The oldest 'onychophoran' *Xenusion*: a link connecting phyla?

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The second specimen of *Xenusion auerswaldae* Pompeckj 1927, found in an erratic boulder of the basal Cambrian Kalmarsund sandstone in Hiddensee island, GDR, appears to represent the part of the body missing in the holotype. This enables reconstruction of the whole animal, which, despite its remarkable size of about 20 cm in length, was of rather simple anatomical organization, lacking any specialized appendages or head organs. It is suggested that *Xenusion* was an ancestral walking articulate which had originated from a priapulid-like crawling ancestor. *Xenusion* may be ancestral for Middle Cambrian *Aysheaia*, which exhibits distinct tardigradan traits. It is proposed to classify these two lobopod animals in a new class Xenusia, ancestral for both the Onychophora and the Tardigrada. Possible derivations of the arthropods and annelids from the Xenusia are discussed. □ *Onychophora, Articulata, Cambrian, phylogeny.*

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Xenusion auerswaldae Pompeckj 1927 is the oldest animal body fossil of the Baltic region. When the first specimen, found in glacial drift at Sewekow in NE Germany, was described by Pompeckj (1927), he estimated the age of the rock as being no younger than the Early Cambrian. Because *Scolithos* tubes, expected by him to be present in Lower Cambrian sandstones of similar lithology, are lacking in the rock, a Precambrian age was suggested for it. This dating was in use by subsequent authors (*inter alia* Heymons 1928) until it was questioned by Neben (*in* Jaeger 1964). After detailed search for a possible source area of the rock, Jaeger & Martinsson (1967) concluded that it was the outcrop of the Early Cambrian Kalmarsund Sandstone in SE Sweden. Even so, *Xenusion* appears to be the oldest among Baltic fossil articulates (cf. Dzik & Lendzion 1988).

The holotype of *Xenusion auerswaldae* was thoroughly redescribed by Jaeger & Martinsson (1967), who also discussed possible relationships of the species. Despite excellent preservation of the specimen, it did not reveal crucial anatomical data which could help its placement in the scheme of zoological classification. This has left an inconveniently wide field for speculations. Jaeger & Martinsson (1967) weakly upheld the view of Pompeckj (1927) that *Xenusion* was related to ancestral onychophoran-like articulates and rejected the reorientation of its body suggested by Heymons (1928). Nevertheless, another basically different interpretation, more and more widely accepted among palaeontologists, was introduced by Tarlo (1967), evidently impressed by the superficial similarity of the holotype of *Xenusion* to the Vendian frond-like Petalonamae. The idea of a petalonamean relationship of *Xenusion* has been accepted as plausible by Whittington (1978) and even further developed by McMenamin (1986).

A new well-preserved specimen of *Xenusion*, found in glacial drift of Hiddensee island, GDR (Krumbiegel *et al.* 1980), provides new data on the anatomy of the animal and enables solution of the question of its relationships. In effect, the old problem of the origin and early diversification of the articulates appears to be in need of general reconsideration, which is the intention of the present paper.

The second specimen of *Xenusion*

In 1979 Mr. Horst Deichfuss and Mrs. Helga Deichfuss deposited (at the Geiseltalmuseum of the Martin-Luther-Universität Halle–Wittenberg) a specimen of what appeared to be the new find of *Xenusion* (Krumbiegel *et al.* 1980;

Schallreuter 1985). It was found on the seashore of Hiddensee island, near Rostock. The specimen is exposed on the surface of a flat block of dark *Xenusion* sandstone, 20 × 17 × 3 cm in dimensions (Fig. 1). The basal side of the block (opposite to that with the fossil) abounds in pebbles of pink to light grey claystone, up to 21 mm in diameter. They are evenly rounded, although some of their casts show a somewhat irregular surface. No evidence of compaction was found, which suggests that the pebbles were already lithified before deposition. The abundance and size of pebbles decreases toward the topmost layers, in which the fossil is preserved (Fig. 2), but a few small ones (2–3 mm in diameter) occur in close proximity to the fossil (see Fig. 3). Because of this gradation in distribution of the pebbles, and indistinctly gradational character of laminae, it is inferred that the side with the fossil was the upper one of the sandstone bed. Both the varve-like lamination and the presence of 'clay galls' are typical features of the *Xenusion* (Kalmarsund) sandstone. Pebbles also occur in the boulder with the holotype housed at the Museum für Naturkunde (Paläontologisches Museum) of the Humboldt Universität Berlin (cf. Jaeger & Martinsson 1967).

The lamination is strictly parallel in most of

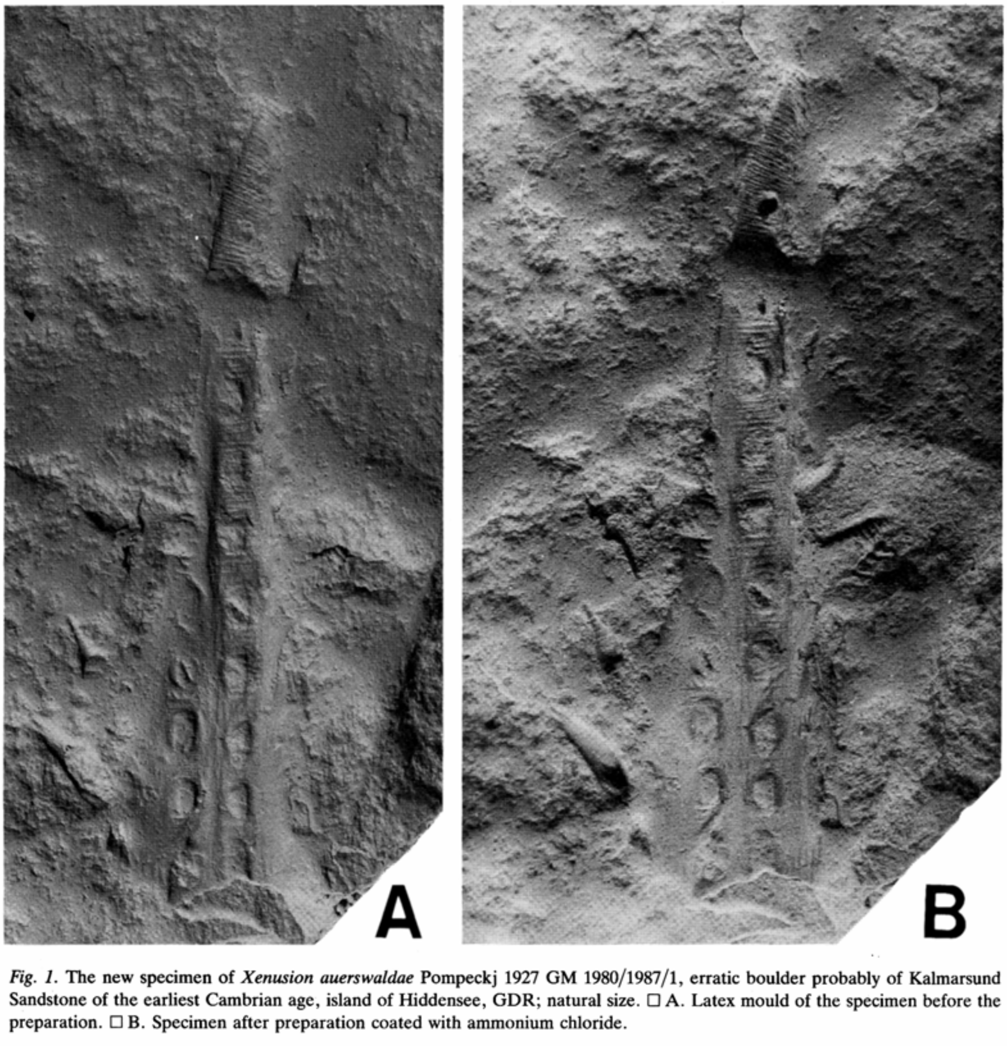

Fig. 1. The new specimen of *Xenusion auerswaldae* Pompeckj 1927 GM 1980/1987/1, erratic boulder probably of Kalmarsund Sandstone of the earliest Cambrian age, island of Hiddensee, GDR; natural size. ☐ A. Latex mould of the specimen before the preparation. ☐ B. Specimen after preparation coated with ammonium chloride.

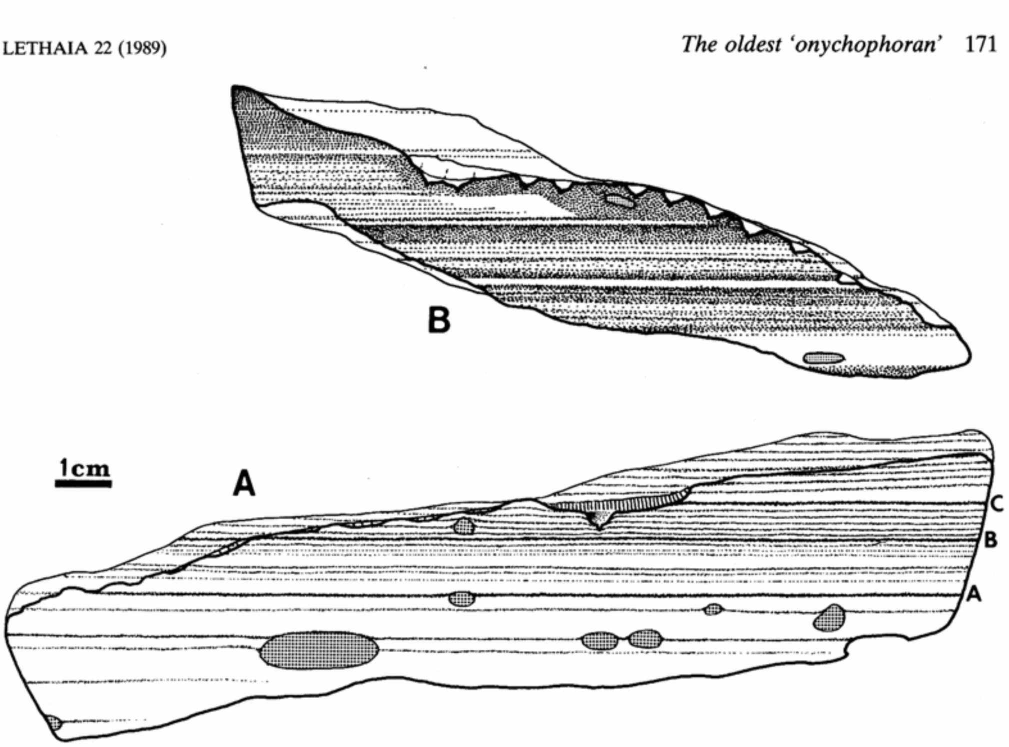

Fig. 2. □ A. Schematic section through the boulder in Fig. 1. Sagittal in relation to the Halle specimen of *Xenusion*. Note angular bending of the specimen and its relation to the lamination and claystone pebbles. □ B. Same for the holotype.

the Geiseltalmuseum boulder except for the part above the level of the fossil, where some layers seem to be slightly diagonal (Fig. 2). The thickness of particular layers bracketed by darker purple-red laminae may differ slightly on particular sides of the boulder, but generally they can be traced around it with ease. They remain undisturbed even in close proximity to the specimen of *Xenusion* (Fig. 1B, 2, 3) and only very insignificant changes in the course of the lamination are detectable.

The fossil itself crosses three major sets of laminae. At the thicker red bands (indicated by letters A–C in Figs. 2 and 3) it is bent angularly and the angle between the body axis and the lamination is different, being smaller in the B–C layer with more prominent red strips than in the underlaying layer of lighter colouration. This is evidently an effect of compaction and indicates that the red strips in the Kalmarsund sandstone are remnants of clay (and/or organic) intercalations. The most significant displacement in the course of lamination is a dune-like elevation on the surface of the red band C (cf. Figs. 1, 3). Because of this slight elevation the specimen there was more bent than on the preceding bedding surfaces (Fig. 2).

It therefore appears that prior to its burial the specimen was anchored in the sand with its now unpreserved part (being outside the boulder) and was standing obliquely above the bottom. Gradually it was covered by rhythmically deposited sand and clay (?organic) sediment. Evidently, the sedimentation took place in conditions of rather low energy of the environment, without strong directional water currents (although a weak current might remain in consistency with the position of the specimen and presence of the little 'dune' around it). The trunk was rather stiff in its longitudinal direction, though numerous longitudinal folds and random orientation of appendages indicate considerable transverse elasticity. It is unclear what the cause of the varve-like appearance of the Kalmarsund Sandstone was, but this clearly puts limits on the possible rate of sedimentation, and we have to accept that the carcass of *Xenusion* was exposed to the action of sea water and bottom scavengers for a long time. It would be hard to imagine such a situation in a Recent environment. We have thus to accept that the conditions of

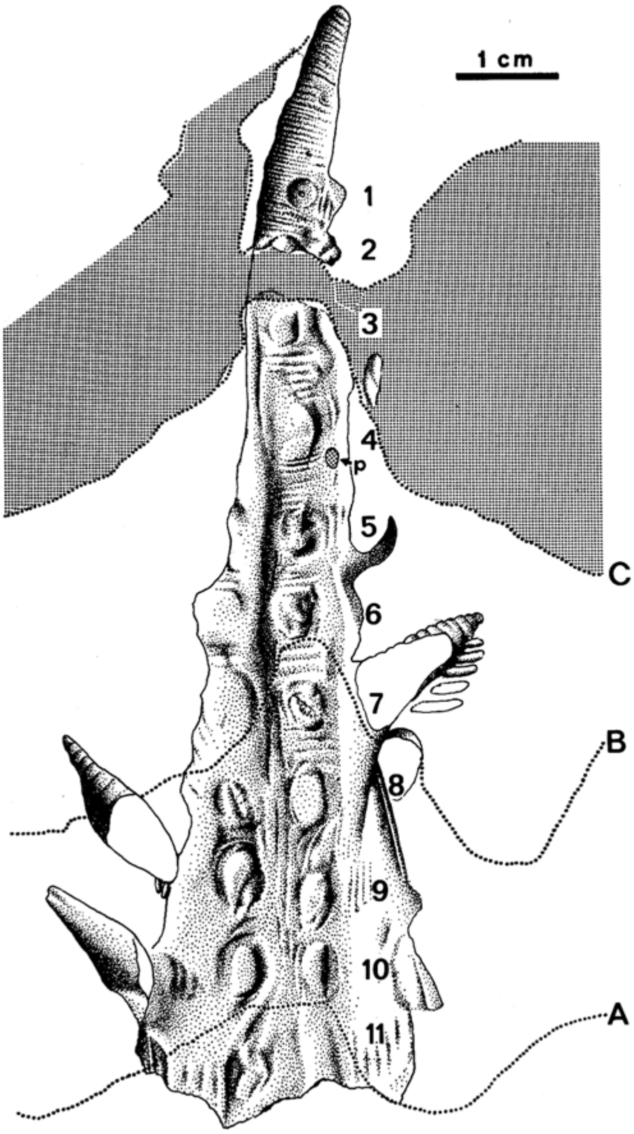

Fig. 3. Interpretative drawing of the Geiseltalmuseum specimen of *Xenusion* in Fig. 1. The course of major red laminae indicated by stippling; the shadowed area presents the surface of lamina C. Numbers refer to appendages and humps. Note the presence of a small pebble (p) in the proximity of the specimen.

fossilization in the Cambrian seas were not actualistic. Both the activity of bottom animals and the bacterial decay in the environment of *Xenusion* were very low. The same conclusion was reached by Whittington (1978:172) regarding conditions of fossilization in the Burgess Shale environment, although he blamed anoxic conditions of sedimentation for the lack of scavengers.

There are no remnants of the original cuticle matter in the specimen, nor is there evidence of any secondary mineralization, except for the red staining of a spine in the centre of the most anterior dorsal hump.

With the exception of the appendages and one end (proposed here to be anterior) of the body, which is preserved in full relief, the rest of the specimen was flattened either strictly dorsoventrally (the posterior end) or obliquely laterally (the anterior part above lamina B). The appendages are preserved three-dimensionally owing to filling of their interiors with sand. It is likely that also the anterior tip of the body, now known only from a depression left after the exfoliated part of the fossil, was filled with sand. The imprint of the proboscis represents not much more than a quarter of its perimeter. As inferred from the concavity of the depression the anterior tip of the proboscis was more or less hemisphaerical in shape. The mouth area is not preserved.

Anteriorly the body surface can be traced around the trunk. It is not possible, however, to detect any discontinuity in the rock, which could correspond to the venter below the well-preserved dorsal structures at the posterior end of the fossil. Most probably it never occurred there. Smooth, unsegmented lateral bands became wider and wider toward the posterior end of the trunk. If one assumes, like Heymons (1928: Fig. 6) did, that it is solely an effect of dorsoventral compression, then the ventral side of the body would be three times as wide as the dorsal one. The cross-section of the body would be widely trapezoidal, despite the evidently round appearance of the body, which can be inferred from the morphology of its anterior part preserved partially in full relief. We thus interpret the present appearance of the fossil as being the result of fossilization of already empty body covers being ruptured longitudinally and widely open along the venter.

Humps. – The humps, which generally occupy strictly dorsal positions and are distributed close to the midline, seem to change their position to an almost lateral one anteriorly. Along with this displacement the cuticular rings, which are posteriorly restricted only to the areas separating particular pairs of humps and are few in number (2 or 3), become more and more closely spaced and can be identified also in between particular humps, as well as on the sides of the body (Figs. 1, 3). All humps standing dorsally from the specimen are strongly compressed, probably not so much in effect of the rock compaction but simply by the weight of sand. Their tips are not preserved, perhaps due to abrasion of the boulder. Although the humps have not preserved their original shapes, circular areas corresponding to their contours are easily recognizable. This indicates that the cuticle of the humps was softer than the surrounding areas of the cuticular rings. Mechanical preparation of the anteriormost hump, imbedded in the rock matrix and seen from its interior, revealed its hemisphaerical shape and distinct morphologic separation from the densely ringed body surface. This hump is approximately 2.8 mm in diameter and is armed with a tubular spine(?) of about 0.3 mm diameter. The spine has its wall stained with red iron oxide minerals.

Appendages. – All appendages are preserved in full relief although fragmentarily. Left appendage 10 shows much of its ventral surface, which appears to be almost completely smooth, although in the next appendage (9) distinct transverse rings can easily be recognized. No other structures are present on the ventral side of the appendages, at least in their distal parts. The most proximal part of the ventral side of appendage 10 was not reached by preparation but no apparent structural changes in the proximity of its base can be noted.

The dorsal part of right appendage 7 was exposed partially by preparation. It was armed with tubular spines which were attached to the posterodorsal side of each ring. At least one distally located ring subdivides anteriorly into two separate rings. Fine longitudinal striation occurs on the surface of the rings. The spines, reaching almost 1 mm in diameter connect smoothly with the appendage without any joint. A slight constriction at the base is recognizable, which may, however, be present only on the dorsal side. The base of appendage 7 is somewhat abraded and its relation to the trunk is not quite clear. Even more complicated is the situation of right appendage 8, which seems to stand almost vertically.

It is generally true that while the dorsal part of the body, bearing distinct cuticular rings and armed with spined humps, was rather stiff along its longitudinal axis (which was a necessary precondition to be covered with sediment in the peculiar way noted above), the appendages are rather haphazardly arranged owing to significant transverse elasticity of the body. This is expressed also in the presence of many longitudinal folds on the lateral bands, which lack any transverse structures. Sets of short longitudinal wrinkles tend to follow the bases of the appendages (Fig. 3).

Reconstruction of the body of *Xenusion*

There are several reasons for believing that the holotype of *Xenusion auerswaldae* Pompeckj

1926, housed at the Museum für Naturkunde of the Humboldt Universität Berlin, and the new specimen of the Geiseltalmuseum represent the opposite ends of the same kind of animal:

(1) The length of the annulated areas between particular pairs of humps increases along the body of the Berlin specimen and the same trend obtains in the Geiseltalmuseum specimen if this is accepted as being the anterior part.

(2) Tubular spines arming appendages are oriented posterodorsally in both specimens, according to the proposed relationship between them.

(3) The distribution of appendages and the shape of the anterior end of the body of *Aysheaia* (Whittington 1978; Robison 1985) are closely similar to those of *Xenusion*.

(4) Both *Xenusion* specimens occur in the same, very peculiar, kind of rock and were found in geographic positions suggesting the same source area.

The anterior segments of the Berlin specimen are of exactly the same morphology as the posterior segments of the second specimen of *Xenusion*. It is not possible to establish the exact number of segments of the body, but it certainly exceeded 20. Otherwise there would be too abrupt a change in distribution of rings in front of the part with 14 segments known from the Berlin specimen.

Both the Berlin and the Geiseltalmuseum specimens are preserved in the same way, with flattened and outspread central parts of the body and with the apical parts, as well as appendages, filled with sand and preserved three-dimensionally. The ventral rupture of the body integument, doubted by Jaeger & Martinsson (1967:440) regarding the holotype, seems now apparent after examination of the new, more completely preserved specimen. It therefore appears that neither of the *Xenusion* fossils are external moulds, as was assumed by Jaeger & Martinsson (1967:436), but three-dimensionally preserved incomplete exuvia. The same mode of preservation was also reported for *Aysheaia(?) prolata* Robison 1985 from the Middle Cambrian of Utah by Robison (1985:231). That specimen was fossilized in a fine-grained clay and subsequent compaction has reduced the filling of the moult to a thin layer of shale. Perhaps also the mode of moulting was different in *Aysheaia*, without the ventral rupture.

Mode of moulting in X*ENUSION*. – The difference in exuviation between *Aysheaia* and *Xenusion* can be explained by some differences in scleritization of their body covers. It has already been noted above that the central dorsal band of the specimens of *Xenusion* was stiff at least in the longitudinal direction, while the rest of the integument was much more elastic, especially regarding transverse directions of deformation. This suggests that the dorsum of *Xenusion* was covered by thicker cuticle (which was also the case in *Aysheaia*; Whittington 1978) and that there was a fibrous, longitudinal component in the cuticle. To free the body from the old integument *Xenusion* had to open it ventrally, and because of inferred cuticle organization the rupture was longitudinal.

With the proposed mode of exuviation as the reason for particular preservation of the specimens it is no longer necessary to envision the appendages of *Xenusion* as being strictly laterally oriented (cf. Jaeger & Martinsson 1967).

The resulting reconstruction of the body of *Xenusion auerswaldae* presents it as an animal with a cylindrical trunk covered with cuticular rings superimposed on segmentation (Fig. 4). Segmental organs are represented by paired ventrolateral appendages and corresponding to them pairs of dorsal or dorsolateral (anteriorly) humps. In the central and posterior parts of the body the cuticle around the humps was firm, which resulted in formation of wider rings and in superficially heteronomous segmentation of the body. Closer to the anterior end of the body the cuticular rings were present also in between humps and on the lateral and ventral sides of the trunk. The humps were armed with tubular spines of unknown length. It seems unlikely that these structures represented only papillae, because they were evidently rather heavily scleritized (cf. Jaeger & Martinsson 1967:439). Somewhat similar spines armed particular cuticular rings of the appendages.

Function of spines. – It seems reasonable that both the spines arming the tips of the humps and the rings of the appendages, being of similar shape and preserved in the same manner, had a similar function. Their inferred strong cuticularization makes unlikely any respiratory function, albeit their distribution on the appendages is suggestive of such a role. Being dorsally or posterodorsally oriented they could not have had any mechanical

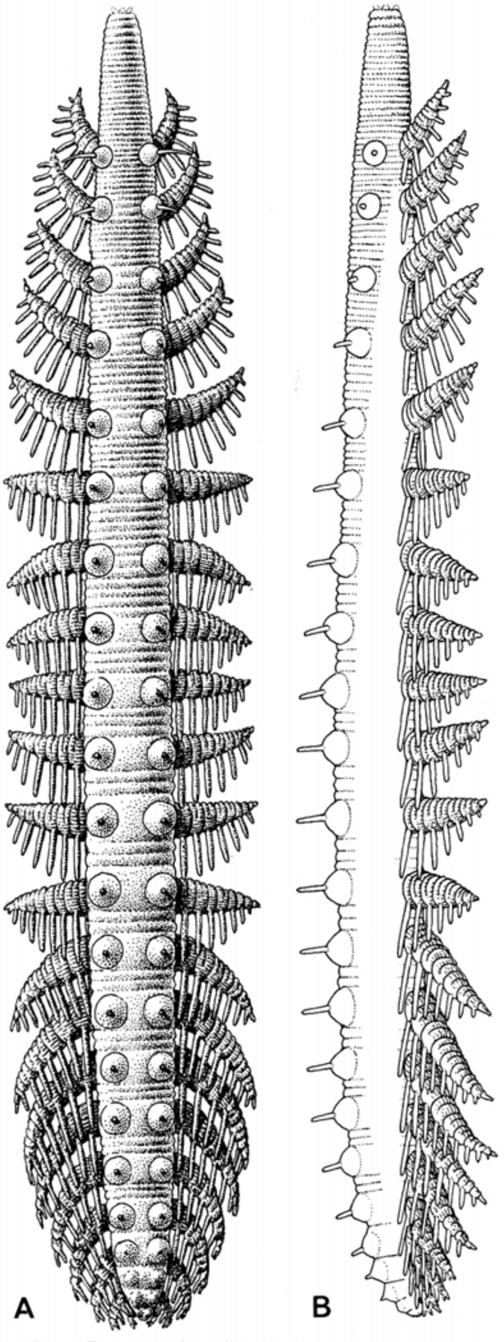

Fig. 4. Reconstruction of the body appearance of *Xenusion auerswaldae* Pompeckj 1927, from the earliest Cambrian of the Baltic region, in dorsal (A) and right lateral (B) views. The length of spines on appendages and humps is conjectural, as is the number of segments. Approximately natural size.

function in catching a prey. Neither does it seem likely that they could be used to produce enough power by flapping to be used in swimming (which is hard to accept for a creature of this morphology anyway).

The most rational explanation we are able to find is a defensive function. Having rather firm and stiff dorsal body covers *Xenusion* was probably able to enroll its body by contraction of longitudinal ventral muscles. The spines extending from humps and appendages would then have formed an armament, as in a hedgehog. All this indicates that there were large predators associated with *Xenusion* (see also Conway Morris & Jenkins 1985). Possibly *Xenusion* itself was a predatory animal, swallowing its prey with evidently movable and possibly extendable proboscis.

Relatives of *Xenusion*

Now, after the discovery of the second specimen of *Xenusion auerswaldae* a close similarity of this fossil animal to the Middle Cambrian *Aysheaia pedunculata* Walcott 1911 becomes apparent. In both cases there is a tubular head region lacking any specialized head organs, lobopod appendages armed with spines at least on some rings, body rings armed with nipple-like processes, each bearing a spine (Whittington 1978: Fig. 78), and the body rings corresponding to particular appendage pairs are separated by a set of intercalatory rings, usually three in number. The dorsum is more heavily scleritized in both animals. The differences are much less significant: tubercles occur on all body rings in *Aysheaia*, instead of being represented only on major rings by pairs of humps. The appendage spines in *Aysheaia* are less numerous and oriented radially, instead of posteriorly, which seems consistent with their proposed defensive function in a relatively short body incapable of being rolled up. What is perhaps more significant, the first appendage pair in this animal shows some features of functional specialization and the head region in front of it is relatively short (Whittington 1978).

There are other Middle Cambrian fossils which allow us to fill the morphologic gap between *X. auerswaldae* and *A. pendunculata.* Thus, the Middle Cambrian *A. (?) prolata* from the Wheeler Formation of Utah (Robison 1985) had a long head region lacking a morphologically specialized

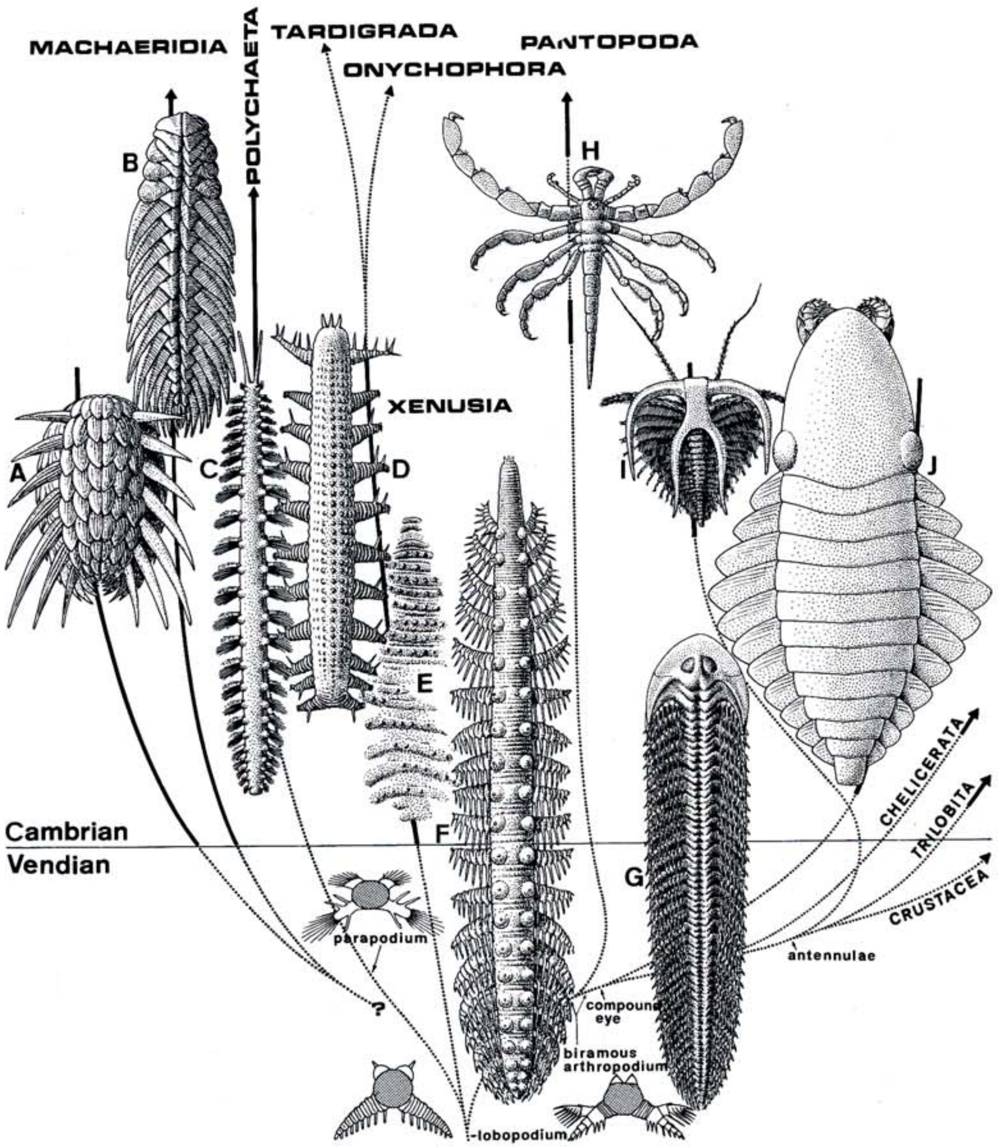

Fig. 5. The most primitive fossil segmented animals and proposed relationships of their classes. □ A. *Wiwaxia corrugata* Matthew 1899 (Conway Morris 1985). □ B. *Plumulites pieckorum* Jell 1979 (Jell 1979). □ C. *Burgessochaeta setiger* (Walcott 1911) (Conway Morris 1979). □ D. *Aysheaia pedunculata* Walcott 1911 (Whittington 1978). □ E. *'Plagiogmus* sp.' (Cloud & Bever 1973). □ F. *Xenusion auerswaldae* Pompeckj 1927. □ G. *Spriggina floundersi* Glaessner 1958 (Birket-Smith 1981). □ H. *Palaeoisopus problematicus* Broili 1923 (Bergström *et al.* 1980). □ I. *Marrella splendens* Walcott 1912 (Whittington 1971). □ J. *Anomalocaris nathorsti* (Walcott 1911) (Whittington & Briggs 1985). Not to scale. Points of origin of diagnostic anatomical features indicated; diagrammatic cross sections show proposed original appearance of appendages in particular major clades.

first appendage pair, both characters typical for *Xenusion*. The mode of preservation of the specimen, which is an exuvium, does not allow the recognition of features of the body ornamentation. This is shown by another Middle Cambrian species from the Flathead Sandstone of Wyoming, two specimens of which were identified as the trace-fossil *Plagiogmus* by Cloud & Bever (1973: Figs. 2, 3). They exhibit a heteronomous pattern of the body annulation, with each wider ring ornamented with seven tubercles and separated by at least one (perhaps 3) very narrow and smooth ring. There are some problematic extensions of wider rings, which may represent appendages associated with them (Fig. 5E).

A possibility of relationship between *Xenusion* and the enigmatic group Tommotiida, widely distributed in Cambrian seas, was mentioned by Bengtson (1970:388). This would require that humps on the dorsal side of the body are transformed into elytrophores to produce conical sclerites. In the tommotiids they were most probably arranged in two longitudinal rows, as in their supposed successors the Turrilepadida (Fig. 5B, Jell 1979; Dzik 1986), and even more complicated body armour occurred in other, possibly related, Cambrian organisms (Fig. 5A, Conway Morris 1985; Dzik 1986). Although there is nothing inconsistent in this interpretation, too little is known about the anatomy of the tommotiids and other representatives of the class Machaeridia to allow elaboration of this theory (Dzik 1986).

There is another fossil organism bearing conical sclerites, the Tremadocian *Dimorphoconus granulatus* Donovan & Paul 1985, which shows a pattern suggestive of heteronomous segmentation of the body covers, thus resembling *Xenusion*. If one assumes a more regular original distribution of sclerites in the fossil than proposed by Donovan & Paul (1985: Fig. 3), then the similarity to the body ornamentation in the *Xenusion–Aysheaia* group becomes apparent. There is no evidence for the presence of appendages in *Dimorphoconus*, so, once again, any suggestion of relationship must remain mere speculation.

Ancestry of *Xenusion*

It is generally acknowledged now that hydraulic mechanism played an important role in the evolutionary origin of the anatomical organization of articulates (Manton 1977:190) and that they originated from peristaltically burrowing ancestors (Clark 1964, 1979:70). A direct peristaltic wave is used by worms not only to burrow in a soft sediment but also to crawl on its surface (Hunter *et al.* 1983). Any extensions of the body surface then move in a way (Hunter *et al.* 1983: Fig. 6) similar to that of walking appendages (cf. Manton 1977).

This makes it tempting to envisage the origin of gait in ancestors of *Xenusion* as an effect of gradual modifications of structures already present on the surface of their bodies. Most burrowing animals have the body surface annulated and armed with anchoring hooks or setae. Structures of this kind occurred in the Cambrian priapulids, too (Conway Morris 1977), presumably the earliest effectively burrowing animals, which were probably responsible for at least some of the

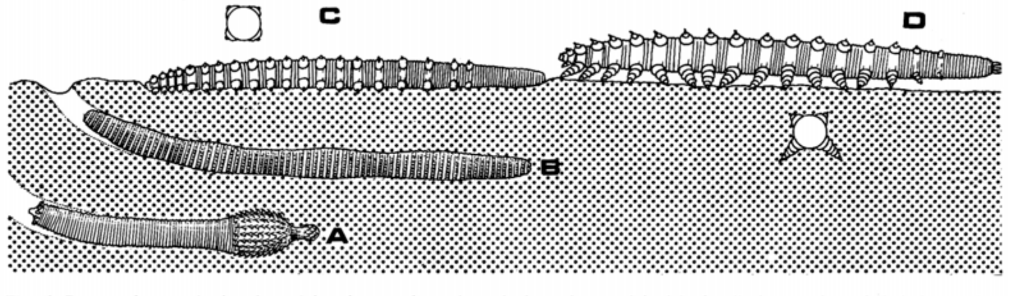

Fig. 6. Proposed scenario for the origin of appendages in articulates from original hydraulic locomotion of their burrowing ancestors. □ A. Burrowing priapulid worm propelled by single direct peristaltic wave. □ B. Burrowing worm of *Palaeoscolex* morphology with few direct peristaltic waves passing along the body. □ C. Hypothetical facultatively crawling stage with still radial distribution of hydraulically strengthened anchoring vesicles on the surface of the body. □ D. Ancestral *Xenusion*-like articulate with functionally ventral vesicles transformed into walking lobopods.

oldest endichnian trace fossils, known since the late Vendian (Crimes 1987). It thus seems noteworthy that the cylindrical trunk of *Xenusion*, with its terminal mouth and body annulation, which is dense anteriorly and more and more regularly heteronomous toward the posterior end of the body, strongly resembles the body of the priapulids.

Notable, also, is the similarity in size, distribution, and inferred softness of dorsal humps to appendages in *Xenusion*. This suggests some relationship in their organogeny and common evolutionary origin. One may envisage the origin of these organs as an effect of differential evolution of tetraradially arranged spined vesicles arming the wider ones of heteronomously distributed annuli. The vesicles occurring on the functionally ventral surface of the crawling ancestor of *Xenusion* were adopted to function as locomotory appendages, while the dorsal ones were to perform a strictly defensive function (Fig. 6).

According to the above model the ancestor of *Xenusion* had a round body cross-section with radial distribution of cuticular structures on its surface. If so, one may wonder whether the distinctly tetraradial organization of the oral apparatus of one of the most primitive arthropods *Anomalocaris* (Whittington & Briggs 1985) is not a remnant of this oldest stage in the evolution of the articulates. Perhaps also tetraradial was the organization of the mouth apparatus in the problematic segmented Cambrian animal *Wiwaxia* (Conway Morris 1985). Of much interest, therefore, is the recent discovery of a worm-like fossil in a burrow of Early Cambrian *Scolithos linearis* (Haldemann 1840); this has a segmented appearance with large bumps arming each body segment, not dissimilar to the humps of *Xenusion* (Troppenz 1986).

Among known Cambrian and Ordovician worm-like fossils the most conspicuous heteronomic annulation with radially distributed tubercles is typical of the *Palaeoscolex* group (Conway Morris & Robison 1986). Whittard (1953) identified, in his Tremadocian *P. piscatorum* Whittard 1953, a mouth apparatus supposedly composed of two small sclerites, and, because of that, interpreted the fossil as an annelid. It has to be noted, however, that the digestive tract, well preserved in some specimens of *P. piscatorum*, is displaced from its central position in such a way that it makes contact with the body wall. This indicates lack of any segmental septa, which should be present in a primitive annelid (Clark 1962), and rather suggests the relationship of *Paleoscolex* to the priapulids.

Xenusion and the phylogeny of articulates

There is general agreement that the Middle Cambrian *Aysheaia* can be considered as an ancestor of both the Tardigrada and the Onychophora (Simonetta & Delle Cave 1975, 1981; Simonetta 1976; Whittington 1978; Bergström 1979; Robison 1985) and this also applies to *Xenusion*, although the tardigradan traits are less apparent in its morphology and it is more primitive than *Aysheaia* in the development of body segmentation and specialization of appendages. It has to be noted that there is no exact correspondence between numbers of intercalatory rings and the segments in *Xenusion*; therefore there seems to be no reason for deducing the presence of legless somites in either *Aysheaia* or *Xenusion* (cf. Whittington 1978:188).

The terminally located radial mouth and cylindrical annulated body are most probably primitive features inherited from ancestors of *Xenusion*, perhaps priapulid-like. Only the presence of the lobopods is the feature of *Xenusion* which seems to indicate the origin of its evolutionary branch. Lobopods persist in the descendants of these Cambrian animals, the onychophorans and tardigradans. There are some features in the anatomy of Recent tardigradans which can be interpreted either as effects of their relationships with the Arthropoda or Nemathelminthes (Kristensen 1981), and which may be used as support for the interpretation of the transitional position of the Lobopodia Snodgrass 1938 proposed here.

Segmentation of appendages of Recent arthropods is of a different nature, even in larval stages. If *Xenusion* really occupied an ancestral position in the phylogeny of articulates, then in the course of evolution to the Arthropoda the annulation of elastic covers, stiff owing to the hydraulic pressure of the body fluids, had to be replaced by an external segmented skeleton stiffened by means of cuticularization. How it could proceed may be illustrated by the morphology of appendages of some Cambrian arthropods, known in details owing to phosphatized fossils. Of special interest is

Martinssonia elongata Müller & Walossek 1986 (Müller & Walossek 1986a) and possibly related forms, known only from larval stages (larva C; Müller & Walossek 1986b). Basal parts of their appendages show annulation of the lobopod type, while the proximal parts are biramous and segmented, presenting typical arthropodia.

A somewhat similar difference in segmentation pattern occurs in Devonian pycnogonids, too (Bergström *et al.* 1980). It may be of some meaning that among Cambrian larvae there are some resembling protonymphs of Recent Pantopoda and having at the same time annulation of appendages similar to *Martinssonia* (larva D of Müller & Walossek 1986b). The most primitive among the oldest known pycnogonids, *Palaeoisopus problematicus* Broili 1928, shared with *Martinssonia* its legless abdomen with elongated telson, but this seems rather to be an effect of mechanisms involved in evolutionary reduction of the abdomen than evidence of any direct relationship. These similarities, however, have to be considered when the presence of a long proboscis, with terminally located radial mouth, in the pycnogonids is interpreted in phylogenetic terms.

It may be suggested that the posteriorly oriented ventral mouth of typical arthropods originated as an effect of transformation of a *Xenusion*-like proboscis into such a directed proboscis of the pycnogonid type and its subsequent unification with the ventral surface of the trunk, which seems to be still uncompleted in *Martinssonia* (see Müller & Walossek 1986a: Fig. 12D). Despite its ventral orientation, the presence of a radially organized mouth apparatus in such primitive Cambrian arthropods as *Anomalocaris* (Whittington & Briggs 1985) can thus be interpreted as a result of a still unfinished evolutionary development of the labrum from a curved proboscis.

The stronger scleritization of the dorsum in *Xenusion* seems to be an arthropodan trait. One may also wonder whether the similarity in presence and position of spines, arming rings of the most anterior appendages in *Aysheaia* and segments in similarly located uniramous appendages of *Anomalocaris* are not effects of a common descent.

If the above presented phylogenetic interpretation of the morphology of appendages in the *Martinssonia* group is correct, then the biramosity of post-antennular appendages of the arthropods originated by terminal splitting of lobopods. With subsequent reduction of the proximal annulated parts (the larva C and *M. elongata* may serve as exemplification of this process) the arthropodan appearance of the appendage, with a comb-like exopodite and an endopodite armed with ventral spines, became more and more apparent.

The oldest known animal showing the presence of biramous segmented appendages with comb-like dorsal branch is *Spriggina floundersi* Glaessner 1958 from the Vendian of Ediacara (Birket-Smith 1981). According to the reconstruction of its external morphology presented by Birket-Smith (1981) it had a trunk armed with paired dorsal structures resembling the humps of *Xenusion* (they also occur in Cambrian larva A of Müller & Walossek 1986b). The first two head segments formed a cephalic shield, parabolic in outline, with long lateral spines, thus resembling the head shield of the Cambrian *Marella splendens* Walcott 1912 (Whittington 1971). *Spriggina*, together with *Marrella*, may thus represent a branch ancestral to the trilobites, different from them in having fewer segments fused into the cephalic shield and lacking wide thoracic pleura.

A few comments are also necessary regarding the relations of the annelids, traditionally believed to occupy a position ancestral to the arthropods (i.e. Grasshoff 1981, but see Manton 1977 and Bergström 1986), to the branch of *Xenusion*, which is proposed here as replacing the annelids in this phylogenetic role. The crucial point of the problem is the relationship between para-, lobo-, and arthropodia.

The oldest anatomically known Cambrian annelids show already well-developed polychaete traits, except for the jaws, aciculae, eyes, the medial tentacle, and palpi, which do not seem to be present yet (Conway Morris 1979). The morphologically distinct head armed with a pair of long smooth tentacles and the neuro- and notopodia, which are not connected proximally, do not allow fitting these animals into any of the stages in the evolutionary development of the articulates proposed above. At least two interpretations are thus possible: (1) that the polychaetes originated from the earliest arthropods as an effect of secondary loss of segmentation in already biramous appendages and transformation of the antennulae into tentacles, or (2) that they shared ancestry with *Xenusion*. In the latter case, neuro- and notopodia could be homologous to the lobopodia and humps, respectively, and the development of head was independent in the arthropods and annelids (Fig. 5). Whatever the real origin of the polychaetes, the organization of their oldest representatives indicates that they mark the next step in the development of locomotory abilities of the earliest articulates, a shift from walking on the bottom to swimming above it, contrary to the opinion of Clark (1969:45).

The cylindrical annulated body of *Xenusion* with a terminal mouth suggests its origin from a burrowing priapulid-like ancestor. Clark's (1964) idea that the hydraulic mode of locomotion was typical for ancestral articulates is thus supported by palaeontological evidence. However, the apparently superficial annulation of the body of *Xenusion*, with rings in the anterior part of the body, not having any relationship to the metameric distribution of appendages and humps, hardly provides any support for the notion of a fully segmental internal organization of the body. There is thus no reason to suppose any crucial role of a segmented coelom in the hydraulic locomotion of *Xenusion*, as both in Recent priapulids, related to its possible ancestors, and in its recent onychophoran successors fluids of the primary body cavity (blastocoel) are used to transfer hydraulically the power of contracting muscles. It is highly unlikely that *Xenusion* was different in this respect. The role performed by the coelomic fluid in locomotion of some Recent annelids thus seems to be a secondary adaptation.

Proposed classification

Little doubt remains that *Xenusion* is directly related to *Aysheaia* and that both are ancestral to Recent Onychophora and Tardigrada. These Cambrian animals should thus be classified together with their successors and they certainly deserve equal taxonomic rank. For nomenclatorial clarity we thus propose restricting the range of the class Onychophora Grube 1853 to terrestrial protracheates having their head appendages transformed into antennae and mouth apparatus. For their marine ancestors, lacking these advanced characters but having lobopods armed with cuticular spines and a terminal, radial mouth, we propose a new taxonomic unit Xenusia, new class. It is proposed including the classes Xenusia, Tardigrada, and Onychophora into the (sub)phylum Lobopodia Snodgrass 1938 of rank equal to the Annelida Lamarck 1809.

Xenusion differs from *Aysheaia* in lacking specialized appendages, in the presence of a long proboscis, and in the strongly heteronomous annulation of the body. These differences do not allow inclusion of *Xenusion* in the family Aysheaiidae Walcott 1911. We thus propose Xenusiidae, new family, defined by the above listed features.

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References

Bengtson, S. 1970: The Lower Cambrian fossil *Tommotia. Lethaia 3*, 363–392.

Bergström, J. 1979: Morphology of fossil arthropods as a guide to phylogenetic relationships. *In* Gupta, A. P. (ed.): *Arthropod Phylogeny*, 3–56. Van Nostrand Reinhold Company, New York.

Bergström, J. 1986: Metazoan evolution – a new model. *Zoologica Scripta 15*, 189–220.

Bergström, J., Stürmer, W. & Winter, G. 1980: *Palaeoisopus, Palaeopantopus* and *Palaeothea*, pycnogonic arthropods from the Lower Devonian Hunsrück Slate, West Germany. *Paläontologische Zeitschrift 54*, 7–54.

Birket-Smith, S. J. R. 1981: A reconstruction of the Precambrian *Spriggina. Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 105*, 237–258.

Clark, R. B. 1962: On the structure and functions of polychaete septa. *Proceedings of the Zoological Society of London 138*, 543–578.

Clark, R. B. 1964: *Dynamics in Metazoan Evolution. The Origin of the Coelom and Segments.* 313 pp. Clarendon Press, Oxford.

Clark, R. B. 1969: Systematics and phylogeny: Annelida, Echiura, Sipuncula. *Chemical Zoology 4*, 1–68.

Clark, R. B. 1979: Radiation of the Metazoa. *In* House, M. R. (ed.): *The Origin of Major Invertebrate Groups. – The Systematic Association Special Volume 12*, 55–102.

Cloud, P. & Bever, J. E. 1973: Trace fossils from the Flathead Sandstone, Fremont county, Wyoming, compared with Early Cambrian forms from California and Australia. *Journal of Paleontology 47*, 883–885.

Conway Morris, S. 1977: Fossil priapulid worms. *Special Papers in Palaeontology 20*, 1–95.

Conway Morris, S. 1979: Middle Cambrian polychaetes from the Burgess Shale of British Columbia. *Philosophical Transactions of the Royal Society of London B 285*, 227–274.

Conway Morris, S. 1985: The Middle Cambrian metazoan *Wiwaxia corrugata* (Matthew) from the Burgess Shale of British Columbia. *Philosophical Transactions of the Royal Society of London B 307*, 507–582.

Conway Morris, S. & Jenkins, R. J. F. 1985: Healed injuries in Early Cambrian trilobites from South Australia. *Alcheringa 9*, 167–177.

Conway Morris, S. & Robison, R. A. 1986: Middle Cambrian priapulids and other soft-bodied fossils from Utah and Spain. *The University of Kansas Paleontological Contributions, Paper 117*, 1–22.

Crimes, T. P. 1987: Trace fossils and correlation of late Precambrian and early Cambrian strata. *Geological Magazine 124*, 97–119.

Donovan, S. K. & Paul, C. R. C. 1985: A new possible armoured worm from the Tremadoc of Sheinton, Shropshire. *Proceedings of the Geological Association 96*, 87–91.

Dzik, J. 1986: Turrilepadida and other Machaeridia. *In* Hoffman, A. & Nitecki, M. H. (eds.): *Problematic Fossil Taxa*, 116–134. Oxford University Press, New York.

Dzik, J. & Lendzion, K. 1988: The oldest arthropods of the East European Platform. *Lethaia 21*, 29–38.

Grasshoff, M. 1981: Arthropodisierung als biomechanischer Prozess und die Entstellung der Trilobiter-Konstruktion. *Paläontologische Zeitschrift 55*, 219–231.

Heymons, R. 1928: Uber Morphologie und verwandtschaftliche Beziehungen des *Xenusion auerswaldae* Pomp. aus dem Algonkium. *Zeitschrift für Morphologie und Ökologie der Tiere 10*, 307–329.

Hunter, R. D., Moss, V. A. & Elder, H. Y. 1983: Image analysis of the burrowing mechanisms of *Polyphysia crassa* (Annelida: Polychaeta) and *Priapulus caudatus* (Priapulida). *Journal of Zoology, London 199*, 305–323.

Jaeger, H. 1964: Das Ratsel *Xenusion*. *Urania 27*, 132–133.

Jaeger, H. & Martinsson, A. 1967: Remarks on the problematic fossil *Xenusion auerswaldae*. *Geologiska Föreningens i Stockholm Förhandlingar 88*, 435–452.

Jell, P. A. 1979: *Plumulites* and the machaeridian problem. *Alcheringa 3*, 253–259.

Kristensen, R. M. 1981: Sense organs of two marine arthrotardigrades (Heterotardigrada, Tardigrada). *Acta Zoologica 62*, 27–41.

Krumbiegel, G., Deichfuss, H. & Deichfuss, H. 1980: Ein neuer fund von *Xenusion*. *Hallesches Jahrbuch für Geowissenschaften 5*, 97–99.

Manton, S. M. 1977: *The Arthropoda: Habits, Functional Morphology and Evolution.* 527 pp. Clarendon Press, Oxford.

McMenamin, M. A. S. 1986: The garden of Ediacara. *Palaios 1*, 178–182.

Müller, J. & Walossek, D. 1986a: *Martinssonia elongata* gen. et sp. n., a crustacean-like euarthropod from the Upper Cambrian Orsten of Sweden. *Zoologica Scripta 15*, 73–92.

Müller, J. & Walossek, D. 1986b: Arthropod larvae from the Upper Cambrian of Sweden. *Transactions of the Royal Society of Edinburgh: Earth Sciences 77*, 157–179.

Pompeckj, J. F. 1927: Ein neues Zeugnis uralten Lebens. *Paläontologische Zeitschrift 9*, 287–313.

Robison, R. A. 1985: Affinities of *Aysheaia* (Onychophora), with description of a new Cambrian species. *Journal of Paleontology 59*, 226–235.

Schallreuter, R. 1985: Das zweite *Xenusion*. *Geschiebekunde Aktuell 1*, 19–23.

Simonetta, A. 1976: Remarks on the origin of the arthropods. *Memorie della Societa Toscana di Scienze naturale (1975) B 82*, 112–134.

Simonetta, A. & Delle Cave, L. 1975: Notes on the morphology and taxonomic position of *Aysheaia* (Onychophora?) and *Scania* (undetermined phylum). *Monitore Zoologico Italiano (N.S.) 9*, 67–81.

Tarlo, L. B. H. 1967: *Xenusion* – onychophoran or coelenterate? *Mercian Geologist 2*, 97–99.

Troppenz, U.-M. 1986: *Scolithos* – Verursacher der Rohrenbauten gefunden? *Geschiebekunde Aktuell 2*, 35–36.

Whittard, W. F. 1953: *Palaeoscolex piscatorum* gen. et sp. nov., a worm from the Tremadocian of Shropshire. *Quarterly Journal of the Geological Society of London 109*, 125–136.

Whittington, H. B. 1971: Redescription of *Marrella splendens* (Trilobitoidea) from the Burgess Shale, Middle Cambrian, British Columbia. *Bulletins of the Geological Survey of Canada 209*, 1–24.

Whittington, H. B. 1978: The lobopod animal *Aysheaia pedunculata* Walcott, Middle Cambrian, Burgess Shale, British Columbia. *Philosophical Transactions of the Royal Society of London 284*, 165–197.

Whittington, H. B. & Briggs, D. E. G. 1985: The largest Cambrian animal, *Anomalocaris*, Burgess Shale, British Columbia. *Philosophical Transactions of the Royal Society of London, B 309*, 569–618.