THE MYRIAPODA

VOLUME 2

Cover: Aphistogoniulus infernalis Wesener, 2009 (Spirobolida, Pachybolidae). Original drawing by Denitsa Peneva.

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THE MYRIAPODA

Edited by
A. MINELLI

VOLUME 2

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PREFACE

Four years after the publication of the first part of this monograph, the second volume is also ready, at last, for publication. Difficulties in completing the project were largely anticipated. The lack of a modern comprehensive monograph for this group, in particular the fact that twenty years ago no author was ready to contribute a chapter on Diplopoda to the well-known series on the *Microscopic Anatomy of Invertebrates*, thus perpetuating the lack of treatment of this group in the original *Traité* directed by Pierre-Paul Grassé — a gap fixed once and for ever by the decision of the publisher to discontinue the production of that series — was clearly a consequence of the immature level of knowledge in many aspects of millipede biology, as well as of the very limited number of specialists worldwide, often overloaded with their original research projects. It was therefore arduous to recruit a team for the long awaited monograph.

Not unexpectedly, this book has been eventually written by a team of authors whose membership has changed in part over the years. Eventually, I have enjoyed the generous participation of several senior researchers (i.e., myriapodologists of my own generation) but also of much younger colleagues who are seriously committed to generate a modern millipede zoology. To any and all of them I acknowledge here in print my deepest gratitude.

Even among the professional zoologists, not very many people are aware of the actual diversity of millipedes. Looking through the clouds of a still unsatisfactory taxonomy we discover indeed a taxon of which the species described to date are more or less as numerous as those of birds, and those that have been estimated to exist are probably in a number comparable to that of the whole of vertebrates.

The readers of this book will become aware of the wonderful diversity of the Diplopoda, not simply under the aspect of external morphology (see colour Plate I at the end of this volume), beginning with number and shape of those unique segmental units into which the trunk of these arthropods is articulated, but also in many other regards ranging from the chemistry of their defensive secretions to the astonishing diversity of their post-embryonic developmental schedules.

At the time I am delivering this manuscript to the publisher, we are still waiting for the first fully sequenced genome of a millipede species. In fact, even if some modern research has been conducted on this group, including gene expression studies on an emerging model species (*Glomeris marginata*), millipede biology is still a wonderfully unexplored area waiting for the efforts of a large number of researchers with diversified interests and skills.

Together with all my co-authors, I present this volume to the scientific community with the hope that our work may represent a useful starting point for future research and a stimulus to go seriously ahead with the study of this largely neglected arthropod group.

My sincere thanks to Michiel Thijssen, Sabine Steenbeek, Wendel Scholma and Marc Jarmuszewski of Brill, for their encouragement and help throughout the years, and to the VTeX team at Kaunas, Lithuania, for the excellent page setting.

Padova, 21 May 2015

ALESSANDRO MINELLI

CHAPTER 1

DIPLOPODA — AN OUTLINE OF RESEARCH HISTORY

BY

ALESSANDRO MINELLI

Detailed information about the history of research on millipedes is found in some classical works, especially in Silvestri (1903) and Verhoeff (1928-1932). The following outline will briefly cover the progress in the knowledge of the Diplopoda as due to the most prominent deceased researchers; current trends will be also noted.

In the X edition of his *Systema Naturae* (1758), Linnaeus (1707-1778) placed most of the few millipede species known at the time in the genus *Julus*, but described as *Scolopendra Lagura* the diplopod currently known as *Polyxenus lagurus*. Additional genera, most of which are now considered to belong to different orders, were first introduced only some decades later: *Pol[l]yxenus*, *Glomeris* and *Polydesmus* by Pierre André Latreille (1762-1833) in 1802/1803, *Craspedosoma* by William Elford Leach (1790-1836) in 1814, *Abacion*, *Narceus* and *Pleuroloma* by Constantine Samuel Rafinesque-Schmaltz (1783-1840) in 1820, *Callipus* by Antonio Giuseppe (= Antoine Joseph) Risso (1777-1845) in 1826, *Fontaria* by John Edward Gray (1800-1875) in 1832, *Spirostreptus* and *Strongylosoma* by Johann Friedrich von Brandt (1802-1879) in 1833.

Besides the contributions of the younger among these authors, around mid-century the knowledge of myriapods, of millipedes in particular, was strongly advanced by authors such as Hippolyte Lucas (1814-1899), François Louis Paul Gervais (1816-1879), Carl Ludwig Koch (1778-1857) and Henri Louis Frédéric de Saussure (1829-1905), as well as by George Newport (1803-1854), who contributed anatomical and biological observations, in addition to describing new species and improving the taxonomic arrangement of the group. Fabre (1855) contributed a first important work on reproduction and development of these arthropods.

A pivotal work in the history of diplopodology is the monograph of the myriapods of the austro-hungarian monarchy published by Robert Latzel (1845-1919) in two volumes (Latzel, 1880-1884). The work contained in fact an extensive introduction and a comprehensive list of the literature hitherto published on the Myriapoda. This may have catalyzed the strong acceleration we observe in studies on the Diplopoda before the end of

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the XIX century. At the time there was is indeed a lively production, especially in taxonomy, e.g. with all or most of the myriapodological works of Ödön (= Edmund) Tömösváry (1852-1884), Antonio Berlese (1863-1927), Charles Harvey Bollman (1868-1889), Reginald Innes Pocock (1863-1947) and Orator Fuller Cook (1867-1949) and the beginnings of the long careers of Filippo Silvestri (1876-1949), Henri Wilfred Brölemann (1860-1933), Karl Wilhelm Verhoeff (1867-1945) and Carl August Theodor Michael Graf von Attems-Petzenstein (1868-1952).

Some of these authors have contributed to the study of millipedes also for aspects other than taxonomy. For example, Tömösváry is much better known for the post-antennal sensory organs named after him than for the few taxa he described as new; Silvestri (1903) published a well-informed, but rarely used compendium of millipede anatomy; Attems (1926) contributed a widely cited compendium of millipede zoology; and Verhoeff was also author of the most extensive encyclopedic treatment of myriapods published to date, within which the volumes on the Diplopoda were published in 1928-1932.

Over the first half of the XX century the activity of these authors was accompanied by the taxonomic works of many others, including Johann Carl (1877-1944), Ralph Vary Chamberlin (1879-1967), Harold Frederick Loomis (1896-1976) and Otto Schubart (1900-1962). The second half of the past century and the first decade of the present one were dominated by the exemplary work of Richard Lawrence Hoffman (1927-2012), accompanied by the taxonomic production of many other authors, among which Carlo Strasser (1903-1981), Nell Bevel Causey (1910-1979) and Bruno Condé (1920-2004), who was for a while the only taxonomist working on Penicillata. Description of new species is continuing today at a sustained pace thanks to the effort of an excellent group of speciastists, who are also progressively improving the systematization of previously described taxa, a great many of which, among those described in the XIX century, are still problematic, with poorly informative diagnoses (but this is also true of a number of those described by later authors, especially Chamberlin and Verhoeff). This persisting problem with the backlog from the past is the reason for the great uncertainty about the number of validly described millipede species, as mentioned in Chapter 16 and also witnessed by the sizeable divergences between the estimates offered by different authors, e.g. Hoffman (1980), Sierwald & Bond (2007), Shear (2011) and Minelli & Golovatch (2013). In the last few decades, precious research tools have been published, such as the nomenclator of genus and family names published in 1970 by Casimir Albrecht Willem Jeekel (1922-2010) and subsequently updated by two supplements (Shelley et al., 2000; Shelley & Golovatch, 2015), Hoffman's (1980) critical overview of millipede classification down to the genus level, and Shelley's (2002) synopsis of families and suprafamilial taxa.

As will be evident from a perusal of the following chapters, millipede morphology is still very incompletely known and — with some exceptions — progress in this area has been much slower, in the last few decades, than in centipede morphology. Ultrastructural research focussed for a while on sperm cells, targeted by Baccio Baccetti (1931-2010) and his school, while the most active area of investigation is currently the fine structure of sense organs (cf. Chapter 9).

A still open problem of comparative morphology is the nature of the segmental units forming the trunk of the millipedes, obviously different from those of the other arthropods. As discussed in Chapter 11, interesting novel insights are offered by the study of the embryonic expression of several classes of developmental genes, as well as by a careful interpretation of naturally occurring teratological specimens with ectopic, possibly homeotic appendages.

As for the functional morphology of the skeletomuscular system and the mechanics of locomotion, we must still rely on the studies of Sidnie M. Manton (1903-1979).

The first studies on the embryonic development of millipedes were those of Ilya Ilich Mechnikov (1845-1916) on *Oranmorpha guerinii* and other species, followed by N. G. Lignau's monograph (1911a, b) on *Polydesmus abchasius*, Otto Pflugfelder's (1904-1994) study of segmentation on *Platyrhacus amauros* (1932) and Wolfgang Dohle's monograph on *Glomeris marginata* (1964). In recent years, *G. marginata* has turned into the millipede model species used in the current studies on developmental genetics summarized in Chapter 11. Previous to the latter, experimental studies on millipede development are essentially limited to those of Lysiane Juberthie-Jupeau on the embryos of *Spelaeoglomeris doderoi* and *Glomeris marginata*, those of Michael W. Berns and William Tinsley Keeton on the post-embryonic production of segments and those of Georges Petit on the regeneration of the appendages in *Polydesmus*; this literature is briefly reviewed in Chapter 11, where the corresponding references are listed.

Knowledge of the diverse post-embryonic developmental schedules of millipedes accumulated over time since the earliest observations published by Newport. Many important observations, including the characterization of the phenomenon of periodomorphosis, are due to Verhoeff. Eventually, in the second half of the XX century there was an explosion of accurate studies of the life histories of many diplopod species, summarized by Enghoff et al. (1993) in a landmark review. A substantial part of the research in this field has been contributed by John Gordon Blower (1923-2001) and collaborators in England, by Yoshiteru Murakami (1925-1997) in Japan and by several living researchers in France.

Most of what we know about courtship behavior in millipedes is still to be found in the papers of Ulrich Haacker (1939-1972), but interesting evidence has been recently gathered on the mechanics of sperm transfer and the associated problems of sperm competition and reproductive isolation by coevolution of the genitalia.

Experimental work on millipede physiology was pioneered by Félix Auguste Joseph Plateau (1841-1911) in the second half of the XIX century, but did not flourish until the last decades. Worth mention are Thomas Eisner's (1929-2011) studies on the chemistry of repugnatory secretions. Details on modern research on millipede physiology are given in Chapters 3 to 9.

The usual abundance of millipedes in litter and soil and their important role in decomposition processes, as well as their potential role in revealing the presence of heavy metals and other contaminants (a topic dear to Stephen P. Hopkin (1956-2006)) explain the growing attention towards millipede ecology. Of general interests are however the studies focusing on the millipedes of special environments, e.g. those of Joachim Ulrich Adis (1950-2007) in the periodically inundated forests of Amazonia, of Clifford Smeed

Crawford (1932-2010) and Michael Warburg in arid zones, of Edwin Meyer on high altitude sites in the Alps, of Jean François David, Jean-Jacques Geoffroy, Wolfram Dunger and Karin Voigtländer on a diversity of European woodlands and other formations.

Discovery and description of fossil millipedes, including representatives of lineages whose classification as crown-group Diplopoda has subsequently been disputed, begun in the second half of the XIX century, and included spectacular forms, e.g. arthropleuridans and archypolypodans. Among the researchers of that time, the most prominent was Samuel Hubbard Scudder (1837-1911). Millipede palaeontology has been flowering again since mid XX century, with the results summarized in Chapter 14.

Millipede phylogeny does not seem to be matter of dispute, but the relationships between the Diplopoda and the other myriapods are, to some extent, still controversial, as summarized by Edgecombe (2011) in the first volume of the present work. Phylogenetic studies within the Diplopoda are still mainly limited to the interrelationships among the major clades (orders) (see Chapter 15), and to species-level studies within a handful of genera.

In the last '60s, two very important and interrelated events have launched a new era in the study of millipedes (and myriapods generally). These were the birth of the Centre International de Myriapodologie, due to Jean-Marie Demange, Otto Kraus and Jean-Paul Mauriès, and the start of a series of International Congresses of Myriapodology, still ongoing — a new edition every three years — since the first congress in 1969.

No comprehensive and at the same time detailed monograph has been dedicated to millipede zoology after the classic works of Attems and especially Verhoeff, cited above. However, useful modern compendia were provided by Hopkin & Read (1992) and Dunger (1993).

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CHAPTER 2

DIPLOPODA — GENERAL MORPHOLOGY

BY

MARKUS KOCH

THE MILLIPEDE BODY — SHAPE AND STRUCTURE

The body of millipedes consists of a head and a largely homonomous trunk composed of units generally called diplosegments or rings. Most trunk rings are typically equipped with two pairs of segmented legs each (diplopodous). The legs are articulated to the trunk paramedially on its ventral side. The total number of leg pairs in adults ranges from 11 up to 375. Body size of adults varies conspicuously; extant species include dwarves with a body length of only 1.4 millimeter as well as giants reaching body lengths of more than 30 cm (Hoffman et al., 2002).

The body is usually elongate. Most common forms are (sub-) cylindrical and worm-like, short-legged and capable of enrolling into a tight spiral when disturbed; or are broadly flattened (flat-backed) and equipped with lateral wing- or keel-like cuticular extensions of the body wall called paranota that may cover the legs. Anterior and/or posterior ends of the body taper in some species. The head may be partially or entirely hidden by the anteriormost body ring(s). The most posterior unit of the body (telson) bears the anal opening and lacks legs but may be equipped with filamentous outgrowths ('spinnerets') onto which fibre-producing glands open. The telson usually forms the rear of the body; in some species it is hidden by the posteriormost body ring(s). Paired genital openings (gonopores) lie medioventrally in the anterior part of the trunk (progoneate condition). In females the gonopores open on eversible devices called vulvae, which are sometimes transformed into elongate ovipositors or into sclerotized, leg-like appendages called cyphopods. In males the gonopores lie directly on leg bases or on paired, rarely unpaired penes. Males that transfer sperm directly onto females show specialized legs for copulation: gonopods closely behind the body ring bearing the gonopores/penes (Helminthomorpha), or modified ultimate legs called telopods (Pentazonia). Spiracles (tracheal openings, also called stigmata) occur close to the leg bases on stigmatic plates. Openings of repugnatorial glands (ozopores) may be present as an unpaired, inconspicuous row along the dorsal midline (Pentazonia: Glomerida), or as paired rows in the lateral

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body wall (Helminthomorpha); in juliformian millipedes they often form a conspicuous longitudinal line of dots on each side of the trunk.

The exoskeleton is soft in penicillate millipedes only; in all other millipedes (Chilognatha), as far as known (reviewed by Enghoff, 1990), the cuticle becomes calcified and therefore hard and rigid in the course of their postembryonic development. The body surface may either be largely smooth, variably microsculptured (e.g., Akkari & Enghoff, 2011), or ornamented with prominent cuticular tubercles, ridges, or spines as in the "dragon millipedes" (e.g., Likhitrakarn et al., 2015). Rarely is the body surface densely covered by setae, as in the thread-like *Mitocybe* species (Platydesmida) (Shelley, 2010). Distinct, often aposematic colouration or colour patterns (longitudinal bands, transverse stripes, or spots) are widespread in millipedes (reviewed by Enghoff, 2011), especially in polydesmidans (e.g., Marek & Bond, 2009) and generally in tropical species. Millipedes of temperate zones are more uniformly brown, gray or black. Some lack pigmentation entirely such as species inhabiting caves.

FUNCTIONAL TYPES

Since Manton's studies on the functional morphology of millipedes (summarized in 1977) five main types of body shapes are related to particular life habits and distinguished as *Lebensformtypen* (e.g., Dunger, 1993), *ecomorphological types* (Hopkin & Read, 1992), or *morphotypes* (Kime & Golovatch, 2000; Golovatch & Kime, 2009). Three of them concern different specializations to burrowing life habits: *Bulldozers* or *rammers* are represented by cylindrical forms with numerous short walking legs and a broad front end, as exemplified by the Juliformia. The front end of the trunk forms a rigid cap used as a ram with the head bent underneath, followed by a stiff, largely inflexible trunk with an even width made of round, relatively short, telescopically invaginated and incompressible body rings. The power needed by the walking legs to push the body through substrate is optimized by the relatively broad size of the path determined by the front end, and by the minimal resistance of the body rings and legs against the penetration of the substrate. In millipedes of the *wedge type*, as represented by the Polydesmida, a tapering front end facilitates entering crevices. The stiff, incompressible body rings are equipped with paranota that broaden the rigid, flat backs and provide a thrust to widen the penetrated crevice laterally in one plane, thus allowing for relatively longer and stronger legs; their power for pulling the body forward is two to five times greater than in juliformian millipedes (Manton, 1977). Another type of wedge-burrowing characterizes the *borers* among the Colobognatha and Nematophora. Borers have strongly tapering front ends, some also possessing keel-like paranota. They basically differ from the 'flat-backed' millipedes of the wedge type in the greater flexibility of their body rings that allows movements in an earthworm-like manner. The three main types of burrowers among millipedes show considerable variation and include transitional forms, such as juliformian species with tapered front ends (Manton, 1977) as well as 'habit reversals' like fast-running species among the Callipodida (Dunger, 1993) and other species that apparently abandoned burrowing in favour of a surface active lifestyle (Shelley, 1999).

The other two main functional types relate to short-bodied species. The pill-millipedes (Pentazonia: Oniscomorpha) represent the *rollers*; they resemble woodlice of the family Armadillidiidae (Isopoda: Oniscidea) in their outer appearance and are similarly able to enroll into a ball when disturbed, this ability being known as volvation. Rollers evolved several times independently among millipedes and also occur in polydesmidans (e.g., Sphaeriodesmidae) and few polyzoniidans (Golovatch, 2003). The bristly millipedes (Penicillata) are unique in their striking ornamentation with tufts of serrate setae (pleural and tergal 'trichomes' of taxonomists) and are categorized as *bark-dwellers* (dwarf type of Dunger, 1993). They lack burrowing capability but can nevertheless enter small crevices due to the minute size of their flat, soft bodies.

Other noteworthy body shapes, the functional significance of which still remains unclear, are particularly shown by termitophilous species of the Glomeridesmida (genus *Termitodesmus*): some of them (*T. ceylonicus*) show extraordinarily dome-shaped trunk rings that appear to form a tent for the body, while others (*T. escherichi*) are extremely flattened and recall "water pennies" (i.e., aquatic beetle larvae of the family Psephenidae) in their peculiar shape of a coin.

SEGMENTS AND BODY REGIONS

The millipede head comprises three leg-bearing segments — the antennal, mandibular, and maxillary segments — and three apparently legless segments, the preantennal (ocular), intercalary (premandibular), and postmaxillary (second maxillary) segments (e.g., Janssen et al., 2004). The head is followed by a tergite called the collum that in millipede systematics is counted as the first trunk ring. The subsequent three (rarely four) trunk rings carry a single pair of legs; this region of the trunk is sometimes specified as the thorax of millipedes (e.g., Brölemann, 1935). More or less numerous rings with two leg-pairs (in adults), usually with the exception of the penultimate ring(s), form the majority of the remaining part of the trunk (abdomen). It terminates posteriorly in a unit called the telson, which consists of a preanal, in helminthomorph millipedes ring-shaped sclerite, paired valves bordering the anal opening, and a subanal plate (Enghoff, 1990).

The majority of the trunk units — here called rings irrespective of their actual shape and number of leg-pairs, and of whether the rings are entire or incomplete — are traditionally considered as diplosegments, i.e. to be formed by fusion of two adjacent segments, such that two leg-pairs and two sets of pleurites, sternites and stigmatic plates are coupled with a single tergite. These exoskeletal elements are primarily linked by arthrodial membranes, as shown by the bristly millipedes (Penicillata; e.g., Manton, 1956; Blower, 1985). In chilognathan millipedes the sclerites undergo fusion to different degrees under formation of composites called pleurotergites or of complete entities lacking arthrodial membrane between the former sclerites entirely (see Wesener et al., 2014, their Fig. 7). The term ring is literally used in a more strict sense in the latter instance only, i.e. for units entirely lacking arthrodial membrane between tergite, pleurites, and sternites (ring sensu Enghoff

et al., 1993). Rings of this kind are characteristic for the Juliformia, Polydesmida, and Siphoniulida, which are sometimes denoted accordingly as the ring-forming millipedes. The correlation between the segmental sclerites in non-ring-forming millipedes (i.e., in millipedes with incomplete rings) is constant in Polyzoniida and Chordeumatida (Enghoff et al., 1993) but difficult to assess in other forms due to apparent displacements of the legs relative to the pleurites and tergites (e.g., Manton, 1956). The question on whether or not the thoracic trunk rings, each with only a single leg-pair, represent diplosegments as well (e.g., Demange, 1967; Kraus, 1990) remained contentious but is nowadays refuted (Enghoff et al., 1993; Wilson, 2002; Janssen, 2011).

The discussion on the segmental nature of the trunk rings was recently challenged by insights obtained from gene expression studies (reviewed by Damen et al., 2009) demonstrating that dorsal and ventral halves of the body are decoupled in their early development (for details see Chapter 11). The trunk rings of millipedes, whether complete or incomplete, are therefore no longer considered as to be comparable to conventional arthropod segments (Akkari et al., 2014). According to this view the distinction of haplo- and diplosegments in the traditional sense is obsolete (Janssen, 2011; Fusco & Minelli, 2013).

HEAD

The cephalic segments of millipedes form a compact head capsule that carries a single pair of antennae and two leg-derived mouthparts, the mandibles and the gnathochilarium. Paired lateral clusters of eyes (commonly called ocelli, but see Chapter 9), trichobothria (Polyxenida only), and organs of Tömösváry primarily represent the main sensory organs on the head capsule but may be partially or entirely absent (see Chapter 9).

In chilognathan species with chewing-biting feeding habits the head capsule is typically short and round in side view, quite broad and trapezoidal in frontal (or posterior) view (Fig. 2.1, also Plate II). Its margins form a sharply defined, inwardly directed duplicature along which the mouthparts are jointed. The duplicature allows distinction of a lower side (bottom) from the arched upper side (roof) of the head capsule (Attems, 1926; Verhoeff, 1928). Along the roof the following regions are usually distinguished: a forehead with labrum and clypeus; the frons between the antennal sockets and ocular fields; and the epicranium comprising vertex and occiput (e.g., Iniesta et al., 2012, their Fig. 3E). Lateral areas of the cranial margin below and behind the antennal sockets are usually denoted as the genae.

The head regions are largely confluent and are not delimited against each other by sutures. A notch (*incisura lateralis*) in the lateral margin of the head capsule below the antennal sockets demarcates the area where the cuticular tentorium is usually attached to the head capsule (Fig. 2.2A, also Plate III; Fig. 2.4C, also Plate V). A more or less distinct *interocular furrow* may traverse the frons between the antennae and eyes. A *parietal furrow* is typically present in eugnathan millipedes (Blanke and Wesener, 2014); in Spirobolida it sets off a distinct parietal sclerite lateral to the antennal sockets (Hoffman, 1979).

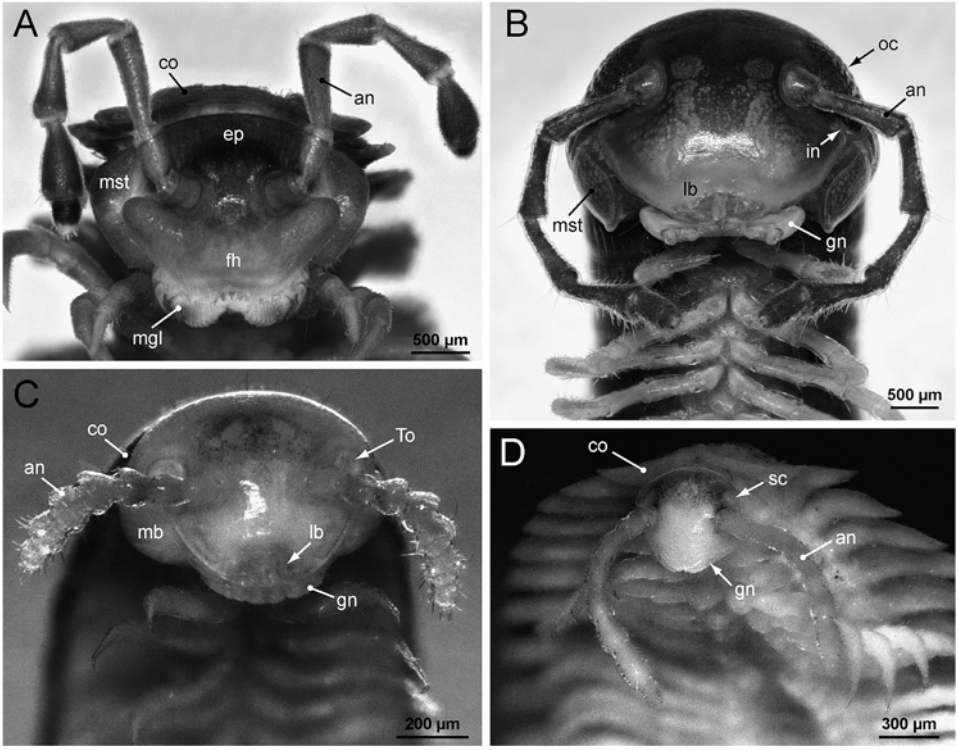


Fig. 2.1. Light micrographs of the head, frontal view. **A** *Polydesmus angustus* (Polydesmida), mandibular gnathal lobes exposed (abducted). **B** *Tachypodoiulus niger* (Julida), mandibular gnathal lobes hidden within preoral chamber (resting state). **C** *Glomeridesmus* sp. (Pentazonia: Glomeridesmida), mandibular base undivided. **D** *Platydesmus* sp. (Colobognatha: Platydesmida), mandibles almost entirely concealed. Originals: M. Koch. Abbreviations: **an** antenna; **co** collum; **ep** epicranium; **fh** forehead; **gn** gnathochilarium; **in** incisura lateralis; **mb** mandibular base; **mgl** mandibular gnathal lobe; **mst** mandibular stipes; **oc** ocular field (eyes); **sc** supra-antennal convexity ('eyespot'); **To** Tömösváry organ. *For a colour version of this figure, see Plate II.*

Spirobolidans are further characterized by a median furrow on the forehead that extends from the clypeus over the labrum onto the epipharynx; the furrow is the external expression of a cuticular septum subdividing the forehead into paired halves. A longitudinal *median furrow* on the epicranium externally demarcates an endoskeletal ridge-like apodeme (median septum of Manton, 1964; Wilson, 2002) expanding the cuticular space for muscle attachments. The occiput is sometimes (especially in juliformians) elevated against the remaining part of the epicranium and may be differently sculptured and/or delimited from it by a transverse groove, line, or ridge. The posterior margin of the occiput sharply bends inwards and forms a semi-circular, dorsolateral flange (postoccipital flange of Manton, 1964; Wilson, 2002) that in the Helminthomorpha gives rise to an endoskeletal *neck phragma* constricting the posterior aperture of the head capsule dorsolaterally (Fig. 2.4B, also Plate V). In the Juliformia the lower edges of this phragma give rise to pointed

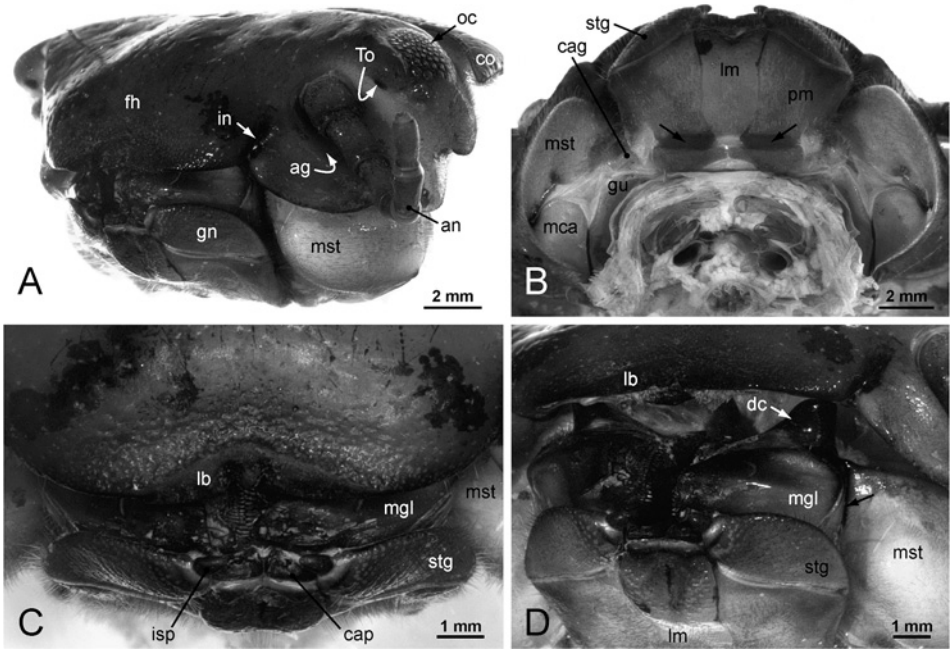


Fig. 2.2. *Zoosphaerium* sp. (Sphaerotheriida), light micrographs of the head of a decapitated specimen. **A** Frontal view on left side. **B** Caudal view; arrows point to areas of flexibility ('joints') between the paramental parts and inclined, apparently paired basal parts of the gnathochilarium. **C** Frontal view on "mouth" (i.e., opening of preoral chamber). **D** Frontal view from left on 'mouth', gnathochilarium and mandibles lowered to display the dorsal condyle of the mandibular gnathal lobe within the preoral chamber; arrow points to upper joint between gnathal lobe and mandibular base (lower joint hidden by the gnathochilarium). Originals: M. Koch. Abbreviations: **ag** antennal groove; **an** antenna; **cag** cardo of gnathochilarium; **cap** cap-like protuberance of endochilarium; **co** collum; **dc** dorsal condyle of mandibular gnathal lobe; **fh** forehead; **gn** gnathochilarium; **gu** gula; **in** incisura lateralis; **isp** inner stipital palp of gnathochilarium; **lb** labrum; **lm** 'lamello-mentum' of gnathochilarium; **mca** cardinal part of mandibular base; **mgl** mandibular gnathal lobe; **mst** stipital part of mandibular base; **oc** ocular field (eyes); **pm** 'paramentum' of gnathochilarium; **stg** stipes of gnathochilarium; **To** Tömösváry organ. *For a colour version of this figure, see Plate III.*

protuberances (internal pseudoccipital processes sensu Manton, 1964). The lower margins of the occiput may also extend backwards into pointed processes (external pseudoccipital processes of Manton, 1964).

Some groups show peculiar modifications of the head capsule in correlation with specialized life and feeding habits. In the Polyxenida the dorsoventral flattening of the body causes a strong inclination of the forehead, such that the clypeus and the mouthparts extend backwards below the remaining part of the head (opisthognathous orientation) (Fig. 2.6A). The antennae are jointed to the head capsule anteriorly on its lower surface in deep emarginations; the antennal bases are accordingly not visible in dorsal view. The eyes are positioned on protruding lateral lobes that are delimited from the frons by a marked furrow (Müller et al., 2007).

In oniscomorph millipedes the head capsule shows adaptations to volvation (Fig. 2.2, also Plate III; Fig. 2.7). The head is markedly shortened (in antero-posterior direction) and can be entirely enclosed by the trunk tergites when enrolled. Sphaerotheriidans and some glomeridans increase the space for the antennae within the sphere by large antennal grooves on the frontal area of the head (e.g., Wesener, 2010). The head lumen provides little space for endoskeletal phragmata; apodemes usually found in helminthomorph millipedes are short (e.g., the cuticular tendon of the mandibular gnathal lobe) or entirely absent (e.g., the median septum). A neck phragma is commonly thought to be absent as well (e.g., Blanke & Wesener, 2014). However, in all pentazonians, markedly in Glomerida, paired triangular endoskeletal processes arise from the occiput that are structurally and functionally comparable to the internal pseudoccipital processes of the neck phragma in helminthomorph millipedes (see, e.g., Silvestri, 1903, his Figs. 21-22; Verhoeff, 1928: 771; Dohle, 1964: 270).

Small pear-shaped heads are characteristic for species with suctorial feeding habits, as shown by the Polyzoniida, most Siphonophorida, and Siphonocryptida among the Colobognatha, as well as by the Siphoniulida. Forehead and mouthparts are acuminate and sometimes drawn out into a long beak (e.g., Enghoff & Golovatch, 1995 and Korsós et al., 2008 for Siphonocryptida; Sierwald et al., 2003 for Siphoniulida; Read & Enghoff, 2009 and Marek et al., 2012 for Siphonophorida). The cheeks formed by the mandibular bases are strongly reduced or entirely absent; the gnathochilarium and genae are laterally approached and seem to coalesce in some species under partial or entire internalization of the mandibular base within the head capsule (entognathy). In siphonorhinids the posterior articulation of the mandibular base with the head capsule may still be externally visible (Marek et al., 2012, their Fig. 2 for *Illacme plenipes*).

Uniquely 'deformed' heads were recently described for adults of the caverniculous species *Pseudotremia peponocranium* (Chordeumatida), in which the frontal area of the head capsule is greatly swollen and forms a conspicuous projection of yet unknown function (Shear, 2011).

Labrum

The apex of the forehead is medially bordered by a narrow, cresecent-shaped labrum. In all millipedes the labrum is fused to the clypeus (e.g., Silvestri, 1903) and usually immovable, except for penicillates in which some flexibility against the clypeus seems to be maintained (Verhoeff, 1928: 956). The labral area is never delimited from the clypeus by a suture but usually contrasts against it by its different colouration, setation, or cuticular ornamentation (Fig. 2.1, also Plate II). The distal margin of the labrum is broadly rounded laterally and slightly to conspicuously emarginated medially. The median margin is usually equipped with teeth that are considered to be primarily adapted to burrowing life habits in Chilognatha (Enghoff, 1990). In the Nematophora, Polydesmida, and most Juliformia, the margin is typically equipped with three teeth, i.e. a median tooth flanked by two paramedian teeth, rarely with a higher number of smaller denticles (Enghoff, 1990; see, e.g., Antić et al., 2015, their Fig. 89 for labral denticles in Chordeumatida). In

spirobolidans (Juliformia) four labral teeth may occur as the forehead, including the former median labral tooth, is medially split by a deep groove extending from the labral margin towards the frons (e.g., Pitz & Sierwald, 2010). In the Pentazonia only a single median tooth is present and is flanked by sharply rounded edges (Fig. 2.2C, also Plate III; Figs. 2.5, 2.7). In penicillate millipedes the labral margin lacks teeth but is sometimes lined along its medial emargination by multiple lamellate denticles (e.g., Nguyen Duy-Jacquemin et al., 2011). Labral teeth are also absent in the Platydesmida among the Colobognatha (e.g., Shear & Marek, 2009) (Fig. 2.1D, also Plate II). In species with suctorial feeding habits within this group as well as in the Siphoniulida the labrum is devoid of teeth but may show denticles bordering the minute, slit- or pore-shaped mouth (i.e., the external opening of the preoral cavity). This especially concerns species with acuminate foreheads devoid of a beak, such as *Illacme plenipes* (Siphonorhinidae; Marek et al., 2012) or *Polyzonium germanicum* (Polyzoniida). In these species the labrum is inclined along the tip of the forehead, such that only the basal part of the labrum — bordered against the clypeus by a shelf- or comb-like protuberance — is visible on the upper surface of the cranial tip. The distal denticulate labral margin is bent downwards and backwards onto its lower surface; left and right parts of the labral margin are medially approached and narrow the former medial emargination of the labral margin into a longitudinal slit that is continuous with the mouth (i.e., the triangular or pore-shaped external opening of the preoral cavity).

Antennae

The antennae of millipedes are primarily composed of seven antennomeres and a short, retractile tip bearing four apical sensory cones (Fig. 2.1, also Plate II; Fig. 2.7). The traditional interpretation of the antennal tip as an 8th antennomere (e.g., Enghoff, 1990; Fontanetti & Camargo-Mathias, 2004; Minelli & Golovatch, 2013; Sombke & Ernst, 2014) is questioned by some authors (e.g., Pitz & Sierwald, 2010) who apparently consider the apical sensory apparatus as a part of the 7th antennomere. The (presumed) 8th antennomere is exceptionally elongate in cavernicolous species of the Lophoproctidae (Penicillata) (Condé & Nguyen Duy-Jacquemin, 2008), while short and conical in other penicillates. In chilognathan millipedes the antennae usually appears 7-segmented as either the antennal tip merely forms a terminal disc (e.g., Sombke & Ernst, 2014), or — less often — as the 7th antennomere is strongly reduced to a short ring as in stemmiulidans (e.g., Riquelme et al., 2014). In the Sphaerotheriida (Pentazonia) only six antennomeres are apparent (Fig. 2.2A, also Plate III), the last terminating in a disc bearing four or more sensory cones (e.g., Wesener & Sierwald, 2005). An increase in the number of apical sensory cones also characterizes some species of the Glomerida, Polydesmida, and Spirobolida (Pitz & Sierwald, 2010). Strikingly elongate, seemingly 9-segmented antennae (including the terminal tip) occur in Callipodida and Stemmiulida, in which the basal part of the second antennomere forms a more or less distinct additional segment termed the antennal trochanter (Verhoeff, 1928; Blanke & Wesener, 2014). Presence (and homology) of the antennal trochanter in these taxa was questioned by Silvestri (1916) as the basal part of the second antennomere in Stemmiulida seems to be delimited from its remaining part

merely by a slight constriction, but not by a joint. Absence of a joint between the antennal trochanter and the remaining part of the second antennomere, however, is typical also for most Callipodida, a distinct joint apparently being present only in *Apfelbeckia* species (Verhoeff, 1928).

The entire length of the antennae relatively to the body as well as the relative length and shape of the antennomeres are quite variable among millipedes, and sometimes also vary between males and females (Verhoeff, 1928). The antennae are rarely straight but usually curved sideward and backwards with the antennal tip directed anteriorly, and are sometimes elbowed between mid-segments. In some species, the curved antennae are placed into antennal grooves on either the head capsule (Sphaerotheriida, some Glomeridae, Spirobolidae) or on the mandibular stipes (Atopetholidae among Spirobolida). Relatively short antennae often appear club-shaped as distal segments, especially the 6th antennomere, tend to be thicker than the basal segments. This is particularly evident in species with suctorial feeding habits, in which the antennae appear conspicuously stout on the small, pear- or beak-shaped heads (e.g., Enghoff & Golovatch, 1995). Apart from the apical sensory cones on the antennal tip, the sensorial equipment commonly involves clusters of specialized sensilla along the apical, retrolateral edges of antennomeres 5-7 (for details see Chapter 9).

Mandibles

Milliped mandibles are gnathobasic, i.e. they consist of the base of the original leg only and its endite(s) forming the gnathal lobe (Scholtz et al., 1998; Prpic & Tautz, 2003). The mandibular base is quite voluminous in chewing-biting millipedes, often surmounting the width of the head capsule, and forms the lateral cheek of the head (*Kopfpleurite* of Verhoeff, 1928). In eugnathan millipedes (Juliformia, Nematophora, and Polydesmida) the base is typically subdivided by a syndetic joint into two main components called cardo and stipes (Fig. 2.4B, also Plate V), with the gnathal lobe jointed to the latter. The cardo and stipes themselves may show further subdivisions by furrows or ridges. In the Polyxenida and Pentazonia the mandibular base is largely entire. This might accordingly represent the ancestral state in millipedes (Blanke & Wesener, 2014), but this view remains ambiguous. Flexible areas in the form of marginal notches (see, e.g., Iniesta et al., 2012, their Fig. 3C for *Glomeridesmus*) or faint furrows (Silvestri, 1903, his Fig. 55 for *Lophoproctus*; Kraus & Brauckmann, 2003, their Fig. 32 for *Polyxenus*) may instead indicate that cardo and stipes are secondarily fused in the respective groups. A fusion of cardo and stipes must be assumed for the Chordeumatida among the Eugnatha, in which the base is no longer divided, the former division being indicated only by a distinct groove in the dorsal (anterior) margin (Blower, 1985). Similar grooves occur in pentazonians on both the dorsal (anterior) and ventral (posterior) margin in comparable position to the joint between cardo and stipes in helminthomorph millipedes (Fig. 2.2B, also Plate III); the grooves in pentazonians provide some flexibility between the (presumable) cardinal and stipital components of the entire mandibular base as well. The bulky extrinsic muscles of the mandibular base, whether entire or composite, primarily originate to large extent

from a rigid collagenous tendon (intergnathal ligament of Snodgrass, 1950; transverse mandibular tendon sensu Manton, 1964). This tendon is maintained, as far as known, in at least Polyxenida, all pentazonian orders (e.g., Verhoeff, 1928, for *Glomeris*, and pers. obs.), Polydesmida (Snodgrass, 1951, and pers. obs.), and all juliformian orders (e.g., Fechter, 1961 for Julida; Manton, 1964 and Wilson, 2002 for Spirostreptida, and pers. obs. for Spirobolida). In Colobognatha, and likely all millipedes specialized on suctorial feeding, the origin of the corresponding mandibular muscles seems to be shifted onto the cuticular tentorium (e.g., Verhoeff, 1928, his Fig. 474 for *Platydesmus*; Blanke & Wesener, 2014 for *Brachycybe*). However, the derivation of the mandibular muscles in taxa with specialized feeding habits has not been comparatively studied thus far. It cannot be excluded that in the respective taxa only the few mandibular muscles are maintained that arise from the cuticular tentorium in chewing-biting millipedes as well (i.e., the muscles primarily arising from the transverse mandibular tendon may be lost in Colobognatha coincident with the loss of this tendon).

Secondary sexual modification of the cardo and stipes or, more often, of only the stipes occur in some male julidans, in which protuberances of the mandibular base serve to clasp the female's head (or antennae) during copulation (Enghoff, 1979) (Fig. 2.4D, also Plate V). Similar modification of the mandibular stipes also occurs in males of some Spirostreptida (see, e.g., Korsós & Johns, 2009) (Fig. 2.4A, also Plate V). In species with suctorial feeding habits the mandibular base is modified into rod-shaped lever arms under elongation of the stipes and shortening of the cardo. In these species the entire mandible is not or only barely visible externally but mostly or entirely hidden within the head capsule (entognathous condition).

The mandibular gnathal lobe lies, in its resting position, largely enclosed within the preoral chamber. It is primarily equipped with a complex armature for chewing and biting, the composition of which shows a common pattern in millipedes (Enghoff, 1990; Köhler & Alberti, 1990; Ishii & Tamura, 1995; Edgecombe et al., 2003): The distal part of the gnathal armature (*pars incisiva*) comprises a stout external tooth, a combed, multi-cusped internal tooth (sometimes referred to as internal teeth), and several rows of hyaline pectinate lamellae (Fig. 2.3, also Plate IV). The proximal part (*pars molaris*) carries a large, rigid crescent-shaped, ovoid or triangular molar plate that in situ flanks the mouth opening (i.e., the opening of the foregut). Distal and proximal parts are separated by an intermediate area equipped with trichoid, fimbriate, or scaly spines. Flexible areas of the cuticle between the components of the gnathal lobe permit independent movements of especially the combed internal tooth, to which intrinsic muscles attach (e.g., Manton, 1964, her Fig. 53). A large (in oniscomorph pentazonians relatively short) laminar or tubular apodeme (*äußeres Tentorium* of Attems, 1926; *Außententorium* of Seifert, 1932) arises from the mesial margin of the gnathal lobe and serves as an attachment for strong adductor muscles (e.g., Fechter, 1961; Manton, 1964; Wilson, 2002). The antagonistic movement (abduction) is coupled with movements of the gnathochilarium, such that its lowering instantaneously causes the mandibular gnathal lobes to open, which is thought to be supported by movements of the tentorium (see below, Peristomatic structures).

Variation in detail of the gnathal lobe's armature is informative for millipede systematics (e.g., Enghoff, 1979 for Julida; Ishii, 1988 for Polyxenida; Ishii & Tamura, 1996 for Polydesmida). The

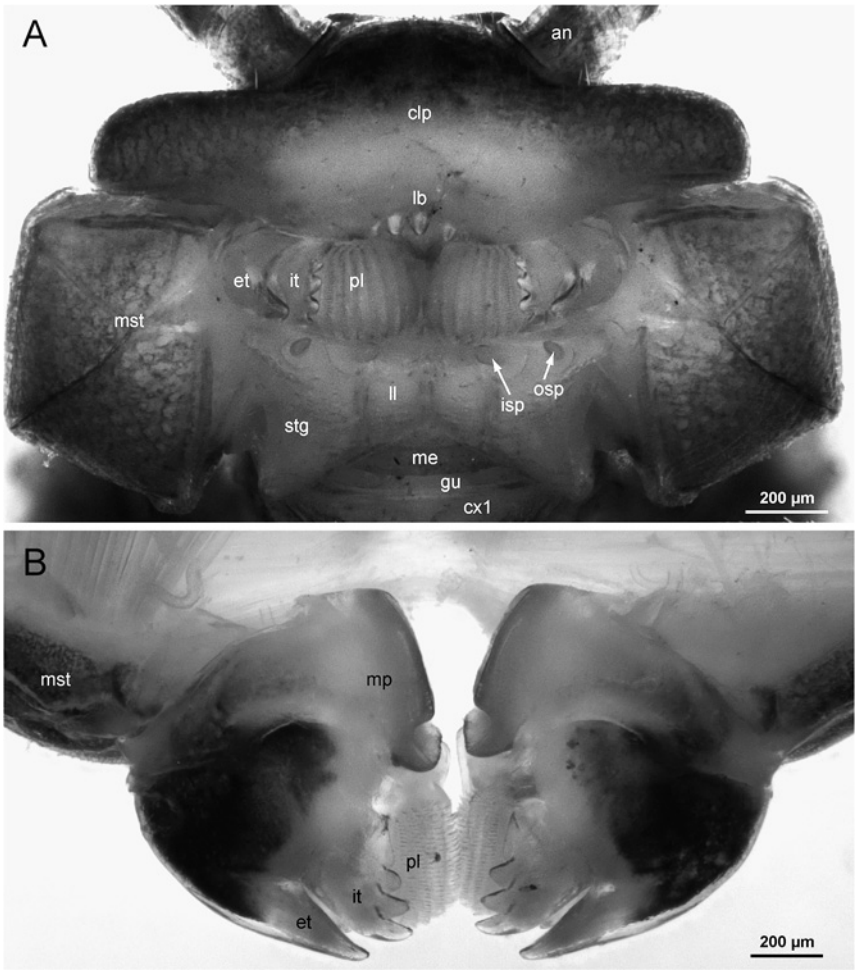


Fig. 2.3. Light micrographs of the mandibular gnathal lobe. **A** *Polydesmus angustus* (Polydesmida), frontal view on abducted gnathal lobes in situ. **B** *Glomeris marginata* (Glomerida), dissected pair of mandibles, dorsal view on gnathal lobes. Originals: M. Koch. Abbreviations: **an** antenna; **clp** clypeus; **cx1** coxa of first trunk legs; **et** external tooth; **gu** gula; **isp** inner stipital palp; **it** internal tooth; **lb** labrum; **ll** lamella lingualis; **me** (duplo-) mentum of gnathochilarium; **mp** molar plate; **mst** mandibular stipes/stipital part of mandibular base; **osp** outer stipital palp; **pl** pectinate lamellae; **stg** stipes of gnathochilarium. *For a colour version of this figure, see Plate IV.*

external tooth may form a single cusp or consists of a large apical cusp and one or several smaller subapical cusps; it may either protrude from or cling to the internal tooth, and is sometimes movable at its base. The internal tooth is usually comb-shaped and comprises three or more (in polydesmids up to seven) apically rounded cusps; rarely it forms a simple, curved edge lacking cusps, as in some spirobolidans (Pitz & Sierwald, 2010). Presence of an additional, isolated simple tooth lateral and proximal to the base of the internal tooth is characteristic for all Spirobolida (Pitz & Sierwald, 2010). The number of rows of pectinate lamellae is primarily high in millipedes (i.e., more than 6, about 10 in adults) and increases during postembryonic growth, but may be secondarily restricted to a lower,

constant number in all postembryonic stages (e.g., 4-5 in some Julida; Enghoff, 1979). The teeth of the pectinate lamella are usually simple and elongate but sometimes show variably branching tips (Enghoff, 1990). The intermediate area in chordeumatids forms a plate-like process protruding over the distalmost part of the molar plate (Köhler & Alberti, 1990). The surface of the molar plate may be flat and smooth, perforated, tuberculate or papillate, or variably fissured by furrows and ridges, and sometimes shows combinations of various states along the proximo-distal or antero-posterior axis. A fringe of spines rarely surrounds the margin of the molar plate circumferentially but is most often restricted to its anterior margin, or lacks entirely. Presence of a single, stout cusp distal and mesial to the molar surface (molar cusp of Enghoff, 1984a) is characteristic for nematophoran millipedes (i.e., Callipodida, Chordeumatida, and Stemmiulida). A similar tooth occurs in some glomerids lateral to the distal end of the molar plate (Wesener, 2012: lateral tooth). The proximalmost part of the molar plate, i.e. the part closest to the mouth, is often followed by a tuft of trichoid spines, the so-called molar tuft, recalling the *Haarpolster* (pulvillus) of centipede mandibles (e.g., Edgecombe et al., 2003).

Specialized feeding habits in favour of scraping or piercing food correlate to different degrees with simplifications of the gnathal armature. Penicillates are characterized by a loss of both external and internal teeth (Ishii & Tamura, 1995) and mainly use the molar plate for crushing food. The former incisor part is restricted to a protruding lobe apically covered by multiple (6-10) rows of broad, rather blunt and sometimes branched denticles (e.g., Kraus, 2001, his Figs. 10, 20-21). These denticles are likely homologous to the teeth of the pectinate lamellae in chilognathan millipedes. Suctorial feeders among the Helminthomorpha are devoid of the molar part and show variable transformations of the incisor part into minute claws — primarily under maintenance of strongly modified external and internal teeth (e.g., Ishii & Tamura, 1995 for Polyzoniida) — or into stylet-like structures (e.g., Silvestri, 1903, his Figs. 63-65, and Marek et al., 2012 for Siphonophorida). Among the Colobognatha, the mandibles of the (presumably) fungivorous platydesmidans still recall the original state of the gnathal armature but show a conspicuous elongation of the intermediate area under modification (including size reduction) of the external and internal teeth, pectinate lamellae, and molar plate (Verhoeff, 1928; Enghoff, 1990; Ishii & Tamura, 1995). The molar plate appears to be entirely reduced in some andrognathid species (e.g., *Pseudodesmus* sp.; Semenyuk et al., 2011).

The articulation of the mandibular base with the head capsule is a firm hinge in chewing-biting millipedes but never involves joints of the ball-and-socket-type (Manton, 1964). The gnathal lobe, in contrast, articulates with the stipes via a hinge that in polydesmidans involves two protruding ball-like condyles (e.g., Nguyen & Sierwald, 2013, their Fig. 11), one each on the dorso-lateral (upper) and ventro-lateral (lower) basal margin of the gnathal lobe, which fit into corresponding sockets on the anterior margin of the stipes. The two condyles (especially the lower condyle) are less conspicuous in other chilognathan millipedes, and are entirely absent in the Pentazonia (e.g., Attems, 1926), which instead show a circumferential syndetic joint — in shaerotheriidans with strenghthened upper and lower margins (Fig. 2.2D, also Plate III) — between gnathal lobe and mandibular base. In polyxenids two condyles occur on the basal margin of the gnathal lobes, one of which consists of three knobs (Attems, 1907 for *Monographis*; Kraus & Brauckmann, 2003 for *Polyxenus*). In the suctorial feeders with simplified mandibles among the Colobognatha a simple syndetic joint each between the cardo and stipes as well as the stipes and gnathal lobe seems to be primarily maintained (Silvestri, 1903; Verhoeff, 1928: 837). Platydesmids in addition also primarily keep at least the upper ball-and-socket type of articulation between stipes and gnathal lobe (Verhoeff, 1928, his Fig. 408).

Pentazonia are unique among millipedes in the presence of an additional condyle on the dorsal surface of the gnathal lobe lateral to the molar plate (Wesener & VandenSpiegel, 2009). The condyle articulates with the lower side of the forehead, but details of this articulation still remain unclear. The condyle is hook-shaped in Glomeridesmida, as in centipedes (Chilopoda). In glomeridans the condyle instead is flatly compressed, or entirely absent, while forming a prominent, thick and cylindrical or wing-like protuberance in sphaerotheriidans (Fig. 2.2D, also Plate III). This condyle likely corresponds to the ancestral articulation of the mandibular gnathal lobe with exoskeletal components of the tentorium in myriapods (e.g., Koch, 2003).

Gnathochilarium

The preoral cavity of millipedes is bordered from below or behind, respectively, by a bowl- or plate-like 'lower lip' called the gnathochilarium (Fig. 2.2B, also Plate III). It consists of the leg bases (cardo and stipes) of the first maxilla, its endites that give rise to two apical sensorial lobes (stipital palps), and a median, often composite plate interconnecting the maxillae and providing another pair of apical sensorial lobes (lingual palps). The ancestral composition and origin of the intermaxillary plate and the homology and evolution of its components among millipedes have traditionally been contentious and still remain partly unclear.

The traditional debate on the nature of the gnathochilarium mainly focused on (i) whether or not the appendages of the postmaxillary segment (second maxillae) give rise to the intermaxillary plate (e.g., Hilken & Kraus, 1994 versus Dohle, 1998 versus Kraus, 2001); and (ii) whether the intermaxillary plate was primarily entire and variably fragmented in chilognathans, or instead was primarily composed of several skeletal elements that among millipedes underlie fusion to different degrees (e.g., Jeekel, 1985; Enghoff, 1990; Mauriès & Enghoff, 1990). Recent gene expression studies on *Glomeris marginata* corroborate the view that appendages of the postmaxillary segment (second maxillae) are not involved in the formation of the gnathochilarium (Prpic & Tautz, 2003; Prpic, 2004; Prpic et al., 2005). They furthermore reveal that not only cardo and stipes, but also the distal part(s) of the intermaxillary plate, the so-called lamellae linguales, are derived from the limb buds of the first maxilla and accordingly have paired anlagen. The nature of the proximal element(s) of the intermaxillary plate, i.e. the mentum and its derivatives in Helminthomorpha (promentum, postmentum, intermentum), was not considered in these studies; traditionally they are interpreted as sternal elements of either the maxillary (Verhoeff, 1928) or postmaxillary segment (Attems, 1926). Basal elements of the gnathochilarium are posteriorly bordered (and sometimes covered) by a skeletal element, the gula (*hypostoma* of Latzel, 1884; *basilare* of Silvestri, 1903) that forms the ventral sclerotic border of the head capsule. There is broad consensus that the gula is a sternal element as well, but there has been disagreement on whether it is derived from the sternum of the postmaxillary segment (Silvestri, 1949; Dohle, 1964, 1980) or of the first trunk segment (Blower, 1985; Hoffman, 1990; Hilken & Kraus, 1994); recent developmental insights (e.g., Janssen, 2011) favour the former interpretation.

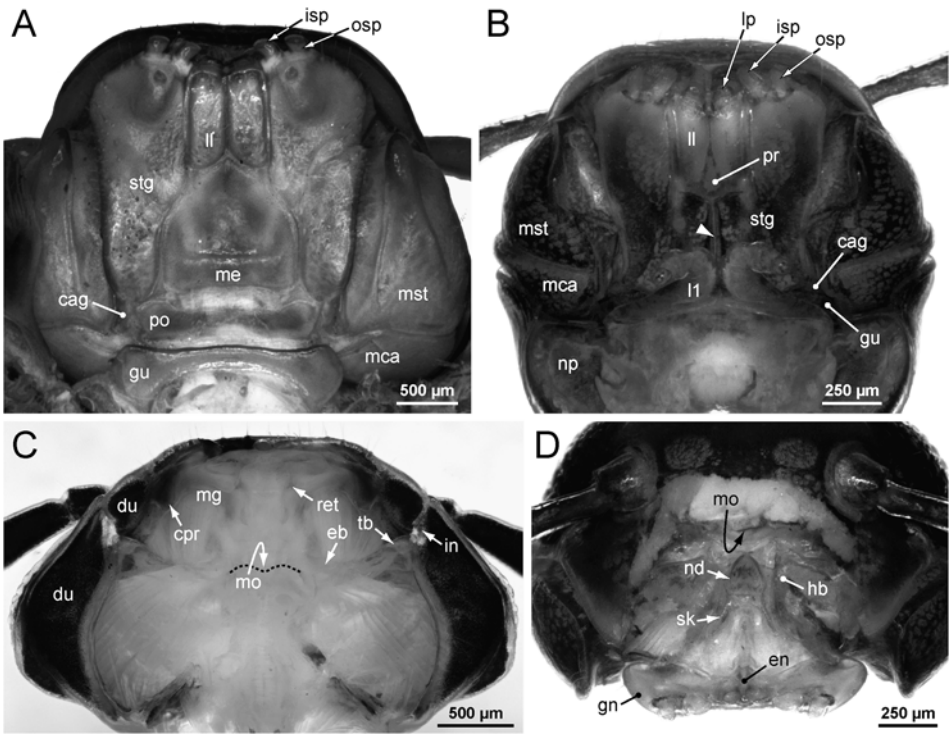


Fig. 2.4. Light micrographs of gnathochilarium (**A-B**) and peristomatic structures (**C-D**). **A** *Sechelleptus* sp. (Spirostreptida), caudal view on dissected head of a male specimen (tip of labrum on top). **B** *Tachypodoiulus niger* (Julida), male specimen, same view as in **A**; arrowhead points to median suture, along which the gnathochilarial stipites appear to be fused. **C** *Glomeris marginata* (Glomerida), same view as in **A** but gnathochilarium, mandibles, and hypopharynx (cutting edge indicated by dotted line) removed to display the epipharynx; the tentorium is largely translucent. **D** *Tachypodoiulus niger* (Julida), frontal view on head, forehead and mandibular gnathal lobes removed to display the hypopharynx. Originals: M. Koch. Abbreviations: **cag** cardo of gnathochilarium; **cpr** clypeolabral protuberance; **du** duplicature; **eb** epipharyngeal bar of tentorium; **en** endochilarium; **gn** gnathochilarium; **gu** gula; **hb** hypopharyngeal bar of tentorium; **in** incisura lateralis; **isp** inner stipital palp; **ll** lamella lingualis; **lp** lingual palp; **l1** first trunk legs; **mca** mandibular cardo; **me** mentum of gnathochilarium; **mg** mandibular groove; **mo** mouth (opening of foregut); **mst** mandibular stipes; **nd** hypopharyngeal node; **np** neck phragma; **osp** outer stipital palp; **po** postmentum; **pr** promentum; **ret** retinacular bar; **sk** serrulate keel; **stg** stipes of gnathochilarium; **tb** transverse bar of tentorium. *For a colour version of this figure, see Plate V.*

In the Eugnatha the gnathochilarium typically forms a rectangular or trapezoidal 'shovel' that is neatly encompassed by the mandibles, often by strong longitudinal ridges on the mandibular stipites (Fig. 2.4A + B, also Plate V). All components of the gnathochilarium are arranged in (almost) one plane. Paired stipites primarily form broad lateral elements that are interconnected distally by paired lamellae linguales and proximally by a trapezoidal or triangular, often composite mentum. The stipites apically bear two conical palps apiece (here referred to as outer and inner stipital palps), the

lamellae linguales each bear a single palp (here referred to as lingual palp). A pair of small, often inconspicuous *cardines* borders baso-laterally against the stipes and mentum. The cuticular interconnections (sutures) show flexibility and provide some limited plasticity to all these elements (Hilken & Kraus, 1994). The suture between each stipes and lamella lingualis in addition houses the opening of the maxillary nephridial organs (e.g., El-Hifnawi & Seifert, 1973; *Putzdrüse* of Verhoeff, 1928). The nephridial openings usually lie at the base of the suture interconnecting stipes and lamella lingualis but are located in a more distal position of the suture in Polydesmida and Chordeumatida (Verhoeff, 1928; Attems, 1937). The frontal surface of the gnathochilarium above the stipites and lamellae linguales gives rise to the so-called endochilarium that interconnects the gnathochilarium with the hypopharynx (Fig. 2.4D, also Plate V). The endochilarium comprises a central body (*Zentralkörper* of Verhoeff, 1928) that in some eugnathans, especially Callipodida, protrudes fronto-medially as a median lobule (*spatula* sensu Silvestri, 1903) between the apical margins of the lamellae linguales and their palps. Behind the lingual palps, a pair of paramedian cap-like protuberances of the endochilarium (*Zäpfchenkappe* of Verhoeff, 1928) houses another cluster of sensorial cones (Fig. 2.5). In contemporary descriptions these protuberances are sometimes referred to as central (located) pads (Wesener et al., 2008, 2009 for Spirobolida), but this term is used ambiguously, sometimes interchangeably, sometimes distinctly from median palp. The term median palp usually refers to the apical lobes roofing the lamellae linguales, but its usage in previous publications is likewise inconsistent; median palp may refer to the lingual palps, to the inner stipital palps, to clusters of sensorial cones on the endochilarium, or to the entire entity comprising the lingual palp and protuberances of the endochilarium. The endochilarial sensory fields lie immediately adjacent to hyaline fringed lobes (*Außenlappen* of Verhoeff, 1928) extending laterally towards and along the stipital palps. The endochilarial components are variably supported by skeletal elements (Verhoeff, 1928: *Zentralzapfen*, *Stützbogen*, *Bogenknoten*; Enghoff, 1981: anterior skeletal elements) that firmly connect the endochilarium to the gnathochilarium. The endochilarial area furthermore houses the paired openings of the posterior salivary glands (*glandula salivalis posterior* of El-Hifnawi & Seifert, 1973).

Variation in the shape of the gnathochilarium in eugnathan millipedes concerns the relative size, composition and arrangement of its components. The stipes most often is quite elongate; it comprises a slender proximal part bordering against the mentum and a broad distal part bordering against the lamellae linguales. Main deviations concern the Spirobolida, in which the stipes appears relatively short and stout and distinctly set off from the cardines by a conspicuously large mentum; and the Julida, in which the proximal parts of the stipites appear to be coalesced along a median suture (symphyognathous), apparently under restriction of the original mentum to an unpaired triangular plate (promentum) above the coalesced parts of the stipites and possibly slender transverse basal plates below them (Fig. 2.4B, also Plate V). The cardines generally receive little attention in contemporary studies. According to the classic surveys (Silvestri, 1903; Attems, 1926; Verhoeff, 1928) they primarily form narrow, triangular or crescent-shaped sclerites immediately below the stipites, but they tend to underlie size reduction, especially in Chordeumatida. Stemmiulida uniquely differ from other Eugnatha in the increased number of cardinal sclerites, apparently as the formerly entire cardo is split into 2-3 sclerites on each side (Silvestri, 1916). The lamellae linguales are

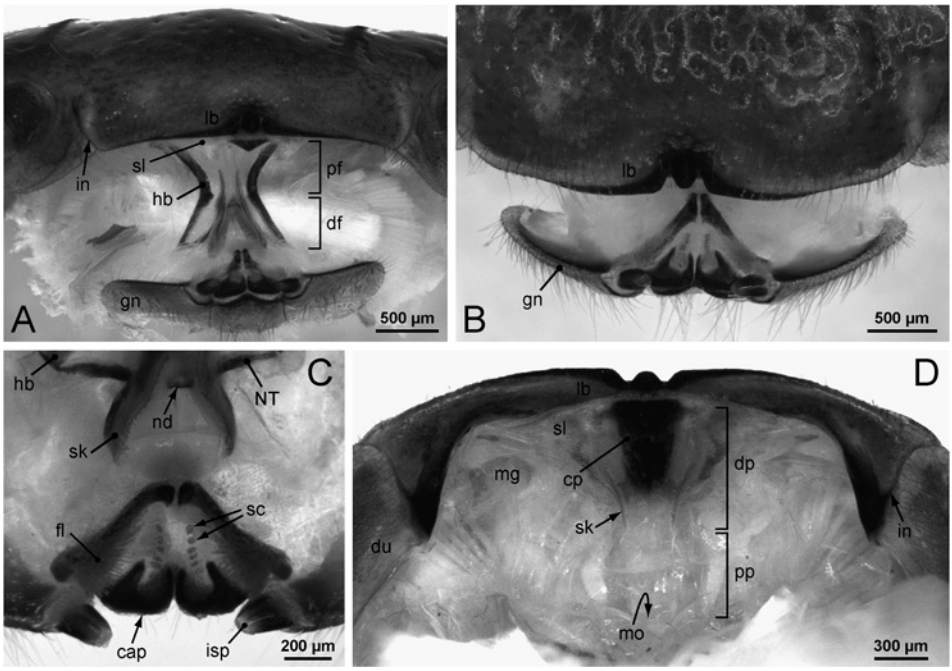


Fig. 2.5. *Zoosphaerium* sp. (Sphaerotheriida), light micrographs of peristomatic structures. **A** Frontal view into the preoral chamber, mandibles removed to display the hypopharynx. **B** Endochilarium, frontal view. **C** Endochilarium and distal field of hypopharynx, dorsal view. **D** Epipharynx, caudal view (tip of labrum on top). Originals: M. Koch. Abbreviations: **cap** cap-like protuberance of endochilarium; **cp** central plate; **df** distal field of hypopharynx; **dp** distal part of epipharynx; **du** duplicature; **fl** fringed lobe; **gn** gnathochilarium; **hb** hypopharyngeal bar of tentorium; **in** incisura lateralis; **isp** inner stipital palp; **lb** labrum; **mg** mandibular groove; **mo** mouth; **nd** hypopharyngeal node; **NT** Nebententorium; **pf** proximal field of hypopharynx; **pp** proximal part of epipharynx; **sc** cluster of sensorial cones; **sk** serrulate keel; **sl** side lobe of epipharynx.

consistently paired in eugnathans but variably separated from each other by the mentum. Depending on how far the mentum protrudes between the lamellae linguales, they may form elongate, rectangular plates that are medially contiguous almost along their entire length; or shorter, triangular plates that are medially interconnected only by their apices, if at all. Conspicuously small lamellae linguales in correlation with an enlarged mentum are characteristic for Spirobolida (Wesener et al., 2008). Median palps are usually stated to be present in eugnathans (except Siphoniulida), irrespective of whether or not palp-like protuberances and/or apical sensory cones occur above the lamellae linguales. Palp-like protuberances in a literal sense — as present, for instance, in Julida (see, e.g., Enghoff, 1981, his Fig. 11) or Chordeumatida (see Reboleira & Enghoff, 2014, their Fig. 3) — occur neither in Polydesmida, nor in Spirobolida above the lamellae linguales. In polydesmidans vestiges of the lingual palps are represented, if present at all, by a few sensorial cones on blunt apical pads roofing the lamellae linguales (see, e.g., Nguyen & Sierwald, 2013, their Fig. 12). In spirobolidans blunt pads likewise roof the lamellae linguales but lack sensorial cones on their apices; instead they show each a small circular cluster of sensorial cones offset subapically towards the endochilarial surface (see, e.g., Wesener et al., 2008, their Fig. 7; Wesener et al., 2009, their Figs. 32, 40, 61). Contemporary descriptions consider them as derived from the endochilarial clusters of sensory cones, supposedly by a split of these clusters each into (sub-) apical and lateral sensory fields.

Unambiguous distinction between the sensory cones from the lingual palps and endochilarium seem to cause problems in Callipodida, in which protuberances roofing the lamellae linguales are or are not considered as palps (see, e.g., Shear et al., 2003: lingual palps are stated as absent in *Sinocallipus* despite documentation of protuberances that in other callipodidans are considered as lingual palps by, e.g., Verhoeff, 1928).

The original state of the sternal elements of the gnathochilarium in Eugnatha still remains unclear. Basically the mentum either forms an entire plate, or is transversely devided into an apical promentum and the mentum proper (sometimes specified as eumentum). The term duplomentum (rarely diplomentum; e.g., Mikhaljova, 2004) was formerly introduced for all chilognathan taxa with an entire mentum but is applied ambiguously in contemporary descriptions either for all taxa with an entire mentum, or only for taxa in which the mentum shows a conspicuous promental area that is not delimited from the proper mentum by a suture, as for instance in Polydesmida. Such ambiguity particularly concerns the Spirostreptidea, which may have a duplomentum (Verhoeff, 1928; Jeekel, 1985) or only the mentum proper (e.g., Enghoff, 1981) for the apparent absence of a promental area. The degree of how far the promentum (or promental area) medially separates the lamellae linguales varies among eugnathans from inconspicuous to almost complete. Usually the promentum forms an unpaired triangular or drop-shaped plate. In some Spirostreptida (some Pseudonannolenidae and Pericambalidae) the promentum exceptionally appears to be split longitudinally into two halves (see, e.g., Iniesta & Ferreira, 2013, their Figs. 4, 8). It remains unclear though whether the respective halves are derived from the promentum, or instead from oblique subdivision of the lamellae linguales (for discussion see Mauriès & Enghoff, 1990). The proximal area of the mentum may further be delimited by a transverse ridge (*Bogenwulst* of Verhoeff, 1928) for the presence of a medial depression on its distal area (*Kinngrube* sensu Verhoeff, 1928). Such a depression delimited by a strong ridge occurs in some Cambalidae, Pseudonannolenidae, Spirostreptidae, and Iulomorphidae among the Spirostreptida (see, e.g., Enghoff, 1981, his Fig. 3; Korsós & Johns, 2009, their Figs. 10, 44; Korsós & Read, 2012, their Fig. 1; Iniesta & Ferreira, 2013, their Figs. 4, 8), as well as in some Chordeumatidae (Chordeumatida) and Callipodidae (Callipodida) (Verhoeff, 1928). An analogous basal 'subdivision' of the mentum by a transverse ledge was recently described for some Pachybolidae (Spirobolida) (Wesener et al., 2009).

Whether entire or composite, the mentum is basally followed by a more or less slender transverse sclerite called the postmentum (Verhoeff, 1928) or *praebasilare* (Silvestri, 1903; Attems, 1926). In some species the postmentum is represented — in addition or exclusively — by a pair of small sclerites adjacent to the cardines called the nodi. The origin of the postmentum (and nodi) from either the mentum or the gula remains unclear. Polydesmida exceptionally seem to lack both a postmentum and nodi (Fig. 2.3A), potentially for being fused to the mentum (Verhoeff, 1928: 912). In Julida the paired or unpaired basal sclerites of the gnathochilarium are variably interpreted as remains of the mentum (e.g., Attems, 1926), as postmentum (e.g., Fechter, 1961), or as intermentum (Verhoeff, 1928), depending on how many transverse bars are differentiated (or recognized) between the basally fused stipites and the gula. Recognition of an intermentum in julidans is based on the contentious view that the stipites are not coalesced basally but fused with the actual mentum into mentostipites, under loss of the original sutures delimiting the stipites from the mentum (Verhoeff, 1928; Jeekel, 1985). Homologisation of the basal sclerites is furthermore hampered by the view that the intermentum is thought to vary in size among Julida with respect to the size of the postmentum; the more obvious, usually depicted pair of basal plates (see, e.g., Enghoff, 1981, his Fig. 3) may either represent the postmentum behind an inconspicuous intermentum (Trichoblaniulidae: Verhoeff, 1928), or instead represent the intermentum while the postmentum — whether conspicuous and equipped with nodi (Blaniulidae: Verhoeff, 1928) or inconspicuous (Julidae: Verhoeff, 1928) — lies hidden below the gula.

Recognition and homologization of the sternal elements of the gnathochilarium accordingly still cause problems in contemporary taxonomic descriptions. For instance, Shear et al. (2003) considered

a small triangular mentum and broad postmentum (*prebasilare*) to be present in *Sinocallipus*, while the corresponding areas in other Callipodida are traditionally interpreted as promentum and (eu-) mentum, respectively, the postmentum being represented only by small nodi (Verhoeff, 1928). Recognition of the mentum in the strongly derived gnathochilarium of Siphoniulida by Sierwald et al. (2003) likewise remains ambiguous. Current descriptions of the basalmost gnathochilarial sclerites in Spirostreptida are inconsistent with traditional interpretations in mistaking the postmentum either for an intermentum (Wilson, 2002), or for the gula (Korsós & Johns, 2009; Iniesta & Ferreira, 2013).

Sexual modifications of the gnathochilarium are particularly known from male Parajuloidea (Julida), in which the promentum is transformed into a soft, enlarged pad completely separating the lamellae linguales, while apparently paired mental sclerites are delimited from the stipites by a more or less obvious suture (e.g., Jeekel, 1985); and from male Stemmiulida, in which the lamellae linguales are strongly enlarged under a shortening of the mentum. A unique instance of transformed gnathochilaria in Polydesmida concerns males of *Ingurtidorgius caprinus* (Trichopolydesmidae), in which the stipites seem to be medially coalesced in correlation with the lack of lamellae linguales, while the promental area of the shortened duplomentum gives rise to an elongate hook (e.g., Golovatch, 2013). In Spirostreptida males instead may show modifications of the maxillary stipites in being slightly expanded distally and/or equipped with additional sensory pits (see, e.g., Korsós & Johns, 2009 for *Eumastigonus*; Pimvichai et al., 2009 for *Thyropygus*; Korsós & Read, 2012 for *Zinagon*); or of the postmentum that is variably dissolved into single sclerites in correlation with the presence of retrose prefemoral lobes on the first trunk legs in males involved in mating (e.g., Krabbe, 1982).

The gnathochilarium of the Colobognatha lacks apical sensorial palps entirely (e.g., Enghoff, 1984a), and the cap-like protuberances of the endochilarium are likewise reduced (Verhoeff, 1928). In the Platydesmida the gnathochilarium still is composed of large stipites, more or less conspicuous cardines, a narrow mentum that may be entire or divided into promentum and (eu-) mentum, and slender lamellae linguales that are variably separated medially (from hardly to entirely) by the promentum or the promental area of the (duplo-) mentum, respectively (e.g., Attems, 1951 and Minelli, 1976 for *Dolistenus*; Kraus & Kraus, 1994 for *Platydesmus*; Blanke & Wesener, 2014 for *Brachycybe*). In other colobognathans the gnathochilarium tends to form a single plate, the composition of which remains ambiguous. According to classic descriptions (Silvestri, 1903 and Attems, 1938 for *Siphonorhinus* and *Kleruchus*) a composite gnathochilarium with well-separated stipites, lamellae linguales, a narrow mentum, and inconspicuous cardines is preserved in some Siphonorhinidae (Siphonophora), while other siphonorhinids seem to have these components indistinguishably fused (Marek et al., 2012 for *Illacme*). The tapering, apparently undivided gnathochilarium of Siphonophoridae (*Siphonophora*) and Siphonocryptida (e.g., Enghoff & Golovatch, 1995) may instead consist of the mentum only. The fate of the maxillae (entire absence?) in these taxa remains unclear though, since Attems (1938) reported presence of cardines in Siphonophoridae, and some classic illustrations (Silvestri, 1903, his Fig. 9) and recent documentations of the siphonophorid head by electron microscopy (Read & Enghoff, 2009, their Figs. 1-2) indicate presence of paired lateral structures along the beak that might correspond to slender stipites or lamellae linguales. Paired stipites and/or lamellae linguales may also occur in some Polyzoniida (Verhoeff, 1928 for *Polyzonium*; Attems, 1951 for *Burinia*), but they are delimited only indistinctly by grooves associated with the openings of the maxillary nephridia, if at all. A relatively large gula covers the base of the gnathochilarium in Platydesmida and may also occur in other colobognathans (denied for Polyzoniida by Verhoeff, 1928). The apparently exceptional presence of a postmentum in some Platydesmida still remains dubious (absent in *Platydesmus* and *Brachycybe*: Verhoeff, 1928 and Blanke & Wesener, 2014, but present in *Dolistenus*: Attems, 1951 and Minelli, 1976, and present in *Brachycybe*: Hoffman, 1990)

Among the Pentazonia the typical components of the helminthomorph gnathochilarium occur in Glomerida as well, comprising paired stipites, paired cardines, lamellae linguales that at least

have paired anlagen but medially fuse during embryonic development (Prpic & Tautz, 2003), and — uniquely among millipedes — a paired mentum, i.e. a mentum that is divided by a median suture into two halves (e.g., Enghoff, 1990, his Fig. 2). The mentum is markedly short in glomeridans, such that the fused lamellae linguales seem to form the majority of the intermaxillary plate, and the stipites do not border against the mentum but only the relatively large cardines. The median fusion of the lamellae linguales is characteristic for Pentazonia in general (see, e.g., Wesener & VandenSpiegel, 2009, their Figs. 58-66). In Glomeridesmida and Sphaerotheriida, however, the fused lamellae linguales are not delimited from the mentum by a suture but seem to be coalesced with the mentum into a large, undivided plate called the lamello-mentum (e.g., Iniesta et al., 2012). It remains unclear though which area of the lamello-mentum can be ascribed to the mentum (e.g., Hoffman, 1976). In Sphaerotheriida the lamello-mentum comprises broad lateral areas called the paramentum that distinctly separate the stipites from small cardines (e.g., Wesener, 2009). The mid-field of the intermaxillary plate between left and right paramentum is entirely or partly elevated, while the narrow basalmost area of the lamello-mentum is flexibly inclined and in at least some species appears paired for the presence of a less sclerotized median bridge (Verhoeff, 1928) (Fig. 2.2B, also Plate III). In Glomeridesmida, in contrast, the lamello-mentum broadens basally only, such that the relatively large cardines remain jointed to both the stipites and the lamello-mentum. Presence of an unpaired or paired postmentum was discussed by Verhoeff (1928) for Glomeridesmida and Sphaerotheriida but is not recognized in comtemporary descriptions. The short, paired mentum in Glomerida is suggestive of considering only the paired or unpaired basalmost areas in Glomeridesmida and Sphaerotheriida as derived from the actual mentum, the main parts of the intermaxillary plate hence being formed by the fused lamellae linguales in all pentazonians (e.g., Attems, 1926, his Fig. 116 for *Glomeridesmus*), but this view still requires more comprehensive anatomical studies of the gnathochilarial musculature. As in Glomerida, the maxillary nephridia of glomeridesmidans open distally into the suture between the stipites and lamellae linguales (pers. obs.), whereas the openings are apparently shifted onto the endochilarium in Sphaerotheriida (Verhoeff, 1928). A broad gula covers the base of the gnathochilarium in Glomerida and Glomeridesmida. In Sphaerotheriida the gula forms an inconspicuous transverse bar that widens laterally only and is fused with its lateral parts to the head capsule (Fig. 2.2B, also Plate III).

Among pentazonians outer and inner palps of the stipes show similar sizes in some glomeridans only. In other Glomerida as well as Glomeridesmida the outer palp is markedly smaller than the inner palp, while in Sphaerotheriida only vestiges of the outer palp occur (Fig. 2.2, also Plate III; Fig. 2.5A-C), i.e. a few (usually four) sensory cones that are no longer elevated on a palp (see, e.g., Wesener & VandenSpiegel, 2009). Lingual palps seem to occur in Glomeridesmida only. In *Termitodesmus* (Silvestri, 1911, and pers. obs.) they resemble the lingual palps of eugnathan millipedes in their conical shape and equipment with short sensory cones, whereas in *Glomeridesmus* they are enlarged — in the same manner as the inner stipital palps — into broad pads with elongate, tubular sensory cones (e.g., Iniesta et al., 2012). In Glomerida and Sphaerotheriida the lingual palps are replaced by pads devoid of apical sensory cones (Fig. 2.5C). Recent descriptions (e.g., Hilken & Kraus, 1994; Wesener & VandenSpiegel, 2009) consider these pads as derived from (i.e., homologous to) median palps. Verhoeff (1928: 872, 878), however, considered the pads as to be formed by the cap-like protuberances of the endochilarium (*Zäpfchenkappen* of Verhoeff, 1928) under loss of the lingual palps. This interpretation is straightforward with regard to the state in Sphaerotheriida, in which the cap-like protuberances of the endochilarium are medially approached and their paramedian clusters of sensorial cones transformed into elongate rows, in some species under subdivision into multiple circular clusters (e.g., Wesener, 2009, his Fig. 33; Golovatch et al., 2012, their Fig. 5). The subapical position of the distalmost sensorial cones in Glomerida, however, causes ambiguity about their derivation from either the lingual palp, or the paramedian clusters of the endochilarium. The latter interpretation, i.e. correspondence to the state in Sphaerotheriida, seems to be favoured by the structure of the endochilarial skeleton in glomeridans (Verhoeff, 1928).

The interpretation of the 'lower lip' in the Polyxenida also remains contentious. It is composed of (i) a broad, unpaired but seemingly bipartite bowl that shows a more flexible, triangular field along its midline; (ii) a flexible, apparently paired membranous field anterior to the bowl bearing sensorial lobes (on each side a roundish paramedian pad continuous with a branch-like, faintly segmented lateral lobe that may be absent as in Lophoproctidae); and (iii) paired, in ventral (caudal) view rod-shaped, apically blunt or faintly bilobed 'appendages' frontally overlying the membranous field anterior to the bowl (see, e.g., Kraus, 2001, his Figs. 20-21) (Fig. 2.6A). Presence of a gula has variably been denied or confirmed (see Manton, 1961: 451). The entire construction is oriented backwards (opisthognathous), such that the basal attachment of the bowl-shaped plate to the body in situ lies anterior to the distal tip of the gnathochilarium. Identification of the first maxillae within this construction still is controversial. Recent taxonomists (e.g., Hoffman, 1982; Enghoff, 1990; Nguyen Duy-Jacquemin et al., 2011) commonly follow Reinicke's (1910) interpretation and consider the sensorial lobes ('palps') as stipital in origin, and the stipites as fused into the bowl-shaped plate. Short lamellae linguales (or remnants of them according to Verhoeff, 1928) were recognized by Reinicke (1910) in front of the paramedian sensorial lobes but are commonly ignored in contemporary descriptions. He furthermore attributed the rod-shaped 'appendages' overlying the bowl-shaped plate to the hypopharynx. Kraus & Kraus (1994), in contrast, revived the view by Carpenter (1905) who considered the rod-shaped 'appendages' to represent the first maxillae proper in polyxenids, because they appear more shell-like in dorsal (frontal) view and basally show faint indication of segmentation into cardo and stipes. They accordingly questioned the presence of a gnathochilarium in Polyxenida as they considered the first maxillae as to be still arranged in front of the intermaxillary plate (versus in the same plane as the intermaxillary plate, as in Chilognatha), similarly as in the millipedes' closest relatives, the Pauropoda.

All previous interpretations suffer from the anatomical problem that the apical sensorial lobes in Polyxenida cannot unambiguously be assigned to the intermaxillary plate as they seem to arise distinctly offset within the membranous field between the rod-shaped 'appendages' and the intermaxillary plate. This position of the sensorial lobes, as well as of the openings of the maxillary nephridia paramedially in front of the sensorial lobes, rather suggests two alternative interpretations that have not been taken into consideration thus far: in following the view that only the rod-shaped 'appendages' represent the first maxilla, either the membranous fields bearing the sensorial lobes correspond to the area differentiated as distinct lamellae linguales in the Chilognatha, the intermaxillary plate of penicillates accordingly being basically sternal in origin (i.e., formed by the mentum); or the components corresponding to the lamellae linguales in Chilognatha form the main parts of the intermaxillary plate in polyxenids, with or without involvement of sternal structures. Both hypotheses basically imply that the sensorial lobes in Polyxenida are homologous to the lingual palps in Chilognatha, stipital palps accordingly being absent in Polyxenida.

An apparent difference between the states in Pauropoda and Polyxenida refers to the independence of the first maxillae from the intermaxillary plate in the former (see, e.g., Kraus, 2001, his Fig. 23), whereas in Polyxenida they form a structural entity with the intermaxillary plate, as in chilognathan millipedes. The assignment of the term gnathochilarium to this entity in Polyxenida accordingly is anatomically justified whatever homologisation of its components with regard to Chilognatha and Pauropoda will prove most likely. In hexamerocerate pauropods, however, the first maxillae were also reported to be "fused together with the intermaxillary plate to a broad probably homogenous combination" (Scheller, 1982: 246). Provided that this interpretation is correct, the possibility deserves consideration that a gnathochilarium was already acquired in the common ancestor of Pauropoda and Diplopoda.

Peristomatic structures: epipharynx, hypopharynx, and tentorium

The actual mouth of millipedes, i.e. the opening of the foregut, lies deeply within a preoral chamber. The roof and floor of this chamber are called the epipharynx and

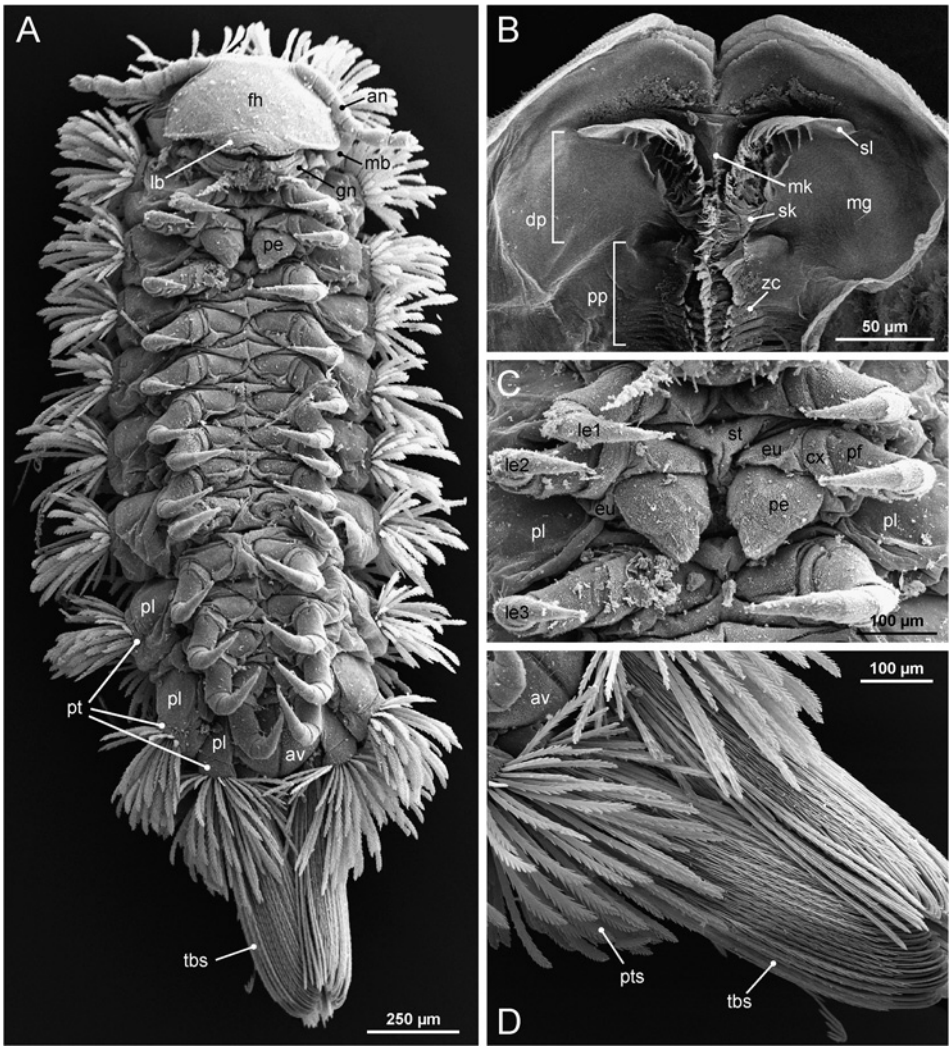


Fig. 2.6. Polyxenida, SEM-micrographs. **A** *Polyxenus lagurus*, ventral view on male body. **B** *Uni-xenus mjoebergi*, epipharynx (tip of labrum on top) (imaging operated by Sue Lindsay, Australian Museum). **C-D** *Polyxenus lagurus*, details of **A**: **C** penes and the ventral skeleton; podomere denotation follows Bäcker et al. (2008); **D** caudal bundles of setae. Originals: M. Koch. Abbreviations: **an** antenna; **av** anal valve; **cx** coxa; **dp** distal part of epipharynx; **eu** eupleurite; **gn** gnathochilarium; **fh** forehead; **le1/le2/le3** trunk legs 1-3; **mb** mandibular base; **mg** mandibular groove; **mk** median keel; **pe** penis; **pf** prefemur; **pl** pleurite (= laterotergite); **pp** proximal part of epipharynx; **pt** 'paratergum'; **pts** paratergal tuft of setae; **sk** spiniferous keel; **st** sternite; **tbs** telsonal bundle of setae; **zc** zipper-like construction.

hypopharynx, respectively. Both surfaces are variably equipped with skeletal structures, lobes and keels as well as microstructures apparently involved in supporting the mandibles in mastication, food transport towards the mouth, and/or grooming of especially the

mandibular gnathal lobes' armature (Verhoeff, 1928). Epipharynx and hypopharynx are continuous lateral to the mouth but are usually bordered transversely by a complex skeleton called the tentorium.

The epipharynx is distally and laterally framed by the marginal duplicature (*Zapfenbogen* of Verhoeff, 1928) of the forehead (Fig. 2.4C, also Plate V; Fig. 2.5D). The surface appears bipartite to different degrees, partly for the occasional presence of a skeletal clypeolabral protuberance (Enghoff, 1981, after Verhoeff, 1928) of the duplicature that laterally subdivides the epipharynx into distal and proximal parts (relative to the mouth). The two parts of the epipharynx are medially confluent but usually differ in their embodiment with cuticular armatures. The bipartition of the epipharynx is reminiscent of the distinction of labral and clypeal parts of the epipharynx in other myriapods, especially scutigeromorph centipedes (see Koch & Edgecombe, 2006; Koch, 2011). Homologies between the epipharyngeal components in centipedes and millipedes have not been discussed thus far, but are proposed here to consider (i) the submarginal versus marginal skeleton to which the mandibular gnathal lobes may be jointed, (ii) the separation of the median labral teeth from the epipharynx by a groove, and (iii) presence of a median keel on at least the labral part of the epipharynx that is laterally bordered by (iv) paired rows of cuticular spines or bristles. The latter distally enlarge in millipedes into spiniferous side lobes (*Seitenlappen* of Verhoeff, 1928) that converge towards paramedian spiniferous keels (lateral denticulate keels of Enghoff, 1981). Side lobes and spiniferous/denticulate keels are absent in Colobognatha (Verhoeff, 1928) and probably all millipedes specialized for sucking feeding modes. When present, the side lobes are strengthened basally by paired sclerotic bars called the retinaculum (Verhoeff, 1928; epipharyngeal bar of Wilson, 2002; for Julida see Enghoff, 1981, his Fig. 10), to which muscles attach (e.g., Wilson, 2002, her muscles *e1* and *e2*). The retinaculum is primarily maintained in Colobognatha despite absence of side lobes (Verhoeff, 1928, his Fig. 435). The paired retinacular bars are fixed to the marginal duplicature in Polyxenida and Helminthomorpha. In the Pentazonia, in contrast, a protruding fold sets off the apex of the epipharynx, including the side lobes, from the marginal duplicature and the median labral tooth, respectively (Fig. 2.4C, also Plate V; Fig. 2.5D). This raises the impression that the epipharynx of pentazonians is loosely attached to the head capsule (versus fixed to it in Polyxenida and Helminthomorpha), which, however, only refers to the epipharyngeal skeleton not being connected to the forehead's duplicature. Paired sclerotic bars laterally border a markedly broad mid-field on the labral epipharyngeal part in Pentazonia. These bars are likely homologous to the retincular bars in Helminthomorpha, but are straight, separate from the marginal duplicature and proximally interconnected by a transverse bar. The mid-field between these bars is largely soft in Glomeridesmida and Glomerida. In Sphaerotheriida, in contrast, it forms a strongly sclerotized central plate with a large median tooth at its distal end (Fig. 2.5D) that in some species continues into a smooth median keel (see, e.g., Wesener & Sierwald, 2005, their Fig. 45; Wesener, 2009, his Figs. 30D, 46C; Golovatch et al., 2012, their Fig. 5). A similar but usually smaller epipharyngeal tooth (*Mittelzapfen* of Verhoeff, 1928) also occurs in some eugnathan millipedes, for instance in Polydesmida and (some?) Chordeumatida. In non-juloid Julida and some Spirostreptida, the marginal duplicature below the labral teeth may

instead give rise to a median triangular projection, which in juloids seems to be replaced by a retrose lobe (Enghoff, 1981). In pachybolids (Spirobolida) the entire epipharyngeal skeleton is markedly rigid (pers. obs.); the mid-field of the labral part forms a strongly sclerotized central plate, similarly as in Sphaerotheriida, that is internally strengthened by a ball-shaped protuberance originating from the median incision of the forehead. The retinacular bars are conspicuously elongate in pachybolids, almost reaching the mouth, and are interconnected by a transverse bar at (apparently) the border between labral and clypeal parts of the epipharynx. Less conspicuous transverse bars also interconnect the short(er) retinacular bars in polydesmidans (Verhoeff, 1928). The transformation of the epipharyngeal skeleton in millipedes with a predominantly sucking feeding mode is still insufficently studied (for Polyzoniida see Attems, 1900; Verhoeff, 1928).

The area between the marginal duplicature and the paramedian keels on the labral part of the epipharynx forms broad, largely soft mandibular grooves (*Mandibulargrube* of Verhoeff, 1928) housing the bulky mandibular gnathal lobes in their resting position. Median and paramedian keels fade out on the clypeal part of the epipharynx in front of the mouth. The clypeal part usually lacks elaborate cuticular armatures, except for Polyxenida in which the median keel continues into a zipper-like construction (*Leistenorgan* of Verhoeff, 1928; Fig. 2.6B) of unknown function. In the Chilognatha one or two pairs of anterior salivary glands, likely homologous to the buccal glands in centipedes (see, e.g., Rosenberg et al., 2011), open onto the clypeal part of the epipharynx but are absent in Polyxenida (El-Hifnawi & Seifert, 1973).

The hypopharynx comprises the area between the endochilarium and the mouth. In millipedes this area never forms a tongue-like protuberance, as is the case in centipedes or symphylans, but usually displays a shallow distal and a more bulging proximal field relative to the mouth (anterior and posterior fields sensu Enghoff, 1981, after Verhoeff, 1928) (Fig. 2.4D, also Plate V). The distal border to the endochilarium may be indicated by a fold, a groove, or — in some Julida — by a joint formed between the skeleton of the endochilarium and a median hypopharyngeal protuberance (*Zwischenzapfen* or *Widerlager* of Verhoeff, 1928). The main skeletal support for the hypopharynx is consistently provided by the hypopharyngeal bars of the tentorium and associated suspensorial sclerites called the *Nebententorium* (Fig. 2.5A, C). On the distal field of the hypopharynx paired paramedian serrulate keels often converge towards the mouth. The keels are sometimes supported by more or less conspicuous sclerotic bars. The shallow, in frontal view trapezoidal or triangular mid-field between the keels is slightly to densely equipped with spines that may delimit a narrow median suture (sensu Enghoff, 1981). In nematophorans and some Julida (Enghoff, 1981, his Fig. 11) the distal serrulate keels continue onto the proximal field into another pair of serrulate keels that diverge towards the lateral angles of the mouth opening (see also Verhoeff, 1928, his Figs. 439-440, 465-466). Distal and proximal keels may be separated each by a sclerotic hump-like protuberance (*Buckel* of Verhoeff, 1928). Julidae and Trichoblaniulidae instead show a strongly scerotized median node at the junction to the proximal field (Fig. 2.4D, also Plate V), which is supposed to support the grinding of food via the mandibular molar plates (Enghoff, 1985). At this junction paired sclerotic plates (*Presshöcker* of Verhoeff, 1928) instead form the most prominent hypopharyngeal

structures in the Polydesmida. The sclerotic plates may be homologous to the hump-like protuberances in nematophoran millipedes (Verhoeff, 1928). In polydesmidans they are followed proximally by a pair of membranous folds (*lobi pharyngis*) that seem to be capable of enclosing the mouth like 'swinging doors' (Verhoeff, 1928: 869). The distal field of the polydesmidan hypopharynx appears relatively short and is distally followed by a markedly elongate endochilarium, both of which are laterally bordered by a pair of spiniferous keels converging to the sclerotic plates in front of the mouth. In spirobolidans a median sclerotic tooth-like protuberance lies in front of the mouth and forms part of a rigid skeleton surrounding the distal mid-field of the hypopharynx (Snodgrass, 1951 for Spirobolidae, and pers. obs. for Pachybolidae). Spirostreptideans show no obvious distinction between proximal and distal fields of the hypopharynx; its largely smooth surface is apparently devoid of keels and instead shows paramedian furrows and a median groove (in some species a chitinous median plate; Manton, 1964) converging along its entire length from the endochilarium to the mouth (Verhoeff, 1928, and pers. obs.).

Among the Colobognatha a median groove laterally bordered by straight keels seems to form the only structures primarily maintained on the floor of the preoral chamber (Verhoeff, 1928, his Fig. 473 for *Platydesmus*). The groove and keels have until now been interpreted as to be formed from the endochilarium, while a hypopharynx is thought to be absent in all colobognathans. The alternative interpretation of the groove and keels as to represent the hypopharynx has not been taken into consideration thus far. This alternative appears equally plausible with regard to the shape of the hypopharynx in Polyxenida and Pentazonia, which share with most eugnathan millipedes the presence of a median hypopharyngeal groove bordered by lateral keels (for Polyxenida see Verhoeff, 1928, his Figs. 468-470). The keels are serrulate in Glomerida (Verhoeff, 1928, his Fig. 461, and pers. obs.) and Sphaerotheriida (see, e.g., Wesener, 2009, his Fig. 44A; Golovatch et al., 2012, their Fig. 5A) and border a median nose-like protuberance at the junction to the proximal field of the hypopharynx (Fig. 2.5A, C). Serrulate keels and a sclerotic median protuberance in front of the mouth (*Hypopharynxhöcker* of Verhoeff, 1928; see Koch, 2003, his Fig. 10) occur in Polyxenida as well and might accordingly represent an ancestral feature of the hypopharynx in millipedes.

The tentorium of millipedes is a complex sclerotic structure comprising exoskeletal bars of the preoral chamber and endoskeletal processes arising from these bars. The entity of all tentorial bars and processes, whether exoskeletal or endoskeletal, was called anterior tentorial apodeme by Manton (1964). It serves as an attachment site for a variety of muscles, including muscles originating from the clypeus, epicranium and its neck phragma, extrinsic muscles of the antennae, mandibles, and gnathochilarium, as well as ventral longitudinal muscles (in Polyxenida and Colobognatha only, as far as known; Manton, 1961) and muscles interconnecting the tentorium with the collagenous endoskeletal tendon system (e.g., Wilson, 2002 for Spirostreptida). The construction of the tentorium is reminiscent of a swing suspended within the largely membranous wall of the preoral chamber between the head capsule and the hypopharynx. The apparent mobility of the tentorium is considered essential for coupling movements of the mandibular gnathal lobes with those of the gnathochilarium, but details on the mechanism remain contradictory (see Fechter, 1961 versus Manton, 1964).

The composition of the tentorium in millipedes basically corresponds to a general pattern in myriapods (Koch, 2003). The exoskeletal components consist of an elongate *transverse bar* that

sends off a short *epipharyngeal bar* and tilts onto the hypopharynx to form a *hypopharyngeal bar*; all these components may give rise to endoskeletal processes, markedly a rod-shaped or laminar *posterior process* (head apodemes sensu Snodgrass, 1951) originating lateral to the mouth. The extent of additional endoskeletal components seems to vary among millipedes but is difficult to infer from previous descriptions (mainly Silvestri, 1903; Voges, 1916; Verhoeff, 1928; Fechter, 1961; Manton, 1964; Wilson, 2002; Blanke & Wesener, 2014) as they lack accurate distinction between exo- and endoskeletal parts. The transverse bar of the tentorium is flexibly attached to the head capsule, consistently at the *incisura lateralis* or, when this notch is absent, at a corresponding area of the head capsule. The recurrent statement that the tentorium originates from or gives rise to the *incisura lateralis* (e.g., Wilson & Shear, 2000) is misleading, since the tentorium may be equipped with a transverse bar despite absence of this notch (Polyxenida, Colobognatha), or exceptionally may lack a transverse bar despite presence of the notch (Sphaerotheriida). The manner of how the transverse bar attaches to the *incisura lateralis* differs among chilognathans depending on whether the opposite margins of the notch remain separate or coalesce ('open' versus 'closed' states of the *incisura lateralis*), but details on the attachment site remain unclear for most millipede orders. In juliformian millipedes the attachment of the tentorium to the head capsule is more firm than in, for instance, Glomerida (Fig. 2.4C, also Plate V) or Polydesmida, in which the tentorium easily detaches from the *incisura lateralis* when manipulated manually. In Julidae (Fechter, 1961 for *Cylindroiulus*) the transverse bar provides a blunt endoskeletal process that seems to articulate against a circular epicranial 'window' formed by the fused margins of the ('closed') *incisura lateralis*. An articulation of this kind between the tentorium and the head capsule is not known from other millipedes thus far. In Spirostreptida and Spirobolida the blunt lateral end of the transverse bar is tightly squeezed in between the opposite margins of the ('open') *incisura lateralis*, apparently without formation of an articular process. Among Spirobolida, however, a 'closed' *incisura lateralis* has recently been recorded for some Pachybolidae (Wesener et al., 2008); the coincident alteration of the tentorial attachment has not yet been described. Previous documentation of the *incisura lateralis* in nematophorans remains ambiguous about whether the notch is 'open' (Callipodida?) or 'closed' (Chordeumatida? see, e.g., Shear, 2011, his Figs. 26, 85); the few studies of their tentorium (mainly Verhoeff, 1928 for Callipodida and Chordeumatida) revealed no basic structural differences and considered the transverse bar as being fused to the notch (i.e., lack of an articulation). The *incisura lateralis* is 'open' in pentazonians (see, e.g., Verhoeff, 1928, his Fig. 359 for *Glomeris*). In Glomerida the transverse bar curls over the forehead's duplicature to attach loosely at the base of the notch (Silvestri, 1903, his Fig. 125; Dohle, 1964, his Fig. 23).

The transverse bar of the tentorium as such generally provides an endoskeletal ridge along its entire length that may enlarge into a massive frontal process, as in Polyxenida (Koch, 2003) or Platydesmida (pers. obs., based on Blanke & Wesener, 2014, their Electronic Supplement ES 2). The tip of the short epipharyngeal bar may also extend into the head lumen to form an endoskeletal process. The hypopharyngeal bar is mainly exoskeletal and apparently used for providing a thrust onto the mandibular gnathal lobes to open when the gnathochilarium is lowered (Manton, 1964, her Figs. 53-54). The tip of the hypopharyngeal bar is jointly connected to a suspensorial sclerite of the hypopharynx called the *Nebententorium* (hypopharyngeal lateral sclerite of Wilson, 2002). The suspensorial sclerite is thought to be derived from subdivision of a formerly entire hypopharyngeal bar (Manton, 1964), as present in Chilopoda or Symphyla. According to classic descriptions (Verhoeff, 1928) the *Nebententorium* varies considerably among millipedes in its shape and relative arrangement; it seems to correspond in some millipedes in providing an endoskeletal process passing below the surface of the hypopharynx, and generally in serving in the origin of muscles inserting on the stipes, lamella lingualis, and mentum of the gnathochilarium.

The endoskeletal posterior process of the tentorium in eugnathans usually forms a short laminar, scute-like apodeme. It extends within the head, as far as known, backwardly inclined against the tentorium towards the gnathochilarium. The process remains distinct from the collagenous transverse

tendon system, in contrast to the corresponding apodemes in centipedes or symphylans that are usually embedded into the collagenous tendons. In Colobognatha the apodemes are transformed into elongate rods that in Polyzoniida and Siphonophorida variably form side branches (Verhoeff, 1928, Manton, 1961, and Blanke & Wesener, 2014 for Platydesmida; Attems, 1900, Silvestri, 1903, and Manton, 1961 for Polyzoniida and Siphonophorida). Among the pentazonians, Glomerida exceptionally seem to lack posterior processes and apparently maintain the typical exoskeletal components only (transverse bar, epi- and hypopharyngeal bars including an inconspicuous paired *Nebententorium*). In Sphaerotheriida, the tentorium is even more reduced to an elongate, remarkably rigid hypopharyngeal bar (plus *Nebententorium*); it remains unclear though whether its proximal part lateral to the mouth invaginates into the head lumen to form a short, straight posterior process (see Verhoeff, 1928, his Fig. 464). Polyxenids instead are characterized by vertically arranged posterior processes passing towards the epicranium in correlation with the opisthognathous head posture (Manton, 1961, her Fig. 34; Koch, 2003).

An articulation between the tentorium and the mandibular gnathal lobe mostly concern their interaction via the hypopharyngeal bar. The additional condyle on the anterior (dorsal) face of the gnathal lobes in pentazonians (see Wesener & VandenSpiegel, 2009, their Figs. 73-76) may interact with the duplicature of the forehead for the apparent absence of other structural devices, but details of the articulation remain unclear.

TRUNK

The trunk of adult millipedes consists of a variable, in some orders constant and/or gender-specific number of uniform body rings, the majority of which bear two pairs of walking legs. Structural deviations from the majority of uniform body rings particularly concern the anteriormost part of the trunk ("thorax"), the trunk ring(s) bearing external genitalia, and the rear of the body terminating in the so-called telson. The original skeletal composition of a diplopodous trunk ring is traditionally considered to be pentazonian (e.g., Enghoff, 1990), i.e. to include one tergite, two pleurites (one on each body side), and two sternites (anterior and posterior sternites), these components being either jointly delimited from each other by arthrodial membranes or partly or entirely fused. Recent considerations of presumed subcoxal elements, however, require a re-interpretation of the pleural and sternal elements in millipedes (Bäcker et al., 2008; Wesener et al., 2014), as outlined below.

The total number of trunk rings is traditionally inferred from the number of tergites that ranges from 11 (apparently only 9 in *Lophoturus madecassus* (Marquet & Condé, 1950)) up to 192. Ventral segmental units instead range in number from 14 up to 380 (summarized for each order by Fusco, 2005, his Table A1, and Fusco & Minelli, 2013, their Table 9.1). In millipedes with pentazonian trunk rings the positional correlation between dorsal and ventral segmental units is often difficult to assess and still provokes debate (see Dohle, 2006; Janssen et al., 2006). The discussion includes the question of whether diplopods are primarily diplopodous or instead formerly show a rather flexible adjustment of the number of legs and tergites, which is ultimately fixed to diplopodous units in millipedes with complete rings (see, e.g., Kraus & Brauckmann, 2003). The original number of trunk

rings in millipedes likewise remains contentious. For Helminthomorpha an increase of body size (Enghoff, 1990) and of trunk ring number to more than 21 (Enghoff, 1984a) is assumed, but this assumption remains questionable with respect to the fossil record (Wilson, 2005; see Chapter 14). A reduction of trunk ring number is commonly accepted to characterize the evolution of the Polyxenida (max. 11 dorsal segmental units; e.g., Nguyen Duy-Jacquemin et al., 2011) and Oniscomorpha (max. 13 dorsal segmental units).

Collum

The region between the head capsule and the first leg-bearing trunk ring forms a neck covered by a tergite called the collum (Fig. 2.1, also Plate II). In millipede systematics this tergite is traditionally counted as the first trunk ring. Early surveys remained contentious though about whether the collum is derived from the head ("*segmento occipitale*" of Silvestri, 1903) or from a trunk segment (e.g., Verhoeff, 1928). The development of the collum indeed seems to involve both the apodous postmaxillary segment of the head and the first leg-bearing trunk segment (e.g., Janssen, 2011). A "collum segment", as inferred from the anatomy of adults (e.g., Fechter, 1961; Manton, 1961), does not exist in millipedes from the developmental point of view; the collum instead superimposes the original segmental border between head and trunk in myriapods. Ventral segmental units are primarily not associated to the collum; the sternite of the postmaxillary segment seems to keep its original participation in head formation, presumably in contributing the gula (e.g., Dohle, 1974), whereas sternite and legs of the first trunk segment primarily become associated with the second trunk tergite (e.g., Janssen et al., 2004). The absence of legs, sternites, and stigmatic plates on the collum ring is accordingly not due to a loss or shift, as has been argued previously (e.g., Manton, 1961); it primarily lacks these structures for not representing a complete body segment. Whether positioned behind or below the collum, the first trunk legs remain distinct from it as well as from the gula in all millipedes, including Spirobolida, in which the first four leg-pairs of the trunk are believed to be shifted forward one segment (e.g., Bodine, 1970; Pitz & Sierwald, 2010; for an alternative interpretation see Janssen, 2011). The traditional consideration of the gula as the first trunk sternite (e.g., Manton, 1961) is accordingly misleading. Rare instances of an apparent displacement of the gula to a more posterior position below the collum do not approach "a more primitive condition" (Manton, 1961 for *Nanogona*) but are unquestionably derived. Pleurites are likewise absent on the collum ring in most (if not all) millipedes, but have been considered as present in some Polyxenida as well as in Polydesmida. In the Polyxenida, some species show small projections adjacent to the collum that are equipped with the same 'trichomes' (i.e., serrate setae) as the lateral protuberances on subsequent trunk rings (e.g., Short & Huynh, 2010) and thus are regarded as serial homologues; whether any of the lateral protuberances are homologous to the pleurites of chilognathan millipedes, however, remains questionable (see below, Structure and composition of diplorings). The 'collum pleurites' of polydesmidans (e.g., Verhoeff, 1928; Attems, 1937) jointly link the gula with the mandibular cardines, as in no other millipedes. Anatomically these 'pleural' sclerites

have nothing in common with the 'pleurites' of subsequent trunk rings and their homology thus is unlikely. With regard to their position the 'collum-pleurites' of polydesmidans instead seem to be almost certainly derived from sternal structures of the postmaxillary head segment.

The presence of the collum functionally allows the head being bent below the trunk to serve "the two outstanding diplopod proficiencies, that of spiraling and of pushing [through substrate]" (Manton, 1961: 443). Morphological adaptations correlated to these proficiencies, however, differ among millipedes and might have been acquired several times convergently (see above, Functional types). In the *bulldozers* the smooth collum is conspicuously larger than subsequent trunk tergites and conceals the posterior part of the head as well as the anterior part of the second trunk tergite like a cap (e.g., Manton, 1961). A collum of this kind is used to shield the head during burrowing and characterizes the Juliformia, Siphoniulida, and (some) Stemmiulida (Enghoff, 1984a). The *wedge-type burrowers* and *borers* (Colobognatha, Polydesmida, Callipodida and Chordeumatida) instead usually have a less pronounced collum that hardly covers the head from above, if at all, and usually lacks reflexed side lobes. In these millipedes the collum largely adopts the sculpture, ornamentation and/or setation of the subsequent trunk tergites (i.e., of their metazonites), including paranotal extensions when present. Still other members of these groups, especially many colobognathans and polydesmidans, may protect their heads by the collum in enlarging it into a roof that partly or entirely hides the head from above. In some Callipodida and Chordeumatida the collum may not overhang the head but is larger or thicker than remaining trunk tergites. Rarely does it distinctly differ from both the head and the remaining trunk in its colouration (e.g., *Rhiscosomides* spp.; Shear, 1973). A marked reduction in size of the collum is characteristic for volvatory species (Oniscomorpha, some polydesmidans; see, e.g., Wesener & VandenSpiegel, 2009; VandenSpiegel & Golovatch, 2012); they do not display the head and collum when rolled-up into a sphere.

The collum structurally differs from other trunk tergites in not telescoping into a preceding tergite and accordingly lacks the typical distinction of prozonite and metazonite of subsequent trunk tergites in helminthomorph millipedes. Depending on its size the collum may instead show distinct articulations with the head capsule. The cap-like collum of juliformian millipedes mainly shows on its lower side lobes articulating with the second trunk tergite. The anterior margin of the cap instead is produced into a stiff duplicature tightly overlying the back of the head. The lower margin of this duplicature is sinuate and medially produced into a small, roundish (Julida, Spirobolida) or tapering (Spirostreptida) process (*Medianzapfen* of Verhoeff, 1928) mainly serving as attachment site for muscles. In Callipodida and most Chordeumatida this process is markedly enlarged into a conspicuous median pivot (*Collumzapfen* of Verhoeff, 1910-1914; *Nackenzapfen* or *Drehzapfen* of Verhoeff, 1928) that articulates with the posterior margin of the head capsule. This articulation, correlated with the absence of an anterior duplicature and of side lobes embracing the body, allows for a greater mobility of the head than in other millipedes.

"Thoracic" trunk rings

The first three trunk rings (rarely four: Spirobolida) behind the collum differ in their architecture from subsequent trunk rings, particularly in having only one pair of legs per ring (*haplorings* sensu Janssen, 2011). These haplorings are often referred to as the thorax of millipedes (Fig. 2.7). Functionally the haplopodous state of these rings is thought to increase the space for the head when bent below the trunk, thus allowing for a tight rolling-up into a protective coil or sphere, respectively (e.g., Manton, 1961). Skeletal alterations of the anterior haplorings correlated to this behavior vary among chilognathan millipedes. The "ring-formers" show a gradual approach towards complete rings from anterior to posterior, with a gradual decrease in the flexibility of the ventral leg-bearing plates (Fig. 2.8C, also Plate VI). Their greater flexibility raises the impression that the first and, to a lesser degree, the second leg-pairs are detached from the second and third trunk ring, respectively. In the Polydesmida the first haploring (systematically counted as the second trunk ring) appears incomplete and to be devoid of legs, because the ventral leg-bearing plates are set off anteriorly by ample arthrodial membrane; still the pleurotergite may be coalesced ventrally and forms a slender ventral bridge without participation of a 'sternite' (according to traditional terminology) (Fig. 2.9C, also Plate VII). The same applies to the second postcollum ring, on which the ventral plate(s) bearing the legs are closer to the ventral bridge formed by the pleurotergite, but still are delimited by a membranous pouch (females) or by sutures (males). The third haplopodous postcollum ring of polydesmidans is the first in the sequence of complete rings, in which the pleurotergites and ventral leg-bearing plates are indistinguishably fused into complete rings. In the Juliformia the first postcollum ring is always incomplete and shows a ventral gap, while the second ring may be partially complete by the ventral fusion of the pleurotergites behind the leg-bearing plates (Fig. 2.8C, also Plate VI). Entire rings including the ventral plates usually start on the third postcollum ring in Julida and Spirobolida, on the first diploring in Spirostreptida (Attems, 1914). The state in Siphoniulida is peculiar in showing a second trunk ring with apparently two leg-pairs followed by an apparently apodous third ring (Sierwald et al., 2003). It is suggested here that this impression is caused by the absence of complete rings on the first and second postcollum rings, coincident with a recession of the first two leg-pairs (and their leg-bearing plates) into the ventral gap between the collum and the pleurotergite of the first postcollum ring; on the second postcollum ring the pleurotergite is coalesced ventrally and forms a broad bridge behind the second leg-pair. According to this interpretation the thorax of Siphoniulida largely corresponds to its state in Juliformia, except for the ventral pleurotergal bridge on the second postcollum ring being far larger in Siphoniulida than in Juliformia.

The leg-bearing plates of the first postcollum ring generally show greater flexibility in the Chilognatha, rarely also the ventral plates of the second and third haplorings (e.g., Sphaerotheriida) in not being jointed to a pleurite (i.e., laterotergite) or pleurotergite, respectively. In the Helminthomorpha all thoracic trunk rings further differ from abdominal trunk rings in lacking defence glands (ozadenes), which (if present) usually start on the fifth trunk ring. Less frequently does the thorax (and head) contrast in its different coloura-

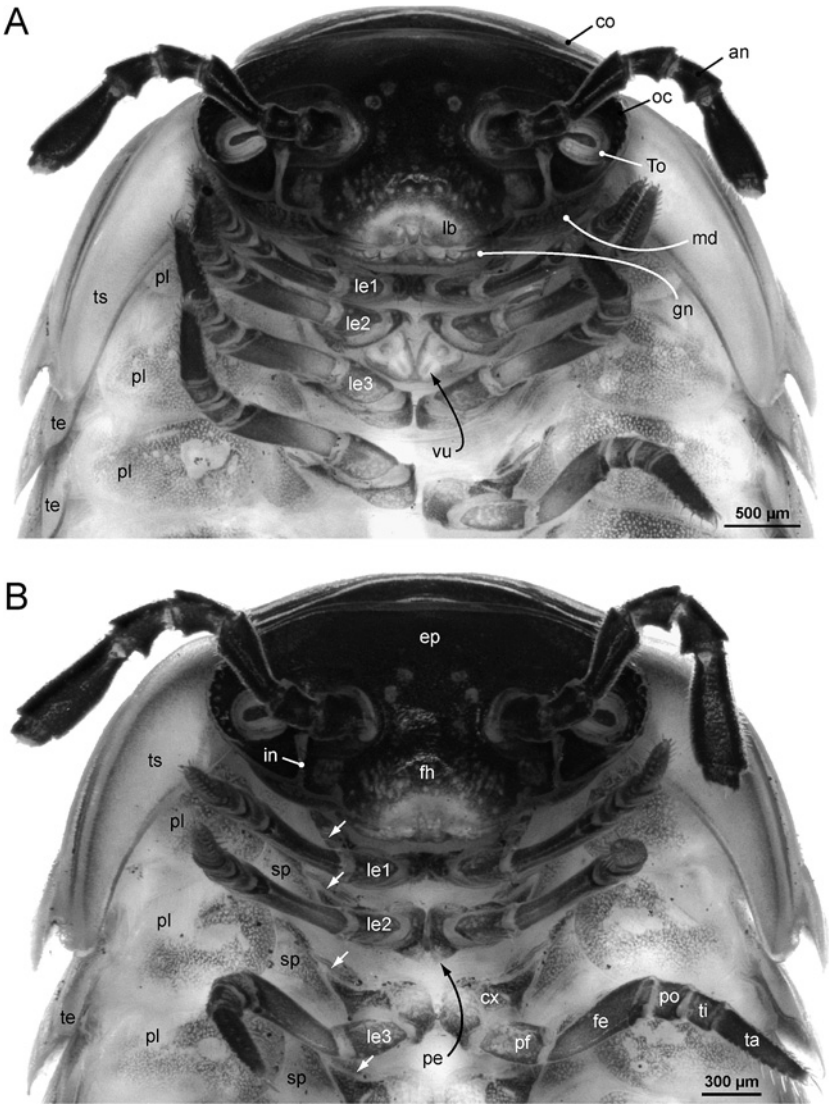


Fig. 2.7. *Glomeris marginata* (Pentazonia: Glomerida), light micrographs of head and thorax, ventral view. **A** Female. **B** Male; straight arrows point to spiracles (= stigmata). Originals: M. Koch. Abbreviations: **an** antenna; **co** collum; **cx** coxa; **ep** epicranium; **fe** femur; **fh** forehead; **in** incisura lateralis; **gn** gnathochilarium; **le1/le2/le3** trunk legs 1-3; **lb** labrum; **md** mandible; **oc** ocular field (eyes); **pe** penis; **pf** prefemur; **pl** pleurite (= laterotergite); **po** postfemur; **sp** stigmatic plate; **ta** tarsus; **te** tergite; **ti** tibia; **To** Tömösváry organ; **ts** thoracic shield; **vu** vulva.

tion against the rest of the trunk (e.g., Polyzoniida: Shelley & Shear, 2005 for *Stenozonium leonardi*; Callipodida: Stoev & Enghoff, 2011 for *Sinocallipus thai*). Helminthomorphs furthermore lack spiracles on the ventral plates of the first two postcollum rings; tracheal

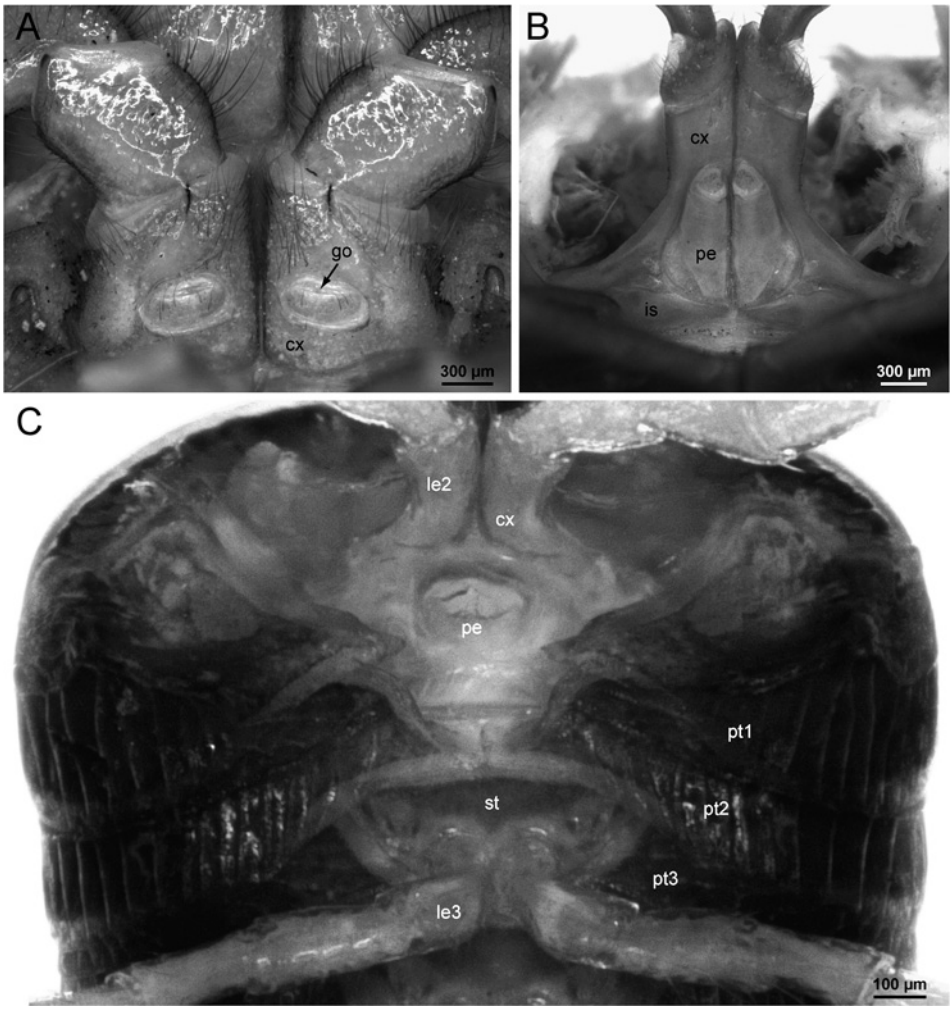


Fig. 2.8. Light micrographs of male genitalia associated to the second pair of trunk legs, ventrocaudal view (anterior is top). **A** *Zoosphaerium* sp. (Sphaerotheriida), merochete state. **B** *Sechelleptus* sp. (Spirostreptida), 'hemipenes'. **C** *Tachypodoiulus niger* (Julida), 'single penis'. Originals: M. Koch. Abbreviations: **cx** coxa; **go** gonopore; **is** intercalary sclerite; **le2/le3** second/third pair of trunk legs; **pe** penis; **pt1/pt2/pt3** pleurotergite of leg-bearing body rings 1/2/3; **st** sternite. *For a colour version of this figure, see Plate VI.*

pouches still occur on these plates but exclusively serve as apodemes for muscle attachment (e.g., Hilken, 1998, and Chapter 6).

The tergites of the thoracic rings are usually shorter than the subsequent tergites of diplorings. In species capable of volvation (Pentazonia: Oniscomorpha; several Polydesmida), in contrast, the second trunk tergite is strongly enlarged into a so-called thoracic shield (Fig. 2.7) and equipped with devices (grooves, pits, or brims) for adjusting the tips of all subsequent tergites, or their paranota, respectively, onto or below the thoracic

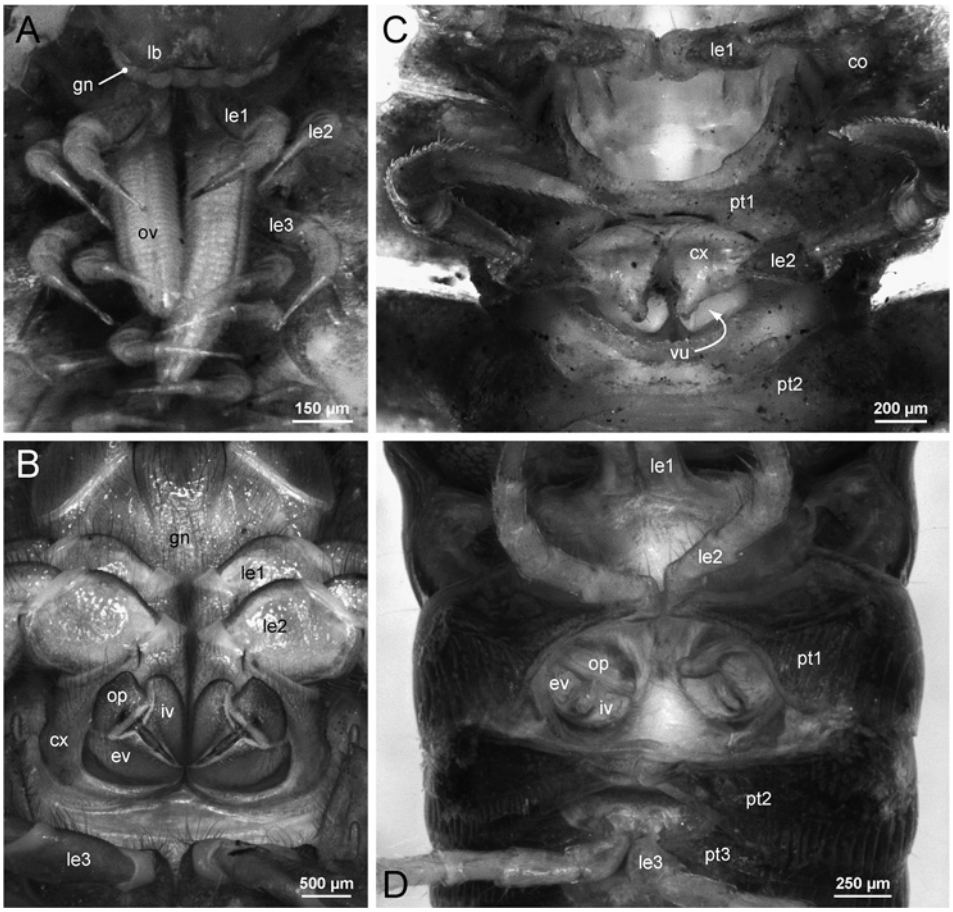


Fig. 2.9. Light micrographs of female genitalia associated to the second pair of trunk legs, ventral view (anterior is top). **A** *Glomeridesmus* sp. (Glomeridesmida). **B** *Zoosphaerium* sp. (Sphaerotheriida). **C** *Polydesmus angustus* (Polydesmida). **D** *Tachypodoiulus niger* (Julida). Originals: M. Koch. Abbreviations: **co** collum; **cx** coxa; **ev** external valve of vulva; **gn** gnathochilarium; **iv** internal valve of vulva; **lb** labrum; **le1/le2/le3** trunk legs 1-3; **op** operculum of vulva; **ov** ovipositor; **pt1/pt2/pt3** pleurotergite of leg-bearing trunk rings 1-3; **vu** vulva. *For a colour version of this figure, see Plate VII.*

shield during enrolling (see, e.g., VandenSpiegel & Golovatch, 2012). Among polydesmidans, the formation of a thoracic shield may alternatively concern the third trunk tergite, or the third and fourth trunk tergites (Golovatch, 2003). The thoracic shield of glomeridans was formerly argued to comprise two fused tergites (second and third trunk tergites), in contrast to the shield in Sphaerotheriida that is thought to be formed by only the second trunk tergite (Attems, 1926; Verhoeff, 1928). This distinction is not followed in recent considerations, but the homology of the thoracic shields in Glomerida and Sphaerotheriida nevertheless remains unclear: features related to volvation are either viewed as potential synapomorphies (Enghoff et al., 1993; Sierwald et al., 2003; Blanke & Wesener, 2014), or

as due to convergence (Sierwald & Bond, 2007). Correspondences in the skeletomuscular system apparently argue against the latter interpretation (Regier et al., 2005).

In the Polyxenida the number of haplopodous postcollum rings still remains contentious (three versus four; see Dohle, 2006). The trunk musculature (Manton, 1956) supports the view that in Polyxenida the first diploring follows behind the third postcollum ring, i.e. on the fifth trunk ring (e.g., Nguyen Duy-Jacquemin et al., 2011, their Fig. 10) as in chilognathan millipedes. The series of ventral skeletal structures, however, is uniform along the trunk of adult polyxenidans and does not provide a marker unambiguously indicating a border between haplorings and diplorings (Fig. 2.6A). Only the first two anterior leg-pairs of polyxenidans differ in showing a gradual increase in podomere number, the composition of the legs of diplorings being adopted on the third haplopodous postcollum ring.

In the Chilognatha the first two pairs of thoracic legs may also differ in podomere number from subsequent legs, for instance in some Callipodida, Stemmiulida, and Polydesmida (e.g., Attems, 1937). Irrespective of podomore number, the first and sometimes also the second legs (rarely all thoracic legs) typically are smaller or shorter. In Juliformia their bases (coxae) are strongly elongated for being recessed deeper than subsequent legs. The thoracic legs furthermore often show gender-specific alterations. Modifications of the first legs in males are usually related to mating behavior (e.g., Krabbe, 1979 for Spirostreptida; Enghoff, 1981 for Julida). In julidans the structure of the first legs of males may underlie periodomorphosis, i.e. alternating changes from less modified in so-called 'intercalary' males to strongly modified in 'copulatory' males (e.g., Sahli, 1990). The first legs are often reduced to different degrees (Fig. 2.4B, also Plate V), in extreme instances under maintenance of only a coxosternite (e.g., some cambalidean Spirostreptida; Hoffman, 1982). In female helminthomorphs the coxae of the first legs are always fused to the 'sternite' (e.g., Brewer & Bond, 2013; Blanke & Wesener, 2014), sometimes also in males, for instance in Spirostreptida (e.g., Krabbe, 1982; Wilson, 2002). In female Pentazonia the coxae of the first legs instead are fused with the so-called stigmatic plates only, whereas the sternite proper remains distinctly separated, if maintained at all (Wesener et al., 2014 for Glomeridesmida).

The structure of the second pair of trunk legs is affected by the association of the gonopores to these legs. Presence and size of devices bearing the gonopores variably impact on the shape and flexibility of these legs and their leg-bearing plates. Among Callipodida, Chordeumatida, and Julida, modifications in females sometimes include a reduction of the podomeres succeeding the coxa (collectively termed the telopodite), in extreme instances under loss of almost the entire leg and maintenance of only the 'sternite' or coxosternite, respectively (e.g., some Blaniulidae among Julida, Kashmireumatidae among Chordeumatida, or some female Callipodida; see, e.g., Enghoff, 1984b; Mauriès, 1988; Stoev & Enghoff, 2005). In most Stemmiulida as well as Parajulidae (Julida) a reduction of the telopodite occurs in both females and males (e.g., VandenSpiegel, 2001; Shelley, 2008). In Polydesmida frequent modifications in females concern the recessement of both the gonopore-bearing genitalia and of the leg bases into large apertures, and the gain of probuterances (some called the epigyne; e.g., Blower, 1985) on the ventral part of

the pleurotergal ring bordering the aperture from behind or entirely sheathing the leg bases (e.g., Hoffman, 2011).

The third pair of trunk legs most often neatly joins the series of uniform walking legs on the diplorings, both in structure and relative arrangement. Similarities of the third leg-pair to subsequent leg-pairs on diplorings also include the eventual presence of coxal vesicles as well as of pregonopodal leg modifications in males (see below, Walking legs). A loss of the third leg-pair is assumed for female Chordeumatidae (e.g., Blower, 1985), in which the second leg-pair (and vulvae) is followed by a legless sternite called the platosternite. Presence of this legless sternite was formerly put forth as evidence for the view that the third postcollum ring represents a haplopodous diploring, on which only the posterior leg-pair is maintained, the platosternite of chordeumatids being the remains of the former anterior leg-pair of this presumed diploring. This view contributed to a discussion on whether the border between thorax and abdomen in millipedes already lies behind the second postcollum ring (e.g., Verhoeff, 1928; Brölemann, 1935 versus Silvestri, 1903), as indicated by the general similiarity of the third legs to subsequent trunk legs on diplorings. This discussion later focused on the question whether all haplopodous postcollum rings represent 'cryptic' diplorings (Demange, 1967; Kraus, 1990). Based on more recent developmental and anatomical evidence (e.g., Wilson, 2002; Janssen, 2011) the assumption of cryptic diplorings is no longer perpetuated; still there are proponents of the view that the genitalia on the second postcollum ring represent leg-derived appendages (e.g., Hoffman, 2011).

Gonopores

In both sexes the paired external openings (gonopores) of the gonads are associated with the bases of the second pair of walking legs (e.g., Enghoff, 1990), often on eversible or permanently everted devices variably called penes, penial apparatus, pseudopenes, genital papilla, or gonapophyses in males, and vulvae, cyphopods, or ovipositors in females (Fig. 2.7). In taxonomic descriptions the terms applied to the respective devices are mostly used interchangeably and without an explanation for the preference of one term over the other. Systematists have placed much emphasis on whether the gonopores (or their devices) lie *on* the coxae of the second pair of trunk legs or immediatlely *behind* them, but there are many intergradational forms in various taxa where such distinction remains subjective and/or requires more accurate description (see, e.g., Enghoff & Golovatch, 1995; Shelley, 1995; both for Colobognatha). Previous considerations of ancestral states in Diplopoda (e.g., Pocock, 1903; Dohle, 1980; Enghoff, 1990) tentatively suggest that the gonopores primarily became associated to lobes reminiscent of coxal vesicles (see below, Walking legs). These lobes apparently emerge variably among millipedes from either subcoxal sclerites surrounding the coxa (*eupleurite* of Bäcker et al., 2008 for Pauropoda and Polyxenida), or directly from the coxa of the second trunk legs, if present at all. An alternative interpretation inferred from the skeletomuscular system of eugnathan millipedes considers the genitalia on the third trunk ring as remnants of legs (e.g., Demange, 1967; Hoffman, 1982, 2011). The anatomical support for this alternative

interpretation is not compelling from the viewpoint of comparative arthropod morphology, given that by far more complex genitalia evolved in insects from mere modification of coxal vesicles (e.g., Klass, 2009). Whatever phylogeny will prove most likely for millipedes, the evolution of their genitalia on the third trunk ring involves positional shifts as well as gain, loss, or transformation of eversible devices, the homology and evolution of which still remains to be clarified.

The male gonopores are traditionally stated to lie on "penes" when the seminal ducts (*vasa deferentia*) open on eversible or permanently everted lobes or tubes (Fig. 2.8, also Plate VI). Some systematists (e.g., Enghoff, 1990) apply the term penis broadly to all millipedes bearing such lobes or tubes on the third trunk ring, irrespective of their position (relative to the second leg-pair) and construction. Others restrict the term penis (in terms of a "true" or "free" penis) to devices located behind the coxae of the second leg-pair, i.e. to structures separate and apparently independent of these legs, as in Julida and Stemmiulida, and distinguish them — merely positionally (e.g., Attems, 1926; Verhoeff, 1928) — from so-called pseudopenes sitting *on* the coxae, as in many Colobognatha. This positional distinction often causes problems (and conflicting description) as in many species the penes are behind but still attached to the posterior side of the coxae, either as permanently everted structures (e.g., Spirostreptida; e.g., Korsós & Johns, 2009, their Fig. 48 for Iulomorphidae), or as eversible pouches (e.g., Glomerida), or as permanently everted lobes (e.g., Siphonocryptida, most Siphonophorida, many Polyzoniida). Apparently differing positions of the penes/pseudopenes either on or behind the coxae need not necessarily rely on a positional shift of the respective genital devices, but can be merely due to a transformation of the coxae under maintenance of the original position of the (pseudo-) penes. A typical example for the latter instance concerns the Siphonocryptida: Its two genera (*Siphonocryptus*, *Hirudicryptus*) have diagnostically been distinguished on whether or not the (pseudo-) penes are delimited from the coxae by a socket (Golovatch & Enghoff, 1995; Korsós et al., 2008). A comparison of the documentation of the two states (*idem*) clearly reveals that the position of the (pseudo-) penes is identical in the two genera, whereas the coxae differ in their construction (among others in being paired versus fused into a syncoxite). This difference can easily be confused with a positional difference of the (pseudo-) penes on or behind the coxae.

Julidae are usually considered a typical example for the presence of a "true" penis; still contemporary systematists seem to disagree on whether the julid penis is distinctly set off behind the second legs (Enghoff, 1996), or originates from the posterior face of their bases (Pitz & Sierwald, 2010 for *Ophyiulus*). The difficulty in precisely locating the origin of the penis may be due to the occasional fusion of the coxae and 'sternite' into a coxosternite that hampers identification of the individual coxal components; or may be due to the occasional presence of paired or unpaired 'intercalary sclerites' (in males of Spirostreptida, derived from the coxae according to Attems, 1914; see also Wilson, 2002) that markedly reduce the space for penes behind the bases of the second leg-pair (Fig. 2.8B, also Plate VI). A different criterion for a distinction of penes from pseudopenes in Juliformia concerns their composition with regard to the presence or absence of sclerotic components. This criterion has been applied to distinguish the (variably) sclerotized penes in Julida and Spirostreptida from the (semi-) membranous, protrusible (pseudo-) penis characteristic of Spirobolida (e.g., Demange, 1967, his Fig. 64; Enghoff, 1977; Wesener et al., 2008; Pitz & Sierwald, 2010). In the context of Juliformia the deviating state of the unpaired, protrusible, apically bifid lobe bearing the paired male gonopores in Spirobolida has caused conflicting descriptions, ranging from lack of a penis (Enghoff, 1981) over presence of a "highly deviant" penis (Enghoff, 1996) to presence of a pseudopenis (Blanke & Wesener, 2014); and is variably considered as "hardly comparable" (Enghoff, 1996), plesiomorphic (Hoffman & Orcutt, 1960), or apomorphic for Spirobolida (Wesener et al., 2008; Pitz & Sierwald, 2010). Julida and Spirostreptida are sometimes stated to share a "double penis" (Diplocheta concept; e.g., Hoffman, 1982) characterized by an unpaired median base from which arise paired apical lobes bearing the gonopores. The extent of

basal fusion and the length of the apical lobes vary tremendously (see Enghoff, 1996 for Julidae). In some non-juloid Julida and most Spirostreptida the unpaired penial base is inconspicuous, the penis being mainly composed of two entirely separate "hemipenes" (Enghoff, 1996) (Fig. 2.8B, also Plate VI); this state (double penis made of hemipenes) indeed is hard to distinguish from paired, unfused penes (see Demange, 1967, his Figs. 66-69). The other extreme with remarkable large extent of basal fusion under shortening of the apical paired lobes is particularly known from some Julidae. In several lineages of non-juloid Julida the fusion of the (hemi-) penes yielded, apparently convergently, an entirely unpaired, so-called single penis (Enghoff, 1981, 1996) (Fig. 2.8C, also Plate VI). A similar transformation from formerly paired (but membranous) penes on the posterior side of the coxae of the second leg-pair into a single, telescopically retractable unpaired penis occurred within Stemmiulida (Mauriès et al., 2010).

From a functional perspective usage of the term penis for any of the eversible or permanently everted devices bearing the male gonopores has been considered improper (e.g., Haacker, 1970; Haacker & Fuchs, 1970), because they almost never serve as intromittent organs in millipedes. Instead, sperm (or spermatophores) are transferred from the gonopore either onto silky threads for an uptake by females without pairing (Polyxenida), or onto other legs (see below, Specialized trunk appendages) that deposite the sperm onto or into the female genitalic system during mating (Chilognatha) (see Chapter 10). This might explain why often indifferent terms like 'pouch', 'sac', or '(genital) papilla' have alternatively been used to describe the organs bearing the male gonopores, particularly in non-juliformian millipedes. The devices called penes (or pseudopenes) in colobognathan millipedes are reminiscent of coxal vesicles in their structure and position (Fig. 2.11A, also Plate IX) but vary in shape from concial over bottle-shaped to fairly elongate (e.g., Enghoff & Golovatch, 1995). The elongate penes of some polyzoniids are medially approached along their entire length as if to form a single penis (e.g., Brölemann, 1935, his Fig. 118 for *Polyzonium germanicum*). The same applies to the exceptional presence of an elongate "double penis" in Chordeumatida (Mauriès, 1990, his Fig. 26 for *Beticosoma longipenis*), which is composed of two entirely separate coxal projections that medially merge along more than half their length.

Other non-juliformian millipedes often lack eversible or everted devices and show the *vasa deferentia* opening flush onto the coxa of the second leg-pair, this state being called merochetism (e.g., Enghoff, 1990). Merochete gonopores represented merely by a hole in the coxae occur in male Glomeridesmida and Sphaerotheriida among Pentazonia (Fig. 2.8A, also Plate VI); in some Platydesmida and some Siphonorhinidae among Colobognatha; as well as in Polydesmida, Callipodida, and Chordeumatida. Still in these taxa the male gonopores may be surrounded or covered by sclerotized plates or membranous folds (Glomeridesmidae: Iniesta et al., 2012; Sphaerotheriida: Wesener, 2014), or they may be elevated on soft, membranous tubules and/or stiff medio-distal extensions of the coxa (e.g., Korsós et al., 2011, their Figs. 9, 16). In Polydesmida the coxal projections elevating the male gonopores are sometimes called gonapophyses ("the hardened openings of the *vas deferens*", Marek, 2010), irrespective of whether or not the coxa is extended medio-distally or whether the projections are flexible or stiff (for soft gonapophyses see, e.g., Hoffman et al., 2002; Hoffman, 2008). Among polydesmidans they presumably evolved convergently in several lineages (Chelodesmidae, Rhachodesmidae,

Sphaeriodesmidae among others; e.g., Hoffman, 1998, 2008). Gonapophyses may also occur in Callipodida (e.g., Shear et al., 2003 for *Sinocallipus*), Chordeumatida (Caseyidae; e.g., Shear & Leonard, 2007; Shear, 2011), and some Colobognatha (Siphonophoridae: Marek et al., 2012 for *Illacme*; Siphonotidae: Golovatch, 2014 for *Burinia*). It remains unclear though whether the structures called gonapophyses in the aforementioned taxa are all of the same kind.

The vulvae or cyphopods of adult females are primarily readily visible behind or on the posterior face of the coxae of the second leg-pair, either as permanently everted papillae (Polyxenida), as largely membranous, eversible pouches or bulbs (Glomerida, Glomeridesmida: Termitodesmidae, most Colobognatha; Fig. 2.7A), or merely as sclerotized plates (Sphaerotheriida; Fig. 2.9B, also Plate VII). In the Synxenidae (Polyxenida) as well as in *Glomeridesmus* (Glomeridesmida) the vulvae are transformed into elongate, pleated tubes (ovipositors; Fig. 2.9A, also Plate VII) that, when everted, extend over several trunk rings (Short and Huynh, 2006, their Fig. 8) or nearly reach full body length (Hoffman et al., 2002 for Glomeridesmidae; see also Iniesta et al., 2012). In the majority of eugnathan millipedes, in contrast, the vulvae are recessed into the body (when resting), in depressions called vulval sacs. The degree of recession varies within the orders, ranging in, for instance, Polydesmida and Spirostreptida from fully exposed under lack of a vulval sac to deeply invaginated into a vulval sac (Demange, 1967; see also Hoffman, 2010 for Polydesmida; Mauriès & Enghoff, 1990 for cambalidean Spirostreptida) (Fig. 2.9C, D, also Plate VII). The vulval sacs are particularly elongate in Callipodida and some Julida (e.g., Enghoff, 1984b for Blaniulidae), thus allowing to serve as ovipositors when fully everted (see Demange, 1967, his Fig. 70 for *Callipus*).

The composition of the vulvae shows a common pattern in millipedes (e.g., Brölemann, 1935): The body of each vulva is called the *bursa* and is represented by a bulbous or globular evagination that is incompletely divided in its centre by an oblique, slit-like depression into a pair of valve-like folds (called external and internal valves, or anterior and posterior valves) covering the opening of the oviduct (i.e. the gonopore) from behind; another fold called the *operculum* covers the gonopore from anterior (Fig. 2.9B, D, also Plate VII). Bursa and operculum are connected via a common base to the vulval sac (when present). Both the two valves of the bursa and the operculum may be sclerotized, or even calcified, and are often densely setose. Chambers of variable shape and number open in the depth of the depression between the valves and serve for sperm storage (*receptaculum seminis*, rarely called *spermatheca*). The seminal receptacles are usually separate from the oviduct; exceptionally they are formed by extension of the oviduct itself (Barnett et al., 1993 for Spirostreptidae), or they lie outside and behind the vulvae ("*extravulvaire*" sensu Mauriès, 1989, in some but not all Stemmiulida; e.g., VandenSpiegel, 2001). In at least eugnathan millipedes a common pattern has also been revealed for the muscular equipment of the vulval apparatus (Demange, 1967: 71). The gonopore and openings of the seminal receptacle(s) are exposed by hemolymph pressure spreading the operculum and bursal valves, which in turn are retracted by muscles partly arising from the (apodemic) tracheal pouches of the sternal plate(s) bearing the second leg-pair; in species with deeply recessed vulval sacs these apodemes may be strongly enlarged. A distinction of operculum and

valves has not yet been applied onto Polyxenida, but the roughly T-shaped opening of the female genital papilla of polyxenids provides the impression of a corresponding tripartition (see, e.g., Kraus, 2005, his Fig. 10 for *Polyxenus*; Short & Huynh, 2013, their Fig. 3H for *Unixenus*).

Variation in the structure of the vulvae concerns almost all components and includes eventual absence of the operculum and of seminal receptacles (e.g., Marek et al., 2012 for *Illacme*, Siphonophorida) as well as fusion of left and right vulvae into a single organ (e.g., Shear et al., 2009 for *Pratherodesmus*, Polydesmida). In more recent times this variation has been attributed systematic significance in some orders (at higher or lower taxonomic levels, including species distinction), especially Sphaerotheriida (e.g., Wesener, 2014), Polyzoniida (e.g., Kurnik & Thaler, 1989), Polydesmida (e.g., Tadler & Thaler, 1993), Chordeumatida (e.g., Kurnik & Thaler, 1985; Tadler, 1993; Shear & Leonard, 2007; Mikhaljova et al., 2013), Stemmiulida (e.g., Mauriès, 1989), Julida (e.g., Enghoff, 1991; Spelda, 1993; Tadler, 1996), and Spirobolida (e.g., Wesener et al., 2009). Modern studies, however, indicate that supposed characters of the female genitalia for species delimitation may prove to be merely based on different degrees of vulval extension in the individual specimens studied (Shear, 2011 for Chordeumatida). For other millipede orders descriptions of the vulvae are scarce, especially for Glomerida (Verhoeff, 1928, his Figs. 292, 295 for *Glomeris*), Termitodesmidae among Glomeridesmida (Silvestri, 1911, his Fig. 67), Platydesmida (Pocock, 1910, his Fig. 5g for *Platydesmus lineatus*; Blanke & Wesener, 2014, 3D-reconstruction for *Brachycybe lecontii*), Siphonocryptida (Korsós et al., 2009), Siphonophorida (Marek et al., 2012), and Callipodida (e.g., Glaubrecht & Spelda, 1993). Except for the latter, these taxa seem to share paired bivalvate vulvae (with or without operculum, bare or setose) readily visible in excavations of the posterior face of the coxae of the second leg-pair, which likely corresponds to the ancestral state of the vulvae in Chilognatha.

Structure and composition of diplorings

On the trunk rings following behind the thoracic haplorings two pairs of legs and their ventral leg-bearing plates traditionally called sternites are associated laterally to one pleurite and dorsally to one tergite, these skeletal components forming a primarily flexible, secondarily firm and eventually constant series of structural entities called diplorings (Fig. 2.10, also Plate VIII). The tergite and pleurites of each diploring are traditionally considered as to comprise the tergites and pleurites of two adjacent body segments that are fused into a diplotergite ("syntergite" sensu Kraus & Brauckmann, 2003) and diplopleurites, respectively (e.g., Enghoff, 1990), but this interpretation is rejected by recent developmental insights (e.g., Janssen, 2011; see Chapter 11). Recent comparative considerations of the pleural skeleton in arthropods (Bäcker et al., 2008) furthermore provide evidence in support of the view that the ventral leg-bearing plates traditionally called sternites in millipedes each comprise a set of sclerites of different origin, i.e. the sternite proper plus a pair of so-called stigmatic plates (Wesener et al., 2014). As has already been presumed by Regier et al. (2005) (initially refuted by Sierwald &

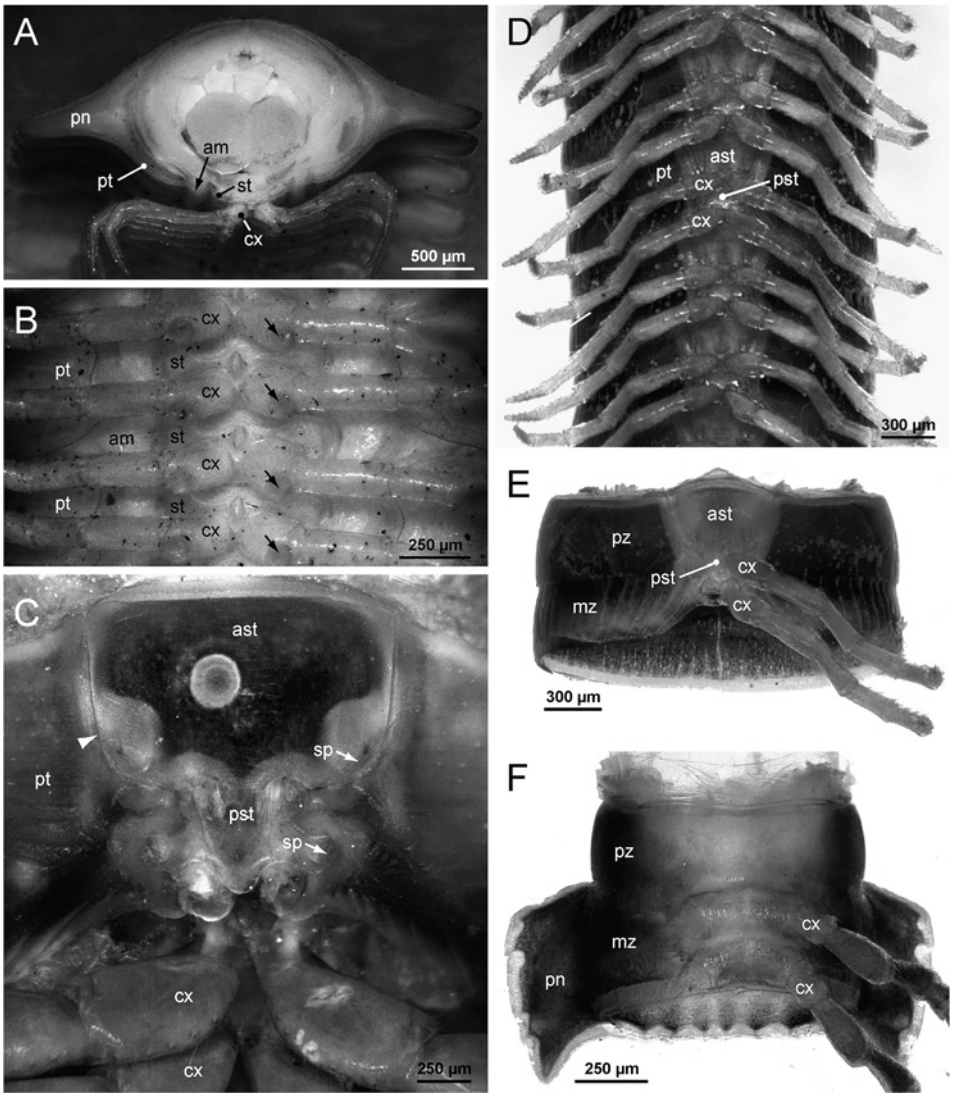


Fig. 2.10. Light micrographs of diplorings. **A-B** *Brachycybe* sp. (Colobognatha: Platydesmida), mid-body rings in (**A**) frontal view, and (**B**) ventral view (anterior is top); arrows point to everted coxal vesicles. **C** *Sechelleptus* sp. (Spirostreptida), ventral skeleton of a mid-body ring, legs removed to display the sternites and leg-sockets (anterior is top); arrowhead points to suture between pleurotergite and sternites. **D-E** *Tachypodoiulus niger* (Julida): **D** ventral view on mid-body rings (anterior is top); **E** skeleton of a single dissected diploring (legs of right body side removed). **F** *Polydesmus angustus* (Polydesmida), skeleton of a mid-body ring in ventral view (anterior is top), legs of right body side removed to display their sockets. Originals: M. Koch. Abbreviations: **am** arthrodial membrane; **ast** anterior sternite; **cx** coxa; **mz** metazonite; **pst** posterior sternite; **pt** pleurotergite; **pz** prozonite; **sp** spiracle (= stigma); **st** sternite. *For a colour version of this figure, see Plate VIII.*

Bond, 2007, Supplemental Appendix 1, for being "unsubstantiated" but corroborated by Wesener et al., 2014), the stigmatic plates are considered as to be derived from subcoxal elements of the legs that are incorporated into the trunk wall and give rise to tracheae or tracheal pouches, respectively, externally reflected by their openings interchangeably called spiracles or stigmata (Fig. 2.7). The stigma-carrying components of the ventral skeleton in millipedes are revealed as corresponding to the pleurites proper in arthropods (*eupleurite* and *trochantinopleurite* of Bäcker et al., 2008); they primarily surround each leg base (coxa) in a more or less arc-shaped manner. In the Polyxenida these pleural arcs are still flexibly delimited from each other and from the sternite proper but have traditionally been interpreted as the coxa and trochanter of the legs (but see Silvestri, 1903, for presumable subcoxal elements across millipedes). In the Chilognatha the pleural arcs are represented by a single pair of stigmatic plates (per leg-pair) that in the Pentazonia remain distinct from the sternite proper (when present), whereas in Helminthomorpha they are indistinguishably fused with the sternite (Wesener et al., 2014).

The current recognition of the "true" pleurites and sternites in millipedes (in the context of comparative arthropod morphology) confirms the early view (e.g., Attems, 1926) that the ventro-lateral plates traditionally called pleurites in millipedes are derived from the tergites; these are extended ventrad in millipedes, primarily under flexible delimitation and strong inclination of their ventral extensions towards the legs. The interpretation of the pleurites as "laterotergites", formerly restricted by Snodgrass (1958) to Oniscomorpha, is accordingly now suggested to concern all millipedes (Wesener et al., 2014). The assumption of two pairs of pleurites per diploring in Polyxenida (Wesener et al., 2014, their Fig. 7), apparently deemed to be fused into a single pleurite in Chilognatha, nevertheless is inconsistent with this interpretation and requires more detailed justification. In the context of the recent discussion of the mismatch between dorsal and ventral segmental units in millipedes (e.g., Dohle, 2006) the pleurites/laterotergites have not been considered explicitly thus far. With respect to their number and development from embryonic 'lateral plates' (*Seitenplatten* of Dohle, 1964) and coincident occurrence with the tergites during postembryonic anamorphosis independent of ventral segmental structures (e.g., Nguyen Duy-Jacquemin, 2006 for Polyxenida), they likely fall into the category of dorsal segmental units, despite their consistently (latero-) ventral position in millipedes.

Adjusted to current insights, the terminology for the skeleton of millipedes suggested by Wesener et al. (2014) preliminarily retains the traditional descriptive terms except for introducing "stigmatic plates" for the pleural sclerites bearing the openings (spiracles or stigmata) of the tracheal pouches; future studies should nevertheless aim at a terminology that is consistent with the terms applied to corresponding structures in non-milliped myriapods (or arthropods in general). According to the current interpretation the skeletal composition of a diploring in chilognathan millipedes primarily comprises one tergite, two pleurites (i.e., laterotergites; one each per body side), four stigmatic plates (i.e., subcoxal pleurites; one pair per leg-pair), and two sternites (anterior and posterior sternites).

The diplorings vary in length among millipedes and are remarkably short in the Juliformia (Fig. 2.10E, also Plate VIII), which is thought to advance the efficiency in burrowing (Manton, 1954: 348). In cross section the diplorings are literally ring-shaped in eugnathans only, irrespective of the design of the trunk ring skeleton, whereas the design

of the diplorings in pentazonians and colobognathans is reminiscent of arch bridges (Wilson & Hannibal, 2005). Generally in chilognathan millipedes (to a lesser degree in Polyxenida) the diplorings overlap telescopically, formerly only dorso-laterally, but entirely in millipedes with complete rings. In the helminthomorphs this overlap correlates with a conspicuous transverse subdivision of both tergite and pleurites of each diploring into anterior and posterior regions called prozonite and metazonite (often interchangeably denoted as prozona and metazona, or protergum and metatergum), with the anterior invaginated part (prozonite) differing in size, shape, and cuticular ornamentation from the posterior exposed part (metazonite) (Fig. 2.10E, F, also Plate VIII). Differences in the cuticular ornamentation concern setation, spination, striation and carination, or microsculpture, the variability of which is attributed systematic significance (e.g., Hoffman, 1977 on "carinotaxy" in cambalopsid Spirostreptida; Akkari & Enghoff, 2011 on microsculptures in Polydesmida). The overlap of the diplorings may coincide with the presence of cuticular devices on or below the posterior tergal margins called the limbus and endotergum, respectively, which are thought to prevent soil particles (and organisms) from obstructing telescopic movements (e.g., Shear, 2009 for Chordeumatida; Wesener, 2009 for Sphaerotheriida; Akkari & Enghoff, 2011 for Polydesmida; Enghoff, 2014 for Spirostreptida).

The zonation of the diplorings is usually maintained among helminthomorphs irrespective of whether or not tergite and pleurites are fused into a pleurotergite. Exceptions concern the Spirobolida, in which three transverse zones are distinguished (prozonite, mesozonite, metazonite), and the Stemmiulida, in which a zonation into pro- and metazonite is less conspicuous (see, e.g., Mauriès, 1989) and often considered absent (e.g., Hoffman, 1982), as in Pentazonia and Polyxenida. Formation of pleurotergites is characteristic of some colobognathan lineages (mainly Platydesmida and Siphonocryptida; Fig. 2.10A, B, also Plate VIII) as well as of the Eugnatha, and is accordingly assumed to underlie convergent evolution among Helminthomorpha (e.g., Wilson & Anderson, 2004). Spirobolida differ from other millipedes with pleurotergites in showing a longitudianal suture on each body side that is thought to indicate the former border between tergite and pleurite (Enghoff, 1984a; Wesener et al., 2008). Another probably convergent transformation of the (pleuro-) tergites concerns the lateral extension of the metazonites into wing- or keel-like paranota in Platydesmida, some Siphonophorida, Polydesmida, and Chordeumatida (Shear et al., 2003) (Fig. 2.10A, F, also Plate VIII). The pleurotergites may also show a longitudinal mid-dorsal sulcus (markedly in Platydesmida, Siphonocryptida, Chordeumatida, and Stemmiulida; e.g., Enghoff, 1990) (Fig. 2.13), the functional significance of which has not been considered thus far.

The metazonital paranota are sometimens interchangeably denoted as "paratergites" or "paraterga" (e.g., Mikhaljova, 2004). These latter terms, however, are less distinctive as they have been applied to various non-homologous structures in millipedes, for instance to the lateral ('pleural') setose protuberances in Polyxenida (e.g., Kraus & Brauckmann, 2003; Nguyen Duy-Jacquemin, 2006), or to short side lobes formed by the ventral margins of the tergites in Sphaerotheriida (e.g., Wesener & Sierwald, 2005) and by the lateral margins of the tergites in Siphonocryptida (e.g., Enghoff & Golovatch, 1995; Korsós et al., 2009), i.e. to taxa commonly considered as lacking paranota. The paranota carry

the openings (*ozopores*) of defence glands (*ozadenes*), which otherwise (in millipedes lacking paranota) open flush on the tergites or pleurotergites, respectively. In either position they are sometimes delimited and/or elevated on short tubular projections called porosteles or peritremata (e.g., Korsós et al., 2008 for Siphonocryptida; Shear & Marek, 2009 for Platydesmida). In Helminthomorpha the ozopores open laterally on each body side, never more than one pair per diploring from the fifth trunk ring backwards. The number of ozopores/ozadenes may be reduced in a taxon-specific manner, including entire loss (Chordeumatida, Siphoniulida, some Polydesmida); rarely is their number increased (some Spirobolida, in which ozopores start on the third trunk ring; e.g., Wesener et al., 2008). In Polydesmida the specific, discontinuous distribution of ozopores along the trunk is expressed in a "pore formula". Defence glands also occur in the Glomerida among Pentazonia but open mid-dorsally in inconspicuous ozopores within the arthrodial membrane behind the posterior margin of the tergites, from the third trunk ring backwards to the antepenultimate trunk ring (Shear et al., 2011). In *Glomeris* the defence glands develop from paired lateral anlagen that migrate during embryogenesis to their definitive, apparently unpaired mid-dorsal position (Dohle, 1964). The homology of the defence glands in Glomerida and Helminthomorpha nevertheless remains uncertain (Brewer & Bond, 2013; Blanke & Wesener, 2014) because of their lack in Glomeridesmida and Sphaerotheriida.

The pleurites (laterotergites) or pleurotergites of chilognathan millipedes primarily remain flexibly separate from the sternal plates (Fig. 2.10B, also Plate VIII) and slightly to conspicuously overlap them in an imbricate manner (e.g., Enghoff, 1990, his Fig. 4 for *Polyzonium*). This overlap is largely or entirely smoothed out in species with complete rings, in which the sternites are fused to the pleurotergites (Fig. 2.10C, also Plate VIII); still some degree of overlap may be maintained, for instance in Julidae, in which the openings of the tracheal pouches (i.e., the spiracles/stigmata) are roofed by the pleurotergal margins (e.g., Enghoff, 1984a, his Figs. 7-10; Hilken, 1998, his Fig. 10a). Homologues of the "free" pleurites in chilognathan millipedes form similarly shaped ventro-lateral plates in Polyxenida (Fig. 2.6A, C), in corresponding position to the pleurites of pentazonians and colobognathans but below lateral protuberances of the body bearing each a tuft of serrate setae (e.g., Brölemann, 1935, his Fig. 61; Kraus & Brauckmann, 2003, their Figs. 31, 37). The delimitation of these lateral protuberances from both the tergite and the ventro-lateral plate has caused ambiguity about the number of pleurites per diploring in Polyxenida: some consider presence of two pleurites on each side of a diploring (the lateral protuberance bearing a tuft of setae plus the plate below it: Brölemann, 1935), others assume a single pleurite represented either by the lateral protuberance under disregard of the ventro-lateral plate (e.g., Manton, 1956); or only by the ventro-lateral plate while the lateral protuberances are denoted as "paraterga" (e.g., Kraus & Brauckmann, 2003). Irrespective of these conflicting views, the ventro-lateral plates below the lateral protuberances are the only structures in polyxenidans that are immediately comparable to the pleurites of chilognathan millipedes in their relation to the sternal plates.

The sternites and stigmatic plates of each diploring are primarily flexibly delimited from each other, as shown by Polyxenida (Bäcker et al., 2008; Fig. 2.6C) and Glomeridesmida (Wesener et al., 2014), and do not participate in telescoping movements of the trunk

rings. From the hourglass-shaped median sternites in Polyxenida only their anterior part seems to be primarily maintained in the Pentazonia, this part being strongly inclined in Glomeridesmida such that the sternal remnant is only visible in frontal view but not from behind. The stigmatic plates are fused to the coxae of the legs in Glomeridesmida, with a suture between coxa and stigmatic plate visible on the first postcollum trunk ring only (Wesener et al., 2014, their Figs. 2, 3). In Oniscomorpha the sternites are entirely reduced under maintenance of only the left and right stigmatic plates (a state formerly interpreted as presence of "divided sternites"; see, e.g., Wilson, 2005), well separated from the coxae. A peculiar feature of Glomeridesmida also concerns the unique position of the stigmata posterior to the leg base (see, e.g., Silvestri, 1903: 106; Wesener et al., 2014), whereas their former position anterior to the leg bases, as shown by Polyxenida, is preserved in Oniscomorpha and Helminthomorpha, albeit in a more lateral position than in Polyxenida.

The fusion of each sternite with two stigmatic plates into a single entity in the Helminthomorpha produces a series of rigid transverse plates (pragmatically called sternites in the following), to which the leg bases are jointed posteriorly. The antero-lateral stigmata on these plates vary in shape from inconspicuous slits to prominent cones (e.g., Mesibov, 2009 for Polydesmida). They open into cuticular pouches that give rise to tracheae and primarily (including Polyxenida) also serve as attachment site for muscles, especially intersegmental longitudinal muscles as well as appendicular muscles; in correlation with the latter function the tracheal pouches of chilognathan millipedes are often enlarged into uniramous or biramous apodemes (e.g., Manton, 1954; Hilken, 1998). The sockets for the leg bases usually have a paramedian position on the sternites and are almost contiguous; rarely are the sockets shifted to a more lateral position (Platydesmidae; e.g., Shelley, 2010). The shape of the sockets is variable; usually they are roundish and more or less elevated, in some species they are raised into cones on the posterior part of each plate, or they are framed into the posterior margin of each plate and may remain posteriorly incomplete, as is the case in Juliformia. Anterior and posterior sternites of each diploring are primarily uniform, i.e. largely alike in shape and in the position of the stigmata (Fig. 2.10B, also Plate VIII), but dimorphic in millipedes with complete rings (Fig. 2.10C-E, also Plate VIII), in which the sternites are coalesced and fused to the pleurotergite.

On the complete diplorings of the Juliformia, in which pleuro-sternal sutures are maintained, the anterior sternite is far longer than the posterior sternite and neatly forms a bridge between the ventral margins of the pleurotergal prozonite, thus allowing the entire anterior part of the diploring to telescop (or to 'slide') into the preceding diploring. The anterior sternite has accordingly been categorized as a "sliding sternite" (*Gleitplatte* fide Verhoeff, 1928; see also Blanke & Wesener, 2014), but this may be considered improper as the sternite itself cannot perform sliding movements independent of the pleurotergite and the posterior sternite, to both of which the anterior sternite is immovably fused. A peculiarity of juliformian diplorings concerns the fixation of the anterior and the posterior sternites in an overlapping position; the posterior margin of the anterior sternite bearing the sockets for the legs roofs the anterior part of the posterior sternite. Presence of elongated anterior "sliding sternites" is also characteristic for the complete

trunk rings of Siphoniulida (Sierwald et al., 2003, their Fig. 10), but these lack the overlap of anterior and posterior sternites typical for Juliformia and may further differ in lacking the anterior pair of stigmata (which have not been documented thus far), these being positioned on the posterior sternite in widened areas that are absent on the narrow anterior sternite. Polydesmida is also tentatively considered to share with Juliformia anterior "sliding sternites" (Enghoff, 1984a; Blanke & Wesener, 2014), but the lack of sutures outlining the sternal components causes ambiguity (Fig. 2.10F, also Plate VIII). An alternative interpretation of the polydesmidan state (Verhoeff, 1928: *sterna conflata*) considers the prozonital part of the pleurotergites as ventrally fused into a complete prozonital ring without participation of the anterior sternite, both anterior and posterior sternites (indistinguishably fused) being restricted to the metazonital part of the diploring (e.g., Attems, 1926, 1937). Whether the transformation of the trunk ring skeleton into complete rings is homologous in Polydesmida and Juliformia accordingly remains uncertain; this transformation may result from convergent evolution (Shear et al., 2003). The diplorings of polydesmidans particularly differ from those in Juliformia in showing a marked constriction between the prozonital and metazonital parts, as well as in the reduced size or entire lack of an endoskeletal ring-shaped flange (*prophragma* of Attems, 1926; *cyclophragma* of Verhoeff, 1928) that in other chilognathan millipedes markedly constricts the anterior aperture of the prozonite and serves as attachment site for the muscles effecting telescopic movements of the diplorings (e.g., Manton, 1954, 1961).

The sternites of non-ring-forming helminthomorphs (Colobognatha, Nematophora) remain flexibly delimited from each other as well as from the pleurites (laterotergites) or pleurotergites, respectively. All sternites are usually uniformly shaped on diplorings with walking legs, except for Stemmiulida which show an alternating sequence of anterior and posterior sternites of different size and shape (e.g., Mauriès et al., 2010). The sternites of nematophorans are characterized by a rib-like transverse ridge (*Rippensternit* of Verhoeff, 1928; see also Blanke & Wesener, 2014) that extends between the stigmata and partitions each sternite into an anterior stigmatal section and a posterior coxal section bearing the sockets for the legs, the former section somewhat roofing the latter. The relative dimensions of anterior versus posterior section vary tremendously (see, e.g., Silvestri, 1903: 108). In Callipodida and Chordeumatida the anterior section usually is more or less U-shaped whereas the posterior section appears roughly triangular for tapering posteriorly in between the leg sockets. A median depression and/or node may be present on the posterior section, which is thought to accommodate the leg bases when the body is flexed (Verhoeff, 1928: 394). Dorso-ventral flexure of the body furthermore causes the sternites to slide onto each other from backwards, a movement of the sternites apparently not seen in colobognathans except Platydesmida (Manton, 1961). The short sternites of colobognathans do not show a bipartition but are usually characterized by a median node-like dilatation (*Knotensternit* of Verhoeff, 1928; see also Blanke & Wesener, 2014; Fig. 2.10B, also Plate VIII) housing extrinsic leg muscles as in no other millipedes (Manton, 1961: 401). Other aspects of the sternites seem to vary among colobognathans in a greater manner than appreciated thus far (Blanke & Wesener, 2014). Known variation concerns the structure of the leg sockets (complete versus anterior half-sockets), the

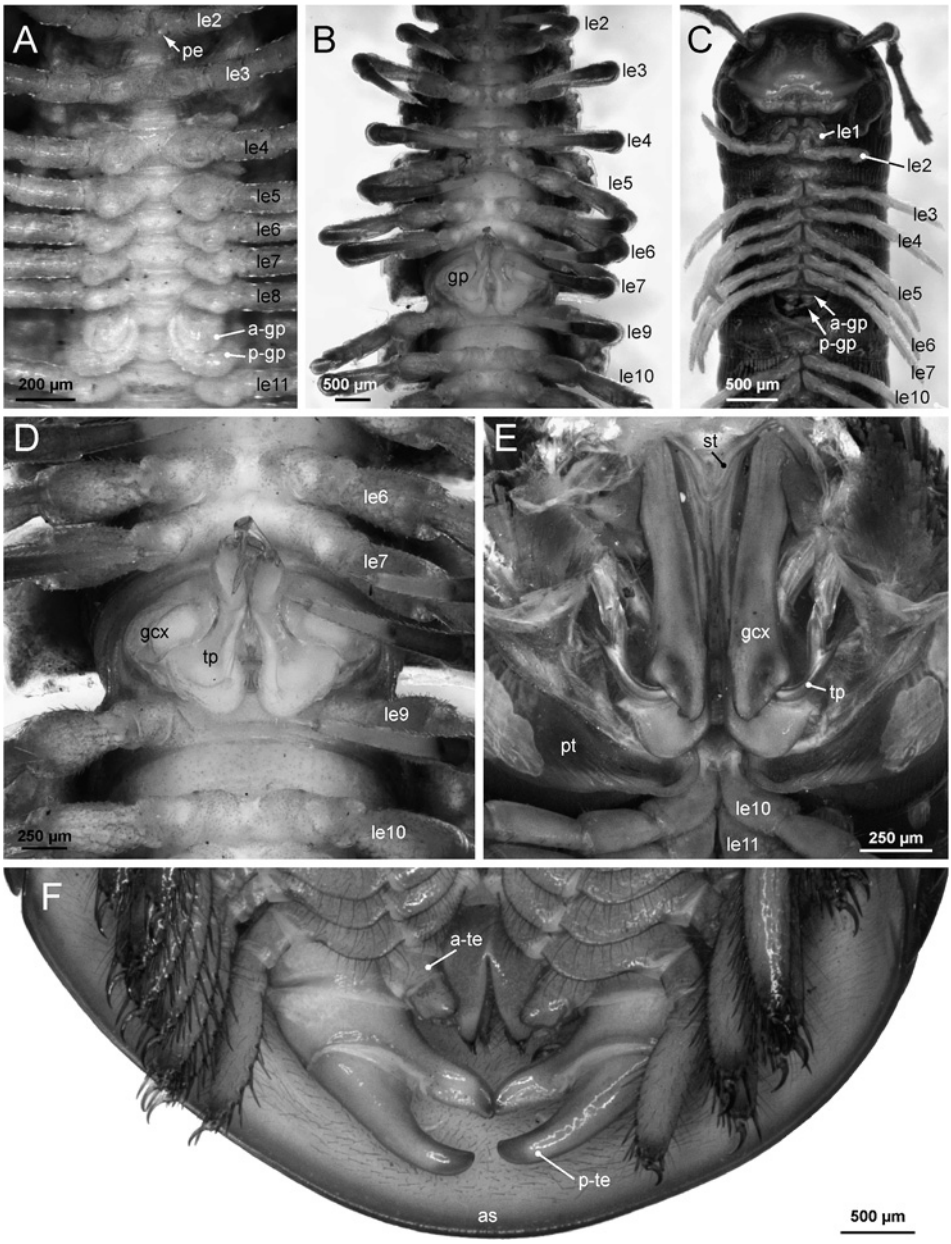
degree of overlap of adjacent sternites (ranging from strong to none), and the size of the tracheal pouches that may be reduced in correlation with the presence of separate 'sternite apodemes' adopting the former function of the tracheal pouches as attachment site for leg and trunk muscles (Manton, 1961).

Walking legs

The walking legs of chilognathan millipedes typically consist of six podomeres, the leg base called the coxa and a telopodite made of five segments conventionally denoted from proximal to distal as prefemur, femur, postfemur, tibia, and tarsus (Fig. 2.7B). The tarsus apically bears a single claw that is sometimes composite and/or equipped with accessory structures (variably shaped processes or pads or paronychia). Additional leg segments may occur by (sometimes incomplete) delimitation of a short trochanter from the coxa and/or bipartition of the tarsus. Due to the lack of intrinsic muscles in these additional segments it is unlikely that they represent "true" podomeres (see Silvestri, 1903; Verhoeff, 1928 versus Manton, 1958). The legs of non-diplopod myriapods show at most six podomeres but homologies have not yet been established (i.e. corresponding terms applied across myriapods need not necessarily refer to homologous leg segments).

The recent interpretation of the basal podomeres in Polyxenida as subcoxal elements (Bäcker et al., 2008) implies that their legs are at most six-segmented, with the podomere considered as the prefemur in previous and contemporary taxonomic descriptions actually representing the coxa (Fig. 2.6C). This interpretation also implies that eversible structures variably denoted in millipedes as coxal vesicles, coxal pouches, coxal sacs, coxal pores, or coxal glands are located on subcoxal elements in Polyxenida. Presence of "sternal" eversible vesicles in the extinct Archipolypoda (Wilson & Anderson, 2004) may support the view that a subcoxal position was primarily maintained in Chilognatha. In extant chilognathans eversible vesicles, when present, are positioned on the coxa, in colobognathans in a continuous series from the third leg-pair backwards (Fig. 2.10B, also Plate VIII; Fig. 2.11A, also Plate IX). Homology of the subcoxal and coxal vesicles is supported by their similar, bivalvate appearance when collapsed or retracted, respectively (see, e.g., Shear and Marek, 2009, their Fig. 12 for Platydesmida). In other extant chilognathans the number of coxal vesicles is reduced to a shorter continuous or discontinuous series (Glomeridesmida, Callipodida), or they are restricted to males to a low number of legs in the vicinity of the gonopods and deemed to serve for sperm storage (Chordeumatida), or their openings are reduced in size and lack evidence for any eversible structure (Stemmiulida). Polydesmida and Juliformia lack coxal vesicles; a gland opening occasionally occuring on the coxae of the second leg-pair in male julidans is denoted as a coxal pore (e.g., Enghoff, 1984a, his Fig. 13; Enghoff, 1991), but its derivation from an eversible vesicle is unlikely, given that no other millipedes are known to have eversible vesicles on the second leg-pair, possibly for the vesicles being transformed into penes and vulvae, respectively.

The two leg-pairs of a diploring are almost always uniform in size and shape. A remarkable instance of disparate leg lengths ("heteropody" sensu Golovatch, 2009) is provided by the chelodesmid *Pandirodesmus disparipes* (Polydesmida). Gender-specific leg modifications often occur in males and are usually related to mating (see Chapter 10).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In Helminthomorpha the modifications mainly concern the legs in front (sometimes also behind) the specialized legs (gonopods) used for sperm transfer. Pregonopodal leg modifications in male juliformians typically concern presence of sole pads (also called pulvilli) on the tarsus (e.g., Pitz & Sierwald, 2010 for Spirobolida) or onto more proximal segments of the telopodite (e.g., postfemoral and tibial pads in Spirostreptida). Male Polydesmida and Chordeumatida instead often show the femora of pregonopodal legs equipped with variably shaped protuberances (e.g., Shear, 2007 for Chordeumatida).

Specialized trunk appendages: gonopods and telopods

Sperm transfer is accomplished in chilognathan millipedes by modified legs in males that firmly attach at the vulvae during mating. In pentazonians the last leg-pair(s) at the rear of the body serves this function and are called telopods (Fig. 2.11F, also Plate IX). The ultimate leg-pair is consistently transformed into a pincer-shaped organ by modification of their telopodites (e.g., Wesener & VandenSpiegel, 2009, their Figs. 37-39). In Oniscomorpha the penultimate and sometimes also the antepenulitmate leg-pair are transformed into accessory telopods. The legs transformed into anterior and posterior telopods are suppressed in females.

In the Helminthomorpha, modified leg-pairs on the seventh and/or eighth trunk rings are transformed into spermatopositors and/or associated structures. Transformation into gonopods may concern solely the eighth leg-pair, the eighth and ninth leg-pairs, or the ninth and tenth leg-pairs (Fig. 2.11A-E, also Plate IX). The gonopods may be readily visible in between the unmodified walking legs (Polydesmida, Chordeumatida, Stemmiulida) but are often deeply recessed into internal pouches (most Juliformia). When two leg-pairs are involved (anterior and posterior gonopods), one of them is used to deposite the sperm (or spermatophore) into the vulvae, while the other leg-pair 'assists' in mostly unknown, probably highly variable manners as accessory gonopods (also called peltogonopods when deemed to serve a protective function). Accessory functions may include to remove or to stratify sperm from prior matings (sperm displacement, see, e.g., Frederiksen & Enghoff, 2015). Further assistance may be provided by the legs (paragonopods) immediately in front or behind the gonopods. The classic systematic distinction of proterospermous and opisthospermous taxa refers to whether the anterior or the posterior gonopods affect the sperm transfer. The 'functional' gonopod may be distinguishable (from 'accessory'

Fig. 2.11. Light micrographs of gonopods (**A-E**) and telopods (**F**). **A** *Platydesmus* sp. (Colobognatha: Platydesmida), anterior part of trunk, ventral view. **B** *Polydesmus angustus* (Polydesmida), anterior part of trunk, ventral view. **C** *Tachypodoiulus niger* (Julida), anterior part of trunk, ventral view. **D** *Polydesmus angustus* (Polydesmida), higher magnification of the gonopods shown in **B**. **E** *Sechelleptus* sp. (Spirostreptida), dissected gonopods in situ, ventral view. **F** *Zoosphaerium* sp. (Sphaerotheriida), rear of the trunk in ventral view. Originals: M. Koch. Abbreviations: **a-gp** anterior gonopod; **as** anal shield; **a-te** anterior telopod; **gcx** gonocoxa; **gp** gonopod; **le1-11** trunk legs 1-11; **pe** penis; **p-gp** posterior gonopod; **p-te** posterior telopod; **pt** pleurotergite; **st** sternite; **tp** telopodite of gonopod. *For a colour version of this figure, see Plate IX.*

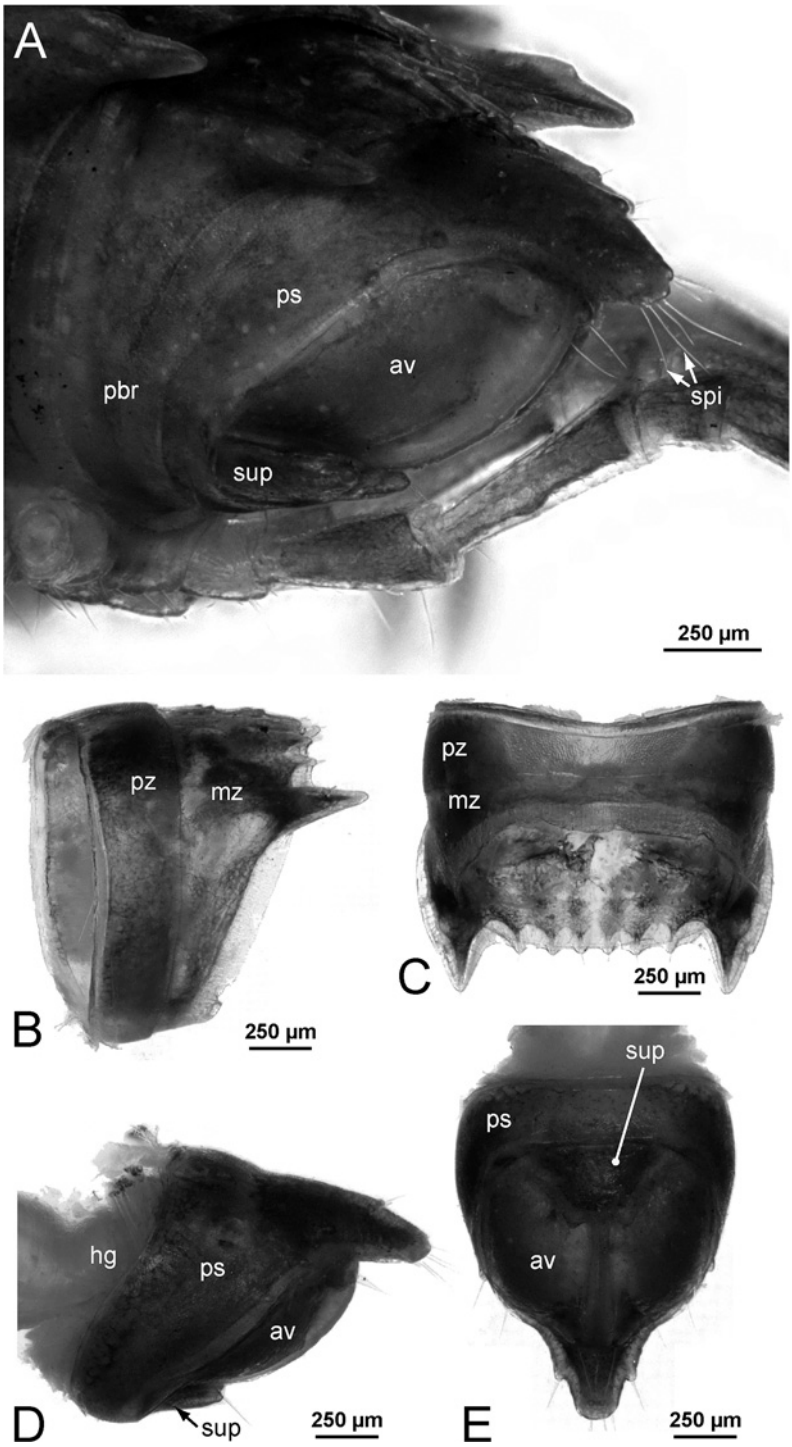
gonopods) by the presence of tube-like devices on its base (gonocoxa) and/or telopodite, used for picking up the sperm/seminal fluid/spermatophore from the male gonopore and for injecting it onto the female vulvae or seminal receptacle, respectively. These tube-like devices, when present, are called the cannula on the (gono-) coxa of the modified leg, and prostatic (or seminal) groove on its telopodite. The part of the telopodite bearing the distal opening of the prostatic groove is generally denoted as the solenomere (see, e.g., Mesibov, 2015 for Polydesmida).

In the Eugnatha the transformation of legs into gonopods is highly complex and most often species-specific; their characters accordingly play a key role in morphological species distinction. The complexity of the leg transformations renders recognition of homologous components extremely difficult, for which multiple, partly not even order-wide terminologies exist to name their components. Contemporary species descriptions often refrain from homology statements and instead provide pictorial representations to ease comprehension and comparisons (e.g., Korsós et al., 2011 for Polydesmida; Enghoff, 2014 for Spirostreptida). Still there are instances of so-called monotonous gonopods among eugnathans (few species of Callipodida, Polydesmida, and each of the juliformian orders; Stoev & Enghoff, 2011), in which the gonopods are largely invariant and non-gonopodal characters show greater variation. In the Colobognatha the transformations are simpler and the gonopods still look leg-like (e.g., Shear & Marek, 2009 for Platydesmida; Fig. 2.11A, also Plate IX). The homology of colobognathan and eugnathan gonopods nevertheless remains questionable (e.g., Brewer & Bond, 2013).

Postpedal trunk segments

The rear of the trunk terminates in a unit called the telson, which systematists count as the last trunk ring (sometimes denoted as "anal segment"; e.g., Golovatch, 2003), if not explicitly excluded from trunk ring number (following Enghoff et al., 1993). It consists of a ring-shaped, posteriorly often tapering preanal sclerite roofing and/or laterally overlapping a pair of large, most often undivided valves (paraprocts) that flank and close off the anal opening of the gut (Fig. 2.12). Below the anal valves usually lies a scale-like sclerite called the subanal plate (hypoproct). The preanal sclerite may form a complete ring or shows a ventral gap. In Polydesmida and Nematophora (possibly also in Siphoniulida) the dorsal posterior margin of the preanal sclerite (sometimes denoted as the epiproct) bears organs presumed to represent modified setae on which fibre-producing glands open (e.g., Shear, 2008; Enghoff & Akkari, 2011). Presence of these 'spinnerets' may form an ancestral feature of eugnathans that were lost in Juliformia (Brewer & Bond, 2013). This view

Fig. 2.12. *Polydesmus angustus* (Polydesmida), light micrographs of the telson. **A** Rear of the body, posterior view on left body side. **B-C** Skeleton of the legless penultimate body ring in (**B**) lateral view (anterior is left) and (**C**) ventral view (anterior is top). **D-E** Dissected telson in (**D**) lateral view (anterior is left) and (**E**) ventral view (anterior is top). Originals: M. Koch. Abbreviations: **av** anal valve; **hg** hindgut; **mz** metazonite; **pbr** penultimate body ring; **ps** preanal sclerite; **pz** prozonite; **spi** 'spinneret'; **sup** subanal plate.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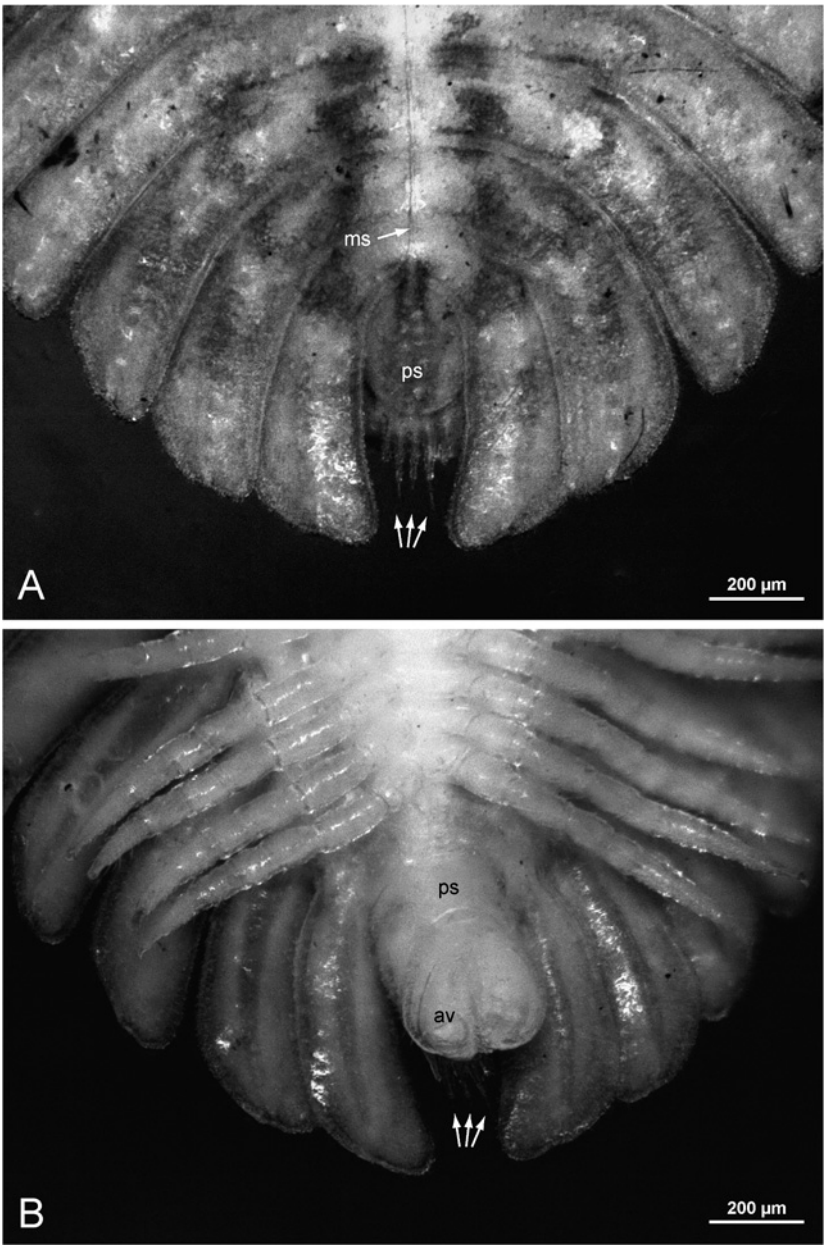

Fig. 2.13. *Platydesmus* sp. (Colobognatha: Platydesmida), light micrographs of the telson. **A** Rear of the body in dorsal view. **B** Same in ventral view. Arrows point to setiferous cones (six in one row, setae partly broken off) resembling 'spinnerets'. Originals: M. Koch. Abbreviations: **av** anal valve; **ms** median sulcus; **ps** preanal sclerite.

possibly finds support by the occurrence of setiferous cones or tubercles (Chamberlin, 1922; Gardner, 1974) on the apex of the epiproct in Platydesmida (Colobognatha) that resemble the 'spinnerets' in Stemmiulida both in number (6) and arrangement (Fig. 2.13), but their fine structure and potential association with fibre-producing glands have not been studied thus far. The telson of polyxenidans instead is equipped with bundles of elongate, barbed and (in part) distally hooked setae (Fig. 2.6A, D) that are splayed when the animal is disturbed (a protective reaction against attack, particularly by ants; Eisner et al., 1996). The telsonal area bearing these modified setae is considered homologous to the preanal sclerite in chilognathans, with the anal valves displaced onto the penultimate trunk ring to accommodate the telsonal bundles of setae (Enghoff, 1990). Whether these bundles of modified setae are serial homologues to the lateral tufts of serrate setae on preceeding trunk rings, proposed by Verhoeff (1928: 452) has not since been considered.

In chilognathans the telson may be readily visible or partly or entirely hidden in dorsal view by the trunk tergite(s) in front of the telson, in Oniscomorpha by a large anal shield (also called the pygidium; Fig. 2.11F, also Plate IX) of unclear, potentially variable composition (for Sphaerotheriida, see Wesener & Sierwald, 2005). The trunk ring immediately in front of the telson often lacks legs (Fig. 2.12A-C), sometimes (particularly in juveniles) also the trunk rings in front of the penultimate trunk ring. In the 'ring-formers' the apodous pre-telsonal trunk ring(s) of adults seems to be formed by the pleurotergite(s) only, without participation of sternites.

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CHAPTER 3

DIPLOPODA — INTEGUMENT

BY

SLOBODAN E. MAKAROV

INTEGUMENT

The integument of millipedes protects internal organs and tissues, represents a barrier against pathogens, parasites, predators and water loss, and enables communication with the external world. The integument consists of two distinct parts: cuticle and epidermal layer. The cuticle is secreted by epidermal cells and covers the entire body surface. The cuticle is composed of several layers but most of the mechanical properties are due to the exo- and endocuticle layers. A calcified cuticle is characteristic for all diplopod taxa except penicillates.

A characteristic feature of integumental origin found in some millipede orders is a pair of glands in many diplosegments that are known as repugnatory, repugnatorial or defensive glands, or ozadenes. When disturbed, diplopods discharge odorous secretions from these glands, indicating a role in chemical defence. These glands may also have additional functions, such as antimicrobial or antifungal protection, and possibly intraspecific communication. The chemistry of millipedes defence secretions represents a source of unique, still largely undiscovered, natural compounds, and an important pool of novel characters for diplopod taxonomy, phylogeny and ecology. Thus, one of the main parts of this chapter reviews data gathered so far in the semiochemistry of the Diplopoda.

Cuticle

Data on the ultrastructure of the millipede cuticle are limited to the following species: *Polyxenus lagurus* (Seifert, 1967), *Glomeris marginata* (Ansenne et al., 1990; Compère et al., 1994, 1996a, b), *Polyzonium germanicum* (Wegensteiner, 1982), *Ommatoiulus sabulosus* (Blower, 1951), *Ophyiulus pilosus* (Thorez et al., 1992), *Pachyiulus varius* (Carmignani & Zaccone, 1977), *Tachypodoiulus niger* (Blower, 1951; Hicking, 1979), *Aulacobolus excellens*, *Cingalobolus bugnioni* (Rajulu & Krishnan, 1968), *Orthoporus ornatus* (Walker & Crawford, 1980), *Gonoplectus malayus* (Shrivastava, 1992), and *'Spirostreptus' asthenes* (Subramoniam, 1974).

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The outermost layer of millipede cuticle is the multi-stratified epicuticle including cement, wax, and cuticulin layer, as well as the inner epicuticle (Fig. 3.1A; Thorez et al., 1992; Compère et al., 1996a, b). The epicuticle covers the procuticle, which is subdivided into exocuticle and endocuticle. All layers are transversed by pore canals and dermal gland ducts (Fig. 3.1A, E).

According to the dual-function model of arthropod cuticle (Compère & Goffinet, 1992), the upper part of the cuticle (superficial layers and cuticulin layer) in diplopods mainly contributes to cuticular permeability, while the lower part (inner epicuticle and procuticle) is responsible for the mechanical properties of the exoskeleton.

The cement layer represents an outer protection consisting of wax-impregnated proteins, while the wax layer consists of stabilized lipid compounds (mostly unsaturated) (Compère et al., 1996a) (Fig. 3.1B, C). Both layers probably represent integumental adaptations to a terrestrial mode of life. The cuticulin layer is multi-laminated and is deposited first during the moult (Fig. 3.1B, C). Between this layer and the fibrous procuticle there is the thickest epicuticular layer, the inner epicuticle (Fig. 3.1B, C). This consists of the lipoprotein matrix surrounding proteinaceous elements and chitin-protein microfibres in peculiar organization with helicoidal twisted arrangement of the exocuticle fibres (Ansenne et al., 1990; Compère et al., 1996a). Microfibres are absent from the inner epicuticle of membranes between tergites.

Both exocuticle and endocuticle (Fig. 3.1E, F) have lamellate structure, due to a chitin-protein microfibre arrangement similar to most other arthropods (twisted plywood system) (Thorez et al., 1992). Moreover, Compère and co-workers found great similarity in structure between the epicuticle and procuticle microfibres in *G. marginata* which have the same origin and morphogenesis (Compère et al., 1996a).

In *O. pilosus* and *G. marginata* the pore canals form a twisted ribbon-like vertical pathway extending from the epidermis up to the epicuticle (Fig. 3.1D, E) (Ansenne et al., 1990; Thorez et al., 1992). Vertical fibres form a twisted sheath around the canal lumen of the axial pore. Dermal gland ducts run through the whole cuticle and open at the surface. Their diameters are larger in the exocuticle than in the endocuticle. These glands probably secrete cement material (Ansenne et al., 1990). Pore canal originate from epidermal cell process. Their lumen persists as hollow unmineralized tubes in the endocuticle and regress after mineral deposition.

In some millipedes cuticular specialization provide tolerance or resistence to submersion in water even for few months. Such adaptations have been reported for a few members of the Polydesmidae, Pyrgodesmidae, Blaniulidae, Julidae, and Siphonotidae (Adis et al., 1998). In *Aporodesminus wallacei* all tergites are covered with a thick secretion layer called cerotegument. This layer is externally hydrophilous and supported by small secretion pillars which are located between the tubercles of the tergite and the cones of the sternite (Adis et al., 1998). The cerotegument covers a hydrophobic cavity filled with air that enables plastron respiration (see Chapter 6).

The cuticle of millipedes, except for penicillates, is mineralized. A few studies showed that Ca and Mg (mainly from carbonates) in the tergites represent approximately 40-70% of the total cuticle dry weight (Thorez et al., 1992; Vohland et al., 2003). In *O. pilosus*

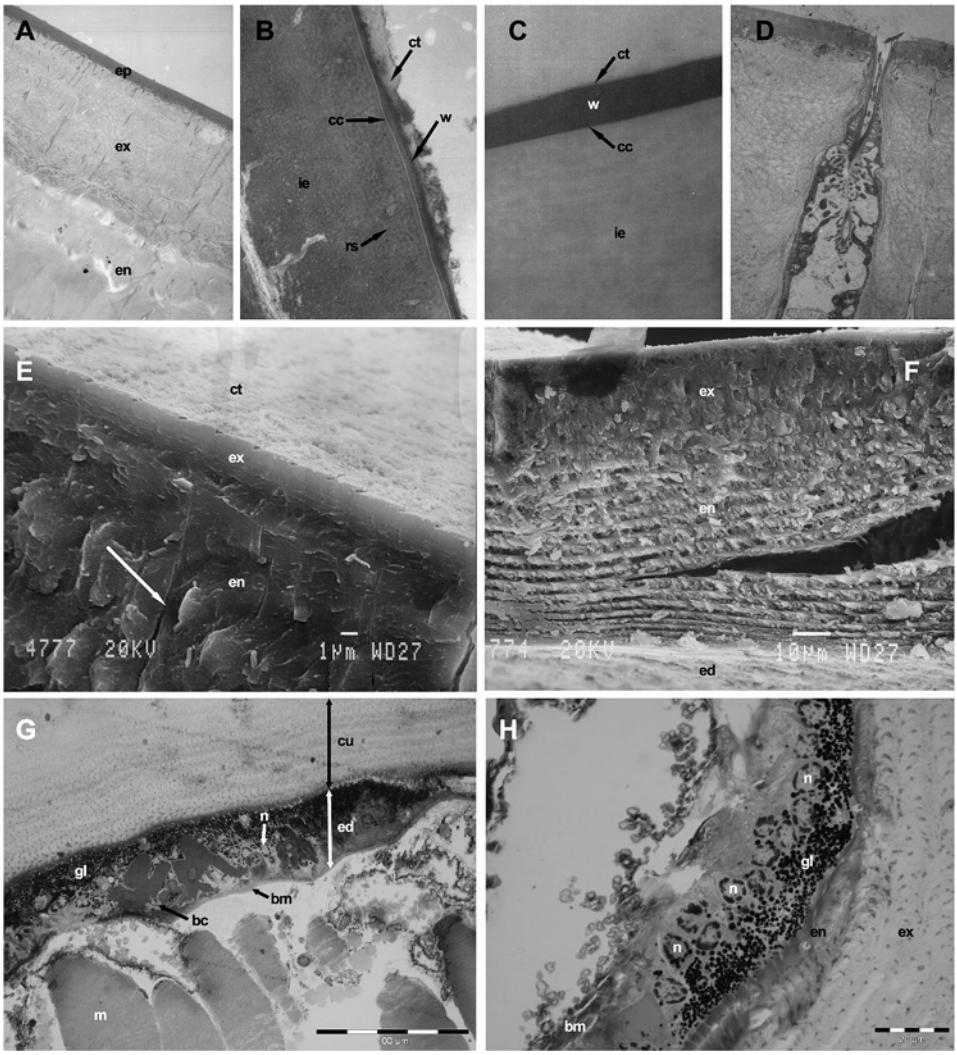

Fig. 3.1. Structure of cuticle. **A** Vertical section through the cuticle in *Glomeris marginata*, general view, ×2000. **B** Transverse section through the tergite of *G. marginata* after classical tissue fixation, ×40 000. **C** Detail of upper epicuticular layers on vertical section through a tergite of *G. marginata* after extraction of free lipids, ×80 000. **D** Dermal gland in *G. marginata*, ×9000. **E** SEM view of a vertical fracture in the mineralized tergite cuticle in *Ophyiulus pilosus*, arrow indicates a pore canal's lumen, ×4200. **F** SEM general view of a vertical fracture through the whole cuticle in *O. pilosus*, ×850. **G** Vertical section through the epidermis in *Apfelbeckia insculpta*. **H** Detail of epidermis in *A. insculpta*. (Reproduction from: Ansenne et al., 1990; Compère et al., 1996; and Thoreze et al., 1992, by kind permission of the Dr P. Compère.) Abbreviations: **bc** basal cell; **bm** basal membrane; **cc** cuticulin layer; **ct** cement layer; **cu** cuticle; **ed** epidermis; **en** endocuticle; **ep** epicuticle; **ex** exocuticle; **gl** apical part of epidermal cell rich in organelles; **ie** inner epicuticle; **m** muscle; **n** nucleus; **rs** rod shaped elements; **w** wax layer.

minerals impregnate both exocuticle and endocuticle (Thorez et al., 1992), while in *'S.' asthenes* and *P. varius* the endocuticle is not mineralized (Subramoniam, 1974; Carmignani & Zaccone, 1977). Vohland et al. (2003) first investigated the chemical composition of the cuticle of two millipede species from contrasting forest habitats and observed no differences in the absolute amount of bioelements in their cuticle. Their relative amount was higher in species from inundation forest, but species from upland forest had greater body mass and a higher fraction of organic compounds (which is the result of substitution of calcium with proteins).

Calcium accumulation in diplopods has a significant influence on the biogeochemical cycle of this element in terrestrial ecosystems (Hopkin & Read, 1992).

Epidermis

The epidermis is a continuous, unistratified layer of epidermal cells separated from the body cavity by a thin basal membrane. Some epidermal cells secrete or deposit a comparatively thick cuticle on its outer surface. In *Apfelbeckia insculpta* the epidermal cells have distinct polarity (Fig. 3.1G). The apical part of some epidermal cells in the same species contains numerous granules (Fig. 3.1H). Abundant pigment granules were also observed in epidermal cells of *Orthoporus ornatus* (Walker & Crawford, 1980).

A variety of specialized cells not concerned primarily with the production of cuticle are also found in millipede epidermis. Diffuse glandular cells in the epidermis might produce specific substance (Haacker, 1974). In the chordeumatids (e.g., *Chordeuma sylvestre*) these cells form a complex of independent bicellular units, but in some glomerids and julids they appear as a multicellular gland with one common efferent duct. Furthermore, Haacker (1974) found single glandular cells, each combined with one canal-forming cell, in the male of *C. sylvestre*. These glandular cells may be aggregated in some pleurotergites to form single-layer field. In other pleurotergites they form multi-layered complex, but each glandular cell still has its own efferent duct opening through dorsal cuticle. Haacker (1974) supposed that these cells probably produce pheromones, involved in the mating behaviour in these millipedes. Unfortunately, there are no additional investigations on this subject.

Colour

Early postembryonic stages of many millipedes are colourless. Adults are often very pale immediately after the moult (even for a few days) and gradually get darker. Cave-dwelling, as well as many geophilic species are usually white, without pigment. In other adult millipedes, a great variety in coloration appear, including red, yellow, orange, pink or red, sometimes as dorsal or lateral spots or lines. Actually, most millipedes show either cryptic or aposematic coloration. A unique aposematic coloration was observed in *Desmoxytes purpurosea* (Enghoff et al., 2007). Living specimens have purple to shocking pink body, brownish head and black antennae (Plate I D). Enghoff (2011) described trans-segmental colour patterns (colour pattern consists of repeated elements, each of which covers several body rings) for several millipede taxa belonging to the orders Spirobolida,

Spirostreptida, Platydesmida, Siphonocryptida, and Chordeumatida. Such colour pattern may have aposematic or camouflaging function. In most cases the adult pattern correlates with postembryonic growth (each pattern element corresponds to a set of body rings added with one moult) (Enghoff, 2011). Marek & Bond (2009) described mimicry complex among seven apheloriine species, endemic for a relatively small area in Norh America. Aposematic coloration and pattern vary considerably within species, but co-occuring species often appear identical. In other words, authors documented case in which unrelated species vary in colour and pattern over geographical space but appear identical where they co-occur (Müllerian mimicry).

There is little information about pigments in diplopods (Hopkin & Read, 1992). Kennedy (1978) distinguished several types of pigments in Myriapoda: quinones, ommochromes, melanins, flavins and tetrapyrroles, while Needham (1968) found three integumental pigments in one polydesmid species.

REPUGNATORY GLANDS

Generally, millipedes are unable to avoid predator attack by escaping, but they possess physical and chemical defence. Only exception is the *Stemmiulus regressus* from Africa; this 3-4 cm long species is capable of jumping 2-3 cm when startled (Evans & Blower, 1973).

The exoskeleton represents a physical barrier against predators, but a more effective protection is chemical defence. In millipedes of the order Polyxenida, which have uncalcified cuticle (soft millipedes) and do not possess chemical defences, a pair of defensive bristle tufts at their rear is likely involved in defence against enemies (Eisner et al., 1996). However, many millipedes possess defensive glands (ozadenes) in the form of integumental sacs arranged segmentally along the body, where defensive compounds are synthesized and stored, to be eventually discharged upon disturbance.

Recent reports showed that members of the orders Siphonophorida, Stemmiulida, Platydesmida and Siphonocryptida have chemical defense system (Kudo et al., 2011; Shear, 2015). Chordeumatida, Sphaerotheriidae, and Polyxenida have long been known to lack ozadenes; Siphoniulida also lack glands; and Glomeridesmida probably lack chemical protection (Shear et al., 2007). Species belonging to the other millipede orders have ozadenes. As a rule, the defensive substances are multifunctional. As repellents, toxins, or antimicrobial substances, they are directed against a wide range of potential target organisms.

The secretions of 140 species from 92 genera have been analyzed to date with more than 80 identified compounds (Tables 3.1-5). Identified compounds can be provisionally grouped into the following chemical classes: alkaloids, quinones, phenols, and cyanogenic compounds (Fig. 3.2). It is necessary to note that in different orders of millipedes a variety of minor compounds also appear (Tables 3.1-5), but their importance and function awaits further studies.

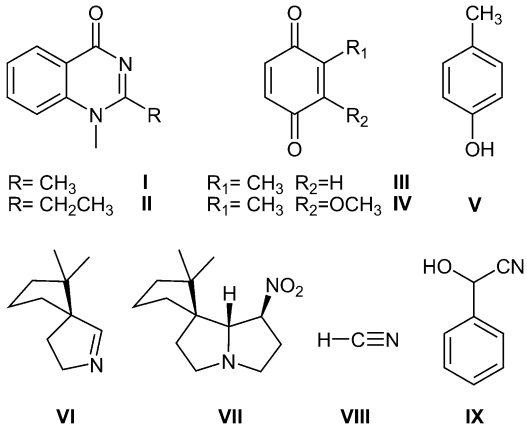

Fig. 3.2. The most common defensive compounds in the Diplopoda: glomerin (I), homoglomerin (II), 2-methyl-1,4-benzoquinone (III), 2-methoxy-3-methyl-1,4-benzoquinone (IV), *p*-cresol (V), polyzonimine (VI), nitropolyzonamine (VII), HCN (VIII), mandelonitrile (IX).

According to the morphology of the glands and the presence of specific defence compounds, three types of defensive glands can be distinguished: *glomerid*, *julid* and *polydesmid type*.

Glomerid type

Members of the order Glomerida are protected against enemies by their exoskeleton and enrolling habit, but these millipedes are also the only representatives of the diplopod infraclass Pentazonia which additionally possess chemical defence (Shear et al., 2011). In these millipedes, paired glands open by ozopores dorsomedially on somites 3-10 and produce single drops of secretion (Eisner et al., 1978; Hopkin & Read, 1992; Shear et al., 2011). Each ozadene consists of a subovoid sac or reservoir and an efferent duct (Fig. 3.3A). Dorsally, two ducts from one tergite are fused in one short common channel, opening through an ozopore to the outside (Fig. 3.3B). Each sac is surrounded by muscles that force secretion through the ozopore (Hopkin & Read, 1992).

The defensive secretions of Glomerida have been studied in five species from three genera (Table 3.1). This secretion comprises only two quinazolinone alkaloids — glomerin (1,2-dimethyl-4(3H)-quinazolinone) and homoglomerin (1-ethyl-2-methyl-4(3H)-quinazolinone). Both compounds are paralyzing agents. For example, wolf spiders tend to reject *G. marginata* on the basis of taste, but they sometimes do so only after having killed the millipede and ingested the secretion. In such case the spider becomes totally paralyzed, sometimes for a few days. These alkaloids can also cause partial paralysis in mice, slowed reactions in birds, and vomit reactions in toads (Schildknecht & Wenneis, 1967b; Carrell & Eisner, 1984).

Carrell (1984) found that secretion of *G. marginata* also contains a very sticky proteinaceous component which provides physical protection against predators, additional to the chemical protection provided by glomerin and homoglomerin. The same author

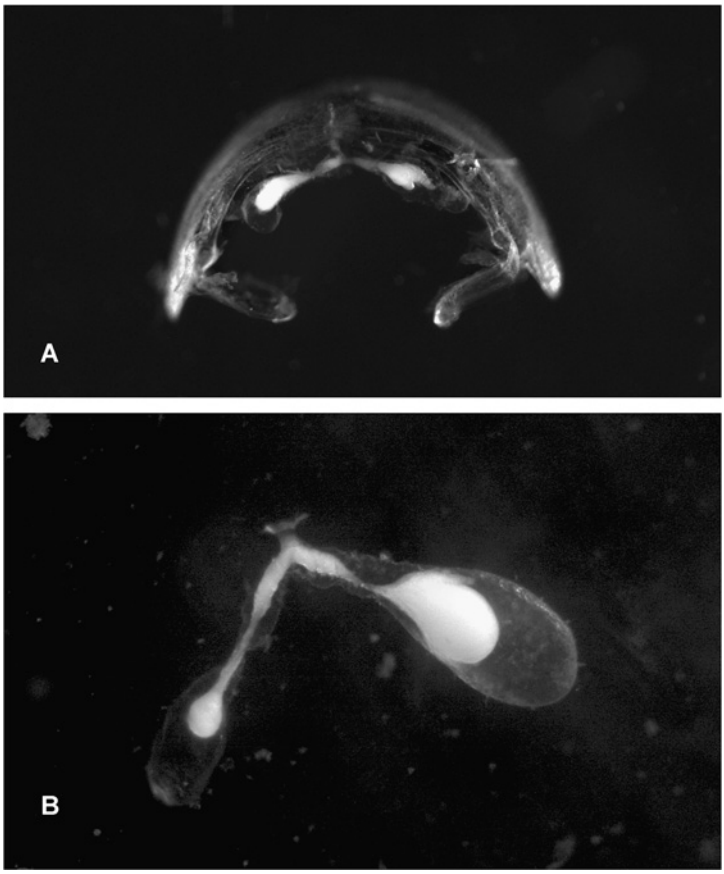

Fig. 3.3. *Hyleoglomeris faberi*. **A** Tergite VI with ozadenes, oral view. **B** Isolated ozadene; the white mass in the vesicles represents proteinaceous components.

TABLE 3.1
Defensive secretions in representatives of the order Glomerida

Species	Glomerin	Homoglomerin	Proteins	References
Glomeris marginata	+	+	+	Meinwald et al., 1966; Schildknecht et al., 1966, 1967; Schildknecht & Wenneis, 1967a, b; Carrell, 1984; Carrell & Eisner, 1984
Glomeris klugii	+	+	−	Schildknecht et al., 1967
Glomeris hexasticha	+	+	−	Schildknecht et al., 1967
Loboglomeris rugifera	+	−	−	Schildknecht et al., 1967
Onomeris sinuata	+	+	−	Shear et al., 2011

noted that adults of this species require more than four months to replenish their defensive reserves after completely discharging them during an attack.

Eisner et al. (1978) grouped glomerids together with polyzoniids as the “alkaloid millipedes”.

Julid type

This type of glands is characteristic for the orders Julida, Spirobolida, Spirostreptida, Callipodida, Polyzoniida and Platydesmida (probably also for the orders Stemmiulida, Siphonophorida and Siphonocryptida; Shear, 2015).

The structure of *julid-type* glands is relatively simple (Hopkin & Read, 1992). It consists of a generally spherical (order Callipodida) (Fig. 3.4B) or more or less distinctly bilobed sac or reservoir (order Julida) (Fig. 3.4D) bordered by secretory cells lined with cuticle, and an efferent duct opening laterally on the body surface via a small ozopore (Fig. 3.5A-C). The terminal portions of the efferent duct wall have inflections with attached muscles that serve to pry open this valve (Eisner et al., 1998). Discharge of defensive compounds is accomplished by contraction of the valvular muscle and

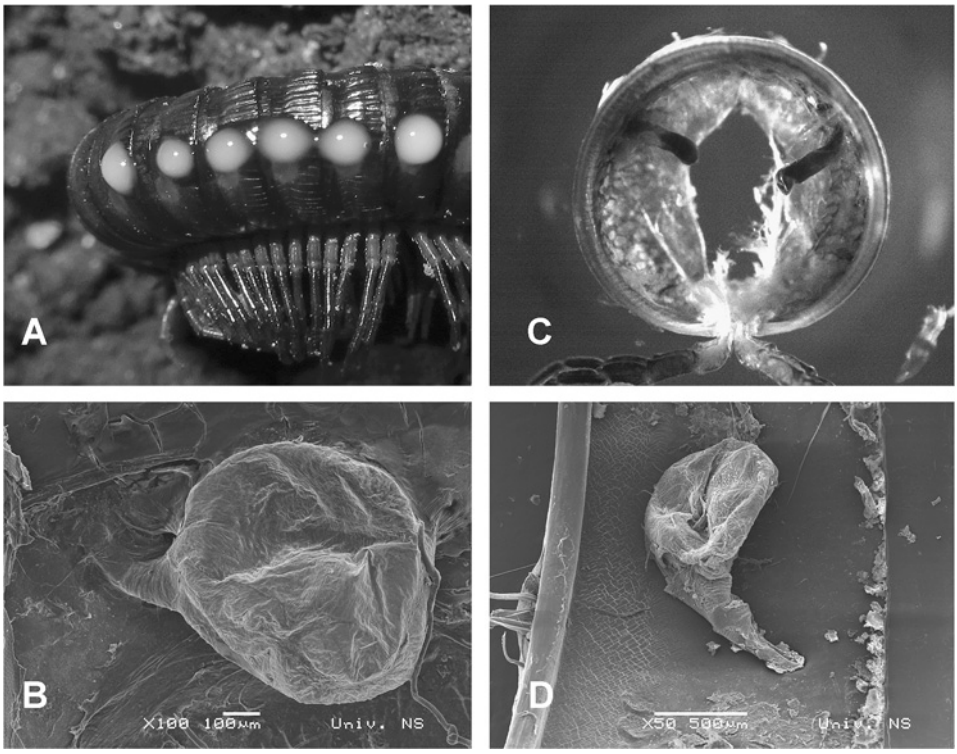

Fig. 3.4. **A** Part of the trunk of *Apfelbeckia insculpta* with droplets of defence fluids. **B** Ozadene of *A. insculpta*, SEM. **C** Pleurotergite XVIII of *Megaphyllum bosniense* with pair of ozadenes, oral view, SEM. **D** Ozadene of *M. bosniense*, SEM.

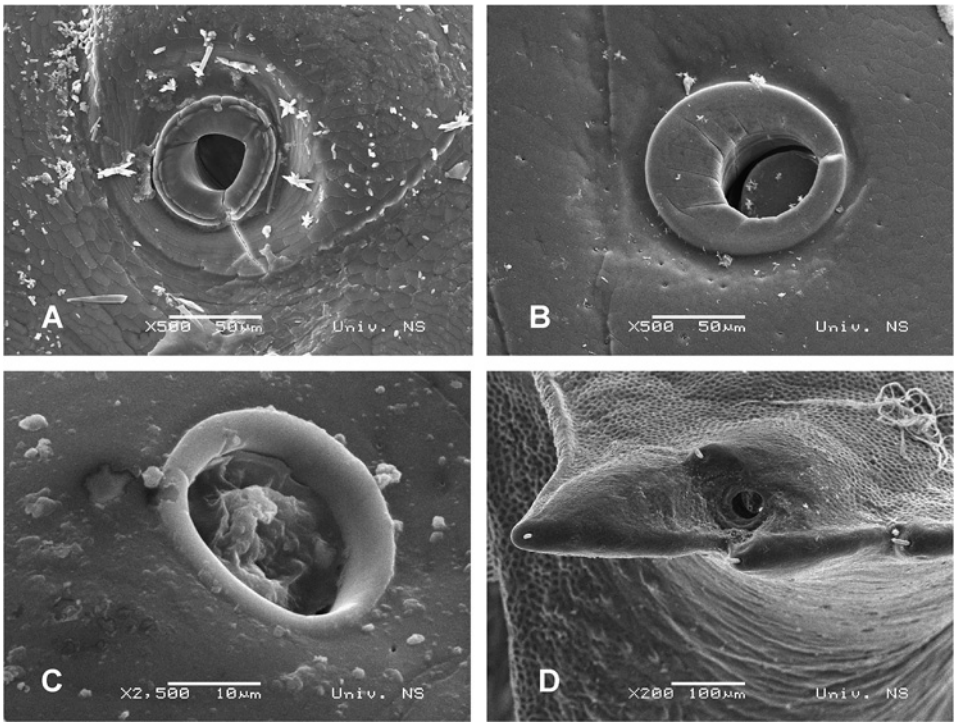

Fig. 3.5. Ozopores. **A** *Apfelbeckia insculpta*. **B** *Pachyiulus hungaricus*. **C** *Polyzonium germanicum*. **D** *Polydesmus complanatus*.

simultaneous compression of the sac. Sac compression should be provoked indirectly by increased hemocoel pressure or by pressure from the integumental muscles that surround the glands (Eisner et al., 1998). However, in some species [*Uroblaniulus canadensis*, *Anadenobolus arboreus*, *Pachyiulus hungaricus* (Woodring & Blum, 1965; Weatherston & Percy, 1969; Makarov et al., 2014)] have been observed that terminal portion of the efferent duct also contains a conical plug, normally closing ozopore (Fig. 3.5B). Weatherston & Percy (1969) showed that the sac wall in *U. canadensis* consists of secretory units. Each such unit consists of a pair of specialized cells and a tubule transporting the secretion generated in these cells to a large cuticule-lined sac. These cells are rich with organelles and their distal portion has numerous secretory granules which are liberated into the sac. Repugnatory glands are distributed laterally on most 'rings' (Fig. 3.4C), and only the first five and last one or two rings are devoid of glands.

According to the type of defensive compounds we can distinguish three groups within the *julid-type* millipedes (Eisner et al., 1978). The first group (Julida, Spirobolida, and Spirostreptida) mainly produce quinones as defensive compounds. The second group (Callipodida and Stemmiulida) has phenol as main chemical, and the third group (Polyzoniida, Platydesmida and Syphonocryptida) has alkaloids in the defensive fluids. Recent studies

have shown, however, that this distinction is not, because some compounds are present in two or more orders (Tables 3.1-5).

The presence of chemical defences in the Julida was known in the nineteenth century, although the compounds involved were not identified. Béhal & Phisalix (1900) first detected benzoquinones as compounds in the defensive secretion of *Julus terrestris*. After that, 20 quinone and 17 nonquinone compounds have been identified in 27 julid species from 18 genera (Table 3.2). All analyzed species showed multi-component secretion patterns consisting of quinones as main compound, accompanied by different minor compounds. The most common compounds are 1,4-benzoquinones, toluquinone, and 2-methoxy-3-methyl-1,4-benzoquinone. The natural function of benzoquinones is generally obscure. In millipedes they fulfil antimicrobial and antifeedant roles. It is known that among terrestrial animals 1,4-benzoquinones are widely produced by arthropods and probably serve to repel predators. Worth of further investigation is Haacker's (1974) suggestion that in some representatives of the orders Julida and Spirostreptida females use their defensive quinones to prevent copulation or as a signal that the female is not ready to copulate.

Non-quinonic compounds in the defensive fluids of julids include esters, alcohols, alkenals, as well as some other chemicals (Table 3.2) (Huth, 2000; Bodner & Raspotnig, 2012; Shimizu et al., 2012). It is possible that combination of benzoquinones and esters could be a more effective millipede defence than other type of compound alone (it is known that some arthropods with defence benzoquinones secrete also liquid hydrocarbons which may serve as solvent for the irritating quinones). Some non-quinones registered by Shimizu et al. (2012) in *Anaulaciulus* sp. have been known so far in some other arthropods as compounds with antimicrobial activity (*n*-hexyl n-tridecanoate), as species recognition signals (*n*-hexyl myristate), or in combination with other compounds as pheromones (*n*-hexyl laurate, *n*-hexyl caprate or *n*-octyl laurate).

Among the most intriguing presences of non-quinone compounds found in the secretion of a member of the Julida are *o*-cresol, found in defensive fluids of the probably most basal parajulid *Oriulus venustus*, *p*-cresol in some typhloiulids, and *p*-cresol and phenol in oncoiulin *Unciger transsilvanicus*. Phenol-based defenses are also widespread among the more distant clades within the order Julida (Raspotnig & Makarov, unpublished). These occurrences may represent a symplesiomorphy of Callipodida, Polydesmida and Juliformia, eventually lost in the majority of the latter.

Bodner & Raspotnig (2012) provided the first data on the ontogenetic development of the secretion in a julids. In *Allajulus dicentrus*, the secretion in early postembryonic stadia (III and IV) include only the benzoquinone fraction. The following stadium V still exhibits a secretion profile dominated by benzoquinone along with small amounts of octenol, whereas the profile of some individuals in stadium VI was found already similar to that of the adults.

Small number of analysed julids limits chemosystematic application of both quinones and non-quinones (Vujisić et al., 2011). For the further study it will be indicative that the lack of toloquinone in the genus *Allajulus* is perhaps a good chemotaxonomical marker (Bodner & Raspotnig, 2012).

TABLE 3.2
Defensive secretions in representatives of the orders Julida, Spirobolida and Spirostreptida

Orders and species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	References
JULIDA																					
Allajulus dicentrus	❶	+	−	−	+	+	−	−	+	−	−	−	−	−	−	−	−	−	−	−	Bodner & Raspotnig, 2012
A. nitidus	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Röper & Heyns, 1977
Anaulaciulus sp.	❷	+	+	+	+	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	Shimizu et al., 2012
Blaniulus guttulatus	❸	+	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Weatherston et al., 1971
Bollmaniulus hewitti	−	+	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Duffey, 1974
Cibiniulus phlepsii	■	+	−	+	−	+	−	+	+	−	+	−	−	−	−	−	−	−	−		Vujisić et al., 2014
Cylindroiulus boleti	❹	+	−	+	+	+	−	+	+	+	+	+	+	+	−	−	−	−	−	−	Vujisić et al., 2011
C. caeruleocinctus	❺	+	+	+	+	+	+	−	−	+	−	−	+	−	+	+	−	−	−	−	Schildknecht & Weiss, 1961; Röper & Heyns, 1977; Huth, 2000
C. luridus	−	+	−	+	−	−	−	+	−	+	−	−	−	−	−	−	−	−	−	−	Röper & Heyns, 1977
C. meinerti	❻	+	+	+	+	+	+	−	−	−	−	−	−	−	+	−	+	−	−	−	Huth, 2000
C. punctatus	❻	+	+	+	+	+	+	−	−	+	−	−	+	−	+	−	+	−	−	−	Röper & Heyns, 1977; Huth, 2000
Enantiulus nanus	❻	+	−	−	+	+	+	−	−	−	−	−	−	−	+	−	−	−	−	−	Huth, 2000
Julus scandinavius	❻	+	+	+	+	+	+	−	−	−	−	−	−	−	+	−	+	−	−	−	Huth, 2000
J. terrestris	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Béhal & Phisalix, 1900; Pavan, 1968
Leptoiulus proximus	❻	+	+	+	+	+	+	−	−	−	−	−	−	−	+	−	+	−	−	−	Huth, 2000
L. trilineatus	❹	+	+	+	+	−	−	+	+	+	+	+	+	+	+	−	−	−	−	−	Vujisić et al., 2011
Megaphyllum bosniense	❹	+	−	+	+	−	−	+	+	+	+	+	+	+	+	−	−	−	−	−	Vujisić et al., 2011
M. unilineatum	−	+	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Schildknecht & Weiss, 1961; Pavan 1968
Nopoiulus kochii	■	+	−	+	+	−	−	+	+	+	−	+	−	+	−	−	−	−	−	−	Vujisić et al., 2014
Ommatoiulus sabulosus	❻	+	+	+	+	+	+	−	−	−	−	−	−	−	+	+	+	−	−	−	Trave et al., 1959; Huth, 2000
Ophyiulus pilosus	−	+	−	+	−	−	−	−	−	+	−	−	+	−	−	−	−	−	−	−	Röper & Heyns, 1977
Oriulus venustus	❼	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Kluge & Eisner, 1971
Saiulus setifer	−	+	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Duffey, 1974
Tachypodoiulus niger	❻	+	+	+	+	+	+	−	−	−	−	−	−	−	+	−	+	−	−	−	Huth, 2000

TABLE 3.2
(Continued)

Orders and species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	References
JULIDA																					
Unciger foetidus	−	+	−	+	−	−	−	−	−	+	−	−	+	−	−	−	−	−	−	−	Röper & Heyns, 1977
U. transsilvanicus	◆	+	+	+	+	+	−	+	+	+	−	+	−	+	−	+	+	+	−	−	Sekulić et al., 2014
Uroblaniulus canadensis	❽	−	+	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Weatherston & Percy, 1969
SPIROBOLIDA																					
Acladocricus setigerus	−	+	+	+	+	−	−	+	+	+	−	+	+	+	+	+	−	+	+	−	Wu et al., 2007
Anadenobolus arboreus	−	+	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Pavan, 1968
A. holomelanus	−	+	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Duffey, 1974
A. monilicornis	−	+	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Duffey, 1974
A. putealis	−	+	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Bedoussac et al., 2007
Chicobolus spinigerus	−	+	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Monro et al., 1962; Pavan, 1968
Epibolus pulchripes	−	+	−	−	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Wood et al., 1975
Eurhinocricus sabulosus	−	+	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Duffey, 1974
Floridobolus penneri	⊗	+	+	+	+	+	−	−	+	−	−	−	−	−	−	−	−	−	+	−	Monro et al., 1962; Attygalle et al., 1993
Leptogoniulus sorornus	−	+	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Duffey, 1974
Narceus americanus	⊗	+	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Monro et al., 1962
N. annularis	−	+	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Percy & Weatherston, 1971
N. gordanus	−	+	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Pavan, 1968
Paraspirobolus lucifugus	−	+	−	−	+	+	−	−	−	−	−	+	+	−	−	−	−	−	−	−	Kuwahara et al., 2002a
Pelmatojulus brachysternus	−	+	−	+	+	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	De Bernardi et al., 1982
P. laminatus	−	−	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Barbier & Ledeber, 1957; Pavan, 1968
P. tigrinus	✷	+	−	+	−	−	−	−	+	+	−	−	−	−	−	−	−	−	−	−	Schmitt et al., 2004
Rhinocricus insularis	❾	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Wheeler et al., 1964
R. padbergi	❿	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Arab et al., 2003
R. varians	−	−	−	+	−	+	−	−	−	−	−	−	−	−	−	+	−	−	−	−	Moussatche et al., 1969; Blum, 1981
Trigoniulus corallinus	−	+	−	+	+	+	−	−	−	+	−	−	+	−	−	−	−	−	−	−	Monro et al., 1962; Kuwahara et al., 2002a
Trigoniulus sp.	−	+	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Pavan, 1968

TABLE 3.2
(Continued)

Orders and species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	References
SPIROSTREPTIDA																					
Archispirostreptus gigas	−	+	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Wood, 1974; Smolanoff et al., 1975a
A. tumuliporus	−	+	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Smolanoff et al., 1975a
Aulonopygus aculeatus	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Barbier, 1959; Smolanoff et al., 1975a
Calathostreptus fulvus	−	+	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Perisse & Salles, 1970; Smolanoff et al., 1975a
Cambala hubrichti	−	+	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Smolanoff et al., 1975a
Congopyge acanthophor	−	+	−	+	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	De Bernardi et al., 1982
Doratogonus annulipes	−	+	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Eisner et al., 1965; Smolanoff et al., 1975a
Glyphiulus septentrionalis	−	+	−	−	−	+	−	−	−	−	−	−	+	−	−	−	−	−	−	−	Kuwahara et al., 2002a
Harpagophoridae unidentified	−	+	+	+	−	+	−	−	−	+	−	+	−	−	−	+	−	+	−	−	Deml & Huth, 2000
Ophistreptus levis	−	+	+	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	De Bernardi et al., 1982
Orthoporus cavicollis	−	+	−	+	−	+	−	−	+	−	−	−	−	+	−	−	−	−	+	−	Williams et al., 1997
O. conifer	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Eisner et al., 1965; Smolanoff et al., 1975a
O. dorsovittatus	−	+	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Weldon et al., 2003
O. flavior	−	+	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Eisner et al., 1965; Smolanoff et al., 1975a
O. ornatus	−	+	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Eisner et al., 1965; Smolanoff et al., 1975a
Peridontopyge aberrans	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Barbier, 1959; Smolanoff et al., 1975a
P. conani	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Smolanoff et al., 1975a
P. rubescens	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Smolanoff et al., 1975a
P. vachoni	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Barbier, 1959; Smolanoff et al., 1975a

TABLE 3.2
(Continued)

Orders and species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	References
SPIROSTREPTIDA																					
Prionopetalum tricuspis	−	+	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Wood, 1974; Smolanoff et al., 1975a
Rhapidostreptus innominatus	−	+	+	+	+	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	De Bernardi et al., 1982
R. virgator	−	−	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Barbier & Ledeber, 1957; Smolanoff et al., 1975a
Spirostreptus castaneus	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Barbier & Ledeber, 1957; Smolanoff et al., 1975a
S. multisulcatus	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Barbier, 1959; Smolanoff et al., 1975a
S. pavani	−	+	+	+	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	Deml & Huth, 2000
Telodeinopus aoutii	−	+	+	+	+	+	−	−	−	+	−	−	+	−	−	+	+	+	−	+	Deml & Huth, 2000

Nonquinone compounds: (1) [❶, (*E*)-2-heptenal, isomer of octenal, (*E*)-2-octenol, isomer of nonenal, (*E*) and (*Z*)-2-nonenal, (*E*)-2-decenal; ❷, *n*-butyl *n*-dodecanoate, *n*-butyl 12-methyltetradecanoate, *n*-pentyl *n*-dodecanoate, *n*-pentyl 11-methyldodecanoate, *n*-hexyl *n*-decanoate (= *n*-hexyl caprate), *n*-hexyl *n*-undecanoate, *n*-hexyl 10-methylundecanoate, *n*-hexyl *n*-dodecanoate (= *n*-hexyl laurate), *n*-hexyl 11-methyldodecanoate, *n*-hexyl *n*-tridecanoate, *n*-hexyl 12-methyltridecanoate, *n*-hexyl *n*-tetradecanoate (= *n*-hexyl myristate), *n*-hexyl 13-methyltetradecanoate, *n*-heptyl *n*-dodecanoate, *n*-octyl *n*-dodecanoate (= *n*-octyl laurate); ❸, hexadecyl acetate, octadecenyl acetate (probably (*E*)-octadec-1-enyl acetate); ❹, hexyl esters of saturated and unsaturated C_{14}-C_{20} fatty acids; ❺, octanol, nonanol, decanol, dodecanol, alkenols, derivates of unsaturated fatty acids; ❻, hexylester of alkanoic acid and derivates of unsaturated fatty acids; ❼, *o*-cresol; ❽, unidentified aliphatic compounds; ❾, *trans*-2-dodecenal; ❿, tetrahydro-pyrrolo-pyridine-2,6-dione and ten linear aliphatic hydrocarbons; ■, hexyl and octyl oleate; ✱, 2,4-dihydroxy-6-methylbenzaldehyde; ◆, *p*-cresol, phenol, isopentylhexacosatetraenoate (isopentyl ester of C26:4 fatty acid), and isopentyl esters of saturated and unsaturated fatty acids with chain lengths from C_{14} to C_{20}; ⊗, uncharacterized components].

Quinone compounds: 2-methoxy-3-methyl-1,4-benzoquinone (2); 1,4-benzoquinone (3); 2-methyl-1,4-benzoquinone (= toluquinone) (4); 2,3-dimethoxy-5-methyl-1,4-benzoquinone (= ubiquinone 0) (5); 2,3-dimethoxy-1,4-benzoquinone (6); 2-methoxy-6-methyl-1,4-benzoquinone (7); 2-methyl-3,4-methylenedioxyphenol (8); 2-hydroxy-3-methyl-1,4-benzoquinone (9); 2-methyl-1,4-hydroquinon (= toluhydroquinone) (10); 2-methoxy-5-methyl-1,4-hydroquinone (11); 2,3-dimethoxy-1,4-hydroquinone (12); 2-methoxy-3-methyl-1,4-hydroquinone (13); 2,3-dimethoxy-5-methylhydroquinone (14); 2-methoxy-5-methyl-1,4-benzoquinone (15); 2-ethyl-1,4-benzoquinone (16); 2-methoxy-1,4-benzoquinone (17); hydroquinone (18); 3-methoxy-2,5-dimethyl-1,4-benzoquinone (= 2-methoxy-3,6-dimethyl-1,4-benzoquinone) (19); 1,4-naphthoquinone (20).

Both quinones and non-quinones have been detected in the defensive fluids of 22 species from 13 genera belonging to the order Spirobolida (Table 3.2). In these species, the quinone fraction is generally dominant.

Beside benzoquinone, the defensive fluid of *Rhinocricus padbergi* (Table 3.2) contains an alkaloid, previously known only from glomerids and polyzoniids (Arab et al., 2003). However, according to Bodner & Raspotnig (2012) the alkaloid in *R. padbergi* according to its molecular weight and chromatographic characteristics is actually reminiscent of the common juliform 2-methoxy-3methyl-1,4-benzoquinone (this is the reason for the current exclusion of Spirobolida from the "alkaloid Diplopoda").

In the defensive fluids of most spirobolids, Attygalle et al. (1993) and Wu et al. (2007) recorded the absence of hydrocarbons or other additives that could serve as solvents of the quinones, which are in crystal form at room temperature. In *Acladocricus setigerus* the secretion remains liquid even without a solvent due to melting point depression effect which results from the presence of benzoquinones with the other components in the mixture. In this way the secretion is a more potent and repulsive especially on mucous integument of vertebrates that are predators of giant spirobolids (Wu et al., 2007).

Schmitt et al. (2004) showed that some quinones could function as kairomones of scarab beetles from West and Southern Africa and in tropical Asia. Eisner et al. (1998) described the mechanism by which the larva of the phengodid beetle *Phengodes laticollis* finds and kills millipedes of the species *Floridobolus penneri*. This predator injects its enteric fluid in the body of spirobolids without inducing the millipede to discharge the defensive secretion and subsequently feeds on the spirobolid without rupturing its repugnatory glands.

Some giant spirobolids produce a considerable amount of defensive fluids which in direct contact with human skin stains it reddish-brown and causes a slight burning sensation, occasionally followed by slight blistering and exfoliation (Buden et al., 2004).

Up to date, 25 spirostreptid species from 12 genera have been analyzed for defence compounds. As in other juliforms, the most common compounds are toloquinone and 2-methoxy-3methyl-1,4-benzoquinone, as well as 14 additional quinones (Table 3.2). Interestingly, no trace of non-quinone chemicals has ever been detected in the secretions of spirostreptids. This may be due to their complete reduction in spirostreptids secretion, but it could instead be the result of earlier incomplete identifications (especially by Smolanoff et al., 1975a) when instruments were less sensitive than today. Our preliminary results on one unidentified spirostreptids (new species, H. Enghoff, pers. comm.) indicated at least few non-quinones in the defensive fluids.

The chemical properties of millipede chemicals are occasionally exploited by other animals. Namely, capuchin monkeys intentionally anoint themselves with secrets of *Orthoporus dorsovittatus*, probably obtaining in this way protection against insects during the rainy season (Valderrama et al., 2000). Also, some other mammals and birds have been observed to use quinones of juliform millipedes for self-anointing in order to control ectoparasites pressure (Birkinshaw, 1999; Weldon et al., 2003; Zito et al., 2003).

The chemical composition of the defensive secretion — exclusively including phenolic compounds — has been documented in only five species from five genera of the order Callipodida (Table 3.3). The first attempt to investigate the defence chemistry in

TABLE 3.3
Defensive secretions in representatives of the order Callipodida

Species	*p*-Cresol	Phenol	*p*-Ethylphenol	References
Abacion magnum	+	+	−	Eisner et al., 1963b; Pavan, 1968
Delophon georgianum	+	−	−	Shear et al., 2007
Tetracion jonesi	+	−	−	Shear et al., 2010
Apfelbeckia insculpta	+	+	−	Ćurčić et al., 2009
Callipodella fasciata	+	+	+	Makarov et al., 2011

callipodids was the work of Eisner et al. (1963b) on *Abacion magnum*. In this species the secretion is discharged as discrete white droplets (similar as in *Apfelbeckia insculpta*; Fig. 3.4A), however not from all glands at once, but only from the glands of the traumatized region. The first glands to secrete defensive fluids are those of the directly stimulated pleurotergites; with persistent stimulation at the same place, the response tends to spread to adjacent pleurotergites (usually never to more than a few on either side of the stimulated place).

In callipodids *p*-cresol is the major component and only two additional minor compounds have been detected (Table 3.3). *p*-Cresol is well known as an effective repellent of insects, especially ants, but also lizards, jays and mice (Eisner et al., 1963b).

The presence of *p*-cresol in callipodidans lead Eisner et al. (1978) to name these arthropods as "cresol millipedes", but — as noted before — this molecule is not exclusive of the defensive secretion of the Callipodida.

The semiochemistry of the Polyzoniida is poorly known (Table 3.4). Polyzoniids have julid-type of defence glands, but with one possibly derivative feature: the presence of an elongated tubular, possibly glandular, vesicle on the posterior side of the reservoir (Fig. 3.6A, B). Polyzoniids have alkaloids (Table 3.4) in their ozadenes which have repellent properties for natural enemies of millipedes such as ants and other insects. Interestingly, some siphonotid polyzoniids represent a dietary source of alkaloids for dendrobatid frogs (Saporito et al., 2003). Remains that further studies confirm appearance of proteinaceous components in the secretion of some polyzoniids, as assumed by Eisner et al. (1978). Newest data on the chemical defense systems of two stemmiulids, a

TABLE 3.4
Defensive secretions in representatives of the order Polyzoniida

Species	1	2	3	4	5	6	References
Buzonium crassipes	−	−	+	+	+	−	Wood et al., 2000
Kiusiozonium okai	+	+	−	−	−	+	Kuwahara et al., 2007
Polyzonium germanicum	−	+	−	−	−	−	Smolanoff et al., 1975b; Röper, 1978
Petaserpes rosalbus	+	+	−	−	−	−	Meinwald et al., 1975; Takagi & Mori, 2000
Rhinotus purpureus	+	−	−	−	−	+	Saporito et al., 2003

Nitropolyzonamine (1), polyzonimine (2), buzonamine (3), limonene (4), β-pinene (5), spiropyrrolizidine *O*-methyloxime 236 (6).

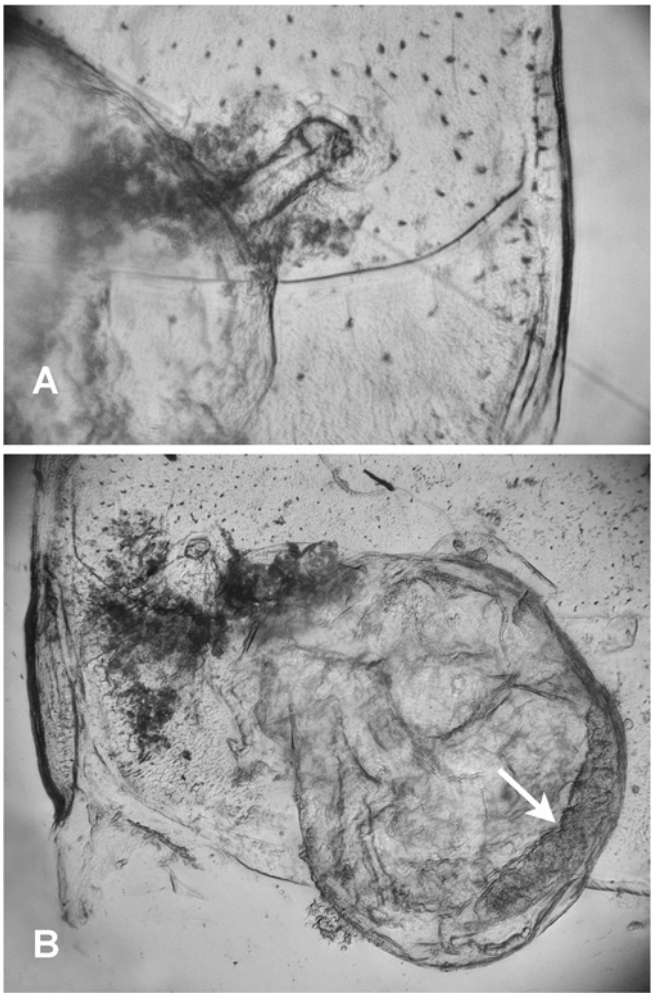

Fig. 3.6. Ozadene of *Polyzonium germanicum*. **A** Efferent duct and ozopore. **B** Vesicle; arrow denotes additional, probably glandular, vesicle.

siphonocryptid and a siphonophorid, indicate that these include *p*-cresol, spiropyrrolyidine oxime and terpenes, respectively (Shear, 2015).

Polydesmid type

The most extensive investigations on the defence secretion in Diplopoda have targeted the polydesmids. The defence secretions have been analyzed in 51 species from 36 genera, with the identification of 26 compounds (Table 3.5).

Polydesmid glands are complex and consist of the following compartments: a large inner membranous sac or reservoir (Fig. 3.7B, D), an efferent duct (Fig. 3.7B, E), a reaction chamber (vestibule) (Fig. 3.7A-C), and the ozopore (Figs. 3.5D, 3.7A). The reservoir leads

TABLE 3.5
Defensive secretions in representatives of the order Polydesmida

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	References
Amplinus bitumidus	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Bedoussac et al., 2007
Anoplodesmus saussurii[a]	+	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Bano & Krishnamoorthy, 1978
Apheloria virginiensis corrugata	+	+	+	−	−	−	+	−	−	−	−	−	−	−	−	−	−	Pavan, 1968; Conner et al., 1977; Blum, 1981
Astrodesmus laxus	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Eisner et al., 1975
Brachoria sp.	+	+	−	+	+	−	+	−	−	−	−	−	−	−	−	−	−	Duffey et al., 1977
Brachydesmus avalae	+	+	−	+	+	+	+	−	−	−	−	−	−	−	−	−	−	Makarov et al., 2010
B. dadayi	+	+	−	+	−	+	+	−	+	−	−	−	−	−	−	−	−	Makarov et al., 2010
B. troglobius	+	+	−	+	+	+	+	−	−	−	−	−	−	−	−	−	−	Makarov et al., 2012
Caraibodesmus sp.	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Blum, 1981
Chamberlinius hualienensis	+	+	−	+	+	−	+	−	−	−	−	−	−	−	−	+	−	Noguchi et al., 1997a
Cherokia georgiana	+	+	−	+	+	−	+	−	−	−	−	−	−	−	−	−	−	Duffey et al., 1977
Cleptoria rileyi	+	+	−	+	+		+	−	−	−	−	−	−	−	−	−	−	Duffey et al., 1977
Cryptocorypha sp.	+	+	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	Kuwahara et al., 2011
Epanerchodus fulvus	+	+	+	+	−	−	+	−	−	−	−	−	−	−	−	−	−	Kuwahara et al., 2011
E. japonicus	+	+	+	−	−	−	−	−	−	−	−	−	−	+	−	−	−	Mori et al., 1994
Epanerchodus sp.	+	+	−	+	−	−	+	−	−	−	−	−	−	−	−	−	−	Kuwahara et al., 2011
Euryurus leachii	+	+	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	Hall et al., 1969; Duffield et al., 1974
E. maculatus	+	+	−	+	−	−	−	−	−	−	+	−	−	+	−	−	−	Duffey et al., 1977
Eutrichodesmus armatus	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	Kuwahara et al., 2003
E. elegans	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	Kuwahara et al., 2002b

TABLE 3.5
(Continued)

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	References
Haplogomphodesmus pavani	+	+	+	+	+	−	−	−	−	−	−	−	−	−	−	−	−	Barbetta et al., 1966; Pavan, 1968; Blum, 1981
Harpaphe haydeniana	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Davenport et al., 1952; Blum, 1981
Kepolydesmus anderisus	+	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Shear et al., 2007
Leonardesmus injucundus	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	Shear et al., 2007
Motyxia sequoiae	+	+	−	+	+	−	+	−	−	−	−	−	−	−	−	−	−	Davenport et al., 1952; Blum, 1981
M. tiemanni	+	+	−	+	+	−	+	−	−	−	−	−	−	−	−	−	−	Duffey et al., 1977
M. tularea	+	+	−	+	−	−	+	−	−	−	−	−	−	−	−	−	−	Duffey et al., 1977
Nearctodesmus cerasinus	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Blum, 1981
N. salix[b]	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Wood & Sorensen, 2005
Nedyopus tambanus	+	+	+	+	−	−	+	−	−	−	−	−	−	−	−	−	−	Kuwahara et al., 2011
N. patrioticus	+	+	−	−	−	−	−	−	−	−	−	−	−	+	+	−	−	Noguchi et al., 1997b
Niponia nodulosa	−	−	−	−	−	−	−	−	−	−	−	+	+	−	−	−	−	Ômura et al., 2002a
Orthomorpha coarctata	+	+	−	−	+	−	−	−	−	−	+	−	−	+	−	−	−	Monteiro, 1961; Pavan, 1968; Blum, 1981
Oxidus gracilis[c]	+	+	+	+	+	−	−	−	−	−	+	−	−	+	+	+	−	Duffey et al., 1977; Taira et al., 2003; Kuwahara et al., 2011
Pachydesmus crassicutis	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Blum & Woodring, 1962; Blum, 1981
Parafontaria laminata	+	+	−	+	+	−	+	−	−	−	−	−	−	−	−	−	−	Mori et al., 1995
P. tonominea	+	+	+	+	−	−	+	−	−	−	−	−	−	−		−	−	Ômura et al., 2002b

TABLE 3.5
(Continued)

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	References
Pleuroloma flavipes	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Hall et al., 1969; Blum, 1981
Polydesmus collaris collaris[d]	+	+	−	+	+	−	−	−	−	−	−	−	−	−	−	−	−	Casnati et al., 1963; Blum, 1981
P. complanatus	+	+	+	+	−	−	+	+	+	−	−	−	−	−	−	−	−	Makarov et al., 2010
Pseudopolydesmus canadensis	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Blum, 1981
P. erasus	+	+	−	+	−	−	−	−	−	−	+	−	−	+	−	−	−	Duffey et al., 1977
P. serratus[e]	+	+	+	+	+	−	+	−	−	−	−	−	−	−	−	−	−	Conner et al., 1977; Blum, 1981
Rhysodesmus vicinus	+	−	+	−	−	−	−	−	−	+	−	−	−	−	−	−	−	Casnati et al., 1963; Pavan, 1968; Blum, 1981
Riukiaria semicircularis	+	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Ômura et al., 2002b
Rudiloria kleinpeteri	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	Blum, 1981
R. trimaculata	+	+	+	−	−	−	+	−	−	−	−	−	−	−	−	−	−	Blum, 1981
Sigmoria nantahalae	+	+	−	−	+	−	+	−	−	−	−	−	−	−	−	−	−	Duffey et al., 1977
Sigmoria sp.	+	+	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	Duffey et al., 1977
Stelgipus agrestis	+	+	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	Duffey et al., 1977
Xystocheir sp.	+	+	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	Duffey et al., 1977

HCN (1); benzaldehyde (2); mandelonitrile (3); mandelonitrile benzoate (4); benzoic acid (5); phenylmethanol (= benzyl alcohol) (6); benzoyl nitrile (= benzoyl cyanide) (7); benzyl methyl ketone (= phenylacetone) (8); benzyl ethyl ketone (9); cuminaldehyde (10); guaiacol (11); 1-octen-3-ol (12); geosmin (13); phenol (14); *p*-cresol (15); methyl benzoate (16); (1Z)- and (1E)-2-nitroethenylbenzenes (17).

[a] Also cyanogenic glucoside, β-glucosidase, mandelonitril lyase, and proteins (Bano & Krishnamoorthy, 1978).

[b] Also 2-methylbutanoic and 3-methylbutanoic acid (= isovaleric acid) (Wood & Sorensen, 2005).

[c] Also creosol (= 2-methoxy-4-methyl phenol) and benzaldehyde dimethyl acetal (Taira et al., 2003).

[d] Also formic acid, acetic acid, and isovaleric acid (Casnati et al., 1963).

[e] Also myristic, stearic, and isovaleric acid (Blum, 1981).

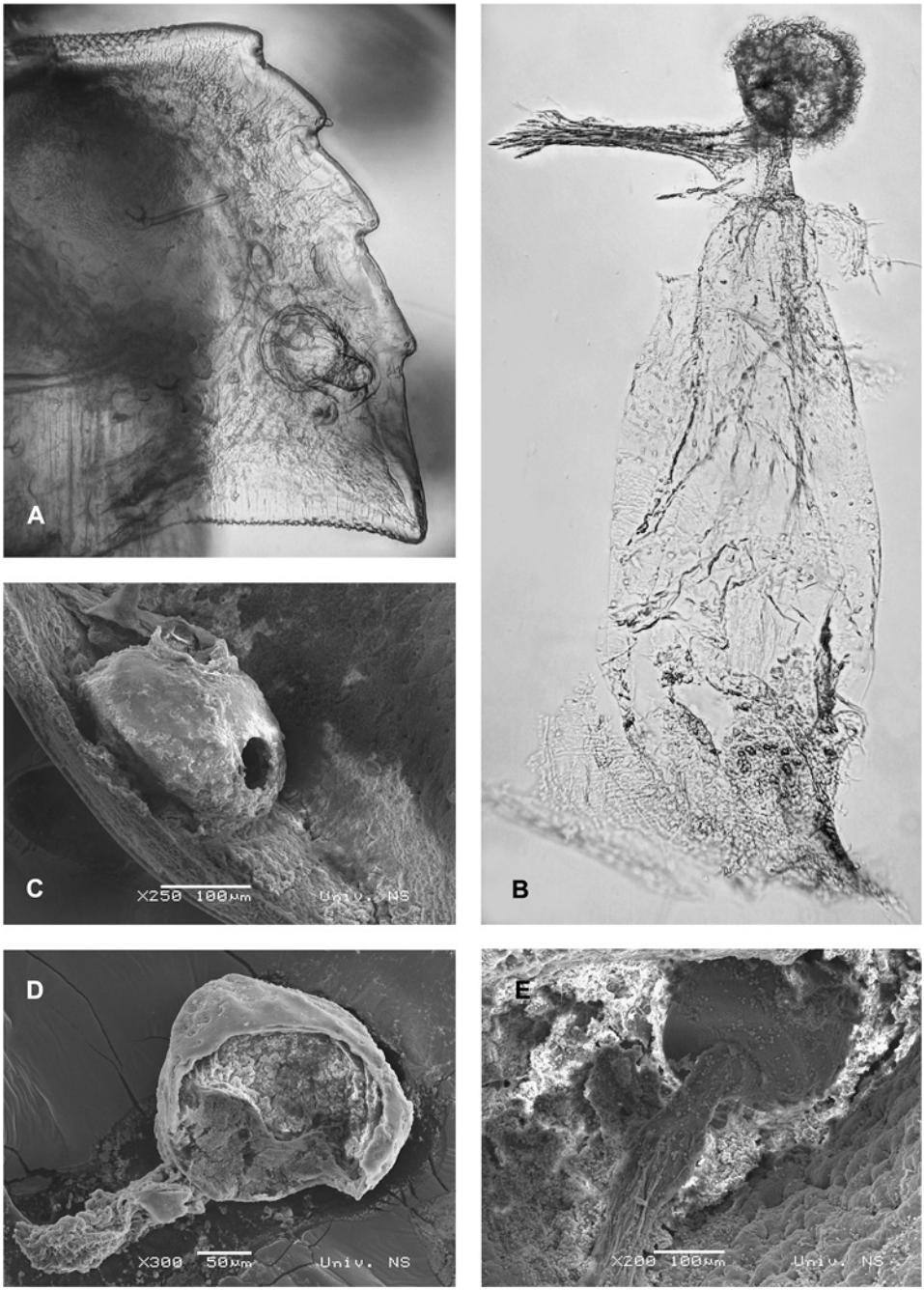

Fig. 3.7. Ozadenes in the Polydesmida. **A** *Brachydesmus mulaomerovici*, paranotum with ozadene, dorsal view. **B** *Polydesmus complanatus*, isolated ozadene. **C** *P. collaris*, reaction chamber, SEM. **D** *P. collaris*, vesicle and efferent duct, SEM. **E** *P. collaris*, terminal portion of efferent duct and reaction chamber, SEM.

into the vestibule by way of a narrow duct, the terminal portion of which is tightly occluded by a spring-like valvular infolding of the duct wall (Eisner et al., 1963a). Muscles serve to open the valve and transfer compounds into the reaction chamber (Fig. 3.7B). However, Woodring & Blum (1963) described tongue-like structure at terminal portion of the duct in *Pachydesmus crassicutis*, closing the reservoir. The ozopores are located on a number of trunk rings starting from the 5th and extending through to the 19th. The most common segmental distribution is 5, 7, 9, 10, 12, 13, 15, 16, 17, 18, 19, but a variety of other combinations occur (it is pertinent to note that some Sphaeriodesmidae have no ozopores). Ozopores usually open at the body surface level, but in some polydesmids they open on short columns termed *porosteles*.

HCN is a characteristic defensive product in most of the polydesmids. It is derived from mandelonitrile or, in some taxa, from p-isopropylmandelonitrile. According to Duffey et al. (1974) phenylalanine is a common precursor in the production of mandelonitrile. Lyase-catalyzed dissociation of the labile mandelonitrile produces hydrogen cyanide and benzaldehyde.

Duffey (1981) also found that *Harpaphe haydeniana* stores mandelonitrile in oily droplets in the reservoir. When the millipede is alarmed, hydrostatic pressure increases in its haemolymph causes the squeezing of mandelonitrile out of the storage chambers through a reaction chamber, where it is mixed with degrading enzymes, to the exterior. Degrading enzymes are stored separately from the cyanogenic precursor in the reaction chamber. Enzyme and substrate are mixed only after stimulation of the millipede, which results in the production of benzaldehyde and HCN (Blum, 1981). However, Kuwahara et al. (2011) have found that Schotten-Baumann reaction represents a new mechanism of hydrogen cyanide release. Here, a reaction of benzoyl cyanide and mandelonitrile under alkaline body fluid conditions results in the formation of HCN and mandelonitrile benzoate. This mechanism might be a more advanced and evolved chemical defence than the natural or lyase-catalyzed dissociation of labile mandelonitrile to HCN and benzaldehyde.

Blum (1981) noted that the cyanogenic glands of *H. haydeniana* contain both β-glucosidase and α-hydroxynitrile lyase activity and also contain β-cyanoalanine synthase and rhodanese for detoxification of the cyanogenic glucosides (CNglc) degradation products. Interestingly, both *H. haydeniana* and *Oxidus gracilis* possess biochemical pathways for CNglc biosynthesis that involve similar or identical intermediates to those known from vascular plants (N-hydroxy aminic acids, oximes, nitriles) (Duffey, 1981). Duffey et al. (1974) showed that *H. haydeniana* detoxifies some of its cyanide by first converting it to β-cyanoalanine which is then transformed to asparagine. Apart from both β-cyanoalanine and asparagine, the secretion of *O. gracilis* contains rhodanese which transforms HCN into the harmless thiocyanate ion. In the same species, phenol can be rapidly converted to tyrosine by tyrosine phenol lyase. Also, phenol is detoxified by being converted to phenyl glycoside and small amounts of arbutin (Blum, 1981).

The major defensive secretion of polydesmids is often accompanied by minor compounds (Table 3.5). Some polydesmids produce phenol and guaiacol in their cyanogenic reaction chambers which are deterrents, and phenol is also a common bacteriostatic agent.

The two phenolics may prevent the growth of soil bacteria that could penetrate the reaction chamber which opens directly to the exterior. Volatiles such as phenol and guaiacol could provide a slight effusion pressure sufficient enough to restrict the entry of free-floating fungal spores. Furthermore, the presence of these minor components may represent the first step in warning predators. The roles of esters (mandelonitrile benzoate) are various: repellents or toxicants, wetting agents, facilitators of penetration through the cuticle, or precursors of highly reactive final compounds (Blum, 1981). Roncadori et al. (1985) showed that mixture of the four defensive compounds detected in two xystodesmids (benzaldehyde, benzoic acid, benzoyl nitrile, and mandelonitrile benzoate) suppressed spore germination more effectively than the individual compounds and appeared to function synergistically.

Recent reports have shown that the cyanogenic apparatus is not universal in the order Polydesmida. In defensive secretion of *Niponia nodulosa* Ômura et al. (2002a) registered only the presence of two noncyanide compounds, 1-octen-3-ol and geosmin. They speculate on two possible roles for this secretion — as defensive allomones and as chemical messenger in intraspecific communication (pheromone). Non-cyanogenic polydesmids are also *Eutrichodesmus elegans* (Kuwahara et al., 2002b), *E. armatus* (Kuwahara et al., 2003) and *Leonardesmus injucundus* (Shear et al., 2007). This has been tentatively explained by Shear et al. (2007) as an adaptive response to local conditions: *L. injucundus* inhabits deep litter and soil layers and does not exhibit aposematic coloration in comparison to species appearing at the surface with red, yellowish, orange, even violet or blue coloration.

According to Bedoussac et al. (2007), the benzaldehyde produced by the polydesmid *Amplinus bitumidus* could function as kairomone for the dung beetle *Canthon morsei*.

The synthesis of defensive products in polydesmids is very slow. *Apheloria virginiensis corrugata* is able to produce and discharge less than 10% of its initial capacity about one week after its cyanogenic glands had been depleted (Blum, 1981).

Intrageneric and interspecific differences in the chemical composition of the defensive secretion exist in some polydesmids (Makarov et al., 2010, 2012) and may serve as chemotaxonomical criteria.

BIOLUMINESCENCE

Luminous species have been recorded from only three genera, *Motyxia* (from Western North America), *Paraspirobolus* (Chuuk Island, Taiwan, and Okinawa), and *Salpidobolus* (New Caledonia) (Rosenberg & Meyer-Rochow, 2009).

Early reports of bioluminescence in millipedes have been reviewed by Hopkin & Read (1992). There are few new reports with additional information of mechanisms and the possible adaptive significance of this phenomenon in millipedes.

The best known and most intensively analyzed luminous form is *Motyxia sequoiae*. This millipede produces a greenish-blue light at a wavelength of 495 nm that gradually intensifies when the animal is disturbed. Emission depends on the interaction of four components: a photoprotein, magnesium ions, molecular oxygen, and ATP (Kuse et al.,

2001). The photoprotein emits light in proportion to its amount, but the luminescence reaction does not require a luciferase (Oba et al., 2011). The photoprotein in this species has a porphyrin chromophore which is responsible for light emission. The fluorescent compounds of *M. sequoiae* were identified as 7,8-dehydropterin-6-carboxylic acid, and pterin-6-carboxylic acid (Kuse et al., 2001). Kuse et al. (2010) also isolated pterin-6-carboxylic acid from the cuticle of *Parafontaria laminata armigera*, but this species does not produce bioluminescence in the dark.

There are speculations and hypotheses on the importance of bioluminescence in millipedes. Marek et al. (2011) demonstrated experimentally that in *M. sequoiae* the luminescence has aposematic function in deterring predators. The mechanisms of biolumeniscence in other millipedes has not been studied to date.

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CHAPTER 4

DIPLOPODA — SKELETOMUSCULAR SYSTEM AND LOCOMOTION

BY

MARKUS KOCH

Comparative accounts on the skeletomuscular system of millipedes are mainly limited to the classic studies by Silvestri (1903), Manton (1954, 1956, 1958, 1961; summarized in 1977), and Demange (1967). These revealed remarkable variation and a complexity that contributes to severe difficulties in providing proper descriptions (Demange, 1967: 17); authors have been reluctant to infer muscular homologies, which accordingly remain ambiguous. An explicit approach towards a robust system of muscular homology by Wilson (2002) was based on a study of a spirostreptid species. This approach has not since been continued, although a broader taxonomic survey has recently been announced based on studies employing micro-tomography to facilitate comprehension and comparisons with three-dimensional reconstructions (Blanke & Wesener, 2014). With respect to these forthcoming studies, only a short survey is provided here that summarizes basic insights related to locomotion (for details on head anatomy see Chapter 2).

MUSCLE TOPOGRAPHY

The skeletomuscular system of the trunk shows a serial repetition of longitudinal muscles (usually partitioned into dorsal, lateral, and ventral sections), deep and superficial oblique muscles, single strands of dorso-ventral and/or latero-ventral muscles, and extrinsic leg muscles. Endoskeletal support for these muscles is mainly provided by cuticular (prozonital) phragmata and the tracheal pouches and their apodemes, respectively. Remnants of a formerly (inter-) segmental collagenous endoskeleton (see, e.g., Shultz, 2007) are retained in Polyxenida (ventral intersegmental trunk tendons of Boudreaux, 1979a) but are considered to be entirely reduced in Chilognatha (e.g. Enghoff, 1984; Blanke & Wesener, 2014). Manton's (1956) descriptions of these remnants in *Polyxenus*, however, remain dubious as she could not properly distinguish them from chitinous (i.e., cuticular) formations. Her descriptions caused Boudreaux (1979b) to consider chitinous rods to be

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embedded into the ventral collagenous tendons, with a unique position of the latter below the ventral nerve cord (versus above the nerve cord in all other arthropods retaining segmental collagenous tendons). This view, as well as the nature of Manton's "V-shaped bars" not considered by Boudreaux, still requires a more thorough re-consideration.

Variation in the complexity of the muscular system as well as variation in the capability of dorso-ventral flexure of the body correlates with the degree of fusion of the exoskeletal components (Manton, 1954). The musculature accordingly is more complex in non-ring-forming millipedes than in the 'ring-formers' (i.e., Polydesmida and Juliformia), and among the ring-formers is more complex in thoracic haplorings than in diplorings (for details on the exoskeleton see Chapter 2). Complexity particularly concerns the ventral musculature; lateral and dorsal longitudinal and oblique muscles form an almost compact subepidermal layer composed of thick, broad packages (most Helminthomorpha) or single strands in a lattice-like arrangement (e.g., Polyxenida, Oniscomorpha). A characteristic part of the diplopodan muscular pattern is the absence of tergo-coxal muscles, i.e. extrinsic leg muscles arising from the tergites and inserting on the coxa of the walking legs. Their loss has thus far been considered an apomorphy of Chilognatha (Boudreaux, 1979b; Enghoff, 1984: "several muscles lost"; Blanke & Wesener, 2014: "certain muscles [absent]") because of their alleged presence in Polyxenida. The recent interpretation of the polyxenidan coxa as a subcoxal element (*eupleurite* of Bäcker et al., 2008; see Chapter 2) instead favours the view that tergo-coxal muscles are absent in all millipedes. This view is supported by the immobility of the podomere traditionally regarded as the coxa of the walking legs in Polyxenida (Manton, 1956), the leg-base being moved by extrinisic muscles inserting on the prefemur (the "true" coxa of the polyxenidan legs sensu Bäcker et al., 2008). The dorso-ventral muscles deemed to be lost in Chilognatha insert on remnants of transverse collaganeous tendons as well as on the eupleurites (stigmatic plates of Wesener et al., 2014). The apparent absence of these muscles in Helminthomorpha is likely correlated with the fusion of the stigmatic plates with the sternites and the loss of the ventral collagenous tendons. Whether all of these muscles are also absent in the Pentazonia, in which the stigmatic plates remain distinct from the sternites (as far as they are present; see Wesener et al., 2014), requires reconsideration.

The walking legs are equipped with a low number of extrinsic muscles (usually 2-4) effecting their forward and backward swing during walking. In chilognathans these muscles mainly arise from the ipsilateral tracheal pouches and their apodemes, respectively. Presence of chiasmatic coxal muscles (*Kreuzungsmuskeln* of Attems, 1926) arising from contralateral tracheal pouches are considered an apomorphy of Nematophora (e.g., Blanke & Wesener, 2014). This view, however, conflicts with the relatively widespread occurence of chiasmatic extrinsic leg muscles in other millipedes (including Polyxenida, Manton, 1956: 165; for Polydesmida see Manton, 1954, her Fig. 3f; in Juliformia apparently restricted to thoracic legs, see, e.g., Wilson, 2002, her Fig. 10 for Spirostreptida), the homology of which still remains unclear. Intrinsic muscles are considered to show a common plan in millipedes (Manton, 1958), the number and complexity of which, however, varies in correlation with leg size (the smaller the leg, the fewer the number of muscle bundles and the less the extension of their insertions). Leg muscles are considered simplest in Juliformia,

while showing greatest divergence from the common plan in Nematophora and Polyxenida (Manton, 1958: 531), i.e. in species capable of fast-running, in which additional intrinsic muscles occur. The distal claws can be bent considerably against the tarsus; their bending is effected by flexor muscles that in all millipedes pull on an elongate cuticular tendon extending from the base of the claw through the tarsus towards the tibia. As in all myriapods, the legs lack an extensor or levator muscle for moving the claw antagonistically (e.g., Snodgrass, 1952: 208).

ULTRASTRUCTURE OF MUSCLE FIBRES

Studies on the ultrastructure of skeletal muscles in millipedes focused on various *Glomeris* species (Glomerida), *Julus terrestris* (Julida), and *Orthoporus ornatus* (Spirostreptida). Dorsal and ventral longitudinal trunk muscles in these species largely correspond in their ultrastructure to tonic skeletal muscles in other arthropods, particularly centipedes (Chilopoda), but show a remarkably low number of mitochondria (Saita, 1970). The myofilaments may or may not be arranged in a regular hexagonal pattern, in either instance typically with a myosin to actin filament ratio of 1:6. The density of actin filaments becomes strikingly high in contracted sarcomeres; in relaxed states about 10-12 actin filaments surround each myosin filament in the A-Band. Sarcomere length varies conspicuously but at no contractile stage does it become shorter than the length of the myosin filaments, the Z-Band being continuous at all physiological conditions (Camatini et al., 1979).

Lateroventral oblique muscles responsible for spiralling or enrolling of the body instead are able to supercontract (Camatini et al., 1979; Candia Carnevali & Valvassori, 1982). Their fibres are characterized by perforated Z-discs that allow the myofilaments to pass through the perforations during contraction. Myofilament arrangements in these muscles are similar to those of tonic muscles (Camatini et al., 1979). A different mechanism for supercontraction has been revealed for *Glomeris marginata* (Candia Carnevali & Valvassori, 1982). In this species the contractile apparatus is relatively weakly expressed in the respective muscle fibres, with a myosin to actin filament ratio of about 1:4. The Z-line is homogenous and continous in relaxed states but rarefies during contraction by dilatation of its components, thus allowing myofilaments to pass through the Z-line.

The ultrastructure of visceral muscles has been exemplified for the muscular layers surrounding the midgut and testis of *Pachyiulus oenologus* (Julida) (Camatini & Ceresa Castellani, 1978). Similarly as in *Lithobius forficatus* (Chilopoda), they differ from skeletal muscles in adopting characteristics of smooth muscles.

MECHANICS OF LOCOMOTION

The detailed analyses of millipede locomotion by Manton (summarized in 1977) revealed a wide range of locomotory habits and capabilities, among which the various

manners of burrowing and spiralling are considered the most intriguing proficiencies. The metachronal waves performed by the legs of juliformian millipedes during undisturbed walking have always attracted the greatest interest, in recent times particularly as a model for revealing basic principles in the evolution of multi-legged animals (e.g., Kuroda et al., 2014) as well as for technical applications (see, e.g., Kassim et al., 2006; Fattahi & Spinello, 2014).

Leg movements basically consist of a propulsive backstroke in contact with the ground followed by a forward stroke through the air. The speed of the animal correlates with the relative duration of backward and forward strokes, the backstroke being of significantly shorter duration in fast-runners. Contralateral legs of a pair step synchronously in chilognathan millipedes, while successive, ipsilateral legs show a variable phase difference in the corresponding movement to avoid their 'collision', which is the main reason for the impression of undulations passing along the trunk from anterior to posterior. Gaits are more powerful, the longer the backstroke lasts and the more legs are involved simultaneously in the same phase. In ring-forming millipedes the pushing force for burrowing is further enhanced by the maintenance of an almost constant body length, i.e. by avoiding body stretching during locomotion. This is achieved by the rigid exoskeleton of the diplorings in the ring-formers, the skeletomuscular anatomy of which is considered to prevent a marked trunk elongation (Wilson, 2003). Because the trunk of the ring-formers has been compared with a spinal column made of a "series of opisthocoelous vertebrae" (Manton, 1954), their locomotive mechanism has been characterized as "spinal locomotion" (Fattahi & Spinello, 2014), as opposed to so-called "concertina locomotion" that involves a significant degree of body stretching. The latter is exerted by the ring-formers to a limited degree at faster gaits (2-5% in Juliformia, almost absent in Polydesmida; Manton, 1954) or to enter very narrow crevices (Fattahi & Spinello, 2014), whereas it is typically found to higher degrees in non-ring-forming millipedes (about 10% body extension in *Glomeris*, 17% in *Polyzonium*, about 5% in *Craspedosoma*; Manton, 1954). Body stretching at faster speeds is also characteristic for the bristly millipedes (Polyxenida), the gaits of which differ, however, from those of chilognathan millipedes in that the contralateral legs step alternately (Wilson, 2003).

Anatomical parameters of the legs impacting on speed were exemplified by Manton (1958) for lysiopetaloid millipedes (Callipodida), members of a clade (Nematophora) comprising the fastest runners among millipedes. Modifications related to fast-running concern the length of the legs and their intrinsic muscles (both being far longer than in burrowers), the orientation of the axis of articulation between the leg-base (coxa) and body (horizontal in burrowers versus vertical in fast-runners), the size of the coxa (being narrowed in fast-runners), the length of the extrinsic leg muscles and of their origin from tracheal pouch apodemes (both of which are elongated in fast-runners), as well as the degree to which the legs can be bent and lifted for a forward stroke (being more obtuse in burrowers than in fast-runners).

Polyxenids are able of moving upside down on rocks or other surfaces, an ability known among chilognathans only from colobognathans (Manton, 1961: 426). While this ability

in polyxenids is mainly based on the presence of adhesive lappets on the claws (Manton, 1956), colobognathans instead show modified proximal limb muscles that allow the legs to cling the body closely to the substrate in a chiton-like manner. Modifications of the last two leg-pairs in synxenids (Polyxenida) enable them to jump (e.g., Nguyen Duy-Jacquemin, 2006); adaptations to jumping include the replacement of the claws on the 'jumping legs' by so-called palettes (see, e.g., Nguyen Duy-Jacquemin et al., 2011, their Fig. 7). Among chilognathans the ability to jump is only known from some stemmiulidans, in which the jumping mechanism seems to be derived from modification of their ability to spiral (Evans and Blower, 1973).

The mechanism for spiralling or enrolling into a ball involves a complex muscular interplay causing dorso-ventral flexure and ventral compression, details of which necessarily vary among chilognathans depending on the flexibility of their exoskeleton. Non-ring-forming millipedes show marked displacements of their 'free' ventral skeleton during spiralling, whereas juliformians among the ring-formers instead avoid ventral compression by markedly raising the ventral anterior part of the entire body rings on their tilted, immobile anterior sternites (for details, see Manton, 1977: 364). Some muscles involved in dorso-ventral flexure, particularly the deep oblique muscles, are able to supercontract and to maintain tension for a long period; whether a catch mechanism keeps the body coiled over longer times, as has been assumed for pill-millipedes (Candia Carnevali and Valvassori, 1982), still remains unclear.

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CHAPTER 5

DIPLOPODA — DIGESTIVE SYSTEM

BY

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The digestive tract of millipedes is a straight tube, differentiated into three large regions: foregut, midgut, and hindgut (Fig. 5.1). Except for the midgut, of mesodermal origin, the other two regions, of ectodermal origin, are internally lined by cuticle (Hopkin & Read, 1992). A pair of salivary glands, or a single one, runs along the foregut and is responsible for the production of a secretion that in addition to lubricating the food, may contain digestive enzymes. From the pylorus, the first portion of the hindgut, a pair of Malphighian tubules arise which play a role in the osmoregulation and excretion of nitrogen residues and inorganic material (Hopkin & Read, 1992; Fantazzini et al., 1998; Moreira-de-Sousa & Fontanetti, 2012).

Histological and, to a very limited extent, ultrastrucural studies have been performed in the last fifty years on representatives of most millipede orders, i.e. Polyxenida: *Polyxenus lagurus* (Schlüter & Seifert, 1985); Glomerida: *Glomeris marginata* (Schlüter, 1980b; Martin & Kirkham, 1989); Polydesmida: *Euryurus erythropygus* (Miley, 1930), *Oxidus gracilis* (Seifert & Rosenberg, 1977), *Polydesmus angustus* (Schlüter, 1980a, b), *Anoplodesmus tanjoricus* (Deshmukh & Deshmukh, 2011); Chordeumatida: *Mycogona germanica* (Köhler et al., 1991), *Mastigona mutabilis* (Meyer & Eisenbeis, 1985); Julida: *Ptyojulus impressus* (Hefner, 1929), *Cylindroiulus londinensis* (Hubert, 1978a, b, 1979a, b, 1981, 1988), *Tachypodoiulus niger* (Schlüter, 1980a); Spirobolida: *Narceus americanus* (Miley, 1930), *N. gordanus* and *Floridobolus penneri* (Bowen, 1968), *Rhinocricus padbergi* (Fantazzini et al., 1998, 2002; Camargo-Mathias et al., 2004, 2011; Miyoshi et al., 2005); Spirostreptida: *Plusioporus setiger*, *Urostreptus atrobrunneus* and *Orthoporus* sp. (Nunes & Crawford, 1977; Schlüter, 1979, 1982, 1983; Crawford et al., 1983; Fontanetti & Camargo-Mathias, 1997; Fontanetti et al., 2001; Miyoshi et al., 2005; Moreira-de-Sousa & Fontanetti, 2012).

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FOREGUT

The foregut runs from the mouth to the esophageal valve. Morphological descriptions of this region are available for *R. padbergi* (Fantazzini et al., 1998), *Plusioporus setiger* (Fontanetti & Camargo-Mathias, 1997), *Urostreptus atrobrunneus* (Moreira-de-Sousa & Fontanetti, 2012), *P. impressus* (Hefner, 1929), *E. erythropygus* (Miley, 1930) and *A. tanjoricus* (Deshmukh & Deshmukh, 2011).

Characteristic for this region are epidermal invaginations whose cells secrete a cuticle with many folds facing the lumen (Fig. 5.1A). The wall of this region is comprised of epithelium, basal membrane, and muscles. Salivary glands surround the entire structure (Figs. 5.1A, 5.2A).

In *R. padbergi*, the foregut is the shortest portion of the alimentary canal, representing approximately one sixth of the total length. The epithelium is formed by columnar cells with nuclei mainly in the cell's central region. A cuticular intima and a thin peritrophic membrane are observed (Fantazzini et al., 1998).

The foregut epithelium of *Anoplodesmus tanjoricus* is composed of columnar cells with oval nuclei in the basal region. In the middle region of this portion, the epithelium exhibits six plicae that occupy most of the lumen, while in the posterior region, the plicae are cranched. The basal membrane is continuous in the plicae, unlike the muscles (Deshmukh & Deshmukh, 2011). Miley (1930) observed the presence of six plicae in the posterior portion of the *E. erythropygus* foregut, while near the mouth the epithelium consisted of a thin layer of small and irregular cells.

In *P. setiger*, the foregut is also the shortest portion of the digestive tract, representing approximately 14% of the total length. Histologically, it is similar to the foregut of *R. padbergi*, but the epithelium is formed by columnar cells in the anterior portion and cuboidal cells in the posterior portion. Approaching the midgut, the cells become columnar again and in the transition region (esophageal valve), they are extremely elongated (Fontanetti & Camargo-Mathias, 1997).

The foregut epithelium of *U. atrobrunneus* (Fig. 5.2B), *P. impressus* and *P. setiger* is composed of cells of different heights depending on the region. In the former species, the cells of the anterior portion are shorter, with central nuclei, while in the middle and posterior portions the cells are taller with nuclei in the basal region. A peritrophic membrane is observed (Moreira-de-Sousa & Fontanetti, 2012). In *P. impressus*, the cells near the mouth are columnar; in the region before the esophageal valve, the cells are cuboidal, but become columnar again approaching the esophageal valve. The esophageal valve exhibits extremely elongated cells (Hefner, 1929).

The transition from the foregut to the midgut is marked by the esophageal valve and the gradual disappearance of the cuticular intima (Fig. 5.2C, D).

MIDGUT

Histologically, the midgut is composed of epithelium, basal membrane, muscle layer, hepatic cells, and an external membrane that lines these structures (Figs. 5.1B, 5.3A). The

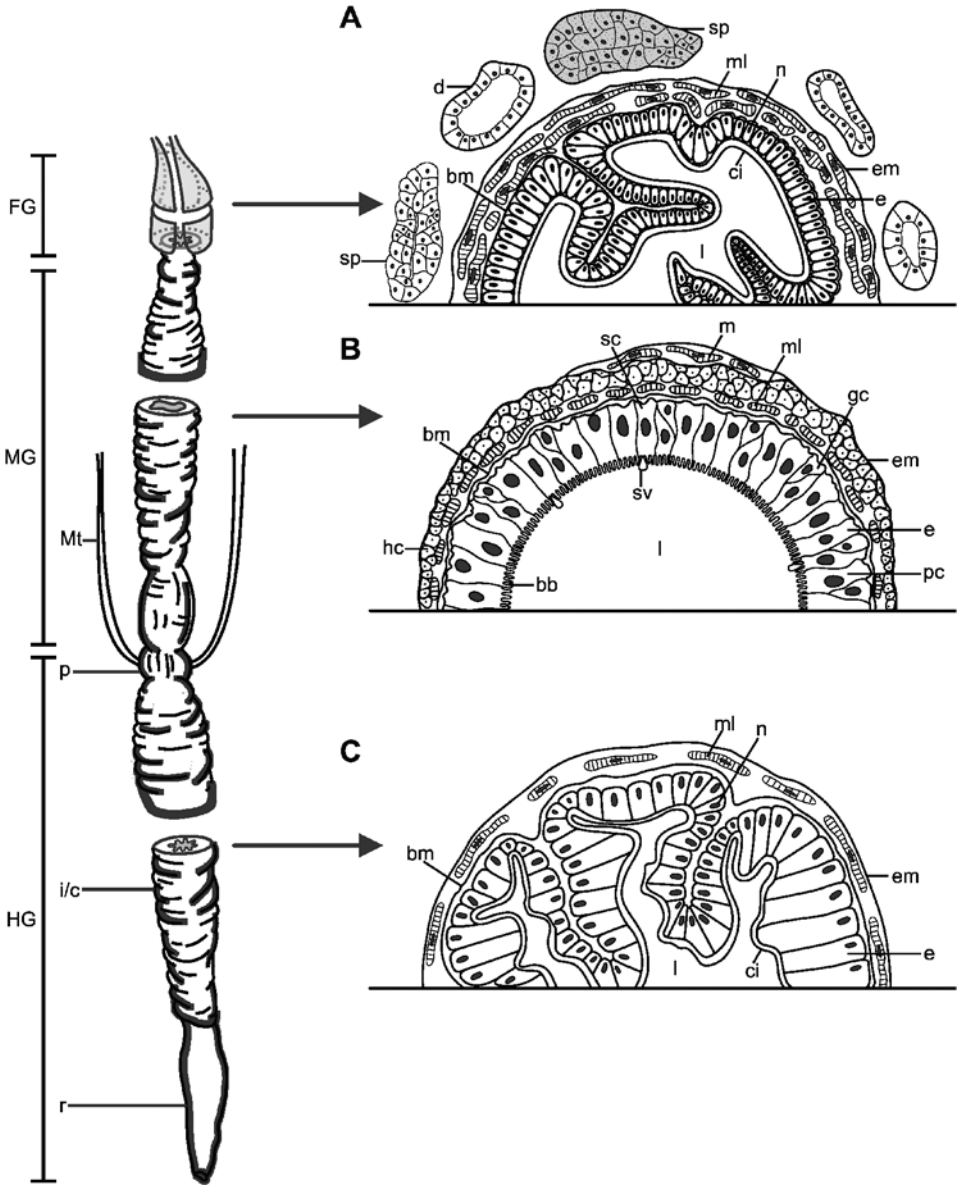

Fig. 5.1. Schematic illustration of the digestive tube and sections of the foregut (**A**), midgut (**B**) and hindgut (**C**) of millipede. Abbreviations: **bb** brush border; **bm** basal membrane; **ci** cuticular intima; **d** duct; **e** epithelium; **em** external membrane; **FG** foregut; **gc** generative cell; **hc** hepatic cell; **HG** hindgut; **i/c** ileo/colon; **l** lumen; **m** musculature; **MG** midgut; **ml** muscular layer; **Mt** Malpighian tubule; **n** nucleus; **p** pylorus; **pc** principal cell; **r** rectum; **sv** secretory vesicle; **sc** secretory cell; **sp** secretory portion.

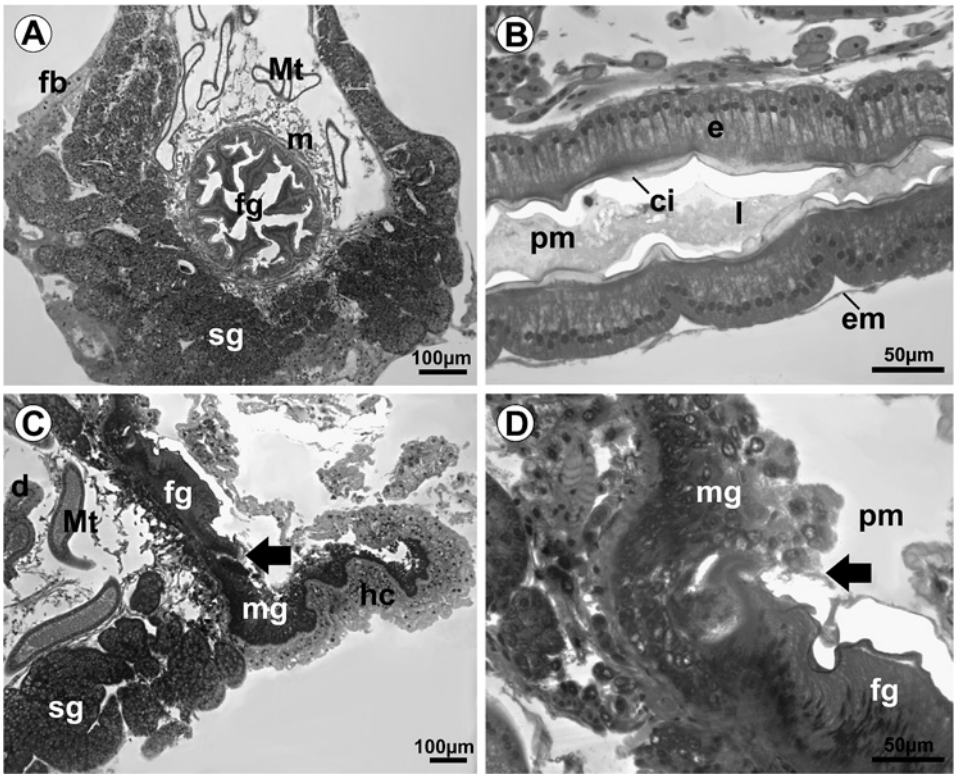

Fig. 5.2. Foregut of *Urostreptus atrobrunneus*. Histological sections stained with hematoxylin-eosin; arrows denote foregut/midgut transition. Abbreviations: **ci** cuticular intima; **d** duct; **e** epithelium; **em** external membrane; **fb** fat body; **fg** foregut; **l** lumen; **hc** hepatic cell; **m** musculature; **mg** midgut; **Mt** Malpighian tubule; **pm** peritrophic membrane; **sg** salivary gland.

midgut of millipedes produces the peritrophic membrane that lines the food in the lumen (De Mets, 1962; Hubert, 1977, 1979a, b). The peritrophic membrane of *G. marginata* was described in detail by Martin & Kirkham (1989).

The midgut epithelium is formed by three cell types: the most abundant ones are the principal, digestive or absorptive cells; there are also smaller cells, termed generative or regenerative cells, alternating with the principal cells at the base of the epithelium; and secretory cells intercalated between principal cells (Figs. 5.3B, 5.4).

Bowen (1968) reported the presence of a pseudostratified columnar epithelium in the midgut of *F. penneri* and *N. gordanus*. In all other species examined, a simple prismatic epithelium was observed. This was confirmed by Hubert (1979b) in her ultrastructurural study of *C. londinensis*. On the other hand, in *R. padbergi* and *U. atrobrunneus*, the epithelium is classified as pseudostratified (Camargo-Mathias et al., 2004; Moreira-de-Sousa et al., unpublished data). The midgut of *Plusioporus setiger* is lined by a columnar epithelium (Fontanetti & Camargo-Mathias, 1997).

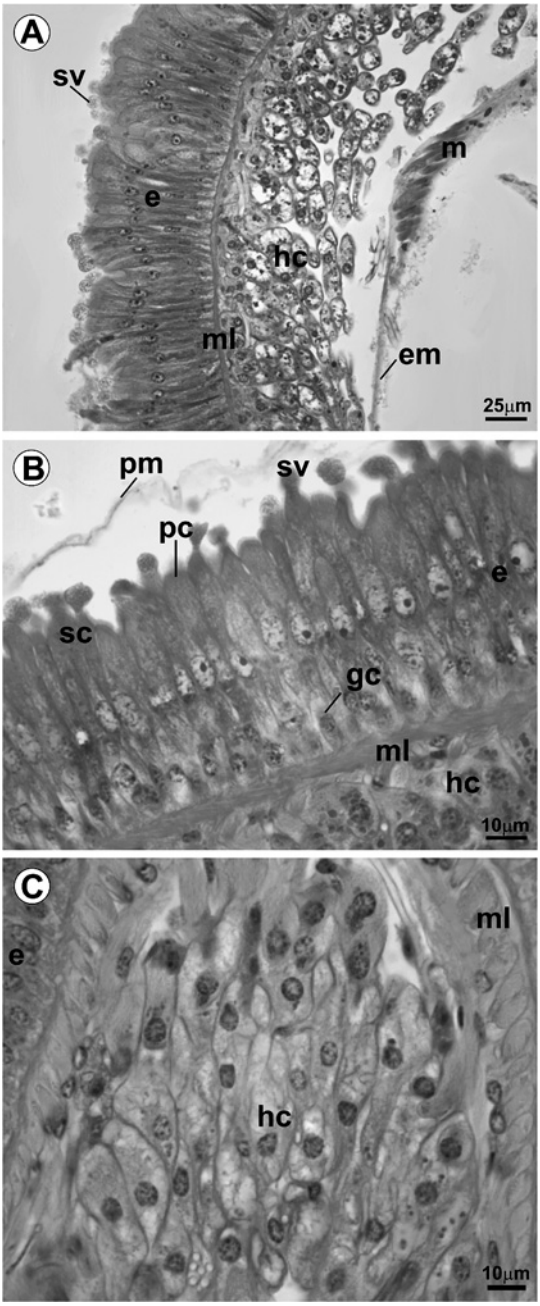

Fig. 5.3. Midgut of *Rhinocricus padbergi*. Histological sections stained with hematoxylin-eosin. **A** General view. **B** Epithelium. **C** Hepatic cells. Photo (C): Vanessa V. Merlini. Abbreviations: **e** epithelium; **em** external membrane; **gc** generative cell; **hc** hepatic cell; **m** musculature; **ml** muscular layer; **pc** principal cell; **pm** peritrophic membrane; **sc** secretory cell; **sv** secretory vesicle.

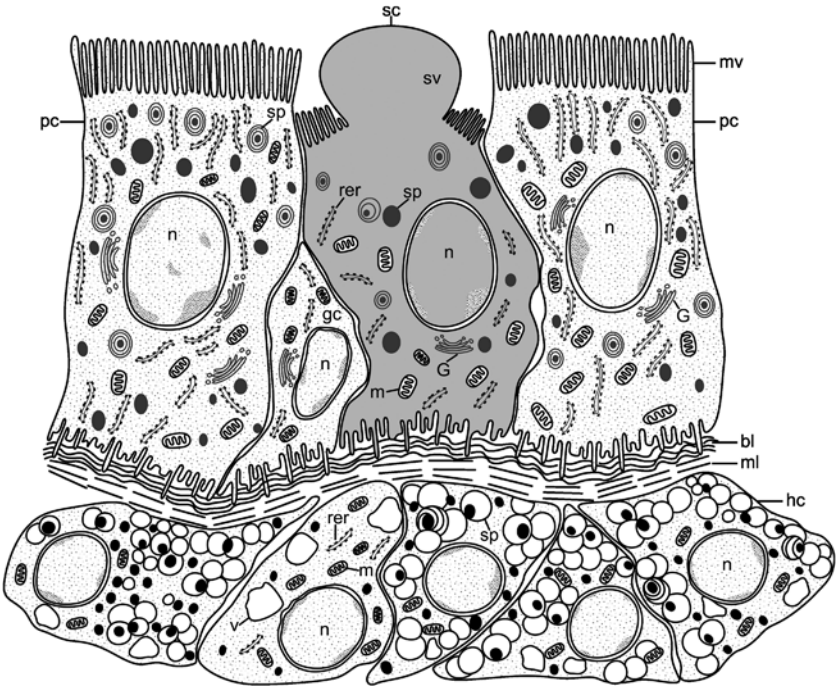

Fig. 5.4. Schematic illustration of the cell types in the midgut of millipedes. Abbreviations: **bl** basal lamina; **G** Golgi apparatus; **gc** generative cell; **hc** hepatic cell; **m** mitochondria; **ml** muscular layer; **mv** microvilli; **n** nucleus; **pc** principal cell; **rer** rough endoplasmic reticulum; **sc** secretory cell; **sp** spherocrystal; **sv** secretory vesicle; **v** vesicle.

Principal, digestive or absorptive cells

The nuclei of the principal cells (Fig. 5.4) are located in the upper half of the cell, with shapes ranging from round to oval. The apical membrane exhibits many microvilli (Fig. 5.5B), forming a distinctive brush border. The intracellular membranes are connected to the smooth septate junctions, which have a structure similar to those of other arthropods (Dallai et al., 1990).

In *R. padbergi*, the cytoplasm of these cells is rich in elongated mitochondria, most of which are located in the apical region. A large amount of rough endoplasmic reticulum (RER), Golgi apparatus, and spherocrystals are also present (Camargo-Mathias et al., 2004). Sosinka et al. (2014) suggested the name of digestive cells since these are responsible for synthesis, secretion and accumulation due to the abundance of RER and SER, and transport, because of the presence of mitochondria in the folds of the basal membrane.

The principal cells also exhibit many granules of concentric layers (spherocrystals) (Fig. 5.5C) (Hopkin & Read, 1992), which may contain calcium salts, in addition to metals such as zinc and copper (Köhler & Alberti, 1992; Köhler et al., 1995).

According to Fontanetti et al. (2006), the spherocrystals, also termed mineralized bodies, vary in structural organization between cells of the different regions of the body.

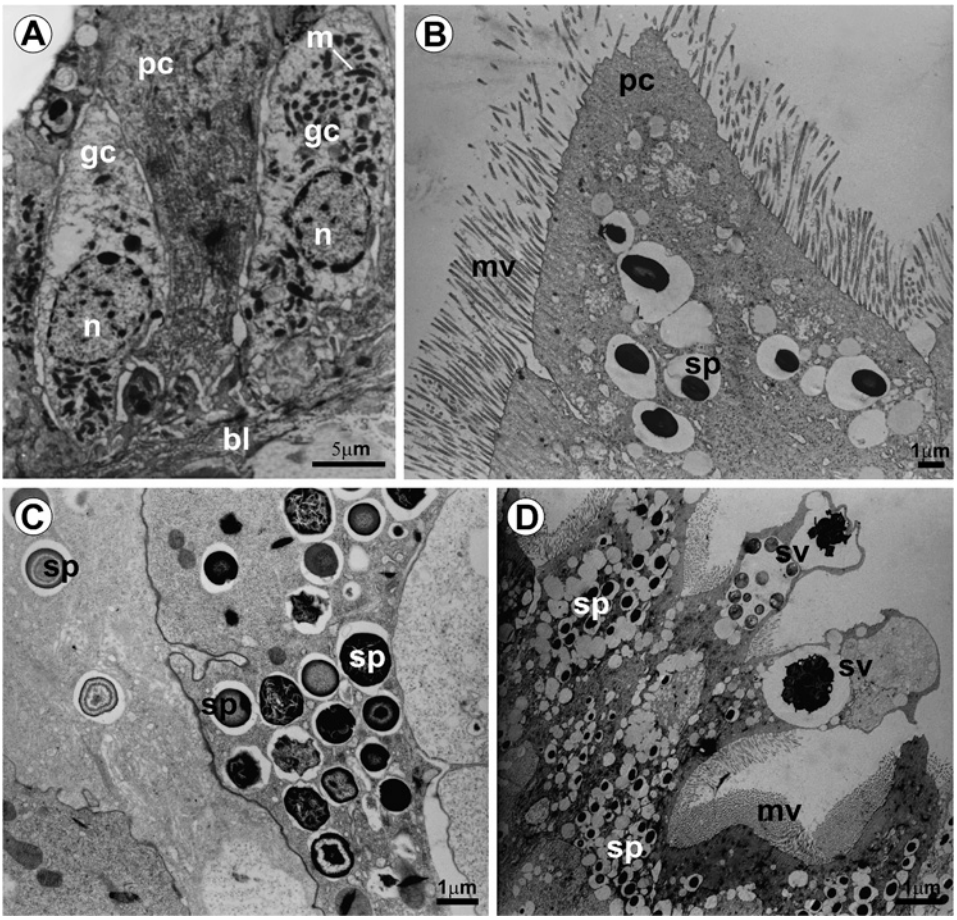

Fig. 5.5. Electron micrographs of midgut cells. **A** *Rhinocricus padbergi*. **B-D** *Urostreptus atrobrunneus*. **A** From Nogarol & Fontanetti (2011). Abbreviations: **bl** basal lamina; **gc** generative cell; **m** mitochondria; **mv** microvilli; **n** nucleus; **pc** principal cell; **sc** secretory cell; **sp** spherocrystal; **sv** secretory vesicle.

The spherocrystals found in the midgut epithelium of *R. padbergi* are enclosed by a membrane and are not associated to organelles such as the endoplasmic reticulum or the Golgi apparatus. In *U. atrobrunneus*, the spherocrystals are also enclosed by a membrane, but are in close contact with the rough endoplasmic reticulum (Moreira-de-Sousa et al., unpublished data).

The accumulation of mineral salts in spherocrystals is considered an important mechanism for the maintenance of the homeostasis in different organisms; this is arguably relevant in many physiological phenomena, especially recycling, storage and excretion of minerals (Hubert, 1979a; Locke, 1984; Fontanetti et al., 2006). According to Fantazzini et al. (2002) the presence of spherocrystals in the principal cells suggests that the epithelium might be involved in the transportation of metals. In this case, metals precipitate as

intracellular granules of different types, that are subsequently excreted by direct discharge into the intestinal lumen or by replacement of the intestinal epithelium (Hubert, 1979a; Godoy & Fontanetti, 2010; Nogarol & Fontanetti, 2010). This mechanism represents a detoxification process (Fontanetti et al., 2006).

Generative or regenerative cells

Midgut epithelial cells have a limited lifespan, due to genetic factors that determine their aging, as well as wearing due to their absorptive and secretory roles and the contact with pathogens and substances present in the foods ingested (Godoy & Fontanetti, 2010; Souza & Fontanetti, 2011). Thus, these cells are constantly being replaced by a population of generative cells, which multiply and grow into principal cells during moulting (Hopkin & Read, 1992). The generative cells are found in the basal region of the epithelium and have basal spherical nuclei (Figs. 5.4, 5.5A). These cells are considered unipotent stem cells of the millipede midgut (Sosinka et al., 2014).

Many studies that used diplopods as bioindicators in impacted soils reported the epithelium replacement as a form of detoxification, since toxic substances are eliminated along with the epithelium, which is replaced by generative cells (Godoy & Fontanetti, 2010; Nogarol & Fontanetti, 2010; Souza & Fontanetti, 2011; Bozzatto & Fontanetti, 2012; Christofoletti et al., 2012).

Secretory cells

Secretory cells (Figs. 5.4, 5.5D, 5.6A) are commonly observed in the intestine of many diplopod species (Hopkin & Read, 1992; Camargo-Mathias et al., 2004).

In diplopods exposed to contaminated soils, an increased amount of mucus was observed on the midgut epithelium, as a response to environmental pollutants (Nogarol & Fontanetti, 2010; Perez & Fontanetti, 2011; Merlini et al., 2012). Secretory cells, however, were seldom observed, in disagreement with the large amounts of glycoprotein secretion present on the epithelium. Because of the presence of large quantities of rough endoplasmic reticulum observed in the principal cells, a morphological trait in agreement with the secretory role (Junqueira & Carneiro, 2008), the secretory cells might be a functional state of the principal cells in advanced maturation stages.

In the principal cells of diplopods, several secretion vesicles in different stages of maturation are observed in the lumen near the microvilli (Fig. 5.6B, C) (Fontanetti & Camargo-Mathias, 1997), indicating that these cells may become secretory cells depending on their physiological state. Hefner (1929) concluded that for diplopods species, the type of principal cells secretion is holocrine, while in *P. impressus*, the presence of fragments of epithelial cells suggests a merocrine secretion by cell constriction. Fontanetti et al. (2001) demonstrated that in the midgut of *P. setiger*, the secretion mode is apocrine (Fig. 5.6D), as part of the cytoplasm is eliminated with the secretion. In *R. padbergi*, Fantazzini et al. (2002) observed secretion vesicles with contents in various condensation levels, suggesting a maturation or dehydration process during the transport from the cytoplasm to the lumen.

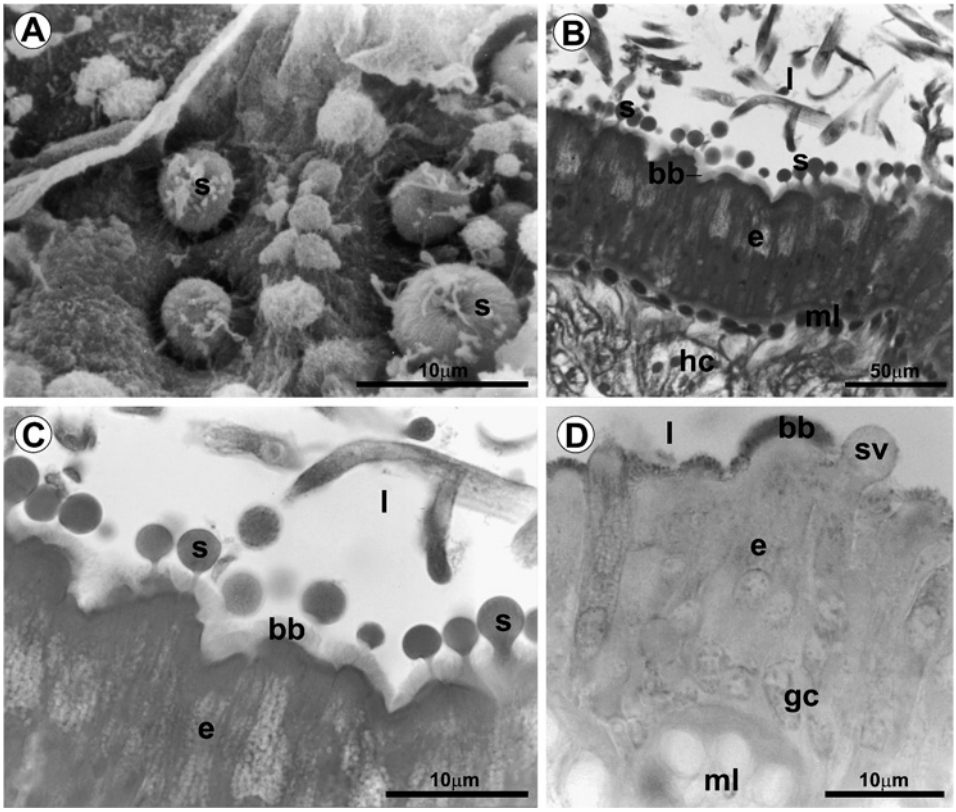

Fig. 5.6. Midgut of *Rhinocricus padbergi*. **A** Scanning electron micrograph. **B-D** Histological sections treated with xylidine ponceau (**B, C**) or PAS/Alcian blue (**D**). Abbreviations: **bb** brush border; **e** epithelium; **gc** generative cell; **hc** hepatic cell; **l** lumen; **ml** muscular layer; **sv** secretory vesicle.

According to these authors, the mode of secretion is aprocrine and the vesicles might contain different materials. In many cases the release of secretory vesicles also means a way of elimination of undesirable substances as spherocrystals (Fig. 5.5D).

Sosinka et al. (2014) first reported the release of microapocrine secretion in the millipedes *Julus scandinavius* and *Archispirostreptus gigas*. The vesicles are formed at the end of microvilli and then discharged into the lumen as double-membrane vesicles.

Hepatic cells

Beyond working as energy storage sites, the hepatic cells may also accumulate metals and other compounds as granules that are released into the hemolymph to be excreted elsewhere in the body (Hubert, 1978a, b, 1979a, b, 1988).

The hepatic cells (Figs. 5.3C, 5.4) have been confused with the fat body by Subramonian (1972), due to their similarities with the trophocytes that comprise the perivisceral fat body. Fontanetti and Camargo-Mathias (1997) and Fantazzini et al. (2002) also incor-

rectly identified them as "fat body layer of the midgut". Actually, the fat body described by Subramonian (1972) and the "fat body layer of the midgut" reported by Fontanetti & Camargo-Mathias (1997) and Fantazzini et al. (2002) are known to be a layer of hepatic cells, comparable to the hepatopancreas of other arthropods. This layer is continuous (Fig. 5.3A), but there are no junctions between the cells. These are of irregular shape; the cytoplasm is heterogeneous with small vacuoles and many mitochondria. Hemocytes and tracheoles are also observed among hepatic cells.

According to Hubert (1988), the hepatic cells exhibit a kind of communication with the principal cells that suggests an open transport between these two cell types. However, no contact between hepatic and principal cells was observed in the spirobolid *R. padbergi* or the spirostreptid *P. setiger* and *U. atrobrunneus* (Fontanetti & Camargo-Mathias, 1997; Fantazzini et al., 2002; Camargo-Mathias et al., 2004).

HINDGUT

The beginning of the hindgut is marked not only by the reappearance of the cuticular intima, but also by a tubular pylorus, to which the Malphigian tubules are inserted (Hubert, 1979a, b). In addition to the pylorus, the number of chambers in the hindgut may vary, typically ileum, colon and rectum (Dallai et al., 1990). A peritrophic membrane facing the lumen is often observed along the entire hindgut (Fig. 5.1C) (Hopkin & Read, 1992).

Spines are present in the cuticular surface of the hindgut and may play a role in filtering the digested food, in the continuous movement of food along the digestive tract, preventing reflux and retaining symbiotic organisms. Schlüter (1980a) suggested that these spines are also able to break the peritrophic membrane, allowing higher exchange of fluids and ions with the fecal matter.

These spines may present species-specific traits (Schlüter, 1980a; Elzinga, 1998). In *T. niger*, there are superficial microspines without a corresponding indentation in the epithelium (Schlüter, 1980a). In *P. angustus*, the spines are inserted into the epithelium and each one has a muscle fibre able to move it (Schlüter, 1980a). In *Orthoporus ornatus*, the hindgut cuticle is characterized by the presence of projections, each one with a central depression that can harbor bacteria (Crawford et al., 1983).

The hindgut epicuticle of *C. londinensis* exhibits small 50-100-nm perforations allowing for increased permeability (Hubert, 1981).

Pylorus

The pylorus is formed by parallel plates covered with microspines (Fig. 5.7A). The corresponding epithelium resembles a fluid-transporting epithelium and its main role is to reabsorb water from feces (Dallai et al., 1990). Under the epithelium, well-developed muscles are observed along the entire structure.

The cuticle may exhibit different denticles, acanthae, spicules, microspines or setae (Elzinga, 1998; Miyoshi et al., 2005) which may appear in different shapes, unispinose (Fig. 5.7B) and/or multispinose (Fig. 5.7C, D).

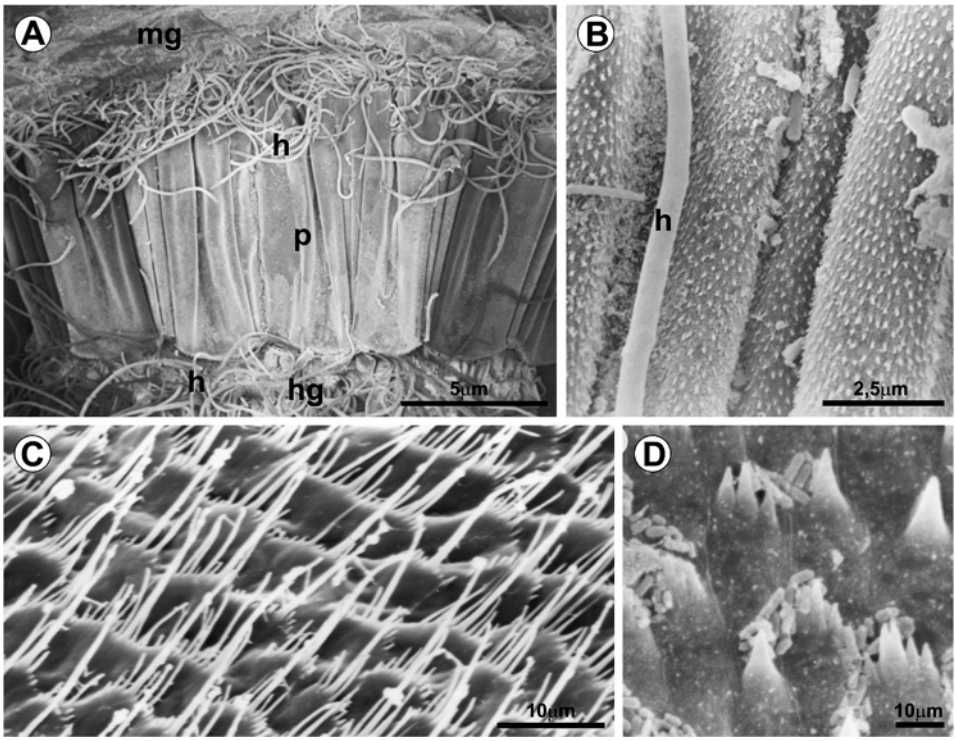

Fig. 5.7. Pylorus. **A, B, D** *Rhinocricus padbergi*. **C** *Pseudonannolene tricolor*. **A** General view. **B** Unispinose microspines. **C, D** Multispinose microspines. Scanning electron micrographs. Abbreviations: **h** hypha; **hg** hindgut; **mg** midgut; **p** pylorus.

In *U. atrobrunneus*, few large microspines are observed at the beginning of the pylorus, decreasing in size and increasing in number toward the end of the region (Moreira-de-Sousa & Fontanetti, unpublished data). In *R. padbergi*, multispinose microspines are observed at the beginning of the pylorus, which gradually decrease in number and increase in size, then arising in unispinose microspines (Fig. 5.7B). In the pylorus/ileum transition, multispinose microspine are observed again (Miyoshi et al., 2005). The microspines in the anterior portion of the pylorus of *Pseudonannolene tricolor* resemble thin setae (Fig. 5.7C) and are heterogeneous in size, density and shape (Miyoshi et al., 2005).

In the midgut/pylorus transition of *Ophyiulus pilosus*, *Cylindroiulus punctatus* (Moss & Taylor, 1996) and *R. padbergi* (Fig. 5.7A) (Miyoshi et al., 2005), clusters of filamentous structures are observed, similar to those of microbionts of the order Eccrinales (Trichomycetes).

The cuticle surface of the pylorus facing the lumen may be covered with secretion from exocrine pyloric glands.

Histologically, the pylorus is formed by a columnar epithelial cells supported by connective tissue and a well-developed musculature (Fig. 5.8A).

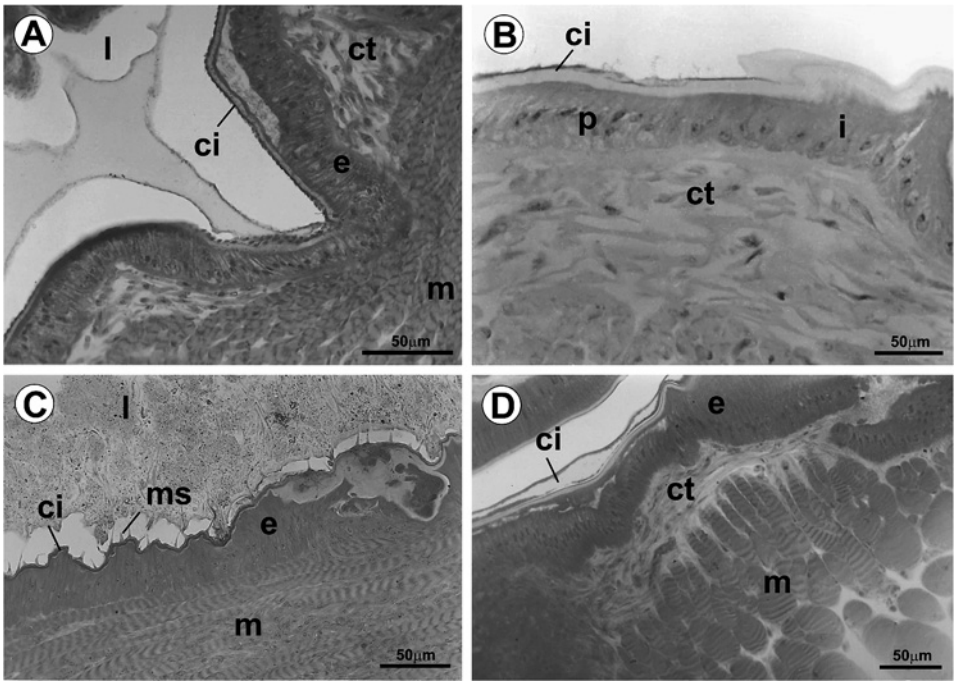

Fig. 5.8. Hindgut of *Rhinocricus padbergi*. **A** Pylorus. **B** Pylorus/ileum. **C** Colon. **D** Rectum. Histological sections stained with xylidine ponceau (**A-C**) or bromophenol blue (**D**) techniques. Abbreviations: **ci** cuticular intima; **ct** connective tissue; **e** epithelium; **i** ileum; **l** lumen; **m** musculature; **ms** microspine; **p** pylorus.

Region between pylorus and rectum

The portion of the intestine between pylorus and rectum has different characteristics in the different species and can be divided into a variable number of chambers.

In *U. atrobrunneus*, the histological composition is essentially the same despite the structural transition between the pylorus and the ileum/colon, with a single columnar epithelium and well-developed muscles. In this region, however, there is a thin layer of connective tissue below the epithelium. The epithelium is formed by shorter cells in the terminal, rectal region. The cuticular intima in this portion also exhibits microspines. Muscles are more developed near the transition of the ileum/colon region toward the rectal region, which is marked by a valve (Moreira-de-Sousa & Fontanetti, unpublished data).

In *R. padbergi*, the ileum is histologically very similar to the pylorus, except for the absence of denticles in the cuticular intima (Fig. 5.8B). The posterior portion of this region exhibits a sudden invagination, from which the colon begins, with taller epithelial cells and thicker cuticular intima provided with long denticles that become thinner toward the rectum. The colon is also characterized by the absence of connective tissue and well-developed muscles (Fig. 5.8C) (Fantazzini & Fontanetti, unpublished data).

In *P. impressus*, the hindgut is divided in six regions, not defined by the author (Hefner, 1929). Crawford et al. (1983) reported the presence of an ileum and a colon for *O. ornatus*,

with a hindgut much longer compared to other parts of the digestive tube. In *P. setiger*, the hindgut is the longer portion of the digestive tube and is not subdivided into ileum and colon; only pylorus and rectum are differentiated (Fontanetti & Camargo-Mathias, 1997).

Ano-rectal region

The ano-rectal region is where feces are formed. In *P. impressus*, the rectum is short, in the shape of a sac with thin walls that can be partially everted through the anal valves during defecation. The epithelial walls are relatively thin and the circular muscle layer consists of few fibers. The chitinous coating is thick, but apparently flexible in the lumen. In some species, such as *M. mutabilis*, the rectum can be turned outward to absorb water from moist substrates (Hefner, 1929).

In *Euryurus erythropygus*, the rectal intima exhibits folds that nearly fill the lumen of the intestine and lack microspines (Miley, 1930). Microspines are observed instead along this entire structure in *U. atrobrunneus* (Moreira-de-Sousa & Fontanetti, unpublished data). In *R. padbergi*, the rectum (Fig. 5.8D) exhibits connective tissue and a well-developed muscle layer (Fantazzini & Fontanetti, unpublished data); in *E. carolinensis*, longitudinal muscles extend until near the rectum, where only circular muscles are observed (Miley, 1930).

In *U. atrobrunneus*, the middle of the rectal portion forms a pre-anal chamber, which opens into the anal valves. This region presents many plicae, an epithelium with a thick cuticular intima and a well-developed and organized muscle layer. The histological structure of the anal region is similar to that of the rectum, with many foldings facing the lumen with an epithelium apparently formed by approximately cubical cells (Moreira-de-Sousa & Fontanetti, unpublished data).

ASSOCIATED STRUCTURES

Salivary glands

The salivary glands surround the foregut (Figs. 5.1A, 5.2A). In *R. padbergi* (Fig. 5.9) the salivary gland is a single structure (Camargo-Mathias et al., 2011), contrary to previous reports of paired structures (Fantazzini et al., 1998). The diameter of the acinous portion is smaller than the diameter of the tubular portion consisting of a pair of excretory ducts.

In *U. atrobrunneus* the salivary glands consist of a secretory portions and the excretory ducts. In the secretory portion, the cells closer to the oral cavity show strong staining, resembling an acinus in shape (Fig. 5.10A); the portion which is closest to the midgut has a tubular shape formed by less stained cells (Fig. 5.10B). The duct (Fig. 5.10A, C) also has different configurations, in some portions it is formed by cubic cells with central nuclei and in others, by taller cells with peripheral nuclei (Moreira-de-Sousa & Fontanetti, 2012).

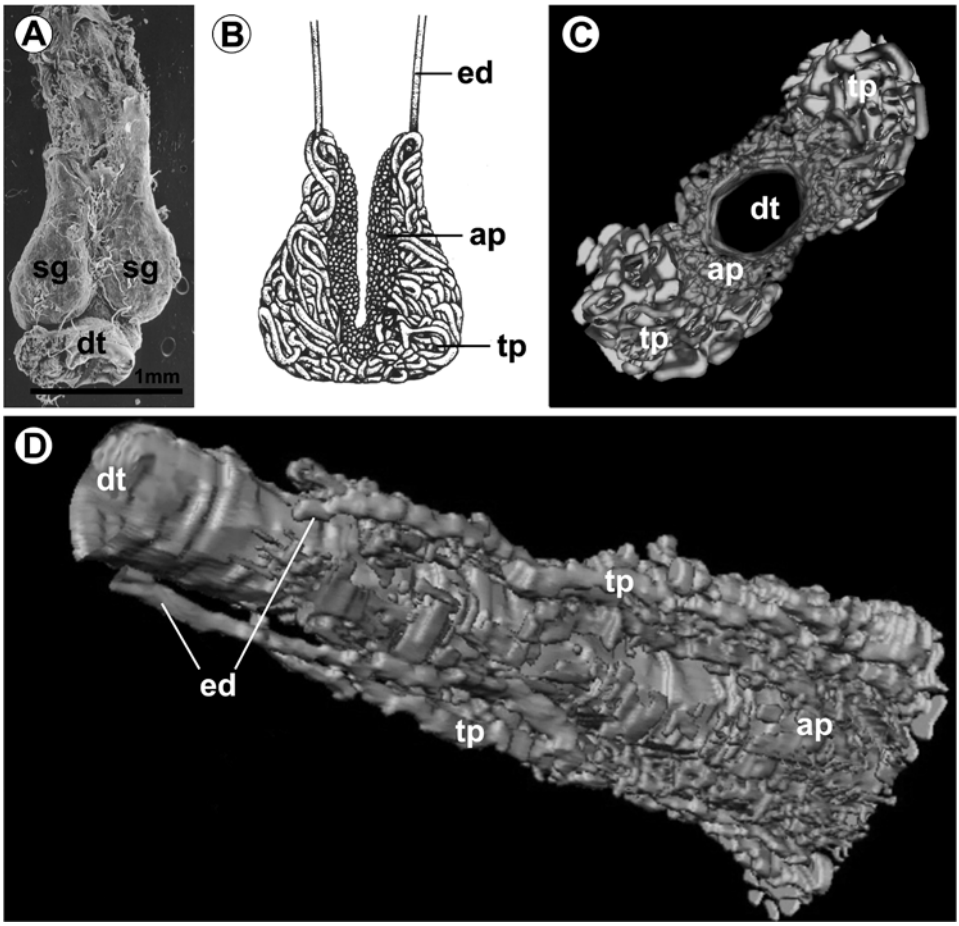

Fig. 5.9. Salivary gland of *Rhinocricus padbergi*. **A** Scanning electron micrograph. **B** General diagram. **C-D** Tridimensional reconstruction. Photos from Camargo-Mathias et al. (2011). Abbreviations: **ap** acinus portion; **dt** digestive tube; **ed** excretory duct; **sg** salivary gland; **tp** tubular portion.

Peritrophic membrane

According to Nunes & Crawford (1977), a peritrophic membrane is well defined in the digestive tube of the Diplopoda, although it has not been observed in the foregut of *P. impressus* (Hefner, 1929), *A. tanjoricus* (Deshmukh & Deshmukh, 2011), *E. erythropygus* (Miley, 1930), or in the foregut and hindgut of *O. ornatus* (Nunes & Crawford, 1977).

In *R. padbergi* (Fantazzini et al., 1998, 2002), *P. setiger* (Fontanetti & Camargo-Mathias, 1997) and *U. atrobrunneus* (Moreira-de-Sousa & Fontanetti, unpublished data) it is possible to identify an acellular peritrophic membrane along the entire alimentary canal, which envelopes the food. Basic proteins, glycoproteins, and mucopolysaccharides have been found in the peritrophic membrane in the midgut of *F. penneri* and *N. gordanus* (Bowen, 1968).

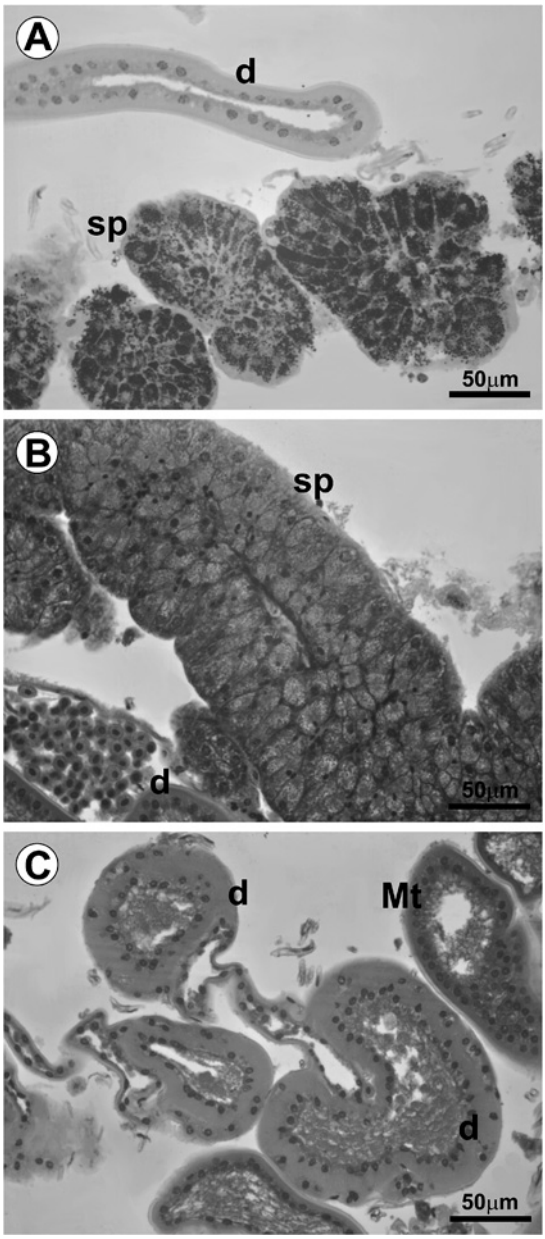

Fig. 5.10. Salivary glands of *Urostreptus atrobrunneus*. Histological sections stained with hematoxylin-eosin. Abbreviations: **d** duct; **fg** foregut; **mg** midgut; **Mt** Malpighian tubule; **sp** secretory portion.

The peritrophic membrane of *G. marginata* has been examined in detail by Martin and Kirkham (1989). A specific golden colloidal marker was developed for chitin, allowing the identification of secretion sites of the chitin and protein components of the peritrophic membrane. Chitin first appears at the base of microvilli along the entire midgut length. Protein components are incorporated to it when there is close physical association between the microvilli and the forming peritrophic membrane.

Pyloric glands

The surface of the cuticle facing the hindgut lumen may be covered by a layer of secretion from exocrine glands situated at the junction between midgut and hindgut. These glands, known as pyloric glands, secrete their products in the longitudinal crevices of the pyloric valve and have been described for a considerable number of species (Schlüter, 1979, 1980b). This secretion layer seems to influence the permeability of the hindgut and is essential for the resorption of water and other components.

In *Orthoporus* sp., secretory cells are easily identified by their insertion in the apical region to canal cells, which are responsible for forming the efferent duct. Usually, one or two secretory cells and many efferent ducts form one functional unit (Schlüter, 1979).

Anal glands

In many species, in addition to pyloric glands, anal glands are also present. In *Rhapidostreptus virgator*, Schlüter (1982, 1983) demonstrated that these glands are more developed in individuals near molting. The secretions produced by these glands are used to glue together grains of feces and soil particles during the construction of moulting chambers.

DIGESTION

In many millipedes, enzymes that participate in the digestion can break down proteins, lipids, and simple carbohydrates. These enzymes originate from salivary glands secretions and epithelial cells of the midgut, but also, according to some authors (Nunes & Crawford, 1977; Hopkin & Read, 1992) by microorganisms located and mixed with food in the gut lumen.

In addition to participating in the digestion process, the midgut acts as a barrier preventing toxic or non-essential compounds from reaching the rest of the body (Hopkin et al., 1985), and plays a role in the detoxification and excretion of xenobiotics (Hopkin et al., 1985; Köhler & Triebskorn, 1998; Souza & Fontanetti, 2011). As a result, ecotoxicological studies on the midgut have been conducted to evaluate the toxicity of soils, to detect alterations and assess the damage caused by the test compound in tissues and cells (Godoy & Fontanetti, 2010; Nogarol & Fontanetti, 2010, 2011; Perez & Fontanetti, 2011; Souza & Fontanetti, 2011; Bozzatto & Fontanetti, 2012; Fontanetti et al., 2012; Merlini et al., 2012).

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CHAPTER 6

DIPLOPODA — TRACHEAL SYSTEM

BY

GERO HILKEN, ANDY SOMBKE, CARSTEN H. G. MÜLLER
AND JÖRG ROSENBERG

It is striking that studies dealing with the structure of tracheal systems of Diplopoda are almost of very old age. Most of them go back to the 19th century and are based on light microscopic methods only. Comparative aspects are lacking in most studies, because authors deal with the tracheal system of a specific species only. Hilken (1997, 1998) was the first who investigated the tracheal systems of some diplopod species under comparative and phylogenetic aspects using light microscopy and EM-techniques (SEM, TEM). The situation is similar sparsely with regards to physiological studies.

It is obvious that 'typical' representatives of some diplopodan subtaxa have been repeatedly investigated. Thus, in Penicillata, only the tracheal systems of *Polyxenus lagurus* was investigated intensively (Bode, 1877; Verhoeff, 1896, 1928-1932; Reinicke, 1910; Hilken, 1998). In Pentazonia, only the tracheal system of *Glomeris marginata* is well described (Brandt, 1841; Voges, 1878; Verhoeff, 1895; Wernitzsch, 1910; Hilken, 1998). In his great monography Verhoeff (1928-1932) offered some data on the tracheal system of the Sphaerotheriida. The tracheal system of representatives of Colobognatha is comparatively poorly known. The best investigated species is *Polyzonium germanicum* (Latzel, 1884; Attems, 1926-1930, 1937; Verhoeff, 1928-1932: 1234; Hilken, 1998). *Craspedosoma simile* is the best investigated species of the Nematophora due to the monographic study of Wernitzsch (1910). Verhoeff (1928-1932: 1275) added some new aspects concerning networks of tracheae formed by anastomoses that surround the spinnerets of theses diplopods. The tracheal systems of representatives of the Polydesmida were investigated mainly under the aspect of taxonomy, due to the striking differences of spiracle structures (Attems, 1937; Mesibov, 2003, 2005, 2006, 2009a, b). However, the tracheal systems of several species were investigated more intensively: *Polydesmus complanatus* (Effenberger, 1907), *Coromus thomsoni* (Verhoeff, 1928-1932: 1227), *Brachydesmus superus* (Hilken, 1998), *Pachydesmus crassicutis* (Stewart & Woodring, 1973). Little is known also about the tracheal system of representatives of the Juliformia. However, the respiratory systems of some representatives of Julida were tentatively investigated, e.g. *Ommatoiulus rutilans*, *O. sabulosus*, as well as the spirostreptid *Orthoporus texicolens* (Rossi, 1901; Krug, 1906; Ziegler, 1907; Wernitzsch, 1910; Verhoeff, 1928-1932: 1200-1205; Stewart & Woodring, 1973; Hilken, 1998).

Details on respiratory metabolism and oxygen consumption in different diplopod species were investigated by a series of authors: Stewart & Woodring (1973), Penteado et al. (1991), Gromysz-Kalkowska (1970, 1974, 1976a, b, 1979, 1980), Gromysz-Kalkowska & Stojalowska (1983), Gromysz-Kalkowska & Tracz (1983), Gromysz-Kalkowska et al. (1986), Dwarakanath (1971) and

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Iatrou (1990), Stamou & Iatrou (1990), Hackstein & Stumm (1994), Schmitz & Harrison (2004), Sustr & Simek (2009). Few Diplopods are able to enter water temporarily (Enghoff, 1985; Burrows et al., 1994; Messner et al., 1996; Adis & Messner, 1997). Submersion tolerance (hours to days) or resistance (weeks to months) is enabled by a well-developed plastron respiration (Adis & Messner, 1997; Adis et al., 1998, 2003). In some large species of the Spirostreptidae, the subsequent O_2-distribution is supported by the circulatory system with help of the respiratory pigment hemocyanin in the hemolymph: this aspect was investigated by Jaenicke et al. (1999) and Kusche & Burmester (2001). Recently has it become evident that hemocyanins are more widespread than expected. Pick et al. (2014) demonstrated the existence of hemocyanin also in *Polydesmus angustus*, but also its absence in *Polyxenus lagurus*, *Cylindroiulus punctatus*, *Glomeris marginata*, *G. pustulata* and *Arthrosphaera brandtii*.

Diplopods are terrestrial arthropods. Most of them live in the upper soil layers, which are relatively poor in oxygen and often waterlogged. The exchange of oxygen and carbon dioxide between atmosphere and animals takes place via a well-developed tracheal system. The tracheal system of Diplopoda consists of spiracles, tracheal pouches with their atria, branched or unbranched tracheal stems, and tracheoles. Tracheal pouches are a characteristic feature of millipedes (and of Pauropoda, their aldelphotaxon) comprising two functions: the pouches surround spacious atria and serve additionally as apodemata (anchoring points) for the attachment of extrinsic muscles of the coxae (Wernitzsch, 1910; Blower, 1985; Kraus & Kraus, 1994; Hilken, 1998; Drago et al., 2011). The primordium 'anlage' of the tracheal system occurs late in development during the embryonic pupoid stage. However, the system is not functional until the first larval stage (Verhoeff, 1928-1932: 245). The larval stages of the representatives of Helminthomorpha are equipped with only one pair of spiracles.

The diplopod tracheal systems follows a more or less uniform segmental arrangement and is generally devoid of tracheal anastomoses (exception: Nematophora) (Verhoeff, 1928-1923: 1186). The cuticle of the ectodermal tracheal system is moulted several times (Verhoeff, 1928-1932: 2248, 1265).

SPIRACLES: GENERAL ASPECTS

The legless collum bears no spiracles (Fig. 6.4A-B). The following three segments (2-4) are single segments with only one pair of legs (Fig. 6.4A). Verhoeff (1901) and Kraus (1990) interpreted them as cryptic double-segments. However, the status of these segments is still a matter of debate. The 'basal' Penicillata and Pentazonia develop a single pair of spiracles at each of segments 2-4 (Fig. 6.4A left). Representatives of the Helminthomorpha possess no spiracles at the 1st and 2nd segment (Fig. 6.4B right; Verhoeff, 1901; Wernitzsch, 1910). From the 5th segment on, all diplopods show a sequence of regular diplosegments with two pairs of spiracles up to the last leg-bearing diplosegment. The last three (legless) segments bear again no spiracles and tracheal pouches. As spiracles appear only on leg-bearing segments, a functional relationship between tracheal systems and the organs of locomotion in Diplopoda seems to exist (see below).

The spiracles of Diplopoda are always located on the sternites, ventrally, beside the leg coxae. Recently, Wesener et al. (2014) reported about the discovery of a ventral so-

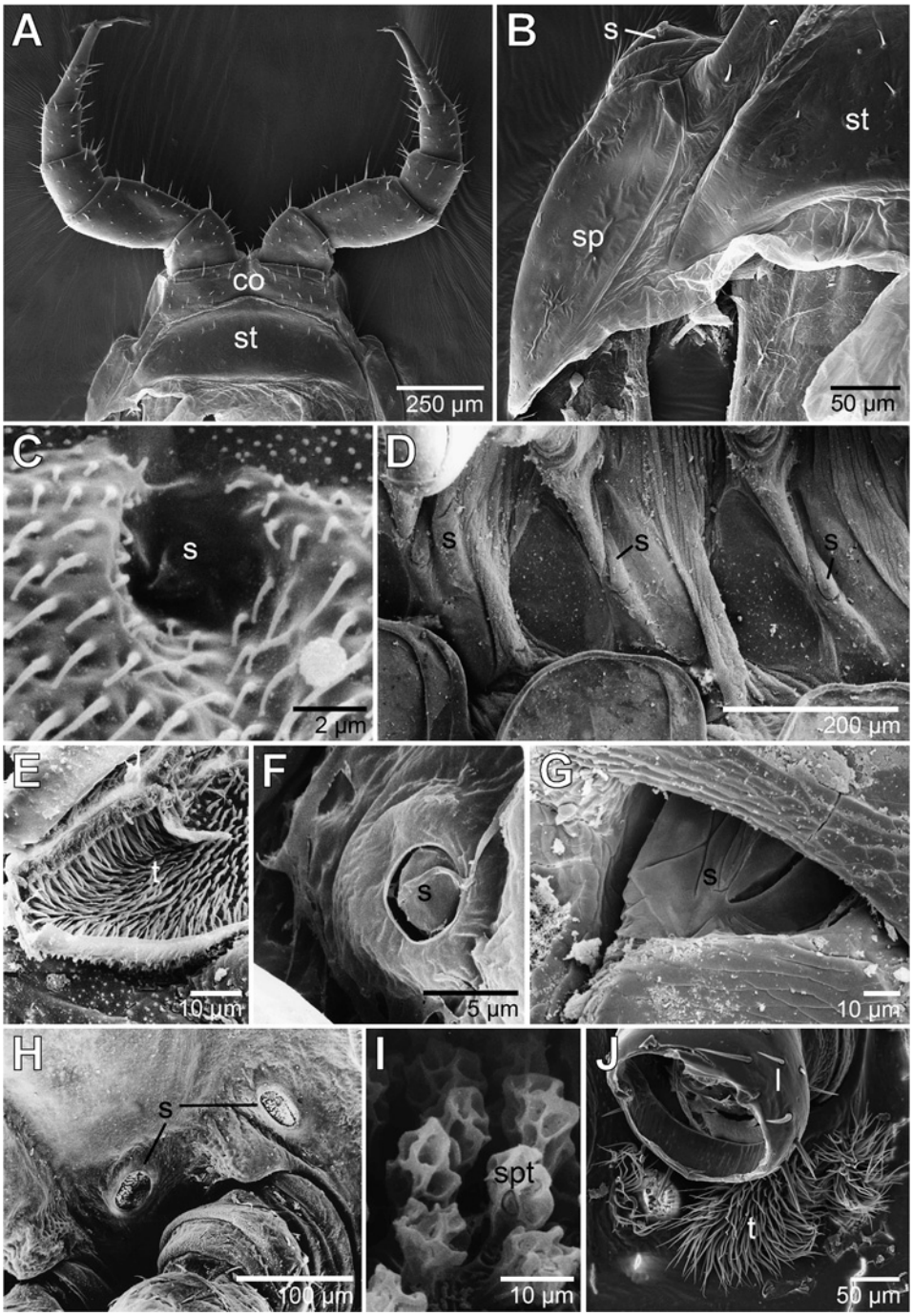
called stigmatic-plate, commonly referred as diplopod sternite (Fig. 6.1A-B). According to these authors, the lateral stigma-carrying plates of the Diplopoda are not sternal, but subcoxal elements, associated with the limb base. Therefore the formerly named sternites would better be referred to as stigma-carrying plate. However, up to now this is only described in the basal clade Glomeridesmida. Therefore, here we provisionally continue using the term sternite. Spiracles differ conspicuously with regards to shape, size, location, and the equipment with trichomes/microsetae within diplopod subtaxa and sometimes even between closely related species. In many species numerous trichomes form a fyke-apparatus (Verhoeff, 1928-1932: 1246; Stewart & Woodring, 1973; Hopkin & Read, 1992). Such apparatuses are mainly found in species with large spiracles (e.g. Polydesmida; Figs. 6.1E, H, 6.2A, C-D), whereas in species with small spiracles, trichomes are not developed (Penicillata; Fig. 6.1C). These trichomes may help protecting the tracheal system from dust, soil pollution, and/or water loss. Densely packed longish and often furcated setaceous microtrichia, described as a dense cluster of emergent hair-like structures, have been described in several Tasmanian Dalodesmidae (Fig. 6.1J; *Dasystigma bonhami*, *D. huonense*, *D. margaretae*, *D. tyleri*, *Lissodesmus anas*, *L. margaretae*, *L. modestus*, *Tasmanopeltis grandis*) and Paradoxosomatidae (*Aethalosoma solum*, *Dicranogonus* sp., *Notodesmus scotius*, *Pogonosternum* sp., *Orthomorpha coarctata*, *Akamptogonus novarae*, *Somethus mesibovi*, *S. tasmani*) (Mesibov, 2003, 2005, 2009b). The function of the hair-like structures and flooding ability of these species remain unclear.

According to Verhoeff (1928-1932: 1241-1243), the spiracles of polydesmid and spirobolid diplopods are actively closable by relaxation of so-called sphincter muscles. Verhoeff assumed active periodical releases of air via the spiracles. In contrast, Stewart & Woodring (1973) found that a spiracular closing mechanism is lacking in representatives of Polydesmidae and Spirostreptida (see below). In many cases, particular protection mechanisms seem not to be necessary, because the spiracles are often covered by sternal edges (*Ommatoiulus* sp.) or by diplosegmental overlap when coiling and close oppression of the coxae (*Orthoporus texicolens*) (Stewart & Woodring, 1973; Hilken, 1998).

Some authors described that the spiracles can be opened by the aid of a muscle, the so-called ‘Voges Muskel‘ that extends from the tracheal pouches to the coxal base of the legs (Voges, 1878; Verhoeff, 1928-1932: 1200). However, this mechanism is not likely in species with massive and sclerotized pouch walls, because they are hardly moveable (Fig. 6.3C-D, H; e.g. *Glomeris marginata*, *Brachydesmus superus*; cf. Stewart & Woodring, 1973; Hilken, 1998). However, in species with very thin-walled pouches (Fig. 6.3A, E; Penicillata, Colobognatha) this mechanism might work. In most species, these muscles function primarily in relationship with the movements of the coxae (Hilken, 1998).

TRACHEAL POUCHES: GENERAL ASPECTS

Tracheal pouches or tracheal pockets (Voges, 1878; Krug, 1906; Verhoeff, 1928-1932: 1186) are developed in all diplopods. The pouch surrounds the atrium and is thus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sometimes called the atrium wall. Voges (1878) interpreted them as metamorphic, modified tracheae, Verhoeff (1928-1932: 1252) as a kind of neoformation. According to Verhoeff (1928-1932: 1243), they function as air-collecting sacks and dust containers.

Tracheal pouches are developed from the first leg-bearing segment to the last but one. In diplosegments, generally two pairs are developed (Fig. 6.4A-F). Pouches are located centrally or marginally on the sternites. In representatives of Helminthomorpha, the early postembryonic stages develop tracheal pouches with small lumina in each of the first two leg-bearing segments, but no spiracles. Thus, these cryptic pouches serve exclusively as apodemata and have no respiratory function (Krug, 1906; Ziegler, 1907; Wernitzsch, 1910). This is the reason why Verhoeff called these structures in Helminthomorpha 'muscle pouches' (Verhoeff, 1928-1932: 1198). Only in representatives of Penicillata and Pentazonia, the pouches of the first two leg-bearing segments have respiratory function, because they form spiracles. However, the anterior pouches of the 7th trunk segment, where the gonopods are located, are modified. These pouches fuse with the femora and completely lack a lumen in adult specimens. They serve exclusively as apodemata (Wernitzsch, 1910). Effenberger (1907) could not detect tracheal pouches in the seventh segment in *Polydesmus complanatus* and the last two segments also lack pouches. These segments are supplied by tracheae from the more anterior segments (Effenberger, 1907).

The shape of the pouches differs among diplopod subtaxa. Generally, they consist of a basal shaft that runs out into a medial and a lateral horn (Fig. 6.3C, E). The tracheae originate, depending on the species, from the tip of the horns (Fig. 6.3C, E), or from the basal part of the shaft (Fig. 6.3H-I). Verhoeff (1928-1932: 1186) mentioned that the variability of diplopod sternites has a significant influence on the shape of the tracheal pouches. The width of the sternites and the localization of the coxae/spiracles seem to be responsible for the dilatation of either the lateral or the medial pouch horns. In diplopods with wide sternites and free pleurites, the lateral horns are especially long (Oniscomorpha, Colobognatha; Fig. 6.3C, E). In some diplopods with merged pleurites and sternites (e.g. Polydesmida), the spiracles and the tracheal pouches are located more laterally, which lead to prolonged medial horns (Fig. 6.3F, H; Hilken, 1998). In Pentazonia, the pouches are connected elastically, and in Helminthomorpha they are firmly adjoined to the sternites (Verhoeff, 1928-1932: 1273).

Fig. 6.1. **A-G** Spiracles of different diplopod species. **A** First leg pair of *Glomeridesmus* sp. (Glomeridesmidae), female, with their stigmatic-plate (SEM). **B** Detail of a stigmatic plate with a spiracle (SEM). **C** Spiracle of *Polyxenus lagurus* (Penicillata) (SEM). **D** Three spiracles of *Glomeris marginata* (Pentazonia, SEM), view from ventrolateral. **E** Numerous trichomes within a spiracle of *G. marginata* (SEM). **F** Spiracle of *Polyzonium germanicum* (Colobognatha) (SEM). **G** Spiracle of *Ommatoiulus sabulosus* (Julida, SEM). **H** Two spiracles of *Brachydesmus superus* (Polydesmida) with trichomes (SEM). **I** Spongiform trichomes within the spiracle of *B. superus* (SEM). **J** *Lissodesmus anas* (Polydesmida) with a "foxtail-like" trichoma equipment around the spiracle (SEM). **A-B** Originals from Thomas Wesener. **C-I** Originals from Gero Hilken. **J** Original from Robert Mesibov. Abbreviations: **co** coxa; **s** spiracle; **sp** stigmatic plate; **spt** spongiform trichomes; **st** sternites; **t** trichomes.

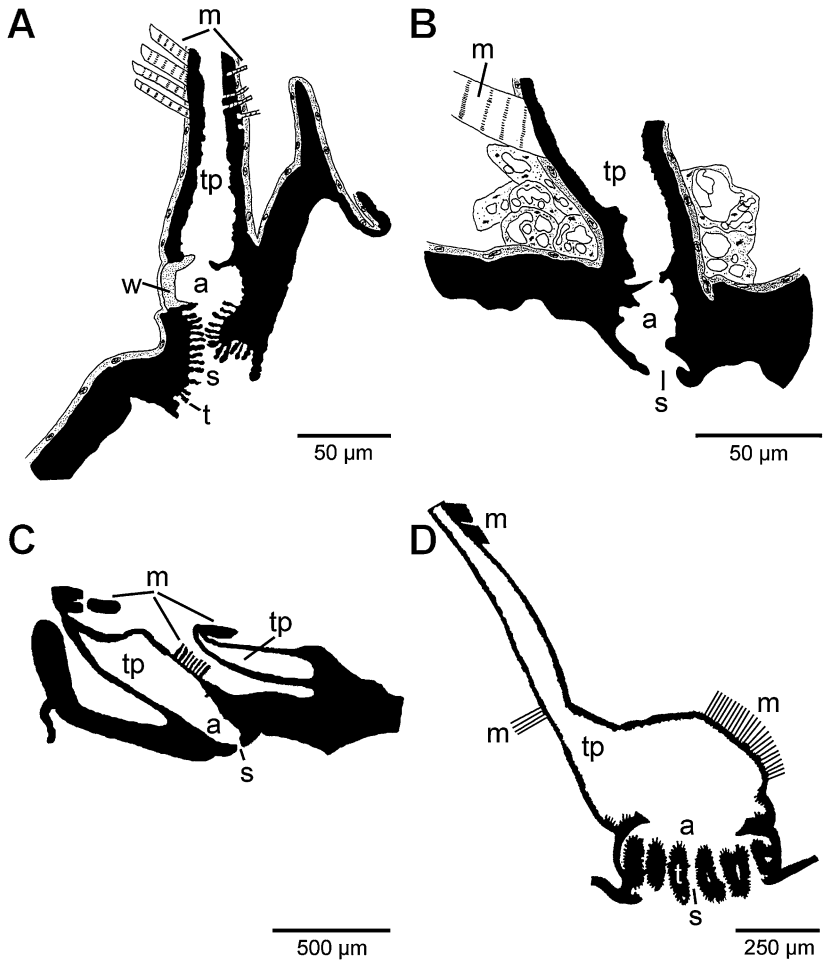


Fig. 6.2. **A-D** Semischematic representations of sagittal sections of diplopod spiracles. **A** *Brachydesmus superus* (Polydesmida). **B** *Polyzonium germanicum* (Colobognatha). **C** Spiracle and tracheal pouch one and part of tracheal pouch two of *Orthoporus texicolens* (Spirobolida). **D** Sagittal section of a tracheal pouch of *Pachydesmus crassicutis* (Polydesmida). **A, B** Modified after Hilken (1998). **C, D** Modified after Stewart & Woodring (1973). Abbreviations: **a** atrium; **m** muscles; **s** spiracle; **t** trichomes; **tp** tracheal pouch; **w** 'window'.

The cuticle of the pouches is extremely massive and sclerotized in most species of Diplopoda. The pouches serve as apodemes (= anchoring points) for the attachments of the extrinsic muscles of the coxae. Depending on the species considered, protractor muscles of the gonopods are attached to the anterior or posterior tracheal pouches of the segments 6 to 10, additionally (Drago et al., 2011). Exceptions from this arrangement are found in representatives of Penicillata and Colobognatha. In Penicillata, the integument and, thus, the tracheal pouches are comparably soft due to the weak sclerotization (Fig. 6.3A-B). In

Colobognatha, the solidity of the pouches might be reduced due to the development of other structures that serve as apodemes for leg musculature.

TRACHEAL SYSTEM: GENERAL ASPECTS

In Penicillata and Pentazonia there are branched tracheae and distinctive supply areas (Fig. 6.4B-C) whereas in Helminthomorpha the tracheae are unbranched and arranged as "wild tracheal bushes" not ordered in a segmental fashion (Fig. 6.4E). The Colobognatha show an intermediate arrangement (Fig. 6.4C). It is likely that unbranched tracheae are an apomorphic feature of Helminthomorpha (Voges, 1916; Hilken, 1998). There seems to be a functional coherence between branched and unbranched tracheae on the one hand and the different shape of the trunk segments on the other (Verhoeff, 1928-1932: 1269; Hilken, 1998). Penicillata and Pentazonia have comparatively short and wide trunk segments. The transversal body-section is crescent-shaped. Here, an equable gas exchange seems to be maintained by branched tracheae, whereas in Helminthomorpha with their long and thin trunks and their ring-like diplosegments oxygen supply is best obtained by bushes of long and unbranched tracheae.

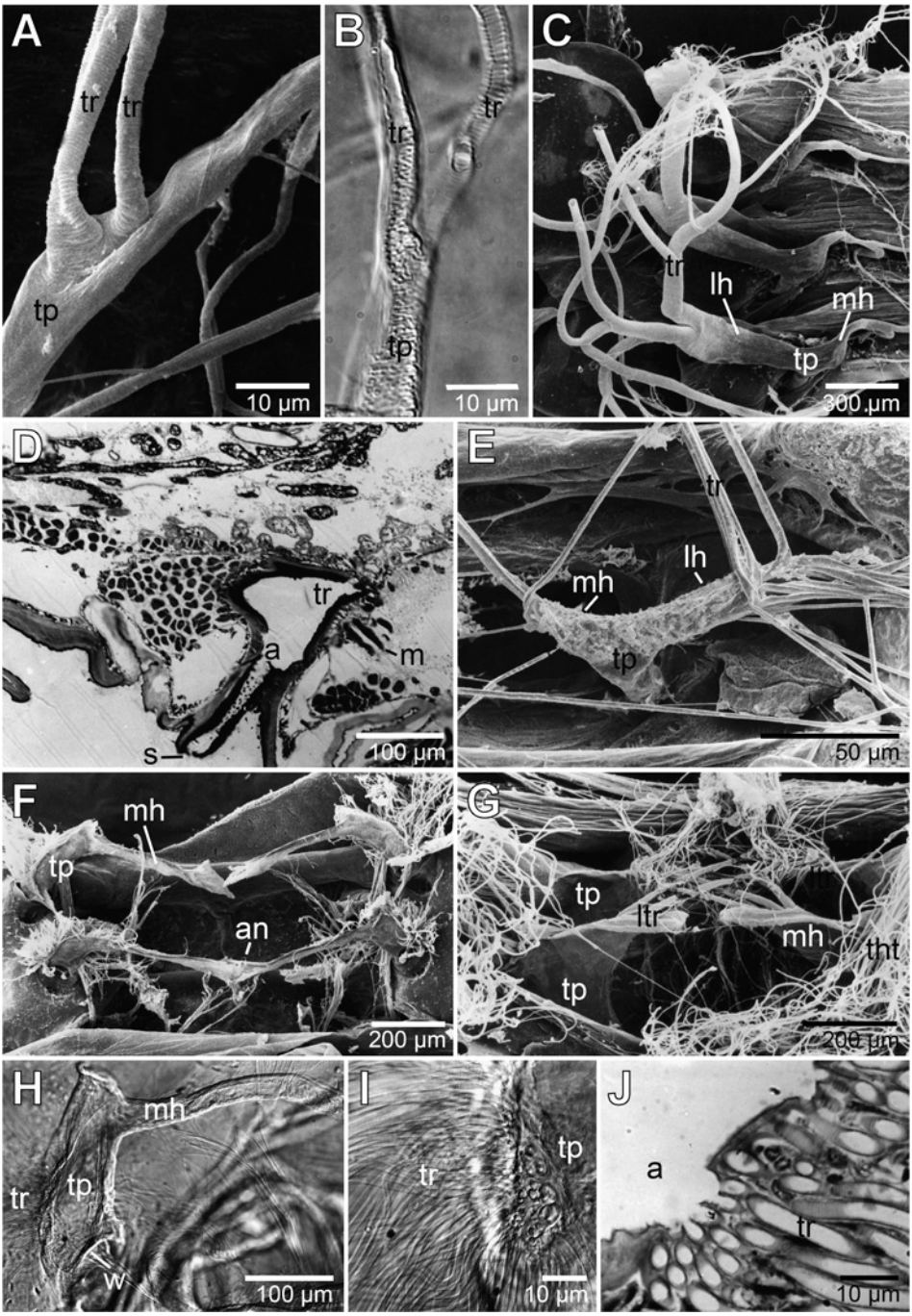
The tracheae of only very few diplopod species were investigated so far using transmission electron microscopy (*Polyxenus lagurus*, Fig. 6.5A-B, E-F; *Glomeris marginata*, Fig. 6.5C-D; *Brachydesmus superus*, Hilken, 1998). As far as we know, the basic organization of diplopod tracheae and tracheoles is comparable to that of Chilopoda and Hexapoda. The tracheae of diplopods always consist of a single-layered epithelium which is covered by three cuticular layers: endo-, exo- and epicuticle. The tracheae are strengthened by sclerotized, epicuticular taenidia which are helically arranged in the tracheal wall (Fig. 6.6A-D), similar to other myriapods, e.g. *Lithobius forficatus* (Chilopoda) (Hilken, 1997, 1998).

TRACHEAL SYSTEMS IN DIFFERENT SUBTAXA OF THE DIPLOPODA

Penicillata

The series of spiracles begins at the first leg-bearing segment (Fig. 6.4A left). Spiracles are located at the edge of the sternites and the pleurites near the coxae of the legs (Fig. 6.1C). The openings are very small (approximately 2 μm in diameter) and hardly visible. This may be the reason why protection mechanisms against water loss or litter pollution are not developed. None of the investigated species form a fyke-apparatus within the spiracular openings. However, Reinecke (1910) described small warts in light microscopy as cuticular modifications in the vicinity of the spiracle.

The occurrence of tracheal pouches and taenidia was challenged by the first investigators (Bode, 1877; Verhoeff, 1896). However, Reinecke (1910) and Hilken (1998) could clearly demonstrate that tracheal pouches are developed. Due to the presence of numerous cuticular papillae, tracheal pouches can be easily distinguished from the tracheae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(Fig. 6.3A-B; Hilken, 1998). It was not until Reinecke (1910) who demonstrated first that coxal muscles are attached to the pouches. Additionally, endoskeletal structures serve as apodemes for the coxal muscles. The very tiny tracheal pouches of *Polyxenus lagurus* (8-19 μm in diameter) are situated on these endoskeletal arches that stabilize the soft exoskeleton. The distal edge of each tracheal pouch is the origin of a single tracheal stem (Fig. 6.4B). This is also the case in *Lophoproctus* sp. (Verhoeff, 1928-1932: 1270).

In *Lophoproctus lucidus*, the pouches consist of a medial and a lateral horn, whereas in *Polyxenus lagurus* only a long medial horn exists (Fig. 6.3A). Tracheal pouches are more massive in *L. lucidus* than in *P. lagurus*. The pouches are only a little wider than the diameter of the attaching trachea (Hilken, 1998).

In *Polyxenus lagurus*, a single trachea originates on top of each lateral horn of the serial pouches and additionally two other tracheal stems arise more laterally (Fig. 6.4B). The latter tracheae branch several times dichotomously in the vicinity of the tracheal pouches. The length of large trachea can reach up to 300 μm. The tracheae supply not only organs of their original segment, but also of neighbouring ones (Fig. 6.5B). The tracheae of the anterior segments run craniad, whereas the tracheae of posterior segment run in caudal direction (Fig. 6.4B). Whereas Verhoeff (1896) denied the presence of taenidia, Bode (1877) and Hilken (1998) showed that the tracheae are strengthened by helically arranged taenidia (Figs. 6.3B, 6.5E-F). The tracheae pass into tracheoles with a diameter of $\leqslant$1.0 μm.

Chilognatha

Pentazonia. — Specific characters of the tracheal system of representatives of the Pentazonia are demonstrated in *Glomeris marginata*, the best investigated species in this taxon (Brandt, 1841; Voges, 1878; Verhoeff, 1895; Hilken, 1998). The Glomerida and Sphaerotheriida show spiracles starting with the first leg-bearing segment (Fig. 6.4A left). The paired spiracles are located in folds of the integument ventrally on the sternites near the coxae (Fig. 6.1D). Caudally, they move over in the direction of the pleurites. The slit-shaped spiracles are medially sunken, the margins are bulging. The inner wall of the atrium

Fig. 6.3. **A-J** Tracheal pouches and tracheae of different diplopod species. **A** *Polyxenus lagurus* (Penicillata, SEM). **B** *Polyxenus lagurus*. Note the different linings of a tracheal pouch (trichomes) and the attaching tracheae (taenidium) (LM, Hoyer's solution). **C** *Glomeris marginata* with branched tracheae of different diameters (Pentazonia, SEM). **D** Sagittal section of a spiracle and a tracheal pouch of *G. marginata* (LM). **E** Tracheal pouch of *Polyzonium germanicum* with its medial and lateral horns and several unbranched tracheae (Colobognatha, SEM). **F** Two pairs of tracheal pouches of *Brachydesmus superus* with its enlarged median horns and several unbranched tracheae (Polydesmida, SEM). **G** Two pairs of tracheal pouches of *Ommatoiulus sabulosus* with unbranched large and thin tracheae (Julida, SEM). **H-J** *B. superus* (LM): **H** Single tracheal pouch with its enlarged median horn and basally originating tracheae (Hoyer's solution). **I** Origin of unbranched tracheae at the tracheal pouch (Hoyer's solution). **J** Sagittal section of a tracheal pouch with branching tracheae (LM). Originals from Gero Hilken. Abbreviations: **a** atrium; **an** anastomosis; **lh** lateral horn; **ltr** large tracheae; **m** muscles; **mh** medial horn; **s** spiracle; **tht** thin tracheae; **tp** tracheal pouch; **tr** tracheae; **w** 'window'.

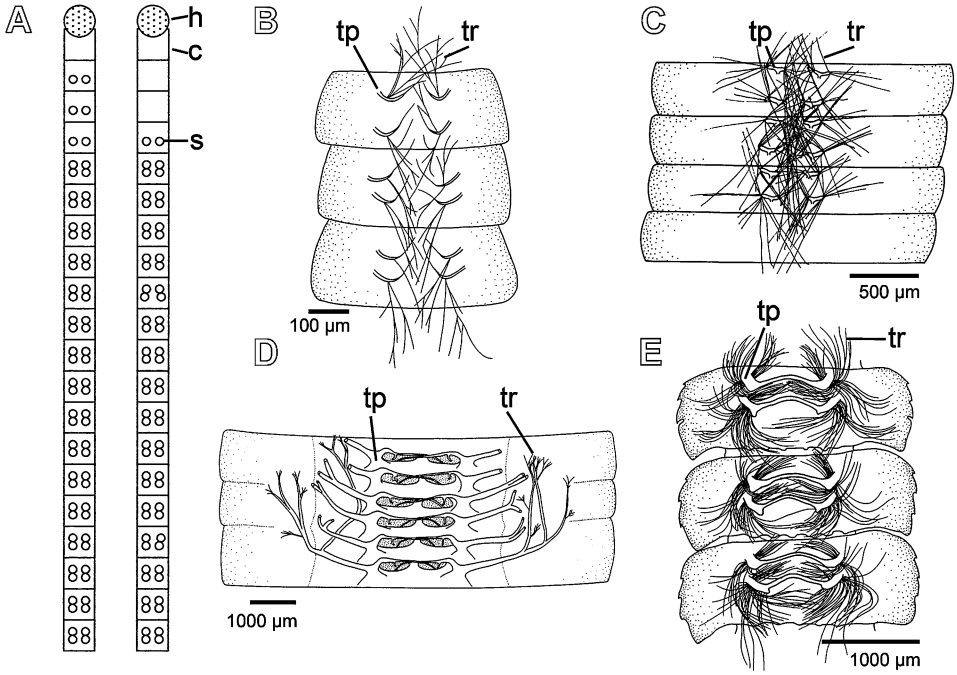

Fig. 6.4. **A** Semischematic representations of the arrangement of spiracles in Diplopoda: **A left** Penicillata and Pentazonia; **A right** Helminthomorpha. **B-E** Semischematic representations of tracheal systems in Diplopoda: **B** *Polyxenus lagurus* (Penicillata); **C** *Glomeris marginata* (Pentazonia); **D** *Polyzonium germanicum* (Colobognatha); **E** *Brachydesmus superus* (Polydesmida). **A-E** Modified after Hilken (1998). Abbreviations: **c** collum; **h** head; **s** spiracle; **tr** tracheae; **tp** tracheal pouch.

is covered by long unbranched trichomes building a fyke-apparatus (Fig. 6.1E) (Hilken, 1998). In *G. marginata*, the large spiracles seem to be closable. This can help to prevent water loss (Hopkin & Read, 1992).

In *G. marginata*, huge and massive tracheal pouches with medial and lateral horns are present (Figs. 6.3C, 6.4E). The elongated lateral horn reaches to the sternite-pleurite border, whereas the medial horn is short. Only in the first leg-bearing segment, the medial horn is larger than the lateral one (Verhoeff, 1928-1932: 1252). The pouches of the last five leg-bearing segments are smaller than those of the anterior ones. The cuticle of the pouch wall is covered by cuticular papillae. Verhoeff (1928-1932: 1248) described that there is no clear separation between the tracheal pouches and the tracheae. He interpreted this observation as a secondary feature of the Glomerida. However, Hilken (1998) showed that towards the origin of the tracheae, first fragments of taenidia appear.

In *G. marginata*, two huge tracheal stems arise from each lateral horn (Fig. 6.3C; Hilken, 1998). Each stem ramifies dichotomly even at longer distance from the pouch. After two to four branchings, the tracheal lumina become tighter and finally the tracheae run out into tracheoles (Fig. 6.3C); diameter $\leqslant 1$ μm. Small tracheae and tracheoles surround the organs web-like and penetrate them. The tracheae of the lateral horns supply

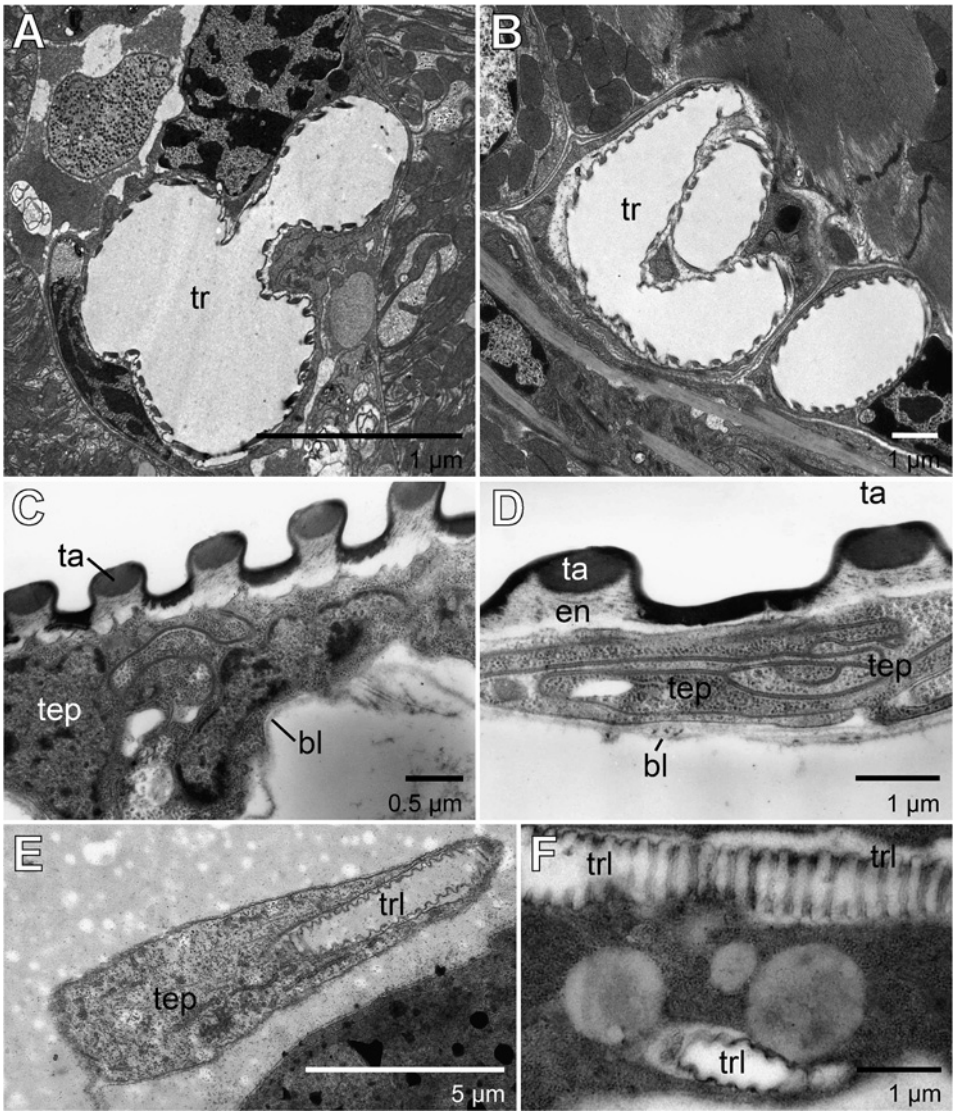

Fig. 6.5. **A-F** Structure of tracheae in Diplopoda. **A-B** *Polyxenus lagurus* (Penicillata, TEM): **A** branching trachea within the tissue; **B** several tracheae within the tissue. **C-D** *Glomeris marginata* (Pentazonia): **C** detail of a longitudinal section of a trachea with its distinct taenidia (TEM); **D** longitudinal section of a trachea with interdigitations of tracheal epithelium. **E-F** Regions of the tracheoles (*Polyxenus lagurus*, Penicillata): **E** tracheole with its surrounding epithelial cell. Taenidia are still visible; **F** tracheole end cell with two tracheoles, strengthened by taenidia. **A, B, E, F** Originals from Carsten Müller. **C, D** Originals from Gero Hilken. Abbreviations: **bl** basal lamina; **en** endocuticle; **ta** taenidium (= exocuticle); **tep** tracheal epithelium; **tr** tracheae; **trl** tracheoles.

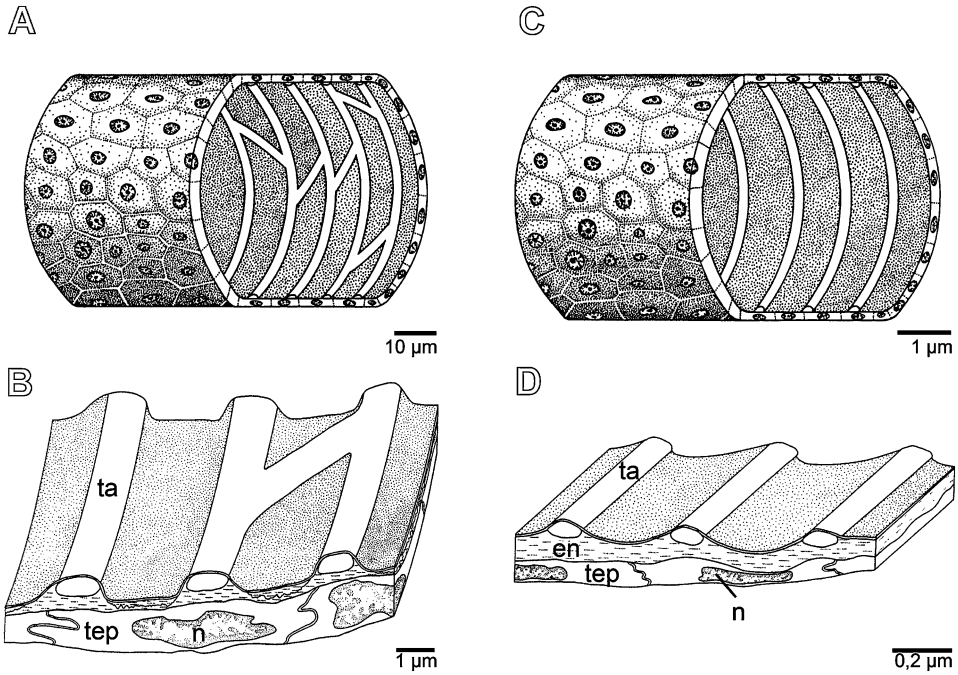

Fig. 6.6. **A-D** Semischematic representations of tracheal structure in Diplopoda. **A-B** *Glomeris marginata* (Pentazonia): **A** overview of a trachea; **B** detail of **A**, with branched taenidia. **C-D** *Brachydesmus superus* (Polydesmida): **C** overview of a trachea; **D** detail of **C**, with unbranched taenidia. Basal lamina not shown. Modified after Hilken (1998). Abbreviations: **en** endocuticle; **n** nucleus; **ta** taenidium (= exocuticle); **tep** tracheal epithelium; **tr** tracheae.

the organs of the relevant diplosegment with the exception of the legs and the ventral nerve cord. From the medial horn two tracheae arise as well. They branch and supply the legs and the ventral nerve cord (Fig. 6.4E). The tracheal arrangement in the trunk of *G. marginata* is more or less segmental. Most of the tracheae remain in their original segments, only few reach into neighbouring segments. The head is supplied by tracheae of the first three segments (Voges, 1897). The course of the tracheal stem originating at the medial horn of the third segment is unusual. It branches into an anterior branch that runs into the head, and a posterior extremely elongated one that runs caudally, close to the ventral nerve cord, through the whole body. In addition, originating from the seventh diplosegment, the tracheal stems of the lateral horns are elongated and extend toward the anal segment (Wernitzsch, 1910; Hilken, 1998). Males show no spiracles and no pouches in the 11th and 12th trunk segment, whereas females possess spiracles and pouches also in the 11th segment (Wernitzsch, 1910). *G. marginata* shows one of the clearest tracheal arrangements of all investigated diplopod species, which achieve nearly the complexity of tracheal systems in Chilopoda and Hexapoda.

The tracheae consist of a single-layered epithelium which is covered by a cuticle (Figs. 6.5C-D, 6.6A-B). Depending of the tracheal diameter, this epithelium is 0.5 to 1.8 μm in height. The epithelial cells are connected by wide interdigitations (Fig. 6.5D). The

cuticle consists of a lamellated endocuticle, a thin sclerotized exo- and a very thin electron-dense epicuticle. The endocuticle is subdivided into a basal layer of low electron-density, and a denser outer layer that is restricted to the areas between the exocuticular taenidia (Fig. 6.6B). The tracheae are strengthened by helically arranged taenidia. In large tracheal stems, the taenidia are 0.5-0.8 μm in width (Hilken, 1998). The taenidia are interconnected by anastomoses (Fig. 6.6A-B; Verhoeff, 1928-1932: 1254; Hilken, 1998). This seems to be quite uncommon in Diplopoda. To date, only representatives of the related Sphaerotheriida have been reported to show the same kind of strengthening structure (Verhoeff, 1928-1932: 1260, 1262).

In Sphaerotheriida, the separation between tracheal pouches and tracheae is much more distinct with regard to their cuticular lining (Verhoeff, 1928-1932: 1264). The wall of the tracheal pouch is extremely massive and structured like the integument. Three different muscles are attached to the tracheal pouches: pleural muscles, abdominal muscles, and coxal muscles (Verhoeff, 1928-1932: 1249). Verhoeff suspected that movements of the distal horn wall via the attached muscles results in an exchange of air in the atrium: The pouches are lined by hair sensilla (Verhoeff, 1928-1932: 1260, 1262), and should be equipped with numerous unicellular glands that discharge their secretion into the anterior pouches. Verhoeff (1928-1932: 1260) observed numerous debris in the pouches of Sphaerotheriidae, but not in those of glomerid species. The arrangement of tracheae in Sphaerotheriidae is very similar to that of *G. marginata*. The sphaerotheriid tracheae are the largest within the Diplopoda (Verhoeff, 1928-1932: 1260, 1262).

Helminthomorpha. — In representatives of Helminthomorpha, the first two leg-bearing trunk segments lack spiracles (Fig. 6.4A right), but show rudimentary tracheal pouches with no spiracles (Krug, 1906; Ziegler, 1907; Wernitzsch, 1910; Verhoeff, 1928-1932: 1198). Generally, the tracheae are long, thin and unbranched.

Colobognatha. — The tracheal system of representatives of Colobognatha is poorly investigated. The large spiracles of *Polyzonium germanicum* (8 μm in diameter) are situated ventrolaterally on the sternites, close to the coxae (Hilken, 1998). The openings are surrounded by convex cuticular rings. Roundish cuticular nubs fit accurately into these rings (Fig. 6.1F; Hilken, 1998). Due to the presence of a small spiracle muscle that extents to the coxa (Verhoeff, 1928-1932: 1234), it is likely that the spiracles can be opened (Fig. 6.2B). Fyke-apparatuses are lacking. In most other species of Colobognatha, the spiracles are very small (Attems, 1926-1930: 64).

Polyzonium germanicum shows very delicate tracheal pouches and a remarkable slender tracheal system (Fig. 6.4C; Hilken, 1998). The narrow base of the pouch is short (Fig. 6.3E). Apically, each pouch passes into two distinct horns. The lateral horn is larger than the medial one and extends nearly to the border of the sternites and pleurites (Fig. 6.3E). Only very few muscles are attached to the pouches (Fig. 6.2B). However, the main portion of the coxal muscles is attached to hook-like anchoring points — a unique feature of diplopods (Verhoeff, 1928-1932: 1234; Hilken, 1998). This partial loss of function as apodemes might be the reason for the weak development of the tracheal pouches in *P. germanicum* (Latzel, 1884; Verhoeff, 1928-1932: 1237; Hilken, 1998). In

Platydesmus sp., the horns are particularly massive. Laterad, the horns point beyond the sternites (Verhoeff, 1928-1932: 1237).

The tracheae are always unbranched (Figs. 6.3C, 6.4D). They originate at the tips of both tracheal horns. Nearly all tracheae are not restricted to their original diplosegment, but project deeply into the neighbouring ones (Fig. 6.4C). Some of them reach a length of 400 μm and extend over five segments. The number of tracheae originating at each horn (15-20) is comparatively small. The tracheal diameter (2-4 μm) is barely reduced from the origin at the tracheal pouch up to the target organ (Hilken, 1998).

Eugnatha. — Wernitzsch (1910) described that there is a tendency in eugnathan diplopods to build longitudinal bundles of tracheae that extend over several segments. Some of these groups build only lateral, other lateral and medial tracheal bundles.

Nematophora. — Due to the investigation of Wernitzsch (1910), *Craspedosoma simile* (Chordeumatidae) is the best investigated species of the Nematophora with regards to its tracheal system. The spiracles of *C. simile* lie deeply invaginated in the wall of the sternites and are well protected by overlapping edges of the pleurites. Fyke-apparatuses are lacking. The tracheal pouches possess very small medial and huge lateral horns. At the base of each pouch, coxal muscles are attached. Generally, the tracheae of this species arise from the anterior bases of the pouches and from the distal parts of the medial and lateral horns. However, it is conspicuous that only the lateral horns of the posterior tracheal pouches build tracheae, whereas the tips of the anterior lateral horns mostly end blind, only in exceptional cases some tracheae were found.

The tracheae originating from the medial horn supply the ventral nerve cord and the legs, those arising from the base of the pouch supply the gut and the gonads. The tracheae of the posterior pouches are longer and reach into neighbouring segments, whereas those of the anterior pouches remain in the original segment. Only the tracheae of diplosegments 4 and 5 form tracheal bundles which supply the spiracle-less segments 1-3 and the head. All tracheae of *Craspedosoma simile* are unbranched and have nearly the same diameter. They are strengthened by taenidia. The tracheal system of other representatives of Nematophora (e.g. *Mastigona* sp. and *Chordeuma* sp.) looks quite similar. However, it shows an additional medio-ventral and longitudinal tracheal stem originating from the medial horns of the 4th and 5th diplosegments which extend to the head (Wernitzsch 1910). In Nematophora, Verhoeff (1928-1932: 1275) described networks of tracheae formed by anastomoses that surround the spinnerets. These are the only anastomoses observed within the Diplopoda.

Polydesmida. — Attems (1937: 9) described the spiracles of Polydesmida as openings situated on more or less crater-like elevations. Recently, the structure of the spiracles in the Dalodesmidae and Paradoxosomatidae (Polydesmida) were described using SEM techniques. The spiracular structure varies strongly and takes several forms that may not be confined to a crater (Mesibov, 2003, 2005, 2006, 2009b). *Lissodesmus anas* (Dalodesmidae) have a foxtail of hair-like structures arising just anterior and ventral to the anterior spiracle (Fig. 6.1J; Mesibov, 2005). The emerging spiracles of *Dasystigma* sp.

and *Tasmanopeltis* sp. (Dalodesmidae) consist of densely packed trichomes resembling the tentacles of sea anemones. The posterior spiracles are more prominently 'tentacled'. In representatives of Paradoxosomatidae, emergent spiracles are also found. In *Tholerosoma* sp. the spiracle are provided with numerous fine, short projections, but in *T. monteithi* the spiracle surface is largely covered by minute, irregular plates (Mesibov, 2006). In most of the examined Australian Paradoxosomatidae, the spiracle consists of numerous fine, short, and densely packed cuticular projections. These may be hidden within the crater or extend well beyond it, i.e. 'recessed' and 'emergent' are arbitrary categories along a continuum of shape. In several genera, the cuticular projections have multi-pronged tips (Mesibov, 2009a). The apparent absence of well-defined spiracles in Australian *Agathodesmus steeli* and *Prosopodesmus* species (Haplodesmidae) is remarkable. Mesibov (2009b, 2012) was unable to detect spiracles neither with light microscopy (cleared specimens) nor with scanning electron microscopy.

The tracheal system of *Polydesmus complanatus* (Effenberger, 1907) and *Brachydesmus superus* (Hilken, 1998) was investigated intensively. The huge spiracles of *B. superus* (70 μm in diameter) are located near of the sternite-pleurite border and thus comparatively far away from the coxae (Fig. 6.1H). The anterior spiracle has a vertical, the posterior spiracle a horizontal orientation (Hilken, 1998). The spongy trichomes (3.0-3.9 μm in length) have a conical shape and a tapered base (Fig. 6.1I). They are characterized by numerous spongy cuticular depressions. The entrance of the pouch is further narrowed by a sclerotized ring (Fig. 6.2A); the transition zone to the tracheal pouch is narrowed in addition by a cuticular ridge (Hilken, 1998). A similar sclerotized ring was also described in *Pachydesmus crassicutis* (Stewart & Woodring, 1973).

Already Voges (1878, 1916) mentioned that the anterior tracheal pouches of polydesmid millipedes are slightly larger than the posterior ones. The atrium wall of the tracheal pouch of *Brachydesmus superus* has an extremely massive cuticle (Fig. 6.3H; diameter 14-15 μm). The pouch runs out into two horns. The lateral horn is small and stub, whereas the medial horn, pointing medio-caudad, is huge (Figs. 6.3H, 6.4E) and fuses with the medial horn of the opposite side (Fig. 6.3F; Hilken, 1998). Ziegler (1907) could not observe suchlike fusions in *P. complanatus*, but Voges (1916) confirmed that fusions of tracheal horns occur in this species. In *Coromus thomsoni*, all four horns of a diplosomite are fused, forming a so-called pouch-plate (Verhoeff, 1928-1932: 1227). In *Pachydesmus crassicutis*, only a single horn of the tracheal pouches is described that tapers to its end (Fig. 6.2D; Stewart & Woodring, 1973). Basally, in *P. crassicutis* and *Brachydesmus superus* the pouch shows an oval 'window' (Figs. 6.2A, 6.3H; Verhoeff, 1911-1914: 493), a characteristic feature of the Polydesmida (Verhoeff, 1911-1914:493; Voges, 1916; Stewart & Woodring, 1973; Hilken, 1998). This 'window' is covered by a fine cuticle. Verhoeff (1911-1914: 493) postulated that a sclerotized ring surrounding the window have function in respiration. He described 'pump muscles' attached to this inflexible cuticular ring and concluded that the whole structure may work as an 'air-pump'. He thought that the muscle contraction leads to an expansion of the pouch wall, causing inhalation of air. Such rings are developed only in Polydesmoidea, possibly due to their immense calcium deposition of their exoskeleton that leads to inflexible segmental rings (Verhoeff, 1911-1914: 493). Voges (1916) and Hilken

(1998) could not find muscles attached to the sclerotized rings. However, in *B. superus* and in *Pachydesmus crassicutis* numerous coxal muscles are attached to the pouch proximally beside the 'window' (Fig. 6.2A, C-D; Stewart & Woodring, 1973; Hilken, 1998). Stewart & Woodring (1973) denied a function as an 'air-pump'. In *Pachydesmus crassicutis*, there is no evidence for a closure mechanism. The lever-muscle arrangement has been shown to be unable to pump air in or out of the tracheal pocket. Further investigations are necessary to clarify the function of the window.

All investigated representatives of Polydesmida have only one type of thin tracheae. The tracheae, all unbranched (Fig. 6.3I-J), are mostly limited to the segment of their origin (Fig. 6.4E). In *Brachydesmus superus* the tracheae originate latero-basal at each pouch in a high numbers, only 1-2 μm in diameter. Only few tracheae extend caudally into the legs of the next diplosegments. Most of the tracheae run through hemolymph spaces and finally tracheoles penetrate different tissues. In *Polydesmus complanatus*, most tracheae extent in the adjacent segments (Effenberger, 1907). In *Pachydesmus crassicutis*, approximately 450 tracheae (2 μm in diameter) arise from the enlarged tracheal pouch (Stewart & Woodring, 1973). In *Polydesmus* sp. tracheae originating at diplosegments 4 and 5 build longitudinal bundles that supply the first 3 segments and the head (Wernitzsch, 1910).

The cuticle of the tracheae shows the typical structure: the lamellated endocuticle, the exocuticle and the very thin epicuticle. Every trachea is strengthened by a single continuous taenidium (0.3 μm in diameter) which is helically arranged. Anastomoses of taenidia are not observable (Hilken, 1998).

Juliformia. — Little is known about the tracheal system of Juliformia. Rossi (1901), Krug (1906), Ziegler (1907), Verhoeff (1928-1932: 1200-1205), and Hilken (1998) investigated the respiratory system of some representatives of Julida only tentatively, e.g. *Ommatoiulus rutilans* and *O. sabulosus*. Stewart & Woodring (1973) investigated *Orthoporus texicolens*, a representative of the Spirostreptida.

Tergites and pleurites are fused in all representatives of the Julida. The spiracles are located on the free sternites that fit perfectly into the homogeneous body rings. In *O. sabulosus*, the spiracles are deeply indented; laterally they abut against the pleurites (Fig. 6.1G; Hilken, 1998). In all the juliformian diplopods investigated so far, a lever muscle is situated in a medial groove near the spiracle. Another small muscle which originates at the base of the nearest coxa is attached to it. It has been suggested that these muscles might be used to open the spiracles (Verhoeff, 1928-1932: 1190, 1200). However, other closing mechanisms are also likely. When specimens are coiled, the posterior edge of the preceding diplosegment covers the anterior portion of the following one, including at least parts of the anterior pair of spiracles (Stewart & Woodring, 1973). The coxae cover the spiracles additionally. Trichomes are not developed at the entrance of the spiracle in *O. rutilans* and *O. sabulosus* (Krug, 1906; Hilken, 1998).

Whereas the second leg-bearing segment of *O. rutilans* bears rudimentary pouches, but no spiracles, the third leg-bearing segment shows neither pouches nor spiracles (Krug, 1906). Due to the very small sternites, the pouches and the spiracles are situated ventromedially. In *O. sabulosus*, the conical, basal tracheal pouch is very long; the upper part

is dilated and ends in a small medial as well as a slightly larger lateral horn. The tracheal pouches of *O. rutilans* have the shape of complanate bottles (Krug, 1906; Ziegler, 1907). In diplosegments, the posterior pouches are larger than the anterior ones. Coxal muscles are attached medially at the posterior pouch walls. These walls are so strongly sclerotized that they do not have a respiratory function (Krug, 1906).

The tracheal system of Julida shows a higher complexity than those of other Helminthomorpha. Two aspects seem to be characteristic features of this taxon. (1) The tracheae originating from the anterior pouches are numerous, long and thin, whereas those originating from the posterior pouches are rarer, but much thicker. (2) The tracheae arising from the medial horns are shorter and thicker than those arising from the lateral horns (Krug, 1906; Ziegler, 1907; Wernitzsch, 1910; Hilken, 1998). In *O. sabulosus*, the numerous unbranched tracheae (2-3 μm in diameter) arising from the lateral horn, occupy wide parts of their diplosegment; only few extend into neighbouring segments. From the medial horn, only few (10-15), but larger tracheae (10-12 μm in diameter) arise (Fig. 6.3G). They intersect with tracheae of the adjacent diplosegments, but show no anastomoses or ramifications (Hilken, 1998). Tracheae occur from the 4th segment on throughout the body (Krug, 1906). The 5th segmental ring shows specialized pouches, because the large type of trachea is missing, only thin tracheae are developed in "*Julus* sp.". *O. rutilans* shows lateral and median longitudinal bundles of tracheae originating at the fourth and fifth diplosegments that supply the first segments and the head. The median bundle contains a particularly high number of tracheae. Whereas most of the helminthomorph diplopods show these bundles only in the anterior trunk segments (segments 4-6; Krug, 1906; Ziegler, 1907), Wernitzsch (1910) described them also in posterior segments in "*Julus* sp.". The tracheae of the posterior segments are more or less disordered (Krug, 1906).

No transmission electron microscopic studies on tracheae are available for representatives of the Juliformia.

RESPIRATION

Air may be conducted through the tracheal respiratory system by active ventilation or by passive diffusion. As to their respiratory metabolism, soil-living millipedes are characterised as oxygen conformers or oxygen regulators.

Gas exchange

In Diplopoda, coxal muscles insert at the tracheal pouches. Verhoeff (1928-1932) speculated that in some species possibly flexion or compression of the tracheal pocket might facilitate ventilation of the trachea. Stewart and Woodring (1973) studied the tracheal apparatus of *Pachydesmus crassicutis* (Polydesmida) and *Orthoporus texicolens* (Spirobolida) under functional aspects. The authors showed that ventilation, eventually achieved by compression of the tracheal pouches, is lacking in both diplopod species. The cuticular walls of the tracheal pockets seem to be too massive to allow flexion. The muscle

arrangement of the tracheal pockets has been proven to be unable to pump air in or out of the tracheal pockets. There is a smooth and continuous rate of oxygen consumption with no peaks or burst of oxygen consumption in the air (oxygen conformers). The ventilation of respiratory gases seems to be a simple process of diffusion of respiratory gases in and out of the spiracles. The effective diameter of their trachea enables a passive exchange of oxygen. An unidentified Australian paradoxosomatid millipede shows continuous gas exchange with evidence of occludible spiracles (Woodman et al., 2007). Contrary, two spirostreptid millipedes (*Plusioporus setiger* and *Pseudonannolene tricolor*), two spirobolid millipedes (*Spirobolus* sp. and *Rhinocricus padbergi*) and the julid *Megaphyllum rossicum* can maintain normal oxygen consumptions down to at least 5 kPa P_{O_2} and are thus considered oxygen regulators (Penteado, 1987). The Brazilian spirostreptid millipede *Pseudonannolene tricolor* is able to regulate oxygen consumption down to at least 71 mm Hg O_2 (10% O_2). A critical P_{O_2} is assumed to lie somewhere between 71 and 35.4 mm Hg O_2, since in experiments from this range downward the millipede started to show oxyconformity. When the millipede was exposed to a stepwise declining P_{O_2} down to about 7 mm Hg O_2, *P. tricolor* did not control oxygen consumption and showed oxygen conformation (Penteado & Hebling-Beraldo, 1991). For a review on hypoxic tolerance in Diplopoda see Schmitz & Harrison (2004).

Further details on respiration metabolism and oxygen consumption in different diplopod species were investigated by Gromysz-Kalkowska (1970, 1974, 1976a, b, 1979, 1980), Dwarakanath (1971), Gromysz-Kalkowska & Stojalowska (1983), Gromysz-Kalkowska & Tracz (1983), Gromysz-Kalkowska et al. (1986), Stamou & Iatrou (1990, 1993) and Penteado et al. (1991).

Plastron respiration

Only very few millipedes (representatives of Polydesmidae, Pyrgodesmidae, Blaniulidae, Julidae, and Siphonotidae from temperate and/or tropical regions) have been noticed or suspected to enter water temporarily (Enghoff, 1985; Burrows et al., 1994; Messner et al., 1996; Adis & Messner, 1997). Submersion tolerance (few hours/days) or submergence resistance (weeks/months) is enabled by plastron respiration. A plastron it defined as a water-repellent hydrophobic structure, which allows air-breathing species to use their respiration system under water. Plastron structures hold a thin layer of air into which oxygen from the surrounding water is added by means of diffusion to the same extent as oxygen is withdrawn through the connected tracheal system by breathing. In addition, plastrons can be actively ventilated. In flowing waters, small bubbles of atmospheric air in the water can be captured and added to the plastron (Adis & Messner, 1997; Adis et al., 1998, 2003). In millipedes, plastron structures can be subdivided into compressible structures as hydrophobic microtrichia/trichomes on the atrium wall of the spiracles and incompressible hydrophobic cuticular secretions (cerotegument) that cover certain body parts connected by stigmata (Adis et al., 1997, 2003; Marx & Messner, 2012).

Hydrophobic microtrichia. — The flooding ability in different millipedes depends on the presence of hydrophobic plastron retaining structures on the atrium wall of the spiracles, allowing plastron respiration under water. It is shown that the hydrophobic structures are short piston-like microtrichia or longish, densely packed setaceous microtrichia.

The wall of the spiracular atrium is deepened and consists of a lattice of short piston-like microtrichia described in the Polydesmida *Serradium semiaquaticum* (Adis et al., 1997), in *Polydesmus denticulatus*, *Brachydesmus superus* (Messner et al., 1996; Hilken, 1998), and in *P. angustus* (Eisenbeis & Wichard, 1985). The species show submersion resistance (see below).

A network of densely packed non-, bi- or polyfurcated setiform microtrichia covers the elevated spiracular atrium wall of the Paradoxosomatidae *Oxidus gracilis*, *Selminosoma chapmani* and *Iulidesmus hylaeicus* and the Platyrhacoidea *Aphelidesmus* sp. (Messner et al., 1996) and *Pycnotropis tida* (Adis & Messner, 1997). The species showed submersion or flood tolerance (see below).

Flood resistance is experimentally shown in the troglobitic European millipede *S. semiaquaticum* (spiracles with piston-like microtrichia) ($\geqslant$28 days in 14°C aerated water $\geqslant$9.6 mg O_2 l^{-1}; 54-158 h in 9-12°C non-aerate water, 4.9-5.3 mg O_2 l^{-1}). Small bubbles of atmospheric air in the water can be captured and added to the spiracular microtrichia if water current is above 75 cm sec^{-1} (Adis et al., 1997). Flood resistance is shown for the European millipedes *Polydesmus denticulatus* and *Brachydesmus superus* (spiracles with piston-like microtrichia): 50-75 days (4-9°C water) (Zulka, 1989; Messner et al., 1996).

Flood tolerance is experimentally shown for *I. hylaeicus* (spiracles with setiform microtrichia) from inundation area of Amazonas-Solimõis (Brazil) that can survive in non-aerate water for 6-8 h (25°C, about 2 mg O_2 l^{-1}), 12-18 h (20°C, about 4 mg O_2 l^{-1}) and 42-48 h (15°C, about 5.4 mg O_2 l^{-1}), in aerate water 24-26 h (25°C, >6.5 mg O_2 l^{-1}), 48-72 h (20°C, 6.6 mg O_2 l^{-1}) and 144-168 h (15°C, >7.9 mg O_2 l^{-1}) (Messner et al., 1996). *Oxidus gracilis* (spiracles with setiform microtrichia) shows a submersion tolerance of 5-7 d (Adis & Messner, 1997).

Hydrophobic secretion layer = cerotegument. — Plastron respiration is possible by a hydrophobic secretion layer (cerotegument, see Adis & Messner, 1997) that extend on tergites to sternites and covers all spiracles in the coxal region in part or thins out into a spiny web network around the uncovered spiracles. The cerotegument is firmly supported by secretion pillars located between cuticular tubercles or cones (compare Fig. 2 in Adis et al., 2003). A thin air casing can be held in the hydrophobic cavity below the cerotegument and by the spiny web network near the spiracles. This enables plastron respiration with high flood resistance. A cerotegument plastron respiration is stated by the neotropical species of the semiaquatic immatures of *Myrmecodesmus adisi* (Polydesmida, Pyrgodesmidae) (Adis, 1986), that can survive submersion in Amazonian floodplains up to 11 month (Adis, 1986; Messner & Adis, 1988; Adis & Messner, 1997; Adis et al., 2003). Similar hydrophobic cerotegumental layer is documented in the semiaquatic species *Aporodesminus wallacei* and *Cryptocorypha ornata* (Polydesmida, Pyrgodesmidae) (Adis et al., 1998). A cerotegumental crust is observed in different

Haplodesmidae (Polydesmida) of the genus *Eutrichodesmus* (*Eutrichodesmus basalis*, *E. armatocaudatus*, *E. communicans*, *E. similis*) (Golovatch et al., 2009). The function remains unclear.

Methane emission

Arthropods release CO_2 and H_2O and consume O_2 via tracheae as a natural consequence of their metabolism and breathing. Beside CO_2 and H_2O several millipedes emit CH_4 as one of the end products of their intestinal (methanogenic bacteria-aided) fermentations. Methane release was firstly reported from all tropical representatives of millipedes belonging to the orders Spirobolida, Spirostreptida, and Polydesmida (*Chicobolus* sp., *Orthoporus* sp., *Pycnotropis acuticollis, Rhapidostreptus virgator*), but not in those living in the temperate European climate (*Glomeris* sp., *Julus* sp., *Polydesmus* sp., *Tachypodoiulus niger*) that may reflect the sensitivity of intestinal methanogens for low temperatures (Hackstein & Stumm, 1994; Bijnen et al., 1996). However, Sustr & Simek (2009) found significant methane emission in several temperate millipedes including some species from the order Julida (*Julus scandinavius*, *Leptoiulus proximus*, *L. trilobatus*, *Megaphyllum projectum*, *M. unilineatum*, *Unciger foetidus*, *U. transsilvanicus*). On the other hand, methane production was not confirmed in *Cylindroiulus boleti*. Members of the other orders (Glomerida and Polydesmida) did not release methane with the exception of one questionable recorded release in *Polydesmus complanatus* (Polydesmida, Polydesmidae). Negative results were obtained from species of the Paradoxosomatidae (*Strongylosoma stigmatosum* and *Iulidesmus hylaeicus*).

Respiratory copper proteins — hemocyanins

In some large diplopod species of the Spirostreptidae, the subsequent O_2-distribution is supported by the circulatory system with the help of the respiratory pigment hemocyanin in the hemolymph, whereas in other diplopod species hemocyanin seems to be lacking. This copper-containing, respiratory protein with high oxygen affinity has been found in the hemolymph of the diplopods *Spirostreptus* sp. and *Telodeinopus aoutii* (Jaenicke et al., 1999; Kusche & Burmester, 2001) and *Archispirostreptus gigas*, but not in the smaller representatives of the Julidae and Glomeridae (Hagner-Holler, 2004).

Although the tracheal system of the Spirostreptidae is similar to that of other helminthomorph diplopods, a high hemocyanin concentration was observed. Hemocyanins have been interpreted as an adaptation to subterrestrial and therefore potentially hypoxic habitats. The protein is composed of one (*Archispirostreptus* sp.) or two immunologically distinct subunits that are most likely arranged in a 36-mer (6×6) native molecule (*Spirostreptus* sp.). It has a high oxygen affinity (*Spirostreptus* sp.: $P_{50} = 4.7$ Torr, *Archispirostreptus* sp.: $P_{50} = 8.7$ Torr) but low cooperativity (*Spirostreptus* sp.: $h = 1.3$, *Archispirostreptus* sp.: $h = 2.1$). The hemocyanin of *Spirostreptus* sp. is structurally similar to the single known hemocyanin from the centipede *Scutigera coleoptrata* (Chilopoda) (Mangum et al., 1985), indicating a rather conservative architecture of the myriapod hemocyanins. Hemocyanins

were identified in the symphylans *Hanseniella audax* and *Symphylella vulgaris*, the chilopod *Scolopendra subspinipes dehaani* and the diplopod *Polydesmus angustus*. No hemocyanins were found in the diplopods *Polyxenus lagurus*, *Cylindroiulus punctatus*, *Glomeris marginata*, *G. pustulata*, and *Arthrosphaera brandtii*, or the chilopods *Lithobius forficatus*, *Geophilus flavus*, and *Strigamia maritima*. This suggests multiple independent losses in myriapod taxa. Two independent hemocyanin subunits were found that were already present in the myriapod stem line (Pick et al., 2014).

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CHAPTER 7

DIPLOPODA — CIRCULATORY SYSTEM

BY

CHRISTIAN S. WIRKNER AND WILLI E. R. XYLANDER

As all euarthropods, diplopods possess a circulatory system which can be described as an open hemolymph vascular system (Wirkner et al., 2013). That means the body cavity is a space filled with hemolymph in which the internal organs are bathed. Being mostly larger than just a few millimetres and therefore not being able to rely only on diffusion as a transport mechanism, diplopods need an active circulation of their hemolymph. This is accomplished by a system including a vascular part (the hemolymph vascular system), the spaces between the organs (the hemolymph lacunar system) and the circulated liquid, the hemolymph itself, in which the hemocytes float. The anatomy of the circulatory system in diplopods has only been studied in very few species. Most relevant contributions are by Newport (1843), Heathcote (1889), Rossi (1902), Seifert (1932), Leiber (1935), Seifert & Rosenberg (1978) and Pass (1991).

ANATOMY AND VASCULAR ULTRASTRUCTURE

The descriptions of the circulatory system follow the division of the diplopod body into head and trunk.

Due to the open circulatory system in Arthropoda the body fluids of the primary and secondary body cavity are a haemolymph (a mixture of lymph and blood). There are several functions taken over by the haemolymph, e.g. transfers of nutrients from the intestine to the tissues, immune response, haemolymph clotting and wound healing, and cuticle tanning.

Hemolymph vascular system

The central pumping structure, the heart, extends through the complete trunk and is located just dorsally to the digestive tract (Fig. 7.1A). Hearts in diplopods are relatively thin-walled tubes (Fig. 7.1B) consisting of a myocard or heart muscle which is covered

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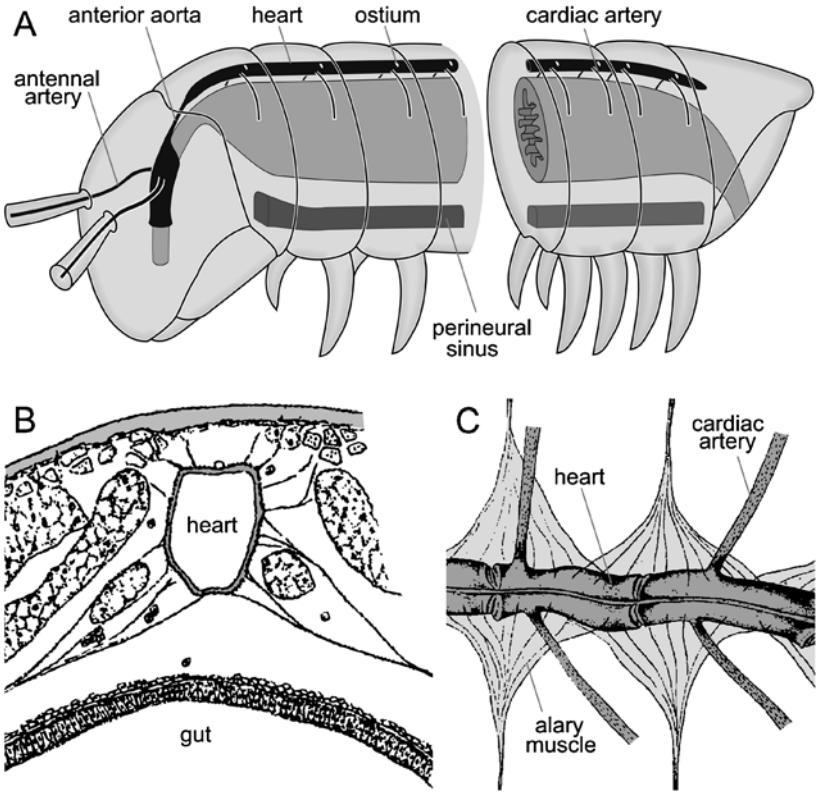


Fig. 7.1. Schematic representation of the cardiovascular system in Diplopoda. **B** Schematic drawing of a cross section through the heart in *Strongylosoma stigmatosum*. **C** Schematic drawing of the heart and alary muscles in *Strongylosoma stigmatosum*. Note that in each diplosegment two pairs of ostia, cardiac arteries and alary muscles occur respectively. **A** Modified after Wirkner et al. (2013). **B, C** Redrawn after Seifert (1932).

by an outer and an inner layer of extracellular material (Seifert & Rosenberg, 1978). The myocard itself is made up of circularly arranged cardiomyocytes. Hearts are suspended in the trunk (a) dorsally via suspending strands which are irregularly distributed along its length, and (b) ventrally through its attachment to the dorsal diaphragm (Fig. 7.1B). The latter contains alary muscles; through their contraction the heart is widened during the diastole (Fig. 7.1C). In each diplosegment, the hearts have two pairs of incurrent ostia, two pairs of lateral cardiac arteries and two pairs of alary muscles (Fig. 7.1C) while in each of the three anteriormost thoracic segments just one pair of ostia and arteries occur (Seifert, 1932). The lips of the ostia which project into the tube of the heart are formed by four peculiarly-shaped cardiomyocytes (Heathcote, 1888). The cardiac arteries are short unbranched vessels and open between the cells of the fat body in the lateral parts of the trunk segments. According to Seifert (1932) and Leiber (1935) cardiac arteries have no valves at their origin to prevent backflow of hemolymph during systole. Based on histological studies the wall of the cardiac arteries is considered to constitute

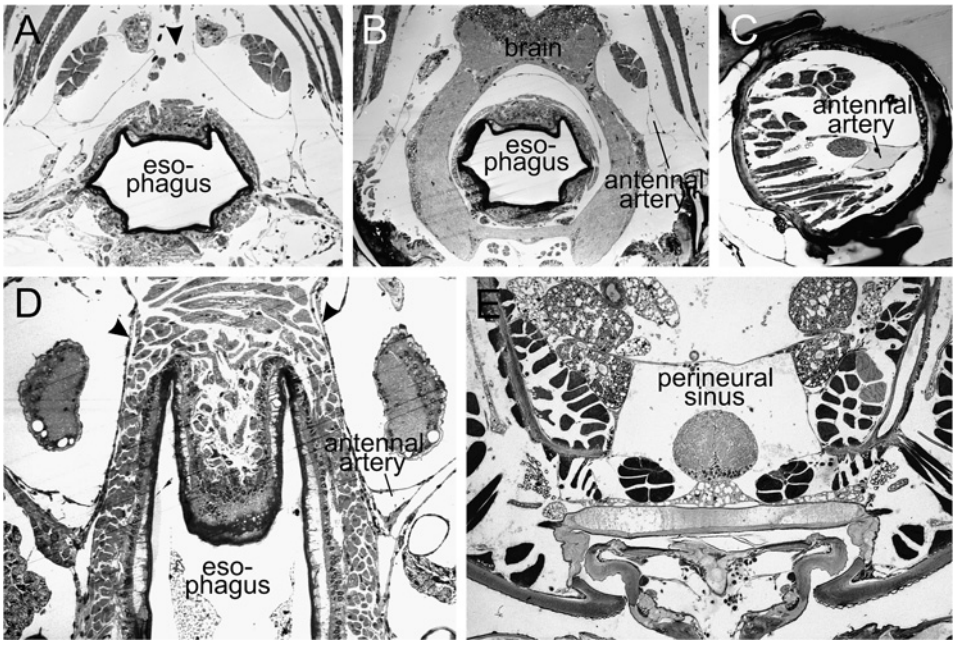


Fig. 7.2. Semi thin sections visualizing vascular structures in *Polydesmus denticulatus*. **A-D** Periesophageal sinus and antennal arteries: **A** Head posterior to brain (cross-section). Antennal arteries arise from periesophageal sinus; latter with dorsal opening (arrow). **B** Head anterior to **A**. Antennal arteries extend lateral to brain. **C** Antenna. Artery attached to antenna1 nerve. **D** Head (horizontal section). Antennal vessels originate from perioesophageal sinus, delimited by thin connective tissue sheath (arrows). **E** Trunk segment. Perineural sinus surrounding ventral nerve cord. **A-E** Originals: G. Pass (University Vienna).

a continuation of the connective tissue sheath of the heart and therefore might not be contractile. Posteriorly, the heart ends blindly, whereas it is prolonged anteriorly by the anterior aorta (Fig. 7.1A). The transition from the heart into the anterior aorta is located in the anteriormost trunk segment. The anterior aorta runs dorsally of the digestive tract towards the region where the oesophagus bends ventrally. Here, the anterior aorta connects dorsally to the oesophagus to ventro-laterally surround it completely thus forming the so-called perioesophageal sinus (Figs. 7.1A, 7.2A-D; Pass, 1991). This sinus opens into the cephalic hemocoel in the shape of a funnel. Off the perioesophageal sinus, a pair of arteries extends into the antennae (Fig. 7.2A-C). Along the dorsal side of the anterior aorta and the heart a dorsal heart nerve runs medially to the end of the heart (Fig. 7.1B). Segmental nervous connections to the ventral nerve cord as described for chilopods (e.g., Wirkner et al., 2011) have not been observed (Seifert, 1967).

Lacunar system

In comparison to the vascular system, even less information exists concerning the lacunar system. From the posterior part of the head towards the ventral nerve cord, it

lies within a so-called perineural sinus (Figs. 7.1A, 7.2E). According to Clarke (1979) just behind the head the anterior aorta communicates through a pair of sinuses with this perineural sinus. In the trunk segments a membrane extends ventro-horizontally thus dividing the hemolymph space into a ventral (perineural) and a perivisceral sinus. The perivisceral sinus itself is separated from the dorsal pericardial sinus by the pericardial membrane or dorsal diaphragm (Fig. 7.1B). Thus, the trunk is all in all divided into three major longitudinal hemolymph spaces.

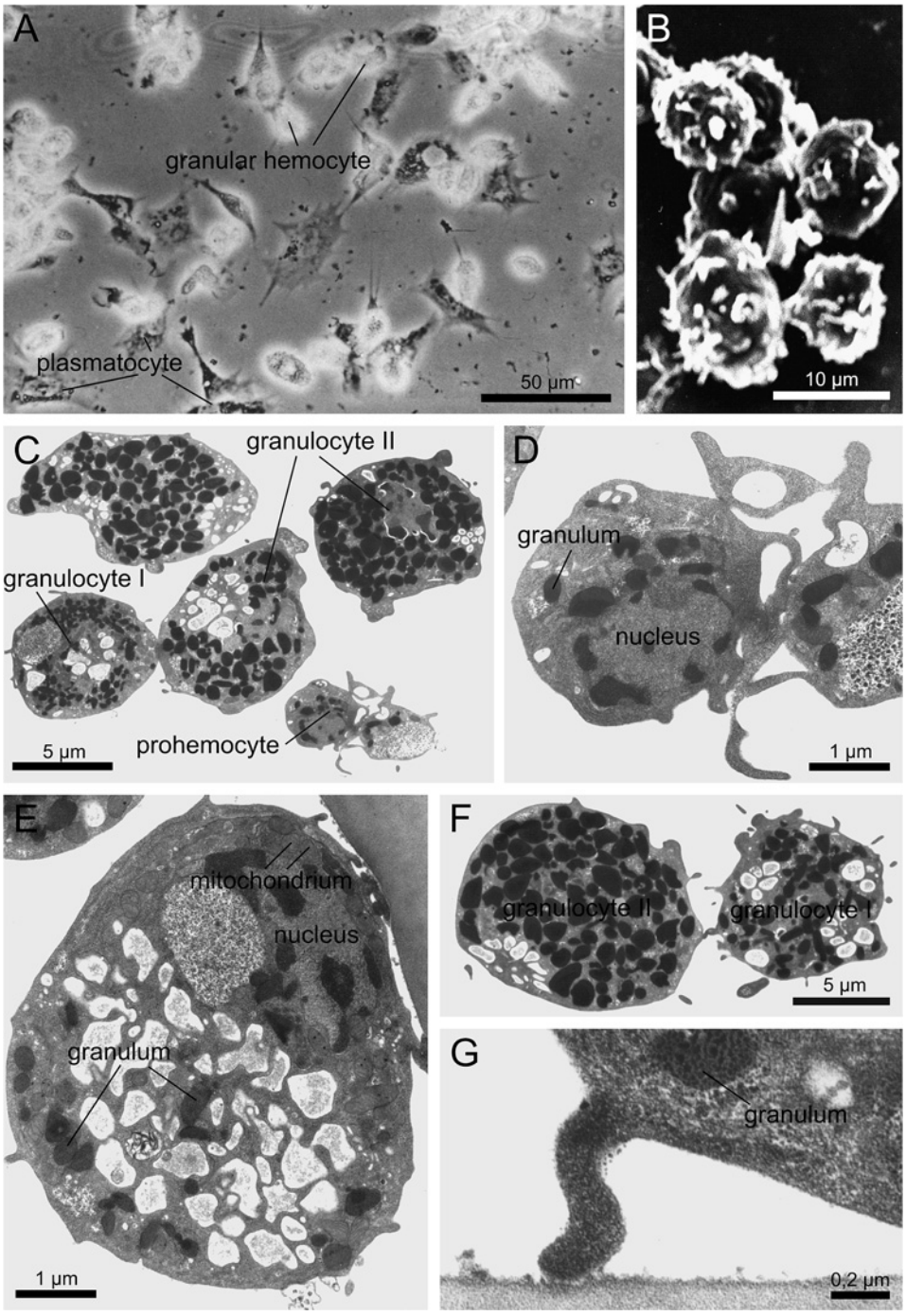
HEMOCYTES

Three types of hemocytes (Fig. 7.3) distinguished by functional and ultrastructural characteristics occur in the investigated diplopod taxa: prehaemocytes, plasmatocytes and granular haemocytes (Xylander & Nevermann, 2006; Xylander, 2009a).

Prohaemocytes are quite rare (<5% of the total haemocyte count). They are considered to be totipotent cells which may develop into other haemocytes types but in most arthropods this hypothesis still has to be proven. Plasmatocytes show little, small or no intracellular grana. They have the capability to spread strongly when getting in contact with xenografts or at wound margins. In Diplopoda, plasmatocytes have extremely little or no phenoloxidase activity (Xylander & Bogusch, 1992, 1997; Xylander & Nevermann, 1993; Xylander, 1996); they comprise about 40% of all haemocytes. In species of Diplopoda investigated, two types of granular haemocytes could be distinguished which differ with regard to their spreading behaviour, the ultrastructure of the grana and the PO activity (see Xylander & Bogusch, 1997; Xylander & Nevermann, 2006; Xylander, 2009a). The function of these cells is not clear but they may be involved in capsule formation during immune response to larger xenografts or parasites.

The number of haemocytes in the few species of Diplopoda investigated so far is significantly lower (2000 to 4000 haemocytes per μl) than in most other arthropod taxa (see Xylander & Nevermann, 2006; Xylander, 2009a for comparative data) probably due to the protective function of the hard cuticle of millipedes which make injuries less probable than e.g. in the soft bodied chilopods. As a consequence clotting is much slower in millipedes than in centipedes. In both taxa, however, wound closure results in dark, melanised scars or clots. Haemolymph chemical properties in millipedes with regard to pH,

Fig. 7.3. Hemocytes in diplopods. From Xylander (2009). **A** Hemolymph preparation with various hemocytes (pure haemolymph, 20 min after puncture, phase contrast). **B** Hemocyte aggregation in vitro observed by scanning electron microscopy (SEM). The hemocytes with short extensions on the cell surface are plasmatocytes. **C** Overview of various hemocytes observed by TEM. **D** TEM photograph of a prehemocyte. **E** Plasmatocyte. Peripheral in the cytoplasm only few grana are visible. In the centre of the cell vesicles filled with flocculent material have gathered. **F** Granular hemocytes of type I and type II observed by TEM. The grana of type II are larger, more spherical and form fewer pseudopodia than type I. **G** TEM observation of a granular hemocyte forming pseudopodia with contact to the substrate.


A
granular hemocyte
plasmatocyte
50 µm
B
10 µm
C
granulocyte II
granulocyte I
prohemocyte
5 µm
D
granulum
nucleus
1 µm
E
mitochondrium
nucleus
granulum
1 µm
F
granulocyte II
granulocyte I
5 µm
G
granulum
0,2 µm

protein content and osmolarity have been recently described and discussed by Xylander (2009b).

CHEMICAL COMPOSITION OF THE HEMOLYMPH

The chemical composition of the hemolymph has only been studied in few species.

Protein content

The protein content of hemolymph ranged between 21 mg ml^{-1} in *Chicobolus* sp. and 56 mg ml^{-1} in *Rhapidostreptus virgator* (Xylander, 2009a). Rajulu (1974) mentioned a total protein content for the hemolymph of the *Cingalobolus bugnioni* of 1.975 mg ml^{-1}. Although protein content may vary between species a 10 to 90-fold difference may rather result from errors during measurement or calculation of protein content. Thus, differences in protein content in Diplopoda will most probably range between 20 to 120 mg ml^{-1} hemolymph. Furthermore, the protein content may vary seasonally as well as with regard to the status within the moulting cycle and sex (Rajulu, 1974; Helbing, 1985, 1989). In specimens of *C. bugnioni* (body weight exceeding 20 g) between 70% (in females) or 30% (in males) higher protein content was found. Rajulu (1974) found 6 hemolymph proteins in male and 7 in female *C. bugnioni* whereas Xylander described 43 to 63 bands in an SDS-PAGE (and 16 larger proteins fractions) für *Chicobolus* sp. and 42 to 53 for *R. virgator* (and 19 larger fractions) (Xylander, 2009c).

Osmolarity

The osmolarity in the hemolymph was found to be 229.6 ± 47.3 mOsm in *Chicobolus* sp. (n = 12) and 200.3 ± 35.4 mOsm in *R. virgator* (n = 10). The variation between single specimens was comparably high (e.g. between 146 mOsm and 250 mOsm in *R. virgator* and 156 mOsm and 289 mOsm in *Chicobolus* sp., respectively). Osmolarity of haemolymph largely depends on environmental factors such as temperature, diet or moisture. As Diplopoda (and Chilopoda) quite rapidly loose body weight and die when kept under too dry conditions (own observations) environmental or rearing conditions obviously play a crucial role for these groups (Xylander, 2009c). Preliminary observations on haemolymph osmolarity from diplopods (W. Xylander, unpubl.) kept under different moisture conditions in artificial habitats or on diets with different water content (potato or cucumber), indicate a higher relevance of the diet in this taxon. This may be due to the fact that the calcified cuticle of most diplopods provides a better short-term protection against evaporation than the thinner cuticle of chilopods.

pH

The hemolymph pH in two diplopod species investigated (*Chicobolus* sp. and *R. virgator*) ranged from slightly to moderately alkaline (pH 8.0 to 8.5 in freshly collected hemolymph and pH 8.5 in frozen hemolymph). Cell-free haemolymph plasma and total haemolymph showed no difference in pH.

Hemocyanin

The hemocyanin of *Spirostreptus* sp. displays the typical arthropod hemocyanin features in terms of subunit size, structural appearance, and spectroscopic properties (Jaenicke et al., 1999). Its sequence contains all amino acids that are required for the function of a true oxygen carrier (Kusche & Burmester, 2001). While the role of the insect protein is not well understood (Sánchez et al., 1998), the myriapod hemocyanins closely resemble that of crustaceans and chelicerates in physiological and structural properties (Kusche & Burmester, 2001).

CARDIAC INNERVATION AND HEART BEAT

After Hertel (2009), who studied *Archispirostreptus gigas* using electrophysiological experiments including electrocardiograms and intracellular recordings from dorsal vessel muscle cells, heartbeat generation in Diplopoda is myogenic. Experiments with tetrodotoxin confirmed this result, and also showed that proctolin, acetylcholine and octopamine have no effect (Hertel, 2009).

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CHAPTER 8

DIPLOPODA — NERVOUS AND NEUROENDOCRINE SYSTEMS

BY

ANDY SOMBKE AND JÖRG ROSENBERG

NERVOUS SYSTEM

No detailed and comparative analysis of the diplopod nervous system is currently available and our present knowledge of the anatomy is anything but complete. The first descriptions were given by Treviranus & Treviranus (1817), Newport (1843), and Owen (1855). Detailed anatomical information were firstly given by Saint-Remy (1890), Holmgren (1916) and Hanström (1928). Sahli (1966) described in detail the nervous system of representatives of the Julida. In parallel, Seifert (1966) provided a comparative overview on the nervous system of representatives of Penicillata, Chordeumatida, Glomerida, Julida, and Spirostreptida.

In mandibulate arthropods, the nervous system can be separated into a central nervous system, composed of brain and ventral nerve cord, and a peripheral nervous system. The brain is a syncerebrum formed by the close association as well as structural and functional transformation of segmental ganglia (Richter et al., 2010; Loesel et al., 2013). Thus, the brain is tripartite and composed of the neuromeres proto-, deuto-, and tritocerebrum. Each neuromere is usually compartmentalized to some degree into definable clusters of neurons in the periphery that surround central neuropils (Richter et al., 2010). In the Myriapoda, the neuraxis (the axis of the nervous system) of the brain is commonly arcuated along the anterior-posterior body axis resulting in a dorsal or even posteriodorsal position of the protocerebrum (Fahlander, 1938; Sombke et al., 2012). Brain neuromeres are not separated by clear borders, but can be distinguished externally by their associated nerves. The neurilemma is thin and composed of two parts: an internal perilemma and an external neural lamella (Joly & Descamps, 1984). The perilemma is composed of different cells types including glial cells. In *Gymnostreptus olivaceus*, Francicso et al. (2015) described an additional external discontinuous and irregular cell sheath whose function appears to be linked to nutrition and protection.

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Protocerebrum

The protocerebrum is the largest part of the brain (Fig. 8.1A-D). It consists of the frontal lobes and extends laterally to include the optic lobes (missing in blind species). Diplopoda possess two optic neuropils commonly termed lamina and medulla (e.g. Holmgren, 1916; Hanström, 1928; Francisco et al., 2015; Sombke & Harzsch, 2015). The second-order optic neuropil (medulla) is also termed 'visual tectum' because it matches the characteristics of the hexapod lobula plate (Strausfeld, 2005). In *Orthoporus ornatus*, Strausfeld (2012) described that photoreceptor axons project into a single planar lamina, from which relays extend centrally to target a group of spindle-shaped neuropils via uncrossed axons. However, older descriptions of '*Julus* sp.' (e.g., Hanström, 1928) mention a layered arrangement of this second-order optic neuropil. The mediodorsal part of the protocerebrum is termed *pars intercerebralis* (Holmgren, 1916). In '*Julus* sp.', Holmgren (1916) distinguished three globuli (I-III) associated with the mushroom bodies that correspond to the '*masse ganglionnaire antérieur*' and the two '*masses ganglionnaire externe et interne*' of Saint-Remy (1890). The globuli are accumulations of small neurons poor of cytoplasm termed globuli- or Kenyon cells. Globulus II corresponds to the *corpora pedunculata* of Hexapoda (Saint-Remy, 1890). According to Sahli (1966), all three globuli belong to the protocerebrum. In general, arthropod mushroom bodies are centers for sensory integration and memory formation, and represent the neuronal basis for associative and flexible behaviors (Loesel et al., 2013). The most prominent input originates in the olfactory lobes through the projection neuron tract which in diplopods was only described for '*Julus* sp.' (Holmgren, 1916) and *Orthoporus ornatus* (Strausfeld et al., 1995; Strausfeld, 2012). Dendritic arborizations of globuli cells form calyces or stalked glomeruli ('Stielglomeruli' sensu Hanström, 1928), axons provide a system of parallel fibers called pedunculi or stalks ('Stiele' sensu Holmgren, 1916). In *Orthoporus ornatus*, Strausfeld (2012) depicted microglomeruli that conjoin the mushroom bodies. A short pedunculus extends laterally, dividing into several parallel lobes and reaching the midline but not crossing it (Strausfeld et al., 1995). Another pedunculus crosses the midline forming a contralateral connection (Strausfeld, 2012). In addition, medial (or median) bodies occur (Holmgren, 1916; Horridge, 1965; Sombke & Rosenberg, in press) (Fig. 8.2C). Here, axons converge and thus establish a contralateral connection of the pedunculi. Histologically, Sahli (1966) described intracerebral structures ('îlot intra-globulaire' or 'organes intra-globulaires') in Julida, Polydesmida and Nematophora situated anterior-dorsal within globulus I. Similar structures ('organes neuraux') were described by Juberthie-Jupeau (1967a) within globulus I of different species of Glomerida (Glomeridae, incl. *Trachysphaera*; Glomeridellidae), and by Nguyen Duy-Jacquemin (1974) in *Polyxenus lagurus*. Jamault-Navarro (1992) interpreted such structures as intracerebral sensory structures ('structures sensorielles intracérébrales'). An unpaired midline neuropil or central body, common in arthropods, seems to be absent (Loesel et al., 2002) or 'insignificant' (Holmgren, 1916; Hanström, 1928) in Diplopoda (compare Fig. 8.2C). According to Holmgren (1916) it is completely embedded in fibers. Strausfeld (2012) interpreted this reduction as expressing a redundant function of leg motor circuits;

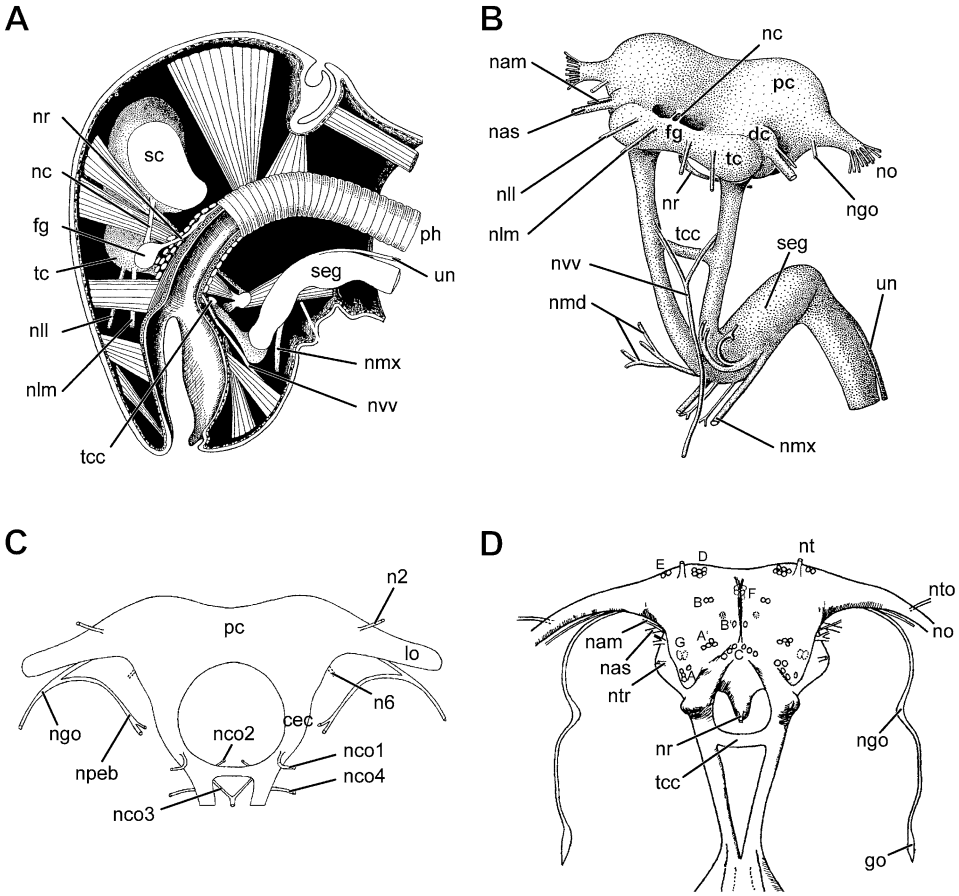

Fig. 8.1. Overview of the diplopod brain. **A** Schematic sagittal section of the head of *Craspedosoma rawlinsii*. **B** Schematic frontolateral view on the brain of *C. rawlinsii*. **C** Schematic frontal view on the brain of *Tachypodoiulus niger*. **D** Schematic frontal view on the brain of *Polyxenus lagurus*. **A** Modified after Seifert (1966). **B** Modified after Seifert (1971). **C** Modified after Sahli (1966). **D** Modified after Juberthie-Jupeau (1983). Abbreviations: **A-F** mark specific neurosecretory cells in the brain of *Polyxenus lagurus*; **cec** circumesophageal connectives; **dc** deutocerebrum; **fg** frontal ganglion; **go** Gabe organ; **lo** lobus opticus; **n2** nerve n2; **n6** nerve n6; **nam** motor antennal nerve; **nas** sensory antennal nerve; **nc** nervus connectivus; **nco1-4** periesophageal nerves; **ngo** Gabe organ nerve; **nll** nervus labralis lateralis; **nlm** nervus labralis medialis; **nmd** nervus mandibularis; **nmx** nervus maxillaris; **no** nervus opticus; **npeb** paraesophageal body nerve; **nr** nervus recurrens; **nt** tegumentary nerve; **nto** nervus tömösváryi; **ntr** trichobothrial nerve; **nvv** nervus visceralis ventralis; **pc** protocerebrum; **ph** pharynx; **sc** syncerebrum; **seg** subesophageal ganglion; **tc** tritocerebrum; **tcc** tritocerebral commissure; **un** unpaired nerve.

as Diplopoda bend their body rather than altering their step length, there seems to be no need for a coordination of locomotion. A protocerebral bridge (associated with the unpaired midline neuropil) was described to be associated with globulus III (Fig. 8.2C), but it was not found again in recent investigations.

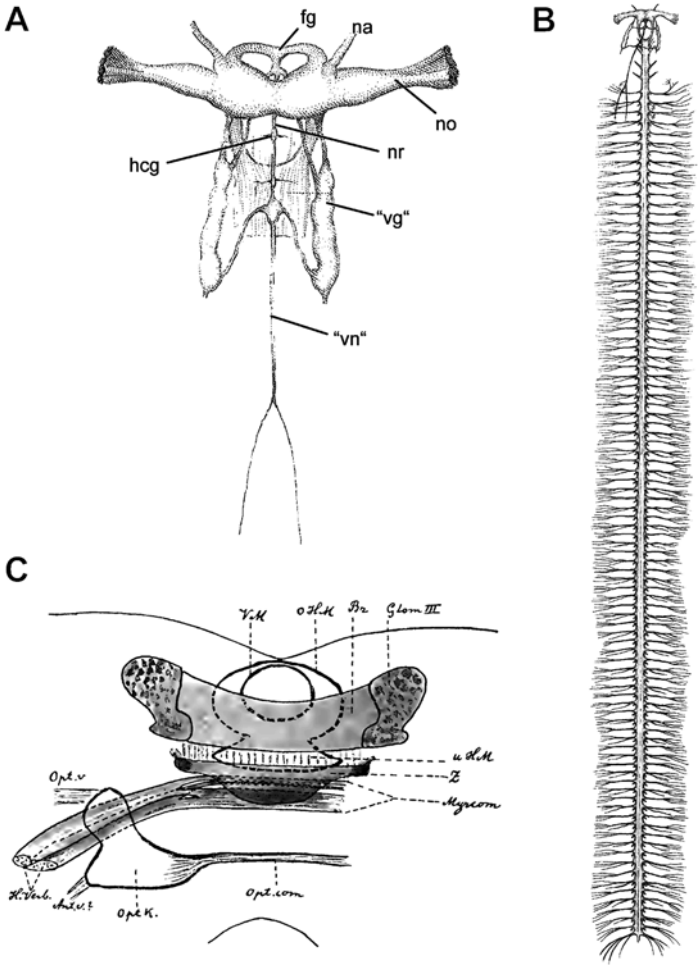

Fig. 8.2. **A** Brain and stomatogastric nervous system of '*Julus* sp.' **B** Brain and ventral nerve cord of '*Julus* sp.' **C** Brain neuropils of *Julus* sp. **A, B** Modified after Newport (1843). **C** After Holmgren (1916) with original labels. Abbreviations: **Ant. v.** antennal connection; **Br** protocerebral bridge; **fg** frontal ganglion; **Glom III** neuropil associated with globuli cell cluster III; **hcg** hypocerebral ganglion; **H. Verb.** posterior connection; **Myrcom** myriapodal commissure; **na** nervus antennalis; **no** nervus opticus; **nr** nervus recurrens; **oHM** and **uHM** posterior medial body; **Opt. com** optic commissure; **opt K** optic body; **Opt. v.** optic connection; **"vg"** visceral ganglion; **VM** anterior medial body; **"vn"** vagus nerve; **Z** midline neuropil.

Deutocerebrum

The deutocerebrum is situated frontal and ventral to the protocerebrum. The two antennal nerves (motor and sensory elements) are associated with the deutocerebrum (Fig. 8.1B, D). Near the emergence of the sensory antennal nerve, several neurosecretory cells are accumulated (Gersch, 1958; Sahli, 1966; Nguyen Duy-Jacquemin, 1971b, 1973). Axons of antennal chemosensory organs (e.g. olfactory and/or gustatory sensilla) project

into the deutocerebrum and form neuropils commonly called 'olfactory glomeruli', collectively forming the olfactory lobe. In Diplopoda, data on olfactory lobes are only available for '*Julus* sp.' (Holmgren, 1916; Hanström, 1928), *Cylindroiulus punctatus* (Nguyen Duy-Jacquemin & Arnold, 1991), *Orthoporus ornatus* (Strausfeld, 2012), and *Gymnostreptus olivaceus* (Francisco et al., 2015). Olfactory lobes are composed of spheroid to ovoid olfactory glomeruli. In *C. punctatus*, two distinct groups of olfactory glomeruli were recognized: a ventral group composed of three larger glomeruli, and a dorsal group with 15-16 smaller glomeruli (Nguyen Duy-Jacquemin & Arnold, 1991). The number of olfactory glomeruli thus could be species-specific. In Chilopoda, olfactory lobes are always composed of olfactory glomeruli (Sombke et al., 2011, 2012) and their number is thought to be species-specific (Sombke et al., 2012).

Mechanosensory input from the antennae is usually processed in a separate deutocerebral neuropil. In Chilopoda, this neuropil is called 'corpus lamellosum' due to its characteristic shape composed of several parallel neuropilar lamellae (Fahlander, 1938; Sombke et al., 2011, 2012). In *Cylindroiulus punctatus*, Nguyen Duy-Jacquemin & Arnold (1991) located a non-glomerular neuropil with parallel subdivisions ventrally of the olfactory lobe that is innervated by antennal afferents. Cobalt backfills showed a tract to the contralateral deutocerebral hemisphere. Both features indicate a similar architecture to the corpus lamellosum described in Chilopoda (Sombke et al., 2012) In *O. ornatus*, Strausfeld (2012) showed four to five small 'allantoidal domains' which could be equivalent to the chilopod corpus lamellosum.

Tritocerebrum and subesophageal ganglion

The tritocerebrum is located ventrally of the deutocerebrum (Fig. 8.1A, B). The tritocerebral lobes are linked to the subesophageal ganglion by two tritocerebral connectives that encompass the foregut (= circumesophageal connectives; Figs. 8.1B-D, 8.3A). In Diplopoda the number of tritocerebral nerves varies and their innervation areas are mostly uncertain which complicates any attempts for homologization. The tritocerebral lobes are medially connected by a stomatogastric or stomodeal bridge that appears as a medial part of the tritocerebrum (Fig. 8.1B, D). From here the stomatogastric nervous system originates entering the stomodaeum (Seifert, 1966) (see Table 8.2). Ventral to the esophagus a free tritocerebral commissure exists (Fig. 8.1B-D). In *Tachypodoiulus niger*, *Polydesmus angustus* and *Oxidus gracilis* (Sahli, 1966), and in *Propolydesmus testaceus* (Gersch, 1958), the tritocerebral connectives contain groups of neurosecretory cells. All investigated Diplopoda (except for Glomerida) possess a paired or unpaired nervus connectivus that connects the frontal ganglion and the syncerebrum (Fig. 8.1A, B). In *Craspedosoma* sp., *Glomeris* sp., *P. lagurus*, and '*Julus* sp.' an unpaired nervus recurrens (Figs. 8.1A-B, D, 8.2A) exhibits a small hypocerebral ganglion (Newport, 1843; Seifert, 1966; Nguyen Duy-Jacquemin, 1971b). The neuromeres of the subesophageal ganglion are completely fused with each other (Figs. 8.1A-B, 8.3A) and usually also fuse with that of the first pair of legs.

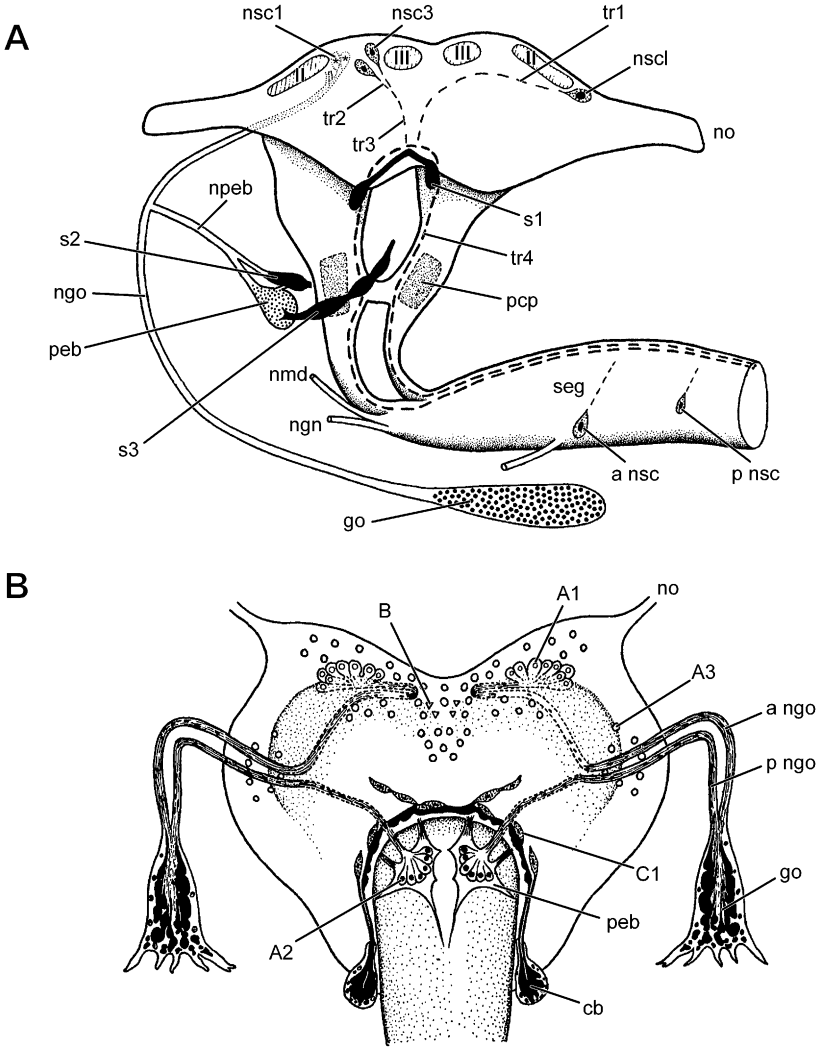

Fig. 8.3. The neuroendocrine system of Diplopoda. **A** Julid brain with neurosecretory cells. **B** Brain and neurosecretory cells in *Anoplodesmus anthracinus*. **A, B** Modified after Juberthie-Jupeau (1983). Abbreviations: **II, III** globuli cell cluster II and III; **A-C** neurosecretory cells; **a ngo** anterior nerve of the Gabe organ; **a nsc** anterior neurosecretory cells of the subesophageal ganglion; **cb** connective body; **go** Gabe organ; **ngn** nerve to gnatochilarium; **ngo** nervus of Gabe organ; **nmd** nervus mandibularis; **no** nervus opticus; **npeb** paraesophageal body nerve; **nsc1** neurosecretory cells near globuli cell cluster I; **nsc3** neurosecretory cells near globuli cell cluster III; **nscl** lateral neurosecretory cells; **pcp** paraesophageal plate; **peb** paraesophageal body; **p ngo** posterior nerve of the Gabe organ; **p nsc** posterior neurosecretory cells of the subesophageal ganglion; **s1-s3** hemolymph sinus 1-3; **seg** subesophageal ganglion; **tr1-tr4** tracts (pathways) of neurosecretory products.

Ventral nerve cord

In diplosegments, the two fused ganglia are sometimes noticeable as slight swellings (Seifert, 1932). In *Cylindroiulus zinalensis*, the ventral nerve cord appears as a homogeneous cord of tissue without these ganglionic swellings (Harzsch, 2004). Connectives are usually fused within a common sheath. However, the segmental nerve roots reveal the metameric organization (Harzsch, 2004). In '*Julus* sp.', the ganglia are almost fused, in *Polydesmus* sp. there is a considerable terminal concentration (Newport, 1843) (Fig. 8.2B). In *Strongylosoma stigmatosum*, Seifert (1932) described a thick leg nerve and a thin ventral nerve ('Bauchnerv') projecting from each ganglion. Harzsch (2004) investigated serotonin-immunoreactive (5HT-ir) neurons in some diplopod species. Bilaterally symmetrical and individually identifiable groups of 5HT-ir somata are arranged in a segmentally repeated pattern. Few somata are present close to the midline, while most 5HT-ir somata are located at the lateral margins of the ganglia. In contrast to Chilopoda, Diplopoda possess an additional group of serotonergic somata.

Brain nerves

Description of brain or cerebral nerves by Treviranus & Treviranus (1817), Newport (1843), and Haller (1904) are only of historical interest. Minor descriptions were given by vom Rath (1885) (Julida) and Seifert (1932) (Polydesmida). More detailed investigations were done by Saint-Remy (1890), Holmgren (1916), Fechter (1961), Sahli (1966), and in a comparable manner on 13 diplopod species by Seifert (1966, 1971).

In *Ommatoiulus sabulosus* (Julida), Saint-Remy (1890) counted six pairs of nerves (protocerebrum: optic nerve and nerve of the Tömösváry organ; deutocerebrum: motor and sensory antennal nerve; tritocerebrum: labral and visceral nerves). Holmgren (1916) counted the same number of brain nerves in '*Julus* sp.' (protocerebrum: optic nerve and frontal nerves; deutocerebrum: motor and sensory antennal nerve; tritocerebrum: two labral nerves) and additionally a nervus protocerebralis originating at the stomatogastric bridge. In *Strongylosoma stigmatosum*, a blind diplopod without Tömösváry organ, Seifert (1932) counted 6 nerves (protocerebrum: none; deutocerebrum: motor and sensory antennal nerves; tritocerebrum: nervus recurrens, labral nerves; as well as the nervus mandibularis and nervus gnathochilarium). Fechter (1961) counted the same brain nerves in *Cylindroiulus caeruleocinctus* as Holmgren (1916); his nervus glandulae cerebralis corresponds to the frontal nerve of Holmgren. In *Tachypodoiulus niger*, Sahli (1966) described in total 14 pairs of brain nerves. Nine pairs of nerves (N1-N9) originate from the brain (protocerebrum: N1-N2; deutocerebrum: N3-N6; tritocerebrum: N7-N9), another four pairs (Nco 1-4) from the circumesophageal connectives (Fig. 8.1C). Additionally, Sahli (1966) described two small brain nerves that connect the frontal ganglion with the brain as well as the stomatogastric nervus recurrens. The neurosecretory brain nerve (nerve of the Gabe organ) branches off from the lateral protocerebrum and innervates the Gabe organ (Figs. 8.1C, D, 8.3A-B) and, after branching, the paraesophageal bodies (see below). Seven pairs of nerves (Nsoe 1-7) originate from the subesophageal ganglion

(Nsoe 1 to the hypopharynx, Nsoe 2 to the mandibles, Nsoe 3 to the gnathochilarium, Nsoe 4 to the posterior salivary glands, Nsoe 5 to the nephridium's labyrinth, Nsoe 6 to the musculus tentorio-phragmo-occipitalis (sensu Fechter, 1961). In parallel to Sahli (1966), Seifert (1966) compared the brain nerves of different diplopod species (*Polyxenus lagurus*, *Craspedosoma rawlinsii*, *Glomeris marginata*, *G. hexasticha*, *G. klugii*, *Polydesmus coriaceus*, *Polydesmus* sp., *Allajulus nitidus*, *Julus scandinavius*, *Tachypodoiulus niger* and *Spirostreptus* sp.). In these species he described up to three protocerebral nerves, up to three deutocerebral nerves, up to eight tritocerebral nerves, and some nerves of the subesophageal ganglion (see Tables 8.1 and 8.2). In *Oxidus gracilis*, an unpaired heart nerve was described by Seifert (1966) that originates from the pars intercerebralis of the protocerebrum and accompanies the aorta caudally up to the telson.

The different numbering of nerves and sometime the vague to imprecise description of the innervation areas makes it difficult to compare the descriptions of these researchers. The brain nerves N2, N5, N6, and N7 of Sahli (1966) were not recognized or described by the other researchers and might represent specific new characters for *Tachypodoiulus niger* (Fig. 8.1C). The nerve N2 innervates the integument near the eyes, the nerves N5-N6 were described as two additional small motoric antennal nerves. The innervation of N7 remains unclear. According to Sahli (1966), the "nerf de Tömösváry" of Saint-Remy (1890), the "Frontalnerv" of Holmgren (1916) and the "nervus glandulae cerebralis" of Fechter (1961) represent probably the equivalent nerve that innervates the Gabe organ. The nervus glandulae cerebralis was misinterpreted by Seifert (1966) as it innervates the Gabe organ, a neurohemal organ (see below). The nerves Nco 1-4 (sensu Sahli 1966) were also not described by Saint-Remy (1890) and Holmgren (1916). Fechter (1961) only described two of them (N.v = Nco3, N.t = Nco 4). The nerve Nco3 of Sahli (1966) probably corresponds to the "Konnektivnerv" of Julida, the nerve Nsoe 2 probably corresponds to the nervus mandibularis, the nerve Nsoe 3 to the nervus maxillaris, and the nerve Nsoe 4 to the "Visceralnerv" described by Seifert (1966).

NEUROENDOCRINE SYSTEM AND ASSOCIATED ORGANS

Neurosecretory cells

Several types of neurosecretory cells (nsc) have been observed in different areas of the diplopod brain. Using light microscopy Gabe (1954) first described neurosecretory cells within the protocerebrum of representatives of Polydesmidae, Chordeumatidae, Glomeridae, and Julidae, situated in the *pars frontalis* near globulus II ("globulus du corps pédonculé" sensu Sahli, 1966). Gersch (1958) observed neurosecretory cells in the *pars frontalis* of a polydesmid. Mainly in *Oxidus gracilis* and *Tachypodoiulus niger*, Sahli (1958, 1966, 1977a) located different types of neurosecretory cells near globulus I (nsc1), near globulus III (nsc3), and in the lateral part of the frontal lobes (nscl) (Fig. 8.3A). In *Anoplodesmus anthracinus*, Prabhu (1962) and Juberthie-Jupeau (1983) described A1-type cells (nsc1 sensu Sahli), A2- and A3-cells in various regions of the protocerebrum, and B-cells within

TABLE 8.1

Nerves of the brain and subesophageal ganglion of different clades of Diplopoda after Seifert (1966) and Nguyen Duy-Jacquemin (1971b, 1973)

	Penicillata	Glomerida	Chordeumatida	Polydesmida	Julida	Spirostreptida
			Protocerebrum			
nervus opticus (no)	+	+	+	−	+	+
nervus Tömösváryi (nto)	+	+	?*	?*	−	−
nervus Gabe organ (ngo)	+	−	+	+	+	+
nervus occipitalis	−	−	−	−	−	+
			Deutocerebrum			
motory antennal nerve (nam)	+	+	+	+	+	+
sensory antennal nerve (nas)	+	+	+	+	+	+
			Tritocerebrum			
nervus connectivus (nc)	+	−	+	+	+	+
nervus recurrens (nr)	+	+	+	+	+	+
nervus procurrens	−	+	−	+	−	+
nervus labri medialis (nlm)	−	+	+	+	+	+
nervus labri lateralis (nll)	−	+	+	+	+	+
nervus visceralis ventralis (nvv)	−	−	+	+	+	+
connective nerve	−	−	−	−	+	−
tritocerebral commissure (tcc)	+	+	+	+	+	+
			Subesophageal ganglion			
visceral nerve	−	+	+	+	+	+
nervus mandibularis (nmd)	+	+	+	+	+	+
nervus maxillaris (nmx)	+	+	+	+	+	+
unpaired nerve (un)	−	−	+	+	−	−

Abbreviations correspond to Fig. 8.1A. The nervus occipitales, procurrens and the subesophageal visceral nerve are not depicted in Fig. 8.1.

* In these taxa, Tömösváry organs are present (see Chapter 9).

TABLE 8.2
Overview of the stomatogastric nerves in different Diplopoda

	Polyxenus lagurus	Glomerida	*Craspedosoma rawlinsii*	Polydesmida	Julida	Spirostreptida
frontal ganglion	+	+	+	+	+	+
nervus connectivus	++	−	++	+	++	++
nervus recurrens	+	+	+	+	+	+
nervus procurrens	−	+	−	+	−	+

+ unpaired; ++ paired nerves; − absent. Modified after Seifert (1966).

the pars intercerebralis (Fig. 8.3B). In *Polyxenus lagurus*, five different types of neurosecretory cells were described (Fig. 8.1D; Nguyen Duy-Jacquemin, 1971b, 1973): A-cells in the anterior part of the frontal lobe, B-cells in the median part of the protocerebrum, C-cells in the *pars intercerebralis*, D-cells in the anterior area of the frontal lobe, and E-cells at the boundary of the frontal and optic lobe. Additionally, F-cells and G-cells are located in the deuto- and tritocerebrum (Fig. 8.1D). In *Anoplodesmus tanjoricus*, three different neurosecretory cell types were described located similarly to those of *A. anthracinus* (Zilpe et al., 2013). The ultrastructure of the nsc1 was only investigated in *Ommatoiulus sabulosus* (Julidae) (Petit & Sahli, 1977). Neurosecretory cells within the deutocerebrum near the innervation site of the sensory antennal nerve were described by Gersch (1958), Sahli (1966), Nguyen Duy-Jacquemin (1971b), and Tripathi (1978). Neurosecretory cells within the tritocerebrum were described along the tritocerebral commissure by Sahli (1958, 1966) and Sahli & Petit (1975a) in *Tachypodoiulus niger*, *Ommatoiulus sabulosus*, *Oxidus gracilis*, and *Polydesmus angustus*. These cells correspond the cells of the "esophageal ganglia" of Saint-Remy (1890). In *Anoplodesmus anthracinus*, neurosecretory C1 cells (Fig. 8.3B) are present along the ventral and medial parts of the brain (Prabhu, 1959, 1961, 1962), however, they were never observed in another Paradoxosomatidae (Sahli, 1966). Nguyen Duy-Jacquemin (1971b, 1973) described neurosecretory cells in *Polyxenus lagurus*. Within the subesophageal ganglion, two paired groups of neurosecretory cells (Fig. 8.3A) were observed in *Tachypodoiulus niger*, *Polydesmus angustus* and *Oxidus gracilis* (Sahli, 1958, 1966) as well as in *Polyxenus lagurus* (Nguyen Duy-Jacquemin, 1973), and a single group in *Propolydesmus testaceus* (Gersch, 1958). Within the ventral nerve cord, neurosecretory cells are metamerically arranged (Gersch, 1958). However, they were only recognized in the anterior ganglia (Prabhu, 1962; Sahli, 1966; Nguyen Duy-Jacquemin, 1973).

Using standard cytochemical techniques, two types of neurosecretory cells were identified in the brain of *Archispirostreptus syriacus* (Warburg & Rosenberg, 1983). One of these cells was also identified using electron microscopy (EM). In addition, three different cells were observed using EM that contained secretory granules of various sizes. Altogether, five neurosecretory cell types have been observed. The secretory products of the nsc1 are stored in the Gabe organ (see below). Neurosecretory axons form the intracerebral root of the Gabe organ nerve: they emerge at the posteroventral side of the optic lobe and reach the Gabe organ (Figs. 8.1C-D, 8.3A-B). In Julidae, Blaniulidae,

Spirobolidae and Spirostreptidae this nerve is divided and gives axons with neurosecretory products to the paraesophageal body (Fig. 8.3A). Only in Spirostreptidae an additional branch projects to the blood sinus formation S2 (Sahli, 1966). Furthermore, the brain contains other pathways of neurosecretory products ("traînées de sécrétions" tr; Fig. 8.3A) (Sahli, 1966). The tr1 projects medially from the lateral neurosecretory cells, tr2 projects from the nsc3 into the posterior part of the brain and tr3 passes in a dorsoventral and lateromedial direction (Fig. 8.3A). In Julidae the pathway to the circumesophageal connective prolongs the trails tr1-3 and is called tr4 (Fig. 8.3A; Sahli, 1966; Sahli & Petit, 1975b). In *Oxidus gracilis*, tr4 originates from several pathways forming a complex system. In this species, the brain exhibits three commissures with many neurosecretory axons (Sahli & Petit, 1975b). In *Anoplodesmus anthracinus* axonal pathways from A1- and A2-cells project to the Gabe organ and that of C1-cells to the connective body (Prabhu, 1962) which is similar in *A. tanjoricus* (Zilpe et al., 2013).

Cephalic organs

Cephalic neurohemal organs have been described in Chilopoda, Symphyla, and Diplopoda (Juberthie-Jupeau, 1983; Descamps et al., 1990). According to Gersch (1964), cephalic neurohemal organs can be categorized into undifferentiated organs (without intrinsic secretory cells) and differentiated organs or glands (with intrinsic secretory cells). In order to classify cephalic organs, undifferentiated ones are termed "organ" and differentiated ones are termed "gland". The cephalic neurohemal organs are always in axonal contact to neurosecretory cells of different brain regions. In Diplopoda, Sahli (1985b) proposed the term "protocerebral neurohemal organs" for organs that are innervated by axons from protocerebral neurosecretory cells. Detailed overviews on the cephalic neurohemal organs in Diplopoda were given by Juberthie-Jupeau (1983) and Descamps et al. (1990) (see Table 8.3).

NEUROHEMAL ORGANS

Gabe organ. — Neurohemal organs were first observed in different Diplopoda by Gabe (1954) and termed "organes glandulaires" (later "glandes cérébrales"). This organ accumulates neurosecretory products of protocerebral neurosecretory cells. In *Propolydesmus testaceus*, Gersch (1958) described similar organs as glands ("Gehirnanhangsdrüsen") and later (Gersch, 1964) as cerebral glands ("Cerebraldrüsen"). In *Anoplodesmus anthracinus*, Prabhu (1959, 1961) described cerebral glands that consist of swollen terminations of neurosecretory cells. In Julida, Sahli (1958, 1961) described similar organs as "glandes endocrines céphalique" or "formations endocrines rétrocérébrales". In *Polyxenus lagurus*, Nguyen Duy-Jacquemin (1971a, b) described a neurohemal organ as cerebral gland ("glande cérébrale") without any statement on secretory activity. As a secretory activity was not detected (= undifferentiated neurohemal organ), Sahli (1963, 1966) termed this organ "organe de Gabe" in memoriam of Gabe. According to Descamps et al. (1990), Gabe mistook this organ for the paraesophageal bodies (see below).

TABLE 8.3
Neurohemal organs in Diplopoda

	Neurohemal organs			Neuroendocrine glands	
	Gabe organ	Connective bodies	Paracommissural plates	Paraesophageal bodies	Blood sinus formation
Polyxenidae	+				
Glomeridae	+			+	
Glomeridellidae	+			+	
Craspedosomatidae	+				
Chordeumatidae	+				
Callipodidae	+			+	+
Spirostreptidae	+				+*
Harpagophoridae	+				
Julidae	+		+	+	+
Blaniulidae	+		+	+	+
Cambalidae	+				
Rhinocricidae	+			+	+
Pseudospirobolellidae	+			+	+
Trigoniulidae	+			+	+
Paradoxosomatidae	+	+	+	+	
Platyrhacidae	+				
Polydesmidae	+		+		

* Blood sinus formations without intrinsic secretory cells (Sahli, 1977b). Modified after Juberthie-Jupeau (1983).

The paired Gabe organs are present in numerous if not in all Diplopoda (summarized by Juberthie-Jupeau, 1983; Descamps et al., 1990). They are located on either side of the subesophageal ganglion in the ventral and posterior part of the head (Figs. 8.1D, 8.3A-B). Their location is variable (Juberthie-Jupeau, 1983; Descamps et al., 1990). In Polyxenidae, Gabe organs are located near the maxillary nephridia (Nguyen Duy-Jacquemin, 1971a, 1973; Seifert & El-Hifnawi, 1972). In Spirostreptida (Shukla & Tripathi, 1976; Sahli, 1977a, b), Julida (Gabe, 1954; Sahli, 1958, 1961, 1966, 1977a, 1979; El-Hifnawi & Seifert, 1972; Sahli & Petit, 1972) and Spirobolida (Sahli, 1977a; Sahli & Petit, 1978), they are located in the ventral and posterior part of the head, on either side of the subesophageal ganglion. In Polydesmida, the organs are located behind the brain (Gabe, 1954; Gersch, 1958; Prabhu, 1959, 1961, 1962; Sahli, 1962, 1966, 1974, 1977a, 1979, 1980, 1985a, b). In Callipodida (Sahli, 1977a, c) and Craspedosomatidae (Gabe, 1954; Palm, 1955; Sahli, 1966, 1977a, c; Seifert, 1971) Gabe organs are situated behind the brain close to the integument of the head capsule. In Glomerida they are located close to the brain (Gabe, 1954; Juberthie-Jupeau, 1967b). Using light microscopy, the Gabe organ appears to be composed of terminals of neurosecretory axons of the protocerebral neurosecretory cells and glial cells. However, ultrastructural investigations have shown the absence of secretory cells and thus, their strictly neurohemal nature (Polyxenidae: Seifert & El-Hifnawi, 1972 ("Neurohämalorgan"), Nguyen Duy-Jacquemin, 1971b, 1973 ("organ de Gabe"); Glomeri-

dae: Juberthie & Juberthie-Jupeau, 1974; Craspedosomatidae: Seifert, 1971; Polydesmidae and Julidae: Sahli & Petit, 1972). Additionally, the organ contains tracheae and occasionally some blood cells (except in *Craspedosoma rawlinsii*: Seifert, 1971). Always, the Gabe organ is innervated by a nerve containing neurosecretory axons arising from protocerebral neurosecretory cells (Fig. 8.3A, B). Only in *Anoplodesmus anthracinus* two nerves were described (Fig. 8.3B; Prabhu, 1961). The organ can be directly (Glomeridae, Glomeridellidae, Callipodidae, Paradoxosomatidae) or indirectly (Juliformia) connected to the paraesophageal bodies and/or the periesophageal blood sinus formation (Sahli, 1966). In Julidae and Polyxenidae, the organs are connected to the subesophageal ganglion by one or two nerves. In *Craspedosoma* sp., the Gabe organ is connected to the periesophageal collar (= tritocerebral commissures and circumesophageal connectives) by a tritocerebral nerve (Descamps et al., 1990). In *Polyxenus lagurus*, Seifert & El-Hifnawi (1971) interpreted a "cerebral gland", situated directly near the tritocerebrum, as a neuroendocrine gland but without a "nervus glandulae cerebralis". This interpretation was rejected by Nguyen Duy-Jacquemin (1978, 1979) who described this gland as the 'tentorium gland' and thus as a true salivary gland.

Connective bodies. — Connective bodies were only described in the polydesmid *Anoplodesmus anthracinus* (Prabhu, 1959, 1961; Nair, 1973) and in the paradoxosomatid *Oxidus gracilis* (Sahli, 1962, 1979). In *O. gracilis* the paired connective bodies are located behind and in the vicinity of each circumesophageal connective (Juberthie-Jupeau, 1983; Descamps et al., 1990). In *Anoplodesmus anthracinus* they are located dorsally near the junction of the connectives with the brain (Fig. 8.3B). Ultrastructural studies confirm that the connective bodies of *O. gracilis* are undifferentiated neurohemal organs. They are composed of terminations of neurosecretory axons and glial cells. Connective bodies receive products from neurosecretory pathway tr4 from globulus I (Sahli, 1966; Sahli & Petit, 1974, 1975b; Descamps et al., 1990) or from neurosecretory cells located on the ventral and medial site of the brain (Prabhu, 1961, 1962) and are essentially storage organs.

Paracommissural plates. — These neurohemal formations were first described by Sahli (1966) in Julidae (Fig. 8.3A) on the posterior sides of the periesophageal collar as trails of neurosecretory products in the neurilemma of the circumesophageal collar ("traînées Tr nv"). Later, these formations were renamed "plages paracommissurales" by Sahli & Petit (1975a; also, Petit & Sahli, 1978). They have been observed in Blaniulidae, Paradoxosomatidae, and Polydesmidae (Sahli & Petit, 1975a) as well as Spirobolida (Descamps et al., 1990). The paracommissural plates are not distinctly separated from the tritocerebral connectives as extracerebral neurohemal organs. The two plates are located near the tritocerebral commissure on the posterior sides of the circumesophageal connectives. Fine structural details were described in *Ommatoiulus sabulosus* and *Tachypodoiulus niger* (Petit & Sahli, 1978). The plates are composed of neurosecretory nerve endings, glia cells, tracheae, and a neurilemma facing a blood sinus. The axons originate in tritocerebral neurosecretory cells lying in the tritocerebral commissure (Sahli & Petit, 1978).

NEUROENDOCRINE GLANDS

Paraesophageal bodies. — First described in Julidae and Blaniulidae as well as in *Oxidus gracilis* as "formations hypocérébrales" (Sahli, 1961, 1962), and later termed "corps para-oesophagiens" (Sahli, 1963). In *Anoplodesmus anthracinus* they were described as "visceral ganglia" (Prabhu, 1961) following former use of the term by Newport (1843). Paraesophageal bodies were described histologically in Glomerida (Juberthie-Jupeau, 1967b), Callipodida (Sahli, 1977c), Juliformia (Sahli, 1966, 1977c; Sahli & Petit, 1978) and Paradoxosomatidae (Prabhu, 1961, 1962; Sahli, 1961, 1962, 1963, 1980; Sahli & Petit, 1978). Fine structural examinations were conducted in *Tachypodoiulus niger* (Sahli & Petit, 1973) and *Ommatoiulus sabulosus* (Petit & Sahli, 1975) (both Julidae), and in the glomerid *Loboglomeris pyrenaica* (Juberthie-Jupeau, 1973). They were not observed in Polyxenidae, Chordeumatidae, Spirostreptida, Cambalidae, Platyrhacidae, and Polydesmidae (see Table 8.3).

Paraesophageal bodies have a spindle to oval shape and are located on each side of the foregut ventrally of the brain and behind the periesophageal collar. The organ contains terminals of neurosecretory axons and essentially intrinsic secretory cells. The axons may originate from the protocerebral neurosecretory cells of globulus I (Sahli & Petit, 1979) and project to the paraesophageal bodies via the part of the nerves of the Gabe organ and the paraesophageal body (Sahli, 1966, 1985b). The secretory cells of the paraesophageal bodies probably send at least a part of their own secretion product to the Gabe organ, as suggested in Glomeridae (Juberthie-Jupeau, 1973), Julidae (Sahli & Petit, 1973, 1979; Petit & Sahli, 1975; Sahli, 1979), and Paradoxosomatidae (Prabhu, 1962). The different types of innervation of the paraesophageal bodies and Gabe organs were described by Sahli (1979, 1980), Juberthie-Jupeau (1983), and Descamps et al. (1990). Sahli (1979) distinguished four different types of connections between Gabe organs and paraesophageal bodies: a juliform type (Julida, Spirobolida), an oniscomorph type (Glomerida), a polydesmid type (Paradoxosomatidae), and a trizonian type (Schizopetalidae).

Periesophageal blood sinus formations. — These homogenous but complex paired blood-sinus formations (S1-S4) (Fig. 8.3A) were first described in Julidae (Sahli, 1966), Spirobolidae (S1-S3) (Petit & Sahli, 1978), Spirostreptidae (S2-S3) (Sahli, 1977b), and in Callipodidae (S2) (Sahli, 1977c). Later on they were called 'blood sinus bodies' by Petit & Sahli (1975). They are closely associated with the periesophageal blood sinus, a forward extension of the cephalic aorta. In light microscopy, the components of all blood sinus formations in Julidae are the same as those of the paraesophageal bodies. Secretory cells are apparently absent only in Spirostreptidae (Sahli, 1977b, 1979). The ultrastructure of S2 blood sinus formation which is linked to the paraesophageal bodies was described in *Ommatoiulus sabulosus* and *Tachypodoiulus niger* (Julidae) as comparable to that of the paraesophageal bodies. Secretory cells and endings of the neurosecretory axons from the paraesophageal bodies are observable. Only in Spirostreptidae, intrinsic secretory cells are not observed. The secretory products of the intrinsic secretory cells are released, partially

at last, in the blood sinus located in the anterior part of the cephalic aorta (Sahli & Petit, 1979).

Clypeolabral formations. — In *Ommatoiulus sabulosus*, El-Hifnawi & Seifert (1972) described a so-called Gabe organ as a neurosecretory gland comparable to cerebral glands in Chilopoda. They are located in the lateral clypeolabrum under the anterior salivary gland. However, this organ is innervated by the tritocerebral nervus labri medialis rather than by the protocerebral Gabe organ nerve with neurosecretory axons originating from protocerebral neurosecretory cells. Therefore, this interpretation as a Gabe organ was rejected (Sahli & Petit, 1972; Descamps et al., 1990) and according to this structure's site in the clypeolabrum the term 'clypeolabral formation' was introduced by Juberthie-Jupeau (1983). This neuroendocrine gland consists of neurosecretory axons extending from protocerebral neurosecretory cells, glial cells, secretory cells (parenchyma cells sensu El-Hifnawi & Seifert, 1972), and tracheae.

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CHAPTER 9

DIPLOPODA — SENSE ORGANS

BY

CARSTEN H. G. MÜLLER AND ANDY SOMBKE

In their book on 'The biology of millipedes' Hopkin & Read (1992) stated that "*despite being one of the better-studied areas of millipede biology, we have still some way to go until structure and function of the sensory receptors and organs are as well-understood as those of insects*" (p. 86).

As a matter of fact, this statement still holds true, as only very few works on either fields of sensory morphology, physiology, or behavior of diplopods have been published since then. So, we are perfectly aware of not coming beyond scratching on the surface of a review on the sensory biology of these animals but in this chapter we rather intend to provide a fresh look on what is currently known morphologically of diplopod sense organs from the perspective of evolutionary morphology. In particular, we evaluate here to which extent present knowledge of diplopod sense organs helps resolving arthropod interrelationships.

Prior to the summary of Hopkin & Read (1992), few reviews of sensory biology of diplopods were released focusing either on external morphology (Eisenbeis & Wichard, 1985), fine structural anatomy (Haupt, 1979) or behavioral implications of their sense organs (Cloudsley-Thompson, 1951a; Barnwell, 1965). Haupt (1979) categorized millipede sense organs as simple or complex. Simple organs are cuticular sensilla, whereas complex organs are eyes, Tömösváry organs, and trichobothria. The diversity of sense organs covered by the current body of literature is pretty much restricted to the millipede's head. Those sense organs undoubtedly occurring on the trunk (sternites, tergites, rings, etc.), walking legs and gonopods are exceedingly understudied.

EYES

History of research

Like eye-bearing Chilopoda (see Müller et al., 2011 for review), all Diplopoda lack median eyes (e.g. Spies, 1981; Sierwald & Bond, 2007). If eyes are present, they always belong to the class of lateral eyes termed ommatidia according to Richter et al. (2010). Small, spherical photoreceptor organs, called accessory lateral eyes, may also be found deeply sunken into fronto-lateral, perioptical compartments of the protocerebrum in some Julidae (Heithier & Melzer, 2005). Single or several up to almost a hundred (e.g., 90 in *Spirostreptus macracanthus*) camera-type, corneal lens eyes are found at either side of the head. Fossil representatives of Diplopoda (e.g. *Glomeropsis*; see also Chapter 16) have been found in *Lagerstätten* of the Upper Carboniferous bearing more than 1000 closely aggregated ommatidia at either side of the head (Kraus, 1974).

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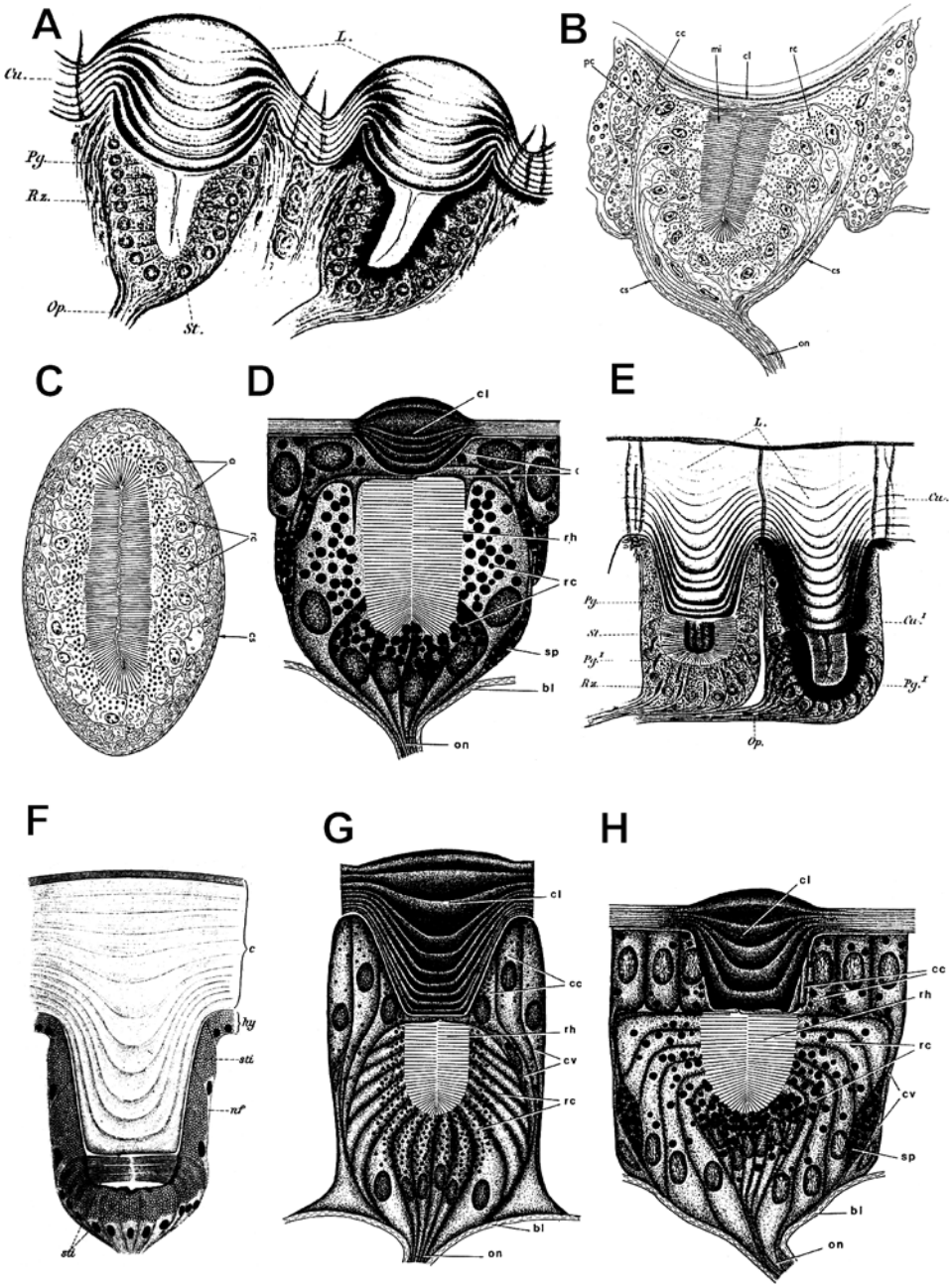
First descriptions of diplopod eyes date back to the 1820s when Müller (1829) provided basic anatomical insights from the eyes of "*Iulus* sp.". Further contributions to millipedes' gross eye anatomy were given by Leydig (1864) and Schultze (1868) and again, more comprehensively, at the end of the 19th century by Grenacher (1879, 1880), Graber (1880), Willem (1892), and Hesse (1901). These works are however limited to representatives of Penicillata (*Polyxenus* sp.), Glomeridae (*Glomeris* spp., Fig. 9.1A), and Julidae ("*Iulus* spp.", Fig. 9.1E, F; *Ommatoiulus sabulosus*). This set of investigated species represents only a fraction of millipedes possessing eyes. The focus on penicillate, glomerid, and julid eyes continues to date. The few transmission electron microscopic (TEM) studies available so far revealed valuable information on the ultrastructural organization of the eyes (Bedini, 1970, Fig. 9.1B, C; Spies, 1981, Fig. 9.1D, G, H; Paulus, 2000; Müller et al., 2007, Fig. 9.7G (colour version, see Plate X; this chapter)), but only Spies (1981) included data on polyzoniid Colobognatha (*Polyzonium germanicum*, Fig. 9.1D) and chordeumatid Nematophora (*Craspedosoma simile*, Fig. 9.1H). Among Penicillata, Müller et al. (2007) contributed new ultrastructural data on the ommatidia including the subtaxon Synxenidae. The anatomy of adult eyes of many recent Chilognatha, such as Sphaerotheriida, Siphonocryptida, Stemmiulida, Callipodida, Spirobolida, and Spirostreptida still remains unknown (e.g. Enghoff et al., 1993; see character matrix of Blanke & Wesener, 2014).

External morphology and occurrence of eyes

Blind taxa are found frequently in Chilognatha, such as in Pentazonia (Glomeridesmida), Colobognatha (Platydesmida, Siphonophorida), some Juliformia (e.g. *Typhloiulus* spp.) as well as all Polydesmida (Attems, 1926; Spies, 1981; Enghoff, 1984; Blanke &

Fig. 9.1. Histological and ultrastructural anatomy of diplopod ommatidia as reconstructed by various authors. The original labelings on the line drawings have been retained. Descriptive terms as preferred by the authors of the present chapter are given in parentheses in the list of abbreviations below. **A-C** Glomerida. **A** *Glomeris* sp., two ommatidia cut medioaxially, left ommatidium light-adapted with dispersed retinular screening pigment granules, right ommatidium dark-adapted with retinular screening pigments aggregated close to the rhabdom. **B-C** *Glomeris romana*, *G. connexa*. Ommatidium in medioaxial-longitudinal view (**B**), cross-cut distal rhabdom formed by corona of distal retinula cells (**C**). **D** Pentazonia: Ommatidium of *Polyzonium germanicum* in medioaxial-longitudinal view. **E-G** Julida. **E-F** Ommatidia of two unidentified species of *Iulus*; two adjoined ommatidia are shown in **E**; left ommatidium in light-adapted state with dispersed retinular screening pigments, right ommatidium in dark-adapted state with screening pigments aggregated around the rhabdom. **F** Ommatidium in medioaxial-longitudinal section. **G** Ommatidium of *Ommatoiulus sabulosus* in medioaxial-longitudinal section as depicted from ultrastructural observations. **H** Nematophora: ommatidium of *Craspedosoma simile* (Chordeumatida) in medioaxial-longitudinal view. **A, E** After Grenacher (1880). **B-C** Based on TEM studies of Bedini (1970). **D** Based on TEM studies of Spies (1981). **F** After Hesse (1901). **G** After Spies (1981). **H** Based on TEM studies of Spies (1981). Abbreviations: **a** Retinularaxone (= retinula axon bundle); **bl** basal lamina (= basal matrix); **c** Kutikula (= cornea), **cc** corneagenous cells, **cl** corneal lamella/lens; **cs** connective sheath (= basal matrix); **Cu** äußere Kutikula (= cornea); **cv** covering cells (= circum-/interommatidial sheath cells); **hy** Hypodermis (= epidermis); **L** Linse (= cornea); **mi** microvilli; **nf** Nervenfaser (= axons of retinula cells); **Op** optic nerve; **on** optic nerve; **pc** pigment cells (= circum-/interommatidial sheath cells); **Pg (PgI-IV)** Pigmentzellen (types I-IV); **rc** retinal/retinular cells (= retinula cells); **rh** rhabdom; **Rz** Retinazellen (= retinula cells); **sp** hypodermal cell processes with screening pigments; **St** Stiftchen (= rhabdomeric microvilli); **sti** Stiftchensaum (= rhabdom); **vb** vitreous body cell (= cone/Semper cell).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Wesener, 2014). The loss of eyes also occurred in subgroups of certain chilognath taxa that most likely possessed eyes primarily, as for instance in the spirobolid family Typhlobolellidae (Bueno-Villegas et al., 2004). As with Chilopoda (cf. Müller et al., 2011), eye loss may also occur at genus or even species level in Diplopoda (e.g. Attems, 1926), mostly linked to adaptation to cave life (Bueno-Villegas et al., 2004).

The number of eyes (ommatidia) varies in most diplopod taxa. There have been attempts to cope with the numerical diversity and to define character states with regard to eye morphology. Variation among adults is often moderate in certain taxa, as for instance within Penicillata (Synxenidae: 9-13 ommatidia in *Phryssonotus* spp., e.g. Fig. 9.7C-D: Short & Huynh, 2006; Müller et al., 2007; Nguyen Duy-Jacquemin et al., 2011; Polyxenidae: 5-6 ommatidia in *Polyxenus* spp.: e.g. Spies, 1981; Nguyen Duy-Jacquemin, 1996a; Condé, 1996; Müller et al., 2007; 6 ommatidia in *Propolyxenus squamatus*: Nguyen Duy-Jacquemin et al., 2011; 8 ommatidia in *Macroxenus enghoffi*: Nguyen Duy-Jacquemin, 1996a; 8 ommatidia in *Afraustraloxenodes* spp.: Nguyen Duy-Jacquemin, 2003; 8 ommatidia in *Unixenus* spp.: Nguyen Duy-Jacquemin & Condé, 1967; Short & Huynh, 2011) and Chordeumatida (2-3 ommatidia in Chaemaesomatidae: Attems, 1926), or all Stemmiulida (1-2 ommatidia: Attems, 1926). In other taxa, interspecific variation of ommatidial numbers in adults is much higher, as for instance in Pachybolidae (e.g. *Crurifarcimen vagans*: 30-39 ommatidia; *Hyperbolus apicomplexus*: 33-39; *Parabolus calceus*: 41-44; *Hadrobolus crassicollis*: 49-51; *Epibolus pulchripes*: 35-57; Enghoff, 2011). In general, species with more than 15 ommatidia are found among Sphaerotheriida, Callipodida, Chordeumatida, Spirobolida, Spirostreptida, and Julida (Blanke & Wesener, 2014; see Fig. 9.6D for *Tachypodoiulus niger* for example).

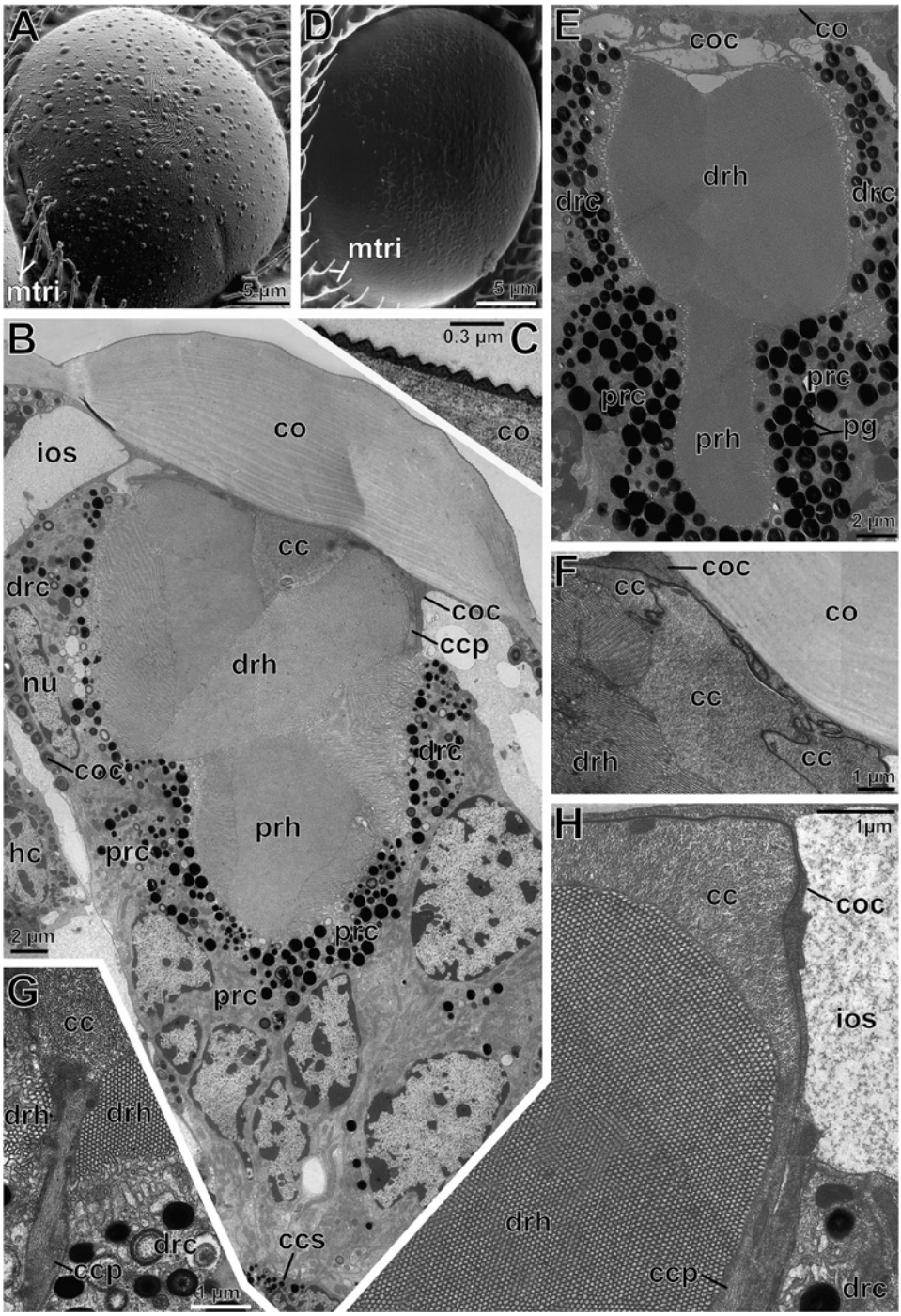
Being closely adjoined and thereby displaying overlapping optical fields, these eyes are similar to ommatidia of compound eyes of crustaceans and hexapods. And indeed, there are arguments to consider them derived from a former compound eye that was still present in the last common ancestor of Myriapoda (see below). When numerous, ommatidia are often arranged in an isosceles or less regular triangle or rhomb, e.g. in Julidae (Fig. 9.6D-F). In any case, the acute anterior apex of the triangle or rhombus is marked by a single ommatidium which is usually the smallest one in the cluster. Posterior of that point, the continuous addition of new ommatidia at moulting events establishes a new row with more ommatidia than the previous one (see below, section Eye development). The triangular/rhomboid pattern is often tight and very accurate, such as in many Arthrosphaeridae (e.g. *Zoosphaerium* spp.: Wesener & Sierwald, 2005), Chordeumatidae (e.g. *Chordeuma proximum*: Blower, 1985), Pachybolidae (e.g. Wesener et al., 2009a, b) and Julidae (*Cylindroiulus* spp.: Enghoff, 1982; Blower, 1985; Harzsch et al., 2007; see also Fig. 9.6D-F). Ommatidial diameters vary immensely among diplopod taxa, depending on size and age, but may also vary in the same species and even the same individual, especially in those diplopods bearing more than 15 ommatidia. If variation is noticeable, the largest eye diameters are found among the oldest ommatidia located at the posterior or postero-ventral end of the cluster (Blower, 1985; Enghoff et al., 1993; Harzsch et al., 2007; Fig. 9.6D). Externally, ommatidia can be recognized by their spherical to oval corneal lens that bulges out the head's cuticle. Diameters of corneal lenses are

sometimes very small, as measured by Müller et al. (2007) in bristly millipedes (15-30 μm in *Phryssonotus platycephalus*, Fig. 9.2A, B; 12-24 μm in *Polyxenus lagurus*, Fig. 9.2D). Usually, ommatidial diameters range between 40 and 150 μm within the ommatidial cluster in small- to medium-sized species. As one example we refer to measurements of Enghoff (1982) conducted in *Cylindroiulus* sp. living on the island of Madeira. Here, the range of ommatidial diameters was 40-80 μm. Another example is *Tachypodoiulus niger* with a range from 50 μm (anterior ommatidia) up to about 120 μm (posterior ommatidia) (see Fig. 9.6D). Ommatidial diameters may considerably exceed the above-mentioned dimensions in very large diplopods like Spirostreptida and Sphaerotheriida (approx. 100-300 μm in *Zoosphaerium arboreale*: Wesener & Sierwald, 2005). The corneal surface is usually smooth (e.g. Julida: Spies, 1981; Eisenbeis & Wichard, 1985; Penicillata Polyxenidae: Müller et al., 2007; see Fig. 9.2D), but sometimes displays a complex sculpture of microridges (Penicillata: Müller et al., 2007; see Fig. 9.2A) or small nipples (Glomerida).

Histological anatomy and ultrastructure

PENICILLATA

The eyes of the penicillates *Polyxenus lagurus* and *Phryssonotus platycephalus* (Fig. 9.7C) are the most thoroughly studied amongst Diplopoda (Spies, 1981; Paulus, 2000; Müller et al., 2007). In both species, the ommatidia are loosely packed and restricted to a small knob-like postero-lateral protuberance of the head, called "eye hill" (Fig. 9.7D) (Eisenbeis & Wichard, 1985; Müller et al., 2007). A distinct suture borders the eye hill from the remaining head capsule. Five ommatidia are present in *Po. lagurus* (Spies, 1981; Müller et al., 2007), 10-13 in *Ph. platycephalus* (Müller et al., 2007; Fig. 9.7D). In longitudinal sections, penicillate ommatidia appear cup-like and have a length of 25-44 μm at their centre, i.e. along the optical axis. Ommatidia are generally composed of a variable number (four or five) of weakly pigmented corneagenous cells forming the slightly biconvex, multilamellated and non-calcified corneal lens (Fig. 9.2B) and a subjacent retinula consisting of two types of photoreceptive retinula cells. There are 4-5 (*Po. lagurus*) or 5-8 (*Ph. platycephalus*, Fig. 9.3A) voluminous distal retinula cells in horizontal circular arrangement around the rhabdom (the photoreceptive structure). In addition, in both species there are always three adjoined proximal retinula cells in upright orientation, i.e. parallel to the optical axis, sitting below the main (distal) rhabdom and contributing to it with an own, but much smaller proximal rhabdom (Figs. 9.2B, 9.3G, 9.7G). Rhabdomeric microvilli are tightly packed in both distal and proximal retinula cells. Microvilli of opposing rhabdomeres never intertwine (Figs. 9.3I, 9.7G). Moreover, proximal retinula cells display a higher abundance of ommochromes (extremely osmiophilic screening pigment granules; e.g. Fig. 9.2B). If compared to eyes of Chilopoda (cf. Müller et al., 2003, 2011), all retinula cells display only a rather weakly developed system of slender perirhabdomeric ER cisternae (Fig. 9.3H). TEM studies revealed that one of the distal retinula cells is considerably smaller and contributes only a minute rhabdomere. Hence, this cell is called the irregular (distal) retinula cell (Fig. 9.3A). In addition, there are reports of either 3 eucone crystalline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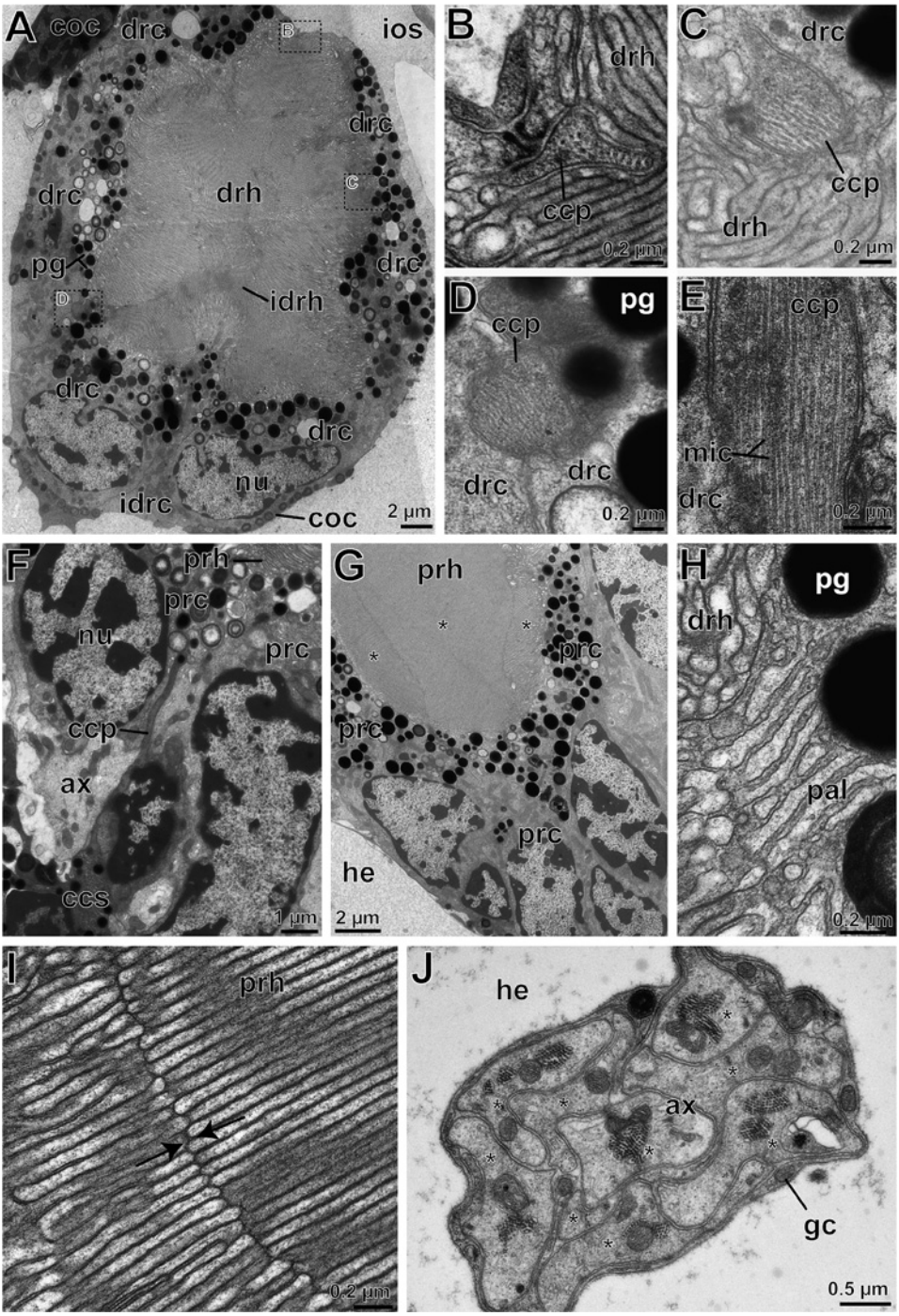
cone cells ("vitreous body cells") in each ommatidium establishing a minute and thus rudimentary tripartite crystalline cone ("vitreous body") crammed into the interface of the corneal lens and the distal rhabdom. However, the existence of such cones was only confirmed for *Ph. platycephalus* (Figs. 9.2B, F-H, 9.3A-G, 9.7G), whereas their presence and number remain ambiguous in *Po. lagurus*. Spies (1981) described two cone compartments ("vitreous bodies") per ommatidium: each compartment is secreted by a single cone cell, a modified hypodermal cell. In total, two cone cells should be present in each ommatidium. In contrast, Paulus (2000) described four cone compartments per ommatidium, thus making it four cone cells present in each eye. Müller et al. (2007) were not able to retrieve any kind of cone cells in the *Po. lagurus* ommatidia (Fig. 9.2E). In *Ph. platycephalus*, the somata of the cone cells are found proximally, sitting on the basal matrix, and contain screening pigment granules more homogenous in electron-density and considerably smaller (diameter: 0.5-0.6 μm) than those found in retinula cells (approx. 0.8 μm) (Figs. 9.2B, 9.3F, 9.7G). From each cone cell soma (Fig. 9.3F), a thin, microtubules-rich process projects distally through the infraretinular spaces, close to the rhabdom (Figs. 9.3A-F, 9.7G). To their terminal end, all three distal cone cell processes become widened (Figs. 9.2G-H, 9.7G) and establish the tripartite crystalline cone (Figs. 9.2F, 9.7G).

When approaching the bottom of the eye cup, axons of all retinula cells are gathered in a distinct axon bundle encapsulated by one or several glial cell(s) (Figs. 9.3J, 9.7G). Retinular axon bundles of the various ommatidia in a eye hill then converge to the optic nerve which projects towards the lamina (see Chapter 8). On their way to the optic nerve, the retinular axon bundles pass through the basal matrix. The basal matrix is made up by the cone cells and, from below, by thin axial processes of strongly pigmented epidermal cells. So far, there is no evidence of specialized external pigment cells (Spies, 1981; Müller et al., 2007), just like those observed below the ommatidia of pleurostigmophoran centipedes (reviewed in Müller et al., 2011). However, specialized muscle fibers may locally attach to the basal matrix implying that the focal length of each ommatidium may be altered by contraction of these eye muscles.

Fig. 9.2. External morphology and cellular anatomy of ommatidia of bristly millipedes (Penicillata): dioptric apparatus. **A-C, F-H** *Phryssonotus platycephalus*. **D, E** *Polyxenus lagurus*. **A** Corneal lens with fingerprint-like sculpturation of nanoridges. SEM. **B** Ommatidium in paramedian (axial) section showing the biconvex corneal lens, rudimentary cone compartments (one cone cell soma is present at the bottom of the micrograph), and double layer comprising distal and proximal retinula cells/rhabdoms. TEM. **C** Close-up of corneal surface showing nanoridges in longitudinal section (line of sawteeth). TEM. **D** Smooth corneal lens. SEM. **E** Ommatidium in longitudinal section lacking crystalline cone compartments (corneal lens cut off). TEM. **F** Oblique-transverse section through dioptric apparatus showing all three cone compartments. TEM. **G-H** Transition zone of proximal cone cell root (ascending from proximal cone cell soma, not shown) and related cone compartment in transverse (**G**) and longitudinal (**H**) sections. TEM. **A, D-F, H** Modified after Müller et al. (2007). **B-C, G** Originals: C. H. G. Müller & A. Sombke. Abbreviations: **cc** cone cell/cone compartment; **ccp** (proximal) cone cell process; **ccs** cone cell soma; **co** corneal lens; **coc** corneagenous cell; **drc** distal retinula cell(s); **drh** distal rhabdom; **hc** hemocyte; **ios** interommatidial space; **mtri** microtrichia; **nu** nucleus; **pg** screening pigment granules (ommochromes); **prc** proximal retinula cell(s); **prh** proximal rhabdom.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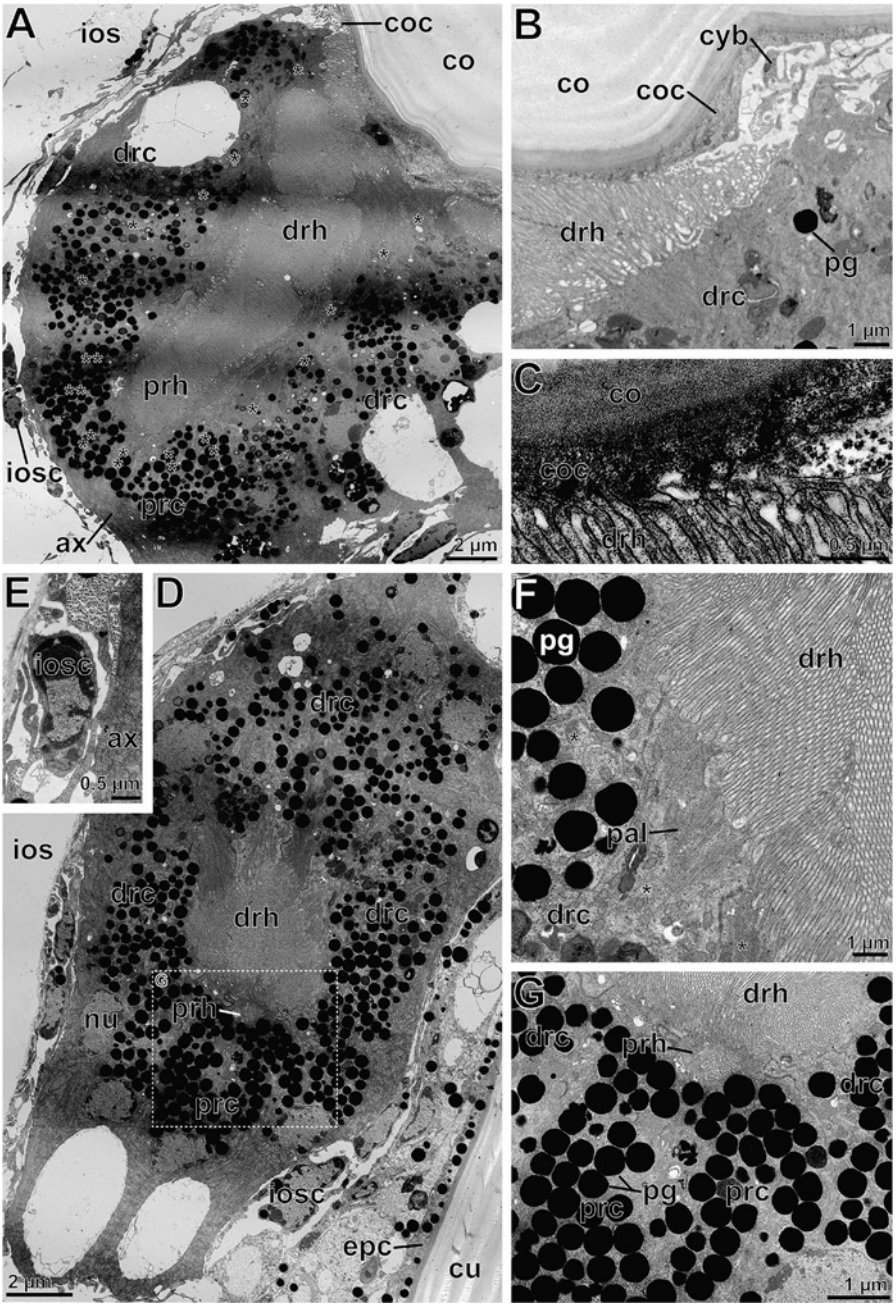
GLOMERIDA

Ultrastructural data are available for *Glomeris romana* and *G. connexa* (Bedini, 1970; see Fig. 9.1B, C) as well as *G. marginata* (this chapter; see Fig. 9.4). In most species of *Glomeris*, 5-9 rounded to ovoid ommatidia, with a diameter of 50-150 μm (Bedini, 1970), are found at either side of the head (e.g. Bedini, 1970; Spies, 1981; Blower, 1985; Golovatch et al., 2009b). The ommatidia are arranged in a slightly curved line bordering the lateral side of the Tömösváry organ (see Fig. 9.8A-B). Only to the posterior end of the ommatidial line, two ommatidia are stacked transversally and build a small row, resulting in an X + 2 arrangement. Ommatidia of *Glomeris* spp. include a biconvex, multilamellated corneal lens secreted by an unspecified number of flattened, pigmented corneagenous cells whose somata are arranged in a circle around the baso-lateral border of the cornea (Fig. 9.4A). The corneagenous cells project thin, often branching axial cytoplasmic processes that adhere tightly to the bottom of the cornea (Fig. 9.4B, C). A crystalline cone is absent. Subjacent to the cornea and the sheath of corneagenous cells, there is the photoreceptive epithelium (retinula) composed of many highly prismatic retinula cells in a cup-like arrangement (Fig. 9.4A). The number of retinula cells was not specified by Bedini (1970), but should exceed 100 or even 200 cells. At their apices, all retinula cells emit rectangular rhabdomeres made of elongated microvilli in compact, strictly parallel formation (Fig. 9.4F). Thus, a more or less compressed hemispherical and fused rhabdom is formed. Beyond the descriptions of Bedini (1970), additional, hitherto unpublished data on the ommatidia of *G. marginata* reveal that specialized retinula cells also contribute to the proximal end of the rhabdom. These cells display a considerably higher abundance of ommochromes (granules 0.5-1.2 μm in diameter, see Fig. 9.4D, G). As the rhabdomeres of these cells are oriented slightly obliquely to or even fully in line with the optical axis, the presence of a dual-type retinula is indicated; these rhabdomeres are usually small (Fig. 9.4A, D, G). Distal retinula cells can also

Fig. 9.3. Cellular anatomy of ommatidia of bristly millipedes (Penicillata) as revealed by TEM: double-type retinula and proximal cone cell system. *Phryssonotus platycephalus*. **A** Oblique-transverse section of distal retinula containing seven cells (one of which forming an irregularly small rhabdomere). Infraretinular locations of the three cone processes are indicated by dashed boxes and are shown at high magnification in **B-D**. **E** Detail of cone cell process strengthened by numerous microtubules. Longitudinal section. **F** Longitudinal section of proximal part of the ommatidium showing proximal aspect of a cone cell process connecting to cone cell soma. **G** Longitudinal section of proximal retinula consisting of three cells, all three rhabdomeres are cut at least in part (asterisks). **H** Bases of rhabdomeric microvilli of distal retinula cell. Note the presence of slender and elongated cisternae of perirhabdomeric ER in palisade-like arrangement. **I** Apical contact zone of two rhabdomeres of proximal retinula cells in longitudinal section. Rhabdomeric microvilli are tightly adjoined and meet without intertwining (arrows). **J** Transverse aspect of axon bundle projecting from ommatidium sheathed by glial cell. Axons are marked by asterisks. **A-J** Originals: C. H. G. Müller & A. Sombke. Abbreviations: **ax** retinular axon(s); **ccp** (proximal) cone cell process; **ccs** cone cell soma; **coc** corneagenous cell; **drc** distal retinula cell(s); **drh** distal rhabdom; **gc** glial cell; **he** hemolymphatic space; **idrc** irregular distal retinula cell; **idrh** irregular distal rhabdomere; **ios** interommatidial space; **mic** microtubules; **nu** nucleus; **pal** perirhabdomeric (palisade) ER cisternae; **pg** screening pigment granule (ommochrome); **prc** proximal retinula cell; **prh** proximal rhabdom.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be distinguished by their highly prismatic soma and are arranged in horizontal circles stacked onto each other in multiple layers (Fig. 9.4A, F). Perirhabdomeric ER cisternae are weakly developed in both cell types. All distal and proximal retinula cells deliver axons, 0.5-2.0 μm in diameter, that are finally bundled (surrounded by glial cells) at the bottom of the ommatidium (Fig. 9.4A). Ommatidial axon bundles are collected in the optic nerve projecting to the lamina. The ommatidia of *G. marginata* apparently possess a nippled corneal surface and are delimitated basally towards the hemolymphatic space by a fibrillous basal matrix ("connecting sheath"), only pierced by the retinular axon bundles. Furthermore, the eye cups are surrounded laterally by processes of pigmented epidermal cells, the interommatidial sheath cells that are partly sunken below the regular epidermis level (Fig. 9.4E). Coverage of these elongated epidermal cells is especially dense at the contact zone between neighboring ommatidia, where they form extensively pigmented pouches and thus create an interommatidial pigment shield.

COLOBOGNATHA

In *Polyzonium germanicum*, three or four ommatidia, approximately 30 μm in diameter, are found at either side of the head, aligned in a single row (Spies, 1981; Fig. 9.1D). Due to the acute shape of the head, the two rows converge medio-frontally in a V-shaped structure. The optical axes of the ommatidia point fronto-dorsally. The cellular architecture of the cup-shaped ommatidia of *P. germanicum* generally resembles those of *Glomeris* spp. by having (1) a biconvex corneal lens (9 μm long, up to 15 μm in diameter) which appears strongly doomed externally, (2) a multilayered retinula, (3) a portion of proximal retinula denser equipped with screening pigment granules (ommochromes) and rhabdomeric microvilli oriented obliquely or in parallel to the optical axis, (4) a compact and fused rhabdom, and (5) interommatidial pouches of condensed screening pigment granules made up by proximal extensions of otherwise randomly pigmented epidermal cells (cf. interommatidial sheath cells in *Glomeris*). As with *Glomeris*, flattened, only randomly pigmented corneagenous cells reach into the interspace between corneal lens and distal rhabdom by the aid of many strongly branching cytoplasmic extensions. However,

Fig. 9.4. Ommatidial anatomy of *Glomeris marginata* (Glomerida). TEM. **A** Overview of cellular composition in paramedian (longitudinal) section. Note the multilayered appearance of the retinula, distal retinula cells are indicated by single asterisks (six layers), proximal retinula cells by double asterisks. **B** Periphery of truncate corneal lens with subjacent distal rhabdom and minute corneagenous interlayer. Longitudinal section. **C** Close-up of corneagenous interlayer in longitudinal section. **D** Oblique section through transition zone of distal and proximal retinula. **E** Close-up of an interommatidial sheath cell on its nuclear level. **F** Three layers (marked by asterisks) of distal retinula cells. Apical region demonstrating weakly developed perirhabdomeric ER cisternae. **G** Sector of **D** (compare dashed box) at higher magnification showing two proximal retinula cells contributing small rhabdomere. **A-G** Originals: C. H. G. Müller & A. Sombke. Abbreviations: **ax** retinular axon(s); **co** corneal lens; **coc** corneagenous cell; **cu** cuticle; **drc** distal retinula cell(s); **cyb** cytoplasmic branches of corneagenous cells; **drh** distal rhabdom; **epc** epidermal cell; **ios** interommatidial space; **iosc** interommatidial sheath cell; **nu** nucleus; **pal** perirhabdomeric (palisade) ER cisternae; **pg** screening pigment granule(s) (ommochromes); **prc** proximal retinula cell; **prh** proximal rhabdom.

the ommatidia of *P. germanicum* differ from those of *Glomeris* in having a considerably lower number of retinula cells. The distal retinula is reduced to a single circle of retinula cells with microvilli aligned perpendicular to the optical axis. Cone cells were never observed.

JULIDA

According to Spies (1981), 35-40 ommatidia flank the head of *Ommatoiulus sabulosus*, arranged in triangular formation (see Fig. 9.1G). The calcified corneal lens is unequally biconvex, displaying a barely doomed and smooth external surface and a deeply sunken proximal part. The cone-shaped lens part is truncated at its base. The cornea is secreted by numerous, weakly pigmented corneagenous cells, their cell bodies encircle its basolateral region. Corneagenous cells project thin, pigment-less processes towards the centre of the ommatidium covering the truncate surface of the corneal lens. The retinula is multilayered comprising numerous horizontal layers of retinula cells in circular formation. Due to the cup-shape of the ommatidia, those of the 300-400 retinula cells being incorporated into most proximal layers show cell bodies and rhabdomeres twisted obliquely or parallel to the optical axis. However, neither the micrographs nor the semischematic drawing yet indicate them to belong to a distinct type of proximal retinula cells (compare descriptions for Penicillata and Glomerida above). The hemispherical rhabdom is compact and fused. The retinula cells taper continuously and form axons that converge into the optic nerve at the base of the ommatidium. Spies (1981) noted the presence of specialized spindle-shaped and pigmented sheath cells ("covering cells") that are somewhat detached from the surrounding, regular epidermal cells, indicated by deeply sunken nuclei, and encompass the ommatidia externally in a multilayered fashion. Basally, they form sac-like dilations upon the basal matrix demonstrating that they should be mainly responsible for establishing the ECM in the entire eye region. According to observations of Spies (1981), the basal matrix ("basal lamina") not only delimitates the ommatidia from below but also envelopes at least a distal part of the optic nerve.

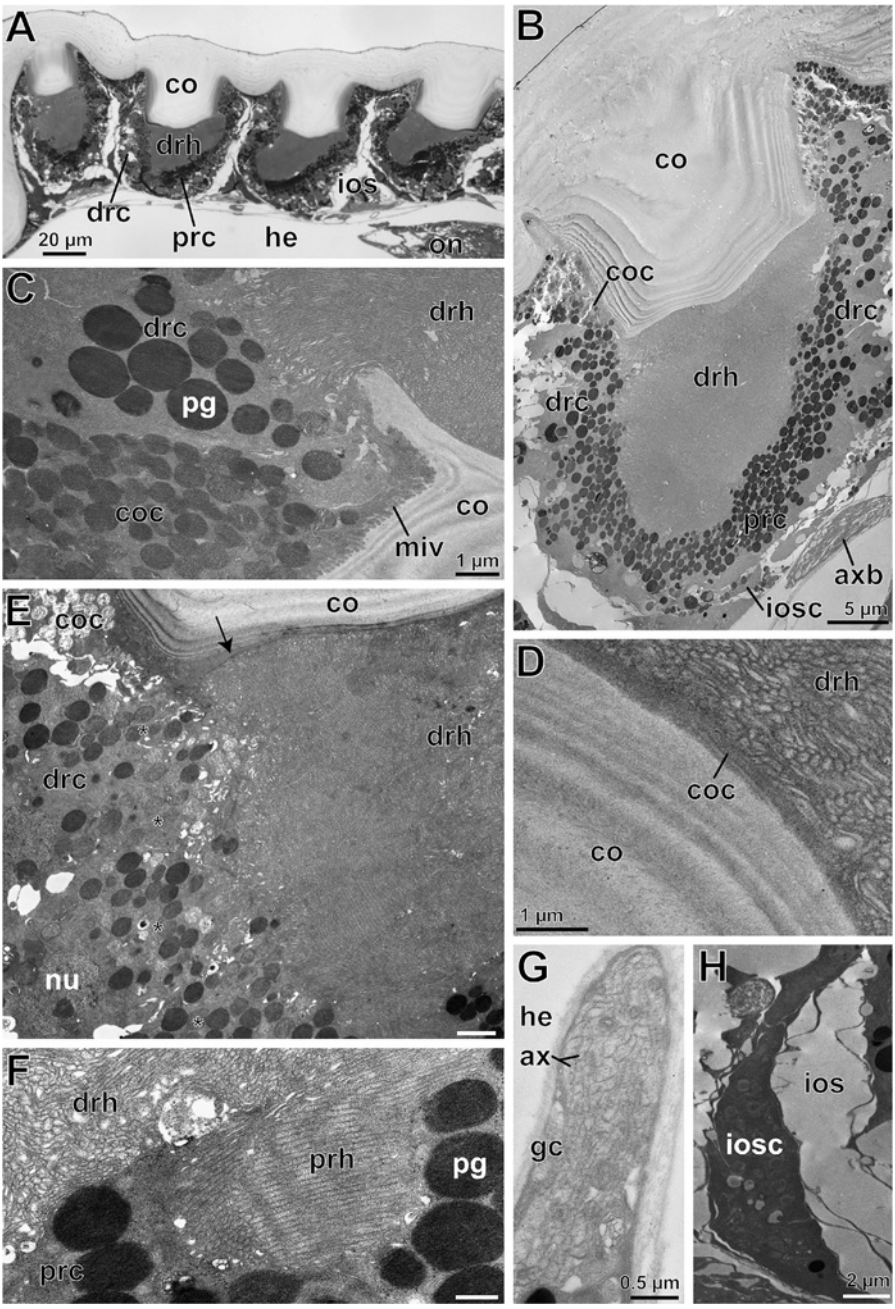
NEMATOPHORA

Among Nematophora, Spies (1981) contributed ultrastructural data for *Craspedosoma simile* (see Fig. 9.1H). Additional, so far unpublished TEM material is provided here (see Fig. 9.5), from a unidentified species of Craspedosomatidae from Pula (Istrian Peninsula, Croatia). About 26 cup-shaped ommatidia (about 60 μm in diameter and 80-100 μm in length) are closely aggregated in a triangular eye field (Fig. 9.5A). Similar to *Ommatoiulus sabulosus*, the ommatidia of *C. simile* consist of an unequally biconvex, deeply bulged corneal lens (with truncate base) and a cup-like arranged photoreceptive epithelium (retinula), stacked horizontally in most parts (Fig. 9.5B, E). Most of the 450-500 high-prismatic distal retinula cells are ordered in circular fashion and enclose the rounded or elliptical distal rhabdom. Proximally and close to the periphery of the ommatidium, the distal retinula cells become axonic and are bent down heading to the bottom's centre of the ommatidium where they bundle, together with axons of proximal retinula cells

(Fig. 9.5G). The content of the screening pigment granules (ommochromes, about 1.2 μm in diameter) of distal retinula cells exhibits heterogeneous electron-density (Fig. 9.5B, E). The proximal third of the retinula is populated by the somewhat smaller and more extensively pigmented proximal retinula cells which, along with their small rhabdomeres, are positioned obliquely or upright, thus being at least roughly in line with the optical axis of the ommatidium. Our observations confirm the distinct nature of these proximal retinula cells in the craspedosomatid ommatidium including clear distinctiveness of their rhabdomeres (Fig. 9.5F). However, it is difficult to recognize the aberrant arrangement of proximal rhabdomeres relative to the optical axis, as it strongly depends on orientation of the section and structural integrity of the retinula after fixation (Fig. 9.5F). Both distal and proximal rhabdoms are of the fused type and merged seamlessly (Fig. 9.5E, F). Ommochromes housed by proximal retinula cells are usually extremely electron-dense and show great homogeneity (Fig. 9.5B). The distal rhabdom directly abuts the truncate base of the corneal lens (Fig. 9.5B-E), only separated from the former by a tiny sheath of radial extensions of radially arranged corneagenous cells (Fig. 9.5D). Pigmented sheath cells ("covering cells") surround the ommatidia and may form several layers between and below them (Fig. 9.5A, B, H). Sheath cells may widen locally and concentrate pigment granules to form pigmented pouches ("hypodermal cell processes with screening pigments") establishing an optical shield between adjacent ommatidia (Fig. 9.5H). Basal terminations of sheath cells also establish the subommatidial basal matrix to which they remain attached constantly.

Intracerebral photoreceptors (accessory lateral eyes)

Additional photoreceptor organs are found in the form of spherical or subspherical bodies deeply sunken into the head and nested in the distalmost lateral protocerebrum, close to the optic neuropils. Histological accounts on these organs, termed neural organs or intercerebral organs (also "ilôts intra-globulaires", "glandes neurales"), have been given for a variety of Diplopoda including Penicillata (*Polyxenus lagurus*: Nguyen Duy-Jacquemin, 1974), Glomerida (Juberthie-Jupeau, 1967), Spirostrepsida (*Peridontopyge junquai*, Odontopygidae gen. sp.: Junqua, 1966; Nguyen Duy-Jacquemin, 1974), Spirobolida (*Narceus annularis*: Junqua, 1966; Nguyen Duy-Jacquemin, 1974), and Julida (*Tachypodoiulus niger*, *Ommatoiulus sabulosus*, *O. rutilans*: Junqua, 1966; Sahli, 1966; Nguyen Duy-Jacquemin, 1974). These organs were described to consist of colloidal cells encasing an spacious extracellular mass and were not identified as photoreceptors at first. That they indeed might be intracerebral eyes became apparent by ultrastructural studies on rhabdomeric intracerebral organs ("spherules rhabdomériques") in the centipede *Lithobius forficatus* (Jamault-Navarro, 1992), and the julid *Cylindroiulus truncorum* (accessory lateral eye sensu Heithier & Melzer, 2005). In *C. truncorum*, a spherule (20 μm in diameter, 5 μm in length) is found on the ventral side of the optic lobe, embedded into a cluster of neuronal somata of the optic neuropils (Fig. 9.6A). Each spherule contains six retinula cells that are overlaid by four cap cells and surrounded by glia-like cells (Fig. 9.6B, C). The retinula cells are arranged in a single circle, their nuclei are however situated on two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different levels. Each retinula cell produces a rhabdomere pointed at the centre of the spherule, thus contributing to a fused rhabdom. The rhabdom looks latticed or star-shaped in cross-sections (Fig. 9.6C), the microvilli of opposing cells may interdigitate locally. All six retinula cells form axons that target the neighboring optic neuropil. However, it is not clear which optic neuropil is innervated (see Chapter 8). Heithier & Melzer (2005) considered accessory lateral eyes to be simple light sensors with no obvious capability of delivering a highly resolved image. According to the authors, there are two, potentially homologous types of accessory lateral eyes in Arthropoda: (1) those still having contact to the cuticle and therefore equipped with a corneal lens or even a dioptric apparatus (in Chelicerata: e.g. *Limulus polyphemus*, *Parabuthus transvaalicus*, or stemmata of various holometabolous Hexapoda), and (2) those lacking contact with the cuticle and embedded into the ventral somata cluster of the optic neuropil (Myriapoda: e.g. *L. forficatus*, *C. truncorum* and further taxa of Chilognatha; accessory medulla system of hemimetabolous Hexapoda; sinus-gland-X-gland-system of Crustacea) (see also Spreitzer & Melzer, 2003).

Development

In millipedes in general and euanamorphic diplopod species (e.g. Julida, e.g. Fig. 9.6D) in particular, it may be very difficult to determine which stadium a certain specimen belongs to, as numerical or morphometrical characters frequently used in this respect (e.g. number of segments or body rings, overall body size, dimensions of segmental defense glands) may become unreliable with age because of considerable variability (Enghoff et al., 1993; compare also Fig. 9.6F). A better way is counting the eye rows that are successively added to the ommatidial cluster (e.g. Vachon, 1947; Saudray, 1952; Sahli, 1955; Blower, 1970, 1985; Peitsalmi & Pajunen, 1991, 1992; Enghoff et al., 1993; Harzsch et al., 2007). Following an eye-less first developmental stadium (stadium I = 0), one row of usually continuously increasing number of ommatidia is added at each moulting event (stadium II = +1, stadium III = +2, etc.) resulting in a multilayer of ommatidia,

Fig. 9.5. Ommatidial anatomy of an unidentified species of Craspedosomatidae from Pula (Istria, Northern Croatia) as depicted from light microscopy (**A**) and TEM (**B-H**). **A** Row of ommatidia in medioaxial and paramedian sections, stained with toluidine-blue. **B** Overview of cellular architecture in paramedian (longitudinal) section. Note multilayered structure of dual type retinula. **C** Densely pigmented corneagenous cells and distal retinula cell located in immediate lateral vicinity of the corneal lens. **D** Detail aspect of axial processes of corneagenous cells crammed between corneal lens and distal rhabdom. **E** Lateral part of distal retinula; three layers of retinula cells are visible (asterisks). Note cornea-rhabdom interlayer of corneagenous cells (arrow). **F** Oblique-tangential section of proximal rhabdom showing orientation of microvilli clearly different from distal rhabdom. **G** Retinula axon bundle in oblique-cross section. **H** Body of interommatidial sheath cell in longitudinal section. Swollen interommatidial space is most likely due to fixation artifact. **A-H** Originals: C. H. G. Müller & A. Sombke. Abbreviations: **ax** retinular axon(s); **axb** retinular axon bundle; **co** corneal lens; **coc** corneagenous cell; **drc** distal retinula cell(s); **cyb** cytoplasmic branches of corneagenous cells; **drh** distal rhabdom; **gc** glial cell; **he** hemolymphatic space; **ios** interommatidial space; **iosc** interommatidial sheath cell; **miv** microvilli; **nu** nucleus; **on** optic nerve; **pg** screening pigment granule (ommochrome); **prc** proximal retinula cell; **prh** proximal rhabdom.

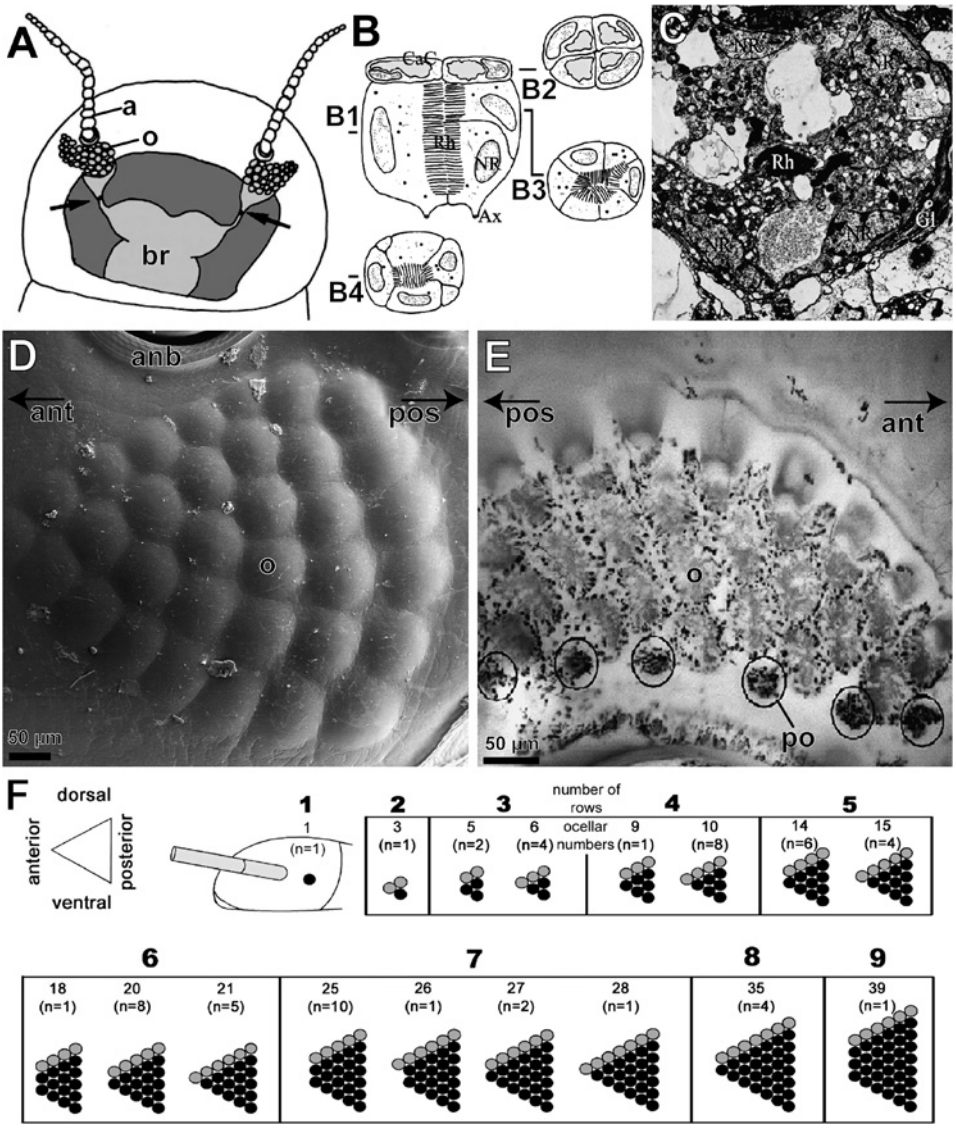

Fig. 9.6. Structure of accessory lateral eyes in *Cylindroiulus truncorum* (**A-C**) as well as distribution and development of diplopod ommatidia (**D-F**). **A** Location of accessory lateral eyes subterminal to the optic nerve (arrows). **B** Cellular organization of accessory lateral eye in longitudinal view (**B1**) and three consecutive cross levels: **B2** level of cap cells; **B3** distal level of retinula displaying an asymmetrical rhabdom; **B4** proximal level of retinula showing symmetrical rhabdom. Retinula consists of heavily transformed retinula cells, termed R-cells. **C** TEM micrograph showing a cross-section through distal part of the retinula. **D** *Tachypodoiulus niger*. Example for ommatidial cluster containing more than 15 ommatidia (cf. character coding in Blanke & Wesener, 2014). Note triangular formation of altogether eight ommatidial rows (eye formula: 1 + 2 + 3 + 4 + 5 + 6 + 6 + 6). SEM. **E** Addition of a new row of protommatidia to juvenile ommatidial cluster of *Archispirostreptus gigas* labeled with

mostly in triangular formation (see Blower, 1970 for example and Fig. 9.6D, F). The row structure is taxon/species-specific and expressed by a formula (e.g. stadium IV: 1 + 2 + 3). Enghoff et al. (1993) remarked that the eye-row-counting-method is not at all applicable to diplopods without or with only few ommatidia. Moreover, some species are known to lose entire ommatidial rows at older stages (cf. Harzsch et al., 2007) or do not clearly display linear arrangements of ommatidia anymore. Nevertheless, counting ommatidial rows is still considered an important method to determine developmental stadia in Julida as well as, but to lesser extent, in Spirostreptida, Spirobolida and Callipodida.

There is also an intercalary growth of already-formed ommatidia — the oldest and largest ommatidia are found at the posterior or posteroventral edge of the ommatidial cluster (e.g. Fig. 9.6D). In *Archispirostreptus gigas*, Harzsch et al. (2007) documented mitotic activities in the various ommatidial constituents during intercalary growth (Fig. 9.6E). The authors concluded that proliferation patterns found in *A. gigas* are remarkably similar to those revealed experimentally in eyes of Xiphosura (Harzsch et al., 2006) and observed on trilobite fossils (Zhang & Clarkson, 1990). Therefore, mechanisms of eye growth in trilobites, xiphosurans, diplopods, and chilopods reflects the ancestral arthropod mode of shaping the visual system (Harzsch et al., 2007).

Evolution and phylogenetic significance

Based on studies of Grenacher (1880), Hesse (1901), Bedini (1970), Spies (1981), and original data presented in this chapter, it can be concluded that the ommatidia ("lateral ocelli", "lateral eyes") of Chilognatha are very similar in structure and most probably homologous. The hitherto investigated ommatidia of various representatives of Glomerida, Colobognatha, Julida and Nematophora all share the following features: (1) a cup-like shape, (2) a biconvex, more or less vaulted corneal lens, (3) a circularly arranged epithelium of pigmented corneagenous cells with thin, elongated cytoplasmic processes projecting axially subjacent to the corneal lens, (4) a multilayered retinula made of high-prismatic distal retinula cells (main axis of cell bodies and rhabdomeres oriented perpendicular to optical axis) and proximal retinula cells (main axis of cell bodies and rhabdomeres oriented obliquely or parallel to optical axis, higher abundance of screening pigment granules), (5) a fused rhabdom made of compact, non-intertwining rhabdomeres, and (6) a circum(inter-)ommatidial, locally multilayered sheath of modified pigmented epidermal cells with elongated cell bodies, somata

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the proliferation marker bromodeoxyuridine (BrdU). Mitotic activity, as depicted by presence and distribution of BrdU-labeled nuclei, is also noticeable in the remaining parts of the cluster comprising already differentiated ommatidia still increasing in size. LM. **F** Postembryonic development of triangular ommatidial cluster in *Cylindroiulus truncorum*. Mappings of ommatidial numbers and distribution as well as patterns of addition of protommatidia in 60 juveniles over various euanamorphic stadia. Specimens are arranged in order of increasing number of ommatidia in a given cluster; n = number of individuals with respective pattern; grey circles indicate units that are new compared to the previous pattern. Ommatidial clusters were composed of 1-39 units arranged in 1-9 ommatidial rows (ROs); observed unit numbers were 1, 3, 5, 6, 9, 10, 14, 15, 18, 20, 21, 25, 26, 27, 28, 35, and 39, so that ommatidial cluster fell into 17 classes. **A-C** Modified after Heithier & Melzer (2005). **E** Modified from Harzsch et al. (2007). **F** Illustration adapted from Harzsch et al. (2007). Abbreviations: **a** antenna; **anb** antennal base; **ant** anterior; **Ax** axon R-cell; **br** brain; **cac** cap cell; **Gl** glial sheath; **NR** nucleus of R-cell; **o** ommatidium/ommatidia; **po** protommatidium; **pos** posterior; **Rh** rhabdom.

sunken deeply below the regular epidermis. In addition, chilognathan ommatidia (7) lack crystalline cones and eucone (Semper) cells.

In contrast, rudimentary tripartite crystalline cones made of three eucone cells with proximally placed somata (= outside crystalline cone) are present in ommatidia of synxenid Penicillata (Müller et al., 2007; see also Fig. 9.7G). Octapartite crystalline cones established by four eucone cells with proximally placed somata have been found in scutigeromorph centipedes (Müller et al., 2003; see also Fig. 9.7A, E). The common presence of cone cells with proximal placed somata suggests suggests that scutigeromorph (Chilopoda) and penicillate (Diplopoda) ommatidia are homologous (Müller et al., 2007, 2011; Müller, 2008). The partly constant cell patterns in the ommatidia of scutigeromorph centipedes and in the miniaturized, disintegrated ommatidia of penicillate millipedes give further evidence to the assumed common origin of penicillate and scutigeromorph ommatidia. These two features may be hypothesized to belong to the ground pattern of the Myriapoda (Harzsch et al., 2007; Müller, 2008). Beyond Myriapoda, common origin of myriapod, crustacean and hexapod ommatidia is indicated by the presence of (1) four eucone (Semper) cells with proximal roots and pigmented terminal swellings, (2) primary pigment cells, (3) a sheath of interommatidial pigment cells, (4) a double-layered retinula, as well as (5) the successive formation of the compound eye from an anterior proliferation zone (Harzsch et al., 2007; Müller et al., 2007, 2011). Due to miniaturization, only a subset of these constitutive mandibulate characters have been retained in Penicillata. According to Harzsch et al. (2007), penicillate and, in particular, scutigeromorph ommatidia probably represent a transitional stage along an extended time axis of evolutionary transformation from cone-less, *Limulus*-like ommatidia displaying highly variable cell numbers to the ommatidia of Tetraconata, highly determined in development and with a constant number of 2 corneagenous, 4 eucone, 8 retinula and 6 interommatidial pigment cells.

Given the distribution of eye character states known so far, it seems more parsimonious to assume that the last common ancestor of Chilognatha had a multilayered distal retinula. This multilayer was reduced to a single layer again in Colobognatha, as exemplified by the ommatidial set-up of *Polyzonium germanicum*. This view was already expressed by Verhoeff (1901) and Spies (1981) who pointed out the peculiar position of Colobognatha within the Helminthomorpha. Similar, but less radical reductions in distal retinular layers may have occurred in lithobiid Lithobiomorpha (*Lithobius forficatus*: see Müller & Rosenberg, 2006; Müller, 2008). A clade Juliformia + (Polydesmida + Nematophora) sensu Blanke & Wesener (2014) may be supported by ommatidia with deep-reaching, basally truncated corneal lenses. A further apomorphy is perhaps the increase in the number of layers of proximal retinula cells. But whether or not proximal retinula cells exist in eyes of Juliformia as a distinct cell type has to be verified by future TEM studies including a wider taxon sampling. The same issue applies to the distinctiveness of circum(inter-)ommatidial sheath cells as independent cell types in diplopod ommatidia which might indeed be homologous to interommatidial pigment cells of mandibulate ommatidia (cf. Müller et al., 2003).

Probably owing to their cup-shaped contours and tendency to dispersion, myriapod eyes others than those of scutigeromorph centipedes that look like true compound eyes (see Müller et al., 2003) have been traditionally termed as "lateral ocellar eyes", "lateral ocelli" or just "ocelli" in countless reviews (e.g. Muñoz-Cuevas, 1984; Hopkin & Read, 1992) and original papers dealing with taxonomy (e.g. Enghoff, 2011), systematics (e.g. Blanke & Wesener, 2014), descriptive morphology (e.g. Grenacher, 1880), and even evolutionary morphology (e.g. Paulus, 1979, 1986, 2000; Spies, 1981; Müller & Meyer-Rochow, 2006a, b; Müller et al., 2007). Bitsch & Bitsch (2005) preferred the more neutral term "simple lateral eyes" to address the cup-shaped, often dispersed eyes of Diplopoda and Pleurostigmophora. However, these terms are misleading as they do not acknowledge the high probability that these eyes have derived from the disintegration of compound eyes formerly present in the ground pattern of Myriapoda. Striking arguments in favor of this view and the presence of "true" compound eyes in the last common ancestor of the Myriapoda are two characters shared by scutigeromorph and penicillate ommatidia: (1) a crystalline cone made up by

three or four eucone (Semper) cells with somata located outside the cone compartments as well as (2) a bi-layered dual type retinula consisting of two circles of distal retinula cells (variable in cell numbers) and proximal retinula cells (constant in cell numbers: *Scutigera coleoptrata*: n = 4; *Phryssonotus platycephalus*: n = 3) (Müller et al., 2003, 2007, 2011; Harzsch et al., 2007; Müller, 2008). As both above-listed characters support homology of ommatidia in Scutigeromorpha and Penicillata, it seems legitimate to assume that penicillate eyes with their rudimentary crystalline cones are highly derived, miniaturized ommatidia (Spies, 1981; Müller et al., 2007). More precisely, penicillate ommatidia might have derived from "*Scutigera*-like" ones (Harzsch et al., 2007) (compare Fig. 9.7B, E and D, G). Therefore, penicillate eyes should better be called ommatidia (Müller et al., 2007). The so-called lateral ocelli of Chilognatha and Pleurostigmophora should also be considered strongly transformed derivates of compound eyes of ancestral myriapods potentially containing "*Scutigera*-like" ommatidia (cf. Spies, 1981) and therefore be called ommatidia (Richter et al., 2010). These transformations happened at least two times independently in both lineages. In this context, mechanisms and pathways that led to the evolution of recent holometabolan stemmata — implying disintegration of protommatidial clusters in early larval stages and subsequent fusion or structural modification of protommatidia — as proposed by Paulus (1979, 1986, 2000) may be a good model explaining the evolution of eyes in Chilognatha and Pleurostigmophora (e.g. the ommatidium of *Lithobius*: cf. Müller & Rosenberg, 2006; Müller, 2008 and Fig. 9.7F). Indeed, this model was introduced at times, when the Tracheata hypothesis was widely accepted, and thus in part suffered from biased assumptions or conclusions (e.g. "pseudofacetted eye" of Scutigeromorpha). Nonetheless, concerning pathways and functional restrictions of evolutionary transformations of lateral eyes Paulus' model is still very helpful, not least because structural correspondences of pleuostigmophoran/chilognathan ommatidia and stemmata of adephagan Coleoptera are striking, especially with respect to their multilayered retinulae and the absence of crystalline cones (cf. Paulus, 1986, 2000). Apparently, a tendency to disintegrate and transform ommatidia into cup-like, more or less dispersed camera-type eyes was a factor in the evolution of lateral eyes including the primary (true compound eyes and their descendants) as well as the accessory ones (accessory lateral eyes, stemmata, intracerebral ocelli).

Visual ecology

Current knowledge of sensory physiology of Diplopoda goes little beyond Cloudsley-Thompson's (1951a) summary. The exact role of vision in millipedes is difficult to assess and poorly studied. To date, not a single electrophysiological study on differential sensitivity of the various retinula cells in a diplopod ommatidium (e.g. color vision) is available. Furthermore, nothing is known about the role of eyes in intra- and interspecific communication/recognition. We need photo-physiological data and in-depth neuroanatomical insights from the optic neuropils to understand millipede motion and spatial vision, and in general, the ability of millipedes to use light for orientation (e.g. perception of polarized light). This would be an important subject of research, as diplopods are known to be generally highly to extremely sensitive to light (e.g. Cloudsley-Thompson, 1951a), may show a diurnal lifestyle (e.g. Cloudsley-Thompson, 1951b; Banerjee, 1967; Wongthamwanich et al., 2012), and, at least some of those millipedes having eyes, may react to light differently by performing both negative and positive phototaxis when illuminated at night (e.g. McKillup, 1988). Studies on visual ecology on eye-bearing diplopods may also be ambiguous as for instance seen in the record on mass-migrating diplopods, such as *Ommatoiulus sabulosus*. In these species, both activity in bright sunlight (i.e. Dziadosz,

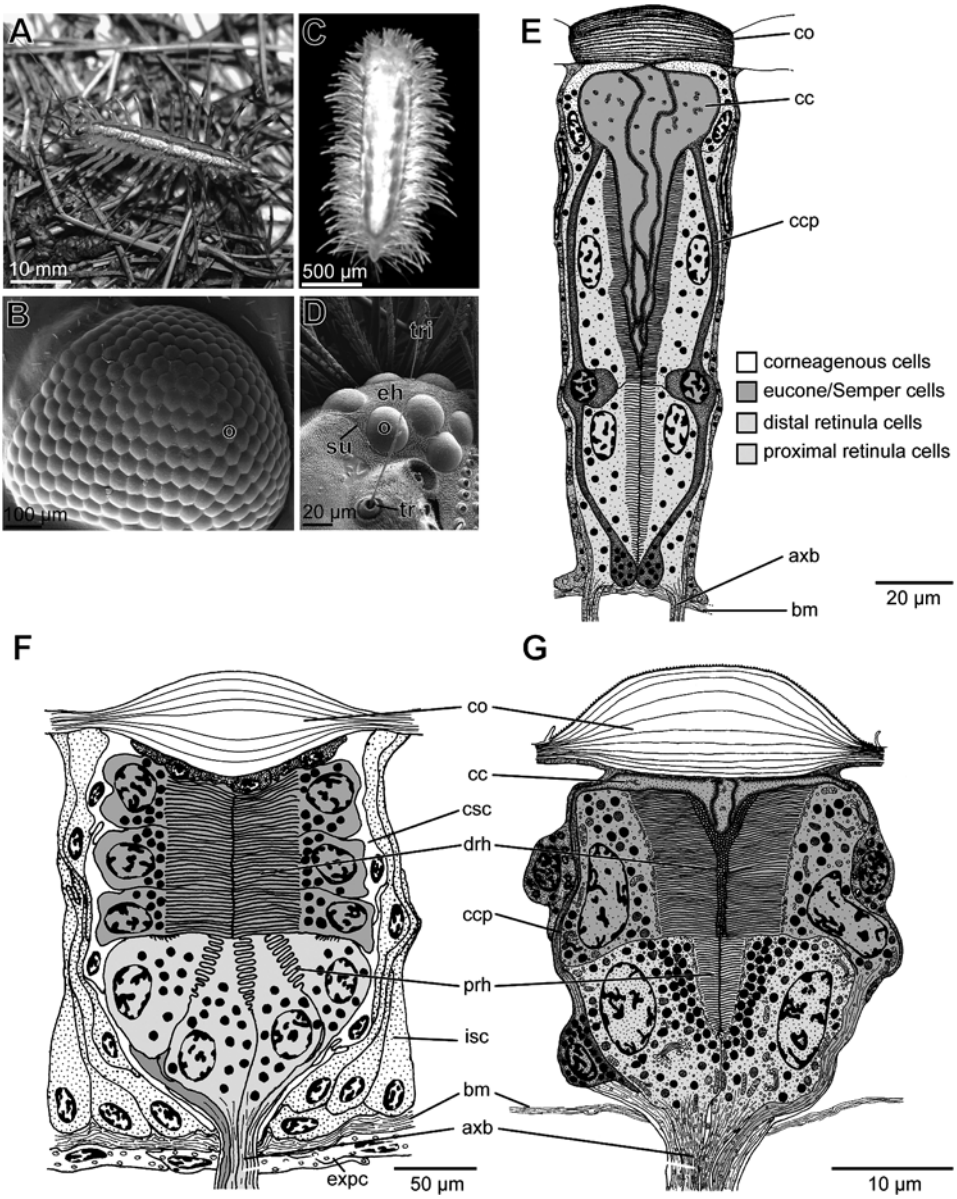


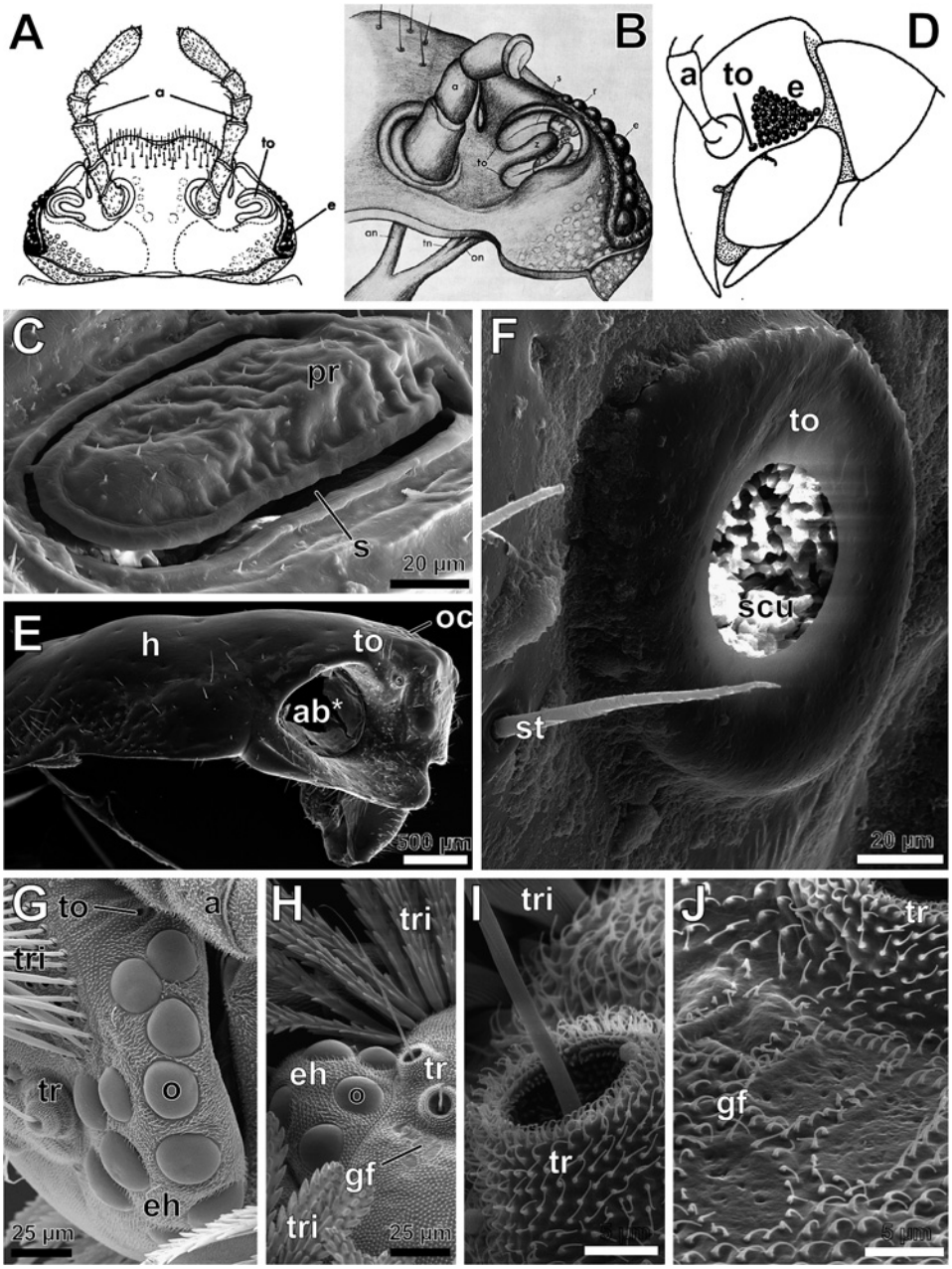
Fig. 9.7. Ultrastructural comparison of ommatidia in Scutigeromorpha, Lithobiomorpha (both Chilopoda) and Penicillata (Diplopoda). **A** Portrait of an adult of *Scutigera coleoptrata* (Scutigeromorpha). **B** Compound eye of *S. coleoptrata* showing over a hundred of hexagonal ommatidia. Lateral view (anterior side to the left). SEM. **C** Portrait of freshly fixed *Phryssonotus platycephalus* (Penicillata). LM. **D** Posterodorsal view of the ommatidial cluster of *P. platycephalus* crammed into minute, suture-delimited eye hill. SEM. **E-G** Semischematic reconstructions of the ommatidia of *S. coleoptrata* (**E**), *Lithobius forficatus* with intertwining proximal rhabdomeres (**F**), and *P. platycephalus* (**G**).

1966; Fairhurst, 1970) as well as at night (Demange, 1960) have been observed. Most recently, Meyer-Rochow (2015) found the polydesmid species *Chamberlinius hualiensis* to undergo mass migrations on the Japanese Izu Island of Hachijojima at night. Despite lacking eyes, this species strongly avoided exposition to light. The same author assumed intracerebral photoreceptors (= accessory lateral eyes) to sustain light sensitivity. In contrast, some diplopod species, such as *Coromus* sp., *Habrodesmus falx*, and *Ommatoiulus moreleti* turned out to be attracted by artificial light at night or under laboratory conditions (Toye, 1966; McKillup, 1988). As a consequence, these millipedes, as with *O. moreleti* in Australia, may invade houses and become a nuisance to the owners (McKillup, 1988). Being attracted to artificial light emitted by house or street sources, may be interpreted as a misled orientation behavior of arthropods basically seeking moonlight as navigation system (McKillup, 1988).

ORGANS OF TÖMÖSVÁRY

The organ of Tömösváry is a paired sense organ in myriapods visible from outside as a variably shaped breakthrough in the head's cuticle and located posteriorly of the antennal base (Fig. 9.8A-G). In longitudinal sections, a peg-like or hemi-spherically arranged epithelium of biciliated receptor cells is found enveloped by numerous sheath cells. The receptor cells project their branched or unbranched dendritic processes into a more variably shaped sensory cavity which is covered by a thin, more or less porous cuticle. The non-myelinated axons of the receptor cells compose the nervus tömösváryi projecting to the dorsolateral protocerebrum (e.g., Haupt, 1971, 1979; Müller et al., 2011; Chapter 8). Sense organs placed posterior to the insertion of the antennae occur in all subtaxa of Myriapoda and some apterygotan Hexapoda. In particular, they have been found in various Chilopoda (Hennings, 1904, 1906; Pflugfelder, 1933; Tichy, 1973; Shear & Bonamo, 1988; Dohle, 1990; Yamana & Toh, 1990; summarized by Müller et al., 2011), Symphyla (Pflugfelder, 1933; Tiegs, 1940; Haupt, 1971), Pauropoda (Haupt, 1973), Diplopoda (e.g. Hennings, 1906; Pflugfelder, 1933; Bedini & Mirolli, 1967a, b; Hopkin & Read, 1992), several Collembola (e.g. Denis, 1926; Altner et al., 1970, 1971; Dallai, 1971; Karuhize, 1971), and Protura (e.g. Bedini & Tongiorgi, 1971; Haupt, 1972). Synonyms for Tömösváry organs are temporal organs, postantennal organs, or pseudoculi (exclusively applied in Pauropoda and Protura).

Note potentially homologous ommatidial structures, in particular if comparing penicillate and scutigeromorph ommatidia, in the respective color code: **violet** corneagenous cells; **orange** eucone/Semper cells; **green** distal retinula cells; **blue** proximal retinula cells. **A** Modified from Sombke et al. (2012). **B** Original. **C-G** Modified from Müller et al. (2007) and Müller (2008). Abbreviations: **axb** retinular axon bundle; **bm** basal matrix; **cc** eucone/Semper cell (crystalline cone compartment); **ccp** cone cell process (connecting cone compartment and proximally located soma); **co** corneal lens; **csc** circumretinular sheath cells; **drh** distal rhabdom; **eh** eye hill; **expc** external pigment cells; **isc** circum-/interommatidial sheath cells; **o** ommatidium/ommatidia; **prh** proximal rhabdom; **su** suture;**tr** trichobothrium; **tri** trichomes.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History of description, typology, histological anatomy

The first discoveries and brief descriptions of Tömösváry organs were made in the 19th century in glomerid millipedes (Brandt, 1839; Leydig, 1864). Simultaneously, Latzel (1883) and Tömösváry (1883) described these organs and called them "Schläfenorgane" (temporal organs). Following Hennings (1904), all postantennal organs in Myriapoda were named after the Hungarian myriapodologist Ödön (= Edmund) Tömösváry. Although widespread (see above), Tömösváry organs of Diplopoda are probably the worst documented postantennal organs among arthropods.

To date, only the works of Zograf (1899), Hennings (1904, 1906), Pflugfelder (1933), and Bedini & Mirolli (1967a, b) (see Fig. 9.8A, B) can be treated as serious accounts, with regard to accuracy and depth of anatomical description. The works of Bedini and Mirolli are the only studies that provide data on the ultrastructure, however they are restricted to a single species, *Glomeris romana*.

Among Penicillata, Tömösváry organs are only convincingly documented in Synxenidae (Short & Huynh, 2006; see Fig. 9.8G). In Chilognatha, Tömösváry organs are present in all subtaxa of Pentazonia (Glomeridesmida; Glomerida, see Fig. 9.8A-C; Sphaerotheriida, see Fig. 9.8E, F) and, among Helminthomorpha, in two subtaxa of Nematophora (Callipodida; Chordeumatida, see Fig. 9.8D) as well as in Polydesmida. In all taxa listed, the external shape of Tömösváry organs varies from spherical, oval, slit- to horseshoe-shaped breakthroughs in the cuticle acting as openings of a more or less deeply sunken receptor cell epithelium. Hennings (1906) defined and discussed developmental stages (see below) as well as two major mature types in glomerid and other diplopods:

(1) Type I: three sensory pits with hairs at either side of the head (trichobothria, see Fig. 9.8H, I): polyxenid Penicillata (see below).

Fig. 9.8. Location and external morphology of Tömösváry organs in Diplopoda. **A-C** Large, horseshoe-shaped Tömösváry organ (type IIa2) in Glomerida. **A** Posteriodorsal view of the head of *Glomeris romana*. **B** Lateral view of the Tömösváry organ and surrounding lateral head region. **C** Detail of Tömösváry organ of *Nearctomeris* sp. (laterodorsal view). Note the peg-like cuticular protuberance causing a curved appearance of the sensory pit, SEM. **D-G** Examples of type IIb Tömösváry organs with spherical sensory pits. **D** Schematic drawing of the head of *Chordeuma proximum*. **E** Posterolateral aspect of the head of *Cyliosoma* sp. (Sphaerotheriida), SEM (trunk removed, antennae lost). **F** Detail of the pore of the sensory pit. Note the highly diversified tube cuticle. SEM. **G** Dorsolateral aspect of the head of *Phryssonotus novahollandiae* (Penicillata) showing the eye (= ommatidial cluster), parts of the antenna, numerous trichomes, and the minute, rounded opening of the Tömösváry organ. SEM. **H** Dorsal view of the eye of *Polyxenus lagurus* (Penicillata) and surroundings with no trace of sensory pits. SEM; potential candidates for Tömösváry organ derivatives. **I** Trichobothrium pointing laterally (basal aspect), *P. lagurus*. SEM. **J** So-called "glandular field" located median of the eye hill (for explanation see main text), *P. lagurus*. SEM. **A, B** Reproduced from Bedini & Mirolli (1967b) with original labels. **C, E, F** Originals: T. Wesener. **D** Modified after Enghoff et al. (1993). **G** Modified after Short & Huynh (2006). **H** Modified after Müller et al. (2007). **I, J** Originals: C. H. G. Müller & A. Sombke. Abbreviations: **a** antenna; **ab*** antennal base; **an** antennal nerve; **e** eye; **eh** eye hill (= ommatidial cluster; ommatidia separated by cuticle of regular epidermal cells); **gf** "glandular fields" trichome-free areas of the cuticle; **h** head; **o** ommatidium; **oc** ommatidial cluster; **on** optic nerve; **pr** peg-like projection of median cuticle; **r** ridge; **s** slit-like opening to horseshoe-shaped sensory pit; **scu** specialized cuticle; **st** sensillum trichodeum; **tn** Tömösváry nerve; **to** Tömösváry organ; **tr** trichobothrium, **tri** trichomes, **z** Zapfen (= **pr**).

(2) Type IIa1: organ in proximate subsurface location; a simple, spherical sensory pit: Glomeridesmidae.
(3) Type IIa2: organ in proximate subsurface location; a horseshoe-shaped, spacious sensory pit: Polydesmidae, Glomeridae (Figs. 9.8A-C, 9.9).
(4) Type IIb1: organ sunken below cuticle and epidermis; a short tube, tube wall cuticle with small protruding teeth: Schizopetalidae.
(5) Type IIb2: organ sunken below cuticle and epidermis; relatively long tube, tube wall cuticle with many protruding teeth and ridges: Sphaerotheriidae (Fig. 9.8E, F).
(6) Type IIb3: organ deeply sunken below cuticle and epidermis; elongated tube, tube wall locally infolded, tube wall cuticle with only a few teeth: Chordeumatidae (Fig. 9.8D).
(7) Type IIb4: organ deeply sunken below cuticle and epidermis; very elongated tube, tube wall with bubble-like widening, tube wall cuticle with many protruding teeth: Craspedosomatidae (Fig. 9.10).

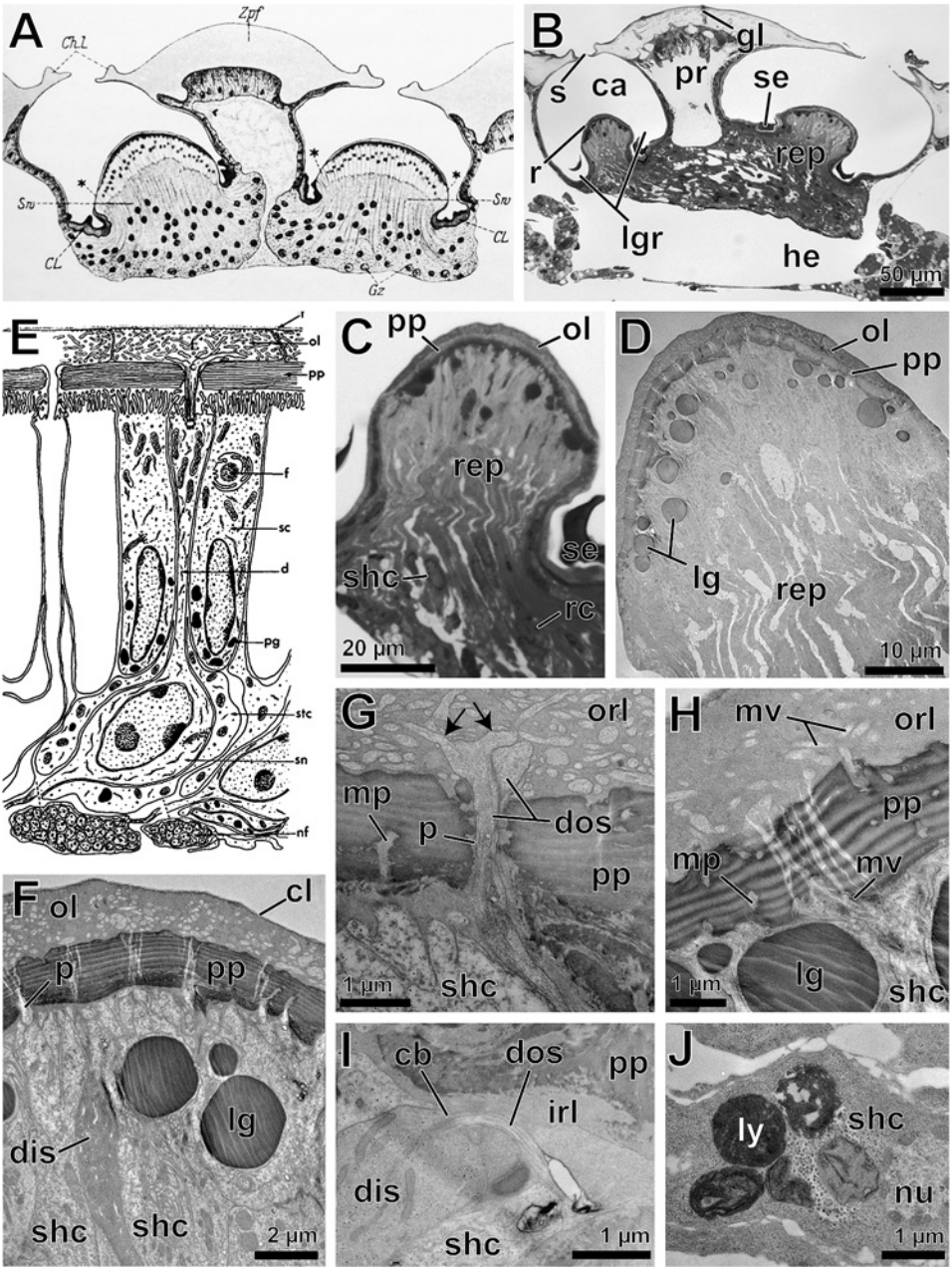
Ultrastructural anatomy

Fine structural investigations on *Glomeris romana* reveal the morphology of a type IIa Tömösváry organ (sensu Hennings, 1906). Bedini & Mirolli (1967a, b) reconstructed the receptor epithelium hidden in a horseshoe-shaped depression of the cuticle (Figs. 9.8A-B, 9.9A-C, E). A slit-like breakthrough along the center of the horseshoe-shaped depression (Fig. 9.8C) widens basally into a hidden, likewise horseshoe-shaped sensory cavity. It comprises two lateral grooves at its bottom separated by a central, cuticularized ridge (Fig. 9.9A-D) and is occupied by numerous bipolar and biciliated receptor cells, granulated sheath cells and glial cells (cf. Fig. 9.9E). The distal tip of this ridge is lined by a thin cuticle ("limiting lamella" sensu Bedini & Mirolli, 1967a, b) that overtops a specialized compartment, called "outer layer", which contains hemolymphatic liquid as well as a complex meshwork of branched dendritic outer segments of the receptor cells (Fig. 9.9E-H). Basally, the outer layer is lined by the "pore plate", a multi-pierced and -lamellate cuticle that leaves space for dendritic outer segments to pass through (Fig. 9.9G). The ciliary bodies are placed shortly below the pore plate (Fig. 9.9E, I) and mark the transition from outer to inner segment of the dendritic process. Once passed through the pore plate, the thinner dendritic outer segments ("cisternae") branch into many "tubules" (Fig. 9.9G) that finally attach to the limiting lamella at different sites. The sheath cells with deeply invaginated apices are grouped by three around a receptor cell, thus forming distinctive sensory units (Fig. 9.9E). The high abundance of biosynthesis-supporting organelles like mitochondria, ER cisternae, and large vesicles with "feospheres" enable the sheath cells to establish and regulate the receptor lymph space, secreting the pore plate, and/or secreting the outer layer including the limiting lamella. The receptor cells possess axons that are collected in the nervus tömösváryi which connects to the lateral protocerebrum (see Chapter 8). Unpublished data on Tömösváry organs of *Glomeris marginata* in general confirms most observations made by Bedini & Mirolli (1967a, b), except for some crucial details. In *G. marginata*, the outer layer

containing branched dendritic outer segments turns out to be a receptor lymph-filled cavity encapsulated proximally by a porous, multi-lamellate cuticle ("pore plate") and distally by the thin epicuticle. Albeit excluded by Bedini & Mirolli (1967a, b), there is evidence that elongated microvilli of the sheath cells pass through the pore plate via separate minute tubules (Fig. 9.9G, H). The massive abundance of lysosomes in the sheath cells (Fig. 9.9J) as well as the absence of Golgi stacks contradict previous conclusions that the sheath cells function primarily as secretory cells. In fact, it is more likely that the sheath cells, besides their main function to encompass the receptor cells, at least temporarily reabsorb substances from the receptor lymph space. Thus, sheath cells may regulate the chemical milieu inside receptor lymph space, especially in the outer layer. An amorphous, electron-dense substance, erroneously described as cuticle ("Chitinleisten": Pflugfelder, 1933), is usually found accumulated in the groove lateral to the central ridge (Fig. 9.9A). This substance may represent secretions by solitary epidermal glands which are especially aggregated at the peg-like projection of the median cuticle ("Zapfen" sensu Pflugfelder, 1933; see Fig. 9.9B). Secretion may pour into the sensory cavity through the slit-like opening, impregnate the specialized ridge cuticle and finally aggregate in the ridges. Secretion coverage may be crucial to bind volatile molecules to the surface of the cuticle, thus enabling reception by receptor cell dendrites. Unpublished data of a type IIb4 Tömösváry organ of an unidentified craspedosomatid millipede shows that the sensory epithelium is deeply sunken into the head flanks, meaning below the cuticle and the level of subjacent epidermis. Numerous receptor cells and sheath cells are grouped together into distinct units and arranged around the bottom of the spiny sensory tube as well as reach into a spine-like body protruding from the tube's bottom center (Fig. 9.10A, B, J). At the tip of the dendritic inner segment, each receptor cell emits two cilia that project into the receptor lymph space (Fig. 9.10E). Whether or not these ciliary processes (= dendritic outer segments) branch distally could not be verified. Depending on the position of the receptor cell soma, the sensory cilia may pass either into the central projection (Fig. 9.10B) or around the basolateral infolds of the sensory tube (Fig. 9.10C, D, F). The cuticle around the bottom of the sensory tube is only locally pierced. Respective pores are traversed by elongated microvilli of the sheath cells, most of which stay in the receptor lymph space (Fig. 9.10D). There are no obvious pore plates or outer lymph compartments as encountered in Tömösváry organs of glomerids. The distal half of the peg-like central projection only shows tapering distal sheath-cell processes with microvilli as well as a voluminous receptor lymph space. As with *Glomeris* spp., the receptor lymph space may contain large granules of high electron-density (Fig. 9.10B).

Distribution and problematic study cases in Diplopoda

Tömösváry organs have not been found in all subtaxa of Colobognatha, including Platydesmida, Polyzoniida, Siphonocryptida, and Siphonophorida (Hennings, 1904, 1906; Attems, 1926; Pflugfelder, 1933; Seifert, 1961; Blower, 1985; summarized in Blanke & Wesener, 2014). Reports on their presence in Stemmiulida (e.g. Verhoeff, 1928-1932) need further confirmation by SEM and TEM. A vast majority of authors argued for the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absence of Tömösváry organs in all subtaxa of Juliformia notwithstanding few conflictive reports such as that of Bueno-Villegas et al. (2004) which, however, seem to be rather unsubstantiated, as proper references to anatomical studies were not provided. The same problem applies to the enigmatic Siphoniulida in which at least some representatives where described to possess Tömösváry organs (Bueno-Villegas et al., 2004). However, these accounts appear to result from misinterpretation of previous studies (compare Sierwald et al., 2003: 89, and Enghoff et al., 1993: 116).

Whether or not all representatives of Penicillata possess Tömösváry organs is still a matter of discussion. Their presence in Synxenidae (e.g. *Phryssonotus novaehollandiae*) is indicated by a pair of tiny spherical openings in the cuticle, found in the direct anterior vicinity of the ommatidial cluster and documented by Short & Huynh (2006) (Fig. 9.8G). However, if we regard other families of Penicillata the literature appears highly ambiguous. On the one hand, hitherto provided semischematic drawings indicate that the Polyxenidae, and namely *Polyxenus lagurus* as a relatively well-studied representative of this group, should possess Tömösváry organs as they possess a pair of Tömösváry nerves projecting into the lateral protocerebrum (Nguyen Duy-Jacquemin, 1973; Juberthie-Jupeau, 1983). On the other hand, there are no anatomical studies clearly showing chilognath-like

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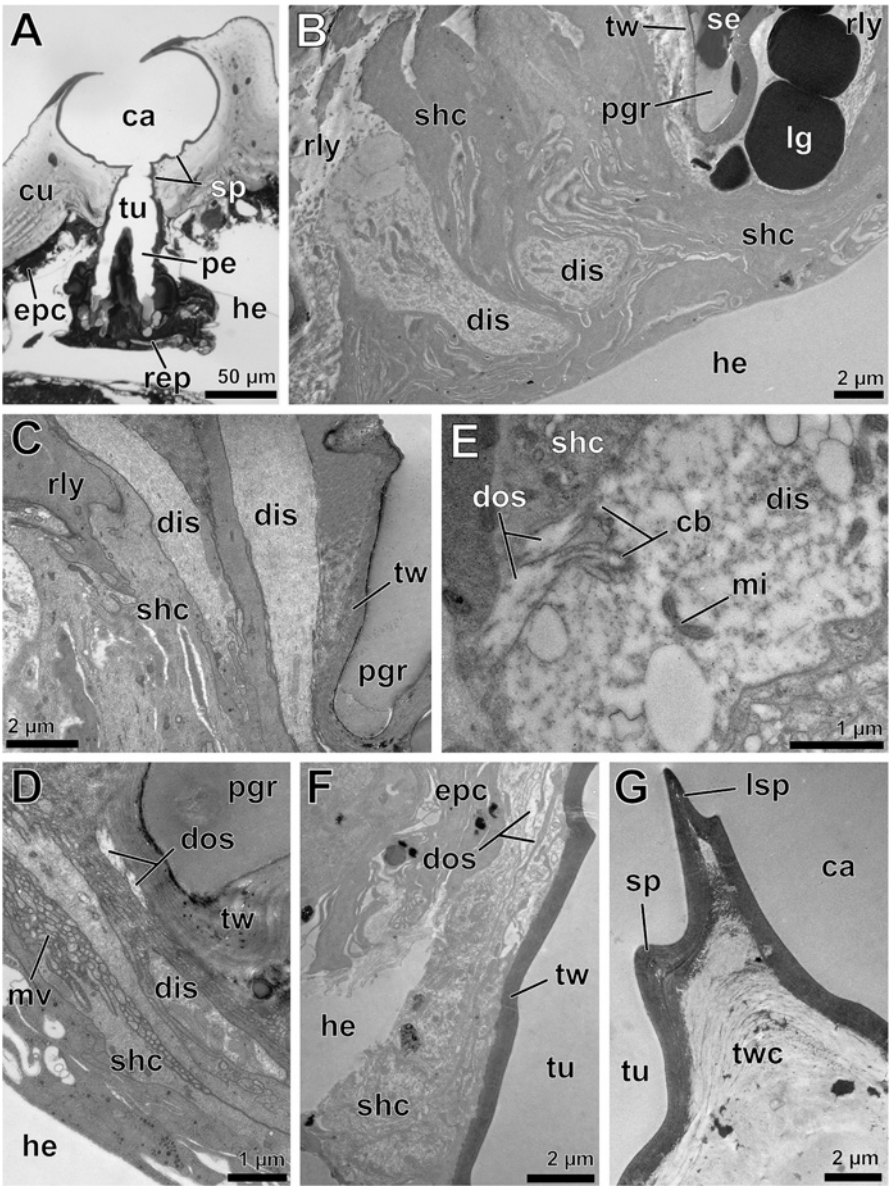
Fig. 9.9. Histological and ultrastructural anatomy of type IIa2 Tömösváry organs in Glomeridae. **A** Transverse section through both branches of horseshoe-shaped Tömösváry organ of *Glomeris* sp. **B-C** Toluidine-blue stained transverse section through Tömösváry organ of *Glomeris marginata*, same orientation as drawn in **A**: **B** Overview of entire section. **C** Detail of central ridge (left branch in **B**) containing the receptor epithelium. Note that receptor cell somata are aligned underneath the somata level of sheath cells. **D** Ultrathin section of central ridge showing numerous, tightly packed distal processes of receptor cells and sheath cells. *Glomeris marginata*. TEM. **E** Semischematic reconstruction of a receptor cell unit in Tömösváry organ of *Glomeris romana* comprising a central biciliated receptor cell and several surrounding sheath cells; cilia (dendritic outer segments) pass through pores of the pore plate reaching the outer layer where they branch. **F-J** Ultrastructural details receptor units in *Glomeris marginata* as documented in TEM. **F** Distal region of receptor epithelium showing the porous, multilamellated cuticle (pore plate) and overlaying outer layer comprising numerous cellular inclusions. **G** Detail of pore plate with a larger pore through which two ciliary processes (dendritic outer segments) or a receptor cell project into the outer layer. **H** Further section of the pore plate containing many micropores providing passage for microvilli of the sheath cells. **I** Transition zone of dendritic inner and outer segments of a receptor cell indicated by the ciliary body (second cilium not cut at this level). **J** Detail of receptor cell soma displaying several lysosomes at various maturation stages. **A** Drawn by Pflugfelder (1933) with original labeling. **B-D, F-J** Originals: C. H. G. Müller & A. Sombke. **E** Reproduced from Bedini & Mirolli (1967b). Abbreviations: **ca** sensory cavity; **cb** ciliary body; **Ch.l.** chitinous ridge ("Chitinleisten"); **CL** chitin lamella ("Chitinlamelle") (= **se**); **cl** (outer) cuticular lamella; **d** dendrite (= **dis**); **dis** dendritic inner segment; **dos** dendritic outer segment; **f** feosphere; **gl** conducting canal of solitary epidermal gland; **Gz** ganglia cells ("Ganglienzellen"); **he** hemolymph space of the head; **irl** (inner) receptor lymph space; **l** limiting lamella (= **cl**); **lg** large extracellular granule(s); **lgr** lateral grooves; **ly** (late) lysosome; **mp** microporus; **mv** microvilli (sheath cells); **nf** nerve fibres; **nu** nucleus; **ol** outer layer; **orl** outer receptor lymph space; **p** large porus; **pg** pigment granule; **pp** pore plate; **pr** projection of median cuticle; **r** ridge; **rc** receptor cell; **rep** sensory (receptor) epithelium; **s** slit-like opening to sensory cavity; **sc** supporting cell (= **shc**); **se** aggregated secretion; **shc** sheath cell(s); **sn** sensory neuron (= **rc**); **stc** satellite cell; **Sw** Sinneswulst (= **rep**); **Zpf** see **pr** ("Zapfen").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postantennal sensory pits. External morphological accounts do exist but remain confusing. Two different structures on the penicillate head have been described as homologous to Tömösváry organs. Based on early attempts of Bode (1878), Hennings (1906) argued that in *P. lagurus* the three trichobothria in postantennal position (see Fig. 9.8G-I) may be strongly modified Tömösváry organs. Seifert (1961) corroborated this idea not least because of Schömann's (1956) behavioral studies that revealed penicillate trichobothria to be detectors for vibrations in the soil rather than being auditory organs as in various Arachnida. Tichy's (1975) first ultrastructural study on penicillate trichobothria indeed brought up some peculiar structures, such as the absence of tubular bodies, the partly pierced hair shaft, a cytoplasmic capsule built by sheath cells invading the hair shaft, or filamentous, desmosome-like structures interconnecting the dendritic outer segments. Nevertheless, Tichy (1975) rejected potential homologies of Tömösváry organs, since he found the available evidence to be far too ambiguous. In contrast, Attems (1926) described Tömösváry organs to be present in Polyxenidae as rudiments located slightly medioanterior of the eye hill and anterior to the three trichobothria, thereby pointing to a different structure. Verhoeff (1928-1932) considered Tömösváry organs of this penicillate as small, simply structured sense organs.

When inspecting SEM images of the penicillate head, a group of approximately five oval cuticular fields devoid of microtrichomes can be found medially of the ommatidial cluster (Fig. 9.8H, J). These structures strongly resemble the "glandular fields" documented on the walking legs by Eisenbeis & Wichard (1985) and were therefore addressed as such by Müller et al. (2007). It is possible that these "glandular fields" are highly aberrant, miniaturized derivatives of Tömösváry organs, but an in-depth SEM and TEM study has to be conducted to verify this suspicion, as synxenid Penicillata display the

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Fig. 9.10. Histological and ultrastructural anatomy of type IIb4 Tömösváry organs in an unidentified representative of Craspedosomatidae. **A** Toluidine-blue stained section, LM. **B-G** TEM. **A** Mediolongitudinal section of the Tömösváry organ showing a distal cavity and a long sensory tube leading to the sensory epithelium which is restricted to the bottom of the tube. Greater part of the sensory epithelium occupies a peg-like structure projecting up from the bottom's center. **B** Bottom of the sensory tube showing a part of the receptor epithelium comprising dendritic inner segments of receptor cells and surrounding sheath cells in modular arrangement; note huge spherical granules located in receptor lymph space. **C-D** Periphery of sensory epithelium showing two dendritic inner segments edging around peripheral groove at bottom site of sensory tube; note the presence of two dendritic outer segments in **D** sent off by the dendritic inner segment on lower right. Sheath cells emit numerous microvilli into receptor lymph space (**D**). **E** Transition zone of dendritic inner and outer segments in biciliated receptor cell indicated by two ciliary bodies. **F** Basolateral aspect of tube wall with numerous closely adjoined processes of sheath cells and dendritic outer segments of receptor cells. **G** Bottom of the distal cavity and subjacent orifice of sensory tube; note spiny protuberances of the wall cuticle. **A-G** Originals: C. H. G. Müller & A. Sombke. Abbreviations: **ca** distal cavity; **cb** ciliary body; **cu** cuticle; **dis** dendritic inner segment; **dos** dendritic outer segment; **epc** epidermal cells; **he** hemolymph space of the head; **lg** large extracellular granule; **lsp** large wall spine; **mi** mitochondrion; **mv** microvilli (sheath cells); **pe** peg-like central projection of sensory epithelium; **pgr** peripheral groove at bottom of sensory tube; **rep** sensory (receptor) epithelium; **rly** receptor lymph space; **se** aggregated secretion; **shc** sheath cell(s); **sp** wall spine(s); **tu** sensory tube; **tw** tube wall; **twc** tube wall cuticle.

same "glandular fields" in addition to what looks like a pore of a proper Tömösváry organ (compare Short & Huynh, 2006). Nonetheless, such a discovery would be anything but surprising because other Progoneata like Pauropoda and Symphyla also display both Tömösváry organs/pseudoculi as well as trichobothria with proximally bulged hair shafts (Haupt, 1979).

Questions on homology, evolution and phylogenetic significance

In the light of the Tracheata hypothesis, the presence of Tömösváry organs was hypothesized as one among many potential synapomorphies of Myriapoda and Hexapoda. In this context, Tömösváry organs were promoted not only because of their similar location at either side of the head, but also because of close resemblance in functional ultrastructure (Haupt, 1973, 1979). Characters of Tömösváry organs have also been used to gain further resolution of phylogenetic interrelationships within Diplopoda (e.g. the Nematophora concept supported by Hennings, 1906; Enghoff et al., 1993; Blanke & Wesener, 2014). Wägele & Kück (2014) recently proposed to add Tömösváry organs to the growing list of morphological synapomorphies of Mandibulata. As main argument in favor of this view, Wägele & Kück (2014) presented a potential homology of Tömösváry organs of myriapods and hexapods to the Bellonci organ described in many Crustacea, such as Mystacocarida, Copepoda, Malacostraca, and probably also Branchiopoda. However, the idea to consider Bellonci organs as the postantennal organs of Crustacea has found strong criticism, as for instance by Bitsch & Bitsch (2004).

Regardless of the plausibility of the above-listed evolutionary scenarios, the significance of Tömösváry organs as phylogenetic key character stands and falls with the question if they can be homologized at all. According to early attempts of Hennings (1906), it was Haupt (1973) who suggested a homology of Tömösváry organs across Myriapoda, Protura and Collembola. In particular, Haupt (1973) referred to the common postantennal location combined with a protocerebral innervation, and moreover stressed the existence of a porous cuticle which allows the dendritic outer segments either to abut or to pass through. However, Haupt (1973, 1979) admitted that the assumption that Tömösváry/temporal organs are homologous is hampered by considerable variations in these organs concerning the (1) overall shape (including the diversification of the cuticle in the sensory pit), (2) number of constituting cells, (3) number of pores in the pore plate, and (4) endo- or exocuticular nature of the pore plate. While there are indeed arguments to support homology of Tömösváry organs in Myriapoda (see below), it has to be noted that for instance the postantennal/temporal organs of many Collembola are so aberrant that it appears challenging even to homologize them among representatives within this group (Altner et al., 1971). This led to general skepticism or even total rejection of their homology (e.g. Hoffmann, 1969; Altner et al., 1971; Dohle, 1980, 1997, 1998; Bitsch & Bitsch, 2000). Beyond any doubt, a well-conceptualized comparative morphological study combining light and electron microscopy (in particular TEM) is highly needed to assess questions of homology and to resolve the massive confusion existing in literature.

In conclusion, we propose to consider at least the Tömösváry organs of Myriapoda to be homologous. Therefore, the term Tömösváry organ sensu stricto should be used when addressing these organs in Myriapoda. Their homology may be established on a combination of the following characters found in a vast majority of, if not all myriapods bearing these organs and investigated so far:

(1) postantennal and periclypeal position, anterior or anteriodorsal to the ommatidium/ ommatidial cluster, primarily not deeply sunken below the cuticle;

(2) horizontal modular arrangement of receptor cells and accompanying sheath cells displaying an elaborated system of microvilli projecting into a spacious receptor lymph space;
(3) each bipolar receptor cell projecting two cilia that taper and branch distally into numerous tubules (with the exception of unbranched cilia in Scutigeromorpha; Yamana & Toh, 1990);
(4) presence of a specialized, either uni- or multiporous cuticular plate through which either single or all dendritic outer segment(s) protrude(s); pore plate primarily internalized, located between inner and outer receptor lymph subcompartments;
(5) receptor cell afferents bundled into the nervus tömösváryi projecting to the lateral protocerebrum.

The modular pattern of receptor and sheath cells as well as the occasional presence of a multiporous cuticular plate (Symphyla, Diplopoda) may indicate an evolution of Tömösváry organs from formerly distinctive, but aggregated chemoreceptive sensilla (according to Haupt, 1979).

Functional considerations

To date, not only the question about homology of Tömösváry organs across arthropods remains unsolved, but also their potential function. The latter issue particularly applies to diplopods. Virtually all kinds of receptor modalities have been discussed with regard to diplopod Tömösváry organs, such as: (1) reception of vibration/sound in *Glomeris* (e.g., Verhoeff, 1928-1932; Pflugfelder, 1933; Schömann, 1956; Meske, 1961), (2) olfaction in *Glomeris* sp. (Zograf, 1899; Bedini & Mirolli, 1967a, b), (3) gravity perception in *Thyropygus* (Krishnan, 1968), or (4) hygroreception in *Glomeris* (Bedini & Mirolli, 1967a, b; compare also Tichy, 1972, 1973 for *Lithobius forficatus*). One might add (5) the perception of CO_2 as based on electrophysiological recordings (Yamana et al., 1986, 1998; Yamana & Toh, 1987). However, the ability to perceive CO_2 was only documented in *Thereuonema hilgendorfi*, a scutigeromorph centipede. Altner & Thies (1976) also inferred that Tömösváry organs may also include (6) thermoreceptive cells as it is impossible to distinguish thermo-, hygro-, and chemoreceptive modalities by the aid of (ultra-)structural data alone. Most speculation was ultimately inspired by behavioral observations or raised while interpreting the functional ultrastructure of the Tömösváry organs in question. Physiological data are mostly missing. Nonetheless, the ubiquity of (a) the horizontal modular arrangement (receptor cells surrounded by their own set of sheath cells), (b) branched dendritic outer segments in receptor cells, and (c) the presence of at least uni-porous plates (Progoneata: Bedini & Mirolli, 1967a, b; Haupt, 1971; see also above in this chapter; Chilopoda: Müller et al., 2011) gives strong support to the assumption that myriapod Tömösváry organs evolved primarily as chemoreceptive or even olfactory organs sensu stricto (cf. Bedini & Mirolli, 1967a, b; see also e.g. Steinbrecht, 1996, 1999; Keil, 2012).

Development

According to Hennings (1904, 1906), the Tömösváry organ of Diplopoda and Chilopoda develops through a pile of neuroectodermal cells that migrate into the frontolateral lobe of the developing brain. Thus, the anlage of the nervus opticus and nervus tömösváryi is being formed which connects the further differentiating epidermis to the subjacent

frontal lobe of the protocerebrum. Later on, coinciding with the subsequent retreat of the frontal lobe from the epidermis and the development of the nervus opticus, the early n. tömösváryi becomes visible and gets stretched but maintains its connection between the epidermis and the brain anlage. Only in those taxa devoid of Tömösváry organs in adult stage, the early n. tömösváryi completely loses contact to the epidermis and vanishes. In taxa with proper Tömösváry organs, the sensory apparatus is established by transformation and elongation of epidermal cells. Simultaneously, each sensory pit ("Schläfengrube" sensu Hennings, 1904, 1906) is formed at either side of the head capsule.

The deepest insight into development of diplopod Tömösváry organs was obtained from *Glomeris pulchra* and *G. marginata*. Hennings (1904) defined six relevant embryogenic stages ranging from early differentiation of the neuroectoderm to a final stage (stages I-VI, see his Figs. 10-16). Stages III and IV are the most crucial ones, as differentiation processes going on in the (neuro-)ectoderm at that time determine the final shape of the Tömösváry organ. For instance, the depth of the sensory tube and arrangement of the sensory epithelium in type IIb organs is determined at stage IV, probably linked to differential mitotic activity in and subsequent elongation of the tube-lining ectoderm. In *Glomeris*, a distal sensory cap of epidermal cells detaches from subjacent tissue that is being transformed into the sensory epithelium (stage III, see Fig. 9.11A). Between this sensory cap and the sensory epithelium there is a hollow space, the later sensory cavity that widens and finally breaks through the cuticle making up a slit-shaped opening on the sensory plate (stage IV, see Fig. 9.11B-C). In chilognath Diplopoda possessing type IIb Tömösváry organs, this pore has a round profile. The tube-like elongation of the sensory pit is correlated with a recession and distortion of the sensory epithelium. According to Hennings (1904, 1906), tube-like formations derive from a *Glomeris*-like stage.

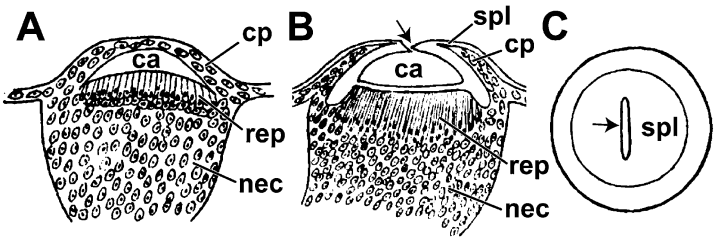

Fig. 9.11. Development of Tömösváry organs in *Glomeris* as reconstructed by Hennings (1904, 1906). **A** Stage III: cellular cap has loosened from hitherto undifferentiated ectoderm, widening of so far still closed sensory cavity, early developmental stage of sensory epithelium present. **B-C** Stage IV: cellular cap is ripped in its center giving rise to slit-shaped opening of the sensory cavity (compare dorsal overview of sensory plate provided in **C**), further differentiation and establishment of sensory epithelium at bottom of sensory cavity, successive elongation of receptor and sheath cells, separating from neuroectoderm (= frontolateral lobe of the developing brain). Modified from Hennings (1906). Abbreviations: **ca** sensory cavity; **cp** cellular cap; **nec** neuroectoderm of frontolateral brain lobe; **rep** differentiating sensory (receptor) epithelium; **spl** sensory plate.

TRICHOBOTHRIA

Myriapod trichobothria in comparison

Trichobothria are a special kind of mechanosensory cuticular sensilla that are described to be (1) usually multi-innervated, (2) possess a directional sensitivity, and (3) primarily detect slow air currents (Hopkin & Read, 1992). In general, trichobothria are considered a great evolutionary achievement of arthropods to conquer terrestrial habitats (Haupt, 1979). Among Myriapoda, trichobothria have been found exclusively in the three subtaxa of Progoneata, i.e. Symphyla (Haupt, 1971), Pauropoda (Haupt, 1976, 1978), and in penicillate Diplopoda (Tichy, 1975). All these trichobothria have in common (1) biciliated receptor cells, (2) a single sensory hair that emerges from a cuticular pit, and (3) a pear- or disk-shaped bulb widening the base of the sensory hair which stays hidden in this cuticular pit (compare Fig. 9.12A-C). However, trichobothria of Progoneata differ in (1) number and location on the body (a single pair on the preanal segment of *Scutigerella immaculata*, Symphyla: Haupt, 1971; single pairs on tergits 2-6 of *Allopauropus* sp., Pauropoda: Haupt, 1976, 1978; each three on either lateroposterior side of the head of *Polyxenus lagurus*, Diplopoda: Tichy, 1975; this chapter), (2) number of receptor cells (16 in *S. immaculata*, 4 in *Allopauropus* sp., 3-4 in *P. lagurus*), (3) ultrastructure of the shaft cuticle (homogeneous and equally thick in *S. immaculata* and *Allopauropus* sp.; heterogeneous, bi-layered and with pore tubules in *P. lagurus*), (4) presence of tubular bodies (present in *S. immaculata* and *Allopauropus* sp.; absent in *P. lagurus*), and (5) ultrastructural appearance of cuticular suspension apparatus at hair base (tubular bodies connected to cuticular projections slightly below the suspension membrane: *S. immaculata*; tubular bodies ensheathed by cuticular projections attached to hair base: *Allopauropus* sp.; without dendrite-to-cuticle attachment system and radial suspension fibres: *P. lagurus*).

Tichy (1975) and Haupt (1979) noticed the outstanding nature of trichobothria of Penicillata by listing up even more unique characters distinguishing their trichobothria from those of symphylans and pauropods, such as the dendritic outer segments (6) entering the sensory hair, (7) maintaining the axoneme configuration of $9 \times 2 + 0$ microtubules over their entire length, (8) being interconnected by desmosome-like junctions ('interciliar junctions'), and (9) being encased by a continuous dendritic sheath established by sheath cells.

Ultrastructure of the penicillate trichobothrium

Being arranged in triangular fashion and thus building a 'cephalic/sensory hair triad' as termed by Tichy (1975) and Haupt (1979), the trichobothria of *P. lagurus* — the only penicillate species so far studied in this respect — point away from each other at level of 90° (Bode, 1878; Verhoeff, 1928-1932; Tichy, 1975; Müller et al., 2007); two of these trichobothria, namely those ones with thicker hairs pointing laterally and posterolaterally, are illustrated on Figs. 9.8H and 9.12D. The hair triad is located in the temporal region, posterior to the antennal base and medially of the ommatidial cluster. Lengths of sensory hairs are around 30 μm, diameters vary between 1.2 and 2.0 μm (Tichy, 1975; see also Fig. 9.13A-B). The cuticular shaft bears ridges (e.g. Figs. 9.8I, 9.13A-B) and pores along its proximal half. Each pore leads into a slit-like hole in the shaft cuticle. Based on application of Dalton's fixative, Tichy (1975) revealed that these slit-like holes are filled by electron-dense material. Each sensory hair emerges from tube-like protuberance ('cuticular

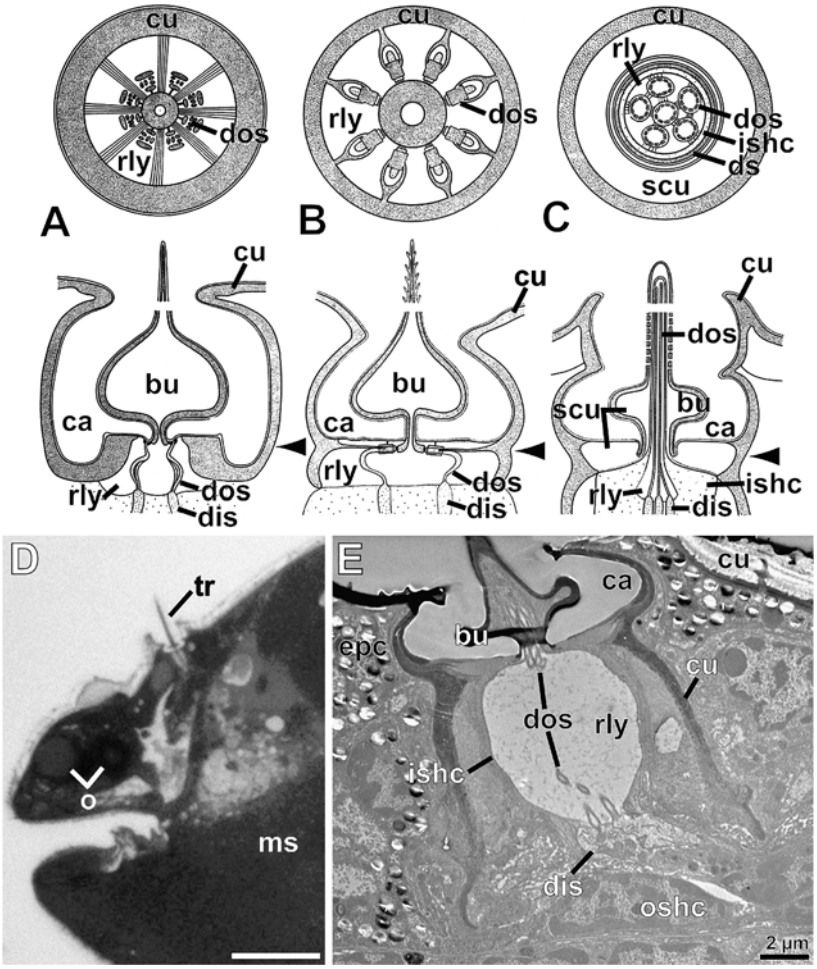

Fig. 9.12. **A-C** Semischematic reconstruction of apical parts of myriapod trichobothria in transverse and longitudinal sections. **A** *Scutigerella* (Symphyla). **B** *Allopauropus* (Pauropoda). **C** *Polyxenus* (Diplopoda). Trichobothria differ greatly in number and modality of receptor cells as well as in interface of stimulus-triggering cuticle and dendritic outer segments (see comparison of cross-sections above longitudinal sections, level of cross-section indicated by black arrowheads). **D-E** Histological (**D**) and ultrastructural (**E**) anatomy of trichobothria of *Polyxenus lagurus*. **D** Semithin cross-section of the posterior part of the head showing trichobothrium pointing laterally in longitudinal section as well as transverse and oblique aspects of several ommatidia. Toluidine-blue stained section, LM. **E** TEM-overview of distal aspect of trichobothrium pointing posteriorly in oblique-longitudinal section, basal bulb of sensory shaft is clearly visible sheltered in the spacious cavity of the cuticle, due to their coiled path the six dendritic outer segments are cut in two places. **A-C** Compilation after Haupt (1979), modified. **D-E** Originals: C. H. G. Müller & A. Sombke. Abbreviations: **bu** basal bulb enwidening hair shaft; **ca** cavity containing shaft bulb; **cu** cuticle; **dis** dendritic inner segment; **dos** dendritic outer segment(s); **epc** epidermal cell; **ishc** inner sheath cell(s); **ms** musculature; **o** ommatidia; **oshc** outer sheath cell(s); **rly** receptor lymph space; **scu** subcuticle; **tr** trichobothrium.

chamber 1') which opens proximally into a spacious pit ('cuticular chamber 2'), conceiling the bulbous widening of the hair base. According to Tichy (1975), those trichobothria pointing laterally and posterolaterally contain three receptor cells (sensilla types I and II), while that one pointing anteromedially posseses four (sensillum type III). Receptor cells are surrounded by sheath cells ('enveloping cells') that are supposed to build and encompass the dendritic sheath as well as three, locally voluminous extracellular spaces. According to Tichy (1975), the first one of these extracellular spaces is homologous to inner receptor lymph cavities of ordinary arthropod sensilla ('type I lymphatic cavity', see his Fig. 6 and our Fig. 9.12C). This cavity is strongly expanded below the bottom of the cuticular cavity ('cuticular chamber 2'). The second extracellular space is restricted to the hair bulb and assumed to correspond to the outer receptor lymph cavities of other arthropod sensilla ('type II lymphatic cavity', see his Fig. 6). A third, circular, but more or less obscure extracellular space ('type III lymphatic cavity', see his Fig. 6) is located at the inner side of the internalized cuticle and does not show an obvious connection to the other receptor lymph cavities.

We revisited the trichobothria of *P. lagurus* using TEM and filled some of the gaps Tichy's (1975) description left over, such as the organization of proximal half of the trichobothrium comprising somata cluster of receptor and sheath cells or aspects of innervation (afferent circuitries and subsequent innervations of the protocerebrum). We can thereby confirm the presence of 3-4 biciliated trichobothrial receptor cells (e.g. Fig. 9.13D, F). Somata of receptor cells are clustered and may bulge deeply below the epidermis into the cephalic hemolymphatic space (Fig. 9.13F). A cluster of trichobothrial receptor cells is completed by more than ten sheath cells. Three of them directly encompass the receptor cells in the center (inner sheath cells) and form the dendritic sheath further up distally (Figs. 9.12C, E, 9.13), while the remaining ones make up a circle of outer sheath cells lining the internalized cuticle. In contrast to Tichy's description, there seems to be only one but particularly expanded and strongly compartimentalized receptor lymph space, corresponding to Tichy's type I lymph cavity. This receptor lymph space contains the dendritic processes of the receptor cells. Receptor lymph compartment 1 extends from the zone of ciliary bodies down to the bottom of the trichobothrium. It is heavily traversed by microvilliform projections of dendritic inner segments and both sorts of sheath cells (Fig. 9.13E). Receptor lymph compartment 2 is balloon-shaped, carries dendritic outer segments on their way into the sensory hair, and is already surrounded by a dendritic sheath built by thin wrap of the inner sheath cells (Figs. 9.12E, 9.13C-D). Receptor lymph compartment 3 is comparatively small and restricted to the sensory hair (Fig. 9.13A-B). The so-called receptor lymph cavity II turned out to be an amorphous, moderately osmiophilic subcuticle which is continuous with subcuticular pads strengthening the thin bottom of the cuticular cavity, called 'drumskin-like cuticular membrane' by Tichy (1975). Likewise, presumed receptor lymph cavity III may also be subcuticle. There are no convincing ultrastructural characteristics yet to call it an outer receptor lymph space. Each dendritic inner segment emits two cilia, representing the dendritic outer segments (Fig. 9.13D). Within the sensory hair, the dendritic inner segments do not transform into tubular bodies, but are interconnected by interciliary junctions and pass through 60-70%

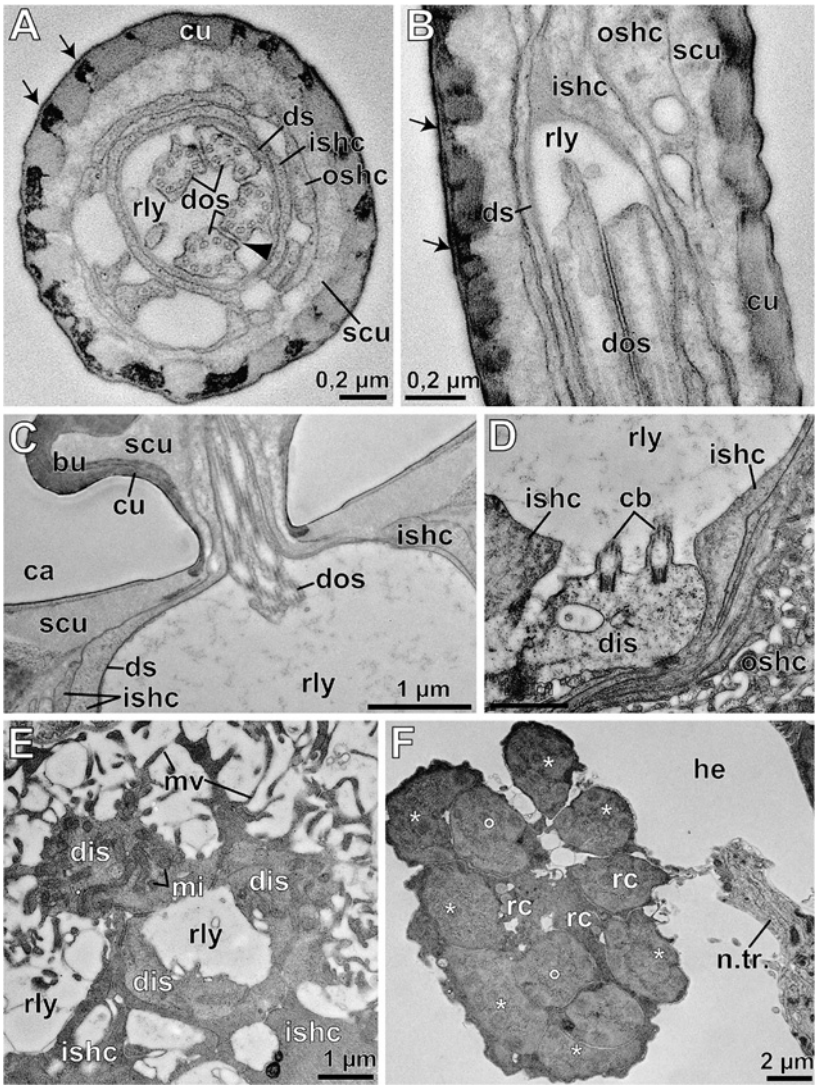

Fig. 9.13. Ultrastructural organization of trichobothria of *Polyxenus lagurus*. TEM. **A-B** Hair shaft above bulb region: **A** Cross-section. **B** Longitudinal section. Note radial projections of subcuticle into peripheral, regularly lamellated cuticle, caps of these tube-like incisions of the cuticle are filled with an electron-dense mass (black arrows), black arrowhead in **A** marks an interciliary junction. At this level, only four of the altogether six dendritic outer segments are cut in the receptor lymph space. **C** Basal region of hair shaft, below bulb structure. Eight dendritic outer segments are seen in oblique-longitudinal section entering enflated receptor lymph space. Note suspension apparatus of hair shaft reinforced by lens-like pads of amorphous subcuticle. **D** Oblique section of two ciliary bodies underlining the biciliated nature of trichobothrial receptor cells. **E** Cross-section of trichobothrium's mid-region showing centered dendritic inner segments emitting elongated microvilli into the receptor lymph space. **F** Cross-section through basal part of trichobothrium including somata of receptor cells as well as of inner (white circles) and outer (asterisks) sheath cells. **A-F** Originals: C. H. G. Müller & A. Sombke.

of the hair's length. They were never observed to break through the dendritic sheath or to make contact with pore tubules which are filled up mainly by radiating spokes of subcuticle (Fig. 9.13A-B). Basally, receptor cell somata taper into axons which leave the cell cluster horizontally rather than terminally (Fig. 9.13F). Receptor cell axons of a hair triad merge into a distinct nerve that projects towards the lateral protocerebrum maintaining a subepidermal path.

Evolutionary and functional aspects

The refined picture of ultastructural organization raises further doubts on homology of symphylan/pauropod and penicillate (diplopod) trichobothria. If they are homologous and synapomorphic for Progoneata at all (sensu Haupt, 1979), one may basically refer only to the basal bulb of the sensory hair as common character. Trichobothria of Symphyla and Pauropoda on the one hand and of Penicillata (Diplopoda) on the other may have derived as a result of independent transformations of different types of cuticular sensilla (mechano- vs. chemoreception) on different body parts (head vs. trunk). As with Penicillata, this ancestral sensillum was most probably chemoreceptive and displayed pore tubules, elongated cilia, etc. It has also been discussed if penicillate trichobothria are strongly transformed organs of Tömösváry (see above). Whether interciliary junctions and/or the basal bulb might enable or support transduction of mechanosensory stimuli on the penicillate trichobothrium and whether chemoreception was not involved still remain open questions. Besides the absence of tubular bodies, there is no unambiguous evidence from ultrastructure that let us assume penicillate trichobothria to be mechanoreceptors, as typically found in other arthropods as for instance arachnids (see review by Reissland & Görner, 1985) or hexapods (e.g. Gnatzy & Schmidt, 1971). Arguments in favour of multidirectional mechanoreception address behavioural observations (Schömann, 1956) or the presence of interciliary junctions. The latter character was found in chordotonal organs of the beetle *Speophyes lucidulus* (see Corbière-Tichané, 1971a, b). This finding brought Tichy (1975) to conclude that penicillate trichobothria include features of insect scolopidia and should thus be capable of receiving mechanical stimuli. However, interciliary junctions also occur in thermo- and hygroreceptive sensilla (of type "Np-is") on the antennae of various holometabolan insects, such as Lepidoptera and Diptera (compare review of Altner & Loftus, 1985). Either way, involvement of hygroreception requires to assume that the dendritic sheath around the dendritic outer segments is permeable to water.

ANTENNAL SENSILLA

Epidermal sensilla are sensory hairs, consisting of two structural components: the receptor cells with their dendritic processes and several sheath cells, which are more or less interspersed into the hair shaft.

Using light microscopy, some species were investigated in the late 19th century by Leydig (1860), Sazepin (1884) and v. Rath (1886) which was summarized and supplemented by Fuhrmann (1922). Ever since the emergence of electron microscopy, few species have been investigated in

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Abbreviations: **bu** basal bulb enwidening hair shaft; **ca** cavity containing shaft bulb; **cb** ciliary body; **cu** cuticle; **dis** dendritic inner segment; **dos** dendritic outer segment(s); **ds** dendritic sheath; **he** hemolymph space of the head; **ishc** inner sheath cell(s); **lg** large extracellular granule; **lsp** large wall spine; **mi** mitochondria; **mv** microvilli; **n.tr.** nerve containing axons of trichobothria; **oshc** outer sheath cell(s); **rly** receptor lymph space; **scu** subcuticle.

detail. In fact, most of what we know of the anatomy of diplopod sensilla on ultrastructural level is based on TEM studies on *Polyxenus lagurus* (Penicillata) (Gaffal et al., 1975; Nguyen Duy-Jacquemin, 1981, 1982, 1983, 1988, 1990, 1997), *Polydesmus coriaceus* (Polydesmida) (Schönrock, 1981) as well as *Blaniulus lorifer* and *Cylindroiulus punctatus* (Nguyen Duy-Jacquemin, 1985a, b, 1989). Furthermore, detailed scanning electron microscopic results are available for julid and other polydesmid species (Nguyen Duy-Jacquemin, 1985a, b, 1989, 1996b; Fontanetti & Camargo-Mathias, 2004; Chung & Moon, 2006a, b; Sombke & Ernst, 2014). In addition, a variety of taxonomic publications depicted and described the occurrences of different antennal sensilla. A typological and comparative overview is, however, not at hand and in this book chapter we will not discuss these accounts. Even though only a low number of diplopod species was investigated specifically with respect to their structure and distribution of antennal sensilla, their terminology and nomenclature varies considerably and therefore hampers classification across Diplopoda. For example, Fuhrmann (1922) described two types of basiconic sensilla ("Zapfen") in Polydesmida. In contrast, Schönrock (1981) and Sombke & Ernst (2014) distinguished five different types, whereas Chung & Moon (2006a) differentiated three types. Using external morphological characters, it is possible to assume the functional modality of specific types of arthropod cuticular sensilla which are known as essential sense organs, performing mechano-, phono-, chemo-, hygro-, thermo- and/or proprioreception (e.g., Haupt, 1979; Altner et al., 1981; Tichy & Barth, 1992; Iwasaki et al., 1999; Steinbrecht, 1999; Yokohari, 1999). Mechanoreceptors are usually innervated by a single receptor cell and possess a tubular body at the terminal end of the dendritic outer segment. The shaft is often held in position by suspension fibers and articulated by a membrane. Contact-chemoreceptors are bimodal and thus possess a mechanoreceptive dendrite attached to the base of the hair as well as chemoreceptive dendrites that extend into the lumen of the hair up to a terminal pore. Olfactory receptors show a cuticular surface that is perforated by numerous tiny pores. Below the cuticle, numerous receptor cells are present.

Millipedes in general tap their antennae on the substrate, likely for gathering environmental information. In blind millipedes, thus, the antennae are suggested to play a major role in sensing the environment (Hopkin & Read, 1992). This is supported by antennal ablation experiments, which showed that male millipedes lacking antennae are not able to mate successfully (Haacker, 1974; Carey & Bull, 1986).

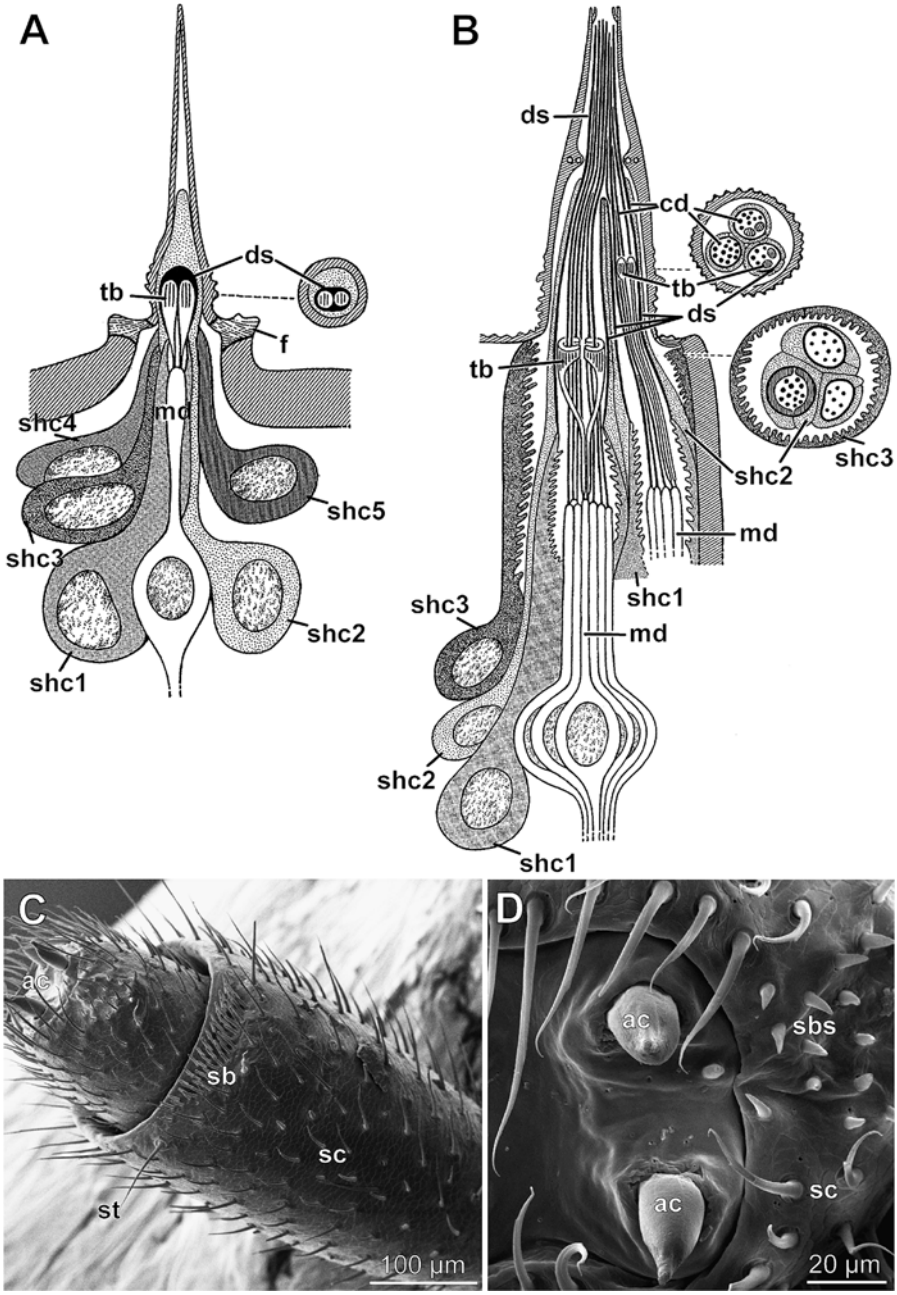
Nguyen Duy-Jacquemin (1990, 1997) summarized data on antennal sensilla of *Polyxenus lagurus*, *Polydesmus coriaceus*, *Blaniulus lorifer* and *Cylindroiulus punctatus* (see Table 9.1). In principle, six different types of sensilla were recorded on diplopod antennae.

Apical cones

A hallmark of diplopod antennae are the apical cones (Fig. 9.14B-D) located on the terminal antennal article (Enghoff, 1990; Hopkin & Read, 1992; Sombke & Ernst, 2014). A variety of different names were applied: sensory cone (e.g. "Sinneskegel", Fuhrmann, 1922; Schönrock, 1981; Wesener & Wägele, 2008; Golovatch et al., 2009a; Wesener et al., 2009a, b), olfactory cone ("Riechkegel": Verhoeff, 1928-1932), large basiconic sensillum (Sakwa, 1978), apical sensory cone (Nguyen Duy-Jacquemin, 1981), sensorial cone (Wesener & Sierwald, 2005), apical antennal cone (Nguyen Duy-Jacquemin, 1996b), apical cone sensillum (Chung & Moon, 2006a, b), or apical cone (Nguyen Duy-Jacquemin, 1997; Fontanetti & Camargo-Mathias, 2004; Marek et al., 2012; Sombke & Ernst, 2014). The presence of four apical cones is considered an autapomorphy of Diplopoda (Enghoff,

TABLE 9.1
Diversity and distribution of antennal sensilla in selected diplopod species (after Schönrock, 1981; Nguyen Duy-Jacquemin, 1990, 1997; Sombke and Ernst, 2014)

Type	Presumed modality	*Polyxenus lagurus*	*Polydesmus coriaceus*	*Oranmorpha guerinii*	*Blaniulus lorifer*	*Cylindroiulus punctatus*
Apical cones	Contact-chemoreception	+	+	+	+	+
Sensilla trichodea	Contact-chemoreception		+	+	+	+
Sensilla basiconica	Olfaction/hygro- and/or thermoreception	+	+	+	+	+
Sensilla coeloconica	Thermo- and hygroreception	+				
Sensilla chaetica/ sensilla setiformia	Mechanoreception	+	+	+	+	+
Cupuliform sensilla	Chemoreception	+				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20 µm

1990; Ax, 1999; Sierwald & Bond, 2007). However, the number may differ inter- and intraspecifically e.g., in Sphaerotheriida with a range of 4 to over 40 (Wesener & Sierwald, 2005; Wesener & Wägele, 2008) or in *Rhinocricus padbergi* (Spirobolida) with a range from 13 to 18 (Fontanetti & Camargo-Mathias, 2004).

In *Polydesmus coriaceus*, an apical cone is composed of more than 500 receptor cells and, thus, represents a compound sensillum (Schönrock, 1981). The shaft is devoid of pores, a terminal pore is always present. In *Polyxenus lagurus*, several units of six to 14 dendrites are surrounded by two sheath cells (Fig. 9.14B). Each sensory unit is composed of several uniciliated chemoreceptive cells and one (per apical cone) biciliated mechanoreceptive cell. All chemoreceptive dendritic outer segments project to the terminal pore. Per apical cone, two tubular bodies are present. At the base of each apical cone, a third sheath cell surrounds all units (Nguyen Duy-Jacquemin, 1981; Fig. 9.14B). Based on fine structural investigations in *P. coriaceus* and *Polyxenus lagurus*, a contact-chemoreceptive function was proposed (Schönrock, 1981; Nguyen Duy-Jacquemin, 1981, 1997). However, Chung & Moon (2006a) proposed an olfactory function.

Sensilla trichodea

Trichoid sensilla were described for numerous chilognath Diplopoda (Polydesmida: Schönrock, 1981; Chung & Moon, 2006a, b; Sombke & Ernst, 2014; Spirobolida: Fontanetti & Carmago-Mathias, 2004; Julida: Nguyen Duy-Jacquemin, 1985b, 1990; Siphonophorida: Marek et al., 2012). The elongated hair is often curved to the top and bears numerous spiral ribs on its surface (Figs. 9.14C, 9.15C, D). The presence of a terminal pore is likely but was not unambiguously proven in all investigations. Fine structural investigations are only available for *Polydesmus coriaceus* (Schönrock, 1981) as well as for *Cylindroiulus punctatus* and *Blaniulus lorifer* (Nguyen Duy-Jacquemin, 1990). There is always one biciliated receptor cell that terminates in two tubular bodies. In *P. coriaceus*, three biciliated receptor cells project into the shaft lumen. In *C. punctatus*

Fig. 9.14. External morphology and ultrastructural anatomy of diplopod antennal sensilla I. **A** Semischematic drawing showing a sensillum setifome of *Polyxenus lagurus* composed of five sheath cells and a single biciliated mechanoreceptive cell comprising two tubular bodies. Added cross-section illustrates the level of tubular bodies enclosed by dendritic sheath. **B** Semischematic drawing showing a dorsal apical cone of *P. lagurus* composed of three sheath cells and several receptor cells. Added cross-sections illustrate further details of dendritic outer segments and the surrounding system of sheath cells divided into three distinct sensory units. Note the presence of chemoreceptive cilia as well as tubular bodies of a mechanoreceptive cilium in particular sensory units. **C** The terminal antennal articles of *Oranmorpha guerinii* (Polydesmida). SEM. At the sixth article sensilla basiconica are accumulated. The terminal article bears four apical cones. Longer sensilla trichodea are distinguishable from shorter sensilla chaetica by their higher angle to the antennal cuticle. **D** Frontal view on the terminal article of *O. guerinii* with two apical cones as well as several sensilla basiconica spiniformia and sensilla chaetica. SEM. **A, B** Modied after Nguyen Duy-Jacquemin (1997). **C, D** Originals: A. Ernst. Abbreviations: **ac** apical cone; **cd** chemoreceptive dendrite; **ds** dendritic sheath; **f** fibrous material; **md** mechanoreceptive dendrite; **sb** sensilla basiconica; **sbs** sensilla basiconica spiniformia; **sc** sensilla chaetica; **shc** sheath cell; **st** sensilla trichodea; **tb** tubular body.

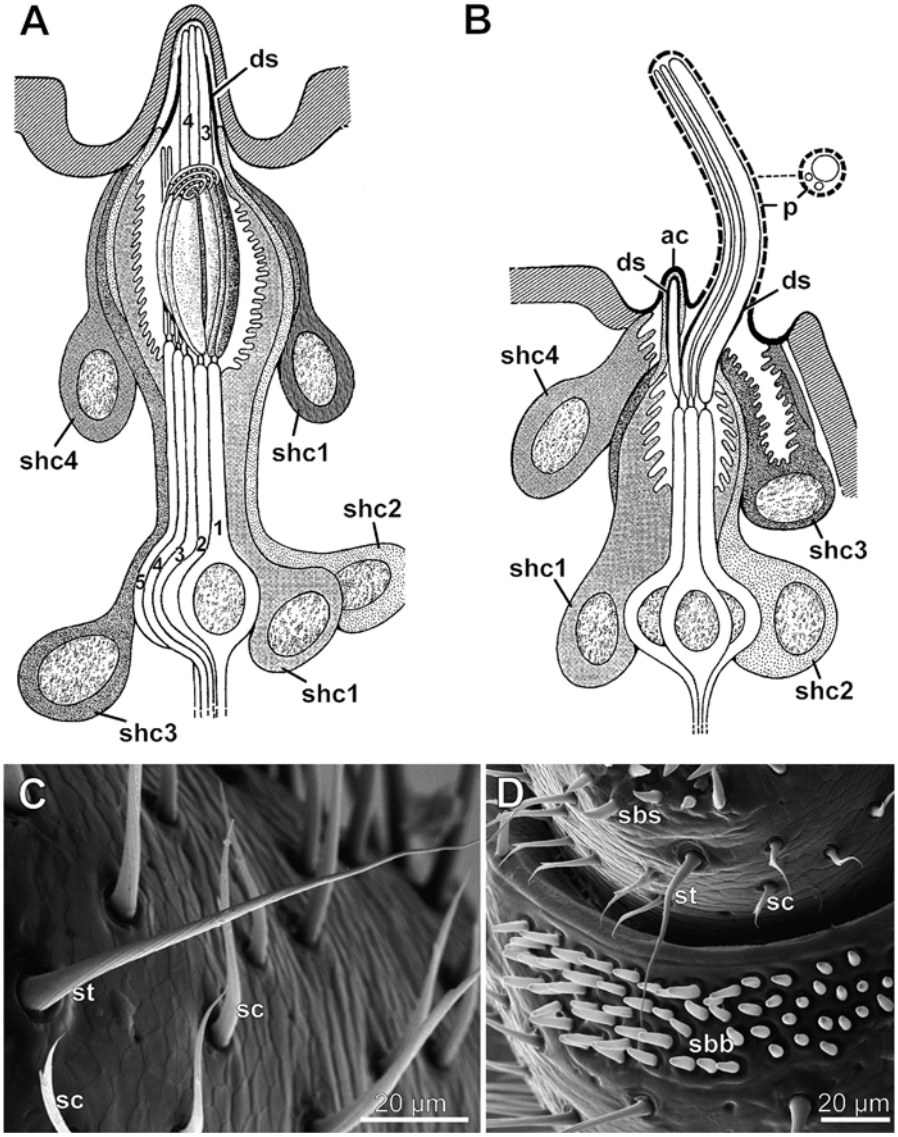

Fig. 9.15. External morphology and ultrastructural anatomy of diplopod antennal sensilla II. **A** Semischematic drawing of a sensillum coeloconicum of *Polyxenus lagurus* composed of four sheath cells and five receptor cells. Note the subcylindrical shape of the dendritic outer segments of receptor cells 1 and 2. Ultrastructure of dendrites of receptor cells 3-5 differs considerably in size (**rc3** with large **dos**), complexity (**rc4** biciliated) and length (**rc5** with short **dos** extending to base of the peg) of the dendritic outer segment (= sensory cilium). **B** Semischematic drawing of a multi-porous thick sensillum basiconicum of *P. lagurus* composed of four sheath cells and three receptor cells. Added cross-section illustrates the porous sensillar shaft traversed by extended chemoreceptive dendritic outer segments. In *P. lagurus*, sensilla basiconica possess an associated cone at their base. **C** Sensilla trichodea and s. chaetica on antennae of *Oranmorpha guerinii* (Polydesmida). SEM.

and *B. lorifer*, the number may vary from four to five including one or two uniciliated receptor cell(s). All receptor cells, and their dendrites in particular, are enveloped by sheath cells, the second (middle) sheath cell reaches up to the base of the sensory hair. Based on these investigations, a contact-chemoreceptive function was suggested. Shorter sensilla microtrichodea at joint membranes between antennal articles were to date only reported to occur in *Oranmorpha guerinii* (Sombke & Ernst, 2014).

Sensilla basiconica

Sensilla basiconica are frequently found at distal antennal articles (Nguyen Duy-Jacquemin, 1990; Sombke & Ernst, 2014; Figs. 9.14C, 9.15D). In Sphaerotheriida, they were also described on the first antennal article (Wesener & Wägele, 2008; Wesener & Van den Spiegel, 2009). On distal antennomeres, basiconic sensilla often occur in groups (summarized in Sombke & Ernst, 2014).

In *Polyxenus lagurus*, Nguyen Duy-Jacquemin (1982) distinguished two subtypes of single-walled, multiporous sensilla basiconica. Thick basiconic sensilla include three uni- and biciliated receptor cells (Fig. 9.15B). Thin basiconic sensilla are supplied by only one receptor cell with a large dendritic outer segment. In both subtypes, longitudinal grooves of the shaft's cuticle are connected to thin openings and pore tubules in the wall. Only the base of the dendritic outer segment is surrounded by the dendritic sheath. In *P. lagurus*, each basiconic sensillum possesses an associated cone at its base (Fig. 9.15B). Similar multiporous sensilla basiconica have been described for *Blaniulus lorifer* (Nguyen Duy-Jacquemin, 1989), *Cylindroiulus punctatus* (Nguyen Duy-Jacquemin, 1989), and *Polydesmus coriaceus* (Schönrock, 1981). Here, sensilla basiconica are also equipped with uni- and biciliated receptor cells. According to the specific morphology of the sensillum basiconicum's apex, the subtypes bacilliformia and spiniformia were introduced (Nguyen Duy-Jacquemin, 1985b, 1989; Sombke & Ernst, 2014). Bacilliform basiconic sensilla (sbb in Fig. 9.15D) possess a rounded apex and longitudinal grooves with small openings, whereas spiniform basiconic sensilla (sbs in Fig. 9.15D) posses a pointed apex which occasionally exhibits a terminal pore (summarized in Sombke & Ernst, 2014). Based on fine-structural investigations, an olfactory function was proposed for thick and thin sensilla basiconica in *P. lagurus* (see Nguyen Duy-Jacquemin, 1982) as well as bacilliform basiconic sensilla in *C. punctatus* and *B. lorifer* (see Nguyen Duy-Jacquemin, 1989) as well as in *P. coriaceus* (see Schönrock, 1981). Sensilla basiconia spiniformia were proposed to fulfill a gustatory function (Nguyen Duy-Jacquemin, 1985b).

Note the shaft protuberance of sensilla chaetica. **D** Accumulation of sensilla basiconica bacilliformia at the distal edge of antennal article 6 and sensilla basiconica spiniformia on antennal article 7 in *O. guerinii*. SEM. **A, B** Modied after Nguyen Duy-Jacquemin (1997). **C, D** Originals: A. Ernst. Abbreviations: **ac** associated cone; **dos** dendritic outer segment(s); **ds** dendritic sheath; **p** pore; **rc** receptor cell; **sbb** sensilla basiconica bacilliformia; **sbs** sensilla basiconica spiniformia; **sc** sensilla chaetica; **shc** sheath cell; **st** sensilla trichodea.

Sensilla coeloconica

Coeloconic sensilla were described on the 6th and 7th antennal article of *Polyxenus lagurus* (Nguyen Duy-Jacquemin, 1997). The sensillum consists of a short and poreless peg situated in a small cuticular depression (Fig. 9.15A). It is equipped with five uni- and biciliated receptor cells. A dendritic sheath around the dendritic outer segments was not observed. Two biciliated receptor cells show a characteristic lamellated ultrastructural appearance typical for thermoreceptive elements (Fig. 9.15A). Thus, a double function as thermo- and hygroreceptor was proposed by Nguyen Duy-Jacquemin (1997).

Sensilla chaetica and sensilla setiformia

Sensilla chaetica are poreless sensilla (e.g. Schönrock, 1981; Chung & Moon, 2006a, b; Marek et al., 2012; Sombke & Ernst, 2014). The hair shaft may display apical protuberances (Marek et al., 2012; Sombke & Ernst, 2014; Fig. 9.15C, D). Fine structural investigations are only available for *Polydesmus coriaceus* (Schönrock, 1981) and, to limited extent, also for *Polyxenus lagurus* (see below). Each sensillum chaeticum contains a single biciliated receptor cell, both dendritic outer segments terminate in two tubular bodies suggesting a mechanoreceptive function. In *P. lagurus*, setiform sensilla (or 'tactile hairs' sensu Gaffal et al., 1975) are present on most antennal articles (Nguyen Duy-Jacquemin, 1988, 1997). The external morphology of setiform sensilla differs from that observed on sensilla chaetica by a bulbous widening of the base of the shaft. Setiform sensilla usually contain a single biciliated mechanoreceptive cell exhibiting two tubular bodies (Gaffal et al., 1975; Nguyen Duy-Jacquemin, 1988; Fig. 9.14A). This is similar to cellular patterns found in sensilla chaetica of *P. coriaceus* (Schönrock, 1981), *Blaniulus lorifer* and *Cylindroiulus punctatus* (Nguyen Duy-Jacquemin, 1990). Thus, sensilla chaetica and setiformia are thought to represent the same type of exclusively mechanoreceptive sensilla.

The sensillum setiforme S' as described from the antennae of *Polyxenus lagurus*, however, comprises three biciliated receptor cells (Nguyen Duy-Jacquemin, 1988, 1997). The six related dendritic outer segments lie inside the inner receptor lymph space which is formed and surrounded by the inner sheath cell (type 1 sheath cell). The occurrence of two tubular bodies attaching to the cuticular fibre system at the base of the sensory hair indicates mechanosensitivity of one receptor cell. The two remaining receptor cells have more extended dendrites/cilia, the one receptor cell has a lamellated dendritic outer segment, whereas the dendritic outer segment of the other receptor neuron displays a subcylindrical and rectilinear shape. For this second and third receptor cells a thermo- and hygroreceptive function may be assumed.

Cupuliform sensilla

Cupuliform sensilla were only described on the 1st, 3rd and 5th article of the antenna of *Polyxenus lagurus* (Nguyen Duy-Jacquemin, 1972, 1997). They can comprise one to three pegs with 5-7 longitudinal grooves. The sensillum is inserted in a deep pit in the distal joint membranes of antennomeres. Fine structural investigations are not conclusive, a chemoreceptive function is however assumed.

Evolution of myriapod sensilla

Arthropod sensilla all share a similar cellular architecture and development (e.g. Keil & Steinbrecht, 1984; Tichy & Barth, 1992; Keil, 1997, 2012; Hallberg & Hansson, 1999; Hallberg & Skog, 2011; Müller et al., 2011, 2014). Axons of receptor cells project mostly into the deutocerebrum of the brain where primary processing neuropils for chemo- and mechanosensory qualities are present (e.g., Loesel et al., 2013; see Chapter 8). Previous studies however reported huge morphological diversity among the various types of cuticular sensilla (e.g., Hexapoda: Altner, 1977; Altner & Thies, 1978; Altner et al., 1983; Crustacea: Hallberg et al., 1997; Cate & Derby, 2002a, b; Chelicerata: Eckweiler et al., 1989; Anton & Tichy, 1994; Talarico et al., 2006; Myriapoda: see citations above as well as Müller et al., 2011 for centipedes) and although believed to be traceable down to a common origin no unambiguous scenario has been presented yet to support this assumption. Amongst many problems preventing proper evaluation of sensilla in an evolutionary context, Hallberg & Hansson (1999) addressed the low number of structural elements and tight functional morphological constraints shaping a given arthropod sensillum. Moreover, at least some types of arthropod sensilla, as for instance those receiving volatile stimuli (olfactory function), have been considered to be prone to convergence, probably due to adaptions to certain environments (e.g. Hallberg & Hansson, 1999). Therefore, it has been questioned in general as to whether characters of arthropod sensilla can be used as phylogenetic markers at all. Although we have a general overview on centipede antennal sensilla (Müller et al., 2011; Sombke et al., 2011, 2014), this discussion is in a far less advanced state with regard to cuticular sensilla of Myriapoda. Moreover, our current knowledge of the external morphology of the various types of diplopod sensilla is often not corroborated by examinations on their cellular anatomy. However, TEM-based studies at least partly revealed considerable variations in cell numbers constituting certain types of myriapod sensilla (e.g. antennal beak-like sensilla of Scutigeromorpha: Müller et al., 2014, various antennal sensilla of scutigeromorph and geophilomorph Chilopoda: Ernst, 2000; Müller et al., 2014). External shapes of sensilla may also vary considerably even though similar cellular set-up, functional ultrastructure and formation patterns disclose them to belong to the same type of sensillum (e.g. Chilopoda: Müller et al., 2014). This variability qualifies current typology of myriapod sensilla as tenuous guesswork, as far as it is based on SEM studies alone. At least, any conclusions on homology and evolution of myriapod sensilla and the applicability of related characters for phylogenetic analyses seem to be far premature unless new morphological data become available. New approaches need to be more consistent and comprehensive with regard to terminology, concept of analysis and methods to be applied.

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CHAPTER 10

DIPLOPODA — REPRODUCTION

BY

ALESSANDRO MINELLI AND PETER MICHALIK

KARYOLOGY
[ALESSANDRO MINELLI]

Chromosome numbers are available for about seventy species of millipedes, unequally distributed among the major taxa of this myriapod class. The list includes ca. 15 species of the sphaerotheriid genus *Arthrosphaera* and several members of the Pachybolidae and the Harpagophoridae, as a result of investigations by Indian authors (largely summarized in Achar, 1987); and a number of Brazilian Spirostreptida, in particular several species of *Pseudonannolene* and a number of Spirostreptidae, studied by Fontanetti and associates. Both schools have also contributed to the study of chromosome numbers in the Polydesmida (ten karyotypes available thus far, including four Japanese Xystodesmidae studied by Tanabe, 1992). The most recent overview by Fontanetti et al. (2002) is the main source for the information summarized in the next lines. Unfortunately, only fragmentary and in part very old reports are available for some major groups, especially Polyxenida (2n = 16 in *Polyxenus* sp.; Sokoloff, 1914), Callipodida (2n = 12 in *Acanthopetalum richii*; Vitturi et al., 1997), Chordeumatida (2n = 24 in a "*Melogona* (*Microchordeuma*)" sp.; Chowdaiah & Kanaka, 1979) and Julida (2n = 22 in *Ommatoiulus oxypygus*; Vitturi et al., 1997, plus a couple of problematic reports for other species). No data for Colobognatha or Stemmiulida.

Warchałowska-Śliwa et al. (2004) confirmed for *Glomeris hexasticha* and *G. connexa* the diploid number 2n = 20 tentatively suggested for *G. annulata* by Bessière (1948). In the Sphaerotheriida, most *Arthrosphaera* species have 2n = 30, others however 28 or 26.

In Polydesmida, the most frequent value is 2n = 12, as found in representatives of different families (Chelodesmidae, Polydesmidae, Xystodesmidae and Paradoxosomatidae); however, Tanabe (1992) reported 2n = 16 for *Riukiaria semicircularis* and Chowdaiah (1966) gave 2n = 24 for a "*Strongylosoma*" sp.

Chromosome numbers are more diverse in Spirobolida (2n = 12, 16, 20, 24, 26, 28) and Spirostreptida (2n = 12, 14, 16, 20, 22, 24, 26, 28). Some variation has been found

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even among members of one genus, e.g. *Rhinocricus* (2n = 20, 24, 28; Fontanetti, 1998a) and *Pseudonannolene* (2n = 12, 14, 16, 20; summarized in Fontanetti et al., 2002).

An XY sex determination system has been suggested in the vast majority of cases; the few putative exceptions deserve further investigation.

SEXUAL DIMORPHISM
[ALESSANDRO MINELLI]

Male millipedes are generally smaller than the conspecific females; in the groups where the number of rings varies intraspecifically, this is lower in males, but in some groups with fixed number of rings the males have a higher number of leg pairs than the females: in the Glomerida, leg pairs are 17 in females, 19 in males; in Sphaerotheriida, 21 in females, 23 in males. Millipede species sexually dimorphic for the number of body rings are known among the Polydesmida (female with 18 + 1 rings, male with 17 + 1, es. *Polydesmus* spp., *Prosopodesmus panporus*, *Eutrichodesmus peculiaris*, *Galliocookia* spp., *Occitanocookia hirsuta*, and several Fuhrmannodesmidae; also dimorphic, but with higher numbers of diplosegments, are the species of the genus *Devillea* species: see p. 285) and the Chordeumatida (male with 25 'rings', female with 29 in *Buotus carolinus*; male with 25 'rings', female with 27 in some Tingupidae; male with 27, female with 29 e.g. in *Xystrosoma beatense* and *Peterjohnsia* spp. (Mauriés, 1987)). In taxa such as Colobognatha or Julida, where intraspecific variation is generally high and, to some extent, 'open', the range of segment numbers found in the males is lower than the corresponding range for the females, partly as a consequence of a lower number of post-embryonic moults, for example a maximum of 11 and 14 postembryonic stadia in males and females of *Ommatoiulus sempervirilis*, respectively (Akkari & Enghoff, 2011); in millipedes with a fixed number of moults, identical in both sexes, the males may develop anyway faster than the females, as in *Pycnotropis tida* (Vohland & Adis, 1999).

In the Polyxenida, sexual dimorphism is mainly expressed as differences in the size, shape and density of some groups of trichomes. For example, in *Unixenus* aff. *broelemanni*, the caudal pencil of the female, including nidamental trichomes, is short, homogeneous, light coloured and furnished with hooked trichomes only; in the male, the pencil is one and half to twice longer, dark coloured in part, and furnished with barbate and serrate trichomes only (Condé & Nguyen Duy-Jacquemin, 1992).

Except for the first post-embryonic stadia, the sex of a millipede can be easily determined by the presence of reduced or modified pairs of appendages in the male. Most conspicuous are the male appendages involved in sperm transfer and/or in grasping the partner during copulation, i.e. the telopods of the Pentazonia and the gonopods of the Helminthomorpha. But other pairs of appendages can be modified, too. The first pair of legs of male Julida are almost always modified, enlarged in Parajuloidea but reduced and more or less hooklike in the other groups: shortened in Blaniulidae, reduced to three articles in some Julidae, to two articles only in *Physiostreptus*. The first pair of legs are also modified in millipedes other than Julida: these appendages lack the pretarsus

in *Iulomorpha*, and have six rather than seven articles in other taxa, The legs of the second pair are reduced in male Parajulidae and Stemmiulidae, while the males of the rhacodesmid *Tancitares michoacanus* have a digitiform accessory processes on the coxae of the second pair of legs (Hoffman, 2011). In the male of *Chelojulus sculpturatus* leg pair 5 is transformed into a pair of forcepts (Enghoff, 1982).

Less widespread are sexual modifications in one or more anterior pair(s) of legs of females. The second pair is reduced in the females of some Chordeumatida, while in Stemmiulida both sexes have strongly modified appendages (leg pairs 1 and 2 in the male, 1 to 3 in the female).

Instances of reversal of this trend are known, for example leg pair 1 of the males of the julid *Typhloiulus ganglbaueri* are normal walking legs (Ceuca, 1970).

Occasionally, sexual dimorphism affects other body features. In most male blaniulids, the mandibles are modified into a kind of forceps used for gripping the antennae of the partner during copulation. Less obvious is the adaptive significance of sex dimorphism in the polydesmidan *Ammodesmus granum*, where the male has high tubercles across the metaterga, lacking in the female, or in the congener *A. congoensis*, where the metaterga of the male are very densely pilose all over, with a few longer setae, but lack the deep median transverse gutter found in the anterior third of the sclerite in the female (VandenSpiegel & Golovatch, 2015).

* * *

Both female and male millipedes have one gonad, extending ventrally to the gut along most of the trunk. From the gonad, paired oviducts resp. a pair of vasa deferentia lead to the also paired gonopores opening between trunk segments II and III. The internal structure of the mature gonads shows more or less ostensibly its nature of fundamentally paired organ, and a more or less large degree of segmental architecture.

FEMALE ORGANS AND GAMETES
[ALESSANDRO MINELLI]

The shape of the millipede ovary varies between a simple sac-like tubule and a distinctly paired set of ovisacs. A simple tubular ovary has been described e.g. in representatives of the Polyxenida (*Polyxenus lagurus*: Seifert, 1960; Kubrakiewicz, 1991b; *Eudigraphis takakuwai nigricans*: Yahata & Makioka, 1994), Glomerida (*Hyleoglomeris japonica*: Yahata & Makioka, 1997), Polydesmida (*Oxidus gracilis*: Kubrakiewcz, 1987), Julida (*Julus terrestris* and *Ophyiulus pilosus*: Kubrakiewicz, 1991a; *Catamicrophyllum* spp.: Gealekman et al., 1996; Warburg & Gealekman, 2000), Cambalidea (*Pseudonannolene* spp.: de Freitas et al., 2003) and Spirostreptidea (*'Spirostreptus' asthenes*: Nadarajalingam & Subramonian, 1984). Ovaries with distinct paired arrangement of ovisacs have been described e.g. in Polydesmida (*Euryurus* '*erythropygus*': Miley, 1930; *Strongylosoma stigmatosum*: Seifert, 1932) and Spirostreptidea (*Urostreptus atrobrunneus*: Fontanetti et al., 2010).

A pair of longitudinally elongated germ zones were found in the dorso-lateral region of the ovaries of four polydesmids (*Nedyopus tambanus*, *Oxidus gracilis*, *Epanerchodus orientalis* and *Eutrichodesmus elegans*), with oogonia and younger oocytes occupying medial positions in respect to the larger oocytes. In some of these species, the ovarian epithelium forms paired folds that extend toward the lumen (Yahata, 2012). In *Eumastigonus* sp. (Cambalidae) oocytes are arranged instead in irregularly shaped clusters including cells at different stages of development (Warburg et al., 1998). In some species (Polydesmida: *Anoplodesmus anthracinus*: Nair, 1981; Julida: *Catamicrophyllum* spp.: Gealekman et al., 1996; Warburg & Gealekman, 2000; Spirobolida: *Rhinocricus padbergi*: Fontanetti & Cunha, 1993), two parallel strands of oocytes are well recognizable in the immature ovary, but the symmetry fades out as long as the oocytes increase in size during vitellogenesis.

The presence of a sac-like ovary instead of one with paired ovisacs is to some extent related to body size or diameter, as suggested by the contrast between smaller and larger species of the same order. Among the Polydesmida, two smaller species (the pyrgodesmids *Poratia salvator* and *Myrmecodesmus hastatus*) have a simple tubular ovary without paired ovisacs, whereas these are present in the chelodesmid *Telonychopus klossae* (Pinheiro et al., 2013).

Among the species with simple tubular ovary, no clustering of oocytes into ovisacs was observed in *M. hastatus*; some degree of grouping was recorded in *P. salvator* (Pinheiro et al., 2013). In the tubular ovary of *'Spirostreptus' asthenes* Nadarajalingam & Subramoniam (1984) recognized an apical germinal zone, a median pre-vitellogenic zone and an anterior vitellogenic zone. A kind of germarium was also described in *Ophyiulus pilosus* (Kubrakiewcz, 1991a) as a dorsolateral cluster of cells in the dorsolateral ovarian wall, and in *P. tocaiensis* (de Freitas et al., 2003) and in *U. atrobrunneus* (Fontanetti et al., 2010) the germarium occupies the apical extremity of the ovary.

The following description was provided by Kubrakiewicz (1991a) for the tubular ovary of *Ophyiulus pilosus*. The organ extends along the body axis between the alimentary canal and the ventral nerve cord. At the anterior end it passes into the oviduct, which is first single and then bifurcated. Lateral to the ovary, there are lobes of fat bodies. The wall of the ovary consists of three layers: external epithelium, striated muscle fibres, and internal epithelium. Germ cells, oogonia, and young oocytes up to the early diplotene stage develop among the cells of the ovary wall, surrounded mainly by epithelial cells of the internal layers, occasionally by muscle fibers. Most germ cells are distributed in clusters in the dorsolateral parts of the ovary wall, and are observed both in juveniles and in sexually mature females.

Yahata & Makioka (1995) studied the development of the ovary of the polyxenid *Eudigraphis takakuwai nigricans* throughout the post-embryonic stadia. In stadium I there is only one cluster of ca. 20 oogonia, accompanied by a few interstitial cells, placed beneath the gut in the third trunk segment. During stadia III to VIII, clusters of previtellogenetic oocytes, still accompanied by interstitial cells, progressively separate from both the anterior and the posterior end of the developing ovary and become arranged

in two parallel vitellarial areas along the ventral wall of the ovary. In stadium VII, oocytes float in the lumen of the ovary, but still retain a connection to the wall.

Oogenesis and eggs

The oogenesis has been described as follicular in Penicillata (*Polyxenus lagurus*) but solitary in the Chilognatha (*Ophyiulus pilosus*, *Polydesmus* sp., *Oxidus gracilis*).

In *U. atrobrunneus* Fontanetti et al. (2012) identified three stages of development: young oocyte with homogeneous cytoplasm of basophilic nature, with large nucleus and well-developed nucleolus; intermediary oocyte (the stage at which chorion deposition initiates) in which vitellogenesis is already ongoing, with less basophilic cytoplasm and a certain granulation in the ooplasm, which increases as the deposition of yolk progresses; and mature oocyte with heterogeneous ooplasm, the stage at which almost all the chorion has been deposited and vitellogenesis has almost finished. Each oocyte is covered by follicular cells, more numerous around the intermediate oocytes.

In *Anoplodesmus anthracinus* Nair (1981) recognized two pre-vitellogenic and two vitellogenic stages. Four stages of oogenesis were also recognized by Warburg & Gealekman (2000) in *Catamicrophyllum caifanum*: (1) oogonia still embedded in the germ layers of the ovarian epithelium; (2) previtellogenic oocytes of two different sizes (<0.1 mm and 0.2 ± 0.45 mm, respectively), entering the ovarian lumen; (3) small, medium and large vitellogenic oocytes; (4) mature, post-vitellogenic oocytes, elliptic in shape and yellowish in colour, appearing towards the end of autumn. In winter only post-vitellogenic oocytes are found, disappearing from the ovary towards the end of winter. The number of mature, post-vitellogenic oocytes is positively correlated with the female's body size.

Vitellogenesis in Diplopoda is of mixed type, i.e. partly endogenous, partly exogenous (Kubrakiewicz, 1991b).

In two millipede of arid habitats, *Archispirostreptus syriacus* and *Orthoporus ornatus*, Crawford & Warburg (1982) demonstrated that desiccation induces resorption of the oocytes.

Millipede eggs are large, yolk-rich, and generally subsphaerical. Their size ranges form 0.2 to 2 mm (rarely more); some examples: *Polydesmus abchasius*, 0.3 mm (Lignau, 1911a, b); *P. angustus*, 0.35-0.45 (Banerjee, 1973); *Spelaeoglomeris doderoi*, 0.5 mm (Juberthie-Jupeau, 1967c); *Pycnotropis tida*, 0.60 ± 0.23 mm (Vohland & Adis, 1999); *Brachycybe nodulosa*, 0.7 (Murakami, 1962b); *Glomeris marginata*, 0.8 (Dohle, 1964), *Cyliosoma* sp., 1-1.2 × 1.27 (Dohle, 1992); *Oranmorpha guerinii*, 1.3 (Metschnikoff, 1874). The chorion, almost smooth and permeable to water, covers the underlying vitelline membrane. The number of egs produced by a female varies extensively, from a few units to more than one thousand. A few examples of fecundity are given in Table 10.1; other data are found e.g. in Verhoeff (1928), Halkka, (1958), Juberthie-Jupeau (1967a) and Blower (1970a, b).

TABLE 10.1
Number of eggs produced by some millipede species

Brachycybe nodulosa	Up to ca. 100	Kudo et al., 2011
Brachydesmus superus	Mean brood size 49	Stephenson, 1961
Cylindroiulus punctatus	Batches of 45-60	Saudray, 1952
Epibolus pulchripes	Batches of 10 to 15	Dhaenens & VandenSpiegel, 2006
Glomeris marginata	Ca. 50 eggs; mean 30, max. 86	Juberthie-Jupeau, 1967b Blower, 1974
Habrodesmus falx	Usually 100-200, max. 1436	Toye, 1967
Polydesmus angustus	1 to 4 ovidepositions, of (in the order) 278 ± 27, 244 ± 25, 153 ± 24 and 85 eggs; max. total 805 eggs in three nests	David & Célérier, 1993
Polydesmus angustus	Field: 125-246, mean 184 Lab: 135-251, mean 157	Banerjee, 1973
Pycnotropis tida	20-140, generally in clusters of ca. 40 eggs	Vohland & Adis, 1999
Spelaeoglomeris doderoi	Mean 4, max. 13	Juberthie-Jupeau, 1967b
Oranmorpha guerinii	200	Metschnikoff, 1874

MALE REPRODUCTIVE SYSTEM, SPERMATOZOA AND SPERMIOGENESIS [PETER MICHALIK]

Morphology and anatomy of the male reproductive system

Research on the male reproductive system of millipedes goes back to the beginning of the 19th century (e.g. Treviranus, 1817; Newport, 1841; Fabre, 1855). So far, a considerable number of species has been studied including representatives of Polyxenida, Pentazonia, Juliformia and Polydesmida (e.g. Seifert, 1932; Warren, 1934; Kanaka & Chowdaiah, 1974; Fontanetti, 1990; de Freitas & Fontanetti, 2003, 2008; for spermatogenesis see also list of studies in Reger & Fitzgerald, 1983 and below). In general, the male reproductive system consists of numerous (segmentally arranged; usually from segment 7 or 8 towards posterior, Fig. 10.1A) testes (testicle vesicles, e.g. Fontanetti, 1990; testis lobes, e.g. Kanaka & Chowdaiah, 1974; testicular lobules, e.g. Demange, 1988; Samenfollikel, e.g. Sokoloff, 1914) and paired (or unpaired, see below) deferent ducts (spermatic duct, e.g. Reger & Cooper, 1968) which lead separately into the gonopores close to base of the second pair of legs or into a bilobed penis behind these legs (e.g. Horstmann & Breucker, 1969a; Hopkin & Read, 1992). In some cases the deferent ducts can be partly fused resulting in a short unpaired region before leading to the paired gonopores (e.g. Effenberger, 1909; Horstmann & Breucker, 1969a). Hopkin & Read (1992) wrongly termed the whole male reproductive system as "testes" resulting in a rather confusing description of this organ system.

Based on Warren (1934) and Kanaka & Chowdaiah (1974) three types of organization can be distinguished, i.e. scaliform, reticular and arthrosphaeroid (Figs. 10.1, 10.2). The *scaliform type* is characterized by long deferent ducts which are connected by small

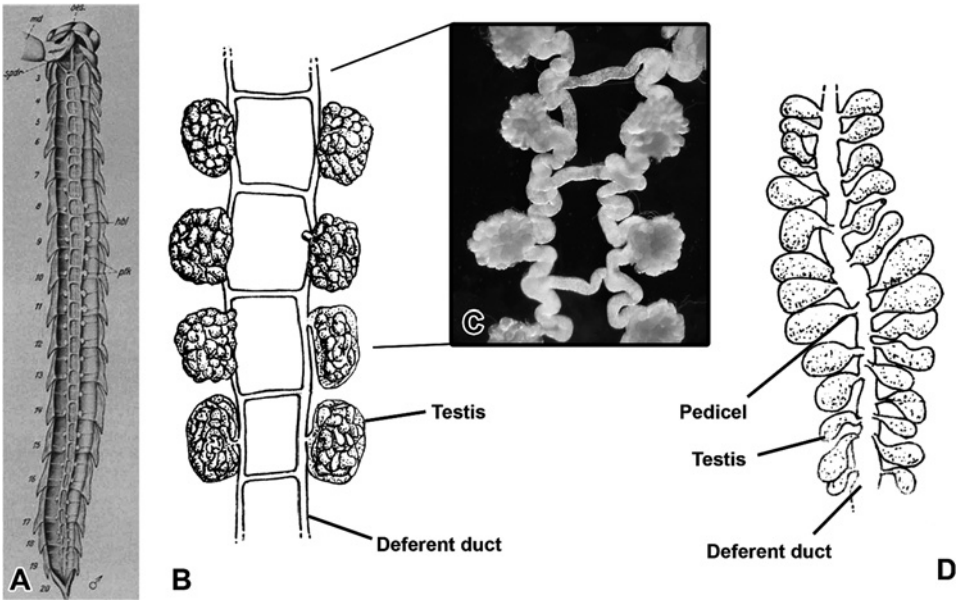

Fig. 10.1. **A** Male reproductive system of *Strongylosoma stigmatosum*. **B, C** Scalariform organization of the male reproductive system. **C** Detail of the male reproductive system of the polydesmidan *Auturus* sp. **D** Schematic drawing of the aberrant organization with an unpaired deferent duct. **A** From Seifert (1932). **B, D** From Fontanetti (1990).

ducts in a ladder-like organization. The globular testes are numerous and directly connected to the deferent ducts (Fig. 10.1A-C). The scaliform organization is most common and reported for the majority of the investigated representatives of Helminthomorpha (see e.g. Fontanetti, 1990; Fujikawa & Yoshida, 2005). The *reticular type* is characterized by reticle-shaped deferent ducts (reported for *Odontopyge*, *Poratophilus* and *Spirostreptus*, all Spirostreptida; Warren, 1934; Kanaka & Chowdaiah, 1974) whereas in the *arthrosphaerid type* connecting tubes are only present distally and the paired deferent ducts are mainly isolated from each other (reported for *Arthrosphaera* (Sphaerotheriida); Kanaka & Chowdaiah, 1974). Moreover, according to Kanaka & Chowdaiah (1974), *Carlogonus robustior* (Spirostreptida) shows a combination of all three types (Fig. 10.2). A rather aberrant type of organization was described by Fontanetti (1988, 1990) for *Pseudonannolene* (Spirostreptida) and *Rhinocricus* (Spirobolida). Here, the deferent duct is rather large and unpaired (!). The numerous testicular vesicles are kidney-shaped and connected to the unpaired deferent duct by a short pedicel (Fig. 10.1D). The unpaired deferent duct bifurcates distally leading to the paired genital openings. According to Fontanetti (1990) this organization resembles also the condition described for *Polyxenus* (Fabre, 1855; Sokoloff, 1914) and *Glomeris* (Bessière, 1948). Fontanetti (1990) considered this type as the most derived. However, as this organization is also present in basal branching lineages (Polyxenida) this scenario is questionable. In contrast, Kanaka & Chowdaiah (1974) suggested the complex reticular genital system to be the primitive organization, which evolved into the scalariform type and with the loss of the connecting ducts into the arthrosphaerid organization.

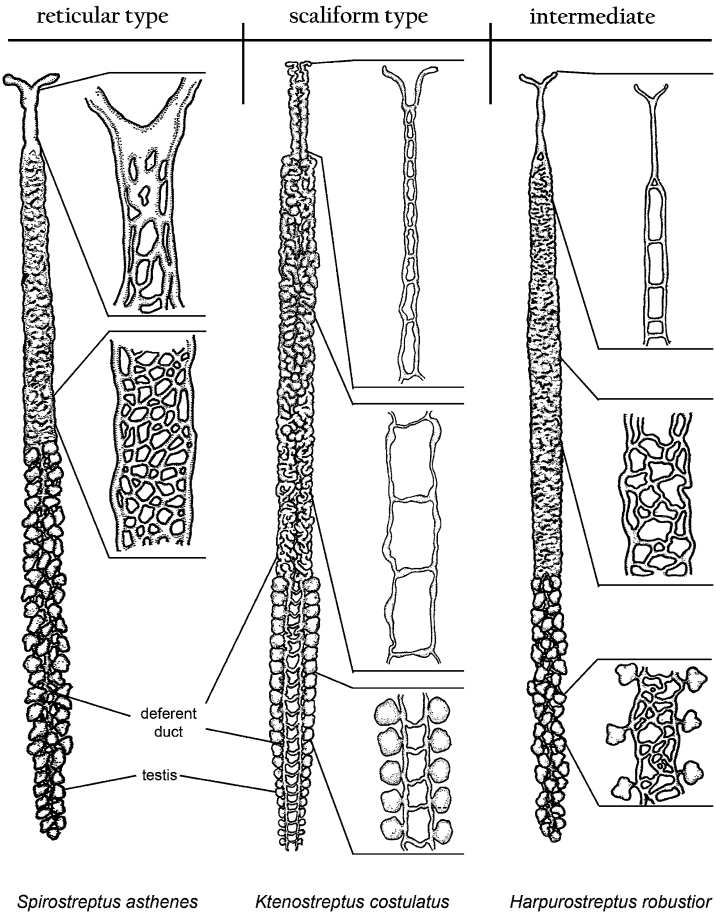

Fig. 10.2. Schematic drawings of some types of organization of the male reproductive system in millipedes. Modified from Kanaka & Chowdaiah (1974).

However, the scalariform organization is only present in Helminthomorpha suggesting an evolution from a simple towards a more complex organization of the male reproductive system of millipedes.

The testes and deferent ducts are surrounded by muscles fibers (Camatini & Castellani, 1978). Histological and ultrastructural observations of the testes revealed the presence of all stages of spermatogenesis in mature specimens (e.g. Sokoloff, 1914; Horstmann & Breucker, 1969b; de Freitas & Fontanetti, 2008). The spermatogenesis can be asynchronous (e.g. Sokoloff, 1914; Reger & Cooper, 1968) or synchronous (e.g. Horstmann & Breucker, 1969a, b; Cecchi & Chelazzi, 1984; de Freitas & Fontanetti, 2008) in each testis. The appearance of a testis depends on the developmental stage of the germ cells, but in general it is characterized by an epithelial layer consisting of somatic and generative cells and a lumen which widen during development containing the mature spermatozoa (e.g. Seifert, 1932; de Freitas & Fontanetti, 2008). Based on the only ultrastructural obser-

vations available so far, de Freitas & Fontanetti (2008) described a secretory function for the somatic cells in the testis of *Pseudonannolene tocaiensis*, which might compensate the absence of male accessory glands (Demange, 1988; Fontanetti, 1998b). As also known for other taxa, also the deferent duct seems to contribute secretion to the seminal fluid (Reger & Fitzgerald, 1983; de Freitas & Fontanetti, 2003-2005). However, the available information is very scarce and only based on few studies on *Pseudonannolene* species. Thus, more studies are needed for more far reaching conclusions concerning the production of the seminal fluid and its components.

Spermiogenesis and spermatozoa

Spermatozoa and spermiogenesis have been described from a variety of taxa in the different millipede clades (reviews: Baccetti & Dallai, 1978; Jamieson, 1987) providing an insight into the evolution of millipede sperm (but see below). In contrast to the other myriapods, millipede spermatozoa are aflagellate and structurally diverse (e.g., Baccetti & Dallai, 1978; Baccetti et al., 1979; Jamieson, 1987; see also Fig. 10.3).

In the pre-electron microscopy era several authors described a flagellum in a number of taxa (e.g., Fabre, 1855; Gilson, 1886; Sokoloff, 1914; Tuzet & Manier, 1955), but this has been disproved by ultrastructural analyses (e.g., Baccetti et al., 1977; Baccetti & Dallai, 1978) and not a single investigated millipede species showed flagellate spermatozoa so far. Thus, it can be assumed

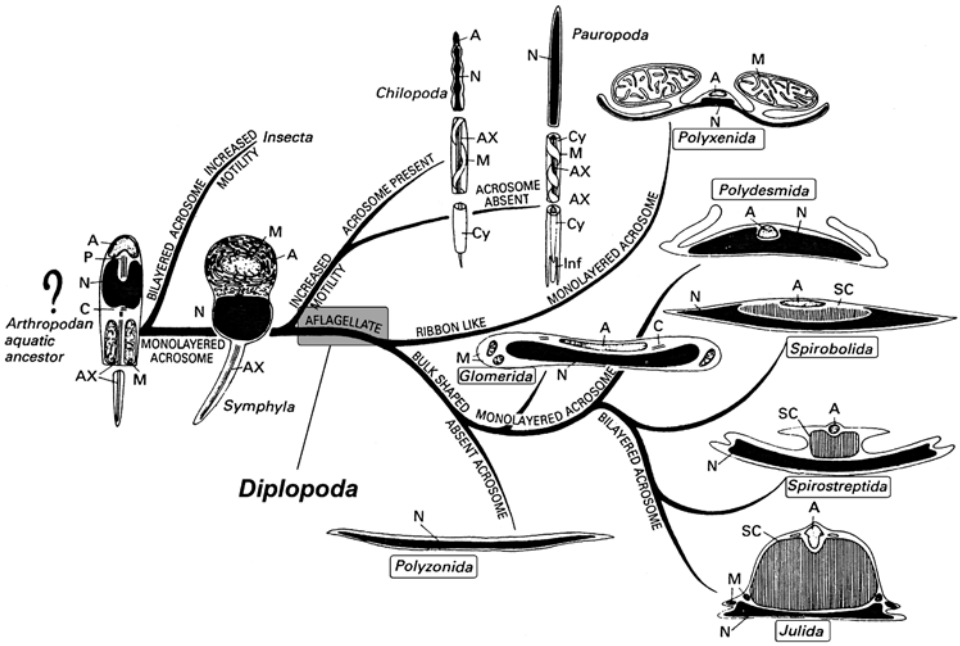

Fig. 10.3. Scenario of the evolution of myriapod spermatozoa. Modified from Hopkin & Head (1992); based on Baccetti et al. (1979). Abbreviations: **A** acrosome; **Ax** axoneme; **C** centriole; **Cy** cylinder; **Inf** infolding; **M** mitochondria; **N** nucleus; **sc** subacrosomal crystal.

that millipede sperm are immotile even though analyses addressing the sperm movement were never performed. However, it is known from other animal taxa that the lack of a flagellum does not necessarily lead to immotile sperm. For example, the aflagellate sperm of nematodes use pseudopodia to move powered by the so-called major sperm protein (MSP; e.g. Klass & Hirsh, 1981; Roberts & Stewart, 1997). Since the formation of a flagellum is costly, aflagellate sperm might have evolved in taxa and/or mating systems without or reduced sperm competition and consequently a relaxed selection on sperm traits occur (e.g., in monandrous mating systems; Morrow, 2004). However, millipedes are polygynandrous and sperm mixing occurs in the female sperm storage organs (e.g. Barnett & Telford, 1994; Barnett et al., 1995). Barnett et al. (1995) revealed that sperm precedence patterns can be mediated by the male (ejaculate displacement by genitalia) or the female (ejaculate depletion) in the spirostreptid *Doratogonus uncinatus*. Wojcieszek & Simmons (2011) found direct evidence for a relationship of paternity success and male genital morphology in the paradoxosomatid *Antichiropus variabilis*. Interestingly, the selection on the male genitalia seems to be non-linear in this species and by comparing different populations evidence for a stabilizing selection on male genitalia was found (Wojcieszek & Simmons, 2012). However, the available data are scarce and the constraints towards an evolution of aflagellate sperm in millipedes are unclear.

The ultrastructural characteristics of spermatozoa of the different millipede taxa are reviewed in detail by Jamieson (1987) and as no ultrastructural analysis was published since then it will be only briefly addressed here.

The division of millipedes in Polyxenida and Chilognatha is also traceable in the sperm morphology. The detailed analyses of the spermatozoa of the only studied polyxenid species *Polyxenus lagurus* revealed a ribbon-like organization (metamorphosis in the female from a barrel to a ribbon shape; Fig. 10.4) with a monolayered acrosome (Sokoloff, 1914, 1918; Baccetti et al., 1974; Dallai et al., 1974) whereas chilognathan taxa are characterized by biscuit-shaped sperm without a transformation in the female reproductive tract (Baccetti & Dallai, 1978). Within Chilognatha a variety of modifications evolved leading to significant differences between the orders.

In pentazonian millipedes only two species of Glomerida (*Glomeris marginata* and *G. pulchra*; e.g., Manier & Boissin, 1978; Baccetti et al., 1979) and one species of Sphaerotheriida (*Cyliosoma* sp.; Jamieson, 1987) were investigated. The spermatozoa of Pentazonia are characterized by the presence of all main cell components, i.e. nucleus, acrosome, mitochondria and centrioles. The cell components are embedded in a small amount of cytoplasm. Furthermore, Jamieson (1987) reported the presence of a continuous layer of vesicles around the cell periphery of the investigated giant pill millipede *Cyliosoma* sp. as a unique feature within millipedes. Moreover, centrioles seem to be absent in this only investigated sphaerotheriid species.

In Helminthomorpha, the available data are rather fragmentary as most studies were undertaken within Juliformia and Polydesmida, but only a single species of Colobognatha (*Hirudisoma* sp.) was studied and no data exist for nematophoran millipedes. The spermatozoa of the only studied colobognathan representative are very aberrant as they lack all cell organelles except the nucleus and thus are very different in respect to all other millipede groups (Baccetti et al., 1979).

In Juliformia, representatives of all three suborders were studied. The spermatozoa of Juliformia are characterized by the lack of centrioles and the presence of conspicuous paracrystalline subacrosomal material (Figs. 10.5, 10.6; subacrosomal crystal: Baccetti

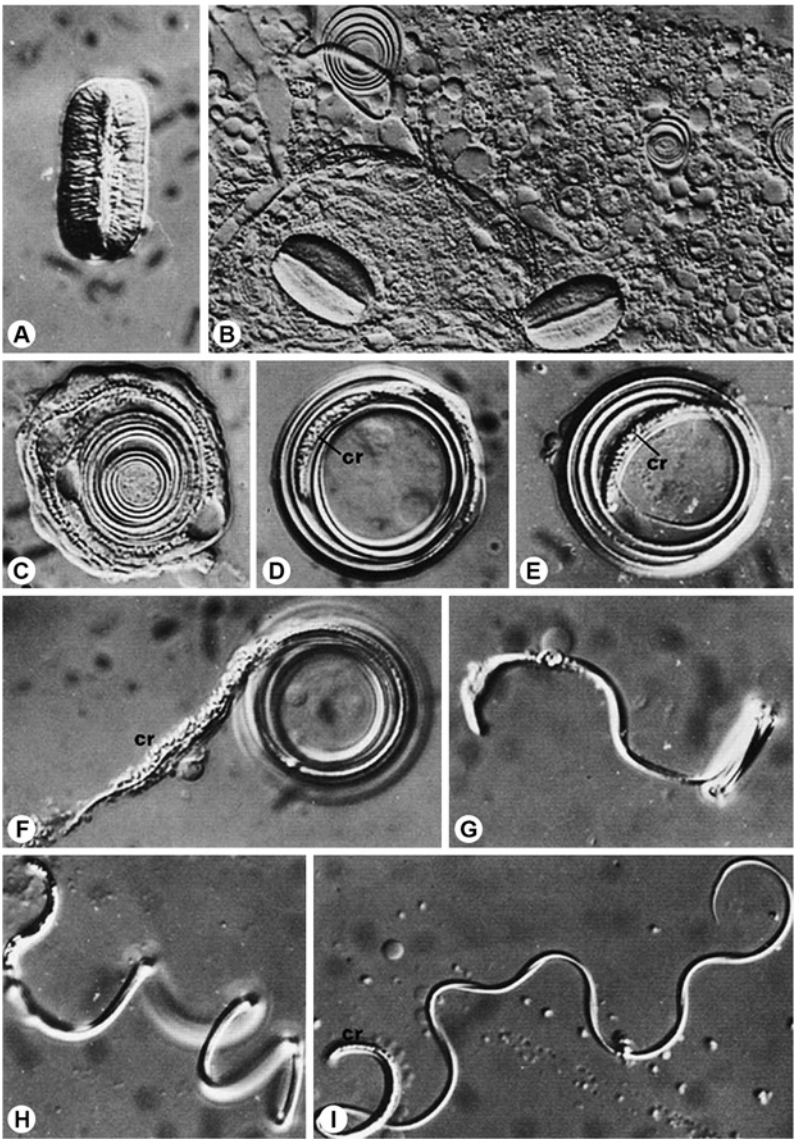

Fig. 10.4. Light microscopy images of spermatozoa of *Polyxenus lagurus*. **A** Barrel-shaped spermatozoon in the deferent duct. **B** Overview of the spermathecal content showing barrel- and spiral-shaped spermatozoa. **C-I** Transformation of a spermatozoon from barrel- into ribbon-shape. From Baccetti et al. (1974).

et al., 1979) which plays an important role in the acrosome reaction during fertilization (e.g., Baccetti et al., 1977). In contrast to Spirostreptida and Spirobolida, the spermatozoa of Julida are transferred individually and not as pairs (e.g., Chevaillier & Prigent, 1969; Camatini & Franchi, 1975, 1978; Baccetti et al., 1977; Baccetti, 1979). As also reflected

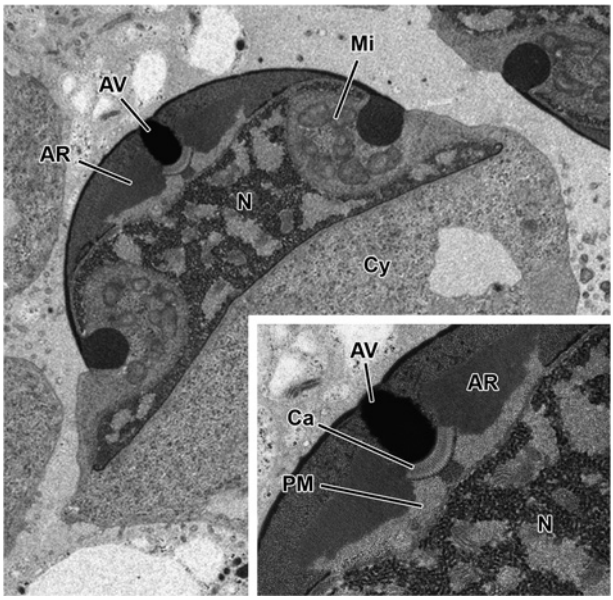

Fig. 10.5. Sagittal section of a spermatid of *Eurhinocricus* sp. (Spirobolida). TEM. The inset depicts a magnification of the acrosomal region with the characteristic paracrystalline subacrosomal material. Abbreviations: **AV** acrosomal vesicle; **AR** acrosomal ring; **Ca** calotte; **Cy** cytoplasm; **Mi** mitochondria; **N** nucleus; **PM** paracrystalline material.

in recent phylogenetic hypotheses (see Chapter 15), the spermatozoa of Julida and Spirobolida are very similar in their organization (for a detailed comparison see Jamieson, 1987) even though the differences in sperm morphology within Spirobolida are remarkable and should be addressed in future analyses.

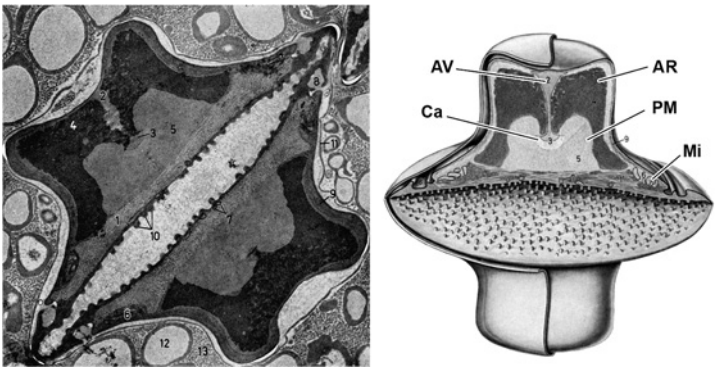

Fig. 10.6. Electron micrograph of a sagittal section (left) and a schematic drawing (right) of a sperm pair of *Spirostreptus* sp. From Horstmann & Breucker (1969a). Abbreviations: **AV** acrosomal vesicle; **AR** acrosomal ring; **Ca** calotte; **Mi** mitochondria; **PM** paracrystalline material.

In Polydesmida, the sperm morphology is described for the genera *Polydesmus*, *Prepodesmus* and *Coromus* (Reger & Cooper, 1968; Petit, 1974; Manier & Boissin, 1975, 1978). The sperm cells of polydesmids are lenticular and the nucleus fills nearly the whole cell. In contrast to Juliformia, mitochondria seems to be always absent in mature spermatozoa.

Based on the available data it seems likely that sperm pairing, which is described for Polydesmida, Polyzoniida, Spirobolida and Spirostreptida, evolved at the base of Heminthomorpha and was subsequently lost in Julida and Spirobolida (*Pelmatojulus ligulatus*: Manier & Boissin, 1976). These pairs are formed by secondary conjugation in the (distal) deferent ducts (Higginson & Pitnick, 2011) at the end of spermiogenesis (Fig. 10.6). Mechanisms of the formation of the pairs and adhesion of sperm cells are largely unknown. In some species the pair is surrounded by an outer sheath (e.g. *Plethocrossus acutiformis*; Manier & Boissin, 1978) or a gutter-shaped ring (*Coromus granulosus*; Manier & Boissin, 1975). The adaptive value of these pairs is unknown for millipedes as no experimental study addressed the fate of the pairs after leaving the primary male reproductive system. Generally, sperm conjugation could be a result of a selection for a variety of traits including efficient and coordinated motility, physical protection from spermicidal environments or enhanced egg penetration (see review by Higginson & Pitnick, 2011). As millipede sperm are non-motile, a protective function or an enhanced competitive fertilization success should be considered since sperm size can be positively correlated with fertilization success (e.g., LaMunyon & Ward, 1999; see also Higginson & Pitnick, 2011).

Even though excellent and detailed descriptions of sperm ultrastructure of millipedes exist (e.g., Horstmann & Breucker, 1969a, b; Horstmann, 1970a, b; Baccetti et al., 1974, 1977), it can be generally concluded that the available data on sperm morphology are still very scarce and studied taxa are unevenly dispersed over the millipede phylogeny (i.e. most studies focus on Juliformia, see above). Thus, well-founded scenarios of the evolution of sperm cannot be given at the present state of knowledge.

EXTERNAL GENITALIA
[ALESSANDRO MINELLI]

The external genitalia are represented in the females by a pair of vulvae, located behind the second pair of legs. The vulvae are complicated ectodermal formations consisting of two main parts, the bursa and the operculum. In the Pentazonia, the vulvae are integrated into the posterior part of the coxae of the second pair of legs, whereas in the Helminthomorpha these structures are morphologically more distinct and are usually protected in a more or less deep invagination, or vulvar sac, out of which they are everted during copulation. The vulvae are usually equipped with glands and contain spermathecae. An ovipositor is present only in *Glomeridesmus*.

Male Polyxenida have a pair of conical, sometimes very long ‘penes’ behind the coxae of the second pair of legs. In Helminthomorpha the male gonopores open directly through

the coxae of the second pair of legs (e.g., in *Polydesmus*; but in the Spirobolida the distal part of the gonoduct are evertible), or through 'penes' located behind the same leg pair. These 'penes' are either paired (more frequently) or unpaired, both morphologies existing even within the same family, as in Stemmiulidae. 'Penis' size and morphology are quite diverse among the Colobognatha. For example, 'penes' are attached to the posterior margin of the coxae in *Hirudicryptus* but open through the coxa in the closely related genus *Siphonocryptus*; 'penes' are short in *Bdellozonium* but elongated, overlappping coxa 6, in *Angarozonium*. The term 'penis' is used here in quotes, because in no millipede these male appendages are used for direct transfer of sperm to the female, as described below.

Male Helminthomorpha possess also one or more pairs of specialized appendages that have a diversity of roles during copulation. In male Pentazonia, the last two (Glomeridesmida and Sphaerotheriida) or three (most Glomerida) pairs of legs are modified in the males as sexual appendages (telopods and paratelopods) used in seizing the female by the antennae prior to copulation and in transferring sperm to the vulvae (Haacker, 1969b).

In male chilognathans, one or more pairs of trunk appendages are modified into highly specialized sexual appendages, generally known as the gonopods. In Colobognatha there are two pairs of gonopods, corresponding to leg pairs 9 and 10. Their derivation from walking legs is clearly visible, especially in the posterior pair, which is articulated into six or seven podomeres, whereas the gonopods of the Eugnatha are strongly modified and often of bizarre shape. In Polydesmida, Callipodida and Siphoniulida there is only one pair of gonopods, corresponding to leg-pair 8. In Chordeumatida, Julida, Spirobolida and some Cambalidea, there are two pairs of gonopods, corresponding to leg pairs 8 and 9. In many Chordeumatida, the leg-pairs adjacent to the gonopods are also strongly modified (paragonopods). In Stemmiulida, Spirostreptidea and some Cambalidea only leg pair 8 are replaced by gonopods, whereas the following pair are completely atrophied. Gonopods of very complex structure are often protected into pouches from which they are pulled out during copulation. The only helminthomorph millipede whose males lack gonopods is the polydesmidan *Aenigmopus alatus*, whose leg pair 8 are not modified in the adult (Loomis & Hoffman, 1962).

Post-telopodal glands open between the telopods and the anus in *Glomeris*, *Trachysphaera*, *Glomeridella* but not in *Spelaeoglomeris*, *Stygioglomeris*, *Protoglomeris* (Juberthie-Jupeau & Tabacaru, 1968). The ultrastructure of these glands in *Glomeris marginata* was described by Juberthie-Jupeau (1976). In the Helminthomorpha, different kinds of gonopodal glands have been described: prostatic glands opening on the coxal part of the posterior gonopods in julids (Attems, 1895) and glands of anterior paragonopods and gonopods in the Chordeumatida (Verhoeff, 1910-1914); moreover, femoral glands are found in some pairs of legs in male Paradoxosomatidae, Julidae and Blaniulidae (Verhoeff, 1910-1914).

MATING BEHAVIOR
[ALESSANDRO MINELLI]

Mate recognition and preliminaries. — In the spirostreptid *Doratogonus uncinatus*, males find mates through random encounters (Telford & Dangerfield, 1993), but in *Ommatoiulus moreleti* females without antennae mate readily, while males without antennae do not, which suggests that males use their antennae to recognise females by contact (Carey & Bull, 1986). In other millipede clades, acustic communication has been occasionally suggested to facilitate mate recognition at distance, but recent investigations point to a different functional interpretation of the stridulatory behaviour in some of these animals. Stridulation is known for three pentazonian taxa: the glomerid genus *Loboglomeris*, where stridulation sounds are actually used by males in courtship behavior (Haacker, 1968), the Arthrosphaeridae, where both sexes possess stridulation organs (Wesener & VandenSpiegel, 2009), and the Sphaerotheriidae, where only males stridulate (Haacker, 1969b) although, usually, only when in contact with a female. This is interpreted by Wesener et al. (2011) as a behaviour preventing the female from volvating into a ball, and stimulating the female to uncoil if already rolled in.

Behavioural sequences were studied by Cooper & Telford (2000) in a few species of *Centrobolus*. Precopulatory interactions between the partners included female coiling and male coercion and uncoiling. During copulation, the male always performed sequences of antennation on the mate's body, followed by production of glandular secretion. In species with very long copulation, the male coiled around the female, whereas in the species with shorter copulation the pair copulated in parallel positions.

Correct positioning of the partners is facilitated in *Chordeuma silvestre* by the presence in the female of a glandular complex between 'rings' 15 to 18, in correspondence of which the male takes contact through specialized projections of its 'ring' 16 (Haacker, 1971).

Sperm transfer. — In the Penicillata, sperm transfer is indirect, as was described by Schömann (1954) in the bisexual form of *Polyxenus lagurus*. The male attaches a bunch of silky threads emerging from its 'penes' to the substrate and places a couple of drops of sperm upon them. Further, longer 'guide' threads are produced by glands opening at the base of leg pairs 8 and 9. As these millipedes are usually gregarious, it is not difficult for a female to find these threads, following which the animal will eventually contact the drops of sperm, onto which the vulvae will be pressed.

In the Chilognatha, sperm transfer is direct, with quite diverse modalities and diverse relative positions of the mating partners during the process.

In *Sphaerotherium* (Haacker, 1968) the partners take contact with their ventral side, the head of one of them facing the posterior body end of the other; the sperm is discharged and moved along the ventral body surface by the help of the legs, until the female's genital opening is reached.

In *Glomeris* (Haacker, 1964, 1969b) the male, in a coiled position that allows gripping the female's vulvae by means of the telopods, shapes by movements of the mandibles a little piece of litter or detritus into a smooth sphere, then puts it in contact with its genital opening, where the sphere is coated with sperm, and finally moves this coated ball down its

ventral surface towards the telopods. Here, the drop of sperm is transferred to the syncoxite processes of the telopods and eventually placed into the female's vulvae.

In julids, the male reaches the partner moving from behind and quietly places itself on the latter's back. The sole-like internal face of femora and tibiae of anterior and middle legs helps keeping hold of the often smooth rings of the female. As soon as the male's head is approximately aligned with the female's head, the male moves head and anterior trunk segments laterally and fixes its modified first pair of legs onto the mouthparts of the female; in some species, e.g. *Kryphioiulus occultus*, the hook-shaped legs 1 are used instead to grasp the female's antennae. The anterior gonopods (protomerites) and the anterior parts (mesomerites) of the posterior gonopods force the vulvae to come out of the vulvar pouches. The posterior parts of the posterior gonopods (opisthomerites) are repeatedly inserted into the vulvae; by a partial rotation towards anterior, the opisthomerites come in touch with the swollen genital papilla of the male, out of which sperm pours out and flows along a spermatic groove of the gonopods. The gonopods are thus inserted again in the vulvae, allowing the transfer of sperm. Similar is sperm transfer in spirostreptidans (Barnett & Telford, 1996). The bulky gonopods are largely concealed within a gonopodal sac, when at rest, but during copulation these appendages are protruded, while spem are transferred from the so-called penes to the coxite of the gonopod; during pairing, sperm will be released into the spermathecae of the vulvae where the sperm mass will be stored. During copulation, the telopodite is repeatedly retracted and released.

In *Craspedosoma*, sperm are simply brushed over the openings of the female's seminal receptacles by cuticular projections (a 'brush') of the male's anterior gonopods, while other parts of the gonopods ensure the correct positioning of the brush against the receptacles. With this mechanism of sperm transfer, mechanical isolation due to differences in genitalic anatomy is very unlikely (Tadler, 1993), but this is quite obvious in other groups.

Tadler (1996) studied the functional anatomy of the genitalia of four species of Julida by serially sectioning the relevant structures of individuals frozen in copula. In *Unciger foetidus* and *Cylindroiulus boleti*, the vulvae are pulled out of the vulval sac through the action of the clasper-like gonopods, whereas in *Brachyiulus lusitanus* and *Nemasoma varicorne* the vulvae remain in the vulval sac. In *N. varicorne*, *U. foetidus* and *C. boleti*, the central funnel of the vulva leading to the receptaculum seminis hosts the solenomerite, the sperm-transferring part of the gonopods.

As described by Tadler (1996), among millipedes there are different degrees of mechanical coaptation between male and female genitalia. Morphological peculiarities of the female organs include the central area of the vulvae in *Nemasoma varicorne*, which is modified to fit with the male solenomerite, and the bursae of the vulvae in *Brachyiulus bagnalli* and *Cylindroiulus boleti*, which are endowed with slits corresponding to projections of the male gonopods.

The tight coevolution of male and female genitalia (Tanabe & Sota, 2014), together with the rapid divergent evolution these structures likely undergo have suggested, in the *Parafontaria tonominea* species complex, speciation through mechanical reproductive isolation between sympatric species (Tanabe et al., 2001; Tanabe & Sota, 2008; Sota &

Tanabe, 2010). Divergence of genitalia and reproductive isolation have been studied also in populations of *Antichiropus variabilis* (Wojcieszek & Simmons, 2011, 2012, 2013).

In this context, the report of natural hybridization between '*Rhymogona cervina*' and '*Rh. silvatica*' described by Pedroli-Christen (1990) deserves revisitation, to show whether the intermediate phenotypes actually represents true secondary hybrids between largely differentiated lineages or local peculiar phenotypes along a primary variation cline, within what is currently regarded as the *Rhymogona montivaga* complex.

Duration of sperm transfer varies quite extensibly: less than 5 minutes in *Cladethosoma clarum* (Rowe, 2010), ca. 10 minutes in *Cylindroiulus punctatus* (Saudray, 1952), 14 minutes in *Chondromorpha severini* (Rangaswamy et al., 1978), but much longer in spirobolids, e.g. ca. 40 minutes in *Centrobolus ruber* and ca. 3 hours in *C. inscriptus* (Cooper & Telford, 2000) and possibly up to two days in *Polydesmus*.

Sperm competition. — Sperm competition is likely high, because females can mate repeatedly (for example, in *Cladethosoma clarum* both males and female mate with two or more individuals of the opposite sex; Rowe, 2010) and fertilization occurs at oviposition, but the females may not need more than one mating to get enough sperm to fertilize all the eggs they will subsequently lay. This has been ascertained in *Polydesmus inconstans*, where the eggs produced by a female after a single mating are distributed over seven to eight ovipositions (Snider, 1981), and comparable observations are available for *Epibolus pulchripes* (Dhaenens & VandenSpiegel, 2006).

Mechanical displacement, by action of the gonopods, of sperm obtained by the female from previous mating, is probably performed by males of many millipedes. This has been demonstrated in the spirostrepid *Orthoporoides pyrhocephalus* (Barnett et al., 1993), Various structures seen on odontopygid gonopods may function in sperm competition by removing sperm from the female receptacula or by stratifying sperm inside the receptacula (Barnett & Telford, 1996). A function in removing sperm from previous copulations has been suggested for the elongated posterior gonopods of *Dolichoiulus parcestriatus* (Enghoff, 1992), the flagella on the gonopods of several julidans (Julidae: Enghoff, 1995; Nemasomatidae: Enghoff, 1985) and the solenomere of the odontopygid gonopod, e.g. in *Raduliverpa serpentispina* and several *Rhamphidarpoides* species (Frederiksen & Enghoff, 2015). But in *Doratogonus uncinatus*, if there is a 24 hours delay between successive matings, the precedence of sperm from the last mating is probably caused either by resorption or by discharge of sperm from previous mating operated by the female rather than by mechanical removal by the gonopods of her later partner (Barnett et al., 1995).

Postcopulatory mate guarding has been described in *Nyssodesmus python*, where the male stands on the back of the female, which continues to move (Adolph & Geber, 1995).

PARTHENOGENESIS
[ALESSANDRO MINELLI]

Thelytokous parthenogenesis has been recorded from a number of millipede species (Table 10.2), but this form of reproduction has been demonstrated experimentally only

TABLE 10.2
Millipede species for which parthenogenesis has been inferred or recorded

Species with geographical parthenogenesis	
Archiboreoiulus pallidus	Palmén, 1949
Cylindrodesmus hirsutus	Enghoff, 1978b; Golovatch et al., 2001
Geoglomeris subterranea	Schubart, 1934; Enghoff, 1994
Nemasoma varicorne	Enghoff, 1976a, c; Jensen et al., 2002; Parker, 2002
Pacifiiulus amurensis	Mikhaljova, 1993
Polyxenus lagurus	Vandel, 1926, 1928; Schömann, 1956; Meidell, 1970; Enghoff, 1976b, 1994
Poratia digitata	Adis et al., 2000; Witzel et al., 2003
Poratia obliterata	Adis et al., 2000
Prolysiopetalum scabratum	Strasser, 1974, 1976
Tessinosoma coelebs	Verhoeff, 1921
Trachysphaera costata	Golovatch, 2008
Underwoodia iuloides	Shelley, 1993
Completely thelytokous species with closely related bisexual species	
Amphitomeus attemsi	Golovatch et al., 2002
Moojenodesmus pumilus	Golovatch, 1992
Okeanobates americanus	Enghoff, 1979
Orinisobates microthylax	Enghoff, 1985
Proteroiulus fuscus	Schubart, 1934; Palmén, 1949; Rantala, 1970; Enghoff, 1978a
Virgoiulus minutus	Enghoff & Shelley, 1979

in a few species, in the other cases it has been simply inferred from the lack or extreme scarcity of males (Enghoff, 1994).

In the species with geographic parthenogenesis, spanandry (the occurrence of rare males in predominantly female populations) may occur at various degrees. In *Nemasoma varicorne*, one male per 200 females was found in a population N of Copenhagen (Enghoff, 1976a); in *Poratia digitata*, one male per 94 females in a hothouse population in Düsseldorf (Adis et al., 2000); in *Proteroiulus fuscus*, values between 6.4 and 24 males per thousand have been recorded (Schubart, 1934; Palmén, 1949; Rantala, 1970). Bisexual populations of otherwise thelytokous millipedes can have a 1:1 sex ratio, as recorded for *Polyxenus lagurus* in Hordaland (Norway) (Meidell, 1970).

In *Nemasoma varicorne*, the females from the probably bisexual populations with many males have well-developed spermathecae, those from populations with few or no males have reduced spermathecae, or virtually none. A few adult individuals of *N. varicorne* (three among several thousands) were described by Enghoff (1976a) as intersexes. Their vulvae were fully developed and the spermathecae were reduced like those of typical parthenogenetic populations, but leg pairs 8 and 9 were reduced as in immature males. Unmated females from bisexual populations occasionally produced a few eggs which do not develop beyond the pupoid stadium. Mated females from bisexual populations produced on average 20.8 eggs, from which ca. equal number of males and females were obtained. Thelytokous females, unmated or mated, produced on average 10.9 eggs, from which only females were obtained.

In contrast to the strict seasonality of oviposition observed in the bisexual millipedes of the temperate regions, in Germany (Schömann, 1956) and in Northern Italy (Minelli, 1968), the parthenogenetic form of *Polyxenus lagurus* lays egg throughout the year.

In other arthropods, parthenogenesis has been found to be related to infections by bacteria of the genus *Wolbachia*. These bacteria have not been found in the thelytokous populations of *Poratia obliterata* (parthenogenetic in European hothouses, bisexual in Amazonia) and *P. digitata* (an obligate parthenogen in European hothouses) (Witzel et al., 2003).

OVIPOSITION AND BROODING
[ALESSANDRO MINELLI]

In *Epibolus pulchripes* oviposition starts two weeks after copulation (Dhaenens & VandenSpiegel, 2006), followed by a second event one week later; similarly, the first oviposition has been observed 14 to 25 days after mating in *Polydesmus angustus* (Banerjee, 1973).

Egg laying can be prolonged over several months. In females of *Polydesmus inconstans* kept in the lab at 15°C, Snider (1981) reported on average 10 ovipositions per female with a total average of 469 eggs.

The females of *Polyxenus lagurus* surround the eggs with a sticky secretion and glue them to the substrate like a string rolled in a flat spiral, protected by a mass ot trichomes detached from the mother's tail brush.

The eggs of most species of Glomerida are protected in individual chambers (only rarely containing 2-3 eggs in *Glomeris*, but up to 7 in *Loboglomeris*; Juberthie-Jupeau, 1967a, c) produced by the mother with fecal matters and/or with earth particles. *Glomeris* females shape egg chambers of 3-5 mm diameter with their hind legs, and eventually abandon them individually in the soil, less frequently store them as a group in soil or litter. Individual cases are also produced by the epigean species of *Trachysphaera*, whereas those living in caves simply lay their eggs in a depression of the soil of even leave them free in detritus (Tabacaru, 1963). In *Cyliosoma*, the egg is covered with glued fragments of rotten wood (Dohle, 1992).

In spirobolids and at least some spirostreptids, the eggs are also protected by individual earthy capsules; those of *Pelmatojulus laminatus* have been described by Aouti (1980), those of *Anadenobolus leucostigma martinicensis* by Nguyen Duy-Jacquemin (1992).

Nematophoran millipedes possess spinnerets and use the silky secretion to produce egg chambers (and also moulting chambers; cf. Chapter 11). The females of Chordeumatida use the secretion of their silk glands to produce a kind of loose cocoon that isolates the eggs, like an air-filled cushion, from direct contact with the substrate.

The females of many polydesmidans use soil matter passed through their gut, together with fecal pellets, to build a kind of earthy bell into which their often numerous eggs are protected. In some species, the chamber is provided with a ventilation chimney. Many other polydesmidans, however, like *Phrurodesmus kinshaensis* (Murakami, 1966), *Apheloria virginiensis corrugata* (Eaton, 1943), *Habrodesmus falx* and *Coromus* sp. (Toye, 1967) lay

TABLE 10.3
Stadium and age at which oviposition occurs in a number of species of Polydesmida and Chordeumatida, all semelparous (after David, 1992)

	Stadium	Number of podous rings	Usual age (years)
POLYDESMIDA			
Brachydesmus superus	VII	17	1
Habrodesmus duboscqui	VIII	18	1-2
Polydesmus angustus	VIII	18	1-2
Polydesmus graecus	VIII	18	2
Polydesmus inconstans	VIII	18	1-2
Tymbodesmus falcatus	VIII	18	2
Xanthodesmus physkon	VIII	18	1
CHORDEUMATIDA			
Anamastigona matsakisi	IX	27	3
Chamaesoma brolemanni	VIII	23	1
Chordeuma proximum	IX	27	1
Chordeuma sylvestre	IX	27	1
Craspedosoma rawlinsii	IX	27	1-2
Haasea fonticulorum	IX	27	3
Melogona gallicum	IX	27	1
Melogona scutellare	VIII	25	1
Nanogona polydesmoides	IX	27	1
Ochogona caroli	IX	27	3
Xylophageuma zschokkei	IX	27	1-2

their eggs loose in the soil. In *Polydesmus angustus* the female remains in the proximity of the 'bell' until the hatching of juveniles and in the case repairs damage. True brooding is limited to the Colobognatha. The female of *Polyzonium germanicum* remains curled up around the eggs until hatching, while secreting a repellent substance that probably also acts as a biocide preventing the rotting of the eggs. Maternal brood care has been also recorded in other Polyzoniida (e.g. *Orsiboe ichigomensis*), in Platydesmida (*Dolistenus* spp.) and also in Polydesmida (*Eutrichodesmus peculiaris*) (reviewed in Enghoff, 1984). Paternal brooding has been recorded in the andrognathids *Brachycybe* spp. (Murakami, 1962a; Gardner, 1974) and *Yamasinaium noduligerum* (Kudo et al., 2009).

Some millipedes are semelparous (Table 10.3), others are iteroparous: following their first mature stadium, after one or more moults males and (more frequently) females mate again and the females start a new series of ovipositions.

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CHAPTER 11

DIPLOPODA — DEVELOPMENT

BY

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EMBRYONIC DEVELOPMENT

Detailed studies on the embryonic development of millipedes are limited to a small number of species. Following the pioneering investigation of Metschnikoff (1874) on *Polyxenus lagurus*, *Oranmorpha guerinii*, *Polydesmus complanatus* and *Ommatoiulus moreleti*, the only monographic studies on the subject described the embryonic development of *Polydesmus abchasius* (Lignau, 1911a, b), *Platyrhacus amauros* (Pflugfelder, 1932) and *Glomeris marginata* (Dohle, 1964, 1974). Useful summaries, with comparisons in respect to other arthropods, have been provided by Johannsen & Butt (1941), Anderson (1973) and Dunger (1993).

Under unspecified culture condition, the embryonic development of *P. amauros*, a tropical species, extended to 19 days; the embryonic development of millipedes from temperate and cold region is expected to last much longer.

Cleavage mitoses of the yolk-rich eggs of millipedes start only after oviposition. The cleavage, adequal but irregular, leads to the formation of a blastoderm that surrounds completely the yolk mass, within which a few yolk-cells remain. Eventually, as described by Dohle (1964, 1974) for *G. marginata*, on the future ventral side of the embryo the blastoderm cells become more crowded and take a columnar shape. This is the first morphological evidence of the would-be germ band. At the posterior end of this area, a plug of cells migrates into the yolk and will form the mesoderm. In *P. amauros*, Pflugfelder (1932) described an additional source of mesoderm from cells immigrating from the intersegmental spaces. The first evidence of segmentation is due to a thickening of the ectodermal cell layer, whereas the mesoderm appears arranged in transversal bands. According to Dohle (1964), these bands hollow out to form coelomic sacs. Along the germ band, small depressions (the so-called ventral organs) indicate the points of invagination of the precursors of the future ganglia of the ventral nerve cord. A distinction emerges between the area that will become extra-embryonic material and a ventral germinal region corresponding to the presumptive anterior portion of the germ band. Here the head

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segments, as well as the first trunk segment, form almost simultaneously. At the caudal end of the germinal region, the posterior growth zone is forming, out of which all remaining segments will be produced.

Segments start to differentiate in the cephalic region, where the stomodaeum invaginates but is soon concealed under the overgrowing labrum. Two segments fail to differentiate anlagen of appendages: these are the intercalary segment between the antennal and the mandibular one, and the postmaxillary segment. However, according to Dohle (1964), the sternites of the post-maxillary segment contribute to the future gnathochilarium.

The first three trunk segments differentiate with the cephalic ones (Janssen et al., 2004), whereas the following segments will emerge sequentially from the posterior proliferation zone, whose mitotic and morphogenetic activity is still poorly known, despite the information provided by Pflugfelder (1932) and Berns (1969), and mainly relative to the addition of new segments during post-embryonic life, in *Platyrhacus amauros* and *Narceus annularis* respectively. In the proliferative zone of *Narceus annularis*, the latter author identified two bursts of mitoses, causing the new segments to extend from it in an anterior direction. The first burst begins during the moult and continues through the third day following the moult. After the third day, a second burst begins in the lateral and dorsal portion of the segment anlagen, in anteroposterior direction, causing great increase in size of the anlagen.

Back to the embryo, the proctodaeum invaginates in the still unsegmented telson area. Up to stage 3 of Dohle (1964), the germ band consists only of presumptive ventral tissue. The dorsal tissue is first located laterally to the ventral tissue, in form of lateral plates, but steadily grows until the lateral plates meet on the dorsal side and eventually fuse together (dorsal closure).

The following developmental step is blastokinesis, i.e. the movement of the germ band into the yolk, accompanied by a flexure at the level of the boundary between head and thorax. At about the same time, the lateral parts of the first leg bearing segment will become the hind border of tergite I or the collum; the second to fourth leg bearing segments will form tergites II to IV, and the following ones will subsequently form one tergite every two leg pairs. The correspondence between dorsal and ventral elements has been subsequently revised, in the context of evidence from the expression patterns of some developmental genes (discussed in the next section).

A certain degree of autonomy between the left and right halves of the body has been observed in the embryonic development of pentazonians: Juberthie-Jupeau (1969) reported a specimen of *Spelaeoglomeris doderoi* with 16 legs on one side, 15 on the other; Dohle (1992) a specimen of *Cyliosoma* sp. with 20 legs on the left side, 21 on the right one.

DEVELOPMENTAL GENETICS

Dorso-ventral autonomy

The obvious mismatch between the dorsal and ventral aspects of trunk segmentation has long suggested some degree of independence between the developmental processes

producing the dorsal vs. ventral serial units of the millipede body. Some arguments from comparative morphology were offered by Enghoff et al. (1993). First, in all species of Glomerida the tergites are added one by one, and the sternites and leg pairs differentiate faster than the production of new tergites although at a slower pace in some species, at a faster pace in others. Second, in *Glomeridesmus* leg pairs are added even after the final number of tergites has been achieved. Third, in platydesmids such as *Brachycybe nodulosa*, there is no correlation across stadia between the number of tergites and the number of sternites and leg pairs.

With the advent of developmental genetics, the developmental origin of the serial units of the millipede trunk has been the subject of a series of studies, largely targeted to the identification, in a model species (*Glomeris marginata*), of homologues of the genes known to be involved in the segmentation process in the embryos of *Drosophila* and other arthropods. These studies revealed strong similarities in the expression patterns of many of these genes, and of other genes involved in other aspects of embryonic patterning, but also noticeable singularities in the expression patterns of some of them. This applies, first of all, to the segment polarity genes. In *Glomeris marginata*, *wingless* is expressed ventrally, but not dorsally; *engrailed* (first expressed in the mandibular segment; Janssen, 2012), *hedgehog* (also expressed in a broad anterior domain corresponding to the ocular and antennal segments; Janssen, 2012), *cubitus-interruptus* and *patched* are expressed both dorsally and ventrally, but the expression pattern in the dorsal side is not compatible with a role in segmentation (Janssen et al., 2004; Damen et al., 2009). Janssen et al. (2008) suggested that the formation of boundaries between segmental units rely dorsally on Decapentaplegic signaling rather than Wingless signalling, mediated by *hedgehod* and *optomotor-blind* expression.

Overall, gene expression analysis suggests that there is no coupling between dorsal and ventral segmentation (Janssen et al., 2006a), and the boundaries between neighbouring tergites are not correlated to the boundaries between embryonic segments (Janssen et al., 2006b).

Despite previous statements (e.g., Janssen, 2011b) that segments are added one by one rather than by double-segment units, the pair-rule gene *pairberry* and other pair rule gene orthologues are expressed in the blastoderm of *Glomeris* in two-segment-wide domains, which at subsequent stages split into two segmental stripes (Janssen et al., 2012). This pattern, however, has no morphological counterpart, neither in the ventral or in the dorsal segmental units.

Only at a later stage, the dorsal segmental units fuse by pairs to form larger elements that subsequently cover two ventral leg-bearing units. Janssen (2011b) finds no evidence supporting the hypothesis that the collum or the anterior trunk segments bearing only one leg pair each represent degenerate diplosegments.

The exceptional finding (Janssen, 2011a) of an abnormally developed embryo lacking dorsal segmental derivatives and dorsal extraembryonic tissue confirms that ventral and dorsal segmental tissues are specified and patterned, to some extent at least, independent of one another.

In addition to *Wingless*/*Wnt1*, another ten *Wnt* genes were identified in *G. marginata* (Janssen et al., 2004, 2010; Janssen & Posnien, 2014). The expression patterns and thus the putative developmental role of many of these genes have been found to be conserved in respect to *Drosophila* and often also to other arthropods (e.g., the spider *Parasteatodea*) and even the onychophoran *Euperipatoides*. Their domains of expressions are as follows:

Gene	*Expression domains and notes*
Wnt2	Ocular region
Wnt4	Throughout the developing embryo. The expression in dorsal tissue implies a role in dorsal segmentation and suggests that *Wnt4* may be the predicted substitute for the missing expression of *wg*/*Wnt1* in dorsal tissue
Wnt5	Ventral nervous system including brain, transverse segmental stripes, labrum and limb primordia (and later the limbs)
Wnt6	Limbs, brain, and segmental expression likely associated with the ventral nervous system
Wnt7	Heart, brain, labrum
Wnt8	Ocular region and mandibular segment
Wnt9	Transient expression in segment-polarity gene-like segmental stripes, in the appendages including the labrum, and in the posterior segment addition zone; later, *Wnt9* is expressed in a dorsal segmental pattern and in form of stripes in the dorsal extraembryonic tissue
Wnt11	First expressed in the posterior segment addition zone; later, in the tips of all appendages
Wnt16	Transverse segmental stripes anterior adjacent to the expression of *engrailed* suggesting that *Wnt16* is involved in segmental boundary formation. Also in the developing brain and in the tips and ventral tissue of the limbs
WntA	Developing brain, heart, limbs and ventral nervous system

The decoupling of dorsal and ventral segmentation is already evident at the time the pair-rule genes are expressed (Janssen et al., 2011b). Nevertheless, components of the gene network known from *Drosophila* and other arthropods are likely to be conserved. Homologues of the pair-rule genes *even-skipped*, *runt*, *sloppy-paired*, *odd-skipped* and *odd-paired* have been found in *G. marginata*.

Some degree of independence between the dorsal and the ventral aspect of the animal is seen also in the patterns of expression of the *Hox* genes. The 10 *Hox* genes of *G. marginata* (including *Hox3* and a *fushi tarazu* homologue) show a broadly conserved expression, in respect to the other arthropods, but the dorsal domains of gene expression are somewhat shifted towards posterior positions relative to the ventral pattern. The three anterior *Hox* genes, i.e. *labial*, *proboscipedia* and *Hox3*, are expressed only ventrally (Janssen & Damen, 2006).

Head and eye

Head patterning genes offer no surprise in *Glomeris* compared to other arthropods. However, while the expression domains of later regulatory genes (i.e. *crocodile*, *cap-n-collar*, *collier*, *orthodenticle*) are highly conserved, those of the primary regulators *hunchback* and *buttonhead-like* show more divergence (Janssen et al., 2011a, c).

Two *Pax6* genes have been found in *G. marginata*, probably the homologues of the *Drosophila* genes *eyeless* and *twin of eyeless*, respectively (Prpic, 2005). During embryonic development, both genes are highly expressed in the optic lobes and the ventral nerve cord. As expected, homologues of other genes involved in the development of the eye (*hedgehog*, *decapentaplegic*, *dachshund*, and *homothorax*) are also expressed in the optic lobes.

Appendages

Proximo-distal patterning. — Homologues of the genes *Distal-less*, *dachshund*, *extradenticle* and *homothorax*, known in *Drosophila* to be among the earliest genes that define positional values along the proximo-distal axis of the developing leg, have been sequenced in *G. marginata*. Their expression in the trunk legs is compatible with a conserved role in defining positional values along the proximo-distal axis, but their role in the head appendages seems to be more complex. In the mandible and gnathochilarium, *Distal-less* does not seem to be involved in proximo-distal patterning, but is expressed in the forming sensory organs. A transient expression of *Distal-less* is observed in the intercalary (post-antennal) segment and in the presumptive maxillary segment; *dachshund* is probably involved both in proximo-distal patterning as well as in the development of sensory organs in the antenna, mandible and gnathochilarium; *homothorax* is expressed in the proximal and medial parts of the legs, *extradenticle* only in the proximal region (Prpic & Tautz, 2003).

In *G. marginata*, *wingless* is expressed along the ventral side of the appendages, comparable with functioning during the patterning of both the proximo-distal and dorso-ventral axes. This gene may also be involved in sensory organ formation in the gnathal appendages by inducing the expression of *Distal-less* and *H15* in the organ primordia (Prpic, 2004).

Dorso-ventral patterning. — In *G. marginata*, an *optomotor-blind* homologue is expressed in the dorsal side of all head and trunk appendages. The lobe-shaped portions of the mouthparts do not express this gene, suggesting ventral nature and thus possible homology to the endites present in the corresponding appendages in insects (Prpic et al., 2005).

Neurogenesis

Glomeris marginata. Groups of neural precursors, rather than single cells as in insects, invaginate from the ventral neurectoderm in a manner similar to what is observed in spiders. Homologues of *achaete-scute*, *Delta* and *Notch* are expressed in a pattern similar to their spider homologues (Dove & Stollewerk, 2003).

POST-EMBRYONIC DEVELOPMENT

Pupoid and stadium I juveniles

The embryonic development ends with the transition to the pupoid stage. In the pupoid, legs and antennae are still unarticulated and the musculature is underdeveloped. This stage becomes visible when the chorion ruptures, sometimes through the action of egg teeth, e.g. in *Polyxenus* and paradoxosomatids, more often because of increased internal pressure. In *Glomeris* the pupoid is still covered by the blastodermal cuticle and the embryonic cuticle; the latter, but not the former, is also visibile in other millipedes.

The pupoid usually remains motionless for several days in the chorion. Eventually, by rupture of the embryonic cuticle a stadium I juvenile with articulated appendages is released. This will however remain in the egg chamber, which is left after one moult, except for *Nemasoma varicorne*, stadium I of which moves, feeds and on occasion overwinters (Brookes, 1974). Sometimes (*Ophyiulus pilosus*) free active life will only start with stadium III.

Stadium I millipedes usually have three pairs of fully developed legs and five tergites. However, four pairs of legs are found in stadium I of *Polyzonium germanicum* and *Brachycybe nodulosa*, six pairs in *Ophyiulus pilosus*, 27 pairs in *Pachyiulus flavipes* (Dirsch, 1937), 41 in *Dolistenus savii* (Silvestri, 1949). Stadium I stemmiulids have three pairs of legs, but also a huge number of apodous pleurotergites: the total number of pleurotergites in stadium I is 24 in *Stemmiulus modicus* (Silvestri, 1916), 29 in *S. regressus* (Silvestri, 1916), 31 in *S. recedens* (Silvestri, 1916), 32 in *S. adisi* (Mauriès, 1984), 34 in *S. bellus* (Cook, 1896a). Very numerous apodous segments (17 or 18) have been also reported for *Pachybolus* (Spirobolida) (Demange, 1974).

Moults

Descriptions of the moulting process in millipedes are very limited beyond an old article by Verhoeff (1901). The topic would deserve targeted research, including a sound investigation of the hormonal control.

Many millipedes moult inside more or less elaborate moulting chambers they built with the help of the silky secretion produced by a posterior spinning apparatus: the nematophorans, some Polydesmida (e.g., *Poratia obliterata* and *P. digitata*; cf. Adis et al., 2000), the Polyxenida and the Siphoniulida possess two or more spinnerets on the telson.

All immature stages of *P. obliterata* and *P. digitata* first build a moulting chamber of soil and/or bark with their mouthparts. Once they are protected within the sealed chamber, they produce a cocoon inside which they moult. Adult females of *P. obliterata* and *P. digitata* were not observed instead to produce silky material during construction of their egg chamber. Moulting chambers have been described also in Callipodida (*Acanthopetalum carinatum*: Fanzago, 1874; *Abacion texense*: Loomis, 1937; *Callipus foetidissimus*: Nguyen Duy-Jacquemin, 1979; *Prolysiopetalum scabratum*: Enghoff & Akkari, 2011) and Chordeumatida (e.g., Cook, 1896a; Verhoeff, 1926-1932; Main, 1931: a good description for *Nanogona polydesmoides*).

ANAMORPHOSIS

Millipedes develop by anamorphosis, that is, their post-embryonic development is articulated in a variable number of stadia, separated by moults at which the number of rings and the number of walking legs generally increase, according to schedules quite different between orders, but uniform within some orders, and to some extent species-specific within other orders. The post-embryonic development has been studies in detail in a number of species, many of which are listed in Table 11.1.

Following the magisterial synthesis of Enghoff et al. (1993), which is the main source of information for the next few pages, the post-embryonic developmental schedules of millipedes are grouped into three alternative forms of anamorphosis:

- in *euanamorphosis* new segments are added at each moult, often also after the achievement of sexual maturity. Only the death of the animal apparently dictates the end of the process;
- in *hemianamorphosis* the addition of new segments stops when a fixed number of segments is reached, but the animal continues to moult and a few 'epimorphic' moults are required for the animal to reach sexual maturity. The number of stadia in the initial, strictly anamorphic phase of development is variable, sometimes even within a species. For example, within the Spirostreptida the transition to the epimorphic phase happens with stadium IX in *Dactylobolus bivirgatus* and *Pelmatojulus* spp., but since IX-XII (with intraspecific variation) in *Rhinocricus padbergi*. Hemianamorphosis has been suggested as the plesiomorphic state in Diplopoda (Enghoff, 1990; Enghoff et al., 1993);
- in *teloanamorphosis* the addition of segments stops when a fixed number of segments is reached, at which the millipede also reaches sexual maturity and definitely stops to moult.

Colobognatha and Julida, plus the Cambalidea within the Spirostreptida, perhaps also the Stemmiulida, develop by euanamorphosis; Polyxenida and Pentazonia by hemianamorphosis; Chordeumatida and Polydesmida by teloanamorphosis. Within these major groups, exceptions are very few. Within the Polydesmida, the species of the genus *Devillea* have a variable number of rings, always higher than in all remaining members of the order, but it is not known if they have actually adopted euanamorphosis; the occasional occurrence of one extra moult has been recorded a couple of times in *Polydesmus* spp. (Verhoeff, 1916, 1928; David & Geoffroy, 2011). Within the Julida, the semelparous males of some species (see below) are somehow borderline between euanamorphic and teloanamorphic. Less uniform, or less easy to classify in respect to post-embryonic developmental schedule, are the Spirobolida and the Spirostreptida Spirostreptidea, most of which are hemianamorphic, but with exceptions; within Callipodida, otherwise teloanamorphic, some species seem to be hemianamorphic: in *Eurygyrus ciliciensis*, Hoffman & Lohmander (1965) described three subadult females with no apodous 'rings'.

This classification is reasonable and useful, but it is too simple to capture the whole diversity of schedules of millipede post-embryonic development. A finer analysis should consider as separate aspects of change, prone to extensive but never universal correlations, the items discussed in the following subsections.

TABLE 11.1
A list of millipede species the post-embryonic development of which has been described

POLYXENIDA	
Lophoturus madecassus	Condé & Terver, 1963; Nguyen Duy-Jacquemin, 1982
Phryssonotus cf. *orientalis*	Condé, 1971
Polyxenus lagurus	Reinecke, 1910
GLOMERIDESMIDA	
Glomeridesmus marmoreus	Mauriés, 1980
SPHAEROTHERIIDA	
Cyliosoma sp.	Dohle, 1992
GLOMERIDA	
Geoglomeris subterranea	Bocock et al., 1973
Glomeris balcanica	Iatrou & Stamou, 1988, 1990
Glomeris marginata	Enghoff et al., 1993
Spelaeoglomeris doderoi	Juberthie-Jupeau, 1967, 1969
Trachysphaera spp.	Tabacaru, 1963
PLATYDESMIDA	
Brachycybe nodulosa	Murakami, 1962a, b, 1963
SIPHONOCRYPTIDA	
Hirudicryptus canariensis	Enghoff et al., 1993
POLYZONIIDA	
Hirudisoma latum	Brölemann, 1935
Polyzonium germanicum	David & Couret, 1983, 1984, 1985
POLYDESMIDA	
Anoplodesmus anthracinus	Bano & Krishnamoorthy, 1985
Brachydesmus dadayii	Ćurčić & Makarov, 1997
Brachydesmus troglobius	Ćurčić & Makarov, 1998
Euryurus erythropygus [probably, a different *Euryurus* species]	Miley, 1927
Oxidus gracilis	
Polydesmus angustus	David et al., 1993
Poratia salvator	
Pseudopolydesmus pinetorum	Youngsteadt, 2009
Streptogonopus phipsoni	Bhakat et al., 1989
CHORDEUMATIDA	
Chamaesoma brolemanni	David, 1989
Chordeuma proximum	Read, 1988b
Craspedosoma rawlinsii	Pedroli-Christen, 1978
Haasea hungarica	Tabacaru, 1965
Melogona voigtii	Tajovský, 1996
Peterjohnsia spp.	Mauriès, 1987
Tianella spp.	Mauriès, 1988

TABLE 11.1
(Continued)

CALLIPODIDA	
Apfelbeckia sp.	Lang, 1935
Callipus foetidissimus	Nguyen Duy-Jacquemin, 1976, 1979
Dischizopetalum illyricum	Verhoeff, 1940
STEMMIULIDA	
Stemmiulus adisi	Mauriès, 1984
JULIDA	
Allajulus nitidus	Biernaux, 1972; Blower & Miller, 1977; David, 1982
Archiboreoiulus pallidus	Brookes, 1963
Blaniulus guttulatus	Brookes & Willoughby, 1978
Boreoiulus tenuis	Brookes, 1963
Brachyiulus lusitanus	Keirallah, 1980; Karamaouna, 1987
Brachyiulus pusillus	Biernaux, 1972
Chelojulus sculpturatus	Enghoff, 1982
Choneiulus palmatus	Peitsalmi & Pajunen, 1996
Cylindroiulus caeruleocinctus	Sahli & Lavrut, 1963; Sahli, 1969c
Cylindroiulus gemellus	Read, 1988a
Cylindroiulus infernalis	Read, 1988a
Cylindroiulus latestriatus	Blower & Gabutt, 1964; Biernaux, 1972; Cotton & Miller, 1974
Cylindroiulus laurisilvae	Read, 1988a
Cylindroiulus lundbladi	Read, 1988a
Cylindroiulus punctatus	Sahli, 1955; Blower & Gabbutt, 1964; Biernaux, 1972
Cylindroiulus rabacalensis	Read, 1988a
Cylindroiulus vulnerarius	Biernaux, 1972
Enantiulus nanus	Kofler & Meyer, 1992
Julus scandinavius	Blower, 1970a
Kryphioiulus occultus	Voigtländer, 1987
Leptoiulus saltuvagus	Meyer, 1985
Megaphyllum bicolor	Karamaouna, 1987
Nemasoma varicorne	Brookes, 1963; Enghoff, 1976b
Nopoiulus kochii	Peitsalmi & Pajunen, 1996; Kheirallah et al., 2000
Ommatoiulus sabulosus	Halkka, 1958; Sahli & Lavoignat, 1964; Fairhurst, 1968; Sahli, 1969c
Ophyiulus pilosus	Blower & Miller, 1974
Orinisobates nigrior	Reeves, 2001
Proteroiulus fuscus	Brookes, 1963
Tachypodoiulus niger	Blower & Fairhurst, 1968; Sahli, 1969c

TABLE 11.1
(Continued)

SPIROBOLIDA	
Anadenobolus leucostigma martinicensis	Nguyen Duy-Jacquemin, 1992
Dactylobolus bivirgatus	Spaull, 1976
Epibolus pulchripes	Dhaenens & VandenSpiegel, 2006
Narceus annularis	Loomis, 1933
Pelmatojulus ligulatus	Demange, 1972; Demange & Gasc, 1972
SPIROSTREPTIDA	
Archispirostreptus syriacus	Crawford et al., 1987
Archispirostreptus tumuliporus	Gillon & Gillon, 1982
Spirostreptus macracanthus	Enghoff et al., 1993
Trachyjulus calvus	Schubart, 1946

Number of stadia and their practical identification

In teloanamorphic millipedes and in the initial, strictly anamorphic part of the post-embryonic development of hemianamorphic ones, the identification of stadia is easy, each stadium being characterized by a fixed number of rings and pairs of legs. In the other cases, especially in euanamorphic millipedes, where individuals with the same number of rings and leg pairs may belong to different stadia, other criteria are adopted, e.g. morphometry (Blower & Gabbutt, 1964) or counting the number of defence glands (Halkka, 1958; Brookes, 1963), but the single best criterion is counting the ommatidia, or the rows of ommatidia. This method, although not exempt from limitations (see Enghoff et al., 1993 for an extensive discussion) has been widely and profitably applied since the works of Vachon (1947), Saudray (1952), Sahli (1955) and Demange (1972); examples include Peitsalmi & Pajunen (1991, 1992), Hornung & Vajda (1988), Frederiksen et al. (2012).

Addition of new pairs of appendages

The plesiomorphic condition in millipedes is probably an increment by one or two leg pairs per moult, as observed in Polyxenida. Pentazonia usually add two or three leg pairs per moult; exceptions are the five pairs added by *Glomeris* at the moult from stadium I to stadium II and the females of *Trachysphaera*, that add only one leg pair between stadium VI and stadium VII.

A very large number of leg pairs is added with the moult from stadium II to stadium III in many Callipodida, Spirobolida and Spirostreptida, e.g. 15-17 in *Archispirostreptus tumuliporus* (Gillon & Gillon, 1982).

Many millipede groups obey an empirical rule known as the ‘law of anamorphosis’. This principle, first proposed by Fabre (1855) with reference to polydesmidans, states that all and only the apodous rings found in a given stadium will become podous in the following stadium. This principle applies also to the Julida (Halkka, 1958; Sahli, 1969) and to the other Juliformia (Spirobolida and Spirostreptida) but, generally, not to the other millipedes. In some species, e.g. the colobognathan *Polyzonium germanicum*, the rule

applies to later developmental stadia, but not to the earlier ones (David & Couret, 1984). Among the millipedes which follow the 'law of anamorphosis' all three types of post-embryonic developmental schedule (hemi-, telo- and euanamorphosis) are represented.

In Polydesmida and Chordeumatida, the segmental increments from a stadium to the next one are very regular, although even in these groups some exceptions have been recorded. For example, stadium II individuals in Polydesmida usually have six pairs of legs, but rare occurrences of specimens with seven pairs have been reported in *Coromus* (Aouti, 1978) and *Streptogonopus phipsoni* (Bhakat et al., 1989). Barring these exceptions, there is thus a strict correlation between the number of stadia and the final number of 'rings' in the adult. All chordeumatids with 29 'rings' are adults in stadium IX; those with 27 in stadium VIII. However, two species with 25 'rings' — *Opistocheiron canayerensis* (see Geoffroy, 1984) and *Chamaesoma brolemanni* (see David, 1989) — are also mature in stadium VIII. In these two species, only one 'ring' (rather than two) is added in stadium VI and again in stadium VII.

The number of segmental units added with a given moult, and thus the number of 'rings' found at a given stadium, are often different between close relatives. For example, all adult Glomerida have 11 tergites and 17 (females) or 19 (males) pairs of legs, but at stadium V with 10 tergites *Glomeris* has 15 pairs of legs, *Trachysphaera* and *Geoglomeris* have 14 and *Spelaeoglomeris* only 13. The number of segments added per moult is very variable in *Polyzonium germanicum* (David & Couret, 1984). As a consequence, individuals with 35 tergites could belong to any stadium between VII and IX, those with 45 to IX-XIV, those with 55 to XII-XVII. Males have generally fewer apodous segments than females. Segmental increments per moult are also very variable in the platydesmids, and can include both odd and even numbers; moreover, the is no correlation between the number of 'rings' and the number of pairs of legs.

In Julida, segmental formulae are generally regular in stadia I to III, but afterwards become variable, due to the rapid and not fixed increments accompanying each of the subsequent moults. In most Julidae and in the blind Blaniulidae the number of podour rings (and leg pairs, in parentheses) are as follows: stadium I, 4 (3); II, 6 (7); III, 11 (17); in the eyed blaniulids, in *Thalassisobates littoralis* and in *Aniulus bollmani*, the corrisponding numbers are I, 4 (3); II, 6 (7); III, 10 (17). Some individual variation in the first two increments has been recorded, however, in *Boreoiulus tenuis* and *Archiboreoiulus pallidus*. In Julida, three developmental phases are generally recognizable according to the amount and regularity of ring and leg pair increments at each moult (Kinkel, 1955). The first phase (stadia I-III, sometimes also IV) follows a fixed schedule; in the second phase, increments are variable, even individually, and generally high; in the third phase, the increments per moult decline.

Intraspecific variation in adult ring number is modest in Spirobolida, the highest range being 10 in *Narceus gordanus* and *Hiltonius mexicanus* (Keeton, 1960). Large intraspecific variation in adult ring number is found instead in some Cambalida: 38-73 rings in *Trachyjulus calvus* (Schubart, 1946), 18-35 in *Jarmilka alba* (Shear, 1973).

Schedules of segment addition and eventual number of 'rings' in the adult vary considerably among the Colobognatha. In *Polyzonium germanicum* there are multiple

segmental formulae since the earliest stadia: four different numbers have been recorded at stadium II, eleven at stadium III; moulting continues in this species at least till stadium XIII (David & Couret, 1983, 1984). However, in another polyzoniid, *Hirudisoma latum*, the number of tergites and legs is apparently fixed at each stadium (Brölemann, 1935). The number of leg pair is even in all stadia in *Polyzonium germanicum*, but odd in all stadia in another colobognathan, *Hirudicryptus canariensis* (Enghoff et al., 1993).

One of the consequences of the uncoupling between achievement of sexual maturity and progress along the schedule of anamorphic development is the fact that apodous rings are often found in adults. Several apodous rings are found in mature specimens of *Exospermitius* sp. (Krabbe, 1982). Even the largest adults of *Callipus foetidissimus*, which is teloanamorphic, have at least one apodous pleurotergite. In *Cladostreptus* spp., individuals with one apodous ring coexist in the same population with others without (Schubart, 1949).

Haplopody

Except for the few anterior, 'thoracic' ones, body rings with one leg pair only (haplopody) are rare throughout the Diplopoda, juvenile and adult stadia included. Exceptions, limited to the last podous ring, are the stadium II juveniles of Polydesmida (few exceptions are known), most stadia of the Nematophora (if we accept the conventional, but somehow arbitrary assignment of individual leg pairs to the individual pleurotergites, to which the sterna in this clade are not attached), plus occasional individuals of a few species of Julida (Enghoff, 1993). Very different and conspicuous is the haplopodous condition observed in stadium III juveniles of the cambalideans *Glyphiulus granulatus* and *Trachyjulus tjampeanus* (Enghoff, 1993). To illustrate this condition, it is useful to describe, as a term of reference, the 'normal' leg distribution found in the related genus *Hypocambala*, where the following ring formulae (podous rings + apodous rings + telson) are observed: probable stadium II: 6 + 14 + T; probable stadium III: 19 + 5 + T, 20 + 4 + T, 20 + 5 + T, 21 + 4 + T; probable stadium IV: 24 + 5 + T, 25 + 5 + T, 25 + 6 + T, 26 + 5 + T. In terms of ring formulae, stadium III of *Glyphiulus granulatus* is not very different from *Hypocambala*, having 16 to 19 podous rings followed by 1 to 3 apodous rings, but rings 7 to 16(-19) have one pair of legs only, probably the posterior one. No haplopodous rings are observed in the following stadia. Haplopody occurs also in stadium III of *Trachyjulus tjampeanus*, with 19 haplopodous rings.

'Larval' characters

Immature millipedes are generally treated as juveniles rather than larvae. The obvious difference in respect to the adults in terms of number of trunk segments and leg pairs is treated as pertaining to growth, and the non-systemic metamorphosis to which one or two leg pairs are subject in the males of the Helminthomorpha, those that will become gonopods (see next section) are regarded as too local as to invite recognizing a developmental change comparable to insect metamorphosis. This is clearly matter of

subjective assessment; however, in this treatise we have preferred to avoid alternative perspectives and corresponding alternative nomenclature, hence all ontogenetic segments of post-embryonic development separated by moults are uniformly described as stadia.

Nevertheless, in a few millipedes the juveniles have peculiar morphological features that are lost with the moult to the mature stadium. For example, 'larval' characters are the lateral keels of *Craspedosoma* spp., that are replaced by rounded paranota in the adults.

Non-systemic metamorphosis of one or more pairs of walking legs into sexual appendages

During the earliest post-embryonic stadia, the pairs of male appendages that will eventually appear as gonopods in the mature millipede are first developed as normal walking legs. At a critical moult, generally different in the different orders but fixed, or largely fixed, within each order, one or more pairs of legs will be replaced by gonopod rudiments, changed at the subsequent moults into more advanced rudiments and eventually into fully differentiated and functional gonopods.

The transformation of walking legs into gonopods is a strongly localized process by which the remaining pairs of legs are not affected, i.e., neither those in front of the future gonopods, or those next to them along the trunk. To express this unusual circumstance, the term *non-systemic metamorphosis* has been suggested (Drago et al., 2008, 2011). The process has been described in some detail in several species, including representatives of the Polydesmida (*Euryurus* '*erythropygus*': Miley, 1927; *Motyxia sequoiae*: Davenport et al., 1982; *Polydesmus angustus* and *Brachydesmus superus*: Petit, 1973a, 1976; *Sigmoria latior*: Filka & Shelley, 1980; *Oxidus gracilis*: Drago et al., 2011), Julida (*Nopoiulus kochii*, *Blaniulus guttulatus* and *Nemasoma varicorne*: Drago et al., 2011), Spirostreptida (e.g., *Spirostreptus* spp., *Archispirostreptus tumuliporus*: Demange, 1967) and Spirobolida (*Narceus annularis*: Berns, 1968; *Epibolus pulchripes*: Dhaenens & VandenSpiegel, 2006). Two examples are described in some detail in the following lines.

In male *Oxidus gracilis* (Fig. 11.1) male leg pair 8 are replaced at stadium IV by a pair of tiny rounded gonopod primordia. These increase slightly in size from stadium V to VII and are abruptly replaced by gonopods with the last moult (to stadium VIII). At stadium IV, the extrinsic muscles of the eighth pair of legs have disappeared, in particular the coxal protractor and retractor muscles that in the previous stadium attached to the tracheal pouch. The gonopod primordia contain a mass of tightly packed, not obviously differentiated cells. In stadia VI and VII, tiny muscles appear proximally, while a mass of tightly packed cells persists in the distal portion of the primordia. At stadium VIII (adult) the internal anatomy of the seventh trunk ring is quite different because of the changes associated with the fully-developed gonopods (Drago et al., 2011).

In male *Nopoiulus kochii*, during stadia III and IV, leg pairs 8 and 9 are ordinary walking legs, but are abruptly replaced by two pairs of gonopod primordia at stadium V, and are then changed into gonopods at stadium VI (VII in some individuals) (Drago et al., 2011). Stadium VI males with completely formed gonopods are not necessarily ready for reproduction, because sometimes the first pair of legs have still to change into

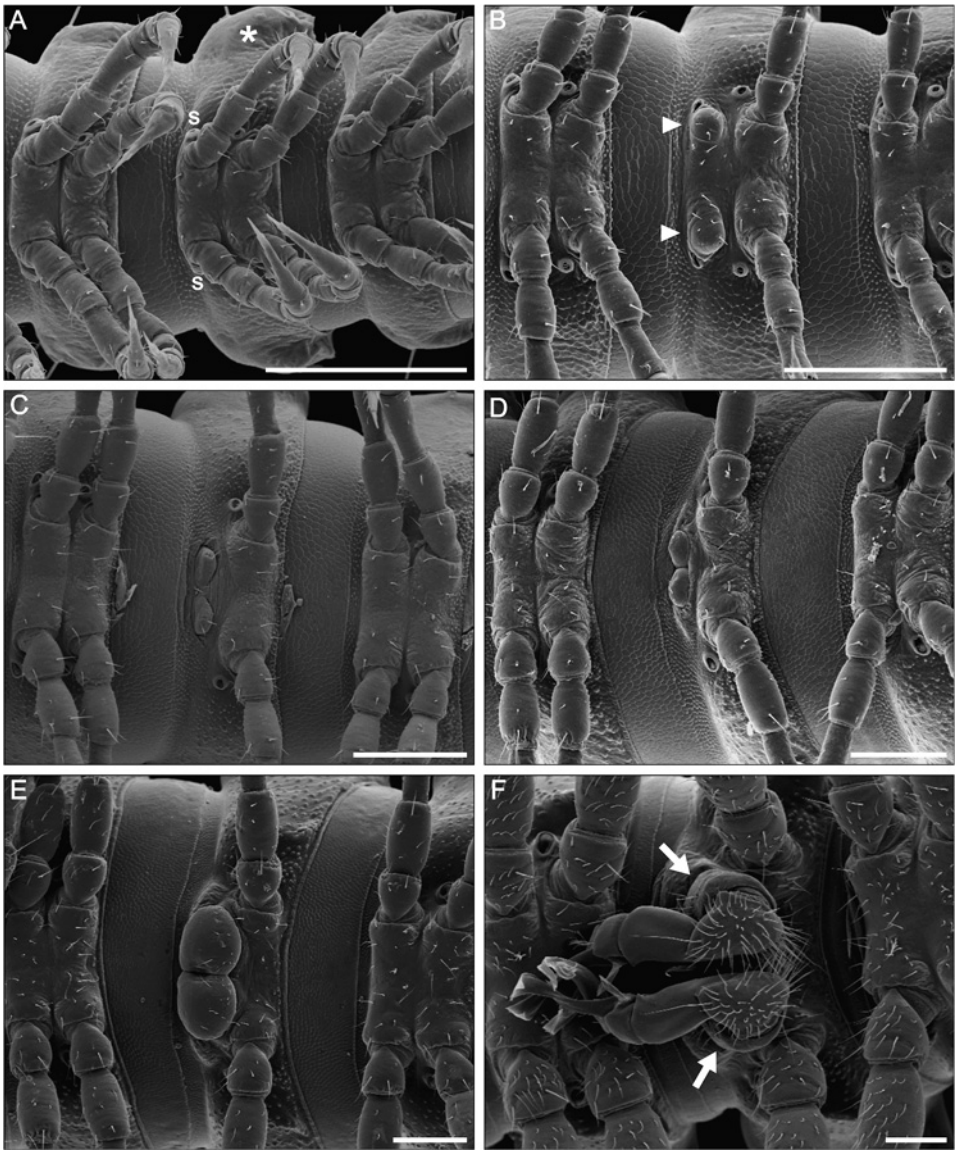

Fig. 11.1. Trunk rings VI-VIII of *Oxidus gracilis* during developmental stadia III-VIII. All male specimens except for the one in **A**, whose sex is undetermined because of the lack of sexual dimorphism at the corresponding developmental stadium. Ventral views, SEM. **A** Stadium III. **B** Stadium IV. **C** Stadium V. **D** Stadium VI. **E** Stadium VII. **F** Stadium VIII. Anterior to the left, scale bars 200 μm. Images and legend correspond to Fig. 11 in Drago et al. (2011). Abbreviation: **s** spiracles associated with the eighth pair of appendages. Arrowheads denote gonopod primordia at their first appearance; arrows denote gonopods, and asterisk denotes trunk ring VII.

the characteristic hooks necessary for grasping the female during copulation (Kheirallah et al., 2000). The development of gonopods in *Blaniulus guttulatus* is similar to the corresponding process in *N. kochii*, but shifted to later stadia: the gonopod primordia only appear in stadium VIII (Drago et al., 2011). In *Nemasoma varicorne*, leg pairs 8 and 9 are replaced by gonopod primordia in stadium IV (Drago et al., 2011) although in some specimens this transformation can be slightly delayed (Enghoff, 1976b).

The number of stadia with gonopod primordia varies among helminthomorph millipedes, sometimes also between closely related taxa. For example, four stadia (IV to VII) with gonopod primordia in *Polydesmus angustus*, but three (IV to VI) in *Brachydesmus superus* (Petit, 1976); in *Pelmatojulus insignis*, gonopod primordia differentiate progressively from stadium IV to IX, eventually approaching the final condition in the subadult stadium X, followed at last by the functional adult as stadium XI (Demange, 1972).

In *Polyzonium germanicum* males, legs 9-10 are transformed in gonopod rudiments in stadium IV, and will appear as full gonopods in the next, mature stadium.

In Julida, Polydesmida and Nematophora, the morphological changes in the external shape of gonopod primordia are abrupt: only minor changes in size and shape of the primordia are noticeable before the final leap from the most advanced anlagen to the fully differentiated gonopods. In other groups, the gradual change from the initially tiny gonopod primordia to the functional gonopods is accomplished across several stadia, as has been documented for the spirobolidan *Pelmatojulus insignis* (Demange, 1972).

In (at least some of) the Chordeumatida, the metamorphosis into gonopods is not synchronous between leg pair 8 and leg pair 9: in the penultimate stadium of male specimens of *Melogona gallica* (David, 1984) and *Cleidogona huebnerae* (Shear, 2013), legs 8 are already reduced, whereas legs 9 are still normal walking legs.

The internal changes accompanying the transformation of ordinary legs into gonopods have been recently described by Drago et al. (2011) in representatives of the Julida and Polydesmida. In those millipedes, as are julidans, in which the gonopods are retracted at rest in a gonopodal sac, the bulky size of the latter, plus the gonopodal muscles and the apodemes at which they are attached cause a dramatic restriction of the lumen of the seventh trunk ring (Fig. 11.2). This has been shown in detail in some julid species (Drago et al., 2011). In *Nopoiulus kochii*, in particular, the ventral nerve cord and the digestive tract are strongly displaced dorsally, likely impairing feeding. The consequent sub-optimal energy intake offers a possible explanation for the existence of intercalary males (see below, in the section on periodomorphosis), in which the reduction of gonopods and associated structures restores internal conditions better compatible with normal feeding, probably a necessary precondition to the eventual change to a further reproductive stadium.

Maturity and subsequent moults

All teloanamorphic millipedes are semelparous, while many hemianamorphic and euanamorphic ones are iteroparous. The stage at which maturity is achieved is largely fixed in millipedes with teloanamorphic development, but in those with euanamorphic development it is often variable, even within a species, depending on sex, population

Fig. 11.2. *Nopoiulus kochii*, adult male. Fused EDF-stack. Seventh trunk ring, after digestion of internal soft tissues. Posterior view. Ventral view, anterior to the top, scale bars 200 μm. Images and legend correspond to Fig. 5A in Drago et al. (2011). Asterisks denote anterior gonopod apodemes.

and external conditions. In the Julida, the stadium at which maturity is first achieved is not fixed; for example, the following variation has been recorded in the British or French populations of some species: *Tachypodoiulus niger*, stadium VII to X (Verhoeff, 1928; Sahli, 1966; Blower, 1970b); *Ophyiulus pilosus*, IX-XI (Blower & Gabbutt, 1964; Blower, 1970a); *Julus scandinavius*, IX-XI (Blower & Gabbutt, 1964; Blower, 1970a); *Cylindroiulus punctatus*, VIII-IX (Blower & Gabbutt, 1964); *C. latestriatus*, VII-IX (Blower & Gabbutt, 1964).

In several groups, males reach sexual maturity one or more stadia earlier than the females; for example, in *Polyzonium germanicum*, males mature in stadium V, female only in stadium VII or even VIII (Couret & David, 1985).

Among the Julida there are both semelparous and iteroparous species. In the latter case, two successive reproductive seasons can be simply separated by a moult, as is nearly always the case for the females, but in the males of several species a non-reproductive intercalary stadium (rarely, more than one) separates a reproductive stadium from the next one. The latter case (periodomorphosis) is described in a distinct section below.

Examples of semelparous julidans, in which both males and females reach maturity, breed and die without moulting further, are *Ophyiulus pilosus* and *Julus scandinavius*. More numerous are the julidan species with iteroparous females, which moult after a first

reproductive phase and then reproduce again. In some species, or at least in some populations, there are no males and the females are thelytokous (e.g., the blaniulids *Proteroiulus fuscus* and *Nemasoma varicorne*; see Brookes, 1963; Enghoff, 1976a; and Chapter 10 in this volume). When males exist, these, according to their reproductive behavior, are either semelparous (e.g., *Cylindroiulus latestriatus*, *C. punctatus*) or periodomorphic (cf. the following section) (e.g., *Tachypodoiulus niger*, *Ommatoiulus sabulosus*), or iteroparous with copulatory-to-copulatory moults (e.g., *Ommatoiulus albolineatus*: Sahli, 1989b; *O. sempervirilis*: Akkari & Enghoff, 2011; *Enantiulus nanus* and *Allajulus nitidus*: Voigtländer, 1987, but Sahli, 1973, 1982 recorded also occasional intercalary males in the latter species; also tentatively suggested for species of *Nepalmatoiulus* and *Dolichoiulus* (Enghoff, 1987, 1992)). If copulatory-to-copulatory moults are uncommon in male julids, this type of succession is, however, known in species of the related families Blaniulidae, Nemasomatidae and Trichoblaniulidae. Based on its occurrence in other millipede orders, e.g. Glomerida and Platydesmida, the copulatory-to-copulatory succession is probably the primitive condition in millipedes.

In Spirostreptida, many species are iteroparous. In *Archispirostreptus syriacus*, maturity is first achieved in stadium XII at 8 years of age (and will be followed by another two mature stadia) in the mesic habitat at Megiddo, but in stadium XIII at 6 years (followed by three more mature stadia) in the xeric habitat at Brosh (both localities in Israel) (Bercovitz & Warburg, 1985). However, other spirostreptidans, e.g. *Spirobolellus trifasciatus* (Loomis, 1964), are sempelparous, as are some individuals of other species, e.g. *Anadenobolus leucostigma* (Nguyen Duy-Jacquemin, 1992) and *Dactylobolus bivirgatus* (Spaull, 1976).

Reversal from reproductive to non-reproductive condition

In some millipedes, subsequent mature stages are separated by intercalary stages which are unable to reproduce and show different degrees of reduction of their sexual appendages. This phenomenon, also known in other arthropods (certain collembolans and female isopods; cf. Minelli & Fusco, 2013), is known in the Diplopoda as *periodomorphosis* (Verhoeff, 1916, 1923, 1933, 1934, 1939; Sahli, 1966, 1968a, b, 1969a, b, c, 1970, 1978, 1980, 1982, 1986a, b, 1990a, b, 1991a, b). The phenomenon is essentially limited to the males of a number of species of Blaniulidae and Julidae; within the latter, periodomorphosis is confined to the clade consisting of the tribes Oncoiulini, Schizophyllini and Cylindroiulini (Enghoff et al., 2011).

Evidence of periodomorphosis is often circumstantial (Akkari & Enghoff, 2011). Direct evidence of the occurrence of this phenomenon is limited to a few species. Males with the characteristic morphology of intercalaries have been observed on reared specimens only for the blaniulids *Blaniulus guttulatus*, *B. lorifer*, *Nopoiulus kochii* and *Proteroiulus fuscus* and the julids *Allajulus nitidus*, *Cylindroiulus caeruleocinctus*, *Ommatoiulus moreleti*, *O. sabulosus* and *Tachypodoiulus niger* (Verhoeff, 1923, 1925; Halkka, 1958; Baker, 1978; Sahli, 1989, 1990b, 1991a, b; Enghoff et al., 1993). Putative intercalary males collected in nature were reported for several additional species, e.g. *O. caspius* (Lohmander, 1936),

O. rutilans (Sahli, 1968a, 1969b), *O. lapidarius* and *O. atlanteus* (Schubart, 1960), *O. dorsovittatus* (Verhoeff, 1893), *O. buchneri*, *O. oxypygus*, *O. punicus*, *Rossiulus kessleri* and *R. vilnensis* (Sahli, 1968a).

In most periodomorphic millipedes, a sexually active stadium is usually separated from the next one by one intercalary only; however, two or more intercalary stadia (up to six in *Proteroiulus fuscus*; Rantala, 1974) can follow before the return to the next fully reproductive stadium.

In *T. niger*, the alternance between mature and intercalary stadia can be repeated several times and different mature stadia with a progressively larger number of rings are morphologically recognizable. The sequence described by Blower & Fairhurst (1968) for the British populations of this species includes: stadium VII, usually immature; VIII, usually the first mature stadium (= f. *typica*); IX, intercalary; X, mature (f. *elongata*); XI, intercalary; XII, mature (f. *elongatissima*); XIII, intercalary; XIV, mature (f. *maxima*); occasionally, the first maturity is anticipated to stadium VII or delayed until stadium IX.

The occurrence of periodomorphosis in female millipedes has been confirmed in one species only, the blaniulid *Blaniulus lorifer* (Sahli, 1984, 1993).

Stephenson's (1961) claim of the existence of an intercalary stage in Polydesmida (*Brachydesmus superus*) has been rejected by Lewis (1972). However, according to Mauriès (1997), periodomorphosis may occur in some species of Spirostreptida, as suggested by the reduced gonopods of the only specimen of *Atopogestus graueri* known to date and by the similarly reduced sexual appendages of some males of the odontopygid *Peridontopyge conani*.

In the intercalary males there is no regression of gonads, and spermatogenesis goes on (Halkka, 1958; Fairhurst, 1974).

Different hypotheses have been formulated as to the adaptive significance of the intercalary males (summarized in Enghoff et al., 1993). These include: (1) to circumvent presumed problems with shedding through consecutive moults the old cuticle from such highly complex structures as gonopods, (2) to provide a resting stage allowing spermatogenesis before the next breeding season, and (3) to maintain a high sex ratio in newly colonized areas by extending the life span of males. However, the main adaptive advantages in having an intercalary stadium with reduced gonopods lies perhaps in the release from the mechanical constraints on the gut caused by the gonopods in resting position. Sexually active males are often slimmer than the last juveniles of their species (Akkari & Enghoff, 2011), and are likely to suffer hunger.

End of post-embryonic development

In Polydesmida, each sex of each species and all stadia have fixed numbers of trunk segments. In the adults, the trunk rings are mostly 18 + 1, but with some exceptions. In several lineages (e.g., in *Brachydesmus*, *Macrosternodesmus*, *Poratia*, *Bacillidesmus*) the number is reduced to 17 + 1. Species with 18 + 1 are also found in the same genus as species with 17 + 1 (e.g. in *Stosatea* and *Cottodesmus*). The single major deviation is represented by the species of the genus *Devillea*, with the following numbers: *D.*

tuberculata: male 19 + 1, female 20 + 1; *D. patrizii* and *D. cerrutii*: female 20 + 1; *D. subterranea*: male 17 + 1 to 21 + 1; *D. doderoi*: male 27 + 1 (23 + 1 to 28 + 1 in specimens of unspecified sex). Unfortunately, the anamorphosis of *Devillea* is still unknown.

All adult Chordeumatida have a fixed number of pleurotergites and a fixed number of stadia, and each stadium has a fixed number of 'rings': mainly 29 in the adult, less commonly 27 and 31; other numbers: 25, 28 in some *Tianella* species, 30 only in *Persedicus martensi* (Mauriés, 1982). For examples of sexual dimorphism in the number of rings, both in Polydesmida and in Chordeumatida, see Chapter 10.

Length of individual stadia and of the whole life cycle

The first data on the duration of individual stadia were provided by Saudray (1952) for *Cylindroiulus punctatus* (Table 11.2); data for many other species have been collected subsequently, especially for European Julida, and are largely found in some of the works cited in Table 11.1.

The length of the individual stadia and of the whole life of the individual are obviously influenced by the environment. In teloanamorphic species, individuals confronted with poor external conditions may be able to postpone breeding until the following season, as observed in *Craspedosoma rawlinsii* by Pedroli-Christen (1978), but eventually the males die after copulation, the females soon after their have deposited their only or final egg batch (see e.g. the behavior of *Streptogonopus phipsoni* as reported by Bellairs et al., 1983 and Bhakat et al., 1989).

Compared to many other arthropods, generation time in millipedes is long or very long. In a number of polydesmidans, the life cycle takes one year, e.g. in *Xanthodesmus physkon* (Northern Nigeria; Lewis, 1971), *Strongylosoma stigmatosum* (Germany; Seifert, 1932), *Brachydesmus superus* (England; Stephenson, 1961), *Oxidus gracilis* (Japan; Murakami, 1962), *Nedyopus hiburizimensis* (Japan; Murakami, 1966), in others one or two years, e.g.

TABLE 11.2
Duration of individual stadia in *Cylindroiulus punctatus* (France)

Stadium	Days
I	1
II	15
III	30
IV	30
V	30
VI	45
VII	60
VIII	60-90
IX	150-180 (first adult stadium)
X	150-180
XI	150-180

in *Habrodesmus duboscqui* (Northern Nigeria; Lewis, 1971), two years, e.g. in *Polydesmus denticulatus* (England; Blower, 1970a) or three years, e.g. in *Ampelodesmus iyonis* (Japan; Murakami, 1965). But in *Glomeris marginata* Blower (1974) reported a maximum age of 10-11 years, approximately the same we can estimate for *Archispirostreptus syriacus*, based on Bercovitz & Warburg's (1985) data. A very high age can be reached also by some teloanamorphic millipedes: in mountain areas (800-2000 m) in central Honshu (Japan), *Parafontaria armigera* moult to adult in the summer of the eighth year, and ovideposition does not occur before the following summer (Fujiyama & Yoshida, 1984).

It is still unclear if the maximum number of stadia recorded in euanamorphic millipede is definitely fixed, or is only limited in practice by the number of moults an individual is able to undertake, given the total sum of external and internal limiting factors to which it is subjected, but could be eventually increased, either to a higher maximum — predetermined but not reached in nature — or even indefinitely. Mechanisms regulating the final, or tendential, number of rings are unknown. The only experimental studies in this context are those of Berns & Keeton (1968a, b), who kept juvenile specimens of *Narceus annularis* in semistarvation: with the first moults since the beginning of the treatment, these millipedes added fewer rings than normally fed specimens, but at later stadia they added instead more rings, thus partially, but never totally, reducing the gap in respect to their well-fed conspecifics.

The maximum number of stadia estimated for a millipede collected in nature is 24, in *Tachypodoiulus niger* (Sahli, 1969c).

TERATOLOGY

The traditional approach to millipede teratology has been descriptive and classificatory: the older literature was summarized by Balazuc & Schubart (1962), but a number of cases have been published thereafter. Monsters as the product of experimental treatment of developing embryos were obtained in *Glomeris marginata* by Juberthie-Jupeau (1968, 1970, 1974). More recent studies try to interpret naturally occurring morphological anomalies in the light of the emerging data on the expression patterns of developmental genes, as described above. These three steps in millipede teratology are briefly summarized in the following.

Three kinds of naturally occurring teratologies have attracted particular interest. A first class includes sexual anomalies:

(i) The presence of a gonopod on one side only of the body, while the contralateral appendage is a normal walking leg, as in a specimen of *Pycnotropis taenia* described by Karsch (1881). Less conspicuous, but of comparable nature, are the cases where only one of the two legs 1 is sexually modified, as in a male of *Amblyiulus cedrophilus* described by Attems (1911) and a male of *Cylindroiulus ibericus* described by Brölemann (1913).

(ii) The presence of supernumerary or ectopic sexual appendages, as in a male of *Ommatoiulus moreleti* with the left leg 11 replaced by a gonopod described by Brölemann (1921), similar to one of legs 6 in a specimen of *Eurydesmus baguassuensis* described by Balazuc & Schubart (1962). An extreme example of this kind of teratology is discussed below.

(iii) The co-occurrence in the same individual of primary or secondary sexual characters of both sexes: a pair of vulvae and a pair of gonopods in a specimen of *Polydesmus inconstans* (Chalande, 1903), a pair of vulvae and a gonopod in the place of left leg 8 (the corresponding right appendage being a normal walking leg) in a specimen of *Aphelidesmus hermaphroditus* (Brölemann, 1898); an overall feminine aspect and a normal ovary but also reduced gonopods like those of intercalary males in a specimen of *Tachypodoiulus niger* (Verhoeff, 1910); a specimen of *Ophyiulus pilosus* with vulvae, ovary with mature eggs, but also two pairs of gonopods intermediate between those of an immature and a mature male (Bigler, 1920); a specimen of *Coonoorophilus monstruosus* with vulvae and ovary full of eggs, but also right gonopods paired with normal walking appendages on the left side (Carl, 1932); a female of *Trichoblaniulus hirsutus* with one of the legs 1 modified as in the male (Verhoeff, 1911).

Occasionally, sexual abnormalities were found to depend on parasitization. In a sample of *Ommatoiulus moreleti* in stadium IX parasitized by larvae of nematomorphs of the genus *Gordius*, Baker (1985) found that the first pair of legs were not modified into hooks and the gonopods were rudimentary; similarly, the vulvae of parasitized females were similar to those of juveniles.

A second class includes segmental anomalies, especially helicomery. In the latter case, two or more consecutive rings are involved. At one end of the perturbed region, the left (or right) half of one ring is fused to the right (or left) half of two (rarely, more) segments. This produces an 'out of frame' pairing that extends for a number of rings until a complementary one-to-many matching re-establishes the normal segmental pattern at the other end of the perturbed region. Three examples of helicomery were described by Balazuc & Schubart (1962), respectively involving rings 44-46 in a *Stenurostreptus stenorhynchus*, rings 34-35 in an *Ommatoiulus moreleti* and two sets of rings (32-36 and 46-48) in a specimen of *Neptunobolus hogei*.

A third class is represented by specimens with branched appendages (schistomely). Binary schistomelies have been found on virtually all kinds of appendages: antennae (*Blaniulus troglobius*: Brölemann, 1923), gnathochilarium (*Pteridoiulus aspidiorum*: Verhoeff, 1913), walking legs (e.g., *Ommatoiulus sabulosus*: Sahli, 1957; *Aporodesmus* sp.: Balazuc & Schubart, 1962), but also the sexually modified legs 1 of a male julidan (*Blaniulus troglodites*: Brölemann, 1923) and even gonopods (posterior gonopods of an *O. sabulosus*: Brölemann, 1917). Much rarer are ternary schistomelies, with a case recorded for one leg 5 with three tips in a specimen of *Salpidobolus anomalus* (Silvestri, 1897).

All these cases of teratology concern adult or subadult specimens, but anomalies have been also reported from pupoids (*Pelmatojulus laminatus*; Aouti, 1980).

A different class of teratologies concern embryos. Janssen (2011a) reported that under laboratory conditions approximately 1 out of 200 embryos of *Glomeris marginata* develops with severe morphological malformations. In most of these abnormally developing embryos, the posterior germ band is duplicated but shares a common anterior pole representing classical cases of duplicitas posterior. These kinds of abnormalities were reported under natural conditions in *Glomeris* (Hubert, 1968). In these cases of duplicitas posterior, at least one appendage of the second trunk segment appeared to be shared by the two germ bands (Janssen, 2013a, b). No examples of duplicitas anterior (duplicated anterior pole) or duplicitas cruciata (duplication with two anterior and two posterior poles) were found, contrary to previous reports by Juberthie-Jupeau (1970). Janssen (2013b) interpreted the lack of axial abnormalities other than duplicitas posterior as evidence of early axis determination. Juberthie-Jupeau (1968, 1974) had described the occurrence of similar abnormally developed embryos of *Glomeris* as a result of temperature shocks at around the time when the blastoderm forms.

The hinge between teratology intended as the description of naturally occurring 'monsters' and developmental biology based on the study of gene expression patterns is represented, in Diplopoda, by a recent study in which a 'monstrous' millipede was used as test case for a *multiplicative model of segmentation* (Akkari et al., 2014). Authors described a male specimen of *Ommatoiulus moreleti* with eight pairs of gonopods, i.e. the normal ones corresponding to walking leg pairs 8 and 9, plus six pairs of ectopic gonopods replacing walking leg-pairs 10-11 and 24-27, respectively (Fig. 11.3). In this specimen there are thus two sets of sexually modified appendages, each of which includes four pairs of gonopods; the posterior set (24-27) is translated by exactly 16 positions in antero-posterior direction in respect to the anterior one (8-11). Akkari et al. (2014) suggested that a body section extending over 16 leg pairs could be, in millipedes with a total number of rings in the range found in most julids, a module deriving from four cycles of regular binary splitting of an embryonic 'primary segment' (Fig. 11.4).

Indeed, a (very likely) early molecular marking of the position(s) where walking legs will later undergo a metamorphosis into gonopods (cf. Drago et al., 2008) may provide an explanation for the distribution of the extra gonopods in the homeotic specimen, provided that segmentation is achieved according to a multiplicative model. It can be hypothesized that the positional marker for gonopods was already present in a primary segment before this eventually split into secondary segments. In the homeotic specimen, the positional marker corresponding to the future gonopods was probably more abundant and/or more extensively distributed, so that (1) it was present both in the first (as in normal specimens) and in the second of the primary trunk segments, and (2) in the progeny of both of these the marker was inherited by a number of secondary segments higher than those normally found marked within the progeny of the first primary segment and eventually revealed by the localized metamorphosis of two pairs of legs only into gonopods.

A likely equivalent teratology was described by Shelley (1975) in a male of the polydesmidan *Nannaria conservata* where two additional pairs of gonopods were found, in the place of leg pairs 4 and 12, respectively, i.e. exactly 4 pairs in front and 4 pairs behind

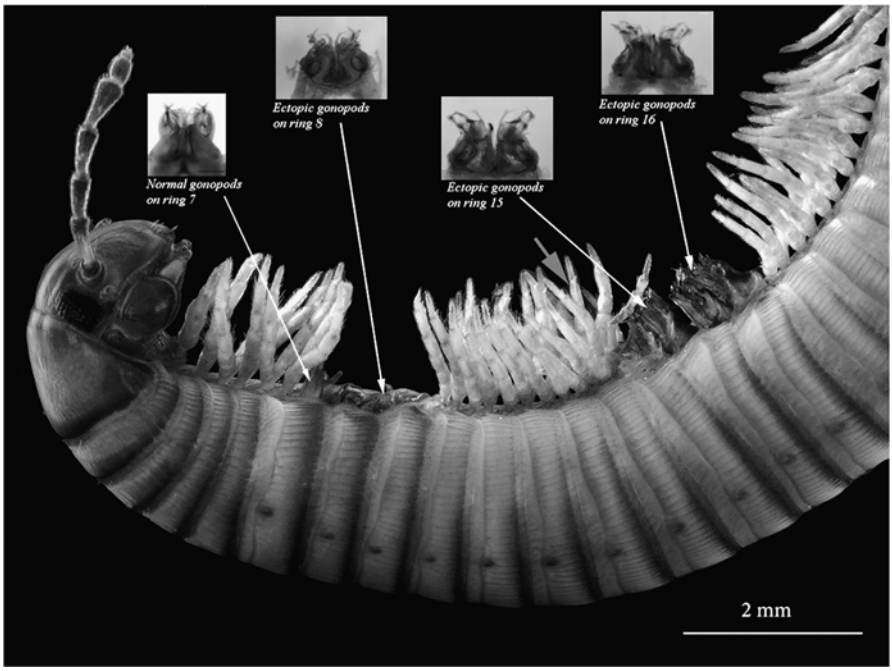

Fig. 11.3. *Ommatoiulus moreleti*, homeotic male with extra pairs of gonopods. Head and first 17 body rings. Images and legend correspond to Fig. 2B in Akkari et al. (2014).

the normal pair of gonopods corresponding to appendage pair 8. The smaller extent (four segmental units) of the interval between pairs of gonopods in this specimen, compared to the 16 units separating the two sets of gonopods in the teratological specimen of *O. moreleti* is interpreted by Akkari et al. (2014) as evidence for a lower degree of segment multiplication in the fomer millipede, in agreement with the fact that in polydesmidans the total number of the animal's body rings is much lower than in julidans.

Outside the diplopods, the case of the two closely related species of the centipede genus *Scolopendropsis*, one with 21 or 23 leg-bearing segments, the other with 39 or 43 (Minelli et al., 2009), similarly supports a multiplicative process of segmentation.

REGENERATION

Evidence of regeneration in millipedes is limited to the following experimental studies on the behavior of damaged appendages.

In the antenna of *Polyxenus lagurus* there is a point of natural autotomy between articles III and IV (Nguyen Duy-Jacquemin, 1972); in the same millipede, amputation of the antenna releases a moult in advance compared to undamaged animals (Seifert, 1966). In *Polydesmus angustus*, the amputated antenna of a juvenile regenerates at all levels of amputation, but there is evidence of a critical zone corresponding to the articulation

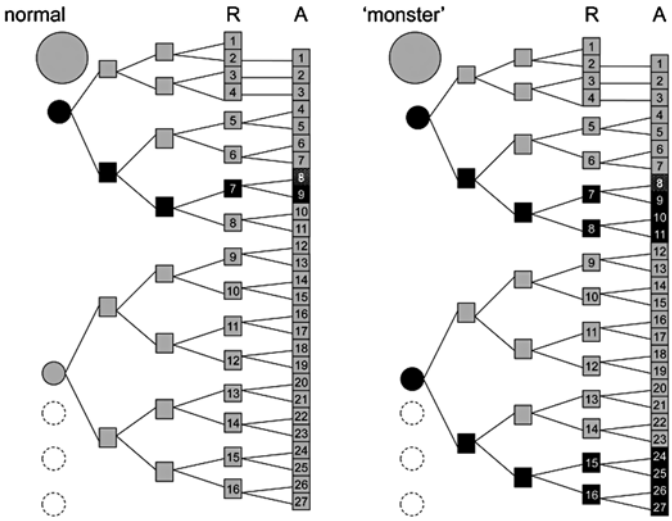

Fig. 11.4. Segmental composition of the anterior part of the body in the homeotic specimen of *Ommatoiulus moreleti* in Fig. 11.3, compared to a normal male, as suggested by the multiplicative segmentation model (Maynard Smith, 1960; Minelli & Bortoletto, 1988; Minelli, 2000, 2001). The first trunk rings are the legless collum and 3 rings with one leg pair each, followed by typical diplosegments. Because of an additional anomaly, in the homeotic specimen only one ring (13 + 14) corresponds to leg pairs 20-23. In each panel, the left vertical sequence of circles represents the embryonic head (big circle) followed by a few primary segments (smaller circles), the number of which is left indeterminate (fading empty circles toward the posterior). Each primary segment is subsequently split, through a sequence of binary AP divisions, into a growing number of secondary (definitive) segments. The intermediate stages from primary to secondary segments as well as the secondary segments (rings, R) and the associated pairs of appendages (A) are represented as squares. Appendage pairs are numbered. Images and legend corresponding to Fig. 15 in Akkari et al. (2014).

between articles II and III: an antenna amputated below this zone regenerates as a juvenile antenna, an antenna amputated above as an adult antenna, complete of all its articles (J. Petit, 1974). In the same species, Petit (1973b) studied also the regeneration of the walking legs.

The only studies hitherto conducted on the legs fated to metamorphose into gonopods are Petit's (1973a) experiments on leg pair 8 of *Polydesmus angustus*, amputated at stadium III. The highest degree of completeness of the regenerated appendage was obtained when the leg was cut at least 30 days before the moult to stadium IV. The regenerated appendage was gonopod-like if the level of cut was equal or distal to the apical end of the prefemur, but intermediate or definitely leg-like if more proximal.

Finally, as mentioned in Chapter 5, the is evidence of a natural process of rejuvenation of the intestinal epithelium. The process was described by Neumann (1985) for the midgut epithelium of *Oxidus gracilis*. Here, the regenerative cells divide at the beginning of a moulting event and push the old differentiated cells into the gut cavity. After the ecdysis, those discarded cells have disappeared.

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CHAPTER 12

DIPLOPODA — ECOLOGY

BY

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HABITATS

Range of habitats

Millipedes are terrestrial arthropods that typically live in decomposing plant litter on the forest floor (Golovatch & Kime, 2009), i.e. an environment that provides food for detritivores and is relatively buffered against temperature and moisture fluctuations. However, while their feeding habits have been highly conserved during evolution (Shear & Selden, 2001), these arthropods are currently represented in a wide variety of habitats and microhabitats.

Many juliformian millipedes which are capable of burrowing have successfully colonized more open, less buffered habitat types. In South Africa, dozens of spirostreptidan species live in savannah, five genera being confined to this biome (Hamer et al., 2006). In Europe, many Julida thrive in grasslands (Kime & Golovatch, 2000). Millipedes also occur in more extreme environments such as deserts and high altitude areas above the timberline. The most common species in warm deserts are large Spirostreptida, whereas the fauna of high mountain habitats is more diverse and dominated by either Chordeumatida or Polydesmida depending on the geographical area (Golovatch & Kime, 2009). Little is known about the biology and ecology of the great majority of species living in extreme environments but, clearly, they must be capable of withstanding long periods of inactivity due to drought or cold. For example, the spirostreptid *Orthoporus ornatus* in deserts of the southwest USA remains dormant for about eight months of dry season (Crawford et al., 1987).

By contrast, many species have evolved in an opposite direction and colonized caves and other subterranean habitats, in which diurnal and seasonal variations in temperature and humidity are much reduced. Millipedes are often numerically dominant in these environments, which are inhabited by both surface-dwelling species that enter caves sporadically or seasonally (troglophiles) and obligate cave dwellers (troglobionts) (Culver

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& Pipan, 2009). Troglobiotic millipedes, although they remain imperfectly known, have been described in large numbers in some countries, e.g. 19 species and subspecies in Bulgaria (16% of the total diplopod fauna) (Stoev, 2007), 37 species in France (Geoffroy, 1997) and 85 species in the USA (Culver & Shear, 2012). Many show morphological adaptations usually found in cave-dwelling organisms, including elongated legs and antennae, and reduced eyes and pigmentation. The 'climatic relict hypothesis' posits that many troglobionts have evolved from surface-dwelling ancestors that sought refuge from climatic stress, notably during the periods of glaciation of the Quartenary (Culver & Pipan, 2009). However, other factors may have been involved in the colonization of caves by millipedes, especially in tropical areas. For example, many troglophilic and troglobiotic cambalopsids from southeast Asia are strongly associated with the presence of guano (Deharveng & Bedos, 2012), and this food source may have been as important as buffered climatic conditions in determining their colonization success.

The presence of millipedes in a variety of unusual habitats has often been reported (Hopkin & Read, 1992; Golovatch & Kime, 2009). A few species are arboreal, even large pill millipedes such as the sphaerotheriids *Sphaerotherium punctulatum* in South Africa and *Zoosphaerium arboreale* in Madagascar, which climb trees more or less regularly for feeding (Haacker & Fuchs, 1972; Wesener & Sierwald, 2005). Other millipedes have adapted to semi-aquatic or aquatic environments. A few species, such as *Thalassisobates littoralis* (Nemasomatidae) and *Dolichoiulus tongiorgii* (Julidae), are exclusively littoral (Barber, 2009). A larger number of species live near rivers and some have adapted to survive periodical flooding. In Amazonian forests subject to seasonal inundation, most millipedes escape flooding by migrating for weeks or months on emerged plants and trees (Adis et al., 1996). The Amazonian pyrgodesmid *Myrmecodesmus adisi* appears to be unique in being capable of surviving under water for months: the species retreats under the bark of submerged tree trunks, where it breathes through a thin air layer trapped along the cuticle (plastron respiration) (Adis et al., 1996). This type of underwater respiration is however used by other polydesmidan species to resist shorter submersions. In caves of northern Italy, for example, the polydesmid *Serradium semiaquaticum* that lives near subterranean streams enters water spontaneously, where it breathes without difficulty (Adis et al., 1997).

A number of habitat analyses were conducted at different spatial scales, mostly in temperate areas, to identify the abiotic and biotic characteristics that best explain the distribution of species in nature (Haacker, 1968; Kime & Wauthy, 1984; David, 1990; Branquart et al., 1995; Lee, 2006; Voigtländer, 2011). They have revealed significant relationships between environmental variables and the presence of particular species, as detailed below. However, as several environmental variables may covary in field studies, laboratory experiments are often necessary to identify which variable(s), singly or in combination, really influence(s) distribution.

Climatic and microclimatic influences

Irrespective of the geographic distribution of species in the major climate zones of the Earth (Chapter 13), differences in climatic conditions within a species' range are

important habitat characteristics for millipedes. Both diurnal and seasonal temperature and moisture regimes greatly differ between grassland and forest ecosystems, which most likely explains the occurrence of many species in either of these habitat types (Haacker, 1968). Likewise, temperature decreases and rainfall often increases with altitude, and such climatic gradients most likely explain why many species occur at a particular elevation. Among representatives of the julid genus *Leptoiulus* in Switzerland, for example, *L. bertkaui* occurs only below 1000 m a.s.l., *L. braueri* and *L. faesi* only above 2000 m a.s.l., and *L. montivagus* in-between (Pedroli-Christen, 1993). At even smaller spatial scales, topography significantly affects microclimatic conditions, which can influence the distribution of millipedes (Ott & Van Aarde, 2014). Specific microclimatic requirements sometimes result in unexpected distributions, as on Cousine Island, Seychelles, where granite rock crevices appear to be key habitat elements for the endemic spirostreptid *Sechelleptus seychellarum*. They form suitable daytime refuges for adults, with favourable microclimate conditions, and the species is more rarely encountered in areas deprived of granite rocks (Lawrence et al., 2013).

Although ecophysiology experiments have only been conducted on a handful of species, they reveal contrasting levels of desiccation resistance, cold hardiness and submersion resistance among species, thus confirming the wide variety of climatic conditions suitable for millipedes. Unsurprisingly, the desert-dwelling *Orthoporus ornatus* has a transpiration rate about 100 times lower than chordeumatidan species from mid-elevation humid forests in Austria (Crawford, 1972; Meyer & Eisenbeis, 1985). However, substantial differences also exist between species occupying the same geographical area. In Europe, the julid *Ommatoiulus sabulosus* is much more resistant to desiccation than other species tested by Haacker (1968), which explains its success in dry habitats, even in the Mediterranean region. The polyzoniid *Polyzonium germanicum* freezes at much lower temperatures than other millipedes (David & Vannier, 1997), which enables the species to overwinter in the surface litter layer of waterlogged sites, in which it lives preferentially (Voigtländer, 2011). In addition, *P. germanicum* is highly resistant to submersion (Tufova & Tuf, 2005), as is the polydesmid *Polydesmus denticulatus* (Zulka, 1996), a species that frequently occurs in temporarily flooded areas. Interestingly, not all experimental results on the temperature and moisture preferences of species agree well with their distribution in the field (Barlow, 1957; Haacker, 1968), suggesting that some populations do not live under ideal conditions. Haacker (1968) argued that temperate millipedes can withstand unsuitable moisture conditions provided they occupy sites consistent with their temperature preferences. However, it is likely that the relative importance of these two factors varies from one species to another.

Influence of soil properties

Overall, more millipede species live in calcareous areas than in acid soil areas (Kime, 1992; Meyer & Singer, 1997; Tajovsky, 1997) and some species such as the west European *Geoglomeris subterranea* (Glomeridae), *Macrosternodesmus palicola* (Macrosternodesmidae) and *Propolydesmus testaceus* (Polydesmidae) are definitely calcicolous (Lee,

2006; Kime & Enghoff, 2011). Although this may be linked to the higher soil pH on calcareous bedrock, alternative explanations must be considered. In calcareous areas, food may be richer in calcium, an element that millipedes accumulate in large amounts in their tissues (Reichle et al., 1969). Based on his experiments, Thiele (1959) concluded that the association of millipedes with calcareous soil is primarily due to the microclimatic characteristics of plant communities occurring on this type of soil.

Soil texture, i.e. the proportions of sand, silt and clay particles, is an important habitat characteristic for millipedes (Kime & Wauthy, 1984; David, 1990; Branquart et al., 1995). Although some species are common in sand dunes (Fairhurst, 1979), many others are rarely found on sandy soil. The underlying causes are not always clear and biological requirements may be important. For example, *Glomeris* females ingest soil during the breeding period to coat their eggs with earthy material (Blower, 1985), which requires soil with sufficiently high silt or clay contents. By contrast, high clay contents inhibit burrowing in the southern African spirostreptid *Doratogonus uncinatus* (Dangerfield & Chipfunde, 1995), which could affect the distribution of field populations because burrowing is essential for survival in the species' dry habitats.

Influence of food resources

The vast majority of millipedes are detritivores, which feed on decaying plant material colonized by microbial decomposers (bacteria and fungi) (Hopkin & Read, 1992). Many species also feed occasionally on a variety of higher-quality foods, such as fallen fruits, seeds, mushrooms, faeces and dead invertebrates (Hoffman & Payne, 1969; Wooten & Crawford, 1975; Dangerfield & Telford, 1996; Koprdova et al., 2010). Close associations with a single species of plant litter are rare and most millipedes tend to be generalist or opportunist detritivores. However, this does not preclude marked food preferences, which have been repeatedly demonstrated after the pioneering works of Lyford (1943) and Dunger (1958). Accordingly, the nature of the food may be an important determinant of the habitat. In the west coast of Canada, the widespread xystodesmid *Harpaphe haydeniana* is more abundant in forests dominated by Douglas fir (*Pseudotsuga menziesii*), which is also the preferred litter species in laboratory feeding tests (Carcamo et al., 2000). Similarly, in a forest dominated by two tree species on Grande-Terre Island, Lesser Antilles, there are more millipede species and they are much more abundant in patches of water mampoo (*Pisonia subcordata*) than in those of West-Indian birch (*Bursera simaruba*). This distribution is consistent with the results of feeding tests, in which *Anadenobolus monilicornis* (Rhinocricidae), *Leptogoniulus sorornus* and *Trigoniulus corallinus* (both Trigoniulidae) consumed five litter species but clearly preferred water mampoo leaf litter (Loranger-Merciris et al., 2008).

More specialized feeding habits occur in species associated with particular habitats or microhabitats. For example, the cave-dwelling *Serradium semiaquaticum*, using modified mouthparts, gathers small organic detritus on wet surfaces along the edge of subterranean streams or under water (Adis et al., 1997). *Myrmecodesmus adisi*, which lives on submerged tree trunks for months in Amazonia, feeds on algae during the flooding periods

(Adis & Junk, 2002). In fact, a number of millipede species are more or less specialized to feed on algae (Dangerfield & Telford, 1996; Mahsberg, 1996), which may impose strict limits on the habitat. The paradoxosomatid *Xanthodesmus physkon* exclusively feeds on this type of food in gallery forests of Ivory Coast and aggregates on tree species that support high densities of algae on their bark (Mahsberg, 1996).

Habitat specialization and possible implications

In millipedes there are both habitat generalists, which occur in a wide range of conditions, and highly specialized species, closely adapted to one type of habitat or microhabitat. Specialization is especially striking when a large number of congeneric species occur in a limited area, such as the dozens of endemic *Cylindroiulus* species (Julidae) studied by Enghoff (1983) on Madeira Island. Among the forest species that live in the laurisilva, *Cylindroiulus gemellus* is a generalist present in all types of microhabitats, but specialists show distinct microhabitat preferences, e.g. soil or soil-litter interface for *C. laurisilvae* and *C. exiguus*, logs for *C. infernalis* and *C. kappa*, and epiphytes on trees for *C. lundbladi*. Moreover, Enghoff (1983) found some correlations between these microhabitat preferences and the morphological characteristics of species, in terms of segment length, leg length, eye size and body coloration. Good soil burrowers, for example, have short segments, short legs, small eyes and are paler. This strongly suggests that microhabitat preferences are traits that have remained stable over long periods of evolutionary time, at least in a number of species.

The distinction between habitat specialists and generalists may be important in terms of response to disturbances that heavily alter habitat conditions. The prevailing view is that specialists should be more vulnerable to habitat alterations than generalists (Hanski, 2005) but this hypothesis has not been tested in millipedes. An example of human-induced habitat alteration is the replacement of old-growth forests by low-diversity tree plantations, which results in a major decrease in resource heterogeneity, in terms of food and microhabitats. Bourdanne (1997) compared millipede species richness in a humid tropical forest and three nearby plantations in Ivory Coast, and found that the number of species decreased from 32 in the natural habitat to 19-24 in the plantations. Although this species loss probably had a relation to the above-mentioned habitat alterations, very little is known about the levels of specialization of the millipede species that were affected.

Habitat specialization is also one possible explanation for shifts in the presence and abundance of different millipede species during the process of ecological succession, whether primary succession at mine sites (Redi et al., 2005; Dunger & Voigtländer, 2009) or secondary succession following cessation of cultivation (Scheu, 1996; Tajovsky, 2000). In Germany, Dunger & Voigtländer (2009) found that millipedes were good indicators of successional stages at former mine sites, with different species predominating in the early stages covered with low vegetation (the craspedosomatid *Craspedosoma rawlinsii*), pre-woodland stages (*Polydesmus inconstans*) and woodland stages (*Glomeris hexasticha* plus other typical species). Habitat characteristics are modified as vegetation changes and

the sequential replacement of millipede species may reflect their adaptation to particular habitat conditions. However, the influence of physiological differences between successive species has not been demonstrated experimentally and alternative explanations of these data, based on increased competitive ability as species richness increases, could be proposed (Giller, 1996).

FACTORS AFFECTING POPULATION DYNAMICS

Seasons and weather

Most millipede species live in seasonal environments and are well adapted to cope with predictable changes in temperature and rainfall (Hopkin & Read, 1992). Under potentially stressful seasonal conditions, populations move to suitable shelters and become inactive for weeks or months. This results in drops in the numbers of specimens collected in leaf litter or caught in pitfall traps but does not necessarily reflect real changes in population density. For example, many species spend the unfavourable seasons buried in the soil, in which temperature and moisture variations dampen with depth (Geoffroy, 1985; Dangerfield, 1998). In North America, the wood-feeding spirobolid *Narceus americanus* burrows into logs in late summer and O'Neill (1969) showed that this behaviour is a response to desiccation. The seasonal activity cycles of millipedes vary tremendously in different climatic zones, showing generally spring and autumn peaks in temperate areas (Geoffroy & Celerier, 1996), but only one summer peak at high elevations (Meyer, 1990) and one winter peak in dry Mediterranean environments (Karamaouna, 1992). Seasonal cycles of activity are closely dependent on the wet season(s) in deserts and tropical areas (Crawford, 1979; Dangerfield, 1998).

Unpredictable weather events during periods of activity or extreme conditions during periods of inactivity can have strong impacts on population abundance. After exceptional droughts in temperate forests, for example, chordeumatidan species have been shown to suffer significant population declines (Schallnass et al., 1992; Geoffroy & Celerier, 1996).

The current climate change is also expected to modify the population dynamics of millipedes, with contrasting effects in different climatic zones. In cool temperate areas, a few degrees of warming with little change in rainfall should result in higher intrinsic rates of increase in many millipede populations, with positive effects on abundance (David & Handa, 2010). This is consistent with signs of northward and eastward range expansion in several species of northwest Europe (Meidell & Enghoff, 1993; Hickling et al., 2006). In most subtropical regions, however, climate warming is predicted to be accompanied by reduced rainfall, which should negatively affect species that are not adapted to withstand severe droughts (David & Handa, 2010). This might be the case in southwestern Australia, for example, where dozens of endemic millipede species are restricted to the coastal mountain region, which presently comprises moist refugia but is predicted to be severely affected by drought in the coming decades (Moir et al., 2009).

Food quality

Experiments have shown that food quality has strong effects on the population dynamics of millipedes, with a considerable influence on life-history traits, mainly growth and reproduction. In *Polydesmus angustus*, females reared from egg to maturity on a mixture of leaf litter have very low fertility, which increases considerably and becomes similar to the fertility of adult females from the field when a pinch of yeast is added monthly to the leaf litter (David & Celerier, 1997). This illustrates the importance of the occasional consumption of nutrient-rich food by millipedes. High-quality food may be even more important for julids, since female *Ophyiulus pilosus* that were reared from egg to maturity on leaf litter alone did not lay any eggs, presumably due to a nutrient deficiency (Blower, 1974). Changes in the species composition of leaf litter that correspond to shifts in nutrient contents also have significant effects on development rate, growth and reproduction, with potentially important implications for population abundance (David & Handa, 2010).

Impacts of predators

Although most millipede orders have defence glands that produce toxic and repellant compounds (see Chapter 3), many animal species are adapted to prey on them. These include, among others, vertebrates (Blower, 1985; Hopkin & Read, 1992), slugs (Herbert, 2000), ants (Suzzoni et al., 2000), scorpions (Carrel & Britt, 2009) and a variety of beetles (Snider, 1984; Eisner et al., 1998; Brunke et al., 2009; Larsen et al., 2009). Some predators may be exclusive millipede specialists, notably among the circumtropical millipede assassin bugs (Hemiptera, Reduviidae, Ectrichodiinae), in which at least 16 species from 12 genera have been documented to feed on millipedes (Forthman & Weirauch, 2012). In Europe, some rove beetles (Staphylinidae) and the hedgehog *Erinaceus europaeus* are key predators that, although being generalists, eat large numbers of millipedes. In Portugal, Baker (1985a) showed that, among many predators that fed on *Ommatoiulus moreleti* in the laboratory, larvae and adults of the rove beetle *Ocypus olens* were particularly voracious. Julid predation by this species was observed in the field and the beetle could complete its life cycle in the laboratory when reared on a millipede-only diet. In Germany, larvae and adults of another rove beetle, *Ocypus similis*, show a marked preference for polydesmid and julid millipedes (Krooss & Schäfer, 1998). Among the vertebrates, the hedgehog eats all the large *O. moreleti* offered in the laboratory, up to 50 individuals within a few minutes (Baker, 1985a).

To what extent can predators influence population density under field conditions? In an original experiment carried out in Portugal, Baker (1985a) tethered *O. moreleti* (stadia IX and X) in the field for eight days and compared the number of survivors when millipedes were either potentially exposed to predators or protected by fine mesh bags. The results showed that, in the absence of fine mesh, the number of survivors was reduced by 37 to 74% depending on the site and the season. In spite of obvious limitations of the method, this provides a first estimate of predation pressure on large-size millipedes under natural conditions. The experiment was repeated in southern Australia, where *O. moreleti* was

introduced by the mid-20th century and became an invasive species, and interestingly, the number of survivors did not differ significantly when the julid was protected or exposed to potential predators. This is consistent with the fact that *O. moreleti* is rejected by most Australia's native predators in the laboratory (Baker, 1985a).

Predation on eggs and juveniles is presumably stronger than for adults (Hopkin & Read, 1992). The earliest stadia are not or not very mobile and, moreover, lack defensive secretions that are effective against a wide range of predators (Eisner et al., 1978). The beetle *Ocypus similis* is known to attack slug eggs and it is likely that it also attacks the eggs of its preferred millipede preys. Krooss & Schäfer (1998) have shown that prey consumption by *O. similis* is maximal from April to June, a period of high reproductive output for European polydesmids, so that predation on eggs and first-stadium juveniles may be strong in these species. High juvenile mortality in the first year of life was recorded in field populations of the julids *Julus scandinavius* (95% mortality) and *Ophyiulus pilosus* (71% mortality) in Great Britain (Blower & Miller, 1974) and also in a field population of *Glomeris balcanica* in Greece (76% mortality) (Iatrou & Stamou, 1991). Although the causes of juvenile mortality were not identified in these studies, predation may be involved.

Impacts of parasites and pathogens

Millipedes are hosts to a wide range of smaller organisms such as bacteria, fungi, protozoans, nematodes, mites and dipteran larvae (Blower, 1985; Hopkin & Read, 1992; Farfan & Klompen, 2012; Carreno et al., 2013). They also serve as intermediate hosts for cestodes and acanthocephalans that parasitize vertebrates (Vaucher, 1971; Richardson, 2006). Some of these organisms may be beneficial, in particular intestinal microorganisms (Byzov, 2006), or have no obvious effect on their host, like ectoparasitic fungi of the Laboulbeniales (Santamaria et al., 2014), but many others are more or less harmful to millipedes. This can affect the population growth rate, e.g. by decreasing fecundity in females and fertility in males, and thereby the abundance of species. Tuzet & Manier (1957) described a number of internal parasites found in *Glomeris marginata* from southern France. The gut is colonized by trichomycetes and gregarines, which do not seem to be harmful, but also by coccidians and nematodes (*Thelastoma*) that are pathogens. The coccidian *Legerella nova* causes substantial deformation of Malpighian tubules, which are invaded by clusters of cysts and grow larger than the gut diameter. Another *Legerella* parasitizes the male reproductive organs and sterilizes testis follicles (in general only one or two follicles out of 30).

Other parasites affect populations more severely. Nematomorphs of the genus *Gordius* are found in several species of julids. When Baker (1985b) looked for *Gordius* larvae in *Ommatoiulus moreleti* specimens from Portugal, the level of parasitism was highly variable depending on the season and habitat. Nematomorphs affect only populations living near streams or ponds because free-living adults require water for breeding. However, in a sample of *O. moreleti* of stadium IX and older collected at one site in late September, 24% of the females and 62% of the males were parasitized. Most of them showed reproductive abnormalities. The first pair of legs of parasitized males was not modified into hooks and

their gonopods were rudimentary. Vulvae of parasitized females were similar to those of juveniles and, more importantly, no parasitized female contained mature eggs, while 98% of unparasitized females were ovigerous.

Some dipteran insects in the genera *Eginia* (Muscidae), *Megaselia* (Phoridae) and *Pelidnoptera* (Phaeomyiidae) are parasitoids of julids. The fly *Pelidnoptera nigripennis* lays eggs on the head, the collum or the first rings and, once hatched, the larva enters the host through ventrally located soft tissues (Bailey, 1989). The larva starts feeding in the anterior region and progresses within the body to pupate. At this stage, the millipede is dead or moribund. Baker (1985b) and Bailey (1989) collected a number of *O. moreleti* parasitized by dipteran larvae at various sites near Lisbon, Portugal. Although the percentage of parasitized individuals was generally low, it could exceed 20% among individuals of stadium VIII and older collected in spring. The prevalence of parasitism increased in successive stadia, which means that larger, potentially more fecund females are the most affected.

There is some evidence that the effects of parasitism (parasites, parasitoids and pathogens) on population density are significant. While *O. moreleti* spread rapidly and reached high population densities following its introduction in southern Australia, its abundance declined markedly in some areas where the species had been established for more than 10 years (Baker, 1985c; McKillup et al., 1988). The latter authors found that a native nematode (*Rhabditis necromena*) was not detected in high-density populations of *O. moreleti*, but was present in over 80% of millipedes in populations with densities below 20 individuals m^{-2}. Experiments showed that the nematode was capable of entering and killing *O. moreleti* in the laboratory and in the field, with some dead and dying millipedes containing up to 300 nematodes. Death appears to be caused not by the parasite itself, but by pathogenic bacteria associated with it, which proliferate inside the millipede (Schulte, 1989). *Rhabditis necromena* was considered efficient enough to be a possible biological control agent.

Population outbreaks

In some millipede species, populations can explode when the above-mentioned factors are ineffective, which results in exceptionally high exponential growth rates. Extremely high levels of abundance can be reached, up to millions of individuals over a small area, and such outbreaks are often accompanied by dramatic mass migrations (Ramsey, 1966; Hopkin & Read, 1992; Sahli, 1996). The intrinsic rate of increase of a millipede in the absence of natural enemies was measured in a well-fed population of *Polydesmus angustus* reared under moderate seasonal conditions (David, 2012). The size of the female population can increase by a factor of about 348 each year, which can explain some outbreaks in annual polydesmidan species. At this rate, a small group of 10 females at the start of the breeding season can potentially grow to >3000 females the next year and >1.2 million females in two years, i.e. >2.4 million individuals including males. These figures are consistent with the outbreak reported by Palmén (1949) for the cosmopolitan *Oxidus gracilis* (Paradoxosomatidae) in Finnish greenhouses. In 1946, a single *O. gracilis* female

was seen in a frost-free greenhouse that contained imported plants; in 1947, the species' abundance increased considerably and the next year it had invaded the whole greenhouse complex. Other instances of mass occurrences reported in the literature are likely to result from the exponential growth of millipede populations in favourable environments (Ramsey, 1966; Sahli, 1996).

Ommatoiulus moreleti is an interesting case because this species, which is moderately abundant in its native range in the Iberian Peninsula (Bailey & De Mendonça, 1990), became invasive following its introduction in a new environment in Australia. The species reached high population densities and became rapidly a significant pest, entering houses in large numbers in autumn and spring (Baker, 1978). The 'enemy release hypothesis' posits that invaders that have evolved high fecundity in their native range to offset losses from predators and parasites, gain a strong advantage when introduced in a system without their natural enemies. As mentioned earlier, there appear to be far fewer millipede predators in South Australia than in Portugal, and *O. moreleti* may be a textbook case of introduced species that becomes a pest due to enemy release.

In other cases, mass occurrences of millipedes are not, strictly speaking, population outbreaks. Concentrations of adults and juveniles of several species may correspond to mass migrations in response to unfavourable weather conditions (Sahli, 1984). Concentrations of adults of only one species may correspond to swarming for reproduction. It is probably the case in the so-called 'train millipedes' of the genus *Parafontaria* (Xystodesmidae), thus named because they periodically invade railway tracks in Japan. Vast gatherings of adults are integral with their life cycles, which are quite unusual for polydesmidan millipedes. *Parafontaria laminata armigera*, for example, has an 8-year life cycle (Niijima, 1998). The species moults only once a year in August, takes seven years to develop in the soil, and adults emerge synchronously and in tremendous numbers one year before the breeding season. Mean adult abundance can exceed 300 individuals m^{-2} in some forests of central Japan (Niijima, 1998; Hashimoto et al., 2004) and, in autumn, adult millipedes swarm on the forest floor and frequently invade roads and railway tracks. This repeats every eighth year in regions inhabited by *P. laminata armigera*.

COMMUNITY ECOLOGY

Species richness in communities

Millipede species richness decreases from communities living under mild environmental conditions to those living under harsh conditions. This pattern is obvious at the global scale, since harsh biomes like tundra and deserts harbour fewer species than temperate forests and far fewer than humid tropical forests (Golovatch & Kime, 2009). Communities in temperate areas generally consist of at most a dozen species, including those occurring at very low densities, whereas the world record for millipede species richness may exceed 30 species at an Amazonian site in Brazil (Adis et al., 2002). Within biomes, however, species richness also decreases at sites where severe environmental constraints, in terms of

soil moisture, soil acidity or other abiotic factors, act as environmental filters that exclude a number of species. In temperate forests, for example, a deep layer of raw humus (also known as mor) develops at sites where the soil is rather cold, acid, sandy or waterlogged. In such environments, very few macro-invertebrate species reach high abundance, e.g. the millipede *Polyzonium germanicum* in acid mor humus under Scots pine (*Pinus sylvestris*) in the Centre of France (David, 1989). Due to the small number of species and strong dominance hierarchy, diversity indices are low and few inter-specific interactions occur in these communities driven by environmental filtering. By contrast, in stable habitats under more favourable conditions, diversity indices increase and inter-specific interactions become increasingly important. When several species utilizing common resources coexist at appreciable population densities, this raises the question of how these communities are organized.

Interactions between millipede species

Differences in resource use among coexisting millipede species have been described, in terms of food preference, activity periods, and especially microhabitats. Using stable isotope analysis, which detects differences in animal diets under natural conditions, Semenyuk & Tiunov (2011) found that trophic differentiation increased with species richness and was much more pronounced in a tropical forest harbouring 23 millipede species in Vietnam than in a more species-poor cold temperate forest in Russia. O'Neill (1967) recorded the exact physical location of seven species in maple-oak forests in Illinois and found that each species was predominant in a different microhabitat. For example, *Narceus americanus*, *Pseudopolydesmus serratus* and the euryurid *Euryurus erythropygus* were found at different depths in logs, while the cleidogonid *Cleidogona caesioannulata* and the abacionid *Abacion lactarium* were found at different depths in leaf litter. Geoffroy (1981) studied in detail the spatial distribution of two julids with broadly similar morphologies, *Cylindroiulus punctatus* and *Allajulus nitidus*, in a mixed forest in France. *Cylindroiulus punctatus* lives mainly in logs, in which it feeds and breeds in summer. *Allajulus nitidus* is a relatively subterranean species that feeds mainly on well-decomposed leaf litter. In winter, many *C. punctatus* move into the soil, but at a smaller depth than *A. nitidus*. When both species co-occur in the litter layer in spring and autumn, they tend to aggregate in monospecific groups. Thus, for much of the time, the two julids are separated spatially, whether vertically or horizontally, as in some *Cylindroiulus* of Madeira referred to above (Enghoff, 1983).

O'Neill (1967) argued that such patterns are evidence for niche segregation due to competitive interactions between co-occurring species. In this classical model of species coexistence, the community is supposed to be saturated with species and represent a state of equilibrium, in which each species is confined to its own ecological niche due to competition (Giller, 1996). However, not all available data are consistent with this theory. First, mutual exclusion is not always so drastic as suggested by O'Neill's (1967) data, even between species with apparently similar feeding habits. In Great Britain, Miller (1974) mentioned woodland sites at which populations of the closely related *Julus*

scandinavius and *Ophyiulus pilosus* were really mixed in leaf litter. Moreover, studies in which millipede communities were sampled repeatedly in different years have shown that not all communities are stable in terms of species composition and abundance distribution. In two British woods, Blower (1979) found that fairly abundant species were totally absent in subsequent years, while species that were initially absent reached appreciable population densities. In the forest of Orleans, France, David (1989) reported that, while some communities remained stable over time, substantial changes occurred in others. For example, the most abundant species at a deciduous forest site were *Polydesmus angustus* (44 individuals m^{-2}) and *Allajulus nitidus* (19 individuals m^{-2}) in a year, but *Glomeris marginata* (54 individuals m^{-2}) and *P. angustus* (20 individuals m^{-2}) in the two following years. Such changes do not support the assumption of equilibrium communities.

Non-equilibrium communities occur under changing environmental conditions and in systems in which disturbance or predation are important (Giller, 1996). Some fire events, for example, can not only reduce the overall abundance of myriapods but also disproportionately favour deep-burrowing species compared with litter-dwelling species (Saulnier & Athias-Binche, 1986). In such circumstances, the composition of post-fire communities bears little relation to competitive interactions. Clearly, there exists a gradient from equilibrium to non-equilibrium conditions and, in general, it is difficult to situate precisely millipede communities along this gradient. Comparisons between temperate and tropical communities might be useful to clarify the issue but, unfortunately, there are no data available on the stability of tropical millipede communities.

Furthermore, the assumption of competitive interactions in limited resource situations requires validation. When there are marked differences in resource use between co-occurring species, this may result from ancestral species-specific adaptations that have been conserved over evolutionary time and not from interspecific competition in contemporary communities. To reach conclusions about competitive interactions, it is necessary to test for shifts in resource use in the absence of potential competitors. For example, it would be interesting to know whether the microdistribution of *Cylindroiulus punctatus* and *Allajulus nitidus*, as reported by Geoffroy (1981), changes depending on whether they occur alone or together at different forest sites. To date, cases of interspecific competition have been documented in this way for many couples of animal species but virtually not for millipedes. Dangerfield & Telford (1996) suspected that competition for food resources could structure millipede communities in the savannah habitats of southern Africa, while admitting that tests of this hypothesis would require long-term monitoring and experimental manipulations. In coastal dune forests of South Africa, Greyling et al. (2001) found that, during the summer, the pachybolids *Centrobolus richardi* and *C. fulgidus* occur predominantly on trees and shrubs, respectively, and that during the winter, when the population density of *C. fulgidus* declines markedly, *C. richardi* goes down in the shrub layer. The authors concluded that the shift in the spatial niche of *C. richardi* could be due to a relaxation of competitive interactions for food resources or space.

Millipede-earthworm interactions

In temperate forests, most taxa of the saprophagous macrofauna (millipedes, woodlice, earthworms, gastropods) reach peak abundance and biomass at the same sites, characterized by mull-type humus, whereas their abundance, biomass and diversity are much lower at sites with moder and mor humus (Schäfer & Schauermann, 1990; David et al., 1993). A degree of spatial segregation between different ecological categories of earthworms is assumed to facilitate their coexistence (Lavelle & Spain, 2001): *epigeic* species live and feed in the litter layer; *anecic* species feed in the litter layer but live in deep, subvertical burrows in the soil; and *endogeic* species live and feed in the soil. However, as most anecic earthworms are large species that dominate the biomass of communities in mull humus, they are expected to exclude epigeic species due to interspecific competition for food (Bouché, 1978). Similar arguments were used for millipedes, most of which are epigeic species that should be excluded from soil communities dominated by large earthworm species (Kime, 1990). This is actually not the case in the field.

A partial solution to this problem was suggested by the study of saprophagous macrofauna communities in mull soils of Mediterranean oak forests on limestone (David, 1999). Earthworms and millipedes, mainly *Glomeris marginata* and *Cylindroiulus caeruleocinctus*, are extremely abundant in these forests. A distinction was made between epi-anecic earthworms such as *Lumbricus terrestris*, which consume or pull into their burrows large amounts of leaf litter, and other anecic species such as *Aporrectodea* spp. and *Scherotheca* spp., the feeding behaviour of which is far less clear. Field data showed that there were negative associations between epigeic millipedes and epi-anecic earthworms, which reached high biomass at different sites; there were however no negative associations between epigeic millipedes and the other anecic earthworms, which were found at very high biomass at the same sites (David, 1999). These observations suggest that both negative and positive interactions may occur between millipedes and earthworms, depending on the species present in communities.

Positive interactions between millipedes and earthworms may be due to ecological facilitation. In laboratory experiments, several earthworm species such as the epigeic *Lumbricus castaneus* and the endogeic *Octolasion lacteum* were shown to feed preferentially on faecal pellets of *Glomeris marginata* rather than on leaf litter (Scheu & Wolters, 1991; Bonkowski et al., 1998). It seems that leaf litter processing by millipedes facilitates earthworm feeding, which may be an example of positive interaction. Unfortunately, this has not been tested so far using anecic earthworm species.

In another experiment, Snyder et al. (2013) demonstrated the occurrence of negative interactions between the xystodesmid *Sigmoria ainsliei* from the Appalachian Mountains and the Asian invasive earthworm *Amynthas agrestis*, which were reared together or separately in the laboratory. Millipedes tended to survive longer when earthworms were absent, while earthworm fecundity was higher when millipedes were absent. As both animals feed on the same well-decomposed leaf material, these negative interactions may be indicative of exploitative competition (Snyder et al., 2013). However, separating the effect of resource use from that of interference is not easy. Mucus secreted by earthworms,

for example, can trap and even kill millipedes when they are kept together in a small volume (personal observations), which may result in interference competition while food resources are not limiting.

ROLE IN DECOMPOSITION PROCESSES

The classical view

Many ecological studies on millipedes have dealt with their role in terrestrial ecosystems as detritivores. Millipedes, like other saprophagous macroarthropods (insects, land hoppers, woodlice) have been functionally classified as 'litter transformers' (Lavelle & Spain, 2001), which consume large amounts of dead plant remains in ecosystems in which they are abundant. Their annual consumption rate, as estimated for glomerids and julids under seasonal temperate conditions, is in the order of 10-14 g (dry mass) of leaf material per g (live mass) per year (Van der Drift, 1975; David, 1987; David & Gillon, 2002). The most visible consequence of these feeding activities is the production of faecal pellets, often in large amounts, which has attracted much interest to determine whether, and how, it enhances litter decomposition.

Classically, a distinction is made between direct and indirect effects of detritivores on decomposition. Direct effects refer mainly to the assimilation of ingested food, which is ultimately mineralized into CO_2 and mineral nutrients. Mineralization is more or less rapid depending on whether food is used for maintenance and respiration (rapid mineralization) or for growth and reproduction with temporary storage in animal tissues (delayed mineralization). Indirect effects include all interactions between detritivores and microbial decomposers (bacteria and fungi), whether in faeces or in unconsumed litter. The dominant view in the soil biology literature is that the direct effects of macroarthropods on decomposition, through assimilation and respiration, are much smaller than their indirect effects on microbially driven decomposition (Lavelle & Spain, 2001). Millipedes and other macroarthropods are thought to enhance decomposition primarily by fragmenting plant litter, thereby increasing the surface area available for microbial colonization and stimulating microbial activity in their faeces. This view dates back to Van der Drift (1951), who enounced that (i) millipedes have low assimilation efficiencies and reject a great proportion of the ingested food as faeces; (ii) fresh faeces examined under a microscope contain almost unaltered litter fragments that show no evidence of chemical breakdown; (iii) litter fragmentation promotes decomposition at a later stage by enhancing microbial activity in faeces. However, a review of the data available shows that the impacts of millipedes on decomposition processes are probably more variable and complicated than in this interpretation.

Direct effects through food assimilation

Remarkably low assimilation efficiencies, often less than 10% on a dry mass basis, have been recorded in millipedes (Bocock, 1963; Van der Drift, 1975; Carcamo et al., 2000;

David & Gillon, 2002). With such low figures, their direct effects on litter decomposition are expected to be weak, even for abundant populations. However, results vary greatly among and within species and many studies have reported assimilation efficiencies above 50% (Geoffroy et al., 1987; Striganova & Prishutova, 1990; Köhler et al., 1991; Pobozsny et al., 1992). Even though some values may be overestimated due to the methods used, laboratory estimates of assimilation efficiency clearly differ by one order of magnitude, with figures below 5% and in excess of 50%.

Among many factors that may be involved in these differences, food quality is probably essential: the higher the concentration of readily assimilable nutrients such as sugars and proteins, the higher the assimilation efficiency. Microbial tissues are very easily assimilated by millipedes, with efficiency values in the 70-90% range for a variety of microorganisms (Bignell, 1989; Byzov et al., 1998), which increases the overall efficiency when microbial biomass is high in leaf litter. Therefore, the variability observed in laboratory studies may result from the use of one arbitrarily selected food in each study, either high or low quality. Natural conditions offer a wider choice in terms of litter species, degree of decomposition and microbial colonization, not to mention additional food types that can be ingested together with leaf litter. If millipedes are able to self-select the most profitable foods in the field, as many insects do (Waldbauer & Friedman, 1991), they may achieve as high assimilation efficiencies as those that are occasionally measured in laboratory studies, i.e. above 50%. This suggests that abundant populations of millipedes may have much greater direct effects on decomposition than generally assumed.

Indirect effects on decomposition through faecal pellet production

The main role of litter transformers is supposed to be litter fragmentation, which increases the surface area available for microbial colonization and stimulates microbial activity in faeces. Compared with leaf litter, fresh faeces of millipedes have a greater proportion of bacteria and a smaller proportion of fungi (Maraun & Scheu, 1996; Byzov et al., 1998). The absolute numbers of bacteria may also be greater in fresh faeces than in leaf litter (Ineson & Anderson, 1985; Byzov et al., 1998), though this is not always the case (Suzuki et al., 2013). As respiration is one measure of microbial activity in plant residues, a number of studies have compared CO_2 release from intact leaf litter and faecal pellets of millipedes at various times after egestion. Taken together, these studies provide no evidence that microbial respiration increases in millipede faeces. Maraun & Scheu (1996) found that, depending on the litter material ingested, respiration in faecal pellets of *Glomeris marginata* was only transiently stimulated (10-20 days after egestion) or not stimulated at all. In another experiment, Scheu & Wolters (1991) recorded a more prolonged stimulation of respiration in faecal pellets, but the cumulative CO_2 production from pellets was not significantly greater than that of unconsumed leaf litter after 23 weeks. Likewise, Suzuki et al. (2013) found that microbial respiration in faecal pellets of *Harpaphe haydeniana* was similar to that of leaf litter over an 8-week period.

Whether or not microbial respiration is transiently increased in faecal pellets, another key point is that no differences between pellets and leaf litter have been detected in terms

of mass loss rates. The few studies that compared mass loss in the two substrates over long time periods (up to one year) have shown that faecal pellets do not loose mass faster than unconsumed leaf litter (Nicholson et al., 1966; Webb, 1977). Other techniques, such as near-infrared spectroscopy analysis, have confirmed that the faecal pellets of *Glomeris marginata* are not more decomposable than leaf litter from which they are derived (Gillon & David, 2001).

Therefore, litter fragmentation by millipedes is not sufficient to enhance microbial decomposition significantly. This may result, at least in part, from the structure of faecal pellets in many species. By forming relatively large and compact pellets, millipedes may actually reduce the surface area available for microbial colonization (Webb, 1977), which was indirectly confirmed by the increased respiration recorded after grinding faecal material (Suzuki et al., 2013). However, the low quality of the resource is the most likely explanation for low mass loss rates in faeces. Faecal pellets of millipedes are comparatively poor in low molecular weight compounds that are readily usable by bacteria, and rich in recalcitrant compounds such as lignin (Bocock, 1963; Gillon & David, 2001; Rawlins et al., 2006). Transient stimulation of microbial respiration after egestion is probably due to small amounts of easily assimilable organic compounds left over in fresh faeces, which may vary with the type of food ingested. However, once readily available resources are exhausted in the faecal material, this prevents any prolonged bacterial activity and therefore any significant increase in mass loss rate. Millipede faeces are increasingly regarded not as microsites of intense microbial activity, but as a stabilized form of organic material (Rawlins et al., 2007).

Interactions with microorganisms in uningested litter

Interactions of millipedes with bacteria and fungi in uningested litter have been largely neglected in view of their potential importance in decomposition processes. Although large amounts of bacterial propagules are dispersed in the litter layers through the deposition of faecal pellets, the consequences for decomposition have been little studied so far (Coulis et al., 2013). Interactions with saprotrophic fungi are somewhat better understood. Owing to the size of their mouthparts, millipedes inevitably damage hyphae when ingesting leaf litter and, as a result, fungal communities are likely to be seriously affected in partially consumed and subsequently abandoned leaf remains. When the blaniulid *Blaniulus guttulatus* grazes directly on mycelium, mycelial extension is stopped beyond the point of grazing (Crowther et al., 2011a). This predation on fungi, whether by attacking dead leaves or grazing on mycelium, has complex effects for several reasons. Firstly, not all fungi are palatable and each millipede species feeds selectively on specific mycelia or plant litter colonized by specific mycelia (Taylor, 1982; Maraun et al., 2003; Crowther et al., 2011b). This greatly reduces the growth of palatable fungi relative to unpalatable species, but the impact on fungal community composition also depends on millipede community composition. Secondly, and most importantly, it has been shown that grazing by millipedes stimulates the production of extracellular enzymes by some basidiomycete fungi (e.g. *Phanerochaete velutina*), and inhibits this production in other

basidiomycetes (e.g. *Resinicium bicolor*) (Crowther et al., 2011b). These changes in the production of fungal cellulolytic and ligninolytic enzymes have repercussions on leaf litter decomposition. Therefore, millipede effects on fungal-mediated decomposition can be positive or negative, depending on the dominant animal and fungal species present, and are expected to vary between soil communities. These complex interactions with litter-decomposing fungi may partly explain why the presence of millipedes and other macroarthropods in litter-soil systems has no consistent effects on overall microbial respiration, which is either enhanced or reduced by their feeding activities (Scheu, 1993; Snyder et al., 2009).

Effects on nitrogen mineralization

Millipedes probably play a more significant role as regulators of nutrient cycling than in enhancing litter decomposition. Their feeding activities considerably increase nitrogen mineralization, i.e. the conversion of organic nitrogen present in leaf material and microorganisms into ammonium-N and/or nitrate-N (Anderson & Ineson, 1984; Kaneko, 1999; Carcamo et al., 2000). In microcosms with optimal numbers of glomerids, julids or polydesmids, levels of nitrogen mineralization can be 10 to 20 times higher than in controls. Experiments using ^{15}N-labelled leaf litter and unlabelled *Glomeris marginata*, and vice versa, have shown that this process is not a direct contribution of millipedes through excretion, as is often suggested, but results predominantly from interactions with microorganisms (Anderson & Ineson, 1984). The enhancement of nitrification by animal feeding activities is also indicative of indirect effects on nitrogen mineralization, since millipedes do not excrete nitrate (Hopkin & Read, 1992). Moreover, nitrogen release does not occur in a step-wise manner when millipedes are added or removed from leaf litter, but can take several weeks to build up or decline (Anderson & Ineson, 1984). Although the detailed mechanisms remain largely unexplained, this timing suggests that nitrogen release only starts after new microbial communities have developed in leaf litter, in response to millipede feeding activities. Considering the essential role of microfauna (protozoa, nematodes) in nitrogen mineralization processes, a possible explanation might be the activation of food chains based on large numbers of bacteria in fresh faecal pellets, which promotes the development of bacterivorous microfauna (Tajovsky et al., 1992). In turn, microfaunal activity is known to stimulate nitrogen mineralization.

Thus, litter-feeding millipedes help to transfer nitrogen and other nutrients to the soil through two distinct pathways, which function on two different time scales: (i) a relatively rapid mobilization (over days or weeks) of organic nitrogen present in the litter layers, presumably due to the stimulation of micro-food webs, which can make nitrogen directly available to plants (Anderson & Ineson, 1984); (ii) a much slower enrichment (over months or years) due to the progressive incorporation of faecal pellets into the soil, i.e. recalcitrant organic matter which is only gradually decomposed by the soil microbial biomass. As mentioned above, the conversion of litter into faeces by millipedes facilitates the feeding activities of earthworms, and this litter processing chain speeds up the process of incorporation and promotes the formation of stable organo-mineral aggregates when both groups of macrofauna co-occur in mull-type humus (Bonkowski et al., 1998).

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CHAPTER 13

DIPLOPODA — GEOGRAPHICAL DISTRIBUTION

BY

HENRIK ENGHOFF

Millipedes occur on all continents except Antarctica. Their known distribution was mapped in great detail by Shelley & Golovatch (2011) who painstakingly accumulated information on the distribution of higher taxa of millipedes, down to the level of order, and presented their findings on numerous maps. They further presented detailed accounts of distribution patterns and used these, together with extensive paleogeographic material, and taking known millipede fossils into consideration, to construct hypotheses about origin and dispersal of higher millipede taxa.

The present treatment provides a brief account of regional millipede faunas and gives examples of distribution patterns at lower taxonomic levels, including the radiations of certain millipede genera on oceanic islands.

MILLIPEDES AS PROVIDERS OF BIOGEOGRAPHICAL EVIDENCE

Most species of millipedes have very small distribution areas, i.e., the level of endemicity is high. An example from the millipede fauna of Europa, incontestably the best studied major part of the World, is provided by volume 1 of the atlas of European species (Kime & Enghoff, 2011). The atlas covers all orders except Julida and Chordeumatida and includes 492 species — roughly a third of the known European fauna. Of these, 183 are known from only one 50 × 50 km square, and 252 — more than half — are known from only 1-3 adjacent 50 × 50 km squares.

Limited distribution — endemicity — also obtains at higher taxonomic levels. For example, 10 out of the 15 families of the order Julida recognised by Enghoff (1991, 1993) are known only from western North America, eastern North America, Europe (including Macaronesia, North Africa and the Middle East), or eastern Asia. Even the largest julidan family, Julidae, is limited to temperate Eurasia (the Palaearctic region).

Millipede endemism is particularly rampant in mountains and on oceanic islands. A mountain example is provided by the endemic Afrotropical family Oxydesmidae, of

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which 21 out of the 27 species described from the Tanzanian Eastern Arc mountains are endemic to just one mountain massif (Hoffman, 1990, 1993, Table 6.1). A study of one genus (*Chaleponcus*) of another endemic Afrotropical family (Odontopygidae) in the Udzungwa Mountains of Tanzania (Enghoff, 2014) has produced 21 species, all endemic to the Udzungwas. Island faunas are treated below.

REGIONAL MILLIPEDE FAUNAS

The following summary of major millipede faunas is by no means complete. Emphasis is on larger groups of mainly larger forms. For example, several families of small Polydesmida (e.g., Fuhrmannodesmidae and Pyrgodesmidae) are very richly represented in all tropical regions.

Holarctic (Palaearctic plus Nearctic)

The Holarctic region is home to three endemic orders: Glomerida, Callipodida and Julida. All three, however, occur marginally in the Oriental region. The large family Julidae is endemic in the Palaearctic region where Glomeridae, Polydesmidae and numerous families of Chordeumatida are also dominant. The Parajulidae are endemic in the Nearctic subregion where Xystodesmidae (shared with the Palaearctic) are also abundant, and Spirobolidae — although with few species, and also shared with the (eastern) Palaearctic — constitute a further conspicuous element.

Afrotropical

Three large families are endemic to sub-Saharan Africa (excl. Madagascar): Oxydesmidae, Gomphodesmidae and Odontopygidae. Other dominant families are Paradoxosomatidae, Chelodesmidae, Pachybolidae and Spirostreptidae, the two latter families in part represented by giant species. Giant pill millipedes occur in southern Africa (Sphaerotheriidae) and Madagascar (Arthrosphaeridae). The S Gondwanan family Dalodesmidae is quite diverse in southern Africa incl. Madagascar. Madagascar further harbours species of the Holarctic + S Gondwanan order Chordeumatida.

Oriental

The large cosmopolitan family Paradoxosomatidae is incredibly diverse in the Oriental region. Harpagophoridae (shared with southern Africa and in part represented by giants) are also abundant. Of giant pill millipedes, Zephroniidae are endemic in SE Asia, and Arthrosphaeridae are shared between India and Madagascar. Rhinocricidae occur marginally in the southern Oriental region, as well as the transitional ‘Wallacea’ and the northern and eastern parts of the Australian region (plus the Neotropics).

Australian

Paradoxosomatidae are also extremely diverse and dominant here. Other characteristic families include Dalodesmidae, Procyliosomatidae (giant pill millipedes), Spirobolellidae, Cambalidae, and Julomorphidae. Chordeumatida also occur.

Neotropical

Chelodesmidae, Spirostreptidae and Rhinocricidae are dominant families. Paradoxosomatidae are less diverse, Dalodesmidae and Chordeumatida occur in the south.

GLOBAL OCCURRENCE OF MILLIPEDE ORDERS

The tendency of higher millipede taxa to have limited distributions is obvious even at ordinal level. Table 13.1 shows the occurrence of the 16 currently recognised millipede orders in each of the six major, non-Antarctic biogeographical regions. Only 3 orders occur in all 6 regions (3 further orders marginally do so). In contrast 30 out of 33 insect orders,[1]) and 4 out of 5 centipede orders,[2]) occur in all 6 biogeographical regions. Each millipede order on average occurs in 3.9 regions if marginal occurrences are excluded.[3])

South East Asia stands out as the most diverse region for millipedes, with all 16 orders recorded (Shelley & Golovatch, 2011).

EXAMPLES OF HISTORICAL BIOGEOGRAPHICAL PATTERNS

Phylogeny-based (cladistic) interpretation of millipede distributions got an early start by Kraus (1966) who analyzed family-level relationships within what is now known as suborder Spirostreptidea of order Spirostreptida. Based on a classical Hennigian analysis, Kraus found the endemic Afrotropical superfamily Odontopygoidea to be the basal clade within Spirostreptidea, sister to a dichomy between Spirostreptidae (Neotropical + Afrotropical) and Harpagophoridae (Afrotropical + Oriental). Kraus argued that the current distribution of Spirostreptidae and Harpagophoridae can be seen as a consequence of the fragmentation of Gondwana and the overlap between both families in Africa as 'secondary'. As to the Odontopygoidea, he argued that their occurrence in Africa is secondary and that they must have arisen as a northern vicariance 'partner' to Spirostreptidae + Harpagophoridae. This,

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[1]) 'Non-cosmopolitic' insect orders are Mantophasmatodea (Afrotropical), Grylloblattodea (Palaearctic and Nearctic) and Raphidioptera (Palaearctic and Nearctic).

[2]) Craterostigmomorpha occur only in the Australian region.

[3]) This comparison is, however, not 'exact science' since taxonomic ranks cannot directly be compared between groups.

TABLE 13.1

The occurrence of the 16 currently recognised millipede orders in the six non-Antarctic biogeographical regions. — AFR: Afrotropical, AUS: Australian, NEA: Nearctic, NEO: Neotropical, ORI: Oriental, PAL: Palaeartic. Marginal occurrences in parentheses. Names of supraordinal taxa after Enghoff (1984). No. of species per order after Sierwald & Bond (2007), except Polyxenida after Nguyen Duy-Jacquemin & Geoffroy (2003) and Siphonocryptida after Enghoff (2010)

	PAL	NEA	NEO	AFR	ORI	AUS	No. of regions	No. of species
Subclass PENICILLATA								
Polyxenida	+	+	+	+	+	+	6	140
Infraclass PENTAZONIA								
Glomeridesmida			+		+		2	28
Sphaerotheriida				+	+	+	3	330
Glomerida	+	+			+		3	271
Subterclass COLOBOGNATHA								
Platydesmida	+	+	+		+		4	69
Siphonophorida		+	+	+	+	+	5	116
Siphonocryptida	+				+		2	6
Polyzoniida	+	+	+	+	+	+	6	127
Superorder NEMATOPHORA								
Stemmiulida			+	+	+	+	4	124
Callipodida	+	+			(+)		2 (+1)	201
Chordeumatida	+	+	+	(+)	+	+	5 (+1)	1237
Superorder MEROCHETA								
Polydesmida	+	+	+	+	+	+	6	5156
Superorder JULIFORMIA								
Spirobolida	(+)	+	+	+	+	+	5 (+1)	1248
Spirostreptida	(+)	+	+	+	+	+	5 (+1)	1894
Julida	+	+			(+)		2 (+1)	1321
Position uncertain								
Siphoniulida			+		+		2	2

although fully logical, however requires extinction of Odontopygoidea in the Holarctic region and thus appears little likely, but an alternative explanation should await a renewed phylogenetic analysis of Spirostreptida.

The Julida is one of the (almost) exclusively Holarctic millipede orders. A biogeographical analysis of Julida was made by Enghoff (1993), based on previous phylogenetic analyses. One of Enghoff's results concerns the sister genera *Nemasoma* and *Orinisobates* (fam. Nemasomatidae) the species of which are allopatrically and disjunctly distribution across the Holarctic region (Fig. 13.1). Based on the cladogram of Enghoff (1985) the author concluded that the North American species of *Orinisobates* most likely derive from a trans-Beringian immigrant from East Asia, the opposite direction of dispersal to that of most amphi-Beringian millipede groups according to Golovatch (1979).

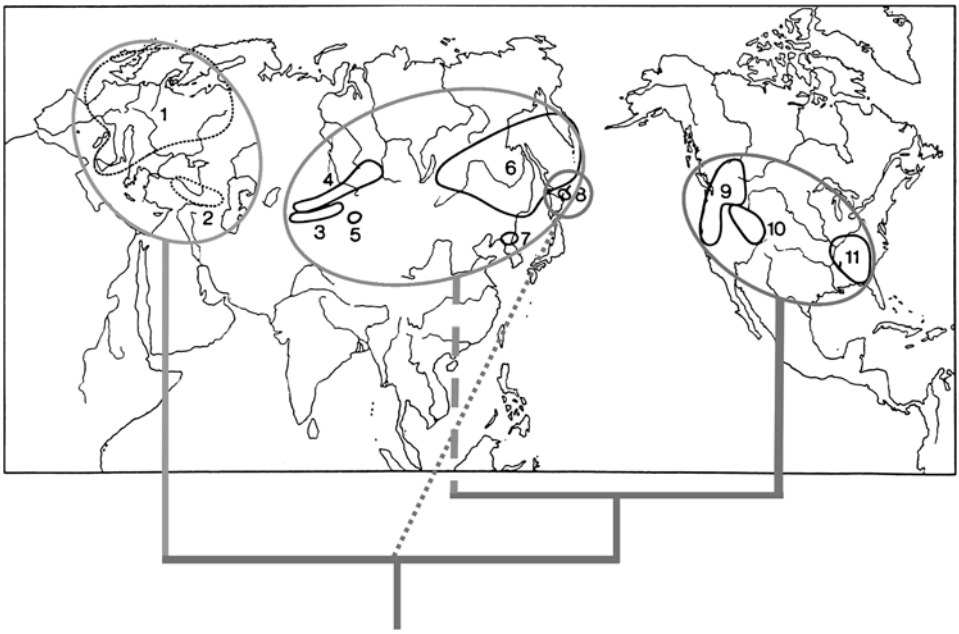

Fig. 13.1. Relationships and distribution of species in the genera *Nemasoma* and *Orinisobates*. Species 1-2: *Nemasoma*, 3-11: *Orinisobates*. The position of species 8 (*Orinisobates soror* Enghoff, 1985) is uncertain, and monophyly of the group of the remaining Asian *Orinisobates* species (3-7) is not supported. Based on Enghoff (1993, Figs. 4, 9).

Wesener & VandenSpiegel (2009) made a modern cladistic analysis of the families of order Sphaerotheriida (giant pill-millipedes). The resulting cladogram is shown on Fig. 13.2, superimposed on a distribution map. Interestingly, Indian giant pill millipedes are most closely related to Malagasy ones, whereas the SE Asian family Zephroniidae is not particularly closely related to the Indian forms.

INSULAR SPECIES SWARMS

In line with millipedes' strong tendency to narrow endemicity, isolated islands very often harbor endemic species. In some cases, an island or archipelago is home to numerous species within a single genus. Examples of such insular species swarms in millipedes include the genus *Eumastigonus* (Spirostreptida, fam. Cambalidae) on New Zealand (Korsós & Johns, 2009), *Nannolene* (also Cambalidae) on the Hawaii islands (Howarth & Mull, 1992) and *Spirobolellus* (Spirobolida, fam. Spirobolellidae) on New Caledonia (Carl, 1926), see also Shelley and Golovatch (2011).

By far the best studied swarms are those of the Atlantic Macaronesian archipalagos, notably the Canary Islands and Madeira. Enghoff (2011) summarized earlier studies on the largest two of those which are in the genera *Cylindroiulus* and *Dolichoiulus* (both

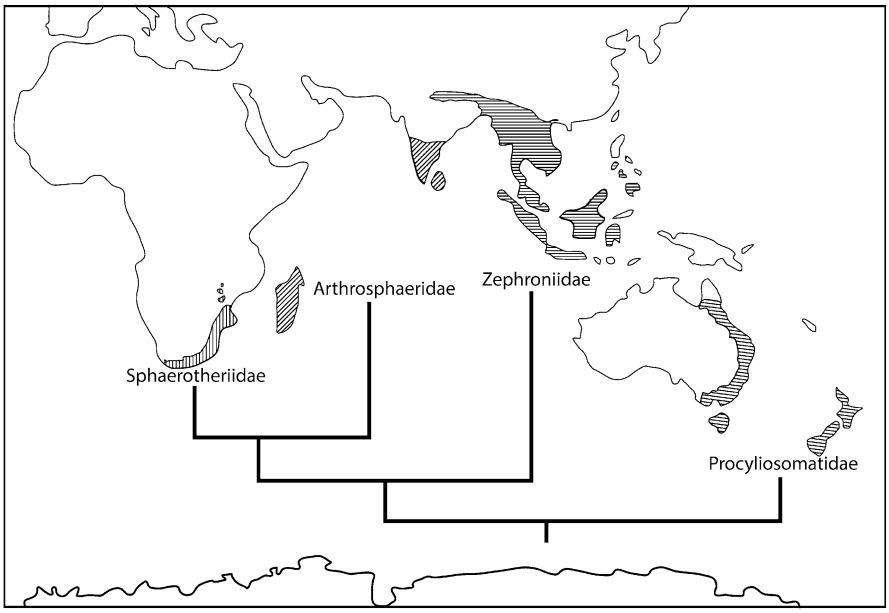

Fig. 13.2. Relationships and distribution of families of giant pill-millipedes, order Sphaerotheriida. From Wesener & VandenSpiegel (2009).

Julida, fam. Julidae). Reboleira & Enghoff (2014) and Enghoff (2012) provided updated information on both genera.

Besides ∼100 species from the European continent, North Africa and east to Central Asia, *Cylindroiulus* has 30 endemic species on the island of Madeira, a further endemic on the satellite island Porto Santo and a 32nd endemic on the Canary Islands. Preliminary phylogenetic studies suggest that this swarm is monophyletic and that the species from Porto Santo and the Canary Islands stem from immigrants from Madeira. There is considerable morphological diversity within the swarm, and most species specialize in a particular (micro)habitat type. Co-existing species mostly are of different sizes.

Dolichoiulus has 50 endemic species on the Canary islands, two further endemics on Madeira and Porto Santo, still another endemic on the tiny Salvage islands situated between Madeira and the Canaries, and three additional endemics on the Cape Verde Islands further south. With one exception, the Canarian species are each confined to one of the seven main islands. Monophyly of the Macaronesian *Dolichoiulus* swarm cannot be ascertained on the available evidence but a preliminary molecular phylogenetic study by I. Sanmartín suggests that the "root" of the Canarian radiation is on the island of Tenerife which has the highest number of species (20). Canarian *Dolichoiulus* species are morphologically as diverse as the Madeiran *Cylindroiulus* and also are habitat specialists, but there is less co-existence at the micro-habitat level.

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CHAPTER 14

DIPLOPODA — FOSSILS

BY

GREGORY D. EDGECOMBE

Because of their calcified exoskeletons, chilognathan millipedes are comparatively well represented in the fossil record for myriapods as a whole, although even the non-biomineralized Penicillata are known from as early as the Cretaceous. Millipedes include probably the earliest terrestrial animal fossils, their body fossil record extending to the mid Silurian (Wilson & Anderson, 2004) and their trace fossil record evidently going back to the Late Ordovician (Wilson, 2006a).

Recent reviews of the diplopod fossil record (Shear, 1997; Shear & Edgecombe, 2010) adopted a stratigraphic ordering, considering the fossils according to the geological period of their occurrence, because a preponderance of the fossil taxa is of uncertain affinities to extant orders. The present account attempts to summarize fossil millipedes systematically, using extinct orders classified as *incertae sedis* where relationships to extant taxa are unclear. Emphasis is placed on Palaeozoic and Mesozoic taxa because Cenozoic fossils (e.g., Eocene Baltic amber) can generally be assigned to extant families.

PENICILLATA: POLYXENIDA

The fossil record of polyxenids is confined to amber, with a record dating back to the Late Cretaceous (earliest Cenomanian, ca. 99 My) and all known fossils can be assigned to the extant families Polyxenidae or Synxenidae. Cretaceous amber of Lebanon is the source of species that underpin two monotypic genera, *Electroxenus jezzinensis* and *Libanoxenus hammanaensis* (Nguyen Duy-Jacquemin & Azar, 2004). Both are members of the family Polyxenidae and are closely related to extant genera. A slightly younger Cretaceous amber species from France belongs to the extant genus *Phryssonotus* (Nguyen Duy-Jacquemin & Azar, 2004). A species from the Late Cretaceous amber of Burma originally described as *Polyxenus burmiticus* Cockerell, 1917, has been reassigned to *Phryssonotus* (Rasnitsyn & Golovatch, 2004).

Eocene Baltic amber has provided five named species of *Polyxenus* and one of *Phryssonotus* (Koch & Berendt, 1854), all in need of restudy.

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Kraus & Brauckmann (2003) and Kraus (2005) proposed that the Silurian-Devonian eoarthropleurids and Carboniferous-Permian arthropleurids were most closely related to penicillates and could be classified as Penicillata (s. lat.). This was based on such shared derived characters as trilobed syntergites, legs bearing movable ventral spines with a terminal bristle, and a "Y skeleton" that extends through the coxa, trochanter and prefemur of the walking legs. This intriguing hypothesis would vastly extend the morphological and stratigraphic range of Penicillata compared to their amber and extant diversity.

DIPLOPODA *INCERTAE SEDIS*: "ARTHROPLEURIDEANS"

One of the most contentious issues in fossil millipede systematics is the monophyly and phylogenetic position of three Palaeozoic orders (Arthropleurida, Eoarthropleurida and Microdecemplicida) sometimes grouped as Arthropleuridea (Shear, 1997; Wilson & Shear, 2000). Arthropleurids and eoarthropleurids had been considered a separate, extinct class of myriapods, though likely allied to Dignatha, until Wilson & Shear (2000) gave evidence for diagnostic features of Diplopoda, notably diplosegmentation. This point has proven contentious in the case of arthropleurids, for which diplopody appears to be unlikely in the case of large individuals (Schneider et al., 2010). Nonetheless, characters of millipedes that are present in arthropleurideans as a whole are an apodous collum segment and paired anal valves (Kraus & Brauckmann, 2003). Wilson & Shear (2000) considered all three orders to form the sister taxon of Chilognatha, although monophyly of Arthropleuridea was supported by only one reliable character, a lateral embayment in the expanded collum segment. Other characters cited as possible synapomorphies of Arthropleuridea (Shear, 1997), such as the parategal lobes being separated from the axis by sutures and a unique system of sclerotized plates (K, B and rosette plates sensu Rolfe & Ingham, 1967) buttressing the leg (Fig. 14.2B) are restricted to Arthropleurida and Eoarthropleurida but are not shared by Microdecemplicida. As noted above, Kraus & Brauckmann (2003) disputed the case for arthropleuridean monophyly and instead placed Arthropleurida and Eoarthropleurida in the Penicillata (s. lat.), while allowing that Microdecemplicida could be sister group to Chilognatha (see Microdecemplicida below).

Eoarthropleurida

Eoarthropleura was originally described as the first Devonian representative of Arthropleurida, based on *E. devonica* Størmer, 1976, from the Emsian of Germany (Størmer, 1976). The morphology of *Eoarthropleura* became better understood with the discovery of various body parts from Devonian rocks in New York and Québec, as well as remains macerated from Upper Silurian shales in the UK (Shear & Selden, 1995). A distinct order, Eoarthropleurida, was formalized based on a few differences from *Arthropleura*/Arthropleurida, specifically the absence of rosette plates (but presence of B and K plates) and tergites lacking nodules or spines (Shear & Selden, 1995). Given that these absences are almost certainly symplesiomorphies, the distinction between the two orders is dubious. The legs of *Eoarthropleura* remain undescribed, but have evidently been identified in the Late Devonian (Shear, 1997).

Arthropleurida

Arthropleurida is composed of about a dozen species in the genus *Arthropleura* Jordan & Meyer, 1854, ranging from the Lower Carboniferous (lower Visean; Rössler & Schneider, 1997) to Lower Permian (Rössler et al., 2012), but the majority deriving from Upper Carboniferous deposits. Their distribution is predominantly Euramerican (Hannibal, 1997a). Body fossil associations have prevalently come from coal swamps, but a comprehensive review of *Diplichnites cuithensis* trackways attributed to *Arthropleura* (Briggs et al., 1979) showed that these animals also inhabited open alluvial environments (Schneider et al., 2010). At an inferred length of two metres for the largest specimens (Hahn et al., 1986), *Arthropleura* includes the largest terrestrial arthropods of all time.

The morphology of *Arthropleura* was comprehensively reviewed by Kraus & Brauckmann (2003) and Kraus (2005). This included documentation of the head, demonstrating that formerly identified "heads" (e.g., Briggs & Almond, 1994; Brauckmann et al., 1997) are actually the collum. The trunk consists of some 29 trilobed paratergal plates, all bearing rather irregular large and small tubercles. Aquatic or semiaquatic habits were favoured by Kraus & Brauckmann (2003) on the basis of a supposed "paper-thin" cuticle. However, Kraus (2005) later suggested that all known *Arthropleura* fossils were of exuvia, which could account for the thin cuticle (also endorsed by Schneider et al., 2010). Shear & Edgecombe (2010) noted that it is difficult to reconcile the subaerial trackways produced by *Arthropleura* with haemolymph pressure alone providing support, and Schneider et al. (2010) regarded the cuticle to have been well sclerotized in order to produce impressions in sand up to 3 cm deep.

Microdecemplicida

Microdecemplex rolfei Wilson & Shear, 2000, is known from partly articulated material macerated from Devonian (Givetian-Frasnian) rocks in New York State. The animals were less than 5 mm long, the trunk having eight diplotergites (the ratio of sternites to tergites confirms strict diplosegmentation) and an anal cone. Although the mandibles, tentorium and gnathochilarium can be readily interpreted by correspondences to extant millipedes (Wilson & Shear, 2000), external morphology of the head is peculiar, apparently involving flared lateral processes that terminate in a foramen, and a pair of short, evidently unsegmented appendages that display little obvious similarity to antennae. *Microdecemplex* had seven-segmented legs (the coxa resembling the B plate of *Arthropleura* and *Eoarthropleura*), and exhibits a form of sexual dimorphism in the posterior limb pair that has been compared to the telopods of Pentazonia (Shear, 1997; Wilson & Shear, 2000).

Irrespective of the controversy over the status of Arthropleuridea and the relationships of arthropleurids, some degree of consensus has been reached over affinities of *Microdecemplex* to Chilognatha (Wilson & Shear, 2000; Kraus & Brauckmann, 2003). *Microdecemplex* shares a tridentate labrum with Chilognatha and a more precise diplopody than is observed in Penicillata or Arthropleurida.

CHILOGNATHA *INCERTAE SEDIS*: ZOSTEROGRAMMIDA

The order Zosterogrammida (Wilson, 2005b) is composed of a single family (Zosterogrammidae) that ranges from the mid Silurian to the Upper Carboniferous. It members are *Casiogrammus ichthyeros* Wilson, 2005, from the Wenlock of Scotland, and the Carboniferous *Zosterogrammus stichostethus* Wilson, 2005 from Illinois, USA, and *Purkynia lata* Fritsch, 1899, from the Czech Republic. They are united by their very broad tergites with terrace lines oriented the same way on different regions. Zosterogrammida cannot be placed with any more precision other than to say that it is very likely Chilognatha, although the broad tergites and medial division of the sternites (known only for *Zosterogrammus*) suggest a relationship to Pentazonia in particular (Wilson, 2005b).

PENTAZONIA

Pentazonia was represented in the Upper Carboniferous by members of the extinct order Amynilyspedida. Membership in Oniscomorpha is supported by the small collum and laterally expanded, shield-like second tergite, and a rounded pygidium. Species of the best-known genus, *Amynilyspes* Scudder, 1882, have been described from North America (Mazon Creek, Illinois, USA) and continental Europe (Nýřany, Czech Republic; Saarland, Germany; Montceau-les-Mines, France) (Fritsch, 1899; Hannibal & Feldman, 1981; Racheboeuf et al., 2004). They were characterized by the presence of 14 arched tergites, a relatively small terminal tergite, long, paired spines on the metatergites, and an apparent lack of ozopores. Three additional genera of Amynilyspedida (*Archiscudderia* Fritsch, 1899, *Glomeropsis* Fritsch, 1899, and *Palaeosphaeridium* Peach, 1914) lacked spines.

An inference that the extant oniscomorph order Sphaerotheriida was also present in the Upper Carboniferous is based on two specimens from Mazon Creek with an apparent count of 13 tergites, as opposed to 15 in the amynilyspedids (Hannibal & Feldman, 1981). This material has, however, alternatively been suggested to possibly belong to *Palaeosphaeridium* and thus may be amynilyspedid (Racheboeuf et al., 2004).

Pentazonians from Cenozoic ambers are assigned to extant genera. These include *Glomeris denticulata* Menge, 1854, from the Eocene Baltic amber and *Glomeridesmus* sp. from Miocene amber in the Dominican Republic (Santiago-Blay & Poinar, 1992).

HELMINTHOMORPHA *INCERTAE SEDIS*: ARCHIPOLYPODA

Archipolypoda was originally conceived (Peach, 1882; Scudder, 1882) as a group to contain Palaeozoic millipedes that were thought to differ from extant Diplopoda in such respects as having alternating haplosegments rather than true diplosegments and longitudinally divided sternites. The group was subsequently excluded from Diplopoda (Hoffman, 1969). The alleged differences from millipedes were subsequently found to be mistaken (Wilson, 2006a), various taxa were reassigned, and Archipolypoda has

been rediagnosed as a likely monophyletic group (superorder Archipolypoda) that is confidently assigned to Diplopoda. It ranges from mid Silurian to Late Carboniferous (Wilson & Anderson, 2004) and comprises four orders: Cowiedesmida, Archidesmida, Palaeosomatida and Euphoberiida. They differ from other helminthomorphs in having a pair of free sternites per diplopleurotergite, these sternites bearing a pair of paramedian pores, often with valve-like closures (Wilson & Anderson, 2004, Fig. 11; Figs. 14.1B, 14.2E herein) that probably contained eversible sacs (Shear, 1997; Wilson, 2006a). Where known, modified legs evidently occur on trunk segment 8 rather than segment 7 as in males of extant Helminthomorpha. The ocellarium, where known, consists of many ocelli arranged in multiple rows, and the pleurotergites bear paranota.

Cowiedesmida

Cowiedesmus eroticopodus Wilson & Anderson, 2004, from the mid Silurian of Scotland, is the only species in its order (Cowiedesmida). Modified legs appear to arise from segment eight in *C. eroticopodus* (Fig. 14.1A) and, assuming that these are gonopods

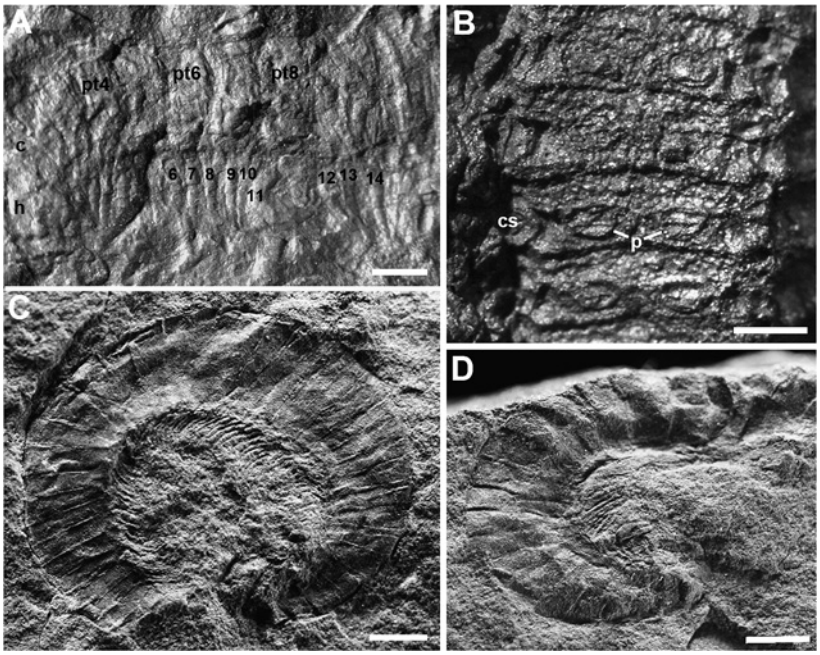

Fig. 14.1. Silurian and Devonian Archipolypoda (**A-B**) and Juliformia (**C-D**). **A** *Cowiedesmus eroticopodus* Wilson & Anderson, 2004, Silurian, Scotland (AM F64845a), head (**h**), collum (**c**) and anterior part of trunk, showing modified leg pair 11 associated with paratergite (**pt**) 8. **B** *Palaeodesmus tuberculatus* (Brade-Birks, 1923), Lower Devonian, Scotland (NHM In. 23803), sternites with bivalved paramedian pores (**p**) and coxal sockets (**cs**). **C-D** *Gaspestria genselorum* Wilson, 2006, Lower Devonian, New Brunswick (**C**) and Québec (**D**), Canada. **C** NBMG D10091, anterior towards right. **D** NBMG 10089, anterior part of trunk. Scale bars: 2.5 mm except **B**, 2 mm.

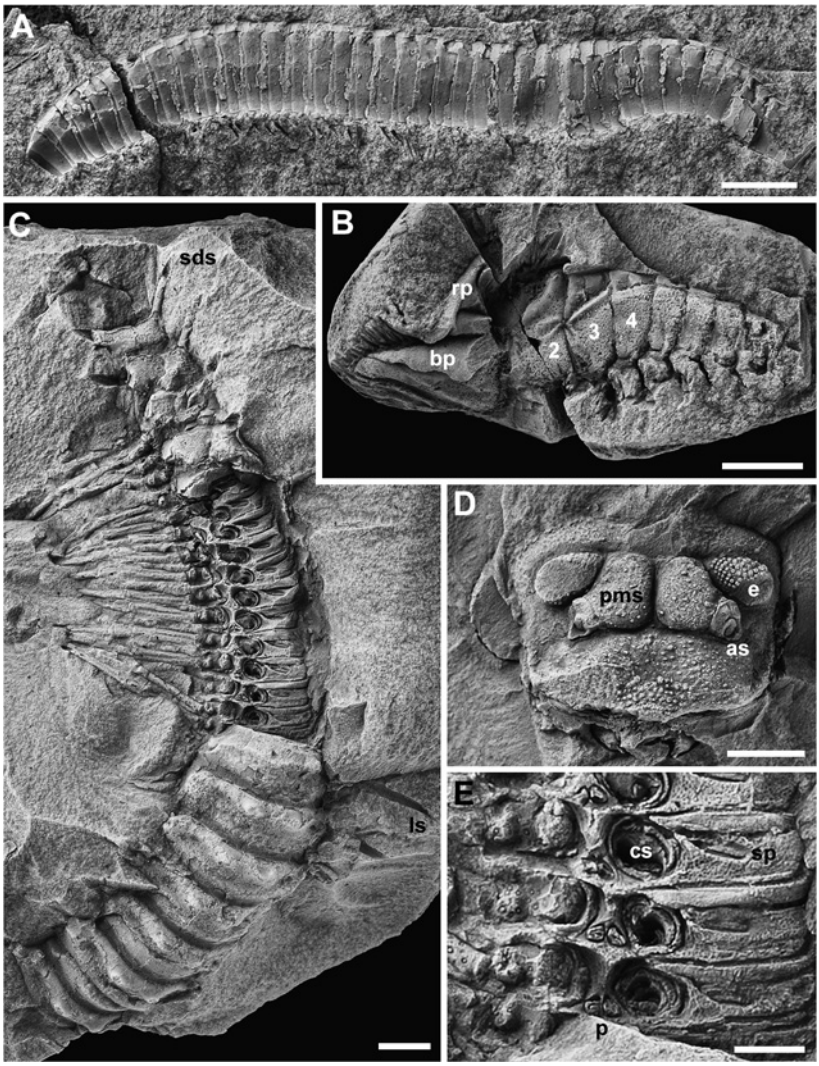

Fig. 14.2. Diplopoda from Upper Carboniferous Coal Measures, UK. **A** *Xyloiulus platti* (Baldwin, 1911) (NHM In. 13738). **B** *Arthropleura* sp., leg (NHM In. 139646), showing B plate (**bp**) and rosette plate (**rp**), podomeres 2-4 numbered. **C-E** *Myriacantherpestes ferox* (Salter, 1863) (Archipolypoda: Euphoberiida). **C, E** Trunk (NHM In. 1050), showing paired subdorsal spines (**sds**) and lateral (**ls**) tergal spines, sternites with coxal sockets (**cs**), paramedian pores (**p**) and spiracles (**sp**). **D** head (NHM In. 1532) in anterior view, showing antennal sockets (**as**), eyes (**e**) and paramedian swellings (**pms**). Scale bars: 5 mm except **E**, 2 mm.

homologous with those in Helminthomorpha, they provide a constraint on the likely time of origin of indirect sperm transfer. The precise segmental placement of these probable gonopods is, however, somewhat contentious because counts of legs anterior to the modified ones may be disputed (Shear & Edgecombe, 2010). Wilson & Anderson

(2004) favoured the modification of the posterior pair of legs of segment 8 (leg pair 11), a condition not seen in any extant millipede order, but evidently shared with at least some other Archipolypoda (see Archidesmida below).

Archidesmida

Like their Silurian relatives, Devonian archipolypodans are restricted geographically to Euramerica. *Archidesmus macnicoli* Peach, 1892, from the Lower Devonian (Lochkovian) of Scotland, was redescribed by Wilson & Anderson (2004) and typifies the Order Archidesmida. As with the Silurian *Cowiedesmus eroticopodus*, *A. macnicoli* has a modified leg pair that can be presumed to be a gonopod, considered by Wilson & Anderson (2004) to be leg pair 10, the anterior pair of segment eight. *Archidesmus* Peach, 1882 and *Cowiedesmus* Wilson & Anderson, 2004 have similar modifications of their presumed gonopods, in both cases being a clavate, multisegmented structure with one to a few hooked spines at the tip, suggesting that these are features of the archipolypodan groundpattern.

A new family of Late Devonian age, Zanclodesmidae, was established by Wilson et al. (2005) based on two species of flat-backed millipedes from Pennsylvania (*Orsadesmus rubecollis* Wilson, Daeschler & Desbiens, 2005) and Québec (*Zanclodesmus willetti* Wilson, Daeschler & Desbiens, 2005). Placement in Archidesmida is based on the similarity in paired lobes on the metazonite to those of *Archidesmus*, since diagnostic sternal characters cannot be seen in the fossils, nor any modified anterior legs that may have been present. The ocellarium of *Zanclodesmus* is large and is composed of numerous ocelli, as in other Archipolypoda (see Euphoberiida below).

Archidesmida evidently survived into the Late Carboniferous, as witnessed by *Anaxeodesmus diambonotusi* Wilson, 2005 from the British Coal Measures (Wilson, 2005b). Although differing from other Archipolypoda in its lack of spines or tuberculation, this species shares characters of sternal morphology with *Archidesmus* and *Palaeodesmus* (e.g., sternites divided into anterior and posterior areas by a transverse groove; coxal sockets widely spaced) that are suggestive of affinities.

Palaeosomatida

The Order Palaeosomatida was erected by Hannibal & Krzemínski (2005) for the monotypic family Palaeosomatidae, consisting of species of *Palaeosoma* Jackson et al., 1919. These occur in Upper Carboniferous (Westphalian) sediments of the British Coal Measures and from the Lower Carboniferous (Namurian) of Poland. Modified limbs are unknown in the existing material, but the sternal morphology (two broad, free sternites per diplosegment; ventral sacs present) are indicative of membership in Archipolypoda. *Palaeosoma* includes large millipedes with 38 or more segments that lack tergal spines, and with ozopores situated on dorsal bosses on the metazonites (Hannibal & Krzemínski, 2005).

Euphoberiida

The morphologically best understood archipolypodans belong to the Order Euphoberiida, composed of three genera from the Upper Carboniferous of Euramerica: *Euphoberia* Meek & Worthen, 1868, *Acantherpestes* Meek & Worthen, 1868, and *Myriacantherpestes* Burke, 1979. They reach a length of up 30 cm, the number of body segments exceeding 20 but not surpassing 60 (Hannibal, 1997b). Their most distinctive character is two sets of long, paired branched spines (a subdorsal pair and a lateral pair) on each metatergite (Fig. 14.2C). Much of the anatomical knowledge of the group derives from revisionary work on *Myriacantherpestes* by Burke (1973, 1979). The heads of euphoberiids differ from those of extant millipedes in their large, possibly compound eyes (Kraus, 1974, Fig. 1; Hannibal, 1997b, Fig. 13.5), small antennae that arose from paramedian swellings (Fig. 14.2D), and the labrum lacking teeth (Burke, 1973). Kraus (1974) interpreted the spiracles of *Acantherpestes* as as being located on pleurites but these elongate openings are clearly lateral to the coxae, in the sternites (Fig. 14.2E). As suspected by Kraus (1974), euphoberiids lack free pleurites and, like other Archipolypoda, instead have free sternites (Wilson & Anderson, 2004, Figs. 6.6, 11). Ozopores are situated at the base of the lateral spine pair. The legs have been interpreted as composed of six podomeres, with an especially elongated femur (Burke, 1979). At least some euphoberiids had modified legs about midlength in the body, although these are inferred to have functioned as claspers rather than as gonopods (Hannibal, 1995). The posterior end of the body features a ventral scale, preanal ring, and pair of anal valves (Wilson, 2005a, Text-fig. 3). Juvenile specimens are observed to have shorter tergal spines and fewer ocelli than adults, and have a series of 6-7 apodous trunk segments posteriorly (Wilson, 2006b).

Archipolypoda incertae sedis

Two Scottish archipolypodans from Silurian rocks of the same age as *Cowiedesmus*, *Albadesmus almondi* Wilson & Anderson, 2004, and *Pneumodesmus newmani* Wilson & Anderson, 2004, are not assigned to orders. *P. newmani* is noteworthy for demonstrating the earliest preserved spiracles in millipedes.

Palaeodesmus tuberculaus (Brade-Birks, 1923), from the Pragian of Scotland (Fig. 14.1B), was originally described as a kampecarid (a group of Dignatha of uncertain position but possibly Diplopoda; Shear & Edgecombe, 2010) but was subsequently recognized to be a millipede (Almond, 1985). It was later assigned to a monotypic genus and shown to belong to Archipolypoda based especially on its sternites bearing a pair of paramedian pores with valves (Wilson & Anderson, 2004). One of the few named taxa of Early Carboniferous millipedes, *Anthracodesmus macconochiei* Peach, 1899, from the Viséan of Scotland, was also re-examined by Wilson & Anderson (2004), although little could be determined about its affinities except that it is probably Archipolypoda based on the apparent lateral (rather than ventral) articulation of its legs.

COLOBOGNATHA

Siphonophorida

The family Siphonophoridae is represented in Miocene Dominican amber by an unnamed species of *Siphonocybe* (Shear, 1981) and by three species of *Siphonophora*, two of which were formally named and described (Santiago-Blay & Poinar, 1992). A citation of Siphonophoridae in the Late Cretaceous (Cenomanian) amber of Burma (Grimaldi et al., 2002) has not yet been documented.

Polyzoniida

Material from Baltic amber (Eocene) has been assigned to the genus *Polyzonium* (Bachofen-Echt, 1942). Although listed in open nomenclature (Weitschat & Wichard, 1998, pl. 23b), an identity as the extant species *Polyzonium germanicum* has been suggested (Hoffman, 1969). A siphonotid from Dominican amber (Miocene) is assigned to *Siphonotus* sp. (Santiago-Blay & Poinar, 1992).

PLEUROJULIDA

The order Pleurojulida was named and diagnosed by Wilson & Hannibal (2005) for two genera, *Pleurojulus* Fritsch, 1899, and *Isojulus* Fritsch, 1899, from Upper Carboniferous sediments of Nýřany in the Czech Republic and at Mazon Creek, Illinois, USA. Pleuroiulidans reached a length of up to 10 cm, and were semicircular in cross-section. Affinities were tentatively suggested between this group and Colobognatha, with which they share free pleurites and sternites (presumed plesiomorphies of Chilognatha as a whole fide Enghoff, 1990). Although the position of the gonopore has not been determined with precision and only one specimen of *Pleurojulus* has been identified as a possible mature male, the gonopod appears to have been situated on either leg pair 10 alone or leg pairs 9 and 10, as in Colobognatha (Wilson & Hannibal, 2005). Sierwald & Bond (2007) depicted uncertainty in the placement of Pleurojulida, placing them in an unresolved trichotomy with Colobognatha and Eugnatha (i.e., Helminthomorpha *incertae sedis*).

JULIFORMIA

Juliformia incertae sedis*: Xyloiulidea*

Hoffman (1963) re-examined specimens of *Xyloiulus* Cook, 1895, and two other Carboniferous genera newly named by him, *Nyranius* and *Plagiascetus*, and later transferred to their own families (Hoffman, 1969). He considered all three (united in a Suborder Xyloiulidea based on a distinctive ornamentation of fine longitudinal grooves and ridges on the pleurotergites) to be possible spirobolidans. The comparison to Spirobolida stressed

"general body form and proportions, and by the lengths and appearances of the legs" (Hoffman, 1963: 168), i.e., rather imprecise characters, and the possible gonopod of *Plagiascetus lateralis* Hoffman, 1963, was identified as spirostreptid-like rather than spirobolid. The superfamily was then thought to be confined to the Upper Carboniferous of Euramerica.

Wilson (2006a) maintained Xyloiuloidea as a superfamily but regarded it to be of uncertain ordinal assignment within Juliformia. Lower Devonian (Emsian) material from Québec and New Brunswick, Canada, that had been reported and compared to Xylioulidea by Shear et al. (1996) but not formally named was formalized as *Gaspestria genselorum* Wilson, 2006 (Fig. 14.1C, D). An even earlier record of Juliformia is provided by *Sigmastria dilata* Wilson, 2006, from the Lochkovian of Scotland. Neither Devonian genus includes much more evidence for systematic placement than a julimorph body plan and diplopleurotergal striations considered as diagnostic for xyloiulideans. These specimens are noteworthy for displaying the first known ozopores, the earliest evidence in millipedes and in all animals of a chemical defense (Wilson, 2006a).

Tomiulus angulatus Dzik, 1981 from the Triassic of Siberia was interpreted by Dzik (1981) as a xyloiulidean, but the taxonomic placement is based only on a striate ornament and has been viewed as suspect (Shear et al., 2009).

Julida

Cenozoic fossils of Julida include members of Blaniulidae, Julidae and Parajulidae (Miner, 1926; Hoffman, 1969), the oldest of which occur in Eocene Baltic amber.

Spirobolida

Possibly the earliest record of Spirobolida is an unnamed species from the Late Carboniferous of New Mexico documented by Hannibal et al. (2004). A few Mesozoic fossils have been assigned to the order, such as the Cretaceous *Gobiulus* Dzik, 1975. In the case of *Gobiulus*, membership in the family Spirobolidae was endorsed by Shelley & Floyd (2014), who classified it in the (now North American) subfamily Floridobolinae and tribe Tylobolini and noted the possibility that it could even be synonymous with the extant genus *Tylobolus*.

MEROCHAETA: POLYDESMIDA

The known fossil record of Polydesmida is confined to the Cenozoic. Families known from amber fossils include Chelodesmidae (Dominican amber: Santiago-Blay & Poinar, 1992; Mexican amber: Riquelme et al., 2014b), Platyrhacidae (Mexican amber: Riquelme et al., 2014b), Polydesmidae (Baltic amber: Hoffman, 1969; Weitschat & Wichard, 1998), and Pyrgodesmidae (Dominican amber: Shear, 1981; Santiago-Blay & Poinar, 1992).

NEMATOPHORA

Hannibaliulus wilsonae Shear, Selden & Gall, 2009, from the Early Triassic of Grès à Voltzia, France, has cylindrical segments composed of diplopleurotergites with a midline suture, and free sternites. In combination with the large eyepatches and the trunk segment count (ca. 43-44 segments), these characters suggest membership in Nematophora (Shear et al., 2009). Comparison with Callipodida is reasonable but has not been upheld with diagnostic apomorphies.

Stemmiulida

A stemmiulid from the Miocene amber of Chiapas, Mexico was described as an extinct genus, *Parastemmiulus* Riquelme et al., 2014a, distinguished from extant genera by the number of ocelli. The only other fossil of the order is an unnamed, generically-unassigned species from the coeval Dominican amber (Santiago-Blay & Poinar, 1992).

Chordeumatida

A few species from Baltic amber have been referred to the extant craspedomsomatid genera *Atractosoma* (Bachofen-Echt, 1942) and *Craspedosoma* (Koch & Berendt, 1854), but none have been subjected to a modern description.

HELMINTHOMORPHA *INCERTAE SEDIS*: HEXACONTASOMATIDAE

Hexacontasoma Hannibal, 2000, was described as the sole member of a new family of Helminthomorpha and left unassigned to an order. Its type, *H. carinatum* Hannibal, 2000, is known from two specimens from the Upper Carboniferous at Mazon Creek, Illinois, USA. The trunk is composed of some 60 segments with prominent paranotae commencing from ca. segment 5. Comparisons were made with Callipodida and Cambalidea (Spirostreptida), the latter especially based on longitudinal ridges on the metazonites (Hannibal, 2000), but too many taxonomically important characters are missing to allow a reliable ordinal placement.

UNASSIGNED CHILOGNATHA

Some poorly known fossil diplopods contribute little to systematic knowledge but are noteworthy as rare representatives from particular geographic regions or parts of the geological time scale, and are recorded here for completeness. For example, *Decorotergum warrenae* Jell, 1983, was formalized for two poorly preserved specimens from the Early Jurassic of Queensland, Australia. This taxon was compared to both Amynilyspedida (not otherwise known later than the Carboniferous) and Polydesmida (Jell, 1983) but neither is especially compelling.

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CHAPTER 15

DIPLOPODA — PHYLOGENETIC RELATIONSHIPS

BY

GREGORY D. EDGECOMBE

Diplopoda has received much more attention from the perspective of classification than it has from the perspective of phylogeny. Although it is of course possible to convey the information content of a classification, i.e., the structure of groups within groups, as a tree diagram (see, e.g., Sierwald & Bond, 2007, Fig. 4, for millipede classification of Hoffman, 1980; Shear & Edgecombe, 2010, Fig. 4, for classification of Shelley, 2003), it need be appreciated that the intent of the classification may not have been strictly phylogenetic. Classifications may reflect groupings of convenience based on easily recognized characters or may contain non-monophyletic groups diagnosed by shared primitive characters or the absence of characters of other groups.

The following account summarizes the existing body of work on the inter-relationships of extant millipede orders based on morphological characters, molecular sequences, or combinations of both kinds of data. Proposed apomorphic characters that underpin the currently endorsed phylogenetic scheme for Diplopoda (Fig. 15.1) are then catalogued. The monophyly of various orders has been defended by explicitly identified autapomorphic characters (e.g., Enghoff, 1981 for Julida; Wesener & VandenSpiegel, 2009 for Sphaerotheriida) and putative autapomorphies for most orders have been listed by Sierwald & Bond (2007, Appendix 1). Phylogenetic analyses conducted for subgroups within some orders, mostly Julida and Polydesmida, were reviewed by Enghoff (2000). Despite the relatively few phylogenetic analyses undertaken for Diplopoda, the correspondence between groups in the latest trees produced using morphological (Blanke & Wesener, 2014) and molecular (Miyazawa et al., 2014) data, and their congruence with the traditional (and current) classification of Diplopoda (Chapter 16) is noteworthy.

MORPHOLOGICAL PHYLOGENIES

Explicit phylogenetic analysis of Diplopoda using Hennig's methods was first undertaken by Kraus (1966) for inferring the relationships of Spirostreptidea. This was followed

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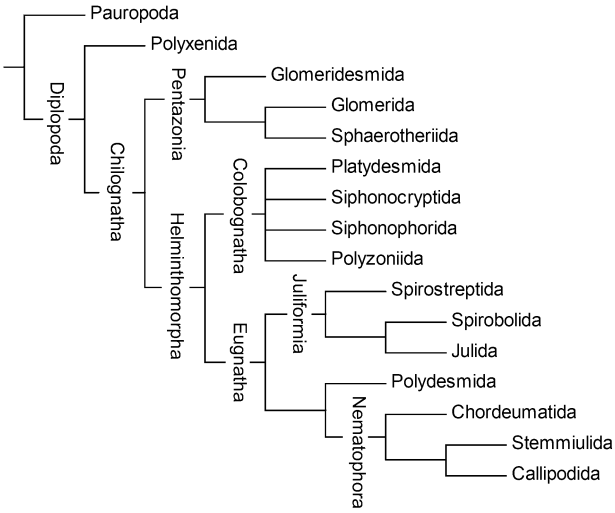

Fig. 15.1. Phylogenetic relationships between orders of Diplopoda based on morphological characters (Blanke & Wesener, 2014). The position of Siphoniulida within Helminthomorpha is uncertain (Sierwald et al., 2003) and the order is not depicted here.

up by cladistic analyses of Enghoff (1981, 1984) for the order Julida and for Diplopoda as a whole, respectively. These were constructed by hand, using Hennigian argumentation applied to morphological characters using inferred ordinal-level groundplans. The Enghoff (1984) cladogram defended the monophyly of numerous clades that had been proposed by taxonomists over the preceding century, such as Chilognatha, Pentazonia, Helminthomorpha, Colobognatha, Eugnatha, Nematophora and Juliformia. This character set was later refined to infer the likely groundplan characters of Chilognatha (Enghoff, 1990). Within Eugnatha, Enghoff et al. (1993) subsequently proposed a resolution for three clades that had previously been an unresolved trichotomy: Merochaeta [Polydesmida] were grouped with Juliformia to the exclusion of Nematophora based on the former two groups sharing the tergites, pleurites and sternites of each diplosegment being fused as complete body rings. This putative clade is colloquially known as "ring-forming" millipedes.

Sierwald et al. (2003) converted Enghoff's (1984) non-numerical character analysis into a matrix and then modified the codings of various characters, resulting in 34 characters coded as groundpatterns for 15 diplopod orders. Analysis without the order Siphoniulida produced a cladogram topology largely the same as that of Enghoff (1984). In contrast to Enghoff et al. (1993), Polydesmida grouped with Nematophora rather than with Juliformia: this was based on two proposed synapomorphies (abrupt male gonopod development, and the male gonopore opening through the coxa of leg 2). The first of these characters was critically discussed by Enghoff (1984), who noted conditions within Julida that rendered the distinction between "abrupt" and "gradual" character states unclear. The position of the male gonopore opening has been noted to need re-evaluation (Blanke & Wesener, 2014, their character 49), and the states for some orders coded by Sierwald et al. (2003) and

followed by Blanke & Wesener (2014) have been subject to alternative interpretations (Enghoff & Golovatch, 1995). An additional character for the polydesmid-nematophoran group is the shared presence of spinnerets (Shear, 2008). Adding Siphoniuliuda to the matrix introduced considerable ambiguity, the strict consensus (Sierwald et al., 2003, Fig. 2) no longer resolving Eugnatha or Nematophora. A new version of the Sierwald et al. (2003) morphological matrix was combined with molecular data for three nuclear protein-coding genes (data from Regier et al., 2005) in a Bayesian analysis by Sierwald & Bond (2007). Results are discussed below in "Molecular phylogenetics".

A morphological cladistic analysis of millipede orders by Blanke & Wesener (2014), again coded as inferred groundplans, drew on 64 characters. Many of these were sourced from early 20th century investigations by Silvestri, Attems and Verhoeff. The most parsimonious cladograms reflect groupings used in the classification of Verhoeff (1932), most of the high-level clades also being those depicted in Enghoff's (1984) phylogeny. These include Chilognatha, Pentazonia, Helminthomorpha, Colobognatha, Eugnatha, Nematophora and Juliformia. Apomorphic characters for these groups are listed below.

MOLECULAR PHYLOGENETICS

The first molecular studies to include exemplars of most orders of millipedes were investigations of myriapod phylogeny using two (Regier & Shultz, 2001, data for 11 diplopod orders) or three nuclear protein-encoding genes (Regier et al., 2005, data for 14 diplopod orders). Both analyses found that the monophyly of ordinal groups could consistently be supported, but relationships between orders were for the most part weakly supported. The more densely sampled, character-rich analysis (Regier et al., 2005) found at least moderate support for monophyly of Pentazonia, Helminthomorpha and Colobognatha, but nodes that conflicted with some traditional groups (e.g., Eugnatha, Nematophora, sometimes Chilognatha) received weak support, and some morphological groupings (e.g., Juliformia) were contradicted.

Combining the Regier et al. (2005) sequences from three loci with ordinal-level groundplan codings of morphology (Sierwald & Bond, 2007) yielded a Bayesian tree that supported the monophyly of all orders represented by more than a single species (as found for the molecules in isolation). It also supported monophyly of Chilognatha, Pentazonia, Helminthomorpha, Colobognatha and Juliformia. Siphoniulida (represented only by morphology) and Stemmiulida were resolved basally in Helminithomorpha, the latter contradicting the monophyly of Nematophora. The position of Polydesmida was arguably the most controversial result, this order grouping with Colobognatha rather than either with other "ring-formers" (Juliformia) or with Nematophora. In contrast, a clade of "ring-formers" was defended in analyses of 18S and 28S rRNA by Cong et al. (2009), although bootstrap support at the node uniting Polydesmida and Juliformia was only 67% and too few other millipede orders were sampled to provide a severe test.

Brewer et al. (2013) sequenced three mitochondrial genomes from millipedes and analyzed these together with mitogenomic data from other arthropods. Data were only avail-

able for five diplopod orders and, apart from monophyly of Juliformia, were incongruent with other data sources. The phylogeny depicted Juliformia + Callipodida and Polydesmida + Platydesmida, thus rejecting Eugnatha.

Maximum likelihood and Bayesian analyses of three nuclear protein-encoding genes for exemplars of 11 diplopod orders by Miyazawa et al. (2014) retrieved a tree that is basically congruent with the morphological scheme in Fig. 15.1. Chilognatha, Pentazonia, Helminthomorpha, Colobognatha, Eugnatha, and Juliformia were all monophyletic, though in some cases with only moderate bootstrap support. Other relationships included Polydesmida + Chordeumatida (the latter the only sampled nematophoran order) to the exclusion of Juliformia.

Molecular work on millipede phylogeny has until very recently been based on conventional Sanger sequencing of PCR products using targeted primers. The first analysis of millipede relationships using the vastly larger gene sampling provided by Next Generation sequencing of transcriptomes was done by Brewer & Bond (2013). Their analysis used 221 nuclear coding genes for nine species of Diplopoda representing the orders Glomeridesmida, Polyzoniida, Platydesmida, Polydesmida, Stemmiulida, Spirostreptida, Callipodida and Chordeumatida. Although the authors stressed "fundamental" differences from existing classifications, the phylogeny retrieved mostly conventional groups, such as Helminthomorpha, Eugnatha and Colobognatha. The main difference was that Stemmiulida grouped with Juliformia, and these collectively with Polydesmida, rather than uniting with the Callipodida and Chordeumatida. This result therefore disputes the homology of spinnerets in stemmiulids and the other two orders of Nematophora.

APOMORPHIC CHARACTERS SUPPORTING MAJOR MILLIPEDE CLADES

The most recent and character-rich morphological cladistic analysis of diplopod interordinal relationships is that of Blanke & Wesener (2014). Characters listed below are from that work and cited as "BW#", with cross-reference to earlier analyses by Enghoff (1984) and Sierwald et al. (2003).

Chilognatha

Monophyly of Chilognatha to the exclusion of Penicillata is defended by the following apomorphic characters:

Trichobothria absent on head [BW8]
Female first stigmatic plate fused with coxa of first leg pair [BW21]
Wide tracheal pouches [BW25]
Cuticle calcified [BW38]
Ventral intersegmental trunk tendons absent [BW40]
Male actively transfers sperm into female genital opening [BW53]

An additional character, formulated as "several muscles lost" (Enghoff, 1984, character 30) or "certain muscles absent" (Blanke & Wesener, 2014, character 41), requires more exact definition. Enghoff (1984, character 26) also listed each diplosegment with a pair of defense glands as an autapomorphy of Chilognatha, but this forced multiple losses, and an alternative coding of lateral and unpaired, mid-dorsal defense glands as non-homologous has been advocated (Blanke & Wesener, 2014, characters 57 and 58).

Monophyly of Chilognatha has rarely been opposed. Some analyses of nuclear protein coding genes by Regier et al. (2005) found weak support for an unconventional grouping of Penicillata with Pentazonia, but others retrieved Chilognatha.

Pentazonia

Monophyly of the three orders of Pentazonia (Glomerida, Glomeridesmida and Sphero-theriida) was defended by Enghoff (1984) and Sierwald et al. (2003) based on two autapomorphies, the last pair of legs transformed into copulatory organs (telopods), and sternites divided in midline. Both of these were instead reinterpreted as symplesiomorphies by Regier et al. (2005), the former because putative telopods were identified in the non-pentazonian fossil *Microdecemplex* (Wilson & Shear, 2000), and the latter based on a reinterpretation of the supposed sternites as leg bases (corroborated by Wesener et al., 2014).

Unambiguous autapomorphies of Pentazonia in the cladogram of Blanke & Wesener (2014) are as follow:

Lamellae linguales of gnathochilarium fused [BW12]
Basal article and gnathal lobe of mandible with a syndetic joint, lacking ball-and-socket-articulations (modified following Chapter 3) [BW14]
Stigmatic plate (= "sternite" of most former studies) divided [BW19]
N-shaped intestine, bent twice [BW43]
Posterior male leg pair telopods with inner horns [BW48]

An additional character cited as apomorphic for Pentazonia is anastomozing tracheae [BW24], but this was optimized with the state in Penicillata coded as unknown. Available data for Penicillata indicate tracheal anastomoses in at least species of *Lophoproctus* (Hilken, 1998), rendering the status of this character as a pentazonian autapomorphy ambiguous.

With respect to the interrelationships of the three pentazonian orders, monophyly of the pill millipedes (Glomerida and Sphaerotheriida) to the exclusion of Glomeridesmida is consistent with their taxonomic grouping as Oniscomorpha, as well as with the recognition that glomeridesmids possess many plesiomorphies that may be retained from the ancestral chilognathan (Enghoff, 1990). Apomorphies of Oniscomorpha fide Blanke & Wesener (2014) are:

Collum much smaller than following tergites [BW31]
Second tergite much larger than following tergites [BW32]
Coxal pouches lacking on legs [BW35]

The only molecular studies to include all three orders of Pentazonia are the three- gene analysis of Regier et al. (2005) and the same dataset combined with morphological data

by Sierwald & Bond (2007). These yielded an unanticipated grouping of Glomeridesmida and Glomerida to the exclusion of Sphaerotheriida, i.e., conflict with Oniscomorpha.

Helminthomorpha

Blanke & Wesener (2014) optimized the following characters as apomorphies of Helminthomorpha:

Muscle attachments at posterior margin of head [BW2]
First and second stigmatic plates lacking tracheae, for muscle attachment only [BW22]
Tracheae arising in a cluster ('Büschel') [BW23]
More than 21 body rings [BW34]
Lateral defence glands [BW57]

As noted above, helminthomorph monophyly was defended (partly using the same characters) in previous morphological analyses (Enghoff, 1984; Sierwald et al., 2003), and has been a consistent and usually strongly supported result of molecular analysis as well (Regier et al., 2005; Brewer & Bond, 2013; Miyazawa et al., 2014). Some additional characters, e.g., short, undivided stigmatic plates [BW20], are helminthomorph apomorphies under particular optimisations.

Colobognatha

The concept of Colobognatha as a group united by reduced mouthparts dates to traditional classifications (Attems, 1926; Verhoeff, 1928). Hoffman (1980) did not employ Colobognatha in his diplopod classification, speculating that its supporting characters could be convergent and are in fact variable (Platydesmida having relatively "normal" mandibles and gnathochilarium compared to most Siphonophorida and Polyzoniida). However, no rival sister groups have been proposed for any subgroup of Colobognatha, and monophyly has consistently been defended in phylogenetic analyses (Enghoff, 1984; Sierwald et al., 2003; Sierwald & Bond, 2007). Characters listed by Blanke & Wesener (2014) as apomorphic are:

Gnathochilarium without palps [BW11]
Mandibular basal article(s) elongate, slender plates [BW15]
Mandibular gnathal lobe with reduced and distorted pectinate lamellae [BW17]
Tenth leg pair in adult males a functional gonopod [BW47]
First post-embryonic stage with four leg pairs [BW50]
Egg protection by adults curling around eggs [BW52]

As noted above, monophyly of Colobognatha also found molecular support from three nuclear protein coding genes (Miyazawa et al., 2014), with a strongly supported clade composed of (Polyzoniida (Platydesmida + Siphonophorida)) resolved as sister group of Eugnatha. Siphonocryptida have not yet been sampled molecularly. The interrelationships between the four orders of Colobognatha were depicted as unresolved by Blanke & Wesener (2014).

Eugnatha

Although discarded by Hoffman (1980) in his classification, monophyly of Eugnatha has been defended in all morphological cladistic analyses of Diplopoda. Unambiguous autapomorphies fide Blanke & Wesener (2014) are:

Labrum bearing three teeth [BW3]
Mandible with two articulated basal articles [BW13]
Pleurites fused to tergites (= pleurotergites) [BW30]
Eighth leg of adult males a functional gonopod [BW45]

The significance of the subdivision of the mandibular base into two basal articles (cardo and stipes) remains questionable because this subdivision is apparently shared by some colobognathans (see Chapter 3). The last two of these characters were likewise optimized by Sierwald et al. (2003) for Eugnatha. Recent molecular analyses based on targeted sequencing (Miyazawa et al., 2014) or transcriptomes (Brewer & Bond, 2013) are also compatible with monophyletic Eugnatha.

Nematophora

The nominate character of Nematophora, preanal spinnerets, had long been considered synapomorphic for its three orders (Stemmiulida, Callipodida and Chordeumatida) (Enghoff, 1984; Sierwald et al., 2003). Its shared presence in Polydesmida (Shear, 2008) has alternatively been cited as synapomorphic for a clade composed of that order together with Nematophora (Blanke & Wesener, 2014, character 42). Under that scheme, autapomorphies of Nematophora are as follow:

Molar cusps in mandible [BW18]
Tracheal pouch with a muscle ('Kreuzungsmuskel' of Attems, 1926) connecting lateral arm with opposite coxa [BW28]
Dorsal suture dividing tergites [BW37]

Transcriptomic data support the union of Callipodida and Chordeumatida (= Coelochaeta Hoffman) (Brewer & Bond, 2013) but do not find Stemmiulida to be their closest relative. Character state reconstruction on the tree of Brewer & Bond (2013) suggested that spinnerets may have been ancestral for Eugnatha as a whole and lost in Juliformia rather than being apomorphic for Nematophora. In contrast, some morphological characters unite Stemmiulida with Callipodida to the exclusion of Chordeumatida, contradicting Coelochaeta: these are an antennal trochanter, and the tarsus divided by a suture but with a continuous tarsal pad (Blanke & Wesener, 2010, characters 10 and 36).

An alternative proposal that challenges the monophyly of Nematophora was advanced by Shear et al. (2003), in which a group composed of (Callipodida (Polydesmida + Stemmiulida)) but not Chordeumatida was based on the shared presence of a cannula, an articulated movable process arising from the gonopod coxa. This character was not used in the analysis by Blanke & Wesener (2014).

Juliformia

Monophyly of Juliformia is a consistent finding of morphological cladistic analyses, but has been supported by different characters depending on whether its sister group was thought to be Polydesmida (Enghoff et al., 1993) or Polydesmida + Nematophora (Sierwald et al., 2003; Blanke & Wesener, 2014). Under the latter scheme, apomorphies are:

Collum enlarged, covering posterior part of head and part of tergite 2 [BW31]
Spermatozoa with a pseudoperforatorium (sensu Baccetti et al., 1979) [BW54]
Defence fluids with benzoquinones [BW61]

Some morphological studies have treated relationships between the three juliformian orders as unresolved (Enghoff et al., 1993), whereas others have united Julida and Spirobolida based on the 8th leg in adult males bearing an accessory gonopod (Sierwald et al., 2003; Blanke & Wesener, 2014). Nuclear ribosomal genes (Cong et al., 2009) and mitochondrial gene rearrangements and amino acid sequences (Woo et al., 2007) instead suggest that Spirobolida and Spirostreptida are sister groups to the exclusion of Julida (Cong et al., 2009), whereas the third possibility (Julida and Spirostreptida as sister groups) was supported by three nuclear protein-coding genes (Miyazawa et al., 2014). Juliform ordinal relationships are, accordingly, an open question.

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CHAPTER 16

DIPLOPODA — TAXONOMIC OVERVIEW

BY

HENRIK ENGHOFF, SERGEI GOLOVATCH, MEGAN SHORT,
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There is no widely accepted consensus about the classification of Diplopoda. The following account basically follows the arrangement by Shear (2011), deviations from this are specified. All currently recognized families are mentioned, and more or less exact numbers of known genera and species in each family are given, as well as the known geographical distribution.

With more than 1800 recognized genera (1868 according to Shear, 2011) mentioning and characterizing them all would require a volume in itself. In the following treatment, which is exhaustive down to the families, all genera are mentioned only for some, mainly smaller orders, whereas only a selection of genera are mentioned for the large orders Polydesmida, Chordeumatida, Julida and Spirostreptida. Likewise, the amount of morphological detail varies greatly between orders, and this chapter cannot in general be used as an identification manual. For those genera which are listed, the (approximate) number of known species and the geographical distribution are given, and as a rule the name of at least one species per listed genus is included. Information on habits is included to a limited extent, e.g., if the members of the family/genus are cavernicolous.

Only Recent taxa are treated here. For fossils see Chapter 14.

Class DIPLOPODA de Blainville in Gervais, 1844

[HENRIK ENGHOFF]

Terrestrial mandibulate and tracheate arthropods with adult body size 1.4-350 mm. Cuticle rarely soft and covered by modified setae (Polyxenida), usually calcified, forming an inflexible, rarely flexible (Glomeridesmida and Polyzoniida), exoskeleton. Body consisting of head, trunk and telson. Head rarely with (Polyxenida), usually without trichobothria. Labrum rarely free (Polyxenida) mostly fused to clypeus, with one (Pentazonia) or three (Eugnatha) teeth. Ommatidia usually present, few or many (up to 100

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per eye), but some orders (Glomeridesmida, Platydesmida, Siphonophorida, Polydesmida) and families entirely blind, and ommatidia lost in many subterranean species. Organ of Tömösváry present as a small pit, rarely larger (Glomeridesmida, Glomerida), sometimes absent (Colobognatha, Stemmiulida, Juliformia). Antennae with six, seven or eight antennomeres, with or without (Polyxenida only) an apical disc carrying generally four, in a few genera more, apical cones. Various sensilla, including sensilla basiconica, usually present on antennomeres, especially dorsally at fifth and sixth (or sixth and seventh in those with eight antennomeres). Epipharynx loosely attached (Pentazonia) or fixed to head capsule (Helminthomorpha). Mandible with one or two (Eugnatha) basal articles and a gnathal lobe. Gnathochilarium variable, order specific, but always consisting of a single, variably subdivided, unpaired plate. Palps of gnathochilarium usually short. Trunk with 9-192 diplosegments (referred to as segments), 11-375 leg pairs. Diplosegments consisting of tergite and (fused or associated) two pleurites, four stigmatic plates, two sternites and two pairs of legs. Sternites, stigmatic plates, pleurites and tergites ranging from free to forming a completely fused ring with barely visible sutures. First segment (collum) legless (except Spirobolida), lacking ventral elements. Anterior segments 2-4 (Spirobolida: 2-5) each with one associated leg pair. Legs consisting of six (coxa, prefemur, femur, postfemur, tibia, tarsus), rarely seven (coxa, trochanter, prefemur, femur, postfemur, tibia, tarsus) or eight (coxa, trochanter, prefemur, femur, postfemur, tibia, tarsus 1, tarsus 2) podomeres. Coxal pores present or absent. Gonopores opening directly through second coxae, or through a pouch just behind leg pair 2, rarely (Stemmiulida) anteriorly of leg pair 3.

Mainly terrestrial decomposers, only a handful of species secondarily adapted to an aquatic lifestyle. Very few species semi-carnivorous (some Callipodida, few Chordeumatida). Many troglobionts in almost every order.

Development by anamorphosis, juveniles hatching with 3, rarely 4 (Colobognatha) exceptionally (*Pachyiulus* spp.) more than 20 leg pairs.

16 orders with 140 families and more than 11 000 species. Numerous species still awaiting assignment to currently valid families and genera are not listed below.

Subclass PENICILLATA Latreille, 1831

[MEGAN SHORT]

Order Polyxenida Verhoeff, 1934

Body length usually 1.5-4 mm, more rarely up to 6 mm. Cuticle soft, not calcified. Head covered in rows of trichomes with large number anteriorly and one or more rows posteriorly on the vertex. Posterior margin of head with 3 + 3 trichobothria. Labrum flexible. Ommatidia often present (11 or less in clusters each side), but absent in Lophoproctidae and in a small number of species in Polyxenidae. Organ of Tömösváry a small, round, circular pit located posterior to the antennal base each side. Antennae with eight segments, lacking a disc. Antennomere 8 with four apical sensory cones,

antennomeres 6 and 7 each with one coeloconic sensillum and a varying number of basiconic sensilla, often with one large setiform sensillum in association. Mandible consisting of basal joint and gnathal lobe. Gnathal lobe composed of three parts: comb-lobe at apex with one row of branched teeth and several rows of comb teeth, intermediate plate which may have an intermediate lobe, sensilla and fimbriate lamella, and the proximal plate with molar plate consisting of serrate limbs, smooth limbs arranged as a comb, granulated zone, a row of molar processes and scattered salivary ostioles. In some there is a submolar process and molar tuft proximally. Gnathochilarium with central pair of palps which may extend into outer palps. Palps covered in sensilla which may be simple, biarticulate or pseudoarticulate. Adult trunk with 9-11 segments excluding telson and 11-17 pairs of legs. Tergites, pleurites and sternites free and undivided. Tracheae with openings in front of the proximal edge of coxae. Each tergite with varying number and pattern of trichomes, with rosettes of trichomes laterally and most commonly one or more transverse rows of trichomes in posterior half of tergites, except for collum. Pleurites associated with segments 2-11, each with dense tuft of trichomes. First tergite (collum) reduced in size, with trichomes not restricted to the posterior and with modified pleurites referred to as lateral protuberances containing a small number of trichomes (commonly three to seven), forward facing. Tergal and pleural trichomes commonly serrate. Trichomes associated with telson comprise a large number of elongate trichomes of two types: hooked with barbs down the stem, and long barbate. The caudal trichomes are shed as a defensive mechanism with replacement occurring via moulting. Females shed caudal trichomes to create a nest to protect eggs and hatchlings. Legs consisting of a variable number of podomeres. First leg with six (lacking trochanter, only one tarsus), second with seven (lacking trochanter), all following with eight podomeres: coxa, trochanter, prefemur, femur, postfemur, tibia, tarsus 1, tarsus 2. Tarsus 2 with claw which commonly has an anterior and posterior process, a lamellate process and an anterior spinous process. Last two pairs of legs in Synxenidae with six podomeres only (lacking coxa and trochanter) and claws replaced with hairy pads. Chaetotaxy of podomeres highly variable. Coxal pores in males varying in number from zero to six pairs, excreting fine threads (and most likely pheromones) on which they deposit their spermatophores. Paired sexual openings located behind and attached to second coxae. Penes more pointed in shape and sometimes shorter than vulvae.

Sperm transfer indirect, males deposit spermatophores. Development anamorphic, first juveniles hatching with three pair of legs. Two species are known to reproduce at least in part parthenogenetically.

Widely distributed on all continents except Antarctica. Ca. 148 species.

Superfamily POLYXENOIDEA Lucas, 1840. — Trichomes associated with telson comprise two dense bundles of elongated trichomes, with a small number in a distinctive medial position dorsal to the caudal bundle(s), referred to as ornamental trichomes. Hooked trichomes may also have barbs along the stem and one to seven proximally facing hooks at the distal end.

Family POLYXENIDAE Lucas, 1840. — 1.2-4.2 mm body length without caudal bundle. 10 tergites plus telson and 13 pairs of legs. Mostly with eyes and pigmented, two to six pairs of coxal pores on leg pairs 6-11 in males. Gnathochilarium with outer palps, leg buds external. 22 genera, ca. 96 species.

Subfamily POLYXENINAE Lucas, 1840. — Tarsus 2 with long spine. Sensilla of the gnathochilarium mostly cylindrical with a conical apex. Telson with two widely separated bundles of trichomes, with a fan-shaped arrangement of long barbate ornamental trichomes inserted dorsally in a tight triangular central area between the bundles. Hooked caudal trichomes with a curved apex forming one to four apical forks, barbs along the stem. Three genera.

Polyxenus Latreille, 1802/1803. — Two transverse rows of trichomes on tergites. Zero to 10 ommatidia each side, most commonly five or six. At least 26 species, worldwide distribution. *Polyxenus lagurus* (Linnaeus, 1758) is widespread in Europe, also occurring in North America and Melbourne, Australia where it is thought to have been introduced. This species has both parthenogenetic and sexually reproducing populations.

Propolyxenus Silvestri, 1948. — Three or more transverse rows of trichomes on tergites. Five or six ommatidia each side. Seven species (incl. *P. forsteri* Condé, 1951, New Zealand and Southern Australia including Tasmania). Other species in Australia, Argentina, South Africa, Italy, Turkey, Rhodes, Greece, Israel. *P. squamatus* Nguyen Duy-Jacquemin, Uys & Geoffroy, 2011. *P. crassisetosus* Marquet & Condé, 1950 has been excluded as it is morphologically distinct, and requires revision.

Typhloxenus Condé, 1954. — No ommatidia. Two species. *T. mirificus* Condé, 1954 (Natal), *T. modestus* Condé, 1959 (South Africa).

Subfamily MONOGRAPHINAE Condé, 2008. — Commonly eight ommatidia each side. Telson with caudal bundles of trichomes closely aligned giving the appearance of a single bundle (hence the prefix 'mono'), and with a linear arrangement of ornamental trichomes inserted anterior to the caudal bundle. The shorter ornamental trichomes are symmetrical around the midline and each side comprises three to fifteen short trichomes in one or two rows, a tight bundle of three to eight long barbate trichomes (most commonly three, arranged in a triangle), and one long thin trichome internal to each bundle. The caudal bundle commonly contains both long barbate trichomes and hooked trichomes which have barbs along the stem and one to seven proximally facing hooks along the stem at the distal end. In some species only adult females possess hooked trichomes. Coxal pores on leg pairs 8 and 9 in male. Median palps of gnathochilarium each with 20-23 cylindrical sensilla, outer palps present. Most commonly antennomere 6 has three basiconic sensilla and antennomere 7 has two basiconic sensilla, with sensilla arranged transversely with a conical sensillum posteriorly and a setiform sensillum more anteriorly. Nine genera.

Anopsxenus Condé & Jacquemin, 1963. — Lacks pigment and ommatidia. Two species, incl. *A. caboverdus* Nguyen Duy-Jacquemin, 1996 from Santiago, Cape Verde Islands; another species from India.

Eudigraphis Silvestri, 1948. — Four species, incl. *E. sinensis* Ishii & Liang, 1990, from China. *E. takakuwai nigricans* (Miyosi, 1947), from Japan. Other species in China, Taiwan, Japan and Okinawa. Very similar to both *Saroxenus* and *Unixenus*.

Mauritixenus Verhoeff, 1939. — Tarsus 2 with thick spine, antennal article 6 with three to five basiconic sensilla only. Six species, incl. *M. gracilicornis* Verhoeff, 1939, Mauritius. Other species from Madagascar, Rodriguez, Réunion and West Africa.

Miopsxenus Condé, 1951. — Lacks pigment. Two species, *M. mootryi* Condé, 1951, Egypt, is the only adult polyxenid with just three ommatidia each side. *M. schubarti* Condé, 1951, Gabon, has no ommatidia.

Monographis Attems, 1907. — Spines on both tarsus 1 and 2. Antennal article 6 with 12-20 basiconic sensilla. Nine species, incl. *M. kraepelini* Attems, 1907, Java. Other species in Vietnam, India, Australia, Brazil, China, Malaysia including Sabah, Singapore.

Pauropsxenus Silvestri, 1948. — Only five ommatidia each side, tarsus 2 with thick spine. Three species, incl. *P. brachyartema* (Brölemann, 1920), Tanzania. Other species in Angola, Congo, Uganda, Madagascar and Gabon.

Saroxenus Cook, 1896. — Four species, incl. *S. alluaudi* (Brölemann, 1920) from Madagascar and Réunion. Other species found in South Africa, Liberia, Mauritus, Ivory Coast, Benin, Angola.

Silvestrus Jones, 1937. — Tarsus 2 with large spine. Setae on tergites in two lateral clusters only, no posterior row. Three species, incl. *S. brevipalpus* (Condé & Jacquemin, 1962) from Madagascar. Other species in India, Sri Lanka, Saint Helena Island, Mauritius, Réunion, Java.

Unixenus Jones, 1944. — Tarsal spine absent, replaced with small setiform hair. At least eight species, incl. *U. broelemanni* (Condé & Jacquemin, 1962) from Madagascar, and *U. mjoebergi* (Verhoeff, 1924), which has a very widespread distribution in Australia. Other species in India, Madagascar, Ivory Coast, and Australia. Further species yet to be described from Vietnam and Papua New Guinea.

Subfamily MACROXENINAE Condé, 2008. — Eight ommatidia each side, telson with two caudal bundles of trichomes with narrow gap between, dorsal to which are the ornamental trichomes comprising a row of barbate trichomes with a gap in midline of row, a group of 10 trichomes below each side extending into the caudal bundle, and one long barbate trichome adjacent internally each side. Gnathochilarium with pseudo-articulated sensilla with a short conical apical fragment; outer palps mostly very developed and carrying up to 28 sensilla (except for *Macroxenus enghoffi* with 44). Four genera.

Afraustraloxenodes Nguyen Duy-Jacquemin, 2006. — Setiform sensillum only on tarsus 2. Four species, incl. *A. namibiensis* Nguyen Duy-Jacquemin, 2003. Other species in Angola and South Africa.

Chilexenus Silvestri, 1948. — One species, *C. rosendinus* (Silvestri, 1903), Chile.

Macroxenodes Silvestri, 1948. — Setiform sensillum only on tarsus 2. Six species, incl. *M. jahnryi* Nguyen Duy-Jacquemin, 2009, Brazil and Argentina. Brazilian specimens were found in the nest of the specialised polyxenid predator ant *Thaumatomyrmex mutilatus* Mayr, 1887. Other species in Amazonas region of Brazil, Venezuela, Greater Antilles, Florida Keys (Florida, USA) and Island Santa Inez Island, Mexico.

Macroxenus Brölemann, 1917. — Spine on tarsus 2, large distance between oval lateral tufts of tergal trichomes. Three species, incl. *M. caingangensis* (Schubart, 1944) found across North Africa in Algeria, Morocco, Malta and Portugal. Of other two species, *M. enghoffi* Nguyen Duy-Jacquemin, 1996 is found in the Canary Islands, the other in Brazil and Venezuela.

Subfamily HYPOGEXENINAE Schubart, 1947. — 1.9 mm body length, caudal bundle 0.4 mm. unpigmented, without ommatidia, antennomere 8 smaller than 7. No sensory cones on antennomere 8. Gnathochilarium with very short outer palps carrying four sensilla each. Hooked caudal trichomes with a curved apex forming three apical forks, barbs along stem. Two transverse rows of short barbate trichomes with small number of trichomes forming rosettes laterally. Telotarsus with narrow lamellate process. Description inadequate, subfamily status may not be warranted. One genus.

Hypogexenus Silvestri, 1903. — One species, *H. pusillus*, found buried deeply in soil at Posadas, Argentina.

Subfamily uncertain.

Ankistroxenus Attems, 1907. — Two species, incl. *A. aethiopicus* (Chalande, 1908), Ethiopia. Other species from Egypt.

Apoxenus Chamberlin, 1947. — One species, *A. micronesius* Chamberlin, 1947, Micronesia.

Mesoxenotus Silvestri, 1948. — One species, *M. primus* Silvestri, 1948, Rhodes.

Family LOPHOPROCTIDAE Silvestri, 1897. — 1.2-4.2 mm body length without caudal bundle. A very homogeneous family mainly inhabiting upper layers of soil and in caves, nine or ten tergites plus telson and 11 (one species only) or 13 leg pairs, leg

buds internal, anophthalmic, lacking pigment, no coxal pores, anterior trichobothrium slightly dilated and ending in short spine hair, gnathochilarium with palps lacking lateral extensions, palps dimorphic with adult males having in the range 30-86 sensilla, while females retain juvenile number around 17-25, antennomeres 6 and 8 elongate with article 6 longest, article 8 with domed apex equal or greater in length than article 7, telotarsus lacking lamella but often with spines and denticles on claws, leg setae pubescent, pear-shaped basally, telson with caudal bundles of trichomes closely aligned giving the appearance of a single bundle and with a linear arrangement of ornamental trichomes each side of the midline consisting of a row of short barbate trichomes interrupted along its length by a cluster comprising two long trichomes plus a single distinct long trichome. Usually only a small number of short barbate trichomes are present external to each cluster. The presence and number of linguiform processes along the anterior edge of the labrum is a key character in distinguishing genera. Six genera, 43 species.

Alloproctoides Marquet & Condé, 1950. — At least three species, incl. *A. xenochilus* Nguyen Duy-Jacquemin, 1982, Papua-New Guinea and Solomon Islands. Other species from Madagascar, Réunion Island, Bismarck Archipelago, and northern Australia.

Ancistroxenus Schubart, 1947. — Two species, incl. *A. comans* (Loomis, 1934), Trinidad, Jamaica, Costa Rica, Colombia, Venezuela and Brazil. The other species from Brazil.

Barroxenus Chamberlin, 1940. — No ommatidia and pigment, antennal shape and proportions typical of Lophoproctidae. Inadequately described, highly likely synonymous with another genus. One species, *B. panamanus* Chamberlin, 1940, Panama.

Lophoproctinus Silvestri, 1948. — Five species, incl. *L. chichinii* Condé, 1951, Egypt. Other species from North Africa and the western Mediterranean region incl. Corsica, Italy, Algeria, Morocco, Tunisia, Balearic, Canary, Madeira and Azores Islands, as well as Mexico and United States.

Lophoproctus Pocock, 1894. — Four species, incl. the troglomorphic *L. pagesi* Condé, 1982 (Plate I A) found in a cave on the island of Majorca. Other species from Portugal, France, Corsica, Italy, Sardinia, Sicily, Lebanon, Algeria, Morocco, Ukraine, Romania, Bulgaria and Russia. *L. lucidus* (Chalande, 1888).

Lophoturus Brolemann, 1931. — At least 28 species, incl. *L. madecassus* (Marquet & Condé, 1950) which is distinctive in possessing only 11 pairs of legs in adults. The species has a circumtropical distribution: southern Algeria, Ivory Coast, Jamaica, Florida, Cape Verde Islands, Tonga, Cook Islands and Barrow Island, northern Australia. Other species in tropical and subtropical areas around the world.

Family uncertain.

Trichoproctus Silvestri, 1899. — Five ommatidia which lack pigment. Inadequately described. One species, *T. biroi* Silvestri, 1899, collected in New Guinea (Tamara Island).

Superfamily SYNXENOIDEA Silvestri, 1923. — All species pigmented and with nine to eleven ommatidia in adults, 10 or 11 tergites plus a telson and with 15 or 17 leg pairs, legs short, with last two leg pairs modified to 'jumping legs', their tarsal claws replaced with hairy pads. Most podomeres bearing long thin setae except for last 2 leg pairs which have 2 setae on femur only. Leg buds external. Insertion of head trichomes in four distinct areas. Gnathochilarial palps with large lateral extensions. Trichobothria with cylindrical funiculi, anterior one (trichobothrium c) with a shorter sensory hair than the more posterior two. Tergites with scale shaped trichomes in two transverse rows with small cluster of barbate trichomes either side at each row end and anterior to anterior scale row. Telotarsus with anterior process with spinous projection shorter than the claw which bears two sharply pointed

latero-anterior and posterior teeth. Vulva strongly elongated into ovipositors, coxal pores present in males, variable in number. Telson cone-shaped, covered anteriorly with a row of scale shaped trichomes with long barbate trichomes each end laterally and remainder of telson covered with long thin trichomes. Found globally in warm and well drained/dry habitats, in litter or under bark.

Family SYNXENIDAE Silvestri, 1923. — 2.4-5 mm body length excluding caudal trichomes. Two genera, eight species.

Condexenus Nguyen Duy-Jacquemin, 2006. — 10 tergites plus telson and 15 pairs of legs. One species, *C. biramipalpus* Nguyen Duy-Jacquemin, 2006, Namibia.

Phryssonotus Scudder, 1885. — 11 tergites plus telson and 17 pair of legs, with the exception of *P. brevicapensis* Nguyen Duy-Jacquemin, 2011 from South Africa with 10 tergites plus telson and 15 pairs legs. A row of sensory trichomes is associated with the anterior trichobothrium, one very long and curved long frontal trichome, with one to five short sensory trichomes adjacent medially. The number of short sensory trichomes is a diagnostic character. Seven species, incl. *P. novaehollandiae* (Silvestri, 1923) widespread throughout Australia with thelytokous populations along the coast in southern Australia. Other species in Uruguay, Chile, Cuba, South Africa, Mozambique, Madagascar, Papua New Guinea, North Africa, Sicily and Spain. *P. orientalis* (Silvestri, 1900), *P. platycephalus* (Lucas, 1846).

Subclass CHILOGNATHA Latreille, 1802/1803

[THOMAS WESENER]

Adult body size 3-350 mm. Cuticle always calcified. Head without trichobothria. Labrum with a single or three teeth (reduced in some orders). Organ of Tömösváry present as a small pit, or absent. Antennae with six or seven podomeres plus disc (rarely with eight antennomeres plus disc), disc carrying four, in very few genera more, apical cones. Various sensilla, including sensilla basiconica are usually present on the antennomeres, especially antennomeres 5 and 6. Gnathochilarium variable, order specific, but always consisting of a single, variously subdivided, unpaired plate. Palps of gnathochilarium short. Trunk with 11-220 segments, and 17-375 leg pairs, and corresponding sternites with often fused stigmatic plates surrounding the coxae. Sternites, stigmatic plates, pleurites and tergites ranging from free to forming a completely fused ring with barely visible sutures. First stigmatic plate in females always fused to coxa 1. Legs consisting of six (coxa, prefemur, femur, postfemur, tibia, tarsus), rarely seven (coxa, trochanter, prefemur, femur, postfemur, tibia, tarsus) or eight (coxa, trochanter, prefemur, femur, postfemur, tibia, tarsus 1, tarsus 2) podomeres. If two tarsi are present, they are still connected by a continuous tarsal pad. Coxal pores present or absent. Gonopores opening directly through second coxae, or through a pouch behind second leg pair. Either posterior male leg pairs modified to telopods, or at least one leg pair of the male segment 7 modified to gonopods (for sperm transfer).

Sperm transfer always direct, male transfers sperm actively into female sexual opening. Development by anamorphosis, juveniles hatching with three, rarely four (Colobognatha) exceptionally (*Pachyiulus* spp.) more than 20 leg pairs.

Ca. 10 000 species in 15 orders, distributed worldwide except Antarctica.

Infraclass PENTAZONIA Brandt, 1833

[THOMAS WESENER]

Head capsule without a median suture, lacking an occipital phragma. Genae (parietal sclerites) absent or strongly reduced. Labrum fused to clypeus, with a single, triangular, anteromedian tooth. Ommatidia absent (Glomeridesmida), few (Glomerida) or numerous (up to 70+, Sphaerotheriida). Organ of Tömösváry present lateral to antennae, of order-specific shape and size. Antennae with six (Sphaerotheriida) or seven (Glomerida and Glomeridesmida) antennomeres plus apical disc carrying four, in numerous genera more, apical cones. Sensilla basiconica present on some antennomeres. Epipharynx loosely attached to head capsule. Mandible consisting of a single basal article and a gnathal lobe. Gnathal lobe often with a condylus (reduced in some Glomerida), generally of order-specific shape. Gnathochilarium variable, order-specific, always with three pairs of palps and fused lamellae linguales. Defence glands absent (Glomeridesmida and Sphaerotheriida) or present, with a single opening located mid-dorsally (Glomerida), secreting alkaloids. Trunk with 10-21 tergites, 10-20 pleurites, 17-36 pairs of legs and corresponding stigmatic plates. Tergites and pleurites free, sternites reduced (Glomerida, Sphaerotheriida) or of small size, visible in anterior view (Glomeridesmida). Stigmatic plates separated from sternites, subdivided and located lateral to (Sphaerotheriida and Glomerida), or fused with (Glomeridesmida) coxae. Spiracles present on first two segments, tracheae dichotomous. Intestine curved, N-shaped. Legs consisting of six podomeres (coxa, prefemur, femur, postfemur, tibia, tarsus). Coxal pores present (Glomeridesmida) or absent (Glomerida and Sphaerotheriida). Last leg-pair in males modified into telopods, consisting of pincer-shaped, three- or four-jointed structures formed by the telopodites and inner horns formed by the fused syncoxite. Female with a free subanal plate. Gonopores opening directly through (Sphaerotheriida), or through a pouch attached posteriorly to, the second coxa (Glomeridesmida and Glomerida).

Sperm transfer little-known, elaborate mating strategies, at least sometimes with the help of mouthparts and soil particles. Includes only millipedes known to stridulate. Development hemianamorphotic, first juveniles hatching with three pairs of legs.

Ca. 675 species in three orders, distributed worldwide except the southern half of South America and Antarctica.

Superorder LIMACOMORPHA Pocock, 1894
Order Glomeridesmida Latzel, 1884

Adult body length usually 4-8 mm, exceptionally up to 15 mm. Head lacking genae, ommatidia absent. Organ of Tömösváry very large, circular, located lateral to antennae. Antennae with seven segments, apparently lacking any sensilla, plus disc carrying four long and slender apical cones. Mandible gnathal lobe with a single external tooth, four to six combed inner teeth, a large area of seven or more rows of pectinate lamellae and a relatively small molar plate which is smaller than the area covered by the pectinate

lamellae. Molar plate always with membranous fringe. A well-developed mandibular condylus always present dorsally. Gnathochilarium with a well-developed, wide gula (hypostoma). Cardines small, separated from gnathochilarium. Mentum and lamellae linguales fused. Stipites large, engulfing the mentum laterally. Two pairs of palps on stipites, lateral pair much smaller than inner pair and with only four to six large sensory cones. A pair of modified median palps on top of lamellae linguales, carrying sensory cones apically, as well as larger and different cones more basally. Ozopores absent. Females with 20 tergites plus anal shield, 19 pairs of pleurites and 36 pairs of legs. Males with 19 tergites plus anal shield, 18 pairs of pleurites and 35 pairs of legs. Tergites weakly calcified and flexible. All tergites of similar shape, size decreasing posteriad. Pleurites present ventrally as large sclerotized plates between tergites and legs. Most pleurites with a dense row of spines posteriorly. Stigmatic plate fused to coxae. Spiracles located laterally. Sternites free, but strongly reduced in size, visible at least in anterior and posterior legs in anterior view between the coxae. Legs consisting of six podomeres (coxa, prefemur, femur, postfemur, tibia, tarsus). Legs long and slender, tarsi apically with a claw and a long, flexible paronychium (a membranolus pad). Coxal pores present, starting from coxae 7, 9 or 11 (species-specific?), each odd numbered coxa with an eversible coxal sac. Penultimate leg-pair in females, third last in males weakly modified, with a narrow coxosternite, and spiracle opening located mesally instead of laterally. Last leg-pair modified, consisting of coxae and three podomeres. Both legs separated from one another, connected by a large, undivided sternite without spiracles. These legs fulfil a sensory function, tarsus posteriorly protruding above the anal shield through special indentations of the last pleurite and tergite. Penultimate male leg-pair modified into a telopod consisting of a syncoxite with inner horns and two four-jointed telopodites. Female and male gonopores opening behind the second coxa, females often with a very long ovipositor.

Development hemianamorphic, with decoupled leg and tergite development.

32 species in two families, distributed in Central and South America, India, SE Asia, the East Indies and Oceania.

Family GLOMERIDESMIDAE Latzel, 1884. — Head visible from above, first tergite (collum) slightly smaller than following tergites. Organ of Tömösváry located on head surface, visible from above. Antennae long and slender, far longer than head width. Modified median palps of gnathochilarium apically with ‘normally’-shaped sensilla. Cardines of gnathochilarium small. Surface of tergites consisting of more than five longitudinal striae with a denticulate margin. All leg podomeres covered with sparse isolated spines. Female gonopore with strongly elongated ovipositors. One genus.

Glomeridesmus Gervais, 1844. — 27 described species distributed from Brazil to Mexico in America, southern India, and various parts of SE Asia together with the East Indies and Oceania. *G. marmoreus* Pocock, 1894, *G. spelaeus* Iniesta & Wesener, 2012 (Plate XII A).

Family TERMITODESMIDAE Silvestri, 1911. — Head not visible dorsally, completely covered by collum, which is slightly larger than following tergites. Organ of Tömösváry located at lateral margin of head capsule, not easy to see from above. Antennae short, shorter than head width, located at lateral margins of head capsule, antennomeres

often as long as wide. Modified median palps of gnathochilarium apically with tube-like sensilla. cardines of gnathochilarium large. Surface of tergites without striae, but always completely covered by Y- or bar-shaped structures. All leg podomeres heavily covered with long spines. Female gonopore a simple vulva, not elongated. Males unknown. The only obligate entomophilous myriapod family. One genus.

Termitodesmus Silvestri, 1911. — Five species, known only from termite mounds in southern India, Sri Lanka and Vietnam. *T. ceylonicus* Silvestri, 1911, *T. escherichi* Silvestri, 1911.

Superorder ONISCOMORPHA Pocock, 1887

Ability to roll into a sphere, possibly evolved independently in the two orders.

Order Sphaerotheriida Brandt, 1833

Adult body length usually 30-45 mm, rolled-up the size of a ping-pong ball, exceptionally up to 100 mm, rolled-up the size of a baseball. Head lacking genae, very wide and short, laterally with large antennal grooves. Each eye with 60-90 ommatidia arranged in a large cluster, always with a single ommatidium located laterally in antennal groove. Organ of Tömösváry a small, circular pit, slightly smaller than an ommatidium, located laterally in antennal groove. Antennae placed laterally on head, accomodated in large lateral antennal grooves, each consisting of six antennomeres plus disc. Antennae short to very short, antennomeres usually cylindrical. Disc usually with four, but in many species of most genera with 15-80, apical cones. Antennomere 6 usually much larger than others, antennomeres 1, rarely 5 and 6, with few isolated sensilla basiconica. Mandible gnathal lobe massive, with a single external tooth, a three-combed (rarely two-combed) inner tooth, six or more pectinate lamellae and a prominently developed molar plate. Molar plate always without membranous fringes. Mandibular condylus prominent, strongly developed. Gnathochilarium with a normal-sized gula. Cardines almost completely reduced. Mentum fused to undivided lamellae linguales forming a large central plate. Stipites large, located lateral to lamellae linguales. Stipites with inner palps only, outer palps rudimentary, reduced to a cluster of four to six tiny sensory cones. Median palps on top of lamellae linguales transformed into centrally located pads, lacking sensory cones in apical half, posterior half of underside with single sensory cones. Ozopores absent. Always with 12 tergites, plus anal shield, 12 pair of pleurites, and 21 (females) or 23 (males) pair of legs. Tergite 13 completely fused to anal shield, in rare cases sutures still visible. First tergite (collum) greatly reduced in size, while second (thoracic shield) greatly enlarged, almost twice as large as the following tergites. Anal shield bell-shaped. All species of the order are capable of complete volvation, where the head and collum fit into the sphere, while the bell-shaped anal shield engulfs the anterior margin of the enlarged second tergite. Second tergite always without a schism (a gap in the lateral margin), except in juveniles, but with deep lateral pits to accommodate the tergite tips of the following segments during

enrolment. Tergite tips and anal shield on underside with special locking carinae that can be moved above the brim of the thoracic shield during enrolment. All tergites very thick and heavily calcified. Underside of posterior margin of tergites ('endotergum') often with special structures to prevent the intrusion of dirt and/or parasites between the tergites when volvation is not complete. Pleurites present ventrally as large sclerotized plates between tergites and stigmatic plates. Stigmatic plates loosely articulated to the coxae, carrying spiracles. Sternites completely reduced. Legs consisting of six podomeres (coxa, prefemur, femur, postfemur, tibia, tarsus). Legs long and massive, knife-shaped, strongly compressed laterally. Femur on posterior side always with a ridge, tarsi always with an apical claw and spine, always lacking a paronychium. Tarsi 1 and 2 always lacking an apical spine. Coxal pores absent. Male leg-pairs 22 and 23 modified into anterior and posterior telopods, respectively, both pairs may carry stridulation organs. Both pairs of telopods with fused coxae. Anterior telopod with three or four podomeres distal to syncoxite, with one or several processes forming chelae or (more often) pincers. Posterior telopods forming chelae, with three podomeres distal to syncoxite, telopoditomere 3 sometimes divided. Telopoditomere 2 of posterior telopods always with a large process forming the immovable finger of chelae, while the sometimes divided telopoditomere 3 forms the movable finger. Syncoxite always with inner lobes and sharp-edged inner horns. Male and female gonopore opening on posterior side of coxa 2. Male gonopore usually covered with a simple plate, female gonopore with a vulva consisting of two sclerotized basal plates ('bursa') and one sclerotized apical plate (operculum), the latter often protruding above the coxa. Females in one family with a stridulation organ on an enlarged subanal plate.

Development hemianamorphic.

More than 340 described species in five families with 24 genera, disjunctly distributed in eastern South Africa, Madagascar, Seychelles, southern India and Sri Lanka, SE Asia from Nepal to SW China, Myanmar to the Philippines, Java and Sulawesi, Australia and New Zealand.

Family PROCYLIOSOMATIDAE Wesener & VandenSpiegel, 2009. — Anterior telopods with four podomeres distal to syncoxite, forming chelae. Posterior telopods with three telopoditomeres. Telopods lacking stridulation organ. Vulva consisting of three plates, apical margin of operculum well-rounded, positioned lower than bursa. Stigmatic plates free. Legs without coxal processes. Tergite 13 incompletely fused to anal shield, a gap and a suture still visible. Endotergum lacking spines, hair or callosities; marginal bristles not organized in rows. Sensory cones on palps of gnathochilarium arranged in a single field. 20-35 mm long. A single genus distributed in E Australia and New Zealand.

Procyliosoma Silvestri, 1917. — 11 species, all smaller than a ping-pong ball when rolled-up.

Family ZEPHRONIIDAE Gray, 1843. — Anterior telopods with three or four podomeres distal to syncoxite, forming clamps, without sclerotized teeth. Vulva consisting of two plates, these plates of bursa being fused. Operculum of vulva rounded, lower margin engulfing vulva apically and partly laterally. Stigmatic plates almost completely covered with pleurites, spiracles protected by coxal processes. Tergite 13 completely fused to

anal shield. Endotergum lacking callosities or spines, marginal bristles arranged in rows. Antennomere 6 often axe-shaped, carrying numerous sensory cones. Sensory cones on palps of gnathochilarium arranged in a single field. 15-50 mm long. 15 genera, 144 species, distributed in SE Asia, from Nepal in the West to SW China in the East, Myanmar in the North to some Philippine islands and Sulawesi in the South. The occurrence of a monotypic genus on a few islands in the Seychelles might be the result of anthropogenic introduction.

Bothrobelum Verhoeff, 1924. — Tergites sulcate, with a U-shaped depression and six oval pits on each site, a unique character for the order. One or two species, Borneo.

Castanotherium Pocock, 1895. — Posterior and anterior telopods with only three podomeres distal to syncoxite. Immovable finger of posterior telopod greatly enlarged, in some species twice as wide as movable finger. Antennae axe-shaped, with numerous apical cones. Tarsi with a single apical spine. 50 species, widely distributed in Indonesia and the Philippines.

Castanotheroides Chamberlin, 1921. — Antennae cylindrical, with only four apical cones. A little-known genus. Three species, Philippines.

Cryxus Leach, 1814. — Anterior telopods with three podomeres distal to syncoxite, telopoditomere 3 heavily bent posteriorly, forming a 'beak' with the process of telopoditomere 2. Telopoditomere 2 of posterior telopod heavily elongated, longer than telopoditomeres 3 and 4 combined. Telopoditomere 4 almost rudimentary, with a 90% torsion so that it overlaps the immovable finger. Tarsus slender, with a single apical spine. Small-bodied, only up to 20 mm long. One species, Vietnam.

Indosphaera Attems, 1935. — Coxae 2 of female completely fused, a unique character in the order. Anterior telopod with four podomeres distal to syncoxite. Telopoditomeres 3 and 4 each almost as long as telopoditomere 1. Process of second telopoditomere of anterior telopods located posteriorly. Posterior telopod with four telopoditomeres, immovable finger with two membranous ledges. Operculum of vulva very narrow. Tarsi with a single apical spine. Tergites hairy. 35-40 mm long. Two species, Myanmar and NE India.

Kophosphaera Attems, 1935. — Anterior telopod with four podomeres distal to syncoxite. Process of second telopoditomere of anterior telopods located posteriorly. Posterior telopod with four telopoditomeres, telopoditomere 4 quite large. Immovable finger short, without any membranes. Antennomere 6 strongly flattened. Legs slender, with a single apical spine. 30-45 mm long. Tergites glabrous. Might fall into synonymy under *Zephronia*. Seven species, northern India and Nepal.

Leptoprotopus Silvestri, 1897. — First two male legs with greatly enlarged claws, claw as long as tarsus, a unique character in the order. Tooth of mandible also enormously enlarged and elongated. Anterior and posterior telopods greatly resembling those of *Sphaeropoeus*. 15 mm long. One species, Sumatra.

Leptotelopus Silvestri, 1897. — Male legs in posterior half modified, uniquely for the order, with enlarged coxa and prefemur, and greatly elongated, but femur, postfemur, tibia and tarsus very slender. Tarsus with fringes of hair at lateral and mesal margins. Anterior telopods with three podomeres distal to syncoxite. Telopoditomere 3 small, forming a clamp with a process of telopoditomere 2. Posterior telopods with four telopoditomeres. A large and ridged plate located on telopoditomere 4 might represent a for the order unique stridulation organ. 15 mm long. One species, Myanmar.

Prionobelum Verhoeff, 1924. — Anterior telopods very similar to those of *Cryxus*. Posterior telopods with four telopoditomeres, telopoditomere 2 elongated. Tarsus with a single apical spine. 20-35 mm long. Seven species, Vietnam and SW China.

Rajasphaera Attems, 1935. — Anterior telopod apparently with three podomeres distal to syncoxite. Posterior telopods unique, telopoditomere 1 massively enlarged and swollen, while telopoditomere 2 is also quite large, with the immovable finger almost fused to its basal parts.

Telopoditomere 3 very slender. Male gonopore located almost mesally instead of posteriorly. Antennomere 6 strongly axe-shaped. Ca. 50 mm long. One species, Borneo.

Sechelliosoma Mauriès, 1980. — Anterior and posterior telopods with three podomeres distal to syncoxite, both pairs strongly elongated and slender. Antennomere 6 cylindrical, disc with only four apical cones. 20+ mm long. One species, Seychelles.

Sphaerobelum Verhoeff, 1924. — Anterior telopod with three or four podomeres distal to syncoxite. Second telopoditomere with a curved process, more distally located telopoditomeres usually simple. Posterior telopods with four telopoditomeres, immovable finger massively enlarged apically, a unique character for the order. 20-45 mm long. Tarsi with single apical spine. Surface variable, hairy to shiny and glabrous. Five described species, Vietnam and Thailand.

Sphaeropoeus Brandt, 1833. — Anterior telopod with four podomeres distal to syncoxite. Telopoditomeres 2 and 3 each almost as long as telopoditomere 1. A specially shaped lateral process of telopoditomere 2 and a process of telopoditomere 3 forming a clamp. Posterior telopods with four telopoditomeres, immovable finger slender. Telopoditomere 3 with small sclerotized teeth. 20-45 mm long. Tarsi with a single, rarely with two apical spines. 21 species, many in need of revision, distributed in Vietnam, Malaysia, Singapore, Sumatra, Borneo, Java and Nias.

Tigridosphaera Jeekel, 2000. — Anterior telopods with three podomeres distal to syncoxite. Telopoditomere 3 bent posteriad, forming clamps with the process of telopoditomere 2. Posterior telopods with four telopoditomeres. Tarsi with a single apical spine. Likely synonymous with *Prionobelum*. Four species, Malay Peninsula.

Zephronia Gray, 1832. — Anterior telopods with four podomeres distal to syncoxite. Telopoditomere 2 with a large, curved process forming a clamp with simple telopoditomeres 3 and 4. Posterior telopod with four telopoditomeres. Immovable finger slender, curved apically, towards telopoditomeres 3 and 4 with two membranous ledges. Telopoditomere 3 also with a membranous ledge and a row of large, crenulated, sclerotized teeth, much larger than telopoditomere 4. Antennae flattened laterally, axe-shaped. 18-50 mm long. Tarsi with several apical spines. 38 species, described from NE India, Myanmar, Cambodia, Vietnam, Singapore, Malaysia, and Thailand.

Family SPHAEROTHERIIDAE Brandt, 1833. — Anterior telopods with three or four podomeres distal to syncoxite, forming clamps. Posterior telopods also consisting of three or four podomeres distal to syncoxite. Inner horns of syncoxite elongated and slender. Telopoditomere 2 of posterior telopods carrying a stridulation organ on its posterior side, a field of ribs that can be moved above special knobs on the anal shield to produce species-specific, audible sounds. Vulva consisting of three plates, operculum mesally often protruding into a single tip. Stigmatic plates free, with a spine-like process protecting the spiracle of the previous stigmatic plate. Coxal lobes absent or present. Tarsi always with a single apical spine, in some species the tibia can carry two apical spines, too. Tergite 13 completely fused to the anal shield. Endotergum always with callosities, and an inner area with triangular spines and hair, marginal bristles always arranged in rows. Antennomere 6 always cylindrical, with four or many apical cones. Sensory cones on the palps of the gnathochilarium arranged in clusters. 20-45 mm long. 55 species in two genera in eastern South Africa, with some isolated, potentially introduced populations as far north as Malawi.

Sphaerotherium Brandt, 1833. — 54 species, incl. *S. dorsale* Gervais, 1847 and *S. punctulatum* Brandt, 1841, and the potentially synonymous ***Kylindotherium*** Attems, 1926, one species.

Family ARTHROSPHAERIDAE Jeekel, 1974. — Anterior and posterior telopods with three or four podomeres distal to syncoxite. Anterior telopod forming a pair of clamps,

telopoditomeres 2 and 3 each always with a field of sclerotized knobs. First telopoditomere of the anterior telopods enlarged, carrying the harp, a stridulation organ consisting of 1-12 large stridulation ribs. Posterior telopods without a stridulation organ, inner horns of syncoxite wide. Vulva consisting of three plates, operculum usually well-rounded, but in some members with a median notch. Inner plate of bursa strongly protruding. Female subanal plate greatly enlarged, forming the washboard, a stridulation organ consisting of 2-24 ribs. Stigmatic plates free, with a spine-like process protecting the spiracle of the previous stigmatic plate. Coxal lobes absent or present. Tarsi always with a single apical spine. Tergite 13 completely fused to anal shield. Endotergum never with callosities, inner area with triangular spines and hair; marginal bristles always arranged in rows. Sensory cones on the palps of the gnathochilarium arranged in a single field. Usually 25-50 mm long, gigantic island forms up to 100 mm long and 48 mm wide, dwarf forms only 8-15 mm long. Four genera, 100 species, distributed in southern India, Sri Lanka and Madagascar, a single species introduced to a former forest garden in the Usambara Hills, Tanzania.

Arthrosphaera Pocock, 1895. — Anterior telopod with four podomeres distal to syncoxite, telopoditomere 4 with lobe covered with sclerotized spots. Harp carrying one or two stridulation ribs. Posterior telopods with three telopoditomeres, telopoditomere 3 carrying two membranous lobes. Operculum of female vulva well-rounded, shorter than bursa. Inner plate of vulva heavily elongated, protruding as far as, or even above, operculum. Female washboard with few, usually four to six stridulation ribs. Legs with a coxal lobe, tarsi usually wide, paddle-like, rarely slender. Underside of anal shield usually with two locking carinae, which are completely reduced in some species. First antennomere without groove, only isolated sclerotized scales, lacking sensilla basiconica like all other antennomeres. Antennomere 6 large, flattened, axe-shaped, carrying numerous apical cones. 25-45 mm long. 40 species, southern India and Sri Lanka. *A. brandtii* (Humbert, 1865) (Plate XI A).

Microsphaerotherium Wesener & VandenSpiegel, 2007. — Anterior telopod with three podomeres distal to syncoxite. Harp carrying a single stridulation rib. Posterior telopods with three telopoditomeres, third with a single membranous lobe. Operculum of vulva narrow, inner plate of vulva protruding. Four to six discontinuous ribs on female washboard. Legs without a coxal lobe, tarsi always long and slender. Underside of anal shield with a single (fused?) locking carina, this being very long, sometimes connecting with the locking carina from the other side. Surface of tergites covered with special tiny 'rotated' (helicoid) setae, dorsally with a sclerotized crest. First antennomere with a groove, few sensilla basiconica, and isolated sclerotized scales. All antennomeres cylindrical, with 5-10 apical cones. Includes the smallest known giant pill-millipedes, e.g. *M. ivohibiense* Wesener & VandenSpiegel, 2007, length less than 10 mm. Two species, rainforests of Madagascar.

Sphaeromimus de Saussure & Zehntner, 1902. — Anterior telopod with four podomeres distal to syncoxite, telopoditomere 4 always with three spines in special positions. Harp carrying 3-10 stridulation ribs. Posterior telopods with three telopoditomeres, third carrying two membranous lobes. Operculum of vulva greatly enlarged and well-rounded, often larger than bursa. Inner plate of vulva not protruding. Female washboard with 8-20 stridulation ribs. Legs with a coxal lobe, tarsi very wide, paddle-like. Underside of anal shield with a single, short, locking carina. First antennomere with neither a groove nor scales, nor sensilla basiconica. Antennomere 6 large and flattened, but not axe-shaped. Number of apical cones sexually dimorphic, females with 40-50, males with 80-90. 20-40 mm long. Ten species, south-eastern Madagascar. *S. musicus* (de Saussure & Zehntner, 1897) (Plate XI B).

Zoosphaerium Pocock, 1895 (Plate XI C-E). — Anterior telopod with three podomeres distal to syncoxite. Harp carrying one or two stridulation ribs (one species with three). Posterior telopods

with three telopoditomeres, third variable, but at least in the *libidinosum* species group carrying two membranous lobes. Operculum of vulva of variable size, but apical margin always with a median notch. Inner plate of vulva protruding. Female washboard with two to eight stridulation ribs. Legs without a coxal lobe, tarsi always long and slender. Underside of anal shield with two locking carinae, posterior one usually two or three times larger than anterior one. First antennomere with a groove, covered with sclerotized scales. Isolated sensilla basiconica always present on first antennomere, rarely also on antennomere 4 or 5. All antennomeres cylindrical, with four or 15-50 apical cones. Usually 20-50, giant species 70-100, mm long. Largest described species, the Emerald Green Giant Pill-Millipede *Z. neptunus* (Butler, 1872). Ca. 55 species, Madagascar. *Z. arboreale* Wesener & Sierwald, 2005, *Z. villosum* Wesener & Sierwald, 2005 (Plate XI F).

Family CYLIOSOMATIDAE Jeekel, 1974. — Anterior telopod with three podomeres distal to syncoxite, syncoxite partly reduced, barely connecting the telopod pair. Telopoditomere 1 massive, more than twice the size of all following podomeres combined. Posterior telopod consisting of three telopoditomeres, third greatly enlarged, always wide and massive, the largest of the three telopoditomeres. Posterior telopod without a stridulation organ, inner horns of syncoxite wide. Vulva consisting of three plates, operculum projecting into a more or less well-rounded tip in the middle axis. Stigmatic plates free, with a spine-like process protecting the spiracle of the previous stigmatic plate. Coxal lobes absent. Tarsi with a single apical spine. Tergite 13 completely fused to anal shield. Endotergum never with callosities, inner area with triangular spines and hair; marginal bristles always arranged in rows. Sensory cones on the palps of the gnathochilarium arranged in a single field. 20-35 mm long. Two genera with 20 species, E and SW Australia.

Cyliosoma Pocock, 1895. — Male anal shield without large groove, only a special field of setae present. Telopoditomere 3 of posterior telopods long and curved. 19 species, E and SW Australia.

Cynotelopus Jeekel, 1986. — Male anal shield heavily modified, with a gigantic groove. Telopoditomere 3 of posterior telopods wide and short. One species, SW Australia.

Order Glomerida Leach, 1814

Adult body length usually 10-15 mm, exceptionally up to 25 mm, in ‘dwarf genera’ only 2.5-5 mm. Head lacking genae, blind or with less than 10 ommatidia arranged in a single row, but usually with a single ommatidium above. Organ of Tömösváry very large, horseshoe-shaped, located lateral to antennae. Antennae placed relatively close to one another, each consisting of seven antennomeres plus disc, laterally flattened fitting into sphere when the animal is rolled-up. Disc usually carrying four, rarely numerous, apical cones. Antennomere 6 usually much larger than others, all antennomeres apparently lacking sensilla basiconica. Mandible gnathal lobe with a single external tooth, two to seven combed inner teeth, six or more pectinate lamellae and a prominently developed molar plate. Molar plate always (?) with a single groove, often lacking a membranous fringe. Mandibular condylus weakly developed (absent in Glomeridae). Gnathochilarium with a wide gula. Cardines very large, almost as large as stipites. Mentum subdivided, small, partly covered by gula. Lamellae linguales fused, very large. Stipites large, located laterally to lamellae linguales. Stipites with smaller lateral and larger inner palps. Median

palps on top of lamellae linguales transformed into centrally located pads, with special sensory cones located at its underside. Paired defence glands opening through a small pore located dorsally in intersegmental membrane behind tergites, starting from third and continuing to penultimate tergite. Secretion consisting of fatty acids and quinazolinone alkaloids. Defence glands reduced in numerous dwarf genera. Usually 11, more rarely 10 tergites, plus anal shield, 10 pairs of pleurites, and 17 (females) or 19 (males) pairs of legs. Collum greatly reduced in size, second (thoracic shield) greatly enlarged, almost twice as large as following tergites. Last tergite (tergite 11) in some genera fused to anal shield or completely reduced. Anal shield bell-shaped. All species of the order are capable of complete volvation, where the head and collum fit into the sphere, while the bell-shaped anal shield engulfs the anterior margin of the enlarged second tergite. Second tergite usually with a groove ('schisma') to accommodate the tergite tips of the following segments during volvation. All tergites thick and, with the exception of some troglobionts, heavily calcified. Pleurites present ventrally as large sclerotized plates between tergites and stigmatic plates. Stigmatic plates loosely articulated to the coxae, carrying spiracles. Sternites completely reduced. Legs consisting of six podomeres (coxa, prefemur, femur, postfemur, tibia, tarsus). Legs long, but, like antennae, compressed laterally. Tarsi with numerous spines, an apical claw and spine, always lacking a paronychium. Coxal pores absent. Leg-pair 17 in males usually modified, with only three or four podomeres distal to coxa, reduced in size ('paratelopods'). Leg-pair 18 in some species (Glomeridellidae) modified into anterior telopods, in others forming a slightly modified second paratelopod, again with only three or four podomeres distal to coxa. Leg-pair 19 always largest, modified into telopods, consisting of a medially fused syncoxite with a central lobe and two inner horns, as well as three- or four-segmented telopodites, often genus-characteristic in shape. Male gonopore opening through a special pouch fused to posterior side of coxa 2. Female sexual opening located in a special, often sclerotized pouch located between leg-pairs 2 and 3.

Development hemianamorphic.

34 genera, more than 300 species, North Africa, Europe through the Caucasus to Iran, isolated findings in central Asia, SE Asia from Nepal to Japan, North Korea to Java and Sulawesi, America from California to Guatemala, and eastern USA.

Family GLOMERIDELLIDAE Cook, 1896. — Male leg-pair 18 modified into anterior telopods. Outer palps of gnathochilarium with only 2-18 sensory cones. Mandible unknown. Two genera, 22 or 23 species, western Spain and France, eastern Alps, Balkans, Caucasus and Asia Minor.

Glomeridella Brölemann, 1913. — Tergite 11 vestigial, visible only laterally. Anal shield without knobs, well-rounded. Opening of Tömösváry organ ridged. Median lobe of syncoxite of posterior telopods simple, podomere 2 of anterior telopods elongated. Tergites pubescent. Species usually less than 7 mm. Seven or eight species, Spain and France, eastern Alps and Balkans. *G. kervillei* (Latzel, 1894).

Typhloglomeris Verhoeff, 1898. — Tergite 11 normally developed. Anal shield in male with two characteristic paramedian tubercles at caudal margin. Opening of Tömösváry organ smooth. Median lobe of syncoxite of posterior telopods trilobate, podomere 2 of anterior telopods swollen. Species up to 11 mm long. Ca. 15 species, many troglobionts, Balkans, Caucasus, Asia Minor.

Family PROTOGLOMERIDAE Brölemann, 1813. — Telopods with four podomeres distal to syncoxite, forming pincers. Telopoditomeres 1-3 of telopod lacking trichosteles (a finger-shaped process with a flagellum on top). Telopoditomere 2 with a non-membranous immovable finger located almost parallel to telopoditomere 3. Mandible with a small condylus. Thoracic shield always with numerous striae. Ommatidia present. Four genera, 20 species, distributed disjunctly in Spain, eastern Mediterranean, Algeria and Sicily, America from Guatemala to California.

Eupeyerimhoffia Brölemann, 1913. — Tergite 11 dorsally reduced. Process of telopoditomere 2 of telopod short and stout. Male leg-pair 17 with four podomeres. Outer palps of gnathochilarium as large as inner palps. One of the largest Glomerida, 18-22 mm long. Two species, Algeria and Sicily.

Glomerellina Silvestri, 1908. — Tergite 11 dorsally reduced. Male leg-pair 17 with three podomeres. Small, less than 6 mm long. Lacking pigment. Antennal grooves present. Two species widespread in the eastern Mediterranean (through historic human commerce?).

Glomeroides Chamberlin, 1922. — All 11 tergites present. Male leg-pair 17 well-developed, with five podomeres. 6-17 mm long. Ommatidia present, except for numerous troglobionts. Outer palps much smaller than inner palps. 15 species, Guatemala to California.

Protoglomeris Brölemann, 1897. — Tergite 11 dorsally reduced. Male leg-pair 17 with four podomeres distal to syncoxite. Up to 15 mm long. Antennal grooves absent. Coxae mesally with a short cone-shaped projection. One species, NE Spain.

Family GLOMERIDAE Leach, 1815. — Telopods with a variable number of podomeres, but telopoditomeres 2 and/or 3 always with some lamellar outgrowth, often with trichosteles on first three telopoditomeres. Mandible without a condylus. Ca. 250 species organized in four subfamilies with 28 genera.

Subfamily HAPLOGLOMERINAE Mauriès, 1971. — Telopod 'simple' and elongated, only second telopoditomere with a membranous extension. Trichosteles either missing or only present on first telopoditomere, or only present on first and second telopoditomeres. Only telopoditomere 2 with a lamellar outgrowth. Potentially an artificial grouping due to parallel reductions in telopod structures. Disjunct distribution in western Europe, Vietnam, Sumatra and Java. Ca. 16 species in nine genera.

Annameris Verhoeff, 1915. — Thoracic shield anteriorly of schisma unusually concave, almost of a swollen appearance, withmore than 14 striae. Up to 20 mm long. Telopods similar to those of *Apiomeris* and *Haploglomeris*. One species, Vietnam.

Apheromeris Silvestri, 1917. — Telopoditomeres 1 and 2 of telopods without trichosteles. Little-known genus. Three species, Java.

Apiomeris Cook, 1896 and ***Malayomeris*** Verhoeff, 1910. — Body dark brown without colour pattern. Male anal shield with two characteristic tubercles. Thoracic shield with 10 or 11 striae, of which five or six crossing the dorsum. Telopods lacking trichosteles, telopoditomeres 2 and 3 fused to a strongly sclerotized, strongly swollen process. Telopoditomeres 3 and 4 forming a pincer. One species each, Sumatra.

Haploglomeris Verhoeff, 1906. — Trichostele absent from first and second telopoditomeres. Four or five species, central Europe and the western Balkans. Potential synonyms are ***Simplomeris*** Verhoeff, 1936, one species, Switzerland, and ***Schismaglomeris*** Verhoeff 1909, one species, *S. occultocolorata* (Verhoeff, 1892) (Plate XII F), Portugal, both genera only known from the original descriptions.

Hyperglomeris Silvestri, 1917. — Four species, Vietnam. Four apical cones on the antennae.

Peplomeris Silvestri, 1917. — Two species, Vietnam. Numerous apical cones on the antennae.

Subfamily GLOMERINAE Leach, 1815. — Telopods generally stout, telopoditomere 2 lacking a complex, distomesal ougrowth. Telopoditomeres 1-3 usually with trichosteles. Four genera, ca. 90 species.

Cantabromeris Mauriès, 2005. — Blackish, more than 10 mm long. Tergite 11 vestigial. Telopoditomere 1 with a small trichostele, telopoditomere 2 with a large, lobe-like projection forming a chela with telopoditomeres 3 and 4. Male leg-pair 17 strongly developed, with 5 podomeres. One species, S Spain.

Glomeris Latreille, 1802. — Always with a colour pattern, except for troglobionts. Telopods only slightly variable, usually with a large, simple, subtriangular, caudomesal lobe on telopoditomere 2 forming neither an obtuse angle to the telopoditomere proper nor a distinct membranous sac on top. Species variable in size, but mainly 10-20 mm long. Male leg-pair 17 reduced, with a maximum of five podomeres, always without spiracles. Ca. 80 species, North Africa, Canary Islands, Europe and Turkey. *G. annulata* Brandt, 1833, *G. balcanica* Verhoeff, 1906, *G. connexa* C. L. Koch, 1847, *G. euganeorum* Verhoeff, 1926 (Plate XII C), *G. hexasticha* Brandt, 1833, *G. intermedia* Latzel, 1884 (Plate I B), *G. klugii* Brandt, 1833, *G. marginata* (Villers, 1789) (Plate I B), *G. oblongoguttata* Verhoeff, 1894 (Plate XII B), *G. pulchra* C. L. Koch, 1847, *G. pustulata* (Fabricius, 1781), *G. romana* Verhoeff, 1900.

Loboglomeris Verhoeff, 1906. — Always a vivid colour pattern. Males with a stridulation organ on posterior side of telopods and at inner margin of anal shield, a character unique for the order. Large (more than 18 mm), colourful species. Three species, NE Spain. *L. pyrenaica* (Latzel, 1886), *L. rugifera* (Verhoeff, 1906).

Onychoglomeris Verhoeff, 1909. — Whitish to brownish, lacking a colour pattern. Telopod telopoditomeres 1 and 2 without trichosteles. Telopoditomere 2 with a large lobe-like projection forming a chela with telopoditomeres 3 and 4. Male leg-pair 17 with six podomeres, almost unmodified, with spiracles. This genus might contain the largest species of the order, 20-25 mm in length. Six species, northern Italy and the Balkans.

Subfamily DODERIINAE Silvestri, 1904. — Telopods usually enlarged and stout, rarely elongated, telopoditomere 2 with a strongly differentiated distocaudal process. 14 genera, ca. 132 species, distributed across the whole range of the order.

Adenomeris Ribaut, 1909. — Special ducts at the posterior margin of each tergite, secreting rod-shaped secretion. Blind. Tergite 11 present. One of the smallest members of the Glomerida, only 2-3 mm long. Two species, eastern Spain and southern Great Britain.

Doderia Silvestri, 1904. — 3-4 mm long. Blind. Posterior half of tergites with massive prominent crests. Tergite 11 present. Five species, SE France, Corsica, N Italy.

Epiromeris Strasser, 1976. — 8-15 mm long. Surface smooth. Tergite 11 extending into a process projecting above anterior part of anal shield. Head with neither a crest nor antennal grooves. One species. Greece.

Geoglomeris Verhoeff, 1908. — Antennomere 7 large, half as long as antennomere 2. Surface smooth. Blind. 3-5 mm long. Tergite 11 present. Outer palps of the gnathochilarium with only three sensory cones. Three or four species, southern and central Europe. *G. subterranea* Verhoeff, 1908.

Hyleoglomeris Verhoeff, 1910 (Plate XI D). — Telopoditomere 1-3 of telopods with trichosteles, telopoditomeres 2 and 3 each also with a large outgrowth. Outgrowth, especially that on telopoditomere 2, large and apically differentiated. Highly variable, 5-16 mm long. Ommatidia present, except for troglobionts. Tergite 11 present. Over 90 species, Eurasia, from Japan and Sulawesi to Balkans. *H. faberi* Makarov et al., 2013, *H. japonica* Verhoeff, 1936.

Nearctomeris Wesener, 2012. — Telopods similar to the morphologically diverse genus *Hyleoglomeris*. With ommatidia. 4-6 mm long. Tergite 11 present. One species, eastern USA.

Onomeris Cook, 1896. — Head with a conspicuous Y-shaped crest and antennal grooves. With ommatidia. 4-6 mm long. Tergite 11 present. Three species, eastern USA. *O. sinuata* (Loomis, 1943).

Rhopalomeris Verhoeff, 1906. — Antennomere 6 greatly enlarged, larger than 3-5 combined, axe-shaped. Antennomere 7 therefore very wide, carrying a disc with numerous sensory cones. Ommatidia and tergite 11 present. Quite large, 16-25 mm long. Three species, Myanmar, Thailand and Malaysia.

Rhyparomeris Ribaut, 1954. — Antennomere 7 small. Entire dorsal surface of head and tergites clothed with small flattened granulations (coagulated secretion) and short pubescence. Blind. Tergite 11 present. Telopods much like in *Hyleoglomeris*. One species, cave-dwelling, NE Spain.

Spelaeoglomeris Silvestri, 1908. — Antennomere 7 small, less than one third the length of antennomere 2. Blind. 4-7 mm long. Tergite 11 present. Head capsule not extending apically to organ of Tömösváry. Four species, France and Spain. *S. doderoi* Silvestri, 1908.

Strasseria Verhoeff, 1929. — 4 mm long. Habitus similar to *Trachysphaera*, but lacking any tubercles or papillae. Posterior margin of each tergite with a dirt-encrusted crest. Colour olive-greenish. Tergite 11 free. One species, Slovenia.

Stygioglomeris Brölemann, 1913. — Antennomere 7 large, as long as antennomere 2. Blind. Unpigmented. 3-5 mm long. Tergite 11 present. Outer palps of the gnathochilarium with only three sensory cones. Five species, southern France and northern Italy, as well as southern Great Britain. Potentially synonymous with *Geoglomeris*.

Tectosphaera Mauriès, 2005. — 3-4 mm long. Thoracic shield laterally with a circular groove to accommodate the lateral tips of the tergites during volvation. Surface smooth. Tergite 11 extending into a process projecting above anterior part of anal shield. Head with a Y-shaped crest and antennal grooves. One species, NW Iberia.

Trachysphaera Heller, 1857. — 3-5.5 mm long. Thoracic shield laterally with a circular groove to accommodate the lateral tips of the tergites during volvation. Surface particular, posterior half of tergites with tubercles and special crests, papillae and other structures also often present. Tergite 11 fused to anal shield. Several cave endemics. 30 species, Europe, Crimea, Caucasus, Turkey and NW Iran. *T. costata* (Waga, 1857), *T. lobata* (Ribaut, 1954) (Plate XI E).

Subfamily MAURIESIINAE Golovatch, 2010. — Telopod stout, podomere 1 reduced in size, with a mesal trichostele. Second podomere with a strongly developed basal apophysis and a strongly developed distal finger. Podomere 3 with a distal finger. One genus, Taiwan.

Mauriesia Golovatch, Mikhaljova & Chang, 2010. — One species, *Mauriesia splendida* Golovatch, Mikhaljova & Chang, 2010, Taiwan.

Infraclass HELMINTHOMORPHA Pocock, 1887

[THOMAS WESENER]

Head capsule with a transverse suture, an occipital phragma present. Genae (parietal sclerites) present. Labrum with three teeth (reduced in Colobognatha). Absence or presence of ommatidia order-, family-, genus- or species-specific. Organ of Tömösváry either a small pit or absent. Antennae with seven podomeres plus disc (very rarely with eight antennomeres plus disc), disc carrying four, in very few genera more, apical cones. Various sensilla, including sensilla basiconica, usually present on antennomeres, especially fifth and sixth. Epipharynx attached to head. Mandible with one or two basal articles (cardo and stipes) and a gnathal lobe. Gnathal lobe always lacking a condylus. Gnathochilarium variable, order-specific, but lamellae linguales always separated from one another. Tentorium attached to head at incisura lateralis. Defence glands present, paired, opening

through lateral ozopores. Trunk with 19-220 segments, and 30-375 leg pairs, and corresponding undivided sternites with fused stigmatic plates surrounding coxae. Sternites, stigmatic plates, pleurites and tergites ranging from free to forming a completely fused ring with barely visible or untraceable sutures. Spiracles absent from first two segments. Tracheae not branching (except for those supporting spinning glands in Nematophora). Tracheae leaving tracheal pouch in a tuft. Intestine a simple, straight tube. Legs consisting of six (coxa, prefemur, femur, postfemur, tibia, tarsus), rarely seven (coxa, trochanter, prefemur, femur, postfemur, tibia, tarsus) or eight (coxa, trochanter, prefemur, femur, postfemur, tibia, tarsus 1, tarsus 2) podomeres. Coxal pores present or absent. Male gonopores opening directly through coxae 2, or through 'penes' located behind leg pair 2. Posterior male leg pairs never modified into telopods, but at least one leg pair of male segment 7 transformed into gonopods, modified for sperm transfer.

Sperm transfer always direct, mostly via gonopods (= spermatopositors). Development by anamorphosis, juveniles hatching with three, rarely four (Colobognatha) exceptionally (*Pachyiulus* spp.) more than 20 leg pairs.

Ca. 9000 species in 12 orders, distributed worldwide except Antarctica.

Subterclass COLOBOGNATHA Brandt, 1834

[THOMAS WESENER]

Adult body size 5-70 mm, body usually flattened. Head capsule small, extended anteriorly, lacking a median suture, but occipital phragma usually present. Labrum without teeth. Eyes with one to four ommatidia (Siphonocryptida, Polyzoniida), or lacking (Platydesmida, Siphonophorida). Organ of Tömösváry absent. Antennae with seven antennomeres, disc always carrying four apical cones. Mandibles more or less strongly reduced, sometimes with a single, very slender, laterally barely visible basal article (*Brachycybe*). Gnathal lobe more or less strongly modified. External tooth of gnathal lobe absent, internal tooth reduced or rarely absent (Siphonophorida: Siphonophoridae), molar plate very small or absent. Pectinate lamellae usually present (except in Siphonophorida: Siphonophoridae). Gnathochilarium with order-characteristic modifications, often forming a hypostoma and a single plate, rarely with a mentum, a promentum and stipites (Platydesmida). Always lacking palps, although special ridges ('pseudopalps') might resemble them. Hypopharynx absent. Epipharynx greatly reduced, only a sclerotized plate instead of fields with spines is present (Platydesmida), or it is even more strongly modified into a 'driller' type structure whose homology is unknown (Polyzoniida). Tentorium present, lateral arms touching head capsule, but not forming an incisura lateralis. Ozopores present, starting from segment 5. Defensive secretions variable, in most groups still unknown. Trunk with 28-192 segments, 45-375 leg pairs. Apparently, mature adults of both sexes of the same species often show great variation in segment number (e.g. 90-182). Sternites fused with stigmatic plates, always free. Pleurites and tergites either free (Siphonophorida, Polyzoniida) or fused with tergites (Siphonocryptida, Platydesmida). Tergites with a dorsal suture in orders where terga and pleura are fused. Sternites with a special nodal point, serving for

muscle attachment instead of the weakly developed tracheal pouches. Legs usually (except in narrow-bodied Platydesmida) in dorsal view covered by the tergites, consisting usually of six (coxa, prefemur, femur, postfemur, tibia, tarsus), in one order (Platydesmida) of seven (coxa, trochanter, prefemur, femur, postfemur, tibia, tarsus), podomeres. Tarsi often with special setae, spines or a paronychium next to the claw. Posterior leg-pair of segment 7 and anterior pair of segment 8 (= legs 9 and 10) modified into gonopods. Gonopods, especially the posterior pair, in some cases still closely resembling legs, usually with 6 or 7 podomeres, apical podomeres elongated and sometimes modified. Coxal pouches present, starting from coxa 3. Male gonopores opening mainly directly through, or in some Siphonocryptida (*Hirudicryptus*) and Polyzoniida (Polyzoniidae and Siphonotidae) behind, the second coxa.

Development by euanamorphosis, first juveniles hatching with four pairs of legs. Males (Platydesmida) or females often guard eggs and juveniles.

Four orders with 8 families and more than 240 species.

Order Platydesmida de Saussure, 1860

Body 7-60 mm long. Two distinct habitus types: a short body with wide paranota or a very slender, elongated body with very short (rarely none) paranota. Head capsule small, pyriform, posteriorly wide, sometimes with laterally projecting lobes. Ommatidia absent, but grooves created by lateral lobes sometimes producing a structure resembling eyes. Antennae slender, antennomeres longer than broad. Mandible basal joint completely reduced to a long, narrow sclerite barely visible laterally. Gnathal lobe slightly distorted, elongated, especially the area with pectinate lamellae elongated. Gnathochilarium large, especially stipites, with usual sclerites, lacking palps. Stipites sometimes with ridges and setae resembling palps. Trunk with 27-110 segments, often with a very large range between mature individuals of the same species. Ozopores starting from segment 5, often located on lateral paranota in a genus-specific position. Composition of secretion unknown. Tergites hirsute and tuberculate, very rarely glabrous. Tergites in some cases with two very large, paramedian, sclerotized and sharpened knobs. Tergites and pleurites strongly fused, without a visible suture, sternites free. Tergites with a strongly developed dorsal suture. In most cases metazonites with horizontal paranota, prozonites particularly narrow. Sterna large, either widely separating coxae (Platydesmidae) or with a large central cone located between the coxae (Andrognathidae). Tracheal pouch apodemes biramous. Legs consisting of seven podomeres (coxa, trochanter, prefemur, femur, postfemur, tibia, tarsus), albeit trochanter often hard to detect. Male leg pairs 9 and 10 modified into gonopods, these being leglike and consisting of distinct podomeres. Number of podomeres variable, but usually both anterior and posterior gonopods consisting of seven podomeres. Apicalmost podomeres often modified. Posterior gonopods usually slenderer than anterior ones, with apical setae. Male gonopore opening directly through coxa 2.

First juveniles hatching with four pair of legs. Males curl around to guard eggs and juveniles.

Two families with 62 species, North and Central America to Panama in the South; SE Asia, including Japan, Korea, mainland China and Taiwan; European Mediterranean, including Caucasus.

Family PLATYDESMIDAE de Saussure, 1860. — Sternites very wide, coxae of legs well separated from one another. Trunk always short with strongly elongated paranota. 15-34 mm long. Two genera with 30 species, Mexico to Panama (Brazil?) in the South.

Desmethus Chamberlin, 1922. — Wide and short. 15-20 mm long. Tergites with a fine layer of setiferous tubercles. Anal segment at posterior margin with small round tubercles carrying setae. Last tergite not surpassing anal valves. Two species, Costa Rica, Guatemala, Panama.

Platydesmus Lucas, 1843 (Plate I C). — Wide and relatively short. Paranota very long, in anterior segments curved anteriorly. 27-52 segments. Surface covered with several rows of tubercles, but never fine, setiferous ones. Anal segment at posterior margin with small, triangular, setiferous tubercles. Last tergite surpassing anal valves. 28 species, Mexico to Panama in the South. *P. lineatus* Pocock, 1903.

Family ANDROGNATHIDAE Cope, 1869. — Sternites narrow, coxae almost in touch medially, but separated by a knob-like extension of sternite. 7-44 mm long. Two divergent habitus types: a short trunk with wide paranota or a very slender, elongated trunk with very short (rarely none) paranota. 12 genera with 36 species, North America, SE and East Asia, including Japan and China, European Mediterranean.

Andrognathus Cope, 1869. — Very long and slender, more than 40 times longer than wide. Paranota short, triangular, those of segment 5 greatly enlarged, with two lobes (a unique character). Body length 12-24 mm, 45-70 segments. Collum wide, but narrow. Terga with setae and tiny tubercles. Hypoproct (subanal scale) lacking. Ozopores opening through large, cone-shaped tubercles. Two species, eastern USA, Mexico.

Brachycybe Wood, 1864. — Colour variable. Trunk very wide, paranota strongly elongated. Terga tuberculate, but glabrous. Eight species, USA, South Korea, Japan, mainland China, Taiwan. *B. lecontii* Wood, 1864, *B. nodulosa* (Verhoeff, 1935), *B. producta* Loomis, 1936, *B. rosea* Murray, 1877.

Dolistenus Fanzago, 1874. — Very slender, thread-like. Paranota very short, rectangular. Body length 6.5-35 mm, 33-108 segments. Tergites densely pilose, apparently without tubercles. Three species, Western Iberia, Italy, Croatia, Greece. *D. savii* Fanzago, 1874.

Ebenostenus Mauriès, 2015. — Monotypic, SW Spain. Metazonites dorsally divided transversally. Body length 12-18 mm, 44-58 segments. Tergites without tubercles. *E. iberoniger* Mauriès, 2015.

Fioria Silvestri, 1898. — Slender, paranota short. Body length 7-14 mm, 28-61 segments. Collum with tubercles. Tergites bent anteriorad, densely pilose, with two rows of round tubercles. Four species, Portugal, Italy, Greece, Caucasus together with adjacent parts of Iran.

Gosodesmus Chamberlin, 1922. — Dark brown to reddish-pink. Long and slender, with short, well-developed, rectangular paranota. Body length 17.5-27 mm, 47-74 segments. Collum large and rectangular, with two or three rows of tubercles. Legs long. One species, western USA (California).

Ischnocybe Cook & Loomis, 1928. — Trunk long and relatively slender, pink. 15-19 mm long, 46-55 segments. Collum wide but narrow, without tubercles. Tergites with tuberculate paranota. Legs long, exceeding paranota. One species, western USA (California).

Mitocybe Cook & Loomis, 1928. — Very long and slender. Paranota present, but only small lateral swellings. 14-25 mm long, 80-110 segments. Collum large and circular. Tergites smooth and densely pilose. Legs very short, not even exceeding pleura. One species, western USA (California).

Plutodesmus Silvestri, 1903. — Large, with relatively wide paranota. Body length 18-22 mm, 46-51 segments. Tergites, including paranota, with 4-5 rows of tubercles. One species, Greece.

Pseudodesmus Pocock, 1887. — Colour variable. Trunk wide, paranota strongly elongated. Body length up to 60 mm, 66-76 segments. Collum with tubercles. Tergites densely pilose, strongly sculptured, with several smaller and one row of larger tubercles. Larger tubercles sometimes forming a ridge or resembling conic spines. Nine species, SE Asia.

Symphyopleurium Attems, 1951. — Reddish. Slender, paranota short. Body 10-16.5 mm long, 43-60 segments. Collum densely pilose, without tuberculations. Tergites pilose, with tubercles not reaching paranota. Margins of paranota without indentations. Opening of defence glands in posterolateral corner. Three species, Japan.

Yamasinaium Verhoeff, 1939. — Grey-yellowish. Slender, paranota short. Body length 8.5-28 mm long, 38-75 segments. Collum with setae and two rows of tuberculations. Tergites, including paranota, with tubercles, covered with short, dense setae. Paranota margins indentate. Three species, Japan (Okinawa), Korea and Taiwan. *Y. noduligerum* Verhoeff, 1939.

Order Siphonocryptida Pocock, 1894

Body lenght 5-15 mm. Head capsule small, pyriform. Two black ommatidia on each side of head. Colour pattern sometimes vivid. Antennae thick, podomeres 1-6 subequal in length, podomere 7 much smaller. Mandibles not studied. Gnathochilarium only superficially studied, apparently consisting of a gula and a single plate with 2 + 2 or 3 + 3 large and several smaller setae. Trunk with 31-55 segments. Ozopores starting from segment 5, located on special peritremata at lateral margin of tergites. Composition of secretion still unknown. Tergites mainly glabrous, with a transverse row of tubercles near caudal margin. Tergites and pleurites fused. Dorsal suture present on all tergites. Last tergite completely overlapping telson, the latter being invisible in dorsal view, at least sometimes fused to penultimate paraterga. Sterna and stigmatic plate 0.8-1.5 as wide as coxa. Legs consisting of six podomeres (coxa, prefemur, femur, postfemur, tibia, tarsus). Tarsi lacking an accessory claw. Male leg pairs 9 and 10 modified into gonopods, these being leglike and consisting of distinct podomeres. Posterior gonopods usually slenderer than anterior ones. Male gonopore opening either directly through (*Siphonocryptus*) or behind coxa 2 (*Hirudicryptus*).

First juveniles still unknown. An adult was observed (Wesener, pers. obs.) guarding young in *Hirudicryptus*, but the sex was not noted.

Second smallest millipede order in terms of species diversity. A single family with two genera and seven species, disjunct (relict?) distribution in Canary Islands and Madeira, Nepal, Taiwan, Malaysia and Sumatra.

Family SIPHONOCRYPTIDAE Pocock, 1894. — Two genera.

Hirudicryptus Enghoff & Golovatch, 1995. — Trunk elongated, at least four times, often even more, longer than wide. Anterior terga overlapping following ones. Head with frontal setae. Collum crescent-shaped, without 'ears'. Male penes attached to posterior margin of coxae 2. Four species, Canary Islands and Madeira, Caucasus, Nepal, and Taiwan. *H. canariensis* Loksa, 1967, *H. taiwanensis* Korsós, Enghoff & Chang, 2008 (Plate I F).

Siphonocryptus Pocock, 1894. — Trunk very wide and rounded, only two to three times longer than wide. Anterior terga overlapping preceding ones. Head without frontal setae. Collum with subrectangular lobes ('ears'). Male penes opening through coxa. Three species, Malaysia, Sumatra.

Order Siphonophorida Newport, 1844

Length 5-70 mm. Trunk usually very slender, width/length ratio less than 1/10. Head capsule small, either pyriform or strongly elongated into a beak. Ommatidia absent. Antennae stout, antennomeres 5 and 6 usually thicker than others. Basal joint of mandibles completely reduced to unusual sclerites, gnathal lobe heavily (Siphonorhinidae) or almost completely reduced (Siphonophoridae). Gnathochilarium strongly modified, either with three sclerites (mentum and stipites?, Siphonorhinidae) or different sclerites completely indiscernible (Siphonophoridae). Trunk with up to 192 segments, being the 'leggiest' millipedes. A range of 50-182 segments is possible in sexually mature adults of the same species. Ozopores starting from segment 5, often located on lateral metatergal projections. Composition of secretion unknown. Tergites either glabrous or, more usually, hirsute. Tergites at least in numerous species with anchor-shaped projections. Tergites, pleurites and sternites free. Tergites without a dorsal suture. In most cases, metazonites with lateral extensions, prozonites therefore appearing particularly narrow. Sterna large, especially the stigmatic part, but coxae almost in touch with each other. Legs consisting of six podomeres (coxa, prefemur, femur, postfemur, tibia, tarsus). Tarsi always with an accessory claw. Male leg pairs 9 and 10 modified into gonopods, these being leglike and consisting of distinct podomeres. Number of podomeres variable in anterior gonopods, posterior gonopods usually with five to seven podomeres. Posterior gonopods usually slenderer than anterior ones. Male gonopore opening directly through coxa 2.

First juveniles with four pair of legs.

14 genera with 115 species, tropical and subtropical regions of America (up to southern USA), southern Africa, numerous islands, Asia (up to northern Pakistan in the north), eastern Australia and New Zealand.

Family SIPHONORHINIDAE Cook, 1895. — Head pyriform, subtriangular, not extended into a 'beak', devoid of setae. Antennae elbowed (geniculate) between antennomeres 3 and 4, pits of sensory cones on antennomeres 5 and 6 absent, only a field of sensilla basiconica present. Antennomere 2 twice as long as 3. Last podomere of posterior gonopod divided into two or more branches. Containing the 'leggiest' millipedes with 192 segments and 750 legs. Four genera with 11 species, western USA (California), southern Africa, Madagascar, India, Vietnam, Laos, Cambodia, Indonesia.

Illacme Cook & Loomis, 1928. — 'Leggiest' millipede known, with 192 segments and 750 legs. Up to 44 mm long and 0.65 mm wide. Can secrete silk-like substance from tergal pores. Anterior and posterior gonopods consisting of six podomeres, apical podomere of posterior gonopod divided into three branches. One species, *Illacme plenipes* Cook & Loomis, 1928, California.

Siphonorhinus Pocock, 1894. — 10-50 mm long. Coxae 1 fused with the sternite. Apical podomere of posterior gonopod divided into two branches lacking spines. Eight species, Indonesia, Vietnam, Cambodia, Laos, India, Madagascar.

Nematozonium Verhoeff, 1939. — Very slender, less than 0.5 mm wide and up to ca. 30 mm long, hirsute, 25-182 segments. Anterior and posterior gonopods each with six podomeres. Apical podomeres of posterior gonopod divided into ventral and dorsal branches with a small spine. One species, South Africa.

Kleruchus Attems, 1938. — 110-135 segments, 35-45 mm long, 1.5-2 mm wide. Mandible with four pectinate lamellae. Anterior telopod with six, posterior with seven podomeres. First leg-pair of male modified, thickened. Coxae 1 loosely articulated with the sternite. One species, Vietnam.

Family SIPHONOPHORIDAE Newport, 1844. — Head strongly extended into a beak whose lower half is formed by gnathochilarium. Head with four macrosetae. Antennae straight and elongated, antennomeres 5 and 6 with a large, conspicuous pit with numerous sensory cones. Antennomere 2 as long as the others. Last podomere of posterior gonopods (when known) apparently undivided. Species in some cases very slender and greatly elongated, with up to 190 segments and 742 legs. Ten genera with 104 species distributed in America, SE Asia (including N Pakistan), Madagascar, Australia and New Zealand.

Balizonium Attems, 1930. — Collum laterally overlapping head in several steps. Anterior gonopods with four podomeres, last podomere twice as long as basal three combined. Beak three fourth as long as head. Suggested to be similar to *Siphonacme*. One species, Indonesia (Bali).

Columbianum Verhoeff, 1941. — Beak reaching four fiths of head length. Anterior gonopods with six or seven podomeres. Up to 120 segments. Four species, Columbia and Peru.

Gonatotrichus Attems, 1951. — Tiny, 5-6 mm long, 0.6-0.8 mm wide, with 30-45 segments. Two species, Malaysia and Seychelles.

Linozonium Attems, 1951. — Trunk worm-like, extremely elongated. Anterior gonopods with six, posterior gonopods with five podomeres. Anterior gonopods simple, similar to those of *Siphonophora* with which this genus might be synonymous. One species, Mexico.

Lomboknium Jeekel, 2001. — 46-78 segments, less than 10 mm long. Anterior gonopods with four or five podomeres, penultimate one longest, last podomere short, thick, unciform. Close to *Gonatotrichus*. Three species, Indonesia (Bali, Java, Lombok).

Okeanozonium Verhoeff, 1941. — 10-23 mm long, 48-67 segments. Anterior gonopods with three or four podomeres, posterior gonopods with six. Antennomeres 3-5 as wide as long. One species, Palau.

Pterozonium Attems, 1951. — Ca. 20 mm long, 1.5 mm wide. Anterior gonopods with five, posterior gonopods with six podomeres. The only genus in the order with paranota. Six species, Seychelles, Malaysia, Sri Lanka, Indonesia.

Rhinosiphora Verhoeff, 1924. — 10-18 mm long, 43-70 segments. Anterior gonopod with five podomeres, third with several setae and slenderer than podomere 1. Podomeres 4 and 5 very slender, elongated. One species, Australia (Queensland).

Siphonacme Cook & Loomis, 1928. — Anterior telopods with five or six podomeres, last podomere of anterior telopods as long as basal three combined. Five species, Vietnam, Cambodia, Laos, Japan(?), Mexico, Panama.

Siphonophora Brandt, 1837. — This genus probably contains a polyphyletic assemblage of species. Currently 80 species, mainly America, with a single species each in Pakistan, Sri Lanka, Vietnam, Myanmar, Malaysia, Indonesia, Philippines, New Caledonia, New Guinea, Australia (Queensland), Fiji, Solomon Islands, New Zealand (here, *S. zelandica* Chamberlin, 1920, Plate I E).

Order Polyzoniida Gervais, 1844

Members 10-15 mm, rarely 4-50 mm long, habitus flat, usually wide, width/length ratio from less than 1/10 to 1/3. One genus (*Cylichnogaster*) capable of limited volvation (unique in Colobognatha). Head capsule small, pyriform, elongated into a well-rounded, rarely sharp-edged (*Orsiboe*) snout. Eyes located laterally, usually with 3 + 3 (rarely 1 + 1, 2 + 2 or 4 + 4) ommatidia. Between the ommatidia with two macrosetae. Antennae relatively thick, antennomeres of equal size, rarely more than two times longer than wide. Mandible basal joint reduced to a slender sclerite, gnathal lobe partly

reduced. Gnathochilarium heavily modified, three sclerites (mentum and stipites?) often still discernable. Ozopores often starting from segment 5, located at the lateral corners of the tergites. Composition of secretion variable, often strongly smelling, polyzonimine, buzonamine, β-pinene and limonene are common. Poison frogs from Madagascar and South America apparently obtain parts of their poison from Polyzoniida. Trunk with as little as 20 up to 88 segments, huge variation in number of segments possible between mature individuals of the same species. Tergites glabrous or hirsute, without any large surface structures. Colour often conspicuous yellowish or even pink, sometimes with characteristic black bands. Tergites, pleurites and sternites free, only rarely are tergites and pleurites fused (*Dawydoffia*). Tergites without a dorsal suture. Posterior margin of tergites in one family (Hirudisomatidae) conspicuously upturned. Sterna large, but coxae almost touching one another. Legs consisting of six podomeres (coxa, prefemur, femur, postfemur, tibia, tarsus). Tarsi in one family (Siphonotidae) with an accessory claw or paronychium. Coxal sacks starting from leg 3. Male leg pairs 9 and 10 modified into gonopods which are usually leglike and consist of distinct podomeres. Number of podomeres variable in the anterior gonopods, posterior gonopods usually with 5-7 podomeres. Last podomeres often modified. Posterior gonopod, especially last podomere, usually slenderer than anterior gonopod. Male gonopore located posterior to coxa 2, rarely opening through the coxa (Hirudisomatidae).

First juveniles with four leg pairs. Female protects eggs.

72 species in 23 genera. Distribution worldwide, but in Africa only in South Africa and Madagascar. One species a worldwide tropical tramp.

Family POLYZONIIDAE Gervais, 1844. — Posterior tergal margin normal, closely touching succeeding tergite. Telson narrow. Collum rarely overlapping part of head. Male gonopore located posterior to coxa 2 (except for *Angarozonium*, which resembles Hirudisomatidae). Tarsal claws without paronychium. Tergites always without tubercles. Animals sluggish. Six genera with 20 species, Europe, western and eastern USA, Mongolia, Siberia and SE Russia and NE China.

Angarozonium Shelley, 1997. — Trunk very wide (usually three to four times longer than wide), up to 11 mm long, with 30-45 segments. Yellowish with few brown spots. Penes elongated, overlappping coxa 6, positioned in caudoventral position. Coxa of anterior gonopod with complex lobe, consisting of two branches; apicalmost podomere simple, densely setose. Five species, Siberia and SE Russia, Mongolia, Korea, NE China.

Bdellozonium Cook & Loomis, 1928. — Slender (four to nine times longer than broad), 15-37 mm long, 35-77 segments. Yellowish. Eyes consisting of three or four ommatidia. Penes short. Anterior gonopod six-jointed, podomere 6 curving anteriorly. Ultimate podomere of posterior gonopod without setae. Two species, western USA (California).

Buzonium Cook & Loomis, 1928. — Large and wide (trunk 3-8 times longer than wide), up to 50 mm long, with 31-81 segments. Eyes consisting of two ommatidia. Penes elongated, overlapping coxa 5. Anterior gonopod six-jointed, podomere 6 small, curving in same axis as basal podomeres. Sterna of legs broad, coxae widely separated (unique character within the family). Labrum dentate, resembling a saw with numerous teeth (unique character within the order). One species, western USA. *B. crassipes* Cook & Loomis, 1928.

Petaserpes Cope, 1870. — Trunk wide (five times longer than broad), 8-15 mm long, 28-58 segments. Yellowish. Eyes consisting of 3 or 4 ommatidia. Penes short, reaching coxa 3. Coxa of

anterior gonopod with simple lobe; anterior gonopod six-jointed, podomere 6 elongated and curved. Posterior gonopods six-jointed, podomere 6 strongly elongated, straight and glabrous. Six species, eastern USA. *P. rosalbus* Cope, 1879.

Polyzonium Brandt, 1837. — Slender (5-8 times longer than broad), 5-20 mm long, 35-60 segments. Yellowish. Eyes consisting of three or four ommatidia. Penes elongated, overlapping coxa 6. Coxa of anterior gonopod with complex lobe, consisting of two branches; apical-most podomere complex, without setae. Anterior gonopod 5-jointed. Posterior gonopod six-jointed; ultimate podomere simple, elongated. Three species, Europe. *P. germanicum* Brandt, 1837 (Plate XIII A).

Stenozonium Shelley, 1997. — Trunk narrow (four to five times longer than wide), 6-16 mm long, with 30-48 segments. Light yellowish. Eyes consisting of three or four ommatidia. Penes short. Anterior gonopod six-jointed, podomere 6 curving anteriorly. Ultimate podomere of posterior gonopod with single barbed seta. Three species, western USA. *S. leonardi* Shelley & Shear, 2005.

Family SIPHONOTIDAE Cook, 1895. — Posterior tergal margin normal, closely in contact with succeeding tergite. Telson narrow. Male gonopore located posterior to coxa 2. Tarsal claws with paronychium. Animals quick and active. 11 genera with 29 species, South America, South Africa, Madagascar, SE Asia, New Zealand (one species an international tramp).

Bdellotus Cook, 1895. — One species, Java.

Burinia Attems, 1926. — Trunk narrow (nine to ten times longer than wide), 7-16 mm long, with 19-88 segments. Eyes consisting of two ommatidia. Gonopods leglike, anterior gonopods with 6, posterior gonopods with seven podomeres. Close to *Siphonotus*. 12 species, South Africa, South America (Brazil, Chile).

Cylichnogaster Verhoeff, 1937. — Trunk wide (two to three times longer than wide), 3-6 mm long, 20-26 segments. Eyes consisting of two ommatidia. Gonopods leglike, anterior gonopods and posterior gonopods with seven podomeres. Apparently able to roll into a ball, with uniquely curved tergites. Two species, South Africa.

Dawydoffia Attems, 1953. — Trunk wide (three times longer than wide), 10-12 mm long, ca. 38 segments. Reddish-brown with black pattern. Eyes consisting of 3 ommatidia. Gonopods leglike, anterior gonopods with seven, posterior gonopods with only four podomeres. Head completely covered by collum. Sternite 2 with conspicuous cone. Apparently pleura fused with terga. One species, Vietnam.

Metriozonium Attems, 1951. — One species, Java.

Rhinotus Cook, 1896. — One species, worldwide tropics. ***Siphonoconus*** Attems, 1930. — Perhaps five species, Indonesia (Java, Flores). Both with strongly modified anterior gonopods. *R. purpureus* (Pocock, 1894).

Rhynchomecogaster Verhoeff, 1937. — Trunk narrow (eight to nine times longer than wide), 16-22 mm long, 48-56 segments. Eyes consisting of two ommatidia. Tergites strongly setose. Gonopods leglike, anterior gonopods and posterior gonopods with 6 podomeres. Two species, South Africa.

Siphonotus Brandt, 1837. — Trunk narrow (nine to ten times longer than wide), 6-9 mm long, 42 segments. Reddish-purple colour. Eyes consisting of two ommatidia. Tergites smooth, with three transverse rows of setae. Metaterga with unique mid-dorsal impression. Gonopods leglike. Two species, Brazil.

Upsima Chamberlin, 1945. — One species, Java (Panaitan). ***Siphonetus*** Chamberlin, 1920. — One species, New Zealand. All in need of revision, some might turn out to be synonyms of the widespread tramp *Rhinotus purpureus*.

Family HIRUDISOMATIDAE Silvestri, 1896. — Posterior tergal margin upturned, elevated above succeeding tergites. Telson broad (rarely narrow). Collum overlapping

part of head up to posterior-most ommatidia. Male penes located ventrally on coxa 2. Tarsal claws without paronychium. Animals sluggish. Six genera with 23 species, Europe, Turkey, Azerbaijan, North America, Japan, Nepal.

Hirudisoma Fanzago, 1881. — Trunk broad or elongated (2.5-6 times longer than wide), 3-10 mm long, 20-36 segments. Telson hidden in dorsal view. Penes conical. Surface granulate. Eyes consisting of three ommatidia. Anterior and posterior gonopod with six podomeres. Anterior gonopod podomere 6 small, with strong, mesal, triangular and sharp-edged projection; sternite without lobes. Apical-most podomere of posterior gonopod slender and strongly elongated. Nine species, Europe, E Anatolia and Caucasus, east to W Azerbaijan.

Kiusiozonium Verhoeff, 1941. — Trunk relatively narrow (four to five times longer than wide), 7.5-23 mm long, 36-62 segments. Coloration tanned with variable number of stripes. Penes conical. Surface glabrous or with few fine setae. Eyes consisting of four ommatidia. Anterior gonopods with five podomeres, podomere 3 with a process. Posterior gonopods with six podomeres, elongated, podomere 6 simple, very slender. Antennomere 6 three times longer than wide. Two species, Japan. *K. okai* (Takakuwa & Miyosi, 1949).

Mexiconium Shelley, 1996. — Trunk narrow (five to six times longer than wide), 6-11 mm long, 27-35 segments. Penes conical. Surface smooth. Posterior tergal margin only weakly upturned. Eyes consisting of two ommatidia. Anterior and posterior gonopod with six podomeres. Anterior gonopod podomere 6 with ventral hirsute lobe, sternite with two large setose lobes. Podomere 6 of posterior gonopod simple, apically trifurcate. One species, Mexico.

Nepalozonium Shelley, 1996. — Trunk broad (2.5 times longer than wide), 3-5 mm long, 22-27 segments. Penes 'bottle'-shaped. Surface smooth and polished. Eyes consisting of three ommatidia. Anterior and posterior gonopod with six podomeres, anterior gonopod sternite with two setose lobes. Podomere 6 of posterior gonopod slender and strongly elongated. One species, Nepal.

Octoglena Wood, 1864. — Trunk broad (two to three times longer than wide), 3-20 mm long, 21-58 segments. Penes conical. Surface granular. Eyes consisting of three ommatidia. Anterior gonopod with six podomeres, podomere 6 divided, sternite with two setose lobes. Podomere 6 of posterior gonopod simple, fimbriate. Six species, USA, Canada.

Orsiboe Attems, 1909. — Head freely visible, extremely elongated into sharp-edged cone. Apical cones on antenna extremely short. Trunk broad (three to four times longer than wide), 4-23 mm long, with ca. 42 segments. Yellow. Penes conical. Eyes consisting of three ommatidia. Anterior gonopod with seven podomeres, last podomere with lobe-like attachment. Posterior gonopods with six podomeres, last podomere fimbriate. Two species, incl. *O. ichigomensis* Attems, 1909, Japan.

Subterclass EUGNATHA Attems, 1898

[THOMAS WESENER]

Head capsule with posterior transverse suture, genae (parietal sclerites) always present. Labrum fused to clypeus, always tridentate. Ommatidia completely absent (Polydesmida), very few (Stemmiulida) or numerous. Organ of Tömösváry absent (Stemmiulida, Juliformia) or present as a small pit (Callipodida, Chordeumatida, Polydesmida). Antennae with seven or eight (e.g. Stemmiulida, Callipodida) antennomeres plus apical disc carrying four, in a few genera more, apical cones. Various sensilla, including sensilla basiconica, usually present on antennomeres, especially laterally on fifth and sixth. Epipharynx attached to head capsule. Mandible consisting of two basal articles (cardo and stipes) in

addition to the massive gnathal lobe. Gnathal lobe always lacking a condylus. Gnathochilarium variable, order- or sometimes family-specific, but lamellae linguales separated from one another, at least by a suture. Trunk with 19-101 segments, and 30 to ca. 200 leg pairs, and corresponding undivided sternites with fused stigmatic plates surrounding coxae. Sternites and stigmatic plates as well as pleurites and tergites always fused together. In some orders all sclerites are fused to body rings with visible or untraceable sutures. Defence glands usually (exception Chordeumatida, a few Polydesmida) present, paired openings located laterally, glands usually simple, rarely bicompartmental (Polydesmida). Defensive secretions of variable composition (but never alkaloids). Legs consisting of six (coxa, prefemur, femur, postfemur, tibia, tarsus), rarely seven (coxa, trochanter, prefemur, femur, postfemur, tibia, tarsus) or eight (coxa, trochanter, prefemur, femur, postfemur, tibia, tarsus 1, tarsus 2) podomeres. Coxal pores present or absent. Male legs 8, often also 9 modified to gonopods.

Sperm transfer always direct, mostly via gonopods (= spermatopositors). Juveniles hatching with three pairs of legs (exception *Pachyiulus* spp.). With few exceptions (some Julida) all males, in some groups (e.g. Chordeumatida) also females, die after one reproductive period.

Superorder MEROCHAETA Cook, 1895

[SERGEI I. GOLOVATCH AND HENRIK ENGHOFF]

Order Polydesmida Leach, 1815

'Flat-backed' millipedes. Length 1.4-134 mm. Head always without eyes, but an inconspicuous organ of Tömösváry sometimes visible as a small pit caudolateral to antennal sockets. Antennae each consisting of seven antennomeres plus disc, apically with four, exceptionally up to at least 20 sensory cones, antennomeres 5-7 normally with sensory fields or pits. Labrum normally tridentate. Mandible: gnathal lobe massive, with a single premandibular tooth (sometimes supplied with up to two lateral denticles or a node), a four- to seven-lobed dentate lamella, 6 pectinate lamellae, an intermediate lobe, and a prominent, but varied molar plate with membranous fringes and dense stairs-like structures, or molar processes. Gnathochilarium with a large gula, but without a prebasilare. Cardines small; mentum large, subtriangular, undivided; stipites large, located lateral to lamellae linguales, with two pairs of palps. Median palps at end of lamellae linguales with no or only very few sensory cones apically. Body composed of head and in the vast majority of species 17 or 18 podous rings plus one apodous ring, plus telson, each ring consisting of fused tergite, pleurites, stigmatic plates and sternites into complete rings with no trace of suture lines. A few species with 16 or up to 27 podous rings; females with one more ring than males in a few species. Collum variable, usually smaller than or subequal to following terga, in a few groups flabellate, covering head from above and with frontal lobulations or radiating furrows. No axial suture. Each ring composed of an anterior, cylindrical smooth or microsculptured prozonite, and a posterior metazonite which normally carries more or less prominent lateral projections

(= paraterga, or paranota); lateral calluses (= peritremata) delimited by a longitudinal sulcus at least dorsally often present. Size, shape, inclination and ornamentation of metaterga and paraterga extremely variable, making the Polydesmida the morphologically most diverse millipede order: The dorsal surface may be smooth, tuberculate or even spinose, often divided into rounded or polygonal tubercles or bosses, sometimes densely covered with tiny cuticular outgrowths which may support a cerotegument (= cuticular secretion layer), sometimes also a soil crust. Often three transverse rows of dorsal setae, sometimes more abundant, irregular pilosity. Tergal setae varying from acuminate to bacilliform, claviform, bi-articulate or dendroid. Paraterga mostly keel-shaped, more rarely spine- or antler-shaped, sometimes nearly absent (small bulges), usually set rather high (at about upper quarter to third of ring height), subhorizontal, less commonly strongly declined, or upturned. Some species capable of full volvation, rolling up into a compact disk due to strongly enlarged paraterga of body ring 2 supplied with a hyposchism (a ledge or gutter delimited by a suture at base) for accommodation of the tips of several following paraterga. So-called pleurosternal carinae sometimes present ventrolaterally. Posterior margin of body rings usually with a limbus (a hyaline extension of the posterior ring margin, often serrated). Telson consisting of a complete preanal ring, two anal valves (paraprocts), each typically with two setae, and a small subanal scale (hypoproct) with two setae; preanal ring often with a dorsal projection (epiproct), tip of epiproct with a group of 4 setiform spinnerets (the spinning function has only been demonstrated in juveniles of some species). Telson in some groups reduced and hidden under the previous paraterga. Defence glands (ozadenes) bicompartmental, usually present, opening through paired ozopores, usually on paraterga or their vestiges of rings 5, 7, 9, 10, 12, 13, 15-17 (18, 19) (normal pore formula). Deviations quite common, particularly in Pyrgodesmidae. In a few groups, especially Pyrgodesmidae, at least some ozopores borne on special stalks (= porosteles). Defensive secretions mostly containing cyanide. Legs consisting of six podomeres (coxa, prefemur, femur, postfemur, tibia, tarsus), sometimes with an additional disk (= trochanter) between coxa and prefemur, highly variable in length and armament, usually longer and more incrassate in males than in females, normally becoming gradually slightly longer towards posterior. Joints between podomeres with special synovial cavities. No coxal pores. Male legs-pair 8 modified into gonopods (except in genus *Aenigmopus*, fam. Tridontomidae), leg-pair 9 normal walking legs. Gonopod aperture on ventral side of body ring 7 transverse. Gonopods usually projecting outside body even when not in use. Gonopod sternum usually reduced or absent, each gonopod bi-articulate, consisting of a coxa and a telopodite. Coxa usually with a distomedial cannula (= hollow coxal horn, or solenite). Telopodite usually directed forward, parallel or crossing, extremely variable in size, shape and ornamentation, but normally with a densely setose basal part conventionally denominated "prefemoral"; part of telopodite distal to prefemoral part, collectively termed "acropodite", usually complex, with various processes and/or other outgrowths, one of which, termed "solenomere", supporting most or part of the seminal groove. Other male leg-pairs sometimes with modifications, in the form of ventral processes (adenostyles) and/or modified ventral setae, modifications multifarious, one example being sphaerotrichomes (= setae with a swollen base). Male gonopores

opening through coxae of leg-pair 2. Female gonopores opening through sclerotized vulvae ('cyphopods') behind leg-pair 2, each vulva consisting of a simple operculum and a complicated bursa.

Postembryonic development teloanamorphotic. First postembryonic stadium with three pairs of legs.

Distributed in all non-Antarctic zoogeographical regions and besides Juliformia usually the dominating group of millipedes.

The descriptive adjective "polydesmoid" refers to polydesmidan millipedes which resemble typical members of the family Polydesmidae, i.e., with small collum, well-developed, laterally at most shallowly dentate paraterga, and metaterga with areolate sculpture of polygonal setigerous bosses.

Suborder Dalodesmidea Hoffman, 1980

Body length 10-35 mm. Sternum of second male leg-pair fused to pleuroterga. Pore formula mostly normal (see above), rarely ozopores only on body rings 8, or 8 and 11, or 8, 11 and 14, or 5, 7 and 9-19. Paraterga from nearly wanting to keel-shaped or even spiniform, normally incised laterally. Dorsal surface of metaterga usually with three, less often more numerous, transverse rows of polygonal to rounded, setigerous bosses or tubercles. Collum typically small, rarely flabellate, covering head from above. Upper seta on anal valves marginal, lower seta discal. Male tarsi, sometimes also some other podomeres, usually with ventral rows or fields of sphaerotrichomes and/or other modified setae, sometimes also with adenostyles. Gonopod coxae usually small, usually coalesced medially into a syncoxite. Gonopod telopodites usually elongate and slender, usually fully separated, but sometimes fused medially at base into a syntelopodite. Accessory seminal chamber usually absent, but hairy pulvillus always absent.

Family DALODESMIDAE Cook, 1896. — Body 10-35 mm long, usually polydesmoid, occasionally capable of volvation, uniformly greyish or brownish, but sometimes with bright markings on paraterga. Collum small, epiproct small and conical, porosteles absent, sphaerotrichomes usually present. About 55 genera and more than 250 species across the southern Hemisphere: New Caledonia, New Zealand, Australia, southern Africa and Madagascar, and southern South America.

Anaulacodesmus Attems, 1989. — 16 species, Chile and Andean parts of Argentina.

Canacophilus Carl, 1926. — Seven species, New Caledonia, Loyalty Islands.

Dalodesmus Cook, 1896. — Four species, Madagascar.

Dasystigma Mesibov, 2003. — Four species, Australia: *D. bonhami* Mesibov, 2003, *D. huonense* Mesibov, 2003, *D. margaretae* (Jeekel, 1984), *D. tyleri* Mesibov, 2003.

Icosidesmus Humbert & de Saussure, 1869. — 18 species, New Zealand.

Lissodesmus Chamberlin, 1920. — 28 species, Australia, incl. *L. anas* Mesibov, 2005, *L. margaretae* Jeekel, 1984, *L. modestus* Chamberlin, 1920.

Tasmaniosoma Verhoeff, 1936. — 21 species, Tasmania. The species pair *T. compitale* Mesibov, 2010 and *T. hickmanorum* Mesibov, 2010 provide a model example of parapatric distributions.

Tasmanopeltis Mesibov, 2005. — Monotypic, *T. grandis* Mesibov, 2005, Tasmania.

Vanhoeffenia Attems, 1908. — Ca. 70 species, S Africa to Mozambique.

Family VAALOGONOPODIDAE Verhoeff, 1940. — 10-20 mm long, paraterga modest, pore-bearing ones with cylindrical porosteles. Collum flabellate, its front margin scalloped or lobulate, covering head from above. Epiproct twice as large and long as in Dalodesmidae. Sphaerotrichomes absent. Three genera and some seven or eight species from southern Africa and Madagascar(?). Some species found associated with ants.

Phygoxerotes Verhoeff, 1939. — Six species, S Africa.

Suborder Leptodesmidea Brölemann, 1916

Trunk of 18 podous plus one apodous body rings excluding telson in the vast majority of species; a few species with up to 27 podous rings, males of a few species with only 17 podous rings. Length 15 (rarely less) to more than 130 mm (by far the largest among the Polydesmida). Colour varied, often with vivid, sometimes aposematic patterns. Sternum of second male leg-pair normally pivoted at lateral ends against sides of third pleurotergum, movable. Pore formula normal, with few exceptions. Paraterga usually large and prominent, wing- or keel-shaped, rarely reduced. Limbus usually smooth. Upper seta on anal valves marginal, lower seta discal. Vestiges of gonopod sternum present, often fused to coxae.

Superfamily CHELODESMOIDEA Cook, 1895.

Family CHELODESMIDAE Cook, 1895. — Length 20-107 mm, 18 podous rings, exceptionally 17 in males, apodous ring 19 sometimes strongly telescoped inside ring 18. Trunk narrow, width/length ratio usually <18%, normally broadest at rings 3-5, thereafter tapering gradually towards telson. Coloration from pallid to black, often with vivid patterns. Antennae with four apical cones forming two unequal dyads separated by inturned distal edges of antennomere 7. Tegument often smooth and shining, but metaterga often dull, roughly granulate and/or tuberculate; tergal setae if any usually simple and inconspicuous. Pore formula mostly normal, rarely reduced, exceptionally only ring 5 with pores. Paraterga usually prominent, sometimes incised/lobate/emarginated laterally, rarely spiniform or strongly reduced. Limbus normally simple, occasionally microdenticulate to microspiculate. Epiproct normally long and conical, but sometimes strongly flattened dorsoventrally, shovel-shaped. Sterna of male leg 3 and/or 4 often, sometimes also other sterna, with paramedian apophyses or cones. Legs normally long and slender, male legs sometimes papillate, often with ventral pads, glands and/or adenostyles; sphaerotrichomes present on postfemora and tibiae. Gonopod coxae fused with sternal vestiges, coxa normally rather long, subequal in length to, occasionally longer than, telopodite. Telopodite usually deeply bipartite, sometimes uni- or tripartite. About 230 genera and 800 species, from southern Mexico and the Antilles to northern Argentina and southern Brazil (but not Chile!); in Africa from Sierra Leone to Angola, and along the coasts of Kenya and Tanzania; one species in Europe (Spain).

Amphelictogon Chamberlin, 1918. — 22 species, Cuba.
Callistocilla Hoffman, 1977. — Three species, E Africa.
Caraibodesmus Chamberlin, 1918. — Ten species, Jamaica.

Cantabrodesmus Mauriès, 1971. — One species, *C. lorioli* Mauriès, 1971, Spain. Only Palaearctic chelodesmid, cavernicolous.

Chondrodesmus Silvestri, 1897. — Ca. 40 species, Ecuador and Brazil to Mexico. *C.* cf. *riparius* Carl, 1914 (Plate XII D) introduced to Europe.

Prepodesmus Cook, 1896. — Three species, Sierra Leone to Nigeria, one species also in the Democratic Republic of the Congo (introduced).

Eurydesmus de Saussure, 1860. — Ca. 17 species, Brazil. *E. baguassuensis* Schubart, 1944.

Leodesmus Mauriès & Geoffroy, 2000. — One species, Brazil. *L. yporangae* (Schubart, 1946), cavernicolous.

Leptodesmus de Saussure, 1859. — 21 species, Brazil.

Odontopeltis Pocock, 1894. — Eight species, Brazil. *O. giganteus* (Schubart, 1949), up to 107 mm long and thus the largest species in the family.

Pandirodesmus Silvestri, 1932. — Two species, one in Tobago, the other, *P. disparipes* Silvestri, 1932, in Guyana, unique among millipedes in having every second leg much longer than the others.

Paracordyloporus Brölemann, 1916. — Ca. 15 species, central Africa.

Telonychopus Verhoeff, 1951. — Two species, Brazil. *T. klossae* Hoffman, 1965.

Thanatomimus Hoffman & Reid, 1990. — One species, Nigeria. *T. enghoffi* Hoffman & Reid, 1990, strongly sculptured, convincingly 'plays dead' when disturbed.

Trichomorpha Silvestri, 1897. — Ca. 35 species, Ecuador to Costa Rica.

Tylodesmus Cook, 1896. — Six species, W Africa.

Superfamily PLATYRHACOIDEA Pocock, 1895. — Epiproct strongly enlarged and flattened dorsoventrally, shovel-shaped. Compound, or tuft, setae (arranged in bundles) present on labrum, telson and legs. Vulvae small and poorly sclerotized.

Family APHELIDESMIDAE Brölemann, 1916. — Length 40-75 mm, colour mostly dark with vivid pattern, tegument mostly smooth and shining. Ozopores crater-shaped, opening laterally on distinct calluses of always well-developed paraterga. Tibiae without a long, tactile, apicodorsal seta. Gonopods with medial sternal remains between coxae; telopodite from very simple to fairly complex, uni-, bi- or triramous. 17 genera, ca. 120 species, Mexico to Brazil and Peru.

Aphelidesmus Brölemann, 1898. — Ca. 30 species, Costa Rica to Ecuador and W Brazil. *A. divergens* Chamberlin, 1918 (Plate XIII B), *A. hermaphroditus* Brölemann, 1898.

Amplinus Attems, 1898. — 28 species, Central America, incl. *A. bitumidus* (Loomis, 1969).

Pycnotropis Carl, 1914. — 26 species, S America, incl. *P. acuticollis* (Attems, 1899), *P. taenia* (Peters, 1864), *P. tida* (Chamberlin, 1941).

Polylepiscus Pocock, 1909. — 11 species, Mexico, Guatemala.

Seminellogon Chamberlin, 1933. — Six species, Costa Rica, Panama.

Family PLATYRHACIDAE Pocock, 1895. — Length 30-134 mm long, thus including the largest species of Polydesmida, colour usually dark, but sometimes with vivid patterns, tegument dull, prozonites granulate, metaterga usually roughly granulate-tuberculate. Lateral calluses of paraterga obliterated to very thin, ozopores usually elevated, ring-like and shifted away from lateral edge, rarely opening laterally at paratergal margin, exceptionally ventrolaterally below paraterga. Spiracles enlarged, especially anterior pair on each body ring often with flared rims. Tibiae of walking legs with a long, tactile, erect, apicodorsal seta on a smooth tubercle. Gonopods with at most very small reduced medial sternal remnants; telopodite usually simple. 40 genera, ca. 250 species, distribution

markedly disjunct: Neotropical region from the Antilles and Nicaragua to Peru and central Brazil; Oriental region, from Myanmar and Indochina through Indonesia and the Philippines, to New Guinea with some adjacent archipelagos of Melanesia and Palau in Oceania.

Acanthodesmus Peters, 1864. — Seven species, Borneo and nearby small islands.

Barydesmus Cook, 1896. — 36 nominal species, Costa Rica to Peru and NW Brazil.

Gigantorhacus Jeekel, 2007. — Five species, Sumatra, Java, Borneo. *G. mirandus* (Pocock, 1894), Sumatra, may reach 134 mm in length and is the largest known species of Polydesmida.

Nyssodesmus Cook, 1896. — 13 species, Nicaragua to Panama. *N. python* (Peters,1864), Costa Rica.

Phyodesmus Cook, 1896. — Nine species, Borneo. *P. pictus* (Peters, 1864), up to 130 mm long.

Platyrhacus C. L. Koch, 1847. — 37 species, SE Asia to Java. *P. amauros* Attems, 1897, *P. andersonii* Pocock, 1895.

Psammodesmus Cook, 1896. — Nine species, Panama to Peru. *P. bryophorus* Hoffman, Martínez & Flórez, 2011, has mosses growing on its dorsum.

Zodesmus Cook, 1896. — Nine species, New Guinea and Moluccas.

Superfamily RHACHODESMOIDEA Carl, 1903. — Pore formula usually normal, rarely extended (5, 7-19), ozopores small. Male coxae 2 with high, slender, apically fimbriate gonapophyses. Gonopods (lacking in one genus) varied, but cannulae always absent.

Family RHACHODESMIDAE Carl, 1903. — Length 10-60 mm. Colour usually intense, often greenish or bluish, but especially in cave-dwelling species may be unpigmented. Tegument usually smooth and shining. Collum small and rounded, like following body rings without spiniform paraterga. 18 genera, 62 species, Mexico to Costa Rica.

Aceratophallus Carl, 1902. — 12 species.

Chromodesmus Loomis, 1976. — Five species.

Rhachodesmus Cook, 1895. — Two species.

Tancitares Chamberlin, 1942. — One species, *T. michoacanus* Chamberlin, 1942, Mexico.

Family TRIDONTOMIDAE Loomis & Hoffman, 1962. — Length 22-28 mm. Colour uniformly greyish. Antennae and legs unusually long and slender. Paraterga on collum spinelike, following paraterga divided into three dorsolateral spines, with ozopores located on ventral side at base between front and middle spines. Two genera, three species, Guatemala.

Aenigmopus Loomis & Hoffman, 1962. — One species, *A. alatus* Loomis & Hoffman, 1962 is the only known helminthomorphan millipede lacking male gonopods.

Tridontomus Loomis & Hoffman, 1962. — Two species.

Superfamily SPHAERIODESMOIDEA Humbert & de Saussure, 1869. — Length 10-50 mm. Body usually, but not always, capable of volvation. Texture smooth to roughly tuberculate, metaterga sometimes with a cerotegument. Paraterga strongly declivous. Ozopores mostly missing, when present very small. Male gonopore on top of a long, slender, usually fringed apophysis of coxa 2. Gonopod coxa always with cannula.

Family CAMPODESMIDAE Cook, 1896. — Length 17-37 mm, obviously capable of imperfect volvation due to a modestly enlarged paraterga on ring 2 and moderately deflexed following paraterga; telson strongly flattened, but fully exposed in dorsal view and

not adapted for volvation. Pore formula either normal or reduced, ozopores being borne on porosteles or present only on rings 5 and 7, and devoid of porosteles, respectively. Coloration uniformly dark. Tegument dull, metaterga roughly granulate-tuberculate, apparently with a cerotegument, often coated with a soil crust as well. Paraterga rounded, at most only slightly dentate laterally, without a callus. Ozopores only on rings 5 and 7. Two genera, W Africa, east to Cameroon.

Campodesmus Cook, 1896. — Nine species, W Africa.

Family HOLISTOPHALLIDAE Silvestri, 1909. — Trunk flat and broad, 10-50 mm long, paraterga prominent, without lateral calluses. Ozopores sometimes present on ring 5. Spiracles displaced strongly anteriad, even posterior ones located inside stricture between pro- and metazonites in front of anterior coxa. Male tarsi 1-5 mostly with prominent bundles of setae (= scopulae). Gonopod aperture sometimes hypertrophied, causing lateral expansion of body ring 7. Gonopods highly variable, ranging from small, slender, coalesced single-segmented remnants to large, apparently 2-segmented appendages with distinct cannulae, very similar to those in some Sphaeriodesmidae. Seven genera, 11 species, Central America from Honduras to S Mexico.

Pammicrophallus Pocock, 1909. — Three species.

Family SPHAERIODESMIDAE Humbert & de Saussure, 1869. — Body mostly very strongly modified for volvation into a tight ball or oblate disk. Length 14-35 mm, width up to 15 mm. Ozopores wanting. Sterna very narrow, much shorter than terga, prozonites often strongly abbreviated to absent ventrally. Antennae and legs mostly long and slender. Tegument smooth to roughly tuberculate. Paraterga strongly declivous to subvertical, distally acute, tergum 3 or terga 3 and 4 enlarged. Telson normally flattened dorsoventrally. Male legs 1 often with femoral adenostyles. Gonopods simple to complex, cannula present. Ca. 14 genera and 91 species, Central America, Greater and Lesser Antilles, extending north to the southern USA.

Desmonus Cook, 1898. — Ten species, southern USA to NE Mexico. *D. inordinatus* Causey, 1958, is one of the northernmost species (Arkansas, Missouri).

Proeilodesmus Hoffman, 1990. — One species, *P. mecistonyx* Hoffman, 1990, Mexico, cavernicolous, has too long and little depressed paraterga to be able to volvate.

Sphaeriodesmus Peters, 1864 (Plate XIII F). — 34 species, Mexico to Panama, Greater Antilles. Many are cavernicolous, e.g., *S. zontehuitz* Shear, 1974.

Superfamily XYSTODESMOIDEA Cook, 1895. — Length ca. 8 to more than 80 mm, exceptionally smaller. Body not capable of volvation, broad and robust, width/length ratio usually >18%, usually parallel-sided on rings 3-16. Antennae rarely with more than four apical cones, these not arranged in dyads. Paraterga mostly prominent, lateral calluses normally evident; metaterga usually without setae. Gonopod coxa with cannula; telopodite with neither accessory seminal chamber nor hairy pulvillus.

Family EURYMERODESMIDAE Causey, 1951. — Length 12-40 mm long; body mostly inflexible (preserved specimens therefore highly fragile), front and, especially, caudal ends of body clearly tapering. Colour frequently vividly red to orange, rarely strongly banded. Mandibular stipes typically with a caudolateral projection, a little larger

in males. Tegument entirely smooth and shining, neither metatergal tuberculations nor transverse sulcus. Prefemora always without a distoventral spine, often bulging dorsally on certain male legs. Tarsal claws gently curved to bisinuate, enlarged basally. Gonopod telopodites directed conspicuously caudoventrad, usually slightly curved to suberect, mostly shorter than coxites, simple, mostly crossing medially, always beset with very long hairs. One genus, 30 species.

Eurymerodesmus Brölemann, 1900. — Southern USA. *E. varius* (McNeill, 1887), southeastern USA.

Family EURYURIDAE Pocock, 1909. — Length up to 35 mm. Tegument smooth and shining; ozopores lateral to dorsolateral, opening on calluses. Epiproct strongly enlarged and flattened dorsoventrally, shovel-shaped. Male coxa 2 usually with an apicoventral, somewhat boletiform cylinder carrying the gonopore. Gonopod coxa with cannula set in a marginal notch, not inside a socket; telopodite very simple, bifid. Two genera, 13 species, eastern USA.

Auturus Chamberlin, 1942. — Six species. *A. evides* (Bollman, 1887).

Euryurus C. L. Koch, 1847. — Seven species. *E. leachii* (Gray, 1832), *E. erythropygus* (Brandt, 1841), *E. maculatus* C. L. Koch, 1847.

Family GOMPHODESMIDAE Cook, 1896. — Length 11-90 mm, body compact, paraterga usually strongly declivous, sometimes strongly reduced; posteriormost body rings (18 and 19) often strongly telescoped. Overall body shape remarkably monotonous. Colour from pale to dark, usually uniform, but sometimes with marked patterns. Antennae usually with four, occasionally 10 or 12, apical sensory cones. Tegument usually smooth and shining, metaterga only seldom rugose; dorsum strongly convex. Intersegmental membranes sometimes (subfamily Marptodesminae) with distinct meshwork pattern. Metaterga without transverse sulcus. Pore formula often reduced or extended (up to 5, 7, 9-19). Lateral calluses of paraterga usually prominent. Epiproct usually conical, never strongly flattened. Some male sterna often with processes. Pregonopodal male legs often with characteristic tarsal pads subtending claws ventrally. Gonopod sternal elements tending to reduction, not fused with coxae; cannula present; telopodites from simple, erect, to very long, arcuate and with a characteristic nodus, i.e. one or more prominent, often armed lobes. 54 genera, 146 species, Africa south of Sahara, but not Madagascar.

Astrodesmus Cook, 1896. — Six species, E Africa. *A. laxus* (Gerstäcker, 1873) is a widespread species.

Haplogomphodesmus Hoffman 2005. — Two species, central Africa, incl. *H. pavani* (Demange, 1965).

Sphenodesmus Cook, 1895. — Four species, from Sierra Leone and the Gambia to Tanzania. *S. sheribongensis* Schiøtz, 1966 serves as food for humans in Burkina Faso.

Tymbodesmus Cook, 1897. — Five species, central Africa. *T. falcatus* (Karsch, 1881) serves as food for humans in Burkina Faso.

Ulodesmus Cook, 1897. — 26 species, South Africa.

Family OXYDESMIDAE Cook, 1895. — Length 30-82 mm; body shape remarkably variable. Colour usually uniform, only seldom with a vivid pattern. Head with a characteristic series or small field of setae above antennal sockets. Antennae always with four

apical cones forming two unequal dyads or even individually separated by inturned distal edges of antennomere 7. Tegument usually dull; metaterga leathery to granulate, areolate or tuberculate, typically with transverse rows of basically setiferous tubercles; sides of metazonites below paraterga often denticulate/spiculate throughout and/or clearly setose at caudal edge; collum and metaterga 2-4 often with strongly differentiated mid-dorsal tuberculations or even caudal horns. Pore formula mostly normal, only rarely somewhat reduced. Paraterga prominent, usually with prominent and elevated lateral calluses, calluses often crenulate or dentate at margin, always with ozopores laterally or dorsolaterally. Epiproct mostly strongly broadened, with enlarged lateral tubercles, rarely conical. Gonopod coxae usually with medial sternal elements, forming a coxosternum, cannulae always present. Telopodites unusually uniform in conformation, usually branched only in distal half, only rarely more deeply bipartite. 34 genera, 153 species. Africa south of Sahara, south to Mozambique and Angola, but not Madagascar; also Socotra Island off the Horn of Africa.

Ceratodesmus Cook, 1896. — Nine species, Kenya, Tanzania. Most species with prominent dorsal projections on body rings 2 and 3. *C. cristatus* (Cook, 1896).

Coromus Gervais, 1847. — 14 species with almost identical gonopods, West Africa, from Guinea to Cameroon. *C. granulosus* (Beauvois, 1805), *C. thomsoni* (Lucas, 1858).

Ctenodesmus Cook, 1896. — Eight species, Kenya, Tanzania. Most species with prominent transverse crest on body ring 3, e.g., *C. pectinatus* (Karsch, 1881).

Exochoromus Hoffman, 1990. — Six species, Nigeria to Congo.

Fontariopsis Pocock, 1903. — Three species, Socotra.

Lyodesmus Cook, 1896. — 22 species, Tanzania, Malawi, Congo. *L. dollfusi* (Cook, 1896), Tanzania, the largest species in the family.

Plagiodesmus Cook, 1896. — Six species, Congo, Angola, Rwanda, Uganda.

Rhododesmus Cook, 1896. — Two species, Kenya, Tanzania.

Family XYSTODESMIDAE Cook, 1895. — Length 8-85 mm, body usually moderately convex, paraterga subhorizontal to clearly declivous, front and, especially, caudal parts of body clearly tapering. Colour from pallid to pitchy black, often with vivid, aposematic patterns. Antennae long and slender, usually with four, seldom with up to 20 apical cones. Tegument smooth and shining, or metaterga dull, modestly to roughly granulate and/or tuberculate, no setae on metaterga. Paraterga usually large and prominent, normally with narrow calluses. Pore formula mostly normal, rarely partly or totally reduced except for body ring 5. Epiproct subtriangular to conical, sometimes clearly flattened dorsoventrally, but tip always narrow. Male coxa 2 usually with apicoventral, somewhat boletiform cylinder carrying gonopore; tarsal claws uncinate to bisinuate, not enlarged basally. Gonopod coxae with or without sternal vestiges. Telopodites from suberect to circular, from simple and unipartite to bipartite, sometimes twisted. 62 genera, 393 species, Holarctic region. Greatest diversity in the Nearctic subregion: N and Central America down to Ecuador, also the Antilles. In the Palaearctic subregion in the circum-Mediterranean area and East Asia from the Russian Far East, to southern China and northern Vietnam, also Taiwan and Japan.

Apheloria Chamberlin, 1921. — Four species, eastern USA. *A. virginiensis corrugata* (Wood, 1864).

Brachoria Chamberlin, 1939. — 34 species, eastern USA.

Cherokia Chamberlin, 1949. — One species, *C. georgiana* (Bollman, 1889), southeastern USA.

Chonaphe Cook, 1904. — Four species, Washington, Oregon to Montana.

Cleptoria Chamberlin, 1939. — Five species, southeastern USA. *C. rileyi* (Bollman, 1889).

Devillea Brölemann, 1902. — Five species, France, Italy. *D. doderoi* Silvestri, 1903, Sardinia, with up to 27 podous rings plus one apodous ring in front of telson. *D. patrizii* Manfredi, 1956, *D. tuberculata* Brölemann, 1902, *D. cerrutii* Manfredi, 1956, *D. subterranea* Verhoeff, 1943.

Falloria Hoffman, 1948. — 17 species, eastern USA.

Harpaphe Cook, 1904. — Three species, western N America. *H. haydeniana* (Wood, 1864) from Alaska to California.

Levizonus Attems, 1898. — Eight species, E Russia, Korea, Japan.

Macellolophus Attems, 1940. — One species, *M. rubromarginatus* (Lucas, 1848), S Spain, Algeria.

Melaphe Cook, 1904. — Six species, N Africa, Cyprus, SE Europe, Turkey. *M. vestita* (C. L. Koch, 1847), Albania, Greece, Cyprus, Turkey.

Motyxia Chamberlin, 1941. — Eight species, California. These are the 'luminous millipedes'. *M. sequoiae* (Loomis & Davenport, 1951), *M. tiemanni* Causey & Tiemann, 1969, *M. tularea* (Chamberlin, 1949).

Nannaria Chamberlin, 1918. — 25 nominal species, USA. *N. conservata* Chamberlin, 1940.

Pachydesmus Cook, 1895. — Two species, southeastern USA. *P. crassicutis* (Wood, 1864).

Parafontaria Verhoeff, 1936. — 12 species, Japan. *P. armigera* Verhoeff, 1936, *P. laminata* (Attems, 1909), *P. tonominea* (Attems, 1999).

Phrurodesmus Takakuwa, 1943. — Two species, Japan. *Ph. kinshaensis* Murakami, 1965.

Pleuroloma Rafinesque, 1820. — Four species, eastern and central USA. *P. flavipes* Rafinesque, 1820, is very widespread.

Rhysodesmus Cook, 1895. — 73 species, El Salvador north to S and W Texas, one species, *R. restans* Hoffman, 1998, in Virginia. *R. vicinus* (de Saussure, 1858).

Riukiaria Attems, 1938. — 36 species, southern and central China, northern Vietnam, Taiwan and Japan. *R. semicircularis* (Takakuwa, 1941).

Rudiloria Causey, 1955. — Five species, northeastern USA. *R. kleinpeteri* (Hoffman, 1949), *R. trimaculata* (Wood, 1864).

Sigmoria Chamberlin, 1939. — 17 species, southeastern USA. *S. ainsliei* (Chamberlin, 1921), *S. latior* (Brölemann, 1900), *S. nantahalae* Hoffman, 1958.

Stelgipus Loomis, 1944. — Two species, southeastern USA. *S. agrestis* Loomis, 1944.

Xystocheir Cook, 1904. — Nine species, California.

Suborder Polydesmidea Pocock, 1887

Length 1.4 to ca. 35 mm. Paraterga usually well-developed, paraterga 2 of volvatory species strongly enlarged. Metatergal setae normally present, usually simple or claviform, less often bacilliform, bi-articulated or otherwise modified. Epiproct usually conical and simple, rarely flattened. Sternite of male legs 2 fused to lower ends of pleuroterga, thus immovable. Upper seta on anal valve marginal, lower seta discal. Gonopod coxae usually large, more or less firmly attached to edges of aperture in body ring 7, thus almost immobile; coxae, but never telopodites, fused medially, often very strongly so, shifted or expanded somewhat laterad in relation to telopodites.

Superfamily ONISCODESMOIDEA de Saussure, 1860. — Length 3-28 mm, body capable of full volvation due to particularly enlarged paraterga 2 and a small collum. Head sometimes with

modifications: an axial keel between antennae or a pair of paramedian projections on frons. Pore formula mostly normal, ozopores inconspicuous, rarely absent. Tegument dull, metaterga mostly microtuberculate to scaly, usually also micropilose, a cerotegument apparently absent. Paraterga following collum very broad, always strongly declined, usually not or only faintly lobulated at lateral margin, normally deeply incised caudally near base. Telson sometimes completely concealed under ultimate paraterga. Limbus absent. Legs short but slender, coxae contiguous medially, sphaerotrichomes and adenostyles absent. Gonopod coxa usually large, fully to largely withdrawn inside aperture, with cannula. Telopodite usually short and stout, with neither an accessory seminal chamber, nor a hairy pulvillus.

Family DORSOPORIDAE Loomis, 1958. — Length about 6 mm. Antennomeres 5 and 6 subequal in length. Tegument smooth and shining; metaterga without transverse sulcus; ozopores located clearly above bases of paraterga. One monotypic genus.

Dorsoporus Loomis, 1958. — *D. barroensis* Loomis, 1958, Panama, male unknown.

Family ONISCODESMIDAE de Saussure, 1860. — Length 3-28 mm. Antennomere 5 longer and larger than sixth. Tegument dull, scaly to microtuberculate, often also micropilose; metaterga often areate and with at least a faint transverse sulcus in caudal third; ozopores located at bases of paraterga. 15 genera, 26 species, from S Mexico to Peru, S Brazil and N Argentina.

Amphitomeus Verhoeff, 1941. — One species, *A. attemsi* (Schubart, 1934), parthenogenetic, original distribution unknown, found in European hothouses.

Oniscodesmus Gervais & Goudot, 1844. — Five species, Colombia, Peru.

Superfamily POLYDESMOIDEA Leach, 1815 (incl. HAPLODESMOIDEA Cook, 1895). — Metaterga usually with an areate sculpture of polygonal bosses; paraterga well-developed, laterally dentate. Collum usually small, transversely ovoid to subtrapeziform, its front margin rarely microlobulate/dentate; sometimes scalloped and then its margin more or less lobulated, covering head from above. Sphaerotrichomes often present. Gonocoxae (coxal part of gonopod) with cannulae and two strong setae, sometimes abundantly setose, telopodites usually subfalcate and rather simple, only moveable in the plane of the main body axis. Seminal groove usually entirely or largely mesal, especially so in basal half of telopodite; an accessory seminal chamber and/or a hairy pulvillus often present.

Family CRYPTODESMIDAE Karsch, 1880. — Length 5-20 mm. Usually without a colour pattern. Body incapable of volvation, usually strongly flattened, very broad (width/length ratio usually close to 0.25). Collum strongly enlarged, flabellate, often with radiating lines, mostly covering head from above, Paraterga always strongly developed, mostly broad and subhorizontal, usually clearly lobulated/incised laterally and caudally, occasionally also at front edge. Pore formula often normal, but sometimes deviating; ozopores occasionally absent, when present never on porosteles, at most on small tubercles, usually removed from lateral edge of paraterga. Metaterga without cerotegument but usually more or less densely setose and/or uniformly tuberculate. Metatergal setae if present mostly simple, occasionally bi-articulated, usually arranged in numerous transverse rows. Limbus usually deeply microcrenulate. Epiproct always fully exposed, from rather simple and subconical to strongly flattened and deeply incised at lateral edges. Legs without sphaerotrichomes, some male legs rather often with adenostyles. Gonopods apparently without an accessory seminal chamber, but often with a hairy pulvillus. 38 genera,

125 species, distribution pantropical: from Mexico to Argentina in the Americas, tropical Africa, and tropical to subtropical Asia to Papua New Guinea and Japan in the East.

Aporodesmus Porat, 1894. — Ca. 25 species, western and central Africa.
Cryptodesmus Peters, 1864. — Three species, Brazil.
Niponia Verhoeff, 1931. — One species, China, Japan. *N. nodulosa* Verhoeff, 1931.
Ophrydesmus Cook, 1896. — Ca. 13 species from SE Asia to the Philippines and New Guinea.
Trichopeltis Pocock, 1894. — Six species, S and SE Asia
Peridontodesmus Silvestri, 1896. — Ca. 11 species, Mexico to Costa Rica.

Family HAPLODESMIDAE Cook, 1895. — Length usually less than 10 mm. Usually without a colour pattern. Body often capable of volvation, then with enlarged paraterga 2. Collum small or, in some non-volvatory species, enlarged, concealing head from above. Paraterga if present usually lobulated laterally, often also fronto- and caudolaterally. Pore formula mostly normal, but sometimes extended (5, 7-19 or 5-19), ozopores always placed dorsally on paraterga, sometimes on porosteles. Metaterga with rough tegument covered by a cerotegument, usually also tuberculate, tuberculation patterns often conspicuously differentiated. Metatergal setae often bi-articulated, sometimes abundant. Epiproct often fully exposed, but sometimes concealed beneath telson, from subconical to strongly flattened and deeply incised at lateral edges. Legs without sphaerotrichomes, but male legs often micropapillate, only rarely modified in other ways. Gonopods with non-globose coxae, telopodites usually simple, uni-, bi- or triramous, usually with evidence of torsion near end of femorite, rarely more basally. Seven genera, ca. 70 species, S Japan, S China, Himalayas, SE Asia to Papua New Guinea and Melanesia, E Australia, and New Caledonia.

Cylindrodesmus Pocock, 1889. — Two species. *C. hirsutus* Pocock, 1889, a pantropical synanthrope, in part parthenogenetic, also in European hothouses.

Agathodesmus Silvestri, 1910. — 22 species, eastern Australia, New Caledonia. *A. steeli* Silvestri, 1919.

Eutrichodesmus Silvestri, 1910. — 46 species, from S Japan in the North, S China, Taiwan, SE Asia to Vanuatu, Melanesia. *E. armatocaudatus* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2003, *E. armatus* (Miyosi, 1956), *E. basalis* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2003, *E. communicans* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2003, *E. elegans* (Myiosi, 1956), *E. similis* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2003, *E. peculiaris* (Murakami, 1966).

Prosopodesmus Silvestri, 1910. — Seven species, mainly in Australia and S. Japan. *P. jacobsoni* Silvestri, 1910, a pan(sub)tropical synanthrope; *P. panporus* Blower & Rundle, 1980, likely native in Australia, but introduced in European hothouses.

Family POLYDESMIDAE Leach, 1815. — Length 4-30 mm. Colour from pallid through brownish or reddish to pitchy black, vivid colour patterns rare. Collum small, transverse-oval, its front margin smooth. Metaterga without a cerotegument. Paraterga usually well-developed, simple, normally dentate laterally. Pore formula usually normal. Limbus microspiculate. Male prefemora often swollen dorsally; adenostyles occasionally present. Sphaerotrichomes usually present. Gonocoxae usually deeply excavated, telopodites usually subfalcate, prefemoral parts without processes. Seminal groove normally making a distolateral loop at base of a mesal branch (endomere) if present, ending inside a more or less large accessory seminal chamber; a solenomere usually present, a distinct hairy pulvillus at its base. Ca. 30 genera, more than 240 species, mostly Holarctic and Oriental, reaching south to N Africa, SE Asia to Java, and Mexico.

Brachydesmus Heller, 1858. — Ca. 75 species, Palaearctic, mainly SE Europe. *B. superus* Latzel, 1884, and *B. proximus* Latzel, 1889, both widespread through commerce. *B. avalae* Ćurčić & Makarov, 1997, *B. dadayi* Verhoeff, 1895, *B. mulaomerovici* Antić et al., 2013, *B. troglobius* Daday, 1889.

Epanerchodus Attems, 1901. — 70+ species, central and E Asia: Russian Far East, Korea, China, Taiwan, Japan. *E. fulvus* Haga, 1956, *E. japonicus* (Carl, 1902), *E. orientalis* Attems, 1901.

Galliocookia Ribaut, 1955. — Four species, three from France, one from the island of Rhodes (Greece).

Polydesmus Latreille, 1802-1803. — Ca. 80 species, Palaearctic, mainly Europe. *P. abchasius* Attems, 1898, *P. angustus* Latzel, 1884, widespread in W Europe; *P. collaris* C. L. Koch, 1847, E Europe, a large, unusually colourful polydesmid; *P. complanatus* (L., 1761), widespread in E Europe. *P. coriaceus* Porat, 1871, *P. denticulatus* C. L. Koch, 1847, *P. graecus* Daday, 1889, *P. inconstans* Latzel, 1884.

Propolydesmus Verhoeff, 1895. — 15 species, western (and central) Europe, Macaronesia. *P. germanicus* (Verhoeff, 1896) (Plate XIII C), *P. testaceus* (C. L. Koch, 1847).

Pseudopolydesmus Attems, 1898. — 12 species, eastern N America. *P. canadensis* (Newport, 1844), *P. erasus* (Loomis, 1843), *P. pinetorum* (Bollman, 1888), *P. serratus* (Say, 1821).

Scytonotus Koch, 1847. — Nine species, N America. *S. granulatus* (Say, 1821), widespread in eastern N America.

Serradium Verhoeff, 1941. — Six species, S Europe. *S. semiaquaticum* Enghoff, Caoduro, Adis & Messner 1997, N Italy, lives in part submerged in subterranean waters.

Superfamily PYRGODESMOIDEA Silvestri, 1896. — Length 1.4-20 mm, mostly 3-10 mm. Body sometimes capable of volvation. Tegument rough, metazonites usually coarsely textured, with abundant cuticular micro-processes supporting a cerotegument (sometimes coated with soil as well). Head often microgranulate on vertex; antennae normally short and clavate. Head often more or less concealed beneath enlarged, frontally scalloped or lobulate collum; body ring 2 often enlarged. Dorsum convex; paraterga usually set low, almost always strongly declined to subvertical; lateral, often also caudal and/or anterior margins more or less lobulated. Metaterga usually coarsely tuberculate, with 2-3 transverse rows of tubercles. Limbus mostly microcrenulate. Pore formula usually different from normal, often variable within genera, some or all ozopores often opening on porosteles at paratergal lateral edge, calluses absent. Legs short, stout (except for tarsi), concealed beneath paraterga, males only rarely with adenostyles, sphaerotrichomes absent, but otherwise modified setae sometimes present. Gonopod coxae usually large, subglobose and clearly exposed, often forming a prominent mesal cavity (gonocoel), usually micropapillate laterally, cannulae present. Telopodites from simple, mostly unipartite, and strongly exposed above coxae, to complex, bi- or tripartite and deeply sunken into coxa. Seminal groove terminating distally, usually on a distinct solenomere, an accessory seminal chamber and/or a hairy pulvillus only exceptionally present.

Family AMMODESMIDAE Cook, 1896. — Length 1.4-5 mm and thus including the shortest known adult millipedes, 16 or 17 podous rings. Body capable of rolling into a tight sphere, paraterga 2 strongly enlarged. Sometimes with distinct colour pattern. Metaterga with a cerotegument. Limbus variable. Pore formula mostly normal, rarely reduced. First and last male legs, sometimes also some others, modified. Gonopod with more or less distinct solenomere, sometimes also with a hairy pulvillus. Two genera, seven species, tropical Africa.

Ammodesmus Cook, 1896. — Three species, W Africa. In addition to showing a remarkable sex dimorphism, this genus seems to be the only one in Polydesmida in which adults of the same species may have 16 or 17 podous body rings regardless of sex. *A. congoensis* VandenSpiegel & Golovatch, 2015, *A. granum* Cook, 1896.

Elassystremma Hoffman & Howell, 1981. — Four species, E Africa.

Family CYRTODESMIDAE Cook, 1896. — Length 5-20 mm, dorsum usually pitchy black, venter pale, antennae pinkish. Body usually capable of volvation due to a strongly hypertrophied and caudobasally excavate paraterga 2 and a reduced collum. Metatergal tuberculations typically not differentiated; paraterga with neither anterior nor posterior marginal lobulations. Pore formula usually normal, porosteles only rarely present. Three genera, 30 species, from Costa Rica and Trinidad to Peru and Brazilian Amazonia.

Cyrtodesmus Gervais, 1847. — Ca. 25 species.

Family PYRGODESMIDAE Silvestri, 1896. — Length 3-16 mm, usually brownish to grayish, rarely variegated. Incapable of volvation: paraterga 2 not particularly enlarged, but collum mostly or entirely covering head from above, with distinct radiating lines or frontal lobulations. Metatergal tubercles typically strongly differentiated, usually with 2 + 2 paramedian rows of particularly strong tubercles; paraterga often with anterior and/or posterior marginal lobulations. Pore formula usually deviating from normal, either reduced or expanded, ozopores often on porosteles. More than 170 genera, mostly monotypic, and nearly 400 species, all tropics, marginally in S Europe, N Africa, southern USA, Japan, Taiwan and central China.

Ampelodesmus Miyosi, 1956. — Five species, Japan, Taiwan. *A. iyonis* Murakami, 1964.

Aporodesminus Silvestri, 1904. — One species, *A. wallacei* Silvestri, 1904, recorded from Hawaii, St. Helena, and Sydney, possibly an anthropochore.

Calymmodesmus Carl, 1914. — 16 species, Colombia to S Mexico.

Cryptocorypha Attems, 1907. — 13 species, Sri Lanka, E and SE Asia, Indonesia, Melanesia. *C. ornata* (Attems, 1938) very widespread on tropical islands, possibly an anthropochore.

Dilophops Loomis, 1934. — One species, *D. bullatus* Loomis, 1934, several tropical islands, probably parthenogenetic, obviously an anthropochore.

Docodesmus Cook, 1896. — 22 species, Caribbean islands to Brazilian Amazonia.

Myrmecodesmus Silvestri, 1910. — 28 species, from Louisiana through southeastern USA, Mexico, and Belize to Brazilian Amazonia. *M. hastatus* (Schubart, 1945), widespread across S America, associated with ants and/or anthropogenic habitats. *M. adisi* (Hoffman, 1985).

Periechodesmus Silvestri, 1947. — One species, *P. caudatus* Silvestri, 1947, Brazil, Cape Verde Islands, probably parthenogenetic, obviously an anthropochore.

Poratia Cook & Cook, 1894. — Seven species, Neotropical. *P. digitata* (Porat, 1889) and *P. obliterata* (Kraus, 1960) have introduced, mostly parthenogenetic populations in European hothouses. *P. salvator* Golovatch & Sierwald, 2001.

Rharodesmus Schubart, 1960. — Two species, N Africa.

Stylodesmus Cook, 1896. — Three species, W Africa.

Tomodesmus Silvestri, 1925. — Two species, Spain.

Superfamily TRICHOPOLYDESMOIDEA Verhoeff, 1910. — Length 2-30 mm, usually less than 10 mm. Body mostly polydesmoid. Paraterga at most with thin calluses, lateral margin typically entire, at most shallowly incised and setigerous; metaterga without cerotegument, mostly with three to four, more or less regular, transverse rows of low setigerous bosses. Ozopores opening flush on dorsal surface of lateral margin of paraterga, pore formula normal. Sphaerotrichomes rather often present on tibiae and tarsi. Gonopods with subglobose coxae, almost always with cannulae; telopodites usually complex, a seminal groove almost always present. An accessory seminal chamber and/or a hairy pulvillus at its orifice only rarely present.

Family TRICHOPOLYDESMIDAE Verhoeff, 1910 (incl. FUHRMANNODESMIDAE Brölemann, 1916, MACROSTERNODESMIDAE Brölemann 1916, MASTIGONODE-

SMIDAE Attems, 1914, and NEARCTODESMIDAE Chamberlin & Hoffman, 1958; cf. Golovatch, 2013). — Length 3-16 mm. Body polydesmoid, only exceptionally paraterga deeply lobulate laterally. Sphaerotrichomes only rarely present. Gonopod coxae usually with cannulae; telopodites sometimes concealed within coxal cavity. Ca. 75 genera, ca. 140 species, mainly northern Hemisphere, both temperate and, especially, tropical.

Bacillidesmus Attems, 1898. — Three species, Bulgaria, ?Hungary.

Coonoorophilus Carl, 1932. — One species, *C. monstruosus* Carl, 1932, southern India.

Cottodesmus Verhoeff, 1936. — Two species, one in Spain, one in Italy. Family assignment uncertain.

Fuhrmannodesmus Carl, 1914. — Seven species, S America (Colombia, Peru).

Heterocookia Silvestri, 1898. — Two species, N Africa.

Ingurtidorgius Strasser, 1974. — One species, Italy (Sardinia). The male has a uniquely modified gnathochilarium with a very long curved process from the mentum, stipites meeting in midline and lamellae linguales missing. *I. caprinus* Strasser, 1974.

Kepolydesmus Chamberlin, 1910. — One species, *K. anderisus* (Chamberlin, 1910), northwestern USA.

Leonardesmus Shelley & Shear, 2006. — One species, *L. injucundus* Shelley & Shear, 2006, northwestern USA.

Macrosternodesmus Brölemann, 1908. — One species, *M. palicola* Brölemann, 1908, widespread (synanthrope) in W Europe.

Mastigonodesmus Silvestri, 1898. — Seven species, S Europe.

Moojenodesmus Schubart, 1945. — Ten species, South America, mainly in Amazonia. *M. pumilus* Schubart, 1945.

Nearctodesmus Silvestri, 1910. — Three species, western N America. *N. insulanus* (Chamberlin, 1941), from British Columbia to Oregon. *N. cerasinus* (Wood, 1864), *N. salix* Chamberlin, 1949.

Occitanocookia Mauriès, 1981. — One species, *O. hirsuta* (Ribaut, 1948), southern France.

Pratherodesmus Shear, 2009. — Three species, western USA.

Sphaeroparia Attems, 1909. — 33 species, tropical Africa, one species in Greece.

Tidesmus Chamberlin, 1943. — Four or five species, western N America.

Trichopolydesmus Verhoeff, 1898. — Two species, Romania.

Family OPISOTRETIDAE Hoffman, 1980. — Length 3-16 mm. Antennae geniculate between antennomeres 5 and 6. Tegument microalveolate, limbus microspiculate. Metaterga with two or three regular, transverse rows of bacilliform, longitudinally ribbed setae sometimes borne on minute knobs; lateral margin of paraterga often slightly incised, with two or three bacilliform setae. Pore formula normal, ozopores opening flush on dorsal side of paraterga. Male legs without sphaerotrichomes, but often with peculiar, bifid or trifid ventral trichomes setae. Gonopods peculiar in having rather small, subglobose, medially fused coxae, with cannulae; telopodites directed dorsolaterad, curving, often very strongly, around coxae 8 along sides of body ring 7; seminal groove running along most of telopodite to terminate distally either on a special solenomere, flush on caudal surface, or inside an accessory seminal chamber which normally is supplied with a hairy pulvillus. Seven genera, 29 species, Ryukyu Islands (Japan), Taiwan, S China and the Himalayas through SE Asia and Indonesia to New Guinea.

Corypholophus Attems, 1938. — Two species, Ryukyu Islands, Vietnam.

Opisotretus Attems, 1907. — Seven species, Indonesia, Papua New Guinea.

Solaenaulus Attems, 1940. — Two species. *S. butteli* (Carl, 1922), Sumatra, introduced to Christmas Isand, Fiji, and New Guinea.

Suborder Strongylosomatidea Brölemann, 1916

Family PARADOXOSOMATIDAE Daday, 1889. — Length 7-70 mm, mostly 10-25 mm. Both setae on anal valve discal, unlike all other Polydesmida. A highly diverse family. Colour from uniformly dark (usually brownish) to pallid, often with a more or less vivid pattern. Paraterga from (nearly) absent to well-developed, keel-, spine- or even antler-shaped; paraterga 2, with very few exceptions, set clearly lower than collum and paraterga 3. Body not capable of volvation; collum never covering head from above, always narrower than ring 2, the latter not enlarged. Tegument smooth and shining in most species, but sometimes rugose or tuberculate, never coated with a cerotegument, polygonal sculpture absent. Pore formula mostly normal, ozopores rarely absent from ring 5, ozopores usually located laterally on typically distinct calluses. Constriction between pro- and metazonites often sculptured at least dorsally: striolate, striate, ribbed or beaded. Limbus smooth. Pleurosternal carinae often present, especially in males until ring 7. Epiproct usually conical, rarely claviform, shovel-shaped or otherwise modified. Sterna sometimes with cones, especially between male coxae 4 and/or some other pregonopodal pairs. Legs quite often very long, normally slightly enlarged in males, sometimes also with dorsally bulged prefemora, ventral apophyses or tubercles (= adenostyles), and/or brushes of particularly dense setae (usually on male tarsi). Gonopod aperture transversely eight-shaped. Gonopods without sternal rudiments; coxae fully separated, parallel, cannulae present; telopodite very diverse, with prefemoral part usually set off from acropodite by oblique sulcus, rarely with one or two processes; telopodite often twisted, with various processes, solenomere often sheathed by a lamellar branch (solenophore) The largest millipede family: 198 genera, 975 species, all regions except the Nearctic part of the Holarctic region, particularly diverse in SE Asia. Several species widespread through commerce.

Aethalosoma Jeekel, 2006. — One species, *Ae. solum* Jeekel, 2006, Tasmania.

Akamptogonus Attems, 1914. — Two species, Australia. *A. novarae* (Humbert & de Saussure, 1869), Australia, widespread through commerce.

Anoplodesmus Pocock, 1895. — 35 species, Nepal, India, Sri Lanka, SE Asia, Indonesia. *A. saussurei* (Humbert, 1865), Sri Lanka, widespread through commerce. *A. anthracinus* Pocock, 1895, *A. tanjoricus* (Pocock, 1892).

Antichiropus Attems, 1911. — 39 species, Australia. *A. variabilis* Attems, 1911.

Aschistodesmus Pocock, 1898. — 15 species, New Guinea, Solomon Islands, Indonesia.

Australiosoma Brölemann, 1913. — Eight species, Australia.

Catharosoma Silvestri, 1897. — 15 species, S America.

Chamberlinius Wang, 1956. — Five species, Taiwan, Japan. *C. hualienensis* Wang, 1956.

Chondromorpha Silvestri, 1897. — Eight species, India, Sri Lanka. *C. severini* Silvestri, 1897, *C. xanthotricha* (Attems, 1898), widespread through commerce.

Cladethosoma Chamberlin, 1920. — Nine species, Australia. *C. clarum* Chamberlin, 1920, *C. trilineatum* (Newport, 1844).

Delarthrum Attems, 1936. — 48 species, mostly Himalaya.

Desmoxytes Chamberlin, 1923. — 30 species, "dragon millipedes", SE Asia. *D. planata* (Pocock, 1895) is widespread through commerce. *D. purpurosea* Enghoff, Sutcharit & Panha, 2007 (Plate I D), Thailand, is "the shocking pink dragon millipede".

Dicranogonus Jeekel, 1982. — One species, *D. pix* Jeekel, 1982, Australia (Victoria).

Eustrongylosoma Silvestri, 1896. — Ca. 35 species, New Guinea, Vanuatu, Solomon Islands, Philippines, Indonesia.

Eviulisoma Silvestri, 1910. — 35 species, Africa.

Gigantomorpha Jeekel, 1963. — Ten species, Borneo, Sulawesi. Very large paradoxosomatids, up to 8 mm wide.

Gigantowales Verhoeff, 1937. — Two species. *G. chisholmi* Verhoeff, 1937, is a very large paradoxosomatid, more than 8 mm wide.

Habrodesmus Cook, 1896. — Six species, tropical Africa. *H. duboscqui* Brölemann, 1919, *H. falx* Cook, 1896.

Helicorthomorpha Attems, 1914. — Three species, SE Asia, Indonesia, New Guinea. *H. holstii* (Pocock, 1895) widespread through commerce.

Iulidesmus Silvestri, 1895. — 61 species, S and Central America, Antilles. *Iulidesmus hylaeicus* (Jeekel, 1963).

Metonomastus Attems, 1937. — 11 species, S Europe.

Nedyopus Attems, 1914. — 13 species, (S)E Asia. *N patrioticus* (Attems, 1898), *N. tambanus* (Attems, 1901), *N. hiburizimensis* Miyosi, 1955.

Notodesmus Chamberlin, 1920. — One species, *N. scotius* Chamberlin, 1920, E Australia, Tasmania.

Oranmorpha Verhoeff, 1941. — Four species, Ethiopia, Eritrea. *O. guerinii* (Gervais, 1836) widespread through commerce.

Orthomorpha Bollman, 1893. — 51 species, SE Asia, Indonesia. *O. coarctata* (de Saussure, 1860), a pantropical anthropochore, is often placed in a separate genus *Asiomorpha* Verhoeff, 1939.

Oxidus Cook, 1911. — Five species, E Asia. *O. gracilis* (C. L. Koch, 1847), widespread through commerce, is "the greenhouse millipede".

Pogonosternum Jeekel, 1965. — Five species, E Australia.

Scolodesmus Cook, 1896. — 18 species, tropical Africa.

Selminosoma Hoffman, 1978. — Monotypic, New Guinea. One species, *S. chapmani* Hoffman, 1978.

Somethus Chamberlin, 1920. — Nine species, Australia. *S. mesibovi* Jeekel, 2006, *S. tasmani* Jeekel, 2006.

Stosatea Gray, 1843. — 15 species, Europe. *S. italica* (Latzel, 1886) (Plate XIII E) is quite widespread.

Streptogonopus Attems, 1914. — Five species, India, Nepal, Pakistan, Bangladesh, Ethiopia and Eritrea. *S. phipsoni* Pocock, 1892.

Strongylosoma Brandt, 1833. — 12 species, (S)E Europe, Middle East, Caucasus. *S. stigmatosum* (Eichwald, 1830) reaches N to Latvia and Kama River, Russia.

Tetrarthrosoma Verhoeff, 1898. — 11 species, Middle East, marginally SE Europe.

Tholerosoma Mesibov, 2006. — Two species, Australia (Queensland). *T. monteithi* Mesibov, 2006.

Tylopus Jeekel, 1968. — 55 species, S China and SE Asia.

Xanthodesmus Cook, 1896. — Four species, tropical Africa. *X. physkon* (Attems, 1898).

Superorder NEMATOPHORA Verhoeff, 1913

[THOMAS WESENER]

Generally cylindrically, but sometimes flat-backed, in part higly mobile millipedes, length 3.5-100 mm. Head usually with eyes, consisting of one or two (Stemmiulida) to many (Callipodida) ommatidia arranged in a triangular patch or a single line. Organ of

Tömösváry present, inconspicuous, smaller than a single occellus. Antennae elongated, consisting of seven (Chordeumatida) or eight (Callipodida, Stemmiulida) antennomeres plus disc with four apical cones. Labrum normally tridentate. Mandibles with a large gnathal lobe consisting of a premandibular tooth, a lobed dentate lamella, four or (often) more pectinate lamellae and a prominently developed molar plate. A unique molar cusp is present between molar plate and pectinate lamellae. Gnathochilarium variably composed, order-specific. Trunk with 25-88 body 'rings', excluding telson. Collum large, but almost never (exception Striariidae) overlapping head. Terga and pleurites fused (pleurotergite), often with a dorsal suture. Stigmatic plates and sternites fused, often with sutures still visible, but free from the pleurotergites. Ozopores present (Callipodida, Stemmiulida) or absent (Chordeumatida). Tracheal pouch with special crossing muscle connecting its lateral arm with the opposite coxa. Telson bearing one to three pairs of spinnerets. Legs consisting of seven (coxa, trochanter, prefemur, femur, postfemur, tibia, tarsus) or eight (coxa, trochanter, prefemur, femur, postfemur, tibia, tarsus 1, tarsus 2) podomeres. Coxal pores at least at a few male leg pairs present. Male leg pair 8, sometimes also 7, 9 and 10 (Chordeumatida) modified into gonopods. Male leg pair 9 either normal walking legs (Callipodida), or atrophied (Stemmiulida), or gonopods (Chordeumatida). Male and female leg pair 1 variably modified, female and male sexual openings highly diverse.

Postembryonic development eu-, telo- or hemianamorphic.

Distributed in all zoogeographical regions excluding Antarctica.

Order Chordeumatida Pocock, 1894

[HENRIK ENGHOFF AND SERGEI I. GOLOVATCH]

Body length 3.5-42 mm, most species 10-25 mm. Colour usually drab, from wholly unpigmented to various hues of brown, a few species with distinct colour patterns. Head elongated, in lateral view clypeus and frons mostly regularly rounded, but flattened or even concave in males of some species, vertex strongly convex, almost always bulging above small collum (in contrast to Juliformia where collum covers posterior part of head). Eyes usually present, mostly more or less triangular and composed of numerous ommatidia. An inconspicuous organ of Tömösváry caudolateral to antennal socket. Antennae usually long and slender, apically with four sensory cones. Mandibular gnathal lobe massive, with a single premandibular tooth, a combed dental lamella, seven to twelve pectinate lamellae (number roughly correlated with body size), an intermediate lobe, and a prominent molar plate with a strong molar cusp. Gnathochilarium with a large gula, a strongly reduced, membranous prebasilare, and small cardines; mentum large, subtriangular, entire or transversely divided; lamellae linguales completely independent; stipites large, located lateral to lamellae linguales, each with two palps. Median palps at end of lamellae linguales also with several sensory cones. Body composed of head, 29 'rings' excluding telson and 50 leg-pairs in most species, less often 25, 27, 28, 30 or 31 'rings' (and correspondingly ±2 leg-pairs per 'ring' number difference), number of 'rings 'and leg-pairs mostly intraspecifically constant. Tergum and pleura fused into pleuroterga, but

sterna + stigmatic plates free (hence 'rings' between inverted commas). Collum usually smaller than following pleuroterga (cf. above). Pleuroterga with a distinct mid-dorsal suture. Each pleurotergum usually with 3 + 3 dorsal/dorsolateral macrochaetae, often mounted on knobs, forming a transverse row or a triangle on each side. Body 'rings' usually with smooth, cylindrical prozonites, but metazonites often with more or less prominent lateral paraterga which may be wing-shaped or humplike, in the latter case imposing an overall moniliform body shape. No defence glands. Telson always visible from above, normally with a truncate, rarely trilobed epiproct carrying two long spinnerets; anal valves (= paraprocts) each composed of a few sclerites; subanal scale (= hypoproct) usually subtrapeziform or semi-circular with a pair of setae at caudal margin. Body never adapted for volvation, usually forming a loose, more seldom tight, spiral when coiled. Legs normally long and slender, consisting of seven podomeres (coxa, trochanter, prefemur, femur, postfemur, tibia, tarsus); anterior legs of males often incrassate and/or with tarsal papillae, occasionally with ventral adenostyles; leg-pair 2 of females sometimes reduced. Male leg-pairs 10 and (mostly) 11, exceptionally also a few other leg-pairs, with coxal sacs. Male leg-pairs 8 and 9 modified into gonopods; both pairs usually at least partially retracted into body. Anterior gonopods usually more modified, extremely varied, often exceedingly complex and difficult to interpret, often with well-developed telopodites which may be fused with the tracheal apodemes, the resulting structure then termed 'cheirite'. Posterior gonopods sometimes little modified, rather resembling normal legs. Both pairs of gonopods may have a pair of long, thin flagella. The leg-pairs adjacent to the gonopods may also be strongly modified and are then termed paragonopods. Male gonopores opening through coxae of leg-pair 2. Female gonopores opening through sclerotized vulvae ("cyphopods") behind leg-pair 2, each vulva consisting of a small operculum and a two-valved bursa.

Postembryonic development teloanamorphotic. First postembryonic stadium with three pairs of legs.

Distributed in all non-Antarctic zoogeographical regions; by far most diverse in the Holarctic region. In the tropics only in S and SE Asia to Australia. Present also in New Zealand and Madagascar, but absent from tropical continental Africa, in S America only in Chile and Andean parts of Argentina. Many species found in caves, troglomorphism (reduced pigmentation and/or eyes, elongated appedages) evolved in numerous lineages.

The internal classification of this order is chaotic, with probably far too many families recognised. We largely follow the scheme of Shear (2011), but multiple major changes are foreseen before a reasonable consensus will be reached (or not). The distinctions between superfamilies and between families are often very subtle, and the short texts provided for each family do not allow at all the assignment of a species to a particularly family; this is particularly obvious for the families of suborder Craspedosomatidea.

Suborder Chordeumatidea Pocock, 1894

Mentum of gnathochilarium undivided, (sub)triangular. Anterior gonopods simple. Posterior gonopods with coxites functioning in sperm transfer in conjunction with anterior

gonopods; telopodites if present reduced to one to three, sometimes more or less inflated segments. Male leg-pairs 7 always, leg-pairs 10 and 11 often, strongly reduced. Leg-pair 11 with coxal glands. Palaearctic subregion.

Family CHORDEUMATIDAE C. L. Koch, 1847. — Length 7-18 mm, 27 or 29 'rings'. Eyes usually present. Body strongly tapering towards posterior, cross-section subcylindrical, paraterga missing. Male leg-pairs 7, 10 and 11 strongly reduced. Females with a unique legless sternum, 'platosternite', behind leg-pair 2, apparently homologous with leg-pair 3. Five genera, 21 species, Europe, especially W Europe.

Chordeuma C. L. Koch, 1847. — 12 species. *C. sylvestre* C. L. Koch, 1847, is quite widespread. *C. proximum* Ribaut, 1913.

Melogona Cook, 1895. — Seven species. *M. gallica* (Latzel, 1884) and *M. voigtii* (Verhoeff, 1899) reach Scandinavia (synanthrope), *M. scutellaris* (Ribaut, 1913).

Mycogona Cook, 1895. — One species, *M. germanica* (Verhoeff, 1892).

Family SPEOPHILOSOMATIDAE Takakuwa, 1949. — Length 4-6 mm long, with 25 'rings'. Eye with four to six ommatidia. Paraterga with lateral humps. Male leg-pair 7 reduced, telopodite divided into several long filaments; male leg-pairs 10 and 11 barely modified, with coxal glands. Female without a platosternite. One genus.

Speophilosoma Takakuwa, 1949. — Six species, Japan.

Suborder Craspedosomatidea Cook, 1895

Mentum of gnathochilarium transversely divided into an apical, triangular promentum and a posterior, trapezoidal eumentum. Anterior gonopods complex, sometimes exceedingly so. Posterior gonopods leglike or variously reduced; telopodites neither inflated nor glandular, often without coxites. Male leg-pairs 10 and 11 with coxal glands; male leg-pair 10 usually not reduced. Palaearctic region, reaching south to Kashmir and Panama.

Superfamily ANTHROLEUCOSOMATOIDEA Verhoeff, 1899. — Antennae long and slender. Anterior gonopods main structures functioning in sperm transfer, mostly massive and complex, usually C-shaped, often with a central, more or less cross-shaped process. Posterior gonopods more or less reduced, often with 1- or 2-segmented telopodites. Flagella mostly absent from both gonopod pairs.

Family ANTHROLEUCOSOMATIDAE Verhoeff, 1899. — Length 3.5-28 mm, 25, 27, 29 or 30 'rings'. Paraterga usually distinct bulges, rarely absent. Anterior gonopods with coalesced coxites, without flagella. Posterior gonopods much simpler, a strong, plate-like sternum or coxosternum with a pair of median colpocoxites (a colpocoxite is a variously shaped structure located more or less caudally on the gonopod coxite and dubiously regarded homologous with everted and sclerotized coxal gland walls) and a pair of lateral angiocoxites; telopodite normally 1- to 3-segmented, often rudimentary, knob- or button-shaped; no flagella. 21 genera, ca. 50 species, mainly Holarctic, most diverse in the circum-Mediterranean area. One monotypic genus in N America.

Anamastigona Verhoeff, 1899. — 17 species, Italy, Balkan, Asia Minor, Israel. *A. matsakisi* Mauriès & Karamaouna, 1984; *A. pulchella* (Silvestri, 1894), relatively widespread through commerce, Italy, France, Macaronesia, Ireland, Germany.

Leschius Shear & Leonard, 2008. — One species, *L. mcallisteri* Shear & Leonard, 2008, N America.

Persedicus Mauriès, 1982. — One species, *P. martensi* Mauriès, 1982, Iran.

Family ACHEROSOMATIDAE Verhoeff, 1929 (= HAASIIDAE Hoffman, 1980). — Length 10-13 mm, 29 'rings.' Unpigmented, mostly blind cave-dwelling species, often with unusually long tergal macrochaetae. Paraterga usually distinct dorsolateral keels or bulges. Anterior gonopods rather massive, complex, caudal syncolpocoxites shield-like, with two characteristic, paramedian bunches of stiff setae on each side. Posterior gonopods (often termed "podosternite") composed of a high, usually cross-shaped, only rarely simple, central sternal process flanked by two rather simple branches. One genus.

Haasia Bollman, 1893. — 12 species in Dinaric and adjacent karsts in S Europe (Slovenia, Croatia).

Family VANDELEUMATIDAE Mauriès, 1970. — Length 4-20 mm, 27 or 29 'rings'. Usually entirely unpigmented, rarely light pinkish. Eyes usually absent. Paraterga small bulges or keels. Five genera, 10-11 species, mostly subterranean, Spain, France, Switzerland.

Typhlopsychrosoma Mauriès, 1982. — Four species, Spain.

Superfamily BRANNERIOIDEA Cook, 1896. — Anterior gonopods main structures functioning in sperm transfer, complex, with telopodite-like colpocoxites, true telopodite absent or reduced, flagella sometimes present. Posterior gonopods simple, leglike but often with reduced telopodites.

Family BETICOSOMATIDAE Mauriès, 2014. — Length 5.5 mm, 29 'rings'. Second pair of male legs with very long 'hemipenial' processes, unlike all other Chordeumatida. One genus.

Beticosoma Mauriès, 1990. — One species, *B. longipenis* Mauriès, 1990, Spain.

Family BRACHYCHAETEUMATIDAE Verhoeff, 1910. — Length 6-11 mm. 29 'rings'. Pale species, blind or with up to seven ommatidia arranged in a line. Paraterga small. One genus.

Brachychaeteuma Verhoeff, 1911. — Eight species, western Europe. *B. bradeae* (Brölemann & Brade-Birks, 1917) is quite widespread.

Family BRANNERIIDAE Cook, 1896. — Length 4.0-4.3 mm, 25 or 27 'rings'. Antennae short, markedly clavate. Pleurotergites with lateral swellings, dorsally strongly sculptured. Anterior gonopods complex. Posterior gonopods and male leg-pair 10 with strongly reduced telopodites. One genus.

Branneria Bollman, 1893. — Two species, southeastern USA. *B. carinata* (Bollman, 1888) is quite widespread.

Family CHAMAESOMATIDAE Verhoeff, 1913 (in the sense of Enghoff & Reboleira, 2013, i.e., incl. ORIGMATOGONIDAE Verhoeff, 1914 which was placed as a separate family in superfam. ANTHROLEUCOSOMATOIDEA by Shear, 2011). — Length 3.3-12 mm, 25, 27 or 29 'rings'. Paraterga small, humplike. Anterior gonopods with mostly

well-developed telopodites and sometimes with flagella. Posterior gonopods with one- or two-segmented telopodites. Many species unpigmented, living in caves. Male leg-pair 10 and/or 11 usually with coxal hooks. 11 genera, 28 species, Europe, N Africa.

Chamaesoma Ribaut & Verhoeff, 1913. — One species, *C. broelemanni* Ribaut & Verhoeff, 1913, epigean, only 25 'rings', France.

Meinerteuma Mauriès, 1982. — One species, *M. lucasii* (Silvestri, 1896), epigean, Tunisia, Algeria.

Scutogona Ribaut, 1913. — Six species, partly cave-dwelling, France, Spain, Portugal.

Xystrosoma Ribaut, 1927. — Eight species, partly cave-dwelling, France, Spain. *X. beatense* Ribaut, 1927.

Family GOLOVATCHIIDAE Shear, 1992. — Length 15-17 mm, 29 'rings'. Paraterga not developed. Anterior gonopods with two-segmented telopodites (unique in order). Male leg-pair 10 strongly reduced. One genus.

Golovatchia Shear, 1992. — One species, *G. magda* Shear, 1992, Russian Far East.

Family HETEROLATZELIIDAE Verhoeff, 1899. — Length 9-21 mm, 29 'rings'. Paraterga small to well-developed. Male leg-pairs 10 and 11 without coxal processes. Anterior gonopods with neither flagella nor telopodites/cheirites. Posterior gonopods with prominent wide ladle-like coxites. Two genera, four species, SE Europe (Balkan Peninsula).

Heterolatzelia Verhoeff, 1897. — Three species.

Family KASHMIREUMATIDAE Mauriès, 1982. — Length 5-14 mm, 25 or 27 'rings'. Body subcylindrical. Anterior gonopods complex. Posterior gonopods simple, with articulated telopodites. Female leg-pair 2 strongly reduced in most species. Two genera, six species, East Asia.

Kashmireuma Mauriès, 1982. — Three species, Himalaya.

Vieteuma Golovatch, 1984. — Three species, including one blind cave-dweller, Vietnam, S China.

Family MACROCHAETEUMATIDAE Verhoeff, 1914. — Length 6 mm, 27 'rings'. Paraterga small. Macrochaetae long and stout. Vulvae each with a huge, clavate appendix, both appendices partly fused medially. One genus.

Macrochaeteuma Verhoeff, 1914. — One species, *M. sauteri* Verhoeff, 1914, Japan.

Family MICROLYMPIIDAE Shear & Leonard, 2003. — Length 4 mm, 27 'rings'. Paraterga small. Posterior gonopods consisting of a single, U-shaped article. Coxae of male leg-pair 10 with unique anterior fringe on the coxal gland openings. One genus.

Microlympia Stear & Leonard, 2003. — One species, *M. echina* Shear & Leonard, 2003, NW USA (Washington).

Family NIPONIOSOMATIDAE Verhoeff, 1941. — Length 7-9 mm, 27 or 29 'rings'. Body smooth, cylindrical. Antennae slender. Anterior gonopod telopodites three-branched, rodlike (character shared with Tingupidae). Two genera, three species, Japan.

Niponiosoma Verhoeff, 1941. — Two species.

Family TINGUPIDAE Loomis, 1966. — Length 2.1-7 mm, 25, 27 or 29 'rings'. Mentum of gnathochilarium transversely divided. Antennae short, clavate. Paraterga pronounced. Characteristic surface sculpture consisting of short, acute ridges running longitudinally, and scattered over the dorsal surface. Two genera, 12 species, E and W USA, marginally in Canada (British Columbia), Alaska.

Tingupa Chamberlin, 1910. — 11 species.

Family TRACHYGONIDAE Cook, 1896. — Length 3.5-4.5 mm, 27 or 29 'rings'. Very few ommatidia, if any. Antennae short, clavate. Often with strongly sculptured dorsal surface. Paraterga well-developed. Three genera, six species, Bosnia-Herzegovina to southern Germany.

Halleinosoma Verhoeff, 1913. — Two species. *H. noricum* Verhoeff, 1913, Austria, Switzerland, Germany.

Superfamily CLEIDOGONOIDEA Cook, 1896.

Family BIOKOVIELLIDAE Mršić, 1992. — Length 12.5-14.5 mm, 29 'rings'. Paraterga very small protuberances. Anterior gonopods with complex telopodites and a pair of clubbed flagella. Posterior gonopods strongly reduced, only represented by a small sternum with a mesal process. One genus.

Biokoviella Mršić, 1992. — One species, *B. mauriesi* Mršić, 1992, Croatia.

Family CLEIDOGONIDAE Cook, 1896. — Length 9-36 mm, 29 'rings'. Paraterga bulge-like. Antennae long, not clavate. Posterior gonopods mostly with more than 2 articles, their coxae enlarged and lobed, locking the anterior gonopod telopodites in place. Eight genera, 152 species, N and Central America.

Cleidogona Cook, 1895. — 83 species, USA (Connecticut) to Panama. *C. caesioannulata* (Wood, 1865), *C. huebnerae* Shear, 2013.
Pseudotremia Cope, 1869. — 47 species, central eastern USA, most species troglobiont. *P. peponocranium* Shear, 2011.

Family ENTOMOBIELZIIDAE Verhoeff, 1899. — Length 7-2 mm, 27 'rings'. Paraterga highly reduced. Posterior gonopods leglike, 5-segmented, with claw. Two genera, four species.

Entomobielzia Verhoeff, 1898. — Three species, Romania.
Tianella Attems, 1904. — Nine species, central Asia, Himalaya.

Family LUSITANIOSOMATIDAE Schubart, 1953. — Length 7 mm, 29 'rings'. Anterior gonopods a syncoxite with two pairs of crossing branches. Posterior gonopods with elongtated coxae and reduced, one-segmented telopodites. One genus.

Lusitaniosoma Schubart, 1953. — One species, *L. machadoi* Schubart, 1953, Portugal.

Family OPISTHOCHEIRIDAE Ribaut, 1913. — Length 5-16 mm, 25 or 29 'rings'. Paraterga small humps, sometimes hardly developed. Connection between tracheal pouches and telopodites of anterior gonopods S-shaped. Posterior gonopods 1-3-segmented. Five genera, 36 species, W Europe, one species in Morocco.

Ceratosphys Ribaut, 1920. — 26 species, Belgium to Morocco.

Opisthocheiron Ribaut, 1913. — Six species, France, marginally Spain. *O. canayerensis* Mauriès & Geoffroy, 1983.

Family TRICHOPETALIDAE Verhoeff, 1914. — Length 3.8-13.5 mm, 27 or 29 'rings'. Tergal setae very well-developed. Anterior gonopods usually with a strong fimbriate branch. Many, but not all, species have distinctive trichomes on the anterior gonopod coxae and angiocoxites. Telopodite of posterior gonopod reduced to a single fused article. Many species in caves. Six genera, 40 species.

Mexiterpes Causey, 1963. — Seven species, Mexico.

Scoterpes Cope, 1872. — 15 species, all in caves, SE USA.

Trichopetalum Harger, 1872. — Seven species, E USA. *T. lunatum* Harger, 1872 extends into S Canada.

Superfamily CRASPEDOSOMATOIDEA Gray in Jones, 1843.

Family ATTEMSIIDAE Verhoeff, 1899. — Length 9-25 mm, 29 'rings'. Mainly differ from Craspedosomatidae by having the seventh male coxae enlarged and modified. Posterior gonopods reduced to pair of segmented or unsegmented rods. 16 genera, ca. 25 species, SE central Europe (Austria and surroundings), many species are cave-dwellers.

Attemsia Verhoeff, 1895. — Five species.

Dendromonomeron Verhoeff, 1912. — One species, *D. oribates* (Latzel, 1884) is the only attemsiid reaching as far north as Germany.

Polyphematia Verhoeff, 1912. — One species, *P. monilifomis* (Latzel, 1884), Austria, Slovenia.

Family CRASPEDOSOMATIDAE Gray in Jones, 1843. — Length 7-24 mm, 29, rarely 27 'rings'. Paraterga 'wing-like', as in polydesmids, or bulge-shaped. Seventh male coxae not enlarged. Posterior gonopods never leglike. 35 genera, 188 species, western and central Europe.

Atractosoma Fanzago, 1876. — 14 species, Italy, a few species in Austria, Croatia, Germany and Switzerland. *A. meridionale* Fanzago, 1876 (Plate XIV E), is the most widespread species.

Bergamosoma Hoffman, 1980. — Four species, Alpine region, northern Italy. *B. canestrinii* (Fedrizzi, 1878) (Plate XIV F).

Craspedosoma Leach, 1814. — 13 species, most species in Italy. *C. rawlinsii* Leach, 1814 (Plate XIV B), widespread in Western Europe.

Dactylophorosoma Verhoeff, 1900. — Two species, northern Italy, Switzerland. *D. nivisatelles* Verhoeff, 1900 (Plate XIV D).

Iulogona Cook, 1896. — Four species, Italy. *I. tirolensis* (Verhoeff, 1894) also in Austria, Germany, Switzerland.

Nanogona Cook, 1895. — Six species, France, but *N. polydesmoides* (Leach, 1814) widespread in W Europe.

Ochogona Cook, 1895. — 19 relatively small species, France to Croatia. *O. caroli* (Rothenbühler, 1900).

Pyrgocyphosoma Verhoeff, 1897. — 41 species, Italy, a few also in neighbouring countries. *P. titianum* (Verhoeff, 1910) (Plate XIV C).

Rhymogona Cook, 1896. — Five species (but the number of valid species is under discussion), Germany, Switzerland, France. *Rh. montivaga* (Verhoeff, 1894).

Family HAPLOBAINOSOMATIDAE Verhoeff, 1909. — Length 19-31 mm, 29 'rings'. Paraterga well-developed. Antennae long and slender. Posterior gonopods 1-3-segmented.

Very similar to Attemsiidae, but seventh male coxae not as enlarged as in the latter family. Four genera, 14 species, SW Europe.

Haplobainosoma Verhoeff, 1900. — One species, *H. lusitanum* Verhoeff, 1900, Portugal, including Azores.

Pyreneosoma Mauriès, 1959. — Ten species, Pyrenees Mountains.

Superfamily HAASEOIDEA Attems, 1899.

Family HAASEIDAE Attems, 1899. — Length 4.5-12 mm, 27 or 29 'rings'. Paraterga well-developed, dorsal macrochaetae very long. Coxae of male 9th legs enlarged. Telopodites of anterior gonopods with a (sperm?) canal. Four genera, 23 species, central and SE Europe.

Haasea Verhoeff, 1895. — 15 species. *H. flavescens* (Latzel, 1884) is the most widespread haaseid. *H. fonticulorum* (Verhoeff, 1910), *H. hungarica* (Verhoeff, 1928).

Xylophageuma Verhoeff, 1911. — Two species, Germany, France, Switzerland. *X. zschokkei* Bigler, 1912.

Superfamily NEOATRACTOSOMATOIDEA Verhoeff, 1901. — European and Altai Mountains, Russian Far East, Japan and China.

Family KIRKAYAKIDAE Özdikmen, 2008 (= ALTAJELLIDAE Mikhaljova & Golovatch, 2001). — Length 7-14 mm, 27 'rings'. Body subcylindrical, no paraterga. Antennae slender. Anterior gonopods with flagella or numerous filamentous outgrowths. Four genera, five species, central Asia.

Kirkayakus Özdikmen, 2008. — One species, *K. pallidus* (Gulička, 1972), Altai Mountains.

Family CYRNOSOMATIDAE Mauriès, 2015. — Length 7-12 mm, 29 'rings'. Anterior gonopods with a pair of flagella arising medially. One genus.

Cyrnosoma Mauriès, 2015. — Three species, Corsica.

Family GUIZHOUSOMATIDAE Mauriès, 2005. — Length 11-15 mm, 27 'rings'. Body subcylindrical, no paraterga. Anterior gonopods simple, triangular, without flagella or filamentous outgrowths, simple triangle. Blind troglobite. One genus.

Guizhousoma Mauriès, 2005. — One species, China, Guizhou.

Family HOFFMANEUMATIDAE Golovatch, 1978. — Length 4-6 mm, 27 'rings'. Paraterga not developed. Anterior gonopods with a flagelliform branch. Male leg-pair 10 reduced, pair 12 with coxal hooks. Two genera, four species.

Hoffmaneuma Golovatch, 1978. — One species, *H. exiguum* Golovatch, 1978, Russian Far East.

Japanoparvus Shear, Tanabe & Tsurusaki, 1998. — Three species, Japan.

Family MASTIGOPHOROPHYLLIDAE Verhoeff, 1899. — Length 9-20 mm, 29 'rings'. Paraterga well-developed. Anterior and posterior gonopods both with flagella. Dorsal macrochaetae long. Second pair of female legs very much reduced. Nine genera, 38 species, central and E Europe.

Mastigona Cook, 1895. — Four species. *M. bosniensis* (Verhoeff, 1897); *M. mutabilis* (Latzel, 1884), quite widespread.

Mastigophorophyllon Verhoeff, 1897. — 15 species, mainly Romania. *M. saxonicum* Verhoeff, 1916, widespread north to Estonia.

Tessinosoma Verhoeff, 1911. — One species, *T. coelebs* Verhoeff, 1911, Italy, Switzerland, seems to be mainly parthenogenetic.

Family NEOACTRACTOSOMATIDAE Verhoeff, 1901, incl. FAGINIDAE Attems, 1926. — Length 6-18 mm, 27 or 29 'rings'. Body with poorly or relatively well-developed, bulge-shaped paraterga. Anterior gonopods with a pair of flagella or bunches of needlelike rods (graphia) arising laterally. Posterior gonopods without flagella, telopodites reduced to erect stumps, more or less independent from the sternite. Nine genera, ca. 22 species, central and SE Europe.

Fagina Attems, 1904. — One species, *F. silvatica* (Attems, 1904), SE Europe.

Pseudocraspedosoma Silvestri, 1898. — Six to eight alpine species, Germany, Switzerland, Italy.

Schizmohetera Mršić, 1987. — Two or three species, Macedonia, Greece.

Superfamily VERHOEFFIOIDEA Verhoeff, 1899.

Family VERHOEFFIIDAE Verhoeff, 1899. — Length 6.5-11 mm, 29 'rings'. Body cylindrical-fusiform, no paraterga. Anterior gonopods simple, without flagella. Posterior gonopods with flagella. One genus.

Haplogona Cook, 1895. — Four species, central Europe. *H. oculodistincta* (Verhoeff, 1893) (Plate XIV A).

Suborder Heterochordeumatidea Shear, 2000

Mentum of gnathochilarium undivided. Posterior gonopods with coxites functioning in sperm transfer in conjunction with anterior gonopods, rarely alone; telopodites usually two-segmented, apical segment swollen and glandular. Male leg-pair 10 with coxal glands, coxae and glands often much enlarged, telopodite often reduced or vestigial; male leg-pair 11 with or without coxal glands. Mainly 'antitropical', i.e., Palaearctic region, Chile, Madagascar, India, Sri Lanka, Australia, New Zealand, but also in SE Asia through Indonesia to New Guinea.

Superfamily CONOTYLOIDEA Cook, 1896. — Antennae long and slender. Paraterga modest to rather prominent dorsolateral bulges. Posterior gonopods with a strong, plate-like sternum, telopodites usually strongly enlarged, 2-segmented and setose. Male legs 10 reduced, male legs 11 without coxal glands.

Family ADRITYLIDAE Shear, 1971. — Length 20-30 mm, 29 'rings'. Anterior gonopods each of a single piece, formed from a fusion of the gonopod with its sternite and the tracheal apodeme. Coxa of male legs 10 strongly enlarged, lobed; telopodites reduced to 2- or 3-segmented vestiges. One genus.

Adrityla Causey, 1961. — Three species, USA.

Family CONOTYLIDAE Cook, 1896. — Length 6.5-25 mm, 29 'rings'. Anterior gonopods not fused to sternite. Male legs 10 often with slightly, exceptionally strongly,

enlarged coxae, sometimes forming a syncoxosternum; telopodites occasionally reduced, 2-segmented. 16 genera, ca. 65 species, mainly Nearctic, three genera with ca. five species in Japan and the Russian Far East.

Conotyla Cook & Collins, 1895. — 12 species, eastern N America.

Superfamily DIPLOMARAGNOIDEA Attems, 1907.

Family DIPLOMARAGNIDAE Attems, 1907. — Length 9-24 mm, 31, exceptionally 28 'rings'. Paraterga from subhorizontal wings to small bulges. Anterior gonopods reduced to a small, inverted T-shaped, strongly sclerotized sternum with a pair of 1- or 2-segmented appendages. Posterior gonopods strongly hypertrophied, with a 1- to 3-segmented setose telopodite. Male legs 10 and 11 with coxal glands, sometimes also with outgrowths on coxae and/or prefemora. 12 genera, 70+ species, from the Volga River region west of the Ural Mountains, through Siberia and Mongolia, to the Russian Far East, Korea, Japan and Taiwan.

Diplomaragna Attems, 1907. — 12 species, East Asia.
Tokyosoma Verhoeff, 1932. — 17 species, Japan, Korea, Taiwan.

Superfamily HETEROCHORDEUMATOIDEA Pocock, 1894. — Antennae short to long, antennomere 2 or 3 occasionally with a knob supporting a fanshaped seta. Paraterga from large keels to small bulges. Posterior gonopods with a strong, usually plate-like sternum sometimes with paramedian apophyses, telopodites strongly enlarged, 2-segmented, setose. Flagella may be present either on anterior or posterior gonopods, but never on both pairs. Male legs 10 reduced, male legs 11 often without coxal glands. Vulvae usually species-characteristic, often fused into a well-sclerotized spermatophore-forming syncyphium with a deep central fossa.

Family EUDIGONIDAE Verhoeff, 1914. — Length 5-7 mm, 29 or 31 'rings'. Antennae rather short, antennomeres 5 and 6 forming a club. Tegument of metazonites finely to roughly granulate-spinulate. Paraterga strongly developed. Anterior gonopods without flagella. Telopodites of posterior gonopod particularly large. Three genera, six species, Chile and Andean parts of Argentina.

Eudigona Silvestri, 1903. — One species, Chile.

Family HETEROCHORDEUMATIDAE Pocock, 1894. — Length 8-16 mm, 29 or 31 'rings'. Collum broader than head and partly concealing it from above. Paraterga very well-developed, polydesmidan- or platydesmid-like. Integument more or less roughened, or velvety, due to a covering of microtrichia. Three genera, six species, SE Asia, Indonesia.

Heterochordeuma Pocock, 1893. — Four species, Myanmar, Indonesia.
Pyrgeuma Shear, 2012. — One species, *P. pyrgodesmoides* Shear, 2012, Malacca Peninsula, resembles a species of the polydesmidan family Pyrgodesmidae.

Family MEGALOTYLIDAE Golovatch, 1978. — Length 10-42 mm, 27 or 29 'rings'. Paraterga distinct keels, small bulges, or missing. Anterior gonopods strongly reduced, sometimes consisting only of sternum. Vulvae usually species-characteristic. Two genera, from the Russian Far East and Himalaya to SE Asia.

Megalotyla Golovatch & Mikhaljova, 1978. — Two species, Russian Far East, N Korea.
Nepalella Shear, 1929. — 23 species, from Nepal to SE Asia.

Family METOPIDIOTRICHIDAE Attems, 1907. — Length 4-17 mm, 31 'rings'. Sometimes with contrastful colour patterns. Antennomere 3 sometimes with a knob supporting a modified seta. Paraterga in form of distinct keels or small bulges. Anterior or posterior gonopods (but never both pairs) sometimes with flagella. Male legs 10 consisting of a coxosternum with two hypertrophied, eversible, at least partly sclerotized coxal glands extending deep into body cavity, often also with a central sternal apophysis, and usually with clearly reduced 1- to 5-segmented telopodites. Males often with secondary sexual modifications of head, antennae, pregonopodal and/or postgonopodal legs. Six genera, 58 species.

Australeuma Golovatch, 1986. — Six species, Australia.
Metopidiothrix Attems, 1907. — 38 species, Taiwan, Indochina, Malaysia, Indonesia, Philippines and Papua New Guinea.
Nesiothrix Shear & Mesibov, 1997. — Two species, Australia.
Nipponothrix Shear & Tanabe, 1994. — Two species, Japan (Kyushu and Ryukyu Islands).
Reginaterreuma Mauriès, 1987. — Six species, Australia.
Schedotrigona Silvestri, 1903. — Four species, New Zealand.

Family PETERJOHNSIIDAE Mauriès, 1987. — Length 3-8 mm, 29 or 31 'rings'. Antennae short, antennomeres 5 and 6 forming a club. Anterior and posterior gonopods rather similar, with mesal coxal processes and lateral telopodites, no flagella; telopodites of posterior gonopods 1-segmented, partially enveloping coxites. Male leg-pair 10 with enlarged coxal glands and strongly reduced telopodites. One genus.

Peterjohnsia Mauriès, 1987. — Four species, Australia.

Superfamily PYGMAEOSOMATOIDEA Carl, 1941. — Length 4.5-12 mm, 29 or 31 'rings'. Antennae rather long and slender. Paraterga in form of distinct subquadrangular keels, small bulges, or missing. Male legs 1 strongly reduced. Male gonopore either borne on a small distomedial knob or opening flush on coxa 2. Anterior gonopods sometimes with flagella. Posterior gonopods quite similar to anterior ones, usually with a strong plate-like sternum, without flagella, telopodites 2-segmented, strongly enlarged, setose. Male legs 10 slightly modified, male legs 11 without coxal glands.

Family LANKASOMATIDAE Mauriès, 1978. — Length 5-12 mm, 31 'rings'. Paraterga in the form of distinct keels, or small bulges, or missing. Anterior gonopods compact, shieldlike, with a pair of flagella. Posterior gonopods with a furrow/canal for accommodation of anterior gonopod flagellum. One genus.

Lankasoma Mauriès, 1981. — Five species, Sri Lanka.

Family PYGMAEOSOMATIDAE Carl, 1941. — Length 4.5-12 mm, 29 or 31 'rings'. Male leg 1 sometimes (*Hendersonula*) strongly reduced to short, 3-segmented appendage. Anterior gonopods without flagella. Vulvae often species-characteristic, contiguous medially, operculum prominent, valves of bursa rather small, differently armed and setose. Two genera, S India and Madagascar.

Betscheuma Mauriès, 1994. — 18 species, Madagascar.
Hendersonula Pocock, 1903. — Two species, S India.

Suborder Striariidea Cook, 1896

Mentum of gnathochilarium transversely divided. Posterior gonopods with telopodites of a single article, usually an inflated, mostly button-shaped, setose, sometimes also spinulate, granulate or tuberculate podomere, serving as a shield for the anterior gonopods which act alone in sperm transfer (posterior gonopod telopodite wanting in Apterouridae); posterior gonopod coxites present, supporting anterior gonopods at rest. Leg-pairs 10 and 11 with coxal glands. Leg-pair 10 not reduced. Nearctic subregion, one species in NE Asia. Two superfamilies.

Superfamily CASEYOIDEA Verhoeff, 1909. — Length 6-20 mm, 29 'rings'. Male coxae 2 usually with gonopores opening through a strong apophysis. Paraterga mostly absent, but exceptionally strong, clearly bilobed and increasing in size towards segment 7. Anterior gonopods complex, with at least one pair of flagella.

Family CASEYIDAE Verhoeff, 1909. — Length 6-20 mm. Antennae moderately to very long, slender, only slightly clavate. Body subcylindrical, no paraterga. Seven genera, 45 species, N America, but one species in the Russian Far East.

Caseya Cook & Collins, 1895. — 21 species, western USA.

Underwoodia Cook & Collins, 1895. — Three species. *U. iuloides* (Harger, 1872), widespread in north-eastern and mid-northern N America, and *U. kurtschevae* Golovatch, 1980, Russian Far East, are probably both predominantly parthenogenetic.

Family UROCHORDEUMATIDAE Silvestri, 1909. — Length 16-19 mm. Antennae long and slender, Paraterga strong, bilobed, growing increasingly prominent towards segment 7. Two nominal, but maybe just one, species in a single genus.

Urochordeuma Silvestri, 1909. — Two species, USA (Washington State).

Superfamily STRIARIOIDEA Bollman, 1893. — Length <4-25 mm, mostly 29 'rings'. Collum usually broader than head, often at least partly covering it from above. Tegument sculptured, usually heavily sclerotized, ornamentation family-characteristic. Paraterga mostly strong at least on some pleuroterga.

Family APTEROURIDAE Loomis, 1966. — Length 5.8-8 mm, 29 'rings'. Antennae rather short and clavate, with particularly enlarged antennomeres 5 and 6. Collum and most following metaterga granulate, with distinct paraterga, but after 'ring' 24 smooth and without paraterga. Collum slightly narrower than head. Anterior gonopods complicated, posterior gonopods strongly reduced, totally concealed between anterior gonopods and sunk into body cavity. One genus.

Apterourus Loomis, 1966. — Two species, USA (California).

Family BUOTIDAE Shear, 2009. — Length 2-4 mm, 25 (males) or 29 (females) 'rings'. Collum broader than head. A pigmented spot instead of ommatidia or an ommatidium on each side of head. Antennae short, clearly clavate, antennomere 5 by far the largest. Postcollum metaterga with short, square paraterga. Tergal macrochaetae very small, flattened and branched apically, bi-articulate, borne on a tubular socket. Anterior and posterior gonopods complicated. One genus.

Buotus Chamberlin, 1940. — One species, *B. carolinus* Chamberlin, 1940, southeastern USA. One of the world's smallest millipedes.

Family RHISCOSOMIDIDAE Silvestri, 1909. — Length 6-7.1 mm, 29 'rings'. Antennae short, clavate, antennomere 5 by far the largest. Tegument of metaterga very densely beset with sharp tuberculations supporting tiny branched setae, appearing almost microhirsute. Collum broader than head. Following paraterga prominent. Anterior and posterior gonopods complicated. One genus.

Rhiscosomides Silvestri, 1909. — Eight species, western N America.

Family STRIARIIDAE Bollman, 1893. — Length 6-15 mm, exceptionally up to 25 mm, 29 'rings'. Antennae long and slender. Head mostly concealed by an enlarged, hood-like collum. Eye with less than 10 ommatidia, arranged on a line. Body subcylindrical, capable of coiling into a tight spiral. Tegument of metaterga thick, distinctly carinate, with 10-12 distinct longitudinal ridges, often covered by a waxy secretion; metatergal setae strongly reduced. Lateral end of male labrum produced into a long, curved process. Anterior gonopods complex, posterior gonopods strongly reduced. Four genera, 15 species, USA.

Striaria Bollman, 1887. — Nine species.

Order Callipodida Pocock, 1894

[PAVEL STOEV]

Body length 12-100 mm. Head usually sexually dimorphic, always convex in females, often medially excavate, occasionally also with frontal bulges, in males. Eyes with numerous ommatidia arranged in a triangular cluster (moderately to strongly reduced in some cave-dwelling species). Organ of Tömösváry always present, circular, situated between the antennal base and the eye. Antennae with antennal trochanter, thus consisting of eight antennomeres and disc. Antennae of variable length, often long and slender, disc always with four apical cones. Antennomere 5 with a distal tuft of sensilla basiconica. Gnathochilarium not sexually dimorphic, mentum transversely divided into promentum and much larger eumentum. Mandible with molar cusps. Mandible usually composed of molar plate surmounted by anterior fringe, intermediate area, pectinate lamellae, internal teeth and external tooth. Molar plate (always?) ridged. Collum usually small and narrower than head and subsequent 'rings' with a pronounced median process on the anterior ridge. Elongated, cylindrical body composed of head, approximately 35 to 88 trunk 'rings' and a telson bearing a pair of spinnerets. Tergite of each segment fused with pleurites to form sub-cylindrical pleurotergites, while sternites are fused to stigmatic plates and remain free and movable. Suture still discernable between sternite and stigmatic plate. Pleurotergites lacking a dorsal suture, but composed of smooth and areolated prozonites and smooth or carinate metazonites, surmounted by trichoid setae arranged in patterns. Metazonites greater in diameter than prozonites, provided with longitudinal crests, ridges, sutures or similar structures. The number of pleurotergites in a given species can be constant or vary. Ozopores present in continuous sequence from pleurotergite 6, lying either between or on lateral crests. Repugnatorial glands of callipodidans produce defensive

secretions that contain para-cresol. Telson usually short, not produced, with a pair of spinnerets at posterior edge of epiproct. Paraprocts always transversely divided by a conspicuous suture. Hypoproct usually divided into three sclerites, but in some species (e.g. *Himatiopetalum ictericum* or *Euxinopetalum dobatorum*) it is a single plate. Legs moderately long, consisting of seven podomeres (coxa, prefemur, femur, postfemur, tibia, tarsus 1, tarsus 2). Tarsi usually divided with a still continuous tarsal pad. Legs vary in size, anteriormost three pairs in males usually shorter than the remaining ones. Coxal vesicles/pouches starting from leg 3 and extending posteriad to leg-pairs 11, 13, 16, 22, 23, etc. in the different taxonomic groups.

Male pre-gonopodal legs often modified, in particular their coxae, trochanters and femora. Tarsal pads usually present on anterior legs of males (none in *Heptium* and some *Colactis*). Males of some species lack claws on anterior legs (e.g., *Dorypetalum*), others undergo complete modification of leg 7 in the shape of a long spine (*Heptium*). The gonopods are formed from the posterior leg-pair of segment 7 and are deeply withdrawn into the body cavity, with distalmost parts usually extending beyond the pleurotergal edge. Leg 9 a normal walking leg. Gonopods very complex and variable, composed of a sternum, coxae and elongated telopodites attached to the coxae by a pivot or hinge articulation, movable by various muscle combinations. Gonosternum (a sclerite lying inbetween the gonopod telopodites, sometimes being fused with gonocoxae to form a single sclerous coxosternal plate) either basal to the gonocoxae (in Sinocallipodidea), or lying in front of the coxae as a large, chitinized, subquadrate, transverse plate (e.g. in some Schizopetalidae), or medially divided and fused with the coxae to form two coxosterna (Dorypetalidae). Other configurations are also known. Coxae usually elaborate, often bearing coxal processes, the latter sometimes as large as the telopodites. Telopodites vary significantly in size and shape across the families. Except for Sinocallipodidea, all members of the order with a prostatic groove running from femoroidal base to the distalmost part of the solenomere. In some taxa, morphological modifications on legs 7 and 9 seem to play a role in copulation too. Male vasa deferentia open through gonopores on coxae 2. Female sexual opening surrounded by two small valves and a small operculum, all retractable into a long, tubular sac extending as far back as the eight or ninth segment and capable of being extended to function as an ovipositor. Second leg-pair in females can be normal or reduced to small sclerites showing a species-specific shape. Body ‘rings’ 2 and 3 of sexually mature females usually enlarged.

Just like most millipedes, callipodidans are detritivores and feed on decaying plant material. However, carnivory and even cannibalism were also documented in some members of the order, such as *Apfelbeckia insculpta*, *Callipus foetidissimus*, *Abacion magnum*. The species were observed feeding on worms, flies, spiders and juvenile millipedes. Most callipodidans live in caves, stony debris or rock crevices. Some species can well resist drought and live in relatively dry desert and steppe habitats.

All callipodidans develop through teloanamorphosis or hemianamorphosis.

Callipodida are currently composed of 3 suborders, 8 families, 36 genera or subgenera and around 140 extant species or subspecies (for more details see Stoev et al., 2008). The order is distributed in the northern and eastern Mediterranean regions, central and SE

Asia, and central and southern North America, with their greatest diversity in the Balkan Peninsula, Asia Minor, southwestern parts of the USA and adjacent parts of Mexico. Some species are distributed by human activities: *Eurygyrus ochraceus* introduced to the Crimea and the Bulgarian Black Sea coast; *Dorypetalum degenerans* to Budapest and Budai Mountains, Hungary; *Callipus foetidissimus* to Paris, France.

Suborder Sinocallipodidea Shear, 2000

Length 40-70 mm. Trunk composed of 55-72 pleurotergites; primary pleurotergal crests low and narrow; secondary and tertiary crests absent; tergal setae thin and pointed, all in an anterior position. Leg-pairs 3-11 with coxal pouches. Head of males convex, pilose, without particular modifications. Leg 9 in males with a distomedial, deeply excavated trochanteral lobe bearing pointed projections, which is suggested to play a role in copulation. Gonosternum extending for the entire breadth of gonopods, lying basal to gonocoxae. Gonocoxa with two medial, clavate processes and a long, slender cannula; telopodite without prostatic groove, with two to four slender, narrowly separated, terminal projections directed anteromesad and overlapping with or terminating close to coxal processes. In contrast to the other suborders, sinocallipodidan have quite uniform gonopods. Differences mainly concern shape and length of cannula, length and shape of certain coxal processes and number of acicular projections of femoroid. Second leg-pair in females normal.

Family SINOCALLIPODIDAE Zhang, 1993. — One genus.

Sinocallipus Zhang, 1993. — Six species, South China (Yunnan), Vietnam, Thailand and Laos. *S. thai* Stoev, Enghoff, Panha & Fuangarworn, 2007.

Suborder Callipodidea Pocock, 1894

Length up to 70 mm. Trunk composed of approximately 55-65 ‘rings’. Head in males convex and lacking particular modifications. Pleurotergal crests missing, instead there are longitudinal grooves. Tergal setae in a posterior position on all ‘rings’. Paraprocts divided into subequal dorsal and ventral halves by transverse suture. Leg-pairs 3-21 with coxal vesicles. Gonopods with a large deltoid sternum on the anterior side and a large transverse intercoxal muscle band posterior to it. The telopodite is not attached to the coxa by a hinged articulation but fussed basally to a long prominent apodeme and capable of in-and-out movements against the coxa by muscle contractions. Female second leg-pair reduced in *Callipus* (females of *Sardopus* unknown).

Family CALLIPODIDAE Bollman, 1893. — Two genera.

Callipus Risso, 1826. — Four species (six subspecies), incl. *C. foetidissimus* (Savi, 1819), France (incl. Corsica), Italy (incl. Sardinia and Sicily), Monaco, Switzerland?

Sardopus Strasser, 1974. — One species, *S. malleiger* Strasser, 1974, Italy, Sardinia.

Suborder Schizopetalidea Hoffman, 1973

Length 12 to approximately 100 mm. Trunk of 35 to 88 'rings'. Pleurotergal crests from well pronounced to very poorly developed. Pleurotergal setae in an anterior position on 'rings' 1-4, 'migration' of setae usually starts on segment 5; all setae usually in a posterior position from 'rings' 6-8 onwards. Paraprocts divided by a transverse suture into a smaller dorsal and a larger ventral half. Coxal pores vary in number across the families, and the following combinations occur: 3-13, 3-16, 3-19, 3-22, 3-23. Suborder characterized by the mode of articulation of the gonopod. The coxal region is expanded and usually fused with the sterna elements. Telopodite attached to the coxa with a pivot or a hinge joint. Female second leg-pair normal or reduced. Northern Mediterranean realm, central and southeastern Asia, North America.

Family ABACIONIDAE Shelley, 1979. — Length 19-59 mm. Trunk composed of approximately 46-61 'rings'. Pleurotergal crests well-developed; poriferous ones larger and more prominent than primary crests in Abacionini and subequal in size in Delophonini. Head in males convex. Leg-pairs 3-13? with coxal pores. Gonopods with variable coxal processes that usually enshield basal part of femorite, with a long acicular postcoxal flagellum with a bulbous base that could represent part of the coxa or a sternal process; flagellum present in Abacionini, missing in Delophonini. The telopodites are composed of a linear femorite and abruptly bent to nearly perpendicular postfemoral part, composed of a solenomere, larger parasolenomere and usually several broader tibiotarsal processes. Female second leg-pair reduced. Eastern USA and northern Mexico.

Subfamily ABACIONINAE Shelley, 1979.

Abacion Rafinesque, 1820. — Five species, USA, northern Mexico. *A. lactarium* (Say, 1821), *A. magnum* (Loomis, 1943), *A. texense* (Loomis, 1937).

Tetracion Hoffman, 1956. — Three species, caves in USA. *T. jonesi* Hoffman, 1956.

Subfamily DELOPHONINAE Shelley, 1979.

Delophon Chamberlin, 1943. — Four species, southeastern USA. *D. georgianum* Chamberlin, 1943.

Family CASPIOPETALIDAE Lohmander, 1931. — Small to moderate-sized Callipodida (28-45 mm), with trunk composed of 53-66 'rings'; tergal crests well developed, poriferous ones prominent. Head of males frontally concave, sometimes with a frontal bulge. Coxae of the male pre-gonopodal legs often modified. Leg-pairs 3-15 with coxal pores. Gonopods relatively simple; gonosternum with a chitinous round-triangular process; gonocoxa subquadrate, prolonged posteriad, bearing an inner coxal process; telopodites simple, attached at the posterior end of the coxae, usually crossing each other in situ and projecting ventrad outside the body cavity; telopodites usually composed of a long, slender and linear femorite and abruptly bent (almost perpendicular) postfemoral part, comprised by a long and straight solenomere and several tibiotarsal processes. Leg-pair 2 in females usually modified. One genus, central and East Asia.

Bollmania Silvestri, 1896. — Eight species, from Iran to southern China.

Family DORYPETALIDAE Verhoeff, 1900. — Length 12-50 mm. Trunk composed of 43-49 'rings'. Pleurotergal crests poorly developed, ozopores situated at base of crests. Head of males either concave or convex. Coxal pores present on leg-pairs 3-13 in Dorypetalinae, on leg-pairs 3-22 in Cyphocallipodinae. Male pre-gonopodal legs often modified, in *Dorypetalum* leg-pairs 4-7 without tarsal claws, and with enlarged prefemora. Gonopods composed of a sternum which is medially divided to form two nearly separate parasterna which in turn are fused with the coxae. Coxosternum very complex, usually with two or three processes: telopodite usually long and slender, bow-shaped, lying between the coxosternal processes. Leg-pair 2 in females normal or modified. Four genera, ten species, Balkan and Iberian peninsulas, Aegean coast of Turkey, southern Romania, one species introduced to Hungary.

Subfamily DORYPETALINAE Verhoeff, 1900.

Dorypetalum Verhoeff, 1900. — Length mostly less than 20 mm. Seven species, incl. *D. degenerans* (Latzel, 1884), Balkan Peninsula and neighbouring parts of Romania and Turkey.

Subfamily CYPHOCALLIPODINAE Verhoeff, 1909.

Cyphocallipus Verhoeff, 1909. — One species, *C. excavatus* Verhoeff, 1909, Spain.
Dorycallipus Verhoeff, 1909. — One species, *D. arcuum* Verhoeff, 1893, Spain.
Lusitanipus Mauriès, 1978. — One species, *L. alternans* Verhoeff, 1893, Portugal.

Family PARACORTINIDAE Wang & Zhang, 1993. — Length 32-60 mm. Trunk of 50-85 'rings'. Pleurotergal crests well-developed, poriferous ones prominent. Head in males convex. Coxal pores on leg-pairs 3-23. Gonosternum reduced or fused with coxae. Gonocoxae freely connected through a medial membranous lamina. Telopodite with one or two prefemoroidal processes, their apical parts usually covered with macrosetae; the basal and proximal parts of femoroidal stem simple, unbranched; distal part usually broadened, with several processes; a parasolenomere is always present. Leg 2 in females reduced to two simple sclerites. Two genera, 12 species, southern China and Vietnam.

Angulifemur Zhang, 1997. — Two species, Yunnan Province, China.
Paracortina Wang & Zhang, 1993. — Ten species, southern China and northcentral Vietnam.

Family SCHIZOPETALIDAE Verhoeff, 1909. — Length 12 to 100 mm. Trunk of 35-56 pleurotegites. Pleurotergal crests either well developed (e.g., *Himatiopetalum*, *Prolysiopetalum*) or nearly lacking (*Callipodella*); ozopores situated at base of crests. Head in males either convex or concave, frontal knobs missing. Coxal pores present on leg-pairs 3-16. Pre-gonopodal legs in males with or without modifications. Gonopods very complex (especially so in *Callipodella*): sternum usually large and transverse and directly anteriad to the coxae; coxae of moderate size and usually with well developed coxal processes; telopodites usually very complex, with highly modified distal parts. Second leg-pair in females normal in all genera, except for *Euxinopetalum*. Ten genera, 53 species, the northeastern Mediterranean realm.

Subfamily ACANTHOPETALINAE Hoffman & Lohmander, 1964.

Tribe ACANTHOPETALINI Hoffman & Lohmander, 1964.

Acanthopetalum Verhoeff, 1900. — Two subgenera (*Acanthopetalum* and *Petalysium* Strasser, 1976), 12 species (15 subspecies), from the Apennines (incl. Sicily and Lipari islands), Balkan

Peninsula (mainly western and southern parts), and Aegean coast of Turkey. One species introduced to Malta. *A. carinatum* (Brandt, 1840), *A. richii* (Gray, 1832).

Balkanopetalum Verhoeff, 1926. — Six species, Bulgaria and Greece.

Eurygyrus C. L. Koch, 1847 (Plate XIV G). — 18 species, incl. *E. ciliciensis* (Verhoeff, 1898). *E. ochraceus* C. L. Koch, 1847, Greece, Turkey, Syria, Lebanon, Palestine, Israel. Some species introduced to the Crimea, Bulgaria and possibly Cyprus.

Tribe APFELBECKIINI Verhoeff, 1900.

Apfelbeckia Verhoeff, 1896. — Three species, western part of the Balkan Peninsula. *A. insculpta* (C. L. Koch, 1847).

Himatiopetalum Verhoeff, 1900. — One species, *H. ictericum* (L. Koch, 1867), the Greek island of Corfu and possibly also southern Albania.

Tribe PROLYSIOPETALINI Verhoeff, 1909.

Prolysiopetalum Verhoeff, 1909. — Two subgenera (*Prolysiopetalum* and *Heterocraspedum* Verhoeff, 1909), five species (six subspecies), Apennine and Balkan peninsulas and the Aegean coast of Asia Minor. *P. scabratum* (L. Koch, 1867).

Subfamily EUXINOPETALINAE Hoffman, 1973.

Euxinopetalum Hoffman, 1973. — One species, *E. dobatorum* Hoffman, 1973, cave in the Asiatic part of Turkey.

Subfamily SCHIZOPETALINAE Verhoeff, 1909.

Tribe DISCHIZOPETALINI Verhoeff, 1909.

Dischizopetalum Verhoeff, 1900. — One species, *D. illyricum* (Latzel, 1884), NE Italy, Slovenia, Croatia, Serbia.

Tribe SCHIZOPETALINI Verhoeff, 1909.

Schizopetalum Verhoeff, 1900. — One species, *S. koelbeli* (Verhoeff, 1895), Croatia.

Callipodella Verhoeff, 1900. — Five species (six subspecies), Apennine and Balkan peninsulas, southern parts of Romania. *C. fasciata* (Latzel, 1882).

Family TYNOMMATIDAE Hoffman, 1980. — Small to moderate-sized Callipodida (13-50 mm), with a trunk composed of 43-88 'rings'. Tergal crests well-developed, lateral poriferous ones usually more prominent. Coxal pores present on legs 3-19 or 3-23 (number unknown in most taxa). Head in males usually convex, the pre-gonopodal legs often modified. Tarsal pads missing in *Heptium* and some species of *Colactis*, leg-pair 7 in the former reduced in a shape of a long spine standing in front of the gonopods. Gonosterna with or without lateral sternal laminae and variable caudal sternal processes; gonocoxae also with or without processes. Telopodites weakly sclerotized, generally long, slender, with or without true prefemoral processes and proximal projections, divided distad into two or three branches. 11 genera, 26 species, southwestern United States, Mexico.

Subfamily ASPIDIOPHONINAE Shelley, 2000.

Aspidiophon Shelley, 2000. — One species, *A. divisum* Shelley, 2000, Sinaloa, Mexico.

Subfamily COLACTIDINAE Hoffman, 1980.

Colactis Loomis, 1937. — Four species, southern Nevada and Utah, USA, to southern Baja California Sur, Tiburon Island (Gulf of California), Sonora, and northwestern Durango, Mexico.

Colactoides Shelley, 1997. — One species, *C. grandis* Shelley, 1997, Chihuahua, Mexico.
Heptium Loomis, 1937. — Two species, extreme southern California, USA.

Subfamily DIACTIDINAE Shelley, 1996.

Diactis Loomis, 1937. — Nine species, southwesternmost California, USA.
Caliactis Shelley, 1996. — One species, *C. bistolata* Shelley, 1996, California, USA.
Florea Shelley, 1996. — One species, *F. sinuata* Shelley, 1996, California, USA.

Subfamily TEXOPHONINAE Shelley, 1989.

Texophon Chamberlin, 1946. — Two species, southern Texas, USA.

Subfamily TYNOMMATINAE Hoffman, 1980.

Idrionaria Shelley, 1996. — One species, *I. dineh* Shelley, 1996, Utah, USA.
Tynomma Loomis, 1937. — Three species, central western California, USA.

Subfamily uncertain.

Mexicopetalum Stoev & Shelley, 2009. — One species, Sonora, Mexico.

Order Stemmiulida Pocock, 1894

[THOMAS WESENER]

Adult body length usually 15-40 mm, largest species up to 50 mm. Head with strongly reduced eyes, consisting of only a single or two ommatidia. Unclear if an organ of Tömösváry exists. Antennae with antennal trochanter, consisting of eight antennomeres and disc. Antennae of variable length, often long and slender, disc always with four apical cones. Gnathochilarium strongly sexually dimorphic, mentum entire, small, placed below the enlarged lamellae lingulaes, the latter heavily striated in males. Mandible with molar cusp, usually composed of molar plate surmounted by anterior fringe, intermediate area, numerous pectinate lamellae, internal teeth and external tooth. Molar plate apparently without deep ridges or grooves. Collum large, larger than following tergites, lacking a cone. Elongated, cylindrical body consisting of 30 to 50 body 'rings', moderately long legs and antennae, as well as a telson bearing a pair of spinnerets. Pleurotergites with a wide dorsal suture, resembling a clearly visible gap and a margin covered by large teeth. Sternites fused to stigmatic plates, remaining free and movable. Suture still discernable between sternite and stigmatic plate. Pleurotergites not subdivided into prozonites and metazonites, always eintirely covered with fine striae. Ozopores present in continuous sequence from segment 5. Defensive secretions unknown. Telson usually short, not produced, with one to three pairs of spinnerets at posterior edge of epiproct. Legs consisting of eight podomeres (coxa, trochanter, prefemur, femur, postfemur, tibia, tarsus 1, tarsus 2). Tarsi divided with a still continuous tarsal pad. Coxal pouches present, starting at leg pair 3. Male leg pair 1 and 2, female leg pairs 1-3 heavily modified. Male leg pair 2 with a reduced telopodite, and an unpaired, undivided penis (except for *Eostemmiulus*). Male leg pair 8 modified to anterior gonopods, leg pair 9 strongly reduced to partly atrophied posterior gonopods. Female genitalia unique, consisting of the vulvae

and two receptacles separate from the former, located between leg pairs 2 and 3, more closely attached to coxa and sternite 3 than 2.

Stemmiulida are fast runners and very mobile, apparently the only known millipedes able to jump. All known Stemmiulida develop through teloanamorphosis or hemianamorphosis.

One family, 155 species, South America, Central Africa, India plus Sri Lanka, Vietnam and Indonesia.

Family STEMMIULIDAE Pocock, 1894. — Three genera, 155 species.

Eostemmiulus Mauriès, 2010. — Leg pair 2 little modified, with paired penes. Posterior gonopods with triarticulated telopodite and a large sternite. Stipes of gnathochilarium lacking a lateral lobe. One species, troglophile, Vietnam.

Scoliogmus Loomis, 1941. — Leg pair 2 with reduced telopodite, single, undivided penis. Posterior telopods with a reduced sternite and rarely articulated telopodite. Stipes of gnathochilarium with a lateral lobe. One species, Puerto Rico.

Stemmiulus Gervais, 1844. — Leg pair 2 with reduced telopodite, single, undivided penis. Posterior telopods with a reduced sternite and rarely articulated telopodite. Stipes of gnathochilarium lacking a lateral lobe. More than 150 species, pantropical. *S. bellus* (Cook, 1895), *S. brasiliensis* Iniesta & Ferreira, 2015 (Plate XIV H), *S. modicus* (Silvestri, 1916), *S. recedens* (Silvestri, 1916), *S. regressus* (Silvestri, 1916).

Superorder JULIFORMIA Attems, 1926

[HENRIK ENGHOFF]

Essentially cylindrical millipedes with an elongate body, length 4-344 mm, diameter 0.4-20 mm. Head usually with eyes, each consisting of one (*Sinostemmiulus*) to at least 68 ommatidia, normally arranged in a triangular to ovoid patch, sometimes on a single line. Organ of Tömösváry absent. Antennae each consisting of six antennomeres plus apical disc, disc with four, exceptionally (some Spirobolida) up to at least 20 sensory cones. Sensilla basiconica present laterally on antennomeres 5 and 6. Labrum normally tridentate. Mandibles: gnathal lobe massive, with a simple or lobed premandibular tooth, a lobed dentate lamella, four or more pectinate lamellae and a prominently developed molar plate. Gnathochilarium variably composed, order and (often) family-specific. Trunk with 18-101 body rings, excluding telson. Collum large, covering posterior part of head. Terga, pleurites, stigmatic plates and sternites fused into complete body rings, except that sterna may be free on the first few rings, very rarely secondarily free on all rings (Nemasomatidae). Defense glands present, consisting of a single compartment, opening through lateral ozopores and mostly secreting benzoquinones. Legs consisting of six podomeres (coxa, prefemur, femur, postfemur, tibia, tarsus). Coxal pores absent, except on leg-pair 2 in some Julida. Tarsal claw often with a paronychium. Male legs-pairs 8 and 9 modified into gonopods (pair 9 almost completely reduced in some Spirostreptida). Gonopod morphology extremely variable. Male gonopores opening through paired (rarely unpaired) penes behind leg-pair 2, or (Spirobolida) distal part of gonoduct eversible.

Female gonopores opening through sclerotized vulvae behind leg-pair 2, each vulva consisting of a simple operculum and a more complicated bursa.

Postembryonic development eu- or hemianamorphic. Numbers of body rings and measurements refer to mature individuals only. First stadium with three pairs of legs in the majority of cases.

Distributed in all non-Antarctic zoogeographical regions and, besides Polydesmida, usually the dominating group of millipedes.

Order Julida Brandt, 1833

[HENRIK ENGHOFF]

Body consisting of head and 24-101 body rings excluding telson, length 4-165 mm, diameter 0.4-8 mm. Head without a median suture extending upwards from labrum. Eyes usually present, each consisting of one (*Sinostemmiulus*) to more than 50 ommatidia, normally arranged in a triangular to ovoid patch, sometimes on a single line. Often a pair of frontal setae. Labrum normally tridentate. Mandibles: gnathal lobe massive, with a simple or lobed premandibular tooth, a lobed dentate lamella, 4 or more pectinate lamellae and a prominently developed molar plate. Gnathochilarium autapomorphic by being 'symphyognathous': the stipites meeting in the midline in their basal part, separating the always hairless promentum from the basal plates of the gnathochilarium (secondarily modified in some male Parajulidae). Body rings often with a posterior whorl of setae, exceptionally (Galliobatidae, Trichoblaniulidae, Trichonemasomatidae) with extensive pilosity. Two pairs of legs associated with fifth body ring. First pair of male legs almost always modified, either enlarged (Parajuloidea) or reduced and more or less hooklike (remaining groups), rarely knoblike or unmodified. Male gonopores opening through paired (rarely unpaired) penes behind leg-pair 2. Following male legs often with ventral pads on femur, postfemur and/or tibia. Male legs-pairs 8 and 9 modified into gonopods. Gonopod morphology extremely variable, but usually the posterior gonopods (modified leg-pair 9) contain the actual sperm-transferring organs, whereas the anterior gonopods (modified leg-pair 8) have a protective function ('peltogonopods'). Anterior gonopods usually with elongate coxal processes, telopodites sometimes well-developed, sometimes completely reduced; a pair of flagella arising from the posterior coxal base often present.

Postembryonic development euanamorphic. Periodomorphosis occurs in some species of Blaniulidae and Julidae.

Distributed in the Holarctic region, marginally also in the Oriental (SE Asia) and Neotropical (Central America) regions. Several species widely distributed through anthropochory.

Superfamily BLANIULOIDEA C. L. Koch, 1847. — Mandibles with 4 pectinate lamellae (except in *Vascoblaniulus*). Promentum of gnathochilarium completely separating the lamellae linguales. Male legs without adhesive pads but with flattened, often leaf-like and ridged setae probably playing the same role (securing a firm grip on the female during copulation).

Family BLANIULIDAE C. L. Koch, 1847. — Body consisting of head plus 24-98 body rings excluding telson, length 5-47 mm, diameter 0.3-1.2 mm. Eyes often absent;

when present, ommatidia arranged in a single line or a narrow triangle. Male mandibles usually modified, by outgrowths from cardo and stipes, into parrot bill-like forceps for gripping the female's antennae during copulation. First male legs strongly modified but clearly derivable from a nemasomatid type with a tibial spine. Penis unpaired. Anterior gonopods without flagella. Vulval invaginations often very deep, reaching beyond body ring 3. 22 genera, 67 species, Europe, N Africa, Caucasus and (only one species) eastern N America.

Acipes Attems, 1937. — Six species on Madeira (insular radiation), five further species in Iberian Peninsula and Canary Islands.

Archiboreoiulus Brolemann, 1921. — Two species, western Europe. *A. pallidus* (Brade-Birks, 1920).

Blaniulus Gervais, 1836. — Ten species, mostly cavernicolous, western Europe. *B. guttulatus* (Fabricius, 1798) (Plate XV D), epigean, widespread by commerce, sometimes pest on sugar beets, strawberries etc. *B. lorifer* Brölemann, 1921, *B. troglobius* Latzel, 1886, *B. troglodites* Brölemann, 1898.

Boreoiulus Brolemann, 1921. — Three species, Europe. *B. tenuis* (Bigler, 1913).

Choneiulus Brolemann, 1921. — Five species, Europe, North Africa. *C. palmatus* (Nemec, 1895).

Cibiniulus Verhoeff, 1927. — Two species, *C. phlepsii* (Verhoeff, 1897), E Europe to Caucasus.

Nopoiulus Menge, 1851. — 11 species, mostly Caucasus. *N. kochii* (Gervais, 1847) widespread by commerce.

Proteroiulus Silvestri, 1897. — Three species. Europe. *P. fuscus* (Am Stein, 1857) widespread in Europe, further north than any other millipede, parthenogenetic.

Vascoblaniulus Mauriès, 1967. — One species, *V. cabidochei* Mauriès, 1967, strongly modified cavernicole, number of mandibular pectinate lamellae enlarged. France.

Virgoiulus Enghoff, 1984. — One species, *V. minutus* (Brandt, 1841), only indigenous blaniulid in N America, parthenogenetic.

Family GALLIOBATIDAE Brolemann, 1921. — Body composed of head plus 62-101 body rings (more than in any other non-colobognathan millipede), length 17-28 mm, diameter 0.6-0.9 mm. No eyes. Body rings with a dense covering of setae, not only a marginal whorl. Penis unpaired. Male legs with flattened, but not leaflike setae. Anterior gonopods with flagella, telopodites with longitudinal excavation for accommodation of long posterior gonopods. One genus.

Galliobates Verhoeff, 1911. — One species, *G. gracilis* (Ribaut, 1909), France.

Family OKEANOBATIDAE Verhoeff, 1942. — Body composed of head plus 35-52 body rings, length 7-20 mm, diameter 0.6-0.8 mm. Eyes each with 7-17 ommatidia arranged in loose, subtriangular group. Anterior gonopods with flagella and well-developed telopodites. Vulval bursa segmented by transverse suture. Two genera, four species.

Okeanobates Verhoeff, 1942 — Two species, one in Japan and one (*O. americanus* Enghoff, 1979, parthenogenetic) in eastern N America.

Yosidaiulus Takakuwa, 1940. — Two species, Japan.

Family ZOSTERACTINIDAE Loomis, 1943. — Body composed of head plus 25-80 body rings, length 5-23 mm, diameter 0.3-0.7 mm. No eyes. Male legs with flattened,

leaflike setae. Anterior gonopods with flagella and telopodites, flagella traversing short posterior gonopods, then entering furrow in anterior gonopod telopodites. Two genera, three species, eastern USA.

Ameractis Causey, 1959. — Two species.
Zosteractis Loomis, 1943. — One species.

Superfamily JULOIDEA Leach, 1814. — Mandibles with 4 pectinate lamellae; molar plate with one or two deep transverse grooves (except in Trichonemasomatidae). Promentum of gnathochilarium short, not completely separating the lamellae linguales (except in Trichonemasomatidae). Second pair of male legs with coxal gland opening (except in Trichonemasomatidae). First pair of male legs often strongly modified, but unmodified in Trichonemasomatidae and only with a retrorse tibial spine in Trichoblaniulidae.

Family JULIDAE Leach, 1814. — Body composed of head plus 28-89 body rings excluding telson, length 6-90 mm, diameter 0.4-7 mm. Eyes mostly present, in a triangular-ovoid group, but absent in many lineages. Mandibular molar plate with two deep transverse grooves. First pair of male legs usually reduced to small hooks, derivable from a nemasomatoid retrorse-tibial-spine type of leg. Male legs often with ventral pads on one or several podomeres. Around 75 genera with more than 700 species, Palaearctic subregion, marginally extending into the Oriental region in SE Asia. Several species widespread through commerce.

Allajulus C. L. Koch, 1847. — Seven species, Europe. *A. dicentrus* (Latzel, 1884), *A. nitidus* (Verhoeff, 1891).

Amblyiulus Silvestri, 1896. — Ca. ten species, Europe, temperate Asia. *A. cedrophilus* (Attems, 1911).

Anaulaciulus Pocock, 1895. — Ca. 50 species, from Himalaya to Japan.

Brachyiulus Berlese, 1884. — About seven species, Europe, N Africa. Several species widespread through commerce, e.g., *B. lusitanus* Verhoeff, 1898. *B. bagnalli* (Brölemann, 1924), *B. pusillus* (Leach, 1814).

Catamicrophyllum Verhoeff, 1900. — Ten species, Middle East. *C. caifanum* Verhoeff, 1900.

Cylindroiulus Verhoeff, 1894. — Ca. 130 species, from Macaronesia to central Asia, in Europe particularly diverse in Italy. An endemic species swarm on Madeira. *C. boleti* (C. L. Koch, 1847), *C. caeruleocinctus* (Wood, 1864), *C. exiguus* Enghoff, 1982, *C. gemellus* Enghoff, 1982, *C. ibericus* Brölemann, 1913, *C. infernalis* Lohmander, 1955, *C. kappa* Enghoff, 1982, *C. latestriatus* (Curtis, 1845), *C. laurisilvae* Enghoff, 1982, *C. londinensis* (Leach, 1815), *C. lundbladi* Lohmander, 1955, *C. luridus* C. L. Koch, 1847, *C. meinerti* (Verhoeff, 1891), *C. punctatus* (Leach, 1815), *C. rabacalensis* Lohmander, 1955, *C. truncorum* (Silvestri, 1896), *C. vulnerarius* (Berlese, 1888), *C. zinalensis* (Faës, 1902).

Dolichoiulus Verhoeff, 1900. — 53 species, almost all on the Canary Islands. *D. parcestriatus* (Brölemann, 1901), *D. tongiorgii* (Strasser, 1973).

Enantiulus Attems, 1894. — Eight species, Europe. *E. nanus* (Latzel, 1884).

Julus Linnaeus, 1758. — A dozen species, Europe, Caucasus, Siberia. *J. scandinavius* Latzel, 1884, widespread in W Europe. *J. terrestris* Linnaeus, 1758.

Kryphioiulus Read, 1990. — One species, *K. occultus* (C. L. Koch, 1847), northern and central Europe.

Leptoiulus Verhoeff, 1894. — Ca. 75 species, Europe (especially the Alps) to Caucasus, NW Iran and Altai Mountains. *L. bertkaui* (Verhoeff, 1896), *L. braueri* (Verhoeff, 1895), *L. faesi* Bigler,

1919, *L. montivagus* (Latzel, 1884), *L. proximus* (Nemec, 1896), *L. saltuvagus* (Verhoeff, 1898), *L. trilineatus* (C. L. Koch, 1847), *L. trilobatus* (Verhoeff, 1894).

Megaphyllum Verhoeff, 1894. — Ca. 20 species, SE Europe, Asia Minor, Altai Mountains. *M. bicolor* (Loksa 1970), *M. bosniense* (Verhoeff, 1897), *M. projectum* Verhoeff, 1894, *M. rossicum* (Timotheew, 1897), *M. unilineatum* (C. L. Koch, 1838).

Nepalmatoiulus Mauriès, 1983. — 55 species, East Asia, from Japan to the Malaccan Peninsula.

Ommatoiulus Latzel, 1884. — Ca. 80 species, mainly in SW Europe and N Africa. *O. sabulosus* (L., 1758) very widespread in Europe, *O. moreleti* (Lucas, 1860) widespread by commerce, a pest in southern Australia. *O. rutilans* (C. L. Koch, 1847). *O. albolineatus* (Lucas, 1845), *O. atlanteus* Schubart, 1960, *O. buchneri* (Verhoeff, 1940), *O. caspius* (Lohmander, 1928), *O. dorsovittatus* (Verhoeff, 1893), *O. lapidarius* (Lucas, 1846), *O. oxypygus* (Brandt, 1841), *O. punicus* (Brölemann, 1894), *O. sempervirilis* Akkari & Enghoff, 2011.

Ophyiulus Berlese, 1884. — Ca. 20 species, most endemic in Italy. *O. pilosus* (Newport, 1842) widespread in W Europe, widespread by commerce.

Pachyiulus Berlese, 1883. — Ca. 15 species, including the largest julids, S and SE Europe, Caucasus and Near East. *P. flavipes* (C. L. Koch, 1847) widespread and synanthropic in S Europe. *P. hungaricus* (Karsch, 1881) (Plate XV A), *P. varius* (Fabricius, 1781).

Pacifiiulus Mikhaljova, 1982. — One, partly parthenogenetic, widespread Siberian species, *P. amurensis* (Gerstfeldt, 1859).

Pteridoiulus Verhoeff, 1913. — One species, *P. aspidiorum* Verhoeff, 1913, Austria, Slovenia.

Rossiulus Attems, 1926. — Two species, E Europe, N Caucasus. *R. kessleri* (Lohmander, 1927), *R. vilnensis* (Jawlowski, 1925).

Tachypodoiulus Verhoeff, 1893. — One species, *T. niger* (Leach, 1815), W Europe.

Typhloiulus Latzel, 1884. — One of several genera of blind cavernicolous julids. Ca. 30 species, mainly in Italy and N Balkan. *T. ausugi* Manfredi, 1953, Italy, with mouthparts modified (pectinate lamellae enlarged), presumably for uptake of semiliquid food (paralleled in a few species in other genera). *T. ganglbaueri* (Verhoeff, 1898).

Unciger Brandt, 1841. — Three species, E Europe, Caucasus, *U. foetidus* (C. L. Koch, 1838). *U. transsilvanicus* (Verhoeff, 1999). Subanal scale with large anteriad hook (paralleled in a few species in other julid genera).

Family RHOPALOIULIDAE Attems, 1926. — Body composed of head plus 49-53 body rings excluding telson, length 12-13 mm, diameter 0.6 mm. Each eye with 7 ommatidia in a group. Mandibular molar plate with a deep transverse groove. Promentum of gnathochlarium short, not completely separating the lamellae linguales. First pair of male legs enlarged and bizarrely modified, but derivable from a nemasomatoid type with a retrorse tibial spine. Anterior gonopods with flagella and well-developed telopodites. One genus.

Rhopaloiulus Attems, 1927. — One species, *R. cameratanus* Attems, 1927, Italy.

Family TRICHOBLANIULIDAE Verhoeff, 1911. — Body composed of head plus 43-59 body rings excluding telson, length 14-35 mm, diameter 0.5-1.3 mm. No eyes. Mandibular molar plate with one deep transverse groove. Promentum of gnathochlarium short, not completely separating lamellae linguales. Body rings with a dense covering of setae, not only a marginal whorl. First pair of male legs unmodified except

for retrorse tibial spine. Anterior gonopods with flagella and large telopodites. One genus.

Trichoblaniulus Verhoeff, 1898. — Four species, Spain, France, Italy. *T. hirsutus* (Brölemann, 1889) (Plate XV B).

Family TRICHONEMASOMATIDAE Enghoff, 1991. — Body composed of head + 34-37 body rings excluding telson, length 10-13 mm, diameter 0.7-0.8 mm. Mandibular molar plate without deep transverse grooves. Body rings with a dense covering of setae, not only a marginal whorl. Penis unpaired. The single known species of this family in many respects resembles a nemasomatoid, but three synapomorphies in the mouthparts places the family in Juloidea (Enghoff, 1991). One genus.

Trichonemasoma Mauriès & Vicente, 1977. — One species, *T. peloponesium* (Mauriès, 1966), Greece.

Superfamily NEMASOMATOIDEA Bollman, 1893. — Mandibles with four pectinate lamellae. Promentum of gnathochlarium completely separating the lamellae linguales (except in male *Dasynemasoma*). First pair of male legs usually with a retrorse tibial spine, otherwise like a normal leg, rarely strongly modified or entirely unmodified. Anterior gonopods with flagella (except in Chelojulidae) and well-developed telopodites (except in *Sinostemmiulus*).

Family CHELOJULIDAE Enghoff, 1991. — Body consisting of head + 30-38 body rings excluding telson, length 10-24 mm, diameter 1.0-1.9 mm. Eyes with up to 52 ommatidia in a triangular-ovoid patch. Body rings strongly cristate; ozopores on large, smooth dorsolateral tubercles (autapomorphy); sterna firmly fused to pleuroterga. First pair of male legs unmodified, but fifth pair strongly incrassate and with a large prefemoral process. Telopodites of anterior gonopods biramous (synapomorphy with Telsonemasomatdae). One genus.

Chelojulus Enghoff, 1982. — One species, *C. sculpturatus* Enghoff, 1982, NW USA.

Family NEMASOMATIDAE Bollman, 1893. — Body consisting of head plus 24-74 body rings excluding telson, length 4-32 mm, diameter 0.4-1.1 mm. Head usually with eyes, each consisting of 1 (*Sinostemmiulus*) to 27 ommatidia, when present arranged in a triangular to ovoid patch. Sterna of body rings secondarily free from pleurotergites, articulating with the latter through intricate overlaps (unique autapomorphy). Male legs (in anterior part of body) with ventral soft pads (except in *Dasynemasoma*). Seven genera, 23 species, Holarctic, mainly in (cool) temperate areas.

Antrokoreana Verhoeff, 1938. — Six species, blind cave dwellers, East Asia.
Dasynemasoma Murakami, 1979. — One species, Japan.
Nemasoma C. L. Koch, 1847. — Two species, Europe, Caucasus, Asia Minor. *N. varicorne* C. L. Koch, 1847, Europe, obligate bark-dweller, exhibits geographical parthenogenesis.
Orinisobates Lohmander, 1933. — Eight species, central and E Asia, N America. *O. microthylax* Enghoff, 1985, *O. soror* Enghoff, 1985, *O. nigrior* (Chamberlin, 1943).
Sinostemmiulus Chamberlin & Wang, 1953. — Two species, Japan, China.
Thalassisobates Verhoeff, 1908. — Three species. *T. littoralis* (Silvestri, 1908), Europe, N Africa, E North America, littoral.

Family PSEUDONEMASOMATIDAE Enghoff, 1991. — Body consisting of head plus 41-63 body rings excluding telson, length 11-20 mm, diameter 0.7-1.0 mm. Eyes each

consisting of 11-15 ommatidia arranged in a rather narrow triangle. Sterna of body rings firmly fused to pleuroterga. Male legs with ventral soft pads, pairs 4-7 with ventral, femoral tubercles (autapomorphy). One genus.

Pseudonemasoma Enghoff, 1991. — One species, *P. femorotuberculatum* Enghoff, 1991, Japan.

Family TELSONEMASOMATIDAE Enghoff, 1991. — Body consisting of head plus 34-70 body rings excluding telson, length 6-12 mm, diameter 0.4-0.6 mm. Eyes each with only two or three ommatidia. Sterna of body rings firmly fused to pleuroterga. Preanal ring (epiproct) with two caudad directed processes. First pair of male legs reduced to small, apparently unsegmented hooks. Telopodites of anterior gonopods biramous. One genus.

Telsonemasoma Enghoff, 1979. — One species, *T. microps* Enghoff, 1979, USA (Oregon).

Superfamily PAEROMOPODOIDEA Cook, 1895. — Mandibles with six or more pectinate lamellae. Promentum of gnathochilarium completely separating the lamellae linguales. First pair of male legs strongly modified, hooklike, probably derived from a nemasomatid type with a tibial spine. Anterior gonopods without flagella.

Family APROSPHYLOSOMATIDAE Hoffman, 1961. — Body consisting of head plus 58 body rings excluding telson, length 16 mm, diameter 1.0 mm. Mandibles with 6 pectinate lamellae. Anterior gonopods without flagella, but with large telopodites. One genus, one species.

Aprosphylosoma Hoffman, 1961. — One species, *A. darceneae* Hoffman, 1961, USA (Oregon).

Family PAEROMOPODIDAE Cook, 1895. — Body consisting of head plus 63-79 body rings excluding telson, length 51-165 mm, diameter 2.2-8 mm. Mandibles with 6 or more pectinate lamellae Anterior gonopods without flagella and telopodites. Two genera, 11 species, western N America.

Californiulus Verhoeff, 1938. — Six species, incl. *C. chamberlini* (Brölemann, 1922) (Plate XV C).

Paeromopus Karsch, 1881. — Five species. *P. paniculus* Shelley & Bauer, 1997, up to 165 mm long, is the largest species of Julida.

Superfamily PARAJULOIDEA Bollman, 1893. — Mandibles with 6-10 pectinate lamellae. Promentum of gnathochilarium completely separating the lamellae linguales in females, in males enlarged and often soft. First pair of male legs enlarged, forming pair of claspers.

Family MONGOLIULIDAE Pocock, 1903. — Body consisting of head plus 38-65 body rings excluding telson, length 15-69 mm, diameter 0.8-4.0 mm. Eyes present or absent. Claw of enlarged first pair of male legs reduced. Second pair of legs at most moderately modified in both sexes. Penis unpaired. Seventh pair of male legs with enlarged coxae and reduced telopodite, except in *Ussuriiulus*. Anterior gonopods with flagella, except in *Ussuriiulus* and *Ikahoiulus*. Second pair of female legs and vulvae not strongly modified. Seven genera, 30 species, temperate East Asia including Japan.

Ikahoiulus Takakuwa, 1941. — One species.

Kopidoiulus Attems, 1909. — Seven species, partly in caves.

Mongoliulus Pocock, 1903. — 15 species.
Ussuriiulus Golovatch, 1980. — One species.

Family PARAJULIDAE Bollman, 1893. — Body consisting of head plus 40-73 body rings excluding telson, length 13-90 mm, diameter 0.8-6 mm. Eyes present, triangular. Claw of enlarged first pair of male legs swollen. Second pair of male legs strongly modified, coxosternum enlarged, telopodites reduced. Penis paired. Seventh pair of male legs unmodified. Anterior gonopods without flagella, or only small vestiges present. Second pair of female legs and vulvae modified: telopodites often reduced, vulval opercula often fused. 28 genera, 115 species, N America, from Alaska southwards, and Central America as far south as El Salvador; one species in China and Japan.

Aniulus Chamberlin, 1940. — 20 species, USA. *A. bollmani* Causey, 1952.
Bollmaniulus Verhoeff, 1926. — 13 species, western N America. *B. hewitti* (Chamberlin, 1919).
Karteroiulus Attems, 1909. — Two species. *K. niger* Attems, 1909, the only Asian parajulid, and *K. alaskanus* (Cook, 1904).
Oriulus Chamberlin, 1940. — One species, *O. venustus* (Wood, 1864), the most widespread North American millipede, covering three-fourths of the continental United States and adjacent southern Canada.
Parajulus Humbert & de Saussure, 1869. — One species, *P. olmecus* Humbert & de Saussure, 1869, Mexico; other Central American species described in *Parajulus* belong to as yet undefined genera.
Pseudoiulus Bollman, 1887. — Five species.
Ptyoiulus Cook, 1896. — Three species, eastern North America. *P. impressus* (Say, 1821).
Saiulus Chamberlin, 1940. — One species, *S. setifer* Chamberlin, 1940, western N America.
Uroblaniulus Attems, 1909. — 11 species. *U. canadensis* (Newport, 1844).

Order Spirostreptida Brandt, 1833

[HENRIK ENGHOFF]

Body length 10-344 mm, diameter 0.6-20 mm. Head usually with eyes, each consisting of up to at least 68 ommatidia. Head without a median suture. Gnathochilarium variable, but stipites always separated by mentum and reaching to base of gnathochilarium. Body consisting of head plus 18-93 body rings excluding telson. Two pairs of legs associated with fifth body ring. Never with frontal setae. Body rings almost always without setae (exception: *Hypocambala*). First pair of male legs often modified, most frequently in the form of a retrorse prefemoral lobe. Posterior gonopods (leg-pair 9) often reduced or even apparently completely absent.

Postembryonic development usually hemianamorphic, at least in suborder Spirostreptidea (Cambalidea are almost unknown in this respect).

A very heterogeneous, possibly non-monophyletic order without clear autapomorphies, unlike Julida and Spirobolida.

Suborder Cambalidea Cook, 1895

Body length 10-90 mm, diameter 0.6-6 mm. Head with eyes (except cave species), ommatidia arranged in a single line or a triangular field. Gnathochilarium very variable:

stipites always reaching base of gnathochilarium; mentum divided or undivided, when divided, promentum may be longitudinally subdivided, mentum/promentum may or may not separate the lamellae linguales, these may be transversely subdivided. 18-93 body rings excluding telson. The first pair of male legs may have femoral processes as in Spirostreptidea. The anterior gonopods may have flagella or not and usually have recognizable telopodites, but the coxites never form a sheath containing the base of the telopodite as in Spirostreptidea The posterior gonopods may be well-developed, strongly reduced, or virtually absent as in Spirostreptidea.

The higher classification of this suborder has been very unstable and seems not yet to have found a balance. The family Pseudonannolenidae has been placed in a separate suborder (Epinannolenidea Chamberlin, 1922), sometimes accompanied by Choctellidae and Iulomorphidae. Authors dealing with Cambalidea tend to lament the state of affairs, an attitude it is difficult to disagree with. At least Pseudonannolenidae may be phylogenetically closer to suborder Spirostreptidea, but until a proper phylogenetic analysis has been made, no further changes in the classification should be made.

Family CHOCTELLIDAE Chamberlin & Hoffman, 1950. — Body consisting of head plus 41-44 body rings excluding telson, length up to 60 mm, diameter 3.2 to ca. 5 mm, body quite stout, bronzy metallic in life, easily confusable with a spirobolid. Eyes each with ca. 30 ommatidia. Gnathochilarium with a separate, undivided promentum. Posterior gonopods reduced to tiny vestiges. One genus.

Choctella Chamberlin, 1918. — Two species, incl. *C. cumminsi* Chamberlin, 1918, eastern USA.

Family PSEUDONANNOLENIDAE Silvestri, 1895. — Body consisting of head plus 44-69 body rings excluding telson, length 10-90 mm, diameter 0.7-6 mm, body quite slender, not bronzy. Eyes each with 4-45 ommatidia, rarely absent. Gnathochilarium variable. Posterior gonopods reduced to tiny vestiges. Seven genera, ca. 90 species, often found in caves.

Epinannolene Brölemann, 1903. — Ca. 30 species, S and Central America, Caribbean islands. *E. pittieri* Brölemann, 1903, widespread (with several nominal subspecies) in the Caribbean, Venezuela and Bermuda.

Physiostreptus Silvestri, 1903. — One species, *Ph. ortonedae* Silvestri, 1903, Ecuador.

Pseudonannolene Silvestri, 1895. — Ca. 45 species, S America. Promentum of gnathochilarium characteristically divided longitudinally. *P. spelaea* Iniesta & Ferreira, 2013, Brazil, is one of several troglobitic species in the genus. *P. tocaiensis* Fontanetti, 1996, *P. tricolor* Brölemann, 1901.

Family IULOMORPHIDAE Verhoeff, 1924. — Anterior gonopods without flagella; posterior gonopods well-developed and elaborate.

Family CAMBALIDAE Bollman, 1893. — Anterior gonopods with flagella; posterior gonopods well-developed.

Family CAMBALOPSIDAE Cook, 1895. — Anterior gonopods without flagella; posterior gonopods typically poorly developed, reduced in size.

No satisfactory delimitation of these three families is possible, despite the characters listed above, and they are therefore treated together. Body consisting of head plus 18-93 body rings excluding telson, length 10-65 mm, diameter 0.6-5 mm. Eyes each with up to at least 55 ommatidia, sometimes absent. Gnathochilarium variable. 40 genera, >200 species. The genera normally assigned to Cambalopsidae are distributed in the Oriental region, whereas those normally assigned to Cambalidae and Iulomorphidae show an 'antitropical' distribution: southern Africa, southern and southeastern Australia, New Zealand, southern S America, N America, Iran.

Atelomastix Attems, 1911 ('Iulomorphidae'). — 28 species, southern Australia.

Cambala Gray, 1832 ('Cambalidae'). — Seven species, N America. *C. annulata* (Say, 1821), eastern USA. *C. hubrichti* Hoffman, 1958.

Chiraziulus Mauriès, 1983 ('Cambalidae'). — Two species, Iran, the only Palaearctic cambalideans. *C. kaiseri* (Mauriès, 1983).

Eumastigonus Chamberlin, 1920 ('Cambalidae'). — Nine species, New Zealand.

Glyphiulus Gervais, 1847 ('Cambalopsidae'). — 55 species, SE Asia, from S China to Java. *G. granulatus* (Gervais, 1847), widespread through commerce. Several species have been shown to have a haplopodous developmental stadium (p. 278). *G. septentrionalis* Murakami, 1975.

Hawaicambala Mauriès, 1983 ('Cambalidae'). — 12 species, Hawaiian archipelago.

Hypocambala Silvestri, 1897 ('Cambalopsidae'). — 13 species, Indian Ocean islands, SE Asia, Indonesia to New Caledonia. *H. anguinea* (Attems, 1900), widespread through commerce.

Iulomorpha Porat, 1872 ('Iulomorphidae'). — 18 species, South Africa.

Jarmilka Shear, 1973 ('Cambalidae'). — One species, *J. alba* Shear, 1973, Belize. May have as little as 18 body rings — the lowest number known in Juliformia and less than most Polydesmida.

Nannolene Bollman, 1887 ('Cambalidae'). — 14 species (Hawaii), nine species (western USA), one species (Japan).

Trachyjulus Peters, 1864 ('Cambalopsidae'). — 31 species, Nepal, India, Sri Lanka through SE Asia to Sulawesi. *T. calvus* (Pocock, 1893), widespread through commerce. Several species have been shown to have a haplopodous developmental stadium. *T. tjampeanus* (Attems, 1903).

Zinagon Chamberlin, 1957 ('Iulomorphidae'). — One or two species, Chile.

Suborder Spirostreptidea Brandt, 1833

Eyes always present, composed of numerous ommatidia arranged in a triangular-ovoid group. Gnathohilarium quite constant: stipites reaching to the prebasilar sclerite on each side of large mentum; mentum not or hardly extending between the lamellae linguales which are therefore contiguous throughout their length. Prefemora of first pair of male legs each with a process pointing towards the base and the mouth. Only one pair of gonopods, corresponding to leg pair 8, pair 9 completely reduced, only a remnant of the sternum is retained. Gonopods consisting of a robust coxal part sheathing the basal part of the telopodite; distal part of telopodite with various spines, lamellae etc.

Superfamily ODONTOPYGOIDEA Attems, 1909.

Family ODONTOPYGIDAE Attems, 1909. — Body composed of head plus 37-77 body rings, length 24-85 mm, diameter 0.8-9.5 mm. Preanal ring without a process. Anal valves almost always with dorsal spine-like processes. Telopodites of gonopods bending mesad and crossing over in midline, distally branching into a solenomere and a telomere, the latter often extremely complex. Sternum of pair 9 of male legs relatively

large, variously shaped. Africa south of the Sahara, not on Madagascar. 32 genera, ca. 370 species.

Bandeirenica Kraus, 1969. — Three species. *B. caboverda* (Pierrard, 1987) is a potato pest on the Cape Verde Islands where it is probably introduced.

Chaleponcus Attems, 1914. — Ca. 40 species, southern Africa, Tanzania.

Congopyge Chamberlin, 1927. — Ca. five species, DR Congo, *C. acanthophor* Chamberlin, 1927.

Cyclotarsus Attems, 1951. — Two species. *C. chapellei* (Demange, 1957), Tchad, Somalia.

Odontopyge Brandt, 1841. — Two species, some of the largest odontopygids, Cameroon, Sudan, Ethiopia.

Peridontopyge Silvestri, 1907. — About 30 species, western Africa. *P. aberrans* Attems, 1914, *P. conani* (Brölemann, 1905), *P. junquai* Demange, 1966, *P. rubescens* Attems, 1927, *P. vachoni* Demange, 1957.

Plethocrossus Attems, 1909. — Six species including some of the largest odontopygids, western, central and eastern Africa. *P. acutiformis* Demange, 1972.

Prionopetalum Attems, 1909. — 24 species, tropical Africa. *P. tricuspis* Brölemann, 1920.

Raduliverpa Frederiksen & Enghoff, 2015. — Four species, incl. *R. serpentispina* Frederiksen & Enghoff, 2015, Tanzania, Kenya.

Rhamphidarpoides Kraus, 1960. — 14 species, Zaire, Tanzania, Ethiopia.

Spinotarsus Attems, 1909. — About 100 species, southern Africa.

Syndesmogenus Attems, 1909. — 13 species, southern, western, central and aastern Africa. *S. fragilis* Vohland, 2013 is the smallest known odontopygid (diameter 0.8 mm).

Superfamily SPIROSTREPTOIDEA Brandt, 1833. — Characterised by having the gonopod telopodites directed caudo-laterad instead of mesad as in Odontopygoidea. Sternum of male legs 9 very strongly reduced.

Family ADIAPHOROSTREPTIDAE Hoffman, 1977. — Body composed of head plus 48-51 rings, length unknown, diameter 2.2-3 mm. Preanal ring without a process: Anal valves without spines. First pair of male legs without prefemoral processes. Gonopod telopodites emerging from posterior side of coxae but bending mesad, then cephalad and projecting between coxae. One genus.

Adiaphorostreptus Hoffman, 1977. — One species, India.

Family HARPAGOPHORIDAE Attems, 1909. — Body composed of head plus 40-79 rings, length 35-250 mm, diameter 2-21 mm. Preanal ring usually with a normally upturned and pointed process. Anal valves without spines. Telopodites of gonopods bending and projecting laterad/caudad, with a spine basal to the bend, with a terminal ‘rake’ of specialised setae (blepharochaetae or xyrochaetae sensu Hoffman, 1975). 44 genera, >220 species, southern Africa, India, Sri Lanka, SE Asia to Indonesia and the Philippines.

Armatostreptus Pimvichai, Enghoff & Panha, 2010. — One species, A. *armatus* (Demange, 1983) (Plate XV F), Thailand.

Anurostreptus Attems, 1914. — Nine species, large millipedes, SE Asia and Indonesia. *A. sculptus* Demange, 1961, Thailand.

Carlogonus Demange, 1961. — Eight species, India. *C. robustior* (Attems, 1936).

Gonoplectus Chamberlin, 1921. — Ca. 20 species, Nepal to Thailand. *G. malayus* (Carl, 1909).

Harpagophora Attems, 1909. — Six species, southern Africa.

Phyllogonostreptus Carl, 1918. — Six species, incl. *P. nigrolabiatus* (Newport, 1844), India.

Poratophilus Silvestri, 1897. — Two species, South Africa.

Thyropygus Pocock, 1894. — 56 species, SE Asia to Java and the Philippines. *T. allevatus* (Karsch, 1881), Thailand and Malaysia.

Stenurostreptus Carl, 1917. — One species, *S. stenorhynchus* (Pocock, 1893), Sri Lanka.

Family SPIROSTREPTIDAE Brandt, 1833. — Body composed of head plus 32-87 body rings, length 16-344 mm, diameter 1.0-20 mm. Preanal ring without a process. Anal valves without spines. Prefemoral processes of first pair of male legs quite variable in shape. Telopodites of gonopods bending and projecting laterad, without a spine basal to the bend, without a terminal 'rake' of specialized setae. 61 genera, 275 species, Africa, marginally N Africa and Middle East, Madagascar; South, Central, and marginally North America.

Archispirostreptus Silvestri, 1895. — Ten large to very large species, tropical Africa, Middle East. *A. gigas* (Peters, 1855), E and S Africa, a common pet millipede, *A. syriacus* (Saussure, 1859), Israel, Syria, Jordan, Arabian Peninsula, *A. tumuliporus* (Karsch, 1881).

Aulonopygus Attems, 1914. — One species, *A. aculeatus* Attems, 1914, W Africa.

Calathostreptus Schubart, 1959. — Two species, Brazil. *C. fulvus* (Schubart, 1960).

Cladostreptus Brölemann, 1902. — Ten species, Brazil.

Doratogonus Attems, 1914. — 37 species, southern Africa, Madagascar. *D. annulipes* Carl, 1917, *D. flavifilis* (Peters, 1855), *D. uncinatus* (Attems, 1914).

Exospermitius Verhoeff, 1942. — Two species, Fernando Poo.

Gymnostreptus Brölemann, 1902. — About 20 species, Brazil and Paraguay. *G. olivaceus* Schubart, 1944.

Ophistreptus Silvestri, 1897. — Nine species, W Africa. *O. guineensis* (Silvestri, 1897) (Plate XV E), *O. levis* (Attems, 1934).

Orthoporoides Krabbe, 1982. — Seven species, S Africa. *O. pyrhocephalus* (L. Koch, 1865).

Orthoporus Silvestri, 1897. — Ca. 80 species, South, Central and southern North America. *O. ornatus* (Girard, 1853), a desert millipede from Mexico and SW USA, *O. cavicollis* (Karsch, 1881), *O. conifer* (Attems, 1950), *O. dorsovittatus* (Verhoeff, 1938), *O. flavior* Chamberlin & Mulaik, 1941, *O. ornatus* (Girard, 1853), *O. texicolens* Chamberlin, 1938.

Plusioporus Silvestri, 1895. — 16 species, S America. *P. setiger* (Brölemann, 1902).

Rhapidostreptus Silvestri, 1910. — Four species, central to E Africa, *R. innominatus* (Chamberlin, 1927), *R. virgator* (Silvestri, 1907).

Sagmatostreptus Hoffman & Enghoff, 2011. — One species, *S. strongylopygus* (Attems, 1950), with an unusual colour patterns consisting of several transverse-triangular black spots on a light brown background, E Africa.

Sechelleptus Mauriès, 1980. — 29 medium-sized to very large species, incl. *S. seychellarum* (Desjardins, 1835), Madagascar and Seychelles.

Spirostreptus Brandt, 1833. — Six large to very large species, southern Africa. *S. castaneus* Attems, 1934, *S. macracanthus* Attems, 1914, *S. multisulcatus* Demange, 1957, *S. pavani* Demange, 1981. The species known as *'S.' asthenes* Pocock, 1892 belongs to a different genus.

Telodeinopus Verhoeff, 1941. — 11 species, W to central Africa. *T. aoutii* (Demange, 1971).

Trachystreptus Cook, 1895. — Two species, incl. *T. cambaloides* Cook, 1895, One of several genera of small spirostreptids with carinate body rings, W Africa.

Urostreptus Silvestri, 1897. — 12 species, South America. *U. atrobrunneus* Pierozzi & Fontanetti, 2006.

Order Spirobolida Bollman, 1893

[THOMAS WESENER]

Adult body length usually 40-80 mm, largest species up to 250 mm, small species 18-30 mm. Some species very broad, resembling sausages, of greater width than similarily long spirostreptids. Head with a very prominent median suture which is interrupted between the antennae but later continuing towards posterior head margin. Head lacking frontal setae. Genae present, as is an usually open, prominent incisura lateralis. A special parietal sclerite is set off in the postantennal area by a suture, often touching or even overlapping the cardo and stipes of the mandible. Labrum with a single median tooth, two (rarely, 4) blunt lateral teeth, one row of marginal setae, and two to eight setiferous foveolae. Usually with more than 20 ommatidia located in an irregular oval cluster. Organ of Tömösváry absent, like in all Juliformia. Antennae with six regular, usually stout, antennomeres plus disc carrying usually four, rarely more, apical cones. Antennomeres 5 and 6 laterally at distal margin with a field of two to four rows of sensilla basiconica. Mandible massive, with a large cardo and slightly smaller stipes. Gnathal lobe with three- or four-combed internal tooth, four or more (often more than six) rows of pectinate lamellae and a large molar plate. Gnathochilarium highly conservative in shape, always consisting of a large mentum which reaches the lateral margins of plate, and each with paired stipites and lamellae linguales. Stipites and lamellae linguales separated by mentum. Each stipes usually with three setae, each lamella lingualis with two setae located behind each other (rare exceptions in some genera). Mentum rarely subdivided by a transverse ledge. Modified median palps of gnathochilarium on underside each with two distinct areas carrying sensory cones, one smaller circular area located apically, more sensory cones located laterally close to the spinigerous fringes. Trunk with 35-60 rings. Body rings always without setae (exception Typhlobolellidae). Ozopores present, usually starting from body ring 5 or 6 (rarely 3, Typhlobolellidae). Each body ring consisting of one tergite, two pleurites and two stigmatic plates which are strongly fused with the sternites, but with suture lines still visible. Tergal part of each ring transversely divided by sutures into pro-, meso-, and metazonites. In mature males, body ring 7 fused ventrally. Surface of body rings smooth and polished, glabrous, very rarely with spines. Telson consisting of a small subanal scale, two well-rounded anal valves which rarely carry a dorso-apical spine, and a dorsal pre-anal scale which can be elongated. Only a single leg pair associated with body ring 5. Body ring 6 and following with 2 leg pairs each. Legs consisting of six podomeres (coxa, prefemur, femur, postfemur, tibia, tarsus). Leg pairs 1 and 2 modified in both sexes, coxae fused to sternites and greatly elongated. Legs 3 and the following ones similar, lacking coxal pores, only male leg pairs 3-7 often with special modifications, especially on coxa. Male tarsi 3 and following ones often with a ventral pad, sometimes also tibiae. Male leg pairs 8 and 9 on body ring 7 modified into anterior and posterior gonopods, respectively, which develop gradually through a few (usually two or three) moults. Gonopod anlagen much simpler than fully developed mature gonopods. Anterior gonopods simple, consisting of a sternite, coxites and telopodites. Sternite and coxite often with sclerotized tracheal apodemes. Sternite often triangular with lateral extensions which

anteriorly engulf basal part of coxite. Coxite and telopodite often extended mesad, forming a pouch for accommodation of the posterior gonopods. Posterior gonopods represent spermatopositors and consist of a coxite with a large tracheal apodeme and a telopodite, both more or less fused. Posterior gonopods connected via membranous tissue or a small sternal remnant (suborder Trigoniulidea). Families and subfamiliesl are mostly based on gonopod (often only posterior gonopod) characteristics. Male gonopore located as a paired membranous, extensible pseudopenis behind coxa 2. Female with vulva attached to the surface of coxosternum 2. Vulva usually consisting of two simple, similar-sized valves and a small operculum.

Postembryonic development by hemianamorphosis (some species may be euanamorphic but evidence is insufficient), females may undergo post-maturity moults, while males as far as known perish after having reached sexual maturity. Eggs deposited individually in earth capsules resembling droppings.

More than 1000 species.

Suborder Rhinocricidea Brölemann, 1913

Characters are those of the only family.

Family RHINOCRICIDAE Brölemann, 1913. — Often with scobinae (shallow, groove-like depressions) on the prozonites. Head always with 2 + 2 setiferous foveolae. Anterior gonopod with large triangular sternite, base of sternite with tracheosclerites and straight and large sternal apodemes. Anterior gonopod with large coxal apodeme. Apodeme of posterior gonopods in same axis as gonopod. Posterior gonopod simple, coxa and telopodite fused and in same line. Telopodite slender, often flagelliform. Posterior gonopods only connected by tissue. Some species (e.g. *Salpidobolus* spp.) can spray their defence secretions. Wide range of sizes, 18-200 mm. 30 genera, more than 575 species. Genera in need of revision, currently impossible to distinguish. North America, Central America, South America, West Indies, southeast Asia, Taiwan, Australia and Oceania.

Acladocricus Brölemann, 1913. — 17 species, Indonesia, Philippines, Oceania, Australia. *A. setigerus* (Silvestri, 1897).

Alcimobolus Loomis, 1936. — One species, Hispaniola.

Anadenobolus Silvestri, 1897. — 78 species. North, Central and South America, West Indies. *A. arboreus* (Saussure, 1859), *A. holomelanus* (Porat, 1894), *A. leucostigma* (Pocock, 1894), *A. l. martinicensis* (Chamberlin, 1918), *A. monilicornis* (Porat, 1876), *A. putealis* (Loomis, 1971).

Andocricus Chamberlin, 1955. — One species, Peru.

Argentocricus Verhoeff, 1941. — Like *Rhinocricus*, but telopodite of anterior gonopod with a mesal vesiculiform structure. Posterior gonopod with a short, simple branch located laterally of the elongated telopodite. Nine nominal species, southern South America.

Auracricus Pérez-Asso, 1998. — One species, Cuba.

Australocricus Jeekel, 2001. — Seven species, Australia.

Baborucocricus Pérez-Asso, 2004. — One species, Haiti.

Carlocricus Jeekel, 2001. — One species, Lombok.

Cubobolus Chamberlin, 1918. — 11 species, Cuba.

Desmocricus Carl, 1918. — One species, Molucca Islands.

Eurhinocricus Brölemann, 1903. — 33 species, North America, Central America, South America, West Indies, Australia, Oceania. *E. sabulosus* (Pocock, 1894).

Fomentocricus Pérez-Asso, 1998. — One species, Cuba.

Haitobolus Mauriés & Hoffman, 1998. — Two species, Haiti.

Jobocricus Pérez-Asso, 1998. — Two species, Cuba, Haiti.

Leiocricus Loomis, 1936. — One species, Haiti.

Lissocricus Chamberlin, 1953. — Four species, Peru, Ecuador, Colombia.

Metacricus Chamberlin, 1953. — One species, Venezuela.

Neocricus Chamberlin, 1941. — Ten species, Guyana, Colombia, Venezuela.

Nesobolus Chamberlin, 1918. — Nine species, Cuba, Haiti, Martinique.

Quisquellacricus Pérez-Asso, 2004. — Three species, Haiti.

Oxypyge Silvestri, 1896. — 11 species, Panama, Guatemala, Peru.

Perucricus Kraus, 1954. — Five species, Peru.

Poecilocricus Schubart, 1962. — One species, Brazil.

Proporobolus Silvestri, 1897. — Nine species, Indonesia, Fiji, Australia.

Rhinocricus Karsch, 1881. — Collection pot for mainly American, but also a few little-known Indonesian and Australian species. 207 species, Central America, South America, West Indies, Indonesia, Oceania. *R. insularis* Schubart, 1948, *R. padbergi* Verhoeff, 1938, *R. varians* (Brölemann, 1901).

Rhytidocricus Hoffman & Keeton, 1960. — One species, Ecuador.

Salpidobolus Silvestri, 1897. — 144 species, South America, West Indies, Taiwan, Indonesia, Australia, Oceania. *S. anomalus* (Silvestri, 1897).

Thyroproctus Pocock, 1894. — Two species, Jamaica.

Yucatobolus Chamberlin, 1938. — One species, Mexico (Yucatan).

Suborder Spirobolidea Bollman, 1893

Without scobinae. Anterior gonopod with large coxal apodeme. Posterior gonopods only connected by tissue. Apodeme of posterior gonopods in same axis as gonopod. Coxite and telopodite of posterior gonopod usually separated and often articulated. Telopodite often modified, rarely simple and slender. 7 families (potentially oversplitted), more than 170 species.

Family SPIROBOLIDAE Bollman, 1893. — Antennae short and located in shallow groove of the parietal sclerite, but never concealed by the collum. Anal scale not protruding above anal valves. Sternite of anterior gonopod mesally arched and narrow, coxite with rounded lobes, telopodites elongated and curved, apically recurved. Posterior gonopod with massive coxa and articulated flexible telopodite, telopodite lacking internal chambers. Massive millipedes of medium length, 35-90 mm long. Seven genera with 33 species, United States, Mexico, Guatemala, China and Taiwan.

Aztecolus Chamberlin, 1943. — Three species, Mexico.

Chicobolus Chamberlin, 1947. — One species, southeastern United States. *C. spinigerus* (Wood, 1864).

Floridobolus Causey, 1957. — Coxites and telopodites of anterior gonopods fused. Apodemes of posterior gonopods strongly elongated. Massive species, 70-80 mm long. Four species, Florida. *F. penneri* Causey, 1957.

Hiltonius Chamberlin, 1918. — About eight species, California, Mexico, Guatemala. *H. mexicanus* (Saussure, 1859).

Narceus Rafinesque, 1820. — Four species, eastern United States. *N. americanus* (Palisot de Beauvois, 1817), *N. annularis* Rafinesque, 1820, *N. gordanus* (Chamberlin, 1943).

Spirobolus Brandt, 1833. — Six species, China and Taiwan.

Tylobolus Cook, 1904. — Seven species, Oregon and California, Utah, Kansas.

Family MESSICOBOLIDAE Loomis, 1968. — Collum laterally narrowed. Anal scale very short. Anterior gonopods large, sternite transverse, with small apodemes, while coxal apodemes are absent. Coxite with large lobes, mesally in contact with one another. Telopodites bent laterally, with an apical notch. Coxite and telopodite of the posterior gonopods fused, without any internal chambers. Species robust, of medium length. Three genera, 25 species, Mexico, Guatemala and Honduras.

Messicobolus Brolemann, 1913. — 14 species, Mexico.

Oxobolus Chamberlin, 1922. — Nine species, Mexico (Chiapas), Guatemala, Honduras.

Petenobolus Loomis, 1968. — Two species, Mexico (Yucatan).

Family ALLOPOCOCKIIDAE Keeton, 1960. — Anal scale short and blunt. Sternite of anterior gonopod small, not produced. Coxite with large lobes and apodemes. Posterior gonopods similar to those of the Spirobolidae, but telopodite separated into more than three apical branches. Tiny species, less than 25 mm. Three genera, seven species, Central America.

Allopocockia Brölemann, 1913. — Two species, Guatemala, El Salvador.

Chelogonobolus Carl, 1919. — Three species, Central America.

Schmidtolus Chamberlin, 1953. — Two species, Guatemala.

Family ATOPETHOLIDAE Chamberlin, 1918. — Head with three to five setiferous foveolae. Antennae of moderate size, located in a groove on the mandibular stipites and overlapped by the collum. Anal scale short and blunt. Anterior gonopods with large triangular sternite with long apodemes. Coxite with large lobe and a distal lobe; telopodite small, often concealed by the coxite. Posterior gonopod massive, with coxite and telopodite fused at a 90 degree angle, lacking internal chambers. Species often adapted to semi-arid habitats. Dull colours. Robust species, up to 80 mm in length. Four subfamilies with 15 genera and 48 species, United States and Mexico.

Anelus Cook, 1911. — Two species, Texas, Mexico.

Arinolus Chamberlin, 1940. — About 11 species, southwestern United States; northern Mexico.

Atopetholus Chamberlin, 1918. — Seven species, southern California, Nevada.

Centrelus Cook, 1911. — Six species, Mexico.

Comanchelus Hoffman & Orcutt, 1960. — Four species, Texas.

Cyclothyrophorus Pocock, 1909. — One species, Mexico.

Eurelus Cook, 1911. — One species, Texas.

Mannobolus Loomis, 1968. — One species, Mexico (Baja California).

Onychelus Cook, 1904. — One species, California, Arizona.

Piedolus Chamberlin, 1930. — One species, Utah.

Tarascolus Chamberlin, 1943. — Four species, Mexico.

Toltecolus Chamberlin, 1943. — Two species, Texas, Mexico (Nuevo Leon).

Uvaldia Loomis, 1968. — One species, Texas.

Watichelus Chamberlin, 1947. — Six species, southern California, Mexico (Northern Baja California).

Family SPIROBOLELLIDAE Brölemann, 1913. — Head with three to five setiferous foveolae. Antennae short. Anal scale short and well-rounded. Anterior gonopod massive and elaborate, but especially the large sternite often hyaline and difficult to see. Posterior gonopods relatively simple, slender and strongly elongated in a unique way, sperm canal opening always located mesally. Slender animals. Most species small less than 40 mm, a few up to 90 mm. Two subfamilies with six genera and 57 species. A few species widely dispersed through commerce, Australia, Oceania, Indonesia, Vietnam, India and Madagascar.

Desmocricellus Attems, 1953. — One species, New Zealand.

Hylekobolus Wesener, 2009. — 30-75 mm long, elongated. Male coxal processes absent, but coxa 7 twice as wide as coxa 6. Posterior gonopod basally at measl margin with triangular sclerite. 11 species; rainforests on Madagascar. All species frequently found in dead wood. *H. brachiosauroides* Wesener, 2009 (Plate XVI E).

Paraspirobolus Brölemann, 1902. — One species, widely dispersed through commerce. *P. lucifugus* (Gervais, 1836).

Physobolus Attems, 1936. — Three species, India and Vietnam.

Spirobolellus Pocock, 1894. — Apparent radiation in New Caledonia (28 species). 50 species, eastern Australia, New Zealand, New Caledonia, Celebes, Loyalty Islands, Caroline Islands, Moluccas, Sumatra, Java. *S. trifasciatus* (Loomis, 1964).

Walesbolus Verhoeff, 1924. — Two species, eastern Australia.

Family TYPHLOBOLELLIDAE Hoffman, 1969. — All species lacking eyes (unique feature of the order). Antennae long and slender. Legs modified: coxae in contact with one another, prefemur and femur dorsally with a hook. Ozopores starting at body ring 3. Tergites covered with setae (unique for the order). Gonopods indistinguishable from the Spirobolellidae. Specimens slender, 20-70 mm long. Four genera with five species, Mexico.

Ergene Chamberlin, 1943. — One species, Mexico (Tamaulipas).

Morelene Chamberlin, 1943. — One species, Mexico (Morelos).

Reddellobus Causey, 1975. — One species, Mexico (Puebla).

Typhlobolellus Hoffman, 1969. — Two species, Mexico (Veracruz).

Family PSEUDOSPIROBOLELLIDAE Brölemann, 1913. — Unclear if monophyletic. Head with 4 + 4 setiferous foveolae. Pro- and mesozonites depressed in comparison to metazonites. Prefemur of legs with eversible pad. Anterior gonopods with invisible sternite, which is small and fused to the coxite. Posterior gonopods simple. Small (<35 mm), slender species. Two genera, four species. One species pantropical, and in hothouses around the globe.

Benoitolus Mauriès, 1980. — Two species, Thailand, Seychelles.

Pseudospirobolellus Carl, 1912. — Two species. *P. avernus* (Butler, 1876) widely dispersed through commerce.

Suborder Trigoniulidea Attems, 1909

Anterior gonopod without coxal apodeme, sternal apodemes tiny. Posterior gonopods orientated parallel to body axis and connected by a distinct remnant of a sclerotized sternite. Apodeme of posterior gonopod forming a 90° angle with gonopod proper. Basal parts of mandible exposed, not even partly covered by head.

Probably including as many higher taxa as the Spirobolidea, still in need of revisions. Currently only a single family is recognized. We follow here Hoffman (1980) and Jeekel (2001) in keeping the Trigoniulinae as a subfamily, rather than a family, since no characters are known which distinguish the Trigoniulinae from the other Pachybolidae.

Family PACHYBOLIDAE Cook, 1897. — Body length 20-100 mm. Very few species with scobinae (*Centrobolus*), head with usually 2 + 2, rarely 3-5 setiferous foveolae. Posterior gonopods large, with long apodemes, coxite usually with one or two internal chambers. Ca. 60 genera and more than 280 species, South America (Brazil, Suriname, Peru), western, eastern and southern sub-Saharan Africa, Madagascar and the Seychelles, India, SE Asia, New Guinea, Australia, Oceania. At least two species are widespread tramp species occurring worldwide in humid tropical environments.

Acanthiulus Gervais, 1844. — Large-bodied (>90 mm long), body rings with spines and ornamentation, otherwise only present in *Eucentrobolus*. Three species, New Guinea.

Ainigmobolus Verhoeff, 1937, one species; ***Zygostrophus*** Chamberlin, 1920, five species; ***Speleostrophus*** Hoffman, 1994, one species; ***Austrostrophus*** Hoffman, 2003, one species. — Small to medium length (30-65 mm). Variable group in need of revision. Grouped together simply because all are Australian.

Amblybolus Keeton, 1964, three species; ***Atlanticobolus*** Hoffman, 1979, one species. — Lateral region of head depressed forming an antennal groove. Posterior gonopod with an articulation at mid-length. 30-40 mm long, only 36-38 body rings. West Africa and an island off Brazilian coast.

Amnestostrophus Hoffman & Keeton, 1960. — 2 + 2 setiferous foveolae. Male legs with tarsal pads. Pre-anal scale not projecting. Gonopods similar to *Trigoniulus*, in need of revision. Small to medium sized, 30-80 mm long, with 43-60 body rings. Three species, Philippines and Guam.

Apeuthes Hoffman & Keeton, 1960, three species, Vietnam; ***Eucarlia*** Brölemann, 1913, 16 species, Seychelles, Indonesia, New Guinea, Solomon Islands. — 2 + 2 setiferous foveolae. Male legs with tarsal pads. Small sized (20-50 mm long), with 35-54 rings. Posterior gonopods relatively simple, not distinctly branched. *Apeuthes* was described as subgenus of *Eucarlia*.

Aphistogoniulus Silvestri, 1897, 12 species, incl. *A. corallipes* (de Saussure & Zehntner, 1902) (Plate XVI A), *A. cowani* (Butler, 1882) (Plate XVI B), *A. erythrocephalus* (Pocock, 1893), *A. infernalis* Wesener, 2009 (Plate XVI C); ***Colossobolus*** Wesener, 2009, seven species; ***Sanguinobolus*** Wesener, 2009, one species. — 2 + 2 setiferous foveolae. Often with blood-red/black colour pattern. Posterior gonopods with coxite elongated into a stalk, telopodite developed as round apical disc. Large-bodied species (>100 mm). Madagascar.

Arostrophus Chamberlin, 1920, two species, New Guinea; ***Plokamostrophus*** Chamberlin, 1920, six species, New Guinea and Solomon Islands; ***Sympastrophus*** Chamberlin, 1920, one species, New Guinea. — Variable group in need of revision. Grouped together simply because all are from New Guinea.

Aulacobolus Pocock, 1903. — Probably not monophyletic, type species with unique and unusual body rings, with low ornaments, no spines, but deeply grooved. Pre-anal scale strongly elongated, forming a hook. Ca. 49 body rings, length ca. 120 mm. Ca. 15 species, India. Two *Aulacobolus* species occur in SE Asia, but it is unclear if their generic assignment is correct. *A. excellens* Silvestri, 1916.

Brachyspirobolus Brölemann, 1914. — 2 + 2 setiferous foveolae. Males with tarsal pads, without coxal processes. Pre-anal scale not projecting. Collum sexually dimorph. Defence gland opening located on the metazonite. Anterior gonopod telopodite elongated into a wide, apically swollen, lateral process. Small (20-45 mm), 36-45 body rings. Four species, central Africa.

Centrobolus Cook, 1897. — 2 + 2 setiferous foveolae. Many species with scobinae. Telopodite of anterior gonopod with a triangular lobe. Posterior gonopod unique, with a very large coxite and a freely articulated telopodite. Small-bodied (up to 30-50 mm long), 40-46 body rings. 44 species, South Africa and Mozambique. *C. fulgidus* (Lawrence, 1967), *C. inscriptus* (Attems, 1928), *C. richardi* (Lawrence, 1967), *C. ruber* Attems, 1928.

Cingalobolus Carl, 1918. — 2 + 2 setiferous foveolae. With scobinae. Male legs without tarsal pads. Antennae short, first antennomere with groove. Defence gland opening located on the metazonite (only shared with the Indian genera *Lankabolus* and *Epombrophilus*). Small species, with 40 body rings, 25-30 mm long. Two species, India. *C. bugnioni* Carl, 1918.

Corallobolus Wesener, 2009. — Red-and-black. Posterior gonopods resemble those of *Spiromanes*. Anterior gonopods simple, telopodite with a triangular mesal process found in numerous spirobolid genera. Large (ca. 100 mm long) massive. One species, Madagascar.

Dactylobolus Golovatch & Korsós, 1992. — Males with tarsal pads, coxae 3-7 with swollen process. Preanal scale not projecting. Anterior gonopod stout, telopodite produced into well-rounded lobe, with mesal ridge on anal side. Posterior gonopod differentiated into coxite and telopodite, telopodite apically with an elongated projection of the sperm canal. Small (25-30 mm), ca. 40 body rings. Two species, Comoros, Seychelles, Zanzibar, NW coast of Madagascar. *D. bivirgatus* (Karsch, 1881).

Epitrigoniulus Brölemann, 1903. — Legs short. Collum overlying antennae. Conspicuous blood-red/black colour pattern. Anterior gonopod simple, without any processes. Coxite and telopodite of posterior gonopod completely fused, elongated, slender, but apex of telopodite wider and rounded. Small (28-50 mm long), 38-42 body rings. Two species, Peru, northern Brazil, Suriname.

Epombrophilus Attems, 1936. — 2 + 2 setiferous foveolae. No scobinae. Male legs with tarsal pads. Pre-anal scale not projecting. Defence gland opening located on the metazonite (only shared with Indian genera *Cingalobolus* and *Lankabolus*). Gonopods similar to *Trigoniulus*. Small species, 20-25 mm long, with 44 body rings. One species, India.

Eucentrobolus Pocock, 1903. — 2 + 2 setiferous foveolae. Body rings with spines and ornamentation only shared with *Acanthiulus* from New Guinea. Preanal scale strongly elongated, apically curved ventrally. 51 + 0 body rings. Large-bodied (160 mm) and relatively slender (12.5 mm wide). One species, India.

Komphobolus Carl, 1941. — 2 + 2 setiferous foveolae. Male legs without tarsal pads. Preanal scale unique, basally with two large, swollen spines, scale itself long, thick, and well-rounded. Body densely covered with grooves. Length 20 mm. One species, India.

Lankabolus Carl, 1941. — 2 + 2 setiferous foveolae. No scobinae. Male legs with tarsal pad. Preanal scale relatively short, barely surpassing anal valves. Defence gland opening located on the metazonite (only shared with Indian genera *Cingalobolus* and *Epombrophilus*). Length 30 mm long, 40 body rings. One species, India.

Leptogoniulus Silvestri, 1897. — 2 + 2 setiferous foveolae. Preanal scale not projecting. Coxa 5 of male overlapping coxa 4. Small, 35-43 mm long, with 49 or 50 body rings. One species. *L. sororrnus* (Butler, 1876) synanthropic with a pantropical distribution.

Litostrophus Chamberlin, 1921. — One species, Gulf of Siam.

Microbolus Lawrence, 1967. — 2 + 2 setiferous foveolae. Male legs with tarsal pad. Described as similar to *Centrobolus* (including gonopods), but smaller. Unique, 'blister-like' secretions on the body rings. Length 27-37 mm, 39 or 40 body rings. One species, Mozambique.

Neptunobolus Schubart, 1949. — 2 + 2 setiferous foveolae. Preanal scale well-rounded, not projecting. Anterior gonopod unusual, with a very slender coxite and telopodite, mesally not

touching triangular sternite. Length 50-80 mm, 46-49 body rings. Two species, Brazil. *N. hogei* Schubart, 1949.

Pachybolus Cook, 1897, one species; ***Hadrobolus*** Cook, 1897, one species, *H. crassicollis* (Peters, 1855); ***Epibolus*** Cook, 1897, one species, *E. pulchripes* (Gestäcker, 1873); ***Crurifarcimen*** Enghoff, 2011, one species, *C. vagans* Enghoff, 2011; ***Hyperbolus*** Enghoff, 2011, two species, incl. *H. apicomplexus* Enghoff, 2011; ***Parabolus*** Enghoff, 2011, two species, incl. *P. calceus* Enghoff, 2011; ***Pelmatojulus*** de Saussure, 1860, seven species, incl. *P. brachysternus* (Cook, 1897), *P. insignis* Saussure, 1859, *P. laminatus* (Cook, 1897), *P. ligulatus* (Voges, 1878) and *P. tigrinus* Hoffman & Mahsberg, 1996; ***Gabolus*** Enghoff, 2008, one species; ***Madabolus*** Wesener & Enghoff, 2008, one species. — Large (more than 100 mm), very broad, resembling sausages. Distinct from all other Trigoniulidea by the following characters: incisura lateralis on head closed; lamellae linguales of gnathochilarium with all setae located at distal edge, not behind one another; female vulva modified, always with a sinuous opening. East and West Africa, Zanzibar, Western Madagascar.

Spiromanes de Saussure & Zehntner, 1902. — Coxite and telopodite of posterior gonopod fused, telopodite apically massive, excavate, without processes. Anterior gonopod simple, telopodite with a short, well-rounded, mesal process. Relatively small bodied (<60 mm), broad. Three or four species, Seychelles.

Spiromimus de Saussure & Zehntner, 1901, 13 species; ***Xenobolus*** Carl, 1918, two species. — 2 + 2 setiferous foveolae. Small to medium sized (40-90 mm), slender millipedes with long legs. Habitus resembling members of the order Spirostreptida. All known species with at least one thin, brightly coloured axial stripe. Sternite, coxite and telopodite of anterior gonopods all elongated mesally into slender processes. Posterior gonopod telopodites curved towards one another, always with a ventral basal process. Madagascar and India.

Stenobolus Carl, 1918. — 2 + 2 setiferous foveolae. Male legs without tarsal pads. Anterior gonopods massive, resembling those of the Spirobolellidae (especially *Hylekobolus*). Species of medium length and slender, 40-60 mm long, 48-50 body rings. One species, India.

Tonkinbolus Verhoeff, 1938. — 2 + 2 setiferous foveolae. Male legs with tarsal pads. Pre-anal scale elongated, apically blunt. Female vulva modified similarly to those of the Pachybolini. Relatively large, 90-120 mm long, 55-57 body rings. Eight species, SE Asia.

Trachelomegalus Silvestri, 1896. — 2 + 2 setiferous foveolae. Male legs without tarsal pad. Slender with long legs and extremely elongated pre-anal scale. Medium sized (up to 85 mm), usually colourful. Three species, Borneo.

Trigoniulus Pocock, 1894, ca. 36 species, incl. *T. corallinus* (Eydoux & Souleyet, 1841) (Plate XVI D); ***Florianus*** Hoffman & Keeton, 1960, two species; ***Arisemolus*** Hoffman, 1980, four species; ***Sumatrobolus*** Verhoeff, 1936, one species; ***Decelus*** Hoffman & Keeton, 1960, one species; ***Gonauchenius*** Hoffman & Keeton, 1960, one species. — Telopodite of posterior gonopod with mesal branch covered by spines, scales or setae. A diverse group in need of revision. 22 additional species are still placed in *Trigoniulus*, but, since they are only known from females, their correct genus placement cannot be decided. Indonesia, Philippines, New Guinea, as well as one species synantropic with a worldwide distribution. *T. corallinus* synanthropic with a Pantropical distribution.

Variulus Wang, 1951. — Male femur, postfemur and tibia apparently with pads. Large, 90-100 mm long, 50 or 51 body rings. One species, Philippines.

Zehntnerobolus Wesener, 2009, two species; ***Flagellobolus*** Wesener, 2009, one species; ***Riotintobolus*** Wesener, 2009, four species; ***Caprobolus*** Wesener, 2009, one species; ***Alluviobolus*** Wesener, 2009, three species; ***Ostinobolus*** Wesener, 2009, four species; ***Pseudocentrobolus*** Wesener, 2009, two species; ***Granitobolus*** Wesener, 2009, two species. — 2 + 2 setiferous foveolae. Vastly different anterior and posterior gonopods, as well as habitus. Mentum of gnathochilarium subdivided by a transverse ridge. Small body size (up to 50 mm). Madagascar.

Genera not assigned to family or suborder.

Banosolus Wang, 1951. — One species, based on an immature male. One species, Philippines.

HELMINTHOMORPHA *incertae sedis*
Order Siphoniulida Pocock, 1894
[THOMAS WESENER]

Small millipedes, 2-7.5 mm long. Body very slender, width/length ratio less than 1/10. Habitus white, pallid, nematode-like with very short legs. Head small, elongated into a beak. No ommatidia. Antennae long, consisting of seven antennomeres. Antennomeres 5-7 latero-apically with special clavate setae, apical disc narrow, with four elongated apical cones. Mandible unknown. Gnathochilarium strongly modified, elongated, but sclerites still distinguishable. Lateral parts of gnathochilarium formed by large stipes, followed centrally by the lingual lamellae separated by a very narrow mentum. Lingual lamellae and stipes each with palps carrying sensory cones. Body with up to 45 polished and nearly glabrous rings. Ozopores absent. Tergites and pleurites fused without any visible suture. Sternites fused to stigmatic plates, and those fused to pleurotergites with visible sutures. Tergites without a dorsal suture. Pleurite region with striae. Sterna large, coxae touching one another. Collum as large as tergite 2 and 3 combined, slightly overlapping head. Telson apically on preanal scale with several spinnerets. Legs consisting of six podomeres (coxa, prefemur, femur, postfemur, tibia, tarsus), all podomeres short, only tarsus elongated. Coxal pores absent. Tarsi always with an accessory claw. Leg pair 8 (anterior leg pair of body ring 7) modified to a gonopod consisting of three different branches, leg pair 9 a normal walking leg. Male gonopore opening unknown.

First juveniles unknown.

One genus, two species.

Family SIPHONIULIDAE Pocock, 1894. — Central America, Sumatra.

Siphoniulus Pocock, 1894. — Two species.

TABLE 16.1
An overview of the suprageneric millipede taxa

Class DIPLOPODA
Subclass PENICILLATA
Order POLYXENIDA
Superfamily POLYXENOIDEA
Family POLYXENIDAE
Family LOPHOPROCTIDAE
Superfamily SYNXENOIDEA
Family SYNXENIDAE
Subclass CHILOGNATHA
Infraclass PENTAZONIA
Superorder LIMACOMORPHA
Order GLOMERIDESMIDA
Family GLOMERIDESMIDAE
Family TERMITODESMIDAE

TABLE 16.1
(Continued)

Superorder ONISCOMORPHA				
	Order SPHAEROTHERIIDA			
			Family PROCYLIOSOMATIDAE	
			Family ZEPHRONIIDAE	
			Family SPHAEROTHERIIDAE	
			Family ARTHROSPHAERIDAE	
			Family CYLIOSOMATIDAE	
	Order GLOMERIDA			
			Family GLOMERIDELLIDAE	
			Family PROTOGLOMERIDAE	
			Family GLOMERIDAE	
Infraclass HELMINTHOMORPHA				
Subterclass COLOBOGNATHA				
	Order PLATYDESMIDA			
			Family PLATYDESMIDAE	
			Family ANDROGNATHIDAE	
	Order SIPHONOCRYPTIDA			
			Family SIPHONOCRYPTIDAE	
	Order SIPHONOPHORIDA			
			Family SIPHONORHINIDAE	
			Family SIPHONOPHORIDAE	
	Order POLYZONIIDA			
			Family POLYZONIIDAE	
			Family SIPHONOTIDAE	
			Family HIRUDISOMATIDAE	
Subterclass EUGNATHA				
Superorder MEROCHAETA				
	Order POLYDESMIDA			
	Suborder DALODESMIDEA			
			Family DALODESMIDAE	
			Family VAALOGONOPODIDAE	
	Suborder LEPTODESMIDEA			
		Superfamily CHELODESMOIDEA		
			Family CHELODESMIDAE	
		Superfamily PLATYRHACOIDEA		
			Family APHELIDESMIDAE	
			Family PLATYRHACIDAE	
		Superfamily RHACHODESMOIDEA		
			Family RHACHODESMIDAE	
			Family TRIDONTOMIDAE	
		Superfamily SPHAERIODESMOIDEA		
			Family CAMPODESMIDAE	
			Family HOLISTOPHALLIDAE	
			Family SPHAERIODESMIDAE	

TABLE 16.1
(Continued)

Superfamily XYSTODESMOIDEA
Family EURYMERODESMIDAE
Family EURYURIDAE
Family GOMPHODESMIDAE
Family OXYDESMIDAE
Family XYSTODESMIDAE
Suborder POLYDESMIDEA
Superfamily ONISCODESMOIDEA
Family DORSOPORIDAE
Family ONISCODESMIDAE
Superfamily POLYDESMOIDEA
Family CRYPTODESMIDAE
Family HAPLODESMIDAE
Family POLYDESMIDAE
Superfamily PYRGODESMOIDEA
Family AMMODESMIDAE
Family CYRTODESMIDAE
Family PYRGODESMIDAE
Superfamily TRICHOPOLYDESMOIDEA
Family TRICHOPOLYDESMIDAE
Family OPISOTRETIDAE
Suborder STRONGYLOSOMATIDEA
Family PARADOXOSOMATIDAE
Superorder NEMATOPHORA
Order CHORDEUMATIDA
Suborder CHORDEUMATIDEA
Family CHORDEUMATIDAE
Family SPEOPHILOSOMATIDAE
Suborder CRASPEDOSOMATIDEA
Superfamily ANTHROLEUCOSOMATOIDEA
Family ANTHROLEUCOSOMATIDAE
Family ACHEROSOMATIDAE
Family VANDELEUMATIDAE
Superfamily BRANNERIOIDEA
Family BETICOSOMATIDAE
Family BRACHYCHAETEUMATIDAE
Family BRANNERIIDAE
Family CHAMAESOMATIDAE
Family GOLOVATCHIIDAE
Family HETEROLATZELIIDAE
Family KASHMIREUMATIDAE
Family MACROCHAETEUMATIDAE
Family MICROLYMPIIDAE

TABLE 16.1
(Continued)

Family NIPONIOSOMATIDAE
Family TINGUPIDAE
Family TRACHYGONIDAE
Superfamily CLEIDOGONOIDEA
Family BIOKOVIELLIDAE
Family CLEIDOGONIDAE
Family ENTOMOBIELZIIDAE
Family LUSITANIOSOMATIDAE
Family OPISTHOCHEIRIDAE
Family TRICHOPETALIDAE
Superfamily CRASPEDOSOMATOIDEA
Family ATTEMSIIDAE
Family CRASPEDOSOMATIDAE
Family HAPLOBAINOSOMATIDAE
Superfamily HAASEOIDEA
Family HAASEIDAE
Superfamily NEOATRACTOSOMATOIDEA
Family KIRKAYAKIDAE
Family CYRNOSOMATIDAE
Family HOFFMANEUMATIDAE
Family MASTIGOPHOROPHYLLIDAE
Family NEOACTRACTOSOMATIDAE
Superfamily VERHOEFFIOIDEA
Family VERHOEFFIIDAE
Suborder HETEROCHORDEUMATIDEA
Superfamily CONOTYLOIDEA
Family ADRITYLIDAE
Family CONOTYLIDAE
Superfamily DIPLOMARAGNOIDEA
Family DIPLOMARAGNIDAE
Superfamily HETEROCHORDEUMATOIDEA
Family EUDIGONIDAE
Family HETEROCHORDEUMATIDAE
Family MEGALOTYLIDAE
Family METOPIDIOTRICHIDAE
Family PETERJOHNSIIDAE
Superfamily PYGMAEOSOMATOIDEA
Family LANKASOMATIDAE
Family PYGMAEOSOMATIDAE
Suborder STRIARIIDEA
Superfamily CASEYOIDEA
Family CASEYIDAE
Family UROCHORDEUMATIDAE

TABLE 16.1
(Continued)

Superfamily STRIARIOIDEA
Family APTEROURIDAE
Family BUOTIDAE
Family RHISCOSOMIDIDAE
Family STRIARIIDAE
Order CALLIPODIDA
Suborder SINOCALLIPODIDEA
Family SINOCALLIPODIDAE
Suborder CALLIPODIDEA
Family CALLIPODIDAE
Suborder SCHIZOPETALIDEA
Family ABACIONIDAE
Family CASPIOPETALIDAE
Family DORYPETALIDAE
Family PARACORTINIDAE
Family SCHIZOPETALIDAE
Family TYNOMMATIDAE
Order STEMMIULIDA
Family STEMMIULIDAE
Superorder JULIFORMIA
Order JULIDA
Superfamily BLANIULOIDEA
Family BLANIULIDAE
Family GALLIOBATIDAE
Family OKEANOBATIDAE
Family ZOSTERACTINIDAE
Superfamily JULOIDEA
Family JULIDAE
Family RHOPALOIULIDAE
Family TRICHOBLANIULIDAE
Family TRICHONEMASOMATIDAE
Superfamily NEMASOMATOIDEA
Family CHELOJULIDAE
Family NEMASOMATIDAE
Family PSEUDONEMASOMATIDAE
Family TELSONEMASOMATIDAE
Superfamily PAEROMOPODOIDEA
Family APROSPHYLOSOMATIDAE
Family PAEROMOPODIDAE
Superfamily PARAJULOIDEA
Family MONGOLIULIDAE
Family PARAJULIDAE

TABLE 16.1
(Continued)

Order SPIROSTREPTIDA
Suborder CAMBALIDEA
Family CHOCTELLIDAE
Family PSEUDONANNOLENIDAE
Family IULOMORPHIDAE
Family CAMBALIDAE
Family CAMBALOPSIDAE
Suborder SPIROSTREPTIDEA
Superfamily ODONTOPYGOIDEA
Family ODONTOPYGIDAE
Superfamily SPIROSTREPTOIDEA
Family ADIAPHOROSTREPTIDAE
Family HARPAGOPHORIDAE
Family SPIROSTREPTIDAE
Order SPIROBOLIDA
Suborder RHINOCRICIDEA
Family RHINOCRICIDAE
Suborder SPIROBOLIDEA
Family SPIROBOLIDAE
Family MESSICOBOLIDAE
Family ALLOPOCOCKIIDAE
Family ATOPETHOLIDAE
Family SPIROBOLELLIDAE
Family TYPHLOBOLELLIDAE
Family PSEUDOSPIROBOLELLIDAE
Suborder TRIGONIULIDEA
Family PACHYBOLIDAE
HELMINTHOMORPHA *INCERTAE SEDIS*
Order SIPHONIULIDA
Family SIPHONIULIDAE

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TAXONOMIC INDEX

In addition to the names of taxa of Diplopoda cited in this volume, the index includes alternative names by which some species have been cited in works mentioned in Chapters 1 to 15. Names of organisms other than millipedes are listed in the Subject Index. Page numbers in *italics* refer to illustrations.

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Plate I. Overview of millipede diversity. **A** *Lophoproctus* cf. *pagesi* (Polyxenida: Lophoproctidae) (Portugal). **B** *Glomeris marginata* and *G. intermedia* (Glomerida: Glomeridae) (Germany). **C** *Platydesmus* sp. (Platydesmida: Platydesmidae) (Mexico). **D** *Desmoxytes purpurosea* (Polydesmida: Paradoxosomatidae) (Thailand). **E** *Siphonophora zelandica* (Siphonophorida: Siphonophoridae) (New Zealand). **F** *Hirudicryptus taiwanensis* (Siphonocryptida) (Taiwan). Photo credits: **A** F. Rasteiro; **B** J. P. Oeyen; **C** E. Recuero; **D** S. Panha; **E, F** Z. Korsós.

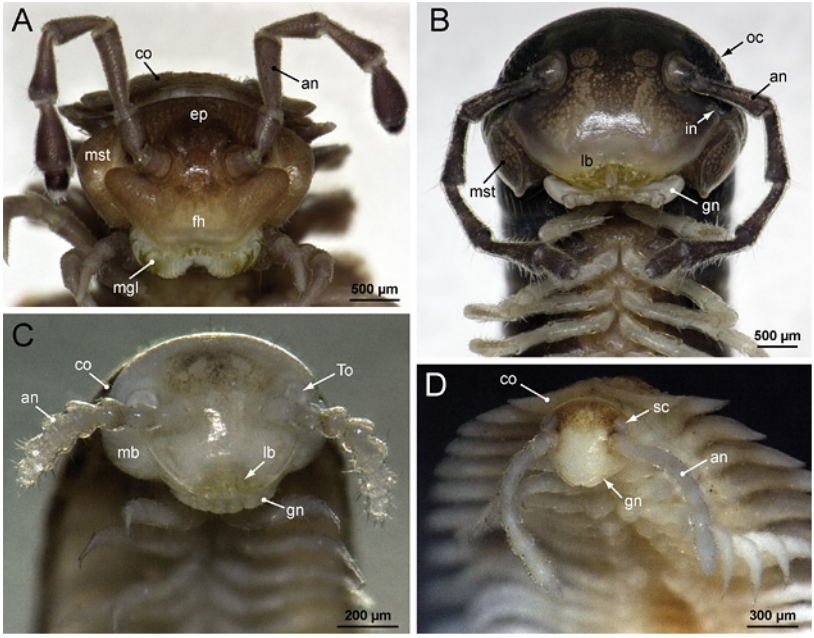

Plate II. Head morphology. **A** *Polydesmus angustus* (Polydesmida). **B** *Tachypodoiulus niger* (Julida). **C** *Glomeridesmus* sp. (Pentazonia: Glomeridesmida). **D** *Platydesmus* sp. (Colobognatha: Platydesmida). Colour version of Fig. 2.1 (see p. 11 for full legend).

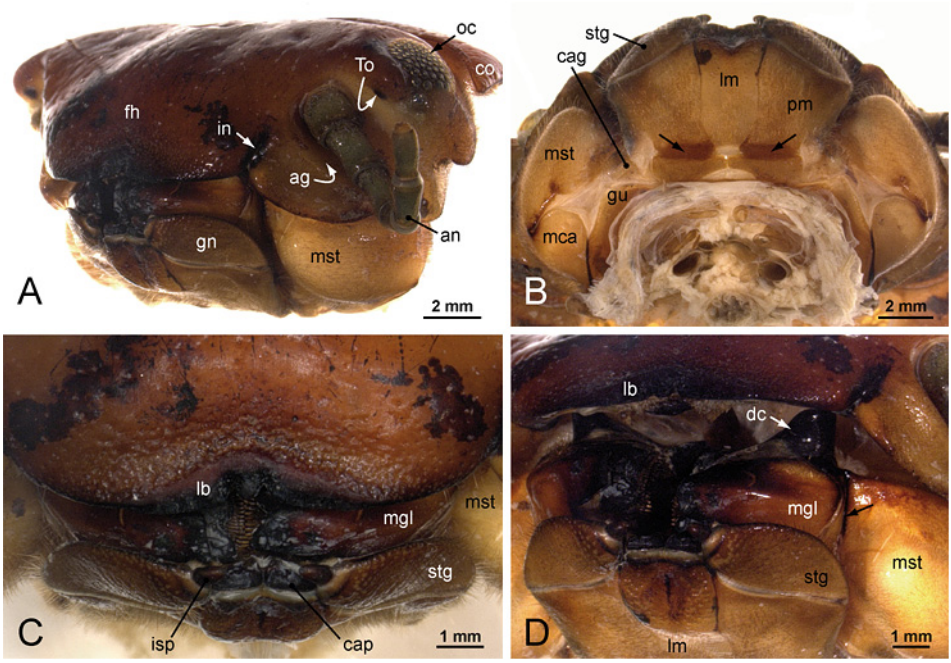

Plate III. *Zoosphaerium* sp. (Sphaerotheriida), morphology of the head. Colour version of Fig. 2.2 (see p. 12 for full legend).

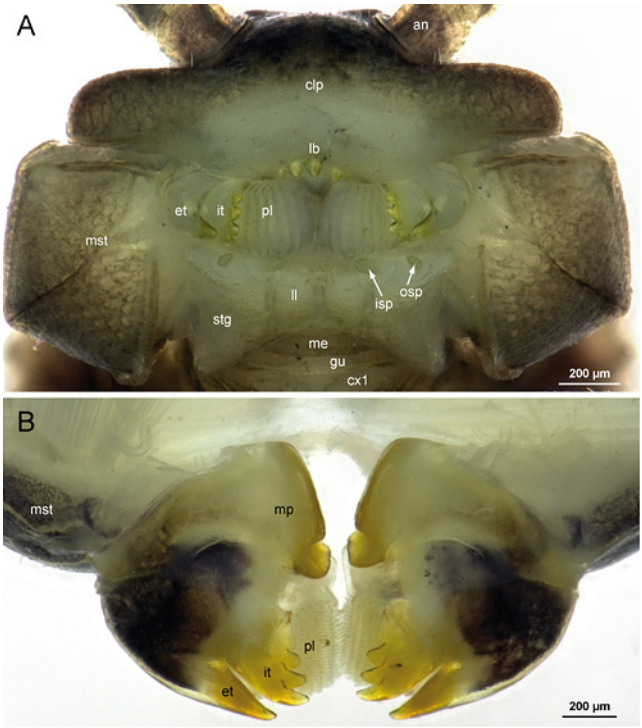

Plate IV. Composition of chewing-biting mandibles. **A** *Polydesmus angustus* (Polydesmida). **B** *Glomeris marginata* (Glomerida). Colour version of Fig. 2.3 (see p. 17 for full legend).

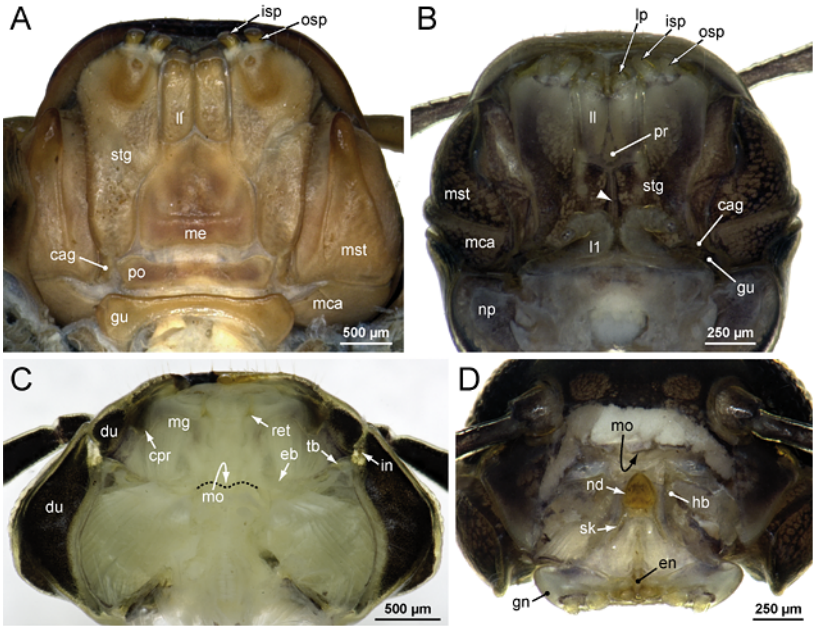

Plate V. Gnathochilarium and peristomatic structures. **A** *Sechelleptus* sp. (Spirostreptida). **B** *Tachypodoiulus niger* (Julida). **C** *Glomeris marginata* (Glomerida), epipharynx. **D** *T. niger* (Julida), hypopharynx. Colour version of Fig. 2.4 (see p. 20 for full legend).

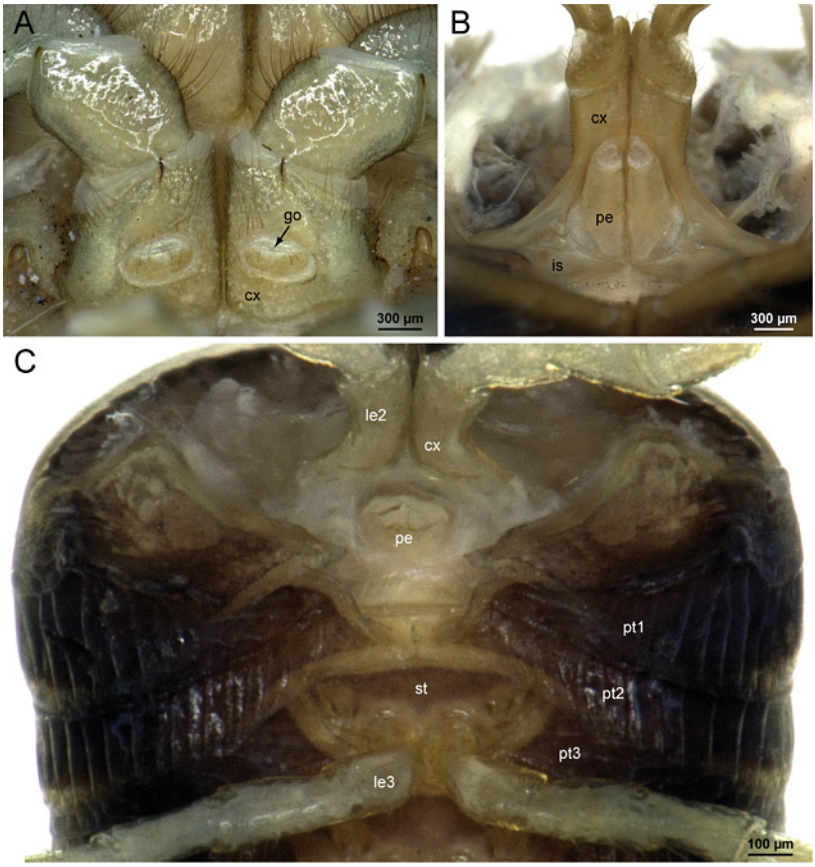

Plate VI. Male genitalia associated to the second pair of trunk legs. **A** *Zoosphaerium* sp. (Sphaerotheriida). **B** *Sechelleptus* sp. (Spirostreptida). **C** *Tachypodoiulus niger* (Julida). Colour version of Fig. 2.8 (see p. 37 for full legend).

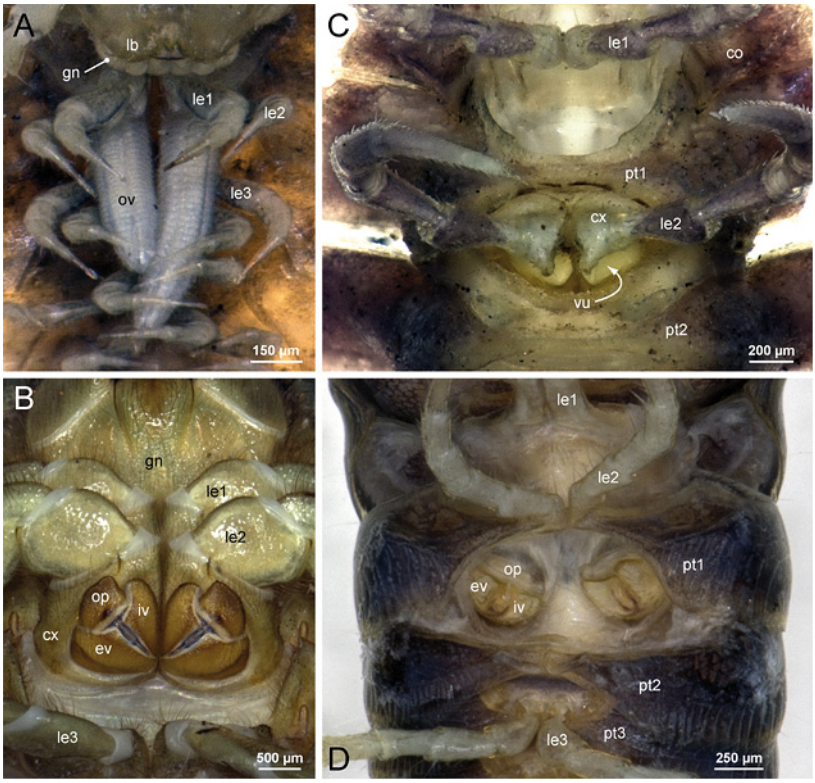

Plate VII. Female genitalia associated to the second pair of trunk legs. **A** *Glomeridesmus* sp. (Glomeridesmida). **B** *Zoosphaerium* sp. (Sphaerotheriida). **C** *Polydesmus angustus* (Polydesmida). **D** *Tachypodoiulus niger* (Julida). Colour version of Fig. 2.9 (see p. 38 for full legend).

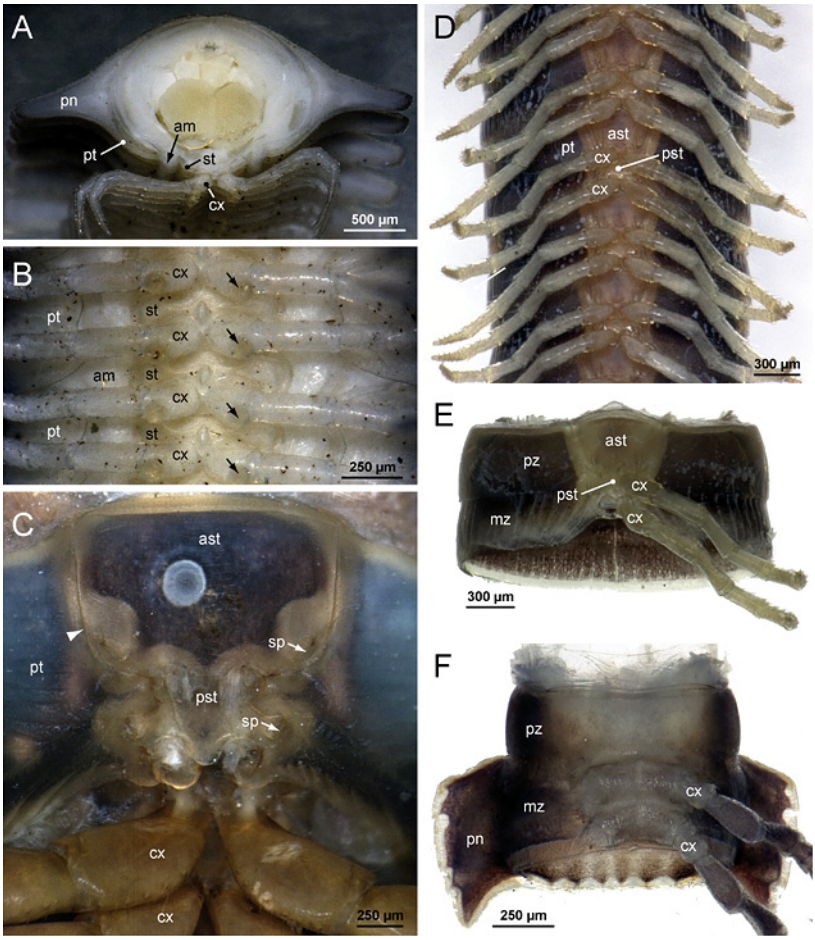

Plate VIII. Morphology of diplorings. **A-B** *Brachycybe* sp. (Colobognatha: Platydesmida). **C** *Sechelleptus* sp. (Spirostreptida). **D-E** *Tachypodoiulus niger* (Julida). **F** *Polydesmus angustus* (Polydesmida). Colour version of Fig. 2.10 (see p. 45 for full legend).

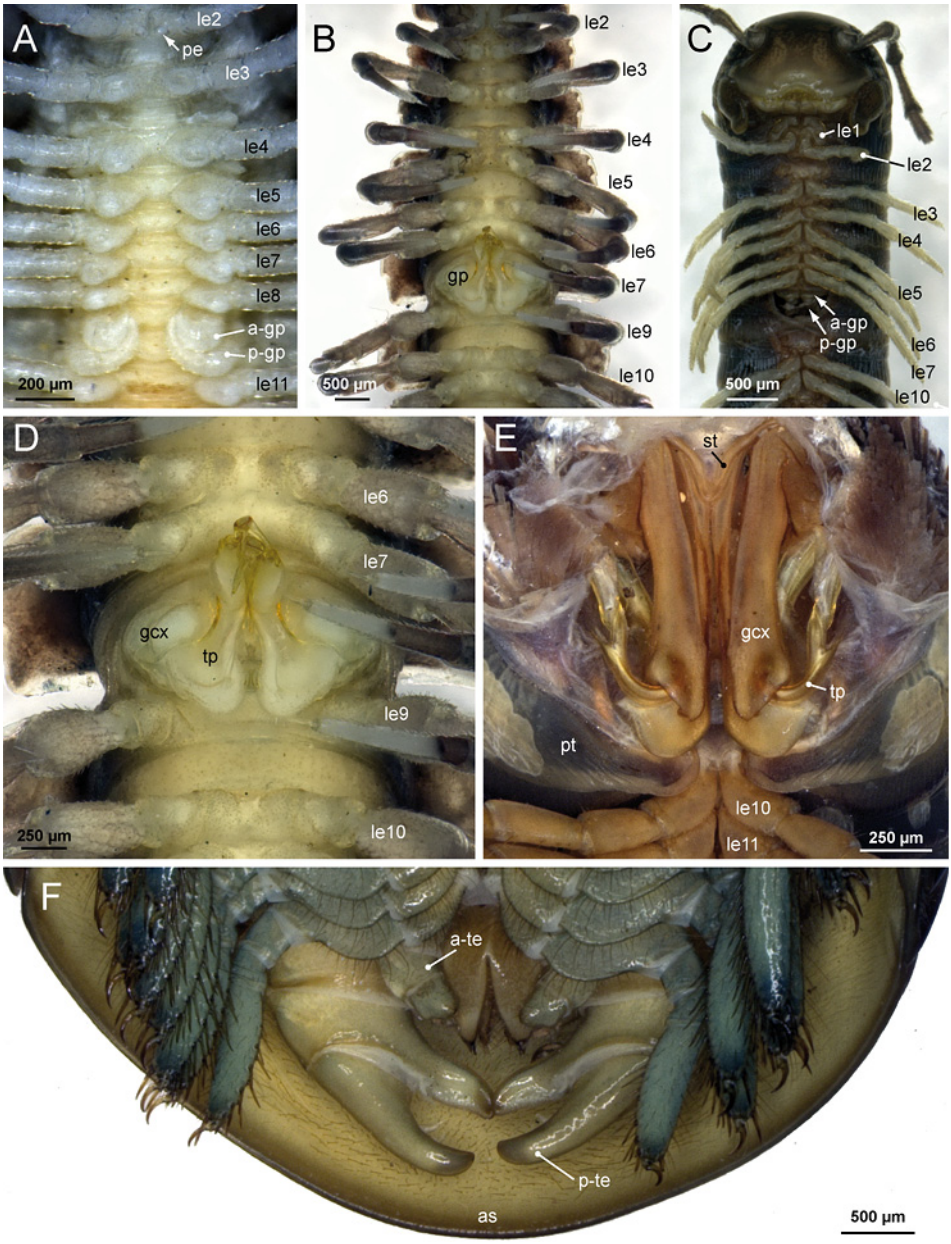

Plate IX. Gonopods (**A-E**) and telopods (**F**). **A** *Platydesmus* sp. (Colobognatha: Platydesmida). **B** *Polydesmus angustus* (Polydesmida). **C** *Tachypodoiulus niger* (Julida). **D** *Polydesmus angustus* (Polydesmida). **E** *Sechelleptus* sp. (Spirostreptida). **F** *Zoosphaerium* sp. (Sphaerotheriida). Colour version of Fig. 2.11 (see p. 53 for full legend).

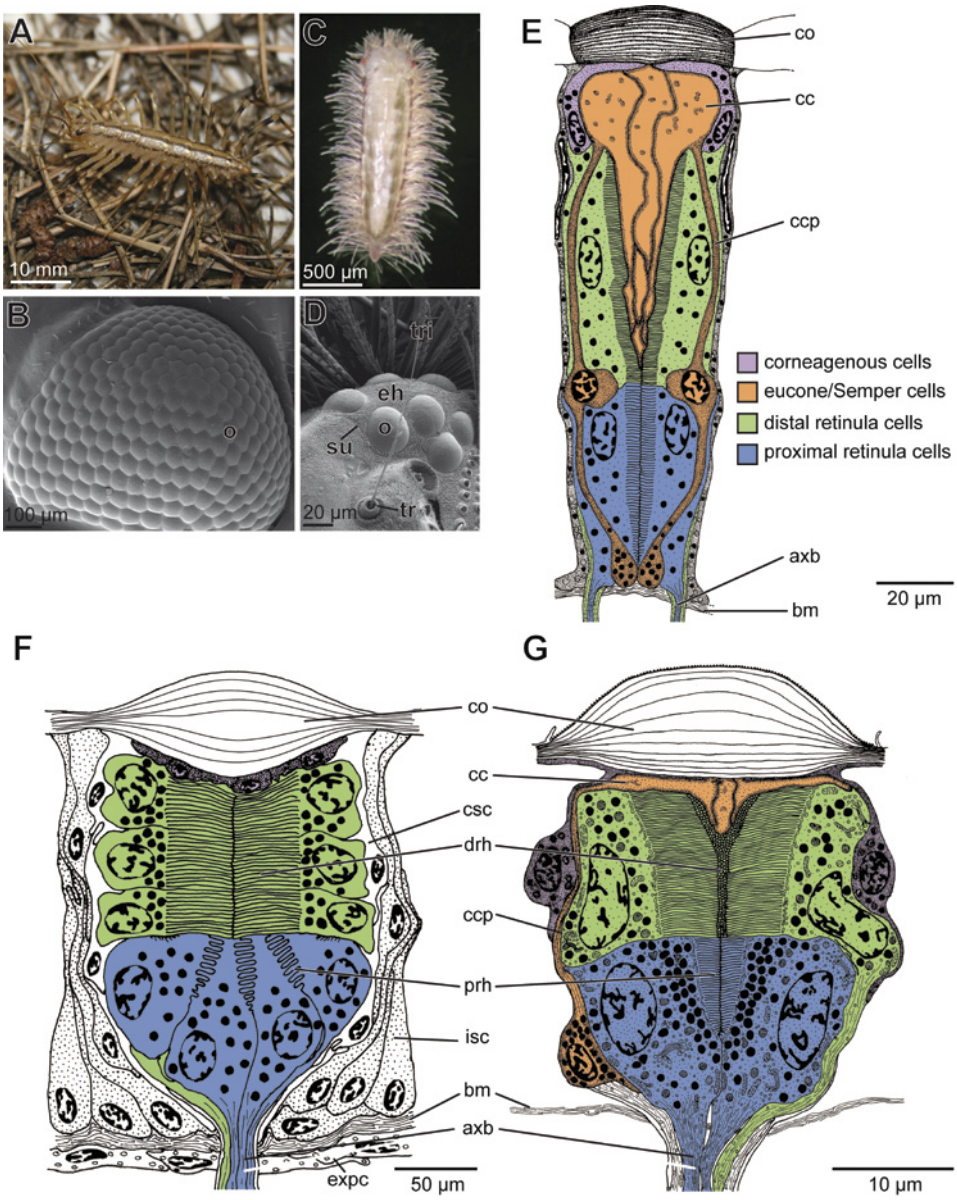

Plate X. Ultrastructural comparison of ommatidia in Scutigeromorpha, Lithobiomorpha (both Chilopoda) and Diplopoda Penicillata (*Phryssonotus platycephalus*). Colour version of Fig. 9.7 (see pp. 200-201 for full legend).

Plate XI. Sphaerotheriida: Arthrosphaeridae. **A** *Arthrosphaera brandtii* (Tanzania, introduced). **B** *Sphaeromimus musicus* (Madagascar). **C** *Zoosphaerium* sp. 1 (Madagascar). **D** *Zoosphaerium* sp. 3 (Madagascar). **E** *Zoosphaerium* sp. (Madagascar). **F** *Z. villosum* (Madagascar). Photo credits: **A, E** J. P. Oeyen; **B** Th. Wesener; **C, D** A. Hartig; **F** K. Schütte.

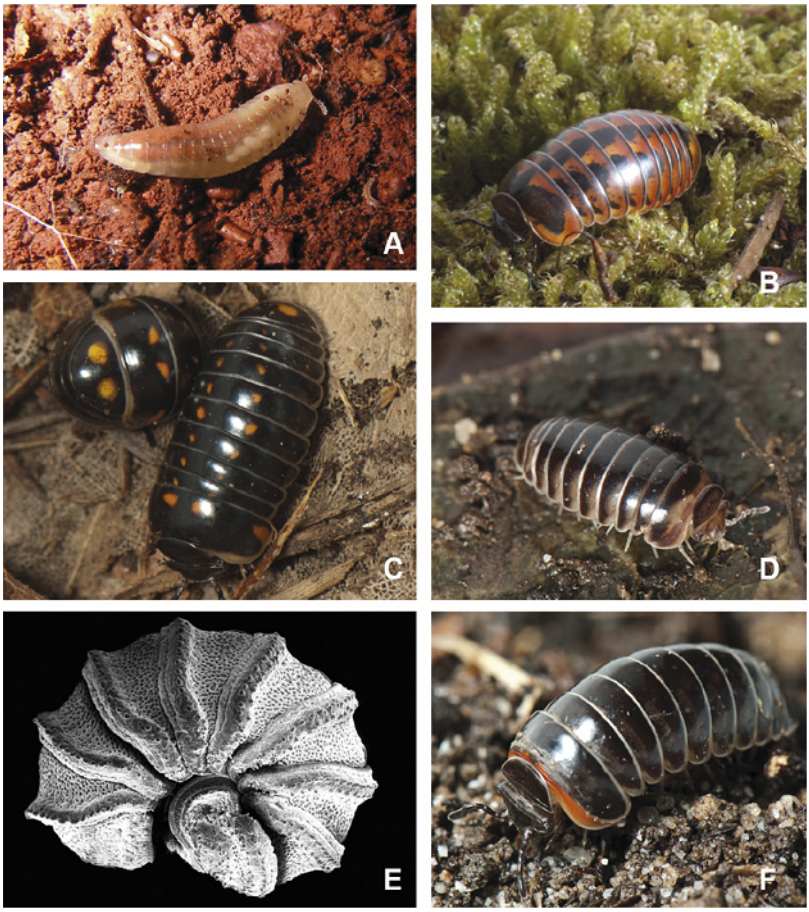

Plate XII. Glomeridesmida (**A**) and Glomerida: Glomeridae (**B-F**). **A** *Glomeridesmus spelaeus* (Brazil). **B** *Glomeris oblongoguttata* (Italy). **C** *G. euganeorum* (Italy). **D** *Hyleoglomeris* sp. (Japan). **E** *Trachysphaera lobata* (SEM) (England). **F** *Schismaglomeris occultocolorata* (Portugal). Photo credits: **A** R. L. Ferreira; **B-D, F** J. P. Oeyen; **E** Th. Wesener.

Plate XIII. Polyzoniida and Polydesmida. **A** *Polyzonium germanicum* (Polyzoniida: Polyzoniidae) (Germany). **B** *Aphelidesmus divergens* (Polydesmida: Aphelidesmidae) (Tobago, introduced). **C** *Propolydesmus germanicus* (id.: Polydesmidae) (Germany). **D** *Chondrodesmus* cf. *riparius* (id.: Chelodesmidae) (Denmark, introduced). **E** *Stosatea italica* (id.: Paradoxosomatidae) (Denmark). **F** *Sphaeriodesmus* sp. (id.: Sphaeriodesmidae) (Mexico). Photo credits: **A-C** J. P. Oeyen; **D** G. Brovad; **E** S. Dupont; **F** E. Recuero.

Plate XIV. Nematophora. **A** *Haplogona oculodistincta* (Chordeumatida: Verhoeffiidae) (Austria). **B** *Craspedosoma alemannicum* (id.: Craspedosomatidae) (Germany). **C** *Pyrgocyphosoma titianum* (id.: id.) (id.). **D** *Dactylophorosoma nivisatelles* (id.: id.) (Austria). **E** *Atractosoma meridionale* (id.: id.) (Germany). **F** *Bergamosoma canestrinii* (id.: id.) (id.). **G** *Eurygyrus* sp. (Callipodida: Schizopetalidae) (Turkey). **H** *Stemmiulus brasiliensis* (Stemmiulida: Stemmiulidae) (Brazil). Photo credits: **A-F** J. Spelda; **G** P. Stoev; **H** R. L. Ferreira.

Plate XV. Julida and Spirostreptida. **A** *Pachyiulus hungaricus* (Julida: Julidae) (Serbia). **B** *Trichoblaniulus hirsutus* (id.: Trichoblaniulidae) (Italy). **C** *Californiulus chamberlini* (id.: Paeromopodidae) (USA). **D** *Blaniulus guttulatus* (id.: Blaniulidae) (USA, introduced). **E** *Ophistreptus guineensis* (Spirostreptida: Spirostreptidae) (Africa). **F** *Armatostreptus armatus* (id.: Harpagophoridae) (Thailand). Photo credits: **A** D. Antic; **B** D. Cheung; **C** M. Hedin; **D** D. Thombs; **E** J. P. Oeyen; **F** P. Pimvichai.

Plate XVI. Spirobolida. **A** *Aphistogoniulus corallipes* (Pachybolidae) (Madagascar). **B** *A. cowani* (id.) (Madagascar). **C** *A. infernalis* (id.) (Madagascar). **D** *Trigoniulus corallinus* (id.) (Tobago, introduced). **E** *Hylekobolus brachiosauroides* (Spirobolellidae) (Madagascar). Photo credits: **A, C, E** Th. Wesener; **B** A. Hartig; **D** J. P. Oeyen.