# A NEW XENUSIID LOBOPOD FROM THE EARLY CAMBRIAN SIRIUS PASSET FAUNA OF NORTH GREENLAND

*by* GRAHAM E. BUDD *and* JOHN S. PEEL

ABSTRACT. Three incomplete specimens of a large lobopod, *Hadranax augustus* gen. et sp. nov. are described from the exceptionally preserved Sirius Passet fauna (Buen Formation, Lower Cambrian, North Greenland). Its overall appearance and size are similar to those of *Xenusion auerswaldi* Pompeckj from the Baltic, but *H. augustus* differs in its possession of four poorly defined dorsal nodes in each row rather than two, and in the probable possession of a pair of long, branched frontal appendages.

The new specimens further demonstrate that the lobopods were a widespread and diverse Cambrian group. The presence of a four-noded xenusiid refutes the hypothesis that lobopods were directly derived from tetra-radial nemathelminthes and shows that both node number and form were fairly flexible, although their primary function remains unclear. The probable presence of a pair of long branched frontal appendages in *H. augustus* removes one of the major reasons for considering *Xenusion* to be a basal lobopod, and adds further to the characters that unite *Anomalocaris*-like taxa to the lobopods.

THE Sirius Passet fauna is an exceptionally well-preserved Early Cambrian fauna from the Buen Formation, which crops out in the far north of Greenland (Conway Morris *et al.* 1987; Text-fig. 1). Three major collecting expeditions, in 1989, 1991 and 1994, have now amassed almost 10 000 specimens. About 40 species are present in the fauna, which is dominated by poorly sclerotized arthropods. Although primary description of Sirius Passet taxa is still at a relatively preliminary stage, 'conventional' Cambrian taxa such as sponges (Rigby 1986) and a nevadiid trilobite (Blaker 1988) have already been described. In addition, a remarkable articulated halkieriid, *Halkieria evangelista* (Conway Morris and Peel 1990, 1995), an *Opabinia*-like gilled lobopod, *Kerygmachela kierkegaardi* (Budd 1993), and an unusual trilobite-like arthropod, *Kleptothule rasmusseni* (Budd 1995), have been described.

## GEOLOGICAL SETTING AND AGE

The Buen Formation consists of siliciclastic deposits which record the subsidence and subsequent transgression of an eroded carbonate platform, represented by the Portfjeld Formation, which developed on the currently southern margin of the Franklinian Basin sequence in North Greenland (Peel and Sønderholm 1991). In its type area of southern Peary Land, the formation is almost 420 m thick but it thickens northwards to about 700 m at the transition into a deep-water basin succession referred to the Polkorridoren Group, the latter cropping out immediately north of the Sirius Passet locality. Regionally, the Buen Formation consists of a lower sandstone-dominated member and an upper mudstone-dominated member, but the mudstones prevail in northern outcrops. The Sirius Passet fauna is derived from mudstones in the lowest part of the formation immediately adjacent to the edge of the underlying carbonate platform (Text-fig. 1).

The Buen Formation yields three stratigraphically distinct faunas of Early Cambrian age in eastern areas of North Greenland. The stratigraphically lowest, from near the base of the formation, contains the nevadiid *Buenellus higginsi* Blaker, 1988, considered by Palmer and Repina (1993) to
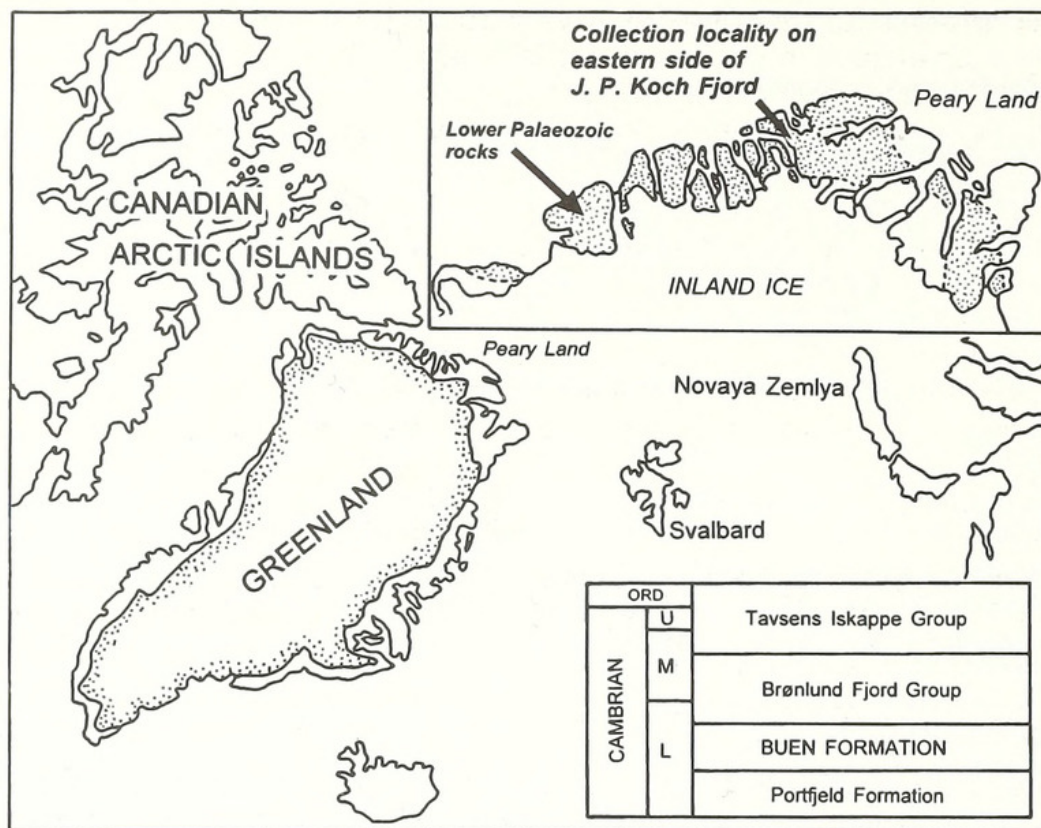
TEXT-FIG. 1. Locality map for the Sirius Passet fauna.

indicate the 'Nevadella' Biozone of North American usage. Exposures in southern Peary Land yield Olenellus (Mesolenellus) hyperboreus Poulsen, 1974 and an undescribed new taxon of nevadiid form from the upper part of the formation, seemingly indicative of the boundary between the 'Nevadella' and Olenellus Biozones. Uppermost beds of the formation yield Olenellus svalbardensis, Kielan, 1960, a typical Olenellus Biozone species, in eastern Peary Land, and the problematical Alacephalus? davisi Lane and Rushton, 1992 from a few kilometres south-west of the Sirius Passet locality.

Acritarchs retrieved from the upper parts of the Buen Formation indicate a general age of the Holmia Biozone (at least in part equivalent to the Olenellus Biozone of North America (Palmer and Repina 1993), and include the diagnostic forms Skiagia ciliosa and Heliosphaeridium dissimilare (Vidal and Peel 1993). Thus, the Sirius Passet fauna seems to be firmly dated as in the 'Nevadella' Biozone. It therefore appears to predate the Chengjiang fauna (see e.g. Shu et al. 1995), which correlates with the Heliosphaeridium dissimilare-Skiagia ciliosa acritarch and Holmia trilobite biozones (Zang 1992).

Correlation within the Lower Cambrian has been thrown into some confusion recently, with the suggestion that the Tommotian may be rather younger than previously thought (Vidal et al. 1995). If this suggestion is correct, then the Buen Formation would correlate with the lower Tommotian as recognized by these authors. It is not clear, however, that such a reorganization of Lower Cambrian correlation will find universal recognition, and under more conventional schemata, the fauna is probably of Late Atdabanian age (Conway Morris and Peel 1995).

## TAPHONOMY

The preservation of the Sirius Passet fauna is puzzling. The fossils show no clear signs of extensive transport, and are associated, perhaps directly, with trace fossils (e.g. Pl. 1; Pl. 2, fig. 1), implying that the environment of deposition was not permanently lethal. Although the central regions of many of the fossils seem certainly to have been mineralized, the outer regions, such as the carapaces

of many of the arthropods, seem also to have been replaced with clay minerals. Originally calcareous forms, such as the trilobite *Buenellus* (Blaker 1988) and the halkieriid *Halkieria* (Conway Morris and Peel 1995), have been decalcified, although they often retain a considerable amount of relief, and the original outer surface of the fossils is retained, implying a replacement process rather than the formation of external moulds.

## SYSTEMATIC PALAEONTOLOGY

### Super-phylum LOBOPODIA Snodgrass, 1938

*Remarks.* This grouping is taken to include all of the lobopodian taxa (including Tardigrada, Onychophora, Pentastomida and Cambrian forms) and all of the arthropods, i.e. the familiar fully sclerotized members of the clade, including the euarthropods (the smallest clade inclusive of all extant arthropods).

### Family XENUSIIDAE Dzik and Krumbiegel, 1989

*Emended diagnosis.* Large lobopodians with robust trunk annulations; trunk nodes large; terminal limb claws apparently absent; annular nodes and long slender branched frontal appendages present in at least some forms.

*Genera.* *Xenusion* Pompeckj, 1927; *Hadranax* gen. nov.

*Remarks.* We do not consider that lobopodian monophyly has been satisfactorily demonstrated (*contra* Ramsköld 1992; Chen *et al.* 1995a). If the proposal of Budd (1993, 1996) that they constitute a paraphyletic assemblage is correct, then the supposed monophyly of any of the lobopodous groups including the Xenusiidae is suspect without further careful character analysis.

### Genus HADRANAX gen. nov.

*Derivation of name.* From the Greek hadros (stout, sturdy) and anax (ruler) in reference to its large size and, no doubt in life, intimidating appearance. The gender is masculine.

*Type species.* *Hadranax augustus* sp. nov.

*Diagnosis.* Large, *Xenusion*-like lobopod, but differing in possessing rows of four trunk nodes instead of two, in the probable presence of annular nodes, and in the lack of fleshy limb outgrowths. *Hadranax* bears a pair of long, branched, probably frontal appendages that are not known from *Xenusion*.

### *Hadranax augustus* sp. nov.

Plates 1–3; Text-figures 2–3

*Derivation of name.* From the Latin *augustus*, august.

*Holotype.* MGUH 24.527 from GGU collection 340103, an incomplete section of the trunk showing limbs and putative frontal appendages (Pls 1–2; Text-fig. 2).

*Type horizon and locality.* From the base of the Buen Formation ('*Nevadella*' Biozone, Lower Cambrian); east side of J. P. Koch Fjord, North Greenland.

*Other material.* MGUH 24.528 (Pl. 3, fig. 1). It is both poorly preserved and confused in the axial region (Text-fig. 3A; Pl. 3, fig. 1), and may represent exuviae (as Jaeger and Martinsson (1967) and Dzik and Krumbiegel (1989) suggested for the known specimens of *Xenusion*); however, a reasonable interpretation of the specimen may be made, showing how some of the limbs have been perturbed to lie under the trunk (Text-fig. 3B). ?MGUH 24.529 (Pl. 3, fig. 2), possibly an isolated pair of limbs, is assigned to this genus with some hesitation,

and may represent two poorly preserved limbs lying next to each other (Pl. 3, fig. 2). Any point of attachment to the body is not visible.

*Diagnosis.* As for the genus.

*Description.* *Hadranax* is a large lobopod: the longest specimen of the body as preserved is 69 mm long, but both terminations are missing. The head and caudal regions of *Hadranax* are unknown, apart from a possible anterior appendage (see below). The trunk is parallel along its preserved length, 11 mm wide, and in the largest specimen consists of eight alternating regions of rows of nodes separated by transverse annulations (see Ramsköld 1992 for terminology and its application to other Cambrian lobopods). There are four sub-equal and rather poorly defined nodes in each row. Five well-defined, broad annulations fill the trunk area between the nodal rows. They show some traces of relatively large but poorly defined 'annular nodes' (Text-fig. 2; Pls 1–2), i.e. small tubercular structures, although the possibility of these being crush structures cannot be discounted. In line with each nodal row is attached a pair of annulated lobopod limbs. Each limb is approximately 17 mm long, and there are 18–20 annulae per limb. The limb annulae bear small projections or tubercles (Pl. 2, fig. 2). The tips of the limbs are moderately pointed, but there is no convincing evidence for the presence of terminal claws.

The best preserved specimen has, mid-way along the trunk, a 28 mm long slender appendage projecting, which appears, as preserved, to underly the limbs (Pl. 1; Pl. 2, fig. 1; Text-fig. 2). It is also characterized by transverse annulations, although these are less prominent and more closely spaced than those along the limbs or the trunk. Near the distal end of the appendage is a short section of a somewhat more slender branch, which also appears faintly annulated. Just proximal to this branch and on the same side is a much smaller protuberance on the main appendage (Pl. 2, fig. 1, arrowed), which probably represents the base of a similar but considerably narrower branch.

The style of preservation and general character (transverse wrinkling and branching or spinosity developed along one margin) are consistent with it representing an appendage of a lobopod (compare the structures in *Aysheaia* (Whittington 1978) and *Kerygmachela* (Budd 1993)). Posterior appendages of lobopods tend to be identical with other trunk appendages, although some, such as in *Hallucigenia*, do appear to be differentiated at the anterior of the animal (Ramsköld 1992; Conway Morris 1997), and appear to be attached laterally, not ventrally, although in this case these appendages are not branched. If the appendage associated with *Hadranax* is either a frontal appendage or some other differentiated appendage, then it is bent backwards and under the body, and for it to be attached to the front of the body it would have to be at least 45 mm long (28 mm preserved plus at least 17 mm concealed under the trunk), and perhaps more than this. Even given these reservations, such an identification seems the most plausible: its overall appearance and preservation is close to that of the overlying specimen, and no other taxa within the fauna are known to possess such appendages.

Triangular extensions of the trunk, complete with annulations that converge distally (Pls 1–2; Text-fig. 2), appear to project out between the limbs of the best specimen. It is difficult to interpret these structures, as they may be taphonomic in origin, perhaps generated by the lateral margins of the trunk being squeezed up by the limbs during burial. However, if this was the case one would expect them to overly the limbs, which they do not, unless these portions are preserved in the (missing) counterpart. Conversely, they may represent genuine extensions of the trunk into fleshy lobes. Unfortunately the best specimen available that shows them does not resolve the issue, and the other convincing specimen is too distorted to be of any help.

*Remarks.* Whilst it is unfortunate that so little material is available (it is among the rarest taxa in the fauna), with only one good specimen, *Hadranax* nevertheless shows several interesting features, although a complete reconstruction will not be presented owing to the lack of knowledge of the head and tail. In particular, it shows the following important similarities to *Xenusion*, especially relative

---

EXPLANATION OF PLATE 1

*Hadranax augustus* gen. et sp. nov.; MGUH 24.527 (holotype). the most complete specimen; note branched appendage emerging from towards the top left of the specimen; the structure at the top right of the specimen is a trace fossil; × 2·7. Compare Text-figure 2.

PLATE 1



BUDD and PEEL, *Hadranax*
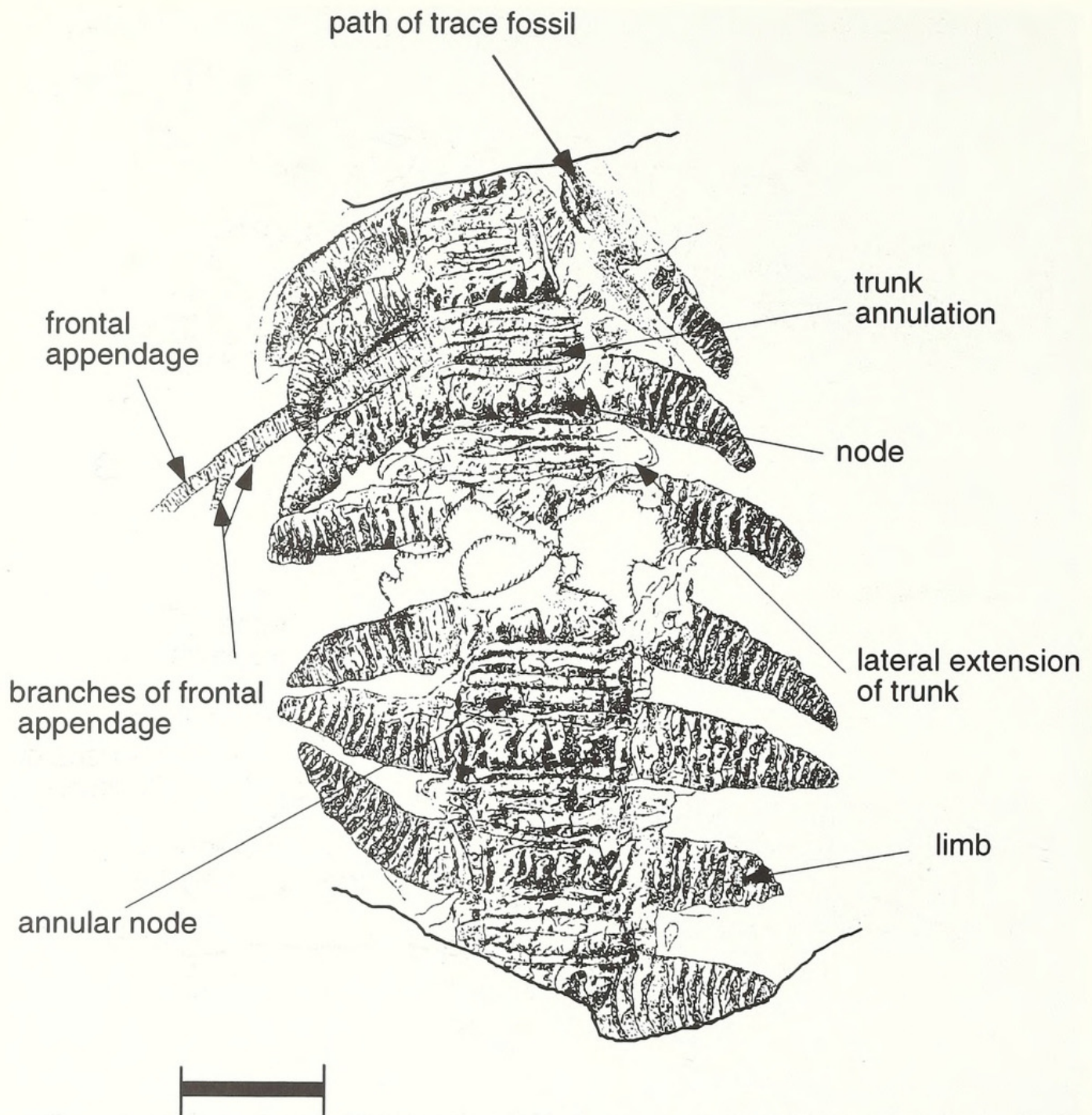
TEXT-FIG. 2. *Hadranax augustus* gen. et sp. nov.; explanatory drawing of MGUH 24.527 (holotype); compare Plate 1. Scale bar represents 10 mm.

to other Cambrian lobopods (no attempt to distinguish apomorphic and plesiomorphic characters is made here).

1. A large size, considerably greater than other Cambrian lobopods. The two known specimens of *Xenusion* have a nodal row spacing of *c.* 5·8 mm and 10 mm (Dzik and Krumbiegel 1989 argued that these two specimens represent posterior and anterior sections of a *c.* 200 mm long animal); for *Hadranax* the values are 8·1 mm for MGUH 24.527 and 8·3 mm for MGUH 24.528. Extrapolating these sizes to give about 20 limb pairs would give a total length of *c.* 150–160 mm, to which should be added the length of the frontal appendages.
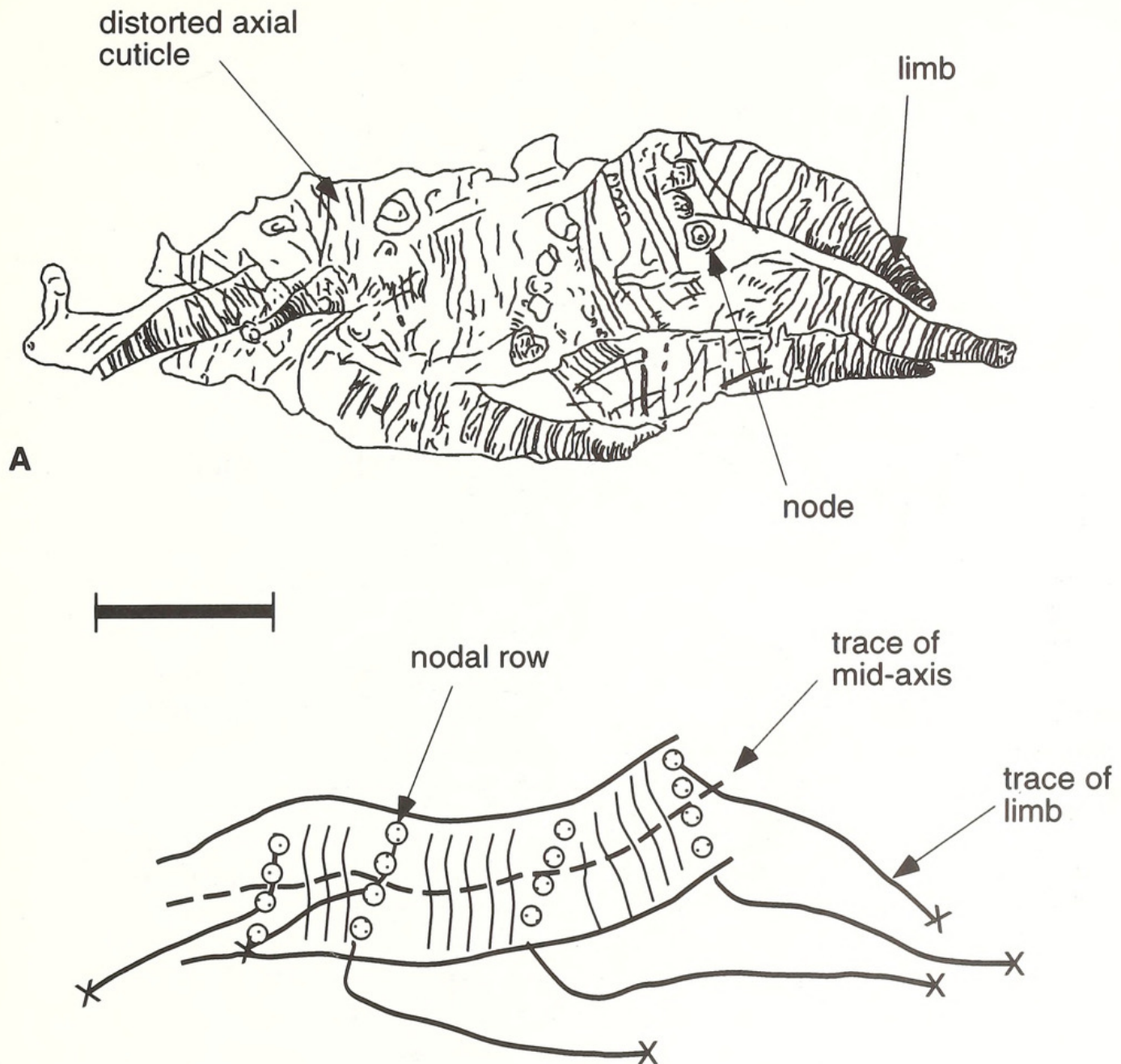
TEXT-FIG. 3. *Hadranax augustus* gen. et sp. nov. A, explanatory drawing of MGUH 24.528. B, schematic interpretation of MGUH 24.528 showing interpreted positions of nodal rows, limbs and their attachment sites. Scale bar represents 10 mm

2. Relatively wide, well-defined trunk annulations.
3. Similar limb morphologies with well-defined annulations and a lack of claws (but in both cases this may be a preservational artefact).
4. Large nodes that lack the plates of taxa such as *Microdictyon* and *Onychodictyon*.
   Relative to *Xenusion*, *Hadranax* also possesses the following autapomorphic characters.

1. Annular nodes (see Ramsköld 1992 for definitions of terminology used herein).
2. Four rather than two nodes in each row, which do not appear to possess spines (although this lack may be a preservational artefact). The appearance of the nodes in the known Cambrian

lobopod genera is rather variable: *Paucipoda* possesses none (Chen *et al.* 1995), *Hadranax* and *Kerygmachela* possess rows of four, *Luolishania* rows of three, *Cardiodictyon*, *Hallucigenia* and *Onychodictyon* pairs and *Ayshaeia* a more irregular array of them.

3. Limbs that do not appear to bear fleshy protuberances, although they do appear to bear paired rows of tubercles.

4. The inferred presence of a pair of long, branched, probably frontal appendages. *Xenusion* is not known to possess such appendages. However, as only two specimens are known (Jaeger and Martinsson 1967 discussed a third specimen, now lost, but it is nowhere figured), and in neither is the preservation good enough to rule out such structures, this judgement is only provisional. The long 'proboscis'-like structure in the reconstruction of *Xenusion* by Dzik and Krumbiegel (1989) may not be accurate (L. Ramsköld, pers. comm.).

Although Pompeckj (1927) considered *Xenusion* to be an onychophoran, Heymons (1928) questioned the orientation of the specimen, and Tarlo (1967), basing his argument on the large size of the fossil and its superficial resemblance to the Vendian form *Rangea*, suggested a pennatulacean affinity, with the organism being interpreted as an upright, frond-like structure. Since then, more recently discovered material (Dzik and Krumbiegel 1989; Dzik 1991), together with the revolution that has occurred in our understanding of Cambrian lobopods (e.g. Ramsköld and Hou 1991; Hou and Bergström 1995) has really settled the question of affinities, although the poor preservation of the *Xenusion* specimens has hampered understanding of how precisely *Xenusion* relates to other lobopods. The xenusiid described here helps clarify the position somewhat, as it possesses a few more characters that other lobopods also possess, notably 'annular nodes' (widespread); four tubercles instead of two (possessed by *Kerygmachela*), and apparently a pair of branched, frontal appendages. In broad terms, this last seems to be most similar to the frontal appendage seen in *Aysheaia*, and also as argued by Budd (1993) to that of *Kerygmachela*, although in detail it is rather different from either of these examples. New discoveries of lobopods will undoubtedly alter our understanding of their systematics, but at present, the possibility that the xenusiids as defined herein will turn out to be paraphyletic (by being a grouping from within which the *Anomalocaris*-like taxa evolved) cannot be discounted.

Despite its pronounced similarity to *Xenusion*, at present the differing characters of *Hadranax*, in the important features of the nodal rows, annular nodes and probable frontal appendages, justify its placement in a new genus. However, this judgment may need amendment in the light of any new discoveries of xenusiid lobopods.


## LOBOPOD DIVERSITY AND ECOLOGY IN THE CAMBRIAN

There are nine described genera of Cambrian taxa which would be broadly classified as 'lobopods' (*Aysheaia*, *Xenusion*, *Hadranax*, *Cardiodictyon*, *Microdictyon*, *Hallucigenia*, *Onychodictyon*, *Paucipodia*, *Luolishania*) and which more-or-less resemble the extant onychophorans (Bergström and Hou 1995; see also Chen *et al.* 1995a, 1995b). In addition to these, there have also been reports of a Cambrian tardigrade (Müller *et al.* 1995); a pentastomid (Walossek and Müller 1994) and a ?pentastomid-like worm, *Facivermis* (Hou and Chen 1989), all of which might be regarded as 'lobopods'. *Kerygmachela* and *Opabinia* should also both be considered to be at the lobopod grade of organization, as should some of the *Anomalocaris*-like taxa (Budd 1993, 1996, 1997).

---

EXPLANATION OF PLATE 2

Figs 1–2. *Hadranax augustus* gen. et sp. nov.; MGUH 24.527 (holotype). 1, details of ?frontal appendage, showing main branch and the tiny branch just proximal to it (arrowed); × 3·1. 2, details of trunk and limbs; note tubercles on limb at bottom left; × 4·5. Lighting in both from north-east. Lt = lateral extension of trunk.

PLATE 2
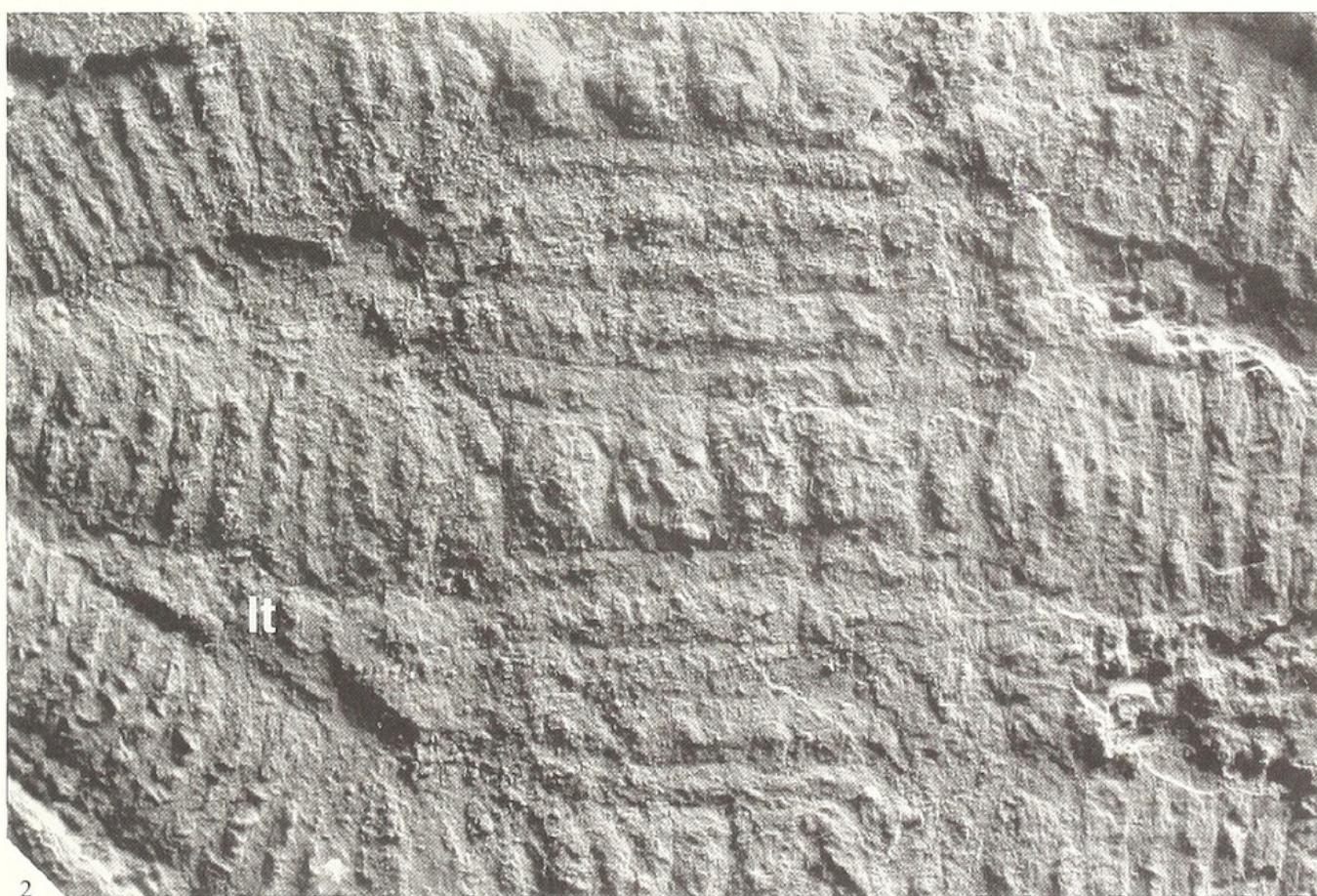
These forms exhibit a much wider morphological diversity than the extant onychophorans, notably in the details of the presence and form of ?defensive spines and frontal appendages. Most, if not all, of these forms, including *Hadranax*, were presumably benthic predators or scavengers, although the suggestion has been made that *Aysheaia* was parasitic on sponges (Whittington 1978), and that *Microdictyon* was a pseudo-pelagic commensal on the holothurian-like *Eldonia* (Chen *et al.* 1995*b*). The Cambrian lobopods may thus have fulfilled an important rôle in Cambrian benthic ecologies, perhaps similar to that occupied by the vagrant polychaetes today (see also Budd in press), although jawless polychaetes seem also to have been fairly diverse by the Mid Cambrian (e.g. Conway Morris 1979).

Almost all of these taxa are known only from exceptionally preserved faunas. It is probably fair to conclude that this broad grouping was widespread, diverse and important in the Cambrian. As was the case with the Cambrian 'arachnomorph' taxa (Briggs and Fortey 1989; Wills *et al.* 1994), this group became severely restricted, perhaps at the Mid-Late Cambrian boundary, and only a few vestiges survived into the rest of the Palaeozoic and beyond. No novel forms of lobopods (*qua* lobopods) seem to have arisen after the Mid Cambrian apart from the extant Tardigrada (first record, Upper Cambrian (Müller *et al.* 1995)) and the Onychophora (first record is probably the Carboniferous *Helenodora* (Thompson and Jones 1980), which most closely resembles *Aysheaia* of the Cambrian taxa). However, it would be a mistake to conclude from this fact alone that the 'lobopods' reached their acme in the Cambrian, as the group is likely to be paraphyletic (Budd 1993, 1997): both the uniramous and biramous arthropods are descended from them. Nevertheless, as a grade of organization, they were probably never as important as in the Early and Mid Cambrian.

There is a necessity, if at least some group of lobopods gave rise to the arthropods, of them having arisen before the arthropods. Unfortunately, at present, the details of Lower Cambrian stratigraphy do not allow any sort of accuracy in determining faunal successions of this nature. The oldest 'Burgess Shale'-like fauna is known from Polish borehole material (Dzik and Lendzion 1988), which may be placed as time-equivalent to the top of the Mazowsze Formation, probably corresponding to the top of the *Platysolenites* zone of Scandinavia and thus predating the earliest trilobites (Moczydłowska 1991; Palacios and Vidal 1995). The Polish material contains a probable relative of *Anomalocaris*, *Cassubia*, and a *Naraoia*-like form, *Liwia*. These taxa probably lie within the stem-group or near the base of the euarthropods respectively (Budd 1996), so at least some lobopods should therefore predate this time period. However, with the possible exception of the enigmatic form *Bomakellia* (Fedonkin 1994, fig. 5c; see also Waggoner 1996), this record is missing, and at present the origins of the lobopods themselves remain obscure; they are unlikely to be derived from annelids, as previously supposed (Eernisse *et al.* 1992, *contra* e.g. Snodgrass 1938). The suggestion of Dzik and Krumbiegel (1989) and Dzik (1991) that *Xenusion* should be considered to be a basal articulate, with its four-fold symmetry suggesting a derivation from the nemathelminth worms, seems also unlikely to be correct. The presence of a closely related form which does not have a four-fold limb and node arrangement probably implies that it is not some fundamental part of the construction of *Xenusion*; and the probable presence of a branched frontal appendage adds evidence that *Xenusion* need not be considered to be a basal form on the basis of its supposed extreme simplicity.

---

EXPLANATION OF PLATE 3

Figs 1–2. *Hadranax augustus* gen. et sp. nov. 1, MGUH 24.528; confused specimen, possibly exuviae; × 2·1. Lighting from south-east. Compare Text-figure 3. 2, MGUH 24.529; ?possible pair of limbs; tip of top limb arrowed; 'Is' indicates the wrinkled edge of an *Isoxys* specimen (see Williams *et al.* 1996); × 3·0. Lighting from west.
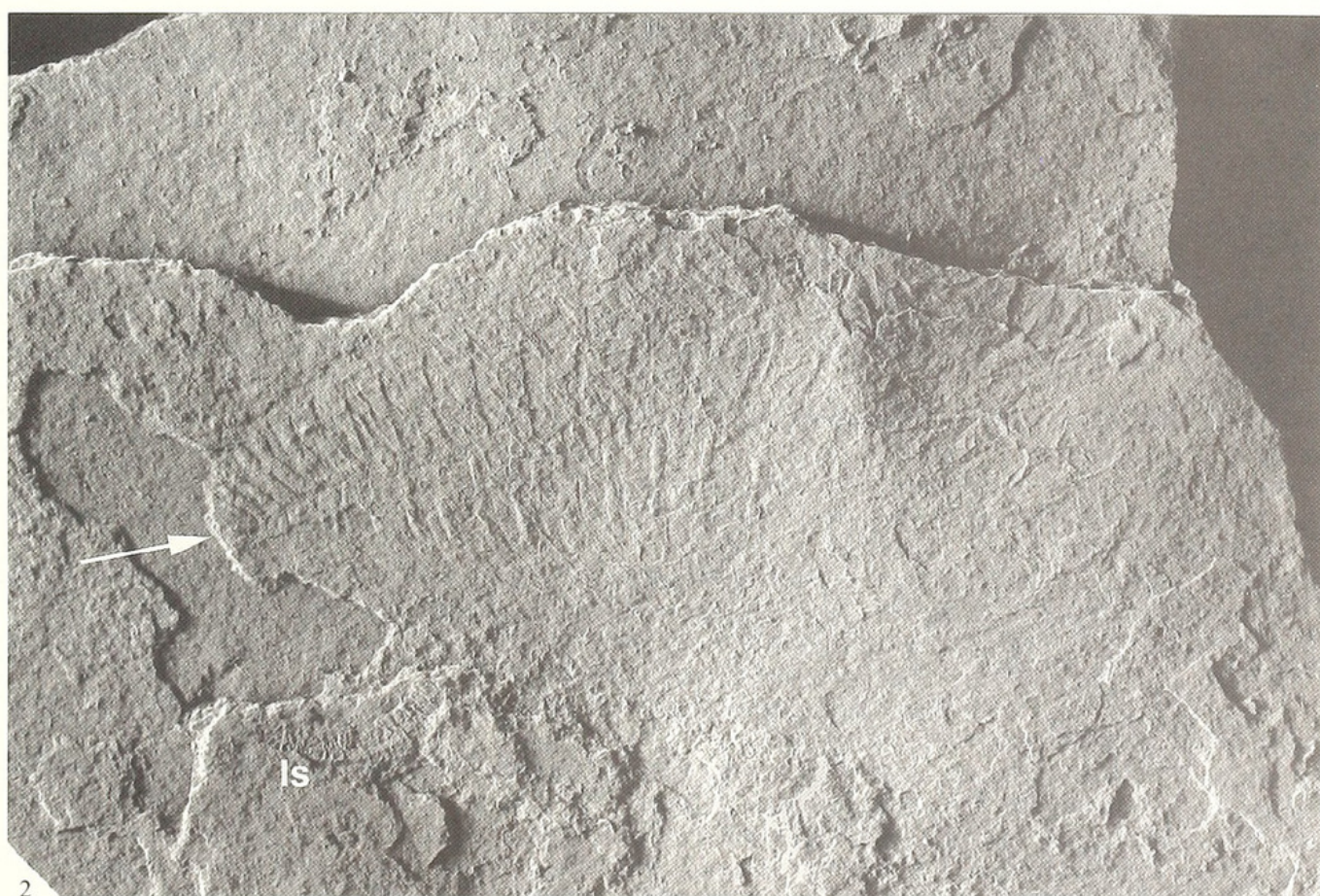
PLATE 3





BUDD and PEEL, *Hadranax*

## REFERENCES

BLAKER, M. R. 1988. A new genus of nevadiid trilobite from the Buen Formation (Early Cambrian) of Peary Land, central North Greenland. *Rapport Grønlands Geologiske Undersøgelse*, **137**, 33–41.

BRIGGS, D. E. G. and FORTEY, R. A. 1989. The early radiation and relationships of the major arthropod groups. *Science*, **246**, 241–243.

BUDD, G. 1993. A Cambrian gilled lobopod from Greenland. *Nature*, **364**, 709–711.

BUDD, G. E. 1995. *Kleptothule rasmusseni* gen. et sp. nov.: an ?olenellinid-like trilobite from the Sirius Passet fauna (Buen Formation, Lower Cambrian, North Greenland). *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **86**, 1–12.

—— 1996. The morphology of *Opabinia regalis* and the reconstruction of the arthropod stem-group. *Lethaia*, **29**, 1–14.

—— 1997. Stem-group arthropods from the Lower Cambrian Sirius Passet fauna of North Greenland. 125–138. *In* FORTEY, R. A. and THOMAS, R. H. (eds). *Arthropod relationships*. Chapman and Hall, London.

—— in press. Cambrian ecology of lobopods and non-trilobite arthropods. *In* ZHURAVLEV, A. YU. and RIDING, R. (eds). *Ecology of the Cambrian radiation*. Columbia University Press, New York.

CHEN JUNYUAN, ZHOU GUIQING and RAMSKÖLD, L. 1995*a*. A new Early Cambrian onychophoran-like animal, *Paucipodia* gen. nov., from the Chengjiang fauna, China. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **85**, 275–282.

—— —— —— 1995*b*. The Cambrian lobopodian *Microdictyon sinicum*. *Bulletin of the National Museum of Natural Science (Taichung, Taiwan)*, **5**, 1–93.

CONWAY MORRIS, S. 1977. A new Metazoan from the Burgess Shale of British Columbia. *Palaeontology*, **20**, 623–640.

—— 1979. Middle Cambrian polychaetes from the Burgess Shale of British Columbia. *Philosophical Transactions of the Royal Society of London, Series B*, **385**, 227–274.

—— and PEEL, S. J. 1990. Articulated halkieriids from the Lower Cambrian of North Greenland. *Nature*, **345**, 802–804.

—— —— 1995. Articulated halkieriids from the Lower Cambrian of North Greenland and their role in early protostome evolution. *Philosophical Transactions of the Royal Society of London, Series B*, **347**, 305–358.

—— —— HIGGINS, A. K., SOPER, N. J. and DAVIS, N. C. 1987. A Burgess Shale-like fauna from the Lower Cambrian of North Greenland. *Nature*, **345**, 802–805.

DZIK, J. 1991. Is fossil evidence consistent with traditional views of the early metazoan phylogeny? 47–56. *In* SIMONETTA, A. M. and CONWAY MORRIS, S. (eds). *The early evolution of Metazoa and the significance of problematic taxa*. Cambridge University Press, Cambridge, ix + 296 pp.

—— and KRUMBIEGEL, G. 1989. The oldest 'onychophoran' *Xenusion*: a link connecting phyla? *Lethaia*, **22**, 169–181.

—— and LENDZION, K. 1988. The oldest arthropods of the East European Platform. *Lethaia*, **21**, 29–38.

EERNISSE, D. J., ALBERT, J. S. and ANDERSON, F. E. 1992. Annelida and Arthropoda are not sister taxa: a phylogenetic analysis of spiralian metazoan morphology. *Systematic Biology*, **41**, 305–330.

FEDONKIN, M. A. 1994. Vendian body fossils and trace fossils. 370–388. *In* BENGTSON, S. (ed.). *Early life on Earth*. Columbia University Press, New York, x + 630 pp.

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.

HOU XIANGUANG and BERGSTRÖM, J. 1995. Cambrian lobopodians – ancestors of extant onychophorans? *Zoological Journal of the Linnean Society of London*, **114**, 3–19.

—— and CHEN JUNYUAN 1989. Early Cambrian tentacled worm-like animal from Chengjiang, Eastern Yunnan. *Acta Palaeontologica Sinica*, **28**, 32–41.

JAEGER, H. and MARTINSSON, A. 1967. Remarks on the problematic fossil *Xenusion auerswaldae*. *Geologiska Föreningens i Stockholm Förhandlingar*, **88**, 435–452.

KIELAN, Z. 1960. On two olenellid trilobites from Vestspitsbergen. *Studia Geologica Polonica*, **4**, 83–92.

LANE, P. D. and RUSHTON, A. W. A. 1992. A problematical trilobite from the Lower Cambrian of Freuchen Land, central North Greenland. *Rapport Grønlands Geologiske Undersøgelse*, **154**, 5–12.

MOCZYDŁOWSKA, M. 1991. Acritarch biostratigraphy of the Lower Cambrian and the Precambrian-Cambrian boundary in south-eastern Poland. *Fossils and Strata*, **29**, 1–127.

MÜLLER, K. J., WALLOSSEK, D. and ZAKHAROV, A. 1995. 'Orsten' type phosphatized soft-integument preservation and a new record from the Middle Cambrian Kuonamka Formation in Siberia. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **197**, 107–118.

PALACIOS, T. and VIDAL, G. 1992. Lower Cambrian acritarchs from northern Spain: the Precambrian-Cambrian boundary and biostratigraphic implications. *Geological Magazine*, **129**, 421–436.

PALMER, A. R. and REPINA, L. N. 1993. Through a glass darkly: taxonomy, phylogeny, and biostratigraphy of the Olenellina. *University of Kansas Paleontological Contributions* (*New Series*), **3**, 1–35.

PEEL, J. S. and SØNDERHOLM, M. (eds). 1991. Sedimentary basins of North Greenland. *Bulletin Grønlands Geologiske Undersøgelse*, **160**, 1–164.

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

POULSEN, V. 1974. Olenellacean trilobites from eastern North Greenland. *Bulletin of the Geological Society of Denmark*, **23**, 79–101.

RAMSKÖLD, L. 1992. Homologies in Cambrian Onychophora. *Lethaia*, **25**, 443–460.

—— and HOU XIANGHUANG 1991. New Early Cambrian animal and onychophoran affinities of enigmatic metazoans. *Nature*, **351**, 225–228.

RIGBY, J. K. 1986. Cambrian and Silurian sponges from North Greenland. *Rapport Grønlands Geologiske Undersøgelse*, **132**, 51–63.

SHU DEGAN, GEYER, G., CHEN LING and ZHANG XINGLIANG 1995. Redlichiacean trilobites with preserved soft-parts from the Lower Cambrian Chengjiang fauna (South China). *Beringeria*, Special Issue 2, 203–241.

SNODGRASS, R. E. 1938. Evolution of the Annelida, Onychophora and Arthropoda. *Smithsonian Miscellaneous Collections*, **97**, 1–159.

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

THOMPSON, I. and JONES, D. S. 1980. A possible onychophoran from the Middle Pennsylvanian Mazon Creek Beds of northern Illinois. *Journal of Paleontology*, **54**, 588–596.

VIDAL, G., MOCZYDŁOWSKA, M. and RUDAVSKAYA, V. R. 1995. Constraints on the early Cambrian radiation and correlation of the Tommotian and Nemakit-Daldynian regional stages of eastern Siberia. *Journal of the Geological Society, London*, **152**, 499–510.

—— and PEEL, J. S. 1993. Acritarchs from the Lower Cambrian Buen Formation in north Greenland. *Bulletin Grønlands Geologiske Undersøgelse*, **164**, 1–35.

WAGGONER, B. M. 1996. Phylogenetic hypotheses of the relationships of arthropods to Precambrian and Cambrian problemation fossil taxa. *Systematic Biology*, **45**, 190–222.

WALOSSEK, D. and MULLER, K. J. 1994. Pentastomid parasites from the Lower Palaeozoic of Sweden. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **85**, 1–37.

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

WILLIAMS, M., SIVETER, D. J. and PEEL, J. S. 1996. *Isoxys* (Arthropoda) from the Early Cambrian Sirius Passet Lagerstätte, North Greenland. *Journal of Paleontology*, **70**, 947–954.

WILLS, M., BRIGGS, D. E. G. and FORTEY, R. A. 1994. Disparity as an evolutionary index: a comparison of Cambrian and Recent arthropods. *Paleobiology*, **20**, 93–130.

ZANG, W. L. 1992. Sinian and Early Cambrian floras and biostratigraphy of the South China Platform. *Palaeontographica*, **224**, 75–119.

GRAHAM E. BUDD

JOHN S. PEEL

Institute for Earth Sciences
Department of Historical
Geology and Palaeontology
Norbyvägen 22
Uppsala S-75236
Sweden