A LARVAL SEA SPIDER (ARTHROPODA: PYCNOGONIDA) FROM THE UPPER CAMBRIAN 'ORSTEN' OF SWEDEN, AND THE PHYLOGENETIC POSITION OF PYCNOGONIDS

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ABSTRACT. Among a set of small, secondarily phosphatised larval arthropods from the Upper Cambrian 'Orsten' of Sweden, described by Müller and Walossek in 1986, one form bears a remarkable resemblance to the hatching protonymph larva of extant Pantopoda. This 'larva D' shares with protonymphs their gross body form, the anteroventral mouth on a slightly off-set forehead region, the cheliceral morphology, two homeomorphic pairs of post-cheliceral limbs, and further detailed similarities. It is described herein as *Cambropycnogon klausmuelleri* gen. et sp. nov. and is proposed as the oldest unequivocal record of both Pycnogonida and Chelicerata. Plesiomorphic features such as a pair of rudimentary pre-cheliceral limbs and the gnathobasic basipods of the two post-cheliceral limbs distinguish it from all known larvae of extant Pantopoda and lead us to propose a phylogeny of the Pycnogonida of the form (*Cambropycnogon klausmuelleri* + (*Palaeoisopus* + (*Palaeopantopus* + Pantopoda))). The fossil may help to resolve the long debate about the relationships of Pycnogonida to other Arthropoda and supports a (Pycnogonida + Euchelicerata) relationship within the Chelicerata. The pre-cheliceral limbs in this fossil support traditional morphological studies in which the chelicera represent the second (a2) head appendage, corresponding to the crustacean 'second antennae', and contradict recent data based on homeobox genes implying that the chelicerae are the first (a1) head appendages homologous with crustacean first antennae.

KEY WORDS: chelicerates, pycnogonids, larvae, antennae, head segments, Cambrian, Orsten.

PYCNOGONIDA (sea spiders; see Discussion for a definition of Pycnogonida and Pantopoda) are an enigmatic group of spider-like, exclusively marine arthropods. They are slow-moving, predominantly benthic animals with a peculiar anatomy. The body is almost tubular, lacking any signs of a dorsal head shield or pleurotergites. The so-called cephalosoma region bears the eyes on a hump or tubercle, the position of which is variable, and the anteroventrally-pointing proboscis, a tubular feeding structure. It also bears up to four pairs of appendages: the chelicerae (also called chelifores or cheliphores), the palps, the ovigers and the most anterior pair of walking legs. Chelicerae, palps and/or ovigers may be absent in adults of certain taxa (see Child 1998 for a recent family key, and Munilla 1999 for a phylogeny based in part on the reduction of cephalic appendages). Posterior to the cephalosoma there are three more tubular segments each bearing a pair of walking legs (plus one or two additional limb-bearing segments in some taxa). This region, sometimes called the thorax or trunk, is followed by a small, unsegmented extension. This is traditionally called the abdomen, although there are indications that in pycnogonids the opisthosomal region comparable to that of Chelicerata actually corresponds to the last limb-bearing segment plus this small 'tail' end (Vilpoux 1999; see also Bullough 1958; Stürmer and Bergström 1981, table 1). As a consequence of the peculiar tubular body design, Pycnogonida have some of their internal structures such as excretory organs either missing or, like the gonads, displaced into the legs. Extant representatives typically feed on sessile organisms such as hydroids (e.g. King 1973), although some species are parasitic on non-vertebrates, either as juveniles or throughout their lives (e.g. Child 1998). There are approximately 1150 living species known, distributed world-wide from the shore down to deep water (Child 1998).

The fossil record of Pycnogonida is very poor. One reason may be that their cuticle is unmineralised, giving them a fairly low preservation potential. However, recent work on Konservatlagerstätten, such as

the Lower Devonian (Lower Emsian) Hunsrück slates of Germany (e.g. Bartels *et al.* 1998) or the Upper Cambrian 'Orsten' (e.g. Müller 1985 and subsequent papers), has shown that under favourable conditions unmineralised material can also be recovered in a state of excellent preservation. The first fossil Pycnogonida were described from the Hunsrück slates (e.g. Broili 1928, 1929, 1930, 1932) and were redescribed in some (significant) detail by Hedgpeth (1978) and Bergström *et al.* (1980). The latter authors recognised three species, two of which, in contrast to extant Pantopoda, have segmented tails, which were noted subsequently as having borne fine setae (Hartenberger 1995). New material from Hunsrück is currently being described (Franz Krapp, pers. comm. 2000). More fossil pycnogonids have been reported from the Jurassic of Solnhofen, Germany, but these have subsequently been recognised as phyllosoma larvae of rock lobsters (Palinurida: Decapoda: Crustacea; compare, e.g. Polz 1969, 1984). There are, however, undescribed and more convincing Pantopoda from Solnhofen (Dunlop, pers. obs.) and fossil Pantopoda have been noted from the Jurassic of France (Wilby *et al.* 1996).

Müller and Walossek (1986) described minute, secondarily phosphatised arthropods from the Cambrian 'Orsten' fauna of Sweden. One of these presumed larval forms, approximately 270 μm long, was named 'larva D' in an open nomenclature. It has a prominent pair of chelate anterior appendages, and was therefore referred to Chelicerata, with possible affinities to the Pantopoda (used by these authors in synonymy to Pycnogonida). The mouth, on a slightly anteroventrally-protruding pre-cheliceral region of the body, is very small in these fossils leading Müller and Walossek (1986, 1988a) to suggest a fluid-feeding, possibly ectoparasitic, mode of life. These authors further discussed the possibility that larva D was a pantopod. Parasitism is well known from larval Pantopoda (see above), and larva D resembles the extant pantopod protonymph, the earliest larval stage, not only in overall size and shape, but in several details such as the large chelate anterior appendages in the vicinity of the small mouth, followed by two more pairs of homeomorphic limbs and a weakly developed head shield.

In contrast to larvae of extant Pantopoda, larva D has a pair of pre-cheliceral structures flanking the mouth. These were discussed by Müller and Walossek (1986) as possible remnants of the antennae of the euarthropodan ground pattern (= first antennae or antennulae of Crustacea), which are not known from any extant Chelicerata. Furthermore, larva D has mesal gnathobases on the basal segment, i.e. the basipod, of the two post-cheliceral appendages. This basipod is traditionally called the coxa in Chelicerata, although in the comparative arthropod terminology developed by Walossek and Müller (1990, 1997) and Walossek (1993, 1999) the basipod is recognised as a homologous element in Euarthropoda bearing the two limb rami whereas the 'coxa' has been redefined as a more proximal element developed in the later crustacean lineage on two limbs second antenna = A2 and mandible = Md (and only these two) at the level of (Phosphatocopina + Eucrustacea) by the enlargement of the proximal endite to a sclerotic ring with a median gnathic elongation. This endite is one of the key innovations of the crustacean evolutionary lineage. Within the Eucrustacea the proximal endite may also be modified to coxal portions on further limbs (e.g. in malacostracans; cf. Walossek 1999).

Gnathobases are unknown in previously described Pantopoda, but are present in various aquatic Chelicerata (e.g. Selden 1981). Antennae, gnathobases and a 'head larva' (see Walossek and Müller 1990, 1997) with four pairs of functional appendages must all be interpreted as symplesiomorphies in the ground-pattern of Chelicerata, because they are characteristic for the ground pattern of Euarthropoda too (see Discussion). The fossil Pycnogonida described thus far are only known from adult specimens and do not show any signs of pre-cheliceral appendages or of gnathobases on their post-cheliceral legs. A more difficult feature is the uniramy of the fossil, since biramous limbs are a ground-pattern character of Euarthropoda. Uniramy holds for all prosomal legs of most extant adult arachnids (there is a possible exception in the mites; see Discussion) and probably for eurypterids too (see e.g. Selden 1981), but not for extant xiphosurids, which retain an exopod on their last prosomal leg (the so-called flabellum).

In this paper we formally name 'larva D' and discuss its relationships with Pantopoda. The implications of its assignment to Pycnogonida, and for the phylogeny of this group and its relationships to Chelicerata, are discussed. Since the morphology has been described in some detail in Müller and Walossek (1986), we concentrate here on those details that are important for the phylogenetic interpretations and present new figures based on improved SEM photographs of all available specimens plus a new reconstruction (Text-fig. 1).

MATERIAL AND METHODS

We re-examined the six specimens of 'larva D' examined and described by Müller and Walossek (1986), plus an additional, previously undescribed specimen (UB Wa118). Both the original and new SEM photographs (Pls 1–4) of the material were analysed and compared to SEM photographs made of the larval sequence of the extant pantopod *Pycnogonum litorale* (Ström, 1762), reared in Ulm for a diploma project (Vilpoux 1999; examples in Pl. 5).

Six of the fossil specimens (including the new UB Wa118) are from a rock sample found in a quarry near Backeborg at the Kinnekulle, a hill at the south-eastern edge of the large Lake Vättern in Västergötland, Sweden. Their age is dated to the lowest zone of the Upper Cambrian Alum Shale succession, the *Agnostus pisiformis* Zone or Zone 1. One specimen is from Zone 2a, etched from a rock sample from near Degerhamn on the Isle of Öland at the eastern coast of Skåne in southern Sweden (see also Müller and Walossek 1986).

The specimens were etched from limestone nodules using a mild (10%) acetic acid, as for the whole 'Orsten' material. During etching (*c.* 14 days) all calcitic material, including the abundant head and tail shields of agnostids is dissolved, whereas the non-calcitic material is retained on sieves of different mesh size (50–500 μm). Suitable cuticular fragments preserved by impregnation of fluoritic apatite (calcium phosphate as in human teeth), were sorted out, after washing and drying, and placed on SEM stubs for gold coating and observation under the SEM.

With respect to preservation (for details of the 'Orsten'-type of preservation and processing, see e.g. Müller 1985), the specimens differ from most other Swedish 'Orsten' fossils in that they appear solid, as can be seen from the fractured rami of the limbs and the caudal outgrowths (Pl. 2, figs 1, 4). Cuticular preservation is generally good, except for some overgrown, particulate matter which has particularly accumulated between the limbs behind the mouth and in the fold between the body and caudal outgrowths, disguising details (Pl. 1, figs 5–7; Pl. 2, fig. 5). Furthermore, the flanks may be covered with particulate matter and some stick-like crystals, such as in UB M801 (Pl. 1, figs 5–7). Six of the seven specimens (UB M800–M805) are almost complete, including the projecting anterior end and at least one of the caudal outgrowths. However, the mouth area on the anterior swollen front end of the body is, in most cases, wrinkled or deformed suggesting that this part of the cuticle was much softer than the surrounding area. The appendages are mostly well preserved except for the annulated rami of the two pairs of post-cheliceral limbs (see below). The seventh specimen, UB Wa118, represents a fragment of the caudal part of the body bearing the left posterior limb and complete caudal outgrowths. Cuticular preservation is uneven, and in some cases the finely micro-folded cuticular surface seems to be ripped off, uncovering a smoother subsurface (Pl. 3, fig. 7).

Terminology (Table 1, including abbreviations used in the plates and figures) generally follows that currently used for Arthropoda and Pycnogonida. Where necessary, we adjusted the terminology for better comparability, adopting that proposed by Walossek in various papers, particularly for portions of limbs (e.g. Walossek 1993, 1999). The term 'antenna' is used in a general sense to refer to the uniramous first head appendage of Euarthropoda, i.e. acting as a feeler (e.g. in insects) and being equivalent to the first antenna or antennula (a1) of Crustacea, where it has a different original function, namely locomotion and feeding (Walossek & Müller 1990). This first head appendage is innervated by the deutocerebrum and should not be confused with the antenna, or better the second antenna (a2), of Crustacea, which corresponds to the second head limb of Euarthropoda. The second antenna is innervated by the tritocerebrum and was sensorial neither in the stem-line of Crustacea nor of Eucrustacea, but acquired this particular function within specific eucrustacean in-group taxa (mainly Malacostraca where it represents an autapomorphy of this taxon; cf. Walossek 1999; Walossek & Müller 1997).

SYSTEMATIC PALAEONTOLOGY

PYCNOGONIDA Latreille, 1810

Genus CAMBROPYCNOGON gen. nov.

Derivation of name. From the Cambrian Period and the suggested relationships with Pycnogonida.

Type species. Cambropycnogon klausmuelleri sp. nov., by monotypy. Known only from early larval instar.

Diagnosis. Characterised, in the known semaphoront, by a chelicera comprising a large, socket-like joint region and two strongly-sclerotised articles forming the chela or claw, two pairs of post-cheliceral appendages with a distinctly pseudo-annulated ramus fringed with fine denticles, absence of spines originating (laterally) on the basal podomere of both the chelicerae and two post-cheliceral appendages, with the basipod of the two post-cheliceral appendages being medially drawn out into a marginally toothed, anteriorly tilted gnathobasic edge, the anterior basipod bearing a stout spine on the outer surface between gnathobase and ramus and a thorn further outwards, and by pointed, laterally flattened pre-cheliceral outgrowths on the rounded forehead flanking the small circular mouth and nesting in a shallow depression. Posterior end of body drawn out into a pair of outgrowths with pseudo-annulation, as in the rami, which are also adorned with denticles that merge into longer setulae towards the posterior of the outgrowth. Outgrowth terminated by a spine.

Cambropycnogon klausmuelleri sp. nov.

Plates 1–4; Text-figure 1

1986   Larva D; Müller and Walossek, pp. 167–175, figs 8–11 (described under open nomenclature).
1988*a*   Larva D; Müller and Walossek, pp. 40–42, 4 figs.
1997   Chelicerate larva; Walossek and Müller, pp. 143, fig. 12.2b–c.

Derivation of name. In honour of Prof. Dr Klaus J. Müller, Bonn, who discovered the 'Orsten' fossil arthropods with their phosphatic preservation and described them over many years together with DW.

Holotype. UB M800, see Müller and Walossek (1986, figs 8a–b, 10d–g, 11a, g); chosen because of its completeness and excellence of preservation.

Type horizon and locality. Quarry near Backeborg at the Kinnekulle, Västergötland, Sweden, Zone 1 of the Upper Cambrian Alum Shale succession (*Agnostus pisiformis* bed).

Additional material. Five specimens, UB M802–M805 and Wa118, from the type locality, the first four of which were figured by Müller and Walossek (1986). One specimen, UB M801, from Degerhamn, Öland, Sweden, Zone 2a of the Upper Cambrian Alum Shale succession. All material is housed in the Institut für Paläontologie, Universität Bonn.

Diagnosis. As for the genus. (The detailed description below is based on a composite of the material with individual specimens noted where appropriate. A reconstruction is presented in Text-fig. 1.)

Description. Body length *c.* 270 μm, width *c.* 110 μm. Body ovoid to barrel-shaped with appendages projecting forwards anteroventrally at an angle of *c.* 30 degrees (Pl. 1, fig. 1) such that the body is highest just behind the second

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EXPLANATION OF PLATE 1

Figs 1–7. *Cambropycnogon klausmuelleri* gen. et sp. nov. SEM micrographs of UB 800 (1–5) and UB 801 (6–7). 1, lateral view of complete specimen with good cuticle preservation, except for the missing rami of the post-cheliceral limbs (anterior to the right, compare with Pl. 3, fig. 8). 2, detailed view of right head region with the forehead slightly off-set and downward-pointing (on right side). 3, same region slightly more from ventral and posterior to show the basipodal gnathobases of the post-cheliceral limbs. 4, caudal outgrowths viewed from dorsolateral; annulation of the rami is not made by complete rings. 5, ventrolateral view of complete but coarsely preserved specimen covered by alien particles and spike-like crystallites. 6, lateral view, demonstrating the similarity in shape of the specimens, with the caudal rami always slightly diverging and held ventrocaudally at an angle of *c.* 45 degrees (cf. Pl. 1, fig. 1). 7, dorsolateral view somewhat from posterior. For abbreviations, see Table 1.

PLATE 1
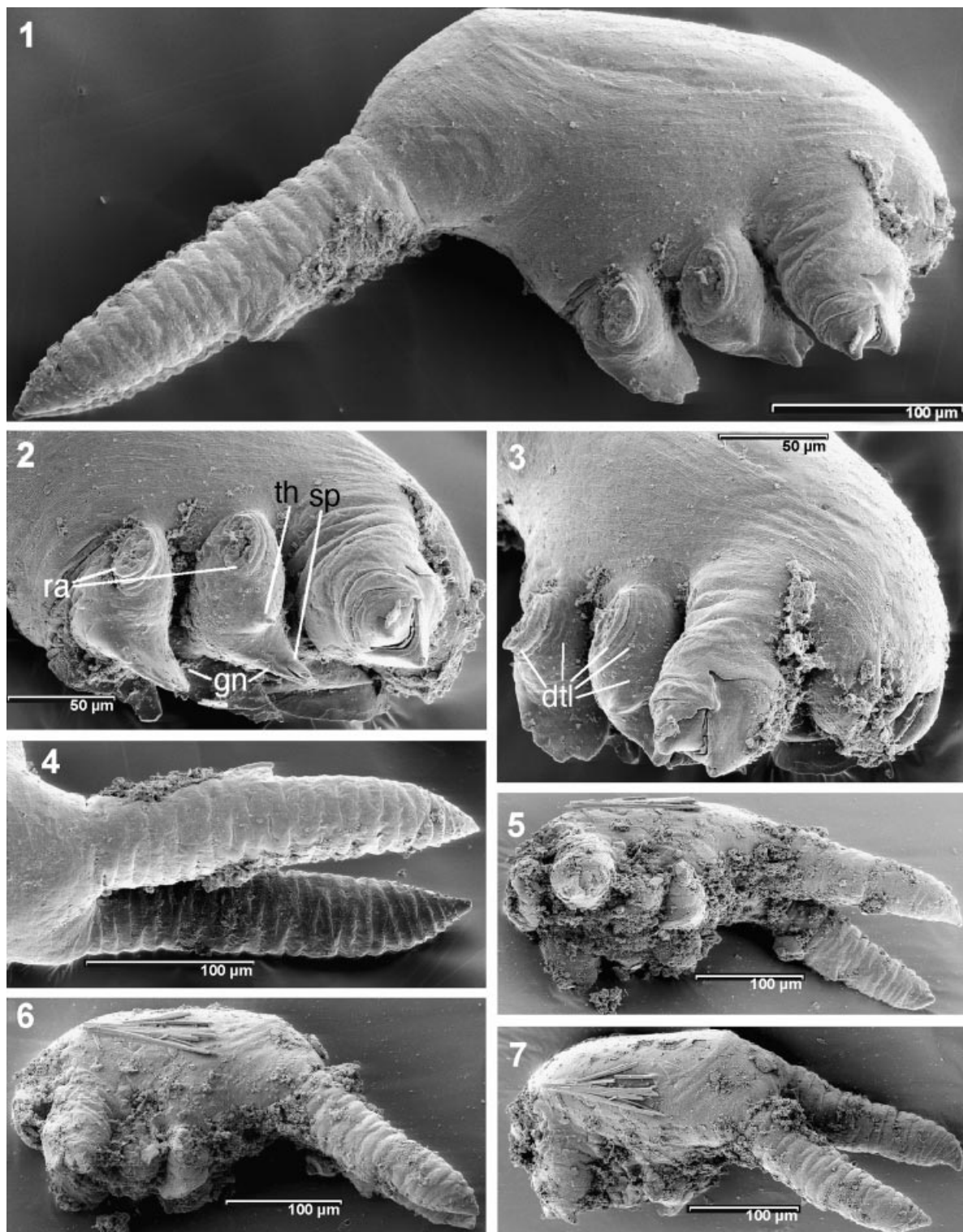
WALOSZEK and DUNLOP, Cambrian larval sea spider

TABLE 1. Abbreviations used in the text, plates and figures (see text for details).

a1?,	possible antenna (corresponding to first antenna or antennula of Crustacea)	gn,	gnathobase of basipod of post-cheliceral limbs
		hs,	head shield
capp,	caudal appendages or outgrowths	hyp,	bulge probably corresponding to hypostome
ch,	chelicera (distal part = chela with fixed and movable finger)	li,	lips around mouth opening
		m,	mouth
chk,	cheek (on forehead)	pchl,	post-cheliceral limb (with appendage number)
den,	dents (of gnathobase)	po,	pore
dtl,	denticle, short cuticular spinule (on various places)	ra,	ramus of post-cheliceral limb
fi fix,	fixed finger of chela	sp,	spine on basipod of first post-cheliceral limb
fi mov,	movable finger of chela (distal podomere of chelicera)	stl,	setula or bristle,
		th,	thorn behind gnathobase of basipod of first post-cheliceral limb
fo,	forehead region		
fld,	folds (above and behind the limbs)	tu,	tubercle on cheek region

post-cheliceral appendage pair. Body with distinct 'forehead' region (*c.* one-fifth of body length), which is slightly off-set and bent ventrally (e.g. Pl. 1, figs 1–3; Pl. 3, fig. 2; Text-figs 1A, C–D). Forehead bears the small circular mouth surrounded by three lips (Pl. 2, fig. 7; Pl. 4, fig. 2, especially evident in UB M804). An infolding of this region obscures the mouth in some specimens (Pl. 4, fig. 1). Slightly domed trapezoidal area in front of the mouth probably represents the hypostome (Pl. 2, fig. 7). Mouth area flanked by a cheek-like smooth area on either side, separated from the mouth area by a cleft, in which a spine-like but laterally compressed outgrowth nests. The spine emerges out of the cuticle slightly ventral of the mouth and extends dorsally almost parallel to the surface, being somewhat pointed distally. The grooves taper distolaterally on either side of the mouth area bordering the cheeks medially and dorsally (Pl. 2, fig. 7; Pl. 4, figs 1–2). The cheeks bear a tiny node or tubercle (Pl. 2, fig. 7; torn out to leave a hole in Pl. 4, fig. 2).

Sides of the body above the limbs with numerous delicate and slightly larger striations or folds (Pl. 1, figs 2–3; Pl. 4, fig. 3); folds much coarser in at least one specimen, UB M804 (Pl. 3, figs 2, 6), possibly because of shrinkage. These striations start distal to the first pair of limbs and run medially with a slight downward curvature, while caudally they surround the last pair of limbs, the caudal rami and the rear of the animal. Striation clearly demarcating off, and forming a belt around, the head shield. Possibly this is the area of the moulting suture. Head shield smooth (Pl. 1, fig. 1), slightly domed and lacking structures, e.g. projections that could be interpreted as the presence of eyes. No clear anterior demarcation between head shield and forehead (Pl. 4, fig. 1). Caudally, the striated cuticle forms two broad areas, one dorsal (Pl. 4, fig. 6), one ventral (Pl. 2, fig. 3), which converge towards, and are separated by the caudal outgrowths (see also Text-fig. 1B).

Main part of the body with three pairs of limbs. Anterior pair chelate, termed chelicerae herein, composed of a thick basal joint portion and two articles forming the fixed and movable part (fingers) of the chela (Pl. 1, fig. 3 and other figures). Chelicerae arising anterolaterally behind the weak transverse furrow between forehead and main part of the body and projecting ventrolaterally, diverging at an angle of 90–100 degrees. Limbs inserting close together leaving

EXPLANATION OF PLATE 2

Figs 1–7. *Cambropycnogon klausmuelleri* gen. et sp. nov. SEM micrographs of UB 802 (1–3), Wa118 (4) and UB 803 (5–7). 1, ventral view of specimen with the rami and margins of the gnathobases of the post-cheliceral limbs and the caudal rami broken off. 2, posterior pair of limbs from posteroventral to show the edges of fracture of the gnathobases. Note the fine wrinkling of the surface between the larger folds. 3, ventral view of the specimen slightly from posterior to show the gape of the limb pairs and the distinct forehead. Right and left sets of limbs approach or almost approach each other at the mid-line. 4, fragmented specimen from ventral, with the anterior body back to last pair of post-cheliceral limbs broken off. Body filled with compact crystalline matter except for a small empty space in the centre. Ramus of left second post-cheliceral limb preserved, somewhat collapsed; coarse matter covering right caudal outgrowth, both apparently shrunken. 5, ventral view of complete specimen, but also here coarse particles surround the limb bases (compare with Pl. 2, fig. 1 and Pl. 3, fig. 1). 6, enlarged view of left chelicera showing fixed and movable finger (compare with Pl. 5, fig. 2 and Pl. 5, fig. 4). 7, anterior view of forehead with central mouth opening, flanked by pointed, dorsally directed outgrowths nesting in depressions that fade out distoposteriorly (possibly the highly reduced pre-cheliceral antennae of the euarthropodan ground pattern = a1). Lateral cheeks with a small tubercle on their dorsal surface.

PLATE 2
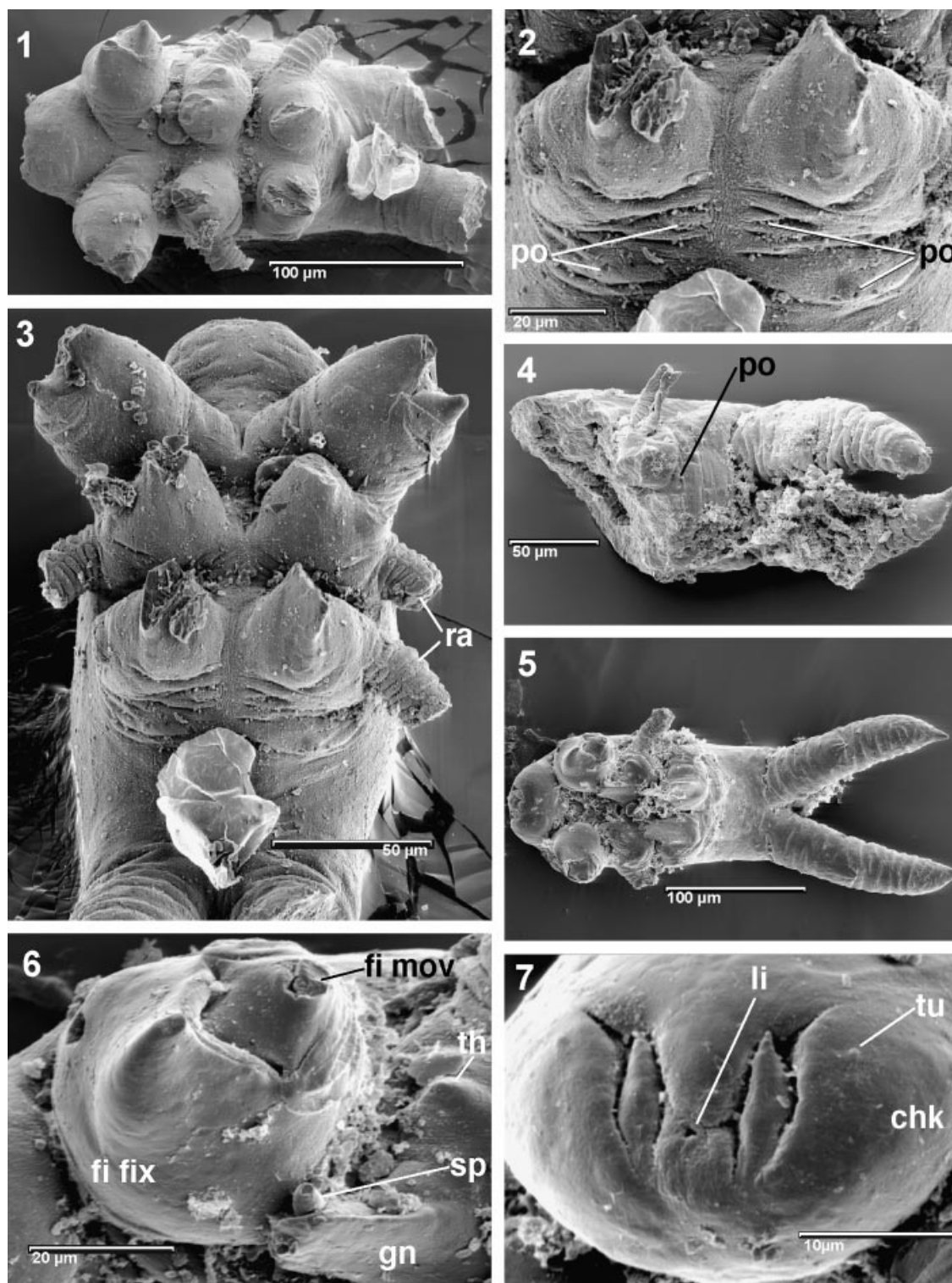
WALOSZEK and DUNLOP, Cambrian larval sea spider
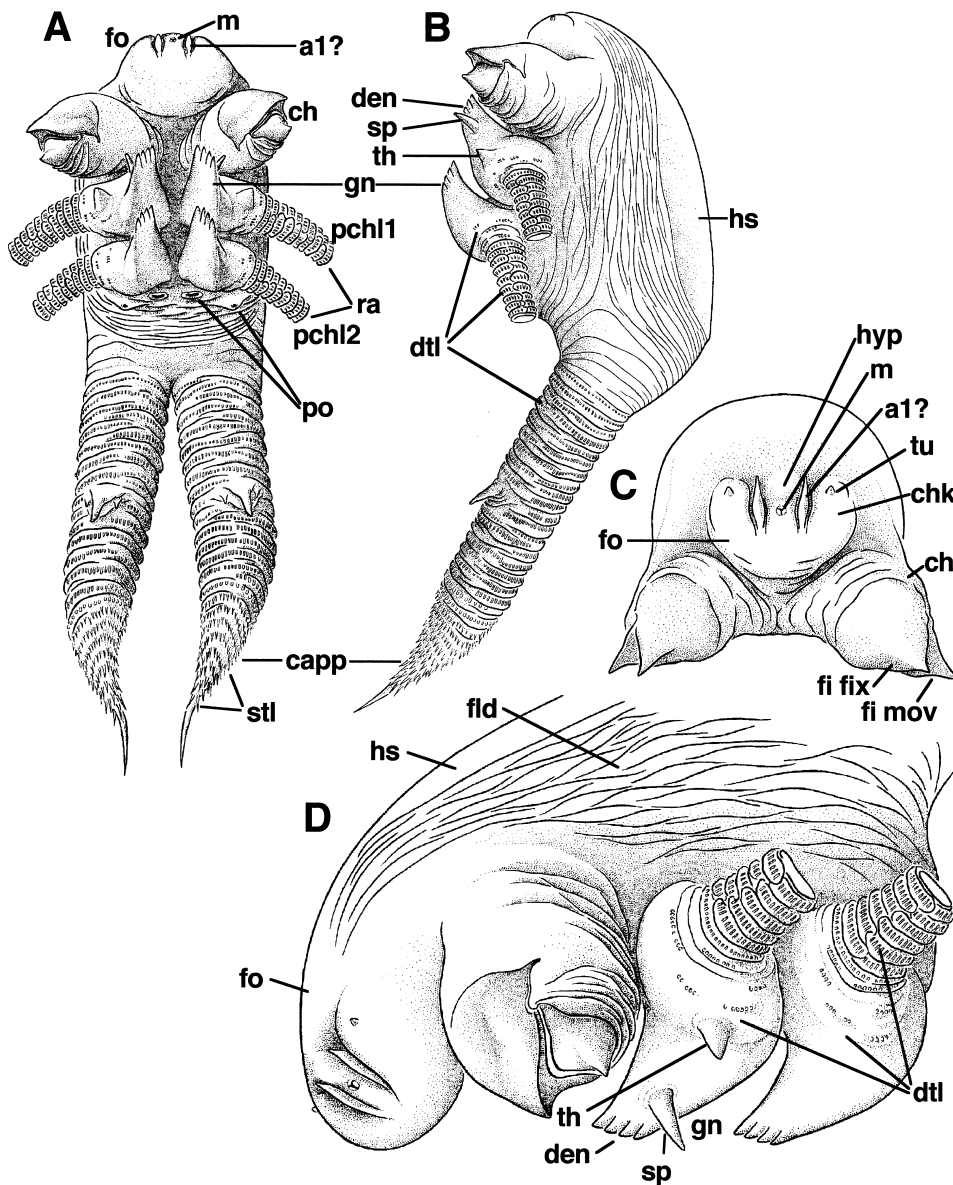
TEXT-FIG. 1. New reconstruction of *Cambropycnogon klausmuelleri* gen. et sp. nov., modified from Müller and Walossek (1986). A, ventral view. B, lateral view. C, anterior view. D, detailed view of left limbs from lateral side showing characteristic ornamentation of the cuticle between limbs and head shield. Rami of post-cheliceral limbs not completed. For abbreviations, see Table 1.

only a deep, narrow furrow between them (Pl. 2, fig. 2; Text-fig. 1C). Both chelicerae tilted some 45 degrees anteriorly and outwardly, resulting in an anteromedial position of the originally medial fixed fingers. Basal part, i.e. the joint area, membranous and slightly annulated (Pl. 1, fig. 3; Pl. 4, fig. 4), almost circular in outline and about one-quarter of the length of the limb. Joint continuing into the proximal article of the chela. Proximal article sub-conical, with its anteromedial edge drawn out to form the triangular, pointed 'fixed finger'. Opposite side of fixed finger slightly concave, its base forming the margin of a transversely extending (originally antero-posteriorly orientated),
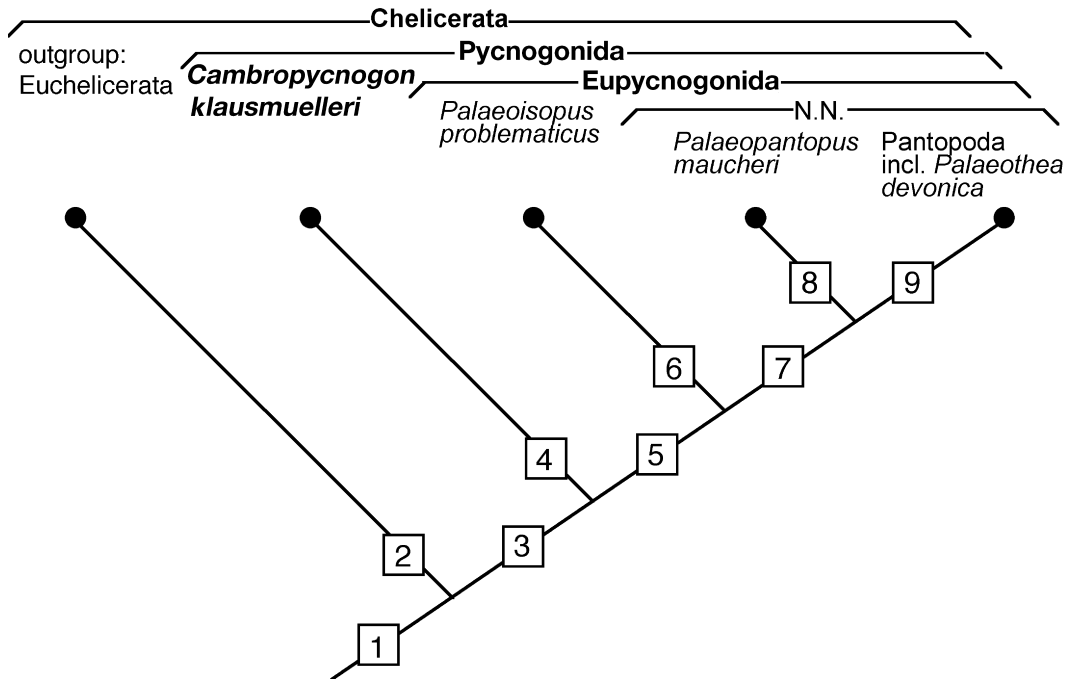
TEXT-FIG. 2. Suggested phylogenetic position of *Cambropycnogon klausmuelleri*, based in part on suggestions by Bergström *et al.* (1980, fig. 32) of the phylogeny within Pycnogonida. For apomorphies of the monophyla and species mentioned (boxes 1–9), see text.

spindle-shaped insertion area of the distal article. This article or podomere is the mobile 'free finger', articulating in the large joint against the fixed finger. Corresponding to the insertion area, the distal article is spindle-shaped at its base but becomes subtriangular and thins out distally (tip broken off in all specimens; Pl. 2, fig. 6; Pl. 3, fig. 4). Length of the two fingers similar. Both fingers of chela may have acted together like pincers. Cuticle around base of free finger highly folded allowing free movement within its bicondylic hinge (pivots recognizable on outer side of proximal article; see Pl. 3, fig. 4). Chela short and stubby in appearance, but the whole chelicera is rather long owing to its large proximal body-limb joint.

The two post-cheliceral limbs are homeomorphic, differing only in minor details of the gnathobase dentition and the presence of a spine and a thorn in the anterior limb. Limbs indistinctly articulated with the body (reduced mobility?), insertion areas oval, with their longer axis in an almost mediolateral orientation (Pl. 2, fig. 3). Thus these limbs appear smaller than the chelicerae in lateral aspect (Pl. 1, figs 1–3). Right and left limbs approaching each other at their bases, similar to the chelicerae, with no sternites or other ventral median structures developed between them. Both limbs comprising only the basipod and a single ramus (e.g. Pl. 3, fig. 3). Basipods with a plate-like gnathobasic extension medially, which is turned sharply anterodistally and ends in a sharply defined dentate rim (dents not well preserved). The gnathobasic plates are tilted laterally or outwardly so that the mesial sides of the basipods diverge at a similar angle as the chelicerae (Pl. 2, figs 1–3; Pl. 3 figs 1–3). Thus, the gnathobases do not oppose each other, implying that they may not have masticated food but were simply evolutionary remnants.

On the anterior post-cheliceral limb, a blunt spine, seemingly oval in cross-section, arises immediately behind (outwards from) the gnathobase pointing slightly more distally than the denticles of the gnathic edge (Pl. 1, fig. 2; Pl. 2, fig. 6; see also Text-fig. 1D). A corresponding spine is lacking on posterior basipod. Furthermore, only the first post-cheliceral limb bears a thorn-like protrusion on its distal surface between gnathobase and ramus (Pl. 1, fig. 1; Pl. 3, figs 3, 7; Text-fig. 1D). The single ramus (distally broken off in all specimens; Pl. 1, figs 2–3; Pl. 2, figs 3–5; Pl. 3, figs 1–3, 5–6) inserts laterally on the basipod in both limb pairs, close to the body wall. Ramus oval to circular in cross-section, not divided into podomeres, weakly off-set from the basipod and with distinct semi-annular folds more distally. Though appearing ring-like, the folds do not encircle the entire ramus (e.g. Pl. 3, fig. 5); instead there is a clear division

into an anterior surface with fewer folds and a posterior surface with more folds, implying that the ramus was more flexible in the posterior direction. Ramus ornamented with bands of raised denticles (originally tiny spiky bristles, less than 1 μm thick) (Pl. 3, fig. 5). This ornament continues more sparsely onto the distal surface of the basipod (Pl. 3, fig. 5), and can also be seen on the inner surface of the gnathic plate (Pl. 3, fig. 7). Similar ornament occurs, on various body parts, widely in crustaceans, particularly in early larvae, both Recent and fossil forms (e.g. Müller & Walossek 1988*b* for *Bredocaris admirabilis*, their pl. 4, figs 3, 5–6; pl. 6, fig. 10; pl. 7, fig. 5; pl. 8, fig. 10).

In profile, the body surface behind the last pair of post-cheliceral limbs steeply inclines dorsally, almost in continuation with the rear of the basipod of these limbs (Pl. 1, fig. 1; Pl. 3, figs 2, 8) to turn parallel to the main axis again thereafter. Two pairs of pores open on the ventral surface of the body in this region (Pl. 2, figs 2, 4; Pl. 3, fig. 3). Anterior pair comprises a slit-like pore with thick margins opening close to the ventral midline directly behind the basipods of the second post-cheliceral limbs. Posterior pair smaller and more widely spaced with a somewhat circular opening on a slightly raised tubercle. Cuticle in this area distinctly folded in most specimens studied.

The caudal region of the body forms an angle of approximately 135 degrees relative to the plane of the head shield in lateral view (Pl. 1, fig. 1; Text-fig. 1B). The posterior end of the body therefore tapers slightly towards the bases of the caudal outgrowths (Pl. 1, figs 4, 7; Pl. 2, fig. 5; Pl. 3, fig. 1). Cuticle between head shield and bases of the caudal outgrowths striated or folded as above the limbs along the sides of the body, but otherwise featureless. At the posterior end two specimens, UB M800 (Pl. 4, fig. 6) and Wa118 (detail not figured), have a small, rounded, knob-like structure located in a depression at the base between the caudal rami. This may be a taphonomic feature but, if genuine, it could also indicate the anal region, representing either a faecal pellet at the anal opening, an anal tubercle and/or the developing tail at the posterior end of the animal. Caudal outgrowths or rami projecting posteroventrally at an angle of about 35–50 degrees relative to the body (which we suspect is their original position because there are no folds suggesting artificial tilting), and are thus orientated in the same plane as the dorsal cuticle behind the head shield (Pl. 1, figs 1, 4–7; Pl. 3, figs 2, 8). Rami diverging from each other at an angle of 35–45 degrees. Rami almost as long as the body and rod-shaped in the first four-fifths of their length. Distal end tapered and curved slightly towards the midline (Pl. 1, figs 4, 6; Pl. 2, figs 4–5). Rami pseudo-annulated, with the folds not forming a complete circle around the ramus, but more or less encircling the ramus, sometimes ending blindly or diverging in a Y-shaped split into two folds (Pl. 4, fig. 7). Ridges with ornament of a row of small denticles (Pl. 4, figs 5, 7), similar to those on the rami described above, but becoming longer posteriorly to form fine bristles or setulae (Pl. 4, figs 5, 7; tentative reconstruction of setulation in Pl. 4, fig. 8 and Text-fig. 1A–B). As on other areas of the cuticle, the surface of the ridges show delicate wrinkles; this does not seem to be a taphonomic artefact but a cuticular substructure (compare Pl. 4, fig. 5 with Pl. 3 fig. 5 and Pl. 4, figs 2–3). Ventrally each ramus bears a lobe approximately one-third of the way up along its length, consisting of a flattened, semicircular structure with a caudally directed spine-like protrusion (e.g. Pl. 1, fig. 4; Pl. 2, fig. 5; Pl. 3, figs 1–2). Distally and more inwardly on the rami, the surface is slightly smoother and carries longer setulae. These are thicker than the more proximal, denticle-like ones and are arranged in rows or a spiral around the tip of the ramus, which fades out in a terminal seta or spine (Pl. 4, figs 5, 7; broken off in all specimens).

Remarks. Among the known arthropods from the Swedish 'Orsten' and similar material yielding such small, secondarily phosphatised animals, there is nothing even remotely similar to *Cambropycnogon klausmuelleri*. Only the slender limbs of the ovoid larva C in Müller and Walossek (1986, figs 5–7) bear some resemblance to the caudal outgrows of *C. klausmuelleri*. Both are finely annulated, and in both taxa

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EXPLANATION OF PLATE 3

Figs 1–8. *Cambropycnogon klausmuelleri* gen. et sp. nov. SEM micrographs of UB 804 (1–7) and UB 805 (8). 1, ventral view of complete specimen, some coarse crystalline matter disguising part of the forehead (right side). Ramus of right anterior post-cheliceral limb partly preserved. 2, ventrolateral view, showing the protruding forehead and the cuticular furrows around the body dorsal to and behind the limbs, which are coarser in this specimen than in most others. 3, ventral view of limb region, slightly from posterolateral to view the gaping facing basipodal surfaces of the limbs. 4, detailed view of the tip of the chela with the movable 'finger' = distal podomere of the chelicera, embedded in a pliable, ample membrane. 5, enlarged view of well-preserved ramus, with fine cuticular folds and rows of minute denticles on the larger ramal folds and on the basipods of limbs. 6, close-up of surface folds dorsal to and behind last limbs (compare with Pl. 4, fig. 3). Fine denticle rows on the folds of the caudal outgrowths (right side). 7, close-up of gnathal surfaces of the basipods of the post-cheliceral limbs, which are angled 90 degrees forward and some 30 degrees outwards. 8, lateral view of complete specimen, showing the weakly defined shield margins (compare with Pl. 1, fig. 1). Profile sharply bending ventrally at posterior edge of head shield (arrowed).

PLATE 3
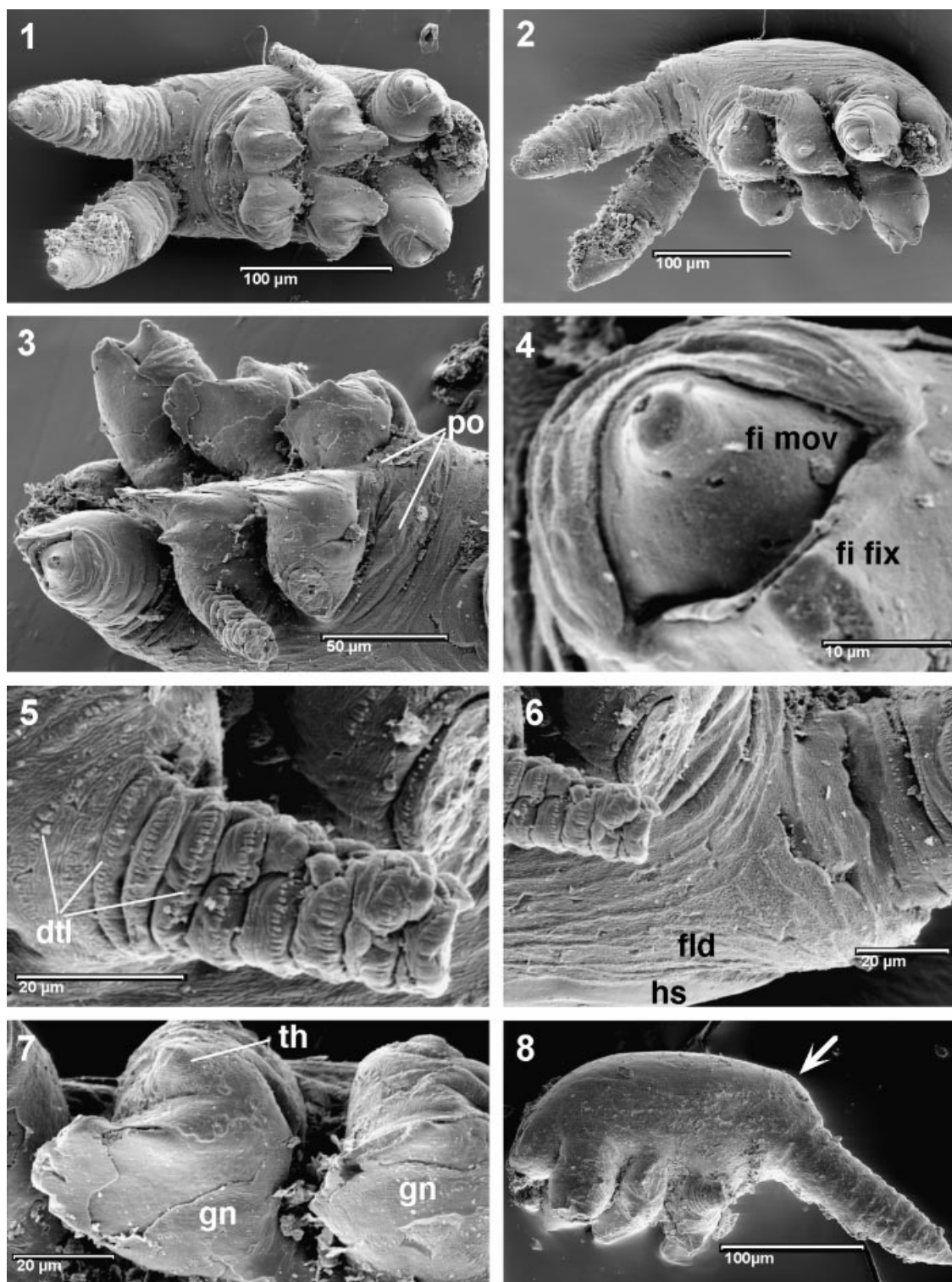
WALOSZEK and DUNLOP, Cambrian larval sea spider

the annuli are adorned with fine spinules or denticles. Moreover, both the rami of *C. klausmuelleri* and the limbs of larva C have a pointed and distally oriented median outgrowth or lobe. However, this is the only comparable feature between the chelicerae-bearing *C. klausmuelleri* and the peculiar, obviously non-feeding larva C (no mouth, no anus, body length *c*. 120 µm), the latter having five pairs of very slender limbs, which are clearly differentiated into uniramous antennulae followed by biramous limbs. In larva C the lobes are clearly sockets of hirsute setae, present on the antennulae, while on limbs 2–4 the seta inserts clearly on the median side of the endopods, and is the only mediodistal structure in limb 5, where only an exopod is clearly defined by its seta-bearing annuli (Müller and Walossek 1986, fig. 6). Furthermore, the lobes of the limbs of larva C insert in the distal third or further distally on the limbs, while that on the caudal outgrowths of *C. klausmuelleri* inserts at less than one-half of the length of the outgrowth.

With regard to the larvae of other Arthropoda, *Cambropycnogon klausmuelleri* resembles only the early semaphoronts, the protonymph and other early stages, of Pantopoda in both gross and detailed morphology. We interpret this as demonstrating a relationship between this fossil and the Pycnogonida, discussed in more detail below within the context of the higher systematics and phylogenetic position of the Pycnogonida.

DISCUSSION

The relationships of the Pycnogonida within the Arthropoda have been debated ever since these animals were first described (see Dohrn 1881 for a comprehensive review of older ideas). These hypotheses generally fall into one of three alternatives: (1) Pycnogonida belong to, or are related to, Chelicerata, generally as the sister group of all other chelicerates (e.g. Wheeler and Hayashi 1998); (2) they are modified crustaceans (e.g. Krøyer 1840); or (3) they are a 'unique' group unrelated to other arthropods (e.g. King 1973). Treating Pycnogonida as unique is unsustainable under phylogenetic systematics and authors supporting hypothesis 3 simply accumulated pycnogonid autapomorphies in a typological fashion as evidence against relationships with other groups. Unfortunately a number of acknowledged pycnogonid workers have long continued to regard these animals as an isolated arthropod taxon (e.g. Hedgpeth 1954).

Relationships with Crustacea (2) were based primarily on superficial comparisons between the pycnogonid protonymph and the crustacean nauplius larva (e.g. Richter 1912) and are not substantiated. Walossek and Müller (1997) recognised the protonymph as an extant example of the retention of the 'head larva' of the euarthropodan ground pattern. This larval type bore antennae and three homeomorphic pairs of post-antennular limbs, and has been retained in the stem line of Eucrustacea. By contrast the 'nauplius' is a special 'part-head larva' with only antennae (here termed antennulae) and two pairs of post-antennular limbs. This nauplius is autapomorphic for Eucrustacea as the crown group of the Crustacea (including all taxa with living derivatives; see particularly Walossek and Müller 1990; Walossek 1999). Other similarities between pycnogonids and crustaceans, such as anameric development, are simply symplesiomorphic for Euarthropoda, while characters which include the Pycnogonida within Chelicerata (see below), as well as the various crustacean autapomorphies (Walossek 1999), preclude any relationship to Crustacea. To avoid too much cross-referencing and circular reasoning, our discussion follows the scheme

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EXPLANATION OF PLATE 4

Figs 1–8. *Cambropycnogon klausmuelleri* gen. et sp. nov. SEM micrographs of details. 1, forehead region of UB 802, anterior mouth area slightly squeezed inwards (coarse cuticular preservation). 2, enlarged view of same area of UB 804. Frontal outgrowths partly lacking their cuticular surface, which is delicately wrinkled and thus clearly visible. Mouth surrounded by three minute lip-like folds (compare with Pl. 2, fig. 7). 3, finely wrinkled surface of UB 800 between limbs and head shield margin. 4, stretched chelicera with fixed and movable finger surrounded by pliable arthrodial membrane. 5, tip of caudal outgrowth of UB 800, with short denticles merging into longer setulae arranged in a spiral pattern. Surface finely wrinkled between the larger folds. Tip of outgrowth continuing into spine or seta (lower left). 6, posterior end of body of UB 800 from posterodorsal, with granular matter disguising the area where the anus might be located. 7–8, caudal rami of UB 800: 7, original with bristles and the terminal seta all broken away distally; 8, with ornamentation added digitally to show the likely original hairiness.

PLATE 4
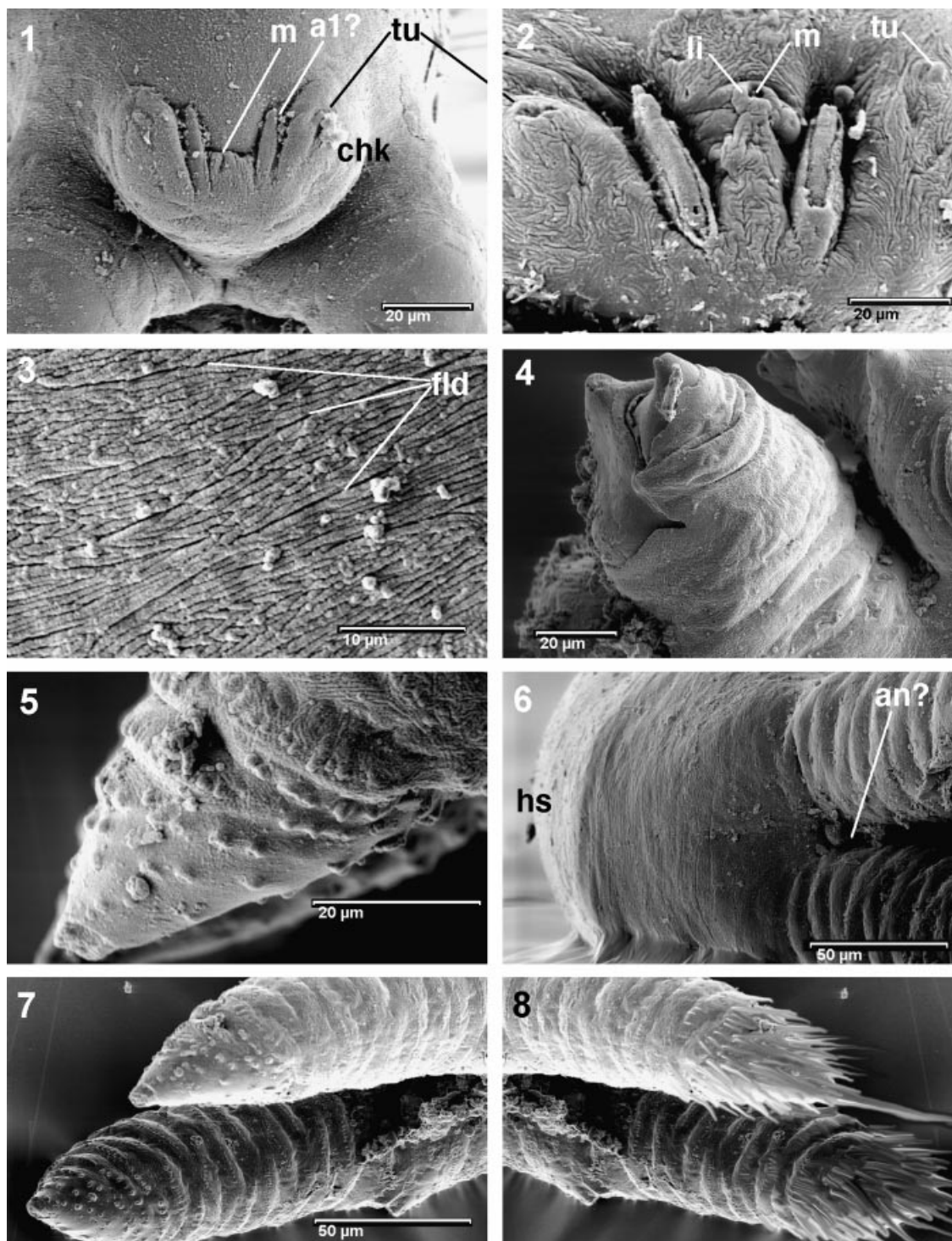
WALOSZEK and DUNLOP, Cambrian larval sea spider

proposed in Text-figure 2, starting with the Chelicerata and ending with the placement of the new fossil rather than vice-versa.

Pycnogonida and Chelicerata

Some early descriptions (e.g. Latreille 1810) include Pycnogonida among the arachnids and many modern textbooks, although providing little evidence for this assumption, classify Pycnogonida (or Pantopoda) either as a class of the Chelicerata or as their sister group. Walossek and Müller (1997) included Pantopoda (= Pycnogonida in the above sense) in the Chelicerata, as the sister group to all other chelicerates. The latter clade was united on the autapomorphy of 'no more head larva' (see above) as the initial stage of the (anameric) larva series. Absence of 'head larvae' is characteristic for arachnids and xiphosurids which, unlike pycnogonids, hatch at much more advanced segmental stages which generally resemble small adults. Wheeler and Hayashi (1998) similarly included Pycnogonida within the Chelicerata, recognising a (Pycnogonida + Euchelicerata) relationship, while Munilla (1999) suggested a (Pycnogonida + Chelicerata) clade for which he used Schram's (1978) name Cheliceriformes. Thus, most recent studies of arthropod relationships have supported chelicerate affinities for pycnogonids, although Giribet and Ribera (2000) did note that under some parameters, and especially for some (molecular) sequence data, the position of Pycnogonida can be unstable and they can emerge in a relatively basal position among the arthropods. However, morphological synapomorphies between Pycnogonida and any non-chelicerate group have not been identified (see also above).

Autapomorphies of Chelicerata. Wheeler and Hayashi (1998) based their hypothesis of the monophyly of Chelicerata (including pycnogonids) on the following autapomorphies: (1) antennae absent; (2) first (developed) appendage chelate; (3) tagmosis into prosoma and opisthosoma; (4) a poorly developed carapace pleural margin, and (5) a telotarsus with three tarsomeres. Munilla (1999) also recognised the tagmosis and chelicerae characters, adding two further autapomorphies: (1) modification of the post-cheliceral limb pair to pedipalps, and (2) four pairs of walking legs. These potential autapomorphies are considered in more detail below.

The presence of antenna-like structures in our fossil (Pl. 2, fig. 7) suggests that loss of antennae does not characterise the ground pattern of Chelicerata (Wheeler and Hayashi's autapomorphy 1), but occurred convergently in at least two chelicerate clades (see below for details). Yet, the reduction of the antennae to vestigial elements, as demonstrated by our fossil, may still hold for the ground pattern of Chelicerata. Chelate chelicerae (Wheeler and Hayashi's autapomorphy 2) were already central to Heymons' (1901) original classification and diagnosis of Chelicerata. Even those Pantopoda lacking chelicerae as adults retain this character in the earliest semaphoront, the protonymph stage. However, the term chelifore has been widely used for Pycnogonida specifically to avoid implying homology with chelicerae (e.g. King 1973). Nevertheless, Winter (1980) clearly demonstrated the homology between the chelicerae of Chelicerata and the chelifores of Pycnogonida based on patterns of innervation in both groups from a 'Chelicerenneuromer'. This neuromer is equivalent to the tritocerebrum (Winter 1980); thus chelicerae are equivalent to the second antennae (a2) of Crustacea (see also below). Chelate second head appendages are not developed in the ground patterns of any other Euarthropoda. Raptorial or even sub-chelate second appendages (similar to araneids) may occur in special in-group crustacean taxa (e.g. certain copepods or branchiurans), but there clearly represent convergently developed structures, since they originate from the 'normal' biramous crustacean second antennae. True chelae never developed in these a2 limbs of any other arthropods. Such structures only occur in certain post-cephalic limbs of particular decapod crustaceans. Within Chelicerata, chelae occur in the post-cheliceral limbs of extant Xiphosura (some Palaeozoic forms apparently lacked terminal chelae; Stürmer and Bergström 1981) and among arachnids in the first post-cheliceral limb, or pedipalp, of Scorpiones, Pseudoscorpiones and Ricinulei. Munilla's (1999) character of transformation of this first post-cheliceral limb to a pedipalp (Munilla's autapomorphy 1) cannot be accepted since this appendage remains unmodified in Xiphosura and most Eurypterida (= unmodified in the ground pattern).

The segmental state of the head region and the prosoma-opisthosoma boundary in Pycnogonida remain

uncertain. Winter (1980) stated that the 'prosoma' in Pycnogonida was not equivalent to the prosoma in other Chelicerata, but gave no clear evidence for this. If the chelicerae are a1, adult Pycnogonida have retained the euarthropodan cephalon (segments I–IV) plus a series of trunk segments. However, in our preferred interpretation (see below) in which chelicerae are a2, adult Pycnogonida have a cephalosoma (segments I–V) in which the first trunk segment is fused with the cephalon to form a discrete tagma, again with additional trunk segments. Pycnogonida lack the distinctly developed head shield, i.e. the shield with marginal extensions from the body proper, as seen in Euchelicerata, and this can be interpreted as a pycnogonid autapomorphy (see below). Wheeler and Hayashi (1998) coded the absence of a broad head shield (or 'carapace') as apomorphic and this character emerged in their analysis as an autapomorphy for Chelicerata (their autapomorphy 4), with a reversal to the plesiomorphic, broad head shield seen in Xiphosura. However, this contradicts the hypothesis, based on the large number of arthropod fossils and Recent Crustacea, that a distinctive shield with marginal extensions (irrespective of its segmental state for this particular argument here) belongs to the ground pattern of, at least, Euarthropoda and Crustacea. If Wheeler and Hayashi are correct in that the absence of tergopleurae-originating marginal shield extensions is apomorphic for Chelicerata, this implies that the head shield should have evolved many times in the euarthropodan lineage, a scenario we find unlikely.

An unequivocal prosomal boundary cannot be identified in Pycnogonida. Therefore, a distinct prosoma-opisthosoma tagmosis (Wheeler and Hayashi's autapomorphy 3) can be interpreted only as autapomorphic for Euchelicerata. It has long been recognised that, compared to extant euchelicerates, Pycnogonida have one leg pair too many in their 'prosoma', if the cephalosoma and limb-bearing trunk are considered as such. However, this interpretation assumes the opisthosoma of Pycnogonida to be represented only by the small tail end seen in living forms. Alternatively, if the post-cheliceral limbs are simply counted sequentially, then the last leg of Pycnogonida would be equivalent to the first opisthosomal appendage in Euchelicerata (see also Bullough 1958; Stürmer and Bergström 1981). Interestingly, this first opisthosomal appendage is lost in most arachnids, although may be retained in scorpions (Dunlop and Braddy 2001). It is clearly retained in other euchelicerates, but not as biramous limbs as the more posterior ones, but in a modified form as the metastoma of Eurypterida and the chilaria of extant Xiphosura, while there is evidence that at least some stem group Xiphosura had, like Pycnogonida, chelicerae plus *six* pairs of fully-developed appendages (Stürmer and Bergström 1981), i.e. a leg on opisthosomal segment 1. This latter observation even led these authors to suggest that the first opisthosomal, or pre-genital, segment should actually be included in the prosoma. Scholl (1977) independently reached a similar conclusion based on embryological data. The prosoma in its traditional sense can, however, be recognised in Euchelicerata as the segments down to, but not including, opisthosomal segment 1.

Accordingly, this segment is an unmodified part of the trunk in Pycnogonida (a plesiomorphy) and its limb is well-developed (another plesiomorphy). In Euchelicerata the segment is shortened or modified (an autapomorphy) into structures such as the microtergite of xiphosurans or the spider pedicel; and its limbs may either be modified, reduced or lost (Shultz 1990). This extreme modification provides no evidence about the ramal status, and uniramy in the limbs of opisthosomal segment 1 may well have developed more than once rather than representing an autapomorphy of Chelicerata as a whole.

In our model, the segmentation and appendages of Pycnogonida and Euchelicerata remain comparable, but simply treating four pairs of walking legs (Munilla's autapomorphy 2) as an autapomorphy of Chelicerata is unsustainable since different groups have apparently developed different limbs as their primary locomotory appendages: IV–VII in arachnids (the so-called walking legs) and V–VIII in pycnogonids (post-larval-head limbs to first opisthosomal limb; see above). As noted above, modification of limb III into a palp occurs in pycnogonids and arachnids, but not in xiphosurans and eurypterids. Based on the Devonian fossil *Palaeoisopus problematicus* Broili, 1928, the tail of Pycnogonida would, in this model, originally have included at least a proximal limb-bearing segment plus four apodous segments and a conical telson portion (= pygidium), possibly carrying the anus. In this model Recent Pantopoda retain the well-developed first opisthosomal segment with appendages, but advanced from the *P. problematicus* condition by compacting the limbless part of the opisthosoma into a rod-shaped portion with a terminal anus, rather than having one leg too many and a small, caudal, rudimentary opisthosoma. Remarkably,

various pantopods have their last limb-bearing segment clearly set off and the limb sockets more posteriorly oriented.

Schram and Hedgpeth (1978) recognised two tarsomeres in the legs of Pycnogonida plus a terminal segment which they called a pretarsus. By contrast, the terminal podomere in arachnid legs is usually called the 'claws' (although it is not a chelate structure), or ungules, and three tarsomeres plus these 'claws' (Wheeler and Hayashi's autapomorphy 5) are therefore an ingroup arachnid apomorphy (e.g. Shultz 1990). Three tarsomeres in the tarsus are neither present in the ground pattern of Pycnogonida nor present in any ingroup pycnogonid taxon (see also Munilla 1999, fig. 5) and are rejected as an autapomorphy of Chelicerata.

In both Pycnogonida and Euchelicerata the chelicerae lack exopods, a further autapomorphy of Chelicerata, while there is a trend towards losing only the exopods on the post-cheliceral prosomal limbs. Exopods are retained as the flabellum of the last leg of extant Xiphosura (see Walossek and Müller 1997) and perhaps as the finger-like Claparède organ of Acari (possibly homologous with the lateral organ of some other arachnids), which derives from the base of the second pair of walking legs (Thomas and Telford 1999). Further exopods are retained, primarily as flat opercula with numerous lamellae serving as respiratory organs, in all opisthosomal limbs behind the so-called chilaria segment in the euchelicerate lineage.

In conclusion, chelate second head appendages, made up of only a few articles (no more than 3–4) and lacking exopods, remain, at present, the most convincing autapomorphy in the ground pattern of Chelicerata (character box 1 in Text-fig. 2) and, hence, a synapomorphy for (Pycnogonida + Euchelicerata). Additional explicit synapomorphies for Pycnogonida and Euchelicerata have not been identified, although King (1973) hinted at similarities in embryogenesis and Miyazaki and Makioka (1989, 1990, 1991) and Ikuta and Makioka (1999) noted a chelicerate-like ovarian structure and oogenesis in Pycnogonida.

Autapomorphies and relationships of Euchelicerata. The monophyly of Euchelicerata is supported by three autapomorphies (character box 2 in Text-fig. 2): (1) loss of the 'head larva' *sensu* Walossek and Müller (1990) (see above); (2) reduction of the four median eyes to two: xiphosurans have two ocelli, plus two vestigial eyes indicating that the four eyes of Pycnogonida are also the chelicerate ground pattern (see also Weygoldt and Paulus 1979); (3) a clear tagmosis into a prosoma, covered by a head shield and bearing six pairs of limbs, and an opisthosoma starting with the modified pre-genital segment and having 13 or fewer segments plus a conical telson with a subterminal ventral anus in the ground pattern. In the ground pattern the retention of exopods with flattened lamellar marginal spines, serving as respiratory organs on the opisthosomal legs, represents a symplesiomorphy (see below). The traditional division of Euchelicerata into (Merostomata + Arachnida) has long been criticised as ecological, rather than phylogenetic (e.g. Kraus 1976). Most recent authors support a phylogeny of the Euchelicerata of the form (Xiphosura (Eurypterida + Arachnida)) (e.g. Weygoldt and Paulus 1979; Shultz 1990, and apomorphies therein). Alternative views centre on the position of the scorpions (see Dunlop and Braddy 2001 for a discussion of characters and additional references) which have been interpreted as (1) basal arachnids, (2) derived arachnids, or (3) a sister group to eurypterids and/or xiphosurans. In the last of these Arachnida, in the traditional sense, would be paraphyletic.

Systematics of Pycnogonida

The names Pycnogonida Latreille, 1810, Podosomata Leach, 1815 and Pantopoda Gerstaecker, 1863 have long been a source of confusion, since they originally represented alternatives (= synonyms) for the same taxon. Of these, Podosomata has rarely been used, but Pycnogonida is found primarily in the English and French literature while Pantopoda has found broad acceptance in German and, to some extent, Russian texts. Hedgpeth (1955, 1956) proposed Pycnogonida for a subphylum consisting of two orders: Pantopoda, which he restricted to Recent taxa, and Palaeopantopoda Broili, 1930, erected exclusively for a single Lower Devonian species, *Palaeopantopus maucheri* Broili, 1929. Palaeopantopoda was principally 'defined' by having a tail of two or three 'abdominal' segments, as compared to the small, undivided

tubercle forming the tail in extant Pantopoda. In terms of phylogenetic systematics, only the Pantopoda were based on an apomorphy, whereas the Palaeopantopoda are therefore characterised by the plesio-morphic character state of the tail (i.e. part of the trunk) being still segmented. The group may, therefore, be a paraphylum.

Hedgpeth (1978) retained his division of Pycnogonida into Palaeopantopoda and Pantopoda and accepted that the Lower Devonian *Palaeisopus problematicus*, which has even more tail segments, was a pycnogonid too. He therefore divided Palaeopantopoda into two new suborders. Palaeopantopodina Hedgpeth, 1978 was erected to include *Palaeopantopus maucheri* and a Jurassic form, subsequently rejected as an obvious misidentified crustacean (Bergström *et al*. 1980). Palaeopantopodina is therefore another higher taxon based on a single species and was defined on a two- or three-segmented tail. Hedgpeth's second suborder, Palaeoisopodina Hedgpeth, 1978, was erected for the single species *Palaeoisopus problematicus* and defined on a five-segmented tail (again a plesiomorphy). Bergström *et al*. (1980) modified Hedgpeth's (1978) classification by raising Palaeoisopoda to even the rank of an order (still only embracing a single species), while recognising a further Hunsrück pycnogonid, *Palaeothea devonica* Bergström, Stürmer and Winter, 1980, as a Devonian representative of the Pantopoda (hitherto embracing only extant forms). This purely classificatory scheme, in which Pycnogonida comprises the three orders Palaeoisopoda (1 species), Palaeopantopoda (1 species) and Pantopoda, has been adopted by some authors (e.g. Arnaud and Bamber 1987; Munilla 1999). Yet, there is still a strong tendency to refer to sea spiders as either Pycnogonida or as Pantopoda along traditional linguistic lines rather than in the systematic context.

Pycnogonid ingroup relationships. Following this argument, Pycnogonida currently comprises the two Devonian species *Palaeisopus problematicus* (= Palaeoisopoda Hedgpeth, 1978) and *Palaeopantopus maucheri* (= Palaeopantopoda Broili, 1930) as derivatives of the stem line of the Devonian–Recent crown group, or Pantopoda *s.s.* Bergström *et al*. (1980), in proposing a relationship of the form (Palaeoisopoda + (Palaeopantopoda + Pantopoda)), recognised an evolutionary trend in the progressive reduction of the tail towards the crown group. Details of apomorphies can be found in Bergström *et al*. (1980) and Munilla (1999), and a slightly modified form of this relationship hypothesis is presented here in Text-figure 2 as set 3.

Monophyly of the Pycnogonida can be characterised by the unique development of a proboscis (in the adults). This tubular feeding structure, reported in all previous fossil (Bergström *et al*. 1980) and Recent taxa, is constructed from three longitudinal elements called antimeres which end distally in chitinous lips, forming a triradiate mouth. The proboscis, which is still absent in the earliest semaphoront, the protonymph, subsequently grows out progressively (e.g. Vilpoux 1999). Progressive reduction in size of all protonymphal limbs, i.e. the chelicerae and the two homeomorphic limbs, during development relative to the remaining limbs (which grow to form the large walking legs) holds for at least all Devonian–Recent pycnogonids and may serve as another autapomorphy in the ground pattern of Pycnogonida. The modification of the third larval appendage pair into ovigers may be another autapomorphy; reports of this character in the fossil taxa are less convincing but are well-documented for *Palaeisopus problematicus*.

Winter (1980) suggested that the cephalosoma bearing four pairs of appendages, i.e. chelicerae plus the next three limb pairs, is autapomorphic for Pycnogonida. However, this character is also present as the propeltidium of the divided head shield (or 'carapace') in arachnids such as Palpigradi, Solifugae and Schizomida. This even raises the possibility that: (1) this cephalosoma (= propeltidium) is part of the ground pattern for Chelicerata retained in pycnogonids and some arachnids; (2) a 'divided carapace' is not an apomorphy within Arachnida (see also Kraus 1976); and (3) fusion of the dorsal part of the trunk segments into a head shield covering the entire prosoma may have occurred more than once within Chelicerata.

A further possible pycnogonid autapomorphy is the complete lack of pleurotergites, or at least their margins, in the whole body, the plesiomorphic state of this character being present in other Chelicerata, at least basally, and in various outgroups such as trilobites, crustaceans or insects (in their tail region). The tubular design of Pycnogonida must also be mentioned as well as the extreme reduction of the tail to, at

most, four segments lacking limbs and a conical element, possibly the telson or pygidium, on which the anus opens in a ventral, subterminal position (Bergström *et al.* 1980; an anal position, which is plesiomorphic within Euarthropoda). A strongly developed eye tubercle is seen in extant Pantopoda and was described in *Palaeoisopus problematicus* by Bergström *et al.* (1980). This character may serve as another autapomorphy of Pycnogonida, although eyes are absent in the earliest semaphoronts of extant pantopods (Vilpoux 1999) and in our larval specimen.

Hou and Bergström (1997) have proposed the presence of specific lamellar spines along the margins of the exopods as a character supporting the monophyly of Lamellipedia, a taxon including trilobites, chelicerates and a number of 'trilobitomorph' groups. The alternative character state is rounded spine-like setae such as in crustaceans, yet the character state is uncertain since it remains unclear which one is plesiomorphic and part of the ground pattern of the common ancestor of these taxa (= stem species of Euarthropoda). Accordingly, this character should have been retained, as a plesiomorphy, in the post-chilarial opisthosomal limbs (and only there) in the stem species of the Chelicerata. These lamellar spines are retained in the exopods of the post-opercular opisthosomal limbs in the stem line of Euchelicerata and were modified (as a eucheliceriate autapomorphy) into plate-like gill lamellae as part of the trend towards flattening of the whole limbs (e.g. Walossek and Müller 1997, fig. 12.9). Uniramy of the trunk limbs with complete absence of any exopods and lamellar spines (they are not seen in *Palaeoisopus problematicus* despite it retaining more of the trunk or 'opisthosoma') must, therefore, be interpreted as an autapomorphy of the Pycnogonida.

Other distinctive pycnogonid characters of the internal anatomy and biology cannot be determined in the fossil taxa (including the Devonian pantopod), so remain putative autapomorphies of Recent Pantopoda (our Eupantopoda, see below). These characters include: (1) absence of excretory organs; (2) gonopores opening on the second limb podomere (typically in all legs in females and the third and fourth legs of males); and (3) cement glands in the chelicerae of the larvae (secondarily absent in some genera; King 1973). Egg-carrying behaviour in males was suggested as a further autapomorphy by Winter (1980).

Affinities and position of Cambropycnogon klausmuelleri

Following Müller and Walossek (1986, 1988*a*) the pair of chelate anterior head appendages made of only a few articles enables us to recognise *Cambropycnogon klausmuelleri* as a representative of the Chelicerata. The presence of an anus remains equivocal in the fossil (it is lacking in the pantopod protonymph), but lack of an anus is simply a consequence of being a non-feeding larval stage (as found in early larvae of many crustaceans of different taxa). At least one pair of pores has been identified in the pantopod protonymph in a similar position to the two pairs of pores in the caudal region behind the second post-cheliceral limb of the fossil (Pl. 2, fig. 2; see also Miyazaki and Suzuki 1997, fig. 2). During larval development of *Pycnogonum litorale*, more such pairs occur progressively with the addition of more legs (Vilpoux 1999 and pers. comm. 2001; Pl. 5, fig. 3). These structures may, therefore, represent pores possibly of the segmental glands presumed to have existed originally in all limb-bearing segments in the Euarthropoda. As such, these pores represent an interesting, but symplesiomorphic, detail in the fossil. In Recent Pantopoda, such as *P. litorale*, these pores later have the appearance of 'Wehrdrüsen' (Vilpoux, pers. comm. 2001), typical for this group. No detailed work has been carried out on these paired pores.

Of the other pantopod-like features noted by Müller and Walossek (1986, 1988*a*), anamorphic development starting with a larva of the 'head larva'-type is symplesiomorphic. However a head larva with chelicerae plus two pairs of homeomorphic limbs occurs exclusively in *Cambropycnogon klausmuelleri* and extant Pantopoda and, therefore, can serve as a further synapomorphy between these taxa and as support for the pycnogonid affinities for *C. klausmuelleri*. The caudal rami of *C. klausmuelleri* (Pl. 1, fig. 5) probably represent a developing pair of limbs. This would be consistent with the ontogeny of extant Pantopoda in which the post-protonymph instar develops a relatively large appendage in this position behind the head larva (Pl. 5, figs 4–5; see also Helfer and Schlottke 1935, fig. 138c–d). Accordingly, *C. klausmuelleri* may actually be at a slightly later developmental stage than the protonymph of extant pantopods. The absence of an even earlier stage, a 'head larva', may, thus, be either an autapomorphy of *C. klausmuelleri* or this stage has simply not been preserved.

We need to establish how much of the larval and ontogeny pattern is a specific part of the character set in the ground pattern of Pycnogonida or if it holds for Chelicerata too and, hence, is plesiomorphic. The finely folded posterolateral putative moulting suture around the weakly demarcated larval head shield might represent a synapomorphy of *Cambropycnogon klausmuelleri* and Pycnogonida, where it has been reported by Behrens (1984) for *Pycnogonum litorale*, but unpublished observations by Vilpoux and Waloszek are unable to confirm this observation for *P. litorale*. By contrast, xiphosurans and arachnids moult with an anterolateral suture. The apparently triradial mouth observed in *C. klausmuelleri* (Pl. 4, fig. 2) is also characteristic for pantopod protonymphs (e.g. Dohrn 1881, pl. 11), and is subsequently expressed in the triradial symmetry of the adult proboscis. However, this character may also be symplesiomorphic as radial to triradial mouths are seen in Tardigrada (e.g. Dewel and Dewel 1997) and larvae of representatives of the stem line of Eucrustacea [Walossek and Müller 1990, for *Henningsmoenicaris scutula* (Walossek and Müller, 1990)]. Even nematodes show triradiality of their mouth openings. In *C. klausmuelleri*, as in pantopod protonymphs, the head shield can be detected by a faint difference in the cuticular surface structure, but true margins are not developed. By contrast, in euchelicerates (including early semaphoronts) there is a clearly developed head shield with amply extending margins (best seen laterally), sometimes called the 'carapace' (for a discussion of head shield versus 'carapace', see Walossek 1993). Since the chelicerate affinities of *C. klausmuelleri* have been established on another character, this shared feature is seen as another synapomorphy of our fossil and Pycnogonida (our Eupycnogonida; see below).

More features in support of pycnogonid affinities of *Cambropycnogon klausmuelleri* are in the forehead and ventral details. In *C. klausmuelleri* and in early larvae of Pantopoda there is a distinct anteroventral projection, a forehead, bearing the small mouth flanked or immediately followed by the pair of chelicerae, which are massive in proportion to the rest of the body (Pl. 5, fig. 2). By contrast, the forehead does not protrude in the anterior region of the body in known euchelicerate larvae, and this morphology, regardless of the fact that these larvae are later semaphoronts, must also be assumed for the ground pattern of Chelicerata and Euarthropoda. Furthermore, the two post-cheliceral limb pairs are not divided into a clear series of podomeres in *C. klausmuelleri* and in early larvae of pantopods, in contrast to known euchelicerate larvae (and presumably in the ground pattern of Euarthropoda), but form a holdfast-like structure in pycnogonids consisting of a basal article and a distal pointed article in Recent larvae (Pl. 5, figs 1–2) and a basal portion and a ramus in the fossil (Pl. 3, figs 1–3). It remains uncertain if this ramus represents a remnant of the endopod or exopod. This limb morphology points towards an ectoparasitic mode of life of the known semaphoront of *C. klausmuelleri*, something characteristic of larval Pantopoda. Given that known Euchelicerata and their larvae are mostly active predators throughout their life (with parasitism restricted to certain in-group Acari), this mode of life appears unlikely for either the ground pattern of Chelicerata or their earliest semaphoronts.

The relationships of *Cambropycnogon klausmuelleri* with Pycnogonida are thus supported by the following synapomorphies: (1) early larva with chelicerae plus two homeomorphic pairs of limbs; (2) massive chelicerae in the earliest larval stages; (3) a weakly defined head shield; (4) a mouth borne on a distinct forehead region in the larva; and (5) two post-cheliceral limbs not divided into a podomere series, but modified to a holdfast, possibly for an ectoparasitic mode of life (character box 3 in Text-fig. 2).

On the other hand, the possession of gnathobases and pre-cheliceral appendages, possibly homologous to euarthropodan antennae, in *Cambropycnogon klausmuelleri* are symplesiomorphies that distinguish it from all other Pycnogonida (our Eupycnogonida; see below). Gnathic-edged basipods on post-antennular appendages are symplesiomorphic, retained from the ground pattern of Euarthropoda, because they occur in various early arthropods, such as trilobites, and they are retained in several euchelicerate groups (e.g. Eurypterida, Xiphosura); and in various arachnids. At least xiphosuran limbs have straight gnathic basipods, as in the ground pattern of Euarthropoda. Devonian and Recent Pycnogonida seem to lack both gnathobases and a1 (i.e. antennae), though this is known only for adult fossils.

Unfortunately we lack later developmental stages from the Cambrian form, and so cannot test the presence of characters appearing in later instars of *Cambropycnogon klausmuelleri* such as ovigers and (perhaps) an eye tubercle. Putative autapomorphies of *C. klausmuelleri* are the specific ornament on the rami of the post-cheliceral limbs (Pl. 3, fig. 5) and the lack of sternites between the head limbs (Pl. 2, fig. 3)

(character box 4 in Text-fig. 2). Pantopod protonymphs have a broad area between their appendages (Pl. 5, fig. 2). More distinctive features of early larvae of extant pantopods are their finely setulate spines on the outer sides of the three pairs of limbs or the long (spaghetti-like) setules on the chelicerae (Pl. 5, fig. 1) as well as the various cuticular pores (Vilpoux 1999), although it remains uncertain when these developed in the larvae along the evolutionary line of Pantopoda. It also remains uncertain whether the fine denticles on the rami, and particularly the caudal outgrowths of *C. klausmuelleri*, represent precursor structures of the fine setulae of extant pantopod larvae.

The alternative to a relationship to Pycnogonida would be to interpret *Cambropycnogon klausmuelleri* as a larval representative of an early stem-group chelicerate (see also Walossek and Müller 1997, fig. 12.8) whose characters reflect the larval ground pattern of the entire chelicerate clade. In this hypothesis loss of the antennae would remain synapomorphic for the Chelicerata (Pycnogonida + Euchelicerata). However, this model is supported by only a single, reductive apomorphy compared to the five for *C. klausmuelleri* and (specifically larval) Pycnogonida (our Eupycnogonida; see below) we have identified above. Furthermore, if our fossil is regarded as an early stem-group chelicerate, characters such as the lack of a distinct forehead region, the unmodified post-cheliceral limbs in the larva, and the clearly defined head shield would have to have become reduced convergently in *C. klausmuelleri* and in Pycnogonida, or to have developed again secondarily, in the stem line of Euchelicerata, because they are present even in, for example, representatives of the basal spiders such as mesothelids. Again, the absence of a forehead, unmodified limbs with a series of podomeres, and a head shield with a margin characterise at least the early instars of arachnids and xiphosurans where this head shield is very broad.

Based on the characters supporting pycnogonid affinities, and building on the model of Bergström *et al.* (1980), we suggest a phylogeny for Pycnogonida of the form: (*Cambropycnogon klausmuelleri* + Eupycnogonida = (*Palaeoisopus problematicus* + N.N. = (*Palaeopantopus maucheri* + Pantopoda [*Palaeothea devonica* Bergstöm *et al.*, 1980 + Eupantopoda]))) (Text-fig. 2). The monophyly of Eupycnogonida is based on two synapomorphies: (1) loss of pre-cheliceral antennae (convergent with Euchelicerata), and (2) reduction of gnathobases on the basipods of the post-cheliceral appendages (convergent with some arachnids, where there is a clear tendency to reduce the gnathobases on the more posterior limbs) (character box 5 in Text-fig. 2). Autapomorphies of *P. problematicus* include annulated leg bases and flattened limbs (Bergström *et al.* 1980) (character box 6 in Text-fig. 2).

The, as yet unnamed, clade N.N. is characterised by the apomorphic reduction of the tail to three or fewer segments (character box 7 in Text-fig. 2), *P. maucheri* by the autapomorphy of annular markings on the abdomen (Bergström *et al.* 1980) (character box 8 in Text-fig. 2) and Pantopoda by reduction of the tail to a single segment (character box 9 in Text-fig 2). We also suggest a Eupantopoda taxon (i.e. all extant taxa) which has the autapomorphies of: (1) absence of excretory organs; (2) gonopores opening on the second limb podomere; (3) cement glands in the larval chelicerae of the larvae; and (4) egg-carrying by males.

Cambrian Chelicerata

Cambrian xiphosuran-like taxa, such as Aglaspidida, have repeatedly been referred to Chelicerata, and aglaspidids were even used as a model 'bauplan intermediate' from trilobites to xiphosurans and arachnids

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EXPLANATION OF PLATE 5

Figs 1–5. SEM micrographs of early larvae of *Pycnogonum litorale* (Ström, 1762) (courtesy K. Vilpoux, Ulm). 1, stage-1 larva = protonymphon. Long setulate, so-called spinning spines, still present in their entire length on the outer sides of the chelicerae. 2, ventral view of same stage. Note the large chelicerae with their fingers orientated in the same way as in the fossil (compare with e.g. Pl. 2, fig. 1). Post-cheliceral limbs of this species more widely separated than in the fossil (compare with Pl. 2, figs 1, 3). 3, posterior end of stage-1 larva with pair of pores in the same position as in the fossil (compare with Pl. 2, fig. 2 and Pl. 3, fig. 3). 4, ventral view of stage-III larva with first 'walking legs' developing on the short, poorly-separated hind body. Note the fine wrinkling of the cuticle. Pores also visible as in 3. More will appear successively with every new pair of limbs. 5, almost lateral view of stage-IV specimen with first walking legs developed and buds of the subsequent pair of limbs. Note the fine folds surrounding the insertions of the caudal limb buds (compare with e.g. Pl. 3, fig. 6 and Pl. 4, fig. 3).

PLATE 5

WALOSZEK and DUNLOP, Cambrian larval sea spider
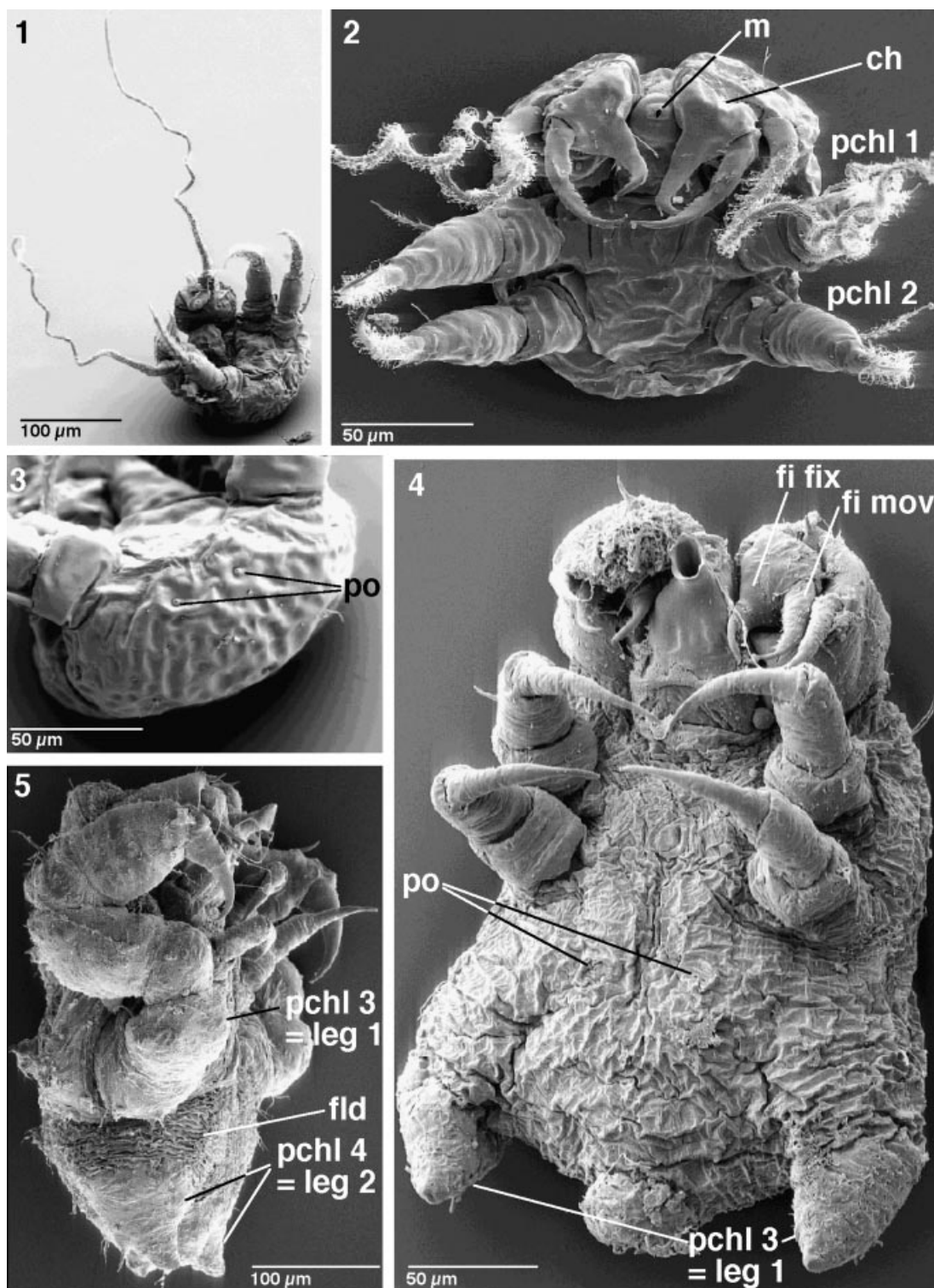
(e.g. Weygoldt and Paulus 1979). Aglaspidida have more recently been excluded from Chelicerata (e.g. Briggs *et al*. 1979; Anderson and Selden 1997; Walossek and Müller 1997). Aglaspidida have a head with four limbs only, the first one representing antennae, thus merely reflecting the euarthropodan ground pattern, and a trunk made of up to 11 segments. Hence, the head does not match the prosoma of Chelicerata and the remaining trunk does not correspond segmentally to the euchelicerate opisthosoma.

Another suggested Cambrian chelicerate, *Sanctacaris uncata* Briggs and Collins, 1988 from the fauna of the Middle Cambrian Burgess Shale, has distinctive lateral eyes ventral to the shield rim (and not dorsal as in Chelicerata), well-developed lateral tergal extensions and a cephalic shield covering more than the euarthropod number of limb-bearing segments, but lacks chelicerae. Subsequent cladistic analyses (e.g. Wills *et al*. 1995) have failed to group it with Chelicerata. Chlupáč (1995) referred some Lower Cambrian fossils to Eurypterida. This rather aglaspidid-like material does preserve appendages similar to those in some eurypterids, but does not show unequivocal apomorphies of either Chelicerata (i.e. chelicerae) or Eurypterida (i.e. a metastoma and genital appendage). An undescribed record of a putative late Cambrian chelicerate was mentioned by both Wahlman and Caster (1978) and Dunlop *et al*. (1999). However, the late Cambrian *Cambropycnogon klausmuelleri* represents the oldest unequivocal record of both Pycnogonida and Chelicerata.

Significance and implications of Cambropycnogon klausmuelleri
The fact that early larval development of Pycnogonida and Euchelicerata includes well-developed chelicerae is in our view the strongest argument to group all of these taxa in a monophylum Chelicerata. Both characters are present in *Cambropycnogon klausmuelleri*. This fossil also demonstrates that gnathobases were originally present in the ground pattern of Pycnogonida (as plesiomorphies retained from the euarthropod ground pattern), but have subsequently become reduced in the Pycnogonida. The possible presence of remains of antennae in *C. klausmuelleri* represents another plesiomorphy for Chelicerata, retained from the euarthropod ground pattern.

However, while larvae of Devonian Pycnogonida are unknown we cannot be certain how long remains of antennae were retained in the line towards the crown group. Yet it is a significant find, as it implies that loss of the antennae is *not* an autapomorphy of the stem species of the Chelicerata (see above), while their reduction to a vestigial state in early developmental stages can, however, still hold as an autapomorphy for Chelicerata, although we are unable to test this in later instars of *C. klausmuelleri* or in any early (i.e. Cambrian) Euchelicerata. According to our interpretation, Chelicerata can be characterised, therefore, by, at least: (1) miniaturised first antennae (plesiomorphic state: well-developed antennae) and (2) chelicerae, at least in early developmental stages (biramous, non-chelate, first post-antennae appendages).

As a consequence, the complete reduction of antennae in any ontogenetic stage may have occurred at least twice among Chelicerata, respectively within the Pycnogonida and Euchelicerata lines. The possible pre-cheliceral appendages in *Cambropycnogon klausmuelleri* provide further support for the hypothesis that Chelicerata started out larval development with a head larva having four pairs of appendages, i.e. (I) antennae (reduced), (II) chelicerae, and two legs (III and IV). Except for the loss of appendage I, this pattern is retained in the protonymph larvae of extant Pantopoda (Walossek and Müller 1997, fig. 12.8; Vilpoux 1999). The development of a longer head tagma (i.e. the prosoma) of the adults in the evolutionary line of Chelicerata cannot be discussed here in detail because *C. klausmuelleri* cannot contribute to this question.

However, the pre-cheliceral appendage pair in *C. klausmuelleri* is also important here. The profound study of the embryonic development of the nervous system in Pantopoda by Winter (1980) and anatomical studies of chelicerates by several other workers (principally Johansson 1933, and further papers summarised in Weygoldt 1985 and Wheeler *et al*. in press), have demonstrated the post-stomodeal origin of the cheliceral ganglion and its retention of a post-stomodeal commissure, thus being homologous to the tritocerebrum of the Euarthropoda (= a2 ganglion of Crustacea). Both the anatomical studies, and now our fossil, provide strong evidence against recent claims based on homeobox genes, that Chelicerata have not lost the deutocerebral head segment, and that chelicerae represent a1 instead, and are thus

homologous with the antennae of insects and myriapods and the first antennae of crustaceans (Damen *et al.* 1998; Telford and Thomas 1998; Damen and Tautz 1999; Abzhanov *et al.* 1999). Wheeler *et al.* (in press) further support our conclusion that chelicerae represent a2. These authors have reviewed the anatomical evidence for a tritocerebrum in the chelicerate brain and also discussed the pre-cheliceral appendages in the fossils described herein, arguing that the expression patterns derived from homeobox genes cannot, in isolation, falsify an established segmental homology pattern based on morphology. Remarkably, Damen *et al.* (1998, fig. 4) depicted a scheme of Hox gene expressions in the body of *Drosophila* showing exactly the head tagma (i.e. ending behind the so-called maxilla-1 segment) that Walossek and Müller (1990), based on their findings of Upper Cambrian stem-line derivatives of the Crustacea in the 'Orsten' material, proposed as characterising the ground pattern of Euarthropoda. This is in contrast to a head including five limb-bearing segments, as has been traditionally presumed for Euarthropoda. This model should also hold for the hatching semaphoront possessing antennae and three, rather than four, pairs of functional limbs (= 'head larvae'; see also Walossek and Müller 1997; Walossek 1999). In line with this, we suggest that our study of *Cambropycnogon klausmuelleri* demonstrates, though possibly at a somewhat later stage (see above), the presence of the same euarthropodan pattern of the larval head tagma in the oldest known, unequivocal member of Chelicerata, a pattern that also remains, in only a slightly modified form, in all extant Pantopoda.

REFERENCES

ABZHANOV, A., POPADIC, A. and KAUFMAN, T. C. 1999. Chelicerate Hox genes and the homology of arthropod segments. *Evolution and Development* **1**, 77–89.

ANDERSON, L. I. and SELDEN, P. A. 1997. Opisthosomal fusion and phylogeny of Palaeozoic Xiphosura. *Lethaia*, **30**, 19–31.

ARNAUD, F. and BAMBER, R. N. 1987. The biology of Pycnogonida. *Advances in Marine Biology*, **24**, 1–94.

BARTELS, C., BRIGGS, D. E. G. and BRASSEL, G. 1998. *The fossils of the Hunsrück Slate — Marine life in the Devonian.* Cambridge Paleobiology Series 3, Cambridge, 323 pp.

BEHRENS, W. 1984. Larvenentwicklung und Metamorphose von *Pycnogonum litorale* (Chelicerata, Pantopoda). *Zoomorphology*, **104**, 266–279.

BERGSTRÖM, J., STÜRMER, W. and WINTER, G. 1980. *Palaeoisopus, Palaeopantopus* and *Palaeothea*, pycnogonid arthropods from the Lower Devonian Hunsrück Slate, West Germany. *Paläontologische Zeitschrift*, **54**, 7–54.

BRIGGS, D. E. G. and COLLINS, D. A. 1988. A Middle Cambrian chelicerate from Mount Stephan, British Columbia. *Palaeontology*, **31**, 779–798.

—— BRUTON, D. L. and WHITTINGTON, H. B. 1979. Appendages of the arthropod *Aglaspis spinifer* (Upper Cambrian, Wisconsin) and their significance. *Palaeontology*, **22**, 167–180.

BROILI, F. 1928. Crustaceenfunde aus dem rheinischen Unterdevon. I. Über Extremitätenreste. *Sitzungsberichte der Bayerischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Abteilung*, **1928**, 197–201.

—— 1929. Beobachtungen an neuen Arthropodenfunden aus den Hunsrückschiefern. *Sitzungsberichte der Bayerischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Abteilung*, **1929**, 253–280.

—— 1930. Über ein neues Exemplar von *Palaeopantopus*. *Sitzungsberichte der Bayerischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Abteilung*, **1930**, 209–214.

—— 1932. *Paleoisopus* ist ein Pantopode. *Sitzungsberichte der Bayerischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Abteilung*, **1932**, 45–60.

BULLOUGH, W. S. 1958. *Practical invertebrate anatomy.* Macmillan, London, 483 pp.

CHILD, C. A. 1998. The marine fauna of New Zealand: Pycnogonida (sea spiders). *National Institute of Water and Atmospheric Research, Biodiversity Memoir*, **109**, 1–71.

CHLUPÁC, I. 1995. Lower Cambrian arthropods from the Paseky Shale (Barrandian area, Czech Republic). *Journal of the Czech Geological Society*, **40** (4), 9–36.

DAMEN, W. G. M. and TAUTZ, D. 1999. Comparative molecular embryology of arthropods: the expression of Hox genes in the spider *Cupiennius salei*. *Invertebrate Reproduction and Development*, **36**, 203–209.

—— HAUSDORF, M., SEYFARTH, E.-A. and TAUTZ, D. 1998. A conserved mode of head segmentation in arthropods revealed by the expression pattern of Hox genes in a spider. *Proceedings of the National Academy of Science, USA*, **95**, 10,665–10,670.

DEWEL, R. A. and DEWEL, W. C. 1997. The place of tardigrades in arthropod evolution. 109–123. *In* FORTEY, R. A. and THOMAS, R. H. (eds). *Arthropod evolution*. Chapman and Hall, London, 383 pp.

DOHRN, A. 1881. Die Pantopoden des Golfes von Neapel und der angrenzenden Meeres-Abschnitte. *Monographie der Fauna und Flora des Golfes von Neapel*, **3**, 1–252.

DUNLOP, J. A. and BRADDY, S. J. 2001. Scorpions and their sister-group relationships. 1–24. *In* FET, V. and SELDEN, P. A. (eds). *Scorpions 2001. In Memoriam Gary A. Polis*. The British Arachnological Society, Burnham Beeches, Bucks, xi + 404 pp.

—— ANDERSON, L. I. and BRADDY, S. J. 1999. A new chasmataspid (Chelicerata: Chasmataspida) from the Lower Devonian of the Midland Valley of Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **89**, 161–165.

GERSTAECKER, C. E. A. 1863. Pantopoda. 248–350. *In* CARUS, J. V. and GERSTAECKER, C. E. A. (eds). *Handbuch der Zoologie*, **2**. W. Engelmann, Leipzig, 642 pp.

GIRIBET, G. and RIBERA, C. 2000. A review of arthropod phylogeny: new data based on ribosomal DNA sequences and direct character optimization. *Cladistics*, **16**, 204–231.

HARTENBERGER, R. 1995. *Palaeoisopus problematicus* Broili, 1928 (Arthropoda) aus dem Hunsrückschiefer (Devon) mit behaartem Abdomen. *Paläontologische Zeitschrift* **69**, 121–123.

HEDGPETH, J. W. 1954. On the phylogeny of the Pycnogonida. *Acta Zoologica*, **35**, 193–213.

—— 1955. Pycnogonida. 163–170. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology, Part P, Arthropoda 2*. Geological Society of America, Boulder, and University of Kansas Press, Lawrence, 181 pp.

—— 1956. On the phylogeny of the Pycnogonida. *Proceedings of the XIV International Congress of Zoology, Copenhagen 1953, section XV*, Copenhagen, 506–507.

—— 1978. A reappraisal of the Palaeopantopoda with description of a species from the Jurassic. *Zoological Journal of the Linnean Society*, **63**, 23–34.

HELFER, H. and SCHLOTTKE, E. 1935. Pantopoda. *H. G. Bronns Klassen und Ordnung des Tierreichs*, Band 5, IV (2). Akademische Verlagsgesellschaft, Leipzig, 314 pp.

HEYMONS, R. 1901. Die Entwicklungsgeschichte der Scolopender. *Zoologica*, **33**, 1–244.

HOU XIANGUANG and BERGSTRÖM, J. 1997. Arthropods of the Lower Cambrian Chengjiang fauna, southwest China. *Fossils and Strata* **45**, 1–116.

IKUTA, K. and MAKIOKA, T. 1999. Evolution of ovarian structure and oogenesis in maxillopodan crustaceans. 91–100. *In* SCHRAM, F. R. and von VAUPEL KLEIN, J. C. (eds). *Crustaceans and the biodiversity crisis, Proceedings of the Fourth International Crustacean Congress, Amsterdam, The Netherlands, July 20–24, 1998*, 1. Brill Academic Publishers, Leiden, 1021 pp.

JOHANSSON, G. 1933. Beiträge zur Kenntniss der Morphologie und Entwicklung des Gehirns von *Limulus polyphemus*. *Acta Zoologica*, **14**, 1–100.

KING, P. E. 1973. *Pycnogonids*. Hutchinson, London, 144 pp.

KRAUS, O. 1976. Zur phylogenetischen Stellung und Evolution der Chelicerata. *Entomologica Germanica*, **3**, 1–12.

KRØYER, H. 1840. Om Pycnogonidernes Forvandlinger. *Naturhistorik Tidsskrift, Kjobenhavn* **1** (3), 299–306.

LATREILLE, P. A. 1810. *Considérations générales sur l'Ordre Naturel des Animaux composant les Classes des Crustacés, des Arachnides et des Insectes*. Paris, 446 pp.

LEACH, W. E. 1815. A tabular view of the external characters of four classes of animals which Linné arranged under Insecta; with the distribution of the genera composing three classes into orders etc. and descriptions of new genera and species. *Transactions of the Linnean Society of London*, **11**, 305–400.

MIYAZAKI, K. and MAKIOKA, T. 1989. Chelicerate-like oogenesis in *Endeis nodosa* (Pycnogonida; Endeidae). *Proceedings of the Arthropod Embryological Society of Japan*, **24**, 11–12.

—— —— 1990. Ovarian structure and oogenesis in pycnogonids: some similarities to those in Chelicerates. *Proceedings of the Arthropod Embryological Society of Japan*, **25**, 1–3.

—— —— 1991. Structure of the adult female reproductive system and oogenetic mode in the sea spider, *Endeis nodosa* (Pycnogonida; Endeidae). *Journal of Morphology*, **209**, 257–263.

—— SUZUKI, H. 1997. External morphology of the protonymphon larvae in a pycnogonid, *Ammothella biunguiculata* (Pycnogonida: Ammotheidae). *Proceedings of the Arthropod Embryological Society of Japan*, **32**, 29–31.

MÜLLER, K. J. 1985. Exceptional preservation in calcareous nodules. *Philosophical Transactions of the Royal Society of London B*, **311**, 67–73.

——— and WALOSSEK, D. 1986. Arthropod larvae from the Upper Cambrian of Sweden. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **77**, 157–179.

—— —— 1988*a*. Eine parasitische Cheliceraten-Larve aus dem Kambrium. *Fossilien*, **1**, 40–42.

—— —— 1988*b*. External morphology and larval development of the Upper Cambrian maxillopod *Bredocaris admirabilis*. *Fossils and Strata*, **23**, 1–70.

MUNILLA, T. 1999. Evolución y filogenia de los Picnogónidos. 273–279. *In* MELIC, A., DE HARO, J. J., MENDEZ, M. and RIBERA, I. (eds). *Evolutión y filogenia de Arthropoda*. Boletin de la Sociedad Entomológica Aragonesa, Zaragoza, **26**, 806 pp.

POLZ, H. 1969. Beobachtungen aus den Solnhofener Plattenkalken. *Natur und Museum*, **99**, 457–467.

—— 1984. Krebslarven aus den Solnhofener Plattenkalken. *Archaeopteryx*, **1984**, 30–40.

RICHTER, F. 1912. Eine Pantopodenlarve von Gabelsflach (Kieler Förde). *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere*, *Supplement*, **15**, 45–50.

SCHOLL, G. 1977. Beiträge zur Embryonalentwicklung von *Limulus polyphemus* L. (Chelicerata, Xiphosura). *Zoomorphologie*, **86**, 99–154.

SCHRAM, F. R. 1978. Arthropods. A convergent phenomenon. *Fieldiana Geologica*, **39**, 61–108.

—— AND HEDGPETH, J. W. 1978. Locomotory mechanisms in Antarctic pycnogonids. *Zoological Journal of the Linnean Society*, **63**, 145–169.

SELDEN, P. A. 1981. Functional morphology of the prosoma of *Baltoeurypterus tetragonophthalmus* (Fischer) (Chelicerata: Eurypterida). *Transactions of the Royal Society of Edinburgh*: *Earth Sciences*, **72**, 9–48.

SHULTZ, J. W. 1990. Evolutionary morphology and phylogeny of Arachnida. *Cladistics*, **6**, 1–38.

STRÖM, H. 1762. *Physisk og Oeconomisk Beskrevelse over Fogderiet Søndmør, beliggende i Bergens Stift i Norge*, **1**, 208–209.

STÜRMER, W. and BERGSTRÖM, J. 1981. *Weinbergina*, a xiphosuran arthropod from the Devonian Hunsrück Slate. *Paläontologische Zeitschrift*, **55**, 237–255.

TELFORD, M. J. and THOMAS, R. H. 1998. Expression of homeobox genes shows chelicerate arthropods retain their deutocerebral segment. *Proceedings of the National Academy of Sciences, USA*, **95**, 10,671–10,675.

THOMAS, R. H. and TELFORD, M. J. 1999. Appendage development in embryos of the oribatid mite *Archegozetes longisetosus* (Acari, Oribatei, Trhypochthoniidae). *Acta Zoologica* (*Stockholm*), **80**, 193–200.

VILPOUX, K. 1999. Zur Ontogenie und der Morphogenese der Extremitäten von *Pycnogonum litorale* (Ström, 1762) (Pycnogonidae, Pantopoda). Unpublished diploma thesis, University of Ulm, 121 pp.

WAHLMAN, G. P. and CASTER, K. E. 1978. Bearing of new Texas Upper Cambrian arthropods on merostome classification. *Geological Society of America, Abstracts with Programme*, **10** (6), 268.

WALOSSEK, D. 1993. The Upper Cambrian *Rehbachiella kinnekullensis* Müller, 1983, and the phylogeny of Branchiopoda and Crustacea. *Fossils and Strata*, **32**, 202 pp, 34 pls.

—— 1999. On the Cambrian diversity of Crustacea. 3–27. *In* SCHRAM, F. R. and von VAUPEL KLEIN, J. C. (eds). *Crustaceans and the biodiversity crisis*, *Proceedings of the Fourth International Crustacean Congress, Amsterdam, The Netherlands, July 20–24, 1998*, **1**. Brill Academic Publishers, Leiden, 1021 pp.

—— and MÜLLER, K. J. 1990. Stem-lineage crustaceans from the Upper Cambrian of Sweden and their bearing upon the position of *Agnostus*. *Lethaia*, **23**, 409–427.

—— —— 1997. Cambrian 'Orsten'-type arthropods and the phylogeny of Crustacea. 139–153. *In* FORTEY, R. A. and THOMAS, R. H. (eds). *Arthropod evolution*. Chapman and Hall, London, 383 pp.

WEYGOLDT, P. 1985. Ontogeny of the arachnid central nervous system. 20–37. *In* BARTH, F. G. (ed.). *Neurobiology of arachnids*. Springer-Verlag, Berlin, 385 pp.

—— and PAULUS, H. F. 1979. Untersuchungen zur Morphologie, Taxonomie und Phylogenie der Chelicerata. *Zeitschrift für Zoologische Systematik und Evolutionsforschung*, **17**, 86–116, 177–200.

WHEELER, W. C. and HAYASHI, C. Y. 1998. The phylogeny of the extant chelicerate orders. *Cladistics*, **14**, 173–192.

—— GIRIBET, G., DESALLE, R. and EDGECOMBE, G. D. in press. Chelicerate segmental homology and homeobox gene expression. *Cladistics*.

WILBY, P. R., BRIGGS, D. E. G. and RIOU, B. 1996. Mineralization of soft-bodied invertebrates in a Jurassic metalliferous deposit. *Geology*, **24**, 847–850.

WILLS, M. A., BRIGGS, D. E. G., FORTEY, R. A. and WILKINSON, M. 1995. The significance of fossils in understanding arthropod evolution. *Verhandlungen der Deutschen Zoologischen Gesellschaft*, **88**, 203–215.

WINTER, G. 1980. Beiträge zur Morphologie und Embryologie des vorderen Körperabschnitts (Cephalosoma) der Pantopoda Gerstaecker, 1863. *Zeitschrift für Zoologische Systematik und Evolutionsforschung*, **18**, 27–61.

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