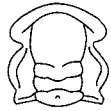


Opisthosomal fusion and phylogeny of Palaeozoic Xiphosura

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Fusion of opisthosomal tergites to form a thoracetrone has previously been considered a characteristic of the xiphosuran superfamilies Euproopioidea Eller, 1938, and Limuloidea Zittel, 1885. Evidence is presented here that fusion also occurs in Bellinuroidea Zittel & Eastman, 1913. Results of a cladistic analysis of Palaeozoic xiphosuran genera indicate that Synziphosurina Packard, 1886, is a paraphyletic assemblage of stem-group Xiphosura. Superfamily Paleolimulidae superfam. nov. is erected for families Paleolimulidae Raymond, 1944, and Moravuridae Přibyl, 1967. □ *Chelicerata, cladistics, evolution.*

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Horseshoe crabs (Xiphosura) have been held up as the prime example of a ‘living fossil’ group – one that has remained conservative in morphology and at low diversity for much of its geological history (Fisher 1984). The distinctive features of a large carapace concealing the prosomal appendages, fused opisthosomal tergites (a thoracetrone), and a styliiform tail spine, can be traced back to Carboniferous times, when the group was apparently much more diverse than today. Three distinct groups of Carboniferous Xiphosura are generally recognized, the superfamilies Bellinuroidea Zittel & Eastman, 1913, Euproopioidea Eller, 1938, and Limuloidea Zittel, 1885. The latter two groups share the possession of a thoracetrone, whilst bellinuroids have hitherto been distinguished by their free opisthosomal tergites. During a restudy of upper Palaeozoic Xiphosura by one of us (LIA), it was discovered that all specimens that could be referred to *Bellinurus* Pictet, 1846 (Fig. 2J), and also *Bellinuroopsis* Chernyshev, 1933 (Fig. 2M), have all post-opercular tergites fused into a thoracetrone (Anderson 1995). This observation has important consequences for xiphosuran taxonomy and phylogeny. We present here the evidence for fusion in the opisthosoma of bellinuroids, followed by a phylogenetic analysis of late Palaeozoic Xiphosura to generic level. The character matrix relies to a large extent on new information resulting from restudy of large numbers of late Palaeozoic xiphosurans, including all available holotypes. Further details are given by Anderson (1996), and taxonomic revisions will be published elsewhere. A major conclusion of this study is that Synziphosurina Packard, 1886, is a paraphyletic assemblage and the name

must be abandoned; xiphosurans with a thoracetrone (and other synapomorphies) are united herein in the order Xiphosurida Latreille, 1802.

Material and methods

Terminology follows Selden & Siveter (1987) and Siveter & Selden (1987). Fig. 2 shows reconstructions of a selection of xiphosuran taxa discussed in the text; see Selden & Siveter (1987, Fig. 1) for drawings of other taxa. In Chelicerata, the first somite (I) bears chelicerae, and somites II–VI bear fully expressed limbs. Somite VII bears the chilidia in *Limulus*, in which animal the tergite is completely lost. Somite VIII is termed the opercular segment in Xiphosura, and its tergite the opercular tergite. We restrict the term *free lobe* to the lateral parts of the opercular segment when they have become distinctly set off from the axial part of the opercular segment. Some authors recognize a pre-chelicerale somite, the acron; if present then this somite could be numbered 0. While Synziphosurina is shown here to be a paraphyletic group, it is convenient to use the term ‘synziphosurine’ in an informal sense to refer to stem-group Xiphosura that lack a thoracetrone (i.e. all Xiphosura except Xiphosurida).

Institutional abbreviations are as follows: BMNH, The Natural History Museum, London, UK; GSM, British Geological Survey, Geological Survey Museum, Keyworth, UK; MM, Manchester Museum, Manchester, UK; NMW, National Museum of Wales, Cardiff, UK; RSM, Royal Museum of Scotland, Edinburgh, UK; USNM, US

National Museum, Smithsonian Institution, Washington, DC.

Cladistic analyses were carried out using MacClade 3.0 software (Maddison & Maddison 1992) on Apple Macintosh computers. MacClade was used to input data, and draw and manipulate trees on-screen, rather than providing solutions; this is because (a) the data are sparse (see 'Discussion', below) and (b) the program is primarily designed for this type of analysis.

Opisthosomal fusion in *Bellinurus*

In his original description of *Bellinurus*, Pictet (1846) described the posterior three opisthosomal segments as fused, and the remainder of the opisthosoma unfused. Xiphosurans were then considered to be crustaceans closely related to the trilobites, so it is likely that trilobite tagmosis coloured Pictet's perception of these animals. The superfamily Bellinuroidea was erected by Zittel & Eastman (1913), characterized by a variable number of fused posterior segments in addition to free tergites in the opisthosoma. Størmer (1955) considered fusion of all opisthosomal tergites into a thoracetrone to be characteristic of Euprooidea Eller, 1938, and Limuloidea Zittel, 1885.

Dix & Pringle (1930) described a number of new species of *Bellinurus* from the South Wales coalfield. They concurred with the generally accepted view of the unfused state of most of the opisthosoma in *Bellinurus*, but introduced complication by erecting new taxa characterized by from 4 free tergites (*B. truemani*) to 7 (*B. morgani*). This material (*B. truemani* NMW 29.197GI; *B. morgani* GSM 49362) was re-examined by LIA, and it was found that Dix & Pringle had miscounted tergites (see Anderson 1996 for details). Schultka (1994) compared a Namurian specimen from Germany with the descriptions of Dix & Pringle (1929) and assigned it to *B. cf. truemani*, believing only the two most posterior tergites to be fused.

Eldredge (1974) divided Limulicina Richter & Richter, 1929, into two superfamilies, Bellinuracea and Limulacea, on the basis of the state of fusion of the opisthosoma. Inclusion of the family Euproopidae in the Limulacea reflected his opinion that the lineage could be traced from *Euproops* (Fig. 2K) through to *Limulus*. Fisher (1981) subsequently showed this to be unlikely. In addition, Eldredge (1974) erected the infraorder Pseudoniscina for *Pseudoniscus* (Fig. 2G) and some, unnamed early bellinurines.

Bergström (1975) described a weakly defined fulcral node on the anterior side of each tergite of *Bellinurus koenigianus* Woodward, 1872, which he believed fitted into the next anterior tergite, in an analogous manner to trilobites. This was probably a misinterpretation of the spine-bearing axial nodes, which are seen clearly in *Euproops danae* (Meek & Worthen, 1865), a related

xiphosuran (Anderson 1994). Bergström (1975) described a microtergite (a term coined by Fisher *in litt.* to Bergström 1975) at the prosoma–opisthosoma boundary which appeared to be fused to the opercular segment (tergite 2). Examination of the holotype of *B. koenigianus* (BMNH In 59227) and additional material of *E. danae* by LIA confirms this observation.

Subsequent workers (e.g., Fisher 1982; Siveter & Selden 1987; Selden & Siveter 1987; Pickett 1993) followed earlier interpretations in considering only the posterior three opisthosomal tergites of *Bellinurus* to be fused, but did not study the type material. Pickett (1993) interpreted the unnamed bellinurines of Eldredge (1974) as being *Bellinurus carterae* Eller, 1940, *Bellinurus alleganyensis* Eller, 1938, and *Bellinuroopsis rossicus* Chernyshev, 1933, and placed them in Kasibelinuridae Pickett, 1993. Anderson (1995) first suggested the possibility of full opisthosomal fusion in *Bellinurus*. Our re-examination of the type material of the Upper Carboniferous Bellinuroidea clearly demonstrates that all true members of the Bellinuroidea exhibit full fusion of the opisthosoma into a thoracetrone.

Criteria for the recognition of fusion

If the opisthosomal tergites of *Bellinurus* were unfused then four criteria should be met:

- 1 On enrollment, the axial portions of the opisthosomal tergites should show some degree of flexure in the vertical plane, as seen in trilobites, synziphosurines which use sphaeroidal enrollment such as *Pseudoniscus*, *Legrandella* (see Eldredge 1974) and *Kasibelinurus* Pickett, 1993, and isopod crustaceans.
- 2 Fully or partially disarticulated free tergites should be found in the rock matrix, as seen in eurypterids, aglaspidids (Hesselbo 1992), chasmataspidids (Caster & Brooks 1956) and trilobites.
- 3 Dorso-ventral compression of the tergites should result in the asymmetrical disposition of the lateral spines in the fossils (see Hesselbo 1992).
- 4 Distinct anterior and posterior boundaries to the opisthosomal tergites should be visible in the fossils.

Observations

- 1 In *Bellinurus*, flexure of the body in enrolled specimens always occurs at the prosoma–opisthosoma junction. This can be seen clearly in specimens of enrolled *Bellinurus trilobitoides* (Fig. 1). Flexure involves the microtergite and the posterior margin of the prosoma, resulting in occlusion of the prosoma onto the opisthosoma (Fisher 1979) in a similar manner to that in *Euproops*, which has a thoracetrone. Bergström (1975, p. 294) referred to Woodward's (1878, p. 242) mention of having seen an enrolled *Bellinurus arcua-*

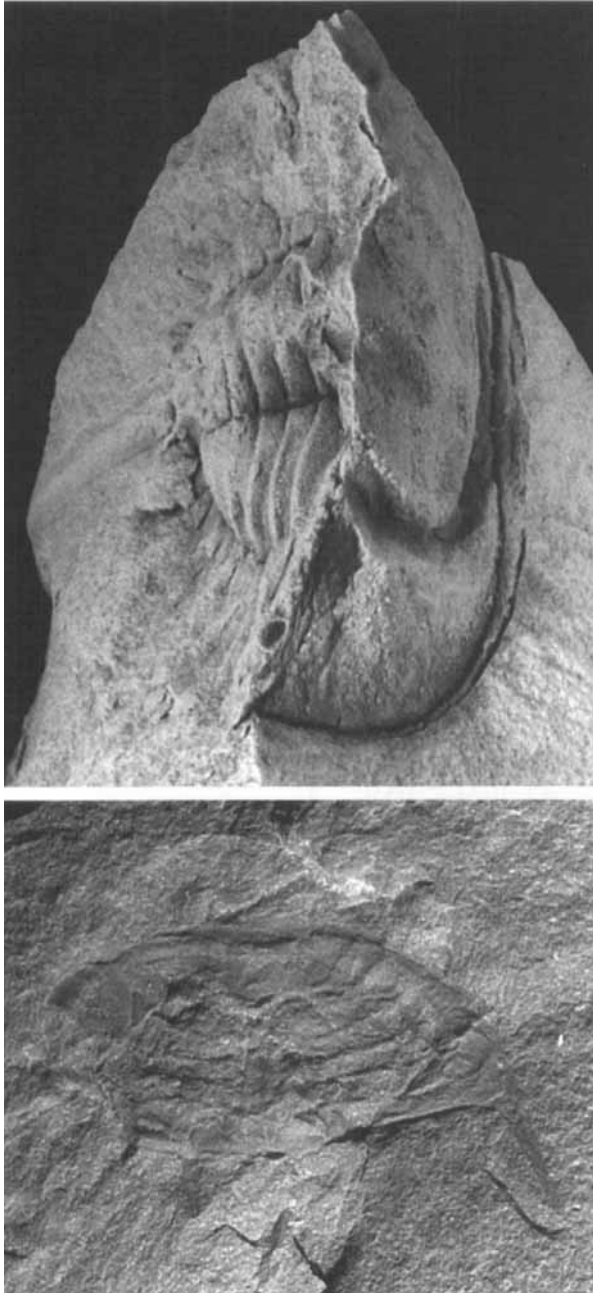


Fig. 1. Enrolled specimens of *Bellinurus trilobitoides* Buckland, 1837; Carboniferous (Westphalian A). □A. RSM GY 1911.6.2, Coseley, West Midlands, UK, $\times 2$. □B. MM LL11055, Bickershaw, Lancashire, UK, $\times 2$.

tus Bailly, 1863, but there is no illustration of the specimen, and it cannot be traced from the description. Bergström (1975, Fig. 1) figured one specimen of *Euproops anthrax* Prestwich, 1840 (BMNH I 2751), and two of *Pringlia birtwelli* Woodward, 1872, in a coaptated position. He termed this form of enrollment 'folding up', and discussed the necessity for a microtergite for this form of coaptation. Probably, Wood-

ward (1878, p. 242) saw a folded-up specimen, especially since he described it thus: 'the body was found to be doubled back upon the head, like an *Ampyx* or *Trinucleus*.'

- 2 Examination of more than one thousand Upper Carboniferous bellinurine specimens in museum collections revealed no free post-opercular opisthosomal tergites. Where opisthosomata show damage, breakage is across transverse ridge boundaries, not along them. This is the case in both *Euproops* and *Bellinurus*. If the opisthosomal tergites of *Bellinurus* were free, then it would be reasonable to expect that breakage would result in disarticulation of tergites, which are separated by lines of weakness. Disarticulated prosomata and opisthosomata have been identified, and these seem to be more common in recently collected material than in museum collections, possibly as a result of collection bias.
- 3 In most specimens, the lateral opisthosomal spines retain their symmetrical relationships and act as a single unit with the (fused) tergites during compression. On the few specimens to show asymmetrical disposition of lateral opisthosomal spines, it has resulted not from compression of free tergites but from extreme compaction and tectonic deformation in coal-seam roof-shale preservation. One example of this is the holotype of *Bellinurus carwayensis* Dix & Pringle, 1930 (NMW 29197.G3). Displacement of the genal spines by compressional deformation is more common. Compression tends to increase the angle between the genal spine and the posterior margin of the prosoma, particularly in specimens where the carapace has disarticulated slightly from the opisthosoma and has been compressed oblique to the bedding plane. Some authors (e.g., Dix & Pringle 1930; Schultka 1994) used the magnitude of this angle as a species diagnostic, but it has been shown to be susceptible to taphonomic effects (Anderson 1994).
- 4 The first two transverse ridges of the opisthosoma in *Bellinurus* (equivalent to the posterior edges of the first two opisthosomal tergites) bifurcate laterally and form the margins of the corresponding lateral spines, each bifurcation being surmounted by a small node.

Timing of opisthosomal fusion

Williams (1885) described a xiphosuran from the Upper Devonian of Erie County, Pennsylvania, which he thought had fused opisthosomal tergites. Because *Bellinurus* was diagnosed at that time as having free tergites, he assigned the new species to the genus *Prestwichia*, naming it *Prestwichia eriensis*. Packard (1886) renamed this specimen *Protolimulus eriensis* because *Prestwichia* had been

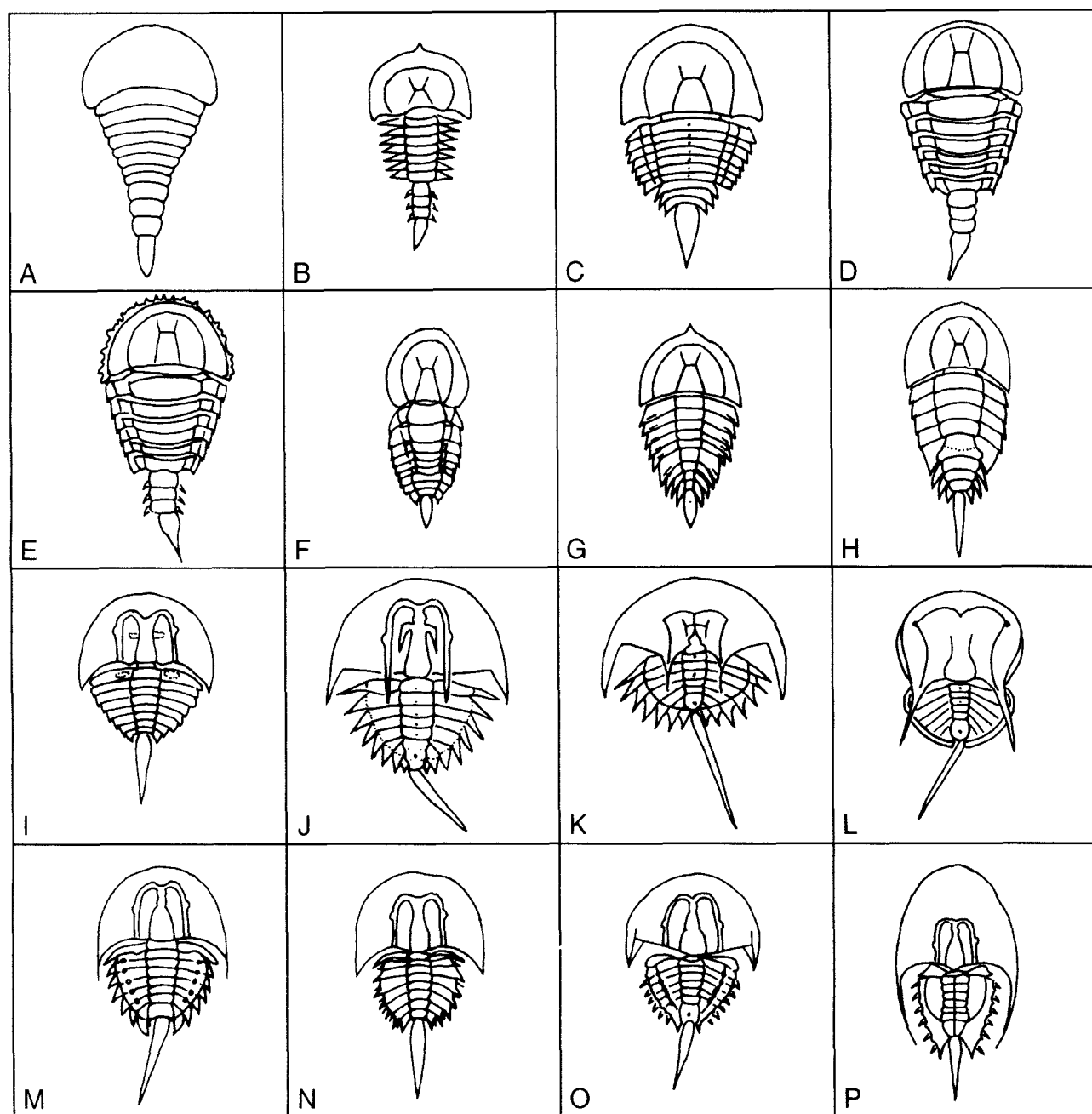


Fig. 2. Diagrammatic reconstructions of xiphosuran taxa mentioned in the text. All views are dorsal; magnifications are approximate. □A. *Lemoneites*; Ordovician; $\times 3.2$. □B. *Legrandella*; Devonian; $\times 0.255$. □C. *Weinbergina*; Devonian; $\times 0.32$. □D. *Bunodes*; Silurian; $\times 0.85$. □E. *Limuloides*; Silurian; $\times 0.85$. □F. *Pasternakevia*; Silurian; $\times 0.85$. □G. *Pseudoniscus*; Silurian; $\times 0.85$. □H. *Cyamocephalus*; Silurian; $\times 0.85$. □I. *Kasibelinurus*; Devonian; $\times 0.255$. □J. *Bellinurus*; Carboniferous; $\times 0.85$. □K. *Euproops*; Carboniferous; $\times 0.64$. □L. *Liomesaspis*; Carboniferous; $\times 0.85$. □M. *Bellinuroopsis*; Carboniferous; $\times 0.6$. □N. *Rolfeia*; Carboniferous; $\times 0.425$. □O. *Paleolimulus*; Carboniferous; $\times 0.255$. □P. *Valloisella*; Carboniferous; $\times 17$.

previously synonymised with *Euproops* (see Anderson 1994 for details of the synonymy). However, re-examination of the specimen described originally by Williams (1885) has shown that it is not a body fossil but a trace fossil (Babcock *et al.* 1995). Caster (1930) figured an additional specimen of *Protolimulus eriensis* from Hanley quarry, Pennsylvania.

Eller (1940) described a new species, *Bellinurus carterae* (see Pickett 1993 for explanation of this spelling of the trivial name), from the same quarry as the fragment of *Protolimulus* described by Caster (1930). Eller suggested that *Bellinurus carterae* might be synonymous with *Protolimulus*.

Pickett (1993) described *Kasibelinurus* (Fig. 2L) from the Upper Devonian of New South Wales, Australia. He noted that articulating half-rings, a character used by Eldredge (1974) to define his new infraorder Pseudoniscina, were absent in this form, but pointed to the presence of articulating facets on the lateral margins of the opisthosomal tergites as an indication of the unfused nature of the opisthosoma. Examination of an enrolled specimen of *Kasibelinurus* (USNM 484524), collected by Mr Scott McKenzie (Erie County, PA), confirms Pickett's observation.

Examination of a photograph of the Upper Devonian *Bellinuroopsis rossicus* Chernyshev, 1933, kindly lent to the authors by Dr John Pickett (Sydney), clearly shows that this form also has a fused opisthosoma, as evidenced by the equal disposition of the lateral fixed spines and the raised opisthosomal platform. Also, the presence of nodes two-thirds of the way along the transverse ridges is a character which may link it to the Moravuridae Příbyl, 1967 (Siveter & Selden 1987) and Paleolimulidae Raymond, 1944. *Bellinuroopsis* clearly does not belong in Kasibelinuridae Pickett, 1993. The fusion event must therefore have occurred prior to the late Devonian. The paucity of Devonian xiphosurid body fossils precludes further stratigraphic constraint at present.

Functional morphology

The advantages of opisthosomal fusion are not entirely clear. In favour of fusion are: reduced musculature, fewer areas of soft cuticle which would be susceptible to predation, and possibly better occlusion than in sphaeroidal enrollment. Fisher (1981) pointed out that fusion of the posterior tergites to produce an O_7 – O_9 tagma would give a larger area for the insertion of muscles to operate the tail spine. The tail spine is vital to the survival of *Limulus*, because it is used to fend off predators and to right the overturned animal. It would be expected that increased fusion would be correlated with a stronger and longer tail spine with greater musculature. Lack of flexibility of the thoracetron would make righting the overturned animal more difficult and may also correlate with a new form of enrollment.

Phylogenetic analysis

Taxa used in the analysis

This analysis is primarily concerned with the interrelationships of late Palaeozoic Xiphosura. All post-Palaeozoic taxa, which all belong to superfamily Limuloidea and were reviewed by Hauschke & Wilde (1991), are excluded

from the analysis. The exception is the Recent *Limulus*, which is included to represent the Limuloidea.

Valloisella Racheboeuf, 1992 (Fig. 2P), originally assigned to Euproopidae but moved to Paleolimulidae by Anderson & Horrocks (1995) because it shows the diagnostic characters of the family, has a carinate axial ridge on the opisthosoma, a character shared with all post-Palaeozoic xiphosurans.

Elleria (Raymond, 1944) and *Moravurus* Příbyl, 1967, are known only from single isolated thoracetrons and so are excluded from the analysis. Re-examination of *Elleria* by LIA (in preparation) revealed characters that support its assignment to Kasibelinuridae.

Raymond (1944) described two very similar xiphosurid genera from the Upper Carboniferous of Mazon Creek, Illinois: *Liomesaspis* and *Pringlia*. Restudy of these forms (Anderson, in press) has indicated that the two genera are synonymous, and *Pringlia* is a junior synonym of *Liomesaspis* (Fig. 2L). *Palatinaspis beimbaueri* Malz & Poschmann, 1993, from the Lower Permian of Germany, was affiliated to *Pringlia fritschii* Remy & Remy, 1959, from the German Stephanian. Study of the illustrations in Malz & Poschmann (1993) suggest to us that *Palatinaspis* is synonymous with *Liomesaspis*, and it is included in the latter genus here. Specimens of *Anacontium* Raymond, 1944, are too poorly preserved to be useful in the analysis; this genus may be synonymous with *Euproops* or *Liomesaspis*.

Bergström (1975) suggested that *Neolimulus* may be a junior synonym of *Pseudoniscus*, a suggestion which our study has supported. The defining character of the only specimen of *Neolimulus*, ophthalmic ridges meeting at the anterior margin of the carapace, results from the carapace being compressed while loosely articulated with the opisthosoma.

The unnamed synziphosurine from the early Silurian (late Llandovery) of Waukesha, Wisconsin, figured by Mikulic *et al.* (1985) was studied by LIA, and it appears to be a poorly preserved example of *Bunodes*.

A number of Cambrian and Ordovician so-called merostomoids with shovel-shaped carapaces (and few other features), together with *Chasmataspis*, aglaspids, and Størmer's (1972) strange arthropods *Diploaspis* and *Heteroaspis*, show essentially plesiomorphic characters with respect to the Xiphosura in the present study. They are excluded from the analysis for the following reasons. *Chasmataspid* Caster & Brooks (1956) was included in Xiphosura by most authors (see Selden & Siveter 1987), though Eldredge (1974) allied this group with the Eurypterida. *Chasmataspis* exhibits the following characters: thirteen opisthosomal tergites, anteriorly positioned eyes, lack of ophthalmic ridges, a carapace morphology similar to aglaspids, and a unique pattern of fusion of opisthosomal tergites. Bergström (1975) included *Diploaspis* Størmer, 1972, and *Heteroaspis* Størmer, 1972, with

Chasmataspida. He considered the paddle-shaped swimming leg of *Diploaspis* to have evolved independently from that of eurypterids. He mentioned the non-chelate nature of the walking appendages as a character that separates *Diploaspis* from all other xiphosurids and chasmataspids. He also considered that the anterior position of the eyes and the lack of other carapace features in *Heteroaspis* indicate no close xiphosuran affinities. Anteriorly positioned eyes are more common in eurypterids. Removal of *Heteroaspis* and *Diploaspis* from Chasmataspida would render it a monotypic group.

The earliest recorded xiphosuran is *Eolimulus* Moberg, 1892, from the Cambrian of Sweden, but it is known only from the carapace, so its identity is doubtful (Selden 1993). We include *Paleomerus* Størmer, 1955, and *Lemoneites* Flower, 1968 (Fig. 2A), as outgroups in the analysis. The morphology of *Paleomerus* is fairly well known from three specimens (Størmer 1956; Bergström 1971); this animal was referred to Aglaspidida Walcott, 1911, by Størmer (1955) and to Merostomoidea Størmer, 1944, by Bergström (1971). *Lemoneites* (Fig. 2A) is from the Ordovician of New Mexico. Flower (1968) placed it in Aglaspidida but remarked on the number of similarities with Synziphosurina. Eldredge (1974) placed *Lemoneites* as *Xiphosura incertae sedis*. Aglaspidids were removed from Chelicerata by Briggs *et al.* (1979) on the grounds that there were only four or five pairs of cephalic appendages, the first of which was not demonstrably chelate. They did not refer them to another higher taxon. Their removal from Chelicerata was criticised by Bergström (1981) who argued that the number of head segments (and hence head appendages) was variable in early chelicerates and other arthropods.

Characters and character states used in the analysis

The characters used in the analysis are discrete; some are multistate where it is clear that a homologous feature is involved. Some characters occur outside the Xiphosura, and therefore outside the scope of this study except where they occur in the two outgroups, *Lemoneites* and *Paleomerus*. All characters are treated as unordered in the cladistic analysis, though character state polarity is discussed below.

Character 1 (thoracetrone). – Fusion of opisthosomal tergites IX–XVII, posterior to the opercular tergite (VIII), produces a thoracetrone, an apomorphy of Xiphosurida. In *Bellinuroopsis*, the fused nature of the opisthosoma is evidenced by the presence of transverse ridge nodes (character 6) and the modified appearance of the opercular tergite (VIII) from the following tergites. The opercular tergite remains unfused in *Rolfeia* (Fig. 2N) and *Bellinuroopsis* (Fig. 2M) and separate from the thoracetrone.

Character 2 (metasoma). – Pseudotagmata may be recognized in the opisthosoma of some early Xiphosura. A metasoma may be formed from the three most posterior opisthosomal segments, the sternites and tergites of which are fused into cylindrical sclerites, clearly distinct from the anterior mesosoma. Where epimera are absent, this character is readily visible, but if epimera are present, as in *Pseudoniscus*, *Pasternakevia* and *Cyamocephalus* (Fig. 2F, G, H) for example, the distinction between mesosoma and metasoma is obscure. The converging axial furrows of the opisthosoma become parallel just anterior to the last three tergites in some of these forms, but the distinction between mesosoma and metasoma is not obvious, as it is in *Lemoneites*, for example. Since the underside of the animal cannot be seen, it is uncertain whether appendages or a fused sternite is present. This character is, to some extent, linked with character 5.

The metasoma, where present, always consists of three segments, but which somites are involved in its formation is not clear. In the most plesiomorphic forms with a metasoma, such as *Lemoneites*, *Legrandella* and *Weinbergina* (Fig. 2A, B, C), it is formed from the ninth to eleventh opisthosomal segments (presumed somites XV–XVII). In *Bunodes* and *Limuloides* (Fig. 2D, E) it is the eighth to tenth opisthosomal segments. These would represent somites XIV–XVI if a segment had been lost posterior to the metasoma but XV–XVII if a segment had been lost anterior to the metasoma. If the latter, then the metasomas of *Lemoneites*, *Legrandella* and *Weinbergina* would be homologous with those of *Bunodes* and *Limuloides*. This would also suggest that either the hypertrophied tergite VIII or the supposed double tergite XIII was indeed formed by fusion of two tergites (Eldredge 1974; Selden & Siveter 1987). *Cyamocephalus* clearly shows two fused tergites (XII and XIII) which could be a further advancement of this trend, but looking at Fig. 2A of Eldredge & Plotnick (1974), there is an alternative possibility. These authors suggested that the tail spine lying to one side of the specimen was broken, its base remaining with the rest of the body. It seems strange that the rigid tail spine should break at its thickest point, yet the rest of the exoskeleton remain fully articulated. If the spine base were actually the posteriormost tergite, then *Cyamocephalus* would represent a more primitive stage in which fusion of tergites was still clearly visible. We have coded the metasoma as absent (0) in *Paleomerus*, present (1) only where it is distinct, and lost (2) elsewhere, thus assuming homology.

Character 3 (tergite VII). – The first opisthosomal segment, expressing tergite VII, is reduced to a microtergite and lacks lateral tergal fields in the apomorphic condition (1). The plesiomorphic state (0) for this character is shown by *Lemoneites*, which has a fully expressed tergite with lateral fields. Eldredge (1974) reported that *Legran-*

della had reduced epimera associated with the microtergite. *Cyamocephalus* also has short epimera on this segment (Eldredge & Plotnick 1974). The microtergite is lost (2) in forms possessing a free lobe.

Character 4 (movable opisthosomal spines). – The presence of movable opisthosomal spines is an autapomorphy of suborder Limulina. Movable opisthosomal spines are absent in all other genera, including *Bellinuroopsis*. *Dubbolimulus* Pickett (1984) lacks movable spines, which is interpreted here as an autapomorphy for this genus, though it is possible that movable spines were present but lost by disarticulation during biostratigraphy. Interestingly, *Rolfeia* lacks both fixed and movable spines on the second opisthosomal tergite (IX) though they occur on all more posterior tergites, and our preliminary observations of *Paleolimulus longispinus* Schram, 1979, show that this animal has the same pattern of fixed and movable spines (*contra* Schram 1979, Fig. 2, but as hinted at by Waterston 1985). Possibly, *P. longispinus* is actually a *Rolfeia*, and the lack of spines on tergite IX is autapomorphic for the genus.

Character 5 (fixed lateral opisthosomal spines). – Opisthosomal tergites in the outgroups of Xiphosura (e.g., *Paleomerus*) show no or very short epimera (0). Synziphosurines show short and broad (sag.) or longer, curved epimera (1), depending on the width of the opisthosomal axis (character 20). True lateral spines (2) are reinforced by the continuation of the corresponding transverse ridge of the thoracetron. Fixed lateral spines on the opisthosoma occur in *Bellinuroopsis*, *Rolfeia*, *Bellinurus* and *Euproops*. Loss of lateral spines (3) may be derived relative to their presence; this occurs in *Liomesaspis* and some later limuloids.

Character 6 (transverse ridge nodes). – Swollen nodes on the transverse ridges of the opisthosoma occur in *Bellinuroopsis*, *Xaniopyramis* and *Paleolimulus*. Undescribed specimens of *Rolfeia* (BMNH In 34941 and I 889) show evidence of transverse nodes as well as longitudinal ridges (see character 7). Presence of nodes is coded as 1, absence as 0, though the absence of these nodes in limuloids probably reflects a secondary loss.

Character 7 (longitudinal opisthosomal ridges). – Longitudinal ridges which link the transverse ridge nodes (forming quadriradiate nodes) occur in *Paleolimulus*, *Xaniopyramis* and *Rolfeia*. They are also useful as indicators of full fusion of the opisthosomal tergites. Their presence in *Bellinuroopsis* is not confirmed from study of the single holotype specimen. Siveter & Selden (1987) reported that 'probable homologues of the longitudinal pleural ridges and associated nodes' were present in *Paleolimulus*; our re-examination of the holotype and new, additional material has shown the presence of well defined longitudinal ridges in this genus.

Character 8 (pyramidal cheek node). – Siveter & Selden (1987) cited the presence of a cheek node with an associated anteriorly running ridge in the Lower Carboniferous *Xaniopyramis* as a possible autapomorphy for the genus. Investigation of new specimens of *Paleolimulus* show that this character is also present in this form. The node appears to be absent in *Rolfeia*.

Character 9 (course of ophthalmic ridges). – Ophthalmic ridges are absent in *Paleomerus* and *Lemoneites* (0). In synziphosurines, the ophthalmic ridges bearing the compound eyes are bowed outwards laterally (convex, 1). In *Euproops* and *Liomesaspis* the ophthalmic ridges follow a concave course to the cardiac lobe (2); this state is presumed to be synapomorphic for these two taxa.

Character 10 (cardiac lobe). – A cardiac lobe is absent from *Paleomerus* (0) and cannot be confirmed in *Lemoneites*. In all other sufficiently well preserved xiphosurans in this analysis a cardiac lobe is present (1).

Character 11 (posterior axial lobe). – The posterior three segments (XIII–XV) of the thoracetron of xiphosurids commonly lose their intersegmental divisions to form a distinct triangular or trapezoidal area, here called the posterior axial lobe (Fisher's (1981) O₇–O₉ tagma). In *Bellinurus*, *Euproops* and *Liomesaspis* the axial region of this lobe is triangular and tapers posteriorly. The corresponding region in *Valloisella*, *Paleolimulus* and *Limulus* is broadly trapezoidal in shape.

Character 12 (ophthalmic spines). – Ophthalmic spines are posterior elongations of the ophthalmic ridges, and we consider their absence to be plesiomorphic, their presence a novelty. Ophthalmic spines occur in *Bellinurus*, *Euproops* and *Liomesaspis*, but they are not always observable (Anderson 1994), so they may yet be shown to occur in other xiphosurids. *Limulus* and *Paleolimulus* bear upwardly pointing thorns at the posterior ends of the ophthalmic ridges; we considered these not to be homologous with true ophthalmic spines.

Character 13 (posterior carapace margin). – The plesiomorphic state (0) for the carapace is a straight posterior margin. Derived states are gently (1) and strongly (2) curved. Character 13 may be linked with character 14.

Character 14. – The carapace genal angles may be rounded (0), pointed (1) or modified into genal spines (2). Genal spines have a dorsal ridge which distinguishes them from pointed genal angles. Character 14 may be linked with character 13.

Character 15 (macrotergites). – A hypertrophied second opisthosomal tergite (VIII) occurs in *Bunodes*, *Limuloides* and *Pasternakevia* (Eldredge 1974; Selden & Drygant 1987).

Character 16 (tergites XII–XIII). – *Cyamocephalus* Currie, 1927, has fused sixth and seventh opisthosomal tergites (Eldredge & Plotnick 1974). Störmer (1955), Eldredge (1974), Störmer & Bergström (1981), and Selden & Siveter (1987) discussed possible fusion of the last mesosomal tergite (XIII and XIV) in *Bunodes* and *Limuloides*, but in all of the material we studied, these tergites appear not to be fused.

Character 17 (metasomal epimera). – Epimera occur on the metasomal tergites of *Pseudoniscus*, *Weinbergina*, *Cyamocephalus*, *Pasternakevia*, *Bunodes* and *Limuloides* and *Kasibelinurus* (1). (Note that these animals do not necessarily show a clear distinction between mesosoma and metasoma.) Since metasomal epimera are lacking in *Paleomerus* and *Lemoneites* (0), their presence appears as apomorphic within the scope of this analysis.

Character 18 (carapace margin). – The cuticular projections that produce a characteristic serrate anterior and anterolateral margin of the carapace of *Limuloides* are autapomorphic for this taxon. The plesiomorphic state is a smooth carapace rim.

Character 19 (precardiac lobe). – In *Bunodes*, *Limuloides*, *Kasibelinurus* and *Pseudoniscus*, the cardiac lobe is divided by a transverse groove forming an H-shaped area. Pickett (1993), in describing *Kasibelinurus*, had access to relatively uncrushed material and named the anterior portion of this H-shaped area the precardiac lobe (1). In *Legrandella* the cardiac lobe is broadly triangular in form and tapers rapidly anteriorly; there is no evidence of a precardiac lobe in this form. The shape of the cardiac lobe was reported to be unknown in *Weinbergina*, however Störmer & Bergström (1981) reconstructed the cardiac lobe of *Weinbergina* as resembling that of *Legrandella*. The illustration of *Pasternakevia* (Selden & Drygant, 1987, Fig 3a) shows a faint H-shaped medial region on the carapace. Re-examination of the holotype (BMNH I 16251) and an additional specimen (BMNH I 25) of *Cyamocephalus* suggests that it, too, has a precardiac lobe. Xiphosurids possess a much smaller node, bearing ocelli, anterior to the apex of the cardiac lobe (2). *Paleomerus* lacks a cardiac, and hence a precardiac, lobe (0).

Character 20 (opisthosomal axis). – *Paleomerus* and *Lemoneites* have no discernible axial region, which is thus coded as 0 in this analysis. All other taxa show a vaulted median axis, but the ratio of the width of the axial to the lateral regions varies. *Bunodes*, *Limuloides* and *Pasternakevia* all have wide opisthosomal axes, with narrow lateral areas (1). *Pseudoniscus*, *Cyamocephalus*, *Kasibelinurus* and all xiphosurids have a narrow axis relative to the lateral areas (2). The axis of *Legrandella* is about half the total width of the opisthosoma, which is here coded as wide.

Character 21 (tail spine). – A short, basally wide, rapidly tapering, tail spine is considered the plesiomorphic con-

dition because it occurs in *Paleomerus* and all synziphosurines. In xiphosurids, the tail spine is longer and thinner and can be equal to, or slightly longer than, the combined length of the prosoma and opisthosoma.

Character 22 (loss of opisthosomal segments). – *Lemoneites*, *Legrandella* and *Weinbergina* show evidence of eleven segments in the opisthosoma (0). Ten segments are seen in *Pseudoniscus*, *Cyamocephalus*, *Bunodes*, *Limuloides* and *Pasternakevia* (1). Further loss of a segment resulted in a segment count of nine in *Kasibelinurus* and all xiphosurids (2). Since we are uncertain exactly which somites are expressed as tergites, a simple count seems the easiest way of scoring this character. The counting of opisthosomal segments in *Limulina* is a little difficult because of the trend towards loss of transverse ridges demarcating separate segments on the lateral fields of the opisthosoma as well as on the axis. Nevertheless, it is possible to count opisthosomal segments by locating the paired apodemes on either side of the axial ridge.

Character 23 (opisthosomal flange). – Fusion of the bases of the fixed lateral spines to form an opisthosomal flange is a synapomorphy of *Euproops* and *Liomesaspis*.

Character 24 (tergite VIII). – The plesiomorphic state for this character is a freely articulating tergite (0). Incorporation of the opercular tergite (VIII) into the thoracetron is a synapomorphy of Bellinuridae and Euproopidae (1). In *Bellinuroopsis* and *Rolfeia* the opercular segment articulates freely with the thoracetron (0). In *Paleolimulus*, *Valloisella*, *Limulus* and *Xaniopyramis*, the opercular tergite has lost the axial part of the tergite and forms the so-called free lobes, which are fused to the thoracetron (2).

Character 25 (anterior medial carapace projection). – Both *Pseudoniscus* and *Legrandella* possess a small median projection on the anterior edge of the carapace. This structure is not encountered in any other xiphosuran taxon and is therefore considered to be derived in these taxa.

Character 26 (axial carina). – The plesiomorphic condition for the opisthosomal axis is a series of rounded nodes, one per segment (0). In *Valloisella* and *Limulus*, the axial lobes of individual tergites are barely distinguishable, and a continuous, carinate ridge runs the full length of the opisthosoma (1).

Discussion

Nineteen taxa and 26 characters were used in this analysis. The resulting cladogram (Fig. 3) has a tree length of 44 and a consistency index of 0.86. Fig. 3A shows all character-state changes; Fig. 3B shows only those changes that are unambiguous. There are a number of unresolved trichotomies, some of which result from a contest between two characters. In Fig. 3B, note the fol-

Table 1. Data matrix of taxa and characters used in the cladistic analysis.

| Character | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 |
|-----------------------|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| <i>Paleomerus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Lemoneites</i> | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Weinbergina</i> | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Legrandella</i> | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Limuloides</i> | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| <i>Bunodes</i> | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| <i>Pasternakevia</i> | 0 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | ? | 1 | 0 | 0 | 0 | 0 |
| <i>Pseudoniscus</i> | 0 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 2 | 0 | 1 | 0 | 0 | 1 | 0 |
| <i>Cyamocephalus</i> | 0 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 0 |
| <i>Kasibelinurus</i> | 0 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 0 |
| <i>Bellinurus</i> | 1 | 2 | 1 | 0 | 2 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 0 | 0 | 0 | 0 | 2 | 2 | 1 | 2 | 0 | 1 | 0 | 0 |
| <i>Liomesaspis</i> | 1 | 2 | 1 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 1 | 1 | 2 | 2 | 0 | 0 | 0 | 0 | 2 | 2 | 1 | 2 | 1 | 1 | 0 | 0 |
| <i>Euproops</i> | 1 | 2 | 1 | 0 | 2 | 0 | 0 | 0 | 2 | 1 | 1 | 1 | 2 | 2 | 0 | 0 | 0 | 0 | 2 | 2 | 1 | 2 | 1 | 1 | 0 | 0 |
| <i>Bellinuroopsis</i> | 1 | 2 | 1 | 0 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 2 | 2 | 1 | 2 | 0 | 0 | 0 | 0 |
| <i>Rolleia</i> | 1 | 2 | 1 | 1 | 2 | 1 | 1 | 0 | 1 | 1 | ? | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 2 | 2 | 1 | 2 | 0 | 0 | 0 | 0 |
| <i>Paleolimulus</i> | 1 | 2 | 2 | 1 | 3 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 2 | 2 | 1 | 2 | 0 | 2 | 0 | 0 |
| <i>Xaniopyramis</i> | 1 | 2 | 2 | 1 | 3 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 2 | 2 | 1 | 2 | 0 | 2 | 0 | 0 |
| <i>Valloisella</i> | 1 | 2 | 2 | 1 | 3 | 0 | 0 | 0 | 1 | 1 | 2 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 2 | 2 | 1 | 2 | 0 | 2 | 0 | 1 |
| <i>Limulus</i> | 1 | 2 | 2 | 1 | 3 | 0 | 0 | 0 | 1 | 1 | 2 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 2 | 2 | 1 | 2 | 0 | 2 | 0 | 1 |

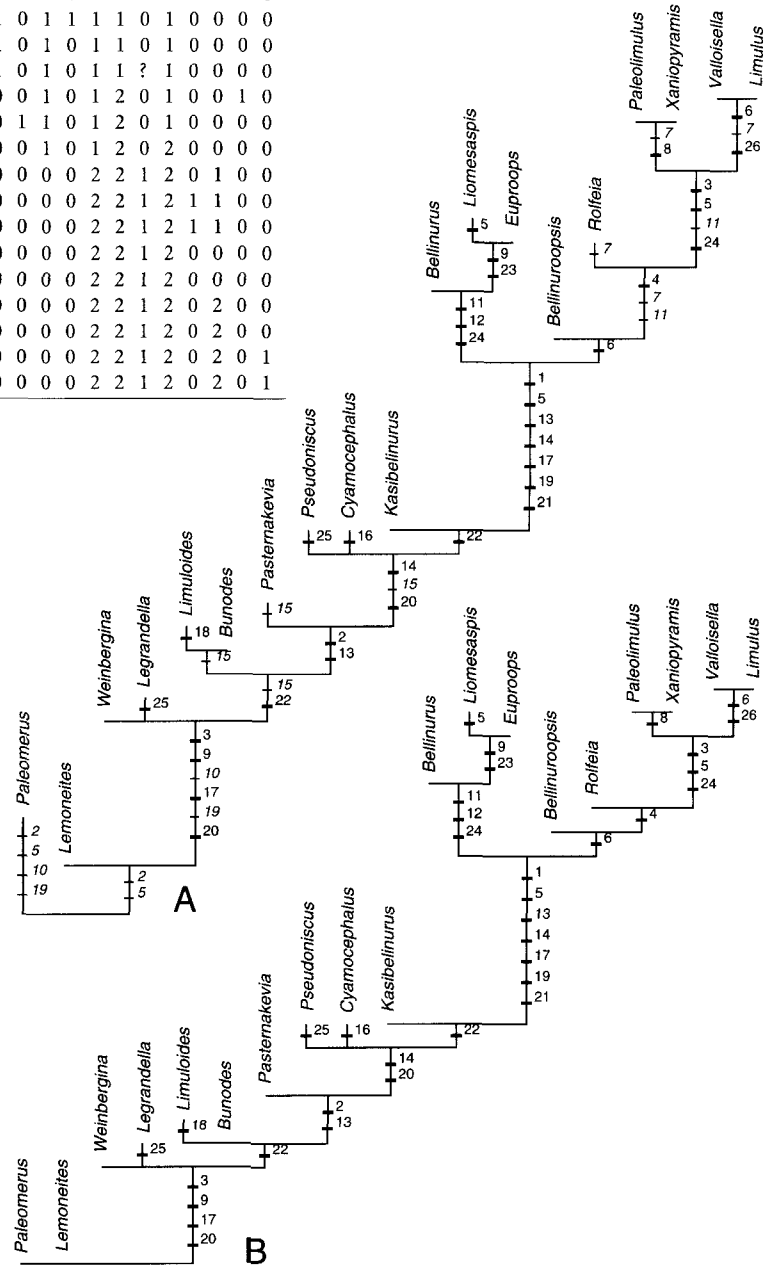


Fig. 3. Cladogram of Palaeozoic Xiphosura, based on data matrix in Table 1. Fat, horizontal bars with plain numerals mark unambiguous character state changes, thin horizontal bars with italic numerals mark ambiguous character state changes. Numerals refer to characters in Table 1 and the text. □A. All character state changes. □B. Unambiguous character state changes only.

lowing trichotomies: (1) at the base of the cladogram (*Paleomerus*, *Lemoneites*, Xiphosura); (2) (*Weinbergina*, *Legrandella*, Unnamed taxon 1); (3) (*Pseudoniscus*, *Cyamocephalus*, Unnamed taxon 4). In general, there are too few characters to fully explore the relationships among these animals, especially among the synziphosurines. However, nodes that are particularly well sup-

ported are: (1) the Xiphosura, where four character state changes differentiate the taxon from its outgroups; and (2) the Xiphosurida, where seven character state changes clearly separate this taxon from the stem-group, the synziphosurines. Also, *Bellinurina* and *Limuloidea* are each distinguished by three character state changes from other xiphosurids.

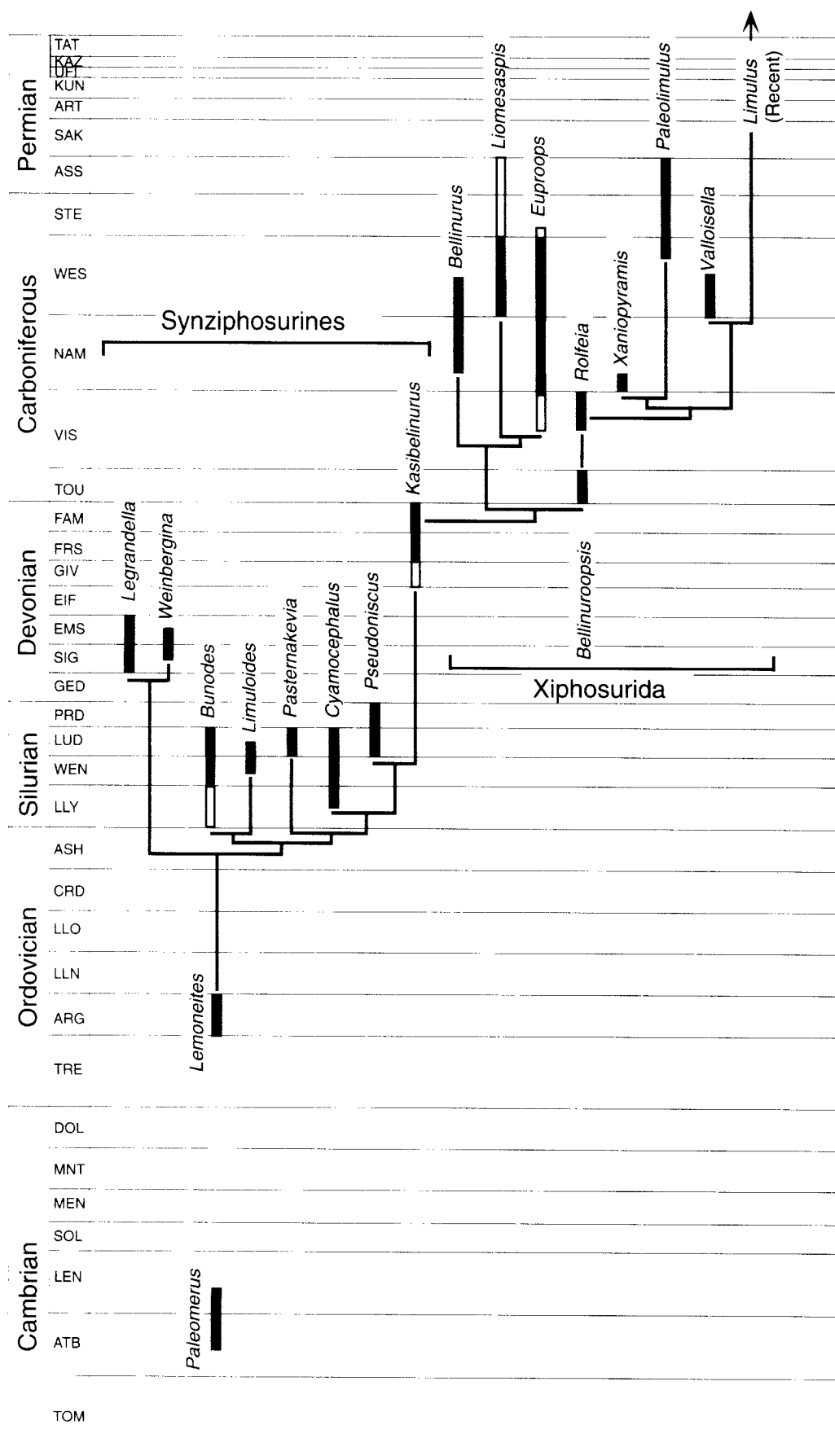


Fig. 4. Evolutionary tree of Palaeozoic Xiphosura and outgroups derived from cladogram (Fig. 3) and stratigraphic record. Standard stages are drawn to scale; names abbreviated as in Benton (1993). Thick black bars = published stratigraphic record of taxon; thick hollow bars = unpublished record or published record of xiphosuran unassigned to genus or reassigned herein (see text); thick grey bars = range extension between known records. Thin horizontal bars denote sister-group relationships; thin vertical bars represent ghost lineages and range extensions concordant with the cladogram (see text for details).

Evolutionary tree

Fig. 4 shows the cladogram in Fig. 3 superimposed on a chart of the stratigraphic occurrence of the taxa used in the analysis. Both published and unpublished stratigraphic information is included for completeness; unpublished records were given by Anderson (1996). The youngest known *Cyamocephalus*, of Ludlow age, is from the Welsh Borderland; Scottish specimens, from the Waterhead Group, could be Llandovery in age (Walton 1965), but Selden & White (1983) referred these rocks, at least in part, to the Ludlow stage.

The evolutionary tree was constructed using the conventional reasoning as outlined by Smith (1994, Chapter 6). Basically, only monophyletic taxa are shown as sister groups; taxa that lack unique apomorphies (and are therefore defined on combinations of character states) either require more information to resolve their true status or are metataxa. Metataxa may be ancestors, so these unresolved taxa are shown as possible ancestors in the phylogenetic tree.

Lemoneites and *Paleomerus* are outgroups; *Lemoneites* is shown in Fig. 4 as a possible ancestor to Xiphosura. In the trichotomy of *Weinbergina*, *Legrandella* and higher Xiphosura (Unnamed taxon 1), note that *Legrandella* and Unnamed taxon 1 have apomorphies, *Weinbergina* does not. *Weinbergina* could be ancestral to *Legrandella*, and together these two genera constitute Weinberginidae Richter & Richter, 1929. *Weinbergina* could also be ancestral to Unnamed taxon 1 but, given the great age difference between Weinberginidae and the oldest member of Unnamed taxon 1 (*Bunodes*), the common ancestor of Weinberginidae is shown as a ghost lineage in Fig. 4. The presence of weinberginids in the late Ordovician is likely. The trichotomy of *Pseudoniscus*, *Cyamocephalus* and higher xiphosurans (Unnamed taxon 5) cannot be resolved because all three taxa have unique apomorphies within the three-taxon problem, so the most recent of the two taxa (*Pseudoniscus* + Unnamed taxon 5) are united as sister taxon to the third (*Cyamocephalus*); the hypothesized stem lineage is plesiomorphic with respect to all three taxa. Note the possible ancestral relationships of *Kasibelinurus*, *Bellinuroopsis* and *Rolfeia*. *Kasibelinurus* appears to be ancestral to the Xiphosurida, and since *Pseudoniscus* is Silurian, the stem of Unnamed taxon 5, and possibly the genus *Kasibelinurus*, should also be found in that period. The greatest number of character state changes occurs between *Kasibelinurus* and Xiphosurida, yet there is a larger stratigraphic gap between *Kasibelinurus* and the other synziphosurines. *Kasibelinurus* lacks autapomorphies, which is why it appears on the diagram as a possible ancestor to Xiphosurida. Should unique characters be found to define *Kasibelinurus* as a discrete taxonomic entity, then *Kasibelinurus* and Xiphosurida would share a common ancestor some time before the middle Devonian. It is possible that *Kasibelinurus* and the

weinberginids are late representatives of a taxa which originated in the lower Silurian or Ordovician. Fig. 4 clearly demonstrates the need for more fossils to be found in Ordovician and Devonian strata if we wish to elucidate further the relationships of these fascinating animals.

Revised classification

A revised classification of the taxa used in this analysis is given below. The convention of the plesion (Patterson & Rosen 1977) is used to reflect the cladogram accurately (Fig. 3). An asterisk denotes that the taxon is plesiomorphic at the level of analysis and further information is required to establish monophyly.

Class Xiphosura Latreille, 1802

Family Weinberginidae Richter & Richter, 1929

Weinbergina Richter & Richter, 1929*

Legrandella Eldredge, 1974

Unnamed taxon 1

Unnamed taxon 2

Bunodes Eichwald, 1854*

Limuloides Woodward, 1865

Unnamed taxon 3

Plesion *Pasternakevia* Selden & Drygant, 1987*

Unnamed taxon 4

Plesion *Cyamocephalus* Currie, 1927

Plesion *Pseudoniscus* Nieszkowski, 1859

Unnamed taxon 5

Plesion (Family) Kasibelinuridae Pickett, 1993*

Kasibelinurus Pickett, 1993*

Order Xiphosurida Latreille, 1802

Suborder Bellinurina Zittel & Eastman, 1913

Family Bellinuridae Zittel & Eastman, 1913*

Bellinurus Pictet, 1846*

Family Euproopidae Eller, 1938

Euproops Meek, 1867*

Liomesaspis Raymond, 1944

Unnamed taxon 6

Plesion *Bellinuroopsis* Chernyshev, 1933*

Unnamed taxon 7

Plesion (Family) Rolfeidae Selden & Siveter, 1987*

Rolfeia Waterston, 1985*

Suborder Limulina Richter & Richter, 1929

Superfamily Paleolimuloidea, new

[Diagnosis: Limulina with a pyramidal cheek node on the carapace]

Family Paleolimulidae Raymond, 1944*

Paleolimulus Dunbar, 1923*

Family Moravuridae Přibyl, 1967*

Xaniopyramis Siveter & Selden, 1987*

Superfamily Limuloidea Zittel, 1885

Plesion *Valloisella* Racheboeuf, 1992*

Family Limulidae Zittel, 1885

Limulus Müller, 1785

This classification differs fundamentally from previously published schemes, principally because synziphosurines are shown to be a paraphyletic group. They appear as a stem lineage to the Xiphosurida, a name that is used here in preference to infraorder Limulicina Richter & Richter, 1929, to which it is equivalent (Selden & Siveter 1987; Pickett 1993). *Lemoneites* is excluded from Xiphosura as perceived by Anderson (1996), because of the lack of ophthalmic ridges on the carapace and absence of an axial ridge on the opisthosoma. Weinberginidae Richter & Richter, 1929, is retained for *Weinbergina* and *Legrandella* for the reasons discussed under *Evolutionary tree*, above. Within Xiphosurida, suborder Bellinurina Zittel & Eastman, 1913, comprises the common Carboniferous xiphosurid families Bellinuridae Zittel & Eastman, 1913, and Euproopidae Eller, 1938. Sister group to Bellinurina is Unnamed taxon 6, containing the metataxa *Bellinuroopsis* and *Rolfeia*, and suborder Limulina Richter & Richter, 1929, a name that is used here in preference to superfamily Limuloidea Zittel, 1885, to which it is equivalent (Selden & Siveter 1987; Pickett 1993). Limuloidea is here used for plesion *Valloisella* and Limulidae, and also includes all Mesozoic and Cenozoic xiphosurids (*Paleolimulus fuchsbergensis* Hauschke & Wilde, 1987, is not a paleolimulid because it lacks the characteristic network of transverse and longitudinal ridges on the thoracetrone). A new superfamily, Paleolimuloidea, is erected here for families Paleolimulidae Raymond, 1944, and Moravuriidae Přibyl, 1967.

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