

Cambrian Derivatives of the Early Arthropod Stem Lineage, Pentastomids, Tardigrades and Lobopodians – An ‘Orsten’ Perspective*

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Abstract. ‘Orsten’-type preservation is the phosphatisation of cuticular surfaces without any further deformation and has yielded completely three-dimensional fossils, mainly arthropods at scale of 100 µm–2 mm. Records of such exceptional fossils are now reported from several continents and from the Early Cambrian (approx. 520 Mi. years BC) to the Early Cretaceous (approx. 100 Mi. years BC). ‘Orsten’-type *konservat-Lagerstätten* from the Middle and Upper Cambrian have brought up mainly crustaceans and representatives of the Euarthropoda, but also derivatives of their early stem lineage. These are larval stages of Upper Cambrian pentastomids, tongue worms, which today are parasites of various tetrapods. A Middle Cambrian representative of the minute tardigrades is currently under description; it possibly represents the adelphotaxon of extant Tardigrada. New to science are fragments of a small tubular, finely annulated organism with similarly annulated segmental tubular limbs. This Upper Cambrian form, currently under investigation, may represent the first lobopodian in an ‘Orsten’-type preservation and expands their record to the late Cambrian. It shares with several of the Lower to Middle Cambrian Chengjiang and Burgess Shale fauna lobopodians the lobopodian design of its limbs, paired segmental dorsal outgrowths, and the finely annulated tubular body, which is smooth in the limb regions. New information presented by this ‘Orsten’ fossil concerns cuticular details undetectable on flattened fossils. Pentastomids, tardigrades and the onychophorans/lobopodians have been called “pro-” or “prot-arthropods” because they still lack, or partly lack, characteristic features known from later derivatives of the evolutionary line of Arthropoda. Among the three taxa, the Pentastomida are assumed to be the latest offshoot because they possess segmented limbs with pivoted joints between the articles. The now established record of all of the “pro-arthropods” and even true crustaceans in the earliest Palaeozoic implies, in our view, that the ancestry of Arthropoda lies even further back well in the Pre-Cambrian.

Key words. Arthropoda, Euarthropoda, calcitic nodules, phosphatisation, arthropodium, arthrodisation, arthropodisation, pivoted joints.

1. INTRODUCTION

‘Orsten’ is an expression for a very exceptional type of preservation and/or type of a so-called *konservat-Lagerstätte* rather than referring to a special geographic point or time level. Sometimes, however, it is also equivalent with the first discoveries made in southern Sweden (Västergötland and Isle of Öland) by the German palaeontologist Klaus J. Müller, Bonn, in the Mid Sixties.

In fact, ‘Orsten’-type preservation is the secondary phosphatisation, by impregnation, of the upper part of cuticle, apparently soon after the death of the animals. Subsequently, no further diagenetic deformation – apart from wrinkling or shrinking effects of the dead carcasses – had occurred. Thus, the ‘Orsten’ yields completely three-dimensional fossils having preserved all details, such as eyes, limbs or hairs, still in place, i.e. in their original topology. This was caused by the post-mortem embedding of the animals within limestones that later formed into nodules (Fig. 1). Since the fossils are phosphatised (fluoritic apatite), they can be etched from their surrounding rock by weak acetic acid. Such limestone nodules have locally been called ‘Orsten’, possibly even originating from “orne sten”

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Fig. 1. Upper Cambrian calcareous 'Orsten' nodule embedded within alum shales (photograph taken in a quarry near Falköping, Västergötland, Sweden, by DW).

(pig stone), which roughly translated means "smelling stone" due to its characteristic smell of rotten eggs at cracking or processing because of a high content of organic matter.

This type of preservation is rather rare and seems to affect mainly arthropods at a size range of approximately 100 up to 2000 µm in body size. Examples are given in Fig. 2 (for details see MÜLLER & WALOSSEK 1985, 1986, 1988; WALOSSEK & MÜLLER 1990, 1998). As is typical for the 'Orsten'-type of preservation, the very soft joint membranes between limb podomeres or body segments are well preserved, as are fine bristles on the limbs, such as depicted in Fig. 2C. Records of such phosphatised fossils are now known from most continents (Fig. 3) and range in age from the early Cambrian (approximately 520 Mio. years old) to the early Cretaceous (approximately 100 Mio. years).

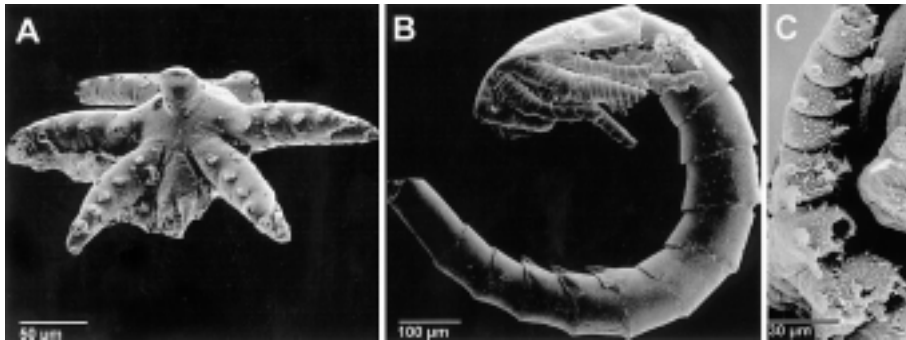


Fig. 2. SEM example pictures of Upper Cambrian Swedish 'Orsten' fossils. **A.** Type-A larva from ventral, antennula (= first appendage) on right side broken off (from MÜLLER & WALOSSEK 1986). **B.** *Skara anulata* Müller, 1983 as a representative of the Skaracarida Müller & Walossek, 1985 (Maxillopoda) (from MÜLLER & WALOSSEK 1985). **C.** First maxilla of an adult specimen of *Bredocaris admirabilis* Müller, 1983 (from MÜLLER & WALOSSEK 1988).

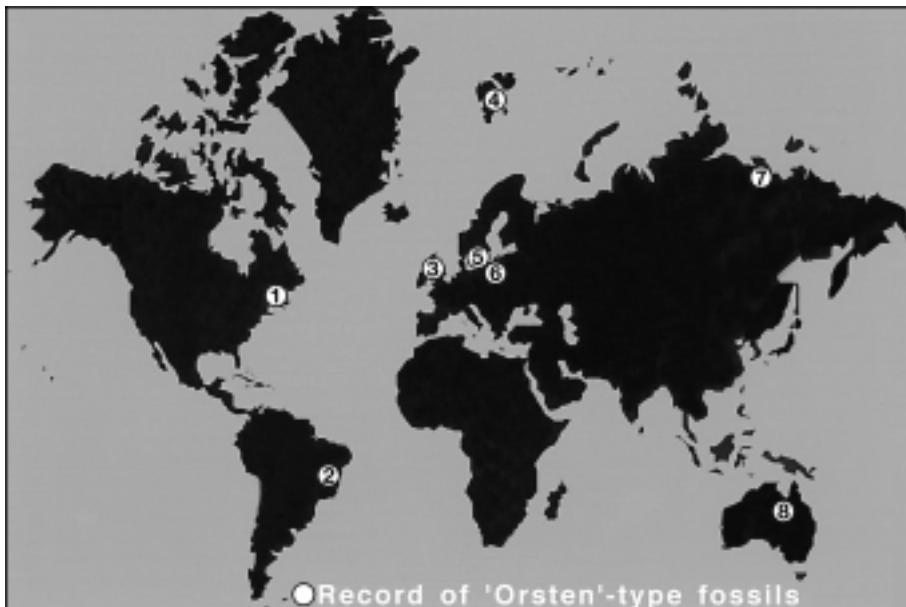


Fig. 3. World map with numbered finds of 'Orsten'-type of preservation. **1.** Newfoundland, Upper Cambrian/Lower Ordovician; **2.** Santana Formation, Brazil, Lower Cretaceous; **3.** Comley, Wales, Great Britain, Lower Cambrian; **4.** Spitsbergen, Norway, Triassic; **5.** Southern Sweden, Upper Cambrian; **6.** Poland, Upper Cambrian/ Lower Ordovician; **7.** Lena area, Siberian plate, Middle Cambrian; **8.** Georgina Basin, Australia, Middle Cambrian (cf. WALOSSEK 1999).

2. ARTHROPODS OF THE SWEDISH 'ORSTEN'

Heading from the euarthropodan level of organisation down the evolutionary line of the Arthropoda (Fig. 4), we will present less well known or still unknown 'Orsten' fossils as representatives of this early line of the Arthropoda. To clarify our understanding of what the taxon Euarthropoda is, we consider the Euarthropoda to embrace at least the taxa †Trilobita, Chelicerata, Crustacea, Atelocerata, i.e. those arthropods sharing, in their ground pattern, a head tagma with one pair of antennae (first antenna, antennula of Crustacea) and 3 pairs of biramous limbs covered by a uniform shield, a segmented, limb-bearing body, and all post-antennular limbs comprising a well-sclerotised basipod carrying two rami. The inner ramus is 7-segmented (endopod) and the outer one is a seta-bearing flap (exopod). This limb design might have been achieved even earlier in the late stem lineage of Euarthropoda, so would represent a plesiomorphy in the ground pattern of this taxon. In evolutionary terms, the endopod is the retained segmented distal end of a formerly uniformly segmented limb, as developed in the Lower Cambrian arthropod †*Fuxianhuia protensa* Hou, 1987, while the basipod is the product of fusion of the proximal segments (WALOSSEK 1999). The exopod was originally just a passive flap (e.g., in *Fuxianhuia protensa*), receiving marginal setation subsequently when arising from the sloping outer edge of the basipod. Free mov-

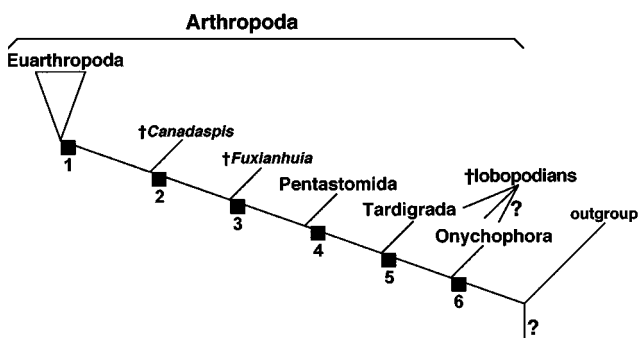


Fig. 4. Argumentation scheme of the phylogeny of Arthropoda. Black squares indicate sets of autapomorphies of the respective stem species. Example features (key developments): **1.** head with antennula + 3 pairs of limbs with a basipod carrying a 7-segmented endopod and flat exopod; **2.** arthropodium with subdivision of stem into locomotory and feeding parts; **3.** biramous arthropodium; **4.** pivot-jointed arthropodium; **5.** arthrodisation = segmental subdivision of cuticle in softer joints and firmer segment parts; **6.** moulting of cuticle (unsure with respect to the Ecdysozoa hypothesis) (numbering according to successive argumentation within the text; fossil taxa indicated by a cross).

ability by internal muscles occurred much later, most likely convergently in the various euarthropodan lines. Thus there was never an equality of the rami and the coxa, which is only developed on some crustacean limbs, and does not belong to the ground pattern of the Euarthropoda. Moreover, there are terms for structures of the early evolution of the arthropod limb like "exites" or "prae-coxa" that do even not exist. They are simply misleading since mixing up quite different outgrowths of the arthropod limbs that evolved at different times and in different groups.

Before this level of Euarthropoda, there are a number of taxa that contribute to the set of characters of Euarthropoda, such as the above mentioned *Fuxianhuia protensa* and †*Canadaspis* (first described: *C. perfecta* (Walcott, 1912); Fig. 4). They cannot be discussed at this place, but only briefly mentioned that they have body segments and articulated legs, so are arthro-dial and arthropodal, but both do not have a basipod and also do not have a head of the amount of segments of the Euarthropoda (WALOSSEK 1999).

Earlier than this, there is a set of taxa in the arthropodan lineage that has been variously termed pro- or prot-arthropods (e.g., PFLUGFELDER 1980). These are the Pentastomida, tongue worms, the Tardigrada, water bears, and the Onychophora, velvet worms, plus the exclusively Cambrian so-called lobopodians ("Lobopodia" Snodgrass, 1938). Authors have discussed the Pentastomida as in-group Eucrustacea closely related to branchiurans (fish lice) (e.g., WINGSTRAND 1972; ABELE et al. 1989), but in our view they are early offshoots of the euarthropodan line (see below for discussion).

Adult Pentastomida are parasites that live exclusively in the respiratory tract including the mouth region and noses of land-living, mostly carnivorous tetrapods, ranging from turtles, snakes, lizards to crocodiles, birds and mammals. Pentastomida feed on blood, mucus or lymph fluid. The larvae of Pentastomida hatch from the eggs, pass through the gut of their host and migrate through its body to live in different organs and finally, depending on the life cycles, in the lung system of their definitive host. The body of the larvae usually comprises a thicker anterior part with the small mouth frontoventrally and two pairs of hook-like limbs and a thinner tail piece carrying little papillae or hooks caudally (Fig. 5).

Remarkably, the only fossil record of Pentastomida is from 'Orsten' occurrences (WALOSSEK & MÜLLER 1994; MÜLLER et al. 1995), thus with a gap of 500 Million years. These fossils range from young stages in a size range of between 500 and 700 µm (Fig. 6) to slightly longer and apparently older stages, found by ANDRES (1989) on the Isle of Öland, Sweden, in only slightly younger rock. These fossil larvae also have a

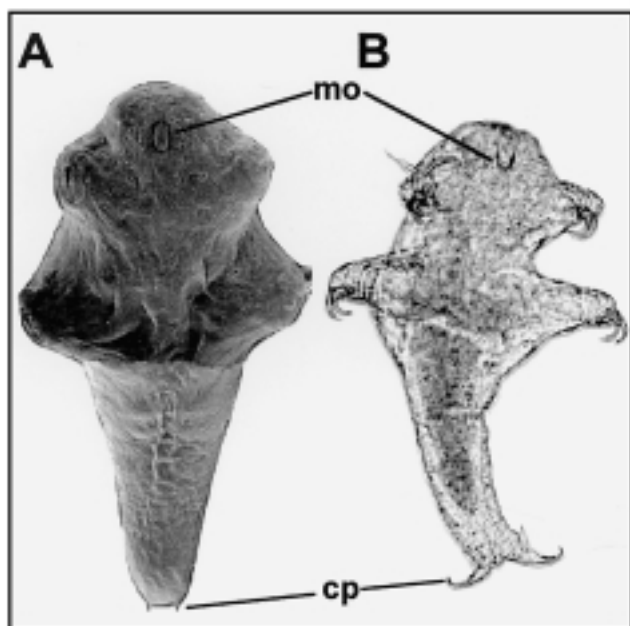


Fig. 5. Recent larval pentastomids. **A.** SEM micrograph of *Reighardia sternae* (Diesing, 1864) from the silver gull *Larus argentatus* Linné, 1758 (courtesy W. BÖCKELER, Kiel). **B.** Photograph of *Subtriquetra subtriquetra* Sambon, 1922 from saurid sauropsids (courtesy J. RILEY, Dundee). Abbreviations: mo: mouth opening; cp: caudal papillae.

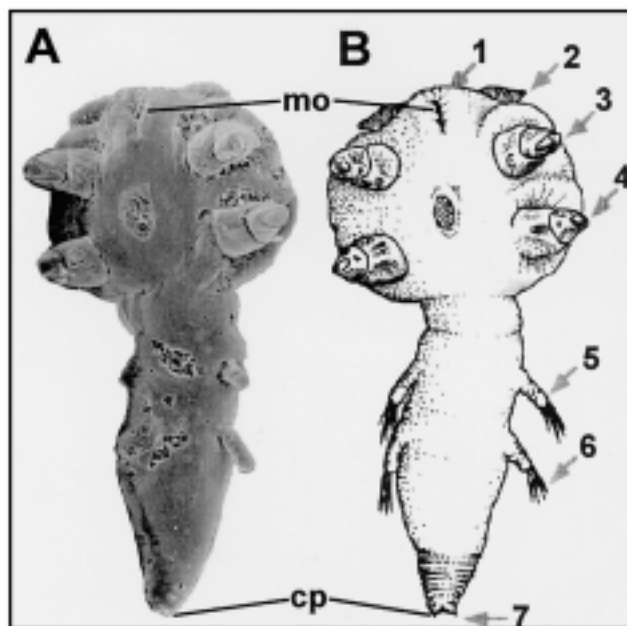


Fig. 6. Cambrian larval pentastomids. **A.** SEM micrograph of *Boecklericambria pelturae* Walossek & Müller, 1994 from the Upper Cambrian *Peltura*-zone of the Swedish 'Orsten', ventral view (from WALOSSEK & MÜLLER 1994). **B.** Reconstruction of this form, arrows point to the palps (1), the mouth (2), the limbs (3–6), and the caudal papillae (7) (from WALOSSEK & MÜLLER 1994).

thicker anterior body and a thinner posterior part (Fig. 6). Some have a mouth frontoventrally, as in the extant larvae, and all have two pairs of large, claw-like limbs. As in the Recent *Reighardia sternae* (Diesing, 1864), there may be another pair of outgrowths frontolateral to the mouth, and also the fine caudal papillae are present.

In striking contrast to extant pentastomid larvae, however, there are up to two pairs of rudimentary limbs on the tail part. Other detailed similarities between fossil and extant larvae concern the limb design: both have small pores on both pairs of limbs. They assisted to identify the 3-segmented nature of these limbs also in the extant forms, which has not been described before (Fig. 7B, D). We consider these limbs as intermediate between a lobopodian leg, as in the lobopodians and onychophorans, and the multi-segmented arthropodium of more advanced arthropods – examples are numerous. The derived state is also apparent from the occurrence of pivot joints and joint membranes between the limb articles (Fig. 7).

Interestingly, the later larval stages of the pentastomid stem lineage derivatives (ANDRES 1989) demonstrate that the three-segmented hind body of the early larvae is retained even with its rudimentary limbs but that it simply elongates strongly. Since ganglial knots remain

reminiscent of these body segments in extant larvae, this demonstrates that the carrot-shaped tail of the fossil representatives of the pentastomids is made of three portions of equal length, while in the living forms the long carrot-shaped or flattened tail is made just out of the last portion. The two anterior tail segments are so close to the head that, because the gonopore is right between these two and the long last part, some authors have considered the pentastomids as progoneate and thus related to the progoneate "myriapods" (e.g. OSCHKE 1963).

The Tardigrada, in our view, comprise an earlier branching down the arthropodan line than the pentastomids (Fig. 4), because they do not have the well-articulated and pivot-jointed limbs of the latter group. What Tardigrada already show of arthropod features is the arthrodisation of the cuticle meaning the cuticle has segmental or metameric thickening and thinning. A representative of the Tardigrada has also been discovered in an 'Orsten' type of preservation, found in Middle Cambrian rocks of the Siberian platform (Fig. 8).

The four possibly juvenile specimens of the new form are between 250 and 350 μm long. With a barrel-like shape, they look much like living tardigrades, particularly when compared with marine ectoparasitic species (KRISTENSEN 1980), such as the arthrotardigrade

Fig. 7. SEM micrographs of details of Recent (A, B) and fossil (C, D) pentastomids; articles of the limbs numbered. **A.** Limbs of a young *Porocephalus crotali* (Humboldt, 1808); arrows point to the soft “secondary hook” arising from joint membrane between articles 1 and 2 (courtesy J. RILEY, Dundee). **B.** Limb of early larva of *Reighardia sterna* (Diesing, 1864), arrows point to the pores, comparable to fig. 7D (from WALOSSEK & MÜLLER 1994). **C.** Right claw limbs of *Heymonsicambria kinnekullensis* Walossek & Müller, 1994 from ventral (from WALOSSEK & MÜLLER 1994). **D.** Right claw limbs of *Boecklericambria pelturae* Walossek & Müller, 1994 from ventral, arrows point to the pores as in Fig. 7B (from WALOSSEK & MÜLLER 1994).

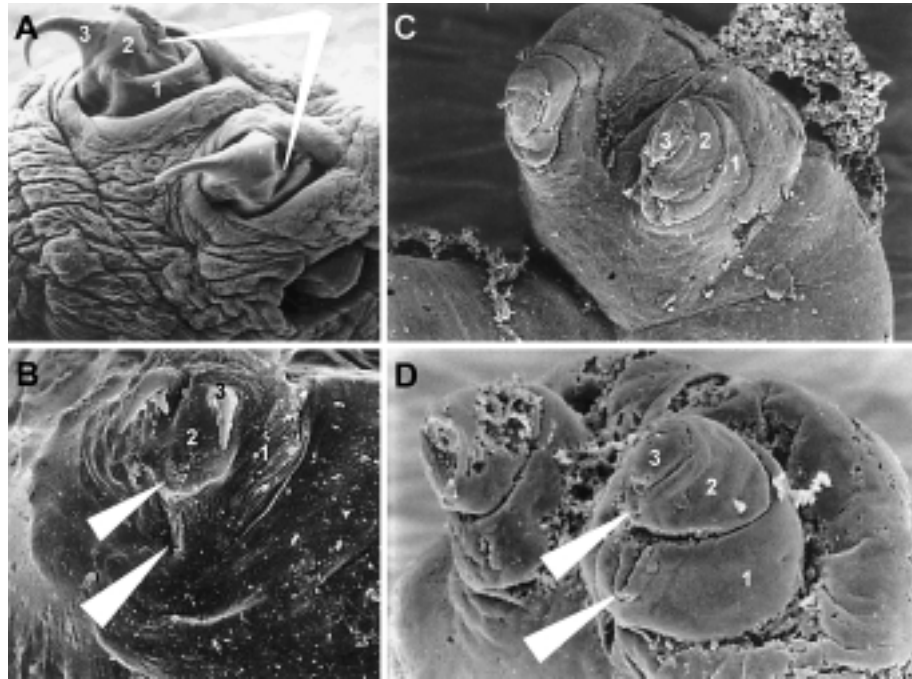
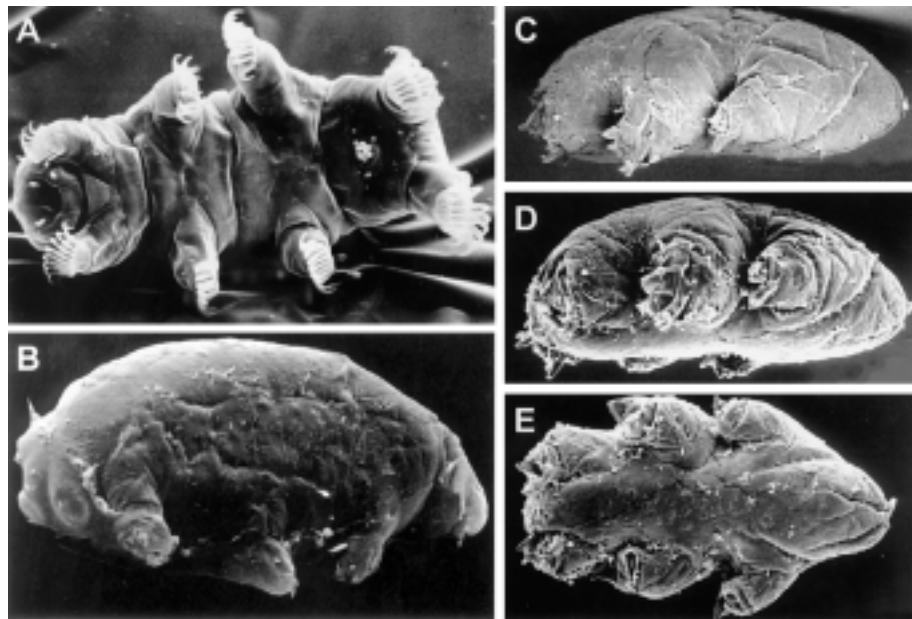


Fig. 8. SEM micrographs of tardigrades. **A.** *Echiniscoides sigismundi* (Schultze, 1865) (Echiniscoididae, Heterotardigrada). **B.** *Tetrakentron synaptae* Cuénot, 1892 (Halechiniscidae, Heterotardigrada). **C–E.** new fossil form, possibly larval, from the Middle Cambrian of Siberia; **C,** from left lateral; **D,** from left ventro-lateral; **E,** from ventral. (A from KRISTENSEN & HALLAS 1980; B from KRISTENSEN 1980; C–E from MÜLLER et al. 1995).



Tetrakentron synaptae Cuénot, 1892. The sistergroup relationship of the fossil form to all living forms is apparent from its segmentation starting with only three pairs of limbs and thus demonstrating plesiomorphic anameric ontogeny, while in their groundpattern state extant tardigrades hatch with the final number of four limbs. Anlagen of a further pair of limbs are developed in one of the four fossil specimens at hand (Fig. 8).

Besides size and general shape there are several even detailed similarities between the fossil form and living tardigrades, such as in the design of the cuticle with a peculiar substructure called pillars (Figs. 9, 10A). These similarities are also discernible in the frontoventral mouth surrounded by fine vela and sensorial structures that correspond to the clavae and cirri of living forms.

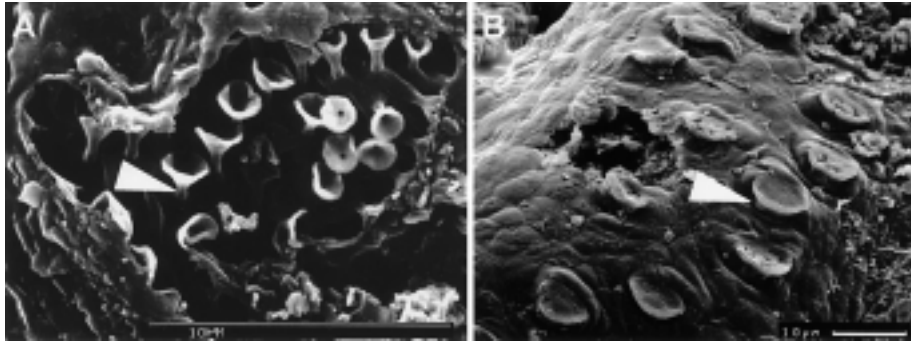


Fig. 9. SEM micrographs of the cuticle of tardigrades with pillar structures (arrowed). **A.** *Batillipes mirus* Richters, 1909 (Batillipediidae, Heterotardigrada) (courtesy R. M. KRISTENSEN, Copenhagen). **B.** new Siberian fossil (from MÜLLER et al. 1995).

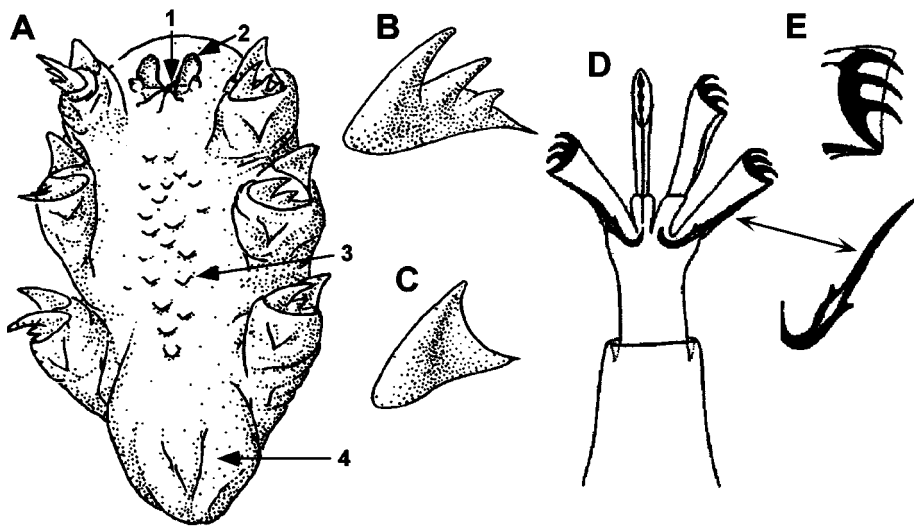


Fig. 10. **A.** Reconstruction of the new Siberian fossil tardigrade; arrow 1 points to the mouth, arrow 2 indicates the sensorial structures, arrow 3 points to the pillar structures (see Fig. 9), arrow 4 indicates the anlagen of the fourth pair of limbs. **B.** Anterior claw with three hooks. **C.** Posterior claw unforked. **D, E.** Recent *Styraconyx craticulus* (Pollock, 1983) (Heterotardigrada). **D.** Limb from the posterior. **E.** View of the three-hooked claw with its supporting apparatus. (A–C from MÜLLER et al. 1995, D, E from KRISTENSEN & HIGGINS 1984).

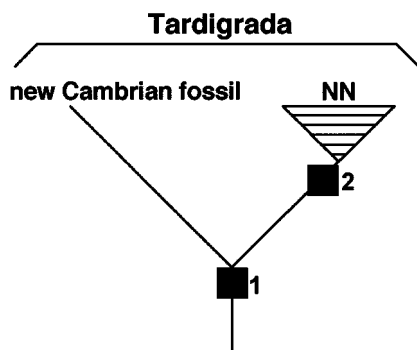


Fig. 11. Argumentation scheme of the phylogeny of Tardigrada; black squares stand for autapomorphies of the respective stem species. It is not clear if epimery is an autapomorphy of the Tardigrada or if it is plesiomorphic. Autapomorphies: 1: pillars; sensorial structures on front of head; 2: epimery, larvae hatch with the final number of four pairs of limbs.

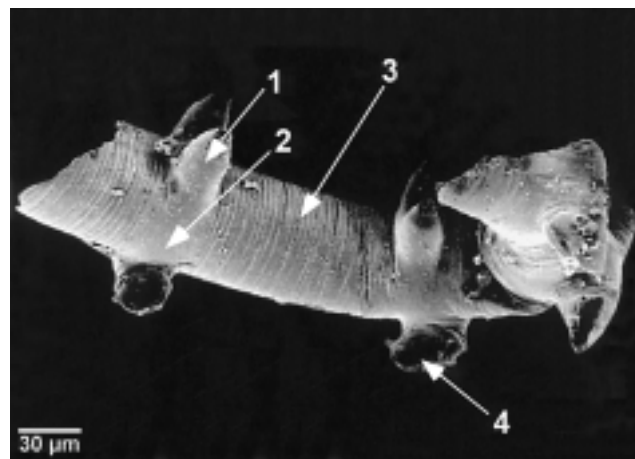


Fig. 12. SEM micrograph of the new fossil supposedly lobe-pod from the Upper Cambrian Swedish 'Orsten'. Arrow 1 points to the dorsal humps, terminating in a spine that are missing in this specimen; arrow 2 indicates the smooth area of the body where limbs and dorsal humps arise; arrow 3 points to the fine annulation of the body between the insertions of the limbs; arrow 4 points to the limbs that are broken off distally.

The limbs of the fossils seem to be outwardly twisted and have two claws each; the anterior being a three-forked claw and the posterior one being unforked (Fig. 10A–C). The claws of Recent tardigrades, for instance the claws of the arthrotardigrade *Styraconyx craticulus* (Pollock, 1983) (Figs. 10D, E) are comparable to the claws of the Siberian fossil (Fig. 10B, C). This suggests that differences in having more toes and hooks may be a secondary modification of this basic pattern evolved in the stem lineage of the modern forms. Like the Tardigrada, the Onychophora and various Cambrian so-called lobopodians (HOU & BERGSTRÖM 1995) also have paired claws (see also RAMSKÖLD 1992a, b). A possible view but uncertain is that the paired claws are a synapomorphy of both groups.

Although it may be considered as a matter of semantics, we prefer to include this new fossil species into the Tardigrada, rather than leaving it outside, because the characters shared are exclusive for the fossil and the Recent Tardigrada. Since the stem lineage is part of a taxon, it might be good to use the name Tardigrada to embrace the fossil and all living representatives of tardigrades (Fig. 11).

The last larger group listed in our diagram are the Onychophora and the exclusively fossil group of worm-like forms called the “lobopodians” due to their soft legs, so far known only from the Early to the Middle Cambrian. Among them are the famous Burgess Shale fossils, such as *Aysheaia pedunculata* Walcott, 1911 and *Hallucigenia sparsa* Conway-Morris, 1977, Chengjiang biota forms like *Microdictyon sinicum* (Chen, Hou & Lu, 1989) and a species from German drift boulders, *Xenusion auerswaldae* Pompeckij, 1927. Onychophorans and lobopodians share a slender body with a series of long legs ending in double claws. Head and tail end are still little understood and variously subject to be re-interpreted by changing them around. Some have added even eyes, antennae-like structures or barbles that may also occur on the body and the legs. Various, the body between the insertion points of the legs is finely annulated, as are the legs, lobopodia, which insert far ventrally.

A characteristic feature of several of the fossil lobopodians is the paired internal sclerotic plates above the limbs insertions (HOU & BERGSTRÖM 1995). These plates have been known for much longer as components of the so-called small-shelly faunal assemblages (e.g., BENGTSO 1991; CHEN et al. 1989b). Yet these could not be assigned to any organism until the lobopodians were found as whole animals in the famous Chengjiang fauna, China (e.g. CHEN et al. 1989a, 1989b, 1992). The plates may be drawn out into spines of different lengths, indicating a much larger variability within species than that known by forms in body preservation. In other cases animals

only with spine-like, sometimes very long outgrowths are known, such as in the famous Burgess Shale form *Hallucigenia sparsa* Conway-Morris, 1977.

Remarkably, at the scale of one tenth of the size of the Lower to Middle Cambrian lobopodians, the fossil material from Upper Cambrian ‘Orsten’ has also yielded a few fragments of similar worm-shaped forms (Fig. 12). They have not yet been described in detail and are introduced herewith as the first Upper Cambrian lobopodian, as well as the first lobopodian in an ‘Orsten’-type of preservation and as the youngest record of this type of derivatives of the early evolutionary line of the Arthropoda.

The ‘Orsten’ lobopodian shares with the Lower to Middle Cambrian lobopodians not only the annulated segmental limbs but also the segmental paired dorsal outgrowths on the finely annulated tubular body, which has a diameter of about 100 to 120 µm. The specimens provide significant new data for this group owing to their fine preservation of cuticular details undetectable on flattened fossils, even though they are incomplete. The body and the limbs are virtually cylindrical, and the limbs were apparently stretched virtually laterally due to a thicker bridge linking right and left legs. It remains uncertain if lobopodians had a thin and layered cuticle, which had to be moulted, but at least the Upper Cambrian representative shows a cell-like surface microstructure that resembles the onychophoran condition. It seems likely that lobopodians are a grade and not a taxon (BUDD 1996, 1997). Some of the forms with a frontal mouth and no associated sensorial frontal appendages may represent the earliest derivatives of the evolutionary line of the Arthropoda, some may be on the onychophoran line, and some may be related to tardigrades, nonetheless altogether having branched off before the pentastomids (Fig. 4).

3. CONCLUSIONS

All three so-called “pro-arthropods” lack or partly lack characteristic features known from forms belonging to the later evolutionary line of the Arthropoda, particularly those that can be assigned to the monophylum Euarthropoda (*sensu* WALOSSEK 1999). This is first seen in details of the head formation that has not reached a stage including the segments of antennae, in the sense of multi-segmented feelers, and three more segments with limbs. None of the limbs of early derivatives of the euarthropodan stem lineage possessed a rigid basipod nor an endopod or a paddle-shaped exopod. And even the clear arthrodisation, the segmental sclerotisations of the cuticle and clearly arthropodial limbs with stem and rami apparently appear later on the evolutionary line. Among the three stem lineage derivatives of the Arthro-

poda, the Pentastomida represent, in our view, the latest offshoot due to their possession of articulated limbs with pivoted joints. Yet the segmental state of their head, the nervous system and the oligomeric segmental state achieved already at hatching is in clear contrast to the euarthropodan level of organisation and, even more, refutes any relationships with taxa within the crustaceans, eucrustaceans, entomostracans and maxillopods (e.g. WALOSZEK & MÜLLER 1998). Consequently, relationships to branchiuran Maxillopoda, as it has been suggested by WINGSTRAND (1972) on the basis of an admittedly striking similarity in sperm morphology and ABELE et al. (1989) on the basis of 18S rRNA data, are difficult to accept for us, as this would require numerous character reversals and convergencies along the evolutionary line of crustaceans, which contrasts the parsimony principle. There is, in our view, no evidence to argue that a gross similarity in shape is simply due to reduction of structures according to the highly parasitic life of the extant pentastomids, as claimed by ABELE et al. (1989). Hosts of pentastomids are mostly amniote Vertebrates, a taxon that might not have existed in the Cambrian, but derivatives of its ancestral line are already abundant, in particular with respect to the diversity of Cambrian conodonts. Therefore, the morphology of a pentastomid might not be considered as reflecting reduction according to parasitism, but may just depict a primarily arthropod set of characters, suitable for parasitism already in the Upper Cambrian. In fact parasitism must not necessarily be accompanied by reductions, and extant pentastomids still have a well-developed cuticle without adaptations to an internalised mode of life in a host. Also the highly parasitic Tantulocarida, a group of maxillopodan Eucrustacea, have retained proximal endites of their thoracic limbs, a feature evolved in the stem species of Crustacea and known from Cambrian derivatives of the eucrustacean stem lineage (see above).

What are the perspectives of the 'Orsten' fossils for our understanding of the early evolution of Arthropoda?

1. First 'Orsten' fossils yield more detailed structural information of fossils than any other preservational type was ever able to demonstrate.
2. Also biological questions of life habits etc. can be touched with more confidence than with fossil material in any other preservation.
3. The preservation of ontogenetic stages, sometimes even in sets, provides another important data set for phylogeny interpretations: the character formation along development, which is also informative for the understanding of the evolution of features.
4. Moreover, the finds of muscles (see ANDRES 1989) indicate the possibility of preserving even internal details.

5. Finds of 'Orsten'-type preservation in older and younger strata and in other localities world-wide demonstrate that we have just reached the edge of the potential of this extra-ordinary data source.

6. More discoveries and more work power will surely yield more and new exciting information to complete our view into the Early Palaeozoic World.

7. Lastly the Early Cambrian record of not only "proarthropods" but even crustaceans suggests that the evolutionary line of the Arthropoda started within the Precambrian.

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