

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 *Xaniopyramis* 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 *Neobelinuropsis* Eller, whilst the euproopoids originated independently later in the Carboniferous via a different bellinuroid line. *Rolfeia* is the oldest limuloid, but the slightly younger *Xaniopyramis* 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 *Xaniopyramis* lies between *Rolfeia* and the Permo-Carboniferous *Paleolimulus* Dunbar, of the Paleolimulidae Raymond. *Xaniopyramis* belongs to the Moravuridae Pfißyl; *Rolfeia*, previously provisionally considered to be a palcolimulid, is placed herein within the monotypic Rolfeidae fam. nov. □ *Chelicerata*, *Xiphosura*, *evolution*, *Carboniferous*.

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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 *Neobelinuropsis* 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 *Bellinuropsis* 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 Rolfeidae fam. nov. erected herein.

Terminology follows that of Siveter & Selden (1987) and references therein. Lankester (1904)

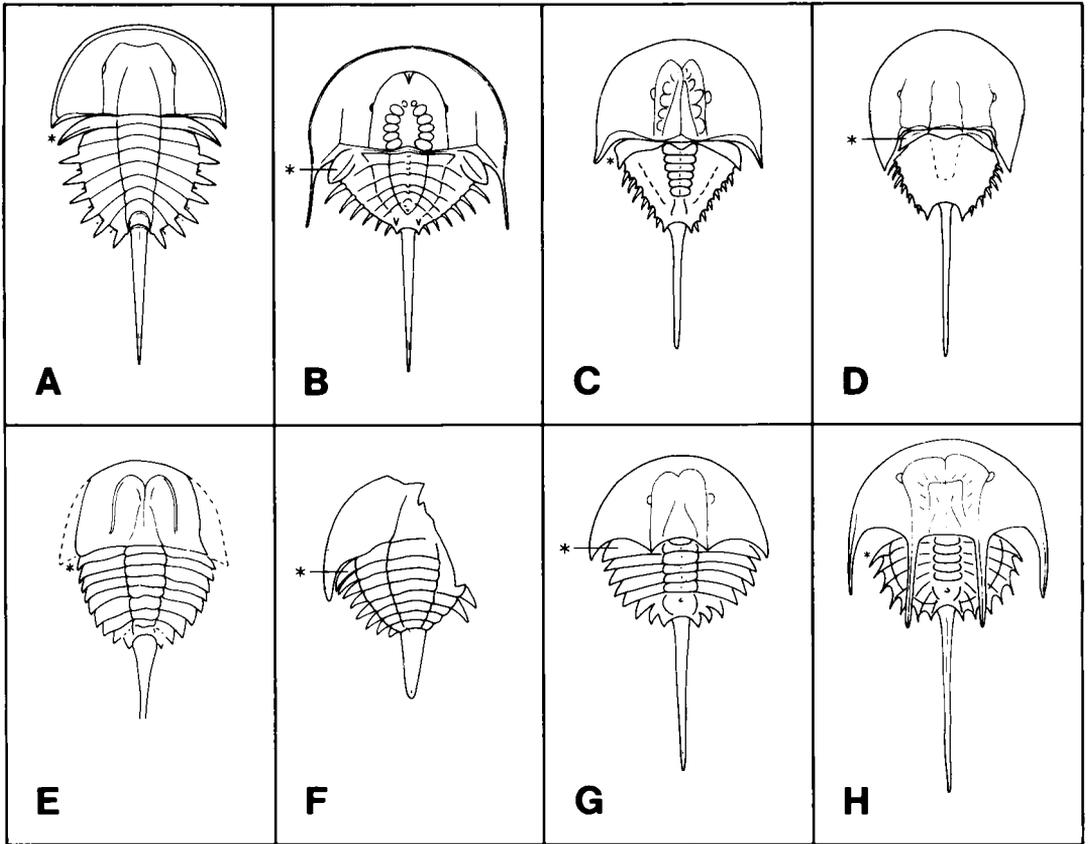


Fig. 1. Diagrammatic reconstruction of xiphosurid taxa representative of the Bellinuroidea, Euproopoidea and Limuloidea. All views are dorsal; all magnifications are approximate. Free lobes or segments expressing somite VIII are marked with an asterisk. □ A. *Rolfia fouldenensis* Waterston, 1985; Lower Carboniferous, Tournaisian; $\times 0.7$; based on Waterston 1985, Fig. 3. □ B. *Xaniopyramis linseyi* Siveter & Selden, 1987; Upper Carboniferous, basal Namurian; $\times 0.16$; based on Siveter & Selden 1987, Fig. 7. □ C. *Paleolimulus avitus* Dunbar, 1923; Lower Permian; $\times 2$; based on Fisher 1981, Fig. 3b and Dunbar 1923, Fig. 1. □ D. *Limulus polyphemus* (Linnaeus, 1858); Recent; $\times 0.06$; after Shuster 1979, Fig. 2. □ E. *Neobelinuroopsis rossicus* (Chernyshev, 1933); upper Devonian; $\times 0.6$; after Størmer 1952, Fig. 1h. □ F. *Bellinurus carteri* Eller, 1940; upper Devonian; $\times 0.75$; after Eller 1940, Fig. 1. □ G. *Bellinurus koenigianus* Woodward, 1872; Carboniferous; $\times 1$; after Fisher 1981, Fig. 3A. □ H. *Euproops danae* Meek & Worthen, 1865; Carboniferous; $\times 0.7$; after Fisher 1979, Fig. 1.

gave a useful account of the terminology of arthropod metamerism, to which reference should be made for further clarification. A somite, or metamer, is a fundamental division of the body, identified and numbered from the first postoral (chelicerar in chelicerates) somite, numbered I. 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 thoracetron (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 classifying 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 aglaspids 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 Størmer & 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 bellinuroids 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, Bellinuroidea and Euproopidea (suffix changed to conform to ICZN Recommendation 29A; spelling of *Bellinurus* and derivatives in agreement with Morris 1980). Fisher's

Table 1. Classification of the Xiphosura followed herein.

Class Xiphosura Latreille, 1802
Order Chasmataspida Caster & Brooks, 1956
Order Xiphosurida Latreille, 1802
Suborder Synziphosurina Packard, 1886
Suborder Limulina Richter & Richter, 1929
Infraorder Pseudoniscina Eldredge, 1974
Infraorder Limulicina Richter & Richter, 1929
Superfamily Bellinuroidea Zittel & Eastman, 1913
Superfamily Euproopidea Eller, 1938
Superfamily Limuloidea Zittel, 1885

(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 Chelicerata; 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 below 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 chilidia 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 chilidia 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 *Limuloides* 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) (Størmer 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 *Neobelinuroopsis 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 *Neobelinuroopsis*, 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 limulicines 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 opisthosomae of some bellinuroids, for example *B. koenigianus* (Bergström 1975:294). *Neobelinuroopsis* 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 *Neobelinuroopsis* 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 *Neobelinuroopsis* 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 $0_7 - 0_9$ 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 thoracetrone of eupropoids, 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 thoracetrone, 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 opis-

thosomae. Nevertheless, we agree with Raymond (1944) and Fisher (1981) that the thoracetrone 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 thoracetrone, 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 eupropoids 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 eupropoids, and that there was a momentous trend reversal to produce the limuloid condition.

An alternative hypothesis supporting a eupropoid-limuloid phylogenetic link is that the most anterior thoracetrone segment in eupropoids 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 thoracetrone which are also found in eupropoids. However, many other changes need to be involved in this proposed eupropoid-limuloid transformation: the loss of the eupropoid 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 eupropoids. Also, since eupropoids show 5 axial rings on the thoracetrone, 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 thoracetrone, yet *Xaniopyramis* shows at least 5 axial rings (Siveter & Selden 1987) and the other limuloids have more than 5 rings or apodeme pairs. Additionally, *Xaniopyramis* is at least as old as the oldest known euproopoid, so it could not be a transitional form between the later limuloids and any known euproopoid. *Rolfeia*, which is from the Tournaisian and hence slightly older than *Xaniopyramis*, shares the characters of fixed marginal opisthosomal spines and rounded opisthosomal 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 *Xaniopyramis* and the coeval *Moravurus* Přibyl, 1967 belong, was alone derived from the Euproopodea and is separate from the Limuloidea. This hypothesis would require the independent 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 limuloids 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 *Xaniopyramis* within the Limuloidea

Figure 2 shows our conclusions regarding the phylogenetic relationships of *Rolfeia*, *Xaniopyramis* 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 & Selden (1987), and those features which are of particular phylogenetic significance are detailed in the legend to Fig. 2. Each genus presents unique derived characters, such as the cheek ridge in

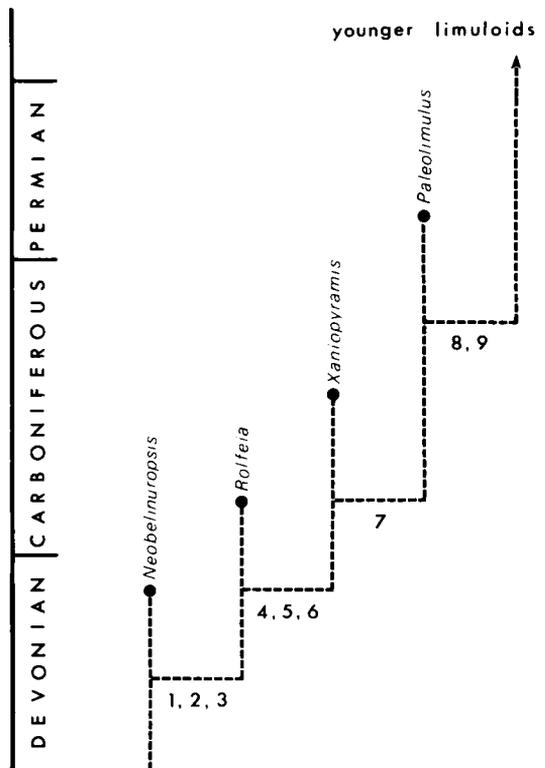


Fig. 2. Phylogeny of taxa discussed in the text; only the most completely known genera relevant to the analysis are included. The numbered homologous character pairs are detailed below:

Primitive state	Derived state
1. Free opisthosomal tergites	Thoracetrone
2. No movable opisthosomal spines	Movable opisthosomal spines
3. Pleura of somite VIII not developed into free lobe	Free lobe
4. Axial part of tergite of somite VIII fully expressed dorsally in opisthosoma	Axial part of tergite of somite VIII mostly encephalized
5. No longitudinal pleural ridges	Longitudinal pleural ridges
6. Fixed opisthosomal spines	No fixed opisthosomal spines
7. Pleural ribs	No pleural ribs
8. Ophthalmic ridges meet anteriorly	Ophthalmic ridges do not meet
9. Axial rings on thoracetrone	No axial rings on thoracetrone

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, Courcyeian 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 posteromarginal 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 thoracetrone, a feature lacking in the Paleolimulidae and all later limuloids. In the Rolfeiidae, the presence on the thoracetrone 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 thoracetrone, 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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