A new Late Cambrian pentastomid and a review of the relationships of this parasitic group

Dieter Waloszek, John E. Repetski and Andreas Maas

ABSTRACT: Pentastomida, tongue worms, are a taxon of about 130 species of parasites, living exclusively in the respiratory tracts of vertebrates. Three-dimensionally preserved Upper Cambrian larvae already demonstrate a high degree of adaptation to parasitism, striking morphological conservatism, and a high diversification by the Late Cambrian, thereby suggesting a likewise diversified host group. Not least due to their highly modified morphology, the systematic affinities of pentastomids remain controversial. The two major alternatives place the group as either close to branchiuran crustaceans or as stem-lineage derivatives of the Euarthropoda. To this set of Cambrian fossil representatives of the pentastomids we can add a new form from Lower Ordovician boundary beds from Sweden, most likely reworked from Upper Cambrian horizons. Based on this new species, named *Aengapentastomum andresi* gen. et sp. nov., and the available information about fossil and Recent pentastomids, we review the diverging ideas on the systematic position of this fully parasitic taxon.

KEY WORDS: Arthropoda stem lineage, parasitism, phylogeny

Pentastomida is a group of about 130 species of worm-shaped parasites of various kinds of tetrapods, mostly land animals, with terminal hosts ranging from amphibians to various sauropsids, such as turtles, snakes, lizards, crocodiles, birds, as well as various eutherian mammals, such as canids, antelopes, reindeer (only calves) and marsupials (Spratt 2003). Humans are not a natural host, but can (rarely) become infected as paratenic hosts, resulting in a disease called pentastomiasis or porocephalosis. It is caused by the porocephalid taxa *Armillifer* Sambon, 1922a, *Linguatula* Fröhlich, 1789 and *Porocephalus* von Humboldt, 1809 (Heymons 1935; Fain 1960; Haugerud 1988; Itakura 1995; Riley 1996; Muller 2002). Actinopterygii, e.g. cichlids and barbs, all the mentioned groups of tetrapods, and also at least one insect species, may act as intermediate hosts in the life cycle of Recent tongue worms. Direct development in a single host also has been reported (Banaja *et al.* 1975; Riley 1986). This diversity of life cycles has caused difficulties in reconstructing the ancestral life cycle (cf. Heymons 1935; Haugerud 1989).

The two main individuals who conducted the earliest studies of pentastomids were Richard Heymons, Berlin (e.g., Heymons 1923, 1926a, b, 1935, 1941) and Konstantin von Haffner, Hamburg (e.g., Haffner 1964, 1971, 1972, 1973, 1974, 1977; Haffner & Rack 1971; Haffner *et al.* 1967, 1969). Few other scientists have studied the Pentastomida thereafter. More recent authorities are Wolfgang Böckeler, Kiel (e.g., Böckeler & Vauk-Hentzelt 1979; Storch & Böckeler 1979, 1982; Böckeler 1982, 1984a–d; Böckeler & Storch 1990; Storch *et al.* 1990; Thomas & Böckeler 1992, Thomas *et al.* 1999a–c) and John Riley, Dundee (e.g., Riley 1972, 1973a, b, 1976, 1983, 1986, 1992, 1994, 1996; Banaja *et al.* 1975; Ali & Riley 1983, 1984; Winch & Riley 1986a, b; Jones & Riley 1991; Jones *et al.* 1992; McAllister *et al.* 1993; Buckle *et al.* 1997; Riley *et al.* 1978, 1985, 1987, 1990, 1991, 1997; Riley & Self 1980, 1981a, b, 1982; Riley & Heideman 1998; Riley & Huchzermeyer 1995, 1996, 2000).

Overall, the particular focus of pentastomid research has been on their taxonomy; less so on life cycles and host-parasite

interactions (e.g., Böckeler 1984a; Haugerud 1989; Junker *et al.* 1998a, b). Examples of the few more recent papers dealing with the phylogeny of the group are by Abele *et al.* (1989) and Lavrov *et al.* (2004) using molecular data, and by Walossek & Müller (1994) based on fossil discoveries from the Cambrian. In a detailed in-group analysis – the only one of its kind ever made – Almeida & Christoffersen (1999) challenged several older ideas (Sambon 1922a, b) such as the division of crown-group pentastomids into two major lineages, Cephalobaenida and Porocephalida. Again, Almeida & Christoffersen (2002) summarised biological data of South American species and presented new hypotheses on the phylogenetic position of pentastomids. As with the in-group status, the phylogenetic relationships of the Pentastomida were unclear for a long time and, historically, the group has been affiliated with a wide range of groups in the past (Table 1).

Eventually (until the 1980s), consensus amongst scientists was to place the group on the stem lineage to the Euarthropoda. This implied a closer alliance to onychophorans (velvet worms) and tardigrades (water bears), together being named 'pro'- (or 'prot')-arthropods (see, e.g., Pflugfelder 1980). Detailed investigation of morphological, anatomical

Table 1 Historical summary of previous ideas on the position of the Pentastomida (after Heymons 1935 and Walossek & Müller 1994 for further discussion).

PLATYHELMINTHES	– either cestodes or trematodes
NEMATHELMINTHES	– nematodes
ARTICULATA	– either Polychaeta, Myzostomida, or Tardigrada
"PROT"-ARTHROPODA	– closer to either Onychophora or Tardigrada
ARTHROPODA	– either mites or pantopods among Chelicerata
	– Tracheata "Myriapoda"
	– either copepods or branchiurans among Eucrustacea

(particularly the nervous system) and embryological/developmental features (Böckeler 1984a–d) supported this view.

This view was challenged, when Wingstrand (1972) observed striking similarities in sperm morphology between the pentastomid *Raillietiella hemidactyli* Hett, 1934 and the crustacean *Argulus foliaceus* (Linnaeus, 1758). Wingstand therefore concluded that pentastomids had close affinities with the ectoparasitic branchiuran crustaceans (fish-lice). This was supported by molecular studies of 18S rDNA (Abele *et al.* 1989, 1992; Zrzavý *et al.* 1998; Giribet & Ribera 2000; Peterson & Eernisse 2001), and later by subsequent studies of sperm morphology (Storch & Jamieson 1992; Jamieson & Storch 2000) in these same two species. This hypothesised relationship of pentastomids and branchiuran crustaceans became rapidly accepted worldwide – in spite of the fact that no other morphological data either support or even contradict this interpretation (but see Maas & Waloszek 2001 or Almeida & Christoffersen 1999 for criticism about the reliability of these interpretations). Again, ontogenetic investigations of *Reighardia sternae* that do not support a crustacean relationship have also been ignored completely so far; no sign of any crustacean larva features have yet been detected during embryogenesis (Böckeler 1982, 1984a–d).

Based on the description of a new [presumed] Upper Cambrian form from Västergötland, Sweden, we reviewed the current information on the morphology of the fossil pentastomids and new information raised about the relationships within and of pentastomids since our first description in 1994 (Waloszek & Müller 1994).

1. Material and methods

1.1. Material
The single specimen of *Aengapentastomum andresi* gen. et sp. nov. now under study was found by one of the present authors [JER] in a sample of glauconitic, sandy, calcareous rock from the *Ceratopyge* Limestone at Stora Backor, Sweden (see Type locality, below). This nodular limestone was processed by standard conodont extraction methods: acid digestion by 10% to 15% acetic acid, followed by wet-sieving, heavy liquid separation, and magnetic separation before hand picking of the remaining insoluble residue. The 75- to 840-micron size fraction was searched for the microfossils. The sample was extremely rich in conodonts and phosphatic brachiopod valve fragments; conodont abundance exceeded several thousand elements per kg of rock processed. The specimen is complete, comprising the head with two pairs of short grasping limbs, and the elongate tail with short, but distinct caudal outgrowths. The fairly smooth preservation of its surface has largely effaced details such as joints and segment boundaries, particularly of the legs. The posterior head legs differ in their orientation, thus demonstrating their range of action, as can be seen also in other 'Orsten'-type material (see particularly Müller & Walossek 1985 for a description of the flexibility of Skaracarida). Rarely seen in the typical 'Orsten'-type preservation, but as with the single specimen of the Canadian pentastomid find, *Heymonsicambria taylori* Walossek, Repetski & Müller, 1994, and possibly also as with Andres' (1989) material, the specimen seems to be solid and not hollow.

1.2. Methods
Original SEM images of the holotype (UB W135) were taken at the Institute of Palaeontology of the University of Bonn, Germany. They were digitised for reproduction and processing using Adobe Photoshop CS™ on Apple computers.

Concerning terminology, the use of Pan- as a prefix in phylogenetic analyses was established by Lauterbach (1989) as a conceptual term in an analysis of phylogeny until apomorphies are found to establish a system. Its use was not intended in a nomenclatorial sense (see also Meier & Richter 1992). Although it should be avoided in classification, it became more and more widely used in a taxonomic sense to encompass larger entities, for example Panarthropoda, or Pancrustacea. The present authors reject this usage, not least since appropriate terms have been validly published, when referring to the monophylum that includes the stem species, stem lineage and crown group. Since the two living taxa Onychophora and Tardigrada are clearly offshoots of the evolutionary lineage toward an undisputed monophylum that includes all arthropodised and arthrodised taxa, a crown group Euarthropoda nests within Arthropoda *sensu stricto* and there is a further evolutionary lineage leading to the Euarthropoda (cf. Maas *et al.* 2004; Waloszek *et al.* 2005). Therefore, we have a compound stem-lineage and not a single lineage leading to Euarthropoda, with all stem-lineage taxa being extinct. In fact, all these constructs/conceptual items are developed to make phylogeny more transparent and flexible if new taxa are to be included or excluded based on new evidence. Again, Arthropoda s. str. is a monophylum, as are the Euarthropoda, and both are established on the basis of numerous autapomorphic features (Maas *et al.* 2004). In any case, a crown group is monophyletic. Nevertheless, it is appropriate to name monophyletic units if necessary.

2. Systematic palaeontology

Pentastomida Rudolphi, 1819

The new form belongs, in our view, to the Pentastomida, as it shares (i) its characteristic head with two pairs of claw-like three-segmented limbs (autapomorphy of Pentastomida), the proximal two segments with pores medially (autapomorphy of Pentastomida) and the distal one acting as a hook in a pliable membrane, articulating against the penultimate segment (autapomorphy of Pentastomida); (ii) an anterior, slightly ventrally oriented mouth (symplesiomorphy); and (iii) a carrot-shaped tail consisting of three metameres (autapomorphy of Pentastomida) and a terminal portion bearing a pair of short caudal outgrowths or papillae (status uncertain). Paired frontal sensilla in other Cambrian pentastomids and extant derivatives are lacking in the new form. They should occur dorsal to a transverse furrow above the anterior pair of limbs (cf. Fig. 2C), but cannot be taken into account due to preservation. Compared to our other material, preservation has smoothed the entire surface to a large degree, thus considerably effacing segment boundaries and other structures. Likewise, trunk limbs on trunk segments two and three, as developed in some of the Upper Cambrian representatives of the stem lineage of Pentastomida, are missing in the new form, and this lack cannot, at present, be taken as an argument for placing the new form closer to the crown group (for which we herein suggest the name Eupentastomida) or, even, closer to any specific Recent crown-group taxon.

Aengapentastomum gen. nov.

Etymology. A combination of the collection locality name, the Änga quarry, and the affinity of the type species to Pentastomida.

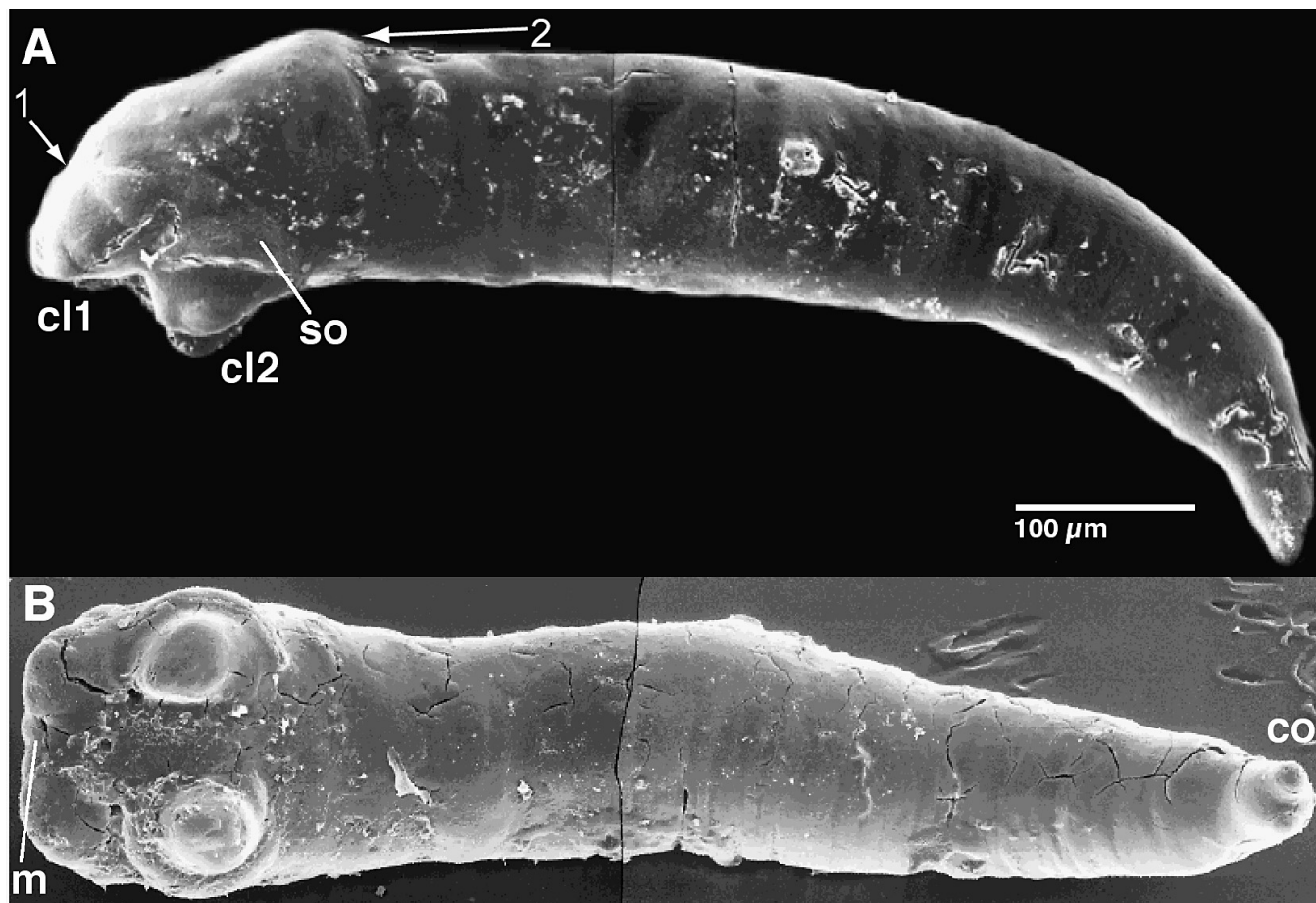**Type and only species.** *Aengapentastomum andresi* sp. nov.

Figure 1. *Aengapentastomum andresi* gen. et sp. nov. (A) Lateral view of the holotype. Arrow 1 points to the anterior head border line, arrow 2 to the posterior rim. (B) Ventral view of holotype. Note the annulated trunk. Abbreviations: (cl1), (cl2) cephalic claw limbs; (co) caudal outgrowth; (m) mouth; (so) limb socket.

Aengapentastomum andresi sp. nov.

?1989 "Seltene Art" – Andres, p. 11; plate 2, fig. 1.

Etymology. In honour of Dietmar Andres, Berlin, who first described Upper Cambrian/Lower Ordovician pentastomid fossils (see Andres 1989).

Holotype. A single complete but smoothly preserved specimen, repository number UB W 135.

Type locality. From the *Ceratopyge* Limestone exposed in the Änga Quarry, at Stora Backor, Västergötland, Sweden. The sample, field number JR8-26-82E, is from a nodule of glauconitic, sand-size phosphatic fossil-rich lime grainstone. It is from the same horizon as Sample 5 of Lindström (1954). This horizon is Late Tremadocian in age (*Paltodus deltifer* Zone), as dated by an abundant conodont fauna of well-preserved elements. However, this interval also contains abundant phosphatic microfossils, very possibly including this pentastomid as well, that clearly have been reworked upwards from Upper Cambrian and Lower Tremadocian strata. These reworked fossils are variously iron-stained, blackened and abraded, and thus visually easily separated from the well-preserved younger faunal elements. This sample is the same as that which yielded the pentastomid *Heymonsicambria repetskii* Walossek & Müller, 1994 (see Walossek & Müller 1994 for details); both of these pentastomid specimens are darkened and abraded, thus we conclude that they belong to the reworked fauna.

Measurements (measured to the nearest 5 μm on the SEM images; approximately). Total length 730 μm, maximum length and width of head region (measured at its rear) 175 μm; height 130 μm. Height of anterior trunk portion 120 μm, last

two thirds decreasing in height from 95 to 75 μm, caudal end decreasing toward the pair of rounded outgrowths from 45 to 20 μm. Anterior head limbs: width above socket 50 μm, posterior head limbs: width above socket 65 μm.

Diagnosis. Pentastomid with rounded head, the anterior head limbs being shorter than the posterior ones, antero-ventrally oriented and with inwardly pointing terminal podomere or segment. Posterior limbs ventrally inserting and posteriorly oriented, subtriangular at their basis. Socket slightly swollen around outer part of limb. Ventral surface of cephalon straight, distal part gently rounded. Trunk smooth, with weakly defined annulation visible by 12–13 folds. Trunk caudally tapering. No signs of vestigial limbs, but caudal outgrowths prominent, peg-like. Holotype is most likely a more advanced larval stage, as derived from its size.

Description. The body of the new pentastomid is distinctly divided into two parts, head and trunk. The head is less high anteriorly than posteriorly (subtriangular in lateral profile, Fig. 1A) and is almost as long as wide (Fig. 1B). There is no distinct head shield or similar structure, although a transverse, gently curved and shallow furrow dorsal to the swollen sockets of the anterior limbs and the distinct posterior head margin in some views give this impression (Fig. 1A). The head cuticle continues anteriorly and laterally around the body proper. Fig. 2B also reveals a round swelling in the middle of the dorsal surface of the head with a shallow furrow around it. Its function and origin are unclear because there is no equivalent structure in any of the known fossil and extant taxa. There are 'dorsal organs' described for Recent pentastomid larvae, but only for embryonic stages (as described by Osche 1959 for *Reighardia sternae*). The posterior head boundary is

distinguished by a slightly swollen margin and a slight decrease in diameter of the anterior trunk portion. The border is less distinct ventrally.

The anterior claw limbs insert antero-laterally and flank, with their indistinct sockets, the mouth area (Figs 1A, B, 2A, B). A spindle-shaped depression anteromedial of the limb sockets bordered laterally by swollen lip-like ridges is interpreted as the mouth (Fig. 2C), as compared to *Boeckelericambria pelturae* (Walossek & Müller 1994, fig. 13b). That the hole is filled and not deep is characteristic of this kind of coarse preservation.

The sockets of the anterior limbs are weakly defined and are visible only as a triangular hump laterally (Fig. 2A–C). The limbs are composed of three segments or podomeres (Fig. 3), but these are only faintly visible on account of indifferent preservation. The proximal segment forms the major part of the limb, from which the oval smaller second section arises. This part carries the triangular 'claw', the distal segment. A faint hump latero-distally on the second segment is actually the pliable membrane from which the terminal segment points medially toward the mouth. The exact situation for such a limb has been reconstructed by Walossek & Müller (1994) on the basis of their better-preserved larvae in the Swedish 'Orsten' material (see also Fig. 3). The distance to the posterior limbs is minor, mainly because of their more prominent limb sockets (part of the body proper). Also the distance between the pair is less than 20 μm.

The posterior limbs, though only slightly larger, appear more prominent due to their sockets that encircle the limbs like a ring, except for the median side. In ventral view, the shape of the limbs is slightly triangular, with the inner edge being straight (a morphology shared with other larvae from the 'Orsten'). These limbs also are composed of three segments, though the boundaries are rather effaced due to imperfect preservation of the holotype (reconstructed in Fig. 3). It is clear that the distal segment points posteriorly. Again, the slightly different orientation of right and left limbs suggests movability of the whole limbs in an anterior-posterior direction. This is also seen in the slight recession of the right limb into its socket posteriorly and of the left limb anteriorly (Fig. 2A, B). The posterior limbs are located at some distance from one another, approximately 50 μm and point straight ventrally (topological orientation).

The trunk is shaped like a carrot. It is, more or less, devoid of any distinct subdivision into segments/metameres. Only the last third starts with a slightly smaller diameter, thus appears slightly offset, and again the last 50 μm are distinctly less wide and may represent the caudal end, as developed in the other fossil larvae from Sweden and Canada. The trunk shows a faint annulation into 12–13 annuli (Figs 1A, B; 3). However, it remains uncertain if this can be regarded as a similar annular subdivision of the trunk end as in the Recent Pentastomida, hence bringing *Aengapentastomum andresi* closer to the crown group. The caudal end continues into a pair of peg-like outgrowths (also named terminal papillae in pentastomid terminology; Fig. 2D). Their shape is slightly unequal, but this may be an individual defect rather than a species-specific feature. Trunk limbs, or even vestigia of them, are missing in *Aengapentastomum andresi*. Certain structures visible in Fig. 1A and B are clearly surface contaminations, as such are common in this kind of Cambrian phosphatic fossil material.

Comparisons (differential diagnosis). *Aengapentastomum andresi* gen. et sp. nov. can be clearly distinguished from any previously described Cambrian pentastomid. In particular, it has a much more elongate trunk and the overall size is larger than all eight Upper Cambrian specimens from Västergötland, Sweden, that represent at least six different species (see

Walossek & Müller 1994). Therefore we consider it as a later semaphoront, also developmentally older than *Heymonsicambria repetskii* from the same sample and developmentally older than a Canadian specimen assigned to the species *H. taylori* Walossek, Repetski & Müller, 1994. However, this would not validate its taxonomic distinction. Sharing morphological features of both the so-called hammer- and the round-headed larvae of Walossek & Müller (1994), it seems that *A. andresi* would either weaken the concept that they are distinct or bridge the morphological gap between the two groups. The specific location and orientation of the cephalic limbs of *A. andresi* (towards different directions) are unknown from those of the 'Orsten' taxa, but show resemblance to some forms examined by Andres (1989; pls. 1:1, 5, 6 and 2:1) in having smaller anterior legs with inwardly oriented distal segments and larger posterior legs with backwardly oriented claws. Accordingly, this parasite may have anchored itself in a shallow depression by dragging the body against the tissue using the anterior limbs as pincers and by backward hooking of the large posterior limbs, eventually pressing the mouth against the tissue for sucking (see Walossek & Müller 1994, fig. 20]. The larva depicted on Andres' (1989) plate 2:1 resembles *A. andresi*, but it is not only much smaller, but also has a single pair of vestigial limbs on its second trunk portion. Since the third metamere and the caudal end are indistinctly divided, it may well be that this larva represents a younger stage of *A. andresi* (geological age would also fit). However, speculations about this must await a detailed re-study of Andres' material. All the larger specimens shown by Andres (1989) are clearly distinguished from *A. andresi* not least by their presence of two pairs of trunk limb vestigia.

Since a mouth is to be expected to show up later in development, its presence in *Aengapentastomum andresi* cannot serve greatly to demonstrate relationships. Walossek & Müller (1994) were able to show that the principal differences between all fossil species/specimens are in the orientation and size relationships of the clawed head limbs and in the presence or absence of trunk legs. *A. andresi* is well within the range of morphologies. Again, the segmental state of the clawed limbs is as in the other taxa. Absence of one or both trunk limb vestigia again is another weak argument, because such variety is present in the Swedish material (Walossek & Müller 1994) as well as in Andres' material (Andres 1989). The distinctive head and trunk of the other Canadian form *Heymonsicambria taylori*, a small hammer-headed larva (Walossek *et al*. 1994), makes it unlikely that we can relate it to *A. andresi*.

Other features worth considering are the fairly large caudal outgrowths of *Aengapentastomum andresi* (Fig. 2D). These are much smaller, tipped or papilliform in all other described 'Orsten' pentastomids, although it is difficult to make a clear interpretation for Andres' (1989) specimens since he showed only a few illustrations. Caudal outgrowths of the size of those of *A. andresi* occur in larvae of certain eupentastomid taxa, e.g., in the early larvae of *Subtriquetra subtriquetra* Sambon, 1922 (Fig. 4B) or in larval *Porocephalus crotali* (von Humboldt, 1809). Drawings of larval *Reighardia sternae* (Diesing, 1864) often also include such large outgrowths, but contrast with the SEM images (cf. Walossek & Müller 1994, fig. 27A). Adult females of *Raillietiella mabuiae* Heymons, 1923 (cf. Walossek & Müller 1994, fig. 26c) also have quite distinctive outgrowths similar to those of the new Cambrian form. It seems, as Almeida & Christoffersen (1999) suggested, that larger caudal outgrowths may have evolved several times.
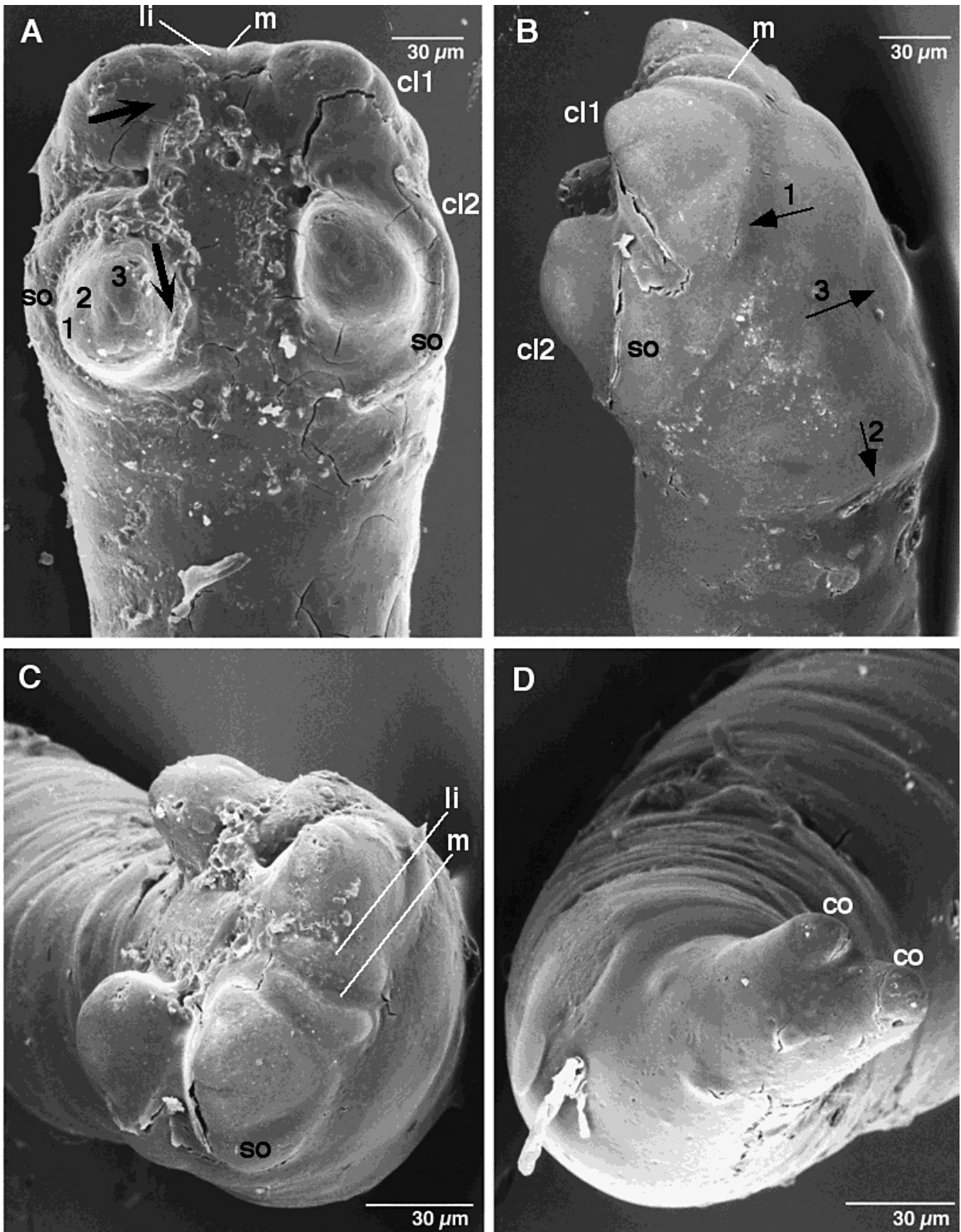
Figure 2. Details of the holotype of *Aengapentastomum andresi* gen. et sp. nov: (A) Head region in ventral view. Inwardly pointing distal (third) article of anterior head limb and posteriorly pointing third article of posterior head limb (articles numbered) almost invisible due to post-mortem abrasion (arrows emphasise orientation); (B) Head from left side. Furrow above socket of anterior limb (arrow 1) represents anterior border of head. Also postero-dorsal border distinct (arrow 2). Dorsal shallow hump encircled by a weak furrow (arrow 3); (C) Head in anterior view; mouth surrounded by lip-like ridges laterally. No sign of frontal papillae dorsal to the mouth; (D) Strongly tapering trunk end in dorso-caudal view; caudal outgrowths somewhat unequal in size. Note that the specimen shown in these pictures has numerous cracks, and thus is quite fragile (abbreviations as in Fig. 1; additionally: (li) lip flanking the mouth).
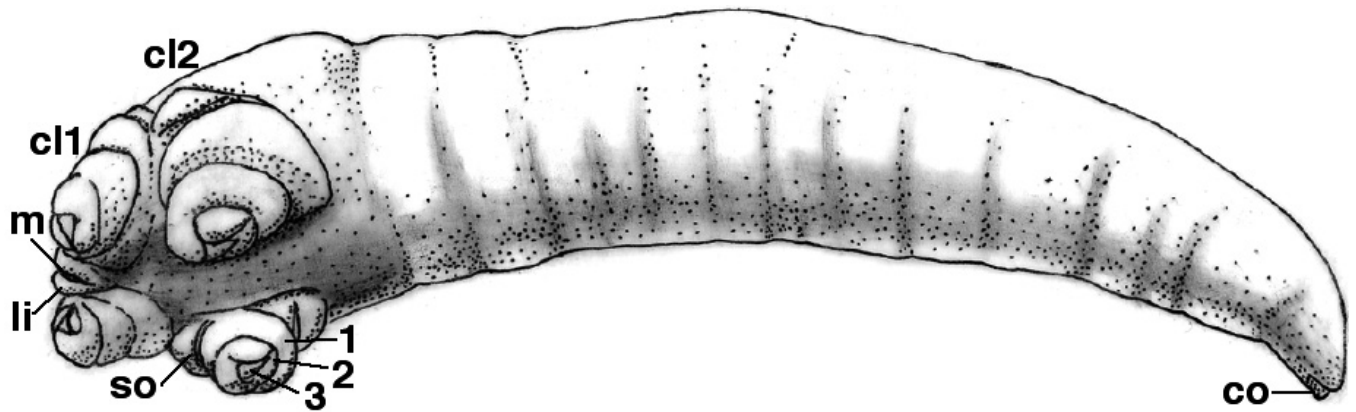
Figure 3. Reconstruction of *Aengapentastomum andresi* gen. et sp. nov. in ventro-lateral aspect. Mouth surrounded by lip-like ridges laterally (abbreviations as in Figures 1 and 2).
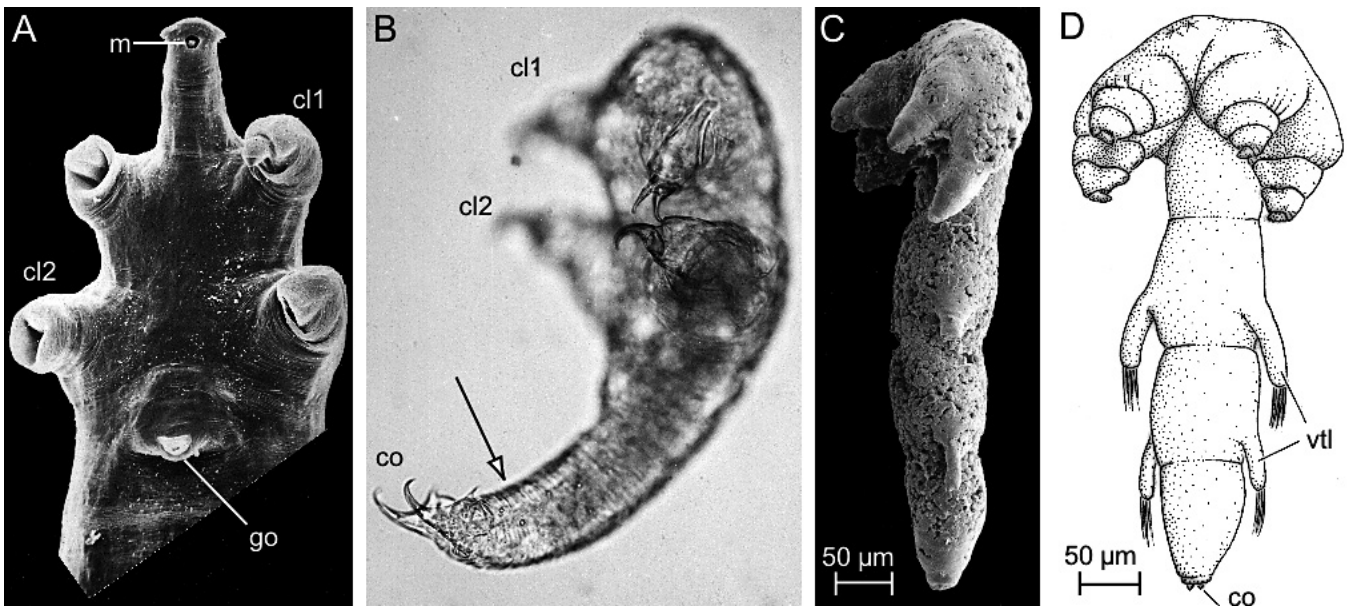

Figure 4. Examples of adults and early larvae of Recent and Cambrian Pentastomida: (A) Head (∼5 mm) of adult of extant *Cephalobaena tetrapoda* Heymons, 1922, from the snake *Philodryas baroni* Berg, 1895, ventral view (courtesy of W. Böckeler, Kiel); (B) Free-living larva of extant *Subtriquetra subtriquetra* Sambon, 1922, from crocodiles, having large caudal outgrowths for locomotion (courtesy J. Riley, Dundee). Note the post-cephalic subdivision of the body (arrow): (C), (D) SEM photomicrograph and reconstruction of larva of Upper Cambrian *Heymonsicambria scandica* Walossek & Müller, 1994, with vestigial trunk limbs (vtl); (go) gonopore; other abbreviations as in Fig. 1.

3. Comparative morphology

3.1. New evidence from Cambrian fossils

Recently, Waloszek (correct spelling of name) and Müller described several three-dimensionally preserved fossils from Upper Cambrian 'Orsten' limestones in Västergötland, Sweden (Walossek & Müller 1994). These 500-million-year-old marine fossils are strikingly similar to early larval stages of pentastomids. Their detailed comparison uncovered even minute details shared with extant tongue worms (Fig. 4A, B), such as small pores on the portions of the two pairs of head limbs and paired cephalic sensilla-like structures on the front of the head and paired outgrowths on the rear of the trunk end (examples in Fig. 4B for extant larvae, Fig. 4C, D for fossil forms). Limb pores were not known previously from extant pentastomids but they were found subsequently also in the larvae and adults of cephalobaenids and porocephalids (Walossek & Müller 1994). Using this information, Walossek & Müller (1994) also traced the three-segmented status of the limbs, as found in the fossils, in extant representatives. Although this had already

been illustrated by Heymons in 1935 (fig. 147 of an uncertain porocephalid called *Pentastomum gracile* Diesing, 1836), limb subdivision had long remained largely misunderstood, such that the distal hooks (= the third portion of the limbs) were regarded as modified legs.

Walossek and Müller were not the first to describe such fossil pentastomids. Dietmar Andres from Berlin had previously reported early larval and ontogenetically more advanced specimens from the isle of Öland, Sweden, although without any detailed and formal systematic description (Andres 1989). Whilst the small stages were either similar to those described by Walossek and Müller (1994) or added new types, the larger specimens importantly showed a characteristic enlargement particularly of the posterior pair of hooks (Andres 1989) – superficially similar to those of the extant *Raillietiella*, and an elongated, carrot-shaped trunk, as found in many living pentastomids. This material may also be Late Cambrian in age. Similar to the sample containing *Aengapentastomum andresi*, it is from Lower Ordovician strata that contain abundant reworked material. With this fossil evidence, not

only evidence of the life cycle of early pentastomids became known, but also anatomical details due to the extraordinary muscle tissue preservation in Andres' material. This permitted reconstruction of the muscle systems of the cephalic legs (segmental muscles and pro- and remotor muscles moving the whole limbs) and trunk (comprising two large paired strands). The only larger discrepancy was that some – not all – of the Upper Cambrian fossil larvae from Västergötland, and also those from Öland, had a more-or-less distinct subdivision of the trunk and short vestigial limbs on it, actually located on the posterior two segments out of a set of three post-cephalic segments. In other fossil forms, only one pair of limbs was present, or none at all – such as in *Aengapentastomum andresi* gen. et sp. nov. and in all extant taxa. All taxa possess a conical, smooth or finely annulated caudal end terminating in a pair of papilla-like outgrowths.

One major problem with extant pentastomid morphology concerns the tagmosis and the segmental status of head and trunk. The head bears only two pairs of uniramous legs, highly modified into hooks. Only the embryo of *Reighardia sternae* has a pair of palp-like structures (Osche 1963, see also Osche 1959, fig. 2b) plus a small protuberance between these 'palps' and the first claw limb. The present authors' studies of an embryo of *R. sternae* did not show such a structure. Osche went far in interpreting the anterior two structures together with the two legs as evidence of an arthropod head and a closer relationship to certain myriapods (Table 1). Whereas Andres' (1989) material does not show any frontal structures, only a single form amongst our fossil material (*Boeckelericambria pelturae*) bears palps similar to those of the *R. sternae* embryo (Walossek & Müller 1994, fig. 25a). Instead, in the so-called hammer-headed forms, the present authors observed paired papillae dorso-frontally, similarly to other extant pentastomids. It has often been cited that there should be two pairs in extant pentastomids (Heymons 1935), but it was not possible to validate this from the literature, with one possible exception – an uncertain, but most likely larval porocephalid *Pentastomum gracile* Diesing, 1936, illustrated by Heymons (1935, fig. 147). It has been suspected that papillae and palps are homologues (Böckeler 1984c). Indeed, the frontal papillae of *Raillietiella* are more palp-like than papillate, but they appear as just a single pair.

The cephalic nervous system comprises only a single anterior ganglial mass in *Reighardia sternae* (Böckeler 1984c), and two pairs of ganglia post-orally corresponding to the legs. Hence, it seems very unlikely that the anterior mass is a compound of ganglia from more than one segment, nor does it innervate two different anterior paired external structures (see below), as was suggested by Almeida & Christoffersen (1999) as evidence of two more anterior limb-bearing segments of the head.

Extant pentastomids possess three pairs of ganglial nodes behind those innervating the cephalic claw limbs. These are indicative of the original presence of three original post-cephalic trunk segments in the sense of metameres (Böckeler 1984c; Walossek & Müller 1994; see also Almeida & Christoffersen 1999). Indeed, all those Cambrian fossil pentastomids (larvae and later stages) with a well-developed segmentation show three distinctive post-cephalic segments – segments 2 and 3 may bear vestigiae of limbs – plus a conically tapering caudal portion (Walossek & Müller 1994). Andres' (1989) material provides supporting evidence that the posterior two of the three segments (the limb-bearing ones) and the conical caudal end eventually elongated extensively to form a carrot-shaped trunk, whilst the anterior trunk segments remained short, apparently having ceased to grow further. Considering these larger forms, Walossek & Müller (1994,

fig. 21) proposed that, during later evolution toward the crown-group pentastomids (Eupentastomida, new name herein, see Fig. 6), all three larval post-cephalic segments ceased to grow but only the conical caudal end of the trunk elongated enormously. This resulted in a trunk of modern forms comprising only the caudal end, which became as long as the combined preceding trunk segments in the fossils.

Already by the Late Cambrian, the far laterally-inserting trunk limbs were little more than small vestiges at most, and the anterior trunk segment had no limbs. The above interpretation of the different development of the carrot shape in the Palaeozoic and the Recent pentastomids is further supported by the fact that Andres' (1989) large specimens have paired dorsal and ventral muscle strands in their anterior trunk (because of the metameric nature; see Andres 1989, pl. 2:4–8), whilst there are small muscle portions relating to the fine annulation of the trunk of crown-group pentastomids. The annulation of extant forms is inferred as secondary and as a pseudo-annulation simply splitting the body and muscles of the caudal portions into short but regular sections. This is corroborated by the 'anterior' position of the gonopore in several of the extant pentastomids, which lies behind the segmented post-cephalic region and in front of the pseudo-annulated portion (hence this is not 'progoneate' [anterior gonopore position as opposed to 'opisthogoneate'] as assumed by Osche 1963, who regarded pentastomids as early myriapods).

Thus, the carrot shape of the fossil and extant pentastomids originated from different allometric growth but from the growth of the same number of segments. This may also be the reason why previous workers did not observe the four trunk muscle strands in extant taxa. Yet, plesiomorphically, modern pentastomids hatch with the adult number of two limb-bearing cephalic (still uncertain) and only three trunk segments plus a caudal end, as in the fossil stem-lineage forms. Hatching with the final, and even such an extremely low, number of body segments, as in pentastomids, is unusual among euarthropods. This does not indicate epimeric development, where the larval phase is completed inside the egg.

3.2. The new taxon *Aengapentastomum andresi* gen. et sp. nov.

The single specimen of the new species discovered in a quarry in the region of Falbygden, Västergötland, Sweden, actually occurred in the same sample that yielded *Heymonsicambria repetskii* Walossek & Müller, 1994. Much of the microfauna, conspicuously including the conodont fauna, has been reworked from older sediments. Therefore, the Early Ordovician age of the surrounding rock gives a misleading impression, but the age of the specimen must be between early Late Cambrian and the Cambro-Ordovician boundary. The approximately 700 µm-long specimen is complete and more advanced in development than any of the larvae described by Walossek & Müller (1994), or *Heymonsicambria taylori* Walossek, Repetski & Müller, 1994 from Canada (Walossek et al. 1994), but comparable to the larger specimens reported by Andres (1989).

It may be argued that the specimen of *Aengapentastomum andresi* represents a later developmental stage of one the Västergötland forms, or *H. repetskii*, but its morphology is different enough to preclude a close relationship. This is particularly true because the specimen of *A. andresi* is not a typical hammer-headed type of larva but has specially shaped and oriented claw limbs: the anterior pair is oriented inwardly and anteriorly and is smaller than the posteriorly and backward pointing second pair. With this design, the new form more closely resembles some of Andres' specimens from the isle of Öland (Andres 1989, pl. 1:1–6, pl. 2:1, 3, 5–8). It may

well be that at least one of Andres' specimens (1989, pl. 2:1) belongs to *A. andresi* gen. et sp. nov. It is possible that the small specimen illustrated in Andres' Plate 1:1 is also con-specific, respectively an earlier semaphoront of the new species. This Öland specimen has, however, vestigial legs on its body, which are missing in *A. andresi*. It also differs in having a clear trunk division, but shares a similarly short and separated caudal end. The larger similar specimens of Andres' (1989) material all have vestigial limbs on their trunk, thereby ruling out a close relationship to *A. andresi*. Neither can gender differences be excluded.

Aengapentastomum andresi also differs in other aspects from all previously described larger forms: (i) the anterior margin of the head is marked by a faint borderline in the form of a furrow (Figs 1A, arrow 1; 2B, arrow 1). Posteriorly the head shows a rim (Figs 1A, arrow 2; 2B, arrow 2). The latter feature is known only from the round-headed type of larva *Boeckelericambria pelturae*; (ii) there is an almost frontal mouth (Figs 1B, 2A, C), which may indicate the ability for active feeding. A mouth – and in a similar position and with flanking 'lips' (Fig. 2C) – has only been described so far from the round-headed larva of *B. pelturae* (cf. Walossek & Müller 1994, fig. 14c); (iii) the trunk is weakly subdivided into some 10–12 annulations (Figs 1–3). There are even more, but less distinct, annulations between these; (iv) the caudal end is rather short and narrower than in any other fossil form, while the caudal outgrowths are the largest of all such outgrowths described so far. The extensions are slightly unequal in size (Fig. 2D), but this may be an individual artefact. The weakly humped centre of the dorsal head region (Fig. 2B) has no counterpart in any of the other fossils, nor is this structure described for extant pentastomids either. *Reighardia sternae* possesses an embryonic organ at a similar position (egg gland, see Osche 1959, 1963; for correct and recent citation of the egg-gland see Stender-Seidel & Thomas 1997), but homology with this is rather unlikely because *R. sternae* is the only extant species possessing this structure.

4. Discussion

4.1. Phylogeny within Pentastomida

The features of *Aengapentastomum andresi* gen. et sp. nov. discussed above enlarge the data set of Cambrian taxa presumed to represent stem-lineage derivatives of Pentastomida, as understood herein. The present morphology- and palaeontology-based assignment of the fossils to Pentastomida rests on numerous shared features ranging from cuticular structures to segmental organisation, development and anatomical features. In particular the neuro-anatomical data provided by Böckeler (1984c) leave very little possibility of interpreting the nervous system as secondarily modified or simplified from a state as developed in in-group eucrustaceans. Almeida & Christoffersen (1999) accepted the affinities of the Cambrian fossils with the modern pentastomids, although taking a more hesitant viewpoint about the systematic affinities of the group within Arthropoda *sensu lato*. Taking all evidence into account, ontogeny also can be considered as an argument for relating the Cambrian forms to living pentastomids. The present authors regard this as the most parsimonious explanation – apart from the fact that this view causes no argumentational discrepancies/conflicts in terms of morphology. If convergent evolution of all these strikingly similar details is assumed, the result can only be confusion – no matter what underlying systematic position of the pentastomids within Arthropoda *sensu lato*. The most problematic features are the limbs and their pores.

The few significant differences between the fossils and the living taxa are mainly the differences in trunk development. This can be explained by differential growth of the segments and elongation of the caudal portion. Moreover the original trunk limbs are already small vestiges in the Upper Cambrian forms – several taxa even lacked them from hatching or lost them during growth. Since *Aengapentastomum andresi* lacks trunk limb vestiges and a distinct subdivision of the trunk region, only a detailed re-analysis of Andres' specimens (more than one thousand according to Andres (pers. comm. 2003)) can shed more light on this taxonomic in-group problem. Remarkably, the new form has a fine annulation along the trunk, a slightly offset caudal end and two fairly large caudal outgrowths (=terminal papillae). These features and the specific position and orientation of the cephalic legs bear resemblance to the extant taxon *Raillietiella hemidactyli*. Re-investigation of Andres' material could provide a better understanding of the evolution of pentastomids from the stem lineage in the direction of the crown group. The pores discovered by Walossek & Müller (1994) on the inner edge of the cephalic limbs on the fossils are differentiated and still occur in the same fashion today in extant forms (a slit pore and round pore, arrowed in Fig. 5).

Recently however, Lavrov *et al.* (2004, p. 544) questioned this assignment of the 'Orsten'-type fossils to pentastomids. Furthermore, trusting exclusively in molecular data, they went as far as stating that fossils cannot be used to prove or disprove systematic hypotheses. Apart from the fact that there is overwhelming literature to demonstrate the usefulness of palaeontological data for phylogenetic interpretations of whatever group of organisms, science cannot prove at all – which holds equally for molecular data. One can only hypothesise on the basis of probability (reliability, credibility). There are indeed features enough, which Lavrov *et al.* (2004) seem to have overlooked in Walossek & Müller (1994). But only discoveries such as the present fossil material can add to our fragmentary knowledge. Only fossils, as once-living organisms, together with specimens from living species, can provide the factual test of any hypothesis based on systematic affinities and morphologies. Specifically, there are enough features in the fossil pentastomids, such as shape, size, and segmentation, as well as details, such as the frontal and caudal papillae, the claw limbs and their two different pores (Fig. 5), which are not just similar to but exactly match those of extant taxa. Fossils can help to reconstruct ground patterns, which no molecular study will ever be able to do.

Discussing possible relationships of and within Pentastomida, one has to clarify first the monophyletic status of this group. Walossek & Müller (1994) postulated the following autapomorphies developed in the stem species of Pentastomida (node 1 in Fig. 6):

- full number of segments at hatching;
- paired uniramous head limbs developed as attachment devices, three-segmented;
- first trunk metamere lacking limbs;
- second and third trunk metameres possessing at most vestigial limbs with a distal tuft of setae (not hooks, as Almeida & Christoffersen 1999 claimed); and
- caudal trunk portion with a pair of caudal outgrowths or papillae.

Crown-group members of the Pentastomida (Eupentastomida new taxon) are distinguished from the Cambrian/Ordovician fossil forms by several characters listed by Walossek & Müller (1994) and Almeida & Christoffersen (1999) (node 2 in Fig. 6). The two most obvious ones are:
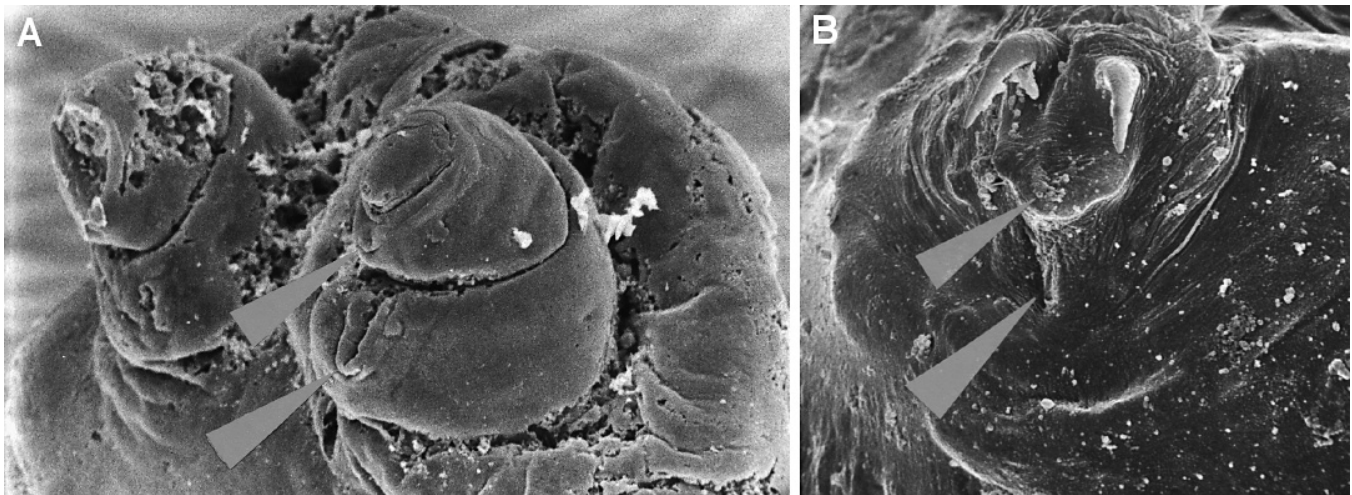
Figure 5. Shared details between early larvae of Cambrian and Recent pentastomids: pores on leg segments: (A) Larva of Upper Cambrian *Boeckelericambria pelturae* Walossek & Müller, 1994 (from Walossek & Müller 1994); (B) Larva of extant *Reighardia sternae* (Diesing, 1864), showing not only the subdivision into three parts, but also two pores (courtesy: W. Böckeler, Kiel).
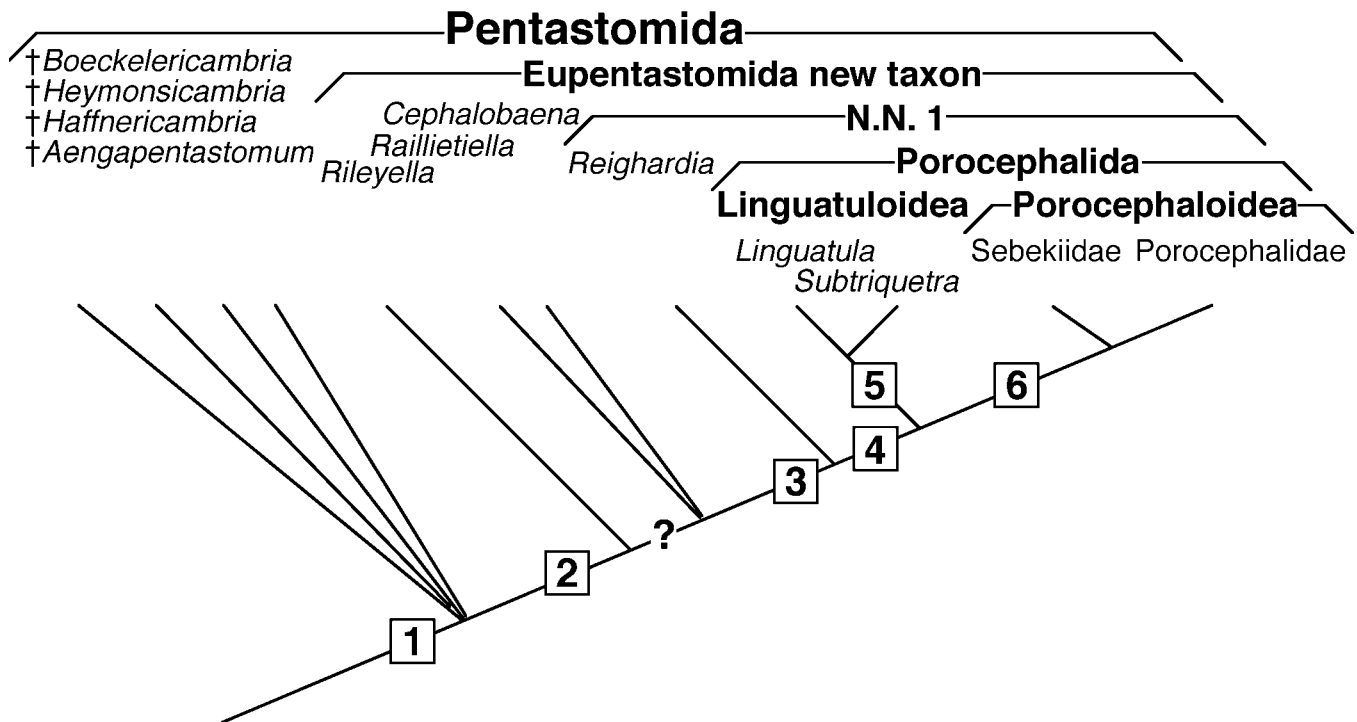

Figure 6. Hypothesised phylogenetic relationships within Pentastomida (modified from and including the data from Almeida & Christoffersen 1999 and Spratt 2003). Possible autapomorphies in the ground patterns of stem species (nodes) along the evolutionary lineage toward Porocephaloidea sensu Almeida & Christoffersen (1999) (*Rileyella* added by Spratt 2003 below *Cephalobaena* and *Raillietiella*; characters unclear, indicated by a questionmark between 2 and 3) are as follows:

1 head with two pairs of grasping limbs, limbs three-segmented (plesiomorphy: leg segments connected by pivot joints); slit pore medially on proximal segment of limb, rounded pore on next segment; trunk made of three metameres and a caudal end; larvae hatch with the final number of segments;

2 larvae with frontal penetrating structures; trunk of later larvae and adults made of 4th trunk portion only; anterior metameres short, close to head; elongate caudal trunk portion finely annulated (pseudo-annulation); cuticular pores all over the body in larvae and adults;

3 loss of terminal papillae (caudal outgrowths) in adults (according to Almeida & Christoffersen 1999);

4 more than 10 characters listed by Almeida & Christoffersen (1999), including the compaction of ganglia to a single sub-oesophageal mass;

5 adult body shape flattened and spatulate;

6 ovoid early larvae (according to Almeida & Christoffersen 1999; see text for details) [Sebekiidae is grammatically correct, not Sebekidae as frequently used in the literature].

● the penetrating apparatus of the larvae; and
● the different fate of the posterior trunk (pseudo-annulation of the caudal portion).

It is most likely that the penetrating apparatus developed in the course of the complication of the life cycle in the stem species of the Eupentastomida. It is less easy, or impossible, at

present to establish the reason for the modification of the trunk. One feature remains problematical: among the early larvae of the Cambrian/Ordovician pentastomids, trunk legs may be present, partly present, or absent. Until now, only the larger specimens reported by Andres (1989) were known, and all have limb vestigia. The specimen of *Aengapentastomum andresi* gen. et sp. nov. is the first of a later stage that lacks legs, and no Recent pentastomids have external trunk legs (only ganglia retained). Yet, lack of structures is problematic in any discussion of phylogeny. As mentioned above, there are more similarities between *A. andresi* and extant pentastomids: the shape, position and orientation of the head limbs (especially *Raillietiella hemidactyli*), the fine trunk annulation (many Recent species), and the rather distinctive caudal outgrowths (*R. hemidactyli*, but also others). Thus, based on the combination of characters, absence of trunk legs in *A. andresi* appears to be a homoplasy.

Considering the situation within the crown-group, Almeida & Christoffersen (1999) concluded that the traditional cephalobaenids (*Cephalobaena tetrapoda*, *Raillietiella hemidactyli* and *Reighardia sternae*) can no longer be considered as monophyletic. They argued convincingly for the paraphyletic status of Cephalobaenida, the taxon being based on plesiomorphic features. According to these authors, *Cephalobaena* Heymons, 1922, *Raillietiella* Sambon, 1910 and *Reighardia* Ward, 1899 branched off successively along the lineage towards the monophyletic Porocephalida, *Reighardia* representing the sister taxon to the Porocephalida. Rather than their three-part division of the evolutionary lineage towards the monophyletic Porocephalida, the present authors can only substantiate a two-part division, based on the following:

- Mouth openings with surrounding swellings are present, e.g., in the fossil *Boeckelericambria pelturae* and the new form *Aengapentastomum andresi* (Fig. 2C) and in the Recent *Reighardia sternae*, but they cannot be termed 'rostra', as Almeida & Christoffersen (1999) did in their analysis. In *Cephalobaena tetrapoda*, the mouth is located at the tip of a cephalic protrusion (Fig. 4A), the 'rostrum' of Almeida & Christoffersen (1999), which the authors interpreted as a plesiomorphy without giving any further information; this implies reduction of this 'rostrum' in *Raillietiella hemidactyli* – which actually has a mouth cone – and its complete loss in all other eupentastomids. Circum-oral internal stiffenings are simply necessary for better sucking (cf. Leeuwen & Muller 1984) and are common to all pentastomids including those from the Upper Cambrian. Therefore, the present authors cannot agree with the character 'rostrum reduced' of Almeida and Christoffersen (1999) as an autapomorphy of eupentastomids except *C. tetrapoda*, and they leave their tree unresolved at node 2 in Figure 6.
- Elongation of the cephalic legs of *C. tetrapoda* is interpreted by Almeida & Christoffersen (1999) as a plesiomorphy. Since there are no indications of such a feature in any of the fossil taxa, it seems more likely that the feature 'elongated legs' represents an autapomorphy of this single taxon – in addition to the protrusion of the mouth area.
- The lack of caudal outgrowths or 'terminal papillae' in adult *R. sternae* and porocephalids is a synapomorphy in the view of Almeida & Christoffersen (1999) (set 3 in Fig. 6). This remains similarly problematical until more comparative studies are available (investigations of larval *Reighardia sternae* by Storch & Böckeler 1982 point out clearly a sensory function and an ultrastructure found amongst arthropods). Since there is no autapomorphy to establish the monophyly of a taxon Cephalobaenida, the present

authors support Almeida & Christoffersen (1999) in regarding them as paraphyletic.

At present, we hesitate to suggest the placement of *Aengapentastomum andresi* closer to the crown-group, Eupentastomida new taxon (see Fig. 6). The name 'Pan-Pentastomida', as proposed by Almeida & Christoffersen (1999), is not valid in a formal classification, and it is suggested that the established taxonomic name Pentastomida is retained for the entire group, including the stem-lineage derivatives, and that the validly available taxon name 'Eupentastomida, new taxon' is obtained for the crown group (autapomorphies as given by Almeida and Christoffersen 1999). The in-group situation remains problematical, because several decisions by these authors within the crown group seem to be based on symplesiomorphies or misinterpretations (e.g., the rostrum). Again, it may well be that the known Lower Palaeozoic stem-lineage pentastomids form a paraphyletic assemblage.

4.2. Phylogeny of Pentastomida within Arthropoda *sensu lato*

Concerning the phylogenetic position of Pentastomida, Walossek & Müller (1994) discussed the uncertainties in estimating relationships on the basis of their discoveries and their reconstructions of the limb system and body tagmosis. In the light of information about the extant forms from embryology (e.g., Korschelt & Heider 1936) and the development of the nervous system (summarised in Böckeler 1984c), they concluded that pentastomids are probably phylogenetically older than the in-group taxa of Euarthropoda. This would match earlier suggestions by Heymons (1926a) and Pflugfelder (1980), or other authors promoting the hypothesis, that pentastomids, tardigrades, and onychophorans, as 'prot-arthropods', form a paraphyletic assemblage of stem taxa on the evolutionary lineage toward the Euarthropoda *sensu* Walossek (1999). Maas & Waloszek (2001; Fig. 6) and Maas *et al.* (2004, fig. 4) based their interpretation of the phylogeny of Arthropoda upon the progressive development of cuticular specialisations. Their analysis led the authors to the following interpretations:

- Onychophorans, lobopodians, and tardigrades are basal because of the lack of sclerotised body segments and arthrodised legs (*arthropodia* are one of the autapomorphies of Arthropoda *sensu stricto*; see Waloszek *et al.* 2005 also for the terms *arthropodisation* and *arthrodisation*);
- The development of jointed legs with pivot joints between the limb segments indicates a progress in the process of *arthropodisation*, from the tubular 'lobopodium' of onychophorans and allied to the euarthropod limb with basipod, endo- and exopod; possession of segments connected by joints represents, therefore, a synapomorphy of Pentastomida and Arthropoda *sensu stricto*;
- Pentastomids branched off before reaching the level of *arthrodisation*, i.e. the development of tri-partite tergal sclerotisations connected by membranous cuticle, an additional autapomorphy of Arthropoda *s. str.* (cf. Maas *et al.* 2004; Waloszek *et al.* 2005 for more autapomorphies of this taxon).

Accepting these interpretations, the present authors exclude pentastomids from the taxon Arthropoda s. str. *sensu* Maas *et al.* (2004). In their view, neither tagmosis of the pentastomids, nor their limbs or any other external and internal features are similar to structures of any eucrustaceans, and particularly not to branchiurans. Virtually all parasitic eucrustaceans can undoubtedly be placed within a specific taxon, e.g., based on details or specific larval features (for

parasitic rhizocephalans as aberrant barnacles, as an example, see, e.g. Høeg 1995).

So, if pentastomids are regarded as in-group eucrustaceans and even as being closely related to branchiurans, this would imply that, already in the Cambrian period, pentastomids would have modified or lost all originally shared features of different levels, such as those apomorphies making them euarthropods, mandibulates, crustaceans, labrophorans, eucrustaceans, maxillopods, and so on (see, e.g., Maas *et al.* 2003 for character sets), hereby disguising the true relationships. Likewise, pentastomids should also have modified other features back into their plesiomorphic ancestral design; for example: head composition, nervous system, limbs (see also Tchesunov 2002). This does not seem very parsimonious. Morphology may indeed become modified during evolution into a parasite, but its systematic origin remains recognisable in virtually all cases known of at present (see also Jenner 2004 for discussion of this phenomenon).

Of course, it cannot be denied that some features are indeed similar between pentastomids and branchiurans:

- Wingstrand (1972) found that the sperm morphology of the branchiuran *Argulus foliaceus* and the pentastomid *Raillietiella hemidactyli* is very much the same. Yet, sperm morphology has not been studied in any other species (see also Storch & Jamieson 1992; Jamieson & Storch 2000);
- On the basis of an 18S rDNA analysis, Abele *et al.* (1989, 1992) supported the idea of a close relationship of pentastomids and branchiurans (see also Spears & Abele 1998; Zrzavý *et al.* 1998);
- Giribet & Ribera (2000) investigated 18S rDNA and 28S rDNA sequences of various metazoans and suggested that pentastomids are most closely related to ostracodes, another possibly maxillopodan group of crustaceans, but are less likely related with branchiurans;
- Lavrov *et al.* (2004) sequenced the mitochondrial DNA of the pentastomid *Armillifer armillatus* (Wyman, 1847) and some crustaceans including the branchiuran *Argulus americanus* Wilson, 1902. From their results on sequences and gene arrangements, they concluded that pentastomids are crustaceans with affinities to branchiurans. As a critical point of their analysis, the authors used the prerequisite that *Limulus polyphemus* Linné, 1758 possessed the ancestral (plesiomorphic) gene-order representing the euarthropod ground pattern. Such a proposition cannot be sustained before investigation of gene arrangement in onychophorans and tardigrades.

Apart from these interpretations, there are no morphological, anatomical, or embryological features available that could, even to a minor degree, support a relationship between pentastomids and branchiurans (see also Zrzavý 2001 for discussion of *pro* and *contra* arguments). In their valuable in-group cladistic analysis of the pentastomids, Almeida & Christoffersen (1999) used a total of 32 morphological, anatomical and developmental characters and refuted any relationship between pentastomids and Eucrustacea. (However, their reconstruction of a 'ur-form' pentastomid cannot be used as an argument because it is a sketch that includes only plesiomorphic features valid for Arthropoda *sensu lato*, and therefore resembles lobopodians and tardigrades more than pentastomids. All legs are of the same lobopodial design and there is no head and tail tagmosis. This body design disagrees with the morphology of the Cambrian fossils presented above). Tchesunov (2002), who revised characters for and against a close relationship between Pentastomida and Branchiura (=Ichthyostraca Zrzavý, Hypsa & Vlaskova, 1998), came to the same conclusion that pentastomids are not closely related to branchiurans.

A feature complex that is used by the 'Ichthyostraca' advocates to support a close relationship between Pentastomida and Branchiura is ovary morphology and oogenesis, studied by Böckeler (1984b) and Ikuta & Makioka (1999). In the present authors' view, these results should be interpreted differently. Böckeler (1984b) studied the ovary and oogenesis of *Reighardia sternae* (Diesing, 1864) and found that the oogenesis of pentastomids is comparable with that of onychophorans and chelicerates rather than with that of other arthropods. The results of the study of Ikuta & Makioka (1999) on ovary structure and oogenesis in maxillopodan crustaceans revealed a close resemblance between pentastomid, cheliceratan and branchiuran growth of the oocytes on the outer surface of the ovary. Since this is very similar to the mode in Onychophora, and with regard to the position of at least some of the taxa in the system of Arthropoda (Maas & Waloszek 2001), ovary morphology and oogenesis of these taxa display the plesiomorphic state and are not shared characters in the sense of uncovering relationships.

From the present point of view, the problem of the systematic position of Pentastomida remains for the moment unresolved. It is not possible to convincingly argue for one or the other hypothesis, so long as so many conflicting characters exist. We are convinced that morphological and molecular characters should be congruent to give final clues about relationships. However, only morphological data can tell us about ground patterns, branchings and evolutionary pathways. They have also a much higher degree of complexity, therefore *per se* have a high reliability.

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DIETER WALOSZEK and ANDREAS MAAS, Section for Biosystematic Documentation, University of Ulm, Helmholtzstrasse 20, D-89081 Ulm, Germany.
e-mail: dieter.waloszek@uni-ulm.de; andreas.maas@uni-ulm.de

JOHN E. REPETSKI, U.S. Geological Survey, Mail Stop 926A National Center, 12201 Sunrise Valley Drive, Reston, VA 20192, USA.
e-mail: jrepetski@usgs.gov