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Phylogeny of the basal swimming eurypterids (Chelicerata; Eurypterida; Eurypterina)

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SYNOPSIS The phylogeny of a broad selection of taxa at the base of the monophyletic Eurypterina (swimming eurypterids) is analysed. The results suggest that *Onychopterella* is the most basal of these forms, in agreement with its early stratigraphic occurrence. One step up from *Onychopterella* is a split between the superfamily Eurypteroidea and a clade comprising the four other clades in Eurypterina: Mixopteroidea, Waeringopteroidea, Adelophthalmoidea and Pterygotoidea. Eurypteroidea is composed of two major clades; the Eurypteridae consists of most species of *Eurypterus* and North American representatives of *Erieopterus*. The Dolichopteridae, numerically less species-rich, but more morphologically diverse, consists of *Dolichopterus*, *Ruedemannipterus*, *Buffalopterus*, *Strobilopterus*, *Syntomopterus* and most likely *'Eurypterus' minor*. Polyphyly of *Eurypterus* and paraphyly of *Onychopterella* differ from present taxonomic assignments. Not surprisingly, the fossil record of the clade is shown to be very poor as expected for animals lacking a mineralised exoskeleton. This is reflected in a low Relative Completeness Index (RCI) value of −41%.

KEY WORDS Eurypterida, swimming, relative completeness index, RCI, cladistics

Contents

Introduction

Eurypterids were a diverse group of Palaeozoic, primarily aquatic chelicerates ranging from the early Late Ordovician (Størmer 1951) to the Late Permian (Ponomarenko 1985). However, they attained their greatest diversity in the Silurian and Lower Devonian of Europe and North America, making Eurypterida the most diverse Palaeozoic chelicerate Order (J. A. Dunlop, pers. comm., 2005). The one major evolutionary step that appears to have brought about the greatest diversity in the Eurypterida was the broadening of the posterior 'leg' allowing its utilisation in swimming: 71% of eurypterid species were swimming forms (Tetlie 2004). According to all phylogenies of the Eurypterida (Plotnick 1983; Braddy

1996; Tetlie 2004), the swimming leg developed only once within the Order (although there is a considerable broadening in the posterior prosomal appendages also in the stylonurid genus *Alkenopterus* Størmer, 1974; see Poschmann & Tetlie 2004). The eurypterids with swimming legs are assigned to the monophyletic Suborder Eurypterina, but the boundaries of Eurypterina are not entirely clear. Most authors have used the broadening of the sixth prosomal appendage into a swimming leg as the criterion for inclusion, while Plotnick (1983) suggested using the presence of podomere 7a in this appendage to qualify for inclusion in Eurypterina. This latter definition would, in addition to all the swimming forms, add the stylonurids (i.e. eurypterids with the sixth prosomal appendage retained as walking legs) *Moselopterus* Størmer, 1974 and *Vinetopterus* Poschmann & Tetlie, 2004 in addition to some species of *Drepanopterus* (see Størmer 1974) to Eurypterina. The hypothesis that the walking appendages with a modified spine, VI-7a, represent secondarily modified or reduced swimming legs should be considered, but there is no physical evidence to suggest this is the case. The presence of three segments in the genital operculum in *Moselopterus* suggest this genus cannot have been derived from higher in the tree than the selection of taxa under consideration here, and this hypothesis is presently considered unlikely.

The phylogeny of most of the swimming forms is relatively well understood at all taxonomic levels (Tetlie 2004; Ciurca & Tetlie 2007), but one part of the tree that has, until now, been poorly characterised is the topology of the basal part of the clade. These taxa are united by a non-spiniferous fifth prosomal appendage (see Tollerton 1989: fig. 9), apparently a symplesiomorphy. Many of these basal taxa have been insufficiently described or have been known from very incomplete material. A series of recent descriptions have changed our views of many taxa (Tetlie 2006 [*Eurypterus*], Tetlie in press [*Strobilopterus* and '*Er. latus*'], and it is now possible to incorporate all this new information into a phylogeny of the basal part of Eurypterina. This part of the tree encompasses the important development of the origin of swimming that allowed the eurypterids to flourish in certain environmental settings and for a time permitted them to fully compete with cephalopods and the emerging gnathostomes as top predators (Dunlop *et al*. 2002). We take the opportunity to use our resulting tree to test the completeness of the fossil record of the eurypterid superfamily Eurypteroidea and some more basal taxa, using the methodology of the Relative Completeness Index (RCI) developed by Benton & Storrs (1994).

Material and methods

Characters were coded from eurypterid descriptions in the literature, both in press and in review, and from personal observations. To get a broad range of basal taxa and to be able to test monophyly of genera, we chose species, rather than genera, as operational units (for a complete list of species included and excluded, see Tables 1 and 2). The phylogenetic analysis was performed using PAUP* 4.0b10 PPC (Swofford 2002). All characters have equal weight and are treated as unordered unless stated otherwise. The Silurian *Parastylonurus ornatus* (Laurie, 1892) and the Devonian *Moselopterus ancylotelson* Størmer, 1974 were selected as outgroup taxa and represent presumed primitive (lacking podomere 7a) and derived (possessing podomere 7a) stylonurid eurypterids, respectively. To be able to test whether the basal swimming forms comprise a monophyletic basal clade or a paraphyletic assemblage, two taxa belonging to more derived clades of swimming forms were also included: the Ordovician *Orcanopterus manitoulinensis* Stott *et al*., 2005 represents a basal member of the Waeringopteroidea (Tetlie 2004), while the Silurian *Hughmilleria socialis* Sarle, 1903 is a basal member of the Pterygotoidea (Tetlie 2004).

Table 1 Taxon and character matrix.

Taxon	5	10	15	20	25	30	35	37
Parastylonurus ornatus	00?00	00000	000?0	0000?	?0000	03000	10000	02
Moselopterus ancylotelson	00?00	11101	00100	00110	00000	0100?	?2300	20
Buffalopterus pustulosus	10?11	11???	?1??1	?????	?????	020??	?0000	31
Dolichopterus jewetti	20?10	2?001	10111	12210	10111	00000	10000	00
Dolichopterus macrocheirus	20?10	2?001	10111	12210	10111	00000	10000	00
Erieopterus eriensis	11100	11100	?0??1	0?211	12000	01???	???00	00
Erieopterus microphthalmus	41100	11100	20121	02211	12000	01100	00000	00
Eurypterus dekayi	41001	10110	30121	02111	13110	010??	01110	00
Eurypterus hankeni	31001	1?100	301?1	02211	12110	120??	?1010	00
Eurypterus henningsmoeni	31001	10100	301?1	02211	13?10	120??	?1101	02
Eurypterus leopoldi	31001	1?10?	????1	?????	?2110	??1??	??010	13
Eurypterus minor	21010	1????	?????	?????	?????	010??	?00?0	00
Eurypterus pittsfordensis	31001	10100	30121	02111	12110	121?0	?1010	13
Eurypterus remipes	31001	10200	30121	02011	14110	12000	02201	01
Eurypterus tetragonophthalmus	31001	10100	30121	02211	13110	12000	01101	02
Onychopterella augusti	50???	?1?0?	?0??1	00110	11?00	?????	?13?0	00
Onychopterella kokomoensis	5????	?110?	?0??1	01110	11?00	??0??	?21?0	40
Ruedemannipterus stylonuroides	60?10	2????	?0??1	12110	0??10	000??	?????	??
Strobilopterus princetonii	10?10	3?00?	?11?1	0?010	11111	011??	10200	??
Syntomopterus richardsoni	10?10	31???	?????	?????	?????	?1???	?????	??
Hughmilleria socialis	70?0?	22300	40131	01111	14010	0301?	12300	00
Orcanopterus manitoulinensis	70?01	2?300	40131	0?011	11010	030??	?2300	40

Table 2 Excluded taxa that possibly belong to the basal part of Eurypterina, or have previously been assigned to genera belonging to this part of the tree.

Taxon	Reason for exclusion
Buffalopterus verrucosus	Not eurypterid (Tollerton 2004)
Dolichopterus antiquus	Not eurypterid (Tollerton 2004)
Dolichopterus asperatus	Problematic taxon (see the text)
Dolichopterus bulbosus	A hughmilleriid? (Tetlie 2004)
Dolichopterus gotlandicus	Poorly known
Dolichopterus (?) *herkimerensis*	Problematic taxon (O. E. Tetlie & V. P. Tollerton Jr, pers. obs., 2005)
Dolichopterus siluriceps	Probable synonym of *Dolichopterus macrocheirus*
Dolichopterus stormeri	Possibly part of *Erieopterus laticeps* (see the text)
Erieopterus brewsteri	Juvenile *Tarsopterella scotica* (Braddy 2000)
Erieopterus chadwicki	Not eurypterid (Tollerton 2004)
Erieopterus hudsonicus	Not eurypterid (Tollerton 2004)
Erieopterus hypsophthalmus	Poorly known and synonym of *Erieopterus eriensis*?
Erieopterus laticeps	Poorly known and problematic identity (see the text)
Erieopterus latus	Juvenile *Strobilopterus princetonii* (Tetlie in press)
Erieopterus limuloides	Relatively poorly known
Erieopterus phillipsensis	Possibly *Eurypterus* (V. P. Tollerton Jr, pers. comm., 2003)
Erieopterus statzi	Similarities to *Parahughmilleria* (Poschmann & Tetlie 2006)
Erieopterus turgidus	Possible synonym of *Erieopterus microphthalmus*?
Eurypterus cephalaspis	Poorly known
Eurypterus cyclophthalmus	Belongs to *Kiaeropterus* (Tetlie *et al.* 2007)
Eurypterus (?) *decipiens*	Not eurypterid (Tollerton 2004)
Eurypterus flintstonensis	Poorly known
Eurypterus laculatus	Poorly known
Eurypterus lacustris	Synonym of *Eurypterus remipes* (Cuggy 1994)
Eurypterus (?) *loi*	Poorly known
Eurypterus ornatus	Poorly known
Eurypterus (?) *pristinus*	Not eurypterid (Tollerton 2004)
Eurypterus quebecensis	Poorly known
Eurypterus serratus	Poorly known
Eurypterus (?) *styliformis*	Poorly known
Eurypterus (?) *trapezoides*	Synonym of *Adelophthalmus sievertsi* (Poschmann 2006)
Eurypterus (?) *yangi*	Poorly known
Megalograptus ohioensis	Hugely incompatible taxon (Tetlie 2004)
Onychopterella (?) *pumilus*	Possible *Drepanopterus* (Plotnick 1999)

Erieopterus (?) *laticeps* (Schmidt, 1883) from Estonia was considered for inclusion, although ultimately rejected due to being too poorly known. It also has been interpreted in two different ways. Following the interpretations of Schmidt (1883) and Holm (1898), the *Erieopterus*-like carapaces, a *Dolichopterus*-like swimming leg, a *Dolichopterus*-like genital operculum and a *Dolichopterus*-like metastoma, all belonged to *Er.* (?) *laticeps*. This view was contested by Caster & Kjellesvig-Waering (1956), who erected the new species *Dolichopterus størmeri* [sic] for the leg, operculum and metastoma. Although no more complete specimens are currently known than in 1898, the interpretation of Schmidt (1883) and Holm (1898) is favoured here, since this would provide a plausible taxon morphologically connecting the clade containing *Dolichopterus* Hall, 1859 and *Ruedemannipterus* Kjellesvig-Waering, 1966 with the clade containing the wide-carapaced swimming eurypterids (e.g. *Strobilopterus* Ruedemann, 1935 and *Buffalopterus* Kjellesvig-Waering & Heubusch, 1962). However, as suggested below, *Er.* (?) *laticeps* should probably not be referred to the genus *Erieopterus* Kjellesvig-Waering, 1958.

The taxa *D. asperatus* Kjellesvig-Waering, 1961 and *Syntomopterus richardsoni* Kjellesvig-Waering, 1961 are problematic. *Dolichopterus asperatus* was based on a carapace and distal parts of three swimming legs, with one of the paddles selected as the holotype. The carapace shape, eye shape and eye position of this carapace are all suggestive of a pterygotid, of which there are representatives in the fauna, rather than a *Dolichopterus*. The three paddles could all possibly be referred to *Syntomopterus richardsoni* Kjellesvig-Waering, 1961. Since *D. asperatus* was described prior to *Sy. richardsoni* in the same publication and the holotype of *D. asperatus* is one of the paddles rather than the possible pterygotid carapace, the name *asperatus* would have priority over *richardsoni*. Furthermore, Tetlie (in press) pointed out that the genus name *Syntomopterus* is preoccupied for a beetle and suggested a replacement name for the eurypterid genus. The coding of *Sy. richardsoni* is based on just the carapace, since the material from the Holland Quarry Shale has not yet been re-evaluated.

One taxon that has a non-spiniferous fifth appendage and is very well-known, but has been excluded from this phylogenetic analysis, is *Megalograptus ohioensis* Caster & Kjellesvig-Waering 1951. Megalograptids have traditionally been interpreted as close to the Mixopteroidea (e.g. Caster & Kjellesvig-Waering, 1964, Størmer 1974, Plotnick 1983).

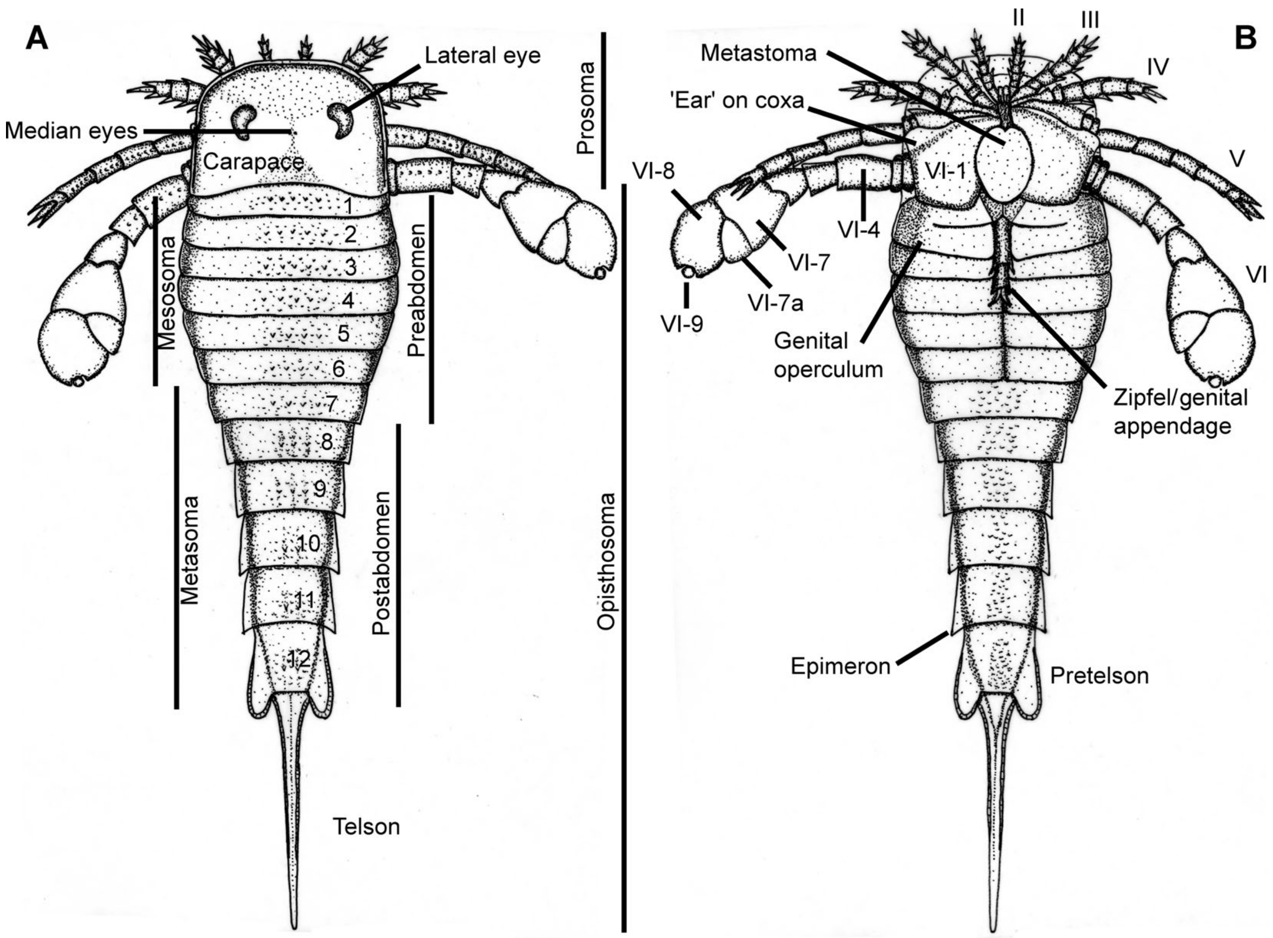

Figure 1 Typical eurypterid belonging to the Eurypteroidea, here represented by *Eurypterus henningsmoeni* (Tetlie, 2002), with major morphological features labelled. **A**, Dorsal side. **B**, Ventral side.

Tetlie (2004) found the taxon to be very problematic, sharing a number of potential synapomorphies with both the Eurypteroidea and the Mixopteroidea, in addition to having a huge number of apomorphies. Tetlie (2004) found *Megalograptus* to be basal in the Mixopteroidea after removing taxa with more than 66.6% missing data, while when removing incompatible characters from the dataset, *Megalograptus* changed position to within the clade analysed herein. Its antiquity (Late Ordovician) suggests it might be very basal, something hinted at by Caster & Kjellesvig-Waering (1951). Resolving the position of megalograptids is beyond the scope of this contribution, since it would necessitate including the entire Mixopteroidea. More material of megalograptids that might show whether or not *M. ohioensis* is an atypical megalograptid, or a redescription of *M. ohioensis* might help resolve some of the phylogenetic problems raised by this taxon.

Morphological terminology mainly follows Tollerton (1989). The term prosoma is used for the entire head-region, including the prosomal appendages, while the term carapace refers to the dorsal head-shield only. Individual prosomal appendages are numbered with Roman numerals from anterior to posterior. Individual podomeres in the prosomal appendages are numbered with Arabic numerals from proximal to distal, thus a combination of a Roman and Arabic numeral is used to identify an individual podomere, i.e. IV-6, denotes the sixth podomere of the fourth appendage. The morphological terms used in this contribution are illustrated in Fig. 1.

Results

Phylogeny

The results of the parsimony analysis of the data in Table 1, utilising the branch-and-bound search algorithm, produced eight most parsimonious trees with tree-lengths of 102 steps after removing uninformative characters (Consistency Index (CI) = 0.62, Retention Index (RI) = 0.75, Rescaled Index (RC) = 0.48). The strict and 50% majority rule consensus trees of these eight trees are seen in Figs 2A and 2B, respectively. The support values of a 10% deletion jackknife analysis with 1000 replicates is shown under the nodes in Fig. 2B. The strict consensus tree is superimposed onto a geological time scale in Fig. 3. The main areas of disagreement between the trees are (1) in the position of '*Eurypterus*' *minor*, which might be basal to a number of the clades identified, and (2) the internal resolution of the *Eu. remipes, Eu. tetragonophthalmus* and *Eu. henningsmoeni* clade, but the sister-group relationship between *Eu. tetragonophthalmus* and *Eu. henningsmoeni* is considered fully resolved by Tetlie (2006).

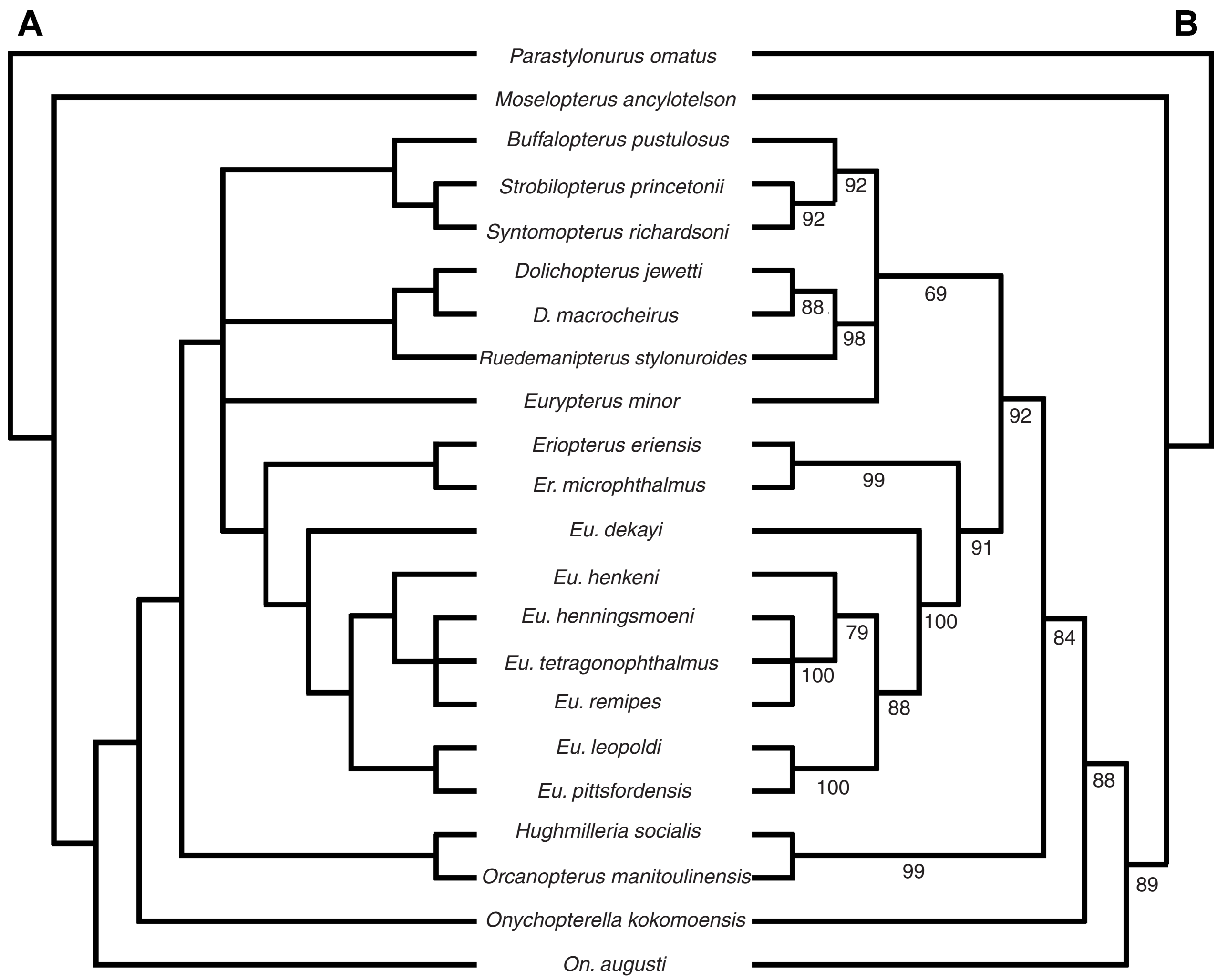

Figure 2 Consensus trees of the 8 most parsimonious trees found when analysing the data from Table 1. **A,** Strict consensus tree. **B,** Majority rule consensus tree with the jackknife support (see the text) values indicated under the nodes.

Relative Completeness Index

The Relative Completeness Index (RCI) is a measure of the relative completeness of the fossil record that uses phylogenetic information to estimate the size of gaps (Benton & Storrs 1994). The RCI is calculated from phylogenetic trees with plotted range data, in our case Fig. 3, by comparing the amount of gap in the fossil record compared to the represented record (Benton & Storrs 1994) using the following formula:

$$\mathrm{RCI} = \left(1 - \frac{\sum(MIG)}{\sum(SRL)}\right) \times 100\%$$

Where *MIG* is the Minimum Implied Gap and *SRL* is the Simple Range Length for each taxon (Benton & Storrs 1994). Values of RCI can range from infinite negative values, where the sum of the gaps exceeds the stratigraphic range, to 100% where there are no gaps in the stratigraphic record (Benton & Storrs 1994). The RCI result of –41% suggests that this clade of eurypterids has a poor fossil record. Benton & Hitchin (1996) considered any RCI < +50% to be poor (see discussion below).

Discussion

By excluding the poorly known taxa, which may or may not belong to this part of the eurypterid tree (Table 2), a relatively robust result was produced. Figure 3 shows that the Eurypteroidea ranged from the Late Ordovician to the Middle Devonian, when this group of eurypterids went extinct. There is generally a good correlation between the order of first occurrences in the fossil record and inferred phylogenetic relationships. This correlation was tested by calculating the Gap Excess Ratio (GER) of Wills (1999), which ranges from 0 (worst fit) to 1 (best fit). The GER calculated for the phylogenetic tree in Fig. 3 was 0.72, which is actually better than for any of the examples calculated by Wills (1999).

The analysis suggests that *Onychopterella augusti* Braddy *et al*. (1995) is the most primitive swimming eurypterid, a result that agrees with the early (Late Ordovician) occurrence of this taxon. The evidence also suggests that *Onychopterella* is not a monophyletic genus, based mainly on the more stylonurid-like dimensions of podomeres VI-4 and VI-5 (character 17) in *On. augusti* compared to *On. kokomoensis*. Adding the two more derived swimming forms demonstrated that the basal forms are not monophyletic,

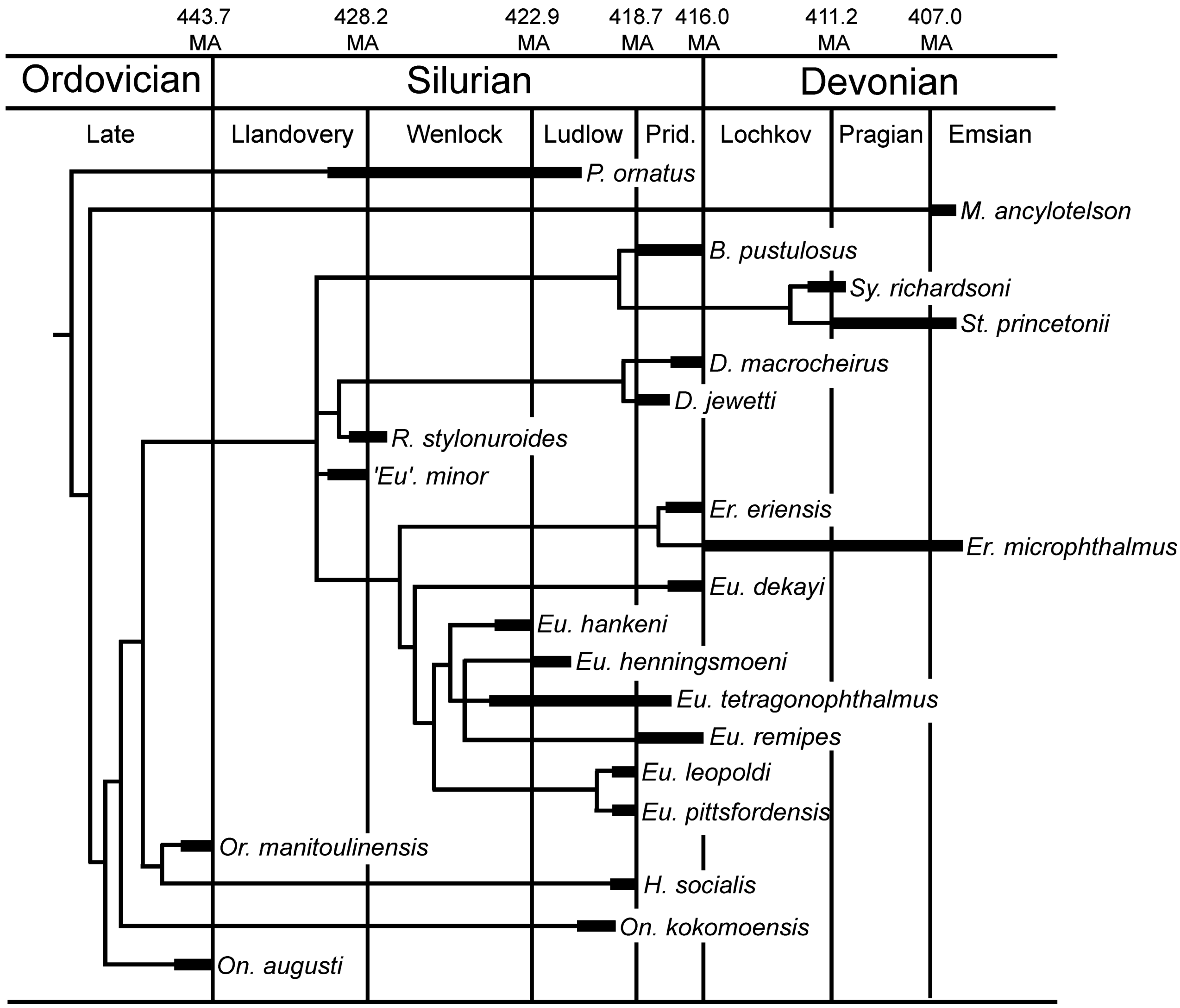

Figure 3 Strict consensus tree superimposed onto a Late Ordovician to Middle Devonian geological time scale. Prid. = Přídolí; B, *Boffalopterus*; D, *Dolichopterus*; Er, *Erieopterus*; Eu, *Eurypterus*; H, *Hughmilleria*; M, *Moselopterus*; On, *Onychopterella*; Or, *Orcanopterus*; P, *Parastylonurus*; R, *Ruedemannipterus*; St, *Strobilopterus*; Sy, *Syntomopterus*.

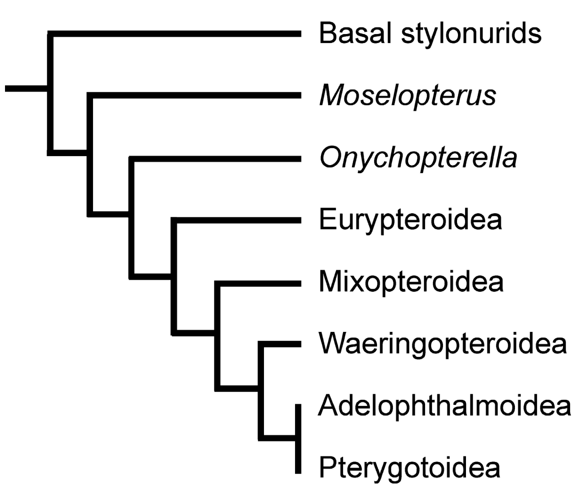

Figure 4 Simplified cladogram showing the relationships between the basal stylonurids, *Moselopterus*, *Onychopterella* and the five major superfamilies in Eurypterina (compiled from Tetlie 2004 and the results found herein).

since the two species of *Onychopterella* are basal to the split between the remaining 'primitive' forms and the more derived forms represented by *Hughmilleria* and *Orcanopterus*. For a summary of the phylogenetic relationships of the superfamilies in Eurypterina, see Fig. 4. However, the remaining 'primitive' swimming forms (to the exclusion of *Onychopterella*) comprise a monophyletic assemblage that could be treated as the superfamily Eurypteroidea, which is defined by a combination of these characters: non-spiniferous appendage V (symplesiomorphy), a relatively long podomere VI-4 (possible synapomorphy, but also present in *Megalograptus*) and a serrated podomere VI-8 (synapomorphy). The Eurypteroidea clade is divisible into two smaller clades. The best supported of these consists of some of the North American representatives of the genus *Erieopterus* and the genus *Eurypterus* (except *Eu. minor*) and is, in most respects, similar to the analysis of Tetlie (2006). This clade is here interpreted as the Family Eurypteridae Burmeister, 1843 and is characterised by separate furca in the genital appendages, a wide VI-7a and a relatively short VI-9. The second clade is more interesting as it accommodates a number of poorly known and previously enigmatic eurypterids, including *Buffalopterus*, *Strobilopterus*, *Syntomopterus*, *Dolichopterus* and *Ruedemannipterus*. That clade is here interpreted as the Family Dolichopteridae Kjellesvig-Waering & Størmer, 1952 and is characterised by a large palpebral lobe, relatively large VI-9, a narrow VI-7a and a long and narrow metastoma, although the metastomal shape is variable among the few taxa where it is known. '*Eurypterus*' *minor* also appears to belong to this clade based on its enlarged palpebral lobes, but evidence is not entirely conclusive, as this species is relatively poorly known (Laurie 1898; Tetlie 2006). This clade can be further subdivided. One clade consists of *Dolichopterus* and *Ruedemannipterus* and is characterised by a very elongate carapace with eyes positioned anteriorly, a fixed angle between VI-3 and VI-4 that is smaller than 180° and by a much enlarged VI-9. The second clade consists of *Buffalopterus*, *Strobilopterus* and *Syntomopterus* and is recognised from its extremely wide carapace with small, centrally positioned eyes and very short swimming legs.

The derived position of the genus *Dolichopterus* is somewhat surprising. The 'stylonuroid' aspect of this form has long been recognised (e.g. Størmer 1955), especially regarding certain aspects of the swimming legs, eyes and metastoma. Having said that, there are no unequivocal apomorphies suggesting a close relationship between the stylonurids and *Dolichopterus*. That *Onychopterella* was closer than *Dolichopterus* to the stylonurids was already pointed out in the 'phylogeny' of Clarke & Ruedemann (1912: 124–125). Considering the more spine-like VI-9 in most stylonurid eurypterids, the swimming leg of *Onychopterella*, with a small spiniferous VI-9, is a better model for a primitive swimming leg compared to the leg of *Dolichopterus*, with VI-9 developed into a large plate (see Fig. 5). Secondly, it is also apparent from the evidence provided by *Ruedemannipterus* that VI-9 was much smaller further down the clade than in *Dolichopterus*. Thirdly, the extremely narrow swimming legs in *Onychopterella* are hardly much more expanded than in many stylonurids, which also suggests that this is truly the primitive swimming leg. It is therefore very likely that the enlarged VI-9 is a synapomorphy of *Dolichopterus* rather than a plesiomorphy within Eurypterina.

The RCI value we found for our cladogram (−41%) is much lower than the average for fossil echinoderms (mean = 62.3%), fish (mean = 69.4%) and continental tetrapods (mean = 49.8%) (Benton & Hitchin 1996). This low RCI value is not unexpected for a number of reasons. Firstly, the numbers presented by Benton & Hitchin (1996) are much higher since the best results will be produced when using high-level category groups (Benton & Storrs 1994), as in the examples above. This is due to the fact that species and genera have much shorter durations than families or orders and thus have shorter Simple Range Lengths (SRLs) (Benton & Storrs 1994). Since the SRLs are so much shorter for species, they can easily overwhelm the MIGs even if the fossil record for a group is well-known. Due to this difference it is difficult to compare our results directly with those of Benton & Hitchin (1996). Similar examples can be seen with the poor RCI score for coelacanth cladograms (Forey 1988; Hitchin & Benton 1997) where the short stratigraphic ranges of the genera caused very short SRLs and thus a negative RCI. More similar results were produced for fossil Scleractinia corals (Johnson 1998) with a RCI of −63.2% (Benton *et al*. 2000), and eusuchians (Brochu 1997) with RCI values ranging from –71.3% to –85.8% (Benton *et al*. 2000). However, other cases using species had very different results showing that it is possible for species data to produce high RCI values, for example Shaffer *et al*. (1997) produced a number of cladograms for species of fossil turtles with results varying from 49.73% to 79.29% (Benton *et al*. 2000).

Benton *et al*. (1999) discuss other scenarios that would cause low RCI scores. In addition to the poor quality of the fossil record, these include poor quality cladograms, stratigraphic problems and sampling density. Any of these could be, at least partially, responsible for the low RCI determined in this study. The most likely reason for the low RCI of our eurypterid cladogram is that eurypterids lack a mineralised cuticle and, therefore, have a low preservation potential. Plotnick (1986) examined the preservation potential of non-mineralised shrimps in both field and laboratory experiments. In all cases, he found that the arthropod cuticle is quickly broken down by chitinoclastic micro-organisms and thus not easily preserved. The main conclusion was that remains of arthropods with non-mineralised cuticles would be generally restricted to settings with little or no bioturbation (Plotnick 1986). The same would be expected to be true for eurypterid remains. According to Plotnick (1999), most of the major eurypterid localities from the Silurian are in finely laminated beds that show little or no evidence of bioturbation. This would imply that there is a reasonable likelihood that most eurypterids would not have been preserved and that this seriously limits the quality of the eurypterid fossil record. However, it should be noted that the Lower Devonian eurypterid localities in Germany often do not show laminated beds and these beds show evidence of bioturbation (M. Poschmann, pers. comm., 2006). In the German Lower Devonian and some Scottish Silurian localities, arthropods are preserved because of decomposition of plant material, which reduces the abundance of oxygen in the sediments.

It should be noted that this is the first time the RCI has been calculated for a group of eurypterids and the results might not be typical of Eurypterida as a whole. It is possible that there are clades that would have higher and lower RCI values. The relatively short-lasting Pterygotoidea (~40 million years), with the largest number of species of any eurypterid superfamily, should have a better RCI if a reasonable phylogeny incorporating many members of this taxon could be found. At the other end of the scale, the long-lasting Adelophthalmoidea (~155 million years), with some large gaps in their fossil record, would probably have a poorer RCI. It is therefore possible that the Eurypteroidea has a RCI value typical of the eurypterids, but until more RCI values are calculated for eurypterid clades, this remains to be seen.

Systematic palaeontology

Phylum **CHELICERATA** Heymons, 1901

Order **EURYPTERIDA** Burmeister, 1843

Suborder **EURYPTERINA** Burmeister, 1843

Diagnosis. Eurypterids with a flattened, modified spine, on the postero-distal corner of podomere VI-7 (modified from Plotnick 1983).

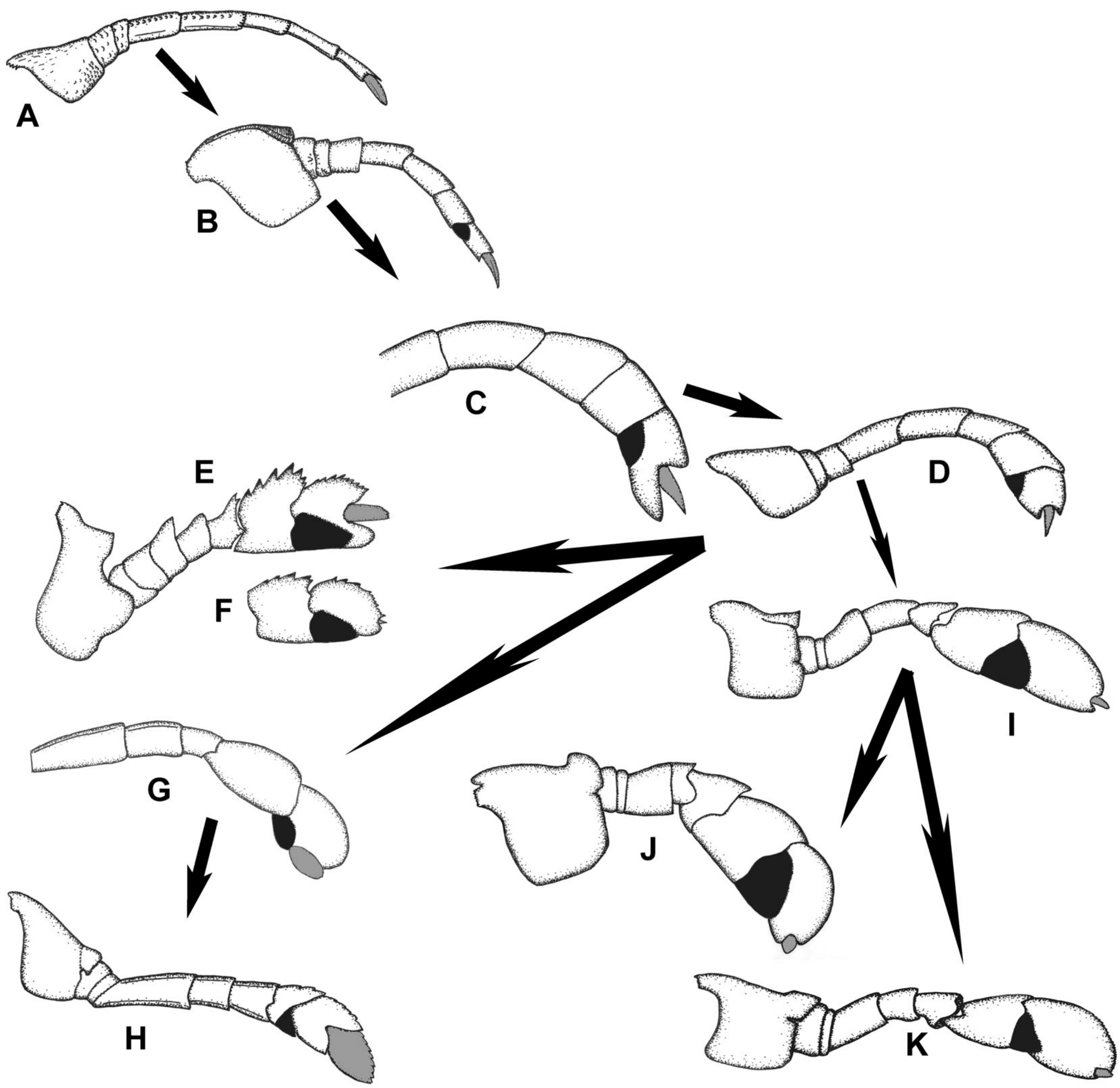

Figure 5 Dendrogram illustrating the development of the swimming leg from a stylonurid walking leg. Podomere 7a is shown in black and podomere 9 in grey. **A**, *Parastylonurus ornatus*; **B**, *Moselopterus ancylotelson*; **C**, *Onychopterella augusti*; **D**, *Onychopterella kokomoensis*; **E**, *Strobilopterus princetonii* (adult); **F**, *Strobilopterus princetonii* (juvenile); **G**, *Ruedemannipterus stylonuroides*; **H**, *Dolichopterus jewetti*; **I**, *Erieopterus microphthalmus*; **J**, *Eurypterus pittsfordensis*; **K**, *Eurypterus tetragonophthalmus*. Redrawn from various sources. Not to scale.

Remarks. Although this definition of Eurypterina is not the one traditionally used, it is preferred here because it is more clear-cut than a definition based on whether the sixth prosomal appendage is a swimming leg or not. The main problem with the old definition is where to draw the line between a walking leg and a swimming leg. Most would agree that the leg of *Moselopterus ancylotelson* (Fig. 5B) is a walking leg and that of *Onychopterella kokomoensis* (Fig. 5D) is a swimming leg. But is the sixth appendage of *O. augusti* (Fig. 5C) a walking leg or a swimming leg?

Superfamily **EURYPTEROIDEA** Burmeister, 1843

Content. *Eurypterus* DeKay, 1825; *Erieopterus* Kjellesvig-Waering, 1958; *Dolichopterus* Hall, 1859; *Ruedemannipterus* Kjellesvig-Waering, 1966; *Strobilopterus* Ruedemann, 1935; *Buffalopterus* Kjellesvig-Waering & Heubusch, 1962; *Syntomopterus* Kjellesvig-Waering, 1961.

Diagnosis. Eurypterina with three segments in the genital operculum; non-spiniferous V; long VI-4 (but slightly reduced in *Strobilopterus*); distal joint of VI-6 modified for rotation of paddle; serrate VI-8; lacking cercal blades.

Occurrence. Laurentia and Baltica (questionable occurrence in South China). Llandovery (Early Silurian) to Eifel (Middle Devonian).

Remarks. The Superfamily does not have any unique synapomorphy and a suite of characters is necessary, especially to separate it from *Onychopterella* and *Megalograptus*. None of these two have the distal joint of VI-6 shaped like the number '3', allowing the paddle to be used for rowing (Selden 1981).

Family **EURYPTERIDAE** Burmeister, 1843

CONTENT. *Eurypterus* Dekay, 1825; *Erieopterus* Kjellesvig-Waering, 1958.

DIAGNOSIS. Metastoma oval (except in *E. remipes*); 'ear' on coxa VI subquadrate; VI-7a wide; VI-9 relatively small; furca on genital appendage not fused.

OCCURRENCE. Laurentia and Baltica (questionable occurrence in South China). Wenlock (Middle Silurian) to Lochkov (Lower Devonian).

REMARKS. The Eurypteridae is, in most respects, more derived morphologically than the Dolichopteridae. *Eurypterus* and *Erieopterus* have a wide VI-7a and, in contrast to the Dolichopteridae, there is a trend towards a smaller VI-9 in the more derived taxa. There is also a general trend towards decreasing the sizes of the epimera. These developments might be indications that while the Eurypteridae preferred a nektonic mode of life, the Dolichopteridae, at least the clade including *Buffalopterus*, *Strobilopterus* and *Syntomopterus*, pursued a benthic lifestyle.

Family **DOLICHOPTERIDAE** Kjellesvig-Waering & Størmer, 1952

CONTENT. *Dolichopterus* Hall, 1859; *Ruedemannipterus* Kjellesvig-Waering, 1966; *Strobilopterus* Ruedemann, 1935; *Buffalopterus* Kjellesvig-Waering & Heubusch, 1962; *Syntomopterus* Kjellesvig-Waering, 1961.

DIAGNOSIS. Palpebral lobe large; metastoma long and narrow; VI-7a narrow; VI-9 relatively large; large epimera on metasoma.

OCCURRENCE. Laurentia and Baltica. Llandovery (Early Silurian) to Eifel (Middle Devonian).

REMARKS. These eurypterids retain the primitive condition of VI-7a as a relatively narrow plate, but the relatively large VI-9 might be homoplastic between *Ruedemannipterus*–*Dolichopterus* and *Strobilopterus* since the juvenile *Strobilopterus* have a simple spine (Fig. 5F). *Eurypterus minor* might belong here, contrary to the conclusions of Tetlie (2006), but since there is considerable doubt about this poorly known taxon, we leave the taxonomy unchanged.

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Appendix: Characters and states

Carapace and metastoma characters

1. *Carapace shape (0 = horseshoe; 1 = semicircular; 2 = quadrate; 3 = trapezoidal; 4 = wide-rectangular; 5 = subquadrate; 6 = campanulate; 7 = parabolic)*. See Tollerton (1989) for illustrations.
2. *Genal facets (0 = absent; 1 = present)*. Genal facets are absent in *Dolichopterus* and present in most species of *Eurypterus* and *Erieopterus*.
3. *Angle of genal facets (0 = low angle; 1 = high angle)*. The angle is low in *Eurypterus* and high in those species of *Erieopterus* that possess them.
4. *Size of palpebral lobe (0 = small; 1 = large)*. Large in *Dolichopterus, Ruedemannipterus, Strobilopterus, Syntomopterus* and *Er. minor*.
5. *Eye shape (0 = crescentric; 1 = reniform)*. *Dolichopterus, Erieopterus, Ruedemannipterus, Syntomopterus, Strobilopterus* and *Er. minor* have crescentric eyes, the rest have reniform eyes.
6. *Eye position (0 = centrilateral; 1 = centrimesial; 2 = antelateral; 3 = central)*. See Tollerton (1989).
7. *Ventral plate type (0 =* Eurypterus *type; 1 =* Erieopterus *type; 2 =* Hughmilleria *type)*. See Tollerton (1989).
8. *Metastoma shape (0 = lyrate and elongate petaloid; 1 = oval, rhombiovate and vase-shaped; 2 = elliptical; 3 = petaloid A)*. See Tollerton (1989).

Prosomal appendage characters

9. *Number of spines per podomere of prosomal appendages II–IV (0 = two spines; 1 = four to six spines)*. *Eurypterus dekayi* uniquely has 4–6 spines on each podomere of appendages II–IV.
10. *'Podomere' 7a on V (0 = absent; 1 = present)*. A spine modified into a 'podomere' 7a is present in *Dolichopterus* and *Moselopterus*, while unknown in *Ruedemannipterus*. Absent in all others where appendage V is known.
11. *Nature of appendage V (0 = non-spiniferous, stylonurid type; 1 = non-spiniferous,* Dolichopterus *type; 2 = non-spiniferous,* Erieopterus *type; 3 = non-spiniferous* Eurypterus *type; 4 = spiniferous,* Hughmilleria *type)*.

These leg types are figured in Tollerton (1989) with the exception of *Erieopterus* type, which is intermediate in morphology between the *Dolichopterus* and *Eurypterus* types.

12. *Length of appendage VI (0 = long; 1 = short (barely projecting from beneath carapace))*. Only *Strobilopterus* and *Buffalopterus* have a very short swimming leg.
13. *'Ear' on coxa VI (Størmer 1974). (0 = absent; 1 = present)*. Present in all taxa except *P. ornatus*.
14. *Shape of 'ear' on coxa VI (0 = elongated triangular; 1 = rectangular; 2 = subquadrate; 3 = semicircular)*.
15. *Appendage VI developed into swimming paddle (0 = absent; 1 = present)*. Present in all taxa where known except *P. ornatus* and *M. ancylotelson*.
16. *Angle between VI-3 and VI-4 (0 = 180°; 1 ≠ 180°)*. In most eurypterids, this angle is 180° (i.e. the leg is straight), but in *Dolichopterus* and *Ruedemannipterus* the anterior angle is always smaller and the posterior angle is always larger than 180°. It therefore appears that this podomere joint was more or less immobile.
17. *Length of podomeres VI-4 and VI-5 (0 = VI-5 > VI-4; 1 = VI-5 ≈ VI-4; 2 = VI-4 > VI-5)*. Most stylonurids including *P. ornatus* and *M. ancylotelson*, but also *On. augusti*, have an appendage VI where podomere 5 is the longest. In *On. kokomoensis*, the two podomeres are the same length, while the other taxa where this character is known have an appendage where podomere 4 is longer than 5.
18. *Morphology of VI-7 and VI-8 (0 = 8 < 7; 1 = 8 ≈ 7; 2 = 8 > 7 (from Størmer 1973))*. The taxa with a distal paddle (2) are *Dolichopterus*, *Erieopterus*, *Eu. hankeni*, *Eu. tetragonophthalmus* and *Eu. henningsmoeni*. *Eurypterus remipes*, *Strobilopterus* and *Orcanopterus* have a proximal paddle (0). The paddles of *Hughmilleria*, *Onychopterella*, *Ruedemannipterus*, *Eu. dekayi* and *Eu. pittsfordensis* have paddles where the two podomeres are approximately the same size.
19. *Podomere VI-7a (0 = absent; 1 = present)*. Present in all taxa where known except *P. ornatus*, possibly a suitable synapomorphy of Eurypterina, i.e. *Moselopterus* and *Vinetopterus* would be included in Eurypterina (*sensu* Plotnick 1983).
20. *Width of VI-7a (0 = narrow (less than 50% of width of VI-7); 1 = wide (more than 50%))*. This is narrow in *Moselopterus*, *Ruedemannipterus*, *Onychopterella*, *Strobilopterus* and *Dolichopterus*.
21. *Shape of VI-7a (0 = oval; 1 = triangular)*. The small podomere 7a is oval in *Moselopterus* and *Ruedemannipterus* and triangular in all other taxa where known.
22. *Length of VI-9 (as ratio of VI-8) (0 = very large (100% of VI-8 length); 1 = large (>50% of VI-8 length); 2 = medium (22–20% of VI-8 length); 3 = small (14–10% of VI-8 length); 4 = tiny (6–7% of VI-8 length))*. Ordered. VI-9 is very large in *Dolichopterus*, *Parastylonurus* and *Moselopterus*, large in *Onychopterella*, *Strobilopterus* and *Orcanopterus*, medium in *Eu. hankeni*, *Eu. leopoldi*, *Eu. pittsfordensis* and *Erieopterus*, small in *Eu. dekayi*, *Eu. tetragonophthalmus* and *Eu. henningsmoeni* and tiny in *Eu. remipes* and *H. socialis*.
23. *Serrated VI-8 (0 = absent; 1 = present)*. Some taxa have a serrated VI-8, especially developed in *Strobilopterus* and *Dolichopterus*, but it is also notable in some species of *Eurypterus*.
24. *Shape of podomere VI-9 (0 = spinose; 1 = triangular, pentagonal or oval)*. Spinose in *Parastylonurus, Moselopterus, Onychopterella* and *Erieopterus*.
25. *Serrated VI-9 (0 = absent; 1 = present)*. The only taxa known to have a serrated podomere VI-9 are *Dolichopterus* and *Strobilopterus*, but the condition is unknown in *Ruedemannipterus*.

Opisthosoma and telson characters

26. *Ornament of large scales in longitudinal rows on opisthosoma (0 = absent; 1 = present)*. Most species of *Eurypterus* have such scales, while these are not present in *Er. minor* and *Eu. dekayi*, or any other taxon. The large scales on *Buffalopterus* are arranged in a different manner and are not considered homologous.
27. *Cuticular sculpture (0 = no sculpture; 1 = pustules; 2 = pustules and scales; 3 = scales)*. The sculpture is a confusing and clearly somewhat homoplastic character, but it is included since it clearly also adds some phylogenetic information.
28. *Anterior tergite (0 = fully developed; 1 = reduced)*. The anterior tergite is fully developed in all taxa where known except *Eu. pittsfordensis*, *Eu. leopoldi*, *Strobilopterus*, *Er. microphthalmus* and *Er. eriensis*, where the width is not complete and the carapace therefore articulates towards the second tergite in the three former species, while the two latter have just a narrow junction between carapace and opisthosoma. For illustrations of this character, see Sarle (1903: pl. 17, fig. 1) and Jones & Kjellesvig-Waering (1985: figs 3.1, 3.2 and 3.4).
29. *Segments in genital operculum (0 = three segments; 1 = two segments)*.
30. *Segments in genital Zipfel (= appendage) type A (0 = three segments; 1 = two segments; 2 = undivided)*. Ordered. Most taxa have three-segmented genital Zipfel, but *Strobilopterus* has an undivided Zipfel.
31. *Fusion of furca in genital zipfel type A (0 = absent; 1 = present)*. *Erieopterus* and *Eurypterus* have free furca, while in *Dolichopterus*, *Strobilopterus* and *Hughmilleria*, these are fused.
32. *Metasoma second order differentiation (0 = large, angular; 1 = small, angular; 2 = very small or absent)*. Large angular epimera on the metasoma are present in *Parastylonurus*, *Buffalopterus*, *Erieopterus*, *Dolichopterus*, *Strobilopterus* and *Er. minor*, while small epimera are present in *On. augusti*, *Eu. hankeni*, *Eu. henningsmoeni*, *Eu. pittsfordensis*, *Eu. tetragonophthalmus* and *Eu. dekayi*. They are very small to not present in *Er. remipes*, *Hughmilleria*, *Orcanopterus* and *Moselopterus*.
33. *Epimera on pretelson (0 = long or medium, angular; 1 = long or medium, rounded; 2 = short, angular; 3 = none)*. The epimera on the pretelson are long and angular in *Parastylonurus*, *Buffalopterus*, *Dolichopterus*, *Erieopterus* and several *Eurypterus* species, long and rounded in *Eu. tetragonophthalmus*, *Eu. henningsmoeni*, *Eu. dekayi* and *On. kokomoensis*, short and angular in *Eu. remipes* and *Strobilopterus* and non-existent in *On. augusti*, *Hughmilleria* and *Orcanopterus*.
34. *Angular striated ornament of pretelson (0 = absent; 1 = present)*. *Eurypterus hankeni*, *Eu. dekayi*, *Eu.*

pittsfordensis and *Eu. leopoldi* have an ornament of angular striations.

35. *Imbricate scale ornament of pretelson (0 = absent; 1 = present). Eurypterus tetragonophthalmus*, *Eu. henningsmoeni* and *Eu. remipes* have an ornament of imbricate scales on the pretelson, while these are not present in other taxa.
36. *Telson shape (0 = lanceolate; 1 = styliform; 2 = short curved styliform; 3 = circular; 4 = clavate)*. The telson shape is lanceolate (Tollerton 1989: fig. 15-1) in most taxa, but more styliform (Tollerton 1989: fig. 15-2) in *Eu. leopoldi* and *Eu. pittsfordensis*, short curved styliform in *Moselopterus*, circular in *Buffalopterus* and clavate in *On. kokomoensis* and *Orcanopterus*.
37. *Telson margin (0 = smooth; 1 = serrated; 2 = imbricate scales; 3 = striated)*. Most taxa do not have any marginal ornament of the telson, but *Buffalopterus* has a serrated telson, *Parastylonurus*, *Eu. henningsmoeni* and *Eu. tetragonophthalmus* have an ornament of imbricate scales on the telson. Striated marginal ornament is present on the telson of *Eu. pittsfordensis*, *Eu. leopoldi* and *Moselopterus*, as indicated by Størmer (1974).