

TREATISE ON ZOOLOGY – ANATOMY, TAXONOMY, BIOLOGY

# THE MYRIAPODA

*Edited by*

Alessandro Minelli

VOLUME 1



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*Cover: The centipede Plutonium zwierleini Cavanna, 1881 (Chilopoda, Scolopendromorpha, Plutoniumidae); see fig. 19.10, p. 396.*

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## Preface

The single major group whose treatment never appeared in Pierre-Paul Grassé's *Traité de Zoologie*, the largest zoological treatise in the second half of the last century, is the Myriapoda. Also incomplete (limited indeed to the Chilopoda) was the text devoted to myriapods in the more recent *Microscopic Anatomy of the Invertebrates* directed by Frederick W. Harrison. Thus, the most recent comprehensive treatment of these arthropods are still Carl Attems' chapters in Willy Kükenthal's *Handbuch der Zoologie* (1926) and the still older, but much more extensive volumes written by Karl Wilhelm Verhoeff for Bronn's *Klassen und Ordnungen des Thier-Reiches* (1902-1934).

The need to fill this major gap in the zoological literature is something about which I have been thinking for 35 years. In the spring of 1975, indeed, I had my first experience with the lively international community of myriapodologists, then gathering in Hamburg for its third meeting, following the establishment, seven years before, of an informal network coordinated by Jean-Marie Demange, Otto Kraus and Jean-Paul Mauriès. It was within this community, responsible for many recent advances in the study of these fascinating animals, that the background (scientific and human alike) took shape, out of which the present monograph could eventually emerge.

Barely five months later, in September 1975, I had my only chance of meeting with Professor Grassé, who had been invited to give the opening address to a congress of the Italian zoological society, meeting that year in Siena. In reply to an obviously expected question from the floor, Grassé explained how he had been steering his huge editorial project through the years.

These recollections from some thirty years before were still very lively in my mind when Michiel Thijssen invited me to encourage a small group of specialists to write for Brill a 2-volume monograph on the Myriapoda, to ideally complement the glorious *Traité*.

Thanks to the generous efforts of a dozen authors, the first part of the monograph is finally ready for the printer. The present volume opens with an introductory chapter on the affinities of the Myriapoda and the relationships among the main myriapod groups while the remaining 20 chapters cover the Chilopoda, the Symphyla and the Pauropoda. I much hope that the second volume, on the Diplopoda, will follow before long.

On behalf of my colleagues, I express here the sincere thanks of our team to Steffen Harzsch (University of Greifswald) and Nicholas J. Strausfeld (University of Arizona) for advice on neuroanatomical issues  
Giuseppe Fusco for advice on centipede development

Wolfram Dunger (Ebresbach) and Jörg Spelda (Zoologische Staatssammlung München) for advice on centipede ecology

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Leandro Drago, Federica Todesco, Roberta Pasotto and Matteo Simonetti for precious help with a diversity of editorial issues

On a personal note, I address very special thanks to two of 'my' authors, Lucio and Greg, whose impact of the pages of this volume extends far beyond the limits of the chapters they have signed. Like associated editors, they have carefully read through the whole text, enormously increasing its readability and the consistency in the use of morphological nomenclature.

Standardization of terms is indeed one, and possibly not the least, of the many benefits one may obtain by browsing through the pages of a treatise. Or by writing them.

Padova, 13 October 2010

Alessandro Minelli

## Chapter 1

# PHYLOGENETIC RELATIONSHIPS OF MYRIAPODA

Gregory D. Edgecombe

Myriapods play a pivotal role in current debates about the interrelationships of life's most diverse clade, the Arthropoda. Whether myriapods are most closely related to hexapods, sister to a crustacean-hexapod clade, or are sister to Chelicerata each finds support from different classes of evidence in contemporary literature. Although molecular data in particular provide good evidence in favour of myriapod monophyly, the possibility that Myriapoda could be paraphyletic or polyphyletic has some adherents. This section reviews these competing hypotheses with an emphasis on recent studies; historical overviews are provided by Dohle (1980, 1988) and Edgecombe and Giribet (2002). The conclusion is that most data favour myriapod monophyly, and there is currently no strong basis for rejecting the traditional systematic arrangement of Chilopoda as sister group to Progonaeta. The division of the progonaetes into Symphyla and Dignatha is challenged by some molecular support for a symphylian-pauropod alliance, though this grouping is morphologically anomalous. The status of Myriapoda as part of Mandibulata (having crustacean and hexapod affinities) or Paradoxopoda (having chelicerate affinities) is an open question that ultimately structures the root of the arthropod crown group.

### *Myriapods are outside a hexapod-crustacean group*

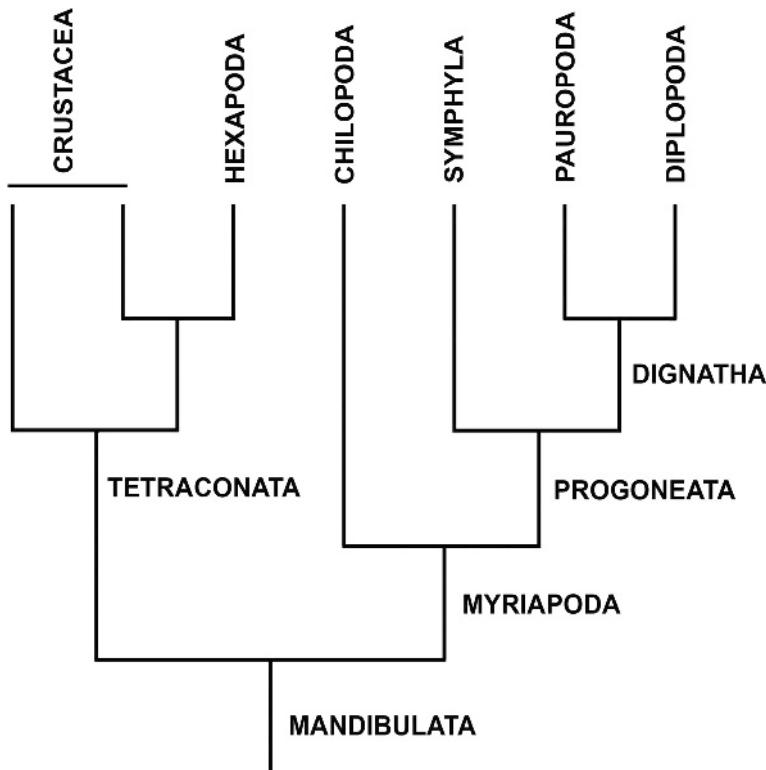
A very long tradition held that the closest relatives of myriapods are the hexapods, that relationship forming the basis for the classical Atelocerata or Tracheata hypothesis. Some morphologists maintain that myriapods and hexapods form a clade, either based on comparative surveys of particular character complexes (Bäcker et al., 2008) or numerical cladistic analysis of a broader sampling of morphological characters (Bitsch and Bitsch, 2004). Klass and Kristensen (2001) provided a detailed review of morphological arguments in favour of Atelocerata and retained that grouping in their classification of mandibulate arthropods, but with recognition that some morphological evidence conformed better to a then-emerging molecular view that hexapods are more closely related to crustaceans than to myriapods.

The morphological support for a monophyletic hexapod-crustacean grouping (that excludes the myriapods) is especially focused on characters from the nervous system. Neurophylogeny arguments in favour of the hexapod-crustacean clade (named Tetraconata by Dohle 2001, but often called Pancrustacea) are outlined in the reviews or analyses of Strausfeld (1998, 2005), Dohle (2001), Loesel et al. (2002), Harzsch (2002, 2004, 2006), Harzsch and Hafner (2006), Stollewerk and Chipman (2006), Strausfeld et al. (2006), Ungerer and Scholtz (2008), and Mayer and Whitington (2009). They include detailed similarities in compound eye ultrastructure, the mode of growth of new visual elements, the optic neuropils, midline neuropils in the brain, serotonin immunoreactivity in the nerve cord, and neuroblasts that express the same markers and produce homologous neurons. When these putative hexapod-crustacean apomorphies are coded in cladistic analyses alongside other morphological systems, they contribute to the retrieval of Tetraconata as a clade, with Myriapoda its sister group (Giribet et al. 2005).

An ever-growing suite of molecular arguments in favour of Tetraconata, and a lack of molecular support for Atelocerata, render it increasingly more convincing that myriapods are excluded from a hexapod-crustacean clade. Molecular evidence for Tetraconata comes from analysis of nuclear ribosomal genes (Mallatt et al., 2004; Petrov and Vladychenskaya, 2005; Mallatt and Giribet, 2006; von Reumont et al., 2009, and many earlier studies cited therein), nuclear protein-coding genes (Regier et al., 2005a, 2008, 2010, and earlier papers by the same authors), mitochondrial genomics (Hassanin, 2006; Gai et al., 2008; Rota-Stabelli et al., 2010), Hox gene sequences (Cook et al., 2001), hemocyanin sequences (Kusche et al., 2003), mitochondrial gene order (Boore et al. 1998), combination of nuclear ribosomal and protein-coding genes with mitochondrial genomes (Bourlat et al., 2008), and Expressed Sequence Tags (Dunn et al., 2008; Roeding et al., 2009). Because it is emphatically supported by diverse molecular data and is readily interpreted morphologically (especially from features of the nervous system), Tetraconata is a working hypothesis for arthropod phylogeny throughout this chapter (Fig. 1.1) except when particular arguments about myriapods are necessarily cast in an Atelocerata framework for historical reasons.

### *Are myriapods monophyletic?*

For more than a century, the monophyly of Myriapoda has come under fire. Pocock (1893), for example, firmly stated that “the so-called group of Myriapoda is an unnatural assemblage of beings”. Interestingly, the influential mid 20<sup>th</sup> century advocates of arthropod polyphyly were convinced of myriapod monophyly. Manton (1964), for exam-



**Fig. 1.1** Inter-relationships of Myriapoda according to the Mandibulata hypothesis. The relationships between myriapod classes are based principally on morphological and developmental evidence.

ple, drew support for a unique origin of the myriapods in the functional morphology of the cephalic tentorial complex, specifically the so-called “swinging tentorium”, and Anderson’s (1973) synthesis of arthropod development likewise treated Myriapoda as “a respectable systematic unit” (1973, p. 128).

Non-monophyly of Myriapoda takes two forms: a long tradition recognised myriapods as paraphyletic with respect to hexapods (Dohle, 1965; Kraus & Kraus, 1994; Kraus, 2001; Willmann, 2003), and considered that only negative characters (e.g., absence of median eyes and absence of scolopidia) could be marshalled in defence of myriapods monophyly (Dohle 1980). The more recent emergence of the Paradoxopoda or Myriochelata (= myriapods + chelicerates) concept has led to some arguments for

myriapods being paraphyletic with respect to Chelicerata (Negrisolo et al., 2004). Alternatively, some morphology-based analyses using neuroanatomical characters have concluded that Myriapoda is polyphyletic, with Diplopoda in a nearly basal position in the Euarthropoda (Strausfeld, 1998; Loesel et al., 2002; Strausfeld et al., 2006) and Chilopoda closer to other mandibulate arthropods.

### *The case for monophyly*

Arguments in favour of myriapod monophyly derive from both morphological and molecular analyses, as well as combination of those data.

#### *Morphology*

Morphological characters that serve as putative autapomorphies of Myriapoda have been discussed in detail in recent reviews by Bitsch and Bitsch (2002, 2004), Koch (2003), and Edgecombe (2004), to whom the reader is referred for additional documentation. The most forceful arguments derive from the structure of the cephalic tentorial endoskeleton and its relationship to the mandible (Manton, 1964; Kluge, 1999; Koch, 2003).

The details of the anterior tentorial arms exhibit a common pattern in the Myriapoda (Fig. 1.2). In particular, the head apodemes ('posterior process of the tentorium' fide Koch 2003; 'pp' in Fig. 1.2) in Chilopoda and Progoneata are fused to a transverse bar (Bitsch and Bitsch, 2002; Koch, 2003) that may extend to the lateral cranial wall. The posterior processes are also merged with sclerites that form a hypopharyngeal bar, and serve as supports for the hypopharynx (Koch, 2003). In the different myriapod classes, the transverse bar supports the apodemes that give rise to mandibular adductor muscles. Symphyla have posterior processes as in the other myriapods but were thought to lack the transverse bar (Snodgrass, 1950). However, a transverse apophysis documented by Ravoux (1975) in *Scutigerella* was later identified as the homologue of the transverse bar found in other myriapods (Bitsch and Bitsch, 2002; Koch, 2003). As such, the transverse bar is a general character for Myriapoda, and since a homologue is not known in Hexapoda or Crustacea it can be considered to be autapomorphic for Myriapoda.

The functional role of the tentorium in myriapods also differs fundamentally from that of hexapods. In Myriapoda, downwards and outwards movements of the tentorial apodemes provide or enhance the abductor force that opens the mandibles, which have a separate, movable gnathal lobe, and the dorsoventral mandibular muscles are shifted to

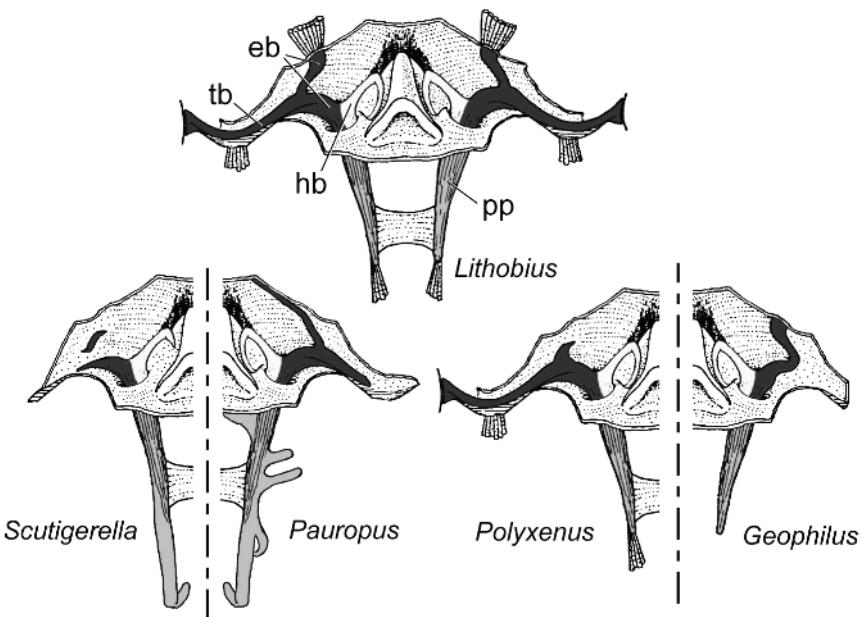


Fig. 1.2 Cephalic tentorial endoskeleton in myriapods, from Koch (2003), depicting Chilopoda (*Lithobius*, *Geophilus*), Syphyla (*Scutigerella*), Paropoda (*Pauropus*) and Diplopoda (*Polyxenus*).

eb epipharyngeal bar; hb hypopharyngeal bar; pp posterior process; tb transverse bar

*For a colour version of this figure, see Plate I*

the tentorial apodeme. These tentorial movements are the basis for the “swinging tentorium” argument viewed by Manton (1964) and Kluge (1999) as a strong indicator of the monophyly of Myriapoda. A counterargument was raised by Klass and Kristensen (2001), who posited that tentorial movements in myriapods, although unique to that group, could be plesiomorphic, i.e., that mobility could be a precursor to an immobile tentorium in Hexapoda. That transformation series is, however, dependent upon the monophyly of the Atelocerata/Tracheata, and is unpolarizable even in the context of Atelocerata. With respect to this and other characters, Koch (2003) accurately noted that myriapod paraphyly only commands serious consideration if Atelocerata is monophyletic. The increasing support for Tetraconata thus strengthens the case for tentorial movement/abduction of the mandibular gnathal lobe being a myriapod autapomorphy. It is confined to Myriapoda, is structurally and functionally complex, and has unique morphological details (e.g., the transverse bar of the tentorium).

Comparison of serotonin reactive neurons by Harzsch (2004) identified two correspondences in Chilopoda and Diplopoda that may serve as additional apomorphic characters for Myriapoda (Harzsch, 2006). Cell group “b” of Harzsch (2004) is an aggregation of two to four cells in chilopods and diplopods that is not found in chelicerates or Tetraconata, and the same pertains to single median serotonergic neurons labelled as neurons “c” and “d”. The most parsimonious optimisation of these myriapod-specific neurons is an autapomorphy of Myriapoda.

Some accounts of eye morphology optimised the lack (inferred phylogenetic loss) of a crystalline cone in the eyes as a myriapod autapomorphy (Ax, 1999) but this interpretation is flawed because Scutigeromorpha (Müller et al., 2003) and Penicillata (Müller et al., 2007) among the Chilopoda and Diplopoda, respectively, have been convincingly reinterpreted as having ommatidia with a crystalline cone. Earlier views of myriapod eyes as uniformly being stemmata or “pseudocompound” eyes in the case of Scutigeromorpha (Paulus, 2000) are inaccurate (Harzsch et al., 2006). A feature shared by the ommatidia of Scutigeromorpha and Penicillata that has been postulated to serve as a possible autapomorphy of Myriapoda is the eucone cells having their nuclei displaced outside (proximal to) the cone compartments (Müller et al., 2007).

When morphological data for a broad range of arthropods are analysed in a cladistic parsimony framework, myriapod monophyly has generally been obtained. The morphology datasets of Edgecombe (2004) and Giribet et al. (2005) retrieved myriapod monophyly, though the jackknife support for Myriapoda is not high (68% in the latter analysis, falling beneath 50% when molecular data were added). A cladistic analysis of arthropod morphology with emphasis on Mandibulata by Bitsch and Bitsch (2004) found Myriapoda to be ambiguous (monophyletic in only some shortest cladograms) under equal character weights, although myriapod monophyly was an unambiguous result after the characters were subjected to reweighting based on their fit to an initial set of trees. However, one of the most compelling morphological apomorphies of Myriapoda, the transverse bar of the tentorium discussed above, was not used as a character in the 2004 analysis (no tentorial character was coded as autapomorphic for Myriapoda). Its inclusion would strengthen support for myriapod monophyly.

#### *Molecular data*

Early molecular analyses generally sampled Myriapoda using exemplars only of Chilopoda and Diplopoda, so while a grouping of those taxa relative to other arthropods was the typical result, the omission of pauropods and symphylans weakened the value of

this finding for postulating myriapod monophyly. When the widely sampled small nuclear ribosomal subunit 18S rRNA was sequenced for pauropods and symphylans, extreme length heterogeneity led to analytical complications, with those two groups being placed in highly labile positions throughout the Arthropoda under different analytical conditions (Giribet and Ribera, 2000; Giribet and Wheeler, 2001). However, in more recent analyses that have included the complete 28S nRNA locus together with 18S, myriapods were retrieved as monophyletic when members of Diplopoda, Symphyla and Chilopoda were analysed (Mallatt et al., 2004). Myriapod monophyly was likewise found when a pauropod was added to a sample that includes symphylans, chilopods and diplopods for these nuclear ribosomal genes (Gai et al., 2006). Other recent analyses based on complete 18S and 28S sequences have, in contrast, found that pauropods and symphylans are resolved in anomalous positions outside the Euarthropoda (von Reumont et al., 2009; Mallatt et al., 2010).

Myriapod monophyly is also found with strong support in analyses of three nuclear coding genes by Regier et al. (2005a,b), these trees including at least two members of each myriapod class. This result is emphatically retrieved when the sampling of nuclear coding genes is inflated to 62 protein-coding genes for a subset of the sampled taxa (Regier et al., 2008, 2010).

Most mitochondrial genomic analyses have included data only for Chilopoda and Diplopoda among the Myriapoda, though the more recent analyses that have broadly sampled across the Arthropoda retrieve myriapod monophyly (Hassanin, 2006; Carapelli et al., 2007). The first analyses of mitochondrial protein-coding genes to include symphylans along with diplopods and chilopods found that Myriapoda is monophyletic but with weak support (Podsiadlowski et al., 2007) or is variably monophyletic and strongly supported (using amino acids) or paraphyletic with respect to chelicerates (using nucleotides) (Gai et al., 2008).

Combination of morphology and nine molecular loci by Giribet et al. (2005) found that Myriapoda was monophyletic under 13 of 20 explored analytical conditions, including the set of gap and transversion:transition costs that optimised congruence between the ten (nine genes + morphology) data partitions.

Thus, Regier et al. (2005b, 2008) reasonably summarise the situation with respect to molecular data in general: when hexapods and crustaceans group together, as they do with nearly all molecular datasets, Myriapoda is a monophyletic group. Indeed Myriapoda is one of the most stable clades in the entire Arthropoda for Regier et al.'s (2008, 2010) data, and I endorse their conclusion that the rediscovery of myriapod monophyly is one of the successes of arthropod molecular systematics.

*The case for paraphyly*

The concept of Myriapoda as a paraphyletic group was rather widely promoted in the context of myriapods being ancestral to hexapods. The growing body of evidence that crustaceans rather than myriapods are the closest relatives of hexapods (see references in the introductory paragraphs) and a rejection of the classical Atelocerata hypothesis by many morphologists carries the consequence that a myriapod ancestry of Hexapoda is unparsimonious. Even if hexapod-crustacean affinities were dismissed, the putative morphological apomorphies that unite progoneate myriapods with hexapods to the exclusion of chilopods (the Labiophora hypothesis of Kraus and Kraus, 1994; Kraus, 2001) are problematic in terms of their proposed homologies (Ax, 1999; Edgecombe and Giribet, 2002).

Another version of myriapod paraphyly involves Symphyla being sister group of Hexapoda (Willmann, 2003), but at a cost of rendering both Progonaeta and Myriapoda paraphyletic.

One analysis of sequence data from mitochondrial coding regions (Negrisolo et al., 2004) agreed with numerous molecular analyses in finding support for myriapods being closest relatives of chelicerates (Paradoxopoda/Myriochelata) but was novel in that some analytical methods resolved the myriapods as paraphyletic. Specifically, the two analysed chilopods were sister to chelicerates, to the exclusion of diplopods, and the same result was found in some mitogenomic analyses using a larger taxonomic sample by Gai et al. (2008, their Fig. 6).

The node contributing to myriapod paraphyly was not, however, strongly supported in either of these analyses, and alternative analytical methods applied to the same data (e.g., using parsimony in the case of Negrisolo et al., 2004; analysing amino acids rather than nucleotides in the case of Gai et al., 2008) retrieved monophyly of Myriapoda, and with strong support in the case of the Gai et al. (2008) data. Myriapod paraphyly in a Paradoxopoda/Myriochelata context is grossly inconsistent with morphology, and it is exceedingly difficult to postulate compelling apomorphies that one or another group of myriapods shares with chelicerates to the exclusion of the other myriapods. If Paradoxopoda is a natural group, myriapods are monophyletic.

*The case for polyphyly*

The most explicit modern arguments for Myriapoda being a polyphyletic assemblage come from studies of brain anatomy (Loesel et al., 2002; Strausfeld et al., 2006). These

data have been argued to resolve Diplopoda at the base of the Euarthropoda whereas Chilopoda are thought to share certain derived characters with a crustacean-hexapod clade (Tetraconata). In these studies, millipedes are represented by the spirostreptids *Orthoporus ornatus* and *Archispirostreptus gigas*. The most important character absence in Diplopoda that is thought to be synapomorphic for other euarthropods is a single midline neuropil. A chilopod/pancrustacean group further shares an additional midline neuropil (ml2 of Loesel et al., 2002) that is lacking in diplopods and chelicerates. Pauropods and symphylans have not been included in the recent analyses of brain anatomy, though symphylans at least have been examined using the same techniques as taxa coded in the phylogenetic analyses (Strausfeld et al., 2006, their fig. 2h).

The new brain data make an invaluable addition to datasets for arthropod phylogeny. Though analyses confined to neuroanatomical characters yield myriapod polyphyly (because of the basal resolution of Diplopoda within Euarthropoda) (Strausfeld et al., 2006), morphological analyses that include brain characters that define deep nodes together with characters from other morphological systems instead unite myriapods as a clade (Giribet et al., 2005), and spirostreptids group with other myriapods rather than at the base of the Euarthropoda in phylogenomic analyses (Roeding et al., 2009). A total evidence perspective interprets the brains of diplopods as exhibiting some reversals/losses rather than signalling the most basal lineage in the arthropod crown group.

#### *Monophyly of the four myriapod classes*

The four main myriapod groups, Chilopoda, Symphyla, Pauropoda and Diplopoda, are each almost universally recognised as monophyletic, drawing on either morphological or molecular characters. Each of these taxa is defended by a set of morphological and developmental characters that can be regarded as apomorphies. These have been reviewed several times (Dohle, 1980, 1997; Kraus, 1997; Edgecombe and Giribet, 2002), and are only succinctly listed here.

*Chilopoda*. – Egg tooth on second maxillae in embryo; appendage of first trunk segment a forcipule housing a poison gland; trunk legs with ring-like trochanter lacking mobility at joint with prefemur; spiral ridge on nucleus of spermatozoon. Under the widely accepted phylogeny of Chilopoda (Notostigmophora-Pleurostigmophora scheme), additional chilopod apomorphies include 15 pairs of locomotory legs, trunk heterotergy (alternation of long and short tergites, with reversal on segments 7-8), and anisostigmophory (spiracles associated with segments bearing long tergites).

*Sympyla*. – Single pair of tracheal stigmata on sides of head capsule. Eyes absent. Labium with distal sensory cones. Female spermathecae formed by paired lateral pockets in mouth cavity. Twelve pairs of trunk legs. Unpaired genital opening. Paired terminal spinnerets. Anal segment with a pair of large sensory calicles (trichobothria), each with a long sensory seta.

*Pauropoda*. – Antennae branching, with a special sensory organ (globulus). Paired pseudocelli on lateral sides of head capsule. Exsertile vesicles on ventral side of postcephalic segment. Trichobothria at margins of tergites.

*Diplopoda*. – Body segments fused into diplosomites. Antenna with eight articles, the distal article bearing apical sensory cones. Aflagellate spermatozoa.

### *Relationships between the myriapod classes*

Even confined to a framework of myriapod monophyly, nearly all possibilities for the interrelationships of the four classes have been endorsed in some study. A few arrangements are limited to single molecular analyses and almost invariably are weakly supported, or were based on morphological arguments that were exposed to be flawed by subsequent workers (but formalised in the taxonomic literature as Trignatha, Opisthogoneata, Monomalata, Atelopoda, Ventrovesiculata, and other rarely-used or now obsolete names). Some of these are noted in the following section, but in general the discussion focuses on groups that have compelling character support and are the topics of contemporary discussion.

#### *Progoneata: support and challenges*

From a morphological perspective, the classical (and still best supported) hypothesis for the basal branching in the Myriapoda is between Chilopoda and Progoneata (Fig. 1.1). Monophyly of Progoneata was defended in detail by Dohle (1980), whose main apomorphies for the group were the gonopore being situated between the second pair of trunk legs (the eponymous “progoneaty”), the midgut developing within yolk, the fat body developing from vitellophages in the yolk, sternal apodemes, and trichobothria with a basal bulb. The style of midgut and fat body development were part of a suite of embryological characters, also including the gonoduct arising as a secondary ectodermal ingrowth, viewed by Anderson (1973) as strong evidence in favour of Progoneata. Largely based on the characters tabulated by Dohle and Anderson, Progoneata is recovered as a

monophyletic group in some numerical cladistic analyses using morphology (Edgecombe, 2004; Giribet et al., 2005). However, the morphology-based analysis of Bitsch and Bitsch (2004) instead retrieved weak support for Symphyla as sister to Chilopoda + Dignatha, rejecting Progoneata. That analysis did not, however, include the putative developmental apomorphies of the group in the dataset, and thus some of the most compelling evidence in support of Progoneata was underemployed.

Molecular support for Progoneata is provided by analyses of mitochondrial genome samples that unite Symphyla and Diplopoda to the exclusion of Chilopoda (Gai et al., 2008; also analyses of amino acids by Podsiadlowski et al., 2007), though without data from Paupropoda. In general, though, molecular analyses to date have not found strong support for the internal nodes grouping the four main myriapod clades. Regier et al's (2008) dataset of 62 protein-coding genes for a subset of the Arthropoda that is more densely sampled for three genes recovers strong support for Myriapoda and each of the four myriapod classes but a weakly supported scheme of inter-class relationships (1.. 3A) (see below under Dignatha). However, Progoneata is bolstered by the addition of more genes to the sample, receiving moderate support (bootstrap support 67–73%) across a range of analytical conditions when the sampling is increased to most of 62 genes for 75 arthropod terminals (Regier et al., 2010). Combination of morphology and nine markers by Giribet et al. (2005) found that Progoneata was monophyletic in the optimal cladogram (Fig. 1.3C) but was weakly supported.

#### *Dignatha: morphological support and molecular challenges*

A grouping of Paupropoda and Diplopoda as Dignatha (Fig. 1.1) has been considered the least controversial taxon within Myriapoda above the class level. Dignatha has been defended by a limbless post-maxillary segment, the vas deferens opening on the tip of conical penis, spiracles at the bases of the walking legs that open to a tracheal pouch that has an apodemal function (present in Hexamerocerata only among the Paupropoda), a motionless pupoid stage after hatching, and the first free-living juvenile having three pairs of legs (Dohle, 1980; Enghoff et al., 1993). The eponymous dignathic condition (first maxillae bordering the mouth and absence of appendage on the second maxillary segment) has been variably supported as apomorphic (Dohle, 1997). Numerous arguments from anatomy (Dohle, 1980, 1997) and gene expression favour the view that the gnathochilarium of diplopods is composed of the first maxillae only (but see Hilken and Kraus, 1994 for a paired maxillae interpretation). Though the argument has been made that the term “gnathochilarium” should be restricted to the maxillary derivative of

Chilognatha alone (Hilken and Kraus, 1994; Kraus and Kraus, 1994), an apomorphic character shared by pauropods and diplopods (including Penicillata) is the maxillae are combined with an intermaxillary plate, and each of these components has similar embryonic relations (e.g., Dohle, 1980, their figs. 10-13). Ax (1999) reasonably argued that the structural and functional union of the maxillae in pauropods and diplopods provides an apomorphy of Dignatha regardless of whether or not second maxillae are considered to be incorporated. Taken together, Dohle's (1997) summary that Dignatha is "a well-founded monophyletic taxon" is an accurate reading of morphology.

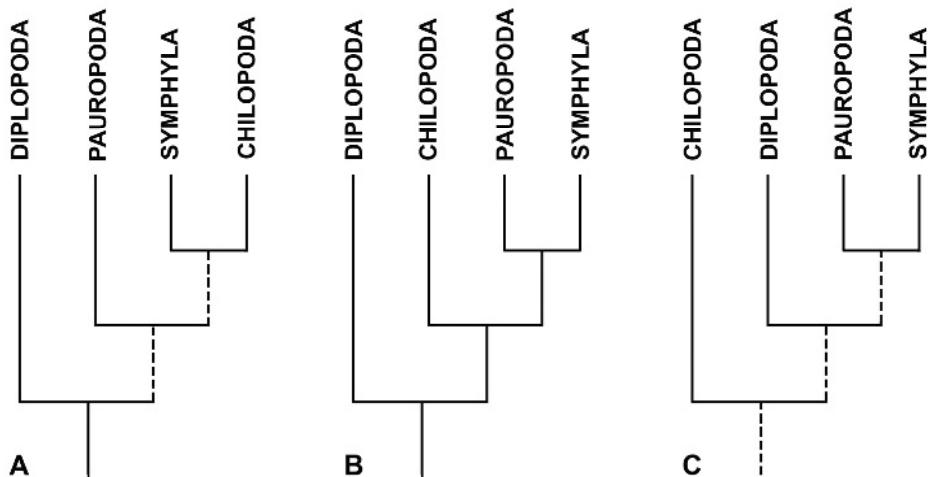


Fig. 1.3 Relationships between myriapod classes based on molecular and combined analyses. Myriapoda is monophyletic in each example. A Likelihood tree based on nuclear protein-coding genes (Regier et al., 2008), with relationships identified by the authors as weakly supported shown by dashed lines. B Bayesian and likelihood trees based on complete 18S and 28S rRNA (Gai et al., 2006) and Bayesian tree based on nucleotide data for three nuclear protein-coding genes (Regier et al., 2005b). The topology is re-rooted between Sympyla and Pauropoda for parsimony analysis of amino acids (Regier et al., 2005b). C Parsimony tree based on morphology and nine genes (Giribet et al., 2005), with intra-class groupings having jackknife support <50% shown by dashed lines. The same topology with strong support for Myriapoda and variable support for the two internal nodes was found in likelihood analyses of 62 nuclear protein-coding genes (Regier et al., 2010).

Analysis of combined small and large nuclear ribosomal RNA by Gai et al. (2006) retrieved a result that is not anticipated by morphology, a sister group relationship between Pauropoda and Sympyla under varied analytical conditions (Fig. 1.3B), and a pauropod-sympylan group was also present (albeit with weak support) in the shortest cladogram based on combined morphological and multi-locus sequence data by Giribet

et al. (2005) (Fig. 1.3C). These results are not wholly independent because Giribet et al. included the 18S and 28S rRNA loci in their analysis as well. A pauropod-sympylan group conflicts with the strong morphological support for the monophyly of Dignatha. The Gai et al. (2006) analyses consistently resolved Chilopoda as sister to the pauropods and symphyllans (Fig. 1.3B), thus also conflicting with monophyly of Progonaeta, but in all figured trees the grouping of non-diplopod myriapods has the lowest support value of any node in the tree. The same groupings were found by Regier et al. (2005b) in their Bayesian analysis of nucleotide data for three nuclear protein-coding genes, though likewise with weak support, and parsimony analysis of amino acids for the same data yields a completely re-rooted topology: Symphyla (Pauropoda (Chilopoda + Diplopoda)) (Regier et al. 2005b, their fig. 2). Dignathan monophyly is also rejected in the analyses of Regier et al. (2008), the most complete sampling again favouring Diplopoda as sister to all other myriapods (Fig. 1.3A). However, the morphologically anomalous groups in the analyses of the nuclear coding genes (i.e., non-diplopod myriapods and groups composed of Symphyla + Chilopoda or Symphyla + Pauropoda) are weakly supported. Expanding the taxonomic coverage for 62 nuclear coding genes (Regier et al., 2010) provided a more stable alliance between Symphyla and Pauropoda (bootstrap support 65–97%) in the context of a monophyletic Progonaeta (Fig. 1.3C). A recurring theme of molecular work to date is that apart from the pauropod-sympylan grouping found by Gai et al. (2006) with nuclear ribosomal genes and by Regier et al. (2010) from a much larger sampling of nuclear ribosomal genes, the low levels of support for surprising inter-class relationships mean that they cannot be used as strong arguments against Progonaeta and Dignatha.

### *Mandibulata or Paradoxopoda?*

In light of the emergence of Paradoxopoda/Myriochelata from several analyses using different kinds of molecular data, morphologists have stressed a considerable body of anatomical evidence in support of Mandibulata. Harzsch et al. (2005) reviewed much of the data in favour of Mandibulata, in the context of Myriapoda as sister to Tetraconata. This includes the mandible itself, including details of gene expression that corroborate its classical interpretation as a coxal endite (Bitsch, 2001; Prpic and Tautz, 2003) and its gnathal edge differentiated into molar and incisor processes (Edgecombe et al., 2003). Mandibulates share paired lateral buds on the mandibular sternum that give rise to either the paragnaths (in crustaceans) or components of the hypopharynx (in myriapods and hexapods), leading Wolff and Scholtz (2006) to propose that such sternal anlagen on the posterior stomodaeal region are homologous in and apomorphic for Mandibulata.

Brain anatomy defends Mandibulata (to the exclusion of Diplopoda) based on several character states, including a conserved midline neuropil that is embedded in the protocerebral matrix, the somata that supply cerebral neuropils being variable in size, and the deutocerebrum containing the olfactory lobe (Strausfeld et al., 2006). The stomatogastric and labral nerves are connected to the tritocerebrum in Mandibulata, rather than to the deutocerebrum as in onychophorans and chelicerates (Scholtz and Edgecombe, 2006). Ommatidial ultrastructure has also been argued to provide mandibulate apomorphies, especially in light of redescriptions of the compound eyes of scutigeromorph chilopods (Müller et al., 2003) and penicillate diplopods (Müller et al. 2007). Details that are apomorphic for Mandibulata include a crystalline cone being developed in the dioptric apparatus, and the cone in *Scutigera* is composed of four cone cells (Müller et al., 2003), just as in general condition for the common ancestor of crustaceans and hexapods according to the Tetraconata hypothesis (Dohle, 2001; Richter, 2002). The lateral eyes of scutigeromorphs and penicillates have dozens of cells in each subunit and, although cell numbers are variable, some individual cells (e.g., cone cells and proximal retinula cells) can be identified (Harzsch et al., 2005). Cell numbers in myriapod ommatidia are intermediate between the low, fixed cell numbers shared by hexapods and crustaceans and the higher, more variable cell numbers in chelicerates. As well, interommatidial pigment cells in scutigeromorphs have been shown to share detailed similarity with those of crustaceans and hexapods (Müller et al., 2003). Correspondences include longitudinal extension of the cell bodies, distal positioning of the nuclei, the cytoplasm absorbing pigment granules, and the specific mode of attachment of the cornea and basement membrane (Müller et al., 2003).

Analogous to the arguments raised above with reference to ommatidial cell numbers, myriapods, hexapods and crustaceans share a lower and more fixed number of serotonergic neurons in the nerve cord than are observed in chelicerates (Harzsch, 2004), in which clusters of ca 10 somata are present. In mandibulates, cells are individually identifiable and typically developed singly or in pairs, to a maximum of four neurons in a group. The reduced, more stable number is viewed as apomorphic for Mandibulata (Harzsch et al., 2005).

Drawing on the above arguments, Mandibulata has been regarded as better supported than Paradoxopoda from the perspective of anatomy, and is more readily interpreted from fossil evidence (Edgecombe, 2010). Until recently the only plausible potential autapomorphy of Paradoxopoda is a mode of neurogenesis that is similar in detail in diplopods (Dove and Stollewerk, 2004), chilopods (Kadner and Stollewerk, 2004; Stollewerk and Chipman, 2006) and chelicerates. This involves groups of postmitotic

neural precursors being recruited for a neural fate, in contrast to the stem-cell-like divisions of neuroblasts in Tetraconata (reviewed by Stollewerk and Chipman, 2006). Pending modern data for neurogenesis in onychophorans, the polarity of these two alternative character states was equivocal. Investigations of nervous system development in Onychophora by Mayer and Whitington (2009) indicate that three characters shared between hexapods, crustaceans and onychophorans are likely to be apomorphies for Onychophora and Euarthropoda as a whole, whereas the alternative states shared by myriapods and chelicerates could be synapomorphies for Paradoxopoda. These characters involve the immigrating clusters of post-mitotic cells noted above, segmental invaginations of the neuroectoderm in each hemisegment that lead to the formation of so-called ventral organs, and the exclusive generation of neurons in the central neuroectoderm (versus a dual role of the neuroectoderm giving rise to both neurons and epidermis in Onychophora and Tetraconata). Expression domains of gap genes along the proximo-distal axis of the onychophoran limb resemble those of hexapods and crustaceans, and provide more evidence for myriapods and chelicerates being sister taxa (Janssen et al., 2010).

With the discovery of these putative anatomical and gene expression apomorphies, Paradoxopoda is no longer a solely molecular grouping, and it need be acknowledged that it has been retrieved in several analyses using different kinds of data. Among these are Hox gene sequences (Cook et al., 2001), hemocyanin sequences (Kusche and Burmester, 2001), mitochondrial genomics (Hwang et al., 2001; Hassanin, 2006), and nuclear genes either separately or in combination with mitochondrial genes (Pisani et al., 2004). Expressed sequence tag data unite the only sampled myriapods (*Scutigera* and *Archispirostreptus*) with chelicerates rather than Tetraconata (Dunn et al., 2008; Roeding et al., 2009) but the limited taxonomic sampling for Myriapoda must be acknowledged. The widely-used nuclear ribosomal genes 18S and 28S rRNA have found support for a Paradoxopoda/Tetraconata split with some taxonomic samples (Mallatt et al., 2004, 2010; Petrov and Vladychenskaya, 2005; von Reumont et al., 2009, apart from the anomalous placement of Symphyla and Pauropoda outside Euarthropoda) but with a different sampling the monophyly of Mandibulata rather than Paradoxopoda could not be rejected when groups were tested with parametric bootstrapping (Mallatt and Giribet, 2006). Likewise, although the mitochondrial genomic citations above have supported Paradoxopoda, exploration of the data by Rota-Stabelli and Telford (2008) showed that Mandibulata is instead retrieved under certain choices of outgroups, and increasingly so as fast evolving lineages are excluded (Rota-Stabelli et al., 2010). Data exploration for nuclear-coding genes by Regier et al. (2008) shows that Mandibulata is

better supported than Paradoxopoda under varied analytical conditions, notably when fast-evolving genes are excluded, and an expanded sampling for these genes retrieves Mandibulata rather than Paradoxopoda with strong support (Regier et al., 2010). Retrieval of Paradoxopoda/Myriochelata from hemocyanin sequence data (Kusche and Burmester, 2001) was reversed in favour of Mandibulata with additional sequences (Kusche et al., 2003). The combination of several nuclear markers with complete mitochondrial genomes likewise resolves the tree with Mandibulata as the better supported clade (Bourlat et al., 2008).

Thus, at present, morphological support for Mandibulata may be stronger than that for Paradoxopoda/Myriochelata, and after several years of emerging signal for the latter from molecular analyses, Mandibulata is the better supported grouping in several recent large-scale molecular compilations. The choice between the two alternatives from the molecular perspective can fairly be described as knife-edge and sensitive to analytical methods (Caravas and Friedrich, 2010). Solving this difficult rooting problem at the base of the Euarthropoda is an ongoing challenge for settling the affinities of the Myriapoda.

### References

- ANDERSON, D. T., 1973. Embryology and phylogeny in annelids and arthropods. – Pergamon Press, Oxford.
- AX, P., 1999. Das System der Metazoa II. Ein Lehrbuch der phylogenetischen Systematik. – Gustav Fischer Verlag, Stuttgart.
- BÄCKER, H., M. FANENBRUCK & J. W. WÄGELE, 2008. A forgotten homology supporting the monophyly of Tracheata: the subcoxa of insects and myriapods re-visited. – *Zoologischer Anzeiger* **247**: 185-207.
- BITSCH, C. & J. BITSCH, 2002. The endoskeletal structures in arthropods: cytology, morphology and evolution. – *Arthropod Structure & Development* **30**: 159-177.
- BITSCH, C. & J. BITSCH, 2004. Phylogenetic relationships of basal hexapods among the mandibulate arthropods: a cladistic analysis based on comparative morphological characters. – *Zoologica Scripta* **33**: 511-550.
- BITSCH, J., 2001. The arthropod mandible: morphology and evolution. Phylogenetic implications. – *Annales de la Société entomologique de France, nouvelle Série* **37**: 305-321.
- BOORE, J. L., D. V. LAVROV, & W. M. BROWN, 1998. Gene translocation links insects and crustaceans. – *Nature* **392**: 667-668.
- BOURLAT, S. J., C. NIELSEN, A. D. ECONOMOU & M. A. TELFORD, 2008. Testing the new animal phylogeny: a phylum level molecular analysis of the animal kingdom. – *Molecular Phylogenetics and Evolution* **49**: 23-31.
- CARAPELLI, A., P. LIÓ, F. NARDI, E. VAN DER WATH & F. FRATI, 2007. Phylogenetic analysis of mitochondrial protein coding genes confirms the reciprocal paraphyly of Hexapoda and Crustacea. – *BMC Evolutionary Biology*, **7**, S8.
- CARAVAS, J. & M. FRIEDRICH, 2010. Of mites and millipedes: Recent progress in resolving the base of the arthropod tree. – *Bioessays* **32**: 488-495.

- COOK, C. E., M. L. SMITH, M. J. TELFORD, A. BASTIANELLO & M. AKAM, 2001. Hox genes and the phylogeny of the arthropods. – *Current Biology* 11: 759-763.
- DOHLE, W., 1965. Über die Stellung der Diplopoden im System. – *Verhandlungen der deutschen Zoologischen Gesellschaft* 1965: 597-606.
- DOHLE, W., 1980. Sind die Myriapoden eine monophyletische Gruppe? Eine Diskussion der Verwandtschaftsbeziehungen der Antennaten. – *Abhandlungen des naturwissenschaftlichen Vereins in Hamburg* 23: 45-104.
- DOHLE, W., 1988. Myriapoda and the ancestry of insects. – *Manchester Polytechnic*, Manchester.
- DOHLE, W. 1997. Myriapod-insect relationships as opposed to an insect-crustacean sister group relationship. – Pp. 306-315 in R. A. FORTÉY, R. & R. H. THOMAS (eds.) *Arthropod relationships*. – Chapman and Hall, London.
- DOHLE, W. 2001. Are the insects terrestrial crustaceans? A discussion of some new facts and arguments and the proposal of the proper name *Tetraconata* for the monophyletic unit Crustacea+Hexapoda. – *Annales de la Société entomologique de France, nouvelle Série* 37: 85-103.
- DOVE, H. & A. STOLLEWERK, 2004. Comparative analysis of neurogenesis in the myriapod *Glomeris marginata* (Diplopoda) suggests more similarities to chelicerates than to insects. – *Development* 130: 2161-2171.
- DUNN, C. W., A. HEJNOL, D. Q. MATUS, K. PANG, W. E. BROWNE, S. A. SMITH, E. C. SEAVER, G. W. ROUSE, M. OBST, G. D. EDGEcombe, M. V. SØRENSEN, S. H. D. HADDOCK, A. SCHMIDT-RHAESA, A. OKUSU, R. M. KRISTENSEN, W. C. WHEELER, M. Q. MARTINDALE & G. GIRIBET, 2008. Broad taxon sampling improves resolution of the Animal Tree of Life. – *Nature* 452: 745-749.
- EDGEcombe, G. D. 2004. Morphological data, extant Myriapoda, and the myriapod stem-group. – *Contributions to Zoology* 73: 207-252.
- EDGEcombe, G. D. 2010. Arthropod phylogeny: an overview from the perspectives of morphology, molecular data and the fossil record. – *Arthropod Structure & Development* 39: 74-87.
- EDGEcombe, G. D. & G. GIRIBET, 2002. Myriapod phylogeny and the relationships of Chilopoda. – Pp. 143-168 in J. LLORENTE BOUSQUETS & J. J. MORRONE (eds.) *Biodiversidad, taxonomía y biogeografía de artrópodos de México: hacia una síntesis de su conocimiento, volumen III*. – Prensas de Ciencias, Universidad Nacional Autónoma de México, México.
- EDGEcombe, G. D., S. RICHTER & G. D. F. WILSON, 2003. The mandibular gnathal edges: homologous structures across Mandibulata? – *African Invertebrates* 44: 115-135.
- ENGHOFF, H., W. DOHLE & J. G. BLOWER, 1993. Anamorphosis in millipedes (Diplopoda) - the present state of knowledge, with some developmental and phylogenetic considerations. – *Zoological Journal of the Linnean Society* 109: 103-234.
- GAI, Y., D. SONG, H. SUN, Q. YANG & K. ZHOU, 2008. The complete mitochondrial genome of *Sympylella* sp. (Myriapoda: Symphyla): Extensive gene order rearrangement and evidence in favour of Progoneata. – *Molecular Phylogenetics and Evolution* 48: 103-111.
- GAI, Y.-H., D.-X. SONG, H.-Y. SUN & K.-Y. ZHOU, 2006. Myriapod monophly and relationships among myriapod classes based on nearly complete 28S and 18S rDNA sequences. – *Zoological Science* 23: 1101-1108.
- GIRIBET, G., S. RICHTER, G. D. EDGEcombe & W. C. WHEELER, 2005. The position of crustaceans within Arthropoda – evidence from nine molecular loci and morphology. – In S. KOENEMANN & R. JENNER (eds.), *Crustacea and arthropod relationships*. – *Crustacean Issues* 16: 307-352.
- GIRIBET, G. & C. RIBERA, 2000. A review of arthropod phylogeny: new data based on ribosomal DNA sequences and direct character optimization. – *Cladistics* 15: 204-231.
- GIRIBET, G. & W. C. WHEELER, 2001. Some unusual small-subunit ribosomal RNA sequences of metazoans. – *American Museum Novitates* 3337: 1-14.

- HARZSCH, S., 2002. The phylogenetic significance of crustacean optic neuropils and chiasmata: a re-examination. – *Journal of Comparative Neurology* **453**: 10-21.
- HARZSCH, S., 2004. Phylogenetic comparison of serotonin-immunoreactive neurons in representatives of the Chilopoda, Diplopoda, and Chelicerata: implications for arthropod relationships. – *Journal of Morphology* **259**: 198-213.
- HARZSCH, S., 2006. Neurophylogeny: architecture of the nervous system and a fresh view on arthropod phylogeny. – *Integrative and Comparative Biology* **46**: 162-194.
- HARZSCH, S. & G. HAFNER, 2006. Evolution of eye development in arthropods: phylogenetic aspects. – *Arthropod Structure & Development* **35**: 319-340.
- HARZSCH, S., R. R. MELZER & C. H. G. MÜLLER, 2006. Mechanisms of eye development and evolution of the arthropod visual system: the lateral eyes of Myriapoda are not modified insect ommatidia. – *Organisms, Diversity and Evolution* **7**: 20-32.
- HARZSCH, S., C. H. G. MÜLLER & H. WOLF, 2005. From variable to constant cell numbers: cellular characteristics of the arthropod nervous system argue against a sister-group relationship of Chelicerata and "Myriapoda" but favour the Mandibulata concept. – *Development Genes and Evolution* **215**: 53-68.
- HASSANIN, A. 2006. Phylogeny of Arthropoda inferred from mitochondrial sequences: strategies for limiting the misleading effects of multiple changes in pattern and rates of substitution. – *Molecular Phylogenetics and Evolution* **38**: 100-116.
- HILKEN, G. & O. KRAUS, 1994. Struktur und Homologie der Komponenten des Gnathochilarium der Chilognatha (Tracheata, Diplopoda). – *Verhandlungen des naturwissenschaftlichen Vereins in Hamburg* **34**: 33-50.
- HWANG, U. W., M. FRIEDRICH, D. TAUTZ, C. J. PARK & W. KIM, 2001. Mitochondrial protein phylogeny joins myriapods and chelicerates. – *Nature* **413**: 154-157.
- JANSSEN, R., B. J. ERIKSSON, G. E. BUDD, M. AKAM & N.-M. PRPIC, 2010. Gene expression patterns in an onychophoran reveal that regionalization predates limb segmentation in pan-arthropods. – *Evolution & Development* **12**: 363-372.
- KADNER, D. & A. STOLLEWERK, 2004. Neurogenesis in the chilopod *Lithobius forficatus* suggests more similarities to chelicerates than to insects. – *Development, Genes & Evolution* **214**: 367-379.
- KLASS, K.-D. & N.-P. KRISTENSEN, 2001. The ground plan and affinities of hexapods: recent progress and open problems. – *Annales de la Société entomologique de France, nouvelle Série* **37**: 265-298.
- KLUGE, N. J., 1999. Mitos en Sistemática y principios de Nomenclatura Zoológica. – *Boletín de la Sociedad Entomológica Aragonesa* **26**: 347-377.
- KOCH, M., 2003. Monophyly of the Myriapoda? Reliability of current arguments. – *African Invertebrates* **44**: 137-153.
- KRAUS, O., 1997. Phylogenetic relationships between higher taxa of tracheate arthropods. – Pp. 295-303 in R. A. FORTEY & R. H. THOMAS (eds.) *Arthropod relationships*. – Chapman & Hall, London.
- KRAUS, O., 2001. "Myriapoda" and the ancestry of the Hexapoda. – *Annales de la Société entomologique de France, nouvelle Série* **37**: 105-127.
- KRAUS, O. & M. KRAUS, 1994. On "Myriapoda"-Insecta interrelationships, phylogenetic age and primary ecological niches (Arthropoda, Tracheata). – *Verhandlungen des naturwissenschaftlichen Vereins in Hamburg* **34**: 5-31.
- KUSCHE, K. & T. BURMESTER, 2001. Diplopod hemocyanin sequence and the phylogenetic position of the Myriapoda. – *Molecular Biology and Evolution* **18**: 1566-1573.
- KUSCHE, K., A. HEMBACH, S. HAGNER-HOLLER, W. GEBAUER & T. BURMESTER, 2003. Complete subunit sequences, structure and evolution of the 6 x 6-mer hemocyanin from the common house centipede, *Scutigera coleoptrata*. – *European Journal of Biochemistry* **270**: 2860-2868.

- LOESL, R., D. R. NÄSSEL & N. J. STRAUSFELD, 2002. Common design in a unique midline neuropil in the brains of arthropods. – *Arthropod Structure & Development* 31: 77-91.
- MALLATT, J. M., J. R. GAREY, & J. W. SHULTZ, 2004. Ecdysozoan phylogeny and Bayesian inference: first use of nearly complete 28S and 18S rRNA gene sequences to classify the arthropods and their kin. – *Molecular Phylogenetics and Evolution* 31: 178-191.
- MALLATT, J. M., & G. GIRIBET, 2006. Further use of nearly complete 28S and 18S rRNA genes to classify Ecdysozoa: 37 more arthropods and a kinorhynch. – *Molecular Phylogenetics and Evolution* 40: 772-794.
- MALLATT, J., C. WAGGONER & M.J. YODER, 2010. Nearly complete rRNA genes assembled from across the metazoan animals: effects of more taxa, a structure-based alignment, and paired-sites evolutionary models on phylogenetic reconstruction. – *Molecular Phylogenetics and Evolution* 55: 1-17.
- MANTON, S. M., 1964. Mandibular mechanisms and the evolution of arthropods. – *Philosophical Transactions of the Royal Society of London, B* 247: 1-183.
- MAYER, G. & P. M. WHITINGTON, 2009. Velvet worm development links myriapods with chelicerates. – *Proceedings of the Royal Society of London B* 276: 3571-3579.
- MÜLLER, C. H. G., J. ROSENBERG, S. RICHTER & V. B. MEYER-ROCHOW, 2003. The compound eye of *Scutigera coleoptrata* (Linnaeus, 1758) (Chilopoda: Notostigmophora): an ultrastructural reinvestigation that adds support to the Mandibulata concept. – *Zoomorphology* 122: 191-209.
- MÜLLER, C. H. G., A. SOMBKE & J. ROSENBERG, 2007. The fine structure of the eyes of some bristly millipedes (Penicillata, Diplopoda): additional support for the homology of mandibulate ommatidia. – *Arthropod Structure and Development* 36: 463-476.
- NEGRISOLI, E., A. MINELLI & G. VALLE, 2004. The mitochondrial genome of the house centipede *Scutigera* and the monophyly versus paraphyly of Myriapoda. *Molecular Biology and Evolution* 21: 770-780.
- PAULUS, H. F. 2000. Phylogeny of the Myriapoda - Crustacea - Insecta: a new attempt using photoreceptor structure. – *Journal of Zoological Systematics and Evolutionary Research* 38: 189-208.
- PETROV, N. B. & N. S. VLADYCHENSKAYA, 2005. Phylogeny of molting protostomes (Ecdysozoa) as inferred from 18S and 28S rRNA gene sequences. – *Molecular Biology* 39: 503-513.
- PISANI, D., L. L. POLING, M. LYONS-WEILER & S. B. HEDGES, 2004. The colonization of land by animals: molecular phylogeny and divergence times among arthropods. – *BMC Biology*, 2, 1-10.
- POCOCK, R. I., 1893. On the classification of the tracheate Arthropoda. – *Zoologischer Anzeiger* 16: 271-275.
- PODSIADŁOWSKI, L., H. KOHLHAGEN & M. KOCH, 2007. The complete mitochondrial genome of *Scutigerella causeyae* (Myriapoda: Symphyla) and the phylogenetic position of the Symphyla. – *Molecular Phylogenetics and Evolution* 45: 251-260.
- PRPIC, N.-M. & D. TAUTZ, 2003. The expression of the proximodistal axis patterning genes *Distal-less* and *dachshund* in the appendages of *Glomeris marginata* (Myriapoda: Diplopoda) suggests a special role of these genes in patterning the head appendages. – *Developmental Biology* 260: 97-112.
- RAVOUX, P., 1975. Endosquelette et musculature céphaliques de *Scutigerella immaculata* Newport (Symphyla: Scutigerellidae). – *Bulletin du Muséum national d'Histoire naturelle, Paris* 332: 1189-1238.
- REGIER, J. C., J. W. SHULTZ, A. R. D. GANLEY, A. HUSSEY, D. SHI, B. BALL, A. ZWICK, J. E. STAJICH, M. P. CUMMINGS, J. W. MARTIN & C. W. CUNNINGHAM, 2008. Resolving arthropod

- phylogeny: exploring phylogenetic signal within 41 kb of protein-coding nuclear gene sequences. – *Systematic Biology* **57**: 920-938.
- REGIER, J. C., J. W. SHULTZ & R. E. KAMBIC, 2005a. Pancrustacean phylogeny: hexapods are terrestrial crustaceans and maxillopods are not monophyletic. – *Proceedings of the Royal Society B* **272**: 395-401.
- REGIER, J. C., J. W. SHULTZ, A. ZWICK, A. HUSSEY, B. BALL, R. WETZER, J. W. MARTIN & C. W. CUNNINGHAM, 2010. Arthropod relationships revealed by phylogenomic analysis of nuclear protein-coding sequences. – *Nature* **463**: 1079-1083.
- REGIER, J. C., H. M. WILSON & J. W. SHULTZ, 2005b. Phylogenetic analysis of Myriapoda using three nuclear protein-coding genes. – *Molecular Phylogenetics and Evolution* **34**: 147-158.
- VON REUMONT, B. M., K. MEUSEMANN, N. U. SZUCSICH, E. DELL'AMPLIO, V. GOWRI-SHAKAR, D. BARTEL, S. SIMON, H. O. LETSCH, R. R. STOCSITS, Y.-X. LUAN, J. W. WÄGELE, G. PASS, H. HADRYS & B. MISOF, 2009. Can comprehensive background knowledge be incorporated into substitution models to improve phylogenetic analyses? A case study on major arthropod relationships. – *BMC Evolutionary Biology* **9**: 119.
- RICHTER, S., 2002. The Tetraconata concept: hexapod-crustacean relationships and the phylogeny of Crustacea. – *Organisms, Diversity and Evolution* **2**: 217-237.
- ROEDING, F., J. BORNER, M. KUBE, S. KLAGES, R. REINHARDT & T. BURMESTER, 2009. A 454 sequencing approach for large scale phylogenetic analysis of the common emperor scorpion (*Pandinus imperator*). – *Molecular Phylogenetics and Evolution* **53**: 826-834.
- ROTA-STABELLI, O., E. KAYAL, D. GLEESON, J. DAUB, J. L. BOORE, M. J. TELFORD, D. PISANI, M. BLAXTER & D. V. LAVROV, 2010. Ecdysozoan mitogenomics: evidence for a common origin of the legged invertebrates, the Panarthropoda. – *Genome Biology and Evolution* **2**: 425-440.
- ROTA-STABELLI, O. & M. J. TELFORD, 2008. A multi criterion approach for the selection of optimal outgroups in phylogeny: Recovering some support for Mandibulata over Myriochelata using mitogenomics. – *Molecular Phylogenetics and Evolution* **48**: 103-111.
- SCHOLTZ, G. & G. D. EDGEcombe, 2006. The evolution of arthropod heads: reconciling morphological, developmental and palaeontological evidence. – *Development, Genes and Evolution* **216**: 395-415.
- SNODGRASS, R. E., 1950. Comparative studies on the jaws of mandibulate arthropods. *Smithsonian Miscellaneous Collections* **116**: 1-85.
- STOLLEWERK, A. & A. CHIPMAN, 2006. Neurogenesis in myriapods and chelicerates and its importance for understanding arthropod relationships. – *Integrative and Comparative Biology* **46**: 195-206.
- STRAUSFELD, N. J., 1998. Crustacean - insect relationships: the use of brain characters to derive phylogeny amongst segmented invertebrates. – *Brain, Behavior and Evolution* **52**: 186-206.
- STRAUSFELD, N. J., 2005. The evolution of crustacean and insect optic lobes and the origins of chiasmata. – *Arthropod Structure & Development* **34**: 235-256.
- STRAUSFELD, N. J., C. M. STRAUSFELD, R. LOESEL, D. ROWELL & S. STOWE, 2006. Arthropod phylogeny: onychophoran brain organization suggests an archaic relationship with a chelicerate stem lineage. – *Proceedings of the Royal Society of London, B* **273**: 1857-1866.
- UNGERER, P. & G. SCHOLTZ, 2008. Filling the gap between identified neuroblasts and neurons in crustaceans adds new support for Tetraconata. – *Proceedings of the Royal Society of London, B* **275**: 369-376.
- WILLMANN, R., 2003. Die phyletischen Beziehungen der Insecta: Offene Fragen und Probleme. – *Verhandlungen des Westdeutscher Entomologentags 2001*: 1-64.
- WOLFF, C. & G. SCHOLTZ, 2006. Cell lineage analysis of the mandibular segment of the amphipod *Orchestia cavimana* reveals that the crustacean paragnaths are sternal outgrowths and not limbs. – *Frontiers in Zoology* **3**, 19.

## Chapter 2

# THE CHILOPODA – INTRODUCTION

### Diagnosis

Alessandro Minelli

CHILOPODA. Terrestrial, tracheate, antennate and mandibulate arthropods with predatory life-style and generally nocturnal habits. Body articulated into head and trunk. The head bears one pair of mostly elongated antennae. Eyes, when present, either in form of a cluster of separate ocelli, or apparently faceted. A temporal organ (Tömösváry organ) is present in two major and likely basal subclades. Mouth ventral, preceded by an inarticulate and variously distinct labrum and provided with one pair of mandibles and two pairs of maxillae, the latter often integrated into a single functional complex. Appendages of the first trunk segment in form of poisonous maxillipedes (forcipules), those of the following segments locomotory uniramous legs, the ultimate pair often modified into grasping or sensory tools. Number of leg pairs always odd in the adult, either fixed in the species or in a whole clade, or intraspecifically variable. Trunk segments frequently heteronomous, especially in the dorsal aspect, with number of tergites sometimes lower or higher than the number of sternites and leg pairs. Frequent alternation between longer segments provided with spiracles and shorter segments without spiracles. Leg-bearing segments followed by two or possibly three terminal segments forming the genital and anal region, which is either devoid of external appendages or provided with one pair of gonopods (but two pairs in males of the Scutigeromorpha) of one to three articles. Genital opening at the posterior end of the body. Tracheal system opening either with lateral spiracles leading into long, frequently branched and partly anastomosed tracheae, or with dorsal stomata connected by short, thin tracheae to the dorsal vessel; respiratory pigment (hemocyanin) present only in the latter case. Excretion by Malpighian tubules, sometimes also through maxillary nephridia. Brain subdivided into proto-, deuto- and tritocerebrum, the protocerebrum sometimes indistinct. Male gonads of variable number and structure, either one, or two, or many, sometimes articulated into a macro- and a microtestis. One ovary. Post-embryonic development either hemianamorphic or epimorphic. Brood care in the epimorphic clade.

## History of research

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Despite a considerable increase in research efforts in the last quarter century, centipedes are still an inadequately known clade of arthropods. The whole scientific literature on this group since Linnaeus (1758) is only about 5000 titles. Even at the level of species description, important additions may still be expected, as witnessed by the recent discovery (Chagas et al., 2008) of *Scolopendropsis duplicata*, a Brazilian scolopendromorph whose unusual segment number (39 or 43) required a change in a main point of the diagnosis of the Scolopendromorpha (all other species in this clade having 21 or 23 pairs of legs) in respect to the sister clade, the Geophilomorpha (27 to 191 pairs of legs).

The old literature on the Chilopoda has been extensively discussed and listed by Lewis (1981), Rosenberg (2009) and Rosenberg and Müller (2009), and will be reviewed here only in outline.

Species description begins with Linnaeus (1758), who placed all the six centipede species known to him in the genus *Scolopendra*. During the XIX century, important taxonomic contributions were provided by George Newport (1803-1854), Frederick Vilhelm August Meinert (1833-1895), Robert Latzel (1845-1919; the author of a still useful monograph on the myriapods of the Austro-Hungarian monarchy, 1880, 1884) (biography: Stagl, 2006), and Orator Fuller Cook (1867-1949). They were followed by six authors whose publications span the last decade of the XIX and the first three to five decades of the XX centuries, who contributed an amazing number of taxonomic studies on the centipedes of all parts of the world, including some major monographs: these authors were Henry Wilfred Brölemann (1860-1933) (biography: Duboscq, 1933), Karl Wilhelm Verhoeff (1867-1945) (biography: Mauermayer, 1962), the count Carl Attems (1868-1952) (biography: Strouhal, 1961), Filippo Silvestri (1873-1949), (biography: Cotronei, 1956) and Ralph Vary Chamberlin (1879-1967). Verhoeff was also the author of the most detailed, although cumbersome, treatment of the Chilopoda in the German zoological encyclopedia *Bronn's Klassen und Ordnungen des Thier-Reiches* (Verhoeff, 1902-25), while Attems signed the much shorter but much more accessible account on the same group in the *Handbuch der Zoologie* (Attems, 1926). These authors were also interested in the other groups of myriapods, while the more recent taxonomists have generally specialized in the study of one of the traditional 'classes'.

During the second half of the XX century and up to present, the continuing description of new genera and species has been paralleled by an increasingly effective revision of previously described taxa. In many subgroups, synonymization has been more extensive than species description. Despite these efforts, many groups still await a modern monographic treatment, the largest of these groups being the North American Lithobiidae and the large, worldwide distributed scolopendromorph genus *Cryptops*.

At present, some 3150 valid species names are recognized, ascribed to the more than 400 genera enumerated in Chapter 19 of this work. A nomenclator of centipede genus group names introduced between 1758 and 1957 is Jeekel (2005); Shelley's (2006) supplement extends it to 2005.

The second half of the XIX century was also the time of the first serious studies on centipede anatomy. This line of enquiry, progressively accompanied by histological studies, has continued until the advent of electron microscopy, to be eventually complemented, and often revolutionized, by the results of the latter. Most of the research on centipede anatomy, histology and ultrastructure has been limited to a few representative species, as specified below; comparative studies on other taxa would be rewarding, even at the level of gross anatomy.

From the point of view of physiology, centipedes have been seldom selected as model animals, with the exception of *Lithobius forficatus*, which has been quite extensively used, e.g. in research on hormones and neurohormones. Other centipedes used more than occasionally in experimental research are *Scutigera coleoptrata* and *Scolopendra* spp.

*Lithobius*, *Scutigera* and *Scolopendra* represent three of the five major clades in the Chilopoda. Of the remaining two clades, our limited knowledge of the Craterostigmomorpha is largely due to the late discovery (Pocock, 1902) of the first of the two currently known representatives, and to their localized geographical distribution, limited to Tasmania and New Zealand, but comparable arguments do not apply to the Geophilomorpha, actually the most species-rich clade in the Chilopoda. But Geophilomorpha are not so easily kept in captivity as are at least some species of the other clades. In particular, to date it has not been possible to have any geophilomorph species completing the life cycle in captivity. However, the recent interest in the mechanisms of arthropod segmentation and their evolution has attracted widespread interest in the Geophilomorpha (see Chapter 13). Eventually, a geophilomorph species (*Strigamia maritima*) has turned into a model species, whose genome has been sequenced, although the results of this effort are still unpublished at the time the present monograph goes to press.

Besides the venomous bite of the scolopender, a biological peculiarity of centipedes already recorded in the pre-Linnaean literature is bioluminescence, although this property is only known from a few species, all of them belonging to the Geophilomorpha. Already in 1547 the voyager and explorer Oviedo described a glowing representative of the Geophilomorpha from St. Domingo Island (cf. Newport, 1845). In Europe bioluminescent centipedes were first recorded in 1670 (Richard, 1885). The literature on centipede bio-luminescence has been reviewed by Minelli (1978), Rosenberg (2009) and Rosenberg and Meyer-Rochow (2009). A history of prelinnean myriapodology has not yet been written.

The following paragraphs recounts the earliest or the most important studies on different aspects of centipede anatomy and histology. Some of the old data are still useful (and even, in several cases, they remain the only available ones) and will be presented in the following chapters, together with the most recent data and interpretations.

*L. forficatus* received special attention through the detailed accounts on its anatomy by Biegel (1922) and later by Rilling (1968). A modern, but incomplete account of centipede anatomy, ultrastructure included, is Minelli (1993).

The earliest studies on the cuticle of the Chilopoda (Duboscq, 1898a; Verhoeff, 1902-1925; Fuhrmann, 1922; Fahlander, 1938; Blower, 1950, 1951) long predate the advent of electron microscopy. As first noticed by Zograff (1880), the centipede integument is rich in pores of epidermal glandular cells. This observation was followed by light microscopic descriptions of unicellular glands (Duboscq, 1898; Fuhrmann, 1922; Brade-Birks and Brade-Birks, 1920; Koch, 1927; Blower, 1951; Rilling, 1968; Maschwitz et al., 1979; Desbalmes, 1992). Fahlander (1938) distinguished between solitary epidermal glands and compound glands, formed by numerous unicellular epidermal glands.

Pore openings on the coxae of the last 2-5 leg pairs (Lithobiomorpha) or those of the ultimate legs only (Scolopendromorpha and Geophilomorpha) or on the anal valves were first described as pori pleurales and pori anales (Geophilomorpha: Meinert, 1870, 1872, 1886; Tömösváry, 1883-84), pori coxaes (Lithobiomorpha: Latzel, 1880; Zograff, 1880; Duboscq, 1898a), or characterized as pleural glands (Scolopendromorpha: Herbst, 1891; Verhoeff, 1892). These pores are the openings of multicellular organs that in the past were mostly regarded to be glandular (Latzel, 1880; Tömösváry, 1883-84; Herbst, 1891; Verhoeff, 1892, 1902-1925, 1931; Willem 1897; Duboscq 1898; Biegel, 1922; Attems 1929; Rilling 1968). The coxal organs were considered to be sensory, or to secrete a spinning secretion (Zograff, 1880), or sticky fibres (Herbst, 1891), that play a role in sperm transfer (Willem, 1897). Modern ultrastructural investigations (Rosenberg and Seifert, 1977; Littlewood, 1983; Rosenberg, 1982, 1983a, b, 1984, 1989; Rosenberg & Greven, 1996;

Borucki and Rosenberg, 1997; Greven et al., 1997; Rosenberg et al. 2006) revealed that the epithelia surrounding the coxal and anal pores are not glandular, and these organs are now known as coxal or anal organs, respectively (Rosenberg, 1985).

Latzel (1884) described a possibly sensory organ in the head of *Scutigera coleoptrata*, subsequently called by Haase (1884b) the maxillary organ.

Neuroendocrine glands in centipedes were first described by Heymons (1901) in *Scolopendra* but initially interpreted as an endocrine organ (glandula cerebralis) by Fahlander (1938). Similar organs were described from all main centipede lineages by Fahlander (1938), Hanström (1940), Gabe (1952, 1956) and Palm (1956). Scheffel (1961) regarded this organ as a storage site for products of the protocerebral neurosecretory cells. But fine structural investigations have revealed that the cerebral glands of *Lithobius forficatus* are composed of the endings of neurosecretory axons and glandular cells that produce secretion themselves (Scheffel, 1965; Joly, 1966). Fine-structural investigations on the cerebral gland of different Chilopoda were done by Ernst (1971), Rosenberg (1976) and Descamps & Joly (1985).

The anatomy of the digestive system of the Chilopoda is still incompletely known despite a lengthy series of contributions (de Serres, 1813; Plateau, 1878; Haase, 1884b; Balbiani, 1890; Willem, 1889; Verhoeff, 1902-1925; Kaufman, 1960c, 1961a, c, 1962a; Shukla, 1964; Jangi, 1966; Rilling, 1968; Sundara Rajulu 1970b), the most recent papers also including histology. The peritrophic membrane enclosing ingested food in the midgut was first detected by Plateau (1878) in *Cryptops* sp. The term peritrophic membrane was introduced by Balbiani (1890). The first experiments on the physiology of digestion were performed by Plateau (1878); enzymatic activities in the gut were studied by Nielsen (1962), Shrewsbury and Barson (1953) described the bacterial flora of the digestive tract of *Lithobius* sp.

The arrangement and structure of the spiracles of geophilomorph species were investigated by Meinert (1870), Chalande (1885), Haase (1884a), Verhoeff (1902-1925, 1941), Füller (1960a), Lewis (1963), Manton (1965), Curry (1974) and Hilken (1998), those of *Lithobius* by Kaufman (1962b), those of the Scolopendromorpha e. g. by Chalande (1885), Haase (1887), Verhoeff (1902-25, 1941), Crabbill (1955, 1960), Füller (1960a), Manton (1965), Curry (1974), Lewis et al. (1996), Hilken, (1998) and Klok et al. (2002). The spiracles of the Scolopendromorpha are the most complex and diverse ones within the Chilopoda and are used, since Newport (1845), in the taxonomy of this group (see also Kohlrausch, 1879, Haase, 1884a, 1887, Verhoeff, 1941).

The nature of the dorsal tracheal system of *Scutigera coleoptrata* was recognized quite early (Tömösváry, 1881, 1883, Sinclair, 1891, 1892, Voges, 1882, Haase, 1884a, 1885; Sinclair,

1891, 1892); Dubuisson (1928), first described the close connection between the tracheae and the circulatory system in *S. coleoptrata*.

The tracheal system of different representatives of the Lithobiomorpha was studied by Zograff (1880), Haase (1884), Chalande (1885), Verhoeff (1902-1925, 1905, 1941). More detailed investigations were devoted to the tracheal system of *Lithobius forficatus* (Voges, 1916; Ripper, 1931; Kaufman, 1961b; Rilling, 1968), also with electron microscopy (Hilken, 1998). The tracheal systems of Scolopendromorpha have been mainly investigated in several species of *Scolopendra* and *Cryptops* (Müller, 1829; Chalande, 1885; Haase, 1884a; Dubuisson, 1928; Kaufman, 1964; Manton, 1965; Jangi, 1966; with electron microscopy by Hilken 1997, 1998), but other taxa were also studied by Kohlrausch (1879) and Verhoeff (1902-1925). Studies on the tracheal systems of different representatives of the Geophilomorpha include Palmén (1877), Haase (1884a), Chalande (1885), Dubuisson (1928), Demange (1942), Kaufman (1960a, b), Manton (1965), and the histological work by Füller (1960b) and Hilken (1998). Early studies on the function of the respiratory system include Chalande (1886), Plateau, (1887, 1890), Dubuisson (1928), and Lewis (1963).

Straus-Durckheim (1828) first described the dorsal heart with its lateral arteries in *Scolopendra*. A decade later Lord (1838) described the supraneural vessel and the maxilliped arch connecting the dorsal and ventral vessels in *Scolopendra*. The first comprehensive and comparative works on the vascular system in Chilopoda were carried out by Newport (1838, 1843) and expanded on by Herbst (1889, 1891). The supraneural vessel in *Scolopendra gigantea* was investigated by Chatin (1883). Duboscq (1896, 1898a) studied the circulatory system of *S. cingulata* in depth, and that of *Cryptops* sp., *Lithobius* sp. and different Geophilidae in lesser detail.

A detailed description of the circulatory system of *S. cingulata*, *L. forficatus*, *S. coleoptrata*, *Thereuopoda clunifera*, and *Thereuonema tuberculata* was published by Fahlander (1938). Jangi (1966) described the circulatory system of Indian scolopenders. Varma (1971) looked at the innervation of the tubular heart in *S. morsitans*. In the same year, Ernst (1971) described the anatomy of the circulatory system, the pericardial sinus and the innervation of the pericardial sinus in *Geophilus flavus*. Wirkner and Pass (2000, 2002) described the circulatory system in *Craterostigmus tasmanianus* for the first time and explored comparative morphological and phylogenetic aspects of the circulatory system of other chilopods (*S. coleoptrata*, *T. longicornis*, *L. forficatus*, *S. cingulata*, *Orya barbarica*, *G. flavus*). Heart beat frequencies were measured in chilopods by Chalande (1886), Dubuisson (1928), Auerbach (1951), more recently, by Hertel et al. (2002). The ontogenetic development of the vascular system was investigated by Heymons (1901)

(*Scolopendra*), Biegel (1922) (*L. forficatus*) and Knoll (1974) (*S. coleoptrata*). Studies on the innervation of the dorsal vessel are Herbst (1891), Fahlander (1938), Seifert (1967a, b), Scheffel (1961), Ernst (1971), Varma (1971), Økland et al. (1982), Jamault-Navarro (1984), Økland (1984) and Wirkner and Pass (2002).

Blood cells (hemocytes) in the hemolymph of chilopods were described by Cattaneo (1889), Cuénnot (1891, 1897) and Duboscq (1898b). More recent studies are those of Sundara Rajulu (1970a, 1973), Ravindranath (1981), Sarojini & Gowri (1981), and especially those of Nevermann et al. (1991), Nevermann (1996) and Hilken et al. (2003a). A cardiac valve found by Herbst (1891) between the aorta and the heart and more accurately described by Fahlander (1938) and Wirkner and Pass (2002).

Maxillary nephridia were first described by Herbst (1889) in *Scutigera coleoptrata* and later found by the same author (Herbst, 1891) in *Lithobius forficatus*. Their nature, however, was only discovered by Fahlander (1938), who provided accurate description of these organs in *Thereuopoda clunifera* and *L. forficatus*. More recent accounts based on light and electron microscopy illustrate the maxillary nephridia of *Scutigera coleoptrata* (Gabe, 1967, 1972; Rosenberg, 1979) and *L. forficatus* (Palm, 1954; Gabe, 1967, 1972; Rilling, 1968; Rosenberg et al., 2009).

Following older descriptions by Dufour (1824), Müller (1829), Plateau (1878), Balbiani (1890) and Kowalevsky (1892/1893), centipede Malpighian tubules were studied histologically by Wang and Wu (1947), Palm (1954), Shukla (1964), Jangi (1966), Rilling (1968), Bertheau (1971) and Prunesco and Prunesco (1996, 2006), and were examined at the ultrastructural level by Füller (1966).

The first anatomical descriptions of glands in the head of centipedes were given by Müller (1829), Dufour (1824), Plateau (1878) and MacLeod (1878). The first comparative anatomical study was done by Herbst (1889, 1891), who investigated the head glands of *Scutigera coleoptrata*, *L. forficatus*, and *Scolopendra cingulata*. Heymons (1901) illustrated the ontogenetic development of head glands in *Scolopendra* sp. and recognized their ectodermal origin. Fahlander (1938) described the occurrence and histology of the glands not only within the head but also in the anterior trunk segments in many representatives of the Notostigmomorpha, Lithobiomorpha, Scolopendromorpha and Geophilomorpha, distinguishing between aggregated epidermal glands, head glands, and vesicular glands located in the first trunk segments. Latzel (1884) described an organ of unknown significance in the head of *Scutigera coleoptrata*. He mentioned the large number of small hairs and microscopic spindle-like bodies within this organ.

Illustrating the anatomy of *Lithobius forficatus*, Rilling (1960, 1968) provided the best account thus far of the musculature of head, trunk and legs of a centipede species.

Detailed descriptions of head muscles were also given by Meinert (1883) for *Scolopendra*, and by Applegarth (1952) for *Pseudolithobius megaloporus*. More numerous studies are available on the musculature of the trunk, including Becker (1926, 1949), Bücherl (1940) and Jangi (1966), all essentially confined to scolopendromorphs. The musculature of the antennae and terminal legs of *Scolopendra* was described by Jangi (1961).

Manton devoted several years of her scientific activity to the morpho-functional study of the arthropod skeleto-muscular system, examining representatives of all the main lineages, including Chilopoda (e.g., Manton, 1965).

The histological structure of the musculature of *Scutigera*, *Geophilus* and *Cryptops* was studied by Füller (1963) shortly before the start of the modern ultrastructural studies summarized in Chapter 5.

The oldest anatomical descriptions of the nervous system of chilopods (*Lithobius*) are found in Treviranus and Treviranus (1817) and Dufour (1824). Subsequent studies revealed detail of the nervous system in the Scutigeromorpha (Newport, 1843; Saint-Remy, 1887, 1889; Herbst, 1891; Chatin, 1893; Duboscq, 1898; Seifert, 1967a), Lithobiomorpha (Saint-Remy, 1887; Chatin, 1893; Duboscq, 1898; Haller, 1905; Jawlowski, 1929; Hanström, 1928; Fahlander, 1938; Henry, 1948; Applegarth, 1952; Rilling, 1960, 1968; Scheffel, 1961), Scolopendromorpha (Saint-Remy, 1887; Herbst, 1891; Chatin, 1893; Fahlander, 1938; Jangi, 1966; Seifert, 1967a; Joshi et al., 1977) and Geophilo-morpha (Newport, 1843; Saint-Remy, 1887; Duboscq, 1898; Fahlander, 1938; Lorenzo, 1960; Seifert, 1967a; Ernst, 1971), but the nervous system of Craterostigmomorpha is still completely unknown. Aspects of brain cytoarchitecture have been illustrated in *S. coleoptrata* (Hörberg, 1931; Sombke et al., 2009), *Thereuopoda clunifera* (Fahlander, 1938) and *Lithobius* sp. (Holmgren, 1916). Loesel et al. (2002) investigated the neuropil structure of the protocerebrum in *Scolopendra* spp. The innervation pattern of the antennal musculature in *S. morsitans* was described by Changulani (1969), and the stomatogastric nervous system of representative Scutigeromorpha, Lithobiomorpha, Scolopendromorpha and Geophilo-morpha by Seifert (1967a).

The histological structure of the scutigeromorph ommatidia has been examined by several authors using light microscopic methods (Grenacher, 1880; Packard, 1880; Adensamer, 1894; Rosenstadt, 1896; Hemenway, 1900; Hesse, 1901; Hanström, 1926, 1934). Adensamer (1894) described the photoreceptor of *Scutigera* as a “pseudo-faceted eye” and thus indicated that this lateral eye represents a secondary type of compound eyes (Paulus, 2000). The first fine structural information concerning the rhabdom and dioptric system of the eye of *Scutigera coleoptrata* was published by Paulus (1979).

The eyes of the Pleurostigmophora were termed ocelli by Bedini (1968), Joly (1969) and Bähr (1971, 1974), but stemmata (like those of the larvae of holometabolous insects) by Borucki (1996), and stemma-like eyes by Bitsch and Bitsch (2005). The lateral ocelli of the Lithobiomorpha have been the objects of classical histological researches (Zograff, 1880; Gruber, 1880; Grenacher, 1880; Willem, 1891; Hesse, 1901; Joly and Herbaut, 1968), followed by electron microscopy studies (Bedini, 1968; Joly, 1969; Bähr, 1971, 1974). The most recent ultrastructural studies (e.g., Müller and Meyer-Rochow, 2006a, b; Müller and Rosenberg, 2006) are presented in Chapter 12.

Behavioural experiments on the vision of *Lithobius* and *Scolopendra* species were reported by Plateau (1886, 1887), Verhoeff (1902-1925), Klein (1934), Scharmer (1935), Bauer (1955), Demange (1956), Görner (1959), Klingel (1960) and Meske (1961). The research of history on epidermal sensilla dates back to Fuhrmann (1922), but most of what is known to date about the fine structure and the typology of scattered and compound sensilla in Chilopoda is due to the studies of a few electron microscopists (Keil, 1975, 1976; Ernst, 1976, 1979, 1981, 1983, 2000; Tichy, 1973; Ernst and Rosenberg, 2003; Ernst et al., 2006, 2009). The best investigated body parts with regard to sensillar equipment are the antennae.

Anatomical descriptions of centipede gonads include Dufour (1824), Fabre (1855), Chalande (1905), Prunesco (1965 b, 1969, 1969/70) and Knoll (1974) for *Scutigera coleoptrata*; Fabre (1855), Zograff (1880), Schaufler (1889), Fahlander (1938), Prunesco (1965a) and Rilling (1968) for *Lithobius forficatus*; Prunesco (1965 d) and Prunesco et al. (1996) for *Craterostigmus*; Fabre (1855), Tuzet and Manier (1953a), Jangi (1957), Prunesco (1965c, 1997), Demange and Richard (1969), Brunhuber (1970) and Brunhuber and Hall (1970) for several scolopendromorph species; and Fabre (1855), Schaufler (1889), Chalande (1905), Tuzet and Manier (1953), Lewis (1961), Prunesco (1967a, 1968) and Breucker (1970) for some geophilomorphs.

Gametogenesis, moulting and their endocrine control were extensively studied by R. Joly and M. Descamps, whose many papers on these subjects are summarized in Chapter 10.

Early work on the embryonic development of Lithobiomorpha (Zograff, 1882), Scolopendromorpha (Heymons, 1901; Ivanov, 1940) and Geophilomorpha (Metschnikoff, 1875; Zograff, 1883; Verhoeff, 1902-25) has been summarized by Johanssen and Butt (1941), Anderson (1973), Gilbert (1997), Rosenberg (2009) and Rosenberg and Müller (2009). The most recent of the traditional studies on centipede embryology is Knoll (1974) on *Scutigera coleoptrata*.

Modern research, including the study of expression patterns of developmental genes, especially in *Lithobius atkinsoni* and *Strigamia maritima*, is presented in Chapter 14.

### References

- ADENSAMER, W., 1894a. Über das Auge von *Scutigera coleoptrata*. – Verhandlungen der zoologisch-botanischen Gesellschaft in Wien 43: 8-9.
- ADENSAMER, T., 1894b. Zur Kenntnis der Anatomie und Histologie von *Scutigera coleoptrata*. – Verhandlungen der zoologisch-botanischen Gesellschaft in Wien 43: 573-578.
- ANDERSON, D. T., 1973. Embryology and phylogeny of annelids and arthropods. – Pergamon Press, Oxford.
- APPLEGARTH, A. G., 1952. The anatomy of the cephalic region of a centipede *Pseudolithobius megaloporus* (Stuxberg) (Chilopoda). – Microentomology 17: 127-171.
- ATTEMS, C., 1926. Chilopoda. – Pp. 239-402 in W. KÜKENTHAL (ed.) Handbuch der Zoologie. 4(1). De Gruyter, Berlin-Leipzig.
- ATTEMS, K., 1929. Myriapoda: I. Geophilomorpha. In: F. E. Schulze, W. Kükenthal, K. Heider, & R. Hesse (eds.). Das Tierreich Bd. 52,– De Gruyter, Berlin & Leipzig.
- AUERBACH, S. I., 1951. The centipedes of the Chicago area with special reference to their ecology. – Ecological Monographs 21: 97-124.
- BAHR, R., 1971. Die Ultrastruktur der Photorezeptoren von *Lithobius forficatus* L. (Chilopoda: Lithobiidae). – Zeitschrift für Zellforschung und mikroskopische Anatomie 116: 70-93.
- BAHR, R., 1974. Contribution to the morphology of chilopod eyes. – Symposia of the Zoological Society of London 32: 383-404.
- BALBIANI, E.-G., 1890. Étude anatomique et histologique sur le tube digestif des *Cryptops*. – Archives de Zoologie expérimentale et générale (2) 8: 1-82.
- BAUER, K., 1955. Sinnesökologische Untersuchungen an *Lithobius forficatus* L. – Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere 65: 237-256.
- BECKER, E. G., 1926. [K evoljucii naruznogo skeleta i muskulatury Tracheata (Atelocerata) 1. Tergal'nyi skelet i dorsal'naja prodol'naja muskulatura Chilopoda] // Zur phylogenetischen Entwicklung des Skellets und der Muskulatur der Ateloceraten (Tracheaten). 1. Das Tergalskelett und die Dorsalmuskulatur von Chilopoden (in Russian – pp. 3-50 - and German translation – pp. 51-67). – Revue zoologique Russe 4: 3-67.
- BECKER, E. G., 1949. [K evoljucii naruznogo skeleta i muskulatury Tracheata (Atelocerata) 2. Plejral'nyj i sternal'nyj skelet i muskulatura Chilopoda Epimorpha] // Zur phylogenetischen Entwicklung des Skeletts und der Muskulatur der Ateloceraten (Tracheaten). 2. Pleural and sternal skeleton and musculature of Chilopoda Epimorpha (in Russian, title translated). – Revue zoologique Russe 28: 39-58.
- BEDINI, C., 1968. The ultrastructure of the eye of a centipede *Polybothrus fasciatus* (Newport). – Monitore zoologico Italiano, Nuova Serie 2: 31-47.
- BERTHEAU, P., 1971. Histologie comparée des tubes de Malpighi de quelques Chilopodes (Myriapodes). – Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, Paris, D 272: 2913-2915.
- BIEGEL, J. H., 1922. Beiträge zur Morphologie und Entwicklungsgeschichte des Herzens bei *Lithobius forficatus* L. – Revue Suisse de Zoologie 29: 427-480.
- BITSCH, J. & C. BITSCH, 2005. Evolution of eye structure and arthropod phylogeny. – In: Koenemann, S. & R. Jenner (Eds), Crustacean and arthropod relationships. – Crustacean Issues 16, Taylor & Francis, New York, pp. 185-214.

- BLOWER, J. G., 1950. Aromatic tanning in the Myriapod cuticle. – Nature 165: 569.
- BLOWER, J. G., 1951. A comparative study of the chilopod and diplopod cuticle. – Quarterly Journal of Microscopical Science 92: 141-161.
- BORUCKI, H., 1996. Evolution und phylogenetisches System der Chilopoda (Mandibulata, Tracheata). – Verhandlungen des naturwissenschaftlichen Vereins in Hamburg, Neue Folge 35: 95-226.
- BORUCKI, H. & J. ROSENBERG, 1997. Transport-active organs within the anal capsule of *Craterostigmus tasmanianus* (Chilopoda, Craterostigmomorpha). – Zoomorphology 117: 49-52.
- BRADÉ-BIRKS, H. K. & S. G. BRADE-BIRKS, 1920. Notes on Chilopoda XX. Luminous Chilopoda, with special reference to *Geophilus carpophagus*, Leach. – Annales and Magazine of Natural History, Zoology, Botany and Geology (9) 5: 1-30.
- BREUCKER, H., 1970. The structure of the male genital ducts of *Geophilus linearis* (Chilopoda). – Zeitschrift für Zellforschung und mikroskopische Anatomie 108: 225-242.
- BRUNHUBER, B.S., 1970. The formation of the Scolopendromorph spermatophore. – Bulletin du Muséum national d'Histoire naturelle, Supplément: 24-28.
- BRUNHUBER, B. S. & E. HALL, E., 1970. A note on the accessory glands of the reproductive system of the scolopendromorph centipede, *Cormocephalus anceps*. – Zoological Journal of the Linnean Society 49: 49-59.
- BÜCHERL, W., 1940. Sobre a musculatura da *Scolopendra viridicornis* Newp. Uma contribuição para o estudo comparativo da musculatura dos quilópodos e insetos. – Memórias do Instituto Butantan 14: 65-107.
- CATTANEO, G., 1889. Sulla morfologia delle cellule ameboidi dei Molluschi e Arthropodi. – Bollettino scientifico, Pavia II: 3-29, 33-57.
- CHAGAS, A. JR., G. D. EDGECOMBE & A. MINELLI, 2008. Variability in trunk segmentation in the centipede order Scolopendromorpha: a remarkable new species of *Scolopendropsis* Brandt (Chilopoda: Scolopendridae) from Brazil. – Zootaxa 1888:36-46.
- CHALANDE, J., 1885. Recherches anatomiques sur l'appareil respiratoire chez les Chilopodes de France. – Bulletin de la Société d'Histoire Naturelle de Toulouse 19: 39-66.
- CHALANDE, J., 1886. Recherches sur le mécanisme de la respiration chez les myriopodes. – Bulletin de la Société d'Histoire Naturelle de Toulouse 20: 137-162.
- CHALANDE, J., 1887. Recherches sur le mécanisme de la respiration chez les myriopodes. – Comptes rendues de l'Académie des Sciences, Paris D 104: 126-127.
- CHALANDE, J., 1905. Recherches histologiques et anatomiques sur les myriapodes du sud-ouest de la France. Bulletin de la société d'Histoire naturelle de Toulouse 38: 48-154.
- CHANGULANI V., 1969. Innervation of the antennal musculature of the centipede *Scolopendra morsitans* Linn. — Journal of Morphology 127: 105-112.
- CHATIN, J., 1893. Sur les noyaux cérébraux des Myriopodes. – Comptes rendues de l'Académie des Sciences, Paris D 117: 291-293.
- COTRONEI, G., 1956. Commemorazione di Filippo silvestri. – Bollettino del Laboratorio di Zoologia generale ed agraria, Portici 33: 1-XXXIX.
- CRABILL, R. E., 1955. On the reappearance of a possible ancestral characteristic in a modern chilopod (Chilopoda: Scolopendromorpha: Cryptopidae). – Bulletin of the Brooklyn Entomological Society 50: 133-136.
- CRABILL, R. E., 1960. A new American genus of cryptopid centipede, with an annotated key to the scolopendromorph genera from America north of Mexico. – Proceedings of the United States National Museum III: 1-15.
- CUÉNOT, L., 1891. Études sur le sang et les glandes lymphatiques dans la série animale. – Archives de zoologie expérimentale et générale (2) 9: 13-90, 365-375, 592-670.

- CUÉNOT, L., 1897. Les globules sanguins et les organes lymphoides des Invertebrés. – Archives d'Anatomie Microscopique I: 153-192.
- CURRY A., 1974. The spiracle structure and resistance to desiccation of centipedes. – Symposia of the Zoological Society of London 32: 365-382.
- DEMANGE, J.-M., 1942. Remarques sur le système trachéen d'*Hydroschendyla submarina* (Grube) et celui des myriapodes géophilomorphes en général. – Bulletin du Muséum national d'Histoire naturelle (2) 14: 422-427.
- DEMANGE, J.-M., 1956. Contribution à l'étude de la biologie, en captivité, de *Lithobius piceus gracilitarsis* Brol. (Myriapode - Chilopode). – Bulletin du Muséum national d'histoire naturelle, 2e série 28: 388-393.
- DEMANGE, J.-M. & J. RICHARD, 1969. Morphologie de l'appareil génital mâle des Scolopendromorphes et son importance en systématique (Myriapodes Chilopodes). – Bulletin du Muséum national d'histoire naturelle, Paris (2) 40: 968-983.
- DESBALMES, G., 1992. Funktions-Anatomie des Fressapparates der Chilopoda: Die Kopfregion von *Theatops erythrocephalus* (C. L. Koch) sowie deren Kauapparat im funktionellen Vergleich mit *Scolopendra cingulata* und *Scutigera coleoptrata*. – Formal- und naturwissenschaftliche Fakultät der Universität Wien.
- DESCAMPS, M. & R. JOLY, 1985. Ultrastructure of the cerebral glands in *Scolopendra cingulata* Latr., *Cryptops savignyi* Leach and *C. hortensis* Leach (Myriapoda: Scolopendromorpha). – International Journal of Insect Morphology and Embryology 14: 105-113.
- DE SERRES, M., 1813. Observations sur les usages des diverses parties du tube intestinal des insects. – Annales du Muséum d' histoire naturelle 20: 213-353.
- DUBOSCQ, O., 1896. Les glandes ventrales et la glande venimeuse de *Chetechaelyne vesuviana* Newp. – Bulletin de la Société Linnéenne de Normandie, 4e série 9: 151-173.
- DUBOSCQ, O., 1898a. Recherches sur les chilopodes. – Archives de zoologie expérimentale et générale (3) 6: 481-650.
- DUBOSCQ, O., 1898b. Sur les globules sanguins et les cellules à carminate des Chilopodes. – Archives de zoologie expérimentale et générale (3) 6: XI-XIV.
- DUBOSCQ, O., 1933. Henry Brölemann. – Bulletin de la Société zoologique de France 58: 257-283.
- DUBUSSON, M., 1928. Recherches sur la ventilation trachéenne chez les chilopodes et sur la circulation sanguine chez les Scutigères. – Archives de Zoologie expérimentale et générale 67: 49-63.
- DUFOUR, L., 1824. Recherches anatomiques sur le *Lithobius forficatus* et la *Scutigera lineata*. – Annales des Sciences Naturelles, Zoologie (1) 2: 81-99.
- ERNST, A., 1971. Licht- und elektronenmikroskopische Untersuchungen zur Neurosekretion bei *Geophilus longicornis* Leach unter besonderer Berücksichtigung der Neurohämialorgane. – Zeitschrift für wissenschaftliche Zoologie 182: 62-130.
- ERNST, A., 1976. Die Ultrastruktur der Sinneshaare auf den Antennen von *Geophilus longicornis* Leach (Myriapoda, Chilopoda). I. Die Sensilla trichoidea. – Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 96: 586-604.
- ERNST, A., 1979. Die Ultrastruktur des Sinneshaare auf den Antennen von *Geophilus longicornis* Leach (Myriapoda, Chilopoda). 2. Die Sensilla basiconica. – Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 102: 510-552.
- ERNST, A., 1981. Die Ultrastruktur der Sinneshaare auf den Antennen von *Geophilus longicornis* Leach (Myriapoda, Chilopoda). 3. Die Sensilla brachyconica. – Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 106: 375-399.

- ERNST, A., 1983. Die Ultrastruktur der Sinneshaare auf den Antennen von *Geophilus longicornis* Leach (Myriapoda, Chilopoda). 4. Die Sensilla microtrichoidea. – Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 109: 521-546.
- ERNST, A., 2000. Struktur und Verbreitung verschiedener Cuticularsensillen bei *Geophilus longicornis* Leach (Chilopoda, Geophilomorpha: Geophilidae). – Fragmenta faunistica, Warszawa 43, Supplement: II3-129.
- ERNST, A. & J. ROSENBERG, 2003. Structure and distribution of sensilla coeloconica on the maxillipedes of Chilopoda. – African Invertebrates 44: 155-168.
- ERNST, A., J. ROSENBERG & G. HILKEN, 2006. Structure and distribution of antennal sensilla in the centipede *Craterostigmus tasmanianus* Pocock, 1902 (Chilopoda, Craterostimomorpha). – Norwegian Journal of Entomology 53: 153-164.
- ERNST, A., J. ROSENBERG & G. HILKEN, 2009. Structure and distribution of antennal sensilla in the centipede *Cryptops hortensis* (Donovan, 1810) (Chilopoda, Scolopendromorpha). – Soil Organisms 81: 399-411.
- FABRE, J.-H. (1855): Recherches sur l' anatomie des organes reproducteurs et sur le développement des Myriapodes. - Annales des Sciences naturelles (4), Zoologie 3: 257-316.
- FAHLANDER, K., 1938. Beiträge zur Anatomie und systematischen Einteilung der Chilopoda. – Zoologiska Bidrag från Uppsala 17: 1-148.
- FUHRMANN, H., 1922. Beiträge zur Kenntnis der Hautsinnesorgane der Tracheaten. I. Die antennalen Sinnesorgane der Myriapoden. – Zeitschrift für wissenschaftliche Zoologie 119: 1-52.
- FÜLLER, H., 1960a. Untersuchungen über den Bau der Stigmen bei Chilopoden. – Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 78: 129-144.
- FÜLLER, H., 1960b. Über die Chiasmen des Tracheensystems bei Geophilomorphen. – Zoologischer Anzeiger 165: 289-297.
- FÜLLER, H., 1963. Vergleichende Untersuchungen über das Skelettmuskelsystem der Chilopoden. – Abhandlungen der Deutschen Akademie der Wissenschaften, Klasse für Chemie, Geologie und Biologie 1962 (3): 1-98.
- FÜLLER, H., 1966. Elektronenmikroskopische Untersuchungen der Malpighischen Gefäße von *Lithobius forficatus* (L.). – Zeitschrift für wissenschaftliche Zoologie 173: 191-217.
- GABE, M., 1952. Sur l'emplacement et les connexions des cellules neurosécrétrices dans les ganglions cérébroside de quelques Chilopodes. – Comptes Rendus de l'Académie des Sciences, Paris, D 235: 1430-1432.
- GABE, M., 1953a. Particularités histologiques de la glande cérébrale des *Scutigera coleoptrata* L. – Bulletin de la Société Zoologique de France 78: 338.
- GABE, M., 1953b. Quelques acquisitions récentes sur les glandes endocrines des arthropodes. – Experientia 9: 352-356.
- GABE, M., 1956. Contribution à l'histologie de la neuro-sécrétion chez les Chilopodes. – In: Wingstrand, K. (ed.): Bertil Hanström, Zoological Papers in honour of his sixty-fifth Birthday, November 20th. – Lund Zoological Institute, Lund: 163-183.
- GABE, M., 1967. Caractères cytologique et histo chimiques du rein maxillaire des Chilopodes. – Comptes Rendus de l'Académie des Sciences, Paris, D 264: 726-729.
- GABE, M., 1972. Contribution à l'histologie du rein maxillaire des Chilopodes. – Annales des Sciences Naturelle – Zoologie et Biologie Animale (12) 14: 105-129.
- GIBSON-CARMICHAEL, T.D., 1885. Notes on the anatomy of the Myriapoda. – Proceedings of the Royal Physical society of Edinburgh 8: 377-381.
- GILBERT, S. F., 1997. Arthropods: the crustaceans, spiders, and myriapods. – In: Gilbert, Scott F.; Raunio, Anne M. [Eds]. Embryology: constructing the organism. – Sinauer Associates, Inc. Sunderland, MA. 1997: i-xii, 1-537: 237-257.

- GÖRNER, P., 1959. Optische Orientierungsreaktionen bei Chilopoden. – Zeitschrift für vergleichende Physiologie 42: 1-5.
- GRABER, V., 1880. Ueber das unikorneale Tracheaten- und speciell das Arachniden- und Myriopoden-Auge. – Archiv für mikroskopische Anatomie 17: 58-94.
- GRENACHER, H., 1880. Ueber die Augen einiger Myriapoden. Zugleich eine Entgegnung an Herrn Prof. V. Graber in Czernowitz. – Archiv für mikroskopische Anatomie 18: 415-467.
- GREVEN, H., J. ROSENBERG & I. LATKA, 1997. Cytochemical notes on the specialized cuticle of the coxal organs in *Lithobius forficatus*: Application of lectins and demonstration of chitin (Chilopoda, Lithobiomorpha: Lithobiidae). – Entomologica Scandinavica, Suppl. 51: 71-76.
- HAASE, E., 1884a. Das Respirationssystem der Symphylen und Chilopoden. – Zoologische Beiträge I: 65-96.
- HAASE, E., 1884b. Schlundgerüst und Maxillarorgan von *Scutigera*. – Zool. Beitr. I: 97-108.
- HAASE, E., 1885. Zur Morphologie der Chilopoden. – Zoologischer Anzeiger 8: 693-696.
- HAASE, E., 1887. Die Stigmen der Scolopendriden. – Zoologischer Anzeiger 10: 140-142.
- HALLER, B., 1905. Über den allgemeinen Bau des Tracheatensyncerebrums. – Archiv für mikroskopische Anatomie 65: 181-279.
- HANSTRÖM, B., 1926. Eine genetische Studie über die Augen und Sehzentren von Turbellarien, Anneliden und Arthropoden. Kungliga Svenska vetenskapsakademiens Handlingar (3) 4: 1-176.
- HANSTRÖM, B., 1928. Vergleichende Anatomie des Nervensystems der Wirbellosen Tiere unter Berücksichtigung seiner Funktion. – Julius Springer Verlag, Berlin.
- HANSTRÖM, B., 1934. Bemerkungen über das Komplexauge der Scutigeriden. – Lunds Universitets Arsskrift, Ny Föld, Avdelning 2 (2) 30: 1-14.
- HANSTRÖM, B., 1940. Inkretorische Organe, Sinnesorgane und Nervensystem des Kopfes einiger niedriger Insektenordnungen. – Kungliga Svenska Vetenskapsakademiens Handlingar 18: 1-165.
- HEMENWAY, J., 1900. The structure of the eye of *Scutigera (Cermatia) forceps*. – Biological Bulletin I: 205-213.
- HENRY, L., 1948. The nervous system and the segmentation of the head in Annulata. V Onychophora, VI Chilopoda, VII Insecta. – Microentomology 13: 27-48.
- HERBST, C., 1889. Anatomische Untersuchungen an *Scutigera coleoptrata*. Ein Beitrag zur vergleichenden Anatomie der Articulata. – Inaugural-Dissertation, Philosophische Fakultät Jena S. 1-37.
- HERBST, C., 1891. Beiträge zur Kenntnis der Chilopoden (Drüsen; Coxalorgan; Gefäßsystem und Eingeweidennervensystem). – Bibliotheca zoologica 3 (9): 1-43.
- HERTEL, W., C. S. WIRKNER & G. PASS, 2002. Studies on the cardiac physiology of Onychophora and Chilopoda. – Comparative Biochemistry and Physiology A 133: 605-609.
- HESSE, R., 1901. Untersuchungen über die Organe der Lichtempfindung bei niederen Thieren. VII. Von den Arthropoden-Augen 2. Die Augen der Myriapoden. – Zeitschrift für wissenschaftliche Zoologie 70: 347-473.
- HEYMONS, R., 1901. Die Entwicklungsgeschichte der Scolopender. – Zoologica (Stuttgart) 13: 1-244.
- HILKEN G., 1997. Tracheal systems in Chilopoda: a comparison under phylogenetic aspects. – Entomologica Scandinavica Supplement 51: 49-60.
- HILKEN, G., 1998. Vergleich von Tracheensystemen unter phylogenetischem Aspekt. – Verhandlungen des naturwissenschaftlichen Vereins in Hamburg, Neue Folge 37: 5-94.
- HILKEN G., C. BROCKMANN & L. NEVERMANN L. 2003a. Hemocytes of the centipede *Scutigera coleoptrata* (Chilopoda, Notostigmophora) with notes on their interactions with the tracheae. Journal of Morphology 257: 181-189.

- HILKEN, G., C. BROCKMANN & J. ROSENBERG, 2003b. The maxillary organ gland: description of a new head gland in *Scutigera coleoptrata* (Chilopoda, Notostigmophora). – African Invertebrates 44: 175-184.
- HOLMGREN, N., 1916. Zur vergleichenden Anatomie des Gehirns von Polychaeten, Onychophoren, Xiphosuren, Arachniden, Crustaceen, Myriopoden und Insekten. – Kungliga Svenska Vetenskapsakademiens Handlingar 56: 1-303.
- HOPKIN, S. P., 1996. Myriapodology before and after Martin Lister's "Journey to Paris in the year 1698". – Mémoires du Museum National d'Histoire Naturelle, 169: 25-34.
- HÖRBERG, T., 1931. Studien über den komparativen Bau des Gehirns von *Scutigera coleoptrata* (L.). – Lunds Universitets Årsskrift, Ny Föld, Afdeling 2 27: 1-24.
- IVANOV, P. P., 1940. Embrional'noje razvitiye skolopendry v svjazi s embriologiej i morfologiej Tracheata. – Izvestiya Akademii Nauk SSR, Otdelenie Biologicheskikh Nauk 6: 831-861.
- JAMAULT-NAVARRO, C., 1984. Arterial walls as cephalic neurohemal organs in *Lithobius forficatus* L. (Myriapoda Chilopoda). – Experimental Biology 43: 97-108.
- JANGI, B.S., 1957. The reproductive system in the male of the centipede, *Scolopendra morsitans* L. (Scolopendridae) – Annals and Magazine of Natural History (12) 10: 232-240.
- JANGI, B. S., 1960. On the antennal musculature of the centipede, *Scolopendra amazonica* Bucherl. – Bulletin of the Zoological Society, College of Science, Nagpur 3: 35-42.
- JANGI, B. S., 1961. The skeletomuscular mechanism of the so-called anal legs in the centipede *Scolopendra amazonica* (Scolopendridae). – Annals of the Entomological Society of America 54: 861-869.
- JANGI, B. S., 1966. *Scolopendra* (The Indian centipede). – The Zoological Society of India, Calcutta.
- JAWLOWSKI, H., 1929. Über die Funktion des Zentralnervensystems bei *Lithobius forficatus* L.. – Acta Biologiae experimentalis, Warsaw 3: 289-316.
- JEEKEL, C.A.W., 2005. Nomenclator generum et familiarum Chilopodorum: A list of the genus and family-group names in the class Chilopoda from the 10<sup>th</sup> edition of Linnaeus, 1758, to the end of 1957. – Myriapod Memoranda Supplement I: 1-130+i-viii.
- JOHANNSEN, O. A. & F. H. BUTT, 1941. Embryology of Insects and Myriapods – The developmental history of insects, centipedes, and milipedes from egg deposition to hatching. – McGraw-Hill, New York-London.
- JOLY, R. 1966. Sur l'ultrastructure de la glandes cérébrale de *Lithobius forficatus* L. (Myriapode, Chilopode). – Comptes rendus de l'Académie des Sciences D 263: 374-377.
- JOLY, R., 1969. Sur l'ultrastructure de l'oeil de *Lithobius forficatus* L. (Myriapode Chilopode). – Comptes rendus hebdomadaires des séances de l'Académie des Sciences D 268: 3180-3182.
- JOLY, R. & C. HERBAUT, 1968. Sur la régénération oculaire chez *Lithobius forficatus* (Chilopode). – Archives de zoologie expérimentale et générale 109: 591-612.
- JOSHI, G., P. HURKAT, & V. CHANGULANI, 1977. Studies on the morphological aspects of the supraoesophageal and suboesophageal ganglia of *Scolopendra morsitans* Linné (Myriapoda, Chilopoda). – Deutsche Entomologische Zeitschrift 24: 175-180.
- KAUFMAN, Z. S., 1960a. The structure of tracheoles in some Chilopoda (in Russian; title translated). – Doklady Akademii Nauk SSSR 130: 693-696.
- KAUFMAN, Z. S., 1960b. The tracheal system of *Geophilus proximus* C. L. Koch (in Russian with English summary). – Zoologicheskii Zhurnal 39: 1802-1810.
- KAUFMAN, Z. S., 1960c. The structure of the digestive tract in *Geophilus proximus* Koch (Chilopoda). – Doklady Akademii Nauk SSSR 135: 992-995.
- KAUFMAN, Z. S., 1961b. Development and structure of the tracheal system in *Lithobius forficatus* L. (in Russian with English summary). – Zoologicheskii Zhurnal 40: 503-511.

- KAUFMAN, Z. S., 1961a. Postembryonic development and structure of the alimentary tract in *Lithobius forficatus* L. (Chilopoda) [in Russian, English summary]. – Entomologiceskoe Obozrenie 40: 109-119.
- KAUFMAN, Z. S., 1961c. Digestive tract structure in *Scutigera coleoptrata* L. – Doklady Akademii Nauk SSSR 139: 740-742.
- KAUFMAN, Z. S., 1962a. The structure and development of stigmata in *Lithobius forficatus* L. (Chilopoda, Lithobiidae) (in Russian with English summary). – Entomologicheskoe Obozrenie 41: 366-371.
- KAUFMAN, Z. S., 1962b. The structure of digestive tract in *Scolopendra cingulata* Latr. (Chilopoda) [in Russian, English summary]. – Zoologicheskii Zhurnal 41: 859-869.
- KEIL, T., 1975. Die Antennensinnes- und Hautdrüsengänge von *Lithobius forficatus* L. Eine licht- und elektronenmikroskopische Untersuchung. – Dissertation, Freie Universität Berlin.
- KEIL, T., 1976. Sinnesorgane auf den Antennen von *Lithobius forficatus* L. (Myriapoda, Chilopoda). I. Die Funktionsmorphologie der "Sensilla trichodea". – Zoomorphology 84: 77-102.
- KLEIN, K., 1934. Über die Helligkeitreaktion einiger Arthropoden. – Zeitschrift für wissenschaftliche Zoologie 145: 1-38.
- KLINGEL, H., 1960. Vergleichende Verhaltensbiologie der Chilopoden *Scutigera coleoptrata* L. ("Spinnenassel") und *Scolopendra cingulata* Latreille (Skolopender). – Zeitschrift für Tierpsychologie 17: 11-30.
- KLOK, C. J., R. D. MERCER & S. L. CHOWN, 2002. Discontinuous gas-exchange in centipedes and its convergent evolution in tracheated arthropods. – Journal of experimental Biology 205: 1019-1029.
- KNOLL, H. J., 1974. Untersuchungen zur Entwicklungsgeschichte von *Scutigera coleoptrata* L. (Chilopoda). – Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 92: 47-132.
- KOCH, A., 1927. Studien an leuchtenden Tieren: I. Das Leuchten der Myriapoden. – Zeitschrift für Morphologie und Ökologie der Tiere 8: 241-270.
- KOHLRAUSCH, E., 1879. Beitrag zur Kenntnis der Scolopendriden. – Journal des Museum Godeffroy 14: 51-74.
- KOWALEVSKY, A., 1892/93. Sur les organes excréteurs chez les Arthropodes terrestres. – Congrès Internationaux d'Anthropologie et d'Archéologie préhistorique et de Zoologie 2: 187-229.
- LATZEL, R., 1880. Die Myriopoden der Österreichisch-Ungarischen Monarchie. I. Die Chilopoden. – A. Hölder, Wien.
- LATZEL, R., 1884. Die Myriopoden der Österreichisch-ungarischen Monarchie. 2. Hölder, Wien.
- LEWIS, J. G. E., 1961. The life history and ecology of the littoral centipede *Strigamia* (=*Scolioplanes*) *maritima* (Leach). – Proceedings of the Zoological Society of London 137: 221-248.
- LEWIS, J. G. E., 1963. On the spiracle structure and resistance to desiccation of four species of geophilomorph centipede. – Entomologia Experimentalis et Applicata 6: 89-94.
- LEWIS, J. G. E., 1981. The biology of centipedes. Cambridge University Press, Cambridge-London-New York.
- LEWIS, J. G. E., T. J. HILL & G. E. WAKLEY, 1996. The structure and possible function of the spiracles of some Scolopendridae (Chilopoda, Scolopendromorpha). – Mémoires du Muséum national d'Histoire naturelle 169: 441-449.
- LINNAEUS, C., 1758. Systema naturae. – Laurentius Salvius, Holmiae.
- LITTLEWOOD, P. M. H., 1983. Fine structure and function of the coxal glands of lithobiomorph centipedes: *Lithobius forficatus* and *L. crassipes* (Chilopoda, Lithobiidae). – Journal of Morphology 177: 157-179.

- LOESEL, R., D. R. NÄSSEL & N. J. STRAUSFELD, 2002. Common design in a unique midline neuropil in the brains of arthropods. – *Arthropod Structure & Development* 31: 77-91.
- LORD, W., 1838. Observations of the anatomy of the organs of circulation in the *Scolopendra*. London Medical Gazette, New Serie I: 892-894.
- LORENZO, M., 1960. The cephalic nervous system of the centipede *Arenophilus bipuncticeps* (Wood) (Chilopoda, Geophilomorpha, Geophilidae). – *Smithsonian miscellaneous collections* 140: 1-43.
- MAC LEOD, J., 1878. Recherches sur l'appareil venimeux des Myriapodes chilopodes. – Description des véritables glandes vénénifiques. – *Bulletin de l'Académie Royale de Belgique* 44: 781-798.
- MANTON, S. M., 1965. The evolution of arthropod locomotory mechanisms. Part 8. Functional requirements and body design in Chilopoda, together with a comparative account of their skeleto-muscular systems and an appendix on a comparison between burrowing forces of annelids and chilopods and its bearing upon the evolution of the arthropodan haemocoel. – *Journal of the Linnean Society of London, Zoology* 46: 251-483.
- MASCHWITZ, U., U. LAUSCHKE, & M. WÜRMLI, 1979. Hydrogen cyanide-producing glands in a Scolopender, *Asanada* n. sp. (Chilopoda, Scolopendridae). – *Journal of Chemical Ecology* 5: 910-907.
- MAUERMAYER, G., 1962. Karl Wilhelm Verhoeff 1867-1945. Selbstdarstellung eines deutschen Zoologen. – *Lebensdarstellungen deutscher Naturforscher* 9: 7-50 – Deutsche Akademie der Naturforscher Leopoldina, Leipzig.
- MEINERT, F., 1870. Myriapoda Musaei Haniensis. Bitrag til Myriapodernes morphologi og systematik. I. Geophile. – *Naturhistorisk Tidsskrift* (3) 7: 1-128.
- MEINERT, F., 1872. Myriapoda Musei Havniensis. Bidrag til Myriapodernes Mophologi og Systematik 2. Lithobini. – *Naturhistorisk Tidsskrift* (3) 8: 281-344.
- MEINERT, F. V. A., 1883. Caput Scolopendrae. The head of the Scolopendra and its muscular system. – Hagerup, Copenhagen.
- MEINERT, F., 1886. Myriapoda Musaei Cantabrigensis, Mass. Part I. Chilopoda. – *Proceedings of the American Philosophical Society* 23: 161-233.
- MESKE, C., 1961. Untersuchungen zur Sinnesphysiologie von Diplopoden und Chilopoden. – *Zeitschrift für vergleichende Physiologie* 45: 61-77.
- METSCHNIKOW, E., 1875. Embryologisches über *Geophilus*. – *Zeitschrift für wissenschaftliche Zoologie* 25: 313-322.
- MINELLI, A., 1978. Secretion of centipedes. – Pp. 73-85 in S. BETTINI (ed.) *Arthropod venoms: Handbook of experimental pharmacology* 48 – Springer, Heidelberg-Berlin.
- MÜLLER, C. H. G. & J. ROSENBERG, 2006. Homology of lateral ocelli in the Pleurostigmophora? New evidence from the retinal fine structure in some lithobiomorph species (Chilopoda: Lithobiidae). – *Norwegian Journal of Entomology* 53: 265-286.
- MÜLLER, C. H. G. & V. B. MEYER-ROCHOW, 2006a. Fine structural description of the lateral ocellus of *Craterostigmus tasmanianus* Pocock, 1902 (Chilopoda: Craterostigmomorpha) and phylogenetic considerations. – *Journal of Morphology* 267: 850-865.
- MÜLLER, C. H. G. & V. B. MEYER-ROCHOW, 2006b. Fine structural organization of the lateral ocelli in two species of *Scolopendra* (Chilopoda: Pleurostigmophora): an evolutionary evaluation. – *Zoomorphology* 125: 13-26.
- MÜLLER, J., 1829. Zur Anatomie der *Scolopendra morsitans*. – *Isis* 22: 549-552.
- NEVERMANN, L., 1996. Untersuchungen an Haemocyten von *Scolopendra cingulata* und *Lithobius forficatus* unter dem Aspekt zellulärer Abwehrreaktionen. Dissertation Justus Liebig Universität Gießen.

- NEVERMANN, L., W. E. R. XYLANDER & G. SEIFERT, 1991. The hemocytes of the centipede *Lithobius forficatus* (Chilopoda, Lithobiomorpha). – Light and electron microscopic studies using in vitro techniques. – *Zoomorphology* 110: 317-327.
- NEWPORT, G., 1838. On the anatomy of certain structures in Myriapoda and Arachnida, which have been thought to have belonged to the nervous system. *London Medical Gazette*, New Series I: 970-973.
- NEWPORT, G., 1843. On the structure, relations, and development of the nervous and circulatory systems, and on the existence of the complete circulation of the blood in vessels, in Myriapoda and macrourous Arachnida. – First series. *Philosophical Transactions of the Royal Society, London* 2: 243-302.
- NEWPORT, G., 1845. Monograph of the class Myriapoda, order Chilopoda; with observations on the general arrangement of the Articulata. – *Transactions of the Linnean Society of London* 19: 265-302, 349-439.
- NIELSEN, C. O., 1962. Carbohydrases in soil and litter invertebrates. – *Oikos* 13: 200-215.
- ÖKLAND, S., 1984. Changes in heart ultrastructure during development of *Strigamia maritima* Leach (Myriapoda, Chilopoda, Geophilidae). – *International Journal of Insect Morphology and Embryology* 13: 233-245.
- ÖKLAND, S., A. TJÖNNELAND, A. NYLUND, L. N. LARSEN & I. CHRIST, 1982. The membrane systems and the sarcomere in the heart of *Lithobius forficatus* L. (Arthropoda, Chilopoda). – *Zoologischer Anzeiger* 208: 124-131.
- PACKARD, A. S. Jr., 1880. The eyes and brain of *Cermatia forceps*. – *American Naturalist* 14: 602-603.
- PAGENSTECHER, H. A., 1878. Allgemeine Zoologie oder Grundgesetze des thierischen Baus und Lebens. – Wiegandt, Hempel & Parey, Berlin.
- PALM, N.-B., 1954. The elimination of injected vital dyes from the blood in Myriapods. – *Arkiv för Zoologi* 6: 219-246.
- PALM, N.-B., 1956. Neurosecretory cells and associated structures in *Lithobius forficatus* L. – *Arkiv för Zoologi* (2) 9: 115-129.
- PALMÉN, J. A., 1877. Zur Morphologie des Tracheensystems. – Engelmann, Leipzig.
- PAULUS, H. F., 1979. Eye structure and the monophyly of the Arthropoda. – Pp. 299-383 in A.P. Gupta (Ed.) Arthropod phylogeny. Arthropod phylogeny. – Van Nostrand, New York.
- PAULUS, H. F., 2000. Phylogeny of the Myriapoda-Crustacea-Insecta: a new attempt using photoreceptor structure. – *Journal of Zoological Systematics and Evolutionary Research* 38: 189-208.
- PLATEAU, F., 1878. Recherches sur les phénomènes de la digestion et sur la structure de l'appareil digestif chez les Myriapodes de Belgique. – *Mémoires de la Académie Royale de Belgique* 42: 1-94.
- PLATEAU, F., 1886. Recherches sur la perception de la lumière par les myriapodes aveugles. – *Journal de l'anatomie et de la physiologie normales et pathologiques de l'homme et des animaux* 22: 431-457.
- PLATEAU, F., 1887. Recherches expérimentales sur la vision chez les arthropodes. – *Bulletin de la Académie royale de Belgique* (3) 14: 407-448.
- PLATEAU, F., 1890. Les myriapodes marins et la résistance des arthropodes à respiration aérienne à la submersion. – *Journal of Anatomy and Physiology* 26: 236-269.
- POCOCK, R. I., 1902. A new and annectant type of chilopod. – *Quarterly Journal of Microscopical Science* (2)45: 417-448.
- PRUNESCO, C.-C., 1965a. Contribution à l'étude anatomique et anatomo-microscopique du système génital femelle de l'ordre Lithobiomorpha. – *Revue roumaine de Biologie, Série de Zoologie* 10: 11-16.

- PRUNESCO, C.-C., 1965b. Le système génital et trachéal de *Craterostigmus* (Craterostigmomorpha, Chilopoda). – Revue roumaine de Biologie, Série de Zoologie 10: 309-314.
- PRUNESCO, C.-C., 1965c. Le système génital femelle d'*Ethmostigmus trigonopodus* (Otostigmini, Chilopoda). – Revue roumaine de Biologie, Série de Zoologie 10: 407-411.
- PRUNESCO, C.-C., 1965d. Système génital femelle du genre *Cryptops* (Scolopendromorpha, Chilopoda). – Revue roumaine de Biologie, Série de Zoologie 10: 231-235.
- PRUNESCO, C.-C., 1967. Le système génital femelle de l'ordre Geophilomorpha. – Revue roumaine de Biologie, Série de Zoologie 12: 251-256.
- PRUNESCU, C.-C., 1968. Le système genital mâle chez quatre espèces de chilopodes de l'ordre des Geophilomorpha. – Revue roumaine de Biologie, Série de Zoologie 13: 57-62.
- PRUNESCO, C.-C., 1969. Le système genital mâle de *Scutigera coleoptrata* (Notostigmophora Chilopoda). – Revue roumaine de Biologie, Série de Zoologie 14: 185-190.
- PRUNESCO, C.-C., 1970. Considérations sur l'évolution du système génital des Chilopodes. – Bulletin du Muséum national d'Histoire naturelle, Paris, (2) 41 (1969) Supplément 2: 108-111.
- PRUNESCU, C.-C., 1997. The anatomy and evolution of the genital system in Scolopendromorpha (Chilopoda). – Entomologica Scandinavica, Supplement 51: 41-48.
- PRUNESCU, C.-C., R. MESIBOV & K. SHINOHARA, 1996. Preliminary data on the anatomy of the genital systems in *Craterostigmus tasmanianus* (Craterostigmomorpha) and *Esastigmatobius longitarsis* (Henicopidae, Lithobiomorpha) (Chilopoda). – Mémoires du Museum National d'Histoire Naturelle 169: 341-346.
- PRUNESCO C.C. & P. PRUNESCO, 1996. Supernumerary malpighian tubules in chilopods. – Mémoires du Muséum national d'Histoire naturelle, Paris 169: 437-440.
- PRUNESCO, P. & C. C. PRUNESCO, 2006. Rudimentary supernumerary Malpighian tubules in the order of Craterostigmomorpha Pocock 1902. – Norwegian Journal of Entomology 53: 113-118.
- RAVINDRANATH, M. H., 1981. Onychophorans and myriapods. Pp. 327-354 In N. A. RATCLIFFE & A. F. ROWLEY (eds.), Invertebrate blood cells 2. Arthropods to urochordates, invertebrates and vertebrates compared. Academic Press, London.
- RICHARD, J., 1885. Un mot sur la phosphorescence des Myriapodes. – Annales de la Société Entomologique de Belgique 29 (2): 15-20.
- RILLING, G., 1960. Zur Anatomie des braunen Steinläufers *Lithobius forficatus* L. (Chilopoda). Skelettmuskelsystem, peripheres Nervensystem und Sinnesorgane des Rumpfes. – Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 78: 39-128.
- RILLING, G., 1968. *Lithobius forficatus*. Grosses Zoologisches Praktikum 13b. – Fischer, Stuttgart.
- RIPPER, W., 1931. Versuch einer Kritik der Homologiefrage der Arthropodentracheen. – Zeitschrift für wissenschaftliche Zoologie 138: 303-369.
- ROSENBERG, J., 1976. Die Ultrastruktur des Gabeschen Organs (Cerebraldrüse) von *Scutigera coleoptrata* L. (Chilopoda, Notostigmophora). – Zoologische Beiträge, Neue Folge 22: 281-306.
- ROSENBERG, J., 1979. Topographie und Feinstruktur des Maxillarnephridium von *Scutigera coleoptrata* L. (Chilopoda, Notostigmophora). – Zoomorphologie 92: 141-159.
- ROSENBERG, J., 1982. Coxal organs in Geophilomorpha (Chilopoda). Organization and fine structure of the transporting epithelium. – Zoomorphology 100: 107-120.
- ROSENBERG, J., 1983a. Coxal organs of *Lithobius forficatus* (Myriapoda, Chilopoda). Fine structural investigation with special reference to the transporting epithelium. – Cell and Tissue Research 230: 421-430.
- ROSENBERG, J., 1983b. Coxal organs in Scolopendromorpha (Chilopoda): Topography, organization, fine structure and significance in centipedes. – Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 110: 383-393.

- ROSENBERG, J., 1984. Ultrastructure of the anal organs in the larval stages of *Lithobius forficatus* L. (Chilopoda, Lithobiomorpha). – International Journal of Insect Morphology and Embryology 13: 25-29.
- ROSENBERG, J., 1985. Untersuchungen zur feinstrukturellen Organisation und Funktion der Coxal- und Analorgane bei Chilopoden. – Bijdragen tot Dierkunde 55: 337-344.
- ROSENBERG, J., 1989. Untersuchungen zur funktionellen Morphologie der Analorgane von Geophilidae (Geophilomorpha). – Pp. 115-123 in A. MINELLI (ed.): Proceedings of the 7th International Congress of Myriapodology. – Brill, Leiden.
- ROSENBERG, J., 2009. Die Hundertfüßer Chilopoda (Die Neue Brehm-Bücherei 285). Westarp Wissenschaften, Hohenwarsleben.
- ROSENBERG, J. & H. GREVEN, 1996. Coxal organs of Chilopoda: The exocrine glands in *Lithobius forficatus*. Mémoires du Museum National d'Histoire Naturelle (Paris) 169: 403-409.
- ROSENBERG, J. & V. B. MEYER-ROCHOW, 2009. Luminescent myriapoda: A brief review. – Pp. 139-146 in V. B. MEYER-ROCHOW (ed.): Bioluminescence in focus - A collection of illuminating essays. – Research Signpost, Trivandrum, Kerala.
- ROSENBERG, J. & C. H. G. MÜLLER, 2009. Morphology in Chilopoda - a survey. Myriapoda and Onychophora of the world - Diversity, biology and importance, – Soil Organisms 81: 1-55; CD-Rom Appendix
- ROSENBERG, J. & G. SEIFERT, 1977. The coxal glands of Geophilomorpha (Chilopoda): Organs of osmoregulation. – Cell and Tissue Research 182: 247-251.
- ROSENBERG, J., C. H. G. MÜLLER & G. HILKEN G., 2006. Ultrastructural organization of the anal organs in the anal capsule of *Craterostigmus tasmanianus* Pocock, 1902 (Chilopoda, Craterostigmomorpha). – Journal of Morphology 267: 265-272.
- ROSENBERG, J., A. SOMBKE & G. HILKEN, 2009. Structure and function of the maxillary nephridium of *Lithobius forficatus* (Chilopoda, Pleurostigmophora). – Journal of Morphology 270: 1531-1540
- ROSENSTADT, B., 1896. Zur morphologischen Beurtheilung der Augen von *Scutigera*. – Zoologischer Anzeiger 19: 369-375.
- SAINT-REMY, G., 1887. Contribution à l'étude du cerveau chez les Arthropodes trachéates. – Archives de Zoologie expérimentale et générale (2) 5 bis, Supplement: 1-274.
- SAINT-REMY, G., 1889. Sur la structure du cerveau chez les Myriapodes et les Arachnides. – Rev. Biol. Nord France 8: 281-298.
- SAROJINI, S. G. & N. GOWRI, 1981. A study of haemocytes in a centipede *Otostigmus* sp. (Chilopoda: Myriapoda). – Indian Zoologist 5: 15-19.
- SCHARMER, J., 1935. Die Bedeutung der Rechts-Links-Struktur und die Orientierung bei *Lithobius forficatus*. – Zoologische Jahrbücher, Abteilung für allgemeine Zoologie und Physiologie der Tiere 54: 459-506.
- SCHAUFLER, B., 1889. Beiträge zur Kenntnis der Chilopoden. – Verhandlungen der zoologisch-botanischen Gesellschaft in Wien 39: 465-478.
- SCHEFFEL, H., 1961. Untersuchungen zur Neurosekretion bei *Lithobius forficatus* L. (Chilopoda). – Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 79: 529-556.
- SCHEFFEL, H., 1965. Elektronenmikroskopische Untersuchungen über den Bau der Cerebraldrüse der Chilopoden. – Zoologische Jahrbücher, Abteilung für allgemeine Zoologie und Physiologie der Tiere 71: 624-640.
- SEIFERT, G., 1967a. Das stomatogastrische Nervensystem der Chilopoden. – Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 84: 167-190.
- SEIFERT, G., 1967b. Der Ursprung des dorsalen Herznervs der Lithobiiden (Chilopoda). – Experientia 23: 452-453.
- SHELLEY, R. M., 2006. Nomenclator generum et familiarum Chilopodorum II: A list of the genus and family-group names in the class Chilopoda from 1958 through 2005. – Zootaxa 1198: 1-20.

- SHREWBURY, F. D. & G. J. BARSON, 1953. The flora of the digestive tract of the common centipede. – Journal of Pathology and Bacteriology 66: 312-315.
- SHUKLA, G. S., 1960. The nervous system of *Scolopendra morsitans*. – Proceedings of the National Academy of Sciences B 170: 131-149.
- SHUKLA, G. S., 1962. Digestive system of *Scolopendra morsitans* L. – Proceedings of the Indian Science Congress 49: 411.
- SHUKLA, G. S., 1964. Studies on *Scolopendra morsitans* Linn., Part II: Digestive and excretory systems. – Entomologische Berichte 24: 55-60.
- SINCLAIR, F. G., 1891. A new mode of respiration in the Myriapoda. — Proceedings of the Royal Society of London 100: 200-201.
- SINCLAIR, F. G., 1892. A new mode of respiration in the Myriapoda. – Philosophical Transactions of the Royal Society of London B 183: 61-72.
- SOMBKE, A., S. HARZSCH & B. S. HANSSON, 2009. Brain structure of *Scutigera coleoptrata*: New insights into the evolution of mandibulate olfactory centers. – Soil Organisms 81: 319-325.
- STAGL, V., 2006. Robert Latzel – his life-work and importance for Myriapodology. – Norwegian Journal of Entomology 53: 223-236.
- STRAUS-DURCKHEIM, H. E., 1828. Considérations générales sur l'anatomie comparée des animaux articulés. – Levrault, Paris.
- STROUHAL, H., 1961. Hofrat Dr. Carl Graft Attems zum Gedanken. – Annalen des naturhistorischen Museums in Wien 64: 1-38.
- SUNDARA RAJULU, G., 1970a. A comparative study of the free amino acids in the haemolymph of a millipede, *Spirostreptus asthenes*, and a centipede, *Ethmostigmus spinosus* (Myriapoda). – Comparative Biochemistry and Physiology 37: 339-344.
- SUNDARA RAJULU, G., 1970b. Studies on the nature of carbohydrases in a centipede *Scolopendra heros*, together with observations of hydrogen ion concentration of the alimentary tract. – Journal of Animal Morphology and Physiology 17: 56-64.
- SUNDARA RAJULU, G., 1973. Free amino acids in the haemolymph Myriapoda. – Symposia of the Zoological Society of London 32: 347-364.
- TAKAKUWA, Y., 1955. Morphology and classification of the *Scutigera*, with a memory of the late Dr. Asajiro Oka (in Japanese). – Gakufu-Shoin Publisher, Tokyo: 1-59.
- TICHY, H., 1973. Untersuchungen über die Feinstruktur des Tömösváryschen Sinnesorgans von *Lithobius forficatus* L. (Chilopoda) und zur Frage seiner Funktion. – Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 91: 93-139.
- TOMÖSVÁRY, E., 1881. A *Scutigera coleoptrata* legzöszervéről (in Hungarian) (On the organ of respiration of *Scutigera coleoptrata*). – Maros-Vásárhelytt, 1-25.
- TOMÖSVÁRY, E., 1883a. Über das Respirationsorgan der Scutigeriden. – Mathematikai és Természettudományi Értesítő 1: 175-180.
- TOMÖSVÁRY, E., On the organ of respiration in the genus *Scutigera* (in Hungarian). – Mathematikai és Természettudományi Értesítő 1:145-150.
- TOMÖSVÁRY, E., 1883-1884. Über den Bau der Spinndrüsen der Geophiliden. – Mathematikai és Természettudományi Értesítő 2: 441-447.
- TREVIRANUS, G. R. & L. C. TREVIRANUS, 1817. Vermischte Schriften anatomischen und physiologischen Inhalts. – Röwer, Göttingen.
- TUZET, O. & J. F. MANIER, 1953. Les spermatozoïdes de quelques Myriapodes Chilopodes et leur transformation dans le receptacle seminalis de la femelle. – Annales des Sciences naturelles, Zoologie II: 221-230.
- VARMA, L., 1971. On the morphology of the heart of the centipede *Scolopendra morsitans* (Chilopoda Epimorpha). – Journal of Animal Morphology and Physiology 18: 111-120.

- VERHOEFF, C., 1892. Zur Kenntnis der Analpleurendrüsen bei Scolopendriden. – Berliner Entomologische Zeitschrift 37: 203-208.
- VERHOEFF, K. W., 1902-1925. Fünfter Band. II. Abteilung Gliederfüssler: Arthropoda Klasse Chilopoda (tables 1-30). – In: Bronn, H.G. (ed.): H. G. Bronn's Klassen und Ordnungen des Tier-Reichs. – Akademische Verlagsgesellschaft m.b.H., Leipzig: p. 1-725.
- VERHOEFF, K. W., 1905. Über die Entwicklungsstufen der Steinläufer, Lithobiiden, und Beiträge zur Kenntnis der Chilopoden. – Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie der Tiere, Supplement. 8: 195-289.
- VERHOEFF, K. W., 1931. Über europäische *Cryptops*-Arten. – Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere 62: 263-288.
- VERHOEFF, K. W., 1941. Zur Kenntnis der Chilopoden-Stigmen. – Zeitschrift für Morphologie und Ökologie der Tiere 38: 96-117.
- VOGES, E., 1882. Das Respirationssystem der Scutigeriden. – Zoologischer Anzeiger 5: 67-69.
- VOGES, E., 1916. Myriapodenstudien. – Zeitschrift für wissenschaftliche Zoologie 116: 75-135.
- VOGT, K. C., YUNG, É., 1894. Traité d'anatomie comparée pratique. – Reinwald, Paris.
- WANG, T. H. & H. W. WU, 1947. On the structure of the Malpighian tubes of the centipedes and their excretion of uric acid. – Sinensis (Nanking) 18: 1-11.
- WILLEM, V., 1889. Note sur l'existence d'un gésier et sur sa structure dans la famille des Scolopendrides. – Bulletin de l'Académie royale de Belgique (3) 18: 532-547.
- WILLEM, V., 1891a. On the structure of the ocelli of *Lithobius*. – Annals and Magazine of Natural history (6) 8: 482-483.
- WILLEM, V., 1891b. Sur la structure des ocelles de la lithobie. – Comptes rendus de l'Académie des Sciences, Paris D 113: 43-45.
- WILLEM, V., 1892. Les ocelles de *Lithobius* et de *Polyxenus* (Myriapoda). – Bulletins de la Société Royale Malacologique de Belgique 27: lxix-lxxi.
- WILLEM, V., 1897. Les glandes filières (coxales) des Lithobies. – Annales de la Société entomologique de Belgique 41: 87-89.
- WIRKNER, C. S. & G. PASS, 2000. Comparative morphology of the circulatory organs in Chilopoda. – Fragmenta faunistica, Warszawa 43, Supplement: 83-86.
- WIRKNER, C. S. & G. PASS, 2002. The circulatory system in Chilopoda: Functional morphology and phylogenetic aspects. – Acta Zoologica (Stockholm) 83: 193-202.
- ZOGRAFF, N., 1880. Anatomie *Lithobius forficatus*. (in Russian, title translated)– Izvestija Imperatorskago Obscestva Ljubitelej Estestvoznanija. –Antropologii i Etnografii/Moskovskij Universitet 32 (2): 1-34.
- ZOGRAFF, N. J., 1882. Zur Embryologie der Chilopoden. – Zoologischer Anzeiger 5: 582-585.
- ZOGRAFF, N. J., 1883. Materialien zur Kenntnis der Embryonalentwicklung von *Geophilus ferrugineus* L. K. und *Geophilus proximus* L. K. (in Russian, title translated) – Izvestija Imperatorskago Obscestva Ljubitelej Estestvoznanija. –Antropologii i Etnografii/Moskovskij Universitet 43(1): 1-77.

## Chapter 3

# CHILOPODA – GENERAL MORPHOLOGY

Alessandro Minelli  
with a section by Markus Koch

### *The centipede body – an external view*

The body of centipedes is elongate to filiform, obviously segmented, and often flattened. Most species are 1–5 cm long, but the smallest adults among the Geophilomorpha and Lithobiomorpha are only ca. 4 mm long and the biggest *Scolopendra* species are approximately 30 cm long.

Scutigeromorphs and lithobiomorphs are quite fragile, due to the softness of their integuments and the ease with which their appendages are detached from the body. Scolopendromorphs are rather more robust, but their appendages, the ultimate legs especially, are also prone to detachment. Geophilomorphs (head capsule, forcipules and forcipular segment excluded) are soft-bodied but also elastic, and their rubber-like trunk and appendages do not easily break apart.

Many centipedes are quite uniformly coloured, in the most diverse hues of yellow, red and brown, but conspicuously coloured and patterned species are common: examples are given in the colour plates in this volume. Some scolopendromorphs alternate red and black or brown and black dorsal stripes, each colour band corresponding either to one complete tergite or to the anterior posterior halves, respectively, of one tergite.

The body is distinctly articulated into head and trunk.

### *Head*

Together with the poisonous forcipules, the head capsule (Fig. 3.1) is usually the most strongly sclerotized part of the centipede body. In the Scutigeromorpha (Fig. 3.1A) the head is nearly globular, whereas in the remaining centipedes it is quite flat.

The mouthparts are covered by the cephalic shield. The two antennae are articulated on the anterior margin of the latter, or immediately underneath. The eyes, if present, are mostly visible on the anterolateral margin. In *Craterostigmus* (Fig. 3.1C) and in many

geophilomorphs (Fig. 3.1E), the distal part of the forcipules (see below) extends anteriorly beyond the anterior margin of the head.

In most lithobiomorphs (Fig. 3.1B), the head shield is approximately circular and bears an evident transversal suture at the level of the lateral ocelli. Towards the lateral margins of the head, the transversal suture splits into an anterior and a posterior longitudinal suture.

In the Scutigeromorpha and Lithobiomorpha, close to the eyes there is another sense organ, the Tömösváry organ (cf. Chapter 12).

In ventral aspect, the head is functionally covered, to a more or less large extent, by the forcipular coxosternite plus the forcipules; thus, the mouthparts and a variably large part of the head can only be seen by detaching the head from the forcipular segment. Ventrally, the anterior part of the head is formed by a plate (the clypeus) whose posterior margin, delimiting the mouth anteriorly, is generally distinguishable as the labrum.

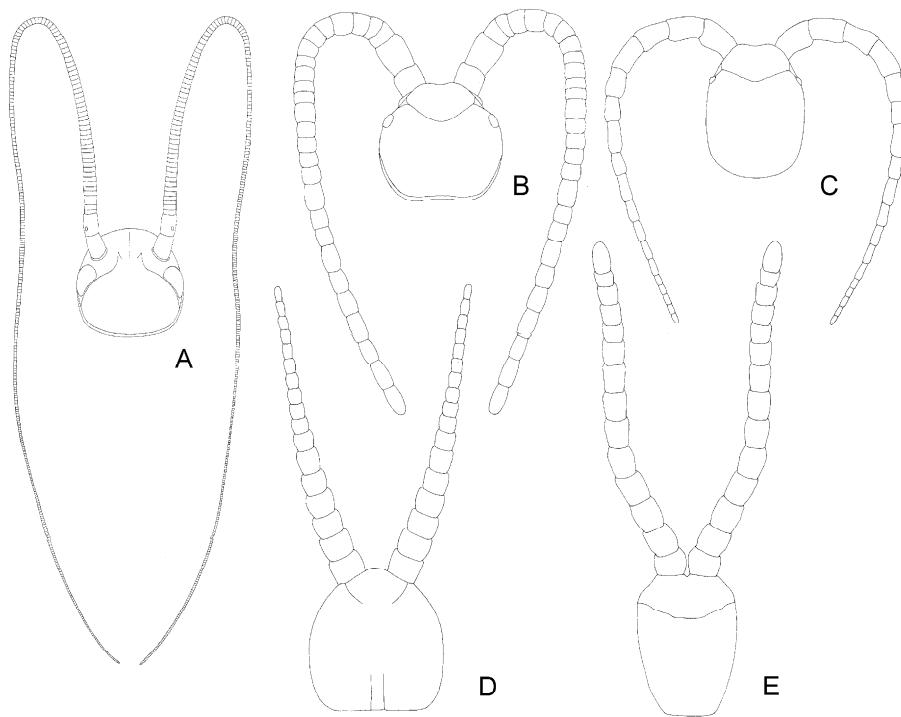
#### *Antennae*

The site of insertion of the antennae on the head is lateral in Scutigeromorpha (Fig. 3.1A), anterolateral in the Lithobiomorpha (Fig. 3.1B) and distinctly anterior in the remaining clades (Fig. 3.1C-E).

In the Geophilomorpha the number of antennal articles is always 14, in the Scolopendromorpha it is very often 17 (always so e.g. in *Cryptops*, *Scolopocryptops*, *Asanada*), but higher in some taxa, up to 34. According to Lewis (2000), numbers lower than 17 recorded for *Tidops simus* and *Kartops guianae* are possibly due to damage. Antennae of 17-18 articles are present in *Craterostigmus*. In the Lithobiomorpha, there are between 14 and more than one hundred antennal articles (e.g., 111 in *Lithobius shordonii*), the number being usually quite constant whenever it is low (i.e., around 20), but variable within the species when higher than ca. 25. Article number may differ between closely related taxa, e.g. 20 antennomeres in *Bothropolys* but many more in *Eupolybothrus*, again 20 in *Lithobius (Monotarsobius)* but many more in *Lithobius (Sigibius)* (Eason, 1991).

The antennae of the Scutigeromorpha are formed by five articles, of which the two proximal ones, or ordinary constitution, form the scape, while the three distal segments, each of which is subdivided into a very large number of annuli, form an extremely long flagellum. Two 'nodes' interrupt the otherwise uniform continuity of the flagellum and mark its trisegmental structure.

For a description of the antennal sensilla, see Chapter 12.



**Fig. 3.1** Head, with antennae (dorsal view, setae omitted). A *Pilbarascutigera incola* (Scutigeromorpha). B *Henicops howensis* (Lithobiomorpha). C *Craterostigmus crabilli* (Craterostigmomorpha). D *Cryptops parisi* (Scolopendromorpha). E *Tygarrup takarazimensis* (Geophilomorpha). Original E. Zamprogno.

### Eyes

As described in detail in Chapter 12, the scutigeromorphs have a pair of conspicuous faceted eyes that occupy a lateral position on the head capsule, behind the antennae. The remaining non-blind centipedes have lateral ocelli, mostly located close to the lateral margin of the head. Their number varies between one pair as in *Craterostigmus*, the scolopendromorph genus *Mimops* and most henicopid lithobiomorphs to the four of scolopendrids up to a maximum of 49 pairs in large lithobiids. All members of the scolopendromorph families Cryptopidae, Scolopocryptopidae and Plutoniumidae and all Geophilomorpha are blind, as are the anopsobiine henicopids and several cavernicolous species of Lithobiidae.

### *Clypeus and labrum* (Fig. 3.2)

The clypeus and cephalic pleurites are anterior and lateral in the Scutigeromorpha, ventral in all other taxa.

In Lithobiomorpha and Scolopendromorpha the mid-piece of the labrum is represented by a single, strong tooth directed posteriorly, the side pieces are larger and provided with a fringe of setae. In *Craterostigmus* the labrum includes a mid-piece with five teeth and side pieces with a fringe of slender projections.

Among the Geophilomorpha there is considerable diversity in the structure of the clypeus and labrum. The labrum is often articulated into a median part, generally with one to many teeth, and two side-pieces, often provided with a posteriorly directed fringe.

Based on morphological observations of the mouth region in *Geophilus carpophagus*, Haswell et al. (2006) suggested that the side pieces of the labrum are distinct morphological units, but the mid-piece is just an extension of the clypeus. This basically agrees with developmental evidence presented by Sakuma and Machida (2005) suggesting that in *Scolopocryptops rubiginosus* the clypeolabrum is a composite structure formed by fusion of a clypeal element with paired labral anlagen.

There are three pairs of gnathal appendages, called the mandibles, the first and the second maxillae, in accordance to the nomenclature adopted for hexapods and crustaceans.

### *Mandibles*

The mandibles (Fig. 3.3) are articulated with the head capsule through a single condyle; the proximal part of the appendage is a curved shank to which the muscles are attached; the trunk of the appendage ends in a broadened and flattened distal end, whose armature, such as serially arranged elongate projections or teeth or both, varies considerably within the group.

In the Lithobiomorpha, the apical ridge of the mandible is provided with a dentate lamina of tricuspid teeth; a tuft of plumose hairs occupies the dorsal angle of the ridge, while a pectinate lamina provided with a number of finely crenulated to shortly pinnate bristles is present on the ventral angle together a series of with plumose hairs, continuing with shorter hairs on the convex part of the ridge. The mandibles of the Scutigeromorpha are similar, except for a larger extension of the apical ridge dorsal to the dentate lamina.

Mandibles are minute in *Craterostigmus* (Fig. 3.3C), distally with a large membranous lobe accompanied by spines, three small tricuspid teeth, and a thick fringe of bristles.

In the Scolopendromorpha (Fig. 3.3D) the trunk of the mandible bears a cruciform suture. On the distal margin there are a dentate lamella with tricuspid teeth (five teeth on one mandible, four on the other), accompanied by pectinate lamellae ventrally and by fine bristles dorsally.

The mandibles of the Geophilomorpha (Fig. 3.3E) are delicate. Their apical armature is very diverse: only a comb-like series of fine teeth (pectinate lamella) in the Geophilidae; a series of pectinate lamellae in the Mecistocephalidae and Oryiidae; a pectinate lamella accompanied by a series of tooth blocks (dentate lamella) in the Schendylidae; a dentate lamella accompanied by several pectinate lamellae in the Himantariidae. These differences in mandible structure have been extensively used in geophilomorph taxonomy, especially as differential characters at the family level. Number of pectinate lamellae and number of teeth borne on each lamella also are common diagnostic characters within the Mecistocephalidae, but this will require a reassessment in the light of the fact that number and complexity of these lamellae increase during post-embryonic development (unpubl. data on *Tygarrup* spp.).

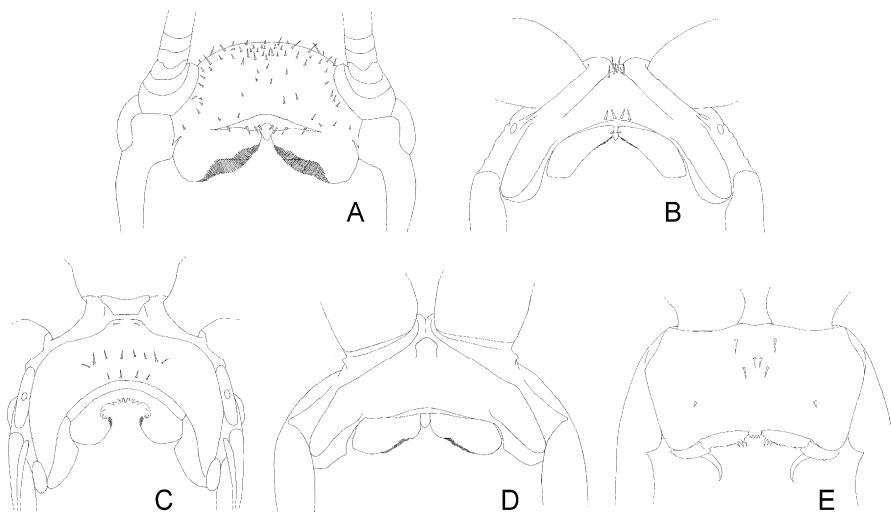


Fig. 3.2 Anterior part of the head (ventral view, maxillae and mandibles removed, antennae only partially drawn). A *Scutigera coleoptrata* (Scutigeromorpha). B *Lithobius pilicornis* (Lithobiomorpha). C *Craterostigmus tasmanianus* (Craterostigmomorpha). D *Scolopendra cingulata* (Scolopendromorpha). E *Geophilus flavus* (Geophilomorpha). Original E. Zamprogno.

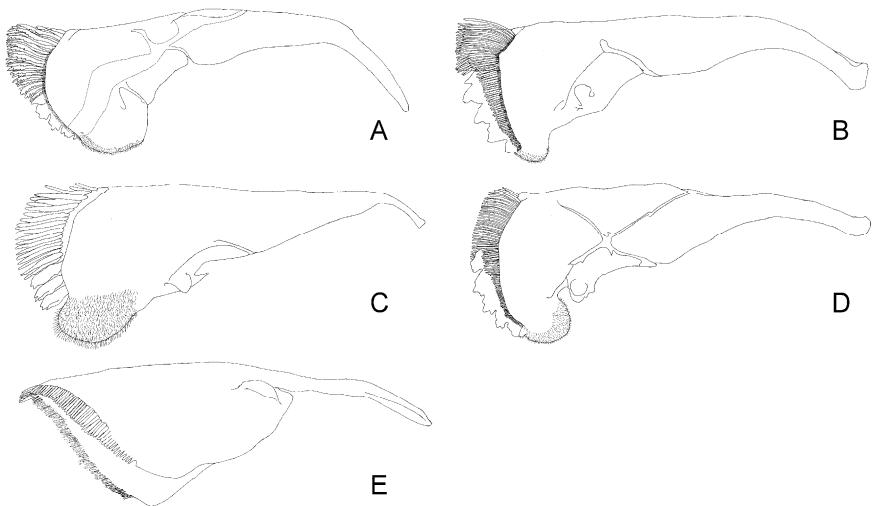


Fig. 3.3 Left mandible (ventral view). A *Scutigera coleoptrata* (Scutigeromorpha). B *Eupolybothrus grossipes* (Lithobiomorpha). C *Craterostigmus tasmanianus* (Craterostigmomorpha). D *Ostostigmus* sp. (Scolopendromorpha). E *Pleurogeophilus mediterraneus* (Geophilomorpha). Original E. Zampogno.

#### Maxillae (Fig. 3.4)

First and second maxillae are integrated into a functional complex that covers the mandibles and often also the labrum when seen from below.

The first maxillae include a proximal coxosternite (resulting from the coalescence of the proximal part of the appendages, the coxa, with the sternite of the corresponding segment) that bears a pair of articulated telopodites (undivided in the Craterostigmomorpha) and usually a pair of fixed coxal projections between the telopodites.

In the Scutigeromorpha, the coxosternite of the second maxillae is very short; the first three articles of the telopodites are provided with 1-4 spine-bristles each; there is no apical claw.

In the Lithobiomorpha (Fig. 3.4B) and Scolopendromorpha (Fig. 3.4D) a median longitudinal division signals the composite nature of the coxosternite of the first maxillae.

The second maxillae are more distinctly leg-like than the first maxillae. The left and right halves of the coxosternite are not always fused medially; the telopodites are generally of three articles (four in the Scutigeromorpha and in the geophilomorph genus

*Macronicophilus*), the last of which is provided with a more or less developed terminal claw.

First and second maxillae of *Craterostigmus* (Fig. 3.4C) are similar to those of the Scolopendromorpha.

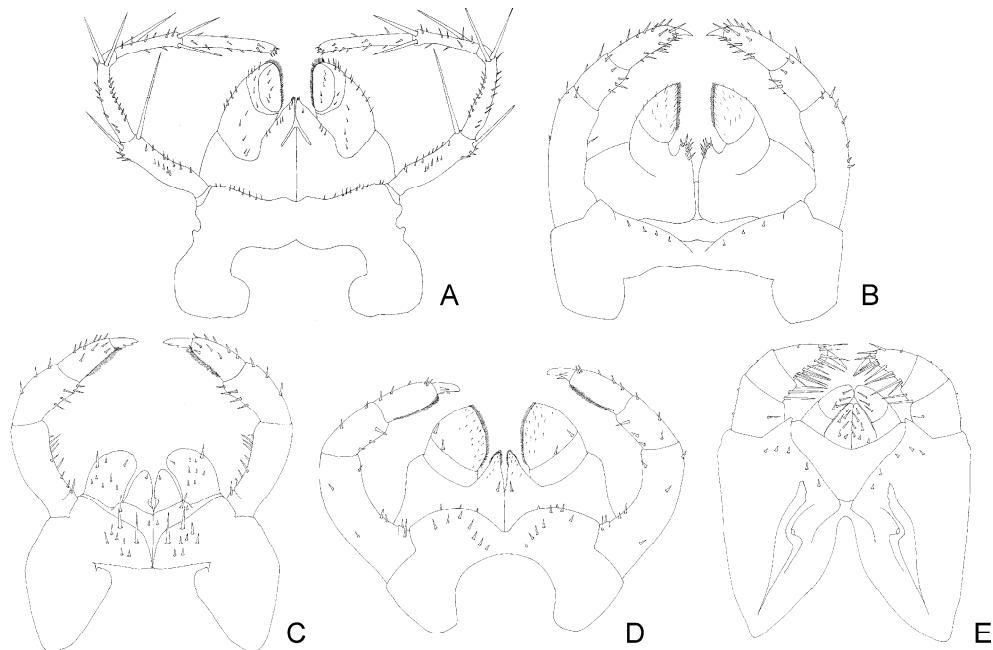


Fig. 3.4 Maxillary complex (ventral view). A *Scutigera coleoptrata* (Scutigeromorpha). B *Lamycetes emarginatus* (Lithobiomorpha). C *Craterostigmus tasmanianus* (Craterostigmomorpha). D *Cryptops anomalans* (Scolopendromorpha). E *Ribautia colcabensis* (Geophilomorpha). Original E. Zamprogno.

#### *Peristomatic structures* by Markus Koch

The mouth of centipedes is situated in a preoral chamber formed by components of the head capsule: anteriorly by the clypeolabrum, posteriorly by a tongue-like median outgrowth of the mandibular sternite. As structures immediately preceding the pharynx, the internal wall of the clypeolabrum and the sternal tongue are called the epipharynx and hypopharynx, respectively. Because they immediately surround the mouth opening, Verhoeff (1902-25) subsumed the epipharynx and hypopharynx together with the pharynx under the term peristomatic organs. Epipharynx and hypopharynx are variably

equipped with sclerites, setae, trichomes, openings of epidermal glands, and sensilla (Fig. 3.5). Details of the shape and arrangement of these peristomatic structures proved to be informative for higher-level systematics (Koch & Edgecombe 2006, 2008; Edgecombe and Koch 2008, 2009).

### *Epipharynx*

A corresponding pattern in the composition of the epipharynx is observed in Scutigeromorpha, Lithobiomorpha, and Scolopendromorpha (Fig. 3.5). Main differences basically seem to correlate with the shape of the head, being either dome-shaped (Scutigeromorpha) or dorsoventrally flattened (Pleurostigmophora). In the latter group, the epipharynx is clearly bipartite in showing distinctive transverse structures (a row of denticle-like spines or a bulge) consistently followed by a median spine field that demarcates the border between distal labral and proximal clypeal parts. At this border, a transverse row of bottle-shaped gland openings immediately in front of the median spine field is characteristic for Lithobiomorpha, whereas a transverse row of bullet-shaped sensilla immediately behind the median spine field characterizes the Scolopendromorpha. A distinctive labral part is differentiated in the Scutigeromorpha, in which a network of sclerites, the labral trapezoid, encompasses a membranous area bearing two median fields of sensilla (Fig. 3.5A). In the Pleurostigmophora, this area is reduced to an unpaired median sclerotized plate devoid of sensilla. Distally, this plate continues into the median labral tooth and therefore is called the tooth plate (Fig. 3.5C,E). Homology of the labral trapezoid and median tooth plate is readily recognizable by the correspondence in how they are laterally flanked by setose plates, the so-called distal bars of a submarginal sclerotized armature. The paired proximal bars of this submarginal armature laterally flank the clypeal part of the epipharynx. These bars are either continuous (Scutigeromorpha) or not (Pleurostigmophora) with the distal bars, but correspond in that they form the so-called epipharyngeal bars of the tentorial complex (Koch, 2003), to which the mandibular gnathal lobes are jointed. The median area of the clypeal part shows further networks of sclerotic cords and bars (forming the so-called clypeal triangle) in the Scutigeromorpha, but is devoid of sclerites in the Pleurostigmophora. Glandular pore fields of the clypeal part variably surround paired lateral and/or unpaired median clusters of sensilla as well as lateral bands of spines and of scale-like trichomes, the size and shape of which form distinctive states.

*Craterostigmus* and geophilomorph centipedes deviate from this pattern, probably in correlation with a suctorial feeding mode. Labral and clypeal parts are less obviously

demarcated than in Scutigeromorpha, Lithobiomorpha, or Scolopendromorpha, nor are corresponding sensilla or spine clusters recognizable. Distal bristle bands are restricted to the Mecistocephalidae among Geophilomorpha, while shape and arrangement of spines and sensilla display enormous variation ranging from dense fields over discrete clusters to entire absence, the evolution of which still remains to be clarified.

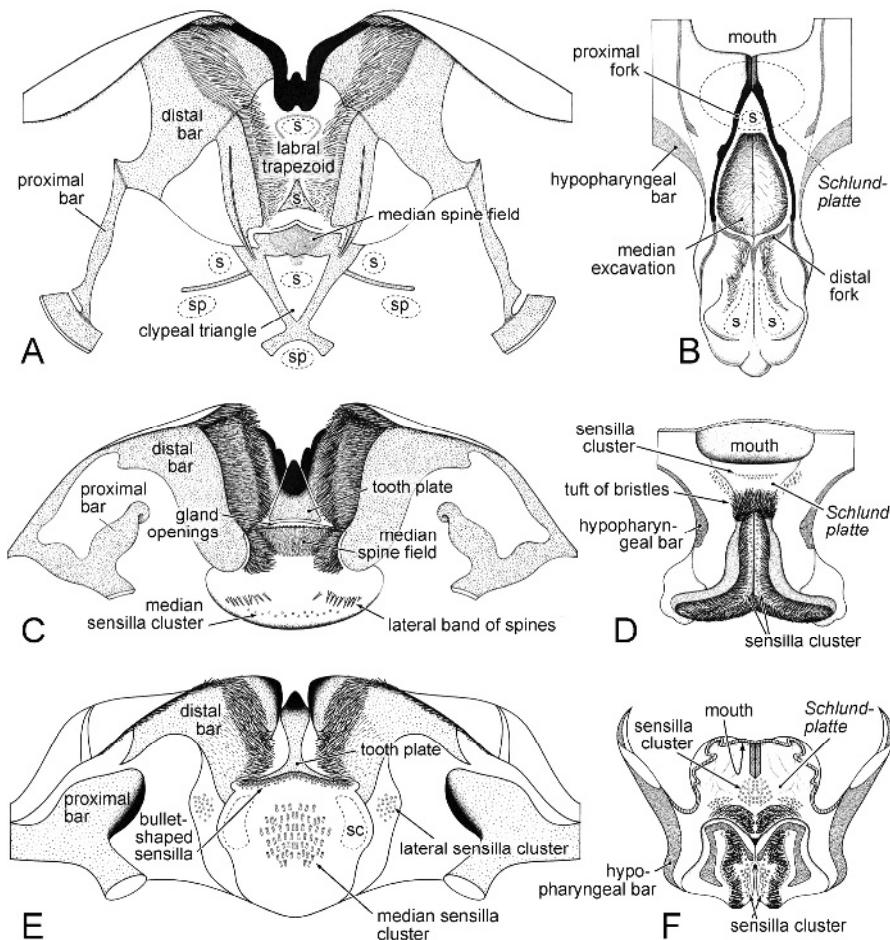


Fig. 3.5 Schematic illustration of epipharynx (left) and hypopharynx (right). A,B Scutigeridae; stippled circles mark clusters of sensilla (s) or spines (sp). C,D Lithobiidae. E,F Scolopendridae; stippled fields mark clusters of scale-like trichomes (sc). A,B modified from Koch and Edgecombe (2006); C,D modified from Koch and Edgecombe (2008); E,F modified from Edgecombe and Koch (2008).

### *Hypopharynx*

The high-ranking centipede subgroups are distinguished each by a specific type of hypopharynx. An elongate, oblique tongue projecting to variable extent into the preoral chamber characterizes the Scutigeromorpha (Fig. 3.5).

The most distinctive feature is the presence of a sclerotized fork, the paired distal parts of which encompass a deep median excavation of unknown function. In the Pleurostigmophora, the hypopharynx is usually much shorter and seems to show no homologue to the area bearing the median excavation in scutigeromorphs. Lithobiomorphs have a short, in ventral view triangular hypopharynx equipped with a median crest, along which rows of bristles are arranged like a moustache (Fig. 3.5D). In the Scolopendromorpha, the hypopharynx forms an elongate, in side view convex pad instead of a tongue (Fig. 3.5F). Common features of all these hypopharyngeal types in Scutigeromorpha, Lithobiomorpha, and Scolopendromorpha are the presence of distinctive button-shaped sensilla arranged on paired median membranous lips extending towards the distal tip of the hypopharynx; and the presence of a proximal, sensilla-bearing plate immediately in front of the mouth, which Verhoeff (1902–25) called the “Schlundplatte”. Shape and arrangement of the “Schlundplatten”-sensilla show significant variation, including loss.

Another peculiar correspondence is the manner of how the hypopharynx is laterally flanked by so-called lateral folds. These folds are continuous with the hypopharyngeal bars of the tentorial complex (Koch 2003) and might represent remnants of superlinguae.

*Craterostigmus* and geophilomorph centipedes again deviate in showing highly variable shapes of the hypopharynx ranging from shallow, trough-like outgrowths over bipartitioned to pointed types, all of which are devoid of button-shaped sensilla.

### *Trunk*

The elongated trunk of centipedes includes a variable and often high number of segments, most of which are each provided with one pair of appendages. The first segment of the trunk, the forcipular segment, bears one pair of poisonous maxillipedes, or forcipules (Fig. 3.6).

This segment is followed by a number of leg-bearing segments, always odd in number in the adults. Posterior to the ultimate leg-bearing segment there is a terminal region of disputable segmental composition.

*Forcipular segment and forcipules*

The tergite of the forcipular segment is free in the Craterostigmomorpha and Geophilomorpha, short but distinct in the Scutigeromorpha and Lithobiomorpha, but not distinct from the following tergite in the Scolopendromorpha.

In the Scutigeromorpha, the sternite is vestigial and the coxites are provided with 3-4 long spine-bristles on the anterior margin. In the other groups, the sternite is fused with the coxae of the segment's appendages to form the massive forcipular coxosternite, with a median longitudinal cleft in the Lithobiomorpha. Between the bases of the two telopodites, the anterior margin of the coxosternite is often provided with individual teeth or with tooth-plates. There are 2-11 teeth on each half of the margin in the Lithobiomorpha, generally accompanied by a peculiar seta (the porodont) at each side, close to the marginal teeth. There are two tooth-plates with 5-8 teeth each in *Craterostigmus*; also one pair of tooth-plates in many Scolopendridae and in Plutoniumidae.

The forcipules are very slender in the Scutigeromorpha and, to a lesser extent, in some Lithobiomorpha. The forcipular telopodites are usually of four articles, usually described as the trochanteroprefemur, femur, tibia and tarsungulum, in the order, but the homology of the individual articles with those of walking legs is still unsettled. In the geophilomorph clade Aphilodontidae, only one article represents the femoral-tibial sector. Femur and tibia form complete rings in the Scutigeromorpha, Lithobiomorpha and Craterostigmomorpha, incomplete in the Scolopendromorpha and Geophilomorpha.

Teeth are frequent along the inner margin of the forcipule. In the Scutigeromorpha, the trochanteroprefemur is armed with a long spine-bristle. There are five or six robust teeth on a trochanteroprefemoral process in *Craterostigmus*, and a similarly large process in many Scolopendromorpha. In Geophilomorpha, all forcipular articles may be devoid of teeth, but in many genera teeth are present on the trochanteroprefemur and (frequently) at the base of the tarsungulum. Particularly rich are the forcipular armatures of the Mecistocephalidae, some Geophilidae (e.g., *Gnathoribautia*, *Pachymerium*) and a few Schendylidae (e.g., *Schendyla armata*).

Shortly before the distal end of the tarsungulum there is the opening of a poison gland. The gland itself is usually located in the proximal part of the forcipular telopodite, but in a few cases it occupies instead a more internal position, thus giving rise to a long or very long secretory duct (Duboscq, 1896; Uliana et al., 2007; Chao and Chang 2006): in the geophilomorph *Henia vesuviana* the gland is located very far away from the forcipules,

around the twentieth segment of the trunk. See Chapter 4 for a description of the fine structure of the poison gland.

#### *Number of leg-bearing segments*

In three of the five main centipede clades, i.e. in the Scolopendromorpha, Lithobiomorpha and Craterostigmomorpha, the adult number of leg-bearing segments is

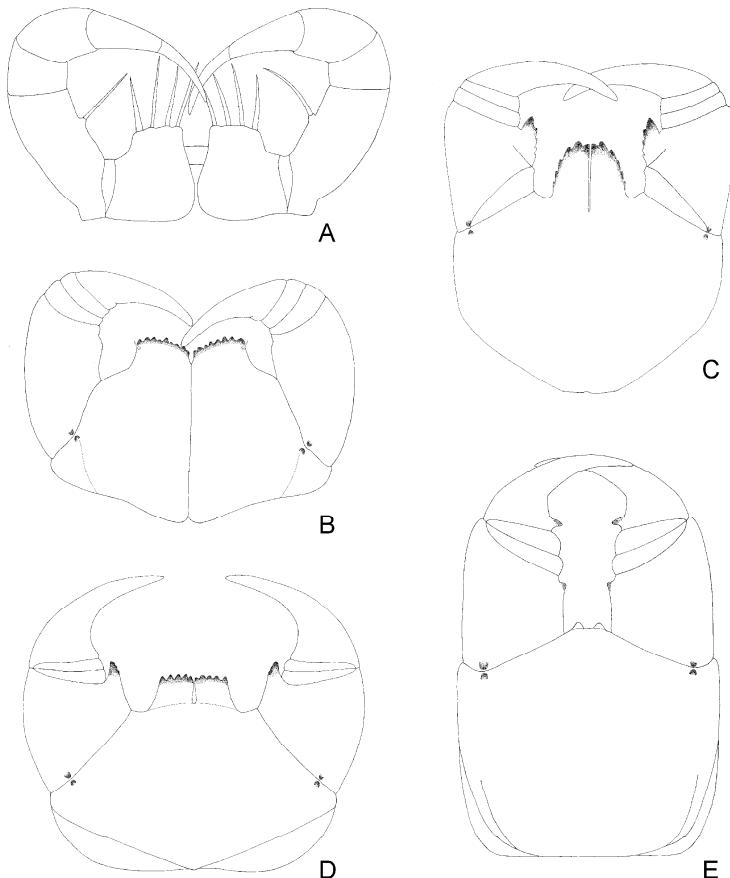


Fig. 3.6 Forcipular segment (ventral view, setae omitted). A *Scutigera coleoptrata* (Scutigeromorpha). B *Bothropolys montanus* (Lithobiomorpha). C *Craterostigmus tasmanianus* (Craterostigmomorpha). D *Scolopendra cingulata* (Scolopendromorpha). E *Pachymerium ferrugineum* (Geophilomorpha). Original E. Zampogno.

always 15. Segment number is higher and less constant in the other two clades. A majority of species in the Scolopendromorpha have 21 pairs of legs, almost all of the others have 23. The only known exceptions are found in the genus *Scolopendropsis*: specimens with either 21 or 23 occur together in *S. bahiensis* (Schileyko, 2006) whereas the recently described *S. duplicata* includes specimens with either 39 or 43 pairs of legs (Chagas et al., 2008).

In the Geophilomorpha, the number of leg-bearing segments ranges from 27 to 191 (Minelli et al., 2000), the lowest numbers being found in *Schendyllops oligopus* (27 or 29 pairs in the males, 31 in females), *Dinoglyphilus oligopodus* (29 in both sexes), *Geophilus persephones* (29 in the only, male, specimen known thus far) and *G. richardi* (29 or 31 in the males, 33 in females). The highest number (191) has been recorded in *Gonibregmatus plurimipes*. In the individual species of the Mecistocephalidae, segment number is generally invariant (mostly 41 or 45 or 49), but in a few species with more than ca. 60 pairs of legs, some degree of intraspecific variation creeps in, most conspicuously in *Mecistocephalus microporus*, with up to 101 leg-bearing segments (Bonato et al., 2001, 2003). In meistocephalids, segment number is also identical between the sexes, whereas in nearly all remaining geophilomorphs the females have more segments than the conspecific males: the distribution of segment numbers within individual populations is usually shifted towards higher numbers by two units in the females in respect to the males, but the differences is higher, up to about eight segments, in species with high or very high segment number, e.g. *Himantarium gabrielis* (Minelli and Bortoletto, 1988).

Post-embryonic developmental stages with an even number of leg-bearing segments occur along the anamorphic development of the Lithobiomorpha (cf. Chapter 14), but all adult centipedes have an odd number of leg-pairs. Only two marginal exceptions to this rule have been recorded thus far. Both of them refer to abnormal specimens, but the kind of anomaly is different between the two cases. One of these exceptions was a male specimen of *Strigamia maritima* with 48 pairs of legs (Kettle et al., 1999, 2000), very likely due to a homeotic mutation changing the gonopods (the appendages of the posterior terminal region of the trunk, see below) into an extra pair of legs, more precisely, into a small-size copy of the usual specialized terminal legs of *Strigamia* males. The other exception was represented by two male specimens of *Haplophilus subterraneus* with 80 pairs of legs, likely due to a localized defective secondary segmentation near the posterior end of the body (Lesniewska et al., 1999).

The impressive difference in segment number between the two species of *Scolopendropsis* mentioned above suggest that this character can evolve, in centipedes, in a saltational way (Minelli et al., 2009; see also Bonato et al., 2001, 2003). In the

Geophilomorpha, the existence of very closely related species morphologically distinguishable only by the number of segments has been repeatedly claimed. This has been confirmed, based on genetic evidence, for a longer (*Geophilus carpophagus*) vs. a shorter (*G. easoni*) species (Arthur et al., 2001), originally recognized by Eason (1979) as two ecologically vicariant forms of *G. carpophagus*. Within a species, segment number may vary along a latitudinal cline (Kettle and Arthur, 2000; Arthur and Kettle, 2001) or other geographical gradients (Simaikis and Mylonas, 2006; Simaiakis et al., 2010). In a species with individual variation in segment number limited to a few classes only (*Strigamia maritima*), evidence for some degree of heritability of this trait (Vedel et al., 2009) and a small effect on segment number of environmental temperature during incubation (Vedel et al., 2008, 2010) have been recently demonstrated.

In the dorsal aspect, all lithobiomorphs and most scolopendromorphs show a more or less obvious alternation of long tergites, corresponding to segments bearing a pair of spiracles laterally, and shorter tergites, corresponding to segments lacking spiracles.

In the Lithobiomorpha, long tergites (1, 3, 5, 7, 8, 10, 12, 14) alternate quite regularly with shorter tergites (2, 4, 6, 9, 11, 13), with a distinct anomaly around segment 6 to 8. This ‘midbody anomaly’ that disrupts an otherwise regular alternation of major and minor segments seems to mark the disappearance (or, better, the lack of formation) of a segment with short tergite and no lateral spiracles (Demange, 1967, 1969; Minelli et al., 2000). Correspondingly, the full series of spiracles in Lithobiomorpha (actually further reduced in most genera) is (1), 3, 5, 8, 10, 12, 14 and 3, 5, (7), 8, 10, 12, 14, 16, 18, 20 in the Scolopendromorpha with 21 pairs of legs, with one additional pair in segment 22 in those with 23 pairs of legs and further pairs at segments 24, 26, 28, 30, 32, 34, 36, 28, (40, 42) in *Scolopendropsis duplicata* (with 39 or 43 pairs of legs respectively). Within the Lithobiomorpha, the presence of spiracles on leg-bearing segment 1 is limited to the Henicopini. Within the Scolopendromorpha, presence vs. absence of spiracles on leg-bearing 7, a trait traditionally considered diagnostic at the genus level, is possibly quite easily evolvable, as shown by the recent discovery (Di et al. 2010.) of a *Theatops* species with spiracles in that position, while the other species in the genus lack them. Interestingly, the genus closest to *Theatops* is *Plutonium*, where spiracles, uniquely among the Scolopendromorpha, are found in an uninterrupted series all along the trunk.

In the Geophilomorpha there is no comparable ‘anomaly’, as tergite length does not alternate between even and odd numbered segments, and all leg-bearing segments from the second on are provided with spiracles. Nevertheless, in many geophilomorphs a segmental position comparable to the one where all lithobiomorphs and most scolopendromorphs have the just described anomaly in the alternation between

segments with longer and shorter tergites is marked either by the localized occurrence of morphological features lacking elsewhere or by the occurrence of a quite abrupt ‘transition’ between an anterior and a morphologically different posterior set of segments.

In several geophilomorphs, localized segmental markers occur on a few segments at ca. 37–45 % of the total number of segments. Examples are the virguliform fossae along the lateral edge of sternites in some *Stigmatogaster* and *Haplophilus* species, the horse-shoe shaped depressions on the sternites in *Bothriogaster* and the posterior transversal fossae in the *Haplophilus* species formerly referred to a separate genus *Nesoporogaster*.

Owing to the intraspecific variation in total segment number, in different individuals of *Stigmatogaster gracilis* the most anterior and the most posterior segments marked with virguliform fossae occur at different absolute positions along the main body axis, but the range of marked segments is always the same, in terms of relative segment position. The range of marked segment is smaller in younger than in older specimens; with age, it increases very little anteriorly, but rather more in the opposite direction (Minelli, 1992).

Among the Geophilomorpha, the only major clade where no evidence of a segmental anomaly has been found thus far is the Mecistocephalidae. Very often, however, the mid-body singularity is not given by a short series or specially marked segments, but by a ‘transition’ between an anterior and a posterior region, with segments differing e.g. in the different shape and thickness of the legs (stouter and shorter in the anterior set), or in the presence (limited to the anterior set) of sternites with a median wide and shallow groove along the anterior margin (the so-called *carpophagus* structure, after the name of a species, *Geophilus carpophagus*, where this condition is very distinct).

#### *Structure of leg-bearing segments*

Basically, each leg-bearing segment is covered by a tergite dorsally and by a sternite ventrally, but in the Scutigeromorpha and Craterostigmomorpha there is a major mismatch between the dorsal and the ventral sclerites.

In the Scutigeromorpha there are only eight tergites compared to the 15 pairs of legs (and sternites). According to the conventional interpretation (e.g., Eason, 1964), the first seven tergites correspond, in the order, to leg-bearing segment 1, 2+3, 4+5+6, 7+8, 9+10, 11+12 13+14, whereas the last leg-bearing segment would apparently lack a tergite. A different interpretation (1, 2+3, 4+5, 6+7, 8+9, 10+11, 12+13, 14+15) was proposed by Murakami (1959). The posterior margin of each tergite is notched; in front of the notch there is a respiratory opening (stoma; cf. Chapter 7).

In *Craterostigmus*, tergites 3, 5, 7, 8, 10, and 12 are each subdivided into two plates, giving the (dorsal only) appearance of 21 segments. All these ‘segments’, except for 1 and 14, are accompanied by a pretergite.

In the Scolopendromorpha and Geophilomorpha, the individual tergites and sternites are more or less distinctly subdivided into pre- and metatergites and pre- and metasternites, respectively. In some scolopendromorphs, e.g. in *Cryptops*, and in the meciostocephalid Geophilomorpha, the metasternites are prolonged as endosternites overlapping the anterior part of the subsequent presternite.

#### *Pleurites*

Laterally, the leg-bearing segments are covered by an extensive area of soft cuticle within which a number of pleural sclerites are dispersed. The pleurites of the Scutigeromorpha are very weakly sclerotized. In the Lithobiomorpha, the segments with spiracles are provided with stigmatopleurites bearing the respiratory openings, otherwise the soft pleural membrane bears only a few very small sclerites.

In *Craterostigmus*, the pleural region of leg-bearing segments 3, 5, 8, 10, 12 and 14 hosts a stigmatopleurite and a poststigmatopleurite; in all segments there are also a procoxa, a katopleure and some smaller sclerites. The pleural area of segments 13-15 is almost wholly covered by the procoxa.

The number of pleurites is the highest in Geophilomorpha, especially in Himantariidae; this must be regarded as a derived condition. In this clade, a common complement of pleurites includes a prescutellum and a stigmatopleurite bearing a spiracle; ventrally a katopleure. The base of the leg is partially encased in an incomplete ring formed by an anterior procoxa and a posterior metacoxa.

The ultimate leg-bearing segment and the postpedal segments are quite different from the preceding ones. None of these segments bear spiracles. The ultimate leg-bearing segment lacks free pleurites; in the Epimorpha there are large and often inflated coxopleura, very often pierced by pores (see Chapter 4).

#### *Legs*

Legs are inserted ventrolaterally on the trunk segments. Most centipede legs are six-segmented, including a coxa and a five-segmented telopodite with trochanter, prefemur, femur, tibia and tarsus. The tarsus usually ends with an apical claw.

The legs of the Scutigeromorpha are extremely long, and of length increasing from the anterior to the posterior pairs. A well-developed coxa provided with a ventral spine is followed by a tiny trochanter. There are 2-3 ridges armed with spines and bristles along the whole length of the prefemur, femur and tibia. There are also spine-bristles at the end of each of these three leg segments. Tarsus I and tarsus II are divided into many annuli, thus forming a kind of flagellum. The apical claw is well-developed on leg-pairs 1-14. The ventral side of the tarsal flagellum is provided with numerous setae, spines and tarsal papillae that help getting firm foot on the substrate. The coxae of the extremely long ultimate legs are aligned parallel to the main body axis; the prefemoral, femoral and tibial ridges are weaker, the distal spine-bristles are reduced and the division between tarsus I and tarsus II is indistinct; overall, there are up to more than 500 tarsal annulations; a terminal claw is lacking.

In lithobiomorphs, the tarsus can be undivided or divided into two secondary articles, or even more than two, as in many *Henicops* and *Cermatobius* species; conditions are often different in the last three pairs of legs in comparison to legs 1-12 (see Chapter 19). A flagellar tarsus is also present in the ultimate pair of legs of the newportiine scolopendromorphs, with 4 to 39 flagellomeres.

Legs with fewer than six articles are rare, an example being the male specimens of the schendylid geophilomorph genus *Nannophilus*.

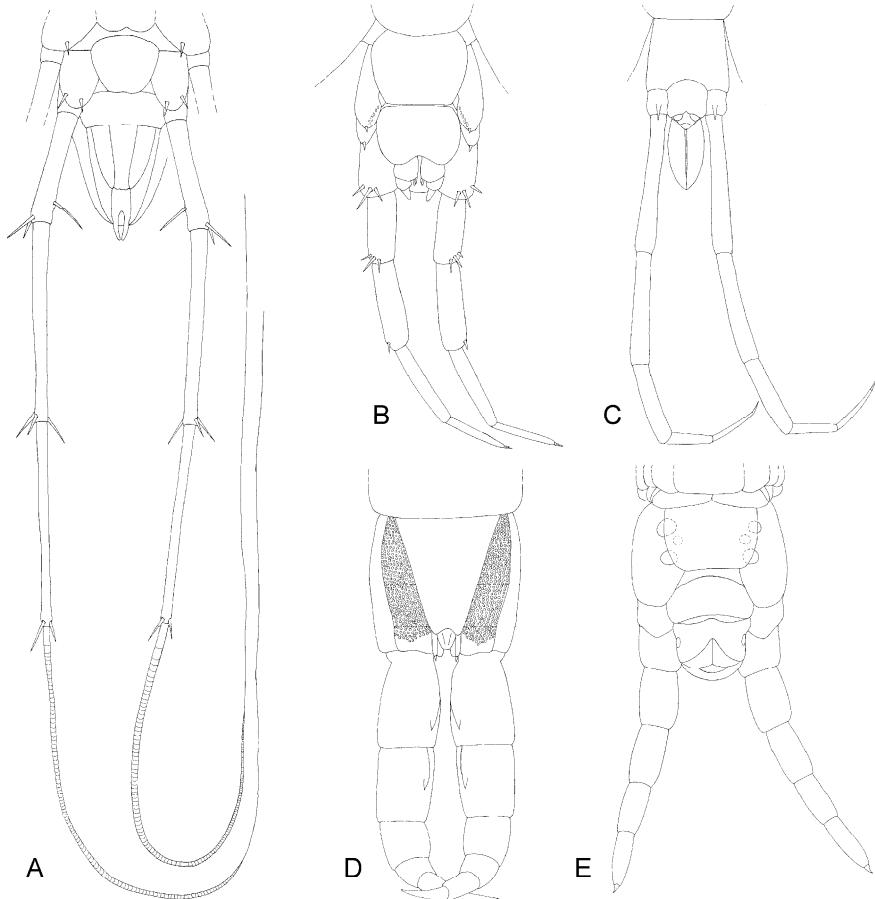
Specialized legs with pincer-like claws are known from three different geophilomorph clades, *Diphyonyx*, *Neogeophilidae*, *Eucratonyx*, in all three cases limited to the segments of the 'mid-body anomaly'.

The ultimate pair of legs are generally modified (Fig. 3.7). Their function is other than locomotory, e.g. grasping or sensory. In the scolopendromorph genus *Alipes*, the tarsus of the ultimate legs is leaf-like and is used as a stridulatory apparatus: a scraper is found on the edge of the tarsus, a file on a ventral expansion of the same leg (Iorio, 2003). Stridulation (frequency of sound in the range 10-80 kHz) occurs when the animal is disturbed, but the sound is also produced by freshly autotomized legs (Skovmand & Enghoff, 1980).

#### *Postpedal segments*

The segmental composition of the trunk posterior to the last leg-bearing segment is uncertain. As many as three segments were recognized there by Brolemann (1930) and Lewis (1981), i.e. an intermediate segment, a first genital segment bearing a pair of gonopods, a second genital segment bearing the penis or the vulva, followed by the telson

with the anus flanked by the anal valves. The homeotic mutant mentioned above seems to disprove the presence of an intermediate segment, in the geophilomorphs at least. In that mutant, the gonopods were replaced by a diminutive duplicate of the terminal legs, without any evidence of the existence of a segment with suppressed appendages in front of the 'first genital segment' (Kettle et al., 1999, 2000).



**Fig. 3.7** Female ultimate leg-bearing segment and postpedal segments (ventral view, setae omitted). A *Scutigera coleoptrata* (Scutigeromorpha). B *Lithobius glacialis* (Lithobiomorpha). C *Craterostigmus tasmanianus* (Craterostigmomorpha). D *Theatops californiensis* (Scolopendromorpha). E *Plateurytion* sp. (Geophilomorpha). Original E. Zamprogo.

In the Scutigeromorpha, the terminal segments are covered by two tergites which, in Brolemann's (1930) disputable interpretation, should belong to the intermediate and the

second genital segment respectively, while the intermediate segment, whose existence is questionable at least, should lack a sternite. In the female (Fig. 3.8A), the large coxosternite of the first genital segment covers the ventral surface of the following segment(s) and bears a pair of two-article gonopods. In the male (Fig. 3.9A), the trapezoidal sternite of the first genital segment is accompanied by a pair of attenuated gonopods; a similar pair of appendages, with a penis in between, is borne on the second genital segment. The last tergite would correspond to the telson.

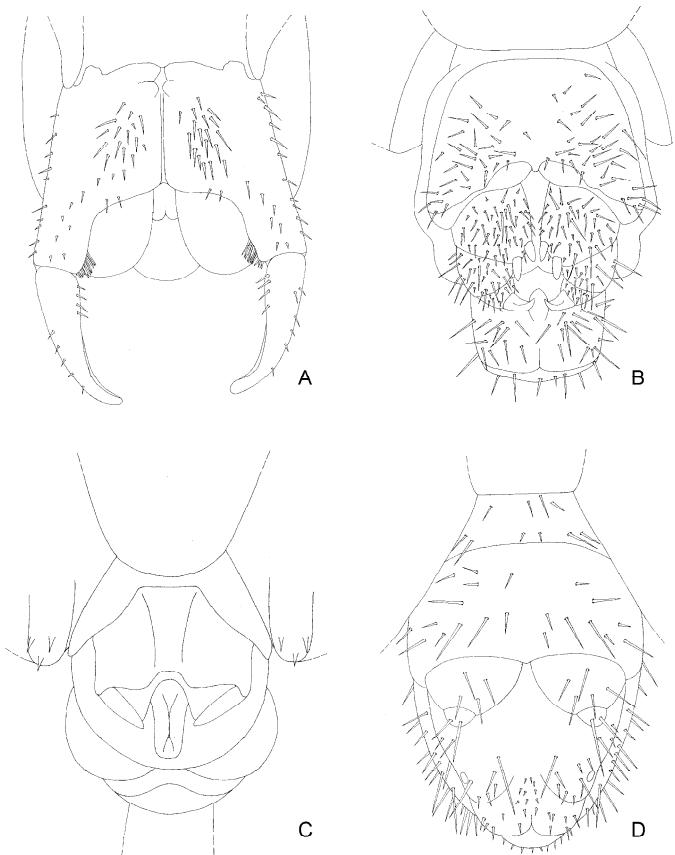


Fig. 3.8 Female postpedal segments, with gonopods (ventral view). A *Scutigera coleoptrata* (Scutigeromorpha). B *Henicops tropicanus* (Lithobiomorpha). C *Scolopendra cingulata* (Scolopendromorpha). D *Escaryus ethopus* (Geophilomorpha). Original E. Zamprogno.

In the Lithobiomorpha, a fairly large tergite is found posterior to the tergite of the ultimate leg-bearing segment and is currently referred to as the intermediate segment. In

*Pleurolithobius* males, the posterior angles of this tergite continue into long, curved horns. The first genital segment has a tergite and a sternite, the latter accompanied by a pair of gonopods. Female gonopods (Fig. 3.8B) are composed of a proximal massive and setose article with two or three large spurs on the inner margin and either one (Lithobiidae) or two (Henicopidae) distal articles and a large and often spoon-like claw, used in manip-

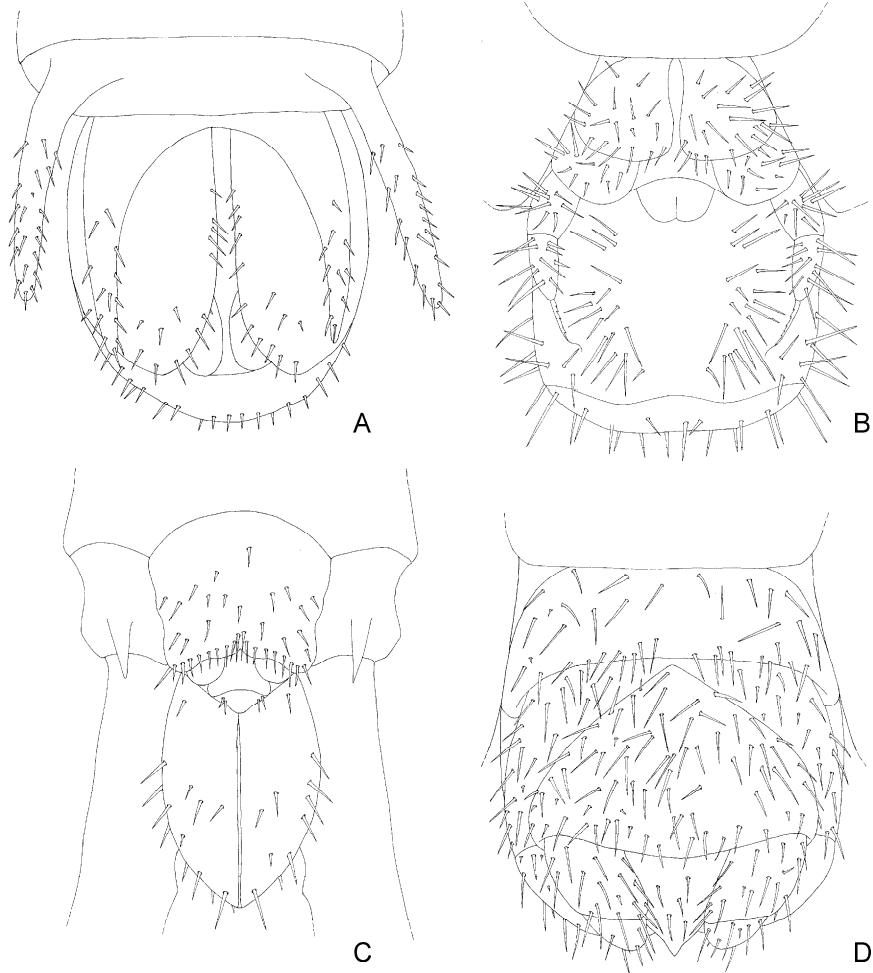


Fig. 3.9 Male terminal segments, with gonopods (ventral view). A *Scutigera coleoptrata* (Scutigeromorpha). B *Henicops milledgei* (Lithobiomorpha). C *Craterostigmus tasmanianus* (Craterostigmomorpha). D *Schendylops* sp. (Geophilomorpha). Original E. Zamprogno.

ating the eggs at deposition. Male gonopods in Lithobiidae are usually inconspicuous and composed of one or two articles, as in *Lithobius*, but in *Eupolybothrus* these appendages are elongate, and in Henicopidae the male gonopod has three articles and a terminal filament (Fig. 3.9B). The second genital segment is represented in the male by the penis, in the female by a narrow, bilobed ventral sclerite. The telson corresponds to a small tergite and a pair of anal valves.

In *Craterostigmus* the anal region is developed as a bivalved capsule that opens ventrally, each side bearing four anal pore-fields separated by cuticular bars (Dohle, 1990; Rosenberg et al., 2006).

The postpedal segments of the Scolopendromorpha are strongly reduced and modified, and not visible from above (Fig. 3.8C).

In the Geophilomorpha, the genital region is dorsally covered by a large tergite, traditionally referred to the intermediate segment; distinct pleurites are present. In the females, gonopods are very short, often of two articles, but sometimes non-articulated (Fig. 3.8D) In the male, the pleurites of the first genital segments are distinct and gonopods are distinctly of 2 articles, with a protrusible structure (the ‘penis’) in between (Fig. 3.9D)

Anal pores corresponding to anal organs (see Chapter 4) are seen on the sclerites at the sides of the anus in juvenile representatives of Geophilomorpha and Lithobiomorpha and persist in adult Henicopidae and many Geophilomorpha

### References

- ARTHUR, W., D. FODDAI, C. KETTLE, J. G. E. LEWIS, M. LUCZYNSKI & A. MINELLI, 2001. Analysis of segment number and enzyme variation in a centipede reveals a cryptic species, *Geophilus easoni* sp. nov., and raises questions about speciation. – Biological Journal of the Linnean Society 74: 489–499.
- ARTHUR, W. & C. KETTLE, 2001. Geographic patterning of variation in segment number in geophilomorph centipedes: clines and speciation. – Evolution and Development 3: 34–40.
- BONATO, L., D. FODDAI & A. MINELLI, 2001. Increase by duplication and loss of invariance of segment number in the centipede *Mecistocephalus microporus* (Chilopoda, Geophilomorpha, Mecistocephalidae). – Italian Journal of Zoology 68: 345–352.
- BONATO, L., D. FODDAI & A. MINELLI, 2003. Evolutionary trends and patterns in centipede segment number based on a cladistic analysis of Mecistocephalidae (Chilopoda: Geophilomorpha). – Systematic Entomology 28: 539–579.
- BROLEMANN, H. W., 1930. Éléments d'une faune des Myriapodes de France. Chilopodes. – Imprimerie Toulousaine, Toulouse.
- CHAGAS, A. JR., G. D. EDGECOMBE & A. MINELLI, 2008. Variability in trunk segmentation in the centipede order Scolopendromorpha: a remarkable new species of *Scolopendropsis* Brandt (Chilopoda: Scolopendridae) from Brazil. – Zootaxa 1888:36–46.

- CHAO, J.-L. & H.-W. CHANG, 2006. Variation of the poison duct in Chilopoda centipedes from Taiwan. – Norwegian Journal of Entomology 53: 139–151.
- DEMANGE, J.-M., 1967. Recherches sur la segmentation du tronc des Chilopodes et des Diplopodes Chilognathes (Myriapodes). – Mémoires du Muséum national d'Histoire naturelle, Paris A44: 1–188.
- DEMANGE, J.-M., 1969. La réduction métamérique chez les chilopodes et les diplopodes chilognathes (Myriapodes). – Bulletin du Muséum national d'Histoire naturelle 40: 532–538.
- DI, Z.-Y., Z.-J. CAO, Y.-L. WU, S.-J. YIN, G. D. EDGEcombe & W.-X. LI, 2010. Discovery of the centipede family Plutoniumidae in Asia: a new species of *Theatops* from China, and the taxonomic value of spiracle distributions in Scolopendromorpha. – Zootaxa (in press).
- DOHLE, W., 1990. Some observations on morphology and affinities of *Craterostigmus tasmanianus* (Chilopoda). – Pp. 69–79 in A. MINELLI (ed.) Proceedings of the 7th International Congress of Myriapodology. – E.J. Brill, Leiden.
- DUBOSCQ, O., 1896. Les glandes ventrales et la glande venimeuse de *Chetechaelyne vesuviana* Newp. – Bulletin de la Société Linnéenne de Normandie, (4) 9: 151–173.
- EASON, E. H., 1964. The centipedes of the British Isles. – Warne, London.
- EASON, E. H., 1979. The effect of the environment of the number of trunk-segments in the Geophilomorpha with special reference to *Geophilus carpophagus* Leach. – Pp. 233–240 in: M. CAMATINI (ed.): Myriapod biology – Academic Press, London.
- EASON, E. H. 1991. On the taxonomy and geographical distribution of the Lithobiomorpha. – Berichte des naturwissenschaftlich-medizinischen Vereins in Innsbruck, Supplement 10: 1–9.
- EDGEcombe, G. D. & M. KOCH, 2008. Phylogeny of scolopendromorph centipedes (Chilopoda): morphological analysis featuring characters from the peristomatic area. – Cladistics 24: 872–901.
- EDGEcombe, G. D. & M. KOCH, 2009. The contribution of preoral chamber and foregut morphology to the phylogenetics of Scolopendromorpha (Chilopoda). – Soil Organisms 81: 295–318.
- HASWELL, M., H. ENGHOFF & W. ARTHUR, 2006. Futher studies on *Geophilus carpophagus* (sensu lato), and a reinterpretation of the structure of its labrum. – Bulletin of the British Myriapod & Isopod Group 21: 2–7.
- IORIO, E., 2003. La fonction stridulatoire des Scolopendres du genre *Alipes* Imhoff, 1854 (Chilopoda, Scolopendromorpha, Scolopendridae, Otostigminae). – Bulletin de Phylle 17: 15–21.
- KETTLE, C. & W. ARTHUR, 2000. Latitudinal cline in segment number in an arthropod species, *Strigamia maritima*. – Proceedings of the Royal Society of London, Series B, Biological Sciences 267: 1393–1397.
- KETTLE, C., W. ARTHUR, T. JOWETT & A. MINELLI, 1999. Homeotic transformation in a centipede. – Trends in Genetics 15: 393.
- KETTLE, C., W. ARTHUR, T. JOWETT & A. MINELLI, 2000. A homeotically-transformed specimen of *Strigamia maritima* (Chilopoda, Geophilomorpha), and its morphological, developmental and evolutionary implications. – Fragmenta faunistica, Warszawa, 43 Supplement: 105–112.
- KOCH, M., 2003. Monophyly of the Myriapoda? Reliability of current arguments. – African Invertebrates 44: 137–153.
- KOCH, M. & G. D. EDGEcombe 2006. The peristomatic structures in Scutigeromorpha (Chilopoda): a comparative study, with new characters for higher-level systematics. – Zoomorphology 125: 187–207.
- KOCH, M. & G. D. EDGEcombe, 2008. The peristomatic structures of Lithobiomorpha (Myriapoda, Chilopoda): comparative morphology and phylogenetic significance. – Journal of Morphology 269: 153–174.

- LESNIEWSKA, M., L. BONATO, A. MINELLI & G. FUSCO. 2009. Trunk anomalies in the centipede *Stigmatogaster subterranea* provide insight into late-embryonic segmentation. – Arthropod Structure & Development 38: 417–426.
- LEWIS, J. G. E., 1981. The biology of centipedes. – Cambridge University Press, Cambridge.
- LEWIS, J. G. E., 2000. Centipede antennal characters in taxonomy with particular reference to scolopendromorphs and antennal development in Pleurostigmophora (Myriapoda, Chilopoda). – Fragmenta Faunistica, Warszawa 43 Supplement: 87–96.
- MINELLI, A., 1992. Towards a new comparative morphology of myriapods. – Berichte des naturwissenschaftlich-medizinischen Vereins in Innsbruck, Supplement 10: 37–46.
- MINELLI, A. & S. BORTOLETTO, 1988. Myriapod metamerism and arthropod segmentation. – Biological Journal of the Linnean Society 33: 323–343.
- MINELLI, A., A. CHAGAS-JÚNIOR & G. D. EDGECOMBE, 2009. Saltational evolution of trunk segment number in centipedes. Evolution & Development 11: 318–322.
- MINELLI A., D. FODDAI, L. A. PEREIRA & J. G. E. LEWIS, 2000. The evolution of segmentation of centipede trunk and appendages. – Journal of Zoological Systematics and Evolutionary Research 38: 103–117.
- MURAKAMI, Y., 1959. Postembryonic development of the common Myriapoda of Japan. I. The anamorphic development of the leg-bearing segments of Scutigeridae and a new aspect on the problem of its tergite. [In Japanese, with English summary] – Zoological Magazine, Tokyo, 68: 193–199.
- ROSENBERG, J., C. H. G. MÜLLER & G. HILKEN, 2006. Ultrastructural organization of the anal organs in the anal capsule of *Craterostigmus tasmanianus* Pocock, 1902 (Chilopoda, Craterostigmomorpha). – Journal of Morphology 267: 265–272.
- SAKUMA, M. & R. MACHIDA, 2005. Clypeolabrum formation in a centipede *Scolopocryptops rubiginosus* L. Koch (Chilopoda: Scolopendromorpha). – Proceedings of the Arthropodan Embryological Society of Japan 40: 1–4.
- SCHILEYKO, A. A., 2006. Redescription of *Scolopendropsis bahiensis* (Brandt, 1841), the relations between *Scolopendropsis* and *Rhoda*, and notes on some characters used in scolopendromorph taxonomy (Chilopoda, Scolopendromorpha). – Arthropoda Selecta 15: 9–17.
- SIMAIAKIS S. M., E. IORIO, P. DJURSVOLL, B. A. MEIDELL, G. ANDERSSON & L. R. KIRKENDALL, 2010. A study of the diversity and geographical variation in number of leg-bearing segments in centipedes (Chilopoda: Geophilomorpha) in north-western Europe. – Biological Journal of the Linnean Society 100: 899–909.
- SIMAIAKIS, S. & M. MYLONAS, 2006. Intraspecific variation in segment number in *Pachymerium ferrugineum* (C. L. Koch, 1835) (Chilopoda: Geophilomorpha) in the south Aegean Archipelago (north-east Mediterranean, Greece). – Biological Journal of the Linnean Society 88: 533–539.
- SKOVMAND, O. & H. ENGHOFF, 1980. Stridulation in *Alipes grandidieri* (Lucas), a scolopendromorph centipede. – Videnskabelige Meddelelser fra den naturhistoriske Forening 142: 151–160.
- ULIANA M., L. BONATO & A. MINELLI, 2007. The Mecistocephalidae of the Japanese and Taiwanese islands (Chilopoda, Geophilomorpha). – Zootaxa 1396: 3–84.
- VEDEL, V., Z. APOSTOLOU, W. ARTHUR, M. AKAM & C. BRENA, 2010. An early temperature-sensitive period for the plasticity of segment number in the centipede *Strigamia maritima*. – Evolution and Development 12: 347–352.
- VEDEL, V., C. BRENA & W. ARTHUR, 2009. Demonstration of a heritable component of the variation in segment number in the centipede *Strigamia maritima*. – Evolution and Development 11: 434–440.
- VEDEL, V., A. D. CHIPMAN, M. AKAM & W. ARTHUR, 2008. Temperature-dependent plasticity of segment number in an arthropod species: the centipede *Strigamia maritima*. – Evolution and Development 10: 487–492.

VERHOEFF, K. W., 1902–25. Chilopoda. – Pp. 1-725 in H. G. BRONN (Ed.) Klassen und Ordnungen Des Tierreichs, 5(2). – Akademische Verlagsgesellschaft, Leipzig.

## Chapter 4

# CHILOPODA - INTEGUMENT AND ASSOCIATED ORGANS

### Integument and cuticle

Jörg Rosenberg, Carsten H.G. Müller & Gero Hilken

#### *Integument*

The integument of Chilopoda consists of a single-layered epidermis that secretes a more or less conspicuous basal matrix and a multi-layered cuticle. Besides the ordinary epidermal cells, the epidermal layer includes isolated epidermal glands. The cuticle covers also invaginated epidermal derivatives such as the tubular tracheal system, the ductules of exocrine glands, the pharynx, the hind-gut, and the openings of the sexual organs. Beside providing apodemata (insertion places for muscles, see Fig. 4.2F), the cuticle is an important barrier between the outer environmental influences and the inner milieu and provides both protection against evaporation and permeation of fluids.

In Chilopoda, moulting occurs lifelong (see Chapter 10).

#### *The cuticle*

Seen from above, the cuticular surface of centipedes often shows a polygonal pattern of scutes (Figs. 4.1A, D; 4.2A-C; 4.3) reflecting the geometry of the external face of epidermal cells at the stage of deposition of the very first layers of the epicuticle (Fusco et al., 2000). The scute-like configuration is stable across subsequent developmental stages. The epidermal cells are usually firmly connected by complex interdigitations of their lateral membranes (Figs 4.1D, 4.2C). Besides sensory setae (see Chapter 12), epidermal cells may create trichomes of different kinds, especially frequent in the preoral chamber and on the mouthpart appendages. For instance, filiform (=foliate) and fusiform (=serrated) trichomes of various length and density are observed within the maxillary organ (Figs. 4.2D-E).

The composition of a centipede's cuticle has been insensively investigated in various *Lithobius* species and generalized to most Chilopoda. The cuticle of *L. forficatus* consists

of a thick multi-lamellated endocuticle, a rigid more electron-dense exocuticle and an external epicuticle up to 1 µm in thickness (Scheffel, 1987) (cf. Fig. 4.1B, *Lithobius mutabilis*). The epicuticle is thin and, as in other chilopod taxa, usually not exceeds 10–20 nm in thickness (Fusco et al., 2000).

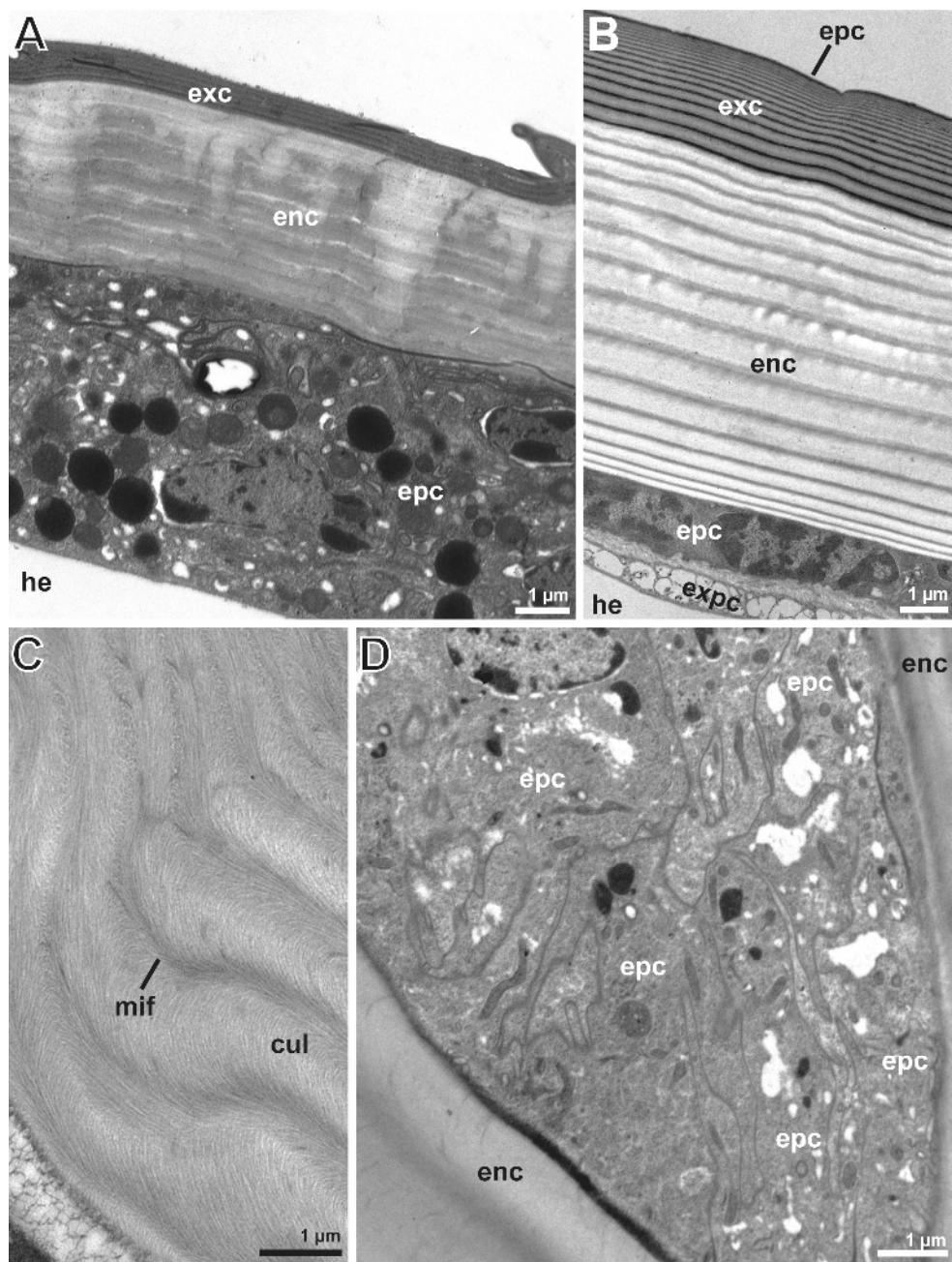
In *L. forficatus*, the endo-, meso-, and exocuticle are composed of alternating lamellae of chitin and protein layers (Fig. 4.1B). The chitin lamellae consist of primary fibrils that merge to secondary fibrils (> 100 nm in length) (Damaschun and Füller, 1965; Füller, 1965a, b). An example of microfibrillar packing in the cuticle of centipedes is given in Fig. 4.1C. Cytochemical analyses have demonstrated the presence of chitinous material in the endocuticle of the coxal organs, whereas within the subcuticle chitin is not detectable (Greven et al., 1997). Specialized epithelia may secrete a subcuticle, as in the coxal organs of various centipedes (Rosenberg, 1985) or in the area of the maxillary organ of *S. coleoptrata* (Hilken and Rosenberg, 2006b) (Fig. 4.2C). A subcuticular matrix is also secreted by canal cells of exocrine epidermal glands.

The exocuticle varies in form and thickness across the different regions of the body. In sternites, pleurites, mouth region and even in some places of otherwise strongly sculpturized tergites the cuticle is rather thin with the exocuticle contributing less than a fifth of the whole thickness (e.g. *Scutigera coleoptrata*, Fig. 4.1A). In *Lithobius forficatus*, the exocuticle is responsible for a quarter to a fifth of the total cuticle thickness (Fig. 4.1B). In contrast, the unsclerotized cuticular areas, connecting sclerites within segments, podomeres and antennomeres (arthrodial membranes) are very thin and flexible. In *Haplophilus subterraneus*, the sclerite exocuticle projects inwards in the form of cones that appear to correspond to individual epidermal cells (Fusco et al., 2000), resulting in the polygonal areas or scutes (Cals, 1974) visible in surface views on the cuticle (Fig. 4.2A–B). The cones of the exocuticle are not preset in the areas of arthrodial membrane.

The chemical composition of the epicuticle still remains unclear; the old and contrasting reports by Krishnan (1956) and Shrivastava (1971) need revisit. The absence of a wax layer in the epicuticle has been considered to be a characteristic feature

**Fig. 4.1** Ultrastructure of the epidermis and cuticle of various centipedes. A Epidermis lateral medio-laterally of the head capsule of *Scutigera coleoptrata*. Note the terrace like profile of the upper cuticular surface displaying the polygonal sculpturation of the cuticle. B Epidermis posterior to the lateral ocellar field of *Lithobius mutabilis*. C Pattern of double-arched microfibrils in the cuticle of *Henia* in oblique section. D Tangential view of the apical region of several epidermal cells and overlaying cuticle, observed nearby the lateral flanks of the head capsule of *Craterostigmus tasmanianus*. TEM. Originals C. H. Müller.

cul cuticular lamella; enc endocuticle; epc epidermal cell; epic epicuticle; exc exocuticle; expc external pigment cell; he hemolymphatic space; mif cuticular microfibrils



of centipedes (Semenova, 1961; Scheffel, 1987; Hochstrate, 1988/89). This is supported by experiments with the abrasive aluminium oxide powder: in *L. forficatus*, the intensity of evaporation is similar between treated and untreated animals (Joly, 1962). Centipedes are therefore constantly threatened by desiccation and are thus confined to environments with a humid atmosphere.

### Solitary epidermal glands

Carsten H. G. Müller, Jörg Rosenberg & Gero Hilken

Several types of epidermal glands (solitary, aggregated and compound) have been recently described and characterized thanks to transmission electron microscopy (Müller et al., 2003a, 2006, 2008, 2009, in press; Hilken et al., 2005) (cf. Table 4.1).

Solitary epidermal glands include at least one secretory cell, one canal cell and also, very often, one intermediary cell. In many cases, additional canal cells and a multiplicity of secretory cell types are found. The maximum cell number hitherto counted in a solitary epidermal gland is six, as found in *Cryptops hortensis*, *Scolopendra oraniensis* and *S. cingulata*, distributed among five functionally differentiated cell types: one or two different secretory cell(s), a single intermediary cell, and one or two different canal cells (Hilken et al., 2005; Müller et al., 2009, in press; Rosenberg, 2009). Even though highly abundant sometimes, solitary epidermal glands are clearly separated from each other by sheaths of epidermal cells encircling them.

In contrast, we define as aggregated epidermal cells unions of several to many closely attached epidermal glands that discharge their secretion to the outside through individ-

**Fig. 4.2** Ultrastructure of the epidermis, cuticle and cuticular differentiations of various centipedes. A Longitudinal section through the upper half of the cuticle of an anterior trunk segment of *Henia*. B Close-up of the upper part of cuticle from two scutes located medially on the head capsule of *Henia*, displaying exocuticular cones. C Lower magnification of an epidermal area in the maxillary organ of *Scutigera coleoptrata*. Note the unlammellated subcuticle and margins of subjacent epidermal layers interconnected by cytoplasmic projections (arrowhead). D-E Filiform and fusiform setae projected into the maxillary organ of *Scutigera coleoptrata* in transverse (D) and oblique-longitudinal (E) sections. F Junctional point of mandibular muscles in the head capsule of *Henia*. Several apodemata are visible, which are attached to striated muscular fibres, arranged via specialized epidermal cells rich in tonofilaments. TEM. Originals C. H. G. Müller.

apo apodeme; con exocuticular cone; enc endocuticle; epc epidermal cell; exc exocuticle; mu mandibular musculature; sbc subcuticle; sc cuticular scute; smtr small filiform (=foliate) trichome; str fusiform (=serrated) trichome; tf tonofilaments

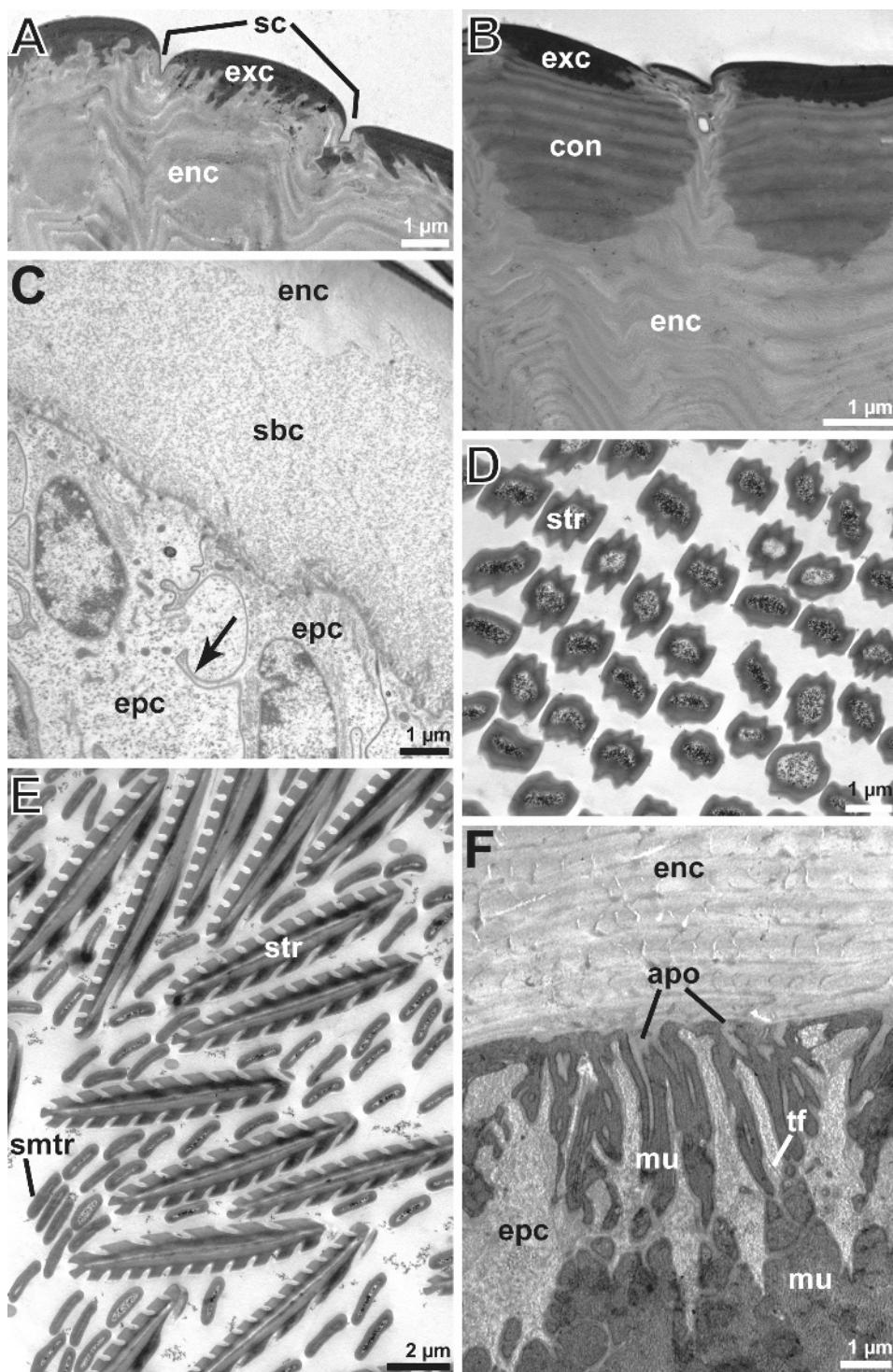


Fig. 4.3. Scanning electron microscopic micrograph showing the polygonal sculpturation (scutes) in a dorsolateral sector of the head capsule of *Scutigera coleoptrata*. The cuticle is pierced by the shafts of several sensilla microtrichoidea. Original C. H. G. Müller.

smi sensillum microtrichoideum

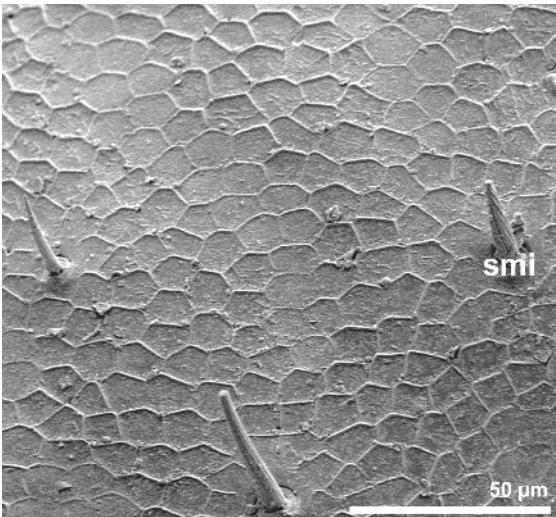
al ducts; their gland pores pierce the cuticle and are thus visible from outside. Examples of aggregated epidermal glands in Chilopoda are the sternal glands of geophilomorphs (Turcato and Minelli, 1990; Fig. 4.10) and the glands surrounding the Tömösváry organ of *L. forficatus* (Tichy, 1973).

Compound glandular organs likewise comprise gland units, each comparable in structure to one solitary epidermal gland, but usually those units differ from the latter by their bigger size and the presence of common ducts. Examples of compound glandular organs are the various head and vesicular glands (see section below) as well as the poison glands, such as known from *L. forficatus* (Rosenberg and Hilken, 2006) and some Scolopendromorpha (Antoniazzi et al., 2009).

According to the number of contributing cells as well as by the structure of the canal cell, its conducting canal, reservoir and of the glandular pore, two different designs of epidermal glands can be distinguished: *recto-canal epidermal glands* with a rather voluminous, untwisted, straightly up-running conducting canal (all but Scutigeromorpha, Fig. 4.4A-E) and *flexo-canal epidermal glands* with an extended, thin and heavily convoluted ('flexuous') conducting canal (all Chilopoda, see Fig. 4.4F) (Müller et al., 2006, 2008, 2009, in press).

#### *Ultrastructure of the recto-canal epidermal glands*

In all chilopod taxa investigated so far, solitary recto-canal epidermal glands are composed of up to five different cell types. Three cell types (secretory, intermediary and canal cell) form recto-canal epidermal glands in Scutigeromorpha and Geophilomorpha (Figs. 4.4A,E; 4.6A,E), whereas four cell types (two different secretory cells, intermediary



cell, canal cell) are found in Lithobiomorpha (Fig. 4.4B). Five cell types (two different secretory cells, intermediary cell, proximal and distal canal cell(s)) form recto-canal epidermal glands in Craterostigmomorpha (Figs. 4.4C, 4.6B,D,F) and Scolopendromorpha (Figs. 4.4D, 4.6C). In the latter taxon the distal canal cell is doubled (Müller et al., in press, Fig. 4.4D) resulting in a total of six contributing cells. Compound recto-canal epidermal glands usually integrate several thousands of glandular units (Hilken et al., 2003, 2005; Hilken and Rosenberg, 2006a,b, 2009; Rosenberg and Hilken, 2006; Antoniazzi et al., 2009). Epidermal glands of the recto-canal type are rarely found in aggregated formation (sternal defence glands glands of Geophilomorpha: Turcato and Minelli, 1990; see also Fig. 4.10).

The more frequent solitary and compound recto-canal epidermal glands can be homologized based on

- (1) high diversity of contributing cell types usually exceeding tricellular arrangement (Figs. 4.4A-E, 4.6A-F)
- (2) a wall- or slit-like structure surrounding the pore opening (Fig. 4.5A-B)
- (3) a straight-uprunning and broad conducting canal that includes many local, spherical or pear-shaped widenings (reservoirs, median and distal cavities) (Figs. 4.4A-E; 4.5C,E-G; 4.6)
- (4) the presence of closely adjoined microvilli or microvilliform infoldings around the apex of the (proximal) canal cell(s) that point to the conducting canal (Figs. 4.4A-E; 4.5E-G; 4.6A-F,H)
- (5) the absence of a central cavity in the (distal) canal cell(s) (e.g. Fig. 4.4A-E)
- (6) a tendency to form huge compound gland organs, e.g. epidermal maxilla-II gland (Hilken et al., 2005)

Recto-canal epidermal glands usually release their secretion through a pore opening surrounded by a wall- or ring-shaped structure (Fig. 4.5A-B). The cuticular ring appears homogeneous in most taxa, only the sternal (defence) glands of himantariid and dignathodontid Geophilomorpha have pore openings surrounded by a wall, which is notched by a suture (Turcato et al., 1995). Wall-lined pore openings of recto-canal epidermal glands may remain rather small and simple in Scutigeromorpha (Müller et al. in press; also interommatidial glands: Müller et al., 2003a, Fig. 4.5A), Lithobiomorpha (telopodite glands: Keil, 1976; periatrial glands: Carcupino, 1996), Craterostigmomorpha (Müller et al., in press) and Geophilomorpha (Müller et al., in press; also Turcato et al., 1995, e. g. sternal glands of *Schendyla carniolensis*), the pore opening then lies on level equal to the wall-like cuticular projection surrounding it. In some telopodite glands of *Lithobius forficatus*, the pore opening is deeply sunk into the cuticle (see Figs. 4a,b-d in Keil, 1976). Likewise structured pore openings are found associated with sternal (defence) glands of various Geophilomorpha (Turcato et al., 1995: e.g. *Schendyla carniolensis*). Larger and structurally elaborated pore openings are observed in solitary epidermal glands close to the lateral ocellar fields of Lithobiomorpha and Scolopendromorpha. There, pore

openings look either triangular or slot-like (*Lithobius dentatus*, Fig. 4.5B). They may be surrounded by a second and thinner inner wall, as in the sternal (defence) glands of some Geophilomorpha (Turcato et al., 1995) or in tarsal glandular pore fields on the telopodites of the scolopendromorph *Ectonocryptoides quadrimeropus* (Koch et al., 2010: see their Fig. 9B). Further pore openings of large diameter are observed in Lithobiomorpha, e.g. on the sides of head capsule (Müller et al., in press). Usually, these enflated pores are covered in part by a cuticular scale resembling a closure apparatus. This slit-like pore appearance is also found in the aggregated sternal glands of various geophilomorphs (Hopkin et al., 1990; Turcato et al., 1995). Depending on location and function, pore structure varies considerably within areas of geophilomorph sternal glands, but the general architecture of the pores does not change with age (Turcato et al., 1995).

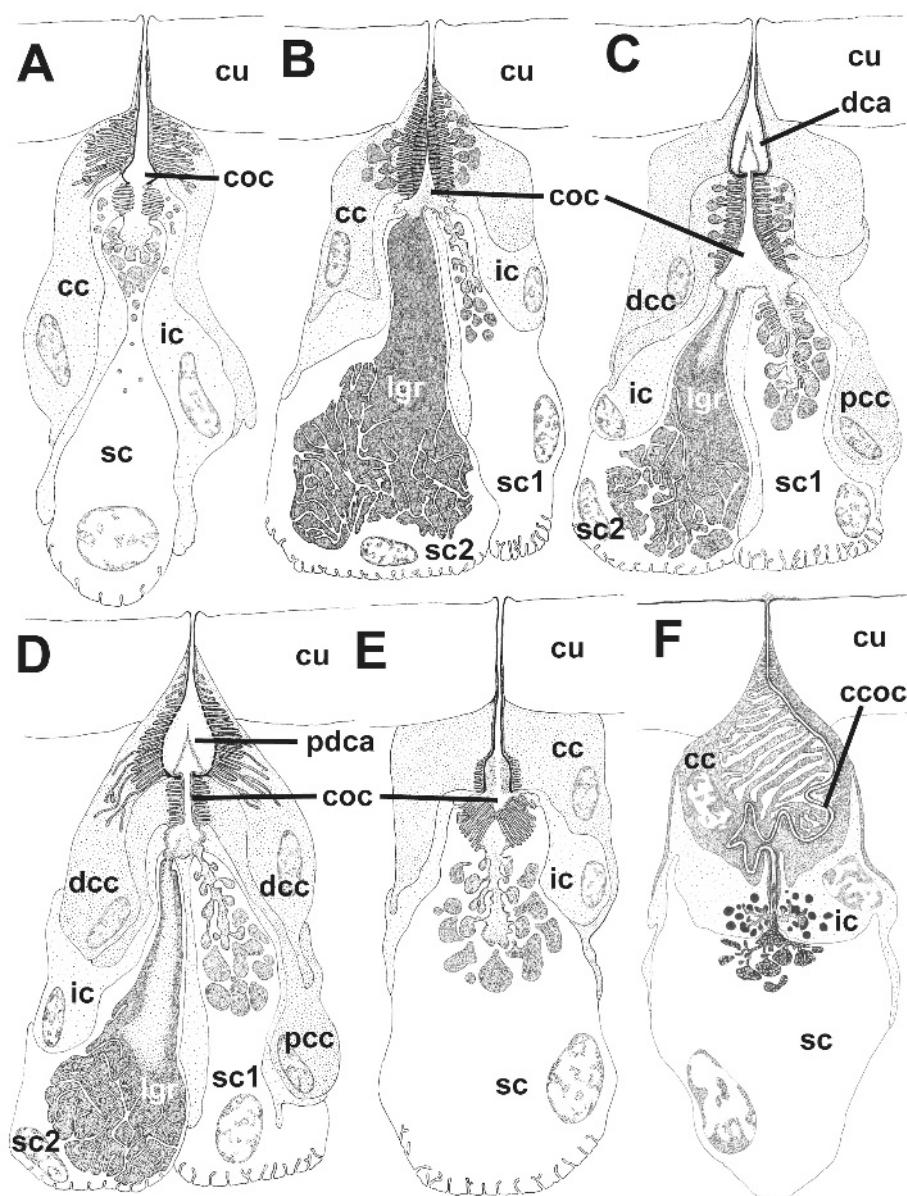
Based on the number of pore openings on the lateral and dorsal regions of the head capsule, the total number of recto-canal epidermal glands is lowest in Scutigeromorpha, intermediate in Lithobiomorpha and Craterostigmomorpha, high in Scolopendromorpha, and extremely high in Geophilomorpha. On the head and the trunk tergites of geophilomorphs, the abundance may become so high, that the sheath of epidermal cells separating one gland from the other may disappear.

#### *Ultrastructure of the flexo-canal epidermal glands*

Flexo-canal epidermal glands may also cluster to form aggregated glands around an associated organ, mostly sense organs. They are much more frequent and found in all chilopod taxa except for Scutigeromorpha (Müller et al., 2009). This gland type is characterized by

- (1) low diversity of contributing cell types (mainly tricellular formations: secretory cell, intermediary cell, canal cell) (Fig. 4.4F)
- (2) a simple glandular pore opening (e.g. Fig. 4.5B)
- (3) a thin, elongated and strongly convoluted conducting canal showing no spacious reservoir or canal widening (Figs. 4.4F; 4.5D,H-I; 4.7A-E)
- (4) the presence of a more or less expanded extracellular space within the canal cell (central cavity) resulting from a complex invagination of the apical membrane (Figs. 4.4F; 4.5D,H-I; 4.7A)
- (5) a stretched, tube-like portion of the canal cell's apex elongating through the intermediary and the secretory cell (e.g. Fig. 4.4F)
- (6) low tendency to form clusters (mostly solitary epidermal glands, aggregated in rare cases)

**Fig. 4.4.** Semischematic reconstructions of solitary recto-canal epidermal glands (A-E) and flexo-canal epidermal glands (E) spread dorsomedially and laterally on the head capsules of various centipedes. In both glands examined, intermediary cells can be found. Units within aggregated and compound glandular organs can mostly be referred to the basic architecture illustrated here. A *Scutigera coleoptrata* (Scutigeromorpha). B *Lithobius* spp., *Eupolybothrus fasciatus* (Lithobiomorpha). C *Craterostigmus tasmanianus* (Craterostigmomorpha). D *Scolopendra* spp., *Cryptops hortensis* (Scolopendromorpha). E *Strigamia crassipes*, *Henia* spp., *Haplophilus dimidiatus* (Geophilomorpha). F *Craterostigmus tasmanianus* (Craterostigmomorpha). Drawings modified after Müller et al. (2009, in press).



cc canal cell; ccoc convoluted conducting canal; coc conducting canal; cu cuticle; ic intermediary cells; dcc distal canal cell; lgr large secretion reservoir (formed by sc2); pcc proximal canal cell; pdca pear-shaped distal cavity (Scolopendromorpha); sc secretory cell; sc1 type-1 secretory cell; sc2 type-2 secretory cells

**Table 4.1.** Solitary, aggregated and compound glands hitherto described in Chilopoda. The table includes classifications according to cell typology (e.g. Hilken et al., 2005), organisation degree and ultrastructure of the conducting canal (Müller et al., 2009).

Taxon	Gland	Cells	N	Organ.	Class	Refs.
<i>Lithobius forficatus</i>	Small epidermal glands (between teleopodite glands, at the base of sensilla trichoidea)	s-c	1	i	f	1
<i>Lithobius forficatus</i>	Interommatidial glands	s-c	2	i/a	f	2
<i>Eupolybothrus fasciatus</i>	Large accessory sex glands (female)	s-c	>1	c	r?	3
<i>Eupolybothrus fasciatus</i>	Small accessory sex glands (female)	s-c	>1	c	r?	3
<i>Lithobius forficatus</i>	Teleopodite glands (on the antennae)	s-i-c	1	i	r	1
<i>Lithobius forficatus</i>	Epidermal gl. assoc. with Tomosváry's organ	s-i-c	1	i/a	f	4
Pleurostigmophora	Epidermal glands assoc. with coxal organs	s-i-c	1	i	f?	5
<i>Lithobius forficatus</i>	Epidermal coxal glands	s-i-s	1	i	f	6
<i>Scutigera coleoptrata</i>	Interommatidial glands	s-i-s	1	i	r	2
<i>Lithobius forficatus</i>	Telopodite glands on the posterior legs	s-i-c	2	a	r	1
Geophilomorpha	Sternal glands	s-i-s	1	a	r	7, 8
<i>Eupolybothrus fasciatus</i>	Periatrial gland	s-i-c	2	i	r?	3
Scutigeromorpha, Geophilomorpha	Epidermal glands on head flanks, in <i>Scutigera</i> around the compound eyes	s-i-c	1	i	r	9
Pleurostigmophora	Epidermal glands on head flanks	s-i-c	1	i/a	r	10
<i>Scutigera coleoptrata</i>	Maxilla-I-gland	s-i-c	1	c	r	11
<i>Scutigera coleoptrata</i>	Maxilla-II-gland	s-i-dc- pc	1	c	r	12
<i>Lithobius forficatus</i>	Poison gland in maxillipeds	s-i-dc- pc	1	c	f	13
Lithobiomorpha	Epidermal glands around ocellar field	s-s'-i-c	2	i	r	9
Craterostigmom., Scolopendrom.	Epidermal glands near by the eyes	s-s'-i- dc-pc	2	i	r	9
<i>Scutigera coleoptrata</i>	Maxillary organ gland	s-s'-i- dc-pc	2	c	r	14, 15
<i>Scutigera coleoptrata</i>	Vesicular gland	s-s'-i- dc-pc	2	c	r	16

**Cells.** – c canal cell; dc distal canal cell; i intermediary cell; pc proximal canal cell(s). – N. – Number of secretory cells per unit gland. – Organization. – a aggregated; c compound; i isolated. – Class. – f flexo-canal epidermal gland; r recto-canal epidermal gland. – Refs. 1. Keil (1976); 2. Müller et al. (2003a); 3. Carcupino (1996); 4. Tichy (1973); 5. Rosenberg (1985); 6. Rosenberg (1994); 7. Turcato and Minelli (1990); 8. Turcato et al. (1995); 9. Müller et al. (in press); 10. Müller et al. (2009); 11. Hilken and Rosenberg (2006a); 12. Hilken et al. (2005); 13. Rosenberg and Hilken (2006); 14. Hilken et al. (2003); 15. Hilken and Rosenberg (2006b); 16. Hilken and Rosenberg (2009).

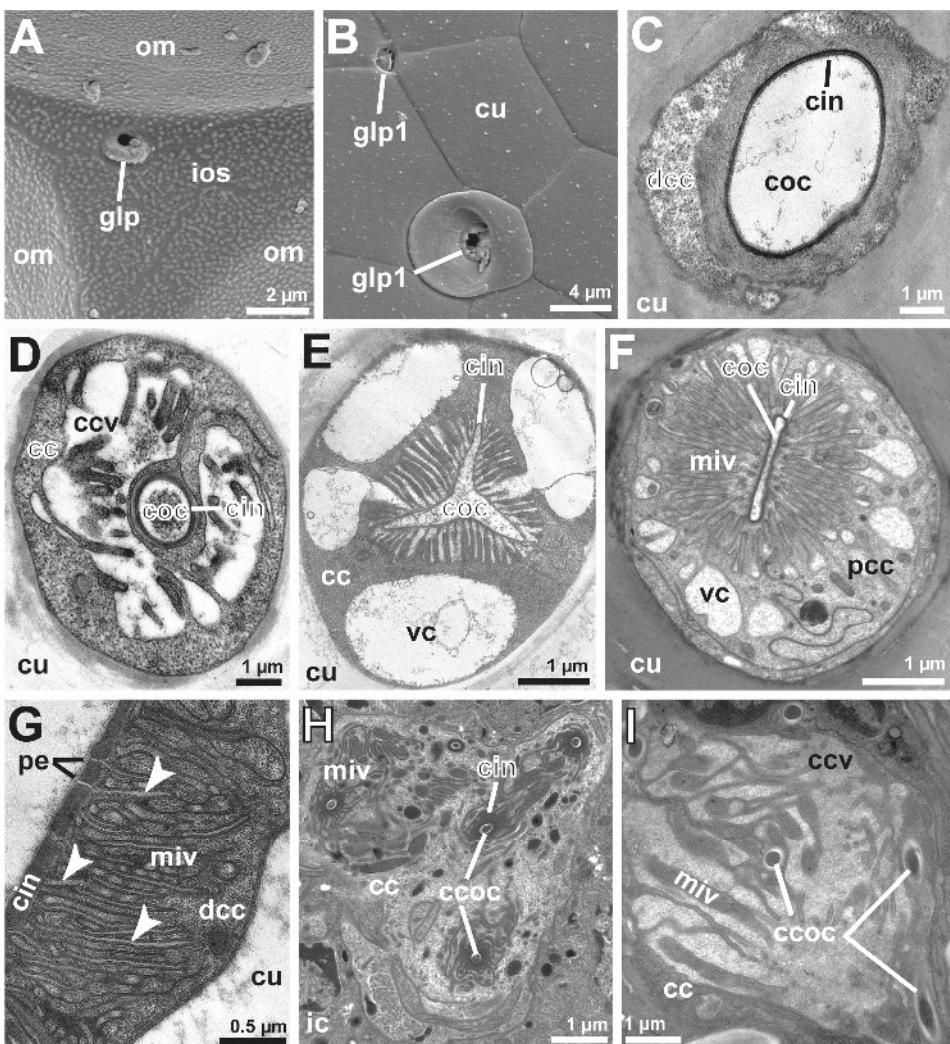
*Cell types in recto-canal and flexo-canal epidermal glands*

**Secretory cell(s).** The voluminous secretory cell is mostly pear-shaped. In recto-canal epidermal glands its narrow apex is invaginated and forms a widened extracellular reservoir (Müller et al., in press, see e.g. Fig. 4.4A-E). The apical cell membrane produces microvilli that may extend deeply into the extracellular reservoir (Figs. 4.4B-E; 4.6B,D-F,H). In flexo-canal epidermal glands, the cell apex forms a complex network of extracellular canals (loculi or glandular reservoir) (Müller et al., 2009, see Figs. 4.4F; 4.7B,E). The canals converge to a common conducting canal secreted by the intermediary cell and the canal cell (e.g. Fig. 4.7B). Both, the extracellular reservoir and the glandular reservoir are free of cuticle. The basal cell membrane of the secretory cell is invaginated, forming a basal labyrinth (Figs. 4.4A-E, 4.7H). The huge nucleus is located in the basal part of the cytoplasm (Fig. 4.4). Cisternae of endoplasmic reticulum, numerous free ribosomes and several elongated mitochondria occur. A huge number of dictyosomes is distributed throughout the cell. The secretory cell in a flexo-canal epidermal gland are filled with large, spherical secretory granules of differing degrees of osmophily and heterogeneity (Figs. 4.4F; 4.7B,F-G). According to cell form and the content in secretion granules, two types of secretory cells are distinguishable in recto-canal epidermal glands of Lithobiomorpha, Craterostigmomorpha and Scolopendromorpha. In type I cells, secretion granules are widely uniform as in the solitary secretory cells in tricellular glands. The granules are especially abundant in the apical cell regions, where they merge with the apical cell membrane and discharge their content into the extracellular cavity or glandular reservoir (Figs. 4.4A-E, 4.6). In type II cells, the whole cell body looks heavily inflated because of a voluminous glandular reservoir. The cytoplasm is a flattened sheath and contains only some small vesicles of higher osmophilic content. The cavity-like reservoir is filled with a moderately electron-dense, finely granular and heterogenous substance. Heterogeneity is caused by highly electron-dense platelets that are tightly stacked and dispersed in the entire cavity (Figs. 4.4B-D; 4.6B-D,F-G). Type I and II secretions meet at the base of the conducting canal (e.g. Fig. 4.6C,G).

**Intermediary cell.** A single intermediary cell is present in all chilopod taxa hitherto studied with TEM. In both recto-canal and flexo-canal epidermal glands, the intermediary cell connects the secretory cell(s) to the (proximal) canal cell and provides a passage for the secretion from the extracellular or glandular reservoir up to the conducting canal (Müller et al., 2009, in press, see Figs. 4.4, 4.6, 4.7B-E).

In most centipedes examined, the body of the intermediary cell looks flattened. Sometimes, it is wrapped locally by the apex of the secretory cell(s) (e.g. Figs. 4.4E-F, 4.7B). In recto-canal epidermal glands containing more than one secretory cell, the intermediary cell establishes a manchette-like structure that holds the tips of both secretory cells in place but also separates them from each other (Figs. 4.4B-D; 4.6B-C,F-G). In both recto-canal and flexo-canal epidermal glands, the intermediary cell is folded and encloses the straight basal portion of the conducting canal, which is covered by a distinct, delicate cuticle only in its distal part (Figs. 4.6G-H, 4.7E). The longer, uncuticularized proximal part may be considerably constricted by microvillar projections of the apex of the intermediary cell. The presence of secretion granules in the cytoplasm indicates the ability of the intermediary cell to function as an accessory gland cell (Figs. 4.4A,F; 4.6A,F; 4.7B,E). However, pinocytosis of primary secretion products can also not be excluded for intermediary glands (Müller et al., in press). Adhering junctions (maculae adhaerentes) make firm contact to the secretory cell(s) and to the proximal canal cell.

**Canal cells.** Recto-canal epidermal glands include either a single canal cell (e.g. Fig. 4.4A,E) or a horizontal multilayer of one proximal and one or two distal canal cell(s) (e.g. Fig. 4.4B-D). All canal cell types contribute equally to the formation of the distal, fully cuticularized part of the con-



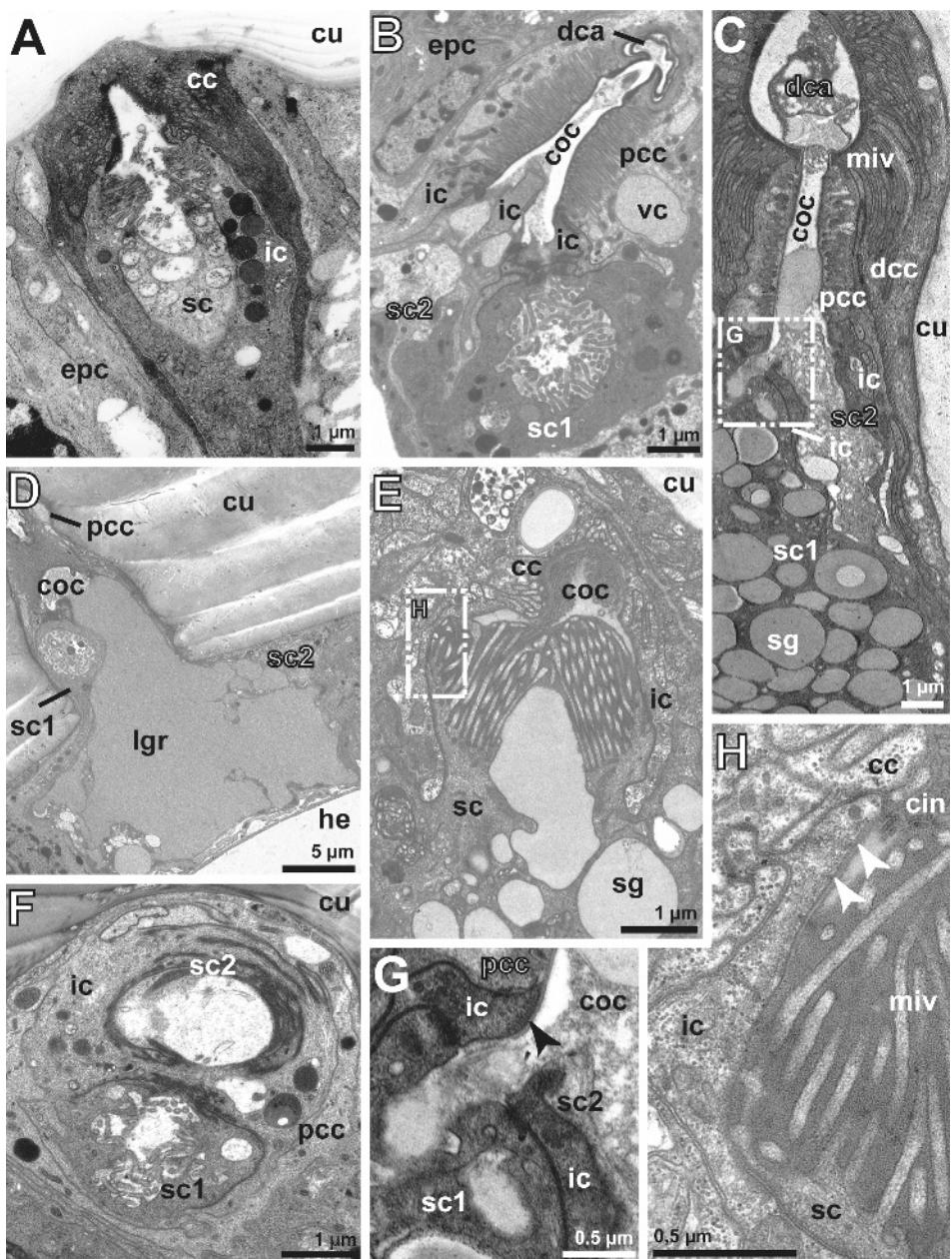
ducting canal, which ranges between 0.5 and 2.5 μm in diameter (Figs. 4.4A-E; 4.5C,E-F; 4.6A-C)). The secretion is finally processed along the conducting canal.

**Proximal canal cell.** – A proximal canal cell is only developed in recto-canal epidermal glands equipped with secretory cell types I and II. The proximal canal cell surrounds the subcuticular compartment of the conducting canal (e.g. Figs. 4.4C-D, 4.5F, 4.6B-C). The apical cell membrane is often differentiated into deep infoldings, embedded in an electron-lucent subcuticular layer beneath the osmiophilic cuticle (e.g. Fig. 4.6B-C, G). Often these apical infoldings disappear in the distal part of the conducting canal. The cytoplasm of the proximal canal cell contains several electron-dense vacuoles, but only a few organelles, including elongated mitochondria are situated in particular near the cell apex.

**Fig. 4.5** Ultrastructure of solitary epidermal glands of the recto-canal (A-C, F-G) and flexo-canal (B, D, H-I) type explored in various chilopod taxa. Outer morphology viewed by scanning electron microscopy (SEM) (A-B) is complemented by transmission electron micrographs (TEM) (C-I) focused on the distal region of the gland comprising the canal cell apparatus and the conducting canal, marking the main difference between both classes of epidermal glands. A Pore region of an interommatidial gland of *Scutigera coleoptrata*. B Pore openings of an recto-canal epidermal gland (with slit-like closure apparatus, glp1) and a flexo-canal epidermal gland (simple breakthrough in the epidermis, glp2) in close vicinity, found lateral to the ocellar field of *Lithobius dentatus*. C Cross section through distal region of the distal canal cell showing a predominating conducting canal. *Craterostigmus tasmanianus*. D Cross section through distal region of a canal cell. *Eupolybothrus fasciatus*. E Cross section through distal region of a canal cell showing a triangular-shaped conducting canal. *Lithobius dentatus*. F Cross section through apikal region of the proximal canal cell showing a compressed, slit-like conducting canal. *Craterostigmus tasmanianus*. G Longitudinal section through lateral, perforated wall of the distal cavity surrounded by distal canal cells. Note the thin tubes connected to the cuticular breakthroughs (white arrowheads). *Craterostigmus tasmanianus*. H-I Cross sections through medioproximal region of canal cells having a thinned, convoluted conducting canal: H with unconnected cuttings of the conducting canal (*Craterostigmus tasmanianus*), I with paired cuttings of the conducting canal being interconnected by a membrane (*Scolopendra oraniensis*). Micrographs modified from Müller et al. (2009, in press).

cc canal cell; ccoc cuttings of the convoluted conducting canal; ccv central cavity; cin cuticular intima lining the conducting canal; coc conducting canal; cu cuticle; dcc distal canal cell; glp glandular pore opening; ic intermediary cell; ios interommatidial space; miv microvilli; om ommatidium; pcc proximal canal cell; pe perforations of the cuticular wall of the distal pear-shaped cavity; vc large vacuole

**Distal canal cell.** – In those recto-canal epidermal glands equipped with a horizontally stacked multilayer of canal cells, a small distal canal cell encloses the distalmost part of the conducting canal (Figs. 4.4B-D; 4.5C,G; 4.6C). This canal compartment is regularly filled with granular material which often adheres to the cuticle (e.g. Fig. 4). The apical cell border is either deeply folded (e.g. 6C) or undifferentiated (e.g. Fig. 4.5C). The conducting canal is narrowed by the microvillar fringe of the (distal) canal cell(s) and may display a rounded/ovoid (e.g. Fig. 4.5C), triangular (Fig. 4.5E) or slot-like (Fig. 4.5F) outline. Besides the bean-shaped nucleus, the cytoplasm contains only mitochondria and bundles of microtubules and microfilaments, usually condensed around the apex. Microfibrils may serve as a clamp attaching the tips of microvillar tips to the cuticular intima of the conducting canal (e.g. telopodite glands in *Lithobius forficatus*: Keil, 1976; solitary epidermal glands on head flanks of *L. forficatus*: Müller et al., in press). In interommatidial glands of *Scutigera coleoptrata*, also pigment granules are observed in proximal protrusions of the cell body (Müller et al., 2003a,b). In Scolopendromorpha, there are two distal canal cells. Here, the cuticular intima lining the widened and pear-shaped distal compartment of the conducting canal is pierced by pores that continue in radial ramifications crammed into the interspace of the microvilli-like outgrowths of the canal cell (Figs. 4.4D, 4.5G, 4.6C). Only a single canal cell is present in flexo-canal epidermal glands (Müller et al. 2009). Each canal cell is characterized by a huge, ramified extracellular cavity traversed by the more or less strongly convoluted conducting canal 0.3-0.5 µm in diameter (Figs. 4.4.4F; 5D,H-I; 4.7A). Around the bottom of the canal cell, there is a cytoplasmic process that reaches deeply into the intermediary cell (Figs. 4.7B-E). The mostly elongated nucleus includes weak concentrations of heterochromatin (Fig. 4.7A), the cytoplasm houses few Golgi stacks and cisternae of the endoplasmic reticulum, locally accumulated free ribosomes, vesicles of



varying shape and electron-density (0.4–0.8 µm in diameter) as well as slim, elongated and multiply bent cristate mitochondria. The median region of the canal cell envelopes a huge space ca-

**Fig. 4.6.** Ultrastructure of solitary recto-canal epidermal glands examined with transmission electron microscopy in various chilopod taxa. Overviews of the gland's architecture are given by oblique-longitudinal sections showing a majority of contributing cell types and parts of the conducting canal (A-E). In addition, the apical region of the intermediary cell is demonstrated for several taxa (F-H). A Tricellular arrangement of an interommatidial/trunk tergite gland in *Scutigera coleoptrata*. B Median apart of a five-cell containing gland situated dorsally of the lateral ocellus of *Craterostigmus tasmanianus*. C Median part of a six-cell containing gland between the lateral ocellar field and antennal base in *Scolopendra oraniensis*. D View of the median and basal part of the same gland as indicated in B. Note the massive glandular reservoir built by a type-2 secretory cell. E Median part of a tricellular gland situated in the midst of the capsule of *Strigamia crassipes*. F Cross section through the apex of both type-1 and -2 secretory cells encompassed by apical manchette of the intermediary cell (gland in the close vicinity of the lateral ocellus of *Craterostigmus tasmanianus*). G Highly magnified view of basal region of the conducting canal surrounded by manchette-like sheath of the intermediary cell. The cuticular intima terminates at the transition zone of the proximal canal cell and the intermediary cell (black arrowhead). The region is indicated by dashed white box in C. *Scolopendra oraniensis*. H Margin of the glandular reservoir of a tricellular gland in *Strigamia crassipes*. The apical membrane of the intermediary cell lacks a cuticular overlayer (white arrowheads). Region is indicated by dashed white box in E. Micrographs modified from Müller et al. (in press).

cc canal cell; cin cuticular intima lining the conducting canal; coc conducting canal; cu cuticle; dca pear-shaped distal cavity of the distal canal cell(s);dcc distal canal cell; epc epidermal cell; he hemolymphatic space; ic intermediary cell; lgr large glandular reservoir; miv microvilli; pcc proximal canal cell; sc secretory cell; sc1 type-1 secretory cell; sc2 type-2 secretory cell; sg granule; vc large vacuole

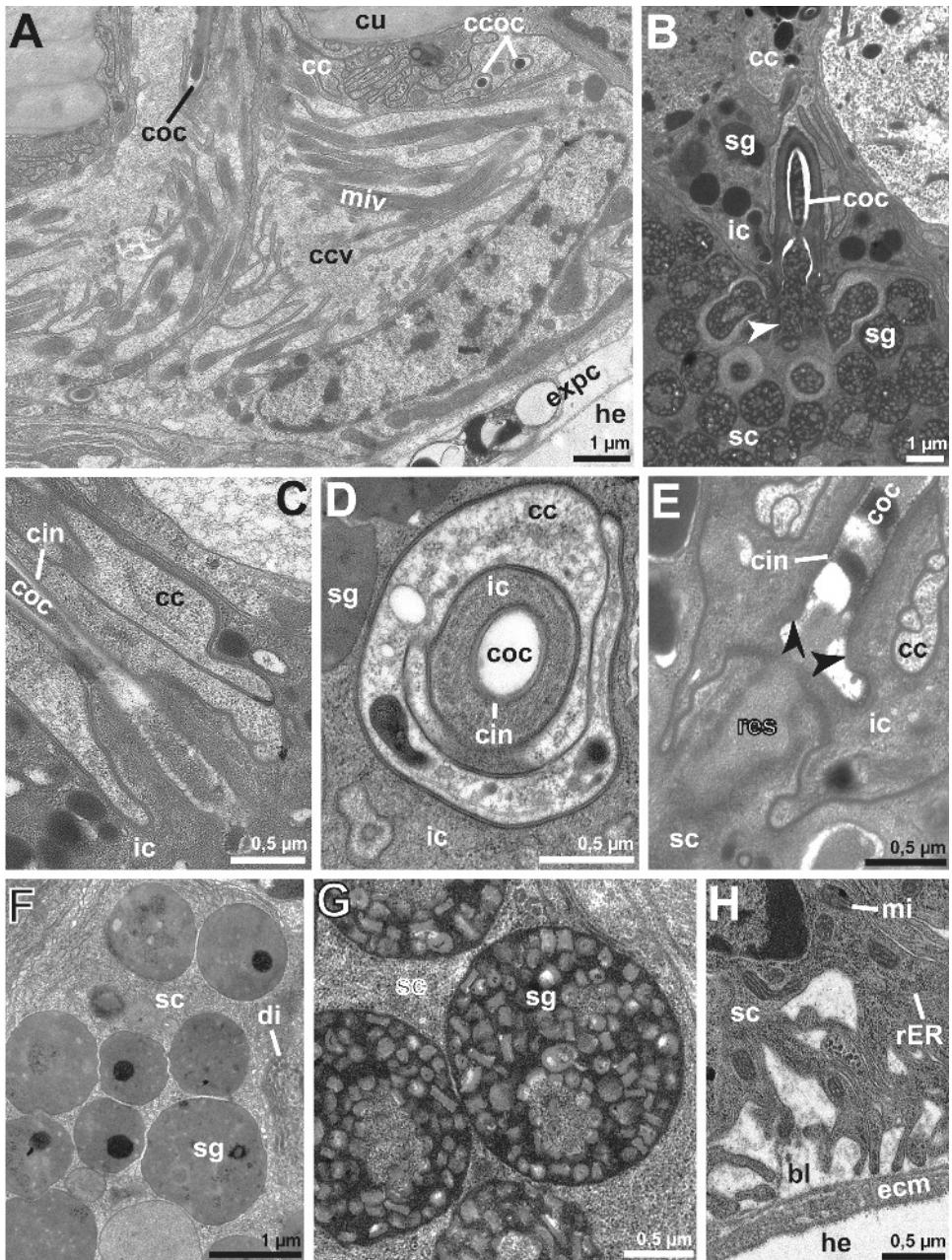
vity filled with a loose meshwork of cytoplasmic projections that emanate from the apex of the canal cell and end near-by the conducting canal. The cytoplasmic projections are rich in mitochondria (Figs. 4.4F, 4.5H-I; 4.7A).

#### *Epidermal gland classification*

Based on Hilken et al. (2005), Rosenberg (2009), and Müller et al. (2009, in press) we can distinguish different types of epidermal glands:

- glands with two cell types (secretory cell(s) + canal cell(s))
- glands with three cell types (secretory cell + intermediary cell + canal cell)
- glands with four cell types (secretory cell + intermediary cell + proximal + distal canal) or (secretory cell type I + II + intermediary cell + canal cell)
- glands with five cell types (secretory cell + intermediary cell + proximal + distal canal cell) or (secretory cell type I + type II + intermediary cell + canal cell(s))

To date, there seems to be enough evidence for the universal presence of intermediary cells in Chilopoda. However, some epidermal glands in lithobiomorph centipedes have been described as only consisting of a secretory cell and a canal cell. In *L. forficatus*, examples for bicellular glands are the 'small epidermal glands', located between the larger telopodite glands (Keil, 1976), as well as the partly compound interommatidial glands (Müller et al., 2003a). Likewise bicellular are the small and large accessory sex glands associated with the ovarian system in females of *Eupolybothrus fasciatus* (Carcupino, 1996). Admittedly, there are more reports for bicellular epidermal glands in



**Fig. 4.7** Ultrastructure of solitary and tricellular flexo-canal epidermal glands examined with transmission electron microscopy on the head capsule of various chilopod taxa (here documented in close vicinity of the lateral ocelli). Overviews of the gland's architecture are given by cross sections (D, G) as well as oblique-longitudinal (A-C, E-F, H) sections. Given TEM micrographs focus on the median transition zone of the canal cell, intermediary cell and secretory cell as well as on the cytoplasmic characteristics of the secretory cell. A Lower magnified view of the central cavity enflating the canal cell. *Scolopendra oraniensis*. B Median part of a gland showing fusion and expulsion zone of the secretory cell (white arrowhead). *Craterostigmus tasmanianus*. C Transition zone of basal projection of the canal cell and apex of the intermediary cell representing the beginning of the conducting canal. *Scolopendra oraniensis*. D Transverse profile of the same transition zone as described in C. Note the still existing cuticular intima lining the conducting canal at the very beginning of the intermediary cell. *Lithobius dentatus*. E Same zone described in C and D, but observed in *Scolopendra cingulata*. Note the disappearance of the cuticular intima in the lower part of the stretched intermediary cell apex (black arrowheads). F-G Ultrastructure of the secretory granules produced by the secretory cell: F Moderately heterogenous granules (*Lithobius dentatus*), G Strongly heterogenous, mosaic-like granules (*Craterostigmus tasmanianus*). H Basis of a secretory cells in a gland found in *Craterostigmus tasmanianus* indicating a small basal labyrinth. Micrographs modified after Müller et al. (in press), E,F. Originals Müller.

bl basal labyrinth; cc canal cell; ccoc cuttings of the convoluted conducting canal; cin cuticular intima lining the conducting canal; coc conducting canal; cu cuticle; di dictyosome; expc external pigment cell; he hemolymphatic space; ic intermediary cell; rER cisternae of the rough endoplasmic reticulum; sc secretory cell; sg secretory granule

Chilopoda (Tab. 4.1). However, in these cases Hilken et al. (2005) and Müller et al. (2009) managed to detect fine structural details in reviewed illustrations manifesting the existence of intermediary cells. The incomplete cuticular lining however could not be confirmed anywhere (Hilken et al., 2005; Rosenberg, 2009). Such still uncertain cases are for instance: 1) the aggregated epidermal glands encompassing the Tömösváry organ of *L. forficatus* (Tichy, 1973), 2) clusters of epidermal cells surrounding the main epithelium of coxal and anal organs (e.g. Rosenberg, 1985; Rosenberg and Greven, 1996) or situated around the last coxae of *L. forficatus* (Rosenberg, 1994).

Intraspecific variation at cellular level is apparently much higher in compound glands. In *Scutiger coleoptrata*, while the solitary epidermal glands are always tricellular, compound epidermal glands have glandular units consisting of three (maxilla-I-glands: Hilken and Rosenberg, 2006a), four (maxilla-II-glands: Hilken et al., 2005) or five cell types (maxillary organ gland: Hilken et al., 2003, Hilken and Rosenberg, 2006b; vesicular gland: Hilken and Rosenberg, 2009). Also, the formation of acini as well as the multiplication of type-equivalent secretory cells is only observed within units of compound epidermal glands, as the maxillary gland of *Scutiger coleoptrata* (Hilken and Rosenberg, 2006a) with more than two secretory cells. Likewise, review of micrographs and description of large and small accessory sex glands in female *E. fasciatus* reveals the existence of several secretory cells building the bottom of glandular units (Carcupino, 1996).

#### Functions of solitary epidermal glands

A possible function of solitary epidermal glands in Chilopoda may be to prevent desiccation of the cuticle or to enhance its elasticity (Blower, 1951, 1952; Rilling, 1968;

Tichy, 1973; Keil, 1976; Desbalmes, 1992). Some epidermal glands possibly release pheromones (Rosenberg, 1994) or mucous substances (Rosenberg, 1985; Rosenberg and Greven, 1996). The secretion of the interommatidial glands may prevent infestation by ectoparasites (Müller et al., 2003a), that of the maxillary organ gland may serve to clean the antennae or extremities (Hilken et al., 2003).

It is not known to which extent either type of secretory cells is responsible for the secretion. In scattered flexo-canal epidermal glands, the canal cell might become important in accumulating and regulating the ion and water balance (Müller et al., 2009).

In solitary recto-canal epidermal glands of Lithobiomorpha, Craterostigmomorpha and Scolopendromorpha, a subcuticular valve reaching into the distal cavity of the conducting canal may also control the flow and release of the secretion (Müller et al., 2010, in press).

### Aggregated and compound epidermal glands

Jörg Rosenberg, Carsten H. G. Müller & Gero Hilken

#### Aggregated epidermal glands

Aggregated epidermal glands are tightly clustered glandular units sitting on a common basal matrix, but pouring their secretion outside via their own conducting canals. Each glandular unit is composed of secretory cell(s), a single intermediary cell, and a proximal and/or a distal canal cell(s).

#### Vesicular glands

Paired vesicular glands are only developed in Scutigeromorpha, Scolopendromorpha, and Craterostigmomorpha (Table 4.2). Their fine structural organization has been only investigated in the Scutigeromorpha (Hilken and Rosenberg, 2009). The role of their secretion is unclear, either defensive, as assumed by Fahlander (1938) for *Scutigera coleoptrata*, or related to ecdysis (Hilken and Rosenberg, 2009).

*Scutigeromorpha.* – There are two pairs of vesicular glands (Fig. 4.8A-B), in the maxilliped and the first leg-bearing segment respectively. The anterior part of these glands opens inter-segmentally via ducts with wide lumen into the upper part of the corresponding pleural region. Both glands consist of wide sac-like cavities that often appear vesicular. The epithelia consist of numerous glandular units each with a single

secretory cell, a small intermediary cell and a proximal and a distal canal cell (Hilken and Rosenberg, 2009).

The pear-shaped secretory cell forms an invaginated extracellular cavity at its cell apex with several longish microvilli. The intermediary cell forms, together with the canal cells, a conducting canal. Proximally, the intermediary cell bears microvilli, whereas its distal part is lined by a distinct cuticle which is in continuation of the cuticle of the canal cells. The distal canal cell forms numerous microvilli embedded into the cuticle.

*Craterostigmomorpha*. - In *C. tasmanianus* only a very large second vesicular gland is developed, extending up to the middle of the second leg-bearing segment and opening under the edge of the first tergite (Manton, 1965).

*Scolopendromorpha*. - The paired vesicular gland (*second vesicular glands = coxal glands*; Jangi, 1966) lies mainly in the second leg-bearing segment, with openings on the first leg-bearing segment immediately under the tergite in front of the leg insertion. In *Scolopendra morsitans* (Jangi, 1966), these glands extend posteriorly up to the third leg-bearing segment (up to the fourth in the Cryptopidae; Fahlander, 1938) and open on the coxa of the first legs.

### *Poison glands*

A poison gland opens via a poison duct near the tip of the forcipular tarsungulum.

The internal part of the poison duct is surrounded by a huge number of the glandular units of the poison gland (Fig. 4.8C). The ultrastructure of the poison glands has been described for *Lithobius forficatus* (Rosenberg and Hilken, 2006) and some scolopendromorphs (*Scolopendra morsitans*: Dass and Jangi, 1978; *Ethmostigmus rubripes*: Ménez et al., 1990; *Cryptops iheringi*, *Ostostigmus pradoi*, *S. viridicornis*: Antoniazzi et al., 2009).

In *L. forficatus*, the glandular epithelium of the poison gland consists of many multicellular units (Fig. 4.8C-D) formed by a huge secretory cell, an intermediary, a proximal and a distal canal cell. The whole glandular epithelium is surrounded by a basal lamina.

The canal cells form the cuticularized conducting canal that opens into the common poison duct (Fig. 4.8D). The distal canal cell encloses a wide atrium, lined by a wide cuticle that opens into the common poison duct. The proximal canal cell is more complex. In its distal part, it surrounds the conducting canal. In the transitional zone between distal and proximal canal cell, the latter forms a nozzle-like cuticular ‘valve’ projecting deep into the atrium (Fig. 4.8D). More proximally, the cuticle is thickened to a ring-shaped cuticular pad, visible even by light microscopy (Fig. 4.8D). In its proximal part, the proximal canal cell forms a thin cytoplasmic leaflet that encloses, together with the intermediary cell, a wide extracellular space. The longish nucleus is in the basal part of the cytoplasmic projection. The intermediary cell connects the proximal canal cell with the following secretory cell. Only in its distal part the intermediary cell is covered by a delicate cuticle, in continuation with the cuticle of the proximal canal cell. The nucleus of the

intermediary cell is in the basal part of the cell. The extracellular space is filled with secretion; its inner boundary is formed by the intermediary cell, surrounded by the proximal canal cell. The voluminous secretory cell is pear-shaped. The invaginated apex forms a widened extracellular reservoir, lined by microvilli (Fig. 4.8E-F). The cytoplasm is filled with numerous osmiophilic spherical vacuoles that merge with the apical cell membrane. The large nucleus is in the basal part of the cell (compare Fig. 4 in Rosenberg and Hilken, 2006).

The venom secreted by the secretory cell and released by exocytosis into the extracellular reservoir of the secretory cell is stored in the extracellular space delimited by the proximal projections of the intermediary and the proximal canal cell and eventually released into the common poison duct.

In the scolopendromorphs, hypodermal cells, basal membrane cells, peripheral and longitudinal muscles have been described. These muscles surround the poison gland and, particular, encapsulate the secretory cells (Dass and Jangi, 1978, Ménez et al., 1990, Antoniazzi et al., 2009). For functional considerations compare Rosenberg and Hilken (2006), Rosenberg (2009) and Antoniazzi et al. (2009).

### *Maxillary organ gland*

This gland, located at the dorsal side of the maxillary organ, is composed of numerous secretory units, each including two secretory cells, a single intermediary cell, a proximal and a distal canal cell (4-cell type gland; Fig. 4.9A).

The pear-shaped secretory cells are invaginated distally, forming a widened extracellular cavity lined by short microvilli. The intermediary cell connects the extracellular cavity of each secretory cell and the extracellular part of the canal cells. The apex of the intermediary cell has a distinct microvillar fringe in its proximal part. In its most distal part, the cell is lined by a cuticular intima that is in continuation with the conducting canal formed by the proximal canal cell. Its cell apex has a distinct microvillar border, which disappears distally. The distal canal cell also contributes to the formation of the conducting canal, which runs through the cuticle and opens into a huge reservoir of the maxillary organ (Hilken et al., 2003).

**Fig. 4.8** Vesicular glands of *Scutigera coleoptrata*. A Light microscopical micrograph of the first (I) and second (II) vesicular gland with their large glandular lumina. B Electron microscopical micrograph of the first vesicular gland. The glandular cells are filled with numerous clear vesicles in its basal part. The cells are covered by a cuticle. C-F Poison gland of *Lithobius forficatus*. C Numerous aggregated glandular units open into a common poison duct. D Overview of the distal part of the glandular units with their valve-like openings and their conducting canals. E The pear-shaped distal part of the secretory cell is surrounded by a small intermediary cell. F Higher magnification of the apex of the secretory and the intermediary cell. Only the distal part of the intermediary cell is lined by a faint cuticle. Originals Rosenberg & Hilken.

c/cu cuticle; cc conducting canal; ep cuticular pad; er extracellular reservoir; gl glandular units; ic intermediary cell; Mg Malpighian tubule; mv microvilli; n nucleus of secretory cell; pc proximal canal cell; pd poison duct; sc secretory cell; v valve

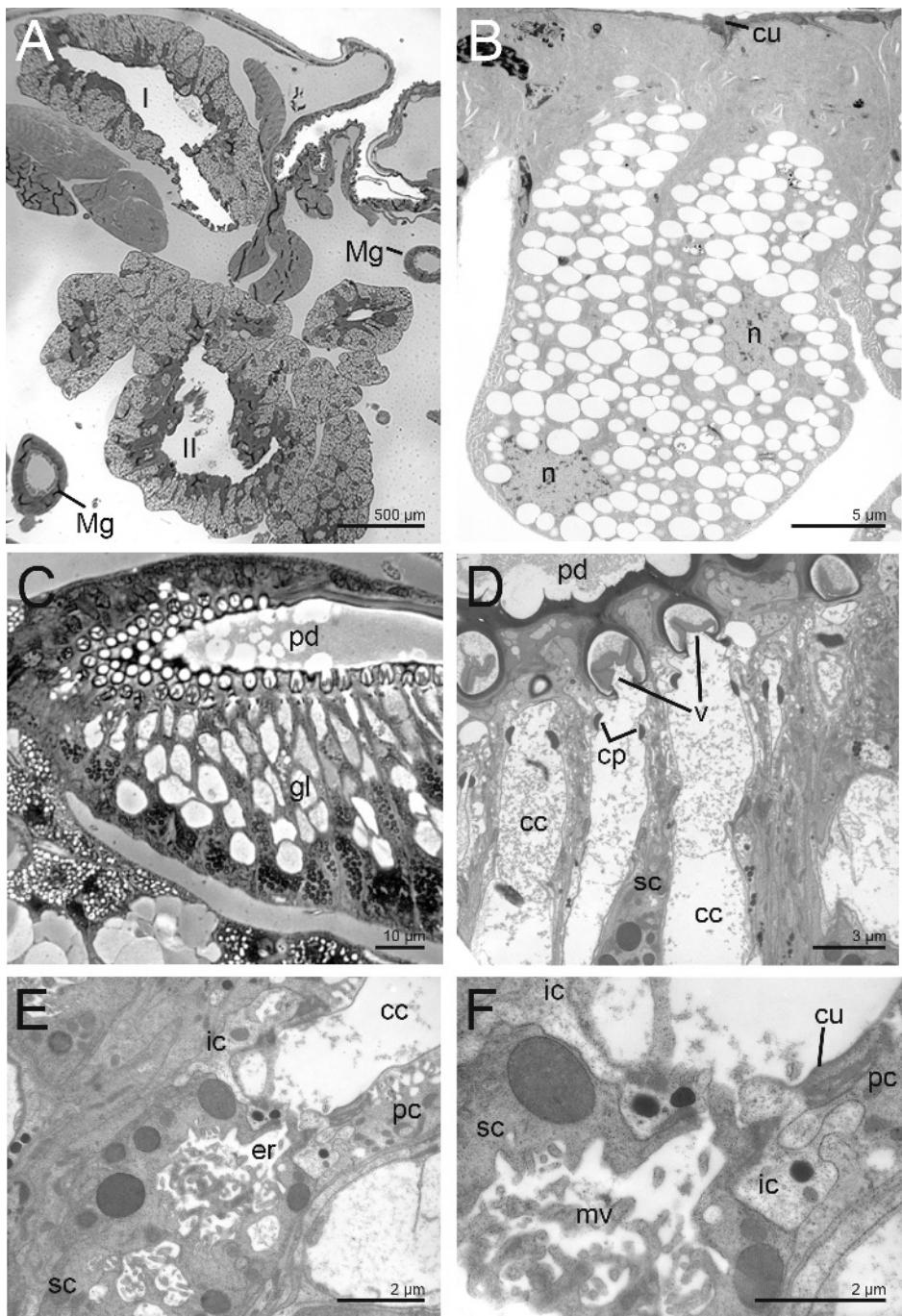


Table 4.2. Overview of the distribution of head and vesicular glands within different taxa of Chilopoda (according to Fahlander, 1938; Manton, 1965; Rilling, 1968).

	median buccal glands	lateral buccal glands	hypopharyngeal glands	mandibular/hypopharyngeal glands	I. maxillary glands	II. maxillary glands	I. vesicular glands	II. vesicular glands
Scutigeromorpha	+	+	-	+	+	+	+	+
Lithobiomorpha	+	+	+	+	?	+	-	-
Craterostigmomorpha	+	+	-	+	-	+	-	+
Scolopendromorpha	+	+	-	+	-	+	-	+
Geophilomorpha	+/-	-	-	+	-	+	-	-

It is assumed that the secretion of the gland improve the function of the maxillary organ as a cleaning organ (Hilken et al. 2003, Hilken and Rosenberg, 2006b).

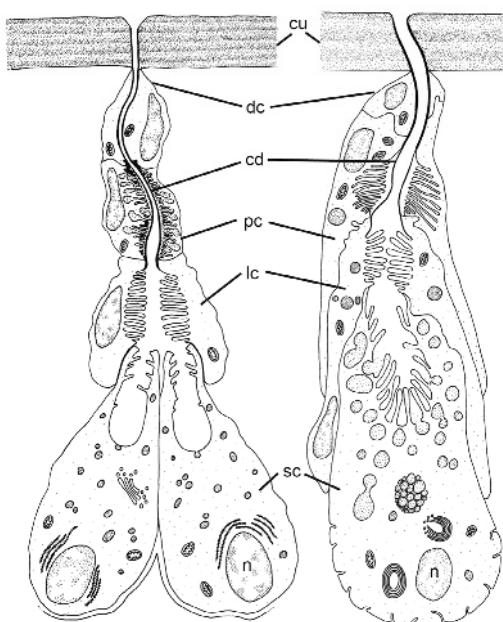
### *Epidermal maxilla II-gland*

The epidermal maxilla II-gland of *Scutigera coleoptrata* surrounds a spacious integumentary cavity at the base of the maxilla II. The gland is an aggregated epidermal gland composed by thousands of epidermal glandular units (Hilken et al., 2005), each of them consisting of a secretory cell, an intermediary cell, a proximal canal cell and a distal canal cell (4-cell type gland) (Fig. 9B).

The voluminous secretory cell is pear-shaped. Its narrow invaginated apex forms a wide extracellular reservoir with longish microvilli. The intermediary cell and the two canal cells form the conducting canal. The intermediary cell is lined by a cuticle only in its distal part; proximally, a microvillar border is formed. In the area of the two canal cells, the conducting canal is completely covered by a cuticle. The function of this gland is still unclear (Hilken et al., 2005)

### Further examples for aggregated glands in Chilopoda

The sternal glands of Geophilomorpha and the telopodal glands of *Lithobius forficatus* consist of numerous glandular units (Keil, 1975, Turcato and Minelli, 1990). Here, they are assigned to the class of aggregated, recto-canal epidermal glands, because each glandular module discharges its secretion separately through a broad, straight-running conducting canal onto the cuticle via a separate pore opening.



**Fig. 4.9** Semischematic drawings showing examples of modular units within aggregated glands in Chilopoda. A *Scutigera coleoptrata*: Schematic drawing of the single glandular unit of the Maxillary organ gland. Modified after Hilken et al. (2003). B *Scutigera coleoptrata*: Schematic drawing of the single glandular unit of the epidermal maxilla II-gland. Modified after Hilken et al. (2005).

cd conducting canal; cu cuticle; dc distal canal cell; ic intermediary cell; n nucleus; pc proximal canal cell; sc secretory cell

### *Sternal glands*

Most geophilomorph centipedes have segmental clusters of sternal or ventral glands with opening pores arranged in more or less well-defined sternal pore areas (Fig. 4.10A-C). In *Pleurogeophilus mediterraneus*, these glands form groups of glandular units, each composed of a huge secretory cell, a neck cell that forms a double fibrillar ring-like structure, a short and wide conducting canal with a wide microvillar border embedded in the cuticle, and an intracuticular chamber that opens on the sternal surface via a pore within a more or less defined pore area or pore field (Turcato and Minelli, 1990; Turcato et al., 1995). It is likely that the neck cell actually represents an intermediary cell with a cuticular intima only in its distal part (compare Fig. 7 in Turcato and Minelli, 1990). The two following cells may be regarded as proximal and distal canal cells.

Recent TEM-examination of *Haplophilus dimidiatus* confirmed the existence of a thin but elongated intermediary cell, crammed into the narrow interspace left by the canal cell(s) (lining the outer (lateral) membrane) and the dominant secretory cell (lining the inner (duct-oriented) membrane). Its apex makes contact with a small area of the wide conducting canal, slightly above a muscular closing apparatus (Fig. 4.10E), and is covered with a cuticular intima only in its distal part (Fig. 4.10F). The valve-like closing apparatus separates the extraordinarily long glandular

reservoir produced by the huge and extended secretory cell, from the upper conducting canal, which is all lined by a cuticle and an microvillar fringe produced by the canal cell(s) (Fig. 4.10E).

The glandular reservoir and the conducting canal have the same width. By approaching the ventromedian pore field (Fig. 4.10A-C), the broad conducting canal tapers slightly and releases its secretion through a pore opening (Fig. 4.10D). Each glandular unit is ensheathed by a longitudinal, musculature that increases in thickness to the bottom of the gland touching the centrally displaced ventral nerve chord (Fig. 4.10B-C,G).

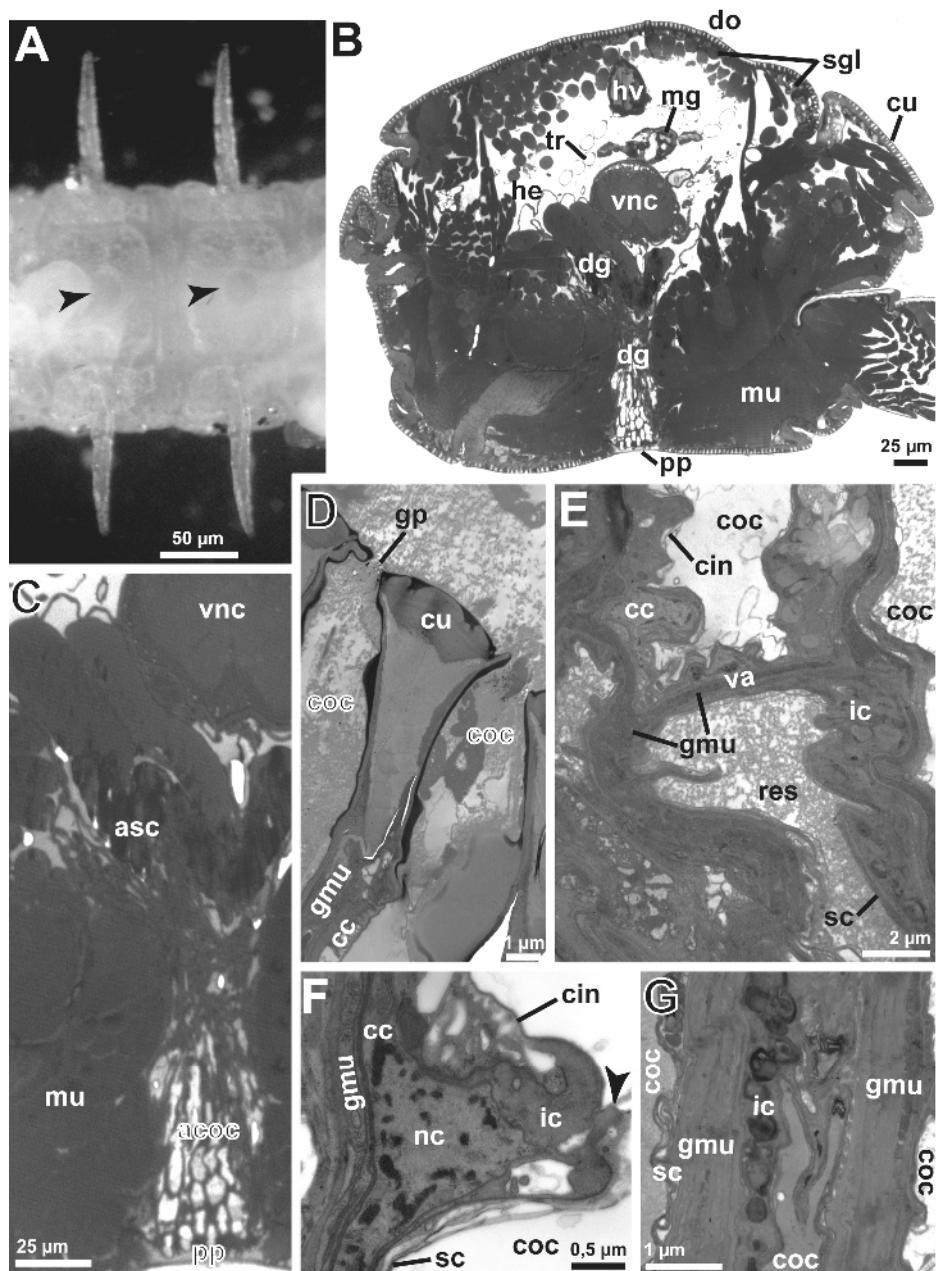
The sternal glands are defensive glands (Lewis, 1981; Hopkin et al., 1990; Hopkin and Anger, 1992; Rosenberg, 2009), in several species also involved in bioluminescence (see below).

### *Telopodal glands*

In *Lithobius forficatus*, numerous pore openings are found on the inner part of the distal telopodites XII-XV, belonging to an aggregation of telopodal glands (Keil, 1976). Each glandular unit is composed of a small and a large secretory cell and two covering cells. The smaller secretory cell is perhaps an intermediary cell and the two covering cells the proximal and distal canal cells respectively (Hilken et al., 2005). The telopodal glands function as defensive glands (Rosenberg, 2009).

**Fig. 4.10.** Ultrastructure of aggregated sternal glands in the geophilomorph *Haplophilus dimidiatus* as seen from stereo microscopy (A), light microscopy (B-C) and transmission electron microscopy (D-G). A Two median trunk segments are seen from ventral perspective. The pore fields, each situated and centred on a given sternite, are highlighted by dark arrowheads. B-C Transverse histological sections through one segment such as photographed in A. The sternal gland complex consists of closely adjoined (aggregated) glandular units that reach deeply into the hemolymphatic space, where they reach the centre of the segment: B overview; C close-up of the ventromedian area demonstrating the massive glandular apparatus. Also note the existence of solitary recto-canal and flexo-canal epidermal cells concentrated in the tergite and paratergite region. D Longitudinal overview of the pore plate showing the orifice of two glandular units via their conducting canals. E Transition zone of the canal cells, the intermediary cell and the secretory cell. The accompanying glandular musculature passes through and reinforces the valve-like closure apparatus separating the conducting canal from the proximal glandular reservoir. Longitudinal section. F Higher magnification of the tiny apex of an intermediary cell. The apical membrane is free of cuticle along its proximal half (black arrowhead). Longitudinal section. G. Longitudinal section through a region more proximal to F. Note the continuous and higher width of the glandular musculature. Originals Müller, Rosenberg, Hilken.

acoc aggregated conducting canals heading towards the pore plate region; asc aggregated, sac-like alignment of secretory cells; cc canal cell; cin cuticular intima lining the conducting canal; coc conducting canal; cu cuticle; dg sternal glands; do dorsal part of the body; gmu gland-associated musculature; he hemolymphatic space; hv heart vessel; ic intermediary cell; mg midgut; mu trunk musculature; nc nucleus; pp pore plate (= pore field); sc secretory cell; sgl solitary epidermal glands of the recto-canal and/or flexo-canal type; tr group of tracheal tubes; va valve-like closure apparatus; vnc ventral nerve chord



### *Hydrogen-cyanide producing glands*

In the scolopendromorph genus *Asanada* there are hydrogen-cyanide producing glands on the margins of sternites, pleurites, tergites, and in the legs. The glands, only histologically described, are elongated with constricted ends. The orifice is a cuticular nozzle, projected halfway into the gland cell (Maschwitz et al., 1979).

### *Periatrial gland*

The periatrial gland of *Eupolybothrus fasciatus* is part of a female accessory sex gland system located on the ventral wall of the atrium into which it opens via several small canals (Carcupino, 1996). It consists of secretory cells and ductule cells. Hilken et al. (2005) assumed that an intermediary cell with incomplete cuticular cover was overlooked (e.g. Carcupino, 1996, Fig. 34).

### *Compound epidermal glands*

Compound epidermal glands are defined by the large size and complex acinar construction of glandular units, distributed at the periphery of an arborescent system of ducts of progressively diminishing calibre. A true compound epidermal gland and the acinar subcompartments, in our sense, have to include functional units with intermediary cells connecting the secretory cells to the canal cells. As the occurrence and potential homology of intermediary cells within the glandular units across Chilopoda is only reliably evaluated by the aid of TEM, the classification status of many obviously acinar epidermal glands remains uncertain, as most anatomical descriptions are based on light microscopy alone (e.g. head glands).

We therefore introduce three subcategories, according to the conduction of TEM studies. To date, only one epidermal gland is well supported to be of the compound type (maxilla-I gland). Furthermore, there are candidate glands with ultrastructural accounts that can be theoretically used but lack certain information to draw convincing homology concepts (accessory sex glands). The majority of potential compound epidermal glands (head glands) still waits for an ultrastructural inspection.

#### **Confirmed compound epidermal glands: maxilla I-gland**

The maxilla-I gland, a salivary gland of *Scutigera coleoptrata* (Hilken and Rosenberg,

2006a). This paired salivary gland opens via the hypopharynx into the foregut and extends up to the third trunk segment. The gland is of irregular shape and consists of numerous acini with several gland units (Fig. 4.12A-B). The secretion is released into an arborescent duct system. Each acinus consists of multiple glandular units, each of them composed of secretory cells, a single intermediary cell, and canal cells (Figs. 4.11A, 4.12C-D) (3-cell type gland).

Each pear-shaped secretory cell is invaginated distally and forms an extracellular reservoir, lined by microvilli. The intermediary cell forms a conducting canal and connects the secretory cell with the canal cell system. Proximally, the intermediary cell bears microvilli, whereas the distal part is covered with a distinct cuticle in continuation with the cuticle of the canal cells (Fig. 4.12C-D). The structure of the glandular units of this salivary gland is comparable to that of the glandular units of solitary and aggregated epidermal gland. The apex of the intermediary cell has a different structure. Microvilli are formed only in its proximal part, distally the apical cell membrane forms a delicate but distinct cuticle, in continuation with that of the canal cells (Fig. 4.12C-D).

#### *Compound epidermal glands of uncertain status: accessory sex glands*

The female reproductive system of *Eupolybothrus fasciatus* includes paired large and small accessory sex glands, situated lateral to the ovary, consisting of secretory cells and ductule cells (Carcupino, 1996). The glands have a conical shape. Glandular units display an acinar organization in both types. But due to lack of specific ultrastructural data on the composition of the acini (e.g. presence of intermediary cells), their affiliation to the class of compound glands still needs an evaluation. Both glands have strongly coiled principal ducts that lack a muscularis and open both in- and outside the genital atrium posteriorly at the bases. It is formed by a circular unilayer of columnar canal cells of second order (termed epithelial cells). Numerous microvilliform extensions project into the principal duct.

Within small accessory sex glands, the large secretory cells, arranged as acini, surround an extracellular lumen and rest on the basal matrix bordering the periphery of the glandular sac.. The apices of the secretory cells stay stably connected among each other by adhering junctions resembling zonulae adhearentes. The directly adjoined ductile cell(s) surround(s) the relatively thin conducting canal, termed 'glandular reservoir', that becomes then further narrowed by the extensive microvillar apparatus produced by the secretory cells. Sometimes, cilia with basal bodies are observed between packages of microvillar extensions. The cytoplasm of the secretory cells contains many rough ER cisternae, dictyosomes, ribosomes and spherical, membrane-delimited secretory granules of moderate and/or high electron density. The nucleus is round and equipped with a prominent nucleus. In contrast, the nucleus of the ductile cell is

described to be of an irregular shape. In principle, the cytoplasm of the ductile cell is electron-lucent and contains few ER cisternae, dictyosomes and lysosomal bodies. A cuticular intima borders the conducting canal and intralobular ductules throughout their entire length (Carcupino, 1996). The large accessory sex glands are estimated to be three times more voluminous than the smaller ones. Their cellular architecture and proportions is widely similar to the smaller gland type, with the exception of the secretory cells showing higher complex contents of the secretory granules (Carcupino, 1996).

#### *Compound epidermal glands of uncertain status: head glands*

Chilopoda possess a number of head glands (Fahlander, 1938): two pairs of buccal glands, a mandibular gland, a first and a second maxillary gland. With the exception of the second maxillary gland, all these glands open into the mouth cavity or the foregut and may function as salivary glands (cf. Tab. 4.2).

#### *Scutigeromorpha*

The largest number of head glands is found in the Notostigmophora. Fahlander (1938) distinguished the following glands.

*Buccal glands.* Two pairs of lateral and median buccal glands open on the epipharynx into the oral cavity. They fill up most of the head region cranial of the oral cavity.

*Mandibular glands.* (= hypopharyngeal glands; Manton, 1965). This gland pair is located mainly in the area of the hypopharynx, with openings in a furrow on the lateral sides of the latter. According to Fahlander (1938), these glands belong to the mandibular segment, but they are actually innervated by the tritocerebrum.

*First maxillary glands.* This paired gland, only present in the Scutigeromorpha, has an irregular shape and consists of numerous acini formed by several glandular units. It opens immediately anterior to the basal articulation of the first maxillae. The secretory part lies ventral to the nerve cord. The gland opens via the hypopharynx into the foregut and extends up to the third trunk segment. The secretion is released into an arborescent duct system (Fahlander, 1938). For its ultrastructure, see Hilken and Rosenberg (2006a).

*Second maxillary glands.* This gland pair extends mainly in the forcipular segment above the foregut and consists of a large number of lobes. They open on both sides of the head, behind and under the coxa of the second maxilla, next to the openings of the maxillary nephridium (Fahlander, 1938).

**Lithobiomorpha (Fig. 4.11B)**

**Buccal glands.** *L. forficatus* possesses two pairs of lateral and medial buccal glands. The median pair lies mostly between the antennal lobes of the brain, the smaller lateral pair is located more ventrally. Both glands open on the labrum into the preoral cavity (Fahlander, 1938).

**Hypopharyngeal glands.** An inconspicuous pair of glands is situated at the base of the hypopharynx and opens on its anterior part (Rilling, 1968). Fahlander (1938) described this gland as a complex of epidermal cells not belonging to the head glands. The structure looks similar to the aggregated epidermal maxilla II-gland of *S. coleoptrata* (see above) (Hilken et al. 2005).

**Mandibular glands.** (=hypopharyngeal gland; Manton, 1965). This gland pair extends ventrally to the foregut up the first trunk segments. The location of the gland openings were described differently: on the hypopharynx medially to the mandibles (Herbst, 1891; Rilling, 1968), whereas Fahlander (1938) assigned these glands to the mandibular segment, but they are actually innervated from the tritocerebrum (intercalary segment). First description of the fine structure of this exocrine gland was given by Rosenberg and Seifert (1975). The glandular part of the mandibular gland is covered by strands of the *glandula ecdysialis* (cf. Chapter 10).

**First maxillary glands.** According to Herbst (1891) and Rilling (1968) these paired but merged gland is situated in the area of the second maxillae and opens paramedially between their coxites. Fahlander (1938) described this gland as a complex of aggregated epidermal cells and did not assign this gland to the head glands.

**Second maxillary glands.** This small gland pair lies between the forcipular and the first leg-bearing segment and opens at the base of the second maxillae near the opening of the maxillary nephridium (Fahlander, 1938). Rilling (1968) characterized this gland as a maxillipedal gland that opens paired or unpaired (Rosenberg et al., 2009) at the base of the forcipules.

**Craterostigmomorpha**

The head glands in *Craterostigmus tasmanianus* seem to be arranged like those in the Scolopendromorpha (Manton, 1965; Borucki, 1996). Two pairs of buccal glands open into the preoral cavity. The secretory part of the hypopharyngeal and the second maxillary gland lies in the trunk (hypopharyngeal gland: fifth to sixth leg-bearing segment; second maxillary gland: third to fifth leg-bearing segment). The glands open on the hypopharynx and on the maxillae II. A first maxillary gland is absent in Craterostigmomorpha (Manton, 1965).

Fig. 4.11 Semischematic drawings showing examples of compound epidermal glands and head glands in Chilopoda. A *Scutigera coleoptrata*: Schematic drawing of the single glandular unit of the maxilla I gland. Modified after Hilken and Rosenberg, 2006. B *Lithobius forficatus*: Schematic drawing of the location of the different head glands and the maxillary nephridium. Modified after Rilling (1968).

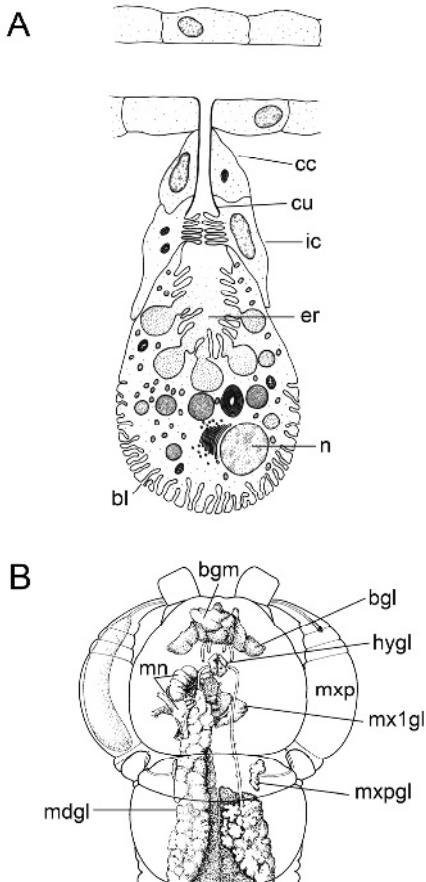
bgl buccal gland lateral; bgm buccal gland medial; bl basal labyrinth; cc canal cell; cu cuticular lining; er extracellular reservoir; hygl hypopharyngeal gland; ic intermediary cell; mdgl mandibular gland; mx1gl maxillary 1-gland; mxp maxilliped; mxpgl maxilliped gland; mn maxillary nephridium; n nucleus

#### *Scolopendromorpha*

**Buccal glands.** Paired median and lateral buccal glands are found in the anterior part of the head, cranial into which they open (Fahlander, 1938). In *Scolopendra morsitans* the epipharyngeal glands open on the epipharynx (Jangi, 1966). In *Theatops erythrocephalus*, median epipharyngeal and lateral tentorial buccal glands open in the preoral cavity (Desbalmes, 1992).

**Mandibular glands.** This gland pair lies on either side of the gut, with the glandular part extending from segment 4 to segment 7 and open near the hypopharynx, medially of the mandibles (Herbst, 1891), or cranial to the 1. maxillae (Fahlander, 1938). On the ventral wall of the head between the labium and the hypopharynx (*Jangi, 1966, S. morsitans*), or on the sides of the hypopharynx (Desbalmes, 1992; *Theatops erythrocephalus*). These glands should belong to the mandibular segment (Heymons, 1901; Fahlander, 1938), but are actually innervated by the tritocerebrum.

**Second maxillary glands.** The secretory part of this gland is situated in leg-bearing segments 3-4, opening on the coxosternite of the second maxilla (Fahlander, 1938).



### *Geophilomorpha*

In Geophilomorpha, two to three pairs of head glands are present (Fahlander, 1938):

*Buccal glands.* A pair of small, possibly the median buccal glands, is developed in *Mecistocephalus diversisternus*, *Geophilus proximus*, and *Pachymerium ferrugineum*, whereas in *Strigamia hirsutipes* no buccal glands have been found (Fahlander, 1938).

*Mandibular glands.* This paired gland opens on the hypopharynx and extends far back into the body (Fahlander, 1938), especially in littoral species as *Hydroschendyla submarina*, *Strigamia maritima* and *Henia bicarinata* (Binyon and Lewis, 1963).

*Second maxillary glands.* The glandular part of these glands extends far back into the trunk, their openings are on the coxosternum of the second maxillae or caudomedially from them (Fahlander, 1938).

### *Other compound glands*

The female reproductive system of *Eupolybothrus fasciatus* includes paired large and small accessory glands, lateral to the ovary, consisting of secretory cells and duct cells (Carcupino, 1996).

### *Function of compound epidermal glands*

The two pairs of buccal glands, the mandibular or hypopharynx gland, and the first maxillary gland are in connection to the digestive tract and are thus supposed to be salivary glands (Duboscq, 1898; Fahlander, 1938; Jangi, 1966; Desbalmes, 1992). Only the second maxillary glands have no connection to the digestive tract.

Physiological experiments on the function of head glands are limited to the old studies of Plateau (1878) and Cornwell (1916). The latter author demonstrated proteolytic and amylolytic activity in the secretion of the mandibular and second maxillary glands of a few scolopendromorph species (for details see Rosenberg, 2009).

It is possible that at least the maxillary gland supplies grooming fluid for cleaning antennae and legs. Grooming *T. erythrocephalus* produced secretion from the second maxillary gland in such great quantities that the preoral cavity was sometimes completely filled (Desbalmes, 1992). Binyon and Lewis (1963) suggested that the large mandibular glands of littoral Geophilomorpha might secrete excess salt.

## Coxal and anal organs

Jörg Rosenberg, Carsten H. G. Müller & Gero Hilken

Coxal and anal pores of pleurostigmophoran centipedes were originally interpreted as the openings of glands (see Rosenberg, 2009). However, comparative fine-structural investigations in Lithobiomorpha (Littlewood, 1983; Rosenberg, 1983a, 1984; Rosenberg and Greven, 1996; Greven et al., 1997), Scolopendromorpha (Rosenberg, 1983b), Craterostigmomorpha (Borucki and Rosenberg, 1997; Rosenberg et al., 2006), and Geophilomorpha (Rosenberg, 1982; 1989; Rosenberg and Seifert, 1977), revealed that the epithelia surrounding the coxal and anal pores are not glandular, but have the character of transporting epithelia. Therefore, it was proposed to term these organs as coxal or anal organs respectively (Rosenberg, 1985). As comparable organs are lacking in Notostigmophora, it is postulated that coxal and anal organs are autapomorphies of pleurostigmophoran centipedes (Rosenberg et al., 2006).

### *Lithobiomorpha*

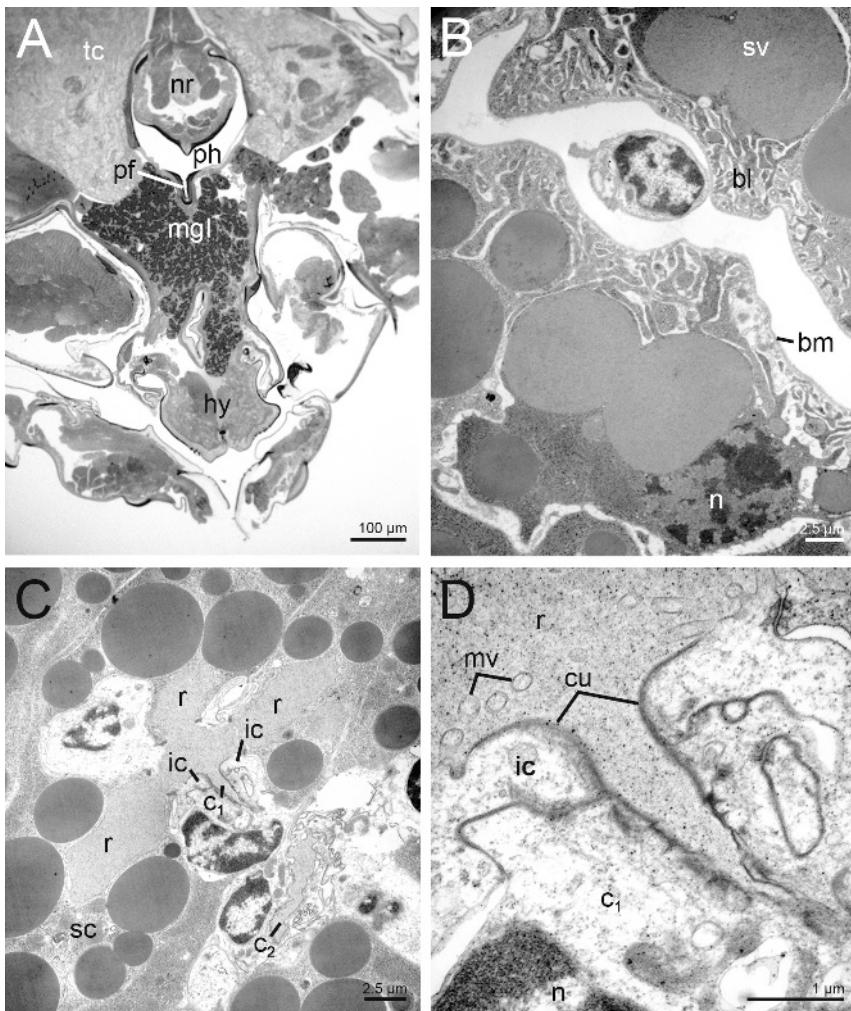
Each coxa of the last two to five pairs of legs bears ventrally a gutter-like depression, the pore field, into which the pores of the coxal organs open (Fig. 4.13B). Coxal pores are present (Littlewood, 1991a; Edgecombe et al., 2002; Edgecombe, 2003a, b) on the last

- 2 pairs of legs in several Henicopidae, e.g. *Anopsobius neozelanicus*, *Dichelobius flavens*
- 3 pairs of legs in *Dakrobius krivolutskyi* (Lithobiidae) and *Paralamyctes newtoni* (Henicopidae)
- 4 pairs of legs in most Lithobiidae and Henicopidae, incl. some Anopsobiinae, e. g. *Ghilaroviella* and *Shikokuobius*
- 5 pairs of legs in *Pseudolithobius* sp. (Lithobiidae), *Hedinobius* sp. and *Zygethobius pontis* (Henicopidae)

The arrangement of the coxal pores within the pore field also varies: the numerous coxal pores are irregularly distributed in the Ethopolyinae, in Lithobiinae the coxal pores

**Fig. 4.12.** Maxilla I-gland of *Scutigera coleoptrata*. A Overview of the maxilla I-gland in the area of the pharynx apparatus (LM). B Overview of two neighbouring glandular acini (TEM). C Apices of three secretory cells with their extracellular reservoir, a single intermediary cell, and two canals of different order (TEM). D Cell apex of the intermediary cell; proximally, microvilli are formed; distally the apex is covered by a distinct cuticle that is continuation with the cuticle of the following canal cell. The apex of the canal cell is completely lined by a cuticle (TEM). Originals Hilken, Rosenberg.

bl basal labyrinth; bm basal lamina; cu cuticular lining; c1 canal of first order; c2 canal of second order; hy hypopharynx; ic intermediary cell; mgl maxilla I-gland; mv microvilli; n nucleus; nr nervus recurrens; pf pharynx furrow; ph pharynx; r extracellular reservoir; sc secretory cell; sv secretory vesicle; tc tritocerebrum



are arranged in a single row and the pore number is variable in most species, e.g. 5 to 9 in *L. forficatus* (Eason, 1964; Andersson, 1981; Littlewood, 1983, 1991a; Rosenberg, 1983a; Barber, 2009). Females have more coxal pores than the males in most postembryonic stadia (Archey, 1937; Tobias, 1969; Andersson, 1976, 1979, 1981). For Russian Lithobiomorpha Zalesskaja (1975, 1978) reports a correlation between size and number of coxal pores and the amount of water in their habitat. A low number and diameter of pores is found in the xeric mountain genus *Hesebius*.

The drier the habitat the fewer pores per coxa are developed. Conversely, pores with very large diameter were reported for Lithobiidae living on river banks. In lithobiids there is a linear correlation between the logarithm of pore field area and head width. This suggests that mature centipedes will have proportionately smaller pore fields than younger stadia. Similarly, log transformations of single-pore area and head width are significantly correlated, suggesting that large centipedes have proportionately smaller coxal pores in relation to the body area than smaller stadia (Littlewood, 1991a).

In *L. forficatus* the first coxal pore appears when the animal bears 12 leg pairs.

During the anamorphic stages, the ventral side of the anal segment bears a single oval anal pore (Fig. 4.13B) leading into a wide cavity lined by cuticle. The base of this common cavity is surrounded by the epithelia of the paired anal organs.

The anal pores gradually disappear during the first epimorphic stage and are completely absent two stages later. In the first epimorphic stage the transporting epithelium of the anal organ is reduced. It is assumed that the functions of the larval anal organs are transferred to the coxal organs (Rosenberg, 1984).

#### *Craterostigmomorpha*

In *Craterostigmus tasmanianus* the last leg-bearing segment is followed by two genital segments and the bivalved anal capsule that projects between the last pair of legs (ano-genital capsule; Pocock, 1902). The two valves of the anal capsule surround a wide cavity opening ventrally by a longitudinal slit. The inner surface of each valve is covered by four pairs of triangular to rectangular anal pore fields.

Neighbouring pore fields are separated by broad cuticular bars (Fig. 4.13C). Each field bears several deeply invaginated openings of circular or oval outline with aggregations of anal pores (Archey, 1916; Dohle, 1990; Borucki, 1996; Borucki and Rosenberg, 1997; Rosenberg et al., 2006).

#### *Scolopendromorpha*

The coxa of the last trunk segment of nearly all Scolopendromorpha bears numerous, small coxal pores situated on a well-defined and restricted area of the ventrolateral aspect of the coxa. In *Cryptops hortensis* and *Scolopendra cingulata*, the diameter of the pores is about 10 µm (Attems, 1930; Eason, 1964; Rosenberg, 1983b).

#### *Geophilomorpha*

The coxal pores opening on the terminal pair of legs in Geophilomorpha display great diversity in number (one to many), size and arrangement. In some species pores cover the whole surface of the coxa. In *Haplophilus subterraneus* the whole slightly swollen coxae

are covered by small and numerous pores, whereas in *Geophilus flavus* each coxa possesses six to ten coxal pores situated ventrally in two irregular rows (Fig. 4.13D), in *Strigamia maritima* the coxa bears several coxal pores distributed over the ventral coxal surface, mostly covered by the margin of the metasternite. Number and arrangement of coxal pores are quite useful in taxonomy (Eason, 1964; Rosenberg, 1982, 1988/89, Barber 2009).

Anal pores are present in both sexes in Geophilidae (Fig. 4.13D), Mecistocephalidae, Oryidae and Himantariidae (Eason, 1964; Foddai and Minelli, 2000; Barber, 2009).

#### *Ultrastructure of coxal and anal organs*

All coxal and anal organs investigated so far (e.g. Rosenberg, 1985) have a largely uniform cellular organization. From each coxal and anal pore a cuticle-lined pore canal leads more or less deep into the coxa. At its base the pore canal is slightly widened and surrounded by a huge radially arranged epithelium (Fig. 4.14A). Coxal and anal organs are not eversible. Littlewood (1983) calculated the approximate volume of coxal organs of mature specimen of *Lithobius forficatus* ( $3.9 \times 10^4 \mu\text{m}^3$ ) and *L. crassipes* ( $2.3 \times 10^4 \mu\text{m}^3$ ).

The main epithelium consists of tall columnar transporting cells, covered by a specialized cuticle. Laterally, junctional cells and solitary epidermal glands surround the main epithelium like a collar. Epidermal glands open into the pore canal, which is lined by an undifferentiated epithelium. Coxal and anal organs are separated from the hemolymph by a reticular sheath of elongated and flattened cells (Littlewood, 1983: connective tissue sheath) that enclose a wide subepithelial sinus (except for the coxal organs of *H. subterraneus* and the anal organs of the anamorphic stages of *Lithobius* sp.), carrying hemocytes. Tracheae, tracheoles and nerve fibres penetrate through the outer cellular sheath into intercellular spaces between the cells of the main epithelium. Axons containing neurosecretory granules are frequently observed.

The main epithelium is composed of columnar cells up to 50  $\mu\text{m}$  high (e.g. Rosenberg, 1983a) (Fig. 4.14B). Adjacent cells are separated by intercellular spaces of varying width, occasionally filled with fine granular material. Desmosomes occur close to the cell apex. In *L. forficatus* and *L. crassipes*, neighbouring cells are linked by junctions that seem unique for transporting epithelia: a strip of electron-dense material which is punctuated at regular 15 nm intervals by lateral thickenings is lying in the electron-lucent gap and gives the epithelium an appearance of a string of beads (Littlewood, 1983). The cells show striking enlargement of the apical and basal surface, typical for transport cells. The numerous infoldings of the apical cell membrane lead very deep into the cell up to the nuclear regions, forming an apical complex up to 4/5 of cell height. The extracellular spaces, up to about 30 nm wide, are filled with porous electron-dense material extending from the subcuticular layer. The cytoplasm contains elongated mitochondria. Clusters of microtubules run toward the top of the infoldings. This transitional zone is only a few micrometers thick, except for the halophilous species *Strigamia maritima*, where it ranges over about one third of the cell apex (Rosenberg, 1982).

Below the transitional zone the foldings become more regular. The extracellular clefts narrow here to about 8 to 10 nm and are completely filled with electron-dense material. These extracellular spaces run through most parts of the transport cell up to the basal labyrinth. Here they become drop-shaped and in Geophilomorpha they are surrounded by smooth endoplasmic reticulum. The

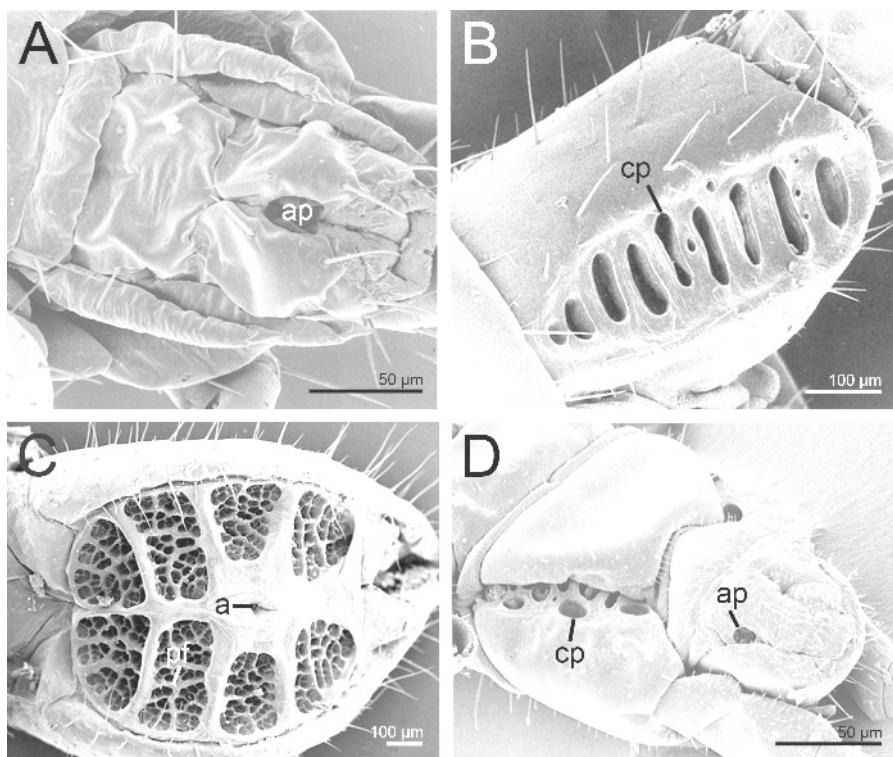
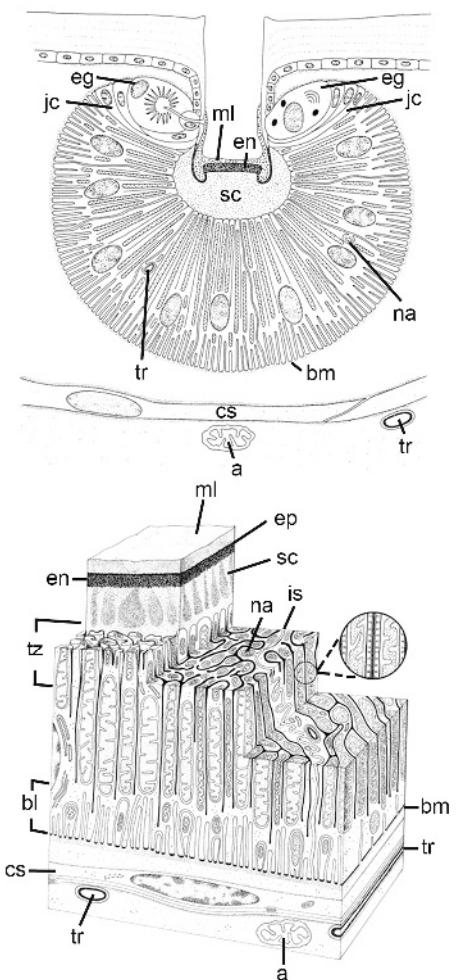


Fig. 4.13. Anal and coxal organs in Pleurostigmophora. A *Lithobius* sp., third anamorphic stage. Terminal segment with unpaired anal pore and posterior segments 11 and 12. B Adult specimen of *Lithobius forficatus*: Coxa of the trunk segment 12 with coxal pores arranged in a pore field. C *Craterostigmus tasmanianus*: Paired anal valves with anal pore fields and openings of the anal pores. D *Geophilus flavus*: coxal pores on the last coxae and paired anal pores on the second genital sternite. Fig. A, B, D: Originals J. Rosenberg, C: Original G. Hilken and J. Rosenberg.

a anus; ap anal pore; cp coxal pore; pf pore field

deeply folded apical cell membranes are coated with particles. The cytoplasm of the infoldings is now entirely occupied by voluminous, strongly elongated mitochondria, several  $\mu\text{m}$  in length, and with a dense matrix. The distance between the outer membranes of the mitochondria and the parallelly arranged apical cell membranes is remarkably constant at about 20 nm. In its regular occurrence this triad of membranes of the apical folds, particles coating the surface of these membranes, and closely associated mitochondria seems to constitute a plasmalemma-mitochondrial complex that dominates most of the entire cell (Fig. 4.14B). Continuous areas of the rough endoplasmic reticulum, Golgi complexes and microtubules are present only around the oval nucleus in the basal third of the cell. In *Cr. tasmanianus* the foldings of the apical cell membrane are



**Fig. 4.14** A Schematic organization of a single coxal organ. B Schematic organization of transport epithelial cells of a coxal organ. Inset: plasmalemma-mitochondrial complexes. Both illustrations after Rosenberg (1983), modified.

a artery; bl basal labyrinth; bm basal lamina; cs cellular sheath; eg epidermal gland; en endocuticle; ep epicuticle; is intercellular space; jc junctional cell; ml mucous layer; na neurosecretory axon; sc subcuticle; tr trachea; tz; transition zone

not closely packed and the plasmalemma-mitochondrial complexes are less pronounced than in coxal or anal organs of other pleurostigmophoran centipedes (Rosenberg et al., 2006).

The basal labyrinth is characterized by infoldings of the cell membrane extending up to one fifth of the height of the epithelium. The cytoplasm contains elongated mitochondria. In *Lithobius*, Littlewood (1983) observed parallel bundles of actin filaments. The basal matrix, which covers each coxal organ as a whole, is about 0.5 µm thick. The matrix contains some profiles of collagen.

The main epithelium is covered by a specialized, three-layered cuticle (Fig. 4.14B). Covered by a thin epicuticle, an endocuticle bulges into the pore canal.

The endocuticle is not lamellated (*Lithobiomorpha*), more or less lamellated (*Geophilomorpha*, *Craterostigmomorpha*), or striated (*Scolopendromorpha*). Between the endocuticle and the tips of the apical infoldings there is a spacious, most often double-layered subcuticle (Fig. 4.14B) (Littlewood, 1983: subcuticular matrix). The thicker outermost stratum exhibits a regular pattern of electron-dense material in *Lithobiomorpha*, an irregular one in *Scolopendromorpha* and *Craterostigmomorpha*, and a honeycomb pattern in *Geophilomorpha*. The thinner innermost stratum consists of fine fibrils of osmophilic material. The inner subcuticle extends deep into the folds of the apical cell membrane. In *Haplophilus subterraneus*, a subcuticle seems to be completely absent (Rosenberg and Seifert, 1977). Chitin was not detectable cytochemically in the subcuticle of *L. forficatus* (Greven et al., 1997).

The main epithelium is surrounded by junctional cells, epidermal glands, and cells of the pore canal (Fig. 4.14A). The slender junctional cells and the small solitary epidermal glands cover the transport epithelium like a collar. The cytoplasm of the junctional cells contains an oval nucleus,

microtubules, Golgi complexes, cisternae of the rough endoplasmic reticulum, and clusters of ribosomes. The cells are covered by a thin cuticle. Each of the solitary epidermal glands consists of a single secretory cell with well developed granular endoplasmic reticulum and Golgi-dictyosomes, an intermediary cell, and a canal cell. The mucous secretion of the secretory cells is dispersed mainly on the cuticle of the main epithelium, forming a distinct and often expanded mucous layer. The intermediary cell with its different cuticular intima was not described correctly before (e.g. Rosenberg, 1983a). In the anal capsule of *Craterostigmus tasmanianus* (Rosenberg et al., 2006) the intermediary cell of the epidermal glands is covered only in its distal part by a thin but distinct cuticle: it is assumed that this also occurs in other coxal and anal organs. The canal cell forms a duct with cuticular intima. The apical cell membrane of the canal cell is differentiated into deep infoldings, along which mitochondria are frequently found. The enlarged surfaces and the conspicuously high number of mitochondria in the canal cells suggests transporting ability. These conspicuous membrane foldings were characterised as an "end-apparatus", formed by the intermediary cell (additional cell: Rosenberg, 1982, 1983 a, b, 1985), but in the light of most recent findings (Hilken et al., 2005; Rosenberg et al., 2006) this structure belongs to the canal cell.

Rosenberg (1983a) and Littlewood (1983) described at the same time the fine structural organisation of the coxal organs of *Lithobius*. But in his fine structural analysis Littlewood (1983) overlooked several morphological characters of the general organization of the coxal organs in *L. forficatus* and *L. crassipes* as junctional cells, epidermal glands which secrete a mucous layer, and the plasmalemm-mitochondrial complexes of the main transport epithelium. A secretory cell was figured (Fig. 4.6 inset), but interpreted as "pore hypodermis". The huge mucous layer on the specialized cuticle was described as a "finely granular substance of high electron opacity", its origin remains unclear (Littlewood, 1983).

#### *Function*

The traditional suggestion that in *Lithobius* sp. the coxal organs produce a sticky defence secretion extruded through the sieve-like cuticle was disproved by the Blower (1952) and Keil (1976), who demonstrated that the defence secretion is produced by the telopodal glands situated in the same four pairs of legs as the coxal pores. For other misinterpreted functions of coxal organs in the past compare Rosenberg (2009).

The main epithelium of the coxal and anal organs is not glandular, but displays infoldings of apical and basal cell membrane and plasmalemma-mitochondrial-complexes, characteristic of transport epithelia which are suggested to take part in uptake of water linked with active ion transport (Berridge and Oshman, 1972). In *L. forficatus* ions are actively transported across the transport epithelium of the coxal organs, resulting in an increase of ion concentration in the hemolymph (Rosenberg and Bähr, 1981). The localization of chloride within the endo- and subcuticle is also regarded as an indication of transepithelial solute transport (Rosenberg and Greven, 1996).

A further feature of organs involved in fluid-transport phenomena are the subcuticular space and the distinct mucous layer. A subcuticle is formed in water transporting epithelia of many terrestrial arthropods (e.g. Noirot and Noirot-Timothée, 1971). Küppers and Thurm (1980) suggested that the subcuticle of the anal sac of *Lepisma* sp. contains hygroscopic material in the form of mucopolysaccharides similar to those demonstrated in the mucous layer and the subcuticle of the centipede coxal organs (Rosenberg, 1983b; Rosenberg and Greven, 1996).

In *L. forficatus* the coxal organs are capable to absorb water from an atmosphere saturated by tritiated water vapour. In dehydrated animals the water vapour uptake increases linear during the first 3 h, reaching a saturation-point after about 40 h. That means that 40–50 µl water can be transported over the whole body into the hemolymph. Blocking the coxal pores by silicone oil leads to a drastic decrease of water vapour uptake within 1 h ( $42 \pm 5\%$ ). The pore field area is only about 2% of the area of the whole integument. This means that the uptake of water vapour with the aid of the coxal organs is about 500 times higher. The coxal organs can be regarded as the most important organs of water vapour uptake in the centipedes. Condensed water is actively transferred across the transport epithelium into the hemolymph (Rosenberg and Bajorat, 1984).

According to Littlewood (1983, 1988, 1991a, b; also Littlewood and Blower, 1987), the coxal organs are not simply responsible for the regulation of the ionic content or osmotic potential of the haemolymph, but also release a pheromone. This hypothesis is supported by behavioural and chemical evidence. However, the ultrastructure of the transport epithelium makes it unlikely that those cells are the actual site of synthesis of the putative pheromone. Instead, this pheromone may be produced in the hemocytes located in the subepithelial sinus beneath the coxal organs. The transport of organic moieties could be reconciled with the diuretic function of "transporting epithelium" of the coxal organ. Therefore, the additional or perhaps primary physiological role of the epithelium is getting rid of excess water (diuresis), not water vapour uptake, and the release of pheromones across the transport epithelium. In *L. forficatus* the coxae of the last trunk segments bear numerous openings of solitary epidermal glands in the vicinity of the coxal organs (Rosenberg, 1994). It is more likely, that pheromone is produced by these glands rather than by hemocytes.

## Bioluminescence

Gero Hilken, Jörg Rosenberg & Carsten H.G. Müller

In centipedes, bioluminescence is only known for some geophilomorphs (reviewed by Minelli, 1978; Rosenberg, 2009; Rosenberg and Meyer-Rochow, 2009).

Brade-Birks and Brade-Birks (1920) and Koch (1927) showed that in *Geophilus carpophagus* and *Strigamia crassipes* the glowing substances is produced in the sternal glands and discharged via the large sternal pore fields.

The luminous secretion has been described as yellowish in *Orya barbarica* (Gazagnaire, 1888), transparent in *Orphnacetus brevilabiatus* (Anderson, 1980) and *Strigamia crassipes* (Brade-Birks and Brade-Birks, 1920), but also bluish in the same *S. crassipes* (Koch, 1927). The colour of the bioluminescence itself is generally described as greenish. The luminous periods may last from seconds to minutes (Koch, 1927; Jones et al., 1976). The light intensity was found so strong to be recorded by a photographic plate (Brade-Birks and Brade-Birks, 1920; Koch, 1927).

Anderson (1980) showed that the luminous substance of *Orphnacetus brevilabiatus* contains a luciferin and a luciferase, as in many other bioluminescent animals. The O<sub>2</sub>-dependent luciferin/luciferase-reaction of *O. brevilabiatus* runs at a pH-optimum of 4.6.

### *References*

- ANDERSON, J. M., 1980. Biochemistry of centipede bioluminescence. – Photochemistry and photobiology 31: 179-182.
- ANDERSSON, G., 1976. Post-embryonic development of *Lithobius forficatus* (L.) (Chilopoda: Lithobiidae). – Entomologica Scandinavica 7: 161-168.
- ANDERSSON, G., 1979. Taxonomic studies on the postembryonic development in *Lithobius*, with a brief comparison with *Lamyctes*. – Ph. D. Dissertation, Department of Zoology, Göteborg University, Sweden.
- ANDERSSON, G., 1981. Taxonomical studies on post-embryonic development in Swedish Lithobiomorpha (Chilopoda). – Entomologica Scandinavica, Supplement 15: 105-124.
- ANTONIAZZI, M. M., C. M. PEDROSO, I. KNYSAK, R. MARTINS, S. P. G. GUIZZE, C. JARED & K. C. BARBARO, 2009. Comparative morphological study of the venom glands of the centipede *Cryptops iheringi*, *Ostostigmus pradoi* and *Scolopendra viridicornis*. – Toxicon 53: 367-374.
- ARCHEY, G., 1916. The occurrence in New Zealand of *Craterostigmus tasmanianus* Pocock (Chilopoda). – Transactions and Proceedings of the New Zealand Institute 49: 319-320.
- ARCHEY, G., 1937. Revision of the Chilopoda of New Zealand, part 2. – Record of the Auckland Institute and Museum 2: 71-100.
- ATTEMS, C. C., 1930. Myriapoda. 2. Scolopendromorpha (Das Tierreich 54). – de Gruyter, Berlin.
- BARBER, A. D., 2009. Centipedes. – Synopsis of the British fauna (New series 58) – Field Studies Council, Shrewsbury.
- BERRIDGE, M. J. & J. L. OSHMAN, 1972. Transporting epithelia. – Academic Press, New York, London.
- BINYON, J. & J. G. E. LEWIS, 1963. Physiological adaptations of two species of centipede (Chilopoda: Geophilomorpha) to life on the shore. – Journal of the Marine Biological Association of the United Kingdom 43: 49-55.
- BLOWER, J. G., 1951. A comparative study of the chilopod and diplopod cuticle. – Quarterly Journal of Microscopical Science 92: 141-161.
- BLOWER, J. G., 1952. Epidermal glands in centipedes. – Nature 170: 166-167.

- BORUCKI, H., 1996. Evolution und phylogenetisches System der Chilopoda (Mandibulata, Tracheata). – Verhandlungen des naturwissenschaftlichen Vereins in Hamburg, Neue Folge 35: 95-226.
- BORUCKI, H. & J. ROSENBERG, 1997. Transport-active organs within the anal capsule of *Craterostigmus tasmanianus* (Chilopoda, Craterostigmomorpha). – Zoomorphology 117: 49-52.
- BRADE-BIRKS, H. K. & S. G. BRADE-BIRKS, 1920. Notes on Chilopoda XX. Luminous Chilopoda, with special reference to *Geophilus carpophagus*, Leach. – Annals and Magazine of Natural History (9) 5: 1-30.
- CALS, P., 1974. Mise en évidence, par la microscope électronique à balayage, de champs morphogénétiques polarisés, exprimés par les cellules épidermiques normales dans l'appendice locomoteur des Arthropodes: *Tylos latreilli* (Audouin) (Crustacé, Isopode) et *Periplaneta americana* (L.) (Insecte, Dictyoptère). – Comptes rendus de l'Académie des Sciences, Paris, D 279: 663-666.
- CARCUPINO, M., 1996. Morphological characterization of female accessory sex glands of *Eupolybothrus fasciatus* (Newport) (Chilopoda, Lithobiomorpha). – Journal of Morphology 228: 61-75.
- CHAO, J.-L. & H.-W. CHANG, 2006. Variation of the poison duct in Chilopoda centipedes from Taiwan. – Norwegian Journal of Entomology 53: 139-151.
- CORNWELL, J. W., 1916. Some centipedes and their venoms. – Indian Journal of Medical Research 3: 541-557.
- DASS, C. M. S. & JANGI, B. S., 1978. Ultrastructural organization of the poison gland of the centipede, *Scolopendra morsitans* L. – Indian Journal of Experimental Biology 16: 748-757.
- DUBOSCQ, O., 1898. Recherches sur les chilopodes. – Archives de Zoologie expérimentale et générale (3) 6: 481-650.
- DAMASCHUN, G. & H. FÜLLER, 1965. Röntgenographische Untersuchungen über die Chitintextur der Cuticula von Chilopoden. – Zoologische Jahrbücher, Abteilung für allgemeine Zoologie und Physiologie der Tiere 71: 415-428.
- DESBALMES, G., 1992. Funktions-Anatomie des Fressapparates der Chilopoda: Die Kopfregion von *Theatops erythrocephalus* (C. L. Koch) sowie deren Kauapparat im funktionellen Vergleich mit *Scolopendra cingulata* und *Scutigera coleoptrata*. – Thesis, Formal- und naturwissenschaftliche Fakultät der Universität Wien.
- DOHLE, W., 1990. Some observations on morphology and affinities of *Craterostigmus tasmanianus* (Chilopoda). Pp. 69-79 in A. MINELLI (ed.) Proceedings of the 7th International Congress of Myriapodology. – Brill, Leiden.
- DUBOSCQ, O., 1898. Recherches sur les Chilopodes. – Archives de Zoologie expérimentale et générale (3) 6: 481-650.
- EASON, E. H., 1964. Centipedes of the British Isles. – Warne, London.
- EDGECOMBE, G. D., 2003a. A new genus of henicopid centipede (Chilopoda: Lithobiomorpha) from New Caledonia. – Memoirs of the Queensland Museum 49: 269-284.
- EDGECOMBE, G. D., 2003b. A new species of the Gondwanan centipede *Anopsobius* (Chilopoda: Lithobiomorpha) from New South Wales, Australia. – Zootaxa 204: 1-15.
- EDGECOMBE, G. D., G. GIRIBET & W. C. WHEELER, 2002. Phylogeny of Henicopidae (Chilopoda: Lithobiomorpha): a combined analysis of morphology and five molecular loci. – Systematic Entomology 27: 31-64.
- FAHLANDER, K., 1938. Beiträge zur Anatomie und systematischen Einteilung der Chilopoda. – Zoologiska Bidrag från Uppsala 17: 1-148.
- FODDAI, D. & A. MINELLI, 2000. Phylogeny of geophilomorph centipedes: old wisdom and new insights from morphology. – Fragmenta Faunistica 43 Supplement: 61-71.

- FUHRMANN, H., 1922. Beiträge zur Kenntnis der Hautsinnesorgane der Tracheaten. I. Die antennalen Sinnesorgane der Myriapoden. – Zeitschrift für wissenschaftliche Zoologie 119: 1-52.
- FÜLLER, H., 1963. Vergleichende Untersuchungen über das Skelettmuskelsystem der Chilopoden. – Abhandlungen der Deutschen Akademie der Wissenschaften zu Berlin, Klasse für Chemie, Geologie und Biologie 3: 1-97.
- FÜLLER, H., 1965a. Dichroitische Anfärbung von Chitin mit Thiazinrot, ein histochemischer Chitinnachweis. – Zoologischer Anzeiger 174: 125-131.
- FÜLLER, H., 1965b. Untersuchungen über die Chitintextur des Integuments der Chilopoden. – Zoologischer Anzeiger 175: 173-181.
- FUSCO, G., C. BRENA & A. MINELLI, 2000. Cellular processes in the growth of lithobiomorph centipedes (Chilopoda: Lithobiomorpha). A cuticular view. – Zoologischer Anzeiger 239: 91-102.
- GAZAGNAIRE, J., 1888. La phosphorescence chez les myriapodes. – Bulletin de la Société entomologique de France 13: 182-186.
- GREVEN, H., J. ROSENBERG & I. LATKA, 1997. Cytochemical notes on the specialized cuticle of the coxal organs in *Lithobius forficatus*: application of lectins and demonstration of chitin (Chilopoda, Lithobiomorpha: Lithobiidae). – Entomologica Scandinavica, Supplement 51: 71-76.
- HERBST, C., 1891. Beiträge zur Kenntnis der Chilopoden (Drüsen; Coxalorgan; Gefäßsystem und Eingeweidennervensystem). – Bibliotheca zoologica 3 (9): 1-43.
- HEYMONS, R., 1901. Die Entwicklungsgeschichte der Scolopender. – Zoologica (Stuttgart) 13: 1-244.
- HILKEN, G., C. BROCKMANN & J. ROSENBERG, 2003. The maxillary organ gland: description of a new head gland in *Scutigera coleoptrata* (Chilopoda, Notostigmophora). – African Invertebrates 44: 175-184.
- HILKEN, G. & J. ROSENBERG, 2006a. Ultrastructural investigation of a salivary gland in a centipede: structure and origin of the maxilla I-gland of *Scutigera coleoptrata* (Chilopoda, Notostigmophora). – Journal of Morphology 267: 375-381.
- HILKEN, G. & J. ROSENBERG, 2006b. Ultrastructure of the maxillary organ of *Scutigera coleoptrata* (Chilopoda, Notostigmophora): description of a multifunctional head organ. – Journal of Morphology 267: 152-165.
- HILKEN, G. & J. ROSENBERG, 2009. Ultrastructural investigation of vesicular glands in *Scutigera coleoptrata* (Chilopoda, Notostigmophora). – Journal of Morphology 270: 451-458.
- HILKEN, G., J. ROSENBERG & C. BROCKMANN, 2005. Ultrastructure of the epidermal maxilla II-gland of *Scutigera coleoptrata* (Chilopoda, Notostigmophora) and the ground pattern of epidermal gland organs in Myriapoda. – Journal of Morphology 264: 53-61.
- HOCHSTRATE, W., 1988/1989. Zum Wasserhaushalt anamorpher Larven des Chilopoden *Lithobius forficatus* (L.). – Wissenschaftliche Beiträge, Friedrich-Schiller-Universität Jena 2: 64-70.
- HOPKIN, S. P., M. J. GAYWOOD, J. F. V. VINCENT & E. L. V. MAYES-HARRIS, 1990. Defensive secretion of proteinaceous glues by *Henia (Chaetechelyne) vesuviana* (Chilopoda, Geophilomorpha). Pp. 175-181 in A. MINELLI (ed.) Proceedings of the 7<sup>th</sup> International Congress of Myriapodology. – Brill, Leiden.
- JANGI, B. S., 1966. *Scolopendra* (The Indian centipede). – The Zoological Society of India, Calcutta.
- JOLY, R., 1962. Etude expérimentale de la résistance à la dessiccation de *Lithobius forficatus* L. (Myriapode, Chilopode) en fonction du degré relative et de la température. – Bulletin de la Société zoologique de France 87: 155-163.
- JONES, T. H., W. E. CONNER, J. MEINWALD, H. E. EISNER & T. EISNER, 1976. Benzoyl cyanide and mandelonitrile in the cyanogenetic secretion of a centipede. – Journal of Chemical Ecology 2: 421-429.

- KEIL, T. A., 1976. Die Antennensinnes- und Hautdrüsengänge von *Lithobius forficatus* L. Eine licht- und elektronenmikroskopische Untersuchung. – Dissertation, Freie Universität Berlin.
- KOCH, A., 1927. Studien an leuchtenden Tieren: I. Das Leuchten der Myriapoden. – Zeitschrift für Morphologie und Ökologie der Tiere 8: 241-270.
- KOCH, M., G. D. EDGECOMBE & R. M. SHELLEY, 2010. Anatomy of *Ectonocryptoides* (Scolopocryptopidae: Ectonocryptopinae) and the phylogeny of blind Scolopendromorpha (Chilopoda). – International Journal of Myriapodology 3: 51-81.
- KRISHNAN, G., 1956. The nature and composition of the epicuticle of some arthropods. – Physiological Zoology 29: 324-337.
- KÜPPERS, J. & U. THURM, 1980. Water transport by electroosmosis. Pp. 125-144 in M. LOCKE & D. S. SMITH (eds.) Insect biology in future. – Academic Press, London.
- LEWIS, J. G. E., 1981. The biology of centipedes. – Cambridge University Press, Cambridge.
- LITTLEWOOD, P. M. H., 1983. Fine structure and function of the coxal glands of lithobiomorph centipedes: *Lithobius forficatus* and *L. crassipes* (Chilopoda, Lithobiidae). – Journal of Morphology 177: 157-179.
- LITTLEWOOD, P. M. H., 1988. The chemosensory behaviour of *Lithobius forficatus* (Myriapoda: Chilopoda). 2. Bioassay and chemistry of the coxal pheromone. – Journal of Zoology 215: 523-535.
- LITTLEWOOD, P. M. H., 1991a. Chilopod coxal organs: morphological considerations with reference to function. – Journal of Zoology 223: 379-393.
- LITTLEWOOD, P. M. H., 1991b. The water relations of *Lithobius forficatus* and the role of the coxal organs (Myriapoda: Chilopoda). – Journal of Zoology 223: 653-665.
- LITTLEWOOD, P. M. H. & J. G. BLOWER, 1987. The chemosensory behaviour of *Lithobius forficatus*. 1. Evidence for a pheromone released by the coxal organs (Myriapoda: Chilopoda). – Journal of Zoology 211: 65-82.
- MANTON, S. M., 1965. The evolution of arthropod locomotory mechanisms. Part 8. Functional requirements and body design in Chilopoda, together with a comparative account of their skeleto-muscular systems and an appendix on a comparison between burrowing forces of annelids and chilopods and its bearing upon the evolution of the arthropodan haemocoel. – Journal of the Linnean Society of London, Zoology 46: 251-483.
- MASCHWITZ, U., U. LAUSCHKE, & M. WÜRMLI, 1979. Hydrogen cyanide-producing glands in a scolopender, *Asanada* n. sp. (Chilopoda, Scolopendridae). – Journal of Chemical Ecology 5: 910-907.
- MÉNEZ, A., K. ZIMMERMAN, S. ZIMMERMAN, & H. HEATWOLE, 1990. Venom apparatus and toxicity of the centipede *Ethmostigmus rubripes* (Chilopoda, Scolopendridae). – Journal of Morphology 206, 303-312.
- MINELLI, A., 1978. Secretion of centipedes. – Pp. 73-85 in S. BETTINI (ed.) Arthropod venoms: Handbook of experimental pharmacology 48 – Springer, Heidelberg-Berlin.
- MÜLLER, C. H. G., G. HILKEN & J. ROSENBERG, 2008. Fine structure and diversity of “flexo-canal epidermal glands” on the head of pleurostigmophoran centipedes (Chilopoda). – Journal of Morphology 269: 1493.
- MÜLLER, C. H. G., J. ROSENBERG & G. HILKEN, 2006. On the fine structure of epidermal glands in Chilopoda: structure and phylogenetic aspects. – Norwegian Journal of Entomology 53: 399.
- MÜLLER, C. H. G., J. ROSENBERG & G. HILKEN, 2009. Fine structure and phylogenetic significance of ‘flexo-canal epidermal glands’ in Chilopoda. – Soil Organisms 81: 269-294.
- MÜLLER, C. H. G., J. ROSENBERG & G. HILKEN, in press. Ultrastructure, functional morphology, and phylogenetic implications of ‘recto-canal epidermal glands’ in Chilopoda with a proposal for an advanced classification of class-III epidermal glands in Euarthropoda. – Arthropod Structure & Development

- MÜLLER, C. H. G., J. ROSENBERG & V. B. MEYER-ROCHOW, 2003a. Hitherto undescribed interommatidial exocrine glands in Chilopoda. – African Invertebrates 44: 185-197.
- MÜLLER, C. H. G., J. ROSENBERG, S. RICHTER & V. B. MEYER-ROCHOW, 2003b. The compound eye of *Scutigera coleoptrata* (Linnaeus, 1758) (Chilopoda: Notostigmophora): an ultrastructural investigation that adds support to the Mandibulata concept. – Zoomorphology 122: 191-209.
- NEWPORT, G. 1845. Monograph of the class Myriapoda, order Chilopoda; with observations on the general arrangement of the Articulata. Transactions of the Linnaean Society of London 19, 265-302.
- NOIROT, C., C. NOIROT-TIMOTHÉE, 1971. Ultrastructure du proctodéum chez le Thysanure *Lepismodes inquilinus* Newmann (= *Thermobia domestica* Packard). II Le sac anal. – Journal of Ultrastructural Research 37: 335-350.
- PLATEAU, F., 1878. Recherches sur les phénomènes de la digestion et sur la structure de l'appareil digestif chez les Myriapodes de Belgique. – Mémoires de l'Académie royale de Belgique 42: 1-94.
- POCOCK, R. J., 1902. A new and annectant type of chilopod. – Quarterly Journal of Microscopic Science, New Series 45: 415-448.
- RILLING, G., 1968. *Lithobius forficatus*. Grosses Zoologisches Praktikum 13b. – Fischer, Stuttgart.
- ROSENBERG, J., 1982. Coxal organs in Geophilomorpha (Chilopoda). Organization and fine structure of the transporting epithelium. – Zoomorphology 100: 107-120.
- ROSENBERG, J., 1983a. Coxal organs of *Lithobius forficatus* (Myriapoda, Chilopoda). Fine structural investigation with special reference to the transporting epithelium. – Cell and Tissue Research 230: 421-430.
- ROSENBERG, J., 1983b. Coxal organs in Scolopendromorpha (Chilopoda): Topography, organization, fine structure and significance in centipedes. – Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 110: 383-393.
- ROSENBERG, J., 1984. Ultrastructure of the anal organs in the larval stages of *Lithobius forficatus* L. (Chilopoda, Lithobiomorpha). – International Journal of Insect Morphology and Embryology 13: 25-29.
- ROSENBERG, J., 1985. Untersuchungen zur feinstrukturellen Organisation und Funktion der Coxal- und Analorgane bei Chilopoden. – Bijdragen tot Dierkunde 55: 337-344.
- ROSENBERG, J., 1988/89. Bestimmungsschlüssel für mitteleuropäische Erdläufer (Geophilomorpha) anhand der Coxalporen. – Acta biologica Benrodis I: 133-141.
- ROSENBERG, J., 1989. Untersuchungen zur funktionellen Morphologie der Analorgane von Geophilidae (Geophilomorpha). – Pp. 115-123 in A. MINELLI (ed.) Proceedings of the 7th International Congress of Myriapodology. – Brill, Leiden.
- ROSENBERG, J., 1994. Fine structure of epidermal glands in vicinity to the coxal organs of *Lithobius forficatus* (Chilopoda). – Acta Biologica Benrodis 6: 37-47.
- ROSENBERG, J., 2009. Die Hundertfüßer Chilopoda. – Die Neue Brehm-Bücherei 285, Westarp Wissenschaften, Hohenwarsleben.
- ROSENBERG, J. & E. BÄHR, 1981. Coxalorgane bei Chilopoden: Feinstruktur und Ionen-Transport. – Verhandlungen der Deutschen Zoologischen Gesellschaft 74: 263.
- ROSENBERG, J. & K. H. BAJORAT, 1984. Einfluß der Coxalorgane von *Lithobius forficatus* L. (Chilopoda) auf die Sorption von Wasserdampf. – Zoologische Jahrbücher, Abteilung für allgemeine Zoologie und Physiologie der Tiere 88: 337-344.
- ROSENBERG, J. & H. GREVEN, 1996. Coxal organs of Chilopoda: the exocrine glands in *Lithobius forficatus*. – Mémoires du Museum National d'Histoire Naturelle, Paris 169: 403-409.
- ROSENBERG, J. & G. HILKEN, 2006. Fine structural organization of the poison gland of *Lithobius forficatus* (Chilopoda, Lithobiomorpha). – Norwegian Journal of Entomology 53: 119-127.

- ROSENBERG, J. & V. B. MEYER-ROCHOW, 2009. Luminescent myriapoda: A brief review. – Pp. 139-146 in V. B. MEYER-ROCHOW (ed.): Bioluminescence in focus - A collection of illuminating essays. – Research Signpost, Trivandrum.
- ROSENBERG, J., C. H. G. MÜLLER & G. HILKEN 2006. Ultrastructural organization of the anal organs in the anal capsule of *Craterostigmus tasmanianus* Pocock, 1902 (Chilopoda, Craterostigmomorpha). – Journal of Morphology 267: 265-272.
- ROSENBERG, J. & G. SEIFERT, 1975. Ist allein die Glandula ecdisialis die Häutungsdrüse von *Lithobius forficatus*? – Experientia 31: 1100-1101.
- ROSENBERG, J. & G. SEIFERT, 1977. The coxal glands of Geophilomorpha (Chilopoda): Organs of osmoregulation. – Cell and Tissue Research 182: 247-251.
- ROSENBERG, J., A. SOMBKE & G. HILKEN, 2009. Structure and function of the maxillary nephridium of *Lithobius forficatus* (Chilopoda, Pleurostigmophora). – Journal of Morphology 270: 1531-1540.
- SCHEFFEL, H., 1987. Häutungsphysiologie der Chilopoden: Ergebnisse von Untersuchungen an *Lithobius forficatus* (L.). – Zoologische Jahrbücher, Abteilung für allgemeine Zoologie und Physiologie der Tiere 91: 257-282.
- SEMENOVA, L. M., 1961. Relation of cuticle structure in chilopods to the condition of existence (Russian with English summary). – Zoologicheskii Zhurnal 40: 686-693.
- SHRIVASTAVA, S. C., 1971. Studies on the cuticle of the Indian common chilopod *Scolopendra morsitans* L. – Indian Journal of Entomology 33: 83-193.
- TICHY, H., 1973. Untersuchungen über die Feinstruktur des Tömösváryschen Sinnesorgans von *Lithobius forficatus* L. (Chilopoda) und zur Frage seiner Funktion. – Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 91: 93-139.
- TOBIAS, D., 1969. Grundsätzliche Studien zur Art-Systematik der Lithobiidae. – Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 523: 1-51.
- TURCATO, A., G. FUSCO & A. MINELLI, 1995. The sternal pore of geophilomorph centipedes (Chilopoda: Geophilomorpha). – Zoological Journal of the Linnean Society 115: 185-209.
- TURCATO, A. & A. MINELLI, 1990. Fine structure of the ventral glands of *Pleurogeophilus mediterraneus* (Meinert) (Chilopoda Geophilomorpha). – Pp. 165-173 in A. MINELLI (ed.) Proceedings of the 7<sup>th</sup> International Congress of Myriapodology. – Brill, Leiden.
- ZALESSKAJA, N. T., 1975. Distribution patterns of Lithobiomorpha on the territory of the USSR. – Pp. 163-166 in J. VANEK & W. JUNK (eds.): Proceedings of the 5th International Colloquium on Soil Zoology, Prague 1975. – BV Puld, Den Haag.
- ZALESSKAJA, N. T., 1978. Adaptive morphology of centipede characteristics (Chilopoda, Lithobiomorpha). – Pp. 55-60 in M. S. Gilharov (ed.) The adaptations of soil animals to environmental conditions. – Nauka, Moscow.



## Chapter 5

# CHILOPODA – MUSCULATURE AND LOCOMOTION

Alessandro Minelli

### *Muscle topography*

Because of page limits, we cannot illustrate here in detail the topographical anatomy of centipede musculature, which is known in great detail only for *Lithobius forficatus*, thanks to Rilling (1960, 1968). Older but still useful descriptions of head musculature are also available for *Pseudolithobius megaloporus* (Applegarth, 1952) and *Scolopendra subspinipes* (Meinert, 1883). Some detail will be provided instead for the musculature of the trunk, as a necessary background to understand locomotory mechanics. The following account follows Manton's (1952, 1965, 1973, 1977) comparative morpho-functional studies of centipede locomotion.

Trunk muscles are arranged in six groups: four sets of longitudinal muscles (superficial, dorsal, lateral, sternal), the deep oblique muscles and the deep dorso-ventral muscles.

In geophilomorphs, the individual longitudinal muscles span only one intersegmental boundary, whereas in the other groups there are also sets of muscles whose posterior point of attachment is further behind than the segment closest to that to which the muscles attach anteriorly. The superficial muscles are always segmental, that is, extending between one tergite and the anterior margin of the next following tergite. In the burrowing geophilomorph centipedes of the genus *Haplophilus*, one pair of superficial muscles is attached to the pretergite, two pairs on the metatergite. In the scolopendromorphs (*Cormocephalus*), where pretergites are not present, there is one pair of superficial longitudinal muscles attaching on each tergite. In the fast running scolopendromorphs, the musculature is arranged in three layers.

Lateral longitudinal muscles are distinct in scolopendromorphs and geophilomorphs, but in scutigeromorphs and lithobiomorphs these sets are fused together with the sternal longitudinal muscles.

Leg muscles are quite numerous, especially in the fast-running forms. There are 34 extrinsic muscles per leg in the Scutigeromorpha, 20 in the Lithobiomorpha, 19 in the Scolopendromorpha, 13 in the Geophilomorpha.

#### *Ultrastructure of muscle fibres*

Following earlier structural investigations in light microscopy (Füller, 1963) centipede muscles – together with sperm cells – were the object of the oldest ultrastructural studies performed on Chilopoda. Those investigations covered the striated muscles of *Scutigera coleoptrata*, *Lithobius forficatus*, *Scolopendra cingulata* and *Himantarium gabrielis* (Camatini and Saita, 1967, 1968, 1969; Camatini, 1970). Various arrangements of myofibrils were described, with phasic fibres arranged in a hexagonal pattern with a myosin to actin filament ratio as 1:3, tonic fibres with ratio 1:6.

The boundary between contiguous sarcomeres, or Z-line, is continuous in the longitudinal muscle fibres of *L. forficatus* (Camatini et al., 1979).

Neuromuscular junctions have been described in *Scolopendra cingulata*, *Scutigera coleoptrata*, *Lithobius* sp. and *Himantarium gabrielis* by Saita and Candia Carnevali (1978).

An atypical myofilament array was described for the visceral muscle fibres of *Lithobius forficatus*, specifically in the testis (Camatini and Ceresa Castellani, 1974, 1978). The fibres of the mid-gut muscles of *Lithobius forficatus* have a peripheral nucleus and measure 2.5 x 4.0  $\mu\text{m}$ . Their T-system is well-developed, the ratio of myosin to actin filaments in the A band is 1:6. Z lines are very irregular (Camatini and Ceresa Castellani, 1978). A single myofibril forms each fibre of the muscular sheath of the testis in *L. forficatus* (Camatini and Ceresa Castellani, 1974, 1978). The external longitudinal fibres (2.6 x 3.5  $\mu\text{m}$ ) have central nucleus, the internal circular fibres (1.9 x 4  $\mu\text{m}$ ) have a lateral nucleus. Z bands are very irregular, the sarcoplasmic reticulum is poorly developed, and the T system apparently absent.

#### *Mechanics of locomotion*

In principle at least, centipedes are a choice group for the study of locomotion. On the one hand, their high to very high number of leg pairs suggests mechanical solutions other than those adopted by terrestrial arthropods with six or eight legs. On the other hand, an important diversity of locomotion styles is also found within the group, the main clades differing conspicuously not only in the number of locomotory appendages, but also in the

elasticity and flexibility of the trunk, in the length to diameter ratio of the latter, in the ratio of leg length to body diameter, and also in swiftness and ability to change direction.

Leg structure and function have been accurately described by Manton (1952, 1965, 1977). The leg can perform a promoter-remotor swing and a rotation on its axis. Leg extension is produced in an indirect way by proximal depressor muscles aided by leg rocking and by hydrostatic pressure of the hemolymph. Function of centipede legs is not restricted to locomotion. The most anterior pairs are commonly used to hold the prey during capture and feeding; prey size dictates how many pairs of appendages are involved in this behaviour (Verhoeff, 1938: *Scutigera coleoptrata*; Lewis, 1961, 1981a: *Strigamia maritima*; Manton, 1964: *Cormocephalus nitidus*; Elzinga, 1994: *Scolopendra viridis*).

Most centipedes spend their life in crevices in the soil, in the interstices between stones, amidst fallen leaves, or under bark. Under these circumstances, their body is often in touch with solid objects with both the ventral and the dorsal side at the same time. This approaches the conditions experienced by burrowing animals, although quite a few chilopods can be regarded as true burrowers as are, for example, most species of earthworms.

Closest to the shape and the locomotory mechanics of typical burrowing animals are a few large geophilomorphs like *Himantarium* and *Haplophilus*. Here, the body is nearly cylindrical, the pleurites are numerous and the flexibility and softness of the body is not much different from those of an earthworm, with which they have thus the opportunity to meet frequently in the soil. Indeed, earthworms are well documented as a prey item of these large himantariid geophilomorphs.

Manton (1965, 1977) provided an account of locomotion in *Haplophilus*. Here, most of the burrowing is accomplished by the segments of the anterior third of the trunk, i.e., those in front of the mid-body ‘transition’ (see Chapter 3). The legs of these segments are stouter than those of the remaining segments. Waves of muscular contraction are created just behind the head: a few segments are shortened and their diameter increases. This way, these segments form a strong *point d'appui* against the soil. This phase of muscular contraction moves as a backwards directed wave, enabling the segment in front of it to elongate, thus advancing in the crevice, until a new wave of shortened and thickened segments forms again just behind the head. These waves eventually vanish towards the mid-body transition and the posterior part of the body is simply dragged forward in a largely passive way. Most of the burrowing force is provided by the dorsal, lateral and sternal longitudinal muscles, with a contribution by deep oblique muscles. Antagonistic to all these muscles are the deep dorso-ventral muscles, whose contraction restores the

condition of segment elongation. This antagonistic activity is effective because the animal contains ample hemocoelic spaces filled with incompressible fluid.

Brought to the surface, burrowers are often helpless: they cannot move forward unless the anterior part of the body is put into a crevice. In the absence of other objects under which to crawl, the only thing under which a burrowing geophilomorph may try to go is the posterior part of its own body. As a consequence, the animal ends up making a coil of its body. This is easily observed with himantariids but also with *Strigamia* species, whose locomotory mechanics, however, have never been investigated.

These burrowing habits are far from being shared by all geophilomorphs. For example, several geophilids, e.g. *Pachymerium ferrugineum*, are not able to burrow, but are reasonably swift when moving on an open surface. The swiftest of all geophilomorphs are the meistocephalids, one trait among many others, anatomical and biological alike, that make them more similar to scolopendromorphs than to the remainder of the Geophilomorpha.

Species-specific differences in locomotory performances are also found among the scolopendromorphs. For example, the arboricolous *Edentistoma octosulcatum* is much less agile than the majority of its relatives (Lewis, 1982). However, as a rule scolopenders are quite effective, speedy runners.

Most of the experimental work on centipede locomotion has been performed on *Scolopendra* species.

At low speed, many legs are in contact with the ground at every time, but this number diminishes at higher speed. Thus, at high speed there are many raised legs on each side between two consecutive legs on the ground. During speedy running, only three out of 40 locomotory legs (those of the ultimate pair are not involved in propelling the animal) are actually propulsive at any time. During faster gait, all legs of one side occupy the same footprints.

During locomotion, the main body axis of the scolopender is not kept straight, but is continuously involved in posteriorly directed undulations. The legs located in the concavity of a bent trunk region all touch the ground at a single point (Anderson and Full, 2001) and are those active in propelling the animal forwards.

Manton (1977) defended the view that in the case of myriapods the lateral undulations do not contribute to increase speed as often happens in vertebrates (Gray, 1968); rather, muscular activity would be spent to reduce the loss of mechanical efficiency due to such undulations. However, subsequent studies on axial kinematics and muscle activity during locomotion of *S. heros* (Anderson et al., 1995) have shown that axial bending

generated by longitudinal muscles does actually contribute to the efficiency and speed of the run.

The maximum recorded speed is 260 mm/sec in a 38 mm *Cryptops anomalans*, 280 mm/sec in a 25 mm *Lithobius forficatus* and as much as 420 mm/sec in a 22 mm *Scutigera coleoptrata* (Manton, 1965).

Although terrestrial, some centipedes are able to swim and this ability may help explaining why they are able to colonize remote islands (Minelli, 1984). Lewis (1981b) reported snake-like swimming movement in *Scolopendra subspinipes*, during which most legs were held against the side of the body; only the head capsule and most of the tergites were above water level.

#### *Energetics of locomotion*

Very little is known on centipede locomotion from the point of view of energetics. Evidence on the enzymatic activity levels of lactate dehydrogenase (highest levels in the fast running *Scutigera* and in the massive *Scolopendra*), intermediate in *Lithobius* and very low in *Himantarium*) are in broad agreement with the different locomotory performances of different taxa (Dell'Agata et al., 1994).

Compared to animals of comparable size, scolopenders consume less oxygen per unit body mass per unit distance (Full, 1989).

#### *References*

- ANDERSON, B. D., R. J. FULL & M. GARCIA, 2000. A spring-mass model of centipede locomotion. – Integrative and Comparative Biology 40: 928.
- ANDERSON, B. D., J. W. SHULTZ & B. C. JAYNE, 1995. Axial kinematics and muscle activity during terrestrial locomotion of the centipede *Scolopendra heros*. – Journal of Experimental Biology 198: 1185-1195.
- APPLEGARTH, A. G., 1952. The anatomy of the cephalic region of a centipede *Pseudolithobius megaloporus* (Stuxberg) (Chilopoda). – Microentomology 17: 127-171.
- CAMATINI, M., 1970. The structure of striated muscle fibers in some Chilopoda. – Bulletin du Muséum national d'Histoire naturelle, Paris, (2) 41 (1969) supplément 2: 31-34.
- CAMATINI, M. & L. CERESA CASTELLANI, 1974. Atypical myofilament array of visceral muscle fibres of *Lithobius forficatus* L. testis. – Journal of Submicroscopic Cytology 6: 353-365.
- CAMATINI, M. & L. CERESA CASTELLANI, 1978. Myofilaments array of some visceral muscle fibers of *Lithobius forficatus* Linnaeus and *Pachybolus enologus* B. – Abhandlungen und Verhandlungen des naturwissenschaftlichen Vereins in Hamburg, Neue Folge 21/22: 243-255.
- CAMATINI, M., E. FRANCHI & I. DE CURTIS, 1979. The Z-line in Myriapoda muscles. – Pp. 157-167 in M. CAMATINI (ed.): Myriapod biology. Academic Press, London-New York.

- CAMATINI, M. & A. SAITA, 1967. L'ultrastruttura dei muscoli intersegmentali del corpo di *Scolopendra*. - Atti della Accademia nazionale dei Lincei, Rendiconti, Classe di Scienze fisiche, matematiche e naturali 42: 704-710.
- CAMATINI, M. & A. SAITA, 1968. Osservazioni sull'ultrastruttura di alcuni muscoli di *Scutiger coleoptrata*. - Atti della Accademia nazionale dei Lincei, Rendiconti, Classe di Scienze fisiche, matematiche e naturali 44: 443-447.
- CAMATINI, M. & A. SAITA, 1969. Studio al microscopio elettronico della muscolatura di *Lithobius forficatus* durante l'anamorfosi. - Atti della Accademia nazionale dei Lincei, Rendiconti, Classe di Scienze fisiche, matematiche e naturali 46: 73-80.
- DELL'AGATA, M., G. PANNUNZIO, M. ZAPPAROLI & S. FERRACIN, 1994. Data on electrophoretic mobility and enzymatic activity levels of lactate dehydrogenase from centipedes (Chilopoda). - Bollettino di Zoologia 61: 53-57.
- ELZINGA, R. J., 1994. The use of legs as grasping structures during prey capture and feeding by the centipede *Scolopendra viridis* Say (Chilopoda: Scolopendridae). - Journal of the Kansas Entomological Society 67: 369-372.
- FULL, R. J., 1989. Mechanics and energetics of terrestrial locomotion: bipeds to polypeds. - Pp. 175-182 in W. WIESER & E. GNAIGER (eds.) Energy transformations in cells and animals. - Thieme, Stuttgart.
- FÜLLER, H., 1963. Vergleichende Untersuchungen über das Skelettmuskelsystem der Chilopoden. Abhandlungen der Deutschen Akademie der Wissenschaften zu Berlin, Klasse für Chemie, Geologie und Biologie 3: 1-97.
- GRAY, J. 1968. Animal locomotion. - Weidenfeld & Nicholson, London.
- LEWIS, J. G. E., 1961. The life history and ecology of the littoral centipede *Strigamia (=Scolioplanes) maritima* (Leach). - Proceedings of the Zoological Society of London 137: 221-248.
- LEWIS, J. G. E., 1981a. The biology of centipedes. Cambridge Univeristy press, Cambridge.
- LEWIS, J. G. E., 1981b. Swimming in the centipede *Scolopendra subspinipes* Leach (Chilopoda, Scolopendromorpha). - Entomologist's Monthly Magazine 116: 121.
- LEWIS, J. G. E., 1982. Observations on the morphology and habits of the bizarre Borneo centipede *Arrhabdotus octosulcatus* (Töömsváry) (Chilopoda, Scolopendromorpha). - Entomologist's Monthly Magazine 117(1981): 245-247.
- MANTON, S. M., 1952. The evolution of arthropodan locomotory mechanisms. Part 2. General introduction to the locomotory mechanisms of the Arthropoda. - Journal of the Linnean Society of London, Zoology 42: 93-117.
- MANTON, S. M., 1964. Mandibular mechanisms and the evolution of arthropods. - Philosophical Transactions of the Royal Society of London, B Biological Sciences 247: 1-183.
- MANTON, S. M., 1965. The evolution of arthropodan locomotory mechanisms. Part 8. Functional requirements and body design in Chilopoda, together with a comparative account of their skeleto-muscular systems and an appendix on a comparison between burrowing forces of annelids and chilopods and its bearing upon the evolution of the arthropodan haemocoel. - Journal of the Linnean Society of London, Zoology 45: 251-484.
- MANTON, S. M., 1973. The evolution of arthropodan locomotory mechanisms. Part II. Habits, morphology and evolution of the Uniramia (Onychophora, Myriapoda, Hexapoda) and comparisons with Arachnida, together with a functional review of uniramian musculature. - Journal of the Linnean Society of London, Zoology 53: 257-375.
- MANTON, S. M., 1977. The Arthropoda. Habits, functional morphology and evolution. - Clarendon Press, Oxford.
- MEINERT, F. V. A., 1883. Caput Scolopendrae. The head of the Scolopendra and its muscular system. - Hagerup, Copenhagen.

- MINELLI, A., 1984. Dispersione e adattamento nella genesi dei popolamenti insulari: l'esempio dei miriapodi. – Atti dei Convegni Lincei 62: 45-65.
- RILLING, G., 1960. Zur Anatomie des braunen Steinläufers *Lithobius forficatus* L. (Chilopoda). Skelettmuskelsystem, peripheres Nervensystem und Sinnesorgane des Rumpfes. – Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 78: 39-128.
- RILLING, G., 1968. *Lithobius forficatus*. Grosses Zoologisches Praktikum 13b. – Fischer, Stuttgart.
- SAITA, A. & M. D. CANDIA CARNEVALI, 1978. Neuromuscular junction in myriapoda electron microscopic observation. – Abhandlungen und Verhandlungen des naturwissenschaftlichen Vereins in Hamburg, Neue Folge 21/22: 279-293.
- VERHOEFF, K. W., 1938. Über die europäische Spinnen-Assel (*Scutigera coleoptrata*). – Natur und Volk 68: 442-448.



## Chapter 6

# CHILOPODA – DIGESTIVE SYSTEM

Markus Koch, Carsten H. G. Müller, Gero Hilken & Jörg Rosenberg

The alimentary canal of centipedes is a muscular tube for unidirectional passage of food from the mouth, which is located in the depth of a preoral chamber, towards the anus at the posterior end of the body. Valve-like constrictions subdivide the gut into at least three main compartments: the foregut, the midgut, and the hindgut. The foregut and hindgut are usually lined by cuticle. In the foregut, the cuticle to different degrees contributes to formations involved in trituration and/or the prevention of back-flow of food. The main digestion and absorption of nutrients occur in the midgut, which produces chitinous peritrophic membranes enveloping the food. Pre-digestion in the foregut and/or preoral chamber by enzymes produced in the midgut and in various head glands is likely a common trait of centipedes. A predominantly suctorial feeding based on a more intense extra-intestinal liquefaction of prey within the prey's body is assumed for *Craterostigmus* and geophilomorph centipedes (e.g., Blower, 1957; Lewis, 1961; Manton, 1965). A survey of previous studies on the anatomy of the gut has been provided by Rosenberg (2009) and Rosenberg and Müller (2009), the most noteworthy of which are listed in Tables 6.1 and 6.2. The results of these studies are complemented here with yet unpublished observations, particularly on geophilomorphs.

### *Foregut*

The foregut of centipedes is formed by a single-layered epithelium lined with cuticle and surrounded by inner longitudinal and outer circular muscle layers allowing peristaltic movements (e.g., Plateau, 1878; Balbiani, 1890; Jangi, 1966). The lumen of the foregut varies considerably in the high-ranking subgroups (Fig. 6.1). In Scutigeromorpha, Lithobiomorpha, and *Craterostigmus* the foregut is relatively short and straight, hardly exceeding the second leg-bearing segment. It extends as a straight tube or via an S-shaped loop up to leg-bearing segments 10-16 in most Scolopendromorpha (Koch et al., 2009), and reaches beyond leg-bearing segment 20 in many Geophilomorpha (e.g., trunk segments 25-27 in *Geophilus proximus*; Minelli, 1993) except for Mecistocephalidae, in which the transition to the midgut occurs in more anterior trunk segments (e.g., leg-

bearing segments 7–8 in *Arrup* and *Tygarrup* species, 12 in *Dicellophilus carniolensis*, 17 in *Mecistocephalus tahitiensis*).

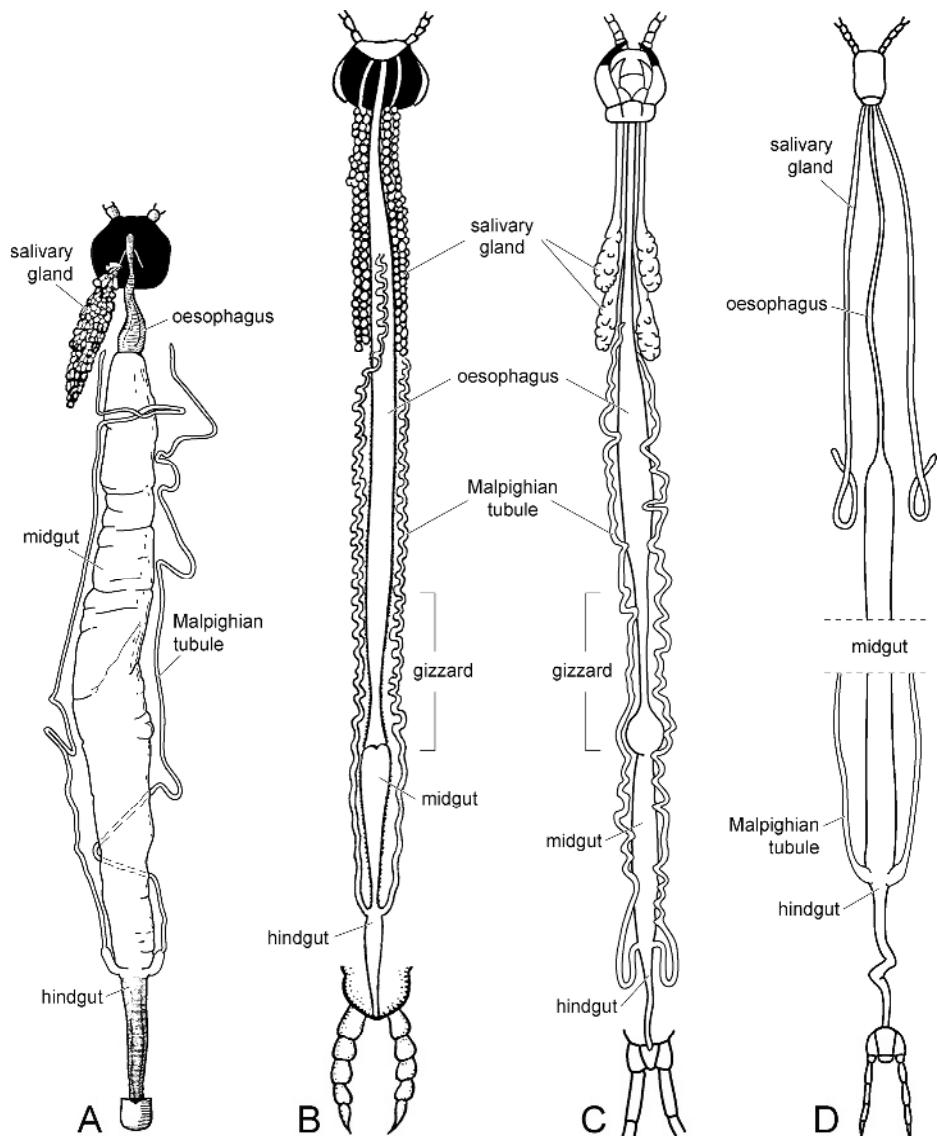


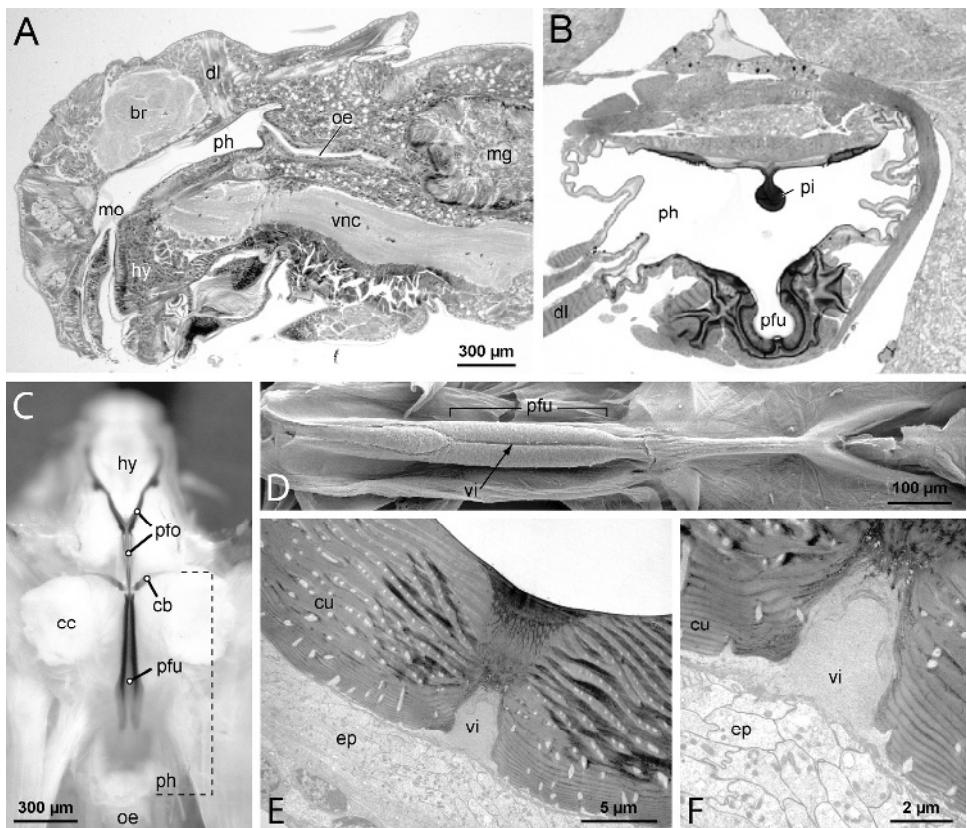
Fig. 6.1 Schematic illustration of the alimentary canal. A *Lithobius forficatus*. B *Scolopendra morsitans*. C *Cryptops anomalans*. D *Geophilus flavus*. A, after Rilling (1968); B, after Shukla (1964), C, after Balbiani (1890), D, after Plateau (1878); A, C-D redrawn by Minelli (1993) and modified by Rosenberg (2009).

Usually, an increase in trunk segment number among geophilomorphs seems to coincide with an elongation of the foregut, albeit non in direct proportion. Its diameter generally is extremely narrowed in geophilomorphs as well as in *Craterostigmus*. The thin tube, which in some species is strongly convoluted in its posterior part (e.g., *Eucratonyx meinerti*; Fig. 6.5B), is hardly thicker than the Malpighian tubules extending anteriorly all along the length of the foregut.

Based on the attachment of cephalic dilator muscles to the anterior part of the foregut, an anterior pharynx is usually distinguished from a subsequent oesophagus, which lacks dilator muscles. The pharyngeal cuticle is thickened or sclerotized at the insertion of the dilator muscles. The floor of the pharynx in particular is frequently equipped with a sclerotized midventral groove or rod, to which tentorial dilator muscles attach (Fig. 6.2B,C). In scutigeromorphs, the midventral groove is continuous with a peculiar hypopharyngeal fork (Fig. 6.2C) (see chapter 1, *Peristomatic structures*). In *Scutigera coleoptrata*, and presumably in other species, the sclerotized groove forms a component of a more elaborate pharyngeal armature, the so-called pharynx apparatus, involved in manipulating swallowed food.

The oesophagus partly acts as a crop and its wall is strongly folded in at least its posterior part. Posteriorly, the foregut ends with a cardiac valve, equipped with a sphincter that entirely or partly invaginates into the midgut lumen. In the Scolopendromorpha, an elongate gizzard (proventricle) variably equipped with cuticular spines and spinous lobes intervenes between the crop and cardiac valve. Posteriorly directed microspines may also be present in the pharynx and oesophagus (Elzinga, 1998). In *Lithobius forficatus*, cuticular formations previously described as spines in the posterior part of the oesophagus (e.g., Rilling, 1968) proved to be reminiscent of trichoid sensilla (Fig. 6.4A) (Koch et al., 2009). The foregut in the Scutigeromorpha and Geophilomorpha seems to be consistently devoid of trichomes.

Minute pores of apparently epidermal glands are scattered around the oesophagus/crop of *Lithobius forficatus* (Fig. 6.4A) and scolopendromorphs and may be more widespread. Presence of epidermal glands within the foregut epithelium was evidenced by Hilken & Rosenberg (2009) for *Scutigera coleoptrata*. Clusters of small compound glands opening into the lumen of the oesophagus were reported by Kaufman (1962) for *Scolopendra cingulata*. Two conical outgrowths (caeca) of the oesophagus are exceptionally present in *Ethmostigmus spinosus* (Sundara Rajulu, 1970a). Although the function of these caeca remains uncertain, secretory activity seems to be likely. Further cellular characteristics of the foregut's epithelium were summarized by Minelli (1993) and Rosenberg (2009).



**Fig. 6.2** *Scutigera coleoptrata*, pharynx apparatus. A Paramedian sagittal section (LM) through head and anterior trunk segments, showing the course of the foregut. B Transverse section through pharynx at the level of the pistil (LM). C Dorsal view on dissected floor of pharynx (LM), showing pharyngeal furrow and interconnected sclerites. D Ventral view on pharyngeal furrow (SEM), after maceration. E Transverse section through pharyngeal furrow (TEM), showing the thin median connection of its two halves along a ventral incision and their cuticle pierced by numerous pore canals. F Detail of E (TEM), showing the ventral incision in higher magnification. A original J. Rosenberg; B from Rosenberg (2009); C: original M. Koch; D-F: from Hilken & Rosenberg (2009).

br brain; cb circular bar; cc circumoesophageal commissure; cu cuticle; dl dilator muscle; ep epithelium; hy hypopharynx; mg midgut; mo mouth opening; oe oesophagus; pfo proximal fork; pfu pharyngeal furrow; ph pharynx; pi pistil; vi ventral incision; vnc ventral nerve cord

#### Pharyngeal armatures

In the Scutigeromorpha, the pharynx distinctively widens to a chamber to which remarkably strong dilator muscles attach (Fig. 6.2A,B). In addition to tentorial dilators

inserting on the midventral groove, cranial dilator muscles attach anteriorly on paired sclerotized bars circumscribing the mouth opening (Fig. 6.2C), and posteriorly on paired plate-like cuticular thickenings of the dorsal pharyngeal wall. In *Scutigera coleoptrata*, the roof of the pharynx additionally forms a middorsal sclerotized ridge that anteriorly tapers off into a stalked knob called a pistil (Fig. 6.2B) (Seifert, 1967; Hilken and Rosenberg, 2009). Laterally, the middorsal ridge is flanked by paired longitudinal bars to which no muscles seem to attach. The composition and musculature of this pharyngeal armature indicate that the pistil can slide and also be locked in the midventral groove, since Haase (1884), without recognizing its origin from the pharyngeal roof, identified a delicate, arrow-shaped rod fixed in between the two halves of the groove. The function of the pharynx apparatus still remains unclear; it may represent a sorting and grinding device that prevents larger food particles to enter the oesophagus. Ultrastructural details of the pharynx apparatus (Fig. 6.2D-F) seem to support this interpretation (Hilken and Rosenberg, 2009). The pistil is likely a common trait of the Scutigeromorpha, but its presence in species other than *Scutigera coleoptrata* still remains to be verified.

#### *Gizzard*

In the Scolopendromorpha, the crop passes over into a bipartite gizzard (Edgecombe and Koch, 2009; Koch et al., 2009, 2010). The anterior elongate part of the gizzard is straight or sometimes looped and shows a regular arrangement of folds (plicae) that strongly contrasts with the irregular folding of the crop. The short posterior part of the gizzard in front of the cardiac valve is characterized by outgrowths of the plicae (elongate projections or lobes) that almost entirely fill the gizzard's lumen. Based on the distinctive armature of both anterior and posterior parts, two types of gizzards are distinguishable (Fig. 6.3).

In the Scolopendridae, the plicae of the anterior part of the gizzard are armed with spiniferous scales and/or posteriorly directed spines (Figs. 6.3B, 6.4C,D). The inconspicuous posterior part of the spine-type of gizzard houses a circlet of flap-like, conical or digitiform lobes armed with spiniferous scales, short spikes, or elongate spines. The spine-type of gizzard particularly varies in the arrangement of the posteriorly directed spines, being either numerous and discrete (e.g., Asanadini), or variably grouped on plates (most Scolopendrini), or absent with spiniferous scales as the only cuticular armature (e.g., Otostigmini).

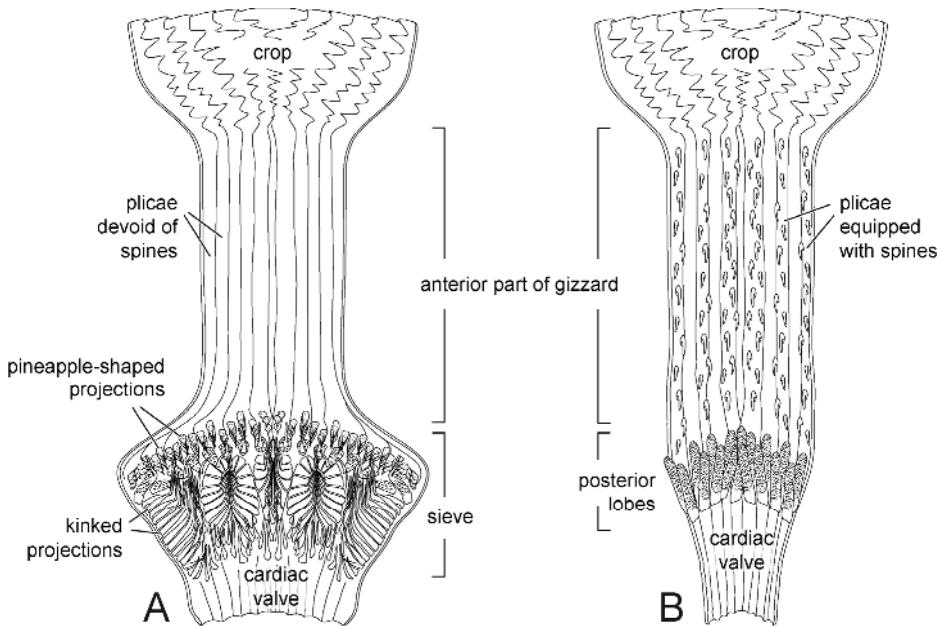
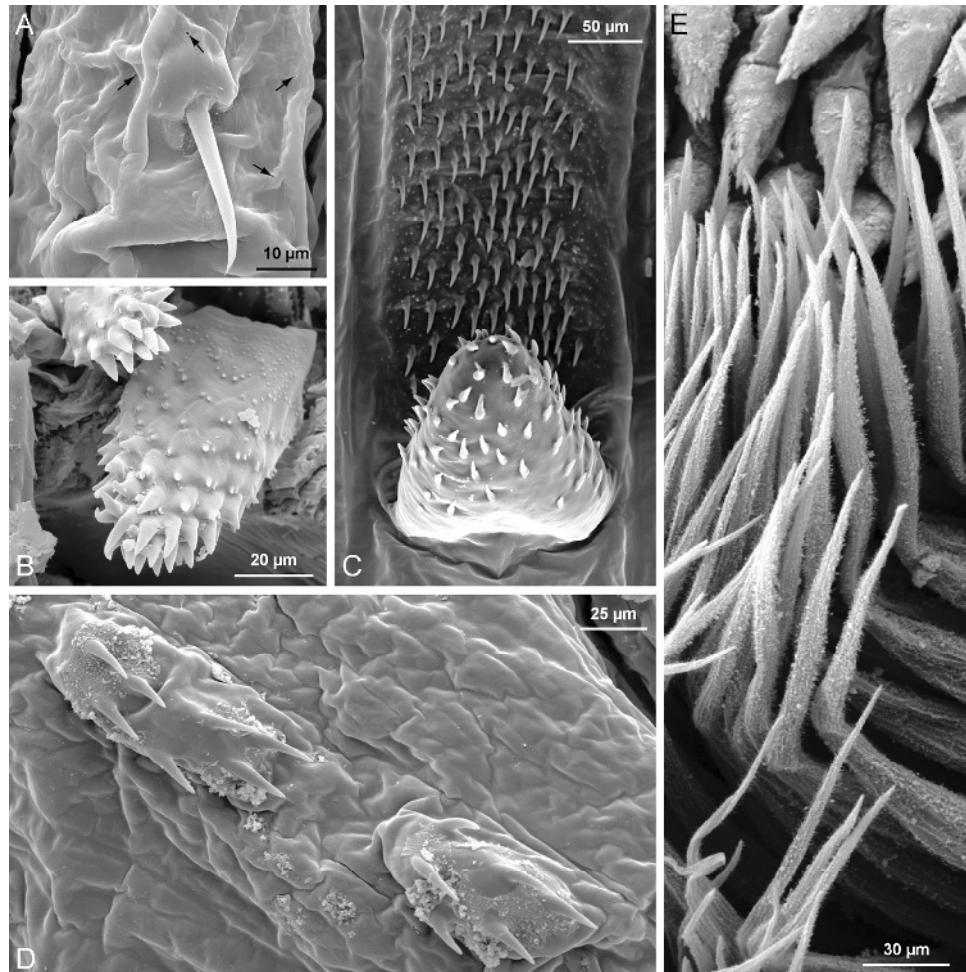


Fig. 6.3 Schematic illustration of the two basic types of gizzards in Scolopendromorpha, fanned out in one plane (anterior is top). A Sieve-type of gizzard, as composed in Scolopocryptopidae. B Spine-type of gizzard in Scolopendridae. From Koch et al. (2009).

Blind scolopendromorphs (Cryptopidae, Plutoniumidae and Scolopocryptopidae) are equipped with a sieve-type of gizzard (Fig. 6.3A). Its inconspicuous but likewise elongate anterior part is devoid of spines or any other cuticular trichomes and therefore was not recognized as a component of the gizzard in early anatomical studies (Plateau, 1878; Willem, 1889; Balbiani, 1890). Its plicae, however, are as regularly arranged as in the Scolopendridae and similarly contrast against the irregular folding of the crop. The more obvious, usually bulbous posterior part is composed of distinctive types of projections that are variably armed with cuticular trichomes. The projections are densely arranged in several transverse rows as to form a sieve (Figs. 6.3A, 6.4E). The sieve may be composed of uniform projections (e.g., *Cryptops hortensis*, Plutoniumidae; Fig. 6.5C) or of differently shaped projections along an antero-posterior zonation (e.g., Scolopocryptopinae, *Cryptops anomalans*; Fig. 6.4B,E), among which the anteriormost closely resemble the posterior lobes of the spine-type of gizzard (Fig. 6.4C). Whether these projections really serve as a sieve or as a masticatory device still remains unclear. Verhoeff (1902-1925) assumed that swallowed food is already pre-digested by enzymes produced in the

midgut before entering the sieve, and transferred into the foregut. Present evidence for glandular cells among the foregut's epithelium favours the view that digestive enzymes may already be produced in the oesophagus, crop, or anterior part of the gizzard.



**Fig. 6.4** Cuticular armatures of the foregut (SEM). A *Lithobius forficatus*, sensilla trichodea on folds of the oesophagus, surrounded by pore openings (arrows) of presumably epidermal glands. B-E Components of the gizzard in Scolopendromorpha. B *Cryptops anomalans*, pineapple-shaped projections of the "sieve". C *Scolopendropsis bahiensis*, spine-bearing plica and posterior lobe. D *Scolopendra laeta*, spiniferous plates on plica of anterior part of gizzard (anterior is left). E *Newportia monticola*, kinked sieve-projections in front of pineapple-shaped projections (anterior is top). Originals: M. Koch and G. Edgecombe.

A remarkable exception of a gizzard lacking any cuticular trichomes and posterior lobes/projections is found in *Edentistoma octosulcatum* (Scolopendridae: Arrhabdotini). A loss of its cuticular armature together with a shortening of the foregut and modifications of both mouthparts and preoral chamber (Edgecombe and Koch, 2008) are assumed to correlate with modified, presumably vegetarian feeding habits in this species (Lewis, 1981a).

Table 6.1 Overview on the components of the foregut and its main anatomical studies.

Taxon	Pharynx	Pharynx apparatus	Oesophagus / crop	Gizzard	Main studies
<b>Scutigeromorpha</b>					1-7
Scutigeridae	+	+	+/+	-	
Scutigerinidae	?	?	?	?	
Psellioididae	?	?	?	?	
<b>Lithobiomorpha</b>					1,2,5,8,9
Lithobiidae	+	-	+/+	-	
Henicopidae	?	?	?	?	
<b>Craterostigmomorpha</b>					5
<i>Craterostigmus</i>	+	-	+/?	-	
<b>Scolopendromorpha</b>					1,2,5,10-15
Cryptopidae	+	-	+/+	+	
Scolopocryptopidae	+	-	+/+	+	
Scolopendridae	+	-	+/+	+	
<b>Geophilomorpha</b>					1,2,5,16,17
Mecistocephalidae	+	-	+/?	-	
Geophilidae	+	-	+/?	-	
Himantariidae	+	-	+/?	-	
Oryidae	+	-	+/?	-	
Other Adesmata	+	-	+/?	-	

Refs.: 1. Plateau 1878; 2. Verhoeff 1902-25; 3. Takakuwa 1955; 4. Kaufman 1961a; 5. Manton 1965; 6. Seifert 1967; 7. Hilken and Rosenberg 2009; 8. Kaufman 1961b; 9. Rilling 1968; 10. Balbiani 1890; 11. Willem 1889; 12. Kaufman 1962; 13. Shukla 1964; 14. Jangi 1966; 15. Koch et al. 2009; 16. Bücherl 1942; 17. Kaufman 1960.

### Midgut

The midgut of centipedes is overall quite uniform among the high-ranking subgroups, the most obvious difference being its variable size in relation to foregut and hindgut length. Apart from the slight constrictions demarcating the midgut from the fore- and hindgut, the former is characterized by its much larger diameter, its distinctive epithelium and musculature, as well as its "mottled" basal surface.

The larger diameter of the midgut is partly due to the remarkable thickness of its epithelium (Figs. 6.2A, 6.5). Its columnar cells are regularly arranged in clusters (villi); the height of these columnar cells increases towards the centre of each cluster (Kaufman, 1960). Alternation between projecting villi and the interposed furrows (crypts)

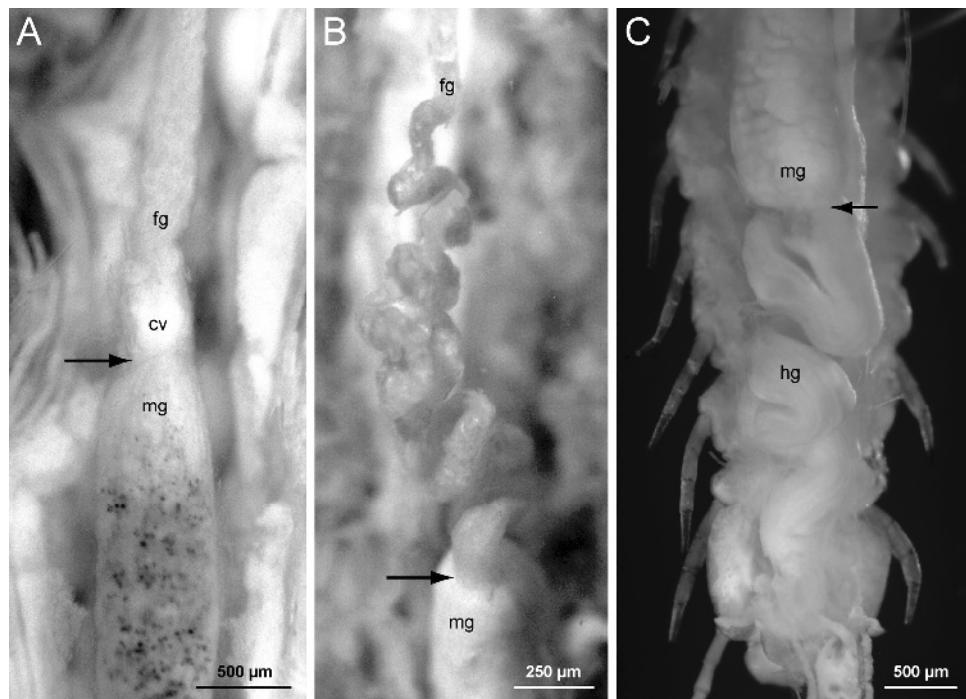


Fig. 6.5 Light micrographs of the foregut-midgut and midgut-hindgut transition in geophilomorphs, dorsal view. A *Dicellophilus carniolensis* (Mecistocephalidae). B *Eucratonyx meinerti* (Gonibregmatidae). C *Himantarium gabrielis* (Himantariidae). Arrows point to the transition zones. Originals: M. Koch and G. Edgecombe.

cv cardiac valve; fg foregut; hg hindgut; mg midgut

contributes to an uneven, fissured relief of the luminal surface. On their basal side, cell clusters determine a mottled appearance of the midgut's basal surface in the form of dark, hexagonal spots shining through the gut in a checkerboard manner (Fig. 6.5A). These spots were identified by Kaufman (1960) as basal aggregations of epithelial nuclei, probably of regenerative cells, within the centre of each cell cluster. Histologically, two cell types can generally be distinguished within the clusters (e.g., Kaufmann, 1960, 1961a,b, 1962; Jangi, 1966; Rilling, 1968). Most cells are cylindrical, with a broadened, striated apex and narrowed base (Fig. 6.6C). The apical striation indicates presence of microvilli (confirmed by electron microscopy for *Lithobius forficatus*; Vandenbulcke et al., 1998). The cylindrical cells apparently fulfil three main functions: digestion (secretion of enzymes, absorption of nutrients), detoxification by accumulation and excretion of indigestible inclusions, and formation of peritrophic membranes enveloping the food mass in the midgut lumen. Digestive enzymes have been analyzed in *Lithobius forficatus* and *Scolopendra* species; they comprise various carbohydrases (including chitinase and cellulase) as well as a trypsin-like protease (surveyed by Lewis 1981b; Minelli, 1993; Rosenberg, 2009). Among inclusions of the midgut epithelium in *Lithobius*, the accumulation and detoxification of heavy metals is most remarkable (Hopkin and Martin, 1983, 1984; Hopkin et al., 1985; Descamps et al., 1996; Vandenbulcke et al., 1998). A chitinous peritrophic envelope has been observed in representatives of each of the high-ranking centipede subgroups except Craterostigmomorpha. In *Geophilus proximus*, the envelope proved to consist of two basic layers with different histological staining properties (Kaufman, 1960). Ultrastructurally, the envelope is characterized in *Lithobius forficatus* as well as scolopendromorph centipedes as a network of microfibrils with minute, rectangular holes (see Peters, 1992, for the most recent survey).

Interspersed among the cylindrical cells are so-called beaker- or goblet-shaped cells (Kaufman, 1960, 1961a, 1962). Apart from their glandular nature, the main function of these cells as well as their scattered, variable distribution along the midgut (partly with accumulations in either its anterior or posterior part) remain unclear.

In *Cryptops anomalans* at least, the epithelium of the midgut degenerates seasonally in winter time (Balbiani, 1890). Regeneration of cylindrical cells occurs from cells constantly proliferating from the crypts between the epithelial cell clusters, whereas the goblet-shaped cells mainly proliferate from the cluster's centre.

While the cells of the fore- and the hindgut are connected by pleated septate junctions (scalariform junctions are also observable in the hindgut of *Scolopendra*), the cells of the midgut exhibit smooth septate junctions (Dallai et al., 1990).

The muscle layers of the midgut are continuous with those of the foregut and hindgut, but their arrangement inverts along the transitions: inner longitudinal muscle strands of the foregut pass through its outer circular layer and extend over the cardiac valve to the midgut to form a continuous outer longitudinal layer above an inner circular layer (Fig. 6.6A).

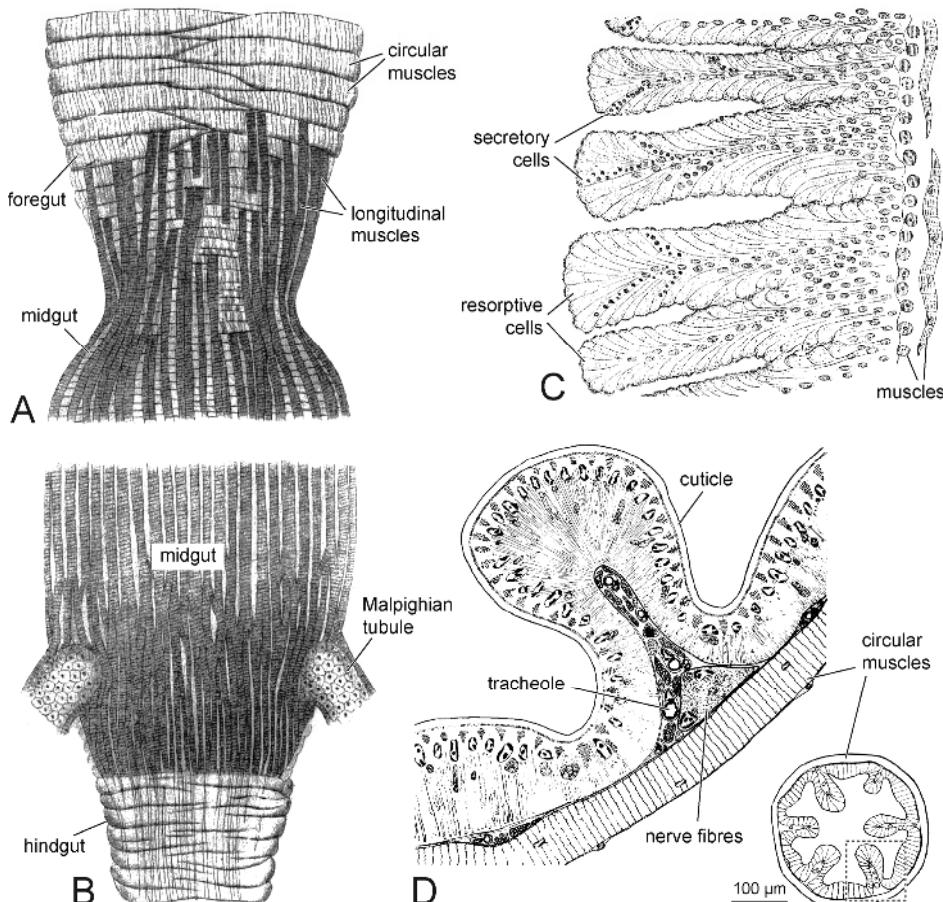


Fig. 6.6 Schematic illustrations of the gut musculature and epithelium. A-B *Cryptops anomalans*, arrangement of the gut muscles along the (A) foregut-midgut transition, and (B) midgut-hindgut transition. C *Scolopendra cingulata*, longitudinal section through the midgut epithelium. D *Lithobius forficatus*, detail of the hindgut wall in transverse section as indicated in the overview, based on electron microscopic studies. A-B from Balbiani (1890); C after Kaufman (1962); D after Wenning (1978) modified by Rosenberg (2009).

In some scolopendromorphs and geophilomorphs, a similar inversion happens at the transition to the hindgut (e.g. Balbiani, 1890; Bücherl, 1942; Shukla, 1964): the outer longitudinal muscle strands of the midgut pass through an outer circular layer of the hindgut to form an inner longitudinal layer (Fig. 6.6B). Additional muscles suspending the anterior part of the midgut to the dorsal body wall were described for *Lithobius forficatus* (Rilling, 1968).

In *Strigamia maritima*, large groups of epithelial cells are budded off from the posterior half of the midgut and form a large proportion of the faeces (Lewis, 1981b).

**Table 6.2** Overview on main previous studies on the anatomy of midgut and hindgut. DE = digestive enzymes, HG = hindgut, LM = light microscopy (histology), MG = midgut, PE = peritrophic envelope, TEM = transmission electron microscopy.

	MG (LM)	MG (TEM)	PE	DE	MT [no.]	HG (LM)	HG (TEM)
<b>Scutigeromorpha</b>							
Scutigeridae	1	2	1,3	?	[4] 4	1	2
<b>Lithobiomorpha</b>							
Lithobiidae	5,6	2,7	8-11	8,12	[2] 13,14	5,6	2,15,16
<b>Craterostigmomorpha</b>							
<i>Craterostigmus</i>	17	-	?	?	[3] 17	17	-
<b>Scolopendromorpha</b>							
Cryptopidae	10	-	10	?	[2] 14	10	-
Scolopocryptopidae	18,19	-	?	?	?	-	-
Scolopendridae	20,21	2	3,22,23	24,25	[2] 14,25	20,21	2
<b>Geophilomorpha</b>							
Mecistocephalidae	-	-	?	?	?	-	-
Geophilidae	27	2	27	?	[2] 14,28	20,21	2
Himantariidae	-	2	8	?	[2] 8	-	2
Oryidae	29	-	?	?	[2] 29	29	-
Other Adesmata	29	-	?	?	[2] 29	29	-

Refs.: 1 Kaufman 1961a; 2. Dallai et al. 1990 [cell junctions only]; 3. Waterhouse 1953; 4. Prunesco and Prunesco 1996; 5. Kaufman 1961b; 6. Rilling 1968; 7. Vandebulcke et al. 1998; 8. Plateau 1878; 9. Gibson-Carmichael 1885; 10. Balbiani 1890; 11. Peters 1968; 12. Nielsen 1962; 13. Füller 1966; 14. Bertheau 1971; 15. Wenning 1978; 16. Wenning 1979; 17. Prunesco and Prunesco 2006; 18. Willem 1889; 19. Koch et al. 2009; 20. Kaufman 1962; 21. Jangi 1966; 22. Peters 1968; 23. Sundara Rajulu 1971; 24. Sundara Rajulu 1967; 25. Sundara Rajulu 1970b; 26. Wang and Wu 1947; 27. Kaufman 1960; 28. Palm 1954; 29. Bücherl 1942.

### *Hindgut*

The short hindgut of scutigeromorphs and lithobiomorphs is usually straight, whereas in scolopendromorph and geophilomorph centipedes it is often looped or even strongly convoluted (e.g., *Himantarium gabrielis*; Fig. 6.5C). Generally, no compartmentalisation is obvious along the hindgut. The transition from midgut to hindgut is indicated by the opening of the Malpighian tubules into the gut, the number of which varies from 2 to 4 (see Table 6.2, and chapter 9). There is, however, still uncertainty as to whether the actual junction lies in front or behind their openings because anatomical markers to identify the midgut-hindgut transition remain ambiguous (e.g., Rilling, 1968). A pyloric valve seems to be usually located behind the opening of the Malpighian tubules, in *Scolopendra cingulata* apparently in front of them (Kaufman, 1962). No central pyloric chamber is formed by the anteriormost part of the hindgut. Instead, each Malpighian tubule basally widens into an ampulla, which may represent functional equivalents to a single, central pyloric chamber. The ampullae of the Malpighian tubules attach to the gut within the musculature of the midgut, while the circular layers of the hindgut as well as its cuticular lining start immediately behind their insertion (Fig. 6.6B). This may be the reason why the Malpighian tubules in *Scolopendra* species were variably described as opening into the midgut (e.g., *S. subspinipes*; Wang and Wu, 1947) versus into the hindgut (*S. morsitans*; Shukla, 1964). Openings of the Malpighian tubules into the midgut have also been documented for *Craterostigmus tasmanianus* (Prunesco and Prunesco, 2006, their Fig. 6.3). Anatomical difficulties in determining the midgut-hindgut junction precisely were also reported for geophilomorph centipedes (Bücherl, 1942). Embryological observations (Heymons, 1901, for *Scolopendra* spp.; Knoll, 1974, for *Scutigera coleoptrata*) favour an ectodermal origin of Malpighian tubules from the anlage of the proctodeum. Heymons (1901), however, also noted transient pouches in the posterior entoderm that closely resemble anlagen of Malpighian tubules.

The cuticular lining of the hindgut epithelium is relatively thin and generally undifferentiated; in *Scolopendra* species, however, it may be uneven (*S. cingulata*; Kaufman, 1962) or equipped with simple microspines (*S. viridis*; Elzinga, 1998). The epithelial cells of the hindgut histologically resemble those of the foregut epithelium, but in *Lithobius forficatus* they ultrastructurally proved to differ in showing typical characteristics of a transporting epithelium (Fig. 6.6D) (Wenning, 1978, 1979). The variable degree of longitudinal infolding of the hindgut epithelium (6 folds in *L. forficatus* and *Scolopendra* spp.; 10-12 folds in *Scutigera coleoptrata* and *Cryptops anomalans*; 3 folds in *Geophilus proximus*) was assumed to correlate with different requirements for water reabsorption and

accordingly to depend on the humidity of the habitat (Kaufman, 1961b). In *L. forficatus*, however, no ultrastructural indication for intense water reabsorption as typically (e.g., in insects) shown by parts of the hindgut differentiated as a rectum or rectal organs was found (Wenning, 1978, 1979).

The musculature of the hindgut consists of strong circular layers and weak longitudinal strands (Fig. 6.6B,D). Towards the anus, the longitudinal strands may gradually strengthen; in *Cryptops*, they posteriorly form a similarly thick layer as the circular muscles (Verhoeff, 1902-1925). Dilators of the hindgut are restricted to the anal segment and apparently promote defecation (Jangi, 1966). The anus is surrounded by a variable number of sclerites and is usually flanked by paired anal valves.

### References

- BALBIANI, E.-G., 1890. Étude anatomique et histologique sur le tube digestif des *Cryptops*. – Archives de Zoologie expérimentale et générale (2) 8: 1-82.
- BERTHEAU, P., 1971. Histologie comparée des tubes de Malpighi de quelques Chilopodes (Myriapodes). – Comptes rendus hebdomadaires des Séances de l'Académie des Sciences, Paris, D 272: 2913-2915.
- BLOWER, J. G., 1957. Feeding habits of a marine centipede. Nature 180: 560.
- BÜCHERL, W., 1942. Estudos morfo-anatômicos sobre Geofilomorpos Neotrópicos. – Memórias do Instituto Butantan 15: 159-223.
- DALLAI, R., E. BIGLIARDI & N. J. LANE, 1990. Intercellular junctions in myriapods. – Tissue & Cell 22: 359-369.
- DESCAMPS, M., M. C. FABRE, C. GRELLE & S. GERARD, 1996. Cadmium and lead kinetics during experimental contamination and decontamination of the centipede *Lithobius forficatus* L. – Archives of Environmental Contamination and Toxicology 31: 350-353.
- EDGEcombe, G. D & M. KOCH, 2008. Phylogeny of scolopendromorph centipedes (Chilopoda): morphological analysis featuring characters from the peristomatic area. – Cladistics 24: 872-901.
- EDGEcombe, G. D. & M. KOCH, 2009. The contribution of preoral chamber and foregut morphology to the phylogenetics of Scolopendromorpha (Chilopoda). – Soil Organisms 81: 295-318.
- ELZINGA, R. J., 1998. Microspines in the alimentary canal of Arthropoda, Onychophora, Annelida. – International Journal of Insect Morphology and Embryology 16: 230-238.
- FÜLLER, H., 1966. Elektronenmikroskopische Untersuchungen der Malpighischen Gefäße von *Lithobius forficatus* (L.). – Zeitschrift für wissenschaftliche Zoologie 173: 191-217.
- GIBSON-CARMICHAEL, T. D., 1885. Notes on the anatomy of the Myriapoda. – Proceedings of the Royal Physical Society of Edinburgh 8: 377-381.
- HAASE, E., 1884. Schlundgerüst und Maxillarorgan von *Scutigera*. – Zoologische Beiträge I: 97-108.
- HEYMONS, R., 1901. Die Entwicklungsgeschichte der Scolopender. – Zoologica [Stuttgart] 13: 1-244.
- HILKEN, G. & J. ROSENBERG, 2009. First ultrastructural investigation of the pharynx apparatus of *Scutigera coleoptrata* (Chilopoda, Notostigmophora). – Soil Organisms 81: 327-335.
- HOPKIN, S. P. & M. H. MARTIN, 1983. Heavy metals in the centipede *Lithobius variegatus* (Chilopoda). – Environmental Pollution Series B 6: 309-318.

- HOPKIN, S. P. & M. H. MARTIN, 1984. The assimilation of zinc, cadmium, lead and copper by the centipede *Lithobius variegatus* (Chilopoda). – Journal of Applied Ecology 21: 535-546.
- HOPKIN, S. P., K. WATSON, M. H. MARTIN & M. L. MOULD, 1985. The assimilation of heavy metals by *Lithobius variegatus* and *Glomeris marginata* (Chilopoda, Diplopoda). – Bijdragen tot de Dierkunde 55: 88-94.
- JANGI, B. S., 1966. *Scolopendra* (The Indian Centipede). – The Zoological Society of India, Calcutta.
- KAUFMAN, Z. S., 1960. The structure of the digestive tract in *Geophilus proximus* Koch (Chilopoda). – Doklady Akademii Nauk SSSR 135: 992-995.
- KAUFMAN, Z. S., 1961a. Digestive tract structure in *Scutigera coleoptrata* L. – Doklady Akademii Nauk SSSR 139: 740-742.
- KAUFMAN, Z. S., 1961b. Postembryonic development and structure of the alimentary tract in *Lithobius forficatus* L. (Chilopoda) [in Russian, English summary]. – Entomologiceskoe Obozrenie 40: 109-119.
- KAUFMAN, Z. S., 1962. The structure of digestive tract in *Scolopendra cingulata* Latr. (Chilopoda) [in Russian, English summary]. – Zoologicheskii Zhurnal 41: 859-869.
- KNOLL H. J., 1974. Untersuchungen zur Entwicklungsgeschichte von *Scutigera coleoptrata* L. (Chilopoda). – Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 92: 47-132.
- KOCH, M., G. D. EDGEcombe & R. M. SHELLEY, 2010. Anatomy of *Ectonocryptoides* (Scolopocryptopidae: Ectonocryptopinae) and the phylogeny of blind Scolopendromorpha (Chilopoda). – International Journal of Myriapodology 3: 51-81.
- KOCH, M., S. PARSCHEK & G. D. EDGEcombe, 2009. Phylogenetic implications of gizzard morphology in scolopendromorph centipedes (Chilopoda). – Zoologica Scripta 38: 269-288.
- LEWIS, J. G. E., 1961. The life history and ecology of the littoral centipede *Strigamia* (=*Scolioplanes*) *maritima* (Leach). – Proceedings of the Zoological Society of London 137: 221-247.
- LEWIS, J. G. E., 1981a. Observations of the morphology and habits of the bizarre Borneo centipede *Arrhabdotus octosulcatus* (Tömösváry) (Chilopoda, Scolopendromorpha). – Entomologists Monthly Magazine 117: 245-248.
- LEWIS, J. G. E., 1981b. The biology of centipedes. – Cambridge University Press, Cambridge, London, New York.
- MANTON, S. M., 1965. The evolution of arthropod locomotory mechanisms. Part 8. Functional requirements and body design in Chilopoda, together with a comparative account of their skeleto-muscular systems and an appendix on a comparison between burrowing forces of annelids and chilopods and its bearing upon the evolution of the arthropodan haemocoel. – Journal of the Linnean Society (Zoology) 46: 251-483.
- MINELLI, A., 1993. Chilopoda. – Pp. 57-114 in F. W. HARRISON AND M. E. RICE (eds.) Microscopic Anatomy of Invertebrates 12: Onychophora, Chilopoda, and lesser Protostomata. – Wiley-Liss, New York.
- NIELSEN, O. G., 1962. Carbohydrases in soil and litter invertebrates. – Oikos 13: 200-215.
- PALM, N.-B., 1954. The elimination of injected vital dyes from the blood in Myriapods. – Arkiv för Zoologi 6: 219-246.
- PETERS, W., 1968. Vorkommen, Zusammensetzung und Feinstruktur peritrophicischer Membranen im Tierreich. – Zeitschrift für Morphologie der Tiere 62: 9-57.
- PETERS, W., 1992. Peritrophic membranes. – Springer, Berlin-Heidelberg-New York.
- PLATEAU, F., 1878. Recherches sur les phénomènes de la digestion et sur la structure de l'appareil digestif chez les Myriapodes de Belgique. – Mémoires de l'Académie royale des Sciences, des Lettres et des Beaux-Arts de Belgique 42: 1-94.

- PRUNESCO, C.-C. & P. PRUNESCO, 1996. Supernumerary malpighian tubules in chilopods. – Mémoires du Muséum national d'Histoire naturelle, Paris 169: 437-440.
- PRUNESCO, C.-C. & P. PRUNESCO, 2006. Rudimentary supernumerary Malpighian tubules in the order Craterostigmomorpha Pocock 1902. – Norwegian Journal of Entomology 53: 113-118.
- RILLING, G., 1968. *Lithobius forficatus*. Grosses Zoologisches Praktikum 13b. – Fischer, Stuttgart.
- ROSENBERG, J., 2009. Die Hundertfüßer (Chilopoda). Neue Brehm-Bücherei 285. – Westarp Wissenschaften, Hohenwarsleben.
- ROSENBERG, J. & C. H. G. MÜLLER, 2009. Morphology in Chilopoda – a survey. – Soil Organisms 81: CD-Rom-Appendix.
- SEIFERT, G., 1967. Der Pharynxapparat von *Scutigera coleoptrata* L. – Zeitschrift für Morphologie und Ökologie der Tiere 58: 347-354.
- SHUKLA, G. S., 1964. Studies on *Scolopendra morsitans* Linn., Part II: Digestive and excretory systems. – Entomologische Berichten 24: 55-60.
- SUNDARA RAJULU, G., 1967. The nature of the proteolytic enzyme systems in *Scolopendra heros*, a chilopod. – Zoologische Jahrbücher, Abteilung für allgemeine Zoologie und Physiologie der Tiere 73: 276-280.
- SUNDARA RAJULU, G., 1970a. Presence of caecal outgrowths in the alimentary canal of a centipede *Ethmostigmus spinosus* Newport (Chilopoda, Myriapoda). – Current Science 39: 564-565.
- SUNDARA RAJULU, G., 1970b. Studies on the nature of carbohydrases in a centipede *Scolopendra heros*, together with observations on hydrogen ion concentration of the alimentary tract. – Journal of Animal Morphology and Physiology 17: 56-64.
- TAKAKUWA, Y., 1955. Morphology and classification of the *Scutigera*, with a memory of the late Dr Asajiro Oka [in Japanese, title translated]. – Gakufū-Shoin, Tokyo.
- VANDENBULCKE, F., C. M. GRELLÉ, C. FABRE, & M. DESCAMPS, 1998. Implication of the midgut of the centipede *Lithobius forficatus* in the heavy metal detoxification process. – Ecotoxicology and Environmental Safety 41: 258-268.
- VERHOEFF, K. W., 1902-1925. Chilopoda. – In H. G. BRONN (ed.) Klassen und Ordnungen des Tierreiches, 5, Abt. 2, Buch 1, pp. 1-725. – Akademische Verlagsgesellschaft, Leipzig.
- WANG, T. H. & H. W. WU, 1947. On the structure of the Malpighian tubules of the centipedes and their excretion of uric acid. – Sinensis, Shanghai 18: 1-11.
- WATERHOUSE, D. F., 1953. The occurrence and significance of the peritrophic membrane with special reference to adult Lepidoptera and Diptera. – Australian Journal of Zoology 1: 299-318.
- WENNING, A., 1978. Struktur und Funktion des Exkretionssystems von *Lithobius forficatus* L. (Chilopoda, Myriapoda). – Zoologische Jahrbücher, Abteilung für allgemeine Zoologie und Physiologie der Tiere 82: 419-433.
- WENNING, A., 1979. Structure and function of the hindgut of *Lithobius forficatus* L. (Myriapoda, Chilopoda). – Pp. 135-142 in M. CAMATINI (ed.) Myriapod Biology. – Academic Press, London.
- WILLEM, V., 1889. Note sur l'existence d'un gésier et sur sa structure dans la famille des Scolopendrides. – Bulletin de l'Académie royale des Sciences, des Lettres et des Beaux-Arts de Belgique 3 : 532-547.

## Chapter 7

# CHILOPODA – TRACHEAL SYSTEM

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Centipedes are terrestrial, tracheate arthropods. Most of them (Pleurostigmophora) have more or less conventional tracheal systems comparable to those of other land arthropods, whereas the Scutigeromorpha (Notostigmophora) rely on a unique respiratory system where a huge number of short tracheae convey O<sub>2</sub> to the hemolymph which enter the dorsal vessel via ostia. The subsequent O<sub>2</sub> distribution is provided by the circulatory system with the help of a respiratory pigment (hemocyanin) in the hemolymph.

### *Spiracles*

Spiracles occur on many or most trunk segments, but never on the forcipular segment or the last leg-bearing segment and genital segments (Fig. 7.1). In Geophilomorpha, and in *Plutonium* among the Scolopendromorpha, the spiracles are arranged in uninterrupted segmental series, while in the other centipedes they are restricted to the leg-bearing segments with long tergites (Haase, 1884; Verhoeff, 1902-1925; Hilken, 1998; Fusco, 2005).

#### *Notostigmophora*

In the Scutigeromorpha there is a median, dorsal spiracle at the posterior edge of each long tergite, corresponding to the leg-bearing segments 1, 3, 5, 8, 10, 12, and 14 (Fig. 7.1A). The size of the spiracles increases up to the fourth long tergite covering leg-bearing segments 7-9, to decrease thereafter. Due to the shape similar to gas-exchange openings on plants leaves, Haase (1884) described the spiracles of the Notostigmophora as “stomata”. Cuticular lips, located directly under the outer opening may narrow the width of the slits (Hilken, 1998). A tubular passage connects the posterior side of the spiracle to a wide atrium (Fig. 7.2A-B). No muscle is attached to either the spiracle or the atrium.

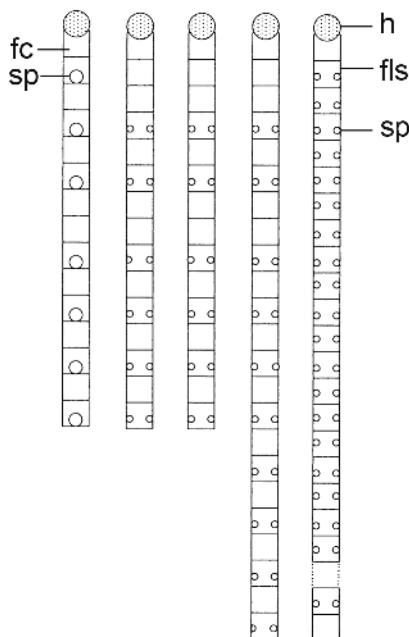


Fig. 7.1 Sequences of spiracles in Chilopoda. From left to right: Scutigeromorpha (Notostigmophora), Lithobiomorpha, Craterostigmomorpha, Scolopendromorpha, Geophilomorpha. There are several variations of the presented scheme especially in the Lithobiomorpha and Scolopendromorpha (for details see text). Some species show segment and spiracle duplicates (*Scolopendropsis duplicita*), *Plutonium zwierleinii* has spiracles on all leg-bearing segments, and several species develop an additional spiracle on leg-bearing segment 7 (e.g. *Rhysida*, see following text). Modified after Hilken (1998).

fc forcipular segment; fls first leg-bearing segment; h head; sp spiracles

#### Pleurostigmophora

All pleurostigmophoran centipedes have paired spiracles on the pleura of trunk segments (Fig. 7.1B-E).

In Lithobiomorpha, number and arrangement of spiracles differs in the different taxa (Tab. 7.1.).

In the Craterostigmomorpha, the spiracles are restricted to leg-bearing segments 3, 5, 8, 10, 12, and 14 (Fig. 7.1C).

Table 7.1 Leg-bearing segments with spiracles in different lithobiomorph taxa.

	I	III	V	VIII	X	XII	XIV	references
Henicopinae	+	+	+	+	+	+	+	1-3
Lithobiidae, many Anopsobiinae		+	+	+	+	+	+	4-6
<i>Anopsobius productus</i> , <i>A. neozelandicus</i> , <i>A. wrighti</i> ,			+	+	+	+	+	5
<i>A. diversus</i> , <i>A. actius</i>								
<i>Dichelobius etnaensis</i>			+	+	+	+	+	7
<i>Anopsobius</i> sp., <i>Rhodobius</i> sp.					+	+		7
<i>Catanopsobius</i> sp.					+			7-8

References. - 1. Haase (1885); 2. Demange (1967); 3. Edgecombe (2001); 4. Rilling (1968); 5. Edgecombe (2003); 6. Edgecombe and Giribet (2004); 7. Edgecombe (2004); 8. Crabbill (1955).

In all Scolopendromorpha (with one exception), spiracles are only present on the pleura of segments with long tergites (Fig. 7.1D). Most species with 21 leg-bearing segments (Scolopendridae, Cryptopidae) have 9 pairs of spiracles (segments 3, 5, 8, 10, 12, 14, 16, 18, 20; Demange, 1967). In *Alluropus*, *Dinocryptops*, *Ethmostigmus*, *Newportia* and *Rhysida*, an additional pair is developed on leg-bearing segment 7. In species with 23 leg-bearing segments a further pair of spiracles is present on segment 22 (e.g., Crabbill, 1960); in *Scolopendropsis duplicata*, with either 39 or 43 pairs of legs, the series continues on all even-numbered leg-bearing segments up to segment 38 or 42 respectively (Chagas et al., 2008). Only *Plutonium zwierleinii* (Plutoniumidae) has 19 pairs of spiracles on all leg-bearing segments from segment 2 to segment 20 (Haase, 1884; Demange, 1967).

All Geophilomorpha have spiracles on all leg-bearing segments, the first and the last one excepted (Fig. 7.1E).

In the Pleurostigmophora, the spiracles and atria are covered by numerous cuticular trichomes (Füller, 1960b; Manton, 1965; Rosenberg 2009). Longer trichomes function as a weir (Füller, 1960a; Kaufman, 1961) or help reducing water loss (Lewis, 1963). Shorter trichomes which cover the septum of the atria serve as a plastron (Manton, 1965; Lewis et al., 1996; Hilken, 1997, 1998, 2003). Between the hydrophobic trichomes, the air can be stocked, thus preventing inflow of water in the tracheal system. In some species, epidermal glands located in the atrial epithelium secrete possibly hydrophobic substances responsible for the water-repellent qualities of the trichomes (Füller, 1960a).

*Lithobiomorpha*. – The spiracles of *Lithobius forficatus* were described by Verhoeff (1941), Füller (1960a), Kaufman (1960a, 1962), Curry (1974), and Hilken (1998). Their size decreases from anterior to posterior. The spiracles are slit-shaped, their lips (peritrema) reinforced by cuticular strips. The opening is followed by a flat atrium that continues

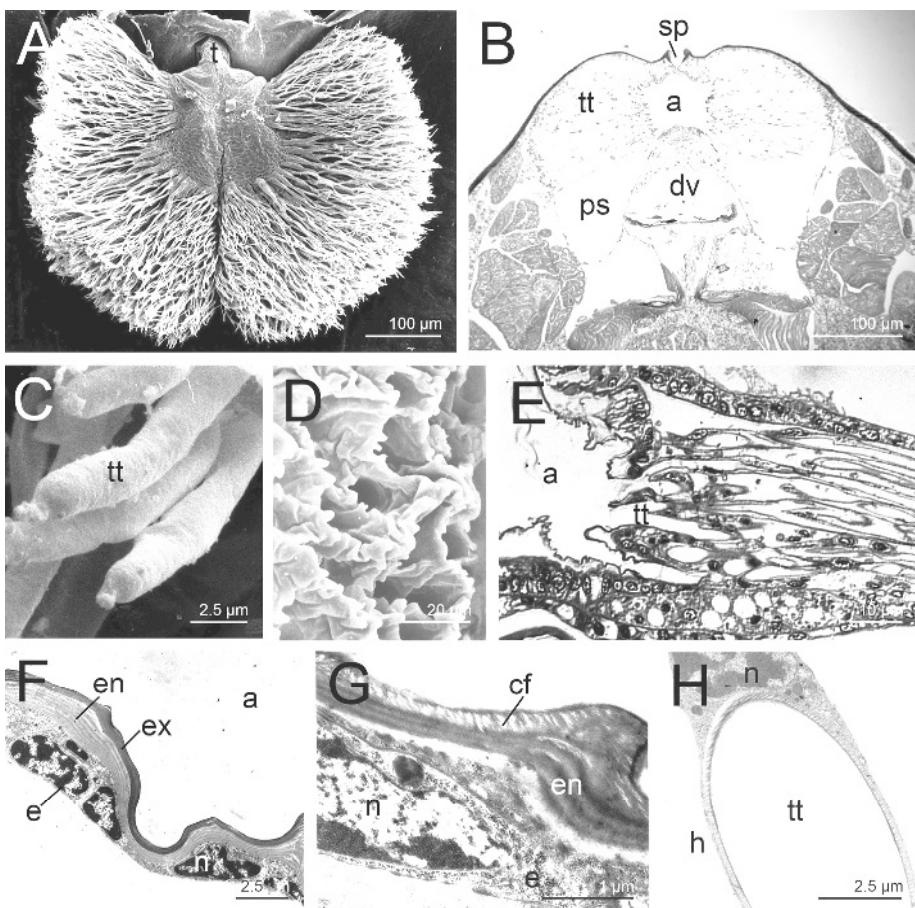
into a small number of short but wide tracheal stems. The high epithelium of the atrium does not contain glands. Based on desiccation experiments, Lewis (1963) assumed that lithobiomorph centipedes are able to regulate the opening width of their spiracles. Spiracle muscles are not developed. However, two muscles attaching at the proximal edges of the stigmapleurite may pull apart the spiracle lips (Füller, 1960a; Rilling, 1968). The walls of these lips are equipped with short and flattened spongiform trichomes (Hilken, 1998), forming a plastron. The wall of the atrium forms cuticular stripes from which large trichomes extend into the atrium. At the transition to the tracheae, the stripes fade into taenidia (Hilken, 1998).

*Craterostigmomorpha.* – The spiracles of *Craterostigmus tasmanianus* (Manton, 1965; Prunesco, 1965; Hilken, 1997, 1998) are crater-like (Fig. 7.4A-B, up to 250 µm) and conspicuously large. They are located on sclerotised stigmapleurites. The atrium wall is covered with numerous complex trichomes that remind spongy mats which form a plastron (Fig. 7.4A) (Hilken, 1998).

*Scolopendromorpha.* – The spiracles of the Scolopendrinae are triangular to lengthwise oval, whereas the roundish spiracles of the Otostigminae are often ear-shaped (Lewis et al., 1996). The inner side of these spiracles is equipped with numerous trichomes and the atrium is subdivided by a diaphragm into an outer and an inner part (Fig. 7.5A) (Haase, 1884; Verhoeff, 1902-25, 1941). In *Scolopendra* spp., both compartments are covered with long trichomes, forming a complex weir apparatus (Lewis et al., 1996; Hilken, 1998; Klok et al., 2002). Some trichomes are interconnected via lateral strips to form a plastron (Lewis et al., 1996).

In *S. cingulata* and *Cormocephalus nitidus calcaratus*, prominent muscles are attached at valve-like protrusions of the tracheal pouches that surround the atria, regulating the width of the atrium and allow an active opening of the spiracle (Fig. 7.5A) (Verhoeff, 1902-25; Dubuisson, 1928; Füller, 1960a; Manton, 1965; Hilken, 1998). Thus, the pouches function as muscular apodemes (Hilken, 1998). It is assumed that the closing of the spiracle is a passive consequence of the elasticity of the cuticle. In *Cormocephalus westwoodi* and *Scolopendra morsitans* (Klok et al., 2002) no spiracle muscles were found. The wide flap-valve allows complete closing of the spiracles in *S. morsitans*, whereas the same structures are so narrow in *C. westwoodi* that they do not seem to be able to close the spiracles completely.

The spiracles of *Cryptops hortensis* (Cryptopidae) have a huge, elliptical outer opening and a sickle-shaped, narrow inner opening (Füller 1960a: “spiracle mouth”). The spiracle is subdivided into an atrium and a tracheal pouch; both parts are covered with tricho-



**Fig. 7.2** Tracheal system of *Scutigera coleoptrata*. A Overview (SEM). B Spiracle and tracheal system (LM, cross section). C Blind ends of tracheal tubules (SEM). D Tracheal tubules branching off from the atrium (SEM). E Section through the atrium with originating tracheal tubules (LM). F Cuticular layers of the atrium wall (TEM). G Transition between atrium and tracheal tubules. The endocuticle is covered by chitin fibres (TEM). H Epithelium of tracheal tubules, covered by a cuticle with chitin fibres (TEM). Modified after Hilken (1998).

a atrium; cf chitin fibres; dv dorsal vessel; e epithelium of atrium and/or tracheal tubules; en endocuticle; ex exocuticle; h haemolymph; n nucleus; ps pericardial sinus; sp spiracle; t tube; tt tracheal tubules

mes. The arrangement looks like the outer and inner atrium of the Scolopendrinae. The longest trichomes are 8 µm long. In the area of the outer atrium, the cuticle is produced by a epithelium of high cylindrical cells. Epidermal glands are not developed. Two

muscles are attached at the beginning of the tracheal pouch (inner atrium). The spiracles are opened by contraction of these muscles and closed by the elasticity of the cuticle (Füller, 1960a; Curry, 1974; Hilken, 1998).

*Geophilomorpha.* – The roundish to oval spiracles are generally located on distinct stigmapleurites, sometimes in the neighborhood of hair-like sensilla, e. g. in *Geophilus flavus* und *Strigamia acuminata* (Füller, 1960a). In many species, spiracles size decreases from anterior to posterior segments.

The spiracles of *G. carpophagus* are roundish and covered with numerous branched trichomes leaving a bare slit in the center of the spiracle (Fig. 7.5D) (Hilken, 1998). Spongy deepenings, typical for the trichomes of many pleurstigmophorans, are uncommon in the outer trichomes of *G. carpophagus*. However, the shape of the trichomes vary in different species, and differ sometimes even within the same specimen (Füller, 1963; Lewis, 1963; Curry, 1974): scale- (*S. acuminata*) or hair-like (*G. flavus*; Füller, 1960a), fungus-shaped (Manton, 1965) or hairlike with a Y-shaped tip (*G. carpophagus*; Hilken 1998). Spiracle muscles are not developed (Fig. 7.5D). However, the spiracles might be closed by the flattening of the atrial wall.

In *Himantarium gabrielis* and *G. flavus*, the spiracle (or tracheal) pouch from which the first tracheal stems originate is conspicuously enlarged. Its wall is covered by trichomes that are basally netlike interconnected (Füller, 1960a). The trichomes build thus a hydrophobic plastron. From the small spaces between the trichomes, the respiratory gases may diffuse even when the animals are digging and the spiracle is closed (Manton, 1965). Spiracle muscles like those in Scolopendromorpha are not developed (Füller, 1960a; Hilken, 1998). Numerous epidermal glands are intermingled in the epithelium of the atrial wall. The spiracle of *G. flavus* is surrounded by large glands (Füller, 1960a).

### *Tracheae and tracheal systems*

#### *Notostigmophora*

From the posterior end of the spiracle, a cuticle-lined tube leads into an atrium with intensively folded walls, but lacking trichomes (Fig. 7.2B, D-E). A high number of short tracheal tubules originate from the lateral and posterior sides of the atrium wall (Fig. 7.2A-B). These tubules form a paired, lung-shaped organ, sometimes termed a tracheal lung (Haase, 1884; Prunesco and Prunesco, 1996). In *Scutigera coleoptrata*, the tracheal tubules branch basally three to four times, in *Allothereua maculata* only once. In *Parascutigera festiva*, the tracheal tubules branch only once in the middle and in some

cases again in the distal part (Hilken, 2003). In *S. coleoptrata*, approximately 500 to 600 tracheal tubules originate at the atrium (Fig. 7.2D-E) (diameter 6-7 µm at their origin, 2 µm at their blind end; Fig. 7.2C). The short tracheal tubules project about 200 µm into the pericardial sinus (Fig. 7.2B). Anastomoses are not observed. The tracheal tubules are built by epidermal cells with large nuclei, and very scarce cytoplasm (Fig. 7.2H). Tracheal tubules originating in the middle part of the atrium are surrounded by scanty connective tissue. Hemocytes were frequently observed in the interspaces between the tracheae, indicating that hemolymph circulates through these spaces (Hilken, 1998).

The single-layered epithelium of the atrium builds a cuticle with a laminated endocuticle (0.7-2.1 µm thick) and a very fine exo- and epicuticle (Fig. 7.2F-G). A typical endocuticle is not developed in the tracheal tubules of *Scutigera coleoptrata* (Fig. 7.2H, 3B); application of chitinase resulted in the complete dissolution of the tracheal system (Hilken, 1998). This result contradicts Sundara Rajulu's (1971) claim that the tracheae of *Thereuopoda longicornis* do not contain chitin, but collagen and acid mucopolysaccharids. Taenidia are not developed, but the tracheae are internally strengthened by circular chitin fibres, up to 60-90 nm in diameter, that form a one- to two-layered network (Fig. 7.2H, 3A-B). The tracheae are formed by a flat single-layered epithelium approximately 30 nm in height, which is only extended in the area of the nuclei. Mitochondria, rough endoplasmatic reticulum and Golgi apparatus are also localized there (Hilken, 1998).

#### *Pleurostigmophora*

In the Lithobiomorpha, Scolopendromorpha and Geophilomorpha, tracheae are a system of deeply invaginated tubules that run through the whole body (Fig. 7.3E-H) and run into different tissues (Fig. 7.5C). Tracheae originate from tracheal pouches (Fig. 7.5A, D-E), lacking only in the Craterostigmomorpha, which also function as apodemes in the Scolopendromorpha.

*Lithobiomorpha*. – Number and course of the tracheae and their degree of branchings are quite variable. Left-right asymmetries are quite often observed: tracheal stems that are lacking on one body side are substituted by tracheae from the other body side (Hilken 1998). Anastomoses between tracheae are lacking (Fig. 7.3E).

Two tracheal stems, originating at the spiracle pair of the third leg-bearing segment, project into the head (Rilling, 1968). The upper head trachea (trachea cephalica superior) supplies via smaller branches also the tergal and pleural regions of leg-bearing segments 1 and 2. This trachea splits within the head into 3 tracheal branches which supply the maxillipedes, the antennae, and the anterior and posterior head region. The lower head

trachea (Tr. cephalica inferior) supplies the first pair of legs, the ventral region of trunk segments 1 and 2 and the segment of the maxillae. Additionally, four small tracheal branches originating at the first pair of spiracles run into the leg-bearing segments 2 and 3 (Rilling, 1968). From each of the following spiracles two to five tracheal stems originate (Voges, 1916; Ripper, 1931; Rilling, 1968; Hilken, 1998), which branch several times and run into the adjacent anterior and posterior spiracle-lacking segments, where they mainly supply the musculature of the body and the legs. The tracheae originating at the last pair of spiracles supply the gut and the terminal body segments (Rilling, 1968).

The diameter of the large tracheal stems is about 40 µm; that of descending tracheae 10-15 µm. The epithelium of the smaller tracheae is 5 µm high (Hilken, 1998) and narrows constantly toward the tip. In the area of the tracheoles, with diameters of less than 1 µm, the height of the epithelium is about 20 nm.

The epithelium of the tracheae is covered by a cuticle: the multi-layered endocuticle (max. 0.5 µm high), is overlaid by a thin exo- and a very thin, electron-dense epicuticle (Fig. 7.3C-D). The tracheae are strengthened by a high number of spirally arranged taenidia (Fig. 7.4F; 1.0-1.5 µm high). Only the tracheoles lack taenidial strengthenings (Hilken, 1998).

*Craterostigmomorpha*. – The tracheal system of *Craterostigmus tasmanianus* is characterized by an unusually high number of unbranched tracheae (1500-2000 according to Hilken, 1998; 3000 according to Manton, 1965) arising directly from each spiracle (Fig. 7.3F, 7.4B-D). No tracheal pouches and tracheal stems are developed and no anastomosis is observed (Hilken, 1998). The tracheal mass fills up a substantial part of each segment (Fig. 7.4B-D). Most of the tracheae remain in the body side where they originate; a few of them extend into the neighbouring segments (Fig. 7.3F).

The tracheae of *C. tasmanianus* are nearly as small as tracheoles in diameter (3-4 µm) and penetrate the tissue directly. Each trachea is strengthened by only one, very long taenidium (Fig. 7.4E, Hilken, 1997, 1998).

*Scolopendromorpha*. – In *Cryptops anomalans* and *C. hortensis*, two paired head tracheae are developed, originating from the first pair of spiracles in the third leg-bearing segment. The five to six huge tracheal stems (10-22 µm in diameter) originating from each spiracle branch several times. Three of these tracheae run contralateral within the same segment, the others project into the legs or reach deeply into the anterior segments that have no spiracles. Anastomoses are common, especially among the smaller tracheal branches (Fig. 7.3G, 5B).

Tracheae are more numerous in larger species. In *Scolopendra cingulata* and *S. morsitans* up to 15 tracheal stems originate at the first pair of spiracles (Fig. 7.3G). In *Scolopendra* spp., ten of these tracheae run into the anterior leg-bearing segments and the head region.

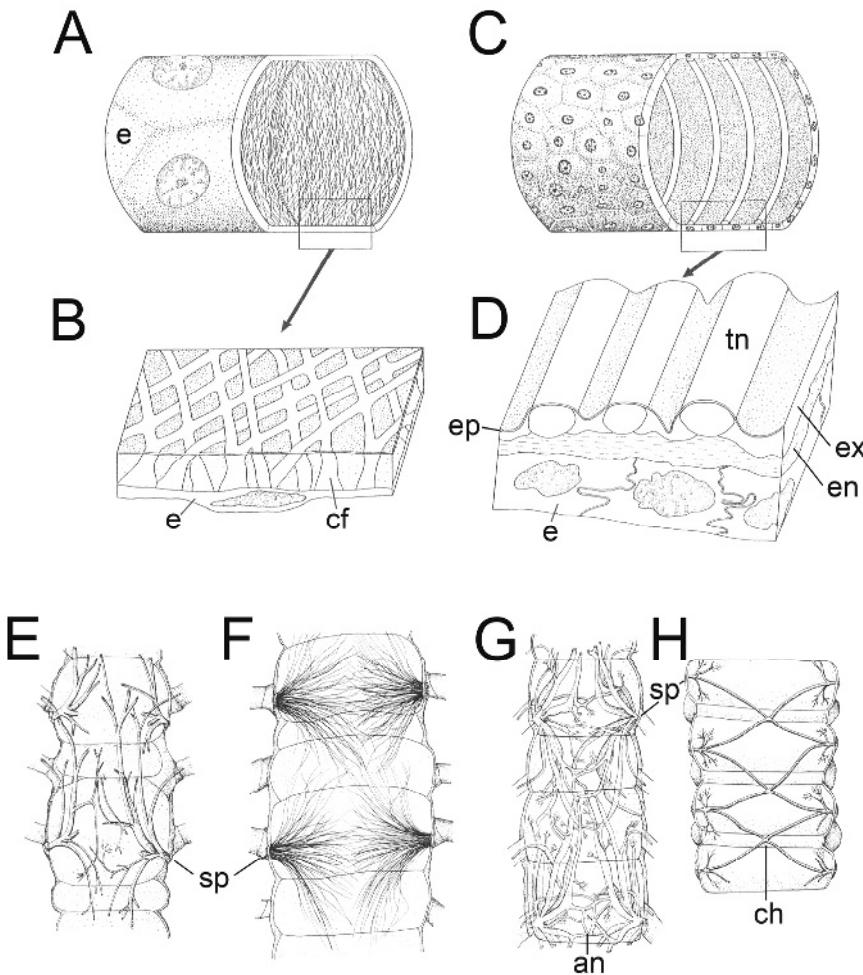
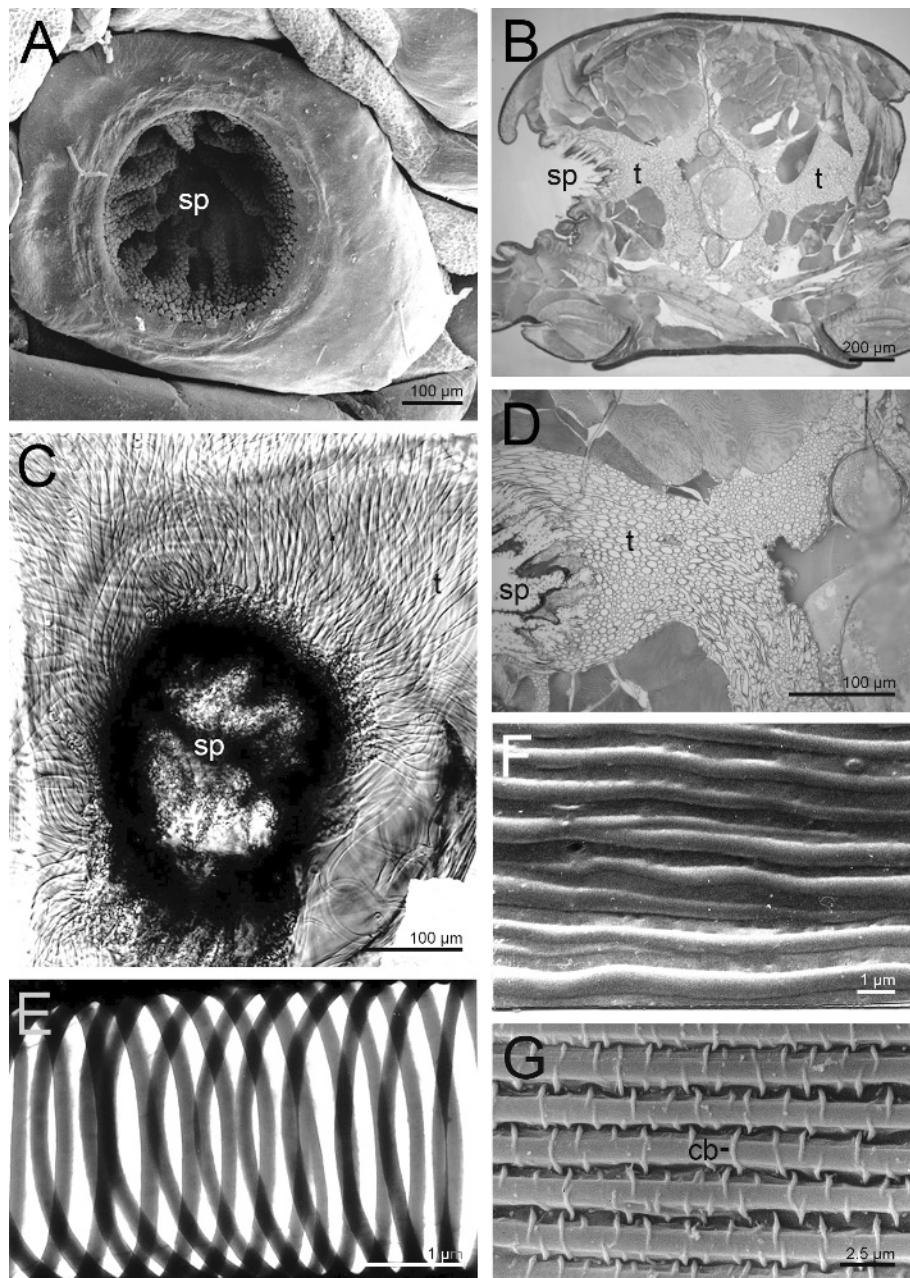


Fig. 7.3 A-D Diagrammic structure of trachea in Chilopoda. A-B: *Scutigerella coleoptrata*, C-D: *Lithobius forficatus*. E-H Diagrammatic representation of tracheal systems of pleurostigmophoran centipedes. E *Lithobius forficatus*, F *Craterostigmus tasmanianus*, G *Scolopendra cingulata*, H *Geophilus carpophagus*. Modified after Hilken (1998).

an anastomosis; cf chitin fibres; ch chiasma; e tracheal epithelium; en endocuticle; ep epicuticle; ex exocuticle; sp spiracle; tn taenidium



**Fig. 7.4** Spiracles and tracheae of pleurostigmophoran centipedes. A-E *Craterostigmus tasmanianus*: A Spiracle (SEM). B Spiracle and tracheal system (cross section, LM). C Spiracle with thousands of originating tracheae (Hoyers mixture, LM). D Tracheae originating from spiracle (LM). E Single helically arranged taenidium (TEM). F *Lithobius forficatus*, several interdigitating taenidia (SEM). G *Scolopendra cingulata*, several taenidia with numerous vertically arranged cuticular bars (SEM). Modified after Hilken (1998).

cb cuticular bar; sp spiracle; t trachea

The legs of segments 3-20 are supplied by two tracheae, the last legs by 3 tracheae each. Both longitudinal and transversal anastomoses are developed.

The tracheae of *Scolopendra morsitans* are strengthened by both shorter and longer taenidia (Merlin, 1901). The helically running taenidia of *S. cingulata* are so short that they end after a few windings; thus, numerous taenidia are involved in strengthening each trachea (Hilken, 1998). The taenidia, up to 1.5 µm in width, are separated by narrow interspaces (0.5-1 µm). Only in tracheal stems with wide lumina (up to 160 µm in diameter), the taenidium is framed by numerous vertically arranged exocuticular bars (Fig. 7.4G). In smaller tracheae (diameter ≤ 0.4 µm) these bars are not present. The tracheal epithelium of *S. cingulata* is covered by the three usual cuticular layers (Hilken, 1997, 1998).

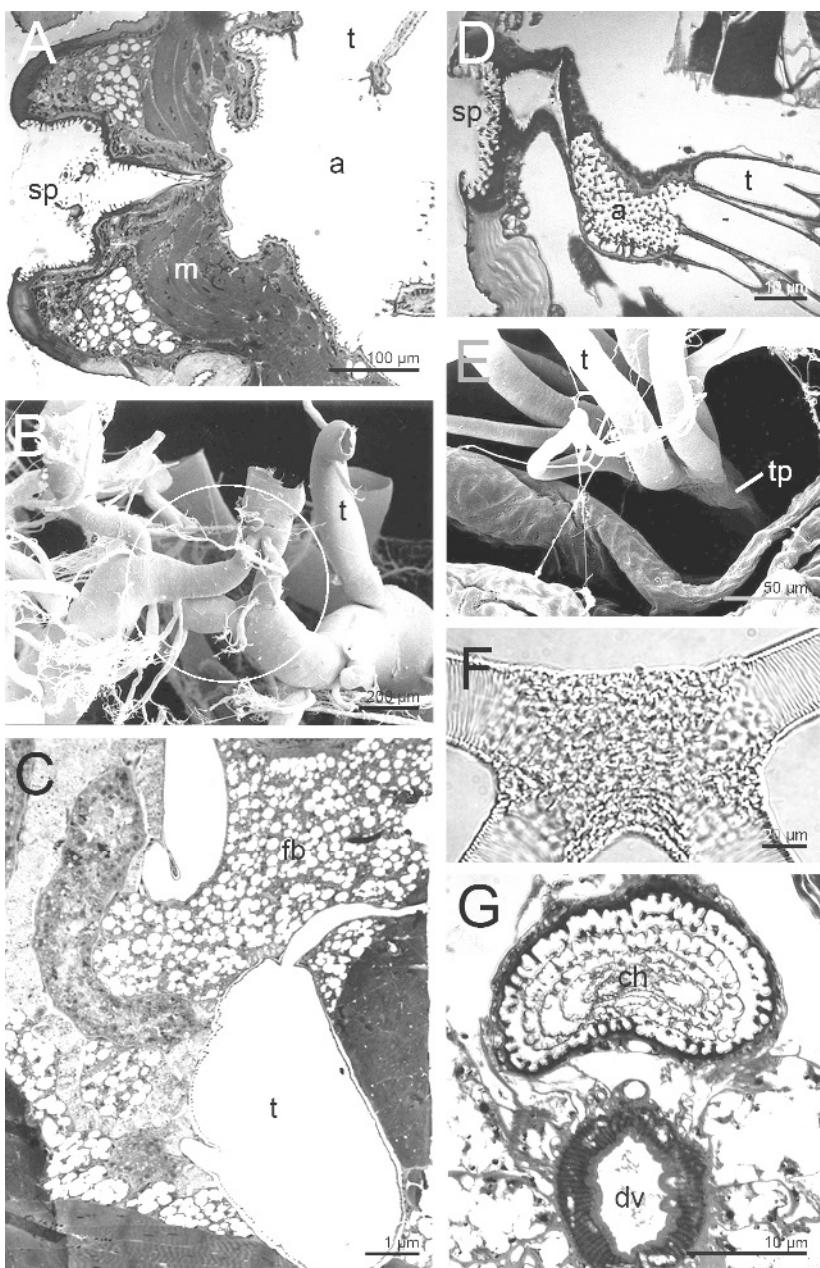
**Geophilomorpha.** – The tracheal system of all Geophilomorpha is characterized by the unique ‘chiasmata’, complex anastomotic bridges uniting four tracheal stems originating from the spiracles of two contiguous segments. Chiasmata are mostly located in the median sagittal plane, dorsally to the heart (Fig. 7.3H, 5F-G).

The course of the tracheae differs among geophilomorph species and is sometimes quite complex. Two types of tracheal arrangement are distinguished (Demange (1942),

- segmental arrangement: two consecutive spiracles of the same body side are interconnected via longitudinal tracheal stems. The corresponding tracheal stems of both sides fuse below the praetergite to form a chiasma
- intersegmental arrangement: the longitudinal tracheal stems skip 1, 2, 3 or 4 spiracles and connect to these via a chiasma

In *Geophilus carpophagus*, a tracheal stem runs craniad, originating at the spiracle of the second leg-bearing segment. After branching in the first leg-bearing segment, the corresponding tracheae of both body sides fuse in the forcipular segment to form a chiasma.

The two descending branches run into the antennae (Dubuisson, 1928). In *G. proximus*, two ventral and dorsal tracheal branches run into the head, originating at the first pair of



**Fig. 7.5.** Tracheae of pleurostigmophoran centipedes. A-C *Scolopendra cingulata*: A Spiracle with attached muscles and huge atrium (cross section, LM). B Tracheal anastomosis (circle, SEM). C Tracheae embedded into muscle and fat body (LM). D-G *Geophilus carpophagus*: D Spiracle pouch and tracheal stems (cross section, LM). E Tracheal pouch and tracheal stems (SEM). F Chiasma with four connecting tracheae (LM). G Chiasma and dorsal vessel (cross section, LM). Modified after Hilken (1998).

a atrium; ch chiasma; dv dorsal vessel; fb fat body; m muscle; sp spiracle; t trachea; tp tracheal pouch

spiracles. The dorsal branches fuse in the anterior head region and run into the antennae; the ventral branches build a chiasma in the first leg-bearing segment and run craniad towards the antennae (Kaufman, 1960b).

The taenidia are not developed in the area of the chiasmata (Chalande, 1885, for *Geophilus electricus*). Histological investigations of the tracheal sytems of *G. flavus*, *G. carpophagus*, *Himantarium gabrielis*, and *Strigamia acuminata* (Füller, 1960b; Minelli, 1985; Hilken, 1998) show that the lumen of the chiasmata is filled with concentrically arranged cuticular layers (Fig. 7.5G).

Each layer represents a residue of an exuvia that was not pulled out during the previous ecdysis. Thus, the number of layers reflects the number of ecdysis events and thus allows an estimation of the animal's age (Minelli, 1985). In the hitherto investigated species, the layers of the chiasmata are covered with different structures: trichome-like structures, analogous to those of the atria (*G. carpophagus*; Füller, 1960b; Hilken, 1998) or a net of cuticular stripes (*G. flavus*, *S. acuminata*). In *H. gabrielis*, the trichomes of the chiasmata are cross-linked via cuticular extensions.

In *H. gabrielis*, the helically arranged taenidia are 1.5-2.4 µm in width; they are separated by 0.2-0.6 µm wide interspaces. In *G. carpophagus* each trachea is strenghtened by numerous short taenidia that follow each other (Hilken, 1998).

### *Respiration*

Air may be conducted through the respiratory system of arthropods by active ventilation or passive diffusion. Active ventilation is extremely rare in Chilopoda.

#### *Notostigmophora*

Specimens of *Scutigera coleoptrata* die after 1.5 h when their stomata are closed with oil (Haase, 1884). Old experiments putatively demonstrating ventilation of the tracheae of *Scutigera coleoptrata* (Dubuisson, 1928) must be dismissed in the light of recent

investigations showing that in *Scutigerina weberi* the gas exchange takes place continuously. The release of CO<sub>2</sub> shows a diffuse pattern, probably due to the stomata, that are permanently open (Fig. 7.6E) (Klok et al., 2002).

The short tracheae of the Notostigmophora are surrounded by the hemolymph which contains a respiratory pigment (Sundara Rajulu, 1969, 1974). In *S. coleoptrata* this pigment shows two absorption peaks at 277 and 336 nm (Mangum et al., 1985; Mangun and Godett, 1986). It is a hemocyanin with a very low O<sub>2</sub>-affinity, which shows, unusually among arthropods, a negative Bohr effect. The O<sub>2</sub>-capacity of the *Scutigera* hemocyanin at 23°C is >3 ml O<sub>2</sub> per 100 ml hemolymph. The molecular weight is about 2,81x10<sup>6</sup>. The polymer consists of six hexamers arranged in octaedric order (Boisset et al., 1990). Kusche et al. (2003) reconstructed the complete aminoacid-sequence and the molecular structure of the *Scutigera* hemocyanin. The structure of the hemocyanin of *S. coleoptrata* is the same as that of the Diplopoda (Kusche and Burmester, 2001). This structure is otherwise unique within the arthropods. Each hexamer consists of two copies each of HcA and HcB and a single copy of HcC and HcD. The O<sub>2</sub>-binding copper atoms are bound to histidine. Molecular phylogenetic analyses show that the hemocyanins of the Myriapoda (Diplopoda and Chilopoda) have a monophyletic origin.

#### *Pleurostigmophora*

*Lithobiomorpha*. – Cyclic ventilation of the tracheal system was observed in *Lithobius melanops*. Once an hour, the animal releases fitfully a high amount of CO<sub>2</sub> („burst phase“). In the following 30 min, the rate of gas exchange decreases constantly. Indirect spiracle muscles have likely an effect in this process. However, a complete closing of the spiracles is not possible. The high CO<sub>2</sub> emission rate in the interburst phase suggests substantial leakage from the spiracles (Fig. 7.6D) (Klok et al., 2002).

In *L. forficatus* star-shaped cells of the connective tissue contain a water-soluble, copper-containing pigment (Attems, 1930; Needham, 1945, 1958, 1960) which, according to Burmester (2002), is most likely a 6-dimere hemocyanin.

*Scolopendromorpha*. – Manton (1965) assumed that the large, sinus-like tracheal stems do not only serve as pipes for the transport of respiratory gases, but also as storage sites for CO<sub>2</sub> to survive in soil layers low in oxygen. In *Scolopendra morsitans* and *Cormocephalus westwoodi anceps* a discontinuous exchange of respiratory gases is measurable (Klok et al., 2002). The spiracles open for a short time and close completely for a longer time (*S. morsitans*, 40 min) or nearly completely (*C. westwoodi anceps*, 2h). CO<sub>2</sub> is either stored in the

hemolymph or released via the periodically opened spiracles. In *C. westwoodi* a cyclic change of the respiratory gases was also observed.

The epidermal cells of *S. morsitans* contain a bluish to greenish pigment with an absorption spectrum showing a maximum at 580 nm (Sundara Rajulu, 1968).

**Geophilomorpha.** – Several representatives of the Geophilomorpha are known to survive under water for conspicuously long time, up to 2 days in *Himantarium gabrielis*) (Haase, 1884; Chalande, 1886; Plateau, 1890). *Pachymerium ferrugineum* survived under water 24-95 days at a water temperature of 19-27°C and even 68-178 days at a temperatur of 6-12°C (Suomalainen 1939). Several species are occasionally exposed to flooding; some of them may rely on plastron respiration. This is suggested by Blower's (1955) observation that the body surface of flooded specimens is sometimes covered by an air sheath.

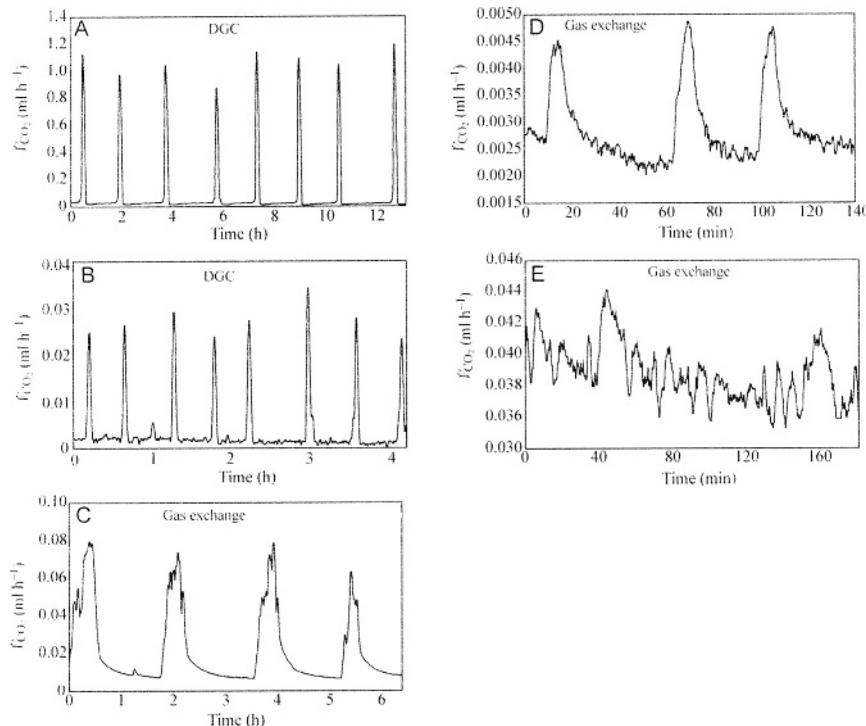


Fig. 7.6 Gas exchange patterns in different species of Chilopoda. A *Scolopendra morsitans*. B *Cormocephalus westwoodi anceps*. C *C. w. westwoodi*. D *Lithobius melanops*. E *Scutigerina weberi*. Modified after Klok et al. (2002).

DGC discontinuous gas exchange cycle

Species such as *Strigamia maritima* and *Hydroschendyla submarina* live in the intertidial zone and are thus exposed to short, recurrent episodes of flooding. These species are able to survive one or two days under seawater (Hennings, 1903; Binyon and Lewis, 1963).

Prolonged flooding is a regular, seasonally occurring condition in some Amazonian forests, where geophilomorph species have developed alternative survival strategies to that. Some species move up on the trees as soon as the water level rises, and down again when the water level lowers, thus actually avoiding being covered by water. Other species, on the contrary, are able to survive under water, thanks to the peculiar meshwork of their atrial trichomes, which provide them with a real plastron (A. Minelli, personal communication).

### References

- ATTEMS, C., 1930. Chilopoda. – Handbuch der Zoologie. Vierter Band, Erste Hälfte: Progoneata, Chilopoda, Insecta I. – Walter de Gruyter, Berlin-Leipzig: 239-402.
- BINYON, J. & J. G. E. LEWIS, 1963. Physiological adaptations of two species of centipede (Chilopoda: Geophilomorpha) to life on the shore. – Journal of the Marine Biological Association of the United Kingdom 43: 49-55.
- BLOWER, J. G., 1955. Millipedes and centipedes as soil animals. – Pp. 138-151 in D. K. M. KEVAN (ed.) Soil Zoology. – Butterworth, London.
- BOISSET, N., J. C. TAVEAU & J. N. LAMY, 1990. An approach to the architecture of *Scutigera coleoptrata* hemocyanin by electron microscopy and image processing. – Biology of the Cell 68: 73-84.
- BURMESTER, T., 2002. Origin and evolution of arthropod hemocyanins and related proteins. – Journal of Comparative Physiology B 172: 95-107.
- CHAGAS, A. JR., G. D. EDGECOMBE & A. MINELLI, 2008. Variability in trunk segmentation in the centipede order Scolopendromorpha: a remarkable new species of *Scolopendropsis* Brandt (Chilopoda: Scolopendridae) from Brazil. Zootaxa 1888: 36-46.
- CHALANDE, J., 1885. Recherches anatomiques sur l'appareil respiratoire chez les Chilopodes de France. – Bulletin de la Société d'Histoire naturelle de Toulouse 19: 39-66.
- CHALANDE, J., 1886. Recherches sur le mécanisme de la respiration chez les myriopodes. – Bulletin de la Société d'Histoire naturelle de Toulouse 20: 137-162.
- CRABILL, R. E., 1955. On the reappearance of a possible ancestral characteristic in a modern chilopod (Chilopoda: Scolopendromorpha: Cryptopidae). – Bulletin of the Brooklyn Entomological Society 50: 133-136.
- CRABILL, R. E., 1960. A new American genus of cryptopid centipede, with an annotated key to the scolopendromorph genera from America north of Mexico. – Proceedings of the United States National Museum III: 1-15.
- CURRY A., 1974. The spiracle structure and resistance to desiccation of centipedes. – Symposia of the Zoological Society of London 32: 365-382.
- DEMANGE, J.-M., 1942. Remarques sur le système trachéen d'*Hydroschendyla submarina* (Grube) et celui des myriapodes géophilomorphes en général. – Bulletin du Muséum national d'Histoire naturelle (2) 14: 422-427.
- DEMANGE, J.-M., 1967. Recherches sur la segmentation du tronc des Chilopodes et des Diplopodes Chilognathes (Myriapodes). – Mémoires du Muséum National d'Histoire Naturelle, Série A Zoologie 44: 1-188.

- DUBUSSON, M., 1928. Recherches sur la ventilation trachéenne chez les chilopodes et sur la circulation sanguine chez les Scutigères. – Archives de Zoologie expérimentale et générale 67: 49-63.
- EDGECOMBE, G. D., 2001. Revision of *Paralamyctes* (Chilopoda: Lithobiomorpha: Henicopidae), with six new species from Eastern Australia. – Records of the Australian Museum 53: 201-241.
- EDGECOMBE, G. D., 2003. A new species of the Gondwanan centipede *Anopsobius* (Chilopoda: Lithobiomorpha) from New South Wales, Australia. – Zootaxa 204: 1-15.
- EDGECOMBE, G. D., 2004. A new species of the henicopid centipede *Dichelobius* (Chilopoda: Lithobiomorpha) from Southeastern Australia and Lord Howe Island. – Proceedings of the Linnean Society of New South Wales 125: 189-203.
- EDGECOMBE, G. D. & G. GIRIBET, 2004. Molecular phylogeny of Australasian anopsobiine centipedes (Chilopoda: Lithobiomorpha). – Invertebrate Systematics 18: 235-249.
- FÜLLER, H., 1960a. Untersuchungen über den Bau der Stigmen bei Chilopoden. – Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 78: 129-144.
- FÜLLER, H., 1960b. Über die Chiasmen des Tracheensystems bei Geophilomorphen. – Zoologischer Anzeiger 165: 289-297.
- FÜLLER, H., 1963. Vergleichende Untersuchungen über das Skelettmuskelsystem der Chilopoden. – Abhandlungen der Deutschen Akademie der Wissenschaften zu Berlin, Chemie, Geologie und Biologie 3: 1-97.
- FUSCO, G., 2005. Trunk segment numbers and sequential segmentation in myriapods. – Evolution & Development 7: 608-617.
- HAASE, E., 1884. Das Respirationssystem der Symphylen und Chilopoden. – Zoologische Beiträge 1: 65-96.
- HAASE, E., 1885. Zur Morphologie der Chilopoden. – Zoologischer Anzeiger 8: 693-696.
- HENNINGS, C., 1903. Zur Biologie der Myriopoden I. Marine Myriopoden. – Biologisches Zentralblatt 23: 720-725.
- HILKEN, G., 1997. Tracheal systems in Chilopoda: a comparison under phylogenetic aspects. – Entomologica Scandinavica Supplement 51: 49-60.
- HILKEN, G., 1998. Vergleich von Tracheensystemen unter phylogenetischem Aspekt. – Verhandlungen des naturwissenschaftlichen Vereins in Hamburg, Neue Folge 37: 5-94.
- HILKEN, G., 2003. Morphologie und evolutionsbiologische Studien an Myriapoden. – Habilitationsschrift Fachbereich 9, Universität Duisburg-Essen.
- KAUFMAN, Z. S., 1960a. The structure of tracheoles in some Chilopoda (in Russian; title translated). – Doklady Akademii Nauk SSSR 130: 693-696.
- KAUFMAN, Z. S., 1960b. The tracheal system of *Geophilus proximus* C. L. Koch (in Russian with English summary). – Zoologicheskii Zhurnal 39: 1802-1810.
- KAUFMAN, Z. S., 1961. Development and structure of the tracheal system in *Lithobius forficatus* L. (in Russian with English summary). – Zoologicheskii Zhurnal 40: 503-511.
- KAUFMAN, Z. S., 1962. The structure and development of stigmata in *Lithobius forficatus* L. (Chilopoda, Lithobiidae) (in Russian with English summary). – Entomologicheskoe Obozrenie 41: 366-371.
- KLOK, C. J., R. D. MERCER & S. L. CHOWN, 2002. Discontinuous gas-exchange in centipedes and its convergent evolution in tracheated arthropods. – Journal of Experimental Biology 205: 1019-1029.
- KUSCHE, K. & T. BURMESTER, 2001. Diplopod hemocyanin sequence and the phylogenetic position of the Myriapoda. – Molecular Biology and Evolution 18: 1566-1573.
- KUSCHE, K., A. HEMBACH, S. HAGNER-HOLLER, W. GEBAUER & T. BURMESTER, 2003. Complete subunit sequences, structure and evolution of the 6 x 6-mer hemocyanin from the common house centipede, *Scutigera coleoptrata*. – European Journal of Biochemistry 270: 2860-2868.

- LEWIS, J. G. E., 1963. On the spiracle structure and resistance to desiccation of four species of geophilomorph centipede. – *Entomologia Experimentalis et Applicata* 6: 89-94.
- LEWIS, J. G. E., T. J. HILL & G. E. WAKLEY, 1996. The structure and possible function of the spiracles of some Scolopendridae (Chilopoda, Scolopendromorpha). – *Mémoires du Muséum national d'Histoire naturelle* 169: 441-449.
- MANGUM, C. P. & G. GODETT, 1986. The hemocyanin of the uniramous Arthropods. In: LINZEN, B. (ed.): *Invertebrate oxygen carriers*. – Springer Verlag, Berlin, Heidelberg: 277-280.
- MANGUM, C. P., J. L. SCOTT, R. E. BLACK, J. I. MILLER & K. E. VAN HOLDE, 1985. Centipedal hemocyanin: Its structure and its implications for arthropod phylogeny. – *Proceedings of the National Academy of Sciences of the United States of America* 82: 3721-3725.
- MANTON, S. M., 1965. The evolution of arthropod locomotory mechanisms. Part 8. Functional requirements and body design in Chilopoda, together with a comparative account of their skeleto-muscular systems and an appendix on a comparison between burrowing forces of annelids and chilopods and its bearing upon the evolution of the arthropodan haemocoel. – *Journal of the Linnean Society of London, Zoology* 46: 251-483.
- MERLIN, A. A., 1901. Tracheae of centipede. – *Journal of the Royal Microscopical Society* (2) 1901: 153.
- MINELLI, A., 1985. Post-embryonic development and phylogeny in geophilomorph centipedes (Chilopoda). – *Bijdragen tot de Dierkunde* 55: 143-148.
- NEEDHAM, A. E., 1945. On relative proportions in serially repeated structures (Seriometry). - I. Limbs and body segments of *Lithobius forficatus* (L.). – *Proceedings of the Linnean Society of London* 115: 355-370.
- NEEDHAM, A. E., 1958. Connective tissue pigment of the centipede, *Lithobius forficatus* (L.). – *Nature* 181: 194-195.
- NEEDHAM, A. E., 1960. Properties of the connective tissue pigment of *Lithobius forficatus* (L.). – *Comparative Biochemistry and Physiology* 1: 72-100.
- PLATEAU, F., 1890. Les myriopodes marins et la résistance des arthropodes à respiration aérienne à la submersion. – *Journal of Anatomy and Physiology* 26: 236-269.
- PRUNESCO, C. C., 1965. Les systèmes génital et trachéal de *Craterostigmus* (Craterostigmomorpha, Chilopoda). – *Revue Roumaine de Biologie - Zoologie* 10: 309-314.
- PRUNESCO, P. & C. C. PRUNESCO, 1996. The ultrastructure of the tracheae of tracheal lungs in *Scutigera coleoptrata* (Notostigmophora, Chilopoda). – *Travaux de l'Institut de Spéléologie "Emile Racovitza"* 35: 63-67.
- RILLING, G., 1968. *Lithobius forficatus*. Grosses Zoologisches Praktikum 13b. – Fischer, Stuttgart: 1-136.
- RIPPER, W., 1931. Versuch einer Kritik der Homologiefrage der Arthropodentracheen. – *Zeitschrift für wissenschaftliche Zoologie* 138: 303-369.
- ROSENBERG, J., 2009. Die Hundertfüßer Chilopoda. – *Die Neue Brehm-Bücherei* Bd. 285, Westarp Wissenschaften Hohenwarsleben.
- SUNDARA RAJULU, G., 1968. On the nature of the pigments of a centipede *Scolopendra morsitans*. – *Science and Culture* 34: 297.
- SUNDARA RAJULU, G., 1969. Presence of haemocyanin in the blood of a centipede *Scutigera longicornis* (Chilopoda: Myriapoda). – *Current Science* 7: 168-169.
- SUNDARA RAJULU, G., 1971. X-ray diffraction and EM studies on the fine structure of the tracheae of a centipede *Scutigera longicornis*, together with observations on their chemical composition. – *Current Science* 17: 467-468.
- SUNDARA RAJULU, G., 1974. A comparative study of the organic components of the hemolymph of a millipede *Cingalobolus bugnioni* and a centipede *Scutigera longicornis* (Myriapoda). – *Symposia of the Zoological Society of London* 32: 347-364.

- SUOMALEINEN, P., 1939. Zur Verbreitungökologie von *Pachymerium ferrugineum* C. Koch (Myriapoda) im finnischen Schärenhof. – Annales zoologice societatis Zoologicae Botanicae Fenniae Vanamo 7: 10-14.
- VERHOEFF, K. W., 1902-1925. Fünfter Band. II. Abteilung Gliederfüssler: Arthropoda Klasse Chilopoda. –In: BRONN, H.G. (ed.): H. G. Bronn's Klassen und Ordnungen des Tier-Reichs. – Akademische Verlagsgesellschaft, Leipzig: 1-725.
- VERHOEFF, K. W., 1941. Zur Kenntnis der Chilopoden-Stigmen. – Zeitschrift für Morphologie und Ökologie der Tiere 38: 96-117.
- VOGES, E., 1916. Myriapodenstudien. – Zeitschrift für wissenschaftliche Zoologie 116: 75-135.



## Chapter 8

# CHILOPODA – CIRCULATORY SYSTEM

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The tracheal and circulatory systems are well developed in centipedes. These differ in this respect from hexapods, which possess a well developed tracheal system but a rather reduced circulatory system.

As in all euarthropods, the circulatory system of chilopods is of the open kind. That is, the body cavity is a space filled with hemolymph that irrigates the internal organs. Being mostly larger then just a few millimeters and therefore not being able to rely only on diffusion as a transport mechanism, chilopods need an active circulation of the hemolymph. This is accomplished by the circulatory system which is made up of a vascular part (the hemolymph vascular system), the spaces between the organs (the hemolymph lacunar system) and the circulated liquid, the hemolymph itself, which includes hemocytes.

### *Anatomy*

In all chilopod species investigated so far, the hemolymph vascular system consists of a dorsal and a ventral longitudinal vessel (Figs. 8.1, 8.2, 8.3A, D, E), which in the first trunk segment are connected through the maxilliped arch (see Figs. 8.1, 8.2, 8.3A, E). Both the dorsal and the ventral vessel can be divided into two regions, respectively in front of the maxilliped arch and behind it. In the dorsal vessel, the two regions are the anterior cephalic aorta (= anterior aorta) and the heart proper, which runs along the trunk, while the ventral vessel is divided by the maxilliped arch into a ventral cephalic vessel and a supraneurial vessel.

The tubular heart, the most important pumping organ, runs the entire length of the trunk. It is contained within a pericardial sinus, which is separated from the rest of the body cavity by a dorsal diaphragm formed by the alary muscles and connective tissue (see below). The heart bears segmentally arranged pairs of ostia that allow the hemolymph to pass out of the pericardial sinus into the lumen of the heart. In all chilopods, except in the Scutigeromorpha (Figs. 8.4B), the lips of the ostia extend deep into the heart lumen (Figs. 8.4C, D), functioning as intracardial valves and hemolymph to

only flow in an anterior direction within the heart (Wirkner and Pass, 2002). The anterior aorta has no ostia.

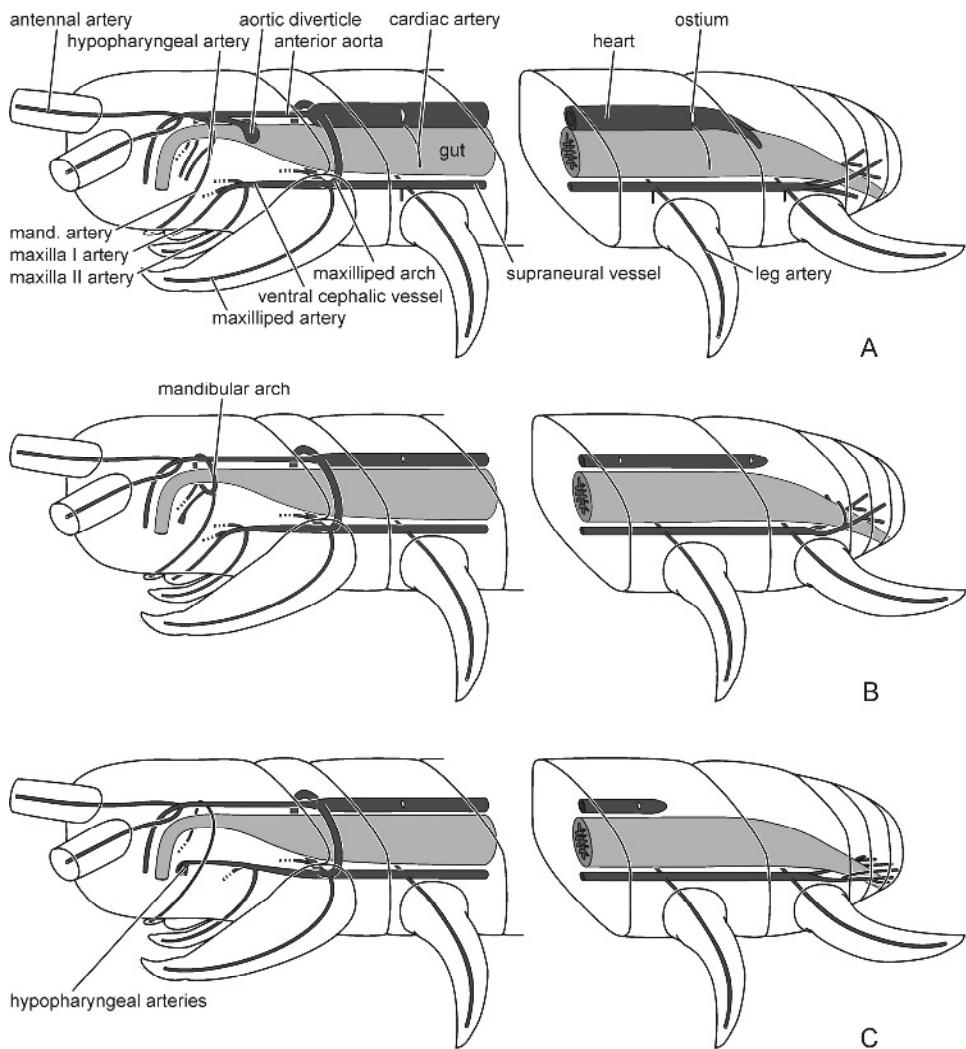


Fig. 8.1 Schematic representations of the hemolymph vascular system in Chilopoda. Only anterior and posterior body regions are shown. Omitted regions are segmental representations of the last segment shown in the anterior part. Arteries on the right body side are depicted by broken lines. Full labelling only in A, in B-E only deviations from the pattern shown in A are labelled. A Scutigeromorpha. B Lithobiomorpha. C Craterostigmomorpha. After Wirkner and Pass (2002).

For a colour version of this figure, see Plate II

Dorsal and ventral vessels give rise to a series of arteries. In all chilopod groups, at least two pairs of arteries branch off from the anterior aorta, supplying the antennae and the mandibles, respectively. Vessels branching off from the mandibular arteries also supply the hypopharyngeal sinus. Off the heart in Scutigeromorpha and Scolopendromorpha, paired cardiac arteries emanate below every pair of ostia. First and second maxillae are supplied by pairs of arteries that branch off from the ventral cephalic vessel. One pair of leg arteries branches off from the supraneurial vessel in each segment of the trunk. The anal and genital region is supplied by arteries emanating from the supraneurial vessel.

A dorsal pericardial sinus is separated from the rest of the body cavity by the dorsal diaphragm (pericardial membrane) which stretches horizontally over the underside of the dorsal longitudinal muscles. Windows in the pericardial membrane near the heart allow hemolymph from the body cavity to pass through. Fan-shaped transversal muscle fibres (alary or pterygoid muscles) are embedded in the dorsal diaphragm; in *Lithobius forficatus* they originate in the pleura or the tergites of trunk segments 1-15 (Rilling, 1968). The muscle fibres fan out and insert into connective tissue fibrils which are connected to the fibrous sheath surrounding the heart (Figs. 8.3A, B, 8.4A, 8.7A).

#### *Scutigeromorpha*

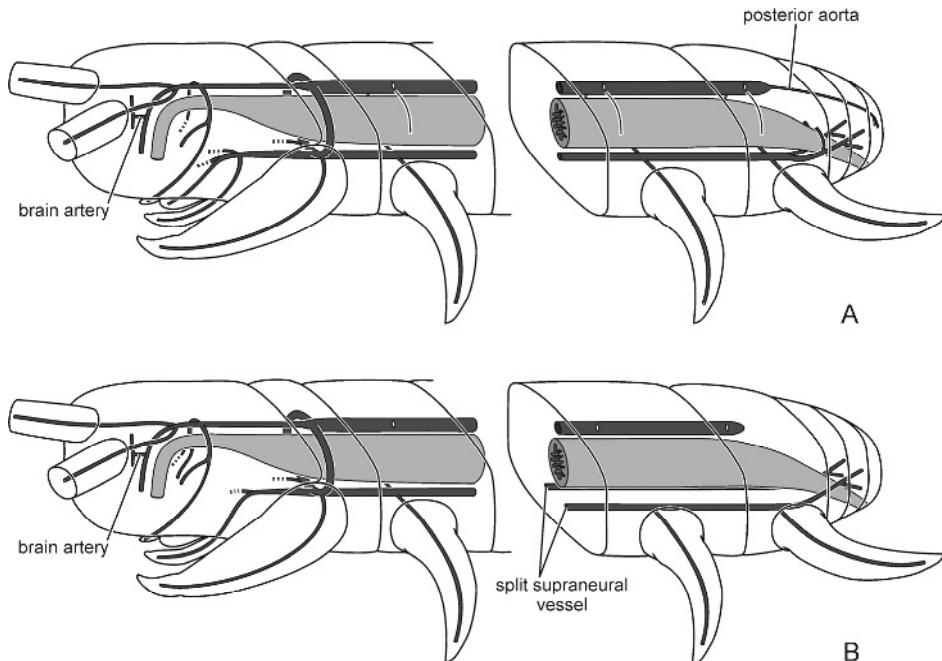
The circulatory system of the Scutigeromorpha (Fig. 8.1A) is more complex than that of the other chilopod taxa, in that numerous fine arteries emanate from all central and peripheral vessels (Wirkner and Pass, 2002).

A cardiac valve formed of two flaps pointing headwards is located between the aorta and the heart. The arteries which branch off the aorta and the fine offshoots of these arteries extend deeply into the brain. Near the mandibles, a short branch diverges ventrally, splitting to form a pair of blind sacs (Herbst, 1891; Fahlander, 1938; Wirkner and Pass, 2002; Hilken et al., 2006). The wall of these aortic diverticules is made up of a single layer of muscle tissue 15-20 µm thick (Fig. 8.4A; see also Hilken et al., 2006). The heart of *Scutigera coleoptrata* (Herbst, 1891; Dubuisson, 1928; Wirkner and Pass, 2002), *Thereuonoda clunifera* and *Thereuonema tuberculata* (Fahlander, 1938) extends from the forcipular segment to the end of leg-bearing segment 13 (tergite 7). In Scutigeromorpha the heart bears 13 pairs of ostia, the last located in the leg-bearing segment 13. The lips of the ostia do not protrude far into the lumen of the heart (Fig. 8.4B). The heart is fixed to the dorsal wall of the body via thin fibres of connective tissue. It does not run in a straight line but broadens below each long tergite and bulges dorsally. Between contiguous tergites its diameter is narrower. At both the beginning and the end of each

enlargement, one pair of ostia is found (Fig. 8.3C), the most anterior of which is always closely associated with the tracheal system (Figs. 8.3C, 8.4B).

In *Scutigera coleoptrata*, the heart is extended posteriorly by two short arteries which run laterally along the gut (Figs. 8.1A; Wirkner and Pass, 2002). In *T. tuberculata* and *T. clunifera*, two arteries differing in diameter branch off the posterior end of the heart (Figs. 8.3D; Fahlander, 1938). The thicker right artery runs in an anterior direction along the dorsal wall of the hindgut and merges into the muscularis of the midgut. Three branches emanate off this artery and run anteriorly. One branch runs posteriorly above the hindgut, the other two run to the midgut.

The supraneurial vessel extends as far as leg-bearing segment 15. A pair of leg arteries branch off in each leg-bearing segment. Small branches off these leg arteries supply the fat body that lies around the ventral ganglia (Figs. 8.1A). An unpaired ventral artery supplies each ganglion (Figs. 8.1A). In the region of the 14<sup>th</sup> and 15<sup>th</sup> pair of legs two addit-



**Fig. 8.2** Schematic representations of the hemolymph vascular system in Chilopoda. Only anterior and posterior body regions are shown. Omitted regions are segmental representations of the last segment shown in the anterior part. Arteries on the right body side are depicted by broken lines. Full labelling only in A, in B-E only deviations from the pattern shown in A are labelled. A Scolopendromorpha. B Geophilomorpha. After Wirkner and Pass (2002).

For a colour version of this figure, see Plate II

ional arteries branch off the supraneural vessel to supply the gonads. In segment 15 the supraneural vessel splits into three branches which divide terminally: the median branch continues underneath the hindgut (Fahlander, 1938).

#### *Lithobiomorpha*

Apart from the maxilliped arch, a mandibular arch can be found in *Lithobius forficatus*, formed by two arteries emanating from the anterior aorta uniting again underneath the foregut (Figs. 8.1B, 8.3A). On each side of the mandibular arch, an artery branches off to supply the mandibles. Ventrally of the foregut, an unpaired artery branches off the mandibular arch in anterior direction. This artery ends funnel-shaped in the hypopharyngeal sinus. At the level of the protocerebrum, the antennal arteries emanate from the anterior aorta. They follow the lobes of the deutocerebrum in a latero-ventral direction. The anterior aorta runs between the pharynx and the brain in an anterior direction and ends in an anterior sinus. The anterior portion and its innervation by neurosecretory axons were described in detail by Jamault-Navarro (1984).

The heart runs from the forcipular segment into leg-bearing segment 15, where it ends blindly (Figs. 8.1B). One pair of ostia is found in each segment with the exception of the forcipular segment. The heart is attached to the dorsal body wall by suspending strands along its entire length. According to Fahlander (1938), segmentally arranged cardiac arteries should exist, but Rilling (1968) and Wirkner and Pass (2002) could confirm their existence only in leg-bearing segment 11 and 12 shortly anterior to the corresponding pairs of ostia.

The supraneural vessel runs along the dorsal side of the ventral nerve cord from the second maxillary segment to leg-bearing segment 15 and splits into terminal arteries which accompany the hindgut into the genital segment. In the head, the supraneural vessel extends into the second maxillary segment. The supply of the first maxillae remains controversial (compare Figs. 8.1B and 3A; Wirkner and Pass, 2002 vs. Rilling, 1968). In the trunk the supraneural vessel is suspended to the transversal musculature (Rilling, 1968).

#### *Craterostigmomorpha*

The anterior aorta runs from the forcipular segment into the labrum where it opens into the labral sinus (Figs. 8.1C). Two pairs of arteries (antennal, mandibular) branch off the anterior aorta. The heart runs from the forcipular segment to leg-bearing segment 14,

where it ends blindly. A pair of ostia can be found in each leg-bearing segment (Figs. 8.4C, os).

In the head, the ventral cephalic vessel runs into the hypopharyngeal sinus and terminates in four open-ending hypopharyngeal arteries (Figs. 8.1C). Only the second maxillae are supplied via a pair of arteries. In the trunk, the supraneurial vessel extends into the leg-bearing segment 15, where it splits and these branches run into the anal capsule where they branch into a number of small vessels.

### *Scolopendromorpha*

In the literature, there are contradicting statements about the number of arteries branching off the anterior aorta. Fahlander (1938) described seven pairs of arteries in *Scolopendra cingulata* (Figs. 8.3E). Of these, the first and second pair of arteries are claimed to belong to the maxillary segment. The third pair of arteries runs into the mandibles. Off one of these mandibular arteries a branch runs to the hypopharynx and posteriorly to the midgut. A fourth pair is said also to belong to the mandibular segment. A fifth pair and the thick antennal arteries also branch off the anterior aorta. Posteriorly to the antennal arteries, a pair of arteries branch off the aorta that run in a posterior direction along the foregut. The aorta terminates in a sinus that lies anterior to the brain. The presence of a mandibular arch as described by Newport (1843) could not be confirmed by Fahlander (1938) or Wirkner and Pass (2002). However, in the different taxa there are intraspecific variations in the number and pattern of minor vessels (Fahlander, 1938). Wirkner and Pass (2002) described two pairs (mandibular and antennal) of arteries branching off the anterior aorta in *S. cingulata* (Figs. 8.2A). These authors confirmed the existence of an unpaired hypopharynx artery. Anterior to the antennal arteries, an unpaired artery branches off the aorta to run through the brain and is therefore termed brain artery. Anterior to the brain, this artery divides into a dorsal and a ventral branch.

The heart extends from the maxilliped segment into the ultimate leg-bearing segment. It is equipped with one pair of ostia (Figs. 8.4D, os) and one pair of cardiac arteries in each leg-bearing segment. At the posterior end, an arterial arch connects the dorsal with the ventral vessel (Fahlander, 1938). Two pairs of arteries branch off this arch, one of which supplies the musculature of the rectum (Fahlander, 1938). The heart tapers in the last leg-bearing segment and merges into the unpaired posterior aorta which ends in the anal segment (Figs. 8.2A; Wirkner and Pass, 2002). The arteries for the ultimate pair of legs branch off the rectal arch. These arteries also supply the coxal organs and give off the anal arteries (Fahlander, 1938). The supraneurial vessel splits after having given off the

arteries for the last pair of legs into a number of terminal arteries that supply the hindgut and the posterior trunk segments (Wirkner and Pass, 2002).

#### *Geophilomorpha*

An unpaired brain artery branches off the anterior aorta anterior to the antennal arteries (Figs. 8.2B). Fahlander (1938) described a mandibular arch in *Mecistocephalus* sp.; the existence of such a vessel ring could not be confirmed by Wirkner and Pass (2000, 2002) in *Geophilus flavus* and *Orya barbarica*. The heart extends from the forcipular segment into the genital segments (Ernst 1971: *G. flavus*) or ends blindly in the ultimate leg bearing segment (Wirkner and Pass, 2002: *G. flavus*, *Orya barbarica*). It is chambered and equipped with a pair of ostia in each leg-bearing segment. The lips of the ostia protrude deeply into the lumen of the heart (Figs. 8.4E).

**Table 8.1.** Distribution of peripheral vessels in chilopods. (+ = present; – = absent. After Wirkner and Pass (2000)).

	Scutigeromorpha	Lithobiomorpha	Craterostigmomorpha	Scolopendromorpha	Geophilomorpha
Arteries off anterior aorta					
antennal arteries	+	+	+	+	+
brain artery	–	–	–	+	+
mandibular arteries	+	+	+	+	+
Mx 1 arteries	+	+	–	+	–
Mx 2 arteries	+	+	+	+	+
mandibular arch	–	+	–	–	–
aortic diverticules	+	–	–	–	–
hyphopharyngeal supply	+	+	–	+	+
Features of the heart					
maxilliped arch	+	+	+	+	+
ostia (segmental)	+	+	+	+	+
ostial valves	–	–	+	+	+
cardiac arteries	+	+	–	+	–
posterior end of heart open	+	–	–	+	–
Features of the SNV					
hyphopharyngeal supply	–	–	+	–	–
leg arteries	+	+	+	+	+
ventral arteries (unpaired)	+	–	–	–	–
splitting SNV	–	–	–	–	+

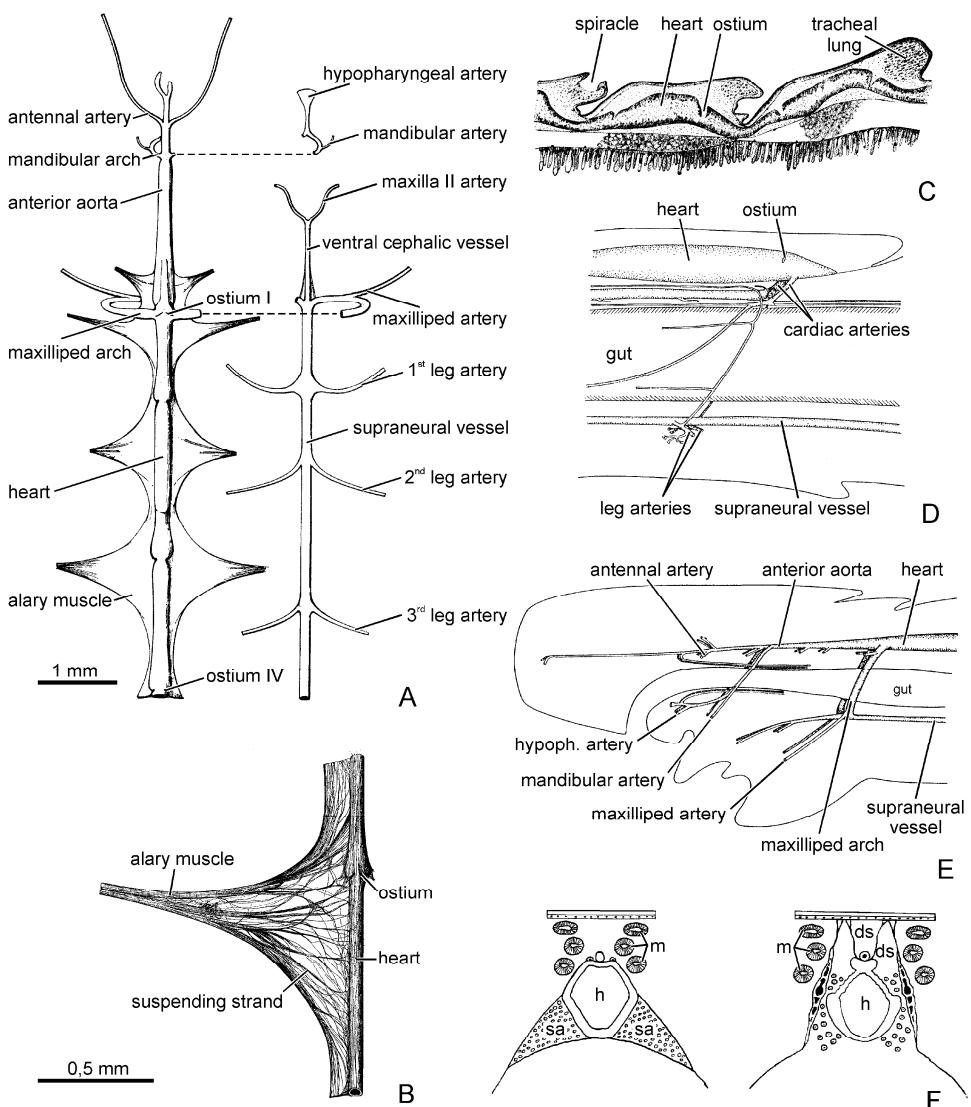


Fig. 8.3 Schematic representations of the hemolymph vascular system in Chilopoda. A *Lithobius forficatus*. Dorsal and ventral vessels are displaced. B One alary muscle in *L. forficatus*. C Sagittal section through trunk segments in *Scutigera coleoptrata*. D Posterior end of the heart in *Scutigera coleoptrata*. E The hemolymph vascular system in the head of *Scolopendra cingulata*. F Two cross sections through the heart in *Geophilus flavus*. A, B after Rillin (1968); C after Dubuisson (1928); D, E, after Fahlander (1938); F after Ernst (1971).

ds sinus dorsalis; h heart; m longitudinal muscles; sa sinus alaeformis

Only the second maxillae are supplied by a pair of arteries from the ventral cephalic vessel. In the posterior trunk segments, the supraneural vessel splits into two main trunks that run ventrolaterally along the gut (Figs. 8.2B, 8.4F; Wirkner and Pass, 2002: *Orya barbarica*).

In *G. flavus*, a tripartite pericardial sinus is described that consists of one dorsal and two lateral partitions. The lateral partitions (Duboscq, 1898a: sinus alaeformes) run along the entire length of the heart and are only interrupted in the regions where the ostia lie. These sinuses are confined by two suspending membranes attached laterally and ventrally to the heart. The dorsal partition (Duboscq, 1898a: sinus dorsalis) is confined to the region of the ostia in each segment. It functions to attach the heart to the tergites and is made up of the ventral sector of the lateral partitions which detaches from the heart wall and runs to the tergite (Figs. 8.3F; Ernst, 1971). In addition, a ligamentum dorsale (Heymons, 1901: ligamentum cordis) spans from the dorsal wall of the heart to the tergite, thus confining the sinus (Ernst, 1971).

### Vascular ultrastructure

Histologically, the outside of the myocardium is covered by a connective tissue sheath (adventitia) and is lined inside by an endocard (intima). However, it is not possible to identify the endocard as a cellular layer through light microscopy.

Ultrastructural studies (Seifert and Rosenberg, 1978; Økland et al., 1982; Økland, 1984; Jamault-Navarro, 1984; Wirkner and Pass, 2002; Hilken et al., 2006) showed that the heart, the supraneural vessel and the aortic diverticules (the latter are only present in Scutigeromorpha) are made up of a single layer of musculature (myocardium), which is covered by a thick basal membrane. The single sarcomeres of the myocardium feature distinct Z, I, and A-bands. In *L. forficatus* und *Strigamia maritima* three different forms of cell borders can be distinguished in the myocardial cells (Økland et al., 1982; Økland, 1984). The tubuli of the T-system arise from invaginations of the sarcolemma and ramify into longitudinal and transversal tubuli. In *L. forficatus*, only smooth sarcoplasmatic reticulum can be found. It accumulates in the region of the I- and Z-bands of the sarcomere but does not form sheaths around the myofibrills. Occasionally, membranes of the sarcoplasmatic reticulum can accompany the transversal tubuli (Økland, 1984). In other chilopod species, smooth sarcoplasmatic reticulum was also reported (Seifert and Rosenberg, 1978; Økland, 1984).

The wall of the arteries is also made up of a single layer of circular musculature which is covered by a thick basal membrane on the epicardial and the luminal sides (Seifert and

Rosenberg, 1973; Rosenberg and Seifert, 1975). Nuclei are in most cases ellipsoid and project out of the wall of the arteries. The contractile system of the myofibrils is weakly developed and poorly patterned. Neurosecretory axons are often attached to the wall of the arteries.

In *S. coleoptrata*, arteries are found in close proximity to the maxillary nephridia that are open on one side. These vessels attach with the open side to the surface of the compact sacculus, while the "closed" side separates the lumen from a narrow hemolymph sinus. The basal laminae of the muscle cells merge with the basal lamina of the sacculus, thus preventing leakage of hemolymph out of the artery into the sinus (Rosenberg and Seifert, 1975).

#### *Tissues associated with the circulatory organs*

The heart tube in chilopods is surrounded by cells that were early on termed lymphatic glands (Cuénot, 1891: *Glandes lymphatiques*) or pericardial cells (Figs. 8.5A, B; Herbst, 1891; Duboscq, 1898a). These groups of cells occur in more or less ordered clusters in the pericardial sinus (*Scolopendromorpha*, *Scutigeromorpha*) (Duboscq, 1898a) or are closely associated with the alary muscles. In *L. forficatus*, the heart is accompanied by pericardial cells arranged as bands. The chilopodan pericardial cells do not conform to pericardial cells described in insects (= nephrocytes) (Rilling, 1968; Palm, 1954). The pericardial cells in *L. forficatus* were seen as connective tissue (Duboscq, 1898b) or modified fat body strands (Kowalevsky, 1895).

In *S. coleoptrata*, the dorsal vessel (anterior aorta, heart) and the emanating arteries in the head are surrounded by cell strands (Figs. 8.4A; pc). The ultrastructure of these cells differs greatly from connective tissue or fat body cells and are therefore termed "perivascular cells" (Hilken & Rosenberg, 2005). The cell clusters are covered by a continuous basal lamina. Only few organelles are found in the cytoplasm that contains a number of lysosome-like structures and a large number of vacuoles. Function and homology of these cells in comparison to the pericardial cells in other chilopods remains unclear.

During the study of pericardial cells, Kowalevsky (1893, 1895) found cells in *Scolopendra* sp. within the fat body that could be stained by vital dyes (ink, ammonium carmine). These cells absorb bacteria and lie at the endings of arteries.

Kowalevsky called these cells lymphatic glands (*glandes lymphatiques*) but they were later on renamed by Duboscq (1896) into Kowalevsky bodies ("corpuscules de Kowalev-

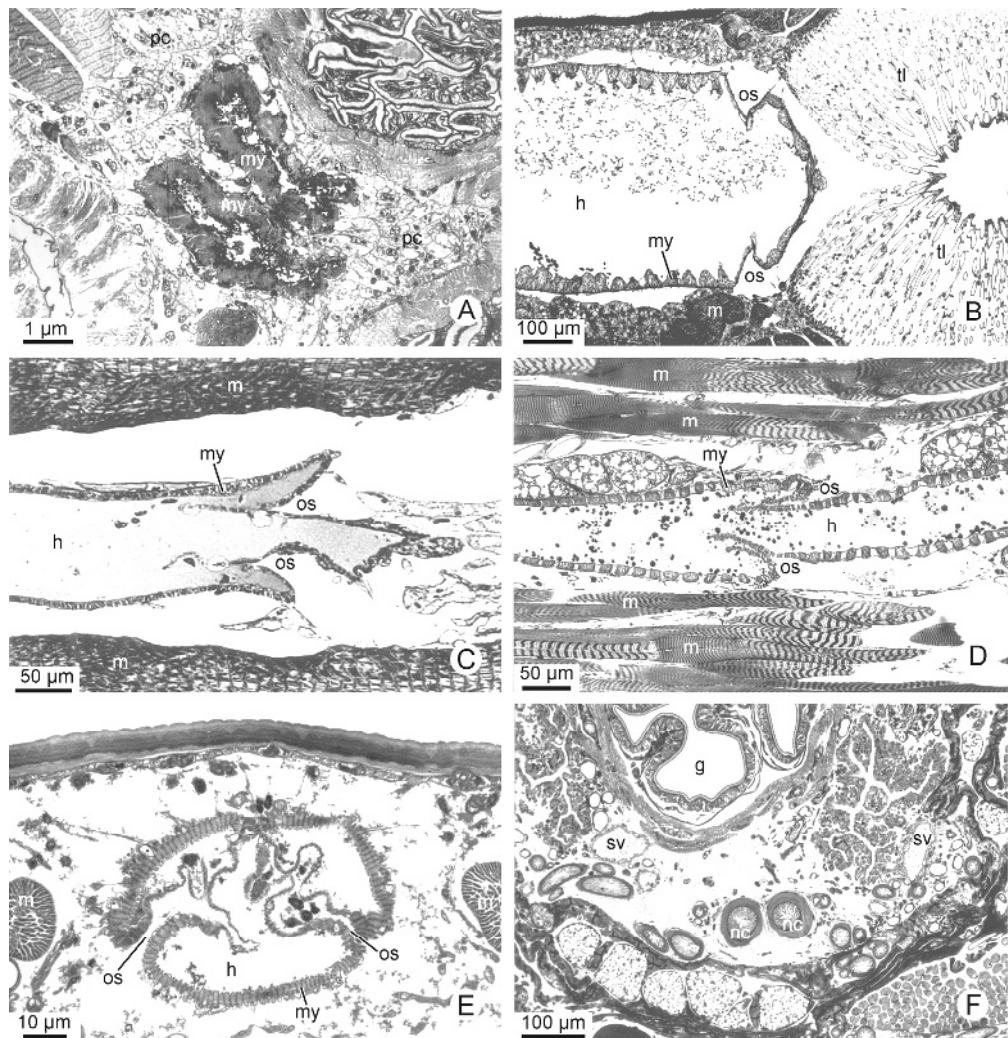


Fig. 8.4 Semi thin sections ( $1\mu\text{m}$ ) through the hemolymph vascular system in Chilopoda. A Cross section through the aortic diverticules in *Scutigera coleoptrata*. B Horizontal section through the heart and tracheal lung in *Scutigera coleoptrata*. C Horizontal section through the heart in *Craterostigmus tasmanianus*. D Horizontal section through the heart in *Scolopendra* sp.. E Cross section through the heart in *Orya barbarica*. F Cross section through the split supraneuronal vessel in *Orya barbarica*. A, D-E original; B-C, F after Wirkner and Pass (2002).

g gut; h lumen of the heart; m muscle; my, myocardium; nc ventral nerve chord; os ostium; pc pericardial cells; sv supraneuronal vessel; tl tracheal lung

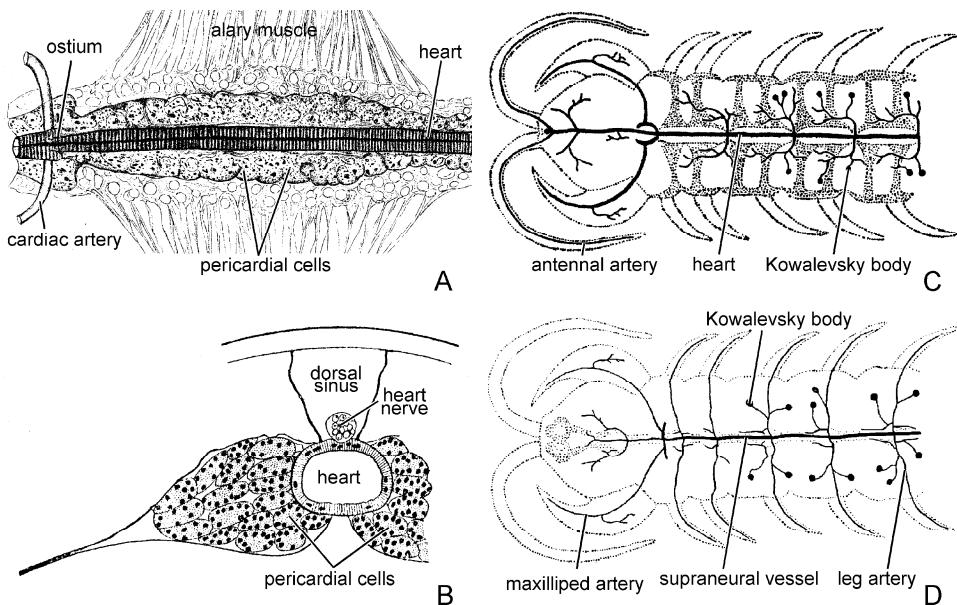
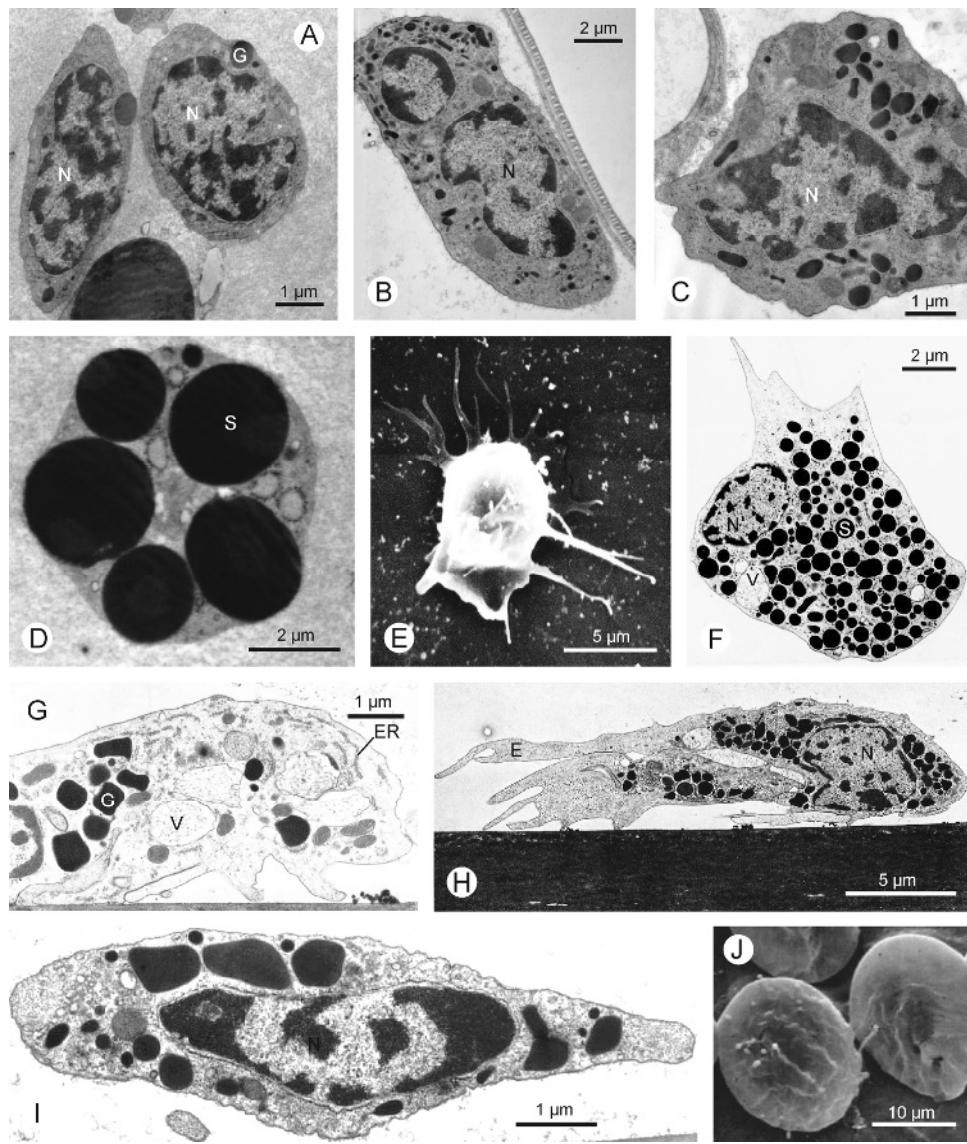


Fig. 8.5 Schematic representations of the tissues associated with the hemolymph vascular system in Chilopoda (*Scolopendra cingulata*). A Heart and dorsal diaphragm. Note pericardial cells along the heart. B Cross section through the heart. C View on the anterior body to show Kowalevsky bodies at the end of cardiac arteries. D Ventral view of the anterior body to show Kowalevsky bodies at the end of arteries branching off the ventral vessel. A after Herbst (1891); B after Duboscq (1898a); C-D after Duboscq (1896).

sky") in honour of their discoverer. In Scolopendromorpha (*Scolopendra cingulata*, *Cryptops hortensis*) these Kowalevsky bodies were found at the endings of cardiac arteries (Figs. 8.5C) and arteries branching off the supraneurial vessel (Figs. 8.5D). In *Lithobius* sp. and Geophilomorpha, however, Kowalevsky bodies could not be detected, and their occurrence in *Scutigera* sp. is unclear (Duboscq, 1898a). Ultrastructural studies are still missing and therefore a detailed description is not possible.

Fig. 8.6. Electron micrographs of different forms of hemocytes in Chilopoda (after different authors). A Prohemocyte (TEM) in *Scutigera coleoptrata*. B Plasmacyte (TEM) in *S. coleoptrata*. C Granulocyte (TEM) with irregular nucleus in *S. coleoptrata*. D Round spherulocyte (TEM) with large circular spherules in *S. coleoptrata*. E Prohemocyte (SEM) in *Lithobius forficatus*. F Spherulocyte (TEM) with large number of spherules in *L. forficatus*. G Plasmacyte (TEM) in *L. forficatus*. H Granulocyte (TEM) with ectoplasmatic protrusions in *L. forficatus*. I Discoid hemocyte (TEM) in *Scolopendra cingulata*. J Discoid hemocytes (SEM) in *S. cingulata*. A-D after Hilken et al. (2003); E-H after Nevermann et al. (1991); I-J after Nevermann (1996.)

E protrusion; ER endoplasmatic reticulum; G granule; N nucleus; S spherule; V vacuole



### *Hemocytes*

Hemocytes contain numerous grana of different size. Mitoses are common. We describe here only the forms that have been characterized by electron microscopy.

*Scutigeromorpha*

In *S. colcoprata*, four types of hemocytes can be distinguished (Hilken, 2003; Hilken et al., 2003a, b).

Prohemocytes (Figs. 8.6A) are rarely found. These cells account for less than 5% of the hemocytes in the vicinity of the tracheae. They are spindle-shaped, 4–6 µm long, and poorly differentiated. Apart from the large nucleus, only a few electron-dense granules, a poorly developed rough endoplasmic reticulum and some mitochondria can be identified.

Plasmatocytes (Figs. 8.6B), 4.3 to 11.6 µm long, predominate (>70%) among the hemocytes in the vicinity of the tracheae. Fusiform and discoid plasmatocytes can be distinguished. The rough endoplasmic reticulum is poorly developed; in some cases, Golgi complexes are large. Additionally, the cells contain small vacuoles and mitochondria, rarely multivesicular bodies.

Granulocytes (Figs. 8.6C), 6 to 10 µm long, are the second most common type of hemocytes (< 20%) in the hemolymph and in the vicinity of the tracheae to which they may adhere through cytoplasmic protrusions. The irregular nuclei have peripheral chromatin and are located in a central position. Abundant granules (diameter 0.03–0.7 µm) occupying most of the cell, irregular, oval or elongated in shape, are concentrated around the nucleus.

Spherulocytes (Figs. 8.6D), 3.4 to 6.1 µm long, account for approximately 5% of the hemocytes found close to the tracheae. They contain only few, but large, more or less electron-dense spherical granules which displace the cytoplasm to narrow interspaces and the nucleus to the margin of the cell.

*Lithobiomorpha*

In the hemolymph of *L. forficatus*, hemocyte number has been determined as  $45\ 200 \pm 21\ 800\ \mu\text{l}^{-1}$ . Four forms of hemocytes can be distinguished (Nevermann et al., 1991; Nevermann, 1996).

The globular prohemocytes (Figs. 8.6E), of diameter < 9 µm, contain only few granules. They account for approximately 2% of the hemocytes. The nucleus is lobular and the cytoplasm contains a number of free ribosomes.

Plasmatocytes (Figs. 8.6G), either discoid or spindle-like (these cells can vary their form quickly), are mitotically active. The cytoplasm of discoid plasmatocytes contains more electron-dense granules than the cytoplasm of the spindle-like cells. Membranes of rough endoplasmatic reticulum, free ribosomes and dictyosomes are rare.

Granulocytes (Figs. 8.6H) are more compact cells of about 9–10 µm x 10–15 µm. The nucleus is lobular; the cytoplasm includes vacuoles and is packed with electron-dense granules. The endoplasmatic reticulum is weakly developed and looks swollen.

Spherulocytes (Figs. 8.6F) are slightly ovoid cells larger than all other types of hemocytes (size up to 20 x 15 x 10 µm). The ovoid nucleus is large; the cytoplasm is filled with globular granules (spherules) of electron-dense, homogeneous material. The endoplasmatic reticulum is weakly developed, dictyosomes are rare.

#### *Scolopendromorpha*

In the hemolymph of *Scolopendra cingulata*, hemocyte number has been determined as  $31\,400 \pm 9\,700 \mu\text{l}^{-1}$ . Three main forms of hemocytes are recognizable (Nevermann, 1996).

The globular to fusiform prohemocytes, diameter 5–10 µm, represent 3.7% of the total hemocyte population. The relatively large nucleus lies centrally; the cytoplasm contains a few small granules, a small number of vesicles, a substantially rough endoplasmatic reticulum, many free ribosomes and some mitochondria.

Discoid hemocytes (Figs. 8.6I, J), ca. 9 µm in diameter and ca. 3 µm thick, are flat, sometimes with filopodial extensions, with a thick equatorial bundle of up to 60 microtubules. The nucleus lies eccentrically and the cytoplasm contains a lot of small and few large, electron-dense granules, sometimes also small vesicles with low electron-density.

The abundant (82% of the total), globular to discoid granulocytes have a diameter of 7–11 µm. The polymorphous nuclei lie eccentrically. The cytoplasm is densely packed with electron-dense granules. The endoplasmatic reticulum is not very well developed and free ribosomes are rare. Granulocytes are highly active in phagocytosis.

#### *Chemical composition of the hemolymph*

The pH of the hemolymph is slightly basic (pH 8) in *S. cingulata*, substantially neutral (pH 6.5–7.5) in *L. forficatus* (Xylander, 1992; Nevermann, 1996) and in the geophilomorph *Mixophilus indicus* (pH value 7.2; Sundara Rajulu, 1972).

Some osmolarity values of the hemolymph have been determined, ranging from 209.0 ± 20.3 mM l<sup>-1</sup> in *Cormocephalus rubriceps* (Bedford and Leader, 1975) and 371.5 ± 7.8 in *S. cingulata* (Xylander, 1992), with intermediate values in *L. forficatus* (Wenning, 1978).

The protein content of the hemolymph is  $65.5 \text{ mg ml}^{-1}$  in *L. forficatus*,  $73.2 \text{ mg ml}^{-1}$  in *S. cingulata* in the average (Xylander, 1992). Much higher and less likely values have been reported for several species by Sundara Rajulu (1970, 1973, 1974).

In *L. forficatus* there are sensible seasonal variations in the total amount of hemolymph proteins ( $20$  to  $120 \text{ mg ml}^{-1}$ ) and the protein spectrum, possibly correlating with the moulting events and the maturation of oocytes and yolk production (Helbing, 1985, 1989).

The supercooling point of the hemolymph is considerably lower in summer than in winter (*Scolopendra polymorpha*: Crawford and Riddle, 1974; Crawford et al., 1975; *L. forficatus*: Tursman et al., 1994; Tursman and Duman, 1995), following seasonal fluctuations in the composition of the hemolymph. In *L. forficatus*, an anti-freezing protein has been demonstrated, enabling the animal to endure temperatures down to  $-15.0 \text{ }^{\circ}\text{C}$  (Tursman et al., 1994; Tursman and Duman, 1995).

#### *Cardiac innervation and heart beat*

In *L. forficatus* and in *Strigamia maritima*, the heart is well innervated and the axons are covered by a myelin sheath. The synaptic clefts are about  $10 \text{ nm}$  wide (Økland et al., 1982; Økland, 1984). The dorsal heart nerve communicates with the stomatogastric nervous system in *L. forficatus* and *L. piceus* (Seifert, 1967 a,b). In the trunk segments of *L. forficatus* the dorsal heart nerve is supplied by axons of neurosecretory cells in the ventral nerve cord. These axons run together with paired nerves that branch off the ventral nerve cord (Fahlander, 1938; Rilling, 1960) in a dorsal direction and merge with the dorsal heart nerve (Scheffel, 1961).

The heart in *Scolopendra morsitans* (Figs. 8.7A, B) is innervated by three major nervous systems (dorsal heart nerve, subesophageal ganglion, ventral nerve cord) (Varma, 1971). The dorsal heart nerve extends along the whole length of the dorsal side of the dorsal vessel (Figs. 8.7A). In the region of the anterior aorta it is made up of six peripheral and one median fibre. Two nerves emanating from the subesophageal ganglion connect to the dorsal heart nerve close to the first pair of ostia. From this point in a posterior direction, the heart nerve consists of 16 to 19 fibres.

Overall, up to 132 bipolar and multipolar neurons were counted. Off the subesophageal ganglion, two pairs of nerves run to the dorsal heart nerve (Nervus VI und X). The first pair (Figs. 8.7; RNI) runs along each side of the anterior aorta and innervates the anterior aorta and the maxilliped arch. Each nerve splits into a ventral and a dorsal branch. The latter connects to the dorsal heart nerve. The ventral branch innervates the

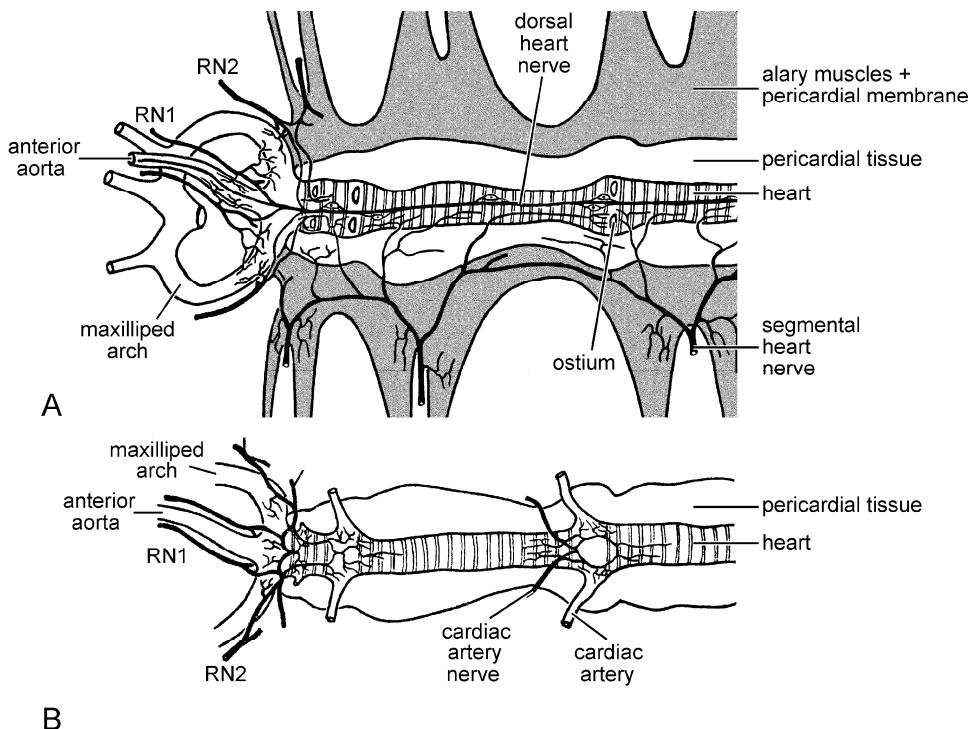


Fig. 8.7 Schematic representations of the innervation of the heart in *Scolopendra morsitans*. A Dorsal view of the anterior part of the heart. B Ventral view of the anterior part of the heart. After Varma (1971).

valve between the heart and anterior aorta. The second pair of nerves (Figs. 8.7A: RN2) runs along the maxilliped arch and also splits into a dorsal and a ventral branch. The former connects to the dorsal heart nerve a short distance posterior to RN1. The ventral branch merges with the ventral branch of RN1 and additionally innervates the maxilliped arch. Off the ventral nerve cord, segmentally arranged cardiac nerves supply the dorsal heart musculature. In each segment, each cardiac nerve splits at the basis of the alary muscles into an anterior and a posterior branch. The anterior branch innervates the alary muscles, the heart, the pericardial tissue and the ostia. Both branches communicate to the branches of the adjacent posterior and anterior cardiac nerves.

Two muscle systems are responsible for the pumping action of the heart, these being the myocardium and the alary muscles, the latter being segmentally arranged. Peristaltic contraction waves propel the hemolymph from posterior to anterior. The diastole is aided by the alary muscles which arise at the pleura and insert at the dorsal diaphragm.

Heart beat is triggered neurogenically (Sundara Rajulu, 1966; Hertel et al., 2002), but is superimposed upon a basic myogenic rhythm in *S. cingulata*. Isolated hearts of *S. morsitans* react positively chronotropic (accelerating) and tonotropic (cumulative) to acetylcholine ( $10^{-8}$ – $10^{-4}$  M) and adrenaline ( $10^{-4}$  M), while histamine ( $10^{-5}$  M) produces a negative chronotropic effect (Sundara Rajulu, 1966).

### References

- BEDFORD, J. & J. P. LEADER. 1975. The composition of the hemolymph of the New Zealand centipede *Cormocephalus rubripes* (Newport). – Comparative Biochemistry and Physiology 50 A: 561-564.
- CRAWFORD, C. S. & W. A. RIDDLE. 1974. Cold hardiness in centipedes and scorpions in New Mexico. – Oikos 25: 86-92.
- CRAWFORD, C. S. & W. A. RIDDLE & S. PUGACH. 1975. Overwintering physiology of the centipede *Scolopendra polymorpha*. – Physiological Zoology 48: 290-294.
- CUENOT, L. 1897. Les globules sanguins et les organes lymphoides des invertébrés. – Archive d'Anatomie Microscopique 1: 153-192.
- DUBOSCQ, O. 1896. La terminaison des vaissaux et les corpuscules de Kowalevsky chez les Scolopendrides. – Zoologischer Anzeiger 19: 391-397.
- DUBOSCQ, O. 1898a. Recherches sur les chilopodes. – Archives de Zoologie expérimentale et générale (3) 6: 481-650.
- DUBOSCQ, O. 1898b. Sur les globules sanguines et les cellules à carminate des chilopodes. – Archives de Zoologie expérimentale et générale (3) 6: XI-XIV.
- DUBUSSON, M. 1928. Recherches sur la ventilation trachéenne chez les chilopodes et sur la circulation sanguine chez les Scutigères. – Archives de Zoologie expérimentale et générale 67: 49-63.
- ERNST, A. 1971. Licht- und elektronenmikroskopische Untersuchungen zur Neurosekretion bei *Geophilus longicornis* Leach unter besonderer Berücksichtigung der Neurohämialorgane. – Zeitschrift für wissenschaftliche Zoologie 182: 62-130.
- FAHLANDER, K. 1938. Beiträge zur Anatomie und systematischen Einteilung der Chilopoda. – Zoologiska Bidrag från Uppsala 17: 1-148.
- HELBLING, G. 1985. Jahreszeitliche Veränderungen des Hämolympheproteinspektrums von *Lithobius forficatus* (L.) (Chilopoda). – Zoologische Jahrbücher, Abteilung für allgemeine Zoologie und Physiologie der Tiere 89: 99-106.
- HELBLING, G. 1989. Postecdysiale Kutikulaprotein-, Hämolympheprotein- und Chitin-Syntheseaktivität bei *Lithobius forficatus* (L.) (Chilopoda). – Zoologische Jahrbücher, Abteilung für allgemeine Zoologie und Physiologie der Tiere 93: 219-226.
- HERBST, C. 1891. Beiträge zur Kenntnis der Chilopoden (Drüsen; Coxalorgan; Gefäßsystem und Eingeweidennervensystem). – Bibliotheca Zoologica 9: 1-43.
- HERTEL, W., C. S. WIRKNER & G. PASS. 2002. Studies on the cardiac physiology of Onychophora and Chilopoda. – Comparative Biochemistry and Physiology A 133: 605-609.
- HEYMONS, R. 1901. Entwicklungsgeschichte der Scolopender. – Zoologica (Stuttgart) 13: 1-244.
- HILKEN, G. 2003. Morphologie und evolutionsbiologische Studien an Myriapoden. – Habilitationsschrift Universität Duisburg-Essen.

- HILKEN, G., C. BROCKMANN & L. NEVERMANN, 2003a. Hemocytes of the centipede *Scutigera coleoptrata* (Chilopoda, Notostigmophora) with notes on their interactions with the tracheae. – *Journal of Morphology* 257: 181-189.
- HILKEN, G., C. BROCKMANN & L. NEVERMANN, 2003b. Exocytosis of fibrous material from plasmacytocytes in *Scutigera coleoptrata* (Chilopoda, Notostigmophora) in relation to wound healing. – *African Invertebrates* 44: 169-173.
- HILKEN, G. & J. ROSENBERG, 2005. A new cell type associated with haemolymph vessels in the centipede *Scutigera coleoptrata* (Chilopoda, Notostigmophora). – *Entomologica Germanica* 27: 201-210.
- HILKEN, G., C. S. WIRKNER & J. ROSENBERG, 2006. On the structure and function of the aortic diverticules of *Scutigera coleoptrata* (Chilopoda, Notostigmophora). – *Norwegian Journal of Entomology* 53: 107-112.
- JAMAULT-NAVARRO, C., 1984. Arterial walls as cephalic neurohemal organs in *Lithobius forficatus* L. (Myriapoda Chilopoda). – *Experimental Biology* 43: 97-108.
- KOWALEVSKY, A., 1892. Sur les organes excréteurs chez les Arthropodes terrestres. – *Travaux du Congrès international de Zoologie Moscou* 2: 187-229.
- KOWALEVSKY, A., 1893. Études expérimentales sur les glandes lymphatiques des Invertébrés (Communication préliminaire). – *Bulletin scientifique publié par l'Académie Imperiale des Sciences de Saint-Pétersbourg* 36: 273-295.
- KOWALEVSKY, A., 1895. Étude des glandes lymphatiques de quelques Myriapodes. – *Archives de Zoologie expérimentale et générale* 3: 591-616.
- NEVERMANN, L., 1996. Untersuchungen an Haemocyten von *Scolopendra cingulata* und *Lithobius forficatus* unter dem Aspekt zellulärer Abwehrreaktionen. – *Dissertation Justus-Liebig-Universität Giessen*.
- NEVERMANN, L., W. E. R. XYLANDER & G. SEIFFERT, 1991. The hemocytes of the centipede *Lithobius forficatus* (Chilopoda, Lithobiomorpha. Light and electron microscopic studies using in vitro techniques. – *Zoomorphology* 110: 317-327.
- NEWPORT, G., 1843. On the structure, relations, and development of the nervous and circulatory systems, and on the existence of the complete circulation of the blood in vessels, in Myriapoda and macrourous Arachnida. - First series. – *Philosophical Transactions of the Royal Society, London* 133 Part II: 243-302.
- ØKLAND, S., 1984. Changes in heart ultrastructure during development of *Strigamia maritima* Leach (Myriapoda, Chilopoda, Geophilidae). – *International Journal of Insect Morphology and Embryology* 13: 233-246.
- ØKLAND, S., A. TJØNNELAND, A. NYLUND, L. N. LARSEN & I. CHRIST, 1982. The membrane system and the sarcomere in the heart of *Lithobius forficatus* L. (Arthropoda, Chilopoda). – *Zoologischer Anzeiger* 208: 124-131.
- PALM, N.-B., 1954. The elimination of injected vital dyes from the blood in Myriapods. – *Arkiv för Zoologi* 6: 219-246.
- RILLING, G., 1960. Zur Anatomie des braunen Steinläufers *Lithobius forficatus* L. (Chilopoda). Skelettmuskelsystem, peripheres Nervensystem und Sinnesorgane des Rumpfes. – *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere* 78: 39-128.
- RILLING, G. 1968. *Lithobius forficatus*. Grosses Zoologisches Praktikum 13b. – Fischer, Stuttgart.
- ROSENBERG, J. & G. SEIFERT, 1975. Offene Hämolympgefäß am Sacculus der Maxillarnephridien von *Scutigera coleoptrata* L. (Chilopoda, Notostigmophora). – *Entomologica Germanica* 2: 167-169.
- SCHEFFEL, H., 1961. Untersuchungen zur Neurosekretion bei *Lithobius forficatus* L. (Chilopoda). – *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere* 79: 529-556.

- SEIFERT, G., 1967a. Das stomatogastrische Nervensystem der Chilopoden. – Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 84: 167-190.
- SEIFERT, G., 1967b. Der Ursprung des dorsalen Herznerfs der Lithobiiden (Chilopoda). – Experientia (Basel) 23: 452-453.
- SEIFERT, G. & J. ROSENBERG, 1973. Poröse Blutgefäße bei *Scutigera coleoptrata* L. (Chilopoda, Notostigmophora). – Experientia (Basel) 29: 1156-1157.
- SEIFERT, G. & J. ROSENBERG, 1978. Feinstruktur der Herzwand des Doppelfüßler *Oxidus gracilis* (Diplopoda: Paradoxosomatidae) und allgemeine Betrachtungen zum Aufbau der Gefäße von Tracheata und Onychophora. – Entomologica Germanica 4: 224-233.
- SUNDARA RAJULU, G., 1966. Cardiac physiology of a chilopod *Scolopendra morsitans*. – Journal of Animal Morphology and Physiology 13: 114-120.
- SUNDARA RAJULU, G., 1970. A comparative study of the free amino acids in the haemolymph of a millipede, *Spirostreptus asthenes*, and a centipede, *Ethmostigmus spinosus* (Myriapoda). – Comparative Biochemistry and Physiology 37: 339-344.
- SUNDARA RAJULU, G., 1972. On the mode of respiration of an estuarine centipede *Mixophilus indicus*. – Journal of Animal Morphology and Physiology 19: 181-190.
- SUNDARA RAJULU, G., 1973. Free amino acids in the hemolymph of Myriapoda. – Current Science 42: 95-96.
- SUNDARA RAJULU, G., 1974. A comparative study of the organic components of the hemolymph of a millipede *Cingalobolus bugnioni* and a centipede *Scutigera longicornis* (Myriapoda). – Symposia of the Zoological Society of London 32: 347-364.
- TURSMAN, D. & J. H. DUMAN, 1995. Cryoprotective effects of thermal hysteresis protein on survivorship of frozen gut cells for the freeze-tolerant centipede, *Lithobius forficatus*. – Journal of Experimental Biology. 272: 249-257.
- TURSMAN, D., J. H. DUMAN & C. A. KNIGHT, 1994. Freeze tolerance adaptations in the centipede, *Lithobius forficatus*. – Journal of Experimental Biology 268: 347-353.
- VARMA, L., 1971. On the morphology of the heart of the centipede *Scolopendra morsitans* Linn. (Chilopoda, Epimorpha). – Journal of Animal Morphology and Physiology 18: 111-120.
- WENNING, A., 1978. Struktur und Funktion des Exkretionssystems von *Lithobius forficatus* L. (Chilopoda, Myriapoda). – Zoologische Jahrbücher, Abteilung für allgemeine Zoologie und Physiologie der Tiere 82: 419-433.
- WIRKNER, C. S. & G. PASS, 2000. Comparative morphology of the circulatory organs in Chilopoda. – Fragmenta Faunistica, Warszawa 43 Supplement: 83-86.
- WIRKNER, C. S. & G. PASS, 2002. The circulatory system in Chilopoda: functional morphology and phylogenetic aspects. – Acta Zoologica (Stockholm) 83: 193-202.
- XYLANDER, W. E. R., 1992. Immunabwehr-Reaktionen bei Diplopoden und Chilopoden. – Habilitationssschrift Fachbereich Biologie Justus-Liebig-Universität Giessen.

## Chapter 9

# CHILOPODA – EXCRETORY SYSTEM

## Main excretory organs

Jörg Rosenberg, Andy Sombke & Gero Hilken

The main excretory organs in Chilopoda are the maxillary nephridia, only present in the Scutigeromorpha and Lithobiomorpha, and the Malpighian tubules. Additional excretory functions are provided by the nephrocytes and the fat body.

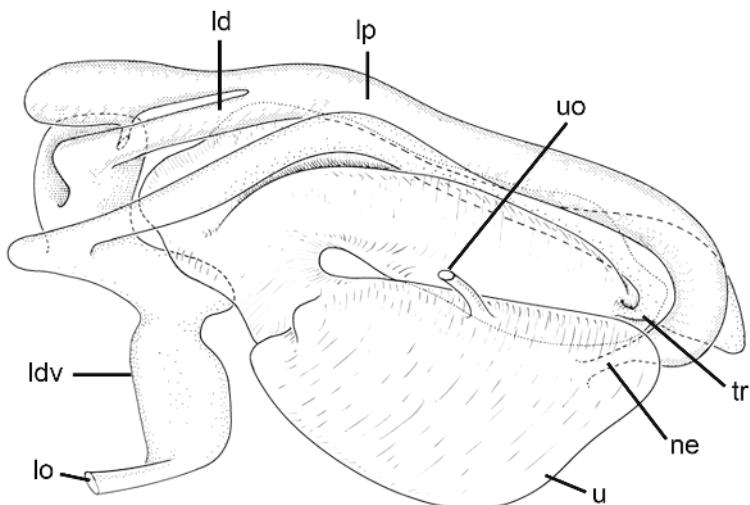
### *Maxillary nephridia*

#### *The maxillary nephridium of Scutigera coleoptrata*

The maxillary nephridium of Scutigeromorpha has been described histologically in *Thereuopoda clunifera* (Fahlander, 1938) and in *Scutigera coleoptrata* (Herbst, 1889, 1891; Gabe, 1967, 1972); the latter has been also studied at ultrastructural level (Rosenberg, 1979b). In this species the main part of the maxillary nephridium is situated between the coxae of the second maxillae. The nephridium is subdivided into a compact sacculus and a nephridial tubule folded four times, with two distinct regions: the labyrinth and the utriculus. Transitional epithelia connect the sacculus with the labyrinth and the labyrinth with the utricle. A dorso-ventral branch of the labyrinth opens into the maxillary organ at the base of the first maxillae. The utricle opens laterally near the base of the coxae of the second maxillae. The compact sacculus is nearly completely surrounded by the horseshoe-shaped utriculus and covers large parts of the nephridial canal (Fig. 9.1A). In *T. clunifera* the hemolymph is supplied by a branch of the artery of the second maxillae (Fahlander, 1938). In *S. coleoptrata* small hemolymph vessels are often in contact with the sacculus; their wall is perforated (Rosenberg and Seifert, 1975). Neurosecretory axons approach to the sacculus.

The surface of the compact sacculus is heavily folded and surrounded by a uniform basal lamina. The sacculus is formed by numerous nephrocytes; a wide cavity is not formed (Fig. 9.2A). The nephrocytes are described in detail below. Characteristic organelles are coated vesicles, tubular structures, and lysosomal bodies.

A



B

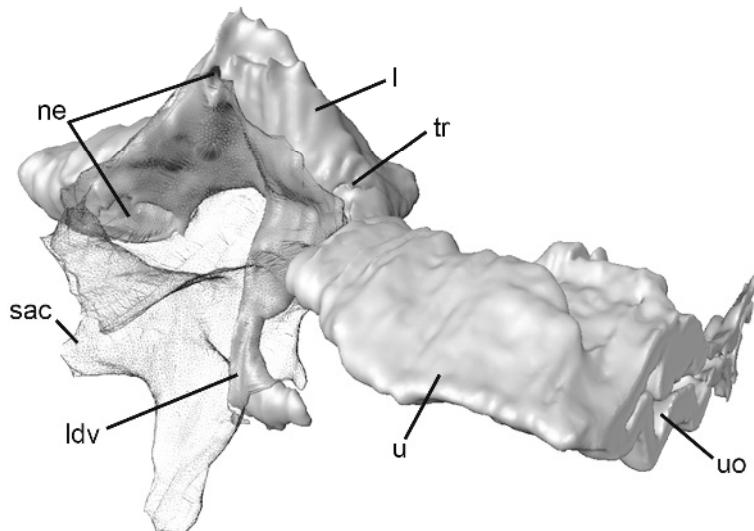


Fig. 9.1 Diagrammatic representation of maxillary nephridia. A *Scutigera coleoptrata*. The compact sacculus is not shown. B *Lithobius forficatus*. A original J. Rosenberg; B original A. Sombke.

l labyrinth; ld distal labyrinth; ldv dorso-ventral branch of labyrinth; lo opening of labyrinth; lp proximal labyrinth; ne nephrostome; sac sacculus; tr transitional zone; u utricle; uo opening of utricle

The nephrostome, a short duct that mediates between the sacculus and labyrinthal canal, described by Fahlander (1938) and Gabe (1972) as a transition segment, is about 20 µm long in *Scutigera coleoptrata*. The epithelium is formed by cubical cells, many of which are ciliated, about 5 µm high. Their cytoplasm is poor in organelles. Besides the nucleus, some Golgi bodies and mitochondria are visible, and glycogen deposits are conspicuous.

The nephridial canal is folded four times and is subdivided into a twice-folded tubular labyrinth and a thick-walled horseshoe-shaped utriculus (Fig. 9.1A). This antidromic canal system should allow concentration of the urine according to the counter-flow principle. The labyrinth and utriculus open separately. The single-layered epithelium of the nephridial canal is formed by transport epithelial cells with a distinct microvillar border and a conspicuous basal labyrinth with accompanying mitochondria.

The labyrinth consists of two nearly parallel, antidromic tubules; cell height is about 12–14 µm in the distal tubule and about 8 µm in the proximal one. At their connection a dorso-ventral tubule branches off and opens via a short cuticularised duct into the maxillary organ. The proximal tubule of the labyrinth opens into the utriculus. In the distal part of the labyrinth the microvillar border reaches up to 0.2 µm height; in the proximal part the microvilli are short. Alkaline phosphatase and PAS are detectable only within the microvillar border of the proximal part (Gabe, 1972). Cell protrusions fill the labyrinth canals, often occluding the distal segment.

The epithelium of the utricle is formed by columnar cells, 30–35 µm high, covered by a thick cuticle (about 1 µm) (Fig. 9.2D). The cells contain numerous microtubules and form a microvillar border about 2 µm high. The microvilli are hexagonally arranged and embedded into a subcuticular layer. The utricle opens to the outside via a short canal. Several epidermal glands are distributed between the canal cells. The labyrinth is connected to the utricle by a transition zone about 25 µm long. The cubic cells are covered by a thin cuticle. The transition zone is surrounded by muscle fibres. Axons are observable between the epithelial cells.

#### *The maxillary nephridium of Lithobius forficatus*

A detailed description of the fine structural organisation of the maxillary nephridium of *L. forficatus*, previously described with histological techniques (Herbst, 1891; Fahlander, 1938; Palm, 1954; Gabe, 1967, 1972; Rilling, 1968) was given by Rosenberg et al. (2009).

The paired maxillary nephridium of *L. forficatus* is situated lateral to the pleuro-ventral longitudinal musculature in the region of the first and second maxillae. The elongated nephridium is subdivided into a luminous sacculus, a sac-like labyrinth, and a bean-like

utriculus. As in Scutigeromorpha, two openings occur. The labyrinth opens at its beginning medially on the coxa of the second maxilla; the utriculus opens paramedially at the base of the first maxilla. There are two funnel-like openings from the sacculus into the labyrinth (Fahlander, 1938) (Fig. 9.1B). Alkaline phosphatase and PAS are detectable only within the microvillar border of the labyrinth (Gabe, 1972).

The sacculus is formed by typical podocytes which enclose a wide lumen (Fig. 9.2B). The nephridial canal (Fig. 9.1B), the labyrinth (Fig. 9.2C) and the utriculus are formed by transporting epithelia; the thick epithelium of the utriculus is covered by cuticle. The connections between sacculus and labyrinth and between labyrinth and utricle are formed by undifferentiated transitional cells, often with apical centrioles. The epithelium of a dorso-ventral branch is formed by unspecialized cells, covered by cuticle. Epidermal glands are intermingled between the ordinary epithelial cells and discharge their secretion into the duct. The utriculus forms a short conducting canal. The conducting canals of both utriculi fuse ventromedially to form a common duct that opens medially at the base of the first maxillae close to the opening of the first maxillary gland.

The gross structure of the maxillary nephridium of *S. coleoptrata* and *L. forficatus* is thus similar in the occurrence of a sacculus and a nephridial canal that is divided into two morphological and functional differentiated compartments, the labyrinth and the utriculus. However, the nephridia of these species differ considerably in detail. In *S. coleoptrata*, the compact sacculus is formed by a cluster of nephrocytes with numerous coated vesicles along the cortical labyrinth; the cytoplasm contains numerous tubular bodies, endosomes, and vacuoles (Rosenberg, 1979b). In *L. forficatus*, the sac-like sacculus is formed by podocytes, not homologous to the nephrocytes of the sacculus in *S. coleoptrata*. The fine structure is in accordance with the typical wide sacci of non-chilopodan arthropods. Sacculus and labyrinth are connected by an unpaired (*Scutigera*) or paired (*Lithobius*) transitional zone. Few vestigial cilia (*Scutigera*) or centrioles (*Lithobius*) are developed. The two conducting canals open on different parts of the head. In *Scutigera*, the dorso-ventral branch of the labyrinth consists of a transporting epithelium of high physiological activity, discharging into the maxillary organ at the base of the first maxilla (Rosenberg, 1979b; Hilken and Rosenberg, 2006). In *Lithobius*, the corresponding branch opens ventrally at the base of the second maxilla. It is formed by an undifferentiated epithelium, covered by a cuticle.

As well, the utriculus opens on different sides of the head: in *Scutigera*, laterally, at the base of the second maxillae; in *Lithobius*, medially, at the base of the first maxillae. In both *S. coleoptrata* and *L. forficatus*, the transport epithelia of the labyrinth and the utriculus are

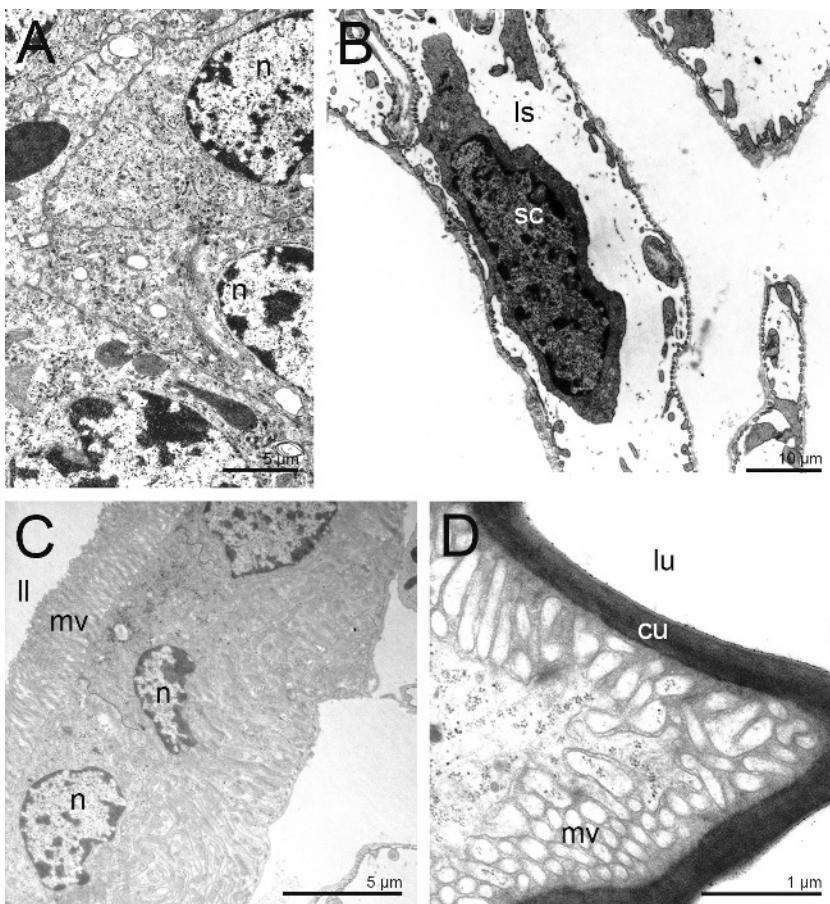


Fig. 9.2 Maxillary nephridium (EM). A *Scutigera coleoptrata*, compact sacculus, formed by nephrocytes. B *Lithobius forficatus*: sacculus, formed by podocytes. C-D *L. forficatus*: labyrinth and utricle. C Labyrinth cells with microvilli border. D Apex of an utricle cell with its cuticular lining. A Original Rosenberg; B-D Originals G. Hilken and J. Rosenberg.

cu cuticle; ll lumen of labyrinth; ls lumen of sacculus; lu lumen of utricle; mv microvilli border; n nucleus; sc cell of the sacculus

thought to minimize the loss of water. However, due to its elaborated folded and antidromic nephridial canal, *S. coleoptrata* seems to be more able to minimize dehydration.

In fact, this species colonizes drier habitats than *L. forficatus*. Actually, *S. coleoptrata* is a specialized surface-living, fast running centipede with long legs that is living above the soil. In contrast, *L. forficatus* requires moist soil habitats (Eisenbeis and Wichard, 1985).

### *Malpighian tubules*

The Malpighian tubules in Chilopoda are long, forwardly running and blind tubules that originate at the junction of the mid- and hindgut and discharge their excretion into the gut by way of a distinct ampulla. Usually, a single pair of Malpighian tubules is developed (exceptions: Scutigeromorpha and Craterostigmomorpha, see below).

*Scutigeromorpha*. – In *S. coleoptrata*, four Malpighian tubules are developed. Two of them discharge laterally into the gut through large ampullae, the other two are connected dorsally and ventrally of the gut by small ampullae (Dufour, 1824; Prunesco and Prunesco, 1996). The epithelium is a typical transporting epithelium (Fig. 9.3A,B).

*Lithobiomorpha*. – The two long Malpighian tubules of *Lithobius tricuspis* extend anteriorly to near the head, continue along the midgut and open into the gut through ampullae. In adult specimens ca. 14–18 mm long, the length of a tubule is about 30 mm, the diameter about 0.2 mm. Several cubical cells with a well developed microvillar border are seen in a tubule's cross-section. The basal part of the cells is striated. Three segments are distinguishable by size and height of the cells. Only some longitudinal muscle fibres

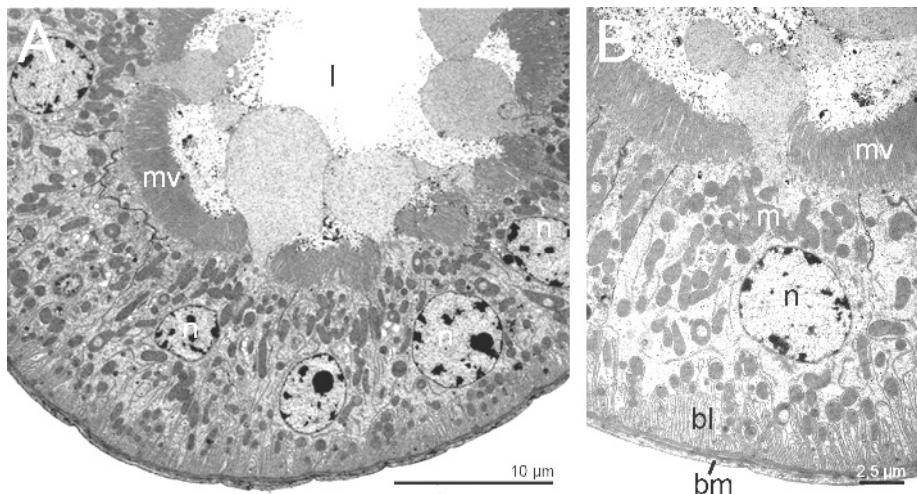


Fig. 9.3 *Scutigera coleoptrata*, Malpighian vessel, distal part. A Overview. B Transport epithelial cell of a Malpighian vessel with an extended microvilli border and basal labyrinth. Original C. H. G. Müller.

bl basal labyrinth; bm basal lamina; l lumen of Malpighian vessel; m mitochondria; mv microvilli border; n nucleus

surround the tubules (Bertheau, 1971). In *L. forficatus* the two Malpighian tubules run slightly convoluted and parallel to the midgut. According to Rilling (1968) the thick-walled ampulla opens into the gut in the posterior part of the midgut. In contrast, Palm (1954) reported that the tubules open into the gut at the border of the mid- and hindgut. The question deserves revisiting.

At ultrastructural level, the Malpighian tubules of *L. forficatus* are formed by a typical transport-active epithelium (Füller, 1966). Apically, the cells develop a thick border of microvilli, less numerous and shorter in the distal part of the tubule. Pinocytotic vesicles are often observable at the cell base. Numerous mitochondria are distributed beneath the microvilli. The cell's middle region contains the nucleus, some endoplasmic reticulum, Golgi complexes, and mitochondria. The basal part of the cell is characterized by a well developed basal labyrinth, whose folded membranes are accompanied by numerous elongated mitochondria. The lumen of the cells contains concentrically stratified excreta (urosphaerites), which probably consist of calcium urate and other calcium salts.

*Craterostigmomorpha*. – There are three Malpighian tubules in both *Craterostigmus tasmanianus* and *C. crabilli*. One pair opens into the midgut via a larger ampulla, the unpaired tubule via a smaller one. Regional differentiations are not observable at a histological level (Prunesco and Prunesco, 1996, 2006; Edgecombe and Giribet, 2008).

*Scolopendromorpha*. – In *Cryptops hortensis*, the two Malpighian tubules discharge excreta via an ampulla into the gut at the boundary between mid- and hind-gut (Plateau, 1878). The ampulla is lined by cells similar to those of the hindgut, hence Balbiani (1890) regarded the tubules as belonging to this part of the digestive tract. Only a few cubical cells with a well-developed microvilli border form in cross-section the Malpighian tubule. The basal part of the cells appears striated. Only some longitudinal muscle fibres surround the tubules (Bertheau, 1971).

In *Scolopendra* spp., the two Malpighian tubules extend forwards up to the second leg-bearing segment and open into the gut at the boundary between mid- and hind-gut. In *S. cingulata*, the tubular epithelium is formed in cross-section by a large number of high prismatic cells with a faint microvillar border; the basal part of the cells appears to some extent striated. A regional differentiation is not observed. A network of longitudinal and transverse muscular fibres is developed (Bertheau, 1971). In *S. subspinipes*, the tubules form a series of undulation or loops. They taper very gradually towards their rounded ends; the narrowest region is 0.2 mm in diameter. In transverse section, a tubule consists of 40 to 75 columnar, non-microvillate epithelial cells; these measure 300 µm in length in the basal region but are shorter in the distal region of the tubule. Regenerative epithelial cells

are developed. External to the basal lamina, the tubule is surrounded by a sheet of flattened cells. Muscular elements as well as an ampulla seem not to be present (likewise for *S. morsitans*; Jangi, 1966). In starved animals, the lumen of the tubules contains a few uric acid crystals, otherwise the fluid is almost clear (Wang and Wu, 1947).

*Geophilomorpha*. – In Geophilomorpha, the two Malpighian tubules extend up to the posterior third of the mid-gut. They open into the digestive tract at the boundary between mid- and hind-gut. In *Stenotaenia linearis* and *Pachymerium ferrugineum*, there are about 10 cubical cells in any distal cross section of the tubule; in the proximal region the number increases to about 20 columnar cells. A microvillar brush border is developed; the basal part of the cells appears striated. A few longitudinal muscle fibres surround the tubules (Bertheau, 1971).

### *Excretion*

Functional data on excretion are available for *L. forficatus*, *L. variegatus* and *S. cingulata* (Bennett and Manton, 1962; Wenning, 1977, 1978, 1979, 1989; Wenning et al., 1991).

The excretory function of the maxillary nephridia is hitherto only inferred from histological and fine-structural investigations. These organs have a structure similar to the well-known nephridia of crustaceans and insects (Fahlander, 1938; Palm, 1954; Gabe, 1972). The excretory function is also suggested by the fine-structural organization of the cells of the sacculus and the labyrinthal canal. In the sacculus, primary urine might be formed by ultrafiltration. Along the transporting epithelia of the labyrinth canal a concentration of the urine occurs by resorptive and secretory processes (Gabe, 1972). Within the utriculus, resorption of water and ions leads to a hypertonic urine. In *L. forficatus*, injected India ink, carmine suspension and trypan blue are accumulated within the sacculus, whereas Congo red, lithium carminate and tolulylene red were found in the lumen of the labyrinth and utriculus (Palm, 1954).

The function of the nephridia in chilopods as excretory organs has been questioned by Bennett and Manton (1962), who remarked that nephridia are only present in the anamorphic centipedes but not in the Epimorpha, which should thus rely on other organs for excretion. A possible function of the nephridia might be the production of grooming fluid (Bennett and Manton, 1962).

*Lithobius* sp. is also able to eliminate vital dyes from the body fluid through the Malpighian tubules (Kowalevsky, 1892, 1892/93, 1895; Palm, 1954). Fluid secretion by Malpighian tubules was studied in *L. forficatus*. Isolated tubules continued to produce urine for 24 hours. Unlike many insects, *L. forficatus* exhibits strongly  $\text{Na}^+$ -dependent,  $\text{K}^+$ -

independent urine formation.  $\text{Cl}^-$  is the main anion in the fluid released from the ampullae and whole isolated tubules. *L. forficatus* is not able to form concentrated urine. The osmotic concentration of the fluid of the hind-gut is lower than in the hemolymph. This leads to the conclusion that in *L. forficatus* the Malpighian tubules contribute greatly to volume regulation, while the rectum is important for ion regulation (Wenning, 1978, 1989; Wenning et al., 1991).

The epithelium of the hind-gut of *L. forficatus* is not able to resorb fluid that is hypotonic compared to the hemolymph. This species seems to produce a hypoosmotic final urine in order to discharge excessive ions ingested by food. Under these circumstances, drastically limited urine production is essential for water conservation (Wenning, 1977, 1979).

It is not clear whether the catabolism of the centipedes is uricotelic or ammoniotelic. Crystalline uric acid was reported from the Malpighian tubules of several Chilopoda (Plateau, 1878; Gibson-Carmichael, 1885; Wang and Wu, 1947), but not in all investigate species (Berthau, 1971). The urosphaerites in *L. forficatus* probably consist of calcium urate and other calcium salts. The fine structural composition varies along the tubules (Fuller, 1966). Bennett and Manton (1962) could not detect crystalline uric acid in the Malpighian tubules of *L. forficatus* over the year. Uric acid is present in a considerable amount in dry faeces: *Scolopendra heros* (8.7%) (Wang and Wu, 1947; Horne, 1969), *L. forficatus* (15%), and *L. melanops* (up to 25%) (Hubert, 1977). In *L. forficatus* only 1-8% of the total nitrogen in the faeces is represented as uric acid nitrogen, whereas 50 to 80% is ammonia nitrogen (Bennett and Manton, 1962). In several Chilopoda (*Scutigera coleoptrata*, *L. forficatus*, *L. piceus*, *L. crassipes*, *L. melanops*, *Geophilus carpophagus*, *G. flavus*, *Strigamia acuminata*, *Haplophilus subterraneus*, *Scolopendra cingulata*, *Cryptops anomalans*, *C. hortensis*), both uric acid as well as ammonia have been demonstrated, together with a uricase. Only in *Henia vesuviana* was uric acid not detected (Hubert and Razet, 1965; Hubert, 1968, 1969, 1977).

## The maxillary organ of the Notostigmophora

Gero Hilken, Jörg Rosenberg & Carsten H. G. Müller

### *Structure*

The maxillary organ is located inside the posterior coxal lobes of the first maxillae (Fig. 9.4B). It consists of two deep, sac-like invaginations of the epidermal integument.

Both sacs are joined dorsomedially by the epithelium of the maxillary organ gland (Hilken et al., 2003). The glandular epithelium surrounds a large reservoir that opens ventrally into the maxillary organ (Fig. 9.4A). The maxillary organ is connected in its most anterior part to the oral cavity. In its posterior end, the large reservoir forms two narrow canals that extend laterally and connect the maxillary organ with the dorsoventral part of the labyrinth canal of the maxillary nephridium (Rosenberg, 1979b; Hilken and Rosenberg, 2006).

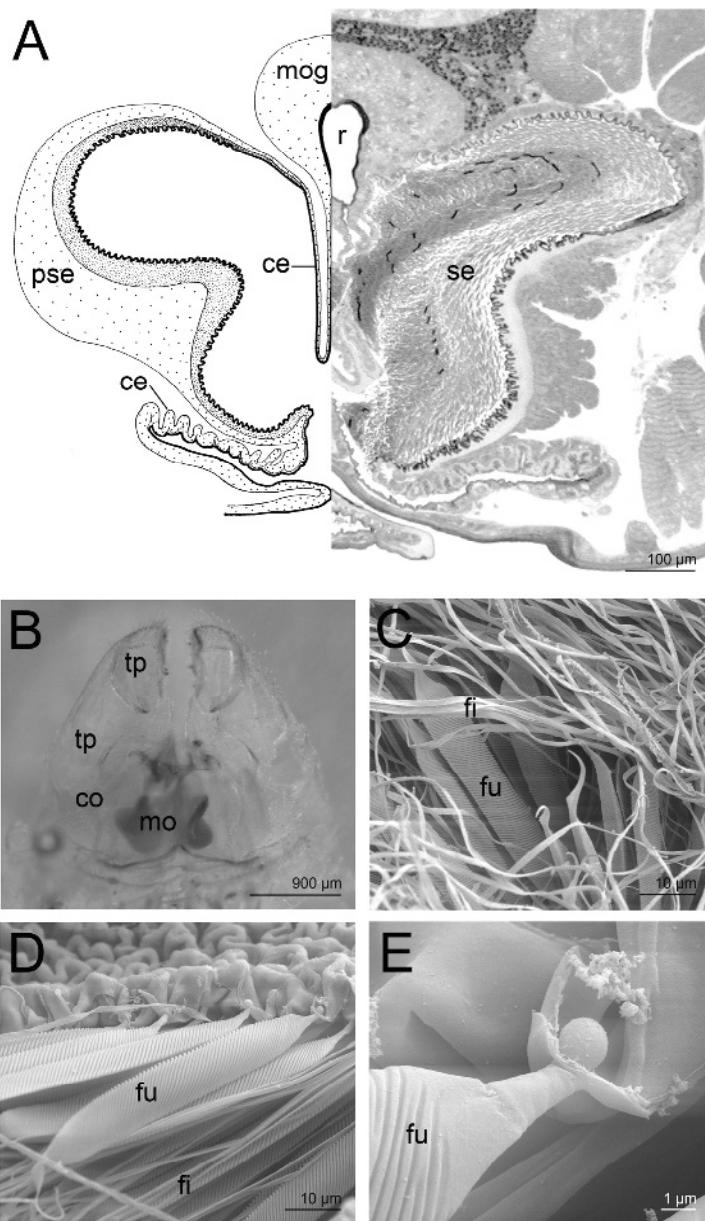
The maxillary organ of *Scutigera coleoptrata* is lined by a single-layered epithelium with its basal lamina. The epithelium is completely covered by a cuticle. According to cell shape, Hilken and Rosenberg (2006) recognize between two types of epithelia: a simple cuboidal epithelium of varying height and differentiation and a pseudostratified columnar epithelium (Fig. 9.4A). The latter is the most prominent feature of the maxillary organ. In light microscopy, the cell nuclei of the epithelium seem to be stacked in several layers. That gives the impression of a “multi-layered epithelium”. Its characteristic feature is the specialized and strongly folded cuticle. The entire cuticle is studded with hundreds of setae that protrude deeply into the maxillary organ. Two different types can be distinguished, filiform (Fig. 9.4C) and fusiform setae (Fig. 9.4D-E), mainly located in the middle and the lateral part of the maxillary organ, respectively. The smooth filiform setae, oval in cross section, are about 180 µm in length and about 1.3 µm in width. The helically grooved fusiform setae, about 70 µm in length and about 10 µm in width, show at the base a ring-like annular notch and a spherical cuticular body (Fig. 9.4E) and distally end in a thin, hooked tip (Fig. 9.4C-E).

### *Function*

Latzel (1880) interpreted this structure as a sense organ, Haase (1884) and Heathcote (1885) suggested that the maxillary organ functions as an auditory organ, whereas several authors suggested that this organ can be everted and acts with its setae as a cleaning organ for preening the antennae and the legs (Verhoeff, 1902-1925; Manton, 1965; Desbal-

Fig. 9.4 Maxillary organ of *Scutigera coleoptrata*. A Combination of semischematic and histological representations of the middle part of the maxillary organ. B Ventral view of the first maxillae with the translucent maxillary organ (Hoyer's solution). C Fusiform seta with its hooked ends and filiform setae (SEM). D Part of the folded cuticle with filiform and mainly fusiform setae (SEM). E Basal connection of a fusiform seta to the cuticle by a spherical cuticular body (SEM). Originals G. Hilken and J. Rosenberg.

ce cuboidal epithelium; co coxa; fi filiform seta; fu fusiform seta; mo maxillary organ; mog maxillary organ gland; pse pseudostratified columnar epithelium; r reservoir; se setae; tp teleopodite



mes, 1992; Borucki, 1996). However, using video recording, the organ's function in cleaning was rejected by Rosenberg et al. (2004, 2005), as the maxillary organ is not everted during preening.

Borucki (1996) noted that the maxillary organ could be squeezed and retracted by different muscles. He compared the setae of the maxillary organ with tracheae and discussed whether this organ has been developed from pairs of tracheal bundles. Hilken and Rosenberg (2006) show that the maxillary organ communicates with the oral cavity, the maxillary organ gland, the maxillary nephridium and a number of epidermal glands. Thus, they described the maxillary organ as a multifunctional organ. On the one hand, it may function as a storage site for part of the excretion fluid from the maxillary nephridia and the secretion from the maxillary organ gland and other epidermal glands. The pseudostratified epithelium with its folded cuticle allows extending the maxillary organ to within the first maxillae, when its lumen is filled up with fluids. The latter, when reaching the mouth cavity, may be used as preening fluid. On the other hand, as the organ stores excreta from the maxillary nephridia, it is thought that ammonia in the excretory fluid evaporates via the setae and the ventral opening of the maxillary organ, while part of the fluid is possibly recovered via the connection to the oral cavity, as an adaptation to dry environments.

## Nephrocytes

Jörg Rosenberg, Carsten H.G. Müller & Gero Hilken

Nephrocytes have been investigated by electron microscopy by Rosenberg (1973, 1974, 1978, 1979a), Seifert and Rosenberg (1974), Rosenberg et al. (1997) and Vandenbulcke et al. (1998). The nephrocytes described by TEM techniques are in a good agreement with the “filament acide” or “cellule à carminates” of the earliest light microscopy investigations.

*Scutigeromorpha*. – In *Scutigera coleoptrata* nephrocytes form a compact endocrine head gland (*glandula capitis*) (Rosenberg, 1974) (see Chapter 10), and the compact sacculus of the maxillary nephridium (Rosenberg, 1979b).

*Lithobiomorpha*. – In *Lithobius forficatus* nephrocytes form an endocrine gland (*glandula ecdysialis*), which surrounds the mandibular glands as so-called lymphatic cell strands (Seifert and Rosenberg, 1974) (see chapter 10).

*Scolopendromorpha*. – In *Cryptops hortensis* strands of nephrocytes surround the Malpighian tubules (Rosenberg, 1979a) and are also distributed along the trunk within the fat body (Rosenberg et al., 1997).

*Geophilomorpha*. – In different Geophilomorpha (*Haplophilus subterraneus*, *Stenotaenia linearis*, *Geophilus flavus*) strands of nephrocytes surround the perineural sinus or the supraneural vessel (Rosenberg, 1978).

### *Fine structure*

Ultrastructurally, centipede nephrocytes are typical podocytes with deep extracellular cortical labyrinth canals of variable width, formed by numerous radiating foot processes with their pedicels (Fig. 9.5A,B). A nephrocyte is surrounded by a distinct and homogenous basal lamina 150-300 nm high (Fig. 9.5B,D). Close to the basal lamina, the clefts of the cortical labyrinth, formed by pedicels, become narrow. At the entrance to the labyrinthine channels narrow slits with a width of up to 15 nm are usually bridged by a single diaphragm; sometimes 2 to 3 diaphragms occur (stitch-like desmosomes) (Fig. 9.5 D). Here the plasma membrane bears an electron-dense deposit that extends into the cytoplasm.

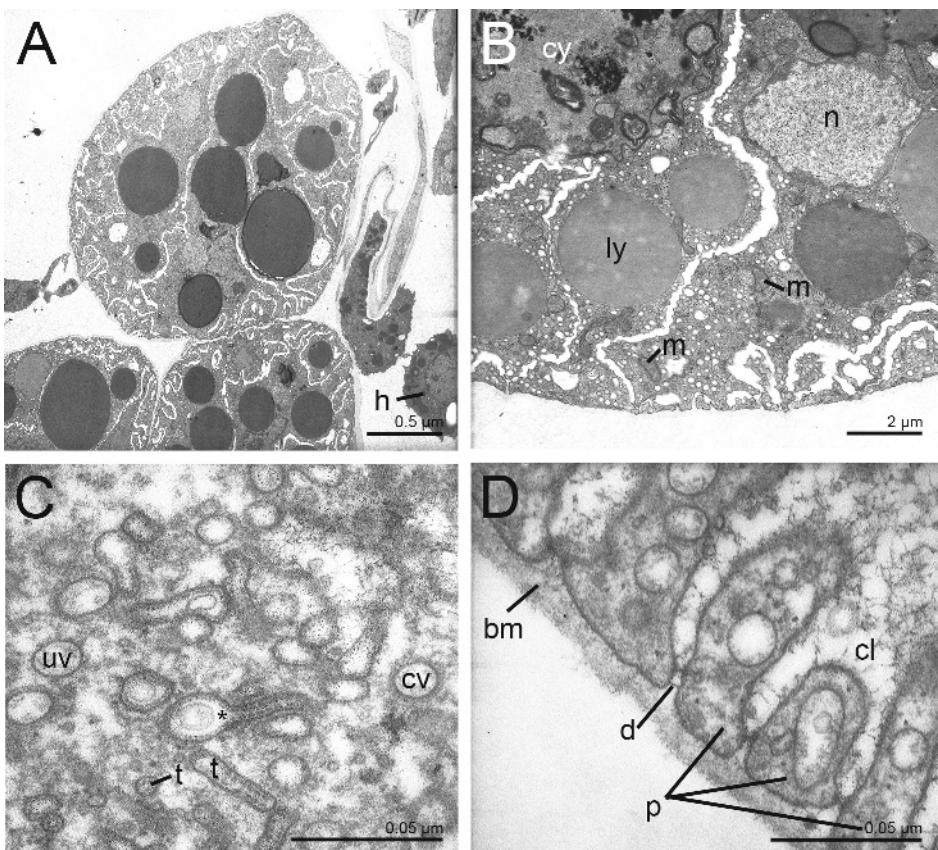
Basal lamina and diaphragms form an extracellular barrier that filters the hemolymph entering the extracellular labyrinthine channels. Rather large particles are able to pass the basal lamina (Crossely, 1984; Rosenberg et al., 1997).

On the luminal side the membranes of the infoldings are covered by a prominent surface coat of filamentous material (Fig. 9.5D). These regions are the site of very intense endocytosis. Filamentous material is still present in these invaginations. On the cytoplasmic side a clathrin coat occurs that not only surrounds the coated pits but also the resulting coated vesicles. Vesicles deeper in the cytoplasm lose the clathrin coat. The diameter of coated and uncoated vesicles ranges from 120-300 nm (Fig. 9.5C). Uncoated vesicles fuse to larger electron transparent vacuoles (endosomes), clearly distinguishable by filamentous material forming a regular pattern along the inner side of their membranes. Fusions of endosomes occur regularly.

Other characteristic elements of nephrocytes are tubular elements about 60 nm in diameter, more than 0.6 µm long. The inner surface of its membrane is lined by electron

Fig. 9.5 Nephrocytes. A-B: *Stenotaenia linearis*. A Overview of several nephrocytes (2.200 x). B Margin of a nephrocyte showing podocytic character (6.000 x). C-D *Cryptops hortensis*. C Part of the cytoplasm with coated vesicles, uncoated vesicles and tubular elements. Note the fusion of a tubular element with an endosome (\*) (40.000 x). D Part of the cortical labyrinth of a nephrocyte (40.000 x). A-D originals J. Rosenberg.

bm basal lamina; cl cortical labyrinth; cv coated vesicles; cy cytolysosome; d diaphragm; h hemocyte; ly lysosome; m mitochondrion; n nucleus; p pedicels; t tubular elements; uv uncoated vesicles



dense particles of about 25 nm in diameter. They are arranged in a helical pattern, leaving an electron-lucent central core of about 20 nm. Frequently tubules fuse with endosomes (Fig. 9.5C). The presence of coated and uncoated vesicles, the fusion of the latter to endosomes, and their connection with tubular elements point to a receptor-mediated endocytosis (Rosenberg et al., 1997).

Two types of vacuoles can be distinguished within the nephrocytes. In the central part of a nephrocyte some often very large vacuoles are present, filled with bulks of osmiophilic material. Membranous residues inside the vacuole indicate that it is a cytolysosome (Rosenberg, 1978, 1979b). Within the cortical and central part of nephrocytes, smaller spherical to oval vacuoles are distributed, filled with fine granular material of different electron density (Rosenberg, 1978, 1979b) (Fig. 9.5A, B).

The nucleus of the nephrocytes is voluminous and lobed. Near the nucleus only a few cisternae of rough endoplasmic reticulum and Golgi complexes are noticeable. Free ribosomes are frequently found, and mitochondria are distributed throughout the cell (Fig. 9.5B).

#### *Function*

There is no clear-cut evidence of the function of nephrocytes in Chilopoda. Early authors suggested that these cells play a role in cleaning body fluids. The elimination of injected trypan blue is surprising: in *Lithobius forficatus*, nephrocytes will completely clear the hemolymph of 10 ml trypan blue (2%) within 4 h. Trypan blue is stored to a large amount within the lymphatic tissue around the mandibular gland and is not excreted by the nephridia or Malpighian tubules (Palm, 1954; Rilling, 1968).

The basal lamina and the diaphragms represent the extracellular site of filtration for hemolymph components before they are taken up by the cells by receptor-mediated endocytosis. Only colloidal gold and cationized ferritin pass through and reach the cytoplasm (Rosenberg et al., 1997).

On the other hand, the nephrocytes of the lymphatic tissue of *L. forficatus* may play an important role in the detoxification of cadmium and lead. The large electron-dense primary lysosomes are the main organelles to accumulate heavy metals. Nephrocytes in Chilopoda might thus be involved in the excretory process involving uptake, accumulation, degradation, and removal of hemolymph constituents (Vandenbulcke et al., 1998).

In *L. forficatus* the nephrocytes of the lymphatic tissue (glandula ecdysialis) might act as an endocrine gland that synthesizes and exports moulting hormones. This is supported by experimental (Scheffel, 1969, 1979, 1987), cytological (Seifert and Rosenberg, 1974), immunological (Bidmon et al., 1987; Seifert and Bidmon, 1988), and biochemical investigations (Leubert et al., 1979; Leubert, 1986; Descamps et al., 1992; Descamps and Lafont, 1993; Dolle et al., 1993) (see chapter 10). Phagolysosomes, resulting from the fusion of endosomes and lysosomes, are thought to be the sites of synthesis of the ecdysteroid hormones from cholesterol or its metabolites taken up from the hemolymph (Seifert, 1990). In vitro isolated glands release ecdysone as well as 20-hydroxyecdysone into the incubation medium (Leubert, 1986) and convert 5 $\beta$ -ketadiol into 2-deoxyecdysone (Descamps and Lafont, 1993). However, the conversion of precursors into ecdysteroids did not occur in these glands (Dolle et al., 1993). Therefore, the nephrocytes might have only storage and releasing function for ecdysteroids synthesized elsewhere in the body. Other possible sites of ecdysteroid synthesis are the

ovaries (Leubert et al., 1982). Nevertheless, Descamps and Lafont (1993) considered these strands of nephrocytes to be the putative ecdysial gland of *L. forficatus*.

### References

- BALBIANI, E.-G., 1890. Étude anatomique et histologique sur le tube digestif des *Cryptops*. – Archives de Zoologie expérimentale et générale (2) 8: 1-82.
- BENNETT, D. S. & S. M. MANTON, 1962. Arthropod segmental organs and Malpighian tubules with particular reference to their function in Chilopoda. – Annals and Magazine of Natural History (13) 5: 545-556.
- BERTHEAU, P., 1971. Histologie comparée des tubes de Malpighi de quelques Chilopodes (Myriapodes). – Comptes Rendus hebdomadaires des Séances de l'Académie des Sciences, Paris, D 272: 2913-2915.
- BIDMON, H. J., G. SEIFERT, & J. KOOLMAN, 1987. Lokalisation von Ecdysteroiden und ihren Rezeptoren in Evertebraten. – Verhandlungen der Deutschen Zoologischen Gesellschaft 80: 157-158.
- BORUCKI, H., 1996. Evolution und phylogenetisches System der Chilopoda (Mandibulata, Tracheata). – Abhandlungen des naturwissenschaftlichen Vereins in Hamburg, Neue Folge 35: 95-226.
- CROSSLEY, A. C., 1984. Nephrocytes and pericardial cells. – Pp. 487-515 in: G. A. KERKUT & L. J. GILBERT (eds.) Comprehensive insect physiology, biochemistry, and pharmacology. – Oxford-New York: Pergamon Press.
- DESBALMES, G., 1992. Funktions-Anatomie des Fressapparates der Chilopoda: Die Kopfregion von *Theatops erythrocephalus* (C. L. Koch) sowie deren Kauapparat im funktionellen Vergleich mit *Scolopendra cingulata* und *Scutigera coleoptrata*. – Dissertation aus der Formal- und naturwissenschaftlichen Fakultät, Universität Wien.
- DESCAMPS, M. & LAFONT, R., 1993. Conversion of different putative ecdysteroid precursors in *Lithobius forficatus* L. (Myriapoda, Chilopoda). – Insect Biochemistry and Molecular Biology 23: 481-489.
- DESCAMPS, M., B. LEU & B. CHARIB, 1992. Ecdysteroid changes during the life cycle of the centipede *Lithobius forficatus* L. (Myriapoda, Chilopoda). – Advances in Comparative Endocrinology 1: 193-196.
- DOLLE, F., C. HETRU, B. ROUSSEAU, F. SOBRIOS, C. BLAIS, R. LAFONT, M. DESCAMPS & B. LUU, 1993. Synthesis of a tritiated 3-dehydroecdysteroid putative precursor of ecdysteroid biosynthesis. – Tetrahedron 49: 2485-2498.
- DUFOUR, L. J., 1824. Recherches anatomiques sur le *Lithobius forficatus* et la *Scutigera lineata*. – Annales des Sciences naturelles, Zoologie (1) 2: 81-99.
- EDGEcombe, G. D. & G. GIRIBET, 2008. A New Zealand species of the trans-Tasman centipede order Craterostigmomorpha (Arthropoda: Chilopoda) corroborated by molecular evidence. – Invertebrate Systematics 22: 1-15.
- EISENBEIS, G. & W. WICHARD, 1985. Atlas zur Biologie der Bodenarthropoden. – G. Fischer, Stuttgart-New York.
- FAHLANDER, K., 1938. Beiträge zur Anatomie und systematischen Einteilung der Chilopoda. – Zoologiska Bidrag från Uppsala 17: 1-148.
- FÜLLER, H., 1966. Elektronenmikroskopische Untersuchungen der Malpighischen Gefäße von *Lithobius forficatus* (L.). – Zeitschrift für wissenschaftliche Zoologie 173: 191-217.

- GABE, M., 1967. Caractères cytologiques et histoquimiques du rein maxillaire des Chilopodes. – Comptes rendus de l'Académie des Sciences, Paris, D 264: 726-729.
- GABE, M., 1972. Contribution à l'histologie du rein maxillaire des Chilopodes. – Annales des Sciences naturelles, Zoologie et Biologie animale (12) 14: 105-129.
- GIBSON-CARMICHAEL, T. D., 1885. Notes on the anatomy of the Myriapoda. – Proceedings of the Royal Physical Society of Edinburgh 8: 377-381.
- HAASE, E., 1884. Schlundgerüst und Maxillarorgan von *Scutigera*. – Zoologische Beiträge I: 97-108.
- HEATHCOTE, F. B., 1885. On a peculiar sense organ in *Scutigera coleoptrata*, one of the Myriapoda. – Quarterly Journal of Microscopic Science 25: 253-260.
- HERBST, C., 1889. Anatomische Untersuchungen an *Scutigera coleoptrata*. Ein Beitrag zur vergleichenden Anatomie der Articulata. – Inaugural-Dissertation, Philosophische Fakultät Jena: 1-37.
- HERBST, C., 1891. Beiträge zur Kenntnis der Chilopoden (Drüsen; Coxalorgan; Gefäßsystem und Eingeweidenervensystem). – Bibliographia zoologica 3 (9): 1-43.
- HILKEN, G., C. BROCKMANN & J. ROSENBERG, 2003. The maxillary organ gland: Description of a new head gland in *Scutigera coleoptrata* (Chilopoda, Notostigmophora). – African Invertebrates 44: 175-184.
- HILKEN, G. & J. ROSENBERG, 2006. Ultrastructure of the maxillary organ of *Scutigera coleoptrata* (Chilopoda, Notostigmophora): Description of a multifunctional head organ. – Journal of Morphology 267: 152-165.
- HORNE, F. R., 1969. Purine excretion in five scorpions, an uropygid and a centipede. – Biological Bulletin 137: 155-160.
- HUBERT, M., 1968. Contribution à l'étude des organes excréteurs et de l'excrétion chez les Myriapodes (Progonéates et Opisthogonéates). – Archives des Sciences physiologiques 22: 93-109.
- HUBERT, M., 1969. A propos de l'excrétion d'acide urique et d'ammoniaque chez les Myriapodes. – Bulletin du Muséum national d'Histoire naturelle (2) 41, Suppl. 2: 72-74.
- HUBERT, M., 1977. Contribution à l'étude des organes excréteurs et de l'excrétion chez les Diplopodes et les Chilopodes. – Ph. D. Thesis, Université de Rennes. No 264.
- HUBERT, M. & P. RAZET, 1965. Sur les principaux éléments du catabolisme azoté chez les Myriapodes. – Comptes rendus de l'Académie des Sciences, Paris, D 261: 797-800.
- JANGI, B. S., 1966. *Scolopendra* (The Indian Centipede). – The Zoological Society of India, Calcutta.
- KOWALEVSKY, A., 1889. Ein Beitrag zur Kenntnis der Exkretionsorgane. – Biologisches Zentralblatt 9: 33-47, 65-76, 127-128.
- KOWALEVSKY, A., 1892. Sur les organes excréteurs chez les arthropodes terrestres. – Travaux du Congrès international de Zoologie, Moscou 2: 187-229.
- KOWALEVSKY, A., 1895. Étude des glandes lymphatiques de quelques Myriapodes. – Archives de Zoologie expérimentale et générale (3) 3: 591-616.
- LATZEL, R., 1880. Die Myriopoden der Österreichisch-Ungarischen Monarchie. Erste Hälfte: Die Chilopoden. – A. Hölder, Wien.
- LEUBERT, F., 1986. Untersuchungen zur Ecdysteroid-Biosynthese durch das Lymphstrang-Gewebe von *Lithobius forficatus* (L.) (Chilopoda). – Wissenschaftliche Zeitschrift der Pädagogischen Hochschule Erfurt-Mühlhausen, Mathematisch-naturwissenschaftliche Reihe 22: 73-77.
- LEUBERT, F., H. EIBISCH, H. KROSCHWITZ & H. SCHEFFEL, 1982. Ecdysteroid Biosynthese durch das Ovar von *Lithobius forficatus* (L.) (Chilopoda). – Zoologische Jahrbücher, Abteilung für Allgemeine Zoologie und Physiologie der Tiere 83: 65-476.

- LEUBERT, F., H. EIBISCH & H. SCHEFFEL, 1979. Isolierung und Charakterisierung des Häutungshormons von *Lithobius forficatus* L. (Chilopoda). – Zoologische Jahrbücher, Abteilung für Allgemeine Zoologie und Physiologie der Tiere 83: 334-339.
- MANTON, S. M., 1965. The evolution of arthropod locomotory mechanisms. Part 8. Functional requirements and body design in Chilopoda, together with a comparative account of their skeleto-muscular systems and an appendix on a comparison between burrowing forces of annelids and chilopods and its bearing upon the evolution of the arthropodan haemocoel. – Journal of the Linnean Society of London, Zoology 46: 251-483.
- PALM, N.-B., 1954. The elimination of injected vital dyes from the blood in Myriapods. – Arkiv för Zoologi 6: 219-246.
- PLATEAU, F., 1878. Recherches sur les phénomènes de la digestion et sur la structure de l'appareil digestif chez les Myriapodes de Belgique. – Mémoires de l'Académie royale des Sciences, des Lettres et des Beaux-Arts de Belgique 42: 1-94.
- PRUNESCO C. C. & P. PRUNESCO, 1996. Supernumerary malpighian tubules in chilopods. In: Acta Myriapodologica, (Geoffroy, J. J., Mauries, J. P., & Nguyen Duy-Jacquemin, M. eds.). – Mémoires du Muséum national d'Histoire naturelle 169: 437-40.
- PRUNESCO, C. C. & P. PRUNESCO, 2006. Rudimentary supernumerary malpighian tubules in the order Craterostigmomorpha Pocock 1902. – Norwegian Journal of Entomology 52: 113-118.
- RILLING, G., 1968. *Lithobius forficatus*. Grosses Zoologisches Praktikum 13b. – Fischer, Stuttgart.
- ROSENBERG, J., 1973. Eine bisher unbekannte Drüse im Kopf von *Scutigera coleoptrata* L. (Chilopoda, Notostigmophora). – Experientia 29: 690-692.
- ROSENBERG, J., 1974. Topographie und Ultrastruktur der endokrinen Kopfdrüsen von *Scutigera coleoptrata* L. (Chilopoda, Notostigmophora). – Zeitschrift für Morphologie der Tiere 79: 311-321.
- ROSENBERG, J., 1978. Zur Ultrastruktur der Nephrocyten von Erdläufern (Chilopoda: Pleurostigmophora: Geophilomorpha). – Entomologica Germanica 4: 24-32.
- ROSENBERG, J., 1979a. Fine structure of the "lymphatic tissue" of *Cryptops hortensis* (Chilopoda, Scolopendromorpha): General organization and intercellular junctions. – In: CAMATINI, M. (ed.): Myriapod Biology. – Academic Press, London, New York: 288-294.
- ROSENBERG, J., 1979b. Topographie und Feinstruktur des Maxillarnephridium von *Scutigera coleoptrata* L. (Chilopoda, Notostigmophora). – Zoomorphologie 92: 141-159.
- ROSENBERG, J., M. BRENNER & H. GREVEN, 2004. Putzverhalten und Trinken bei *Scutigera coleoptrata* L. (Chilopoda, Scutigeromorpha). – Entomologie heute 16: 83-92.
- ROSENBERG, J., M. BRENNER & H. GREVEN, 2005. Preening and drinking in *Scutigera coleoptrata* (Chilopoda: Scutigeromorpha) (Video-film) – Peckiana 4: addendum: coverback.
- ROSENBERG, J., E. KRÜGER & W. PETERS, 1997. Intense receptor-mediated endocytosis in nephrocytes of Myriapoda. – Entomologica Scandinavica Supplement 51: 15-23.
- ROSENBERG, J. & G. SEIFERT, 1975. Offene Hämolympghälfte am Sacculus der Maxillarnephridien von *Scutigera coleoptrata* L. (Chilopoda, Notostigmophora). – Entomologica Germanica 2: 167-169.
- ROSENBERG, J., A. SOMBKE & G. HILKEN, 2009. Structure and function of the maxillary nephridium of *Lithobius forficatus* (Chilopoda, Pleurostigmophora). – Journal of Morphology 270: 1531-1540.
- SCHEFFEL, H., 1969. Untersuchungen über die hormonale Regulation von Häutung und Anamorphose von *Lithobius forficatus* (L.) (Myriapoda, Chilopoda). – Zoologische Jahrbücher, Abteilung für Allgemeine Zoologie und Physiologie der Tiere 74: 436-505.
- SCHEFFEL, H., 1979. Probleme der hormonalen Regulation von Häutung und postembryонаler Morphogenese bei Chilopoden. – Wissenschaftliche Zeitschrift der Pädagogischen Hochschule Erfurt-Mühlhausen, Mathematisch-naturwissenschaftliche Reihe 15: 111-119.

- SCHEFFEL, H., 1987. Häutungsphysiologie der Chilopoden: Ergebnisse von Untersuchungen an *Lithobius forficatus* (L.). – Zoologische Jahrbücher, Abteilung für Allgemeine Zoologie und Physiologie der Tiere 91: 257-282.
- SEIFERT, G., 1990. Morphology, histology, and ultrastructure of the ecdysial glands in Myriapoda. – Pp. 309-341 in A. P. GUPTA (ed.): Morphogenetic hormones of Arthropods. Vol. 1; 2. Embryonic and postembryonic sources. – Rutgers University Press, New Brunswick, London.
- SEIFERT, G. & H. J. BIDMON, 1988. Immunohistochemical evidence forecdysteroid-like material in the putative molting glands of *Lithobius forficatus* (Chilopoda). – Cell & Tissue Research 253: 263-266.
- SEIFERT, G. & J. ROSENBERG, 1974. Elektronenmikroskopische Untersuchungen der Häutungsdrüsen ("Lymphstränge") von *Lithobius forficatus* L. (Chilopoda). – Zeitschrift für Morphologie der Tiere 78: 263-279.
- VANDENBULCKE, F., C. GRELLE, M. C. FABRE & M. DESCAMPS, 1998. Ultrastructural and autometallographic studies of the nephrocytes of *Lithobius forficatus* L. (Myriapoda, Chilopoda): Role in detoxification of cadmium and lead. – International Journal of Insect Morphology and Embryology 27: 111-120.
- VERHOEFF, K. W., 1902-25. Gliederfüssler: Arthropoda, Klasse Chilopoda. In: H. G. BRONN (ed.) Klassen und Ordnungen des Tierreichs, 5(II). – Akademische Verlagsgesellschaft, Leipzig.
- WANG, T. H. & H. W. WU, 1947. On the structure of the Malpighian tubes of the centipedes and their excretion of uric acid. – Sinensis (Nanking) 18: 1-11.
- WENNING, A., 1977. Zur Struktur und Funktion des Exkretionssystems von *Lithobius forficatus* L. (Myriapoda, Chilopoda). – Dissertation Fachbereich 23 (Biologie), Freie Universität Berlin: 1-57.
- WENNING, A., 1978. Struktur und Funktion des Exkretionssystems von *Lithobius forficatus* L. (Chilopoda, Myriapoda). – Zoologische Jahrbücher, Abteilung für allgemeine Zoologie und Physiologie der Tiere 82: 419-433.
- WENNING, A., 1979. Structure and function of the hindgut of *Lithobius forficatus* L. (Myriapoda, Chilopoda). – Pp. 135-142 M. CAMATINI (ed.) Myriapod biology. - Academic Press, London.
- WENNING, A., 1989. Transporteigenschaften der Malpighischen Gefäße von *Lithobius forficatus* L. (Myriapoda, Chilopoda). – Verhandlungen der Deutschen Zoologischen Gesellschaft 82: 215-216.
- WENNING, A., U. GREISINGER & J. P. PROUX, 1991. Insect-like characteristics of the malpighian tubules on a non insect: fluid secretion in the centipede *Lithobius forficatus* (Myriapoda: Chilopoda). – Journal of Experimental Biology 158: 165-180.



## Chapter 10

# CHILOPODA – ENDOCRINE SYSTEM

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Studies on structure and function of the endocrine system, and the hormonal control on moulting and gametogenesis, are essentially limited to anamorphic and adult stages of *Lithobius forficatus* (reviewed in Juberthie-Jupeau, 1983; Joly and Descamps, 1988; Descamps, 1990).

### *Anatomy and fine structure of the endocrine system*

#### *Neurosecretory cells in the brain*

In all centipede groups, neurosecretory cells (Fig. 10.2A) are chiefly located in the protocerebrum (Gabe, 1952, 1953a, 1956, 1966; Palm, 1956; Scheffel, 1961; Joly, 1966c; Joly and Descamps, 1968; Ernst, 1971; Jamault-Navarro and Joly, 1977; reviewed in Juberthie-Jupeau, 1983). These cells form paired groups in the anterior-lateral area of the frontal lobe and in the posterior-dorsal areas of the pars intercerebralis.

In *L. forficatus*, most of the axons of the neurosecretory centres from the frontal lobe (type A, B<sub>1-2</sub>, C) and some axons of the pars intercerebralis (type B<sub>3-5</sub>) form the nerve of the cerebral gland (*nervus glandulae cerebralis*) (Fig. 10.1A).

Several other pathways, with axons poor in secretory granules, issue from neurosecretory cells of the frontal lobe and the pars intercerebralis and innervate areas of the brain or branches of the cephalic arteries (Jamault-Navarro and Joly, 1977; Jamault-Navarro, 1981).

Activity of the neurosecretory cells is first detected during the second anamorphic larval stadium shortly before ecdysis (age 10-12 d) (Scheffel, 1961). In *Geophilus flavus*, the nerve of the cerebral gland is formed by axons of the neurosecretory cells of the frontal lobe and the pars intercerebralis (Ernst, 1971).

Seven types of neurosecretory cells with different neurosecretory granules (type A, B<sub>1-5</sub>, C) can be distinguished in *L. forficatus* (Fig. 10.1A) and *G. flavus* (Ernst, 1971; Jamault-Navarro and Joly, 1977; Jamault-Navarro, 1981).

### *Neurosecretory cells in the ventral nerve cord*

In *Scutigera coleoptrata* neurosecretory cells are observed in both the cranial and caudal part of the ganglia (Prunesco, 1970a).

In *L. forficatus*, neurosecretory cells are observable within the suboesophageal ganglion, the forcipular ganglion, and in the ganglia of the ventral nerve cord. Paired groups of neurosecretory cells are developed in the anterior and in the posterior region of each ganglion. Neurosecretory axons innervate the dorsal heart nerve via the segmental heart nerve (Scheffel, 1969). Activity of the posterior neurosecretory cells of the ventral ganglia is first detected during the III larval stadium, whereas the activity of other neurosecretory cells is only observed in older larvae (Scheffel, 1961). Prunesco (1970b) described histologically anterior and posterior neurosecretory areas within the ganglia of the nerve cord of *Scolopendra cingulata* and *Plutonium zwierleini*, with three types of neurosecretory cells. In *G. flavus* neurosecretory cells (type A, B, C) are situated near the origin of the segmental heart nerve. Neurosecretory axons innervate the segmental pericardial organs and the dorsal heart nerve (Fig. 10.1C). Sporadically neurosecretory cells (type C) are observable in the anterior part of the ganglia. In the ganglion of the hind extremity, axons of the anterior neurosecretory cells run into the previous ganglion and innervate the heart. Neurosecretory cells are absent within the ganglia of the first and second genital segment (Ernst, 1971).

### *Neurohemal organs*

Neurohemal organs were only investigated in *L. forficatus* (Jamault-Navarro, 1984) and *G. flavus* (Ernst, 1971).

In *L. forficatus* cephalic neurohemal organs consist of dilated neurosecretory axons with numerous secretory granules near the walls of the aorta and antennal arteries (Fig. 10.1B). The axons can be differentiated according to their different types of neurosecretory granules originating from the neurosecretory areas of the pars intercerebralis.

In *G. flavus*, segmental neurohemal organs are situated along the heart in the region of the ostia. These pericardial organs are innervated by the posterior neurosecretory cells of the ventral nerve cord ganglia via the segmental heart nerve (Fig. 10.1C).

The neurosecretory axons contain different types of granules (type A, B, C). Most axons remain in the pericardial organs, fewer of innervating the dorsal heart nerve (Ernst, 1971).

### *Neuroendocrine glands*

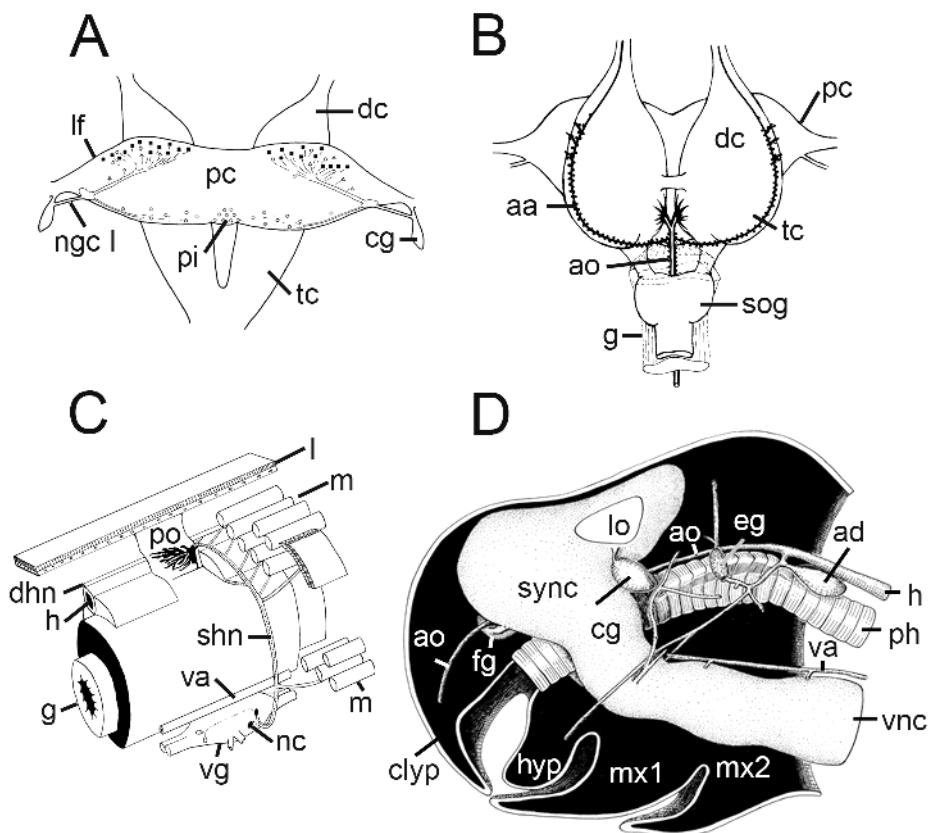
In all Myriapoda, with the exception of Paupropoda, neuroendocrine glands seem to exist as cerebral glands, innervated by the neurosecretory areas of the protocerebrum. Fahlander (1938) documented this organ (glandula cerebralis) in nearly all subtaxa of Chilopoda and recognized its endocrine function. The cerebral gland was investigated by light microscopy in different Chilopoda by Gabe (1952, 1953a, b, 1956) and Palm (1956) and by electron microscopy by Scheffel (1965c) and Joly (1966a) (*L. forficatus*), Ernst (1971) (*G. flavus*), Rosenberg (1976) (*S. coleoptrata*), and Descamps and Joly (1985) (*S. cingulata*, *Cryptops anomalans*, *C. hortensis*). A comparative light-microscopic study on the location and innervation of the cerebral gland in different pleurostigmophorans is given by Joly and Descamps (1968) and Descamps and Joly (1985). Reviews on the cerebral glands in Chilopoda are by Juberthie-Jupeau (1983) and Descamps et al. (1990).

The cerebral glands are located either in the vicinity of the brain (Scutigeromorpha Fig. 10.1D, Geophilomorpha) or laterally, under each ocellar zone (Lithobiomorpha, Scolopendromorpha). In most cases, the cerebral gland is connected by a single nerve to the protocerebrum (Fig. 10.2B). In *Lithobius forficatus* two nerves are developed (Fig. 10.1A) (Rilling, 1960, 1968; Scheffel, 1961; Descamps et al., 1990a), though only one nerve has been described in the anamorphic larval stadia of *L. forficatus* (Scheffel, 1961). In all Chilopoda studied by TEM, the major part of the cerebral gland is occupied by axonal endings (Fig. 10.2C) issued from neurosecretory centres of the frontal lobe and the pars intercerebralis (Ernst, 1971; Joly and Jamault-Navarro, 1978; Jamault-Navarro, 1981). The axons contain neurosecretory granules, within which peptides, 5-hydroxytryptamine, and noradrenaline have been demonstrated in *L. forficatus* (Joly and Devauchelle, 1970; Descamps et al., 1985).

The axons are accompanied by glial cells and by glandular cells (Fig. 10.2C) containing granules of different diameter (Scutigera sp.: 170-270 nm, *Lithobius* sp.: 200-500 nm, *Scolopendra* sp.: 200-600 nm, *Cryptops* sp.: 160-520 nm, *Geophilus* sp.: max. 410 nm). In *L. forficatus* they contain cystine, cysteine, arginin, and lysine, but no polysaccharides and lipids and are not digested by proteolytic enzymes (Joly and Devauchelle, 1970).

### *Endocrine glands*

In anamorphic larvae of *L. forficatus*, Scheffel (1963, 1965a,b 1969, 1987) demonstrated that the tissue surrounding the mandibular gland (Fig. 10.2E, F) (Seifert and Rosenberg, 1974), produces a hormone that stimulates ecdysis.



**Fig. 10.1** A-B *Lithobius forficatus*. A Diagrammatic representation of the distribution of neurosecretory cells in the protocerebrum. B Schematic drawing of the cephalic neurohemal organs. Neurosecretory axons and neurohemal organs in black. C *Geophilus flavus*. Diagrammatic representation of a segmental pericardial organ, the segmented heart nerve and the neurosecretory cells of a ventral ganglion. Neurosecretory axons and neurohemal organs in black. D *Scutigera coleoptrata*. Sagittal section of the head to illustrate the location of the cerebral and the endocrine head gland. A, modified after Jamault-Navarro and Joly (1977); B, modified after Jamault-Navarro (1984); C, modified after Ernst (1971); D, modified after Rosenberg (1974).

aa antennal artery; ad aortic diverticule; ao aorta; cg cerebral gland; clyp clypeus; dc deutocerebrum; dhn dorsal heart nerve; eg endocrine gland; fg frontal ganglion; g gut; h heart; hyp hypopharynx; i integument; If lobus frontalis; lo lobus opticus; m longitudinal muscles; mx1 maxilla I; mx2 maxilla II; nc neurosecretory cells; ngl nervus glandulae cerebralis I; pc protocerebrum; ph pharynx; pi pars intercerebralis; po pericardial organ; shn segmental heart nerv; sog suboesophageal ganglion; syn syncerebrum; va ventral artery; vg ventral ganglion; vnc ventral nerve cord

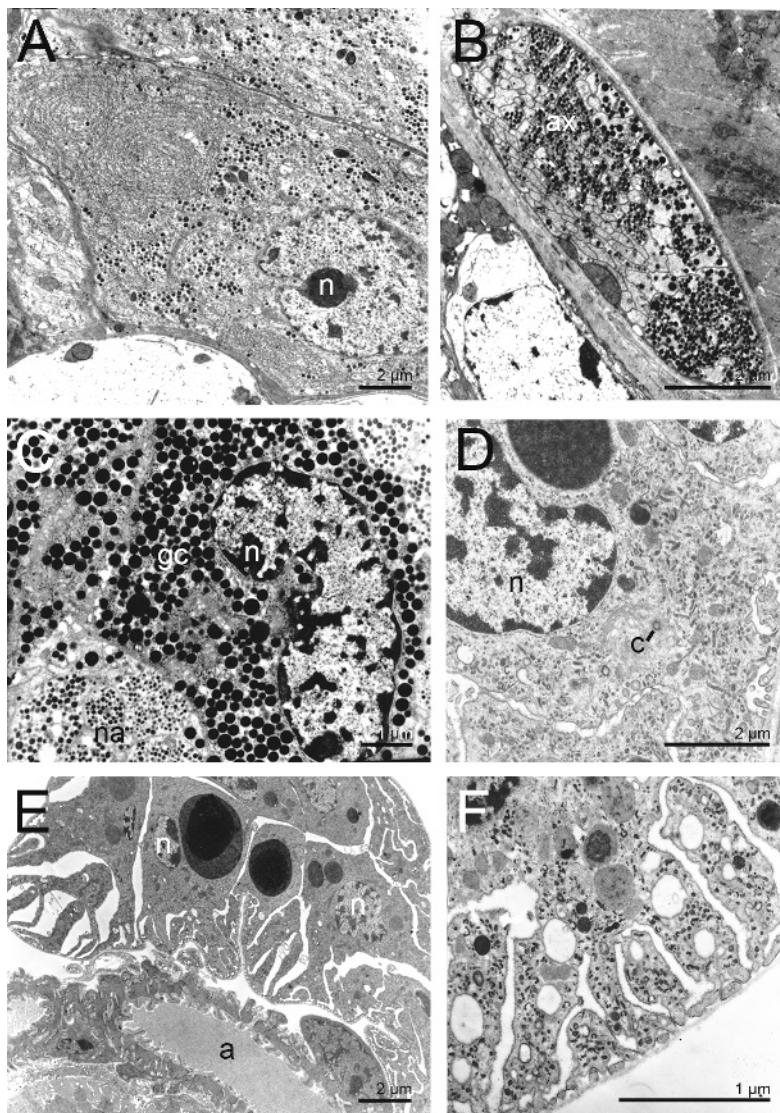


Fig. 10.2 A-C *Scutigera coleoptrata* (TEM). A A single protocerebral neurosecretory cell. B Nervus glandularis cerebralis of with numerous neurosecretory axons filled with neurosecretory granules. C Part of the cerebral gland with glandular cells (gc) and sections of neurosecretory axons (na), filled with neurosecretory granules. D-F *Lithobius forficatus* (TEM). D Endocrine gland near a small artery. E Cortex of the ecdysial gland. The podocyte-like cell shows typical pedicels. F Margin of the ecdysial gland, showing the podocytic character of the cells. Originals J. Rosenberg.

a artery; ax neurosecretory axons; c centriole; gc glandular cells; n nucleus; na neurosecretory axons

Cytological (Seifert and Rosenberg, 1974), immunocytochemical (Bidmon et al., 1987; Seifert and Bidmon, 1988) and biochemical investigations (Leubert et al., 1979; Descamps et al., 1992) support its function as an ecdysial gland. Leubert (1986) demonstrated the release into the culture medium from isolated glands of ecdysone and 20-hydroxyecdysone. In adult centipedes, secretions from cerebral glands probably have an effect on the secretory activity of the ecdysial glands and lead to an increase of ecdysteroids in the hemolymph (Joly, 1979).

An endocrine gland of comparable ultrastructure was described in the head of *S. coleoptrata* (Rosenberg, 1974). Its putative function as an ecdysial gland has still to be proven experimentally.

A review on endocrine glands in Chilopoda was given by Seifert (1990).

### *Hormonal control of moulting*

#### *Moultling process*

The moultling cycle of adult *L. forficatus* is divided into three phases: a post-ecdysial period (about 10 d), an intermolt period (about 20 d) and a pre-ecdysial period (about 20 d), during which apolysis is observable. The cerebral gland is only active in the intermolt period, followed by a period of about 20 d during which moultling is no longer influenced by neuroendocrine or external factors (Joly, 1966b,c,d).

In adult (Joly, 1961, 1966a,b,c, 1980) and larval (Scheffel, 1965b, 1969) *L. forficatus*, the moultling process is controlled by the neurosecretory cells/cerebral gland complex (reviewed in Scheffel, 1987; Joly and Descamps, 1988). These studies establish the existence of a moderating and a stimulating endocrine system in centipedes (Fig. 10.3).

#### *Regulation of the moultling cycle*

The neurosecretory cells of the frontal lobe and the pars intercerebralis are the supraordinate system, controlling the formation of a neurohormone in the cerebral gland (Joly, 1976; Joly and Jamault-Navarro, 1978). Both the moderating and stimulatory systems influence the moultling cycle. It is likely that the moderating effect of the neurosecretory cell of the frontal lobes – cerebral gland complex is exerted at the epidermal level. This complex controls the activity of the ecdysial gland, which is inhibited until the start of the critical period during preecdysis. In the second anamorphic larval stage of *L. forficatus* Scheffel (1969) demonstrated that destruction of

the ecdysial gland before a critical period (< 24 h after moult) leads to a delay of the moult.

A moderating role of the cerebral gland on the moulting processes was demonstrated in larval *L. forficatus* (Scheffel, 1965b, 1969) and in adult *L. forficatus* and *S. cingulata* (Joly, 1962). In adult specimens, removal of the cerebral gland (Joly, 1961, 1962, 1966b,c), cutting of the nervus glandulae cerebralis, or destruction of the neurosecretory cells of the frontal lobes induce an increase in the percentage of moulting and a shortening of the moulting cycle (Joly, 1966c, 1976, 1980). After removal of the cerebral gland, the amount of ecdysteroids in the hemolymph decreases (Joly, 1979). Implantations of cerebral glands in animals deprived of their own glands can delay moulting induction and even inhibit moulting, if implantation is repeated every 20 d (Joly, 1966b,c, 1980).

Electrical stimulation of the neurosecretory cells of the frontal lobes or of the pars intercerebralis induces a release of secretion through their axons into the cerebral gland. Stimulation of the frontal lobes is followed by a longer secretory activity of the glandular cells of the cerebral gland and induces lengthening of the moulting cycle. Experiments suggest a neurohormonal control of the cerebral gland by the neurosecretory cells of the frontal lobe. The glandular cells of the cerebral gland produce a hormone that inhibits moulting (Joly and Descamps, 1977; Joly, 1982, Joly and Jamault-Navarro, 1978).

In adult *L. forficatus*, the neurosecretory cells of the pars intercerebralis exert a stimulatory action on the moulting cycle (Fig. 10.3). Destruction of the pars intercerebralis induces a decrease of moulting and a lengthening of the moulting cycle. This effect is inhibited by the implantation of parts of a pars intercerebralis. Electrical stimulation of the neurosecretory cells of the pars intercerebralis also induces an increase in the percentage of moulting individuals, especially among immature animals (Joly, 1966c; Joly and Descamps, 1977; Joly and Jamault-Navarro, 1978). The stimulatory role of the pars intercerebralis is probably exerted via the cerebral gland. Destruction of the pars intercerebralis leads to a stimulation of the activity of the glandular cells of the cerebral gland and to a lengthening of the moulting cycle. The glandular cells of the cerebral gland then show lysosomes, large vacuoles, and sometimes autophagic bodies (Joly and Jamault-Navarro, 1978). However, the stimulatory action of the neurosecretory cells of the pars intercerebralis seems to be less effective in larval stages. Decapitation of starved larvae of the third anamorphic stadium leads to a partial and sometimes complete moult (Scheffel, 1969, 1987).

The neurosecretory cells of the frontal lobe and the pars intercerebralis are thus the supraordinate system controlling the formation of a neurohormone in the cerebral gland. It is likely that the moderating effect of the neurosecretory cells of the frontal lobes/

cerebral gland complex is exerted at the epidermal level and controls the activity of the ecdysial gland, which is inhibited until the start of the critical period during preecdysis (Joly, 1976; Joly and Jamault-Navarro, 1978). In the second anamorphic larval stage of *L. forficatus* Scheffel (1969) demonstrated that destruction of the ecdysial gland before a critical period (< 24 h after moult) leads to a delay of moult.

Later on Descamps (1992) argues that the *Lithobius* model controlled simply by the balance between a moderating and a stimulating system has evolved toward a more elaborate system in which the origin of some of the factors is either hypothetical or unknown.

Joly and Descamps (1988) regarded the endocrine control of moulting in centipedes as more similar to that of decapod crustaceans than to that of insects. Both Crustacea and Chilopoda have inhibitory systems that delay moulting in larvae as well as in adults. In Crustacea, the X-organ-sinus gland complex controls the moulting process. Injection of eyestalk extracts with the X-organ-sinus gland complex from the crab *Carcinus maenas* delays, after removal of the cerebral gland, an induced ecdysis in adult *L. forficatus* (Joly, 1972).

#### *Influence of external and internal factors on the moulting cycle*

Feeding and temperature are the main external factors that play a role in the moulting process in larvae and adults of *L. forficatus* (Fig. 10.3). External factors such as feeding and temperature seem to act directly on the cerebral gland. Starved larvae of the third anamorphic stadium do not moult because of hormonal blocking of the neuroendocrine system. Food intake removes this effect. Adult specimens do not moult when starved. Inhibition of moulting may at first be related to an increase in activity of the cerebral gland. Later on it is induced mainly by a metabolic action. When starved adult animals are allowed to feed again, the cerebral gland starts secreting again. In adults, the optimal temperature for moulting is about 24°C; no moulting occurs below 5°C (Roberts, 1957; Joly, 1966b,c, 1977; Scheffel, 1969).

Moulting can be induced experimentally. In starved I-III stadium larvae of *L. forficatus*, antennectomy induces moulting, possibly by stimulating the secretion of moulting hormone (Scheffel, 1980). In starved II stadium larvae, phytecdysone from *Taxus baccata* induces apolysis (Pollak and Scheffel, 1973). In adult *L. forficatus*, antennectomy (Joly and Lehouelleur, 1972; Descamps, 1977a; Joly, 1977; Joly and Descamps, 1981) or removal of walking legs 10-12 during the intermolt period (Joly, 1966b,c; Descamps, 1977a) lead to a shortening of the moulting cycle, likely through a decrease in the moderating action of

the cerebral gland (Joly, 1982). A similar effect of removal of walking legs was described in *S. coleoptrata* (Cameron, 1926). Injection of bovine insulin (0.002 µg or 0.02 µm) leads to an increase in the percentage of moulting individuals, if performed in May, the period of intense physiological activity, but had lower or no effect in January (end of the period of the physiological rest) or September (decrease of the physiological activity), respectively (Descamps et al., 1988).

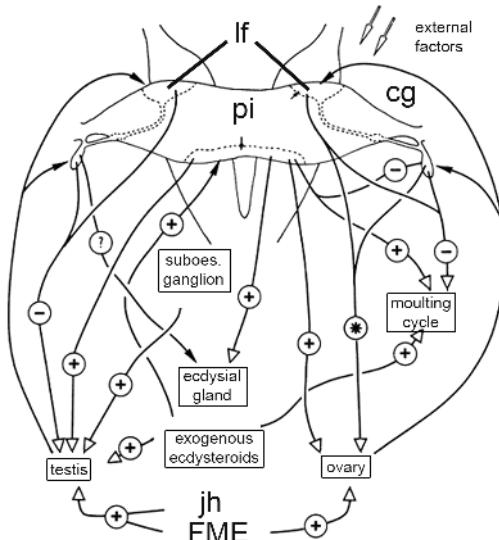


Fig. 10.3 *Lithobius forficatus*. Schematic drawing of the main endocrine actions and interactions. Modified after Joly and Descamps (1988).

cg cerebral gland; FME Farnesylmethylether; jh juvenile hormone; If lobus frontalis; pi pars intercerebralis. (-) moderating effect; (+) stimulating effect; (\*) necessary for normal oocyte growth and vitellogenesis

#### *Ecdysteroid hormone in Chilopoda*

Ligature experiments on II stadium larvae of *L. forficatus* demonstrate that moulting is controlled by a postcephalic ecdisial centre (Scheffel, 1969). In starved III stadium larvae of *L. forficatus* exogenous ecdysteroids induce the activation of the ecdisial process as apolysis in the regions of antennae and leg buds (Scheffel, 1969, 1978, 1983, 1986; Pollak and Scheffel, 1973; Scheffel and Wilke, 1974; Scheffel et al., 1974; Pollak, 1977; Leubert and Schütz, 1985). Ecdysteroids also stimulate the synthesis of chitin during the formation of

the cuticle (Scheffel and Küchenmeister, 1981; Küchenmeister and Scheffel, 1982; Kriewald and Scheffel, 1986).

In adult *L. forficatus*, the stimulating effect of exogenous ecdysteroids (20-OH ecdysone) on the moulting cycle has been demonstrated (Joly, 1964; Descamps, 1977a). In the longer term, ecdysteroids act essentially by activating the epidermal cells and inducing precocious apolysis (Joly and Descamps, 1988). Exogenous ecdysteroids induced an increase of brain electrical activity in the pars intercerebralis after a latency of 20 to 60 sec and an increase in the synthetic activity of the neurosecretory cells (type B<sub>5</sub>) of the pars intercerebralis. (Descamps and Lasalle, 1981; Jamault-Navarro et al., 1983; Descamps et al. 1986).

The presence of ecdysteroids in the hemolymph of Chilopoda has been demonstrated (Joly et al., 1979; Leubert et al., 1979), with two fractions, corresponding to ecdysone and 20-OH ecdysone respectively. Throughout the moulting cycle, ecdysteroid levels in the hemolymph vary between 20 and about 200 ng/ml (Joly et al., 1979), being low during the autumn-winter resting period, with an increase in April before the moulting activity starts (Descamps et al., 1992). Ecdysone and 20-OH ecdysone are found in the ovary and in mature eggs of *L. forficatus* (Leubert et al., 1982). Ecdysteroid biosynthesis is detected in the ecdysial (lymphatic) gland, releasing *in vitro* ecdysone and 20-OH ecdysone into the culture medium (Leubert 1986). In a preliminary report Descamps et al. (1990b) demonstrated that the ecdysial gland is able to hydroxylate a putative precursor to ecdysone or 20-OH ecdysone.

In *L. forficatus*, 3H-ecdysone is hydrolysed to 20-hydroxyecdysone (Leubert and Schütz, 1985). The ecdysial gland and the gonads are the most effective tissues to convert 2,22,25-trideoxyecdysone into 2-deoxyecdysone *in vitro*, but at rather low levels (Descamps and Lafont, 1993). The different precursors from cholesterol to ecdysone seem to be unidentified hitherto (Dolle et al., 1993).

#### *Hormonal control of gametogenesis*

##### *Oogenesis*

In *L. forficatus*, oogenesis is influenced by temperature and by feeding (Herbaut, 1975b, 1976b). Three phases can be distinguished: premeiosis, previtellogenesis, and maturation. There are two main periods of vitellogenesis, in autumn and spring respectively (Herbaut and Joly, 1972; Leubert and Scheffel, 1984). The development of the gonads begins during the epimorphic phase of post-embryonic development. The growth of the oocytes is very

slow and the largest cells reach the end of the previtellogenesis during the sixth epimorphic stage (pseudomaturus II). Oocyte maturation is only observed in the following stadia (matus junior, matus senior) (cf. Chapter 14) and is not dependent on mating. When cerebral glands of adult animals are implanted in pseudomaturus I juveniles, vitellogenesis can be triggered, but oocyte maturation was never observed. When portions of ovaries from young females (praematurus, pseudomaturus I) are implanted into an adult female, the donor's oocytes do not grow and some of them degenerate (Herbaut, 1977a). Juvenile hormone-like substances has a stimulating effect on the oogenetic cycle (Joly et al., 1980).

Herbaut and Joly (1972) and Herbaut (1975a) demonstrated the stimulating action of the neurosecretory cells of the pars intercerebralis during the oogenetic cycle and the required presence of the cerebral gland to insure normal oogenesis (Herbaut, 1976a). Ovarectomy resulted in an increased activity of the cerebral glands (Joly, 1984). Sareen and Adiyodi (1983) suggested that hormone(s) produced by the neurosecretory cells of the protocerebrum and the cerebral gland promote ovarian growth by preventing moulting (Fig. 10.3).

In spring time, exogenous ecdysteroids can disturb oogenesis and block vitellogenesis; in autumn, oocyte growth is little impaired (Herbaut, 1977b). Descamps (1989) demonstrated that excessive ecdysteroid levels lead to the release of a moderating factor by the cerebral gland. Nevertheless, ecdysteroids are necessary for oogenesis (Leubert et al., 1982; Descamps and Lasalle, 1986). Herbaut (1977b) demonstrated in long-term experiments that ecdysone injections lead to problems in oocyte growth and in some cases to a blockage of vitellogenesis. The rise of ovarian ecdysteroids observed during the vitellogenic phases (Descamps et al., 1992) is more likely related to the storage of ecdysteroid conjugates than to signals controlling vitellogenesis (Descamps, 1992) (Fig. 10.3). Moreover Descamps (1992) challenged to reinvestigate the endocrine control of oogenesis taken into account the exogenous origin of yolk proteins (e.g. vitellogenins).

### *Spermatogenesis*

In *L. forficatus* two spermatogenetic cycles normally occur during the year, one starting in early spring, the second in late spring or early summer. Spermatophores are produced in July and in mid-December (Joly and Descamps, 1969). A spermatogenetic factor released from the neurosecretory cells of the pars intercerebralis stimulates the spermatogenetic cycle (Fig. 10.3) (Descamps and Joly, 1971; Descamps, 1972, 1974, 1977b,

1978, 1990). The suboesophageal ganglion seems to play a secondary stimulating role on the spermatogenetic cycle (Descamps, 1979).

The neurosecretory cells of the frontal lobe and the cerebral glands have an inhibitory effect (Descamps, 1975, 1978, 1990) (Fig. 10.3).

Exogenous ecdysteroid stimulates RNA and protein synthesis in the spermatocytes of *L. forficatus* (Descamps, 1977b, 1981, 1985, 1986; Beniouri et al., 1983, 1985; Beniouri, 1984) and *L. crassipes* and is documented by ultrastructural studies (Beniouri et al., 1983). Juvenile hormone-like substances, farnesylmethylether (Fig. 10.3) as a juvenile hormone mimic, and 5-hydroxytryptamine have a stimulating effect on the spermatogenetic cycle (Descamps, 1980, 1985; Descamps et al., 1990c). Ecdysteroids (20-OH ecdysone) increase the permeability of the testis-blood barrier. A recovery period takes place during the meiotic phase (Beniouri et al., 1983; Descamps et al., 1986). Neither injection of 20-OH ecdysone nor electrostimulation of the pars intercerebralis can stimulate spermatocyte syntheses during this phase. Removal of antennae or limbs results in a delay in the appearance of spermatids and spermatozoa in the testes (Descamps, 1977a).

It is likely that hormones act only on spermatogonia and on spermatocytes at the beginning of the spermatogenetic cycle (Descamps, 1990, 1992).

### *Metabolic regulation*

The removal of the pars intercerebralis leads in *L. forficatus* to a significant decrease in weight, but does not seem to exert a role in the diuretic function (Joly, 1971). Destruction of the pars intercerebralis or the removal of the cerebral glands seem to induce an alteration of hemolymph proteins, especially albumin and prealbumin (Joly and Descamps, 1988).

The heart of *Scolopendra morsitans* is neurogenic, the cardiac activity regulated through the release of an unidentified neurohormone, present in the brain and in the heart (Sundara Rajulu, 1966). Joly and Decamps (1988) suggested the neurohormone may be conveyed by the segmental cardiac nerve and pericardial organs similar as described by Ernst (1971) in *G. flavus*.

### *References*

- BENIOURI, R., 1984. Testis-blood barrier control by 20-hydroxyecdysone in *Lithobius forficatus* (Myriapoda, Chilopoda). - *Cytobios* 40: 159-170.

- BENIOURI, R., M. DESCAMPS, M. PORCHERON & R. JOLY, 1983. Corrélations naturelles et expérimentales entre croissance spermatocytaires et taux d'ecdystéroïdes chez les Lithobiidae (Chilopoda). – Revue Canadienne de biologie expérimentale 42: 183-189.
- BENIOURI, R., M. DESCAMPS & G. TORPIER, 1985. The spermatocyte membrane in *Lithobius forficatus* L. (Myriapoda Chilopoda). Changes induced by hormonal actions. Preliminary results. – Reproduction Nutrition Développement 25: 83-92.
- BIDMON, H. J., G. SEIFERT, & G. KOOLMAN, 1987. Lokalisation von Ecdysteroiden und ihren Rezeptoren in Evertebraten. – Verhandlungen der Deutschen Zoologischen Gesellschaft 80: 157-158.
- CAMERON, J. A., 1926. Regeneration in *Scutigera forceps*. – Journal of Experimental Biology II: 169-179.
- DESCAMPS, M., 1972. Rôle de la pars intercerebralis dans la régulation du cycle spermatogénétique chez *Lithobius forficatus* L. – General and Comparative Endocrinology 18: 586.
- DESCAMPS, M., 1974. Etude du contrôle endocrinien du cycle spermatogénétique chez *Lithobius forficatus* L. (Myriapode, Chilopode). Rôle de la pars intercerebralis. – General and Comparative Endocrinology 24: 191-202.
- DESCAMPS, M., 1975. Étude du contrôle endocrinien du cycle spermatogénétique chez *Lithobius forficatus* L. (Myriapode Chilopode). Rôle du complexe "cellules neurosécrétrices des lobes frontaux du protocérébron - glands cérébrales". – General and Comparative Endocrinology 25: 346-357.
- DESCAMPS, M., 1977a. Influence de la croissance somatique sur le cycle spermatogénétique de *Lithobius forficatus* (Chilopodes, Myriapodes). – General and Comparative Endocrinology 33: 412-422.
- DESCAMPS, M., 1977b. Recherches expérimentales sur la régulation du cycle spermatogénétique au cours du développement post-embryonnaire chez *Lithobius forficatus* L. (Myriapode Chilopode). – Archives de Biologie 88: 203-215.
- DESCAMPS, M., 1978. Rôle des centres endocrines céphaliques dans la régulation de la spermatogenèse chez *Lithobius forficatus* L. (Myriapode, Chilopode). – Bulletin de la Société zoologique de France 103: 367-373.
- DESCAMPS, M., 1979. Influence of the ventral nerve cord on the spermatogenetic cycle in *Lithobius forficatus* L. (Myriapode, Chilopode). – International Journal of Invertebrate Reproduction 1: 205-208.
- DESCAMPS, M., 1980. Influence d'un mimétique de l'hormone juvénile sur la cycle spermatogénétique de *Lithobius forficatus* L. (Myriapode, Chilopode). – Bulletin de la Société zoologique de France 105: 57-63.
- DESCAMPS, M., 1981.  $\beta$ -ecdysone influence on the spermatocyte growth in *Lithobius forficatus* L. (Myriapoda, Chilopoda). Autoradiographic (optical level) and ultrastructural studies. – Archives de Biologie 92: 53-65.
- DESCAMPS, M., 1985. Hormonal control of spermatogenesis in the Myriapode *Lithobius forficatus*. – Pp. 317-320 in B. LOFTS & W. N. HOLM (eds.): Current trends in comparative endocrinology. – Hong Kong University Press, Hong Kong.
- DESCAMPS, M., 1986. Endocrine control of spermatogenesis in the Lithobiidae (Myriapoda, Chilopoda). – Pp. 145-149 in M. POUCHET, J. ANDRIES, & A. DHAINAUT (eds.): Advances in invertebrate reproduction. – Elsevier, Amsterdam.
- DESCAMPS M., 1989. Influence of 20-hydroxyecdysone on oogenesis in *Lithobius forficatus*: high dose levels lead to the involvement of a moderation factor. – General and Comparative Endocrinology 74: 321.
- DESCAMPS, M., 1990. Role of morphogenetic hormones in spermatogenesis in Myriapoda. – Pp. 567-592 in A. GUPTA (ed.) Morphogenetic hormones of Arthropoda. Vol. I, part 3: Roles in

- histogenesis, organogenesis, and morphogenesis. – Rutgers University Press, New Brunswick, London.
- DESCAMPS, M., 1992. Endocrine events during the life cycle of *Lithobius forficatus* L. (Myriapoda, Chilopoda). – Berichte aus dem naturwissenschaftlichen-medizinischen Verein Innsbruck, Supplement 10: 111-16.
- DESCAMPS, M., C. CARDON & B. LEU, 1986. Influence of brain electrical stimulation on 20-OH-ecdysone injection on the CAMP-level in the testis of *Lithobius forficatus* (Myriapoda, Chilopoda). – P. 506 in M. POUCHET, J. ANDRIES & A. DHAINAUT (eds.): Advances in invertebrate reproduction. – Elsevier, Amsterdam.
- DESCAMPS, M., M. CHARLET & B. LEU, 1990b. Conversion of 2,22,25-trideoxyecdysone ( $5\beta$ -ketodiol) by body parts and gonads of *Lithobius forficatus* L. (Myriapoda, Chilopoda). – Invertebrate Reproduction and Development 18: 111.
- DESCAMPS, M., C. JAMAULT-NAVARRO, & R. JOLY, 1988. Influence of vertebrate insulin on molting in *Lithobius forficatus* L. (Myriapoda, Chilopoda). – Life Science Advances/General Endocrinology 7: 35-38.
- DESCAMPS, M. & R. JOLY, 1971. Role de la pars intercerebralis dans la déroulement du cycle spermatogénétique de *Lithobius forficatus*. – Comptes rendus de l'Académie des Sciences, Paris, Série D 273: 768-770.
- DESCAMPS, M., R. JOLY, R. BENIOURI & C. JAMAULT-NAVARRO, 1990c. Involvement of 5-hydroxytryptamine in the endocrine control of spermatogenesis in *Lithobius forficatus* (L.) (Myriapoda, Chilopoda). – Pp. 183-196 in A. MINELLI (ed.): Proceedings of the 7th International Congress of Myriapodology. – Brill, Leiden-New York-København-Köln.
- DESCAMPS, M. & R. LAFONT, 1993. Conversion of different putative ecdysteroid precursors in *Lithobius forficatus* L. (Myriapoda, Chilopoda). – Insect Biochemistry and Molecular Biology 23: 481-489.
- DESCAMPS, M. & B. LASALLE, 1981. Electrophysiological evidence for direct ecdysteroid action on the brain in *Lithobius forficatus* L. (Myriapoda, Chilopoda). – Reproduction, Nutrition, Développement 21: 681-687.
- DESCAMPS, M. & B. LASALLE, 1986. 20-hydroxyecdysone effects on the oocytes resting potential in *Lithobius forficatus* L. (Myriapoda, Chilopoda). – P. 505 in M. POUCHET, J. ANDRIES & A. DHAINAUT (eds.): Advances in invertebrate reproduction. – Elsevier, Amsterdam.
- DESCAMPS, M., B. LEU & B. CHARIB, 1992. Ecdysteroid changes during the life cycle of the centipede *Lithobius forficatus* L. (Myriapoda, Chilopoda). – Advances in Comparative Endocrinology 1: 193-196.
- DESCAMPS, M., F. SAHLI, C. JAMAULT-NAVARRO & J. CAPLET, 1990a. Morphology, histology, and ultrastructure of cephalic neurohemal organs and their roles in morphogenetic processes in Myriapoda. – Pp. 195-232 in A. P. GUPTA (ed.): Morphogenetic hormones of Arthropods, Vol 1, Part 2: Embryonic and postembryonic sources. – Rutgers University Press, New Brunswick, London.
- DOLLE, F., C. HETRU, B. ROUSSEAU, F. SOBRI, C. BLAIS, R. LAFONT, M. DESCAMPS & B. LUU, 1993. Synthesis of a tritiated 3-dehydroecdysteroid putative precursor of ecdysteroid biosynthesis. – Tetrahedron 49: 2485-2498.
- ERNST, A., 1971. Licht- und elektronenmikroskopische Untersuchungen zur Neurosekretion bei *Geophilus longicornis* Leach unter besonderer Berücksichtigung der Neurohämialorgane. – Zeitschrift für wissenschaftliche Zoologie 182: 62-130.
- FAHLANDER, K., 1938. Beiträge zur Anatomie und systematischen Einteilung der Chilopoda. – Zoologiska bidrag från Uppsala 17: 1-148.

- GABE, M., 1952. Sur l'emplacement et les connexions des cellules neurosécrétrices dans les ganglions cérébrosides de quelques Chilopodes. – Comptes Rendus de l'Académie des Sciences, Paris, D 235: 1430-1432.
- GABE, M., 1953a. Particularités histologiques de la glande cérébrale des *Scutigera coleoptrata* L. – Bulletin de la Société Zoologique de France 78: 338.
- GABE, M., 1953b. Quelques acquisitions récentes sur les glandes endocrines des arthropodes. – Experientia 9: 352-356.
- GABE M., 1956. Contribution à l'histologie de la neuro-sécrétion chez les Chilopodes. – Pp. 163-183 in K. WINGSTRAND (ed.): Bertil Hanström, Zoological papers in honour of his sixty-fifth birthday, November 20th. – Lund Zoological Institute, Lund.
- GABE, M., 1966. Neurosecretion. – Pergamon Press, Oxford and Elmsford, New York: 1-872.
- HERBAUT C., 1975a. Etude expérimentale de la régulation endocrinienne de l'ovogénèse chez *Lithobius forficatus* L. (Myriapode, Chilopode). Rôle de la pars intercerebralis. – General and Comparative Endocrinology 27: 34-42.
- HERBAUT, C., 1975b. Influence des facteurs externes sur le cycle ovogénétique chez *Lithobius forficatus* L. (Myriapode, Chilopode). – Archives de Zoologie expérimentale et générale 116: 293-302.
- HERBAUT C., 1976a. Étude expérimentale de la régulation endocrinienne de l'ovogénèse chez *Lithobius forficatus* L. (Myriapode, Chilopode). Rôle du complexe "cellules neurosécrétaires protocérébrales-glandes cérébrales". – General and Comparative Endocrinology 28: 264-276.
- HERBAUT, C., 1976b. Les processus de dégénérescence des cellules sexuelles au cours de l'ovogénèse chez *Lithobius forficatus* L. (Myriapode Chilopode). – Archives d'Anatomie microscopique et de Morphologie expérimentale 65: 175-182.
- HERBAUT, C., 1977a. Évolution du cycle ovogénétique au cours du développement postembryonnaire chez *Lithobius forficatus* L. (Myriapoda, Chilopoda). – Archives de Biologie 88: 67-77.
- HERBAUT, C., 1977b. Influence de la croissance somatique sur l'ovogénèse chez *Lithobius forficatus* (L.) (Myriapode Chilopode). – Archives de Zoologie expérimentale et générale 118: 63-72.
- HERBAUT, C. & R. JOLY, 1972. Activité ovarienne et cycle ovogénétique chez *Lithobius forficatus* L. (Myriapode Chilopode). – Archives de Zoologie expérimentale et générale 113: 215-225.
- JAMAULT-NAVARRO, C., 1981. Cellules neurosécrétrices et trajets axonaux protocérébraux chez *Lithobius forficatus* L. (Myriapode Chilopode). Etude ultrastructurale. – Archives de Biologie 92: 203-218.
- JAMAULT-NAVARRO, C., 1984. Arterial walls as cephalic neurohemal organs in *Lithobius forficatus* L. (Myriapoda, Chilopoda). – Experimental Biology 43: 97-108.
- JAMAULT-NAVARRO, C. & R. JOLY, 1977. Localisation et cytologie des cellules neurosécrétrices protocérébrales chez *Lithobius forficatus* L. (Myriapode Chilopode). – General and Comparative Endocrinology 31: 106-120.
- JAMAULT-NAVARRO, C., R. JOLY & M. DESCAMPS, 1983. Activation of neurosecretory cerebral cells by 20-hydroxyecdysone in *Lithobius forficatus* L. (Myriapoda Chilopoda). – General and Comparative Endocrinology 50: 36-42.
- JOLY, R., 1961. Déclenchement expérimental de la mue chez *Lithobius forficatus* L. (Myriapode, Chilopode). – Comptes rendus de l'Académie des Sciences, Paris, D 252: 1673-1675.
- JOLY, R., 1962. Les glandes cérébrales, organes inhibiteurs de la mue chez les Myriapodes Chilopodes. – Comptes rendus de l'Académie des Sciences, Paris, D 254: 1679-1681.
- JOLY, R., 1964. Action de l'ecdysone sur la cycle de mue de *Lithobius forficatus* L. (Myriapode, Chilopode). – Comptes rendus de la Société de Biologie, Paris 158: 548-550.

- JOLY, R., 1966a. Sur l'ultrastructure de la glandes cérébrale de *Lithobius forficatus* L. (Myriapode, Chilopode). – Comptes rendus de l'Académie des Sciences, Paris, D 263: 374-377.
- JOLY, R., 1966b. Étude expérimentale du cycle du mue et de sa régulation endocrine chez les Myriapodes Chilopodes. – General and Comparative Endocrinology 6: 519-533.
- JOLY, R., 1966c. Contribution à l'étude du cycle de mue et de son déterminisme chez les Myriapodes Chilopodes. – Bulletin biologique de France et Belgique 3: 379-480.
- JOLY, R., 1966d. Étude expérimentale du cycle du mue et de sa régulation endocrine chez les Myriapodes Chilopodes. – General and Comparative Endocrinology 6: 519-533.
- JOLY, R., 1971. Effet de la destruction de la pars intercerebralis sur l'évolution pondérale chez *Lithobius forficatus*. – Comptes rendus de l'Académie des Sciences, Paris, D 273:1208-1209.
- JOLY, R., 1972. Effet de l'injection d'extraits de pédoncules oculaires de crabe sur la cycle de mue de *Lithobius forficatus* L. (Myriapode, Chilopode). – General and Comparative Endocrinology 18: 560-564.
- JOLY, R., 1976. Influence de quelques interventions expérimentales sur l'activité sécrétoire des glandes cérébrales chez *Lithobius forficatus* L. (Myriapode, Chilopode). – General and Comparative Endocrinology 30: 301-312.
- JOLY, R., 1977. Influence de quelques facteurs externes sur l'activité sécrétoire des glandes cérébrales chez *Lithobius forficatus* (Myriapode, Chilopode). Étude en microscopie photonique et électronique. – General and Comparative Endocrinology 32: 167-178.
- JOLY, R., 1979. Neurosecretion and endocrine glands in Chilopoda. – Pp. 263-72 in M. CAMATINI (ed.) Myriapode Biology. – Academic Press. London.
- JOLY, R., 1980. Evolution ultrastructurale et actions de greffons de glandes cérébrales sur le cycle de mue chez *Lithobius forficatus* L. (Myriapode Chilopode). – Bulletin de la Société zoologique de France 105: 49-56.
- JOLY, R., 1982. Influence d'interventions expérimentales provoquant le déclenchement de la mue sur l'activité sécrétoire des glandes cérébrales chez *Lithobius forficatus* (Myriapode Chilopode). – Journal de Physiologie 78: 586-594.
- JOLY, R., 1984. Effect of gonadectomy on the secretory activity of the cerebral glands in *Lithobius forficatus* L. (Myriapoda, Chilopoda). – Experimental Biology 43: 109-117.
- JOLY, R. & M. DESCAMPS, 1968. Étude comparative du complexe endocrine céphalique chez les Myriapodes Chilopodes. – General and Comparative Endocrinology 10: 364-375.
- JOLY, R. & M. DESCAMPS, 1969. Évolution du testicule, des vésicules séminales et cycle spermatogénétique chez *Lithobius forficatus* L. (Myriapode Chilopode). – Archives de Zoologie expérimentale et générale 110: 341-348.
- JOLY, R. & M. DESCAMPS, 1977. Influence de l'électrostimulation cérébrale sur l'histologie ultrastructurale et le rôle physiologique des glandes cérébrales chez *Lithobius forficatus* (Myriapode, Chilopode). – Archives de Biologie 88: 333-347.
- JOLY, R. & M. DESCAMPS, 1981. Effect of brain electrostimulation on antennal regeneration in *Lithobius forficatus* L. (Myriapoda: Chilopoda). Preliminary note. – Reproduction Nutrition Développement 21: 377-382.
- JOLY, R. & M. DESCAMPS, 1988. Endocrinology of Myriapodes. – Pp. 429-449 in H. LAUFER, & G. H. DOWNER (eds.): Invertebrate Endocrinology, Vol. 2: Endocrinology of selected invertebrate types. – Alan R. Liss, New York.
- JOLY, R., M. DESCAMPS & C. HERBAUT, 1980. Actions et régulations endocrinienches chez *Lithobius forficatus* L. (Myriapode Chilopode). – Bulletin de la Société zoologique de France 105: 250.
- JOLY, R. & G. DEVAUCHELLE, 1970. Étude cytochimique de la glande cérébrale de *Lithobius forficatus* L. (Myriapode, Chilopode); nature des sécrétions. – Journal de Microscopie 9: 631-642.

- JOLY, R. & C. JAMAULT-NAVARRO, 1978. Rôle de la pars intercerebralis sur l'activité sécrétoire des glandes cérébrales chez *Lithobius forficatus* L. (Myriapode, Chilopode). Étude ultrastructurale. – Archives de Zoologie expérimentale et générale 119: 487-496.
- JOLY, R. & J. LEHOUELLEUR, 1972. Effet de la section antennaire sur le déclenchement de la mue chez *Lithobius forficatus* L. (Myriapode Chilopode). – General and Comparative Endocrinology 19: 320-324.
- JOLY, R., P. PORCHERON & F. DRAY, 1979. Étude des variations du taux d'ecdysteroïdes au cours du cycle de mue dans l'hémolymphe de *Lithobius forficatus* L. (Myriapode Chilopode), par dosage radio-immunologique. – Comptes rendus de l'Académie des Sciences, Paris, D 288: 243-246.
- JUBERTHIE-JUPEAU, L., 1983. Neurosecretory systems and neurohemal organs of myriapoda. – Pp. 204-278 in A. GUPTA (ed.): Neurohemal organs of arthropods: Their development, evolution, structures and functions. – Thomas, Springfield, Illinois.
- KRIEWALD, M. & H. SCHEFFEL, 1986. In-vitro-Untersuchungen über die Intensität der Chitinsynthese im larvalen Integument des Chilopoden *Lithobius forficatus* (L.). – Zoologische Jahrbücher, Abteilung für allgemeine Zoologie und Physiologie der Tiere 90: 249-256.
- KÜCHENMEISTER, J. & H. SCHEFFEL, 1982. Regionsspezifische zeitliche Veränderungen der Chitinsynthese-Aktivität während larvaler Häutungszyklen von *Lithobius forficatus* (L.) (Chilopoda). – Zoologische Jahrbücher, Abteilung für allgemeine Zoologie und Physiologie der Tiere 86: 53-59.
- LEUBERT, F., 1986. Untersuchungen zur Ecdysteroid-Biosynthese durch das Lymphstrang-Gewebe von *Lithobius forficatus* (L.) (Chilopoda). – Wissenschaftliche Zeitschrift der Pädagogischen Hochschule Erfurt-Mühlhausen MNR 22: 73-77.
- LEUBERT, F., H. EIBISCH, H. KROSCHWITZ & H. SCHEFFEL, 1982. Ecdysteroid-Biosynthese durch das Ovar von *Lithobius forficatus* (L.) (Chilopoda). – Zoologische Jahrbücher, Abteilung für allgemeine Zoologie und Physiologie der Tiere 83: 65-476.
- LEUBERT, F., H. EIBISCH & H. SCHEFFEL, 1979. Isolierung und Charakterisierung des Häutungshormons von *Lithobius forficatus* L. (Chilopoda). – Zoologische Jahrbücher, Abteilung für allgemeine Zoologie und Physiologie der Tiere 83: 334-339.
- LEUBERT, F. & H. SCHEFFEL, 1984. Moulting and reproduction in *Lithobius forficatus* (Chilopoda). – Acta Entomologica Bohemoslovaca 81: 22-28.
- LEUBERT, F. & R. SCHÜTZ, 1985. Untersuchungen zum Stoffwechsel des Ecdysons bei *Lithobius forficatus* (L.) (Chilopoda). – Wissenschaftliche Zeitschrift der Pädagogischen Hochschule Erfurt-Mühlhausen, Mathematisch-naturwissenschaftliche Reihe 21: 111-116.
- PALM, N.-B., 1956. Neurosecretory cells and associated structures in *Lithobius forficatus* L. – Arkiv för Zoologi (2) 9: 115-129.
- POLLAK, W., 1977. Untersuchungen zur quantitativen Wirkung von Ecdysteron auf die postembryonale Morphogenese des Chilopoden *Lithobius forficatus* (L.). – Zoologische Jahrbücher, Abteilung für allgemeine Zoologie und Physiologie der Tiere 81: 383-394.
- POLLAK, W. & H. SCHEFFEL, 1973. Häutungsauslösung bei Chilopoden-Larven durch Phytecdysone der Eibe (*Taxus baccata*). – Zoologischer Anzeiger 191: 86-92.
- PRUNESCO, C. C., 1970a. Les cellules neurosécrétrices des ganglions ventraux des chilopodes anamorphes. – Revue Roumaine de Biologie - Zoologie 15: 147-151.
- PRUNESCO, C. C., 1970b. Les cellules neurosécrétrices des ganglions ventraux des chilopodes épimorphes. – Revue Roumaine de Biologie - Zoologie 15: 323-327.
- RILLING, G., 1960. Zur Anatomie des braunen Steinläufers *Lithobius forficatus* L. (Chilopoda). Skelettmuskelsystem, peripheres Nervensystem und Sinnesorgane des Rumpfes. – Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 78: 39-128.
- RILLING, G., 1968. *Lithobius forficatus*. Grosses Zoologisches Praktikum 13b. – Fischer, Stuttgart.

- ROBERTS, H., 1957. An ecological study of the arthropods of a mixed beech-oak woodland, with particular reference to Lithobiidae. – Ph. D. Thesis, University of Southampton.
- ROSENBERG, J., 1974. Topographie und Ultrastruktur der endokrinen Kopfdrüsen von *Scutigera coleoptrata* L. (Chilopoda, Notostigmophora). – Zeitschrift für Morphologie der Tiere 79: 311-321.
- ROSENBERG, J., 1976. Die Ultrastruktur des Gabeschen Organs (Cerebraldrüse) von *Scutigera coleoptrata* L. (Chilopoda, Notostigmophora). – Zoologische Beiträge (NF) 22: 281-306.
- SAREEN M. L. & K. G. ADIYODI, 1983. Arthropoda - Myriapoda. – Pp. 497-520 K. G. ADIYODI & R. G. ADIYODI (eds.) Reproductive biology of invertebrates. – Wiley, New York.
- SCHEFFEL, H., 1961. Untersuchungen zur Neurosekretion bei *Lithobius forficatus* L. (Chilopoda). – Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 79: 529-556.
- SCHEFFEL, H., 1963. Zur Häutungsphysiologie der Chilopoden. – Zoologische Jahrbücher, Abteilung für allgemeine Zoologie und Physiologie der Tiere 70: 284-290.
- SCHEFFEL, H., 1965a. Der Einfluß von Dekapitation und Schnürung auf die Anamorphose der Larven von *Lithobius forficatus* L. (Chilopoda). – Zoologische Jahrbücher, Abteilung für allgemeine Zoologie und Physiologie der Tiere 71: 359-370.
- SCHEFFEL H., 1965b. Über die Wirkung implantierter Cerebraldrüsen auf die Larvenhäutungen von *Lithobius forficatus* L. (Chilopoda). – Zoologischer Anzeiger 174: 173-178.
- SCHEFFEL, H., 1965c. Elektronenmikroskopische Untersuchungen über den Bau der Cerebraldrüse der Chilopoden. – Zoologische Jahrbücher, Abteilung für allgemeine Zoologie und Physiologie der Tiere 71: 624-640.
- SCHEFFEL, H., 1969. Untersuchungen über die hormonale Regulation von Häutung und Anamorphose von *Lithobius forficatus* (L.) (Myriapoda, Chilopoda). – Zoologische Jahrbücher, Abteilung für allgemeine Zoologie und Physiologie der Tiere 74: 436-505.
- SCHEFFEL, H., 1978. Probleme der neuroendokrinen und endokrinen Regulation bei Chilopoden. – In: Penzlin, H. (ed.): Probleme der Korrelation neuronaler und endokriner Regulation bei Evertebraten. – Friedrich-Schiller-Universität, Jena: 133-152.
- SCHEFFEL, H., 1980. Der Einfluss der Temperatur auf die Häutungsauslösung durch Antennenamputation bei hungernden Larven des Chilopoden *Lithobius forficatus* (L.). – Zoologische Jahrbücher, Abteilung für allgemeine Zoologie und Physiologie der Tiere 84: 67-83.
- SCHEFFEL, H., 1983. In vitro-Untersuchungen über die häutungsauslösende Wirkung von Ecdyson und 20-Hydroxyecdyson bei Chilopoden. – Zoologische Jahrbücher, Abteilung für allgemeine Zoologie und Physiologie der Tiere 87: 425-438.
- SCHEFFEL, H., 1986. Weitere Untersuchungen über die Ecdysteroid-Sensitivität der larvalen Epidermis von *Lithobius forficatus* (L.) (Chilopoda). – Zoologische Jahrbücher, Abteilung für allgemeine Zoologie und Physiologie der Tiere 90: 77-83.
- SCHEFFEL, H., 1987. Häutungsphysiologie der Chilopoden: Ergebnisse von Untersuchungen an *Lithobius forficatus* (L.). – Zoologische Jahrbücher, Abteilung für allgemeine Zoologie und Physiologie der Tiere 91: 257-282.
- SCHEFFEL, H. & J. KÜCHENMEISTER, 1981. Influence of diflubenzuron on moult initiation and chitin biosynthesis in the centipede *Lithobius forficatus* (L.). – P. 83 in F. SEHNAL, A. ZABZA, J. J. MENN & B. CYMBOROWSKI (eds.): Regulation of insect development and behaviour. – Wroclaw Technical University Press, Wroclaw.
- SCHEFFEL, H. & C. WILKE, 1974. Fördernder Einfluss von Actinomycin D auf die Häutungsauslösung durch exogenes Ecdysteron bei Chilopoden-Larven. – Zoologische Jahrbücher, Abteilung für allgemeine Zoologie und Physiologie der Tiere 78: 33-39.

- SCHEFFEL, H., C. WILKE & W. POLLAK, 1974. Die Wirkung von exogenem Ecdysteron auf Larven des Chilopoden *Lithobius forficatus*. – Acta entomologica Bohemoslovaca 71: 233-238.
- SEIFERT, G., 1990. Morphology, histology, and ultrastructure of the ecdysial glands in Myriapoda. – Pp. 309-341 in A. P. GUPTA (ed.): Morphogenetic hormones of Arthropods. 1 Part 2. Embryonic and postembryonic sources. – Rutgers University Press, New Brunswick, London.
- SEIFERT, G. & H. J. BIDMON, 1988. Immunohistochemical evidence for ecdysteroid-like material in the putative molting glands of *Lithobius forficatus* (Chilopoda). – Cell and Tissue Research 253: 263-266.
- SEIFERT, G. & J. ROSENBERG, 1974. Elektronenmikroskopische Untersuchungen der Häutungsdrüsen ("Lymphstränge") von *Lithobius forficatus* L. (Chilopoda). – Zeitschrift für Morphologie der Tiere 78: 263-279.
- SUNDARA RAJULU, G., 1966. Cardiac physiology of a chilopod *Scolopendra morsitans*. – Journal of Animal Morphology and Physiology 13: 114-120.



## Chapter 11

# CHILOPODA – THE NERVOUS SYSTEM

Andy Sombke, Jörg Rosenberg & Gero Hilken

## The central nervous system

The nervous system of chilopods is divided into the central nervous system, composed of the brain and ventral nerve cord, and the peripheral nervous system with its projecting nerves. The central nervous system (brain or syncerebrum) is divided into the proto-, deuto-, and tritocerebrum. The peripheral nervous system is linked by nerves from the brain or ventral nerve cord to sense- and locomotion organs.

### *The protocerebrum*

The protocerebrum is the largest part of the brain. It is well developed in Lithobiomorpha, Scolopendromorpha, and, especially, in Scutigeromorpha. In analogy to the Hexapoda, the posterodorsal region is called pars intercerebralis (Joly and Descamps, 1987). The protocerebrum extends laterally and includes the optic lobes. Geophilomorpha and eyeless Scolopendromorpha have reduced protocerebral lobes. The optic lobes in Scutigeromorpha (Fig. 11.3 A) comprise two neuropils: (1) the lamina, which supplies uncrossed axons to the optic tectum (Melzer et al., 1996; Strausfeld, 2005), the latter consisting of a thin plate-like neuropil extending out from the lateral edge of the protocerebrum; (2) the optic or visual tectum (formerly called medulla) is equipped with large relay neurons that send their axons into the brain. After Strausfeld (2005) the second neuropil matches the characteristics of the hexapod lobula plate. Therefore, it should be named optic tectum to avoid the assumption of a homology between the medulla of Hexapoda and malacostracan Crustacea and the second optic neuropil of Chilopoda. In *Lithobius forficatus*, long axons branch within the optic tectum and possess long collaterals that project to different regions of the neuropil. Large interneurons connect the optic lobes with the dorsal and ventrolateral protocerebrum. The neurons possess large neurites projecting from the optic tectum region medially and dorsally (Melzer et al., 1996). In Scutigeromorpha, the lamina has a simple organization; for each ommatidium, there are two relay neurons (monopolar cells) but no evidence of

local interneurons. The second optic neuropil is equipped with large tangential neurons that send their axons from its inner edge into the protocerebrum, where they terminate at the dendrites of descending neurons (Strausfeld, 2005). According to Strausfeld, the cell arrangements in the optic tectum are identical to the organization of neurons in optic neuropils of hexapods exemplified by the lobula plate of dipterous insects.

Laterally, above the protocerebrum, a large cluster comprising many small globuli cells (characterized by a minute amount of perikaryal cytoplasm and by nuclei with condensed chromatin) provide a system of parallel fibers that provide two substantial lobate neuropils, one lateral and one close to the brain's midline. Together these structures have been termed the mushroom bodies or corpora pedunculata or globuli (Joly and Descamps, 1987). However, homology with structures having the same name in hexapods is unclear. In Scutigeromorpha, the pedunculus is divided into two strands. In Lithobiomorpha and in Scolopendromorpha, only undivided pedunculi are present, whereas they are lacking in Geophilomorpha.

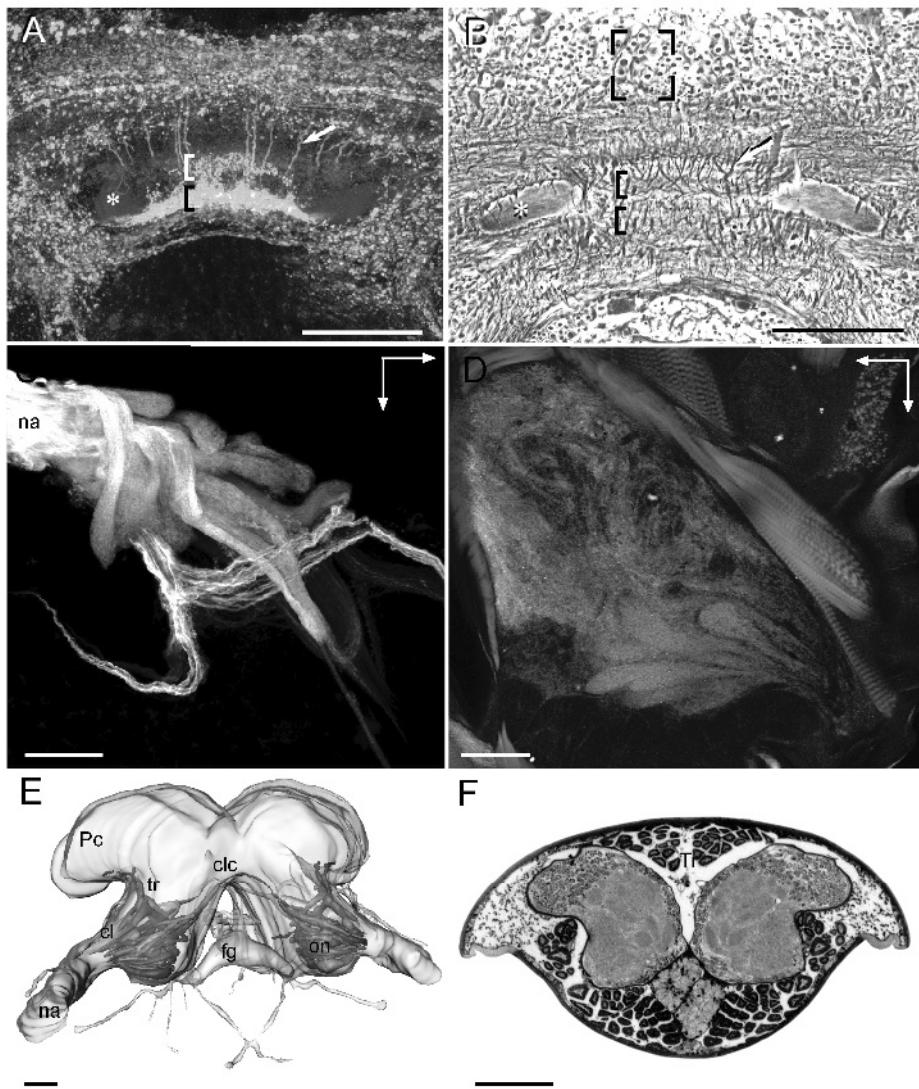
The midline neuropil (or central complex) in *Scolopendra* spp. has been described by Loesel et al. (2002). In the investigated species, the central complex is roughly hemi-ellipsoid in shape and situated between the proximal tips of the medial lobes of the corpora pedunculata (Fig. 11.1 A, B). The central complex neuropil consists of at least three horizontal layers: a ventral, a medial, and a dorsal. In *Scolopendra* spp., the midline neuropil is innervated by fine fibers that are arranged in a more or less columnar manner and show an immunoreactivity against the neurotransmitter allatostatin. The medial lobes of the corpora pedunculata are immunonegative. Many delineated lateral brain regions, as well as commissural tracts, are immunoreactive to allatostatine and tachykinine-related peptide. In addition, Bodian staining of *S. polymorpha* revealed a system of

**Fig. 11.1** A *Scolopendra polymorpha*, columnar array of allatostatin-like immunoreactive fibres that innervate the unique midline neuropil from its upper surface. The arrow indicates columnar fibres. The asterisk indicates the tip of the medial lobe of the mushroom body (corpora pedunculata). B *S. polymorpha*, Bodian staining shows an additional system of interwoven fibres. Square brackets show corresponding layers of the midline neuropil in A and B. The open bracket indicates cluster of large cell bodies. C Dextranbiotin backfill of the left deutocerebral lobe of *Scutigera coleoptrata*. D Immunolocalization of synaptic proteins and phalloidin labeling in the left deutocerebral lobe of *Scutigera coleoptrata* (horizontal section). E 3D-reconstruction of the brain of *Scutigera coleoptrata*. corpus lamellosum (posterior) and olfactory neuropils (anterior). F Cross section of the head of *Cryptops hortensis*. All scale bars 100 µm. A and B after Loesel et al. (2002), C-E modified after Sombke et al. (2009), F original A. Sombke.

Cl Corpus lamellosum; clc contralateral connection; d dorsal; Dc deutocerebrum; f frontal; fg frontal ganglion; m median; Na nervus antennalis; On olfactory neuropil; Pc protocerebrum; Tr tracheae; tr afferent tracts

interweaving fibers in the midline neuropil. The central body is well developed in Scutigeromorpha, whereas in Geophilomorpha it is vestigial.

The cerebral nerves were first described by Holmgren (1916) and Fahlander (1938) and later compared by Seifert (1967b) (see Table 11.2). Rilling (1968) and Joshi et al. (1977) described the cerebral nerves from *Lithobius forficatus* and *Scolopendra morsitans*. In *Lithobius forficatus*, the nervus Tömösváryi (only known in Scutigeromorpha and Lithobiomorpha),



which originates in the proximal region of the postantennal organ (= temporal or Tömösváry organ; see p. 000), projects posteriorly and medially to the cell body rind of the optic lobes (Petykó et al., 1996). Here, the nerve runs medially near the anterior surface of the brain. Adjacent to the optic tectum, its fibers pass through the cell body layer and enter the neuropil proper. They terminate in the neighborhood of the ipsilateral globuli cell cluster and pedunculus of the corpora pedunculata. The paired cerebral gland is connected with the protocerebrum over the nervus glandulae cerebralis. Only in Lithobiomorpha is this nerve paired. According to Rilling (1968), the pathways of these nerves are comparable to that of the allatocardiac nerves in hexapods.

### *The deutocerebrum*

The deutocerebrum is the most anterior part of the brain with regard to the body axis, but is caudal to the protocerebrum with respect to the neuraxis. A visible transition between the proto- and deutocerebrum is, however, not obvious. The deutocerebrum receives the antennal nerves at its frontolateral edges. The deutocerebrum is densely packed with both hemispherical and elongated partitions called olfactory neuropils (Sombke et al., 2009). These extend anteriorly through the deutocerebrum. In contrast to the other Chilopoda, Geophilomorpha show medially fused deutocerebral lobes.

In *Scutigera coleoptrata*, the deutocerebral lobes contain dense neuropils that have the shape of elongated cylinders (Fig. II.1 C, D). In analogy to hexapods, the sum of these neuropils is called the antennal lobe. In *S. coleoptrata* one neuropil provides a contralateral connection. In hexapods, antennal lobe neuropils are organized as numerous and approximately spherical glomeruli. In crustaceans, the olfactory lobes are divided into

Table II.1 Stomatogastric nerves. Number of positive signs equals the pairs of nerves. After Seifert (1967a).

	Scutigeromorpha	Lithobiomorpha	Scolopendromorpha	Geophilomorpha
Stomodeal bridge	-	+	+	+
Frontal connectives	+	-	-	-
Nervus labralis	+	++	+	+
Nervus recurrens	+	+	+	+
Nervus connectivus I	+	+	++	+
Nervus connectivus II	-	+	-	-

elongated columnar subunits (reviewed in Schachtner et al., 2005). Elongated to spherical olfactory neuropils are also present in Lithobiomorpha, Scolopendromorpha (Fig. II.1 F), and Geophilomorpha.

In *S. coleoptrata*, the antennal nerve divides into two branches: (1) the dorsofrontal part innervates the olfactory neuropils (as mentioned above), and (2) the ventrocaudal part innervates the corpus lamellosum (Fig. II.1 C, E). Seifert (1967a) argued that the second antennal nerve serves to process mechanosensory signals. Therefore, the corpus lamellosum, which is also present in Scutigeromorpha, Lithobiomorpha and Scolopendromorpha, may represent a specialized mechanosensory neuropil.

### *The tritocerebrum and stomatogastric nervous system*

The tritocerebrum is the smallest part of the brain and is located ventrally on both sides of the esophagus. The tritocerebral lobes presumably are linked by two commissures: (1) a supra-oesophageal commissure or stomatogastric/stomodeal bridge, and (2) a subesophageal commissure or tritocerebral commissure.

The stomatogastric nervous system innervates the mouth- and the preoral region as well as the frontal part of the gut and carries both motor and sensory axons. There is a stomatogastric bridge in Scutigeromorpha, Lithobiomorpha, Scolopendromorpha and Geophilomorpha. Only in Scutigeromorpha is it substituted by long frontal connectives linking the tritocerebral lobes with the frontal ganglion. All centipedes have a nervus recurrens, which leaves the frontal ganglion ventrocaudally. Through the dorsal dilators of the foregut, the nerve enters the musculature of the pharynx. The n. recurrens then extends caudally between the outer ring musculature layer and the inner longitudinal musculature of the epithelium of the gut. A nervus recurrens dorsalis is present exclusively in Geophilomorpha (Fig. II.5 D, Nrd). In all taxa a hypocerebral ganglion is formed in the course of the n. recurrens (Figs. II.4, II.5; Hcg). Although Fahlander (1938) described a nervus frontalis in Scutigeromorpha and Lithobiomorpha (Fig. II.4 A, B; Nf) the existence of this nerve was not verified and Seifert (1967a) thought it to be an artifact. In Lithobiomorpha, a connective nerve (nervus connectivus II, Table II.1) is present, from which branches a thin nerve between the frontal ganglion and the brain.

This is the dorsal cardiac nerve (Fig. II.4 D; Ncd) that projects to the roof of the cephalic aorta and runs almost the entire length of the dorsal vessel. Labral nerves also have their origin in the tritocerebrum. In Scutigeromorpha, Geophilomorpha and Scolopendromorpha, there is one pair of labral nerves whereas in Lithobiomorpha there are two pairs. A pair of nerves (nervus connectivus I; Figs. II.4 C, D; II.5 C; Nc) leaves the

esophageal connectives ventrally. In Scolopendromorpha, a second pair of connective nerves can be found (Fig. 11.5A, Nc). They were misinterpreted as a free tritocerebral commissure (Seifert, 1967a). In contrast to diplopods where a free tritocerebral commissure occurs, in chilopods the tritocerebral commissure takes its course within the subesophageal ganglion.

### Subesophageal ganglia and the ventral nerve cord

The ventral nervous system is segmentally organized, with a pair of fused ganglia serving each segment. In the Lithobiomorpha and Geophilomorpha, the ventral nerve cord innervates the heart via segmental heart nerves (not studied in other taxa) (Scheffel, 1961; Ernst, 1971).

In *Lithobius forficatus*, the ganglia associated with the mandibles and both maxillae are fused as a single mass. This is caudally linked by paired connectives to a sequence of sixteen well-separated ganglia that innervate the trunk limbs. A terminal ganglion - possibly a fusion product of several neuromeres - succeeds the sixteenth trunk ganglion (Harzsch, 2004).

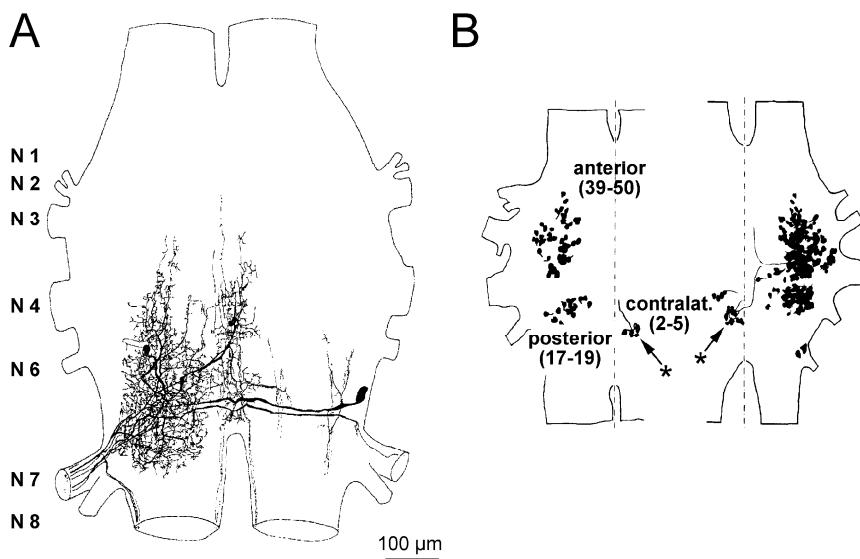
In *Geophilus flavus* the pregenital and genital ganglia are linked via short connectives (Ernst, 1971).

In *L. forficatus*, eight pairs of nerves arise from the ganglia (Fig. 11.2 A). Three are purely motor nerves innervating musculature, while the others also contain sensory axons. Exclusively sensory nerves have not been described (Rilling, 1968). The innervation pattern of dorsolateral motor neurons and interneurons differs considerably from that seen in hexapods, although in all euarthropods the motor neurons supplying an appendage derive from two populations belonging to two adjacent ganglia (Kutsch & Breidbach, 1994; Kutsch & Heckmann, 1995; Heckmann & Kutsch, 1995). All axons exit via the posterior nerve of the anterior ganglion. The fibers from the posterior ganglion ascend via the lateral region of the connective. All axons exit via an intersegmental nerve. The fibers that stem from the anterior and posterior neuron group run through the lateral region of the connective (Heckmann & Kutsch, 1995).

Somata of excitatory leg motor neurons in Euarthropoda in general seem to be arranged in three clusters in the ventral ganglionic cell cortex. These clusters are subdivided into smaller soma groups. Single cells appear to innervate the walking appendages (arrows in Fig. 11.2 B). In *L. forficatus*, there is a contralateral cluster composed of up to five cell bodies, which apparently correspond to the contralateral clusters observed in scorpions, crustaceans, and hexapods (Fig. 11.2B). At least one of

these cell bodies is GABA-immunoreactive (arrow with asterisks in Fig. II.2 B) (Harzsch et al., 2005). Three median pairs of serotonin immunoreactive neurons and one pair on the lateral border of the ganglion are identifiable (Harzsch, 2004).

The extremely rapid escape responses of centipedes suggest that the ventral nerve cord contains fast through-conducting pathways. Babu (1964) studied the giant fibers in the ventral nerve cord in Scolopendromorpha. According to their conducting speeds, three groups of giant fibers can be distinguished: (1) 3–4.5 m/s, (2) 3–3.5 m/s, and (3) 2–3 m/s. Giant fibers with slower conducting speed are responsible for the leg movement. In *Scolopendra morsitans*, the giant fibers are arranged in three groups: (1) dorso-lateral, (2) dorso-intermediate, and (3) dorso-medial. The diameters of giant fibers range between 28–58  $\mu\text{m}$ . The dorso-medial and dorso-intermediate groups correspond to the ascending pathway of crustacean and hexapods, the dorso-lateral group to the descending pathway (Varma, 1971).



**Fig. II.2 A** Selective drawing of some of the neurites belonging to the anterior set supplying the dorsal longitudinal muscles in ganglion 8 in *Lithobius forficatus*. There are large contralateral and two small midline somata. N 1-4, 6-8 Lateral nerve roots. **B** Distribution of walking leg motor neuron somata in the ventral soma complex in *Lithobius forficatus*. The anterior cluster contains the largest number of somata. Putative inhibitors are marked by arrows with asterisks. Only the ipsilateral portions of the ganglia are shown; broken lines indicate ganglion midlines. A modified after Heckmann & Kutsch (1995); B modified after Harzsch et al. (2005).

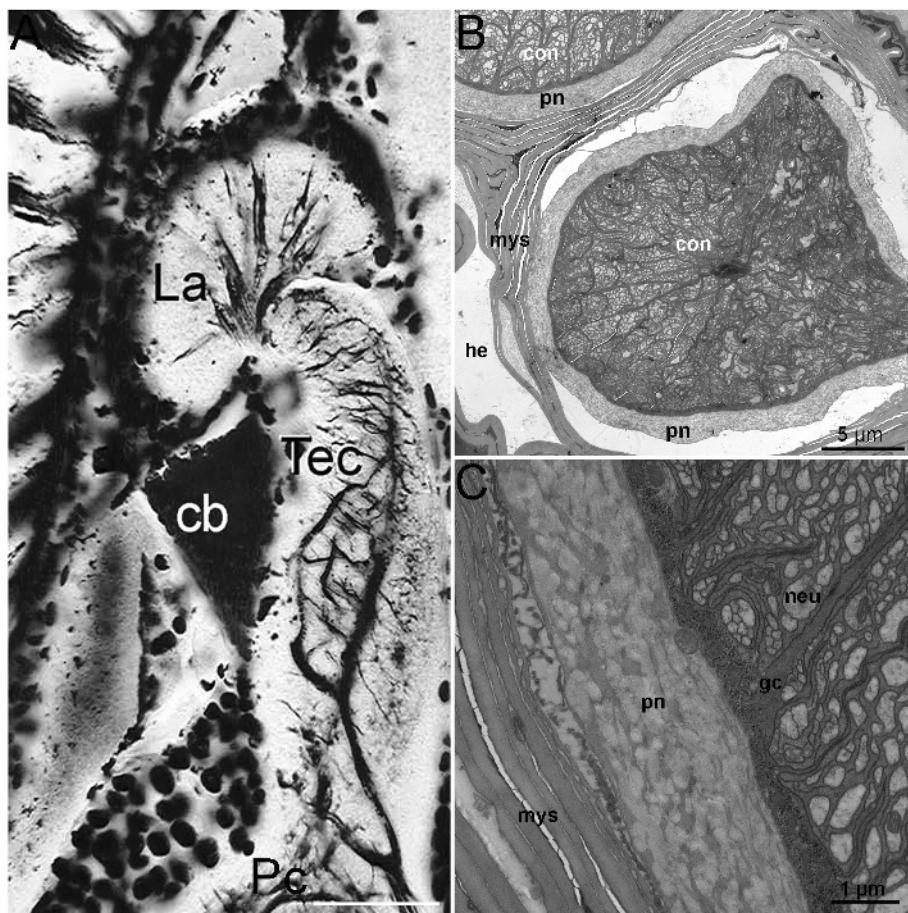


Fig. 11.3 A Bodian staining of optic neuropils in *Scutigera coleoptrata*. The passage of axons is constricted midway between the lamina and visual tectum. The two neuropils are connected by uncrossed axons. B Cross section of a connective of the ventral nerve cord with myelin sheath. C Magnification of connective and myelin sheath. A modified after Strausfeld (2005); B, C originals C. H. G. Müller.

cb cell bodies of neurones associated with the tectum (location behind the tectum's inner surface); con connective; gc glial cells; he hemolymph; La lamina; mys myelin sheath; neu neurite; Pc protocerebrum; pn perineurium; Tec visual tectum

#### *The nervous system of Scutigeromorpha*

Due to their roundish head shape, the appearance of parts of the central nervous sys-

tem in representatives of the Scutigeromorpha differs from that of other chilopod taxa (Fig. 11.4 A, C). The protocerebrum extends as a huge mass dorsally from the deutocerebrum. The elongated optic lobes, which extend contiguously from the lateral protocerebrum, are well developed compared to those of other chilopods in that they serve a sophisticated compound retina and are composed of orderly organized neurons. The cerebral glands (endocrine organs) are connected with the lateral protocerebrum by the nervus glandulae cerebralis (Fig. 11.4 A, Ngc).

The deutocerebrum, which is the second neuromere of the brain, actually extends forward to receive the robust antennal nerves. Within the deutocerebrum, the olfactory neuropils and the corpus lamellosum (mechanosensory neuropil) are visible as separate structures (Fig. 11.1 C, D, E) (Sombke et al., 2009). Like in hexapods, the deutocerebrum is partitioned into many discrete neuropils receiving what are thought to be olfactory receptor axons. However, these subunits have a cylindrical form instead of the spherical glomeruli that typify many insect olfactory lobes. Saint-Remy (1887, 1889) and Hörberg (1931) described these cylinders as irregular, convoluted ribbons. Dextranbiotin backfills reveal that these neuropils are first order processing units in the deutocerebrum (Fig. 11.1 C). In *Scutigera coleoptrata*, thirty-four distinct and uniquely identifiable subunits have been identified that are invariant between individuals. At least one subunit is typically linked to its contralateral counterpart. There is no evidence of further partitions within the cylindrical subunits, in contrast to the layering that hallmarks columns in the olfactory lobe of malacostracan crustaceans (Sandeman et al., 1992; Harzsch and Hansson, 2008). The ventrocaudal part of the antennal nerve innervates the presumed mechanosensory neuropil of the corpus lamellosum, which is composed of approximately eight lamellae divisible into two classes: (1) the outer two lamellae that form a 180° loop, (2) the inner lamellae that project further on dorsomedially (Fig. 11.1 E) (Sombke et al., 2009). In the Scutigeromorpha and Scolopendromorpha, these neuropils are connected contralaterally by the posterior antennal commissure (Fahlander, 1938). By analogy with the Hexapoda, a chemosensory function for the olfactory neuropils and a mechanosensory function for the corpus lamellosum have been suggested (Sombke et al., 2009).

A demarcation between the tritocerebrum and deutocerebrum is not apparent although the nervi frontales are supposed to indicate the anterior margin of the tritocerebrum, just posteroventral to the antennal lobe. The frontal connectives of the tritocerebrum project slightly caudad and converge medially at the frontal ganglion. They are distinguished from the stomodeal bridge by the absence of a layer of tritocerebral gangliar cells (see also Table 11.1). The nervus recurrens projects dorsally

from the frontal ganglion on top of the pharynx and esophagus. The nerve descends into the hypocerebral ganglion and its axons disperse over the foregut epithelium and musculature of the pharynx. Fahlander (1938) described a nervus frontalis (Fig. 11.4 A, B Nf) in *Thereuopoda clunifera* and *L. forficatus* but this was disputed by Seifert (1967a), who suggested that most likely Fahlander described a trachea. A pair of labral nerves emerges in the front of the tritocerebrum. These nerves converge and innervate the musculature of the clypeolabral region and the labral gland (buccal gland) (Fig. 11.4 A, C Nl). Paired connective nerves leave the tritocerebrum posteriorly and merge with the subesophageal ganglion. From the subesophageal ganglion an unpaired nerve projects between the pharynx and the musculus tentorio-pharyngealis medialis. In *T. clunifera*, Fahlander (1938) described a free tritocerebral commissure (Fig. 11.4 A, Tcc). According to Seifert (1967a), in *S. coleoptrata* this commissure lies within the subesophageal ganglion (Fig. 11.4 C, Tcc).

### *The nervous system of Lithobiomorpha*

In *Lithobius forficatus*, the brain (Fig. 11.4 B) is located in the frontal part of the head above and in front of the pharynx (Fig. 11.4 D). The nerve to the cerebral glands is paired. A transition between the deutocerebrum to the large tritocerebrum is not visible. The tritocerebral lobes are connected to the frontal ganglion over a short stomodeal bridge.

A short unpaired nerve projects from the frontal ganglion to the pharyngeal musculature that connects to the ventral side of the protocerebrum (Fig. 11.4 D, Nc II). According to Seifert (1967a), this nerve projects as the nervus connectivus II (see Table 1) into the medial part of the brain. Rilling (1968), however, was unsure about the destination of this nerve. Herbst (1891) first discovered the dorsal heart nerve (Fig. 11.4 D, Ncd), which projects to the ending of the aorta cephalica and follows it thereon (Seifert, 1967b). The nervus recurrens projects caudally from the frontal ganglion and supplies the frontal part of the alimentary tract dilators of the pharynx. Ganglionic swellings mark the hypocerebral ganglion.

A nerve projects to the hypopharynx from each connective of the tritocerebrum. The two nerves merge after entering the hypopharynx.

According to Rilling (1968) this is the free tritocerebral commissure, which innervates the musculature of the hypopharynx. However, Seifert (1967a) claims that a free tritocerebral commissure does not exist and that the tritocerebral commissure continues within the subesophageal ganglion.

### *The nervous system of Scolopendromorpha*

In representatives of the Scolopendromorpha the head is flattened and the shape of the brain reflects this shape (Fig. 11.5 C). The protocerebrum is located dorsally and caudal to the deutocerebrum. It provides short optic lobes that receive four visual nerves. Eyeless species, like *Cryptops* spp., have vestigial optic lobes (Fig. 11.1 F). In all Scolopendromorpha, the nervus glandulae cerebralis projects from the ventral border of the protocerebrum to the protocerebral glands (Fig. 11.5 B). Postantennal organs and nervi Tömösváryi are not present.

The deutocerebrum, although the second neuromere, extends forward from the protocerebrum. The dorsal antennal flexor muscle is innervated by a nerve that arises caudally from the antennal basis. A second nerve arises caudally in the ventrolateral part of the deutocerebrum. This carries the axons of motor neurons to antennal muscles and the axons of sensory neurons from receptors on the antenna. The deutocerebrum merges with the tritocerebrum without any noticeable border. The tritocerebral lobes are connected to the frontal ganglion by a short stomodeal bridge.

The nervus recurrens projects dorsally from the frontal ganglion and enters the outer and inner ring musculature of the pharynx. Caudally, the nerve swells into a hypocerebral ganglion equipped with a few neurons (Seifert, 1967a; Joshi et al., 1977). Two nerves arise from the tritocerebral ganglia in the vicinity of the frontal ganglion and split up into three branches (Fig. 11.5 A, C, NI). According to Seifert (1967a) these nerves are the basis of the nervus labralis. Joshi et al. (1977) claimed that yet another nerve arises from the tritocerebrum. Fahlander (1938) and Joshi et al. (1977) described a free tritocerebral commissure which, according to Seifert (1967a), is covered with a joint neural lamella inside the subesophageal ganglion. The caudal connective nerves arising laterally from the esophageal connectives project into the mandibles. Varma (1971) described the dorsal heart nerve of *S. morsitans* that extends from the head up to the segment 21.

### *The nervous system of Geophilomorpha*

The brain of the Geophilomorpha, all of which are eyeless, is relatively flattened and is also the most modified in Chilopoda (Fig. 11.5 B, D). Correlated with the absence of a visual system, the protocerebrum is reduced. Ventrally, the paired nervus glandulae cerebralis emerge and project to the cerebral gland. This nerve was misleadingly described as nervus Tömösváry by Saint-Remy (1887). However, a postantennal organ is missing in Geophilomorpha.

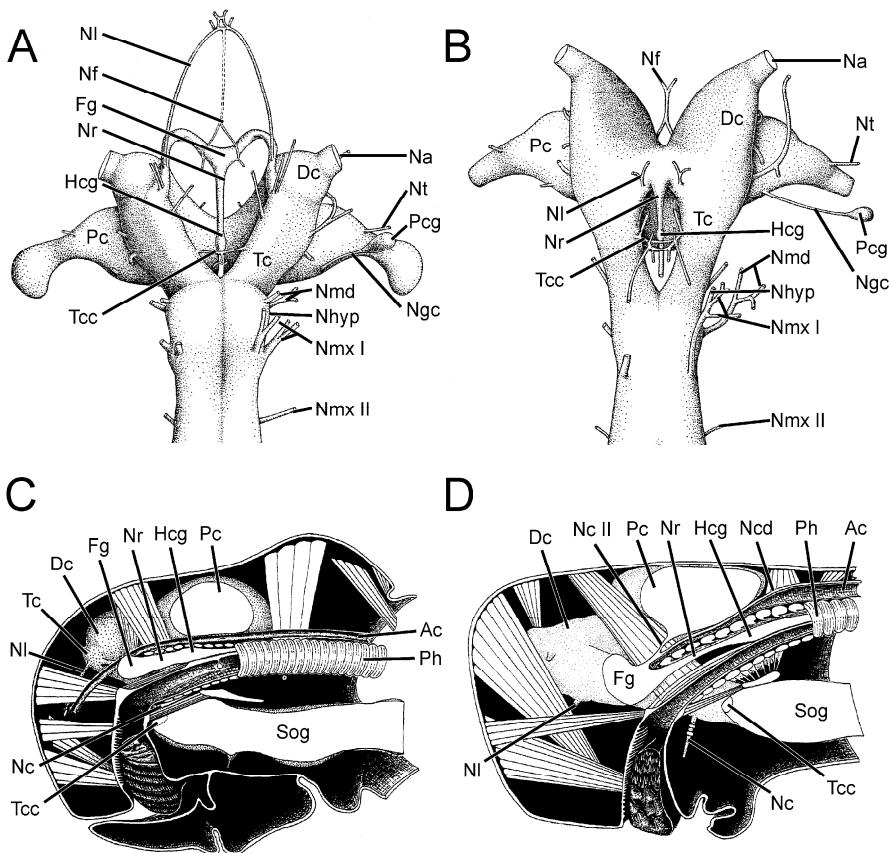


Fig. 11.4 A Nervous system of *Thereuopoda clunifera* (Scutigeromorpha). Ventral view. B Nervous system of *Lithobius forficatus* (Lithobiomorpha). Ventral view. Only one nervus glandulae cerebralis is shown. Nervus connectivus not shown. C Mediosagittal section through the head of *Scutigera coleoptrata* (Scutigeromorpha). D Mediosagittal section through the head of *Lithobius forficatus* (Lithobiomorpha). A-B modified after Fahlander (1938); C-D modified after Seifert (1967a).

Ac Aorta cephalica; Dc Deutocerebrum; Fg Frontal ganglion; Hcg Hypocerebral ganglion; Na nervus antennalis; Nc nervus connectivus I; Nc II nervus connectivus 2; Ncd nervus cephalicus dorsalis; Nf nervus frontalis (existence unclear after Seifert); Ngc nervus glandulae cerebralis; Nhyp nervus hypopharyngealis; NI nervus labralis; Nmd nervus mandibularis; Nmx I nervus maxillaris 1; Nmx II nervus maxillaris 2; Nr nervus recurrens; Nt nervus tömosváry; Pc Protocerebrum; Pcg Protocerebral gland; Ph Pharynx; Sog Subesophageal ganglion; Tc Tritocerebrum; Tcc Tritocerebral commissure

Table II.2 Areas innervated by nerves of the brain and the subesophageal ganglion of *L. forficatus*; nerve numbers after Fahlander (1938) (first column) and Rilling (1968) (second column).

Protocerebrum		
N1	N1	ocelli
N3	N2	organ of Tömösváry
	N3	cerebral gland
N4	N4	cerebral gland
N6 (Dc)	N5	ocellar region, epicranium
	N6	ocellar region, epicranium
N2	N7	ocellar region, epicranium
	N8	?
Deutocerebrum		
N7	N9	antennal nerve (motor/sensory)
	N10	antennal musculature-sensory organ
	N11	free nerve endings on antennifer/antenna articulation
	N12	?
N10	N13	basal antennal musculature
N12	N14	basal antennal musculature
N11	N15	basal antennal musculature
Tritocerebrum		
N13	N16	stomodeal bridge/frontal ganglion
N15	N17	pharynx dilator 122/N. connectivus
N14	N18	nervus recurrens
	N19	epipharyngeal muscle, labral muscles
	N20	clypeo-labral and clypeo-tentorial musculature
N18	N21	lateral preoral cavity
N19+N20	N22	hypopharyngeal muscle and wall
	N23	epicranial tentorial muscles
Subesophageal ganglion		
Nhyp + Nmx 1	Nmd	mandible
	N hph & Nmx I	hypopharynx, first maxillae
	Nmx II, N 1 – 5	second maxillae
Forcipular ganglion		
Mxp N 1 – 4		forcipules

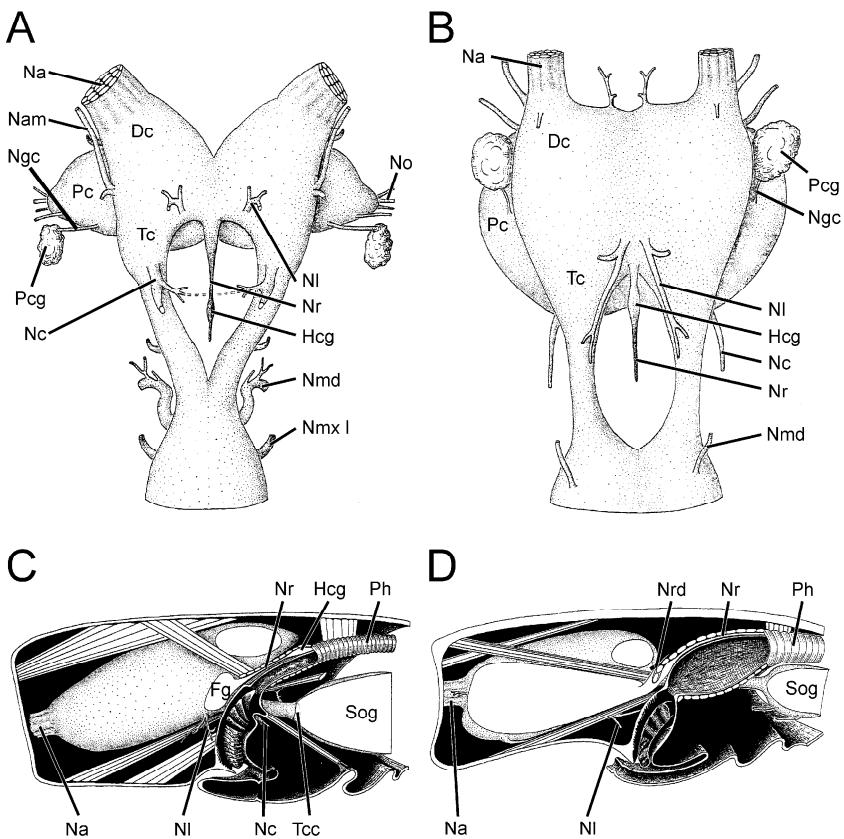


Fig. II.5 A Nervous system of *Scolopendra cingulata* (Scolopendromorpha), ventral view. B Nervous system of *Geophilus* sp. (Geophilomorpha), ventral view. C Mediosagittal section through the head of *Cryptops hortensis* (Scolopendromorpha). D Mediosagittal section through the head of *Geophilus flavus* (Geophilomorpha). All modified after Seifert (1967a).

Dc Deutocerebrum; Fg Frontal ganglion; Hcg Hypocerebral ganglion; Na nervus antennalis; Nam nervus antennalis (motor); Nc nervus connectivus; Ngc nervus glandulae cerebralis; NI nervus labralis; Nmd nervus mandibularis; Nmx I nervus maxillaris I; No nervus opticus; Nr nervus recurrens; Nrd nervus recurrens dorsalis; Pc Protocerebrum; Pcg Protocerebral gland; Ph Pharynx; Sog Subesophageal ganglion; Tc Tritocerebrum; Tec Tritocerebral commissure

The largest section of the brain is the deutocerebrum. Again, a clear transition between the proto- and deutocerebrum is not noticeable. The antennal nerves contain

10-15 bundles of sensory neurons and three motor nerves (Lorenzo, 1960) that innervate the ventral flexor muscles of the antenna. According to Lorenzo (1960), another motor nerve arises from the protocerebrum and innervates the sensory organs in the lateral clypeus region.

The tritocerebrum is little developed and is contiguous with deutocerebral lobes without any visible border in between. The lobes of the tritocerebrum are connected by a short stomodeal bridge. The nervus recurrens projects from the frontal ganglion to the epithelia and musculature of the pharynx. A nervus recurrens dorsalis is present only in Geophilomorpha (Fig. 11.5 D, Nrd). Ventrally, the n. recurrens swells to a small hypocerebral ganglion and splits into two branches in the vicinity of the second maxillae. According to Lorenzo (1960), the labral nerve originates near the n. recurrens and innervates the frontodorsal dilators and the lateral areas of the labrum. Seifert (1967a) instead stated that the labral nerve emerges from the frontal ganglion (Fig. 11.5 D, Nl). Fahlander (1938) described a free tritocerebral commissure that has not been confirmed by Lorenzo (1960) or Seifert (1967a).

### Histology and ultrastructure

As in other arthropods, the brain of *Lithobius forficatus* is enclosed within a neurilemma that serves as a barrier between it and the hemolymph. The neurilemma is divided into two components. (1) The external neural lamella is composed of collagen fibers (maximal 0.3 µm) (Füller, 1964). (2) The more internal discontinuous perilemma (or perineurium) is composed of glial cells (Jamault-Navarro and Joly, 1977; Jamault-Navarro, 1981). Both act as a blood-brain barrier. Along with septate junctions, glial cells are connected over linker junctions, which are apparently characteristic for chilopods (Lane, 1989, 1991). The neuropil of the brain lies within a rind composed of neuronal somata. Three types of these can be found: (1) small perikarya (10-15 µm in diameter) with a round and voluminous nucleus and reduced cytoplasm, (2) larger neurons (about 20 µm diameter) with occasionally lobate nuclei and voluminous cytoplasm, and (3) large neurosecretory cells filled with neurosecretory granules (NCSs). NSCs are located in paired symmetrical groups in the anterolateral area of the frontal lobes and in the ventral nerve cord (Gabe, 1966; Jamault-Navarro & Joly, 1977).

The nerves of the peripheral nervous system are coated by a distinctive double-layered neural lamella. The inner layer is composed of mucopolysaccharides with a specific alignment of collagen fibers. The outer lamella is composed of connective tissue (Füller, 1964; Füller & Ude, 1969). In different species of Geophilomorpha, ganglia, connectives

and peripheral nerves of the ventral nerve cord are coated by a convoluted multicellular myelin-like sheath (Fig. 11.3 B, C) (Rosenberg & Seifert, 1978). The number of cells and convolutions is variable. Sheath cells contain lentiform nuclei and only little cytoplasm.

Mitochondria, cytosomes, granular endoplasmatic reticulum, ribosomes, and Golgi complexes can be found. No cytoplasm is visible within the myelinated areas. Cell membranes are coated with a broad polysaccharide matrix. Hemocoel clefts are visible between the myelinated cells. Filaments of cells overlap and are connected via septate desmosomes. The main function of the myelin-like sheath is thought to be a substantial barrier to the hemolymph (Rosenberg & Seifert, 1978).

### Neuroactive substances

In *Lithobius forficatus*, acetylcholine, GABA, serotonin (5-hydroxytryptamine), noradrenalin (norepinephrine), and dopamine have been documented as neuroactive substances (Descamps & Lasalle, 1983, 1986). The effect of dopamine differs according to seasons and is thus thought to play a role in the control of seasonal rhythms. Serotonin and noradrenaline have been localized in the frontal lobes and the lateral areas of the deuto- and tritocerebrum, as well as in the ventral nerve cord (Descamps et al., 1985). Its effect on the growth of spermatocytes has been shown. GABA ( $\gamma$ -aminobutyric acid) has been suggested as the inhibitory transmitter whereas serotonin is thought to play a role in the maturation of sperm with dopamine having an inhibitory effect (Beniouri, 1983).

### References

- BABU, K. S., 1964. Through-conduction systems in the ventral nerve cord of centipedes. – Zeitschrift für vergleichende Physiologie 49: 114-129.
- BENIOURI, R., 1983. Contribution à l'étude de la spermatogénèse et de son déterminisme chez les Myriapodes Chilopodes. – Thèse 3ème cycle, Université de Lille.
- DESCAMPS, M., R. JOLY & C. JAMAULT-NAVARRO, 1985. Autoradiographic localization of 5-hydroxytryptamine and noradrenaline in the central nervous system of *Lithobius forficatus* L. (Myriapoda, Chilopoda). – Bijdragen tot de Dierkunde 55: 47-54.
- DESCAMPS, M. & B. LASALLE, 1983. Influence of putative neurotransmitter on brain electrical activity in *Lithobius forficatus* L. (Myriapoda, Chilopoda). – Comparative Biochemistry and Physiology 76 C: 237-240.
- DESCAMPS, M. & B. LASALLE, 1986. 20-hydroxyecdysone effects on the oocytes resting potential in *Lithobius forficatus* L. (Myriapoda, Chilopoda). – P. 505 in M. POUCHET, J. ANDRIES & A. DHAINAUT (eds.) Advances in invertebrate reproduction. – Amsterdam: Elsevier.
- ERNST, A., 1971. Licht- und elektronenmikroskopische Untersuchungen zur Neurosekretion bei *Geophilus longicornis* Leach unter besonderer Berücksichtigung der Neurohämialorgane. – Zeitschrift für wissenschaftliche Zoologie 182: 62-130.

- FAHLANDER, K., 1938. Beiträge zur Anatomie und systematischen Einteilung der Chilopoda. – *Zoologiska Bidrag från Uppsala* 17: 1-148.
- FÜLLER, H., 1964. Über Struktur und Chemismus der Neurallamelle bei Chilopoden. – *Zeitschrift für wissenschaftliche Zoologie* 169: 203-215.
- FÜLLER, H. & J. UDE, 1969. Elektronenmikroskopische Untersuchungen über den Feinbau der Neurallamelle bei Chilopoden. – *Zeitschrift für wissenschaftliche Zoologie* 180: 21-33.
- GABE, M., 1966. Neurosecretion. – Pergamon Press, Oxford.
- HARZSCH, S., 2004. Phylogenetic comparison of serotonin-immunoreactive neurons in representatives of the Chilopoda, Diplopoda, and Chelicerata: implications for arthropod relationships. – *Journal of Morphology* 259: 198-213.
- HARZSCH, S. & B. S. HANSSON, 2008. Brain architecture in the terrestrial hermit crab *Coenobita clypeatus* (Anomura, Coenobitidae), a crustacean with a good aerial sense of smell. – *BMC Neuroscience* 9: 58.
- HARZSCH, S., C. H. G. MÜLLER & H. WOLF, 2005. From variable to constant cell numbers: cellular characteristics of the arthropod nervous system argue against a sister-group relationship of Chelicerata and „Myriapoda“ but favour the Mandibulata concept. – *Development, Genes and Evolution* 215: 53-68.
- HECKMANN, R. & W. KUTSCH, 1995. Motor supply of the dorsal longitudinal muscles. II. Comparison of motoneuron sets in Tracheata. – *Zoomorphology* 115: 197-211.
- HERBST, C., 1891. Beiträge zur Kenntnis der Chilopoden (Drüsen; Coxalorgan; Gefäßsystem und Eingeweidenervensystem). – *Bibliotheca zoologica* (3) 9: 1-43.
- HOLMGREN, N., 1916. Zur vergleichenden Anatomie des Gehirns von Polychaeten, Onychophoren, Xiphosuren, Arachniden, Crustaceen, Myriopoden und Insekten. – *Kungliga Svenska Vetenskapsakademiens Handlingar* 56: 1-303.
- HÖRBERG, T., 1931. Studien über den komparativen Bau des Gehirns von *Scutigera coleoptrata* (L.). – *Lunds Universitets Årsskrift N. F. Avd, 2, 27(19)*: 1-24.
- JAMAULT-NAVARRO, C., 1981. Cellules neurosécrétrices et trajets axonaux protocérébraux chez *Lithobius forficatus* (L.) (Myriapode Chilopode). Etude ultrastructurale. – *Archives de Biologie* 92: 203-218.
- JAMAULT-NAVARRO, C. & R. JOLY, 1977. Localisation et cytology des cellules neurosécrétrices protocérébrales chez *Lithobius forficatus* (L.) (Myriapode Chilopode). – *General and Comparative Endocrinology* 31: 106-120.
- JOLY, R. & M. DESCAMPS, 1987. Histology and ultrastructure of the myriapod brain. – Pp. 135-157 in A. GUPTA (ed.) *Arthropod brain*. – Wiley, New York.
- JOSHI, G., P. HURKAT, & V. CHANGULANI, 1977. Studies on the morphological aspects of the supraoesophageal and suboesophageal ganglia of *Scolopendra morsitans* Linné (Myriapoda, Chilopoda). – *Deutsche entomologische Zeitschrift* 24: 175-180.
- KUTSCH, W. & O. BREIDBACH, 1994. Homologous structures in the nervous system of Arthropoda. – Pp. 1-113 in P. D. EVANS (ed.) *Advances in Insect Physiology* 24. – Academic Press, London-Sydney.
- KUTSCH, W. & R. HECKMANN, 1995. Homologous structures, exemplified by motoneurones of mandibulates. – Pp. 220-248 in O. BREIDBACH & W. KUTSCH (eds.) *The nervous system of invertebrates: An evolutionary and comparative approach*. – Birkhäuser, Basel.
- LANE, N. J., 1989. Novel arthropod cell junctions with restrictive intercellular "linkers". – *Journal of Neurocytology* 18: 661-669.
- LANE, N. J., 1991. Morphology of glial - blood barriers. – *Annals of the New York Academy of Sciences* 633: 348-362.
- LOESEL, R., D. R. NÄSSEL & N. J. STRAUSFELD, 2002. Common design in a unique midline neuropil in the brains of arthropods. – *Arthropod Structure & Development* 31: 77-91.

- LORENZO, M., 1960. The cephalic nervous system of the centipede *Arenophilus bipuncticeps* (Wood) (Chilopoda, Geophilomorpha, Geophilidae). – Smithsonian Miscellaneous Collections 140: 1-43.
- MELZER, R. R., Z. TETYKO & U. SMOLA, 1996. Photoreceptor axons and optic neuropils in *Lithobius forficatus* (Linnaeus, 1758) (Chilopoda, Lithobiidae). – Zoologischer Anzeiger 235: 177-182.
- PETYKÓ, Z., T. ZIMMERMANN, U. SMOLA & R. R. MELZER, 1996. Central projections of Tömösváry's organ in *Lithobius forficatus* (Chilopoda, Lithobiidae). – Cell and Tissue Research 283: 331-334.
- RILLING, G., 1968. *Lithobius forficatus*. Grosses Zoologisches Praktikum 13b. – Fischer, Stuttgart.
- ROSENBERG, J. & G. SEIFERT, 1978. Die Myelinscheide um Zentralnervensystem und peripherie Nerven der Geophilomorpha (Chilopoda). – Zoomorphology 89: 21-31.
- SAINT-REMY, G., 1887. Contribution à l'étude du cerveau chez les Arthropodes trachéates. – Archives de Zoologie expérimentale et générale (2) 5 bis, supplément: 1-274.
- SAINT-REMY, G., 1889. Sur la structure du cerveau chez les Myriapodes et les Arachnides. – Revue biologique du Nord de la France 8: 281-298.
- SANDEMAN, D., R. SANDEMAN, C. DERBY & M. SCHMIDT, 1992. Morphology of the brain of crayfish, crabs, and spiny lobsters: A common nomenclature for homologous structures. – Biological Bulletin 183: 304-326.
- SCHACHTNER, J., M. SCHMIDT & U. HOMBERG, 2005. Organization and evolutionary trends of primary olfactory brain centers in Tetraconata (Crustacea + Hexapoda). – Arthropod Structure & Development 34: 257-299.
- SCHEFFEL, H., 1961. Untersuchungen zur Neurosekretion bei *Lithobius forficatus*. – Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 83: 529-556.
- SEIFERT, G., 1967a. Das stomatogastrische Nervensystem der Chilopoden. – Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 84: 167-190.
- SEIFERT, G., 1967b. Der Ursprung des dorsalen Herznervs der Lithobiiden (Chilopoda). – Experientia 23: 452-453.
- SOMBKE, A., S. HARZSCH & B. S. HANSSON, 2009. Brain structure of *Scutigera coleoptrata*: New insights into the evolution of mandibulate olfactory centers. – Soil Organisms 81: 319-325.
- STRAUSFELD N. J., 2005. The evolution of crustacean and insect optic lobes and the origin of chiasmata. – Arthropod Structure & Development 34: 235-256.
- VARMA, L., 1971. On the morphology of the heart of the centipede *Scolopendra morsitans* Linn. (Chilopoda, Epimorpha). – Journal of Animal Morphology and Physiology 18: 111-120.

## Chapter 12

# CHILOPODA – SENSE ORGANS

Carsten H. G. Müller, Andy Sombke, Gero Hilken & Jörg Rosenberg

### *Photoreceptor organs*

Based on their recently published electron microscopic examinations, Müller and Meyer-Rochow (2006a) defined two types of lateral eyes in Chilopoda according to the presence or absence of a crystalline cone:

- compound eyes constructed of ommatidia possessing a crystalline cone formed by four cone cells (Scutigeromorpha; Müller et al., 2003b) (Fig. 12.1A-B)
- lateral ocelli without a crystalline cone, but with a unicorneal lens (Lithobiomorpha: Müller and Rosenberg, 2006; Scolopendromorpha: Müller and Meyer-Rochow, 20006a; Craterostigmomorpha: Müller and Meyer-Rochow, 2006b) (Fig. 12.1E-L)

### *The compound eyes of Scutigeromorpha*

Because their fine structure did not seem to correspond to that described in the Mandibulata, scutigeromorph ommatidia were generally believed to form a “pseudo-compound eye” or “pseudo-faceted eye”, that is, not being homologous with other arthropod compound eyes. However, Paulus (1979) considered the eye of *Scutigera* a secondary construct built by modified ommatidia putatively emerged from a dissolution of a primary faceted eye. Recently, a comprehensive examination of the fine structural organisation of the compound eye of *S. coleoptrata* has been provided by Müller et al. (2003b), forming the basis for the following description.

### *General organization of a notostigmophoran ommatidium*

The triangular compound eye of adult *S. coleoptrata* usually contains about 150 ommatidia (Fig. 12.1A). Higher numbers, up to 600 ommatidia, are reached in the larger species *Thereuopoda clunifera* and *Thereuonema tuberculata* (Hanström, 1934). Each cuticular lens displays an approximately biconvex profile, particularly curved along its distal surface. In the apical region of the eye, the ommatidia are of a hexagonal shape with average diameters of 50 µm (Fig. 12.1B). Pentagonally shaped facets are found at the margins of the eye. The total number of cells contributing to an ommatidium varies

within the eye region. Each ommatidium contains a dioptric apparatus, a photoreceptive dual-type retinula and accessory pigment cells. Interommatidial exocrine glands are located in the interspace between the ommatidia (Müller et al. 2003a,b) (Fig. 12.1B).

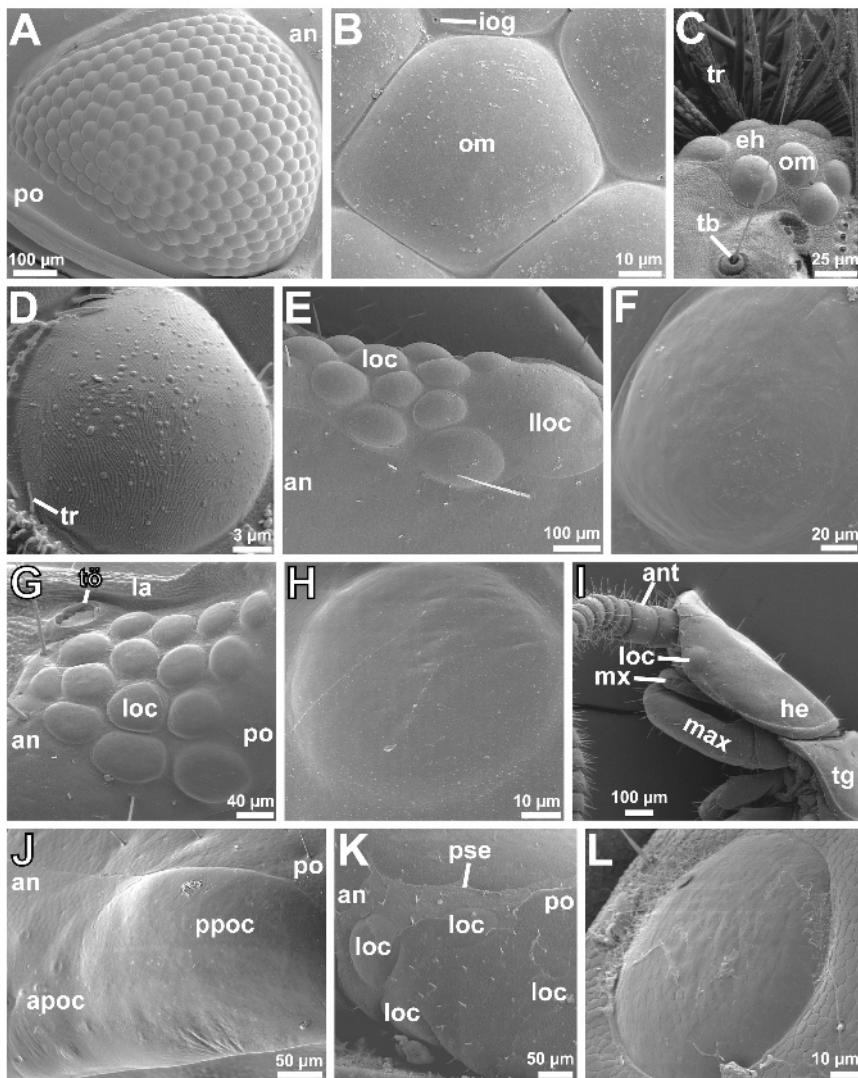
#### *Dioptric apparatus*

The dioptric apparatus includes a biconvex corneal facet, made up by 8-10 corneagenous cells, and a multipartite crystalline cone formed by four cells (Fig. 12.2B,D). The corneagenous cells are arranged in a circle around the distalmost part of the crystalline cone and directly underly the corneal facet (Fig. 12.2B). The cytoplasm is filled with numerous pigment granules showing various degrees of osmophilicity. Some pigment granules have diameters (0.5-1.2 µm) slightly higher than in the retinula cells (Fig. 12.3B).

Corneagenous cells show a similar appearance and cytoplasmic composition to the primary pigment cells in hexapod ommatidia, in which the same cell type secretes the cornea and produces a primary pigment shield around the crystalline cone. In crustaceans, however, the corneagenous cells are always free of pigment granules (Paulus, 1979, 2000). Nevertheless, the occurrence of electron-dense pigment granules and the widely accepted homology of the crustacean and hexapod ommatidia (cf. Paulus,

**Fig. 12.1.** Various eye types of Chilopoda (A-B, E-L) and penicillate Diplopoda (C-D) observed by scanning electron microscopy. A-B *Scutiger coleoptrata*: A Right compound eye. B One ommatidium and its surrounding interommatidial spaces housing pore openings of interommatidial glands. C-D *Phryssonotus platycephalus* (Penicillata): C Eye hill bearing 9-12 modified ommatidia, D Detailed view of an ommatidium with streak-like sculpturation on the corneal surface. E-F *Eupolybothrus fasciatus*: E Dorsal view of right lateral ocellar field with far distanced posterior ocellus pointing towards lateroposterior direction, F Detailed view of a lateral ocellus in the middle of lateral ocellar field. G-H *Lithobius dentatus*: G. Dorsal view of right lateral ocellar field with subjacent organ of Tömösváry, H Detailed view of a lateral ocellus placed medioposteriorly in the cluster. I *Lamyctes emarginatus*: Lateral view of the left half of the head and first trunk segment. Note the occurrence of one lateral ocellus on the side of the head capsule. J *Craterostigmus tasmanianus*: Detailed view of the left lateral ocellus. K-L *Scolopendra oraniensis*: K Left ocellar field with four ocelli in decussate formation. L Anterior ocellus in the same ocellar field as in K, higher magnification. A-B originals Pohl/Müller, C-D after Müller et al. (2007), E, G after Müller and Rosenberg (2006), F,H-I originals Müller, J. Müller and Meyer-Rochow (2006b), K-L after Müller and Meyer-Rochow (2006a).

an anterior direction; ant antenna; apoc anterior part of the ocellus not covered by the corneal vault; eh eye hill; he head capsule; iog opening of the interommatidial exocrine gland; la lateral direction (lateral end of the head capsule); lloc large ocellus at the posterior end of the cluster; loc lateral ocellus; max forcipule (maxilliped); mx maxilla; om ommatidium; po posterior direction; ppoc posterior; regular part of the ocellus; pse secretion plaque on the cuticle and corneal lens; tb trichobothrium; tg tergit of first trunk segment; tr (feathered) trichome; tō organ of Tömösvary



1979, 2000; Dohle, 2001; Richter, 2002) may support a common origin of scutigeromorph and tetracanate corneagenous cells. The only argument against this assumption would be the differing number of corneagenous cells.

Each spheroidal crystalline cone houses up to eight compartments, unequally distributed across the cone corpus (Figs. 12.2A-C, 12.3A,C,E). These cone compartments are mostly produced by four eucone cells with their somata displaced to the proximal

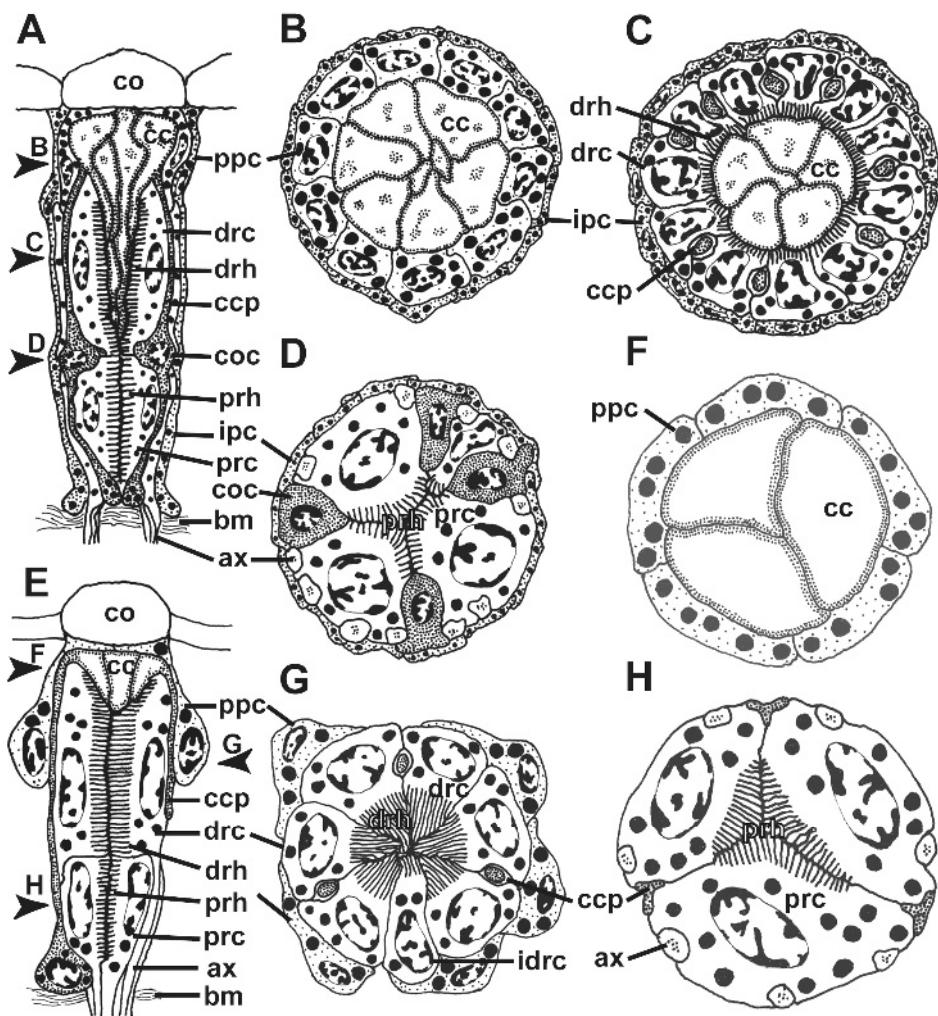
region of the ommatidium. The nuclear zone of the cone cells is located between the four proximal retinula cells (Figs. 12.2D, 12.3F). The cone cell somata are linked to either one or two cone segment(s) by cytoplasmic strands (Figs. 12.2A,C, 12.3A-B,E-F). Directly above the rhabdomeres of the distal retinula cells, each cytoplasmic process unites with one crystalline cone compartment (e.g. Figs. 12.2A, 12.3B). It is, however, impossible to propose a general distribution pattern of the distal processes of the cone cells in the sense of Melzer et al. (1997) or Dohle (2001) because the number of distal retinula cells as well as infraretinular spaces is not fixed. The cone cell somata emit four proximal cytoplasmic processes running towards the basal matrix where they widen to sac-like terminals containing numerous pigment granules (Figs. 12.2A, 12.3G). Most basally, the terminals come into contact and surround the proximal tip of the proximal rhabdome (Figs. 12.2A, 12.3H).

#### *Retinula cells and rhabdom*

The retinula of scutigeromorph ommatidia is arranged in two stacked horizontal coronae of retinula cells of distinct typology (Figs. 12.2A, 12.3A). In the distal retinula, one can count 9-13 cells forming a ring-like rhabdome around the middle and proximal third of the crystalline cone (Figs 12.2A,C, 12.3E).

**Fig. 12.2** Schematic reconstructions of scutigeromorph and penicillata ommatidia based on light microscopic and transmission electron microscopic studies. A-D *Scutigera coleoptrata* (Chilopoda): A Mediosagittal section through an ommatidium containing a dual type retinula comprising a single corona of distal and proximal retinula cells. B-D Transverse sections through different regions of an ommatidium (section planes indicated by black arrowheads in A): B Mediodistal region of the crystalline cone surrounded by primary pigment cells. C Medioproximal region of the crystalline cone surrounded by distal retinula cells, D Nuclear level of proximal retinula cells and intermediate cone cells surrounded by interommatidial pigment cells. E-H *Phryssonotus platycephalus* (Diplopoda): E Mediosagittal section through miniaturized ommatidium containing a dual type retinula (distributed among a distal and proximal layer of retinula cells). F-H Transverse sections through different regions of an ommatidium (section planes indicated by black arrowheads in E): F Distomedian region of the tripartite crystalline cone (cut directly beneath the corneal lens) surrounded by primary pigment cells, G Nuclear level of the corona of distal retinula cells surrounded by primary pigment cells, H Nuclear level of ring of proximal retinula cells. Drawings modified after Müller (2008).

ax axonic process of a retinula cell; bm basal matrix; cc; crystalline cone (compartment); ccp distal (or proximal) process of a cone cell; co corneal lens; coc eucone cell; drc distal retinula cell; drh distal rhabdome; idrc irregular (small) distal retinula cell; ipc interommatidial pigment cell; ppc primary pigment cell; prc proximal retinula cell; prh proximal rhabdome



The proximal retinula cells are always four in number and create a closed rhabdome with wider, less ordered microvilli (diameter 100-150 nm). The first to third cells are of equal size, the fourth is smaller and of irregular shape (Figs. 12.2D, 12.3G). The rhabdomeric microvilli of both distal and proximal retinula cells are closely attached to each other and do not interdigitate. Because of the absence of interdigitating rhabdomeres in the proximal retinula in *Scutigera* ommatidia, a homology of the dual type retinulae of notostigmophoran ommatidia and pleurostigmophoran lateral ocelli is not convincingly supported (Müller and Rosenberg, 2006). A homology of dual type retinulae

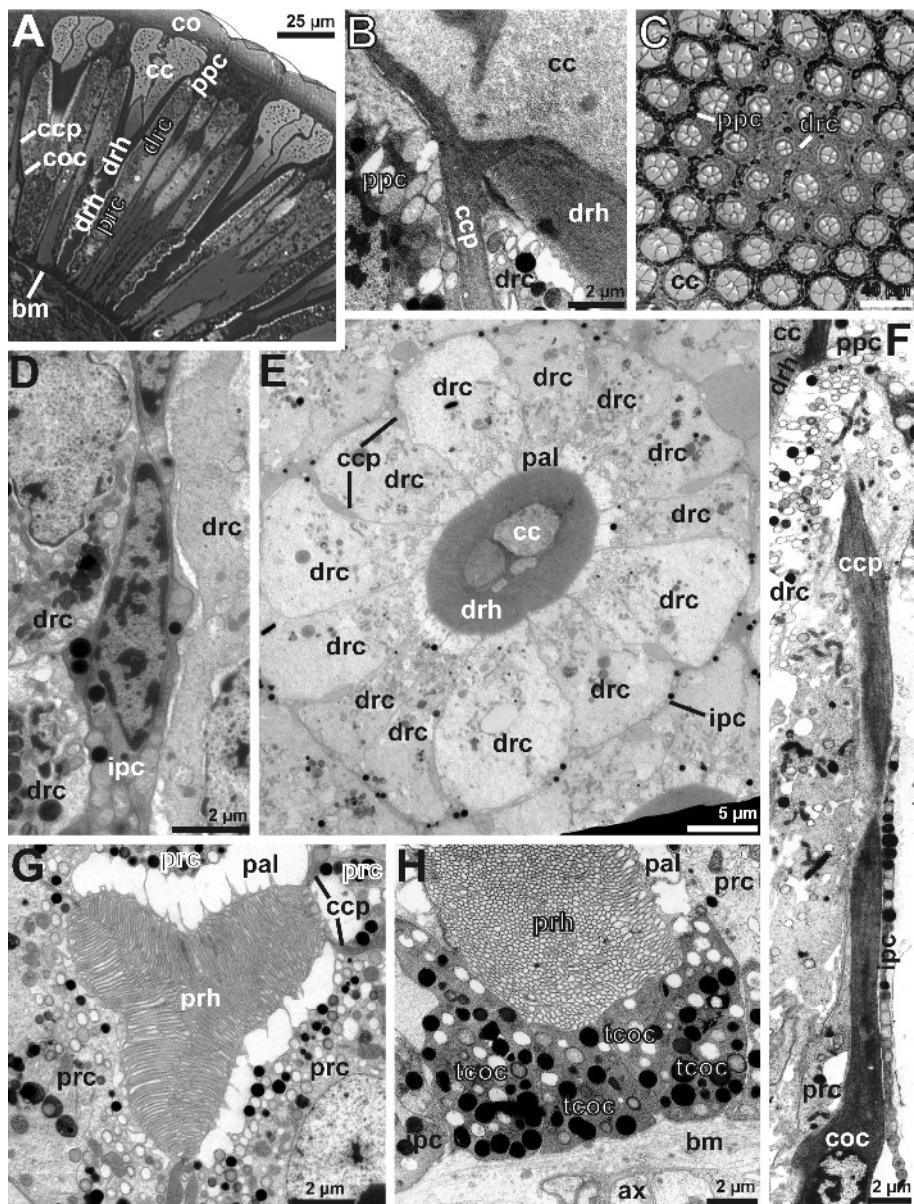


Fig. 12.3 Organization of compound eye and ommatidia of *Scutigera coleoptrata* as observed by light microscopy (A,C) and transmission electron microscopy (B,D-H). A Longitudinal section through the middle of the compound eye showing several ommatidia in longitudinally and tangentially cut perspective. B Distal process of a cone cell connecting to associated cone compartment. C Trans-

of Notostigmophora and some Hexapoda could be questioned due to different absolute numbers of retinula cells. Additionally, there is a slight intraspecific variation of distal retinula cell numbers among the Notostigmophora, a condition unknown in crustacean and hexapod ommatidia.

#### *Accessory pigment cells*

The pigment shield is composed of several elongated cells surrounding the entire ommatidium. Interommatidial pigment cells, 14–16 in number, extend from the cornea down to the basal matrix (Figs. 12.2A, 12.3D–E). In its most distal and proximal regions, an interommatidial pigment cell is densely filled with pigment granules (diameter 0.4–0.8 µm), mostly rather osmiophilic. Other typical organelles are large vesicles of lower electron density (diameter 0.5–1.2 µm). A distinct nuclear zone begins on the proximal level of the primary pigment cells (Fig. 12.3D). With their specific equipment of cytoplasmic granules, the interommatidial pigment cells may provide optical isolation between adjacent ommatidia. Moreover, the elaborated system of microtubules may offer a stabilisation to the extended ommatidia.

#### *Basal matrix and optic neuropils*

The entire compound eye is lined by a complex basal matrix separating the retinal region of the eye from the subjacent neuropil and the hemolymphatic space (Fig. 12.2A, D–H). Figure 12.2A shows a transverse section through a compound eye showing ommatidia cut at in their distal part at different levels of the crystalline cone, the deepest cuts being found in the centre of the image. D Longitudinal section through an interommatidial space occupied by interommatidial pigment cells that here surround the distal retinulae of neighbouring ommatidia. E Overview of a corona of 13 distal retinula cells at the proximal level of the crystalline cone. Distal processes of the four cone cells are found in the infraretinular spaces. F Oblique-longitudinal section through the periphery of a distal retinula cell providing an almost complete view of a distal cone cell process extending from the proximal soma to related cone compartment. G Cross section through the corona of proximal retinula cells shortly below the transition zone to distal retinula. Note the four proximal cone cell projections running down to the basal matrix through infraretinular spaces. H Oblique-longitudinal section through proximal tip of the proximal rhabdom produced by proximal retinula cells. Swollen and pigmented terminations of proximal cone cell processes are assembled below the rhabdom. A,C,D–E,G originals Müller, B,F,H micrographs modified after Müller et al. (2003b).

ax axonic process of a retinula cell; bm basal matrix; cc; crystalline cone (compartment); ccp; distal (or proximal) process of a cone cell; co corneal lens; coc eucone cell; drc distal retinula cell; drh distal rhabdom; ipc interommatidial pigment cell; pal swollen cisternae of the perirhabdomeric ('palisade') endoplasmic reticulum (ER); ppc primary pigment cell; prc proximal retinula cell; prh proximal rhabdom; teoc swollen termination of a cone cell

3A). The basal matrix consists of an extracellular (basal lamina of the cone and interommatidial pigment cells) and cellular (terminally swollen processes of the cone and interommatidial pigment cells, retinular axons, underlying muscle bundles, hemocytes, glial cells) portion (Fig. 12.3H). The basal lamina, 0.9–1.5 µm in thickness, is apparently a dense mat of collagen fibrils and microfilaments. The basal matrix is pierced by bundles of retinular axons enveloped by thin sheaths of glial cells (e.g. Fig. 12.3H). The structure and pattern of the basal matrix fit well with the description of the quite simply arranged ‘Blattodean-Orthopteran type’ (Odselius and Elofsson, 1981).

The optic lobe of *S. coleoptrata* and *T. clunifera* comprises only two retinotopic neuropils, the lamina and medulla. The two neuropils are connected by uncrossed axons. The medulla is equipped with large tangential neurons that send their axons from the inner edge into the protocerebrum, where they terminate at the dendrites of descending neurons (Fahlander, 1938; Strausfeld, 2005).

#### *Interommatidial exocrine glands*

There are up to four interommatidial glands of the ‘recto-canal’ type (cf. Chapter 4) per hexagonal ommatidium (Müller et al., 2003a), located in the interommatidial spaces. Each exocrine gland is capped by a canal cell producing an axial channel lined by cuticle. This conducting canal opens between the corneal facets and terminates into a wall-like opening where the secretion is released to the outside (Fig. 12.1B). An intermediary cell is also found between the distal canal and the proximal secretory cell.

#### *Electrophysiology*

The compound eyes enable *Scutigera* to respond to flashes of light of different intensity and quality, including high sensitivity to the UV-A region. Peak sensitivity is at a wavelength of 448 nm (blue). Two, perhaps three kinds of visual pigments are possibly distributed among the distal and proximal retinula cells. It is assumed that the sensitivity to UV radiation may help the animal to avoid open illuminated spaces or to detect exits from concealed hiding places in soil crevices and from the underside of boulders (Meyer-Rochow et al., 2006).

#### *Development*

Structures of the distal and proximal retinula cells (including the distal rhabdome)

are observed in histological sections of the first anamorphic instar, which already reacts to light stimuli. Crystalline cone cells are not observable. During the following anamorphic stages the size and the number of ommatidia increase continuously. In 7 mm juveniles, eye anatomy corresponds to that of the adult. The growing eyes of adults are entirely surrounded by a proliferation zone of high mitotic activity. Differentiated functional ommatidia do no exhibit further trace of cell proliferation (Harzsch et al., 2007).

#### *Vision and behaviour*

Bright lateral light at different times of the day has no influence on the running direction of the nocturnal *S. coleoptrata*, which thus does not exhibit negative phototaxis, but under bright light conditions the animals move preferentially towards dark-coloured plates (positive skototaxis). A reaction to polarized light has never been observed (Görner, 1959), even though at least the rhabdomeres of some distal and proximal retinula cells have strictly parallel, unidirectional microvilli that in principle should enable the photoreceptors to detect light polarization (Müller et al., 2003b).

Based on experiment, Klingel (1960) stated that *S. coleoptrata*, although a fast-running predator, does not seem to use its eyes for detecting prey, only recognizing its prey when stimulated by direct physical contact (antenna or legs) or chemical attraction.

#### *The lateral ocelli of the Pleurostigmophora*

When present, the lateral ocelli in the Pleurostigmophora are located on the frontolateral margins of the head capsule, directly behind the antennae. They can occur as a single pair, like in many Lithobiomorpha (Henicopidae, see Fig. 12.II, some smaller Lithobiidae), the Craterostigmomorpha (Fig. 12.IJ) and the scolopendromorph family Mimopidae. A second pattern is given by four lateral ocelli in a decussate arrangement, quite distant from each other (Scolopendridae, Fig. 12.IK). Finally, there are the so-called ocellar fields containing several or numerous lateral ocelli of varying diameter (most members of the Lithobiidae, Fig. 12.IE,G). Within an ocellar field of a lithobiid, there is a size gradient from the single so-called giant ocellus, confining the field posterioventrally, towards the anteroventral field margin where the smallest ocelli are visible (Fig. 12.IE,G). Some henicopid and lithobiid Lithobiomorpha as well as all Cryptopidae, Plutoniumidae and Scolopocryptopidae (Scolopendromorpha) and Geophilomorpha are blind. The corneal lens' surface often shows the same polygonal sculpturation as seen on a centipede's cuticle in general (Fig. 12.IF,H,J,L).

The cup-like lateral ocelli of the Pleurostigmophora are of fairly uniform structure. The corneal lens, mostly biconvex and deeply vaulted, is produced by an unpigmented epithelium (Fig. 12.4, 6C-D). In *Craterostigmus*, the ellipsoid lateral ocellus is subdivided into two distinct anterior and posterior regions (Fig. 12.4D), whereas the elevated corneal lens covers the entire subjacent retinula in lateral ocelli of the Lithobiomorpha and Scolopendromorpha (Fig. 12.4A-C). A crystalline cone is never present in the pleurostigmophoran lateral ocelli. The often multilayered dual-type retinula is divided into rings of horizontally oriented distal retinula cells with a circumapical, compact rhabdomeres, and a more or less homogeneous epithelium of proximal retinula cells parallel to the optical axis (Fig. 4).

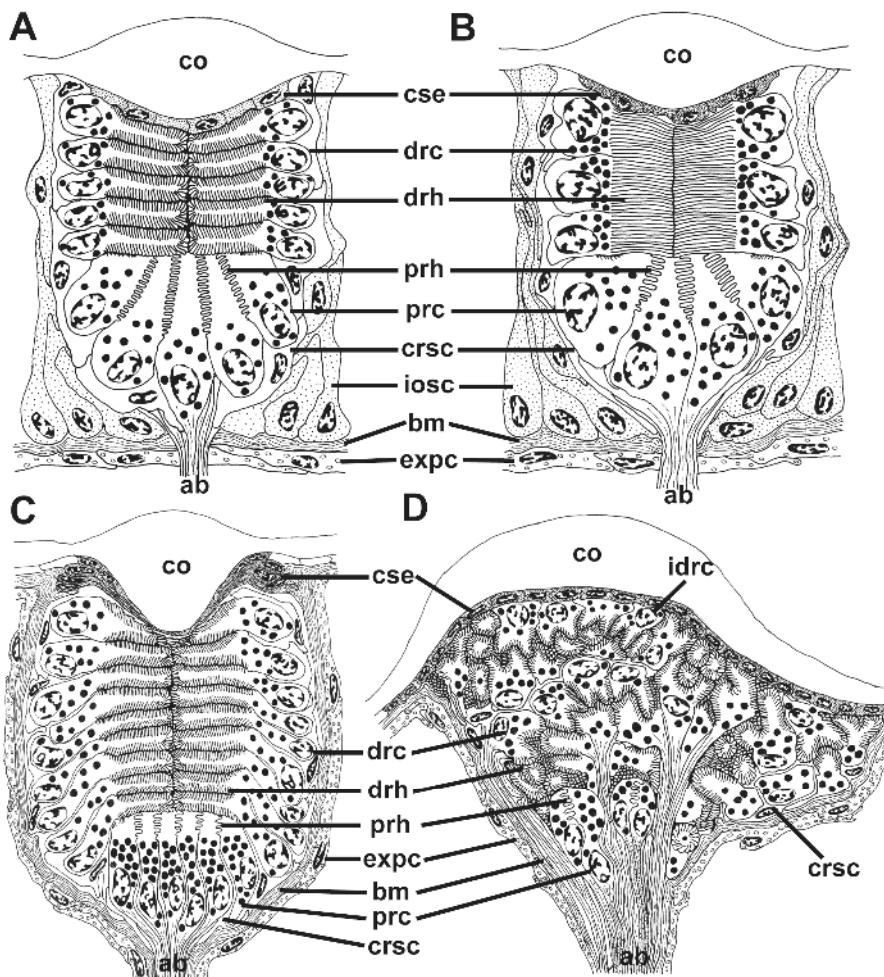
Contiguous proximal rhabdomeres interdigitate and generate diffuse but fused rhabdomes. Nearly all retinula cells belong to the everse type, and only the strongly modified distal retinula of *Craterostigmus* includes some inverse cells (Fig. 12.4D). 1-2 types of sheath cells envelop the dual-type retinula (Fig. 4). External pigment cells surround either the whole eye cup (Lithobiomorpha, Craterostigmomorpha) or all the lateral ocelli within a single ocellar field (Scolopendromorpha) (Müller and Meyer-Rochow, 2006a,b, Müller and Rosenberg, 2006, Müller, 2008).

#### *Cornea and corneagenous epithelium*

Each corneal lens has a plane-convex (*Craterostigmus*, Fig. 4D) or biconvex longitudinal profile (Fig. 12.4A-C). Seen from above, the lenses look circular or ellipsoid, except for

**Fig. 12.4** Schematic reconstructions of different forms of lateral ocelli of various Pleurostigmophora based on light microscopic and transmission electron microscopic examinations. A Longitudinal section through a lateral ocellus of *Eupolybothrus fasciatus* (Lithobiomorpha, Lithobiidae) with a multilayered distal retinula, the apex of the distal retinula cells is elongated and carries circumapical fringe of microvilli. B Longitudinal section through a lateral ocellus of *Lithobius* sp. (Lithobiomorpha, Lithobiidae) containing a dual type retinula with 2-6 layers of distal retinula cells and two types of sheath cells. C Longitudinal section through a lateral ocellus of *Scolopendra* sp. (Scolopendromorpha, Scolopendridae) containing a dual type retinula with up to 20 layers of distal retinula cells. D Longitudinal section through the lateral ocellus of *Craterostigmus tasmanianus* (Craterostigmomorpha) consisting of a highly complex network of distalretinula cells interfused by bicellular units of proximal retinula cells. The lateral ocellus is divided into an anterior portion and a larger posterior portion covered by a prominent corneal lens. Drawings modified after Müller (2008).

ab (primary) axon bundle; bm basal matrix; cse cornea-secreting epithelium (- corneagenous cell); co corneal lens; crsc circumretinular sheath cell; drc distal retinula cell; drh distal rhabdom; expc external pigment cell; idrc inverse distal retinula cell; iosc interocellar sheath cell; prc proximal retinula cell; prh proximal rhabdom



the postero-lateral ocellus in *Scolopendra* which may adopt an 8-shape (Fig. 12.1E-L). In lithobiomorph and scolopendromorph ocelli, the internal lens surface is either sunk into the eye cup, moderately sunk (slightly asymmetrical) as in *Lithobius* and *Eupolybothrus* or deeply invaginated (very asymmetrical) as in *Scolopendra*. The corneal lens is produced by a corneagenous epithelium of 30-2240 mostly flattened cells without pigment granules but showing a very electron dense cytoplasm (Figs. 12.4, 12.6C-D). The homogeneity of the corneagenous epithelium strongly depends on the amount of inner curvature of the corneal lens. In *Craterostigmus*, a layer of cubical cells is homogeneously distributed below the corneal lens. A more complex corneal lens, formed by a partly heterogenous

corneagenous epithelium, is found in *Lithobius*, *Eupolybothrus* and *Scolopendra*. The corneagenous epithelium includes numerous stretched somata that can still be found directly under the corneal vault. There is a tendency to dislocate the thinned somata to the periphery of the cornea. This process of displacement reaches its final stage in *Scolopendra*. Here one can distinguish two types of cornea-secreting epithelial cells. One type is characterized by short, plate-like cells that only surround the lateral margins of the corneal lens and are firmly attached to it by cone-like protusions of the cornea linked to microtubular bundles (Fig. 12.6C). The other type is limited to the most proximal part of the corneal lens. Four to six extremely flattened cells with their nuclei are clustered around the proximolateral region of the corneal lens (Figs. 12.4C, 12.6C). Minute cytoplasmic processes emanate from the corneagenous cell bodies heading towards the central subcorneal zone (Fig. 12.6D). Each cell process becomes thereby attached to a small central sector of the cornea (Müller and Meyer-Rochow, 2006a,b, Müller and Rosenberg, 2006, Müller, 2008).

#### *Dual-type retinula and rhabdome*

Depending on the animal's age and the relative position of the lateral ocellus within the ocellar field, the retinula of *Lithobius*, *Eupolybothrus* and *Scolopendra* contains 36-1160 retinula cells. Cell number is the highest in the lateral ocellus of *Craterostigmus* with approximately 1300 photoreceptive cells. All pleurostigmophoran taxa examined have a dual-type retinula comprising distal and proximal retinula cells.

The distal retinula cells are mostly rectangular or cylindrical and are oriented perpendicular to the optical axis. They are aligned in a circle and thus build distinctive horizontal layers. Many of these layers are stacked onto each other (*Lithobius*: 1-6 layers (Fig. 12.4B), *Eupolybothrus*: 4-12 (Fig. 12.4A), *Scolopendra*: 10-20 (Fig. 12.4C)). The distal retinula of *Craterostigmus* deviates considerably from this pattern by having disintegrated the circular arrangement and the stacks of horizontal layers. Here, the distal retinula cells have a laminar extension, and are arranged in clusters (Figs. 12.4D, 12.5G,H).

The pattern of the distal retinula cells and the structure of their rhabdomeres influence the complexity of the likewise multilayered rhabdome. Distal retinula cells with straight apex (*Lithobius*) produce rectangular or orthogonal rhabdomeres which get in contact within the axial region of the eye to form a simple fused rhabdome (Figs. 12.4B, 12.5A-D). A second type of distal rhabdome is observed in *Eupolybothrus* and *Scolopendra*, where the cell apices are extended to form circumapical rhabdomeres and a fused but more complex rhabdome, respectively (Figs. 12.4A,C, 12.6A-B,E-F). Knob-like

or bilobed apices forming cap- or W-shaped circumapical rhabdomeres are found in the distal retinula of *Craterostigmus*. The rhabdome of *Craterostigmus* is heavily branched (Figs. 12.4D, 12.5H).

In a pleurostigmophoran lateral ocellus, approximately 10% of all retinula cells belong to the proximal type, differing from the distal ones in shape, orientation, arrangement, pigmentation (*Scolopendra*) and interaction of their rhabdomeres (Figs. 12.4, 12.5F,I, 12.6G). A homogenous layer of proximal retinula cells occupies the bottom of each eye cup in *Lithobius* (Figs. 12.4B, 12.5A), *Eupolybothrus* (Fig. 12.4A) and *Scolopendra* (Figs. 12.4C, 12.6A). In the same taxa, the proximal retinula cells look conical or club-shaped and are aligned parallel to the optical axis (perpendicular to the distal retinula cells, see Figs. 12.4, 12.6G)). Around the apex a uni- or bidirectional rhabdome is formed which can be very short and un conspicuous (*Scolopendra*, Fig. 12.6G) or elongated (*Lithobius*, *Eupolybothrus*). The microvilli of a proximal rhabdome are considerably distanced from each other, which allow contiguous rhabdomeres to interdigitate and form an extensively fused, zip-like structure (Figs. 12.4, 12.5F,I, 12.6G). Thus, the entire proximal rhabdome looks stellate (*Lithobius*) or like a complex network in cross sections (*Eupolybothrus*, *Scolopendra*, e.g. Fig. 12.6B). In the latter case, the complexity increases with the total number of proximal retinula cells (*Scolopendra*). Most distally, the tips of the proximal rhabdomeres may abut to the rhabdomeres of the last layer of the distal retinula. Again, the proximal retinula of *Craterostigmus* is very different from those described above because of the disintegration of the multilayered coronal system. There is instead a pattern of loosely dispersed units, each of two drop-like proximal retinula cells clumped together along the entire length (Fig. 12.4D). At the apex of a proximal dual-cell unit, each straight inner contact membrane produces a pectinate rhabdome which, like in Lithobiomorpha and Scolopendromorpha, intertwine with the one of the partner cell (Fig. 12.5I).

In general, the cytoplasm of both retinula cell types is moderately osmophilic and is endowed with organelles typical for photoreceptive cells in Arthropoda, such as polymorphous screening pigment granules, vacuoles of various content and osmophilicity, cristate mitochondria, Golgi stacks, cisternae of rough and smooth endoplasmic reticulum, and succession stages of lysosomal bodies.

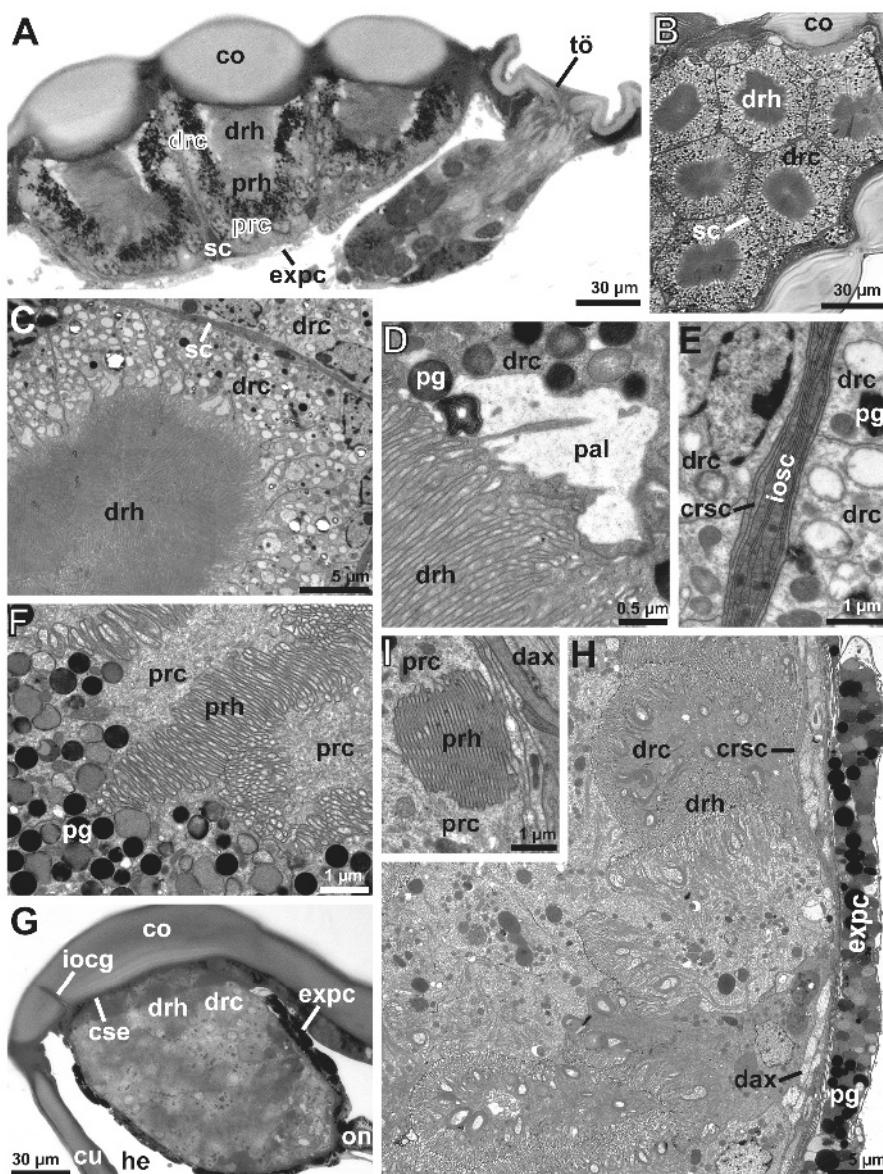
The retinula cells, in particular the distal ones, may also develop a more or less conspicuous system of perirhabdomeric ('palisade') endoplasmic reticulum. In *Lithobius* and *Eupolybothrus*, the cisternae of the latter appear swollen and surround the axial rhabdome as a distinct ring (Bedini, 1968; Bähr, 1971, 1974) (Fig. 12.5D). The volume of the cisternae varies according to the state of dark-light adaptation (Bähr, 1972). The perirhabdomeric endoplasmic reticulum is also found in the distal retinula cells of *Scolopendra*, where it displays a dense palisade of lengthened cisternae (Fig. 12.6F). In contrast, there is no evidence of swollen perirhabdomeric cisternae in *Craterostigmus*, where a massive and highly ordered smooth endoplasmic reticulum is traversed by thin cytoplasmic bridges in the distal retinula cells (Fig. 12.5H).

### *Sheath cells*

Two types of sheath cells (circumretinular and interocellar) are distinguishable by shape, location in relation to the eye cup and cytoplasmic composition. In all taxa examined, distal and proximal retinulae are tightly enveloped by loosely dispersed circumretinular sheath cells, 20-300 in number (Fig. 12.4). The thin circumretinular sheath cell bodies are usually utricular in shape and have an electron lucent cytoplasm without pigment granules. Small projections are sent in a vertical direction towards the bottom and the tip of the eye cup. Additionally, axial processes may emerge from the soma and penetrate the retinula, running through the infraretinular spaces. Both axial and vertical cell processes often branch and aggregate; as a result, the sheet of circumretinular sheath cells appears multilayered. However, some circumretinular sheath cells of *Lithobius* and *Eupolybothrus* lack axial processes (Figs. 12.4A-B, 12.5E). The

**Fig. 12.5** Organization of lateral ocelli of various Lithobiomorpha and Craterostigmomorpha as observed by light microscopy (A-B,G) and transmission electron microscopy (C-F,H-I). A Transverse section through the lateral margin of the head capsule of *Lithobius forficatus* providing a longitudinal profile of the lateral ocellar field and anteroventrally adjoined organ of Tömösváry. B Cross section through one lateral ocellar field showing several ocelli at the level of the distal retinula. *L. forficatus*. C Overview of one half of a lateral ocellus placed in the middle of the eye cluster. Note the dense packing of prismatic distal retinula cells contributing to an almost rectangular central rhabdom. *L. forficatus*. D Higher magnified view of the apex of a distal retinula cell from which highly ordered rhabdomeric microvilli emanate. *Lithobius dentatus*. E Detailed view of an interocellar space between two lateral ocelli filled with a multilayer of circumretinular and interocellar sheath cells. *L. forficatus*. F Two proximal retinula cells, each of which forms an apical cytoplasmic process surrounded by interdigitating microvilli. *Lithobius mutabilis*. G-I *Craterostigmus tasmanianus*: G Posterior part of the lateral ocellus in longitudinal section. H. Distal periphery of the lateral ocellus showing the complex network of distal retinula cells and rhabdomeres. I Close-up of a bicellular module of proximal retinula cells presenting an interdigitating rhabdom unit. A. LM images modified from Müller (2008), B,F,H originals Müller, C-E modified after Müller and Rosenberg (2006), G,I modified after Müller and Meyer-Rochow (2006b).

co corneal lens; crsc circumretinular sheath cell; cse cornea-secreting epithelium (= corneagenous cells); cu cuticle; dax axon of a distal retinula cell; drc distal retinula cell; drh distal rhabdom; expc external pigment cell; he hemolymphatic space; iocg conducting canal of an intraocular exocrine gland; iosc interocellar sheath cell; on optic nerve; pal swollen cisternae of the perirhabdomeric ('palisade') endoplasmic reticulum; pg highly osmophilic pigment granule; prc proximal retinula cell; prh proximal rhabdom; sc sheath cell; tö organ of Tömösváry



wrapping of retinula cells by axial processes is most elaborated in *Craterostigmus*, where numerous cuneiform clusters of somata of circumretinular sheath cells, located near the margin of the eye cup, emanate bundles of axial processes between the clusters of distal retinula cells. On their way to the centre of the eye cup, these axial processes envelop the

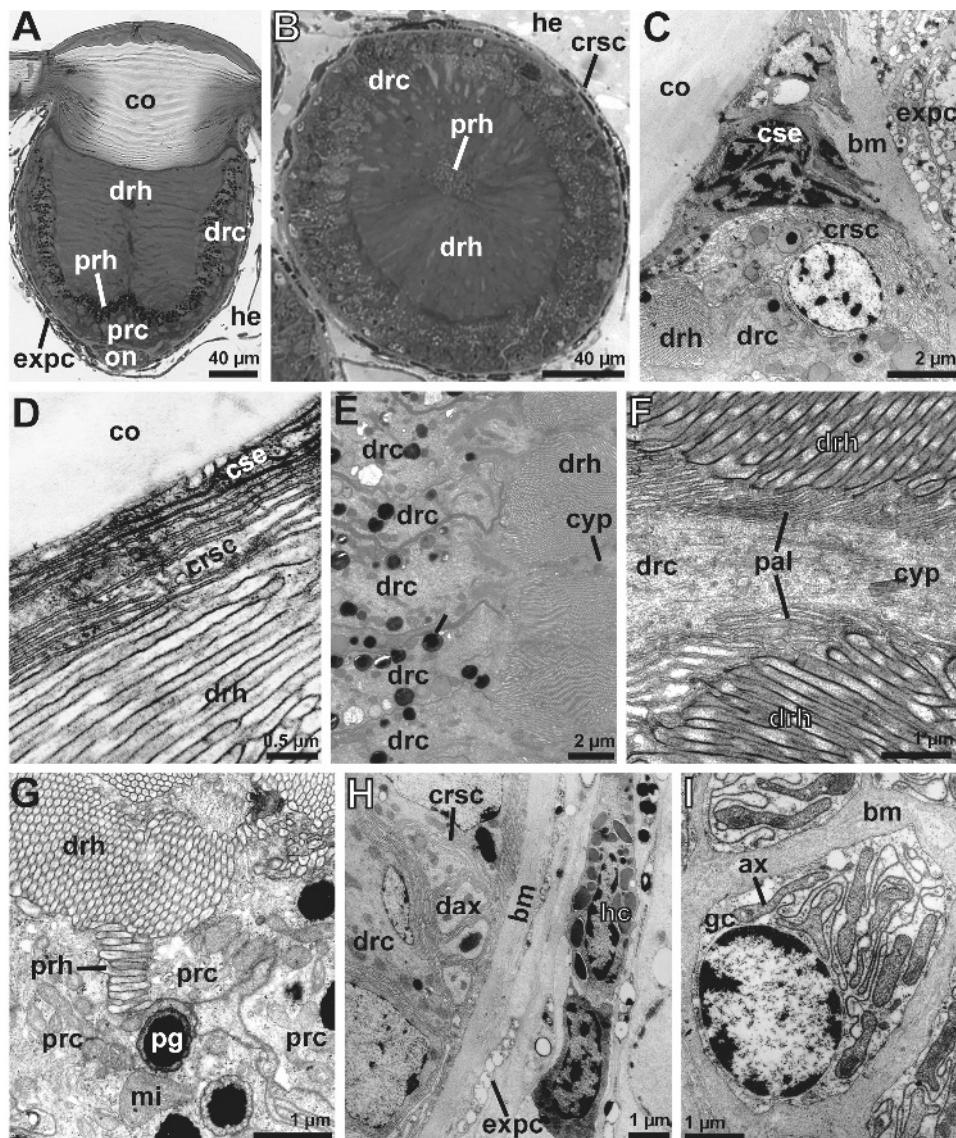
peripheral bundles of retinular axons (Fig. 12.H-I). In *Scolopendra*, the wrapping of the retinula cells by axial processes of the circumretinular sheath cells reaches the highest degree (Figs. 12.4C, 12.6C,H). Processes of distally located sheath cells run between cornea-secreting cells and the distal layer of distal retinula cells (Fig. 12.6D).

Only in *Lithobius* and *Eupolybothrus*, the interocellar space is filled with 20-200 interocellar sheath cells, extending from the cornea down to the basal matrix (Fig. 12.4A-B). Comparable to the circumretinular sheath cells, small vertical and axial cell processes, emanating from the somatic part of the cell, branch and intertwine with processes of neighbouring cells. Thereby, the interocellar sheath cells usually form 6-10 cell layers (Fig. 12.5E). The cytoplasm is generally more electron-dense than in the circumretinular sheath cells. In dark-adapted animals, the entire cytoplasm is heavily endowed with polymorphic, hyaline vacuoles, 0.5-1.2 µm in diameter.

Sheath cells may improve bioelectric isolation between retinula cells and between retinular axon bundles, possibly allowing to transmit rapid, unambiguous signals and to maintain spatial resolution. The sheath cells provide a multilayered system of cytoplasmic compartments with high and low refractive indices. According to Land (1972), only ten of those layers are needed to reflect nearly 100% of the incident light. Since centipedes are strongly nocturnal, having an internal reflecting layer would lead to a significant increase in their eyes' visual sensitivity.

**Fig 12.6 Organization of lateral ocelli of Scolopendromorpha reconstructed by the aid of light microscopy (A-B) and transmission electron microscopy (C-I).** A Longitudinal section through the dorsal ocellus of *Scolopendra oraniensis* (Scolopendridae). B Cross section through the transition zone of the distal and proximal retinula, the slight axial protrusion of the proximal rhabdomeres is clearly visible by the change from radial to net-like pattern of rhabdomeres. C Lateral cluster of cornea-secreting epithelial cells and subjacent soma of a circumretinular sheath cell. Longitudinal view. D Detailed view of the complex membrane staples present below the corneal lens representing axial processes of the cornea-secreting cells, circumretinular sheath cells as well as distal rhabdomeric microvilli. E Longitudinal overview of a couple of horizontally stapled distal retinula cells at the base of the axial cytoplasmic processes and distal rhabdomeres. F Higher magnification of proximal end of finger-like cytoplasmic process of a distal retinula cell. Note the vestigial perirhabdomeric ER apparatus. G Transition zone of distal and proximal retinula, two interdigitating proximal rhabdomeres are illustrated. H Lateral margin of a distomedian region of a lateral ocellus bordered by a complex, ramified basal matrix and a diffuse multilayer of external pigment cells. I. Cross section through a subretinal axon bundle entering the optic nerve. Note the extensive glial sheathing of the retinular axons. A modified from Müller (2008), B-C,E-F,H originals Müller, D,G,I. modified after Müller and Meyer-Rochow (2006a).

ax axonic process of a retinula cell; bm basal matrix; co corneal lens; crsc circumretinular sheath cell; cse cornea-secreting epithelium (= corneagenous cells); cyp thin cytoplasmic process of a distal retinula cell; dax axon of a distal retinula cell; drc distal retinula cell; drh distal rhabdom; expc external pigment cell; gc glial cell sheath; hc hemocyte; he hemolymphatic space; mi mitochondrion; on optic nerve; pal swollen cisternae of the perirhabdomeric ('palisade') endoplasmic reticulum (ER); pg highly osmiophilic pigment granule; prc proximal retinula cell; prh proximal rhabdom



#### *External pigment cells/basal matrix*

The lateral ocelli of the Scolopendromorpha and Craterostigmomorpha are lined along the entire periphery of the eye cup by a basal matrix (Fig. 12.4C-D) which consists of an extracellular portion (basal laminae of sheath cells, cornea-secreting epithelial cells,

external pigment cells, occasionally also epidermal cells) and a cellular portion (peripheral sheath cells and the projections of the external pigment cells).

In *Craterostigmus*, the extracellular portion is only about 0.5-0.9 µm thick. In contrast, the basal matrix is massively developed in *Scolopendra*. Particularly, the extracellular portion exhibits a broad network of collagen fibres; still a compact layer in the middle and proximal (about 1.4 µm thick) but branched and even more enlarged close to the distalmost part (up to 15 µm thick) of the eye cup (Figs. 12.4C, 12.6C,H-I).

In *Eupolybothrus* (Fig. 12.4A) and *Lithobius* (Fig. 12.4B), a thin basal matrix separates the whole ocellar field from the subjacent plexus of external pigment cells (see below). Therefore, only the bottoms of the mostly contiguous lateral ocelli are bordered by the very thin extracellular portion (< 0.5 µm thick).

In all pleurostigmophoran ocelli, the basal matrix is only perforated near the base of the eye cup. There, the entirety of retinular axon bundles, ensheathed by glial cells, runs into the adjacent optic nerve (e.g. Fig. 12.6I).

A plexus of one or two contiguous rows of external pigment cells delimits the single eye cup (*Craterostigmus*, *Scolopendra*) or the entire ocellar field (*Lithobius*, *Eupolybothrus*) against the hemolymphatic space (Figs. 12.4, 12.5A,H, 12.6A,C,H). The innermost layer contributes to and usually adjoins the extracellular portion of the basal matrix. The cytoplasm of the external pigment cells is filled with small electron lucent vacuoles (0.9-1.4 µm in diameter), polymorphic granules of moderate osmiophilicity (about 0.5 µm in diameter), and numerous electron dense pigment granules (0.4-0.8 µm in diameter). Large polymorphic granules with an inhomogeneous matrix dominate the cytoplasm in *Lithobius* and *Eupolybothrus*.

Within the external pigment cells of *Scolopendra*, rounded granules of higher electron density are visible (e.g. Fig. 12.6C). In *Craterostigmus*, regions rich in electron lucent granules (distal part of the eye cup) alternate with zones in which more osmiophilic granules are accumulated (Fig. 12.5H). In *Scolopendra* and *Craterostigmus*, the external pigment cells are not restricted to the region around the lateral ocelli(us) as they underlie the adjacent epidermis over a certain distance. External pigment cells cover the distal part of the optic nerve (e.g. *Craterostigmus*, Fig. 12.5G).

#### *Interommatidial and intraocellar organs*

In lithobiid centipedes (*Lithobius*, *Eupolybothrus*), the interocellar spaces are sometimes pierced by the openings of interommatidial glands (Müller et al., 2003a). As in *Scutigera*, these glands consist of a canal and a secretory cell. The existence of a third cell type, the

so-called intermediary cell, was however assumed by Müller et al. (2009), based on critical evaluation of broader set of TEM micrographs.

Intraocellar organs are curious structures within the lateral ocellus of the *Craterostigmus*. Pores of flexo-canal epidermal glands are observed near the margins of its eye (Fig. 12.5G). The glandular apparatus breaks through the corneagenous epithelium and extends down to the uppermost layer of the distal retinula. In addition, the anterior, uncurved part of the cornea of *Craterostigmus* is also pierced by sockets and hair shafts of *Sensilla microtrichodea* (see below) (Müller and Meyer-Rochow, 2006b).

#### *Photoreceptor axons and optic neuropils*

As shown by Holmgren (1916) and Hanström (1926, 1928) for *Lithobius*, the optic lobes are composed of two optic neuropils (lamina, medulla), situated one after another. Two types of central projections originating from the lateral ocelli have been identified in *L. forficatus* (Melzer et al., 1996/97). Short retinular axons terminate within the first optic neuropil of the lamina. They possess varicose swellings throughout the depth of the neuropil. Long axons pass through the first neuropil and terminate within the medulla, where up to five long collaterals are observed that diverge to various synaptic sites.

#### *Light- and dark adaptive changes and circadian rhythm*

Following earlier investigations by Bähr (1972), Müller and Rosenberg (2006) observed fine structural changes within the lateral ocelli of *Lithobius* species in full darkness vs. light adapted state (12:12 h light:dark cycle). When light adapted, the distal retinula cells show a conspicuous ring of swollen cisternae of perirhabdomeric endoplasmic reticulum around the axial rhabdome. In dark adapted lateral ocelli, these cisternae are lesser voluminous. Osmiophilic pigment granules aggregate and build up a screening shield around the retinula. Most important, rhabdomeric microvilli are extended in dark adapted eyes. As typical for arthropod eyes, increase in rhabdome diameter raises the absolute sensitivity of the photoreceptors during the night (Meyer-Rochow, 1999). Bähr (1965, 1967) carried out extracellular recordings from the ocellar field of *Lithobius forficatus*. The electroretinograms reveal that dark adaptation occurs at high stimulus intensities in a biphasic manner and seems to be complete after 20 minutes. Based on the experimental results, Bähr (1967) thought that *L. forficatus* orientates itself from light to dark environments. It could be excluded that *L. forficatus* is able to recognize single images or movements.

### *Development and regeneration of the ocelli*

In embryonic development, the first sign of an anlage of a lateral ocellus is detectable in *Scolopendra* at a time when the embryo has completely folded inward (Heymons, 1901). The spherically shaped eye anlage is covered by the first embryonic cuticle. Before hatching, retinula cells and the nervus opticus are developed. After hatching, the four lateral ocelli are recognizable.

Continuous mitotic activity affects all cellular components of all four lateral ocelli of *Scolopendra oraniensis* in the course of moulting events in adult specimens. Therefore, a persistent proliferation (intercalary growth) goes on within the lateral ocelli ('ocellar ommatidia') of the Scolopendromorpha (Harzsch and Hafner, 2006; Harzsch et al., 2007). The occurrence of intercalary growth can be also suggested for the lateral ocelli of lithobiomorphs (cf. Andersson, 1981).

Ablation of the lateral ocelli in matures junior specimens of *Lithobius forficatus* is followed by regeneration; the new ocelli are innervated by the optic nerve (Joly and Herbaut, 1968). In one case, a heterotypic, antenna-like regenerate was obtained.

### *Vision and behaviour*

Positive skototaxis, i.e. orientation towards dark-coloured objects under bright conditions has been reported for *Lithobius forficatus* (Klein, 1934; Görner, 1959) and *Scolopendra subspinipes* (Plateau, 1887), but also for representatives of the blind Cryptopidae and Geophilomorpha (Plateau, 1886, 1887). Negative phototaxis has been described in *L. forficatus* (Verhoeff, 1902-1925; Klein, 1934; Scharmer, 1935; Bauer, 1955; Görner, 1959; Meske, 1961), but negated in *L. piceus gracilis* (Demange, 1956) and *S. cingulata* (Plateau, 1887). No reaction to polarized light has been found in either *Lithobius* or *Scolopendra* (Görner, 1959).

### *Phylogenetic implications of myriapod eye characters*

Anatomy and ultrastructure suggest that ommatidia of Myriapoda, Crustacea and Hexapoda share a common origin. This is supported by features like primary pigment cells, a sheath of interommatidial pigment cells, a double-layered retinula built by two distinct retinula cells as well as the successive formation of the compound eye from an anterior proliferation zone, but probably the most important homologous character is the crystalline cone formed by four eucone cells (Müller et al., 2003b, 2007; Harzsch et al., 2007; Müller, 2008). Tripartite crystalline cones, connected to proximally placed cone cell somata by thin infraretinular processes have also been found recently in the penicillate diplopod *Phryssonotus platycephalus* (Müller et al., 2007) (Figs. 12.1C-D, 12.2E-

H). This specific fine structural correspondence suggests that scutigeromorph and penicillate ommatidia are homologous (Müller et al., 2007).

Moreover, the partly constant cell patterns in the ommatidia of scutigeromorph centipedes and in the miniaturized, disintegrated ommatidia of penicillate millipedes are thought to be closer to the ground pattern of Mandibulata than are the ommatidia of the Tetraconata. If so, eucone cells with their nuclei placed outside the light-focusing cone compartments are most likely ancestral (Müller et al., 2003b, 2007; Harzsch et al., 2007; Müller, 2008). In this context, scutigeromorph ommatidia are however also unique, because each distal cone cell process bifurcates and gives rise to the formation of two distinct compartments within the multipartite crystalline cone. One cone cell forming two cone compartments therefore is a potential apomorphy of the Scutigeromorpha.

A phylogenetic analysis carried out by Müller (2008) integrated 28 new eye characters into an updated and corrected matrix of Edgecombe and Giribet (2004) containing 222 morphological characters of various centipedes. The results of this analysis revealed that eye characters, such as 1) unpigmented, flattened epithelial cells producing a more or less vaulted corneal lens, 2) unpigmented sheath cells encompassing the retinula, 3) external pigment cells lining the ocellar field against the hemolymphatic space, 4) a multilayered dual type retinula, and 5) interdigitating rhabdomeres of the proximal retinula cells provide further support for the Pleurostigmophora concept. The assumed derived state of lateral ocelli of Pleurostigmophora implies that cone-less, camera-type eyes surrounded by a mantle of external pigment cells have evolved independently in Chilopoda and Diplopoda. Due to transformation processes, it is only the dual type retinula that remains in favour of homology of scutigeromorph/penicillate ommatidia and pleurostigmomorph/chilognath lateral ocelli.

### *Epidermal sensilla*

#### Sensory hairs (setae)

Epidermal sensilla are sensory setae, consisting of two structural components: the sensory cells with their dendritic processes and several sheath cells, more or less interspersed into the hair shaft.

#### *Scattered epidermal sensilla*

Scattered sensilla are defined here as small epidermal sensilla dispersed on the centipede's cuticle. Sensilla of differing structure and function may be tightly adjoined but do not occur in specialized, encapsulated cuticular compartments to perform specific functions. Scattered sensilla, especially those located on the antennae, cover a wide range of functions, comprising mechano-, chemo-, hygro- and thermoreception. Numerous types of scattered epidermal sensilla have been identified. Eleven sensilla types are presented here in detail. Some of them are restricted to the

antennae. Only five sensillar types are comprehensively understood with regard to their histological anatomy and ultrastructure, examined with light microscopy as well as scanning and transmission electron microscopy. Based on TEM examinations, epidermal sensilla were assumed to be bimodal with regard to their function. The functions of certain types of antennal sensilla have been assumed on the basis of TEM studies. However, experimental evidences (e.g. from behavioural studies or electrophysiology) are still lacking.

1) *Sensilla trichodea*. – Trichoid sensilla are by far the most common and widespread sensilla found on a centipede's body (Fig. 12.9A). Contrary to many other types of sensilla they occur on any body part lined by a hardened cuticle. However, to date only the antennal trichoid sensilla have been thoroughly investigated. In this review, some TEM observations on the organization of cephalic sensilla trichodea are presented for *Craterostigmus tasmanianus*, *Lithobius dentatus* and *Scolopendra cingulata* (Fig. 12.8B-H). Counting several dozens to hundreds in Scutigeromorpha (e.g. *Scutigera coleoptrata*) (Ernst et al. unpubl.) and Geophilomorpha (e.g. *Geophilus flavus*) (Ernst, 1976, 1994, 2000b), up to 4,000 sensilla of this type can be found on each lithobiomorph (*Lithobius forficatus*), craterostigmomorph (*Craterostigmus tasmanianus*) and scolopendromorph (e.g. *Cryptops hortensis*, *Newportia monticola*) antenna (Keil, 1975, 1976; Ernst, 2000b; Ernst et al., 2006, 2009; Koch et al., 2010). The main information on the fine structural architecture of sensilla trichoidea is owed to the thorough EM studies of Ernst (1976, 1994, 1996, 1999, 2000b) on *G. flavus* and Keil (1975, 1976) on *L. forficatus*.

The elongated hair shaft (length: *L. forficatus*: 100-150 µm, *G. flavus*: 20-120 µm, *C. tasmanianus*: 17-50 µm on median antennomeres, 50-390 µm in other areas, *S. coleoptrata*: 48-73 µm) is often curved to the top and bears numerous spiral ribs on its surface. Ernst et al. (2009) define two subtypes of trichoid sensilla in *Cryptops hortensis*: straight type-1 sensilla, frequently distributed on the lateral side of the antennomeres (length: 17-88 µm long, keenly ribbed) and slightly curved type-2 sensilla, less frequent in the central area of the antennomeres (length: 6-16 µm long, roughly ribbed). Apically, these sensilla have a terminal pore. The highly flexible shaft is fixed to the cuticle surrounding the socket by a membranous cuticular joint. A constant number of 18 uniciliate sensory cells is noticeable in antennal sensilla trichodea of *L. forficatus*. Among these 18 dendritic processes, 17 smaller ones run through the entire sensillum, penetrate the lumen of the shaft and head to the terminal pore opening (cf. Fig. 12.8B), whereas one single and thicker dendrite transforms apically into a tubular body attached to a fibrillous network in the cuticular socket membrane (Figs. 12.7A, 12.8C-D). In contrast, sensory cells vary in composition and number in *G. flavus*. Antennal trichoid sensilla have 15 to 17 uniciliate sensory cells (cf. Fig. 12.8G), those situated on the maxillae are however smaller and

include only 6 to 9 sensory cells, one of which is biciliate and ends up in two tubular bodies at their hair base (Fig. 12.7B).

Each sensillum includes a thecogen cell, a trichogen cell and a tormogen cell as in hexapods. Inner and outer receptor lymph cavities extend deeply into the lumen of the hair shaft (Figs. 12.7A-B, 12.8D-E,G-H). The dendritic sheath is distinct and channels most of the thin outer dendritic segments to the terminal pore opening (Fig. 12.8B-E).

Bimodal sensilla trichodea most likely integrate contact chemoreception and mechanoreception. The extraordinarily high abundances of antennal trichoid sensilla in Geophilomorpha are perhaps correlated with the loss of eyes.

2) *Sensilla microtrichodea*. – Because of many ultrastructural similarities, the sensilla microtrichodea are easily characterized as miniaturized sensilla trichodea (Fig. 12.9B). To date, only antennal sensilla microtrichodea have been studied in detail. They have never been found on the antennae of Scutigeromorpha, whereas either a few (*Craterostigmus tasmanianus*; Ernst et al., 2006), one hundred (*Cryptops hortensis*; Ernst et al., 2009) or several hundred (*Lithobius forficatus*; Keil, 1975; *Geophilus flavus*; Ernst 1983, 2000b) have been counted. Hair shafts of antennal sensilla microtrichodea are hardly visible externally, even by scanning electron microscopy. This is due to their strict alignment along the basis of each antennomere, which is overlapped by an anterior projection of the subjacent antennomere. In *L. forficatus*, sensilla microtrichodea occur in three distinct groups of 2-5 sensilla, measuring between 5 and 10 µm in length. The sensory apparatus consists of two uniciliate sensory cells surrounded by three sheath cells. Both outer dendritic segments are tightly encased by a thick dendritic sheath produced by the thecogen cell. Both dendrites run up to the slender and smooth hair shaft 5-10 µm in length. Neither tubular bodies nor terminal pores have been found.

More details are known for the microtrichoid sensilla on the antennae of *G. flavus*. The widely smooth hair shafts are longer (7-17 µm), have a terminal pore opening and they are aligned in three circles of 2-5 sensilla at the base of most antennomeres. A slightly variable number of 6-8 sensory cells is surrounded by three sheath cells. Two sensory cells are biciliate, the remaining ones only form a single dendritic process. The slender four outer dendritic segments of the two biciliate sensory cells are connected to the socket membrane via four tubular bodies. The thecogen cell, which is rich in cytoplasmic granula, secretes a thick and far-upreaching dendritic sheath wrapping the dendrites and the inner receptor lymph cavity. An outer receptor lymph cavity, formed by the tormogen sheath cell, is also present. The location at the base of the antennomeres as well as the specific orientation of the tubular bodies relative to the hair shaft and socket membrane may indicate a proprioceptive function (Ernst, 1983, 2000b).

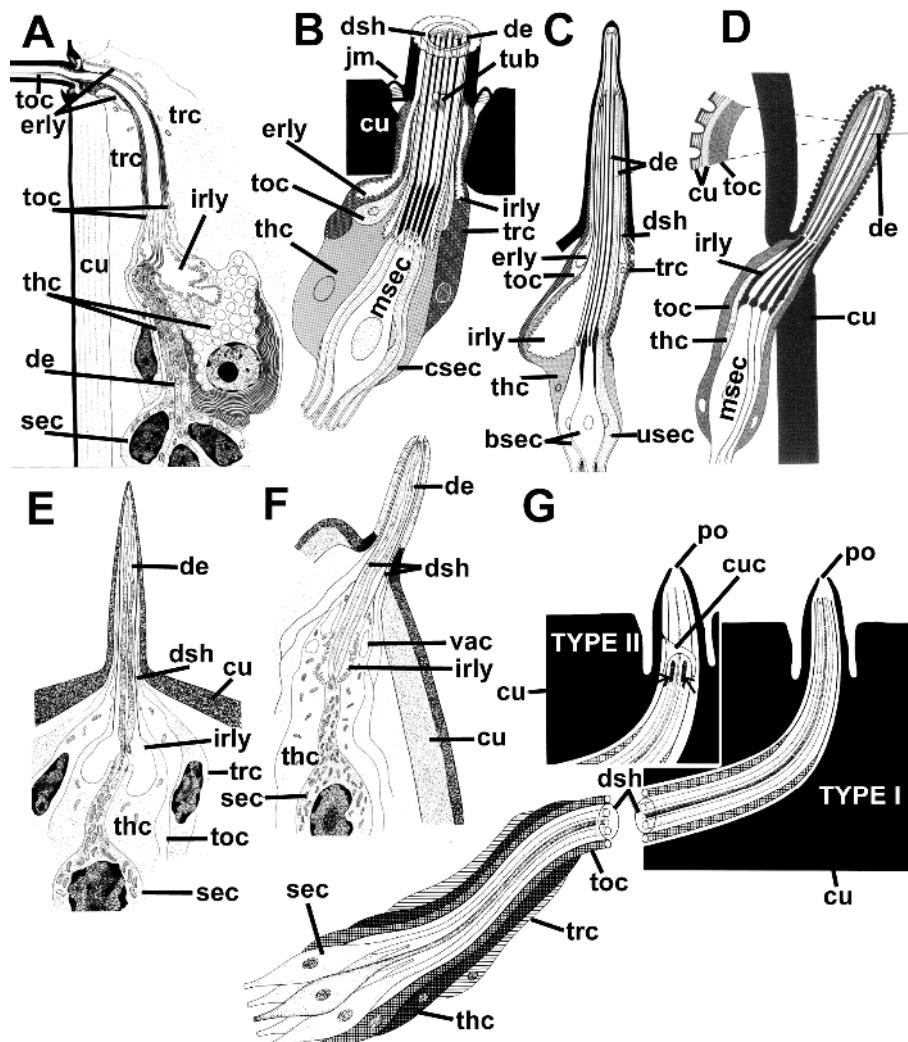


Fig. 12.7 Semischematic reconstructions of various types of scattered epidermal sensilla located on the antennae (A-F) or tip of the forcipules of different chilopod subgroups. A Sensillum trichodeum in *Lithobius forficatus*. B Sensillum trichodeum in *Geophilus flavus*. The sensillar shaft is cut at its base. C Sensillum brachyconicum in *G. flavus*. D Sensillum basiconicum in *G. flavus*. E Sensillum basiconicum (subtype: long cone shaped sensillum basiconicum) in *L. forficatus*. F Sensillum basiconicum (subtype: short peg sensillum basiconicum) in *L. forficatus*. G Two subtypes of sensilla coeloconica found on the forcipules of *L. forficatus* (Types I and II). Tubular bodies of Type II are indicated by small black arrowheads. Drawings modified after following authors: A after Ernst (1976), B,D after Ernst (2000b), C original Ernst, E-F after Keil (1975), G after Ernst and Rosenberg (2003).

3) *Sensilla basiconica*. – Sensilla basiconica are so far only known from the antennae of lithobiomorph, craterostigmomorph, scolopendromorph and geophilomorph centipedes (Fig. 12.9C). They may appear scattered or, as for instance in Geophilomorpha, ordered in two groups on the terminal antennal article. Keil (1975) distinguished two morphs of sensilla basiconica on the antennae of *Lithobius forficatus*: 1) short pegs, fingerlike, slightly curved sensory cones and 2) long cones, elongated (prismatic) sensory cones. In *L. forficatus*, approximately 40 peg- and cone-shaped sensilla can be counted on each antenna. The number of sensilla basiconica is much less in the Epimorpha (1 in *Craterostigmus tasmanianus*: Ernst et al. 2006; 61-114 in *C. hortensis*: Ernst et al., 2009; 36-53 in *G. flavus*: Ernst 1979, 2000a,b; at least 2 in *Newportia monticola*: Koch et al., 2010). A common feature is a system of perforations (appr. 0.1 µm in diameter) or deep, longitudinal grooves (*G. flavus*) in the cuticle of the hair shaft. The hair shafts of all sensilla basiconica studied so far are inflexible. The shaft wall continues into the surrounding cuticle without a membranous articulation. Terminal pore openings do occur, but are often inconspicuous.

Studies with transmission electron microscopy, although limited to *L. forficatus* (Keil, 1975) and *G. flavus* (Ernst, 1979, 1996, 2000a,b), show that sensilla basiconica in Chilopoda may vary enormously with respect to the external appearance of the hair shaft and the internal cellular organization. The hair shafts are principally short in peg-shaped sensory cones and vary slightly between the groups: e.g. 10-20 µm in *L. forficatus* (2-4 µm in diameter: Keil, 1975) or 10-14 µm in *G. flavus* (Ernst, 1979). In contrast, the long cones become much longer, for instance 10-50 µm in *L. forficatus* (Keil, 1975). Further intra- and interspecific variations concern sensory and sheath cells.

In the peg-shaped sensilla basiconica of *L. forficatus*, three biciliate sensory cells are encased by three sheath cells (thecogen, trichogen and tormogen cell) that accompany the dendritic outer segments up the entire shaft to the terminal pore (Fig. 12.7F). The inner receptor lymph cavity (formed by the thecogen cell), delimited along the whole length by the dendritic sheath, likewise extends to the sensillum's tip and houses all dendrites. Outer dendritic segments run peripherally in the shaft, close to the cuticular pores, which are continuous with the shaft lumen.

Peg-shaped sensilla basiconica of *G. flavus* are also innervated by three sensory cells, but the size of their somata is different and each of them produces only one uniciliate dendritic process. Two of the three outer dendritic segments are larger and, while being

bsec biciliate sensillar sense cell; cu cuticle; cuc cuticular cap; csec (contact) chemoreceptor cell; de dendritic process (inner and outer segment); dsh sheath enclosing outer dendritic segments ('Dendritenscheide'); erly external receptor lymph cavity; irly internal receptor lymph cavity; jm joint (socket) cuticle; msec mechanoreceptor cell; po terminal shaft pore; sec sensillar sense cell; thc thecogen cell; toc tormogen cell; trc trichogen cell; tub tubular body; usec uniciliate sensillar sense cell; vac vacuole

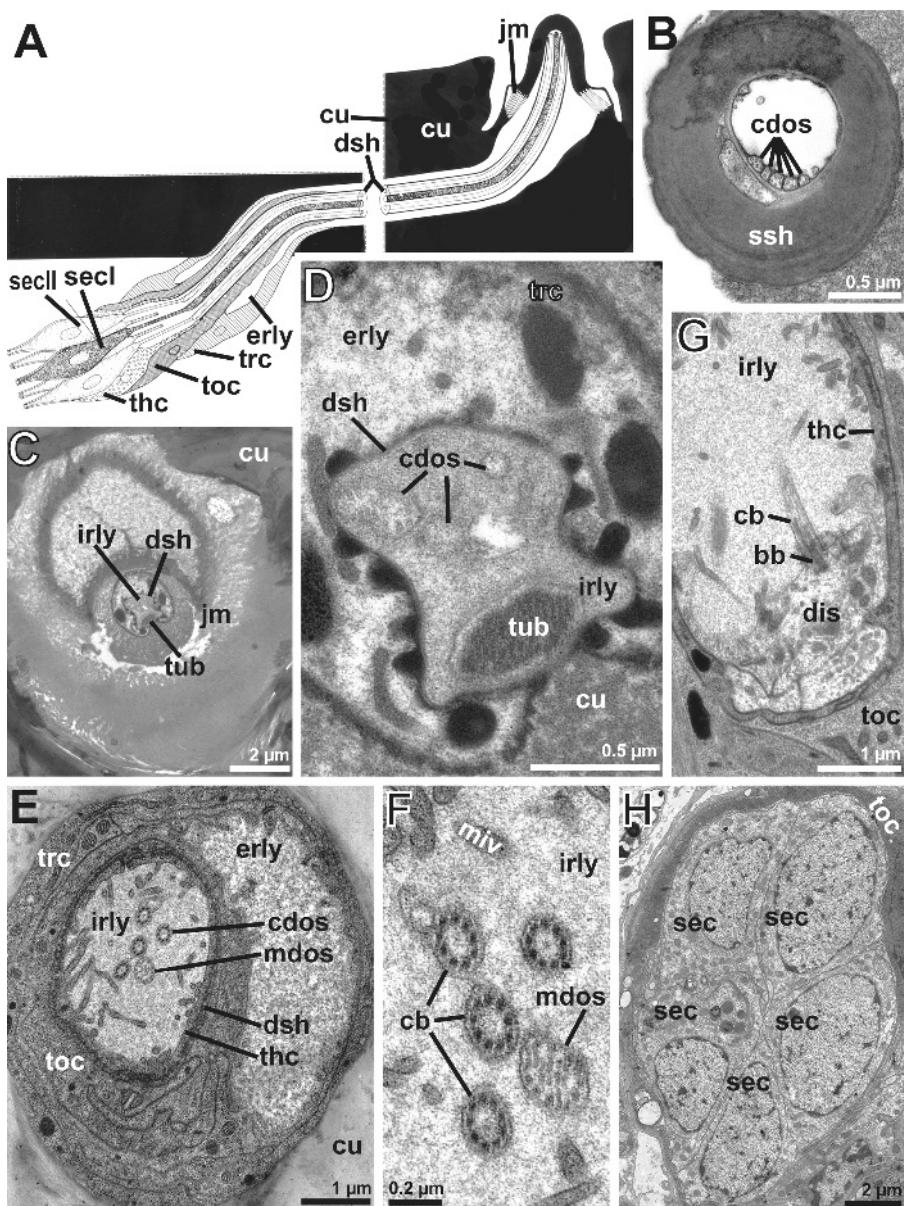
embedded into the inner receptor lymph space, become enveloped by a tube-like, cytoplasmic sheath of the thinner third outer dendritic segment. This constellation likely enlarges the perceptive dendritic surface. The thecogen cell is replaced by a second tormogen cell (1 trichogen cell + 2 tormogen cells). Both tormogen cells send off extensions into the lumen of the hair shaft (Fig. 12.7D).

Cone-shaped sensilla basiconica of *L. forficatus* possess 4-6 uniciliate sensory cells. The 4-6 outer dendritic segments include up to 50 microtubules. The outer dendritic segments enter the shaft lumen. The sheath cell apparatus consists of a thecogen cell surrounding the inner receptor lymph and the proximal part of the dendritic sheath, a trichogen cell surrounding the median and distal parts of the dendritic sheath and running up to the hair shaft, and a tormogen cell enclosing and joining the two latter sheath cells without forming an obvious outer receptor lymph cavity (Fig. 12.7E).

The porous shaft of the sensillum basiconicum seems to enable volatile odors to reach the tips of the thinned and extended outer dendritic segments and thereby supports an interpretation in favour of olfaction. Passing of volatile odor molecules through the perforated wall of peg-shaped sensilla basiconica of *G. flavus* is also considered possible, presuming at least a selective permeability of the thin cuticle at the bottom of the hair shaft grooves (Tichy and Barth, 1992). Hygro- and/or thermoreception are assumed for the sensilla basiconica in *L. forficatus* (Keil, 1975).

**Fig. 12.8** A Semischematic reconstruction of type-I sensilla coeloconica inserted on the tip of forcipules of *Geophilus flavus*. B-H Collection of original transmission electron micrographs showing sections of sensilla trichodea located near-by the lateral ocellar field of *Lithobius dentatus* (B), *Craterostigmus tasmanianus* (C-G) and *Scolopendra cingulata* (H): B Cross section through the sensillar shaft loaded with several profiles of outer dendritic segments running through the shaft lumen (probably contact chemoreceptors). C Oblique cross section on the level of the cuticular socket showing dendrites enclosed by dendritic sheath structure. D Cross section through same region, but with higher magnification of dendritic outer segments, one tubular body is clearly visible in the inner receptor lymph cavity. E Cross section through sensillum trichodeum at the level of ciliate bodies. Note the presence of inner and outer receptor lymph cavities, three types of sheath cells and several dendritic outer segments. F Close-up of the center of the inner receptor lymph cavity housing several mechano- and (contact-) chemoreceptive dendrite populations distinguishable by their size and occurrence of ciliate bodies. G Transition zone of inner and outer segment of a sensillar sensory cell recognizable by the basal body structure. H Cluster of five sensillar sensory cells (nuclear level) at the bottom of a sensillum trichodeum. A modified after Ernst and Rosenberg (2003).

bb basal body anchoring the cilium; cb ciliate body; cdos outer dendritic segment of a putative contact chemoreceptor cell; csec (contact) chemoreceptor cell; cu cuticle; dis inner dendritic segment of a sensillar sensory cell; dsh sheath enclosing outer dendritic segments ('Dendritenscheide'); erly external receptor lymph cavity; irly internal receptor lymph cavity; jm joint (socket) cuticle; mdos outer dendritic segment of a mechanoreceptor cell; miv microvillus; sec sensillar sense cell; secI type-I sensillar sensory cell; secII type-II sensillar sensory cell; ssh sensillar hair shaft; the thecogen cell; toc tormogen cell; trc trichogen cell; tub tubular body



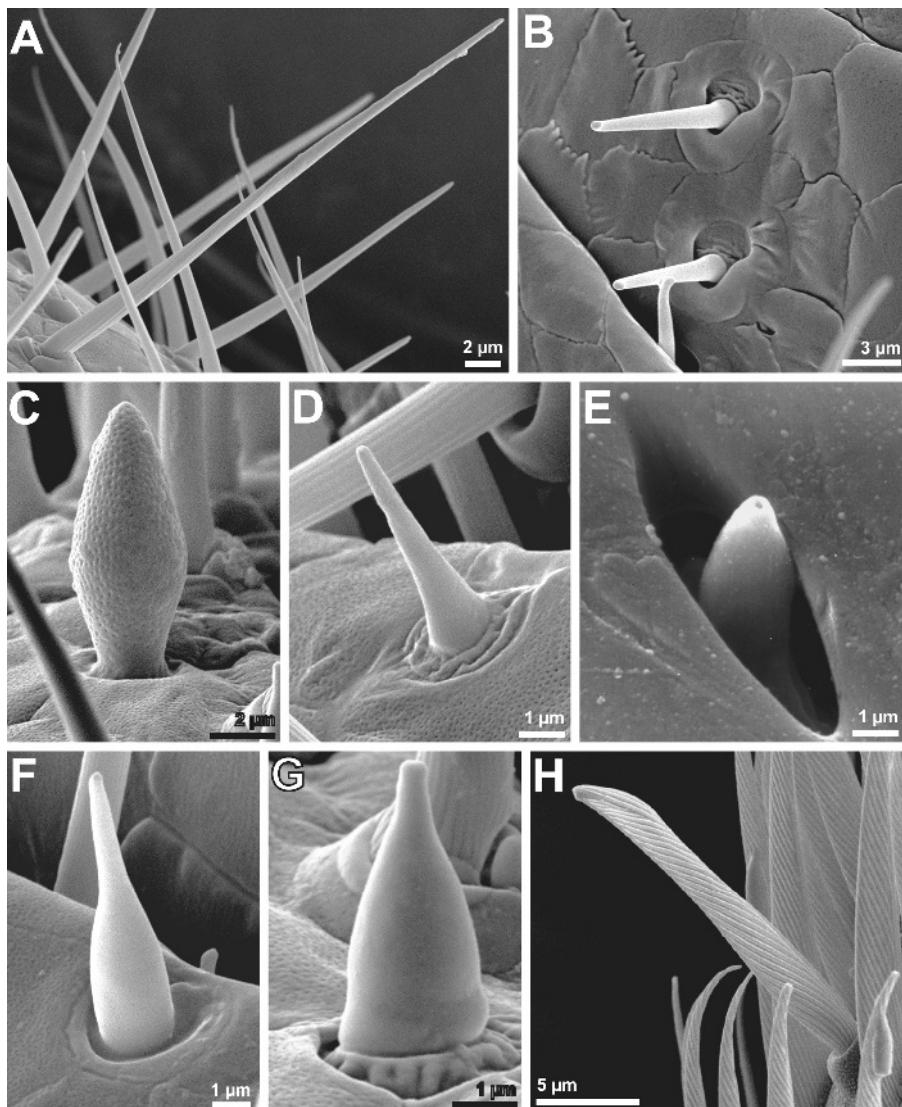
4) *Sensilla brachyconica*. – In *Cryptops hortensis*, Ernst et al. (2009) distinguish two classes of sensilla brachyconica depending on hair length and insertion place on the antennae: terminal sensilla brachyconica and upper-edge sensilla brachyconica (compare

also Fig. 12.9D). Based on external morphology, the upper-edge sensilla brachyconica are here homologized with the large and small sensory cones on the nodes of the antennae of *Scutigera coleoptrata* (Ernst et al., unpubl.). With numbers of 72 per antenna in *L. forficatus* (Keil, 1975) and up to 15 per antenna in *C. hortensis* (Ernst et al., 2009), sensilla brachyconica with short, spine-like hair tapering continuously to the tip (diameter ranging from 1.6–2.1 µm at the base to 0.3 µm at the tip) are frequent on the anteroventral and anterodorsal edge of antennomeres 2 to 16. Their length is approximately 10 µm in *L. forficatus* and between 4.4 and 6.8 µm in *C. hortensis* (Fig. 12.9D). At the base, upper-edge sensilla brachyconica are inserted in a wide and shallow cavity allowing for movements in all directions. The existence of a terminal pore opening is mostly uncertain, only in *Scutigera coleoptrata* does such a pore opening seem to exist (Ernst et al., unpubl.).

The sensilla brachyconica on the distal tip of the terminal antennomere may become considerably longer, e.g. those of *S. coleoptrata* (5.5 µm), *G. flavus* (14–18 µm; Ernst, 1981, 1999, 2000b) or the so-called ‘Sinneskegel’ of *L. forficatus* (50 µm; Keil, 1975). Terminal spine-shaped sensilla are fewer in number, e.g. 3 per antenna in *S. coleoptrata*, 7 per antenna in *G. flavus*, 8 in *L. forficatus*, 5–11 in *C. hortensis*. The shape of the hair is slender, sometimes slightly curved towards the tip, which bears a rounded pore opening. In *C. hortensis*, the hair looks smooth and velvety, decreasing in diameter from 1.6 to 2.1 µm at the occasionally striated base to 0.3 µm at the distal tip. Scanning electron microscopy showed that the socket of both terminal and upper-edge sensilla brachyconica is firmly connected to the surrounding cuticle (*G. flavus*, *L. forficatus*, *C. hortensis*).

A transmission electron microscopic description of sensilla brachyconica is only available for *G. flavus* and *L. forficatus* (Ernst, 1981, 2000b; Keil, 1975). In *G. flavus*, Ernst (1981, 2000b) described a bimodal sensory apparatus made up of one uniciliate and two biciliate sensory cells enclosed by three sheath cells (Fig. 12.7C). The total of five outer dendritic segments have different diameters and terminate on different levels in relation to the hair shaft. Tubular bodies are absent, indicating the inability of these sensilla to process mechanosensory stimuli. A higher number of 4–6 uniciliate sensory cells is present in *L. forficatus* (Keil, 1975). The exposed position on the tip of the terminal antennomere suggests a thermoreceptive function in *L. forficatus*, whereas the bimodal arrangement of sensory cells enables the addition of hygroreceptors in *G. flavus* (Ernst et

Fig. 12.9 Compilation of types of epidermal sensilla in Chilopoda, documented on the antennae of *Cryptops hortensis* (A–D,F–G) and *Scutigera coleoptrata* (H) as well as recessed on the maxillipedes of *Lithobius forficatus* (E). The sensilla have been ordered according to their appearance in the text. A Sensillum trichodeum. B Sensillum microtrichodeum. C Sensillum basiconicum. D Sensillum brachyconicum. E Sensillum coeloconicum. F Club-shaped sensillum. G Hat-shaped sensillum. H Beak-shaped sensillum.



al., 2009). The possible existence of a terminal pore in *C. hortensis* suggests a functional combination of hygro- or thermoreceptors with contact chemoreceptors (Ernst et al., 2009).

5) **Sensilla coeloconica.** – Sensilla coeloconica are structurally highly diverse and seem to be widespread among the five main chilopod subtaxa. Although variations in hair shape do occur, these sensilla are reliably distinguishable from all other types (Fig.

12.9E). The majority of sensilla coeloconica is described on the forcipular claw (Jangi and Dass, 1977, Ménez et al. 1990; Ernst, 1995; Rosenberg and Ernst, 2001; Ernst et al., 2002; Ernst and Rosenberg, 2003). Others are known from the antenna of *Craterostigmus tasmanianus* (Ernst et al., 2006) or the epi- and hypopharyngeal regions of some Scutigeromorpha (Koch and Edgecombe, 2006) and many Scolopendromorpha ('nipple-and/or bullet-shaped' sensilla: Edgecombe and Koch, 2009; Koch et al., 2010). The sensory cone is centered into a deep cavity of ovoid or spherical shape. The cone mostly has a terminal pore and barely overlaps the level of the surrounding cuticle. We distinguish three subtypes according to size differences and local patterns of distribution.

Type-I: Sensilla coeloconica with broad and conical hair shafts (2-5 µm in length) can be seen in large numbers on the ventral and dorsal side of the forcipular tarsungulum (Fig. 12.9E). Sensory cells and sheath cells are connected to the sensory cone via a long, S-shaped channel. In *L. forficatus*, 7-9 uniciliate sensory cells are surrounded by one thecogen cell, one trichogen cell, and one tormogen cell. Thick (0.6-1.2 µm in diameter) and thin (0.2-0.4 µm in diameter) outer dendritic segments pass through the cuticular channel and center of the sensory cone where they abut the apical pore opening. On their way up the channel, the dendrites are wrapped by the dendritic sheath and the thecogen sheath cell. (Rosenberg and Ernst, 2001; Ernst and Rosenberg, 2003) (Fig. 12.7G). In *G. flavus*, approximately 60 type-I sensilla coeloconica occur at the tip of the tarsungulum. Deviations from type-I sensilla in *L. forficatus* are a mostly lesser number of sensory cells (n=3-8), smaller diameters of outer dendritic segments (thick dendrites: 0.4-0.7 µm, thin dendrites: 0.2-0.3 µm) and absence of a terminal pore on the sensory cone. The basis of the sensory cone is hinged to the cuticle of the socket cavity by a membranous joint and stiff radial microfibrils, limiting shaft mobility (Ernst and Rosenberg, 2003) (Fig. 12.8A).

Type-II: Sensilla coeloconica with slender hairs shafts and rounded tips (1.5-2.7 µm in length) can be observed in low numbers on the uppermost tip region of the forcipular tarsungulum. Type-II sensilla are similar to those of type-I in general configuration but there are considerable differences in receptor composition. In hemianamorphic larval stages and adults of *L. forficatus*, the two outer dendritic segments with widest diameters are associated with tubular bodies (mechanoreception), allowing for stable connection of the dendrites to a cap-like differentiation of the socket cuticle. All remaining, putatively chemoreceptive dendrites run further up, enter the hair shaft and terminate close to the apical pore opening (Ernst and Rosenberg, 2003) (Fig. 12.7G).

Type-III: Sensilla coeloconica with long and acute hair shafts (2-4.5 µm in length) can be found in almost elliptical cavities at the inferior edge of the tarsungulum tip. A terminal pore opening exists.

With exception of the antennae of *C. tasmanianus* where the existence of terminal pores on tumbler switch-shaped sensilla is dubious, type-I sensilla coeloconica are thought to function as contact chemoreceptors (Rosenberg and Ernst, 2001; Ernst and Rosenberg, 2003). This assumption is supported by behavioural experiments conducted by Jangi and Dass (1977) in *S. morsitans*. The existence of dendritic outer segments of thick and thin diameters in type-I sensilla coeloconica in Lithobiomorpha and Geophilomorpha indicates a dual function, possibly a combination of thermo- and hygrocceptors (Ernst, 1995, 2000b; Ernst and Rosenberg, 2001). In type-II sensilla coeloconica of *L. forficatus*, mechano- and chemoreceptors are coupled, and the former receptor function appears obvious because of the existence of tubular bodies (Rosenberg and Ernst, 2001).

6) **Collared bottle-shaped sensilla.** – Based on SEM data, collared bottle-shaped sensilla, hitherto exclusively found on the antennae of *Craterostigmus tasmanianus*, are compound sensory hairs distinguished by a smooth, collar-like shaft and a smooth, tapered distal flagellum without apical pore opening (Ernst et al., 2006). Owing to a joint-like structure connecting its base to the shaft, the flagellum is assumed to be movable. Variations of antennal bottle-shaped sensilla do occur in *C. tasmanianus*. Edgecombe and Giribet (2004) illustrated a short as well as a long subtype to be frequent on the dorsal side at the anterior edge of antennomere 16 and a single long bottle-shaped sensillum on the ventral side at the anterior edge of the same antennomere. Sensilla of both subtypes are abundant on the anterior edges of antennomeres 2, 6 and 11.

7) **Collared tube-shaped sensilla.** – Based on SEM data, tube-shaped sensilla are hitherto only known from the apical tip of the terminal antennomere of *Craterostigmus tasmanianus* (Ernst et al., 2006). Like bottle-shaped sensilla, they appear compound, being divided into a shaft and flagellar region. In contrast to the latter type, however, tube-shaped sensilla have a long and slender shaft contrasting with a much shorter flagellum without an apical pore opening. Sensilla of similar collared form have been documented on the antenna of *Scolopocryptops sexspinosa*. Here, the length ratio between shaft and flagellum is about 1:2. The hair looks striated as in typical antennal trichoid sensilla (see above and Edgecombe and Giribet, 2004). Bipartite sensilla also seem to occur in other *Scolopocryptops* species (Attems, 1930) as well as in *Dinocryptops miersi* (Lewis, 2000).

8) **Club-shaped sensilla.** – SEM observations reveal that simple and blunt club-shaped sensilla of *Cryptops hortensis* are superficially similar to bottle-shaped sensilla of *Craterostigmus tasmanianus*. Club-shaped sensilla are not subdivided into distinct segments (Ernst et al., 2009). The base of the sensillum is inserted in a plain cavity (Fig. 12.9F). Only a few of them (2-4) have been mapped on each antenna of *C. hortensis*. At the tip of the sensillum, a terminal pore opening is present. Termed as ‘bottle-shaped sensilla’,

club-shaped sensilla have also been documented grouped together on the apical antennomeres of the scolopendromorphs *Newportia monticola* and *Ectonocryptoides quadrimeropus* (Koch et al., 2010). The cavity around the socket is spacious.

9) **Hat-shaped sensilla.** – To date, hat-shaped sensilla were exclusively found on the antennae of various Scolopendromorpha. The 2-6 hat-shaped sensilla, observed in *Cryptops hortensis*, are by far the smallest sensilla ever found on chilopod antennae (up to 5.7 µm in diameter, see Fig. 12.9G)) (Ernst et al., 2009). Often, the bulky and smooth sensory hair sits on a furrowed, plate-like pedestal embedded into a flat, bowl-like depression of the cuticle. The form of the sensory hairs rather resembles a mitre. A terminal pore is present. This type of sensillum seems to be also present on the terminal antennomere of *Newportia monticola* ('bottle-shaped sensilla', Koch et al., 2010).

10) **Button-shaped, rimmed sensilla.** – This rather unique type of epidermal sensilla belongs to the group of hypopharyngeal sensilla and was found by Koch and Edgecombe (2006) on the tongue of scutigeromorphs (e.g. *Thereuopoda longicornis*) in paired paramedial rows, innervated by paired neuropils sitting below the frontal epidermis of distal hypopharynx. Cuticular structures formed by these sensilla display resemble a buzzer structure ('button') on which the small, peg-like sensilla are mounted. According to Koch and Edgecombe (2006), inturned cuticular rims of these sensilla bear an irregularly folded, whereas the outer rim displays a more regular, concentric ornament. Subsequently Koch and Edgecombe (2008) discovered distinct rows of button-like sensilla on the hypopharynx of Lithobiomorpha.

11) **Beak-shaped sensilla.** – Based on SEM data alone (Ernst et al., unpubl.), over 4.000 beak-like sensilla were observed on the antennae of *Scutigera coleoptrata* (Fig. 12.9H). The long, broad and flattened sensory hairs resemble an elongated beak. The shaft bears a pattern of spiralled, strongly convex ribs separated from each other by deep furrows, probably the roughest rib pattern among all hitherto described types of chilopod sensilla. The tip of the shaft is thickened, often curved, and carries a terminal pore opening. By being inserted on the anterior margin of every second or third antennomere and by keeping constant distance from each other in this circular arrangement, beak-shaped sensilla are aligned accurately along the entire antenna, probably forming a grid pattern of chemoreceptors.

#### *Large or compound epidermal sensilla*

These are complex structures with more or less closely assembled sensilla which may contain one or several types of sensilla. Compound epidermal sensilla often appear in

module-type arrangements and are sunk into a deep depression of the epidermis, only visible from outside by a more or less spacious pore opening. The axons of their sensory units are grouped together in a specialized nerve targeting in one or several parts of the brain.

#### *Tömösváry organ*

The Tömösváry organ is a sense organ assumed to function as a carbon dioxide detector. The name Tömösváry organ refers to the first discoverer, the Romanian myriapodologist Ödön Tömösváry (1852–1884), and was introduced by Vogt and Yung (1883). Common English synonyms are ‘temporal organ’ or ‘postantennal organ’. In accordance with Haupt (1979) and Tichy and Barth (1992), the Tömösváry organ is assigned here to the category of compound sensilla organs.

The Tömösváry organ is located behind the basis of each antenna in the Scutigeromorpha (*Scutigera coleoptrata*: Tichy and Barth, 1992; *Thereuonema tuberculata*: Yamana and Toh, 1990) and Lithobiomorpha (Lithobiidae: *Lithobius forficatus*: Tichy, 1972, 1973a; Tichy and Barth, 1992; various Henicopidae: Edgecombe, 2004). In Lithobiomorpha, the broad, crater-like Tömösváry organs are variously placed anteriolaterally to the ocellar field (or posteriolaterally to the antennal basis in blind species) often nested against the edge of the head capsule (most Lithobiidae; e.g. Müller and Rosenberg, 2006) (see also Fig. 12.5A). In some Henicopidae of the genus *Paralamyctes*, the openings to the Tömösváry organ are placed in a depression of the bending edge of the head capsule (Edgecombe et al., 2002, Edgecombe, 2004), but in *Lamyctes caeculus* and *Haasiella* spp. they are displaced posteriorly to the cephalic pleurite and are thereby not visible from above (Edgecombe, 2004). In Craterostigmomorpha, a triangular plate surrounded by a prominent cuticular ring lateral to the clypeus is possibly a Tömösváry organ (Dohle, 1990).

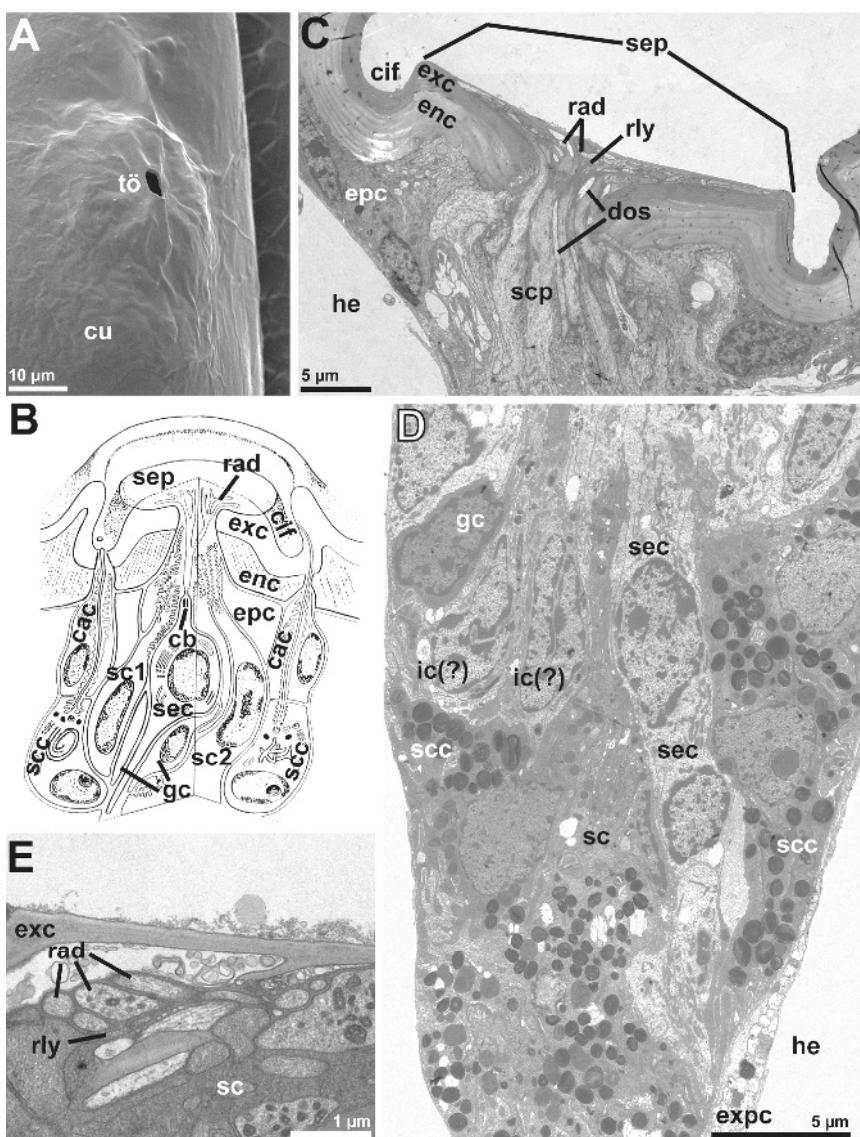
Besides the Chilopoda, Tömösváry organs are found in all remaining subgroups of the Myriapoda as well as in Protura and Collembola (see summary in Haupt, 1979).

The most thoroughly studied Tömösváry organ in Chilopoda is that of *Lithobius forficatus* (Tichy, 1972, 1973a, b; Tichy and Barth, 1992). It consists of a sensory apparatus of twelve closely packed biciliate sensory cells enveloped by an outer mantle of at least twice as many sheath cells (Fig. 12.10B,D). The dendritic processes emanating from each sensory cell are divided into three compartments according to the 1) distance to the soma, 2) the occurrence of ciliary structures and 3) the extension of the inner receptor lymph cavities (Fig. 12.10B). The outer dendritic segment consists of an unpaired ciliary segment and paired dendrites that project distally and finally come into contact with the cuticle. The cuticle forms an elevated sensory plate lining the bottom of the crater-

shaped opening (Figs. 12.5A, 12.10B-C). On the level of the ciliate body, the sheath cells transform into elongated distal extensions that withdraw from the dendrites but form small inner receptor lymph cavities around one pair of cilia, the third dendrite compartment, the so-called outer segment. The liquid content of the receptor lymph cavities is controlled by continuous secretion activity by the sheath cells. When approaching the sensory plate, the small inner receptor lymph cavities fuse to build the outer receptor lymph cavity. More distally, however, the ciliary processes divide into second order branches (Fig. 12.10C,E). All branches and subbranches are still embedded in the outer receptor lymph cavity and finally make contact to the inner surface of the thin exocuticle that lines the bottom of the crater-shaped opening of the organ. In its center, the sensory cuticular plate is raised above the level of the surrounding circular furrow, which is covered by a cuticular bulge. The circular furrow is rich in pore openings of numerous flexo-canals epidermal glands that enclose the entire sensory apparatus (Figs. 12.5A, 12.10B-C). Tichy (1972, 1973a) described these accessory flexo-canals epidermal glands as including only canal cells and secretory cells, but according to new observations the presence of intermediary cells cannot be excluded. Potential candidates for intermediary cells are marked in Fig. 12.10D. From the bottom of the sensory cell's soma, an axonic process is sent off to enter the nervus Tömösváryi, with thick neurilemm and glial cell sheaths. Tichy (1972, 1973a) described the afferent axonic processes that transmit stimuli to the subjacent neuropils without synaptic connections, but the absence of synapses appears problematic. The Tömösváry organ afferents innervate three compartments within the ipsilateral protocerebrum: the second

Fig 12.10 External morphology (SEM: A) and cytomorphology (TEM: C-E) of the Tömösváry organ in *Scutigera coleoptrata* (A) and *Lithobius forficatus* (B-E). A Tömösváry organ, note the dome-like elevation of the cuticle leaving a small central pore opening on the summit. B 3D cut-away drawing showing the ultrastructural organization of the Tömösváry organ in *L. forficatus* (adapted from Tichy, 1973a). C Longitudinal section through the apical region of the Tömösváry organ with the sensory plate crossed by numerous ramified projections of the outer dendritic segments, processes of the sheath cells and receptorlymph interspaces. D Organization of the median and proximal regions of the Tömösváry organ housing a high diversity of cell types, same individual as in C. E Highly magnified sector within the sensory plate region (longitudinal view). Ramifications of outer dendritic segments abut the thinned cuticle. A original Ernst, Sombke; C-E originals Müller.

cac canal cell (of an accessory flexo-canal epidermal gland); cb ciliate body; cif circular furrow around the sensory plate; cu cuticle; dos outer dendritic segment; enc endocuticle; epc epidermal cell; exc exocuticle; expc external pigment cell; gc glial cell; he hemolymphatic space; ic(?) putative intermediary cell(s); rad ramified tip of an outer dendritic segment; rly receptor lymph space; sc sheath cell; scl type-1 sheath cell; sc2 type-2 sheath cell; scc secretory cell (of an accessory flexo-canal epidermal gland); scp sheath cell process (with microvillar fringe); sec sensory cell constituting Tömösváry organ; sep sensory plate; tō opening of the Tömösváry organ



optic neuropile (medulla), the dorsolateral protocerebrum, and the pedunculi of the so-called mushroom bodies (Petykó et al., 1996).

The fine structure of Tömösváry organs in *T. tuberculata* (Yamana and Toh, 1990) and *S. coleopterata* (Tichy and Barth, 1992) widely corresponds to conditions in *L. forficatus*.

Similar are number, proportions, compartmentalization and dendritic ramification of the sensory cells. So too is the arrangement of sheath cells and the merging of inner receptor lymph cavities into one distal outer receptor lymph cavity. However, scutigeromorph Tömösváry organs have both mono- and biciliate sensory cells and strongly differ from those in Lithobiomorpha by their outer appearance and distal expansion of the sensory apparatus. In *T. tuberculata* and *S. coleoptrata*, the sensory apparatus, which is lined by thin, fibrous cuticle, forms a mushroom-like bulbus protruding into a spacious cuticular cavity covered by a cuticle with a small central opening only (Fig. 12.10A).

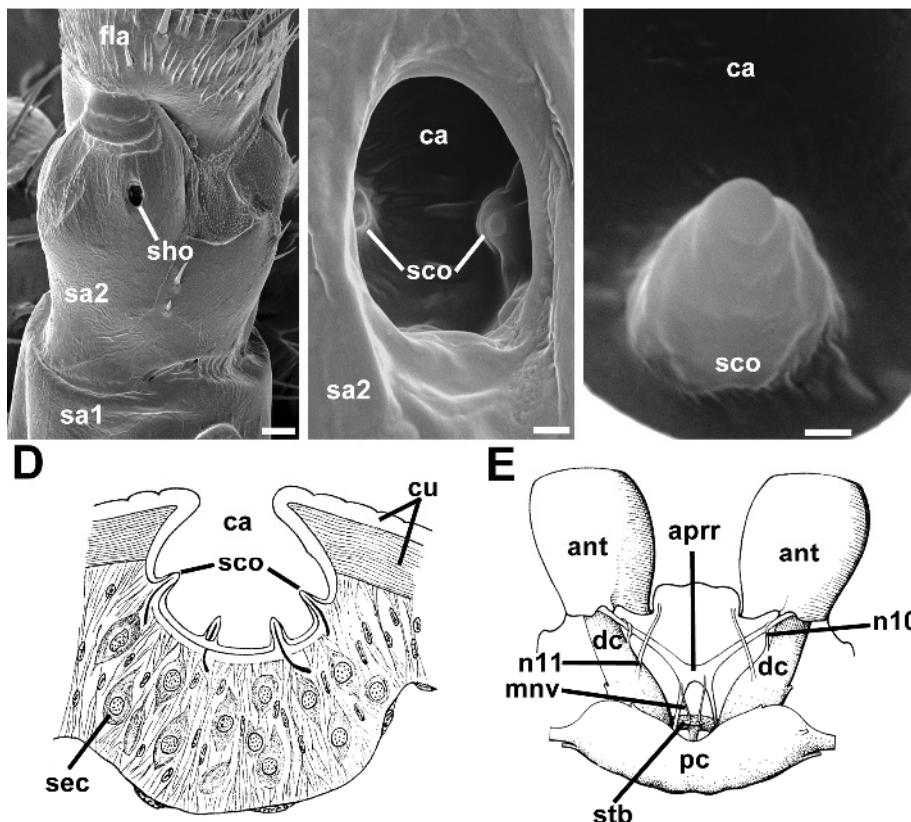
There have been speculations on the function of Tömösváry organs, ranging from hygrocception (Bauer, 1955; Tichy, 1973a,b) to vibration detection (Meske, 1960, 1961). However, electrophysiological recordings on *T. tuberculata* have shown the sensitivity of Tömösváry receptor cells against H<sub>2</sub>O and, in particular, CO<sub>2</sub> (Yamana et al., 1986, 1998; Yamana and Toh, 1987). The receptor cells are assumed to detect changes in ion concentrations within the receptor lymph cavities. Sensitivity to CO<sub>2</sub> molecules is considered to be especially advantageous for predators living in or close to the soil (e.g. hidden underneath stones or in rocky/wooden crevices). Functional constraint to tune and enhance the sensitivity towards H<sub>2</sub>O and/or CO<sub>2</sub> perception may have led to enormously enlarged Tömösváry organs in cave-inhabiting centipedes, just like described by Hennings (1904, 1906). Some blind Henicopidae (e.g. *Paralamyctes (Haasiella) trailli*, *Lamyctes caeculus*) carry larger Tömösváry organs than their relatives equipped with eyes (Serra, 1981, Edgecombe et al., 2002).

#### *Shaft organ ('Schaforgan')*

Verhoeff (1904) described a dorsomedian pit on the distal (second) antennomere of the antennal shaft of scutigeromorph centipedes and termed it the 'Schaftorgan' (see also Fig. 12.11A-C). The English term 'shaft organ' was introduced by Lewis (1981). Within this

**Fig 12.11** External morphology (SEM data: A-C) and anatomy (LM data: D) of the shaft organ on the antennae of *Scutigera coleoptrata*. A Overview of the second shaft antennomere of one antenna photographed from dorsal perspective. The shaft organ is clearly visible as a round breakthrough in the cuticle. B Higher magnification of the cavity of the shaft organ from dorsal perspective. Bumps at the bottom of the cavity represent sensory cones. C Detail of the cavity and close-up of one sensory cone. D Longitudinal section of the shaft organ and schematic reconstruction of the sensory cell pattern situated below the bottom of the cavity. E Cut-away drawing of a dissected antennal muscle sense organ in *Lithobius forficatus*. Example for a proprioceptor in Chilopoda. A-C, originals Ernst, Sombke; D modified after Fuhrmann (1922); E modified after Rilling (1968).

ant antenna; appr antennal proprioceptor (muscle sense organ); ca cuticular cavity of the shaft organ; cu cuticle; dc deutocerebrum; fla proximal antennomere of the flagellum; mnv motoric nerve; nI0-II 10<sup>th</sup> and 11<sup>th</sup> nerve; pc protocerebrum; sa1 first antennal (shaft) article; sa2 second antennal (shaft) article; sec sensory cell constituting the shaft organ; sco sensory cone; sho opening of the shaft organ; stb stomodeal bridge (-frontal connective)



pit, approximately 20 cone-shaped sensilla with a length of 3 µm are present in *Scutigera coleoptrata* (Fig. 12.11D). The function of the shaft organ is completely unknown. Fuhrmann (1922) suggested that these sensilla may have an olfactory function. However, due to their insertion within the shaft organ it is not likely that the sensilla are gustatory or mechanoreceptors (Ernst et al., unpubl.). However, in SEM studies the sensillar shaft seems to be unstructured and the rounded tip does not possess a terminal pore (Ernst et al., unpubl.). Typologically, the sensilla assembled in the shaft organ resemble the sensilla brachyconica that have also been observed on the antennae of other chilopods.

### *Proprioreceptors*

Proprioreceptors have been described by Rilling (1960, 1968) in *Lithobius forficatus*, as specialized muscle receptors and sensory cells with free terminations structures. Proprioreceptive sensory cells are often constant in number and show equal distribution

patterns on their target structures. Ramified dendritic processes of the sensory cells cover wide parts of the unsclerotized cuticle typically found in the intersegmental or interpodomeric membranes. Compression or stretching of the articular membranes then results in depolarization of the proprioceptors. Otherwise, proprioceptive nerve elements are associated with thin muscular bands. These filigree muscular bands connect moveable cuticular plates (tergites, pleurites, sternites) and tentorial structures with each other. The terminology of these so-called muscle receptors is based on their location in the centipede's body. For instance, there are pedal muscle receptors that consist of a simple muscle band innervating a pair of primary sensory cells and receive input from the coxa-trochanter-joint in the walking legs. Pedal muscle receptors of principally identical structure are likewise present at the bases and within the maxillae II, the maxillipedes as well as the antennae, there forming the so-called antennal muscle sensory organ (Fig. 12.11E). Furthermore, there are tergal muscle receptors that are placed at the attachment points of the dorsal longitudinal musculature which extends between two succeeding large tergites. Afferents of tergal muscle receptors extend to the ventral nerve chord.

Besides Scutigeromorpha, tergal muscle receptors have also been reported in the dorsal longitudinal musculature of *Scolopendra morsitans*. Varma (1972) found receptors consisting of 13 bi- and multipolar sensory cells. Each receptor is innervated by the N-IV nerve projecting from the ventral ganglia 1-20. Muscle receptors arranged at different parts of the trunk have been described in a further *Scolopendra* species as well as in *Lithobius* sp. and the geophilomorph *Haplophilus* sp. (Osborne, 1961; Finlayson, 1976).

### References

- ANDERSON, G., 1981. Taxonomical studies on the post-embryonic development in Swedish Lithobiomorpha (Chilopoda). – *Entomologica Scandinavica* (Supplement) 15: 105-124.
- ATTEMS, C. C., 1930. Myriapoda. 2. Scolopendromorpha (Das Tierreich, 54). – Walter de Gruyter, Berlin.
- BAHR, R., 1965. Ableitung lichtinduzierter Potentiale von den Augen von *Lithobius forficatus* L. – *Naturwissenschaften* 52: 459.
- BAHR, R., 1967. Elektrophysiologische Untersuchungen an den Ozellen von *Lithobius forficatus* L. – *Zeitschrift für Vergleichende Physiologie* 55: 70-102.
- BAHR, R., 1971. Die Ultrastruktur der Photorezeptoren von *Lithobius forficatus* L. (Chilopoda: Lithobiidae). – *Cell and Tissue Research* 116: 70-93.
- BAHR, R., 1972. Licht- und dunkeladaptive Änderungen der Sehzellen von *Lithobius forficatus* L. (Chilopoda: Lithobiidae). – *Cytobiologie* 6: 214-233.
- BAHR, R., 1974. Contribution to the morphology of chilopod eyes. – *Symposium Zoological Society London* 32: 388-404.

- BAUER, K., 1955. Sinnesökologische Untersuchungen an *Lithobius forficatus*. – Zoologische Jahrbücher, Abteilung für Physiologie der Tiere 65: 267-300.
- BEDINI, C., 1968. The ultrastructure of the eye of a centipede *Polybothrus fasciatus* (Newport). – Monitore Zoologico Italiano (N.S.) 2: 31-47.
- DEMANGE, J.-M., 1956. Contribution à l'étude de la biologie, en captivité de *Lithobius piceus gracilis* Brölemann (Myriapode – Chilopode). – Bulletin du Muséum national d'Histoire Naturelle, Paris 28 Supplément 2: 388-393.
- DOHLE, W., 1990. Some observations on morphology and affinities of *Craterostigmus tasmanianus* (Chilopoda). – Pp. 69-79 in A. Minelli (ed.). Proceedings of the 7<sup>th</sup> International Congress of Myriapodology. E.J. – Brill, Leiden.
- DOHLE, W., 2001. Are the insects terrestrial crustaceans? A discussion of some new facts and arguments and the proposal of the proper name 'Tetraconata' for the monophyletic unit Crustacea + Hexapoda. – Pp. 85-103 in T. DEUVE (ed.). Origin of the Hexapoda. Annales de la Société Entomologique de France (N.S.) 37.
- EDGEcombe, G. D., 2004. The henicopid centipede *Haasiella* (Chilopoda: Lithobiomorpha): new species from Australia, with a morphology-based phylogeny of Henicopidae. – Journal of Natural History 38: 37-76.
- EDGEcombe, G. D. & G. GIRIBET, 2004. Adding mitochondrial sequence data (16S rRNA and cytochrome c oxidase subunit I) to the phylogeny of centipedes (Myriapoda: Chilopoda): an analysis of morphology and four molecular loci. – Journal of Zoological Systematics and Evolutionary Research 42: 89-134.
- EDGEcombe, G. D., G. GIRIBET & W. C. WHEELER, 2002. Phylogeny of Henicopidae (Chilopoda: Lithobiomorpha): a combined analysis of morphology and five molecular loci. – Systematic Entomology 27: 31-64.
- EDGEcombe, G. D. & M. KOCH, 2009. The contribution of preoral chamber and foregut morphology to the phylogenetics of Scolopendromorpha (Chilopoda). – Soil Organisms 81: 295-318.
- ERNST, A., 1976. The ultrastructure of the sensory hairs on the antenna of *Geophilus longicornis* Leach (Myriapoda, Chilopoda). I. The sensilla trichoidea. – Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 96: 586-604.
- ERNST, A., 1979. The ultrastructure of the sensory hairs on the antenna of *Geophilus longicornis* Leach (Myriapoda, Chilopoda). II. The sensilla basiconica. – Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 102: 510-532.
- ERNST, A., 1981. The ultrastructure of the sensory hairs on the antenna of *Geophilus longicornis* Leach (Myriapoda, Chilopoda). III. The sensilla brachyconica. – Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 106: 375-399.
- ERNST, A., 1983. The ultrastructure of the sensory hairs on the antenna of *Geophilus longicornis* Leach (Myriapoda, Chilopoda). IV. The sensilla microtrichodea. – Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 109: 521-546.
- ERNST, A., 1994. Verteilung und Ultrastruktur der Sensilla trichodea auf den Maxillen des Chilopoden *Geophilus longicornis* Leach. – Verhandlungen der Deutschen Zoologischen Gesellschaft 87: 239.

- ERNST, A., 1995. Die Ultrastruktur der Sensilla coeloconica auf den Maxillipeden des Chilopoden *Geophilus longicornis* Leach. – Verhandlungen der Deutschen Zoologischen Gesellschaft 88: 160.
- ERNST, A., 1996. Biciliarität von Sinneszellen in verschiedenen Cuticularsensillen des Chilopoden *Geophilus longicornis* Leach. – Verhandlungen der Deutschen Zoologischen Gesellschaft 89: 272.
- ERNST, A., 1999. Fine structure and distribution of different cuticular sensilla in *Geophilus longicornis* Leach (Chilopoda, Geophilomorpha: Geophilidae). – Zoology (Supplement II) 102: 39.
- ERNST, A., 2000a. Fine structure and distribution of basiciconic sensilla in the centipede *Necrophilocophagus longicornis* Leach. – Zoology 103: 56.
- ERNST, A., 2000b. Struktur und Verbreitung verschiedener Cuticularsensillen bei *Geophilus longicornis* Leach (Chilopoda, Geophilomorpha: Geophilidae). – Fragmenta Faunistica, Warszawa 43 Supplement: 113-129.
- ERNST, A. & J. ROSENBERG, 2003. Structure and distribution of sensilla coeloconica on the maxillipedes of Chilopoda. – African Invertebrates 44: 155-168.
- ERNST, A., J. ROSENBERG & G. HILKEN, 2006. Structure and distribution of antennal sensilla in the centipede *Craterostigmus tasmanianus* Pocock, 1902 (Chilopoda, Craterostigmomorpha). – Norwegian Journal of Entomology 53: 153-164.
- ERNST, A., J. ROSENBERG & G. HILKEN, 2009. Structure and distribution of antennal sensilla in the centipede *Cryptops hortensis* (Donovan, 1810) (Chilopoda, Scolopendromorpha). – Soil Organisms 81: 399-411.
- ERNST, A., J. ROSENBERG, R. MESIBOV & G. HILKEN, 2002. Sensilla coeloconica on the maxillipede of the centipede *Craterostigmus tasmanianus* Pocock, 1902 (Chilopoda, Craterostigmomorpha). – Abhandlungen und Berichte des Naturkundemuseums Görlitz 72: 207-214.
- FAHLANDER, K., 1938. Beiträge zur Anatomie und systematischen Einteilung der Chilopoda. – Zoologiske Bijdragen fran Uppsala 17: 1-148.
- FINLAYSON, L. H., 1976. Abdominal and thoracic receptors in insects, centipedes, and scorpions. – Pp. 153-211 in P.J. MILL (ed.). Structure and function of proprioceptors in the invertebrates. – Chapman & Hall, London.
- FUHRMANN, H., 1922. Beiträge zur Kenntnis der Hautsinnesorgane der Tracheaten. I. Die antennalen Sinnesorgane der Myriapoden. – Zeitschrift für Wissenschaftliche Zoologie 119: 1-52.
- GÖRNER, P., 1959. Optische Orientierungsreaktionen bei Chilopoden. – Zeitschrift für Vergleichende Physiologie 42: 1-5.
- HANSTRÖM, B., 1926. Eine genetische Studie über die Augen und Sehzentren von Turbellarien, Anneliden und Arthropoden (Trilobiten, Xiphosuren, Eurypteriden, Arachnoiden, Myriapoden, Crustaceen und Insekten). – Kongliga Svenska Vetenskaps Academiens Handlingar 4: 1-176.
- HANSTRÖM, B., 1928. Vergleichende Anatomie des Nervensystems der Wirbellosen Tiere unter Berücksichtigung seiner Funktion. – Springer Verlag, Berlin.
- HANSTRÖM, B., 1934. Bemerkungen über das Komplexauge der Scutigeriden. – Lunds Universitets Arskrift (2 N.F.) 30: 1-14.
- HARZSCH, S. & G. HAFNER, 2006. Evolution of eye development in arthropods: phylogenetic aspects. – Arthropod Structure & Development 35: 319-340.

- HARZSCH, S., R. R. MELZER & C. H. G. MÜLLER, 2007. Mechanisms of eye development and evolution of the arthropod visual system: the lateral eyes of Myriapoda are not modified insect ommatidia. – *Organisms, Diversity & Evolution* 7: 20-32.
- HAUPT, J., 1979. Phylogenetic aspects of recent studies on myriapod sense organs. – Pp. 391-406 in M. CAMATINI (ed.). *Myriapod Biology* – Academic Press, New York.
- HENNINGS, C., 1904. Das Tömösvárysche Organ der Myriapoden I. – *Zeitschrift für Wissenschaftliche Zoologie* (Leipzig) 76: 26-53.
- HENNINGS, C., 1904. Das Tömösvárysche Organ der Myriapoden II. – *Zeitschrift für Wissenschaftliche Zoologie* (Leipzig) 80: 576-641.
- HEYMONS, R., 1901. Die Entwicklungsgeschichte der Scolopender. *Zoologica* (Stuttgart) 33: 1-244.
- HOLMGREN, N., 1916. Zur vergleichenden Anatomie des Gehirns von Polychaeten, Onychophoren, Xiphosuren, Arachniden, Crustaceen, Myriopoden und Insekten. – *Kongliga Svenska Vetenskaps Academiens Handlingar* 56: 1-303.
- JANGI, B. S. & C. M. S. DASS, 1977. Chemoreceptive function on the poison fang in the centipede, *Scolopendra morsitans* L. – *Indian Journal of Experimental Biology* 15: 803-804.
- JOLY, R. & C. HERBAUT, 1968. Sur la régénération oculaires chez *Lithobius forficatus* L. (Myriapode Chilopode). – *Archive de Zoologie Expérimentale & Générale* 109 : 591-612.
- KEIL, T. A., 1975. Die Antennen- und Hautdrüsengänge von *Lithobius forficatus* L. Eine licht- und elektronenmikroskopische Untersuchung. – Ph. D. thesis, Free University Berlin, 61p.
- KEIL, T. A., 1976. Sinnesorgane auf den Antennen von *Lithobius forficatus* L. (Myriapoda, Chilopoda). I. Die Funktionsmorphologie der "Sensilla trichodea". – *Zoomorphology* 84: 77-102.
- KLEIN, K., 1934. Über die Helligkeitsreaktionen einiger Arthropoden. – *Zeitschrift für Wissenschaftliche Zoologie* 145: 1-38.
- KLINGEL, H., 1960. Vergleichende Verhaltensbiologie der Chilopoden *Scutigera coleoptrata* L. („Spinnenassel“) und *Scolopendra cingulata* Latreille („Scolopender“). – *Zeitschrift für Tierphysiologie* 17: 11-30.
- KOCH, M. & G. D. EDGEcombe, 2006. Peristomatic structures in Scutigeromorpha (Chilopoda): A comparative study, with new characters for higher-level systematics. – *Zoomorphology* 125: 187-207.
- KOCH, M. & G.D. EDGEcombe, 2008. The peristomatic structures of Lithobiomorpha (Myriapoda, Chilopoda): comparative morphology and phylogenetic significance. – *Journal of Morphology* 269: 153-174.
- KOCH, M., G. D. EDGEcombe & R. M. SHELLEY, 2010. Anatomy of *Ectonocryptoides* (Scolopocryptidae: Ectonocryptopinae) and the phylogeny of blind Scolopendromorpha (Chilopoda). – *International Journal of Myriapodology* 3: 51-81.
- LAND, M. F., 1972. Mechanism of orientation and pattern recognition by jumping spiders. – Pp. 231-247 in R. WEHNER (ed.). *Information processing in the visual systems of arthropods*. – Springer Verlag, Berlin.
- LEWIS, J. G. E., 1981. The biology of centipedes. – Cambridge University Press, Pp. 1-476.
- LEWIS, J. G. E., 2000. Centipede antennal characters in taxonomy with particular reference to scolopendromorphs and antennal development in Pleurostigmophora (Myriapoda, Chilopoda). – *Fragmenta Faunistica*, Warszawa 43 Supplement: 87-96.

- MATIC, Z., 1960. Beiträge zur Kenntnis der blinden *Lithobius*-Arten (Chilopoda: Myriapoda) Europas. – Zoologischer Anzeiger 164: 443-448.
- MELZER, R. R., R. DIERSCH, D. NICASTRO & U. SMOLA, 1997. Compound eye evolution: highly conserved retinula and cone cell patterns indicate a common origin of the insect and crustacean ommatidium. – Naturwissenschaften 84: 542-544.
- MELZER, R. R., Z. PETYKÓ & U. SMOLA, 1996/97. Photoreceptor axons and optic neuropils in *Lithobius forficatus* (Linnaeus, 1758) (Chilopoda, Lithobiidae). – Zoologischer Anzeiger 235: 177-182.
- MÈNEZ, A., ZIMMERMAN, K., ZIMMERMAN, S. & H. HEATWOLE, 1990. Venom apparatus and toxicity of the centipede *Ethmostigmus rubripes* (Chilopoda, Scolopendridae). – Journal of Morphology 206: 303-312.
- MESKE, C., 1960. Schallreaktionen von *Lithobius forficatus* L. (Chilopoden). – Zeitschrift für Vergleichende Physiologie 43: 526-530.
- MESKE, C., 1961. Untersuchungen zur Sinnesphysiologie von Diplopoden und Chilopoden. – Zeitschrift für Vergleichende Physiologie 45: 61-77.
- MEYER-ROCHOW, V. B., 1999. III Photoreceptors and photo-environments. III-2 Compound eye: circadian rhythmicity, illumination, and obscurity. – Pp. 97-124 in E. EGUCHI & Y. TOMINAGA (eds.). Atlas of arthropod sensory receptors. Dynamic morphology in relation to function. – Springer, Tokyo.
- MÜLLER, C. H. G., 2008. Vergleichend-ultrastrukturelle Untersuchungen an Augen ausgewählter Hundertfüßer (Mandibulata: Chilopoda) und zur Bedeutung von Augenmerkmalen für die phylogenetische Rekonstruktion der Euarthropoda. – Ph.D. thesis, University of Rostock, Cuvillier Verlag, Göttingen.
- MÜLLER, C. H. G. & V. B. MEYER-ROCHOW, 2006a. Fine structural organization of the lateral ocelli in two species of *Scolopendra* (Chilopoda: Pleurostigmophora): an evolutionary evaluation. – Zoomorphology 125: 13-26.
- MÜLLER, C. H. G. & V. B. MEYER-ROCHOW, 2006b. Fine structural description of the lateral ocelli of *Craterostigmus tasmanianus* Pocock, 1902 (Chilopoda: Craterostigmomorpha) and phylogenetic considerations. – Journal of Morphology 267: 850-865.
- MÜLLER, C. H. G. & J. ROSENBERG, 2006. Homology of lateral ocelli in the Pleurostigmophora? New evidence from the retinal fine structure in some lithobiomorph species (Chilopoda: Lithobiidae). – Norwegian Journal of Entomology 53: 265-286.
- MÜLLER, C. H. G., J. ROSENBERG & G. HILKEN, 2009. Fine structure and phylogenetic significance of 'flexo-canal epidermal glands' in Chilopoda. – Soil Organisms 81: 269-294.
- MÜLLER, C. H. G., J. ROSENBERG & V. B. MEYER-ROCHOW, 2003a. Hitherto undescribed interommatidial exocrine glands in Chilopoda. – African Invertebrates 44: 185-197.
- MÜLLER, C. H. G., J. ROSENBERG, S. RICHTER & V. B. MEYER-ROCHOW, 2003b. The compound eye of *Scutigera coleoptrata* (Linnaeus, 1758) (Chilopoda: Notostigmophora): an ultrastructural reinvestigation that adds support to the Mandibulata concept. – Zoomorphology 122: 191-209.

- MÜLLER, C. H. G., A. SOMBKE & J. ROSENBERG, 2007. The fine structure of the eyes of some bristly millipedes (Penicillata, Diplopoda): additional support for the homology of mandibulate ommatidia. – Arthropod Structure & Development 36: 463-476.
- ODSELIUS, R. & R. ELOFSSON, 1981. The basement membrane of the insect and crustacean compound eye: definition, fine structure, and comparative morphology. – Cell and Tissue Research 216: 205-214.
- OSBORNE, M. P., 1961. Studies on the sensory of insects and centipedes. – Ph.D. thesis, University of Birmingham.
- PAULUS, H. F., 1979. Eye structure and the monophyly of the Arthropoda. – Pp. 299-383 in A. P. GUPTA (ed.). Arthropod phylogeny. – Van Nostrand, New York.
- PAULUS, H. F., 2000. Phylogeny of the Myriapoda – Crustacea – Insecta: a new attempt using photoreceptor structure. – Journal of Zoological Systematics and Evolutionary Research 38: 189-208.
- PETYKÓ, Z., T. ZIMMERMANN, U. SMOLA & R. R. MELZER, 1996. Central projections of Tömösváry's organ in *Lithobius forficatus* (Chilopoda, Lithobiidae). – Cell and Tissue Research 283: 331-334.
- PLATEAU, F., 1886. Recherches sur la perception de la lumière par les Myriapodes aveugles. – Journal de l'Anatomie et Physiologie 22: 431-457.
- PLATEAU, F., 1887. Recherches expérimentales sur la vision chez les Arthropodes. – Bulletins de l'Académie des Sciences, des Lettres et des Beaux-Arts de Belgique (14) 3: 407-448.
- RICHTER, S., 2002. The Tetraconata concept: hexapod-crustacean relationships and the phylogeny of Crustacea. – Organisms Diversity & Evolution 2: 217-237.
- RILLING, G., 1960. Zur Anatomie des braunen Steinläufers *Lithobius forficatus* L. (Chilopoda). Skelettmuskelsystem, peripheres Nervensystem und Sinnesorgane des Rumpfes. – Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 78: 39-128.
- RILLING, G., 1968. *Lithobius forficatus*. Großes Zoologisches Praktikum 13b. – Gustav Fischer Verlag, Stuttgart.
- ROSENBERG, J. & A. ERNST, 2001. Sensilla coeloconica on the poison fang (maxilliped) of *Lithobius forficatus* (Chilopoda): Distribution, SEM and TEM investigations. – Zoology (Supplement IV) 104: 42.
- SCHARMER, J., 1935. Die Bedeutung der Rechts-Links-Struktur und die Orientierung bei *Lithobius forficatus* L. – Zoologische Jahrbücher, Abteilung für Physiologie der Tiere 54: 459-506.
- SERRA, A., 1981. Alguns caràcters adaptatius dels Lithobiomorpha (Chilopoda) al medi cavernicola. – SIS 8: 258-262.
- STRAUSFELD, N. J., 2005. The evolution of crustacean and insect optic lobes and the origin of chiasmata. – Arthropod Structure & Development 34: 235-256.
- TICHY, H., 1972. Das Tömösvárysche Sinnesorgan des Hundertfüßlers *Lithobius forficatus* L. – ein Hygrosezeptor. – Naturwissenschaften 59: 315.
- TICHY, H., 1973a. Untersuchungen über die Feinstruktur des Tömösváryschen Sinnesorgans von *Lithobius forficatus* L. (Chilopoda) und zur Frage seiner Funktion. – Zoologische Jahrbücher Abteilung für Anatomie und Ontogenie der Tiere 91: 93-139.
- TICHY, H., 1973b. Bau und Funktion des Tömösváryschen Sinnesorgans von *Lithobius forficatus* L. – Verhandlungen der Deutschen Zoologischen Gesellschaft 36: 55-56.

- TICHY, H. & F. G. BARTH, 1992. Fine structure of olfactory sensilla in myriapods and arachnids. – *Microscopy Research and Technique* 22: 372-391.
- VARMA, L., 1972. Muscle receptor organs in the centipede *Scolopendra morsitans* Linn. – *Zoologischer Anzeiger* 188: 400-407.
- VERHOEFF, K. W., 1902-1925. Fünfter Band. II. Abteilung Gliederfüßer: Arthropoda Klasse Chilopoda. – Pp. 1-725 in H. G. BRONN (ed). H. G. Bronn's Klassen und Ordnungen des Tierreiches. – Akademische Verlagsgesellschaft, Leipzig.
- VERHOEFF, K. W., 1904. Mittheilungen über die Gliedmassen der Gattung *Scutigera* (Chilopoda). *Sitzungsberichte der Gesellschaft der naturforschenden Freunde Berlin* 9: 198-236.
- VOGT, K.C. & E. YUNG, 1883. *Traité d'anatomie comparée pratique*. – Reinwald, Paris.
- YAMANA, K., D. NAOMI & Y. TOH, 1998. Ionic mechanisms of the carbon dioxide reception in the Japanese house centipede, *Thereuonema hilgendorfi*. – *Zoological Science* 15: 691-697.
- YAMANA, K. & Y. TOH, 1987. Intracellular recordings from receptor cells of the temporal organ of the Japanese house centipede, *Thereuonema hilgendorfi*: receptor potential and conductance changes. – *Journal of Experimental Biology* 131: 205-213.
- YAMANA, K. & Y. TOH, 1990. Structure of the temporal organ of the Japanese house centipede *Thereuonema hilgendorfi* Verhoeff. – *Journal of Morphology* 203: 311-319.
- YAMANA, K., Y. TOH & H. TATADA, 1986. Electrophysiological studies on the temporal organ of the Japanese house centipede, *Thereuonema hilgendorfi*. – *Journal of Experimental Biology* 126: 297-314.

## Chapter 13

# CHILOPODA – REPRODUCTION

Alessandro Minelli

### *Sexes and secondary sexual characters*

Centipedes are gonochoric, like the vast majority of arthropods. In mature animals, sexes are easily distinguished on external characters in all major centipede groups to the exception of the Scolopendromorpha, where the widespread absence of secondary sexual characters adds to the general absence of externally visible genital appendages (cf. Chapter 3).

Size differences between the sexes are often modest (with females being larger than the males, sometimes distinctly so, e.g. in *Strigamia*) but in most geophilomorph species, the Mecistocephalidae excepted, females have higher average and modal numbers of leg-bearing segments than the conspecific males.

In the Lithobiomorpha, specialized structures such as sulci or apical warts are very common in the posterior leg-pairs of the males, especially on the tibia of leg 15, sometimes also on leg 14. In *Pleurolithobius*, male tergite 16 is distinctive for its two long posterior ‘horns’. In the subgenus *Dacolithobius* of *Lithobius*, male tergite 14 is very elongated and bears a posterior fringe of setae. In *Pterygotergum*, male tergites 10, 12 (especially) and 14 are prolonged laterally into ‘wings’ resembling the distinctive pleurotergal lobes of many millipedes. Male *Lithobius* deprived of legs 15 may develop secondary sexual characters (grooves, warts) on leg 14 (Eason, 1993), a circumstance that caused regenerated specimens to be described as distinct species. Uniquely, in *Paitobius zinus* the male is provided with enormous forcipules (Crabill, 1960).

Specializations in the ultimate leg-pair of males are also present in some Scolopendromorpha, e.g., in *Alipes*, *Digitipes*, *Otostigmus* (*Parotostigmus*) and a few *Scolopendra* and *Cryptops* species; lesser specialization is found in the penultimate legs of some *Cryptops* species. Male sexual traits also include the modified tergites of the posterior segments in male *Otostigmus* (*Otostigmus*), eventually also a modified sternite 21; a long caudal process of tergite 21 in the male suggested the name of *O. (Dactylotergitus) caudatus*.

In the Geophilomorpha, males are nearly universally characterized by the thicker and often more setose condition of the ultimate leg pair. In many species of the

mecistocephalid genus *Tygarrup*, males, but not females, are provided with sternal pores (Crabill, 1968). In a few mecistocephalid and schendylid species the two sexes differ in the relative length and setation of the antennae and the length or diameter of some antennomeres (Pereira, 1999; Pereira et al., 2002; Bonato and Minelli, 2004).

#### *Gynandromorphism and intersexuality*

A gynandromorph *Lithobius forficatus* was described, with one male and one female gonopod (Matic, 1958), whereas a specimen of *Lithobius (Monotarsobius) austriacus* was found to have both the ultimate leg and the gonopod of the left side of female aspect, and the corresponding appendages of the right side of male aspect (Borek, 1969).

A small ovary was found by Descamps & Herbaut (1971) in a specimen of *L. forficatus* with male gonopods and an apparently normal male genital system.

#### *Chromosomes*

Chromosome size is very large in the Lithobiomorpha, less so in the Scutigeromorpha and Scolopendromorpha, and very small in the Geophilomorpha. The lowest diploid number ( $2n=14$ ) was found in *Mecistocephalus takakuwai* (Ogawa, 1961). The scanty cytogenetic literature on the group was summarized by White (1979). His table can be supplemented with the more recent data in Table 13.1.

Table 13.1. Diploid chromosome numbers of some centipede species.

Refs.: 1. Zanazzo et al., 1994; 2. Colmagro et al., 1987.

	male	female	Ref.
<i>Eupolybothrus fasciatus</i>	24	24	1
<i>Eupolybothrus grossipes</i>	27? 28?	28	1, 2
<i>Eupolybothrus nudicornis</i>	44		2
<i>Eupolybothrus tridentinus</i>	38	39?	2
<i>Lithobius dentatus</i>		46	2
<i>Lithobius forficatus</i>	44		2
<i>Lithobius pilicornis</i>		42	2
<i>Lithobius tricuspis</i>		50	2
<i>Lithobius validus</i>	54	54	2
<i>Scolopendra cingulata</i>	26	26	2
<i>Scutigera coleoptrata</i>	34	34	2

Multiple (male?) sex chromosomes were reported for the scolopendromorph *Otocryptops sexspinosis* (Ogawa, 1954). No other reliable record of sex chromosomes is available.

### *Parthenogenesis*

Males have been reported as absent in most populations of *Lamyctes emarginatus* (exceptions in the Azores, the Canary Islands and New Zealand) and *L. caeculus* (with males, however, abundant in Cuba) (Enghoff, 1975). Males are also lacking in the British, German and Scandinavian populations of *Lithobius macilentus*, but occur in the Netherlands (Eason, 1964; Albert, 1978, 1982). *Geophilus proximus* is most probably parthenogenetic in a large part of northern and eastern Europe (e.g., Zograff, 1882; Palmén, 1948; Bonato et al., 2005).

### *Sexual maturity*

Except for the temperate opportunist *Lamyctes emarginatus* (Albert, 1983; Andersson, 2006) and possibly for a few tropical scolopendromorphs (Lewis, 1970), all data suggest for centipedes a life expectancy of two or more years: e.g., at least three years in *Pachymerium ferrugineum* (Palmén and Rantala, 1954), five years in *Lithobius mutabilis* (Voigtländer, 2007), with maturity in the second year and even later. In the lab, the first eggs are laid by *L. erythrocephalus* at 12-16 months, by *L. mutabilis* at 1.5 year at the earliest (Voigtländer, 2007), by *Geophilus flavus* and *Stenotaenia linearis* at 21 months (Weil, 1958). Female *Scolopendra cingulata* only start laying when in their third year (Radl, 1992).

### *Gonads and gonoducts*

#### *Female organs*

Centipede females have a dorsal ovary, prolonged anteriorly as a long, thin terminal filament. In *L. forficatus* (Prunesco, 1965a; Rilling, 1968) this extends forwards up to trunk segment 6, in *S. cingulata* variably to segment 5-8. Posteriorly, the ovary continues into a short oviduct, which in most centipedes soon divides into a left and a right branch; these unite again ventrally to the gut to form the genital atrium into which open also one pair of seminal receptacles and (generally) two pairs of accessory glands. In the Scolopendromorpha, the oviduct splits into a left and a right genital duct, with separate

openings into the genital atrium. The left duct is longer and forms a genital arch around the gut. In *Ethmostigmus trigonopodus*, the right duct is actually absent (Prunesco 1965b), while in *Cryptops* it is the left branch that is apparently missing (Prunesco 1965c). Only one pair of accessory glands is usually found in the Scolopendromorpha (Prunescu, 1997).

Oocytes generally arise from the ventral wall of the ovary, in *Scutigera* however from two dorso-lateral ridges: this suggests that the single ovary derives from an originally paired gonad (Knoll, 1974).

Minor differences within each of the main groups of centipedes have been recorded, mainly involving in the Lithobiomorpha the shape of the seminal receptacles (e.g., sausage-like in *L. forficatus*, ovoid in *Eupolybothrus* spp.) and the degree of coiling of their ducts (Prunesco, 1965a).

#### *Male organs*

Centipede male organs are very diverse. Scutigeromorpha and Geophilomorpha (very unlikely is a similar record for the scolopendromorph *Cryptops trisulcatus*; Tuzet and Manier, 1953) have one pair of testes; only one large, dorsal testis is found in Lithobiomorpha; in Craterostigmomorpha and Scolopendromorpha, the male gonad resolves into a number of small testicular follicles, eventually connected to a single vas deferens. There are also two or more pairs of accessory glands, partly involved in the production of spermatophores.

There is no clear divide between paired and unpaired structures, however. The coiled vas efferens issuing from each of the two testes in Scutigeromorpha and Geophilomorpha unites with the vas efferens issuing from the other testis to form a single vas deferens. In *Scutigera coleoptrata* the vas deferens divides into three branches, of which the lateral ones go into the upper part of the ejaculatory canal, while the median one ends into the sinus issued from the fusion of the two seminal vesicles (Prunesco, 1969; Demange, 1988).

Elements of duplication are also found in *Lithobius forficatus*, where the single tubular testis derives embryonically from the fusion of paired rudiments (Biegel, 1922). Two gonad rudiments also form in the embryo of *Scolopendra*, and unite into a single sac that eventually resolves into numerous quasi-metameric units (Heymons, 1901).

The testis of *Lithobius forficatus* is so long as to need two loops and extends anteriorly as a terminal filament up to ca. tergite 6 or 7. Posteriorly, the mature testis narrows into a vas efferens, followed by the short vas deferens. Similar to the female oviduct, the latter splits into two branches, respectively passing left and right of the gut before uniting again ventrally. There are one dorsal and two ventral pairs of accessory glands, all of

them large in *Lithobius* (Rilling, 1968), whereas the dorsal ones are very small in *Harpolithobius* and in the Ethopolyinae. In other species, the testis is more or less coiled, from just once as in *Harpolithobius banaticus* up to six times as in *L. erythrocephalus* (Prunescu, 1963).

Further evidence of the secondary nature of the unpaired testis of Lithobiidae is provided by the diverse condition of the male gonad(s) in Henicopidae. Here, an additional, rudimentary gonad has been reported for *Anopsobius neozelanicus* (Prunescu & Johns, 1969) and *Dichelobius* sp. (Prunescu, 1970), whereas in *Lamyctes anderis* and *Cermatobius longitarsis* there is only one, unpaired testicular sac (Prunescu and Prunescu, 1999).

In the Scutigeromorpha, each testis is actually subdivided into an anterior macrotestis and a posterior microtestis (*Scutigera coleoptrata*: Bouin, 1934; *Thereuonema tuberculata*: Fahlander, 1938), producing sperm of corresponding larger and smaller size (see below). Similarly, the male gonad of henicopids is divided in a proximal microtestis and a distal microtestis, the former producing macrospermatocytes 2.5 µm in diameter, the latter macrospermatocytes with a diameter 10-20 times larger (Prunescu and Johns, 1969).

In the Scolopendromorpha, the number of follicles is variable: 7-13 pairs in the Scolopendrinae, 5-12 pairs in the Otostigminae, 4-26 pairs in the Cryptopidae, 11 pairs in *Plutonium*. The individual fusiform follicles are provided with a vas efferens at either end; the single vas deferens into which they unite differentiates posteriorly into a spermatophoral pouch (Demange and Richard, 1969; Prunescu, 1997). In the Scolopendridae, but not in the Cryptopidae, the posterior part of the vas deferens splits into two branches, like the female oviduct. There are two pairs of accessory glands; in *Scolopendra valida*, the dorsal, larger pair opens into the terminal segment of the vas deferens (ductus ejaculatorius), while the smaller ventral pair opens into the genital atrium (Demange and Richard, 1969); an opposite arrangement has been described in *S. cingulata* (Prunescu, 1997).

In the Geophilomorpha, the two spindle-like, dorsal testes extend in the posterior half of the trunk. At either end, each testis goes on into a very thin vas efferens (55-75 µm in *Stenotaenia linearis*; Breucker, 1970). The single vas deferens into which the v. efferentes eventually unite splits, like the female oviduct, into two branches which unite again ventrally to the gut to form an ejaculatory duct that receives also the ducts from two pairs of accessory glands.

The testis wall, well described histologically in *Lithobius*, consists of an internal layer of extremely interdigitating cells (Camatini and Franchi, 1975; Camatini and Castellani Ceresa, 1974) surrounded by a conspicuous layer of large collage fibers accompanied by

circular ring muscles, followed in turn by a layer of longitudinal muscles and finally by an outer epithelial sheath, supported by a thin basal membrane.

### *Gametogenesis and gametes*

#### *Oogenesis*

Oogenesis has been studied in *S. coleoptrata* (Knoll, 1974) and *L. forficatus* (Herbaut, 1972a, b, 1974, 1976).

Four phases can be distinguished: premeiosis, previtellogenesis, vitellogenesis and maturation. Oocytes are initially arrested in diplotene. At the start of previtellogenesis, a rapid increase in the number of ribosomes and mitochondria signals a strong increase of metabolic activity. Subsequently, yolk starts accumulating in the cytoplasm, while the number of ribosomes and mitochondria decreases. In *L. forficatus*, the growth of the oocytes starts during late epimorphic stages preceding the adult (Zerbib, 1966; Herbaut 1977). Older oocytes migrate from the extensively folded ventral wall of the ovary where they first differentiate towards the anterior part of the ovary.

During the maturation phase, the epithelium of the ovary secretes a chorion 10-15 µm thick (Herbaut, 1974). Egg cells are surrounded by follicular cells (Tönniges, 1902; Rilling, 1968; Herbaut, 1976). Maturation is triggered by the assumption of the spermatophore (Radl, 1993).

#### *Spermatogenesis*

In *L. forficatus*, spermatogonia and spermatocytes are already present in the third anamorphic instar (cf. Chapter 14) of post-embryonic development (Zerbib, 1966), but the spermatogenetic cycle is only completed in the maturus junior and maturus senior instars (Descamps, 1971a). Four phases can be recognized (Joly and Descamps, 1969), starting with the resting phase when the spermatogonia, 30 µm in diameter, are still laying in the testis wall and subsequently start growing to spermatocytes I, 100 µm in diameter, which fill the lumen of the testis. The spermatogenesis gives rise to tetrads of spermatids (Descamps, 1969). The following differentiation and release of mature sperm cells are followed by a recovery phase. Degenerating spermatocytes and spermatids are often seen being phagocytised by other spermatocytes (Descamps, 1971a, b).

#### *Gametes*

Eggs. – Centipede eggs are large and yolk. Those of *Scutigera coleoptrata* are slightly ovoid, 1.1 x 1.2-1.25 mm, covered by two membranes 7 µm each in thickness: the outer one is granular and provided with processes which likely favour adhesion of soil particles (Dohle, 1970), the inner one is transparent and homogeneous. In *Lithobius forficatus*, the egg is spherical, hardly 1 mm in diameter, but becomes much larger (ca. 1.5 mm in diameter) when covered by soil particles (Brocher, 1930). Eggs of *Scolopendra cingulata* measure 3.5 x 3.3 mm (Radl, 1992), those of *Strigamia maritima* ca. 1 mm (Chipman et al., 2004).

*Sperm cells.* – In the literature there are many descriptions of mature sperm cells of centipedes, including studies on Scutigeromorpha (Camatini et al., 1977; Mazzini et al., 1992), Lithobiomorpha (Descamps, 1972; Camatini et al., 1974; Reger et al., 1980), Craterostigmomorpha (Carcupino et al., 1996), Scolopendromorpha (Camatini and Franchi, 1979; Beniouri and Descamps, 1985; Jamieson, 1986; Mazzini et al., 1993), and Geophilomorpha (Horstmann, 1968; Cotelli et al., 1978) and also some comparative studies (Franchi et al., 1978; Saita et al., 1979; Mazzini et al., 1991a, b, 2000). However, the oldest descriptions mixed together elements pertaining to the two different kinds of sperm, the macrosperm and the microsperm, which are produced by most of the centipedes, to the exception, as far as known, of the Geophilomorpha. These two types of sperm are often produced in anatomically well-differentiated parts of the testis. This duality of centipede sperm is however known for more than a century, at least in Scutigeromorpha (Ancel and Bouin, 1908; Bouin, 1934; Ansley, 1954) and Scolopendromorpha (Bouin, 1903, 1925; Aron, 1920; Carcupino et al., 1999).

Centipede macrosperm are very large, e.g. 1.4 mm in *Scutigera* (Ansley, 1954), while microsperms are nearly ten times smaller. All centipede sperm cells are filiform, with a cylindrical acrosome. The nucleus is helically coiled. The connective piece linking the sperm head to the tail has different shape in the different groups. The tail axoneme, with typical 9+2 microtubule arrangement, terminates with a characteristic end piece or plume, also morphologically different in the different groups.

#### *Mating behaviour, spermatophores and sperm transfer*

Sperm is generally transferred to the female by means of spermatophores, the exception being the Geophilomorpha, where the males release instead an uncoated mass of sperm. It is likely that centipede females receive sperm only once in their life, or at

most once a year. Iorio and Ythier (2007) reported an *Ethmostigmus trigonopodus* female that, having mated only once, laid eggs twice, 144 days apart.

The spermatophores of the Scutigeromorpha are lemon-shaped, 4.5 x 2.3 mm in *Scutigera coleoptrata* (Klingel, 1960a), 7 x 3.5 mm in *Thereuopoda longicornis* (Klingel, 1962). Spermatophores are spherical in *Lithobius*, with a diameter of 1 mm in *L. piceus* (Demange, 1956), 2.5 mm in *L. forficatus* (the sperm drop inside is 0.6-0.8 mm) (Klingel, 1960b). Relatively small spermatophores, e.g. 1.5-2.5 mm in length in *Scolopendra* and *Cormocephalus*, with a shape like a wheat grain and a flattened side provided with a longitudinal sulcus, are produced by the Scolopendromorpha (Klingel, 1960a). Spermatophores are formed in the posterior part of the vas deferens (Scolopendromorpha: Brunhuber, 1970a; Craterostigmomorpha; Carcupino et al., 1996).

In *Scutigera coleoptrata* (Klingel, 1956, 1960a) and *Thereuopoda longicornis* (Klingel, 1962) the spermatophore is laid on the ground. In the Lithobiomorpha (Demange, 1956: *Lithobius piceus*; Klingel, 1960b: *L. forficatus*) and Scolopendromorpha (Klingel, 1957, 1960a: *Scolopendra cingulata*; Brunhuber, 1969: *Cormocephalus westwoodi anceps*) the spermatophore is deposited by the male onto a web and removed from there by the female. A web is also produced by male geophilomorphs as a substrate for the sperm drops.

In *L. forficatus* courtship begins with the male (more active than the partner) and the female touching each other with vibrating antennae, often taking contact with the partner's terminal appendages. This may last for hours. Then the male produces a web of ca. 120 strands, while the female continues tapping with her antennae the terminal legs of the male. A few minutes after the production of the spermatophore, the male continues spinning, now producing one to three slime strips behind the spermatophore. This work completed, the male turns back. The two partners are now facing head to head and reciprocally in touch with the tip of the antennae. After further stereotyped movements, the female collects the spermatophore with her gonopods and eventually ingests part of it, while the male will shortly eat the web. The whole behavioural sequence from the beginning of courtship to the ingestion of spermatophore or web remains may last more than four hours. (Klingel, 1960b).

In Scolopendromorpha, following an initial approach by which both partners display what seems to be a defence position, the male initiates courtship by tapping the posterior legs of the female with his antennae. This may last up to 14 hours in *Cormocephalus*. Then the male spins a web through a narrow space in the soil and deposits a spermatophore on the threads. In the meantime, the female either maintains contact with the partner (*S. cingulata*) or not (*C. westwoodi anceps*). Eventually, by moving through the narrow spaces through which the web has been spun, the female touches it with her posterior segments and seizes the spermatophore through her genital valves. The spermatophore breaks apart and a mass of sperm is poured into the genital atrium. What remains of the spermatophore is eventually eaten by the female.

Direct transfer of the spermatophore between the two partners whose genital openings are kept in contact for an adequate amount of time has been described for *Ethmostigmus rubripes spinosus* (Sundara Rajulu, 1970). This behaviour, so unusual in centipedes, awaits confirmation by new studies.

### *Egg laying and parental care*

A major divide splits the centipedes in two groups, in respect to the relationships between mother and offspring. Intriguingly, this distinction overlaps to a very large extent with the alternative between anamorphic and epimorphic post-embryonic development (cf. Chapter 14). Scutigeromorpha and Lithobiomorpha, that is, the centipedes with most obvious anamorphic development, lay their eggs individually, over a long time span, and do not take care of them after they have covered them individually with fine earth particles from the substrate where the female eventually abandons them. In *Scutigera coleoptrata*, the egg covered by soil particles is eventually dropped into a crevice (Dohle, 1970), but sometimes simply abandoned on the surface, or clustered into a 'nest' eventually containing 7-10 eggs (Knoll, 1974). In *Lithobius forficatus* (Brocher, 1930) the female keeps for a long while the egg between the genital valves, turning it continuously. In the meantime she uses the gonopods to obtain from the substrate fine-grained material which is eventually glued onto the egg's surface, likely by the help of a secretion. After one hour of this behaviour, the egg is wholly camouflaged, but the actual egg laying will occur only two or three hours later. In the meantime, the female remains inactive, still holding the egg. The soil capsule concealing the egg is approximately spherical in *L. forficatus*, but it is flattened like a poached egg in the case of *L. piceus* (Demange, 1956).

Opposite to the Scutigeromorpha and Lithobiomorpha, the epimorphic centipedes (Scolopendromorpha and Geophilomorpha) plus the Craterostigmomorpha, in which the anamorphic phase of the post-embryonic development is reduced to a very limited increase in segment number with the first moults, lay all their eggs in a single batch and the female remains coiled around her offspring until hatching, or even longer.

In *Craterostigmus*, eggs are laid in crevices or chambers in decaying logs, in 'egg capsules' over which the female remains coiled as in scolopendromorphs (Manton, 1965). In all scolopendromorph species of which brooding females have been observed, the mother rolls her body around the mass of eggs of juveniles presenting their ventral surface to them, but the opposite position is generally observed in the geophilomorphs. Here, the ventral surface of the brooding female is exposed to the outside. It has been suggested that this behaviour is related to the presence, in this clade, of sternal glands whose secretion is thus more quickly and effectively offered as a weapon against predators. This hypothesis is circumstantially supported by the fact that the meciostocephalid geophilomorph *Dicellophilus carniolensis* behaves in this respect like the Scolopendromorpha, in intriguing correlation with the likely plesiomorphic lack of

sternal glands in mecistocephalid females (Bonato et al., 2002), but this is not supported by the newly observed brooding behaviour of another mecistocephalid species, *Mecistocephalus togoensis* (Edgecombe et al., 2010), which behaves like the majority of geophilomorphs. Eggs are generally brooded by the female inside a brood cavity in the soil. Eggs and embryos are loosely glued together into a ball by a sticky secretion. Grooming activities have been observed (*Cormocephalus westwoodi anceps*, *Scolopocryptops sexspinous*; Auerbach, 1951). It has been repeatedly suggested that this may involve the use of a fungicide, but this has never been shown experimentally. Disturbing a brooding female causes her to abandon the eggs or even to eat them (Brunhuber, 1970b).

Egg laying and brooding takes place during the summer in scolopendromorphs and geophilomorphs of the temperate regions (Verhoeff, 1902-25; Palmén & Rantala, 1954; Weil, 1958; Vaitilingham, 1960; Lewis, 1961, 1962). The minimum brooding time so far recorded is 18 days (*Scolopendra heros*; Iorio, 2003).

Fecundity is not easily ascertained in the case of the anamorphous centipedes because their eggs are laid individually over a long time span. In the lab, *Scutigera coleoptrata* females lay as a rule four eggs (but up to 20) per day, with a highest recorded number of 151 over the whole season (Knoll, 1974). A maximum of 30-40 eggs per season has been recorded for *Lithobius mutabilis* (Albert, 1983; Voigtländer, 2007), but the fecundity of larger lithobiomorphs can be higher. In some *Lithobius* species from temperate regions, eggs are laid in several periods throughout the year (Voigtländer, 2000).

In the epimorphic centipedes, the yearly production of eggs is limited to one batch whose size is easily established. For the Scolopendromorpha, numbers recorded span from just 7 to 9 eggs in *Cryptops hyalinus* (Cornwell, 1934; Johnson, 1952) to 15-30 in *Otostigmus tibialis*, *O. scabricauda* and *Scolopocryptops ferrugineus* (Bücherl, 1971), 15-23 in *Scolopendra* spp. (Heymons 1901), up to 40 in *Cormocephalus multispinus* (Lawrence, 1947), 49-65 in *Scolopocryptops sexspinosis* (Auerbach, 1951) and up to 86 in *Scolopendra morsitans* (Lewis, 1970). Up to 47 eggs have been recorded in broods of *Geophilus flavus* (Weil, 1958); 44-77 in those of *Craterostigmus tasmanianus* (Mesibov, 1995).

#### References

- ALBERT, A. M., 1978. Bodenfallenfänge von Chilopoden in Wuppertaler Wältern (MB 4708/09). – Jahresberichte des naturwissenschaftlichen Vereins in Wuppertal 31: 41-45.
- ALBERT, A. M., 1982. Deviations from Dyar's rule in Lithobiidae. – Zoologischer Anzeiger 208: 192-207.
- ALBERT, A. M., 1983. Life cycle of Lithobiidae - with a discussion of the r-and K-selection theory. – Oecologia 56: 272-279.

- ANCEL, P. & P. BOUIN, 1908. Sur l'existence d'une double spermatogenèse chez *Scutigera coleoptrata* - Comptes rendus de la Société de Biologie 65: 287-289.
- ANDERSSON, G., 2006. Habitat preferences and seasonal distribution of developmental stadia in *Lamyctes emarginatus* (Newport, 1844) (*L. fulvicornis* Meinert, 1866) and comparisons with some *Lithobius* species (Chilopoda, Lithobiomorpha). - Norwegian Journal of Entomology 53: 33-320.
- ANSLEY, H. R., 1954. A cytological and cytophotometric study of alternative pathways of meiosis in the house centipede (*Scutigera forceps* Rafinesque). - Chromosoma (Berlin) 6: 656-659.
- ARON, M., 1920. Sur l'existence d'une double spermatogenèse chez le *Cryptops* (Myriapode). - Comptes rendus de la Société de Biologie 83: 241-242.
- AUERBACH, S. I., 1951. The centipedes of the Chicago area with special reference to their ecology. - Ecological Monographs 21: 97-124.
- BENIOURI, R. & M. DESCAMPS, 1985. Étude ultrastructurale du spermatozoïde de *Cryptops hortensis* Leach (Myriapode Chilopode). - Archives de Biologie 96: 195-207.
- BIEGEL, J. H., 1922. Beiträge zur Morphologie und Entwicklungsgeschichte des Herzens bei *Lithobius forficatus* L. - Revue suisse de Zoologie 29: 427-480.
- BONATO, L. & A. MINELLI, 2002. Parental care in *Dicellophilus carniolensis* (C. L. Koch, 1847): New behavioural evidence with implications for the higher phylogeny of centipedes (Chilopoda). - Zoologischer Anzeiger 241: 193-198.
- BONATO L. & A. MINELLI, 2004. The centipede genus *Mecistocephalus* Newport 1843 in the Indian Peninsula (Chilopoda Geophilomorpha Mecistocephalidae). - Tropical Zoology 17: 15-63.
- BONATO, L., A. MINELLI & V. SPUNGIS, 2005. Geophilomorph centipedes of Latvia (Chilopoda, Geophilomorpha). - Latvijas Entomologs 42: 5-15.
- BOREK, V., 1969. Nalez gynandromorpha *Monotarsobius austriacus* Verhoeff, 1937 (Chilopoda). - Acta Musei Reginaehradecensis A 10: 33-34.
- BOUIN, P., 1903. Sur l'existence d'une double spermatogenèse et de deux sortes de spermatozoïdes chez *Scolopendra morsitans*. - Archives de zoologie expérimentale et générale (4) 1: iii-vi.
- BOUIN, P., 1925. Les cinèses de maturation et la double spermatogenèse chez *Scolopendra cingulata* L. - Cellule 35: 371-423.
- BOUIN, F., 1934. Recherches sur l'évolution d'un chromosome spécial (hétérochromosome?) au cours de la double spermatogenèse chez *Scutigera coleoptrata* (Lin.). - Archives de zoologie expérimentale et générale 75: 595-613.
- BREUCKER, H., 1970. The structure of the male genital ducts of *Geophilus linearis* (Chilopoda). - Zeitschrift für Zellforschung und mikroskopische Anatomie 108: 225-242.
- BROCHER, F., 1930. Observations biologiques sur la ponte et les premiers stades du *Lithobius forficatus* L. - Revue suisse de Zoologie 37: 375-383.
- BRUNHUBER, B. S., 1969. The mode of sperm transfer in the scolopendromorph centipede: *Cormocephalus anceps anceps* Porath. - Zoological Journal of the Linnean Society 48: 409-420.
- BRUNHUBER, B. S., 1970a. The formation of the Scolopendromorph spermatophore. - Bulletin du Muséum national d'Histoire naturelle, Paris (2) 41 (1969), supplément 2: 24-28.
- BRUNHUBER, B. S., 1970b. Egg laying, maternal care and development of young in the scolopendromorph centipede, *Cormocephalus anceps anceps* Porath. - Zoological Journal of the Linnean Society 49: 225-234.
- BUCHERL, W., 1971. Venomous chilopods or centipeds. - Pp. 169-196 in W. BÜCHERL. & E. E. BUCKLEY (eds.) Venomous animals and their venoms. - Academic Press, New York-London.
- CAMATINI, M. & L. CASTELLANI CERESA, 1974. Atypical myofilament array of visceral muscle fibres of *Lithobius forficatus* L. testis. - Journal of Submicroscopic Cytology 6: 353-365.

- CAMATINI, M. & E. FRANCHI, 1975. Aspetti ultrastrutturali del testicolo in larve di *Lithobius forficatus* L. – Atti dell'Accademia nazionale dei Lincei, Rendiconti, Classe di Scienze fisiche, matematiche e naturali 58: 49-56.
- CAMATINI, M. & E. FRANCHI, 1979. Ultrastructural morphology of spermatozoa from *Scolopendra morsitans* (Myriapoda Chilopoda). – Journal of Submicroscopic Cytology II: 335-343.
- CAMATINI, M., E. FRANCHI, A. SAITA & L. BELLONE, 1977. Spermiogenesis in *Scutigera coleoptrata* (Myriapoda Chilopoda). – Journal of Submicroscopic Cytology 9: 373-387.
- CAMATINI, M., A. SAITA & F. COTELLI, 1974. Spermiogenesis of *Lithobius forficatus* (L.) at ultrastructural level. – Symposia of the Zoological Society of London 32: 231-235.
- CARCUPINO, M., A. BALDACCI, A. M. FAUSTO, G. SCAPIGLIATI & M. MAZZINI, 1999. Sperm dimorphism in Chilopoda: comparison of Scolopendromorpha and Geophilomorpha. – Invertebrate Reproduction and Development 35: 45-53.
- CARCUPINO, M., A. M. FAUSTO, M. L. BERNARDINO ORTEGA, M. ZAPPAROLI & M. MAZZINI, 1996. Spermatophore development and sperm ultrastructure in *Craterostigmus tasmanianus* (Chilopoda, Craterostigmomorpha). – Zoomorphology II6: 103-110.
- CHIPMAN, A. D., W. ARTHUR & M. AKAM, 2004b. Early development and segment formation in the centipede, *Strigamia maritima* (Geophilomorpha). – Evolution and Development 6: 78-89.
- COLMAGRO, R., A. MINELLI, G. PALUDETTI & M. B. RASOTTO, 1987. Chromosome studies in centipedes (Chilopoda: Lithobiomorpha). – Caryologia 39: 309-323.
- CORNWELL, W. S., 1934. Notes on egg-laying and nesting habitus of certain species of North Carolina myriapods and various phases of their life histories. – Journal of the Elisha Mitchell Scientific Society 42: 289-291.
- COTELLI, F., M. FERRAGUTI, M. & C. LORA LAMIA DONIN, 1978. Morphologie ultrastructurale du spermatozoïde de *Himantarium gabrielis* Linnaeus. – Abhandlungen und Verhandlungen des naturwissenschaftlichen Vereins in Hamburg, Neue Folge 21/22: 219-229.
- CRABILL, R. E., 1960. A remarkable form of sexual dimorphism in a centipede (Chilopoda: Lithobiomorpha: Lithobiidae). – Bulletin of the Brooklyn Entomological Society 55: 121-133.
- CRABILL, R. E. JR., 1968. A bizarre case of sexual dimorphism in a centipede, with consequent submergence of a genus (Chilopoda: Geophilomorpha: Mecistocephalidae). – Entomological News 79: 286-287.
- DEMANGE, J.-M., 1956. Contribution à l'étude de la biologie, en captivité, de *Lithobius piceus gracilitarsis* Brol. (Myriapode - Chilopode). – Bulletin du Muséum national d'histoire naturelle, Paris, (2) 28: 388-393.
- DEMANGE, J.-M., 1988. Arthropoda - Myriapoda. – Pp. 473-485 in K. G. ADIYODI & R. G. ADIYODI (eds.) Reproductive biology of invertebrates. Volume 3. Accessory sex glands. – Wiley, Chichester-New York.
- DEMANGE, J.-M. & J. RICHARD, 1969. Morphologie de l'appareil génital mâle des Scolopendromorphes et son importance en systématique (Myriapodes Chilopodes). – Bulletin du Muséum national d'histoire naturelle, Paris (2) 40: 968-983.
- DESCAMPS, M., 1969. Sur la présence de deux mitoses non réductionnelles après la phase de croissance spermatocytaire chez *Lithobius forficatus* L. (Myriapode Chilopode). – Comptes rendus hebdomadaires des Séances de l'Académie des Sciences D 268: 1942-1944.
- DESCAMPS, M., 1971a. Le cycle spermatogénétique chez *Lithobius forficatus*. I. Evolution et étude quantitative des populations cellulaires du testicule au cours du développement post-embryonnaire – Archives de zoologie expérimentale et générale II2: 199-209.
- DESCAMPS, M., 1971b. Le cycle spermatogénétique chez *Lithobius forficatus*. II. Influence de facteurs externes sur l'évolution du testicule et des vésicules séminales – Archives de zoologie expérimentale et générale II2: 731-746.

- DESCAMPS, M., 1972. Étude ultrastructurale du spermatozoïde de *Lithobius forficatus* L. (Myriapode Chilopode). – Zeitschrift für Zellforschung und mikroskopische Anatomie 126: 193-205.
- DESCAMPS, M. & C. HERBAUT, 1971. Sur un cas d'intersexualité chez *Lithobius forficatus* (Myriapoda Chilopoda). – Comptes rendus hebdomadaires des séances de l'Académie des sciences D 272: 1648-1651.
- DOHLE, W., 1970. Über Eiablage und Entwicklung von *Scutigera coleoptrata* (Chilopoda). – Bulletin du Muséum national d'Histoire naturelle, Paris (2) 41 (1969) supplément 2: 53-57.
- EASON, E. H., 1964. The centipedes of the British Isles. – Warne, London.
- EASON, E. H., 1993. Displacement of the male secondary sexual characters in *Lithobius calcaratus* C.L. Koch and other species of *Lithobius*. – Bulletin of the British Myriapod Group 9: 21-23.
- EDGEcombe, G. D., L. BONATO & G. GIRIBET, 2010. Brooding in *Mecistocephalus togensis* (Geophilomorpha: Placodesmata) and the evolution of parental care in centipedes (Chilopoda). – International Journal of Myriapodology 3.
- ENGHOFF, H., 1975. Notes on *Lamyctes coeculus* (Brölemann), a cosmopolitan, parthenogenetic centipede (Chilopoda: Henicopidae). – Entomologica Scandinavica 6: 45-46.
- FAHLANDER, K., 1938. Beiträge zur Anatomie und systematischen Einteilung der Chilopoda. – Zoologiska Bidrag från Uppsala 17: 1-148.
- FRANCHI, E., M. CAMATINI & F. COTELLI, 1978. Comparative analysis of mature spermatozoa in Chilopoda (Arthropoda Myriapoda). – Journal of Submicroscopic Cytology 10: 112-113.
- HERBAUT, C., 1972a. Etude cytochimique et ultrastructurale de l'ovogénèse chez *Lithobius forficatus* L. (Myriapode, Chilopode). Evolution des constituants cellulaires. – Wilhelm Roux' Archiv für Entwicklungsmechanik der Organismen 170: 115-134.
- HERBAUT, C., 1972b. Nature et origine des réserves vitellines dans l'ovocyte de *Lithobius forficatus* L. (Myriapode, Chilopode). – Zeitschrift für Zellforschung und mikroskopische Anatomie 130: 18-27.
- HERBAUT, C., 1974. Étude cytochimique et origine des enveloppes ovocytaires chez *Lithobius forficatus* (L.) (Myriapode, Chilopode). – Symposia of the Zoological Society of London 32: 237-247.
- HERBAUT, C., 1976. les processus de dégénérescence des cellules sexuelles au cours de l'ovogénèse chez *Lithobius forficatus* (L.) (Myriapode, Chilopode). – Archives d'anatomie microscopique et morphologie expérimentale 65: 175-182.
- HERBAUT, C. 1977. Évolution du cycle ovogénétique au cours du développement post-embryonnaire chez *Lithobius forficatus* (Myriapoda Chilopoda) – Archives de biologie 88: 67-78.
- HEYMONS, R., 1901. Die Entwicklungsgeschichte der Scolopender. – Bibliotheca zoologica 33: 1-244.
- HORSTMANN, E., 1968. Die Spermatozoen von *Geophilus linearis* Koch (Chilopoda). – Zeitschrift für Zellforschung und mikroskopische Anatomie 89: 410-429.
- IORIO, E., 2003. Notes sur la reproduction et l'éthologie de quelques scolopendres (Chilopoda, Scolopendromorpha, Scolopendridae). – Bulletin de Phylie 14: 3-8.
- IORIO, E. & E. YTHIER, 2007. Quelques observations concernant la reproduction d'*Ethmostigmus trigonopodus* (Leach, 1817) (Chilopoda, Scolopendromorpha, Scolopendridae, Otostigminae). – Bulletin d'Arthropoda 33: 3-12.
- JAMIESON, B. G. M., 1986. The spermatozoa of the Chilopoda (Uniramia): An ultrastructural review with data on dimorphism in *Ethmostigmus rubripes* and phylogenetic discussion. – Journal of Submicroscopic Cytology 18: 543-558.
- JOHNSON, B. M., 1952. The centipedes and millipedes of Michigan. – Dissertation, University of Michigan.

- JOLY, R. & M. DESCAMPS, 1969. Évolution du testicule, des vésicules séminales et de cycle spermatogénétique chez *Lithobius forficatus* L. (Myriapode Chilopode). - Archives de zoologie expérimentale et générale 110: 341-348.
- KLINGEL, H., 1956. Indirekte Spermatophorenübertragung bei Chilopoden (Hundertfüßer), beobachtet bei der "Spinnenassel" *Scutigera coleoptrata* Latzel. - Die Naturwissenschaften 43: 311-312.
- KLINGEL, H., 1957. Indirekte Spermatophorenübertragung beim Skolopender (*Scolopendra cingulata* Latreille; Chilopoda, Hundertfüßer). - Die Naturwissenschaften 44: 338-340.
- KLINGEL, H., 1960a. Vergleichende Verhaltensbiologie der Chilopoden *Scutigera coleoptrata* L. ("Spinnenassel") und *Scolopendra cingulata* Latreille (Skolopender). - Zeitschrift für Tierpsychologie 17: 11-30.
- KLINGEL, H., 1960b. Die Paarung des *Lithobius forficatus* L. - Verhandlungen der Deutschen Zoologischen Gesellschaft 1959: 326-332.
- KLINGEL, H., 1962. Das Paarungsverhalten des malaiischen Höhlentausendfußes *Thereuopoda decipiens cavernicola* Verhoeff (Scutigeromorpha, Chilopoda). - Zoologischer Anzeiger 169: 458-460.
- KNOLL, H. J., 1974. Untersuchungen zu Entwicklungsgeschichte von *Scutigera coleoptrata* L. (Chilop.) - Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 92: 47-132.
- LAWRENCE, R. F., 1947. Some observations on the post-embryonic development of the Natal forest centipede, *Cormocephalus multispinus* (Kraep.). - Annals of the Natal Museum II: 139-156.
- LEWIS, J. G. E., 1961. The life history and ecology of the littoral centipede *Strigamia* (-*Scolioplanes*) *maritima* (Leach). - Proceedings of the Zoological Society of London 137: 221-248.
- LEWIS, J. G. E., 1962. The ecology, distribution and taxonomy of the centipedes found on the shore in the Plymouth area. - Journal of the Marine Biological Association of the United Kingdom 42: 655-664.
- LEWIS, J. G. E., 1970. The biology of *Scolopendra amazonica* in Nigerian Guinea Savannah. - Bulletin du Muséum national d'Histoire naturelle, Paris (2) 41 (1969) supplément 2: 85-90.
- MANTON, S. M., 1965. The evolution of arthropodan locomotory mechanisms. Part 8. Functional requirements and body design in Chilopoda, together with a comparative account of their skeleto-muscular systems and an appendix on a comparison between burrowing forces of annelids and chilopods and its bearing upon the evolution of the arthropodan haemocoel. - Journal of the Linnean Society of London, Zoology 45: 251-484.
- MATIC, Z., 1958. Doua Lithobiidae noi pentru fauna R.P.R. si unele observatii interesante la *Lithobius forficatus*. - Studii si Cercetari de Biologie, Seria Zoologie 9: 81-89.
- MAZZINI, M., M. CARCUPINO & A. M. FAUSTO, 2000. Myriapoda. - Pp. 117-141 in B. G. M. JAMIESON (ed.) Progress in male gamete ultrastructure and phylogeny, volume 9C of K. G. ADIYODI & R. G. ADIYODI (eds.) Reproductive biology of invertebrates. - Wiley, Chichester.
- MAZZINI, M., M. CARCUPINO, A. M. FAUSTO, C. PURI & M. ZAPPAROLI, 1992. Further observations on the ultrastructure of mature sperm of *Scutigera coleoptrata* (L.) (Chilopoda, Scutigeromorpha). - Journal of Submicroscopic Cytology and Pathology 24: 251-256.
- MAZZINI, M., M. CARCUPINO, A. M. FAUSTO & M. ZAPPAROLI, 1991a. Comparative sperm structure in Chilopoda. - Pp. 990-995 in B. BACCETTI (ed.) Comparative spermatology 20 years after. - Raven Press, New York.
- MAZZINI, M., A. M. FAUSTO, C. PURI, M. ZAPPAROLI & M. CARCUPINO, 1991b. The terminal appendage (plume) of chilopodan sperm. - Acta embryologiae et morphologiae experimentalis 12: 117-119.
- MAZZINI, M., A. M. FAUSTO, C. PURI, M. ZAPPAROLI & M. CARCUPINO, 1993. End-piece formation during spermiogenesis of Scolopendromorpha (Chilopoda). - Journal of Submicroscopic Cytology and Pathology 25: 257-262.

- MESIBOV, R., 1995. Distribution and ecology of the centipede *Craterostigmus tasmanianus* Pocock, 1902 (Chilopoda: Craterostigmomorpha: Craterostigmidae) in Tasmania. — Tasmanian Naturalist 117: 2-7.
- OGAWA, K., 1954. Chromosome studies in the Myriapoda. VII. A chain association of the multiple sex-chromosomes found in *Otocryptops sexspinosis* (Say). — Cytologia 14: 265-272.
- OGAWA, K., 1961. Chromosome studies in the Myriapoda. XVI. The chromosome of five species of chilopods. — Zoological Magazine, Tokyo 70: 203-206.
- PALMÉN, E., 1948. The Chilopoda of eastern Fennoscandia. — Annales zoologici Societatis zoologico-botanicae fenniae Vanamo 13: 1-44.
- PALMÉN, E. & M. RANTALA, 1954. On the life-history and ecology of *Pachymerium ferrugineum* (C. L. Koch) (Chilopoda, Geophilidae). — Annales zoologici Societatis zoologico-botanicae fenniae Vanamo 16: 1-44.
- PEREIRA L. A., 1999. Un nouveau cas de dimorphisme sexuel chez les Schendylidae; *Schendyllops virgincordae* (Crabill, 1960), espèce halophile nouvelle pour la Martinique (Myriapoda, Chilopoda, Geophilomorpha). — Zoosystema 21: 525-533
- PEREIRA L. A., D. FODDAI & A. MINELLI, 1999. A new Brazilian schendylid centipede (Chilopoda: Geophilomorpha) with unusually structured antennae. — Zoologischer Anzeiger 241: 57-65.
- PRUNESCO, C.-C., 1963. [Anatomical observations of male reproductive system order Lithobiomorpha (Chilopoda, Tracheata)]. — Revue roumaine de biologie 8: 357-366 [in Russian].
- PRUNESCO, C.-C., 1965a. Contribution à l'étude anatomique et anatomo-microscopique du système génital femelle de l'ordre Lithobiomorpha. — Revue roumaine de biologie, série de zoologie 10: 11-16.
- PRUNESCO, C.-C., 1965b. Le système génital femelle d'*Ethmostigmus trigonopodus* (Otostigmidae, Chilopoda). — Revue roumaine de biologie, série de zoologie 10: 407-411.
- PRUNESCO, C.-C., 1965c. Système génital femelle du genre *Cryptops* (Scolopendromorpha, Chilopoda). — Revue roumaine de biologie, série de zoologie 10: 231-235.
- PRUNESCO, C.-C., 1969. The male genital system in *Scutigera coleoptrata* (Notostigmophora Chilopoda). — Revue roumaine de biologie, série de zoologie 14: 185-190.
- PRUNESCO, C.-C., 1970. Considérations sur l'évolution du système génital des Chilopodes. — Bulletin du Muséum national d'Histoire naturelle, Paris (2) 41 (1969) supplément 2: 108-111.
- PRUNESCU, C.-C., 1997. The anatomy and evolution of the genital system in Scolopendromorpha (Chilopoda). — Entomologica scandinavica, supplement 51: 41-48.
- PRUNESCU, C.-C. & P. M. JOHNS, 1969. An embryonic gonad in adult males of *Anopsobius neozelandicus* Silvestri (Chilopoda). — Revue roumaine de biologie, série de zoologie 14: 407-409.
- PRUNESCU, C.-C. & P. PRUNESCU, 1999. The genital system in *Lamyctes anderis* (Hemicopidae, Lithobiomorpha, Chilopoda). — Revue roumaine de biologie, série de biologie animale 44: 35-39.
- RADL, R. C., 1992. Brood care in *Scolopendra cingulata* Latreille (Chilopoda: Scolopendromorpha). — Berichte des naturwissenschaftlich-medizinischen Vereins in Innsbruck, Supplement 10: 123-127.
- RADL, R. C., 1993. Über Lebenszyklus, Fortpflanzung und Brutpflege des Hundertfüßlers *Scolopendra cingulata* (Chilopoda, Scolopendromorpha). — Dissertation, Universität Würzburg.
- REGER, J. F., M. E. C. FITZGERALD & M. CAMATINI, 1980. A correlated thin-section freeze-fracture study on plasmalemmal and mitochondrial membrane specializations in the principal piece of spermatozoa from the chilopodan *Lithobius forficatus* L. — Journal of Ultrastructure Research 73: 157-168.

- RILLING, G., 1968. *Lithobius forficatus*. – Großes zoologisches Praktikum 13. – Fischer, Stuttgart.
- SAITA, A., M. CANONACO, M. E. FRANCHI & S. TRIPEPI, 1979. The formation of membranous or mitochondrial derivates in the sperm tail of the chilopods. – Pp. 105-111 in M. CAMATINI (ed.) Myriapod biology. – Academic Press, London.
- SUNDARA RAJULU, G. 1970. A study on the nature and formation of the spermatophore in a centipede *Ethmostigmus spinosus* (Scolopendromorpha: Myriapoda). – Bulletin du Muséum national d'histoire naturelle, Paris 41 (1969), supplément 2: 116-121.
- TÖNNIGES, C., 1902. Beiträge zur Spermatogenese und Oogenese bei den Myriopoden. – Zeitschrift für wissenschaftliche Zoologie 71: 328-358.
- TUZET, O. & J. F. MANIER, 1953. Les spermatozoïdes de quelques Myriapodes Chilopodes et leur transformation dans le réceptacle seminal de la femelle. – Annales des sciences naturelles, zoologie (11) 15: 221-230.
- VAITILINGHAM, S., 1960. The ecology of the centipedes of some Hampshire woodlands. – Ph.D. thesis, University of Southampton.
- VERHOEFF, K. W., 1902-1925. Chilopoda. Pp. 1-725 in H. G. BRONN (ed.) Klassen und Ordnungen des Tierreichs, 5, Abteilung 2, Buch 1. – C. F. Winter'sche Verlagshandlung, Leipzig.
- VOIGTLÄNDER, K. 2000. Vergleichende Untersuchungen zur Postembryonalentwicklung von *Lithobius*-Arten (Chilopoda, Lithobiidae). Mitteilungen der Deutschen Gesellschaft für allgemeine und angewandte Entomologie 12: 535-540.
- VOIGTLÄNDER, K., 2007. The life cycle of *Lithobius mutabilis* L. Koch, 1862 (Myriapoda: Chilopoda). – Bonner zoologische Beiträge 55 (2006): 9-25.
- WEIL, E., 1958. Zur Biologie der einheimischen Geophiliden. – Zeitschrift für angewandte Entomologie 42: 173-209.
- WHITE, M. J. D., 1979. The present status of myriapod cytogenetics. – Pp. 3-8 in M. CAMATINI (ed.) – Myriapod biology. Academic Press, London.
- ZANAZZO, G., M. G. FILIPPUCCI, A. BOATO & A. MINELLI, 1994. Allozymic and karyological evidence concerning Italian populations of the *Eupolybothrus fasciatus*-group (Chilopoda, Lithobiomorpha). – Zoologischer Anzeiger 232: 77-95.
- ZERBIB, C., 1966. Étude descriptive et expérimentale de la différentiation de l'appareil génital du myriapode chilopode *Lithobius forficatus* L. – Bulletin de la Société zoologique de France 91: 203-216.
- ZOGRAFF, N. J., 1882. Zur Embryologie der Chilopoden. – Zoologischer Anzeiger 5: 582-585.

## Chapter 14

# CHILOPODA – DEVELOPMENT

Alessandro Minelli  
with a section by Andy Sombke

### *Embryonic development*

The earliest studies on centipede embryonic development mentioned in Chapter 2 are still useful, but contain some heavy errors of interpretation. Most seriously, in his detailed and widely cited monograph on the embryonic development of *Scolopendra* spp., Heymons (1901) described the fore end of the germ band as the rear one, as demonstrated by Sakuma and Machida (2002, 2004) and confirmed by Chipman et al. (2004b).

Before the advent of developmental genetics, centipede embryology had been the object of more recent studies by Dohle (1970) and Knoll (1974) on *Scutigera coleoptrata*, by Hertzel (1983, 1984) on *Lithobius forficatus* and by Whitington et al. (1991) on *Ethmostigmus rubripes*. However, the present short account will be mainly based on the current work where descriptive embryology is integrated with the study of the expression patterns of ‘developmental genes’.

### *Developmental genes*

Data on gene expression during embryonic development are essentially limited to three centipedes: *Lithobius atkinsoni* (Hughes and Kaufman, 2002a, b, c), *L. forficatus* (Kadner and Stollewerk, 2004) and *Strigamia maritima* (Kettle et al., 2003; Chipman et al., 2004a, b; Brena et al., 2006; Chipman and Stollewerk, 2006; Chipman and Akam, 2008).

In *L. atkinsoni*, expression patterns have been examined for three segmentation genes (*even-skipped*, *engrailed* and *wingless*) (Hughes and Kaufman, 2002a) and for all the 10 *Hox* genes (*labial*, *proboscipedia*, *Hox3*, *Deformed*, *Sex combs reduced*, *fushi tarazu*, *Antennapedia*, *Ultrabithorax*, *abdominal A* and *Abdominal B*) whose presence was expected in these arthropods (Hughes and Kaufman, 2002b).

As for *S. maritima*, expression data are available for *hunchback*, *Krüppel*, *Delta*, *Notch*, *even-skipped*, *hairy*, *enhancer of split* (Chipman and Stollewerk, 2006; Chipman and Akam, 2008), for *caudal* and an *odd-skipped-related* gene (Chipman et al., 2004a), for the segment polarity genes *engrailed* (Kettle et al., 2003; Chipman et al., 2004b) and for the *Hox* genes (Brena et al., 2006).

Earlier work on the homologues of these genes in a diversity of centipedes (Grenier et al., 1997; Bastianello and Minelli, 2001; Cook et al., 2001; Bastianello et al., 2002) revealed independent

duplications of *engrailed* in *Lithobius forficatus* and *Geophilus carpophagus* and the presence of two *Deformed* homologues in *Pachymerium ferrugineum*.

#### Cleavage to germ-band segmentation

Chipman et al. (2004b) characterized the embryonic development of *S. maritima* as an extreme case of short germ-band development, because nearly all body segments are formed sequentially. The same authors also acknowledged, however, that at the blastoderm stage the embryo already contains cells that will later contribute to all of the body segments, a circumstance that does not pertain to most short-germ insects.

As in the other centipedes, in *S. maritima* the cleavage of the yolk egg results in the formation of yolk pyramids leaving a central uncleaved volume. A blastoderm is eventually formed, containing perhaps 20 000–35 000 nuclei. Chipman et al. (2004b) were unable to ascertain whether the blastoderm is cellular or syncytial at this stage. Many blastoderm nuclei eventually accumulate on a restricted area of the egg surface, forming a blastodisc, the presumptive rudiment of the embryo, which covers about one half of the total surface.

Segmentation of the germ band is first manifested in the periodic expression of segmentation genes.

A periodic pattern of expression of *caudal* and an *odd-skipped-related* gene starts at the margin of the blastodisc, preceding overt segmentation. The latter gene is expressed in concentric cell rings around the proctodeum. *caudal* is expressed continuously throughout the blastodisc, but this expression breaks down into rings anteriorly, towards the zone where overt segmentation is becoming observable. Both of these genes are expressed initially in double-segment periodicity.

The one-segment periodicity is eventually established by the expression of *engrailed*, which forms one stripe for every primary *caudal* stripe; more or less at the same time, secondary stripes of *caudal* expression intercalate within the primary *caudal* stripes. The subsequent expression of *engrailed* overlaps the primary and secondary *caudal* strips, eventually establishing the final segmental periodicity of the germ band.

Still in *S. maritima*, the pair-rule gene *even-skipped* is represented by two duplication products, *evel* and *eve2*, both of them expressed in concentric rings like those of an *odd-skipped-related* 1 and *Delta*, in double-segment periodicity.

In *S. maritima*, the first stripe of *engrailed* expression appears close to the margin of the blastodisc and defines the presumptive anterior pole of the latter, eventually marking one of the gnathal segments, possibly the mandibular one. Anterior to this stripe, two patches of *engrailed* expression will soon mark the position of the antennal segment.

Further transversal stripes will be added progressively posterior to the first one (Kettle et al., 2003; Chipman et al., 2004b). The eventual addition of an *engrailed* stripe to mark an intercalary segment between the antennal and the mandibular ones is uncertain.

In pace with the formation of new stripes of *engrailed* expression goes the elongation of the germ-band in the form of an increasingly elongated stripe projecting out of the blastodisc, whose area shrinks more and more. The proctodeal and stomodeal invaginations are visible at the time the sixth and the fifteenth to twentieth stripes, respectively, of *engrailed* have been expressed.

As soon as all segments have been formed, the two halves of the germ-band split apart like an opening zipper, beginning with the midlength of trunk and extending towards either body end. At the same time, the germ-band sinks progressively into the yolk (blastokinesis). The lateral margins of the germ band, corresponding to the left and right halves of the future dorsal side of the centipede, extend over the yolk mass and eventually meet along the dorsal midline. At this stage, because of the folded position of the germ band, the embryo's head comes close to touch its opposite end.

#### *Hox gene expression*

The expression patterns of *Hox* genes in *Lithobius atkinsoni* are intermediate between those of chelicerates and those of pancrustaceans. *Hox3* seems to have a typical *Hox*-like role, rather than the different functions of its homologues *zen* and *bicoid* in the Pancrustacea. In *L. atkinsoni*, *fushi tarazu* has a double function, as a *Hox*-like gene as in arachnids, and as a segmentation gene, as in insects. *Hox* gene expression patterns correlate with the boundaries between tagmata, as the domains of expression of *labial*, *proboscipedia*, *Hox3* and *Deformed* span over the head, those of the remaining *Hox* genes span over the trunk. In particular, *Scr*, *ftz* and *Antp* are expressed in the forcipular segment (Hughes and Kaufman, 2002b).

In *Strigamia maritima*, persistent expression of *Antennapedia* characterizes the forcipular segment; all leg-bearing segments express three *Hox* genes, i.e. *Antennapedia*, *Ultrabithorax* and *Abdominal-A*; the expression of *Abdominal-B* is restricted to a posterior area around the proctodaeum (Brena et al., 2006).

#### *Neurogenesis and axonogenesis* by Andy Sombke

The development of the chilopod nervous system has been the subject of recent investigations whose results have been intensively discussed in a phylogenetic perspective (e.g., Whitington, 2006). In the scolopendromorph *Ethmostigmus rubripes* (Whitington, 1991; Whitington et al., 1995), the onset of neurogenesis is marked by a thickening of the ventral ectoderm associated with

proliferative divisions of the surface ectodermal cells. The inner layer of ectodermal cells may retain cytoplasmatic connections with the surface (Tiegs, 1940). The second major event in neurogenesis is the migration of nuclei from a superficial to a basal position in certain ventral ectodermal cells. These cells retain a connection to the surface by a thin cellular process. The surface of the ectoderm flattens at the site of convergence of the cell processes. This nuclear migration has been regularly found in the Chilopoda (Heymons, 1901; Knoll, 1974; Hertzel, 1984; Whitington et al., 1991; Kadner and Stollewerk, 2004) and also reported in all other myriapod groups. It is therefore highly likely to represent a basal character for the Myriapoda. After internal nuclear migration, the neuroectoderm thickens rapidly, and the anlagen of the segmental ganglia begin to take shape. A distinctive morphogenetic event takes place in the ganglion rudiment: the surface of the anlagen invaginates to form a vesicle, which becomes trapped inside the ganglion (Heymons, 1901; Whitington et al., 1991). Heymons (1901) claimed that these invagination sites are the seat of productions of neurons in *Scolopendra*. In *Ethmostigmus* (Whitington et al., 1991), nuclei labeled with bromodeoxyuridine are often found on the outer edge of clusters of cells that radiate out from the invagination site in the ganglion. However, the fact that invagination takes places well after the clusters have begun to form indicates that it is probably incidental to neural generation.

The first axons appear on the dorsal surface of the ganglion anlagen following internal nuclear migration and the onset of mitotic activity within the thickened neuroectoderm. Axonogenesis takes place in a rostrocaudal sequence, beginning in head neuromeres, then progressing to more posterior segments. In *Ethmostigmus*, a wide bundle of caudally directed axons (primary tract) descends from the brain to posterior segments well before axon growth begins in any of the trunk neuromeres. This tract becomes progressively wider as development ensues. Heymon's (1901) description of axon growth in *Scolopendra* suggests that a primary tract also forms in this embryo. In *Ethmostigmus*, at early stages, many neurons in the central nervous system can be individually identified, allowing a comparison with the detailed descriptions of axon growth from identified neurons in embryos of hexapods and malacostracan crustaceans. The pattern of axon growth in the centipede appears to be substantially different to that seen in insects and malacostracan crustaceans.

### *Teratology*

Teratological specimens of Chilopoda are not rare in nature. A range of defects have been documented, including bifurcation of the main body axis and a diversity of serious disturbances of trunk segmentation, and bi- and trifurcations of the appendages. An overview of centipede teratology was offered by Minelli and Pasqual (1986). Unique is the frequency of specimens with developmental defects in the geophilomorph *Haplophilus subterraneus* (Leśniewska, 2004; Leśniewska et al., 2009a). From a Polish population of this species are known the only adult specimens of Chilopoda ever recorded with an even number of leg pairs (Leśniewska et al., 2009b).

### *Moult*

Details of the moulting process are best known for some *Lithobius* species (e.g., Deman-

ge, 1944; Dunger, 1993). In the anamorphic instars of these centipedes, apolysis is first visible at the level of the posterior growth zone, along the intersegmental membranes and in the appendages. Mitoses of epidermal cells are rare outside the proliferation zone. The old cuticle is last released at the points where musculature is attached, therefore the centipede is still capable of movement when the moulting process has already begun. Contraction of the dorsoventral musculature of the head triggers the ecdysis. The frontal suture is broken, followed by the lateral head sutures. The cuticular lining of the foregut is released together with the cuticle of the forehead and the antennae. The second anamorphic instar of *Lithobius* spends up to 60 hours in the moulting process, that is, ca. 80% of the whole duration of that instar. Ecdysis takes 15 minutes in the youngest juveniles, but up to 30-40 minutes in the adult. In adult *L. forficatus*, it takes two days for the new cuticle to become hard and fully pigmented.

Moults are preceded by a non-feeding period, 2-4 days in *Lithobius*, 10-11 days in *Ethmostigmus*. In *Lithobius*, the two earliest post-embryonic instars do not feed, but still rely on residual yolk, but the following instars do not moult if not fed.

### *Postembryonic development*

Two different models of post-embryonic development oppose the Scutigeromorpha, Lithobiomorpha and Craterostigmomorpha to the Scolopendromorpha and Geophilomorpha. The former are anamorphic, that is, leaving the egg with a still incomplete number of articulated trunk segments and appendages, whereas the latter are epimorphic, that is, they acquire all their segments, and all their legs, before hatching.

Contrary to the evolutionary trend in insects, where the early post-embryonic instars (the larvae) of the holometabolans are thought to correspond to late embryonic instars of their developmentally plesiomorphous relatives, in a large clade of centipedes the main evolutionary transition has brought to the embryonalization of originally post-embryonic stages. Indeed, plotting developmental schedules onto centipede phylogeny reveals epimorphosis as the derived state, anamorphosis as the primitive.

Irrespective of phylogeny, the contrast between the two development schedules is so conspicuous that Haase (1880) used it as a main foundation for his proposal to divide the Chilopoda into the subtaxa Anamorpha (Scutigeromorpha and Lithobiomorpha; the Craterostigmomorpha, where a less obvious amount of anamorphosis is also present, were unknown at the time) and Epimorpha (Scolopendromorpha and Geophilomorpha).

The use of the term larva for the anamorphic stages of the hemianamorphic centipedes is very widespread, but ill-advised (Pflugfelder, 1932) as these stages are just incomplete as to the development of posterior segments and their appendages, but otherwise have no distinct characters and live under the same environmental conditions as the adult. Following Voigtländer (2007, on a suggestion by W. Dohle) we can use, for the whole sequence of post-embryonic instars, a single series of Roman numerals, to which an Arabic number in parenthesis is added for the post-anamorphic stages. Thus, for example, I, II, III, IV, V, VI(1), VII(2) etc.

During the post-embryonic development, the number of antennal articles increases conspicuously in the Lithobiomorpha, but only to a very limited extent in the Scolopendromorpha and not at all in the Geophilomorpha. Lewis (1968) recorded in *Scolopendra amazonica* a slight increase from the 17 antenomeres of early adolescens stadia up to 19 (occasionally 20), by subdivision of subterminal antenomeres.

The sequence of splitting of the antenomeres along the earliest post-embryonic instars of *L. forficatus* has been established by Scheffel (1969). Lewis (2000) suggested a common morphogenetic programme for the antenna of pleurostomophoran centipedes, considering that the antenna of *Lithobius* passes through conditions which seem to be equivalent to mature antennae of geophilomorphs and scolopendromorphs, respectively. In *L. forficatus*, indeed, that antenna of the newly hatched L0 larva has 7 antenomeres, which become 11 in the next instar, then 14 (cf. geophilomorphs), 17 and so on up to the final, usually higher, number. Articles 2, 4 and 6 of the primary set of seven articles are responsible for the origination of most of the secondary antenomeres eventually form, whereas the most distal of them never divides.

### *Hemianamorphosis*

During the anamorphic phase of the development, mitotic activity is essentially continuous, irrespective of the phase of the moulting cycles. Different serial structures proceed at different pace with growth and differentiation. In particular, posterior neuromeres differentiate in advance with respect to the corresponding tergites and sternites (Minelli et al., 2006).

Centipede anamorphosis is, in fact, a hemianamorphosis, in that the post-embryonic increase in trunk segment number is completed within a few moults, following which the animal continues moulting but does not add segments anymore. In all hemianamorphic centipedes, the final number of leg pairs is 15, but this target is obtained following different schedules. In *Scutigera coleoptrata*, the six post-embryonic anamorphic stages are characterized by the presence of 4, 5, 7, 9, 11 and 13 pairs of legs, respectively (Verhoeff, 1905b).

In *S. coleoptrata*, sexual maturity is obtained at the sixth epimorphic stage; the previous stages (sometimes called the agenitalis I, agenitalis II, immaturus, prematurus and pseudomaturus, respectively) are recognizable by the increasingly larger body size and higher number of antennal flagellomeres, and by the progressive development of the gonopods.

In *Lithobius forficatus*, the five anamorphic stages are characterized instead by 7, 7 (or 8), 8, 10 and 12 pairs of legs. The first post-embryonic instar has 8 pairs of legs in *Cermatobius longitarsis* (Murakami, 1961).

Detailed descriptions of the sequence of post-embryonic stages in several European and Japanese lithobiomorphs are available (e.g. Murakami, 1958, 1960a, b; Eason, 1964; Andersson, 1976, 1978a, b, 1980, 1981, 1982a, b, 1983, 1984a, b; Fründ, 1983; Voigtländer, 2000, 2007).

The number of epimorphic stages is different in the different species and apparently variable within the species, at least when this number is high, as in *L. mutabilis* (9 to 15). Eight to nine epimorphic stages have been also recorded in *L. forficatus*, eight in *L. erythrocephalus*, *L. melanops*, *L. tenebrosus*, seven in *L. curtipes*, *L. crassipes*, *L. microps*, six in *L. variegatus*, five in *Lamyctes emarginatus*, three in *Henicops* sp., two in *L. (Sigibius) burzenlandicus*.

The first five of the nine epimorphic instars identified by Andersson (1978a) in *L. forficatus* correspond, respectively, to the agenitalis I, agenitalis II, immaturus, prematurus, and pseudomaturus primus of Verhoeff (1902-25, 1905a) and Joly (1966), whereas the sixth and the seventh are both apparently equivalent to the pseudomaturus secundus of these authors. Maturity is finally obtained with the eighth instar (maturus junior) which eventually moults once more to matus senior. In *Craterostigmus*, 12 pairs of legs are already present at hatching and the final number is obtained after the first moult.

In *Lithobius* species, the hemianamorphic development is accompanied by deviation from Dyar's rule, that is, body length does not increase through the series of moults as a regular geometric progression (Albert, 1982). Instead, the growth rate is lower during the earliest post-embryonic and the immature epimorphic stages, higher during most of the anamorphic phase and again in the adults (Albert, 1982).

### *Epimorphosis*

A slight increase in segment number during early embryonic life has been claimed for some geophilid species (Johnson, 1952; Misioch, 1978) but until present this has not been demonstrated on convincing evidence (Minelli, 1985; Horneland and Meidell, 1986).

In hatching geophilomorphs the chorion splits into two halves. The centipede is still embryoid, its anterior part being still filled with yolk, the antennae still are not recognizably segmented and all other head and trunk appendages are still represented by

buds. An egg tooth is borne on the future second maxilla (Metschnikoff, 1875; Verhoeff, 1902-25; Weil, 1958).

A moult of the last embryonic cuticle gives rise to the peripatoid stadium. At this stage, the antennae are vaguely segmented, but spiracles, tracheae and setae are still lacking and the margins of tergites and pleurites are still indistinct; sternal glands and coxal pores are lacking.

In the following foetus stadium all head and trunk segment are distinctly segmented, the antennae are provided with sparse setae and the legs bear their claws. Tergites, pleurites and coxal sclerites are distinct. There is evidence of a differentiating although still not functional spiracular and tracheal system; the ventral glands are still without pores, and the coxal organs still devoid of external outlet. The foetus eventually moults to adolescens I, which is the last instar to which the mother offers brooding care. In the adolescens I, all appendages are functional, spiracles and sternal pores are open, as are the pores of the coxal organs. The animal still remains with the mother, relying on residual yolk. Independent life and active feeding will only start with the third instar. This instar and the following ones preceding maturity are called the adolescens stages. Their number is probably different in different species, but reliable evidence is limited.

From specimens reared in the lab, Weil (1958) recognized five adolescens instars in *Geophilus flavus* and *Stenotaenia linearis*, followed by three mature instars, whereas Lewis (1961), based on field collections, identified three adolescens instars and three to four mature instars in *Strigamia maritima*. Three adolescens instars were also recorded by Verhoeff (1902-25) in *Dicellophilus carniolensis*.

Most efforts aiming at identifying adolescens instars based on the degree of differentiation of the genital region, or the number of coxal pores or the whorls of setae on the antennal articles (e.g., Verhoeff, 1902-25), have at most value for individual species. For example, the number of sensilla on antennal articles 5, 9 and 13 appears to discriminate instars in *Hydroschendyla submarina* (Demange, 1943), but is invariant with age in *Strigamia maritima* (Lewis, 1961). A different approach has been suggested by Manton (1965) and applied by Minelli (1985), based on the regular increase with each moult of the number of cuticular rings lining the median 'atrium' where left and right tracheal stems anastomose. On this evidence, Minelli (1985) demonstrated the occurrence of three adolescens instars in *Schendyla nemorensis*, *D. carniolensis* and *Henia bicarinata*, four in *Strigamia crassipes* and *Geophilus carpophagus*, six in *Stigmatogaster gracilis*, followed by two (*S. gracilis*, *S. nemorensis*), three (*S. crassipes*) or four (*D. carniolensis*, *H. bicarinata*, *G. carpophagus*) mature instars.

Scolopendromorpha hatch in conditions comparable to those of a geophilomorph peripatoid. Three adolescens instars have been also recorded in this taxon (Verhoeff, 1902-25; Lawrence, 1947; Lewis, 1966; Brunhuber, 1970).

### *Regeneration*

Regeneration of centipede appendages is well documented in Scutigeromorpha and Lithobiomorpha (e.g., Weise, 1991; reviewed in Minelli et al., 2000; Maruzzo et al., 2005). Lithobiomorphs with regenerated appendages are commonly found in the field. Regeneration power is poor in the Scolopendromorpha, but evidence for this phenomenon is provided by occasional findings of specimens, e.g. of *Cryptops* species, with distal antennal articles of smaller diameter and with sparse setae, or with small, delicate terminal legs. Autotomy of the terminal legs is known for several scolopendromorphs (*Cryptops*, *Asanada*, *Alipes* and, possibly, *Rhysida*).

No certain proof of regeneration is available for the Geophilomorpha (Minelli et al., 2000). Geophilomorph antennae with less than 14 antennae are likely the product of early developmental defects, rather than incomplete regeneration.

Worthy of note is a case of regenerated poison claws recorded in *Lithobius latro* (Verhoeff, 1940), but the left forcipule described as regenerated in a specimen of the geophilomorph *Plateurytion dudichii* (Verhoeff, 1940) was possibly the outcome of a developmental trouble. The same is likely true of the occasional reports of geophilomorphs with one to several rudimentary legs, including the holotype of *Geophilus persephones* (Foddai and Minelli, 1999; Minelli, 2000).

In *Scolopendra*, regeneration of a damaged antenna may produce a new appendage with more antennomeres than in the normal antenna. A bifurcated (schistomelic) regenerate of an ultimate leg was described in a specimen of *S. morsitans* (Lewis, 1968).

In Scutigeromorpha and Lithobiomorpha, lost or experimentally removed appendages can regenerate. Surgical removal of ocelli of postlarval specimens of *Lithobius forficatus* is followed by regeneration with the first following moult (Joly and Herbaut, 1968).

### *References*

- ALBERT, A. M., 1982. Deviations from Dyar's rule in Lithobiidae. – *Zoologischer Anzeiger* 208: 192-207.  
ANDERSSON, G., 1976. Post-embryonic development of *Lithobius forficatus* (L.) (Chilopoda: Lithobiidae). – *Entomologica Scandinavica* 7: 161-168.  
ANDERSSON, G., 1978a. An investigation of the post-embryonic development of the Lithobiidae - some introductory aspects. – *Abhandlungen und Verhandlungen des naturwissenschaftlichen Vereins in Hamburg, Neue Folge* 21/22: 63-71.

- ANDERSSON, G., 1978b. Post-embryonic development of *Lithobius erythrocephalus* C. L. Koch (Chilopoda: Lithobiidae). – Entomologica scandinavica 9: 241-246.
- ANDERSSON, G., 1980. Post-embryonic development of *Lithobius melanops* Newport (Chilopoda: Lithobiidae). – Entomologica scandinavica II: 225-230.
- ANDERSSON, G., 1981. Post-embryonic development and geographical variation in Sweden of *Lithobius crassipes* L. Koch (Chilopoda: Lithobiidae). – Entomologica scandinavica 12: 437-445.
- ANDERSSON, G., 1982a. Post-embryonic development of *Lithobius calcaratus* C. L. Koch, (Chilopoda: Lithobiidae). – Entomologica scandinavica 13: 435-440.
- ANDERSSON, G., 1982b. Post-embryonic development of *Lithobius microps* Meinert (Chilopoda: Lithobiidae). – Entomologica scandinavica 13: 89-95.
- ANDERSSON, G., 1983. Post-embryonic development of *Lithobius curtipes* C. L. Koch (Chilopoda: Lithobiidae). – Entomologica scandinavica 14: 387-394.
- ANDERSSON, G., 1984a. Post-embryonic development of *Lamyctes fulvicornis* Meinert (Chilopoda: Henicopidae). – Entomologica scandinavica 15: 9-14.
- ANDERSSON, G., 1984b. Post-embryonic development of *Lithobius tenebrosus fennoscandicus* Lohmander (Chilopoda: Lithobiidae). – Entomologica scandinavica 15: 1-7.
- BASTIANELLO, A. & A. MINELLI, 2001. engrailed sequences from four centipede orders: Strong sequence conservation, duplications and phylogeny. – Development, Genes and Evolution 21I: 620-623.
- BASTIANELLO, A., M. RONCO, P. A. BURATO & A. MINELLI, 2002. Hox gene sequences from the geophilomorph centipede *Pachymerium ferrugineum* (C. L. Koch, 1835) (Chilopoda: Geophilomorpha: Geophilidae): Implications for the evolution of the Hox class genes of arthropods. – Molecular Phylogenetics and Evolution 22: 155-161.
- BRENA, C., A. D. CHIPMAN, A. MINELLI & M. AKAM, 2006. Expression of trunk Hox genes in the centipede *Strigamia maritima*: sense and anti-sense transcripts. – Evolution and Development 8: 252-265.
- BRUNHUBER, B. S., 1970. Egg laying, maternal care and development of young in the scolopendromorph Centipede, *Cormocephalus anceps anceps* Porath. – Zoological Journal of the Linnean Society 49: 225-234.
- CHIPMAN, A. D. & M. AKAM, 2008. The segmentation cascade in the centipede *Strigamia maritima*: Involvement of the Notch pathway and pair-rule gene homologues. Dev. Biol. 319, 160-169
- CHIPMAN, A. D., W. ARTHUR & M. AKAM, 2004a. A double segment periodicity underlies segment generation in centipede development. – Current Biology 14: 1250-1255.
- CHIPMAN, A. D., W. ARTHUR & M. AKAM, 2004b. Early development and segment formation in the centipede, *Strigamia maritima* (Geophilomorpha). – Evolution and Development 6: 78-89.
- CHIPMAN, A. D. & A. STOLLEWERK, 2006. Specification of neural precursor identity in the geophilomorph centipede *Strigamia maritima*. – Developmental Biology 290: 337-350.
- COOK, C. E., M. L. SMITH, M. J. TELFORD, A. BASTIANELLO & M. AKAM, 2001. Hox genes and the phylogeny of the arthropods. – Current Biology 11: 759-763.
- DEMANGE, J.-M., 1943. Sur le développement post-embryonnaire et la chaetotaxie d'*Hydropschendyla submarina* (Grube). Myriapodes. – Bulletin du Muséum national d'Histoire naturelle, Paris (2) 15: 418-423.
- DEMANGE, J.-M., 1944. Quelques mots sur la mue de *Lithobius forficatus* L. (Myriapodes, Chilopodes). – Bulletin du Muséum national d'Histoire naturelle, Paris (2) 15: 235-237.
- DOHLE, W., 1970. Über Eiablage und Entwicklung von *Scutigera coleoptrata* (Chilopoda). – Bulletin du Muséum national d'Histoire naturelle, Paris, (2) 41 (1969) supplément 2: 53-57.
- DUNGER, W. 1993. Überklasse Antennata. – Pp. 1031-1160 in H.-E. GRUNER, M. MORITZ & W. DUNGER: Arthropoda (ohne Insecta) in H.-E. GRUNER (ed.) Wirbellose Tiere in A. KAESTNER

- (founder) Lehrbuch der Speziellen Zoologie. Vierte Auflage. – Fischer, Jena-Stuttgart-New York.
- EASON, E. H., 1964. Centipedes of the British Isles. – Warne, London.
- FODDAI, D. & A. MINELLI, 1999. A troglomorphic geophilomorph centipede from southern France (Chilopoda: Geophilomorpha: Geophilidae). – Journal of Natural History 33: 267-287.
- FRUND, H.-C., 1983. Postlarvale Entwicklungsstadien von *Lithobius mutabilis* L. Koch 1862 (Chilopoda Lithobiidae) - mit einem Schlüssel zu ihrer Erkennung. – Zoologischer Anzeiger 211: 81-94.
- GRENIER, J. K., T. L. GARBER, R. W. WARREN, P. M. WHITINGTON & S. CARROLL, 1997. Evolution of the entire arthropod Hox gene set predated the origin and radiation of the onychophoran/arthropod clade. – Current Biology 7: 547-553.
- HAASE, E., 1880. Schlesiens Chilopoden. I. Chilopoda anamorpha. Inaugural-Dissertation, Universität Breslau.
- HERTZEL, G., 1983. Cuticulare Hüllen in der Embryogenese von *Lithobius forficatus* (L.) (Myriapoda, Chilopoda). – Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere II0: 395-401.
- HERTZEL, G., 1984. Die Segmentation des Keimstreifens von *Lithobius forficatus* (L.) (Myriapoda, Chilopoda). – Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere II2: 369-386.
- HEYMONS, R., 1901. Die Entwicklungsgeschichte der Scolopender. – Zoologica (Stuttgart) 13: 1-244.
- HORNELAND, E. O. & B. A. MEIDELL, 1986. The epimorphosis of *Strigamia maritima* (Leach, 1817) (Chilopoda: Geophilidae). – Entomologica Scandinavica 17: 127-130.
- HUGHES, C. L. & T. C. KAUFMAN, 2002a. Exploring myriapod segmentation: The expression patterns of *even-skipped*, *engrailed*, and *wingless* in a centipede. – Developmental Biology 247: 47-61.
- HUGHES, C. L. & T. C. KAUFMAN, 2002b. Exploring the myriapod body plan: Expression patterns of the ten Hox genes in a centipede. – Development 129: 1225-1238.
- HUGHES, C. L. & T. C. KAUFMAN, 2002c. Hox genes and the evolution of the arthropod body plan. – Evolution and Development 4: 459-499.
- JOHNSON, B. M., 1952. The centipedes and millipedes of Michigan. – Ph.D thesis, University of Michigan.
- JOLY, R., 1966. Contribution à l'étude du cycle de mue et de son déterminisme chez les myriapodes chilopodes. – Bulletin biologique de France et Belgique 3 : 379-480.
- JOLY, R. & C. HERBAUT, 1968. Sur la régénération oculaire chez *Lithobius forficatus* L. (Myriapode Chilopode). – Archives de Zoologie expérimentale et générale 109: 591-613.
- KADNER, D. & A. STOLLEWERK, 2004. Neurogenesis in the chilopod *Lithobius forficatus* suggests more similarities to chelicerates than to insects. – Development, Genes and Evolution 214: 367-379.
- KETTLE, C., W. ARTHUR, T. JOWETT & A. MINELLI, 1999. Homeotic transformation in a centipede. – Trends in Genetics 15: 393.
- KETTLE, C., W. ARTHUR, T. JOWETT & A. MINELLI, 2000. A homeotically-transformed specimen of *Strigamia maritima* (Chilopoda, Geophilomorpha), and its morphological, developmental and evolutionary implications. – Fragmenta faunistica, Warszawa, 43 Supplement: 105-112.
- KETTLE, C., J. JOHNSTONE, T. JOWETT, H. ARTHUR & W. ARTHUR, 2003. The pattern of segment formation, as revealed by *engrailed* expression, in a centipede with a variable number of segments. – Evolution and Development 5: 198-207.
- KNOLL, H. J., 1974. Untersuchungen zu Entwicklungsgeschichte von *Scutigera coleoptrata* L. (Chilop.). – Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 92: 47-132.

- LAWRENCE, R. F., 1947. Some observation on the post-embryonic development of the Natal forest centipede *Cormocephalus multispinosus* (Kraep.). – Annals of the Natal Museum II: 139–156.
- LESNIEWSKA, M., 2004. Bifurcation of one antenna in *Stigmatogaster subterraneus* (Shaw, 1794) (Chilopoda: Geophilomorpha). Biological Letters 41: 51–53.
- LESNIEWSKA, M., L. BONATO & G. FUSCO. 2009a. Morphological anomalies in a Polish population of *Stigmatogaster subterranea* (Chilopoda: Geophilomorpha): a multi-year survey. Soli Organisms 81: 347–358.
- LESNIEWSKA, M., L. BONATO, A. MINELLI & G. FUSCO. 2009b. Trunk anomalies in the centipede *Stigmatogaster subterranea* provide insight into late-embryonic segmentation. – Arthropod Structure & Development 38: 417–426.
- LEWIS, J. G. E., 1961. The life history and ecology of the littoral centipede *Strigamia* (=*Scolioplanes*) *maritima* (Leach). – Proceedings of the Zoological Society of London 137: 221–248.
- LEWIS, J. G. E., 1966. The taxonomy and biology of the centipede *Scolopendra amazonica* in the Sudan. – Journal of Zoology 149: 188–203.
- LEWIS, J. G. E., 1968. Individual variation in a population of the centipede *Scolopendra amazonica* from Nigeria and its implications for taxonomic discrimination in the Scolopendridae. – Journal of the Linnean Society (Zoology) 47: 315–326.
- LEWIS, J. G. E., 2000. Centipede antennal characters in taxonomy with particular reference to scolopendromorphs and antennal development in pleurostigmomorphs (Myriapoda, Chilopoda). – Fragmenta faunistica, Warszawa 43, Supplement: 87–96.
- MANTON, S. M., 1965. The evolution of arthropodan locomotory mechanisms. Part 8. Functional requirements and body design in Chilopoda, together with a comparative account of their skeleto-muscular systems and an appendix on a comparison between burrowing forces of annelids an. – Journal of the Linnean Society of London, Zoology 45: 251–484.
- MARUZZO, D., L. BONATO, C. BRENA, G. FUSCO & A. MINELLI, 2005. Appendage loss and regeneration in arthropods: a comparative view. – Pp. 215–245 in S. KOENEMANN & R. JENNER (eds.) Crustacea and arthropod phylogeny. Crustacean Issues 16 – Balkema, Rotterdam.
- METSCHNIKOW, E., 1875. Embryologisches über *Geophilus*. – Zeitschrift für wissenschaftliche Zoologie 25: 313–322.
- MINELLI, A., 1985. Post-embryonic development and the phylogeny of geophilomorph centipedes (Chilopoda). – Bijdragen tot de Dierkunde 55: 143–148.
- MINELLI, A., 2000. Holmeric vs. meromeric segmentation: A tale of centipedes, leeches, and rhombomeres. – Evolution & Development 2: 35–48.
- MINELLI, A., C. BRENA, G. DEFLOIAN, D. MARUZZO & G. FUSCO, 2006. From embryo to adult. Beyond the conventional periodization of arthropod development. – Development Genes and Evolution 216: 373–383.
- MINELLI, A., D. FODDAI, L. A. PEREIRA & J. G. E. LEWIS, 2000. The evolution of segmentation of centipede trunk and appendages. – Journal of Zoological Systematics and Evolutionary Research 38: 103–117.
- MINELLI, A. & C. PASQUAL, 1986. On some abnormal specimens of centipedes (Chilopoda). – Società veneziana di Scienze naturali, Lavori II: 135–141.
- MISIOCH, M., 1978. Variation of characters in some geophilid centipedes. – Abhandlungen und Verhandlungen des naturwissenschaftlichen Vereins in Hamburg, Neue Folge 21/22: 55–62.
- MURAKAMI, Y., 1958. The life history of *Bothropolyx asperatus* Koch (Chilopoda Lithobiidae). – Zoological Magazine, Tokyo 67: 217–223 [in Japanese, with English summary].
- MURAKAMI, Y., 1960a. Postembryonic development of the common Myriapoda of Japan. III. *Lithobius pachyptedatus* Takakuwa. I. Anamorphic stadia. – Zoological Magazine, Tokyo 69: 121–124 [in Japanese, with English summary].

- MURAKAMI, Y., 1960b. Postembryonic development of the common Myriapoda of Japan. IV. *Lithobius pachypterus* Takakuwa. 2. Epimorphic stadia. - Zoological Magazine, Tokyo 69: 163-166 [in Japanese, with English summary].
- MURAKAMI, Y., 1961. Postembryonic development of the common Myriapoda of Japan. IX. Anamorphic stadia of *Esastigmatoibis longitarsus* Verhoeff (Chilopoda; Henicopidae). - Zoological Magazine, Tokyo 70: 430-434 [in Japanese, with English summary].
- PFLUGFELDER, O., 1932. Über den Mechanismus der Segmentbildung bei der Embryonalentwicklung und Anamorphose von *Platyrrhacus amarus* Attems. - Zeitschrift für wissenschaftliche Zoologie 140: 649-723.
- SAKUMA, M. & R. MACHIDA, 2002. Germband formation of a centipede *Scolopocryptops rubiginosus* L. Koch (Chilopoda: Scolopendromorpha). - Proceedings of the Arthropodan Embryological Society of Japan 37: 19-23.
- SAKUMA, M. & R. MACHIDA, 2004. Germband formation of a centipede *Scolopendra subspinipes* L. Koch (Chilopoda: Scolopendromorpha). - Proceedings of the Arthropodan Embryological Society of Japan 39: 41-43.
- SCHEFFEL, H. 1969. Untersuchungen über die hormonale Regulation von Häutung und Anamorphose von *Lithobius forficatus* (L.) (Myriapoda, Chilopoda). - Zoologische Jahrbücher, Abteilung für allgemeine Zoologie und Physiologie der Tiere 74: 436-505.
- VERHOEFF, K. W., 1902-1925. Chilopoda. In BRONN, H. G. (ed.): Klassen und Ordnungen des Tierreichs, 5, Abteilung 2, Buch I. - C. F. Winter'sche Verlagshandlung, Leipzig: 1-725.
- VERHOEFF, K. W., 1905a. Über die Entwicklungsstufen der Steinläufer, Lithobiiden, und Beiträge zur Kenntnis der Chilopoden. - Zoologische Jahrbücher, Supplement 8: 195-289.
- VERHOEFF, K. W., 1905b. Zur Morphologie, Systematik und Hemianamorphose der Scutigeriden. - Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin 1902(2): 9-60.
- VERHOEFF, K. W. 1940. Chilopoden-Kieferfuß-Regenerate in freier Natur. - Zeitschrift für Morphologie und Ökologie der Tiere 36: 645-650.
- VOIGTLÄNDER, K. 2000. Vergleichende Untersuchungen zur Postembryonalentwicklung von *Lithobius*-Arten (Chilopoda, Lithobiidae). - Mitteilungen der Deutschen Gesellschaft für allgemeine und angewandte Entomologie 12: 535-540.
- VOIGTLÄNDER, K., 2007. The life cycle of *Lithobius mutabilis* L. Koch, 1862 (Myriapoda: Chilopoda). - Bonner zoologische Beiträge 55 (2006): 9-25.
- WEIL, E., 1958. Biologie der einheimischen Geophiliden. - Zeitschrift für angewandte Entomologie 42: 173-209.
- WEISE, R., 1991. Antennenregeneration bei dritten Larven von *Lithobius forficatus* (L.). (Myriapoda, Chilopoda). - Zoologischer Anzeiger 227: 343-355.
- WHITINGTON, P. M., 1995. Conservation versus change in early axonogenesis in arthropod embryos: a comparison between myriapods, crustaceans and insects. - Experientia, Supplementum 72: 181-219.
- WHITINGTON, P. M., 2006. The evolution of arthropod nervous systems: Insights from neural development in the Onychophora and Myriapoda. - Pp. 318-336 in J. H. KAAS, G. F. STRIEDTER & J. L. R. RUBENSTEIN (eds.) Evolution of nervous systems: A comprehensive reference. - Elsevier, Academic Press, Oxford.
- WHITINGTON, P. M., T. MEIER & P. KING, 1991. Segmentation, neurogenesis and formation of early axonal pathways in the centipede, *Ethmostigmus rubripes* (Brandt). - Roux's Archives of Developmental Biology 199: 349-363.
- WÜRMLI, M., 1980. Statistische Untersuchungen zur Systematik und postembryonalen Entwicklung der *Scolopendra canadensis*-Gruppe (Chilopoda: Scolopendromorpha:

Scolopendridae). - Sitzungsberichte, Österreichische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Abteilung I 189: 315-353.

# Chapter 15

## CHILOPODA – ECOLOGY

Karin Voigtländer

### *Life-forms and ecological strategies*

#### *Life-forms*

Basically all chilopods are predatory soil inhabitants that avoid light and show distinct preference for moist microhabitats. Their habit is generally cryptozoic, as they spend the day under stones, bark and leaf litter or inside the soil and go out for hunting during the night. Ecological preferences and adaptations to special habitats are mirrored by body construction plans as ecomorphotypes or life-forms.

Based on locomotion, Manton (1977) distinguished three centipede ecomorphotypes.

The burrowing type is found in the Geophilomorpha and best represented by the polypodous, worm-like Himantariidae. With their very elongated body, these centipedes are especially adapted for a life in deeper soil layers and narrow soil galleries and clefts, where they live predominantly or exclusively.

An intermediate type is found in most representatives of the Scolopendromorpha. These centipedes can reach a relatively high running speed, but have also developed a special technique to burrow that allows them to produce deep branched burrow systems, in which they retreat during hot and dry times. In hard soil areas the strongly developed forcipules and the anterior three to four leg pairs tackle soil particles or small stones. Either these pieces are pushed in front of the body or they are pushed backwards out of the gallery by alternately lengthening and shorting of the body with simultaneous motion of the legs.

The Craterostigmomorpha have a running form similar to the Scolopendromorpha, but use a different burrowing technique. *Craterostigmus* stretches forward the very large forcipules by hydrostatic pressure, grasps prey and pulls it backwards by muscular power, like mole crickets.

The running type is represented by the Lithobiomorpha and Scutigeromorpha. With their flattened body, the Lithobiomorpha live preferentially in the leaf litter and the upper soil layer, often penetrating into small and flat cavities of the soil surface as well as sheltering under stones and bark. The species of Scutigeromorpha, mostly hunting on open surfaces, are fast-running.

### *Ecological strategies*

*Reproduction pattern.* The growth rate of centipedes living in tropical or subtropical regions is very high during the rainy season. Many species have an annual life-cycle, e.g., *Ethmostigmus trigonopodus*, *Asanada sokotranica*, *Rhysida nuda togoensis* (Lewis, 1973, 1974). In Nigeria, *Scolopendra amazonica* shows the most rapid development known for Chilopoda, becoming adult already after 6 to 12 months. This is the only centipede species known to have two generations in one year (Lewis, 1970).

In temperate regions with small extremes, as in large parts of Europe, most centipedes are perennial (Weil, 1958; Lewis, 1961, 1981; Andersson, e.g., 1976, 1984; Voigtländer, 2000, 2006). They are characterized by a low reproductive potential, long life span and a high intraspecific variability in duration and number of developmental stages. Almost all European Chilopoda are such equilibrium species or k-strategists (Albert, 1983; Fründ, 1991).

In Europe a r-selected species (adapted to frequent disturbance) is the introduced, parthenogenetic henicopid *Lamyctes emarginatus*. The life-cycle of this lithobiomorph is annual and in Europe strongly adapted to the water regime in floodplains (Zulka, 1991; Zerm, 1997; Andersson, 2006). The species survives the winter and spring-high-water in the egg-stage and is ready to breed parthenogenetically only some weeks after the drying-up. Thus, *L. emarginatus* develops large populations in a short time. Other chilopod species with life cycles spanning over two or more years survive the first winter as juveniles.

Such different developmental strategies are one possibility for the coexistence of species which have otherwise nearly the same claims for living conditions, for example *Lamyctes emarginatus* and *Lithobius (Monotarsobius) curtipes*. Both species are of the same size and therefore competitors for food. Nevertheless they live together in the same habitat (litter layer of floodplain forests). The annual species *Lamyctes emarginatus* is present as adults only in times with high nutrient supply (late summer and autumn) and therefore influences only a little the population of the perennial species *L. curtipes* (Zulka, 1999).

*Survival strategies.* A lot of centipede species all over the world use seasonal migrations between different strata as a possibility to survive unfavorable environmental conditions.

In humid tropics (Amazonian upland forests) Geophilomorpha can be found more abundantly in the upper 7 cm soil layer during the rainy season and more abundantly in deeper soil layers (7 to 14 cm) during the dry season (Adis et al., 1996). Some geophilid species are well-adapted to survive periodical inundations in forests by climbing up on

tree trunks and outlasting the periodical floods in the canopy (Adis et al., 1996; Morais et al., 1997; Foddai et al., 2002).

In tropical savannah regions chilopods abandon the soil surface during the dry seasons (Lewis, 1970, 1974). They crawl in soil galleries, often dug by themselves. During the rainy season these galleries are filled up with water and the chilopods return quickly to the soil surface. Only *Scolopendra amazonica* is active on the soil surface over the whole year as well as, but less commonly, another scolopendromorph, *Asanada walkeri* (Lewis, 1970).

In the temperate zone, centipedes show a distinct maximum of activity in spring (May/June), often correlated with a maximum in reproductive activity, and an autumn maximum in mesic forests in September, at dry sites from October to November. Centipedes evade winter low temperatures by moving down into deeper soil layers. Arborial species also overwinter in the soil (Spelda, 1999). During summer dry months, geophilids behave like earthworms by curling up in deeper hollows.

Seasonal habitat changes between stumps or rotten wood and leaf litter were found to be likely in North American and English Lithobiidae (Auerbach, 1951; Roberts, 1957; Lloyd, 1963), but could not be established in German woods (Fründ, 1987; Poser, 1989).

#### *Environmental factors*

The most important abiotic factor influencing centipede distribution is humidity. In laboratory experiments (Fründ, 1987), *Lithobius mutabilis*, *L. curtipes* and *L. macilentus* showed a preference for 100 % relative humidity. A longer survival time in dry air for *L. mutabilis* compared with *L. curtipes* may indicate a larger ecological range of this species. Long persistent inundation periods can only be survived by a few species.

Temperature preferences have been studied by Grgič and Kos (2002) for a few Central European species. Experimentally established optimal temperatures for European Lithobiidae are between 12 and 22°C. Irreversible damage occurs at temperatures above 35°C. Centipedes from temperate zones survive low temperatures in an inactive state without feeding (*Pachymerium ferrugineum* up to -26°C). *Lithobius forficatus* is able to survive an exposure to temperatures up to -6°C without damage (Tursman et al., 1994).

As predators, centipedes are only indirectly sensitive to the quality of the vegetation as influencing the quality of the humus layer and space structure, but they are sensitive especially to the availability of prey species (Albert, 1982; Fründ, 1983; Poser, 1990a; Schäfer, 1990; Schäfer and Schauermann, 1990; Schatzmann, 1990). Special conditions are found near the basis of tree trunks or stumps (Fründ, 1987; Poser, 1989; Scheu and Poser,

1996). Here the site factors are modified by the increased thickness of the litter layer, higher humidity, changed food supply and lower pH-value.

Occurrence and frequency of scars in centipedes can be used as a measure of stress factors, e.g., predation pressure, intrapopulation interference, or shortage of resting places in times of climatic stress (Fründ, 1991, 1992, 1996; Fründ et al., 1997).

### *Horizontal and vertical distribution*

Horizontal zonal distribution has been best studied in central European deciduous woods (Fründ 1987, 1991; Poser, 1989, 1990b; Scheu and Poser, 1996; Spelda, 1999; Jabin et al., 2007). Morphologically very similar species can be separated by their choice of microhabitats as tree-trunk-dwellers (e.g., *Lithobius pelidnus*, *L. valesiacus*, *L. piceus*), surface active dwellers (e.g., *L. mutabilis*) or rotten stump-dwellers (e.g., *L. macilentus* and *L. crassipes*, the latter species also on tree trunks).

As for the vertical zonal distribution, the epedaphic and hemiedaphic life styles are dominant within the Chilopoda, especially the Lithobiomorpha and Scolopendromorpha. The euedaphic life style is mainly represented by Geophilomorpha dwelling in mineral soil, usually implying body elongation, shortening of appendages and loss of eye pigment.

In European deciduous woods the vertical zoning of the centipedes differs between the various types of the humus layer. Moder-humus beech forests show a very clear stratification whereas in calcareous beech woods a mull humus layer is developed under the influence of Lumbricidae, which causes a more horizontal heterogeneity. As an example of vertical zoning in a European deciduous wood, Fründ (1991) divided such a soil profile according to the preferences of the dominant species for three zones:

- preference for F- and L-layer: *Lithobius mutabilis* and *Strigamia acuminata* (epedaphic life-form),
- preference for F- and H-layer: *L. macilentus*, *L. pygmaeus* (hemiedaphic life-form),
- main preference for H-layer, additionally also F-layer: *Geophilus alpinus* (euedaphic life-form).

### *Feeding habits*

As predators Chilopoda feed predominantly on living animals. However, there are numerous references that vegetable food is not disdained (indeed it can even be essential). Centipedes can endure long periods of hunger (up to 6 months). Differences in the food spectrum exist between the different species as well as the different stadia

within one species (Poser, 1989) depending on the body size. Geophilomorpha, living in deeper soil layers, prefer slow but relatively large prey animals (e.g., Lumbricidae, larvae of Diptera), whereas the more surface-active Lithobiomorpha feed on small, more active forms (e.g., Collembola).

#### *Centipede venom*

Investigations on the effects on animals of centipede venom are summarized in Lewis (1981) and Rosenberg (2009). Arthropods are killed or benumbed in a few seconds by very small amounts of venom. For example, the amount of venom delivered by *L. forficatus* with one bite is sufficient to benumb 16 larvae of the wax moth *Galleria mellonella*. The extract of a third of a poison gland of *Ethmostigmus rubripes* (Scolopendromorpha) kills a migratory locust (*Locusta migratoria*) in seconds.

Venom effects on vertebrates range from marginal consequences (e.g., *Lithobius mordax* on mice or rats) to death. The lethal amount of the venom of *E. rubripes* on white mice is one-hundredth of one poison gland per gram body weight of the mice. Following bite by *E. rubripes* in the pad a dog may die within one day, whereas no lethal effect has been recorded for other test vertebrates (rats, cavies, amphibians).

Regarding the action of centipede venom on humans, the bite of *Lithobius* causes intense pain decreasing after 10–15 min, reddening and appearance of wheals. To some extent egression of blood at the biting place can be observed. Similar phenomena appear after a bite by *Scutigera*, whereby the pain is stronger and can persist for up to 36 h. The most intensive pain, local ignitions or oedemas which often decay no more than after hours or days are caused by the bite of scolopendrids. Sometimes (bites of *Scolopendra subspinipes*) it may come to swellings of lymph glands. Seldom headache, giddiness, sickness and emesis occur. Hitherto only two cases of death of children are known.

#### *Prey spectrum and feeding*

In the Scutigeromorpha, the feeding spectrum and mechanism were investigated in *Scutigera coleoptrata* (summarized in Lewis, 1981 and Rosenberg, 2009) and *Thereuonoma tuberculata* (Murakami, 1958). Both species accept as food a wide variety of spiders, insects (from springtails to flies and butterflies) and, more rarely, lithobiomorph centipedes. Isopods were attacked only after moulting. Cannibalism is not rare. Olfactory and tactile stimuli with antennae, legs or mouthparts are necessary to elicit prey-catching behaviour. The very elongated lasso-like tarsi entangle the prey which is

not only sucked, but also quickly chewed with the mandibles. The forcipules are not used for mastication (as in Scolopendromorpha).

Lithobiomorphs feed on a very wide spectrum of soft-bodied prey, especially springtails and mites, larvae of flies and other insects, nematodes, annelids (Enchytraeidae and small Lumbricidae), slugs, spiders, juvenile or just moulted woodlice or millipedes and many insect species. Species often climbing up tree trunks (*Lithobius piceus*, *L. crassipes*) mostly capture scale-insects and aphids (Poser, 1988). In laboratory experiments, in addition to animal food, offered plants were clearly nibbled off by *L. mutabilis* (Voigtländer, 2006). Cannibalism is common. In lithobiomorph centipedes, food selection depends on the availability of the different items. They detect prey either by walking about (*Lamyctes emarginatus*) or by ambush from a hiding place (*Lithobius*). Prey animals must have a certain relation to the body size of the predator. For *L. forficatus* the proportions are established as predator : prey = 5 : 1 (Simon, 1960) and seem to be true also for other species. Small collembolans (*Folsomia* sp.) were only attacked by juveniles of *L. forficatus* and *L. mutabilis* and by smaller species of the subgenera *Monotarsobius* and *Sigibius*. In most cases juveniles feed on different prey than the adults. Lithobiomorphs notice the prey only when their antennae come into direct contact with it.

Regarding the food spectrum of *Craterostigmus tasmanianus* little is known and mostly from observations in captivity. Manton (1965) reported that termites were pulled out of crevices in dead wood using the very long forcipules, but Mesibov (1995) could not find any relations between *Craterostigmus* and termites in natural habitats. Copious fluid is poured out from the mouth and the semi-digested prey is sucked.

As for scolopendromorphs, most observations on feeding behaviour and food selection were undertaken in the laboratory and suggest a very wide food spectrum: earthworms, snails, spiders, cockroaches, locusts, larvae of beetles and flies, wasps, bees and many other insects, up to vertebrates as amphibians and small reptilians, birds, mice and bats. However, vegetable food and fluids such as milk, tea and coffee are not avoided, possibly for compensation of fluid loss. Cannibalism is common. Field observations confirm that large scolopendrids attack vertebrates, slugs and various winged insects. Investigation of gut content reveals fragments of spiders, mites, centipedes, flies, beetles, termites and ants (Lewis, 1966). Unexpected records from the field have recently shown that scolopendromorphs, occasionally at least, are able to feed on prey such as scorpions (the European *Scolopendra cingulata* on *Euscorpius flavicaudis*; Iorio, 2006), bats (*Sc. gigantea* in a Venezuelan cave; Molinari et al., 2005); tree frogs (*Otostigmus tibialis* on the hylid *Dendropsophus elegans*; Forti et al., 2007) and even sea anemones (*Otostigmus scabricauda* on *Bunodosoma caissarum*; Moraes and Chagas, 2009). The food spectrum of the smaller

*Cryptops* species is limited to small annelids and arthropods, e.g., collembolans, spiders, centipedes, millipedes, and flies. Vegetable residues were also found in investigations of gut contents.

Geophilomorphs are basically carnivorous but they also sometimes ingest vegetable food. The prey spectrum of species living in the litter layer is broader than that of species hunting in deeper soil layers. Manton (1965) discussed the feeding mechanism and the structure of the head and concluded that geophilomorphs are suctorial feeders. The best documented feeding habits are those of *Strigamia maritima* and *S. acuminata* (Blower, 1957, Lewis, 1961; Poser, 1988; Weil, 1958). In captivity a huge number of invertebrates were attacked, e.g., small annelids (Enchytraeidae), larvae of dipterans and other insects, snails, arachnids, millipedes, woodlice, thysanurans, diplurans, and various pterygote insects. In most cases larger and low mobility prey such as earthworms are preferred. In contrast to lithobiomorphs, geophilomorphs are active hunters. Because all species are blind the perception of prey seems to be realised by chemical stimuli or ground motion. The coastal species *Strigamia maritima* feeds on barnacles (Lewis 1961, 1981).

#### *Enemies and competition for food*

The list of centipede enemies is large and ranges from (tropical) terrestrial planarians to arachnids and predatory insects to amphibians, lizards, birds and mammals, of the latter especially moles and mice.

Spiders have an important and complex influence on centipede populations: it is probably dependent on the difference of body size, whether a specimen occurs as prey, predator or concurrent (Fründ, 1996).

#### *Habitats*

Habitat preferences of centipede species have been studied in several European countries, including the British Isles (Barber, 2005), Netherlands (Jeekel, 1999), Belgium (Lock and Dekoninck, 2001; Lock et al., 2001), Spain (García-Ruiz and Serra, 2003), Italy (Minelli and Iovane, 1987), Slovenia (Kos, 1996; Grgič and Kos, 2005a), Germany (Voigtländer, 2005), the Czech Republic (Tuf, 2000; Wytrwer and Tajovský, 2005) and Poland (Wytrwer, 1990, 1992, 2000; Leśniewska, 2000; Tracz, 2000).

Human disturbance of habitats has important impact on centipede communities (e.g., Schmitt and Roth, 1998; García-Ruiz, 1999a, 2003). Chilopods are obviously sensitive to pollution by heavy metals (Grelle et al., 2000). In natural heavy metal contaminated

grassland in Germany only *L. forficatus* and *L. melanops* occur in noteworthy abundances (Voigtländer, 2003a, b)

Centipedes, although not the most fashionable bioindicators, have been nevertheless used to assess the effects of environmental management (Grgič and Kos, 2005b; Leśniewska et al., 2005), following the example of their changing composition along ecological successions (Grgič and Kos, 2003), including those following extensive fires (García-Ruiz, 1999b, 2001) or on recultivated sites after coal-mining (e.g., Dunger & Voigtländer, 2009).

*Urban biotopes.* – Most of the wood-inhabiting species are replaced by synanthropic or settlement-typical species (e.g., Wytwer, 1995, 1996). Mediterranean species have found their way to towns of central Europe (*Henia vesuviana*, *Haplophilus subterraneus*, *Cryptops anomalans*). Also species from S-E Asia or Western Europe (*Tygarrup javanicus*, *Schendyla dentata*) have become inhabitants of central European towns.

The fauna of North European towns is represented by species from central Europe or even Mediterranean regions.

*Fauna of high mountains.* – True high-alpine species are hardly found among the Chilopoda, but there are *Lithobius* species up to 5545 m on Nepal Himalaya (Eason, 1989).

In Europe, all species known from above 2000 m (timberline) are mostly eurytopic with a broader range of altitudinal preference. The species spectrum of the alpine zone above 2500 m is dominated by *Lithobius* species. In the Alps and the mountains of the Balkan peninsula (Franz, 1975; Iorio, 2008, 2010; Stoev, 2002) *L. forficatus*, *L. erythrocephalus* and *L. latro* are all found up to 2600 m, *L. pilicornis*, *L. tricuspidis*, *L. valesiacus* and *L. lapidicola* up to 2700 m, *L. schuleri* up to 2900 m and *L. lucifugus* up to 3200 m. After Spelda (1999) and Pilz et al. (2008), *L. glacialis* and *L. lucifugus* are the only high-montane species in the Alps. They were found exclusively in the alpine zone of the Allgäuer Alps. Three further subalpine to alpine European species (*L. borisi*, *L. electron* and *L. schukeri*) are of uncertain taxonomical status (Stoev, 2002).

Geophilomorph species are mostly recorded up to ca. 2300 m. The highest record of a geophilomorph species in Europe is for *Strigamia crassipes* at 2750 m (Stoev, 2002).

In the Andes, species of *Lamyctes* are frequently recorded from the area of Lake Titicaca up to 4000 m, *Lamyctes andinus* up to 4400 m.

A list of centipedes found above 3500 m on the East African mountains (Beron, 2000) include one *Mecistocephalus* and three *Cryptops* species at 3500 m and *Scolopendra afra* at 4000 m on Mt. Elgon, *M. insularis* at 3900 m on Mt. Nyiragongo, *L. emarginatus* at 4000 m on Mt. Kenya and *L. africanus* at 4200 m on Mt. Ruwenzori.

*Coastal areas.* – Some chilopods species are, partly exclusively, inhabitants of clifffy seashores, where they live near by the surge zone. Special adaptations allow them to tolerate high salt contents as well as temporary flooding (Binyon and Lewis, 1963). Notably, among the Geophilomorpha several species in different genera and from different sites around the world have been recorded as halophilic (Barber, 2009). Among these, *Pachymerium ferrugineum*, *Tuoba poseidonis*, *Strigamia maritima*, *Hydroschendyla submarina* and *Geophilus seurati*. *S. maritima* feeds on *Orchestia* amphipods (Lewis, 1961), barnacles (*Balanus balanoides*) and periwinkles (*Littorina saxatilis*) (Blower, 1957). *Henia bicarinata* and *Geophilus flavus* occasionally also occur on the coasts of the Mediterranean Sea.

*Floodplains.* – Centipedes living in inundation endangered areas have two opportunities to survive the high water: to run away or to resist (Tufová and Tuf, 2005). Among the European lithobiomorphs, *L. microps*, *L. forficatus*, *L. mutabilis* and *L. curtipes* show a very high inundation tolerance. At favourable oxygen conditions they can survive between 25 and 40 hours underwater; *L. curtipes* was found alive after 22 days inundation (Zulka, 1991). High water temperatures, oxygen-poor or stagnant water cause the species to leave the water and climb e.g., on tree trunks.

*Selected tropical biotopes.* Little is known about habitat preferences and ecology of Chilopoda in tropical regions. Only in central Amazonia have some biotopes been investigated more intensively (Adis, 2002). According to their habitat preferences, scolopendromorph centipedes can be divided into two main groups (Schileyko, 2002). The first group consists of nocturnal solitary hunters that during daytime are usually hidden under stones, logs, bark, in the canopies or in litter (e.g., *Rhysida*, *Scolopendra*, *Cormocephalus*, *Arthrorhabdus*). They are large (up to 200-220 mm) to medium-sized creatures (40-70 mm). The second group includes smaller (10-40 mm), mainly eyeless forms characterised by a hypogean way of life (some *Cryptops* and *Tidops*). They are active all over the day in the lowest litter layers, at the litter-soil interface, or in the uppermost soil, leaving their usual habitat only occasionally. Species of the genus *Newportia* belong both to the first and second group.

In two Amazonian species of Geophilomorpha morpho-anatomical modifications for surviving submersion are known (Adis, 1992). All scolopendromorph and geophilomorph centipedes have an adapted behaviour to climb on the trees and to living there during the inundation period (Foddai et. al., 2002; Schileyko, 2002), while the henicopid lithobiomorph *Lamyctes adisi* has a dormant submerged egg stage (Zalesskaja, 1994).

*Fauna of caves.* – True cave species (troglobionts) spend their whole life in caves and show such morphological adaptations as very long antennae and legs as well as reduction of pigment and ocelli.

True troglobionts are known from Spain, Sardinia (several *Lithobius* species, including *Lithobius (Trogololithobius) sbordonii*) South-France (e.g., *Geophilus persephones*), Crete, Romania and Bulgaria, Central America and Australia (e.g., Negrea and Minelli, 1994; Chagas and Shelley, 2003; Edgecombe, 2005, 2006).

*Nest dwelling Chilopoda.* – The presence of geophilomorphs in nests of the mole (*Talpa europaea*), although frequent (Minelli, 1979), is probably due to generic environmental opportunities. By contrast, the presence of some Lithobiidae in nests seems to show a preference of such habitats, especially in the case of *Lithobius crassipes*. The scolopendromorph *Cryptops hortensis* seems to have a preference for nests of the rodent *Clethrionomys glareolus*.

Chilopoda show no obligate myrmecophily. However, they were often found as facultative visitors in ant-nests (e.g., Stoev and Lapeva-Gjonova, 2005). Most observations are known from nests of *Formica rufa*. Here species of *Lithobius*, *Monotarsobius* and *Sigibius* and others were found to pass through the egg- and youth-development, whereas the adults left the ant-nests. The ants obviously tolerate these guests, provided that the chilopods do not get into the brood chambers.

#### *Parasitism and commensalism*

A few species of fungi (*Oesophagomyces lithobii*, *Rhabdomyces lobjoyi*, *Mononema moniliforme*, *Omphalocystis plateaui*) were found in the foregut of some *Lithobius* and *Cryptops* species.

More than 40 species of gregarines (Apicomplexa) are known to live as extracellular commensals in the mid-gut or to penetrate with their front end into the mid-gut cells of centipede hosts. With the exception of *Stigamia maritima*, all chilopods investigated in this respect host gregarines. No information exists for *Craterostigmus*. Strong infection with *Grebnickiella pixella* can lead to gut occlusion in the host *Scolopendra morsitans*.

Coccidia found as extracellular parasites in the middle and posterior part of the mid-gut of centipedes belong to the Adeleidae (recorded from Lithobiomorpha and Scolopendromorpha) and Eimeriidae (recorded from Lithobiomorpha and Geophilomorpha).

As for the Nematomorpha, *L. forficatus* is known as host of larval *Gordius emarginatus* and *G. aquaticus*.

Representatives of the nematode genus *Cephalobellus* have been reported in *Geophilus*. Whereas a strong affection on young stages is lethal, adult specimens live without visible damage.

Larvae of Tachinidae (Diptera) parasitize in the visceral cavity of their hosts, *?Loewia foeda* and *Helocera delecta* in adult *Lithobius*, *Exoristoides harrisi* in *Geophilus*. Their pupation takes place in the empty skin of the centipede. As for the parasitoid Hymenoptera, larvae of proctotrupids (*Phaneroserphus calcar* and *Proctotrupes ater*) and chalcidoids attack *Lithobius* species.

#### *Phoresy*

Phoretic connections with arthropods, including centipedes, are widespread in the mite cohorts Uropodina, Astigmatina and Heterostigmata. About 40 centipede species of all orders are known used as “omnibus” by hypopi or nymphs of mites (e.g. Lewis, 1961, 1981; Mašán, 2001; Błoszyk et al., 2006). For this, the species of the carrier is mostly of no importance. Only *Oodinychus ovalis* and *Uroobovella pulchella* belonging to the Uropodina are exclusively associated with *L. forficatus*. The majority of the mites were located on the sides of anterior segments of the centipedes, mostly on the second segment. The centipedes observed in the study by Błoszyk et al. (2006) normally carried from 1 to a maximum of 16 phoretic uropodine deutonymphs.

#### *References*

- ADIS, J., 1992. How to Survive Six Months in a Flooded Soil: Strategies in Chilopoda and Symphyla from Central Amazonian Floodplains. – Studies on Neotropical Fauna and Environment 27: 117-129.
- ADIS, J. (ed.), 2002. Amazonian Arachnida and Myriapoda. – Pensoft, Sofia-Moscow.
- ADIS, J., A. MINELLI, J. W. DE MORAIS, L. A. PEREIRA, F. BARBIERI, & J. M. G. RODRIGUES, 1996. On abundance and phenology of Geophilomorpha (Chilopoda) from Central Amazonian upland forests. – Ecotropica 2: 165-175.
- ALBERT, A. M., 1982. Species spectrum and dispersion patterns of chilopods in three Solling habitats. – Pedobiologia 23: 337-347.
- ALBERT, A. M., 1983. Life cycle of Lithobiidae - with a discussion of the r- and K-selection theory. – Oecologia 56: 272-279.
- ANDERSSON, G., 1976. Post-embryonic development of *Lithobius forficatus* (L.) (Chilopoda: Lithobiidae). – Entomologica scandinavica 7: 161-168.
- ANDERSSON, G., 1984. Post-embryonic development of *Lithobius tenebrosus fennoscandicus* Lohmander (Chilopoda: Lithobiidae). – Entomologica scandinavica 15: 1-7.

- ANDERSSON, G., 2006. Habitat preferences and seasonal distribution of developmental stadia in *Lamyctes emarginatus* (Newport, 1844) (*L. fulvicornis* Meinert, 1868) and comparison with some *Lithobius* species (Chilopoda, Lithobiomorpha). – Norwegian Journal of Entomology 53: 311-320.
- AUERBACH, S. I., 1951. The centipedes of the Chicago area with special reference to their ecology. – Ecological Monographs 21: 97-124.
- BARBER, A. D., 2005. Recording distribution and habitat preferences for myriapods in the British Isles. – Peckiana 4 : 15-34.
- BARBER, A. D., 2009. Littoral myriapods: a review. – Soil Organisms 81: 735-760.
- BERON, P., 2000. Non-insect Arthropoda (Isopoda, Arachnida, and Myriapoda) on the high mountains of tropical Africa. – Bonner Zoologische Monographien 46: 153-188.
- BINYON, J. & J. G. E. LEWIS, 1963. Physiological adaptations of two species of centipede (Chilopoda: Geophilomorpha) to life on the shore. – Journal of the Marine Biology Association of the United Kingdom 43: 49-55.
- BŁOSZYK, J., J. KŁIMCZAK & M. LEŚNIEWSKA, 2006. Phoretic relationships between Uropodina (Acar: Mesostigmata) and centipedes (Chilopoda) as an example of evolutionary adaption of mites to temporary microhabitats. – European Journal of Entomology 103: 699-707.
- BLOWER, G., 1957. Feeding habits of a marine centipede. – Nature 180: 560-560.
- DUNGER, W. & K. VOIGTLÄNDER, 2009. Soil fauna (Lumbricidae, Collembola, Diplopoda and Chilopoda) as indicators of soil ecosubsystem development in post-mining sites of Eastern Germany – a review. – Soil Organisms 81: 1-51.
- CHAGAS, A. Jr. & R. M. SHELLEY, 2003. The centipede genus *Newportia* Gervais, 1847, in Mexico: description of a new troglomorphic species; redescription of *N. sabina*; revival of *N. azteca*; and a summary of the fauna (Scolopendromorpha: Scolopocryptopidae: Newportiinae). – Zootaxa 379: 1-20.
- EASON, E.H., 1989. Lithobiidae from the Nepal Hymalayas. With Description of Ten New Species of *Lithobius* and *Australobius* (Chilopoda: Lithobiomorpha). – Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere II6: 335-372.
- EDGEcombe, G. D., 2005. A troglomorphic species of the centipede *Cryptops* (*Trigonocryptops*) (Chilopoda: Scolopendromorpha) from Western Australia. – Records of the Western Australian Museum 22: 315-323.
- EDGEcombe, G. D., 2006. A troglobitic cryptopid centipede (Chilopoda: Scolopendromorpha) from Western Queensland. – Records of the Western Australian Museum 23: 193-198.
- FODDAI, D., A. MINELLI, & L. A. PEREIRA, 2002. Chilopoda. Geophilomorpha. – Pp. 459-474 in J. ADIS (ed.) Amazonian Arachnida and Myriapoda. – Pensoft, Sofia-Moscow.
- FORTI, L. R., H. Z. FISCHER & L. C. ENCARNACÃO, 2007. Treefrog *Dendropsophus elegans* (Wied-Neuwied, 1824) (Anura: Hylidae) as a meal to *Ostostigmus tibialis* Brölemann, 1902 (Chilopoda: Scolopendridae) in the Tropical Rainforest in southeastern Brazil. – Brazilian Journal of Biology 67: 583-584.
- FRANZ, H., 1975. Die Bodenfauna der Erde in biozönotischer Betrachtung. – Steiner, Wiesbaden.
- FRÜND, H.-C., 1983. Untersuchungen zur Koexistenz verschiedener Chilopodenarten im Waldboden. – Dissertation, University of Würzburg.

- FRÜND, H.-C., 1987. Räumliche Verteilung und Koexistenz der Chilopoden in einem Buchen-Altbestand. – *Pedobiologia* 30: 19-29.
- FRÜND, H.-C., 1991. Zur Biologie eines Buchenwaldbodens. 14. Die Hundertfüßer (Chilopoda). – *Carolinae* 49: 83-94.
- FRÜND, H.-C., 1992. The occurrence and frequency of scars in centipedes. – Berichte aus dem naturwissenschaftlich-medizinischen Verein in Innsbruck, Supplement 10: 269-275.
- FRÜND, H.-C., 1996. Chilopoda. – Pp. 113-121 in J. RÖMBKE, L. BECK, B. FÖRSTER, H. C. FRÜND, F. HORAK, A. RUF, C. ROSCICZESKI, M. SCHEURIG & S. WOAS. (eds.) Boden als Lebensraum für Bodenorganismen: bodenbiologische Standortsklassifikation – Literaturstudie. – <http://www.lubw.baden-wuerttemberg.de/servlet/is/17027>.
- FRÜND, H.-C., B. BALKENHOL & B. RUSZKOWSKI, 1997. Chilopoda in forest habitat-islands in north-west Westphalia, Germany. – *Entomologica Scandinavica* Supplement 51: 107-114.
- GARCÍA-RUIZ, A., 1999a. Estudio comparativo de las comunidades de quilópodos en zonas con vegetación natural y repobladas de Madrid. – *Boletín de la Sociedad Entomológica Aragonesa* 25: 25-27.
- GARCÍA-RUIZ, A., 1999b. Estudio post-fuego de las comunidades de quilópodos en coscojares de Castilla-La Mancha. – A post-fire study of centipedes in oak stands in Castille-La Mancha. – *Ecología Madrid* 13: 283-288.
- GARCÍA-RUIZ, A., 2001. Estudio de los efectos de un incendio sobre las poblaciones de miriápidos. – Study of the effects of fire on myriapod populations. – *Ecología Madrid* 15: 269-273.
- GARCIA-RUIZ, A., 2003. Ecología de las comunidades de quilópodos en áreas modificadas por depósito de residuos sólidos urbanos inertes. – *Ecología Madrid* 17: 191-197.
- GARCÍA-RUIZ, A. & A. SERRA, 2003. Studies on centipede communities (Chilopoda) from three habitats in Toledo Province, Spain. – *African Invertebrates* 44: 227-236.
- GRUELLE, C., M. C. FABRE, A. LEPRETRE & M. DESCAMPS, 2000. Myriapod and isopod communities in soils contaminated by heavy metals in northern France. – *European Journal of Soil Science* 51: 425-433.
- GRGIČ, T. & I. KOS, 2002. Temperature preference in some centipede species of the genus *Lithobius* Leach, 1814 (Chilopoda: Lithobiidae). – *Acta Biologica Slovenica* 44: 3-12.
- GRGIČ, T. & I. KOS, 2003. Centipede diversity in patches of different development phases in an unevenly-aged beech forest stand in Slovenia. – *African Invertebrates* 44: 237-252.
- GRGIČ, T. & I. KOS, 2005a. Centipede diversity in differently structured forests in Slovenia. – *Peckiana* 4: 49-56.
- GRGIČ, T. & I. KOS, 2005b. Influence of forest development phase on centipede diversity in managed beech forests in Slovenia. – *Biodiversity and Conservation* 14: 1841-1862.
- IORIO, E., 2006. Le scolopendromorphe *Scolopendra cingulata* Latreille, 1829 (Scolopendromorpha, Scolopendridae), un prédateur du scorpion *Euscorpius (Tetrarichobothrius) flavicaudis* (De Geer, 1778) (Scorpiones, Euscorpiidae). – *Bulletin d'Arthropoda* 30: 60-62.
- IORIO, E., 2008. Contribution à l'étude des chilopodes (Chilopoda) des Alpes-Maritimes, incluant une clé d'identification des lithobiomorphes Lithobiidae de Provence-Alpes-Côte d'Azur. – *Bulletin de la Société linnéenne de Provence* 59: 127-190.

- IORIO, E., 2010. Les Lithobies et genres voisins de France (Chilopoda, Lithobiomorpha). Révision de plusieurs espèces méconnues et nombreux apports inédits à la connaissance du genre *Lithobius* Leach, 1814. Avec une clé des familles, des genres et de toutes les espèces de l'ordre. – Revue de l'Association Roussillonnaise d'Entomologie 19, Supplément.
- JABIN, M., W. TOPP, J. KULFAN & P. ZACH, 2007. The distribution pattern of centipedes in four primeval forests of central Slovakia. – Biodiversity and Conservation 16: 3437-3445.
- JEEKEL, C. A. W., 1999. Qualitative analysis of the chilopods and diplopods occurring in some woodland biotopes in the Netherlands. – Myriapod Memoranda 1: 81-93.
- KOS, I., 1996. Centipedes (Chilopoda) of some forest communities in Slovenia. – Pp. 635-646 in J. J. GEOFFROY, J. P. MAURIES & M. NGUYEN DUY-JACQUEMIN (eds.) Acta Myriapodologica – Mémoires du Museum National d'Histoire Naturelle, 169.
- LEŚNIEWSKA, M., 2000. Centipede (Chilopoda) communities of three beech forests in Poland. – Fragmenta faunistica, Warszawa 43 Supplement: 343-379.
- LEŚNIEWSKA, M., E. KORALEWSKA-BATURA & J. BŁOSZYK, 2005. Centipede communities in oak-hornbeam forests of different ages and exploitation in Wielkopolska (Poland). – Peckiana 4: 67-77.
- LEWIS, J. G. E., 1961. The life history and ecology of the littoral centipede *Strigamia* (=*Scolioplanes*) *maritima* (Leach). – Proceedings of the Zoological Society of London 137: 221-248.
- LEWIS, J. G. E., 1966. The taxonomy and biology of the centipede *Scolopendra amazonica* in the Sudan. – Journal of Zoology 148: 188-203.
- LEWIS, J. G. E., 1970. The biology of *Scolopendra amazonica* in Nigerian guinea savannah. – Bulletin du Muséum national d'Histoire naturelle, Paris, (2) 41 (1969), Supplément 2 85-90.
- LEWIS, J. G. E., 1973. The taxonomy, distribution and ecology of centipedes of the genus *Asanada* (Scolopendromorpha: Scolopendridae) in Nigeria. – Journal of the Linnean Society, Zoology 52: 97-112.
- LEWIS, J. G. E., 1974. The ecology of centipedes and millipedes in Northern Nigeria. – Symposia of the Zoological Society of London 32: 423-431.
- LEWIS, J. G. E., 1981. The biology of centipedes. – Cambridge University Press, Cambridge.
- LLOYD, M., 1963. Numerical observations on the movement of animals between beech litter and fallen branches. – Journal of Animal Ecology 32: 157-163.
- LOCK, K., D. DE BAKKER & B. DE VOS, 2001. Centipede communities in the forests of Flanders. – Pedobiologia 45: 27-35.
- MANTON, S. M., 1965. The evolution of arthropodan locomotory mechanisms. Part 8. Functional requirements and body design in Chilopoda, together with a comparative account of their skeleto-muscular systems and an Appendix on a comparison between burrowing forces of annelids and chilopods and its bearing upon the evolution of the arthropodan haemocoel. – Journal of the Linnean Society of London, Zoology 45: 251-484.
- MANTON, S. M., 1977. The Arthropoda. Habits, functional morphology and evolution. – Clarendon Press, Oxford.
- MAŠÁN, P., 2001. Mites of the cohort Uropodina (Acarina, Mesostigmata) in Slovakia. – Annotationes Zoologicae et Botanicae 223: 1-320.

- MESIBOV, R., 1995. Distribution and ecology of the centipede *Craterostigmus tasmanianus* Pocock, 1902 (Chilopoda: Craterostigmomorpha: Craterostigmidae) in Tasmania. — Tasmanian Naturalist 117: 2-7.
- MINELLI, A., 1979. Centipedes from the burrows of *Talpa europaea* L. in Italy north of Po River. — Bollettino del Museo civico di Storia naturale, Verona, 5 (1978): 573-579.
- MINELLI, A. & E. IOVANE, 1987. Habitat preferences and taxocenoses of Italian centipedes (Chilopoda). — Bollettino del museo civico di storia naturale di Venezia 37: 7-34.
- MOLINARI, J., E. E. GUTIERREZ; A. A. DE-ASCENCAO, J. M. NASSAR, A. ARENDS & R. J. MARQUEZ, 2005. Predation by giant centipedes, *Scolopendra gigantea*, on three species of bats in a Venezuelan cave. — Caribbean Journal of Science 41: 340-346.
- MORAES, F. & A. Jr. CHAGAS, 2009. Border between two worlds: the first record of sea anemone feeding on centipede. — International Journal of Myriapodology 2: 215-217.
- MORAIS, J. W., J. ADIS, E. BERTI-FILHO, L. A. PEREIRA, A. MINELLI & F. BARBIERI, 1997. On abundance, phenology and natural history of Geophilomorpha from mixedwater inundation forest in Central Amazonia (Chilopoda). — Entomologica scandinavica Supplement 51: 115-119.
- MURAKAMI, Y., 1958. Food habit of *Thereuonema hilgendorfi* Verhoeff (Chilopoda Scutigeridae). — Zoological Magazine, Tokyo 67: 138-141.
- NEGREA, S. & A. MINELLI, 1994. Chilopoda. — Pp. 249-254 in C. JUBERTHIE & V. DECU (eds.) Encyclopedia Biospeologica, I. — Société de Biospéologie, Moulis-Bucarest.
- PILZ, C., R.R. MELZER & J. SPELDA, 2008. Morphometric and SEM analysis of the species pair *Lithobius mutabilis* L. Koch, 1862 and *L. glacialis* Verhoeff, 1937 (Chilopoda: Lithobiomorpha). — Organisms, Diversity & Evolution 7: 270e1-270e20.
- POSER, T., 1988. Chilopoden als Prädatoren in einem Laubwald. — Pedobiologia 31: 261-281.
- POSER, T., 1989. Aufteilung der Ressourcen innerhalb der Chilopodengemeinschaft eines Kalkbuchenwaldes. (Zur Funktion der Fauna in einem Mulmbuchenwald 12). — Verhandlungen der Gesellschaft für Ökologie 17: 279-284.
- POSER, T., 1990a. The influence of litter manipulation on the centipedes of a beach wood. — Pp. 235-245 in A. MINELLI (ed.) Proceedings of the 7th International Congress of Myriapodology. Brill, Leiden.
- POSER, T. (G.), 1990b. Die Hundertfüßer (Myriapoda, Chilopoda) eines Kalkbuchenwaldes: Populationsökologie, Nahrungsbiologie und Gemeinschaftsstruktur. — Dissertation, University of Göttingen.
- ROBERTS, H., 1957. An ecological survey of the arthropods of a mined beech-oak woodland with particular reference to the Lithobiidae. — Ph. D Thesis, University of Southampton.
- ROSENBERG, J., 2009. Die Hundertfüßer (Chilopoda). — Neue Brehm-Bücherei 285. Westarp Wissenschaften, Hohenwarsleben.
- SCHÄFER, M., 1990. The soil fauna of a beech forest on limestone: trophic structure and energy budget. — Oecologia 82: 128-136.
- SCHÄFER, M. & J. SCHAUERMANN, 1990. The soil fauna of beech forests: comparison between a mull and a moder soil. — Pedobiologia 34: 299-314.
- SCHATZMANN, E., 1990. Weighting of habitat types for estimation of habitat overlap-application to a collection of Suiss centipedes. — Pp. 299-309 in A. MINELLI (ed.) Proceedings of the 7th International Congress of Myriapodology. Brill, Leiden.

- SCHEU, S. & G. POSER, 1996. The soil macrofauna (Diplopoda, Isopoda, Lumbricidae and Chilopoda) near tree trunks in a beech wood on limestone: indications for stemflow induced changes in community structure. – Applied Soil Ecology 3: 115-125.
- SCHILEYKO, A. A., 2002. Scolopendromorpha. – Pp. 479-500 in J. ADIS (ed.): Amazonian Arachnida and Myriapoda. Pensoft, Sofia-Moscow.
- SCHMITT, G. & M. ROTH, 1998. Centipede and millipede communities in cultural landscapes of Northeast-Germany. – Pp. 191-197. in V. PIŽL & K. TAJOVSKÝ (eds.) Soil Zoological Problems in Central Europe. Institute of Soil Biology, České Budějovice.
- SIMON, H. R., 1960. Zur Ernährungsbiologie von *Lithobius forficatus* (Myriapoda, Chilopoda). – Zoologischer Anzeiger 164: 19-26.
- SPELDA, J., 1999. Ökologische Differenzierung südwestdeutscher Steinläufer (Chilopoda: Lithobiida). – Verhandlungen der Gesellschaft für Ökologie 29: 389-395.
- STOEV, P., 2002. A Catalogue and Key to the centipedes (Chilopoda) of Bulgaria. – Pensoft, Sofia-Moscow.
- STOEV, P. & A. LAPEVA-GJONOVA, 2005. Myriapods from ant nests in Bulgaria (Chilopoda, Diplopoda). – Peckiana 4: 131-142.
- TRACZ, H., 2000. The Diplopoda and Chilopoda of selected ecotones in northwestern Poland. – Fragmenta faunistica, Warszawa 43 Supplement: 351-360.
- TUF, I. H., 2000. Communities of centipedes (Chilopoda) in three floodplain forests of various age in Litovelské Pomoraví (Czech Republic). – Fragmenta faunistica, Warszawa 43 Supplement: 327-332.
- TUFOVÁ, J. & I. H. TUF, 2005. Survival under water - comparative study of millipedes (Diplopoda), centipedes (Chilopoda) and terrestrial isopods (Oniscidea). – Pp. 195-198 in K. TAJOVSKÝ, J. SCHLAGHAMERSKÝ & V. PIŽL (eds.) Contributions to Soil Zoology in Central Europe I. Institute of Soil Biology, České Budějovice.
- TURSMAN, D.; J. G. DUMAN & C. A. KNIGHT, 1994. Freeze tolerance adaptations in the centipede, *Lithobius forficatus*. – Journal of Experimental Zoology 268: 347-353.
- VOIGTLÄNDER, K., 2000. Vergleichende Untersuchungen zur Postembryonalentwicklung von *Lithobius* – Arten (Chilopoda, Lithobiidae). – Mitteilungen der Deutschen Gesellschaft für allgemeine und angewandte Entomologie 12: 535-540.
- VOIGTLÄNDER, K., 2003a. Hundertfüßer (Chilopoda). – Pp. 26-29, 54-55, 71, 88-89, 107-108, 123-124, 194-195 in P. SCHNITTER, M. TROST & M. WALLASCHEK (eds.): Tierökologische Untersuchungen in gefährdeten Biotoptypen des Landes Sachsen-Anhalt. I. Zwergrastwiesen, Trocken- und Halbtrockenrasen. – Entomol. Mitteilungen Sachsen-Anhalts, Sonderheft 2003.
- VOIGTLÄNDER, K., 2003b: Species distribution and assemblages of centipedes (Chilopoda) on open xeric sites in Saxony-Anhalt (Germany). – Pp. 283-291 in M. Hamer (ed.) Myriapodology in the new Millennium – African Invertebrates 44.
- VOIGTLÄNDER, K., 2005. Habitat preferences of selected Central European centipedes. – Peckiana 4: 163-179.
- VOIGTLÄNDER, K., 2006. The life cycle of *Lithobius mutabilis* L. Koch, 1862 (Myriapoda: Chilopoda) – Bonner zoologische Beiträge (2007) 55: 9-25

- WEIL, E., 1958. Zur Biologie der einheimischen Geophiliden. – Zeitschrift für angewandte Entomologie 42: 173-209.
- WYTWER, J., 1990. Chilopoda of linden-oak-hornbeam (Tilio-Carpinetum) and thermophilous oak forests (Potentillo albae-Quercetum) of the Mazovian Lowland. – Fragmenta faunistica, Warszawa 34: 73-94.
- WYTWER, J., 1992. Chilopoda communities of the fresh pine forest of Poland. – Pp. 205-211 in E. MEYER, K. THALER & W. SCHEDL, (eds.) Advances in Myriapodology – Berichte des naturwissenschaftlich-medizinischen Vereins in Innsbruck, Supplement 10.
- WYTWER, J., 1995. Faunistical relationships between Chilopoda of forest and urban habitats in Mazowia. – Fragmenta faunistica, Warszawa 38: 87-133.
- WYTWER, J., 1996. Chilopoda of urban greens in Warsaw. – Pp. 213-220 in J. J. GEOFFROY, J. P. MAURIES & M. NGUYEN DUY-JACQUEMIN (eds.) Acta Myriapodologica – Mémoires du Museum National d'Histoire Naturelle 169.
- WYTWER, J., 2000. Centipede (Chilopoda) communities of some forest habitats of Puszcza Białowieża in Poland. – Fragmenta faunistica, Warszawa 43 Supplement: 333-342.
- WYTWER, J. & K. TAJOVSKÝ, 2005. Centipedes in the spruce forests of the Moravskoslezske Beskydy Mountains, Czech Republic. – Pp. 211-215 in K. TAJOVSKÝ, J. SCHLAGHAMERSKÝ & V. PIŽL (eds.) Contributions to Soil Zoology in Central Europe I. Institute of Soil Biology, České Budějovice.
- ZALESSKAJA, N. T., 1994. The centipede genus *Lamyctes* Meinert, 1868, in the environs of Manaus, Central Amazonia, Brazil (Chilopoda, Lithobiomorpha, Henicopidae). – Amazoniana 13: 59-64.
- ZERM, M., 1997. Distribution and phenology of *Lamyctes fulvicornis* and other lithobiomorph centipedes in the floodplain of the Lower Oder Valley, Germany (Chilopoda, Henicopidae, Lithobiidae). – Entomologica Scandinavica Supplement 51: 125-132.
- ZULKA, K. P., 1991. Überflutung als ökologischer Faktor: Verteilung, Phänologie und Anpassungen der Diplopoda, Lithobiomorpha und Isopoda in den Flussauen der March. – Dissertation, University of Vienna.
- ZULKA, K. P., 1999. Terrestrische Arthropoden. – Pp. 259-271 in J. KELEMEN & I. OBERLEITNER (eds.) Fließende Grenzen. Lebensraum March Thaya-Auen. Umweltbundesamt, Wien.



## Chapter 16

# CHILOPODA – GEOGRAPHICAL DISTRIBUTION

Lucio Bonato & Marzio Zapparoli

Chilopoda have an almost worldwide distribution, inhabiting most continents, major islands and oceanic islands. No records are known from Antarctica, most parts of Greenland, the American and Asiatic arctic islands, as well as from a large part of the western Saharan Africa, the latter probably for lack of research.

As far as is known, maximum phyletic diversity and species richness are in temperate and subtropical North America and in southern Europe; relatively high diversity and richness are also found in southern Africa and in the Japanese archipelago. A gradient of species richness from higher latitudes to temperate and subtropical areas, and a less evident gradient from the equatorial belt to subtropical and temperate regions are recognizable. However, it is hard to assess how much this pattern is affected by a geographical bias in faunistic investigation.

### *Distribution of major lineages*

SCUTIGEROMORPHA (ca. 95 spp.) are present in all continental lands with the exception of the northernmost areas, also in major islands and many oceanic islands. No records are known from some subtropical and temperate areas of South America and from some sub-Saharan regions. Maximum diversity and richness are in southern and eastern Africa, the Indian peninsula, south-eastern Asia and Australia.

Scutigeridae (ca. 50 spp.) are almost worldwide, distributed in all continental lands to the exception of the northernmost areas, in all major islands and many oceanic islands. Many records refer to introduced populations, e.g., of *Scutigera coleoptrata*. Maximum diversity and richness are in Australia and south-eastern Asia; within the Americas, Europe and Africa, species numbers are higher in temperate than in tropical regions.

Pselliodidae (ca. 3 spp.) are restricted to tropical and subtropical regions of the Americas and Africa.

Scutigerinidae (3 spp.) inhabit only southern Africa and Madagascar.

LITHOBIOMORPHA (ca. 1100 spp.) are almost worldwide in distribution, including some northernmost and southernmost regions and islands. No records are known from some

tropical and subtropical regions in the Americas, Saharan and sub-Saharan areas, Arabia and south-eastern Asia. Maximum diversity and richness are in all temperate continental areas.

Lithobiidae (ca. 1000 spp.) are present mainly in the continental areas of the Boreal hemisphere. The few records from tropical regions and the Austral hemisphere are mostly due to introductions (e.g. *Lithobius forficatus*, *L. obscurus*, *L. peregrinus*, *Bothroplys rugosus*), though some native taxa occur (e.g., species of *Australobius*). Maximum diversity and richness in North America, but the status of many taxa needs to be revised (Eason, 1974); high species numbers also from the Mediterranean region and continental Asia.

Henicopidae (ca. 120 spp.) range in all continents to the exception of Antarctica, in major islands and some oceanic islands; only scattered records are known from tropical regions. Maximum diversity and richness are in temperate continental areas of the Austral hemisphere, secondarily in the temperate part of North America. Many records from the Boreal hemisphere refer to introduced taxa (e.g., *Lamyctes caeculus*, *L. emarginatus*, *Ghilaroviella*, *Rhodobius*).

CRATEROSTIGMOMORPHA (2 spp.) are restricted to Tasmania and New Zealand.

SCOLOPENDROMORPHA (ca. 700 spp.) inhabit all continents to the exclusion of Antarctica, and are also present on all major islands and many oceanic islands. No records are known from most of the western Sahara and some areas in Asia. Maximum diversity and richness are in all tropical and subtropical regions.

Scolopendridae (ca. 400 spp.) inhabit continental areas to the exception of Antarctica and a large temperate part in the Boreal hemisphere, northwards reaching the internal part of North America, southern Europe and central Asia; also all major islands and many oceanic islands. Many records are due to introductions, mainly to oceanic islands (e.g. *Scolopendra morsitans*, *S. subspinipes*). Maximum diversity and richness are in all subequatorial regions and in some subtropical areas in the Austral hemisphere.

Cryptopidae (ca. 170 spp.) range almost worldwide, being present in most continents, all major islands and some oceanic islands. No records are known from some parts of Central and South America, south-eastern Asia, and a large area including Sahara throughout the Arabian peninsula to central Asia. Maximum diversity and richness are in the temperate North and South America, Europe and the Mediterranean region, central and southern Africa, Madagascar, and Australasia.

Mimopidae (1 sp.) are limited to northern China.

Plutoniumidae (6 spp.) are present in the south-western and eastern part of North America, as well as the Mediterranean region.

Scolopocryptopidae (ca. 80 spp.) are present in the Americas, excepting the northernmost and southernmost regions, and in easternmost Asia, from China and the Japanese region to the Malay archipelago, as well as in Africa and the Fiji islands. Maximum diversity and richness are in tropical Americas.

GEOPHIOMORPHA (ca. 1250 spp.) are distributed in continental areas to the exclusion of Antarctica, including the northernmost and southernmost regions, all major islands and most oceanic islands. No records are available from some areas in western Africa, in South America, and in continental Asia. Maximum diversity and richness are in the temperate and subtropical part of North America, most of South America, the Mediterranean basin, the southernmost Africa, the Japanese region and south-eastern Asia.

Geophilidae (ca. 560 spp.) are almost worldwide, to the exclusion of Antarctica and some areas in western Africa and southern and south-eastern Asia. Maximum diversity and richness are in the south-western part of North America and in southern Europe; a high number of species is also found in South America, southern Africa and Australasia.

Aphilodontidae (ca. 15 spp.) range in temperate South America and southernmost Africa. Maximum diversity is in South America.

Ballophilidae (ca. 80 spp.) are present in tropical and subtropical Americas and Africa, Madagascar, islands in the Indian Ocean, south-eastern Asia and Oceania. Maximum diversity and richness are in the Americas, with a high species number also found in Africa and south-eastern Asia.

Dignathodontidae (ca. 20 spp.) inhabit the whole Mediterranean region, from Macaronesia to the Caucasus, northwards reaching western and central Europe. Maximum diversity and richness are in the eastern part of the range.

Eriphantidae (1 sp.) are restricted to the Baja California peninsula.

Gonibregmatidae (ca. 15 spp.) inhabit Madagascar, the Indian peninsula, south-eastern Asia, Australasia and the Fiji islands. Maximum diversity and richness are in Indonesia.

Himantariidae (ca. 70 spp.) are distributed from south-western North America to Mexico; from Macaronesia, through the Mediterranean region and central Asia, to the Indian peninsula; also in the Korean peninsula and Japanese islands. The few records from other regions are probably due to introduction. Maximum diversity and richness are in the Californian-Mexican region and in southern Europe.

Linotaeniidae (ca. 50 spp.) are mainly distributed in the Boreal hemisphere (North America southwards to Mexico, and temperate Eurasia); also in the southern Andes. Maximum diversity and richness are in North America, central Europe and Japan.

Macronicophilidae (4 spp.) are restricted to subequatorial South America.

Mecistocephalidae (ca. 170 spp.) range mainly in most tropical and subtropical lands. Maximum diversity and richness are in eastern Asia from Japan to the Malay archipelago; a high number of species is also found in southern Asia.

Neogeophilidae (4 spp.) inhabit a limited area in Central America.

Oryidae (ca. 45 spp.) are distributed in most of the Americas, some areas in Africa, Madagascar, southern and eastern Asia, Australia and Pacific islands. Maximum diversity and richness are in the tropical South America, south-eastern Africa and Madagascar.

Schendylidae (ca. 220 spp.) are spread in the Americas, most of Eurasia, the whole of Africa, Madagascar, western Australia, New Caledonia, Hawaii and Fiji islands. Maximum diversity and richness are in North and South America and southern Europe, with a high number of species also in Japan and southern Africa.

### *Distributional patterns*

Some taxa richest in species have a very broad geographic range (among the genera, *Scutigera*, *Lamyctes*, *Lithobius*, *Cormocephalus*, *Cryptops*, *Scolopendra*, *Geophilus*), but their current circumscription is often composite, being possibly polyphyletic or paraphyletic, and distribution is altered by extensive introductions through human activity (Eason, 1974). Some lineages are also largely widespread because of the high dispersal ability of some species (*Pachymerium*, *Tuoba*). Of the genera and other main lineages with a narrower range, the most frequent distributional patterns are highlighted in the following (see also Bonato et al., 2009). Selected examples are in parentheses.

Within the temperate regions of the Boreal hemisphere only a few lineages are widespread in large parts of both North America and Eurasia (*Lithobiidae* to the exclusion of introduced populations, *Ethopolyinae*, *Arctogeophilus*, *Escaryus*, *Strigamia*) (Eason, 1992; Pereira & Hoffman, 1993). Some are distributed in both North America and eastern Asia (*Arrup*), a few also extending to south-eastern Asia or to Australia (*Bothropolys*, *Zygethobiini*, *Queenslandophilus*).

Some lineages are widespread in the tropical parts of all or almost all continents (*Scolopendrini*, particularly *Arthrorhabdus*; *Otostigmata*, particularly *Otostigmus* and *Rhysida*; *Ballophilidae*, particularly *Ballophilus*; *Oryidae*, particularly *Orphnacetus*). Others are limited to the tropical regions of some continents only: America and Africa (*Psellioididae*, *Ctenophilus*; Pereira & Demange, 1997); Africa, Asia and Oceania (*Asanadini*, particularly *Asanada*).

In the Austral hemisphere, only a few lineages are present on all the temperate continental lands, including South America, southernmost Africa, Madagascar, Indian peninsula, Australia, New Zealand and subantarctic islands (*Paralamyctes*; Edgecombe, 2001; Giribet & Edgecombe, 2006). Instead, different lineages are distributed on more than one subcontinent: the southernmost parts of both South America and Africa (Aphilodontidae, particularly *Aphilodon*; *Plateurytion*); the most southern parts of South America and the Australian region (*Anopsobius*, possibly introduced to southern Africa; *Pachymerinus*); Indian region and Australia (*Thereuopodina*).

Many lineages, mostly of lithobiomorphs and geophilomorphs, are exclusive or almost exclusive of the temperate part of North America. Some of them are widespread in the region (*Zygethobius*, *Arenophilus*; the latter possibly introduced in England), others are limited to the eastern or the south-eastern parts (*Sonibius*), or range along the western regions (*Oabius*, *Damothus*). Many lineages are limited to the south-western part of North America, namely California and surrounding areas (*Gosibius*, *Pseudolithobius*, *Kethopinae*, *Eriphantidae*), sometimes also extending to Mexico (*Chomatobius*).

Some lineages are distributed in most of tropical America, including the continental lands of Central America, the Antilles and the northern part of South America (*Newportiinae*, *Notiphilides*). Many lineages are present in the continental part of Central America only (*Atethobius*, *Cruzobius*, *Ectonocryptopinae*, *Chomatophilus* and *Neogeophilidae*), sometimes extending northwards to south-eastern North America (*Hemiscolopendra*, *Gosipina*, *Nothobius*, *Sogona*). A few are limited to Central America and the Antilles (*Piestophilus*, *Polycricus*, *Telocricus*).

Some lineages are limited to the subequatorial and tropical South America (*Scolopendropsis*, *Hyphydrophilus*, *Macronicophilus*) or to temperate South America (*Brasiloscutigera*, *Analamyctes*, *Apogophilus*, *Chilenophilus*, *Schendyloides*).

Many lineages, especially in Geophilomorpha, are distributed around the Mediterranean basin. Some of them are widespread in most of the Mediterranean region (*Eupolybothrus*, *Himantarium*, *Gnathoribautia*), sometimes extending to Macaronesia and the Caucasus (Dignathodontidae including *Dignathodon* and *Henia*, *Nannophilus*). Some of these are limited to the western part of the region (*Tachythereua*, *Plutonium*, *Stigmatogaster*), some others to the eastern part (*Harpolithobius*, *Pleurolithobius*, *Clinopodes*, *Stenotaenia*, *Thracophilus*).

Some lineages are limited to a narrow area in central Asia (*Dzhungaria*, *Ghilaroviella*, *Schizotergitus*, *Krateraspis*, *Taschkentia*). Others extend from central Asia to the Mediterranean basin (*Hessebius*, *Bothriogaster*, *Polyoporogaster*), or to east and south-eastern Asia (*Cermatobius*). Lineages restricted to areas in the eastern continental part of Asia

include *Dakrobius*, Pterygoterginae, *Validifemur*, Mimopidae. Others are exclusive to the Japanese islands (*Shikokuobius*, *Takashimaia*).

Some lineages are limited to tropical Africa (*Schizotaenia*), others to southernmost Africa (*Polygonarea*), sometimes also to Madagascar (Scutigerinidae, particularly *Scutigerina*).

Many lineages are distributed in south-eastern Asia and surrounding regions (*Thereupoda*, *Anopsobiella*, *Australobius*, Arrhabdotini, Sterropristini, *Anarrup*, *Eucratonyx*, *Tygarrup*).

Many other lineages are restricted to the Australian region, including mainland Australia and Tasmania, New Zealand, New Caledonia and other islands (*Henicops*; Edgecombe et al., 2006), most often only in some of these islands (Craterostigmomorpha, *Maoriella*, *Zelanophilus*). Some are exclusive to Australia (*Prionopodella*, *Prothereua*, *Pilbarascutigera*, *Notiasemus*, *Australoschendyla*), or to New Caledonia (*Easonobius*, *Campylostigmus*).

Highly disjunct geographic ranges, probably relics of a former more widespread distribution, are also known. Many of these encompass disjunct areas in the Boreal hemisphere, e.g. *Pseudolithobiinae* (south-western North America and south-western Asia; Eason, 1992), *Plutoniumidae* and particularly *Theatops* (southern part of North America and Mediterranean region), and *Dicellophilus* (south-western North America, central Europe and Japan; Bonato et al., 2010). Other unusual disjunct geographic ranges are those of *Anopsobiinae* (most species in Australasia, South America and southern Africa, but also a few species isolated in central Asia, Japan and Indochina; Edgecombe & Giribet, 2003, 2004), *Dinocryptops* (Neotropics and eastern Asia), *Paracryptops* (Indian peninsula to New Guinea, and Antilles), *Marsikomerus* (a restricted area of North America and the Hawaii Islands; Hoffman & Pereira, 1991), and *Mesocanthus* (Indian peninsula and northern Africa).

### *The centipede fauna of major regions*

The following major sub-continental regions are broadly identifiable as hosting a distinct centipede fauna. For each region exemplary genera, selected among the most rich in species, are given in parentheses.

*Temperate North America, to the exclusion of the south-western regions.* – This area is very rich in representatives of the Lithobiomorpha, chiefly Lithobiidae (*Bothropolys*, *Gosibius*, *Neolithobiuss*, *Oabius*, *Paitobius*), with some exclusive genera such as *Garibius*, *Nambabius*, *Sonibius*. Also rich in species are Geophilomorpha, mainly represented by Geophilidae (*Arctogeophilus*, *Arenophilus*, *Geophilus*), with many endemic genera; also present are

Himantariidae, Linotaeniidae (*Strigamia*), and Schendylidae (*Escaryus*). Scolopendromorpha include Scolopendridae (*Scolopendra*), Cryptopidae (*Cryptops*), Plutoniumidae (*Theatops*), and Scolopocryptopidae (*Scolopocryptops*), with the exclusive Kethopinae. Only a few Scutigeromorpha are present.

*Between the south-western part of North America and Mexico.* – This region hosts one of the richest centipede faunas in the world, with almost half of the genera endemic to the region. Dominant in diversity are Lithobiomorpha, mostly Lithobiidae (*Gosibius*, *Neolithobius*, *Oabius*), and Geophilomorpha, mainly represented by Geophilidae (*Polycricus*, *Sogona*), secondarily Himantariidae (*Chomatobius*), Schendylidae (*Nyctunguis*) and other families. Exclusive to the region are many genera of lithobiomorphs and geophilomorphs, and two families of the latter group (Eriphantidae and Neogeophilidae). Scolopendromorpha include Cryptopidae (*Cryptops*), Scolopendridae (*Scolopendra*), Scolopocryptopidae (*Newportia*), and the exclusive Ectonocryptopinae. A few Scutigeridae and Pselliodidae are also present.

*Caribbean region, including Antilles and surrounding islands.* – The fauna is dominated by Geophilomorpha and Scolopendromorpha. Geophilomorpha mostly include Ballophilidae (*Ityphilus*), Geophilidae (*Polycricus*, *Telocricus*), Oryidae, and Schendylidae, with a few exclusive genera. Scolopendromorpha include mainly Scolopendridae (*Cormocephalus*), as well as Cryptopidae and Scolopocryptopidae (*Newportia*). Lithobiomorpha and Scutigeromorpha are very poorly represented (the latter with single species of *Dendrothereua* and *Sphendononema*).

*Tropical South America.* – Most species belong to Scolopendromorpha, mainly to Scolopendridae (*Cormocephalus*, *Otostigmus*, *Rhysida*), with the exclusive *Scolopendropsis*, and to Scolopocryptopidae (*Newportia*, *Scolopocryptops*). Also very diverse are the Geophilomorpha, mainly represented by Ballophilidae (*Ityphilus*), Geophilidae (*Ribautia*) and Schendylidae (*Pectiniunguis*, *Schendylops*); many genera are exclusive, as is the family Macronicophilidae (Pereira et al., 1997). Poorly represented are Scutigeromorpha, with species of Pselliodidae and Scutigeridae, and Lithobiomorpha, mainly Henicopidae (*Lamyctes*).

*Southern, temperate part of South America.* – Geophilomorpha are dominant and mainly represented by Geophilidae (*Plateurytion*), Schendylidae (*Schendylops*), and Aphilodontidae; many genera are exclusive, e.g. *Apogeophilus*, *Chilenophilus*, *Dinogeophilus*, *Mecistauchenus*, *Mecophilus*, *Metaxythus*, *Schendyloides*, and *Trematorya*. Less rich are Scolopendromorpha, mostly represented by Cryptopidae (*Cryptops*) and Scolopendridae (*Otostigmus*) with the exclusive *Akymnopellis*, and Lithobiomorpha, mainly represented by

Henicopidae (*Anopsobius*, *Lamyctes*) with the exclusive *Analamyctes* and *Catanopsobius*. Scutigeromorpha are very few, all belonging to Scutigeridae.

*Temperate Eurasia.* – Most species belong to Lithobiomorpha, mainly Lithobiidae (*Lithobius*), with the exclusive *Dakrobius*, *Pterygotergum* and *Schizotergitus*, but also a few Henicopidae, with the exclusive *Ghilaroviella* and *Hedinobius*. Geophilomorpha are highly diverse and include mainly Geophilidae (*Geophilus*) and Schendylidae (*Escaryus*, *Schendyla*); also present are Linotaeniidae (*Strigamia*) and other families. Relative few Scolopendromorpha are present, including Cryptopidae, Scolopendridae and the exclusive, localized Mimopidae. Scutigeromorpha are only represented by Scutigeridae.

*Mediterranean region, eastwards to Caucasus and westward to Macaronesia.* – This region hosts one of the richest centipede fauna of the world (more than 500 species in more than 50 genera), with almost 40% of the genera restricted to this region. Most species belong to Lithobiomorpha, mainly Lithobiidae (*Harpolithobius*, *Lithobius*), with some endemic genera such as *Eupolybothrus* and *Pleurolithobius*. Geophilomorpha are diverse as well (Bonato & Minelli, 2009), mainly with Dignathodontidae (*Henia*), Geophilidae (*Geophilus*), Himantariidae (*Haplophilus*) and Schendylidae (*Schendyla*), but also Linotaeniidae and other families; many genera are exclusive, e.g. *Clinopodes*, *Dignathodon*, *Gnathoribautia*, *Haploschendyla*, *Nannophilus* and *Thracophilus*. Less numerous are Scolopendromorpha, mainly represented by Cryptopidae (*Cryptops*) and Scolopendridae (*Scolopendra*), but also including Plutoniumidae, with the exclusive *Plutonium*. Scutigeromorpha only include few Scutigeridae, notably the endemic, localized *Tachythereua*.

*Japanese archipelago, Korean peninsula and Taiwan.* – Lithobiidae (*Bothropolys*, *Lithobius*) form the bulk of Lithobiomorpha but Henicopidae are also present, with the exclusive *Shikokuobius*. Geophilomorpha mainly include Mecistocephalidae (*Arrup*, *Mecistocephalus*), with the exclusive *Proterotaiwanella* and *Takashimaia*; also present are Geophilidae (*Geophilus*), Linotaeniidae (*Strigamia*) and Schendylidae (*Escaryus*), with the exclusive *Falcaryus*, and fewer representatives of other families. Also relatively rich are Scolopendromorpha, which include especially Scolopendridae (*Otostigmus*), but also Cryptopidae and Scolopocryptopidae (*Scolopocryptops*). Scutigeromorpha are represented only by Scutigeridae (*Thereuopoda*, *Thereuonema*).

*Central Africa.* – Most species belong to Scolopendromorpha, which include Cryptopidae (*Cryptops*) and Scolopendridae (*Alipes*, *Cormocephalus*, *Otostigmus*), secondarily to Geophilomorpha, mainly represented by Geophilidae (*Ribautia*, *Schizotaenia*), but also Ballophilidae (*Ballophilus*), Mecistocephalidae, Schendylidae and Oryidae, these latter with exclusive genera, e.g. *Lamotteophilus*. Also quite diverse are Scutigeromorpha,

represented by Scutigeridae and Psellioididae. The number of Lithobiomorpha is very low, all Henicopidae (*Lamyctes*, *Lamyctopristus*).

*Southernmost part of Africa.* – The fauna is dominated by Geophilomorpha and Scolopendromorpha. Geophilomorpha are mainly represented by Geophilidae (*Geoperingueyia*, *Polygonarea*), with some exclusive genera, but also Aphilodontidae (*Aphilodon*), Schendylidae and Oryidae, with the exclusive *Aspidopleres* and *Diphtherogaster*. Scolopendromorpha mainly include Scolopendridae (*Cormocephalus*), but also Cryptopidae. Lithobiomorpha are mostly represented by Henicopidae (*Lamyctes*, *Lamyctopristus*, *Paralamyctes*). Scutigeromorpha are few, but include the geographically restricted Scutigerinidae.

*Madagascar.* – Most species belong to Scolopendromorpha, especially Cryptopidae (*Cryptops*) and Scolopendridae (*Cormocephalus*), and Geophilomorpha, mainly Mecistocephalidae (*Mecistocephalus*) and Oryidae (*Orphnaeus*). Low in diversity but not uncommon are Scutigeromorpha, which are represented by Scutigeridae (*Scutigera*) and Scutigerinidae, the latter with the exclusive *Madagassophora*, and Lithobiomorpha, only represented by Henicopidae.

*Indian peninsula and surrounding regions, including Ceylon and Maldives, northwards to the Himalayas.* – Scolopendromorpha are very rich in species and predominantly represented by Scolopendridae (*Otostigmus*, *Rhysida*, *Scolopendra*), but also Cryptopidae. Relatively rich are also Lithobiomorpha, which mainly include Lithobiidae (*Australobius*, *Lithobius*), and Geophilomorpha, especially Himantariidae (*Mesocanthus*, *Polyporogaster*) and Mecistocephalidae (*Mecistocephalus*). Scutigeromorpha are represented only by Scutigeridae (*Thereuonema*, *Thereuopoda*, *Thereuopodina*).

*South-eastern Asia, from the Indochinese peninsula to the Malay Archipelago.* – Scolopendromorpha are rich and diverse, including Scolopendridae (*Otostigmus*, *Scolopendra*), with the exclusive Arrhabdotini and Sterropristini, Cryptopidae (*Cryptops*), with the exclusive *Tonkinodentus*, and Scolopocryptopidae. Also diverse are Geophilomorpha, which mainly include Mecistocephalidae (*Mecistocephalus*), with the exclusive *Anarrup*, but also Ballophilidae (*Ballophilus*), Geophilidae with some exclusive genera, Gonibregmatidae (*Gonibregmatus*) and other families. Lithobiomorpha mainly include Lithobiidae (*Australobius*, *Lithobius*), but also Henicopidae, including the exclusive *Anopsobiella*. Scutigeromorpha are represented by Scutigeridae only (*Parascutigera* and *Thereuopoda*).

*New Guinea.* – Scolopendromorpha are diverse and represented mainly by Scolopendridae (*Cormocephalus*, *Ethmostigmus*, *Otostigmus*), but also Cryptopidae (*Paracryptops*) and Scolopocryptopidae (*Scolopocryptops*). Much less diverse are

Geophilomorpha, which include mainly Mecistocephalidae (*Mecistocephalus*), some Gonibregmatidae and a few species of other families. Scutigeromorpha are present with Scutigeridae, including the endemic *Ballonema* and *Podothereua*, whereas Lithobiomorpha are represented by a few Lithobiidae only (*Australobius*).

*Australia.* – Scutigeromorpha are relatively rich, although represented only by Scutigeridae (mostly *Allothereua* and *Parascutigera*), with the some exclusive genera such as *Pilbarascutigera*, *Prionopodella* and *Prothereua* (Edgecombe, 2008). Relatively lower is the number of representatives for all other orders. Indigenous Lithobiomorpha only include Henicopidae (mostly *Anopsobius*, *Dichelobius*, *Henicops*, and *Paralamyctes*). Scolopendromorpha mainly include Scolopendridae (*Arthrorhabdus*, *Cormocephalus*, *Ethmostigmus*, *Rhysida*, *Scolopendra*) and Cryptopidae (*Cryptops*). Geophilomorpha are represented mainly by Geophilidae (*Ribautia*), secondarily by Mecistocephalidae (*Mecistocephalus*) and fewer Ballophilidae, Oryidae and Schendylidae, the last one with the exclusive *Australoschendyla*. Tasmania is part of the distributional range of Craterostigmomorpha.

*New Zealand.* – Most species belong to Geophilomorpha, mainly Geophilidae (*Maoriella*, *Steneurytion*, *Zelanophilus*) but also Ballophilidae, and Scolopendromorpha, which are represented by Cryptopidae (*Cryptops*) but few Scolopendridae (*Cormocephalus*). Lithobiomorpha include only Henicopidae (*Anopsobius*, *Lamyctes*, *Paralamyctes*), whereas Scutigeromorpha are present with a single species. Craterostigmomorpha are widely distributed but with a single species only.

*Pacific islands.* – A large number of species are Geophilomorpha, mainly Mecistocephalidae (*Mecistocephalus*) but also Ballophilidae, Geophilidae, Gonibregmatidae, Oryidae, and Schendylidae. Quite rich are also Scolopendromorpha, which are represented by Cryptopidae (*Cryptops*), Scolopocryptopidae and Scolopendridae (*Cormocephalus*, *Otostigmus*), with *Campylostigmus* exclusive to New Caledonia. Scutigeromorpha are mainly represented by few Scutigeridae (*Parascutigera*). Poorly represented are Lithobiomorpha, with a small number of Henicopidae (*Lamyctes*), including *Pleotarsobius*, which is exclusive to the Hawaii islands.

### References

- BONATO, L., S. BEVILACQUA & A. MINELLI, 2009. An outline of the geographical distribution of world Chilopoda. – Contributions to Natural History, Bern 12: 489–503.  
BONATO, L., L. DANYI & A. MINELLI, 2010. Morphology and phylogeny of *Dicellophilus*, a centipede genus with highly disjunct distribution (Chilopoda, Mecistocephalidae). – Zoological Journal of the Linnean Society 158: 501–532.

- BONATO, L. & A. MINELLI, 2009. Geophilomorph centipedes in the Mediterranean region: revisiting taxonomy opens new evolutionary vistas. – *Soil Organisms* 81: 489–504.
- EASON, E. H., 1974. On certain aspects of the generic classification of the Lithobiidae with special reference to geographical distribution. – *Symposia of the Zoological Society of London* 32: 65–73.
- EASON, E. H., 1992. On the taxonomy and geographical distribution of the Lithobiomorpha. – *Bericht des naturwissenschaftlich-medizinischen Vereins in Innsbruck, Supplement* 10: 1–9.
- EDGECOMBE, G. D., 2001. Revision of *Paralamyctes* (Chilopoda: Lithobiomorpha: Henicopidae) with six new species from Eastern Australia. – *Records of the Australian Museum* 53: 201–241.
- EDGECOMBE, G. D., 2008. Gonopod segmentation and the Australian centipede *Prionopodella* (Chilopoda): testing a basal position in the Scutigeromorpha. – *Journal of Natural History* 42: 1289–1301.
- EDGECOMBE, G. D., D. J. COLGAN & D. SHARKEY, 2006. Phylogeny and biogeography of the Australian centipede *Henicops* (Chilopoda: Lithobiomorpha): a combined morphological and molecular approach. – *Insect Systematics & Evolution* 37: 241–256.
- EDGECOMBE, G. D. & G. GIRIBET, 2003. Relationships of Henicopidae (Chilopoda: Lithobiomorpha): new molecular data, classification and biogeography. – *African Invertebrates* 44: 13–38.
- EDGECOMBE, G. D. & G. GIRIBET, 2004. Molecular phylogeny of Australasian Anopsobiinae centipedes (Chilopoda: Lithobiomorpha). – *Invertebrate Systematics* 18: 235–249.
- GIRIBET, G. & G. D. EDGECOMBE, 2006. The importance of looking at small-scale patterns when inferring Gondwanan biogeography: a case study of the centipede *Paralamyctes* (Chilopoda, Lithobiomorpha, Henicopidae). – *Biological Journal of the Linnean Society* 89: 65–78.
- HOFFMAN, R. L. & L. A. PEREIRA, 1991. Systematics and biogeography of *Marsikomerus* Attems, 1938, a misunderstood genus of centipedes (Geophilomorpha: Schendylidae). – *Insecta Mundi* 5: 45–60.
- PEREIRA, L. A. & J.-M. DEMANGE, 1997. Nouvelle contribution à la connaissance du genre *Ctenophilus* Cook, 1896, à répartition géographique disjointe (Myriapoda, Chilopoda, Geophilomorpha, Schendylidae). – *Zoosystema* 19: 293–326.
- PEREIRA, L. A., D. FODDAI & A. MINELLI, 1997. Zoogeographical aspects of Neotropical Geophilomorpha. – *Entomologica Scandinavica* 51 supplement: 77–86.
- PEREIRA, L. A. & R. L. HOFFMAN, 1993. The American species of *Escaryus*, a genus of holoartic centipedes (Geophilomorpha, Schendylidae). – *Jeffersoniana* 3: 1–72.



## Chapter 17

# CHILOPODA – PHYLOGENY

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Chilopod phylogenetics is in a relatively advanced state for myriapods as a whole. Extensive comparative studies of morphology, a phase of Hennigian argumentation followed up by numerical cladistic analyses, and sampling of the major chilopod groups for several molecular loci that are widely used in arthropod phylogenetics have led to the relationships of the main chilopod clades being well resolved. The scheme of ordinal interrelationships on which this review is based (Fig. 17.1) is widely endorsed by morphologists, and all nodes are strongly supported with relatively little character conflict between different kinds of morphological data. The results are largely congruent with the genes that to date have the most exhaustive taxonomic coverage, nuclear ribosomal 18S and 28S rRNA (Edgecombe et al., 1999; Giribet et al., 1999; Edgecombe and Giribet, 2002, 2004), though the relationships of Craterostigmomorpha in particular present a conflict with morphology (Mallatt and Giribet, 2006; Mallatt et al., 2010; Murienne et al., 2010) that has also been identified using nuclear protein-coding genes (Regier et al., 2005, 2010).

Historical perspectives on the interrelationships of the major chilopod groups were summarised in a landmark analysis by Dohle (1985), addressing such classical questions as whether the most basic division of chilopods is between taxa with anamorphic and epimorphic development (Anamorpha and Epimorpha) or, alternatively, between taxa with dorsal or ventral spiracles (Notostigmophora and Pleurostigmophora, respectively). Dohle concluded that morphological evidence decisively supports the latter scheme, and his cladogram is similar to phylogenetic trees produced earlier by Prunescu (1965) and Shinohara (1970), and anticipated by the classifications of Pocock (1902) and Verhoeff (1902–25) as well as the phylogenetic reasoning of Fahlander (1938). With the application of cladistic argumentation, Anamorpha was exposed as a paraphyletic group (anamorphic development in scutigeromorphs and lithobiomorphs is shared with members of the other three myriapod classes and thus a primitive character).

Throughout this chapter, the numbering scheme for apomorphic characters in the text corresponds to the character support shown in Fig. 17.1. Discussions of most of these characters and supporting literature for their documentation can be found in

earlier analyses (Edgecombe et al., 1999; Edgecombe and Giribet, 2004). Among the morphology-based reviews either of chilopod phylogeny as a whole or evolution of particular organ systems, the scheme of relationship in Fig. 17.1 is endorsed and defended by Prunescu (1965, 1970, 1996), Shinohara (1970), Dohle (1985, 1990), Shear and Bonamo (1988), Borucki (1996), Hilken (1997), Minelli et al. (2000), Wirkner and Pass (2002), and Müller and Meyer-Rochow (2006a). Additional morphological evidence that has come to light since the Edgecombe and Giribet (2004) analysis is from descriptive and comparative studies on the eyes (Scutigeromorpha: Müller et al., 2003; Lithobiomorpha: Müller and Rosenberg, 2006; Craterostigmomorpha: Müller and Meyer-Rochow, 2006a; Scolopendromorpha: Müller and Meyer-Rochow, 2006b) and the peristomatic structures (Koch and Edgecombe, 2006, 2008 for Scutigeromorpha and Lithobiomorpha, respectively; Edgecombe and Koch, 2008, for Scolopendromorpha). Literature citations are mostly provided only for characters that post-date Edgecombe and Giribet (2004).

### *Chilopod monophyly*

Chilopods unite to the exclusion of other myriapods based on a few unambiguous autapomorphic characters identified by Dohle (1985):

1. second maxillae bearing embryonic egg teeth
2. first trunk appendage modified as a maxillipede (forcipule) housing a poison gland. Although not typically cited in the diagnosis of Chilopoda, specific details of the proportions of the forcipules can be identified as unique to Chilopoda, e.g., the enlarged, medially-confluent coxae with a reduced sternum, as well as the presence of three specific types of forcipular sensilla (Ernst and Rosenberg, 2003)
3. nucleus of the sperm bearing a spiral ridge

Additional characters that are autapomorphic for Chilopoda with the cladogram topology in Fig. 17.1 (but forced to reverse in Phylactometria or Epimorpha) include:

4. 15 pairs of locomotory trunk legs
5. alternation of long and short trunk tergites (heterotergy) apart from the two successive long tergites on the seventh and eighth segments. In the case of Scutigeromorpha, the corresponding region is part of a composite tergite covering leg-bearing segments 7–9
6. anisostigmophory (spiracles exclusively on segments bearing long tergites)
7. female gonopods that manipulate single egg

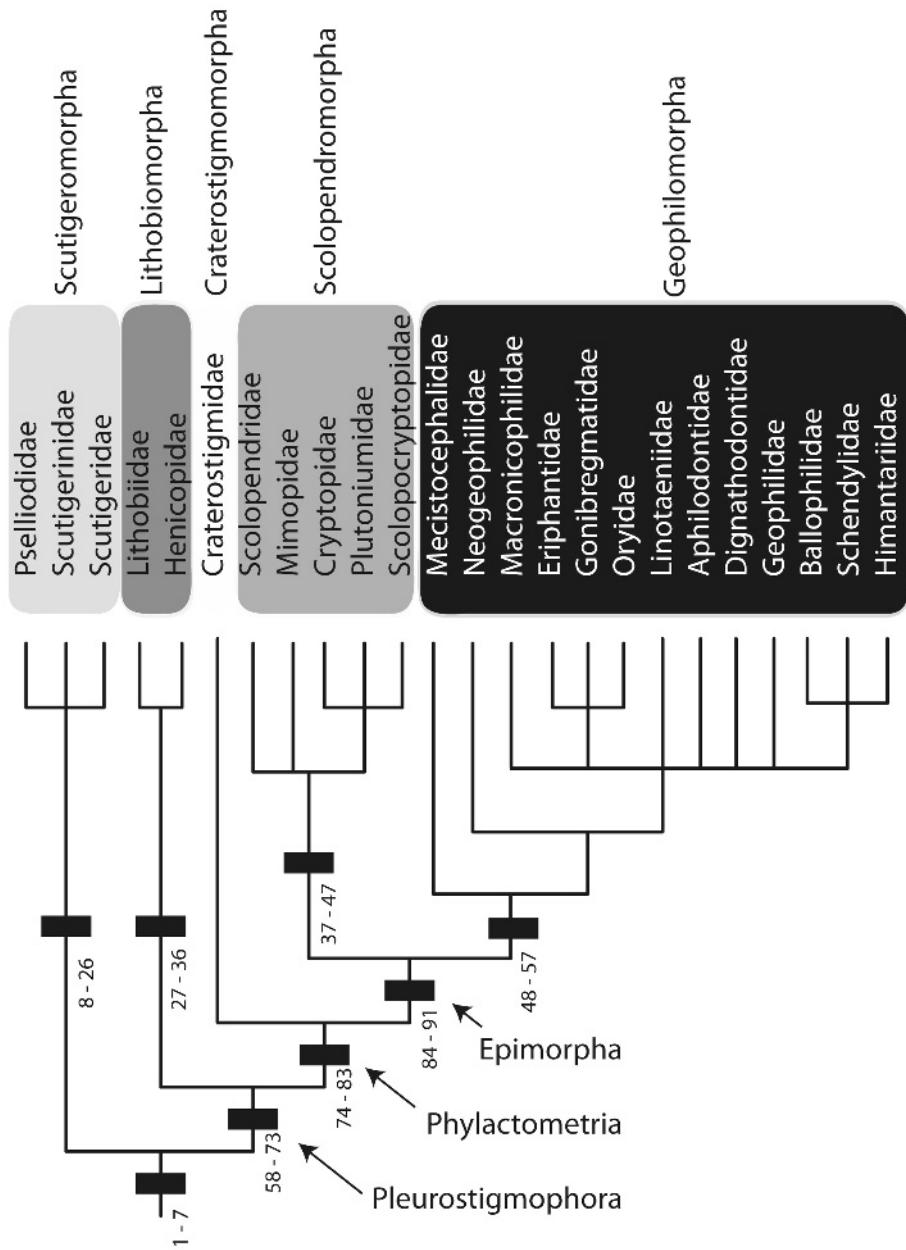


Fig. 17.1. Relationships of extant chilopod orders based on morphology, and the fundamental splits within the four large orders. Apomorphic characters 1-91 are listed in the text.

Sperm dimorphism (macrosperm and microsperm) is an ambiguous apomorphy for Chilopoda. This character is shared with Symphyla (Dallai and Afzelius, 2000), and is thus either a myriapod apomorphy that is lost in Dignatha (and in Geophilomorpha) or is convergent in chilopods and symphylans.

### *Monophyly of the extant chilopod orders*

Monophyly of Scutigeromorpha and Geophilomorpha has generally been considered a non-controversy because these groups possess obvious suites of unique characters. Paulus (1979, his fig. 6.33) was unable to specify any autapomorphies for Scolopendromorpha on a cladogram for chilopod groups, but this deficiency was rectified by Dohle (1985), who identified the single tergite covering the forcipular and first pedigerous segments and the bean-shaped spermatophore with its tough wall as strictly autapomorphic. In fact, scolopendromorph monophyly can be defended by a much larger suite of characters (Chagas et al., 2008). The only chilopod order for which monophyly has regularly been viewed as either weakly supported or even explicitly stated to be paraphyletic (Prunescu, 1996) is Lithobiomorpha. This misconception was addressed by Edgecombe (2004) and Edgecombe and Giribet (2004), who identified morphological details that are unique to Lithobiomorpha (with no necessity to posit that they are primitive characters for Pleurostigmophora as a whole), and lithobiomorph monophyly is strongly supported by molecular and combined morphological and molecular analyses (Edgecombe and Giribet, 2004; Giribet and Edgecombe, 2006).

Autapomorphic characters of the four large orders of Chilopoda are enumerated in the following section. Because Craterostigmomorpha consists of only two congeneric species that are distinguished by subtle morphological differences and the monophyly of the order is non-controversial, autapomorphies of *Craterostigmus*/Craterostigmomorpha are not listed here (see, e.g., seven autapomorphic characters from eye morphology alone identified by Müller and Meyer-Rochow, 2006a, their fig. 6).

#### *Scutigeromorpha*

8. antennae multiannulated flagella, divided into two or three sections by elongate nodes
9. antennal scape bearing the so-called Schaftorgan
10. distal cytoplasmic cone cell processes that each branch into two secondary processes and form two cone cell compartments (Müller et al., 2003; Müller and

Rosenberg, 2006)

11. hypopharynx projecting as an elongate tongue with pair of sclerotized forks on its frontal surface (Koch and Edgecombe, 2006)
12. button-like sensilla with ovate rims on the apex of the hypopharynx (Koch and Edgecombe, 2006)
13. epipharynx with a labral trapezoid delimited by lateral bars, with two groups of sensilla coeloconica medially (Koch and Edgecombe, 2006)
14. a chevron-shaped row of transversely-compressed, triangular denticles at the border between the labral and clypeal parts of the epipharynx (Koch and Edgecombe, 2006)
15. main laminae of the mandible separated by a broad membranous region, with the pulvillus (Haarpolster) situated on a discrete sclerite on the dorsal side of this desclerotised region
16. a maxillary organ housed in the coxal process of the first maxilla
17. second maxillae lacking terminal claws
18. rows of trichomes on the inner side of the tarsus of the second maxilla
19. forcipular coxosternite with four pairs of elongate spine-bristles and a corresponding spine-bristle on the forcipular prefemur
20. eight elongate tergites covering the trunk segments, including a single tergite over segments 7-9
21. tracheal lungs opening to a spiracle on the posterior part of each tergite
22. tracheae strengthened by a network of chitin fibres
23. legs pentagonal in cross-section, with the angles developed as ridges (carinae) that bear serrate files of spines
24. trunk legs with greatly elongated tarsi, subdivided into many annulations
25. paired tarsal papillae (Tarsalzapfen) and resilient sole hairs (federnde Sohlenhaare) on the ventral side of tarsus 2
26. female gonopods forcipulate, with a single articulation

*Lithobiomorpha*

27. a single transverse seta projecting medially from the labral side piece
28. a band of four clypeal setae in front of the labrum
29. bottle-shaped glandular openings at the border between the labral and clypeal parts of the epipharynx (Koch and Edgecombe, 2008)
30. brush-like setae on the inner margin of the distal article of the first maxillary

telopodite developed as paired rows of plumose setae that branch as slender hairs

31. plumose setae on the inner surface of the tarsus of the second maxillae
32. a translucent seta (porodont) on the lateral part of the forcipular dental margin
33. pretarsal accessory claws with an ornament that changes from pitted on its proximal part to linear ridges and grooves on its distal part (Edgecombe, 2004)
34. coxal pores on the last four legs (leg pairs 12-15), secondarily modified in some lineages to the last two, three or five pairs
35. female gonopod with its basal article bearing spurs (macrosetae) and terminal article with a broad claw. The claw has cuticular pits that each house a sensillum coeloconicum on the dorsodistal surface
36. first post-embryonic stage with seven leg pairs. A larger number of leg-bearing segments in the hatchling compared to Scutigeromorpha is a plausible apomorphy of Pleurostigmophora as a whole, but there is little basis for assuming that the fundamental number of seven leg pairs in Lithobiomorpha (modified to six or eight in a few lineages) is part of the pleurostigmophoran ground pattern rather than being a lithobiomorph autapomorphy.

#### *Scolopendromorpha*

37. the four laminae of the mandible intersecting at a cruciform suture
38. curled setae along the inner margin of the telopodite of the first maxilla
39. tarsus of the second maxillae bearing a dorsal brush on its inner face
40. a single row of bullet-shaped sensilla at the border between the labral and clypeal parts of the epipharynx (Edgecombe and Koch, 2008)
41. a single tergite covering the forcipular and first leg-bearing trunk segments
42. foregut relatively long (extending at least to trunk segment 5), differentiated into a crop and gizzard, the latter of which has plicate walls (Koch et al., 2009)
43. muscles attaching to the dorsal and ventral sides of spiracular pouches
44. genital segments retracted above the ultimate sternite
45. gonopods lacking in the female and usually in males (a genital appendage on the first genital segment in some species of a few scolopendrid genera is the only plausible homologue of a gonopod but its restriction to certain Scolopendriini makes it most unlikely that it is a retained primitive character);
46. left ejaculatory duct rudimentary or absent
47. spermatophores bean-shaped, with a multilayered wall

Two eye characters documented in *Scolopendra* by Müller and Meyer-Rochow (2006b) - a deeply sunken corneal lens that serves to differentiate the corneagenous layer and a much expanded and ramified basal matrix - were cited by Müller and Meyer-Rochow (2006a) and Müller and Rosenberg (2006) as apomorphies for Scolopendromorpha as a whole. This optimization is only valid if Scolopendridae retain characters of the common ancestor of all scolopendromorphs (including those that have lost the visual organs).

#### *Geophilomorpha*

48. ocelli lacking (the relatively compact brain of geophilomorphs is in part correlated with the suppression of optic neuropils)
49. a fixed number of 14 antennal articles
50. two lateral areas bearing sensilla basiconica on the terminal antennal article
51. mandibles relatively small and abducted by muscular movements without mobility of the anterior tentorial arms
52. trunk composed of at least 27 leg-bearing segments
53. trunk homonomous (no alternation of long and short tergites)
54. tergum of each trunk segment with two strongly delimited sclerites, a pretergite and metatergite
55. spiracles on all leg-bearing trunk segments apart from the first and ultimate
56. tracheal chiasmata (moultling rings), separated by spongiform trichomes
57. antennae and legs lacking regenerative capacity

#### *Notostigmophora vs. Pleurostigmophora*

The Pleurostigmophora hypothesis posits that Notostigmophora/Scutigeromorpha is sister group of all other chilopods. Numerical cladistic analyses (Edgecombe and Giribet, 2004) have strongly corroborated earlier Hennigian argumentation schemes (Dohle, 1985; Borucki, 1996) in defending the monophyly of Pleurostigmophora. Shared derived characters of this group include:

58. a flattened head capsule with the clypeus being bent ventrally and antennae shifted to the front of the head with their bases close together
59. mandible lacking a molar plate
60. greater rigidity of the second maxillary coxae
61. absence of a complete joint between the second maxillary trochanter and prefemur, which together comprise a trochanteroprefemur

- 62. medial coalescence of the forcipular coxae
- 63. coxal apodemes (Coxalplatten) on the forcipules
- 64. a forcipular tarsungulum formed by an unjointed tarsus and pretarsus
- 65. ultrastructurally similar coxal organs (see Chapter 4)
- 66. deposition of the spermatophore on a web that is produced by a penis or Spinngrieffel

Numerous details of eye morphology and ultrastructure are apomorphic for Pleurostigmophora under the Mandibulata concept, in which the faceted eye of Scutigeromorpha is viewed as plesiomorphic relative to the lateral ocelli of pleurostigmophorans (see “Phylogenetic relationships of Myriapoda” for evidence in favour of and against Mandibulata). These include the following characters (Müller and Rosenberg, 2006, their fig. 8):

- 67. cup-like lateral ocelli lacking a crystalline cone
- 68. a flat corneagenous epithelium lacking pigment grains
- 69. a multilayered distal retinula with cells forming compact, primarily circumapical rhabdomeres
- 70. a star- or net-like rhabdom composed of a single-layered proximal retinula with cells forming bi-directional, interdigitating rhabdomeres
- 71. unpigmented circumretinular sheath cells
- 72. a subretinal plexus of external pigment cells
- 73. a sculptured corneal surface

The polarity of pleural (versus dorsal) spiracles has long been controversial (e.g., Dohle, 1985 vs Klass and Kristensen, 2001 for different functional and phylogenetic scenarios), and the status of pleural spiracles as an additional apomorphic character of Pleurostigmophora is ambiguous. Another character that may prove to be an autapomorphy of Pleurostigmophora is specialised sensilla on antennal articles 2, 5, 9, and 13 of at least immature stadia (Lewis, 2000). Precise details of similar sensilla types are needed to strengthen this homology.

### *Phylactometria*

The systematic position of *Craterostigmus tasmanianus* (from which a second species in New Zealand, *C. crabilli* Edgecombe and Giribet, 2008, has been recently separated) has been one of the most intensely considered questions in chilopod systematics. Although relationships to Lithobiomorpha (Attempts, 1926) or to Scolopendromorpha (Manton,

1965) were advanced in early studies, most morphologists have agreed that *Craterostigmus* is sister group to Epimorpha (Prunescu, 1965, 1970, 1996; Shinohara, 1970; Dohle, 1985, 1990; Shear and Bonamo, 1988; Borucki, 1996; Hilken, 1997; Edgecombe et al., 1999; Minelli et al., 2000; Wirkner and Pass, 2002; Müller and Meyer-Rochow, 2006a; Müller and Rosenberg, 2006). The monophyletic group composed of Craterostigmomorpha and Epimorpha forms the basis for the taxon Phylactometria (Edgecombe and Giribet, 2004), united by the following apomorphic characters:

74. brooding involving the mother guarding the egg cluster by wrapping her body around it (primitively with the ventral side of the body against the eggs)
75. extraordinarily high cell numbers in the lateral ocelli (e.g., more than 1000 retinula cells) (Müller and Meyer-Rochow, 2006a, b)
76. proximal retinula cells partly with monodirectional rhabdomeres (Müller and Meyer-Rochow, 2006a, b)
77. maxillary nephridia lacking in postembryonic stadia
78. rigidity of the forcipules, a character complex including the forcipular pleurite arching over the coxosternite, the hinge of the coxosternite being sclerotized, and the coxosternite being deeply embedded into the cuticle above the first pedigerous trunk segment
79. presternites distinct
80. separate sternal and lateral longitudinal muscles
81. lateral testicular vesicles linked by a central, posteriorly extended deferens duct
82. coxal organs confined to the last leg pair
83. internal valves formed by lips of the ostia projecting deeply into the heart lumen

### *Epimorpha*

Apart from the curiously rerooted tree of Ax (1999), the monophyly of Epimorpha has been a staple of morphology-based cladistic studies of Chilopoda. Epimorpha is defended by the following synapomorphic characters of Scolopendromorpha and Geophilomorpha:

84. strictly epimorphic development (in contrast to a single anamorphic stage in *Craterostigmus*)
85. at least two post-embryonic stages with non-functional limbs (peripatoid and foetoid stages) guarded by the mother
86. an absence of Tömösváry organs (more generally shared with the extinct order

- Devonobiomorpha)
- 87. an unpaired brain artery (Wirkner and Pass, 2002)
  - 88. a shared hinge between four articles on the forcipular telopodite (spanning the trochanteroprefemur to the tarsungulum)
  - 89. trunk heterotergy either slight, being distinct in at least anterior segments (Scolopendromorpha), or wholly absent (Geophilomorpha)
  - 90. paramedian sutures on the trunk tergites
  - 91. longitudinal and transverse connections between segmental tracheal branches

### *Molecular phylogenies*

To date, four sources of molecular data have been applied to the higher-level relationships of centipedes:

*Nuclear coding genes.* To date three markers have been widely sampled across the Chilopoda, Regier et al. (2005) providing the most recent analysis. The first analysis based on these genes was a sampling of elongation factor-1 $\alpha$  sequences for five species that yielded the morphologically anomalous grouping of Scolopendromorpha + Scutigeromorpha, with Lithobiomorpha its sister group and Geophilomorpha basal to that assemblage (Shultz and Regier, 1997). When the taxonomic sample was increased to 11 species and RNA polymerase II sequences were added (Regier and Shultz, 2001), analysis under parsimony and maximum likelihood frameworks recovered the monophyly of Epimorpha but other ordinal relationships were incongruent with morphology. A 27 species chilopod sample that added a third gene, elongation factor-2, generally retrieved monophyly of the four large chilopod orders but ordinal interrelationships remained grossly incongruent with morphology (Regier et al., 2005). These markers resolve Craterostigmomorpha basally in Chilopoda, with Lithobiomorpha as sister to Geophilomorpha and a clade composed of Scutigeromorpha + Scolopendromorpha. A large increase in the number of genes (62 genes) for four chilopod species in a broader arthropod phylogeny analysis recovered the split between Scutigeromorpha and Pleurostigmophora but resolved *Craterostigmus* as sister to a grouping of *Lithobius* and *Scolopendra* (Regier et al., 2010) rather than retrieving a grouping of Phylactometria;

*Nuclear ribosomal genes.* Fragments of the small (18S rRNA) and large (28S rRNA) nuclear ribosomal subunits were the first molecular data source for which all five extant orders of centipedes were sampled (Giribet et al., 1999), a 12 species analysis yielding a

cladogram for ordinal relationships that is completely congruent with the morphological hypothesis in Fig. 17.1. The same pattern was retrieved using the same markers when the taxonomic sample was increased to 38 species and different analytical methods were explored (multiple alignments versus Direct Optimization) (Edgecombe et al., 1999). A sampling of these genes in 70 terminals (Edgecombe and Giribet, 2004) continued to retrieve Pleurostigmophora and Epimorpha as clades, but inverted the branching order of Craterostigmomorpha and Lithobiomorpha compared to morphology and the earlier 18S + 28S analyses. Smaller taxonomic samples for Chilopoda that included longer fragments of the 28S rRNA locus reiterated the more basal resolution of *Craterostigmus* in Pleurostigmophora (Mallatt and Giribet, 2006; Mallatt et al., 2010) that was also found for nuclear protein-encoding genes (Regier et al., 2010). *Craterostigmus* was likewise sister to other Pleurostigmophora when complete 18S and 28S rRNA and two mitochondrial genes were analysed for 97 centipede species (Murienne et al., 2010).

**Mitochondrial genes.** Sequence data for ribosomal 16S rRNA and the coding gene cytochrome c oxidase subunit I (COI) are widely applied to phylogenetic problems within chilopod orders, and have been included in a four gene sampling with nuclear ribosomal 18S and 28S nRNA (Edgecombe and Giribet, 2004, updated for more taxa by Murienne et al., 2010). Addition of the mitochondrial markers contributed more incongruence with morphology than is the case for the nuclear ribosomal genes alone (e.g., the four-gene analysis grouped Craterostigmomorpha + Geophilomorpha, with Lithobiomorpha their sister and failed to retrieve the monophyly of Scolopendromorpha).

**Engrailed.** Sequences for the *engrailed* gene have been surveyed for eight centipede species that include all orders except for Scutigeromorpha (Bastianello and Minelli, 2001). Rooted on Lithobiomorpha, Scolopendromorpha united with *Craterostigmus* rather than with Geophilomorpha, thus conflicting with Epimorpha. Whether paralogous genes are contributing to this result requires further exploration.

Combination of the three nuclear coding genes of Regier et al. (2005), two nuclear ribosomal genes, two mitochondrial genes and morphology for a 24-species sample found that two mutually incongruent topologies emerge under different costs for analytical parameters (Giribet and Edgecombe, 2006).

When gaps (insertions or deletions) are assigned a relatively high cost, signal from morphology and the nuclear ribosomal genes comes to the fore (because of the length heterogeneity of these markers) and the shortest trees correspond to Fig. 17.1. At lower gap costs, the nuclear ribosomal genes contribute most of the signal, and the optimal

cladogram is the same as found for those genes alone (i.e., highly incongruent with respect to morphology).

### *Phylogenetic relationships within the four large orders*

Although this chapter is principally concerned with the interrelationships between the five extant orders of Chilopoda, brief mention is made here of recent studies that have focused on the deep relationships within the four large orders. These studies have informed the taxonomic groupings employed elsewhere in this volume.

*Scutigeromorpha*. – A century lapsed between Verhoeff's (1905) pioneering attempt at a phylogenetic tree for the scutigeromorph genera and cladistic analyses of the internal phylogeny of the order. A three-family classification is supported by combination of morphological characters and sequence data for five or six genes in that the three families are monophyletic and represent the deepest splits in the cladogram (Edgecombe and Giribet, 2006, 2009). However, the morphological resolution (Scutigerinidae as sister to Psellioididae and Scutigeridae) conflicts with the molecular signal, which instead favours either a basal resolution of Psellioididae or a sister group relationship between Psellioididae and Scutigerinidae.

*Lithobiomorpha*. – To date, cladistic analyses have focused on Henicopidae, sampling morphology and five molecular loci (Edgecombe et al., 2002; Edgecombe and Giribet, 2003). A basal split into monophyletic Anopsobiinae and Henicopinae is found in the optimal combined analyses, though under some analytical conditions Anopsobiinae is instead paraphyletic, with the Boreal and Gondwanan members separated.

*Scolopendromorpha*. – The first morphology-based cladistic analysis based of scolopendromorphs sampled all genera as terminal taxa, but was restricted in its character sampling (Schileyko and Pavlinov, 1997). Subsequent studies have aimed to increase the number of characters applied to this problem by documenting and coding new characters from understudied anatomical systems. New characters from the peristomatic area (Edgecombe and Koch, 2008) and the foregut (Koch et al., 2009) have allowed the relationships between most of the major groups of Scolopendromorpha to be assessed, though some high-ranking groups based on single species (notably Mimopidae) have not been sampled for the new characters. From the perspective of morphology, blind scolopendromorphs have been resolved as a grade at the base of the order (Edgecombe and Koch, 2008) or a polyphyletic group (Schileyko and Pavlinov, 1997), but the recognition of a distinctive sieve-type of gizzard shared by Cryptopidae,

Plutoniumidae and Scolopocryptopidae is consistent with a single origin for blind lineages (Koch et al., 2009; Edgecombe and Koch, 2009).

Monophyly of blind scolopendromorphs has also been found in molecular analyses, though to date the taxonomic sampling is limited. Analyses of nuclear ribosomal genes, their combination with mitochondrial genes, and all of those data together with morphology found a blind scolopendromorph clade (Edgecombe and Giribet, 2004), as did three nuclear coding genes (Regier et al., 2005). The latter unite members of Plutoniumidae and Scolopocryptopidae as a clade to which Cryptopidae is sister, a pattern of relationships that corresponds to gizzard morphology (Koch et al., 2009, their fig. 11).

*Geophilomorpha.* – A basal split between Mecistocephalidae and all other geophilomorphs, recognised in Verhoeff's (1908 in Verhoeff, 1902–1925) classification of the order into Placodesmata and Adesmata, has been corroborated in combined analyses of morphological and molecular data (Edgecombe et al. 1999; Edgecombe and Giribet, 2002, 2004), or either data source on its own. The only cladistic analysis of the order to sample exemplars of all families, the morphology-based analysis of Foddai and Minelli (2000), also recognised this basal division. Adesmata, which have sternal glands opening to sternal pore areas as an autapomorphic character, have a compelling behavioural apomorphy in the observation that the mother broods the eggs and hatchlings with her sternum facing up. This character was formerly regarded as diagnostic of Geophilomorpha as a whole (Dohle, 1985) until it was discovered that members of Mecistocephalidae (Placodesmata) resemble Scolopendromorpha and *Craterostigmus* in brooding with the sternum facing down (Bonato and Minelli, 2002). Within Adesmata, numerous families have not yet been sampled with sequence data, so the morphological hypothesis of Foddai and Minelli (2000) provides the current phylogenetic framework. These data favour a clade that unites strongly multisegmented families (Eriphantidae, Gonibregmatidae, Oryidae) and are congruent with molecular evidence that groups Himantariidae, Ballophilidae and Schendylidae (Edgecombe and Giribet, 2004).

### References

- ATTEMS, C. 1926. Chilopoda. – Pp. 239–402 in W. KÜKENTHAL & T. KRUMBACH (eds.) Handbuch der Zoologie, 4(1). – De Gruyter, Berlin-Leipzig.
- Ax, P., 1999. Das System der Metazoa II. Ein Lehrbuch der phylogenetischen Systematik. – Gustav Fischer, Stuttgart.
- BASTIANELLO, A. & A. MINELLI, 2001. *engrailed* sequences from four centipede orders: strong sequence conservation, duplications and phylogeny. – Development Genes and Evolution 211: 620–623.

- BONATO, L. & A. MINELLI, 2002. Parental care in *Dicellophilus carniolensis* (C. L. Koch, 1847): new behavioural evidence with implications for the higher phylogeny of centipedes (Chilopoda). – *Zoologischer Anzeiger* **241**: 193-198.
- BORUCKI, H., 1996. Evolution und Phylogenetisches System der Chilopoda (Mandibulata, Tracheata). – *Verhandlungen des naturwissenschaftlichen Vereins in Hamburg, Neue Folge* **35**: 95-226.
- CHAGAS, JR., A., G. D. EDGEcombe & A. MINELLI, 2008. Variability in trunk segmentation in the centipede order Scolopendromorpha: a remarkable new species of *Scolopendropsis* Brandt (Chilopoda: Scolopendridae) from Brazil. – *Zootaxa* **1888**: 26-46.
- DALLAI, R. & B. A. AFZELIUS, 2000. Spermatozoa of the 'primitive type' in *Scutigerella* (Myriapoda, Symphyla). – *Tissue & Cell* **32**, 1-8.
- DOHLE, W., 1985. Phylogenetic pathways in the Chilopoda. – *Bijdragen tot de Dierkunde* **55**: 55-66.
- DOHLE, W., 1990. Some observations on morphology and affinities of *Craterostigmus tasmanianus* (Chilopoda). Pp. 69-79 in: A. MINELLI (ed.) *Proceedings of the 7<sup>th</sup> International Congress of Myriapodology*. – Brill, Leiden.
- EDGEcombe, G. D., 2004. Monophyly of Lithobiomorpha (Chilopoda): new characters from the pretarsal claws. – *Insect Systematics and Evolution* **35**: 29-41.
- EDGEcombe, G. D. & G. GIRIBET, 2002. Myriapod phylogeny and the relationships of Chilopoda. Pp. 143-168 in J. LLORENTE BOUSQUETS & J. J. MORRONE (eds.) *Biodiversidad, taxonomía y biogeografía de artrópodos de México: hacia una síntesis de su conocimiento*, 3. – Prensas de Ciencias, Universidad Nacional Autónoma de México, México.
- EDGEcombe, G. D. & G. GIRIBET, 2004. Adding mitochondrial sequence data (16S rRNA and cytochrome c oxidase subunit I) to the phylogeny of centipedes (Myriapoda, Chilopoda): an analysis of morphology and four molecular loci. – *Journal of Zoological Systematics and Evolutionary Research* **42**: 89-134.
- EDGEcombe, G. D. & G. GIRIBET, 2006. A century later – a total evidence re-evaluation of the phylogeny of scutigeromorph centipedes (Myriapoda, Chilopoda). – *Invertebrate Systematics* **20**: 503-525.
- EDGEcombe, G. D. & G. GIRIBET, 2009. Phylogenetics of scutigeromorph centipedes (Myriapoda: Chilopoda) with implications for species delimitation and historical biogeography of the Australian and New Caledonian faunas. – *Cladistics* **25**: 406-427.
- EDGEcombe, G. D., G. GIRIBET, & W. C. WHEELER, 1999. Phylogeny of Chilopoda: Combining 18S and 28S rRNA sequences and morphology. – *Boletín de la Sociedad Entomológica Aragonesa* **26**: 293-331.
- EDGEcombe, G. D. & M. KOCH, 2008. Phylogeny of scolopendromorph centipedes (Chilopoda): morphological analysis featuring characters from the peristomatic area. – *Cladistics* **24**: 872-901.
- EDGEcombe, G. D. & M. KOCH, 2009. The contribution of preoral chamber and foregut morphology to the phylogenetics of Scolopendromorpha (Chilopoda). – *Soil Organisms* **81**: 295-318.
- ERNST, A. & J. ROSENBERG, 2003. Structure and distribution of sensilla coeloconica on the maxillipedes of Chilopoda. – *African Invertebrates* **44**: 155-168.
- FAHLANDER, K., 1938. Beiträge zur Anatomie und systematischen Einteilung der Chilopoden. – *Zoologiska Bidrag från Uppsala* **17**: 1-148.
- FODDAI, D. & A. MINELLI, 2000. Phylogeny of geophilomorph centipedes: old wisdom and new insights from morphology. – *Fragmenta faunistica, Warszawa* **43** supplement: 61-71.
- GIRIBET, G., S. CARRANZA, M. RIUTORT, J. BAGUÑA & C. RIBERA, 1999. Internal phylogeny of the Chilopoda (Myriapoda, Arthropoda) using complete 18S rDNA and partial 28S rDNA sequences. – *Philosophical Transactions of the Royal Society of London* **354**: 215-222.

- GIRIBET, G. & G. D. EDGEcombe, 2006. Conflict between data sets and phylogeny of centipedes: an analysis based on seven genes and morphology. – Proceedings of the Royal Society of London B 273: 531–538.
- HILKEN, G., 1997. Tracheal systems in Chilopoda: a comparison under phylogenetic aspects. – Entomologica Scandinavica Supplement 51: 49–60.
- KLASS, K.-D. & N.-P. KRISTENSEN, 2001. The ground plan and affinities of hexapods: recent progress and open problems. – Annales de la Société entomologique de France, nouvelle Série 37: 265–298.
- KOCH, M. & G. D. EDGEcombe, 2006. Peristomatic structures in Scutigeromorpha (Chilopoda): a comparative study, with new characters for higher-level systematics. – Zoomorphology 125: 187–207.
- KOCH, M. & G. D. EDGEcombe, 2008. The peristomatic structures of Lithobiomorpha (Myriapoda, Chilopoda): comparative morphology and phylogenetic significance. – Journal of Morphology 269: 153–174.
- KOCH, M., S. PARSCHEK & G. D. EDGEcombe, 2009. Phylogenetic implications of gizzard morphology in scolopendromorph centipedes (Chilopoda). – Zoologica scripta 38: 269–288.
- LEWIS, J. G. E., 2000. Centipede antennal characters in taxonomy with particular reference to scolopendromorphs and antennal development in pleurostigmomorphs [sic] (Myriapoda, Chilopoda). – Fragmenta faunistica, Warszawa 43 Supplement: 87–96.
- MALLATT, J. M. & G. GIRIBET, 2006. Further use of nearly complete 28S and 18S rRNA genes to classify Ecdysozoa: 37 more arthropods and a kinorhynch. – Molecular Phylogenetics and Evolution 40: 772–794.
- MALLATT, J., C. WAGGONER & M.J. YODER, 2010. Nearly complete rRNA genes assembled from across the metazoan animals: effects of more taxa, a structure-based alignment, and paired-sites evolutionary models on phylogenetic reconstruction. – Molecular Phylogenetics and Evolution 55: 1–17.
- MANTON, S. M., 1965. The evolution of arthropodan locomotory mechanisms. Part 8. Functional requirements and body design in Chilopoda, together with a comparative account of their skeleto-muscular systems and an appendix on a comparison between burrowing forces of annelids and chilopods and its bearing upon the evolution of the arthropodan haemocoel. – Journal of the Linnean Society (Zoology) 45: 251–484.
- MINELLI, A., D. FODDAI, L. A. PEREIRA & J. G. E. LEWIS, 2000. The evolution of segmentation of centipede trunk and appendages. – Journal of Zoological Systematics and Evolutionary Research 38: 103–117.
- MÜLLER, C. H. G. & V. B. MEYER-ROCHOW, 2006a. Fine structural description of the lateral ocellus of *Craterostigmus tasmanianus* Pocock, 1902 (Chilopoda: Craterostigmomorpha) and phylogenetic considerations. – Journal of Morphology 267: 850–865.
- MÜLLER, C. H. G. & V. B. MEYER-ROCHOW, 2006b. Fine structural organization of the lateral ocelli in two species of *Scolopendra* (Chilopoda: Pleurostigmophora): an evolutionary evaluation. – Zoomorphology 125: 13–26.
- MÜLLER, C. H. G. & J. ROSENBERG, 2006. Homology of lateral ocelli in the Pleurostigmophora? New evidence from the retinal fine structure in some lithobiomorph species (Chilopoda: Lithobiidae). – Norwegian Journal of Entomology 53: 165–186.
- MÜLLER, C. H. G., J. ROSENBERG, S. RICHTER, & V. B. MEYER-ROCHOW, 2003. The compound eye of *Scutigera coleoptrata* (Linnaeus, 1758) (Chilopoda: Notostigmophora): an ultrastructural reinvestigation that adds support to the Mandibulata concept. – Zoomorphology 122: 191–209.
- MURIENNE J., G. D. EDGEcombe & G. GIRIBET, 2010. Including secondary structure, fossils and molecular dating in the centipede tree of life. – Molecular Phylogenetics and Evolution 57:

- 301-313.
- POCOCK, R. I., 1902. A new and annectant type of chilopod. – Quarterly Journal of Microscopic Science, new series **45**: 417-448.
- PAULUS, H. F., 1979. Eye structure and the monophyly of the Arthropoda. Pp. 299-383 in A. GUPTA (ed.), *Arthropod phylogeny*. – Van Nostrand Reinhold, New York.
- PRUNESCU, C. C., 1965. Contribution à l'étude de l'évolution des Chilopodes. – Revue roumaine de Biologie, Zoologie **10**: 89-102.
- PRUNESCU, C. C., 1970. Quelle est la place occupée par *Cermatobius*, *Craterostigmus* et *Plutonium* dans la phylogénie des chilopodes? – Bulletin du Muséum national d'Histoire naturelle, Paris, (2) **41** (1969) supplément 2: 112-115.
- PRUNESCU, C. C., 1996. Plesiomorphic and apomorphic characters states in the Class Chilopoda. – Mémoires du Muséum national d'Histoire naturelle, Paris **169**: 299-306.
- REGIER, J. C. & J. W. SHULTZ, 2001. A phylogenetic analysis of Myriapoda (Arthropoda) using two nuclear protein-encoding genes. – Zoological Journal of the Linnean Society **132**: 469-486.
- REGIER, J. C., J. W. SHULTZ, A. ZWICK, A. HUSSEY, B. BALL, R. WETZER, J. W. MARTIN & C. W. CUNNINGHAM, 2010. Arthropod relationships revealed by phylogenomic analysis of nuclear protein-coding sequences. – Nature **463**: 1079-1083.
- REGIER, J. C., H. M. WILSON & J. W. SHULTZ, 2005. Phylogenetic analysis of Myriapoda using three nuclear protein-coding genes. – Molecular Phylogenetics and Evolution **34**: 147-158.
- SCHILEYKO, A. A. & I. J. PAVLINOV, 1997. A cladistic analysis of the order Scolopendromorpha (Chilopoda). – Entomologica scandinavica **51** Supplement: 33-40.
- SHEAR, W. A. & P. M. BONAMO, 1988. Devonobiomorpha, a new order of centipedes (Chilopoda) from the Middle Devonian of Gilboa, New York State, USA, and the phylogeny of centipede orders. – American Museum Novitates **2927**: 1-30.
- SHULTZ, J. W. & J. C. REGIER, 1997. Progress toward a molecular phylogeny of the centipede orders (Chilopoda). – Entomologica scandinavica **51** Supplement: 25-32.
- SHINOHARA, K., 1970. On the phylogeny of Chilopoda. – Proceedings of the Japanese Society of Systematic Zoology **65**: 35-42.
- VERHOEFF, K. W., 1902-1925. Chilopoda. In BRONN, H. G. (ed.): *Klassen und Ordnungen des Tierreichs*, 5, Abteilung 2, Buch 1. – C. F. Winter'sche Verlagsbuchhandlung, Leipzig: 1-725.
- VERHOEFF, K.-W., 1905. Über Scutigeriden. – Zoologischer Anzeiger **29**: 73-119.
- WIRKNER, C. S. & G. PASS, 2002. The circulatory system in Chilopoda: functional morphology and phylogenetic aspects. – Acta Zoologica **83**: 193-202.

## Chapter 18

# CHILOPODA – FOSSIL HISTORY

Gregory D. Edgecombe

The lightly sclerotised cuticle of chilopods, coupled with their predominantly litter and soil-dwelling habits, set constraints on their fossilisation potential. In spite of this, of the five extant chilopod orders, two (Scutigeromorpha and Scolopendromorpha) have a fossil record extending back to the Palaeozoic, and an extinct order in the Middle Devonian (Devonobiomorpha) dates the divergence of Lithobiomorpha and Phylactometria to at least that age, ca 385 million years ago. In addition to a few recent discoveries in Jurassic and Cretaceous rocks, chilopods are known from several species in Cretaceous and Cenozoic ambers.

### *Scutigeromorpha*

The earliest known fossil centipedes, ca 418 million years old, can be confidently assigned to the Scutigeromorpha. The Silurian-Devonian genus *Crussolum* Shear et al., 1998 (Shear et al. 1998; Anderson and Trewin, 2003) has the polygonal cross section of the leg articles, with sawblade-like rows of spines along the ridges (carinae) at each angulation (Fig. 18.1D, E), that is retained by extant scutigeromorphs. Unlike extant scutigeromorphs the tarsus is not clearly differentiated into a tarsus 1 and tarsus 2, and several unique tarsal characters that are invariably observed in all extant scutigeromorphs (tarsal papillae, resilient sole-hairs) are lacking in the mid-Palaeozoic fossils. As such, *Crussolum* can be identified as a stem-group scutigeromorph.

The forcipules of *Crussolum* have a separation between the coxae that indicates flexibility, and has robust socketed setae along the margin of the coxae (Anderson and Trewin, 2003) (Fig. 18.1C). These latter setae differ from the invariable four spine-bristles on the coxal margin of crown-group Scutigeromorpha, an apomorphic character that reinforces the stem-group position of *Crussolum*. In the Windyfield Chert (Lower Devonian, Scotland), an antenna assigned to *Crussolum* sp. has at least 21 short articles, but its complete length is unknown, and Fayers and Trewin (2005) allowed that the material could be hexapod rather than chilopod. *Crussolum* is known from the Upper

Silurian (Přidolian) Ludford Lane deposits in England, the Lower Devonian (Pragian) Rhynie and Windyfield Cherts of Scotland, and the Middle Devonian (Givetian) of Gilboa, New York.

Stratigraphically later scutigeromorphs include the Upper Carboniferous *Latzelia* Scudder, 1890, and the Lower Cretaceous *Fulmenocursor* Wilson, 2001. *Latzelia* is known from a single species, *L. primordialis* Scudder, 1890, from the Mazon Creek deposits of Illinois, U.S.A. (Scudder, 1890; Mundel, 1979). It has been separated as a monotypic family, Latzeliidae, though diagnosed only as "a small-headed robust scutigeromorph" (Mundel, 1979). One feature that might place *Latzelia* outside the scutigeromorph crown group is its relatively short fourth tergite (plate covering leg-bearing segments 7–9), but in most respects it is decidedly similar to extant Scutigeromorpha. *Fulmenocursor* is likewise monotypic, based on *F. tenax* Wilson, 2001, from the Crato Formation (Aptian) in northeastern Brazil. The shape of the antennal articles (wider than long), presence of paired spine-bristles on the tibia of the second maxillae, and apparently styliform (male?) gonopods (Wilson, 2001) suggest that *Fulmenocursor* may be referable to the family Scutigeridae. Two scutigerid taxa, *Scutigera illigeri* and *S. leachi*, were named by Koch & Berendt (1854) from Eocene Baltic amber, though they have since been regarded as a single species (Keilbach, 1982).

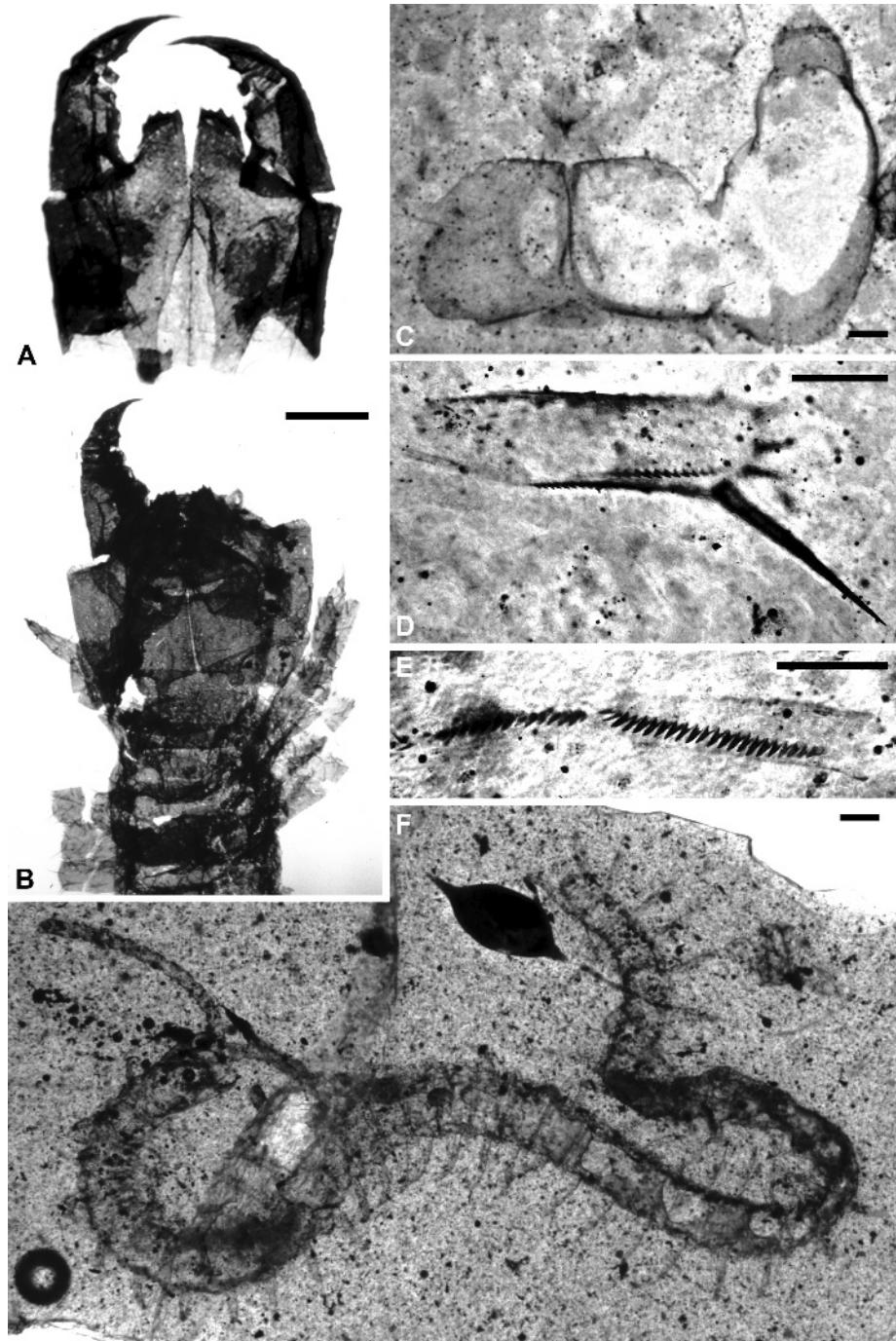
### *Lithobiomorpha*

Although the widely endorsed cladogram for Chilopoda and available palaeontological data (occurrence of *Devonobius*; Shear and Bonamo, 1988) predict that stem-group lithobiomorphs should have evolved no later than the Middle Devonian, the record of fossil lithobiomorphs is confined to the Cenozoic. A specimen referred to *Lithobius* from the Rubielos de Mora site in Spain (Peñalver, 1998) is of Early Miocene age. The published drawing identifies it as a lithobiid rather than a henicopid based on the presence of spurs encircling the distal parts of leg articles, and the relative thickening of the ultimate legs is more typically lithobiid.

Additional fossil lithobiomorphs are represented in Cenozoic ambers. Baltic amber in-

**Fig. 18.1** Fossil Chilopoda. Scale bars 0.2 mm. A–B *Devonobius delta*, Middle Devonian, Gilboa, New York, USA. A Forcipules. B Head and anterior part of trunk. C–E Stem-group scutigeromorph *Crussolum* sp., Windyfield Chert (Lower Devonian), Scotland. C Forcipules. D Prefemur of a trunk leg. E Tibia of a trunk leg. F *Buziniphilus antiquus*, Upper Cretaceous amber, western France. A, B, W. A. Shear; C–E, L. I. Anderson; F, original G.D. Edgecombe.

For a colour version of this figure, see Plate III.



cludes a few named lithobiid species (*Lithobius longicornis*, *L. maxillosus*, *L. planatus*; all by Koch & Berendt, 1854; plus several nomina nuda referred to *Lithobius* by Menge (1854)). None of this material has been examined in modern times and the detailed affinities of these species are unknown.

Fossils preserved in volcanic tephra in the Rhine floodplain, dated at ca 11,000 years, are identified as *Lithobius* cf. *forficatus* (Waldmann et al., 1996).

### *Devonobiomorpha*

*Devonobius delta* Shear and Bonamo, 1988, from the Middle Devonian of Gilboa, New York, is known from magnificently preserved cuticular remains, with even fine details of setation known for parts of the exoskeleton. The head and anterior part of the trunk are preserved (Fig. 18.1A, B), including legs, but the complete number of segments is unknown, and the structure of the posterior segments is not well understood, being represented by a single telescoped exuvium.

*Devonobius delta* lacks ocelli. The antenna is composed of at least 13 articles but the most complete specimen (Shear and Bonamo 1988, their fig. 25) is fragmentary. The trunk has at least 16 segments with distinct alternation of long and short tergites (heterotergy). The most distinctive character is a pair of long ventral apodemes on the forcipular coxosternite, not known in other chilopods; like other pleurostigmophorans, *Devonobius* also has a pair of dorsal apodemes (Coxalplatten of Verhoeff). The coxosternite has “can opener” serrate endites as in *Craterostigmus* and many Scolopendromorpha (Fig. 18.1A).

Shear and Bonamo (1988) considered *Devonobius* to be sister group of Scolopendromorpha and Geophilomorpha based on the shared absence of a Tömösváry’s organ. Borucki (1996) instead regarded *Devonobius* to be most closely related to *Craterostigmus*. The characters cited in support of this relationship, involving purported specializations of the forcipules, a sclerotized bridge between the antennal bases, and size and position of the mandible, were critiqued by Edgecombe and Giribet (2004), whose morphological analysis was unable to choose between the two alternatives (both were equally parsimonious).

### *Scolopendromorpha*

Palaeozoic scolopendromorphs are known exclusively from the Upper Carboniferous of Mazon Creek, Illinois, USA. Two Mazon Creek species have been described,

*Palenarthrus impressus* Scudder, 1890, and *Mazoscolopendra richardsoni* Mundel, 1979. The better known *Mazoscolopendra* is a 21-segmented species that is currently unassignable to either of the main 21-segmented families (Cryptopidae and Scolopendridae). Taxonomically critical characters such as ocelli are inadequately preserved (pers. obs., Field Museum collections), and classification more detailed than Scolopendromorpha is not possible.

The Mesozoic record of scolopendromorphs is based on two species from the Lower Cretaceous Crato Formation in northeastern Brazil, *Velocipede betimar*, named and described by Martill and Barker (1998), and *Cratoraricrus oberlii* Wilson, 2003. The latter is the better understood of the two, though known from a single specimen. It possesses some characters typical of Scolopendridae, such as bipartite tarsi, and sternites having paired paramedian grooves (Wilson, 2003). More specifically, sternal paramedian grooves along the length of the trunk are apomorphic for Asanadini and Scolopendrini (Scolopendrinae). The presence of ocelli in *Cratoraricrus* can neither be confirmed nor discounted. An unassigned Crato Formation scolopendromorph with 21 pairs of trunk legs is distinct from *Cratoraricrus* but requires further comparison with *Velocipede* (Menon et al., 2003).

Baltic amber is the source of an unnamed cryptopid (*Cryptops* sp. of Bachofen-Echt, 1942) and *Scolopendra avita* Menge in Koch & Berendt, 1854. A scolopendromorph illustrated from Dominican amber (Poinar & Poinar, 1999, their fig. 87) is a member of Scolopocryptopinae, with a single large ventral spinous process on the ultimate leg prefemur that is consistent with a more precise identity as one of the two extant genera in the Neotropics, *Scolopocryptops* and *Dinocryptops*.

### *Geophilomorpha*

Shear and Bonamo (1988) suggested that *Ilyodes attenuata* Matthew, 1894, from the Upper Carboniferous of New Brunswick, Canada, is a potential geophilomorph, but a subsequent examination of the material in the New Brunswick Museum by W. A. Shear (pers. comm.) leaves it doubtful that it is a chilopod.

The earliest well established geophilomorph is *Eogeophilus jurassicus* Schweigert and Dietl, 1997, from the Upper Jurassic Nusplingen Plattenkalk of southwestern Germany. Though the habitus of this species is unquestionably geophilomorph, based on the elongated body with a large number (50+) of trunk segments, its original description from a single specimen presents a puzzling incongruence with extant geophilomorphs in the form of the forcipules. Extant geophilomorphs share a joint between the first and

fourth articles of the telopodite, completely reducing the second and third articles (femur and tibia) on the outer side of the telopodite. This modification is shared with scolopendromorphs (observed in the Cretaceous *Cratoraricrus*: Wilson, 2003, their fig. 4) and has classically been regarded as a synapomorphy for Scolopendromorpha and Geophilomorpha. *Eogeophilus* was depicted as having a complete femur and tibia on the forcipule (Schweigert and Dietl, 1997, their fig. 4) but this may be based on a mistaken anterior limit of the coxosternum (Edgecombe et al., 2009).

The only other Mesozoic geophilomorph is *Buziniphilus antiquus* Edgecombe, Minelli & Bonato, 2009, from La Buzinie amber (Late Cretaceous, early Cenomanian) in western France. This species is known from a single, evidently immature specimen (Fig. 18.1F) but it preserves sufficient morphological information to make membership in either of the families Geophilidae or Schendylidae probable.

Another geophilomorph, *Calciphilus abboti* Chamberlin, 1949, is known from a single incomplete specimen preserved in onyx of Late Cenozoic age from Arizona. It is apparently a member of the Geophilidae (Chamberlin, 1949).

Geophilomorphs from Baltic amber (e.g., Weitschat & Wichard 1998, their pl. 22, fig. d) have not received a recent taxonomic treatment, though a few species have been in the literature since the mid-19<sup>th</sup> century. A series of names proposed by Menge in Koch & Berendt (1854), including *Geophilus brevicaudatus*, *G. crassicornis* and *G. filiformis*, were regarded by Keilbach (1982) as nomina nuda.

### References

- ANDERSON, L. I. & N. H. TREWIN, 2003. An Early Devonian arthropod fauna from the Windyfield Cherts, Aberdeenshire, Scotland. – *Palaeontology* **46**: 457–509.
- BACHOFEN-ECHT, A., 1942. Über die Myriapoden des Bernsteins. – *Palaeobiologica* **7**: 394–403.
- BORUCKI, H., 1996. Evolution und phylogenetisches System der Chilopoda (Mandibulata, Tracheata). – *Verhandlungen des naturwissenschaftlichen Vereins in Hamburg, Neue Folge* **35**: 95–226.
- CHAMBERLIN, R. V., 1949. A new fossil centipede from the Late Cenozoic. – *Transactions of the San Diego Society of Natural History* **II**: 117–120.
- EDGEcombe, G. D. & G. GIRIBET, 2004. Adding mitochondrial sequence data (16S rRNA and cytochrome c oxidase subunit I) to the phylogeny of centipedes (Myriapoda, Chilopoda): an analysis of morphology and four molecular loci. – *Journal of Zoological Systematics and Evolutionary Research* **42**: 89–134.
- EDGEcombe, G. D., A. MINELLI & L. BONATO, 2009. A geophilomorph centipede (Chilopoda) from La Buzinie amber (Late Cretaceous: Cenomanian), SW France. – *Geodiversitas* **31**: 29–39.
- FAYERS, S. R. & N. H. TREWIN, 2005. A hexapod from the Early Devonian Windyfield Chert, Rhynie, Scotland. – *Palaeontology* **48**: 1117–1130.

- KEILBACH, R., 1982. Bibliographie und Liste der Arten tierischer Einschlüsse in fossilen Harzen sowie ihrer Aufbewahrungsorte. – Deutsche entomologische Zeitschrift, Neue Folge 29: 129-286, 301-391.
- KOCH, C. L. & G. C. BERENDT, 1854. Die im Bernstein befindlichen Crustaceen, Myriapoden, Arachniden und Apteran der Vorwelt. – Nicolaische Buchhandlung, Berlin.
- MARTILL, D. M. & M. J. BARKER, 1998. A new centipede (Arthropoda, Chilopoda) from the Crato Formation (Lower Cretaceous, Aptian) of N.E. Brazil. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 207: 395-404.
- MENGE, A. 1854. [Footnotes to] C. L. KOCH & G. C. BERENDT, Die im Bernstein befindlichen Myriapoden, Arachniden und Apteran der Vorwelt. – Nicolaische Buchhandlung, Berlin.
- MENON, F., D. PENNEY, P. A. SELDEN & D. M. MARTILL, 2003. A new fossil scolopendromorph centipede from the Crato Formation of Brazil. – Bulletin of the British Myriapod and Isopod Group 19: 62-66.
- MUNDEL, P., 1979. The centipedes (Chilopoda) of the Mazon Creek. – Pp. 361-378 in M. H. NITECKI (ed.) Mazon Creek Fossils. – Academic Press, New York.
- PEÑALVER, E., 1998. Rubielos de Mora y Ribesalbes: dos yacimientos españoles del Neógeno con insectos fósiles. – Cidaris 13-14: 17-29.
- POINAR, G., JR. & R. POINAR, 1999. The amber forest. – Princeton University Press, Princeton.
- SCHWEIGERT, V. G. & G. DIETL, 1997. Ein fossiler Hundertfüssler (Chilopoda, Geophilida) aus dem Nusplinger Plattenkalk (Oberjura, Südwestdeutschland). – Stuttgarter Beiträge für Naturkunde B (Geologie und Paläontologie) 254: 1-11.
- SCUDDER, S. H., 1890. New Carboniferous Myriapoda from Illinois. – Boston Society of Natural History Memoirs 4: 417-442.
- SHEAR, W. A. & P. M. BONAMO, 1988. Devonobiomorpha, a new order of centipeds (Chilopoda) from the Middle Devonian of Gilboa, New York State, USA, and the phylogeny of centiped orders. – American Museum Novitates 2917: 1-30.
- SHEAR, W. A., A. J. JERAM & P. A. SELDEN, 1998. Centiped legs (Arthropoda, Chilopoda, Scutigeromorpha) from the Silurian and Devonian of Britain and the Devonian of North America. – American Museum Novitates 3231: 1-16.
- WALDMANN, G., B. BERENDONCK & M. STEVENS, 1996. Fossile Hundertfusser (Chilopoda) in spätglazialer Tephra der Rheinaue bei Sinzig, Rheinland-Pfalz. – Acta Biologica Benrodis 8: 149-155.
- WEITSCHAT, W. & W. WICHARD, 1998. Atlas der Pflanzen und Tiere im Baltischen Bernstein. – Pfeil, München.
- WILSON, H. M., 2001. First Mesozoic scutigeromorph centipede, from the Lower Cretaceous of Brazil. – Palaeontology 44: 489-495.
- WILSON, H. M., 2003. A new scolopendromorph centipede (Myriapoda: Chilopoda) from the Lower Cretaceous (Aptian) of Brazil. – Journal of Paleontology 77: 73-77.



## Chapter 19

# CHILOPODA – TAXONOMIC OVERVIEW

## Order Scutigeromorpha

Gregory D. Edgecombe

Adult body length usually 2-3.5 cm, exceptionally up to 8 cm. Cephalic capsule strongly domed, with antennae inserting dorsolaterally, widely separated at their bases. Eyes faceted, ommatidia with a crystalline cone. Multiannulated flagella of the antennae divided into two or three sections by elongate nodes, with a sensory organ (Schaftorgan) on the scape. Mandible large, gnathal edge subdivided into numerous pectinate lamellae, three multi-cusped teeth and pulvilli with a slender molar plate. Maxillary organs housed in coxal projections of first maxillae. Second maxillae slender, lacking terminal claw, with rows of trichomes on inner side of tarsus; four elongate spine-bristles encircling distal end of femur, one on dorsodistal side of prefemur, and variably one on ventrodistal side of prefemur and a pair at distal end of tibia. Forcipular coxae separate, flexible along midline; anterior margins of coxae with four pairs of elongate spine-bristles similar to single spine-bristle on inner edge of forcipular prefemur. Hypopharynx projects as elongate tongue with a pair of sclerotized forks on its frontal surface and button-like sensilla on its tip. Epipharynx with A-shaped bars delimiting labral trapezoid and clypeal triangle; labral trapezoid with two median clusters of sensilla coeloconica. Tracheae opening to slit-like, unpaired stomata on posterior part of tergites; tergites swollen as “stoma-saddles” above tracheae; hemocyanin used as oxygen transport molecule. Eight elongate stomatotergites cover 15 pairs of trunk legs, including single plate over segments 7-9. Tergites bearing bristles (trichoid mechanosensilla set in sockets), many of which are commonly associated with spines, generally with hairs (spiculae or spinulae) between the bristles. Legs with carinae at the angles on prefemur, femur and tibia bearing files of spines. Each coxa bears a spine ventrally. Tarsi greatly elongate, subdivided into many annulations (tarsus 1 with at least four annulations, tarsus 2 with at least 15), most annulations of tarsus 2 bearing paired papillae and resilient sole-hairs on their ventral side. Ultimate legs antenniform, much longer than all others, tarsus subdivided into as many as 500 annulations without clear division into tarsus 1 and 2, lacking pretarsal claw. Female gonopods forcipulate, with single articulation. Two pairs of male gonopods, on first and second genital segments. Coxal and anal organs lacking.

Development anamorphic, where known hatching from the egg with four leg-bearing segments.

Tropical and temperate parts of all continents except Antarctica. Ca 95 extant species in three families.

Family PSELLIODIDAE Chamberlin, 1955 (Fig. 19.1). – Cephalic suture complex lacking an antennal branch, terminating as a pair of anterior projections. Antennal articles

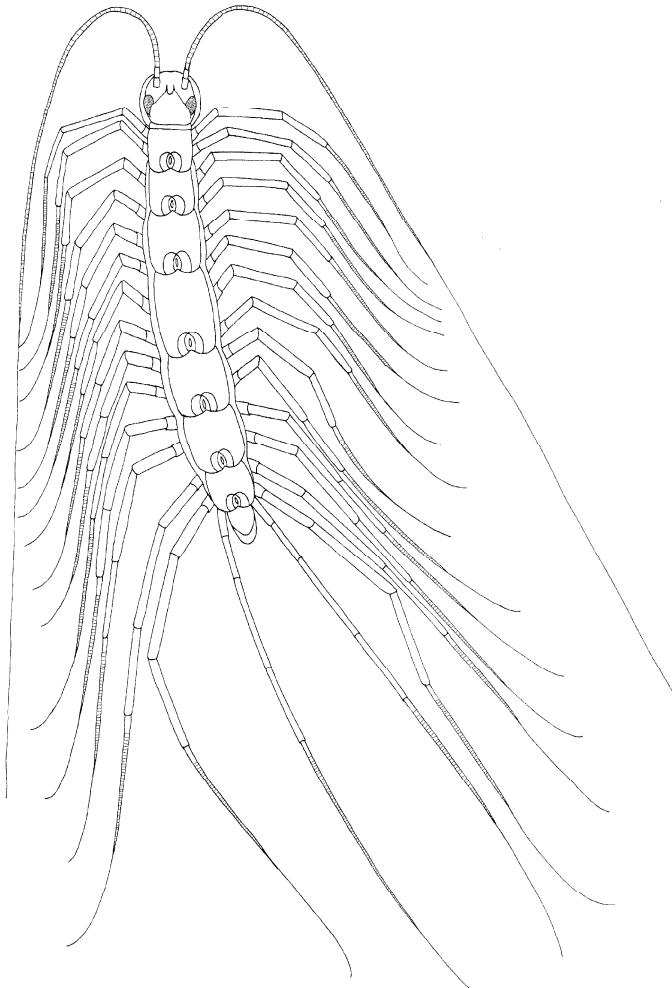


Fig. 19.1 *Sphendonenema guildingii* (Scutigeromorpha, Pselliodidae). Habitus, dorsal view, spine-bristles omitted. Original E. Zamprogno.

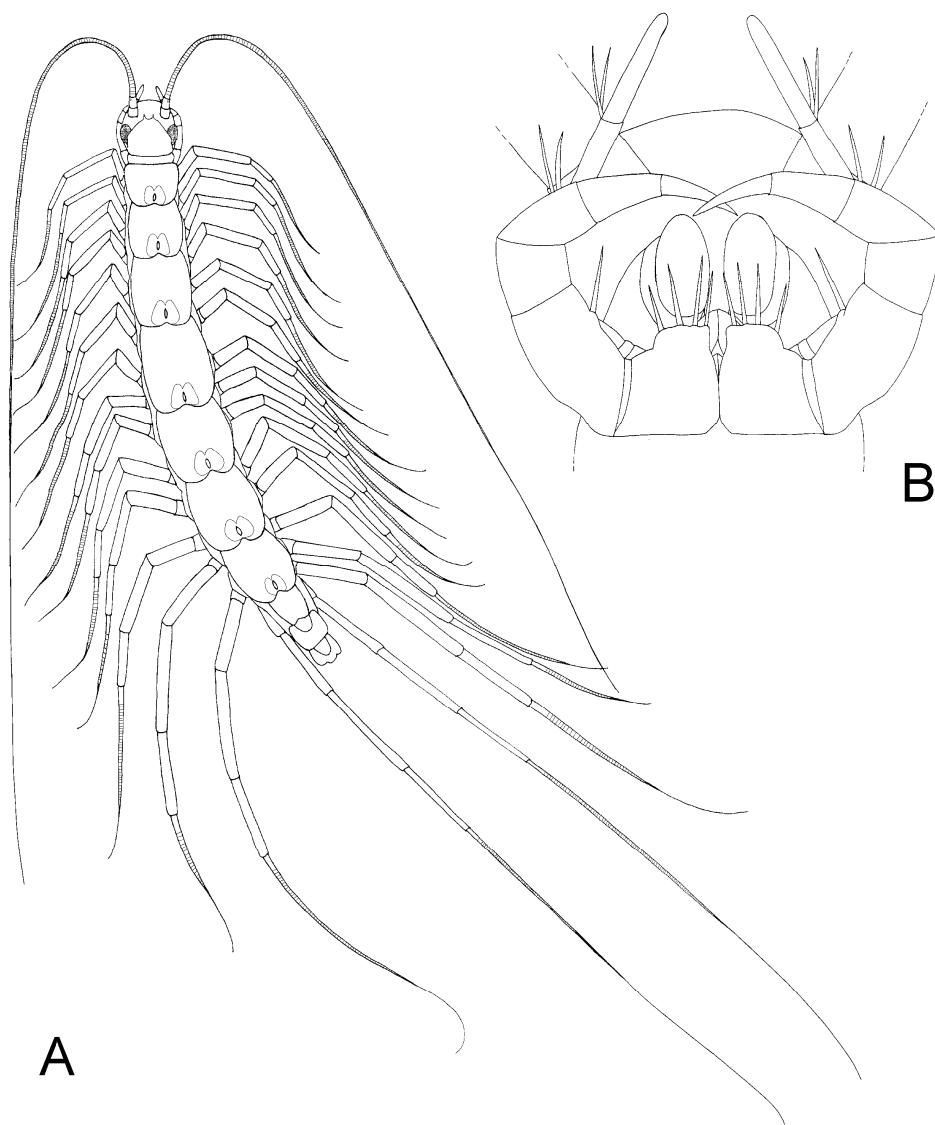


Fig. 19.2 *Scutigera coleoptrata* (Scutigeromorpha, Scutigeridae). A Habitus, dorsal view, spine-bristles omitted. B Anterior part of the body, ventral view. Original E. Zampogno.

longer than wide. Sclerotized lateral bulge lacking in proximal fork of hypopharynx. Bristles on labral trapezoid of epipharynx uniformly simple. Tergites having most bristles associated with a strong spine; spinulae/spiculae elongate triangular. Stoma-

saddles strongly vaulted. Carinae on legs strong. Female gonopods elongate, with relatively short proarthron and long mesarthron. Male gonopods on first genital segment short, lamelliform; gonopods on second genital segment style-like. Neotropics, tropical west and east Africa. At least three species in a single genus.

*Sphendononema* Verhoeff, 1904. – At least three species, incl. *S. guildingii* (Newport, 1844) (lightly pigmented band on medial part of tergites wide, spines on tergites mostly half length of associated bristle; Mexico, Central America incl. Caribbean, South America to Paraguay), *S. rugosa* (Newport, 1844) (lightly pigmented band on medial part of tergites narrow, spines on tergites as long as or slightly shorter than associated bristle; widespread in tropical east Africa, also west Africa).

Family SCUTIGERIDAE Leach, 1814 (Fig. 19.2). – Cephalic suture complex lacking an antennal branch, terminating as a pair of anterior projections. Antennal articles wider than long. Sclerotized lateral bulge in proximal fork of hypopharynx. Labral bristles differentiated into wide inner band of simple bristles and narrow outer band of pectinate bristles; median sensilla cluster on clypeal part of epipharynx arranged as a transversely ovate cluster separated from dense median spine field. Carinae on legs strong. Male gonopods on first and second genital segments both developed as slender styles. South Europe to east and south-east Asia, north and tropical Africa, Madagascar, Australian region, Central America incl. Caribbean, southern South America; distribution greatly expanded by the synanthropic introduction of *Scutigera coleoptrata* (incl. north Europe, North America, south Africa).

Subfamily SCUTIGERINAE Leach, 1814. – Pair of spine-bristles at distal end of tarsus 1 on legs 6-14 (variably present on legs 4 and 5). Ca 15 species in five genera.

*Scutigera* Lamarck, 1801. – Legs 1-9 with tarsal papillae, lacking on legs 10-14. Tergites with numerous bristles (Stachelborsten) paired with a strong spine. Legs 2-14 with one dorsal and two ventral tibial spine-bristles. Mediterranean region, Caucasus, Madagascar, southern South America. Number of species exaggerated because most “*Scutigera*” species are artefacts of unrevised 19<sup>th</sup> century taxonomy, but incl. *S. coleoptrata* (Linnaeus, 1758) (spinulae short and sparse, tarsal papillae on alternating annulations, angle at median distal end of proarthron of female gonopods at least 75 degrees; native to Mediterranean region, synanthropic throughout much of world), *S. nossibei* Saussure and Zehntner, 1902 (dark brown with yellow median band, spiculae robust and almost half length of spines, lateral margins of proarthron and mesarthron divergent; Madagascar), *S. tonsoris* Würmli, 1977 (spiculae slender, setiform, abundant; angle at median distal end of proarthron 50 degrees, lateral margins of proarthron and mesarthron parallel; Iberian peninsula, north Africa).

*Ballonema* Verhoeff, 1904. – First flagellum of antenna with 112-140 articles. Tergites with evenly distributed bristles (Stachelbortsen), lacking unpaired spines. Spiculae densely arranged. Stomata elongate. Legs 1-2 with one ventral tibial spine-bristle, legs 3-4 with one dorsal and one ventral, legs 5-14 with one dorsal and two ventral. New Guinea. A single species, *B. gracilipes* Verhoeff, 1904.

*Ballonemella* Verhoeff, 1944. – First flagellum of antenna with 52–62 articles. Tergites with scattered bristles (Stachelbortsen), lacking spines. Spinulae sparse. Stomata short. Legs 1–2 with one ventral tibial spine-bristle, legs 3–7 with one dorsal and one ventral, legs 8–14 with one dorsal and two ventral. Tanzania. A single species, *B. jeanneli* (Ribaut, 1914).

*Brasiloscutigera* Bücherl, 1939. – First flagellum of antenna with 114–124 articles. Tergites 1–4 with bristles but lacking spines; spines on tergites 5–7 short, rather few in number. Legs 3–14 with one dorsal and two ventral tibial spine-bristles. Tarsal papillae on consecutive articles of legs 1–14, large on legs 1–7, reduced in size on legs 8–14. Margins of proarthron and mesarthron of female gonopods divergent; mesarthron less than half length of metarthron. South Brazil. A single species, *B. viridis* Bücherl, 1939.

*Dendrothereua* Verhoeff, 1944. – Median sensilla of tripartite cluster on proximal labral part of epipharynx arranged as an antero-posteriorly aligned pair. Sclerotized lateral bulge in proximal fork of hypopharynx lacking. Labral trapezoid on epipharynx with a few rows of branching bristles, single inner row of simple bristles. Spines lacking on tergites; hairs (spiculae) about half length of bristles (Stachelborsten). Sternites and coxae of posterior trunk segments with dense hairs. Female gonopods 1.9–2.8 times longer than wide; metarthron short, 0.25–0.3 times length of proarthron + mesarthron, claw-like. Southern North America and Central America incl. Caribbean. At least two species, *D. linceci* (Wood, 1867) (southern North America to Mexico), *D. nubila* (Chamberlin, 1921) (Central America).

Subfamily THEREUONEMINAE Verhoeff, 1905. – Pair of spine-bristles lacking at distal end of all tarsi 1. Mostly in Asian-Australian region. Ca 35 species in 12 genera.

*Thereuonema* Verhoeff, 1904. – Bands of pigmentation along tergites rather diffuse. Hairs on tergites developed as long, needle-like spiculae. East Africa and the Near East, central and east Asia. Four species, incl. *T. microstoma* (Meinert, 1886) (light brown to dark purple-brown, 80–90 bristles associated with a spine on tergite 6, spiculae parallel-sided, female gonopods 1.4–1.9 times longer than wide; east Africa, Near East), *T. tuberculata* (Wood, 1861) (blue-green, 50–80 bristles associated with a spine on tergite 6, spiculae parallel-sided; female gonopods 2.1–2.8 times longer than wide; east Asia), *T. turkestanica* Verhoeff, 1905 (170–200 isolated bristles on tergite 6, spiculae tapering; central Asia).

*Allothereua* Verhoeff, 1905. – Some bristles on tergites 6 and 7 accompanied by unpaired spines. Some spines on border of tergites 6–7 as strong as bristles (Stachelborsten). Sinus of mesarthron of female gonopods mostly narrow, deep, subparallel-sided. Probably non-monophyletic as traditionally delimited (mixed with *Parascutigera*). Central Asia to Australia. Seven species, incl. *A. kirgisorum* Lignau, 1929 (first flagellum of antenna with 66–67 articles, stoma-saddles of tergite 6 with 8+6 spines, tergite 7 with 4+2; Kazakhstan), *A. maculata* (Newport, 1844) (stoma saddles orange, those of tergites 6 and 7 each with few spines; west and south Australia), *A. serrulata* Verhoeff, 1925 (thickened spiculae clustered around spines and bristles, stoma-saddles of tergite 6 with 7–9 spines, tergite 7 with 6–8; Australia), *A. wilsonae* Dobroruka, 1979 (first flagellum with 60 articles, stoma-saddles of tergite 6 with 12+12 spines, tergite 7 with 6+6; Himalayas).

*Parascutigera* Verhoeff, 1904. – Tergites (including borders) with paired spines associated with bristles, often as long as bristle or exceptionally even longer, wholly lacking unpaired spines. Sinus of mesarthron of female gonopods narrow, deep, subparallel-sided. South-east Asia, Australian region, New Caledonia. 12 species, incl. *P. dahlia* Verhoeff, 1904 (first flagellum of antenna with more than 135 articles, one dorsal and two ventral tibial spine-bristles from leg 10; New Britain), *P. festiva* Ribaut, 1923 (first flagellum with ca 80 articles, spiculae nearly setiform, dense, about as large as spines at bristle bases on tergite 6; New Caledonia), *P. guttata* Verhoeff, 1925 (paired spines at bases

of bristles on tergites 6-7 up to half length of bristle; spiculae short, triangular, fairly sparse; Australia).

*Pesvarus* Würmli, 1974. – Stoma-saddles bearing strong, short bristles with short basal spines, the latter either paired and symmetrical or one distinctly larger; spinulae triangular. One dorsal and two ventral tibial spine-bristles from leg 9. Metarthron of female gonopods massive, hook-shaped, as wide as mesarthron, more than 80% length of combined proarthron and mesarthron. West Australia. A single species, *P. pachypus* Würmli, 1974.

*Pilbarascutigera* Edgecombe & Barrow, 2007. – Predominantly orange-brown pigmentation. Anterior projection of cephalic sutures short, parallel. Anterior tergites having scattered setiform bristles (Stachelborsten) and slender, needle-like bristles (Tastborsten) but lacking spines; tergites 5-7 (and tergites 3-4 in some specimens) with numerous spines, each paired with a Tastborste, along each side of midline, on stoma-saddles, and on lateral parts of tergites. Tergal spinulae triangular, relatively sparse. Stoma-saddles weakly vaulted. Sinus between inner margins of mesarthron of female gonopods broad, parabolic to almost rectangular; margins of metarthron relatively straight in ventral view. Female subanal plate drop-shaped, with blunt, rounded distal end. West Australia. A single species, *P. incola* (Verhoeff, 1925).

*Podothereua* Verhoeff, 1905. – Pigmentation predominantly grey-yellow to yellow-brown. Tergites with numerous isolated bristles (Tastborsten), few of them associated with spines. Stomata elongate. Stoma-saddles strongly vaulted; saddles of tergites 6-7 lacking spines or at most with a few small ones. Spinulae short, numerous. Borders of tergites with a weak fringe of saw-like spines. Prefemur of legs 2-4 with a saw-like row of spines. Legs 11-14 with conspicuously long spines on first 10-18 articles of tarsus 2. Sinus between inner margins of mesarthron of female gonopods moderately divergent. Female subanal plate with a pointed process. Bismarck Archipelago. A single species, *P. insularum* Verhoeff, 1905.

*Prionopodella* Verhoeff, 1925. – Tergites lacking pronounced longitudinal bands of dark pigment. Few spine/bristle pairs on tergites, spines lacking on stoma-saddles of tergites 6-7; isolated bristles (mix of Stachelborsten and Tastborsten) with short paired spines at their bases. Spinulae fairly sparse. Stomata short. Inner margins of mesarthron of female gonopods with very wide, shallow sinus; pseudoarticulation variably developed between proarthron and mesarthron. Australia. A single species, *P. pectinigera* Verhoeff, 1925 (Queensland).

*Prothereua* Verhoeff, 1925. – Tergites with bristles accompanied by a pair of short spines on each side of the bristle base (including on border), no unpaired spines. Median region of tergites without ordered longitudinal rows of bristles. Spiculae moderately densely arranged, triangular or more elongate. Stomata 6 and 7 short. Female gonopods with fairly wide sinus, angle at median distal end of proarthron ca 135 degrees; mesarthron divergent. West Australia. A single species, *P. annulata* Verhoeff, 1925.

*Tachythereua* Verhoeff, 1905. – Tergites with many unpaired spines associated with a bristle but wholly lacking hairs (spiculae or spinulae). Posterior margin of sternites with strong median embayment. Female gonopods with very wide sinus; angle at the median distal end of proarthron almost transverse; proarthron 1.8-2.5 times length of mesarthron; small denticles along inner margin of metarthron. Morocco, south Spain. A single species, *T. hispanica* (Meinert, 1886).

*Thereuopoda* Verhoeff, 1904. – Body length 3-8 cm. Anterior projection of cephalic sutures with divergent posterior part such that suture is kinked. Spines often present on proximal half of first antennal flagellum. Stoma-saddles strongly vaulted; stomata elongate. Unpaired spines accompanying bristles (Tastborsten) relatively strong and numerous, typically 12+12 or many more on stoma-saddles of tergite 6; unpaired spines often present on tergites 1-2. Borders of tergites 6 and 7 with heavy spines in saw-like fringe. Female subanal plate with ventral margin straighter than dorsal margin, posterior termination pointed or with a process. South, east, and south-east Asia, Australia. At least two species, *T. clunifera* (Wood, 1862) (in general blue-green, posterior bor-

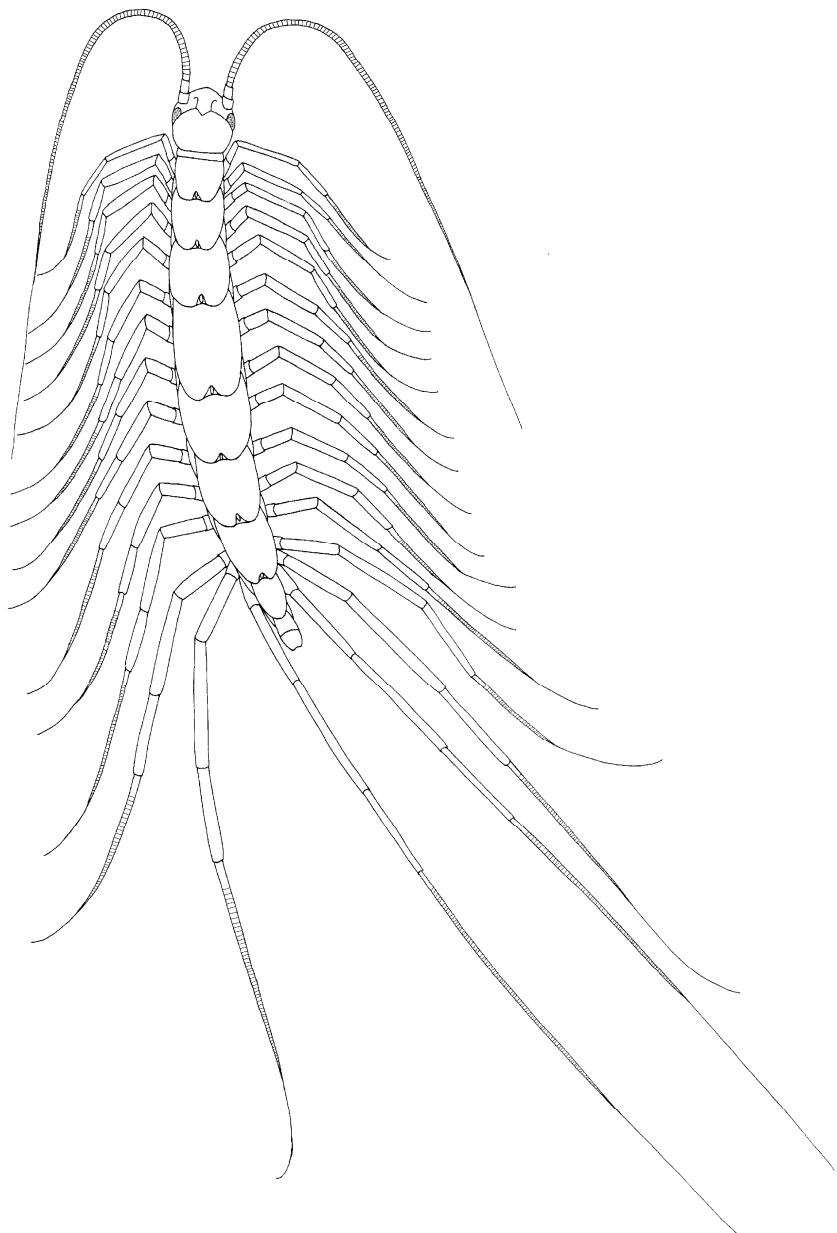


Fig. 19.3 *Madagassophora hova* (Scutigeromorpha, Scutigerinidae). Habitus, dorsal view, spine-bristles omitted. Original E. Zamprogno.

ders of tergites evenly rounded; China, Japan), *T. longicornis* (Fabricius, 1793) (brown or dark brown; posterior borders of tergites unevenly rounded; south, east and south-east Asia).

*Thereuopodina* Verhoeff, 1905. – Stomata elongate; stoma-saddles moderately vaulted; saddle of tergite 6 bearing 3-17 spines on each side. Prefemur of legs 2-4 lacking a saw-like row of spines. Margin of proarthron and mesarthron of female gonopods diverging posteriorly. Female subanal plate with a rounded posterior termination, lacking a process. South Asia and Australia. Three species, *T. adjutrix* Verhoeff, 1936 (first flagellum with 40 articles, 6-7 spines on each stoma-saddle of tergite 7; India), *T. queenslandica* Verhoeff, 1925 (yellow-brown, first flagellum with 58-69 articles, 0-5 spines on each stoma-saddle of tergite 7; Australia), *T. tenuicornis* Verhoeff, 1905 (dirty olive pigmentation, first flagellum of antenna with 76-85 articles, 2-3 spines on each stoma-saddle of tergite 7; Sri Lanka).

*Thereuoquima* Bücherl, 1949. – Only one (dorsal) spine-bristle on prefemur of second maxillae; ventral spine-bristle lacking. Margins of proarthron and mesarthron of female gonopods weakly converging; sinus considerably narrower than width of mesarthron; metarthron longer than short mesarthron. Brazil. A single species, *T. admirabilis* Bücherl, 1949.

Poorly known genera of Scutigeridae known only from single immature specimens are *Diplacrophor* Chamberlin, 1920 (Solomon Islands), *Phanothereua* Chamberlin, 1958 (Solomon Islands), and *Thereuella* Chamberlin, 1955 (Peru), all evidently Thereuoneminae, and *Gomphor* Chamberlin, 1944 (New Guinea), an apparent member of Scutigerinae.

Family SCUTIGERINIDAE Attems, 1926 (Fig. 19.3). – Antennal branch of cephalic suture complex present, continuing towards antennal socket. Antennal articles wider than long. Sclerotized lateral bulge lacking in proximal fork of hypopharynx. Second maxillae lacking pair of spine-bristles at distal end of tibia and on ventral side of prefemur. Lateral bar of labral trapezoid covered with low tubercles; labral bristles all pectinate; median sensilla of tripartite cluster on proximal labral part of epipharynx arranged as an antero-posteriorly aligned pair, situated between lateral clusters; median sensilla cluster on clypeal part of epipharynx arranged as a transverse band immediately proximal to dense median spine field. Tergites beset with bristles (Stachelborsten) but lacking unpaired spines associated with them. Legs relatively short, with weak carinae. Sternites with strong posteromedian embayment; sternites and coxae of posterior segments covered with elongate hairs between bristles. Metarthron of female gonopods with numerous (5-20) denticles along its inner margin. Short, blunt gonopods on first and second genital segment of male. South Africa, Madagascar. Three species in two genera.

*Scutigerina* Silvestri, 1903. – Tergites lacking spiculae; tarsus of second maxillae a single article. South Africa, Madagascar. Two species, *S. malagassa* (Saussure & Zehntner, 1902) (tergites uniformly blackish, 15-20 denticles on metarthron of gonopod; Madagascar), *S. weberi* Silvestri, 1903 (tergites yellow, with dark median and lateral bands, ca 10 denticles on metarthron of female gonopod; south Africa).

*Madagassophora* Verhoeff, 1936. – Tergites with slender, dense spiculae. Tarsus of second maxillae divided into two articles. Madagascar. A single species, *M. hova* (Saussure & Zehntner, 1902).

## Order Lithobiomorpha

Marzio Zapparoli & Gregory D. Edgecombe

Pleurostigmophoran centipedes with 15 leg-bearing trunk segments and pronounced heterotergy. Adult body length from 3.5 mm, as in the widespread subcosmopolitan *Lamyctes caeculus*, to 45–50 mm, as in some European *Eupolybothrus* s. str. or in the central Asiatic *Lithobius giganteus*. Antenna with 14–20 or up to 110 articles. Eye arranged in a cluster of 2–3 to 49 ocelli, single ocellus or absent. Cephalic plate with transverse and antennocellar sutures. Post-ocellar part of head and trunk tergites with margination. Bottle-shaped gland openings at border between labral and clypeal parts of epipharynx. Single transverse seta projecting medially from labral side piece. Mandible composed of two sclerites; gnathal edge with four strong, bicuspid teeth. Brush-like setae on inner margin of distal article of first maxillary telopodite developed as paired rows of plumose bristles that branch as slender hairs. Plumose setae on inner surface of article 3 of second maxillae; second maxillary claw composed of five elongate spines. Forcipular coxosternite bisected by median suture; anterior margin bearing 2+2 or more teeth (lacking in *Anodontobius*) and usually a pair of translucent, seta-like or sclerotized, tooth-like porodonts, rarely absent in Lithobiidae. Spiracles in at least leg-bearing segments 3 and 10 but generally present on segments 3, 5, 8, 10, 12 and 14, also segment 1 in Henicopini. Coxal pores usually on legs 12–15, rarely also on legs 11 (*Dzungaria*; *Pseudolithobiinae*) or restricted to legs 13–15 (*Dakrobius*; *Paralamyctes newtoni*) or 14–15 only (Gondwanan *Anopsobiinae*). Female gonopods with basal article bearing two or more spurs and terminal (third) article a broad claw.

Development anamorphic. First postembryonic stage generally with seven leg pairs (six or eight in some Henicopidae).

Ca 1100 valid species in nearly 130 extant genera/subgenera, in two families.

Family HENICOPIDAE Pocock, 1901. – Single ocellus on each side of head or blind (not a cluster of ocelli as in Lithobiidae). Tömösváry's organ on cephalic pleurite on ventral side of head. Forcipular pleurites connected ventrally, forming a continuous band between coxosternite and sternite of first leg-bearing segment. Distal spinose projection on tibiae of at least legs 1–11, variably present on legs 12–15; distinguished from Lithobiidae by lack of socketed spurs at distal ends of leg articles. Legs 14 and 15 without obvious sexual dimorphism. Male gonopods composed of four articles including terminal filament. Anal pores usually present in adults. Temperate and tropical parts of all

continents, exceptionally in cold boreal regions (e.g., *Lamyctes emarginatus* in Greenland). Ca 120 valid species in 20 genera.

Subfamily HENICOPINAE Pocock, 1901 (Fig. 19.4). – Basal article of telopodite of first

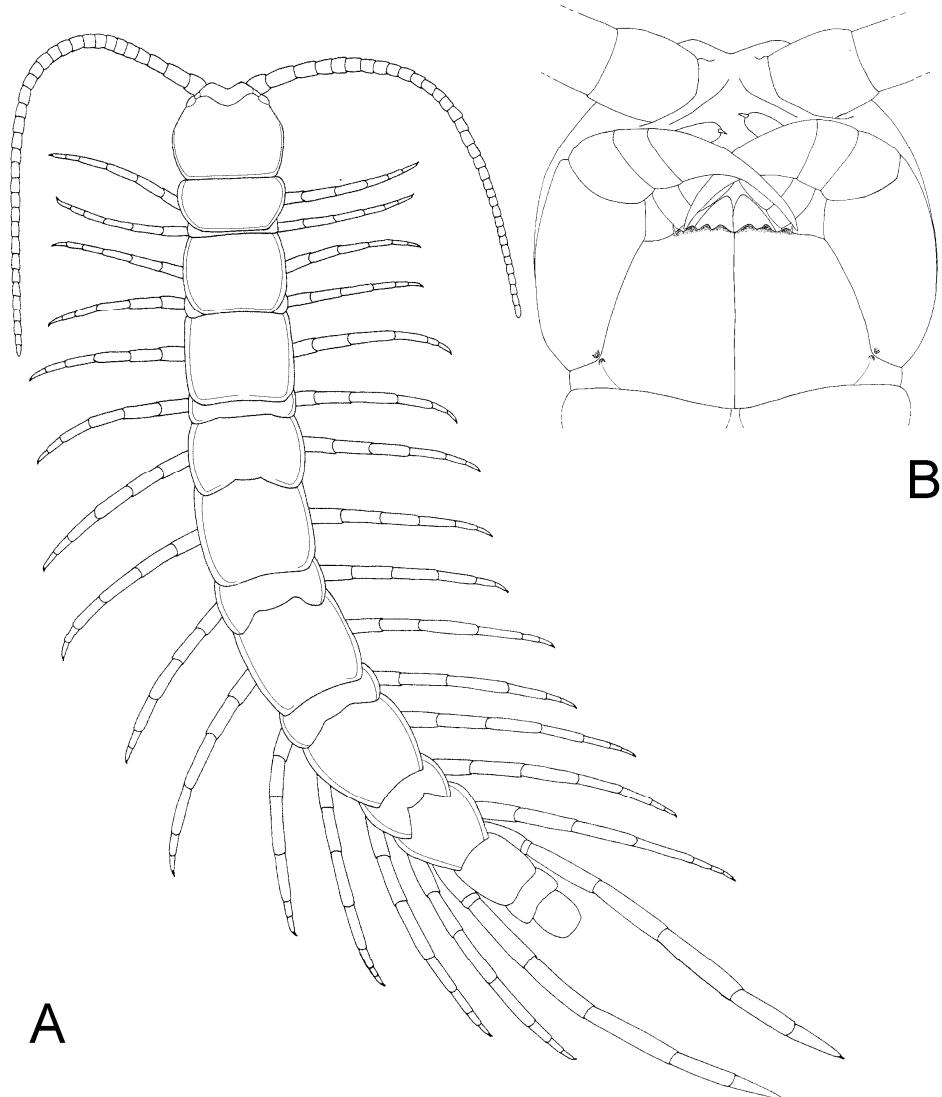


Fig. 19.4 *Henicops dentatus* (Lithobiomorpha, Henicopidae, Henicopinae). A Habitus, dorsal view. B Anterior part of the body, ventral view. Original E. Zamprogno.

maxillae fused on inner side to coxal projection. Distinguished from Anopsobiinae by lack of coxal process on legs 15 (except for *Hedinobius*), usually by presence of ocellus. Cosmopolitan, most diversity in southern hemisphere apart from Zygethobiini. Ca 100 species in 18 genera.

Tribe HENICOPINI Pocock, 1901. – First leg-bearing segment bearing spiracles. Cosmopolitan, most diversity in southern hemisphere (northern hemisphere diversity limited to few species of *Lamyctes* and *Pleotarsobius*). Ca 80 species in seven genera.

*Henicops* Newport, 1844. – Antenna with 26-51 articles. Forcipular coxosternal margin moderately wide, with 3+3 teeth except for *H. washpoolensis* (often 4+4), lacking porodonts. Mandibular aciculae abundant, arranged in two (inner and outer) rows. Several laciniate or plumose setae amidst simple setae on coxal projections of first maxillae. Posterior triangular projections on (at least) tergites 9, 11 and 13 (except *H. brevilabiatus*). Last distal spinose projection of tibia on legs 14 (except *H. brevilabiatus*, on legs 13). Subdivision of tarsus 1 of legs 1-12 indicated by paired larger setae and variably by articulation; tarsi of legs 13 and 14 divided into three or four articles; tarsus 2 of legs 15 divided into at least two articles. First genital sternite of male divided longitudinally into two sclerites. Male and female gonopods abundantly setose, with numerous distally curved setae on male gonopods. Australia, New Zealand, New Caledonia. Five species, incl. *H. brevilabiatus* (Ribaut, 1923) (tergites 11 and 13 without projections, tarsi of legs 1-12 undivided; New Caledonia), *H. howensis* Edgecombe, 2004 (26-30 antennal articles; Lord Howe Island), *H. maculatus* Newport, 1844 (tarsus 2 of legs 14 and 15 divided into three and four, exceptionally five, articles, respectively; south-east Australia, New Zealand), *H. milledgei* Hollington & Edgecombe, 2004 (legs 13-15 with undivided tarsus 1; south-east Australia), *H. tropicanus* Hollington & Edgecombe, 2004 (tarsus 2 of legs 13 and 14 divided into two and three articles, respectively; north-east Australia).

*Analamyctes* Chamberlin, 1955. – Antenna with at least 34-43 articles. Posterior angles of tergites rounded, none produced. Tarsal articulation distinct on all legs. Forcipular coxosternal teeth 2+2 or 3+3. Argentina. Two species, *A. andinus* (Silvestri, 1903) (coxosternal teeth 2+2, last distal spinose projection on tibia of legs 14; Mendoza), *A. tucumanus* Chamberlin, 1955 (coxosternal teeth 3+3, no porodonts, last distal spinose projection on tibia of legs 13; Tucumán).

*Easonobius* Edgecombe, 2003. – Antenna with 26-33 articles. Mandible with single row of exclusively bipinnulate aciculae. Coxal projections of first maxillae with laciniate or plumose setae near dorsal margin. Forcipular coxosternal teeth 2+2 or 3+3. Posterior angles of tergites 7, 9, 11 and 13 produced. Tarsal articulation distinct on all legs. Distal spinose projections on tibiae of legs 1-13. New Caledonia. Two species, *E. humilis* (Ribaut, 1923) (2+2 teeth on narrow coxosternal margin, Tömösváry's organs large), *E. tridentatus* Edgecombe, 2003 (3+3 teeth on moderately wide coxosternal margin, Tömösváry's organs small).

*Lamyctes* Meinert, 1868. – Narrow, curved forcipular coxosternal margin, usually with 2+2 teeth and seta-like or conical porodonts. Tergite margins rounded, lacking projections. Legs 1-12 with single article, tarsi of legs 13-15 bipartite. Cosmopolitan. Ca 40 species.

*L. (Lamyctes)* Meinert, 1868. – First genital sternite of male undivided. Cosmopolitan. Ca 33 species, incl. *L. adisi* Zalesskaja, 1994 (Brazil), *L. albipes* Pocock, 1894 (porodont a tiny spine on lateral shoulder, 2+2 or often 3+3 spurs on female gonopods; Java, Guadalupe, Canary Islands, Seychelles), *L. andinus* Kraus, 1954 (30-32 antennal articles, 2+2 forcipular coxosternal teeth and blunt lateral shouders; Peru, Chile), *L.*

*caeculus* (Brölemann, 1889) (ocellus absent, 24 antennal articles, mostly parthenogenetic; Americas, European greenhouses, Canary Islands, Australia, Hawaii, central Africa, Madagascar, Réunion), *L. emarginatus* (Newport, 1844) (parthenogenetic through much of distribution, 24-29 but usually 25 antennal articles, 2+2 forcipular coxosternal teeth and robust, tooth-like porodonts; New Zealand, Fiji, Kermadec Islands, Australia, widespread in Europe and North America, Hawaii, Greenland, Iceland, Kurile Islands, east Africa, Amazonas, Canary and Azores Islands, New Caledonia), *L. inermipes* (Silvestri, 1897) (35-40 antennal articles; porodonts spine- or tooth-like) (Argentina), *L. pachypes* Takakuwa, 1941 (25 antennal articles, forcipular coxosternal teeth 3+3; Japan, Russia).

*L. (Metalamyctes)* Verhoeff, 1941. – First genital sternite of male divided medially into two sclerites. South Africa, south Atlantic islands. Seven species, incl. *L. africanus* (Porat, 1871) (25-38 antennal articles, ocellus circled by dark pigment, last distal spinose projection on tibia of legs 12; central and south Africa, Madagascar, Juan Fernandez, Hawaii, west Australia), *L. castaneus* Attems, 1909 (33-35 antennal articles, last distal spinose projection on tibia of legs 11; south Africa), *L. tristani* (Pocock, 1893) (20-26 antennal articles, last distal spinose projection on tibia of legs 11; Tristan d'Acunha, Madagascar).

*Lamyctopristus* Attems, 1928. – Forcipular coxosternal margin narrow like *Lamyctes*, with 2+2 or 3+3 teeth. Tergites densely granulated, more pronounced in male than female. Legs 1-12 with undivided tarsi; distal part of tarsi of anterior legs distinctly curved but without distinct articulations. Temperate and tropical Africa. About six species.

*L. (Lamyctopristus)* Attems, 1928. – Basal article of female gonopods hatchet-shaped, bearing 5-7 spurs. Cape region. A single species, *L. validus* Attems, 1928.

*L. (Eumyctes)* Chamberlin, 1951. – Projections on tergites 9, 11 and 13. Female gonopods bearing 2+2 spurs. Africa. Five species, incl. *L. denticulatus* (Attems, 1907) (ca 29 antennal articles, forcipular coxosternal teeth 2+2; central and south Africa), *L. numidicus* Latzel, 1886 (26-29 antennal articles, forcipular coxosternal teeth 3+3; Algeria, Gabon), *L. sinuatus* (Porat, 1893) (ca 34 antennal articles, forcipular coxosternal teeth 3+3; south Africa).

*Paralamyctes* Pocock, 1901. – Median sulcus on cephalic plate continuous to transverse suture. Coxosternite on first maxillae large, bell-shaped. Temperate and tropical parts of southern hemisphere. 24 species.

*P. (Paralamyctes)* Pocock, 1901. – Mandibular aciculae with strong, distally pointed pinnules along one (dorsal) side only. Strong joints between articles on all legs (except *P. bipartitus* Lawrence, 1960). South Africa, Madagascar, India, Australia, New Zealand. 12 species, incl. *P. harrisii* Archey, 1922 (17-20 antennal articles, forcipular coxosternal teeth 2+2; New Zealand), *P. newtoni* (Silvestri, 1917) (17 antennal articles, forcipular coxosternal teeth 5+5, coxal pores lacking on legs 12; India), *P. rahuensis* Edgecombe, 2004 (New Zealand), *P. spenceri* Pocock, 1901 (19-23, usually 20, antennal articles, forcipular coxosternal teeth 5+5 to 8+7; south Africa, Madagascar), *P. tridens* Lawrence, 1960 (23-25 antennal articles, 3+3 small forcipular coxosternal teeth; Madagascar).

*P. (Haasiella)* Pocock, 1901. – Median sulcus on cephalic plate variably impressed behind transverse suture. Antenna with 17-24 articles. Ocellus relatively posteriorly positioned. Forcipular coxosternal teeth decreasing in size medially. Mandibular aciculae with barbs or pinnules along both margins. Tarsal articulation indistinct on legs 1-12. Australia, New Zealand. Six species, incl. *P. cammoensis* Edgecombe, 2004 (17 antennal articles; east Australia), *P. insularis* (Haase, 1887) (19 antennal articles; New Zealand), *P. subiculus* Edgecombe, 2004 (forcipular coxosternal teeth 7-10, strong projections on tergites 11 and 13; Tasmania), *P. trailli* (Archey, 1917) (ocellus absent; New Zealand).

*P. (Edgecombebegdus)* Özdikmen, 2009. – Forcipular coxosternal margin narrow, curved, with 4+4 to 5+5 teeth. Tergite 1 relatively small. Basal article of female gonopods extended as a process

bearing 3+3 spurs. Australia. Two species, *P. cassisi* Edgecombe, 2001 (spur-bearing process on gonopods moderately long; south-east Australia), *P. mesibovi* Edgecombe, 2001 (spur-bearing process on gonopods long, slender; Tasmania).

*P. (Thingathinga)* Edgecombe, 2001. – Simple mandibular aciculae. Forcipular coxosternal margin wide, transverse, bearing 6-12 small teeth. Articulations between articles of anterior legs developed ventrally only. Australia, New Zealand. Three species, incl. *P. grayi* Edgecombe, 2001 (forcipular coxosternal teeth blunt, legs 15 without distal spinose projection on tibia; Australia), *P. validus* Archey, 1917 (forcipular coxosternal teeth pointed, legs 15 with distal spinose projection on tibia; New Zealand).

*Pleotarsobius* Attems, 1909. – Antenna with 19 articles. Tarsus 2 of legs 15 subdivided into ca 15 articles, otherwise like *Lamyctes*. Hawaii. A single species, *P. heterotarsus* (Silvestri, 1904).

Tribe ZYGETHOBIINI Chamberlin, 1910. – Antenna with more than 30 articles. Forcipular coxosternal margin relatively wide, not produced anteriorly. First leg-bearing segment lacking spiracles. Northern hemisphere, incl. North America, central and east Asia. 18 species in five genera.

*Zygethobius* Chamberlin, 1903. – Ocellus present. Forcipular coxosternal teeth 3+3. Posterior angles of tergites 9, 11 and 13 (and sometimes 6 and 7) produced. Tarsal articulation distinct on all legs. Coxal pores on legs 11-15. North America. Five species, incl. *Z. dolichopus* (Chamberlin, 1902) (legs 14 but not 15 with distal spinose projection on tibia; western North America), *Z. pontis* Chamberlin, 1911 (legs 15 with distal spinose projection on tibia; eastern North America).

*Buethobius* Chamberlin, 1911. – Ocellus absent. Forcipular coxosternal teeth 3+3. Posterior angles of tergites 9, 11 and 13 not produced. Tarsal articulation indistinct on legs 1-13. North America. Five species, incl. *B. conjugans* Chamberlin, 1911 (antenna with 43-45 articles, less than half length of body; California), *B. oabitus* Chamberlin, 1911 (antenna with 36 articles, more than half length of body; Mississippi).

*Cermatobius* Haase, 1885. – Ocellus present. Forcipular coxosternal teeth 5+7 to 8+9. Sharp posterior projections on tergites 9, 11 and 13. Distal spinose projections on tibiae of legs 1-13. Tarsi subdivided into up to 30 articles. 3+3 to 6+6 spurs on female gonopods. Central, east and south-east Asia. Six species, incl. *C. martensi* Haase, 1885 (ca 42 antennal articles, 5+5 spurs on gonopods; Indonesia), *C. japonicus* (Silvestri, 1909) (forcipular coxosternal teeth 7+7, 3+3 spurs on gonopods; Japan), *C. kirgisicus* (Zalesskaja, 1972) (44-71 antennal articles, 6+6 spurs on gonopods; Kirghizia), *C. longicornis* (Takakuwa, 1939) (45-56 antennal articles, 4+4 spurs on gonopods; south China, Korea, Japan), *C. longitarsis* (Verhoeff, 1934) (Japan, Taiwan).

*Hedinobius* Verhoeff, 1934. – Ocellus absent. Forcipular coxosternal teeth 3+3. Tergites not notched medially, all posterior angles rounded. Tarsal articulation distinct on legs 5-15, faint on legs 1-4. Coxal pores on legs 11-15. Coxa of legs 15 with a distal process. Spines on trochanter and prefemur of legs 14 and 15. 2+2 spurs on female gonopods. A single species, *H. hummelii* Verhoeff, 1934 (west China).

*Yobius* Chamberlin, 1945. – Ocellus absent. Tarsal articulation distinct on all legs. Utah. A single species, *Y. haywardi* Chamberlin, 1945.

Subfamily ANOPSABIINAE Verhoeff, 1907 (Fig. 19.5). – Body length mostly 5-7 mm, only 3 mm in *Catanobsobius* and *Rhodobius*, up to 14 mm in *Dzungaria*. Ocellus absent. Antenna with 14-18 articles apart from *Dzungaria*. Tergites usually yellow-pale brown;

all posterior angles rounded. Coxa of legs 15 with long, lobate process ending in a spine. Prefemur of legs 15 usually with a single ventral spur. 20 species in eight genera.

*Anopsobius* Silvestri, 1899. – Usually 15 antennal articles. Spiracles on segments 3, 5, 8 (except *A. giribeti*), 10, 12 and 14, also on segment 1 in *A. macfaydeni*. Distal spinose projection on tibiae of legs 1-12. Posteroventral spine on pretarsi short. Coxal pores on legs 14-15 only. Southern South America, Falkland Islands, Australia, New Zealand, south Africa (possibly introduced). 11 species, incl. *A. actius* Chamberlin, 1962 (porodont distal to outer tooth; Chile), *A. diversus* Chamberlin, 1962 Chamberlin, 1962 (6+6 forcipular coxosternal teeth, porodont between two outer teeth; Chile), *A.*

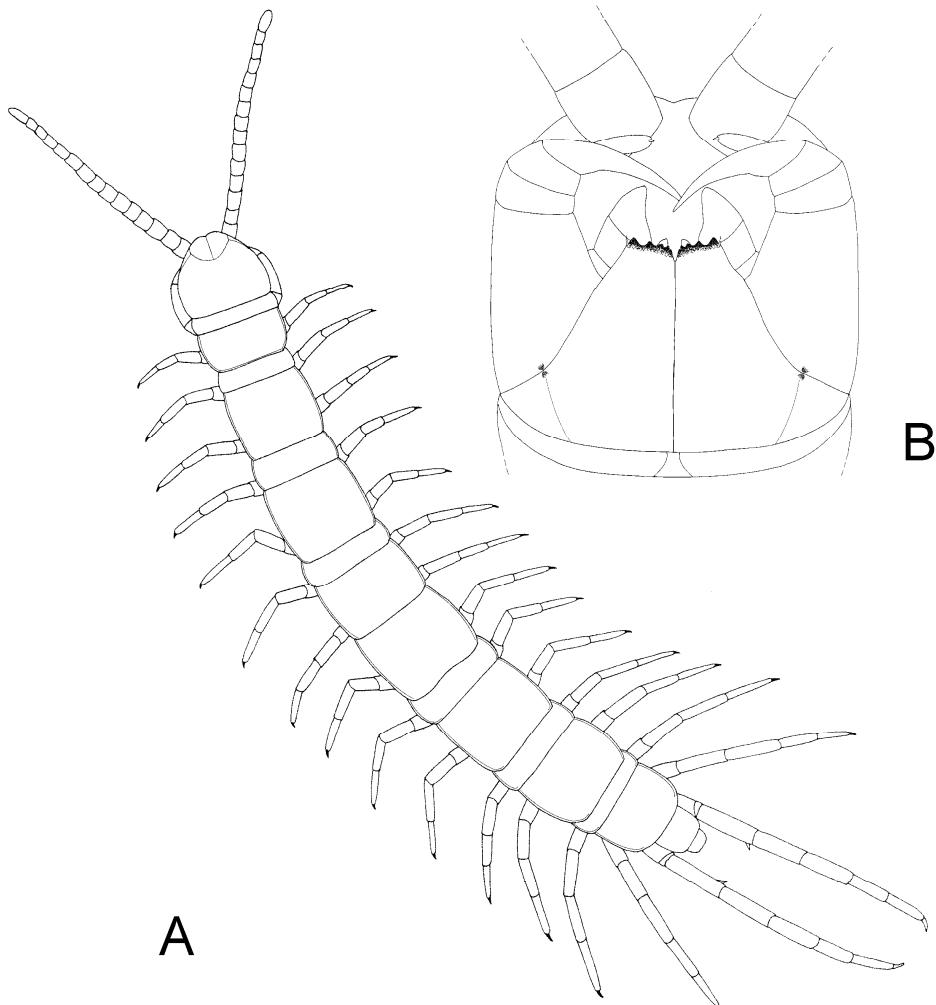


Fig. 19.5 *Anopsobius wrighti* (Lithobiomorpha, Henicopidae, Anopsobiinae). A Habitus, dorsal view. B Anterior part of the body, ventral view. Original E. Zamprogno.

*macfaydeni* Eason, 1993 (spiracles present on segment 1; Falkland Islands), *A. neozelanicus* Silvestri, 1909 (forcipular coxosternal teeth up to 8+8, 2,2 coxal pores on legs 14 and 15 of males; New Zealand), *A. productus* Silvestri, 1899 (leg 15 trochanter lacking ventrodistal spur; Chile), *A. wrighti* Edgecombe, 2003 (usually 5+5 forcipular coxosternal teeth; south-eastern Australia).

*Anopsobiella* Attems, 1938. – Antenna with 18 articles. Forcipular coxosternal teeth 2+2. Spiracles on segments 3, 5, 8, 10 and 12. Legs 9-13 with a small ventrodistal spur on prefemur, femur and tibia. Last distal spinose projection on tibia of legs 13. Legs 14 with robust tarsus 1 that has a dorsal prolongation about 1/3 of its total length that overhangs the short, very slender tarsus 2; legs 15 markedly longer and thicker than legs 14, with tibia stouter than prefemur or femur, developed as a dorsal prolongation about 1/5 its total length, both articles very slender, articulated to ventral extremity of tibia. Coxal pores on legs 12-15. Vietnam. A single species, *A. dawyoffi* Attems, 1938.

*Catanopsobius* Silvestri, 1909. – Length 3 mm. Spiracles on leg-bearing segments 3 and 10 only. All tarsi undivided. Single coxal pore on legs 14 and 15. Legs 15 lacking ventral spine on prefemur. Chile. A single species, *C. chilensis* Silvestri, 1909.

*Dichelobius* Attems, 1911. – Antenna with 17 articles. Coxal pores on legs 14-15 only. Prefemora of legs 15 (and variably 14) with ventrodistal spur. Australia, New Caledonia. Three species, *D. bicuspis* Ribaut, 1923 (spiracles on segments 3, 10 and 12 only, long posteroventral spine on pretarsi, ventrodistal spur on prefemora of legs 14 and 15, tibia of legs 12 with spinose distal projection; New Caledonia), *D. etnaensis* Edgecombe and Giribet, 2004 (spiracles on segments 3, 5, 8, 10, 12 and 14; short posteroventral spine on pretarsi, ventrodistal spur on prefemur of legs 15 but not 14; Queensland), *D. flavens* Attems, 1911 (like *D. bicuspis* but tibia of legs 12 with short, blunt distal projection; west Australia).

*Dzhungaria* Farzalieva, Zalesskaja & Edgecombe, 2004. – Length up to 14 mm. Coxal pores on legs 11-15. Tarsal articulation distinct on legs 2-15. Poorly-developed but evident coxoventral processes on legs 1-10. Last distal spinose projection on tibia of legs 13. Differs from *Ghilarioviella* in absence of a distally-spined coxal process on legs 14, 30-38 antennal articles, forcipular coxosternal teeth 3+3, and less distinct differentiation of porodonta. Kazakhstan. A single species, *D. gigantea* Farzalieva, Zalesskaja & Edgecombe, 2004.

*Ghilarioviella* Zalesskaja, 1975. – Antenna with 16 articles. Forcipular coxosternal teeth 2+2; slender porodonta. Spiracles on segments 3, 5, 8, 10, 12 and 14. Legs 14 and 15 with coxal process terminating in a spine. Coxal pores on legs 12-15. Tajikistan, introduced to a botanic garden in Austria. A single species, *G. valiachmedovi* Zalesskaja, 1975.

*Rhodobius* Silvestri, 1933. – Antenna of 15 articles. Spiracles on segments 3, 12 and 14. Coxal pores on legs 12-15. Legs 15 lacking ventral spine on prefemur. Rhodes, probably introduced. A single species, *R. lagoi* Silvestri, 1933.

*Shikokuobius* Shinohara, 1982. – Antenna of up to 18 articles. 3+3 small forcipular coxosternal teeth. Spiracles on leg-bearing segments 3, 5, 8, 10, 12 and 14. Coxal pores on legs 12-15. Legs 15 only with coxal process. Prefemur and trochanter of legs 15 with ventral spine. Some posterior legs with spine at dorsodistal end of each prefemur. Japan. A single species, *S. japonicus* (Murakami, 1967).

Family LITHOBIIDAE Newport, 1844. – Body length 5-50 mm. Antenna usually with at least 18-20 articles (up to 110 in the troglobitic *Lithobius matulici* Verhoeff, 1899). Ocelli usually three or more on each side, in a cluster of a single usually large posterior ocellus and a group of two or more ocelli decreasing in size (here denoted by the formula 1+n); blind species also known. Tömösváry's organ positioned anteroventral to ocellar cluster. Labrum with side-pieces notched posteromesally at the level of their transverse setae,

resulting in the formation of two blunt teeth. Coxal projections of first maxillae fairly prominent. Forcipular pleurites not meeting each other at base of coxosternite. First leg-bearing segment without spiracles. At least some legs with regularly disposed distal spurs on various articles. Tibiae of all legs without distal spinose projection. Coxae of legs 12-15 (generally), 11-15 (rarely) or 13-15 (very rarely) with more or less numerous coxal pores regularly or irregularly arranged. Tarsal articulation of legs 1-13 distinct or not, always distinct on legs 14 and 15. Legs 14 and 15 often exhibit sexual dimorphism. Ultimate legs with one or two apical claws. No anal organs at the end of anamorphic phase. Male gonopods of one or two articles. Mainly confined to northern hemisphere, apart from few species of *Lithobius* and *Bothropolys*, introduced through commercial trade and established in South America, south Africa and the Australoasiatic region. More than 1000 species/subspecies are currently referred to this family, but many taxa need revision.

Subfamily LITHOBIINAE Verhoeff, 1907 (Fig. 19.6). – Body length 5-50 mm. Antenna with 20 or more articles. Ocelli present or absent. Forcipular coxosternal teeth 2+2 or more, more or less developed, absent in *Anodontobius* Matic, 1983. Tarsal articulation of legs 1-13 distinct or not. Coxae of legs 12-15 with few ventral pores almost regularly disposed in a single row. Holarctic region. More than 900 species/subspecies in ca 100 genera/subgenera but many species are of doubtful identity pending revision. Ca 70 genera/subgenera have been named from North and Central America, most of them are poorly known and of uncertain identity. Few taxonomic reviews have been recently done and a sound inventory of valid taxa is at present unavailable.

*Lithobius* Leach, 1814. – Body length 5-50 mm. Antenna with 20 or more articles. Ocelli 1+1 to 1+38, absent in some troglobitic species. Forcipular coxosternal teeth 2+2-8+8 or few more, more or less developed. Tergites with or without posterior triangular projections. Tibia of the anterior pair of legs not modified. Tarsal articulation of legs 1-13 distinct or not. Secondary sexual modifications sometimes on legs 14 and 15 of male. Female gonopods with uni-, bi- or tridentate claw, 2+2-4+4 spurs. Mostly Palearctic, some species also in North America. A very large and heterogeneous assemblage including more than 500 species/subspecies arranged in eight subgenera.

*L. (Lithobius)* Leach, 1814. – Body length 10-25 mm. Antenna with more than 25 articles. Ocelli 1+9-1+38, less numerous to absent in some cave species. Forcipular coxosternal teeth 2+2-8+8 or little more; porodonts generally slender, setiform, rarely short and stout. Tergites with or without posterior triangular projections, tarsal articulation of legs 1-13 distinct. Secondary sexual modifications sometimes on legs 14 and 15 of male. Female gonopods with uni-, bi- or tridentate claw, 2+2-3+3 spurs. Mostly in the west Palearctic region but also in eastern North America; wide range of epigeic habitats, mostly in forest but also in open arid and semi-arid habitats and in alpine environments, from sea level to 4400 m; species more or less adapted to cave habitat are also known. Ca 300 known species/subspecies, incl. *L. antipai* Matic, 1969 (high altitude, Iran), *L. atkinsoni* Bollman, 1887 (south-eastern North America), *L. borisi* Verhoeff, 1928 (S Balkans), *L. castaneus* Newport, 1844 (porodonts stout; Mediterranean region), *L. dentatus* Koch, 1844 (Central

and Southern Europe), *L. electron* Verhoeff, 1928 (Rhodope Mt.), *L. erythrocephalus* Koch, 1847 (Europe and SW Asia), *L. forficatus* (Linnaeus, 1758) (synanthropic and very common in Europe, introduced elsewhere), *L. glacialis* Verhoeff, 1937. (Central Europe), *L. lapidicola* Meinert, 1872 (one of the smaller representatives; Europe), *L. latro* Meinert, 1872 (Central Europe), *L. lucifugus* L. Koch, 1862 (common in European alpine habitats), *L. macilentus* Koch, 1862 (Europe), *L. melanops* Newport, 1845 (often synanthropic; western Palearctic, introduced in North America), *L. mutabilis* Koch, 1862. (Europe), *L. obscurus* Meinert, 1872 (Spain, Canary Is., Azores Is., Morocco), *L. pelidnus* Haase, 1880 (Central Europe), *L. peregrinus* Latzel, 1880 (South Europe), *L. piceus* L. Koch, 1862 (Europe), *L. pilicornis* Newport, 1844 (western Europe), *L. punctulatus* C.L. Koch, 1847 (Europe), *L. pygmaeus* Latzel, 1880 (Central Europe), *L. sibordoni* Matic, 1969 (no ocelli; caves in Sardinia), *L. schulzeri* Verhoeff, 1925 (Central Europe), *L. tenebrosus* Meinert, 1872 (mainly central Europe), *L. tricuspidis* Meinert, 1872 (Europe), *L. valesiacus* Verhoeff, 1935 (Central Europe), *L. variegatus* Leach, 1814 (dorsal

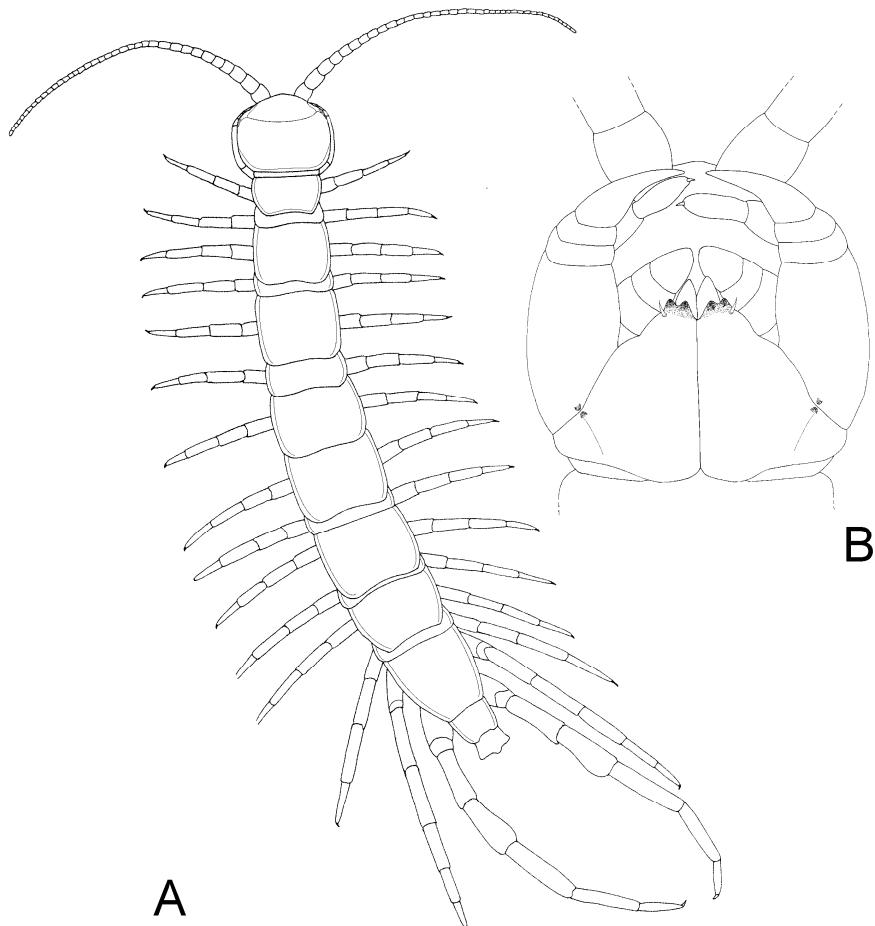


Fig. 19.6 *Lithobius tenebrosus* (Lithobiomorpha, Lithobiidae, Lithobiinae). A Habitus, dorsal view, plectrotaxy omitted. B Anterior part of the body, ventral view. Original E. Zamprogno.

colour pattern of living specimens unmistakable, pale brown marbled with dark violet, posterior legs with pale and dark bands; western Europe).

*L. (Chinobius)* Verhoeff, 1934. – Body length 10-15 mm. Antenna with 17-21 articles. Ocelli 1+5-1+8. Forcipular coxosternal teeth 2+2; porodonts setiform. Tergites 9, 11, 13 with or without posterior triangular projections. Tarsal articulation of legs 1-13 distinct. Legs 14 and 15 of male swollen, with dorsal sulci. Female gonopodial claw bearing two or more medial denticles, variable intraspecifically, conferring a pectinate appearance, 2+2 spurs. Central and east Asia; fragmentary records from temperate coniferous forests, up to 1200 m. 14 species, incl. *L. sachalini* Verhoeff, 1933 (far east Asia), *L. uralensis* Farzalieva, 2004 (Middle Urals, the westmost species).

*L. (Dacolithobius)* Matic, 1961. – Body length 10-12 mm. Antenna with 37-51 articles. Ocelli 1+9-1+15. Forcipular coxosternal teeth 2+2; porodonts spiniform. Tarsal articulation of legs 1-13 distinct. Male tergite 14 very extended posteriorly, covering tergite 15 and part of tergite 16; posterior margin of tergite 14 with setae and having the appearance of a broom. Female gonopods with tridentate claw, 2+2 spurs. South-east Europe; mostly epigeic, but also in caves. A single species of uncertain identity, *L. domogledicus* Matic, 1961.

*L. (Ezembius)* Chamberlin, 1919. – Body length mostly 19-20 mm but an extreme intra- and interspecific variation is known, from 9-10 mm in *L. enghoffi* Eason, 1986 to 22-50 mm in the very variable *L. giganteus* Sselivanoff, 1881. Antenna with ca 20 articles. Ocelli 1+4-1+20. Forcipular coxosternal teeth usually 2+2; porodonts generally setiform, sometimes stout. Tergites generally without posterior triangular projections. Tarsal articulation of legs 1-13 distinct. Female gonopods with uni-, bi- or tridentate claw, 2+2-3+3, rarely 4+4, spurs. Mostly Asia, also western North America; wide range of habitats, from arctic and sub-arctic to tropical and sub-tropical forests, to steppe and overgrazed stony areas of central Asia, to Himalayan montane forests, from sea shore up to 5500 m (Himalayas). Ca 60 species/subspecies, incl. *L. ostiacorum* Stuxberg, 1876 (posterior triangular projections on tergites 11, 13; Siberia), *L. readae* Eason, 1997 (porodonts stout; Kirghizia), *L. schwalleri* Eason, 1989 (more than 2+2 teeth on the forcipular coxosternite; Himalayas), *L. stejenegeri* (Bollmann, 1893) (one of the northmost Lithobiidae known; Alaska and Beringia), *L. tibiotenuis* Eason, 1989 (posterior triangular projections on tergites 9, 11, 13; Himalayas).

*L. (Monotarsobius)* Verhoeff, 1905. – Body length 5-11 mm. Antenna with 20 articles or thereabouts. Ocelli generally few, 1+1-1+11, absent in some cave species. Forcipular coxosternal teeth 2+2; porodonts setiform. Tergites without posterior triangular projections. Tarsal articulation of legs 1-13 very faint or indistinct. Secondary sexual modifications sometimes on male legs 14 and 15. Female gonopods with uni-, bi- or tridentate claw and usually 2+2 spurs. Chiefly Eurasia, introduced elsewhere; wide range of epigeic habitats, from low altitude sites to 4200 m, also caves. Ca 114 species/subspecies, incl. *L. austriacus* (Verhoeff, 1937) (Central and Eastern Europe), *L. bolognai* Zapparoli, 1991 (female gonopods with 4+4-4+5 spurs; Middle East), *L. crassipes* L. Koch, 1862 (common in Europe), *L. curtipes* C. L. Koch, 1847 (temperate Asia, westward up to Europe), *L. ferganensis* (Trotzina, 1894) (temperate Asia, westward up to Europe), *L. fugax* Stuxberg, 1886 (female gonopods with 4+4-4+5 spurs; Siberia), *L. materiatus* Silvestri, 1936 (high altitude; India), *L. speleovolcanus* Serra, 1984 (caves; Canary Islands).

*L. (Porobius)* Attems, 1926. – Body length 12-20 mm. Antenna with 20 articles. Ocelli 1+4. Forcipular coxosternal teeth 2+2-3+3, very small; porodonts spiniform. Tergites without posterior triangular projections. Tarsal articulation of legs 1-13 distinct. Female gonopods with unidentate claw, 2+2 spurs. Middle East; ± thermophilous habitats, incl. *Pinus* forests and Mediterranean scrubs, sea level to 2200 m. Two species, *L. pamukkalensis* Matic, 1980 and *L. paricornis* Porat, 1893.

*L. (Sigibius)* Chamberlin, 1913. – Body length 7-10 mm. Antenna with 25 or more articles. Ocelli 1+2-1+6, rarely absent. Forcipular coxosternal teeth 2+2; porodonts setiform, rarely short and stout. Tergites without posterior triangular projections. Tarsal articulation of legs 1-13 indistinct. Female

gonopods generally with tridentate claw, 2+2 spurs. Mostly west Palearctic but with apparently native species in central and North America; wide range of habitats, including caves, from near sea level to 2000 m. Ca 40 species/subspecies, incl. *L. burzenlandicus* Verhoeff, 1931 (E Europe), *L. bullatus* Eason, 1990 (the only species known in Asia; Hong Kong, probably introduced, primary range unknown), *L. electrinus* (Verhoeff, 1937) (caves in N Italy), *L. microps* Meinert, 1868 (Europe, introduced in North America and Australia), *L. trebinjanus* Verhoeff, 1900 (porodont stout; Balkans).

*L. (Thracolithobius)* Matic, 1962. – Body length 12-15 mm. Antenna with 37-61 articles. Ocelli absent to 1+11-1+13. Forcipular coxosternal teeth 2+2. Tarsal articulation of legs 1-13 distinct. Male tergite 14 peak-shaped, posterior margin completely rounded. Female gonopods with bi- or tridentate claw, 2+2 spurs. South-east Europe; epigeic, but also in cave. Three species, *L. dacicus* Matic, 1959, *L. inexpectatus* Matic, 1962, *L. remyi* Jawlowski, 1933.

Some other species-groups worthy of generic/subgeneric status are recognizable within *Lithobius* s. str., e.g., *Alokobius* Attems, 1926, to include species with more than 20 antennal articles and secondary sexual modifications on legs 14 and 15 of males, but its identity is controversial.

*Anodontobius* Matic, 1983. – Body length 11-13 mm. Antenna with 39-46 articles. Ocelli 1+11-1+13. Forcipular coxosternite wide and short, similar in shape to *Harpolithobius*. First leg not swollen; all legs with blue-black spots. Tarsal articulation of legs 1-13 distinct. Female gonopods with tridentate claw bearing a fourth lateral denticle, 2+2 spurs. Anatolia; from 500 to 1800 m, mostly in mesophilous forests. A single species, *A. osellai* Matic, 1983.

*Arebius* Chamberlin, 1916. – Body length 12 mm and less. Antenna with 20 articles. Ocelli 1+7-1+23. Tergites almost without posterior triangular projections. Female gonopods with 2+2 spurs. Tarsal articulation of legs 1-13 distinct. Posterior legs slender in both sexes, without special modification in male. Western North America from Mexico to Alaska. Ca 25 epigeic species, incl. *A. kochii* (Stuxberg, 1875), *A. medius* Chamberlin, 1916, *A. obesus* (Stuxberg, 1875).

*Australobius* Chamberlin, 1920. – Body length 16-23 mm. Antenna mostly with 20 articles, rarely more than 24. Ocelli few (e.g., 1+3-1+6); large Tömösváry's organ below the inferior row of ocelli. Forcipular coxosternal teeth at least 3+3. Tergites with more or less distinct posterior triangular projections. Legs 15 of male not conspicuously modified. Female gonopods with uni-, bi-, tridentate claw, 3+3-4+4 spurs. Tarsal articulation of legs 1-13 indistinct in some species. Mostly in south-east Asia and east Australia; temperate montane forests to alpine meadows, up to 4850 m, rain to wet sclerophyll forest habitats, from near sea level to 1560 m (Australia). Ca 30 species, incl. *A. magnus* (Trozina, 1894) (antenna with 25-30 articles; widespread in Asia), *A. scabrior* Chamberlin, 1920 (the only species of the genus in Australia), *A. sechellarum* (Brölemann, 1895) (Seychelles).

*Dakrobius* Zalesskaja, 1975. – Body length 6-7 mm. Antenna with 19-20 articles. Three ocelli. Forcipular coxosternal teeth 2+2; porodonts long and setiform. Tarsal articulation of legs 1-13 indistinct. Ventral pores on coxae of legs 13-15. Female gonopods with an additional claw and 2+2 spurs. Far east Russia. A single species, *D. krivolutskyi* Zalesskaja, 1975.

*Enarthrobius* Chamberlin, 1926. – Body length 9-18 mm. Antenna with 25-35 articles. Ocelli 1+5-1+16. Tergites 6, 7, 9, 11, 13 or 7, 9, 11, 13 or only 9, 11, 13 with posterior triangular projections. Tarsal articulation of legs 1-13 distinct. Female gonopods with bi- or tridentate claw; 2+2 spurs. Femur of legs 15 of male with dorsal distal lobe. Six species, most from south-eastern North America, incl. *E. bullifer* Chamberlin, 1926 and *E. covenus* Chamberlin, 1944.

*Eulithobius* Stuxberg, 1875. – Body length 23-29 mm. Antenna with 35-47 articles. Ocelli 1+24-1+49. Forcipular coxosternal teeth 5+5-13+13. Tergites 6, 7, 9, 11, 13 with posterior triangular projections. Female gonopods with uni- or tridentate claw, 2+2-3+3 spurs. Tarsal articulation of legs 1-13 distinct. Legs 14 and 15 long, slender in both sexes, without special modifications in male. South-eastern North America; epigeic, but also in caves. Three species, *E. fattigi* Chamberlin, 1945, *E. hypogaeus* Chamberlin, 1940 and *E. sphactes* Crabill, 1958.

*Garcibius* Chamberlin, 1942. – Body length 21 mm. Possibly related to *Neolithobius*. Antenna very long, with 61 articles. Ocelli rudimentary or absent. Forcipular coxosternal teeth 6+6. Tergites II and 13 with small posterior triangular projections. Female gonopods with tridentate claw, 2+2 spurs. Central America. A single species, *G. osoroi* Chamberlin, 1942 (highly specialized troglobitic species, depigmented, with large Tömösváry's organ; only known from a cave in Mexico).

*Garibius* Chamberlin, 1913. – Body length 5-9.5 mm. Body considerably wider from leg-bearing segment 1 to 10. Tergite 1 much narrower than the head. Antenna with 20 articles. Ocelli 1+6-1+14. Forcipular coxosternal teeth 2+2. Legs 15 of male long, inflated, with a low setigerous tibial lobe pierced by a distinct gland canal. Mostly south-eastern North America; epigeic, chiefly in coniferous or broadleaved forests, rarely in caves. Seven to eight species, incl. *G. monticolens* Chamberlin, 1913 and *G. opicolens* Chamberlin, 1913.

*Gonibius* Chamberlin, 1925. – Body length 18-22 mm. Antenna with 20 articles. Ocelli 1+15-1+18. Forcipular coxosternal teeth 6+6-9+9. Tergites 4, 6, 7, 9, 11, 13 or only 9, 11, 13 with posterior triangular projections. Southern North America; epigeic, 1000 and 2400 m. Two species, *G. glyptocephalus* (Chamberlin, 1903) and *G. rex* (Bollman, 1888).

*Harpolithobius* Verhoeff, 1904. – Body length 9-24 mm. Antenna with 36-78 articles. Ocelli 1+9-1+25, absent in troglobitic species. Forcipular coxosternal teeth generally 2+2, small; forcipular coxosternite narrow, not prominent, with anterior border almost straight, not incised medially; tarsi of the forcipules very long, slender, arched. Tergites 9, 11, 13 with posterior triangular projections. Legs 1 without or with very reduced plectrotaxy, tibia and femur generally swollen. Prefemur, femur, tibia and tarsus of all legs with numerous tegumentary ventro-lateral (posterior) irregular blue-violaceous pigmented spots. Tarsal articulation of legs 1-13 distinct. Tibiae of legs 14 and 15 of male generally modified with a distal dorsolateral setose swelling and a dorsal sulcus respectively. Female gonopods with uni- (rarely), bi- or tridentate claw, 2+2, rarely 3+3, spurs. South-east Europe and south-west Asia; mostly in forests but also in caves, from near sea level to 2100 m. 25 nominal species/subspecies, incl. *H. anodus* (Latzel, 1880) (south Europe, Near East), *H. banaticus* Matic, 1961 (Romania), *H. oltenicus* Negrea, 1962 (no ocelli; caves in Romania), *H. vignatagliantii* Zapparoli, 1989 (no ocelli; only known from a cave in Anatolia).

*Hessebius* Verhoeff, 1941. – Body length 13-30 mm. Antenna with 17-22 articles (generally 20). Ocelli 1+2-1+9. Forcipular coxosternal teeth 2+2. Tergites without posterior triangular projections. Legs 14 and 15 thicker than the anterior ones in female, both thicker in male. Female gonopods with a massive expansion and projection on the dorsolateral ridge, a long claw sometimes with a stout lateral tooth at its base and 2+2-5+5 spurs. South-west and central Asia, north-east Africa; thermophilous habitats, from near sea level to 2250 m in E-Mediterranean area and Middle East, up to 4200 m in Mongolia. Ca 10 species, incl. *H. barbipes* (Porat, 1893) (widespread in E-Mediterranean basin), *H. jangtseanus* Verhoeff, 1942 (central Asia), *H. major* Zaleskaja, 1978 (up to 30 mm; central Asia).

*Nampabius* Chamberlin, 1913. – Body length 5-7.5 mm. Body attenuated anteriorly, tergite 1 much narrower than the head and than tergite 3. Antenna with 20 articles. Ocelli few (e.g. 1+3, 1+6). Forcipular coxosternal teeth 2+2. Tergites 11, 13 or at least 13 with small posterior triangular projections. Tarsal articulation of legs 1-13 indistinct. Tibia of legs 14 of male with dorsal or dorsomedial small subcylindrical or distally expanded lobe bearing a number of setae. Legs 15 of male short, moderately and uniformly inflated. Eastern North America; mostly in forests, both broadleaved and coniferous, also in caves. 17 species, incl. *N. lundii* (Meinert, 1886), *N. turbator* Crabill, 1952 (Appalachian caves).

*Neolithobius* Stuxberg, 1875. – Body length 17-30 mm. Antenna with 30-50 articles. Ocelli 1+25-1+50. Forcipular coxosternal teeth 5+5 to 10+10; porodonts slender and mostly bristle-like. Tergites 7, 9, 11, 13 with posterior triangular projections. Femur of male legs 15 enlarged at least distally, conspicuously widened, and especially bowed ventrad, or at least with dorsal surface depressed or

incurved, rarely with dorsal surface not depressed but elevated at distal end. Southern North America and Central America; epigeic, in a wide range of habitats from forest to open habitats, from near sea level to 3400 m, sometimes in caves. Ca 20 species, incl. *N. mordax* (L. Koch, 1862), *N. transmarinus* (L. Koch, 1862), *N. vorax* (Meinert, 1872) (all in southern North America). Close to *Neolithobius* are *Sozibius* Chamberlin, 1912 (seven species, probably forest dwellers, e.g. *S. tuobukus* (Chamberlin, 1911), mostly inhabiting south-eastern North America), *Nuevobius* Chamberlin, 1941 (two poorly specialized cave species, *N. cottus* Crabbill, 1960 and *N. cavigolens* Chamberlin, 1941, from south-eastern North America and Central America, respectively), *Pholobius* Chamberlin, 1940 (two epigeic species from southern North America, e.g. *P. goffi* Chamberlin, 1940) and *Serrobius* Causey, 1942 (one forest species from south-eastern North America, *S. pulchellus* Causey, 1942).

*Oabius* Chamberlin, 1913. – Body length 10-12 mm. Apparently close to *Lithobius* (*Monotarsobius*). Antenna with 20 articles. Ocelli 1+3-1+12. Tergites without posterior triangular projections. Tarsal articulation of legs 1-13 indistinct. Posterior legs moderately uniformly inflated. Western North America, from Alaska to Arizona. Ca 30 species, incl. *O. aiolus* Chamberlin, 1938, *O. decipiens* Chamberlin, 1916, *O. tiganus* (Chamberlin, 1910). Closely related to *Oabius* are *Tigobius* Chamberlin, 1916 (a single species; California), *Banobius* Chamberlin, 1938 (a single species; Oregon), *Alaskobius* Chamberlin, 1946 (four species; Alaska), *Escimobius* Chamberlin, 1949 (a single species; Alaska) and *Calcibius* Chamberlin & Wang, 1952 (a single species; Washington), all epigeic.

*Paitobius* Chamberlin, 1912. – Body length 6-12 mm. Antenna with 26-34 articles. Ocelli 1+6-1+19, rarely 1+3. Forcipular coxosternal teeth 2+2, inner tooth more anteriorly projected than the outer. Tergites 6, 7, 9, 11, 13, or 7, 9, 11, 13, or 9, 11, 13, or only 11, 13 with posterior triangular projections; posterior triangular projections may be absent in some species. Female gonopods with tridentate, rarely bidentate, claw and 2+2 long and thin spurs. Tarsal articulation of legs 1-13 more or less distinct. Legs 14 and 15 of male without special modifications. Prefemur, femur and tibia of legs 15 with a more or less distinct dorsal longitudinal furrow, a little more crassate in male. Body entirely or partly suffused by a characteristic violaceous hue. South-eastern North America; epigeic, mostly in broadleaved forests; sparse records also from caves. 15 species, incl. *P. carolinae* (Chamberlin, 1911), *P. juventus* (Bollman, 1887), *P. zinus* (Chamberlin, 1922) (forcipules with remarkable sexual dimorphism).

*Pampibius* Chamberlin, 1922. – Body length 6.5-7 mm. Close to *Enarthrobius*. Antenna with 24 articles. Ocelli 1+5-1+8. Forcipular coxosternite with 2+2 teeth; porodonts slender and distally bristle-like. Tergites without posterior triangular projections. Female gonopods with tridentate claw, 2+2 long and slender spurs. Tarsal articulation of legs 1-13 indistinct. Femur of legs 15 of male conspicuously crassate with a lobe at proximal end from which projects a brush of very long setae. South-eastern North America; mostly epigeic, up to 1160 m, one record from a cave. A single species, *P. paitius* (Chamberlin, 1911).

*Pleurolithobius* Verhoeff, 1899. – Body length 9.5-19 mm. Antenna with 27-49 articles. Ocelli 2+2. Forcipular coxosternal teeth 2+2. Tergites 11 and 13 with posterior triangular projections more or less developed. Tarsal articulation of legs 1-13 distinct. Female gonopods with unidentate claw, 3+3 spurs. Male with tergite 16 humped in the middle and with more or less expanded lobed projections on the posterior angles. Femur and tibia of legs 13 very swollen, tibia of legs 15 with a setose distal dorsolateral depression. South-east Europe, north Africa (introduced?); from near sea level to 1300 m, open and shrub Mediterranean habitats, mixed broadleaved and mountain coniferous forests. Two species: *P. orientis* (Chamberlin, 1952), *P. patriarchalis* (Berlese, 1894).

*Schizotergitus* Verhoeff, 1930. – Body length 22-25 mm. Antenna with 20 articles. Ocelli 1+5. Forcipular coxosternal teeth 2+2; porodonts stout, spiniform. Tarsal articulation of legs 1-13 distinct. All tergites without posterior triangular projections; a posterior median notch on tergites 3, 5, 8, 10 and 12. Female gonopods with unidentate claw, 2+2 spurs. Central Asia; steppe habitats

up to 2500 m. Two species: *S. altajicus* Loksa, 1978 (Mongolia), *S. longiventris* Verhoeff, 1930 (Tajikistan).

*Sonibius* Chamberlin, 1912. – Body length 8-12.5 mm. Antenna generally with 20 articles. Ocelli 1+12-1+23. Forcipular coxosternal teeth 2+2, 3+3 or 4+4; porodonts slender. Tergites 9, 11 and 13 with posterior triangular projections. Female gonopods with tridentate claw, 2+2 spurs. Tarsal articulation of legs 1-13 distinct. Legs 14 and 15 of male without special lobes or modifications. Eastern North America; mostly in forest habitats. About five species, incl. *S. bius* (Chamberlin, 1911). Close to *Sonibius* are a number of mostly western North American taxa: *Pokabius* Chamberlin, 1912 s.l. (ca 30 species incl. *P. bilabiatus* (Wood, 1867), *P. centurio* (Chamberlin, 1904)); *Kiberbius* Chamberlin, 1916 (six or seven species with a longitudinal latero-internal furrow on legs 15 in both sexes; incl. *K. nampus* Chamberlin, 1916); *Paobius* Chamberlin, 1916 (seven species, incl. *P. boreus* Chamberlin, 1916); *Simobius* Chamberlin, 1922 (three species, incl. *S. ginampus* (Chamberlin, 1909)); *Nadabius* Chamberlin, 1913 (16 species; incl. *N. jowensis* (Meinert, 1886), *N. pullus* (Bollman, 1887)).

*Taiyubius* Chamberlin, 1912. – Body length 9-15 mm. Antenna with 28-35 articles. Ocelli 1+5-1+13. Forcipular coxosternal teeth 2+2, rarely 3+3; porodonts long, distally bristle-like. Tergites 9, 11 and 13 with posterior triangular projections. Female gonopods with tridentate claw, 2+2, occasionally 3+3, spurs. Tarsal articulation of legs 1-13 distinct. Legs 15 of male without special modifications. South-western North America; epigeic. Three species, incl. *T. angelus* (Chamberlin, 1903).

*Tidabius* Chamberlin, 1913. – Body length 5.5-10 mm. Antenna with 25-35 articles. Ocelli 1+8-1+13. Forcipular coxosternite with 2+2 teeth; porodonts bristle-like. Body considerably attenuated from tergite 10 to the head; tergite 1 always and considerably narrower than tergite 3. Tergites 11 and 13 or only 13 with posterior triangular projections. Female gonopods with tridentate claw, 2+2 or, rarely, 3+3 spurs. Tarsal articulation of legs 1-13 distinct. Legs 14 and 15 short and moderately inflated in both sexes; prefemur, femur and tibia with a more or less distinct dorsal longitudinal furrow; male legs 14 and 15 without special modifications or little more incrassate than in the female. North America; wide range of broadleaved forests, rarely in caves. 14 species, incl. *T. suitus* (Chamberlin, 1911) and *T. tivius* (Chamberlin, 1909).

*Validifemur* Ma, Song & Zhu, 2007. – Body length 9-12 mm. Antenna with 20 articles. Ocelli 1+5-1+7. Forcipular coxosternal teeth 2+2; porodonts feebly thicker. Tergites without posterior triangular projections. Tarsal articulation of legs 1-13 with a trace of division. Male legs 14 thicker than legs 13, but evidently thinner than legs 15; male legs 15 remarkably modified, with strong falciform thorns and prefemur, femur and tibia unusually incrassate. Female gonopods with tridentate claw, 2+2 spurs. North China; open and mixed coniferous-broadleaved forests; 550 m. Two species: *V. pedodontus* Ma, Song & Zhu, 2007, *V. zapparolii* Ma, Song & Zhu, 2007.

Probably related to *Nambabius* and *Garibius* are *Liobius* Chamberlin & Mulaik, 1940 (a single species), *Llanobius* Chamberlin & Mulaik, 1940 (four species), *Physobius* Chamberlin, 1945 (a single species), all from eastern North America, and *Planobius* Chamberlin & Wang, 1952 (a single species), from an unrecorded locality. Probably related to *Paitobius*, *Taiyubius* and *Tidabius* are the monospecific *Juanobius* Chamberlin, 1928 (south-western North America) and *Georgibius* Chamberlin, 1944 (south-eastern North America). Of uncertain identity is *Typhlobius* Chamberlin, 1922 (two species; North America).

Subfamily ETHOPOLYINAE Chamberlin, 1915 (Fig. 19.7). – Body length 15-45 mm. Antenna with 20 or more articles. Ocelli present or not. Forcipular coxosternal teeth small

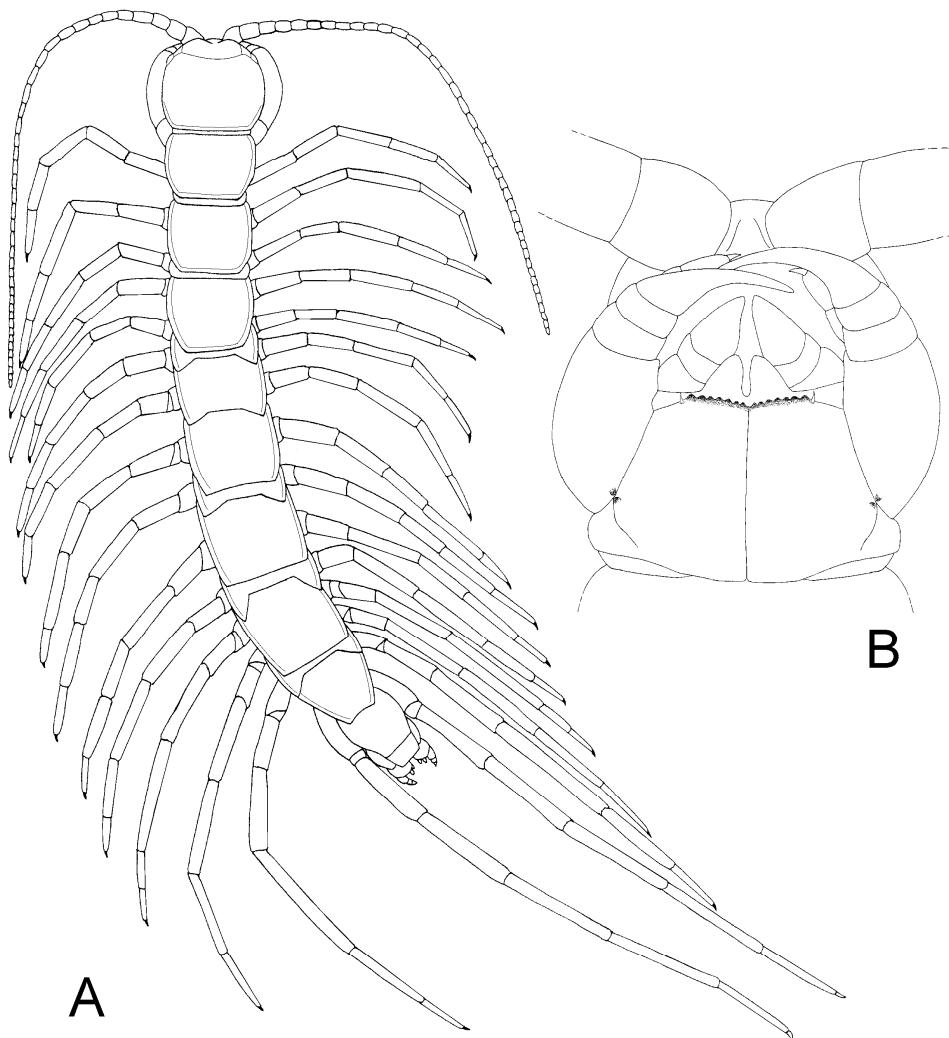


Fig. 19.7 *Eupolybothrus tridentinus* (Lithobiomorpha, Lithobiidae, Ethopolyinae). A Habitus, dorsal view, plectrotaxy omitted. B Anterior part of the body, ventral view. Original E. Zamprogno.

and numerous, usually 7+7 to 11+11. Coxae of legs 12-15 with numerous ventral pores irregularly arranged in more than one row. Tarsal articulation of legs 1-13 distinct. Nearctic and Palearctic regions. Ca 60 species, mostly in the two genera cited here.

*Bothropolys* Wood, 1862. – Body length 15-40 mm. Antenna with 20 articles or thereabouts. Ocelli 1+10-1+40. Forcipular coxosternal teeth usually 5+5 to 11+11. Tergites with or without posterior triangular projections. Female gonopods with tridentate claw, 2+2-4+4 spurs. North America and east Asia; mostly in temperate forests, both coniferous and broadleaved, from low altitude sites up to 2300 m; sometimes in caves, but specialized species are unknown. Ca 40 species, incl. *B. californicus* (Daday, 1889) (western North America), *B. montanus* Verhoeff, 1938 (Japan), *B. multidentatus* (Newport, 1845) (eastern North America), *B. rugosus* (Meinert, 1872) (widely distributed in east Asia, introduced to Hawaii). Allied genera are *Archethopolys* Chamberlin, 1925 and *Zygethopolys* Chamberlin, 1925, with few species from North America.

*Eupolybothrus* Verhoeff, 1907. – Body length 16-45 mm. Antenna with more than 20 articles. Ocelli numerous (e.g., 1+16 to 1+24), absent in some troglobitic species. Forcipular coxosternal teeth numerous (usually 7+7, 10+10); porodonts inserted lateral to the teeth. Tergites with or without posterior triangular projections. Female gonopods invariably with unidentate claw, 2+2 spurs. Near and Middle East, south-east Europe, north Africa; mostly in forests, but also in open or shrub Mediterranean habitats, some species also in caves, from sea level up to 2800 m. Ca 20 species, incl. *E. fasciatus* (Newport, 1845) (mainly Italian peninsula), *E. grossipes* (C.L. Koch, 1847) (widespread in south-east Europe), *E. nudicornis* (Gervais, 1837) (north Africa), *E. obrovensis* Verhoeff, 1930 (troglobitic, north Balkans), *E. transsylvaniaicus* (Latzel, 1882) (Europe, mostly Balkans), *E. tridentinus* (Fanzago, 1874) (the smallest species in the genus, south-east Europe).

Subfamily GOSIBIINAE Chamberlin, 1912. – Body length 6-37 mm. Antenna with 20 or more articles. Forcipular coxosternal teeth 2+2-7+7. Female gonopods with claw always large and strictly entire, without trace of lateral denticles; spurs large and stout, generally 2+2, sometimes 3+3 (*Gosibius* Chamberlin, 1912, *Gallitobius* Chamberlin, 1933), exceptionally more (*Zinapoly* Chamberlin, 1912); first article broad, conspicuously and characteristically excavated at base; coxae of legs 12-15 with ventral pores almost regularly disposed in a single row; males with either legs 14 or 15 or both 14 and 15 with special lobes or other secondary sexual modifications. North and Central America. Ca 90 species in about 30 ill-defined genera/subgenera.

*Gosibius* Chamberlin, 1912. – Body length 15-30 mm. Antenna with 24-35 articles, ocelli 1+13-1+19, rarely less, forcipular coxosternal teeth 2+2, sometimes 3+3, porodonts usually bristle-like, tergites with or without posterior triangular projections, male tibia 14 elevated distally and thicker than proximally, with or without a nodular protuberance on the elevated portion; male femur 15 usually longitudinally furrowed above and widened, male tibia 15 sometimes also more or less widened and bowed ventrally, legs 15 rarely without modifications. Southern North America; epigaeic, mostly in arid habitats, from mixed brush to forest, from low elevation sites up to 3350 m. Ca 20 species, incl. *G. arizonensis* Chamberlin, 1917, *G. intermedius* Chamberlin, 1917 (with a characteristic denticulation on the lateral margins of tergites 7-10 and male tergite 14 of unusual shape), *G. paucidens* (Wood, 1862).

*Arenobius* Chamberlin, 1912. – Body length 15-17 mm. Antenna with 20 articles. Ocelli 1+8. Forcipular coxosternal teeth 2+2. Tergites 9, 11, 13 with posterior triangular projections. Tarsal articulation of legs 1-13 distinct. Legs 14 and 15 of male strongly modified. South-eastern North America; forest habitats, 80-190 m. A single species, *A. manegitus* (Chamberlin, 1911).

*Atethobius* Chamberlin, 1915. – Body length 22-24 mm. Close to *Kunobius* but with tergite 14 greatly enlarged, distinctly wider than the more anterior tergites, extending over and concealing

the reduced tergite 15 and coxae 15. Antenna with 40-44 articles. Ocelli 1+13. Forcipular coxosternal teeth 2+2; porodonts stout and tooth-like. Tergites 7, 9, 11, 13 with strong posterior triangular projections. Tarsal articulation of legs 1-13 distinct. Tibia of male legs 15 with lobe at distal end on mesal side. Central America; epigeic. Two species, incl. *A. mirabilis* Chamberlin, 1915. Similar to *Atethobius* is *Uncobius* Chamberlin, 1943, a taxon of uncertain identity with tergite 14 enlarged but not covering tergite 15, tibia of legs 15 of male without process or secondary sexual modifications. Central America; epigeic, habitat details unknown but altitudinal range from 3100-4100 m. Two species: *U. llanicolens* Chamberlin, 1943, *U. tolucanus* Chamberlin, 1943.

***Delobius*** Chamberlin, 1915. – Body length 19-21 mm. Antenna with 36-46 articles. Ocelli 1+7-1+10. Forcipular coxosternal teeth 3+3-3+4. Tergites 9, 11 and 13 with posterior triangular projections. Tibia of legs 14 of male with a longitudinal swelling or crest at distal end on mesal or caudal surface; legs 15 of male not specially modified. Central America; epigeic, up to 3000 m. Four species, incl. *D. simplex* Chamberlin, 1915.

***Guambius*** Chamberlin, 1912. – Body length 9-16 mm. Antenna with 24-35 articles. Ocelli 1+8-1+13. Forcipular coxosternal teeth 2+2; porodonts varying from slender and distally bristle-like to spiniform. Tergites with or without posterior triangular projections. Tibia of legs 14 of male obliquely planate or excised at distal end above and there bearing a conspicuous lobe or crest of characteristic form. Femur of legs 15 of male more or less conspicuously crassate and longitudinally furrowed above; tibia commonly much less crassate, somewhat elevated along dorsal side but not conspicuously modified. Southern North America; epigeic, one record at 2130 m. Nine species, incl. *G. coloradanus* (Chamberlin, 1912), *G. euthus* (Chamberlin, 1904).

***Kunobius*** Chamberlin, 1912. – Body length 18-27 mm. Antenna with 50-55 articles. Ocelli 1+8-1+9. Forcipular coxosternal teeth 2+2. Tergites 7, 9, 11 and 13 with posterior triangular projections. State of tarsal articulation of legs 1-13 unknown. Male legs 14 unmodified; male legs 15 with secondary sexual modifications. Central America; epigeic. Three species, incl. *K. humberti* (Pocock, 1895), *K. pontifex* (Pocock, 1895). Close to *Kunobius* are *Mexicobius* Chamberlin, 1915, *Friobius* Chamberlin, 1943 and *Mayobius* Chamberlin, 1943, a group of ill-defined genera characterized by body length 14-25 mm but also smaller (*Friobius*, *Mayobius*), antenna with numerous articles (27-47), ocelli generally 1+6-1+9 but also 1+13 (*Friobius*) or 1+25 (*Mexicobius*), forcipular coxosternal teeth generally 2+2, rarely 3+3 (*Mexicobius*), tergites 7, 9, 11, 13 or only 9, 11, 13 with posterior triangular projections, male legs 15 with secondary sexual modification (*Kunobius*, *Friobius*) or not (*Mexicobius*, *Mayobius*). Central America; epigeic, from 450 to 3000 m.

***Labrobius*** Chamberlin, 1915. – Body length 10-13 mm. Antenna with 29-57 articles. Ocelli 1+7-1+13. Forcipular coxosternal teeth 2+2. Tergites 7, 9, 11, 13 or only 9, 11, 13 with posterior triangular projections. Tibia of legs 15 of male with a conspicuous, laterally compressed crest at distal end on dorsal or dorsomesal surface. Central America; epigeic, from 450 to 2400 m. A dozen species, incl. *L. bolivari* Chamberlin, 1943 and *L. minor* Chamberlin, 1915. Close to *Labrobius* is *Vulcanbius* Chamberlin, 1942, a taxon of uncertain identity from Central America, with five epigeic species (e.g., *V. pedrigalus* Chamberlin, 1942) mostly from forest habitats, up to 2000 m.

***Nothembius*** Chamberlin, 1916. – Body length 8-13 mm. Close to *Arenobius*. Antenna with 21-22 articles. Ocelli 1+5-1+10. Forcipular coxosternal teeth 2+2-3+3. Only tergite 13 with posterior triangular projections. Tarsal articulation of legs 1-13 more or less distinct. Legs 14 and 15 of male moderately thickened; tibia of legs 15 of male bearing a distal pilose lobe on its ventral surface. South-western North America; epigeic. Four species, incl. *N. insulac* Chamberlin, 1916.

***Sotimpíus*** Chamberlin, 1912. – Body length 10-37 mm. Antenna with 42-59 articles. Ocelli 1+8. Forcipular coxosternal teeth 4+4-6+6. Tergites 7, 9, 11 and 13 with posterior triangular projections. Central America; epigeic, from 600 to near 2900 m. Four or five species, incl. *S. decodontos* (Pocock,

1895) and *S. macroceros* (Pocock, 1895). Close to *Sotimpus* is *Gallitobius* Chamberlin, 1933, Central America, with two species.

*Zinapolis* Chamberlin, 1912. – Body length 6-20 mm. Antenna with 20 articles. Ocelli 1+20. Forcipular coxosternal teeth 4+4-7+7. Female gonopods with 2+2-6+6 spurs. State of tarsal articulation of legs 1-13 unknown. Tergites 9, 11 and 13 with posterior triangular projections or not. Western North America; epigeic. Two species: *Z. uticola* Chamberlin & Wang, 1952 (Utah), *Z. zippius* Chamberlin, 1912 (Idaho).

Subfamily PSEUDOLITHOBIINAE Matic, 1973. – Body length 13-41 mm. Antenna with 20 or more articles. Forcipular coxosternal teeth 3+3-6+6. Coxal pores arranged in a single row on coxae of legs 11-15. Female gonopods with unidentate claw, 3+3-4+4 spurs. Holarctic. Two genera, three species.

*Pseudolithobius* Stuxberg, 1875. – Body length 13-41 mm. Antenna with 20-22 articles. Ocelli 1+5-1+11. Forcipular coxosternal teeth 3+3-4+4. Tergites 9, 11 and 13 with or without posterior triangular projections. Female gonopods with a large, unidentate claw, 2+2 or 4+4 spurs. Tibia of legs 14 of male enlarged distally; tibia of legs 15 of male conspicuously longitudinally furrowed dorsally and bowed ventrally. South-western North America; epigeic. Two species: *P. festinatus* Crabill, 1953 (California), *P. megaloporus* Stuxberg, 1875 (Arizona).

*Ottobius* Chamberlin, 1952. – Body length 23-34 mm. Antenna with 58-78 articles. Ocelli 1+11-1+17. Forcipular coxosternal teeth 3+4-6+6. Tarsal articulation of legs 1-13 distinct. Tergites 9, 11 and 13 with more or less developed posterior triangular projections. Legs 14 and 15 of male without modifications. Female gonopods with unidentate claw, 3+3-4+4 spurs. South-west Asia; epigeic, in mixed mesophilous broadleaved forests, from 90 to 320 m. A single species, *O. hopanus* Chamberlin, 1952.

Subfamily PTERYGOTERGINAE Verhoeff, 1933. – A subfamily morphologically close to Lithobiinae, from which is distinguishable especially in the shape of the large tergites of the male, notably the enormous lateral expansion of tergite 12 with denticulate margin. East Palearctic. A single species.

*Pterygotergum* Verhoeff, 1933. – Body length 25-28 mm. Antenna with 20 articles. Forcipular coxosternite prominent, with 3+3 very small teeth, both inner ones can be considered as typical teeth whereas the outer one represents a shortened and thickened spiniform seta. Ocelli few (1+1, 4). Tarsal articulation of legs 1-13 distinct. North-west China; epigeic. A single species, *P. svenhedini* Verhoeff, 1933.

Subfamily WATOBIIINAE Chamberlin, 1912. – Body length 5-9 mm, rarely up to 11 mm. Antenna with 19-22 to 24-33 articles. Ocelli few. Forcipular coxosternal teeth 2+2. Tergites without posterior triangular projections or only on tergites 9, 11 and 13. Coxae of legs 12-15 with ventral pores arranged in a single row. Tarsal articulation of legs 1-13 indistinct; plectrotaxy almost totally absent except at least an antero-dorsal spur on tibiae of anterior legs. In south-eastern North and Central America. Five genera, ca 10 species.

*Watobius* Chamberlin, 1911. – Body length 8-9 mm. Antenna with 20-22 articles. Ocelli 1+8. Forcipular coxosternal teeth 2+2; porodonts hair-like. Tergites 9, 11, 13 with posterior triangular projections. Female gonopods with tridentate claw, 2+2 spurs. Tibiae of legs 14 and 15 of male enlarged at the distal end. South-eastern North America; epigeic, detailed habitats unknown, one record from cave. A single species, *W. andersonus* Chamberlin, 1911.

*Arkansobius* Chamberlin, 1938. – Body length 7-8 mm. Antenna with 19 articles. Ocelli 3+2, 4+2 or 4+3. Forcipular coxosternal teeth 2+2; porodonts unknown. State of posterior triangular projections on tergites unknown. Female gonopods with a long unidentate claw, 2+2 acute spurs. Legs 15 of both sexes crassate, more strongly in male, especially femur and tibia. South-eastern North America; epigeic, details on habitat preferences unknown. A single species, *A. lamprus* Chamberlin, 1938.

*Cruzobius* Chamberlin, 1942. – Body length 5-11 mm. Antenna mostly with 20 articles, rarely 22-24. Ocelli 1+4-1+3. Forcipular coxosternal teeth 2+2. Tergites without posterior triangular projections. Male tibia 15 with a disto-dorsal fungiform lobe. Female gonopods with unidentate claw (tridentate in *C. viganus* Chamberlin, 1944; Central America), 2+2 spurs. Most legs of middle with a slender, almost setiform antero-dorsal spur on tibia. Tibiae without ventral spurs. Central America; epigeic, also in caves but not troglobitic. Four species, incl. *C. pococki* Crabbill, 1962, *C. verus* Chamberlin, 1942.

*Malbius* Chamberlin, 1943. – Body length 8 mm. Antenna with 31-33 articles. Ocelli 3+2. Forcipular coxosternal teeth 2+2; porodonts spine-like. Tergites without posterior triangular projections. Legs 14 and 15 of male moderately inflated. Posterior pairs of legs with spurs on articles other than tibia. Central America; epigeic. A single species, *M. lucens* Chamberlin, 1943.

*Tropobius* Chamberlin, 1943. – Body length 5-6 mm. Antenna with 24-25 articles. Ocelli 1+3-2+3. Forcipular coxosternal teeth 2+2; porodonts spine-like. Tergites without posterior triangular projections. Female gonopods with unidentate claw, 2+2 spurs. Central America; epigeic. Two species, incl. *T. sylvanus* Chamberlin, 1943.

Probably included in this group is *Texobius* Chamberlin & Mulaik, 1940 (southern North America), with a single epigeic species.

## Phylactometria

Ocelli when present composed of extremely numerous cells. No maxillary nephridia. Forcipular coxosternite entire, the mid-longitudinal hinge fully sclerotized, and deeply embedded inside the first leg-bearing segment. Forcipular pleurites arched above the coxosternite. Leg-bearing segments with pre sternites between the main sternites (metasternites).

Heart with internal valves formed by lips of the ostia projecting deeply into the lumen. Lateral testicular vesicles linked by a central, posteriorly extended deferens duct. Coxal organs present on the legs of the ultimate pair only.

Parental care with the mother guarding the eggs and the juveniles by wrapping her body around them. Anamorphic phase of the post-embryonic development reduced to a single stage (Craterostigmomorpha only) or entirely absent; hatchlings with at least 12 leg-bearing segments.

## Order Craterostigmomorpha

Gregory D. Edgecombe

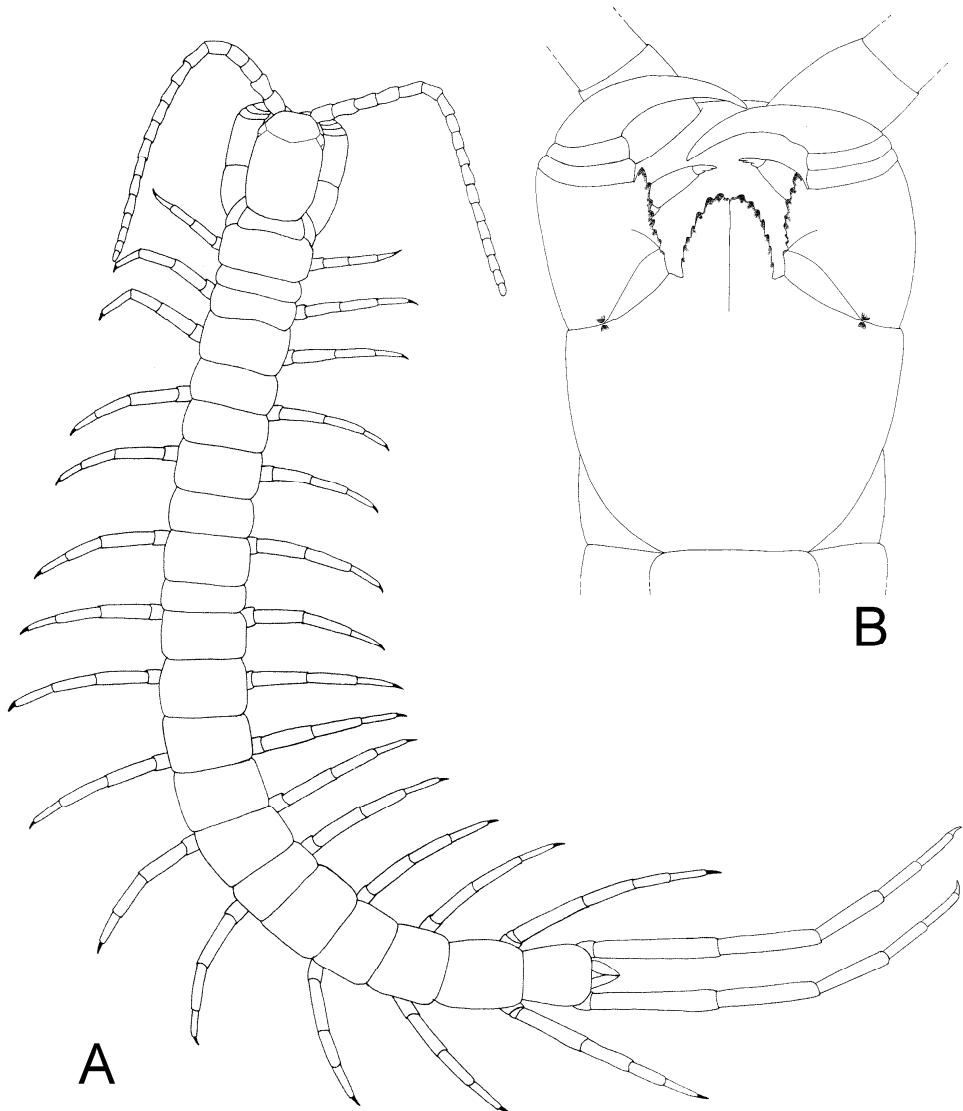


Fig. 19.8 *Craterostigmus crabilli* (Craterostigmomorpha, Craterostigmidae). A Habitus, dorsal view. B Anterior part of the body, ventral view. Original E. Zamprogno.

Pleurostigmophoran centipedes with 15 leg-bearing trunk segments covered by 21 tergites; segments 3, 5, 7, 8, 10 and 12 each with two tergites. Body length to 50 mm. Antenna with 17-18 articles, strongly attenuated distally. A single ocellus on each side of head; ocellus has a bipartite cup, inverse retinula cells, distal retinular cells with bilobed apices that contribute to an irregular, branching rhabdom, and separated pairs of proximal retinular cells. Cephalic plate with transverse and antennocellar sutures. Labrum with five teeth in mid-piece and inner edge of side-pieces; side-pieces bearing slender spines. Mandible with three tricuspid teeth, serrate aciculae, and pulvilli differentiated as a large lobe; two mandibular sclerites, laminae condylifera and dentifera. Telopodite of first maxillae with a single undivided article. Article 3 of the telopodite of second maxillae bearing a fringe of bifurcating or multi-branched spines; claw with a robust median spine and two pairs of more slender lateral spines. Anterior margin of the forcipular coxosternite with a pair of serrate tooth-plates, trochanteroprefemur bearing a similar serrate process. Head and tergites lacking paramedian sutures and marginal ridges. Spiracles on trunk segments 3, 5, 8, 10, 12, and 14. More than 1500 tracheae per spiracle; tracheae unbranched, each strengthened by a single taenidium. Pleural glands open on six trunk segments bearing long tergites. Trochanter of legs 15 and variably legs 13 and 14 bearing a single ventral spine. Metasternites separated by a pair of presternites. Ultimate leg-bearing segment with all sclerites merged as an undivided ring. Anal region developed as a bivalved capsule that opens ventrally, each side bearing four anal pore-fields separated by cuticular bars; capsule supplied with branched arteries. Ultimate legs elongate, slender. Male gonopod a small, elliptical flap.

Female coiling around the egg clutch and one post-embryonic stadium in which the hatchlings have 12 pairs of legs. Adult number of trunk segments attained early in post-embryonic development. Tasmania and New Zealand. Two species in a single family, Craterostigmidae, and genus, *Craterostigmus* (Fig. 19.8).

*Craterostigmus* Pocock, 1902. – Two species, *C. crabilli* Edgecombe & Giribet, 2008 (body length to 37 mm, ventral spine on legs 14 trochanter short and thorn-like or absent; New Zealand), *C. tasmanianus* Pocock, 1902 (body length to 50 mm, ventral spine on legs 14 trochanter strong; Tasmania).

## Epimorpha

No Tömösváry's organ. All four articles of the forcipule sharing a single hinge, so that the two intermediate articles appear incomplete on the external side. Number of pairs of legs 21 to 191, often variable within a single species. Trunk heterotergy slight or

completely absent. Trunk tergites usually with paramedian sulci. Tracheal branches with longitudinal and transverse connections. Brain artery unpaired.

Development strictly epimorphic. At least two post-embryonic stages with non-functional limbs and guarded by the mother.

## Order Scolopendromorpha

Gregory D. Edgecombe & Lucio Bonato

Body flattened, moderately elongate. Colour varied, sometimes vivid. Adult body length from 9 mm to 30 cm. Antenna mostly attenuated gradually, with 14-34 (usually 17-21) articles. Eye a cluster of four ocelli, single ocellus or absent. Labrum with a single medial tooth. Epipharynx with a row of bullet-shaped sensilla at border between labral and clypeal parts. Mandible with four or five strong teeth, several pectinate lamellae, and a pulvillus dorsally; the four laminae composing the mandible intersecting at a cruciform suture. Distal article of the first maxillary telopodite with the inner side fringed by setae with slender stalks and short branches along a distal, curled part. Distal article of the second maxillary telopodite bearing a dense fringe of simple bristles (dorsal brush) along its dorsal side. Anterior margin of the forcipular coxosternite often with a pair of tooth-plates, but sometimes without projections. Forcipules often with a sclerotized process on the mesal side of the basal article, the other articles without projections. A single tergite covering forcipular and first leg-bearing segment. Number of pairs of legs 21 or 23 in all but one known species (with 39 or 43), usually invariant within a single species. Most trunk tergites with paramedian sutures. Trunk heterotergy slight, distinct in at least anterior segments. Spiracles confined to segments with long tergites apart from *Plutonium* (on all leg-bearing segments except ultimate). Spiracular pouches with muscles attaching to their dorsal and ventral sides. Foregut relatively long, differentiated into crop and gizzard. Ultimate leg-bearing segment with coxopleura enlarged; coxal organs opening through scattered pores (except Asanadini). Ultimate legs different from the other legs, varied in shape. Terminal part of the trunk retracted above the sternite of the ultimate leg-bearing segment. Left ejaculatory duct rudimentary or absent. Gonopods lacking in female and usually in males, the latter with genital appendages on first genital segment in some species only.

Female coiling around the egg clutch and newly hatched juveniles with sternum inward. Spermatophore bean-shaped, with multilayered wall.

Almost worldwide; maximum species richness in tropical and subtropical regions. Ca 700 species in five families, 34 extant genera and four extinct genera.

Family CRYPTOPIDAE Kohlrausch, 1881 (Fig. 19.9). – Eyes absent. Median cluster of sensilla coeloconica on clypeal part of epipharynx rhomboid, with lids covering the distal edge of the sensilla. Claw of second maxillae hook-like, accompanied by a ventral flange, exceptionally simple. Forcipular coxosternite without tooth-plates, having either scattered setae along the margin, a sclerotized band or non-denticulated, hyaline lobes. Forcipules without tubercles or projections. 21 leg-bearing segments. Trunk tergites with lateral crescentic sulci; pretergites relatively strongly developed. Sternites usually with transverse line of skeletal thickening, without paramedian grooves, with endosternites usually well developed in the anterior part of trunk. Most legs with a single tarsal article (except for *Trigonocryptops*). Gizzard with stiff anteriorly-directed projections; projections without a distinct kink near their midlength. Coxopleura without processes. Ultimate legs a clasping structure, with strongly bent terminal articles; tibia and tarsus 1 usually having a row of saw teeth. Almost worldwide, both in temperate and tropical regions. More than 170 species in two genera.

*Cryptops* Leach, 1815. – Body length 9-ca 80 mm. Forcipular coxosternal margin at most with a sclerotized marginal rim, lacking lobes; tarsungulum moderately developed. Temperate and tropical regions throughout the world. More than 170 species in four subgenera.

*C. (Cryptops)* Leach, 1815. – Cephalic plate overlying or overlain by tergite 1. Clypeus without an anterior setose area delimited by sutures. Anterior transverse suture variably present or absent on tergite 1. Trigonal sutures lacking on posterior part of sternites. Spiracles often round or ovate, may be slit-like. Tarsus of most legs a single article. Temperate and tropical regions throughout the world. More than 140 species, incl. *C. anomalans* Newport, 1844 (tergite 1 with a cruciform suture; west Palearctic), *C. hortensis* (Donovan, 1810) (forcipular coxosternite relatively short, with slender forcipules; widespread in the world as often introduced), *C. leucopodus* (Rafinesque, 1820) (U.S.A.), *C. parisi* Brölemann, 1920 (labral side-piece notched; ultimate leg tibial and tarsal saw teeth closely set; most of Europe; most part of Europe), *C. polyodontus* Attems, 1903 (ultimate legs with many, unorderd saw teeth; Chatham Island), *C. trisulcatus* Brölemann, 1902 (Mediterranean Region).

*C. (Chromatanops)* Verhoeff, 1906. – Tergum with longitudinal bands of dark pigment. Sternites lacking transverse line of skeletal thickening; endosternites not strongly developed. Spiracles rounded or oval. Leg tarsi a single article. Central and South America. A single species, *C. bivittatus* Pocock, 1893.

*C. (Haplocryptops)* Verhoeff, 1934. – Second maxillary claw simple, pointed rather than with a ventral flange; dorsal brush on second maxillae composed of very short setae. Forcipular coxosternite lacking median suture. Mexico. A single species, *C. acapulcensis* Verhoeff, 1934.

*C. (Trigonocryptops)* Verhoeff, 1906. – Cephalic plate overlying tergite 1. Anterior setose area on clypeus delimited by sutures. Anterior transverse suture on tergite 1. Trigonal sutures on posterior part of sternites, immediately anterior to endosternite. Spiracles slit-like. Leg tarsi generally bipartite. Mostly tropical regions throughout the world. Ca 20 species, incl. *C. gigas*

Kraepelin, 1903 (large size, to 80 mm; Cameroon), *C. iheringi* (Brölemann, 1902) (Brazil) *C. longicornis* (Ribaut, 1915) (antennae and legs very elongate; caves in Iberian peninsula),

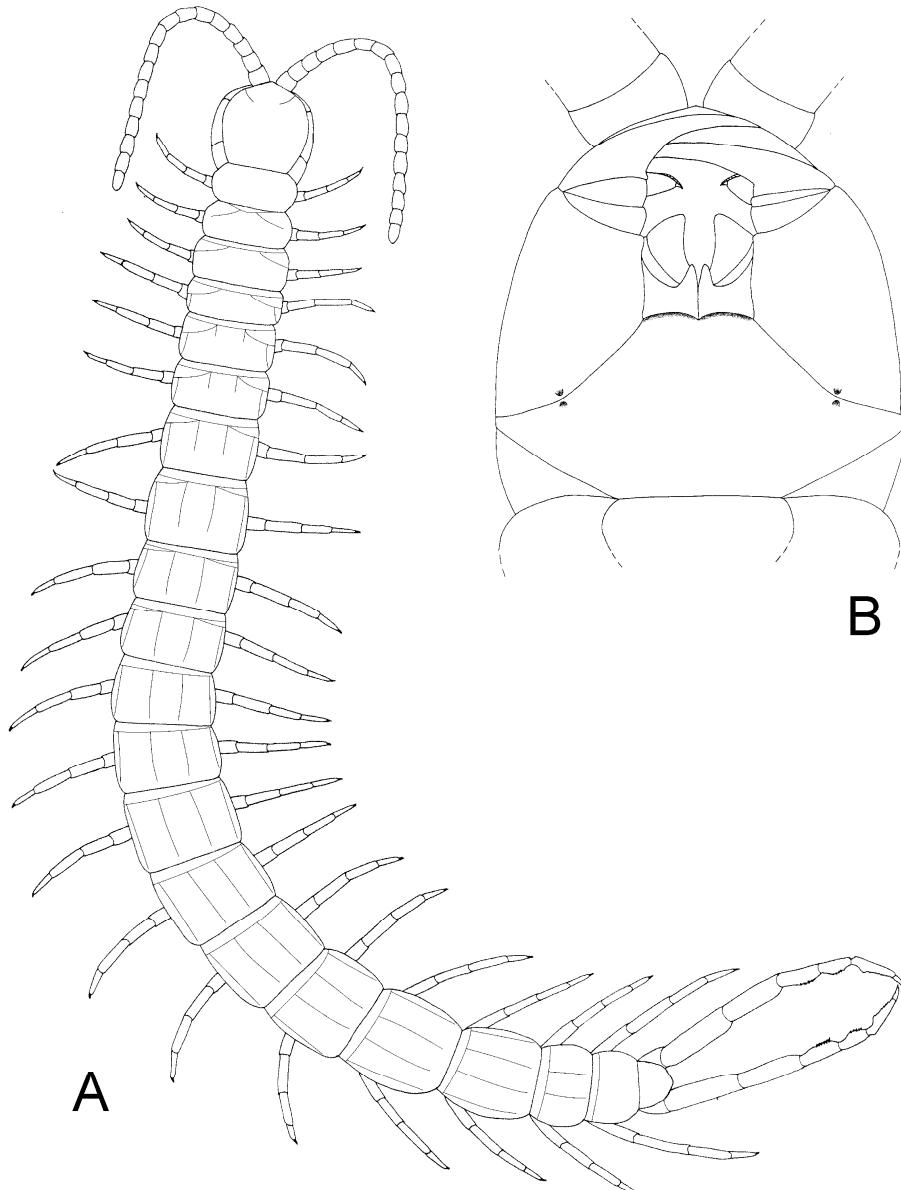


Fig. 19.9 *Cryptops hortensis* (Scolopendromorpha, Cryptopidae). A Habitus, dorsal view. B Anterior part of the body, ventral view. Original E. Zamprogno.

*Paracryptopeltis* Pocock, 1891. – Body length 16–24 mm. Forcipular coxosternal margin with blunt, rounded or slightly flattened, hyaline lobes; tarsungulum very short. From Indian peninsula to New Guinea, and Antilles (the latter possibly introduced). Five species, incl. *P. breviunguis* Silvestri, 1895 (coxosternal marginal lobes conspicuous; New Guinea), *P. spinosus* Jangi & Dass, 1978 (anterior margin of coxosternal lobes somewhat flattened; ultimate legs with a lateral spine distally on femur and lateral and median spines on tibia; India).

Family MIMOPIDAE Lewis, 2006. – Single ocellus on each side of cephalic plate. Forcipular coxosternal marginal plates rounded, without teeth. Tergite 1 with anterior transverse sulcus. 21 leg-bearing segments. All legs with bipartite tarsi. Coxopleura with elongate process, covered with small spines, tip rounded. Ultimate leg-bearing segment, including most articles of the ultimate legs with numerous small spines. North China. A single species.

*Mimops* Kraepelin, 1903. – Body length ca 45 mm. Shanxi. A single species, *M. orientalis* Kraepelin, 1903.

Family PLUTONIUMIDAE Bollman, 1893 (Fig. 19.10). – Depigmented eye spots. Forcipular coxosternite with tooth-plates. Poison calyx extending into the forcipular coxosternite. 21 leg-bearing segments. Gizzard with stiff anteriorly-directed projections; projections evenly curved, covered by multifurcating scales that spirally encircle the projection, branching into slender, needle-like spines. Tergite of the ultimate leg-bearing segment nearly twice as long as that of the penultimate segment, usually with median suture. Coxopleura without process but variably acuminate and bearing an apical spur. Ultimate legs swollen, strongly sclerotized, forcipulate. Mediterranean region, south-west and east part of North America, east Asia. Seven species in two genera.

*Plutonium* Cavanna, 1881. – Body length to ca 150 mm. Spiracles on all leg-bearing segments except the first and the ultimate. Seashore and woodlands. Sardinia, Sicily, Iberian peninsula. A single species, *P. zwierleini* Cavanna, 1881.

*Theatops* Newport, 1844. – Body length 45–77 mm. Spiracles only on the nine or ten segments bearing long tergites. Mediterranean region, south-west and east part of North America, China. Six species, incl. *T. californiensis* Chamberlin, 1902 (ultimate legs usually with a single spine on ventral side of prefemur and femur), *T. erythrocephalus* C. L. Koch, 1847 (median suture on tergite 21 incomplete, ultimate legs lacking dorsal distomedial prefemoral spurs, coxopleura apically acuminate with a dark subapical spur; Iberian peninsula and west Balkan peninsula), *T. posticus* (Say, 1821) (coxopleura apically rounded, without spur, ultimate legs mostly without spines on ventral side of prefemur and femur; south part of North America).

Family SCOLOPENDRIDAE Leach, 1814. – Basal few antennal articles sparsely setose, with abrupt transition to more distal articles that have short, dense setae. Eye usually present, a rhomboid cluster of four ocelli. Labral bristle field completely covering distal sclerotisation of epipharynx (except *Notiasemus*); elongate, figure-eight shaped groups of two smooth depressions surrounding each sensillum on clypeal part or epipharynx. Tufts

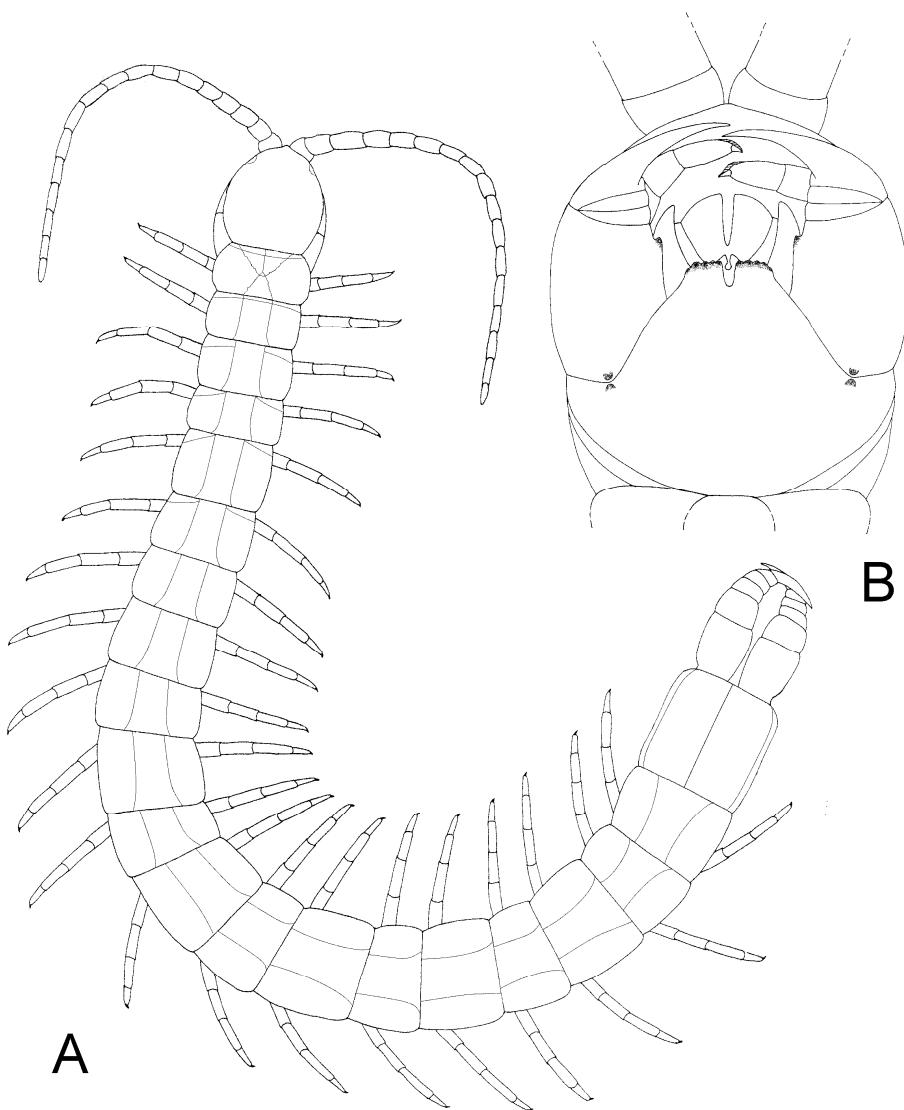


Fig. 19.10 *Plutonium zwierleinii* (Scolopendromorpha, Plutoniumidae). A Habitus, dorsal view. B Anterior part of the body, ventral view. Original E. Zamprogno.

of bristles on lateral flaps of hypopharynx form a continuous field with identical bristles medially. Anterior margin of forcipular coxosternite usually with tooth-plates. Poison

calyx extending at least as far as proximal part of forcipular trochanteroprefemur. Number of leg-bearing segments invariably 21 apart from *Scolopendropsis*. Trunk sternites usually with two paramedian sutures, without transverse groove. Locomotory legs with sparse setae, and with two tarsal articles. Spermatophore with a ventral invagination. Almost worldwide, mainly in tropical regions. More than 400 species in 21 genera.

Subfamily SCOLOPENDRINAE Leach, 1814 (Fig. 19.11). – Spiracles with atrium covered by a three-valved flap, usually triangular with at least the anterior angle pointed, often compressed dorsoventrally. Paramedian sutures on trunk sternites complete. Posteriorly directed spines along plicae of gizzard. Temperate and tropical parts throughout the world. More than 220 species in 12 genera.

Tribe SCOLOPENDRINI Leach, 1814. – Antennae relatively long, extending behind tergite 2. Anterior part of tergites not delimited by a strong transverse furrow. A variable number of marginate tergites in addition to ultimate tergite. Ultimate leg prefemur with dorsomedial process and rows of spines on ventral and medial sides. Mostly tropical and subtropical regions throughout the world. More than 210 species in 10 genera.

*Scolopendra* Linnaeus, 1758. – Body length 23-275 mm. Cephalic plate usually overlapping tergite 1. Coxosternal tooth-plates short to moderately long. Legs with tarsal spurs. Pretarsal claws of the ultimate legs usually with accessory spurs. Most tropical and subtropical regions throughout the world. Ca 90 species, incl. *S. cingulata* Latreille, 1829 (yellowish, ultimate legs with short coxopleural process, few ventral spines on prefemur; south Europe and south-west Asia), *S. gigantea* Linnaeus, 1758 (large size, cephalic plate with complete longitudinal sutures; northern South America), *S. heros* Girard, 1853 (variably red and black, cephalic plate with two diverging longitudinal sutures for more than half its length; south and south-western North America), *S. laeta* Haase, 1887 (17-21, mostly 18, antennal articles, porose area not reaching posterior edge of coxopleuron; Australia), *S. morsitans* (Linnaeus, 1758) (variably coloured, ultimate legs with short coxopleural process and many prefemoral spines, usually in three rows; Africa, Madagascar, south-east Asia and Australia, introduced in other tropical regions; possibly including *S. amazonica* Bucherl, 1946), *S. oraniensis* Lucas, 1846 (body length to 55 mm, blue-grey, coxopleura with slender process; west Mediterranean basin), *S. polymorpha* Wood, 1861 (7-12 glabrous antennal articles, usually four tubercles on distomedial prefemoral process; western part of North America to Central America), *S. spinosissima* Kraepelin, 1903 (ultimate legs with coxopleural process and prefemoral spines very elongate; Philippines), *S. subspinipes* Leach, 1815 (ultimate legs elongate, with few ventral prefemoral spines; south-east Asia, introduced in most tropical regions), *S. valida* Lucas, 1840 (Old World tropics), *S. viridicornis* Newport, 1844 (South America), *S. viridis* Say, 1821 (4-7 glabrous antennal articles, usually two tubercles on distomedial prefemoral process; southern part of North America to Central America).

*Akymnopellis* Shelley, 2008. – Body length 34-85 mm. Transition from sparsely to densely hirsute antennal articles varying from articles 3-6. Tergite 1 without anterior transverse suture. Setae lacking on all tergites and legs other than the ultimate. Tarsus 1 of all legs without spur. South America. Three species, incl. *A. chilensis* (Gervais, 1847) (tergite 21 lacking median suture, ultimate leg prefemur, femur and tibia elongate, oblong; south part of South America), *A. laevigata*

(Porat, 1876) (tergite 21 with incomplete median suture, ultimate leg prefemur, femur and tibia clavate; throughout South America).

*Arthrorhabdus* Pocock, 1891. – Body length 35-50 mm. Cephalic plate and tergite 1 entirely separate, without overlap. Coxosternal tooth-plates relatively long, narrow. Leg tarsus 1 with weak ventrodistal spurs. Ultimate legs lacking pretarsal accessory spurs or having one or two small accessory spurs. North and Central America, Africa, Australia, and possibly India. Four or five species, incl. *A. formosus* Pocock, 1891 (claws of ultimate legs longer than tarsus 2; south Africa), *A. mjobergi* Kraepelin, 1916 (antennae relatively short and composed of 17 articles, claws of ultimate legs

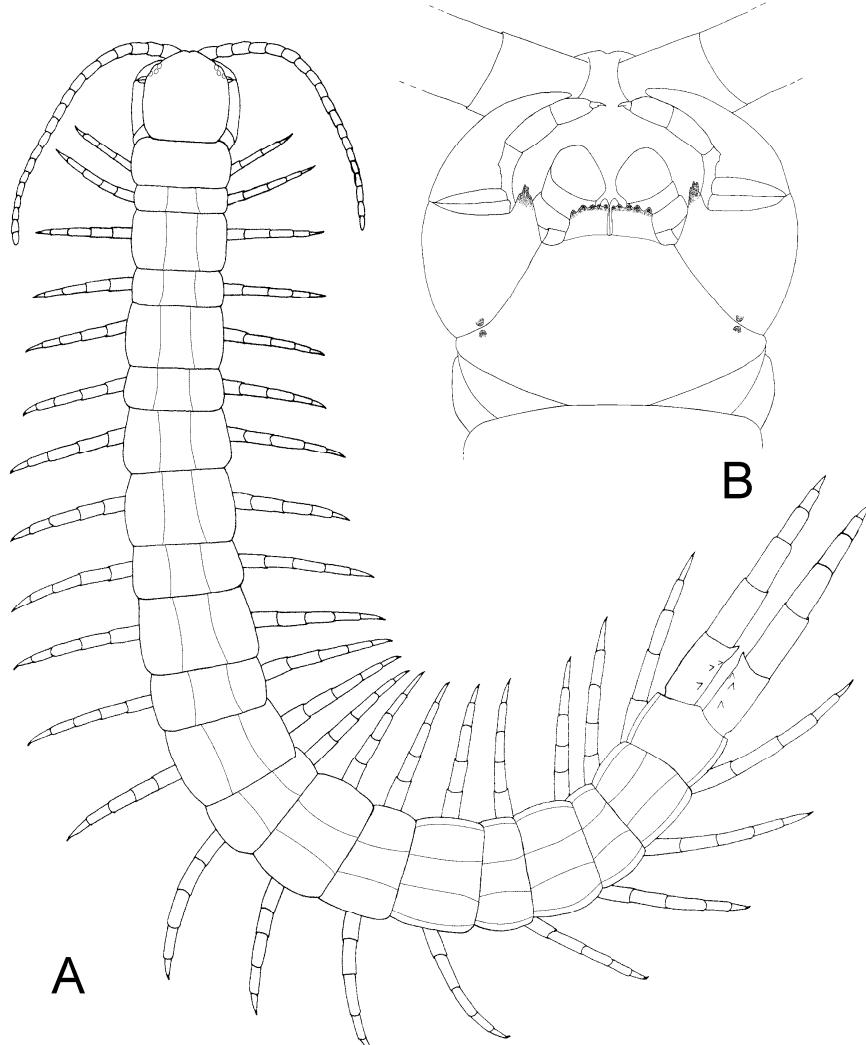


Fig. 19.11 *Scolopendra cingulata* (Scolopendromorpha, Scolopendridae, Scolopendrinae). A Habitus, dorsal view. B Anterior part of the body, ventral view. Original E. Zamprogno.

shorter than tarsus 2; Australia), *A. pygmaeus* (Pocock, 1895) (antennae elongate and composed of 20-26 articles; Central America, northwards to Texas).

*Campylostigmus* Ribaut, 1923. – Body length 39-53 mm. Cephalic plate covered posteriorly by tergite 1, the former with basal plates at posterolateral corners. Mandibles with small teeth; fan bristles covering entire face of lamina dentifera. Spiracles concave dorsally, recurved at their extremities; dorsal edge of peritreme curved ventrad at least in the spiracles at the front and back of body. Legs without tarsal spurs. New Caledonia. Six species, incl. *C. crassipes* Ribaut, 1923 (coxopleura with two apical spines, ultimate leg prefemur moderately elongate; New Caledonia), *C. orientalis* Ribaut, 1923 (coxopleura with 5-6 apical spines, ultimate leg prefemur very elongate; New Caledonia).

*Cormocephalus* Newport, 1844. – Body length 21-160 mm. Antenna usually with 17 (rarely 16 or 18-21) articles. Cephalic plate covered posteriorly by tergite 1, the former with basal plates at posterolateral corners and usually a pair of longitudinal sutures along posterior half. Legs without tarsal spurs. Tropical, subtropical and warm temperate regions throughout world. Almost a hundred species, incl. *C. aurantiipes* (Newport, 1844) (Australia), *C. cupipes* Pocock, 1891 (ultimate legs swollen, forcipulate, with large puncta on prefemur, femur and tibia; south Africa), *C. gervaisianus* (C.L. Koch, 1841) (coxopleural processes short, claws of the ultimate legs finely serrate; south Iberian peninsula, north-west Africa and Caucasus), *C. hartmeyeri* Kraepelin, 1908 (Australia), *C. multispinus* (Kraepelin, 1903) (ultimate legs with many spines; south Africa), *C. nitidus* Porat, 1871 (forcipular coxosternite with ramifying transverse sulci, ultimate leg pretarsus typically lacking accessory claws; south Africa and Madagascar), *C. rubriceps* (Newport, 1843) (brown, coxopleural processes long, only one ventrolateral row of spines on prefemur of ultimate legs; Australia, New Zealand, New Caledonia and other Pacific islands), *C. westwoodi* (Newport, 1844) (length to 105 mm, forcipular coxosternite lacking transverse sulcus; Australian region, circum-Indian), incl. *w. anceps* Porat, 1871.

*Hemiscolopendra* Kraepelin, 1903. – Body length to 57 mm. Transition from sparsely to densely hirsute antennal articles varying from articles 6-9. Cephalic plate overlapping tergite 1. Tergite 1 with prominent anterior transverse suture. Legs without tarsal spurs. From south-east part of North America to Mexico. A single species, *H. marginata* (Say, 1821).

*Notiasemus* Koch, 1895. – Body length to 43 mm. Cephalic plate abuts tergite 1 across its width, without overlap by either. Narrow band of uniformly long, simple bristles on each side of the labral tooth. Legs without tarsal spurs. Coxopleura with spine but no process. West Australia. A single species, *N. glauerti* Koch, 1895.

*Psiloscolopendra* Kraepelin, 1903. – Cephalic plate overlapping tergite 1. Paramedian sutures lacking on tergite 1, present on tergites 2-20; tergite 21 lacking longitudinal median suture. Legs without tarsal spurs. Coxopleural processes short, conical. Ultimate legs with tiny distomedial prefemoral process, bearing a single spine; pretarsal accessory spurs lacking or barely detectable. Burma. A single species, *P. feae* (Pocock, 1891).

*Scolopendropsis* Brandt, 1841, incl. *Rhoda* Meinert, 1886. – Body length 31-78 mm. Head relatively small, distinctly narrower than tergites, with posterior median suture. Number of leg-bearing segments either fixed or variable within a species, when variable either 21-23 or 39-43. Membranous part of pleura reduced at expense of numerous relatively large pleurites, including a set of longitudinal pleurites. Tarsus 1 of locomotory legs half the length of tarsus 2. Coxopleura without processes, variably bearing one or two small spines along posterior margin. Ultimate legs forcipulate; dorsal and medial faces of prefemur and femur flat; claws strongly falcate, their ventral surface bearing a serrated ridge. South America. Four species, incl. *S. bahiensis* (Brandt, 1841) (21 or 23 leg pairs; Brazil), *S. duplicata* Chagas, Minelli & Edgecombe, 2008 (39 or 43 leg pairs; central Brazil).

*Tonkinodentus* Schileyko, 1992. – Body length to 45 mm. Eyes absent. Tooth-plates of forcipular coxosternite with five-eight teeth arranged in two parallel rows; trochanteroprefemoral process bisected sagittally. Femur, tibia, and tarsus 1 of ultimate legs each with an apically-rounded distoventrolateral process. Central and south Vietnam. A single species, *T. lestes* Schileyko, 1992.

Tribe ASANADINI Verhoeff, 1907. – Antennae relatively short, not extending behind tergite 1, tapering distally. Claws of second maxillae without accessory spines. Anterior part of tergites distinctly delimited from the remaining tergite by a strong transverse furrow. Tergites lacking margination apart from tergite 21. Coxopleura lacking process and pores. Ultimate legs forcipulate, with longitudinal groove along dorsal side of femur (and variably prefemora and tibia). Tropical and subtropical regions of Africa, Asia and Oceania. Ca 14 species in two genera.

*Asanada* Meinert, 1886. – Body length 25-38 mm. Antennae reaching tergite 1, markedly tapering distally. Dorsal brush on tarsus of second maxillae relatively small. Lateral margins of tergites 1 and 2 convex outwards. Sternite of segment 21 variably overhanging coxopleura. Tropical and subtropical regions of Africa, Asia and Pacific islands. 13 species, incl. *A. brevicornis* Meinert, 1886 (prefemur of ultimate legs with dorsal groove, sternite of segment 21 as long as wide, with rounded posterior margin; south Asia, Australian region and Pacific islands), *A. socotrana* Pocock, 1899 (prefemur of ultimate legs lacking dorsal groove, sternite of segment 21 wider than long, with straight posterior margin; mainly Africa), *A. walkeri* (Pocock, 1891) (Nigeria to India).

*Asanadopsis* Würmli, 1972. – Body length ca 26 mm. Antennae not reaching tergite 1, moderately tapering distally, flattened. Dorsal brush on tarsus of second maxillae strongly developed. Lateral margins of tergites 1 and 2 straight. Sternite of segment 21 overhanging coxopleura. Sulawesi. A single species, *A. nueschi* Würmli, 1972.

Subfamily OTOSTIGMINAE Kraepelin, 1903 (Fig. 19.12). – Sensilla coeloconica on clypeal part of epipharynx organised as a pair of lateral clusters. Spiracles round or ovate, their long axis generally oriented vertically; floor of spiracular atrium usually raised into humps. Tropical and subtropical regions throughout the world. Ca 200 species in nine genera.

Tribe OTOSTIGMINI Kraepelin, 1903. – Border between labral and clypeal part of epipharynx strongly curved forwards. Forcipular coxosternite with tooth-plates. Leg tibiae and tarsi with spurs, the latter sometimes paired. Testicular vesicles oriented oblique to central deferens duct. Most tropical and subtropical regions throughout the world. Ca 200 species in six genera.

*Otostigmus* Porat, 1876. – Body length 20-150 mm. Leg-bearing segment 7 lacking spiracles. Most parts of tropical and subtropical regions. Ca 120 species, in three subgenera.

*O. (Otostigmus)* Porat, 1876. – Prefemur of ultimate legs bearing spines. Coxopleural process with apical spines. Africa and Indo-Australian region. Ca 60 species, incl. *O. astenus* (Kohlrausch, 1878) (ultimate leg prefemur with short spines; mainly Australia and Pacific islands), *O. scaber* Porat, 1876 (20-21 antennal articles; tergites with up to seven longitudinal keels; mainly east and

south-east Asia), *O. spinicaudus* (Newport, 1844) (only tergite 21 marginate, ultimate leg prefemur with strong spines, each on a prominent base; north Africa and Canary islands).

*O. (Dactylotergitius) Verhoeff, 1937.* – Second article of second maxillary telopodite without distal spine; claws lacking accessory spines. Tergite 21 of male with digitiform median prolongation bearing a tuft of setae set in a socket on each side of its termination. Prefemur of ultimate legs without spines. South America. Two species, *O. caudatus* Brölemann, 1902 (male lacking coxopleural processes; Brazil), *O. cavalcantii* Bücherl, 1939 (male with pointed coxopleural processes; Brazil and Argentina).

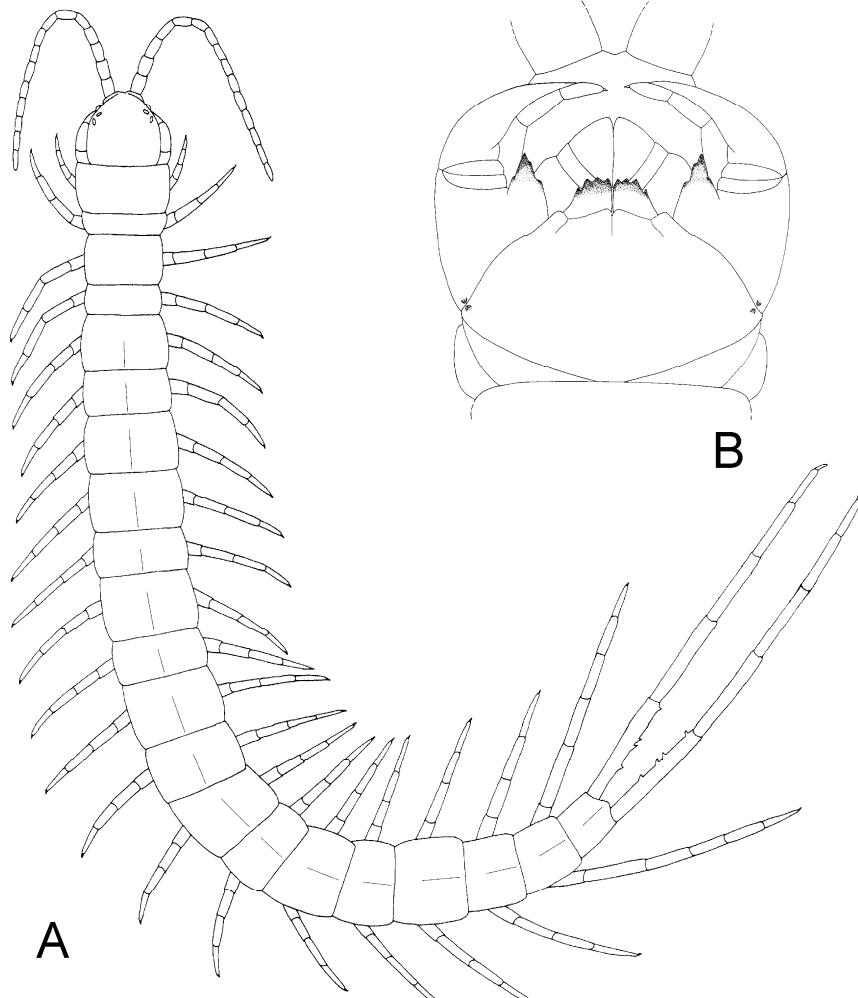


Fig. 19.12 *Rhysida afra* (Scolopendromorpha, Scolopendridae, Otostigminae). A Habitus, dorsal view. B Anterior part of the body, ventral view. Original E. Zampogno.

*O. (Parotostigmus)* Pocock, 1896. – Prefemur of ultimate legs without spines. Coxopleural process short or lacking, without apical spines. Male ultimate legs often with a cylindrical projection from the base of the prefemur. Mainly Neotropical, also in west and central Africa. More than 50 species, incl. *O. carabicus* Kraepelin, 1903 (two tarsal spurs on legs 1-16 or 17; Virgin Islands), *O. insignis* Kraepelin, 1903 (projection on male ultimate legs long, distally swollen; Ecuador) *O. pradoi* Bücherl, 1939 (Brazil), *O. scabricauda* (Humbert & Saussure, 1870) (S America), *O. tibialis* Brölemann, 1902. (Argentina, Brazil).

*Alipes* Imhoff, 1854. – Body length 64-120 mm. Tergites with longitudinal keels that bear tubercles, spaces between keels granulated. Leg-bearing segment 7 lacking spiracles. Ultimate legs elongate, the basal articles slender, the distal articles flattened, leaf-like, stridulating by friction between articles. Central and south Africa. Seven species, incl. *A. appendiculatus* Pocock, 1896 (ultimate legs in male with a sub-cylindrical projection at the base of prefemur; south-east Africa), *A. crotalus* (Gerstaeker, 1854) (distal part of ultimate legs remarkably expanded; central to south Africa).

*Alluropus* Silvestri, 1911. – Body length ca 36 mm. Ultimate legs with a row of shallow tubercles on the prefemur, and a distal projection on the first tarsal article. Vietnam. A single species, *A. demangei* Silvestri, 1912.

*Digitipes* Attems, 1930. – Body length 32-65 mm. Leg-bearing segment 7 lacking spiracles. Claws of second maxillae lacking accessory spines. Male femora of ultimate legs with a distal short subcylindrical process. Central Africa and Indian peninsula. Nine species, incl. *D. coonoorensis* Jangi & Dass, 1984 (male ultimate legs with long coxopleural process and short femoral process; Deccan), *D. verdascens* Attems, 1930 (male ultimate legs with short coxopleural process and long femoral process; equatorial forests in central Africa).

*Ethmostigmus* Pocock, 1898. – Body length 33-160 mm. Forcipules lacking trochanteroprefemoral processes. Leg-bearing segment 7 with spiracles. Africa, south Asia and Oceania. 17 species, incl. *E. pygomegas* (Kohlrausch, 1878) (coxopleural process elongate and with long spines; Himalayas and surrounding mountains), *E. rubripes* (Brandt, 1840) (tooth-plates with 3+3 teeth; coxopleural processes with two small spines on tip and a row of spines on dorsomesial edge; south east Asia, Australia, to Solomon Islands and New Zealand) incl. *r. spinosus* (Newport, 1845), *E. trigonopodus* (Leach, 1817) (body length to 130 mm, tooth-plates with 4+4 teeth; Africa).

*Rhysida* Wood, 1862. – Body length 39-200 mm. Forcipules with prominent trochanteroprefemoral processes. Leg-bearing segment 7 with spiracles. Neotropics, Indo-Australian region, east Africa. Ca 40 species, incl. *R. afra* (Peters, 1855) (trunk tergites almost smooth; south Africa and Himalayas), *R. carinulata* (trunk tergites with distinct additional keels; from south-east Asia to north Australia), *R. immarginata* (Porat, 1876) (coxopleura with moderately elongate process; tropical regions worldwide with the spp. *Rh. i. togoensis* Kraepelin, 1903 (West Africa), *R. monticola* (Pocock, 1891) (large size, coxopleura with very elongate process; Borneo).

Tribe ARRHABDOTINI Attems, 1930. – Median tooth on labrum small. Entire surface of lamina dentifera of mandible and epipharynx densely covered with hairs. Anterior margin of forcipular coxosternite broad, bearing transverse, blade-like sclerotisation, without tooth-plates; pretarsal part of tarsungula relatively long. Tergites much wider than sternites, rigid, bearing seven pronounced longitudinal ridges. Sternites without paramedian sutures, instead with a median sulcus, deepest in mid third of sternite. Legs

relatively short. Ultimate legs pincer-like. Slow-moving, arboreal. Philippines and Borneo. A single species.

*Edentistoma* Tömösváry, 1882. – Body length ca 90 mm. Rainforests of Sarawak and Philippines. A single species, *E. octosulcata* Tömösváry, 1882.

Tribe STERROPRISTINI Verhoeff, 1937. – Forcipular tarsungula bearing blunt serrations along inner margin. Coxopleura lacking process. Ultimate leg pretarsus longer than tarsus 2, lacking accessory spurs. Malay region. Two species in two genera.

*Sterropristes* Attems, 1934. – Body length ca 33 mm. Antennae composed of 17 articles, strongly tapering, their bases not separated medially; seven glabrous articles. Forcipular tarsungula with nine teeth. Legs 1 with two tibial spurs, legs 2-18 with one. Sternite of segment 21 wide posteriorly. Ultimate legs moderately thickened, femur more than twice as wide as long, lacking groove on dorsal side; ventral side of tarsus with distal bulge. Sulawesi. A single species, *S. sarasinorum* Attems, 1934.

*Malaccolabis* Verhoeff, 1937. – Body length ca 43 mm. Antennae composed of 12-15 articles, moderately tapering, their bases separated medially; four glabrous or sparsely setose articles. Forcipular tarsungula with 13 teeth. Legs 1 and 2 with two tibial spurs, legs 3-20 with one. Sternite of segment 21 strongly narrowing posteriorly. Ultimate legs greatly thickened, prefemur and femur both approximately as wide as long; dorsal side of femur with deep groove on its distal half; ventral side of tarsus lacking distal bulge. Malay peninsula. A single species, *M. metallica* Verhoeff, 1937.

Family SCOLOPOCRYPTOPIDAE Pocock, 1896. – Eyes absent. Second maxillary claw pectinate. Forcipular coxosternite without prominent serrate tooth-plates, having at most a few shallow teeth. Number of leg-bearing segments invariably 23. Gizzard with stiff, pineapple-shaped, projections; main zone of projections having a kink near their midlength. Mostly in the Americas and east Asia; recorded also in west Africa, Fiji, and New Guinea. Ca 80 species in eight genera.

Subfamily SCOLOPOCRYPTOPINAE Pocock, 1896 (Fig. 19.13). – Antennae densely covered with collared sensilla apart from basal few articles. Anterior margin of forcipular coxosternite entirely sclerotized or with few shallow teeth. Forcipular trochanteroprefemoral processes present. Tergites with margination from ca. segments 5-9. Coxopleura with process. Ultimate legs straight and relatively slender, prefemur with single strong ventral and dorsomedial spiniform processes. Tropical and temperate regions in the Americas, Africa, east Asia to New Guinea. Ca 24 species in two genera.

*Scolopocryptops* Newport, 1844. – Body length 33-69 mm. Leg-bearing segment 7 without spiracles. Americas, west Africa, east Asia to New Guinea. 22 species, incl. *S. ferrugineus* Linnaeus, 1867 (forcipular coxosternite with four shallow teeth; tropical Africa, Central America, Caribbean), *S. rubiginosus* Koch, 1878 (complete paramedian sutures starting from tergites 3-8; ultimate legs with sparse, scattered setae; east Asia, central part of North America), *S. sexspinous* (Say, 1821) (paramedian sutures confined to posterior part of tergites, none complete; east and central part of North America).

*Dinocryptops* Crabbill, 1953. – Body length 24–106 mm. Leg-bearing segment 7 with spiracles. Antilles, South America and east Asia. Two species, *D. broeckmanni* (Kraepelin, 1903) (cephalic plate with marginal ridges, trunk sternites with shallow transverse grooves; east China, Vietnam), *D. miersii* (Newport, 1845) (cephalic plate finely punctate, lacking marginal ridges; Antilles, South America).

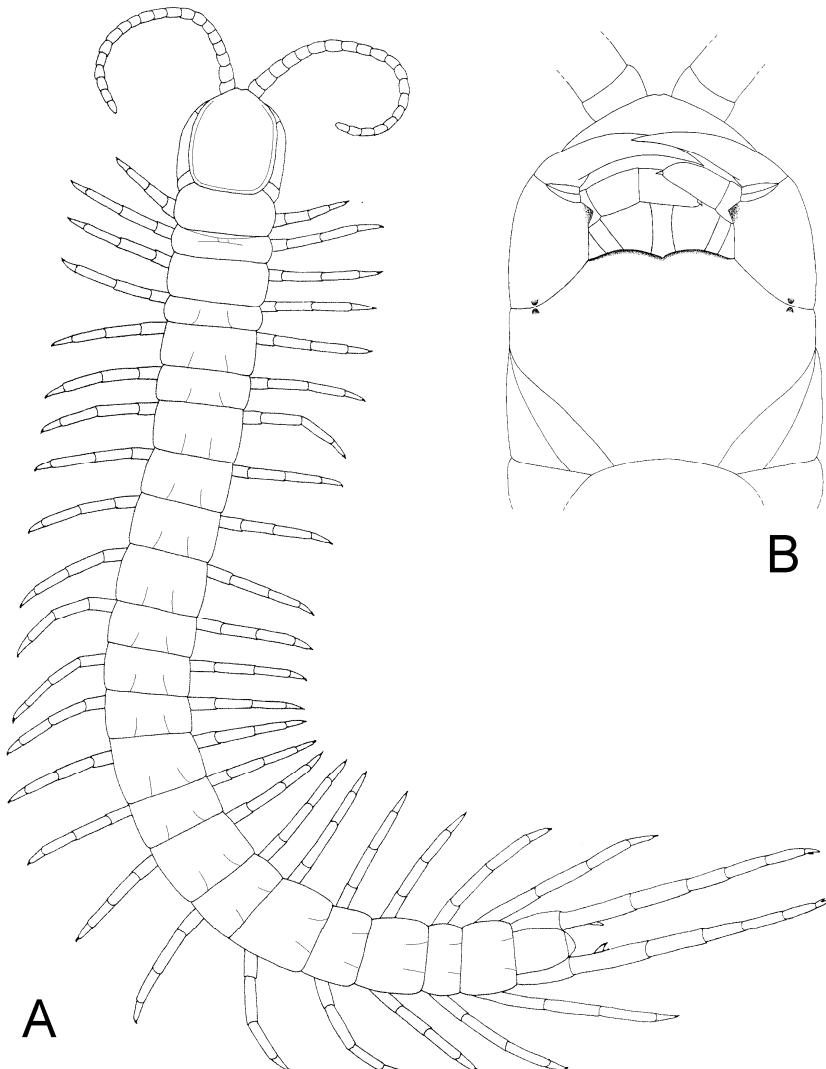


Fig. 19.13 *Scolopocryptops sexspinosis* (Scolopendromorpha, Scolopocryptopidae, Scolopocryptopinae). A Habitus, dorsal view. B Anterior part of the body, ventral view. Original E. Zamprogno.

Subfamily ECTONOCRYPTOPINAE Shelley & Mercurio, 2005. – Small, slender body. Forcipules and coxosternal margin without projections. Coxopleura with short process bearing an acuminate apical spine. Ultimate legs subclavate, tarsus 1 inflated, tarsus 2 small, claw absent. Ultimate leg prefemur and femur with three and two ventral spinose processes, respectively; tibia and tarsus 1 with dense glandular pores. Central America. Three species in two genera.

*Ectonocryptops* Crabbill, 1977. – Body length 11 mm. Ultimate legs with five articles, incl. small, rounded tarsus 2; tibia longest, with distomedial uncinate lobes; prefemur and femur lacking small spiniform setae; glandular pores on medial side of tibia. Mexico. A single species, *E. kraepelini* Crabbill, 1977.

*Ectonocryptoides* Shelley & Mercurio, 2005. – Body length 10-17 mm. Ultimate legs with diminutive tarsus 2, small subapical spur on tarsus 1 adjacent to tarsus 2; tibia and tarsus 1 inflated, subequal in length; prefemur and femur with small spiniform setae in addition to ventral spinose processes; glandular pores on ventral side of tibia and tarsus 1. Mexico, Belize. Two species, *E. quadrimeropus* Shelley & Mercurio, 2005 (Mexico), *E. sandrops* Schileyko, 2009 (Belize).

Subfamily KETHOPINAE Shelley, 2002. – Anterior margin of forcipular coxosternite weakly sclerotized, without projections. Coxopleura with process. Ultimate legs a clasping structure, tarsus 2 flexed against tarsus 1, prefemur unarmed, tibia and tarsus 1 with row of saw teeth. West part of North America. Three species in two genera.

*Kethops* Chamberlin, 1912. – Body length 21-27 mm. Sternites with distinct definition of a marginal band delineated by longitudinal sulci. West part of North America. Two species, *K. atypus* Chamberlin, 1943 (tergite 1 overlapping cephalic plate, the former lacking grooves and sutures; Utah), *K. utahensis* (Chamberlin, 1909) (cephalic plate overlapping tergite 1, latter with anterior transverse suture merging with W-shaped sutures; south-west part of North America).

*Thalkethops* Crabbill, 1960. – Body length ca 35 mm. Sternites without longitudinal sulci laterad. New Mexico, in caves. A single species, *T. grallatrix* Crabbill, 1960.

Subfamily NEWPORTIINAE Pocock, 1896 (Fig. 19.14). – Anterior margin of forcipular coxosternite without well developed tooth-plates, either smooth or with blunt projections. Coxopleura with process. Ultimate legs very elongate, filiform; tarsus 2 divided into at least four (as many as 39) variably-distinct articles, mostly lacking claw. Central America incl. Caribbean, South America. Ca 60 species in two genera.

*Newportia* Gervais, 1847. – Body length 10-94 mm. Anterior margin of forcipular coxosternite smooth, variably with transverse sclerotized band but without projections. Forcipular tarsungulum moderately large. Leg-bearing segment 7 with spiracles. Central America incl. Caribbean, South America. More than 50 species, incl. *N. adisi* Schileyko & Minelli, 1999 (semicircular anterior transverse sulcus on tergite 1; Peru, Brazil), *N. longitarsis* (Newport, 1845) (tarsus 2 of ultimate legs with up to 11 articles; Caribbean, Antilles and tropical part of South America), *N. monticola* Pocock, 1890 (tarsus 2 of ultimate legs well distinct from tarsus 1; Central America and tropical part of South America), *N. unguifer* Chamberlin, 1921 (ultimate legs with claw-like pretarsus; Guyana).

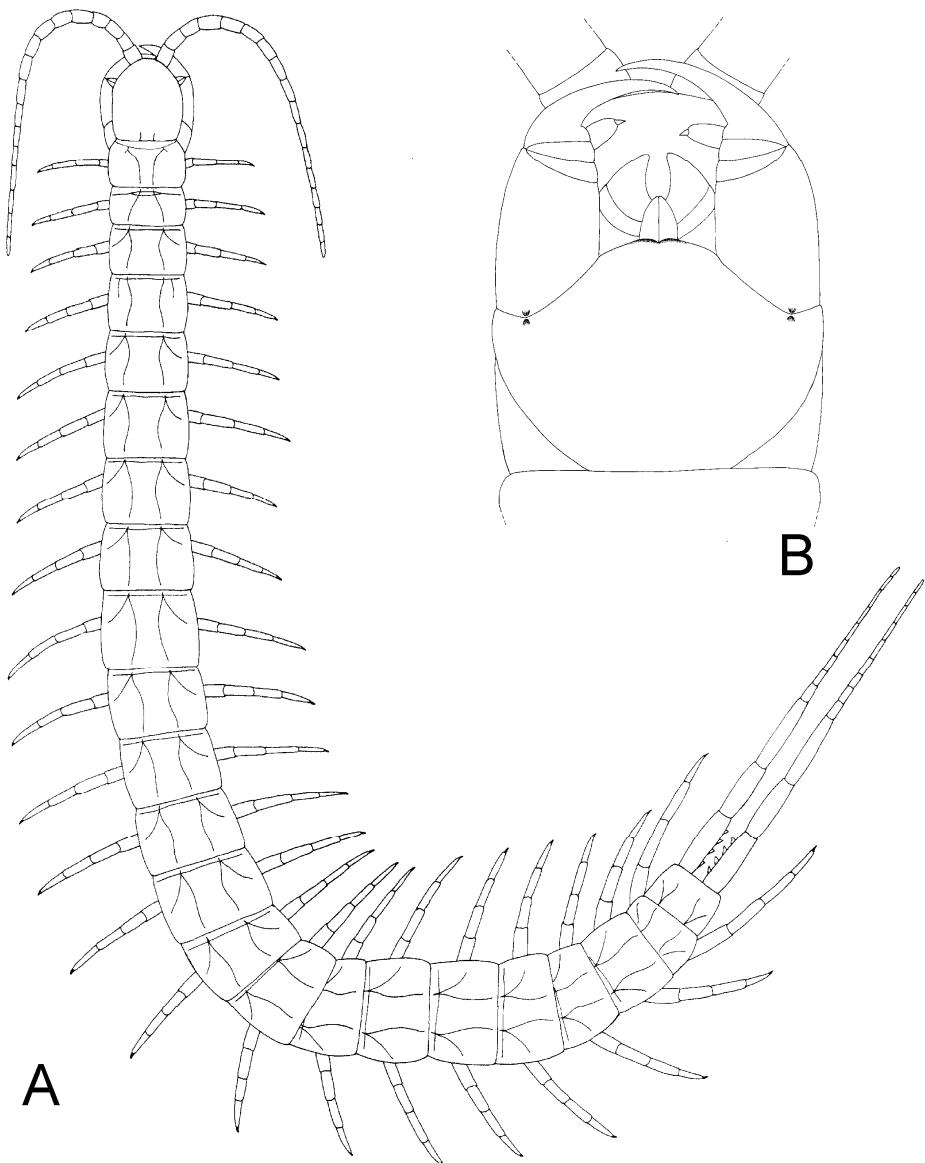


Fig. 19.14 *Newportia adisi* (Scolopendromorpha, Scolopocryptopidae, Newportiinae). A Habitus, dorsal view. B Anterior part of the body, ventral view. Original E. Zamprogno.

*Tidops* Chamberlin, 1915, possibly incl. *Kartops* Archey, 1923 with *K. guianae* Archey, 1923 (Guyana). – Body length 19–30 mm. Anterior margin of forcipular coxosternite with two short, blunt projections. Forcipular tarsungula short. Leg-bearing segment 7 lacking spiracles. Tropical

part of South America and Lesser Antilles. Three species, incl. *T. collaris* (Kraepelin, 1903) (marginal coxosternal projections truncate; north part of South America), *T. simus* Chamberlin, 1915 (Grenada).

## Order Geophilomorpha

Lucio Bonato

Body conspicuously narrow and elongate. Colour usually yellow to brown. Adult body length from ca 1 cm to 22 cm. Antennae invariably composed of 14 articles, usually slightly attenuated. A cluster of club-like sensilla (sensilla basicornica) on the internal and the external sides of the terminal antennal article. Eyes absent. Labrum highly variable in structure, often fringed by a row of denticles or bristles. Mandibles delicate, with the gnathal edge subdivided into a variable number of dentate and/or pectinate lamellae. Telopodites of first maxillae either smooth or covered with tiny scales. Anterior margin of the forcipular coxosternite either smooth or bearing at most a pair of denticles. Forcipules emerging along the anterior margin of the coxosternite, often with sclerotized projections on the mesal side of the articles. Number of pairs of legs from 27 to 191, often variable within each species, usually higher in females than in males. A shorter pretergite and a longer metatergite for each leg-bearing segment from the second to the ultimate. No heterotergy along the trunk, the metatergites changing in size and shape only gradually along the trunk. Spiracles and a particular pattern of well distinct pleurites on the sides of all leg-bearing segments from the second to the penultimate. Ultimate leg-bearing segment with coxopleura usually enlarged; coxal organs opening through either independent pores, variably arranged on the coxopleura, or inside common pits. Ultimate legs variously different from the other legs, sometimes sexually dimorphic, the tarsus most often composed of two articles. Female gonopods either a pair of distinct stout appendages, usually biarticulate, or an entire short lamina. Male gonopods a pair of appendages, usually biarticulate, with a conical projection (penis) in between. A pair of anal organs usually present.

Female coiling around the egg clutch and the newly hatched juveniles with the sternites either inward or outward.

Almost worldwide, except Antarctica and most Arctic regions. Ca 1250 species in 13 families, ca 215 extant genera and three extinct genera.

Family APHIODONTIDAE Silvestri, 1909 (Fig. 19.15). – Body tapering towards the anterior tip. Head usually only slightly elongate. Antennae slightly attenuated. Labrum not clearly distinct, without marginal projections. Each mandible with a single pectinate

lamella only. Telopodites of second maxillae much tapering, without claw. Forcipular coxosternite narrowing anteriorly and forcipules evidently tapering, with a single intermediate article only, the tarsungulum small. Number of leg-bearing segments variable within each species, the overall range 35-87. No sternal pores along the trunk. Coxal organs opening through distinct pores scattered ventrally. Ultimate legs sometimes with a single tarsal article and without claw. Female gonopods an entire lamina. South America and southernmost Africa. More than 15 species in three genera.

*Aphilodon* Silvestri, 1898. – Body length 1-6 cm. 43-87 pairs of legs. Forcipules moderately elongate, with tubercles. Ultimate legs swollen in male and slender in female, sometimes with a single tarsal article and without claw. Paraguay and Paraná basins in South America, and southernmost Africa. More than a dozen species, incl. *A. brevipes* Verhoeff, 1938 (male ultimate legs with a single tarsal article and without claw; south Africa), *A. cibellatus* (Attems, 1928) (ultimate legs with two tarsal articles and with claw in both sexes; south Africa), *A. modestus* Silvestri, 1909 (small size; Paraguay basin), *A. spegazzinii* Silvestri, 1898 (ultimate legs with a single tarsal article and without claw in both sexes; Paraná basin).

*Mecistauchenius* Brölemann, 1907. – Body length ca 5 cm. About 59 pairs of legs. Second maxillae with midlongitudinally divided coxosternite, the telopodites ending with a tubercle. Brazil. A single species, *M. micronyx* (Brölemann, 1902).

*Mecophilus* Silvestri, 1909. – Body length less than 1 cm. About 35 pairs of legs. Telopodites of second maxillae with an apical spine. Forcipular coxosternite and trochanteroprefemora remarkably narrow and elongate. Ultimate legs with a single tarsal article, without claw. Paraná basin. A single species, *M. neotropicus* Silvestri, 1909.

Family BALLOPHILIDAE Cook, 1896 (Fig. 19.16). – Body distinctly tapered towards anterior tip. Variably coloured, often with dark purple patches corresponding to sternal glands. Head short and antennae from slightly attenuated to conspicuously inflated distally, the club being flexed in respect to the more proximal part of the antenna. Labrum poorly sclerotized. Each mandible with a dentate lamella and a pectinate lamella. Claws of second maxillae fringed by two rows of filaments. Forcipular segment very stout, anterior margin of coxosternite medially concave, tergite very wide, forcipules slender and well apart. Number of leg-bearing segments variable within each species, the overall range 37-113. Sternal pores usually either in a single or two paired fields. Each coxopleuron most often provided with one or two pores close to metasternite. Ultimate legs usually remarkably swollen and without claw. Female gonopods an undivided lamina. Most tropical regions. Ca 80 species in 12 genera.

*Ballophilus* Cook, 1896. – Body length 1-7 cm. 37-91 pairs of legs. Antennae distinctly club-like. Sternal pore-fields well circumscribed, subcircular to transversally elliptical. Each coxopleuron

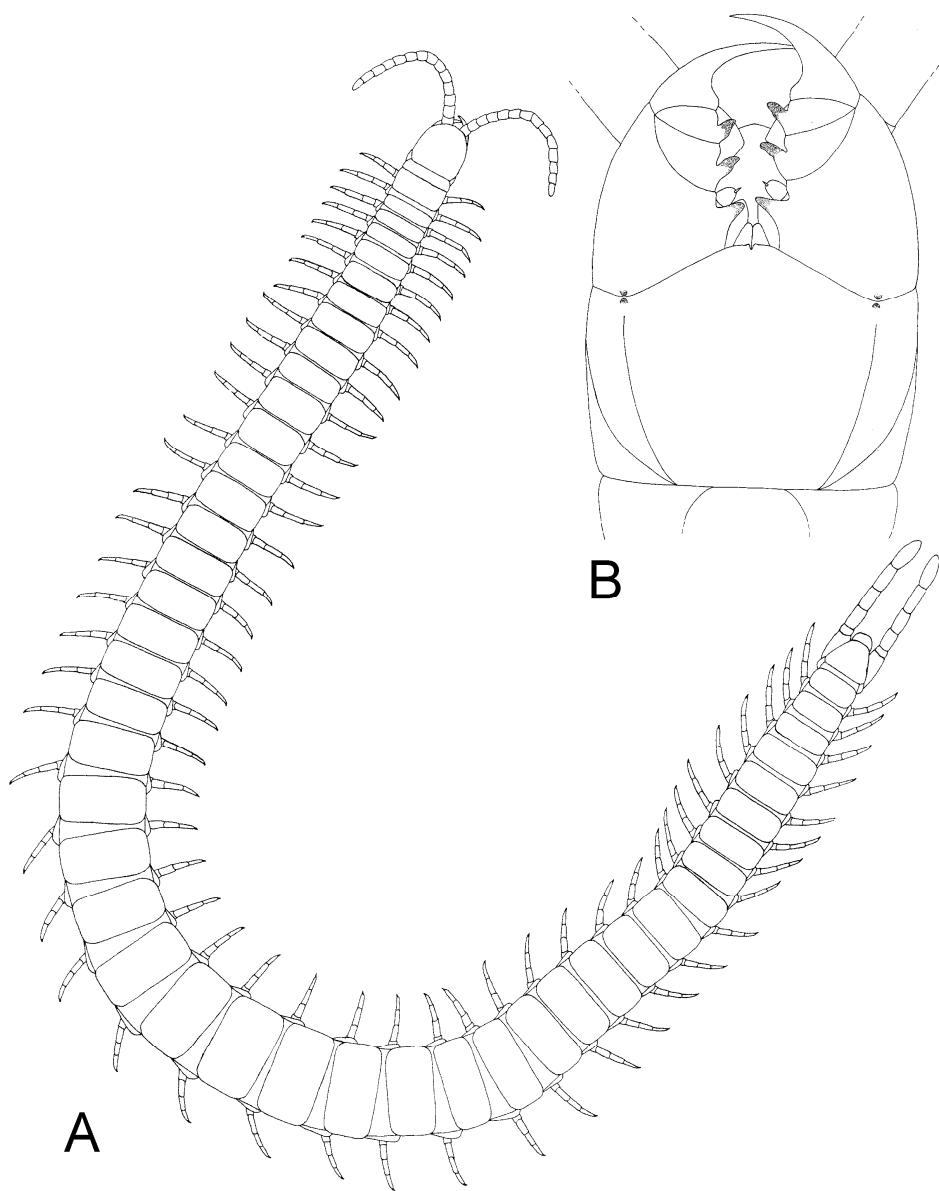


Fig. 19.15 *Aphilodon* sp. (Geophilomorpha, Aphilodontidae). A Habitus, dorsal view. B Anterior part of the body, ventral view. Original E. Zamprogno.

usually with two pores. Tropical and subtropical regions throughout the world, mainly in Africa and south-east Asia. About 40 species, incl. *B. hounsellii* Archey, 1936 (purple sternal glands, opening

in transversely elongate pore-fields; New Zealand), *B. latisternus* Lawrence, 1960 (second maxillary claws fringed by coalescent filaments; Madagascar), *B. ramirezi* Pereira, Foddai & Minelli, 1997 (purple sternal glands; temperate South America), *B. smaragdus* Demange, 1963 (large size, green-blue colour; west Africa).

*Afrotaenia* Chamberlin, 1951. – Body length ca 2 cm. About 59 pairs of legs. Trunk metasternites without patterned pore-fields, only scattered pores. Ultimate legs with claw. Tropical forests in central Africa. A single species, *A. machadoi* Chamberlin, 1951.

*Caritohallex* Crabill, 1960. – Body length ca 1 cm. 39-43 pairs of legs. Antennae slender. No coxal pores. Ultimate legs with a single tarsal article. Lesser Antilles. A single species, *C. minyrrhopus* Crabill, 1960.

*Cerethmus* Chamberlin, 1941. – Body length ca 4 cm. About 81 pairs of legs. Antennae geniculate and abruptly swollen distally. Venezuela. A single species, *C. naiquatanus* Chamberlin, 1941.

*Clavophilus* Chamberlin, 1950. – Body length 2-3 cm. About 89 pairs of legs. Sternal pore-fields ill-defined. Each coxopleuron with a single pore. Puerto Rico. A single species, *C. maricaonus* Chamberlin, 1950.

*Diplethimus* Cook, 1899. – Body length 4-6 cm. 61-79 pairs of legs. Sternal pores in two paired circular fields. Tropical America. Half a dozen species, incl. *D. pulchellus* Turk, 1955 (violet-patched; north Andes).

*Itypophilus* Cook, 1899. – Body length 2-9 cm. 41-113 pairs of legs. Antennae distinctly club-like. Forcipular coxosternite with well marked sclerotized lines. Margin of forcipular tarsungula sometimes denticulate. Each coxopleuron with two pores. Mainly tropical and subtropical America; also Seychelles, east Asian islands and some Pacific islands. About 20 species, incl. *I. grandis* (Turk, 1955) (large size; north Andes), *I. perrieri* (Brölemann, 1909) (forcipular tarsungula evidently denticulate; Amazonas), *I. tenuicollis* (Takakuwa, 1934) (sternal pore-fields biscuit-like; Japanese islands).

*Koinethmus* Chamberlin, 1958. – Body length ca 2 cm. About 71 pairs of legs. Antennae slender. Sternal pores in transverse stripes. Ultimate legs with a single tarsal article. Venezuela. A single species, *K. guanereus* Chamberlin, 1958.

*Leucolinum* Chamberlin, 1945. – Body length ca 1 cm. About 37 pairs of legs. Antennae slender. Ultimate legs only slightly swollen. Lesser Antilles. A single species, *L. trinidadense* Chamberlin, 1945.

*Taeniolinum* Pocock, 1894. – Body length 1-2 cm. 43-51 pairs of legs. Antennae slender. Labrum lined with small tubercles. Sternal pores in ill-defined transverse fields. Rainforests in the Isthmus of Panama, Lesser Antilles and Amazonas. A few species, incl. *T. arborum* Pereira, Minelli & Barbieri, 1994 (tree-dwelling; Amazonas).

*Tanophilus* Chamberlin, 1921. – Body length ca 3 cm. About 79 pairs of legs. Coxal organs opening in a common ventral pit on each coxopleuron. Central America. A single species, *T. hondurasanus* Chamberlin, 1921.

*Zygethmus* Chamberlin, 1957. – Body length ca 2 cm. About 47 pairs of legs. Antennae slender. Sternal pores in two paired subcircular fields. Each coxopleuron with a single pore. Ecuador. A single species, *Z. pantenus* Chamberlin, 1957.

Family DIGNATHODONTIDAE Cook, 1896 (Fig. 19.17). – Body gradually tapering towards the anterior tip. Head short, with antennae not evidently attenuated. Labrum usually poorly sclerotized, with tubercles. Mandibles with a single pectinate lamella only.

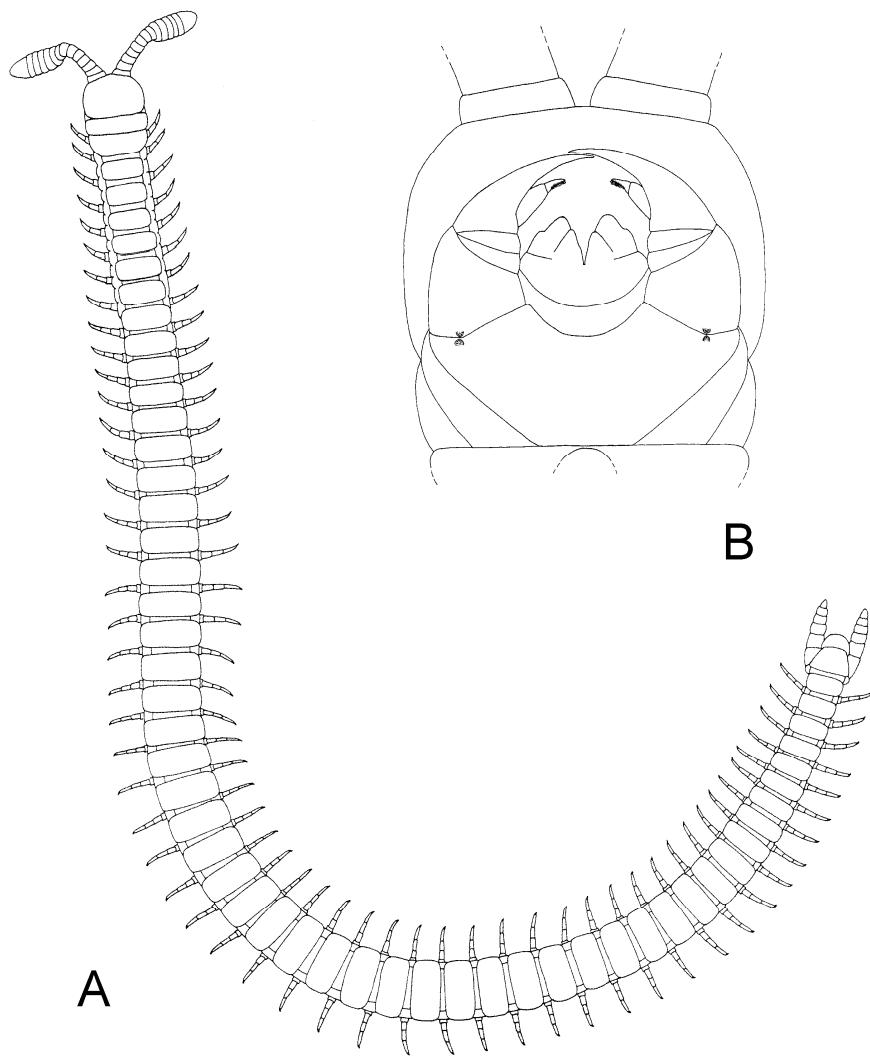


Fig. 19.16 *Ballophilus ramirezi* (Geophilomorpha, Ballophilidae). A Habitus, dorsal view. B Anterior part of the body, ventral view. Original E. Zamprogno.

Second maxillae with slender telopodites and small claws. Forcipular coxosternite short, with paramedian sclerotized lines, the anterior margin usually deeply concave; tergite wide; forcipules without denticles. Number of leg-bearing segments variable within each species, the overall range 43-153. Sternal pores usually present, in a single medial field. Coxal organs usually present, most often in a ventral pit on each coxopleuron. Ultimate

legs swollen, at least in males. Female gonopods an undivided lamina. Whole Ca 20 species in four genera. Mediterranean region from Macaronesia to Caucasus, reaching west and central Europe.

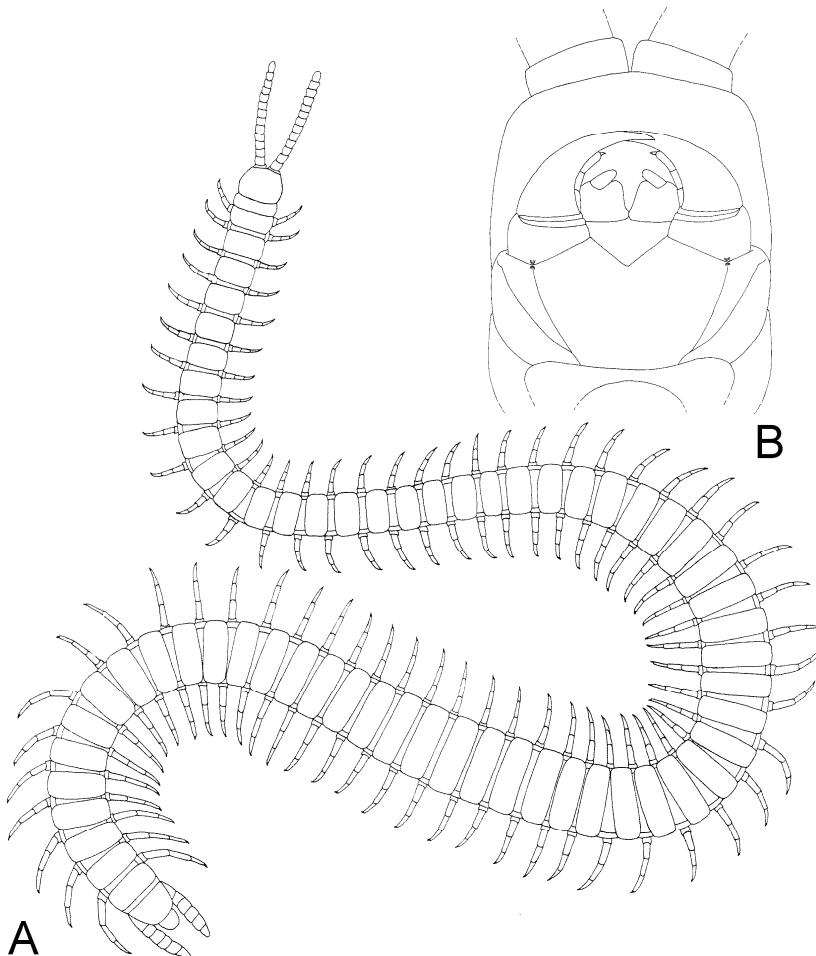


Fig. 19.17 *Henia bicarinata* (Geophilomorpha, Dignathodontidae). A Habitus, dorsal view. B Anterior part of the body, ventral view. Original E. Zamprogno.

**Dignathodon** Meinert, 1870. – Body length 3-11 cm. 65-89 pairs of legs. Body remarkably narrow anteriorly. Antennae slightly swollen distally. A few denticles along the internal margin of each forcipular tarsungulum. No sternal pore-fields. Ultimate legs swollen in both sexes. Most part of the Mediterranean region. Two species, incl. *D. microcephalus* (Lucas, 1846) (more than 60 leg pairs; south Europe and north-west Africa).

*Agnathodon* Folkmanovà & Dobroruka, 1960. – Body length ca 2 cm. 63-69 pairs of legs. Antennae slightly swollen distally. No denticles along the forcipular tarsungula. No sternal pore-fields. Coxal pores opening in two pits on each coxopleuron. Ultimate legs swollen in both sexes. East coast of Black Sea. A single species, *A. paradoxus* Folkmanovà & Dobroruka 1960.

*Henia* Koch, 1847. – Body length 1-15 cm. 43-153 pairs of legs. Forcipular tarsungula remarkably slender and flattened. Sternal pores in a single medial field of various shape. From Macaronesia, through central Europe and Mediterranean region, to Caucasus. More than 15 species, incl. *H. bicarinata* (Meinert, 1870) (labrum with tubercles, ultimate legs with a single tarsal article; mainly littoral sites throughout most of the Mediterranean region), *H. brevis* (Silvestri, 1896) (small size, sternal pore-fields longitudinally elongate; west Mediterranean region), *H. devia* C.L. Koch, 1847 (large size, more than 140 leg pairs, no coxal pores; east Mediterranean region), *H. illyrica* (Meinert,

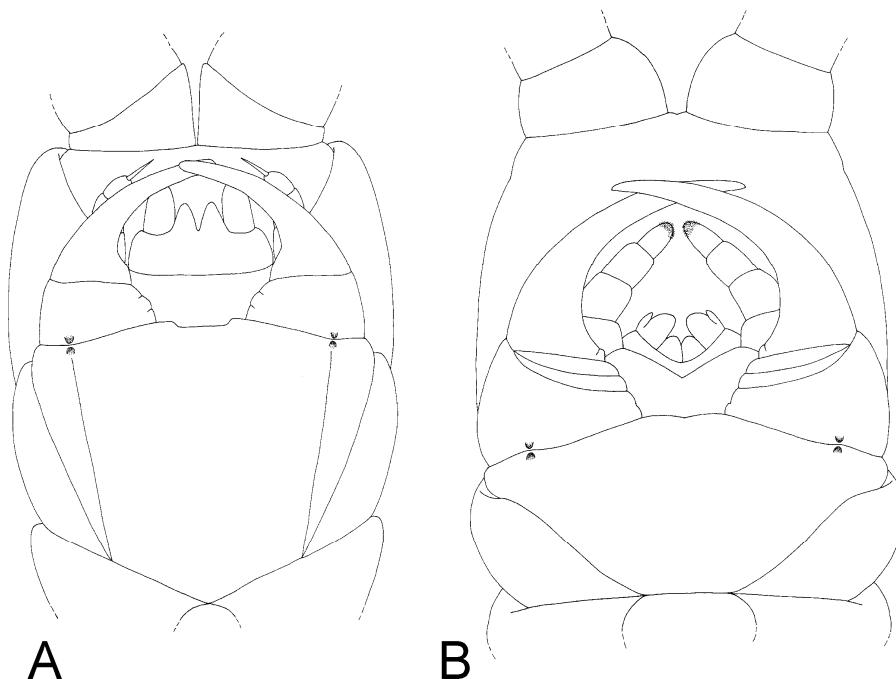


Fig. 19.18 A *Eriphantes telluris* (Geophilomorpha, Eriphantidae). Anterior part of the body, ventral view. B *Macronicophilus unguiseta* (Geophilomorpha, Macronicophilidae). Anterior part of the body, ventral view. Original E. Zampogno.

1870) (Europe, mostly Balkans), *H. vesuviana* (Newport, 1845) (labrum with dense filiform projections, poison glands extended deeply into the trunk, sternal pore-fields subcircular; west and south Europe, north-west Africa).

*Orthognathus* Folkmanovà, 1958. – Body length ca 4 cm. 83-85 pairs of legs. Forcipular trochanteropremora very short, tarsungula long, almost straight and flat. Sternal pore-fields subcircular. Few, distinct coxal pores. Caucasus. A single species, *O. arnoldii* Folkmanovà, 1958.

Family ERIPHANTIDAE Crabbill, 1970 (Fig. 19.18A). – Body very elongate. Head short and antennae stout. Labral margin projecting posteriorly and fringed by tubercles. Mandibles bearing a single row of small teeth. Claws of second maxillae slender and straight. Forcipules composed only of a basal stout article and the tarsungulum, without intermediate articles. Number of leg-bearing segments variable within the species. Anterior trunk metasternites each with two transversely elliptical pore-fields, one anterior to the other. Coxal organs of each coxopleuron opening along the metasternite in an anterior common pit and a posterior pore. Ultimate legs with claw. Female gonopods an undivided lamina. Baja California peninsula. A single species.

*Eriphantes* Crabbill, 1970. – Body length ca 6 cm. 123-145 pairs of legs. Baja California peninsula. A single species, *E. telluris* Crabbill, 1970.

Family GEOPHILIDAE Leach, 1815 (Fig. 19.19). – Body frequently slender but variable in shape. Head usually slightly or moderately elongate; antennae slender. Labrum often composed of a narrow intermediate part with tubercles and two wider lateral parts with bristles. Mandibles with a single pectinate lamella only. Second maxillae variable, the coxosternite frequently undivided and the claws usually without rows of filaments. Forcipular segment variously elongate and broad, the coxosternite usually with two paramedian sclerotized lines. Number of leg-bearing segments variable within each species, the overall range 29-125. Sternal pores often present, with variable arrangement. Coxal organs usually present, opening either through distinct pores or in pits. Female gonopods usually an undivided lamina. Almost worldwide. Ca 560 species in ca 100 genera.

*Geophilus* Leach, 1814. – Body length 1-8 cm. 29-89 pairs of legs. Head only slightly elongate. Labral intermediate part with tubercles. Coxosternite of second maxillae undivided. Forcipules usually poorly elongate, with a single small tubercle at the base of each tarsungulum. Anterior trunk metasternites usually with an anterior medial socket and a posterior transversely elongate pore-field. Most coxal pores close to metasternite. Whole Holarctic. Ca 140 species, incl. *G. algarum* Brölemann, 1909 (slender, ultimate legs with few coxal pores and small claw; littoral sites along the European Atlantic coast), *G. alpinus* Meinert, 1870 (second maxillae with small claws, trunk metasternites with wide anterior sockets; west Palearctic), *G. carpophagus* Leach, 1815 (trunk metasternites with narrow anterior sockets; west Palearctic), *G. cayugae* Chamberlin, 1904 (coxal pores scattered, ultimate legs short; eastern part of North America), *G. easoni* Arthur, Foddai, Kettle, Lewis, Luczynski & Minelli, 2001 (United Kingdom), *G. electricus* (Linnaeus, 1758) (chitin-lines complete; central and northern Europe), *G. flavus* (De Geer, 1778) (antennae elongate, forcipular segment broad; mainly west Palearctic), *G. mordax* Meinert, 1886 (coxal pores along both metatergite and metasternite; mainly eastern North America), *G. persephones* Foddai & Minelli, 1999 (France), *G. richardi* Brölemann, 1904 (France, Italy), *G. seurati* Brolemann, 1924 (Algeria), *G. procerus* L. Koch, 1878 (large size, more than 70 leg pairs; Japan), *G. proximus* Koch, 1847 (often parthenogenetic; northern Eurasia), *G. richardi* Brölemann, 1904 (France, Italy). *G. seurati*

Brolemann, 1924 (Algeria), *G. truncorum* Bergsøe & Meinert, 1866 (small size, no distinct sternal pore-fields, only two pores on each coxopleuron; mainly north and central Europe), *G. vittatus* (Rafinesque, 1820) (dark patches along the trunk, coxal organs opening in ventral pits; central and eastern North America).

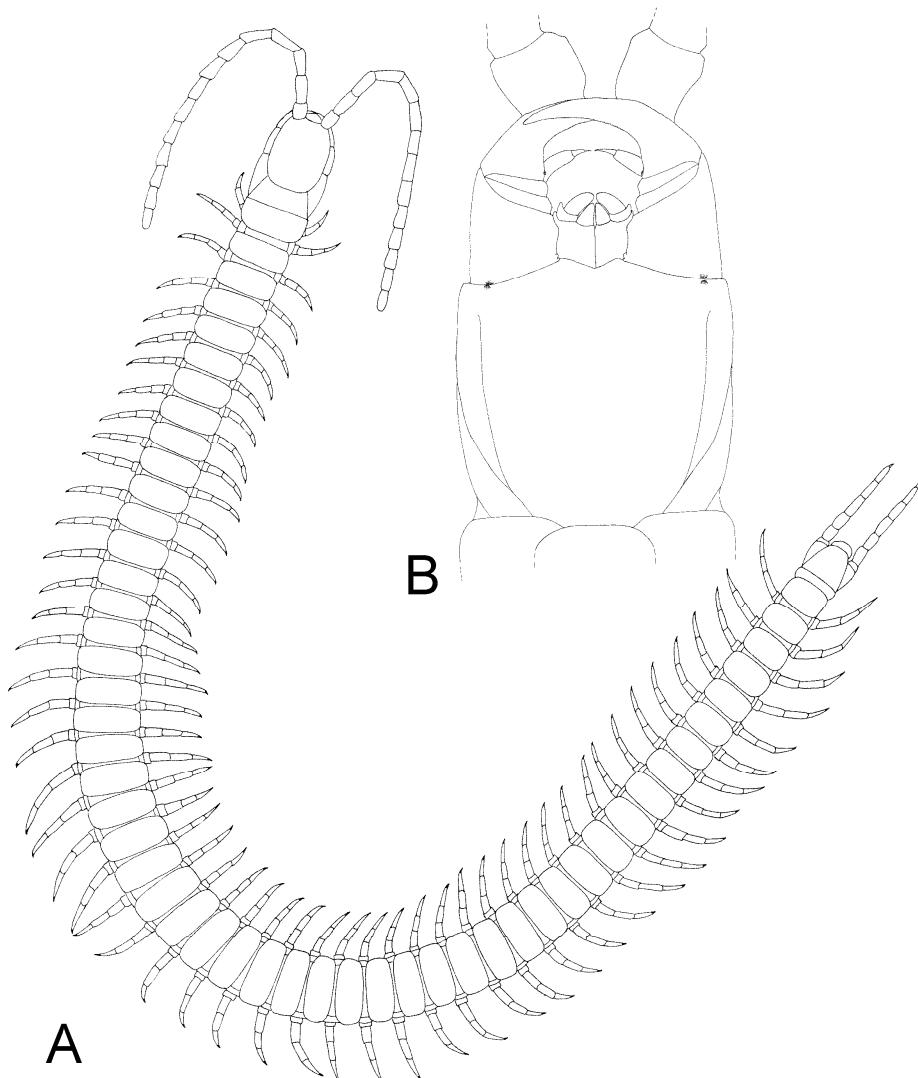


Fig. 19.19 *Geophilus flavus* (Geophilomorpha, Geophilidae). A Habitus, dorsal view; B Anterior part of the body, ventral view. Original E. Zamprogno.

*Abatorus* Chamberlin, 1965. – Body length 4-5 cm. About 70 pairs of legs. Sternal pores in a posterior transverse band. Coxal organs opening in two ventral pits on each coxopleuron. Southwest part of North America. A single species, *A. allredi* Chamberlin, 1965.

*Acanthogeophilus* Minelli, 1982. – Body length 2-3 cm. 67-71 pairs of legs. Very slender. Sternal pores in a posterior transversally elongate area. Coxal pores scattered. Ultimate legs with peculiar spine-like processes. Centro-west part of the Mediterranean region. Two species, incl. *A. spiniger* (Meinert, 1870) (north-west Africa).

*Achilophilus* Attems, 1926. – Body length 2-4 cm. 49-55 pairs of legs. Head elongate. Labrum indistinct. Forcipules with a small tubercle at the base of the tarsungulum. Sternal pores grouped in the posterior part of anterior metasternites. Each coxopleuron with a single, ventral pore. Southernmost Africa. Two species, incl. *A. pachypus* Verhoeff, 1937 (forcipules elongate, ultimate legs with gland-like organs; Cape region).

*Alloschizotaenia* Brölemann, 1909. – Body length 1-2 cm. 37-39 pairs of legs. Head and forcipules elongate. Coxosternite of second maxillae divided mid-longitudinally, with sclerotized ridges. No sternal pores. Each coxopleuron with few pores, close to metasternite. A spinous tubercle on the tip of the ultimate legs. Central-east Africa. A few species, incl. *A. minuta* (Silvestri, 1907) (each coxopleuron with two pores; east Africa).

*Apogeophilus* Silvestri, 1905. – Body length 1-2 cm. 51-59 pairs of legs. Forcipules stout, without denticles. Sternal pores mainly in posterior groups. Coxal pores very few, close to metasternite. Male ultimate legs evidently clavate, with a single tarsal article, without claw. Temperate part of South America. Two species, incl. *A. claviger* Silvestri, 1905 (small size, a single pore on each coxopleuron; Chile).

*Arctogeophilus* Attems, 1909. – Body length 2-5 cm. About 35-69 pairs of legs. Head and forcipules elongate. Labral lateral parts almost touching medially, the intermediate part inconspicuous. Sternal pores usually lacking. Coxopleura with scattered pores. Temperate and sub-artic regions of Asia and North America; also west Europe. A dozen species, incl. *A. fulvus* (Wood, 1862) (forcipular denticles small, ultimate legs without claw; Appalachians), *A. glacialis* (Attems, 1909) (forcipular denticles pointed, ultimate legs without claw; Alaska and surrounding areas), *A. sachalinus* Verhoeff, 1934 (some pores on anterior trunk metasternites; Hokkaido and Sakhalin islands).

*Arenophilus* Chamberlin, 1912. – Body length 1-6 cm. 45-63 pairs of legs. Head and forcipules elongate. Sternal pores in a posterior area. Coxal organs opening in two ventral pits on each coxopleuron. A spinous tubercle on the tip of the ultimate legs. Mainly most part of North America. Half a dozen species, incl. *A. bipuncticeps* (Wood, 1862) (dorsal dark stripes along the trunk; transversally elongate sternal pore-fields; North America), *A. peregrinus* Jones, 1989 (small size; Cornwall and nearby islands), *A. watsingus* Chamberlin, 1912 (subcircular sternal pore-fields; eastern North America).

*Barrophilus* Chamberlin, 1940. – Body length ca 1-2 cm. About 41 pairs of legs. Coxosternite of second maxillae with sclerotized ridges and peculiar anterior projections. Forcipules elongate and with denticles. No sternal pores. Ultimate leg-bearing segment with very wide metasternite, and each coxopleuron with three pores close to the metasternite and a densely setose posterior lobe. Isthmus of Panama. A single species, *B. isolatus* Chamberlin, 1940.

*Bebekium* Verhoeff, 1941. – Body length ca 1 cm. 39-41 pairs of legs. Labral intermediate part without projections. No sternal pores. Coxal organs opening in two ventral pits on each coxopleuron. Balkan peninsula. A single species, *B. mirabile* Verhoeff, 1941.

*Brachygonarea* Ribaut, 1911. – Body length 4-5 cm. 55-65 pairs of legs. Head and forcipules elongate. Coxosternite of second maxillae with sclerotized ridges and peculiar anterior

projections. No sternal pores. Coxal pores close to metasternite. Southernmost Africa. Two species, incl. *B. apora* (Attems, 1909).

*Caliphilus* Chamberlin, 1941. – Body length ca 3 cm. About 65 pairs of legs. Sternal pores in a posterior transverse field. Coxal pores scattered. A small spine at the tip of the ultimate legs. California. A single species, *C. alamedanus* Chamberlin, 1941.

*Cephalodolichus* Verhoeff, 1938. – Body length ca 2 cm. About 35 pairs of legs. Head very elongate. Forcipules with denticles. No sternal pores. Ultimate leg-bearing segment with wide metasternite, two pores on each coxopleuron. Southernmost Africa. A single species, *C. siccus* Verhoeff, 1938.

*Chilenophilus* Attems, 1909. – Body length 5-7 cm. 61-69 pairs of legs. Head and forcipules elongate. Lateral parts of labrum almost touching medially, the intermediate part inconspicuous. Coxosternite of second maxillae divided mid-longitudinally, with sclerotized ridges. Coxal pores scattered. Temperate part of Chile. A few species, incl. *C. corralinus* (Attems, 1903) (sternal pores in a posterior transverse band and a pair of anterior groups; central Chile).

*Chomatophilus* Pocock, 1896. – Body length 3-9 cm. 47-115 pairs of legs. Intermediate part of labrum fringed by bristles. Forcipular segment stout, with trochanteroprefemora short but tarsungula relatively long. Sternal pores in a posterior transverse band extending mid-longitudinally. Coxal organs opening in two ventral pits on each coxopleuron. Mexico. Three species, incl. *C. smithi* Pocock, 1896 (more than 80 leg pairs, ultimate legs slightly inflated in both sexes; Mexico).

*Clinopodes* Koch, 1847. – Body length ca 2-7 cm. 51-81 pairs of legs. Labral margin fringed only by bristles, without tubercles. Forcipular coxosternite with a pair of anterior denticles. Forcipules short, without denticles. Sternal pores in a posterior transverse band. Coxal organs opening mainly close to metasternite. Ultimate legs without claw. Mainly south-east Europe, from Alps to Caucasus. A dozen species, incl. *C. flavidus* C.L. Koch, 1847 (forcipular coxosternal denticles conspicuous, coxal organs opening in a few pits; south-east Europe), *C. trebevensis* (Verhoeff, 1898) (forcipular coxosternal denticles shallow, coxal organs opening through distinct pores, including a posterior isolated pore; east Alps and west Balkan peninsula).

*Condylona* Chamberlin, 1941. – Body length 2-4 cm. 59-85 pairs of legs. Anterior trunk metasternites with an anterior medial socket. No sternal pores. Coxal pores scattered. California. Two species, incl. *C. isabella* Chamberlin, 1941 (forcipules elongate; central California).

*Dekanphilus* Verhoeff, 1938. – Body length ca 4 cm. About 85 pairs of legs. Head and forcipules elongate. Intermediate part of labrum wide. Second maxillae with long claws. Anterior trunk metasternites with an ovate pore-field. Ultimate legs with coxal pores close to the wide metasternite. California. A single species, *D. gracillimus* Verhoeff, 1938.

*Dinogeophilus* Silvestri, 1909. – Body length less than 1 cm. About 29-31 pairs of legs. Forcipular tarsungula relatively large, each with two acute spines on the margin. Anterior trunk metasternites with a longitudinally elongate pore-field. Dense, tiny tubercles on the most posterior trunk segments, on both dorsal and ventral sides. A single pore on each coxopleuron. Ultimate legs of male with a single tarsal article, without claw. Paraná and Uruguay basins. Two species, incl. *D. oligopodus* Pereira, 1984 (Argentina). *D. pauporus* Silvestri, 1909 (adult length ca. 0.5 cm).

*Diphyonyx* Bonato, Zapparoli & Minelli, 2008. – Body length 4-6 cm. 65-81 pairs of legs. Forcipular coxosternite with a pair of anterior tubercles. No sternal pores. Claws of some anterior legs enlarged and with an elongate basal spine. Most coxal organs opening in a single pit on each coxopleuron. South-east Europe and Anatolian peninsula. Three species, incl. *D. conjungens* (Verhoeff, 1898) (each coxopleuron with an additional posterior pore; Anatolian peninsula and surrounding regions).

*Dyodesmophilus* Verhoeff, 1938. – Body length 4-5 cm. About 81 pairs of legs. Head elongate. Forcipules without denticles. Sternal pores in a posterior transverse band. Coxal organs opening in two ventral pits on each coxopleuron. California. A single species, *D. longissimus* (Verhoeff, 1938).

*Dysmesus* Chamberlin, 1944. – Body length ca 1.5 cm. 45-51 pairs of legs. Coxosternite of second maxillae divided mid-longitudinally. Forcipules short, the tarsungulum with a small basal tubercle. No sternal pores. Coxal pores scattered. South Appalachians. A single species, *D. orytes* Chamberlin, 1944.

*Ecuadoron* Chamberlin, 1955. – Body length ca 2-3 cm. About 59 pairs of legs. Coxosternite of second maxillae divided mid-longitudinally. Forcipules elongate. Sternal pores in a subcircular field. Coxal organs opening in a single pit on each coxopleuron. Ultimate legs without claw. Puna island, off Ecuador. A single species, *E. punac* Chamberlin, 1955.

*Eremerium* Chamberlin, 1941. – Body length ca 2 cm. About 43 pairs of legs. Forcipules elongate, with denticles. No sternal pores. Ultimate leg-bearing segment with narrow metasternite and scattered coxal pores. Arizona. A single species, *E. apachum* Chamberlin, 1941.

*Eremorus* Chamberlin 1963. – Body length ca 4 cm. About 85 pairs of legs. Labral intermediate part with small tuberculate plates. No sternal pores. Coxal organs opening in a single ventral pit on each coxopleuron. Nevada. A single species, *E. becki* Chamberlin 1963.

*Eriophilus* Cook, 1899. – Body length ca 1.2 cm. 45-51 pairs of legs. Anterior trunk metasternites with an anterior medial socket and a posterior transverse band of pores. Coxal organs opening in two ventral pits on each coxopleuron. Ultimate legs swollen but the two distal articles abruptly slender. Florida Keys. A single species, *E. neopus* Cook, 1899.

*Eurygeophilus* Verhoeff, 1899. – Body length 2-4 cm. 33-57 pairs of legs. Body stout at both anterior and posterior ends. Forcipular segment very short, forcipules with needle-like tarsungula. Sternal pores in a posterior transverse band. West Europe. Two species, incl. *E. multistiliger* (Verhoeff, 1899) (trunk metasternites with short swollen setae, coxal pores on both dorsal and ventral sides; Iberian peninsula and Sardinia).

*Filipponus* Chamberlin, 1962. – Body length unknown. About 63 pairs of legs. Head and forcipules elongate. Labral lateral parts almost touching medially, the intermediate part inconspicuous. Coxosternite of second maxillae with peculiar anterior projections. No sternal pores. Coxal pores scattered. Chiloë island. A single species, *F. holdgati* Chamberlin, 1962.

*Folkmanovius* Dobroruka, 1957. – Body length ca 1 cm. 67-69 pairs of legs. Intermediate part of labrum fringed by bristles, lateral parts without projections. Forcipular coxosternite with a pair of anterior denticles. Sternal pores in a posterior transverse band. A single coxal pore on each coxopleuron. A tubercle on the tip of the ultimate legs. Bohemia. A single species, *F. paralellus* Dobroruka, 1957.

*Galliophilus* Ribaut & Brolemann, 1927. – Body length ca 5 cm. 73-85 pairs of legs. Forcipular coxosternite anteriorly projecting, forcipules short, the internal margin of tarsungula straight. Trunk metasternites with very few pores. Coxal pores scattered. Ultimate legs without claw. South-west Europe. A single species, *G. beatensis* Ribaut & Brolemann, 1927.

*Geomerinus* Brolemann, 1912. – Body length 5-7 cm. About 71 pairs of legs. Head and forcipules elongate. Claws of second maxillae very small. No sternal pores. Ultimate leg-bearing segment with narrow metasternite, coxal pores scattered, legs with a single tarsal article. South-east Australia. A single species, *G. curtipes* (Haase, 1887).

*Geoperingueyia* Attems, 1926. – Body length mainly 2-5 cm. 41-85 pairs of legs. Head and forcipules short. Telopodites of second maxillae small, with an apical spine. Ventral surface of trunk densely porose. Coxal pores scattered. Ultimate legs with a single tarsal article, often evidently clavate in males, the claw reduced to completely absent. East part of south Africa, often

at high altitude. 10 species, incl. *G. conjungens* Attems, 1928 (female ultimate legs with claw), *G. dentata* Verhoeff, 1938 (ultimate legs without claw in both sexes).

*Gnathoribautia* Brölemann, 1909. – Body length 3-11 cm. About 67-87 pairs of legs. Head elongate. Forcipular coxosternite broad, forcipules elongate and with denticles. No sternal pores. Ultimate legs elongate, without claw. Mediterranean region. A few species, incl. *G. bonensis* (Meinert, 1870) (west Mediterranean basin and Macaronesia).

*Gosipina* Chamberlin, 1940. – Body length 1-2 cm. 55-63 pairs of legs. Labrum not distinctly tripartite. Forcipules without denticles. Sternal pores in a posterior transverse band. Metasternite of the ultimate leg-bearing segment wide. Coxal glands opening in a few ventral pits on each coxopleuron. A spinous tubercle on the tip of the ultimate legs. Texas and Mexico. Two species, incl. *G. hexara* Chamberlin, 1940 (a single pit on each coxopleuron; Texas).

*Hapleurytion* Verhoeff, 1940. – Body length ca 5 cm. 57-61 pairs of legs. Head and forcipules elongate. Claws of second maxillae elongate. Anterior trunk metasternites with a subcircular pore-field. No coxal pores. South-west Africa. A single species, *H. aporus* (Attems, 1922).

*Harmostela* Chamberlin, 1941. – Body length ca 3 cm. 57-59 pairs of legs. Forcipules elongate. No sternal pores. Each coxopleuron with two pores. A long peg at the tip of the ultimate legs. California. A single species, *H. hespera* Chamberlin, 1941.

*Harpacticellus* Verhoeff, 1941. – Body length ca 3 cm. 45-49 pairs of legs. Intermediate part of labrum without projections. Sternal pores in a transverse posterior band and a pair of anterior areas. Coxal pores close to metasternite. Ultimate legs without claw. Bioko island, Gulf of Guinea. A single species, *H. arborum* (Verhoeff, 1941).

*Horonia* Chamberlin, 1966. – Body length ca 4 cm. About 49 pairs of legs. Intermediate part of labrum wide, fringed by bristles. No sternal pores. Coxal pores scattered. South-west part of North America. A single species, *H. bella* Chamberlin, 1966.

*Hovanyx* Lawrence, 1960. – Body length ca 2 cm. About 43 pairs of legs. Labrum poorly distinct, with denticles. Forcipules with a basal denticle on each tarsungulum. Anterior trunk metasternites with a medial subcircular pore-field. No coxal organs. Madagascar. A single species, *H. waterloti* Lawrence, 1960.

*Hyphydrophilus* Pereira, Minelli & Barbieri, 1994. – Body length ca 1-2 cm. 37-43 pairs of legs. Coxosternite of second maxillae divided mid-longitudinally, with sclerotized ridges. Forcipules elongate, the tarsungula with a basal denticle. Sternal pores few. Each coxopleuron with two ventral pores. Amazonas. Two species, incl. *H. projectus* Pereira, Minelli & Barbieri, 2000 (small size, second maxillae with external spinous projections).

*Ketampa* Chamberlin, 1955. – Body length ca 2-3 cm. About 57 pairs of legs. Intermediate part of labrum with tubercles, lateral parts without projections. No sternal pores. Coxal organs opening in a pouch on each coxopleuron. South Andes. A single species, *K. brattstroemi* Chamberlin, 1955.

*Kurdistanius* Verhoeff, 1941. – Body length ca 7 cm. About 63 pairs of legs. Sternal pores in a posterior transverse band. Coxal pores grouped along the lateral margins of the metasternite. Kurdistan. A single species, *K. kosswigii* Verhoeff, 1941.

*Lionyx* Chamberlin, 1960. – Body length 2-3 cm. About 49 pairs of legs. Labral margin with bristles, without tubercles. Each forcipular tarsungulum with a small basal denticle. No sternal pores. Coxal organs opening through distinct pores. California. A single species, *L. hedgpethi* Chamberlin, 1960.

*Maoriella* Attems, 1903. – Body length 3-9 cm. 41-91 pairs of legs. Head and forcipules very elongate. Coxosternite of second maxillae divided mid-longitudinally, without sclerotized ridges. Sternal pores in two pairs of groups. Coxal organs opening in pits close to metasternite. New Zealand; also recorded in Australia and Tahiti. Half a dozen species, incl. *M. ecdema* Crabbill, 1964

(forcipules with long denticles; Chatham island), *M. macrostigma* Attems, 1903 (forcipules with short denticles; New Zealand).

*Mixophilus* Silvestri, 1929. – Body length ca 2 cm. 55-57 pairs of legs. Forcipules short. Trunk metasternites with a posterior transverse band of pores. Coxal organs opening in a single ventral pit on each coxopleuron. Estuarine sediments in the Indian peninsula. A single species, *M. indicus* Silvestri, 1929.

*Nabocodes* Chamberlin, 1940. – Body length ca 2 cm. About 49 pairs of legs. Coxosternite of second maxillae with sclerotized ridges. Forcipules elongate and with conspicuous denticles. No sternal pores. Coxal pores close to metasternite. Ultimate legs without claw. Isthmus of Panama. A single species, *N. mimellus* Chamberlin, 1940.

*Navajona* Chamberlin, 1930. – Body length ca 3 cm. About 51 pairs of legs. Head and forcipules elongate. Lateral parts of labrum almost touching medially. Second maxillae with sclerotised ridges. No sternal pores. Most coxal pores close to metasternite. Ultimate legs of male swollen, with a single tarsal article, without claw. Arizona. A single species, *N. miuropus* Chamberlin, 1930.

*Nesomerium* Chamberlin, 1953. – Body length 4-5 cm. About 69 pairs of legs. Lateral parts of labrum almost touching medially. Mandibles apparently with more than one pectinate lamella. Forcipules elongate, with denticles. Sternal pores in a posterior transverse band. Each coxopleuron with a single ventral pore. Ultimate legs without claw. Hawaii Islands. A single species, *N. hawaiiense* Chamberlin, 1953.

*Nicopus* Attems, 1947. – Body length ca 4 cm. About 69 pairs of legs. Head elongate. Intermediate part of labrum inconspicuous. Forcipules with tubercles. No sternal pores. Coxal pores scattered. Chile. A single species, *N. chilensis* Attems, 1947.

*Nothogeophilus* Lewis, Jones & Keay, 1988. – Body length ca 1 cm. 37-39 pairs of legs. Forcipular coxosternite remarkably elongate. Anterior trunk metasternites with a posterior transverse pore-field. Coxal organs opening through grouped pores or in a single ventral pit on each coxopleuron. Islands off the south coast of Great Britain. A single species, *N. turki* Lewis, Jones & Keay, 1988.

*Oligna* Chamberlin, 1943. – Body length ca 3 cm. About 45 pairs of legs. Labral margin fringed with bristles only. Forcipules without denticles. No sternal pores. Coxal organs opening in two ventral pits on each coxopleuron. Ultimate legs without claw. Central highland of Mexico. A single species, *O. pueblana* Chamberlin, 1943.

*Orinomerium* Chamberlin, 1955. – Body length ca 4 cm. About 49 pairs of legs. Forcipules elongate, with denticles. Anterior metasternite with a transversally elliptical pore-field. Coxal organs opening in a ventral pit on each coxopleuron. South Andes. A single species, *O. andes* Chamberlin, 1955.

*Pachymerellus* Chamberlin, 1920. – Body length 3-4 cm. About 55 pairs of legs. Claws of second maxillae with small filaments. Forcipular coxosternite and tarsungula with small denticles. No sternal pores. Coxal pores scattered. Tasmania. A single species, *P. zygethus* Chamberlin, 1920.

*Pachymerinus* Silvestri, 1905. – Body length 3-8 cm. 47-81 pairs of legs. Head elongate. Intermediate part of labrum narrow, without denticles. Forcipules elongate, with denticles. Sternal pores few or absent. Coxal pores scattered. Chile and south-east Australia. Half a dozen species, incl. *P. froggatti* Brölemann, 1912 (forcipules with an additional basal denticle; south-east Australia), *P. millepunctatus* (Gervais, 1847) (surface evidently punctuated, claws of second maxillae small, metasternite of ultimate leg-bearing segment very small; central Chile).

*Pachymerium* C.L. Koch, 1847. – Body length 2-8 cm. 37-79 pairs of legs. Head elongate. Forcipular coxosternite broad, tarsungula with a conspicuous basal denticle. Sternal pores in a pair of anterior groups and a posterior transverse band. Coxal pores scattered. Mainly west Palearctic and south Africa. A dozen species, incl. *P. ferrugineum* (C.L. Koch, 1835) (less than 60 leg pairs; west

Palaearctic, often introduced throughout the world), *P. grandiceps* (Porat, 1893) (large size, more than 70 leg pairs; Cape region).

*Pagotaenia* Chamberlin, 1915. – Body length ca 2 cm. About 43 pairs of legs. Forcipules elongate, without denticles. Sternal pores in a transverse band. Coxal organs opening in two ventral pits on each coxopleuron. Male ultimate legs swollen, without claw. Central highlands of Mexico. A single species, *P. lestes* Chamberlin, 1915.

*Pandineum* Chamberlin, 1955. – Body length 3-5 cm. 45-73 pairs of legs. Intermediate part of labrum inconspicuous, lateral parts almost touching medially. Forcipules elongate, with denticles. No sternal pores. Most coxal pores close to metasternite. Atlantic coastal regions of South America. 10 species, incl. *P. pauronyx* Chamberlin, 1955 (a tubercle at the tip of the ultimate legs; Chiloé island).

*Peruphilus* Chamberlin, 1944. – Body length ca 1.5 cm. About 43 pairs of legs. Head and forcipules elongate. Anterior trunk metasternites with an anterior medial socket, and with pores in a posterior transverse band. Coxopleura with scattered pores. Peruvian Andes. A single species, *P. sanborni* Chamberlin, 1944.

*Photophilus* Folkmanová, 1928. – Body length 2-3 cm. 49-53 pairs of legs. Forcipules without denticles. Anterior trunk metasternites with an anterior medial socket, and a posterior transverse band of pores. Ultimate leg-bearing segment with metasternite wide, few pores on each coxopleuron, male legs swollen. Bohemia. A single species, *P. griseus* Folkmanová, 1928.

*Piestophilus* Cook, 1896. – Body length 1-4 cm. 45-85 pairs of legs. Forcipules short, without denticles. Trunk metasternites with an anterior medial socket and pores in a posterior transverse band. Coxal organs opening in two ventral pits on each coxopleuron. Ultimate legs strongly swollen, but the second tarsal article abruptly slender, at least in males. Caribbean region. Three species, incl. *P. neopus* (Cook, 1899) (small size, about 50 leg pairs; south Florida and Cuba), *P. tenuitarsis* (Pocock, 1888) (large size, about 85 leg pairs; Lesser Antilles).

*Plateurytion* Attems, 1909. – Body length 2-6 cm. 39-89 pairs of legs. Head and forcipules elongate. Coxosternite of second maxillae divided mid-longitudinally, the metamerous pores with sclerotized rims. Anterior trunk metasternites with a subcircular or slightly transversally elongate pore-field. Temperate part of South America and south Africa. More than 20 species, incl. *P. dudichii* (Verhoeff, 1940) (South Africa), *P. lethifer* (Crabill, 1968) (coxal organs opening in ventral pits; Peruvian Andes), *P. michaelseni* (Attems, 1903) (coxal organs opening in distinct pores close to metasternite; central Chile), *P. paucipes* (Lawrence, 1955) (small size; south Africa), *P. sabulosus* (Attems, 1909) (large size; south Africa).

*Pleurogeophilus* Verhoeff, 1901. – Body length 2-11 cm. 47-89 pairs of legs. Intermediate part of labrum fringed mainly by bristles. Forcipules short, without denticles. Sternal pores usually in a posterior subcircular field. Coxal pores scattered. Ultimate legs elongate, without claw. Some Palaearctic areas, from Mediterranean region to Japan, and east tropical Africa. A dozen species, incl. *P. mediterraneus* (Meinert, 1870) (sternal pore-fields small; NW Africa and South Europe).

*Poaphilus* Chamberlin, 1912. – Body length less than 1 cm. About 37 pairs of legs. Forcipules elongate and with denticles. A few coxal pores, close to metasternite. Internal part of North America. A single species, *P. kewinus* Chamberlin, 1912.

*Polycricus* Saussure & Humbert, 1872. – Body length 2-5 cm. 43-79 pairs of legs. Head and forcipules elongate. Coxosternite of second maxillae divided mid-longitudinally, with sclerotized ridges. Sternal pores in two anterior paired groups and a posterior area. Coxal pores scattered. Ultimate legs without claw. Central America. More than 15 species, incl. *P. brachyceps* Chamberlin, 1944 (head moderately elongate; Mexican highlands), *P. nesiotes* (Chamberlin, 1915) (more than 70 leg pairs; Hispaniola), *P. toltecus* (Saussure & Humbert, 1872) (head very elongate, around 50 leg pairs; Mexican highlands).

*Polygonarea* Attems, 1909. – Body length 3-6 cm. 45-67 pairs of legs. Head elongate. Forcipular coxosternite broad, forcipules elongate with a conspicuous basal denticle on the tarsungulum. Sternal pores in a transverse posterior band and a pair of anterior areas. Coxal organs opening close to metasternite. Southernmost Africa. About 15 species, incl. *P. oligopus* Attems, 1909 (Cape region to Natal), *P. robusta* Lawrence, 1955 (large size; Cape region), *P. zambesia* Lawrence, 1963 (Mozambique).

*Porethus* Chamberlin, 1952. – Body length ca 2 cm. 43-63 pairs of legs. Forcipular coxosternite broad. Coxal pores scattered. Anatolian peninsula. Three species, incl. *P. pauciporus* Chamberlin, 1952 (sternal pore-fields transversally elongate; west and south Anatolia).

*Portoricona* Chamberlin, 1950. – Body length ca 2 cm. 39-53 pairs of legs. Labral margin convex, fringed by tubercles. Forcipules elongate, with a large tubercle at the base of each tarsungulum. No sternal pores. Coxal pores scattered. Puerto Rico. Two species, incl. *P. adjunta* Chamberlin, 1950 (about 40 leg pairs; Puerto Rico).

*Proschizotaenia* Silvestri, 1907. – Body length ca 1 cm. 43-45 pairs of legs. Head and forcipules elongate. Coxosternite of second maxillae with sclerotized ridges and peculiar anterior projections. Sternal pores in a subcircular field. Coxal pores close to metasternite. A tubercle with a small spine at the tip of the ultimate legs. Usambara Mountains, Tanzania. A single species, *P. mediocris* Silvestri, 1907.

*Purcellinus* Attems, 1926. – Body length ca 3 cm. 39-41 pairs of legs. Head and forcipules elongate. Sternal pores in a posterior transverse band. Coxal pores scattered. Cape region. A single species, *P. robustus* Attems, 1926.

*Queenslandophilus* Verhoeff, 1925. – Body length 2-6 cm. 37-75 pairs of legs. Lateral parts of labrum almost touching medially. Second maxillae with sclerotized ridges on the coxosternite. No sternal pores. Coxopleura with many, scattered pores. Ultimate legs most often with claw. East Australia, Japanese archipelago, west part of North America. A few species, incl. *Q. elongatus* Verhoeff, 1938 (more than 70 leg pairs, ultimate legs without claw; California), *Q. sjoestedti* Verhoeff, 1925 (medium size; east Australia).

*Ribautia* Brölemann, 1909. – Body length 1-7 cm. 31-125 pairs of legs. Head and forcipules elongate. Mandibles with long bristles. Coxosternite of second maxillae with sclerotized ridges and peculiar anterior projections. Sternal pores in a single or two paired fields. Coxal pores most often close to metasternite. South America, tropical Africa, Madagascar, south Arabian peninsula, Australia, New Zealand, Melanesian islands. More than 40 species, incl. *R. bouvieri* Brölemann, 1909 (coxal pores distinct, ultimate legs without claw; north Brazil), *R. colcabensis* Kraus, 1957 (Peruvian Andes), *R. conifera* (Attems, 1911) (large size, forcipules with strong denticles, coxal organs opening in a few pits; Australia), *R. ducalis* Pereira, Minelli & Barbieri, 1995 (ultimate legs with an apical spine; Amazonas), *R. taeniata* Ribaut, 1923 (forcipules with a hook-like denticle, more than a hundred leg pairs; New Caledonia).

*Schendyloides* Attems, 1897. – Body length 1-2 cm. 33-53 pairs of legs. Second maxillary claws long and slender. Forcipules elongate, with denticles. Anterior trunk metasternites with pores in a posterior transverse area. Coxal pores close to metasternite. Southernmost part of South America. Two species, incl. *S. psilopus* (Attems, 1897) (more than 40 pairs of legs; from Patagonia to Tierra del Fuego).

*Schizonampa* Chamberlin, 1914. – Body length 1-2 cm. 37-53 pairs of legs. Head and forcipules elongate. Telopodites of second maxillae with lateral projections. No sternal pores. Coxal organs opening on two ventral pits on each coxopleron. A spinous tubercle on the tip of the ultimate legs. Tropical regions of South America and Africa. A few species, incl. *S. manni* Chamberlin, 1914 (Brazil).

*Schizonium* Chamberlin, 1955. – Body length 2-3 cm. 33-61 pairs of legs. Coxosternite of second maxillae divided mid-longitudinally. Forcipules elongate, with denticles. No sternal pores. Coxal pores close to metasternite. Ultimate legs without claw. Central and south Andes. Half a dozen species, incl. *S. talcanum* Chamberlin, 1955 (more than 50 pairs of legs; Chilean Andes).

*Schizotaenia* Cook, 1896. – Body length 1-3 cm. 41-59 pairs of legs. Head and forcipules elongate. Second maxillae with sclerotised ridges. No sternal pores. Coxopleura with few pores, close to metasternite. A spinous tubercle at the tip of the ultimate legs. Tropical Africa. Half a dozen species, incl. *S. prognatha* Cook, 1896 (small size; west Africa).

*Sepedonophilus* Attems, 1909. – Body length 2-5 cm. 49-79 pairs of legs. Lateral parts of labrum almost touching medially, the intermediate part inconspicuous. Coxosternite of second maxillae with peculiar anterior projections, the claws stout. No sternal pores. Coxal pores scattered. Australia. A few species, incl. *S. perforatus* (Haase, 1887) (more than 70 leg pairs; east Australia).

*Serrona* Chamberlin, 1941. – Body length unknown. About 63 pairs of legs. Forcipules with only a denticle at the base of each tarsungulum. No sternal pores. Coxal organs opening in two ventral pores on each coxopleuron. California. A single species, *S. kernensis* Chamberlin, 1941.

*Sogona* Chamberlin, 1912. – Body length 1-5 cm. 41-75 pairs of legs. Labrum not distinctly tripartite, fringed by bristles. Forcipules short, without denticles. Sternal pores in a posterior transverse band and two paired anterior groups. Coxal organs opening in two ventral pits on each coxopleuron. Pretarsi of ultimate legs usually bearing many small spines. South part of North America to Central America. More than a dozen species, incl. *S. poretha* Chamberlin, 1918 (large size, ultimate legs with a spinous tubercle; Gulf Coastal Plain), *S. vera* Chamberlin, 1943 (small size, ultimate legs with a spinous claw; Mexican highlands).

*Steneurytion* Attems, 1909. – Body length 2-4 cm. 37-53 pairs of legs. Head and forcipules elongate. Lateral parts of labrum almost touching medially. Second maxillae with sclerotized rims surrounding the metamerid pores, claws particularly elongate. No sternal pores. Ultimate leg-bearing segment with narrow metasternite and scattered coxal pores. Australia, Tasmania, New Zealand and Hawaii islands. Five species, incl. *S. antipodum* (Pocock, 1891) (ca 40 leg pairs; New Zealand and Tasmania), *S. incisunguis* (Attems, 1911) (ca 50 leg pairs; west Australia).

*Stenotaenia* C.L. Koch, 1847. – Body length 1-8 cm. 43-115 pairs of legs. Labral margin fringed mainly with bristles. Forcipules very short, without denticles, intermediate articles sometimes inconspicuous. Sternal pores in a posterior ovate field. Coxal organs opening in a few ventral pits. Central-east Mediterranean region. A dozen species, incl. *S. linearis* (C.L. Koch, 1835) (medium size; central Europe), *S. romana* (Silvestri, 1895) (small size, possibly paedomorphic; Italian peninsula and Sardinia), *S. sturanyi* (Attems, 1903) (about one hundred pairs of legs; Macedonia and Crete).

*Synerium* Chamberlin, 1955. – Body length ca 4 cm. About 57 pairs of legs. Forcipules with denticles. Anterior trunk metasternites with a subcircular pore-field. Coxal organs opening in a ventral pit on each coxopleuron. South Andes. A single species, *S. nubile* Chamberlin, 1955.

*Synthophilus* Chamberlin, 1946. – Body length ca 2 cm. 45-47 pairs of legs. Forcipular coxosternite without distinct sclerotized lines. Forcipules with a basal denticle on each tarsungulum. No sternal pores. Coxal pores scattered. Alaska. A single species, *S. boreus* Chamberlin, 1946.

*Taiyuna* Chamberlin, 1912. – Body length 1-7 cm. 41-87 pairs of legs. Head and forcipules elongate. Trunk metasternites with an anterior medial socket, without pores. Ultimate leg-bearing segment with narrow metasternite, coxal pores ventral, and most often without claw. Mainly North America, also South America. Half a dozen species, incl. *T. idahoana* Chamberlin, 1941 (head wider anteriorly, ultimate legs with claw; Idaho), *T. occidentalis* (Meinert, 1886) (large size, coxal pores including an isolated posterior pore; California).

*Tampiya* Chamberlin, 1912. – About 125 pairs of legs. Forcipular coxosternite with a pair of anterior denticles. Coxal pores scattered. California's Coastal Mountains. Only one species, *T. pylorus* Chamberlin, 1912.

*Taschkentia* Verhoeff, 1930. – Body length 4-7 cm. 59-69 pairs of legs. Forcipular tarsungula with a basal small denticle. Sternal pores apparently in two anterior pairs of groups and a posterior transverse band. Coxal pores scattered. Central Asia. Two species, incl. *T. parthorum* (Pocock, 1891) (Alay Mountains, central Asia).

*Tasmanophilus* Chamberlin, 1920. – Body length 2-5 cm. 39-69 pairs of legs. Claws of second maxillae with small filaments. Forcipular coxosternite broad; forcipules short, with denticles. Anterior trunk metasternites with a peculiar medial depression and pores arranged into an anterior pair of groups and a posterior transverse band. Coxal pores scattered. Female gonopods distinct and biarticulate. Australia, New Zealand. A few species, incl. *T. opinatus* (Newport, 1845) (more than 50 pairs of legs; Tasmania and mainland Australia).

*Telocricus* Chamberlin, 1915. – Body length 3-8 cm. 47-113 pairs of legs. Head and forcipules elongate. Sternal pores in two pairs of groups. Ultimate leg-bearing segment with narrow metasternite. Scattered coxal pores. Ultimate legs without claw. Central America. A dozen species, incl. *T. cubae* Chamberlin, 1915 (coxopleura and ultimate metatergite very elongate; Cuba), *T. multipes* Chamberlin, 1915 (more than a hundred leg pairs; Hispaniola).

*Timpina* Chamberlin, 1912. – Body length ca 5 cm. Number of leg pairs unknown. Labrum not distinctly tripartite. Forcipules without denticles. Sternal pores in a posterior transverse band. Coxal organs opening in a single ventral pit on each coxopleuron. Ultimate legs with a single tarsal article, without claw. Texas. A single species, *T. texana* Chamberlin, 1912.

*Tuoba* Chamberlin, 1920. – Body length 2-5 cm. 39-73 pairs of legs. Forcipules short, with a denticle at the base of each tarsungulum. Anterior trunk metasternites with an anterior medial socket and a posterior transverse band of pores. Leg claws with a particularly elongate basal spine. Coxal organs opening in a single ventral pit on each coxopleuron. Coastal regions and islands in the Atlantic, Mediterranean, Indian and Pacific oceans; mainly littoral sites. About 15 species, incl. *Tuoba poseidonis* (Verhoeff, 1901) (Mediterranean basin), *Tuoba sydneyensis* (Pocock, 1891) (small size; from Australia to Hawaii islands), *Tuoba xylophaga* (Attems, 1903) (large size; New Zealand).

*Tylonyx* Cook, 1899. – Body length unknown. About 47 pairs of legs. Each coxopleuron with two pores. A spinous tubercle at the tip of the ultimate legs. Florida. A single species, *T. tampae* Cook 1899.

*Watophilus* Chamberlin, 1912. – Body length 1-5 cm. 41-81 pairs of legs. Head and forcipules elongate. Coxosternite of second maxillae with sclerotised ridges. No sternal pores. Coxopleura with scattered, ventral pores. A spinous tubercle on the tip of the ultimate legs. South part of North America. Half a dozen species, incl. *W. alabamae* Chamberlin, 1912 (telopodites of second maxillae with projections; Gulf Coastal Plain), *W. errans* Chamberlin, 1912 (small size; California).

*Zelanoides* Chamberlin, 1920. – Body length 2-4 cm. About 33-41 pairs of legs. Head and forcipules elongate. Claws of second maxillae particularly elongate. No sternal pores. Ultimate leg-bearing segment with metasternite wide and coxal pores close to the metasternite. Tasmania, New Zealand, possibly also Australia. A single species, *Z. similis* (Chamberlin, 1920) (New Zealand).

*Zelanophilus* Chamberlin, 1920. – Body length 4-7 cm. 59-77 pairs of legs. Lateral parts of labrum almost touching medially, the intermediate part inconspicuous. Claws of second maxillae with small filaments. Forcipules without denticles. Anterior trunk metasternites with a single, posterior pore-field. Coxopleura with many, scattered pores. Female gonopods distinct and biarticulate. New Zealand and south-east Australia. Two species, incl. *Z. provocator* (Pocock, 1891) (most posterior trunk metasternites densely setose, ultimate leg-bearing segment very elongate; New Zealand).

*Zygonia* Chamberlin, 1960. – Body length ca 3 cm. About 53 pairs of legs. Head elongate. Forcipules without denticles. No sternal pores. Coxal organs opening in two ventral pits on each coxopleuron. Arizona. A single species, *Z. duplex* Chamberlin, 1960.

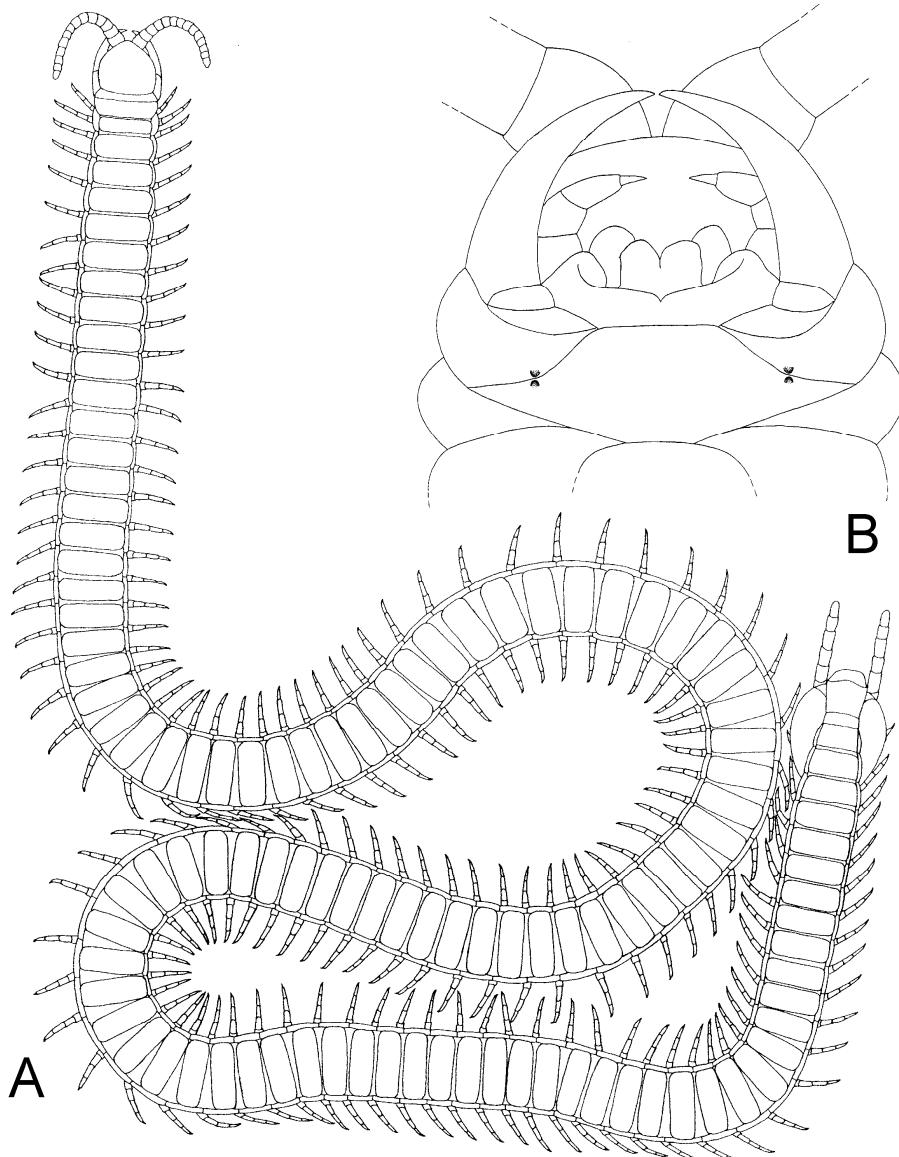


Fig. 19.20 *Gonibregmatus anguinus* (Geophilomorpha, Gonibregmatidae). A Habitus, dorsal view. B Anterior part of the body, ventral view. Original E. Zampogno.

Family GONIBREGMATIDAE Cook, 1896 (Fig. 19.20). – Head short. Labral margin usually fringed by bristles or denticles. Mandibles with a single row of many short teeth. Claws of second maxillae usually with small filaments. Forcipular coxosternite short. Forcipules without denticles, the tarsungula relatively elongate. Number of leg-bearing segments variable within each species, the overall range 57-191. Sternal pores usually in a posterior transverse band and smaller anterior groups. Coxopleura with several pores scattered. Ultimate legs usually with two tarsal articles and without claw. Madagascar, Indian peninsula, south-east Asia, Australasia and west Pacific islands. Ca 15 species in about eight genera.

*Gonibregmatus* Newport, 1843. – Body length 10-15 cm. 99-191 pairs of legs. Labral margin convex, fringed by bristles. First maxillae with uniarticulate telopodites. Claws of second maxillae without filaments. Additional sclerites flanking trunk tergites. Sternal pores in two transverse bands. Coxopleura remarkably expanded. From Philippines and Malay archipelago to Fiji islands. Half a dozen species, incl. *G. anginus* Pocock, 1898 (about 130 pairs of legs; New Guinea, New Britain and nearby islands, *G. plurimipes* Chamberlin, 1920. (Fiji Islands)).

*Australiophilus* Verhoeff, 1925. – Body length 7-12 cm. 109-117 pairs of legs. Labral lateral parts with dense bristles. Pretarsi of the ultimate legs reduced. East Australia and New Zealand. Two species, incl. *A. longissimus* Verhoeff, 1925 (east Australia).

*Disargus* Cook, 1896. – Body length ca 4 cm. About 69 pairs of legs. Sternal pores in an anterior medial field and a posterior band. Female gonopods distinct and biarticulate. Ultimate legs with a single tarsal article, with claw. Indian peninsula. A single species, *D. striatus* (Pocock, 1890).

*Eucratonyx* Pocock, 1898. – Body length 8-13 cm. 103-129 pairs of legs. Labral margin concave, fringed by denticles. Sternal pores in two anterior paired groups and a posterior band. Claws of some anterior legs enlarged, with a basal branch very elongate. Female gonopods coalescent. From Andamans to New Britain. Two species, incl. *E. meinerti* (Pocock, 1889) (coxopleura remarkably elongate; Indochinese peninsula).

*Geoporophilus* Silvestri, 1919. – Body length 5-6 cm. About 107 pairs of legs. Forcipular coxosternite with a pair of anterior denticles. Anterior trunk metasternites with paired pore-fields. Ultimate legs with scattered ventral pores. Sumatra. A single species, *G. angustus* Silvestri, 1919.

*Himantosoma* Pocock, 1891. – Body length 2-7 cm. 57-81 pairs of legs. Labral margin concave, fringed by bristles. Sternal pores in an anterior medial field and a posterior band. Female gonopods distinct and biarticulate. Ultimate legs with claw. From Indian peninsula to Great Sunda. A few species, incl. *H. typicum* (Pocock, 1891) (large size, forcipular tarsungula quite straight; Mergui islands).

*Madageophilus* Lawrence, 1960. – Body length ca 3 cm. About 101 pairs of legs. Labral margin concave, with tubercles and bristles. Sternal pores in an anterior medial field and a posterior band. Ultimate legs with claw. Madagascar. A single species, *M. pauliani* Lawrence, 1960.

*Sogophagus* Chamberlin, 1912. – Body length ca 9 cm. 131-135 pairs of legs. Labrum without projections. Halmahera. A single species, *S. serangodes* (Attems, 1897).

Family HIMANTARIIDAE Bollman, 1893 (Fig. 19.21). – Head short and antennae usually stout. Labral margin medially concave, bearing a row of denticles. Each mandible with a single, entire dentate lamella and some pectinate lamellae. Telopodites of second maxillae strongly tapering, the claws slightly spatulate. Forcipular segment very stout,

with coxosternite and forcipules very short, pleurites displaced on the ventral side, and tergite very wide. Number of leg-bearing segments variable within each species, the overall range 47-181. Sternal pores usually present, a single field on each metasternite. Coxal organs opening either through scattered pores or inside pouches close to the relevant metatergite or metasternite. Ultimate legs usually without pretarsus. Female gonopods distinct and biarticulate. Mainly from west part of North America to central Mexico, and from Macaronesia through the Mediterranean region and central Asia to Indian peninsula; also in the Korean peninsula and Japanese islands. Ca 70 species in ca 19 genera.

*Himantarium* C.L. Koch, 1847. – Body length 10-20 cm. 87-179 pairs of legs. Trunk swollen, posteriorly stout. Each mandible with a robust dentate lamella and few pectinate lamellae. Sternal pore-fields on almost all trunk segments, subcircular. Coxopleura much inflated, completely covered with scattered pores. Metasternite of the ultimate leg-bearing segment very small. Most Mediterranean region; mainly in arid substrates with open vegetation. A few species, incl. *H. gabrielis* (Linnaeus, 1767) (south Europe and north-west Africa).

*Arcophilus* Chamberlin, 1943. – Body length ca 2 cm. About 61 pairs of legs. Sternal pore-fields transversally elongate. Coxal pores scattered on the whole surface of the coxopleura. Ultimate legs swollen in males. Central Mexico, at high altitude. A single species, *A. toltecus* Chamberlin, 1943.

*Bothriogaster* Sselwanoff, 1879. – Body length ca 7-14 cm. 85-129 pairs of legs. Coxosternite of second maxillae expanded anteriorly. Peculiar horseshoe-shaped depressions on some anterior trunk metasternites. Coxal organs opening inside a dorsal and a ventral pouch. From east Mediterranean region to central Asia. Possibly, a single species, *B. signata* (Kessler, 1874).

*Californiphilus* Verhoeff, 1938. – Body length 5-6 cm. 67-135 pairs of legs. Coxosternite of second maxillae anteriorly notched. Trunk without additional sclerites flanking tergites, and sternal pore-fields on almost all segments. Coxal organs opening inside a dorsal and usually two ventral pouches. Metasternite of the ultimate leg-bearing segment trapezoid, the posterior margin distinctly concave. South-west part of North America and Japanese region. Three species, incl. *C. japonicus* (Takakuwa, 1935) (lateral furrows on some trunk metasternites; Korea and Japan).

*Chomatobius* Humbert & Saussure, 1870. – Body length 4-15 cm. 55-181 pairs of legs. Trunk with additional sclerites flanking tergites, and sternal pore-fields on almost all segments. Coxal organs opening inside a dorsal and a ventral pouch. Metasternite of the ultimate leg-bearing segment trapezoid, the posterior margin distinctly concave. South-west part of North America, south to central Mexico. Half a dozen species, incl. *C. laticeps* (Wood, 1862) (about 80 pairs of legs; south-west part of North America), *C. mexicanus* (Saussure, 1860) (about 120-130 pairs of legs; Mexican highlands).

*Diporocyclus* Attems, 1951. – Body length ca 6 cm. About 83 pairs of legs. Sternal pore-fields on almost all trunk segments, transversally strongly elongate. Coxal pores clustered in two groups on the ventral side of each coxopleuron. Iranian steppes. A single species, *D. deserticola* Attems, 1951.

*Empherozoster* Crabbill, 1959. – Body length ca 4 cm. About 63 pairs of legs. Sternal pore-fields on almost all trunk segments, transversally strongly elongate. Coxal organs opening inside a dorsal pouch and inside some ventral pits close to the metasternite; the latter particularly elongate. Anal pores present. New Mexico. A single species, *E. antaeus* Crabbill, 1959.

*Garriscaphus* Chamberlin, 1941. – Body length ca 2-3 cm. 47-55 pairs of legs. Forcipular sclerotized lines weakly visible. Coxal organs opening through distinct pores along the margins of

both metatergite and metasternite. California. A few species, incl. *G. oreines* Chamberlin, 1941 (small size; California).

*Geoballus* Crabbill, 1969. – Body length 4-5 cm. 61-91 pairs of legs. Coxosternite of second maxillae expanded anteriorly. Sternal pore-fields on almost all trunk segments, transversally strongly elongate. Coxal organs opening through distinct pores grouped along the margins of both metatergite and metasternite; the latter trapezoid, its posterior margin distinctly concave. South Mexico. Two species, incl. *G. caputalbus* Crabbill, 1969.

*Gosothrix* Chamberlin, 1923. – Body length ca 8-9 cm. About 159 pairs of legs. Trunk metasternites lacking pore-fields. Coxal pores grouped close to the metasternite. Ultimate legs bearing a well developed claw. Gulf of California. A single species, *G. insulanus* Chamberlin, 1923.

*Haplophilus* Cook, 1896. – Body length 7-18 cm. 69-165 pairs of legs. Trunk metasternites with pore-fields moderately elongate transversally, sometimes also with peculiar structural markings. Coxal pores scattered on the whole surface of the coxopleura. West Europe, north-west Africa and Macaronesia, in sub-mediterranean or sub-oceanic climate. A dozen species, incl. *H. dimidiatus* Meinert, 1870 (S Europe), *H. souletinus* Brölemann, 1907 (formerly in *Nesoporogaster* Verhoeff, 1924; peculiar posterior sockets on some trunk metasternites; west Europe), *H. subterraneus* (Shaw, 1794) (lateral furrows on some trunk metasternites; north-west Europe), *H. superbus* (Meinert, 1870) (large size; west Mediterranean region).

*Himantariella* Chalande & Ribaut, 1909. – Body length 8-18 cm. 113-169 pairs of legs. Mandibles with a relatively small dentate lamella and many pectinate lamellae. Sternal pore-fields on almost all segments, subcircular. Dense coxal pores scattered on the whole surface of the coxopleura, the latter remarkably inflated. West Mediterranean region. Three species, incl. *H. maroccana* Chalande & Ribaut, 1909 (Morocco).

*Mesocanthus* Meinert, 1870. – Body length 4-9 cm. 57-91 pairs of legs. Sternal pore-fields on almost all trunk segments, transversally elongate. Coxopleura poorly enlarged, without coxal organs. Males with swollen ultimate legs, usually with paired groups of spines on some posterior trunk metasternites. North Africa and south Asia from Iranian highlands to Indian peninsula; either in subdesertic or montane climate. Half a dozen species, incl. *M. albus* Meinert, 1870 (Saharan region), *M. brevis* Silvestri, 1919 (Indian peninsula).

*Nothobius* Cook, 1899. – Body length ca 10-15 cm. 119-169 pairs of legs. Sternal pore-fields on almost all trunk segments, only slightly transversally elongate. Coxal organs opening inside a dorsal and a ventral pouch. Ultimate legs with well developed claws. California. A single species, *N. californicus* Cook, 1899.

*Polyporogaster* Verhoeff, 1899. – Body length 5-10 cm. 67-99 pairs of legs. Sternal pore-fields on almost all trunk segments, transversally strongly elongate. Metasternite of the ultimate leg-bearing segment quadrangular. Coxopleura poorly inflated, coxal organs opening inside a dorsal pouch only. North-west Africa and montane regions in central Asia between Iran and Burma. Half a dozen species, incl. *P. indica* (Meinert, 1885) (Himalayas and surrounding areas), *P. tunetana* Verhoeff, 1899 (Atlas).

*Stenophilus* Chamberlin, 1946. – Body length 4-10 cm. 67-97 pairs of legs. Sternal pore-fields limited to anterior trunk or lacking at all. Coxal pores scattered on the whole surface of coxopleura. North America from Pacific coast to Great Plains. Half a dozen species, incl. *S. fieldsi* on the anterior part of trunk; northern Rocky Mountains).

*Stigmatogaster* Latzel, 1880. – Body length 5-10 cm. 83-111 pairs of legs. Trunk relatively slender. Sternal pore-fields on almost all trunk segments, transversally slightly elongate. Peculiar lateral furrows on some trunk metasternites. Most coxal organs opening inside a dorsal pouch covered by the metatergite. Central-west part of Mediterranean basin. A single species, *S. gracilis* (Meinert, 1870).

*Straberax* Crabbill, 1969. – Body length ca 6 cm. 77-97 pairs of legs. Forcipular trochanteroprefemora strongly sclerotized on their internal margin. Tracheal anastomoses between non-contiguous segments. Sternal pore-fields on almost all trunk segments, transversally elongate. Coxal organs opening inside a dorsal and a ventral pouch. Mexican highlands. A single species, *S. morelensis* Crabbill, 1969.

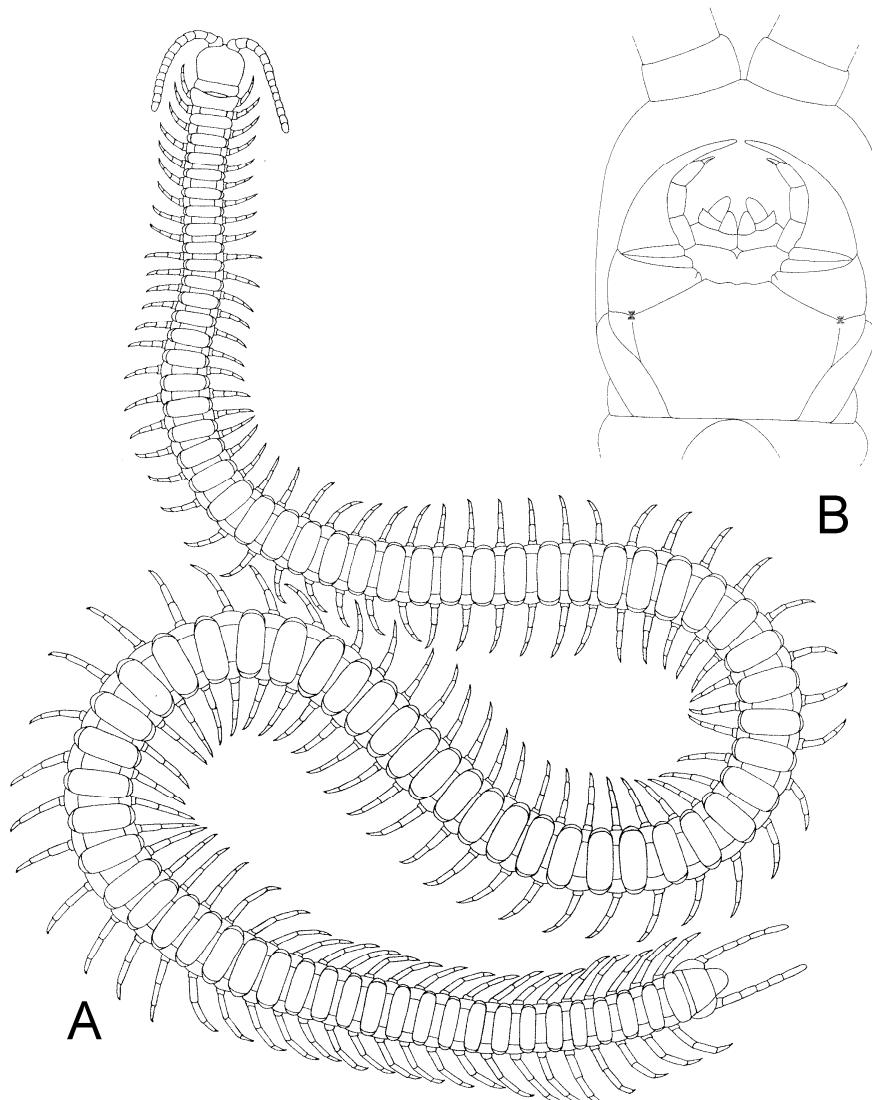


Fig. 19.21 *Stigmatogaster gracilis* (Geophilomorpha, Himantariidae). A Habitus, dorsal view. B Anterior part of the body, ventral view. Original E. Zamprogno.

*Thracophilus* Verhoeff, 1926. – Body length 3-9 cm. 71-103 pairs of legs. Forcipular tarsungula bearing a robust basal tooth. Coxal organs opening inside a ventral pouch, sometimes also inside a dorsal pouch. From west Mediterranean region to central Asia. Half a dozen species, incl. *T. bulgaricus* Verhoeff, 1926 (large size, both dorsal and ventral coxal pouches; montane forests in internal Balkan peninsula).

Family LINOTAENIIDAE Cook, 1899 (Fig. 19.22). – Body usually tapering towards the anterior tip, stout at the posterior tip. Head short, with slender antennae. Margin of the intermediate part of labrum often slightly projecting anteriorly and fringed by tubercles. Mandibles with a single pectinate lamella only. Second maxillae with coxosternite usually undivided and claws without projections. Forcipular segment short, with tergite remarkably wide, forcipules evidently tapering, tarsungula usually with a large tooth at the base. Number of leg-bearing segments variable within each species, the overall range 33-83. Sternal pores usually present, on the posterior part of each metasternite, as either an entire transverse band or two paired fields. Coxal organs opening through distinct pores on the ventral surface of the coxopleura. Ultimate legs shorter than the penultimate legs. Female gonopods an undivided lamina. Most part of the Holarctic, mainly in temperate regions; also south Andes. Ca 50 species in seven genera.

*Strigamia* Gray, 1843. – Body length 2-6 cm. 33-81 pairs of legs. Basal tooth of the forcipular tarsungula usually large. Sternal pores most often in two paired fields. Ultimate leg-bearing segment with metasternite usually narrow, and coxal pores quite scattered. Ultimate legs of males distinctly swollen, the claw sometimes very small. Temperate regions of the Holarctic. Ca 40 species, incl. *S. acuminata* (Leach, 1815) (trunk metasternites flat, metasternite of the ultimate leg-bearing segment narrow; forest soils of most Europe), *S. bothriopus* Wood, 1862 (around 50 pairs of legs; North America), *S. chionophila* Wood, 1862 (around 40 pairs of legs; sub-arctic and temperate regions of North America), *S. crassipes* (C.L. Koch, 1835) (trunk metasternites with sclerotized mid-longitudinal furrow, metasternite of the ultimate leg-bearing segment narrow; forest soils of most Europe), *S. hirsutipes* (Attems, 1927) (basal tooth of the forcipular tarsungula relatively small, ventral surface of the trunk densely setose, legs covered with long setae; Japanese archipelago), *S. maritima* (Leach, 1817) (ventral circular depressions along the trunk; seashores of northern Europe).

*Agathothus* Bollman, 1893. – Body length ca 5 cm. 77-83 pairs of legs. Forcipules without denticles. Ultimate leg-bearing segment with wide metasternite and coxal pores grouped close to it. South Appalachians. A single species, *A. gracilis* (Bollman, 1888).

*Araucania* Chamberlin, 1955. – Body length ca 3 cm. About 43 pairs of legs. Sternal pores in two paired groups. Coxal pores scattered on the ventral surface of coxopleura. South Andes. A single species, *A. araucanensis* (Silvestri, 1899).

*Damothus* Chamberlin, 1960. – Body length ca 1 cm. 37-39 pairs of legs. Two denticles at the base of each forcipular tarsungulum. Rocky Mountains. Two species, incl. *D. alastus* Crabill, 1962 (sternal pores in two paired fields, coxal pores scattered; Utah).

*Malochora* Chamberlin, 1941. – Body length ca 3 cm. About 63 pairs of legs. Second maxillae with coxosternite almost divided mid-longitudinally, and short claws. No sternal pores. Ultimate leg-bearing segment with metasternite very wide and coxal pores grouped along its lateral margins. California. A single species, *M. linsdalei* Chamberlin, 1941.

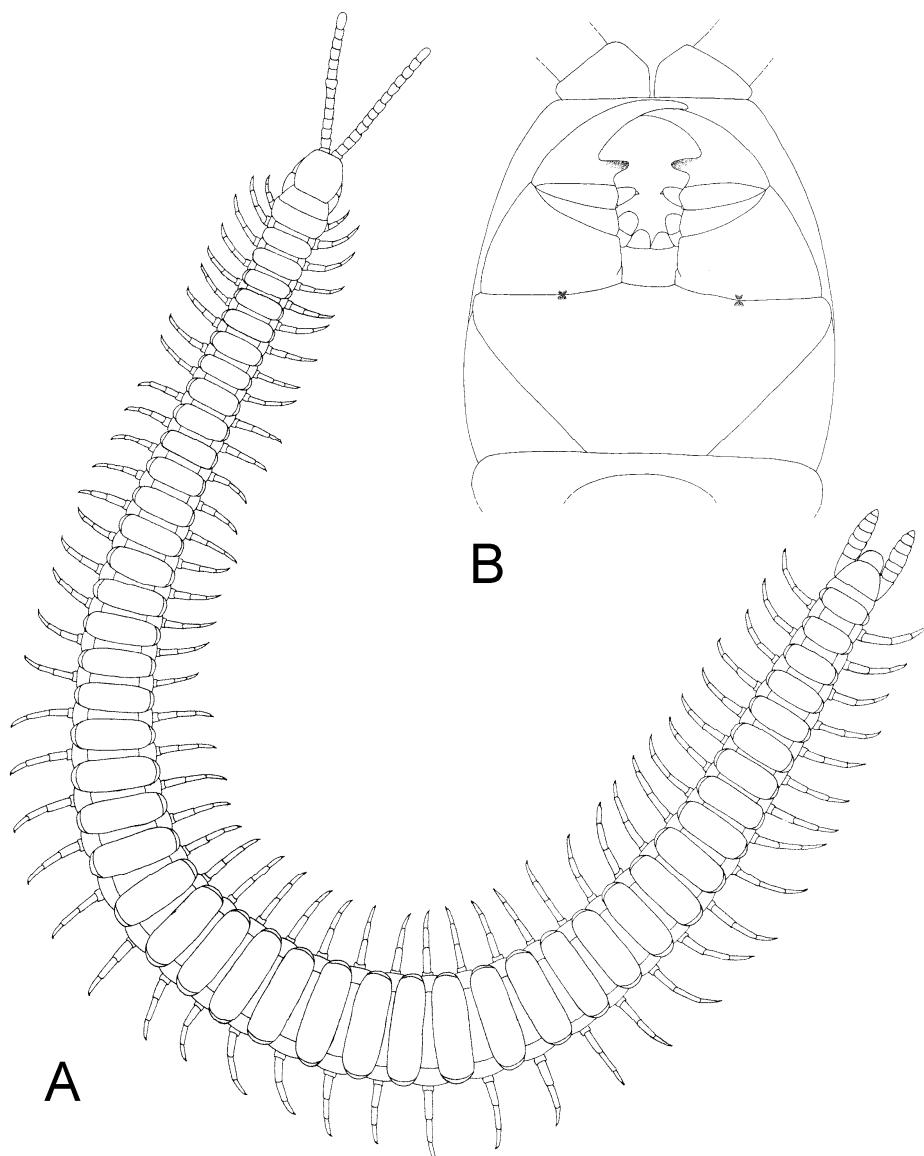


Fig. 19.22 *Strigamia crassipes* (Geophilomorpha, Linotaeniidae). A Habitus, dorsal view. B Anterior part of the body, ventral view. Original E. Zamprogno.

*Tomotaenia* Cook, 1895. – Body length 1-14 cm. 39-83 pairs of legs. Sternal pores in two paired fields. Ultimate leg-bearing segment with very wide metasternite and coxal pores grouped along

its lateral margins. West part of North America and east part of continental Asia. Ca 10 species, incl. *T. epileptica* (Wood, 1862) (large size, red color; west part of North America), *T. fusata* (Attems, 1903) (large size; California and Baja California peninsula), *T. svenhedini* (Verhoeff, 1933) (most coxal pores grouped but for a single isolated pore on each coxopleuron; highlands of China).

*Zantaenia* Chamberlin, 1960. – Body length 4-5 cm. 51-55 pairs of legs. Forcipules without denticles. Ultimate leg-bearing segment with metasternite narrow, coxal pores scattered, without claw in male. Rocky Mountains. A single species, *Z. idahona* Chamberlin 1960.

Family MACRONICOPHILIDAE Verhoeff, 1925 (Fig. 19.18B). – Head short and antennae slightly attenuated. Labrum composed of two distinct lateral parts, entirely fringed by bristles. Mandibles with a single row of many short teeth. Telopodites of second maxillae bearing a fourth additional article covered with small scales, without claw. Forcipular coxosternite and forcipules very short, without denticles, the tarsungula relatively elongate. Number of leg-bearing segments variable within each species. Sternal pores in a large posterior field. Coxopleura with scattered pores. Ultimate legs with a single tarsal article, with claw. Female gonopods uniarticulate. Northern Andes and Amazon basin. Four species in 1 genus.

*Macronicophilus* Silvestri, 1909. – Body length 1-3 cm. 39-61 pairs of legs. Northern Andes and Amazon basin; mainly humid forests. Four species, incl. *M. abbreviatus* Pereira, Foddai & Minelli, 2000 (about 40 pairs of legs; Amazon basin), *M. ortonedae* Silvestri, 1909 (about 60 pairs of legs; northern Andes), *M. unguiseta* Pereira, Foddai & Minelli, 2000 (terminal article of the telopodites of second maxillae particularly small; Amazon basin).

Family MECISTOCEPHALIDAE Bollman, 1893 (Fig. 19.23). – Cephalic shield and forcipular segment often obviously more sclerotized and darker than remaining body. Head elongate. Labrum composed of a narrow, pointed mid-piece, and two wide side-pieces, each of them crossed by a transverse sclerotized line. Mandibles with a series of pectinate lamellae only. Forcipular segment relatively large, with coxosternite very broad, pleurites displaced on the dorsal side flanking a narrow tergite, and forcipules elongate. Number of leg-bearing segments usually invariant within each species but variable between species, the overall range 41-101. Sternal pore-fields usually lacking. Coxopleura bearing tens of pores, scattered on most of their surface. Ultimate legs distinctly longer than the penultimate legs, slender in both sexes, without claw. Female gonopods distinct and biarticulate. Most tropical and subtropical lands, with highest diversity in east Asia, but also some boreal temperate regions. Ca 170 species in 11 genera.

*Mecistocephalus* Newport, 1843. – Body length 2-10 cm. Number of pairs of legs most often 45-51 and invariant within each species, but up to 101 and variable in a few species. Head, forcipular segment and their appendages often much elongate. A pair of sclerotized teeth projecting from the cephalic pleurites. Each forcipular trochanteroprefemur often bearing a pair of denticles, one proximal to the other. Most tropical and subtropical lands, mainly in south and east Asia; only localised in the Americas; also some temperate areas. From subdesertic sites to moist forests. Ca

140 species, incl. *M. diversisternus* (Silvestri, 1919) (variably 57 or 59 pairs of legs; Honshu to Taiwan), *M. insularis* (Lucas, 1863) (described from Réunion I.; distribution uncertain), *M. microporus* Haase, 1887 (large size, variably 93-101 pairs of legs; Philippines), *M. punctifrons* Newport, 1843 (variably melanised, invariably 49 pairs of legs; Indian peninsula), *M. spissus* Wood, 1862 (stout forcipules, invariably 45 pairs of legs; Hawaii islands), *M. tahitiensis* Wood, 1862 (invariably 47 pairs of legs; Australia and Pacific islands), *M. takakuwai* Verhoeff, 1934 (Japan, Taiwan), *M. togenensis* (Cook, 1896) (Africa).

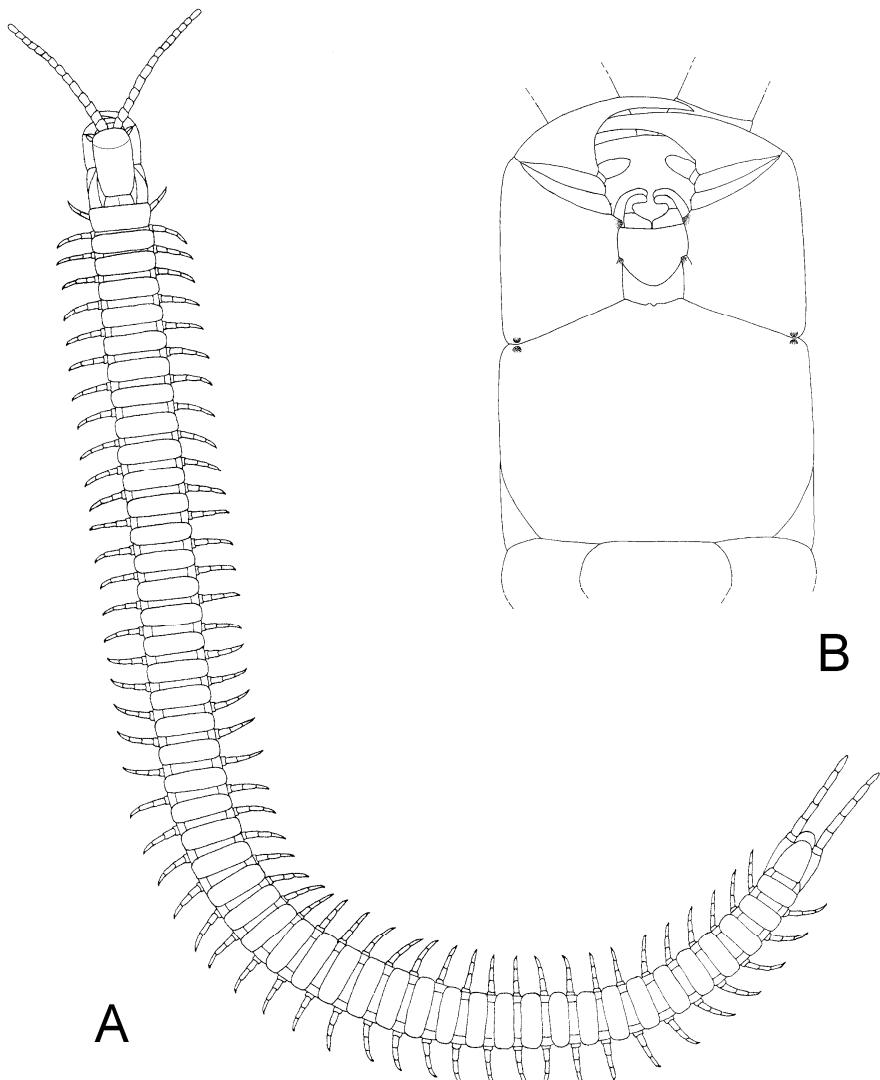


Fig. 19.23 *Mecistocephalus punctifrons* (Geophilomorpha, Mecistocephalidae). A Habitus, dorsal view. B Anterior part of the body, ventral view. Original E. Zamprogno.

*Agnostrup* Foddai, Bonato, Pereira & Minelli, 2003. – Body length 2-3 cm. Invariably 41 pairs of legs. Telopodites of second maxillae relatively small, without claw. Forcipular tarsungulum with a robust basal denticle. Temperate east Asia. Three species, incl. *A. paucipes* (Miyosi, 1955) (Honshu).

*Anarrup* Chamberlin, 1920. – Body length 6-8 cm. Invariably 41 pairs of legs. Clypeus with areolation and setae limited to a short anterior marginal band. Coxosternite of second maxillae divided mid-longitudinally, telopodites swollen and densely setose. Some islands in the Malay Archipelago. Two species, incl. *A. flavipes* (Attems, 1930) (Little Sunda islands).

*Arrup* Chamberlin, 1912. – Body length 1-5 cm. Invariably 41 pairs of legs. Head and forcipular segment poorly elongate. Clypeus almost completely areolate. Coxosternite of first maxillae entire. Telopodites of second maxillae relatively small. Poison glands of adult males often well deep inside the forcipules. Mainly temperate east Asia, but also disjunct regions in central Asia and south-west part of North America. A dozen species, incl. *A. dentatus* (Takakuwa, 1934) (claws on the second maxillae, peculiar pattern of forcipular denticles; Sikhote-Alin, Hokkaido, Kuril islands) and *A. sauteri* (Silvestri, 1919) (large size, forcipules almost without denticles; Taiwan).

*Dicellophilus* Cook, 1896. – Body length 5-7 cm. 41-45 pairs of legs, invariant within each species. Clypeus widely covered by scattered setae. Labrum with longitudinal folds and fringed by marginal bristles. A ventral coxal pore distinctly larger than all other pores. Ultimate legs bearing an apical tubercle covered with small spines. Highly disjunct distribution in central Europe, Honshu and south-west part of North America; mainly in mesophilous, montane forests. Four species, incl. *D. carniolensis* (C.L. Koch, 1847) (central Europe), *D. limatus* (Wood, 1862) (California).

*Krateraspis* Lignau, 1929. – Body length 5-6 cm. Either 45 or 53 pairs of legs. Clypeus with peculiar pattern of setae and areolation. Forcipules relatively stout. Central Asia between Turkestan and Tian Shan. Two species, incl. *K. meinerti* (Sselivanoff, 1881) (south-east Turkestan).

*Nannarrup* Foddai, Bonato, Pereira & Minelli, 2003. – Body length ca 1 cm. Invariably 41 pairs of legs. Coxal pores few, not reaching dorsal side of coxopleura. Recorded in New York only, probably introduced. A single species, *N. hoffmani* Foddai, Bonato, Pereira & Minelli, 2003.

*Partygarrupius* Verhoeff, 1939. – Body length ca 3 cm. Invariably 41 pairs of legs. Clypeal areolation limited to the anterior margin. Telopodites of second maxillae slender, provided with claw. Hokkaido. A single species, *P. moiwaensis* (Takakuwa, 1934).

*Proterotaiwanella* Bonato, Foddai & Minelli, 2002. – Body length ca 3 cm. Either 45 or 49 pairs of legs. Head relatively elongate. Labrum with peculiar marginal notches. Telopodites of second maxillae small, provided with claw. Ultimate legs bearing an apical tubercle covered with small spines. Ryukyu islands and Taiwan. Two species, incl. *P. tanabei* Bonato, Foddai & Minelli, 2002 (Ryukyu islands).

*Takashimaia* Miyosi, 1955. – Body length 2-5 cm. Invariably 45 pairs of legs. A pair of sclerotized teeth projecting from the cephalic pleurites. Telopodites of second maxillae slender, provided with claw. Forcipular tarsungulum bearing a robust tooth along its dorso-internal side. Japanese archipelago. A single species, *T. ramungula* Miyosi 1955.

*Tygarrup* Chamberlin, 1912. – Body length 2-6 cm. Invariably 45 pairs of legs in most species, 43 in an undescribed species. Sometimes patchily melanised. Sternal glands present in males of most species. Mainly south-east Asia, from Seychelles to Hawaii islands; from sea level to high montane forests. A dozen species, incl. *T. javanicus* Attems, 1929 (delicate; mainly Sunda islands), *T. nepalensis* Shinohara, 1965 (large size, melanised; Himalayas), *T. takarazimensis* Miyosi, 1957 (no sternal pores; a few Japanese islands).

Family NEOGEOPHILIDAE Silvestri, 1918 (Fig. 19.24). – Body slender, slightly tapering at both tips, Head short, with slender antennae. Labrum delicate, fringed by

short bristles. Each mandible with a single row of short teeth. First maxillae with coxosternite divided mid-longitudinally, bearing a single pair of stout uniarticulate appen-

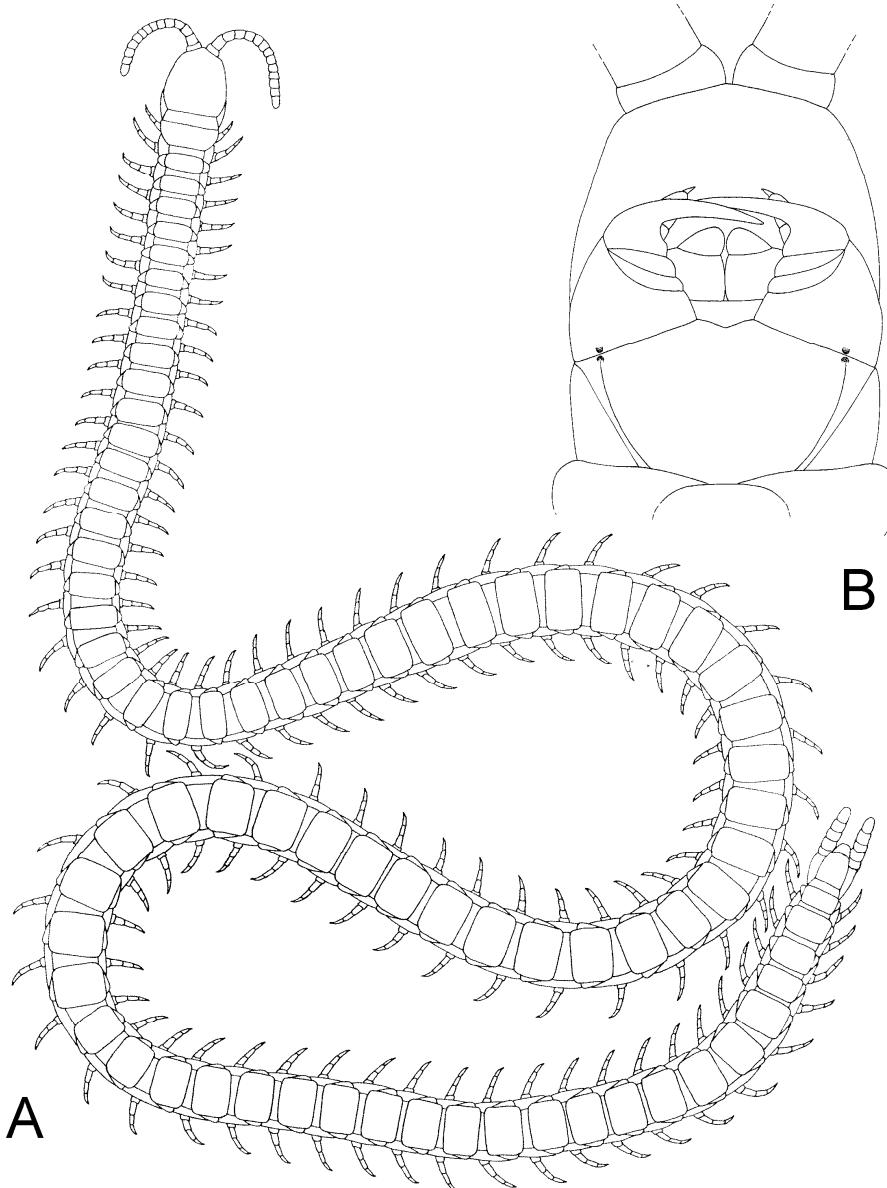


Fig. 19.24 *Neogeophilus primus* (Geophilomorpha, Neogeophilidae). A Habitus, dorsal view. B Anterior part of the body, ventral view. Original E. Zampogno.

dages. Claws of second maxillae with a few short marginal filaments. Forcipular coxosternite stout. Forcipules short, without denticles, the tarsungula flattened. Number of leg-bearing segments variable within each species, the overall range 63-81. Claws of some anterior legs enlarged, with an elongate basal branch. Coxal pores scattered. Ultimate legs swollen, with a single tarsal article in male, without pretarsus. Highlands of Central America. A total of four species in two genera.

*Neogeophilus* Silvestri, 1918. – Body length 3-4 cm. 69-81 pairs of legs. No sternal pores. Central Mexico to Guatemala, mainly in forests. Three species, incl. *N. ixion* Crabill, 1969 (enlarged claws with a basal small spine; Mexico), *N. primus* Silvestri, 1918 (enlarged claws with a rounded tubercle; Mexico).

*Evallogeophilus* Silvestri, 1918. – Body length ca 3 cm. 63-67 pairs of legs. Some most posterior leg-bearing segments with peculiarly enlarged pleurites, metasternites with scattered pores and coalescent with subcoxae. Central Mexico. A single species, *E. mexicanus* Silvestri, 1918.

Family ORYIDAE Cook, 1896 (Fig. 19.25). – Head short and antennae stout. Labral margin slightly concave to almost straight, bearing a row of denticles or bristles. Mandibles with a series of pectinate lamellae only. Telopodites of first maxillae usually uniarticulate. Claws of second maxillae often fringed by two rows of filaments. Forcipular segment stout, coxosternite and forcipules very short and without denticles, pleurites displaced on the ventral side, tergite very wide. Trunk tergites usually flanked by small additional sclerites. Number of leg-bearing segments variable within each species, the overall range 53-169. Sternal pores mainly clustered as two pairs of groups, variably coalescent into a quadrangular frame. Coxopleura poorly enlarged, most often without coxal organs. Ultimate legs usually without pretarsus. Female gonopods distinct, usually biarticulate. Tropical and sub-tropical Americas, Africa, Madagascar, south Asia, Australia and some Pacific islands. Ca 45 species in ca 18 genera.

*Orya* Meinert, 1870. – Body length 5-22 cm. About 81-125 pairs of legs. Claws of second maxillae without marginal filaments. Trunk segments with a peculiar pattern of pleurites. North-west Africa, also recorded from south Iberian peninsula. Three species, incl. *O. barbarica* (Gervais, 1835) (large size; mainly north-west Africa).

*Aspidopleres* Porat, 1893. – Body length 11-12 cm. 87-105 pairs of legs. Sternal pores in four broad groups on each metasternite. Ultimate legs very short. Female gonopods uniarticulate. South-west Africa. A single species, *A. intercalatus* (Porat, 1893).

*Chamberlinia* Machado, 1951. – Body length ca 10 cm. 67-113 pairs of legs. Angolan highlands. A single species, *C. lineata* Machado, 1951.

*Ctenorya* Cook, 1896. – Body length ca 9 cm. 111-115 pairs of legs. Telopodites of second maxillae geniculate. Ultimate legs very elongate. Female gonopods uniarticulate. East tropical Africa. Two species, incl. *C. sjostedti* Attems, 1909 (Tanzania).

*Diphtherogaster* Attems, 1909. – Body length ca 11 cm. 111-139 pairs of legs. Trunk metasternites with evidently areolate posterior areas. Ultimate legs with a single tarsal article. South-west Africa, in arid sites. A single species, *D. flava* Attems, 1909.

*Endoptelus* Chamberlin, 1939. – Body length 3-4 cm. About 79 pairs of legs. Peculiar processes basal to legs of the most posterior pairs. New Guinea. A single species, *E. papuicola* Chamberlin, 1939.

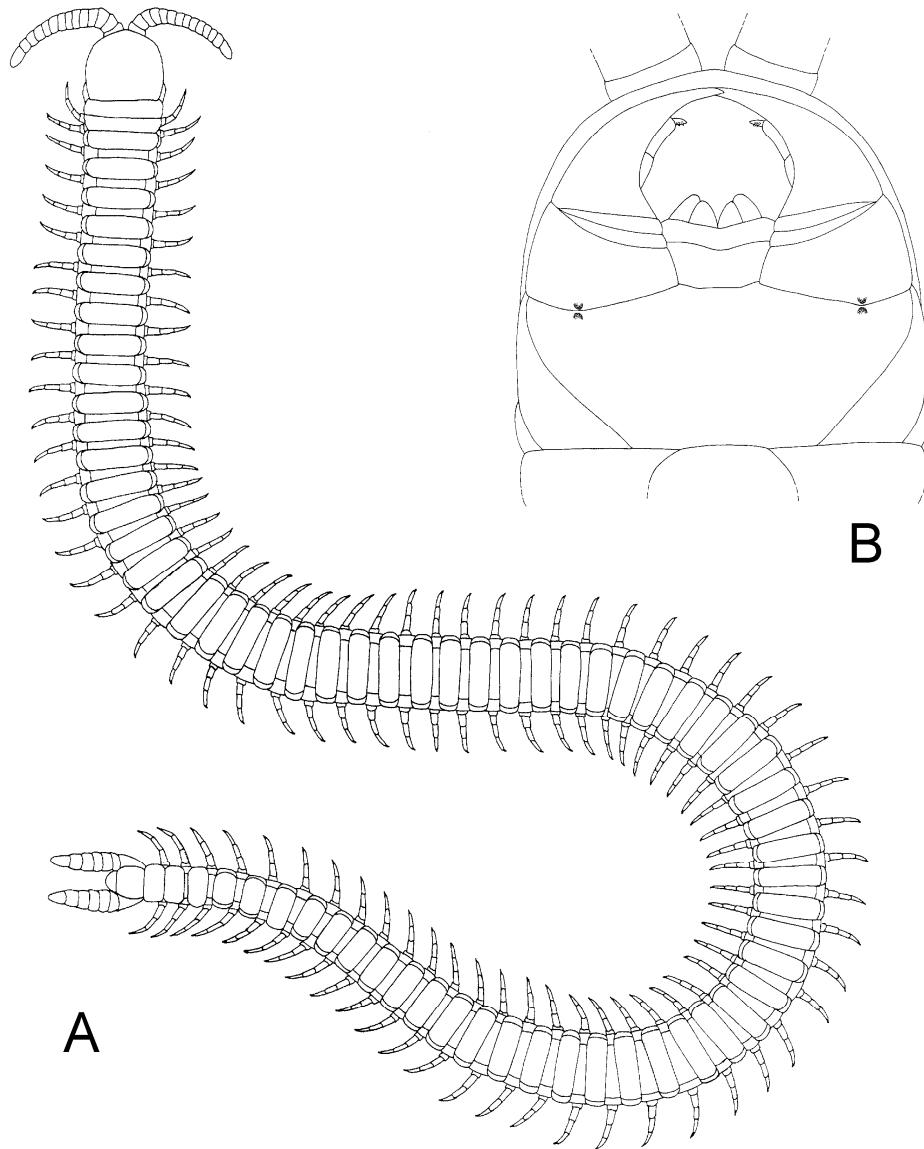


Fig. 19.25 *Orphnacetus brevilabiatus* (Geophilomorpha, Oryidae). A Habitus, dorsal view. B Anterior part of the body, ventral view. Original E. Zamprogno.

*Heniorya* Cook, 1896. – Body length unknown. About 161 pairs of legs. Claws of second maxillae without marginal filaments. Sternal pores arranged mainly in two transverse bands on each metasternite. Brazil. A single species, *H. longissima* Cook, 1896.

*Lamotteophilus* Demange, 1963. – Body length 8-9 cm. 97-133 pairs of legs. Each mandible with a single pectinate lamella and some rows of spines. Claws of second maxillae with some filaments. Guinea. A single species, *L. spinosus* Demange, 1963.

*Marshallopus* Verhoeff, 1937. – Body length 2-3 cm. About 69 pairs of legs. Patchily melanised. Ultimate legs basally swollen and distally flattened. Marshall Islands. A single species, *M. platypedatus* (Takakuwa, 1934).

*Metaxythus* Crabill, 1968. – Body length ca 11 cm. About 113 pairs of legs. Labrum tripartite. Claws of second maxillae without marginal filaments. Trunk metasternites without peculiar markings. Each coxopleuron with coxal organs opening in two pits close to the metasternite. Ultimate legs with claw. Female gonopods an undivided lamina. Anal pores present. Juan Fernández Islands. A single species, *M. austrinus* Crabill, 1968.

*Notiphilides* Latzel, 1880. – Body length mainly 9-15 cm. 83-151 pairs of legs. Ultimate legs short, with a single tarsal article. Tropical America. A few species, incl. *N. maximiliani* (Humbert & Saussure, 1870) (Mexico to Peru).

*Nycternyssa* Crabill, 1959. – Body length 4-7 cm. About 77-83 pairs of legs. Ultimate legs short. Female gonopods uniarticulate. Tropical Africa, south and south-east Asia. Four species, incl. *N. conspersa* (Verhoeff, 1937) (darkly patched; Indian peninsula).

*Orphnaeus* Meinert, 1870. – Body length 3-13 cm. 53-131 pairs of legs. Ultimate legs short. Most part of tropical regions. A dozen species, incl. *O. brasilianus* (Humbert & Saussure, 1870) (uniform colour, sternal pores in a quadrangular frame on each metasternite; tropical America), *O. brevilabiatus* (Newport, 1845) (dark longitudinal stripes, sternal pores in four separate groups on each metasternite; tropical regions worldwide, often introduced), *O. maculatus* Lawrence, 1960 (dorsal and ventral black patches, small size; Madagascar).

*Parorya* Cook, 1896. – Body length ca 12 cm. About 113 pairs of legs. Peculiar pattern of trunk pleurites. South part of North America. A single species, *P. valida* Cook, 1896.

*Pentorya* Cook, 1896. – Body length 10-19 cm. 93-141 pairs of legs. Sternal pores arranged mainly in two transverse bands on each metasternite. Ultimate legs short, with a single tarsal article. Central Africa and Indian peninsula. Two species, incl. *P. indica* Silvestri, 1919 (large body; Indian peninsula).

*Stenorya* Crabill, 1968. – Body length 7-8 cm. About 161 pairs of legs. Claws of second maxillae with only few, very short filaments. Forcipular coxosternite with sclerotized lines. Tanganyika. A single species, *S. vermiculata* Crabill, 1968.

*Titanophilus* Chamberlin, 1915. – Body length 8-20 cm. 101-169 pairs of legs. Claws of second maxillae without filaments. Ultimate legs with a single tarsal article. Antilles and tropical part of South America. Four species, incl. *T. maximus* Chamberlin, 1915 (large size; Hispaniola).

*Trematorya* Brölemann, 1909. – Body length ca 8 cm. About 117 pairs of legs. Claws of second maxillae without filaments. Most trunk metasternites with a mid-longitudinal furrow, a few metasternites in the anterior part of the trunk each with a peculiar socket in the centre. Each coxopleuron with coxal organs opening in two pits close to the metasternite. Ultimate legs with claw. Mid-part of Chilean Pacific coast. A single species, *T. sternalis* Brölemann, 1909.

Family SCHENDYLIDAE Cook, 1896 (Fig. 19.26). – Body slender, gradually tapering towards the posterior tip. Head slightly elongate, antennae slender. Labral margin medially concave, fringed by denticles gradually diminishing towards the convex lateral

parts. Each mandible with a single dentate lamella and a single pectinate lamella. Claws of second maxillae usually slightly spatulate, often fringed by small spines or rows of filaments. Forcipular segment broad, tergite subtrapezoid and narrower than the subsequent tergite, forcipules relatively large and close to each other. Number of leg-bearing segments variable within each species, the overall range 27-87. Sternal pore-fields usually present, most often a single one on each metasternite. Each coxopleuron most often with only one or two ventral pores. Female gonopods distinct, either biarticulate or uniarticulate. Mainly Americas, Palearctic, Africa and Madagascar; also south-east Asia, Australia and some Pacific islands. Ca 220 species in ca 35 genera.

*Schendyla* Bergsøe & Meinert, 1866. – Body length 1-4 cm. 31-57 pairs of legs. Claws of second maxillae with a few spines only. Sternal pore-fields limited to the anterior part of trunk or lacking at all. Each coxopleuron with two pores. Ultimate legs without claw. Most part of the west Palearctic. About two dozen species, incl. *S. armata* Brölemann, 1901 (small size, forcipules with elongate denticles, no sternal pores; west Mediterranean regions), *S. carniolensis* Verhoeff, 1902 (forcipules without denticles; mainly continental Europe), *S. dentata* (Brölemann & Ribaut, 1911) (W Europe), *S. mediterranea* Silvestri, 1898 (ultimate legs very inflated proximally; Mediterranean basin), *S. nemorensis* (C.L. Koch, 1837) (forcipules with small denticles; most part of W Palearctic).

*Algunguis* Chamberlin, 1950. – Body length ca 3 cm. About 69 pairs of legs. Claws of second maxillae fringed by two rows of filaments. Coxal organs of each coxopleuron opening into two pores. Ultimate legs with claw. Puerto Rico. A single species, *A. toronus* Chamberlin, 1950.

*Apunguis* Chamberlin, 1947. – Body length 1-2 cm. About 43 pairs of legs. Claws of second maxillae without projections. Coxopleura with many scattered pores. Ultimate legs with claw. South part of North America. A single species, *A. prosoicus* Chamberlin, 1947.

*Australoschendyla* Jones, 1996. – Body length 1-2 cm. 41-47 pairs of legs. Claws of second maxillae fringed by a single row of filaments. Forcipules short. Sternal pore-fields subcircular. Each coxopleuron with one or two pores. Ultimate legs with claw. West Australia. Two species, incl. *A. capensis* Jones, 1996 (forcipules very short, each coxopleuron with a single pore).

*Bimindyla* Chamberlin, 1952. – Body length ca 5 cm. About 79 pairs of legs. Claws of second maxillae fringed by two row of filaments. Forcipules without denticles. No sternal pores. No coxal organs. Ultimate legs without claw. Bahamas. A single species, *B. gertschi* Chamberlin, 1952.

*Ctenophilus* Cook, 1896. – Body length 2-7 cm. 43-79 pairs of legs. Claws of second maxillae fringed by two rows of filaments. Sternal pore-fields subcircular to trasversally elliptical. Coxal organs of each coxopleuron opening through two pores. A spinous tubercle on the tip of the ultimate legs. Greater Antilles and west tropical Africa. About a dozen species, incl. *C. amicti* (Demange, 1963) (sternal pore-fields on the anterior part of trunk only, metasternite of the ultimate leg-bearing segment very wide; Ivory Coast), *C. nesiotes* Chamberlin, 1918 (sternal pore-fields lacking on the intermediate part of trunk; Hispaniola).

*Cymochilus* Chamberlin, 1947. – Body length and number of leg pairs unknown. Claws of second maxillae fringed by two rows of filaments. Each coxopleuron with two pores. Ultimate legs with claw. Isthmus of Panama. A single species, *C. panamicola* Chamberlin, 1947.

*Escaryus* Cook & Collins, 1891. – Body length 1-7 cm. 31-65 pairs of legs. Claws of second maxillae fringed by two rows of filaments. No sternal pores. Coxopleura with many scattered pores. Ultimate legs with claw, and swollen in male. Holarctic, in temperate and subarctic regions.

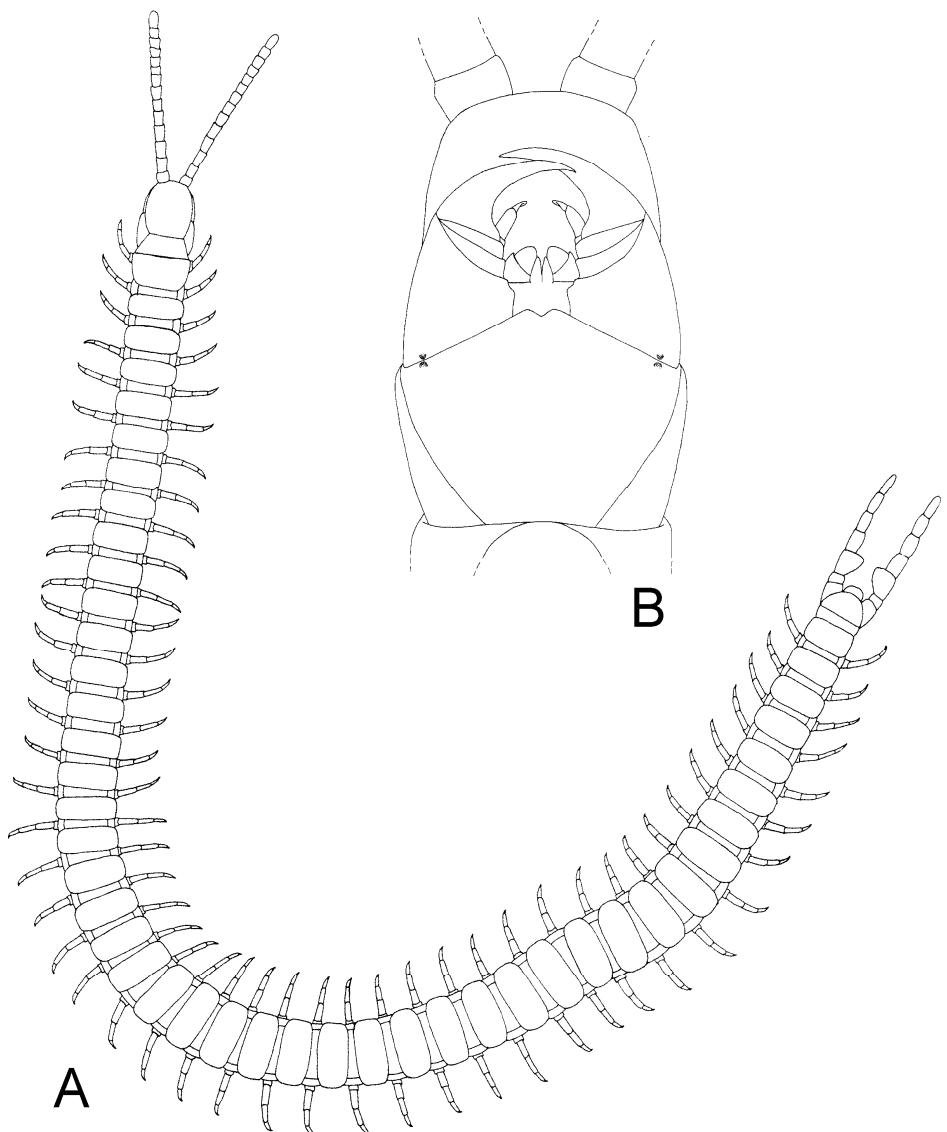


Fig. 19.26 *Schendyla mediterranea* (Geophilomorpha, Schendylidae). A habitus, dorsal view. B anterior part of the body, ventral view. Original E. Zamprogno.

More than 30 species, incl. *E. ethopus* (Chamberlin, 1920) (large size, trunk metasternites without anterior sockets; Alaska and nearby areas), *E. retusidens* Attems, 1904 (ultimate legs with small claw; Tian Shan), *E. urbiculus* (Meinert, 1886) (anterior trunk metasternites with marginal medial socket; east part of North America).

*Espagnella* Attems, 1952. – Body length ca 1 cm. 37-41 pairs of legs. Claws of second maxillae with a few spines only. No sternal pores. Each coxopleuron with two pores. Ultimate legs with claw. Iberian peninsula. A single species, *E. franzi* Attems, 1952.

*Falcaryus* Shinohara, 1970. – Body length ca 1 cm. About 33 pairs of legs. Claws of second maxillae with spines. Forcipular tarsungula with a basal denticle and with the internal margin expanded in a low triangular projection. Legs with serrate claws. No sternal pores. Coxal pores scattered. Ultimate legs with claw. Honshu. A single species, *F. nipponicus* Shinohara, 1970.

*Gosendyla* Chamberlin, 1960. – Body length ca 2 cm. About 49 pairs of legs. Claws of second maxillae fringed by two rows of filaments. No sternal pores. Coxopleura inflated, with scattered pores. Ultimate legs of male swollen, without claw. Middle part of Rocky Mountains. A single species, *G. socaria* Chamberlin, 1960.

*Haploschendyla* Verhoeff, 1900. – Body length 3-6 cm. 47-57 pairs of legs. No coxal pores. Ultimate legs without claw. Mediterranean coastal regions and Madeira. A few species, incl. *H. barbarica* (Meinert, 1870) (north-west Africa and Sicily).

*Holitys* Cook, 1899. – Body length 1-2 cm. About 45 pairs of legs. Ultimate leg-bearing segment with wide metasternite. Ultimate legs with claw. Middle part of Rocky Mountains. A single species, *H. neomexicana* Cook, 1899.

*Hydroschendyla* Brölemann & Ribaut, 1911. – Body length 3-4 cm. 45-53 pairs of legs. Labrum deeply concave. Claws of second maxillae with few spines. Sternal pores very few. Each coxopleuron with two pores. Ultimate legs without claw. Littoral sites around Europe. A single species, *H. submarina* (Grube, 1872).

*Leptoschendyla* Attems, 1953. – Body length ca 2 cm. About 39 pairs of legs. Claws of second maxillae fringed by two rows of filaments. No sternal pores. Each coxopleuron with two pores. Ultimate legs with claw. Indochinese peninsula. A single species, *L. paucipes* Attems, 1953.

*Marsikomerus* Attems, 1938. – Body length 1-5 cm. 39-61 pairs of legs. Claws of second maxillae fringed by two rows of filaments. Sternal pore-fields subcircular. Each coxopleuron with a single, elongate pore. Ultimate legs with claw, swollen and densely setose in male. South part of North America and Hawaii islands. Four species, incl. *M. bryanus* (Chamberlin, 1926) (forcipules with denticles; Hawaii), *M. texanus* (Chamberlin, 1940) (forcipules without denticles; Texas).

*Mesoschendyla* Attems, 1909. – Body length 1-4 cm. 31-63 pairs of legs. Sternal pore-fields on the anterior part of trunk only, subcircular to transversally elliptical. Ultimate leg-bearing segment with a single pore on each coxopleuron, metasternite wide and legs without claw. Mainly south Africa; also central Africa, Madagascar and Java. Eight species, incl. *M. monopora* (Attems, 1909) (large size, about 60 leg pairs; south Africa) and *M. javanica* (Attems, 1907) (small size, less than 40 pairs of legs; Java).

*Mexiconyx* Chamberlin, 1922. – Body length ca 2 cm. About 55 pairs of legs. Sternal pore-fields on the anterior part of trunk only. Each coxopleuron with a single pore. Ultimate legs with claw. Central Mexico. A single species, *M. hidalgensis* Chamberlin, 1922.

*Momophilus* Takakuwa, 1937. – Body length 3-4 cm. About 45-49 pairs of legs. Claws of second maxillae fringed by two rows of filaments. Sternal pore-fields subcircular. Each coxopleuron with two pores. Ultimate legs with claw. Momotori island near Honshu. A single species, *M. serratus* Takakuwa, 1937.

*Morunguis* Chamberlin, 1943. – Body length ca 1 cm. About 47 pairs of legs. No sternal pores. Each coxopleuron with a single pore. Ultimate legs with claw. Central Mexico. A single species, *M. morelus* Chamberlin, 1943.

*Nannophilus* Cook, 1896. – Body length 3-5 cm. 55-77 pairs of legs. Claws of second maxillae fringed by two rows of filaments. Each coxopleuron with two pores. Ultimate legs swollen, with a

single tarsal article, without claw. Macaronesia and Mediterranean basin. Four species, incl. *N. melanostictus* (patchily melanised, ultimate legs of male of five articles only; Canary islands).

*Nannopodellus* Chamberlin, 1924. – Body length 1-2 cm. About 53 pairs of legs. Margin of forcipular tarsungula serrate. No sternal pores. Each coxopleuron with two pores. Ultimate legs with a single tarsal article, without claw. Galapagos islands. A single species, *N. purpurascens* Chamberlin, 1924.

*Nesonyx* Chamberlin, 1923. – Body length 2-3 cm. About 55 pairs of legs. Claws of second maxillae fringed by two rows of filaments. Sternal pore-fields on anterior part of trunk only. No coxal organs. Ultimate legs with claw. Gulf of California. A single species, *N. flagellans* Chamberlin, 1923.

*Nyctunguis* Chamberlin, 1914. – Body length 2-5 cm. 39-65 pairs of legs. Claws of second maxillae fringed by two rows of filaments. Sternal pore-fields on anterior part of trunk only. Each coxopleuron with two pores. Ultimate legs with claw. South part of North America and Mexico; also recorded from Peruvian Andes and Anatolia. More than a dozen species, incl. *N. dampfi* (Verhoeff, 1926) (small size; Mexico), *N. montereus* (Chamberlin, 1914) (large size; California).

*Orygmadyla* Hoffman & Pereira, 1997. – Body length 4-5 cm. About 55 pairs of legs. Forcipular segment relatively short. Anterior trunk metasternites with two paired pore-fields and a peculiar anterior marginal pit. Each coxopleuron with a single pore. Ultimate legs without claw. Peruvian Andes. A single species, *O. spelaea* (Kraus, 1957).

*Parunguis* Chamberlin, 1941. – Body length 1-3 cm. 37-49 pairs of legs. Trunk metasternites with an anterior marginal socket and without sternal pores. Each coxopleuron with two pores. Ultimate legs with claw. California and central Mexico. A few species, incl. *P. kernensis* Chamberlin, 1941 (California).

*Pectiniunguis* Bollman, 1889. – Body length 3-6 cm. About 35-69 pairs of legs. Claws of second maxillae fringed by two rows of filaments. Sternal pore-fields transversally elliptical, on almost all trunk segments. Each coxopleuron with two pores. Ultimate legs without claw. Tropical and subtropical Americas, also recorded from Fiji islands and west Africa. More than 20 species, incl. *P. americanus* Bollman, 1889 (patchily melanised; littoral sites in Central America), *P. bollmani* Pereira, Minelli & Foddai, 1999 (leg claws with very elongate accessory spurs; littoral sites in Central America), *P. ducalis* Pereira, Minelli & Barbieri, 1995 (antennae elongate, more than 60 leg pairs; Amazonas), *P. plusiodontus* Attems, 1903 (mandibular dentate lamellae with many teeth; south Brazil).

*Plesioschendyla* Ribaut, 1923. – Body length 3-4 cm. 43-55 pairs of legs. Claws of second maxillae without projections. Mandibular dentate lamellae with small teeth. Sternal pores in a transverse band. Each coxopleuron with a single pore. Ultimate legs swollen in male, without claw. New Caledonia. A single species, *P. confossa* Ribaut, 1923.

*Portoricellus* Chamberlin, 1950. – Body length ca 1 cm. About 45 pairs of legs. Coxosternite of first maxillae divided mid-longitudinally. No sternal pores. Each coxopleuron with two pores. Ultimate legs with a single tarsal article, without claw. Puerto Rico. A single species, *P. mundus* Chamberlin, 1950.

*Schendylellas* Chamberlin, 1920. – Body length ca 1 cm. About 35 pairs of legs. Claws of second maxillae very small. Sternal pores in a transverse band. Each coxopleuron with two pores. Central America. A single species, *S. hodites* Chamberlin, 1920.

*Schendyllops* Cook, 1899. – Body length 1-7 cm. 27-87 pairs of legs. Claws of second maxillae with two rows of filaments. Sternal pore-fields subcircular to subtriangular, sometimes two paired fields on some metasternites. Each coxopleuron with two pores. Ultimate legs without claw. South America, Africa and Madagascar. More than 60 species, incl. *S. bakeri* (Chamberlin, 1914) (pore-fields on most metasternites, coxal organs bilobate; Amazonas), *S. grandidieri* (Saussure &

Zehntner, 1902) (forcipules short, with a small denticle; Madagascar), *S. interfluvius* (Pereira, 1984) (pore-fields only on anterior metasternites; Paraná valley), *S. maroccanus* (Attems, 1903) (large size, antennae elongate, forcipules with denticles; north-west Africa), *S. oligopus* (Pereira, Minelli & Barbieri, 1995) (Brazil), *S. virgingordae* (Crabill, 1960) (antennae very elongate in male, dense setae on the cephalic pleurites; littoral sites in Lesser Antilles).

*Serrunguis* Chamberlin, 1941. – Body length ca 2 cm. About 65 pairs of legs. Margin of forcipular tarsungula finely crenulate. No sternal pores. Each coxopleuron with two pores. Ultimate legs without claw. California. A single species, *S. paroicus* Chamberlin, 1941.

*Sogodes* Chamberlin, 1922. – Body length ca 1 cm. About 63 pairs of legs. Claws of second maxillae without projections. No sternal pores. Each coxopleuron with two pores. Ultimate legs with claw. Central America. A single species, *S. difficilis* Chamberlin, 1922.

*Sogolabis* Chamberlin, 1920. – Body length ca 1 cm. About 39 pairs of legs. Claws of second maxillae without projections. Forcipules with denticles. No sternal pores. Coxopleura with scattered pores. Ultimate legs without claw. Central America. A single species, *S. scapheus* Chamberlin, 1920.

*Thindyla* Chamberlin, 1955. – Body length ca 6-7 cm. 59-65 pairs of legs. A series of deep invaginations on the ventral side of the anterior trunk segments, each opening on the anterior margin of a metasternite. Pacific coast of South America. A single species, *T. litoralis* (Kraus, 1954).



## Chapter 20

# SYMPHYLA

Nikola Szucsich & Ulf Scheller

### *Diagnosis*

Elongate, weakly sclerotized and unpigmented terrestrial arthropods with 11 or 12 pairs of legs (Fig. 20.1). Head obviously distinct from trunk. Eyes lacking. One pair of long, filiform antennae, a pair of mandibles and first maxillae, and an unpaired second maxilla. Genital openings at trunk segment 4 (progoneate condition, as in Diplopoda and Paurotopoda). Hatchlings with 6-7 pairs of legs and anamorphic development.

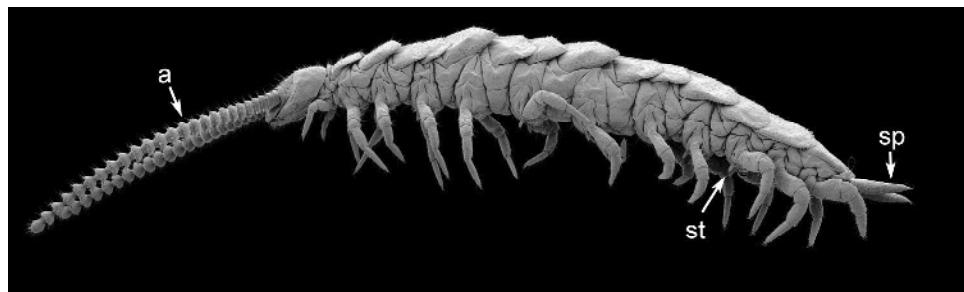


Fig. 20.1 SEM-photograph of *Scutigerella* sp. Original H. Pohl.  
a antenna; sp spinneret; st stylus

### *General morphology*

#### *Head*

The dorsal head surface is strongly sclerotized, forming the head capsule. On the ventral side the sclerotized basal portions of the mouthparts are surrounded by regions of weakly sclerotized cuticle.

Only a small number of sutures are recognizable on the symphytan head. Three of these, common to all species, form an inverted Y pattern. Starting at the antennal condyles on each side, a pair of sutures converges in posterior direction, eventually fusing

together into a coronal suture that runs further caudad, separating the head capsule along the dorsal midline into two hemispheres. At the caudal end of this suture an apodeme protrudes into the head, which serves as an attachment site both for muscles from the trunk and a part of the antennal musculature. An additional post-frontal suture is present at least in *Scutigerella* (Ravoux, 1975).

#### *Antennae and organs of Tömösváry*

The long filiform antennae articulate to the head capsule with a single median joint. During development, new antennomeres form from a weakly sclerotized basal growth zone (Tiegs, 1945). All antennomeres are provided with musculature.

In the weaker sclerotized area posterior to the antennae lies a pair of sensory organs, the temporal organs or organs of Tömösváry. A pair of pit-like invaginations of the head capsule is partly filled up by a branching and anastomosing network of cuticular projections. These have a thin, perforated cuticle and ensheathe the distal projections of about ten sensory cells. Innervated from the protocerebrum, the temporal organs most probably serve as olfactory sense organs and hygroreceptors (Haupt, 1971, 1979).

#### *Mouthparts*

The drop-shaped head of the Symphyla tapers towards the mouth-cone, which encloses the oral cavity. The clypeo-labrum closes the oral cavity dorsally and anteriorly, the mandibles and maxillae laterally, and the second maxillae or labium ventrally and posteriorly. The hypopharynx protrudes into the oral cavity.

On the clypeo-labrum no suture is recognizable to demarcate a clypeal from a labral area. On the ventral or epipharyngeal surface, a pair of furrows functions as guiding structures for the movements of the mandibles, by interacting with a knob-like protrusion of the dorsal surface of the mandibular gnathal lobes (Manton, 1964; Ravoux, 1975).

The mandibles are not uniformly sclerotized but, like in other myriapod groups, are made of distinct sclerites. In Symphyla a basal mandibular sclerite is surrounded by areas of weakly sclerotized cuticle. It articulates proximally with a lateral protrusion of the head capsule, distally with the mandibular gnathal lobe, which is the portion that freely protrudes into the oral cavity. At the gnathal edge, a lacinia mobilis inserts in a weakly sclerotized area (Richter et al., 2002). At the base of the gnathal portion, the mandibular apodeme protrudes medially as an endoskeletal structure into the head cavity. A high

number of fibre bundles of the main mandibular adductor muscle inserts with a common tendon to this apodeme (Fig. 20.2). These bundles originate at the head capsule, while the greater part of the remaining mandibular muscles has tentorial origin.

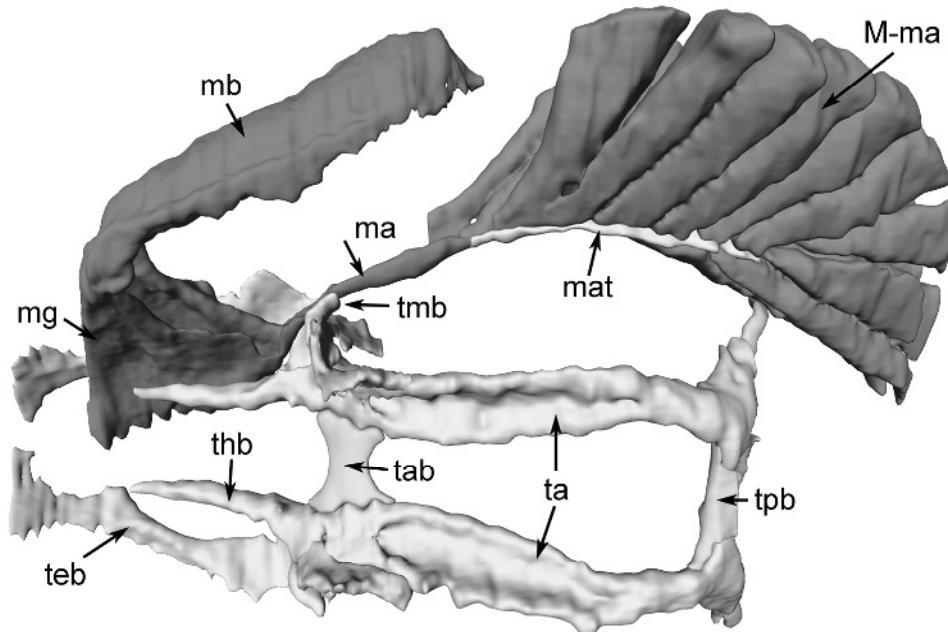


Fig. 20.2 Mandible and tentorium. Original N. Szucsich.

ma mandibular apodeme; mat tendon of mandibular adductor muscle; mb mandibular basal portion; mg mandibular gnathal portion; M-ma mandibular adductor muscle; ta tentorial arm; tab anterior tentorial bridge; teb epipharyngeal bar of tentorium; thb hypopharyngeal bar of tentorium; tmb mandibular bar of tentorium; tpb posterior tentorial bridge

In the maxillae, a basal portion can be likewise differentiated from a gnathal portion. However, the connection between these two parts is not represented by a true articulation, but includes a slender link of continuously sclerotized cuticle. The gnathal portion is bilobate, with an outer galea and an inner lacinia. A peg-like protrusion at the distal end of the basal portion is assumed to represent the remnant of a maxillary telopodite (Hansen, 1903). Like the mandibles, the maxillae articulate to the lateral head capsule with a monocondylic joint.

The second maxillae or labium closes the oral cavity posteriorly. There is no clear border between the basal and gnathal portion. The former consists of an unpaired distal part, which is continuous with paired proximal rods. These rods articulate with cervical sclerites, thus the second maxilla is exceptional among the mouthparts in that it does not articulate with the head capsule. The gnathal portion at its distal end has three pairs of tooth-like protrusions. The two inner pairs are separated from the remaining surface by a slender band of weakly sclerotized cuticle, and thus are assumed to represent labial lobes. The cuticle of the outer pair is continuous with the remaining labial surface and homologized with the labial telopodite (Hansen, 1903). Most of the labial and maxillary muscles have tentorial origins (Domínguez Camacho, 2009; N.U.Szucsich, M. Pennerstorfer & C.S. Wirkner. unpublished). The hypopharynx includes a ventral unpaired part and a pair of dorsolateral superlinguae.

#### *Tentorium*

The head endoskeleton is represented by a pair of cuticular rods, the so called tentorial arms, by structures of connective tissue, plus the associated musculature. The tentorial arms are continuous with three sclerotized structures of the cephalic exoskeleton, a hypopharyngeal, an epipharyngeal and a mandibular bar respectively (Fig. 20.2). All these branches lie at the cranial end of the tentorial arms. The tentorium has no continuously sclerotized connection to the head capsule neither at its anterior nor at its posterior end. This allows for movements of the tentorium relative to the head capsule, hence the notion of swinging tentorium of different authors (Manton, 1964; Koch, 2003; Edgecombe, 2004).

#### *Trunk*

The trunk is usually assumed to include 14 segments and a telson. The anterior 12 segments bear a pair of legs each, except in some groups, where the first leg pair is vestigial to totally absent. Segment 13 bears a pair of spinnerets. A pair of conspicuous bothriotricha on segment 14 is assumed to be serially homologous to trunk appendages, corresponding to degenerating embryonic appendages of the anal segment (Tiegs, 1945).

#### *Trunk segments*

The trunk segments of Symphyla are characterized by a unique mismatch between the

dorsal and the ventral side (Tiegs, 1945; Ravoux, 1947; Manton, 1974; Minelli, 2003; Janssen et al., 2006). This mismatch is most obvious in the Scolopendrellidae, where 15 to 24 distinct dorsal scuta can be differentiated, compared to 11 or 12 pairs of locomotory appendages. But even in Scutigerellidae the tergites deviate from homonomous segmentation. In *Hansenella* the first tergite is very small, the segments 4, 6 and 8 have two tergites each, and the 12<sup>th</sup> segment lacks a tergite (Tiegs, 1945).

Manton (1966, 1974) additionally mentions the presence of intercalary tergites on all trunk segments. These small sclerites lie covered by the regular segment anterior of the latter. Their capacity to swing against the regular sclerites strongly enhances the flexibility of the trunk.

### Appendages

The walking legs are built up of six podomeres, usually called coxa, trochanter, femur, tibia, tarsus, and pretarsus (Ewing, 1928; Ravoux, 1962; Dunger, 1993; Kluge, 1999; Pennerstorfer, 2007). Some authors refer to the trochanter as prefemur (Verhoeff, 1933–1934; Attems, 1926–1930), and the pretarsus as claw (Tiegs, 1940; Manton, 1966). A high number of leg muscles (12 extrinsic, 22–23 intrinsic) is described for *Scutigerella* (Pennerstorfer, 2007).

### Endoskeleton

Each trunk segment is equipped with a ventral, cuticular endoskeleton, built up of a pair of coxal apodemes (Tiegs, 1940; Manton, 1964; Pennerstorfer, 2007). From their invagination sites at the anterior surface of each coxa, the curved rod-like apodemes of both sides converge in a posterior direction. The rods meet in the midline and are reciprocally united by connective tissue (Manton, 1964) or musculature (Ravoux, 1962). Additionally, an endoskeleton of connective tissue has been described by Pennerstorfer et al. (2008).

### Spinnerets

A pair of specialized appendages is situated at the dorsolateral side of the preanal segment (Fig. 20.1); these are usually referred to as spinnerets, occasionally as cerci. At the tips of these spinnerets open the ducts of very conspicuous spinning glands, which extend anteriorly up to the 8<sup>th</sup> abdominal segment (Tiegs, 1945). A viscous fluid is

excreted by contraction of the muscular layer surrounding the gland; when exposed to air it hardens to form elastic spinning threads.

### *Integument*

Symphlans are weakly sclerotized arthropods, with a soft, unpigmented cuticle consisting of five layers: a lamellate endocuticle, a homogeneous exocuticle, and three distinct, very thin layers of epicuticle (Haupt, 1971).

### *Nervous system*

#### *Central nervous system*

The nervous system consists of the brain and the subesophageal nerve mass, which is continuous with the ventral nerve cord. The brain consists of a proto-, a deuto- and a tritocerebrum.

The protocerebrum innervates the postantennal organ and comprises a huge central body and a protocerebral bridge (Hanström, 1928).

The deutocerebrum is build up of a pair of bulges which form the continuation of the antennal nerves. Each antenna is innervated by two nerves, each of them including both sensory and motoric fibers (N. Szucsich, unpublished). The deutocerebral neuropil exhibits a high number of glomerular condensations.

The tritocerebral neuropil lies ventrolaterally of the pharynx. Caudally it continues directly into the subesophageal nerve mass. Since the pairs of ganglia are not clearly separated from each other, most probably due to the small body size, the tritocerebral commissure is not free as in other myriapods (Hanström, 1928). The mandibular, maxillary and labial nerves emanate from the subesophageal nerve mass. Along both the maxillary and the labial nerves there are swellings, presumably with neurosecretory function (N. Szucsich, unpublished)

#### *Stomatogastric nervous system*

At the ventro-cranial end of the tritocerebrum a pair of nerves emanates, which run at either side of the pharynx and interconnect dorsally, forming a stomatogastric bridge. A nervus recurrens emanating from the caudal side of this bridge runs along the dorsal midline of the pharynx.

*Sensilla*

On the pre-anal trunk segment, all symphylans possess a pair of bothriotricha (or trichobothria) of highly complicated ultrastructure (Haupt, 1970, 1979). Cilia of 16 sensory cells connect to the arthrodial membrane at the base of the bothriotrichum. At least eight different directions can be distinguished depending on the deflection of the hair. The bulbous base of the bothriotrichum lies in a cuticular pit (Fig. 20.3). A similar arrangement is known from pauropods and penicillate diplopods, and has been regarded as an apomorphy supporting the monophyly of a taxon Progonyeata (Haupt, 1979).

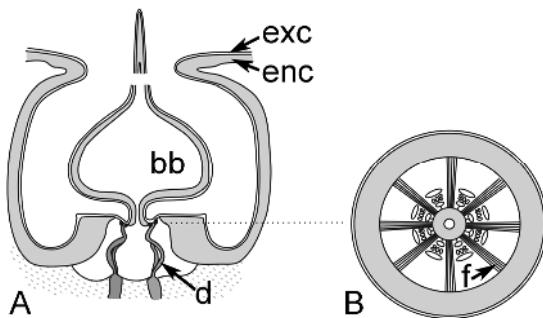


Fig. 20.3 Bothriotrichium (trichobothrium) A Longitudinal section. B Cross section. Modified after Haupt (1979).

bb bulbous base; d dendrites; enc endocuticle; exc exocuticle; f suspension fibrils

*Skeletomuscular system and locomotion*

The trunk musculature of Symphyyla is characterized by a high number and complex arrangement of longitudinal, dorsoventral and oblique muscles (Ravoux, 1947, 1962; Manton, 1964, 1966, 1974). This muscular complexity, along with the high number of distinct (particularly dorsal) sclerites allows a high flexibility of the trunk. Symphyyla can twist and turn their body sharply in any plane.

The locomotion of Symphyyla is characterized by a longer duration of the backwards stroke, compared to the forward stroke (Manton, 1966). Depending on speed every 4<sup>th</sup>, 3<sup>rd</sup> or 2<sup>nd</sup> leg is in phase during locomotion. Usually, the legs of the opposite sides are likewise in phase, thus the animal does not undulate along the main axis.

*Digestive system*

The alimentary canal includes the ectodermal foregut, with an anterior pharynx and a posterior esophagus, the entodermal midgut and the ectodermal hindgut. A detailed description is available for *Hansenella agilis* (Tiegs, 1945).

The short pharynx has a rectangular cross section; its roof is in continuation with the epipharynx, its bottom with the hypopharyngeal roof. A number of pharyngeal dilator muscles insert at the pharyngeal walls. The alimentary canal passes through the CNS between the tritocerebral lobes and runs horizontally into the trunk. No clear border can be observed to mark the transition from the pharynx into the esophagus, since the cross-section of the foregut changes continuously. The esophagus runs nearly straight until it passes, in the fifth trunk segment, into the midgut. The cells of the midgut are cubical to columnar, according to the animal's nutritional status. In the hindgut, a short pylorus with a sphincter can be differentiated from an ileum, a muscular colon and a thin-walled rectum.

*Excretory and osmoregulatory system**Malpighian tubules*

A single pair of Malpighian tubules open into the hindgut shortly after its connection to the midgut (Tiegs, 1940, 1945).

*Glands of the head*

Four pairs of cephalic glands have been described from Symphyla, which develop from coelomic sacs during embryogenesis (Tiegs, 1940; Juberthie-Jupeau, 1971; Haupt, 1976).

A premandibular gland present during earlier phases of the postembryonic development is described as degenerate in the adult, leaving pericardial nephrocytes as the only remnant, without any opening to the exterior.

A mandibular gland opens with its duct between mandible and maxilla. The secretory portion reaches into the fourth trunk segment, dorsal of the nervous system.

Of all cephalic glands the maxillary glands alone are entirely located in the head. The gland starts with a sacculus, surrounded by the anterior opening of the cephalic artery. The excretory duct of the highly convoluted gland opens between the first and the

second maxillae. While the function of the podocytes of the sacculus is most probably ultrafiltration, the tubular part may be involved in re-absorption (Haupt, 1969, 1976).

The excretory duct of a labial salivary gland opens close to the maxillary gland orifice between the first and the second maxilla (Fahlander, 1940; Juberthie-Jupeau, 1971). The secretory part first runs laterad of the pharynx and the gut, reaching into the 5<sup>th</sup> trunk segment.

### *Circulatory system*

In *Hanseniella*, the heart spans from about the 3<sup>rd</sup> segment to the pre-anal segment (Tiegs, 1940). From the 6<sup>th</sup> trunk segment backwards, each segment bears a pair of lateral ostia. The heart is closed at its caudal end, but at its cranial end it is continued by the aorta which runs along the roof of the esophagus. A pair of cephalic arteries splits off the heart shortly before it passes into the aorta, from which it is separated by a valve (N. Szucsich et al., in prep.). These cephalic arteries run in an anterior direction, and their open ends envelop the sacci of the maxillary glands (Juberthie-Jupeau, 1971; Haupt, 1976). Dorsal of the foregut, the aorta runs into the head, where it opens anterior of the brain with a funnel-shaped end. A pair of arteries split off the aorta and run between the two antennal nerves into the antennae. Shortly caudal of it, a single artery splits off, which turns half-circle around the gut to continue ventrally, where it opens into the hemocoel. Before its end a branch (the supraneural vessel) splits off, which forms the ventral longitudinal component of the circulatory system (Tiegs, 1940; N. Szucsich et al., in prep.). In *Hanseniella*, the heart is connected to the supraneural vessel at the caudal end of the aorta, while the anterior part of the supraneural vessel is described to have no vascular connection to the posterior portion. At the caudal end of the animal two branches split off the supraneural vessel, and open near the bothriotricha of the 14<sup>th</sup> segment (Tiegs, 1940).

### *Tracheal system*

The tracheal system opens with a single pair of spiracles anterior of the basal part of the mandibles. A strong tracheal stem runs in a dorsal direction and serves as the insertion site for a number of muscular bundles. Tracheal branchings supply the mandibular adductors; the main stem makes a loop and runs again towards the ventral side. Tracheal branches supply the nervous system and some head muscles, some branches reach into the anterior trunk. The tracheae of the opposite sides anastomose in

the midline at a single point in the head, ventral of the pharynx (Tiegs, 1945; N. Szucsich et al., unpublished).

### *Reproductive system and reproduction*

#### *Female organs*

The female internal genitalia span from the 4<sup>th</sup> to the 12<sup>th</sup> trunk segment. A pair of sac-like, thin-walled ovaries lies ventro-lateral of the gut (Bilinski, 1979). The ovaries pass into paired ectodermal oviducts which themselves open into an unpaired atrium. The single genital opening lies between the coxae of the 4<sup>th</sup> trunk segment (Tiegs, 1945).

#### *Male organs*

Like in the female, the male internal genitalia span from the 4<sup>th</sup> trunk segment to nearly the caudal end of the animal. They are represented by a pair of partly fused testes (Tiegs, 1945) which open with genital ducts on the 4<sup>th</sup> trunk segment. The genital ducts comprise a pair of vasa deferentia which build the connection to the testes, a paired triangular system of vesiculae seminales which fuse above the gut before the vasa deferentia emanate from them, and the paired ejaculatory ducts. The male genital orifice is enclosed by curved genital plates, which are the only external trait of sexual dimorphism reported thus far for symphylans (Tiegs, 1945).

#### *Gametes and gametogenesis*

The sac-shaped ovaries are filled with synchronously developing oocytes (Bilinski, 1979). The latter have spherical to oval nuclei, partly covered by a coat of granular material, and a homogeneous cytoplasm. During early vitellogenesis the nucleus increases in size and yolk spheres appear in the cytoplasm by micropinocytosis. Microvilli develop at the oocyte's surface. The yolk spheres fuse later to form larger complexes.

The eggs are spherical and enveloped by an outer, sculptured chorion. There is contradictory evidence regarding the presence or absence of an inner vitelline membrane. While not reported from Tiegs (1940) for *Hansenella agilis*, it is mentioned for different species of *Scutigerella* and *Hansenella agilis* by Juberthie-Jupeau (1963).

The sperms of Symphyla are dimorphic, with differentiation into longer euspermatozoa and shorter paraspermatozoa (Rosati et al., 1970). The former are assumed to closely agree with the arthropod ground pattern (Baccetti et al., 1979; Dallai and Afzelius, 2000), with a 9+2 axoneme, and centrioles with microtubular triplets, one of these centrioles acting as a basal body. A most probably plesiomorphic feature exclusively found in Symphyla among all arthropods is the presence of a cytoplasmic canal housing the proximal flagellum (Dallai and Afzelius, 2000).

#### *Spermatophores, sperm transfer and egg laying*

The symphylans have indirect sperm transfer with spermatophores (Juberthie-Jupeau, 1959, 1963; Schaller, 1971). The males deposit stalked sperm drops in the absence of a female (Fig. 20.4). The females bite off the sperm drops and store them in gnathal pockets. The eggs are fertilized just shortly after egg laying. They are pulled out from the genital chamber with the mouthparts, deposited in soil or on plants and then smeared with sperm (Juberthie-Jupeau, 1963) (Fig. 20.5).

#### *Parental care*

Eggs are guarded by the female, which waits beside the eggs until the larvae hatch (Jones, 1935; Tiegs, 1945). If under laboratory conditions the adult is removed the majority of eggs fail to hatch (Edwards, 1961).

#### *Development*

##### *Embryonic development*

The spherical eggs have a sculptured chorion, with ridges forming a mesh of triangles, and spines at the intersections of these ridges (Tiegs, 1940). After a first equal division, the cleavage becomes irregular and unequal, lacking strict synchronization of cell divisions. Early in development the blastomeres form yolk pyramids, while a cleavage cavity forms in the center of the egg. At a later stage, with the beginning of tangential divisions, polygonal cells start to appear in the interior of the developing embryo. These large internal cells develop into yolk cells; only the much smaller cells on the surface give rise to the blastoderm. On the ventral side, the germ band forms, which by ingrowth of lateral clefts becomes U-shaped. At the end of this ventral flexure of the embryo, the

developing head region pairs with the caudal end of the trunk. Even before germ band formation, large cells start to grow into the yolk, keeping contact to the surface only by their tapering ends. From each cell of this dorsal organ, filamentous threads start to grow under the chorion until they reach the opposite pole of the egg. The dorsal organ then begins to degenerate. The yolk cells do not become enclosed by the mesoderm to form the midgut, but develop into the fat body, which in the adult lies along the lateral walls of the whole trunk.

The post-embryonic development is hemianamorphic, the hatching larva having but 6-7 pairs of legs (Tiegs, 1940, 1945; Ravoux, 1962; Minelli and Bortoletto, 1988; Machida et al., 1990; Minelli, 2003).

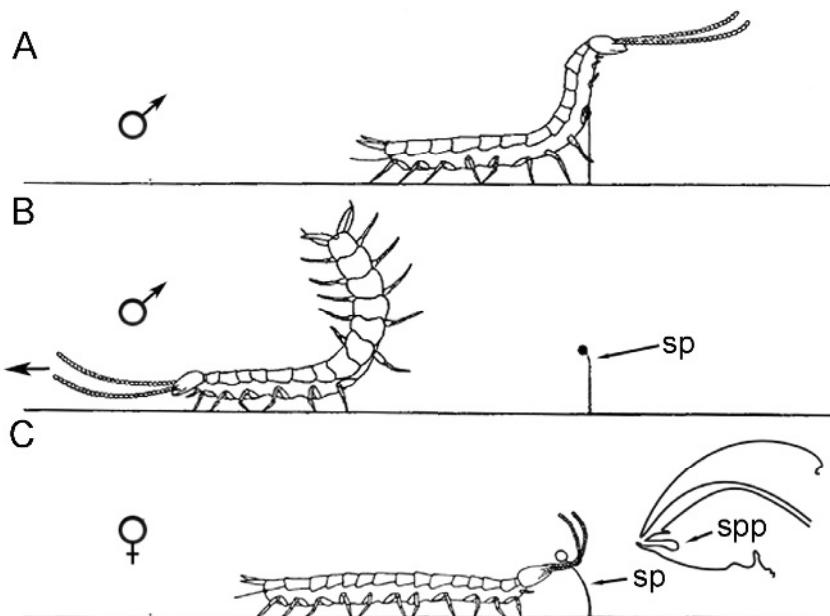


Fig. 20.4 Spermatophore emission and uptake A End stage of spermatophore deposition; The anterior trunk is raised to deposit the stalked spermatophors. C the male turns away from the spermatophore, raises the posterior trunk and leaves. C the female explores the spermatophore with the antennae; successively the sperma is taken up and deposited in a spermal pouch between hypopharynx and maxilla 2 (inset). Modified after Juberthie-Jupeau (1963).

sp Spermatophore; spp spermal pouch

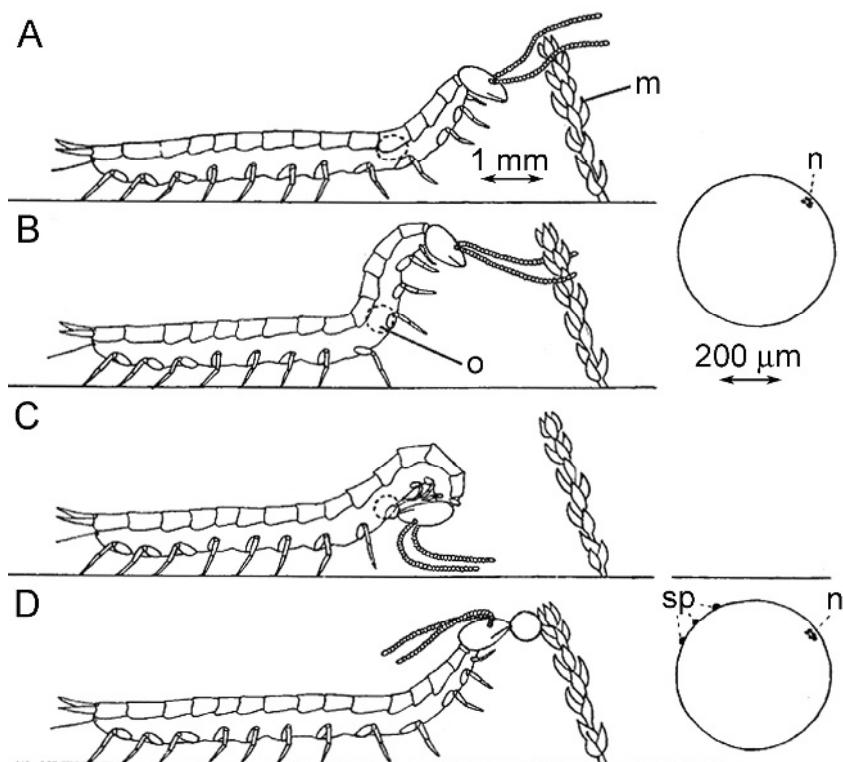


Fig. 20.5 Egg laying and fertilization A a moss plantlet is explored with the antennae. B the female raises the anterior trunk. C the egg is taken from the atrium of the genital tract with the mouthparts. D the female fixes the egg to the moss, and after chewing away a part of the eggs envelop, sperm is deposited from the pouch onto the egg (inset). Modified after Juberthie-Jupeau (1963).

m moss; n individualized chromosomes in the egg cell; o egg in atrium of the genital tract; sp Spermatozooids at egg surface

#### *Post-embryonic development*

With each of the first five post-embryonic moults, an additional pair of legs is formed, starting from a first larva with 6 or 7 pairs (Tiegs, 1945). Many more moults will follow the achievement of the final number of segments and appendages. In larva 2 and 4 accessory spinnerets appear lateral of the actual spinnerets, which replace the older spinnerets after the following moult. Each moult is likewise accompanied by the addition of new antennomeres from the basal zone of the antennae.

*Ecology**Habitat*

Symphylans occupy different kinds of soil, with highest population densities in loams and lowest densities in clay and pure sands. Population densities seem likewise to be low in very acid soil (Edwards, 1958). Survival is strongly dependent on soil moisture. For longer periods animals can live only under 100% relative air moisture between soil particles (Edwards, 1961). The regions of optimal moisture, especially important for moulting and egg-laying, are left only for feeding. While the range of preferred soil temperature lies between 15° and 21° C, symphylans are very tolerant to temperature changes. Seemingly they possess mechanisms of acclimatization to lower temperatures. Only below 5° do the animals become completely inactivated. In species feeding on living plant tissue seasonal vertical soil migrations additionally are dependent on plant growth (Edwards, 1959, 1961).

*Autecology and community ecology*

Sympyla have a relatively long life cycle, with four to six months required to reach sexual maturity from the egg. Expected maximum age is likewise high, with individuals in laboratory conditions surviving up to four years (Edwards, 1958).

*Feeding habits*

Feeding preferences differ between species (Scheller and Adis, 2002). Some species, like *Sympylella vulgaris*, seem to be exclusively saprophagous, while others like the crop pest *Scutigerella immaculata* seem to additionally feed on living plant tissue (Edwards, 1958). However, current knowledge should be taken cautiously, since the analysis of gut contents of *Sympylella* sp. indicate that at least some species are predators on nematodes and small arthropods (Walter et al., 1989).

*Relations to humankind*

The garden symphylan *Scutigerella immaculata* and a number of species of the genus *Hansenella* are recorded as serious agricultural pests (e.g. Michelbacher, 1938, 1949; Murray and Smith, 1982; Peachey et al., 2002; Umble and Fisher, 2003).

### *Geographical distribution*

Sympyla are distributed worldwide with the exception of the Antarctic continent. Caution, however is demanded, since data are still missing for many areas. The following summary thus only reflects our present knowledge on the distribution of genera.

Of the thirteen genera recognized here, four are subcosmopolitan in distribution: *Hansenella*, *Scutigerella*, *Syphylella* and *Scolopendrellopsis*. Others are widely distributed, but either restricted to the Old World (*Remisymphyla*), or to the Ethiopic and Nearctic Regions (*Ribautiella*), or to all major areas, the Palaearctic excluded (*Scolopendrelloides* and *Millotellina*). *Geophilella* is only found in the Holarctic Region and the three remaining genera have still more restricted distributions: *Scolopendrella* to the middle and southern West Palaearctic Region, *Parviapiciella* to the Mediterranean, North Africa and Central Europe, *Neosymphyla* to the Ethiopian region and *Scopoliella* to Mexico.

### *Fossils*

The fossil record on symphylans is very scarce and restricted to specimens from Eocene amber (Bachofen von Echt, 1942; Poinar and Edwards, 1995; Scheller and Wunderlich, 2004; Shear and Edgecombe, 2010). All fossil species (*Scutigerella dominicana* Poinar & Edwards, 1995; *S. baltica* Scheller & Wunderlich, 2004; *Hansenella baltica* Scheller & Wunderlich, 2004; *Scolopendrella* sp.) were assigned to recent genera. The figure given for the undescribed fossil *Scolopendrella* sp. (Bachofen von Echt, 1942) shows that it likewise belongs to Scutigerellidae, thus Scolopendrellidae still remain unknown from the fossil record.

### *Phylogeny*

The position of Symphyta within the Arthropoda is still controversial. The name (Greek for “uniting the phyla”) (Ryder, 1880) refers to the long accepted hypotheses that this taxon is somehow intermediate between myriapods and hexapods (Imms, 1936; Snodgrass, 1938; Tiegs, 1947; Sharov, 1966). As possible synapomorphies supporting a sister group relationship of Symphyta and Hexapoda, Willmann (2003) listed the presence of coxal styli and eversible coxal vesicles, stalked spermatophores, legs articulated into six podomeres, and second maxilla with glossa and paraglossa. A similar list of characters was presented by other authors to support a sister-group relationship between Progoneata and Hexapoda (Kraus and Kraus, 1994; see also Ax, 1999). Both the

homology hypotheses pertaining to character states and the polarization of characters, however, remain disputable, and these traditional hypotheses must be abandoned, as all molecular and combined studies strongly support a close relationship of a taxon Pancrustacea (or Tetraconata) including hexapods and crustaceans to the exclusion of all myriapod groups (e.g., Giribet et al., 2005; von Reumont et al., 2009; Regier et al., 2010). With respect to the sister group of symphylans, these modern studies have still to be taken cautiously, since both symphytan and pauropod sequences remain underrepresented in the available data sets, and an unusual rate of evolution may mislead interpretation (Regier and Shultz, 2001; Edgecombe and Giribet, 2002; Regier et al., 2005, 2010; Gai et al., 2006; Mallatt and Giribet, 2006; von Reumont et al., 2009). While morphological data most strongly support a sister group relationship of Symphyla with Dignatha, i.e. Pauropoda+Diplopoda (Edgecombe, 2004; Edgecombe, 2010; Shear and Edgecombe, 2010), some molecular studies seem to favour monophyly of a taxon comprising Symphyla and Pauropoda alone (Gai et al., 2006; Regier et al., 2010). Mitochondrial genome data still cannot contribute to the question; complete mt genomes are available for Symphyla (Podsiadlowski et al., 2007; Gai et al., 2008), but not yet for pauropod representatives.

Due to the scarce coverage of sequence data, no molecular evidence is available to evaluate the monophyly of Scolopendrellidae and Scutigerellidae (e.g. Bagnall, 1913) or any other question of internal symphytan relationships.

### Taxonomy

The 195 species of Symphyla described to date are currently classified in two families and 13 genera.

Family SCUTIGERELLIDAE Bagnall, 1913. – Head distinctly separated from neck; central rod not interrupted in the middle. Antennae usually with more than 20 articles and with large branched organ on terminal article. 15 simple tergites, first one reduced, all others except last with posterior margins rounded or emarginated. Pit of paired bothriotricha with many setae irregularly distributed around margin. Legs pairs each corresponding to a single tergite, except the 4th, 6th and 8th which correspond to two tergites each; first pair of legs well developed and more than half the length of following pair. Styli at base of legs well developed and bearing two or more setae. Coxal sacs 8 or 9 in number. Cerci with smooth terminal area. Length usually more than 4 mm.

*Scutigerella* Ryder, 1882. – Head pyriform; spiracle opening in anterior part of each side; central rod sharply defined at posterior end but less distinct anteriorly, main rod interrupted at posterior

end by circular area. Antennae of 20-50 segments with two main types of setae, one thicker and stronger, the other thinner; one whorl of setae on the most proximal articles; small sensory organs and fine sensory hairs present; tergites 3, 6, 9, 12 and 14 longer, with deeper indentations of the posterior margins than in other tergites; margins of tergites with many setae of different length; anterolateral setae of tergites not prominent, directed mainly backwards and outwards; last tergite with cavity between cerci. Legs densely setose with intricate sculpture patterns on some segments; 1<sup>st</sup> leg 4-segmented, the others 5-segmented. Styli on legs 3-12. Palaearctic, Nearctic, Neotropical, Ethiopian, Oriental regions (introduced In Australian and Micronesian regions). 29 species, incl. *Scutigerella immaculata* (Newport, 1845).

*Hansenella* Bagnall, 1913. – Head rounded; central rod only distinct in middle. Antennae of 20-50 articles with two main types of setae, one thicker and stronger, the other thinner; one whorl of setae on the most proximal articles; small sensory organs and fine sensory hairs present; anterolateral macrochaetae, usually long and directed mainly forwards and outwards, on at least tergite 2; tergites 3, 6, 9, 12 and 14 longer, with deeper indentations of the posterior margins than in other tergites; margins of tergites with many setae of different length; posterior margin of last tergite straight, no cavity present under last tergite between cerci. Legs densely setose with intricate sculpture patterns on some segments; 1<sup>st</sup> leg 4-segmented, the others 5-segmented. Styli on legs 3-12. Subcosmopolitan, particularly distributed in the southern hemisphere. 82 species, incl. *Hansenella nivea* (Scopoli, 1763).

*Millotellina* Jupeau, 1955. – Body with 15 tergites, the first rudimentary, some tergites with lateral macrochaetae at broadest part of tergite, first pair of legs with 4 segments. Styli and coxal sacs well developed. One or two processes with coarse surface between coxal sacs of legs 5-11. Ethiopian, Oriental, Australian, Micronesian regions. 9 species, incl. *Millotellina splendens* Jupeau, 1955.

*Scolopendrelloides* Bagnall, 1913. – Last tergite with deep posteriomedian depression (cavity). Styli of posterior legs short, shorter than the width of the tarsus. Oriental and Australian region. 3 species, incl. *Scolopendrelloides crassicornis* (Hansen, 1903).

*Scopoliella* Scheller, 1986. – Posterior margin of last tergite forms a rounded disciform lobe projecting backwards between the cerci. Posterior margins of tergites 2-14 crenate. Inner side of proximal part of cerci with some short, thick, conical setiform teeth. Subapical seta of styli consisting of two portions, a proximal one and a distal one, the latter tapering pointed and separated by a knee-like flexure. Nearctic region (Mexico only). 1 species (*Scopoliella crenata* Scheller, 1986).

Family SCOLOPENDRELLIDAE Bagnall, 1913. – Head not distinctly separated from neck; central rod interrupted in middle. Antennae usually of less than 20 articles, with two kinds of setae and some kinds of circular or branched sensory organs, only small branched sensory organs on terminal segment. Tergites 15-24 in number, of which the first may be very reduced or quite well developed; some tergites divided into protergite and metatergite; tergites oval (*Geophilella*); posterior lobes, when present, triangular in shape, longer than broad and present on 13-14 tergites. Pit of bothriotricha with smooth margin. First pair of legs never more than half the length of following pair. Styli poorly developed to rudimentary. Coxal sacs never more than 7 in number. Cerci with striated terminal area. Length usually less than 4 mm.

*Scolopendrella* Gervais, 1839. – Head oval; central rod distinct in both anterior and posterior portions; post-antennal organ small. Antennae with 15-20 segments. 17 tergites, the first vestigial, 13 other tergites with paired triangular processes on posterolateral margins; all tergites except last two separated by intertergal areas, only last two divided by a simple suture; posterior margins of tergites with transverse belt of longitudinal striae between posterolateral processes. Legs short, sparsely setose; first pair of legs well-developed, 3-segmented. Styli rudimentary. Coxal plates with fully developed sacs at bases of legs 3-9. Cerci short, sharply pointed, nearly conical, terminal area with intricate pattern of striae. Middle and southern West Palaearctic regions. 1 species. (*Scolopendrella notacantha* Gervais, 1839).

*Geophilella* Ribaut, 1913. – Central rod of the head broken in the middle. 22 posteriorly rounded tergites, 1<sup>st</sup> tergite well developed. Cerci with scaly cuticular pattern, distal part of cerci not striated. Tergites represented only by paired oval plaques bearing a few setae, no posterior processes. Palaearctic and Nearctic region. 2 species, incl. *Geophilella pyrenaica* Ribaut, 1913.

*Parviapiciella* Mas & Serra, 1993. – Eleven tergites with a pair of finger-like posterior projections, 1<sup>st</sup> pair of legs well developed, tarsi there almost as long as tarsi of the following pair. Southern West Palaearctic region. 1 species (*Parviapiciella balcanica* (Remy, 1943)).

*Scolopendrellopsis* Bagnall, 1913. – 16 or 17 tergites, some of them transversely divided, so that at least 20 plates are eventually present. First pair of legs 3-segmented, with claws, not more than one-half the length of the following pair. Palaearctic, Nearctic, Neotropical, Ethiopian, Oriental, Australian regions (Micronesian region). 15 species, incl. *Scolopendrellopsis microcolpa* (Muhr, 1881).

*Neosymphylla* Edwards & Belfield, 1967. – Head longish oval; 21 tergites, those associated with legs 5, 7, 9 and 11 subdivided; 14 tergites with posterior triangular projections; first pair of legs three-segmented; seven pairs of coxal sacs at legs 3-9. Ethiopian region. 1 species (*Neosymphylla ghanensis* Edwards & Belfield, 1967).

*Remysymphylla* Aubry & Masson, 1953. – 15 tergites, the first rudimentary; tergites 2-14 with a pair of subtriangular posterior processes. Styli poorly developed. Terminal area of cerci striated. First pair of legs reduced, 3-segmented, with terminal setae instead of claws, length half of the length of tarsus of leg 12. Southern West Palaearctic, Ethiopian (Malagasy subregion) and Oriental regions (Indian subregion). 3 species, incl. *Remysymphylla maura* Aubry & Masson, 1953.

*Sympylella* Silvestri, 1902. – Head longer than broad; central rod broken and distinct in both anterior and posterior portions. Antennae with 14-22 segments. 17 tergites or fewer, the first vestigial, 13 other tergites with triangular processes on posterior margins, no belts of longitudinal striae. First pair of legs vestigial, only represented by small protuberances with a few setae. Styli rudimentary. Coxal plates with sacs only fully developed on legs 3-9. Cerci relatively long; terminal area bulbous and with transverse stripes, ending in a single long seta. Subcosmopolitan. 41 species, incl. *Sympylella isabellae* (Grassi, 1886).

*Ribautiella* Brolemann, 1926. – 24 tergites, 13 of them with a pair of posterior processes. First pair of legs rudimentary. 8 pairs of coxal sacs at legs 3-10. Styli poorly developed. Cerci with smooth terminal area. Ethiopian and Neotropical regions. 9 species, incl. *Ribautiella zagnanadina* Brolemann, 1926.

### References

- ATTEMS, C.G., 1926-1930. Myriapoda. – Pp. 1-402 in N. Kükenthal & T. Krumbach T (ed.). Handbuch der Zoologie. Eine Stammesgeschichte der Stämme des Tierreiches, Band 4, 1. Hälfte. de Gruyter, Berlin.
- Ax, P., 1999. Das System der Metazoa II. Ein Lehrbuch der phylogenetischen Systematik 1 – Fischer, Stuttgart.

- BACCETTI, B., A.G. BURRINI, R. DALLAI & V. PALLINI, 1979. Recent work in myriapod spermatology (The spermatozoon of Arthropoda XXXI). – Pp. 97-104 in M. CAMATINI (ed.) Myriapod biology. – Academic Press, London.
- BACHOFEN VON ECHT, A.F., 1942. Über die Myriapoden des Bernsteins. – *Palaebiologica* 1942: 394-403.
- BAGNALL, R.S., 1913. On the classification of the order Symphyla. – *Journal of the Linnean Society (Zoology)* 32: 195-199.
- BILINSKI, S.M., 1979. Ultrastructural studies on oogenesis in Symphyla. – *Cell and Tissue Research* 202: 145-153.
- DALLAI, R. & B.A. AFZELIUS, 2000. Spermatozoa of the primitive type in *Scutigerella* (Myriapoda, Symphyla). – *Tissue and Cell* 32: 1-8.
- DOMÍNGUEZ CAMACHO, M., 2009. Phylogeny of the Symphyla. – Doctoral Thesis: Department of Biology, Chemistry and Pharmacy; Freie Universität Berlin.
- DUNGER, W., 1993. Antennata. – Pp. 1031-1160 in H.E. GRUNER (ed.) *Lehrbuch der speziellen Zoologie I(4)* -Fischer, Jena.
- EDGEcombe, G.D., 2004. Morphological data, extant Myriapoda, and the myriapod stem-group. – *Contributions to Zoology* 73: 207-252.
- EDGEcombe, G.D., 2010. Arthropod phylogeny: An overview from the perspectives of morphology, molecular data and the fossil record. – *Arthropod Structure & Development* 39: 74-87.
- EDGEcombe, G.D. & G. GIRIBET, 2002. Myriapod phylogeny and the relationships of Chilopoda. – Pp. 143-168 in J. LLORENTE BOUSQUETS & J.J. MORRONE (eds.). *Biodiversidad, taxonomía y biogeografía de artrópodos de México: Hacia una síntesis de su conocimiento*, 3. Universidad Nacional Autónoma de México, México.
- EDWARDS, C.A., 1958. The ecology of Symphyla Part I. Populations. – *Entomologia experimentalis et applicata* 1: 308-319.
- EDWARDS, C.A., 1959. The ecology of symphyla. Part II. Seasonal soil migrations. – *Entomologia experimentalis et applicata* 2: 257-267.
- EDWARDS, C.A., 1961. The ecology of symphyla part III. Factors controlling soil distributions. – *Entomologia experimentalis et applicata* 4: 239-256.
- EWING, H.E., 1928. The legs and leg-bearing segments of some primitive arthropod groups, with notes on leg-segmentation in the Arachnida. – *Smithsonian Miscellaneous Collections* 80(II): 1-41.
- FAHLANDER, K., 1940. Die Segmentalorgane der Diplopoda, Symphyla und Insecta Apterygota. – *Zoologiska Bidrag från Uppsala* 18: 243-251.
- GAI, Y., D. SONG, H. SUN, Q. YANG & K. ZHOU, 2008. The complete mitochondrial genome of *Sympylella* sp. (Myriapoda: Symphyla): Extensive gene order rearrangement and evidence in favor of Progoneata. – *Molecular Phylogenetics and Evolution* 49: 574-585.
- GAI, Y., D. SONG, H. SUN & K. ZHOU, 2006. Myriapod monophly and relationships among myriapod classes based on nearly complete 28S and 18S rDNA sequences. – *Zoological Science*, Tokyo 23: 1101-1108.
- GIRIBET, G., S. RICHTER, G.D. EDGEcombe & W.C. WHEELER, 2005. The position of crustaceans within Arthropoda - Evidence from nine molecular loci and morphology. – Pp. 307-352 in S. KOENEMANN & R. JENNER (eds.) *Crustacea and arthropod relationships (Crustacean Issues 16)*. Balkema, Rotterdam.
- HANSEN, H.J., 1903. The genera and species of the order Symphyla. – *Quarterly Journal of Microscopical Science* 47: 1-101.
- HANSTRÖM, B., 1928. *Vergleichende Anatomie des Nervensystems der wirbellosen Tiere unter Berücksichtigung seiner Funktion*. – Springer, Berlin.

- HAUPT, J., 1969. Zur Feinstruktur der Maxillarnephridien von *Scutigerella immaculata* Newport (Symphyla, Myriapoda). – Cell and Tissue Research 101: 401-407.
- HAUPT, J., 1970. Beitrag zur Kenntnis der Sinnesorgane von Symphylen (Myriapoda), I. Elektronenmikroskopische Untersuchung des Trichobothriums von *Scutigerella immaculata* Newport. – Cell and Tissue Research 110: 588-599.
- HAUPT, J., 1971. Beitrag zur Kenntnis der Sinnesorgane von Symphylen (Myriapoda). II. Feinstruktur des Tömösváryschen Organs von *Scutigerella immaculata* Newport. – Cell and Tissue Research 122: 172-189.
- HAUPT, J., 1976. Die segmentalen Kopfdrüsen von *Scutigerella* (Symphyla, Myriapoda). – Zoologische Beiträge 22: 19-37.
- HAUPT, J., 1979. Phylogenetic aspects of recent studies on myriapod sense organs. – Pp. 391-406 in M. CAMATINI (ed.). Myriapod biology. – Academic Press, London.
- IMMS, A. D., 1936. The ancestry of insects. – Transactions of the Society for British Entomology 3: 1-32.
- JANSSEN, R., N.-M. PRPIC & W. DAMEN, 2006. A review of the correlation of tergites, sternites, and leg pairs in diplopods. – Frontiers in Zoology 3(1): 2.
- JONES, S., 1935. A note on the distribution, oviposition and parental care of *Scutigerella unguiculata* Hansen var. *indica* Gravely. – Journal of the Bombay Natural History Society 38: 209-211.
- JUBERTHIE-JUPEAU, L., 1959. Sur une modalité nouvelle de prise des spermatophores et sur l'existence de poches spermatiques gnathales chez les Scutigerellidae (symphyles, myriapodes). – Comptes rendus de l'Académie des Sciences, Paris 248: 862-865.
- JUBERTHIE-JUPEAU, L., 1963. Recherches sur la reproduction et la mue chez les Symphyles. – Archives de Zoologie expérimentale et générale 102: 1-172.
- JUBERTHIE-JUPEAU, L., 1971. Glandes à sécrétion externe de la tête des symphyles. – Revue d'Écologie et de Biologie du Sol 8: 617-629.
- KLUGE, N., 1999. Mitos en sistemática y principios de nomenclatura zoológica. – Boletín de la Sociedad entomológica aragonesa 26: 347-377.
- KOCH, M., 2003. Monophyly of the Myriapoda? Reliability of current arguments. – African Invertebrates 44: 137-153.
- KRAUS, O. & M. KRAUS, 1994. Phylogenetic system of the Tracheata (Mandibulata). On "Myriapoda"-Insecta interrelationships, phylogenetic age and primary ecological niches. – Verhandlungen des naturwissenschaftlichen Vereins in Hamburg 34: 5-31.
- MACHIDA, R., T. NAGASHIMA & H. ANDO, 1990. The early embryonic development of the jumping bristletail *Pedetontus unimaculatus* Machida (Hexapoda: Microcoryphia, Machilidae). – Journal of Morphology 206: 181-195.
- MANTON, S.M., 1964. Mandibular mechanisms and the evolution of arthropods. – Philosophical Transactions of the Royal Society, London B 247: 1-183.
- MANTON, S.M., 1966. The evolution of arthropodan locomotory mechanisms. Part 9. Functional requirements and body design in Symphyla and Paupropoda and the relationship between Myriapoda and pterygote insects. – Journal of the Linnean Society (Zoology) 46: 103-141.
- MANTON, S.M., 1974. Segmentation in Symphyla, Chilopoda and Paupropoda in relation to phylogeny. – Symposia of the Zoological Society of London 32: 163-199.
- MALLATT, J.M. & G. GIRIBET 2006. Further use of nearly complete 28S and 18S rRNA genes to classify Ecdysozoa: 37 more arthropods and a kinorhynch. – Molecular Phylogenetics and Evolution 40: 772-794.
- MICHELBACHER, A.E., 1938. The biology of the garden centipede *Scutigerella immaculata*. – Hilgardia 11: 55-148.
- MICHELBACHER, A.E., 1949. The ecology of Symphyla. – Pan-Pacific Entomology 25: 1-12.

- MINELLI, A. & S. BORTOLETTO, 1988. Myriapod metamerism and arthropod segmentation. – *Biological Journal of the Linnean Society* 33: 323-343.
- MINELLI, A., 2003. The development of animal form. – Cambridge University Press, Cambridge.
- MURRAY, D.A.H. & D. SMITH, 1983. Effect of Symphylla, *Hansenella* sp., on establishment of pineapples in south-east Queensland (Australia). – *Queensland Journal of Agricultural and Animal Sciences* 40: 121-124.
- PEACHEY, R. E., A. MOLDENKE, R. D. WILLIAM, R. BERRY, E. INGHAM & E. GROTH, 2002. Effect of cover crops and tillage system on symphytan (Symphylla: *Scutigerella immaculata*, Newport) and *Pergamasus quisquiliarum* Canestrini (Acari: Mesostigmata) populations, and other soil organisms in agricultural soils. – *Applied Soil Ecology* 21: 59-70.
- PENNERSTORFER, M., 2007. The anatomy of the locomotory apparatus of *Scutigerella* sp. (Symphylla, „Myriapoda“): a re-investigation and comparison to other myriapods. Unpublished diploma thesis, Department of Evolutionary Biology, University of Vienna.
- PENNERSTORFER, M., N.U. SZUCSICH & G. PASS, 2008. Leg musculature and thoracic endoskeleton in Symphylla. Useful structures for homologization of podomeres? -- *Journal of Morphology* 269: 1494.
- PODSIADLOWSKI, L., H. KOHLHAGEN & M. KOCH, 2007. The complete mitochondrial genome of *Scutigerella causeyae* (Myriapoda: Symphylla) and the phylogenetic position of Symphylla. – *Molecular Phylogenetics and Evolution* 45: 251-260.
- POINAR, G.O. & C.A. EDWARDS, 1995. First description of a fossil symphytan, *Scutigerella dominicana* sp. n. (Scutigerellidae, Symphylla), in Dominican amber. – *Experientia* 51: 391-393.
- RAVOUX, P., 1947. La musculature du tronc de *Scutigerella immaculata* Newport. – *Annales des Sciences naturelles (Zoologie)* (11) 9: 63-107.
- RAVOUX, P., 1962. Étude sur la segmentation des symphyles (fondée sur la morphologie définitive et la postembryogenèse suivie de considérations sur la segmentation des autres myriapodes). – *Annales des Sciences naturelles, Zoologie* (12) 4: 141-472.
- RAVOUX, P., 1975. Endosquelette et musculature céphaliques de *Scutigerella immaculata* Newport (Symphylla: Scutigerellidae). – *Bulletin du Muséum national d'Histoire naturelle, Paris* 332: II89-1238.
- REGIER, J.C. & J.W. SHULTZ, 2001. A phylogenetic analysis of Myriapoda (Arthropoda) using two nuclear protein-encoding genes. – *Zoological Journal of the Linnean Society* 132: 469-486.
- REGIER, J.C., H.M. WILSON & J.W. SHULTZ, 2005. Phylogenetic analysis of Myriapoda using three nuclear protein-coding genes. – *Molecular Phylogenetics and Evolution* 34: 147-158.
- REGIER, J.C., J.W. SHULTZ, A. ZWICK, A. HUSSEY, B. BALL, R. WETZER, J.W. MARTIN & C.W. CUNNINGHAM, 2010. Arthropod relationships revealed by phylogenomic analysis of nuclear protein-coding sequences. – *Nature* 463: 1079-1083.
- RICHTER, S., G.D. EDGECOMBE & G.D.F. WILSON, 2002. The lacinia mobilis and similar structures - a valuable character in arthropod phylogenetics? – *Zoologischer Anzeiger* 241: 339-361.
- ROSATI, F., B. BACCETTI & R. DALLAI, 1970. The spermatozoon of Arthropoda. X. Araneids and the lowest myriapods. – Pp. 247-254 in B. BACCETTI (ed.). Comparative spermatology. – Academic Press, New York.
- RYDER, J.A. 1880. *Scolopendrella* as the type of a new order of Articulates (Symphylla). – *American Naturalist* 14: 375-376.
- SCHALLER, F., 1971. Indirect sperm transfer by soil arthropods. – *Annual Review of Entomology* 16: 407-446.
- SCHELLER, U. & J. ADIS, 2002. Symphylla. – Pp. 547-554 in J. ADIS (ed.). Amazonian Arachnida and Myriapoda. – Pensoft, Sofia.

- SCHELLER, U. & J. WUNDERLICH, 2004. Two fossil symphylan species, *Scutigerella baltica* n. sp. and *Hanseniella baltica* n. sp. (Tracheata, Scutigerellidae), in Baltic amber. – Stuttgarter Beiträge zur Naturkunde Series B (Geologie und Paläontologie) 351: 1-11.
- SHAROV, A.G., 1966. Basic arthropodan stock with special reference to insects. – Pergamon Press, Oxford.
- SHEAR, W.A. & G.D. EDGECOMBE, 2010. The geological record and phylogeny of the Myriapoda. – Arthropod Structure & Development 39: 174-190.
- SNODGRASS, R.E., 1938. Evolution of the Annelida, Onychophora and Arthropoda. – Smithsonian Miscellaneous Collections 97: 1-159.
- TIEGS, O.W., 1940. The embryology and affinities of the Symphyla, based on a study of *Hanseniella agilis*. – Quarterly Journal of Microscopical Science 82: 1-225.
- TIEGS, O.W., 1945. The post-embryonic development of *Hanseniella agilis* (Symphyla). – Quarterly Journal of Microscopical Science 85: 191-328.
- TIEGS, O.W., 1947. The development and affinities of the Pauropoda, based on a study of *Pauropus sylvaticus*. – Quarterly Journal of Microscopical Science 88: 275-336.
- UMBLE, J.R. & J.R. FISHER, 2003. Influence of below-ground feeding by garden symphyllans (Cephalostigmata: Scutigerellidae) on plant health. – Environmental Entomology 32: 1251-1261.
- VERHOEFF, K.W., 1933-1934. Symphyla und Pauropoda. – Pp. 1-200 in H. G. Brönn (ed.). Klassen und Ordnungen des Tierreichs, Band 5, Abteilung 2, Buch 3. – Akademische Verlagsgesellschaft, Leipzig.
- VON REUMONT, B.M., K. MEUSEMANN, N.U. SZUCSICH, E. DELL'AMPIO, V. GOWRI-SHANKAR, D. BARTEL, S. SIMON, H.O. LETSCH, R.R. STOCSITS, Y.-X. LUAN, J.W. WÄGELE, G. PASS, H. HADRYS & B. MISOF, 2009. Can comprehensive background knowledge be incorporated into substitution models to improve phylogenetic analyses? A case study on major arthropod relationships. – BMC Evolutionary Biology 9: 119.
- WALTER, D.E., J.C. MOORE & S.J. LORING, 1989. *Sympylella* sp. (Symphyla: Scolopendrellidae) predators of arthropods and nematodes in grassland soils. – Pedobiologia 33: 113-116.
- WILLMANN, R., 2003. Die phylogenetischen Beziehungen der Insecta: Offene Fragen und Probleme. – Verhandlungen Westdeutscher Entomologentag 2001: 1-64.

Chapter 21

# PAUROPODA

Ulf Scheller

*Diagnosis*

Pauropods (Figs. 21.1, 21.2) are whitish-brownish minuscule terrestrial arthropods, length 0.3-2 mm; the trunk has 11 segments and a horizontally cleft pygidium with a uni-

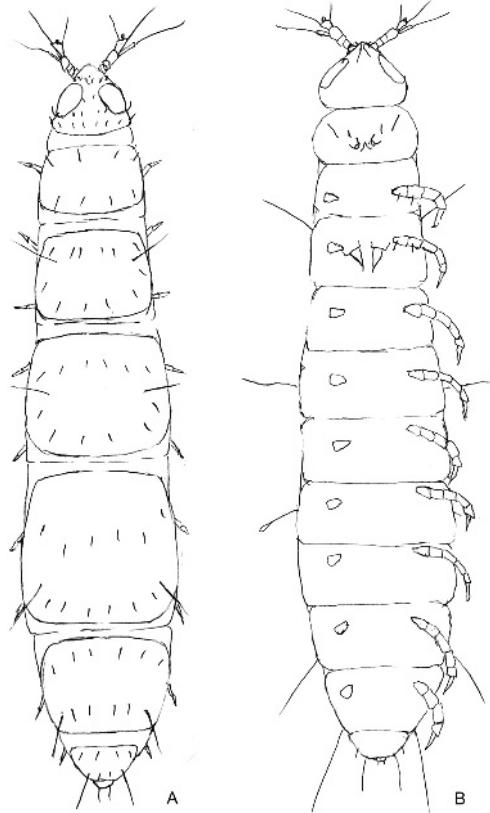


Fig. 21.1 Habitus of typical pauropodoid Paupropoda. (*Decapauropus* sp.) A dorsal view, 120x. B ventral view, male. 120x.

que anal plate. These myriapods are progoneate, with genital apertures between the second pair of legs.

Adults have 8-11 pairs of legs of 5-6 segments; the number of tergites is less than the number of legs; the antennae have a four- or six-segmented shaft and are biramous, with three flagella and a unique candelabra-shaped or globular sense organ; the head has one pair of temporal organs and the mouthparts are mandibles and one pair of maxillae. The tergites have five pairs of long bothriotricha.

The egg develops into a pupoid phase preceding the first larval instar. Post-embryonic development is anamorphic.

#### *Historical account*

Pauropods are found in a diversity of terrestrial habitats and compared to other myriapods have attracted limited attention: although about 150 years have passed since they were discovered near London by Sir John Lubbock (1867), they are still poorly known. Most studies have dealt with descriptions of new species and taxonomical problems.

Lubbock described two species, which both had only nine pair of legs, hence the name of the group, from the Greek pauros = few, pous = foot. He found them fascinating and described one of his species, *Paropus huxleyi*, as "a bustling, active, neat, and cleanly little creature. It has, too, a look of cheerful intelligence, which forms a great contrast to the dull stupidity of the Diplopods, or the melancholy ferocity of most Chilopods". One who once has seen a living pauropod, like a miniature mouse scurrying around on the dark underside of a stone with quick elegance, will certainly concur with him.

A few years after the original discovery, pauropods were collected in Switzerland (Humbert, 1872) and North America (Packard, 1870) and by the beginning of the 20<sup>th</sup> century, when two still valuable monographs were published (Hansen (1902) concentrating on history and description of new species, and Silvestri (1902) concentrating on anatomy and south European species), the number of species was still fewer than 30. Now, particularly thanks to P.A. Remy (France), U. Scheller (Sweden) and Y. Hagino (Japan), the number of species has risen to about 835.

Studies outside taxonomy and systematics are few and therefore for many aspects of pauropod anatomy and biology generalized descriptions are not possible at present. Thus, the following account will often make specific reference to the individual species actually investigated.

*External morphology*

In most pauropods the trunk is whitish in all stages. In Eurypauropodidae and Sphaeropauropodidae, however, the cuticle of the adults is yellow-brownish to brown, even dark brown, but the juveniles have often a lighter tone and can be whitish. Exceptionally light brownish or yellowish pigmented cuticle can be found in weakly sclerotized species too. One species, *Pauropus salvatgei*, can be almost black, but coloured pauropods are extremely rare outside the Eurypauropodidae and Sphaeropauropodidae.

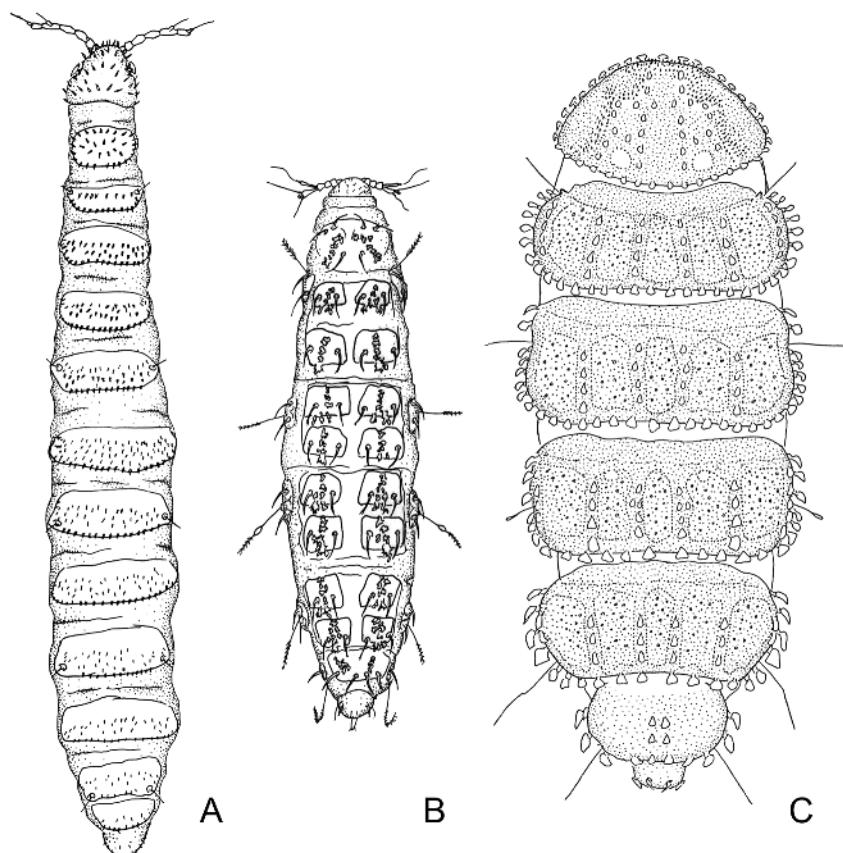


Fig. 21.2 Habitus of representative taxa of Pauropoda. A *Millotauporus* (Hexamerocerata), dorsal view, 75x. B *Brachypauropus hamiger* (Brachypauropodidae), dorsal view, 130x. C *Acopauporus* sp. (Eurypauropodidae), dorsal view, 75x.

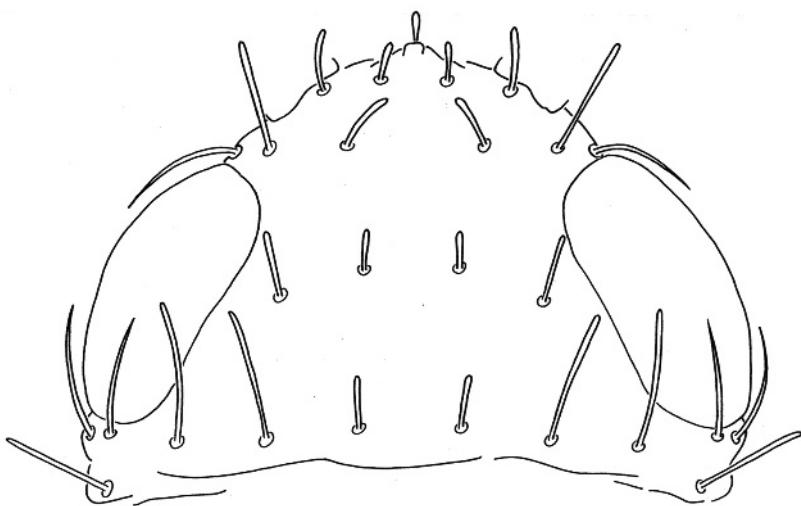


Fig. 21.3 Head of paupropodid paupropod, arrangement of dorsal setae.

#### *Head*

The head (Fig. 21.3) is small to very small, broadly connected with the trunk but well demarcated, in dorsal view triangular with convex sides, in some genera hidden under the first tergite. The mouth is more or less protruding, blunt, most often directed downwards, but in a few species extended and directed anteriorly. The dorsal side may have a transversal fold (some species of *Allopauporus*, *Decapauporus*, *Hemipauporus* and *Diplopauporus*); in *Donzelotauropus* there may be a postero-median cleft. On the dorso-lateral or latero-ventral sides there are paired oval to circular temporal organs. Dorsal and lateral sides are covered with setae, which can be cylindrical, tapering, lanceolate, foliform, ovoid, hastiform or tuft-like. These setae are glabrous, pubescent or annulated, generally simple, while short branched setae occur in *Hexamerocerata*. The most anterior dorsal seta in *Tetramerocerata* is unpaired while the remaining setae are generally arranged in four transversal rows, the first and third rows with two setae on each side of the head ( $a_1$ ,  $a_2$ ), the second with three ( $a_1 - a_3$ ), and the fourth with four setae ( $a_1 - a_4$ ). The head setae can also be placed in a more complicated pattern as in *Euryphaupopodidae* and *Sphaeropaupopodidae*, or inserted irregularly, mainly in *Millotaupopodidae* and *Brachypaupopodidae*. In most paupropods there is a lateral group of three setae ( $l_1 - l_3$ ) below and posterior to the temporal organs. Rarely dorsal setae can be strongly modified,

e.g. large, corniform macrochaetae in *Donzelotauropus* or cup-shaped protuberances in *Virginopauropus necopinatus*. A subcuticular and most often spatulate mediodorsal plate is present in the median part of the dorsal side of the head capsule in *Polypauropus* and *Polypauropoides*.

#### *Antennae*

The antennae have a basal segmented shaft and are distally biramous. The shaft is 6-segmented and strongly telescopic in Hexamerocerata (Fig. 21.4), with numerous pubescent setae arranged in one or two whorls. In Tetramerocerata (Fig. 21.5) the shaft is 4-segmented, not telescopic, and the number of setae is less, particularly on the first two segments. The distal segment is the largest, shortly subcylindrical, rarely longish. The cuticle has often a dense, short pubescence, in a few species distinct. The chaetotaxy of the last segment in Hexamerocerata, the last two segments in Tetramerocerata, is of great importance in identifying species.

In Hexamerocerata the two branches are subcylindrical and subsimilar, and originate from the distal part of the outer dorsal side of the fifth and the sixth segment, respectively.

In Tetramerocerata the branches proceed from the distal part of the fourth segment. The two branches are here generally distinctly longer than wide, the dorsal *t* most often cylindrical-fusiform, longest in *Pauropus* and *Stylopauporus*, and the ventral *s* of more varying shape, often thicker than the *t* branch and obliquely truncated distally. Both branches can be very short, particularly in *Polypauropoides*, *Polypauropus* and *Amphipauropus*, sometimes not longer than wide. The setae of the *s* branch and those of the fourth shaft segment vary in number, shape and length.

The antennal branches have long flagella, in Hexamerocerata one on each antennal branch, in Tetramerocerata one ( $F_1$ ) on *t*, two (the anterior  $F_2$  and the posterior  $F_3$ ) on *s*.

Pauropod antennae also bear sensilla of unusual shape: a candelabra-shaped organ on the sixth shaft segment in Hexamerocerata (Remy, 1953) and a simple or double (Remy, 1932) spheroid sense organ, the globulus *g*, on the distal part of the ventral antennal branch in Tetramerocerata. In the latter group there can also be an additional, rudimentary globulus *g'* on the third segment of the shaft (Remy, 1937) and in Hexamerocerata a small globulus-like organ has been found in some species at the antennal base (Remy, 1953).

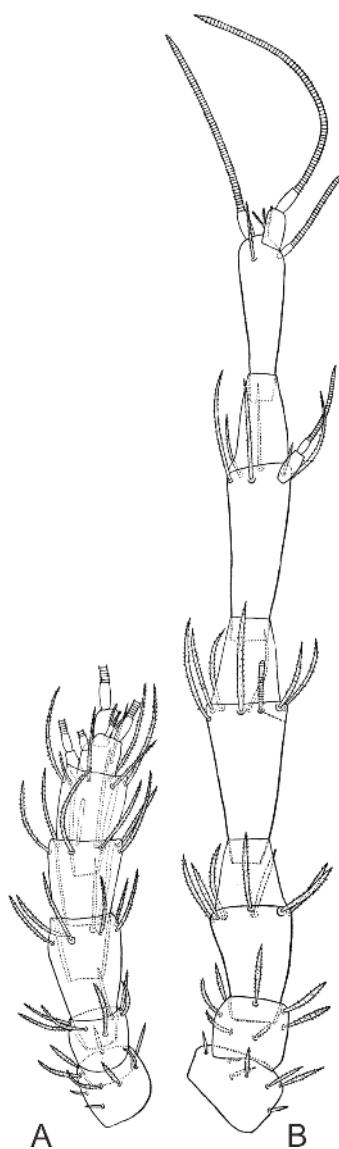


Fig. 21.4 Left Antenna of *Millotauporus*. A almost wholly contracted. B extended. Redrawn after Remy (1953).

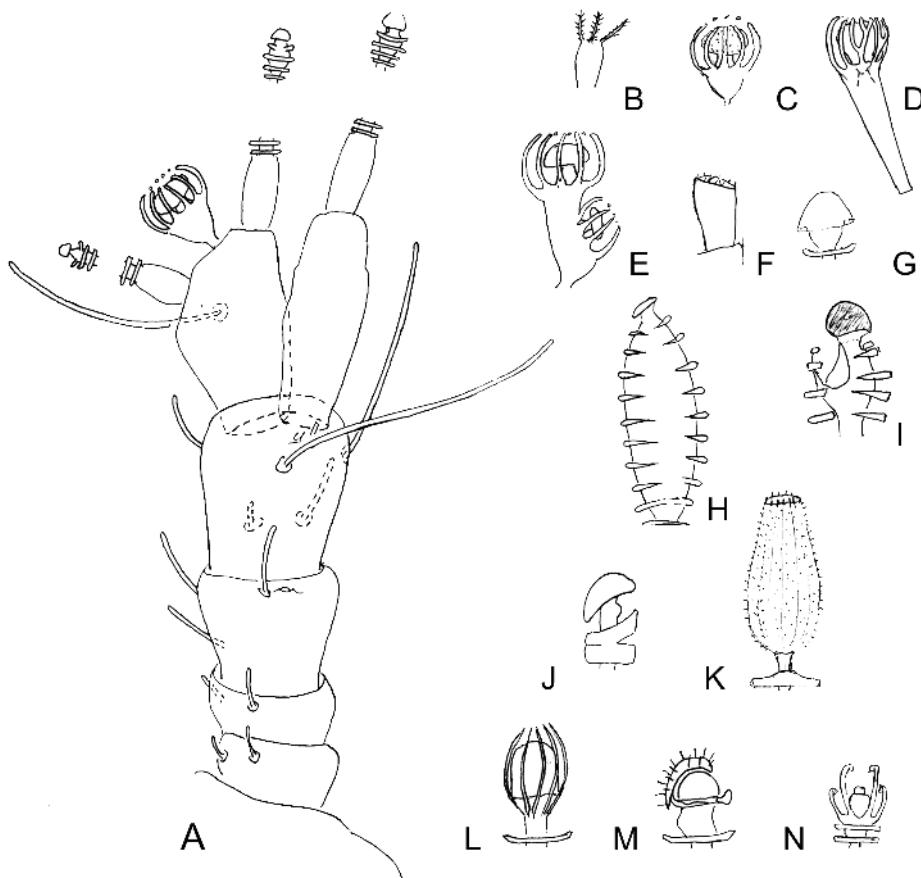


Fig. 21.5 Antennae. A Generalized left antenna of a tetramerocerate pauropod, dorsal view. B *Millo-tauropus silvestrii* (Hexamerocerata), candelabra-shaped organ, 1535x. C Globulus of generalized pauropodid. D *Stylopauropus pubescens*, long-stalked globulus with partly branched bracts, 680x. E *Polypauropodidae*, two joined globuli with flattened capsules, 2230x. F *Rabaudauropus dispar*, rudimentary globulus on third antennal segment, 1675x. G-N calyces of antennal flagella. G A most common type, helmet-shaped calyx and small swelling below. H *Decapauropus binodulosus*, calyx small, oblique, large fusiform swelling below, 2230x. I *Rabaudauropus expandens*, distinct subdistal cavity in the sub-apical swelling, 2790x. J *Amphipauropus* sp., large oblique calyx, almost no subdistal swelling, 2230x. K *Hemipauropus piriformis*, cup-shaped, 2230x. L *Hemipauropus* sp., with bracts surrounding the capsule,  $F_2$ , 2780x. M *Hemipauropus* sp., with hairy cap over distal capsule,  $F_3$ , 2790x. N *Polypauropus afrioccidentalis*, curved bracts surrounding two-parted calyx, 1675x.

The flagella in Tetramerocerata are long, cylindrical, attached with a shaft, which most often is barrel-shaped but distinctly longer than its diameter in Eurypauropodidae and Sphaeropauropodidae. The flagella are hollow, made of disc-shaped elements with

0.5-1.0 µm interdistance. The discs are densely set with short hairs in two or three whorls (Massoud, 1969) and each flagellum terminates with an apical organ.

The flagella are innervated by nine sensory cells (*Acopauropus ornatus*) (Tichy, 1987), but their function has not been investigated. When in activity, pauropods always move the antennae, often with a very rapid, rotating motion, suggesting that these appendages provide crucial information on the environment. They may have an olfactory function, or contain thermo- or CO<sub>2</sub>-receptors. In addition, because of their very large surface, they may be important in regulating water balance.

#### *Temporal organs*

On the dorso-lateral or latero-ventral sides of the head there are two large temporal organs. These are eye-like (Figs. 21.1, 21.3), but pauropods are blind, these organs have other sensory or regulatory functions. In Hexamerocerata they are cup- or umbrella-like (21.6A), with the central part attached to a shallow depression in the head capsule. In Tetramerocerata they are flat or somewhat raised and convexly rounded, in dorsal view oval-triangular. In *Decapauropus gracilis* and *D. vulgaris* their cuticle is two-layered, with many pores, and with about 16 sensory cells connected to them (Haupt, 1973). Accessory structures often occur in Tetramerocerata (Fig. 21.6B-E). Many species have pores of various shapes and position, or the margin can be partly lifted up or has tube-like extensions as in Brachypauropodidae (Fig. 21.6F), *Polypauropoides* and some species in *Samarangopus*. Sometimes the extensions protrude particularly anteriorly, reaching close to the mouth. The temporal organs can also be equipped with exterior or interior vesicles, or canals. In some taxa (e.g., *Allopauropus novicaledonicus*, Eurypauropodidae, Sphaeropauropodidae) other small fungiform or hemispherical organs occur close to the temporal organs (Scheller, 1993, 2000).

#### *Mouthparts*

The mouthparts are similar to those of Diplopoda, but weakly chitinized. The two pairs of mouthparts, the mandibles and the maxillae, are closely connected with each other. In the Hexamerocerata, the mandibles are like those in Diplopoda, strong, with ability to chop up solid nutrient into pieces (Remy, 1953), but in Tetramerocerata these appendages are weakly chitinized, adapted for sucking liquids (Hüther, 1959). The mouth is covered anteriorly by a maxillary plate. Behind the mandibles there is a lower lip, the composition of which is controversial.

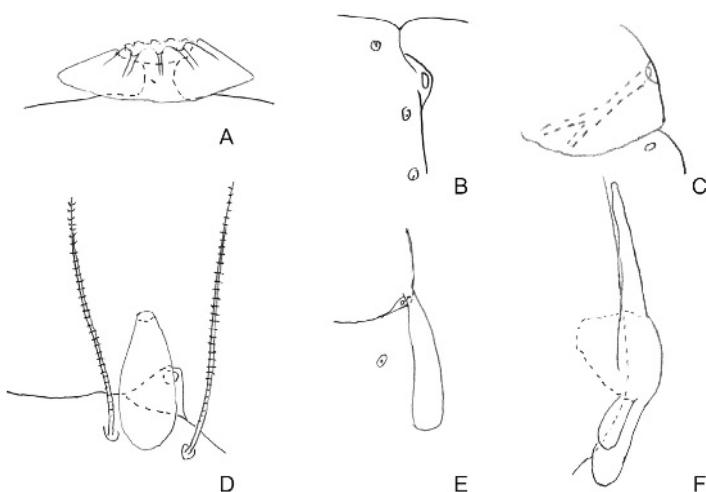


Fig. 21.6 Temporal organs. A *Milloptauropus* sp., umbrella-shaped, 955x. B *Decapauporus cederholmi*, with pore at the posterior margin, 1145x. C *Nesopauporus proprius*, thin canal in the posterior part, 2145x. D *Diplopauropus vesiculosus*, pore and posteriorly directed exterior vesicle, 1715x. E *Stylopaupropoides dytanekes*, pore and posteriorly directed exterior vesicle, 1140x. F *Zygopauporus hesperius*, with tube-like extensions, 1140x. A redrawn after Hagino (2000).

#### Trunk segments

The body is fusiform to cylindrical in the Hexamerocerata and in the weakly sclerotized genera of the Tetramerocerata, often broadest behind the middle. In strongly sclerotized genera the body is broad, rounded both anteriorly and posteriorly, but with the median part of posterior margin almost straight. In Sphaeropaupropodidae the first tergite has even become greatly enlarged, broadened and strongly convex, allowing volvation of the animal to a compact sphere.

The trunk has 12 segments followed by an apodus anal segment, the pygidium, with complicated structure. Adults in Hexamerocerata have one pair of walking legs on each segment except for the collum segment, the final number of tergites is 12 and walking legpairs being 11. In Tetramerocerata segments IV, VI, VIII, X and XII are shortened as is the dorsal part of the collum segment in such a way that whole dorsal side is covered by the tergites belonging to segments II, III, V, VII, IX and XI. When viewed from above, tetramerocerate pauropods appear to have two pairs of legs on most of the apparent body segments, but seen from below it is clear that they actually have just one pair on each segment. Sometimes in the genus *Decapauporus*, and rarely in *Polypauropus*, segment

XI too can be leg-bearing so the maximum number of walking leg pairs is 10 (Remy, 1931). The tergites in both Hexamerocerata and Tetramerocerata are generally weakly sclerotized, roundly rectangular, sometimes distinctly pubescent. In *Hemipauropus* many tergites have a cuticular mesh pattern (Silvestri, 1902), in *Colinauropus* the tergites are coarse (Remy, 1956), so too in many *Scleropauropus* species, and in *Propepauropus* the last tergite is strongly corrugated (Scheller, 1985). In Brachypaupropodidae, *Colinauropus* and *Pounamupauropus* the tergites are divided transversely and/or longitudinally into smaller sclerites with or without posterior appendages. In Eirmopaupropodidae, Antichtopaupropodidae, Brachypaupropodidae, Eurypaupropodidae and Sphaeropaupropodidae the tergites are more or less heavily sclerotized, grainy or sculptured, showing a large variation in thickness and surface structures.

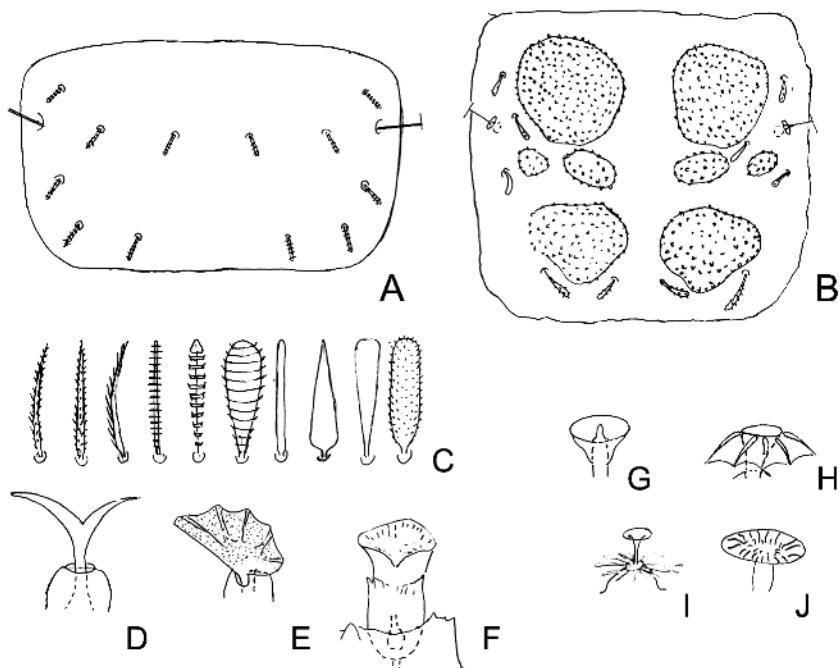


Fig. 21.7 A Paupopodidae. Typical arrangement of tergal setae in transversal rows. B *Colinauropus regis*, tergite III divided into sclerites. C Tergal setae of Paupopodidae. D-F Modified tergal setae. D *Brachypauporus meyeri*, 500x. E *Acpauporus tetrastichus*, 625x. F *Samarangopus umbonifer*, 1000x. G-J Organs of unknown function on the tergites of Eurypaupropodidae. G *Samarangopus poculifer*, 1000x. H *S. umbraculus*, 1000x. I *S. trilix*, 750x. J *S. umbonifer*, 1000x.

The setae of the tergites (Fig. 21.7) are few in number and placed in two regular transversal rows in most genera in Pauropodidae, in Eirmopauropodidae and some genera of Brachypauropodidae (*Brachypauropus*, *Aletopauropus*, *Deltopauropus* and *Zygo-pauropus*). There is most often a reduced number of setae on most anterior and most posterior tergites, e.g. 4+4 setae on tergite I, 6+6 on tergites II-IV and 4+2 on tergite VI. Many irregularly distributed setae occur in *Multipauropus*, *Hystrichopauropus*, *Adaktopauropus* and *Sphaeropauropodidae*, an irregular pattern is dominating in other groups too as in Brachypauropodidae and Eurypauropodidae. However, in *Antillauropus* and *Virginopauropus* (Hansenauropodidae) the setae are placed in regular transversal rows and in *Borneopauropus* and *Brachypauropoides* (Brachypauropodidae) there is a tendency towards transversal rows on most posterior tergites (Scheller, 2009). Deviating types of regular patterns occur rarely in *Acopauropus*.

The dorsal setae are sometimes strongly modified, lanceolate, ovoid, fusiform, Y-shaped, winged, cup-shaped; various other cuticular extensions or protuberances may occur. In some genera, particularly in *Samarangopus*, there are often cuticular organs of unknown function with peculiar shapes such as umbrellas, candelabra flames, funnels, mushrooms, all probably functioning as sensilla (Scheller, 1993, 2000).

#### *Collum segment*

The first trunk segment, the collum, is short, without walking legs, with a smooth ventral surface in Hexamerocerata, but with two appendages and an anteriorly directed process in between in Tetramerocerata. These appendages have sometimes been interpreted as exsertile vesicles but more likely they are rudiments of a pair of legs, which is indicated by their division into two parts, a thickening of the nervous cord corresponding with the last head segment and their specific position. There are also two pairs of setae anterolateral of the appendages, the most lateral one usually the longest. The median process is a cuticular plate, more or less triangular, protruding in anterior direction from the posteromedian part of the collum segment. It is most often small to very small. The appendages are conical to subcylindrical, generally directed posteriorly inwards. They have a distal, flat to hemispherical cap, rarely stalked, sometimes with a collar at the base. They can be indistinctly segmented, and the caps can be distally divided into 2, 3 or 4 sections (Scheller, 1997). In one species of *Polypauropoides* there is no process at all and in two other species, one in *Allopauropus* and the other in *Cauvetauropus*, both process and appendages are lacking. In a few species of Pauropodidae and often in

Eurypauropodidae and Sphaeropaupropodidae the process and/or appendages are conspicuously large (Scheller, 2000).

### *Pygidium*

The last abdominal segment, the pygidium, is apodus (Fig. 21.8); the posterior margin of its sternum is more variable in shape than that of the corresponding tergum. The anal plate, a characteristic of the Paupropoda, is attached to the postero-median part of the sternum. The pygidium is well developed already in the first instar and with the great morphological variation in its shape, paired setae and the anal plate, the shape and arrangement of which remain unvaried during the life cycle, the pygidium is of great importance for the identification of genera and species.

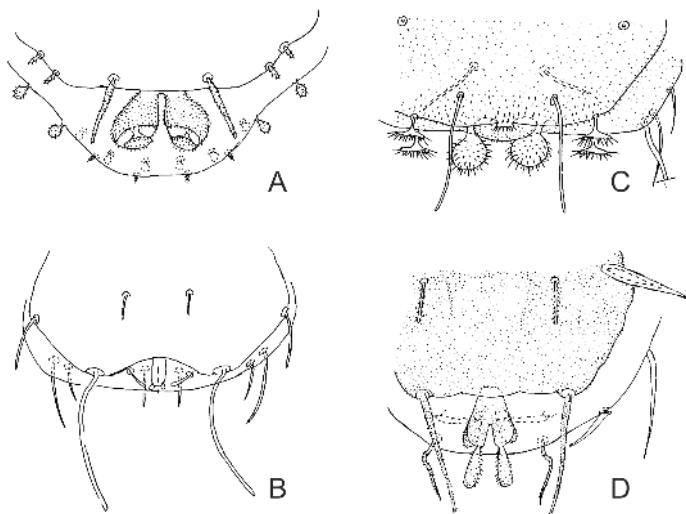


Fig. 21.8 Pygidium. A, *Millotauporus acostae* (Hexamerocerata), ventral view, 430x. B, Tetramerocerata, generalized, ventral view. C, *Polypauropus afrioccidentalis* (Polypauropodidae), ventral view, 615x. D, *Eurypauropus washingtonensis* (Eurypauropodidae), ventral view, 445x.

*Tergum.* – The posterior margin is most often rounded, rarely straight. In a few species in *Stylopauporus* it has a dorsal postero-median cleft (Remy, 1958), in some other species there are postero-median or postero-lateral lobes. In Hexamerocerata there are five to eight pairs of setae, generally short, pointed or hastiform, in Tetramerocerata four pairs,  $a_1-a_3$  and st. In the former order they have not been investigated and seem to be of limited

value for the identification of species, in the latter they vary strongly in length, direction and shape, and are of great taxonomical importance.

*Sternum.* – The posterior margin is straight or somewhat indented, sometimes with a smaller median bulge and/or with low submedian lobes. It always bears an anal plate and a pair of strong postero-lateral setae,  $b_1$  generally longer than their interdistance. In addition there are one or two further pairs of setae,  $b_2$  and/or  $b_3$ , in most genera.

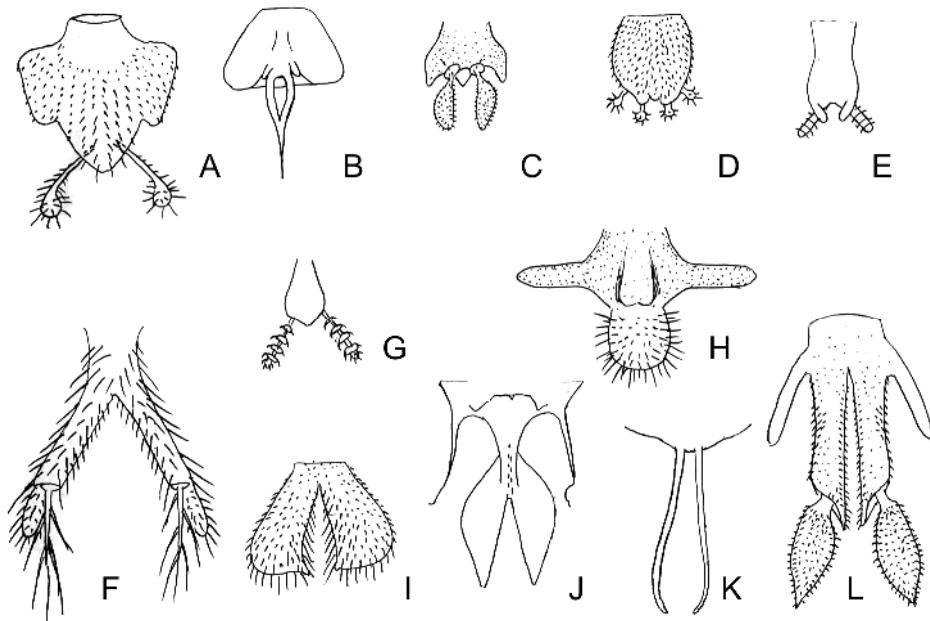


Fig. 21.9 Anal plate. A *Allopauporus sphaeruliger*, 2005x. B *A. akonesis*, 1085x. C *A. carolinensis*, 1030x. D *Decapauporus intonsus*, 1355x. E *D. tenuellus*, 2330x. F *Perissopauporus tridens*, 1355x. G *Nesopauporus proprius*, 2710x. H *Donzelotauporus cruciatus*, 2060x. I *Stylopaupoides bilobatus*, 1625x. J *Hemipauporus piriformis*, 1625x. K *Rabaudauporus dispar*, 1625x. L *Trachypauporus cordatus*, 2005x.

#### Anal plate

All pauropods have one or two anal plates (Figs. 21.8, 21.9) of 10-20  $\mu\text{m}$  attached to the postero-median part of the sternum, in Polypaupropodidae replaced by two posteriorly directed clavate appendages often with a rudimentary plate in between (Fig. 21.8C). The shape of the plate varies from species to species and offers a unique system of characters that often help to immediately identify a species. In most species there is one plate projecting backwards, backwards-upwards or backwards-downwards from the

postero-median margin of the sternum just above the anal opening. The plate is generally provided with one to six branches and/or appendages of various size and shape. In some genera of Brachypauropodidae and in Eurypauropodidae and Sphaeropaupropodidae the anal plate is built up fairly uniformly, but the morphological variation of the plate is enormous.

In Diplopauropodidae there are two anal plates, besides the sternal one, there is also a plate protruding backwards from the tergum. There is an additional tergal plate also in *Decapauporus manausensis* (Scheller, 1994).

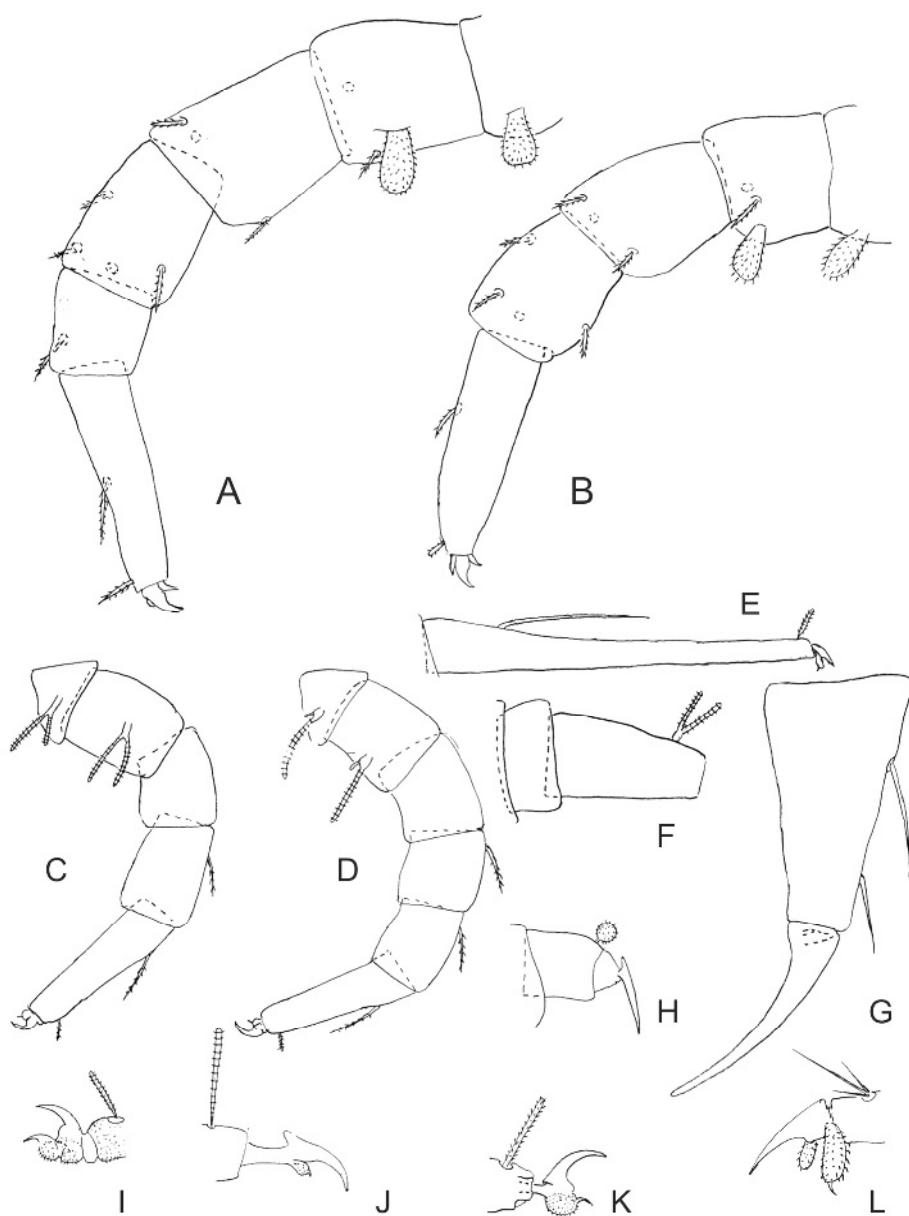
#### Legs (Fig. 21.10)

The numbers of pairs of walking legs in adults varies from 8 to 11. In Hexamerocerata there are 11 pairs on the trunk segments II-XII. Legs 1 and 9 are 5-segmented, the interposed pairs 6-segmented. Sometimes the adults can have 6 segments in the last pair of legs, indicating moulting after the adult phase has been reached.

Adults in Tetramerocerata have 8, 9 or 10 pairs of walking legs on trunk segments II-IX, II-X or II-XI (Remy, 1931), and vestiges only of a pair of legs on the first trunk segment. In most genera in Paupropodidae the first and the last pair of legs are 5-segmented and the remaining pairs 6-segmented; but in Amphiupaupropodidae, most Brachypauropodidae and Sphaeropaupropodidae all walking legs are 5-segmented, a segmentation pattern sometimes also occurring in Paupropodidae, Polypauropodidae and Eurypauropodidae. In species which can have adults with 10 pairs of legs (some *Decapauporus* and *Polypauropus*) legs 1 and 10 are 5-segmented, those remaining 6-segmented.

All walking legs are of similar shape but vary in the number of segments. The coxae are widely separated and in large species, Hexamerocerata and the genera *Pauropus*, *Stylopauporus*, *Donzelotauporus* and *Hemipauporus* in Tetramerocerata, they lengthen distinctly posteriorly. The last pair of legs in *Stylopauporus* can reach 0.3-0.4 of the length

**Fig. 21.10** Legs of Paupropoda. A-B *Millotauropus acostae* (Hexamerocerata). A Leg II, anterior view, 770x. B Leg I, anterior view, 770x. C-D Tetramerocerata, generalized legs, anterior view. C, A 5-segmented leg. D A 6-segmented leg. E *Decapauporus leptotarsus*, long and slender tarsus of ultimate leg, 770x. F *D. anomoius*, short tarsus of ultimate leg, no proximal seta, distal seta Y-shaped, metatarsus ring-shaped, 2055x. G *Samarrangopus proekes*, tarsus of ultimate leg, subconical, main claw very long, stiletto-shaped posterior appendage, 770x. H *Amphiupauporus* sp., tarsus of ultimate leg short, cylindrical, only one globular seta, main claw almost straight, 1540x. I *Allopauporus longisetus*, ultimate leg, distal part of tarsus with empodium, anterior view, 960x. J *Decapauporus janauariensis*, stalked empodium, anterior view, 2055x. K *D. seychellicus*, stalked empodium, anterior view, 1285x. L *Perissopauporus tridens*, distal part of tarsus with empodium, anterior view, 3-forked distal seta, anterior pad-like processes with claw, 1285x.



of the animal. In slow-moving genera the legs are short, sometimes, as in *Amphipauropus* and Brachypauropodidae, less than one tenth of the body length and uniform throughout

the series. There are five or six segments: coxa, trochanter, femur, tibia and a 1- or 2-segment tarsus, the latter bearing a distal empodium with a main claw flanked by one or two rudimentary claws, one of them sometimes on a pad-like structure, which may function as a fastening apparatus on smooth surfaces. The metatarsus is annulated in some species of Pauropodidae. In all pauropods the coxa and trochanter have each at least one large seta. These setae are foliform in Hexamerocerata and accompanied by one or two short pubescent setae. All the following segments have a small and varying number of short setae. In Tetramerocerata there is only one single seta on the upper part of the coxa and trochanter, but of very varying shape: cylindrical, foliform, branched, simple, furcate with subsimilar branches or with one of them more or less reduced. The coxal setae of the second pair of legs in adult males often have an aberrant shape. The femur has no setae, the tibia has one and the tarsus has two to four setae, the distal one on the dorsal side varying extensively in shape.

The empodium consists of a weakly curved main claw and two lateral processes (Massoud, 1970). The main claw can be almost straight to sickle-shaped, in *Amphipauropus* very thin. It is sometimes stalked (a few species in *Allopauropus*, *Decapauropus*, *Stylopauropus*, *Polypauropoides*), or can have a narrow collar, as in *Borneopauropus penanorum*. In Hexamerocerata and most genera in Tetramerocerata, the anterior processes are pad-like with a distal pointed and sometimes claw-like appendage, the posterior one claw- or stiletto-like. In Eurypaupropodidae and Sphaeropaupropodidae both lateral processes can be well developed (*Acopauropus*, *Eurypauropus*) or only the anterior one (*Samarangopus*, *Sphaeropauropus*).

The distal seta of the tarsus is generally short, pointed, cylindrical or somewhat clavate, but can have the shape of a trident, or is Y-shaped or spatulate-globular.

Pauropods are strikingly agile, their locomotory mechanisms result in speedy running and in agility by means of a fast pattern of gait, and the body is kept high and is markedly rigid as they run. The rigidity is supported by the large distance between the coxae, the low number of tergites, no intercalary tergites as in Symphyla and some Chilopoda, the deep dorso-ventral and oblique muscles and extrinsic muscles of adjacent segments as well as the intrinsic musculature.

### *Integument*

Trunk tergites are weakly sclerotized except in Eirmopaupropodidae, Antichtopaupropodidae, Eurypaupropodidae, Sphaeropaupropodidae and, to a lesser degree, in Colinauropodidae and some genera of Brachypaupropodidae. Sternites are lacking or

divided and small, only the sternite of the anal segment is somewhat sclerotized. Between the firmer parts of the integument the cuticle is soft, as in the intersegmental and pleural membranes, and allows for expansion of the trunk to adjust to the nutritional and reproductive state of the animal. No pleurites are present. The soft integument contributes to the high agility often shown. Many, maybe most, species in Pauropodidae can curve the body 90-180° in all directions.

### *Nervous system*

#### *Central nervous system*

In *Pauropus silvaticus*, the brain is comparatively large with its hind end intruding deep into the second trunk segment (Tiegs, 1947). It is triangular in dorsal view with the narrowest corner of the triangle directed forward. The protocerebrum is relatively large and its broad hindmost part consists of three lobes, of which the posterior one forms an inverted trough arching over the nerve cord. The deutocerebrum has two lateral expansions which extend in the direction of the temporal organs. Some cerebral nerves have been observed: one pair from the temporal organs and two unpaired nerves ending in the frontal ganglion of the stomatogastric system, a pair of probably sensory nerves associated with the setae of the roof of the head, two antennary nerves, a pair of presumably motor nerves to the antennae, a pair of nerves supplying the antennary sense organs and a pair of clypeal nerves.

The ventral nerve cord consists of (1) a small sub-oesophageal ganglion formed by the fusion of the mandibular and a single maxillary ganglion, (2) a single collum ganglion and (3) a succession of nine large ganglia, one in each leg-bearing segment. From each trunk ganglion arise five pairs of nerves. Four of them innervate leg muscles and dorsoventral muscles, the fifth goes to the dorsal body wall and is joined in alternate segments by a large sensory nerve from each of the bothriotricha.

#### *Sensilla*

Sensilla have been found on the head, particularly on the antennae, and on the dorsal side of the trunk. In Hexamerocerata there is a small basiantennal organ, a small shallow indentation in the antennal base, containing an organ of similar structure as the antennal globulus described below, and in *Allopauropus novicaledonicus* and some Eurypauropodidae

and Sphaeropauropodidae species there is a pair of small fungiform organs near the temporal organs.

The antennal globulus is the most conspicuous sensillum in Tetramerocerata. It protrudes outward from the cuticle of the ventral antennal branch between the bases of the flagella  $F_1$  and  $F_2$ . It is generally small but sometimes it can be conspicuous, as large as the antennal branch on which it is situated. It consists of a stalk, which generally is more or less conical, sometimes however almost cylindrical (particularly in Eurypauropodidae), and one or two chitin capsules, the latter surrounded by a palisade of 4 to ca. 20 bracts that arch over the capsule(s), distally tapering, subparallel, exceptionally branched.

The capsule in the middle is generally spherical or somewhat flattened, rarely ovoid, in a few species in *Decapauropus* and *Polypauropoides* it is umbrella-shaped (Scheller, 2005). The globulus is innervated by eight sensory cells (*Acopauropus ornatus*) and may contain gustatory receptors or may function as a hygroreceptor (Tichy, 1987). Hexamerocerata have no globuli but a possibly equivalent structure in the candelabra-like organ on the distal antennal shaft segment. It is generally three-forked but the arms can be branched near the tip. A rudimentary globulus is present on the ventral side of the third antennal segment in many genera in Pauropodidae, Brachypauropodidae and Eurypauropodidae. It is most often very small but can be distinctly stalked in *Rabaudauropus* and a few genera in Eurypauropodidae.

In the antenna of Tetramerocerata there is also a distal organ on the flagella, the calyx, of unknown function. This is generally a shortly pubescent hemispherical or conical, rarely asymmetrical, structure, with a small indentation in the underside and/or in the more or less distinct swelling of the axis of the flagellum just below. The calyx can be replaced by a structure similar to the antennal globulus built up by a central capsule surrounded by two to six bracts as in *Hemipauropus*, *Polypauropoides* and *Polypauropus*. In a few species the calyx can be exceedingly small (e.g., *Decapauropus bovistellus*).

All pauropods have long sensory hairs, the bothriotrichs (Fig. 21.11), more or less pubescent and inserted laterally on some tergites. Adults have five pairs of bothriotrichs on tergites II, V, VII, IX and XI in Hexamerocerata, on tergites II-VI or corresponding places in Tetramerocerata.

Each bothriotrich protrudes from a cuticular cavity into which its basal conical bulb is inserted and connected with the underlying tissue with a thin stalk by which it has contact with eight radially arranged nervous cells (*Decapauropus gracilis*, *D. vulgaris*).

Bothriotrichs seem to be mechanoreceptors which make it possible to get information about air currents from eight directions (Haupt, 1978).

Most bothriotrichs are simple and similar to each other, but the third pair ( $T_3$ ) is often deviating, e. g. with end-swelling, or may be thickened further downwards with one to three distinct swellings or their axes are clavate, or they have branches and simple or branched pubescence hairs of various structure. Morphological variation is highest in Pauropodidae, Polypauropodidae and Amphipauropodidae.

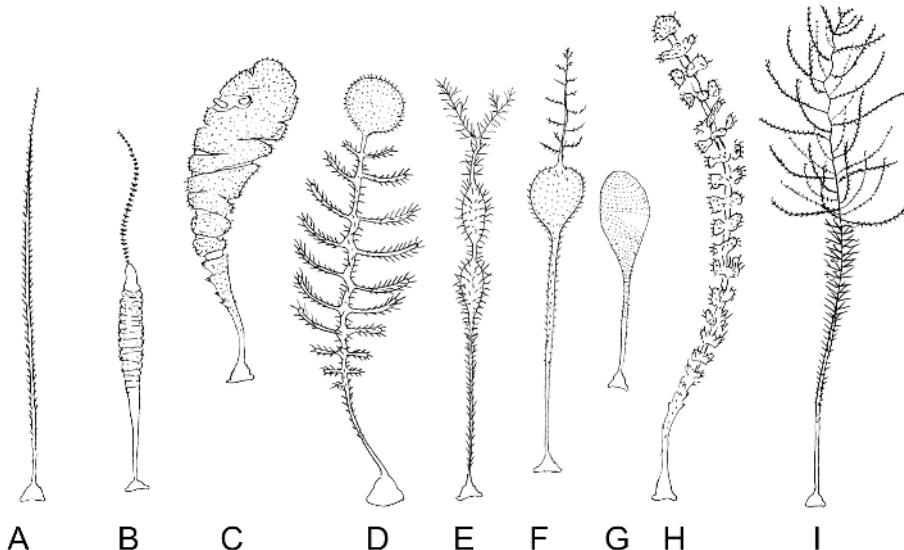


Fig. 21.11 Bothriotrichs. A A common type. B *Brachypauropoides prolatus*, proximal half fusiform, distal half thin, simple, with small discs,  $T_3$ , 640x. C *Amphipauropus* sp., clavate, with irregularly sculptured surface,  $T_3$ , 1770x. D *Decapauporus multiarcuatus*, distal plate and subcylindrical curved branches in pairs,  $T_3$ , 1060x. E *Allopauporus brachycaulis*, two submedian swellings and branched distal part,  $T_3$ , 1275x. F *Stylopaupropoides subantarcticus*, subglobular median swelling, distal third very thin, branched,  $T_3$ , 810x. G *Virginopauropus asperimus*, clavate,  $T_3$ , 850x. H *Amphipauropus* sp., irregular discs,  $T_5$ , 1700x. I *Allopauporus semiputatus*, distal polyramose section,  $T_3$ , 1060x.

#### Stomatogastric nervous system

The visceral nervous system of *Pauropus silvaticus* consists of a stomatogastric and a caudal system (Tiegs, 1947).

The visceral system includes a frontal ganglion on the floor of the clypeus, a pair of small oesophageal ganglia close to the oesophagus and a minute ganglion at the posterior end of the oesophagus at its entrance into the midgut.

The caudal system, arising from the terminal ganglion, consists of a band of nerve fibres that passes back along the floor of the terminal segment onto the rectum's lower surface.

### *Skeletomuscular system and locomotion*

The body structure is correlated with the ability to both elongate the body and to shorten it by contraction to a very high degree, but also to greatly curve the body particularly in the horizontal plane and to use a fast pattern of gait. The high agility is largely due to a well developed musculature and to the soft integument (*P. sylvaticus*).

The most important dorsal muscles of the head are the abductor and adductor muscles for the antennae, two large muscles which probably adjust the convexity of the chitinous cover of the temporal organs and the retractor and depressor muscles for the mandibles. Most sternal muscles of the head insert on the hypopharyngeal apophyses: two muscles which may have a rotatory effect upon the antennae, a strongly developed set of muscles to the mandibles and small muscles associated with the maxillae. Besides the mentioned rotatory muscles, the antennae have flexor and extensor muscles both for the shaft and for the two branches. The muscles associated with the foregut and the preoral cavity are two sets of short buccal dilators and depressors, a retractor to the clypeus and a set of strongly developed dilator muscles.

The musculature of the trunk consists of dorsal and ventral longitudinal muscles, two sets of oblique abdominal muscles, dorso-ventral and crossed ventral muscles and three muscles responsible for the movements of the head, a rotatory, a levator and a retractor.

The extrinsic leg musculature comprises three muscles for each leg, a large promotor, a weaker abductor and an exceptionally large backward directed remotor. There are no muscles in the three distal leg segments.

### *Mechanics of locomotion*

In addition to a putatively primitive locomotory mechanism allowing them to creep in narrow irregular spaces, adult pauropods also run swiftly in short rushes with markedly rigid body. Only young instars use a slow pattern of gait. The presence of many trunk muscles, soft integument and widely separated coxae allow both a slow gait similar to that of the epimorphic Chilopoda and a fast gait. The relative duration of the backward stroke can be as short as in the swiftest chilopod, one-quarter of the duration of a pace.

When creeping with slow gait the body keeps soft and can be turned in U-shape in all directions, at least in most weakly sclerotized species (Manton, 1953, 1966, 1974).

### *Digestive system*

#### *The alimentary canal*

The digestive system has been described by early authors (Latzel, 1884; Silvestri, 1902; Schmidt, 1894, 1895; Verhoeff, 1934) and in later times by Tiegs (1947) in *Pauropus silvaticus*, and by Zanger (1986) in *P. huxleyi*. The alimentary canal begins with a small preoral cavity in which the mandibles work and a pair of salivary glands open out. It is anteriorly delimited by the clypeolabrum/epipharynx, posteriorly by the maxilla. Posteriorly it is followed by a cylindrical undifferentiated ectodermal foregut extending rectilinear to the third trunk segment. The entodermal midgut, beginning in segment IV, is convoluted (*P. huxleyi*) or straight (*Allopauropus brevisetus*) and about twice as wide as the foregut. It has no muscles and ends in the tenth segment, where it abruptly narrows to a short winding tube just before the rectum. The latter is ovoid, muscular, with an outer wall with heavy ring-muscles and a thin inner layer of longitudinal muscles.

### *Excretory and osmoregulatory organs*

#### *Malpighian tubules*

Malpighian tubules lie along the posterior part of the ventrolateral surface of the midgut. They are longish and somewhat clavate in *Eurypauropus*, tapering anteriorly in *Allopauropus*, markedly degenerate without connection with the midgut in *Pauropus silvaticus* (Tiegs, 1947). In studies on *Pauropus* (Zanger, 1986) they have been looked for but not found.

The presence of crystals forming in the midgut epithelium and their secretion into the lumen indicate that the midgut may be the principal excretory organ (Zanger, 1986). It is unknown if special osmoregulatory organs exist.

#### *Glands*

Among the salivary glands of *Pauropus silvaticus*, the clypeal glands are small with an unbranched lumen (Tiegs, 1947). They lie on the floor of the clypeus and open into the

preoral cavity whereas the premandibular glands are relatively large and located dorsolaterally in the second abdominal segment. The latter are devoid of a lumen and open with thin ducts lateral to the bases of the mandibles.

The maxillary glands are largest and reach into the collum segment. They are long and tubular and end in the preoral cavity just behind the bases of the mandibles. The intermaxillary glands are a pair of bilobed masses of glandular tissue, sometimes even fused into a single compact mass lying in part of the floor of the head capsule and the collum segment.

The pseudocular glands lie flattened out against the whole of the epithelium of the temporal organs. Their function is unknown.

#### *Fat-body*

A fat body is present in the trunk of *P. silvaticus*, where it may fill the haemocoel from the floor of the collum segment and backwards. If not laden with reserves it is disposed dorsally. In adult animals in good nutritional condition and with ripe gonads it is obliterated.

There is a relatively spacious cavity to either side of the nerve cord but there are very rarely cells having the appearance of blood cells (Tiegs, 1947).

#### *Tracheal system*

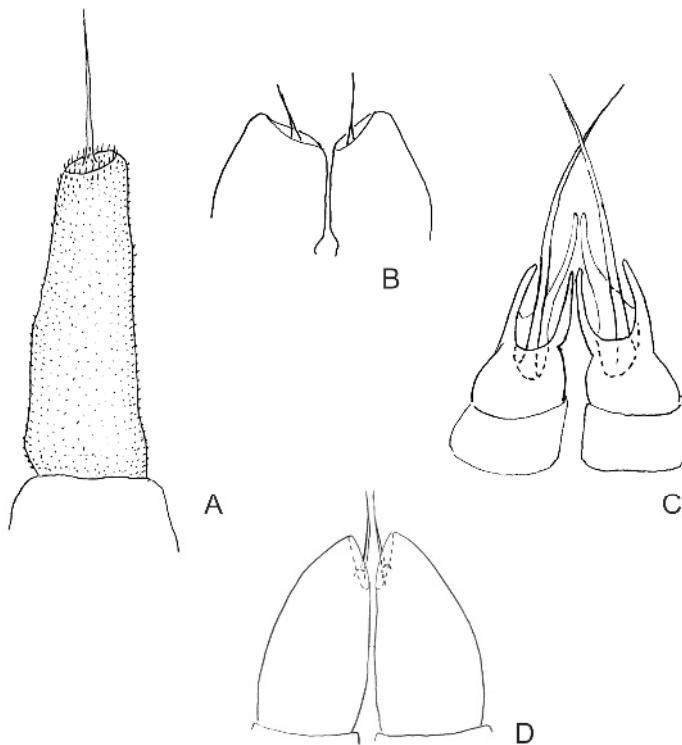
Most pauropods lack tracheae, these having only been found in Hexamerocerata. In this group there are two thin tubes on each side, without spiral thickenings running anteriorly from a stigma at the base of the coxa of the first pair of legs. They reach into the posterior part of the head and one of the two submedian tubes is curved over the other (Remy, 1953). Short rudiments of tracheae are at the bases of the other legs. The thin cuticle covering the lateral parts of the trunk is probably the main surface involved in gas exchange.

#### *Reproductive organs and reproduction*

The Pauropoda are bisexual and progoneate with the gonopores on the ventral side between the second pair of legs: a median, unpaired, almost concealed aperture in females, paired apertures in large, submedian, generally conical papillae in males (Fig. 21.12).

### Female organs

The ovary of *P. silvaticus* is an unpaired thin-walled sac lying between the nerve cord and the intestine from the fifth to the eighth segment, and when replete with eggs, even into the tenth. The eggs are produced from a germarium in its bottom. Four to six eggs may be found growing simultaneously, accompanied by numerous undeveloped ones. They are attached to the ovarian wall with a thin follicular membrane. Between the ovary and the short oviduct there is a thick-walled ductus glandularis in the fifth to third abdominal segment. The oviduct is unpaired and may lie either to the left or to the right of the nerve cord. It ends in the genital atrium, a slight depression in the floor of the third segment, into which the flask-shaped receptaculum seminis opens above the orifice of the oviduct (Tiegs, 1947). No genital sclerites are associated with the sexual opening.



21.12 Genital papillae of Pauropoda. A *Millotauporus angustiramosus*, right papilla, inner view, 1200x. B *Allopauporus brevisetus*, subcylindrical, short papilla, truncate, 790. C *Samarangopus ternarius*, with three distal extensions, anterior view, 630x. D Most common type, Pauropodidae, anterior view, 1200x.

*Male organs*

The testes of *Pauropus huxleyi* and *P. silvaticus* (Tiegs, 1947) are four sac-like organs lying above the alimentary canal just below tergites IV-VI. The four vasa deferentia, two on either side, continue forward below the intestine, to become four vesiculae seminales which become confluent in the sixth segment, forming there two ejaculatory ducts which pass, one on each side, to the genital papillae. The latter are well developed in the adult stages, 10 and 11 pairs of legs in Hexamerocerata, and in the last stage in genera with at most 8 or 9 pair of legs in Tetramerocerata.

Occasionally, well developed genital papillae can be found in the stage with 6 pairs of legs in Brachypauropodidae. In most species, the genital papillae are close to each other, generally conical and roundly distally with a single short thin apical seta.

In one *Brachypauropus* species the genital papillae are two-segmented with both parts of the same length, in a few species the distal seta is as long as the papilla and in *Samarangopus* there are species having the distal part of the papilla enlarged and tube-like or 3-branched. In subadult stages the papillae are conical too, but small, often transparent, and difficult to see, sometimes with a rudimentary seta.

*Gametes*

The eggs of *Pauropus silvaticus* are minute (diameter 0.05-0.16 mm) (Silvestri, 1902; Tiegs, 1947), spherical, pearly white and are laid singly or in clumps.

The sperm cells of the Paupropodidae are flagellate and needle-like (Rosati et al., 1970; Bacetti & Dallai, 1978; Bacetti et al., 1979).

*Chromosomes*

A diploid number of 12 chromosomes was found in both sexes in *Allopauropus brevisetus*, with no evidence of heterochromosomes;  $2n=24$  was reported for *A. danicus*, with XY male heterogamety. An X0 condition was suggested instead for *Pauropus furcifer* and *P. huxleyi*, of which however only male specimens were studied (Fratello and Sabatini, 1990).

*Sperm transfer to egg-laying*

The transfer of sperm is indirect, details being known only for a few species (Laviale, 1964; Schuster and Hasenhütl, 1983). In *Stylopauropus pedunculatus*, *Trachypauropus latzeli*,

*Acopauropus ornatus* and an undescribed species of Eurypauropodidae, a drop containing some hundreds of sperm cells is deposited upon a small web fixed to the substratum and stretched between soil particles or over uneven substrate. The web (diameter 0.2–0.6 mm) consists of hundreds of thin threads on the top of two thick knotty ones in a V-position, under them a web of smooth branched and anastomosing thin threads on which the sperm drop is placed (*Stylopauropus pedunculatus*). A similar web with two types of threads is made in the three species of Eurypauropodidae mentioned above but there the knotty threads are thinnest and the web consists of three layers: at the bottom a layer of glabrous threads on which the sperm drop is placed, above a probably supporting web made of strings of both glabrous and knotty threads up to >0.5 mm long, and topmost a web of smooth threads partly covering the sperm drop.

The females take up the sperm drop and after fertilization the eggs are laid, isolated or in clumps, between soil particles in secluded clefts in the soil or in decaying vegetable matter.

#### *Sexual dimorphism and parthenogenesis*

Sexual dimorphism is rare but small sexual differences in the shape of the anal plate and the pygidial setae have been observed in *Decapauropus*.

In some species of Pauropodidae males are rare, suggesting the occurrence of parthenogenesis. In some *Decapauropus* species living in areas with unfavourable environmental conditions males can be very rare or even lacking and at the same time a high proportion of females of the additional adult stage with 10 pairs of legs may occur. Such spanandric populations (Scheller and Adis, 2000) with probable parthenogenetic reproduction as an adaptation to a mode of reproduction suitable for areas where the species has difficulties in reproducing or colonizing with bisexual individuals, have been reported from North Europe and North Africa.

#### *Development*

##### *Embryonic development*

The egg of *Pauropus silvaticus* is spherical and the chorion is densely covered with minute spines, amongst which there is a single spine of much greater size. The interior of the egg is mainly occupied by yolk. There is neither periplasm nor a vitelline membrane (Tiegs, 1947).

After the 4-cell stage, the cleavage is markedly asynchronous. A short blastula stage with about 80 cells outermost is followed by a gastrula which lasts until about 160-180 cells have been formed in the outer layer. During the third day the gastrula develops into a blastoderm phase. There is much variation between individual blastoderms but eventually in all cases a ventral thickening develops for the impending formation of the germ-band. During the fifth day this thickening is differentiated, the lower part to the germ-band and the dorsal will become the provisional body wall.

By about the end of the fifth day the head-lobes have appeared, a small stomodeal orifice has arisen and the proctodeum begins to form. By the seventh day the stomodeal opening is conspicuous, the head lobes have enlarged, the antennae are now sharply defined and evidence of two new segments has appeared. The stomodeal opening has become a wide cleft, antennae and mandibles are more distinct and a first outline of the maxillae is distinguishable. The first leg-bearing segment is recognizable by its appendages. During the eighth day the first leg pair has enlarged, the second has appeared, the first embryonic cuticle develops and three rows of setae appear on the head.

#### *Pupoid phase*

A few days before the animal is due to emerge from the egg the embryo has developed into a pupoid phase (Tiegs, 1947). This is quiescent and lasts for a few days. Its cuticle is setose and may have outgrowths corresponding to the position of the antennae and, more or less, the first three pairs of legs (*Pauropus silvaticus*, *Trachypauropus latzeli*). The pupoid itself is smooth, white, about 0.2 mm in length, immobile, with minute oral and anal apertures. It is surrounded by a second embryonic cuticle adorned with long thin setae over its dorsal and lateral surfaces. Its sheath shows the impression, from within, of the bifurcated tips of the antennae and of the tips of the first and second, but not third, legs. After three or four days a split appears along the dorsal surface and the first instar larva is hatched. In at least one species in Eurypaupodidae there are two pupoid phases; in this case, the antennae and two pairs of legs are only visible beginning with the second phase (Hasenhütl, 1987).

#### *Post-embryonic development*

The total time required for the post-embryonic development is unknown, but it may well last three to four months. The life-span of the adult is unknown too, but more than a

year has been recorded in laboratory conditions. At least in some species in both orders moulting continues after the full number of body segments have developed.

The sequence of post-embryonic stages observed in the Hexamerocerata and Tetramerocerata is given in Tab. 21.1 and 21.2 respectively (Bagnall, 1935; Tiegs, 1947; MacSwain & Lanham, 1948; Scheller, 1970).

In all stages, the first and the last legs are 5-segmented, the others 5- or 6-segmented.

In the first instar larva of *Pauropus silvaticus* the head already possesses most of the characters of the adult, with temporal organs, developed mandibles and maxillae; in the pygidium all setae and the anal plate are developed with proportions similar to those of

Tab. 21.1 Post-embryonic developmental stages in the Hexamerocerata

	leg pairs	penultimate leg podomeres	antennal shaft segments	trunk segments	tergites	botriotrichs
L I = juv. 6	6	6	4	9	8	4
L II = juv. 8	8	5	5	11	10	4
L III = juv. 9	9	6	5	11	10	5
L IV = juv. 10 = subadult 10	10	6	6	11	11	5
Adult	11	6	(5-)	11	12	5

Tab. 21.2 Post-embryonic developmental stages in the Tetramerocerata

	leg pairs	antennal shaft segments	trunk segments	tergites	botriotrichs
L I = juv. 3	3	2	7	3	2
L II = juv. 5	5	3	8	4	3
L III = juv. 6	6	3	10	5	4
L IV = subadult 8	8	4	11	5	4
adult	8(-10)	4	12	6	5

the adult animal. After about three weeks the larva moults to the following stage (second instar larva) with 8 abdominal segments, the new segment being the seventh abdominal, which has developed between the sixth segment and the anal segment of the previous instar; the antennal shaft has 3 segments, the new segment having been generated at the base of the antenna; 4 tergites; 5 pairs of legs, the newly formed legs being 5-segmented with undivided tarsi, but the hitherto unsegmented tarsi of the second and third legs have divided into two segments.

In the third instar larva, with 10 abdominal segments, segment VIII and IX are new; segment VIII, like IV and VI, is wedge-shaped and without a tergite; segment IX, like V and VII, is a large segment, with a tergite and bears the new fourth bothriotrich. On segment VII the sixth pair of legs has formed, its tarsi being unsegmented; the tarsi of the fourth and fifth legs are now divided. A stage with 7 pairs of legs has been reported from *Amphipauropus* only but has not been studied yet.

In the fourth instar larva, with 11 abdominal segments, the tenth is new and like the alternate segments that precede it, it is wedge-shaped and without tergite and legs; 8 pairs of legs, of which two segment VIII and IX, which were the new segments of the previous instar, the seventh and eighth legs have unsegmented tarsi, the tarsi of the sixth legs have become bisegmented. In some genera the adult stage with fully developed genital papillae may be achieved already in this stage. Adults with more than eight pairs of legs are unknown in *Cauvetauropus*, *Amphipauropus*, *Aletopauropus* and *Zygopauropus* and at least some species have well developed genital papillae in this stage, also in *Allopauropus*, *Juxtapauropus* and *Brachypauropus*.

In the adult there are 12 trunk segments, the newly acquired segment being the eleventh, the pre-anal segment, with tergite, bothriotrichs and sclerotized sternite but devoid of legs, 9 (or 10) pairs of legs, a new pair of legs has been formed on the tenth segment, the new segment of the previous instar; if not all legs are 5-segmented, the first and last pairs are 5-segmented and remaining pairs 6-segmented.

### *Ecology*

#### *Habitat*

Though the number of species diminishes greatly northwards (15 species together in Norway, Sweden and Finland vs. about 90 in a subequal area in Central Europe), several species are able to survive very cold winters. There are finds in east Siberia up to 68°N, in Sweden up to 65.9°N, in Alaska up to 65°N (Scheller, 1986, 1990). In the southern hemisphere, pauropods have been collected on the subantarctic Crozet Islands and Stewart Island, 46°S and 47°S respectively. In cold areas the animals probably migrate to frostless depths before the winter.

Most species are sensitive to dry air and aggregate where humidity is high. Resistance to drought is likely conspicuous in *Euryopauropodidae* and especially in *Sphaeropauropodidae*, both of which are characterized by thick cuticle, the latter also having the capability to coil to a compact, tight sphere. Two species of *Decapauropus* have

been collected from the Negev desert in Israel. On the other side, pauropods generally avoid wet environments, but *Amphipauropus* species might be more dependant than the others on damp saturated air, as they seem to live in close connection with the ground-water surface. In general, moisture is likely more important in influencing vertical distribution than is soil temperature.

Pauropods cannot burrow, thus pore space in the soil is of prime importance, but they can inhabit strata from litter to the subsoil in a variety of plant communities and soil types, agricultural habitats included (Lagerlöf & Scheller, 1989; Bedano et al., 2006). Rarely, however, they occur in heavy soils. Generally they are much more common in broad-leaved than in coniferous forests (Meyer & Scheller, 1992), very rare in peaty soils. Pauropods live also sometimes in decaying logs or under bark and moss carpets and have even been found in odd habitats such as tree-fern crowns, on living tree-trunks and walking up the walls of a cellar. Adaptations for life in caves are rare (Scheller et al. 1997)

The small body size allows them to penetrate into deep layers, and pauropods have to be included in the edaphic faunal constituent, they even tend to be deep-soil inhabitants. Sampling below a depth of half a meter has at times shown considerable numbers there, they follow root canals and earthworm burrows down to the ground water surface and have been collected at depths of 1.5-3.1 m (Price, 1975).

However, the large and strongly sclerotized species in Eurypauropodidae and Sphaeropauropodidae (among them the largest species found, the Indonesian *Samarangopus amplissimus*, 2.04 mm) prefer litter before soil.

In most environments their occurrence is very patchy and the populations sparse (Meyer & Scheller, 1992), but locally up to several hundred specimens/dm<sup>2</sup> have been found, e.g. in damp deciduous forests and agricultural habitats (Hågvar & Scheller, 1998).

Occasionally, pauropods are most abundant near the surface, in a zone about 10-20 cm deep (Price, 1975; Moore, 1982; Adis et al. 1999, Hågvar, 1997) characterized by favourable humidity, temperature and darkness conditions, sufficient aeration rates, accumulation of organic debris and living roots, but there are signs showing that in certain soils at least 10% of the population is living deeper than 1.1 m. When pauropods occur in the uppermost layers they often live together with springtails, various types of mites, insect larvae, diplurans and symphylans. Results from deeper sampling indicate association with proturans and earthworms. Pauropods are shy of light and exposed to light they try to disappear in crevices and soil clumps as soon as possible.

Vertical migration occurs induced by seasonal changes in soil temperature and moisture.

### *Feeding habits*

The feeding habits of most species are unknown, but the main food items seem to be fluids from fungus hyphae and root hairs (Hüther, 1959).

The mouthparts are proportionally strong in Hexamerocerata and allow consumption of solid material. The midgut can contain fungus hyphae, spores, plant tissue, small mineral particles, rarely arthropod setae (Remy, 1953).

The mouthparts in Tetramerocerata are weaker, pointed-sucking. No solid particle has been observed in the lumen of the midgut. The mandibles are used for penetrating the cell walls and the fluid is sucked up, aided by peristaltic movements in the midgut.

Pauropods are not serious plant pests but a species widespread in the tropics, *Decapauropus proximus*, has been found damaging *Saintpaulia* cuttings in a greenhouse by sucking out root-hairs (Scheller et al., 2004).

### *Geographical distribution*

In general pauropods are susceptible to changes in humidity, temperature and light but in spite of that they are more widespread with a greater richness in species and specimens than has been presumed for long time.

They are known from almost anywhere in the world, except for Antarctica, but the distribution areas of the individual species are still very incompletely known because active search for pauropods in new areas has been limited. The approximate range can be estimated only for some widespread genera.

The family Paupodidae is best known, rich in species and found nearly everywhere if the living conditions are suitable. *Decapauropus* and *Allopauporus* are subcosmopolitan and *Pauporus* shows a similar picture, however it is unknown from Amazonas and a few well-studied tropical islands. *Stylopauporus* too is a very widely distributed genus, having a range covering the temperate areas of the Holarctic with extensions to south Asia, Madagascar and Notogaea. Other genera occurring in all the main zoogeographical regions are *Hemipauporus*, rare in temperate areas, and *Polypauropus*, not yet found in East Palaearctic. Moreover, *Rabaudauporus* and *Polypauropoides* have wide ranges, the former not yet found in the Nearctic and the latter seems to be lacking in the Notogaean region and in the eastern parts of the Palaearctic and Oriental regions. Another wide-range genus is *Cauvetauporus*, known from southern West Palaearctic, the Neotropical, Ethiopian and Oriental regions.

In Eurypauropodidae, *Samarangopus* is the most widely distributed genus occurring in four of the main regions, most species in the Oriental region but occurring also in the Ethiopian region, the easternmost Palaearctic and Notogaea.

These ten widespread genera contrast with at present 13 other genera (*Afrauropus*, *Antillauropus*, *Borneopauropus*, *Desmopauropus*, *Diplopauropus*, *Eburnipauropus*, *Hystrichopauropus*, *Multipauropus*, *Propepauropus*, *Ataktopauropus*, *Eirmopauropus*, *Antichtopauropus*, *Zygopauropus*), all with one or at most two species known from a single country only.

As far as known, 12 genera are confined to the Holarctic region, *Acopauropus*, *Aletoptauropus*, *Amphipauropus*, *Brachypauropus*, *Deltopauropus*, *Desmopauropus*, *Eurypauropus*, *Hystrichopauropus*, *Multipauropus*, *Propepauropus*, *Trachypauropus*, *Zygopauropus*. Three more genera are mainly Holarctic: *Donzelotauropus*, but it extends southwards to middle China, and *Scleropauropus* and *Fagepauropus*, both extending southward into the tropics.

Some genera seem to be tropical (*Afrauropus*, *Eburnipauropus*, *Ferepauropus*, *Millotauropus*; *Nesopauropus*, *Virginopauropus*). Others seem to have their main occurrence in the tropics but have extension of range northwards (*Cauvetauropus*, *Colinauropus*, *Sphaeropauropus*), or southwards (*Brachypauropoides*, *Hansenauropus*, *Perissopauropus*, *Stylopauropoides*). Endemism may be more common in the tropics than known at present.

### *Evolutionary history*

There are no fossils before the time of Baltic amber, from which a single species is known, *Eopauropus balticus* Scheller and Wunderlich, 2001, probably belonging to the Pauropodidae (Scheller and Wunderlich, 2001).

However, pauropods seem to be an old group with several characters showing their monophyletic origin: the branched antennae which primarily are six-segmented, the temporal organs of the head, the triangular plate of the 2<sup>nd</sup> pair of maxillae, the five pairs of bothriotrichs and the anal plate.

### *Classification*

An updated system of the Pauropoda has been recently provided by Scheller (2008) and will be adopted in this work.

Order HEXAMEROCERATA Remy, 1950. – Antennal stalk 6-segmented, strongly telescopic; dorsal antennal branch *t* projecting from segment 5, ventral branch *s* from segment 6; ventral antennal branch with one flagellum; temporal organs circular, cup-shaped; trunk with 12 entire tergites; tracheae opening at the base of the first pair of legs;

adults with at most 11 pairs of walking legs; developmental stages with 6, 8, 9, 10 and 11 pairs of legs. Mainly tropical.

Family MILLOTAUROPODIDAE Remy, 1950.

*Millotauporus* Remy, 1950. – Palaearctic region: Japan. Neotropical region: Brazil. Ethiopian region: tropical continental Africa, Madagascar, Seychelles. 8 species, incl. *M. acostae* Scheller, 1997 (Brazil), *M. angustiramosus* Remy, 1955 (Madagascar), *M. silvestrii* Remy, 1953 (Madagascar).

Order TETRAMEROCERATA Remy, 1950. – Antennal stalk 4-segmented, not telescopic; antennal branches projecting from segment 4; ventral antennal branch s with two flagella, at least one globulus and one seta; temporal organs irregularly oval, at least the central part flattened, margins not or only partly lifted up; trunk with 6 entire or partly divided tergites; no tracheae; one rudimentary pair of legs on the first trunk segment; adults with at most 10 pairs of walking legs; developmental stages with 3, 5, 6, (7), 8, 9 and 10 pairs of legs. Distributed worldwide.

Family PAUROPODIDAE Lubbock, 1867. – Ventral antennal branch with one globulus and one seta, q, setae on head and tergites most often cylindrical or tapering. Tergites I and VI leaving head and pygidium free. Dorsal side of head with one anterior unpaired seta and 4 transversal rows of setae; tergites entire, insignificantly or weakly sclerotized, setae of tergites generally in regular transversal rows, rarely modified; adults with 8-10 pairs of legs; first and last pair of legs 5-segmented and remaining pairs 6-segmented, or all pairs 5-segmented; empodia with well-developed median claw and anterior and posterior appendages; one anal plate; body fusiform-cylindrical, generally whitish.

*Pauropus* Lubbock, 1867. – Anterior and posterior margins of ventral antennal branch s subsimilar in length; antennal globulus g short-stalked; antennal ventral branch with one seta, q; adults with at most 9 pair of legs; first and last pair 5-segmented, remaining pairs 6-segmented; pygidial sternum with three pairs of setae,  $b_1+b_2+b_3$ . Subcosmopolitan. 52 species incl. *P. huxleyi* Lubbock, 1867 (in the sense of Lubbock known from Europe, North America, New Zealand), *P. salvatgei* Remy, 1960 (Madagascar), *P. silvaticus* Tiegs, 1943 (Australia).

*Allopauporus* Silvestri, 1902. – Pygidial sternum with three pairs of setae,  $b_1+b_2+b_3$ , pygidial tergum in subadult stage with setae  $d_1+d_2$ , adults with at most 9 pairs of legs, first and last pairs 5-segmented, remaining pairs 6-segmented, anterior margin of ventral antennal branch most often shorter than posterior margin, margins rarely subequal in length; antennal ventral branch with one seta, q; anterior flagellum of ventral antennal branch shorter than to as long as posterior flagellum. Subcosmopolitan. 96 species incl. *A. akonesis* Scheller, 2005 (Gabon), *A. brachycaulis* Scheller, 1968 (Chile); *A. brevisetus* Silvestri, 1902 (southern Europe from France to Greece, Bulgaria and Romania, also Great Britain and Switzerland, and USA), *A. carolinensis* (Starling, 1943) (USA), *A. longisetus* Remy, 1945 (France, Ukraine, Bulgaria); *A. danicus* (Hansen, 1902) (possibly subcosmopolitan); *A.*

*novicaledonicus* Scheller, 1993 (New Caledonia), *A. semiputatus* Scheller, 1975 (Angola); *A. sphaeruliger* Remy, 1948 (tropical Africa, southern Asia, Japan).

*Ataktopauropus* Scheller, 2010. – Anterior and posterior margins of ventral antennal branch  $s$  of the same length, antennal ventral branch with one seta,  $q$ ; tergites I–V with many setae inserted irregularly, first and last legs 5-segmented, remaining pairs 6-segmented, pygidial sternum with two pairs of setae,  $b_1+b_2$ . Australian region. 1 species: *A. adaios* Scheller, 2010 (New Zealand).

*Decapauporus* Remy, 1931. – Pygidial sternum with two pairs of setae,  $b_1+b_2$ ; pygidial tergum in subadult stage with setae  $d_2$  only; adults with 9 pairs of legs, females sometimes with 10 pairs, first and last pair 5-segmented, remaining pairs 6-segmented, anterior margin of ventral antennal branch most often shorter than posterior margin, margins rarely subequal in length; antennal ventral branch with one seta,  $q$ ; anterior flagellum of ventral antennal branch most often shorter than (rarely subequal in length with) posterior flagellum. Subcosmopolitan. 377 species incl. *D. anomoioides* Scheller, 1997 (Brazil), *D. binodulosus* Scheller, 1995 (Sierra Leone), *D. bovisstellus* Scheller, 2005 (Gabon), *D. cederholmi* Scheller, 1995 (Sierra Leone), *D. dischides* Scheller, 1997 (Brazil), *D. gracilis* (Hansen, 1902) (subcosmopolitan), *D. grandicollis* Scheller, 1995 (Thailand), *D. intonsus* (Remy, 1956) (Madagascar, Sri Lanka, Japan, USA), *D. janauariensis* Scheller, 2002 (Brazil), *D. leptotarsus* Scheller, 2004 (Vietnam), *D. ligulosus* Hagino, 1970 (Japan), *D. multiarcuatus* Scheller, 1970 (Sri Lanka), *D. pirlis* Scheller, 1970 (Sri Lanka), *D. proximus* (Remy, 1943) (tropics and subtropics of the Americas, Africa and Asia), *D. seychellicus* Scheller, 1982 (Seychelles), *D. stenogros* Scheller, 2005 (Gabon), *D. tenellus* Scheller, 1971 (Europe, Canada), *D. vulgaris* (Hansen, 1902) (Europe, also reported from Africa, Sri Lanka, North America).

*Desmopauporus* Scheller, 2005. – Anterior margin of ventral antennal branch  $s$  only somewhat shorter than posterior margin; antennal ventral branch with one seta,  $q$ ; pygidial tergum in subadult stage with setae,  $d_1+d_2$ ; temporal organ with anteriorly directed interior vesicle; pygidial sternum with two pairs of setae,  $b_1+b_2$ . Nearctic region. 1 species: *D. dukensis* (Starling, 1943) (USA).

*Perissopauporus* Scheller, 1997. – Ventral antennal branch  $s$  with equally truncated distal corners; antennal ventral branch with one seta,  $q$ ; exterior vesicle protruding backward from posterior part of temporal organ; pygidial tergum in subadult stage with setae  $d_1+d_2$ , pygidial sternum with two pairs of setae,  $b_1+b_2$ . Neotropical region: Brazil, Chile. Ethiopian region: Cameroon, Sierra Leone, Angola, Ivory Coast, Gabon, Uganda. 4 species, incl. *P. tridens* (Scheller, 1975) (Sierra Leone, Angola).

*Ferepauporus* Scheller, 2008. – Anterior and posterior margins of ventral antennal branch  $s$  subsimilar in length; antennal ventral branch with one seta,  $q$ ; antennal globulus  $g$  short-stalked; temporal organs with inner vesicle; adults with at most 9 pair of legs; first and last pair 5-segmented, remaining pairs 6-segmented; pygidial sternum with two pairs of setae,  $b_1+b_2$ . Ethiopian region: Sierra Leone. Australian region: New Caledonia. 2 species, incl. *F. freetownensis* (Scheller, 1995) (Sierra Leone).

*Juxtaupauporus* Scheller, 2007. – Anterior margin of ventral antennal branch  $s$  shorter than posterior margin; antennal ventral branch with one seta,  $q$ ; antennal globulus  $g$  short-stalked; adults with at most 9 pair of legs; first and last pair 5-segmented, remaining pairs 6-segmented; pygidial sternum with two pairs of setae,  $b_1+b_2$ . Palaearctic region: Israel, Morocco. Neotropical region: Jamaica, Brazil, Argentina, Chile. Australian region: New Zealand. 9 species, incl. *J. dugdalei* (Remy, 1956) (Argentina, Chile, Australia, New Zealand).

*Propepauporus* Scheller, 1985. – Anterior margin of ventral antennal branch  $s$  distinctly longer than posterior margin; antennal ventral branch with one seta,  $q$ ; stalk of antennal globulus  $g$  longer than globulus itself; globulus  $g'$  on third antennal segment without stalk; first tergite with 4+4 setae, last tergite with corrugated surface; adults with at most 9 pair of legs; first and last pair 5-

segmented, remaining pairs 6-segmented; pygidial sternum with two pairs setae,  $b_1+b_2$ . Nearctic region: USA. 1 species: *P. corrugatus* (Scheller, 1985) (USA).

*Kionopauropus* Scheller, 2009. – Anterior margin of ventral antennal branch s shorter than posterior margin, antennal ventral branch with one seta, q; antennal globulus g with stalk longer than globulus, first and last pair of legs 5-segmented, remaining pairs 6-segmented, pygidial sternum with two pairs of setae,  $b_1+b_2$ . Oriental region: SE Asia. 3 species, incl. *K. sumatraensis* Scheller, 2009 (Indonesia).

*Stylopauropus* Cook, 1896. – Anterior margin of ventral antennal branch s distinctly longer than posterior margin; stalk of antennal globulus g longer than globulus itself; antennal ventral branch with one seta, q; globulus g' on third antennal segment without stalk; first tergite with 4+4 setae; adults with at most 9 pair of legs; first and last pairs 5-segmented, remaining pairs 6-segmented; pygidial sternum with one pair of setae,  $b_1$ . Nearctic region: USA, Canada. Palaearctic region: most European countries, Tanger, Morocco, Algeria; Azores; Uzbekistan, Japan. Oriental region: SE Asia. Australian region: mainland Australia. 23 species, incl. *S. pedunculatus* (Lubbock, 1867) (most European countries, north Africa, North America, Australia), *S. pubescens* (Hansen, 1902) (middle and south Europe, north Africa).

*Donzelotauropus* Remy, 1957. – Anterior margin of ventral antennal branch s distinctly longer than posterior margin; antennal ventral branch with one seta, q; stalk of antennal globulus g longer than globulus itself; globulus g' on third antennal segment without stalk; first tergite with 4+4 setae; adults with at most 9 pair of legs; first and last pair 5-segmented, remaining pairs 6-segmented; pygidial sternum with two pairs of setae,  $b_1+b_3$ . Widely distributed in the Nearctic and Palaearctic regions. 27 species, incl. *D. cruciatus* Scheller, 1973 (south France, Andorra), *D. longipes* Scheller, 1986 (Alaska), *D. securiger* Remy, 1958 (California).

*Stylopauropooides* Remy, 1956. – Anterior and posterior margins of ventral antennal branch s subsimilar in length; antennal ventral branch with one seta, q; adults with at most 9 pair of legs; first and last pair 5-segmented, remaining pairs 6-segmented; st setae on pygidial tergum widely separated; pygidial sternum with one or two pairs of setae,  $b_1$  or  $b_1+b_3$ ; anal plate with large posteromedian cleft or indentation. Neotropical region: Brazil, Argentina, Crozet Islands. Ethiopian region: Ivory Coast, Madagascar. Australian region: New Caledonia, Australia, New Zealand. 25 species, incl. *S. bilobatus* Scheller, 1993 (New Caledonia), *S. dytanekes* Scheller, 1999 (Brazil), *S. subantarcticus* Scheller, 1974 (Crozet Islands).

*Rabaudauropus* Remy, 1953. – Anterior and posterior margins of ventral antennal branch s subsimilar in length; ventral antennal branch with setae  $q+q'$ ; globulus g' of third antennal segment long-stalked; adults with at most 9 pairs of legs, first and last pair 5-segmented, remaining pairs 6-segmented. Palaearctic region: France, Romania, Greece, Morocco, Japan. Neotropical region: Chile. Ethiopian region: Mauritius, Seychelles. Oriental region: Sri Lanka, Sabah. Australian region: New Caledonia. Not recorded from the Nearctic region. 5 species, incl. *R. dispar* Scheller, 1994 (Sabah), *R. expandens* Scheller, 1968 (Chile).

*Cauvetauropus* Remy, 1952. – Anterior margin of ventral antennal branch s shorter than posterior margin; antennal ventral branch with one seta, q; all legs 5-segmented; adults with at most 8 pairs of legs; pygidial sternum with one pair of setae,  $b_1$ . Palaearctic region: France, North Africa. Neotropical region: Brazil. Ethiopian region: Ivory Coast, Madagascar. Oriental region: Sri Lanka. 5 species incl. *C. cyclonicus* Scheller, 1970 (Sri Lanka).

*Nesopauropus* Scheller, 1997. – Anterior margin of ventral antennal branch s shorter than posterior margin; antennal ventral branch with one seta, q; all legs 5-segmented; adults with at most 9 pairs of legs; pygidial sternum with two pairs of saetae,  $b_1+b_2$ . Ethiopian region: Gabon,

Seychelles. Oriental region: Sri Lanka. Australian region: New Zealand. 8 species incl. *N. proprius* (Scheller, 1982) (Seychelles).

***Multipauropus*** Scheller, 1977. – Preanal segment much narrower than other body segments, longer than broad; tergites with cuticular net pattern, particularly on most anterior and posterior parts; tergite I-V in adult stage with numerous irregularly arranged setae; anterior margin of ventral antennal branch s shorter than posterior margin; antennal ventral branch with one seta, q; pygidial sternum with one pair of setae,  $b_1$ . Palaearctic region: Greece. 1 species: *M. hauseri* Scheller, 1977.

***Hemipauporus*** Silvestri, 1902. – Preanal segment much narrower than other body segments, longer than broad; tergites with cuticular net pattern, particularly on most anterior and posterior parts; tergite I-V in adult stage with few setae arranged in transversal rows; anterior margin of ventral antennal branch s shorter than posterior margin; antennal ventral branch with one seta, q; pygidial sternum with one pair of setae,  $b_1$ . Palaearctic region: Italy, Greece. Neotropical region: Virgin Islands, Jamaica, Colombia, Brazil. Ethiopian region: Sierra Leone, Ivory Coast, Gabon, Angola, Madagascar, Mauritius. Oriental region: Sri Lanka. Australian region: New Caledonia, Guam. 20 species incl. *H. leonensis* Scheller, 1995 (Sierra Leone), *H. piriformis* Scheller, 1994 (Brazil).

***Eburnipauporus*** Scheller, 2008. – Preanal segment much narrower than other body segments, longer than broad; tergites with cuticular net pattern, particularly on most anterior and posterior parts; tergite I-V in adult stage with few setae arranged in transversal rows; anterior margin of ventral antennal branch s shorter than posterior margin; antennal ventral branch with one seta, q; pygidial sternum with two pairs of setae,  $b_1+b_3$ . Ethiopian region: Ivory Coast. 2 species, incl. *E. africanus* (Remy, 1948).

***Hystrichopauporus*** Remy, 1942. – Anterior margin of ventral antennal branch s shorter than posterior margin; ventral antennal branch with one seta, q; dorsal side with at least partly coarse cuticle and many asymmetrically inserted lanceolate setae on tergites I-V; pygidial sternum with two pairs of setae,  $b_1+b_3$ . 1 species. Palaearctic region: France. 1 species: *H. portitor* Remy, 1935.

***Scleropauporus*** Silvestri, 1902. – Anterior margin of ventral antennal branch shorter than posterior margin; antennal ventral branch with one seta, q; dorsal side with at least partly coarse cuticle and lanceolate setae arranged in regular transversal rows; pygidial sternum with one or two pairs of setae,  $b_1$  or  $b_1+b_3$ . Nearctic region: USA, Mexico. Palaearctic region: Norway, Germany, Great Britain, France, Switzerland, Austria, Romania, Portugal, Italy, Greece, Algeria, Morocco. Neotropical region: Brazil. Ethiopian region: Ivory Coast, Angola, Madagascar. 14 species incl. *S. chapaneus* Remy, 1957 (Mexico), *S. lyrifera* Remy, 1936 (many European countries, Algeria, USA).

***Pounamupauporus*** Scheller, 2010. – Anterior margin of ventral antennal branch shorter than posterior margin, antennal ventral branch with one seta, q; tergites I and VI entire, interposed ones divided, II-V transversely and protergites of IV and V also 3-parted by submedian longitudinal divisions, setae on head and tergites not modified, low in number, arranged in regular transversal rows, first and last legs 5-segmented, remaining pairs 6-segmented, pygidial sternum with three pairs of setae,  $b_1+b_2+b_3$ . Australian region: New Zealand. 1 species: *P. bartonae* Scheller, 2010.

***Afrauporus*** Remy, 1959. – Anterior margin of ventral antennal branch s shorter than posterior margin; antennal ventral branch with one seta, q; globulus of ventral antennal branch with long-stalked capsule; dorsal side of head with a few setae only; tergites II-VI with bothriotrichs only, no other setae present; pygidial sternum with two pairs of setae,  $b_1+b_2$ . Ethiopian region: Guinea. 1 species: *A. occiduus* Remy, 1959.

Family COLINAUROPODIDAE Scheller, 1985. – Head and pygidium free, tergites divided into sclerotized coarse plates, partly of irregular shape; body fusiform, one anal plate.

*Colinauropus* Remy, 1956. – Palaearctic region: Japan. Ethiopian region: Réunion. Oriental region: Philippines. 3 species incl.: *C. regis* Remy, 1956 (Réunion).

Family EIRMOPAUROPODIDAE Scheller, 2010. – Head and pygidium free, head and tergites sclerotized with setae in regular transversal rows.

*Eirmopauropus* Scheller, 2010. Australian region: New Zealand. 1 species: *E. distichos* Scheller, 2010.

Family POLYPAUROPODIDAE Remy, 1932. – Ventral antennal branch with two globuli joined to a single stalk and two setae, *q* and *q'*; anal plate replaced by two posteriorly directed more or less thickened appendages; body fusiform.

*Polypauropus* Remy, 1932. – Head with mediodorsal plate; adults with 9 pair of legs, all legs 5-segmented; pygidium with additional setae  $t_1+t_2$ . Nearctic region: USA. Palaearctic region: Great Britain, France, Switzerland, Romania, Spain, Italy, Bosnia and Herzegovina, Greece; Morocco, Algeria. Neotropical region: Brazil, Argentina. Ethiopian region: Guinea, Gambia, Sierra Leone, Ivory Coast, Angola, Kenya, South Africa, Madagascar, Mauritius, Réunion. Oriental region: Pondichéry, Sri Lanka. Australian region: Western Australia. 15 species incl. *P. afrioccidentalis* Scheller, 1995 (Sierra Leone).

*Fagepauropus* Remy, 1951. – Head lacks mediodorsal plate; adults with at most 9 pairs of legs, first and last pair 5-segmented, those remaining 6-segmented; pygidium without additional setae  $t_1+t_2$ . Nearctic region: Canada. Palaearctic region: Morocco; Mongolia, Japan. Ethiopian region: Gambia. 2 species. incl. *F. hesperius* Remy, 1951 (Canada, Morocco, Mongolia, Gambia).

*Polyparopoides* Remy, 1956. – Head with mediodorsal plate; adults with at most 9 pairs of legs, first and last pair 5-segmented, remaining pairs 6-segmented; pygidium without additional setae  $t_1+t_2$ . Nearctic region: USA. Palaearctic region: France. Neotropical region: Brazil, Argentina. Ethiopian region: Ivory Coast, Mauritius. Oriental region: Sri Lanka. 12 species incl. *P. americanus* Scheller, 1988 (USA).

Family AMPHIPAUROPODIDAE Scheller, 2008. – Anterior margin of ventral antennal branch *s* longer than posterior margin; this branch with one antennal globulus *g* and two setae, *q+q'*; dorsal antennal branch *t* very short; setae on tergites very short, strongly clavate; adults with at most 8 pairs of legs, all 5-segmented; tarsus without proximal seta, empodium with one claw only; one anal plate; body cylindrical.

*Amphipauropus* Scheller, 1984. – Nearctic region: Canada. Palaearctic region: Iceland, Norway, Sweden, Denmark, Germany, France, Japan. 2 species incl. *A. rhenanus* (Hüther, 1971) (Iceland, Norway, Sweden, Denmark, Germany).

Family DIPLOPAUROPODIDAE Scheller, 1988. – Ventral antennal branch *s* with one globulus *g* and one seta, *q*; adults with at most 9 pairs of legs, first and last pair 5-segmented, remaining pairs 6-segmented; two anal plates, body fusiform.

*Diplopauropus* Scheller, 1988. – Temporal organs with exterior vesicle; anterodistal margin of ventral antennal branch s only slightly shorter than posterodistal margin; pygidial sternum with one pair of setae,  $b_1$ . Nearctic region: USA. Neotropical region: Virgin Islands. 2 species incl. *D. vesiculosus* Scheller, 1988 (USA).

Family ANTICHTOPAUROPODIDAE Scheller, 2010. – Tergites I and VI leaving head and pygidium free, tergites entire and sclerotized, without true setae but with many protuberances inserted irregularly, antennal ventral branch with one seta,  $q$ .

*Antichtopauropus* Scheller, 2010. – Anterodistal corner of ventral antennal branch s more truncate than posterodistal corner, stalk of antennal globulus g distinctly shorter than globulus, first and last pair of legs 5-segmented, remaining pairs 6-segmented, pygidial sternum with setae  $b_1+b_2+b_3$ , Australian region: Western Australia. 1 species: *A. brevitarsus* Scheller, 2010.

Family BRACHYPAUROPODIDAE Silvestri, 1902. – Tergite I entire, at least tergites II-IV each divided into 4-6 sclerites; setae on tergites more or less modified; antennal ventral branch with one seta,  $q$ ; one anal plate, pygidial sternum with two or three pairs of setae,  $b_1+b_3$  or  $b_1+b_2+b_3$ .

*Brachypauropus* Latzel, 1884. – Temporal organs with at most one tube-like extension; most setae on tergites hastiform; adults with 8-9 pairs of legs, all 5-segmented; pygidial sternum with two pairs of setae,  $b_1+b_3$ . Nearctic region: USA. Palaearctic region: Germany, Poland, France, Austria, Switzerland, Romania, Spain, Italy, Greece. 9 species incl. *B. hamiger* Latzel, 1884 (southern half of Europe), *B. inopinabilis* Scheller, 1986 (Alaska), *B. meyeri* Scheller, 1991 (Austria).

*Aletopauropus* MacSwain & Lanham, 1948. – Head with three transversal rows of setae; temporal organs with 3 tube-like extensions; tergite V with one entire median sclerite; setae on tergites bristle-shaped, bent posteriorly near base; adults with at most 8 pairs of legs, all 5-segmented; pygidial sternum with two pairs of setae,  $b_1+b_3$ . Nearctic region: USA. Palaearctic region: Japan. 2 species incl. *A. latus* MacSwain & Lanham, 1948 (California).

*Borneopauropus* Scheller, 2008. – Temporal organs with 3 uplifted extensions; tergites II-IV partly divided transversally into a pro-and metatergite; setae on tergites foliform-ovoid; adults with 9 pairs of legs, all 5-segmented; pygidial sternum with setae  $b_1+b_2+b_3$ . Oriental region: Indonesia, Sabah. Australian region: Tasmania, New Zealand. 5 species incl. *B. penanorum* (Scheller, 1994) (Sabah).

*Brachypauropoides* Remy, 1952. – Temporal organs with at most 3 tube-like extensions; tergites II-IV split up longitudinally and transversely into 4 sclerites; setae on tergites foliform to ovoid; adults with at most 9 pairs of legs, all 5-segmented; pygidial sternum with three pairs of setae,  $b_1+b_2+b_3$ . Ethiopian region: Madagascar. Australian region: New Zealand. 7 species incl. *B. pistillifer* Remy, 1951 (New Zealand), *B. prolatus* Scheller, 2001 (Sabah).

*Deltopauropus* MacSwain & Lanham, 1948. – Temporal organs with 3 tube-like extensions; setae on tergites scutiform; adults with at most 9 pairs of legs, all 5-segmented; pygidial sternum with two pairs of setae,  $b_1+b_3$ . Nearctic region: USA. Palaearctic region: Japan. 4 species incl. *D. luteus* MacSwain & Lanham, 1948 (California), *D. reticulatus* Hagino, 1989 (Japan).

*Zygopauropus* MacSwain & Lanham, 1948. – Temporal organs with 3 tube-like extensions; head with 4 transversal rows of setae; tergite V with two submedian sclerites; setae on tergites bristle-shaped, bent posteriorly near base; adults with at most 8 pairs of legs, all 5-segmented;

pygidial sternum with two pairs of setae,  $b_1+b_3$ . Nearctic region: USA. 1 species: *Z. hesperius* MacSwain & Lanham, 1948 (California).

Family HANSENAUROPODIDAE Remy, 1954. – At least tergites I and VI entire, tergites II-IV or II-V divided transversally into pro- and metatergite; adults with at most 9 pairs of legs; pygidial sternum with two or three pairs of setae,  $b_1+b_2$  or  $b_1+b_2+b_3$ .

*Hansenauropus* Remy, 1954. – Nine sclerites without true setae but with many small protuberances with transparent distal structure inserted irregularly; all legs 5-segmented; pygidial sternum with two or three pairs of setae,  $b_1+b_2$  or  $b_1+b_2+b_3$ . Neotropical region: Panama. Ethiopian region: Madagascar. Australian region: New Zealand. 3 species incl. *H. gratus* Remy, 1954 (New Zealand).

*Antillauporus* Remy, 1958. – Tergites I and VI entire, interposed tergites transversely split into pro- and metatergite, setae on tergites scutiform, regularly inserted; pygidial sternum with two pairs of setae,  $b_1+b_2$ . Neotropical region: Jamaica. 1 species: *A. eucharis* Remy, 1958.

*Virginopauropus* Scheller, 1990. – Tergites I and VI entire, interposed tergites transversely split into pro- and metatergite, setae on tergites hastiform or modified into cup-like protuberances; pygidial sternum with two pairs of setae,  $b_1+b_2$ . Neotropical region: Virgin Islands. Ethiopian region: Sierra Leone. 2 species: *V. asperrimus* Scheller, 1990 (US Virgin Islands), *V. necopinatus* (Scheller, 1995) (Sierra Leone).

Family EURYPAUROPODIDAE Ryder, 1879. – Six entire strongly sclerotized tergites, body flattened dorsoventrally; lateroventral sides of tergites without longitudinal furrows; no ability to coil the body; tergite I distinctly narrower than tergites II-IV; surface of tergites yellow-brownish to brown, coarse, ornamented, without simple setae but with many types of tubercles, modified setae and marginal protuberances; first and last pair of legs 5-segmented, remaining pairs 6-segmented, or all legs 5-segmented.

*Eurypauporus* Ryder, 1879. – Fourth antennal segment with at least 4 well-developed setae; globulus g of ventral antennal branch long-stalked; setae of tergites inserted in rounded crater-shaped structures; first and last pair of legs 5-segmented, remaining pairs 6-segmented; empodia of legs 3-8 with 2 accessory claws; anal plate V-shaped with straight or almost straight lateral margins; interdistance of pygidial setae  $a_1$  at most twice as long as distance  $a_2-a_3$ . Nearctic region: USA. Palaearctic region: Japan. 5 species incl. *E.washingtonensis* Scheller, 1985 (USA).

*Acopauropus* Cook, 1896. – Fourth antennal segment with at least 4 well-developed setae; globulus of ventral antennal branch long-stalked; setae of tergites inserted in the anterior part of longish crater-shaped structures; first and last pairs of legs 5-segmented, remaining pairs 6-segmented; empodia of legs 3-8 with two accessory claws; interdistance of pygidial setae  $a_1$  distinctly longer than distance  $a_2-a_3$ ; st longish, generally fusiform with distinct pubescence. Palaearctic region: Germany, France, Switzerland, Austria, Czech Republic, Romania, Spain, Greece, European Turkey, Algeria, Georgia, South and North Korea. 12 species incl. *A. consobrinus* (Remy, 1937) (France, Austria, Switzerland, Greece), *A. hastatus* (Attems, 1895) (from Switzerland and France to Greece and European Turkey), *A. ornatus* (Latzel, 1884) (Austria, France). *A. tetrastichus* (Scheller, 1981) (Georgia; Turkey).

*Samarangopus* Verhoeff, 1934. – Fourth antennal segment with 3 well-developed setae; globulus g of ventral antennal branch s short-stalked: all legs 5-segmented; empodia with one anterior accessory claw. Palaearctic region: Japan. Ethiopian region: Rwanda, Madagascar,

Mauritius, Réunion. Oriental region: Nepal, Thailand, Vietnam, Borneo, Indonesia, Philippines. Australian region: Papua New Guinea; mainland Australia, New Caledonia, New Zealand. 35 species incl. *S. amplissimus* Scheller, 2009 (Sumatra), *S. papuensis* Scheller, 1996 (Papua New Guinea), *S. poculifer* Scheller, 1995 (Thailand)), *S. prockes* Scheller, 2001 (Sabah), *S. ternarius* Scheller, 2001 (Sabah), *S. trilix* Scheller, 2007 (Malaysia), *S. umbonifer* Scheller, 1995 (Thailand), *S. umbraculus* Scheller, 1993 (New Caledonia).

*Trachypauropus* Tömösváry, 1882. – Fourth antennal segment with at least 4 well-developed setae; globulus  $g$  of ventral antennal branch  $s$  long-stalked; setae of tergites inserted in posterior part of longish crater-shaped structures; first and last pair of legs 5-segmented, remaining pairs 6-segmented; empodium of legs 3-8 with one accessory claw; interdistance of pygidial setae  $a_1$  shorter than distance  $a_2-a_3$ ; st very short, cylindrical-clavate, glabrous or with short pubescence. Palaearctic region: Great Britain, France, Switzerland, Austria, Hungary, Romania, Yugoslavia, Spain, Italy, Greece; Turkey, Israel. 10 species incl. *T. britannicus* Scheller, 1990 (Great Britain), *T. cordatus* Scheller, 1974 (Switzerland, Austria, Spain, Italy, Greece, Turkey), *T. latzeli* (Cook, 1896) (suthern half of Europe from France to Slovenia).

Family SPHAEROPAUROPODIDAE Verhoeff, 1934. – Six entire strongly sclerotized tergites, body strongly vaulted, lateroventral sides of tergites II-V with deep furrows, can roll up completely; tergite I at least as broad as tergite II-IV; surface of tergites smooth with short pubescence and tuft-like trichomes; all legs 5-segmented.

*Sphaeropauropus* Silvestri 1930. – Palaearctic region: Japan. Oriental region: Nepal, Tibet, Réunion, Sri Lanka, Thailand, Vietnam, Indonesia, Philippines, Borneo. 14 species, incl. *S. arcuatus* Scheller, 2001 (Sabah), *S. convolvolutus* Scheller, 1995 (Thailand), *S. nepalensis* Scheller, 2000 (Nepal).

### References

- ADIS, J., U. SCHELLER, J. WELLINGTON DE MORAIS & J. M. G. RODRIGUES, 1999. Abundance, species composition and phenology of Paupropoda (Myriapoda) from a secondary upland forest in Central Amazonia. – Revue suisse de Zoologie 106: 555-570.
- BACCETTI, B., A. G. BURRINI, R. DALLAI & V. PALLINI. 1979. Recent work on myriapod spermatology. – Pp. 97-104 in M. CAMATINI (ed.) Myriapod Biology. – Academic Press, London.
- BACCETTI, B. & R. DALLAI. 1978. The evolution of myriapod spermatozoa. – Abhandlungen und Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg, Neue Folge 21/22: 203-217.
- BAGNALL, R. S. 1935. An extended classification of the Paupropoda to include two new families. – Annals and Magazine of natural History (10) 16: 619-629.
- BEDANO, J. C., M. P. CANTU & M. E. DOUCET, 2006. Soil springtails (Hexapoda: Collembola), symphylans and paupropods (Arthropoda: Myriapoda) under different management systems in agroecosystems of the subhumid Pampa (Argentina). – European Journal of Soil Biology 42: 107-119.
- FRATELLO, B. & M. A. SABATINI, 1990. Chromosomes of Paupropoda. – Pp. 109-114 in A. MINELLI (ed.) Proceedings of the 7th International Congress of Myriapodology. – Brill, Leiden.
- HAGINO, Y., 2000. A list of Paupropoda from the Imperial Palace, Tokyo, Japan. – Memoirs of the National Science Museum 35: 115-121.
- HÅGVAR, S., 1997. Protura, Paupropoda and Symphyla in Norwegian coniferous forest soils: abundance and vertical distribution. – Pedobiologia 41: 56-61.

- HÄGVAR, S. & U. SCHELLER, 1998. Species composition, developmental stages and abundance of Paupropoda in coniferous forest soils of southeast Norway. – *Pedobiologia* 42: 278-282.
- HANSEN, H. J., 1902. On the genera and species of the order Paupropoda. – *Videnskabelige Meddelelser fra den naturhistoriske Forening i Kjøbenhavn* 53: 323-424.
- HASENHÜTL, K., 1987. Die Pupoidstadien der Eurypauropodinae, am Beispiel von *Gravieripus latzelii* (Cook, 1896) (Myriapoda, Paupropoda). – *Mitteilungen des naturwissenschaftlichen Vereins für Steiermark* II/7: 167-171.
- HAUPT, J., 1973. Die Ultrastruktur des Pseudoculus von *Allopaupopus* (Paupropoda) und die Homologie der Schlafengänge. – *Zeitschrift für Morphologie der Tiere* 76: 173-191.
- HAUPT, J., 1978. Ultrastruktur der Trichobotrien von *Allopaupopus (Decapaupopus)* (Paupropoda). – *Abhandlungen und Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg, Neue Folge* 21/22: 271-277.
- HUMBERT, A., 1872. P. 188 in: SAUSSURE, H. & HUMBERT, A., Etude sur les myriapodes. *Recherches zoologiques publiées par M. Milne Edwards*, 6.
- HÜTHER, W., 1959. Zur Ernährung der Paupropoden. – *Die Naturwissenschaften* 46: 563-564.
- LAGERLÖF, J. & U. SCHELLER, 1989. Abundance and activity of Paupropoda and Symphyla (Myriapoda) in four cropping systems. – *Pedobiologia* 33: 315-321.
- LATZEL, R. 1884. Die Myriapoden der österreichisch-ungarischen Monarchie, 2. Hölder, Wien.
- LAVIALE, M.-L. 1964. Présence de spermatophores chez *Stylopaupopus pedunculatus* (Lubb.) (Paupropode, Myriapode). – *Comptes rendus hebdomadaires des Séances de l'Academie des Sciences, Paris* 259: 652-654.
- LUBBOCK, J., 1867. On *Paupopus*, a new type of centipede. – *Transactions of the Linnean Society of London* 26: 181-190.
- MACSWAIN, J. W & U. N. LANHAM, 1948. New genera and species of Paupropoda from California. – *Pan-Pacific Entomologist* 24: 69-84.
- MANTON, S. M., 1953. Locomotory habits and the evolution of the larger arthropodan groups. – *Society of Experimental Biology, Symposium* 7: 339-376.
- MANTON, S. M., 1966. The evolution of arthropodan locomotory mechanisms. Part 9. Functional requirements and body design in Symphyla and Paupropoda and the relationship between Myriapoda and pterygote insects. – *Journal of the Linnean Society of London, Zoology* 46: 103-141.
- MANTON, S. M., 1974. Segmentation in Symphyla, Chilopoda and Paupropoda in relation to phylogeny. – *Symposia of the Zoological Society of London* 32: 163-190.
- MASSOUD, Z., 1969. Étude de l'ultrastructure des Paupropodes. I. Flagelles et globules des antennes. – *Revue d'Écologie et de Biologie du Sol* 6: 315-323.
- MASSOUD, Z., 1970. Étude de l'ultrastructure des Paupropodes. II. Les organes apicaux des tarses. – *Revue d'Écologie et de Biologie du Sol* 7: 87-94.
- MEYER, E. & U. SCHELLER, 1992. Abundance and species composition of Paupropoda in forest soils of Western Austria (Vorarlberg, Tirol). – *Berichte des naturwissenschaftlich-medizinischen Vereins in Innsbruck, Supplementum* 10: 431-439.
- MOORE, R., 1982. Ecology of the Paupropoda from a coal shale heap in Lancashire, England. – *Pedobiologia* 24: 309-317.
- PACKARD, A. S. 1870. A remarkable Myriapod. – *American Naturalist* 4: 2.
- PRICE, D. W., 1975. Vertical distribution of small arthropods in a California pine forest soil. – *Annals of the Entomological Society of America* 68: 174-180.
- REMY, P. A. 1931. Un nouveau type de Paupropode: *Decapaupopus Cuenoti*, nov. gen., nov. sp. – *Archives de Zoologie expérimentale et générale, Notes et Revue* 71: 67-83.

- REMY, P. A. 1932. Un pauropode de Banyuls-sur-Mer type d'une famille nouvelle: *Polypauropus duboscqi* nov. gen., nov. sp. – Archives de Zoologie expérimentale et générale **74**: 287-303.
- REMY, P. A. 1937. Die Eurypauropodidae (Myriapoda, Paupropoda) des Naturhistorischen Museums zu Wien. – Verhandlungen der zoologisch-botanischen Gesellschaft in Wien, **86/87**: 5-34.
- REMY, P. A. 1950. Les *Millotauropus*, types d'un nouveau groupe de Paupropodes. – Comptes rendus hebdomadaires des Séances de l'Académie des Sciences, Paris, **230**: 472-473.
- REMY, P., 1953. Description de nouveaux types de Paupropodes: "Millotauropus" et "Rabaudauropus". – Mémoires de l'Institut Scientifique de Madagascar (A) **8**: 25-41.
- REMY, P., 1956. Un nouveau Paupropode de l'Ile de la Réunion: *Colinauropus regis* n.g., n.sp. – Bulletin du Muséum national d'Histoire naturelle, Paris (2) **28**: 119-123.
- REMY, P., 1958. Paupropodes des États-Unis d'Amérique et de la Jamaïque. – Mémoires de la Société nationale des Sciences naturelles et mathématiques de Cherbourg, (5) **48** (1957-58): 33-109.
- ROSATI, F., B. BACCHETTI, & R. DALLAI. 1970. The spermatozoon of Arthropoda. X. Araneids and the lowest Myriapods. Pp. 247-254 in B. BACCHETTI (ed.) Comparative spermatology. Proceedings of the international symposium held in Rome and Siena, 1969.
- SCHELLER, U., 1970. The Paupropoda of Ceylon. (Reports from the Lund University Ceylon Expedition in 1962. Vol. I) – Entomologica Scandinavica, Supplementum **1**: 5-97.
- SCHELLER, U., 1985. Taxonomic and distributional notes on paupropods from the United States (Myriapoda, Paupropoda: Paupropodidae, Eurypauropodidae). – Entomologica Scandinavica **16**: 237-257.
- SCHELLER, U., 1986. Beringian Paupropoda (Myriapoda). – Entomologica Scandinavica **17**: 363-391.
- SCHELLER, U., 1990. Northern paupropod faunas. – Pp. 431-441 in A. MINELLI (ed.) Proceedings of the 7<sup>th</sup> international Congress of Myriopodology. – Brill, Leiden.
- SCHELLER, U., 1993. Paupropoda (Myriapoda) from New Caledonia. – Mémoires du Muséum national d'Histoire naturelle, Paris **157**: 27-71.
- SCHELLER, U., 1994. Paupropoda of a secondary forest near the Tarumã Mirim River, Amazonas, Brazil (Myriapoda, Paupropoda, Paupropodidae). – Amazoniana **13**: 65-130.
- SCHELLER, U., 1997. Paupropoda from upland and inundation forests in Central Amazonia, Brazil (Myriapoda, Paupropoda: Millotauropodidae, Paupropodidae). – Amazoniana **14**: 223-300.
- SCHELLER, U., 2000. Eurypauropodidae from the Nepal Himalaya. – Senckenbergiana biologica **80**: 101-126.
- SCHELLER, U., 2005. First records of Paupropoda (Millotauropodidae; Paupropodidae) from Gabon with the description of 16 new species (Paupropoda and Symphyla of the Geneva Museum XIV). – Revue suisse de Zoologie **112**: 457-509.
- SCHELLER, U., 2008. A reclassification of the Paupropoda. – International Journal of Myriopodology **1**: 1-38.
- SCHELLER, U., 2009. New species of Paupropoda (Myriapoda) from Tasmanian temperate rainforests. – Memoirs of Museum Victoria **66**: 289-329.
- SCHELLER, U. & J. ADIS, 2000. Possible parthenogenesis in *Allopauropus* (Myriapoda: Paupropoda). – Fragmenta faunistica, Warszawa **43** Supplement: 171-177.
- SCHELLER, U., M. P. BERG & M. G. M. JANSEN, 2004. Paupropoda (Myriapoda), a class new to the Dutch fauna, with description of a new species. – Entomologische Berichten **64**: 3-9.
- SCHELLER, U., B. P. M. ĆURČIĆ & S. E. MAKAROV, 1997. *Pauropus furcifer* Silvestri (Paupropodidae, Paupropoda): towards an adaptation for life in caves. – Revue suisse de Zoologie **104**: 517-522.
- SCHELLER, U. & J. WUNDERLICH, 2001. First description of a fossil paupropod, *Eopauropus balticus* n. gen. n. sp. (Paupropoda: Paupropodidae), in Baltic amber. – Mitteilungen aus dem geologisch-paläontologischen Institut der Universität Hamburg **85**: 221-227.

- SCHMIDT, P. 1894. Zur Kenntnis des inneren Baues des *Pauropus huxleyi*. – Zoologischer Anziger 17: 189-196.
- SCHMIDT, P. 1895. Beiträge zur Kenntnis der niederen Myriopoden. Morphologie des *Pauropus*. – Zeitschrift für wissenschaftliche Zoologie 59: 436-510.
- SCHUSTER, R. & K. HASENHÜTL, 1983. Die Spermatophore der Eurypaupropodiden (Myriapoda, Paupropoda). – Zoologischer Anzeiger 211: 187-196.
- SILVESTRI, P. 1902. Ordo Paupropoda. – Pp. 1-84 in fasc. 92-96 of A. BERLESE (ed.) Acari, Myriopoda et Scorpiones hucusque in Italia reperta. Typ. Vesuviana, Portici.
- TICHY, H., 1987. Antennal sensory organs in the millipede *Eurypaupropus ornatus*: fine structure of the flagella and globulus. – Journal of Morphology 193: 159-171.
- TIEGS, O. W. 1947. The development and affinities of the Paupropoda, based on a study of *Pauropus silvaticus*, I; II. – Quarterly Journal of Microscopical Science 88: 165-267; 275-336.
- VERHOEFF, K. W., 1933-1934. Gliederfüßler: Arthropoda, II. Abteilung: Myriapoda. 3. Buch: Symphyla und Paupropoda. – In H. G. BRONN (ed.) Klassen und Ordnungen des Tierreichs 5(2): 1-200.
- ZANGER, K., 1986. Topographie, Histologie und Ultrastruktur des Darmtrakts von *Pauropus huxleyi* (Paupropoda: Tetramerocerata). – Zoologische Beiträge 29: 453-467.

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Additionally to the names of taxa of Chilopoda, Symphyla and Pauropoda cited in the present monograph, the index includes alternative names by which some species have been cited in works cited in Chapters 2-15. Page numbers in *italics* refer to figure legends.

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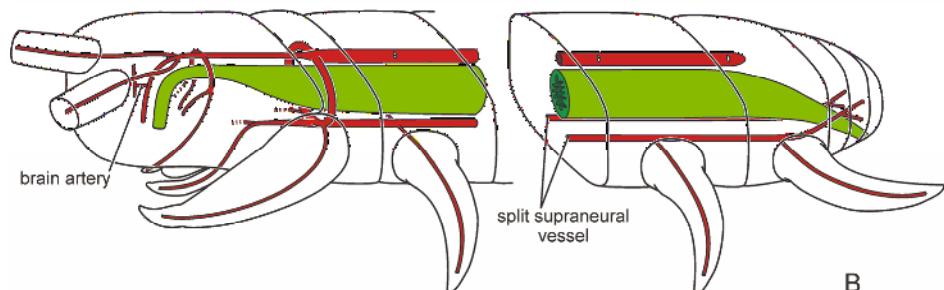
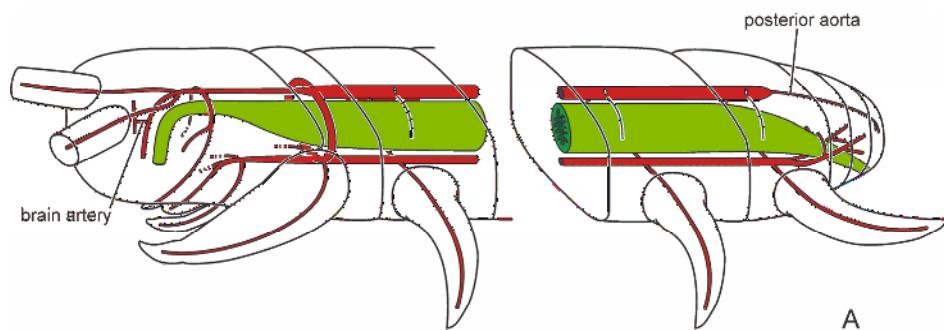
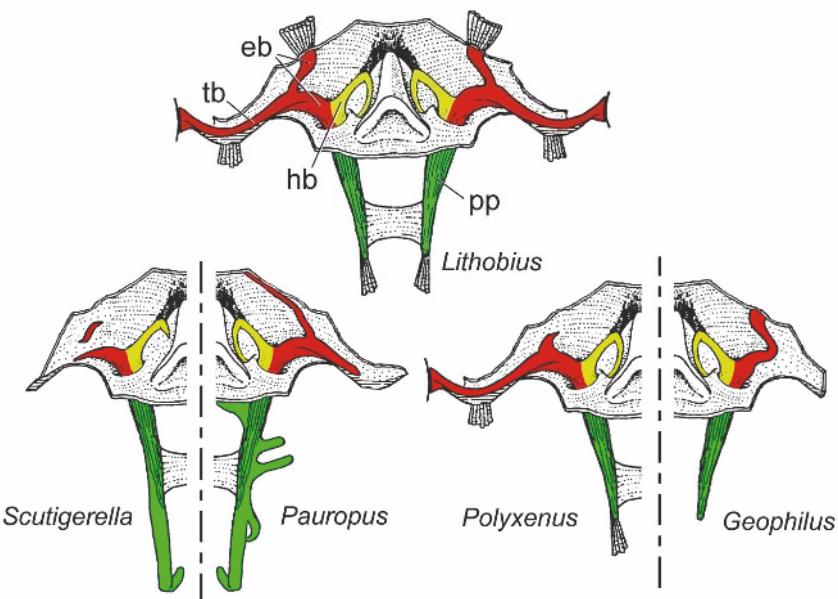


Plate I. (above) Cephalic tentorial endoskeleton in myriapods. For the complete legend, see page 5. (below) Hemolymph vascular system in Chilopoda. For the complete legend, see page 160.

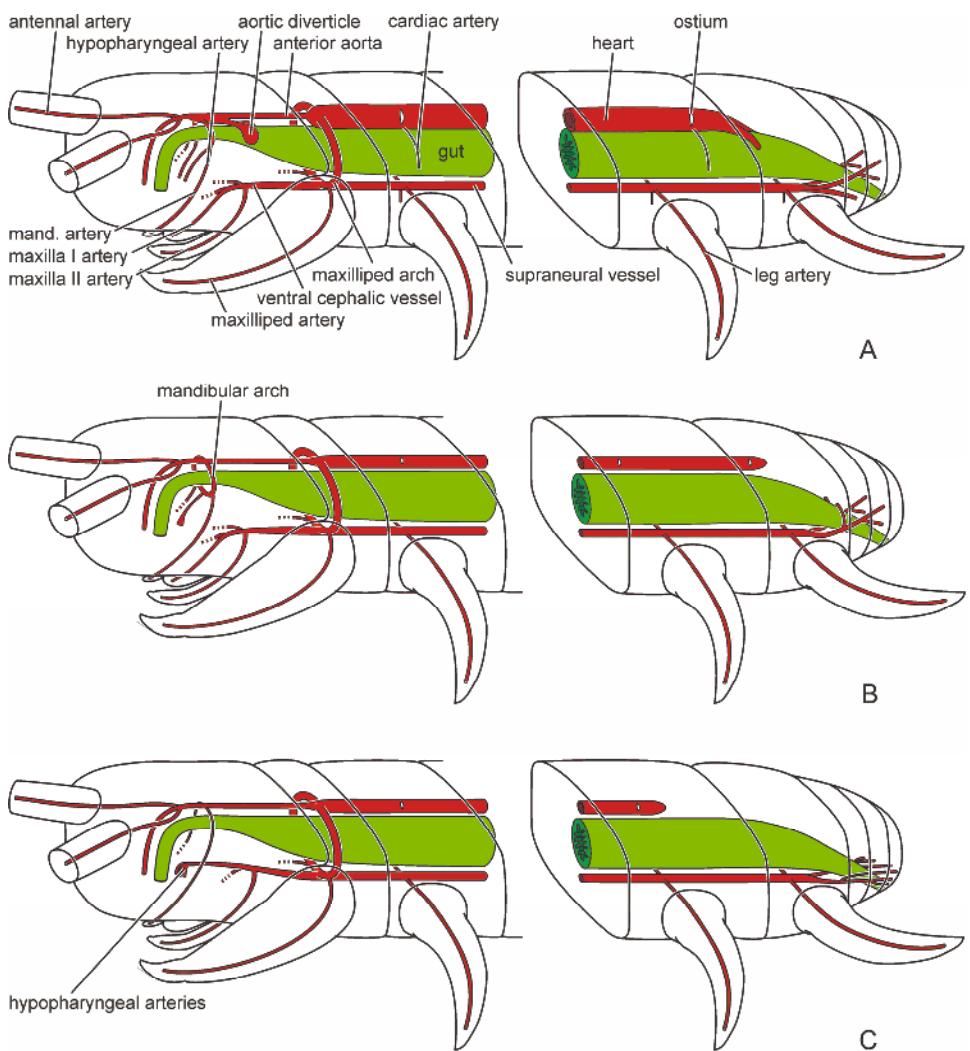


Plate II. Hemolymph vascular system in Chilopoda. For the complete legend, see page 158.

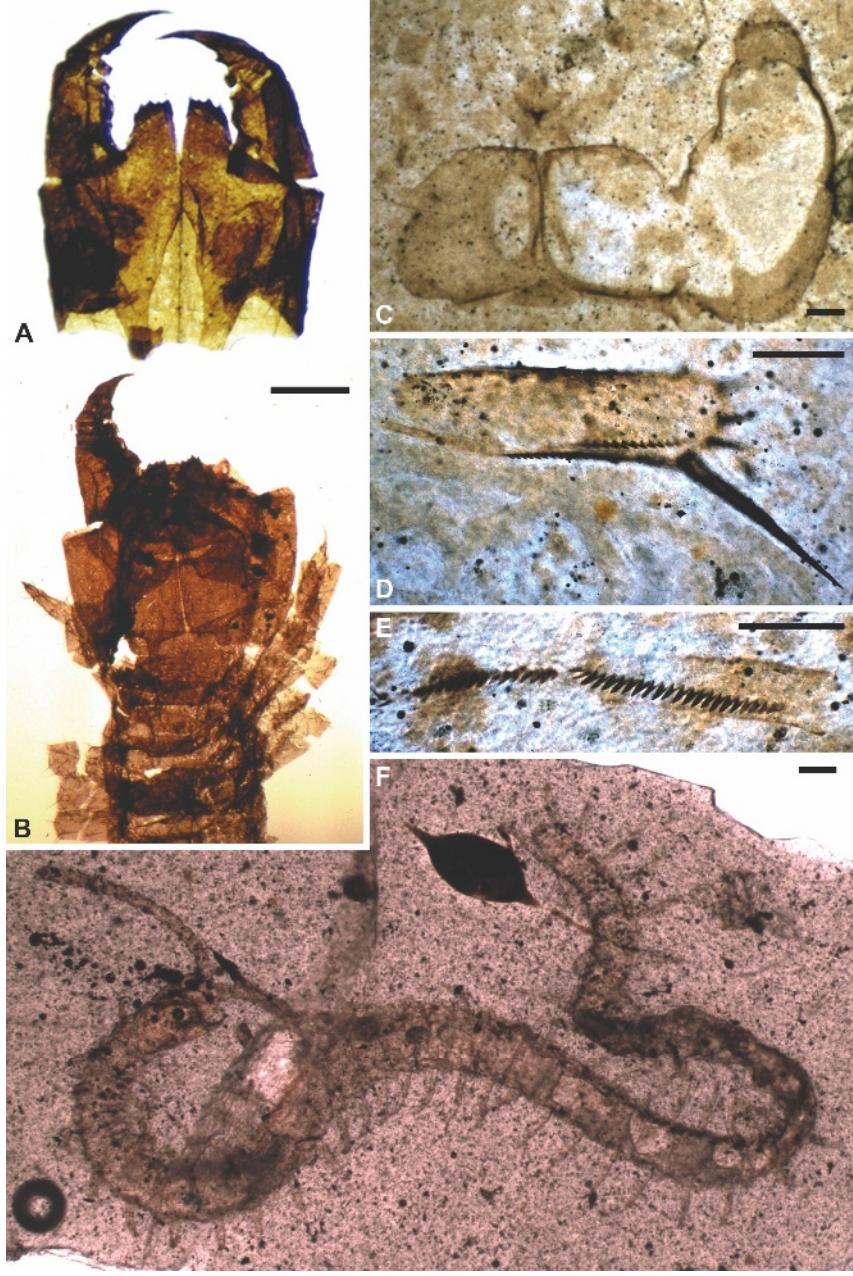


Plate III. Fossil Chilopoda. For the complete legend, see page 356.



Plate IV. A-D Scutigeromorpha. A *Scutigera coleoptrata* (Scutigeridae, Scutigerinae). B *S. coleoptrata*. C *Sphendononema guildingii* (Pselliodidae). D *Thereuopoda longicornis* (Scutigeridae, Thereuoneminae). E-F Craterostigmomorpha. E *Craterostigmus tasmanianus* (Craterostigmidae). F, C. *crabilli* (id.). Photo credits: A M. Uliana, B L. Bonato, C A. Anker, D, E Z. Korsós, F G. Giribet.

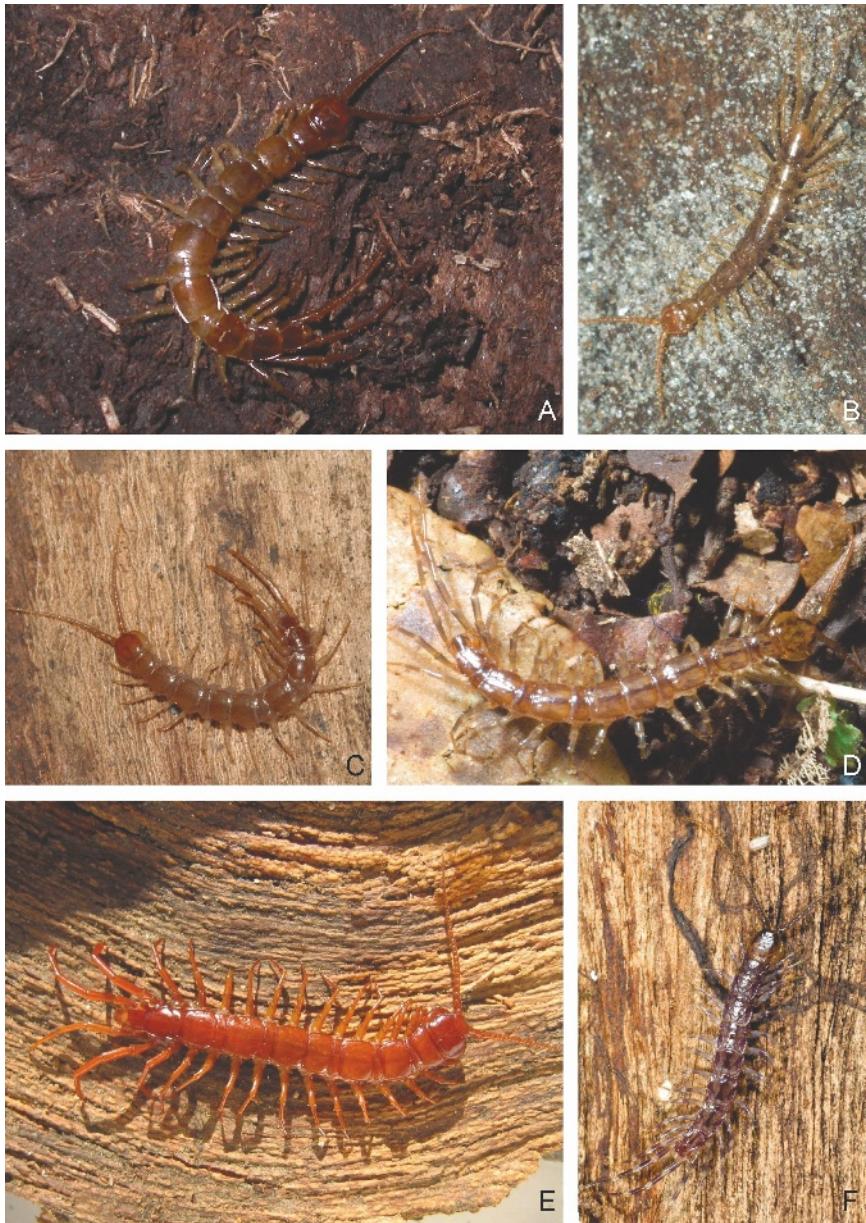


Plate V. Lithobiomorpha. A *Lithobius* sp. (Lithobiidae, Lithobiinae). B *Anopsobius neozelanicus* (Henicopidae, Anopsobiinae). C *L. forficatus* (Lithobiidae, Lithobiinae). D *Paralamyctes rahuensis* (Henicopidae, Henicopinae). E *Eupolybothrus transsylvanicus* (Lithobiidae, Ethopolyinae). F *Henicops dentatus* (Henicopidae, Henicopinae). Photo credits: A M. Uliana, B, D, F G. Giribet, C, E I. Tuf.



Plate VI. Scolopendromorpha. A *Scolopendra cingulata* (Scolopendridae, Scolopendrinae). B *Scolopendra* sp. (id., id.). C *S. cingulata* (id., id.). D *Cormocephalus aurantiipes* (id., id.). E *Cryptops parisi* (Cryptopidae). F *Theatops erythrocephalus* (Plutoniumidae). Photo credits: A L. Bonato, B, E I. Tuf, C M. Uliana, D, F G. Giribet.



Plate VII. A-B Scolopendromorpha. A *Otostigmus scaber* (Scolopendridae, Otostigminae). B *Cormocephalus hartmeyeri* (id., Scolopendrinae). C-F Geophilomorpha. C *Henia bicarinata* (Dignathodontidae). D *Dicellophilus carniolensis* (Mecistocephalidae). E *Orya barbarica* (Oryidae). F *Clinopodes flavidus* (Geophilidae). Photo credits: A Z. Korsós, B G. Giribet, C-D L. Bonato, E-F I. Tuf.



Plate VIII. Geophilomorpha. A *Stigmatogaster gracilis* (Himantariidae). B *Strigamia crassipes* (Linotaeniidae). C *Himantarium gabrielis* (Himantariidae). D *Escaryus* sp. (Schendylidae). E *Henia illyrica* (Dignathodontidae). F *Mecistocephalus* sp. (Mecistocephalidae). Photo credits: A, B L. Bonato, C M. Uliana, D, E I. Tuf, F A. Anker.