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The xenusian-to-anomalocaridid transition within the lobopodians

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ABSTRACT - The morphological series composed of large xenusiids of the Chengjiang fauna of China and the basal anomalocaridids Pambdelurion *and* Kerygmachela *from the Sirius Passet fauna of Greenland is supplemented with another xenusiid lobopodian,* Siberion lenaicus *gen. et sp. nov., from the Early Cambrian Sinsk Formation of central Siberia. Reduction and ventral bending of the proboscis in* Siberion *and the Chengjiang* Megadictyon *and* Jianshanopodia *may be a synapomorphy uniting these representatives with the anomalocaridids. Throughout the series, the raptorial appendages became larger and more sclerotised, while the gill-like structures on the trunk appendages were transformed from their originally tubular shape into a pinnate form and may eventually have given rise to the wide anomalocaridid flaps. Such a tendency can be rooted in the* Aysheaia*-like xenusians, that have raptorial appendages associated with a prominent proboscis. This results in a scenario of almost complete transition from early lobopodians to ancestral arthropods within the xenusian-anomalocaridid segment of the phylogenetic tree.*

RIASSUNTO - [Il passaggio evolutivo da xenusiidi ad anomalocarididi all'interno dei lobopodi] - *La sequenza morfologica costituita dai grandi xenusiidi presenti nella fauna cinese di Chengjiang e dai primi anomalocarididi appartenenti ai generi Pambdelurion e Kerygmachela presenti nella fauna del Sirius Passet della Groenlandia viene integrata da un altro lobopode xenusiide, Siberion lenaicus gen. et sp. nov., proveniente dalla Formazione di Sinsk del Cambriano Inferiore della Siberia centrale. La riduzione ed il ripiegamento ventrale della proboscide di Siberion documentata anche in Megadictyon e Jianshanopodia (entrambi presenti a Chengjiang) potrebbero rappresentare una sinapomorfia che permette di collegare questi rappresentanti agli anomalocarididi. In questa sequenza, le appendici raptatorie divennero via via più grandi e più sclerotizzate, mentre le strutture „a branchia" presenti sulle appendici del tronco modificarono la loro forma originariamente tubolare in una forma pinnata per dare forse origine alla fine agli ampi "flaps" degli anomalocarididi.Tale tendenza può aver avuto inizio con gli xenusiidi tipo Aysheaia, dotati di appendici raptatorie associate ad una pronunciata proboscide. Il quadro che si viene così a delineare permette di definire una transizione quasi completa dai primi lobopodi agli artropodi ancestrali all'interno del segmento xenusiidi-anomalocarididi dell'albero filogenetico.*

INTRODUCTION

The Cambrian lobopodians Xenusia are of crucial importance in understanding relationships among the present-day phyla of the Ecdysozoa. In the anatomy of various xenusians, traits elsewhere restricted to the tardigrades, onychophorans, arthropods or pentastomids are recognisable, but their meaning continues to be controversial. A possible transition between typical xenusians and the anomalocaridids seems of special interest, because of apparent arthropod affinities of the latter. The anomalocaridids share with some xenusians a pair of large raptorial appendages but differ in several other aspects of their anatomy, especially in location and structure of the mouth, presence of lobate gill-like serial appendages, as well as cerci-like caudal structures. Already Budd (1999) has proposed a xenusian affinity for the *Anomalocaris*-like *Kerygmachela* and *Pambdelurion* from the Early Cambrian Sirius Passet fauna of Greenland, but Bergström & Hou (2001) and Hou et al. (2006) opposed any relationship. The latter authors rejected any possibility for the anomalocaridids to be related to arthropods because of their derived 'peytoiid' mouth apparatus. However, the recent finding of an Early Devonian anomalocaridid with three-dimensionally preserved anatomical structures strongly supports arthropod affinities of the group (Kühl et al., 2009).

In the present paper an almost complete specimen of a new xenusian from the late Early Cambrian Sinsk Formation of central Siberia is described and restoration of its external morphology, as well as some aspects of its internal anatomy, is attempted. The Siberian lobopodian may serve as a link connecting the typical Cambrian lobopodians with their *Anomalocaris*-like relatives, supporting thus Budd's (1999) interpretation. The data on the anatomy of the new Siberian species are compared with those on other Cambrian xenusians. An inferred scenario of evolutionary transformations, that resulted in formation of particular branches of the Xenusia, is proposed.

MATERIALS AND METHODS

The occurrence of xenusians in the 'Algal lens' on the right bank of the Lena River (opposite to the Sinsk village) about 300 m E of the Ulukhan-Tuoidakh Creek mouth was reported by Ivantsov (in Ivantsov et al., 2005). He described the only specimen available to him (PIN 4349/820), represented by part and counterpart of a 27 mm long piece of the body with series of five appendages, but found it too incomplete to establish a new taxon.

Another specimen of the same xenusian species (ZPAL V37/1) was found in the scree at the locality 'Algal lens' by myself in 2006. The fossils of unmineralised algae and soft-bodied or weakly sclerotized animals occur there abundantly, covering a single lamina (possibly two), along which the rock tends to split, within a 5 cm thick limestone

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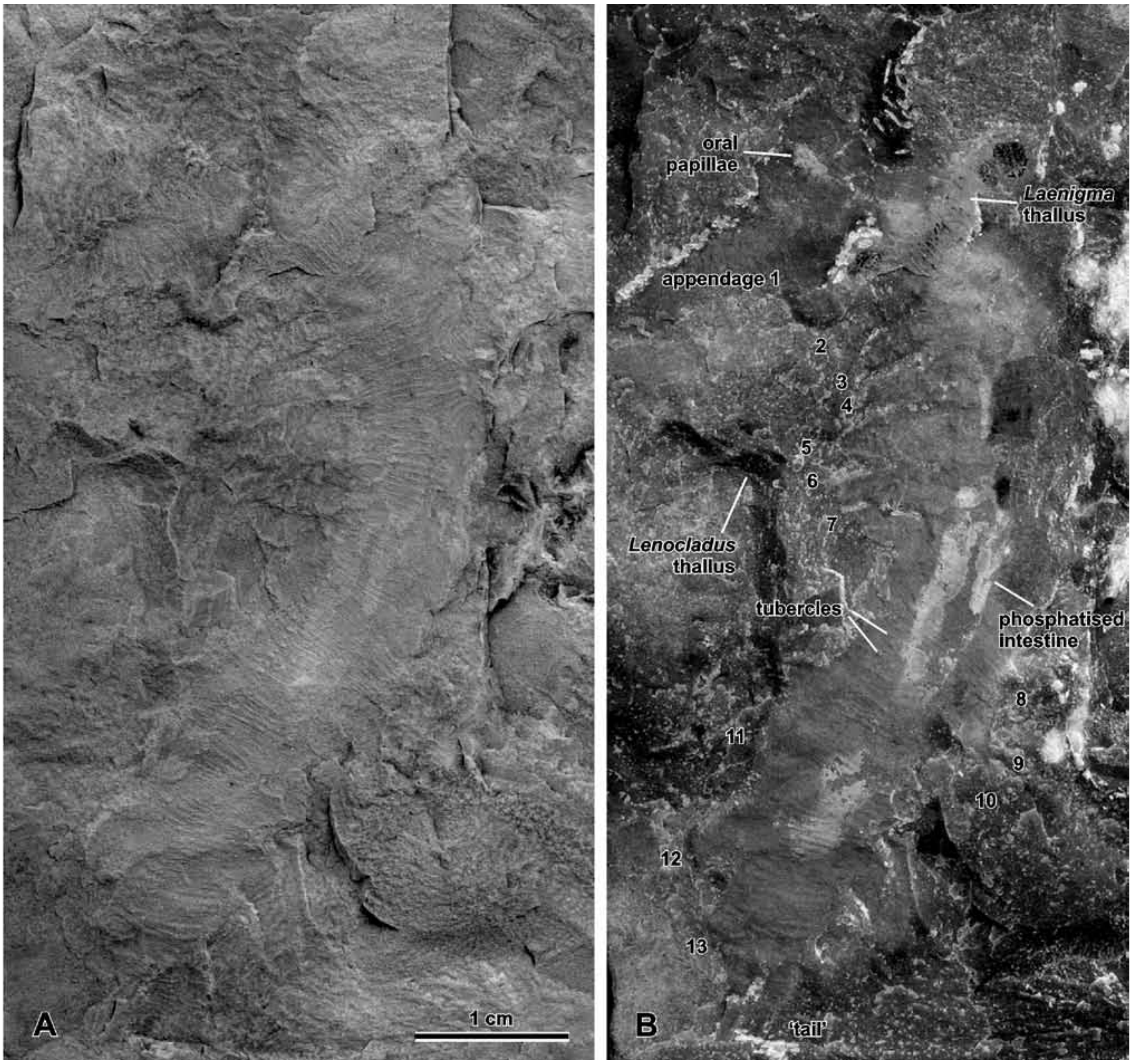

Fig. 1 - *Siberion lenaicus* gen. et sp. nov., holotype ZPAL V37/1 collected from the Early Cambrian (Botomian) Sinsk Formation at the locality 'Algal lens' on the Lena River. (A) Specimen whitened with ammonia chloride. (B) Specimen photographed under water; the appendage numbers are given; compare with Fig. 2.

bed topping the Tuoidakh shale intercalation within the Sinsk Formation (Ivantsov et al., 2005). Associated are numerous trilobites, inarticulate brachiopods, and bradoriids, but also secondarily phosphatised or organic fossils of various affinities. The bed, exploited since 1996 by the team of the Palaeontological Institute of the Russian Academy of Sciences led by Andrey Yu. Ivantsov, has been recently removed by commercial fossil collectors. The Sinsk Formation is of Botomian age, representing the *Bergereniellus gurarii* and early part of *B. asiaticus* trilobite zones. The Formation is represented by a dark bituminous bedded limestone unit about 79 m thick with a few intercalations of black shale (Ivantsov et al., 2005).

The specimen, about 55 mm long, is preserved in faint relief along a split lamina of a bituminous dark limestone slab of 16×7 cm dimensions (Figs. 1, 2A). The specimen does not differ in coloration from the surrounding rock matrix except for a whitish (probably phosphatic) band along its midline, almost certainly representing the intestine (Fig. 2B). The specimen differs from associated algal thalli, which are much darker than the rock matrix and in places preserve black carbonized tissue, in the lack of dark staining. Algae occur in the rock randomly at different levels. A thallus of the alga *Laenigma striatum* Krassilov, 2005 (Krassilov, 2005) crosses the specimen in its anterior part, but belongs to another lamina of the sediment. A phosphatic valve of a lingulid brachiopod is also preserved within the slab.

Actually, the rock does not split strictly along laminae except in regions represented by the xenusian and algae. In places, there is a continuity between the body imprint and its surroundings, suggestive of a microbial mat originally

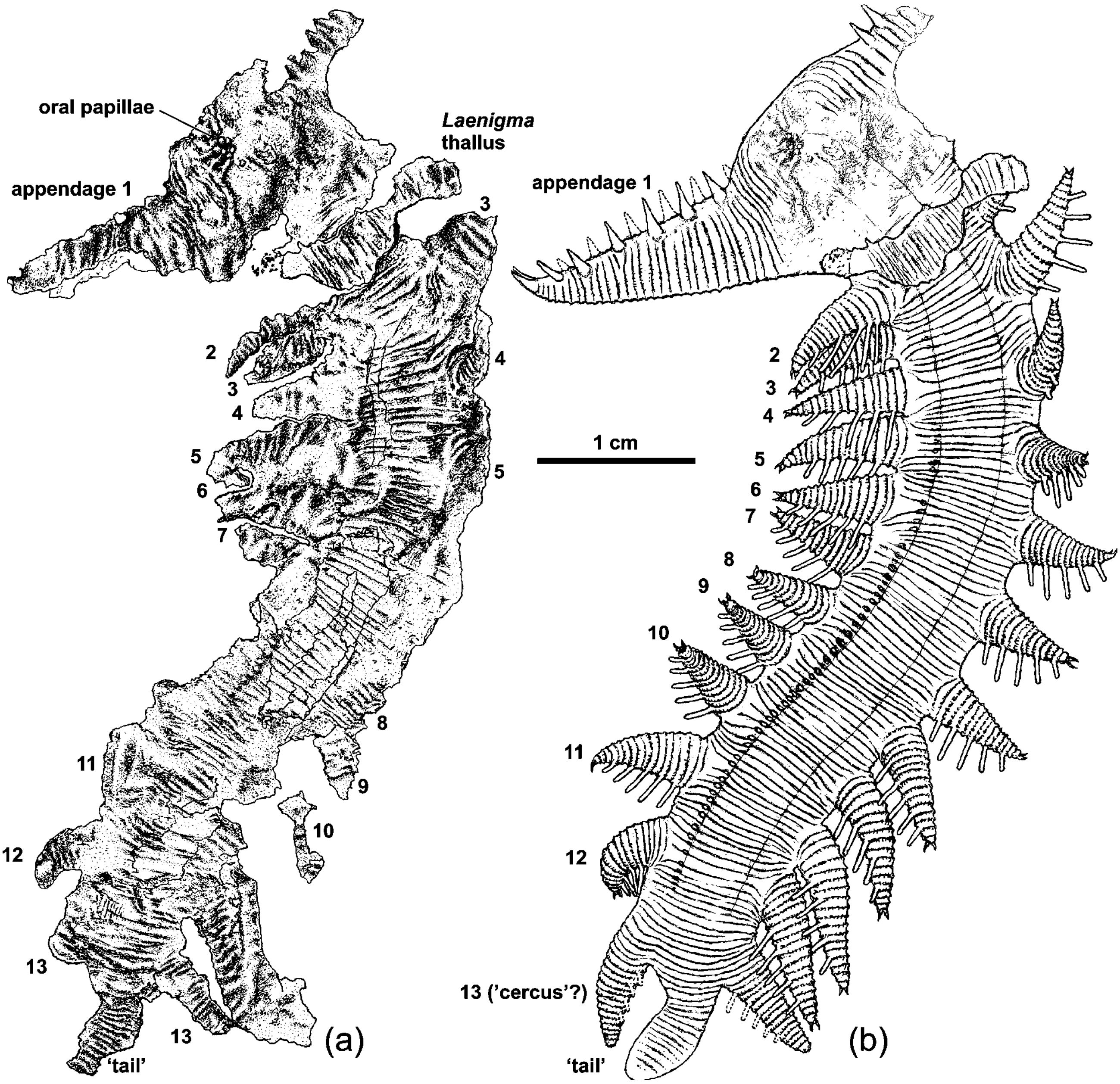

Fig. 2 - *Siberion lenaicus* gen. et sp. nov. from the Botomian of Siberia. (A) Camera lucida drawing of the holotype ZPAL V37/1. B. Proposed interpretation of the holotype specimen with tentative restoration of appendages; note medial location of the annulated 'tail'.

being present there. The rock is hard and preparation with a needle did not give good results because the rock does not exfoliate easily even along the imprint. Crushing the limestone with a hammer was a little more effective, but also in this case splits did not necessarily follow the desired levels.

The holotype was photographed under water and whitened with ammonia chloride. A large magnification camera lucida drawing was prepared, with changing direction of illumination to identify details of the sculpture. The drawing was then transformed into an interpretative diagram by removing probable artefacts of preservation and by replicating details preserved only in some places to all serially homologous regions. While deciding on the meaning of equivocal information, analogy with other xenusians was taken into account. Some aspects of the final reconstruction remain conjectural (for instance length and shape of spines or papilli on appendages).

DESCRIPTION

Interpretation of soft-bodied organisms based on their fossils alone usually suffers from their incomplete preservation and complex taphonomic history. This is also the case with the Siberian lobopodian. The presence of a probable phosphatised intestine indicates that this was not an exuvium, as happens with other xenusian fossils (Robison, 1985; Dzik & Krumbiegel, 1989), but a cadaver. Preservation of other soft-bodied organisms in the same bed may offer some insight into the degree of sclerotisation of its body covers. The most diverse and best preserved palaeoscolecid worms (possible nematomorphs) from the bed (Ivantsov & Wrona, 2004) have their body rings covered with probably originally phosphatic sclerites and are actually skeletal fossils, not especially informative in this respect. The discoidal eldoniids (probable lophophorates) preserve mostly only the dark-stained intestine within incomplete discs, rarely in relief (Ivantsov et al., 2005). The degree of sclerotisation varies within the group very much, as known from other localities. Perhaps the closest analogues of the xenusiid body covers are the originally unmineralised and thin sclerites of the halkieriid *Wiwaxia* (annelid or basal mollusc) and the rather thick organic tubes of *Cambrorhytium* (Ivantsov et al., 2005). The lobopodian specimens from the 'Algal lens' are intermediate in elevation of relief and staining between the sclerites of *Wiwaxia* and discs of the eldonioids. Thus, it is likely that the original degree of sclerotisation of its cuticle was rather low. Not only the annulation of the body and appendages are preserved less prominently than the homologous parts in the two known specimens of *Xenusion* (Dzik & Krumbiegel, 1989), but even the spinose structures arming appendage annuli are obscure in the Siberian fossil.

Trunk

Preservation of the holotype is far from being perfect and it is difficult even to decide, which side of the body it replicates. There are several lines of inference that could potentially be used to solve this question, but in different parts of the body they give conflicting results. Thus, the belt of whitish (presumably calcium phosphate) matter along the body midline most probably represents the intestine and its location above the cuticle imprint suggests that it is seen from the inside of the body. In its posterior part, the cuticle annuli are represented by narrow impressions separated by wider flat areas, which suggests that there were regularly distributed transverse riblets on the body surface. Anteriorly, however, the picture is opposite - with flat areas separating these riblets in positive relief, although the phosphatic belt continues to run above them.

Immediately behind the raptorial appendages, where the algal thallus covers the animal´s body, only one surface is discernible, which suggests that one is dealing with the external surface of the body.

A possible conclusion from these observations is that the specimen mostly represents a palimpsest, with dorsal and ventral parts so closely pressed each to the other that the distinction between them cannot be easily traced. In its anterior part, mostly the dorsum is represented but in the posterior part the venter contributed mainly to the relief. This makes problematic the meaning of the radially arranged probable oral structures and the series of minute oval structures bordering the intestine along its left side but apparently connected with cuticular annuli. Rather arbitrarily, it is proposed that the round objects in the head region represent mineralised bases of oral papillae located ventrally but seen from the dorsum across the cuticle. In case of similar but linearly arranged minute objects on the trunk, it is suggested that these are cuticular papillae arming the dorsal surface of the body.

The location of the circle of possible oral papilli (or spines) significantly backwards in respect to the anterior end of the body indicates that the mouth was not strictly terminal but directed somewhat ventrally.

There are about nine annuli per trunk appendage pair. The spacing of annuli is not strictly regular. Some of them disappear, others insert from the sides. The Moscow specimen PIN 4349/820 is preserved as laterally compressed piece of the body. There seems to be an indistinct zone of change from the dorsal dense annulation to a sparser annulation over the ventral belt (Ivantsov et al., 2005).

'Head' appendages

The appendages of anteriormost pair are much larger than the appendages located behind. They are oriented almost transversely to the body axis, with their anterior margin only slightly behind the frontal end of the body. The annulation is not well demarkated by riblets or furrows and seems rather irregular. Near the anterior margin a series of elevations and depressions, more prominent than regular annuli, occur. Their tips are cut by the split rock surface but they are likely to be bases of spinose protrusions and are interpreted as such (Fig. 2B).

The posterior margin of the head appendages is not preserved on either side of the body but on the left side of the holotype its base extends well behind. This makes them about three times as large as the following 'trunk' appendages.

Trunk appendages

No appendage is completely preserved, but bases of most of them are discernible on sides of the body. Tracing the body annulation helps in matching appendages from both sides of the body (Fig. 2). There is a rather good evidence for 12 appendages of apparently uniform size.

Potentially, the relief and superposition of appendages could help in deciding whether the specimen's venter faces upward or downward. Those in the anterior part of the body are slightly convex, with margins dipping slightly down, and seem to have their caudal side margins located above the frontal margin of an appendage behind. This is a pattern suggestive of the specimen being seen from its dorsum. The opposite seems true for the posterior appendages and the medial caudal extension (the 'tail'), which are slightly concave, with raised margins. These observations do not help in deciding whether the surface of appendages was covered by swollen annuli or rather ridges.

Wrinkles running obliquely to the regular annulation of left appendage 3 and even less distinct traces of such structures on other appendages (Fig. 2) provide a weak evidence that elongated papilli (or spine-like structures) protruded backward from some annuli on each appendage. Their length would be similar to the appendage diameter. The tubercles distributed along the appendages mentioned by Ivantsov et al. (2005, p. 58) may possibly represent bases of the papilli. Similar tubercles occur along the body, well visible on its left side in the holotype specimen (Fig. 2), delimiting the dorsal region with a more dense annulation (Ivantsov et al., 2005, p. 58).

In the first found specimen PIN 4349/820, the tips of some appendages are dark, suggestive of hooklets being present there.

'Tail'

The appendage bases match well in pairs, up to the posteriormost 12th pair, but there is an appendage-like structure even further behind (Fig. 2). Its size is similar to that of the nearby appendages but its axis strictly follows the axis of the body and, although this part of the body was exposed and carefully cleaned from the rock matrix with a needle, no sign of any additional structure that could serve as the second appendage of the same pair was encountered. As discussed below, such terminal structures are known in other Early Cambrian xenusians, which make interpretation of this structure as a legless 'tail' plausible.

EVOLUTIONARY RELATIONSHIPS OF THE SIBERIAN XENUSIAN

Ma et al. (2009) performed computer cladistic analysis based on a matrix of characters chosen and defined by them. In the run with assumed equal value of characters, the group of taxa encompassing large xenusids with grasping appendages appeared as unresolved (Ma et al., 2009, Fig. 12a). Only after arbitrary weighting of characters the desired pattern of clades emerged (Ma et al., 2009, Fig. 12b). The Siberian form, being close morphologically to *Megadictyon*, found to be a sister taxon of the Onychophora, does not influence this proposal. Therefore, I restrict the discussion here to an attempt to arrange body plans represented among the known Cambrian members of the Xenusia into chronomorphoclines, using a somewhat different methodological approach. It may be expected that with increasing geological age of a species the probability increases that it is close to the ancestor of its group. This is a self-evident outcome of the fundamental assumption of any phylogenetic inference (morphological, genetical or molecular) - that difference is proportional to time of evolution. From such perspective the most parsimonious interpretation of a fossil material is that its succession corresponds to the actual course of evolution; additional evidence is necessary to alter such hypothesis. This methodology of inference is discussed in detail elsewhere (Dzik, 1991, 2005). A tentative scenario of evolutionary transformations is then suggested (Fig. 3), in which *Xenusion* is given a central position, consistent with its probable age and anatomy interpretable as being derived from the nemathelminthan body plan (Dzik & Krumbiegel, 1989).

Unspecialised xenusians

Probably *Xenusion auerswaldae* Pompeckj, 1927 (Dzik & Krumbiegel, 1989; Dzik, 2003) is the geologically oldest xenusian, known from two specimens from glacial drift boulders presumably derived from the southern Swedish basal Cambrian Kalmarsund sandstone (Jaeger & Martinsson, 1967). *Xenusion* shows an almost homonomous distribution of unspecialised appendages along its cylindrical body, which seems to be a status plesiomorphic for the Xenusia. The number of appendage pairs remains unknown in *Xenusion*, but it was much higher than 15, as represented in the incomplete holotype. Among other known xenusians only *Paucipodia inermis* Chen, Zhou & Ramsköld, 1995 from the Chengjiang biota is anatomically simpler than *Xenusion*, with nine pairs of cylindrical appendages, lacking any spines except for the terminal claws (Hou et al., 2004, 2007). In the tubular shape of its appendages, but not in the lack of dorsal spines, *Paucipodia* is similar to *Orstenotubulus evamuellerae* Maas et al., 2007, the smallest of all known xenusians. Probably a rather generalised body plan, but relatively large size, characterises the poorly known latest Ordovician member of the group (Whittle et al., 2009).

Sclerite-bearing xenusians

A whole group of the Chengjiang xenusians share such a simple organisation of appendages with *Paucipodia* but are different from other members of the class in being armed with mineralised dorsal sclerites, a pair of them corresponding to each appendage pair (Bengtson et al., 1986). Morphologies of these sclerites ranges from spinose in *Hallucigenia fortis* Hou & Bergström, 1995 (Hou & Bergström, 1995; Hou et al., 2007) to plate-like in *Cardiodictyon catenulum* Hou et al., 1991 (Hou et al., 1991; Ramsköld, 1992; Hou & Bergström, 1995) and *Microdictyon sinicum* Chen et al., 1989 (Chen et al., 1989, 1995). Isolated sclerites of transitional shapes suggest that an evolutionary continuum covers all this series (Bengtson, 1991; Demidenko, 2006). The dorsal sclerites of these lobopodians are thus likely to be derived from dorsal spines of the kind known in *Xenusion*, probably the geologically oldest member of the group.

The last sclerite pair tends to be of a different shape and larger than others in *Microdictyon*, and transformed into oval valves enclosing the swollen terminal part of the body from its sides in *Cardiodictyon* and *Hallucigenia*. The latter genus is represented also in the Mid Cambrian Burgess Shale by the celebrated *Hallucigenia sparsa* Conway Morris, 1977 (Ramsköld & Hou, 1991). However, whether this swollen part of the body represents its posterior end, or the opposite, is a matter of controversy.

In fact, the polarity of the body of most xenusians remains disputable. The Mid Cambrian *Aysheaia* had a cylindrical proboscis and with its body terminating at the opposite end with the last, eleventh pair of appendages (Whittington, 1978). In his restoration there is no caudal part of the body and the appendages do not diminish in size near the posterior end, which suggests that the final number of appendages emerged early in the ontogeny, possibly at the embryonic stage. The polarity of the *Aysheaia* body seems well supported by the presence of apparently raptorial appendage pair near the proboscis. A similar interpretation of the body ends was proposed by myself for *Xenusion* (Dzik & Krumbiegel, 1989), although no appendages are functionally specialised there.

The opposite interpretation of body polarity was proposed for the Burgess Shale *Hallucigenia sparsa* by Ramsköld & Hou (1991) and Hou & Bergström (1995), who considered the appendage-free narrower part of the body to be posterior. This may be an analogy with the posterior part of the onychophoran body (e.g., Mayer, 2006b). The allegedly anterior swollen end of the body of *H. sparsa* was covered by enlarged sclerites, identified by Hou & Bergström (1995), and bears two crowded pairs of appendages in the Chengjiang *Hallucigenia fortis*, *Cardiodictyon catenulum*, and *Microdictyon sinicum* (Chen et al., 1995). These appendages were interpreted as functionally specialised in connection with their

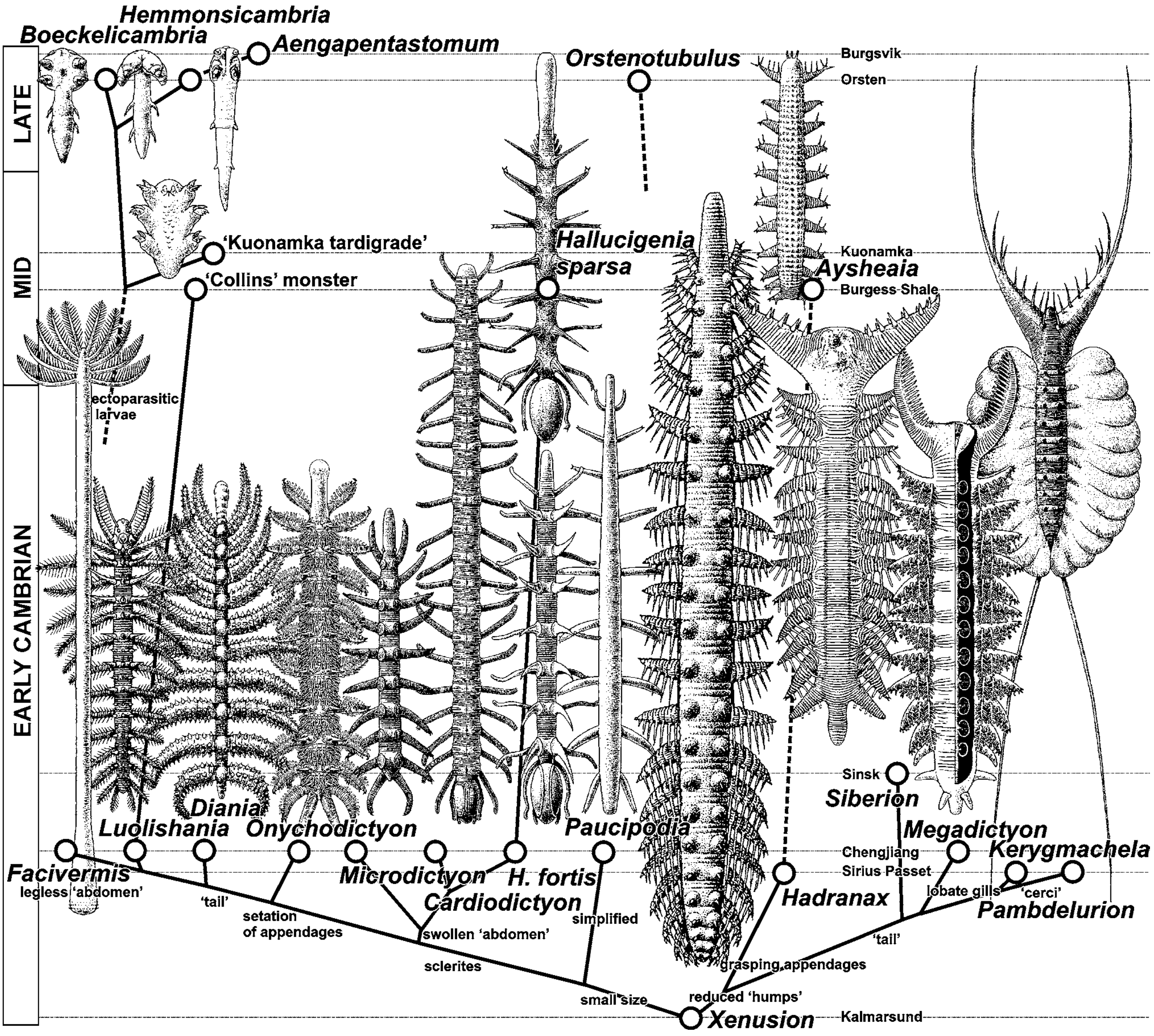

Fig. 3 - Inferred pattern of chronophyletic relationships among known Cambrian Xenusia. Restoration of body appearance given in dorsal view, except for the Mid Cambrian 'tardigrade' (after Müller et al., 1995) and Late Cambrian 'pentastomids' (after Walossek & Müller, 1994), which are shown from their venter. Sources of data given in the text.

perioral location. A possible alternative is that both in *Xenusion* and the sclerite bearing xenusians these are underdeveloped appendages at the posterior end of the body (Ramsköld, 1992). In arthropods such a gradient in size of the posteriormost appendages may be an expression of formation of the body units during successive moults. Moreover, it has to be noticed that in nemathelminthan ecdysozoans reproductive organs open to the hind intestine and the swelling of the posterior part of the body in these xenusians may correspond to the location of gonads.

A similar body organisation characterises another Chengjiang xenusian, *Onychodictyon ferox* Hou et al., 1991 (Bergström & Hou, 2001; Liu et al., 2008c), but its homonomous sclerites seem to represent plesiomorphic traits. Its possible spiny relative, *Diania cactiformis* Liu et al., 2011, has been interpreted as having prominent a proboscis together with a short legless region behind the last strongly sclerotised appendage pair. Although Liu et al. (2011) proposed location of *Diania* well above *Anomalocaris*, based on computer cladistic analysis, the body plan suggests its relationship to another group of possibly sessile Chengjiang xenusians characterized by appendages armed with long sharp setae (Fig. 3).

Sessile xenusians

Minute dorsal sclerites occur in *Luolishania longicruris* Hou & Chen, 1989b (Hou & Chen, 1989b; Hou & Bergström, 1995) from Chengjiang, but there are three longitudinal rows of them instead of two. This xenusian is peculiar in having an anterior series of long appendages armed with hair-like spines suggestive of filtratory mode of feeding (Hou et al., 2007; Liu et al., 2008a, b; Ma et al., 2009). The appendages behind are much shorter (Ma et al., 2009). Minute eyes have been identified in some forms of closely similar morphology (Liu et al., 2006b; Schoenemann et al., 2009). Virtually indistinguishable five anterior appendage pairs are present in *Facivermis*, a bizarre sedentary xenusian characterized by a legless posterior part of the body with a hooks-bearing swollen end (Hou & Chen, 1989a; Liu et al., 2006a). This peculiar body plan throws some light on the possibly ectoparasitic larvae known from three-dimensionally preserved specimens from the Mid and Late Cambrian. Notably, the 'stem-group tardigrade' of Müller et al. (1995) from the Mid Cambrian Kuonamka Formation of northern Siberia had a legless posterior end of the body, which anteriorly was armed with three pairs of appendages. These two aspects of their body plan disclose possible facivermid (less likely siberiid) xenusian affinity, although it does not show any hooks and is much shorter, which may be connected with its early ontogenetic stage of development. Even more derived are the Late Cambrian to earliest Ordovician (the latter possibly reworked from the latest Cambrian) 'pentastomids' of Walossek & Müller (1994). They had only two pairs of appendages with regular claws, whereas rudimentary (or incipient) posterior appendages bore hair-like modified claws similar to those of *Luolishania*.

Xenusians with raptorial appendages

The sclerite-bearing xenusians seem to have evolved towards minute mature size (Fig. 3). The large size of other xenusians, with enlarged raptorial appendages of the first pair, may be a trait inherited after *Xenusion*, which is among the largest xenusians known. Possible walking traces of a Mid Cambrian xenusian (Lane et al., 2003) may help in understanding the locomotory abilities of these animals. Unlike *Xenusion* and sclerite-bearing minute forms, their dorsum was either covered by numerous tubercles or was smooth. In robust tuberculation of the appendage-bearing annuli (instead of 'humps'), *Hadranax augustus* Budd & Peel, 1998 from the North Greenland Sirius Passet fauna (Buen Formation) is transitional between *Xenusion* and the Mid Cambrian Burgess Shale *Aysheaia pedunculata* Walcott, 1911 (Whittington, 1978). Only a small portion of the body of *Hadranax* is known and the structure originally interpreted as a remnant of a long branched frontal appendage may represent an unrelated fossil accidentally superimposed on the holotype. The Sirius Passet fauna is dated as the 'Nevadella' Biozone and predates the Chengjiang fauna, which according to Budd & Peel (1998) correlates with the Baltic Holmia Zone.

Large xenusians with raptorial appendages were present also in the Early Cambrian of China. *Megadictyon haikouensis* Luo & Hu, 1999, as redescribed by Liu et al. (2007) is closely similar, if not conspecific with, *Jianshanopodia decora* Liu *et al*., 2006c. Both have an annulated cylindrical body of a size comparable with *Xenusion*, strong frontal appendages, serial reniform caeca (or rather intestinal glands) and complex radially organised mouth parts. *Megadictyon* Luo & Hu, 1999 shares some features with the Early Cambrian possible anomalocaridids *Pambdelurion* Budd, 1997, and *Kerygmachela* Budd, 1993, i.e., the large frontal appendages, an oral apparatus, and reniform mid-gut diverticula (Budd, 1993, 1997; Liu et al., 2006b). These possible intestinal glands may have a phylogenetic significance. The lack of mud in the intestine of all known xenusians suggests selectivity in feeding (Bergström & Hou, 2001), and perhaps a predatory mode of life, as suggested by their common association with sponges or eldonioids (Chen et al., 1995). Intestinal diverticulae were proposed to enter the appendages in *Hallucigenia* (Conway Morris, 1977) and *Paucipodia* (Chen et al., 1995; Hou et al., 2004). The reniform caeca of *Megadictyon* and *Jianshanopodia* occupy the place corresponding to the dorsal humps in *Xenusion*, proposed to be serially homologous with appendages (Dzik & Krumbiegel, 1989). They may have originated from serial intestinal caeca radiating from the intestine and entering the dorsal appendages, which eventually swelled into the humps. In the Siberian form the phosphatised structure probably corresponding to the intestine has straight smooth lateral sides. There is no evidence for caeca.

Basal anomalocaridids

Pambdelurion whittingtoni Budd, 1997 from the Sirius Passet fauna of Greenland was an animal of almost 30 cm length, its ventral mouth being armed with cuneiform plates, 11 pairs of flaps along the body, and possibly two or three additional flaps in the head region (Budd, 1997). Limbs bearing about fifty annuli were present in conjunction with lateral flaps. In these respects it occupies, together with anatomically more advanced coeval *Kerygmachela*, an intermediate position between xenusians with grasping anterior appendages and the more typical anomalocaridids.

There is a variety of opinions regarding morphology of usually poorly preserved appendages of the anomalocaridids, but there is a possibility that they were biramous, with the annulated ventral part corresponding to the arthropod endopods and the flaps corresponding to the exopods. Instead of paddle-shaped, movable lateral flaps characterising both *Pambdelurion* and *Kerygmachela*, *Jianshanopodia* possessed appendages that bore dorsally emerging series of pinnate extensions of possible respiratory function. The homologous posterior extensions of appendage annuli were weakly sclerotised in the Siberian form and in this respect they resembled the *Jianshanopodia* 'gills' but they were hardly pinnate. The Siberian xenusian fits best in this morphocline as basal to *Megadictyon-Jianshanopodia* and above the less derived *Hadranax*-like xenusians (Fig. 3).

RELATIONSHIPS OF THE XENUSIANS TO OTHER APPENDAGE-BEARING ECDYSOZOANS

A long time distance and a deep morphological difference separate the Cambrian xenusians from their probable relatives, onychophorans and tardigrades (Bergström & Hou, 2001; Budd, 2001; Podsiadlowski et al., 2008). Indeed, the oldest known terrestrial velvet worm *Helenodora inopinata* Thompson & Jones, 1980 from the Francis Creek Shale of Illinois lived almost two hundred million years later. Its anatomy seems to be already close to the Recent onychophorans: it had a pair of antenna-like head appendages and poorly preserved jaws. In the number of walking appendages (probably

22-23 pairs; Thompson & Jones, 1980) only *Xenusion* and *Cardiodictyon* among the known xenusians are similar to *Helenodora* in this respect.

In the lack of intermediates between the Xenusia and Onychophora, only the developmental features of the latter can be used to restore the body plan of their possible ancestors. The crucial point is actual homology of the 'head' appendages and the original location of the mouth. In fact, the innervation of the onychophoran mouth from three different regions of the brain suggests that the mouth was originaly terminal (Eriksson & Budd, 2000; Eriksson et al., 2003), as it is in the Tardigrada and was in the xenusians. Bergström & Hou (2001) suggested homology of the 'antennae' of Onychophora with the grasping appendage of *Aysheaia* and loss of appendages corresponding to the onychophoran jaws in the course of evolution from the xenusian ancestor. Transient Anlagen of nephridial organs found by Mayer & Koch (2005) in the anteriormost segment indicate that the onychophoran antennae are truly modified legs. However, there is no need to make *Aysheaia* the ancestor of onychophorans. They could have originated from much less derived xenusians as well, although this must remain conjectural until the post-Cambrian stage in the lobopodian evolution is documented with fossils.

Mayer & Harzsch (2007) demonstrated that ganglia are not segmental in the Onychophora and the paired leg nerves are the only segmental structures associated with the onychophoran nerve cord. Also in tardigrades, the paired ventral ganglia do not show segmental commissures typical for the ladder-like nervous system of arthropods (Zantke et al., 2008). Significant change is thus required to make a lobopod segmented. But this is necessary as long as there is no reasonable alternative for the ancestry of arthropods.

Some hints regarding possible lobopodian-arthropod relationships are offered by neuroanatomical studies. Strausfeld et al. (2006a, b) pointed out some similarity in the organization of the onychophoran brain to that of the brains of chelicerates. Mayer (2006a) suggested homology between the onychophoran eyes and the median ocelli of euarthropods. The eyes develop posteriorly to the antenna and are not serially homologous with compound eyes of the arthropods (Eriksson et al., 2003). Both developmental data and palaeontology significantly contributed to understanding homology of the head between arthropods and lobopodians (Scholtz & Edgecombe, 2005, 2006).

From the palaeontological point of view, an answer to the question of the lobopodian-arthropod connections has to be sought in checking the xenusian-anomalocaridid segment of the phylogenetic tree. As suggested above, the new Siberian form extends backwards the morphocline connecting *Xenusion* with the anomalocaridids. It initiates a series with *Megadictyon*, *Pambdelurion,* and *Kerygmachela*, in which the raptorial appendages become more and more sclerotised, while dorsally emerging protuberances on trunk appendages transform into pinnate gill-like structures and finally into wide flaps. This generally accepted sequence of events (e.g., Liu et al., 2011) implies that the change from *Peripatus*-like to compound eyes, proposed by Schoenemann et al. (2009), took place well within the anomalocaridid clade.

TAXONOMIC IMPLICATIONS AND DIAGNOSES OF NEW TAXA

It appears thus that except for *Xenusion* and *Paucipodia*, other completely segmented xenusians form two easily defined groups: those with an anterior pair of spinose raptorial appendages and those with mineralised dorso-lateral sclerites. I propose to use the raptorial appendages as a basis to unite these xenusians into a separate new order, which would encompass a new lower rank taxa for the Siberian lobopod. Diagnoses of these Linnean (paraphyletic) taxa are presented below in terms of evolutionary (non-cladistic) taxonomy (as in Hou & Bergström, 1995).

Phylum Lobopodia Snodgrass, 1938
Class Xenusia Dzik & Krumbiegel, 1989
Order Siberiida ord. nov.

Diagnosis - Large xenusiids with prominent grasping first pair of appendages, reduced proboscis, and tail-like terminal extension of the body; appendages with weakly sclerotised serial gill-like structures extending dorsally from some annuli.

Remarks - Members of the new order differ from those of the Xenusiida Dzik & Krumbiegel, 1989 in having large grasping appendages, from Protonychophora Hutchinson, 1930 *sensu* Hou & Bergström, 1995 (for the Aysheaiidae Walcott, 1911) in a reduced proboscis and from the anomalocaridid arthropods in lacking flaps and/or arthropodial appendages of the first pair.

Family Siberiidae fam. nov.

Diagnosis - As for the order.

Genera included - *Megadictyon* Luo & Hu, 1999, *Jianshanopodia* Liu et al., 2006b, *Siberion* gen. nov.

Genus *Siberion* gen. nov.

Type species - *Siberion lenaicus* gen. et sp. nov.

Diagnosis - 'Tail' with annulation, a row of minute tubercles on sides of the body with about 9 annuli per appendage pair; all 12 postoral appendage pairs of similar size and shape bear probably tubular extensions, serially emerging from annuli; the cylindrical gut probably lacks caeca.

Remarks - Most characters making *Siberion lenaicus* gen. et sp. nov. different from other members of the family reflect a rather homonomous organization of its body, which is probably plesiomorphic. However, the age difference between them is such that an ancestor descendant relationship is unlikely and any phylogenetic evaluation of traits remains conjectural. The material from the Sinsk Formation available for study is regrettably limited but there is little chance of additional specimens being found in the predictable future as the fossil locality was recently destroyed by commercial fossil collectors.

Species included - Only the type species.

Siberion lenaicus gen. et sp. nov.

Holotype - ZPAL V37/1 (Figs. 1A-B).

Type horizon and locality - 'Algal lens' on the right bank of the Lena River near the mouth of the Ulukhan-Tuoidakh Creek, Sinsk Formation, Early Cambrian, Botomian, *Bergereniellus gurarii* or early *B. asiaticus* trilobite Zone.

Diagnosis - As for the genus.

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