

Distribution and dispersal history of Eurypterida (Chelicerata)

O. Erik Tetlie *

Department of Geology and Geophysics, Yale University, P.O. Box 208109, CT 06520-8109, USA

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Abstract

The distribution and dispersal histories of Eurypterida are examined in a phylogenetic and palaeogeographic context. It is suggested that all the eurypterid clades originated and had most of their evolutionary history on the palaeocontinents of Laurentia, Baltica, Avalonia, the Rheno–Hercynian Terrane and some presence in Siberia. The Siluro–Devonian Stylonurina and the eurypterine superfamilies Eurypteroidea and Waeringopteroidea are confined in their entirety to these continents. The Late Palaeozoic records of Adelophthalmoidea and Hibbertopteroidea in China, South America and Africa can be explained by ‘rafting’ on the continental plates that amalgamated into the supercontinent Pangaea. However, two clades have distributions that suggest abilities to cross open stretches of ocean; the Silurian and Devonian pterygotoids and some Devonian adelophthalmoids. However, one Silurian mixopteroid and the basal swimming form *Onychopterella* outside the ‘core-area’ suggest the dispersal patterns are more complicated. The pterygotoids might be the only clade whose members frequently undertook oceanic excursions. Since almost all eurypterid evolution took place in Laurentia, Baltica and Avalonia (and some in the Early Devonian of the Rheno–Hercynian Terrane) prior to the Carboniferous, it is unlikely that many taxonomically rich pre-Carboniferous eurypterid faunas will be encountered outside of these palaeocontinents.

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1. Introduction

The eurypterids, commonly referred to as sea scorpions, were the most diverse chelicerate Order in the Palaeozoic, with around 200 valid species. There are around 235 species listed in [Tables 1–7](#), but not all of these are based on diagnostic material (pers. obs.), and revisions are still ongoing. The eurypterids were primarily aquatic animals, but a potential dual respiratory system has been described that might have made it possible for them to undertake short terrestrial excursions ([Selden, 1985](#);

[Manning and Dunlop, 1995](#); [Braddy, 2001](#)). Amongst the eurypterids, we find the largest known arthropods; the pterygotids from the Early Devonian of Germany ([Poschmann pers. comm., 2002](#)), with estimated total lengths (excluding their long chelicerae) of 2.5 m. However, even many of the smaller forms might have been formidable predators in their time, and sizes approaching 100 cm were common in most clades. The earliest known eurypterid is from the early Late Ordovician (Sandbian — ca 460 million years ago (Ma)) of Wales (*Brachyopterus stubblefieldi* [Størmer, 1951](#)) and the last record is from the Late Permian (250 Ma) of Russia (*Hibbertopterus permianus* [Ponomarenko, 1985](#)), giving a total range of approximately

* Tel.: +1 203 432 8744; fax: +1 203 432 3134.

E-mail address: erik.tetlie@yale.edu.

Table 1
Stylonurid taxa and their distribution

Taxon	Age	Distribution	Group
<i>Alkenopterus brevitelson</i>	Early Emsian	Alken, Germany	Rhenopterid
<i>Alkenopterus burglahrensis</i>	L. Pragian or E. Emsian	Westerwald, Germany	Rhenopterid
<i>Brachyopterella pentagonalis</i>	Late Wenlock	Ringerike, Norway	Laurieipterid
<i>Brachyopterella ritchiei</i>	Early Wenlock	Ayrshire, Scotland	Laurieipterid?
<i>Brachyopterus stubblefieldi</i>	Sandbian	Montgomeryshire, Wales	Primitive stylonurid?
<i>Campylocephalus oculatus</i>	Guadalupian?	Dourasovo?, Russia	Hibbertopterid
<i>Campylocephalus permianus</i>	Late Permian	Komi ASSR, Russia	Hibbertopterid
<i>Campylocephalus (?) salmi</i>	Visean	Czech Republic	Hibbertopterid
<i>Clarkeipterus (?) otisius</i>	Llandovery	NY, Pennsylvania, US	Laurieipterid?
<i>Clarkeipterus testudineus</i>	Přidolí	NY, US	Laurieipterid?
<i>Ctenopterus cestrotus</i>	Llandovery–Ludlow	Otisville, New York	Laurieipterid
<i>Cyrtoctenus caledonicus</i>	Visean	East Lothian, Scotland	Hibbertopterid
<i>Cyrtoctenus dewalquei</i>	Famennian	Belgium	Hibbertopterid
<i>Cyrtoctenus dicki</i>	Givetian?	Thurso, Scotland	Hibbertopterid
<i>Cyrtoctenus ostraviensis</i>	Bashkirian	Czech Republic	Hibbertopterid
<i>Cyrtoctenus peachi</i>	Visean	Berwickshire, Scotland	Hibbertopterid
<i>Cyrtoctenus stevensoni</i>	Visean	Berwickshire, Scotland	Hibbertopterid
<i>Cyrtoctenus wittebergensis</i>	Tournaisian	South Africa	Hibbertopterid
<i>Drepanopterus abonensis</i>	Frasnian?	Somerset, England	Hibbertopterid?
<i>Drepanopterus pentlandicus</i>	Llandovery	Pentland Hills, Scotland	Hibbertopterid?
<i>Hallipterus excelsior</i>	Late Devonian	New York, US	Hardieopterid?
<i>Hallipterus lacoanus</i>	Late Devonian	Pennsylvania, US	Hardieopterid?
<i>Hallipterus (?) perspicillum</i>	Emsian	Willwerath, Germany	Hardieopterid?
<i>Hardieopterus (?) lanarkensis</i>	Llandovery to Wenlock	Lesmahagow, Scotland	Hardieopterid?
<i>Hardieopterus macrophthalmus</i>	Llandovery	Pentland Hills, Scotland	Hardieopterid
<i>Hardieopterus megalops</i>	Přidolí	Herefordshire, England	Hardieopterid?
<i>Hardieopterus myops</i>	Llandovery	NY, Pennsylvania, US	Hardieopterid?
<i>Hastimima whitei</i>	Sakmarian	Minas and Tatui, Brazil	Hibbertopterid
<i>Hibbertopterus (?) hibernicus</i>	Tournaisian	Kiltorcan, Ireland	Hibbertopterid
<i>Hibbertopterus scouleri</i>	Visean	West Lothian, Scotland	Hibbertopterid
<i>Kiaeropterus cyclophthalmus</i>	Llandovery	Pentland Hills, Scotland	Primitive stylonurid?
<i>Kiaeropterus ruedemanni</i>	Late Wenlock	Ringerike, Norway	Primitive stylonurid?
<i>Kokomopterus longicaudatus</i>	Early Přidolí	Indiana, US	Hardieopterid
<i>Lamontopterus knoxae</i>	Late Llandovery	Pentland Hills, Scotland	Hardieopterid?
<i>Laurieipterus elegans</i>	Llandovery	Pentland Hills, Scotland	Laurieipterid
<i>Megarachne servinei</i>	Carboniferous–Permian	Argentina	Hibbertopterid
<i>Mycterops (?) blairi</i>	Serpukhovian	Scotland	Hibbertopterid
<i>Mycterops matthieui</i>	Westphalian	Charleroi, Belgium	Hibbertopterid
<i>Mycterops ordinates</i>	Westphalian	Pennsylvania, US	Hibbertopterid
<i>Mycterops (?) whitei</i>	Kasimovian	Iowa, US	Hibbertopterid?
<i>Pagea sturrocki</i>	Lochkovian or Pragian	Arbroath, Scotland	Laurieipterid
<i>Pagea symondsii</i>	Lochkovian	Ewyas Harold, England	Laurieipterid
<i>Parastylonurus hendersoni</i>	Llandovery	Pentland Hills, Scotland	Parastylonurid
<i>Parastylonurus ornatus</i>	Llandovery	Scotland	Parastylonurid
<i>Parastylonurus (?) sigmoidalis</i>	Přidolí	Shropshire, England	Parastylonurid?
<i>Rhenopterus diensti</i>	Emsian	Willwerath, Germany	Rhenopterid
<i>Rhenopterus macrotuberculatus</i>	Early Emsian	Alken, Germany	Rhenopterid
<i>Rhenopterus tuberculatus</i>	Pragian	Overath, Germany	Rhenopterid
<i>Stylonurella (?) arnoldi</i>	Famennian	Pennsylvania, US	Enigmatic stylonurid
<i>Stylonurella (?) beecheri</i>	Famennian	Pennsylvania, US	Enigmatic stylonurid
<i>Stylonurella spinipes</i>	Early Wenlock	Ayrshire, Scotland	Enigmatic stylonurid
<i>Stylonuroides dolichoapteroides</i>	Late Wenlock	Ringerike, Norway	Enigmatic stylonurid
<i>Stylonurus powriensis</i>	Lochkovian or Pragian	Arbroath, Scotland	Enigmatic stylonurid
<i>Stylonurus (?) shaffneri</i>	Famennian	Pennsylvania, US	Enigmatic stylonurid
<i>Tarsopterella scotica</i>	Lochkovian or Pragian	Arbroath, Scotland	Hardieopterid
<i>Vernonopterus minutisculptus</i>	Westphalian	Lanarkshire, Scotland	Hibbertopterid?
<i>Woodwardopterus scabrosus</i>	Early Carboniferous	Scotland	Hibbertopterid
<i>Stylonurus</i> sp.	Lochkovian to Pragian	Cornwallis Island Canada	Enigmatic stylonurid

Table 2
Basal Eurypterina and Megalograptoida and their distribution

Taxon	Age	Distribution	Group
<i>Drepanopterus</i> (?) <i>bembycoides</i>	Llandovery	Pentland Hills, Scotland	Basal Eurypterina?
<i>Drepanopterus</i> (?) <i>lobatus</i>	Llandovery	Pentland Hills, Scotland	Basal Eurypterina?
<i>Drepanopterus</i> (?) <i>nodosus</i>	L Ludlow – E Přídolí	West Virginia, US	Basal Eurypterina?
<i>Hughmilleria</i> (?) <i>lata</i>	Late Wenlock	Ringerike, Norway	Basal Eurypterina?
<i>Moselopterus</i> <i>ancyloctelson</i>	Early Emsian	Alken, Germany	Basal Eurypterina
<i>Moselopterus</i> <i>elongatus</i>	Early Emsian	Alken, Germany	Basal Eurypterina
<i>Moselopterus</i> (?) <i>lanemani</i>	Eifelian	Plavinas, Latvia	Basal Eurypterina?
<i>Nanahughmilleria</i> (?) <i>conica</i>	Llandovery	Pentland Hills, Scotland	Basal Eurypterina?
<i>Onychopterella</i> <i>augusti</i>	Hirnantian?	Clanwilliam, South Africa	Basal Eurypterina
<i>Onychopterella</i> <i>kokomoensis</i>	Early Přídolí	Indiana, US	Basal Eurypterina
<i>Onychopterella</i> (?) <i>pumilus</i>	Early Llandovery	Essex, Illinois, US	Basal Eurypterina?
<i>Vinetopterus</i> <i>struvei</i>	Early Emsian	Alken, Germany	Basal Eurypterina?
<i>Vinetopterus</i> <i>martini</i>	L. Prag. or E. Ems.	Westerwald, Germany	Basal Eurypterina?
<i>Echinognathus</i> <i>clevelandi</i>	Katian	Oneida Co, NY, US	Megalograptoida
<i>Megalograptus</i> <i>alveolatus</i>	Late Ordovician	Lyons Gap, Virginia, US	Megalograptoida
<i>Megalograptus</i> <i>ohioensis</i>	Katian	Manchester, Ohio, US	Megalograptoida
<i>Megalograptus</i> <i>shiderleri</i>	Katian	Oxford, Ohio, US	Megalograptoida
<i>Megalograptus</i> <i>welchi</i>	Katian	Warren Co, Ohio, US	Megalograptoida
<i>Megalograptus</i> <i>williamsae</i>	Katian	Waynesville, Ohio, US	Megalograptoida
<i>Megalograptus</i> sp.	Katian	Quebec, Canada	Megalograptoida
<i>Megalograptus</i> sp.	Katian	Georgia, US	Megalograptoida
<i>Megalograptus</i> sp.	Katian	Shawangunk Mt, NY, US	Megalograptoida

210 Ma. They are most diverse between the Middle Silurian and Early Devonian and have their absolute peak of diversity in the latest Silurian (Přídolí — ca 418.7 to 416.0 Ma). The eurypterids can broadly be divided into two groups (Fig. 1), the basal Stytonurina (which is here interpreted as monophyletic, but might in fact be paraphyletic when a broader range of taxa are considered) and the monophyletic Eurypterina. These two groups are differentiated most easily on the morphology of the posteriormost prosomal appendage; in Stytonurina, this is a long slender walking leg, lacking a modified spine (termed podomere 7a). In Eurypterina, this leg is usually broadened into a swimming paddle, but always has a podomere 7a (Tetlie and Cuggy, in press). The swimming forms dominate and following the definition of Eurypterina possessing a podomere 7a, they represent around 75% of the known species, while the walking forms represent the remaining 25%. In terms of specimen numbers, the swimming forms are even more dominant, representing somewhere between 95 and 99% of known specimens. However, the morphology of walking forms appears almost as diverse as in swimming forms, and it is likely that the fossil record of the swimming forms is vastly more complete than for the walking forms (see also Fig. 1), possibly because of varying habitat preferences. Both the oldest and the youngest eurypterids are walking forms, so they existed for the entire 210 Ma interval, while the swimming forms existed for around 185 Ma (455 to 270 Ma). Almost all eurypterids have been found in near-

shore marine, estuarine, fluvial or lacustrine environments. The vast majority of eurypterid occurrences are from eastern North America and Europe, and whether this pattern represents the true distribution of eurypterids, or a research and collecting bias has been questioned (Plotnick, 1983, 1999). Scotland and eastern North America have the most diverse assemblages, both in terms of species numbers and morphology, followed by England/Wales, the Baltic region, western Germany and Siberia. The rest of the world has a very poor record of eurypterids.

Herein the eurypterid fossil record is interpreted from both a palaeogeographic and phylogenetic perspective, providing some evidence for origination and dispersal of different eurypterid clades. The results suggest that the observed fossil record with a vast eurypterid diversity in Laurentia and Baltica, at least partly represents a true signal and not primarily a collecting or research bias. It is concluded that almost all eurypterids were inhibited from crossing vast expanses of ocean and were limited to dispersal along coastlines, or the slow movements of the continents they ‘rafted’ on. The only clear exception to this seems to have been the pterygotoids, that apparently could cross open oceans, and are found throughout the world in the short time span of their existence (~40 Ma).

2. Previous work

It has long been known that there is a prevalence of eurypterid fossils in certain parts of the world (e.g.

Table 3

Eurypteroidea and their distribution. The three Chinese records of *Eurypterus* are very dubious and might not even represent eurypterids (see Table 7)

Taxon	Age	Distribution	Group
<i>Buffalopecterus pustulosus</i>	Přidolí	New York and Ontario	Dolichopteridae
<i>Dolichopterus asperatus</i>	L. Lochkov.–Prag	Toledo, Ohio, US	Dolichopteridae
<i>Dolichopterus gotlandicus</i>	Early Wenlock	Gotland, Sweden	Dolichopteridae
<i>Dolichopterus jewetti</i>	Přidolí	New York, US	Dolichopteridae
<i>Dolichopterus macrocheirus</i>	Přidolí	New York and Ontario	Dolichopteridae
<i>Dolichopterus siluriceps</i>	Přidolí	New York and Ontario	Dolichopteridae
<i>Dolichopterus stoermeri</i>	Ludlow	Saaremaa, Estonia	Dolichopteridae
<i>Erieopterus eriensis</i>	Přidolí	S. Bass Island, Ohio, US	Eurypteridae
<i>Erieopterus hypsophthalmus</i>	Přidolí	S. Bass Island, Ohio, US	Eurypteridae
' <i>Erieopterus</i> ' <i>laticeps</i>	Wenlock	Saaremaa, Estonia	Dolichopteridae
<i>Erieopterus</i> (?) <i>limuloides</i>	Early Přidolí	Indiana, US	Eurypteridae
<i>Erieopterus microphthalmus</i>	Lochkovian, Emsian	East US, North Canada	Eurypteridae
<i>Erieopterus</i> (?) <i>phillipsensis</i>	Early Wenlock	Cornwallis Is., Canada	Eurypteridae
<i>Erieopterus turgidus</i>	Přidolí	Detroit, Michigan, US	Eurypteridae
<i>Eurypterus cephalaspis</i>	Přidolí	Herefordshire, England	Eurypteridae
<i>Eurypterus dekayi</i>	Přidolí	New York and Ontario	Eurypteridae
<i>Eurypterus flintstonensis</i>	L Ludlow, E Přidolí	Maryland, West Virg., US	Eurypteridae
<i>Eurypterus hankenii</i>	Wenlock	Ringerike, Norway	Eurypteridae
<i>Eurypterus henningsmoeni</i>	Wenlock	Bærum, Norway	Eurypteridae
<i>Eurypterus laculatus</i>	Přidolí	New York, US	Eurypteridae
<i>Eurypterus lacustris</i>	Přidolí	New York and Ontario	Eurypteridae
<i>Eurypterus leopoldi</i>	L Ludlow, E Přidolí	Somerset Is., Canada	Eurypteridae
' <i>Eurypterus</i> ' <i>minor</i>	Llandovery	Pentland Hills, Scotland	Dolichopteridae?
<i>Eurypterus ornatus</i>	Přidolí	Ohio, US	Eurypteridae
<i>Eurypterus pittsfordensis</i>	Late Ludlow	Pittsford, NY, US	Eurypteridae
<i>Eurypterus quebecensis</i>	Early Ludlow	Québec, Canada	Eurypteridae
<i>Eurypterus remipes</i>	Přidolí	New York, US	Eurypteridae
<i>Eurypterus serratus</i>	Early Wenlock	Gotland, Sweden	Eurypteridae
<i>Eurypterus tetragonophthalmus</i>	Wenlock to Přidolí	Baltica	Eurypteridae
<i>Ruedemannipterus stylonuroides</i>	Llandovery–Ludlow	Otisville, New York, US	Dolichopteridae
<i>Strobilopterus princetonii</i>	Pragian	Wyoming, US	Dolichopteridae
<i>Strobilopterus</i> sp.	Eifelian?	Wyoming, US	Dolichopteridae
<i>Syntomopterus richardsoni</i>	L. Lochkov.–Prag.	Toledo, Ohio, US	Dolichopteridae

Clarke and Ruedemann, 1912; Størmer, 1955). Other parts of the world have proved more or less devoid of eurypterids, especially so in pre-Carboniferous strata. Every time a eurypterid occurrence from outside North America and Europe has been described, the authors have usually pointed out the rarity of these occurrences (e.g. Kjellesvig-Waering, 1964; Kjellesvig-Waering, 1973; Waterston et al., 1985; Braddy et al., 1995; Braddy et al., 2002; Burrow et al., 2002; Tetlie et al., 2004; Selden et al., 2005; Shpinev, 2006; Tetlie et al., 2007) but rarely has any explanation for these patterns been sought. Plotnick (1999, p. 114) wrote “eurypterids probably lived in a wider range of environments and geographic regions than are currently known” suggesting that he, at least partly, believed there is a research and collecting bias in the eurypterid fossil record. It is obvious that historically, more intense palaeontological research and fossil collecting has taken place in North America and Europe than in most other parts of the

world, and this would necessarily bias measures of eurypterid diversity and abundance in different geographic locations. However, the recent surge of palaeontological research in China has not produced more than one complete eurypterid specimen (Tetlie et al., 2007). An alternative explanation is therefore that the fossil record is showing a true (albeit incomplete) picture of eurypterid distribution, and that not all eurypterid groups enjoyed a cosmopolitan distribution. Distinct faunal provincialism has been observed in comparable groups like trilobites (e.g. Cocks and Fortey, 1982) and fish (e.g. Turner and Turner, 1974). For trilobites, the faunal provincialism is high in the early Palaeozoic (Cambrian and Ordovician), but decreases throughout the Silurian (Lees et al., 2002).

The only previous attempts to track eurypterid occurrences throughout the world were those of O'Connell (1916), Depitout (1962) and Plotnick (1983). O'Connell (1916) misinterpreted all eurypterid occurrences as

Table 4
Mixopteroidea and Waeringopteroidea and their distribution

Taxon	Age	Distribution	Group
<i>Carcinosoma</i> (?) <i>harleyi</i>	Late Ludlow	Ludlow, England	Mixopteroidea
<i>Carcinosoma</i> <i>libertyi</i>	Late Llandovery	Manitoulin Island, Canada	Mixopteroidea
<i>Carcinosoma</i> <i>newlini</i>	Early Přídolí	Indiana, US	Mixopteroidea
<i>Carcinosoma</i> (?) <i>punctatum</i>	Ludlow	Leintwardine, England	Mixopteroidea
<i>Carcinosoma</i> <i>scorpioides</i>	Wenlock	Lesmahagow, Scotland	Mixopteroidea
<i>Carcinosoma</i> <i>scoticum</i>	Llandovery	Pentland Hills, Scotland	Mixopteroidea
<i>Carcinosoma</i> (?) <i>spiniferum</i>	Late Ludlow	Pittsford, NY, US	Mixopteroidea?
<i>Lanarkopterus</i> <i>dolichoschelus</i>	Wenlock–Ludlow	Ayrshire, Scotland	Mixopteroidea
<i>Mixopterus</i> <i>kiaeri</i>	Late Wenlock	Ringerike, Norway	Mixopteroidea
<i>Mixopterus</i> <i>multispinosus</i>	Late Ludlow	Pittsford, NY, US	Mixopteroidea
<i>Mixopterus</i> <i>simonsoni</i>	Ludlow	Saaremaa, Estonia	Mixopteroidea
<i>Paracarcinosoma</i> <i>acrocephalus</i>	Přídolí, Lochkovian	Barrandian, Czech Rep.	Mixopteroidea
<i>Paracarcinosoma</i> <i>obesus</i>	Wenlock	Lesmahagow, Scotland	Mixopteroidea
<i>Paracarcinosoma</i> <i>scorpionis</i>	Přídolí	New York and Ontario	Mixopteroidea
<i>Rhinocarcinosoma</i> <i>cicerops</i>	Llandovery–Ludlow	Otisville, New York	Mixopteroidea
<i>Rhinocarcinosoma</i> <i>dosonensis</i>	Late Silurian	Do Son Peninsula, Vietnam	Mixopteroidea
<i>Rhinocarcinosoma</i> <i>vanningeni</i>	Ludlow	Clinton, New York	Mixopteroidea
<i>Grossopterus</i> <i>inexpectans</i>	Frasnian	Gilboa, New York	Waeringopteroidea
<i>Grossopterus</i> <i>overathi</i>	Early Emsian	Overath, Germany	Waeringopteroidea
<i>Orcanopterus</i> <i>manitoulinensis</i>	Hirnantian	Manitoulin Island, Canada	Waeringopteroidea
<i>Waeringopterus</i> <i>apfeli</i>	Přídolí	Syracuse area, NY, US	Waeringopteroidea
<i>Waeringopterus</i> <i>cumberlandicus</i>	L Ludlow–E Přídolí	Maryland, West Virg., US	Waeringopteroidea

evidence of fluvial environments. She traced the distribution of eurypterids on Silurian palaeogeographical maps developed by Grabau (1913) long before plate tectonics had been accepted, who postulated the existence of large palaeocontinents in areas today covered by ocean, such as ‘Appalachia’ and ‘Atlantica’ (Plotnick, 1999). O’Connell (1916) tried to explain the disjunct distribution and endemism in Eurypterida as a result of the distribution of eurypterids in rivers draining these palaeocontinents. Depitout (1962) explained eurypterid distribution from the stabilist palaeogeographical maps developed by Termier and Termier (1952). These maps illustrated a number of stable shields bordered or joined by geosynclines (Plotnick, 1999). Eurypterida was considered by Depitout (1962) to have originated in eastern North America in the Ordovician and spread from there to Europe and other continents, mainly migrating along coasts. Plotnick (1983) plotted the eurypterid record on palaeogeographical maps that were relatively similar to those used today, and he also produced the first phylogeny of Eurypterida. However, his phylogeny was on the generic level and the palaeogeographical plots were not interpreted in a phylogenetic sense. Plotnick (1983, pp. 256–257) noted that “...the overall pattern of occurrence is not very enlightening...”, but also (p. 257) that “...the pattern is far more interesting at lower taxonomic levels...”. Plotnick (1983) found that pterygotids and carcosomatids were the only eurypterids known from Gondwana in the Silurian and Devonian, while these two groups also represent the most

marine biofacies described by Kjellesvig-Waering (1961). Plotnick drew parallels between the distribution pattern and the fact that these two groups are also the only two eurypterid groups found in deeper waters (Kjellesvig-Waering, 1961). Plotnick also pointed out that the Carboniferous and Permian eurypterids were widely distributed and very similar all over the world, and suggested that eurypterids were part of the “Carboniferous Faunal Continuum” coined by Schram (1979).

3. Material and methods

Information about the phylogenetic relationships of most complete eurypterids is now available (Tetlie, 2004, 2006a, b; Ciuca and Tetlie, 2007; Tetlie and Cuggy, in press; Tetlie and Poschmann, in review). Even many eurypterids whose phylogenetic position has not been precisely determined can be confidently placed in one of the major clades and this assignment is shown in Tables 1–6, and the few that cannot currently be placed are shown in Table 7. All the detailed information about the individual clades has been combined with the relationships found between the larger clades by Tetlie (2004) into a summary tree shown in Fig. 1. It should be pointed out that this tree is not a supertree, merely a spliced species-level tree, based on the species level analyses of the individual clades (Tetlie, 2006b; Ciuca and Tetlie, 2007; Tetlie and Cuggy, in press; Tetlie and Poschmann, in review; Tetlie, unpub. data).

Table 5
Adelophthalmoidea and their distribution

Taxon	Age	Distribution	Group
<i>Adelophthalmus approximatus</i>	Famennian?	Pennsylvania, US	Adelophthalmidae
<i>Adelophthalmus asturica</i>	Westphalian	Spain	Adelophthalmidae
<i>Adelophthalmus bradorensis</i>	Westphalian	North Campbelltown, Canada	Adelophthalmidae
<i>Adelophthalmus cambieri</i>	Bashkirian	Charleroi, Belgium	Adelophthalmidae
<i>Adelophthalmus (?) carbonarius</i>	Unknown	Unknown, Russia	Adelophthalmidae
<i>Adelophthalmus chinensis</i>	Asselian?	Zhaozhuang, China	Adelophthalmidae
<i>Adelophthalmus corneti</i>	Bashkirian	Quaregnon, Belgium	Adelophthalmidae
<i>Adelophthalmus douvillei</i>	Asselian or Sakmarian	Bussaco, Portugal	Adelophthalmidae
<i>Adelophthalmus dumonti</i>	Westphalian	Mechelen-sur-Meuse, Belgium	Adelophthalmidae
<i>Adelophthalmus granosus</i>	Moscovian	Saarland, Germany	Adelophthalmidae
<i>Adelophthalmus imhofi</i>	Westphalian	Vlkys, Czech Republic	Adelophthalmidae
<i>Adelophthalmus irinae</i>	Tournaisian	Krasnoyarsk, Russia	Adelophthalmidae
<i>Adelophthalmus kidstoni</i>	Westphalian	Radstock, Avon, England	Adelophthalmidae
<i>Adelophthalmus (?) lohesti</i>	Famennian	Pont de Bonne, Belgium	Adelophthalmidae?
<i>Adelophthalmus luceroensis</i>	Gzelian or Asselian	New Mexico, US	Adelophthalmidae
<i>Adelophthalmus mansfieldi</i>	Westphalian–Asselian	Pennsylvania, US	Adelophthalmidae
<i>Adelophthalmus mazonensis</i>	Westphalian	Mazon Creek, Illinois, US	Adelophthalmidae
<i>Adelophthalmus moyseyi</i>	Westphalian	England and Belgium	Adelophthalmidae
<i>Adelophthalmus nebraskensis</i>	Sakmarian?	Nebraska, US	Adelophthalmidae
<i>Adelophthalmus pennsylvanicus</i>	Westphalian	Pennsylvania, US	Adelophthalmidae
<i>Adelophthalmus (?) perornatus</i>	Early Carboniferous	Scotland	Adelophthalmidae?
<i>Adelophthalmus pruvosti</i>	Westphalian	Lens, France	Adelophthalmidae
<i>Adelophthalmus (?) raniceps</i>	Moscovian	Saarland, Germany	Adelophthalmidae?
<i>Adelophthalmus sellardsi</i>	Artinskian?	Oklahoma and Kansas, US	Adelophthalmidae
<i>Adelophthalmus sievertsi</i>	Early Emsian	Willwerath and Alken, Germany	Adelophthalmidae
<i>Adelophthalmus waterstoni</i>	Frasnian	Kimberley, Western Australia	Adelophthalmidae
<i>Adelophthalmus wilsoni</i>	Westphalian	Radstock, Avon, England	Adelophthalmidae
<i>Adelophthalmus zadrai</i>	Bashkirian	Moravo–Silesia, Czech Rep.	Adelophthalmidae
<i>Bassipterus virginicus</i>	L Ludlow to E Přídolí	West Virginia, US	Basal form
<i>Nanahughmilleria clarkei</i>	Llandovery–Ludlow	Otisville, New York, US	Basal form?
<i>Nanahughmilleria norvegica</i>	L Wenlock to E Ludlow	Norway and Scotland	Basal form
<i>Nanahughmilleria (?) patteni</i>	Ludlow	Saaremaa, Estonia	Basal form
<i>Nanahughmilleria (?) prominens</i>	Llandovery	Cayuga, New York	Basal form?
<i>Nanahughmilleria pygmaea</i>	Přídolí	Herefordshire, England	Basal form?
<i>Nanahughmilleria (?) schiraensis</i>	Lochkovian or Eifelian	Khakassia, Lake Shunet, Russia	Basal form?
<i>Parahughmilleria bellistriata</i>	L Ludlow to E Přídolí	West Virginia, US	Adelophthalmidae?
<i>Parahughmilleria hefteri</i>	L. Pragian to E. Emsian	Alken, Germany, Luxembourg	Adelophthalmidae?
<i>Parahughmilleria major</i>	Early Emsian	Alken, Germany	Adelophthalmidae?
<i>Parahughmilleria maria</i>	Llandovery	NY and Pennsylvania, US	Adelophthalmidae?
<i>Parahughmilleria matarakensis</i>	Lochkovian or Eifelian	Khakassia, Lake Shunet, Russia	Adelophthalmidae?
<i>Parahughmilleria salteri</i>	Přídolí	Herefordshire, England	Basal form?
<i>Pittsfordipterus phelpsae</i>	Late Ludlow	Pittsford, New York, US	Basal form
<i>Unionopterus anastasiae</i>	Early Carboniferous	Kazakhstan	Adelophthalmidae?

The palaeomaps (Figs. 2–5) are uninterrupted Mollweide projections that were downloaded with permission from the website of Professor R. Blakey (<http://jan.ucc.nau.edu/~rcb7/RCB.html>; Blakey (2007)) and eurypterid occurrences were plotted onto these maps as precisely as possible with the locality and palaeogeographic information available. The naming of the palaeocontinents is taken from Cocks and Torsvik (2002) and Torsvik and Cocks (2004). The most central palaeocontinents in the discussion of eurypterid occurrences are: *Laurentia* (USA (except Florida), Canada, Greenland and Scotland), *Baltica*

(Scandinavia, the Baltic states, Russia west of the Ural mountains, Ukraine, Romania and Moldova), *Avalonia* (England, Wales and Belgium), the *Rheno–Hercynian Terrane* (western Germany, Luxembourg) and *Siberia* (Russia between the Ural Mountains and the Cherskiy Range). In the Middle to Late Ordovician, Avalonia collided with the southern margin of Baltica (Torsvik and Rehnström, 2003). In the Late Silurian, Baltica/Avalonia and Laurentia collided and created a new palaeocontinent termed *Laurussia*. Some time in the Devonian, the Rheno–Hercynian Terrane became sutured onto the southern

Table 6

Pterygoteia and their distribution. In addition to these named records, pterygotid fragments have been recorded from at least Venezuela, Saudi Arabia, Libya, Morocco, Algeria, Siberia and France

Taxon	Age	Distribution	Group
<i>Hughmilleria</i> (?) <i>saetiger</i>	Ludlow	Pennsylvania, US	Pterygoteia?
<i>Hughmilleria shawangunk</i>	Llandovery	Pennsylvania, NY, US	Pterygoteia
<i>Hughmilleria socialis</i>	Late Ludlow	Pittsford, NY, US	Pterygoteia
<i>Hughmilleria wangi</i>	Llandovery	Hunan, China	Pterygoteia
<i>Herefordopterus banksii</i>	Přidolí	Herefordshire, England	Pterygoteia
<i>Salteropterus abbreviatus</i>	Přidolí	Herefordshire, England	Pterygoteia
<i>Slimonia acuminata</i>	Late Llandovery to Wenlock	Lesmahagow, Scotland	Pterygoteia
<i>Slimonia boliviana</i>	Ludlow or Přidolí	Pojo, Bolivia	Pterygoteia
<i>Slimonia dubia</i>	Llandovery	Pentland Hills, Scotland	Pterygoteia
<i>Slimonia</i> (?) <i>stylops</i>	Přidolí	Herefordshire, England	Pterygoteia?
<i>Jaekelopterus howelli</i>	Pragian	Wyoming, US	Pterygoteia
<i>Jaekelopterus</i> (?) <i>marylandicus</i>	Early Wenlock	Maryland, US	Pterygoteia
<i>Jaekelopterus rhenaniae</i>	Pragian and Emsian	Western Germany	Pterygoteia
<i>Pterygotus anglicus</i>	Lochkovian or Pragian	Scotland, New Brunswick	Pterygoteia
<i>Pterygotus arcuatus</i>	Ludlow	Leintwardine, England	Pterygoteia
<i>Pterygotus</i> (?) <i>australis</i>	Ludlow?	Melbourne, Australia	Pterygoteia
<i>Pterygotus barrandei</i>	Přidolí	Czech Republic, Spain?	Pterygoteia
<i>Pterygotus bolivianus</i>	Emsian or Eifelian	Belen, Bolivia	Pterygoteia
<i>Pterygotus carmani</i>	Lochkovian–Pragian	Ohio, US	Pterygoteia
<i>Pterygotus cobbi</i>	Přidolí	New York and Ontario	Pterygoteia
<i>Pterygotus denticulatus</i>	Late Ludlow	Ludlow, England	Pterygoteia
<i>Pterygotus floridanus</i>	Lochkovian	Florida, US	Pterygoteia
<i>Pterygotus gaspesiensis</i>	Middle Devonian	Quebec, Canada	Pterygoteia
<i>Pterygotus</i> (?) <i>grandidentatus</i>	Wenlock	Dudley, England	Pterygoteia
<i>Pterygotus impacatus</i>	Ludlow	Saaremaa, Estonia	Pterygoteia
<i>Pterygotus kopaninensis</i>	Ludlow	Czech Republic	Pterygoteia
<i>Pterygotus lightbodyi</i>	Late Ludlow	Ludlow, England	Pterygoteia
<i>Pterygotus ludensis</i>	Přidolí	Herefordshire, England	Pterygoteia
<i>Pterygotus</i> (?) <i>mediocris</i>	Ludlow	Czech Republic	Pterygoteia
<i>Pterygotus minor</i>	Lochkovian or Pragian	Scotland	Pterygoteia
<i>Pterygotus taurinus</i>	Přidolí	Ewyas Harold, England	Pterygoteia
<i>Pterygotus</i> (?) <i>ventricosus</i>	Early Přidolí	Indiana, US	Pterygoteia
<i>Pterygotus waylandsmithi</i>	Late Ludlow	NY, US	Pterygoteia
<i>Acutiramus bohemicus</i>	Přidolí	Czech Republic, Australia	Pterygoteia
<i>Acutiramus floweri</i>	Late Ludlow	NY, US	Pterygoteia
<i>Acutiramus cummingsi</i>	Přidolí	New York and Ontario	Pterygoteia
<i>Acutiramus macrophthalmus</i>	Přidolí	New York, US	Pterygoteia
<i>Acutiramus</i> (?) <i>nobilis</i>	Ludlow	Czech Republic	Pterygoteia
<i>Acutiramus perneri</i>	Late Lochkovian	Czech Republic, Spain?	Pterygoteia
<i>Acutiramus perryensis</i>	Přidolí	Ohio, US	Pterygoteia
<i>Acutiramus suwanneensis</i>	Přidolí?	Florida, US	Pterygoteia
<i>Erettopterus bilobus</i>	Late Llandovery to Wenlock	Lesmahagow, Scotland	Pterygoteia
<i>Erettopterus brodiei</i>	Přidolí	Herefordshire, England	Pterygoteia
<i>Erettopterus</i> (?) <i>canadensis</i>	Late Wenlock	Ontario, Canada	Pterygoteia
<i>Erettopterus exophthalmus</i>	Late Ludlow to Early Přidolí	West Virginia, US	Pterygoteia
<i>Erettopterus gigas</i>	Přidolí	Herefordshire, England	Pterygoteia
<i>Erettopterus globiceps</i>	Llandovery	New York, Pennsylv., US	Pterygoteia
<i>Erettopterus grandis</i>	Přidolí	NY, US	Pterygoteia
<i>Erettopterus</i> (?) <i>holmi</i>	Late Wenlock	Ringerike, Norway	Pterygoteia
<i>Erettopterus laticauda</i>	Ludlow	Saaremaa, Estonia	Pterygoteia
<i>Erettopterus marstoni</i>	Ludlow	Leintwardine, England	Pterygoteia
<i>Erettopterus megalodon</i>	Late Ludlow	Lugwardine, England	Pterygoteia
<i>Erettopterus osiliensis</i>	Ludlow	Estonia and NY, US	Pterygoteia
<i>Erettopterus serricaudatus</i>	Early Wenlock	Gotland, Sweden	Pterygoteia
<i>Erettopterus spatulatus</i>	Přidolí	Herefordshire, England	Pterygoteia
<i>Erettopterus</i> (?) <i>vogti</i>	Lochkovian	Spitzbergen	Pterygoteia

Table 7
Problematic eurypterids not considered

Taxon	Age	Distribution	Problem
<i>Borchgrevinkium taimyrensis</i>	Early–Middle Devonian	Norilsk, Russia	Chasmataspid?
<i>Dolichopterus</i> (?) <i>bulbosus</i>	Přídolí	Herefordshire, England	Unknown affinity in Eurypterina
<i>Dolichopterus</i> (?) <i>herkimerensis</i>	Přídolí	New York, US	Unknown affinity in Eurypterida
<i>Eurypterus</i> (?) <i>loi</i>	Wenlock	Hsin Tan, Hubei, China	Not a eurypterid?
<i>Eurypterus</i> (?) <i>styliformis</i>	Wenlock	Hsin Tan, Hubei, China	Not a eurypterid?
<i>Eurypterus</i> (?) <i>yangi</i>	Wenlock	Hsin Tan, Hubei, China	Not a eurypterid?
<i>Holmipterus suecicus</i>	Early Wenlock	Gotland, Sweden	Unknown affinity in Eurypterina
<i>Hughmilleria</i> (?) <i>lanceolata</i>	Llandovery to Wenlock	Lesmahagow, Scotland	Unknown affinity in Eurypterina
<i>Tylopterella boylei</i>	Ludlow	Elora, Ontario, Canada	Unknown affinity in Eurypterida
<i>Tylopterella</i> (?) <i>menneri</i>	Lochkovian	Norilsk, Siberia, Russia	Unknown affinity in Eurypterida

margin of Laurussia. Many of the remaining landmasses were concentrated over the southern polar region in the large continent *Gondwana*, but much of what is today central and eastern Asia were small isolated terranes from the Ordovician to the Carboniferous/Permian (or in some cases even later), e.g. the *North China Block*, the *South China Block*, *Annamia* (Vietnam, Cambodia, Laos, eastern Thailand), *Sibumasu* (western Thailand, eastern Myanmar) and many smaller plates (Cocks and Torsvik, 2002; Torsvik and Cocks, 2004). Towards the end of the Palaeozoic, when the eurypterids became extinct, *Pangaea* was forming from the amalgamation of almost all the landmasses present.

The ages in Tables 1–7 have as far as possible been correlated to the adopted ICS stage names (Gradstein and Ogg, 2004). In addition, Ordovician stage names that were earlier called Ordovician V and Ordovician VI have recently been given the names Sandbian and Katian (Bergström et al., 2006), and these stages are important as the earliest eurypterid occurrences and apparently many of the deep divergences occurred during these intervals.

4. Results

The results are discussed cladewise, but more than one clade is plotted on each palaeomap. Figs. 2–5 demonstrate that Laurussian occurrences dominate; however the dominance of eurypterids in the Laurussian area is actually much greater than indicated by the figures. For instance, Silurian stylonurids from Scotland are only indicated once, but there are a total of nine taxa present (Table 1). Similar simplifications were made for many of the eurypterid core areas of Laurussia (e.g. New York, Indiana, Ontario, England, Norway, Estonia, western Germany), while for occurrences outside of Laurussia, almost all identifiable occurrences have been given individual markers. The eurypterid fossil record is continuous through 210 Ma, while the maps had to be limited to 6 different time slices. This means that all Ordovician occurrences are constrained to one map, all

Silurian to one map, all Devonian to one, all Permian to one, while the Carboniferous have been divided into two; one map representing the Lower Carboniferous (=Mississippian) and one map the Upper Carboniferous (=Pennsylvanian). It is obvious that the longer the period combined onto a single map, the more inaccurate the palaeogeographic position and palaeocoastline of the continent will be. The longest interval on a single map here is the Devonian. These simplifications of the figures should not introduce any more severe errors than the occasional marine occurrence plotted onto land areas. A potentially more serious source of error is present in the taxonomic/phylogenetic assignment of taxa. However, no attempt has been made to divide the stylonurids, phylogenetically the most poorly understood group, into smaller clades, or plot the problematic taxa (Table 7), reducing the risk of taxonomic errors.

4.1. *Stylonurina*

Presently, the phylogeny for the stylonurid eurypterids is not stable. As discussed earlier, they are rarely encountered compared to the swimming forms, and the taxa (Table 1) are generally known from few specimens and most are incompletely known. The oldest and most basal eurypterids are stylonurids, but they are very rare in the Ordovician (Fig. 2A) and Silurian (Fig. 2B). The radiation of the hibbertopterid eurypterids in the Late Devonian and Carboniferous represent the last major genus-level radiation within Eurypterida (Table 1; Fig. 5). The stylonurids are mainly found in rocks formed in fluvial or brackish sedimentary settings, and their ability to disperse might have been inhibited by both the localised nature of their preferred habitats and the salinity barriers caused by their adaptation to a more brackish environment. However, since the distribution of the pre-Pangaean stylonurids is very simple (Fig. 2), the poorly known phylogeny of the stylonurids is actually not much of a problem in this case. The oldest stylonurid (and eurypterid) is from the early Late

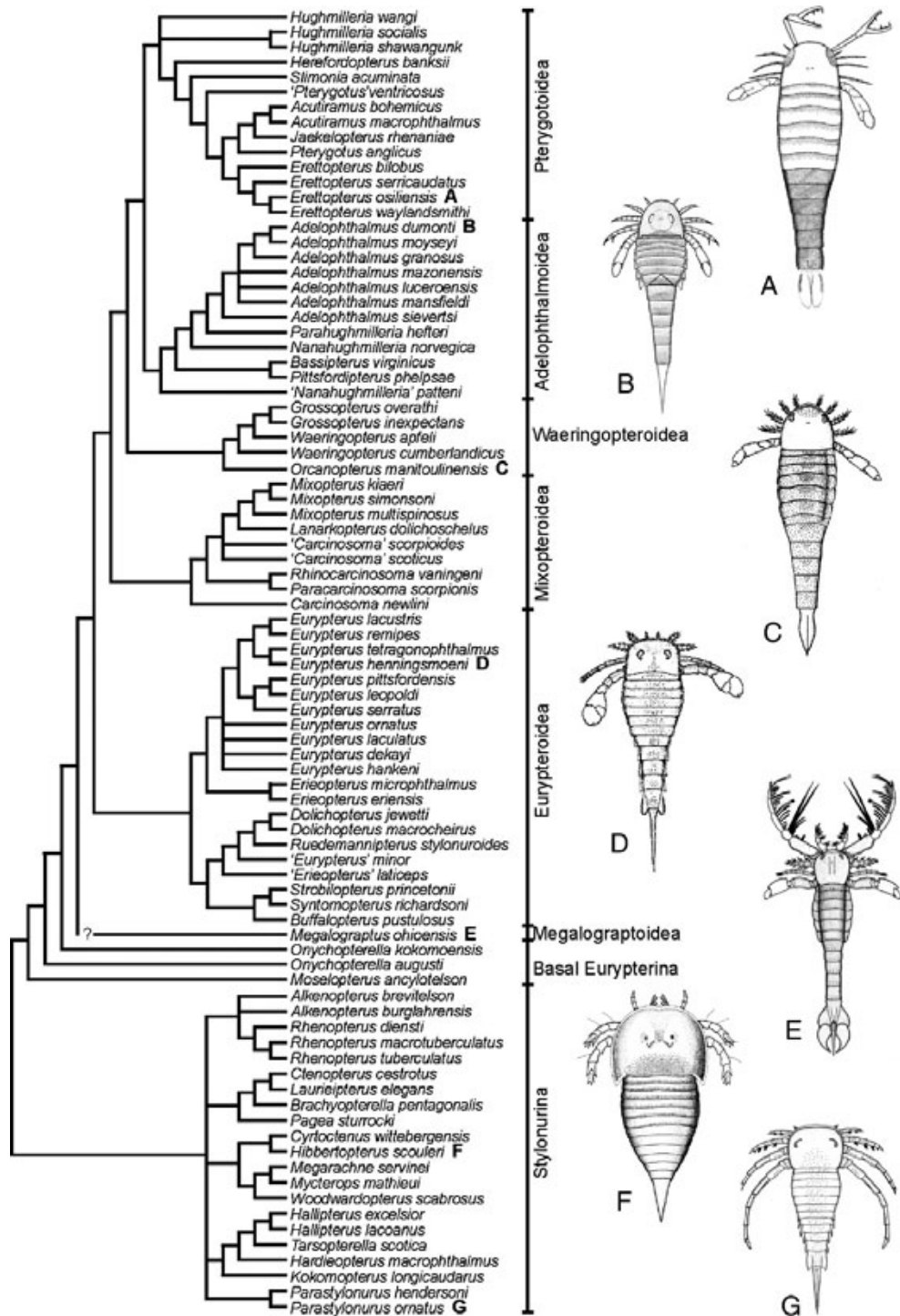


Fig. 1. Phylogeny of Eurypterida. Mainly based on Tetlie (2004), Ciurca and Tetlie (2007), Tetlie and Cuggy (in press), Tetlie and Poschmann (in review) and personal observations. The position of the megalograptids is uncertain. The stylonurids are problematic, and a stripped down version of their phylogeny is presented, with many taxa of uncertain affinity removed. Graphic representatives of most major clades of Eurypterida are also shown with letters indicating their name and phylogenetic position.

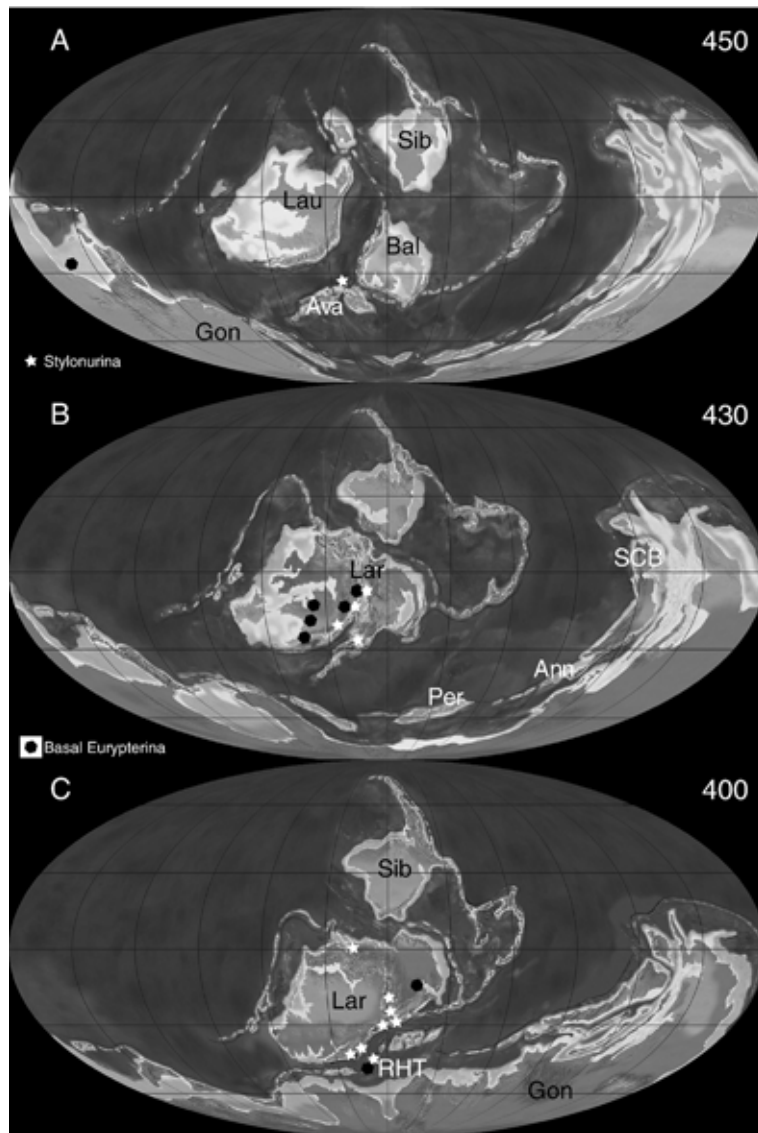


Fig. 2. Distribution of stylonurid eurypterids (white stars) and basal Eurypterina (black hexagons). A) Late Ordovician; B) Silurian; C) Devonian. Abbreviations are: Ann — Annamia, Ava — Avalonia, Bal — Baltica, Gon — Gondwana, Lar — Laurussia, Lau — Laurentia, Per — Perunica, RHT — Rheno–Hercynian Terrane, SCB — South China Block, Sib — Siberia.

Ordovician (Sandbian) of Avalonia (Wales — [Størmer, 1951](#)). It is from a graptolitic shale and thus represents one of very few known records of eurypterids from putative deep-water deposits (other examples are the Czech pterygotids, e.g. [Chlupáč, 1994](#)). Whether this single, complete Ordovician specimen was found in its natural habitat or has been transported into this setting is not known. It is therefore not immediately clear in what geographic region Eurypterida originated, or to what degree the early derivatives were able to migrate between Laurentia and Avalonia/Baltica. Avalonia was moving very fast towards the north during the Ordovician, and by the

Sandbian, Avalonia might have been adjacent to Baltica and approaching Laurentia ([Lees et al., 2002](#); [Torsvik and Rehnström, 2003](#)). Most Silurian and Devonian stylonurids are known from Scotland (then a part of eastern Laurentia) but quite a few taxa were also able to enter Avalonia and Baltica in the Silurian and the Rheno–Hercynian Terrane in the Devonian. Since one of the stylonurid clades, the hibbertopterids, persisted past the end of the Devonian, they were able to spread from Laurentia to South America and Africa during the Late Devonian. With the amalgamation of Pangaea, the hibbertopterids gained a more cosmopolitan distribution.

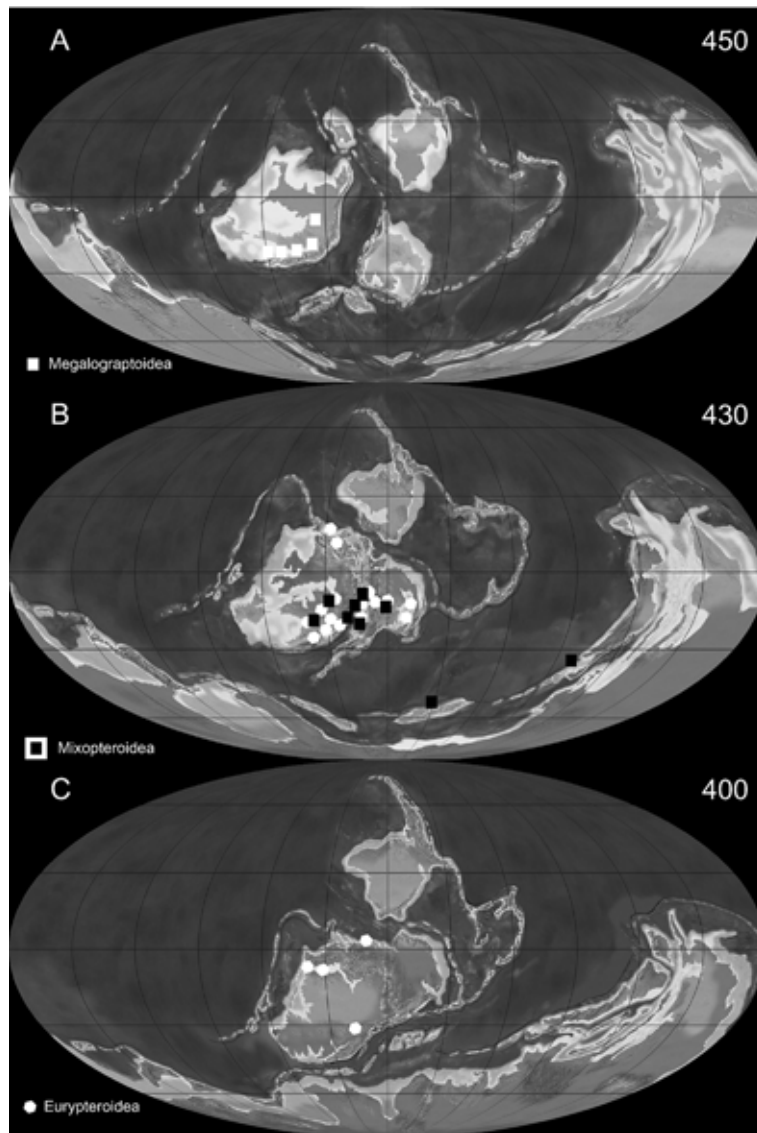


Fig. 3. Distribution of megalopterids (white squares), Eurypteroidea (white hexagons) and Mixopteroidea (black squares). A) Late Ordovician; B) Silurian; C) Devonian. Identity of palaeocontinents as in Fig. 2.

One stylonurid clade that is limited to the Rheno–Hercynian Terrane has been identified. This is the clade consisting of *Rhenopterus* and *Alkenopterus* (see Poschmann and Tetlie, 2004; Poschmann and Franke, 2006). Its origin is unknown (Fig. 1), but its ancestors probably came from among the large stock of primitive stylonurids from eastern Laurentia (Scotland) or Baltica.

4.2. Eurypterina

As mentioned earlier, the Eurypterina includes all the forms with the sixth prosomal appendage developed into a swimming paddle but also the walking forms

possessing a podomere 7a on this appendage (Tetlie and Cuggy, in press). The most basal forms with swimming legs are known from the east coast of Gondwana close to the equator (what today is South Africa) of the Late Ordovician (Braddy et al., 1995). It is not known if they originated there, but it is more likely that they had migrated from Laurentia, since most stylonurids and basal swimming forms are predominantly from Laurentia (Figs. 2A,B, 3A).

4.2.1. Basal swimming forms

The most basal swimming forms (Table 2) include the two species in the genus *Onychopterella*. The oldest

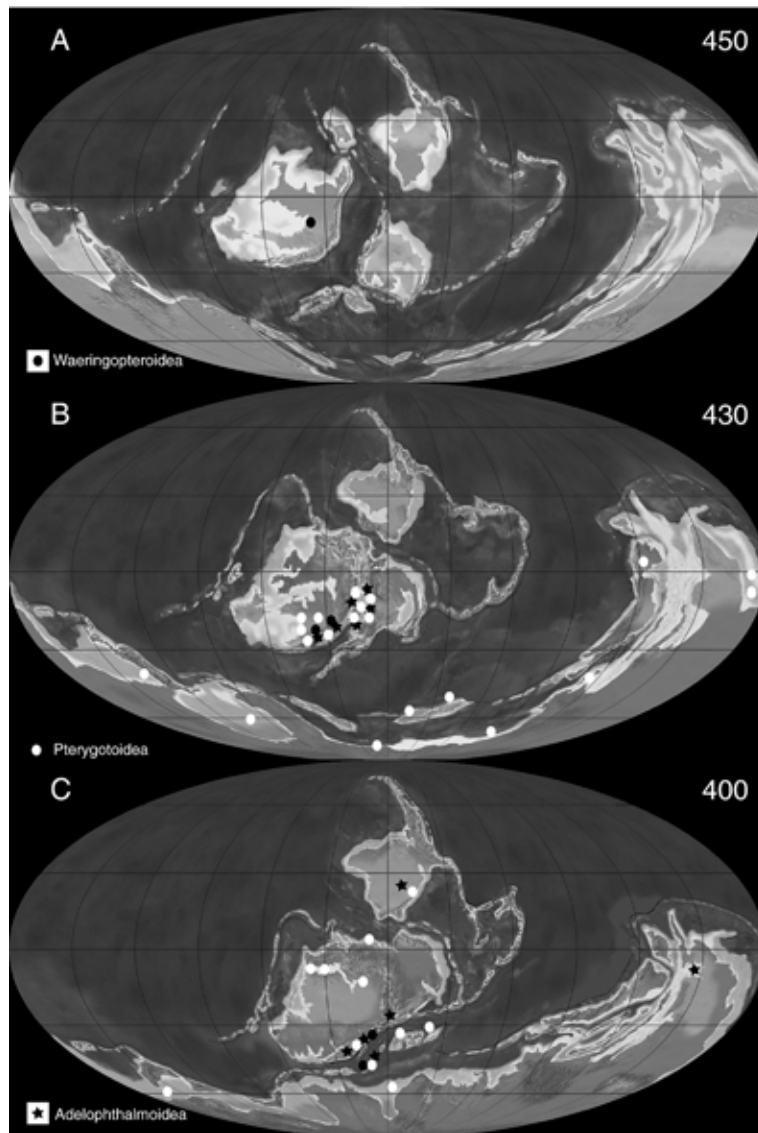


Fig. 4. Distribution of Waeringopteroidea (black circles), Adelophthalmoidea (black stars) and Pterygopteroidea (white circles). A) Late Ordovician; B) Silurian; C) Devonian. Identity of palaeocontinents as in Fig. 2.

(Fig. 2A), and clearly most primitive of these two (see Tetlie and Cuggy, *in press*) is from the Late Ordovician of South Africa (Braddy *et al.*, 1995), while the other is known from the Late Silurian of Laurentia (e.g. Clarke and Ruedemann, 1912). It is most likely that the South African *Onychopterella* arrived from Laurentia. It seems unlikely that the swimming forms originated in Gondwana since there is no trace of the basal stylonurids or the other basal swimming groups in the rest of Gondwana. It is also likely that the stock represented by the South African *Onychopterella* went extinct without establishing a viable Gondwanan eurypterid population. A few forms still retaining the plesiomorphic condition of the sixth prosomal appendage

as a walking leg belong to this part of the phylogenetic tree. With the exception of *Moselopterus ancylotelson* Størmer, 1974 from the Devonian of Germany, the remaining forms of mostly Silurian age are very poorly known.

4.2.2. *Megalograptoidae*

This superfamily (Table 2) is thought to be relatively primitive (between *Onychopterella* and the Eurypteroidea) because they lack a synapomorphy of all more derived swimming forms, the modified distal margin of the sixth podomere of the swimming leg. However, this position (Fig. 1) must be treated with caution since it has never been recovered in a phylogenetic analysis, and is mainly based

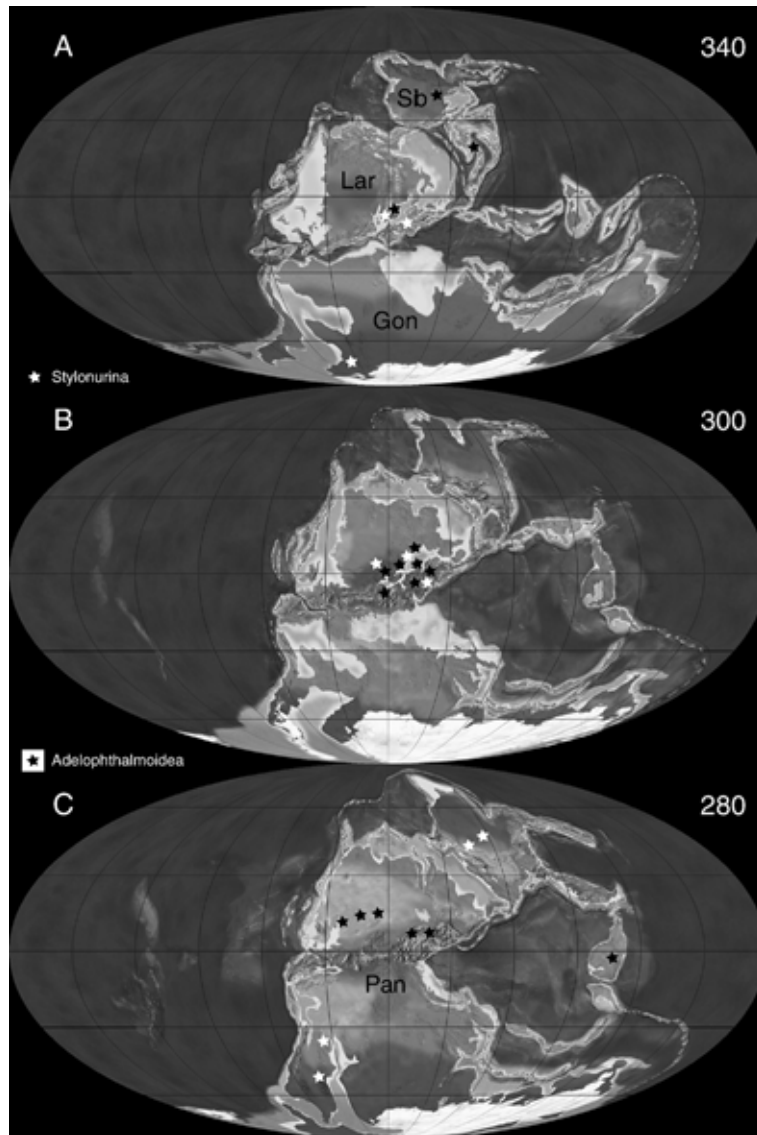


Fig. 5. Distribution of Late Palaeozoic eurypterids (stylonurids — white stars; Adelophthalmoidea — black stars). A) Early Carboniferous; B) Late Carboniferous; C) Permian. Abbreviations are: Gon — Gondwana, Lar — Laurussia, Pan — Pangaea, Sib — Siberia.

on the lack of this character and other presumed primitive traits. It is possible that this clade instead belongs between the Eurypteroidea and the Mixopteroidea, since the sixth podomere in the swimming leg resembles the reduced podomere found in the Mixopteroidea, in addition to numerous similarities with both the Eurypteroidea and the Mixopteroidea. It was probably the first major successful eurypterid group, as evidenced by the Late Ordovician megalograptoid radiation (Fig. 3A). All the records of the Megalograptoidae are from the Late Ordovician of Laurentia (Fig. 3A), although *Holmipterus suecicus* Kjellesvig-Waering, 1979 (Table 7) represents a very questionable record from the Middle Silurian of Baltica.

The megalograptoid affinity of this taxon was questioned by Tollerton (1989), and this view is followed herein. However, even from Laurentia, only one well-known species exists (Caster and Kjellesvig-Waering, 1964), but several other scattered records of the superfamily are known from many parts of the palaeocontinent (Miller, 1874; Walcott, 1882; Caster and Kjellesvig-Waering, 1964; Rindsberg and Chowns, 1986; Brenner et al., 1996; Chartier et al., 2002).

4.2.3. Eurypteroidea

In contrast to the Megalograptoidae, the Eurypteroidea (Table 3) is a rather well-known clade consisting

of the genera *Eurypterus*, *Erieopterus*, *Dolichopterus*, *Ruedemannipterus*, *Buffalopterus*, *Strobilopterus* and *Syntomopterus*. There are a number of poorly known species in this clade that might add new genera, but all species that can be unequivocally assigned to this clade existed in Laurentia and Baltica, with one species from Avalonia (Table 3). Many of the most common and best-known eurypterids belong to this clade; in most rich Silurian eurypterid Lagerstätten, around 90% of eurypterid specimens belong to this clade. Since *Eurypterus* and the other members of the Eurypteroidea were unable to spread beyond Laurussian waters (Fig. 3B, C), it is not surprising that few eurypterids have been found outside the palaeocontinents making up Laurussia. Three species of *Eurypterus* from China were described by Chang (1957). However, there is no evidence suggesting these represent *Eurypterus*; they are maybe not even eurypterids, and are therefore excluded (Table 7) until their eurypterid nature can be convincingly demonstrated.

The genus *Eurypterus* dominates many of the Silurian eurypterid faunas of Laurentia. *Eurypterus* is by far the most common eurypterid in museum collections, probably representing more than 95% of known eurypterid specimens. However, it does not appear that the genus originated in Laurentia. All the earliest records of the genus (disregarding '*E.* *minor*', which appears to belong to the Dolichopteridae; Tetlie and Cuggy, in press) are from Baltica. *Eurypterus* is therefore probably an invasive species in Laurentia, but seems to have adapted well to its new territory.

4.2.4. Mixopteroidea

The internal phylogeny of the Mixopteroidea is still poorly resolved. Only a selection of taxa is presented in Fig. 1, but the taxa belonging to the clade (Table 4) are easily recognized by their scorpion-like appearance and heavily spinose appendages. Some of the genera in the clade have been suggested as fully marine (Kjellesvig-Waering, 1961), as opposed to more near-shore brackish or hypersaline. In this clade, the majority of taxa are also from Laurentia, Baltica and Avalonia. Isolated records from the Late Silurian (?) of Viet Nam (Braddy et al., 2002) and the Czech Republic (e.g. Prantl and Přibyl, 1948), show that the terranes of Annamia and Perunica were within dispersal range of these eurypterids (Fig. 3B). If the palaeogeographical hypotheses of Torsvik and Cocks (2004) and Cocks and Torsvik (2002) are correct, Annamia was drifting just north of the equator, east of Laurussia and north of Gondwana while Perunica was further south and west of Annamia. As indicated by Kjellesvig-Waering (1961), only some

presumed basal genera (*Carcinosoma*, *Paracarcinosoma* and *Rhinocarcinosoma*) of the Mixopteroidea have been found in deeper waters, while *Mixopterus* and *Lanarkopterus* have not. It is therefore worth noting that it is representatives of these basal forms that were found in Vietnam and the Czech Republic. It therefore appears that the carcinomatids (basal mixopteroids) had a distribution that was very similar to that of the pterygotoids. It can be predicted that members of the Mixopteroidea could have been able to spread world-wide, but could not have been as common or successful as the pterygotoids.

4.2.5. Waeringopteroidea

The Waeringopteroidea is a very rare group comprising only 5 species (Figs. 1, 4A–C; Table 4). Four of these are from Laurentia, while one of the Devonian forms is from Germany (Dunlop et al., 2002). It is thought that this clade also originated in Laurentia before spreading to Germany in the Devonian after the Rheno–Hercynian Terrane was sutured onto the southern margin of Laurussia. However, the fossil record of this clade is extremely poor, and very little is known about both morphology and true distribution of the taxa in the clade.

4.2.6. Adelophthalmoidea

The Adelophthalmoidea is a taxonomically diverse clade with 43 species (Table 5). It is also the longest lasting of the clades in the Eurypterina (swimming forms), with a net longevity of at least 170 Ma, becoming extinct in the Middle Permian (270 Ma — Fig. 5C). It is the survival of the genus *Adelophthalmus* (and the poorly known and monospecific *Unionopterus* from Kazakhstan) that solely contributes to the survival of the clade past the Middle Devonian (Tetlie and Poschmann, in review). *Adelophthalmus* is first encountered in western Germany in the Early Devonian (Poschmann, 2006), but after the amalgamation of Pangaea (Carboniferous and Permian), the genus gained an almost cosmopolitan distribution (Figs. 4, 5). The most basal species identified so far in the clade is from Baltica (Estonia), but it is not possible presently to pinpoint where the clade originated, probably it was in Baltica or Laurentia. Like many of the other clades, the Adelophthalmoidea has all the evolution of its basal members taking place in Laurussia. However, the adelophthalmoids were streamlined, slippery-looking animals and were apparently able swimmers. By the Devonian (Fig. 4C), representatives are found both in Siberia and Australia, long before Pangaea was assembled.

4.2.7. Pterygotoidea

The Pterygotoidea is the taxonomically most diverse of all the eurypterid clades comprising 56 species (Table 6).

Although the clade only existed for around 40 Ma in a period when most continents were widely separated, it clearly is the clade to have the most cosmopolitan distribution (Fig. 4B, C). High species diversity might suggest species level endemism, but it is likely the clade is presently oversplit. Like the other clades, these eurypterids are most commonly found in Laurentia, Baltica, Avalonia and the Rheno–Hercynian Terrane, but unlike the other Silurian and Early Devonian forms, they are also relatively commonly found in other palaeocontinents. They have been reported from Australia (McCoy, 1899; Burrow et al., 2002), Libya (Kjellesvig-Waering, 1964), Algeria (Depitout, 1962), Morocco (Waterlot and Lévêque, 1960; Berry and Boucot, 1973), Florida (Kjellesvig-Waering, 1950; 1955), Saudi Arabia (Al-Hajri and Paris, 1998), Iberia (Chlupáč et al., 1997), China (Tetlie et al., 2007), South America (Kjellesvig-Waering, 1964; 1973; Chris Berry pers. comm., 2004), all the former parts of Gondwana, Bohemia (e.g. Barrande, 1872; Semper, 1898; Seemann, 1906; Prantl and Přibyl, 1948; Chlupáč, 1994) just off the northern coast of Gondwana, and Siberia (Novojilov, 1959). The earliest fossils of this clade occur in the latest Llandovery, and are found dispersed in Scotland, Laurentia and South China. This mobility makes it difficult to pin down exactly where the clade originated, but alike its sister-clade, the Adelophthalmoidea, the Pterygotoidea likely had their origins in or close to Laurentia. Until a more inclusive phylogeny of the clade is in place, it cannot be known to what extent the pterygotoids crossed oceans as isolated occurrences or on a regular basis. Like the adelophthalmoids, the pterygotoids were obviously very good swimmers, something that can help to explain the dispersal patterns between continents seen in these two clades.

5. Discussion

Eurypterids are non-mineralized arthropods and their fossil record is therefore relatively incomplete (Tetlie and Cuggy, in press; Tetlie and Poschmann, in review). However, recent advances in resolving the phylogeny of the group have resulted in this first attempt to put together a spliced tree containing all the major clades of swimming eurypterids and some walking forms (Fig. 1). The distribution of eurypterids is here interpreted from both a phylogenetic and palaeogeographical perspective. It has long been noted that almost all described eurypterid taxa have been recorded from the palaeocontinents of Laurentia, Baltica, Avalonia and the Rheno–Hercynian Terrane. It has not been known whether this distribution represent a true signal or a research and collection bias (e.g. Plotnick, 1999).

The majority of eurypterid taxa are known from a time interval when Laurentia, Avalonia, Baltica and the Rheno–Hercynian Terrane were in close proximity. Several clades are confined only to these palaeocontinents. For instance, the Megalogrptoidea are known only from Laurentia, Waeringopteroidea from Laurentia and the Rheno–Hercynian Terrane and the Eurypteroidea from Laurentia, Baltica and Avalonia (one potential record has also been discovered in the Rheno–Hercynian Terrane; Poschmann, in press). Also, it seems clear that most of the clades originated in Laurentia, and the palaeocontinent has a central role in the evolution of every single clade, with the exception of the *Rhenopterus–Alkenopterus* clade that is confined to the Rheno–Hercynian Terrane in its entirety. The Australian species assigned to *Rhenopterus* by Tetlie et al. (2004) was correctly reassigned to *Adelophthalmus* by Poschmann (2006).

The earliest records of Euryptera are from Avalonia and Laurentia, but the origin of the Order is not possible to identify any closer until its Ordovician fossil record is better documented. Most of the stylonurid eurypterids are found in Scotland, originally a part of Laurentia that sutured onto Avalonia, possibly in the Wenlock (Lees et al., 2002). Scotland continued to be the main area for stylonurids until at least the Early Devonian, when many stylonurids are found in what is today western Germany. The Rheno–Hercynian Terrane was sutured onto Laurussia some time in the Devonian, allowing stylonurids to migrate into this new area. The only stylonurids to survive into the Carboniferous and Permian, the hibbertopterids and woodwardopterids dispersed to Gondwana (Brazil, Argentina, South Africa) and Siberia, apparently before the continents were fused into Pangaea, but the existence of one major continent would have allowed further dispersal and radiation of both the stylonurids and the only surviving swimming forms, the adelophthalmids.

The most primitive known form with a swimming leg is *Onychopterella augusti* from South Africa. However, this occurrence is isolated and it is suggested here that the swimming forms probably also originated in Laurentia, since both the stylonurids (including those that are ancestral to *Onychopterella*) and other primitive swimming forms are known mainly from Laurentia (or Laurussia). How *O. augusti* managed to get to South Africa is an open question, but there must have been a population since several specimens are known.

The megalogrptooids and the eurypterooids are the two most primitive larger clades of swimming eurypterids, although their position relative to each other is not entirely clear. The Megalogrptoidea are found only in Laurentia while Eurypteroidea are found predominantly in Laurentia and Baltica with additional sparse records

from Avalonia and the Rheno–Hercynian Terrane. This clade probably originated in Laurentia, but by the Middle Silurian, there was a continuous exchange between the Laurentian and Baltic faunas of eurypteroids, as indicated by the common intermixing of Laurentian and Baltic taxa in this clade. The genus *Eurypterus*, the signature eurypterid of the famed sequences of New York State had its first occurrences in Baltica and apparently later invaded Laurentia.

The mixopteroids probably originated in Laurentia. The more primitive forms were able swimmers and some forms spread all the way to the Annamia and Perunica palaeocontinents, now Vietnam and the Czech Republic. The more derived forms were probably not very mobile, and the evolution of these forms (*Mixopterus* and *Lanarkopterus*) took place in Scotland at the start of the Silurian. These forms did not spread beyond Laurussia. The waeringopteroids were also first documented in Laurentia, but this poorly known group has only been found there and later in the Rheno–Hercynian Terrane (western Germany) when it became a part of Laurussia.

The two remaining clades, the Adelophthalmoidea and the Pterygotoidea, were likely the most able swimmers among the eurypterids both based on their morphology and because they were the most dispersed throughout the world. This mobility and the fact that Laurentia and Baltica were adjacent when these two clades developed make it hard to determine the place of origin for both clades. The Adelophthalmoidea has most of its basal representatives in Laurentia, Avalonia and Baltica. However, when the Rheno–Hercynian Terrane is added to Laurussia, many Devonian forms are found here, including the earliest known *Adelophthalmus*. The clade spread to Siberia in the Early Devonian and Gondwana (Australia) in the Late Devonian. From the Carboniferous, the distribution of *Adelophthalmus* is approximately circumequatorial (Fig. 5).

The Pterygotoidea also has a geographic origin that is troublesome to trace. The clade appeared more or less simultaneously in the Llandovery of Scotland, eastern North America and China. The first two are in Laurentia, but the latter is on the South China Block, far into the Panthalassic ocean. This wide dispersal is probably a testament to the substantial swimming abilities found in these eurypterids. This trend is continued by the presence of pterygotoids in Venezuela, Bolivia, Morocco, Libya, Algeria, Saudi Arabia, Spain, Florida, Australia, and Siberia in addition to the continual presence in Laurentia, Baltica, Avalonia and the Rheno–Hercynian Terrane.

The distribution patterns of eurypterids are in broad agreement with the positions of continents in the Palaeozoic as ascertained by palaeomagnetism and fish and trilobite

faunas (e.g. Cocks and Fortey, 1982; Cocks and Fortey, 1988; Young, 1990; Torsvik, 1998; Blicek and Janvier, 1999; Cocks, 2001; Cocks and Torsvik, 2002; Torsvik and Cocks, 2004). However, one would expect more diverse eurypterid faunas in Siberia if this palaeocontinent was close to Baltica and Laurentia, but this entire palaeocontinent is probably severely undersampled.

Sampling bias is undoubtedly present and have to be considered, even if the parts of the world that once formed Gondwana are catching up in sampling density. As demonstrated by Smith (2001), area of outcrop is an important factor for the palaeodiversity derived from these outcrops. It is for instance well-known that South America has very limited outcrops of Silurian age, severely limiting the potential for South American eurypterid occurrences. The eurypterids are also commonly found in the dolomitic sequences ('waterlimes') of Laurentia and Baltica, and these types of sediments are rarely known outside of these continents. However, it should be noted that less than half of Silurian occurrences listed from Laurentia and Baltica by Plotnick (1999) are known from 'waterlimes'. It is important to consider these biases even when their effect is difficult to assess.

In summary, the distribution of eurypterids from a phylogenetic perspective suggest that the distinct lack of Siluro–Devonian eurypterid occurrences outside of Laurentia, Baltica, Avalonia, the Rheno–Hercynian Terrane and Siberia is a true signal, and not just a bias from the elevated palaeontological research and fossil collecting in these parts of the world. It may be possible to make some predictions regarding the nature and geographic locality of potential future eurypterid finds. Future discoveries of hibbertopterids and adelophthalmoids in Late Devonian to Permian strata should be possible all over the world. However, the prospects of finding any major Ordovician and Silurian eurypterid occurrences outside of North America and Europe seems small, except for adelophthalmoids, pterygotoids and certain types of mixopteroids. Scattered records of eurypterids in Siberia suggest there is a potential for more discoveries of eurypterids in this sparsely sampled region. There should also be possibilities in Greenland since this landmass was associated with Laurentia and pretty close to Scotland in the Silurian. More discoveries also seem possible in Barentsia (Spitzbergen), Kara (Novaya Zemlya) and the different Kasakh plates. All were approaching Laurussia in the Devonian. With these few exceptions, it seems like we mainly have to rely on further discoveries in Laurentia, Baltica, Avalonia and the Rheno–Hercynian Terrane for furthering our knowledge of eurypterids. Continuing exploration of areas without recorded eurypterid remains is important to test and refine the observed distribution patterns.

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