The origin of the limuloids

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A reassessment of the origin of the Limuloidea (Xiphosura) has been facilitated following recent descriptions of the two earliest known examples, of Carboniferous age: Rolfeia Waterston, 1985 from the Tournaisian of Scotland and Xuniopyramis Siveter & Selden, 1987 from the basal Namurian of England. Analysis of the nature of segment reduction from the more primitive to the advanced xiphosurids indicates that in the bellinuroid (limulicine) line caudal fusion was dominant, and supports the notion that the limuloids arose from an early bellinuroid in the late Devonian or earliest Carboniferous, from such as the late Devonian Neobeliuropsis Eller, whilst the euproopoids originated independently later in the Carboniferous via a different bellinuroid line. Rolfeia is the oldest limuloid, but the slightly younger Xuniopyramis is believed to be the first with a partially encephalized somite VIII, a feature thereafter diagnostically present in the limuloid lineage to Recent forms. Phylogenetically Xuniopyramis lies between Rolfeia and the Permo-Carboniferous Paleolimulus Dunbar, of the Paleolimulidae Raymond. Xaniopyramis belongs to the Moravuridae Pfab; Rolfeia, previously provisionally considered to be a Paleolimulidae, is placed herein within the monotypic Rolfeiidae fam. nov. Chelicerae, Xiphosura, evolution, Carboniferous.


The Limuloidea Zittel, 1885 comprises some late Palaeozoic and all post-Palaeozoic xiphosurids. It has persisted from at least the early Carboniferous to the present day at low species diversity and represents a relatively good example of bradytely (Fisher 1984). The origins of this superfamily lie within the other, far more diverse, Palaeozoic Xiphosurida, and the interrelationships of the various groups of Palaeozoic xiphosurids has been the subject of much debate over the years (e.g. Bergström 1975; Eldredge 1974; Størmer 1952). During the Palaeozoic there were two intervals, the late Silurian and the late Carboniferous, when species diversity greatly exceeded the otherwise low level shown by the later limuloids (Fisher 1984, Fig. 2), but it is in the intervening Devonian and early Carboniferous that we seek the origin of the limuloids amongst relatively few described xiphosurid taxa. Two new limuloid genera from the Lower and basal Upper Carboniferous were described recently: respectively Rolfeia Waterston, 1985 and Xaniopyramis Siveter & Selden, 1987 (Fig. 1A, B). These enable us to determine the phylogenetic and temporal origin of the limuloids with greater accuracy than before and to reconsider the possible evolutionary events which led up to the origin of this major group of xiphosurids.

Consideration of the means by which the primitive number of segments in the Xiphosura has progressively reduced and segments have become fused in more advanced forms, based on evidence from morphological, functional and embryological data, leads to the conclusion that the limuloids originated from early bellinuroids, as suggested by Fisher (1981, 1982). The phylogeny presented in Fig. 2 results from examination of the relationships of the earliest limuloids, Rolfeia and Xaniopyramis, with the Permo-Carboniferous Paleolimulus Dunbar, 1923 (Fig. 1C) and the upper Devonian bellinuroid Neobeliuropsis Eller, 1938 (Fig. 1E; this generic name should now be discontinued since Selden & Siveter (in press) have presented evidence that it is a junior objective synonym of Bellinuroopsis Chernyshev, 1933). Rolfeia is not considered by us to belong in the Paleolimulidae Raymond, 1944, to which it was tentatively assigned by Waterston (1985), but to form the monospecific Rolfeiidae fam. nov. erected herein.

Terminology follows that of Siveter & Selden (1987) and references therein. Lankester (1904)
A. Rolfeia fouldensis Waterston, 1985; Lower Carboniferous, Tournaisian; ×0.7; based on Waterston 1985, Fig. 3. B. Xaniopyramis limsiyi Siveter & Selden, 1987; Upper Carboniferous, basal Namurian; ×0.16; based on Siveter & Selden 1987, Fig. 7. C. Paleolimulus avitus Dunbar, 1923; Lower Permian; ×2; based on Fisher 1981, Fig. 3b and Dunbar 1923, Fig. 1. D. Limulus polyphemus (Linnaeus, 1858); Recent; ×0.06; after Shuster 1979, Fig. 2. E. Neobelinus rossicus (Chernyshev, 1933); upper Devonian; ×0.6; after Steirmer 1952, Fig. 1h. F. Bellinurus carteri Eller, 1940; upper Devonian; ×0.75; after Eller 1940, Fig. 1. G. Bellinurus koenigianus Woodward, 1872; Carboniferous; ×1; after Fisher 1981, Fig. 3A. H. Euproops danae Meek & Worthen, 1865; Carboniferous; ×0.7; after Fisher 1979, Fig. 1.

Fig. 1. Diagrammatic reconstruction of xiphosurid taxa representative of the Bellinuroidea, Euproopoidea and Limuloidea. All views are dorsal; all magnifications are approximate. Free lobes or segments expressing somite VIII are marked with an asterisk.

gave a useful account of the terminology of arthropod metamericism, to which reference should be made for further clarification. A somite, or metamere, is a fundamental division of the body, identified and numbered from the first postoral (cheliceral in chelicerates) somite, numbered 1. The individual parts of a somite were termed by Lankester meromes; one merome important in our discussion is the tergite: the dorsal sclerite belonging to one somite. In the following discussion, where segmentation is obvious but somites are not identified, the general term segment is used, as for example when referring to the axial rings or segments of the thoracetrion (fully fused dorsal shield of the opisthosoma; Raymond 1944: 476).

Xiphosurid classification

Debates concerning xiphosurid evolution have resulted in a number of conflicting classification schemes in the literature; these are now briefly reviewed to provide a framework (Table 1) for the discussion following.

Since their removal from the Crustacea and their recognition as chelicerates (Lankester 1881), the Xiphosura have traditionally been allied with
the Eurypterida in the class Merostomata. However, recent attempts at classifyng the Chelicerata have concluded that the Xiphosura is the sister group of either all other chelicerates (e.g. Boudreaux 1979; Grasshoff 1978; Paulus 1979; Weygoldt 1980; Weygoldt & Paulus 1979) or a group which includes the Scorpionida (e.g. Bergström 1979, 1981; Bergström et al. 1980; van der Hammen 1985b, 1986), and therefore this concept of the Merostomata must be discarded (Kraus 1976). Since the rejection of agласpidids as chelicerates by Briggs et al. (1979), only the xiphosurids, synziphosurids and chasmataspids remain in the class Xiphosura according to most authors, but there is no consensus on the relationship of these three taxa. Størmer (1952, 1955), Eldredge (1974) and Fisher (1982, 1984) included the Synziphosurina Packard, 1886 as a suborder of the Xiphosurida, an arrangement which we follow, whereas Bergström (1968, 1975) and Stürmer & Bergström (1981) preferred to place the synziphosurines as a separate order. The Chasmataspida Caster & Brooks, 1956 is regarded by most authors as an order within the class Xiphosura, and we concur, though Eldredge (1974) allied the group with the Eurypterida.

Within the Xiphosurida there are two suborders: the Synziphosurina and the Limulina Richter & Richter, 1929, and it is the relationship of the taxa in the latter group which forms much of the discussion herein. Størmer (1952, 1955) recognized within the Limulina three superfamilies, the Belinuracea Zittel & Eastman, 1913, the Euproopacea Eller, 1938, and the Limulacea Zittel, 1885. Bergström (1975) recognized the Limulina, containing only the Limulacea, and he erected the new suborder Belinurina for the Belinuracea, Euproopacea and Eolimulacea Bergström, 1968. Eldredge (1974) provided evidence for removing some genera from the Synziphosurina and placing them with some primitive belinurinoids in the new infraorder Pseudoniscina, which he considered to be the sister group of the Limulicina Richter & Richter, 1929 in the Limulina. In Eldredge's (1974) scheme, the Limulicina contained the Belinuracea and the Limulacea, the latter embracing the Euproopidae and Limulidae. We follow Eldredge’s reasoning herein but prefer to retain the three superfamilies Limuloidea, Belinuroidea and Euproopoidae (suffix changed to conform to ICZN Recommendation 29A; spelling of Bellinurus and derivatives in agreement with Morris 1980). Fisher’s (1981, 1982) analyses, referred to further below, and his phylogenetic diagrams (1982, Fig. 1; 1984, Fig. 2) supported mainly by unpublished evidence, indicate that a classification scheme for the xiphosurids which reflects phylogeny would require the erection of some new names and emendation of old diagnoses.

In the following section we outline the mechanisms by which the ancestral xiphosuran body plan became modified to produce the limuloid condition.

### Segmentation

The general principles of arthropod segmentation were enumerated by Lankester (1904) in thirteen 'laws', a number of which are relevant to this discussion; reference should be made to his paper for further elaboration. The maximum number of somites in an arthropod group is fixed and their full expression of all meromes is primitive: such a condition is rarely found and is usually hypothetical. Usually meromes (e.g. tergites, appendages) are adapted in some way, from a hypothetical ancestral form, into specialized forms, or atrophied. Thus investigation of the embryology of a group is commonly necessary to reveal ancestral somites which are suppressed in later ontogeny. The maximum number of somites recorded in the Chelicerata is 19, and this number has been identified in the eurypterids, scorpions, ricinuleids and anactinotrichid mites for example (van der Hammen 1985a). The maximum number of somites yet found in the Xiphosura is 18, in the chasmataspids which show 12 opisthosomal tergites (6 somites are present in the prosoma of chelicerates). In fossil chelicerates only those somites which have an expression in the exoskeleton as a tergite, pleural ribs, movable spines or other merome can be identified; ancestral
somites expressed only internally, as neural ganglia for example, cannot be seen. It is possible that a xiphosuran with 19 somites expressed in the exoskeleton may yet be found. Living Xiphosura are sufficiently distant from the ancestral chelicerate body plan to have lost external expression of many somites, but 18 have been identified in embryological studies (Scholl 1977). A major theme in the phylogenetic history of the Xiphosura is the gradual reduction in the number of somites expressed externally, particularly in the opisthosoma. Lankester (1904) described a number of processes by which somites can be suppressed; the details are not relevant to the present discussion but that such processes can be recognized to have occurred is important.

A feature of all arthropod groups is tagmosis: the development of tagmata, major divisions of the body. At least two tagmata are recognizable in the Chelicera; an anterior prosoma with 6 postoral somites (I–VI) and a posterior opisthosoma with up to 13 somites (VII–XIX). Additionally, a preoral region and a telson may be distinguished. The opisthosoma is commonly divisible into an anterior mesosoma of 8 somites and a posterior metasoma of 5 somites. These two opisthosomal tagmata are not expressed in all chelicerates and have therefore been termed pseudotagmata by van der Hammen (1980). It was noted by Lankester (1904) that fusion, suppression or other changes in the expression of somites normally occurs at the boundaries of tagmata; most commonly this involves the formation of a ‘head’, but in the Xiphosura changes will also be noted to have occurred at the prosoma–opisthosoma, mesosoma–metasoma, and metasoma–telson junctions. Changes can occur which involve a somite of one tagma apparently moving, wholly or in part, to the adjacent tagma and forming a functional part of the adopting tagma. The absorption of an opisthosomal somite into the prosoma is here termed encephalization; the importance of this process, and those of fusion of meromes (usually fusion of tergites) at the mesosoma–metasoma and metasoma–telson junctions, in the evolution of the Xiphosura is our next concern.

Encephalization. – The embryological studies of Scholl (1977) and Sekiguchi et al. (1982) of Limulus (Fig. 1D) established that the opisthosomal somites VII and VIII (in part) are absorbed into the prosoma during embryonic development. In the adult Limulus, somite VII is expressed externally as a pair of chilaria situated ventrally on the prosoma, and it has no dorsal expression. Somite VIII is fully developed ventrally on the opisthosoma with the genital operculum but dorsally this somite forms the prosoma–opisthosoma joint and is shared by these tagmata; the free lobe on the opisthosoma also belongs to somite VIII. Thus whilst these somites are opisthosomal in origin, in the adult Limulus they form part of the prosoma, in whole or in part, in terms of functional morphology.

In the lower Devonian synziphosurine Weinbergina Richter & Richter, 1929 (Stürmer & Bergström 1981) and a new, possible synziphosurine from the Lower Silurian of Wisconsin (Mikulic et al. 1985a, b) a sixth pair of walking legs occurs on the prosoma, in the position occupied by the chilaria in Limulus, which must therefore belong to somite VII. The only other genus in the Weinberginidae Richter & Richter, 1929, Legrandella Eldredge, 1974, does not have appendages preserved but shows a dorsal, axial half-ring (i.e. greatly reduced tergite) belonging to somite VII, on the opisthosoma. This reduced tergite in the opisthosoma is not preserved in the four known specimens of Weinbergina, but was probably present (Stürmer & Bergström 1981). Thus almost complete encephalization of somite VII had occurred in these most primitive xiphosurids. We note here that Bergström (1975, 1979, 1981) and Bergström et al. (1980) regarded somite VII in the Xiphosura as prosomal in origin; discussion of this concept is beyond the scope of the present paper and irrelevant to subsequent somatic transformations within the class.

Fusion within the opisthosoma. – In the Weinberginidae, the mesosoma shows evidence of 8 somites: 7 tergites and the half-ring belonging to somite VII (see above), and 3 tergites are present in the metasoma (Eldredge 1974; Stürmer & Bergström 1981). Despite being older than the Weinberginidae, the Silurian Bunodes Eichwald, 1854 and Limuloids Salter in Woodward, 1865 are more advanced synziphosurines with respect to fusion within the opisthosoma since they exhibit only 7 mesosomal segments including the half-ring belonging to somite VII, and 3 metasomal tergites (Eldredge 1974). The posterior mesosomal tergite appears to be double in these genera and probably represents 2 fused tergites (somites XIII and XIV) (Störmer 1955:16).
in the Pseudoniscina, which are primitive members of the Limulina and thus more advanced than the Synziphosurina, some species of the Silurian *Pseudoniscus* Nieszkowski, 1859 and *Cyamocephalus* Currie, 1927 exhibit only 9 segments in the opisthosoma (Eldredge 1974). The sixth segment appears double and is probably composed of the tergite of somite XII joined to the already fused tergites of somites XIII and XIV; the last 3 segments (somites XV to XVII) form the metasoma, which is not clearly distinguished, at least dorsally, in these genera. Additionally, in *Cyamocephalus* the seventh segment is hypertrophied (Eldredge & Plotnick 1974). This may reflect its original formation by fusion, but could represent true hypertrophy since in *Bunodes*, *Limuloides*, and a new pseudoniscine from the Silurian of Podolia (Selden & Drygant 1987) a hypertrophied second opisthosomal tergite (of somite VIII) occurs, which does not appear to have been formed by fusion of two somites.

**Caudal fusion.** – In *Limulus* the most posterior mesosomal somite (XIV) is represented externally by the most posterior movable spine, but the metasomal somites are expressed internally by neural ganglia belonging to somites XV to XVIII (Scholl 1977). The bellinuroids show 2 or 3 fused tergites posteriorly in an opisthosoma of otherwise free tergites. This fusion was initiated for functional reasons: it enabled musculature of somites more anterior than the pretelsonic one to be used in operating the telson, thus increasing the excursion of the telson for more effective righting of the overturned animal (Fisher 1981, 1982).

**Relationships among the limulicine superfamilies**

The traditional view of limulicine relationships, as expressed by Størmer (1952:632, 1955:P19), was of a linear progression from the Bellinuroidea through the Euproopoidea to the Limuloidea. This view was put into the form of a phylogenetic tree by Bergström (1975, Fig. 3). However, nearly every writer on xiphosurid phylogeny has commented that the Bellinuroidea is a diverse and probably unnatural group which needs re-evaluation. Eldredge (1974) restricted the Bellinuroidea to those advanced bellinuroids (*Bellinurus* s.s., apparently including *B. bellulus* König, 1851, type species, and *Neobelinuropsis rossicus* (Chernyshev, 1933)) which have the cardiac and axial furrows aligned, and a well-developed articulation between the prosoma and opisthosoma, and he (Eldredge 1974, Fig. 13) portrayed its sister-group as the Limuloidea, the latter comprising the Euproopidae and the Limulidae. Fisher (1981) examined the relationships among the limulicine superfamilies in terms of a species-based three-taxon problem. He concluded that *Bellinurus koenigianus* Woodward, 1872 (Fig. 1G) was closer to *Euproops danae* Meek & Worthen, 1865 (Fig. 1H) than either was to the early limuloid *Paleolimulus avitus* Dunbar, 1923, and that a thoracetron was independently acquired in the limuloids and the euproopoids. He has since published a detailed phylogenetic tree (Fisher 1982, Fig. 1, 1984, Fig. 2) which shows the Limuloidea as most closely related to certain upper Devonian bellinuroids, such as *Neobelinuropsis*, and the bellinuroid–euproopoid line with *Bellinurus carteri* Eller, 1940 (Fig. 1F) as the oldest representative. The notion that the Limuloidea and the Euproopoidea were derived from separate ancestors within the Bellinuroidea appears to have been previously put forward by Raymond (1944:479–481).

**The Bellinuroidea.** – The bellinuroids are distinguished from other limulicides by their free opisthosomal tergites. It is probable that the most anterior complete, free tergite belongs to somite VIII because: the dorsal expression of somite VII had almost completely disappeared in much older, more primitive (non-limulicine) xiphosurids (see above, Weinberginidae), and an axial remnant of somite VII is present in the opisthosome of some bellinuroids, for example *B. koenigianus* (Bergström 1975:294). *Neobelinuropsis* bears 7 free tergites and a caudal region of 2 fused segments (Størmer 1952:632, Fig. 1h; see Chernyshev 1933). Probably the free tergites represent somites VIII to XIV since, as mentioned above, the opisthosomal tergite of somite VII is greatly reduced in more primitive xiphosurids and also somites VIII to XIV are still expressed externally in some form in the later limuloids (Scholl 1977). In *Neobelinuropsis* therefore, and in the bellinuroid (limulicine) line caudal fusion was the dominant process, in contrast to the pseudoniscines in which, as mentioned above, fusion mainly occurred at the mesosoma-metasoma junction. Thus *Neobelinuropsis* was
not a direct descendant of the pseudoniscines but the two taxa share a common ancestor with free tergites of somites VIII to XVII; this relationship is shown in Fisher’s concept of xiphosurid phylogeny (1982, Fig. 1, 1984, Fig. 2).

The number of free tergites in Neobelinuropsis is greater than in any other bellinuroid with the possible exception of Bellinurus morgani Dix & Pringle, 1930 (see below). Bellinuroids generally possess 5 free tergites and a caudal region with traces of 3 fused segments (the $o_1$ -- $o_3$ tagma of Fisher 1981), but as Eller (1938:134) discussed, there is some variation in the interpretation of free and fused tergites by authors of bellinuroid taxa, particularly by Dix & Pringle (1929, 1930). These authors described bellinuroids from the South Wales coalfield with from 4 free tergites in B. truemanni Dix & Pringle, 1929 to 7 in B. morgani, and with 2 or 3 fused tergites in the caudal region. It seems to us that a number of miscounts are likely to be found in the literature. A count of less than 5 free tergites seems unlikely since this is the number of axial rings preceding the caudal region in the thoracetron of euproopoids, which are thought by all authors to be derived from the bellinuroids.

In his three-taxon analysis, Fisher (1981:51 et seq.) used the shared characters of a caudal region of 3 fused tergites and a rounded opisthosomal outline in dorsal view as indicators of a greater affinity between B. koenigianus and E. danae than either of these taxa to P. avitus which does not have these characters. Fisher’s analysis works for these species but not necessarily for all members of the superfamilies which they represent. First, most limuloids also show a distinct caudal region on the thoracetron, posterior to the last trace of axial segmentation; if the number of fused tergites in the caudal region of the bellinuroids is indeed variable, then it could be possible to find a bellinuroid species with a caudal region composed of somites homologous to one of a limuloid species. Raymond (1944:505) made a tentative suggestion that the caudal region in P. avitus was movable in life; we agree with the doubts expressed by Pickett (1984:611) on this idea. Second, all bellinuroid opisthosomae are not rounded, they vary from subsemicircular to subtriangular in outline, and Raymond (1944:480) emphasized this variation in establishing Koenigiella. Also, we now know that some primitive limuloids, for example Rolfeia and Paleolimulus longispinus Schram, 1979, have rounded opisthosomae. Nevertheless, we agree with Raymond (1944) and Fisher (1981) that the thoracetron of the Limuloidea was derived independently from that of the Euproopoidea, and with Fisher (1981) that the Limuloidea are closer to upper Devonian bellinuroids such as Neobelinuropsis than to later bellinuroids, for the reasons outlined below.

The Euproopoidea. – In spite of the reservations regarding the general application of Fisher’s (1981) three-taxon analysis expressed above, his functional arguments remain valid. The Euproopoidea can readily be derived from bellinuroids with rounded opisthosomae, 5 free tergites and a caudal region showing 3 fused segments, by simple fusion of the free tergites into a thoracetron, and they form a coherent and specialized group. Bergström (1975) argued for the traditional view of a derivation of the Limuloidea from the Euproopoidea, and considered that the ophthalmic spines in euproopoids migrated backwards to become free lobes in the Limuloidea. Since the free lobes belong to somite VIII this hypothesis would require that encephalization of this somite had occurred in the euproopoids, and that there was a momentous trend reversal to produce the limuloid condition.

An alternative hypothesis supporting a euproopoid–limuloid phylogenetic link is that the most anterior thoracetron segment in euproopoids belongs to somite VIII and that this was partly absorbed into the prosoma to leave the free lobe in the opisthosoma of the limuloids. The lower Namurian limuloid Xaniopyramis may at first sight seem to support this alternative since it bears transverse pleural ridges on the thoracetron which are also found in euproopoids. However, many other changes need to be involved in this proposed euproopoid–limuloid transformation: the loss of the euproopoid characters of ophthalmic spines, fixed marginal opisthosomal spines and a semicircular opisthosomal doublure, and the development of the limuloid features of movable opisthosomal spines, longitudinal pleural ridges and a dorsally facing occipital band (post-eromarginal facet), the latter character having been considered (Fisher 1981:56) unlikely to have been derived from the similar but ventrally facing feature seen in euproopoids. Also, since euproopoids show 5 axial rings on the thoracetron, limuloids derived from them with the partial absorption of somite VIII into the prosoma would be expected to show no more than 4 axial
rings or their traces (e.g. pairs of apodemes) on
the thoracetrion, yet *Xaniopyramid* shows at least
5 axial rings (Siveter & Selden 1987) and the other
limuloids have more than 5 rings or apodeme
pairs. Additionally, *Xaniopyramid* is at least as
old as the oldest known euproopoid, so it could
not be a transitional form between the later limu-
loids and any known euproopoid. *Rolfeia*, which
is from the Tournaisian and hence slightly older
than *Xaniopyramid*, shares the characters of fixed
marginal opisthosomal spines and rounded opis-
thosomal outline (Waterston 1985) with the
euproopoids, but these characters also occur in
the bellinuroids. It differs from the euproopoids
in many ways and as convincingly argued by
Waterston (1985), *Rolfeia* must be considered the
earliest known limuloid.

A further evolutionary scenario is that the
Moravuridae Přibyl, 1967, the family to which
*Xaniopyramid* and the coeval *Moravurus* Přibyl,
1967 belong, was alone derived from the
Euproopoidea and is separate from the Limu-
loidea. This hypothesis would require the inde-
pendent evolution of all the characters which the
Moravuridae share with the Limuloidea. The law
of parsimony necessitates the rejection of this
hypothesis.

To conclude this section, we concur with Fisher
(1982, 1984) and Waterston (1985) that the limu-
loids originated amongst primitive bellinuroids
such as *Neobelinuropsis* possibly in the late
Devonian. In the transition from the bellinuroid
to the limuloid condition, somite VIII became
partly encephalized, the axial part of the tergite
forming the prosoma-opisthosoma hinge (Scholl
1977). Details of the transition are discussed in
the following section.

The positions of *Rolfeia* and
*Xaniopyramid* within the
Limuloidea

Figure 2 shows our conclusions regarding the
phylogenetic relationships of *Rolfeia*, *Xaniopy-
ramid* and allied taxa (cf. Waterston 1985, Fig.
4). The characters which distinguish these genera
and their respective families are given below
(Systematic palaeontology) and in Siveter & Sel-
den (1987), and those features which are of par-
ticular phylogenetic significance are detailed in
the legend to Fig. 2. Each genus presents unique
derived characters, such as the cheek ridge in

<table>
<thead>
<tr>
<th>Primitive state</th>
<th>Derived state</th>
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<tbody>
<tr>
<td>1. Free opisthosomal tergites</td>
<td>Thoracetrion</td>
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<tr>
<td>2. No movable opisthosomal spines</td>
<td>Movable opisthosomal spines</td>
</tr>
<tr>
<td>3. Pleura of somite VIII not developed into free lobe</td>
<td>Free lobe</td>
</tr>
<tr>
<td>4. Axial part of tergite of somite VIII fully expressed dorsally in opisthosoma</td>
<td>Axial part of tergite of somite VIII mostly encephalized</td>
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<tr>
<td>5. No longitudinal pleural ridges</td>
<td>Longitudinal pleural ridges</td>
</tr>
<tr>
<td>6. Fixed opisthosomal spines</td>
<td>No fixed opisthosomal spines</td>
</tr>
<tr>
<td>7. Pleural ribs</td>
<td>No pleural ribs</td>
</tr>
<tr>
<td>8. Ophthalmic ridges meet anteriorly</td>
<td>Ophthalmic ridges do not meet</td>
</tr>
<tr>
<td>9. Axial rings on thoracetrion</td>
<td>No axial rings on thoracetrion</td>
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At each dichotomy, the taxa to the left exhibit the primitive
character state and those to the right the derived one. Note
that within the younger limuloids some secondary loss of derived
characters occurs for functional necessity; e.g. *Limulitella
bronni* Schimper, 1850 has no free lobe and *Dubbolimulus
peetae* Pickett, 1984 has no movable opisthosomal spines.
Xaniopyramis (Siveter & Selden 1987), so that no taxon is directly ancestral to any other. The main difference between our phylogeny (Fig. 2) and that of Waterston (1985, Fig. 4) is in the position of Rolfeia, which he provisionally placed in the Paleolimulidae. Rolfeia exhibits primitive characters not found in later limuloids but which it shares with Neobelinuropsis, indicating a likely derivation of these two genera from a common ancestor. These are: the full expression dorsally on the opisthosoma of the axial part of the tergite belonging to somite VIII, the lack of longitudinal pleural ridges and the possession of fixed opisthosomal spines (Fig. 2, nos. 4–6). Waterston (1985) refrained from creating a new family for Rolfeia because although many features in his reconstruction of the genus set it apart from the Paleolimulidae, these were based on uncertain evidence. Since the discovery of Xaniopyramis indicates that the Moravuridae is in fact closer than Rolfeia is to the Paleolimulidae, and that Rolfeia is certainly not a moravurid (see above and next section), this argues for the establishment of the Rolfeiidae fam. nov. to receive the Scottish genus.

Rolfeia is the only limuloid known with the axial ring of somite VIII fully expressed in the opisthosoma, thus whilst the partially encephalized state of somite VIII is indicative of the Limuloidea, it cannot be diagnostic of the superfamily. The basal Upper Carboniferous Xaniopyramis is the oldest limuloid known which shows partial encephalization of somite VIII to leave the free lobe (Siveter & Selden 1987), therefore this event must have occurred before this time. The early Carboniferous age of Rolfeia does not provide a firm date for the encephalization event but suggests it occurred during this interval or the late Devonian at the earliest.

Systematic palaeontology

Family Rolfeiidae fam. nov.

Type genus. – Rolfeia Waterston, 1985; Carboniferous, late Tournaisian, Courceyan Stage, Foulden, Berwickshire, By monotypy.

Other genera. – None.

Diagnosis. – As for Rolfeia (see Waterston 1985:25).

Discussion. – The Rolfeiidae shares with the Moravuridae and the Paleolimulidae a free lobe, dorsal postero-marginal facet, parallel ophthalmic ridges posteriorly which curve anteriorly to meet in front of the eyes, and movable spines on the opisthosoma. The Rolfeiidae and Moravuridae show pleural ribs on the thoraceton, a feature lacking in the Paleolimulidae and all later limuloids. In the Rolfeiidae, the presence on the thoraceton of the axial portion of the segment bearing the free lobe (somite VIII; see above), the lack of longitudinal pleural ridges and the possession of fixed opisthosomal spines, distinguish it from the Paleolimulidae and the Moravuridae. P. longispinus Schram, 1979, from the Namurian Bear Gulch Limestone of Montana, has a rounded thoraceton, apparently supernumerary movable spines on the opisthosoma and it seemingly lacks free lobes. As Waterston (1985:26) pointed out, re-examination of this species is necessary in order to clarify its generic and familial taxonomic position.

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References


