Selectivity in the evolution of Palaeozoic arthropod groups, with focus on mass extinctions and radiations: a phylogenetic approach

By

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Submitted to the graduate degree program in Geology and the Graduate Faculty of the University of Kansas in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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Abstract: Mass extinctions are known to be extraordinary events during which the normal rules of natural selection do not apply. Evidence points to the operation of a different selective regime, one where clade-level properties are selected upon; however, it is still unclear whether survivorship rules apply across different extinction events, the consequences of differential responses in diversity and disparity during extinction events, and the factors governing subsequent recoveries. This dissertation explores these issues by studying three clades of arthropods that experience multiple extinction events, allowing for the effect of different mass extinctions on the same group to be compared utilizing phylogenetic methodology. Three phylogenies where generated, one each for Stylonurina, Eurypterina, and Aulacopleuroidea. Variations in diversity, disparity, and volatility, are compared across these clades for two extinction events: the end-Ordovician (443 Ma) and the late Devonian (385–359 Ma). Consistent differences in how morphospace occupation changes across the end-Ordovician and late Devonian mass extinction events reveal that the underlying driving factors of individual extinction events can result in very different selective pressures, suggesting that it may not be possible to identify general survivorship rules for all mass extinctions. Ecology is revealed to be a major factor behind the responses of individual species to the late Devonian biodiversity crisis. The somewhat contradictory selective signal exhibited by the studied clades reveals how different aspects of ecology can influence diversity, disparity and volatility in different ways, each influencing aspects of clade survival and recovery in different ways. The results also demonstrate the bearing of the evolutionary history of a clade on such studies. Contingency is an important factor in determining the response of clades to mass extinctions, and only through having a firm understanding of the history of a group can such factors be appropriately accounted for.

It’s always difficult to know exactly how to thank all those people who have supported you through some interminable period of time while you frittered around working on ephemeral projects that seemed to take a lot of hours but produce nothing in the way of physical results. These acknowledgements were initially very short, as I was in the midst of the traditional ‘pressed for time’ period of dissertation writing (the one that begins somewhere near the start of the second year and precedes the ‘bargaining’ phase). For posterity, I leave those words here:

This dissertation is dedicated to my parents and my brother, who have always supported me; my friends, who put up with an awful lot; my advisor, who offered me an amazing opportunity; and Kevin Spacey.

This of course is characteristically glib, and so I want to take the time to expand upon it and thank people properly.

First of all I thank my parents, Chris and Denise Lamsdell, who instilled in me a love of the natural world at a young age through numerous holidays, copious nature documentaries, and an often unappreciated fondness for birdwatching (a hobby which I actually share, however spending an hour or so waiting for a small bird to appear from a thicket while you stand next to an electric fence is always going to prove problematic in some way when you’re ten). They have always supported me, both financially and emotionally, and I can never repay them for everything they've done. Thanks to them I've been able to pursue a career I genuinely enjoy, and I will always be thankful for that. I also thank my brother, Antony Lamsdell, who has always been a good sport and listened to stuff that doesn't really interest him, but has also done me the honour of occasionally being genuinely interested in what I do. He is an excellent artist who was always happy to take the time to play games with me when I was home for Christmas, and I hope we get to spend more time together in the future.

I had a number of years in limbo between my Master's degree and my PhD, and I am grateful to my advisor, Paul Selden, for giving me an amazing opportunity to continue my research. Paul has also been a very understanding advisor, allowing me to design my own project and leaving me to work on it in my own fashion, despite the disappointment that I would not be working on spiders. Every member of my committee exhibited extraordinary patience when faced with a barrage of emails whenever I needed forms signed or some sort of committee meeting, as well as reading through the seven hundred pages of dissertation that follows these words.

Numerous other people not bound by the ties of family or academic bureaucracy have also supported me tremendously over the past few years, and it is because of these friends on both sides of the pond that I have been able to remain (relatively) sane throughout my studies. From the UK, Gary Chisholm, Matt Frith, Dave Marshall, Avril Simister and Marc Williams all spent time communicating via instant messenger or email, stayed up late playing games online, or met up during one of my infrequent visits back home. Avril was particularly kind and read through a number of the dissertation chapters, improving their overall quality and making sure all my argumentation was clear and understandable, while Matt spent many nights with me driving jeeps around the Battlefield servers. I also spent many hours chatting with Dave about various aspects of chelicerate phylogeny, podcasting, and the issues of being a sleepwalker on an oilrig. From America I first wish to thank my officemates, Erin Saupe, Matt Downen and Leah Moelling, all of whom have spent an inordinate amount of time listening to me get angry at various things. Ben Rickards and Kathryn Hoffmeister were great fun to live with during my first year here, and Alicia Rosales (whose faux-English accent resembles that of a Dickensian street orphan) and Anya Hess are both great people to spend time with. I also learnt a lot from the other palaeobiologists in the Lieberman lab; Cori Myers, Wes Gapp, Curtis Congreve, Úna Farrell (our long-suffering collections manager who I always just seemed to create problems for) and Michelle Casey. Curtis and I in particular struck up a great friendship, and have spent a lot of time drinking and discussing movies. Curtis and I also spent many evenings expanding the numbers of films that Paula Richter (one of the sweetest people you could ever meet) has seen. Finally, I must thank Amanda Falk, with whom I have willfully spent far too much time over the last two years, and who frequently has me look after her cat, Sir David Attenborough fon Ronsenburg, Duke of Burble (AKA Mr Jowls, AKA Mr Man, AKA Sir David, AKA Burble, AKA Mr Burble, AKA His Grace, AKA Jowls, AKA Mr Butt, AKA Butt, AKA Mr Butts, AKA Butts, AKA Mr Buttus, AKA Doof), who is the dumbest and cuddliest cat I have ever met. I also had the great fortune to meet Martin Stein during my time at Kansas, from whom I learnt everything I know about Cambrian arthropods and the German sense of humour.

I must also acknowledge Thai Siam for providing excellent food and the bare minimum of service required to entice you into coming back. Curtis, Alicia, Paula, Amanda and myself have eaten there far too often over the years.

Finally (really, this time) I also wish to thank all my coauthors and everybody who provided access to specimens, the details of which are presented in the relevant chapters.

Table of Contents

Introduction

Mass extinctions are known to be unique events in earth history, often marked by extreme faunal turnovers that have drastically altered the trajectory of evolution. During these extraordinary periods the normal rules of natural selection do not apply and an alternative selective regime holds sway; different criteria influence survival than during background extinctions, with other factors such as geographic range at the clade level playing a greater role. The study of mass extinctions and their aftermath is a major cornerstone of paleobiology, yet despite decades of research there remain a number of issues to which solutions have proved elusive. These include whether there are general survivorship rules that apply across different mass extinction events, the consequences of inexact correlations between taxonomic and morphological diversity, and the factors governing the dynamics and outcome of recoveries. This dissertation seeks to explore these issues by studying clades that experience multiple extinction events, allowing for the effect of different mass extinctions on the same group to be compared. Through incorporating data from multiple clades across the same time period it is also possible to compare how the different groups react to the same extinction events. These studies utilize phylogenetic methodology to ascertain the internal relationships of the target clades. Accurate phylogenetic relationships are integral for any meaningful understanding of the responses these groups exhibit to mass extinction events to be possible. Three arthropod groups are included as part of the study, the eurypterid suborders Stylonurina and Eurypterina and the trilobite superfamily Aulacopleuroidea. All three clades have evolutionary histories spanning the majority of the Paleozoic, from the Ordovician to the Permian, and as such pass through two mass extinctions, the end-Ordovician and late Devonian. The end Ordovician mass extinction has been linked to the rapid formation of an unstable icehouse in the middle of otherwise greenhouse conditions, with the sudden glaciation and subsequent return to greenhouse conditions resulting in pulsed periods of cladal turnover, therefore exhibiting heightened rates of extinction mediated by rapid climate change. This is not true of the late Devonian event, however, during which the biodiversity loss has been linked to a drop in speciation rates due to a decrease in endemism, with a shutdown in vicariant speciation attributable to widespread interbasinal species invasions mediated by a global increase in sea level. This affords an excellent opportunity to compare the impacts of two very different mass extinction events on three arthropod groups.

This dissertation comprises a series of taxonomic and phylogenetic works that form the basis of detailed analyses of the influence of Paleozoic mass extinctions on three arthropod clades. The first part of the dissertation (Chapters 1–6) consists of works focusing on eurypterid phylogeny; the redescription of *Drepanopterus pentlandicus* and *Melbournopterus crossotus* have deep implications for stylonurine phylogeny, while the redescription of *Stoemeropterus conicus* and the description of three new eurypterine species helps provide a strong groundwork for a robust phylogeny of the Eurypterina. The second part (Chapters 7–8) focuses on aulacopleuroid phylogeny, the first chapter consisting of a broader analysis of trilobites in order to ascertain the status of proetide monophyly while the second comprises a detailed analysis of aulacopleuroid relationships. The final part (Chapters 9–10) constitutes studies on variations in diversity and disparity across the end-Ordovician and late Devonian mass extinctions along with comparisons of rate of character change and volatility between the three clades.

Part 1

On eurypterid phylogeny

Chapter 1

Redescription of *Drepanopterus pentlandicus* Laurie 1892, the earliest known mycteropoid (Chelicerata: Eurypterida) from the early Silurian (Llandovery) of the Pentland Hills, Scotland

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(Formatted for submission to *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*)

ABSTRACT: *Drepanopterus pentlandicus* Laurie, 1892 is redescribed from the original type material along with previously unfigured specimens. A cleft metastoma is confirmed as a characteristic of the genus along with the armature of the second and third prosomal appendages being modified into flattened blades, while the species is shown to possess a somewhat enlarged second tergite and lateral prosomal margins that overlap the first opisthosomal tergite. Different ontogenetic stages of *D. pentlandicus* are described and it is revealed that these latter characters develop only later in ontogeny, suggesting that described specimens of *Drepanopterus abonensis* Simpson, 1951 may represent juveniles. Cladistic analysis of Stylonurina shows the genus *Drepanopterus* to be monophyletic consisting of *D. pentlandicus*, *D. abonensis* and *D. odontospathus* sp. nov., and forms a basal clade of mycteropoids. Hibbertopteroidea Kjellesvig-Waering, 1959 is shown to be a junior subjective synonym of Mycteropoidea Cope, 1886, with the synonymy of many of the hibbertopterid genera hypothesised and *Hibbertopterus* Kjellesvig-Waering, 1959 suggested to represent juvenile specimens of *Cyrtoctenus*

Størmer & Waterston, 1968. *Hibbertopterus permianus* Ponomarenko, 1985 is transferred to *Campylocephalus* Eichwald, 1860. The role of heterochrony in the morphological development of the mycteropoid lineage is discussed, with both hibbertopterids and mycteropids suggested to be hypertrophic and pre displacement peramorphs respectively.

The description of the Pentland Hills arthropod fauna in two seminal papers by Laurie (1892; 1899) marked a turning point in eurypterid research. The co-occurrence of so many species at a single locality makes it the most diverse eurypterid locality in the world (Plotnick 1999) while the style of preservation means that vast amounts of morphological detail can be observed, especially of the organisms' ventral surface. Laurie was the first to assign a stylonurine (i.e. eurypterids with a swimming paddle lacking a modified podomere 7a on appendage VI) to a genus other than *Stylonurus* Page, 1856, and while this view was later temporarily rejected in favour of creating various subgenera of *Stylonurus* by Clarke & Ruedemann (1912) it is now recognised that the erection of *Drepanopterus* Laurie, 1892 was the first concession to the true morphological diversity of Stylonurina.

Laurie's morphological descriptions were generally highly detailed and accurate, however it is only recently that they have been viewed in a context beyond their initial taxonomic assignments, which were somewhat constrained by the framework at the time. Waterston (1979) reviewed many of the stylonurine eurypterids, although it is only in recent years that there has been serious renewed interest in the Pentland fauna with the recognition of *Bembicosoma pomphicus* Laurie, 1899 as a synziphosurine (Anderson &

Moore 2004) and *Kiaeropterus cyclophthalmus* (Laurie, 1892) as a member of the Stylonurina (Tetlie *et al*. 2007) and not a *Eurypterus* as initially described. Reinvestigation of the various further *Drepanopterus* species described by Laurie (1899) revealed that the genus was polyphyletic and that '*Drepanopterus*' *bembycoides* Laurie, 1899 and '*Drepanopterus*' *lobatus* Laurie, 1899 were synonyms of '*Nanahughmilleria*' *conica* Laurie, 1892 and belonged in a distinct genus closely related to members of the basal Eurypterina (Lamsdell 2011) while *Drepanopterus pentlandicus* Laurie, 1892 remained within the Stylonurina.

Redescription of *Drepanopterus abonensis* Simpson, 1951 from the Upper Devonian of Portishead, Somerset showed it to be a basal member of the predominantly Carboniferous-Permian sweep-feeding mycteropoids, a derived stylonurine clade marked by their bizarre morphology and generally large size (Lamsdell *et al*. 2009). Comparison with Laurie's (1892; 1899) published figures suggested that *D. abonensis* and *D. pentlandicus* were indeed congeneric, and if so this would make *D. pentlandicus* the earliest mycteropoid, being from the Llandovery (early Silurian). However, the temporal gap between the two species (some 54 million years) and the limitations inherent in studying the figures from Laurie's original works mean that restudy of *D. pentlandicus* is needed in order to confirm the monophyly of the genus. When studying the Pentland Hills material in 2009 the author discovered over 30 well preserved specimens of *Drepanopterus pentlandicus*, much more than the three described and figured by Laurie, and these make up the basis of the work herein.

1. Previous Work

The Silurian eurypterid fauna of the Pentland Hills was first described by Laurie (1892, 1899) and is possibly one of the most important eurypterid fossil sites in the world, accounting for 15% of all known stylonurine eurypterid species. In total nine genera are known from the site, along with one genus of scorpion and a single genus of xiphosuran. The Hardie and Henderson collections (housed in the National Museums of Scotland) provided the material for Laurie's original work, and these specimens were also the subject of extensive study by Lamont (1955) and Waterston (1979). Renewed interest in the site in recent years has resulted in the redescription of several of Laurie's original taxa, including the xiphosuran *Bembicosoma pomphicus* (Anderson & Moore 2004) and the eurypterids *Kiaeropterus cyclophthalmus* (Laurie, 1892) (Tetlie *et al.* 2007), *Stoermeropterus conicus* (Laurie, 1892) (Lamsdell 2011), and *'Eurypterus' minor* Laurie, 1899 (Tetlie 2006), which has been shown to represent a genus separate from *Eurypterus sensu stricto* (Tetlie & Cuggy 2007).

Drepanopterus pentlandicus was among the first Pentland eurypterids to be described and was originally known from only two specimens within the Henderson collection (Laurie 1892). The acquisition of the Hardie collection greatly increased the number of known specimens for the species, however only one of these was described and figured (Laurie 1899), leaving most of the details of the ventral aspect unknown. Despite a number of relatively complete, unfigured specimens the species has received no further treatment, aside from the Hardie collection specimen figured by Laurie being re-figured in Clarke & Ruedemann (1912, fig. 69) and for a photograph of the holotype to be figured by Anderson (2007, pl. 26 fig. 3). A number of other *Drepanopterus* species have been described however, although most have since been removed from the genus; '*D.*' *bembycoides* Laurie, 1899 and '*D.*' *lobatus* Laurie 1899 were shown to be synonyms of the basal eurypterine *Stoermeropterus conicus* (Lamsdell 2011), *Kokomopterus longicaudatus* (Clarke & Ruedemann, 1912) was transferred from the genus by Kjellesvig-Waering (1966), *D. ruedemanni* O'Connell, 1916 was shown to be a lithic clast by Tollerton (2004), *Vinetopterus struvei* (Størmer, 1974) was removed by Poschmann & Tetlie (2004) and '*D.*' *nodosus* Kjellesvig-Waering & Leutze, 1966 is considered congeneric with *S. conicus*. Therefore aside from *D. pentlandicus* only two other species of *Drepanopterus* are currently recognised as valid – *D. abonensis* Simpson, 1951 from the Upper Devonian of SW England and an unnamed species described by Braddy & Dunlop (2000) from the Lower Devonian of Arctic Canada. The genus received its most recent treatment when *Drepanopterus abonensis* was restudied by Lamsdell *et al*. (2009), where it was considered to have affinities with the large sweep-feeding mycteropoids, and subsequent phylogenetic analysis supports this theory (Lamsdell *et al*. 2010a).

Two other eurypterid species have been suggested to have affinities with *Drepanopterus*. *Onychopterella* (?) *pumilus* (Savage, 1916) was suggested to be a *Drepanopterus* by Plotnick (1999) and an unnamed, undescribed drepanopterid was partially figured by Størmer & Kjellesvig-Waering (1969, fig. 2d), however both of these assignments were suggested before it was realised that the genus was polyphyletic. *O*. (?) *pumilus* is reportedly reposited at the University of Illinois, although its accession number is unknown and so restudy has proved impossible. Details of the morphology as suggested by the only known figure (Savage 1916, pl. 17, fig. 8), specifically the form of the metastoma, genital appendage and telson, suggests its affinities lie with *Stoermeropterus* Lamsdell, 2011 rather than *Drepanopterus*. The known morphology of the undescribed drepanopterid however corresponds well to that of *Drepanopterus pentlandicus* and *D. abonensis*, having a broad body, short and robust spatulae and a long type A genital appendage. Aside from its mention in Størmer & Kjellesvig-Waering (1969), however, no trace of this specimen is known and at present it must be considered lost.

2. Material and methods

All the known specimens of *Drepanopterus pentlandicus* are held at the National Museums of Scotland (NMS) in the Hardie (NMS G.1897.32) and Henderson (NMS G.1885.26) collections. Specimens were photographed under low-angle light using a Panasonic Lumix DMC-FZ50 digital camera. Interpretative drawings were prepared using Adobe Illustrator CS4, on a MacBook Pro running OS X, while reconstructions were prepared in outline in Adobe Illustrator CS4 and shaded in Adobe Photoshop CS4 using the methodology described by Coleman (2003). Phylogenetic analysis consisting of 80 characters coded for 36 taxa was performed using random addition sequences followed by branch swapping (the *mult* command) with 100,000 repetitions with all characters unordered and of equal weight in TNT (Goloboff *et al*. 2008; made available with the sponsorship of the Willi Hennig Society). Jackknife (Farris *et al*. 1996), Bootstrap (Felsenstein 1985) and Bremer support (Bremer 1994) values were calculated in TNT and the Consistency, Retention and Rescaled Consistency Indices were calculated in Mesquite 2.73 (Maddison & Maddison 2010). The matrix is deposited in morphobank

(O'Leary & Kaufman 2007) with the project code p586 and can be accessed from http://morphobank.org/permalink/?P586. The previous incarnations of the phylogenetic matrix from Lamsdell *et al*. (2010a and b) have also been reposited in morphobank with the project codes p537 (http://morphobank.org/permalink/?P537) and p541 (http://morphobank.org/permalink/?P541) respectively.

Eurypterid terminology largely follows Tollerton (1989) for morphology of the carapace, metastoma, lateral eyes, prosomal appendages, genital appendage, opisthosomal differentiation, telson, and patterns of ornamentation, however the terminology for the ventral plate morphologies follows the revised types of Tetlie *et al*. (2008) and Tollerton's *Drepanopterus*-type prosomal appendage was shown to be absent on *Drepanopterus sensu stricto* by Lamsdell *et al*. (2009). Selden (1981) is followed for prosomal structures and cuticular sculpture and the labelling of the appendages. Terminology for the segmentation of the genital operculum follows Waterston (1979), while mycteropoid morphological features are as defined in Lamsdell *et al*. (2009); the term 'blade' is used for the broad, flattened spines bearing sensory setae on the anterior prosomal appendages (Selden *et al*. 2005), 'rachis' (pleural 'rachises') refers to the comb-like spines in *Cyrtoctenus* (Waterston *et al*. 1985) and the term 'lade' (pleural 'laden') refers to the plate-like structures that overlie the coxae (Waterston 1957).

2.1 Institutional Abbreviations

BMAG, Bristol Museum and Art Galleries, Bristol, UK; CMN, Canadian Museum of Nature, Ottawa, Canada; MBA, Museum für Naturkunde, Berlin, Germany; NMS, National Museums of Scotland Collection Centre, Edinburgh, Scotland, UK; PIN, Paleontological Institute, Moscow, Russia.

3. Geological Setting

All known specimens of *Drepanopterus pentlandicus* originate from the Eurypterid Bed at Gutterford Burn [GR NT155579] in the Pentland Hills, located SW of Edinburgh, Scotland. The Gutterford Burn succession was recently described in detail by Anderson *et al*. (2007) and the Eurypterid Bed placed at the base of the Deerhope Formation which is considered to be a shallow marine phase of a continuous marine regression (Clarkson 2000). The Eurypterid Bed is located near the base of the exposure of the Gutterford Burn, situated 3 m up from where the succession dips beneath the water level, however the strata here have been overturned and so the Eurypterid Bed is one of the chronologically younger beds. The Eurypterid Bed itself is *c.* 55 cm thick, with its lower surface not directly conformable with the underlying siltstones suggesting the infilling of a pre-existing irregular sea floor topography (Anderson *et al*. 2007). 13 cm from the base of the bed is a calcareous-rich horizon containing crinoid ossicles, stick bryozoans, monograptids and brachiopods, while two thin clay bands exist, the first 8 cm up from the bed's base while the second covers the top of the Eurypterid Bed with an irregular topology suggesting it draped the underlying beds.

The bed was recognised as a Konservat-Lagerstätte by Anderson *et al*. (2007), citing the presence of eurypterids, scorpions and synziphosurines which have a non-mineralised cuticle that is rarely preserved in the fossil record (Gupta *et al*. 2007). The arthropod specimens within the Eurypterid Bed are mostly entire individuals associated with articulated crinoids, echinoids and starfish and this, coupled with the layers of volcanic clay, suggests that the bed represents a smothering event caused by the seabed being rapidly covered by a sudden influx of fine-grained, volcanic ash sediment (Anderson *et al*. 2007). Similar events are thought to be responsible for the exceptional preservation in the upper Ordovician Elkhorn Formation, Ohio (Caster & Kjellesvig-Waering 1964) and the Wenlock Herefordshire Lagerstätte (Orr *et al*. 2000). Anderson *et al*. (2007) suggested that the localised preservation of the eurypterids in 'hollows' of the bedding surface was due to infilling of the pre-existing topography while the concentration of faunal elements such as starfish could be explained by their clustering at the bottom of such hollows in the sea floor. This is a similar depositional environment to that proposed for the fauna preserved in submarine channel slides from Leintwardine in England which also includes both eurypterids and synziphosurines (Whitaker 1962).

Alongside *Drepanopterus pentlandicus* the eurypterids *Parastylonurus ornatus* (Laurie, 1892), *Parastylonurus hendersoni* Waterston, 1979, *Hardieopterus macrophthalmus* (Laurie, 1892), *Laurieipterus elegans* (Laurie, 1899), '*Eurypterus*' *minor* Laurie, 1899 '*Carcinosoma*' *scoticum* (Laurie, 1899), *Slimonia dubia* Laurie, 1899 and *Stoermeropterus conicus* (Laurie, 1892) are also found in the same bed, as are the scorpion *Dolichophonus loudonensis* (Laurie, 1899) and synziphosurine *Bembicosoma pomphicus*. Aside from the chelicerates the Eurypterid Bed fauna consists of *Dictyocaris ramsayi* Salter, 1860, now considered to be a benthic marine alga (Botting 2007), polychaete burrows (Allan 1927), octocorals, bryozoans, abundant crinoids, stelleroids, the echinoid *Aptilechinus caledonensis* Kier, 1973, brachiopods, the gastropod *Euomphalopterus* cf. *apedalensis* Pitcher, 1939 and the cephalopod *Geisonoceras maclareni* (Murchison, 1859), and monograptid graptolites.

The Eurypterid Bed was interpreted as marginal marine (BA1) by Plotnick (1999), possibly representing a tidal flat setting, and Waterston (1979) mentioned large amounts of plant material found in the Eurypterid Bed, which could suggest a terrestrial influence and an external source for some of the faunal elements. Excavation of the Eurypterid Bed itself however yielded no plant material (Anderson *et al*. 2007), and a detailed study of the specimens held at NMS confirmed that no terrestrial plant material is found in association with the Eurypterid Bed fauna. Furthermore, the associated fauna of echinoids, starfish and brachiopods indicates that the Eurypterid Bed was preserved under normal marine salinity and the most recent work by Anderson *et al*. (2007) supports the depositional environment suggested by Clarkson & Taylor (2002) of suspension flows below wave-base on the seaward side of an offshore bar.

4. Systematic Palaeontology

Eurypterida Burmeister, 1843

Stylonurina Diener, 1924

Superfamily Mycteropoidea Cope, 1881

(= Hibbertopteroidea Kjellesvig-Waering, 1959)

Emended diagnosis. Stylonurina with posterior cleft on metastoma; annular cuticular thickening surrounding lateral eyes; posterolateral carapace margins overlap first opisthosomal tergite; anterior appendages with armature modified into flattened blades (emended from Lamsdell *et al*. 2010a).

Remarks. Hibbertopteridae Kjellesvig-Waering, 1959, Drepanopteridae Kjellesvig-Waering, 1966, and Mycteropidae Cope, 1886 were included in a single superfamily by Lamsdell *et al*. (2010a) under the name Hibbertopteroidea Kjellesvig-Waering, 1959.

However, the family Mycteropidae formed the type family for the superfamily Mycteropoidea by Novojilov (1962), and following the Principle of Coordination (International Code of Zoological Nomenclature articles 36, 43 and 46) the correct author of this superfamily is also Cope 1886. Hibbertopteroidea is therefore a junior subjective synonym of Mycteropoidea.

The diagnosis for the superfamily is modified from Lamsdell *et al*. (2009, 2010a) which makes reference to 'round lenses overlying the lateral eyes'. While there is a circular structure surrounding each of the lateral eyes in mycteropoids, herein termed the annular cuticular thickening as in its original description by Waterston (1957), there is no direct evidence that this structure bore a lens. The concept appears to stem from Tetlie (2004) who referred to 'calcareous lenses', probably based on the fact that a thin film of calcite covered the ocular region on one specimen of *Hibbertopterus* (Waterston 1957) and the only known specimen of *Woodwardopterus* has its eye region obscured by calcium carbonate pustules (Selden *et al*. 2005). The calcite is probably diagenetic in origin however as chelicerates have an unmineralised cuticle and calcareous lenses have not been preserved in any of the numerous other mycteropoid fossils displaying the lateral eyes.

Family Drepanopteridae Kjellesvig-Waering, 1966

Drepanopterus Laurie, 1892

Type species. *Drepanopterus pentlandicus* Laurie, 1892 by original designation.

Emended diagnosis. Drepanopteridae with crescentic lateral eyes; prosomal appendages II–III spiniferous with spines modified into flattened blades; prosomal appendages IV–VI nonspiniferous *Kokomopterus*-type; metastoma oval, cleft posteriorly with anterior notch; type A genital appendage long, reaching to fifth segment of mesosoma, and with spatulae; cuticle displays pustular ornamentation with paired median tubercles on tergites 2–5 (emended from Lamsdell *et al*. 2009).

Remarks. The diagnosis for the genus is updated from Lamsdell *et al*. (2009) as several characteristics such as the cleft metastoma previously only known from *D. abonensis* can now also be confirmed in *D. pentlandicus*.

Drepanopterus pentlandicus Laurie, 1892

Figures 1, 3–21

Emended diagnosis. *Drepanopterus* with a dorsal ornamentation of pustules grading into acicular scales towards the margins of the carapace and tergites; lateral eyes crescentic, lacking enlarged palpebral lobe; small angular prosomal posterolateral lobes present resulting in the tergite of somite VIII being partially overlapped by the carapace in adults; tergite of somite IX elongated in adults; Blattfüsse of somites X and XI lack medial fusion; telson clavate in adult individuals (emended from Laurie 1892).

Type material. NMS G.1885.26.72.5 and G.1885.26.72.6, part and counterpart (holotype), NMS G.1885.26.72.15 (paratype).

Additional material. NMS G.1885.26.72.3, G.1885.26.72.10, G.1885.26.72.11, G.1885.26.72.12, G.1897.32.18, G.1897.32.71, G.1897.32.72, G.1897.32.91, G.1897.32.92, G.1897.32.94, G.1897.32.97, G.1897.32.98, G.1897.32.99, G.1897.32.100, G.1897.32.101, G.1897.32.102, G.1897.32.103, G.1897.32.105, G.1897.32.106, G.1897.32.107, G.1897.32.108, G.1897.32.109, G.1897.32.110, G.1897.32.111, G.1897.32.112, G.1897.32.113, G.1897.32.114, G.1897.32.115, G.1897.32.117, G.1897.32.119, G.1897.32.188, G.1897.32.209, G.1897.32.219, G.1897.32.221, G.1897.32.122, G.1897.32.868, G.1897.32.869.

Remarks. Laurie (1899) figured a single specimen from the Hardie collection, unfortunately this specimen could not be traced and appears to have been lost. One specimen, NMS G.1891.39.18, was identified as its counterpart, however it does not preserve the full detail of the lateral eyes and lacks the distal parts of the prosomal appendages, the metasoma and telson, and so Laurie's figure of the original specimen is reproduced here (Fig. 1). Laurie (1892) referred another specimen (NMS G.1885.26.72.15) to *Drepanopterus pentlandicus* with reservations, however the ornamentation clearly shows that this small specimen is indeed *D. pentlandicus*. The specimen confirms a phenomenon also seen in *D. abonensis* (but omitted from the discussion of Lamsdell *et al*. (2009)), that the telson shape in *Drepanopterus* changes through ontogeny with smaller individuals possessing a lanceolate telson which becomes clavate in adults.

There are a number of key differences between *D. pentlandicus* and the two Devonian species; it lacks the reniform palpebral lobe, retains a cuticular ornament of acicular scales towards the margins of the carapace and tergites and lacks the striate ornament on its marginal rim. While the lack of an enlarged palpebral lobe in particular might suggest that it is further removed from the other mycteropoids than either Devonian *Drepanopterus* species a number of characteristics including the broad marginal rim, pustular ornamentation and paired tubercles suggest that the *Drepanopterus* clade is a monophylum and that *D. pentlandicus* has retained a number of plesiomorphic character states; either these represent reversals or the enlarged palpebral lobes evolved independently in *Drepanopterus* and the remaining mycteropoids, however this at present remains equivocal.

Drepanopterus odontospathus sp. nov.

Drepanopterus sp. Braddy & Dunlop 2000, p. 1172, fig. 4

Diagnosis. *Drepanopterus* with crescentic lateral eyes with a reniform palpebral lobe; marginal rim with striated ornament; telson margin serrate.

Etymology. Named *odontospathus* after the Greek οδοντωτή meaning notched or serrated and σπαθί, meaning sword, in reference to its serrated telson.

Holotype. CMN 51123, carapace part and partial counterpart.

Additional material. CMN 51120b and MBA 934 (paratypes), telson part and counterpart.

Remarks. The two specimens assigned to this species were described by Braddy & Dunlop (2000) from the Emsian of Arctic Canada. While the remains are fragmentary they are clearly those of a *Drepanopterus* with a distinct telson morphology, and so the specimens are assigned to this new species. The species is an important one, as it is the first record of a mycteropoid, and the only Drepanopteridae, from North America. Of the existing *Drepanopterus* species *D. odontospathus* is morphologically closer to *D. abonensis*, with the carapace appearing almost identical. The lateral eyes preserve perhaps the best example in the genus of the annulated cuticular thickening within the genus, preserving the reniform palpebral lobe faintly within an oval, grooved outline (Braddy & Dunlop 2000 fig. 4a). The initial size estimate of 70 cm given by Braddy & Dunlop is based on the old, incorrect reconstruction of *Drepanopterus abonensis* according to Simpson (1951). Scaling the Canadian specimens to the new reconstruction of Lamsdell *et al.* (2009) gives a size estimation of 40 cm. The serrate margin of the telson is reminiscent of the ornamentation on the telson of the mycteropid *Hastimima* (White 1908) while the gross morphology is less clavate than in the other *Drepanopterus* species and appears broader and more lanceolate, closer to the morphology of *Hibbertopterus* (Jeram & Selden 1994).

Family Hibbertopteridae Kjellesvig-Waering, 1959

Campylocephalus Eichwald, 1860

Type species. *Limulus oculatus* Kutorga, 1838.

Emended diagnosis. Hibbertopteridae with subelliptical prosoma broadest at midsection; lateral eyes with reniform palpebral lobe, located on posterior half of carapace (emended from Kjellesvig-Waering 1959).

Remarks. The lack of annular cuticular thickening around lateral eyes of *Campylocephalus oculatus* is probably preservational, as the eyes themselves are preserved only in outline and cuticular thickening structures around the lateral eyes have been observed in *Campylocephalus permianus*.

Campylocephalus permianus (Ponomarenko, 1985)

Hibbertopterus permianus Ponomarenko, 1985, p. 104, fig. 2

Diagnosis. *Campylocephalus* with lateral eyes converging markedly posteriorly.

Holotype. PIN N1209/2, incomplete carapace.

Remarks. The characteristics listed by Ponomarenko as separating this species from other *Hibbertopterus* species, namely the posterior position of the lateral eyes and their non-circular shape, are actually diagnostic of *Campylocephalus*. The characters used to separate the species from *Campylocephalus*, the presence of annular cuticular thickening around the eyes and a different carapace shape, are invalid as *Campylocephalus oculatus* does not preserve the detail of the eye structure and the carapace of *Campylocephalus* is incomplete and flattened, meaning its original shape cannot be ascertained.

5. Morphological Interpretation of *Drepanopterus pentlandicus*

The *Drepanopterus pentlandicus* fossils are preserved in a form typical of the Pentland Hills eurypterids; individuals are relatively intact with the unmineralised cuticle preserved as a brown-green film over impressions of the body. The impressions are sufficiently detailed as to preserve the cuticular ornamentation, even when the cuticle itself has been worn away. There is a distinct phenomenon among the Pentland Hills eurypterids of being preserved in ventral view with the dorsal structures such as lateral eyes and tergite boundaries being superimposed through compression (see Lamont 1955; Waterston 1979) in a manner exceedingly similar to the preservation of some of the eurypterids from Alken an der Mosel, Germany (Størmer 1973; 1974) and may be due to the fine-grained sediment and the coarse nature of the dorsal ornamentation making the rocks more likely to split across the smoother ventral plane of the animal. While this form of preservation is advantageous as the ventral structures such as the genital appendage and metastoma are extremely useful for resolving the relationships of eurypterids it does make reconstructing the dorsal morphology somewhat difficult. Although *Drepanopterus* *pentlandicus* does follow the trend for ventral preservation a greater proportion of its specimens reveal the dorsal aspect, possibly due to its thick dorsal cuticle. In this respect it has the potential to be one of the most completely known Pentland eurypterids, however the anterior appendages are often absent or poorly preserved. A similar problem was noted in *Drepanopterus abonensis* (Lamsdell *et al*. 2009), and it might be that if these appendages were relatively robust they may have regularly broken off at the coxal joint if the carcass or exuviae underwent any transportation. Prosomal appendages II and III are short and robust in *Hibbertopterus scouleri* (Hibbert, 1836) and are only rarely preserved (Waterston 1957); only the most proximal podomeres of these appendages are preserved in *Cyrtoctenus wittebergensis* Waterston, Oelofsen & Oosthuizen, 1985, and *Megarachne servinei* Hünicken, 1980 does not preserve any trace of either appendage pair (Selden *et al*. 2005). *Woodwardopterus scabrosus* (Woodward, 1887) possesses a more gracile appendage III with blades however it is not well preserved and appendage II is absent, and so it appears that these appendages were frequently broken off before preservation in mycteropoids.

The complete nature of the specimens, including the intact ventral prosomal plates and articulated appendages, suggests that they represent mortalities rather than exuviae. Distinguishing between carcasses and moults can be difficult, however the ventral prosomal unit and the carapace and opisthosomal segment one both detach independently from the rest of the exoskeleton during ecdysis (Tetlie *et al*. 2008) and therefore these specimens in all likelihood do represent mortalities. Conversely, while the specimens of *Drepanopterus abonensis* where initially theorised to represent mortalities by Lamsdell *et al*. (2009) the patterns of disarticulation, including having coxa VI preserved with the metastoma, isolated ventral plates and the carapace associated with opisthosomal segment one suggests that these are actually exuviae that have undergone a degree of transportation and further disarticulation after the ecdysial event.

The largest, most complete specimen (NMS G.1897.32.91) has an estimated length of *c.* 38.5 cm, while the largest complete carapace (NMS G.1897.32.869) indicates a total length of *c.* 40 cm, however the average length of the specimens is *c.* 27 cm with the holotype (NMS G.1885.26.72.5) having an estimated total length of *c.* 33 cm. The smallest specimen (NMS G.1885.26.72.15) meanwhile has an estimated length of *c.* 6 cm with other juvenile specimens having estimated lengths of *c.* 18 cm (NMS G.1897.32.18), *c.* 14 cm (NMS G.1897.32.94) and *c.* 9 cm (NMS G.1897.32.108). The animal was broad, with the largest specimens reaching at least 10 cm in width, and deep-bodied down its centre. In adult individuals the carapace accounts for approximately 20% of the total length with the mesosoma accounting for a further 25%, the metasoma 30% and the telson the remaining 25%.

The following descriptions are of the animal in life and are based on a composite of all the available material with individual specimens noted as appropriate. An overall reconstruction of the animal in life is shown in figure 2.

5.1 Prosoma

5.1.1 Carapace and visual structures. The carapace is well represented by fourteen specimens (Table 1), however in only three (NMS G.1885.26.72.5, Figs. 3, 4; G.1897.32.18, Fig. 5c, d; G.1897.32.107, Fig. 6c) is it preserved in its entirety. It is recognisably similar to that of *Drepanopterus abonensis*, being horseshoe-shaped with its widest point being approximately halfway along its length. The carapace is comparatively narrower with a more rounded anterior margin in juvenile specimens such as NMS G.1897.32.18 however it still falls within the boundaries of the horseshoe-shaped morphology. A marginal rim, generally 2–3 mm wide, extends all the way around the front and lateral edge of the carapace and narrows towards its posterior, however unlike *Drepanopterus abonensis* there is no pustule ridge along the marginal rim's inner border, even on well-preserved specimens (e.g. NMS G.1897.32.102, Fig. 6b). The marginal rim also lacks striations, which are present on both *Drepanopterus abonensis* and *Drepanopterus odontospathus*. The posterior margin of the carapace in *Drepanopterus pentlandicus* is somewhat recurved, so that its lateral portions completely overlap the first visible tergite (as in NMS G.1885.26.72.5 and G.1897.32.102) – posterolateral extensions of the carapace are also seen in several specimens of *Drepanopterus abonensis* (Lamsdell *et al*. 2009 pl. 1 fig. 2, pl. 3 fig. 2, pl. 5 fig. 2, pl. 6 fig. 2) although these were not noted in the species redescription. This observation also has ramifications for a specimen of *Drepanopterus abonensis*, BMAG Cb4668 (Lamsdell *et al*. 2009, pl. 3 fig. 2), which was originally considered to show telescoping in the metasoma. However the first tergite is actually somewhat recessed underneath the carapace and the alleged telescoping is actually preservation of the enlarged articulation devices.

The lateral eyes are well preserved, with the visual surface directly observable in five specimens (NMS G.1897.32.18; G.1897.32.97, Figs. 7a, 8; G.1885.26.72.15, Fig. 5b; G.1897.32.868, Fig. 9; G.1897.32.869, Fig. 10), and their general position and outline preserved in several more (e.g. NMS G.1897.32.110, Fig. 11). Among smaller specimens (NMS G.1897.32.18; G.1897.32.98, Fig. 7b; G.1897.32.110) the lateral eyes are closer to around 20% of the carapace length, generally increasing in larger specimens to around

30% of the carapace length, although a number of larger specimens (e.g. NMS G.1897.32.869) exhibit lateral eyes that are only 20% of the carapace length (Table 2). The lateral eyes of juveniles differ in shape, being lunate (NMS G.1897.32.18) rather than arcuate (NMS G.1897.32.102); in those larger specimens that have relatively shorter eyes the degree of curvature of the visual surface is greater, and so all larger specimens consistently have a greater visual surface area than juveniles. In all specimens the lateral eyes are positioned centrimesially, however in the juvenile specimens they are located slightly more anteriorly, similar to the position of the lateral eyes in *Drepanopterus abonensis*. Contra to the expectations of Laurie (1892) none of the *D. pentlandicus* specimens show any indication of a raised palpebral lobe which further serves to differentiate it from the Devonian *Drepanopterus* species, both of which have reniform palpebral lobes. In some of the more poorly preserved *D. pentlandicus* specimens however the lateral eyes appear circular (NMS G.1897.32.110) while on others there are circular grooves surrounding the lateral eyes (NMS G.1897.32.869) and this is due to annular cuticular thickening around the lateral eye (see Waterston 1957). The median ocelli are rarely preserved in Pentland Hills material and are largely obscured in the available specimens of *Drepanopterus pentlandicus*, however in NMS G.1897.32.102 the ocelli are preserved as two indentations on the carapace. They are circular and relatively large, each being 3 mm wide, and positioned centrally between the two lateral eyes at the midpoint of their length.

The cuticular ornamentation of the carapace is much as Laurie (1892) initially described. For the most part the carapace is covered in a pustular ornamentation that slowly grades into broad lunule scales (*sensu* Selden 1981) towards the lateral margins, however even where the scales are at their most prevalent they are interspersed with pustules (NMS G.1885.26.72.3, Fig. 12). The scales on the carapace in *D. pentlandicus* are much more apparent than those of the Devonian species, however some scales are present on the carapace of well preserved *D. abonensis* (Lamsdell *et al*. 2009, pl. 3 fig. 2).

5.1.2 Ventral prosomal plates, prosomal appendages and metastoma. The ventral plates widen anteriorly and in NMS G.1885.26.72.5 and G.1897.32.869 a single median suture is preserved showing that their morphology is also of *Eurypterus*-type. No clear transverse suture is apparent in the majority of specimens, however creases on the ventral plates caused by compression are common and it is likely that the transverse suture has been lost among these taphonomic structures. One specimen, NMS G.1897.32.869 does show a clear suture running across the ventral plate posterior to the marginal rim.

The appendages of *Drepanopterus pentlandicus* are relatively well preserved, however the chelicerae are only preserved in NMS G.1897.32.91 (Fig. 13), where they are shown to be small (6 mm long by 4 mm wide) and angled back towards the mouth presumably through an ‘elbow-joint’ at the attachment of the peduncle and the fixed finger of the chelicera. This morphology corresponds to that of the chelicerae of the other Stylonurina, and of the non-pterygotoid Eurypterina. The same specimen also preserves the only evidence of the second prosomal appendage in the form of the coxae, being 10 mm long and 5 mm wide. Appendage III is known from three specimens, comprising both juvenile and adult individuals (Table 3), and bears similarity to both *D. abonensis* and *Hibbertopterus*. Of the two specimens that preserve more than just the coxa, the larger (NMS G.1897.32.92, Fig. 14a, b) has a podomere structure similar to that of *H. scouleri* as described by Waterston (1957, fig. 4), having short robust podomeres with short fixed spines projecting from the ventral side of each podomere along with moveable blades that are occasionally flexed dorsally so as to appear projecting above the appendage. The appendage is better preserved than the appendage in *D. abonensis* (Lamsdell *et al*. 2009, pl. 1 fig. 9) and shows that, as in *Hibbertopterus*, the cuticular ornamentation becomes more concentrated along the antero-ventral of each podomere and on each blade, possibly consistent with an increase in setal density. The terminal podomere is elongated, as in *D. abonensis*, and curved to resemble a hook-like blade in a manner similar to the terminal podomere of *H. scouleri*. The smaller appendage (NMS G.1897.32.18) differs in having comparatively longer podomeres, and therefore a comparatively longer appendage, with the terminal podomere still appearing elongate but lacking the extreme curvature of the adult specimen. In many ways the juvenile appendage more closely matches the appendage in *D. abonensis* than does the adult, with the blades also appearing to be shorter and less robust.

The three posterior pairs of appendages are all of the *Kokomopterus*-type, with each consecutively posterior pair being longer than the preceding pair. Although appendage IV is preserved in a number of individuals (Table 4) only NMS G.1897.32.18 shows details of more than just the coxa. The appendage is long and nonspiniferous with podomeres that thicken distally, clearly used for locomotion and not for prey capture and comparable to appendage IV in *D. abonensis* and *Woodwardopterus scabrosus*. Appendage V is more frequently preserved (Table 5), although like appendage IV no specimen preserves the terminal podomeres, while appendage VI is the most commonly preserved appendage and is also the most completely known (Table 6). Both appendage pairs have distally expanding podomeres with paired grooves running along their lengths, however with the exception of the juvenile NSM G.1897.32.18 they are comparatively shorter than the corresponding appendages in *D. abonensis*. One specimen (NMS G.1897.32.868) preserves a complete appendage VI and shows several key features that differentiate the Stylonurina from the Eurypterina; there is no modified 'podomere' 7a at the joint between VI-7 and VI-8, VI-5 is longer than VI-4, and there is no coxal 'ear'.

The metastoma is preserved in a fair number of specimens (Table 7), with the largest having the same dimensions as the largest metastoma of *Drepanopterus abonensis* (Lamsdell *et al*. 2009, pl. 5 fig. 3). The metastoma also corresponds in general morphology with *D. abonensis*, being oval in shape with an angular anterior notch and a deep posterior cleft that is obvious on almost every specimen including the holotype (NMS G.1885.26.72.5), with a similar cleft seen in the metastoma of *Hibbertopterus scouleri* (Waterston 1957, pl. 1).

5.2 Opisthosoma

5.2.1 Mesosoma and genital operculum. The mesosoma is represented by a total of 21 specimens (Table 8) that reveal details of both the dorsal and ventral anatomy (e.g. Figs. 15–18). Several features, such as the first tergite being shorter than the succeeding ones and the broadest point of the animal being at the fourth segment, are common to most other eurypterids, while others such as the pustular ornamentation and the presence of paired median tubercles on at least tergites 2–5 are characteristics of *Drepanopterus*.

There are two main differences in the adult specimens that serve to differentiate *D. pentlandicus* from *D. abonensis*; the third opisthosomal segment (second opisthosomal tergite) showing a positive third order differentiation (*sensu* Tollerton 1989) and further paired median tubercles on tergites 6–11. The enlarged third segment (equivalent to somite IX) can be seen in the holotype (NMS G.1885.26.72.5) and is also expressed ventrally as indicated by the enlarged posterior opercular plate in NMS G.1897.32.868.

The genital operculum is preserved in only two specimens, however both genital appendage type A (NMS G.1897.32.71, Fig. 19) and type B (NMS G.1897.32.868, Fig. 9) are represented. Of the two the type B appendage is better preserved and bears some resemblance to the genital appendage of *Hibbertopterus scouleri* as described by Waterston (1957, fig. 6). The appendage is 12 mm long and 8 mm wide and consists of two parts, a broader anterior plate (10 mm by 8 mm) with an anterior notch and a smaller, narrow plate (2 mm by 2 mm) with an angular termination. The genital appendage differs from that of *Hibbertopterus* in the anterior plate that narrows posteriorly, being more cardioid than oval, and is also differentiated from the type B appendage of *Stoermeropterus conicus* by the anterior notch. There is also a median ridge running down the centre of the genital appendage, and although this may be taphonomic – the area around the genital appendage is crumpled, making it difficult to easily discern in photographs – it appears that it may represent the remnants of the original convexity of the appendage. The type A appendage is by comparison preserved as a flat imprint, however while the specimen is overall less well preserved than the type B specimen the appendage is easier to discern due to its sheer size. The type A appendage is 56 mm long, extending down to the fourth Blattfüsse (somite XIII), however the specimen has begun to disarticulate, with the carapace and first tergite along with the narrow anterior opercular plate somewhat displaced anteriorly to (but confusingly still in contact with) the genital operculum and the rest of the opisthosoma. The genital operculum has been compressed, with the median and posterior opercular plates crumpled into one another; thus the genital appendage is positioned slightly more posteriorly than it would have been in life, and so would likely have reached only to the third Blattfüsse (somite XII, corresponding to the fifth tergite). Despite this details of the genital appendage morphology can still be made out. Although it is impossible to make out the number of segments in the genital appendage a pair of grooves can be seen running down its length, absent only from the top third and bottom quarter of the appendage, and this may indicate a three-segmented genital appendage. Paired grooves are also present on the type A appendage of *Drepanopterus abonensis* (Lamsdell *et al*. 2009, pl. 1 fig. 11), which also possesses triangular deltoid plates at the base of the appendage. A single triangular deltoid plate can also be seen to the right of the genital appendage base in NMS G.1897.32.71, which is also flanked by a pair of robust, angular genital spatulae. These are also seen in *D. abonensis* (Lamsdell *et al*. 2009) and in the undescribed drepanopterid figured by Størmer & Kjellesvig-Waering (1969, fig. 2d) which also possesses the triangular deltoid plates.

The remaining opercular plates form the book-gill bearing Blattfüsse, although details of the respiratory structures themselves are not preserved in any of the available specimens. As in most eurypterids the third and fourth Blattfüsse (corresponding to the appendages of somites XII and XIII, or tergites five and six) are medially fused, retaining a visible median suture (NMS G.1897.32.91; G.1897.32.103; G.1897.32.104, Fig. 20b), however the first and second Blattfüsse still retain each half of the operculum as an independent limb as shown by NMS G.1897.32.114 (Fig. 21).

5.2.2 Metasoma and telson. The metasoma is known from 17 specimens (Table 9), however only six of these preserve it in its entirety and only seven show the telson. The metasoma is much the same as in *Drepanopterus abonensis*, narrowing evenly towards the telson, with the pretelson being somewhat more elongated than the preceding segments in at least some specimens (e.g. Figs. 5a, 12, 13). It is notable that the anterior articulations on the tergites, which are comparatively narrow in the mesosoma (Fig. 5) become much larger in the metasoma (Fig. 9), possibly indicating a greater degree of dorso-ventral flexibility. The juvenile paratype specimen (Fig. 5a,b) possesses short, angular epimera on its metasomal segments, as do the supposed adults of *D. abonensis*, however none of the adult specimens of *D. pentlandicus* show any indication of epimera on any of the opisthosomal segments, and it may be that this is another juvenile trait of the genus. The main difference from *D. abonensis* however is the possession of large dorsal median tubercles on the metasomal segments as well as those on tergites 2-5. These are only observed in NMS G.1897.32.868 (Fig. 9) which is also the only individual with a verifiable type-B appendage and so the posterior tubercles may be a sexually dimorphic trait, however more specimens preserving the genital appendage would be required before that possibility could be explored.

The telson is clearly clavate in NMS G.1897.32.72 (Fig. 11), G.1897.32.91 (Fig. 12) and G.1897.32.109 (Fig. 11a) but lanceolate in the juvenile NMS G.1885.26.72.15 (Fig. 5a, b). This appears to confirm a trend first tentatively recognised in *D. abonensis*; that the telson in *Drepanopterus* changes through ontogeny. The ratio of body:telson length does not appear to vary between juveniles and adults, however, and both telson morphologies possess a dorsal median keel which is also present in the other two *Drepanopterus* species.

6. Discussion

The description of unfigured, relatively complete specimens of *Drepanopterus pentlandicus* (the adult morphology of which is shown in Figure 2) allows for a better understanding of the species and permits its relationship to the two other *Drepanopterus* species to be considered in full. The *D. pentlandicus* material is more complete than that of either *D. abonensis* or *D. odontospathus* and confirms the presence of a number of characters within the genus. *D. pentlandicus* clearly retains a number of plesiomorphic characters, such as the lack of an enlarged palpebral lobe and the presence of acicular scales in the cuticular ornament, but also possesses the *Drepanopterus* autapomorphies of pustules in the cuticular sculpture and paired axial tubercles on the tergites. A posteriorly cleft oval metastoma, previously known only from a few disarticulated specimens of *D. abonensis*, is consistently observed in articulated individuals of *D. pentlandicus* while an isolated appendage and an articulated juvenile specimen also verify the occurrence of flattened spines modified into broad blades in the anterior appendages of *Drepanopterus*, albeit in a more recognisable form than in *D. abonensis*. Genital spatulae and deltoid plates on the type A operculum, previously only tentatively known from two isolated genital opercula in *D. abonensis*, are again observed in a more complete specimen of *D. pentlandicus* associated with an elongate type A genital appendage that previously has been known from only the basal portions. The type B genital appendage, meanwhile, shows no indication of deltoid plates or spatulae, however does somewhat resemble the type B appendage of *Hibbertopterus scouleri*.

Drepanopterus pentlandicus also possesses a number of characteristics that suggest further links to the mycteropoids. The most obvious is the cleft metastoma, which is also present in *Hibbertopterus scouleri*. Selden *et al*. (2005) proposed that the metastoma in *H. scouleri* actually represented the fused coxae of appendage VI, with the underlying genital appendage being the true metastoma, however this interpretation is rejected both on the grounds of evidence from *Drepanopterus* and the fact that in ventral view the metastoma overlies the coxae and so the small plate suggested by Selden *et al*. to be the metastoma could not be as it would underlie the coxae. Another similarity is the morphology of the ventral prosomal plates, which until known have not been well known in *Drepanopterus* is not well known with most of the evidence from *D. abonensis* consisting of isolated plates that show the diagnostic stylonurine transverse suture but do not indicate the form of the median join (Lamsdell *et al*. 2009 pl. 1 figs. 6–8), however the median join is relatively well preserved in *D. pentlandicus* and consists of a single *Eurypterus*-type suture. *Hibbertopterus scouleri* has also been demonstrated to possess ventral plates of *Eurypterus*-type (Waterston 1957 pl. 2 fig. 2) and it has been assumed that this plate morphology was part of the mycteropoid ground plan. The ventral plates of *D. pentlandicus*, like those of *Hibbertopterus*, are very broad (NMS G.1897.32.105, Fig. 6d) and this may be linked to having a deep carapace.

The condition in *Drepanopterus pentlandicus* of the posterolateral margins completely overlapping the first tergite is also unusual. The posterolateral margins of the carapace often curve back in eurypterids, however it is mostly only in Eurypterina that the carapace covers the first visible tergite to any great extent (e.g. *Eurypterus tetragonophthalmus* Fischer, 1839). Among Stylonurina the posterolateral margins only greatly overlap the tergite in Hibbertopteridae, where they are drawn out to form lobes. It seems likely that the recurved margins of *D. pentlandicus* are homologous to the hibbertopterid posterolateral lobes, although neither are present in mycteropids, however it is noteworthy that the juvenile *D. pentlandicus* specimens do not show this overlap and it is likely that it only developed in adult individuals. The positive third order differentiation of somite IX appears to be a similar phenomenon. While this segment is somewhat enlarged in *D. pentlandicus* – being one and a half times larger than the following segment – it is not truly hypertrophied as in seen in somite VIII of some synziphosurines (Anderson & Moore 2004, Eldredge 1974, Krzeminski *et al*. 2010) and somites VIII and IX in mycteropids (Pruvost, 1924, Selden *et al*. 2005). *Woodwardopterus*, *Megarachne* and *Mycterops* all have somite IX massively hypertrophied, while in *Mycterops* somite VIII is also hypertrophied. It is possible that the enlarged segment in *D. pentlandicus* is a precursor to the hypertrophied segment in mycteropids. *Drepanopterus abonensis* meanwhile shows no evidence of an enlarged segment, yet neither do the juvenile specimens of *D. pentlandicus* (NMS G.1885.26.72.15, Fig. 5a, b, and G.1897.32.18), and so its lack in *D. abonensis* may be ontogenetic. Similarly, the paired tubercles on tergites 6–11 are not found on the juveniles, although tubercles are seen on tergites 2–5 of the larger specimen (NMS G.1897.32.18), and so their absence in *D. abonensis* may again be due to ontogeny.

A number of characters found in *Drepanopterus pentlandicus* therefore bear resemblance to structures found in either the hibbertopterid of mycteropid lineages, including a lateral overlap of the first tergite by the prosomal carapace margins (hibbertopterids), a somewhat enlarged somite IX (mycteropids) and short, robust prosomal appendages II and III (hibbertopterids). None of these characters are present in the juvenile specimens, however, which exhibit more gracile appendages, a straight carapace posterior and more uniform mesosomal tergite length. Somewhat troublingly none of these characteristics are present in *D. abonensis*, which appears to exhibit more of the juvenile morphology. Two characteristics from the original redescription would seem to suggest that the *D. abonensis* specimens represent adult individuals; the eyes are positioned more centrally on the carapace, a more lateral placement of the eyes being a characteristic of juvenile eurypterids (Cuggy 1994), and the clavate morphology of the telson (Lamsdell *et al*. 2009). However, the lateral eyes of *D. abonensis* are positioned more laterally than shown in Lamsdell *et al*.'s reconstruction, as the figured specimens show, while the majority of telson specimens are lanceolate with those few that do exhibit a somewhat clavate morphology not being as pronouncedly so as in *D. pentlandicus*. Furthermore, the median ridge described as being present in *D. abonensis* probably actually represents taphonomic wrinkling in the cardiac lobe region of some specimens, being undoubtedly absent from several others and inconsistent in morphology among those where it is present. The anterior appendages of *D. abonensis* also more closely resemble those of the juvenile *D. pentlandicus*, being more gracile and lacking the antero-ventral extensions of the podomere cuticle with a conical terminal podomere in contrast to the hook-like podomere of the adult *D. pentlandicus*, which is similar in morphology to that of *Hibbertopterus scouleri*. The armature of the *D. abonensis* appendage is also unusual, appearing to consist of flattened blades at the most distal podomeres but the more usual conical spines proximally. Morphological change in appendage shape has previously been documented in the sixth appendage of

Strobilopterus princetonii (Ruedemann, 1934) (Tetlie 2007a) and in all appendages of '*Carcinosoma*' *scorpioides* (Woodward, 1868) (Lamsdell pers. obs.) and can comprise both changes in relative appendage length and armature. Unfortunately, the juvenile specimen of *D. pentlandicus* does not preserve the proximal armature, however a single blade is preserved distally and it is possible that its morphology may further match that preserved in *D. abonensis*.

Two other differences between *D. abonensis* and *D. pentlandicus* may also be a function of ontogeny. The absence of axial nodes on the mesosomal segments of *D. abonensis* is also observed in the juveniles of *D. pentlandicus*, the smaller of which has no nodes at all, however it is also possible that this difference could be due to sexual dimorphism in adults. Prosomal posterolateral lobes are absent from the juvenile *D. pentlandicus* and were not described in *D. abonensis* by Lamsdell *et al*. (2009), however some specimens (Lamsdell *et al*. 2009, pl. 3 fig. 2, pl. 5 fig. 2) do indicate that posterolateral lobes may in fact be present but are very much reduced in comparison to *D. pentlandicus*. At present there is not enough data to determine whether the described specimens of *D. abonensis* represent juveniles or adults that had paedomorphically retained juvenile traits, however their closer resemblance to the juvenile specimens of *D. pentlandicus* than to the adult in a number of morphological details is conspicuous. The *D. abonensis* specimens have been assumed to be adults largely due to their size but eurypterid discoveries elsewhere have shown that juveniles of large species could themselves reach an impressive size while retaining juvenile characteristics (Lamsdell *et al*. 2010b), something well worth bearing in mind.

6.1 Phylogenetic Implications

In order to ascertain whether the new data for *Drepanopterus pentlandicus* at all alters the current hypotheses of relationships among the Stylonurina the taxon was recoded for the analysis presented by Lamsdell *et al*. (2010b). Three new taxa, *Hastimima whitei* White, 1908, *Campylocephalus oculatus* (Kutorga, 1838), and *Drepanopterus odontospathus* sp. nov., were also included so as to give the mycteropoids a more comprehensive treatment along with nine new characters pertaining to carapace morphology, overlying lens shape, reduction of the median ridge, expansion of the second opisthosomal segment and telson serration. The genera *Vernonopterus* Waterston, 1968 and *Dunsopterus* Waterston, 1968, while clearly mycteropoids, are known only from fragmentary material so were not included in the matrix. Analysis of this expanded data matrix as detailed in the Material and Methods resulted in a single most parsimonious tree (Fig. 22) with a Tree Length of 149, an ensemble Consistency Index of 0.550 and a Retention Index of 0.725. The overall topology of the tree remains unchanged from that in Lamsdell *et al*. (2010b), with Stylonurina consisting of rhenopteroid, stylonuroid, kokomopteroid and mycteropoid clades, nor has the composition or relationships of taxa within these clades altered. *Drepanopterus odontospathus* resolves as the sister taxon to *Drepanopterus abonensis*, as befitting its intermediate stratigraphic position between *Drepanopterus abonensis* and *Drepanopterus pentlandicus*, while *Campylocephalus oculatus* and *Hastimima whitei* fall within the hibbertopterids and mycteropids respectively. *Hastimima whitei* was included within Hibbertopteridae by Lamsdell *et al*. (2010a), however given its provinciality (Brazil) and age (Sakmarian) it is perhaps not surprising that it resolves in the analysis as sister taxon to *Megarachne servinei* from the Permo-Carboniferous of Argentina. *H. whitei* is only known from fragmentary material, however the ornamentation is more reminiscent of mycteropids than hibbertopterids while the preserved tergite may be hypertrophied and has a similar morphology to the first tergite of *M. servinei*. Further, more complete material of *H. whitei* may show that it is congeneric with *M. servinei*, however this is just speculation at present beyond the similarities in tergite and coxa morphology. The inclusion of *C. oculatus* within hibbertopterids is not unexpected; the holotype, consisting of a single carapace, closely resembles the carapace of *Hibbertopterus scouleri* (the two species were considered congeneric by Størmer (1951)), differing solely in the shape and more posterior position of the lateral eyes and point of greatest carapace width. It is intriguing that *C. oculatus*, long considered to be closely related to *H. scouleri*, should in fact form the sister taxon to a clade consisting of *H. scouleri* and *Cyrtoctenus wittebergensis*. While clearly related, these two taxa exhibit a number of differences in appendage morphology (which is unknown in *C. oculatus*) and carapace shape, *Cyrtoctenus wittebergensis* possessing an anterior projection that is lacking in both *H. scouleri* and *C. oculatus*. Both *Hibbertopterus* and *Cyrtoctenus* are found predominantly from the Carboniferous, with one supposed Permian record of *Hibbertopterus* (Ponomarenko 1985) (representing the youngest known eurypterid occurrence) and a single late Devonian occurrence of *Cyrtoctenus* (Fraipont 1889), while the only reliable records of *Campylocephalus* are from the Permian. The Permian '*Hibbertopterus*' material is however more diagnostic of *Campylocephalus* and is herein transferred to that genus. The remaining valid species of *Cyrtoctenus* and *Hibbertopterus* frequently co-occur, with *Cyrtoctenus* largely known from isolated rachises (see Størmer & Waterston 1968) in association with fragments of cuticle from the large eurypterids *Dunsopterus* and *Vernonopterus* (Waterston 1968) and smaller (but still sizeable), more complete specimens of *Hibbertopterus* (Jeram & Selden 1994). An exception to this trend is the single, relatively complete specimen of *Cyrtoctenus wittebergensis* from the Carboniferous of South Africa, which occurs in strata devoid of other eurypterid material (Waterston *et al*. 1985). In their description of *Cyrtoctenus wittebergensis*, Waterston *et al*. noted several similarities with *Dunsopterus* including carapace and tergite morphology, form of the prosomal appendages and cuticular ornamentation, although rachises have never been observed articulated with *Dunsopterus* appendages, and suggested the two may be synonyms. Lamsdell *et al*. (2010a) also briefly summarised similarities between *Dunsopterus*, *Vernonopterus* and *Cyrtoctenus*, noting that *Vernonopterus* and *Cyrtoctenus* both possessed opisthosomal ridges either side of the axial region and suggesting that all three genera may be synonyms. Jeram & Selden (1994) also suggested that *Hibbertopterus* and *Cyrtoctenus* may be synonyms, with *Hibbertopterus* simply representing the juvenile ontogenetic stages and *Cyrtoctenus* the adult forms. Given our knowledge of how appendage armature changes through the development of *Drepanopterus* it is not inconceivable that *Hibbertopterus* could develop rachises in its later moult stages; grooves on the podomeres, present in *Cyrtoctenus*, mycteropids and *Drepanopterus*, are also absent in *Hibbertopterus* suggesting that these too may be a feature that developed later in ontogeny. Furthermore, the lateral eyes of *Cyrtoctenus wittebergensis* are located exceedingly close together towards the carapace centre while those of *Hibbertopterus scouleri* are found in a slightly more lateral (but still overall central) position; as noted earlier, a migration of the lateral eyes towards the carapace centre during ontogenetic development has been previously documented in eurypterids. Finally, a small carapace closely resembling that of *Hibbertopterus scouleri* was described by Waterston (1957) as possibly being a juvenile specimen of *Dunsopterus stevensoni* (Etheridge, 1877). It seems almost certain that *Dunsopterus*, *Vernonopterus* and *Cyrtoctenus* are all synonyms, with *Dunsopterus* having priority, while *Dunsopterus* is also likely to be a junior synonym of *Hibbertopterus*. Such a major systematic revision is beyond the scope of the current work, however.

6.2 Heterochrony and evolutionary trends in mycteropoids

All current knowledge on eurypterid ontogenetic trends largely comes from three studies, focusing on the genera *Eurypterus* De Kay, 1825 (Andrews *et al*. 1974, Cuggy 1994) and *Adelophthalmus* Jordan *in* Jordan & von Meyer, 1854 (Kues & Kietzke 1981), although none of these include representatives of the earliest instars. One species, *Hardieopterus myops* (Clarke 1907), has been theorised to represent juveniles including later described early instars (Clarke & Ruedemann 1912) which display abnormally large eyes and a possible reduction in tergite count, however these specimens have remained virtually forgotten since the early 1900s, and warrant reinvestigation in light of current understanding. The smallest specimens (some not more than a millimetre in size) representing the earliest instars need particular scrutiny given the large amount of inorganic material misidentified by Ruedemann (Tollerton 2006); an initial review of the specimens suggests that several are pseudofossils and some of the larger individuals represent more than one taxon (Tollerton pers. comm.). Given the apparent paucity of ontogenetic data for eurypterids it is perhaps understandable that there have been no studies on heterochronic trends within the various lineages, however there are clues that such trends exist. Two clades are of particular note, both exhibiting a marked increase in size and deviation from the familiar eurypterid morphology through their evolution. Pterygotoidea, well-known as being a highly predatory clade, exhibit a number of juvenile characteristics that become increasingly exaggerated in more derived species and probably lies along a paedomorphocline. The other lineage of interest, Mycteropoidea, show a different trend; both hibbertopterids and mycteropids appear to lie along peramorphoclines. Hibbertopterids exhibit a number of morphological characteristics that can be considered extreme expressions of the *Drepanopterus*-type morphology; the lateral eyes exhibit extreme curvature of the visual surface (as noted in the largest *Drepanopterus* specimens) and are positioned more centrally on the carapace (trends recognised as part of eurypterid ontogenetic development), the lateral overlap of the carapace posterior with the first opisthosomal tergite (a characteristic that only appears in later ontogenetic stages of *Drepanopterus*) becomes more prominent with the genal regions drawn out into posterolateral lobes, the prosomal appendages become shorter and more robust (another observable trend in the ontogeny of other eurypterid species (Lamsdell pers. obs.)) while the appendage armature undergoes a marked expansion into large, broad blades, some of which develop enlarged and robust setae to form rachises. The fourth prosomal appendage, which is nonspiniferous in *Drepanopterus*, also develops armature similar to the second and third appendages but retains its locomotary function. The most obvious expression of the peramorphocline however is the dramatic increase in size diagnostic of the Carboniferous and Permian species, with *Cyrtoctenus* reaching lengths of at least 135 cm and trackway evidence indicating lengths of 150 cm to 250 cm (Whyte 2005, Almond 2002), suggesting that hypermorphosis may be the underlying process. Mycteropids, meanwhile, exhibit the same central positioning of the lateral eyes, increase in appendage armature size and thickening of the calcareous lenses, however do not appear to undergo the same drastic size increase that characterises the hibbertopterids. A number of other characters also appear to buck the peramorphic trend; the podomeres of the anterior appendages remain long and do not shorten into adulthood, the fourth appendage is devoid of armature, and the blades do not develop into rachises. All these characteristics however are also absent from *Drepanopterus* (although the anterior appendages of *Drepanopterus* do get shorter in ontogeny, they do not reduce to the extent seen in *Hibbertopterus*) and so it is likely that mycteropids represent a separate offshoot from the mycteropoid lineage prior to the morphological developments observed in hibbertopterids.

Mycteropids also show no evidence of the lateral margins of the carapace overlapping the first opisthosomal tergite. That said, the first tergite is actually sutured onto the carapace (Selden *et al*. 2005) and, in *Megarachne servinei* and *Woodwardopterus scabrosus*, is drawn out into structures strongly resembling the hibbertopterid posterolateral lobes. It seems that when the tergite fused to the carapace it took on the developmental identity (through changes in expression of the *Hox* genes that determine cell fates in the segments and appendages – see McGinnis & Krumlauf 1992, Gellon & McGinnis 1998) of the carapace posterior, with the posterolateral lobes forming at the posterior of the tergite rather than the true carapace posterior, an interesting possibility as it would mean that the number of segments incorporated into the carapace is greater than the number of somites comprising the prosomal tagma (as indicated by appendage differentiation). This decoupling between carapace shield and cephalic tagma has been noted in other arthropods (e.g. trilobites, Scholtz & Edgecombe 2006; decapod crustaceans, Abzhanov & Kaufman 2004) but is uncommon in chelicerates, which show a remarkable conservatism of tagmation into the prosoma and opisthosoma (although modern horseshoe crabs incorporate part of the tergite of the eighth somite into the prosoma (Scholl 1977, Sekiguchi *et al*. 1982)).

Further evidence that mycteropids represent peramorphs is provided by the extreme hypertrophy of the second tergite into a large, circular structure. The lack of a marked size increase between species however suggest that the main process underlying the developmental shift is not hypermorphy as in hibbertopterids but more likely to be pre displacement, an earlier increase in trait development leading to a more extreme morphology without increasing development time so that overall size stays largely unchanged.

7. Acknowledgements

Thanks are extended to Andrew Ross (NMS) for access to material in his care, Victor Tollerton Jr. (New York) for discussions on the nature of *Drepanopterus*, information on *Hardieopterus myops* and for suggesting restudy of the lateral eye position and median ridge in *Drepanopterus abonensis*, Dave Marshall (Manchester) for discussion on chelicerate morphology and intriguing theories on segment hypertrophy, and Paul Selden (University of Kansas) for support and guidance. Jason Dunlop (MBA) and an anonymous reviewer provided detailed comments that greatly improved the manuscript. This work was made possible by a Palaeontographical Society research grant to restudy the eurypterid fauna of the Pentland Hills.

8. References

Abzhanov, A. & Kaufman, T. 2004. *Hox* genes and tagmatization of the higher Crustacea. *In* Scholtz, G. (ed) *Evolutionary developmental biology of Crustacea*, 43–74. Balkema, Lisse.

Allan, R. S. 1927. *Keilorites* (a new generic name for a Silurian annelid from Australia). *Geological Magazine* **64**, 240.

Almond, J. E. 2002. Giant arthropod trackway, Ecca Group. *Geobulletin* **45**, 28.

Anderson, L. I. 2007. Unmineralised arthropods. *In* Clarkson, E. N. K., Harper, D. A. T., Taylor C. M. & Anderson, L. I. (eds) *Silurian Fossils of the Pentland Hills, Scotland*, 133–156. The Palaeontological Association, London.

Anderson, L. I., Clarkson, E. N. K., Stewart, S. E. & Mitchell, D. 2007. An Upper Llandovery Konservat–Lagerstätte in a depositional context: the Pentland Hills Eurypterid Bed, Midlothian. *Scottish Journal of Geology* **43**, 41–50.

Anderson, L. I. & Moore, R. A. 2004. *Bembicosoma* re-examined: a xiphosuran from the Silurian of the North Esk Inlier, Pentland Hills, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **94**, 199–206.

Andrews, H. E., Brower, J. C., Gould, S. J. & Reyment, R. A. 1974. Growth and variation in *Eurypterus remipes* De Kay. *Bulletin of the Geological Institutions of the University of Uppsala* **4**, 81–114.

Botting, J. P. 2007. Algae, receptaculitids and sponges. *In* Clarkson, E. N. K., Harper, D. A. T., Taylor C. M. & Anderson, L. I. (eds) *Silurian Fossils of the Pentland Hills, Scotland*, 36–49. The Palaeontological Association, London.

Braddy, S. J. & Dunlop, J. A. 2000. Early Devonian eurypterids from the Northwest Territories of Arctic Canada. *Canadian Journal of Earth Sciences* **37**, 1167–1175.

Bremer, K. 1994. Branch support and tree stability. *Cladistics* **10**, 295–304.

Burmeister, H. 1843. *Die Organisation der Trilobiten, aus ihren lebenden Verwandten entwickelt; nebst systematische Uebersicht aller seitherbeschriebenen Arten*, 1–148. G. Reimer, Berlin.

Caster, K. E. & Kjellesvig-Waering, E. N. 1964. Upper Ordovician eurypterids from Ohio. *Palaeontographica Americana* **4**, 300–358.

Clarke, J. M. 1907. The *Eurypterus* shales of the Shawangunk Mountains in eastern New York. *New York State Museum Bulletin* **107**, 295–310.

Clarke, J. M. & Ruedemann, R. 1912. The Eurypterida of New York. *New York State Museum Memoire* **14**, 1–439.

Clarkson, E. N. K. 2000. Pentland Odyssey. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **36**, 8–16.

Clarkson, E. N. K. & Taylor, C. M. 2002. The Deerhope Formation in the North Esk Inlier, Pentland Hills, Scotland. *Special Papers in Palaeontology* **67**, 29–44.

Coleman, C. O. 2003. “Digital inking”: How to make perfect line drawings on computers. *Organisms Diversity & Evolution* **3**, Electronic supplement 14, 1–14.

Cope, E. D. 1886. An interesting connecting genus of Chordata. *American Naturalist* **20**, 1027–1031.

Cuggy, M. B. 1994. Ontogenetic variation in Silurian eurypterids from Ontario and New York State. *Canadian Journal of Earth Sciences* **31**, 728–732.

De Kay, J. E. 1825. Observations on a fossil crustaceous animal of the order Branchiopoda. *Annals of the New York Lyceum of Natural History* **1**, 375–377.

Diener, C. 1924. Fossilium Catalogus, I: Animalia; Pars 25: Eurypterida, 1–28. Berlin.

Eichwald, C. E. d' 1860. *Lethaea rossica* **1**, 1–1360. Schweizerbart, Stuttgart.

Eldredge, N. 1974. Revision of the suborder Synziphosurina (Chelicerata: Merostomata), with remarks on merostome phylogeny. *American Museum Novitates* **2543**, 1–41.

Etheridge, R. Jr. 1877. On the remains of a large crustacean, probably indicative of a new species of *Eurypterus*, or allied genus (*Eurypterus*? *stevensoni*), from the lower Carboniferous series (Cementstone Group) of Berwickshire. *The Quarterly Journal of the Geological Society of London* **33**, 223–228.

Farris, J. S., Albert, V. A., Källersjö, M., Lipscomb, D. & Kluge, A. G. 1996. Parsimony jackknifing outperforms neighbor-joining. *Cladistics* **12**, 99–124.

Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* **39**, 783–791.

Fischer de Waldheim, G. 1839. Notice sur un crustacé fossile du genre *Eurypterus* de Podolie. *Bulletin de la Societe Imperiale des Naturalistes de Moscou* **11**, 125–128.

Fraipont, J. 1889. Euryptérides nouveaux du Dévonien supérieur de Belgique (Psammites du Condroz). *Annales del la Société Géologique de Belgique* **17**, 53–62.

Gellon, G. & McGinnis, W. 1998. Shaping animal body plans in development and evolution by modulation of *Hox* expression patterns. *BioEssays* **20**, 116–125.

Goloboff, P. A., Farris, J. S. & Nixon, K. C. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* **24**, 774–786.

Gupta, N. S., Tetlie, O. E., Briggs, D. E. G. & Pancost, R. D. 2007. The fossilization of eurypterids: a result of molecular transformation. *Palaios* **22**, 439–447.

Hibbert, S. 1836. On the freshwater limestone of Burdiehouse in the neighbourhood of Edinburgh, belonging to the Carboniferous group of rocks. With supplementary notes on freshwater limestones. *Transactions of the Royal Society of Edinburgh* **13**, 169–282.

Hünicken, M. A. 1980. A giant fossil spider (*Megarachne servinei*) from Bajo de Véliz, Upper Carboniferous, Argentina. *Boletin de la Academia Nacional de Ciencias, Córdoba, Argentina* **53**, 317–341.

Jeram, A. J. & Selden, P. A. 1994. Eurypterids from the Viséan of East Kirkton, West Lothian, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **84**, 301–308.

Jordan, H. & von Meyer, H. 1854. Ueber die Crustaceen der Steinkohlenformation von Saarbrücken. *Palaeontographica* **4**, 1–15.

Kier, P. M. 1973. A new Silurian echinoid genus from Scotland. *Palaeontology* **16**, 651–663.

Kjellesvig-Waering, E. N. 1959. A taxonomic review of some late Paleozoic Eurypterida. *Journal of Paleontology* **33**, 251–256.

Kjellesvig-Waering, E. N. 1966. A revision of the families and genera of the Stylonuracea (Eurypterida). *Fieldiana, Geology* **14**, 169–197.

Kjellesvig-Waering, E. N. & Leutze, W. P. 1966. Eurypterids from the Silurian of West Virginia. *Journal of Paleontology* **40**, 1109–1122.

Krzemiński, W., Krzemińska, E. & Wojciechowski, D. 2010. Silurian synziphosurine horseshoe crab *Pasternakevia* revisited. *Acta Palaeontologica Polonica* **55**, 133–139.

Kues, B. S. & Kietzke, K. K. 1981. A large assemblage of a new eurypterid from the Red Tanks Member, Madera Formation (late Pennsylvanian-early Permian) of New Mexico. *Journal of Paleontology* **55**, 709–729.

Kutorga, S. S. 1838. *Beitrag zur Kenntniss der organischen Ueberreste des Kupfersandsteins am westlichen Abhange des Urals*, 1–38. St. Petersburg.

Lamsdell, J. C. 2011. The eurypterid *Stoermeropterus conicus* from the lower Silurian Pentland Hills, Scotland. *Palaeontolographical Society Monograph*, 1–84, pls 1–15.

Lamsdell, J. C., Braddy, S. J. & Tetlie, O. E. 2009. Redescription of *Drepanopterus abonensis* (Chelicerata: Eurypterida: Stylonurina) from the late Devonian of Portishead, UK. *Palaeontology* **52**, 1113–1139.

Lamsdell, J. C., Braddy, S. J. & Tetlie, O. E. 2010a. The systematics and phylogeny of the Stylonurina (Arthropoda: Chelicerata: Eurypterida). *Journal of Systematic Palaeontology* **8**, 49–61.

Lamsdell, J. C., Braddy, S. J., Loeffler, E. J. & Dineley, D. L. 2010b. Early Devonian stylonurine eurypterids from Arctic Canada. *Canadian Journal of Earth Sciences* **47**, 1405–1415.

Lamont, A. 1955. Scottish Silurian Chelicerata. *Transactions of the Geological Society of Edinburgh* **16**, 200–216.

Laurie, M. 1892. On some eurypterid remains from the Upper Silurian rocks of the Pentland Hills. *Transactions of the Royal Society of Edinburgh* **37**, 151–162.

Laurie, M. 1899. On a Silurian scorpion and some additional eurypterid remains from the Pentland Hills. *Transactions of the Royal Society of Edinburgh* **39**, 575–589.

Maddison, W. P. & Maddison, D. R. 2010. Mesquite: A modular system for evolutionary analysis. Version 2.73. http://mesquiteproject.org

McGinnis, W. & Krumlauf, R. 1992. Homeobox genes and axial patterning. *Cell* **68**, 283–302.

Murchison, R. I. 1859. *Siluria* (Third edition), 1–592. John Murray, London.

Novojilov, N. J. 1962. [Order Eurypterida]. *In* Orlov, Y. A. (ed) [*Fundamentals of Paleontology, Volume 9; Arthropoda, Tracheata, Chelicerata*], 404–423, pls. 18–22, Moscow. [In Russian].

O'Connell, M. 1916. The habitat of the Eurypterida. *Bulletin of the Buffalo Society of Natural Sciences* **11**, 1–277.

O'Leary, M. A. & Kaufman, S. G. 2007. MorphoBank 2.5: Web application for morphological phylogenetics and taxonomy. http://www.morphobank.org

Orr, P. J., Briggs, D. E. G., Siveter, D. J. & Siveter, D. J. 2000. Three-dimensional preservation of a nonbiomineralized arthropod in concretions in Silurian volcaniclastic rocks from Herefordshire, England. *Journal of the Geological Society, London* **157**, 173–186.

Page, D. 1856. *Advanced Text-book of Geology* (1st edition), 1–326. Blackwood, Edinburgh and London.

Pitcher, B. L. 1939. The Upper Valentian gastropod fauna of Shropshire. *Annals and Magazine of Natural History* **11**, 82–132.

Plotnick, R. E. 1999. Habitat of Llandoverian-Lochkovian eurypterids. *In* Boucot, A. J. &

Lawson, J. D. (eds) *Paleocommunities: a case study from the Silurian and Lower Devonian*, 106–131. Cambridge, Cambridge University Press.

Ponomarenko, A. G. 1985. King crabs and eurypterids from the Permian and Mesozoic of the USSR. *Paleontological Journal* **3**, 115–118.

Poschmann, M. & Tetlie, O. E. 2004. On the Emsian (Early Devonian) arthropods of the Rhenish Slate Mountains: 4. The eurypterids *Alkenopterus* and *Vinetopterus* n. gen. (Arthropoda : Chelicerata). *Senckenbergiana lethaea* **84**, 175–196.

Pruvost, P. 1924. Un Euryptéride nouveau du terrain houiller de Charleroi. *Annales de la Société geologique du Nord* **46**, 143–151.

Ruedemann, R. 1934. Eurypterids from the Lower Devonian of Beartooth Butte, Wyoming. *Proceedings of the American Philosophical Society* **73**, 163–167.

Salter, J. W. 1860. On new fossil Crustacea from the Silurian rocks. *Annals and Magazine of Natural History* **5**, 153–162.

Savage, T. E. 1916. Alexandrian rocks of northeastern Illinois and eastern Wisconsin. *Bulletin of the Geological Society of America* **27**, 305–324.

Scholl, G. 1977. Beiträge zur Embryonalenentwicklung von *Limulus polyphemus* L. (Chelicerata, Xiphosura). *Zoomorphologie* **86**, 99–154.

Scholtz, G. & Edgecombe, G. D. 2006. The evolution of arthropod heads: reconciling morphological, developmental and palaeontological evidence. *Development Genes and Evolution* **216**, 395–415.

Sekiguchi, K., Yamamichi, Y. & Costlow, J. D. 1982. Horseshoe crab developmental studies I. Normal embryonic development of *Limulus polyphemus* compared with *Tachypleus tridentatus*. *In* Bonaventura, J., Bonaventura, C. & Tesh, S. (eds)

Physiology and Biology of Horseshoe Crabs: Studies on Normal and Environmentally Stressed Animals, 53–73. Liss, New York.

Selden, P. A. 1981. Functional morphology of the prosoma of *Baltoeurypterus tetragonophthalmus* (Fischer) (Chelicerata: Eurypterida). *Transactions of the Royal Society of Edinburgh: Earth Sciences* **72**, 9–48.

Selden, P. A., Corronca, J. A. & Hünicken, M. A. 2005. The true identity of the supposed giant fossil spider *Megarachne*. *Biology Letters* **1**, 44–48.

Simpson, S. 1951. A new eurypterid from the Upper Old Red Sandstone of Portishead. *Annals and Magazine of Natural History* **12**, 849–861.

Størmer, L. 1951. A new eurypterid from the Ordovician of Montgomeryshire, Wales. *Geological Magazine* **88**, 409–422.

Størmer, L. 1973. Arthropods from the Lower Devonian (Lower Emsian) of Alken an der Mosel, Germany. Part 3: Eurypterida, Hughmilleriidae. *Senckenbergiana lethaea* **54**, 119–205.

Størmer, L. 1974. Arthropods from the Lower Devonian (Lower Emsian) of Alken an der Mosel, Germany. Part 4: Eurypterida, Drepanopteridae, and other groups. *Senckenbergiana lethaea* **54**, 359–451.

Størmer, L. & Kjellesvig-Waering, E. N. 1969. Sexual dimorphism in eurypterids. *In* Westermann, G. E. G. (ed) *Sexual dimorphism in fossil Metazoa and taxonomic implications*, 201–214. Stuttgart.

Størmer, L. & Waterston, C. D. 1968. *Cyrtoctenus* gen. nov., a large late Palaeozoic Arthropod with pectinate appendages. *Transactions of the Royal Society of Edinburgh* **68**, 63–110.

Tetlie, O. E. 2004. *Eurypterid phylogeny with remarks on the origin of arachnids*. 1–320. Unpublished PhD thesis, University of Bristol.

Tetlie, O. E. 2006. Two new Silurian species of *Eurypterus* (Chelicerata: Eurypterida) from Norway and Canada and the phylogeny of the genus. *Journal of Systematic Palaeontology* **4**, 397–412.

Tetlie, O. E. 2007a. Like father, like son? Not amongst the eurypterids (Chelicerata) from Beartooth Butte, Wyoming. *Journal of Paleontology* **81**, 1423–1431.

Tetlie, O. E. & Cuggy, M. B. 2007. Phylogeny of the basal swimming eurypterids (Chelicerata; Eurypterida; Eurypterina). *Journal of Systematic Palaeontology* **6**, 237–249.

Tetlie, O. E., Anderson, L. I. & Poschmann, M. 2007. *Kiaeropterus* (Eurypterida; Stylonurina) recognized from the Silurian of the Pentland Hills. *Scottish Journal of Geology* **43**, 1–7.

Tetlie, O. E., Brandt, D. S. & Briggs, D. E. G. 2008. Ecdysis in sea scorpions (Chelicerata: Eurypterida). *Palaeogeography, Palaeoclimatology, Palaeoecology* **265**, 182–194.

Tollerton, V. P. Jr 1989. Morphology, taxonomy, and classification of the Order Eurypterida Burmeister, 1843. *Journal of Paleontology* **63**, 642–657.

Tollerton, V. P. Jr 2004. Summary of a revision of New York Ordovician eurypterids: implications for eurypterid palaeoecology, diversity and evolution. *Transactions of the Royal Society of Edinburgh, Earth Sciences* **94**, 235–242.

Tollerton, V. P. Jr 2006. Strabismus and pseudofossils: a case study of Rudolf Ruedemann (1864-1956). *Earth Sciences History* **25**, 239–250.

Waterston, C. D. 1957. The Scottish Carboniferous Eurypterida. *Transactions of the Royal Society of Edinburgh, Earth Sciences* **63**, 265–288.

Waterston, C. D. 1968. Further observations on the Scottish Carboniferous eurypterids. *Transactions of the Royal Society of Edinburgh, Earth Sciences* **68**, 1–20.

Waterston, C. D. 1979. Problems of functional morphology and classification in stylonuroid eurypterids (Chelicerata, Merostomata), with observations on the Scottish Silurian Stylonuroidea. *Transactions of the Royal Society of Edinburgh, Earth Sciences* **70**, 251–322.

Waterston, C. D., Oelofsen, B. W. & Oosthuizen, R. D. F. 1985. *Cyrtoctenus wittebergensis* sp. nov. (Chelicerata : Eurypterida), a large sweep-feeder from the Carboniferous of South Africa. *Transactions of the Royal Society of Edinburgh, Earth Sciences* **76**, 339–358.

Whitaker, J. H. McD. 1962. The geology of the area around Leintwardine, Herefordshire. *Quarterly Journal of the Geological Society of London* **118**, 319–351.

White, D. 1908. Report on the fossil flora of the coal measures of Brazil. *In* White, J. C. (ed) *Final report on the coal measures and associated rocks of South Brazil*, 377–607. National Press, Rio de Janeiro.

Whyte, M. A. 2005. A gigantic fossil arthropod trackway. *Nature* **438**, 576.

Woodward, H. 1868. On some new species of Crustacea from the Upper Silurian rocks of Lanarkshire &c.; and further observations on the structure of *Pterygotus*. *Quarterly Journal of the Geological Society* **24**, 289–296.

Woodward, H. 1887. On a new species of *Eurypterus* from the Lower Carboniferous shales of Glencartholm, Eskdale, Scotland. *Geological Magazine* **4**, 481–484.

NMS specimen	Carapace length	Carapace width	Lateral eye length	Lateral eye width	Marginal rim width
G.1885.26.72.5	63	98	18	2	2
G.1897.32.18	35	40	8	0.6	1.2
G.1897.32.71	61.5	60*	–	–	3
G.1897.32.91	73	76*	–	–	3
G.1897.32.94	25	32*	–	–	1
G.1897.32.98	46	88*	11	3	3
G.1897.32.100	31*	52*	15	2	–
G.1897.32.102	58	80*	16	3	3
G.1897.32.103	66	78*	16	4	4
G.1897.32.107	51	92	–	–	2.5
G.1897.32.108	16.5	27.5*	–	–	1.5
G.1897.32.110	48	46*	10	2 (9)	3
G.1897.32.868	44*	80*	12	3 (8)	3
G.1897.32.869	76	106*	14	2 (10)	2

Table 1. Dorsal prosomal measurements. Dimensions in mm. The numbers in brackets for lateral eye width include the annular cuticular thickening. *=incomplete

NMS specimen	Distance from carapace lateral margin	Percentage of carapace length	Percentage of carapace width
G.1885.26.72.5	23 (centrimesial)	28.6	2
G.1897.32.18	7 (outer centrimesial)	22.8	1.5
G.1897.32.98	18 (centrimesial)	23.9	–
G.1897.32.102	13 (centrimesial)	27.6	–
G.1897.32.103	19 (centrimesial)	24.2	–
G.1897.32.110	16 (outer centrimesial)	20.8	–
G.1897.32.868	20 (centrimesial)	–	–
G.1897.32.869	23 (centrimesial)	18.4	–

Table 2. Summary statistics for position of lateral eye position from the carapace lateral margin and relative size of eye compared to carapace size (expressed as a percentage of carapace size). NMS G.1897.32.868 does not preserve the full carapace length and so the proportional size cannot be calculated, while only NMS G.1885.26.72.4 and G.1897.32.18 preserve the full carapace width allowing for the relative width of the lateral eyes to be calculated. The current data indicates relatively little alteration in lateral eye proportion and position through ontogeny, however the lateral eyes of the smaller specimens are position at the outermost limits of the centrimesial quadrant whereas in larger specimens they are unquestionably centrimesial.

NMS specimen	**Appendage III**
G.1897.32.18	(podomeres 3 – 8): **3**; 4/3. **4**; 3.5/3. **5**; 3.5/3. **6**; 3.5/3. **7**; 4/3. **8**; 7/3.
G.1897.32.91	(podomere 1): **Coxa**; 12/6.
G.1897.32.92	(podomeres 4 – 8): **4**; 26/10. **5**; 10/10. **6**; 9/9. **7**; 9/6. **8**; 13/5.

Table 3. Appendage III measurements (length/width) in mm.

NMS specimen	Appendage IV
G.1897.32.18	(podomeres 3 – 6): **3**; 5*/4.5. **4**; 10/4.3. **5**; 8/3*. **6**; 6*/4.
G.1897.32.91	(podomere 1): **Coxa**; 16/8.
G.1897.32.98	(podomere 1): **Coxa**; 12/7.
G.1897.32.107	(podomere 1): **Coxa**; 19/10.

Table 4. Appendage IV measurements (length/width) in mm.

NMS specimen	Appendage V
G.1897.32.18	(podomeres 3 – 4): **3**; 9*/5. **4**; 8*/5.
G.1897.32.71	(podomere 1): **Coxa**; 12/5.
G.1897.32.91	(podomeres 1 – 6): **Coxa**; 26/12. **2**; 5/11. **3**; 6/11. **4**; 23/10. **5**; 17/9. **6**; 19/8.
G.1897.32.98	(podomere 1): **Coxa**; 15/8.
G.1897.32.103	(podomere 1): **Coxa**; 20/8.
G.1897.32.107	(podomeres 1 – 5): **Coxa**; 25/12. **2**; 5/10. **3**; 5/10. **4**; 15/9. **5**; 20/8.
G.1897.32.108	(podomeres 4 – 6): **4**; 8/4. **5**; 6/3. **6**; 2.5*/3.
G.1897.32.868	(podomeres 4 – 5): **4**; 24/8. **5**; 20/7.

Table 5. Appendage V measurements (length/width) in mm.

NMS specimen	**Appendage VI**
G.1885.26.72.5	(podomeres 1 – 7): **Coxa**; 22/36. **2**; –. **3**; –. **4**; 40/12. **5**; 35/12. **6**; 18/10. **7**; 19/10.
G.1897.32.18	(podomeres 1 – 6): **Coxa**; 10/12. **2**; 2/6.5. **3**; 2.5/6.5. **4**; 12.5/6. **5**; 13/5. **6**; 9*/4.
G.1897.32.71	(podomeres 1): **Coxa**; 19/30.
G.1897.32.91	(podomeres 1): **Coxa**; 22/33.
G.1897.32.98	(podomeres 1 – 5): **Coxa**; 18/23. **2**; 3/10. **3**; 3/ 10. **4**; 14/7. **5**; 12/7.
G.1897.32.103	(podomeres 1 – 2): **Coxa**; 22/36. **2**; 6/15.
G.1897.32.107	(podomeres 1): **Coxa**; 21/36.
G.1897.32.868	(podomeres 1 – 9): **Coxa**; 22/32. **2**; 4/14. **3**; 4/14. **4**; 18/11. **5**; 24/10. **6**; 21/9. **7**; 17/9. **8**; 16/5*. **9**; 13/4*.
G.1897.32.869	(podomeres 1 – 3): **Coxa**; 23/38. **2**; 6/16. **3**; 6/15.

Table 6. Appendage VI measurements (length/width) in mm.

NMS specimen	Metastoma length	Metastoma width	Notch depth	Cleft length
G.1885.26.72.5	37	28	4	20
G.1897.32.18	10*	10.5	–	–
G.1897.32.91	32	21	3	20
G.1897.32.94	13	9*	–	8
G.1897.32.98	28	19	2	18
G.1897.32.103	30*	26	–	20
G.1897.32.107	22*	18	2	–
G.1897.32.868	15*	18	–	15*
G.1897.32.869	33	26	3	20

Table 7. Metastoma measurements. Dimensions in mm. *=incomplete

NMS specimen	**1**	**2**	**3**	**4**	**5**	**6**
G.1885.26.72.5	12/101*	25/105*	15/101*	14/94*	14/85*	14/73*
G.1885.26.72.10	5*/4*	12/15*	10/22*	10/23*	10/24*	10/25*
G.1885.26.72.15	–	2.5/6.5*	2.5/12.5	2.3/12.5*	2/12	2/11
G.1897.32.18	5/34	10/40	10/35*	9/28*	9/24*	5*/13*
G.1897.32.71	15/61*	24/61*	15/59*	15/59*	15/55*	14/53
G.1897.32.72.1	–	10/42*	10/43*	10/49	9/48	10/47
G.1897.32.91	14/42*	25/88*	16/75*	16/84	14/80	15/58*
G.1897.32.94	5/34*	9/33*	8/10*	6/28*	8/26*	8/25*
G.1897.32.98	13/70*	20/65*	14/88*	14/84*	14/78*	15/57*
G.1897.32.100	13/104*	19/102*	15/78*	15/68*	14/58*	10*/42*
G.1897.32.102	9/72*	15/66*	10/56*	11/45*	11/38*	6*/35*
G.1897.32.103	12/82	20/85	14/89	15/92	14/88	15/82
G.1897.32.106	8/32*	18/58*	14/52*	14/43*	14/30*	–
G.1897.32.108	4.5/25*	7.5/30.5*	7/33*	6/33*	6.5/30*	6/30*
G.1897.32.109	–	–	10/105	10/101*	11/95	11/93
G.1897.32.110	10/51.5*	15/56.5*	11/55*	11/59*	5*/26*	–
G.1897.32.111	8/32*	15/41*	10/44*	10/47*	10/55*	10/55*
G.1897.32.114	4/46*	6/45*	5/32*	5/30*	5/27*	5/26*
G.1897.32.117	5/22*	9/38*	6/42*	6/47*	6/52*	6/52*
G.1897.32.188	9/31*	20/36*	15/41*	15/42*	16/42*	16/41*
G.1897.32.868	10/85	18/99	12/103	12/104	11/102	11/96

Table 8. Mesosoma (length/width) in mm. *=incomplete

NMS specimen	7	8	9	10	11	12	Telson
G.1885.26.72.5	12/62*	11/55*	–	–	–	–	–
G.1885.26.72.10	10/50*	10/45*	10/30*	12/30*	13/32*	15/20*	–
G.1885.26.72.15	2/10	2/8	2/6.5	4/6	4/4.5	5.3/5	19/3
G.1897.32.71	12*/51	–	–	–	–	–	–
G.1897.32.72.1	6/34*	8/19*	8/18*	8/10*	10/14	12/12	25*/6
G.1897.32.72.2	–	4*/5*	12/12*	17/24*	18/26*	22/23	50*/12
G.1897.32.72.3	–	–	–	–	–	9*/16	54*/10
G.1897.32.91	15/43*	16/47*	15/50*	19/53	22/47	29/32	65*/16
G.1897.32.98	14/55*	14/48*	15/44*	15/36*	18/30*	23/22	57*/15
G.1897.32.103	13/76	12/72	15/48*	15/34*	–	–	–
G.1897.32.108	4*/27*	6.5/16*	8/26.5	8/26.5	8/21	14/14	10.5*/7.5
G.1897.32.109	10/89	9/70*	10/71	11/58	12/50	19/38	70*/20
G.1897.32.111	9/50*	10/43*	10/43*	10*/31*	–	–	–
G.1897.32.114	5/33*	5/22*	4*/5*	–	–	–	–
G.1897.32.117	6/49*	6/38*	6/33*	6/24*	6/15*	4*/7*	–
G.1897.32.188	15/36*	13/33*	–	–	–	–	–
G.1897.32.868	10/89	11/76	12/72	14/55*	14/51*	–	–

Table 9. Metasoma and telson (length/width) in mm. *=incomplete

Figure 1. *Drepanopterus pentlandicus* Laurie, 1892. Original figure of a juvenile individual (part to specimen NMS G.1897.32.18?) in Laurie, 1899, specimen now considered lost.

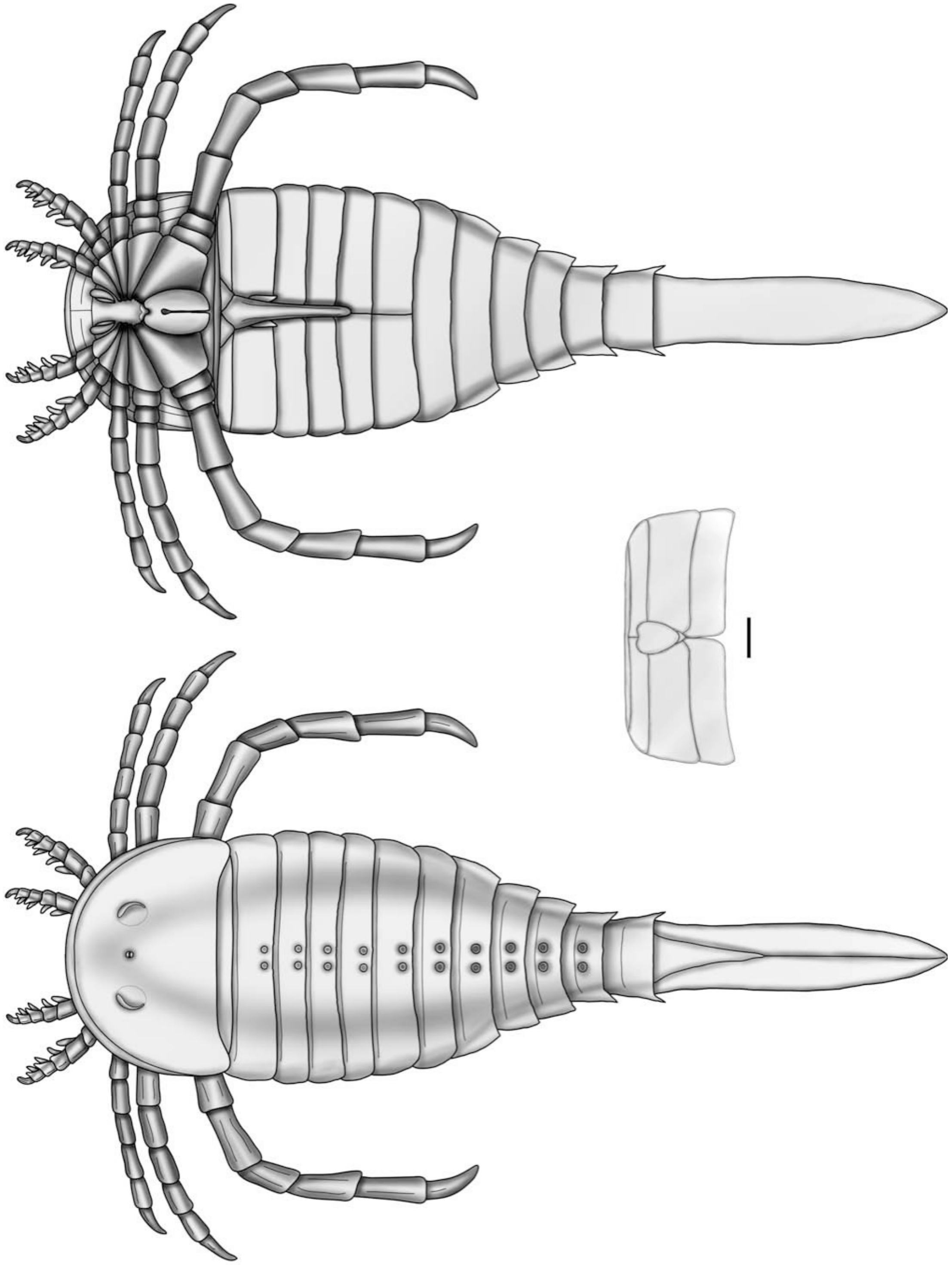

Figure 2. Reconstruction of adult *Drepanopterus pentlandicus* Laurie, 1892. Dorsal and ventral views of a type-A individual are shown either side, while a type-B genital operculum is shown in the centre. Scale bar = 10 mm.


a

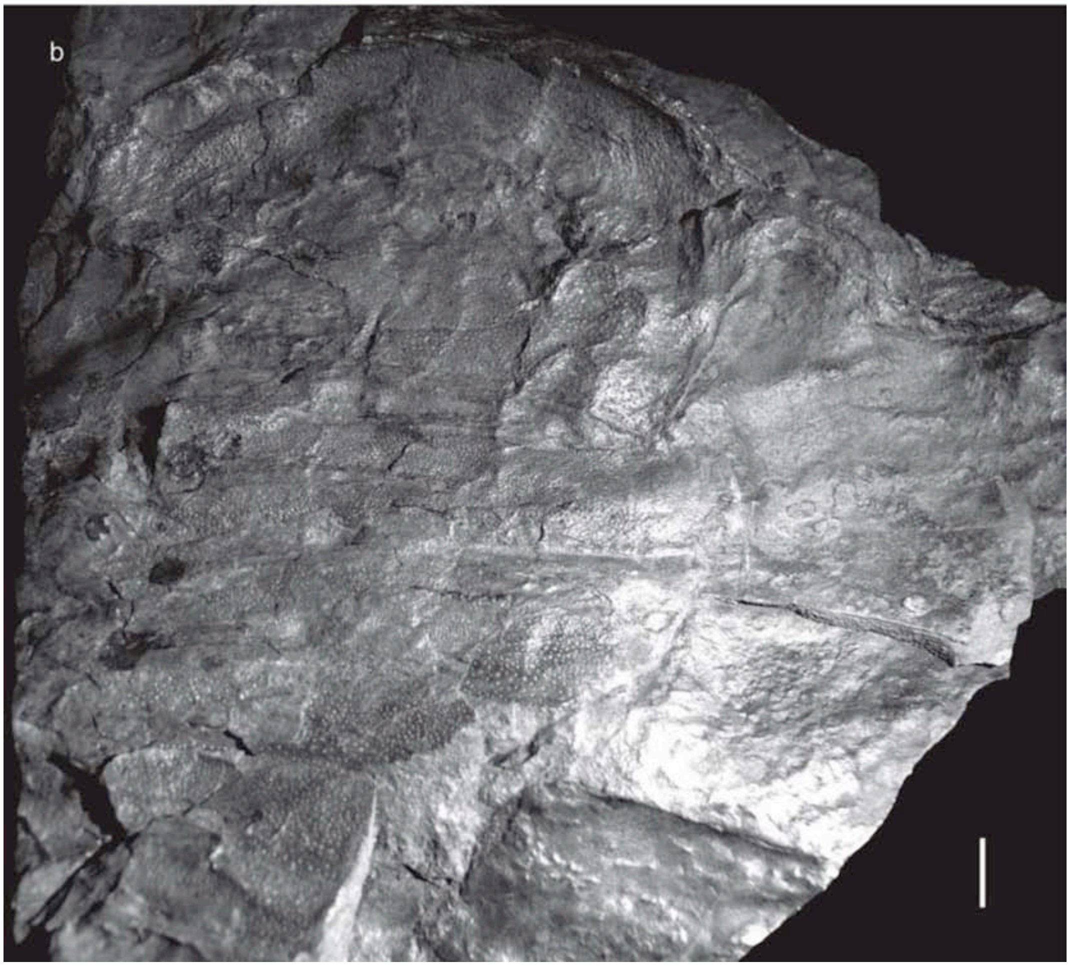
b

Figure 3. *Drepanopterus pentlandicus* Laurie, 1892. a: Holotype, NMS G.1885.26.72.5, consisting of carapace, mesosomal segments and proximal portions of appendage VI, b: NMS G.1885.26.72.5, counterpart. Scale bar = 10 mm.

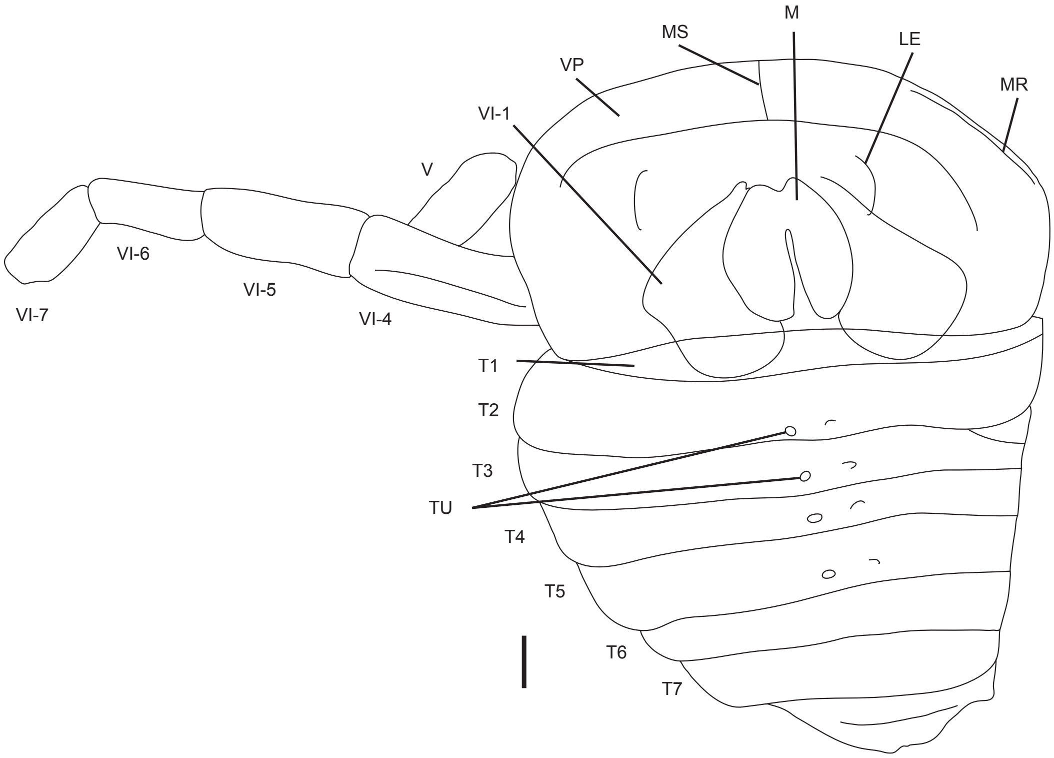

Figure 4. *Drepanopterus pentlandicus* Laurie, 1892. Interpretive drawing of holotype NMS G.1885.26.72.5. Abbreviations: LE, lateral eyes; M, metastoma; MR, marginal rim; MS, median suture; TU, tubercles; T1–T12, tergites 1–12; VP, ventral plate. Prosomal appendages are labelled with Roman numerals (I–VI), and individual podomeres are labelled with Arabic numerals (1–9), proximally to distally. Scale bar = 10 mm.

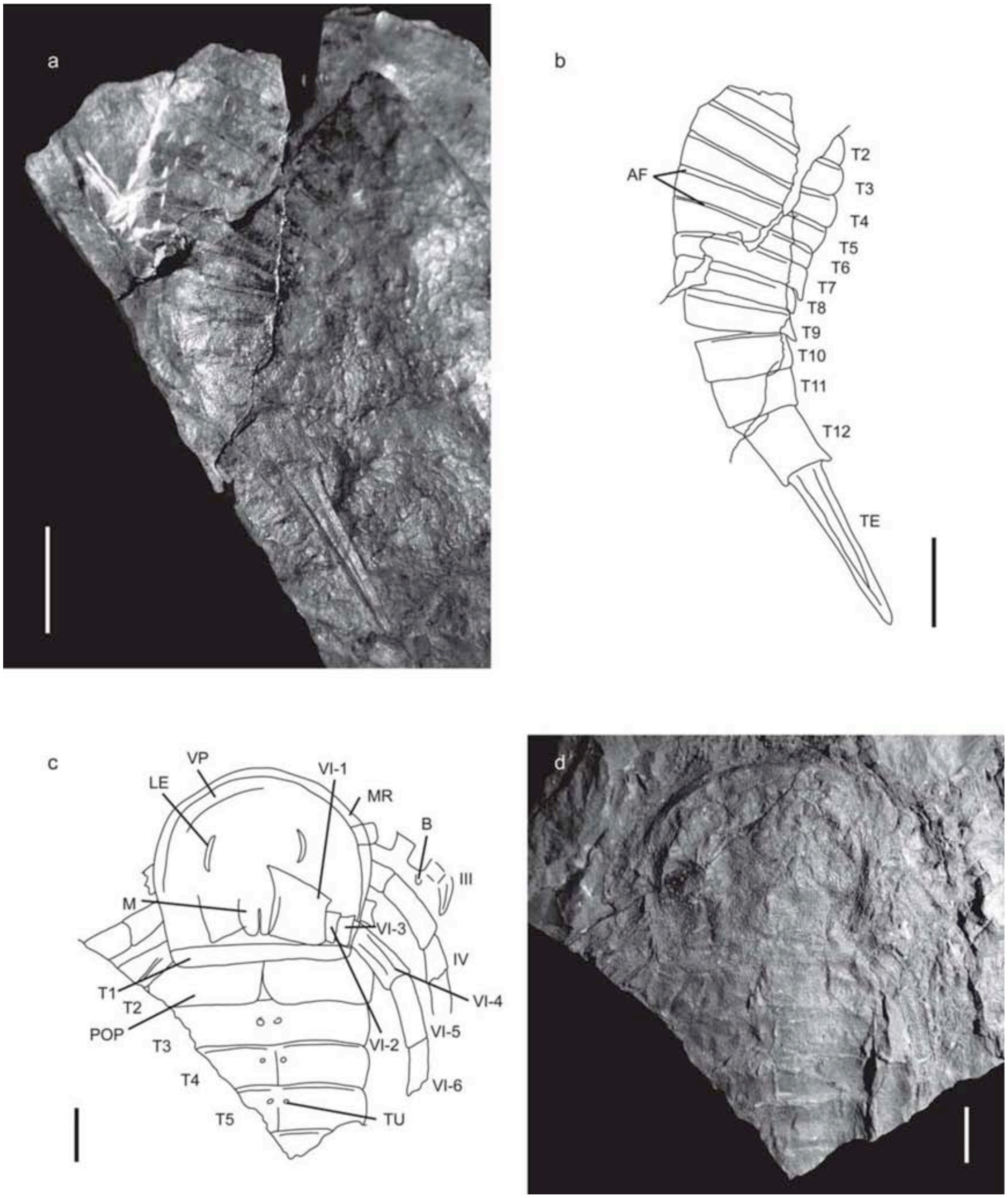

Figure 5. *Drepanopterus pentlandicus* Laurie, 1892. a: Paratype, NMS G.1885.26.72.15, opisthosoma of juvenile individual, b: Interpretive drawing of NMS G.1885.26.72.15, c: Interpretive drawing of NMS G.1897.32.18, d: NMS G.1897.32.18, juvenile individual consisting of carapace, anterior mesosomal segments and parts of prosomal appendages III, IV and VI. Abbreviations: AF, articulating facet; B, blade; LE, lateral eyes; M,

metastoma; MR, marginal rim; TU, tubercles; T1–T12, tergites 1–12; TE, telson; VP, ventral plate. Prosomal appendages are labelled with Roman numerals (I–VI), and individual podomeres are labelled with Arabic numerals (1–9), proximally to distally. Scale bars = 10 mm.

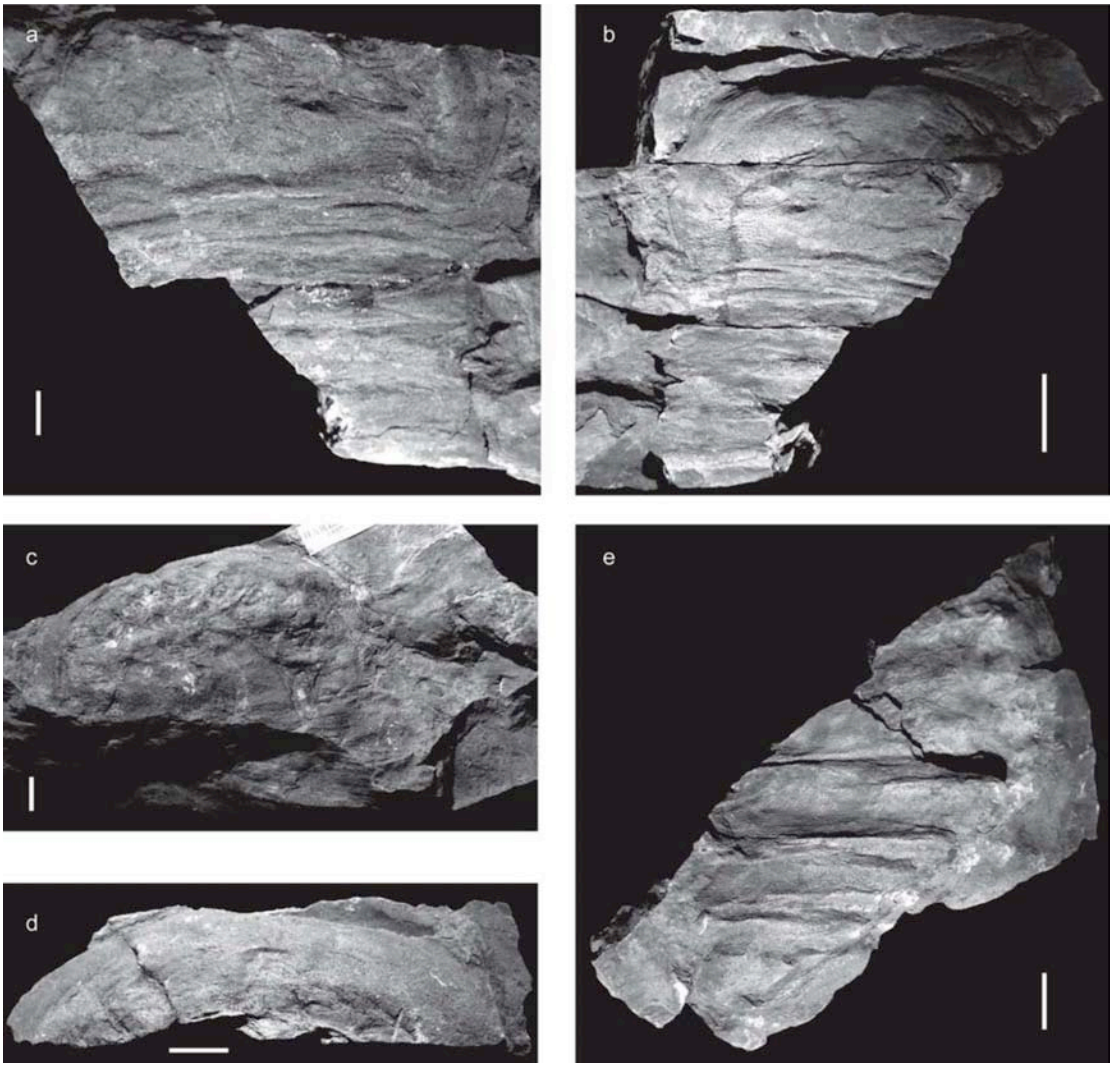

Figure 6. *Drepanopterus pentlandicus* Laurie, 1892. a: NMS G.1897.32.101, partial carapace and mesosomal segments, b: NMS G.1897.32.102, counterpart to NMS G.1897.32.101, c: NMS G.1897.32.107, prosoma showing ventral structures, d: NMS G.1897.32.105, anterior of prosoma showing ventral plates, e: NMS G.1897.32.106, opisthosomal segments. Scale bars = 10 mm.

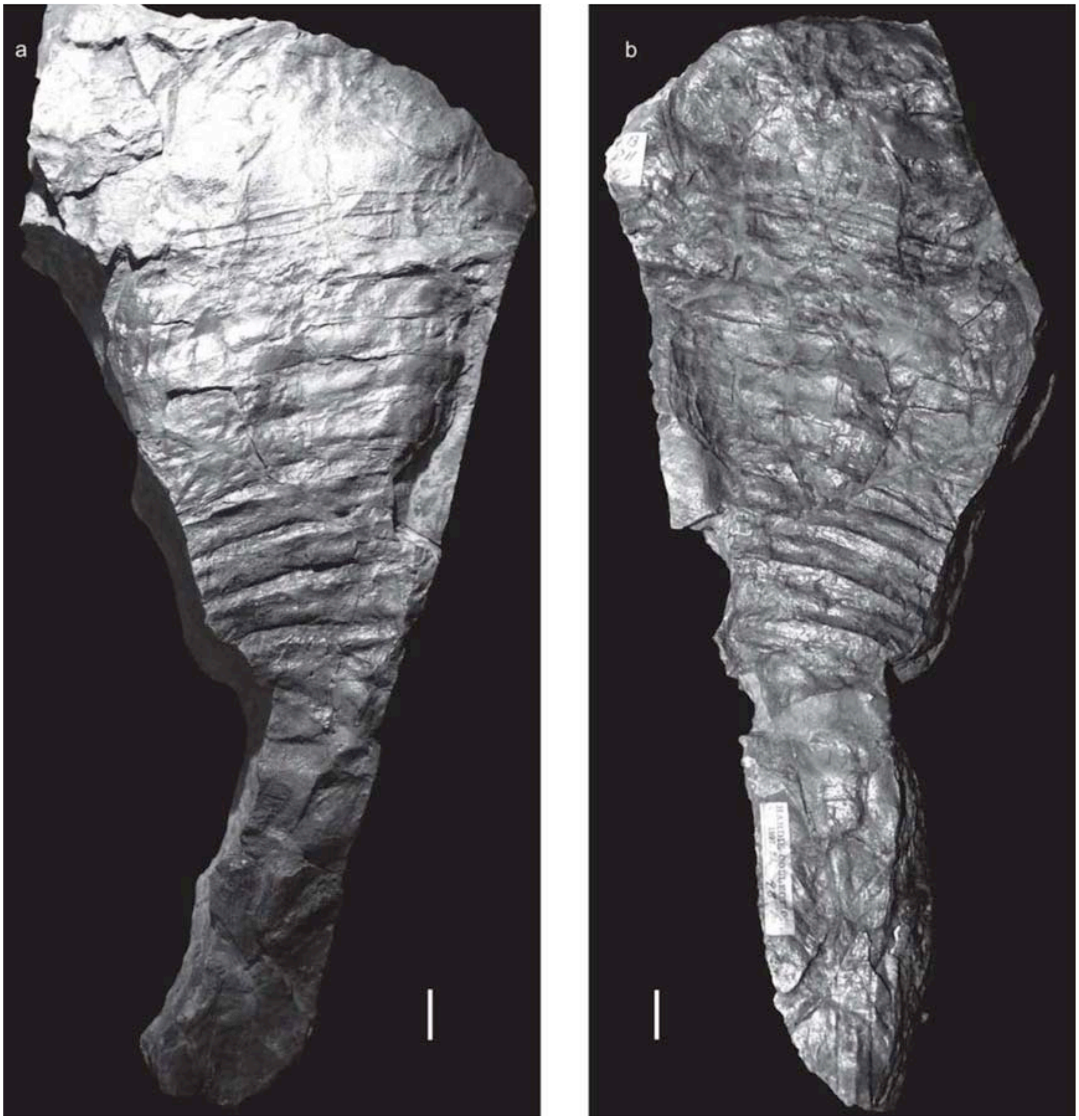

Figure 7. *Drepanopterus pentlandicus* Laurie, 1892. a: NMS G.1897.32.97, relatively complete individual including carapace, opisthosoma and telson, b: NMS G.1897.32.98, counterpart to NMS G. 1897.3.97. Scale bars = 10 mm.

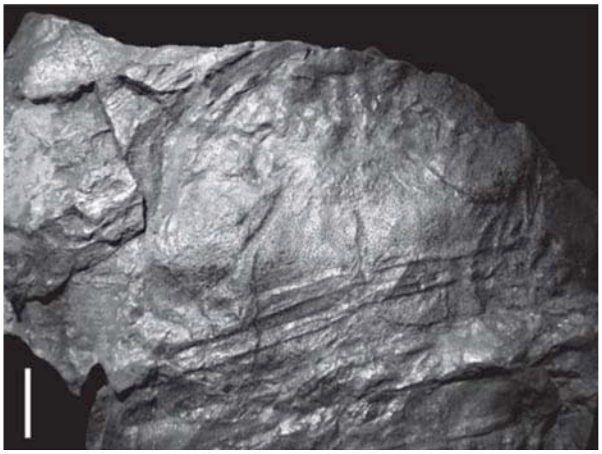

Figure 8. *Drepanopterus pentlandicus* Laurie, 1892. Enlarged view of carapace of NMS G.1892. 897.32.97. Scale bar = 10 mm.

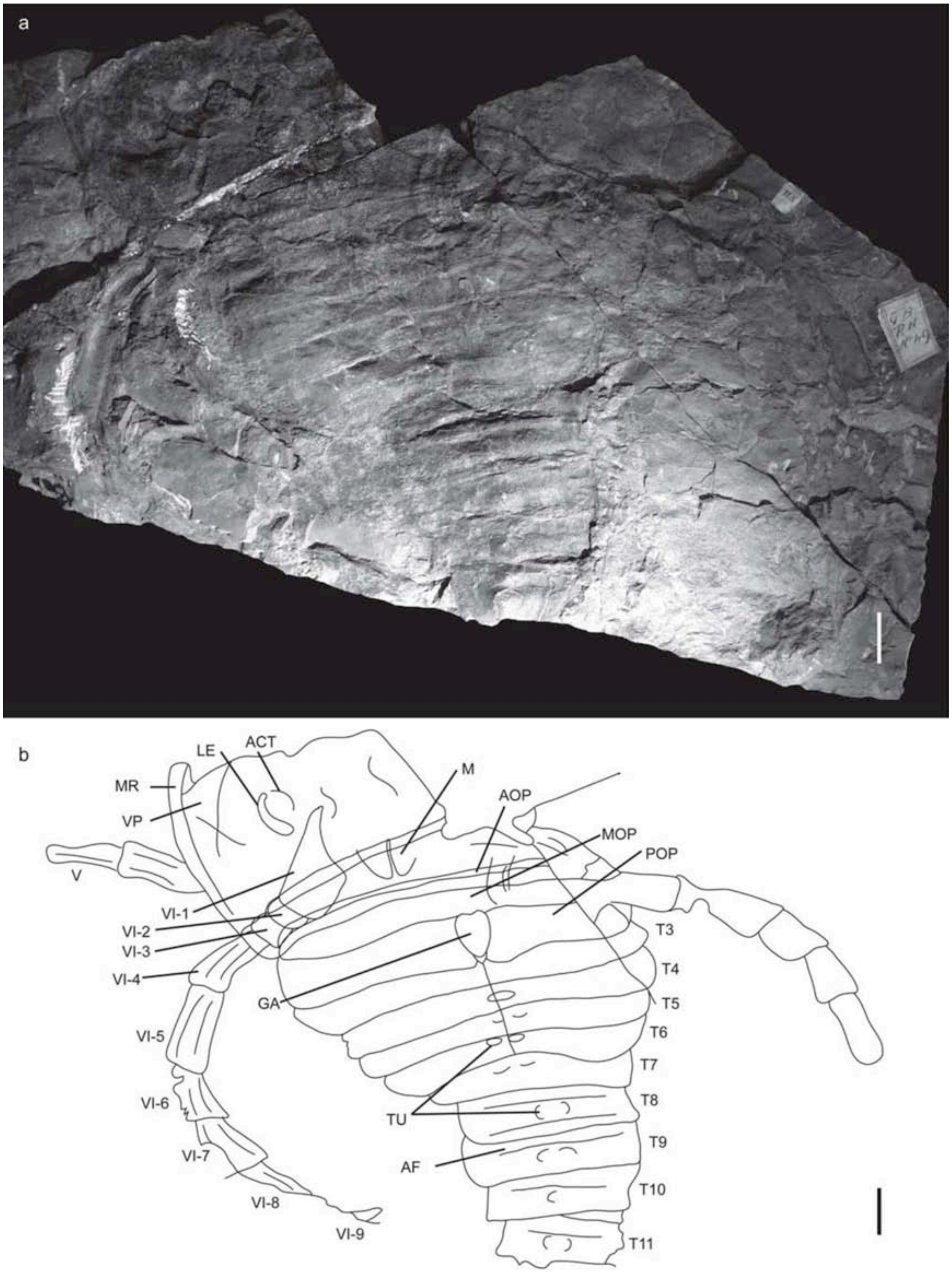

Figure 9. *Drepanopterus pentlandicus* Laurie, 1892. a: NMS G.1897.32.868, almost complete specimen consisting of carapace and opisthosoma, including appendage VI and type B genital appendage, b: Interpretive drawing of NMS G.1897.32.868. ACT, annular

cuticular thickening; Abbreviations: AF, articulating facet; AOP, anterior opercular plate; GA, genital appendage; LE, lateral eyes; M, metastoma; MOP, median opercular plate; MR, marginal rim; POP, posterior opercular plate; TU, tubercles; T1–T12, tergites 1–12; TE, telson; VP, ventral plate. Prosomal appendages are labelled with Roman numerals (I–VI), and individual podomeres are labelled with Arabic numerals (1–9), proximally to distally. Scale bars = 10 mm.

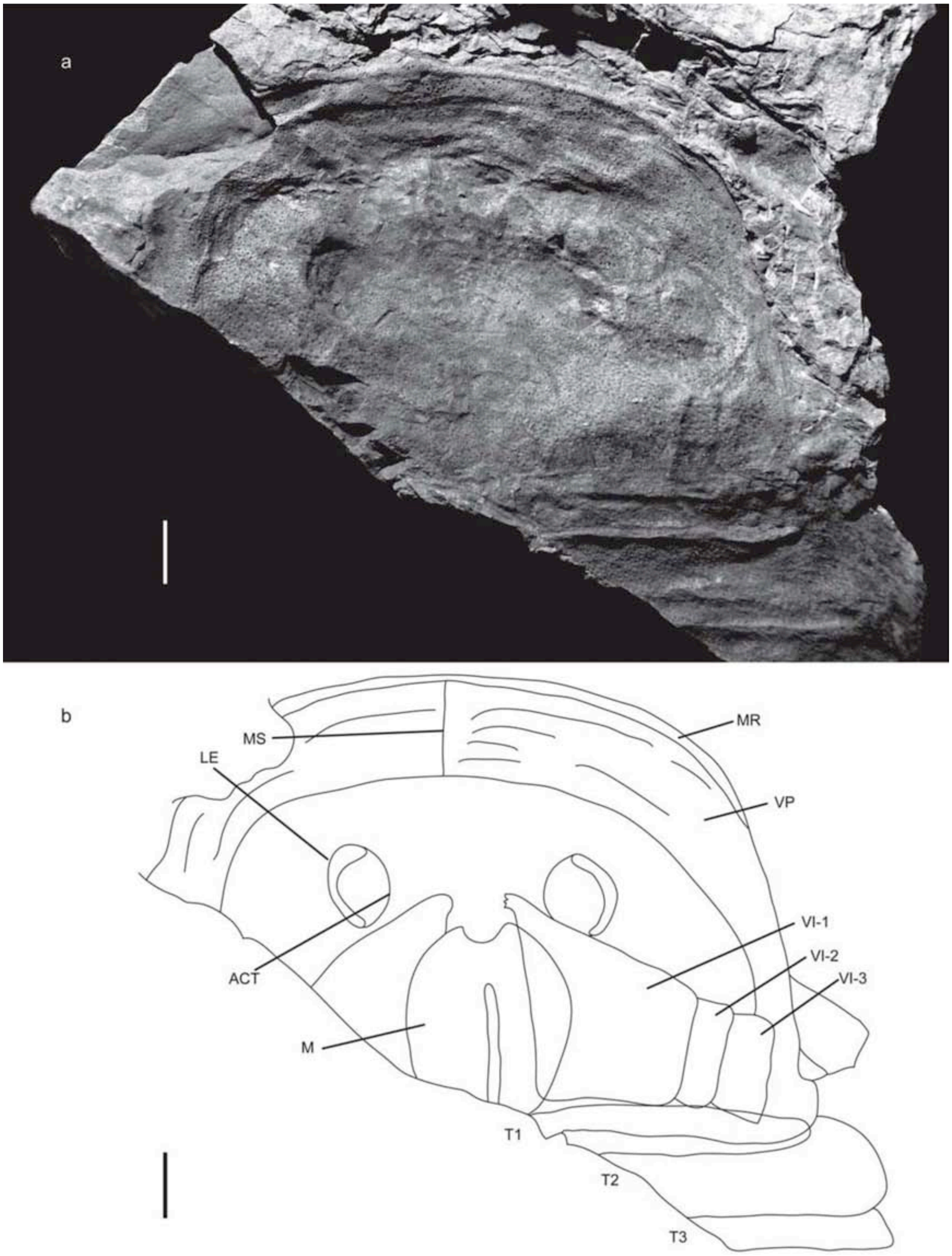

Figure 10. *Drepanopterus pentlandicus* Laurie, 1892. a: NMS G.1897.32.869, prosoma showing lateral eyes, ventral plates, metastoma and coxa of appendage VI, b: Interpretive drawing of NMS G.1897.32.869. Abbreviations: ACT, annular cuticular thickening; LE,

lateral eyes; M, metastoma; MR, marginal rim; MS, median suture; T1–T12, tergites 1–12; VP, ventral plate. Prosomal appendages are labelled with Roman numerals (I–VI), and individual podomeres are labelled with Arabic numerals (1–9), proximally to distally. Scale bars = 10 mm.

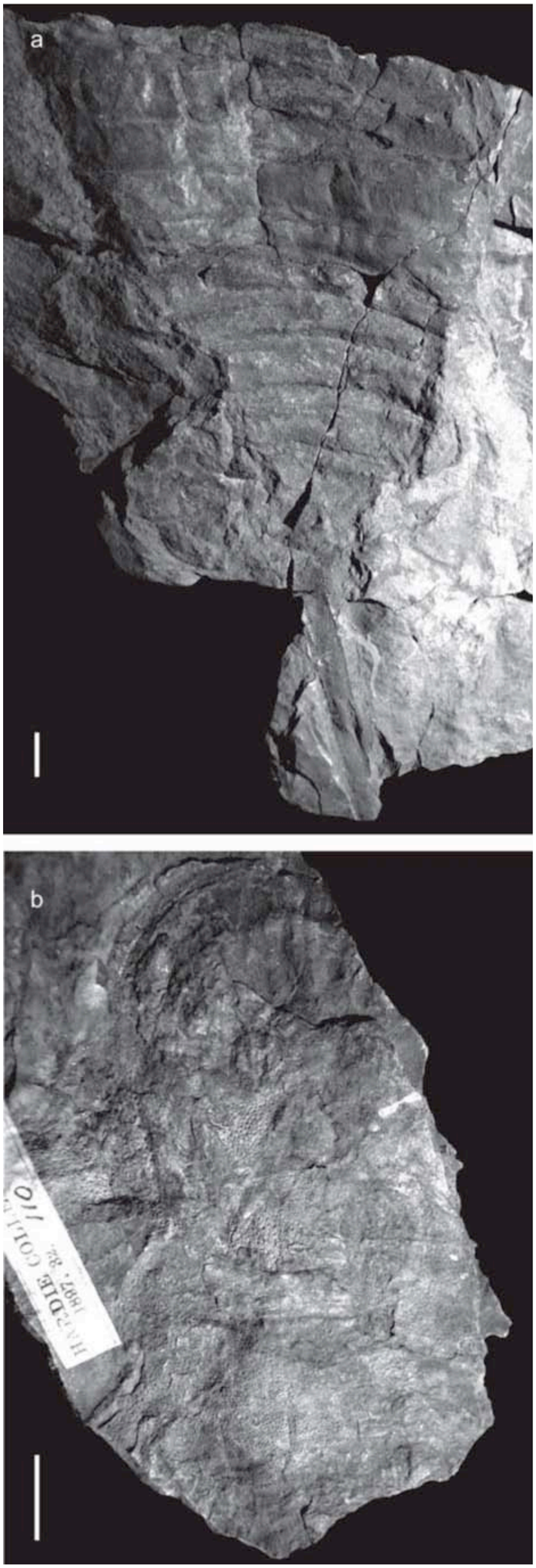
a
b
DIE COLL
1887. 32.
110

Figure 11. *Drepanopterus pentlandicus* Laurie, 1892. a: NMS G.1897.32.109, metasoma and telson, b: NMS G.1897.32.110, carapace with apparently round lateral eye and mesosomal segments. Scale bars = 10 mm.

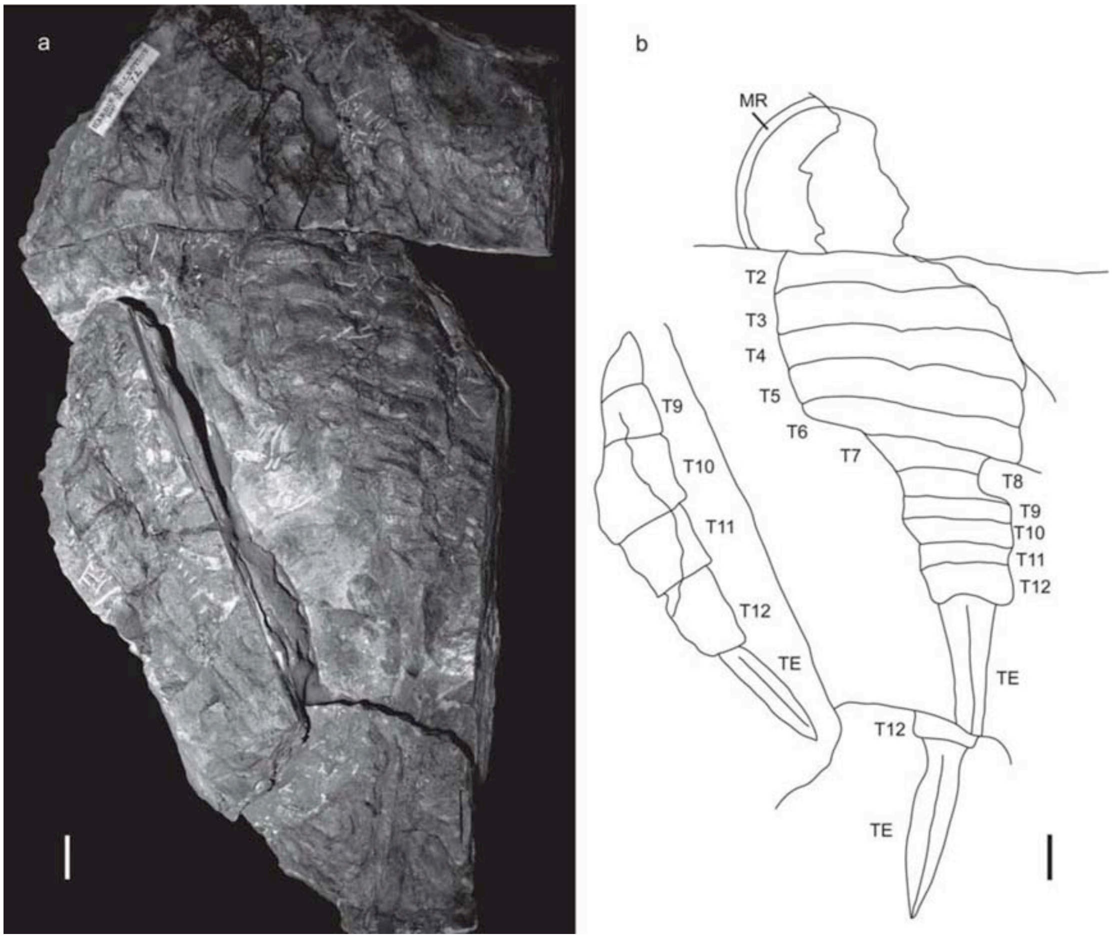

Figure 12. *Drepanopterus pentlandicus* Laurie, 1892. a: NMS G.1897.32.72, multiple specimens preserved in different levels of sediment on the same slab, b: Interpretive drawing of NMS G.1897.32.72. Abbreviations: MR, marginal rim; T1–T12, tergites 1–12; TE, telson. Scale bars = 10 mm.

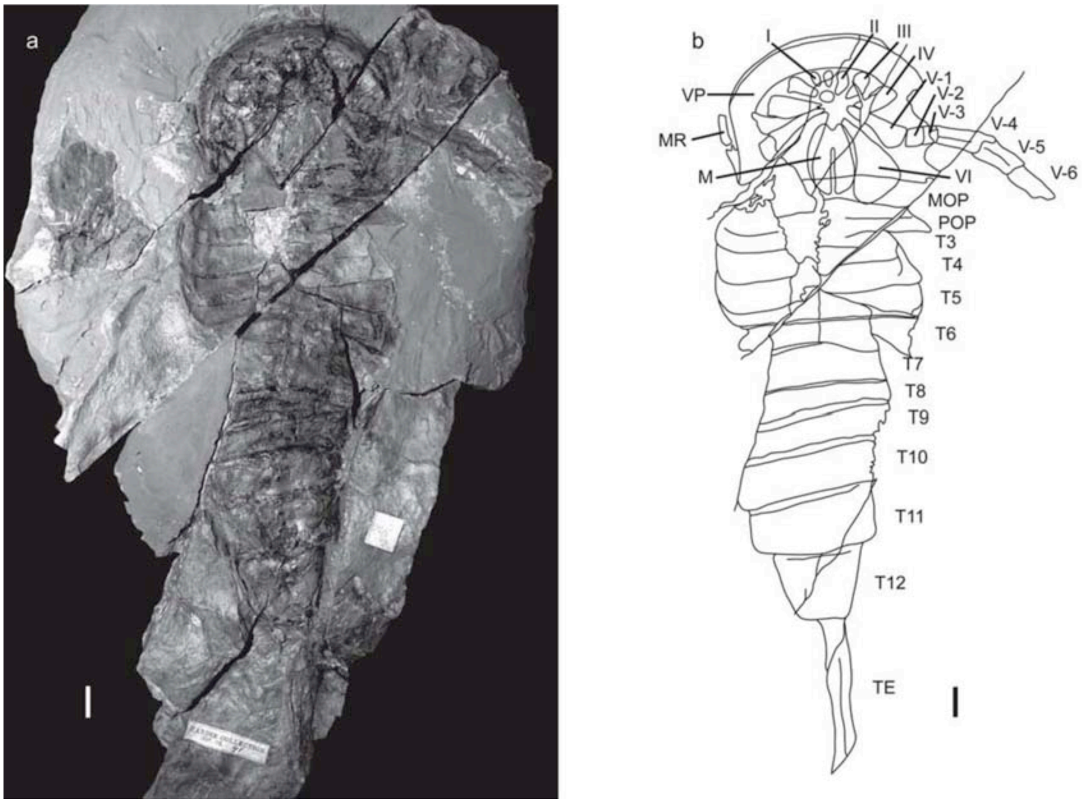

Figure 13. *Drepanopterus pentlandicus* Laurie, 1892. a: NMS G.1897.32.91, remarkably well preserved specimen showing details of the ventral prosomal structures and the median sutures on the Blattfüsse, b: Interpretive drawing of NMS G.1897.32.91. Abbreviations: M, metastoma; MOP, median opercular plate; MR, marginal rim; POP, posterior opercular plate; T1–T12, tergites 1–12; TE, telson; VP, ventral plate. Prosomal appendages are labelled with Roman numerals (I–VI), and individual podomeres are labelled with Arabic numerals (1–9), proximally to distally. Scale bars = 10 mm.

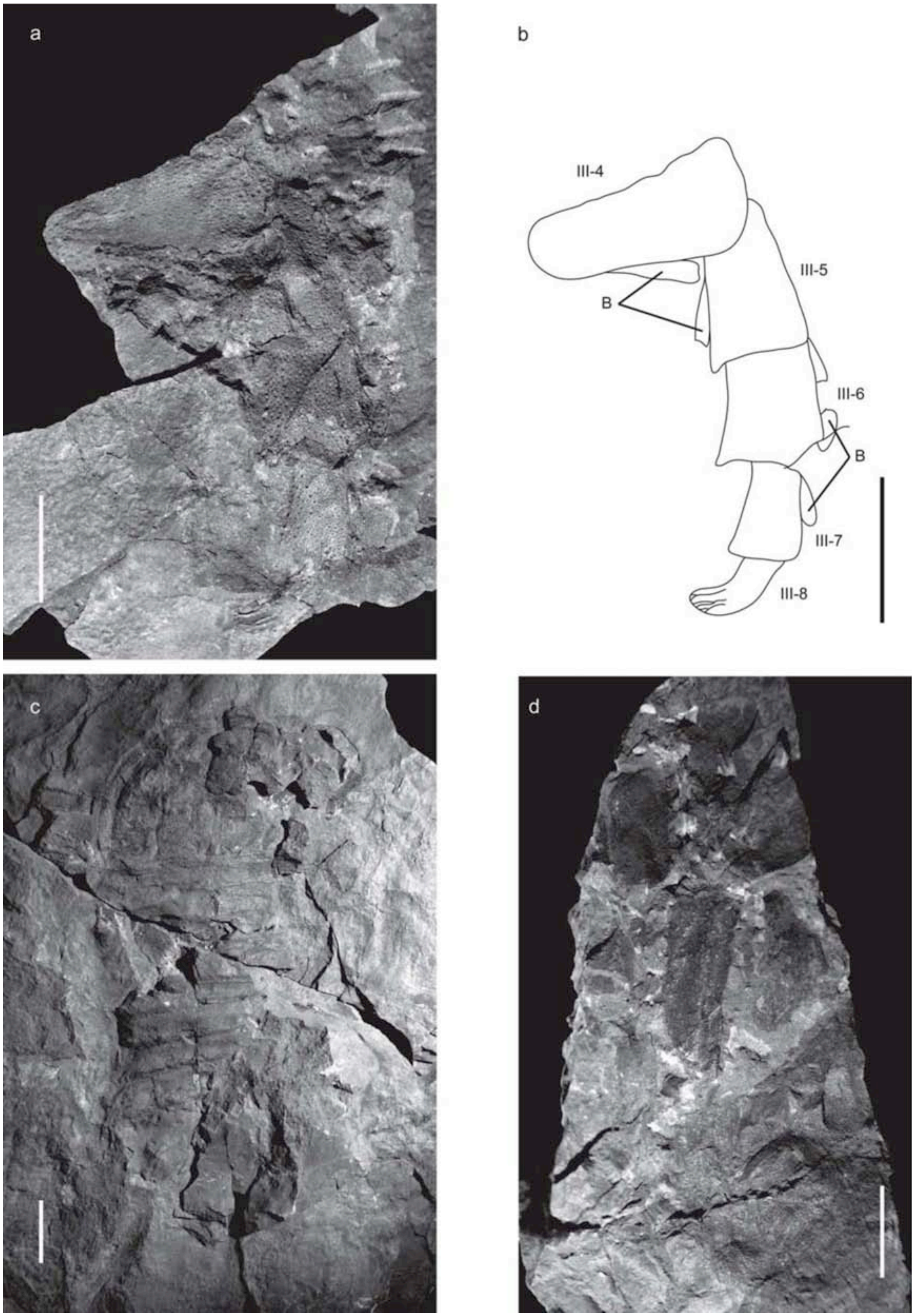
a
b
III-4
III-5
B
III-6
B
III-7
III-8
c
d

Figure 14. *Drepanopterus pentlandicus* Laurie, 1892. a: NMS G.1897.32.92, isolated appendage (III?) with blades, b: Interpretive drawing of NMS G.1897.32.92, c: NMS G.1897.32.94, weathered specimen showing fragments of cuticle, d: NMS G.1897.32.99, tangle of appendage podomeres. Abbreviations: B, blade. Prosomal appendages are labelled with Roman numerals (I–VI), and individual podomeres are labelled with Arabic numerals (1–9), proximally to distally. Scale bars = 10 mm.

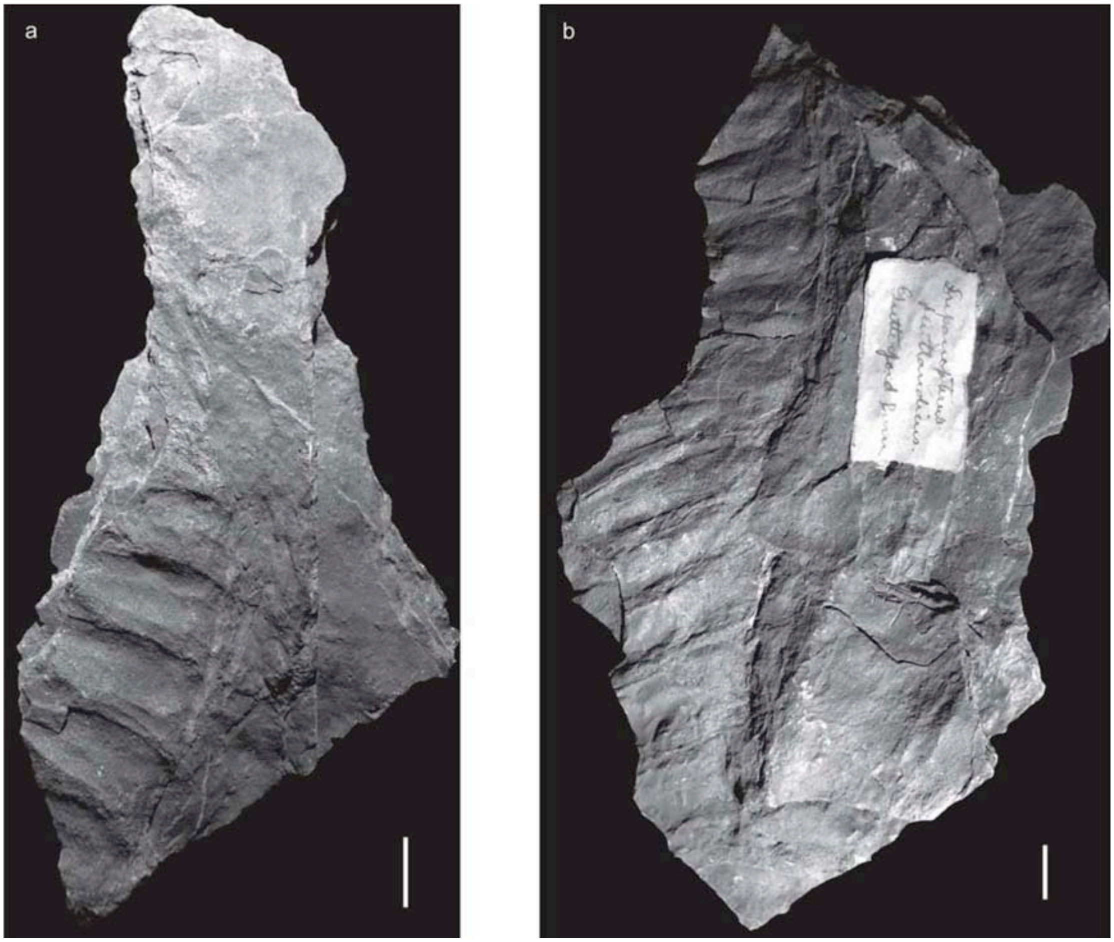

Figure 15. *Drepanopterus pentlandicus* Laurie, 1892. a: NMS G.1885.26.72.12, lateral portions of mesosomal segments, b: NMS G.1885.26.72.10, portion of mesosoma and metasoma. Scale bars = 10 mm.

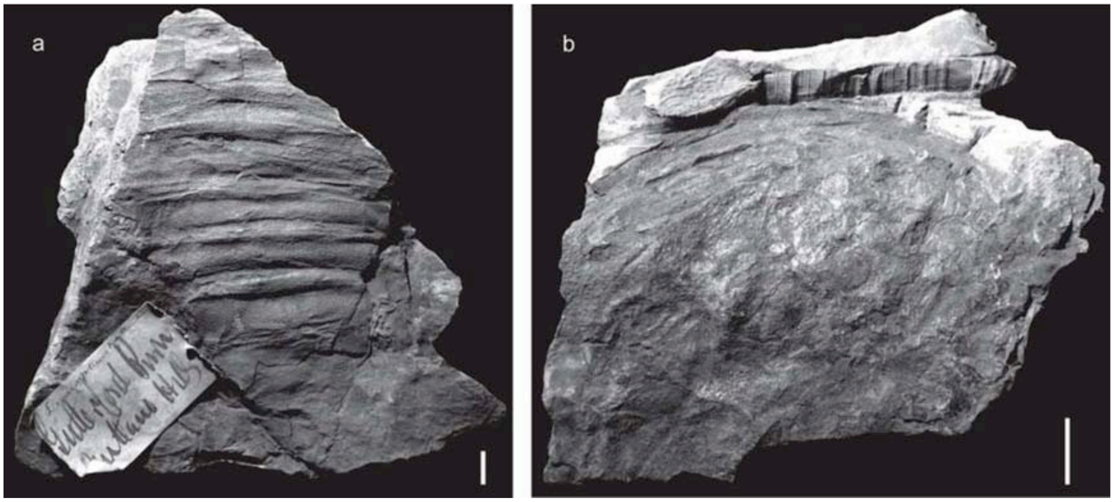

Figure 16. *Drepanopterus pentlandicus* Laurie, 1892. a: NMS G.1885.26.72.11, opisthosomal segments, b: NMS G.1885.26.72.3, fragment of large, flattened carapace showing compressed lateral eye and cuticular ornament. Scale bars = 10 mm.

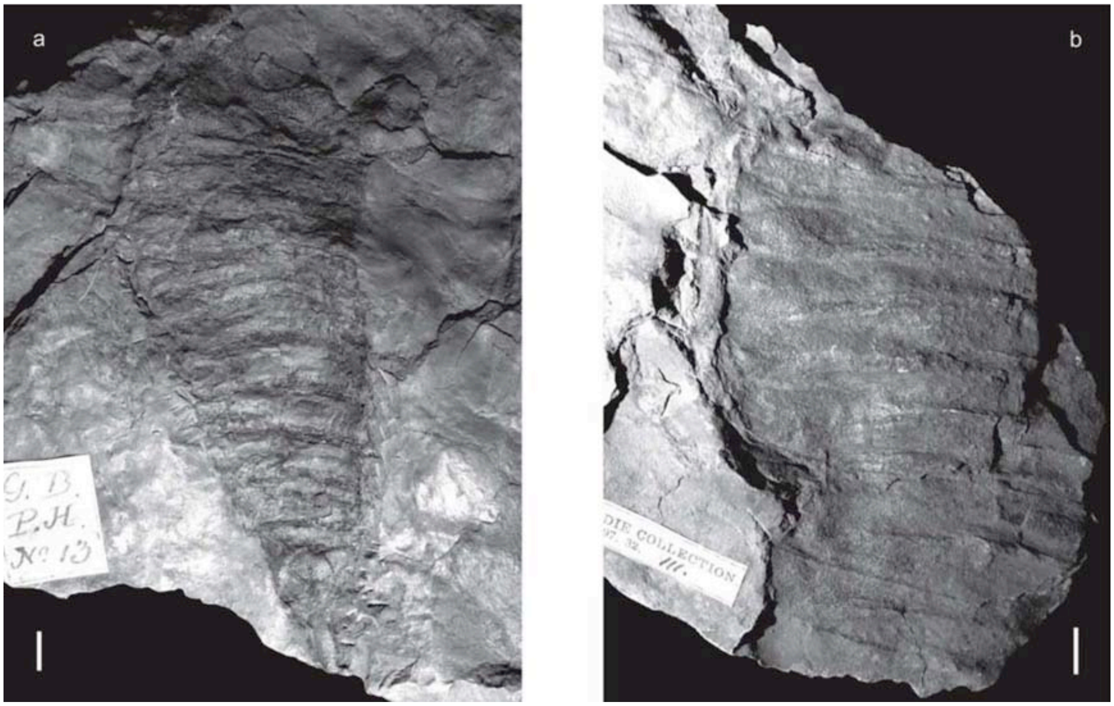

Figure 17. *Drepanopterus pentlandicus* Laurie, 1892. a: NMS G.1897.32.108, showing opisthosoma and base of telson, b: NMS G.1897.32.111, lateral portions of opisthosomal segments. Scale bar = 10 mm.

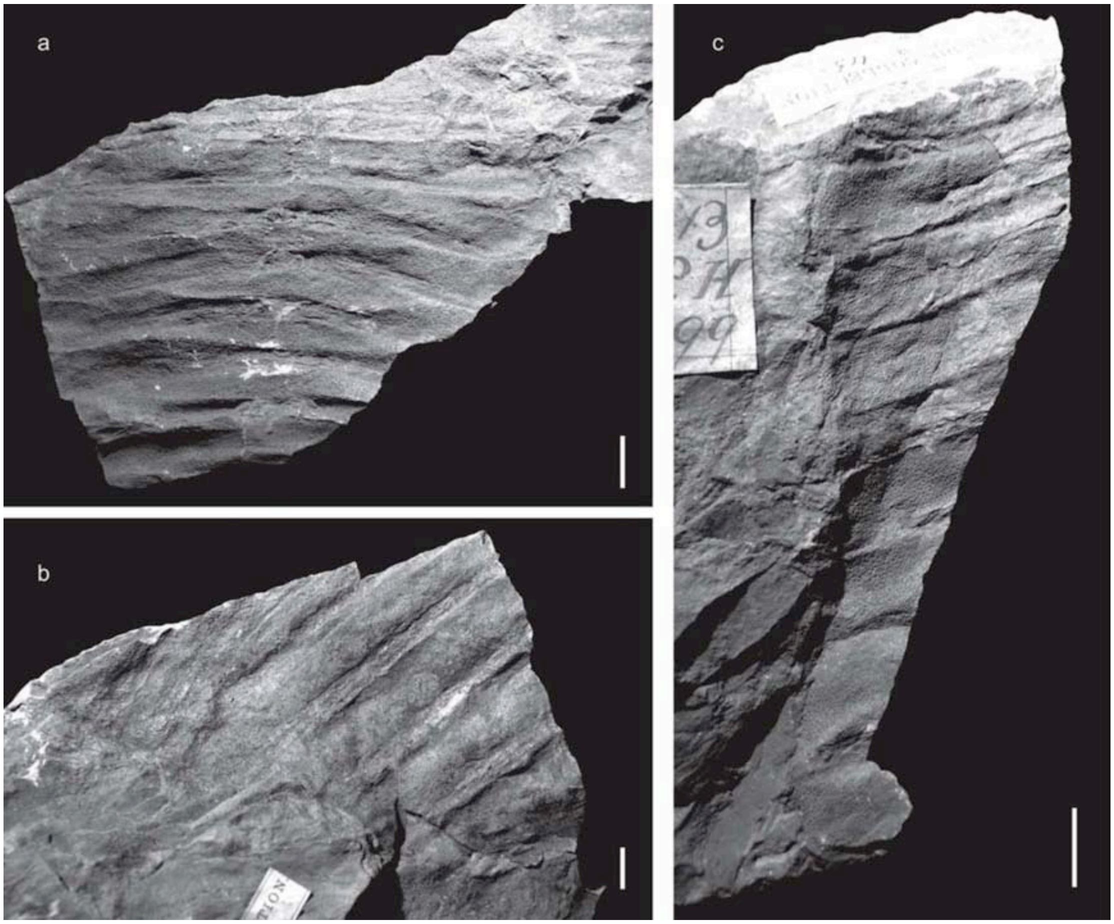

Figure 18. *Drepanopterus pentlandicus* Laurie, 1892. a: NMS G.1897.32.112, ventral view of tergites showing median tubercles, b: NMS G.1897.32.113, lateral portions of tergites, c: NMS G.1897.32.115, tergites showing cuticular sculpture. Scale bars = 10 mm.

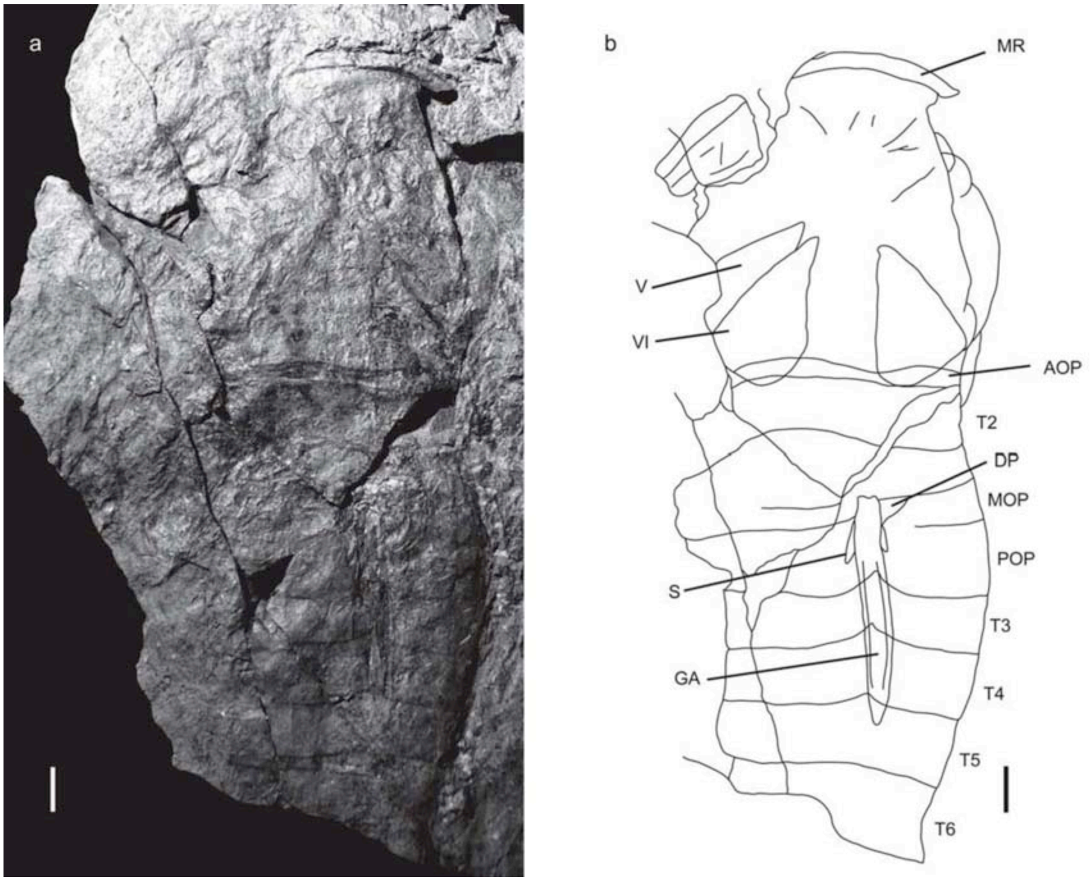

Figure 19. *Drepanopterus pentlandicus* Laurie, 1892. a: NMS G.1897.32.71, specimen preserving the type A genital appenda, b: Interpretive drawing of NMS G.1897.32.71. Abbreviations: AOP, anterior opercular plate; DP, deltoid plate; GA, genital appendage; MOP, median opercular plate; MR, marginal rim; POP, posterior opercular plate; S, spatula; T1–T12, tergites 1–12. Prosomal appendages are labelled with Roman numerals (I–VI). Scale bar = 10 mm.

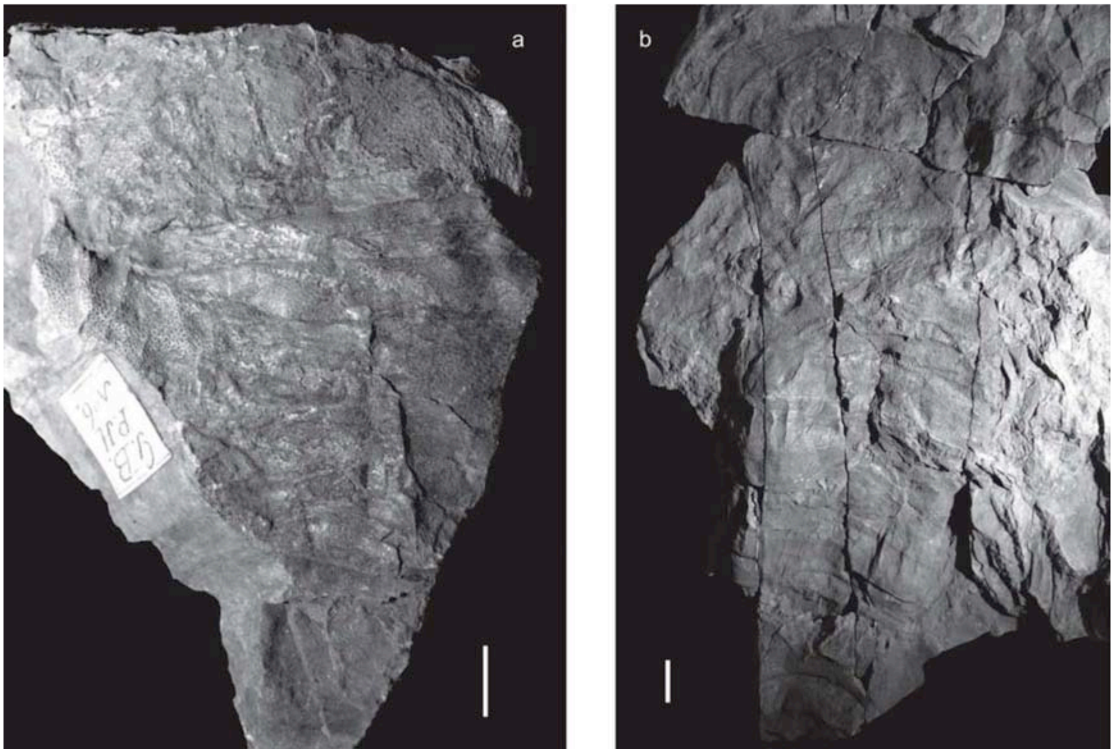

Figure 20. *Drepanopterus pentlandicus* Laurie, 1892. a: NMS G.1897.32.100, poorly preserved specimen with carapace and mesosomal segments, b: NMS G.1897.32.103, fractured specimen showing details of carapace structures and anterior opisthosoma. Scale bar = 10 mm.

Figure 21. *Drepanopterus pentlandicus* Laurie, 1892. NMS G.1897.32.114, specimen showing various degrees of suturing of the blattfüsse. Scale bar = 10 mm.

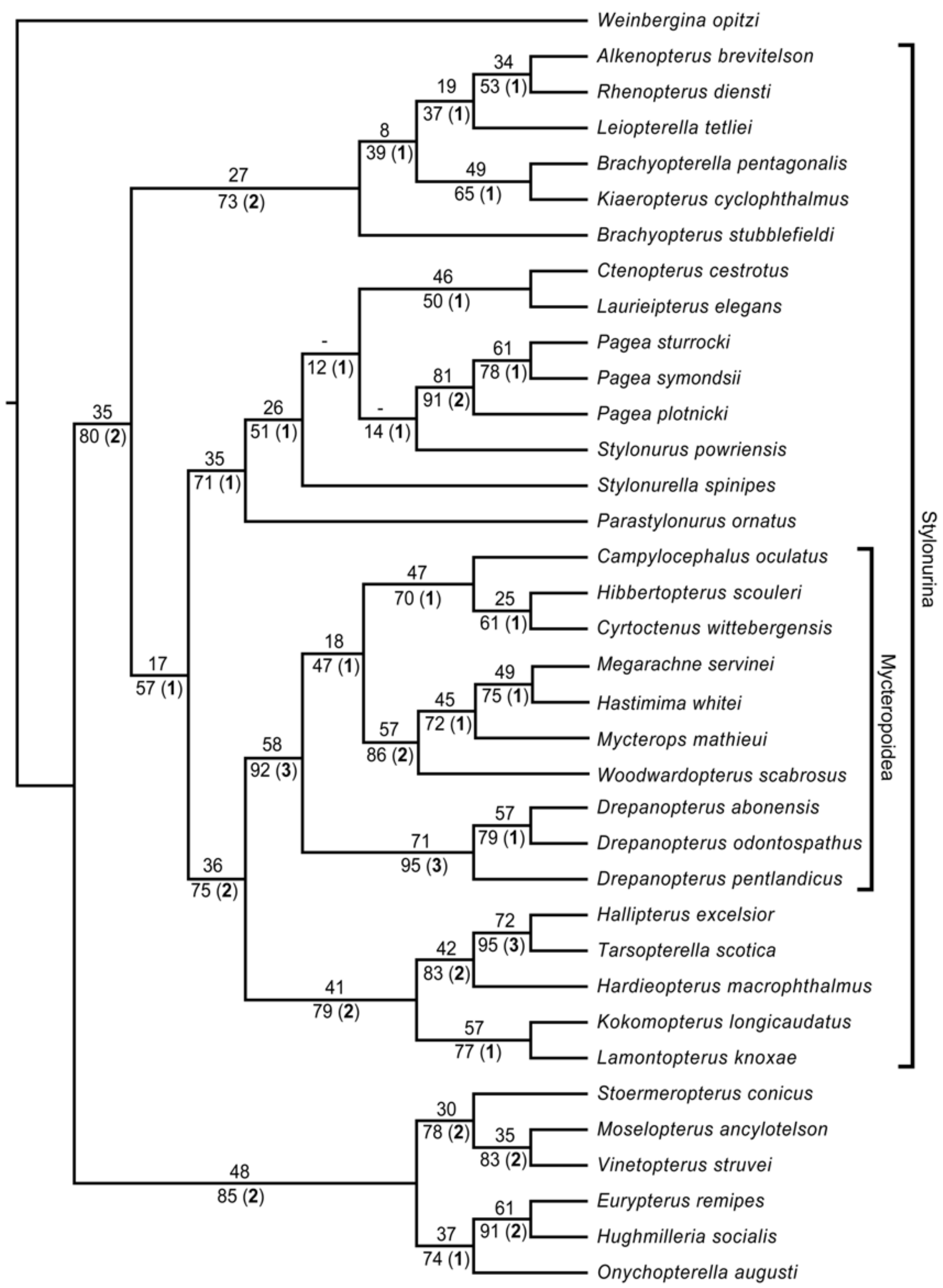

Figure 22. Single most parsimonious tree derived from the matrix shown Appendix 1, analysed as detailed in the material and methods section. Bootstrap values are shown above the branches, generated from 50% character resampling with 1000 repetitions,

while shown beneath the branches are jackknife values with 20% character resampling with 1000 repetitions, with bremer support values shown in bold within parentheses.

Chapter 2

The problematic 'chelicerate' *Melbournopterus crossotus* Caster & Kjellesvig-Waering: a case of mistaken identity

James C. Lamsdell, Ian G. Percival and Markus Poschmann

(Formatted for submission to *Alcheringa*)

The type (and only known) specimen of *Melbournopterus crossotus* Caster & Kjellesvig-Waering, an enigmatic late Silurian fossil that was initially assigned to the eurypterid family Stylonuridae, is critically examined for the first time in 60 years. It is reinterpreted as most likely the dorsal valve of a craniate brachiopod, with prominent paired adductor muscle scars (described originally as 'lateral eyes') situated anteromedially, a short hingeline, and a spinose anterior margin.

MELBOURNOPTERUS CROSSOTUS Caster & Kjellesvig-Waering, 1953 is known from a single enigmatic specimen in part and counterpart, described from the upper Silurian (*Monograptus nilssoni* Zone) Dargile Formation near Heathcote in central Victoria, Australia. The fossil, originally assigned to the eurypterid family Stylonuridae, was interpreted as the external mould of an isolated carapace displaying external cuticular ornamentation and lateral eyes. However, the morphology of these "lateral eyes" is unlike those of any other stylonurid; they are rectangular, positioned on the posterior half of the carapace and angled so they converge anteriorly at the centre of the carapace. Furthermore, the posterior margin possesses short, blunt spines. These unusual characteristics have led to uncertainty over the specimen's assignment. Tollerton (1989) placed it in Eurypterida *incertae sedis*, but Plotnick (1999) suggested that *Melbournopterus* was not a eurypterid, instead considering that it may be a xiphosuran, whereas Tetlie (2004) retained *Melbournopterus* within Eurypterida but as a mycteropid.

Xiphosurans are represented in Australia by only a handful of occurrences, including *Victalimulus mcqueeni* Riek & Gill, 1971 from the Lower Cretaceous Koonwarra Fossil Bed within the Strzelecki Group of Victoria, *Austrolimulus fletcheri* Riek, 1955 from a shale lens within the Middle Triassic Hawkesbury Sandstone of the Sydney Basin, New South Wales, *Paleolimulus* (=*Dubbolimulus*) *peetae* (Pickett, 1984) from the Middle Triassic Ballimore Formation and *Kasibelinurus amicorum* Pickett, 1993 from the Upper Devonian Mandagery Sandstone, both in central NSW, and *Paleolimulus* sp. from the Upper Permian Jackey Shale in Tasmania (Ewington *et al*. 1989). Interestingly, all these specimens have been found in rocks interpreted as freshwater deposits, either lacustrine or fluvial in origin. Two other species referred to xiphosurans by Chapman (1932) were reviewed and rejected by Pickett (1984). There are even fewer records of indisputable eurypterids from Australia (see the review by Selden 1993), with occurrences limited to *Acutiramus* cf. *bohemicus* (Barrande, 1872) from the Lower Devonian of Victoria (Burrow *et al*. 2002) and *Adelophthalmus waterstoni* (Tetlie, Braddy, Butler & Briggs, 2004) (originally assigned to *Rhenopterus*) from the Upper Devonian of Western Australia, whereas *Pterygotus* (?) *australis* McCoy, 1899 from the upper Silurian of Melbourne, and other fragments from strata of similar age in the Cootamundra district of southern NSW that were referred to *Hughmilleria* by Gill (1951) or to *Pterygotus* by Caster & Kjellesvig-Waering (1953) are based on undiagnostic material. Considerable fragmentary eurypterid material from upper Silurian rocks in the Melbourne region remains undescribed in the collections of Museum

Victoria (David Holloway pers. comm., in Burrow *et al*. 2002). All known Australian eurypterids occur in marine strata.

If *Melbournopterus* was a xiphosuran it would be the earliest representative of the group in Australia. Alternatively, if its eurypterid affinities could be established conclusively, this would have important implications for eurypterid biogeography and evolution. Although pterygotids and adelophthalmids were good dispersers capable of traversing the oceans between continents, the same does not apply to either stylonurids or mycteropids (Tetlie 2007), hence the occurrence of a representative of either group in the Silurian of Australia would lend support to the possibility of a Gondwanan origin for Eurypterida (Lamsdell *et al.* in press). If *Melbournopterus* was a mycteropid it would also be the oldest known member of the group.

Very few morphological characters support its assignment to either group, however, and there is a very strong possibility that the phylogenetic position of this enigmatic fossil lies elsewhere. Surprisingly, despite the uncertainty of its affinities, the specimen itself has never been restudied in the six decades since the original description, making its critical re-examination essential. Furthermore, Caster & Kjellesvig-Waering's (1953) alleged image of the counterpart (their figure 2) actually is the same as their illustration of the part specimen (their figure 1), the photograph margins simply having been trimmed. The counterpart of the specimen is, therefore, figured here for the first time.

Material and terminology

The unique specimen preserved as part and counterpart, now housed in Museum Victoria (in Melbourne) with catalogue number MV P.134779, was collected from the upper Silurian Dargile Formation (*Monograptus nilssoni* Graptolite Zone: Ludlow) at a locality 4.2 km east-southeast of

Heathcote Railway Station, approximately 50 km north of Melbourne city centre. The host rock is a light brown laminated micaceous siltstone, lacking other fossils except for a poorly-preserved graptolite stipe. Plaster casts of the holotype are housed in the Field Museum of Natural History, Chicago, USA (FMNH PE22018) and the Naturhistorisk Museum in the University of Oslo, Norway (PMO A40620, A40621). An unidentified Ordovician craniiate brachiopod from the Fossil Hill Limestone that is illustrated in Fig. 2 for comparison with *Melbournopterus* is housed in the Palaeontological Collection of the Geological Survey of New South Wales at Londonderry in outer Sydney, with catalogue number MMF 45232. Brachiopod morphological terminology follows Williams & Brunton (1997).

Characteristics of the holotype

The specimen is subquadrate in outline and planar in profile. As oriented in Figure 1, the specimen measures 44.5 mm from posterior margin (top) to anterior margin (bottom), and is at least 45 mm wide. The posterior margin is slightly emarginate medially and is estimated to attain about half the maximum width. Posterolateral and lateral margins are incompletely exposed, but appear at least on the left side to be broadly and evenly convex. The anterior margin is about equal to the maximum width, and is very broadly convex; its most characteristic feature is a fringe of evenly-spaced, short (2.5 mm), blunt, cylindrical spines that protrude perpendicularly along the entire anterior margin. Whether these spines are solid or hollow can not definitively be determined, although there is a suggestion that they are tubular in one or two places. Incompleteness of the lateral margins prevents an assessment of how far around the shell the spines extend.

Internal details display strong bilateral symmetry, with a low, irregular median ridge dividing the posterior half, away from the hingeline. A conspicuous, well-defined pair of subrectangular depressions with convex corners (the “eyes” of the original interpretation) diverge anterolaterally from the anterior extremity of the median ridge and are relatively shallowly excavated into the shell floor. Slightly deeper and considerably smaller pit-like excavations separate the large paired depressions from the median ridge. Other possible indistinct scars extend in an arc from each end of the hingeline to the vicinity of the lateral extremities of the large paired subrectangular depressions. Several small conical pits are present immediately in front of (anterior to) the hingeline (one is especially prominent on the right-hand side of Figure 1A, expressed as a raised pimple-like feature on the left side of the counterpart, Figure 1B). The floor of the shell in its anterior half is crossed by several indistinct shallow meandering trail-like depressions, extending from the end of the median ridge almost to the spinose anterior margin. The original shell material is not preserved, but the broken edge of the internal mould suggests that it was quite thin.

Discussion

An objective analysis of the part and counterpart of the specimen, and comparison with representatives of other phyla that are likely to have co-existed in a late Silurian marine setting, has resulted in only one possible match – the dorsal valve of a craniate brachiopod. Our reassessment requires a reorientation of the specimen, relative to that in the original description by Caster and Kjellesvig-Waering (1953), who regarded the narrower margin of the specimen as anterior and the spinose margin as posterior. In our interpretation (Figs 1, 2A), the narrower, slightly emarginated edge of the specimen represents a hingeline and hence is posterior in position, whereas the spinose margin is anterior. The large paired subrectangular depressions may be interpreted as the anterior adductor muscle scars (rather than eyes), the medial indentations either side of the anterior end of the median ridge are possibly scars of the brachial protractors, and the arcuate linear excavations and isolated pit-like depressions in the posterior half of the valve can be attributed to other muscle scars such as the posterior adductors and oblique internals (cf. Bassett 2000, fig. 89). The meandering shallow trail-like features in the anteromedian part of the valve are interpreted as *vascula media*. The peripheral fringe of spines is also compatible with a brachiopod interpretation, though this feature is more generally associated with acrothelids such as *Acrothele* and *Orbithele*, and occasionally occurs in zhanatellids (e.g. *Thysanotos*); peripheral spines are unknown in craniids (M. Mergl, pers. comm.).

The similarity between *Melbournopterus crossotus* and craniate brachiopods is most apparent when comparing the former with the Ordovician craniids *Orthisocrania* (Bassett 2000, figs 103f, j) and *Pseudocrania* (Bassett 2000, fig. 93a). Dorsal valves of both these craniids are planar and exhibit an array of morphological features comparable to *M. crossotus*, though they are considerably smaller (20–22 mm maximum width and length, only half the dimensions of *Melbournopterus*). However, another group of craniate brachiopods, the trimerellids (which became extinct by the end of the Silurian), commonly exceed 50 mm in maximum dimension.

To further support the comparison with craniate brachiopods, we illustrate an undescribed example of Late Ordovician age from the Fossil Hill Limestone at Cliefden Caves in central NSW (Fig. 2B, C). This brachiopod, known only from this specimen (MMF 45232), is nearly identical in outline to *Melbournopterus*, and displays comparable paired posterior adductor and oblique internal muscle scars, and a remarkably similar median septum. Like *Orthisocrania*, it shows traces of radial ornament anteriorly, but as the periphery of the specimen is not preserved we can not tell whether these ribs may have been produced as short spines as in *Melbournopterus*. Width of the specimen (18 mm) is again less than half that of *Melbournopterus*.

This reinterpretation is not without its problems, the main one being that the conspicuous paired features, thought to be anterior adductor scars in *Melbournopterus*, diverge in the opposite direction to those in the known craniate brachiopods. An anterolaterally divergent configuration should still allow the muscles to contract to close the valves, so this does not negate the brachiopod hypothesis. We considered inverting *Melbournopterus* so that the spinose margin was uppermost; although in this orientation the presumed adductor muscle scars are more reminiscent of craniates, these muscles would be inserted within the posterior half of the valve, so imparting less of a mechanical advantage in valve closure. Furthermore, because the spines would then lie behind the hingeline, they may interfere with valve opening. Spines (and non-preserved sensory setae that may have occupied interspaces between the spines) are most likely to have protected the anterior opening of the shell.

Lack of preservation of the shell material also hinders a definitive identification of the specimen as a brachiopod. Craniids have a calcitic or aragonitic shell, and lingulate brachiopods (including lingulides, acrotretides and siphonotretides) have a phosphatic shell. As suggested by the presence of graptolite fragments in the rock containing *Melbournopterus*, we interprete the depositional environment as relatively deep water in which it is possible that aragonite – if this in fact was the original composition of the shell – may have dissolved, leaving only the internal mould preserved.

Given the rarity of available material (restricted to a solitary valve internal), some discrepancies in morphological features – such as the combination of external spines with an internal morphology that is more consistent with a group of brachiopods that are normally lacking in spines, and divergence of the large paired adductor scars that is opposite from normal – and the lack of knowledge regarding contemporaneous late Silurian craniate brachiopod taxa, it is prudent not to assign *Melbournopterus* to a genus or species at present. Our reinterpretation provides an alternative explanation of the affinities of this enigmatic fossil, certainly removing it from the eurypterids or xiphosurans and their kin, and potentially establishing it as a craniate brachiopod, although questions remain as to its exact phylogenetic position.

Acknowledgements

J.C.L thanks Lars Holmer (Uppsala Universitet) and Curtis Congreve (University of Kansas) for discussion on the specimen and Paul Selden (University of Kansas) for support. M.P. thanks Ulrich Jansen (Frankfurt) and Christian Franke (Wallendorf) for useful discussions on brachiopods. The paper benefitted from reviews by John Pickett (Geological Survey of NSW) and Michal Mergl (University of West Bohemia). I.G.P. publishes with permission of the Executive Director, NSW Trade & Investment. We are grateful to David Holloway (Museum Victoria) for facilitating the loan of the holotype. David Barnes (NSW Trade & Investment) photographed the specimens. This is a contribution to IGCP 591: The Early to Middle Paleozoic Revolution.

References

BARRANDE, J., 1872. Système silurien du centre de la Bohême. *Supplément au vol. 1 (Trilobites, Crustacés divers et Poissons)*, 647 pp.

BASSETT, M.G., 2000. Order Craniida. In WILLIAMS, A., *et al*. Brachiopoda, volume 2 (Linguliformea, Craniiformea and Rhynchonelliformea (part)). *Treatise on Invertebrate*

Paleontology, Part H, Brachiopoda (2nd edition). KAESLER, R.L., ed., Geological Society of America, Boulder, Colorado and University of Kansas Press, Lawrence, Kansas. 169–183.

BURROW, C.J., BRADDY, S.J. & DOUGLAS, J.G., 2002. Pterygotid eurypterid chelicera from the Lower Devonian of Victoria. *Alcheringa 25*, 263–268.

CASTER, K.E. & KJELLESVIG-WAERING, E.N., 1953. *Melbournopterus*, a new Silurian eurypterid from Australia. *Journal of Paleontology 27*, 153–156.

CHAPMAN, F., 1932. Two new Australian fossil king-crabs. *Proceedings of the Royal Society of Victoria 44,* 100–102.

EWINGTON, D.L., CLARKE, M.J. & BANKS, M.R., 1989. A Late Permian fossil horseshoe crab (*Paleolimulus*: Xiphosura) from Poatina, Great Western Tiers, Tasmania. *Papers and Proceedings of the Royal Society of Tasmania 123,* 127–131.

GILL, E.D., 1951. Eurypterida – scorpions of the sea. A glimpse into the oceans of the distant past. *Victorian Naturalist 68,* 128–133.

LAMSDELL, J.C., HOŞGÖR, İ. & SELDEN, P.A., in press. A new Ordovician eurypterid (Arthropoda: Chelicerata) from southeast Turkey: evidence for a cryptic Ordovician record of Eurypterida. *Gondwana Research*.

MCCOY, F., 1899. Note on a new Australian *Pterygotus*. *Geological Magazine 6*, 193–194.

PICKETT, J.W., 1984. A new freshwater limuloid from the middle Triassic of New South Wales. *Palaeontology 27,* 609–621.

PICKETT, J.W., 1993. A Late Devonian xiphosuran from near Parkes, New South Wales. *Memoirs of the Association of Australian Palaeontologists 15*, 279–287.

PLOTNICK, R.E., 1999. Habitat of Llandoverian-Lochkovian eurypterids. In *Paleocommunities: A case study from the Silurian and Lower Devonian*. BOUCOT, A.J. & LAWSON, J., eds, Cambridge University Press, 106–131.

RIEK, E.F., 1955. A new xiphosuran from the Triassic sediments at Brookvale, New South Wales. *Records of the Australian Museum 23*, 281–282.

RIEK, E.F. & GILL, E.D., 1971. A new xiphosuran genus from Lower Cretaceous freshwater sediments at Koonwarra, Victoria, Australia. *Palaeontology 14*, 206–210.

SELDEN, P., 1993. Fossil chelicerates of Australia. *The Fossil Collector, Bulletin 41 (September 1993),* 11–20.

TETLIE, O.E., 2004. Eurypterid phylogeny with remarks on the origin of arachnids. PhD thesis, University of Bristol, 320 pp. (unpublished)

TETLIE, O.E., 2007. Distribution and dispersal history of Eurypterida (Chelicerata). *Palaeogeography, Palaeoclimatology, Palaeoecology 252*, 557–574.

TETLIE, O.E., BRADDY, S.J., BUTLER, P.D. & BRIGGS, D.E.G., 2004. A new eurypterid (Chelicerata: Eurypterida) from the Upper Devonian Gogo Formation of Western Australia, with a review of the Rhenopteridae. *Palaeontology 47*, 801–809.

TOLLERTON JR, V.P., 1989. Morphology, taxonomy, and classification of the Order Eurypterida Burmeister, 1843. *Journal of Paleontology 63*, 642–657.

WILLIAMS, A. & BRUNTON, C.H.C., 1997. Morphological and anatomical terms applied to brachiopods. In WILLIAMS, A., *et al*. Brachiopoda, volume 1 (Introduction). *Treatise on Invertebrate Paleontology, Part H, Brachiopoda* (2nd edition). KAESLER, R.L., ed., Geological Society of America, Boulder, Colorado and University of Kansas Press, Lawrence, Kansas. 423–440.

Fig. 1. *Melbournopterus crossotus* Caster & Kjellesvig-Waering, 1953, from the Upper Silurian Dargile Formation, near Heathcote, Victoria, Australia. Holotype and sole specimen. **A**, part MV. P134779B (painted black to enhance details); **B**, counterpart MV. P134779A (natural colour). Scale bars = 10 mm.

Fig. 2. **A**, *Melbournopterus crossotus* Caster & Kjellesvig-Waering, 1953, holotype MV. P134779B, coated with ammonium chloride, and annotated to show features indicative of a

craniate brachiopod affinity. A = posterior margin and hingeline; B = median septum; C = paired posterior adductor and oblique internal muscle scars; D = paired anterior adductor muscle scars; E = brachial protractor muscle scars; F = traces of *vascula media* mantle canals; G = anterior margin fringed with spines. Scale bar = 10 mm.

B, C, undescribed craniate brachiopod MMF 45232, from the Kalimna Limestone Member of the Fossil Hill Limestone (Late Ordovician: early Katian age), Cliefden Caves, N.S.W., Australia, showing interior of dorsal valve (B) and corresponding internal mould (C). Note similarity of morphological features to those exhibited by *Melbournopterus crossotus*. See text for further explanation. Scale bars = 5 mm.

Chapter 3

The eurypterid *Stoermeropterus conicus* from the lower Silurian Pentland Hills, Scotland

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(Formatted for submission to *Palaeontographical Society Monographs*)

ABSTRACT

Stoermeropterus conicus (Eurypterida: Eurypterina), from the Telychian (Upper Llandovery, Silurian) of Pentland Hills near Edinburgh, Scotland, is described from material originally assigned to three different species (*Nanahughmilleria conica*, *Drepanopterus bembycoides* and *Drepanopterus lobatus*). Two other existing eurypterid species, *Hughmilleria lata* from the Wenlock of Norway and *Drepanopterus nodosus* from the Pridoli of North America are recognized as being congeneric with *S. conicus*, united principally by their possession of moveable mesosomal spines on the mesosoma, genital spatulae and a bulbous telson 'boss'. Several characters support the assignment *Stoermeropterus* to Moselopteridae, the most basal eurypterine clade, including its possession of a pediform appendage VI with a modified 'podomere' 7a and the possession of a coxal 'ear', which may represent the remains of a much-reduced exopod. *Stoermeropterus conicus* resolves phylogenetically as the most basal known eurypterine, and can aid in reconstructing the eurypterid ground plan. As such an attempt is made to reconstruct the characteristics that are plesiomorphic for Eurypterida through comparison with basal Eurypterina, Stylonurina, chasmataspidids and synziphosurines. Several characteristics previously thought to be autapomorphies of Stylonurina, such as a three-segmented genital operculum, are now shown to actually be plesiomorphic conditions, while other apparently derived characteristics such as an epistoma and genital spatulae may be characters that are present in all eurypterids but are respectively either paedomorphically retained into adulthood or become hypertrophied in various species. Following the identification of a metastoma and genital appendage in some chasmataspidid species, the sole currently known eurypterid autapomorphy is identified as the fusion of the opercular plates of somites VIII and IX. Evolutionary relationships among the traditional 'merostome' groups primarily in light of segment articulations and the development of the appendage of somite VII and the concept that synziphosurines may represents a paraphyletic stem grade to a group inclusive of xiphosurids, chasmataspidids, eurypterids and arachnids is proposed.

INTRODUCTION

Eurypterids, an extinct order of predominantly predatory Palaeozoic aquatic chelicerates with a fossil record spanning the mid-Ordovician to the end-Permian, have been known from the Silurian strata of the Pentland Hills since the late 1800s. The fauna, first described by Laurie (1892, 1899), is possibly one of the most important eurypterid fossil sites in the world; consisting of a diverse eurypterid community. A total of nine genera are known from the site, including both eurypterids with their posterior prosomal appendages modified into paddle-like organs (Eurypterina) and those with entirely pediform appendages (Stylonurina). This results in a high local morphological diversity

(Text-fig. 1). Overall, the locality accounts for 15% of all known stylonurine eurypterid species, and is currently the most diverse eurypterid locality in the world (Plotnick 1999).

Both eurypterine and stylonurine eurypterids are found in a variety of salinities, indicating a euryhaline mode of life (Braddy 2001), however by the Carboniferous stylonurines were limited to freshwater environments. The nektonic Eurypterina reached their acme in the Silurian before declining drastically through to the end Devonian, however Stylonurina diversity remained more or less constant from the Silurian through to the order's eventual extinction towards the end of the Permian (Lamsdell & Braddy 2010). Recent phylogenetic analyses have confirmed the monophyly of the two suborders within Eurypterida (Tetlie 2007a; Lamsdell *et al.* 2010a,b), and these have shown that the most basal members of the Eurypterina had their sixth appendage as a walking leg bearing a modified 'podomere 7a' lobe-like spine. Further study of these basal members is required in order to more accurately determine the nature of the evolutionary transition from a benthic to nektonic habitat and the relationships between the basal taxa of the Eurypterina and the Stylonurina.

Revised interest in the Pentland fauna over recent years has resulted in the redescription of a number of genera, including the recognition of *Bembicosoma pomphicus* Laurie, 1899 as a synziphosurine (Anderson & Moore 2004) and *Kiaeropterus cyclophthalmus* (Laurie, 1892) as a member of the Stylonurina (Tetlie *et al*. 2007), while simultaneously new investigation of the Drepanopteridae (Poschmann & Tetlie 2004; Lamsdell *et al*. 2009) suggested that the family was polyphyletic, containing both derived stylonurines and basal Eurypterina. This culminated in the realization that several of the Pentland species (*Nanahughmilleria* (?) *conica* (Laurie, 1892), '*Drepanopterus*' *bembycoides* Laurie, 1899 and ‘*Drepanopterus*’ *lobatus* Laurie, 1899) represented a distinct genus of basal eurypterine. Lamsdell *et al*. (2010a) assigned ‘*Drepanopterus*’ *bembycoides*, as the most completely known species, to their new family Moselopteridae, however the lack of an accurate, modern anatomical description of these species has limited attempts to include them in broader treatments of Eurypterina phylogeny.

Herein a new genus, comprising the newly synonymized species ‘*Nanahughmilleria*’ *conica*, ‘*Drepanopterus*’ *bembycoides* and ‘*Drepanopterus*’ *lobatus*, is described for the first time as *Stoermeropterus* gen. nov., including a complete description of all known specimens with illustrations and photographs. Based on these specimens and comparisons with other eurypterid taxa a phylogenetic analysis of the basal Eurypterida is presented and the position of *Stoermeropterus* is commented upon, along with its importance for understanding basal eurypterid phylogeny, character evolution, and palaeoecology. This detailed description aims to provide data for *Stoermeropterus* to be included in future studies of eurypterid evolution, including phylogenetic analyses that would previously have excluded *Stoermeropterus* despite its completeness and importance for resolving plesiomorphic character states.

MATERIAL

The material of *Stoermeropterus* gen. nov. *conicus* described here includes all known specimens, held at the National Museums of Scotland in the Hardie (NMS G.1897.32) and Henderson (NMS G.1885.26) collections.

Institutional abbreviations: **AMNH**, American Museum of Natural History, New York, USA; **AU**, University of Aberdeen, Aberdeen, Scotland, UK; **BGS**, British Geological Survey, Keyworth, Nottingham, UK; **BMAG**, Bristol Museum and Art Galleries, Bristol, UK; **BMNH**, British Museum of Natural History, London, UK; **BMS**, Buffalo Museum of Science, Buffalo, New York, USA; **BRSUG**, University of Bristol, Bristol, UK; **CMN**, Canadian Museum of Nature, Ottawa, Canada; **CORD**, Universidad Nacional de Córdoba, Córdoba, Argentina; **ELRC**, Early Life Research Centre, Nanjing, China; **FMNH**, Field Museum of Natural History, Chicago, Illinois, USA; **GIL**, Geological Institute of Lithuania, Vilnius, Lithuania; **GLAHM**, Hunterian Museum, Glasgow, Scotland, UK; **GSC**, Geological Survey of Canada, Ottawa, Canada; **GSE**, Institute of Geological Sciences, Edinburgh, Scotland, UK; **GSSA**, Geological Survey of South Africa, Silverton, Pretoria, South Africa; **HU**, University of Hull, Hull, UK; **IGMR**, Institute of Geology and Mineral Resources, Hanoi, Vietnam; **KM**, Kelvingrove Museum, Glasgow, UK; **LM**, Lapworth Museum, Birmingham, UK; **LSM**, L'viv State Museum of Natural History, L'viv, Ukraine; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; **MfN**, Museum für Naturkunde, Berlin, Germany; **MM**, Manitoba Museum, Winnipeg, Canada; **MNHM**, Muséum National d'Histoire Naturelle, Paris, France; **MR**, Muzeum Dr. Bohuslava Horáka v Rokycanech, Rokycanech, Czech Republic; **NBMG**, New Brunswick Museum, New Brunswick, Canada; **NMS**, National Museums of Scotland Collection Centre, Edinburgh, Scotland, UK; **NRM**, Naturhistoriska Riksmuseet, Stockholm, Sweden; **NYSM**, New York State Museum, Albany, New York, USA; **OSU**, Orton Geological Museum, Ohio State University, Columbus, Ohio, USA; **OUM**, Oxford University Museum of Natural

History, Oxford, UK; **PIN**, Paleontological Institute, Moscow, Russia; **PMO**, Naturhistorisk Museum (formally the Paleontologisk Museum), Universitetet i Oslo, Oslo, Norway; **PU**, Princeton University Geological Museum, New Jersey, USA; **PWL**, Landessammlung für Naturkunde Rheinland-Pfalz, Mainz, Germany; **ROM**, Royal Ontario Museum, Toronto, Ontario, Canada; **SLK**, Collection of Robert Leunissen, Kreuzau, Germany; **SM**, Sedgewick Museum, Cambridge, UK; **SMF**, Naturmuseum und Forschungsinstitut Senckenberg, Frankfurt am Main, Germany; **SPW**, Collection of Markus Poschmann, Waldesch, Germany; **UA**, University of Alberta, Edmonton, Alberta, Canada; **UCM**, University of Cincinnati Museum, Cincinnati, USA; **UI**, University of Illinois, Urbana, Illinois, USA; **UMMP**, University of Michigan Museum of Paleontology, Ann Arbor, Michigan, USA; **USNM**, United States National Museum, Washington, D.C., USA; **USS**, University of Stellenbosch, Stellenbosch, South Africa; **UW**, University of Wisconsin Madison Geological Museum, Madison, Wisconsin, USA; **YPM**, Peabody Museum, Yale University, New Haven, Connecticut, USA.

ACKNOWLEDGEMENTS

I thank Andrew Ross (NMS) for access to the Scottish specimens, Markus Poschmann for access to and discussion on German moselopteroids, and Erik Tetlie for his work on *Stoermeropterus latus* and for originally bringing this material to my attention. Thanks are also due to Lyall Anderson (Cambridge University) for information on the Pentland Hills site, Dave Marshall (Ichron) for discussions on chasmataspidids, Paul Selden (University of Kansas) for support and discussion on sexual dimorphism in chelicerates, Erin Saupe (University of Kansas) for information regarding arachnid genital operculae and general encouragement, Martin Stein (University of Kansas) for discussions on arthropod development and help with drawing methods, and Marc Williams (Spectro/jetcare) for confirming the absence of plant material in the Eurypterid Bed. Victor Tollerton, Jr. aided in ascertaining the ages of the various North American eurypterid faunas, and Curtis Congreve (University of Kansas) provided direction in regards to Ordovician glaciation events. Avril Simister also assisted with discussion and observations on the day-to-day habit of *Limulus*. Paul Mayer (FMNH) is thanked for providing photographs of *Stoermeropterus nodosus*. Jason Dunlop (MfN) provided many valuable comments that greatly improved the manuscript during the review process. I also thank the Palaeontographical Society for the financial grant into Silurian Scottish eurypterid systematics that allowed this work to be carried out.

GEOLOGICAL SETTING

All known fossil specimens of *Stoermeropterus* gen. nov. *conicus* originate from the Telychian (Upper Llandovery, Silurian) rocks (see Loydell 2005; Molyneux *et* al. 2008) of the Pentland Hills, located south-west of Edinburgh, Scotland. The majority of the Pentland Hills strata consists of Old Red Sandstone deposited in the Devonian and early Carboniferous, however Silurian rocks are exposed in three inliers; Bavelaw, Loganlea-Craigenterrie, and the North Esk Inlier (Clarkson & Taylor 2007). The North Esk Inlier is the largest and most fossiliferous outcrop and is divided into five distinct subgroups; the Reservoir, Deerhope, Cock Rig, Wether Law Linn and Henshaw formations (Tipper

1976; Robertson 1989). The succession, with its changing faunas, can be directly linked with phases of a continuous marine regression (Clarkson 2000), with the oldest beds (the Reservoir Formation) deposited in relatively deep-water conditions. The overlying Deerhope Formation represents a shallower marine environment and in places preserves an abundant fauna, while the Cock Rig Formation above it represents the growth and development of a persistent barrier island system after a period of rapid shallowing (Clarkson *et al*. 2001). The large lagoon enclosed behind the offshore barrier forms the Wether Law Linn Formation, the initial typical-marine faunas giving way to a composition dominated by fluctuating salinity as deposition progresses before they become increasingly scarce. The youngest part of the succession is the Henshaw Formation, a series of red sandstones and conglomerates deposited in a semi-arid desert.

The eurypterids are located in an exposure at Gutterford Burn (GR NT155579; Text-fig. 2a), located at the base of the Deerhope Formation (Anderson *et al*. 2007). Anderson *et al*. undertook a detailed examination of the site and presented a sedimentary log of the strata, reproduced in a simplified form here (Text-fig. 2b). The Gutterford Burn succession consists of 23 metres of exposed strata divided into eight lithologies by Anderson *et al*.; micaceous siltstones, the Gutterford Burn Limestones, green shales, the graptolite flags, sandstone with weathered clasts, green clay, the Eurypterid Bed, and purple siltstones. The micaceous siltstones are the oldest beds in the exposed succession, comprising 3 m of green-brown siltstones deposited in beds 50 – 100 mm thick. Some of the beds at the base of the succession are bioturbated by branching *Chondrites* Sternberg, 1833 burrows while a bed of fine-grained green siltstone 2.5 m into the section contains the coral *Favosites multipora* Lonsdale, 1839, stick bryozoans, lingulid brachiopods and monograptid graptolites. The Gutterford Burn Limestones are a series of 18 calcareous beds that extend for 9.5 m, with individual bed thicknesses increasing upwards through the section. The calcareous beds are rich in shelly fossils including brachiopods, bivalves, corals, bryozoans and rare trilobites along with reported finds of the conodont *Pterospathodus amorphognathoides* Walliser, 1964. The surfaces of the individual beds are often covered with *Dictyocaris ramsayi* Salter, 1860 in association with small branching bryozoans and monograptids such as *Monograptus priodon* (Bronn, 1835). The next 1.9 m of the succession consists of the massively bedded green shales and contains the corals *Favosites multipora* and *Palaeocyclus porpita* (Linnaeus, 1767) preserved in their life position. Following the green shales lies 3.4 m of graptolite flags, consisting of dark green shales with six interbedded massive grey-green micaceous flagstones. These are planar laminated with an average bed thickness of 10 – 15 cm, the lower surfaces of which are covered with densely packed *Dictyocaris ramsayi*. Dendroid graptolites, monograptids, the graptolite *Oktavites excentricus* (Bjerreskov, 1975), the putative hexacoral *Mirmor andreae* Lamont, 1978, small starfish and the large orthocone *Orthoceras politum* M'Coy, 1851 have also been reported from these beds. The final 1.5 m before the Eurypterid Bed consists of the non-fossiliferous sandstone with weathered clasts, consisting of 'flinty' sandstone with weathered decalcified clasts 10 – 20 mm thick, succeeded by a 5 cm thick bed of soft green clay interpreted as a band of altered volcanic ash. The Eurypterid Bed itself is *c.* 55 cm thick, the lower surface of which is not directly conformable with the underlying siltstones indicating infilling of a pre-existing irregular sea floor topography. A thin clay band exists 8 cm up from the Eurypterid Bed's base, while 13 cm from the base is a calcareous-rich horizon containing crinoid ossicles, stick bryozoans, monograptids and brachiopods. The top of the Eurypterid Bed is covered by another green clay band with irregular topology suggesting it draped the underlying beds. Above the Eurypterid Bed the remainder of the exposed succession consists of 1.2 m of sandstones capped by finely laminated blue-purple micaceous siltstones.

The Eurypterid Bed is located near the base of the slope rising up from the banks of the Gutterford Burn, approximately 3 m up from where the succession dips beneath the water level. The strata here have overturned, leading to the chronologically youngest beds being located at the base of the exposure. The bed was recognized as a Konservat-Lagerstätte by Anderson *et al*. (2007), citing the presence of eurypterids, scorpions and synziphosurines. Eurypterids (like other chelicerates) have a non-mineralized cuticle (Gupta *et al*. 2007) that is rarely preserved in the fossil record and highly dependent on environmental conditions, so any locality where eurypterid cuticle is preserved in abundance should be considered a Konservat-Lagerstätte. The Eurypterid Bed of Gutterford Burn is one of a series of predominantly Scottish eurypterid Lagerstätten found in the United Kingdom, including the Lower Wenlock Slot Burn Formation of Seggholm, Ayshire (Peach and Horne 1899; Cocks *et al*. 1971), the Patrick Burn Formation of Logan Water (Late Llandovery/Wenlock) and the Kip Burn Formation (Wenlock) of Lesmahagow (Ritchie 1968a; Cocks *et al*. 1971), the Lochkovian age Dundee Formation of Kelly Den near Arbroath (Braddy 2000), the Viséan East Kirkton Quarry near Bathgate, West Lothian (Jeram 1994; Jeram & Selden 1994), and the Pridoli age Downton Castle Sandstone from Ludlow and Kington, Herefordshire (Tetlie 2006). Of these the Gutterford Burn Eurypterid Bed is one of the most diverse, and the most important for stylonurine research. The arthropod specimens are mostly entire individuals and are associated with articulated crinoids, echinoids and starfish. This, coupled with the layers of volcanic clay, suggests that the bed represents a smothering event caused by the sea bed being quickly covered by a sudden influx of fine-grained, volcanic-ash-influenced sediment (Anderson *et al*. 2007), preserving the sea floor community relatively intact (note however that Donovan *et al*. (2011) recently considered the majority of echinoderms from the North Esk Inlier to be allochthonous). The echinoderms are thought to have perished due to the blocking of the ambulacral system by fine-grained sediment as in the Lower Jurassic Gmünd obrution deposit (Seilacher *et al*. 1985). A similar event is thought to have occurred in the upper Ordovician Elkhorn Formation, Ohio, where hundreds of *Megalograptus* specimens are preserved in a largely inflated condition in association with a marine invertebrate fauna (Caster & Kjellesvig-Waering 1964), and the Wenlock-aged Herefordshire Lagerstätte is interpreted to be an ashfall accumulation in an outer shelf environment (Orr *et al*. 2000a). Anderson *et al*. (2007) suggested that the localized preservation of eurypterids in ‘hollows’ on the bedding surface may be explained by the infilling of the pre-existing topography and that concentrations of faunal elements such as starfish may be explained by their clustering at the bottom of such hollows in the sea floor, a similar preservational environment to that proposed for the fauna preserved in submarine channel slides from Leintwardine in England (Whitaker 1962).

The associated fauna of echinoids, starfish and brachiopods indicates that the Eurypterid Bed was preserved under normal marine salinity. Eurypterids are thought to have been largely euryhaline, capable of tolerating a wide range of salinities (Braddy

2001), however the majority of specimens (stylonurines in particular) are known from lagoonal or freshwater deposits. Waterston (1979) mentioned large amounts of plant material found in the Eurypterid Bed, which could suggest a terrestrial influence and an external source for some of the faunal elements. Excavation of the Eurypterid Bed itself (Anderson *et al*. 2007) yielded no plant material however, and a detailed study of the specimens held at NMS confirmed that no terrestrial plant material is found in association with the Eurypterid Bed fauna. This, coupled with the extraordinary levels of articulation of the chelicerates, indicates that all components of the fauna are preserved in their living habitat, indicating that the paucity of Siluro-Devonian marine eurypterid localities is related to preservation potential of eurypterid cuticle rather than a genuine ecological trend.

There are four main components of the fauna preserved in the Eurypterid Bed (Text-fig. 3). The infaunal component is represented solely by the presumed annelid *Keilorites* Allan, 1927. The general lack of infaunal organisms is probably due to the extraordinary preservation being limited to the seabed surface and the lack of a hard exoskeleton in the burrowing organisms. The fossils of *Keilorites* are thought to represent the membrane lined burrows of polychaete worms (Allan 1927) and this structured organic component to the burrow wall may be the reason for their preservation.

The benthic community is the most abundant and diverse component of the fauna, consisting of the majority of the chelicerates and all of the echinoderms. There is also an abundant sessile constituent; by far the most common organism preserved in the Eurypterid Bed is *Dictyocaris ramsayi*, now considered to be a benthic marine alga (Botting 2007), which formed large sheets on the sea floor. The octocoral *Atractosella* *andreae* (Lamont, 1978) and stick bryozoan *Stictopora* Hall, 1847 are also found within the association, along with the moderately abundant crinoids *Macrostylocrinus silurocirrifer* Brower, 1975, *Dimerocrinites pentlandicus* Brower, 1975, *Myelodactylus parvispinifer* (Brower, 1975), and *Dendrocrinus extensidiscus* Brower, 1975. The remainder of the sessile aspect is composed of a moderately abundant brachiopod fauna consisting of *Erinostrophia undata* (M'Coy, 1846)*, Strophochonetes cornuta* (Hall, 1843), *Skenidioides lewisii* (Davidson, 1848), *Isorthis* (*Ovalella*) aff. *mackenziei* Walmsley *in* Walmsley & Boucot, 1975, *Visbyella visbyensis* (Lindström, 1861), *Dicoelosia* aff. *alticavata* Whittard & Barker, 1950, *Sphaerirhynchia sphaeroidalis* (M'Coy, 1852), *Oglupes* aff. *alba* (Lamont, 1978), and *Pseudolingula* Mickwitz, 1909. The motile benthos is dominated by eurypterids and stelleroids. While the stelleroid population is diverse, consisting of *Schuchertia wenlocki* Spencer, 1922, *Taeniactis wenlocki* Spencer, 1922, *Lepyriactis nudus* Spencer, 1927, *Urasterella gutterfordensis* Spencer, 1918, *Protactis wenlockensis* (Spencer, 1922), *Crepidosoma wenlocki* Spencer, 1930 and *Furcaster leptosoma* (Salter, 1857), they are not especially abundant. The echinoid *Aptilechinus caledonensis* Kier, 1973 is also a rare component of the fauna. The benthic chelicerates comprise rare scorpions, *Dolichophonus loudonensis* (Laurie, 1899), and uncommon synziphosurines, *Bembicosoma pomphicus*, but are composed mostly of the stylonurine eurypterids *Parastylonurus ornatus* (Laurie, 1892), *Parastylonurus hendersoni* Waterston, 1979, *Hardieopterus macrophthalmus* (Laurie, 1892), *Drepanopterus pentlandicus* Laurie, 1892 and *Laurieipterus elegans* (Laurie, 1899). There is also a single eurypterine eurypterid restricted to the benthic environment, *Stoermeropterus conicus*, which is the single most common arthropod present in the fauna. Finally a single species of gastropod, *Euomphalopterus* cf. *apedalensis* Pitcher, 1939, is also present in the community.

The demersal component of the fauna is restricted to two species of eurypterids; ‘*Eurypterus*’ *minor* Laurie, 1899 and ‘*Carcinosoma*’ *scoticum* (Laurie, 1899). ‘*Eurypterus*’ *minor* is comparatively rare and would have been limited to swimming close to or walking on the substrate, while ‘*Carcinosoma*’ *scoticum* is known from a handful of specimens that likely represent only two or three large individuals. Unlike ‘*Eurypterus*’ *minor*, ‘*Carcinosoma*’ *scoticum* probably had the capability to be a strong swimmer, moving from site to site via the pelagic environment before returning to the demersal system to hunt. It could also have lain on, or partially in, the substrate waiting for prey to come within reach. Fully pelagic organisms are also preserved in the Eurypterid Bed, albeit as a very small fraction of the fauna restricted to rare specimens of the eurypterid *Slimonia dubia* Laurie, 1899, the more common cephalopod *Geisonoceras maclareni* (Murchison, 1859), and very rare monograptid graptolites *Retiolites angustidens* Elles & Wood, 1908, *Monograptus priodon*, *Monoclimacis geinitzi* (Bouček, 1932) and *Monoclimacis vomerina* (Nicholson, 1872).

The nature of preservation in the Eurypterid Bed provides a rare view into a single moment within a relatively complete fossil community, with a number of different trophic levels preserved in direct association with each other. This can provide additional information on the environment and on the potential relationships and life habits of the faunal constituents. The presence of a benthic primary producer such as *Dictyocaris* in large quantities indicates that the sea floor must have been within the photic zone, and also provides an abundant source of food. Modern echinoids generally graze on algae but will also feed on sponges, bryozoans and other seafloor detritus, and so it is likely that *Aptilechinus* and the gastropod *Euomphalopterus* fed predominantly on the vast sheets of *Dictyocaris*. The brachiopods, octocorals, crinoids and bryozoans meanwhile would have taken their food out of suspension, capturing organic particles and microfauna that passed within reach as they fell out of the pelagic environment. The stelleroids could have fed on the brachiopods, bryozoans and corals in the same manner as modern starfish do. The eurypterids *Parastylonurus* and *Hardieopterus* along with the synziphosurine *Bembicosoma* were probably detritivores, scavenging for food on the sediment surface, however the forward-placed lateral eyes with a forward and lateral field of vision and small chelicerae and anterior spinous appendages of *Parastylonurus* led Waterston (1979) to suggest that it may have browsed the abundant algal matter. *Hardieopterus* meanwhile could have lived partially buried in the substrate as indicated by the somewhat flattened prosomal appendages that appear well adapted for shovelling, the pedunculate epimera that could have acted in a manner similar to the lunules and notches on the tests of scutellinid and rotulinid echinoids, the large centrally-placed lateral eyes that would have afforded an all-round field of vision and the dorsal pustular ornamentation which would have provided camouflage and sensory input (Waterston 1979). This sort of niche separation among organisms living in the same environment would be logical so as to avoid direct competition with each other, particularly when given the large number of individuals preserved in the Eurypterid Bed. Another variation on the scavenging mode of life is exhibited by *Drepanopterus* and *Laurieipterus*, sweep-feeders (Lamsdell *et al*. 2009; 2010a) that may also have taken invertebrate prey such as *Keilorites* out of the substrate. *Stoermeropterus* would undoubtedly also have scavenged for food, however may have also hunted for live prey. The scorpion *Dolichophonus* was a medium-sized predator that could have hunted *Bembicosoma* and '*Eurypterus*' *minor* along with smaller specimens of *Stoermeropterus*. '*Eurypterus*' *minor* is another predator that could have scavenged as well as taken small invertebrates from the substrate. *Slimonia* and *Geisonoceras*, larger predators from the pelagic system, would have been able to tackle larger prey such as *Hardieopterus* and adult *Stoermeropterus*, however only the giant carcinosomatid '*Carcinosoma*' *scoticum* was capable of dispatching the larger eurypterids such as *Parastylonurus* and *Drepanopterus*. An apex predator within the community, '*Carcinosoma*' *scoticum* would have made short work of any of the other chelicerates.

HISTORY OF RESEARCH

The Silurian eurypterid fauna of the Pentland Hills was first described by Malcolm Laurie (1892) as a result of the collecting of some 54 specimens by John Henderson, who discovered the Eurypterid Bed in 1880. Five new species – including '*Eurypterus'* *conicus* – were described, along with a new genus, *Drepanopterus* Laurie, 1892. During this time most eurypterids were assigned to one of two genera; *Stylonurus* Page, 1856 (if the sixth prosomal appendage was modified for walking) or *Eurypterus* De Kay, 1825 (if the sixth appendage was modified into a paddle) – exceptions were *Pterygotus* Agassiz, 1839 and *Slimonia* Page, 1856, both swimming eurypterids but of large size and with oval lateral eyes positioned on the carapace margin. Thus the erection of *Drepanopterus* was the first step in recognizing the true generic diversity of eurypterids, assigning greater taxonomic importance to appendage morphology beyond the obvious function of appendage VI. The acquisition of David Hardie's collection (237 specimens) and excavations conducted by Laurie himself resulted in the description of a further eight new species, including a scorpion, and two new genera (Laurie 1899). The site was recognized as being of extreme importance, with only the Bertie Waterlime of New York State, USA, yielding a greater diversity of species.

No further extensive collecting was carried out until the late 1940s, when Lamont began to collect and describe many specimens from the Pentland region. He was the first to recognize the pre-Wenlock age of the strata (Lamont 1952), and described in detail the structure of the telson in '*Stylonurus' ornatus* and the cuticular sculpture of '*Hughmilleria' conica* (Lamont 1955). All works since then have consisted of restudies of the original material. The prosoma of '*Ctenopterus*' *elegans* (transferred to the genus by Clarke and Ruedemann (1912), later becoming type species of the new genus *Laurieipterus* Kjellesvig-Waering, 1966) was described in detail by Waterston (1962), with particular focus on the well-preserved ventral structures characteristic of the Pentland Hills material, while ventral structures and the prosomal appendages of '*Drepanopterus*' *bembycoides* were figured by Størmer (1974). Waterston (1979) undertook a detailed review of Scottish Silurian 'stylonuroids', including a detailed redescription of *Parastylonurus ornatus*, making it one of the most completely known stylonurines. The new species *Parastylonurus hendersoni* was also erected, along with the genus *Hardieopterus* Waterston, 1979 (type species *H. macrophthalmus*), and in-depth analysis of their relationships and functional morphology attempted.

Work on the Pentland Hills material largely ground to a halt until the turn of the century, when renewed interest in the site resulted in the further redescription of several of Laurie's original taxa; *Bembicosoma pomphicus* was shown to be a xiphosuran (Anderson & Moore 2004) and further specimens of '*Eurypterus*' *minor* were identified (Tetlie 2006), which has since been shown to probably represent a genus separate from *Eurypterus sensu stricto* (Tetlie & Cuggy 2007) while *Kiaeropterus cyclophthalmus*, originally considered to be another species of *Eurypterus* from the site, was shown to be a stylonurine (Tetlie *et al*. 2007). Finally Anderson *et al*. (2007) described the Eurypterid Bed in its depositional context and revised the stratigraphy of the Pentland Hills and an updated list of the eurypterid fauna was compiled by Anderson (2007).

'*Eurypterus*' *conicus* was among the first eurypterids described by Laurie (1892), based on two figured specimens. Both showed a long, conical body in ventral view that gave the species its name but did not preserve much of the prosomal appendages beyond the proximal segments, the posterior-most of which was interpreted as a broad paddle. One also showed details of the genital appendage and metastoma, which was oval with an anterior notch. Several years later Laurie (1899) figured a further specimen preserving the postabdomen and telson, along with two new species of his genus *Drepanopterus*. The first, '*D.*' *lobatus*, was based on largely fragmentary material preserving lobate epimera on the pretelson, while '*D.*' *bembycoides* was represented by a series of relatively complete, broad specimens. Both species preserved good examples of the prosomal appendages with '*D.*' *bembycoides* also preserving the genital appendage and metastoma. At the time Laurie noted that '*D.*' *bembycoides* and '*E*'. *conicus* looked similar, but differentiated them based on the proportions of the body.

Laurie had more specimens to draw on than the handful he described, and these formed the basis of further work. ‘*Eurypterus*’ *conicus* was transferred to the genus *Hughmilleria* Sarle, 1903 based on lateral eye shape by Kjellesvig-Waering (1950). Lamont (1955) then described in detail the cuticular sculpture and ventral structures of the prosoma for the first time, also altering the species name to ‘*conica*’, before Kjellesvig-Waering (1961) transferred the species again to his then subgenus *Nanahughmilleria* Kjellesvig-Waering, 1961, elevated to full generic status by Kjellesvig-Waering & Leutze (1966). The prosomal appendages and genital appendage of ‘*Drepanopterus*’ *bembycoides* were studied in detail by Størmer (1974), who was the first to note the presence of a podomere 7a on appendage VI. Tetlie (2007a) suggested that these three species belonged within the basal Eurypterina, an opinion shared by Lamsdell *et al*. (2009) who further suggested they may all by synonyms before assigning ‘*Drepanopterus*’ *bembycoides* to their new family Moselopteridae (Lamsdell *et al*. 2010a) at the base of the Eurypterina.

TERMINOLOGY

Eurypterid terminology largely follows Selden (1981) for prosomal structures and cuticular sculpture, Tollerton (1989) for morphology of the carapace, metastoma, lateral eyes, prosomal appendages, genital appendage, opisthosomal differentiation, telson, and patterns of ornamentation, and Waterston (1979) for segmentation of the genital operculum. Where discussed, chasmataspidid terminology follows that for eurypterids but as applied by Dunlop *et al.* (2001), Dunlop (2002) and Tetlie & Braddy (2004).

Prosomal appendages are labeled with Roman numerals, and individual podomeres are labeled with Arabic numerals, proximally to distally. Podomere 1 is termed the coxa. The systematics of the basal Eurypterina families follows Tetlie & Cuggy (2007) while Lamsdell *et al.* (2010a) is followed for Stylonurina. The relationships of the remaining Eurypterina families are as set out by Tetlie (2007a).

While Tollerton's (1989) morphological standards greatly aid in the standardization of eurypterid descriptions it has become apparent that, in the decades since their initial publication, there exist several morphological variants not covered by his criteria while some of his morphologies represent either preservational or combinational variants, or are named based on what is now outdated taxonomy. As such, the morphological standards applied to eurypterids ideally need updating, utilizing current understanding of eurypterid systematics, however this is far beyond the scope of the current work. Despite this, several revisions to Tollerton's system have to be adopted herein.

The terminology for the different morphologies of ventral plates and sutures follows the revised types of Tetlie *et al*. (2008), note however that where Tetlie *et al*. figure the different ventral plates (their figure 12) they have confused the *Hallipterus*- and *Brachyopterella*-types: the transverse suture of *Brachyopterella* curves in at the midline, whereas in *Hallipterus* it continues without deviation. Also, the *Eurypterus*-type of ventral plate occurs in stylonurines with an additional transverse suture.

Tollerton's *Drepanopterus*-type prosomal appendage was shown to be absent on *Drepanopterus sensu stricto* by Lamsdell *et al*. (2009), but is a diagnostic feature of moselopteroids and so is herein referred to as being of *Moselopterus*-type. The *Brachyopterella*-type prosomal appendage is as described by Tollerton, however its cuticular ornamentation is variable and a distinction is here made between ornamented and unornamented forms. A new type of prosomal appendage is also recognized, one where there are no moveable spines but each podomere has a pair of small, fixed spine-like projections on the ventral side of its distal margin. These appendages are predominantly found on rhenopterids and are referred to herein as *Rhenopterus*-type. Furthermore an additional carapace shape is described herein, its morphology intermediate between that of the existing semicircular and horseshoe-shaped carapaces. Characterized by a lateral angle ranging from 60˚ to 85˚ and a length: width ratio of between 0.50 and 0.70, this new type is specified as wide horseshoe-shaped.

The eurypterid opisthosoma has traditionally been divided into the mesosoma (segments 1-6) and metasoma (segments 7-12) or the preabdomen (segments 1-7) and postabdomen (8-12). The latter, based on the contraction of the opisthosoma, has become adopted as the standard terminology in most recent literature. However there are problems with this system, as identifying the point of contraction can be somewhat arbitrary, with the sixth segment shown to contract into the postabdomen in *Megalograptus* (Caster & Kjellesvig-Waering 1964), *Onychopterella* (Braddy *et al*. 1995) and *Rhenopterus* (Poschmann & Franke 2006) while other eurypterids can show no differentiation at all. Dividing the opisthosoma into mesosoma and metasoma is a much more natural system: the anterior six segments consist of a tergite/unsclerotized sternite pairing and bear operculae (the non-genital operculae being termed Blattfüsse), while the posterior six are predominantly single ankylosed rings (the first of which consists of a tergite and sclerotized sternite joined via soft integument as in scorpions) lacking externally expressed trunk appendages. This is true of all eurypterids, and is considered herein a preferable division as there is a clear-cut differentiation in form and function between the two.

Explanations for the abbreviations used in the interpretive drawings are as follows: **1–12**: individual segments of the opisthosoma (somites VIII–XIX); **II–VI**: prosomal appendages II-VI; **VI-1–VI-9**: the individual podomeres of prosomal appendage VI; **AF**: articulation facet; **AOP**: anterior opercular plate (somite VII); **C**: carapace; **CE**: coxal ‘ear’; **CH**: chelicera (appendage I); **CL**: cardiac lobe; **DP**: deltoid plate; **EC**: epicoxa; **EN**: endostoma; **EP**: epimeron; **ES**: epistomal sutures; **GA**: genital appendage; **LA**: labrum; **LE**: lateral eye; **ME**: metastoma; **MOP**: median opercular plate (somite VIII); **MR**: marginal rim; **MS**: moveable spine; **POP**; posterior opercular plate (somite IX); **O**: oral opening; **T**: telson; **TB**: telson boss; **TL**: ‘terrace lines’; **VK**: ventral telsonic keel; **VP**: ventral plate.

SYSTEMATIC PALAEONTOLOGY

Order EURYPTERIDA Burmeister, 1843

Diagnosis. Aquatic chelicerates with a genital operculum consisting of two fused opercular plates from somites VIII and IX.

Suborder EURYPTERINA Burmeister, 1843

Diagnosis. Eurypterida with the anterior of coxa VI developed into an 'ear'; a flattened, modified spine, on the postero-distal corner of podomere VI-7; without transverse sutures on the prosomal ventral plates (emended from Lamsdell *et al.* 2010a).

Superfamily ONYCHOPTERELLOIDEA superfam. nov.

Diagnosis. Eurypterina with appendage VI forming a narrow paddle with spinous terminal podomere; metastoma narrow ovate.

Remarks. While the basal Eurypterina (comprising the superfamilies Moselopteroidea and Onychopterelloidea) were considered a plesion by Tetlie (2007a) the fact that they form two distinct clades in the phylogenetic analysis is deemed justification enough to segregate them here into two superfamilies.

Family ONYCHOPTERELLIDAE fam. nov.

Type genus. Onychopterella Størmer, 1951.

Included genera. Onychopterella Størmer, 1951, *Tylopterella* Størmer, 1951.

Diagnosis. Onychopterelloidea with legs II-IV spiniferous, *Hughmilleria*-type; legs V-VI non-spiniferous, V of *Eurypterus*-type and VI a paddle of *Erieopterus*-type, occasionally with spurs on podomere VI-8; preabdomen and postabdomen consisting of six segments each; telson lanceolate.

Occurrence. Upper Ordovician to late Silurian.

Remarks. Tylopterella is an enigmatic genus, and has been considered to be allied to *Drepanopterus* based on the paired tubercles on tergites 2-5. Paired tubercles can be found on a number of eurypterid genera, however, and the shape of the carapace and lateral eyes and the preabdominal/postabdominal divide at the sixth and seventh segments shows the genus to be an onychopterellid.

Superfamily MOSELOPTEROIDEA Lamsdell, Braddy & Tetlie, 2010

Diagnosis. Eurypterina with prosomal appendage VI modified into a walking leg; metastoma ovate, notched anteriorly; type A genital appendage with spatulae (emended from Lamsdell *et al*. 2010a).

Remarks. The reported podomere 7a on appendage V of *Moselopterus* is not convincing – study of the type material showed several examples of appendage V clearly without a 7a, and the previously supposed appendage V could well be a VI.

Family MOSELOPTERIDAE Lamsdell, Braddy & Tetlie, 2010

Type genus. Moselopterus Størmer, 1974.

Included genera. Moselopterus Størmer, 1974, *Stoermeropterus* gen. nov, *Vinetopterus* Poschmann & Tetlie, 2004.

Diagnosis. Moselopteroidea with legs II-IV spiniferous, *Rhenopterus*-type; legs V-VI non-spiniferous, V of unornamented *Brachyopterella*-type and VI of *Moselopterus*-type (emended after Lamsdell *et al.* 2010a).

Occurrence. Early Silurian to Lower Devonian.

Remarks. Moselopterus purportedly has a podomere 7a on appendage V, although the evidence for this is not convincing.

Genus STOERMEROPTERUS gen. nov.

Name. In honour of Professor Leif Størmer, who published many detailed works on eurypterids from the 1930s to the 1970s and first described the eurypterid fauna including *Stoermeropterus latus* from Rudstangen, Ringerike, Norway in 1934.

Type species. *Eurypterus conicus* Laurie, 1892.

Other species. *Stoermeropterus latus* (Størmer, 1934a), *Stoermeropterus nodosus* (Kjellesvig-Waering & Leutze, 1966).

Diagnosis. Moselopteridae with ventral prosomal plates of *Hallipterus*-type lacking transverse suture; carapace wide horseshoe-shaped; opisthosoma with posterior second order differention; mesosoma with moveable lateral spines; base of telson with bulbous ventral boss.

Remarks. FMNH PE6212, figured by Kjellesvig-Waering & Leutze (1966) may be a further specimen of *S. nodosus*, based on the ornamentation and similarities with a genital appendage (PMO H1808) assigned to *S. latus* by Tetlie (2000). Also, some specimens previously assigned to *Nanahughmilleria clarkei* Kjellesvig-Waering, 1964a (e.g. YPM 204297), from the Shawangunk Formation of Otisville, New York State, should probably be assigned to the new genus *Stoermeropterus*.

The genus name was first proposed by Tetlie (2000) to accommodate '*Hughmilleria*' *lata* (of which is known the carapace, postabdomen and telson, prosomal appendage VI and the base of the type A genital appendage) in an unpublished MSc thesis. '*Nanahughmilleria*' *conica* and *'H'. lata* are co-generic, and as *'N'. conica* is the more completely known it is here designated the type species. The diagnosis remains largely unchanged, if somewhat expanded from Tetlie's original, and while the genus is published here for the first time the name *Stoermeropterus* is retained for consistency.

Stoermeropterus conicus (Laurie, 1892) Plates 1–16; Text-figs 4–5, 7–10, 12–14, 17–18

v* 1892 *Eurypterus conicus* n. sp.; Laurie, p.157, pl. 2, figs 12-13, pl. 3 fig. 14.

v. 1899 *Drepanopterus lobatus* n. sp.; Laurie, p. 582, pl. 2, fig. 16, pl. 3, figs 17-18.

v. 1899 *Drepanopterus bembycoides* n. sp.; Laurie, p. 583, pl. 3, figs. 20-21.

v. 1899 *Eurypterus conicus* Laurie; Laurie, pl. 5, fig. 29.

1924 *Eurypterus conicus* Laurie; Diener, p. 16 [Listed].

1924 *Drepanopterus bembicoides* Laurie; Diener, p. 22 [Listed].

1924 *Drepanopterus lobatus* Laurie; Diener, p. 22 [Listed].

1950 *Hughmilleria conicus* (Laurie); Kjellesvig-Waering, p. 228 [Listed].

1955 *Drepanopterus bembicoides* Laurie; Lamont, p. 201 [Listed].

1955 *Drepanopterus lobatus* Laurie; Lamont, p. 201 [Listed].

v. 1955 *Hughmilleria conica* (Laurie); Lamont, p. 202, pl. 2 figs 1-2.

1958a *Hughmilleria conica* (Laurie); Kjellesvig-Waering, p. 1140 [Listed].

1961 *Hughmilleria (Nanahughmilleria) conica* (Laurie); Kjellesvig-Waering, p. 796.

1966 *Drepanopterus bembicoides* Laurie; Kjellesvig-Waering, p.186.

1966 *Drepanopterus lobatus* Laurie; Kjellesvig-Waering, p. 186.

v. 1974 *Drepanopterus bembycoides* Laurie; Størmer, p. 379, text-figs. 14-16.

1999 *Drepanopterus bembycoides*; Plotnick, p. 120.

1999 *Nanahughmilleria conica*; Plotnick, p. 120.

v. 2007 *Nanahughmilleria conica* (Laurie); Anderson, p. 136, text-fig. 12.1A.

v. 2007 *Drepanopterus lobatus* Laurie; Anderson, p. 147, pl. 26, fig 1.

v. 2007 *Drepanopterus bembicoides* Laurie; Anderson, p. 147, pl. 26, fig 2.

2007a *Drepanopterus* (?) *bembycoides*; Tetlie, table 2.

2007a *Drepanopterus* (?) *lobatus*; Tetlie, table 2.

2007a *Nanahughmilleria* (?) *conica*; Tetlie, table 2.

2009 *Drepanopterus bembycoides*; Lamsdell, Braddy and Tetlie, table 1 [Suggested synonym of *Nanahughmilleria* (?) *conica*].

2009 *Drepanopterus lobatus*; Lamsdell, Braddy and Tetlie, table 1 [Suggested sexual dimorph of *Drepanopterus bembycoides*].

2010 *'Drepanopterus' bembycoides* Laurie; Lamsdell, Braddy and Tetlie, p. 51.

Diagnosis. *Stoermeropterus* lacking extensive dorsal scale ornamentation; lunate lateral eyes positioned centrilaterally; ventral prosomal plates with prominent striate sensory grooves and pits; opisthosoma with anterior second order differentiation; posterior margin of opisthosomal segments 10, 11 and 12 serrate.

Type material. Holotype, NMS G.1885.26.72.14 part and counterpart. Paratype, NMS G.1885.26.72.13.

Referred material. NMS G.1885.26.72.1; G.1885.26.72.17; G.1885.26.72.19; G.1897.32.12.9; G.1897.32.85; G.1897.32.88 (holotype of *Drepanopterus lobatus*); G.1897.32.89; G.1897.32.121; G.1897.32.123–126; G.1897.32.130–131; G.1897.32.132 (holotype of *Drepanopterus bembycoides*); G.1897.32.133 (paratype of *Drepanopterus bembycoides*); G.1897.32.134; G.1897.32.136–140; G.1897.32.145; G.1897.32.164 (paratype of *Drepanopterus lobatus*); G.1897.32.165; G.1897.32.167; G.1897.32.170; G.1897.32.172–174; G.1897.32.176; G.1897.32.180; G.1897.32.182; G.1897.32.184–186; G.1897.32.191–192; G.1897.32.197–198; G.1897.32.207–208; G.1897.32.211.

It should be noted that specimens in the NMS collections often have a letter as opposed to a final number; Anderson (2007) changed all these letters to a numerical value according to their position in the alphabet (i.e. a = 1, b = 2, c = 3, etc.); this convention is followed herein.

Distribution. Known only from the Llandovery age Gutterford Burn Eurypterid Bed, Deerhope Formation, Pentland Hills, Scotland.

Remarks. Originally considered three separate species, two of *Drepanopterus* and one of *Eurypterus* (later *Nanahughmilleria*), these are herein synonymized with *Nanahughmilleria conica* having priority. *Drepanopterus lobatus* (NMS G.1897.32.88; G.1897.32.164; G.1897.32.165; G.1897.32.167; G.1897.32.173; G.1897.32.197) is shown to be defined on sexually dimorphic traits whilst *Drepanopterus bembycoides* (NMS G.1897.32.132; G.1897.32.133; G.1897.32.136) represents large, undeformed specimens.

ANATOMICAL DESCRIPTION

PROSOMA

The prosomal region of *Stoermeropterus* is well known from a number of specimens which between them preserve the entirety of its external anatomy. The most commonly preserved structures besides the carapace are the large lateral eyes and the coxae of the appendages, often on the same specimen with either the eyes or coxae projecting through to the exposed surface due to flattening. Prosomal appendages II and III are rarely preserved, likely due to their comparatively delicate nature, while appendages IV-VI more frequently remain articulated to the carapace. The holotype (NMS G.1885.26.72.14:

Text-fig. 4a, Pl. 2, figs. 1&3) retains appendages II, IV and VI, the latter imperfectly preserved although obviously a pediform walking leg. The articulated nature of the appendages suggests that these specimens represent mortalities rather than exuviae, as Tetlie *et al*. (2008) have demonstrated that the prosoma rapidly disarticulated after ecdysis.

Carapace and visual structures. The carapace is known from a total of 32 specimens and accounts for about 17% of the animal's total length, ranging in length from 6.5 mm to a maximum of 38 mm and from 10 mm to 41 mm in width (Table 1), with an overall shape similar to that of *Onychopterella augusti* Braddy, Aldridge & Theron, 1995. Their length: width ratios range from 0.52 to 1.11, which extends beyond the remit of any one of the fourteen carapace shapes set out by Tollerton (1989), however many of the specimens have undergone post-mortem distortion and are laterally compressed. Several have had their carapace compacted such that is has an almost parabolic shaped with a lateral angle of between 90–100° (NMS G.1885.26.72.13: Text-fig. 5b, Pl. 1, figs. 3&4; G.1897.32.85: Pl. 3, fig. 3; G.1897.32.174: Pl. 12, figs. 1&3), however these just represent the most extreme examples of a series of increasingly compacted specimens resulting in higher length: width ratios (Text-fig. 6). As recognized by Laurie (1892) the lower ratios in the spectrum represent *Stoermeropterus* that have retained their original shape with a length: width ratio of between 0.50 and 0.70 and a lateral angle of 60° to 85° (NMS G.1885.26.72.14; G.1897.32.132: Text-fig. 7, Pl. 7, figs. 2–4; G.1897.32.133: Text-fig. 8, Pl. 8, figs. 1&3; G.1897.32.136: Text-fig. 9, Pl. 8, figs. 2&4; G.1897.32.139: Text-fig. 10a, Pl. 10) – this lateral angle is based on the angle of widening after the waist of the carapace, as the posterior flare gives angles ranging from 100°–120°. As these dimensions fail to resolve within any of Tollerton's (1989) existing carapace shapes they form the basis for the new wide horseshoe-shape.

An alternative potential cause for the differences in carapace shape is ontogeny, although this is considered unlikely. The carapace of eurypterids is known to change shape throughout their ontogeny, with juveniles having a more rounded anterior margin (Andrews *et al*. 1974), however the length: width ratio of the carapace remains largely unchanged throughout growth (Cuggy 1994). Furthermore it is considered unlikely that the different *Stoermeropterus* carapace proportions represent different ontogenetic stages as comparing the carapace lengths to their length: width ratios reveals no correlation between length: width ratio and specimen size (Text-fig. 11). While there is some indication that certain individuals where comparatively narrower than others in life (see *Sexual dimorphism in Stoermeropterus conicus*), NMS G.1885.26.72.17 (Text-fig. 12; Pl. 2, fig. 2) confirms the influence of post-mortem compression on the specimens, partial lateral deformation having warped the carapace into an asymmetrical shape.

The carapace has a rounded anterior margin (NMS G.1885.26.72.14; G.1897.32.134: Pl. 7, fig. 5; G.1897.32.139) and straight sides that constrict slightly along the mid third of their length to form a 'waist' in some specimens (NMS G.1885.26.72.17; G.1897.32.12.9: Pl. 6, fig. 2; G.1897.32.131: Pl. 7, fig. 1). A constriction or 'waist' in the carapace is also seen in a number of other Eurypterina (*Waeringopterus cumberlandicus* (Swartz, 1923): FMNH PE6131; *Slimonia acuminata* Salter, 1856: GLAHM 131299; *Grossopterus overathi* (Gross, 1933): MfN MB.A. 2a) and some Stylonurina (*Brachyopterus stubblefieldi* Størmer, 1951: BGS D 3124), although these all vary from the form of *Stoermeropterus conicus*. A constriction almost identical to that of

Stoermeropterus is seen in the 'carapace' of the problematic *Melbournopterus crossotus* Caster & Kjellesvig-Waering, 1953, however the specimen is probably not a eurypterid (Plotnick 1999), and may not even be an arthropod. The marginal rim of *Stoermeropterus conicus* is narrow, usually 1 mm in width, maintaining this width to the carapace posterior (NMS G.1885.26.72.14; G.1885.26.72.17; G.1897.32.85). A narrow marginal rim is often associated with the marginal rim being present only anterior to the lateral eyes, as in *Herefordopterus banksii* (Salter, 1856) (BGS GSM Zf2866), however continuous narrow marginal rims are seen in a number of adelophthalmoids (e.g. *Nanahughmilleria norvegica* (Kiær, 1911): PMO H1632; *Parahughmilleria hefteri* Størmer, 1973: SMF 26054; *Pittsfordipterus phelpsae* (Ruedemann, 1921): NYSM 10102). Among Stylonurina narrow marginal rims are only known from the Rhenopteroidea, and often appear to be folded underneath the carapace such that there is seemingly no marginal rim when viewed dorsally (e.g. *Brachyopterus stubblefieldi*: BGS D 3124; *Rhenopterus diensti* Størmer, 1936a: MfN 48/48a). The marginal rim clearly appears folded under the carapace in a number of *Stoermeropterus conicus* specimens (NMS G.1897.32.85; G.1897.32.134) and therefore appears to be more homologous to the rhenopteroid narrow marginal rim than to the adelophthalmoid form.

The lateral eyes are often well preserved (NMS G.1885.26.72.13; G.1885.26.72.14; G.1897.32.123: Pl. 5, fig. 1; G.1897.32.12.9; G.1897.32.131; G.1897.32.133; G.1897.32.134; G.1897.32.137.2: Pl. 8, fig. 5; G.1897.32.140: Pl. 9, figs. 2&4; G.1897.32.172: Pl. 13, fig. 4; G.1897.32.174; G.1897.32.191: Pl. 14, fig. 4; G.1897.32.208: Pl. 15, fig. 2), sometimes visible in ventral views due to flattening of the specimens, and bear comparison with *Pittsfordipterus phelpsae*. The eyes are lunate, ranging from 4 to 9 mm in length and 0.5 to 2.3 mm in width, and placed centrilaterally on the carapace. The visual surface itself accounts for approximately half of the eye's width, the rest consisting of a narrow palpebral lobe; a similar lateral eye but with a more expanded palpebral lobe is seen in *Moselopterus ancylotelson* Størmer, 1974 (SPW 999-D), while this form of a narrow visual surface on an expanded palpebral lobe occurs in all Stylonurina (e.g. *Alkenopterus brevitelson* Størmer, 1974: SMF VIII 150; *Stylonurella spinipes* (Page, 1859): NMS G.1891.92.33; *Drepanopterus abonensis* Simpson, 1951: BGS GSM 84718). The eyes are comparatively large, averaging around a third of the length of the carapace, however the narrow visual strip means the field of vision would have been limited to the dorsal plane, instead giving an almost 360° lateral view. The form of the lateral eyes is almost identical to those of *Pittsfordipterus phelpsae* (NYSM 10102), although these are half the length of the carapace and are positioned centrimesially. In *Stoermeropterus conicus* the eyes are positioned abnormally close to the carapace edge, reaching almost as far as the marginal rim along their anterior curve, however they just fall short of being semimarginal and are considered intramarginal. Their proximity to the marginal rim is similar to that of the reniform lateral eyes of *Orcanopterus manitoulinensis* Stott, Tetlie, Braddy, Nowlan, Glasser & Devereux, 2005 (ROM 56451) where their anterior curve all but touches the marginal rim.

The median ocelli are not clearly represented in any known specimen, despite the carapace being otherwise well-preserved. One specimen (NMS G.1897.32.134) displays a poorly preserved paired structure between the lateral eyes, situated towards their posterior limit, but the superimposition of the ventral coxae means any interpretation of these structures is extremely tentative. *Parastylonurus ornatus*, the other predominant

Pentland eurypterid species, also fails to preserve any median ocelli (Waterston 1979). Despite the lack of evidence from the specimens it is considered almost certain that *Stoermeropterus conicus*, along with all other eurypterids, had median ocelli. Their lack of preservation is probably due to their small, delicate anatomy and the flattened nature of the specimens, with the superimposition of the dorsal and ventral structures obliterating any trace of them. Assuming they would be similar to the median ocelli preserved in *Stoermeropterus latus* (PMO H1874) they would be simple, separate eyes without an ocellar tubercle and located between the lateral eyes, which is similar to the observed structures in NMS G.1897.32.134.

Ventral plates and sutures. The prosomal ventral plates and sutures are preserved in ten specimens, three of which only preserve the gross morphology of the plates without any visible sutures (NMS G.1885.72.1: Text-fig. 5a, Pl. 1, figs. 1&2; G.1885.26.72.19: Pl. 3, fig. 1; G.1897.32.139). The plates are broader anteriorly, narrowing posteriorly along the lateral edge as in *Eurypterus lacustris* Harlan, 1834 (YPM 209023), and are preserved intact which is the strongest indication that these specimens represent mortalities. The remaining seven specimens (NMS G.1885.72.13; G.1885.72.14; G.1885.26.72.17; G.1897.32.12.9; G.1897.32.132; G.1897.32.134; G.1897.32.174) show that the ventral plates are divided by two sutures, forming a medial epistoma that is around one third the width of the carapace (Table 2). The epistoma differs from that found in other Eurypterina, not remaining the same width for its length or widening posteriorly as it does in the Adelophthalmoidea (e.g. *Nanahughmilleria norvegica*: PMO H192; *Adelophthalmus sievertsi* (Størmer, 1969): PWL 2004/5008-LS) and the Pterygotoidea (e.g. *Herefordopterus banksii*: BGS GSM 88910; *Erettopterus bilobus*

(Salter, 1856): BMNH In 59343) but rather widening anteriorly as in the Stylonurina (e.g. *Brachyopterella pentagonalis* (Størmer, 1934a): PMO H1792; *Hallipterus excelsior* (Hall, 1884): USNM 25673). The sutures in *Stoermeropterus* most closely resemble the *Hallipterus*-type, being situated just either side of the midline resulting in a narrower epistoma (NMS G.1897.32.12.9), however it lacks the transverse suture seen in Stylonurina such as *Parastylonurus ornatus* (NMS G.1897.32.12).

Sutures with an almost identical morphology are however seen in the 'trilobite' larval stage in modern *Limulus* Müller, 1785 (Størmer 1934a, fig. 10) and the chasmataspidids '*Eurypterus*' *stoermeri* Novojilov, 1959 (PIN 1138/1) and *Diploaspis casteri* Størmer, 1972 (SMF VIII 39). This provides compelling evidence that *Stoermeropterus* may represent the plesiomorphic condition for ventral plates and not *Megalograptus* Miller, 1874 as suggested by Tetlie *et al.* (2008) (see *Plesiomorphic states within the Eurypterida*).

Prosomal appendages and metastoma. The prosomal appendages and metastoma, when known, are always preserved articulated to the rest of the prosomal unit. Appendages are preserved in part on seventeen specimens, although most commonly preserved are the coxae (Table 3). The chelicerae are preserved as rounded outlines in six specimens (NMS G.1885.26.72.14; G.1885.26.72.17; G.1897.32.12.9; G.1897.32.85; G.1897.32.123; G.1897.32.132) and range from 2 to 7 mm in length and 1.5 to 4 mm in width (Table 2). The chelicerae, while neither enlarged nor denticulated, appear to have been relatively robust. Morphologically they are similar to the chelicerae seen in most other eurypterids (e.g. *Parastylonurus ornatus*: NMS G.1897.32.12; *Strobilopterus princetonii* (Ruedemann, 1934a): YPM 204947; *Eurypterus tetragonophthalmus* Fischer, 1839: NRM Ar 49952), however their more robust structure is reminiscent of the rhenopterid *Leiopterella tetliei* Lamsdell, Braddy, Loeffler & Dineley, 2010b (CMN 53573) and the chasmataspidid *Loganamaraspis dunlopi* Tetlie & Braddy, 2004 (NMS G.1957.1.649). Appendages II-IV are of the newly diagnosed *Rhenopterus*-type and increase in size posteriorly, appendage II being much slighter in form than appendage IV. Appendage II is known from only two specimens (NMS G.1897.32.123; G.1897.32.133), consists of seven podomeres and in NMS G.1897.32.133 has a total length (including coxa) of 36 mm while the other, smaller specimen would have been about half that length (Table 4). While appearing much more delicate than the other appendages its short length, not extending much beyond the carapace, means it was unlikely to have a tactile sensory function like that suggested for the 'antenniform' second appendage in *Slimonia* (Laurie 1893). Appendage III is known from three specimens (NMS G.1885.26.72.14; G.1897.32.123; G.1897.32.133) and consists of eight podomeres and has a total length ranging from 17.5 mm in the smallest complete specimen to 53 mm in the largest (Table 5). Appendage IV is very robust with the podomeres thickening somewhat distally and having a clear depression running along their length. Known in its completeness from one specimen (NMS G.1885.26.72.14) it has eight podomeres, with a total length of 30 mm, however there are five specimens that preserve incomplete appendages (NMS G.1897.32.123; G.1897.32.133; G.1897.32.136; G.1897.32.137.1; G.1897.32.138: Text-fig. 13b, Pl. 9, figs. 1&3), some of which indicate a prosomal appendage IV with a length of 67.5 mm (Table 6).

The 'spines' on these appendages are difficult to make out due to their small size but fit with the general morphology of the *Rhenopterus*-type (e.g. *Rhenopterus diensti*: MfN

48/48a), being fixed cuticular extensions of the distal edge of the podomeres (e.g. NMS G.1897.32.133), however on the smaller individuals (NMS G.1885.26.72.14; G.1897.32.123) the podomeres appear to lack these cuticular extensions and more closely resemble the unornamented *Brachyopterella*-type. This is probably due to the smaller specimens being earlier instars, and indicates that the spines only begin to form during later moults through the eurypterid's ontogeny.

Appendage V is known completely from three specimens (NMS G.1897.32.133; G.1897.32.136; G.1897.32.137.1), incompletely from another two (NMS G.1897.32.138; G.1897.32.140), and may be tentatively identified in NMS G.1885.26.72.17. Unlike the three preceding appendage pairs appendage V lacks any form of ventral spiniferous extensions on the podomeres, even on the larger specimens, and corresponds to the unornamented *Brachyopterella*-type. It comprises nine podomeres which again thicken slightly distally and bear a depression along their length while podomere 6 has a slight dorsal anterior spur (NMS G.1897.32.136), also seen on appendage VI (NMS G.1897.32.132). The longest preserved appendage has a total length of 83 mm, while the shortest is 38.5 mm long (Table 7). This appendage is unlike any other known from the Eurypterina, with the exception of *Vinetopterus martini* Poschmann & Tetlie, 2004 (PWL 2000/5015b LS), which preserves some fragmentary appendages with a similar podomere morphology. Among the Stylonurina, *Alkenopterus brevitelson* (SPW 697-Da) shows similarly robust appendages however these are crested rather than depressed and have more rounded podomere lateral edges. The depressions are reminiscent of the grooves found on the appendages of hibbertopteroids (e.g. *Drepanopterus pentlandicus*: NMS G.1897.32.91; *Dunsopterus stevensoni* (Etheridge Jr., 1877): NMS G.1964.6.4), however the *Stoermeropterus* appendages are not as deeply grooved nor overall as stocky. The closest resemblance is found in *Brachyopterella ritchiei* Waterston, 1979 (NMS G.1968.14), appendages V and VI of which are well preserved. These bear both a ridge and a depression and are heavily ornamented with scales; however the general podomere shape, their relative dimensions, and the tendency for the podomeres to expand distally all matches the morphology of appendage V in *Stoermeropterus*.

The posterior-most prosomal appendage, appendage VI, is different again in morphology. Preserved completely in five specimens (NMS G.1885.26.72.13; G.1897.32.132; G.1897.32.133; G.1897.32.136; G.1897.32.140), incompletely in NMS G.1885.26.72.14 and possibly G.1885.26.72.17, it is pediform and consists of nine podomeres with an ancillary, posteriorly situated podomere 7a at the joint between podomeres 7 and 8. Podomere 7a is triangular in shape and about half the length of podomere 8 in larger specimens (e.g. NMS G.1897.32.133) but only a quarter the length of podomere 8 in smaller specimens (e.g. NMS G.1885.26.72.13). The podomeres themselves are similar to those in appendage V, being robust, flaring slightly distally and with a depression running along their length. The coxae are distinguished from the others not only by their increased size but by the possession of an anterior cuticular extension, termed the 'ear' (e.g. NMS G.1897.32.12.9). This appendage was the morphotype for the *Drepanopterus*-type appendage of Tollerton (1989), here reclassified as the *Moselopterus*-type appendage. The largest preserved appendage is 102 mm long, while the smallest is 41.5 mm (Table 8). Only two other currently known eurypterids bear similar appendages, and both of these are also grouped in the Moselopteridae alongside *Stoermeropterus*. *Moselopterus elongatus* Størmer, 1974 (SMF VIII 184a) – potentially a synonym of *M. ancylotelson* – also has an appendage VI with distally thickening podomeres and a triangular podomere 7a. The appendage differs in lacking the longitudinal depressions, appearing generally more gracile and in having a more developed 'ear' on the coxa. *Vinetopterus struvei* (Størmer, 1974) (SPW 614-D) also has an appendage VI with podomere 7a, although it is poorly preserved and lacks the coxa. The appendages are again relatively robust and have longitudinal depressions; however podomere 7a is more oval than triangular. On the holotype, where coxa VI is faintly preserved (SMF VIII 191a) there is some indication of an 'ear' however it is closer to the *Stoermeropterus* morphology and is not as prominent as in *Moselopterus* Størmer, 1974. The occurrence of podomere 7a and the coxal 'ear' - often associated with a swimming function in eurypterid paddles (Selden 1981) - in a pediform appendage is of some interest as it suggests that their development was not initially linked to swimming and may suggest an alternative function for the paddles as has been hypothesized in some of the Eurypterina (Laurie 1893; Størmer 1934a; Tetlie 2007b) (see *Plesiomorphic states within the Eurypterida*).

The metastoma, or post-oral feeding plate, is preserved in only four specimens (NMS G.1885.26.72.17; G.1897.32.85; G.1897.32.132; G.1897.32.136) however these offer a comprehensive view of its morphology. The average length: width ratio of the specimens is 1.65, while the lateral angle and angle of cordation (*sensu* Tollerton 1989) of 70˚ and 140˚ respectively indicate that the metastoma fits closest to the oval type in shape. In NMS G.1885.26.72.17 the length: width ratio is only 1.25, however this specimen has undergone distortion and the metastoma has been laterally squeezed, as indicated by the offsetting and acuter angle of the right-hand anterior shoulder. Another specimen (NMS

G.1877.32.132) has a metastoma with a length: width ratio of 2.1, however this specimen does not appear to have undergone preservational warping. It is however larger than the other three animals, and so suggests that the metastoma became relatively narrower in larger animals and therefore comparative width decreased throughout ontogeny, something also observed in *Moselopterus* (Lamsdell pers. obs.). The posterior of the metastoma is rounded, as in the majority of Eurypterina, while the anterior bears a shallow notch flanked by rounded shoulders (NMS G.1877.32.132); the notch is deeper and the shoulders more angular in NMS G.1885.26.72.17 but this is probably due to distortion as in juveniles of *Moselopterus* the notch is, if anything, less expressed than in the adults (SPW 704-D).

The metastoma in *Stoermeropterus* resembles that seen in a number of other eurypterids, particularly among the Eurypterina. Of the Stylonurina only *Drepanopterus* has an oval metastoma, however this laterally divided by a deep posterior cleft (e.g. *Drepanopterus abonensis*: BRSUG 28647; *Drepanopterus pentlandicus*: NMS G.1897.32.91), and the rhenopterids have a metastoma with a rounded posterior margin but the anterior is altogether much narrower giving it an overall turbinate shape (e.g. *Rhenopterus diensti*: MfN 48/48a; *Leiopterella tetliei*: CMN 53573). Within the Eurypterina similar metastoma morphologies are observed within all of the superfamilies bar the Mixopteroidea and its sister group consisting of *Orcanopterus* Stott, Tetlie, Braddy, Nowlan, Glasser & Devereux, 2005, *Grossopterus* Størmer, 1934b and *Waeringopterus* Leutze, 1961. Within the Pterygotoidea the metastoma has a deeper, more angular anterior notch among pterygotids (e.g. *Jaekelopterus rhenaniae* (Jaekel, 1914): PWL 2004/5051-LS) while in the hughmilleriids the metastoma is narrower, again with a deeper anterior notch but also with a flattened posterior (e.g. *Herefordopterus banksii*: BGS GSM 89481). The nanahughmillerids of the Adelophthalmoidea have a very prominent, angular anterior notch and a narrow posterior (e.g. *Nanahughmilleria norvegica*: PMO H1778) while the adelophthalmids have a broad, rounded posterior and an anterior with a shallow notch. The metastoma narrows somewhat towards the anterior (e.g. *Adelophthalmus mazonensis* (Meek & Worthen, 1868): UI X345) in a fashion similar to the rhenopterids. Among the Eurypteroidea the metastoma has a deeply notched anterior and truncated posterior in *Dolichopterus* Hall, 1859 (e.g. *Dolichopterus macrocheirus* Hall, 1859: UMMP 62642) however in more basal dolichopterids the metastoma is a narrower, petaloid shape with a rounder posterior and angular notched anterior (e.g. *Strobilopterus princetonii*: YPM 204947), a morphology shared with the Eurypteridae (e.g. *Eurypterus lacustris*: UMMP 62582A). *Stoermeropterus* shares an almost identical metastoma morphology with the onychopterellid *Onychopterella kokomoensis* (Miller & Gurley, 1896) (FMNH UC6638) and the other moselopterid *Moselopterus ancylotelson* (SMF 26061). Poorly preserved metastomae have also been described from the chasmataspidids *Loganamaraspis dunlopi* (NMS G.1957.1.649b) and *Octoberaspis ushakovi* Dunlop, 2002 (GIL 35/712), but in both these specimens the metastoma narrows drastically towards the posterior and has a relatively well-developed anterior notch, giving it an almost heart-shaped morphology.

Prosomal cuticular sculpture. The carapace is only preserved in dorsal aspect in six specimens (NMS G.1897.32.88: Text-fig. 4b, Pl. 3, fig. 2; G.1897.32.137; G.1897.32.138; G.1897.32.164: Text-fig. 10b, Pl. 11, fig. 2; G.1897.32.172; G.1897.32.191), however in half of these the preservation is too poor to permit study of the cuticle. Of the three that do show the sculpture, two (NMS G.1897.32.164; G.1897.32.172) do not preserve much detail, just giving an indication of a fine, granular sculpture with the impressions of the coxae obscuring much of the detail in NMS G.1897.32.164. NMS G.1897.32.138 shows the ornament in much greater detail, revealing the dorsal part of the carapace to be devoid of scales but covered in a scattered granular sculpture consisting of very fine pustules and is not tuberculate as suggested by Poschmann *et al*. (2005). These are much finer than those of *Drepanopterus abonensis* (BGS GSM 84718), *Hardieopterus macrophthalmus* (NMS G.1897.32.84) or *Chasmataspis laurencii* Caster & Brooks, 1956 (USNM 125099), similar instead to the ornament of *Moselopterus ancylotelson* (SPW 999-D).

While the majority of specimens are preserved in ventral aspect, the prosomal sculpture is only known from seven specimens (NMS G.1885.26.72.13; G.1885.26.72.14; G.1885.26.72.17; G.1885.26.72.19; G.1897.32.85; G.1897.32.132; G.1897.32.134; G.1897.32.139). The sculpture in all of the specimens bar NMS G.1885.26.72.17 is limited to the ventral marginal prosomal plate and is composed of a mixture of 'terrace lines' (*sensu* Selden 1981) grading anteriorly into broad lunules and pits (e.g. NMS G.1885.26.72.13, G.1897.32.139). NMS G.1885.26.72.17 preserves the ventral plate sculpture in exquisite detail, consisting of 'terrace lines' along the lateral edge postero-lateral edge of the ventral plate that are angled anteriorly along up to the margin of the doublure (ventral expression of the marginal rim). Along the anterior of the ventral plates, where they curve around to meet at the epistoma, the 'terrace lines' follow the contours of the carapace margin and are arranged into several rows that between them extend from the anterior to ventral margin of the plates. The foremost 'terrace lines' break up into broad, rounded lunules and pits. Pits are also directly associated with the lunules and 'terrace lines' themselves, where they follow the folliculated pattern of being situated centrally within the structure. Macerated cuticle from the Lower Devonian of Willwerath, Germany shows eurypterids to have been quite hirsute (Braun 1997) and hairs can be seen without visual aid on well preserved Scottish *Pterygotus* specimens (Lamsdell pers. obs.) and so it seems likely that these pits were the attachment points for setae, as seen in *Eurypterus tetragonophthalmus* (NRM Ar 50013b), *Hibbertopterus scouleri* (Hibbert, 1836) (GLAHM A23078) and exuviae of the extant xiphosuran *Limulus polyphemus* Linnaeus, 1758 (Selden 1981, fig. 23d). NMS G.1885.26.72.17 also preserves sculpture on the coxae. This takes the form of 'terrace lines' that run along the length of each coxa, concentrated particularly along the anterior edge. An exception is the greatly expanded coxa of appendage VI, where the 'terrace lines' are more evenly spread out across the entirety of its surface.

The 'terrace lines' of NMS G.1885.26.73.19 were studied under the scanning electron microscope by Miller (1975) as part of a broader treatment of terrace lines in trilobites. The eurypterid 'terrace lines' Miller described as sub-parallel concentric ridges with a scarp slope and a dip slope of low relief ranging from 30 – 50 μ with the ridges facing forwards and peripherally as on a trilobite cephalic doublure. The ridges on NMS G.1885.26.73.19 were spaced from 200 – 1000 μ apart and became more sinuous and increased in anastomosis frequency on the 'genal' part of the plates. Passing inwards across the width of the ventral plates Miller reported that the ridges became shorter and more curved, eventually assuming a scale-like appearance but with the outward facing being consistently maintained. At the inner part of the plates in the midline region was a field of deep, circular hollows in the matrix that Miller considered to be the moulds of setae originally projecting from the cuticle.

Terraced cuticular sculpture patterns are also found in several other eurypterids. Well-preserved specimens of *Eurypterus tetragonophthalmus* (e.g. NRM Ar 35320) reveal similar terrace patterns, with rows of closely spaced terraces running parallel to the plate outer margin and angling towards the peripheral along the lateral edge, while the ventral plates of *Parahughmilleria hefteri* (SMF VIII 60) bear an almost identical sculpture to *Stoermeropterus conicus* with a series of terraces running parallel to the margin that develop anteromedially into small squamae. Fine 'creases' similar to terrace lines have also been described on the inner margin of the ventral plates of *Parastylonurus ornatus* (NMS G.1897.32.13), however while having a similar morphology to the 'terrace lines' in *S. conicus*, *E. tetragonophthalmus* and *Parahughmilleria hefteri* the creases are absent from the majority of the ventral plate and were considered by Waterston (1979) to be where the plates passed into the thinner, flexible integumen connecting the bases of the prosomal appendages. The rest of the ventral plates is ornamented by rounded squamae and as the specimens come from the same locality as *S. conicus* combined with the fact that 'terrace lines' are found on some of the abdominal segments of *Parastylonurus* their absence from the ventral plates is not considered preservational. Dorsal structures similar to the ventral 'terrace lines' described above are also seen in a number of Eurypterina (i.e. *Parahughmilleria bellistriata* (Kjellesvig-Waering, 1950): USNM 115448; *Eysyslopterus patteni* (Størmer, 1934c): AMNH 32720; *Orcanopterus manitoulinensis*: ROM 56462) located on the carapace anterior and between the lateral eyes. These terraces probably performed the same function as the ventral terraces, as they are located on the same region of the animal (the prosoma anterior) in both cases, however the homology of the dorsal and ventral terraces is unclear and it is possible that 'terrace lines' have developed independently at least twice in eurypterids.

Outside of eurypterids, 'terrace lines' are known from a number of arthropod groups, including trilobites (Miller 1975; Schmalfuss 1981) and decapod crustaceans (Schmalfuss 1978; Savazzi 1985). The most obvious analogue to the 'terrace lines' seen in *Stoermeropterus* are those of trilobites, as they share many features including their basic structure and attitude (Miller 1975), consisting of a terrace with the overhang angled anteriorly and towards the peripheral of the carapace margin (e.g. *Holotrachelus punctillosus* (Törnquist, 1884): NRM Ar 45493). There are several differences however, as trilobite terrace lines are frequently found on the dorsal cuticular surface as well as the ventral doublure (Schmalfuss 1981), and are continuous across the anterior of the doublure (e.g. *Paralejurus rehamnanus* Alberti, 1970: SMF 86050) unlike the 'terrace lines' in *Stoermeropterus* that become broken up into discrete scales towards the anterior of the ventral plates (e.g. NMS G.1897.32.139). The cuticular terraces of extant decapods differ somewhat in their pattern to those of trilobites and *Stoermeropterus*, being largely localized to the appendages and the lateral margins of the carapace (Savazzi 1985). When present on the carapace dorsal or ventral surfaces the terraces are discontinuous and tend to have the overhang angled anteriorly irrespective of their position on the carapace. These cuticular terraces are found almost exclusively in burrowing decapods (Schmalfuss 1978), and are thought to function by increasing friction against the burrow wall as the animal wedges itself to avoid being extracted by predators. Discussion on the function of terrace lines in trilobites has been necessarily speculative, however they have been suggested to act as a way of strengthening the exoskeleton (Whittington 1961), a current-monitoring system (Miller 1975), as an aide for burrowing and providing increased friction against soft sediments (Schmalfuss 1981), as increasing frictional resistance to movement during enrollment (Fortey 1986), and as an aid in maintaining the enrolled position or in preventing sediment particles gripping articulation surfaces (Feist *et al.* 2010).

Sensory organs consisting of isolated or loose groups of slits in the cuticle known as slit sensilla are found in arachnids and perform a range of sensory functions including detecting loads on the cuticle, gravitational forces and substrate vibrations (Barth 1985). While possible slit sensilla have been reported from well-preserved eurypterids (Dunlop & Braddy 1997) the 'terrace lines' in *Stoermeropterus* are not considered homologous to arachnid slit sensilla as they occur on the carapace rather than the appendage podomeres where they are most common and are far larger and extensive than any known slit sense organ. Despite this they may have served a similar function; the 'terrace lines' likely had some sensory role, as indicated by their co-occurrence with setae. Their positioning on the ventral surface of the prosoma may indicate that they also served in some frictional function, especially if the animal was scavenging or hunting within the substrate surface, while it is considered extremely unlikely that a eurypterid could enroll itself in a manner similar to trilobites and so their function as some form of locking mechanism can be discounted.

OPISTHOSOMA AND TELSON

The opisthosoma is preserved in its entirety in several specimens while the majority of specimens preserve at least some opisthosomal segments. The telson is also well represented although due to its delicate nature it appears to have been frequently broken off before its natural termination. Again, the entirety of the external anatomy is preserved, and although there is no evidence for the internal respiratory organs or reproductive systems both types of genital appendage are represented in the material and one specimen (NMS G.1897.32.145: Pl. 11, fig. 3) may preserve an alimentary canal. Due to the superimposition of dorsal and ventral structures the Blattfüsse are difficult to distinguish from the associated tergite in many specimens; furthermore the mesosoma is occasionally crumpled antero-posteriorly to around half of its usual length (e.g. NMS G.1885.26.72.1; G.1897.32.89: Pl. 4, fig. 1; G.1897.32.132; G.1897.32.138; G.1897.32.176: Pl. 13, fig. 3) in a manner very similar to specimens of *Moselopterus ancylotelson* (e.g. SMF VIII 56; VIII 164; SPW 701-D) and *Vinetopterus struvei* (e.g. SMF VIII 191; VIII 165). In these cases the metasoma is left intact and un-distorted, presumably because of the more robust nature of the ankylosed rings that form the posterior body segments. This form of taphonomic distortion is distinct to segment telescoping, when the body segments pull in into each other so their boundaries overlap. Telescoping segments are undocumented in xiphosurans and taphonomic experiments have shown telescoping to be present only occasionally in scorpion moults and never in carcasses (McCoy & Brandt 2009), while in eurypterids telescoping is recorded in the metasoma of *Tylopterella boylei* (Whiteaves, 1884) (GSC 2910), *Jaekelopterus rheninae* (PWL 2004/5057-LS), *Vinetopterus martini* (PWL 2000/50156), *Nanahughmilleria norvegica* (PMO H1656; H1642; H1633), questionably from a poorly preserved specimen of *Herefordopterus banksii* (BGS GSM Zf2871), and *Drepanopterus abonensis* (BMAG Cb4668) – although this last example may actually be flattening of the ankylosed segments causing the dorsal and ventral margins to be superimposed as described in *Loganamaraspis dunlopi* (NMS G.1957.1.649) by Tetlie & Braddy (2004). Telescoping involving the metasoma and posterior segments of the mesosoma has also been identified in *Parahughmilleria hefteri* (SMF VIII 43) and *Brachyopterus stubblefieldi* (BGS D 3124). Despite this list of documented cases, telescoping in eurypterids is relatively rare, like scorpions occurring in a minority of presumably exuvial specimens. Postabdominal telescoping is however widespread in chasmataspidids; *Octoberaspis ushakovi* (GIL 35/735; 35/707; 35/379; 35/336; 35/337) showed telescoping in so many specimens that at one point they were considered to potentially be examples of sexual dimorphism or even a separate species (Dunlop 2002), while *Diploaspis casteri* (SMF VIII 36; VIII 39; VIII 73; PWL 1999/8-LS), *'Eurypterus' stoermeri* (PIN 1138/1), and *Diploaspis muelleri* Poschmann, Anderson & Dunlop, 2005 (PWL 2002/5020-LS; 2002/5021-LS) also all display postabdominal telescoping. While the fossils of the two *Diploaspis* species were considered to represent mortalities by Dunlop *et al*. (2001) and Poschmann *et al.* (2005), the evidence for this is circumstantial and the telescoping would suggest that some, at least, are exuviae. This disparity in telescoping frequency between eurypterids and chasmataspidids may indicate a difference in moulting techniques between the two groups, possibly due to the fused nature of the buckler in chasmataspidids.

As previously stated the mesosomal crumpling in *Stoermeropterus conicus* does not indicate that the specimens are the result of exuviae. Despite the correlation between opisthosomal telescoping and moulting there is greater evidence that the specimens represent mortalities (namely the lack of isolated carapaces, the in situ preservation of the prosomal ventral plates and the articulated nature of the prosomal appendages), and based on the way the segments have been distorted rather than displaced between each other, and the lack of metasomal telescoping, the indication is that this is a separate taphonomic phenomenon. Its co-occurrence in specimens of *Moselopterus* (which are considered exuviae – see Størmer 1974) and *Vinetopterus* would seem to suggest it is a characteristic of the Moselopteridae, however the holotype of *Cyrtoctenus wittebergensis* Waterston, Oelofsen & Oosthuizen, 1985 (USS IT01) - a clear mortality - also shows mesosomal crumpling (referred to as telescoping by Waterston *et al*.). Both *Cyrtoctenus* and moselopterids were deep-bodied compared to most other eurypterids and it seems likely that the crumpling is due to the segments being compacted during the taphonomic process due to the increased size of the body cavity offering less resistance to external pressure.

Mesosoma and genital appendage. The mesosoma is known from a total of 34 specimens, ranging in total length from 13 to 40 mm (Table 9), accounting for approximately 23% of the animal's total length in un-crumpled specimens (e.g. NMS G.1885.26.72.13; G.1885.26.72.14; G.1897.32.12.9; G.1897.32.88; G.1897.32.121: Pl. 4, fig. 2). The smallest specimens (e.g. NMS G.1897.32.137.2) have a maximum width of around 12 mm while the largest (e.g. NMS G.1897.32.133) have a maximum width of 55 mm, the widest point occurring at the fourth segment as in most eurypterids. Tergites 2–6 (equivalent to somites IX–XIII) are generally all very similar in length, being about 5 mm long on average with a maximum length of 10 mm seen in some of the larger specimens (e.g. NMS G.1885.26.72.17). Tergite 2 is marginally shorter than 3–6, however tergite 1 (somite VIII) is clearly reduced, ranging from two-thirds to half the length of the following segments. A reduction in the first visible opisthosomal tergite is seen in most eurypterids (e.g. *Stylonurella spinipes*: NMS G.1891.92.33; *Pagea plotnicki* Lamsdell, Braddy, Loeffler & Dineley, 2010b: CMN 53570; *Eurypterus tetragonophthalmus*: NRM Ar 35307; *Mixopterus kiaeri* Størmer, 1934a: PMO H2044; *Nanahughmilleria norvegica*: PMO H2199), both extinct scorpions (e.g. *Proscorpius osborni* (Whitfield, 1885): AMNH 2257, which also shows a slight reduction in segment 2) and their extant counterparts, and synziphosurines (e.g. *Bembicosoma pomphicus*: NMS G.1897.32.149; *Willwerathia laticeps* (Størmer, 1936a): SLK 1a, a plaster cast of which is stored in NMS under G.2007.23.2). Chasmataspidids however do not follow this trend, as the first reduced tergite or microtergite is considered homologous to the reduced opisthosomal segment found folded underneath the prosoma-opisthosoma junction belonging to somite VII (Dunlop & Webster 1999). While this massively reduced true first tergite is not observed in *Stoermeropterus*, this is probably due to the cryptic nature of the segment which is likely present in the majority of eurypterids at least as a plesiomorphic trait, and it is considered likely that the 'posterior doublure' of Kjellesvig-Waering & Heubusch (1962) and Caster & Kjellesvig-Waering (1964) - in *Buffalopterus pustulosus* (Hall, 1859) (BMS E2866) and *Megalograptus ohioensis* Caster & Kjellesvig-Waering *in* Størmer, 1955 (UCM 24113) respectively - and the 'posterior ventral plate' in *Kiaeropterus cyclophthalmus* (NMS G.1885.26.72.16) of Tetlie *et al.* (2007) may in fact represent the tergite. Therefore the second segment in the chasmataspidid opisthosoma corresponds to the commonly held first segment in eurypterids and is the anterior-most segment to be fused into the buckler. Well-preserved specimens show it to be of equal length to the other buckler segments (e.g. *Octoberaspis ushakovi*: GIL 35/324, 35/336;

Forfarella mitchelli Dunlop, Anderson & Braddy, 1999: BMNH In 60023; '*Eurypterus*' *stoermeri*: PIN 1138/1; and well preserved *Diploaspis casteri*: SMF VIII 39).

Some *Stoermeropterus* specimens (NMS G.1885.26.72.1; G.1897.32.12.9; G.1897.32.137.2) appear to show trilobation of the mesosoma, however the majority of well-preserved specimens show the mesosoma to be undifferentiated. Trilobation in eurypterids is delineated by furrows running along the length of the body (e.g. *Megalograptus ohioensis*: UCM 24122A; *Mixopterus kiaeri*: PMO H2044; *Hardieopterus macrophthalmus*: NMS G.1897.32.95) – trilobation suggested by ridges on the opisthosoma (as in *Stylonurus powriensis* Page, 1856: NMS G.1891.92.102 and *Cyrtoctenus wittebergensis*: USS IT01) is not considered homologous to this type – which is not apparent in the Pentland Hills specimens. Furthermore those that do appear to show trilobation have been either laterally compressed or completely flattened, and so it is considered a taphonomic artefact caused by compression and the deep-bodied nature of the specimens.

All the tergites bear an articulation point along their dorsal margin, consisting of a smooth facet followed by a slight ridge before the normal dorsal ornamentation begins. This is best seen in NMS G.1897.32.88 and G.1897.32.138 but can be made out in a few others (e.g. NSM G.1885.26.72.13; G.1897.32.139; G.1897.32.173: Pl. 12, fig. 2) and probably represents the point of overlap with the preceding tergite, with the following segment slotting underneath it. A similar 'smooth articulating facet' was described by Lamsdell *et al*. (2009) in specimens of *Drepanopterus abonensis* (e.g. BGS GSM 84694, GSM 84718). While it has been recognized for some time that the segments of the eurypterid opisthosoma would have overlapped, and implied that a ridge on the tergite marks the maximum point of overlap with the preceding tergite (see Wills 1965 and Caster & Kjellesvig-Waering 1964), the articulation points have been largely neglected in descriptions by previous authors or have been described without the articulation function of the structure being realized (e.g. Kjellesvig-Waering & Heubusch 1962, Tetlie & Dunlop 2005), a notable exception being the description of *Adelophthalmus sievertsi* by Poschmann (2006), where a transverse furrow on the anterior third of each segment was stated to delineate the maximum overlap of the preceding segment. Such articulation points are actually known from many eurypterids (e.g. *Eurypterus lacustris*: BMS E6468; *Eurypterus henningsmoeni* (Tetlie, 2002): PMO 70705; *Adelophthalmus granosus* Jordan *in* Jordan & von Meyer, 1854: MfN MB.A. 890; *Buffalopterus pustulosus*: BMS E2866; *'Carcinosoma' scorpioides* (Woodward, 1868): NMS G.1986.34.5; *Drepanopterus pentlandicus*: NMS G.1885.26.72.5; *Rhenopterus diensti*: MfN 48/48a), and appear to be consistent within the group. Recognizing the morphology of tergite articulations is important for several reasons; several species may have had their total body lengths overestimated by not accounting for the fact that the articulation point would have been slotted beneath the preceding tergite, also the mode of articulation can give some indication of the degree of movement possible between the segments and can be useful for working out functional morphology including locomotion, posture, and the potential or otherwise for enrollment. The morphology of segment articulation may also have some phylogenetic signal useful for resolving the relationships of basal chelicerates and their ancestors (see *Excursus on segment articulations in arthropods*).

One of the more unusual features of *Stoermeropterus conicus* is its possession of moveable spines on the lateral margin of the mesosoma as evidenced from seven specimens (NMS G.1885.26.72.13; G.1885.26.72.14; G.1885.26.72.17; G.1897.32.85; G.1897.32.131; G.1897.32.139; G.1897.32.165: Pl. 11, fig. 1). These spines are also known from the other *Stoermeropterus* species (i.e. *S. latus*: PMO H1715, H1734, H1808; *S. nodosus*: FMNH PE6214) and so appear to be a defining characteristic of the genus. The spines appear to attach beneath the tergite and are most frequently preserved flattened against the body, making them difficult to discern, however occasionally a spine will be shown projecting out giving clear indication of their mobile nature. Despite being positioned between the tergite and operculae the spines appear to be more closely associated with the unsclerotized sternite as they are absent from the first (genital) segment which ventrally has fused with the second segment to form the genital operculum. The spines are narrow, never more than 3 mm in width, and extend for about half the length of the following segment but are otherwise undifferentiated. The mesosomal segments rarely bear any form of lateral ornamentation in eurypterids; fixed epimeral projections consisting of lateral cuticular extensions of the tergite are found in some species of *Adelophthalmus* Jordan *in* Jordan & von Meyer, 1854 (e.g. *A. sievertsi*: PWL 2004/5000-LS, 2004/5002-LS; *A. granosus*: MfN MB.A. 890; *A. mazonensis*: UI X345) and *Strobilopterus princetonii* (PU 13854), but these are clearly not homologous to the articulating spines in *Stoermeropterus*. Moveable spines are unknown in the remaining chelicerates (and potentially all arthropods) with the exception of limuloid xiphosurids as defined by Selden & Siveter (1987). In these taxa the freely articulating abdominal tergites have fused to form a thoracetron and the moveable spines originate from the ventrum of each segment, being interspersed with dorsal fixed epimera (e.g. *Rolfeia fouldenensis* Waterston, 1985: NMS G.1984.67.1) that are highly reduced in more modern species (e.g. *Mesolimulus walchi* (Desmarest, 1822): ROM 53253), and function as mechanoreceptors that aid in righting behaviour (Fisher 1981) and in monitoring the posture of the opisthosoma in relation to the substrate (Waterston 1985). The moveable spines in *Stoermeropterus* and limuloids clearly developed through the same developmental process, being associated with the ventral surface of the preabdomen, having a non-appendicular origin and consisting of a conical spine situated within a semi-spherical socket, probably formed from enlarged and highly sclerotized setae. Furthermore they both lack the spines on the genital segment. Direct homology is unlikely however, as limuloids have six pairs of moveable spines (with the exception of *Rolfeia*, which is also lacking spines on the second tergite for a total of five pairs) and the fusion of tergites into the thoracetron probably occurred in xiphosurans before the development of the moveable spines (Anderson & Selden 1997). The moveable spines therefore probably represent an example of parallelism (Simpson 1961) via generative homology (Butler & Saidel 2000).

Unusually for eurypterids, which are usually preserved so that the rock splits along the specimen's dorsal surface because of the thinner nature of the ventral cuticle (Simpson 1951), the rocks containing *Stoermeropterus conicus* are often split to reveal the ventral structures. A similar phenomenon is seen in *Moselopterus*, and in both cases the cause is likely to be the granular dorsal ornament of the exoskeleton that hinders the splitting of the rock along that surface (Størmer 1974), instead dividing along the smooth ventral cuticle. Despite this, observing the ventral mesosomal structures can be difficult because of the aforementioned thinness of the cuticle combined with compression during preservation resulting in superimposition of the dorsal tergites. The genital operculum and genital appendage can be seen in seven specimens (NMS G.1885.26.72.1; G.1885.26.72.13; G.1885.26.72.17; G.1897.32.12.9; G.1897.32.133; G.1897.32.136; G.1897.32.137) which between them demonstrate the dimorphic morphology of both sexes. The genital operculum itself consists of three fused plates, the median and posterior plates corresponding to the appendages of somite VIII and IX and the anterior plate potentially representing the true sternite of somite VII (see *Plesiomorphic states within Eurypterida*). The anterior opercular plate is little more than a strip that can be seen on only well preserved specimens and accounts for about a tenth of the operculum's length (NMS G.1885.26.72.17). Anterior opercular plates are known among the Stylonurina (*Parastylonurus ornatus*: NMS G.1897.32.8; *Stylonurella spinipes*: BGS GSM 87357; *Drepanopterus abonensis*: BGS GSM 84704) and other relatively basal Eurypterina (*Eurypterus tetragonophthalmus*: BNHM In 59752; *Dolichopterus jewetti* Caster & Kjellesvig-Waering, 1956: NYSM I13138) but appear to be lost in more derived Eurypterina (*Parahughmilleria hefteri*: SMF VIII 59; *Erettopterus bilobus*: KM 09.123.go), while it has also been reported in the chasmataspidid *Loganamaraspis dunlopi* (NMS G.1957.1.649). The median and posterior opercular plates are approximately equal in length with a clear transverse suture at the point where the first and second opercular plates are joined (NMS G.1897.32.136). This is very similar to the stylonurine condition, where there is a prominent transverse opercular suture (as in *Rhenopterus diensti*: MfN 48/48a), whereas in Eurypterina the transverse suture becomes less obvious (*Eurypterus lacustris*: UMMP 62582A) before being lost entirely with the only indication that the genital operculum consists of two segments being a difference in cuticular ornamentation between the two (*Slimonia acuminata*: KM 09.123.aa).

As in all eurypterids, the genital appendage in *Stoermeropterus conicus* is sexually dimorphic, with a long type A appendage (NMS G.1885.26.72.1; G.1885.26.72.13; G.1897.32.12.9) and a short type B (NMS G.1885.26.72.17; G.1897.32.133; G.1897.32.136; G.1897.32.137). The type A appendage is longer comparatively, however the individuals preserving the type B tend to be larger and so both appendages appear to be of a similar size (Table 10), however comparing two similarly sized specimens (NMS G.1885.26.72.1 and G.1897.32.137) reveals that while the appendages have a similar width (about 4 mm at the base) the type A appendage is approximately double the length of the type B (11 mm compared to 6 mm).

The type A genital appendage is associated with deltoid plates that are apparent even in the most poorly preserved specimen (NMS G.1885.26.72.1) that are shown to be almost pentagonal in outline (NMS G.1897.32.12.9), similar to the deltoid plates of *Eurypterus tetragonophthalmus* (BMNH I 3406) rather than the more triangular plates of *Parahughmilleria hefteri* (SMF VIII 256) and *Adelophthalmus sievertsi* (PWL 2004/5018-LS). The deltoid plates are situated at the base of the genital appendage and extend back for the length of the median opercular plate. The posterior opercular plate bears a pair of spatulae that lie either side of the genital appendage and have rounded terminations that marginally extend beyond the posterior plate margin (NMS G.1885.26.72.13; G.1897.32.12.9). Spatulae are generally only known from the Adelophthalmoidea where they vary in morphology from having a pointed termination (*Adelophthalmus sievertsi*: PWL 2004/5018-LS; *Parahughmilleria hefteri*: SMF VIII 256) to a rounded termination like that seen in *Stoermeropterus* (*Adelophthalmus mazonensis*: UI X345; *Adelophthalmus moyseyi* (Woodward, 1907): LM 751). Spatulae have also been reported in *Dolichopterus jewetti* (NYSM I13138) and the Stylonurina *Parastylonurus ornatus* (NMS G.1897.32.7) and *Drepanopterus abonensis* (BGS GSM 84700) and these appear to have angular terminations. The genital appendage itself is lanceolate and originates from the median opercular plate, extending down to the posterior margin of the first Blattfüsse. The number of appendage segments is difficult to ascertain, however it appears there is a long tubular proximal segment and two short distal segments (NMS G.1897.32.12.9). The termination appears unicate in NMS G.1897.32.12.9 but bifurcate in NMS G.1885.26.72.13, and as this is the better preserved of the two this morphology is assumed to be the correct one. This morphology of type A genital appendage appears unique among Eurypterida, being somewhat similar to genital appendages found in adelophthalmoids (for example *Nanahughmilleria norvegica*: PMO H1873 and *Adelophthalmus mazonensis*: UI X345) but the appendage is broader at its base than in *N. norvegica* and far shorter than in *A. mazonensis*.

The type B genital appendage is also associated with a genital operculum that consists of an anterior, median and posterior opercular plate with the transverse suture between the median and posterior opercular plates curving towards the anterior as it extends laterally and the posterior opercular plate bowing downwards around the appendage (NMS G.1897.32.136). There are no deltoid plates on the type B operculum despite this region being well preserved in some specimens, something that is also seen in *Parastylonurus ornatus* (NMS G.1897.32.8). Spatulae may be faintly present, however NMS G.1885.26.72.17 and G.1897.32.136 appear to show narrow structures with angular terminations while on NMS G.1897.32.133 and G.1897.32.139 there appears to be no structures present. An alternative explanation for these structures could be as lateral lamellae; the ‘rim’ and ‘flange’ structures described by Størmer (1974) on the type B operculum of *Moselopterus* and also observed in *Eurypterus tetragonophthalmus* (Braddy & Dunlop 1997) and *Parastylonurus ornatus* (Waterston 1979). The genital appendage itself initially appears lozenge-shaped in specimens where the preservation is poor (NMS G.1897.32.136; G.1897.32.139), however this is largely due to the spatulae partially folding under the appendage compounded by the very tip of the appendage breaking off. NMS G.1885.26.72.17 and G.1897.32.133 show the type B appendage to be obpyriform with its distal termination narrowing to a point. NMS G.1885.26.72.17 also shows the genital appendage narrowing towards its base, however the appendage in this specimen has been displaced from its natural position and it appears that this structure would normally project underneath the median opercular plate as shown in the type B appendage of *Eurypterus tetragonophthalmus* (Braddy & Dunlop 1997).

Posterior to the genital operculum the remaining operculae (the Blattfüsse) are represented by only a handful of specimens (NMS G.1885.26.72.14; G.1885.26.72.17; G.1897.32.12.9; G.1897.32.136). The sternites, being fully covered by the operculae, are unsclerotized in eurypterids and so are not preserved (Størmer 1934a). Of the specimens preserving Blattfüsse, NMS G.1897.32.12.9 shows the central suture between the opercular plates but does not preserve enough detail to provide a verifiable count of the number of plates, while the holotype (NMS G.1885.26.72.14) shows that there were five operculae covering the area corresponding to tergites 1-6 and that at least the posterior three Blattfüsse are medially fused. The clearest indication of opercular morphology comes from NMS G.1885.26.72.17, which shows five operculae, the genital operculum extending for the length of the first two dorsal tergites. The operculae bear strong ornamentation (see *Opisthosomal cuticular sculpture*) and slightly overlap, being marginally longer than their corresponding tergite. Each operculum spans the width of the body and bears a faint suture, while the first Blattfüsse may be unfused; most eurypterids have the Blattfüsse fused with a clear suture (e.g. *Parahughmilleria hefteri*: SMF VIII 57b2; *Stoermeropterus latus*: PMO H1650), while a suture is lacking in the Blattfüsse of *Megalograptus ohioensis* (UCM 24100E), *Erettopterus osiliensis* Schmidt, 1883 (YPM 174601), *Rhinocarcinosoma dosonensis* Braddy, Selden & Doan Nhat, 2002 (IGMR BT166/1), *Hibbertopterus scouleri* (KM G55/76), *Adelophthalmus mazonensis* (UI X345) and *Adelophthalmus moysei* (LM 751). The first Blattfüsse in *Stoermeropterus conicus* is clearly unfused (as shown by NMS G.1897.32.136), unlike the first Blattfüsse in the other moselopterids (e.g. *Vinetopterus struvei*: SMF VIII 145; *Moselopterus ancylotelson*: SMF 26061) which appears to be fused, a condition shared with many eurypterids (e.g. *Onychopterella augusti*: GSSA C373; *Onychopterella kokomoensis*: FMNH UC6638; *Nanahughmilleria norvegica*: PMO H1795; *Parastylonurus ornatus*: NMS G.1897.32.8; *Carcinosoma newlini* Claypole, 1890: AMNH 502; *Eurypterus henningsmoeni*: PMO 70696) although several do also have the first Blattfüsse unfused (e.g. *Slimonia acuminata*: SM A16237; *Orcanopterus manitoulinensis*: ROM 56459; *Eurypterus remipes*: YPM 9003; *Drepanopterus pentlandicus*: NMS G.1897.32.71; *Leiopterella tetliei*: CMN 53573; *Rhenopterus diensti*: MfN 48/48a). There appears to be no clear phylogenetic pattern for Blattfüsse suturing within Eurypterida however, with the fusion of the Blattfüsse apparently variable even within genera while the presence or absence of median sutures on the operculae does not correlate with whether the first Blattfüsse is fused or not (*Leiopterella* has an unfused first Blattfüsse with visible sutures on the remainder while *Orcanopterus* also has the first Blattfüsse unfused but no sutures on the fused operculae) while *Mixopterus kiaeri* unusually has not only the first Blattfüsse unfused but a deep cleft in the second and a notch in the third before the fourth is fully fused (PMO H2044). However, the fusion of opercular plates may have ramifications for broader chelicerate phylogeny (see *Plesiomorphic states within the Eurypterida*).

Metasoma and telson. The metasoma (comprising the last six opisthosomal segments) and the telson are preserved in a total of 33 specimens (Table 11) and are about 108 mm long in larger specimens (e.g. NMS G.1897.32.138), of which the telson accounts for 35 mm, and 43 mm long including a 15 mm telson in smaller individuals (e.g. NMS G.1897.32.164). Altogether the metasoma and telson accounts for 60% of the animal's total length, 34% of the total being the metasoma and 26% being the telson. The anterior three metasomal segments have an average length of 6 mm, while the last three become progressively longer until the pretelson is approximately double the length of segment 7. The metasomal segments are ankylosed, each forming a single sclerotized ring that completely encases the body, and so better withstand the taphonomic warping, resulting in some specimens appearing to have a proportionally longer metasoma (e.g. NMS G.1897.32.89) or a proportionally narrower, apparently undifferentiated prosoma and mesosoma (e.g. NMS G.1897.26.72.13); unwarped specimens show the opisthosoma to begin slightly narrowing from the fourth segment onwards, with an increased contraction at the seventh opisthosomal segment that continues constricting regularly until the pretelson (NMS G.1885.26.72.14; G.1897.32.88). Segment 7 is around 44 mm wide in the largest specimens (NMS G.1897.32.132; G.1897.32.133; G.1897.32.136) but has an average width of 21 mm while the largest pretelson has a width of 20 mm with the average width being 10 mm. The pretelson itself varies, being as long as or longer than it is broad in some specimens but broader than it is long in others.

All metasomal segments bear lateral epimera although these are only preserved on just under a third of the specimens, a phenomenon seen in other Pentland Hills eurypterids such as *Hardiopterus macrophthalmus*, which occasionally appears to lack its distinctive pedunculate epimera (e.g. NMS G.1885.26.72.11). This is also seen in the chasmataspidids *Achanarraspis reedi* Anderson, Dunlop & Trewin, 2000 (AU 12242) and *Chasmataspis laurencii* (USNM 125099) which preserve some but not all of their epimera and was noted to be common in the adelophthalmid eurypterid *Adelophthalmus sievertsi* by Poschmann (2006), who stated that the lateral epimera tended to break off during collection and that the presence or absence of postabdominal epimera should be used as taxonomic criterion only after detailed taphonomic investigation. Waterston (1979) explained this propensity for missing the epimera as due to the postabdominal segments being dorso-ventrally deep while the epimera are positioned only slightly ventral to the dorsal surface of the segments, therefore when a specimen is split along the dorsal surface the epimera are well represented while if the specimen splits along a more ventral plane the epimera may not be well seen or even absent. This explains their apparent absence in many of the *Stoermeropterus* specimens, most of which are exposed in ventral view. Of further interest is the apparent difference in epimeron morphology between certain specimens, with most appearing to have angular epimera on the pretelson (NMS G.1885.26.72.1; G.1897.32.89; G.1897.32.124: Pl. 5, fig. 3; G.1897.32.126: Pl. 6, fig. 1; G.1897.32.130: Text-fig. 13a, Pl. 6, fig. 3; G.1897.32.170: Pl. 11, fig. 4;

G.1897.32.185: Text-fig. 14c; G.1897.32.192: Pl. 14, fig. 3; G.1897.32.198: Pl. 15, fig. 4) while in others they appear lobate (NMS G.1897.32.88; G.1897.32.164; G.1897.32.167: Pl. 13, figs. 1&2; G.1897.32.197: Pl. 15, fig. 3). These lobate specimens were separated into their own species as *Drepanopterus lobatus* by Laurie (1899), however Lamsdell *et al*. (2009) suggested that *D. lobatus* represented a sexual dimorph of *D. bembycoides*. Restudy of these specimens suggests that sexual dimorphism is indeed the cause of the variation, as there is also a consistent difference in pretelson length: width ratios that correlates between the epimeral morphology and the two types of genital appendage (see *Sexual dimorphism in Stoermeropterus conicus*).

The epimera of segments 7-11 are angular even on those specimens with lobate epimera on their pretelson (e.g. NMS G.1897.32.88). These are comparatively small – the first being about the same length as the moveable spines on the mesosoma – and increase in size only slightly in each succeeding segment. By segment 11 the epimera have approximately doubled in size, while the epimera on the pretelson are double the size of those on segment 11. Waterston (1979) considered the epimera of *Parastylonurus ornatus* to be part of a hydrodynamic stabilization system hypothesized for several long-legged Stylonurina generally consisting of a lengthening of the pretelson or telson, however such a system would not seem to apply for *Stoermeropterus* as with the exception of the pretelson the epimera do not drastically project out from the curve of the body and the prosomal appendages are much shorter in relation to the animal's length. It is possible that the epimera served a function similar to that proposed by Waterston (1979) in *Hardieopterus macrophthalmus*, acting to facilitate the working of sediment during excavation and burial.

The telson is known from 22 specimens, ranging in total length from 20 mm to 54 mm (Table 11), with a minimum width of 4 mm and a maximum width of 10 mm at its base. The telson appears lanceolate in the majority of specimens (e.g. NMS G.1897.32.138; G.1897.32.164), however some specimens appear to possess a styliform telson (NMS G.1885.26.72.1; G.1897.32.89) and one seems to have a needle-shaped telson (NMS G.1897.32.12.9), but again these differences are taphonomic in origin. The overall telson shape was lanceolate, however at its base the telson has a ventral 'boss' that was probably the site of muscle attachments allowing for flexure of the telson and an associated ventral carina. A similar telson morphology is seen in *Onychopterella augusti* (GSSA C373a) which possesses both a ventral boss and carina, however the overall telson length is short in comparison to that of *Stoermeropterus*, which is almost equal in length to the postabdomen (e.g. NMS G.1885.26.72.13). Dorsally the telson lacked any form of keel or carina (NMS G.1897.32.138), making it almost identical to the telson of *Parahughmilleria hefteri* (SMF VIII 55; VIII 59; VIII 97), which also lacks a dorsal carina but clearly displays the ventral carina and 'boss' with and an overall telson length almost equal to the postabdomen. The *Parahughmilleria* specimens also apparently show a number of telson variants, and it seems likely that the different observed morphologies merely reflect differences in preservation; the telson morphologies noted in *Stoermeropterus* represent various planes of splitting through the three-dimensional telson structure; the lanceolate shape encompasses the whole telson, while the styliform shape preserves the ventral 'boss' and carina while the single needle shape preserves only the carina.

This telson type also appears similar to the isolated telson representing *Marsupipterus sculpturatus* Caster & Kjellesvig-Waering, 1955 (BGS GSM 89467) which was considered a ceratiocarid crustacean by Rolfe (1963). Braddy *et al*. (1995) suggested that the ‘pouch’ of *Marsupipterus* might be a ventral ‘boss’ where the cuticle has broken away to reveal the hollow attachment site within and returned it to Eurypterida, drawing attention to similarities with *Onychopterella augusti*. It is also possible that the telson has been interpreted upside down, and that the dorsal carina is actually ventral. This, combined with the elongate nature of the telson, could suggest its affinities lie closer to *Stoermeropterus*.

Opisthosomal cuticular sculpture. The opisthosomal ornament is visible in several specimens, but in only one (NMS G.1897.32.138) is the dorsal sculpture preserved. As on the carapace it consists of fine pustules forming a granular sculpture to the exclusion of scales. The pustules do not appear to show any openings for setae to attach and so probably did not serve a sensory function, however due to the very small nature of the structures any attachment points that were there may not have been preserved or would be very difficult to identify. The ventral ornament is again quite different from the dorsal, lacking pustules but possessing a seemingly random scattering of broad lunule scales (NMS G.1885.26.72.13; G.1897.32.12.9; G.1897.32.133; G.1897.32.136) that can be seen across the operculae and underside of the postabdominal segments. Again these appear to lack follicles, and are orientated so that the ‘tip’ of the scale points posteriorly, as is usual in eurypterids.

‘Terrace lines’ similar to those on the prosoma are also located on the ventral surface of the opisthosoma, with the majority localized on the operculae (NMS G.1885.26.72.17;

G.1897.32.131; G.1897.32.136; G.1897.32.139; G.1897.32.176) where they form a series of anastomising veins. These are best seen on NMS G.1885.26.72.17 and were suggested by Lamont (1955) to represent the position of the respiratory organs (Kiemenplatten) due to similarities with the supposed Kiemenplatten of *Slimonia acuminata* as reconstructed by Laurie (1893). The ornament on *Stoermeropterus conicus* consists of three furrows that originate at the lateral margin of the operculae and run inwards along the anterior of the plate, splitting into veins that curve down towards the plate posterior, each vein itself splitting once more and petering out just before the posterior margin where they are almost perpendicular to the main furrows. The main furrows themselves continue to the median join between the two opercular plates, where they deflect slightly towards the posterior before intersecting with the suture. Thus they cover almost all of the operculum's surface area. Although three-dimensionally preserved Kiemenplatten have been retrieved from macerated cuticle (Manning & Dunlop 1995, Filipiak & Zatoń 2010), several species are known to possess imperfectly preserved 'scars' that were thought to be due to the attachment of the Kiemenplatten on the body wall and transposed onto the underlying operculae by compaction during burial, however the observation of similar scars on modern *Limulus* operculae, which does not possess Kiemenplatten, makes this unlikely. *Limulus* does however have book-gills, and book-gills have been described from well-preserved *Onychopterella augusti* (Braddy *et al*. 1999), although these appear to be oriented so the gill lamellae are arranged vertically as in scorpions as opposed to the horizontal lamellae in xiphosurans. However, the book-lungs of scorpions are actually oriented horizontally at their point of attachment and then curve up into the vertical position (Kamenz & Prendini 2008) and it is probable that the lamellae in *O. augusti* had a similar structure, with the observed vertical orientation just representing the distal-most part of the book-gills. Therefore it is likely that these scars represent the attachment of the book-gills onto the actual operculae. Direct comparison with the structures in *Stoermeropterus* therefore can only be made with these scars. These have been described in detail from *Slimonia acuminata* by Moore (1941), *Eurypterus tetragonophthalmus* by Wills (1965) and *Tarsopterella scotica* (Woodward, 1872) by Waterston (1975), and in all cases the book-gill occupies less than half the surface area of the operculum. The scars are situated within a darkened, oval area that probably represents organic staining from the respiratory organs themselves, something that is absent from the *Stoermeropterus* specimens. The 'veins' of the book-gills also originate from the lateral edge of the operculum and run inwards, however the main veins are situated centrally on the segment as shown well in *Slimonia acuminata* (SM A16237a) and branch towards both the anterior and posterior of the plate (e.g. *Tarsopterella scotica*: NMS G.1891.92.103; *Eurypterus tetragonophthalmus*: MCZ 109062, 109063, NRM Ar 47265), giving them a more dendritic appearance. The number of main veins appears to be three in *Slimonia* but is more difficult to ascertain in *Eurypterus* and *Tarsopterella*, however in all three genera the main veins stem from a single, large channel rather than having individual originations.

The clear differences in structure between the opercular ornamentation of *Stoermeropterus conicus* and the form of the book-lung imprints shared between *Eurypterus*, *Slimonia* and *Tarsopterella* indicates that these are not in fact the remains of respiratory organs but the actual ornamentation of the operculae. An almost identical ornamentation is seen on the operculae of *Parahughmilleria hefteri* (SMF VIII 57:

30033) and *Parahughmilleria major* Størmer, 1973 (SMF VIII 148), from which gill areas have also been identified that are independent of the opercular ornamentation (Størmer 1973). *Stoermeropterus conicus* also has a distinct striate ornament on the ventral surface of the postabdominal segments (NMS G.1897.32.125: Pl. 5, fig. 2) that it shares with *Parahughmilleria hefteri* (SMF VIII 55) which consists of a series of four grooves angled postero-laterally. Postabdominal 'terrace lines' are also found on *Parastylonurus ornatus* where they are associated with the epimera (NMS G.1897.32.43), and although these are on the dorsal side of the postabdomen and therefore probably not homologous they are angled away from the body at an angle similar to those in *Stoermeropterus*. The 'terrace lines' in *Parastylonurus* have been interpreted as functioning in sensing water flow across the body (Waterston 1979) and the striations in *Stoermeropterus* may have had a similar function, although it is also possible that they acted in order to increase friction between the animal and the substrate surface (see *Prosomal cuticular sculpture*), or to aid in the movement of sediment when burying itself, as the striae angle so as to move particles backwards and away from the body and could facilitate a forward motion through the sediment surface.

The final three segments have a dentate (*sensu* Tollerton 1989) posterior margin in several specimens (NMS G.1897.32.89; G.1897.32.126; G.1897.32.184: Text-fig. 14a), however these are heavily dependent on preservation with the majority of specimens not exhibiting any sign of ornamentation on segments 10–12 and so it is not clear whether their apparent absence in the specimens with lobate pretelsonic epimera is significant or a taphonomic relic. Dentate posterior margins are present on all the metasomal segments of *Moselopterus ancylotelson* (SMF VIII 146, SPW 701-D, 703-D) and crenulate margins on every tergite are reported from *Vinetopterus struvei* and *V. martini* (Poschmann & Tetlie 2004). Ornamented tergite margins are rare outside of the moselopterids, however a posterior crenate ornamentation is also known from all segments of *Parastylonurus ornatus* (NMS G.1885.26.27.12) and the last two or three postabdominal segments of *Parahughmilleria hefteri* have dentate posterior margins (SMF VIII 42; VIII 59; VIII 98; PWL 2004/5042-LS; 2004/5044-LS).

DISCUSSION

SEXUAL DIMORPHISM IN *STOERMEROPTERUS CONICUS*

Sex determination. Woodward (1866-1878) first recognized sexual dimorphism in the Eurypterida through differences in the genital appendage and, although compared to two separate genera of extant xiphosurid erroneously believed by Woodward to be different genders of the same species, a long and a short morphology of genital appendage were accurately determined in *Slimonia* and *Erettopterus* Salter *in* Huxley & Salter, 1859. Holm (1898) identified the two genital appendage morphologies in *Eurypterus* and noted an increased complexity of the longer appendage, including the possession of internal horn organs, and the association with the short appendage of a hook-like clasping organ on the third prosomal appendage. The clasping organ is found only in the males of modern *Limulus* (although on the second prosomal appendage), and so Holm determined the short genital appendage to represent the male and the long appendage the female. Gaskell (1908), however, concluded the opposite based on comparison with the extant uropygid *Thelyphonus* Latreille, 1802 rather than xiphosurans which have operculae lacking sexual dimorphism (Pocock 1902) or scorpions which are differentiated by the males having genital papillae which project from underneath the operculum (Crucitti *et al*. 1998). It was Holm's interpretation that became adopted for wide use in the literature (e.g. Sarle 1903; Clarke & Ruedemann 1912) until Størmer (1934a) described *Mixopterus kiaeri* based on two remarkable specimens from Ringerike, Norway. These preserved a long genital appendage associated with a clasping organ on the second prosomal appendage, the same as male *Limulus*, and after comparison with other chelicerates (modern amblypygids in particular) Størmer adopted the view of Gaskell, that the long appendage (which he termed type A) is the male and the short appendage (type B) the female; the claspers described from the third prosomal appendage of *Eurypterus* were considered analogues to similar structures found on the third appendages of female amplypygids. This determination of the sexes was accepted by the majority of subsequent workers, including Prantl & Přibyl (1947), Kjellesvig-Waering (1951, 1958a,b, 1959, 1961, 1963), Lamont (1955), Caster & Kjellesvig-Waering (1956), Waterston (1960), and Størmer (1936a, 1955) himself, however Wills (1964) rejected Størmer's assignments, favouring Holm's original conclusions. The following year this view was further expounded (Wills 1965), dismissing any comparisons between aquatic Palaeozoic chelicerates and Recent terrestrial arachnids due to the great disparity in adaptation to their environments. Prior to this second paper however Kjellesvig-Waering (1964a) had adopted the convention of referring to the type A as female, while Waterston (1964) cites too great a controversy to attribute either appendage type to a sex. Ritchie (1968b) followed Waterston in mentioning the controversy but not assigning a sex to either morphology. Despite Kjellesvig-Waering (1966) reverting to a female type B and male type A and an attempted revival of Størmer's interpretations (Størmer & Kjellesvig-Waering 1969) only Størmer (1973), Andrews *et al*. (1974) and Hanken & Størmer (1975) continued to use Gaskel's assignments. Kjellesvig-Waering (1979a) re-adopted the classification of Holm and Wills, and this has been followed by Kues & Kietzke (1981), Selden (1981, 1984) and Braddy & Dunlop (1997). This last publication has set the standard for sex determination in recent years (e.g. Braddy 2000, 2001; Braddy *et al*. 2002; Tetlie *et al*. 2004; Tetlie 2006, 2007b; Poschmann & Franke 2006), however many authors simply refer to the different morphologies as type A and B without attempting to assign a gender (e.g. Tollerton 1989, Miller 2007, Lamsdell *et al*. 2009, 2010b). Recently however this assignment has been questioned again through comparison with modern arachnids, with Kamenz *et al*. (2009) interpreting the horn organs found on the type A appendage as hemispermatophores rather than spermathecae as espoused by Braddy & Dunlop (1997), resulting in a male type A appendage and female type B. This view is tentatively supported herein, however the different appendage morphologies shall be referred to simply as type A and type B without any inferred sex determination from hereon.

Primary sexual dimorphism. Following the considerations of Darwin (1871), primary sexually dimorphic traits are considered to be those directly concerned with and necessary for reproduction; in eurypterids this is limited to the genital appendage and operculum, and possibly the clasping organs on the second appendage (assuming an analogy with the similar structures in male *Limulus*). Only one specimen of *Stoermeropterus conicus* preserves all the podomeres of appendage II (NMS G.1897.32.133) and this does not possess any form of clasper as found in *Brachyopterus* *stubblefieldi* (BGS D 3124) and *Mixopterus kiaeri* (PMO H 2044), although as the specimen has a type B genital appendage this would not be considered unusual. No scimitar lobe is present on appendage III either (NMS G. 1885.26.72.14; G.1897.32.133), as is known from specimens of *Eurypterus tetragonophthalmus* (BMNH I3406/1; I3406/11) and *Stylonurella spinipes* (NMS G.1891.92.33; BGS GSM 87357) with type B appendages, however other well-known species (e.g. *Eurypterus remipes*) also lack scimitar lobes on this appendage, and it seems likely that the occurrence of claspers on appendage II of type A individuals and scimitar lobes on appendage III on type B individuals varies from species to species.

The genital appendage of *Stoermeropterus* is similar to other Eurypterida in having a long, type A morphology consisting of three segments and a shorter type B morphology consisting of two segments. There are exceptions to this rule, as pterygotid eurypterids have a type A genital appendage that is comparatively short, not extending much beyond the genital operculum, and composed of a single segment (Waterston 1964) that probably represents the fused three segments of the primitive condition. The pterygotid type B appendage is short and broad and also consists of a single segment, although there is a clear suture in some taxa where the two segments have fused (e.g. *Erettopterus bilobus*: KM 09.123.go, BGS GSM 87331). *Parahughmilleria hefteri* has been described as having three segments in its type B genital appendage (Størmer 1973), although the terminal two segments are small and poorly preserved and the available material needs reanalyzing to verify this. *Slimonia acuminata* also has a type B appendage apparently consisting of three segments (Waterston 1960), although the genital appendages of this taxon are highly unique compared to other eurypterids with the distal segments of the type B appendage potentially being eversible as part of an ovipositor. In *Stoermeropterus conicus* the type A appendage consists of three segments, the posterior segment of which has a bilobed termination, and extends as far as the posterior margin of the first Blattfüsse (Text-fig. 15a). Anterior to the appendage where it joins with median opercular plate are a pair of deltoid plates which have been interpreted as functioning as articulations for the lowering of the appendage during flexure of the operculum (Braddy & Dunlop 1997), while alongside it are paired, narrow spatulae with slightly rounded terminations. None of the available specimens preserve any evidence of horn organs, however as these are internal structures it is considered likely that *Stoermeropterus* did possess them. The type B appendage consists of two segments, the proximal segment being expanded and oval with a small, triangular terminal segment giving it an overall obpyriform shape (Text-fig. 15b). Deltoid plates are not apparent despite the area being well preserved, however when deltoid plates are present on the type B appendage (e.g. *Parahughmilleria hefteri*: SMF VIII 206; *Slimonia acuminata*: NMS G.1859.35.7) they are less defined than on the type A and so their absence in *Stoermeropterus* could still be preservational. On balance however it is thought likely that the deltoid plates are genuinely absent given their absence in *Eurypterus tetragonophthalmus* (LM 735), *Parastylonurus ornatus* (NMS G.1897.32.8), *Moselopterus ancylotelson* (SMF 26061) and *Rhenopterus diensti* (MfN 48/48a); their occurrence in *Parahughmilleria* and *Slimonia* appears to be a derived trait. Spatulae are also absent from the type B appendage, with the associated lateral structures being interpreted as the dorsal portion of the genital appendage which is usually covered by the operculum – the 'wing' of Wills (1965), 'flange' of Størmer (1974), 'lateral lamella' of Waterston (1979), which is the term used herein, and the 'dorsal surface of the proximal joint' according to Braddy & Dunlop (1997). The lateral lamellae closely resemble those of the type B appendage in *Moselopterus* (SMF VIII 184a; 26061) and *Vinetopterus* (SMF VIII 145), existing as a narrow rim around the genital appendage and being visible between the appendage and the ala of the operculum. Spatulae have been known to be present on both types of genital appendage (e.g. *Parahughmilleria hefteri*: SMF VIII 256, VIII 266), and Caster & Kjellesvig-Waering (1956) state that spatulae are probably usually present in eurypterids but concealed by the operculae, only being apparent in some species in which they have hypertrophied and so become visible. The spatulae however have an opercular origin as they are sutured onto the margin between the ala and the genital appendage, and so they are not homologous to the lateral lamellae.

Secondary sexual dimorphism. Secondary sexual dimorphism has been poorly studied in eurypterids, largely due to the small number of specimens available for any given species and the difficulty in identifying the different sexes when the genital appendage is absent or obscured. When studies of sexual dimorphism have been attempted they have naturally focused on the form and structure of the genital appendage, however variations in body proportions and ornamentation have also been noted. Wills (1965) suspected, but could not prove, that the body of the type B *Eurypterus tetragonophthalmus* was broader than that of type A individuals, as did Holm (1898) who thought that type B individuals were generally larger but again could not prove this by measurement, however Andrews *et al*. (1974) found no evidence for sexual dimorphism (but see comments by Waterston (1979, p. 257) on the limitations of this study). Størmer & Kjellesvig-Waering (1969) measured a limited number of *E. tetragonophthalmus* specimens that, despite the small sample size, suggested that the type B is wider than type

A. Tetlie *et al*. (2004) suggested that specimens of *Rhenopterus* with a type B appendage are broader than those that supposedly possess a type A, although a type A genital appendage has not been directly observed in the genus, and type B specimens in *Moselopterus* appear broader than type A individuals (Lamsdell pers. obs.). However, Waterston (1979) noted that type A specimens of *Parastylonurus ornatus* seem broader than those of type B. Waterston also reported two clusters of length: width ratios for *Hardieopterus macrophthalmus*, although none of these preserve genital appendages and so determination as to which type is broader is impossible.

Despite the lateral compression of the *Stoermeropterus conicus* specimens (see *Carapace and visual structures*) there is evidence for some degree of variation in the width of morphotype A (those with a type A genital appendage and/or angular pretelsonic epimera) specimens and those of morphotype B (type B genital appendage and/or lobate pretelsonic epimera); undistorted specimens of morphotype A (e.g. NMS G.1885.72.14) are narrower than those of morphotype B (e.g. NMS G.1897.32.133), having a carapace length: width ratio range that overlaps with the standard horseshoe-shaped carapace of Tollerton (1989), while morphotype B specimens are also overall larger. The most obvious dimorphic characteristic of *S. conicus* however is the form of the pretelson and its associated epimera, which are so distinct as to have resulted in the two dimorphs initially being described as separate species (Laurie 1892, 1899). The most obvious difference between the two is the epimera, with morphotype A possessing angular epimera while morphotype B bears lobate epimera, however the epimera are often broken off and so identifying the morphotypes using this criterion can be problematic. The other difference in pretelson morphology is, however, frequently preserved, and this is a difference in length: width ratio; morphotype A individuals have an elongated pretelson with a length: width ratio range of 1–1.5, while morphotype B possesses a pretelson with a length: width ratio between 0.6 and 0.7 (Text-fig. 16). The elongate telson morphology is found exclusively with angular epimera, as is the lobate epimera with the 'short' type, and type A genital appendages are found exclusively associated with the elongate pretelson morphology (NMS G.1885.26.72.1; G.1885.26.72.13; G.1897.32.12.9). Only one specimen preserving a type B appendage also shows the pretelson (NMS G.1897.32.133), which is of the short morphology, however no lobate epimera or short pretelson are found associated with type A genital appendages. This, alongside the overall broader nature of the specimens, permits the differences in pretelson morphology to be assigned to sexual dimorphism with some certainty.

As well as correlation with other fossil species, comparison with extant chelicerates may be of use in identifying sexually dimorphic traits and in assigning the different morphotypes to a specific gender. Modern *Limulus* does not generally exhibit secondary sexual dimorphism, although females are generally larger than males (Botton & Loveland 1992), however extant scorpions often show a number of distinct sexually dimorphic traits. Females are often (but not always) larger than the males (Koch 1977), while the males themselves can be more gracile with elongated metasomal segments, particularly the pretelson (Kraepelin 1907). However the most obvious dimorphic trait of *Stoermeropterus*, the form of the epimera, currently appears to be unique among Chelicerata although this may change as more eurypterids are described.

There is also some indication that the telson in *S. conicus* is broader and somewhat shorter in the morphotype B individuals, yet the propensity for the telson to break off from about halfway along its length makes comparison difficult. Specimens of *Ciurcopterus ventricosus* (Kjellesvig-Waering, 1948) do however appear to show a difference in length: width ratio which Tetlie & Briggs (2009) suggested could be due to sexual dimorphism, among other things, while variation in the length of the telson of the synziphosurine *Willwerathia laticeps* was considered a potentially sexually dimorphic trait (Anderson *et al*. 1998), although intraspecific variation in telson length of extant *Limulus* is conspicuous (as Anderson *et al*. noted) and telson width is known to change through eurypterid ontogeny (Poschmann & Tetlie 2006). Finally, the granulation of the chitinous integuments has been reported to vary slightly between the two sexes in eurypterids, with Wills (1965) recording that individuals with type A genital appendages have a more conspicuous and continuous ornament of granules on the triangular area between the front of the prosoma and the lateral eyes than do those with type B appendages, and that the genital appendage of type A is more strongly ornamented than type B. Unfortunately, the integument of *Stoermeropterus conicus* is not well enough known to permit comparison. In modern scorpions the cuticular ornamentation also varies between the sexes, with males having a coarser granulation (Polis & Sissom 1990), similar to type A eurypterids. Although some aspects of secondary sexual dimorphism obviously varied somewhat between eurypterid species, as in modern scorpions, comparison with the secondary sexual dimorphism of *Limulus* and extant scorpions supports the interpretation of eurypterids with a type B genital appendage as being female and those with a type A appendage as male.

Gender frequency within populations. As noted by Størmer & Kjellesvig-Waering (1969) the ratio of males to females is characteristic for several chelicerate groups.

Within scorpions the sex ratio of litters at hatching is 1:1 for non-parthenogenetic species, a ratio that is widespread among arachnids (Savory 1977), however high rates of male mortality result in adult populations with average male: female ratios between 1:2 and 1:3 (Polis 1990). Scorpions however are generally solitary, interacting with other members of their species only at birth or during courtship (or during cannibalism), with social or sub-social occurrences mentioned specifically due to their infrequency (Polis & Lourenço 1986; Shivashankar 1994). Eurypterids have been hypothesized to congregate during mass-moult-mate events through comparison with horseshoe crabs (Braddy 2001) and are often preserved en masse as both accumulations of exuviae and as sites of mass mortality (something never encountered for Palaeozoic scorpions), and so may be closer to *Limulus* in terms of sex ratios. Studies of *Limulus* have shown that, away from breeding grounds, the average male: female ratio is 1:1 (Hata & Berkson 2003), although this could partly be due to the preferential capture of adult females by commercial fishers (Botton & Ropes 1987), while at the breeding grounds the sex ratio is invariably dominated by males, with a male: female average of 3:1 (Rudloe 1980; Shuster & Botton 1985).

Data are limited for eurypterids due to the small sample sizes and propensity for individuals to fail to preserve the genitalia. Størmer & Kjellesvig-Waering (1969) presented a brief overview of sex ratios in eurypterids, suggesting that type A individuals were more common in *Eurypterus* while type B individuals were predominant in *Parahughmilleria* Kjellesvig-Waering, 1961, *Hughmilleria socialis* Sarle, 1903 and *Herefordopterus banksii*, however half of these reported ratios are erroneous. Tetlie *et al.* (2008) showed the type A appendages are more common in *Eurypterus* from the Fiddlers Green Formation, New York and Williamsville Formation, Ontario, with a type A: type B ratio of 6.4:1 and 5.3:1 respectively and a ratio of 1:1.25 is retrieved from the nine genital-bearing specimens of *Herefordopterus banksii* figured by Kjellesvig-Waering (1951) and Tetlie (2006), while among the specimens of *Parahughmilleria* described by Størmer (1973) (comprising both *P. hefteri* and *P. major* which still, admittedly, is a small sample size consisting of only fourteen specimens) the type A: type B ratio is 1.3:1 and in *Hughmilleria socialis* Sarle (1903) reported that the type A and type B appendages were approximately equally represented, the type A: type B ratio from his thirteen published genital appendages being 1.1:1. Due to the small number of specimens involved (bar *Eurypterus*, where the ratios are derived from 37 and 51 specimens respectively) these ratios are only extremely rough estimates but, as most of weighting towards one appendage or the other is due to the occurrence of only one or two extra specimens, the frequency of the sexes tend to be more or less equal. Of the eurypterid species that are known by a number of specimens, but where not considered by Størmer & Kjellesvig-Waering (1969), *Nanahughmilleria norvegica* shows a clear preponderance for type A appendages, with fourteen specimens preserving genital structures (Størmer 1934a) resulting in a type A: type B ratio of 1.8:1, while *Parastylonurus ornatus* exhibits a type A: type B ratio of 2:1 from six preserved genital appendages with a ratio of 1.75:1 when all eleven of Waterston's (1979) morphotype A and B individuals are included. Two species of *Adelophthalmus* Jordan in Jordan & von Mayer, 1854 are preserved in numbers but with very few genitalia; *A. sievertsi* has a type A: type B ratio of 3:1 from four specimens (Poschmann 2006) and *A. luceroensis* Kues & Kietzke, 1981 has a ratio of 6:1 from seven specimens, however in both cases the type B appendage is known only from a single specimen and the high disparity in occurrence of the sexes is likely to be an artefact of small sample size. In *Stoermeropterus conicus* seven genital appendages are known and give a type A: type B ratio of 1:1.3, however when all 25 specimens assignable to one of the two morphotypes are considered the ratio essentially inverts to 1.5:1, highlighting the danger on relying on very small sample sizes, especially considering that the type B appendage is more robust and may be more likely to survive the taphonomic process.

Many eurypterid species are known only from isolated or very few specimens, however when these are found with genitalia preserved the appendage is commonly of type A – e.g. *Hughmilleria* sp. (Braddy 2000), *Rhinocarcinosoma dosonensis* (Braddy *et al*. 2002), *Dolichopterus jewetti* (Caster & Kjellesvig-Waering 1956), *Carcinosoma newlini* (Kjellesvig-Waering 1958b), *Drepanopterus abonensis* (Lamsdell *et al*. 2009), *Lanarkopterus dolichoschelus* Størmer, 1936b (Ritchie 1968b), *Mixopterus simonsoni* Schmidt, 1904, *Mixopterus kiaeri* (Størmer 1934a), *Strobilopterus princetonii* (Tetlie 2007b), *Ciurcopterus ventricosus* (Tetlie & Briggs 2009), *Brachyopterella ritchiei* (Waterston 1979), *Adelophthalmus mazonensis* and *Adelophthalmus moyseyi* (Wills 1964), and *Brachyopterus stubblefieldi* (Størmer 1951), as well as *Megalograptus ohioensis* (Caster & Kjellesvig-Waering 1964) and *Jaekelopterus rhenaniae* (Størmer 1936a; Poschmann & Tetlie 2006) which do each have a single type B appendage preserved but are known from multiple type A appendages – with only comparatively few possessing a type B appendage – e.g. *Grossopterus overathi* (Dunlop *et al*. 2002), *Leiopterella tetliei* (Lamsdell *et al*. 2010b), *Rhenopterus diensti* (Størmer 1936a; Poschmann & Franke 2006), *Orcanopterus manitoulinensis* (Stott *et al*. 2005), and *Stylonurella spinipes* (Waterston 1979) – indicating that, overall, type A genital appendages are more common in the fossil record. Assuming that eurypterid populations followed similar gender ratio dynamics as in modern *Limulus*, these results support the observed secondary sexually dimorphic characters in suggesting a male assignment to the type A appendage and a female assignment to the type B, although further work on the structure of the genitalia themselves will be needed to resolve this issue.

COMPARISON WITH OTHER SPECIES ASSIGNED TO *STOERMEROPTERUS*

Besides the specimens dealt with herein, two other currently known species can be assigned to *Stoermeropterus*. *S. latus*, from the late Wenlock of Ringerike, Norway, is known from 26 disarticulate specimens (Størmer 1934a), while *S. nodosus,* from the early Pridoli of Virginia, USA, is represented by its holotype and counterpart and potentially an isolated genital appendage and operculum (Kjellesvig-Waering & Leutze 1966). The known morphology of both species fits well with that of *S. conicus* in regard to the carapace shape, ventral telson boss and carina, moveable mesosomal spines, and type A genital appendage with spatulae. Although unknown from *S. nodosus* the morphology of prosomal appendage VI and the epistomal sutures of *S. latus* correspond well with those of *S. conicus*.

Stoermeropterus latus (Text-fig. 17a,b) in particular strongly resembles *S. conicus*, especially in regard to the features of the carapace (PMO H1839; H1874) which preserve a clear waist and large lunate lateral eyes located centrilaterally. The median ocelli are also preserved and situated between the lateral eyes in a position similar to possible ocellar structures found in *S. conicus* (NMS G.1897.32.134). Only prosomal appendage VI is known from *S. latus* and this is comparatively short and robust (PMO H2194), also possessing a podomere 7a (PMO H1874), while only a single genital operculum with the proximal portion of a type A appendage can be recognized from the available material (PMO H1753). The genital appendage appears relatively short, consists of at least two segments, and is flanked by rounded spatulae. The mesosoma clearly displays moveable spines (PMO H1753), while the metasoma shows some indication of angular epimera (PMO H1713; H1875) with at least segments 11 and 12 having a dentate posterior margin (PMO H1715; H1875; H1920). Four specimens of *S. latus* preserve the pretelson (PMO H1713; H1734; H1875; H1920), all of which resemble the pretelson associated with the type A genital appendage in *S. conicus*, being elongated so they are longer than broad (L:W >1) and having large angular epimera. Despite there being no indication of a second pretelson morphology in the Ringerike material the small sample size and absence of any type B appendages means that it is equally likely that only one sex is present, a possibility reinforced by the far greater occurrence of type A specimens than type B in the Pentland Hills. The telson of *S. latus* is all but identical to *S. conicus*, with its ventral boss (PMO H1713) and carina (PMO H1734; H1920) and smooth dorsal surface (PMO H1875). *S. latus* differs from *S. conicus* principally in the nature of its cuticular ornamentation; although the ventral side is not well known the 'terrace line' ornament is not present on a specimen which has been prepared to show the epistomal sutures (PMO H1839) nor on the genital operculum (PMO H1753) or Blattfüsse (PMO H1650). Furthermore, the dorsal sculpture includes angular and semi-lunate scales (PMO H1808) in addition to the fine granulation seen in *S. conicus*. Another notable difference in *S. latus* is that the metasoma appears to undergo a much more gradual narrowing than in *S. conicus*, giving the animal a more squat appearance (PMO H1713). The Ringerike *Stoermeropterus* probably represent exuviae, as indicated by the fragmentary nature of the specimens and the occurrence of one of the carapaces articulated with the first tergite to the exclusion of the rest of the opisthosoma (Tetlie *et al*. 2008), and therefore the broader postabdomen could theoretically be due to telescoping of the metasomal segments, however it is repeated in several specimens and the relative length of the metasoma compared to the total length of the animal is the same as in *S. conicus*, and so it is considered to be a genuine feature of the species.

In comparison *Stoermeropterus nodosus* (Text-fig. 17c,d), while clearly belonging to the genus, shows marked difference from *S. conicus*. The lateral eyes, while still lunate, are comparatively smaller and located more anteriorly on the carapace in the most forward possible centrimesial position. Again, the median ocelli are located between the lateral eyes and consist of two separate pits on the carapace surface. The carapace anterior margin is somewhat flatter than in *S. conicus*, and the lateral margins appear to lack a clear waist (FMNH PE6214). The metastoma (FMNH PE6215), which is unknown from *S. latus*, is identical to that of *S. conicus.* An isolated type A genital appendage and operculum previously assigned to *Parahughmilleria bellistriata* (FMNH PE6212) strongly resembles the type A appendage of *S. conicus* in having a short, three-segmented appendage with a bilobed termination and spatulae, and so is herein considered to be assignable to *S. nodosus.* The spatulae are similar to those of *S. latus,* being rounded and marginally broader distally. The mesosoma preserves some indication of moveable spines, while the metasoma bears short, rounded epimera on every segment culminating in large, lobate epimera on the pretelson. The pretelson itself is not elongate and it seems likely that the holotype represents a type B individual; if this is the case it is unclear whether the rounded epimera on segments 7-11 would be consistent between the two sexes. The posterior margins of segments 10-12 are unornamented, potentially reinforcing the possibility that the dentate margins are a sexually dimorphic trait, however the difference could also be preservational. Segments 7 and 8 contract markedly in width so the postabdomen more closely resembles that of *S. conicus* than *S. latus*, while the ventral telson boss is comparatively shorter than either species. The dorsal cuticular ornamentation, mainly consisting of a faint granular sculpture, is dominated by a row of node-like scales which give the species its name located along the posterior of the carapace and each mesosomal segment. It is unclear if these continued onto the metasoma as this is known only from the ventral surface. Angular and semi-lunate scales are found on the isolated genital operculum, which lacks any 'terrace line' ornamentation.

Stoermeropterus conicus (Text-figs. 18–19) shares characteristics of both *S. latus* and *S. nodosus,* somewhat fitting given its older stratigraphical (and hence presumably ancestral) position. Although both non-Scottish species differ from *S. conicus, S. nodosus* appears the most distinct as befits its occurrence in North America and as the youngest occurrence of the genus.

PHYLOGENETIC POSITION OF *STOERMEROPTERUS*

Stoermeropterus conicus represents one of the best-preserved eurypterid species and, along with *Parastylonurus ornatus* from the same locality, is the earliest eurypterid for which the external morphology is almost comprehensively known. Given the age and completeness of *S. conicus* the species is conceivably of considerable importance for studies on eurypterid phylogeny, however not being particularly well known and lacking a modern description it has been omitted from most recent studies (e.g. Tetlie 2007a; Tetlie & Cuggy 2007). When it has been included only those specimens published by

Laurie (1892, 1899) as *Drepanopterus bembycoides* were used to derive the morphological detail, the synonymy of the various Pentland species being at the time only conjectural. These analyses placed *S. conicus* at the base of a moselopteroid clade also including the genera *Moselopterus* and *Vinetopterus* (Lamsdell *et al*. 2010a,b), which itself resolved at the base of the Eurypterina when *Vinetopterus* and *S. conicus* were incorporated into the analysis of basal Eurypterina by Tetlie & Cuggy (Lamsdell *et al*. 2010a). Due to the potential for *Stoermeropterus* to yield important information about a poorly understood period of eurypterid evolution, namely the radiation of forms during the early Silurian and the evolution of swimming in the Eurypterina, it is important that it should be included in future analyses of eurypterid and chelicerate phylogeny. In pursuit of this a limited analysis is presented utilizing the new data for the three *Stoermeropterus* species in order to preliminarily test whether the topology of the tree presented by Tetlie (2007a) has been affected by the reinterpretation of these taxa.

Methodology. For the analysis a matrix of 43 characters for 24 taxa was compiled (Table 12) using novel characters (17, 22, 32, 35-37, 39, 41, 43), characters derived directly from previous analyses (5: Dunlop & Selden 1997; 2, 11, 13, 19-21, 24, 29: Tetlie & Cuggy 2007; 1, 7, 12, 16, 25: Lamsdell *et al*. 2010a), or characters modified from previous analyses (34: Dunlop & Selden 1997; 3-4, 6, 10, 14-15, 18, 23, 28, 38, 40: Tetlie & Cuggy 2007; 30-31, 33: Tetlie & Poschmann 2008; 8-9, 26-27, 42: Lamsdell *et al*. 2010a) (Table 13). All three species of *Stoermeropterus* were included in the analysis, along with the two known species of *Vinetopterus* and two species of *Moselopterus* in order to test the intra-relationships of the Moselopteroidea as defined by Lamsdell *et al*. (2010a). A third species of *Moselopterus*, *M. lancmani* (Delle, 1937), was excluded from the analysis due to it being based on undiagnostic material and the inability to trace the location of the holotype. The synziphosurine *Weinbergina opitzi* Richter & Richter, 1929 was specified as the outgroup following Lamsdell *et al*. (2010a,b) as it supposedly represents the most plesiomorphic known xiphosuran (Anderson & Selden 1997) which are sister group to Eurypterida (Selden & Dunlop 1998), however this is done with reservations given the unclear nature of synziphosurine intra-relationships and their uncertain position within the chelicerate phylogeny (see *Excursus on segment articulations in arthropods*); it is feasible that a chasmataspidid or one of the other 'arachnomorph' arthropods (*sensu* Cotton & Braddy 2004) would be a more suitable outgroup, and although a more comprehensive analysis of chelicerate phylogeny is required before this can be properly assessed. The chasmataspidids *Loganamaraspis dunlopi*, *Diploaspis casteri* and *Octoberaspis ushakovi* are included due to their potential to help inform on the plesiomorphic character states in eurypterids and to test whether chasmataspidids fall outside Eurypterida or are a clade within Eurypterina (as suggested by Shultz (2007)).

Several other eurypterid groups are also included in the analysis, each represented by multiple exemplars as they more accurately represent the character states and transitions of the group than a single exemplar, such as a single species or a composite taxon, would (see Brusatte 2010). Three stylonurines (*Brachyopterus stubblefieldi*, *Rhenopterus diensti* and *Parastylonurus ornatus*) were included in order to help polarize the characters that typify the transition towards swimming among the basal Eurypterina. The other major group of basal Eurypterina as defined by Tetlie & Cuggy (2007), Eurypteroidea, is represented by *Eurypterus remipes* De Kay, 1825 and *Erieopterus microphthalmus* (Hall,

1859) for Eurypteridae and *Dolichopterus macrocheirus* along with *Strobilopterus princetonii* for Dolichopteridae. Two species of *Onychopterella*, *O. augusti* and *O. kokomoensis*, were included as the genus appears to occupy a position in eurypterid evolution where appendage VI has begun to expand into a paddle (indeed, Tetlie & Cuggy (2007) resolved the genus as paraphyletic based on the development of the sixth appendage, suggesting that the paddle might have developed *within* the genus as currently defined). Unfortunately a third species, *O.* (?) *pumilis* (Savage, 1916), was not included in the analysis due to the unavailability of the holotype for study and the insufficient quality of the published figure, however it has been suggested by Kjellesvig-Waering in Plotnick (1999) to be a *Drepanopterus*, and is therefore another species in dire need of redescription. *Tylopterella boylei* was included as several characters (namely the shape of the carapace, position of the lateral eyes and preabdominal/postabdominal division between the sixth and seventh segments) suggest a relationship with the basal Eurypterina and *Onychopterella* in particular. *'T'. menneri* (Novojilov, 1959), from the early Devonian of Siberia, was however excluded from the analysis. Originally described as a *Stylonurus* (clearly erroneous given the paddle-like morphology of appendage VI), it was transferred to *Tylopterella* by Novojilov (1962) based on its possession of paired tubercles located centrally on the dorsal tergites, a characteristic only doubtfully present in the *'T'. menneri* holotype. Restudy of the available figures suggests that the paddles of *'T'. menneri* have an anterior podomere 7a and that the opisthosoma is divided into a three-segmented fused buckler and a nine-segmented postabdomen (Lamsdell pers. obs.) indicating that the specimen in fact represents a new genus of chasmataspidid, a fact to which D. Marshall has been made aware and is now working on a full description of the taxon. *Megalograptus ohioensis* was also included due to its uncertain position within Eurypterida, being hypothesized to be both allied with the Mixopteroidea (Caster & Kjellesvig-Waering 1964) and nestled among the basal Eurypterina (Tetlie & Cuggy 2007), in an attempt to ascertain its relationships phylogenetically. To this end *Mixopterus kiaeri* was also incorporated into the analysis. Finally, *Hughmilleria socialis* was included to represent the remainder of the derived Eurypterina.

The analysis was performed using TNT (Goloboff *et al*. 2008; made available with the sponsorship of the Willi Hennig Society) employing implicit enumeration with all characters unordered and of equal weight. Jackknife (Farris *et al*. 1996) and Bremer support (Bremer 1994) values were calculated in TNT and the Consistency, Retention and Rescaled Consistency Indices were calculated in Mesquite 2.73 (Maddison & Maddison 2010). Nonparametric bootstrapping is often difficult with morphological data due to the limited size of the dataset (Zander 2003) and so was not performed for this analysis. Jackknifing was performed using simple addition sequence and tree bisection-reconnection (TBR) branch swapping, with 1,000 repetitions and 30% character deletion rather than the 20% (e.g. Lamsdell *et al*. 2010a,b) or 10% (e.g. Tetlie & Cuggy 2007; Tetlie & Poschmann 2008) deletion used in previous analyses. Another departure from recent analyses is that the Relative Completeness Index (Benton & Storrs 1994), Stratigraphic Consistency Index (Huelsenbeck 1994), Gap Excess Ratio (Wills 1999) and Modified Gap Excess Ratio (Wills *et al*. 2008) were not calculated for the resulting consensus tree, the reasoning being that the analysis contains representatives of several diverse clades that, without including all their constituent taxa (something beyond the scope of the current study), will only serve to negatively impact these indices and so produce skewed results.

The matrix has been reposited in the online MorphoBank database (O'Leary & Kaufman 2007) under the project code p542 and can be accessed from http://morphobank.org/permalink/?P542.

Results. Analyzing the matrix as detailed above yielded a single most parsimonious tree with a tree length of 105, an ensemble Consistency Index of 0.514, Retention Index of 0.726, and Rescaled Consistency Index of 0.373 (Text-fig. 20a). Of primary importance the three species herein assigned to *Stoermeropterus* are retrieved as one of the most strongly supported monophyletic clades (based on their possession of an epistoma, a deeply notched metastoma anterior, moveable preabdominal spines, an undifferentiated postabdomen and a bulbous expansion at the base of the telson) with *S. conicus* at its base (due to it having angular spatulae) as befitting its stratigraphic position, although the relationships of the species are less well supported. *S. latus* and *S. nodosus* are united by their possession of rounded genital spatulae, while the various characteristics that would seem to unite *S. conicus* and *S. latus* (the position of the lateral eyes and the carapace 'waist') are actually plesiomorphic. The analysis also recovers a monophyletic Moselopteridae (united by a ridged podomere cuticular sculpture, having spatulae on the type A genital appendage, and dentate posterior margins of segments 10-12) again with strong support, with *Stoermeropterus* as sister-group to a clade consisting of *Vinetopterus* and *Moselopterus* (sharing dentate posterior margins of segments 7-9), both of which are also shown to be monophyletic. The *Moselopterus* clade has the best support in the analysis, which is unsurprising given that the species are probably synonyms and are coded identically in the matrix bar for three characters, which are uncertain in *M. elongatus*. The Moselopteridae are resolved as the basalmost family of the Eurypterina (due to a pediform appendage VI, oval VI-7a, and lacking a recessed VI-8/9 joint), which is itself monophyletic (although with remarkably low support, however this is likely to be due to low sampling of the Stylonurina), with a monophyletic Stylonurina as sister-group to the suborder and chasmataspidids as sister-group to Eurypterida (again, however, with low support). The next clade within Eurypterina consists of *Onychopterella* and *Tylopterella* which comprise the new family Onychopterellidae (see *Systematic Palaeontology*), defined by having a preabdomen and postabdomen of six segments each and separated from the other Eurypterina by having a triangular coxal ear, VI-5 longer than VI-4, an unmodified distal margin to VI-6, and a spinose VI-9. *Onychopterella* is here resolved as monophyletic contra to the results of Tetlie & Cuggy (2007), and the jackknife support for this is among the higher in the analysis. Removing *Tylopterella* did not render *Onychopterella* paraphyletic, and so its monophyly is accepted here (paraphyly in *Onychopterella* would of course also render Onychopterellidae paraphyletic and invalidate it as a family). The results deviate from Tetlie & Cuggy (2007) in another major way; resolving Eurypteroidea as paraphyletic. *Dolichopterus* and *Strobilopterus* (representative of Dolichopteridae) here form the monophyletic sister-group to Eurypteridae and the remaining derived Eurypterina, separated based on having a narrow VI-7a, a long VI-9 and possessing large postabdominal epimera. Eurypteridae (*Erieopterus* Kjellesvig-Waering, 1958a and *Eurypterus* in this analysis) is also monophyletic, and separated from the remaining Eurypterina based on having a centralized lateral eye position and a genital operculum consisting of three visible segments. Interestingly, *Megalograptus* resolves as sister-taxon to *Mixopterus* due to its trilobation, supporting the views of Caster & Kjellesvig-Waering (1964) over Tetlie & Cuggy (2007). A more comprehensive analysis including the remaining mixopteroids and further members of Eurypteridae is ideally needed to confirm this placement though, as its Ordovician age and several seemingly primitive character states strongly argue against *Megalograptus* being a derived member of Mixopteroidea. It seems likely that *Megalograptus* may in fact belong at the base of the mixopteroids, or intermediate between Eurypteridae and the derived Eurypterina, and it is unlikely that its brief treatment here will be the final word on this enigmatic taxon.

Of further interest is the position of the chasmataspidids. In in this analysis they form the monophyletic sister-group to Eurypterida, similar to the scenario envisioned by Tetlied & Braddy (2004). *Chasmataspis laurencii* was however not included in the analysis, and its greater age and distinctly different morphology to the diploaspids means that although diploaspid monophyly can be supported the concept of Chasmataspidida as a monophyletic group is still uncertain.

BIOGEOGRAPHICAL AND STRATIGRAPHICAL IMPLICATIONS

The confirmation of *Stoermeropterus conicus* as a member of the Moselopteridae places the earliest known record of the family in the Llandovery (early Silurian) (Text-fig. 20b), an important discovery as this apparently basal family was previously only known from the late Pragian and Emsian of the early Devonian (Størmer 1974; Poschmann & Tetlie 2004). The temporal gap between *S. conicus* and the Devonian genera is breached somewhat by *S. latus* and *S. nodosus*, which are known from the Wenlock and late Ludlow to early Pridoli respectively (Størmer 1934a; Kjellesvig-

Waering & Leutze 1966). The existence of late Ordovician moselopterids is heavily implied by the occurrence of *Brachyopterus stubblefieldi* from the Sandbian of Wales (Størmer 1951) and *Onychopterella augusti* from the Hirnantian-Rhuddanian boundary (see Vandenbroucke *et al*. 2009) of South Africa (Braddy *et al*. 1995) which phylogenetically bracket the Moselopteridae, indicating that the stylonurine and eurypterine lineages split during Darriwilian at the very latest and that, even allowing for another more basal, currently undiscovered eurypterine clade, moselopterids must have diverged by the end of the Hirnantian. Furthermore, if the position of *Megalograptus* (from the Katian: Caster & Kjellesvig-Waering 1964) retrieved here is accepted then the Dolichopteridae and Eurypteridae clades, as well as some of the more derived eurypterine families, should also diverge by the Katian. Currently, the earliest known unequivocal dolichopterid is *Dolichopterus gotlandicus* Kjellesvig-Waering, 1979b from the early Wenlock of Gotland, Sweden, while the earliest Eurypteridae are jointly *Eurypterus serratus* Kjellesvig-Waering, 1979b from the same formation and *Erieopterus* (?) *phillipsensis* Copeland, 1971 (potentially a *Eurypterus* according to Tetlie & Cuggy 2007) from the early Wenlock of Cornwallis Island, Canada. The first occurrence of Dolichopteridae is a matter of some debate however, as *Ruedemannipterus stylonuroides* (Clarke & Ruedemann 1912) from the Shawangunk Formation, New York, may be older (located at the Llandovery-Wenlock boundary) however uncertainty as to the age of the exact age of the Shawangunk Formation make this uncertain (Epstein 1993), and '*Eurypterus*' *minor* Laurie, 1899 known from the same formation as *Stoermeropterus conicus* (hence being upper Llandovery in age) is probably a basal dolichopterid (Tetlie & Cuggy 2007). Even with these occurrences, there is still a 20 MY discrepancy between the first occurrences of the eurypteroids (*sensu* Tetlie & Cuggy 2007) and their inferred origination based on the phylogenetic position of *Megalograptus*. Other derived eurypterid clades are also known to have originated by the Ordovician; *Orcanopterus manitoulinensis*, from Manitoulin Island, Canada, is the basalmost member of an unnamed clade including *Waeringopterus* and *Grossopterus* (Tetlie & Poschmann 2008), while *Eysyslopterus patteni*, the basalmost member of the Adelophthalmoidea, may be present in biotas from Manitoba, Canada (MM I-4064A; Young *et al*. 2007), both from the Hirnantian-Rhudanian boundary, and so even invoking a more basal position for *Megalograptus* it seems that the fossil record for the early evolution of the Eurypterina is incredibly patchy.

Eurypterid biogeography has been analyzed by Tetlie (2007a), who investigated their known occurrences based on a phylogenetic hypothesis formed from a composite of published analyses and unpublished data. Eurypterids are predominantly found around the palaeocontinents of Laurentia, Avalonia and Baltica during the Silurian, when all three were in close proximity to one another, with their range expanding into the Rheno-Hercynian Terrane when it was sutured onto Laurussia during the Devonian, while the formation of Pangaea during the Carboniferous and Permian allowed the surviving eurypterid groups to gain a more global distribution. The palaeocontinent of Siberia was also close to Laurentia and Baltica during the Silurian and Devonian, and the reports of eurypterid faunas from the region (e.g. Novojilov 1959) indicate that their sparse record from the area may be due to lack of sampling rather than a real biogeographic signal. As noted by Tetlie (2007a), placing the origin of Eurypterida is difficult due to the paucity of its Ordovician record, however it is clear that its origins lie within the mid Ordovician at the latest. The oldest stylonurine is known from Avalonia (Størmer 1951), however this is a probable exuviae preserved in a graptolite shale and so its provenance cannot be known with certainty. Of the remaining Ordovician eurypterid occurrences, only one is not from Laurentia; *Onychopterella augusti*, from South Africa which at the time was part of Gondwana. Gondwanan eurypterids are rare, and usually only consist of Pterygotoidea, Adelophthalmoidea or Carcinosomatidae, which are thought to have been able to disperse across ocean bodies. The occurrence of *O. augusti*, which does not have an overly broad sixth prosomal appendage and was therefore not likely to be a good swimmer, is something of a puzzle. Avalonia and Laurentia were last within easy reach of Gondwana for a population of non-oceanic eurypterids during the early Cambrian, however it is exceedingly unlikely that their origins predate the Ordovician and so some other method must have presented itself for the ancestors of the *O. augusti* population to reach Gondwana. One possibility is that periods of sea level lowstand during the Late Ordovician allowed the eurypterids to cross to Gondwana as they would traverse shallow seas. Two potential lowstand events present themselves, the first during the Sandbian and the second during the Hirnantian itself (Saltzman & Young 2005), both giving the South African population plenty of time to establish itself, and this hypothesis of dispersal during a period of lowstand seems more likely than invoking a non-existent Cambrian record for eurypterids.

The phylogenetic position of *Stoermeropterus conicus*, combined with its Llandovery age, lends further support to a Laurentian origination for the Order. While there may have been opportunities for limited dispersal between palaeocontinents prior to the Silurian the morphology of basal forms (broad bodies and short limbs lacking any form of swimming paddle) makes it appear unlikely that they would have spread far and the great concentration of Laurentian occurrences during the Ordovician and early Silurian make it the more likely point of origin.

PLESIOMORPHIC STATES WITHIN THE EURYPTERIDA

The recognition and redescription of *Stoermeropterus conicus* as a basal member of the Eurypterina, combined with a better understanding of the evolution of the Suborder (Tetlie & Cuggy 2007) and a well-resolved stylonurine phylogeny (Lamsdell *et al*. 2010a), permits the exploration of evolutionary trends within Eurypterida and is crucial to the identification of plesiomorphic characters and the resolution of the eurypterid ground pattern. Key to this is the identification of the eurypterid outgroup and the development of the swimming paddle in the Eurypterina, along with shared traits of the basalmost families in both suborders.

The eurypterid outgroup. The relationship of eurypterids to the other merostome groups is something that has been the subject of much debate over the years of research. Laurie (1893), in the first attempt to explore the relationships of the various eurypterid groups, considered them to have evolved from a trilobite ancestor – presumably a view derived from the conclusions of Walcott (1881) – however workers soon began to search for additional forms to bridge the gap between the distinctive trilobite morphology of a variable number of trilobate segments, divided into a cephalon, thorax and pygidium, and the conservative eurypterid morphology of a prosoma, twelve segmented opisthosoma and telson. The description of a number of Ordovician eurypterids, predominantly by Clarke & Ruedemann (1912) and Ruedemann (1916, 1926, 1934b, 1942) (incidentally all of which have since been shown to be pseudofossils by Tollerton (2004), who reduced the number of valid Ordovician species by 75%), meant that the search for the last common eurypterid ancestor was focused on the Cambrian, leading to a degree of ‘merostome spotting’ (an almost identical phenomenon and rationale to the ‘crustacean spotting’ of Edgecombe (2010)) that has only recently begun to be abandoned. Clarke & Ruedemann (1912) found their proto-eurypterid in *Strabops thacheri* Beecher, 1901, while Raymond (1920) considered *Sidneyia inexpectans* Walcott, 1911 and *Emeraldella brocki* Walcott, 1912 to be merostomes bridging the trilobite and eurypterid morphologies. While a relationship between xiphosurans and eurypterids had been recognized since M’Coy (1849) proposed to unite them as a tribe within the Entomostraca, a group formalized under Merostomata Woodward, 1866 (defined as including eurypterids, xiphosurans, and trilobites) which was transferred intact to Chelicerata when Lankester (1881) described *Limulus* as a chelicerate, the exact nature of this association remained largely unexplored until Raasch (1939) hypothesized an origin for synziphosurines and eurypterids from an aglaspidid ancestor. Størmer (1944), in a revision of the Arachnomorpha, maintained xiphosurans as the sister-group of eurypterids however considered aglaspidids to be basal xiphosurans and erected a ‘prochelicerata’, including *Sidneyia* Walcott, 1911 and *Leanchoilia* Walcott, 1912, as ancestral to both xiphosurans (including aglaspidids) and eurypterids. Størmer later added *Emeraldella* Walcott, 1912 to the ‘prochelicerata’, considering them transitional forms between trilobites and xiphosurans (Størmer 1952), and also considered *Strabops* Beecher, 1901 to be an aglaspidid rather than a primitive eurypterid along with the other problematic Cambrian arthropods *Paleomerus* Størmer, 1956, *Neostrabops* Caster & Macke, 1952 and *Beckwithia* Resser, 1931 (Størmer 1955). Raw (1957) however did not consider the aglaspidids to have given rise to either the xiphosurans or the eurypterids; instead the Aglaspidida represented a separate group of primitive chelicerates from which *Weinbergina* Richter & Richter, 1929 and *Pseudoniscus* Nieszkowski, 1859 were directly descended, the remaining synziphosurans formed a group distinct of the Xiphosura, which were sister-group to Eurypterida. Furthermore, the chelicerates were considered to share a common ancestor with olenellid trilobites, a concept later taken further by Lauterbach (1980) who considered olenellids to be separate from other trilobites and part of the chelicerate stem lineage.

The description of two taxa in the latter half of the twentieth century (*Chasmataspis laurencii* and *Kodymirus vagans* Chlupáč & Havlíček, 1965) have since dominated much of the discussion surrounding the relationship of eurypterids to the other aquatic chelicerates. Bergström (1968) considered *Chasmataspis* to be a xiphosuran while maintaining aglaspidids as a separate, more primitive, group while *Kodymirus* (considered an aglaspidid in its initial description) was evoked as a Cambrian proto-eurypterid much as *Strabops* had been almost six decades before. *Kodymirus* was largely accepted as a proto-eurypterid (Bergström 1975, 1979; Chlupáč 1995), although Cotton & Braddy (2004) clearly considered it an aglaspidid, until it was transferred into a group of 'aglaspidid-like' arthropods by Van Roy (2006). The exact affinities of *Kodymirus* are still uncertain, however the 'epistoma' of Chlupáč & Havlíček (1965) bears closer resemblance to a hypostome and contrary to the proposed reconstruction bearing six pairs of appendages (Chlupáč 1995, fig. 4) only one pair of appendages ever appears to be present on articulated specimens (MR 65789, 20490, 65794, 65795, 65796, 65783, 20690) with the appendages themselves composed of six podomeres (MR 65789, 65798).

In this it seems to correspond with the 'great appendage' arthropods such as *Leanchoilia illecebrosa* (Hou, 1987a) which have an enlarged first pair of appendages consisting of a bipartite peduncle and four distal articles (Liu *et al*. 2007), and it is possible that *Kodymirus* may be a megacheiran. Aglaspidids meanwhile were removed from the Chelicerata by Briggs *et al*. (1979) – a revision disputed by Weygoldt & Paulus (1979) and Bergström (1980) but corroborated by subsequent phylogenetic analyses (Briggs & Fortey 1989; Briggs *et al*. 1992; Cotton & Braddy 2004) – while *Chasmataspis* was retained within the Xiphosura and placed in a group with the newly described *Diploaspis casteri* (Størmer 1972).

With a consensus forming on the sister-group relationship between xiphosurans and eurypterids attention increasingly turned to whether chasmataspidids formed a natural group and their position in relation to the two other merostome groups (monophyletic Merostomata having been abandoned as a concept when Weygoldt & Paulus (1979) suggested that its represented a paraphyletic grade with eurypterids being the sister-group to arachnids). They were largely considered to be a monophyletic group of xiphosurans (e.g. Selden & Siveter 1987), although Eldredge (1974) separated chasmataspidids from the xiphosurans and placed them as the monophyletic sister-group to eurypterids, a view more recently shared by Dunlop & Selden (1997). Bergström (1975, 1980) however considered chasmataspidids to be polyphyletic, retaining *Chasmataspis* basally within xiphosurans but placing *Diploaspis* as the ancestor to terrestrial arachnids. Selden & Dunlop (1998) once again envisaged a monophyletic Chasmataspidida but considered them to be the sister group to aglaspidids, outside of Chelicerata, resolving a xiphosuran clade consisting solely of synziphosurines and xiphosurids as sister-group to eurypterids.

Paraphyly of chasmataspidids has been proposed once (Tetlie & Braddy 2004) where diploaspids were considered to be sister-group to eurypterids while *Chasmataspis* was sister-taxon to the diploaspid/eurypterid group. Due to their problematic morphology chasmataspidids have been left out of a number of larger-scale phylogenetic analyses, most of which retrieved a monophyletic Xiphosura as sister-group to Eurypterida and arachnids with a paraphyletic stem of 'great appendage' arthropods (e.g. Briggs & Fortey 1989; Cotton & Braddy 2004), however there have also been a few anomalous results; Wills (1996) placed *Fuxianhuia* Hou, 1987b as the sister-taxon to eurypterids and scorpions to the exclusion of xiphosurans, however *Fuxianhuia* is more likely to be a derivative of the euarthropod stem lineage (Chen *et al*. 1995; Edgecombe & Ramsköld 1996), while Wills *et al*. (1998) considered xiphosurans to be paraphyletic with synziphosurines sister-group to xiphosurans and eurypterids (but see *Excursus on segment articulations in arthropods*). Shultz (2007) did include chasmataspidids in his phylogenetic analysis of chelicerates and resolved them as a monophyletic group *within* Eurypterida, with Stylonurina being sister-group to Chasmataspidida plus Eurypterina. This result is probably due to the paucity of eurypterids in the analysis (only two species were coded) but is a hypothesis that will require more rigorous testing in the future. This uncertainty about chasmataspidid relationships resulted in Lamsdell *et al*. (2010a,b) using *Weinbergina* as the outgroup for their analyses of the Stylonurina, however the presence of a metastoma and genital appendage in diploaspids (Dunlop 2002; Tetlie & Braddy 2004) indicates that these would be a more appropriate outgroup for eurypterid analyses, although the position of *Chasmataspis* is more uncertain. Ideally an analysis including xiphosurans, chasmataspidids and eurypterids as ingroup taxa with a euchelicerate stem lineage taxon as the outgroup needs to be undertaken in order to resolve this matter. A megacheiran would probably make a suitable outgroup (see Dunlop 2006) however this interpretation of ‘great appendage’ arthropods is not yet universally accepted (Budd & Telford 2009). The issue of the relationships between xiphosurans, chasmataspidids and eurypterids is still very much a current one in need of further study, especially as certain characters in the form of the seventh appendage and the form of tergite articulations might suggest that synziphosurines are a paraphyletic with respect to the remaining Euchelicerata and not just Xiphosurida as in the analysis of Anderson & Selden (1997).

Excursus on segment articulations in arthropods. The plesiomorphic state for segment articulations in Arthropoda is difficult to determine, however for several groups (such as Artiopoda, Megacheira and Chelicerata) the ground pattern for articulations appears to involve a narrow transverse ridge on the tergite preceded by a smooth articulation facet. Chen *et al*. (1995) described the stem-euarthropod *Fuxianhuia protensa* Hou, 1987b (ELRC 19250a) as having tergites that connect through ‘articulating half-rings’ consisting of a central projection in front of a transverse articulating furrow with a smooth facet along the anterior of the tergopluerae, however the central projection is highly variable and is probably not a true half-ring articulation. Articulating half-rings have also been initially described from trilobites (e.g. *Hydrocephalus carens* Barrande, 1846: SM A1345; *Gyrometopus lineatus* (Angelin,1854) NRM Ar 47940) which also have a central half-ring with pleural facets or flanges (Whittington 1990), while euthycarcinoids such as *Schramixerxes gerem* (Schram & Rolfe, 1982) (MNHN SOT89291) also have half-ring-type articulations however the projecting ring is raised above the tergite and there appears to be no pleural articulation (Racheboeuf *et al*. 2008);

it seems likely that the use of the term half-ring needs to be reconsidered, and a distinction made between articulating half-rings *sensu stricto* (e.g. the trilobite-type) and the half-ring articulations found in euthycarcinoids and other arthropods which have probably evolved independently.

The aglaspidids *Aglaspis barrandei* Hall, 1862 (UW 4002/9) and *Chlupacaris dubia* Van Roy, 2006 (NMS G.2005.103.1) have a raised articulating ridge along the tergite anterior preceded by a smooth articulating facet (Hesselbo 1992; Van Roy 2006) that seems more similar to the eurypterid style of articulation. *Emereldella brocki* (USNM 136642, 144933) also bears articulating ridges on the tergites that bear close similarity to the aglaspidid articulating ridges (Stein & Selden in press) as does *Leanchoilia superlata* Walcott, 1912 (USNM 155655). Aglaspidids and *Emereldella* have been considered closely allied to chelicerates in the past (e.g. Dunlop & Selden 1997; Hou & Bergström 1997; Cotton & Braddy 2004) while *Leanchoila* is considered by some to belong to the euchelicerate stem lineage (Chen *et al*. 2004) and the morphology of their tergite articulations may support this, however the majority of synziphosurine xiphosurids appear to have articulated using a narrow, flattened half-ring system (Eldredge 1974; Eldredge & Plotnick 1974). This type of articulation appears to be part of the ground pattern for at least xiphosurids as it can be confirmed in a number of well-preserved specimens (e.g. *Bunodes lunula* Eichwald, 1854: AMNH 28734, 29279; *Legrandella lombardi* Eldredge, 1974: AMNH 29273; *Pseudoniscus roosevelti* Clarke, 1902: NYSM 10164; *Cyamocephalus loganensis* Currie, 1927: BMNH I 25; *Willwerathia laticeps*: PWL 472-D) and appears to be vestigial in the fused thoracetron of the earliest xiphosurids (e.g. *Lunataspis aurora* Rudkin, Young & Nowlan, 2008: MM I-3990). The tergite articulations of fossil scorpions are identical to those of eurypterids (e.g. *Compsoscorpius elegans* Petrunkevitch, 1949: BMNH In 15862; *Proscorpius osborni*: BMS E25162), being a smooth, flattened facet with a slight ridge posterior to it, as are the articulations in the postabdomen of the newly-identified chasmataspidid '*Tylopterella*' *menneri* (PIN 5116-1), and all three are considered homologous. Interestingly the holotype of *Chasmataspis laurencii* (USNM 125099) may show indications of articulating half-rings at its postabdominal articulations, while the synziphosurines *Kasibelinurus amicorum* Pickett, 1993 (USNM 484524) and *Weinbergina opitzi* (SMF VIII 7a) have articulating facets as opposed to articulating half-rings. Further work (and ideally specimens of *Chasmataspis*) is needed before this can be confirmed but if correct is further evidence suggesting that chasmataspidids may not be a natural monophyletic group, while *Kasibelinurus* and *Weinbergina* may suggest that at least some synziphosurines were ancestral to all the more derived chelicerates as opposed to just Xiphosurida. While the segment articulations in these taxa are probably plesiomorphic, further evidence for them being derivatives of a stem lineage to all other merostomes and arachnids may exist in the presence of free lobes (*sensu* Selden & Siveter 1987) on the genital segment in as yet undescribed chasmataspidids from Siberia (Marshall pers. comm.); also if the proposed homology of the xiphosuran chilaria and the eurypterid metastoma (Dunlop & Webster 1999) is accepted then the fully pediform appendage VII of *Weinbergina* (probably the plesiomorphic state, as pycnogonids also have a fully pediform VII) must be accounted for. A more parsimonious model of evolution would be for the fully pediform appendages for *Weinbergina* to be reduced into the chilaria through the synziphosurine lineage (some of which, such as *Venustulus* *waukeshaensis* Moore in Moore *et al*. 2005b, clearly only have five post-cheliceral pediform appendages) that were retained in xiphosurids but fused to form the metastoma in eurypterids. While chilaria have ostensibly not been observed in fossil xiphosurans (Rachebeouf *et al*. 2002; Moore *et al*. 2005b) this may be preservational as they are very small and easily lost among the coxae, sometimes difficult to pick out even in extant individuals. As an aside, one specimen of *Alanops magnificus* Rachebeouf, Vannier & Anderson, 2002, MNHN SOT1784, may actually show the chilaria between the coxae of appendage VI, and undescribed specimens of *Paleolimulus signatus* (Beecher, 1904) held at the University of Kansas clearly show the chilaria (Lamsdell pers. obs.).

Despite the stratigraphic problems of some synziphosurines being basal, paraphyletic euchelicerates (*Kasibelinurus* and *Weinbergina* are known from the Devonian), the discovery of Ordovician xiphosurids (Rudkin *et al*. 2008; Van Roy *et al.* 2010) suggests that the monophyly of Xiphosura needs to be questioned and should be fully tested phylogenetically, monophyly being something most previous studies have assumed *a priori*, therefore including no non-xiphosuran taxa except the outgroup (Anderson & Selden 1997) or including only a single taxon for the whole order (Cotton & Braddy 2004). Two exceptions are the analyses of Dunlop & Selden (1997) and Shultz (2007), however two of the three synapomorphies listed by Dunlop & Selden for the order (namely the presence of a cardiac lobe and a reduced first opisthosomal segment) are also known from both chasmataspidids and eurypterids, while it appears that Shultz used Xiphosura as his outgroup and so essentially forced their monophyly. Wills *et al*. (1998) included a synziphosurine (*Weinbergina*) and a xiphosurid (*Tachypleus* Leach, 1819) in their analysis of arthropod phylogeny and did retrieve a paraphyletic Xiphosura, however successive reweighting of the dataset refashioned the topology of the chelicerate clade and rendered Xiphosura polyphyletic and so it seems that without a more comprehensive analysis their status as a monophyletic group is still uncertain.

Plesiomorphic condition of gross body form. The basalmost eurypterid groups (specifically Rhenopteroidea and Moselopteroidea) comprise a number of species that have traditionally been difficult to differentiate phylogenetically, being as they seem to possess little in the way of quantifiable characters to differentiate them. The recognition that many of the stylonurine taxa belong within a redefined rhenopterid clade (Lamsdell *et al*. 2010a) has done much to resolve some of the issues surrounding basal eurypterids, however the similarities between the early representatives of Stylonurina and Eurypterina are truly striking and can sometimes lead to confusion regarding their phylogenetic placement. It seems that the more 'quaint' aspects of morphology of these taxa are due to them being very plesiomorphic; both *Brachyopterus stubblefieldi* and *Stoermeropterus conicus* are rather short-limbed, squat species with broad, deep bodies that are appreciably synziphosuran-like. The differentiation of the opisthosoma into a pre- and post-abdomen is often indistinct and the telson is lanceolate. The presence of metasomal epimera are considered equivocal, as they appear to be absent in rhenopterids, however their presence in the other Stylonurina (e.g. *Parastylonurus ornatus*: NMS G.1897.32.43; *Drepanopterus abonensis*: BGS GSM 84707) along with their occurrence plesiomorphically in moselopterids (e.g. *Stoermeropterus conicus*: NMS G.1897.32.88; *Vinetopterus martini*: PWL 2002/5010-LS), many of the other basal Eurypterina (e.g. *Onychopterella augusti*: GSSA C373a; *Dolichopterus macrocheirus*: AMNH 2250) and their being seemingly vestigial in *Eurypterus lacustris* (YPM 207290) suggests that their absence is an apomorphy of rhenopterids.

An opisthosoma of thirteen segments is shared by eurypterids and scorpions (Dunlop & Webster 1999) as well as chasmataspids, and it seems likely that this segment count was shared by their most common ancestor. Dunlop & Webster also showed that the ventral structures could be homologized between eurypterids, scorpions and synziphosurans, with synziphosurans having eleven opisthosomal segments. This segment count for synziphosurans is somewhat contentious: Eldredge (1974) described eleven tergites in the opisthosoma of *Legrandella lombardii* Eldredge, 1974, the first of which was partially covered by the carapace, and stated that *Limuloides* Woodward, 1865, *Bunodes* Eichwald, 1854, *Pseudoniscus* and *Weinbergina* also had eleven opisthosomal segments. Eldridge & Plotnick (1974) however considered *Pseudoniscus* to possess only ten opisthosomal tergites while Anderson *et al*. (1998) concluded that it was unlikely that any synziphosuran had more than ten opisthosomal somites. Moore *et al*. (2005a) however stated that while *Weinbergina* showed no dorsal expression of an independent somite the first opisthosomal segment may have been fully incorporated into the prosoma. *Bunodes* at least does seem to genuinely possess a small tergite usually covered by the carapace anterior to the first tergite as identified by Anderson *et al*. (1998) (Lamsdell pers. obs. on BMNH 92774) and the unnamed synziphosurine figured by Van Roy *et al*. (2010, fig. 2d) also seems to possess eleven opisthosomal tergites with the first partially covered by the carapace. The homologization of structures as presented by Dunlop & Webster (1999) therefore appears to be valid (incidentally giving them the same number of somites as the megacheirans *Haikoucaris ercaiensis* Chen, Waloszek &

Maas, 2004 and *Tanglangia longicaudata* Luo & Hu *in* Luo, Hu, Chen, Zhang & Tao, 1999) whereby the ancestor of chasmataspidids, eurypterids and scorpions gained two metasomal segments, which they implicitly assume occurred posterior to the existing segments but before the telson.

The plesiomorphic state of the cuticular sculpture is also difficult to determine. Several rhenopterids (*Brachyopterus stubblefieldi*, *Alkenopterus brevitelson*, *Leiopterella tetliei* and possible *Kiaeropterus cyclophthalmus*) possess an integument devoid of ornamentation, however the widespread occurrence of cuticular sculpture in the other Stylonurina, Eurypterina, chasmataspidids and synziphosurines means that this is again probably a rhenopterid apomorphy. Scales are frequently found on eurypterids (e.g. *Parastylonurus ornatus*: NMS G.1885.26.72.7; *Eurypterus dekayi*: YPM 212043; *Hibbertopterus scouleri*: NMS G.1955.15; *Pterygotus anglicus*: NBMG 10000), including (sparsely) on *Stoermeropterus*, but are not recorded on chasmataspidids or xiphosurans, however *Stoermeropterus conicus* (NMS G.1897.32.138) and *Moselopterus ancylotelson* (SPW 999-D) predominantly have a granular cuticular sculpture. Granular ornamentation and pustules are known from several chasmataspidids (*Chasmataspis laurencii*: USNM 125099; *Diploaspis muelleri*: PWL 2002/5022-LS; *Octoberaspis ushakovi*: GIL 35/707) and synziphosurines (*Weinbergina opitzi*: SMF VIII 7a; *Limuloides limuloides* (Woodward, 1865): BMNH In 60018) and this is likely to be the plesiomorphic condition for eurypterids, with scales and pustules developing from modified granules. The terrace ornamentation of *Stoermeropterus conicus* could be apomorphic, however *Parahughmilleria hefteri* bears almost identical ornamentation (SMF VIII 55) and terrace lines are present on the prosomal ventral plate of *Eurypterus* *tetragonophthalmus* (NRM Ar 35320) while a specimen displaying striae on the ventral plates assigned to *Erieopterus* sp. was described by Poschmann & Tetlie (2006). Dorsal terrace lines also occur on a number of other eurypterine eurypterids, and while it is possible that terrace lines evolved a number of times in Eurypterina it is also possible that they are an inherited characteristic. A potential argument against this is the lack of any terrace lines in synziphosurines, chasmataspidids or Stylonurina (although *Parastylonurus* does have similar cuticular structures associated with its postabdominal epimera), however the ventral structures of synziphosurines and chasmataspids are largely unknown and specimens of *Eurypterus tetragonophthalmus* that have not been prepared through acid etching do not preserve enough detail to show the terrace lines, and these structures may be more widespread in aquatic chelicerates than is currently recognized.

Plesiomorphic condition of the carapace, visual structures and marginal rim. The plesiomorphic condition of the carapace shape in eurypterids is difficult to determine as, utilizing the definitions set out by Tollerton (1989), carapace shape varies considerably between different genera and the issue is further complicated by the ease with which the carapace shape is modified by taphonomic distortion. Some plesiomorphic characteristics can be discerned, however. The median constriction of the carapace (the 'waist') in *Stoermeropterus* is also known from *Onychopterella augusti* (GSSA C373a), implying it is a plesiomorphy for Eurypterina, and may also be present in *Brachyopterus stubblefieldi* (BGS D 3124) although it is difficult to discern due to the anterior of the carapace being broader than the posterior. This would indicate that a 'waist' to the carapace is the plesiomorphic state for Eurypterida as a whole, something that may be corroborated by the possible occurrence of similar constrictions in the carapaces of the chasmataspidids *Loganamaraspis dunlopi* (NMS G.1957.1.649) and undistorted specimens of *Diploaspis casteri* (SMF VIII 39). The chasmataspidid specimens also indicate that the broadest point being anterior in the carapace of *Brachyopterus* is not a plesiomorphic condition, and it appears that the plesiomorphic carapace shape was likely to have been largely equal in length and width with its widest point at the carapace posterior. The carapace marginal rim is narrow in rhenopterids (*Brachyopterus stubblefieldi*: BGS D 3124; *Rhenopterus diensti*: MfN 48/48a) and in *Stoermeropterus* and largely deflected ventrally to partially overlap the ventral plates (thus forming the true doublure), a condition shared with the xiphosurids *Alanops magnificus* (Rachebeouf *et al*. 2002, pl. 3 figs. 1 & 3), *Lunataspis aurora* (MM I-4000A), *Paleolimulus signatus* (USNM 484407, 484409) and modern *Limulus*, and the synziphosurines *Bembicosoma pomphicus* (NMS G.1897.32.149) and *Legrandella lombardii* (AMNH 29273). Chasmataspidids meanwhile have rather broad marginal rims (*Chasmataspis laurencii*: USNM 125099; *Diploaspis casteri*: SMF VIII 39), with the anteriorly broadening marginal rim of *Octoberaspis ushakovi* (GIL 35/324) bearing particular resemblance to the marginal rim of the synziphosuran *Pasternakevia podolica* Selden & Drygant, 1987 (LSM 35611), however, while the marginal rim remains narrow in Eurypterina some more derived stylonurines (e.g. *Stylonurus powriensis*: NMS G.1891.92.102; *Drepanopterus abonensis*: BRSUG 28635;) and xiphosurids (e.g. *Euproops danae* (Meek & Worthen, 1865): BMNH It.61012) also have broad marginal rims, possibly linked to a sediment-grubbing mode of life, and it is clear that marginal rim thickness is a somewhat variable character.

The lateral eyes of all known Stylonurina are lunate or arcuate while those of moselopterids are lunate, and neither moselopterids nor rhenopterids show an enlarged palpebral lobe associated with the lateral eye as is seen in more derived Eurypterina (e.g. *Eurypterus remipes*: YPM 211408; *Parahughmilleria hefteri*: SMF VIII 55) and some Stylonurina (*Stylonurella spinipes*: NMS G.1891.92.33; *Drepanopterus abonensis*: BGS GSM 4718), so it seems the plesiomorphic condition of the lateral eyes was as a narrow visual surface abutted by small palpebral lobe that could conceivably be the reduced remnants of the opthalmic ridge found in xiphosurans (e.g. *Weinbergina opitzi*: SMF VIII 7a; *Legrandella lombardii*: AMNH 29273; *Limuloides limuloides*: BMNH In 60018; *Xaniopyramis linseyi* Siveter & Selden, 1987: HU P1986; *Paleolimulus signatus*: USNM 484408). Support for this homology may be found in the chasmataspidid *Octoberaspis ushakovi* (GIL 35/324, 35/336) which appears to possess a reduced but clearly definable ophthalmic ridge in association with its lateral eyes. The median ocelli are often poorly preserved or completely obliterated in the fossil material due to their small, delicate structure, and definite ocelli are not preserved in *Stoermeropterus conicus*, however *Stoermeropterus latus* shows them to be positioned separately on the carapace without a median eye tubercle (PMO H1839, H1874), as does *Stoermeropterus nodosus* (FMNH PE6214). This appears at odds with the condition seen in other aquatic chelicerates, however, as the synziphosurine *Limuloides limuloides* may have the ocelli positioned atop a tubercle (BGS GSM 32393) and the same condition was reported in *Bunodes lunula* by Bergström (1975, pl. 1 fig. 8) while the ocelli are positioned on a median tubercle in the xiphosurid *Alanops magnificus* (MNHN SOT1951) and are interpreted to be so in the Ordovician *Lunataspis aurora* by Rudkin *et al*. (2008) while the median eye tubercle has merged with the median ridge in modern *Limulus*. Among chasmataspidids the ocelli are clearly located on a median eye tubercle in *Chasmataspis laurencii* (USNM 125099, 125101), *Diploaspis casteri* (PWL 1999/5-LS, 1999/6a-LS, SMF VIII 39), and *Octoberaspis ushakovi* (GIL 35/324, 35/713) and so appears to be a constant feature – the report of paired ocellar tubercles in *Diploaspis muelleri* is based on a specimen (PWL 2002/5023) that has been interpreted upside down (Marshall pers. comm.) – while Palaeozoic scorpions also have their ocelli located on a large median eye tubercle that is observable on their earliest Silurian representatives, *Dolichophonous loudenensis* (NMS G.1897.32.196) and *Proscorpius osborni* (Dunlop *et al*. 2008, pl.1 fig. 5). The lack of a median eye tubercle in *Stoermeropterus* is therefore likely to be a reversal, however the lack of an eye tubercle in the other moselopterids (*Vinetopterus struvei*: SPW 614-D; *Moselopterus ancylotelson*: SPW 999-D), dolichopterids (*Strobilopterus princetonii*: YPM 204949), Eurypteridae (*Eurypterus lacustris*: BMS E6468; *Eurypterus tetragonophthalmus*: NRM Ar55307; *Erieopterus hypsophthalmus* Kjellesvig-Waering, 1958a: OSU 19572) *Nanahughmilleria norvegica* (PMO H1798; H1799), *Parahughmilleria hefteri* (PWL 2004/5040-LS, 2004/5041-LS), *Eysyslopterus patteni* (AMNH 32720), *Orcanopterus manitoulinensis* (ROM 56450) and pterygotids (*Herefordopterus banksii*: BGS GSM 88910; *Jaekelopterus rhenaniae*: PWL 2004/5055-LS) suggests that the loss of the median eye tubercle is not an apomorphy solely of *Stoermeropterus*. The lack of a median eye tubercle in rhenopterids (*Kiaeropterus cyclophthalmus*: NMS G.1885.26.72.16; *Kiaeropterus ruedemanni* (Størmer, 1934a): PMO H1733; *Brachyopterella pentagonalis*: PMO H1792, H2050; *Alkenopterus brevitelson*: SPW 624-Da; *Alkenopterus burglahrensis* Poschmann & Tetlie, 2004: PWL

2002/5011-LS; *Rhenopterus diensti*: MfN 48a), the probable rhenopterid *Stylonuroides dolichopteroides* (Størmer, 1934a) (PMO H2179) and the parastylonurid *Stylonurella spinipes* (BGS GSM 87357) of Stylonurina suggests that the lack of a clear median eye tubercle is a characteristic that developed prior to the split of the two suborders. In a number of these taxa the ocelli are positioned on a slight inflation of the carapace that may be the remnant of a median tubercle, however the compressed nature of many eurypterid specimens makes determining the presence or otherwise of a carapace inflation difficult; several rhenopterids (*Brachyopterus* Størmer, 1951, *Kiaeropterus* Waterston, 1979 and *Brachyopterella* Kjellesvig-Waering, 1966) have their ocelli preserved within an ocellar area (*sensu* Tetlie *et al*. 2007), however this is considered a rhenopterid apomorphy that is secondarily lost in *Alkenopterus* Størmer, 1974 and *Rhenopterus* Størmer, 1936a. Both of the more derived Stylonurina and Eurypterina possess the median eye tubercle, however among stylonurines the tubercle is only ever found associated with a median carapace ridge in stylonurids (*Pagea plotnicki*: UA 10477), hardieopterids (Tetlie 2008), drepanopterids (*Drepanopterus abonensis*: BGS GSM 84718, BMAG Cb4168), and with the ridge secondarily reduced in hibbertopterids and mycteropids (*Megarachne servinei* Hünicken, 1980: CORD-PZ 2110; *Hibbertopterus scouleri*: KM G55/76; *Cyrtoctenus wittebergensis*: USS IT.01), while in the Eurypterina it is found as an isolated tubercle (*Adelophthalmus sievertsi*: PWL 1995/7511-LS, 2004/5001-LS, 2004/5002-LS; *Lanarkopterus dolichoschelus*: NMS G.1967.65.3; GSE 12433), suggesting that the median eye tubercle in the two suborders has re-evolved independently.

Plesiomorphic condition of prosomal appendages I-V. The anterior five pairs of prosomal appendages are primarily divided into the preoral chelicerae and the four pairs of postoral locomotary appendages. The chelicerae were previously used to differentiate the two suborders, separating Eurypterida into the small chelicera-bearing Eurypterina and the Pterygotina with enlarged chelicerae (Caster & Kjellesvig-Waering 1964), however this distinction has been abandoned since enlarged chelicerae have been shown to evolve within the Eurypterina (Tetlie 2007a). The plesiomorphic condition of the chelicerae in eurypterids (which varies little throughout much of the Order) is as in Xiphosura, consisting of a proximal peduncle articulating with a podomere that folds back inwards towards the body and extends into a single fixed finger with the terminal podomere forming the movable finger. The morphology of the non-pteryotid chelicerae is observed best in the macerated specimens of *Eurypterus tetragonophthalmus* (Selden 1981, fig. 24j), however the orientation and general morphology can also be seen in a number of stylonurine (*Parastylonurus ornatus*: NMS G.1978.28.3; *Rhenopterus diensti*: MfN 48a) and eurypterine (*Strobilopterus princetonii*: YPM 204947; *Parahughmilleria major*: SMF VIII 148; '*Carcinosoma*' *scoticum*: NMS G.1897.32.153) taxa. Although the fossil pycnogonid *Palaeoisopus problematicus* Broili, 1928 has five segments in the chelicerae (Bergström *et al*. 1980) and the Silurian pycnogonid *Haliestes dasos* Siveter, Sutton, Briggs & Siveter, 2004 (OUM C.29571) along with the possible basal chelicerate *Offacolus kingi* Orr, Siveter, Briggs & Siveter, 2000b (Sutton *et al*. 2002) have chelicerae composed of four segments, no eurypterid possesses anything other than three-segmented chelicerae, Kjellesvig-Waering's (1964b) hypothesis that pterygotids possessed a fourth segment having been disproved by Laub *et al*. (2010).

Størmer (1963, 1974) believed the plesiomorphic state for all the non-cheliceral prosomal appendages to be the *Hughmilleria*-type of appendage, based on comparison with the spinosity of the legs of supposedly ancestral trilobites, however this hypothesis is not supported by the current theories of eurypterid phylogeny. Appendages II-IV of *Stoermeropterus conicus* are of the *Rhenopterus*-type, lacking socketed spines but possessing paired fixed cuticular projections anteroventrally, a characteristic shared with *Vinetopterus martini* (PWL 2002/5010-LS) within Moselopteridae and rhenopterids (*Brachyopterus* stubblefieldi: BGS D 3124; *Brachyopterella pentagonalis*: PMO H1792; *Leiopterella tetliei*: CMN 53573; *Rhenopterus diensti*: MfN 48a) at the base of Stylonurina. The *Rhenopterus*-type appendage being plesiomorphic for eurypterids is further suggested by the occurrence of appendages with short, fixed cuticular extensions in the chasmataspidid *Diploaspis casteri* (SMF VIII 171), while several eurypterids also possess slight cuticular extensions on the podomeres of their fifth and sixth appendages (*Stoermeropterus conicus*: NMS G.1897.32.133; *Moselopterus ancylotelson*: SMF VIII 146; *Brachyopterella ritchiei*: NMS G.1968.14; *Brachyopterus stubblefieldi*: BGS D 3124; *Parastylonurus ornatus*: NMS G.1897.32.57) suggesting that fixed projections are the plesiomorphic condition on every prosomal limb. Another probable plesiomorphic characteristic is the possession of denticulations on the distal podomere margins; while such denticulations have been recognized in *Slimonia* (e.g. *S. acuminata*: BMNH 59658) and *Adelophthalmus* (e.g. *A. mazonensis*: MCZ 7162) they are also present in *Parastylonurus ornatus* (NMS G.1885.26.72.7; G.1897.32.57), *Eurypterus tetragonophthalmus* (BMNH I 3406/12), *Parahughmilleria major* (SMF VIII 148) and *Strobilopterus princetonii* (PU 13854), and it is considered likely that they are present on more (if not all) species but that their small and delicate structure means they are often not preserved.

Plesiomorphic condition of prosomal appendage VI. Størmer (1974) considered the sixth appendage in eurypterids to have followed different evolutionary pathways from a generalized *Hughmilleria*-type of spiniferous appendage. In the case of the Stylonurina the spines were lost completely to form the non-spiniferous walking legs, however among the Eurypterina the swimming paddle developed through the *Moselopterus*-type appendage before separately evolving into the *Dolichopterus*-type paddle and the *Eurypterus*-type, from which the other types of paddle were hypothesized to have arisen. Størmer also considered the paddle of *Onychopterella kokomoensis* to potentially have independent origins from the other paddle types, and suspected that the *Carcinosoma*- and *Slimonia*-type paddles may also be independently derived. In contrast, Tetlie & Braddy (2004) considered *Dolichopterus* to be intermediate between Stylonurina and the remaining Eurypterina, presumably placing *Moselopterus* within the Stylonurina, invoking a single evolution of the paddle from a non-spiniferous, pediform appendage. *Dolichopterus* had traditionally been placed within the Stylonurina (e.g. Kjellesvig-Waering 1966) or positioned as its sister-group (e.g. Waterston 1979), necessitating either a dual origin of the swimming paddle or presenting the *Dolichopterus*-type paddle as the primitive state within Eurypterina. Subsequent phylogenetic analysis by Tetlie & Cuggy (2007) however showed that *Dolichopterus* was not closely allied with Stylonurina but was sister-group to Eurypteridae and they proposed a single origin of the swimming paddle from a non-spiniferous pediform appendage, through the *Moselopterus*-type appendage and the *Onychopterella* paddles (as they considered the genus paraphyletic) before diverging into the dolichopterid paddles and those of the Eurypteridae. This latter interpretation of paddle evolution is supported here, as the phylogenetic position of *Stoermeropterus* shows that the plesiomorphic condition of appendage VI is as pediform, with the paddle evolving only once within Eurypterida. Evidence for all the paddle morphologies having evolved through the same pathway comes from juvenile specimens of forms which, as adults, have radically distinct paddle morphologies from those seen in *Onychopterella kokomoensis* and *Erieopterus* (which are considered to be among the most basic forms of paddle); *Strobilopterus princetonii* has a heavily serrated paddle with a large ninth podomere set into a recess on the posterior margin of the eighth (Tetlie 2007b), however a juvenile specimen (PU 13854) preserves a paddle with a much smaller podomere nine set within a much shallower recess, resembling a more serrated and slightly broader *Erieopterus*-type of paddle. '*Carcinosoma*' *scorpioides*, meanwhile, has a variation on the *Carcinosoma*-type paddle with an elongated eighth podomere and a large, rounded podomere nine set into it (BGS GSM 103939), however *Paracarcinosoma obesus* (Woodward, 1868) from the same locality probably represents a juvenile of the same species (Lamsdell pers. obs.) and has a more rounded eighth podomere and smaller podomere nine that again bears a closer resemblance to the *Erieopterus*-type paddle.

While the expansion of the appendage into a paddle demonstrably occurs within the eurypterine lineage, the coxal ear and podomere 7a appear suddenly in the basalmost members of the Suborder and so ascertaining whether they are plesiomorphic or derived characters is more problematic. Neither occur in the Stylonurina, which would seem to indicate that they are autapomorphies of Eurypterina, however it is possible that these characters were present in the eurypterid ancestor and lost in the Stylonurina. There may be some argument for suggesting that podomere 7a is homologous to one of the tarsal spurs found in some Palaeozoic scorpions, which are located overlying the telotarsus (equivalent to the eighth podomere in eurypterids, which have a divided femur) but originate from the distal margin of the basitarsus (equivalent to the seventh podomere in eurypterids); the similarity is particularly striking in *Palaeophonus nuncius* Thorell & Lindström, 1884 (NRM Ar 32235) where the triangular spurs appear to almost lie flat against the appendage. These tarsal spines may be homologous to the 'spatulate organs' (*sensu* Moore *et al*. 2005a) which are located between the tibial-tarsal joint on appendage VI of *Limulus* (which has both a fused femur and tarsus, resulting in an appendage with only seven podomeres), however these would therefore overlie the seventh podomere in eurypterids (sixth in scorpions) and so the evidence for direct homology is not compelling. The sixth appendage of *Weinbergina opitzi*, with a fused femur but divided tarsus as in scorpions, possesses several lobate spines at the distal margin of the tibia which are probably homologous to those in *Limulus* and a pair of lobate spines originating at the distal margin of the basitarsus (Stürmer & Bergström 1981) that may be homologous to the tarsal spurs in scorpions and potentially podomere 7a in Eurypterina. It is unclear whether a similar structure occurs in chasmataspidids; the chelate supposed sixth appendage of *Chasmataspis laurencii* (USNM 125106) shows no evidence of a podomere 7a or any accessory spines while the pediform sixth appendage of *Loganamaraspis dunlopi* (NMS G.1957.1.649) does not preserve the distal podomeres. Where paddles are known from the Devonian diploaspids (*Diploaspis casteri*: SMF VIII 171; *Octoberaspis ushakovi*: GIL 35/735) they appear to possess a podomere 7a on the anterior edge of the appendage, however this difference in position suggests it may have an independent origin from the posterior 7a of Eurypterina. The coxal ear has no clear homologues in other chelicerates although the dorsally expanded coxae of xiphosurans sometimes bear a semblance to the state, but these more closely resemble an extension of the basipod itself rather than a differentiated dorsal structure as appears to be the case in eurypterids (the cuticle is often preserved as darker than the rest of the coxa). A somewhat similar structure is found at the attachment of the exopod to the basipod in *Chasmataspis laurencii*, which forms an ear-like dorsal projection from which the rest of the exopod projects. It could be that the ear in Eurypterina represents the vestiges of the sixth appendage exopod (which is retained as the flabellum in *Limulus*), however the evidence for this is currently equivocal. If this were the case the coxal ear represents a plesiomorphic state that is lost in the stylonurine lineage.

The expanded sixth appendage of Eurypterina has traditionally been considered primarily as an adaptation for swimming (e.g. Størmer 1974; Selden 1981; Plotnick 1985), with the 'ear' on coxa VI serving to lock the proximal segment against the other coxae, immobilizing it to allow greater generation of thrust by the paddle while the expanded lobe ('podomere' 7a) served to increase the surface area of the paddle and allowed podomere eight to fold back almost completely against podomere seven during the recovery stroke (Selden 1981, figs. 16 & 17). It has also sometimes been suggested that the 'paddle' evolved as an aid for digging into the substrate (Laurie 1893; Størmer 1934a; Tetlie 2007b) in a manner similar to the sixth appendage 'pusher' of *Limulus*, and the possession of a podomere 7a and coxal ear by moselopterids like *Stoermeropterus* which were clearly not swimmers lends support to this alternative hypothesis. The initial function of the ear was likely the same, to immobilize the coxa to allow for greater force to be applied by the posterior appendages in an anterior-posterior sweeping motion, while podomere 7a may have been incidental or more likely acted to strengthen and support the appendage during digging as was suggested in *Moselopterus* by Størmer (1974). The balance of evidence therefore suggests that the modifications of the sixth prosomal appendage during the early evolution of the Eurypterina were related to digging at the substrate surface rather than swimming, and that the function of the paddle as a swimming aid was a secondary adaption that developed within the eurypterine lineage as denoted by the modification of the distal margin of the sixth podomere to allow for greater manoeuvrability of the paddle, a characteristic that seems to be genuinely linked with the adoption of swimming as a regular method of locomotion. Stylonurina, the moselopterids and *Onychopterella* all lack this modified podomere margin, and so when they did swim they would not have been particularly efficient. Dolichopterids such as *Strobilopterus*, meanwhile, probably remained relatively poor swimmers and may have used the sixth appendage for both digging and swimming (Tetlie 2007b), while it is only the most derived taxa such as pterygotids (see e.g. Plotnick & Baumiller 1988) that were capable of swimming for longer durations and so able to disperse across a wider geographical range (Tetlie 2007a).

As the plesiomorphic condition of appendage VI in eurypterids is that of a pediform non-spiniferous appendage homology between the eurypterid swimming paddle and that of diploaspid chasmataspidids is rejected. There are both good morphological and stratigraphical grounds for this; the diploaspid paddle appears to lack a small ninth podomere (e.g. *Diploaspis casteri*: SMF VIII 171; *Octoberaspis ushakovi*: GIL 35/735) while the podomere 7a is located on the anterior side of the appendage; either the paddle in diploaspids has one less podomere than in eurypterids and an anterior podomere 7a has developed independently or podomere 8 has been reduced into a 7a-like structure and the enlarged, terminal paddle podomere is podomere 9. Furthermore, paddle-bearing diploaspids are only known from the Devonian, while the only known Silurian chasmataspidid, *Loganamaraspis dunlopi*, has a pediform appendage VI, and so it appears that the diploaspid paddle developed some time after the eurypterid paddle.

Plesiomorphic condition of the prosomal ventral plates and sutures. Tetlie *et al*. (2008) considered the plesiomorphic condition of the ventral plates in eurypterids to be the *Megalograptus*-type due to the ventral plates being two distinctly separate units. Størmer (1934a) however had considered the *Hughmilleria*-type ventral plates, with a central epistomal plate, to be the plesiomorphic form and that the innovation of the other ventral plate types had occurred through the merging of these three initial plates, with an epistomal plate retained in forms such as pterygotids with well-developed chelicerae. The occurrence of an epistoma in *Stoermeropterus conicus* and *Stoermeropterus latus* (PMO H1839) and some rhenopterid species (*Kiaeropterus ruedemanni*: PMO H1733; *Brachyopterella pentagonalis*: PMO H1792) seems to suggest that Størmer's theory is correct, reinforced by the apparent identification of epistomal sutures in the chasmataspidids *Diploaspis casteri* (SMF VIII 39) and '*Eurypterus*' *stoermeri* (PIN 1138/1), however the sutures of modern *Limulus* more closely resemble those of the *Erieopterus*-type (Størmer 1934a, fig. 11g), as seemingly does the doublure of *Rolfeia fouldenensis* (NMS G.1984.67.1b), the synziphosurine *Venustulus waukeshaensis* (UW 4001/1b) and the Silurian chasmataspidid *Loganamaraspis dunlopi* (NMS G.1957.1.649a). Tetlie *et al*. (2008, p. 192) reported that Tollerton now believes the

Erieopterus-type of ventral plate to be indistinguishable from the *Eurypterus*-type, however those taxa with the *Eurypterus*-type ventral plate clearly display a median suture at the joint between the two plates with the plates remaining a constant width as they curve anteriorly (e.g. *Eurypterus remipes*: YPM 9003A; *Parastylonurus ornatus*: NMS G.1885.26.72.7) while the *Erieopterus*-type appears to consist of two plates (not a single plate as originally described by Kjellesvig-Waering (1958a), which is presumably the reason that Tollerton and Tetlie *et al*. considered them identical to the *Eurypterus*-type) that narrows anteriorly with the true doublure forming a 'triangular area' as recognized by Størmer (1974, p. 384 & fig. 18). This type of ventral plate morphology is seen in *Vinetopterus struvei* (SMF VIII 191), *Moselopterus ancylotelson* (SMF VIII 164), *Erieopterus eriensis* (Whitfield, 1882) (OSU 19614, 19571, USNM 155678) and potentially *Strobilopterus princetonii* (YPM 204947), *Buffalopterus pustulosus* (AMNH 2249), *Onychopterella augusti* (GSSA C373a) and *Onychopterella kokomoensis* (FMNH UC6638), all of which are members of the three basalmost eurypterine clades. It is worth noting that, given current understanding of eurypterid phylogeny, the *Erieopterus*-type ventral plate is the only one that does not develop convergently in different groups, as the *Eurypterus*-type is shown to develop independently in rhenopterids (Størmer 1936a; Lamsdell *et al*. 2010b), parastylonurids and basal hardieopterids (Waterston 1979), hibbertopterids (Waterston 1957) and *Eurypterus* (Clarke & Ruedemann 1912) while epistomal sutures are found in *Stoermeropterus*, basal rhenopterids (Størmer 1934a), stylonurids (Waterston 1962), hardieopterids (Hall & Clarke 1888), adelophthalmoids (Størmer 1934a, 1973; Poschmann 2006) and pterygotoids (Sarle 1903; Kjellesvig-Waering 1964b), further suggesting that the *Erieopterus*-type ventral plate morphology may be the plesiomorphic type. The convergence of ventral plate morphology between Stylonurina and Eurypterina is further reinforced by the occurrence of transverse ventral sutures on the ventral plates of Stylonurina, which are an autapomorphy of the suborder.

One obstacle to this is the presence of epistomal sutures in *Stoermeropterus, Brachyopterella* and *Kiaeropterus*. The ventral plates of *Brachyopterus* are unknown while *Stoermeropterus* is the only moselopterid to possess an epistoma and so it tempting to consider the epistoma apomorphic in *Stoermeropterus* and the *Brachyopterella*/*Kiaeropterus* clade, however the morphology of the epistomal plate in *Stoermeropterus* bears closer relation to the epistomae of the Stylonurina groups than those of the other Eurypterina, and so it is feasible that the possession of an epistoma is the plesiomorphic characteristic that was rapidly lost in both suborders. However, the larvae of modern *Limulus* possess epistomal sutures (Størmer 1934a, figs. 10 & 11f) that are lost in adult instars whilst eurypterids that possess an epistoma often exhibit the traditional juvenile characteristics of large lateral eyes, reduced or absent socketed spines on the prosomal appendages, and (in the case of pterygotids) enlarged chelicerae, suggesting that these characteristics have been paedomorphically retained into adulthood. If larval eurypterids also possessed an epistoma then this could account for its repeated, convergent occurrence within the group, and could explain the similarities between *Stoermeropterus* and Stylonurina as the evolution of epistoma morphology within the Eurypterina would be largely unobservable until it is retained in the adult pterygotoids and adelophthalmoids, both of which are highly derived groups.

Plesiomorphic condition of the metastoma. The metastoma, along with the genital appendage, was traditionally considered the defining autapomorphic character for

Eurypterida (Dunlop & Selden 1997), however the identification of both structures in diploaspid chasmataspidids (Dunlop 2002; Tetlie & Braddy 2004) has left eurypterids without any clear autapomorphies, until the identification of the fused operculae of somites VIII and IX as a potentially unique eurypterid characteristic in this volume. The metastoma is considered to be part of the first (reduced) opisthosomal segment and may have either an appendicular or sternal derivation, however the presence of paired muscle scars on many well-preserved metastomae (e.g. *Hardieopterus macrophthalmus*: NMS G.1897.32.106; *Eurypterus tetragonophthalmus*: BMNH I 3406/20) and a possible fused median suture in others (e.g. *Pagea sturrocki* Waterston, 1962: NMS G.1956.14.11; *Eurypterus hankeni*: PMO 206.625) along with the identification of the anterior opercular plate as the sternite of the first opisthosomal segment suggests that the metastoma is indeed appendicular in nature. The metastoma has been suggested to be homologous to the xiphosuran chilaria and the scorpion sternum (Jeram 1998; Dunlop & Webster 1999), of which the chilaria has been shown developmentally to comprise the appendages of somite VII (Farley 2010) while scorpions possess an embryonic limb pair (Brauer 1895) anterior to the remaining trunk limbs that is not expressed in adults (its eventual fate is currently unknown) that could conceivably form the sternum (Dunlop & Webster 1999). The presence of the metastoma in chasmataspidids suggests that the fusion of the seventh appendage pair occurred some time before the eurypterid lineage diverged, and although known from only two species (*Octoberaspis ushakovi*: GIL 35/712; *Loganamaraspis dunlopi*: NMS G.1957.1.649b) the metastoma of chasmataspidids appears to be fairly uniform in morphology, consisting of a broad anterior portion with a shallow notch and narrowing posteriorly, giving it an overall heart-shape distinct from any of Tollerton's

(1989) metastoma shapes but closest to the cardioid form. An anterior metastomal notch is common in eurypterids and is found both in moselopterids (*Stoermeropterus conicus*: NMS G.1885.26.72.17; *Moselopterus elongatus*: SMF VIII 184) and rhenopterids (*Leiopterella tetliei*: CMN 53573; *Rhenopterus diensti*: MfN 48a) and so appears to be the plesiomorphic condition. Few eurypterids however have a narrow posterior margin, and those that do (e.g. *Acutiramus cummingsi* (Grote & Pitt, 1875): UMMP 62581; *Hughmilleria socialis*: BMNH I7505; *Slimonia acuminata*: SM A16237a; *Mixopterus kiaeri*: PMO H2032; *Lanarkopterus dolichoschelus*: NMS G.1954.26.3) occupy a derived position within eurypterid phylogeny and have a very different overall metastoma morphology to the chasmataspidids. More common in eurypterids is having a rounded metastoma posterior with an overall oval metastoma morphology, which is present in Moselopteridae, Onychopterellidae, Eurypteridae, Adelophthalmidae, and most Pterygotidae, and this is considered the plesiomorphic state. The metastoma of Stylonurina is less conservative in its morphology than in Eurypterina, possibly due to each clade being highly specialized and probably inhabiting a distinct ecological niche with separate feeding strategies (it is worth noting that among the Eurypterina the highly specialized predatory mixopteroids show the most distinct metastoma morphology), however the rhenopterids possess an obturbinate metastoma that greatly resembles the oval form but which narrows anteriorly and *Drepanopterus* (a relatively derived stylonurine) has an oval metastoma but with a posterior cleft (*D. abonensis*: BRSUG 28647; *D. pentlandicus*: NMS G.1897.32.91), suggesting that an oval metastoma is part of the ground plan for Stylonurina too.

Plesiomorphic condition of the genital appendage and operculum. As with the metastoma, the genital appendage was considered an autapomorphy for eurypterids until it was also identified in two species of chasmataspidid (Dunlop 2002; Tetlie & Braddy 2004). The genital appendage is known to be sexually dimorphic in all eurypterids where it is preserved on multiple specimens, and the presence of sexual dimorphism of the appendage in both Stylonurina and Eurypterina as well as potentially in *Octoberaspis ushakovi* (Dunlop 2002, fig 6c,d) indicates that dimorphism of the genital appendage developed before chasmataspidids and eurypterids diverged, and it is possible that genital appendages were always sexually dimorphic.

The most in-depth study of eurypterid genital appendages was undertaken by Braddy & Dunlop (1997), who studied well-preserved material of *Eurypterus tetragonophthalmus*, and the type A appendage was shown to consist of three segments while the type B appendage consisted of only two segments (the terminal 'segment' in both appendages consisting of the furca). In some more derived eurypterine taxa such as pterygotids (see Waterston 1964) the type A appendage has become fused into a single segment, and while the rhenopterid *Brachyopterella ritchiei* (NMS G.1968.14) and the chasmataspidid *Octoberaspis ushakovi* (GIL 35/711) appear to possess a type A appendage consisting of a single segment the preservation in *Brachyopterella* is relatively poor while the morphology of the chasmataspidid appendage (with a seemingly trilobed termination possibly representing the furca) is distinctly different to anything found in eurypterids. Furthermore the supposed type A appendage of *Loganamaraspis dunlopi* NMS G.1957.1.649b) consists of two segments and so it seems likely that the single-segmented appendage in *Octoberaspis* is a derived condition. Based on the presence of a three-segmented type A genital appendage in *Stoermeropterus conicus*, the proliferation of three-segmented type A appendages in the non-pterygotoid Eurypterina, and the presence of a three-segmented type A appendage in *Parastylonurus ornatus* (NMS G.1885.26.72.3) it is considered likely that this represents the plesiomorphic state. The plesiomorphic condition of the type B appendage is even more complicated. The condition in *Eurypterus tetragonophthalmus* is of a short plate with two long furca projecting from it (Braddy & Dunlop 1997, fig. 2b) with a larger portion of the proximal plate hidden dorsally behind the operculum. In pterygotids (Waterston 1964), *Parahughmilleria hefteri* (Størmer 1974) and *Nanahughmilleria norvegica* (Størmer 1934a) however the entire basal plate is visible, being broad and oval shaped, with the furca appearing only as a small terminal segment, while in other taxa the furca appear to fuse into a single elongate plate (Dunlop *et al*. 2002). Dunlop *et al*. considered both these morphologies to be derived from the *Eurypterus* type B appendage, however the type B genital appendage in *Stoermeropterus* and *Moselopterus* most resembles the oval type of *Parahughmilleria* and *Nanahughmilleria*. The morphology of the apparent type B appendage of *Octoberaspis ushakovi* (GIL 35/712) is more similar to the moselopterid type of genital appendage and so this morphology as exemplified in *Stoermeropterus*, rather than that of *Eurypterus*, is considered the plesiomorphic type. Among Stylonurina the type B appendage appears closer in morphology to the type A, consisting of a narrow proximal segment with the tips of the furca projecting from underneath (*Parastylonurus ornatus*: NMS G.1897.32.8; *Stylonurella spinipes*: BGS GSM 87357; *Leiopterella tetliei*: CMN 53573; *Rhenopterus diensti*: MfN 48a; and possibly *Brachyopterus stubblefieldi*:

BGS D 3124) which may represent another stylonurine autapomorphy that became secondarily modified into a broad lobe in *Hibbertopterus* (Waterston 1957, fig. 6).

Genital spatulae associated with the genital appendage have traditionally been considered a defining characteristic of adelophthalmoids, however similar structures have also been described from *Dolichopterus jewetti* (Caster & Kjellesvig-Waering 1956), *Parastylonurus ornatus* (Waterston 1979) and *Drepanopterus abonensis* (Lamsdell *et al*. 2009) and so appear to be more widespread in eurypterids than is generally supposed. Caster & Kjellesvig-Waering (1964, p, 312) lamented the '*Eurypterus* influence' affecting interpretation of eurypterid morphology and it could be argued that a similar phenomenon still exists today; as *Eurypterus* lacks genital spatulae they are considered to be rare occurrences whereas their presence in a number of different eurypterid clades would appear to suggest the opposite. The occurrence of genital spatulae in *Stoermeropterus conicus* may suggest that their possession is a plesiomorphic character within Eurypterida, however current knowledge of their occurrence in other eurypterid clades (including the remaining moselopterids) is too scant to determine this with any certainty. Caster & Kjellesvig-Waering (1956) considered that the spatulae may have been present in all eurypterids but commonly concealed above the operculum, becoming hypertrophied in a number of eurypterids in which they are easily observable. If this were to be the case it would explain why they seem to appear multiple times throughout both the eurypterine and stylonurine lineages.

The possession of deltoid plates anterior to the genital appendage was considered to be a defining characteristic of Eurypterina by Tetlie & Braddy (2004), who stated categorically that stylonurines possess no deltoid plates, however Lamont (1955, pl. 4, fig. 6) figured a genital operculum of *Parastylonurus ornatus* bearing deltoid plates as did Waterston (1979, pl. 6, fig. 6) in *Brachyopterella ritchiei* and deltoid plates were subsequently described in specimens of *Drepanopterus abonensis* (Lamsdell *et al*. 2009, pl. 1, fig. 11 & pl. 2, fig. 1). Considering that different specimens of the same species can appear both to possess and lack deltoid plates (e.g. *Parastylonurus ornatus*: NMS G.1897.32.7 compared to G.1885.26.72.3; *Eurypterus remipes*: YPM 210824 compared to YPM 9003B; *Nanahughmilleria norvegica*: PMO H1632 compared to PMO H1795) it is likely that the apparent presence or otherwise of deltoid plates is heavily dependent on preservation.

The number of segments in the genital operculum has been suggested to be another character of taxonomic importance at subordinal level (Tetlie & Braddy 2004), with the possession of an anterior opercular plate being the primitive state retained in stylonurines. However with Moselopteridae at the base of the Eurypterina and the basal eurypterine taxa *Dolichopterus* (Caster & Kjellesvig-Waering 1956), *Eurypterus* (Wills 1965) and *Erieopterus* (Tetlie & Cuggy 2007) also possessing this anterior opercular plate it seems that this character, like the pediform appendage VI, is the plesiomorphic state in both suborders and is gradually lost along the eurypterine lineage. The anterior opercular plate described by Wills (1964) in *Adelophthalmus* is actually a taphonomic artefact formed by the impression of the posterior margins of the enlarged coxae VI on the genital operculum, and it is thought that the anterior opercular plate was completely lost by the time the mixopteroids diverged from the main eurypterine lineage. The chasmataspidid *Loganamaraspis dunlopi* (NMS G.1957.1.649b) also possesses an anterior opercular plate which is much closer in morphology to a fully expressed ventral segment than that found in eurypterids, and this fits with its origination from somite VII which is also more strongly expressed dorsally than it is in eurypterids. Whether it is homologous to the appendages of somite VII or the sternite has been a subject of some speculation (e.g. Tetlie & Braddy 2004), however Holm (1898) and Wills (1965) showed the anterior opercular plate to be positioned above the metastoma and the operculae with the genital operculum articulating with it, a morphology and position more in line with it being a true sternite than a reduced appendage. This then allows for the metastoma to be derived from the appendages of somite VII, and in turn the endostoma to be formed from the fused epicoxa of appendage VI (see Laurie 1893 and Lamsdell *et al*. 2009 for evidence of the lack of separate epicoxa on appendage VI).

The median and posterior opercular plates represent the appendages of somites VIII and IX and are fused into a single functional operculum in all eurypterids (as recognized by Wills (1965) and shown by the manner in which the operculum is always preserved with both segments, even when complete disarticulation of the rest of the animal has occurred), a characteristic that may be the only reliable eurypterid autapomorphy; the genital operculum of xiphosurans and scorpions consists of a single appendage pair originating from somite VIII (Dunlop & Webster 1999) while the genital appendage of *Octoberaspis ushakovi* is located on the operculum of somite VIII which is preserved distinctly separate from somite IX (GIL 35/711, 35/712) (the genital operculum of *Loganamaraspis dunlopi* is too poorly preserved to differentiate the operculae of somite VIII and IX). Despite the operculae being fused in eurypterids a clear, non-functional suture is visible in Stylonurina (e.g. *Parastylonurus ornatus*: NMS G.1885.26.72.3, G.1897.32.8; *Rhenopterus diensti*: MfN 48a; *Drepanopterus abonensis*: BGS GSM

84700) and the basal Eurypterina e.g. *Stoermeropterus conicus*: NMS G.1885.26.72.17; *Moselopterus ancylotelson*: SMF 26061; *Eurypterus tetragonophthalmus*: BMNH I. 3406.3, I. 3406.23; *Dolichopterus jewetti*: NYSM I13138), however this suture is lost in many more derived taxa, resulting in the median and posterior opercular plates being distinguishable only by the change in cuticular ornamentation (e.g. *Megalograptus ohioensis*: UCM 24117E; *Slimonia acuminata*: SM A16237a; *Pterygotus anglicus*: NBMG 10000); see Dunlop *et al*. (2002, figs. 4 & 5) for an overview of the development of the eurypterine genital operculum.

Plesiomorphic condition of the non-genital trunk appendages. The presence of plate-like operculae on the ventral surface of the opisthosoma is one of the defining characters for Euchelicerata (Weygoldt & Paulus 1979) and can be reliably observed in many eurypterid fossils, as well as the Devonian synziphosurine *Weinbergina* (Stürmer & Bergström 1981), the xiphosurids *Alanops magnificus* (Racheboeuf *et al*. 2002) and *Paleolimulus signatus* (Babcock *et al*. 2000) and the chasmataspidids *Loganamaraspis dunlopi* (Tetlie & Braddy 2004) and *Octoberaspis ushakovi* (Dunlop 2002). Xiphosurans possess six pairs of opercular plates, the first pair being the genital operculum, while the genital operculum and the succeeding opercula has fused in eurypterids (potentially the sole autapomorphy for eurypterids) while some Palaeozoic scorpions have five operculae after the genital segment (Jeram 1998) which is reduced to four in modern forms. Embryological work on scorpions has shown the abdominal ‘sternites’ to actually represent the opercular plates that have fully fused onto the body wall (Farley 2001) and the first two ‘sternites’ of uropygids have also been shown to be sutured operculae (Shultz 1993), suggesting the possession of operculae is a plesiomorphic state for arachnids. Where operculae have been identified in chasmataspidids they appear to be restricted to the buckler region and are therefore found only on three segments, however the Cambrian trace fossil first described by Wahlman & Caster (1978) and later figured by Dunlop *et al*. (2004, fig. 9) as possibly belonging to a chasmataspidid producer seems to show the imprints of six operculae, corresponding to the number found in xiphosurans and suggesting that despite the presence of the fused buckler the mesosoma/metasoma division is the same as in eurypterids and scorpions.

Within eurypterids the four operculae following the genital operculum are usually medially fused, however in the stylonurines *Stylonurella spinipes*, *Leiopterella tetliei*, *Rhenopterus diensti* and *Drepanopterus pentlandicus* the first postgential opercular plate is unfused, a condition shared with *Stoermeropterus conicus*, *Eurypterus remipes*, *Orcanopterus manitoulinensis*, *Slimonia acuminata* and *Mixopterus kiaeri*. The presence of this opercular plate being fused in *Eurypterus henningsmoeni* and the first two operculae being unfused in *Mixopterus kiaeri* however suggests that its fusion is a highly variable character. Evidence from embryological work on scorpions and *Limulus* (Farley 2001, 2010) suggests that a lack of fusion of the anterior operculae may be a paedomorphic characteristic, which would again explain why it appears independently so many times within different eurypterid clades; the presence of unfused opercular appendages in xiphosurans and the chasmataspidid *Loganamaraspis* suggests that this is the plesiomorphic state which is lost in most eurypterid groups but with several species undergoing paedomorphic reversals.

IMPLICATIONS FOR FUTURE EURYPTERID RESEARCH.

Recent work has made much progress in resolving the phylogenetic relationships of the eurypterid groups, however further discoveries may force a reconsideration of these views. As shown by the redescription of *Stoermeropterus conicus*, revisiting specimens held in museum collections, particularly those that have not received much scientific attention for several decades, can yield much new information when they are treated in a modern systematic context, while the discovery of new specimens and fossil localities is also of key importance. Two Canadian localities, the Silurian Eramosa Lagerstätte (von Bitter *et al*. 2007) and the late Ordovician Manitoba biotas (Young *et al*. 2007) have both yielded as yet undescribed eurypterid specimens that have the potential to inform greatly on a poorly-understood period of eurypterid evolution, namely its origins within the Ordovician and radiation into the Silurian. Tollerton (2004) rightly showed that many of the Ordovician records of eurypterids were incorrectly identified, reducing the then recognized number of Ordovician eurypterids to just ten named species, however a number of discoveries since then, including the Manitoba biotas, has shown that Ordovician eurypterids were probably not as rare an occurrence as has been assumed. Our current understanding of eurypterid phylogeny suggests that a number of basal eurypterine clades (namely moselopterids and dolichopterids) probably have a currently undiscovered Ordovician record, and so description of Ordovician eurypterids such as those of the Middle Ordovician St. Peter Formation in Iowa (Liu *et al*. 2006) – which is Darriwilian in age and therefore would represent the oldest record of Eurypterida to date – is of extreme importance. These earliest eurypterids may help resolve the relationships of the basal Chelicerata (xiphosurans, chasmataspidids and eurypterids) which, as shown by the analysis of Shultz (2007), are still poorly resolved phylogenetically and are important to unravel as it has implications for the plesiomorphic character states of Arachnida and hence may provide a solution to the competing hypotheses of scorpions being derived arachnids within a Dromopoda clade or resolving as sister group to all other arachnids.

REFERENCES

AGASSIZ, J. L. R. 1839. Fishes of the Upper Ludlow rock. p. 605–607. *In* MURCHISON, R. I. (Ed.) *The Silurian System, Part 1. Founded on geological researches in the counties of Salop, Hereford, Radnor, Montgomery, Caermarthen, Brecon, Pembroke, Monmouth, Gloucester, Worcester, and Stafford: with descriptions of the coal-fields and overlying formations*. John Murray, London, 768 pp.

ALBERTI, G. K. B. 1970. Trilobiten des jüngeren Siluriums sowie des Unter-und Mitteldevons. II. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, **525**, 1–233.

ALLAN, R. S. 1927. *Keilorites* (a new generic name for a Silurian annelid from Australia). *Geological Magazine*, **64**, 240.

ANDERSON, L. I. 2007. Unmineralised arthropods. p. 133–156. *In* CLARKSON, E. N. K., HARPER, D. A. T., TAYLOR C. M. & ANDERSON, L. I. (Eds.) *Silurian Fossils of the Pentland Hills, Scotland*. The Palaeontological Association, London, 218 pp.

____, CLARKSON, E. N. K., STEWART, S. E. & MITCHELL, D. 2007. An Upper Llandovery Konservat-Lagerstätte in a depositional context: the Pentland Hills Eurypterid Bed, Midlothian. *Scottish Journal of Geology,* **43**, 41–50.

____, DUNLOP, J. A. & TREWIN, N. H. 2000. A Middle Devonian chasmataspid arthropod from Achanarras Quarry, Caithness, Scotland. *Scottish Journal of Geology*, **36**, 151–158.

____, POSCHMANN, M. & BRAUCKMANN, C. 1998. On the Emsian (Lower Devonian) arthropods of the Rhenish Slate Mountains: 2. The synziphosurine *Willwerathia*. *Paläontologische Zeitschrift*, **72**, 325–336.

____ & MOORE, R. A. 2004. Bembicosoma re-examined: a xiphosuran from the Silurian of the North Esk Inlier, Pentland Hills, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **94**, 199–206.

____ & SELDEN, P. A. 1997. Opisthosomal fusion and phylogeny of Palaeozoic Xiphosura. *Lethaia*, **30**, 19–31.

ANDREWS, H. E., BROWER, J. C., GOULD, S. J. & REYMENT, R. A. 1974. Growth and variation in *Eurypterus remipes* De Kay. *Bulletin of the Geological Institutions of the University of Uppsala*, **4**, 81–114.

ANGELIN, N. P. 1854. *Palaeontologica Scandinavica. Pars 1. Crustacea Formationis Transitionis. Fasc. II– Holmiae*. Norstedt & Söner, Stockholm, 92 pp., 41 pls.

BABCOCK, L. E., MERRIAM, D. F. & WEST, D. R. 2000. *Paleolimulus*, an early limuline (Xiphosurida), from Pennsylvanian–Permian Lagerstätten of Kansas and taphonomic comparison with modern *Limulus*. *Lethaia*, **33**, 129–141.

BARRANDE, J. 1846. *Notice Préliminaire sur le Systéme Silurien et les Trilobites de Bohême*. Hirschfeld, Leipzig, 97 pp.

BARTH, F. G. 1985. Slit sensilla and the measurement of cuticular strains. p. 162–188. *In* BARTH, F. G. (Ed.) *Neurobiology of Arachnids*. Springer-Verlag, Berlin, 400 pp.

BEECHER, C. E. 1901. Discovery of eurypterid remains in the Cambrian of Missouri. *American Journal of Science*, **12**, 364.

____ 1904. Note on a new Permian xiphosuran from Kansas. *American Journal of Science*, **17**, 23–24.

BENTON, M. J. & STORRS, G. W. 1994. Testing the quality of the fossil record: paleontological knowledge is improving. *Geology*, **22**, 111–114.

BERGSTRÖM, J. 1968. *Eolimulus*, a Lower Cambrian xiphosurid from Sweden. *Geologiska Föreningens i Stockholm Förhandlingar*, **90**, 489–503.

____ 1975. Functional morphology and evolution of xiphosurids. *Fossils and Strata*, **4**, 291–305, 1 pl.

____ 1979. Morphology of fossil arthropods as a guide to phylogenetic relationships. p. 3–56. *In* GUPTA, A. P. (Ed.) *Arthropod Phylogeny*. Van Nostrand Reinhold Company, New York, 762 pp.

____ 1980. Morphology and systematics of early arthropods. *Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg (Neue Folge)*, **23**, 7–42.

____, STÜRMER, W. & WINTER, G. 1980. *Palaeoisopus*, *Palaeopantopus* and *Palaeothea*, pycnogonid arthropods from the Lower Devonian Hunsrück Slate, West Germany. *Paläontologische Zeitschrift*, **54**, 7–54.

VON BITTER, P. H., PURNELL, M. A., TETREAULT, D. K. & STOTT, C. A. 2007. Eramosa Lagerstätte – Exceptionally preserved soft-bodied biotas with shallow-marine shelly and bioturbating organisms (Silurian, Ontario, Canada). *Geology*, **35**, 879–882.

BJERRESKOV, M. 1975. Llandoverian and Wenlockian graptolites from Bornholm. *Fossils and Strata*, **8**, 1–94.

BOTTING, J. P. 2007. Algae, receptaculitids and sponges. p. 36–49. *In* CLARKSON, E. N. K., HARPER, D. A. T., TAYLOR C. M. & ANDERSON, L. I. (Eds.) *Silurian Fossils of the Pentland Hills, Scotland*. The Palaeontological Association, London, 218 pp.

BOTTON, M. L. & LOVELAND, R. E. 1992. Body size, morphological constraints, and mated pair formation in four populations of horseshoe crabs (*Limulus polyphemus*) along a geographic cline. *Marine Biology*, **112**, 409–415.

____ & ROPES, J. W. 1987. The horseshoe crab, *Limulus polyphemus*, fishery and resource in the United States. *Marine Fisheries Review*, **49**, 57–61.

BOUČEK, B. 1932. Preliminary report on some new species of graptolites from the Gothlandian of Bohemia, part 2. *Věstníku Stáního Geologického ústavu Republiky Československe*, **8**, 150–155.

BRADDY, S. J. 2000. Eurypterids from the Early Devonian of the Midland Valley of Scotland. *Scottish Journal of Geology*, **36**, 115–122.

____ 2001. Eurypterid palaeoecology: palaeobiological, ichnological and comparative evidence for a 'mass–moult–mate' hypothesis. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **172**, 115–132.

____, ALDRIDGE, R. J., GABBOTT, S. E. & THERON, J. N. 1999. Lamellate book-gills in a late Ordovician eurypterid from the Soom Shale, South Africa: support for a eurypterid–scorpion clade. *Lethaia*, **32**, 72–74.

____, ____ & THERON, J. N. 1995. A new eurypterid from the Late Ordovician Table Mountain Group, South Africa. *Palaeontology*, **38**, 563–581, 3 pls.

____ & DUNLOP, J. A. 1997. The functional morphology of mating in the Silurian eurypterid, *Baltoeurypterus tetragonophthalmus* (Fischer, 1839). *Zoological Journal of the Linnean Society*, **121**, 435–461.

____, SELDEN, P. A. & DOAN NHAT, T. 2002. A new carcinosomatid eurypterid from the Upper Silurian of Northern Vietnam. *Palaeontology*, **45**, 897–915.

BRAUER, A. 1895. Beiträge zur Kenntnis der Entwicklungsgeschicte des Skorpiones, II. *Zeitschrift für wissenschaftliche Zoologie*, **59**, 351–433.

BRAUN, A. 1997. Vorkommen, Untersuchungsmethoden und Bedeutung tierischer Cuticulae in kohligen Sedimentgesteinen des Devons und Karbons. *Palaeontographica, Abteilung A*, **24**, 83–156, 15 pls.

BREMER, K. 1994. Branch support and tree stability. *Cladistics*, **10**, 295–304.

BRIGGS, D. E. G. & FORTEY, R. A. 1989. The early radiation and relationships of the major arthropod groups. *Science*, **246**, 241–243.

____, BRUTON, D. L. & WHITTINGTON, H. 1979. Appendages of the arthropod *Aglaspis spinifer* (Upper Cambrian, Wisconsin) and their significance. *Palaeontology*, **22**, 167–180.

____, FORTEY, R. A. & WILLS, M. A. 1992. Morphological disparity in the Cambrian. *Science*, **256**, 1670–1673.

BROILI, F. 1928. Crustaceenfunde aus dem rheinischen Unterdevon. *Sitzungsberichte der Bayerischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Abteilung*, **1928**, 197–201.

BRONN, H. G. 1835. *Lethaea geognostica*, **1**, Stuttgart, 544 pp.

BROWER, J. C. 1975. Silurian crinoids from the Pentland Hills, Scotland. *Palaeontology*, **18**, 631–656, pls. 73–75.

BRUSATTE, S. L. 2010. Representing supraspecific taxa in higher-level phylogenetic analyses: guidelines for palaeontologists. *Palaeontology*, **53**, 1–9.

BUDD, G. E. & TELFORD, M. J. 2009. The origin and evolution of arthropods. *Nature*, **457**, 812–817.

BURMEISTER, H. 1843. *Die Organisation der Trilobiten, aus ihren lebenden Verwandten entwickelt; nebst systematische Uebersicht aller Seitherbeschriebenen Arten.* G. Reimer, Berlin. 148 pp.

BUTLER, A. B. & SAIDEL, W. M. 2000. Defining sameness: historical, biological, and generative homology. *BioEssays*, **22**, 846–853.

CASTER, K. E. & BROOKS, H. K. 1956. New fossils from the Canadian-Chazan (Ordovician) hiatus in Tennessee. *Bulletin of American Palaeontology*, **36**, 157–199.

____ & KJELLESVIG-WAERING, E. N. 1953. *Melbournopterus*, a new Silurian eurypterid from Australia. *Journal of Paleontology*, **27**, 153–156.

____ & ____. 1956. Some notes on the genus *Dolichopterus* Hall. *Journal of Paleontology*, **30**, 19–28.

____ & ____. 1964. Upper Ordovician eurypterids from Ohio. *Palaeontographica Americana*, **4**, 300–358, pls 43–53.

____ & MACKE, W. B. 1952. An aglaspid merostome from the Upper Ordovician of Ohio. *Journal of Paleontology*, **26**, 753–757, pl. 109.

CHEN, J., EDGECOMBE, G. D., RAMSKÖLD, L. & ZHOU, G. 1995. Head segmentation in Early Cambrian *Fuxianhuia*: implications for arthropod evolution. *Science*, **268**, 1339–1343.

____, WALOSZEK, D. & MAAS, A. 2004. A new 'great-appendage' arthropod from the Lower Cambrian of China and homology of chelicerate chelicerae and raptorial antero-ventral appendages. *Lethaia*, **37**, 3–20.

CHLUPÁČ, I. 1995. Lower Cambrian arthropods from the Paseky Shale (Barrandian area, Czech Republic). *Journal of the Czech Geological Society*, **44**, 79–92.

____ & HAVLÍČEK, V. 1965. *Kodymirus* n. g., a new aglaspid merostome of the Cambrian of Bohemia. *Sborník Geologických věd, Paleontologie, Praha*, **6**, 7–20.

CLARKE, J. M. 1902. Notes on Paleozoic crustaceans. *New York State Museum Report*, **54**, 83–110.

____ & RUEDEMANN, R. 1912. The Eurypterida of New York. *New York State Museum Memoirs*, **14**, 1–439, 88 pls.

CLARKSON, E. N. K. 2000. Pentland Odyssey. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **36**, 8–16.

____, HARPER, D. A. T. & TAYLOR, C. M. 2001. Scottish Silurian shorelines. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **91**, 479–487.

____ & TAYLOR, C. M. 2007. Silurian rocks and fossils in the Pentland Hills. p. 8–29. *In* CLARKSON, E. N. K., HARPER, D. A. T., TAYLOR C. M. & ANDERSON, L. I. (Eds.) *Silurian Fossils of the Pentland Hills, Scotland*. The Palaeontological Association, London, 218 pp.

CLAYPOLE, E. W. 1890. *Carcinosoma newlini. American Geologist*, **6**, 400.

COCKS, L. R. M., HOLLAND, C. H., RICKARDS, R. B. & STRACHAN, I. 1971. A correlation of Silurian rocks in the British Isles. *Journal of the Geological Society of London*, **127**, 103–136.

COPELAND, M. J. 1971. Additional Silurian Arthropoda from Arctic and eastern Canada. *Geological Survey of Canada, Bulletin*, **200**, 19–35.

COTTON, T. J. & BRADDY, S. J. 2004. The phylogeny of arachnomorph arthropods and the origin of Chelicerata. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **94**, 169–193.

CRUCITTI, P., MORELLI, R. & SERAFINO, A. 1998. The genital papillae of the species of scorpions (Scorpiones: Chactidae): a SEM study. *Doriana*, **7**, 1–8.

CUGGY, M. B. 1994. Ontogenetic variation in Silurian eurypterids from Ontario and New York State. *Canadian Journal of Earth Sciences*, **31**, 728–732.

CURRIE, L. D. 1927. On *Cyamocephalus*, a new synziphosuran from the Upper Silurian of Lesmahagow, Lanarkshire. *Geological Magazine*, **64**, 153–157.

DARWIN, C. R. 1871. *The descent of man, and selection in relation to sex*. John Murray, London, 898 pp.

DAVIDSON, T. 1848. Sur les brachiopods du système Silurian supérieur de l'Angleterre. *Le Bulletin de la Société Géologique de France*, **5**, 309–338, 370–374.

DIENER, C. 1924. Fossilium Catalogus, I: Animalia; Pars 25: Eurypterida. Berlin, 28 pp.

DE KAY, J. E. 1825. Observations on a fossil crustaceous animal of the order Branchiopoda. *Annals of the New York Lyceum of Natural History*, **1**, 375–377.

DELLE, N. 1937. Zemgales lidzenuma, Augszemes un Lietuvas devona nogulumi. *Acta Universitatis Latviensis, Matēmatikas un Dabas Zinātnu Fakultātes Serija*, **2(5)**, 105–384.

DESMAREST, A.-G. 1822. Les crustacès proprement dits. p. 66–154. *In* BRONGNIART, A. & DESMAREST, A.-G. *Histoire naturelle des crustacès fossiles, sous les rapports zoologiques et geologiques.* F.-G. Levrault, Paris, Strasbourg, 154 pp, 11 pls.

DONOVAN, S. K., FEARNHEAD, F. E., CLARKSON, E. N. K. & DONOVAN, M. 2011. Aspects of crinoid palaeontology of the North Esk Inlier, Scotland (Silurian, Llandovery, Telychian). *Palaeontology*, **54**, 241–252.

DUNLOP, J. A. 2002. Arthropods from the Lower Devonian Severnaya Zemlya Formation of October Revolution Island (Russia). *Geodiversitas*, **24**, 349–379.

____ 2006. New ideas about the euchelicerate stem-lineage. p. 9–23. *In* DELTSHEV, C. & STOEV, P. (Eds.) European Arachnology 2005. *Acta zoologica bulgarica*, Supplement 1, 343 pp.

____, ANDERSON, L. I. & BRADDY, S. J. 1999. A new chasmataspid (Chelicerata: Chasmataspida) from the Lower Devonian of the Midland Valley of Scotland. *Transactions of the Royal Society of Edinburgh, Earth Sciences,* **89**, 161–165.

____, ____ & ____. 2004. A redescription of *Chasmataspis laurencii* Caster & Brooks, 1956 (Chelicerata: Chasmataspidida) from the Middle Ordovician of Tennessee, USA, with remarks on chasmataspid phylogeny. *Transactions of the Royal Society of Edinburgh, Earth Sciences,* **94**, 207–225.

____ & BRADDY, S. J. 1997. Slit-like structures on the prosomal appendages of the eurypterid *Baltoeurypterus*. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1**, 31–38.

____, ____ & TETLIE, O. E. 2002. The Early Devonian eurypterid *Grossopterus overathi* (Gross, 1933) from Overath. Germany. *Mitteilungen aus dem Museum für Naturkunde in Berlin, Geowissenschaftliche Reihe,* **5**, 93–104.

____, POSCHMANN, M. & ANDERSON, L. I. 2001. On the Emsian (Early Devonian) arthropods of the Rhenish Slate Mountains: 3. The chasmataspidid *Diploaspis*. *Paläontologische Zeitschrift,* **75**, 253–269.

____ & SELDEN, P. A. 1997. The early history and phylogeny of the chelicerates. p. 221–235. *In* FORTEY, R. A. & THOMAS, R. H. (Eds.) *Arthropod relationships*. Systematics Association Special Volumes Series, No. 55, London, Chapman & Hall, 400 pp.

____, TETLIE, O. E. & PRENDINI, L. 2008. Reinterpretation of the Silurian scorpion *Proscorpius osborni* (Whitfield): integrating data from Palaeozoic and Recent scorpions. *Palaeontology,* **51**, 303–320, 3 pls.

____ & WEBSTER, M. 1999. Fossil evidence, terrestrialization and arachnid phylogeny. *The Journal of Arachnology*, **27**, 86–93.

EDGECOMBE, G. D. 2010. Arthropod phylogeny: an overview from the perspectives of morphology, molecular data and the fossil record. *Arthropod Structure and Devlopment*, **39**, 74–87.

___ & RAMSKÖLD, L. 1996. Classification of the arthropod *Fuxianhuia*: Response. *Science*, **272**, 747–748.

D'EICHWALD, C. E. 1854. Die Grauwackenschichten von Live- und Esthland. *Bulletin de la Société Imperiale des Naturalistes de Moscou*, **27**, 1–211.

ELDREDGE, N. 1974. Revision of the suborder Synziphosurina (Chelicerata, Merostomata), with remarks on merostome phylogeny. *American Museum Novitates*, **2543**, 1–41.

____ & PLOTNICK, R. E. 1974. Revision of the pseudoniscine merostome genus *Cyamocephalus* Currie. *American Museum Novitates*, **2557**, 1–10.

ELLES, G. L. & WOOD, E. M. R. 1908. A monograph of British graptolites. Part 7. *Palaeontographical Society Monograph*, **62**, cxxi–cxlviii, 273–358, pls. 32–35.

EPSTEIN, J. B. 1993. Stratigraphy of Silurian rocks in Shawangunk Mountain, southeastern New York, including a historical review of nomenclature. *U.S. Geological Survey Bulletin*, **1839**, **Chapter L**, 40 pp.

ETHERIDGE JR., R. 1877. On the remains of a large crustacean, probably indicative of a new species of *Eurypterus*, or allied genus (*Eurypterus*? *stevensoni*), from the Lower Carboniferous Series (Cementstone Group) of Berwickshire. *Quarterly Journal of the Geological Society*, **33**, 223–228.

FARLEY, R. D. 2001. Abdominal plates, spiracles and sternites in the ventral mesosoma of embryos of the desert scorpion *Paruroctenus mesaensis* (Scorpiones, Vaejovidae). *Invertebrate Reproduction and Development*, **40**, 193–208.

____ 2010. Book gill delevopment in embryos and first and second instars of the horseshoe crab *Limulus polyphemus* L. (Chelicerata, Xiphosura). *Arthropod Structure & Development*, **39**, 369–381.

FARRIS, J. S., ALBERT, V. A., KÄLLERSJÖ, M., LIPSCOMB, D. & KLUGE, A. G. 1996. Parsimony jackknifing outperforms neighbor-joining. *Cladistics*, **12**, 99–124.

FEIST, R., LEROSEY-AUBRIL, R. & JOHNON, R. 2010. Coaptative devices, enrollment, and life habits in *Paralejurus*, a particular case in scutelluid trilobites. *Palaeobiodiversity and Palaeoenvironments*, **90**, 125–137.

FILIPIAK, P. & ZATOŃ, M. 2010. Plant and animal cuticle remains from the Lower Devonian of southern Poland and their palaeoenvironmental significance. *Lethaia*, DOI: 10.1111/j.1502-3931.2010.00251.x.

FISCHER DE WALDHEIM, G. 1839. Notes sur un crustacé fossile du genre *Eurypterus* de Podolie. *Bulletin de la Societe Imperiale des Naturalistes de Moscou*, **11**, 125–128.

FISHER, D. C. 1981. The role of functional analysis in phylogenetic inference: examples from the history of the Xiphosura. *American Zoologist*, **21**, 47–62.

FORTEY, R. A. 1986. The type species of the Ordovician trilobite *Symphysurus*: systematics, functional morphology and terrace ridges. *Paläontologische Zeitschrift*, **60**, 255–275.

GASKELL, W. H. 1908. *The origin of vertebrates*. Longmans, Green, and Co., London, 537 pp.

GOLOBOFF, P. A., FARRIS, J. S. & NIXON, K. C. 2008. TNT, a free program for phylogenetic analysis. *Cladistics*, **24**, 774–786.

GRADSTEIN, F. M., OGG, J. G. & SMITH, A. G. 2004. *A geologic time scale 2004*. Cambridge University Press, 610 pp.

GROSS, W. 1933. Die unterdevonischen Fische und Gigantostraken von Overath. *Abhandlungen der Preußischen Geologischen Landesanstalt, Neue Folge*, **145**, 41–77.

GROTE, A. R. & PITT, W. H. 1875. On new species of *Eusarcus* and *Pterygotus* from the Water Lime Group at Buffalo. *Buffalo Society of Natural Science, Bulletin*, **3**, 17–20.

GUPTA, N. S., TETLIE, O. E., BRIGGS, D. E. G. & PANCOST, R. D. 2007. The fossilization of eurypterids: a result of molecular transformation. *Palaios*, **22**, 439–447.

HALL, J. 1843. Natural History of New York, Geology of New York. Part 4. *Survey of the fourth geological district*, Albany, 683 pp.

____ 1847. Descriptions of the organic remains of the lower divisions of the New York System. *New York Natural History Survey, Palaeontology of New York,* **1**, 362 pp., 84 pls.

____ 1859. *Natural History of New York: Palaeontology, III*. New York State Museum, 532 pp.

____ 1862. A new crustacean from the Potsdam Sandstone. *Canadian Naturalist*, **7**, 443–445.

____ 1884. Description of a new species of *Stylonurus* from the Catskill Group. *New York State Museum (36th Annual Report)*, 76–77.

____ & CLARKE, J. M. 1888. *Palaeontology of New York, Volume 7.* Albany, C. Van Benthuysen, 236 pp.

HANKEN, N.-M. & STØRMER, L. 1975. The trail of a large Silurian eurypterid. *Fossils and Strata*, **4**, 255–270, 3 pls.

HARLAN, R. 1834. Critical notices of various organic remains hitherto discovered in North America. *Transactions of the Geological Society of Pennsylvania*, **1**, 46–112.

HATA, D. & BERKSON, J. 2003. Abundance of horseshoe crabs (*Limulus polyphemus*) in the Delaware Bay area. *Fishery Bulletin*, **101**, 933–938.

HESSELBO, S. P. 1992. Aglaspidida (Arthropoda) from the Upper Cambrian of Wisconsin. *Journal of Paleontology*, **66**, 885–923.

HIBBERT, S. 1836. On the fresh-water limestone of Burdiehouse in the neighbourhood of Edinburgh belonging to the Carboniferous Group of rocks. With supplementary notes on other fresh-water limestones. *Transactions of the Royal Society of Edinburgh,* **13**, 169–282.

HOLM, G. 1898. Über die Organisation des *Eurypterus fischeri* Eichw. *Mémoires de L'Académie Impériale des Sciences de St.-Pétersbourg*, **8(2)**, 1–57.

HOU, X. 1987a. Two new arthropods from Lower Cambrian, Chengjiang, eastern Yunnan. *Acta Palaeontologica Sinica*, **26**, 236–256.

____ 1987b. Three new large arthropods from Lower Cambrian Chengjiang, eastern Yunnan. *Acta Palaeontologica Sinica*, **26**, 272–285.

____ & BERGSTRÖM, J. 1997. Arthropods from the Lower Cambrian Chengjiang Fauna, southwest China. *Fossils and Strata*, **45**, 1–116.

HUELSENBECK, J. P. 1994. Comparing the stratigraphic record to estimates of phylogeny. *Paleobiology*, **20**, 470–483.

HÜNICKEN, M. A. 1980. A giant fossil spider (*Megarachne servinei*) from Bajo de Véliz, Upper Carboniferous, Argentina. *Boletin de la Academia Nacional de Ciencias, Córdoba, Argentina*, **53**, 317–341.

HUXLEY, T. H. & SALTER, J. W. 1859. On the anatomy and affinities of the genus *Pterygotus* and description of new species of *Pterygotus*. *Memoires of the Geological Survey of the United Kingdom*, **1**, 105 pp.

JAEKEL, O. 1914. Ein großer *Pterygotus* aus dem rheinischen Unterdevon. *Palaeontologische Zeitschrift*, **1**, 379–382.

JERAM, A. J. 1994. Scorpions from the Viséan of East Kirkton, West Lothian, Scotland, with a revision of the infraorder Mesoscorpionina. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **84**, 283–299.

____ 1998. Phylogeny, classification and evolution of Silurian and Devonian scorpions. p. 7–31. *In* SELDEN, P. A. (Ed.) *Proceedings of the 17th European Colloquium of Arachnology, Edinburgh, 1997*. The British Arachnological Society, Burnham Beeches, 350 pp.

____ & SELDEN, P. A. 1994. Eurypterids from the Viséan of East Kirkton, West Lothian, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **84**, 301–308.

JORDAN, H. & VON MEYER, H. 1854. Ueber die Crustaceen der Steinkohlenformation von Saarbrücken. *Palaeontographica*, **4**, 1–15.

KAMENZ, C. & PRENDINI, L. 2008. An atlas of book lung fine structure in the Order Scorpiones (Arachnida). *Bulletin of the American Museum of Natural History*, **316**, 1–359, 156 pls.

____, DUNLOP, J. A. & STAUDE, A. 2009. The true nature of the eurypterid 'horn organs'. *The Palaeontological Association 53rd Annual Meeting, Programme and Abstract*, 56.

KIÆR, J. 1911. A new Downtonian fauna in the sandstone series of the Kristiana area: a preliminary report. *Skrifter utgitt av Det Norske Videnskaps-Akademi i Oslo I. Matematisk-Naturvidenskapelig Klasse*, **7**, 1–22.

KIER, P. M. 1973. A new Silurian echinoid genus from Scotland. *Palaeontology*, **16**, 651–663, pls. 80–83.

KJELLESVIG-WAERING, E. N. 1948. Two new eurypterids from the Silurian of Indiana. *Journal of Paleontology*, **22**, 465–472, pls. 71–72.

____ 1950. A new Silurian *Hughmilleria* from West Virginia. *Journal of Paleontology*, **24**, 226–228, pl 38.

____ 1951. Downtonian (Silurian) Eurypterida from Perton, near Stoke Edith, Herefordshire. *Geological Magazine*, **88**, 1–22, pls. 1–3.

____ 1958a. The genera, species and subspecies of the Family Eurypteridae, Burmeister, 1845. *Journal of Paleontology*, **32**, 1107–1148, 6 pls.

____ 1958b. Some previously unknown morphological structures of *Carcinosoma newlini* (Claypole). *Journal of Paleontology*, **32**, 292–303, pls. 41–43.

____ 1959. A taxonomic review of some late Paleozoic Eurypterida. *Journal of Paleontology*, **33**, 251–256, pl. 38.

____ 1961. The Silurian Eurypterida of the Welsh Borderlands. *Journal of Paleontology*, **35**, 789–835, 3 pls.

____ 1963. Pennsylvanian invertebrates of the Mazon Creek area, Illinois. *Fieldiana, Geology*, **12**, 85–106.

____ 1964a. Eurypterida: Notes on the subgenus *Hughmilleria* (*Nanahughmilleria*) from the Silurian of New York. *Journal of Paleontology*, **38**, 410–412.

____ 1964b. A synopsis of the Family Pterygotidae Clarke & Ruedemann, 1912 (Eurypterida). *Journal of Paleontology*, **38**, 331–361, pls. 53–56.

____1966. A revision of the families and genera of the Stylonuracea (Eurypterida). *Fieldiana, Geology*, **14**, 169–197.

____1979a. Eurypterida. p. 290–296. *In* FAIRBRIDGE, R. & JABLONKSI, D. (Eds.) *The Encyclopedia of Paleontology*. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania, 886 pp.

____1979b. Eurypterids. p. 121–136. *In* JAANUSSON, V., LAUFELD, S. & SKOGLUND, R. (Eds.) *Lower Wenlock Faunal and Floral Dynamics – Vttenfallet Section, Gotland*. Sveriges Geologiska Undersökning, 294 pp.

____ & HEUBUSCH, C. A. 1962. Some Eurypterida from the Ordovician and Silurian of New York. *Journal of Paleontology,* **36**, 211–221, pls. 36–38.

____ & LEUTZE, W. P. 1966. Eurypterids from the Silurian of West Virginia. *Journal of Paleontology,* **40**, 1109–1122, 2 pls.

KOCH, L. E. 1977. The taxonomy, geographic distribution and evolutionary radiation of Australo-Papuan scorpions. *Records of the Western Australian Museum*, **5**, 83–367.

KRAEPELIN, K. 1907. Die sekundären Geschlechtscharaktere der Skorpione, Pedipalpen und Solifugen. *Mitteilungen aus dem Naturhistorischen Museum in Hamburg*, **25**, 181–225.

KUES, B. S. & KIETZKE, K. K. 1981. A large assemblage of a new eurypterid from the Red Tanks Member, Madera Formation (Late Pennsylvanian-Early Permian) of New Mexico. *Journal of Paleontology*, **55**, 709–729, 3 pls.

LAMONT, A. 1952. Ecology and correlation of the Pentlandian - a new division of the Silurian System in Scotland. Pp. 27-32. *In* Dighton-Thomas, H (Ed.). *Faunal and floral facies and zonal correlation.* Report of the 18th Session of the International Geological Congress, Great Britain, 1948. Part 10.

____ 1955. Scottish Silurian Chelicerata. *Transactions of the Geological Society of Edinburgh*, **16**, 200–216, 4 pls.

____ 1978. Pentlandian miscellany: Mollusca, Trilobita etc. *Scottish Journal of Science*, **1**, 245–302.

LAMSDELL, J. C. & BRADDY, S. J. 2010. Cope's Rule and Romer's theory: Patterns of diversity and gigantism in eurypterids and Palaeozoic vertebrates. *Biology Letters*, **6**, 265–269.

____, ____ & TETLIE, O. E. 2009. Redescription of *Drepanopterus abonensis* (Chelicerata: Eurypterida: Stylonurina) from the Late Devonian of Portishead, UK. *Palaeontology* **52**, 1113–1139, 7 pls.

____, ____ & ____. 2010a. The systematics and phylogeny of the Stylonurina (Arthropoda: Chelicerata: Eurypterida). *Journal of Systematic Palaeontology*, **8**, 49–61.

____, ____, LOEFFLER, E. J. & DINELEY, D. L. 2010b. Early Devonian stylonurine eurypterids from Arctic Canada. *Canadian Journal of Earth Sciences*, **47**, 1405–1415.

LANKESTER, E. R. 1881. *Limulus* an arachnid. *Quarterly Journal of Microscopical Science*, **21**, 504–548.

LATREILLE, P. A. 1802. *Histoire naturelle, generale et particulière, des Crustacés et des Insectes, volume 7*. Dufart, Paris, 391 pp.

LAUB, R. S., TOLLERTON, V. P. JR. & BERKOF, R. S. 2010. The cheliceral claw of *Acutiramus* (Arthropoda: Eurypterida): functional analysis based on morphology and engineering principles. *Bulletin of the Buffalo Society of Natural Sciences*, **39**, 29–42.

LAURIE, M. 1892. On some eurypterid remains from the Upper Silurian rocks of the Pentland Hills. *Transactions of the Royal Society of Edinburgh*, **37**, 151–162, 3 pls.

____ 1893. The anatomy and relations of the Eurypteridæ. *Transactions of the Royal Society of Edinburgh*, **37**, 509–528, 2 pls.

____ 1899. On a Silurian scorpion and some additional eurypterid remains from the Pentland Hills. *Transactions of the Royal Society of Edinburgh*, **39**, 575–589, 5 pls.

LAUTERBACK, K. E. 1980. Schlüsselereignisse in der Evolution des Grundplans der Arachnata (Arthropoda). *Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg (Neue Folge)*, **23**, 163–327.

LEACH, W. E. 1819. Entomostracés, p. 524–543. *In* LEVRAULT, F. G. (Ed.) *Dictionnaires des Sciences Naturelles*, *volume 14*. Paris, 558 pp.

LEUTZE, W. P. 1961. Arthropods from the Syracuse Formation, Silurian of New York. *Journal of Paleontology*, **35**, 49–64.

LINDSTRÖM, G. 1861. Bidrag till kännedomen om Gotlands brachiopoden. *Öfversigt af Konglingun Vetenskaps-Akademians Förhandlingar*, **17**, 337–382, pls. 12–13.

LINNAEUS, C. 1758. *Systema Naturae*, **1**, 1–824. Editio Decima Reformata, Stockholm.

____ 1767. *Systema Naturae*, **1(2)**, 533–1327. Editio Duodecima Reformata, Stockholm.

LIU, H. B., MCKAY, R. M., YOUNG, J. N., WITZKE, B. J., MCVEY, K. J. & LIU, X. 2006. A new Lagerstätte from the Middle Ordovician St. Peter Formation in northeast Iowa, USA. *Geology*, **34**, 969–972.

LIU, Y., HOU, X. & BERGSTRÖM, J. 2007. Chengjiang arthropod *Leanchoilia illecebrosa* (Hou, 1987) reconsidered. *GFF*, **129**, 263–272.

LONSDALE, W. 1839. Corals. p. 675–694. *In* MURCHISON, R. I. (Ed.) *The Silurian System, Part 1. Founded on geological researches in the counties of Salop, Hereford, Radnor, Montgomery, Caermarthen, Brecon, Pembroke, Monmouth, Gloucester, Worcester, and Stafford: with descriptions of the coal-fields and overlying formations*. John Murray, London, 768 pp.

LOYDELL, D. K. 2005. Graptolites from the Deerhope Formation, North Esk Inlier. *Scottish Journal of Geology*, **41**, 189–190.

LUO, H., HU, S., CHEN, L., ZHANG, S. & TAO, Y. 1999. *Early Cambrian Chengjiang fauna from Kunming region, China*. Yunnan Science and Technology Press, Kunming, China, 129 pp.

MADDISON, W. P. & MADDISON, D. R. 2010. Mesquite: A modular system for evolutionary analysis. Version 2.73. http://mesquiteproject.org

MANNING, P. L. & DUNLOP, J. A. 1995. The respiratory organs of eurypterids. *Palaeontology*, **38**, 287–297, 2 pls.

M'COY, F. 1846. *A synopsis of the Silurian fossils of Ireland collected from the several districts by Richard Griffith, F. G. S.* Dublin, 72 pp., 5 pls.

____ 1849. On the classification of some British fossil Crustacea, with notices of new forms in the university collection at Cambridge. *Annals and Magazine of Natural History, including Zoology, Botany, and Geology,* **24**, 392–414.

____ 1851. On some new Silurian Mollusca. *Annals and Magazine of Natural History, including Zoology, Botany, and Geology,* **77**, 45–65.

____ 1852. *A synopsis of the classification of the British Palaeozoic rocks, with a systematic description of the British Palaeozoic fossils in the Geological Museum of the University of Cambridge with figures of the new and imperfectly known species.* Parker & Son, London, 661 pp., 25 pls.

MCCOY, V. E. & BRANDT, D. S. 2009. Scorpion taphonomy: criteria for distinguishing fossil scorpion molts and carcasses. *The Journal of Arachnology*, **37**, 312–320.

MEEK, F. B. & WORTHEN, A. H. 1865. Notice of some new types of organic remains from the Coal Measures of Illinois. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **17**, 41–45.

____ & ____ 1868. Palaeontology of Illinois. *Geological Survey of Illinois*, **3**, 289–565.

MICKWITZ, A. 1909. Vorlaeufige Mitteiling über das genus *Pseudolingula* Mickwitz. *Mémoires de l'Académie Impériale des Sciences de St. Petersbourg (series 6),* **3**, 765–772.

MILLER, J. 1975. Structure and function of trilobite terrace lines. *Fossils and Strata*, **4**, 155–178.

MILLER, R. F. 2007. *Pterygotus anglicus* Agassiz (Chelicerata: Eurypterida) from Atholville, Lower Devonian Campbelltown Formation, New Brunswick, Canada. *Palaeontology*, **50**, 981–999, 1 pl.

MILLER, S. A. 1874. Notes and descriptions of Cincinnatian Group fossils. *Cincinnati Quarterly Journal of Science,* **1**, 343–351.

____ & GURLEY, W. F. E. 1896. New species of Echinodermata and a new crustacean from the Paleozoic rocks. *Illinois State Museum Natural History Bulletin*, **10**, 1–91.

MOLYNEUX, S. G., BARRON, H. F. & SMITH, R. A. 2008. Upper Llandovery–Wenlock (Silurian) palynology of the Pentland Hills inliers, Midland Valley of Scotland. *Scottish Journal of Geology*, **44**, 151–168.

MOORE, P. F. 1941. On gill-like structures in the Eurypterida. *Geological Magazine*, **78**, 62–70, 1 pl.

MOORE, R. A., BRIGGS, D. E. G. & BARTELS, C. 2005a. A new specimen of *Weinbergina opitzi* (Chelicerata: Xiphosura) from the Lower Devonian Hunsrück Slate, Germany. *Paläontologische Zeitschrift*, **79**, 399–408.

____, ____, BRADDY, S. J., ANDERSON, L. I., MIKULIC, D. G. & KLUESSENDORF, J. 2005b. A new synziphosurine (Chelicerata: Xiphosura) from the late Llandovery (Silurian) Waukesha lagerstätte, Wisconsin, USA. *Journal of Paleontology*, **79**, 242–250.

MÜLLER, O. F. 1785. *Entomastraca, seu, Insecta testacea quae in aquis Daniae et Norvegiae reperit, descripsit et iconibus illustravit.* Hauniae, Thiele, 134 pp.

MURCHISON, R. I. 1859. *Siluria* (Third edition). John Murray, London, 592 pp.

NICHOLSON, H. A. 1872. *A monograph of the British Graptolidae. Part 1. General introduction*. Blackwood and Sons, Edinburgh and London, 133 pp.

NIESZKOWSKI, J. 1859. Zusatze zur Monographie der Trilobiten der Ostseeprovinzen, nebst der Beschriebung einiger neuen obersilurischen Crustaceen. *Archiv für die Naturkunde Liv.-, Ehst.- und Kurlands (Ser. 1)*, **1**, 345–384.

NOVOJILOV, N. J. 1959. Mérostomes du Dévonian inférieur et moyen de Sibérie. *Annales de la Société Géologique du Nord*, **78**, 241–258.

____ 1962. Order Eurypterida [in Russian]. p. 404–423, pls. 18–22. *In* ORLOV, Y. A. (Ed.) *Fundamentals of Paleontology, Volume 9; Arthropoda, Tracheata, Chelicerata* [in Russian], Moscow, 894 pp.

OGG, J. G., OGG, G. & GRADSTEIN, F. M. 2008. *The concise geological time scale*. Cambridge University Press, 184 pp.

O'LEARY, M. A. & KAUFMAN, S. G. 2007. MorphoBank 2.5: Web application for morphological phylogenetics and taxonomy. http://www.morphobank.org.

ORR, P. J., BRIGGS, D. E. G., SIVETER, D. J. & SIVETER, D. J. 2000a. Three-dimensional preservation of a nonbiomineralized arthropod in concretions in Silurian volcaniclastic rocks from Herefordshire, England. *Journal of the Geological Society, London,* **157**, 173–186.

____, SIVETER, D. J., BRIGGS, D. E. G., SIVETER, D. J. & SUTTON, M. D. 2000b. A new arthropod from the Silurian Konservat-Lagerstätte of Herefordshire, England. *Proceedings of the Royal Society of London, B*, **267**, 1497–1504.

PAGE, D. 1856. *Advanced textbook of geology*. William Blackwood and Sons, Edinburgh, 326 pp.

____ 1859. *Advanced textbook of geology, 2nd edition*. William Blackwood and Sons, London, 403 pp.

PEACH, B. N. & HORNE, J. 1899. The Silurian rocks of Britain, I. Scotland. *Memoir of the Geological Survey of the United Kingdom.* Hedderwick and Sons, 749 pp.

PETRUNKEVITCH, A. I. 1949. A study of Palaeozoic Arachnida. *Transactions of the Connecticut Academy of Arts and Sciences*, **37**, 69–315.

PICKETT, J. W. 1993. A Late Devonian xiphosuran from near Parkes, New South Wales. *Memoirs of the Association of Australian Palaeontologists*, **15**, 279–287.

PITCHER, B. L. 1939. The Upper Valentian gastropod fauna of Shropshire. *Annals and Magazine of Natural History*, **11**, 82–132.

PLOTNICK, R. E. 1985. Lift based mechanisms for swimming in eurypterids and portunid crabs. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **76**, 325–337.

____ 1999. Habitat of Llandoverian-Lochkovian eurypterids. p. 106–131. *In* BOUCOT, A. J. & LAWSON, J. (Eds.), *Paleocommunities: A case study from the Silurian and Lower Devonian*. Cambridge University Press, 912 pp.

____ & BAUMILLER, T. K. 1988. The pterygotid telson as a biological rudder. *Lethaia*, **21**, 13–27.

POCOCK, R. I. 1902. The taxonomy of the recent species of *Limulus*. *Annals and Magazine of Natural History*, **9**, 246–266.

POLIS, G. A. 1990. Ecology. p. 247-293. *In* POLIS, G. A. (Ed.), *The biology of scorpions*. Stanford University Press, Stanford, California, 587 pp.

____ & LOURENÇO, W. R. 1986. Sociality among scorpions. *Actas X Congreso Internacional de Aracnologia*, **1**, 111–115.

____ & SISSOM, W. D. 1990. Life history. p. 161–223. *In* POLIS, G. A. (Ed.), *The biology of scorpions*. Stanford University Press, Stanford, California, 587 pp.

POSCHMANN, M. 2006. The eurypterid *Adelophthalmus sievertsi* (Chelicerata: Eurypterida) from the Lower Devonian (Emsian) Klerf Formation of Willwerath, Germany. *Palaeontology*, **49**, 67–82, 1 pl.

____, ANDERSON, L. I. & DUNLOP, J. A. 2005. Chelicerate arthropods, including the oldest phalangiotarbid arachnid, from the Early Devonian (Siegenian) of the Rhenish Massif, Germany. *Journal of Paleontology*, **79**, 110–124.

____ & FRANKE, C. 2006. Arthropods and trace fossils from the Lower Devonian (Emsian) of the West Eifel region ⁄ Germany and the Grand Duchy of Luxembourg. *Ferrantia*, **46**, 97–115, 7 pls.

____ & TETLIE, O. E. 2004. On the Emsian (Early Devonian) arthropods of the Rhenish Slate Mountains: 4. The eurypterids *Alkenopterus* and *Vinetopterus* n. gen. (Arthropoda : Chelicerata). *Senckenbergiana lethaea*, **84**, 175–196.

____ & ____ 2006. On the Emsian (Lower Devonian) arthropods of the Rhenish Slate Mountains: 5. Rare and poorly known eurypterids from Willwerath, Germany. *Paläontologische Zeitschrift*, **80**, 325–343.

PRANTL, F. & PŘIBYL, A. 1948. Revise Různorepých (Eurypterida) z Českého Siluru. *Rozpravy - Státního Geologického ústavu Československé Republiky*, 1–116, 8 pls.

RAASCH, G. O. 1939. Cambrian Merostomata. *Geological Society of America, Special Papers*, **19**, 1–146.

RACHEBOEUF, P. R., VANNIER, J. & ANDERSON, L. I. 2002. A new three-dimensionally preserved xiphosuran chelicerate from the Montceau-les-Mines lagerstätte (Carboniferous, France). *Palaeontology*, **45**, 125–147, 3 pls.

____, ____, SCHRAM, F. R., CHABARD, D. & SOTTY, D. 2008. The euthycarcinoid arthropods from Montceau-les-Mines, France: functional morphology and affinities. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh,* **99**, 11–25.

RAW, F. 1957. Origin of chelicerates. *Journal of Paleontology*, **31**, 139–192.

RAYMOND, P. E. 1920. The appendages, anatomy and relationships of trilobites. *Memoirs of the Connecticut Academy of Arts and Sciences*, **7**, 1–169.

RESSER, C. E. 1931. A new Middle Cambrian merostome crustacean. *Proceedings of the United States National Museum*, **79**, 1–4.

RICHTER, R. & RICHTER, E. 1929. *Weinbergina opitzi* n. g., n. sp., ein Schwertträger (Merost. Xiphos.) aus dem Devon (Rheinland). *Senckenbergiana*, **11**, 193–209.

RITCHIE, A. 1968a. New evidence on *Jamoytius kerwoodi* White, an important Ostracoderm from the Silurian of Lanarkshire, Scotland. *Palaeontology*, **11**, 21–39.

____ 1968b. *Lanarkopterus dolichoschelus* (Størmer) gen. nov., a mixopterid eurypterid from the Upper Silurian of the Lesmahagow and Hagshaw Hills inliers, Scotland. *Scottish Journal of Geology*, **4**, 317–338, 1 pl.

ROBERTSON, G. 1989. A palaeoenvironmental interpretation of the Silurian rocks in the Pentland Hills, near Edinburgh, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **80**, 127–141.

ROLFE, W. D. I. 1963. Morphology of the telson in *Ceratiocaris*? *cornwallisensis* (Crustacea: Phyllocarida) from Czeckoslovakia. *Journal of Paleontology*, **37**, 486–488.

RUDKIN, D. M., YOUNG, G. A. & NOWLAN, G. S. 2008. The oldest horseshoe crab: a new xiphosurid from Late Ordovician konservat-lagerstätten deposits, Manitoba, Canada. *Palaeontology*, **51**, 1–9.

RUDLOE, A. 1980. The breeding behaviour and patterns of movement of horseshoe crabs, *Limulus polyphemus*, in the vicinity of breeding beaches in Apalachee Bay, Florida. *Estuarie*s, **3**, 177–183.

RUEDEMANN, R. 1916. *Spathiocaris* and Discinocarina. *New York State Museum Bulletin*, **189**, 98–112.

____ 1921. A recurrent Pittsford (Salina) fauna. *New York State Museum Bulletin*, **219–220**, 205–222.

____ 1926. The Utica and Lorraine Formations of New York, Part 2, Systematic Paleontology, no. 2, Mollusks, Crustacea and Eurypterids. *New York State Museum Bulletin*, **272**, 1–227.

____ 1934a. Eurypterids from the Lower Devonian of Beartooth Butte, Wyoming. *Proceedings of the American Philosophical Society*, **73**, 163–167.

____ 1934b. Eurypterids in graptolite shales. *American Journal of Science*, *5th Series*, **27**, 374–385.

____ 1942. Some new eurypterids from New York. *New York State Museum Bulletin*, **327**, 24–29.

SALTER, J. W. 1856. On some new Crustacea from the uppermost Silurian Rocks. *Quarterly Journal of the Geological Society of London*, **12**, 26–34.

____ 1857. On some new Palaeozoic star-fishes. *Annals and Magazine of Natural History* **20**, 321–334

____ 1860. On new fossil Crustacea from the Silurian rocks. *Annals and Magazine of Natural History,* **5**, 153–162.

SALTZMAN, M. R. & YOUNG, S. A. 2005. Long-lived glaciation in the Late Ordovician? Isotopic and sequence-stratigraphic evidence from western Laurentia. *Geology*, **33**, 109–112.

SARLE, C. J. 1903. A new eurypterid fauna from the base of the Salina in western New York. *New York State Museum Bulletin*, **69**, 1080–1108.

SAVAGE, T. E. 1916. Alexandrian rocks of northeastern Illinois and eastern Wisconsin. *Bulletin of the Geological Society of America,* **27**, 305–324.

SAVAZZI, E. 1985. Functional morphology of the cuticular terraces in burrowing terrestrial brachyuran decapods. *Lethaia*, **18**, 147–154.

SAVORY, T. H. 1977. *The Arachnida*. 2nd ed. London: Academic Press, 340 pp.

SCHMALFUSS, H. 1978. Structure, patterns and function of cuticular terraces in Recent and fossil arthropods. I. Decapod crustaceans. *Zoomorphologie*, **90**, 19–40.

____ 1981. Structure, patterns and function of cuticular terraces in trilobites. *Lethaia*, **14**, 331–341.

SCHMIDT, F. 1883. Nachtrag zur Monographie der Rußischen Leperditen II. Die Crustaceenfauna der Euryptereenschichten von Rootziküll auf Oesel. Miscellanea silurica III. *Memoires of the Academy of Science de St. Petersbourg,* **31**, 28–84.

____ 1904. Über die neue Merostomenform *Stylonurus* (?) *simonsoni*. *Bulletin de l'Académie Impériale des Sciences de St.-Pétersbourg, series 5*, **20**, 99–105, 2 pls.

SCHRAM, F. R. & ROLFE, W. D. I. 1982. New euthycarcinoid arthropods from the Upper Pennsylvanian of France and Illinois. *Journal of Paleontology*, **56**, 1434–1450.

SEILACHER, A., REIF, W. -E. & WESTPHAL, F. 1985. Sedimentological, ecological and temporal patterns of fossil Lagerstätten. p. 5–24. *In* WHITTINGTON, H. B. & CONWAY MORRIS, S. (Eds.), *Extraordinary Fossil Biotas: Their Ecological and Evolutionary Significance,* Cambridge University Press, Cambridge, 192 pp.

SELDEN, P. A. 1981. Functional morphology of the prosoma of *Baltoeurypterus tetragonophthalmus* (Fischer) (Chelicerata : Eurypterida). *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **72**, 9–48.

____ 1984. Autecology of Silurian eurypterids. *Special Papers in Palaeontology*, **32**, 39–54.

____ & DRYGANT, D. M. 1987. A new Silurian xiphosuran from Podolia, Ukraine, USSR. *Palaeontology*, **30**, 537–542.

____ & DUNLOP, J. A. 1998. Fossil taxa and relationships of chelicerates. p. 303–331. *In* EDGECOMBE, G. D. (Ed.) *Arthropod fossils and phylogeny*. Columbia University Press, New York, 347 pp.

____ & SIVETER, D. J. 1987. The origin of the limuloids. *Lethaia*, **20**, 383–392.

SHIVASHANKAR, T. 1994. Advanced sub social behaviour in the scorpion *Heterometrus fulvipes* Brunner (Arachnida). *Journal of Biosciences*, **19**, 81–90.

SHULTZ, J. W. 1993. Muscular anatomy of the giant whipscorpion *Mastigoproctus giganteus* (Lucas) (Arachnida: Uropygi) and its evolutionary significance. *Zoological Journal of the Linnean Society*, **108**, 335–365.

____ 2007. A phylogenetic analysis of the arachnid orders based on morphological characters. *Zoological Journal of the Linnean Society*, **150**, 221–265.

SHUSTER JR., C. N. & BOTTON, M. L. 1985. A contribution to the population biology of horseshoe crabs, *Limulus polyphemus* (L.), in Delaware Bay. *Estuaries*, **8**, 363–372.

SIMPSON, G. G. 1961. *Principles of animal taxonomy*. Columbia University Press, New York, 247 pp.

SIMPSON, S. 1951. A new eurypterid from the Upper Old Red Sandstone of Portishead. *Annals and Magazine of Natural History*, **12**, 849–861, pls. 15–16.

SIVETER, D. J. & SELDEN, P. A. 1987. A new, giant xiphosurid from the lower Namurian of Weardale, County Durham. *Proceedings of the Yorkshire Geological Society*, **46**, 153–168.

____, SUTTON, M. D., BRIGGS, D. E. G. & SIVETER, D. J. 2004. A Silurian sea spider. *Nature*, **431**, 978–980.

SPENCER. W. K. 1918. A monograph of the British Palaeozoic Asterozoa. *Monograph of the Palaeontographical Society, London* **1916(3)**, 109–168

____ 1922. A monograph of the British Palaeozoic Asterozoa. *Monograph of the Palaeontographical Society, London* **1920(5)**, 197–236.

____ 1927. A monograph of the British Palaeozoic Asterozoa. *Monograph of the Palaeontographical Society, London* **1925(7)**, 325–388.

____ 1930. A monograph of the British Palaeozoic Asteroidea. *Monograph of the Palaeontographical Society, London* **1828(8)**, 389–436.

STEIN, M. & SELDEN, P. A. In press. A restudy of the Burgess Shale (Cambrian) arthropod *Emeraldella brocki* and reassessment of its affinities. *Journal of Systematic Palaeontology.*

VON STERNBERG, G. K. 1833. *Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt*. C. E. Brenk, Regensburg, 80 pp., 26 pls.

STOTT, C.A., TETLIE, O. E., BRADDY, S. J., NOWLAN, G. S., GLASSER, P. M. & DEVEREUX, N. G. 2005. A new eurypterid (Chelicerata) from the Upper Ordovician of Manitoulin Island, Ontario, Canada. *Journal of Paleontology*, **79**, 1166–1174.

STØRMER, L. 1934a. Merostomata from the Downtonian Sandstone of Ringerike, Norway. S*krifter utgitt av Det Norske Videnskaps-Akademi i Oslo I. Matematisk-Naturvidenskapelig Klasse*, **10**, 1–125, 12 pls.

____ 1934b. Uber den neuen von W. Gross beschriebenen Eurypteriden aus dem Unterdevon von Overath im Rheinland. *Jahrbuch der Preußischen Geologischen Landesanstalt,* **55**, 284–291.

____ 1934c. A new eurypterid from the Saaremaa-(Oesel-)Beds in Estonia. *Publications of the Geological Institution of the University of Tartu,* **37**, 1–8.

____ 1936a. Eurypteriden aus dem Rheinischen Unterdevon. *Abhandlungen der Preußischen Geologischen Landesanstalt, Neue Folge,* **175**, 1–74.

____ 1936b. *Mixopterus dolichoschelus* (Laurie MS), a Downtonian eurypterid from Scotland. *Memoirs of the Geological Survey, Summary of Progress for 1934*, **2**, 41–46.

____ 1944. On the relationships and phylogeny of fossil and recent Arachnomorpha. *Skrifter utgitt av Det Norske Videnskaps-Akademi i Oslo I. Matematisk-Naturvidenskapelig Klasse*, **5**, 1–158.

____ 1951. A new eurypterid from the Ordovician of Montgomeryshire, Wales. *Geological Magazine,* **88**, 409–422.

____ 1952. Phylogeny and taxonomy of fossil horseshoe crabs. *Journal of Paleontology,* **26**, 630–640.

____ 1955. Merostomata. p. 4–41. *In* MOORE, R. C. (Ed.) *Treatise on Invertebrate Paleontology Part P. Arthropoda 2: Chelicerata, Pycnogonida and Palaeoisopus*. University of Kansas Press, 181 pp.

____ 1956. A Lower Cambrian merostome from Sweden. *Arkiv för Zoologi, serie 2,* **9**, 507–514.

____ 1963. *Gigantoscorpio willsi* a new scorpion from the lower Carboniferous of Scotland and its associated preying microorganisms. *Skrifter utgitt av Det Norske Videnskaps-Akademi i Oslo I. Matematisk-Naturvidenskapelig Klasse, Ny Serie*, **8**, 1–171, 22 pls.

____ 1969. Eurypterids from the Lower Devonian of Willwerath, Eifel. *Senckenbergiana lethaea,* **50**, 21–35.

____ 1972. Arthropods from the Lower Devonian (Lower Emsian) of Alken an der Mosel, Germany. Part 2: Xiphosura. *Senckenbergiana lethaea*, **53**, 1–29, 6 pls.

____ 1973. Arthropods from the Lower Devonian (Lower Emsian) of Alken an der Mosel, Germany. Part 3: Eurypterida, Hughmilleriidae. *Senckenbergiana lethaea*, **54**, 119–205, 13 pls.

____ 1974. Arthropods from the Lower Devonian (Lower Emsian) of Alken an der Mosel, Germany. Part 4: Eurypterida, Drepanopteridae, and other groups. *Senckenbergiana lethaea*, **54**, 359–451, 15 pls.

____ & KJELLESVIG-WAERING, E. N. 1969. Sexual dimorphism in eurypterids. p. 201–-214. *In* WESTERMANN, G. E. G. (Ed.) *Sexual dimorphism in fossil Metazoa and taxonomic implications*. Stuttgart, 251 pp.

STÜRMER, W. & BERGSTRÖM, J. 1981. *Weinbergina*, a xiphosuran arthropod from the Devonian Hunsrück Slate. *Paläontologische Zeitschrift*, **55**, 237–255.

SUTTON, M. D., BRIGGS, D. E. G., SIVETER, D. J., SIVETER, D. J. & ORR, P. J. 2002. The arthropod *Offacolus kingi* (Chelicerata) from the Silurian of Herefordshire, England: computer based morphological reconstructions and phylogenetic affinities. *Proceedings of the Royal Society of London, B*, **269**, 1195–1203.

SWARTZ, C. K. 1923. Order Eurypterida. p. 716–778. *In* SWARTZ, C. K., PROUTY, W. F., ULRICH, E. O. & BASSLER, R. S. (Eds.) *Silurian Volume*. Maryland Geological Survey, 795 pp.

[TETLIE, O. E. 2000. *Eurypterids from the Silurian of Norway.* Unpublished Cand. Scient. Thesis, Universitetet i Oslo, 152 pp.]

____ 2002. A new *Baltoeurypterus* (Eurypterida: Chelicerata) from the Wenlock of Norway. *Norwegian Journal of Geology*, **82**, 37–44.

____ 2006. Eurypterida (Chelicerata) from the Welsh Borderlands, England. *Geological Magazine*, **143**, 723–735.

____ 2007a. Distribution and dispersal history of Eurypterida (Chelicerata). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **252**, 557–574.

____ 2007b. Like father, like son? Not amongst the eurypterids (Chelicerata) from Beartooth Butte, Wyoming. *Journal of Paleontology*, **81**, 1423–1431.

____ 2008. *Hallipterus excelsior*, a stylonurid (Chelicerata: Eurypterida) from the Late Devonian Catskill Delta complex, and its phylogenetic position in the Hardieopteridae. *Bulletin of the Peabody Museum of Natural History*, **49**, 19–30.

____, ANDERSON, L. I. & POSCHMANN, M. 2007. *Kiaeropterus* (Eurypterida; Stylonurina) recognized from the Silurian of the Pentland Hills. *Scottish Journal of Geology*, **43**, 1–7.

____ & BRADDY, S. J. 2004. The first Silurian chasmataspid, *Loganamaraspis dunlopi* gen. et sp. nov. (Chelicerata: Chasmataspidida) from Lesmahagow, Scotland, and its implications for eurypterid phylogeny. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **94**, 227–234.

____, ____, BUTLER, P. D. & BRIGGS, D. E. G. 2004. A new eurypterid (Chelicerata: Eurypterida) from the Upper Devonian Gogo Formation of Western Australia, with a review of the Rhenopteridae. *Palaeontology*, **47**, 801–809.

____, BRANDT, D. S. & BRIGGS, D. E. G. 2008. Ecdysis in sea scorpions (Chelicerata: Eurypterida). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **265**, 182–194.

____ & BRIGGS, D. E. G. 2009. The origin of pterygotid eurypterids (Chelicerata: Eurypterida). *Palaeontology*, **52**, 1141–1148.

____ & CUGGY, M. B. 2007. Phylogeny of the basal swimming eurypterids (Chelicerata; Eurypterida; Eurypterina). *Journal of Systematic Palaeontology*, **5**, 345–356.

____ & DUNLOP, J. A. 2005. A redescription of the Late Carboniferous eurypterids *Adelophthalmus granosus* von Mayer, 1853 and *A. zadrai* Přibyl, 1952. *Mitteilungen aus dem Museum für Naturkunde Berlin, Geowissenschaftliche Reihe*, **8**, 3–12.

____ & POSCHMANN, M. 2008. Phylogeny and palaeoecology of the Adelophthalmoidea (Arthropoda; Chelicerata; Eurypterida). *Journal of Systematic Palaeontology*, **6**, 237–249.

THORELL, T. & LINDSTRÖM, G. 1884. Discovery of a Silurian fossil scorpion. *The Glasgow Herald*, Dec. 19, 1884.

TIPPER, J. C. 1976. The stratigraphy of the North Esk Inlier, Midlothian, Scotland. *Scottish Journal of Geology*, **12**, 15–25.

TOLLERTON, V. P. JR 1989. Morphology, taxonomy, and classification of the Order Eurypterida Burmeister, 1843. *Journal of Paleontology*, **63**, 642–657.

____ 2004. Summary of a revision of New York State Ordovician eurypterids: implications for eurypterid palaeoecology, diversity and evolution. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **94**, 235–242.

TÖRNQUIST, S. L. 1884. Undersökningar öfver Siljansomrĺdets trilobitfauna. *Sveriges Geologiska Undersökning C,* **66**, 1–101.

VANDENBROUCKE, T. R. A., GABBOTT, S. E., PARIS, F., ALDRIDGE, R. J. & THERON, J. N. 2009. Chitinozoans and the age of the Soom Shale, an Ordovician black shale Lagerstätte, South Africa. *Journal of Micropalaeontology*, **28**, 53–66.

VAN ROY, P. 2006. An aglaspidid arthropod from the Upper Ordovician of Morocco with remarks on the affinities and limitations of Aglaspidida. *Transactions of the Royal Society of Edinburgh: Earth Sciences,* **96**, 327–350.

____, ORR, P. J., BOTTING, J. P., MUIR, L. A., VINTHER, J., LEFEBVRE, B., EL HARIRI, K. & BRIGGS, D. E. G. 2010. Ordovician faunas of Burgess Shale type. *Nature*, **465**, 215–218.

WAHLMAN, G. P. & CASTER, K. E. 1978. Bearing of new Texas Upper Cambrian arthropods on merostome classification. *Geological Society of America, Abstracts with Programs*, **10**, 268.

WALCOTT, C. D. 1881. The trilobite: new and old evidence relating to its organization. *Bulletin of the Museum of Comparative Zoölogy at Havard College*, **8**, 191–224.

____ 1911. Cambrian geology and paleontology II. Middle Cambrian Merostomata. *Smithsonian Miscellaneous Collections*, **57**, 17–40.

____ 1912. Cambrian geology and paleontology II. Middle Cambrian Branchiopoda, Malacostraca, Trilobita and Merostomata. *Smithsonian Miscellaneous Collections*, **57**, 145–229.

WALLISER, O. H. 1964. Conodonten des Silurs. *Abhandlungen des Hessischen Landesamtes für Bodenforschung*, **41**, 106 pp.

WALMSLEY, V. G. & BOUCOT, A. J. 1975. The phylogeny, taxonomy and biogeography of Silurian and Early to mid-Devonian Isorthinae (Brachiopoda). *Palaeontographica, Abteilung A*, **148**, 34–108, 10 pls.

WATERSTON, C. D. 1960. The median abdominal appendage of the Silurian eurypterid *Slimonia acuminata* (Salter). *Palaeontology*, **3**, 245–259, pls. 42–43.

____ 1962. *Pagea sturrocki* gen. et sp. nov., a new eurypterid from the Old Red Sandstone of Scotland. *Palaeontology*, **5**, 137–148.

____ 1964. Observations on pterygotid eurypterids. *Transactions of the Royal Society of Edinburgh*, **66**, 9–33, 4 pls.

____ 1975. Gill structures in the Lower Devonian eurypterid *Tarsopterella scotica*. *Fossils and Strata*, **4**, 241–254, 2 pls.

____ 1979. Problems of functional morphology and classification in stylonuroid eurypterids (Chelicerata, Merostomata), with observations on the Scottish Silurian Stylonuroidea. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **70**, 251–322, 6 pls.

____ 1985. Chelicerata from the Dinantian of Foulden, Berwickshire, Scotland. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **76**, 25–33.

____, OELOFSEN, B. W. & OOSTHUIZEN, R. D. F. 1985. *Cyrtoctenus wittebergensis* sp. nov. (Chelicerata: Eurypterida), a large sweep-feeder from the Carboniferous of South Africa. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **76**, 339–358.

WEYGOLDT, P. & PAULUS, H. F. 1979. Untersuchungen zur Morphologie, Taxonomie und Phylogenie der Chelicerata. *Zeitschrift für zoologische Systematik und Evolutionsforschung*, **17**, (85–116), 177–200.

WHITAKER, J. H. MCD. 1962. The geology of the area around Leintwardine, Herefordshire. *Quarterly Journal of the Geological Society of London,* **118**, 319–351.

WHITEAVES, J. F. 1884. On some new, imperfectly characterized or previously unrecorded species of fossils from the Guelph Formations of Ontario. *Palaeozoic Fossils of Canada*, **3(1)**, 1–43.

WHITFIELD, R. P. 1882. Descriptions of new species of fossils from Ohio, with remarks on some of the geological formations in which they occur. *Annals of the New York Academy of Science*, **2**, 193–244.

____ 1885. An American Silurian scorpion. *Science*, **6**, 87–88.

WHITTARD, W. F. & BARKER, G. H. 1950. The Upper Valentian brachiopod fauna of Shropshire. *Annals and Magazine of Natural History*, **12**, 553–590.

WHITTINGTON, H. B. 1961. A natural history of trilobites. *Natural History*, **70**, 8–17.

____ 1990. Articulation and exuviation in Cambrian trilobites. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **329**, 27–46.

WILLS, L. J. 1964. The ventral anatomy of the Upper Carboniferous eurypterid *Anthraconectes* Meek and Worthen. *Palaeontology*, **7**, 474–507, pls. 77–79.

____ 1965. A supplement to Gerhard Holm's "Über die Organisation des *Eurypterus fischeri* Eichw." with special reference to the organs of sight, respiration and reproduction. *Arkiv för Zoologi*, **2 (18)**, 93–145.

WILLS, M. A. 1996. Classification of the arthropod *Fuxianhuia*. *Science*, **272**, 747–747.

____ 1999. Congruence between phylogeny and stratigraphy: randomization tests and gap excess ratio. *Systematic Biology*, **48**, 559–580.

____, BARRETT, P. M. & HEATHCOTE, J. F. 2008. The modified Gap Excess Ratio (GER*) and the stratigraphic congruence of dinosaur phylogenies. *Systematic Biology*, **57**, 891–904.

____, BRIGGS, D. E. G., FORTEY, R. A., WILKINSON, M. & SNEATH, P. H. A. 1998. An arthropod phylogeny based on fossil and recent taxa. p. 33–105. *In* EDGECOMBE, G.

D. (Ed.), *Arthropod Fossils and Phylogeny,* Columbia University Press, New York, 347 pp.

WOODWARD, H. 1865. On a new genus of Eurypterida from the Lower Ludlow Rocks of Leintwardine, Shropshire. *Quarterly Journal of the Geological Society*, **21**, 490–492.

____ 1868. On some new species of Crustacea from the Upper Silurian rocks of Lanarkshire &c.; and further observations on the structure of *Pterygotus*. *Quarterly Journal of the Geological Society*, **24**, 289–296.

____ 1872. Notes on some British Palaeozoic Crustacea belonging to the order Merostomata. *Geological Magazine*, **9**, 433–441.

____ 1866-1878. A monograph of the British fossil Crustacea belonging to the order Merostomata. *Monograph of the Palaeontographical Society*, London, 263 pp, 36 pls.

____ 1907. Two new species of *Eurypterus* from the Coal-Measures of Ilkeston, Derbyshire. *Geological Magazine*, **4**, 277–282.

YOUNG, G. A., RUDKIN, D. M., DOBRZANSKI, E. P., ROBSON, S. P. & NOWLAN, G. S. 2007. Exceptionally preserved Late Ordovician biotas from Manitoba, Canada. *Geology*, **35**, 883–886.

ZANDER, R. H. 2003. Reliable phylogenetic resolution of morphological data can be better than that of molecular data. *Taxon*, **52**, 109–112.

NMS specimen	Carapace length	Carapace width	Lateral eye length	Lateral eye width	Marginal rim width
G.1885.26.72.1	23	25	-	-	-
G.1885.26.72.13	20	22	8.5	2	-
G.1885.26.72.14	23	27	8.3	1.6	-
G.1885.26.72.17	30	41	-	-	1
G.1885.26.72.19	35	40*	-	-	1
G.1897.32.12.9	20	22	6	0.5	-
G.1897.32.85	32	35	-	-	1
G.1897.32.88	-	26.5	-	-	-
G.1897.32.121	14	15	-	-	-
G.1897.32.123	18	20	5	0.5	-
G.1897.32.125	10	12	-	-	-
G.1897.32.131	12.5	24	7.5	1.2	-
G.1897.32.132	38	55	-	-	-
G.1897.32.133	35	50	9	2	-
G.1897.32.134	19.2	28.8	7.5	2.3	0.5
G.1897.32.136	27.5	44	-	-	1
G.1897.32.137.1	23	30	-	-	-
G.1897.32.137.2	10	10	4	0.5	-
G.1897.32.138	32	35*	-	-	1
G.1897.32.139	34	35*	-	-	2
G.1897.32.140	18	31	7	1	-
G.1897.32.164	14	22	-	-	-
G.1897.32.165	27.5	33	-	-	-
G.1897.32.167	11.5	13*	-	-	-
G.1897.32.172	15*	13*	6	0.5	-
G.1897.32.173	17*	19*	-	-	-
G.1897.32.174	39	35	9	1.5	1
G.1897.32.176	22	20	-	-	-
G.1897.32.186	10	15	-	-	-
G.1897.32.191	17	23	5	0.5	-
G.1897.32.207	16	20	-	-	-
G.1897.32.208	17	15*	6	1.5	-

TABLE 1. Dorsal prosomal measurements (in mm) for *Stoermeropterus conicus* (Laurie, 1892). An asterisk indicates an incomplete measurement.

NMS specimen	Chelicerae	Metastoma	Epistoma
G.1885.26.72.13	-	-	6.5/5
G.1885.26.72.14	3/3	-	5/7
G.1885.26.72.17	7/4	19/9	7.5/10
G.1897.32.12.9	4/2.5	-	5/5
G.1897.32.85	3/3	15/9	-
G.1897.32.123	2/1.5	-	-
G.1897.32.132	5/3	25/11	11/13
G.1897.32.134	-	-	9.5/10.5
G.1897.32.136	-	22/14	-
G.1897.32.174	-	-	5/5

TABLE 2. Ventral prosomal (length/width) measurements (in mm) for *Stoermeropterus conicus* (Laurie, 1892).

NMS specimen	II	III	IV	V	VI
G.1885.26.72.1	-	-	8/3	10/3	12/12
G.1885.26.72.13	3/1.5	3.5/2	4/3	6/3	8/10
G.1885.26.72.14	3/2	5/2.5	8/3	8/3	10/12
G.1885.26.72.17	7/4	8/5	12/5	13/6	13/18
G.1885.26.72.19	6/4	10/5	16/6	16/6	16/20
G.1897.32.12.9	3/2	4/3	5/3	7/4	8/11
G.1897.32.85	6/3	8/4	11/5	12/6	12/16
G.1897.32.123	4/2	5/2.5	6/3	7/4	8/11
G.1897.32.132	8/4	10/5	13/6	15/8	15/25
G.1897.32.133	10/5	12/5	17/7	20/10	20/34
G.1897.32.134	4/2	7/2	9.5/3	10/3	11/11
G.1897.32.136	-	12/4	18/6	22/7	22/18
G.1897.32.174	5/2.5	7/4	8/4	10/6	10/18

TABLE 3. Prosomal appendage coxae (length/width) measurements for *Stoermeropterus conicus* (Laurie, 1892).

NMS specimen	**Appendage II**
G.1897.32.123	(podomeres 1 – 3): **Coxa**; 4/2. **2**; 2/2. **3**; 2/2.
G.1897.32.133	(podomeres 1 – 7): **Coxa**; 10/5. **2**; 5/4. **3**; 5/3.5. **4**; 5/3. **5**; 4/3. **6**; 4/2.5. **7**; 3/2.

TABLE 4. Prosomal appendage II (length/width) measurements (in mm) for *Stoermeropterus conicus* (Laurie, 1892).

NMS specimen	**Appendage III**
G.1885.26.72.14	(podomeres 1 – 8): **Coxa**; 5/2.5. **2**; 2/2.5. **3**; 1.5/2. **4**; 1.5/2. **5**; 1.5/1. **6**; 1.5/1. **7**; 1.5/0.75. **8**; 3/0.75.
G.1897.32.123	(podomeres 1 – 4): **Coxa**; 5/2.5. **2**; 2.5/2.5. **3**; 2.5/2. **4**; 2/2.
G.1897.32.133	(podomeres 1 – 8): **Coxa**; 12/5. **2**; 5/5. **3**; 5/4.5. **4**; 7/4.5. **5**; 8/4. **6**; 6/3.5. **7**; 5/3. **8**; 5/2.5.

TABLE 5. Prosomal appendage III (length/width) measurements (in mm) for *Stoermeropterus conicus* (Laurie, 1892).

NMS specimen	**Appendage IV**
G.1885.26.72.14	(podomeres 1 – 8): **Coxa**; 8/3. **2**; 3/2.5. **3**; 2.5/2. **4**; 3.5/2. **5**; 4/2. **6**; 3/2. **7**; 3/1.5. **8**; 3/1.5.
G.1897.32.123	(podomeres 1 – 5): **Coxa**; 6/3. **2**; 2.5/3. **3**; 2/2.5. **4**; 2.5/2. **5**; 2/2.
G.1897.32.133	(podomeres 1 – 2, 7 – 8): **Coxa**; 17/7. **2**; 6/7. — **7**; 6/3. **8**; 6/3.
G.1897.32.136	(podomeres 1 – 4): **Coxa**; 18/6. **2**; 6/6. **3**; 7/5. **4**; 7/5.
G.1897.32.137.1	(podomeres 1 – 6): **Coxa**; 6.25/2.5. **2**; 2/2.5. **3**; 2/2.5. **4**; 3.75/2. **5**; 3/2. **6**; 3.75/2.
G.1897.32.138	(podomeres 4 – 6): **4**; 10/4. **5**; 7.5/4. **6**; 7.5/3.

TABLE 6. Prosomal appendage IV (length/width) measurements (in mm) for *Stoermeropterus conicus* (Laurie, 1892).

NMS specimen	**Appendage V**
G.1885.26.72.17	(podomeres 1 – 5): **Coxa**; 13/6. **2**; 5/5. **3**; 5/5. **4**; 8/4. **5**; 7/4.
G.1897.32.133	(podomeres 1 – 9): **Coxa**; 20/10. **2**; 6/7. **3**; 5/7. **4**; 10/7. **5**; 13/6. **6**; 9/4. **7**; 6/3.5. **8**; 8/3. **9**; 6/3.
G.1897.32.136	(podomeres 1 – 9): **Coxa**; 22/7. **2**; 3/5. **3**; 3/5. **4**; 7.5/5. **5**; 6/4. **6**; 5.5/4. **7**; 5.5/2. **8**; 5/2. **9**; 4/1.5.
G.1897.32.137.1	(podomeres 1 – 9): **Coxa**; 7.5/3.75. **2**; 1.75/4.5. **3**; 2/4. **4**; 5.5/3.5. **5**; 5/3.5. **6**; 5/3. **7**; 4/2.5. **8**; 4/2.5. **9**; 3.75/2.
G.1897.32.138	(podomeres 4 – 8): **4**; 10/4. **5**; 10/4. **6**; 9/4. **7**; 9/3.5. **8**; 9/3.
G.1897.32.140	(podomeres 1 – 6): **Coxa**; 11/3. **2**; 3/3. **3**; 3/3. **4**; 6/3. **5**; 5/2.5. **6**; 5/2.5.

TABLE 7. Prosomal appendage V (length/width) measurements (in mm) for *Stoermeropterus conicus* (Laurie, 1892). The appendage in NMS G.1885.26.72.17 is very poorly preserved and is not shown on any of the figures.

NMS specimen	**Appendage VI**
G.1885.26.72.13	(podomeres 1 – 9): **Coxa**; 8/10. **2**; 2.5/3. **3**; 3/ 3. **4**; 6/ 3. **5**; 5.5/3. **6**; 5/2.5. **7**; 4/ 2.5. **7a**; 1/0.5. **8**; 4/1.5. **9**; 3.5/1.
G.1885.26.72.14	(podomeres 1 – 7): **Coxa**; 10/12. **2**; 3/4. **3**; 3/4. **4**; 5.5/ 4. **5**; 5/4. **6**; 4/3. **7**; 5/3.
G.1885.26.72.17	(podomeres 1 – 4): **Coxa**; 13/18. **2**; 6/6. **3**; 6/ 6. **4**; 10/5.
G.1897.32.132	(podomeres 1 – 9): **Coxa**; 15/25. **2**; 6/7. **3**; 7/7. **4**; 12/7. **5**; 11/6. **6**; 10/6. **7**; 9/5.5. **7a**; 5/2.5. **8**; 7.5/5. **9**; 7.5/3.5.
G.1897.32.133	(podomeres 1 – 9): **Coxa**; 20/34. **2**; 5/9. **3**; 5/9. **4**; 17/7. **5**; 14/7. **6**; 10/7. **7**; 11/6. **7a**; 5/2.5. **8**; 10/5. **9**; 10/4.5.
G.1897.32.136	(podomeres 1 – 9): **Coxa**; 22/18. **2**; 8/6. **3**; 8/6. **4**; 12.5/6. **5**; 9/5. **6**; 7.5/4. **7**; 6/3. **7a**; 1.5/1. **8**; 6/3. **9**; 4/2.
G.1897.32.140	(podomeres 1 – 9): **Coxa**; 11/12. **2**; 4/4. **3**; 4/4. **4**; 7/4. **5**; 5/4. **6**; 5/3.5. **7**; 4/3.5. **7a**; 2.5/1. **8**; 5/3. **9**; 5/3.

TABLE 8. Prosomal appendage V (length/width) measurements (in mm) for *Stoermeropterus conicus* (Laurie, 1892). The appendage in NMS G.1885.26.72.17 is very poorly preserved and is not shown on any of the figures.

NMS specimen	1	2	3	4	5	6
G.1885.26.72.1	4/25	5/25	5/26	6/27	6/26	6/25
G.1885.26.72.13	3/20	5/20	5/21	5/22	5/20	5/18
G.1885.26.72.14	2/24	4/24	5/25	5/26	5/25	6/24
G.1885.26.72.17	5/41	6/41	8/42	9/43	10/41	10/23*
G.1885.26.72.19	5/31*	7/27*	7/25*	-	-	-
G.1897.32.12.9	3/20	5/20	5/21	5/22	5/21	5/20
G.1897.32.85	4/34	6/35	6/35	6/36	7/34	7/32
G.1897.32.88	3/24	4/25	4/26	5/27	5/25	5/22
G.1897.32.89	-	-	2.5/21	3/20	3/20	4/20
G.1897.32.121	2/16	4/17	4/17	4/18	4/16	4/15
G.1897.32.123	2/20	4/22	4/23	4/24	4/22	5/12*
G.1897.32.125	2/12.5	2.5/13	2.5/13.5	3/14	3/12	2.5/11
G.1897.32.130	-	-	3/6*	3/7*	3/13	3/11
G.1897.32.131	1/23	2/23	3/22	3/22	3/20	4/20
G.1897.32.132	4/55	6/53	6/52	6/50	7/48	6/47
G.1897.32.133	4/49	6/49	6/50	7/55	6/50	6/45
G.1897.32.136	3/44	4/44	4/45	4/46	5/45	5/44
G.1897.32.137.1	1.5/25	3/26	3/30	4/33	5/31	4/29
G.1897.32.137.2	2/10	4/11	3/12	3/12.5	3/12	3/10
G.1897.32.138	5/35*	7/35*	7/43*	7/44*	7/42	7/40
G.1897.32.139	3/35	5/36	5/38	6/40	5/38	5/36
G.1897.32.140	3/31	4/30*	4/26*	4/34	5/33	5/32
G.1897.32.164	2/22	3/22	4/23	4/24	4/23	4/22
G.1897.32.165	4/35	4/31*	5/31*	5/32*	6/25*	5/20*
G.1897.32.167	3/14*	3/16*	3/17*	4/17*	4/15*	4/12*
G.1897.32.172	3/15*	3/15*	4/15*	4/16*	4/16*	4/16*
G.1897.32.173	3/20*	4/21*	4/22	4/23	4/22	4/21
G.1897.32.176	2/19	3/20	4/20*	3/20*	3/18*	2/17
G.1897.32.180	4/14*	6/13*	5/12*	5/14*	4/12	4/10
G.1897.32.182	2/26	3/26	3/28	3/29	4/27	4/26
G.1897.32.186	2/14	3/14	3/13	3/13	3/10*	3/7*
G.1897.32.191	5/20*	5/16*	5/16*	4/12*	4/11*	3/10*
G.1897.32.207	3/20	4/21	5/22	5/23	5/15*	-
G.1897.32.208	3/15*	4/15*	4/10*	-	-	-

TABLE 9. Mesosomal segment measurements (length/width in mm) for *Stoermeropterus conicus* (Laurie, 1892). An asterisk indicates an incomplete measurement.

NMS specimen	Type	Appendage Length	Appendage Width	Deltoid Plate Length	Deltoid Plate Width
G.1885.26.72.1	A	11	4	3	2.5
G.1885.26.72.13	A	7	3	3.5	2.5
G.1885.26.72.17	B	11	4	-	-
G.1897.32.12.9	A	8	3	3	2.5
G.1897.32.133	B	13	8	-	-
G.1897.32.136	B	8	4.5	-	-
G.1897.32.137	B	6	4	-	-

TABLE 10. Genital appendage measurements (in mm) for *Stoermeropterus conicus* (Laurie, 1892).

NMS specimen	7	8	9	10	11	12	Telson
G.1885.26.72.1	8/21	10/21	10/20	10/18	10/16	15/15	32/7
G.1885.26.72.13	6/16	7/14	7/12	7/10	7/9	8/7	32/6
G.1885.26.72.14	6/21	6/19	6/18	6/16	7/13	11/11	31/6
G.1897.32.12.9	6/18	6/17	6/15	6/13	8/10	9/8	32/5
G.1897.32.88	5/19	5/17	5/15	5/12	5/10	6/9	21/5
G.1897.32.89	5/17	6/15	8/14	8/12	8/11	10/10	18*/4
G.1897.32.121	4/14	5/13	5/11	5/10	6/9	7/6	24/6
G.1897.32.124	4/13	4/12	4/11	5/8*	7/8	8/7	21*/4
G.1897.32.125	2.5/10	2.5/10	3/10	4/9	4/7	5/5	-
G.1897.32.126	5/15*	8/15*	8/14*	8/16	10/15	15/13	54/5
G.1897.32.130	3/11	3/10	3/9	3.5/7	3/6	5/5	26/4
G.1897.32.131	4/18	6/17	7/12*	-	-	-	-
G.1897.32.132	8/45	9/40	9/34	10/29	12/25	13/20	25*/10
G.1897.32.133	7/43	7/40	8/35	8/30	10/20	9/14	-
G.1897.32.136	5/44	6/41	9/38	8/35	10/31*	-	-
G.1897.32.137.1	5/27	5/26	5/25	-	-	-	-
G.1897.32.137.2	2.5/8	2.5/6	2.5/5	2/4	2/3	2/2	-
G.1897.32.138	7/35	9/31	10/30	14/29	15/23	18/18	35/8
G.1897.32.139	6/31	8/27	8/25	8/23	10/20	5*/13	-
G.1897.32.145	4/12	4/9	4/8	4/8	3/7	3/5	15*/4
G.1897.32.164	4/21	4/20	4/17	5/14	5/12	6/9	15/3
G.1897.32.167	4/12*	3/11*	3/10*	3/5*	-	-	-
G.1897.32.170	5/8*	5/16	5/15	6/13	7/10	8/7	10*/6
G.1897.32.173	5/18	4/16	5/15	5/12	5/10	7/5*	-
G.1897.32.176	5/16	6/15	6/12	8/11	8/10	8/8	-
G.1897.32.180	5/9	5/8	5/7	4/6	4/5	4/4	-
G.1897.32.182	5/25	5/23	6/20	7/18	8/16	8/13	25*/4
G.1897.32.184	-	-	-	10/20*	12/19	18/18	30/5
G.1897.32.185	-	-	-	13/18	14/17	23/16	27*/6
G.1897.32.192	-	-	-	-	-	-	20/6
G.1892.32.197	-	-	-	5/10	4/9	5/7.5	20/5
G.1897.32.198	-	-	6/24	8/22	10/20	15/15	30/6
G.1897.32.211	-	-	-	5/12	5/10	7/5*	25/4

TABLE 11. Metasomal segment and telson measurements (length/width in mm) for *Stoermeropterus conicus* (Laurie, 1892). An asterisk indicates an incomplete measurement.

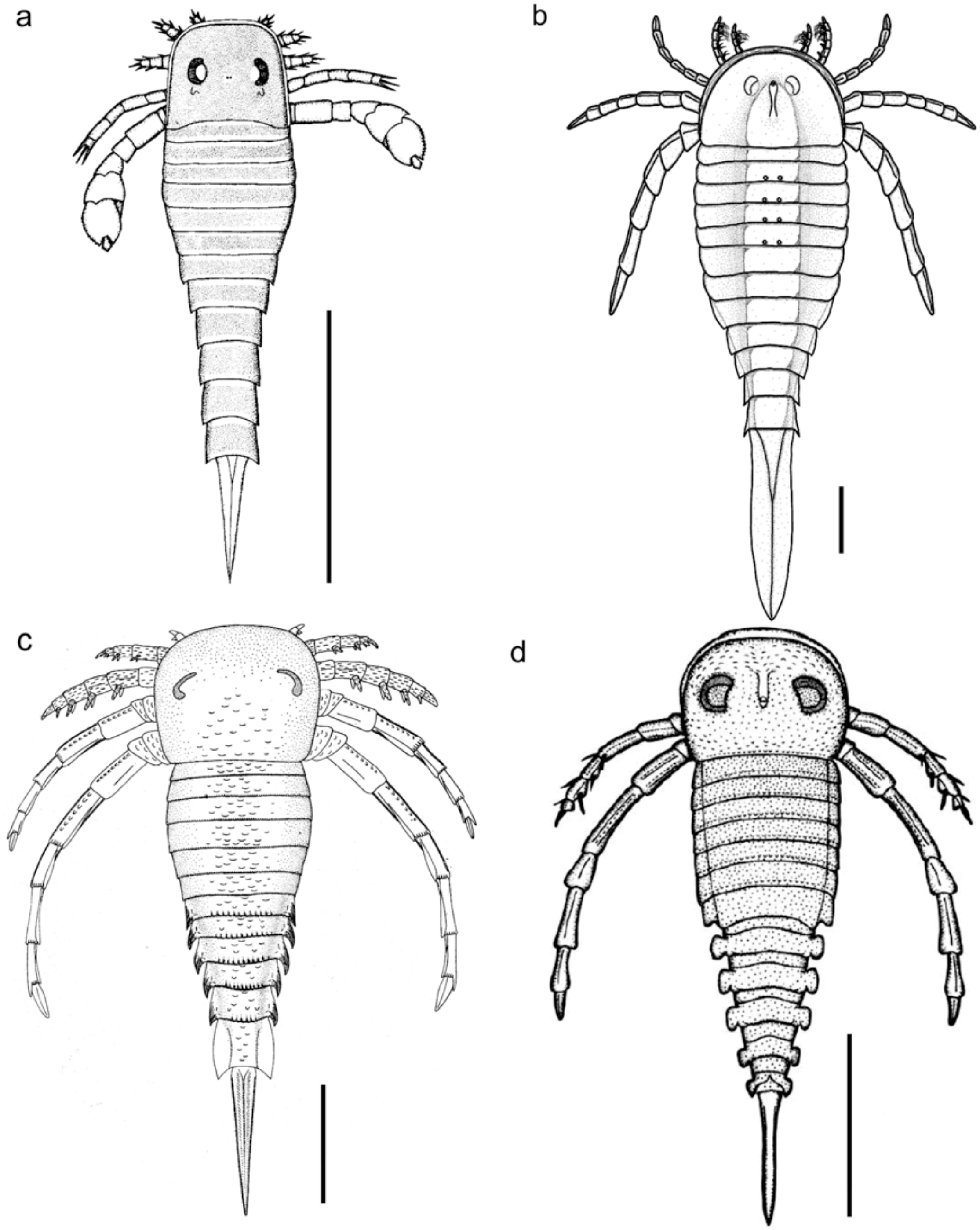
Taxon	Coding				
Weinbergina opitzi	0 0 0 0 0	3 1 1 1 0	0 1 0 – 0	0 0 0 – –	0 0 0 0 0
	– – 2 – –	– 0 0 0 0	0 0 0 0 0	0 1 0	
Brachyopterus stubblefieldi	0 0 0 1 1	? 0 0 0 0	0 0 0 – 0	0 0 0 – –	0 0 0 0 1
	0 ? ? ? ?	? 0 ? 0 0	0 0 0 0 0	0 2 0	
Rhenopterus diensti	0 0 0 0 1	0 0 0 0 0	0 0 0 – 0	0 0 0 – –	0 0 0 0 1
	0 0 0 0 0	– 0 0 1 1	0 0 1 0 0	0 0 0	
Parastylonurus ornatus	0 0 0 0 1	0 0 1 1 0	0 0 0 – 0	0 0 0 – –	0 0 0 0 0
	1 1 0 0 1	0 0 0 0 1	0 0 0 0 0	0 0 0	
Stoermeropterus conicus	0 0 0 0 1	1 1 0 0 0	0 1 1 0 0	0 0 1 0 0	0 0 0 0 1
	1 0 0 0 1	0 1 0 0 0	0 1 0 1 0	0 1 0	
Stoermeropterus latus	0 0 0 0 1	1 1 ? 0 ?	0 ? ? ? 0	0 0 1 0 0	0 0 0 0 1
	? ? 0 ? 1	1 1 0 0 0	0 1 0 1 0	0 0 0	
Stoermeropterus nodosus	0 0 0 0 1	? ? ? 0 ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?
	0 0 0 0 1	1 1 0 0 0	0 ? 0 1 0	0 1 1	
Vinetopterus struvei	1 0 0 0 1	3 1 0 0 0	0 1 1 0 0	0 0 1 0 0	0 0 0 0 1
	0 0 0 ? ?	? 0 0 0 1	1 1 0 ? 0	0 1 1	
Vinetopterus martini	1 0 ? 0 1	3 1 0 0 0	0 ? ? ? 0	0 0 1 0 0	0 0 0 0 1
	? 0 ? ? ?	? 0 0 0 1	1 1 0 ? 0	0 1 1	
Moselopterus ancylotelson	0 0 0 0 1	3 1 1 0 0	0 1 1 0 0	0 0 1 0 0	0 0 0 0 1
	0 0 0 ? 1	0 0 1 0 1	1 1 1 0 1	0 1 1	
Moselopterus elongatus	0 0 0 0 1	3 1 1 0 0	0 1 1 0 0	0 0 1 0 0	0 0 0 0 1
	0 0 0 ? ?	? 0 1 0 1	1 1 1 0 1	0 1 ?	
Onychopterella augusti	0 0 ? 0 1	? ? 1 1 ?	1 1 1 0 0	0 0 1 0 1	0 1 0 0 0
	? ? ? ? 0	– 0 0 1 1	0 0 0 1 0	0 0 0	
Onychopterella kokomoensis	0 0 1 0 1	3 1 1 1 0	1 1 ? ? 0	0 0 1 0 1	0 1 0 0 0
	0 0 0 ? 0	– 0 0 1 1	0 0 0 1 0	0 0 0	
Dolichopterus macrocheirus	0 0 0 0 1	0 1 1 1 0	1 1 1 1 1	1 1 1 0 1	1 1 0 1 0
	1 1 0 0 1	0 0 0 0 1	0 0 0 0 0	0 0 0	
Strobilopterus princetonii	0 0 0 0 1	? ? 1 0 ?	1 1 1 1 0	1 1 1 0 1	1 1 0 1 0
	1 ? ? 0 1	0 0 0 0 1	0 0 ? ? ?	0 0 0	
Eurypterus remipes	0 1 1 0 1	0 1 1 1 1	1 1 1 1 1	1 0 1 1 1	1 1 1 1 0
	0 0 0 1 0	– 0 1 0 1	0 0 0 0 1	0 0 0	
Erieopterus microphthamus	0 1 0 0 1	3 1 1 0 1	1 1 1 1 1	1 0 1 1 1	0 1 1 0 0
	0 1 0 1 0	– 0 1 0 1	0 0 1 0 0	0 0 0	
Hughmilleria socialis	0 0 1 1 1	1 1 1 1 0	1 1 1 1 1	1 0 1 1 1	0 1 1 1 0
	1 1 1 0 0	– 0 1 0 1	0 0 0 0 0	0 0 0	
Tylopterella boylei	0 0 1 0 1	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?
	? ? ? ? ?	? 0 0 1 1	0 0 0 0 0	0 0 0	
Megalograptus ohioensis	1 1 1 1 1	2 1 2 1 1	1 1 1 1 1	1 0 1 1 1	0 1 2 – 0
	0 0 1 0 0	– 0 1 1 1	0 0 0 0 0	1 0 0	
Mixopterus kiaeri	0 1 1 1 1	? 1 2 1 0	1 1 1 1 1	1 0 1 1 1	0 1 1 1 0
	0 0 1 0 0	– 0 1 0 1	0 0 1 0 0	1 0 0	
Loganamaraspis dunlopi	0 0 ? ? ?	3 1 ? ? ?	0 0 0 – ?	? ? ? ? ?	? ? ? ? 0
	0 2 2 0 0	– 0 1 2 1	0 0 0 ? ?	0 2 0	
Diploaspis casteri	0 0 1 1 0	1 ? 0 0 ?	1 ? ? ? ?	0 0 2 – –	0 0 2 – 0
	? ? 2 ? ?	? 0 0 2 1	0 0 2 0 1	0 3 1	
Octoberaspis ushakovi	0 0 0 0 0	? ? ? ? 0	1 ? ? ? ?	? 0 2 – –	0 0 2 – 0
	0 2 2 0 0	– 0 0 2 1	0 0 0 0 0	0 3 0	

TABLE 12. Full data matrix for the phylogenetic analysis.

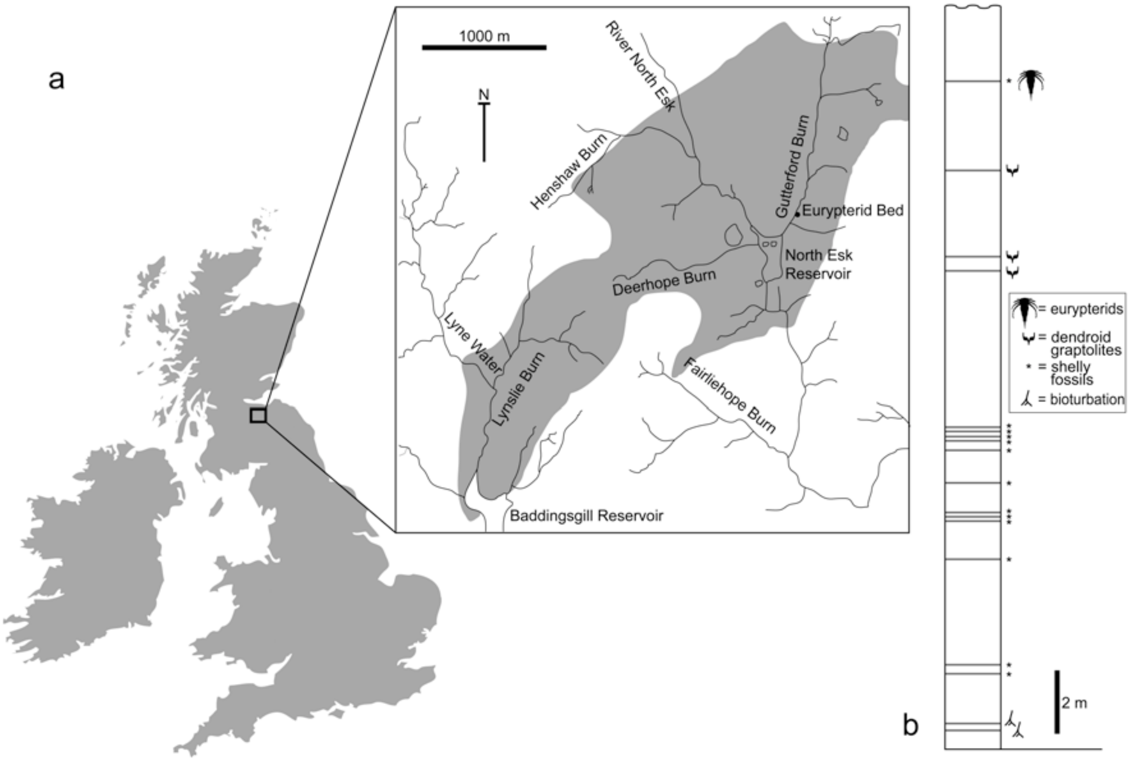
01. Anterior margin of carapace. [0 = unornamented; 1 = denticulate].
02. Carapace genal facets. [0 = absent; 1 = present].
03. Lateral eye shape. [0 = crescentic; 1 = expanded].
04. Lateral eye position on carapace. [0 = central; 1 = anterior].
05. Lateral eyes associated with ophthalmic ridge. [0 = present; 1 = absent].
06. Suture on ventral plates. [0 = *Eurypterus*-type; 1 = *Hughmilleria*- or *Hallipterus*-type; 2 = *Megalograptus*-type; 3 = *Erieopterus*-type].
07. Transverse suture on ventral plates. [0 = present; 1 = absent].
08. Morphology of spines prosomal appendages II–IV. [0 = reduced (length < width of podomere); 1 = regular (length ≈ width of podomere); 2 = enlarged (length > width of podomere)].
09. Mobility of spines on appendages II–IV. [0 = fixed, 1 = moveable].
10. Function of appendage V. [0 = solely walking or prey-capture; 1 = adapted to aid in balance during swimming].
11. Prosomal appendage VI. [0 = walking leg; 1 = swimming leg].
12. Shape of proximal podomere of appendage VI. [0 = narrow (L/W≥2.0); 1 = expanded (L/W<2.0)].
13. Anterior margin of coxa VI. [0 = undifferentiated; 1 = expanded to form ‘ear’].
14. Shape of ‘ear’ on coxa VI. [0 = triangular; 1 = rectangular/subquadrate].
15. Length of podomeres VI-4 and VI-5. [0 = VI-5≥VI-4; 1 = VI-4>VI-5].
16. Distal podomere margin of VI-6 modified. [0 = absent; 1 = present].
17. VI-7 lateral margins. [0 = unornamented; 1 = serrated].
18. Podomere 7a on appendage VI. [0 = absent; 1 = present on posterior of appendage; 2 = present on anterior of appendage].
19. Width of posterior VI-7a. [0 = narrow (less than 50% of width of VI-7); 1 = wide (more than 50%)].
20. Shape of posterior VI-7a. [0 = oval; 1 = triangular].
21. VI-8 lateral margins. [0 = unornamented; 1 = serrated].
22. Morphology of VI-8/VI-9 joint. [0 = joint flush; 1 = VI-9 set into VI-8].
23. Length of VI-9 (as ratio of VI-8). [0 = large (>50% of VI-8 length); 1 = small (<22% of VI-8 length); 2 = totally absent].
24. Shape of podomere VI-9. [0 = spinose; 1 = triangular, pentagonal or oval].
25. Podomere cuticular morphology. [0 = rounded; 1 = ridged].
26. Metastoma anterior. [0 = smooth or shallow notch; 1 = deeply notched].
27. Shape of posterior margin of metastoma. [0 = rounded; 1 = flattened or recurved; 2 = angular].
28. Genital operculum morphology. [0 = consisting of three visible segments; 1 = consisting of two visible segments; 2 = unfused].
29. Morphology of type-A genital appendage furca. [0 = fused; 1 = unfused].

30. Spatulae on type-A genital appendage. [0 = absent; 1 = present].
31. Morphology of genital spatulae. [0 = angular; 1 = rounded].
32. Moveable preabdominal spines. [0 = absent; 1 = present].
33. Postabdominal epimera. [0 = present; 1 = absent].
34. Preabdominal/postabdominal boundary. [0 = between 7th and 8th segments; 1 = between 6th and 7th segments; 2 = between 4th and 5th segments].
35. Postabdomen. [0 = undifferentiated; 1 = narrowing from preabdomen].
36. Posterior margin of segments 7-9. [0 = smooth; 1 = dentate].
37. Posterior margin of segments 10-12. [0 = smooth; 1 = dentate].
38. Telson shape. [0 = straight; 1 = curved; 2 = paddle-like].
39. Telson base. [0 = flattened; 1 = bulbous expansion].
40. Telson margin. [0 = smooth; 1 = serrated].
41. Opisthosoma lateral division. [0 = none; 1 = trilobed].
42. Primary dorsal ornamentation. [0 = scales; 1 = closely spaced pustules; 2 = none; 3 = coarse pustules].
43. Row of node-like scales on dorsal opisthosomal segments. [0 = absent; 1 = present].

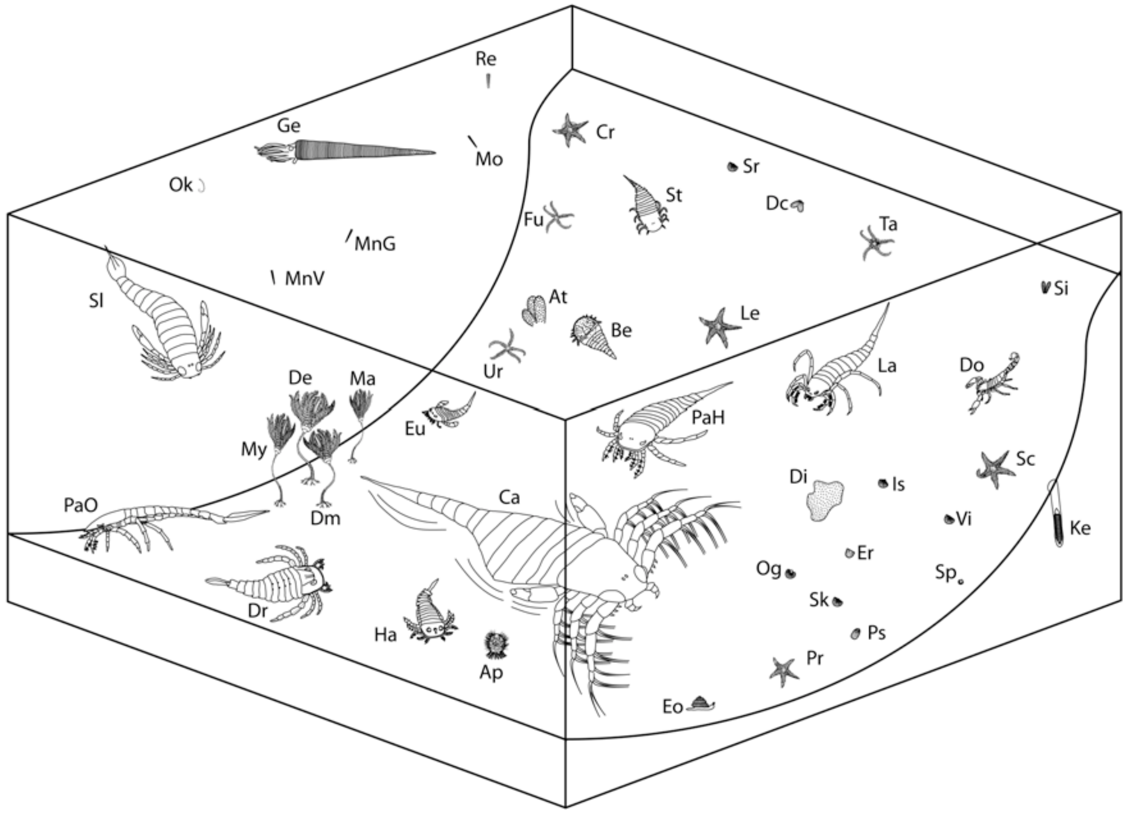
TABLE 13. Character list for the data matrix in Table 12.



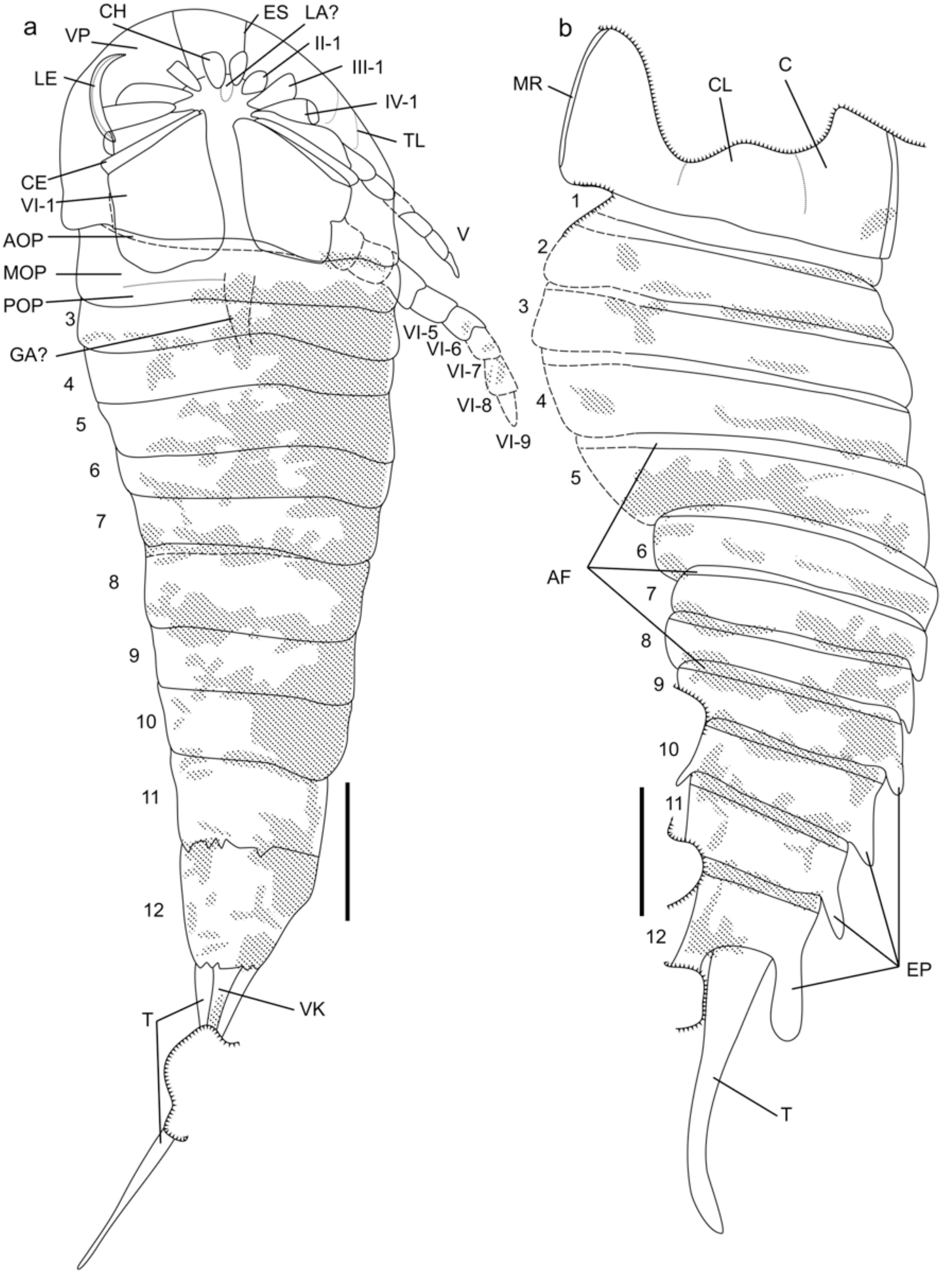
TEXT-FIG. 1. Eurypterids from the Pentland Hills Gutterford Burn Eurypterid Bed: **a**, '*Eurypterus minor*' Laurie, 1899, from Tetlie (2006); **b**, *Drepanopterus pentlandicus* Laurie, 1892, modified from Lamsdell *et al*. (2009); **c**, *Parastylonurus ornatus* (Laurie, 1892), from Waterston 91979); **d**, *Hardieopterus macrophthalmus* (Laurie, 1892), from Tetlie (2008). Scales bars equal 50 mm.



TEXT-FIG. 2. Locality and horizon for *Stoermeropterus conicus* (Laurie, 1892): **a**, map of the British Isles with inset map of the Pentland Hills showing the position of the Eurypterid Bed outcrop; **b**, simplified geological column of the Gutterford Burn section showing fossiliferous horizons and the horizon in which eurypterids are found.



TEXT-FIG. 3. Palaeoenvironmental reconstruction of the Eurypterid Bed: **Ap**, *Aptilechinus caledonensis*; **At**, *Atractosella andreae*; **Be**, *Bembicosoma pomphicus*; **Ca**, ‘*Carcinosoma*’ *scoticum*; **Cr**, *Crepidosoma wenlocki*; **Dc**, *Dicoelosia* aff. *alticavata*; **De**, *Dendrocrinus extensidiscus*; **Di**, *Dictyocaris ramsayi*; **Dm**, *Dimerocrinites pentlandicus*; **Do**, *Dolichophonus loudonensis*; **Dr**, *Drepanopterus pentlandicus*; **Eo**, *Euomphalopterus* cf. *apedalensis*; **Er**, *Erinostrophia undata*; **Eu**, ‘*Eurypterus*’ *minor*; **Fu**, *Furcaster leptosoma*; **Ge**, *Geisonoceras maclareni*; **Ha**, *Hardieopterus macrophthalmus*; **Is**, *Isorthis* (*Ovalella*) aff. *mackenziei*; **Ke**, *Keilorites*; **La**, *Laurieipterus elegans*; **Le**, *Lepyriactis nudus*; **Ma**, *Macrostylocrinus silurocirrifer*; **MnG**, *Monoclimacis geinitzi*; **MnV**, *Monoclimacis vomerina*; **Mo**, *Monograptus priodon*; **My**, *Myelodactylus parvispinifer*; **Og**, *Oglupes* aff. *alba*; **Ok**, *Oktavites excentricus*; **PaH**, *Parastylonurus hendersoni*; **PaO**, *Parastylonurus ornatus*; **Pr**, *Protactis wenlockensis*; **Ps**, *Pseudolingula*; **Re**, *Retiolites angustidens*; **Sc**, *Schuchertia wenlocki*; **Si**, *Stictopora*; **Sk**, *Skenidioides lewisii*; **Sl**, *Slimonia dubia*; **Sp**, *Sphaerirhynchia sphaeroidalis*; **Sr**, *Strophochonetes cornuta*; **St**, *Stoermeropterus conicus*; **Ta**, *Taeniactis wenlocki*; **Ur**, *Urasterella gutterfordensis*; **Vi**, *Visbyella visbyensis*.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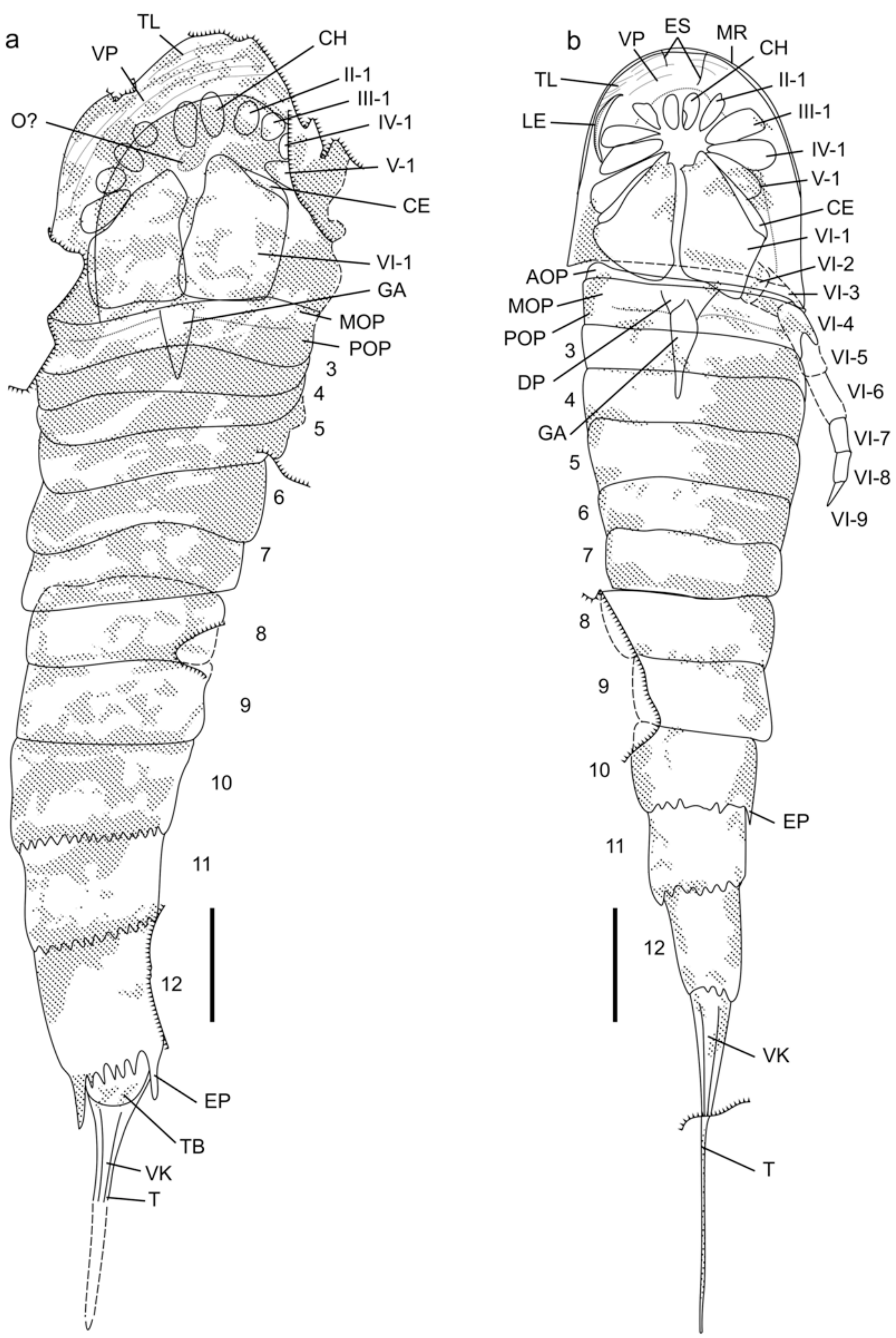
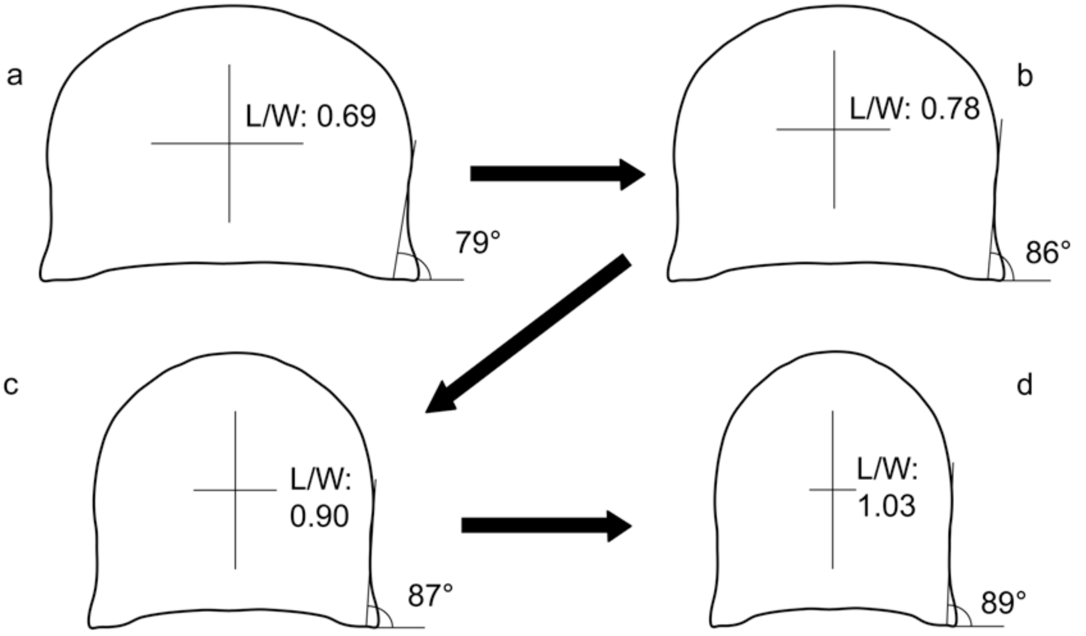
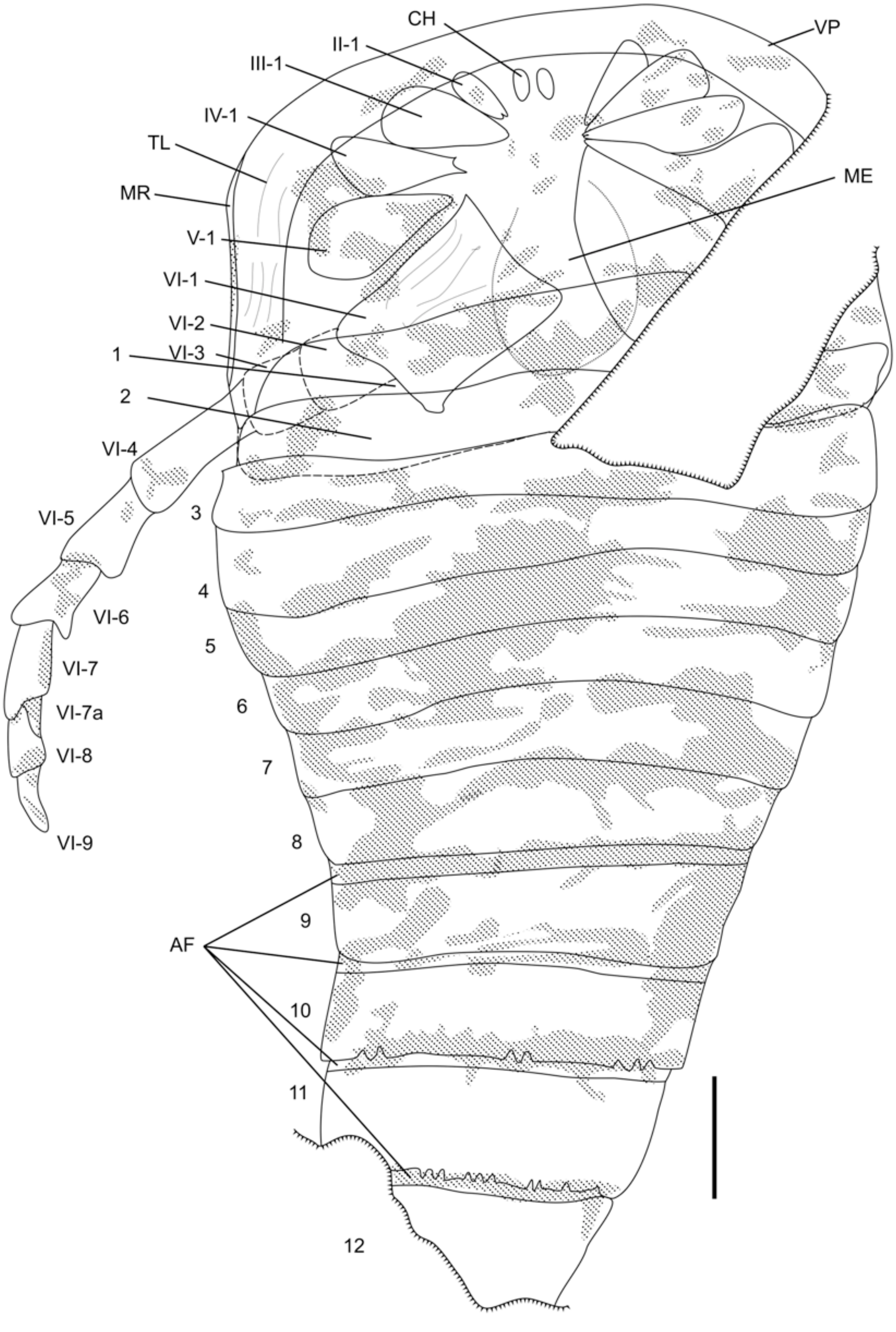
TEXT-FIG. 4. *Stoermeropterus conicus* (Laurie, 1892): **a**, Sketch of NMS G.1885.26.72.14; **b**, Sketch of NMS G.1897.32.88. The shading represents where the original cuticle has been preserved. Scale bars equal 10 mm.



TEXT-FIG. 5. *Stoermeropterus conicus* (Laurie, 1892): **a**, Sketch of NMS G.1885.26.72.1. The circular structure beneath the chelicerae may represent the oral opening, however the prosomal region between the coxae is crumpled and such an assignment cannot be made with certainty; **b**, Sketch of NMS G.1885.26.72.13. The shading represents where the original cuticle has been preserved. Scale bars equal 10 mm.



TEXT-FIG. 6. Diagram detailing taphonomic warping in carapaces of *Stoermeropterus conicus*: **a**, Unwarped carapace; **b**, **c**, intermediate forms created due to lateral compression of the carapace; **d**, 'narrow' form caused due to severe lateral compression of the carapace as exemplified by NMS G.1897.32.174.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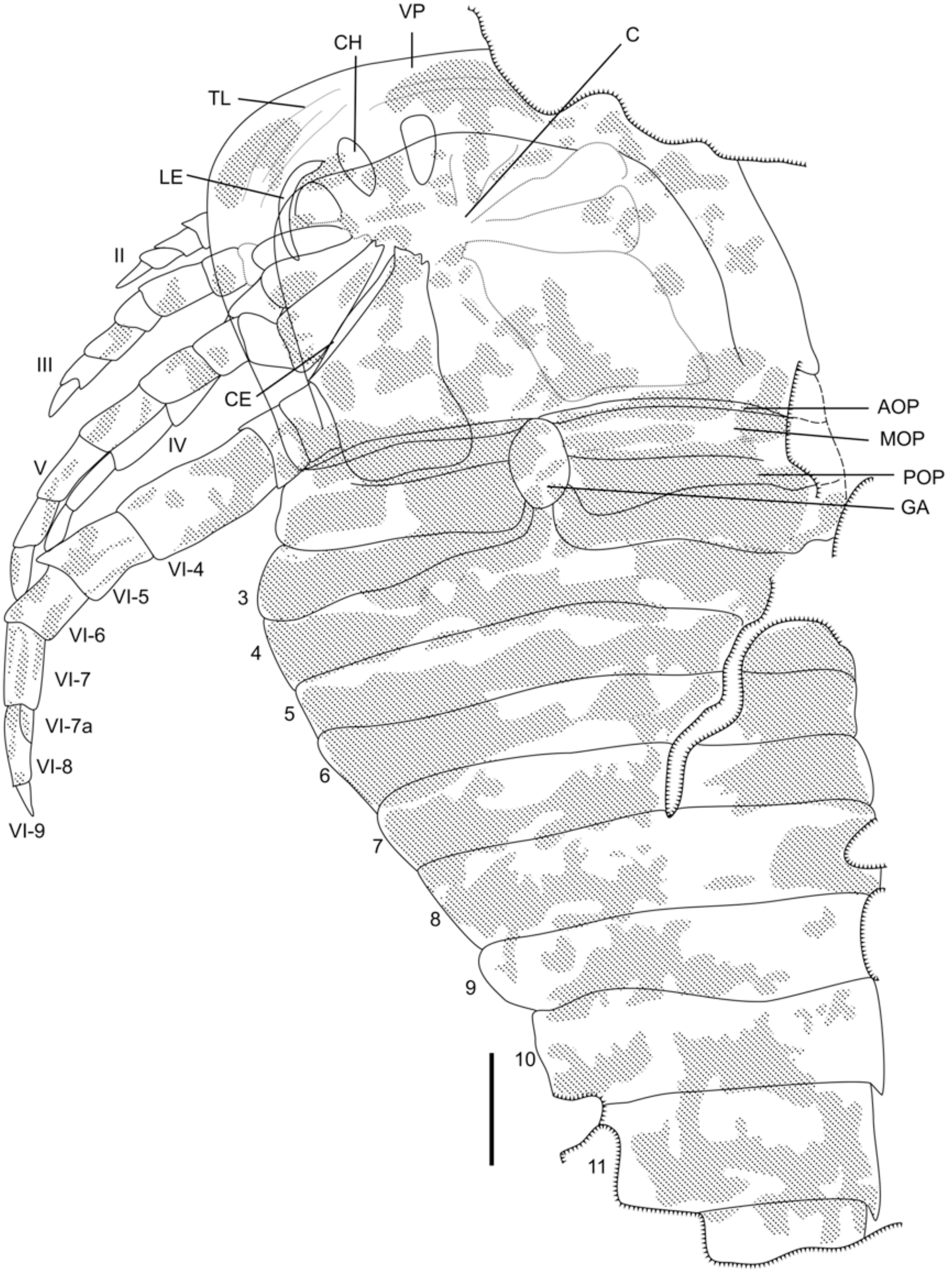
TEXT-FIG. 7. *Stoermeropterus conicus* (Laurie, 1892). Sketch of NMS G.1897.32.132. The shading represents where the original cuticle has been preserved. Scale bar equals 10 mm.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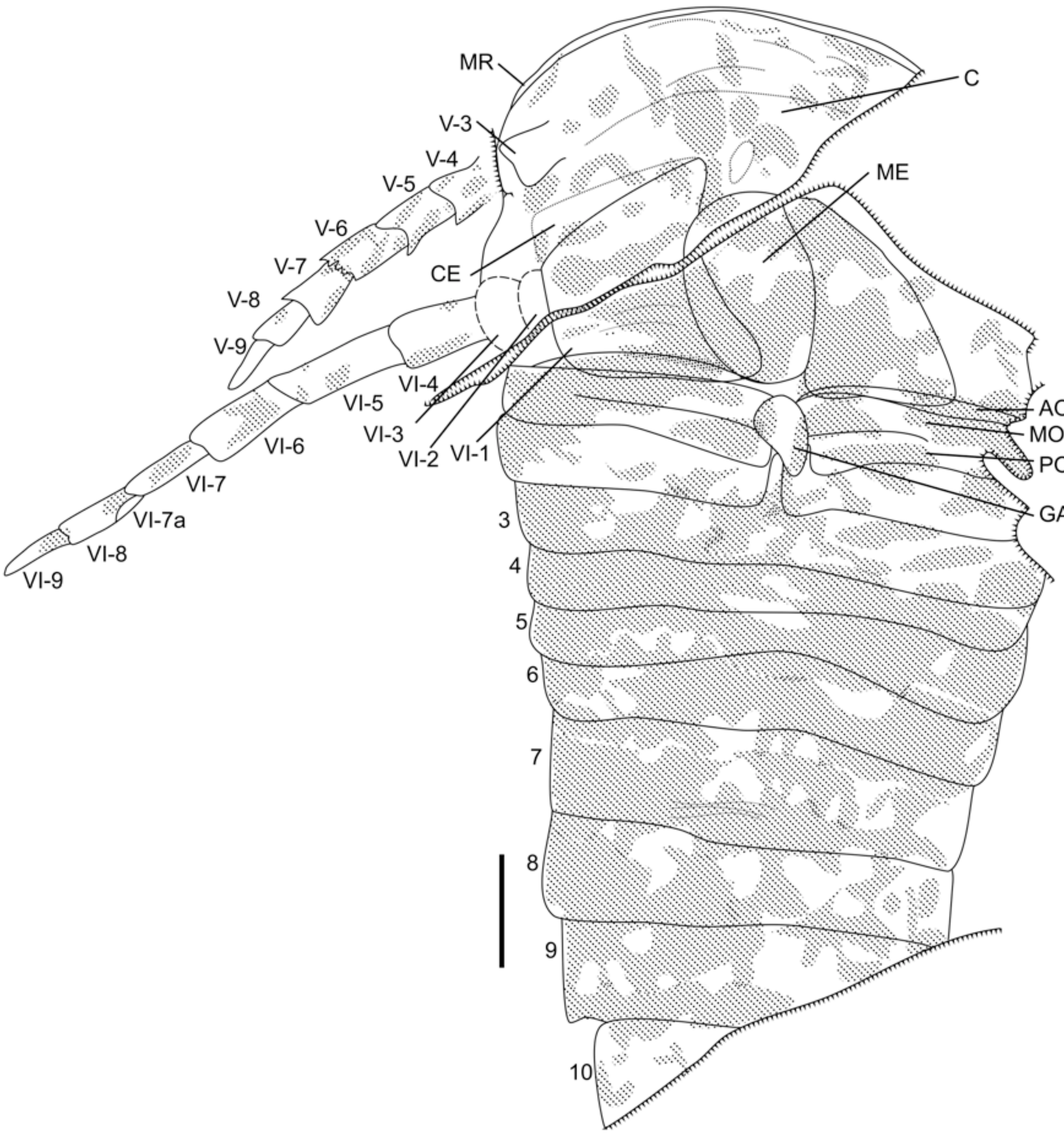
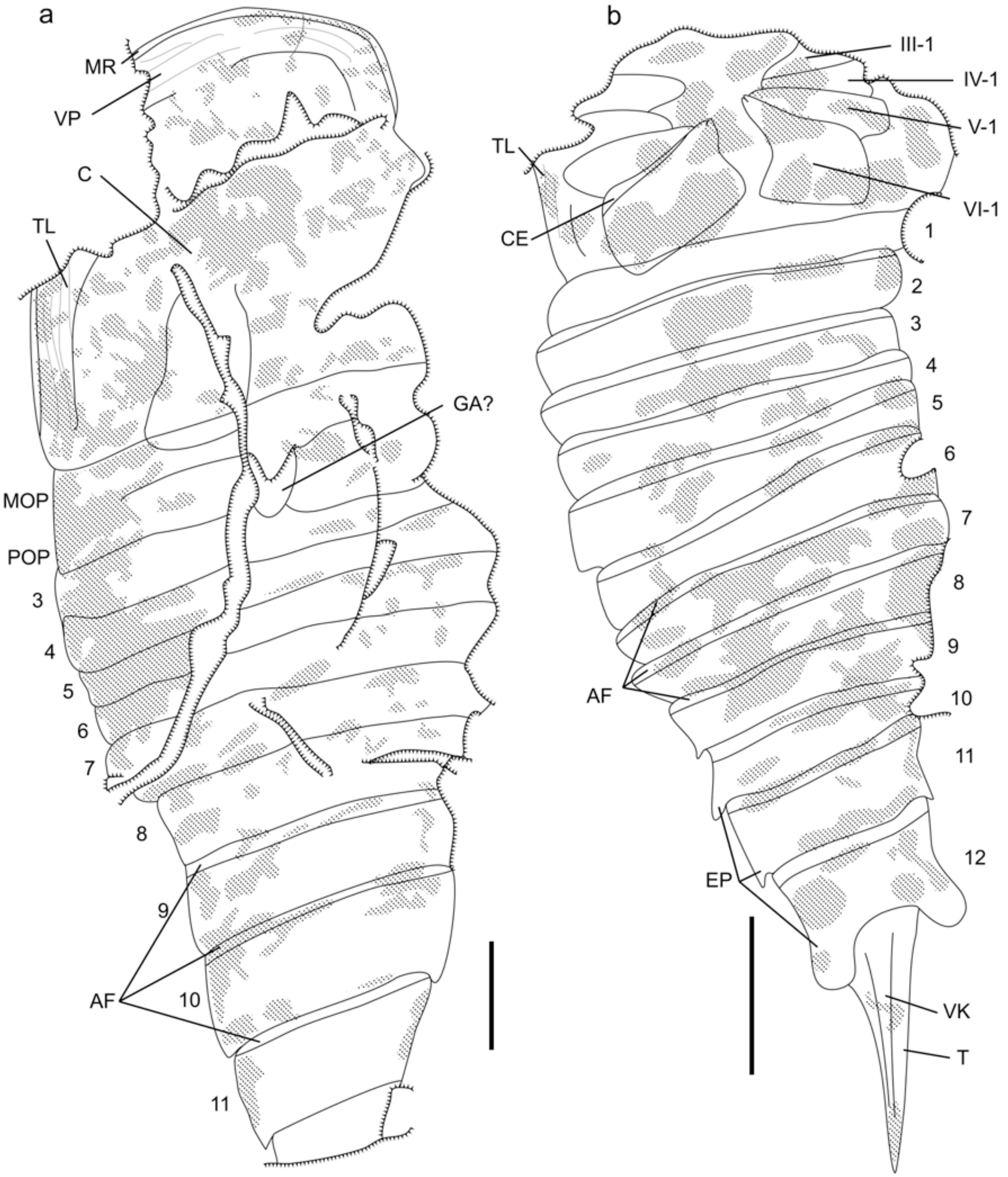
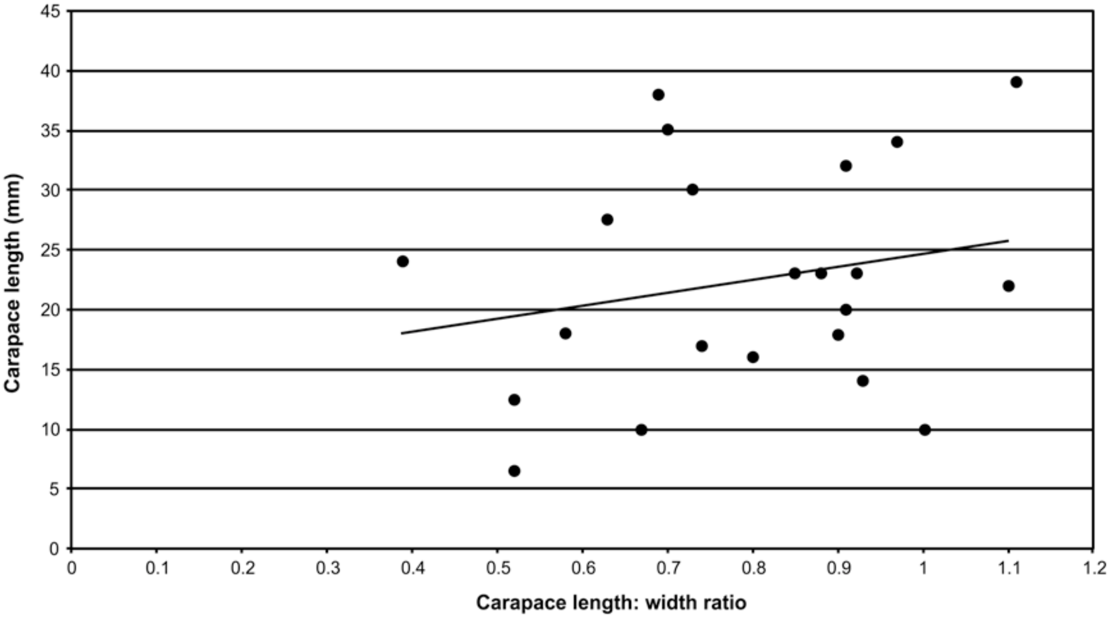
TEXT-FIG. 8. *Stoermeropterus conicus* (Laurie, 1892). Sketch of NMS G.1897.32.133. The shading represents where the original cuticle has been preserved. Scale bar equals 10 mm.



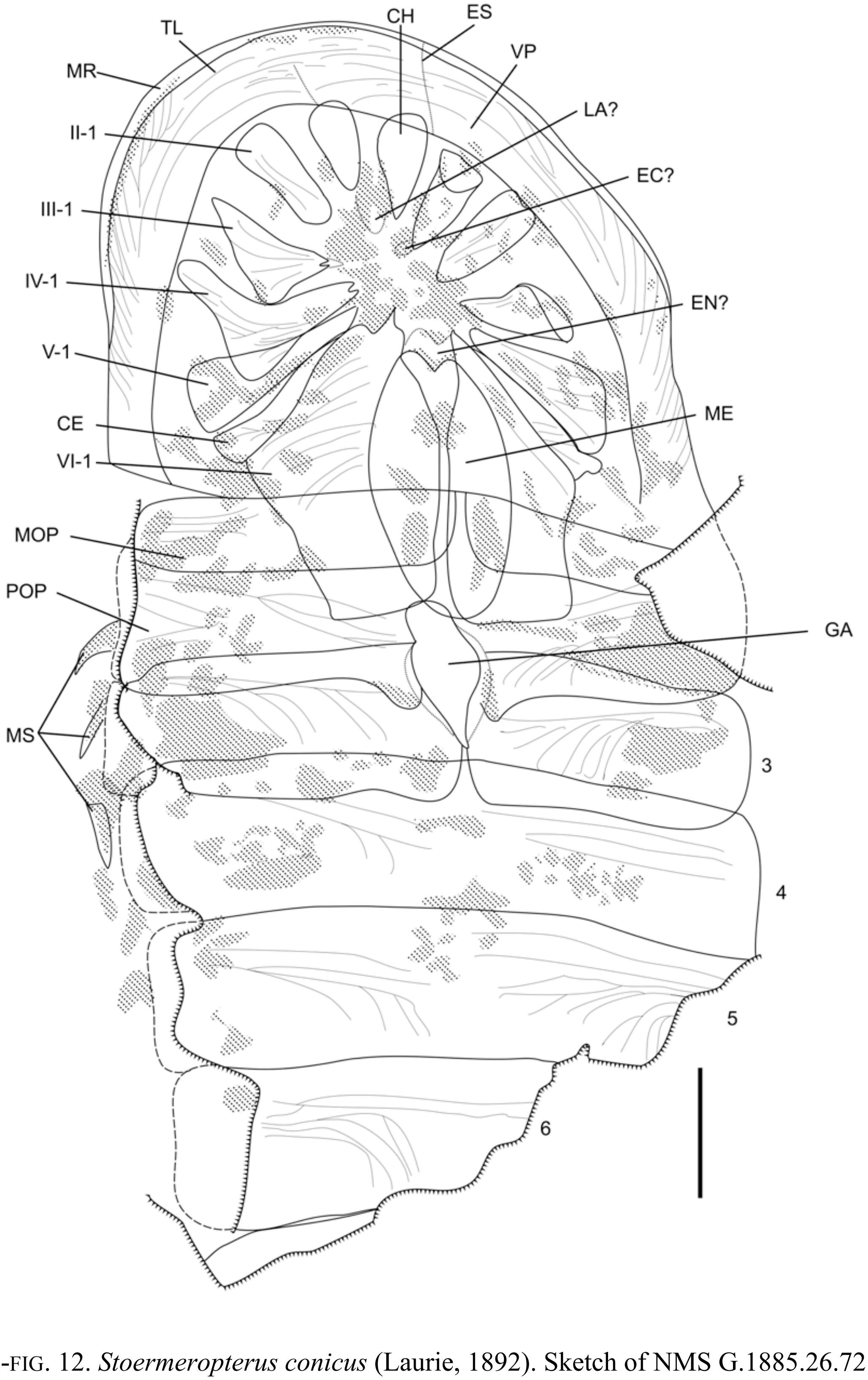
TEXT-FIG. 9. *Stoermeropterus conicus* (Laurie, 1892). Sketch of NMS G.1897.32.133. The shading represents where the original cuticle has been preserved. Scale bar equals 10 mm.



TEXT-FIG. 10. *Stoermeropterus conicus* (Laurie, 1892): **a**, Sketch of NMS G.1897.32.139; **b**, Sketch of NMS G.1897.32.164. The shading represents where the original cuticle has been preserved. Scale bars equal 10 mm.



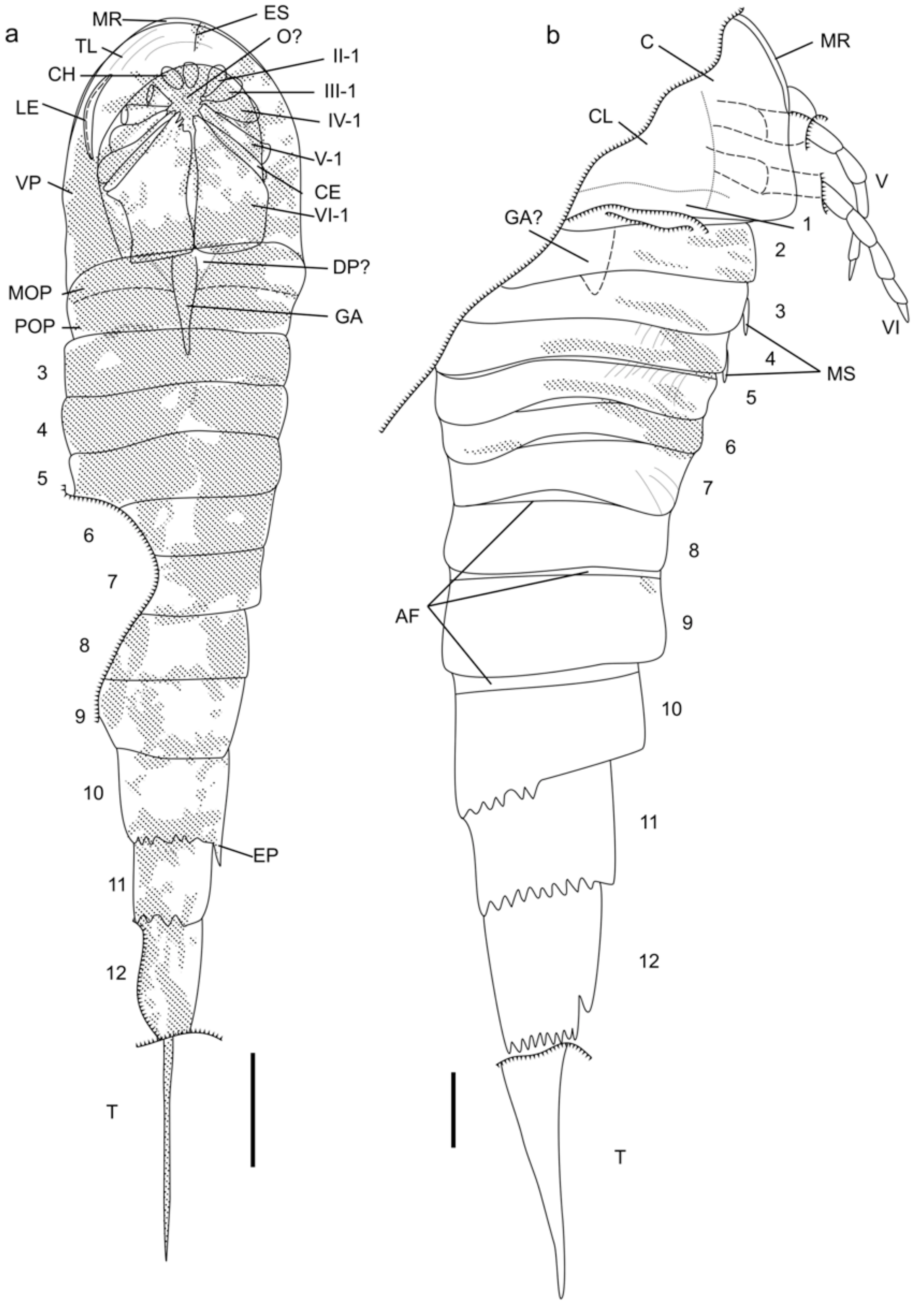
TEXT-FIG. 11. Graph plotting the carapace length: width ratio of all *Stoermeropterus conicus* specimens against carapace length. The regression line is length: width ratio = 11.068(length) + 13.447 and is not significant (r^2 = 0.053, 21 degrees of freedom, p = 0.292) indicating that the relationship between carapace length and carapace length: width ratio is highly variable and likely to be caused by taphonomic warping, not due to ontogeny.



TEXT-FIG. 12. *Stoermeropterus conicus* (Laurie, 1892). Sketch of NMS G.1885.26.72.17.

The lobe-like structure located between the chelicerae may be the labrum as described by

Selden (1981) in *Eurypterus tetragonophthalmus*, while small cuticular structures located proximally on some of the coxa may represent the epicoxa and the seemingly notched structure anterior to the metastoma may be the endostoma, however as in the other *Stoermeropterus* specimens the area between the coxa is poorly preserved and so none of these structures can be confidently identified. The shading represents where the original cuticle has been preserved. Scale bar equals 10 mm.



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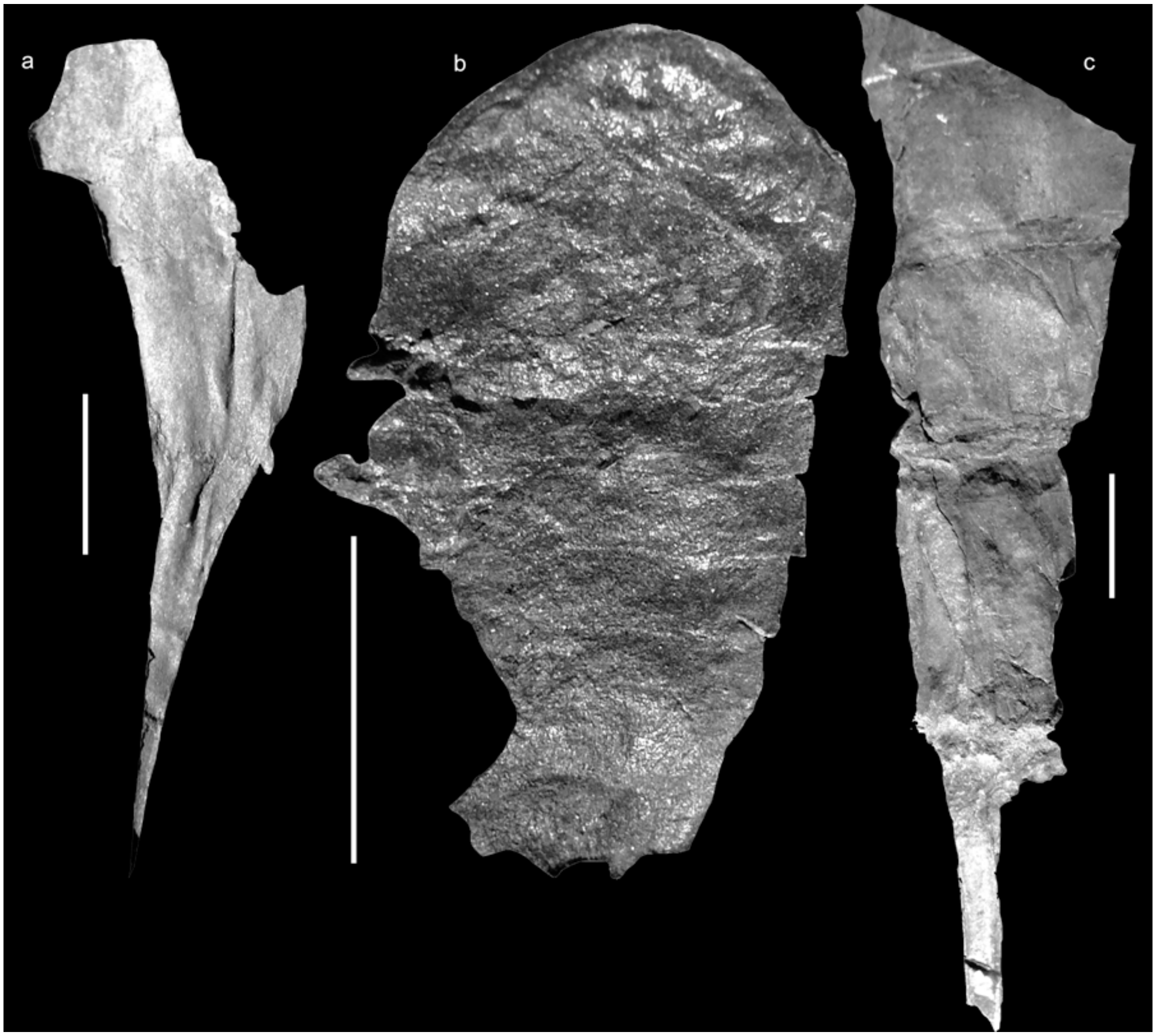
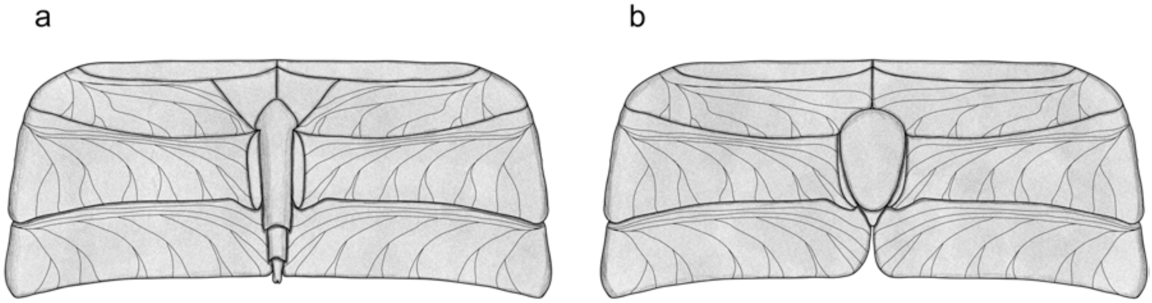
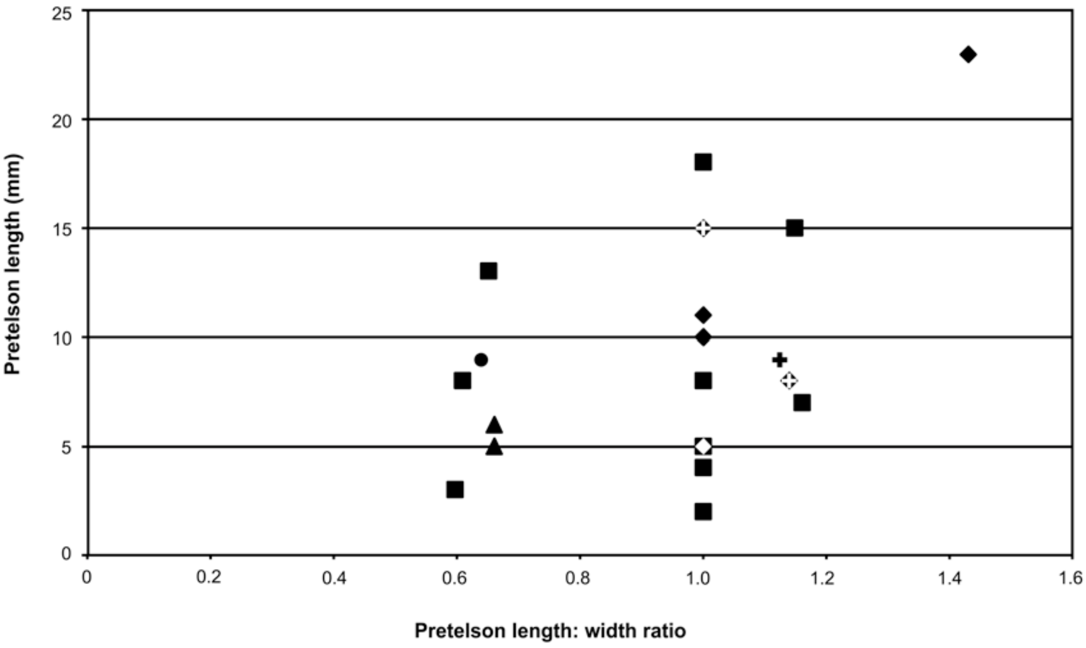
TEXT-FIG. 13. *Stoermeropterus conicus* (Laurie, 1892): **a**, Sketch of NMS G.1897.32.130, which may also show the oral opening; **b**, Sketch of NMS G.1897.32.138. The shading represents where the original cuticle has been preserved. Scale bars equal 10 mm.



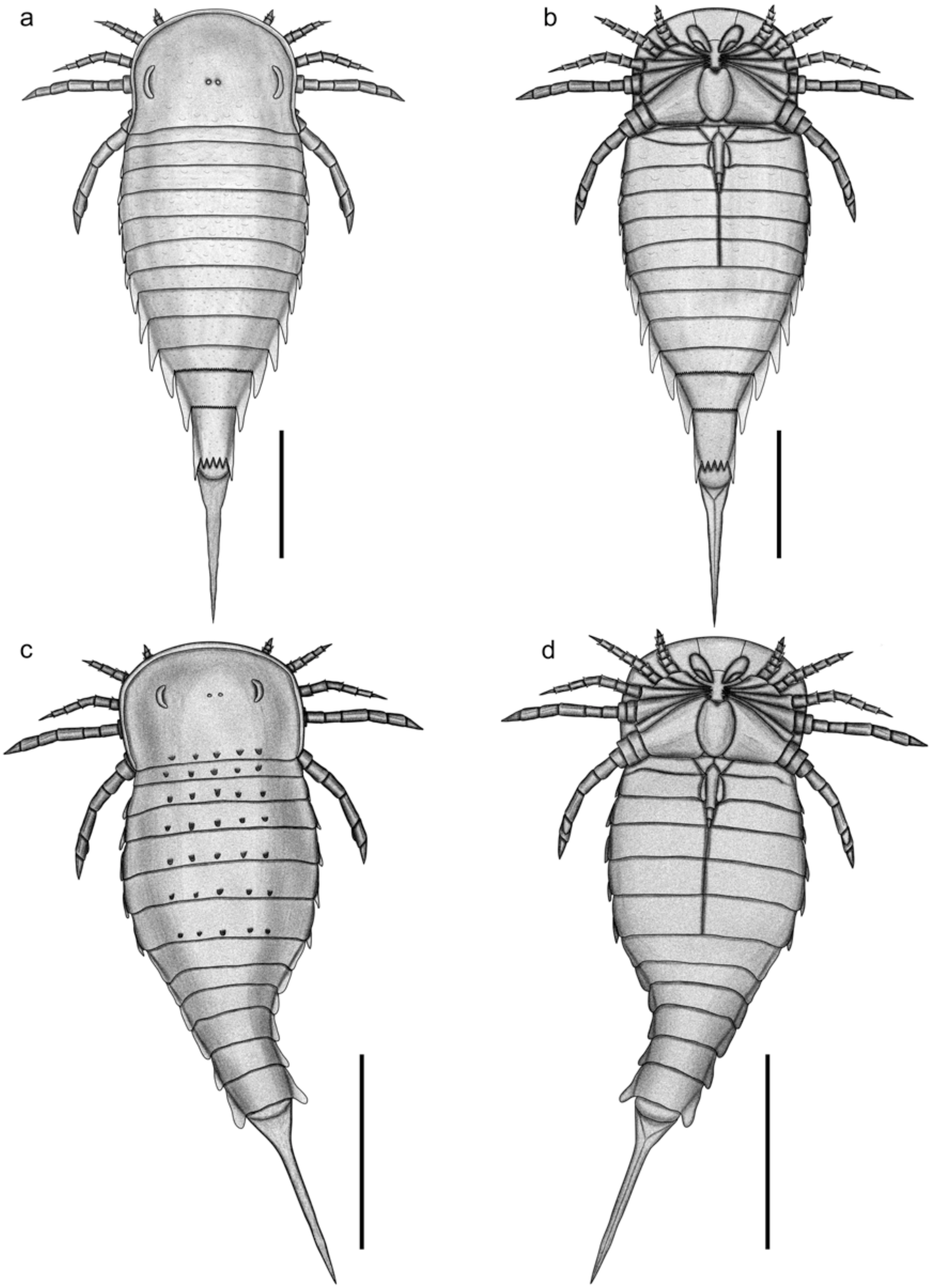
TEXT-FIG. 14. *Stoermeropterus conicus* (Laurie, 1892): **a**, Telson and posterior metasomal segments (NMS G.1897.32.184) showing serration of the pretelson. Orientation unknown; **b**, Prosoma and mesosoma (NMS G.1897.32.186) in ventral view showing the arrangement of the coxae and chelicerae; **c**, Telson and posterior metasomal segments (NMS G.1897.32.185) with epimeron preserved on the pretelson. Orientation unknown. Scale bars equal 10 mm.



TEXT-FIG. 15. Reconstructions of the genital appendage of *Stoermeropterus conicus* (Laurie, 1892): **a**, Reconstruction of the type A appendage; **b**, reconstruction of the type B appendage. Not drawn to scale.

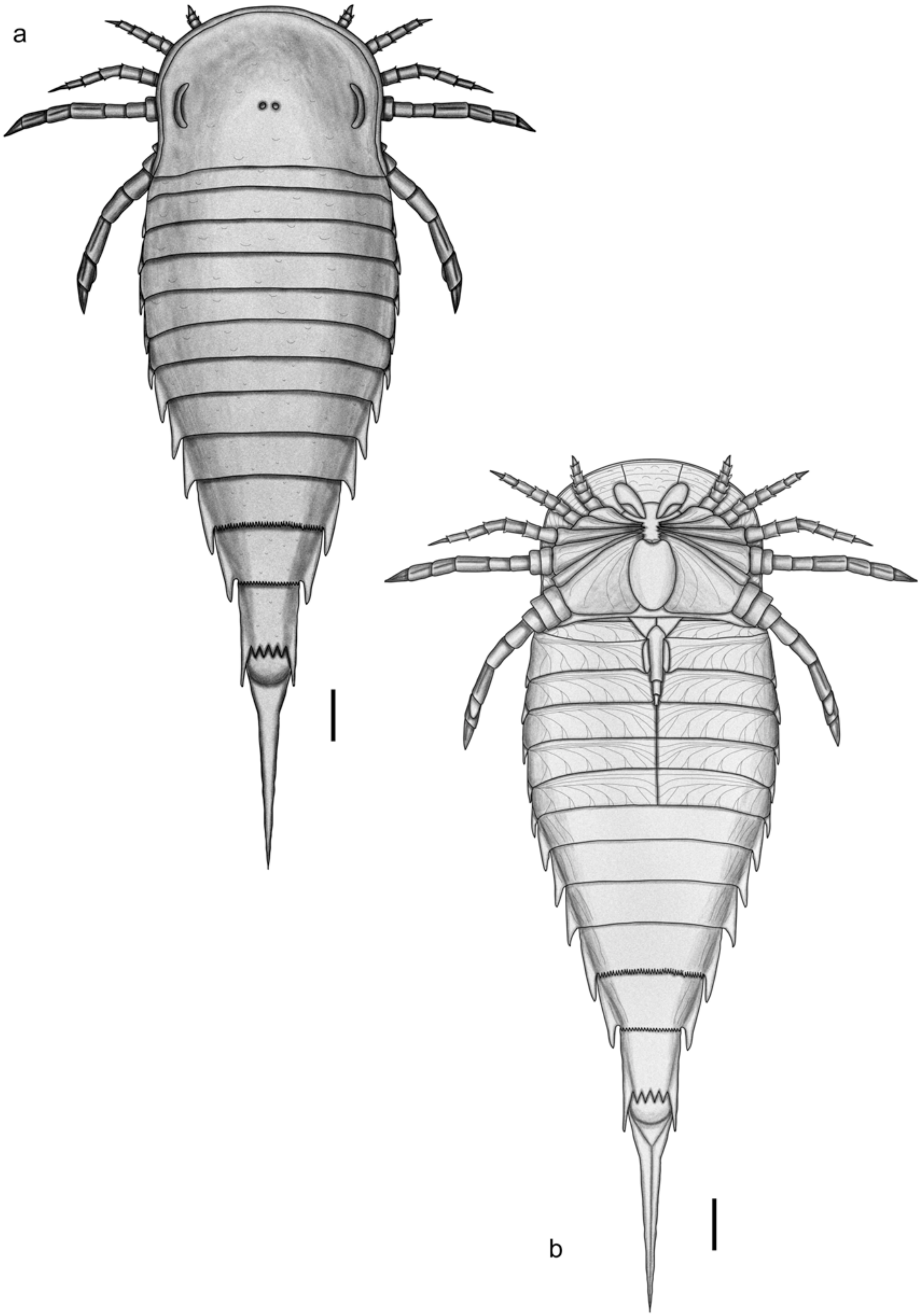


TEXT-FIG. 16. Graph plotting the pretelson length:width ratio of all known specimens of *Stoermeropterus conicus* (Laurie, 1892) against pretelson length. Diamonds indicate specimens preserving angular epimera, crosses represent specimens with a preserved type A genital appendage, triangles are specimens with lobate epimera and circles are those with a type B genital appendage, while squares represent specimens that lack either epimera or a genital appendage. Where two specimens plotted in the same position one point as been marked in white above the other. The distribution clearly shows two discrete concentrations, the first with a length: width ratio between 0.6 and 0.7 and the second with a length: width ratio between 1.0 and 1.4, which is considered strong evidence for a bimodal distribution through sexual dimorphism.

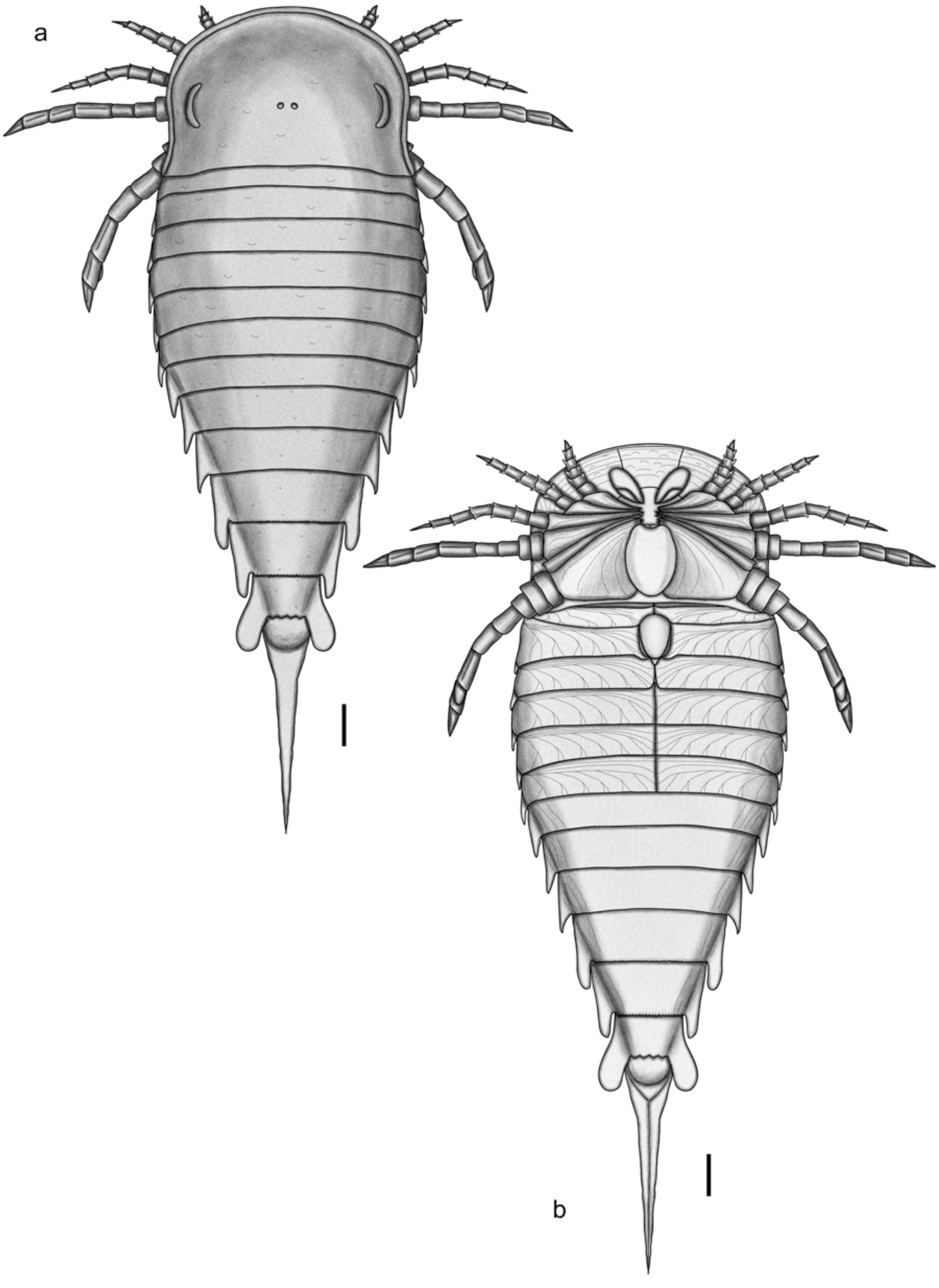


TEXT-FIG. 17. Reconstructions of *Stoermeropterus latus* (Størmer, 1934a) and *Stoermeropterus nodosus* (Kjellesvig-Waering & Leutze, 1966): **a**, dorsal view of *S.*

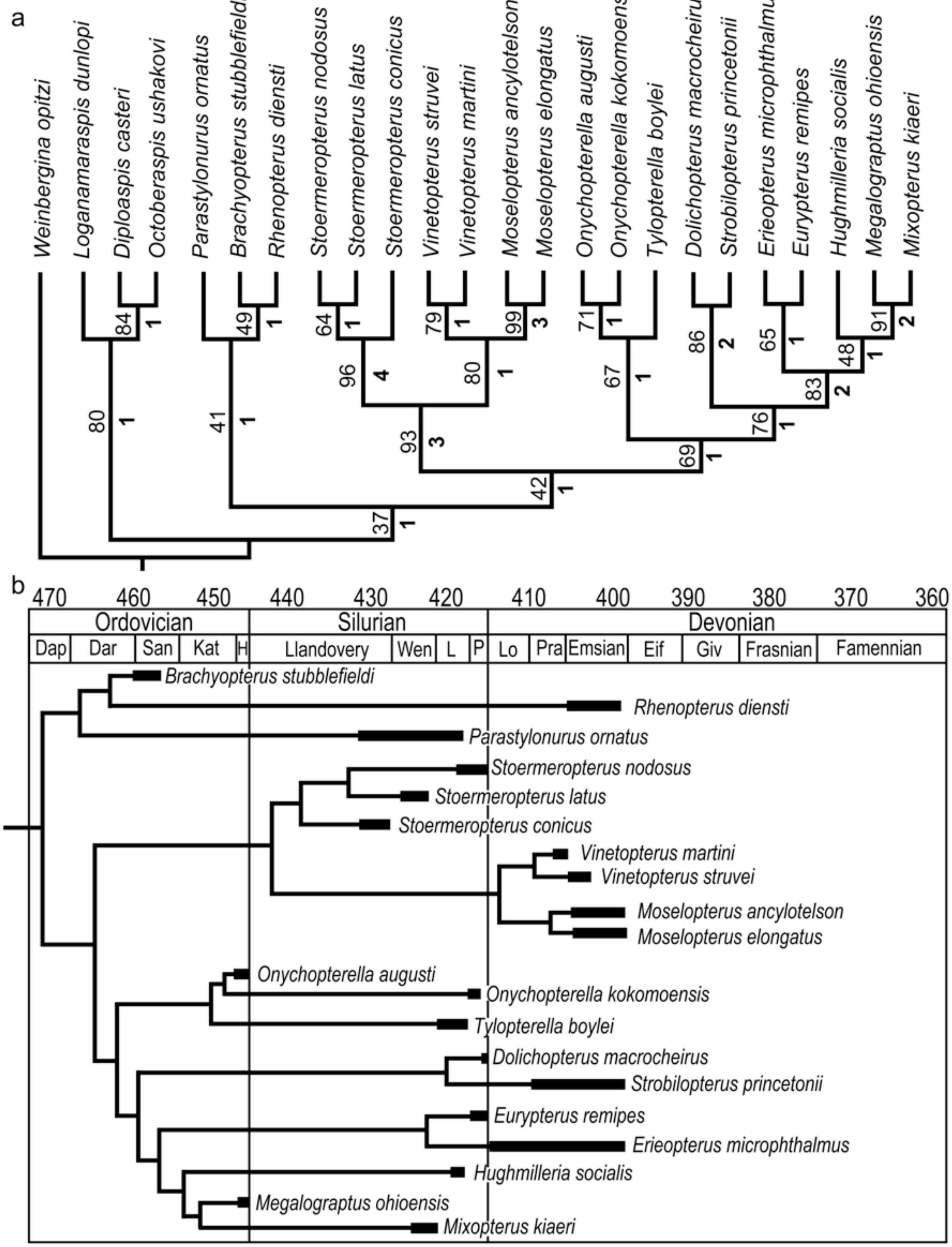
latus. Appendages II–V are reconstructed from *S. conicus*; **b**, ventral view of *S. latus* with type A appendage. Appendages II–V are reconstructed from *S. conicus*, while the distal portion of the genital appendage is reconstructed from comparison with *S. conicus* and *S. nodosus*; **c**, dorsal view of *S. nodosus*, all appendages reconstructed from *S. nodosus*; **d**, ventral view of *S. nodosus* with type A appendage. Appendages I–VI reconstructed from *S. conicus*. The genital appendage is from the specimen FMNH PE6212, herein interpretd as belonging to *S. nodosus*. The appendage is isolated however, and it is possible that the reconstruction presented here is actually the body of a type B individual. Scale bars equal 10 mm.



TEXT-FIG. 18. Reconstruction of *Stoermeropterus conicus* (Laurie, 1892) bearing type A genital appendage: **a**, dorsal view; **b**, ventral view. Scale bars equal 10 mm.



TEXT-FIG. 19. Reconstruction of *Stoermeropterus conicus* (Laurie, 1892) bearing type B genital appendage: **a**, dorsal view; **b**, ventral view. Scale bars equal 10 mm.



TEXT-FIG. 20. Results of the phylogenetic analysis performed using the data matrix in Table 12: **a**, Single most parsimonious tree. The labels to the left of each branch represent jackknife values, while those in bold to the right are Bremer support: **b**, Evolutionary tree derived from plotting the ranges of taxa to the tree from part a. Ages are in Ma and are derived from Gradstein *et al*. (2004) and Ogg *et al*. (2008). Epoch/Age abbreviations are: **Dap**, Dapingian; **Dar**, Darriwilian; **San**, Sandbian; **Kat**, Katian; **H**, Hirnantian; **Llandovery**, Llandovery; **Wen**, Wenlock; **L**, Ludlow; **P**, Pridoli; **Lo**, Lochkovian; **Pra**, Pragian; **Emsian**, Emsian; **Eif**, Eifelian; **Giv**, Givetian; **Frasnian**, Frasnian; **Famennian**, Fammenian.


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PLATE 1

Fig.

Stoermeropterus gen. nov. *conicus* (Laurie, 1892)

1 Specimen lacking appendages (NMS G.1885.26.72.1) in ventral view, showing type A genital appendage.

2 Counterpart of specimen in figure 1 (NMS G.1885.26.72.1) showering lateral edges of mesosomal segments and carapace base.

3 Paratype. Almost complete specimen with partially preserved prosomal appendage VI (NMS G.1885.26.72.13) in ventral view, showing type A genital appendage.

4 Expanded view of specimen in figure 3 (NMS G.1885.26.72.13) showing the arrangement of the coxae and the genital appendage.

Scale bars represent 10 mm.

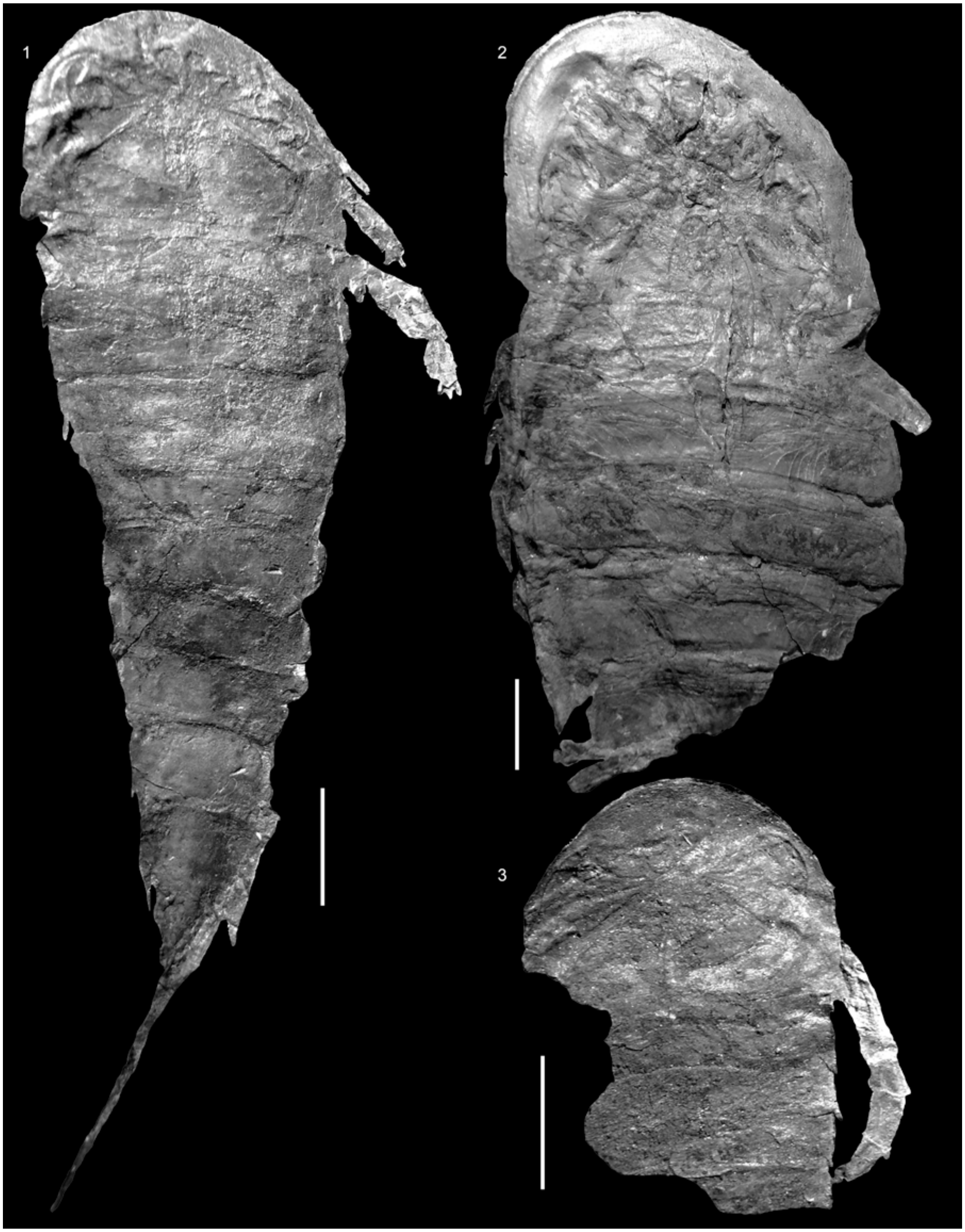
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PLATE 2

Fig.

Stoermeropterus gen. nov. *conicus* (Laurie, 1892)

1 Holotype. Almost complete specimen preserving prosomal appendages III, IV and VI (NMS G.1885.26.72.14) in ventral view.

2 Well-preserved specimen (NMS G.1885.26.72.17) detailing the ornamentation of the prosomal and mesosomal regions in ventral view showing metastoma and type B appendage.

3 Counterpart of holotype specimen in figure 1 (NMS G.1885.26.72.14) showing the position of the chelicerae and more complete appendage VI.

Scale bars represent 10 mm.

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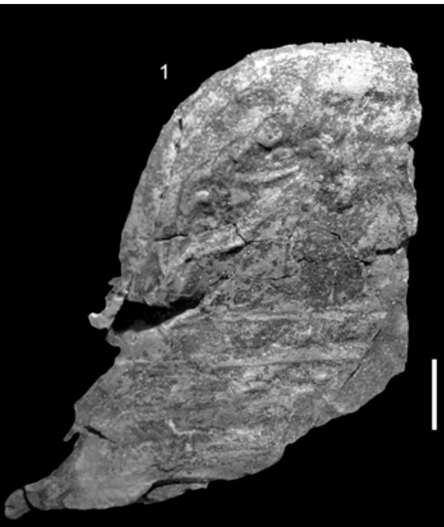

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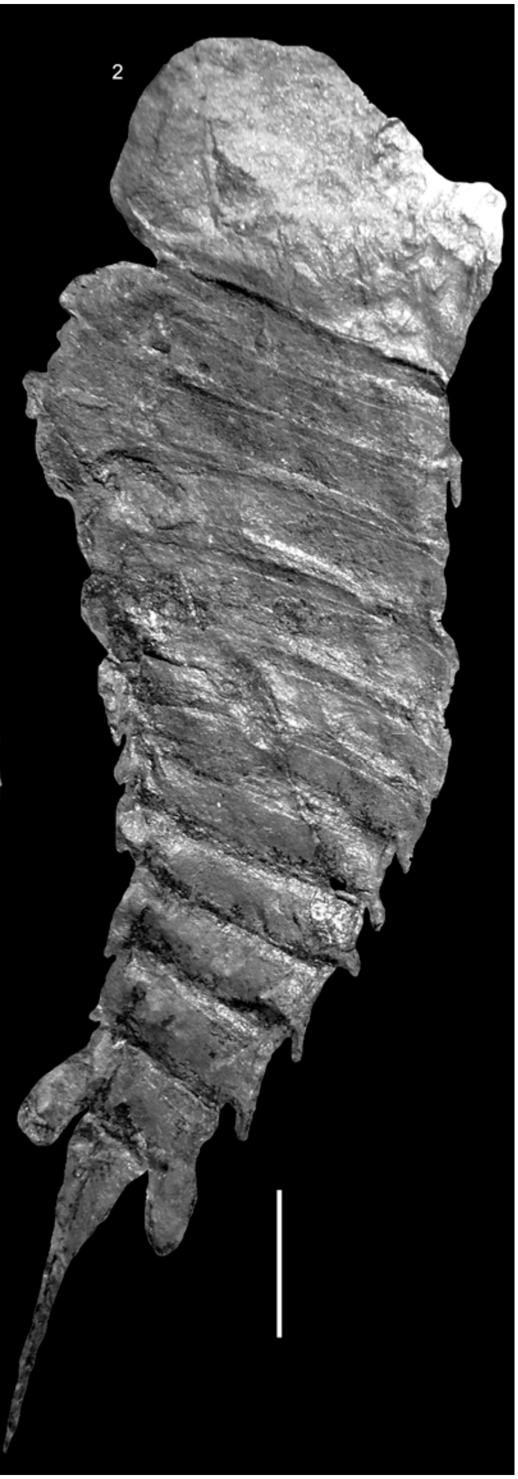

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PLATE 3

Fig.

Stoermeropterus gen. nov. *conicus* (Laurie, 1892)

1 Partial carapace and mesosoma (NMS G.1885.26.72.19) in ventral view.

2 Holotype of *Drepanopterus lobatus*. Specimen lacking appendages (NMS G.1897.32.88) in dorsal view showing lobate epimera on the pretelson.

3 Specimen lacking appendages (NMS G.1897.32.85) in ventral view.

Scale bars represent 10 mm.

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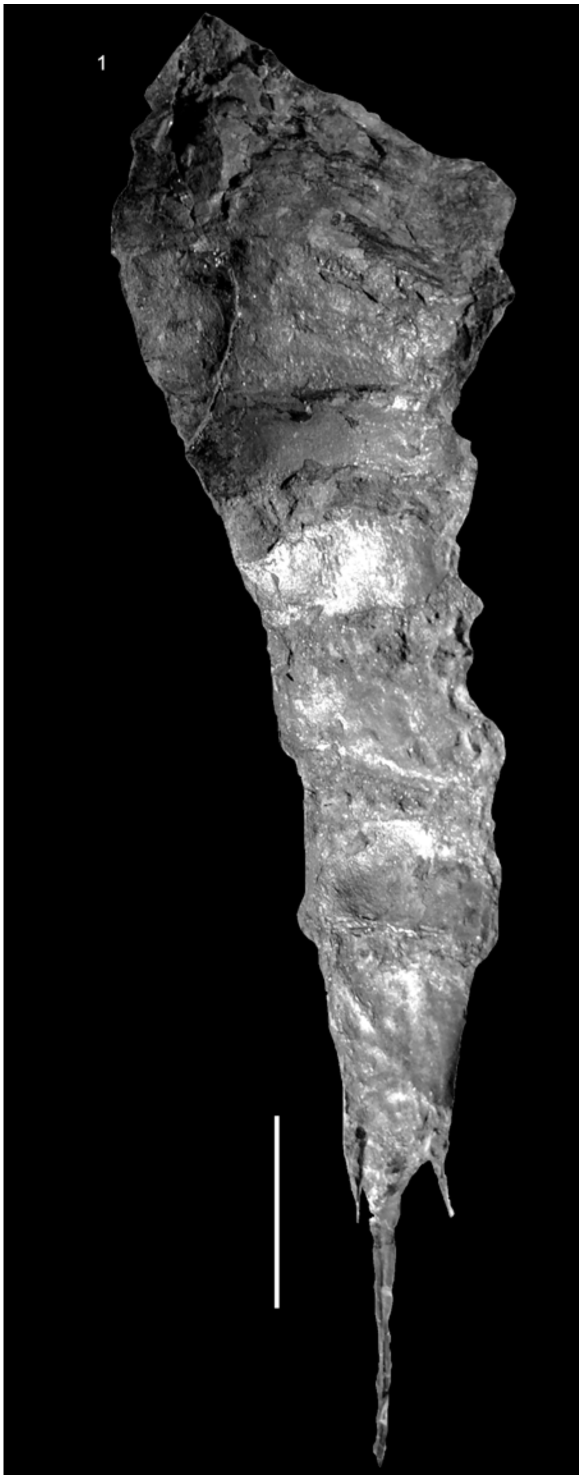

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PLATE 4

Fig.

Stoermeropterus gen. nov. *conicus* (Laurie, 1892)

1 Specimen lacking prosoma and showing the typical crumpling of the mesosoma (NMS G.1897.32.89), possibly in dorsal view.

2 Specimen lacking appendages or detail of the prosoma (NMS G.1897.32.121), orientation uncertain.

Scale bars represent 10 mm.

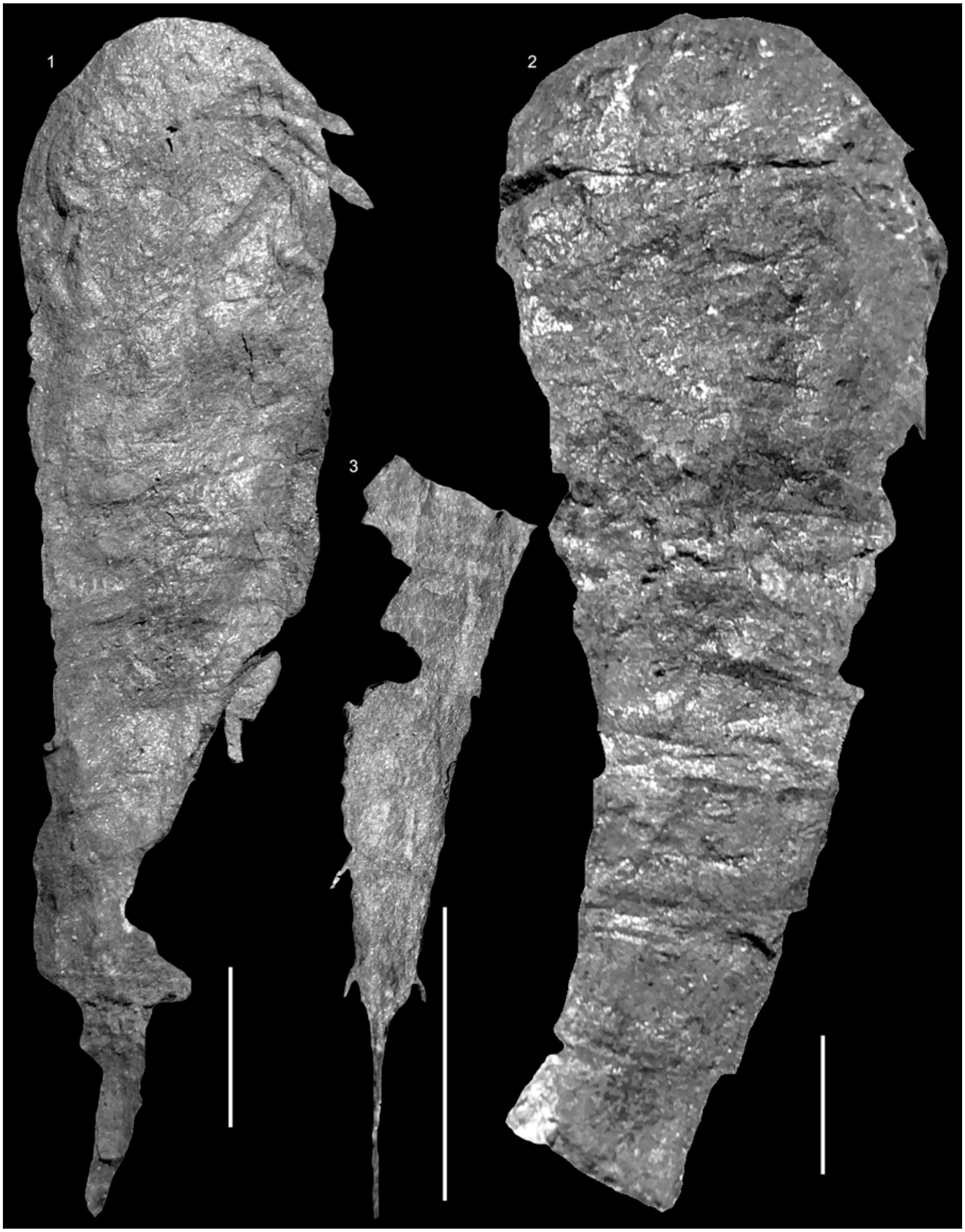
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PLATE 5

Fig.

Stoermeropterus gen. nov. *conicus* (Laurie, 1892)

1 Specimen lacking telson (NMS G.1897.32.123) in ventral view preserving prosomal appendages II-IV.

2 Small specimen (NMS G.1897.32.125) showing ornamentation of the metasomal segments in ventral view.

3 Metasoma and telson (NMS G.1897.32.124) possibly in dorsal view showing pretelsonic epimera.

Scale bars represent 10 mm.

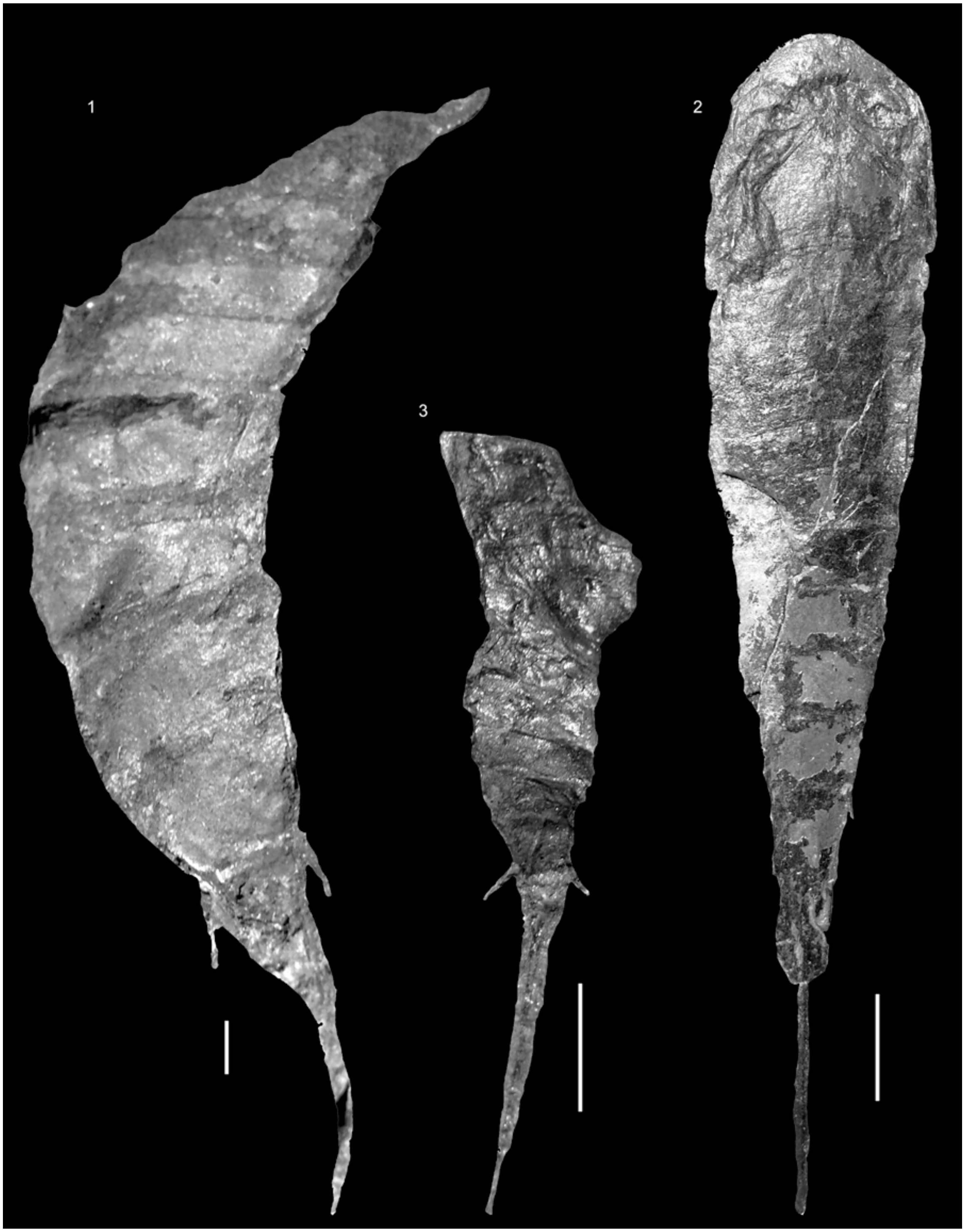
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PLATE 6

Fig.

Stoermeropterus gen. nov. *conicus* (Laurie, 1892)

1 Metasoma and telson (NMS G.1897.32.126) showing pretelsonic epimera, orientation uncertain.

2 Specimen lacking appendages (NMS G.1897.32.12.9) in ventral view showing the arrangement of the coxae and the position of the type A genital appendage.

3 Metasoma and telson (NMS G.1897.32.130) probably in dorsal view showing epimera on the pretelson and the central keel of the telson.

Scale bars represent 10 mm.


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PLATE 7

Fig.

Stoermeropterus gen. nov. *conicus* (Laurie, 1892)

1 Carapace and mesosoma (NMS G.1897.32.131) in ventral view showing mesosomal epimera and cuticular ornamentation.

2 Holotype of *Drepanopterus bembycoides*. Prosoma, appendage VI and opisthosoma minus pretelson and telson (NMS G.1897.32.132) in ventral view.

3 Expanded view of appendage VI from figure 2 (NMS G.1897.32.132).

4 Telson from specimen in figure 2 (NMS G.1897.32.132).

5 Carapace and coxae (NMS G.1897.32.134) in ventral view showing the cuticular sculpture of the marginal plates and the position of the lateral eyes pressed through the flattened carapace.

Scale bars represent 10 mm.

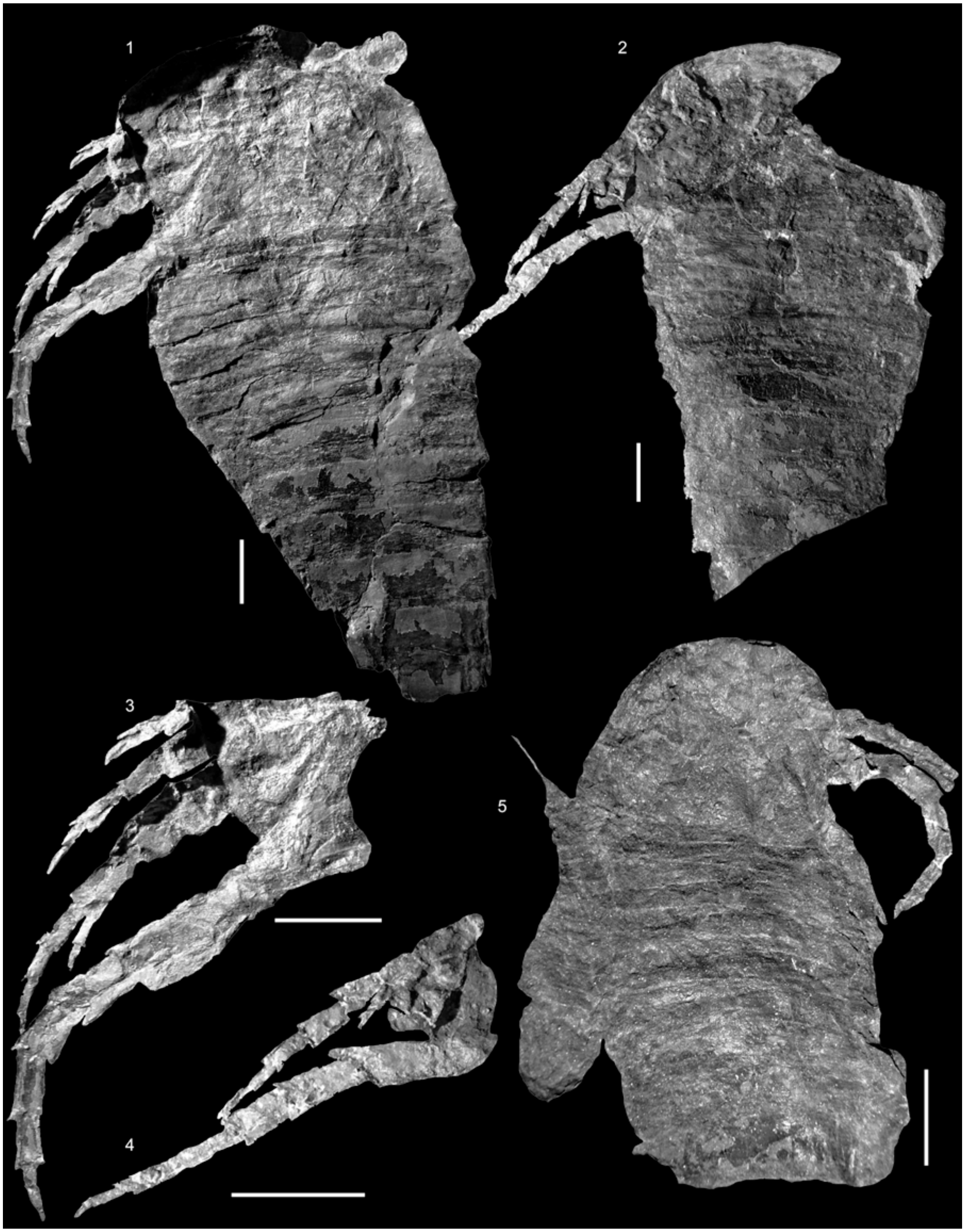
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PLATE 8

Fig.

Stoermeropterus gen. nov. *conicus* (Laurie, 1892)

1 Paratype of *Drepanopterus bembycoides*. Almost complete specimen lacking telson (NMS G.1897.32.133) in ventral view showing type B genital appendage and the position of the lateral eyes through the carapace.

2 Specimen with complete prosomal appendages V and VI but lacking posterior part of metasoma (NMS G.1897.32.136) showing type B genital appendage and metastoma in ventral view.

3 Expanded view of prosomal appendages from specimen in figure 1 (NMS G.1897.32.133).

4 Expanded view of prosomal appendages from specimen in figure 2 (NMS G.1897.32.136).

5 Associated specimens, the larger (NMS G.1897.32.137.1), consisting of prosoma with appendages IV and V and mesosoma in ventral view. Smaller specimen (NMS G.1897.32.137.2) in dorsal view almost complete but lacking appendages.

Scale bars represent 10 mm.


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PLATE 9

Fig.

Stoermeropterus gen. nov. *conicus* (Laurie, 1892)

1 Specimen consisting of opisthosoma and telson with partial carapace and prosomal appendages V and VI (NMS G.1897.32.138) in dorsal view showing telescoping of the mesosoma.

2 Counterpart of specimen in figure 4 (NMS G.1897.32.140) showing the ventral marginal prosomal plates.

3 Expanded view of specimen in figure 1 (NMS G.1897.32.138) showing the lateral edge of the carapace and the prosomal appendages.

4 Specimen consisting of prosoma and mesosoma (NMS G.1897.32.140) in ventral view showing prosomal appendages V and VI and the position of the lateral eyes. Scale bars represent 10 mm.

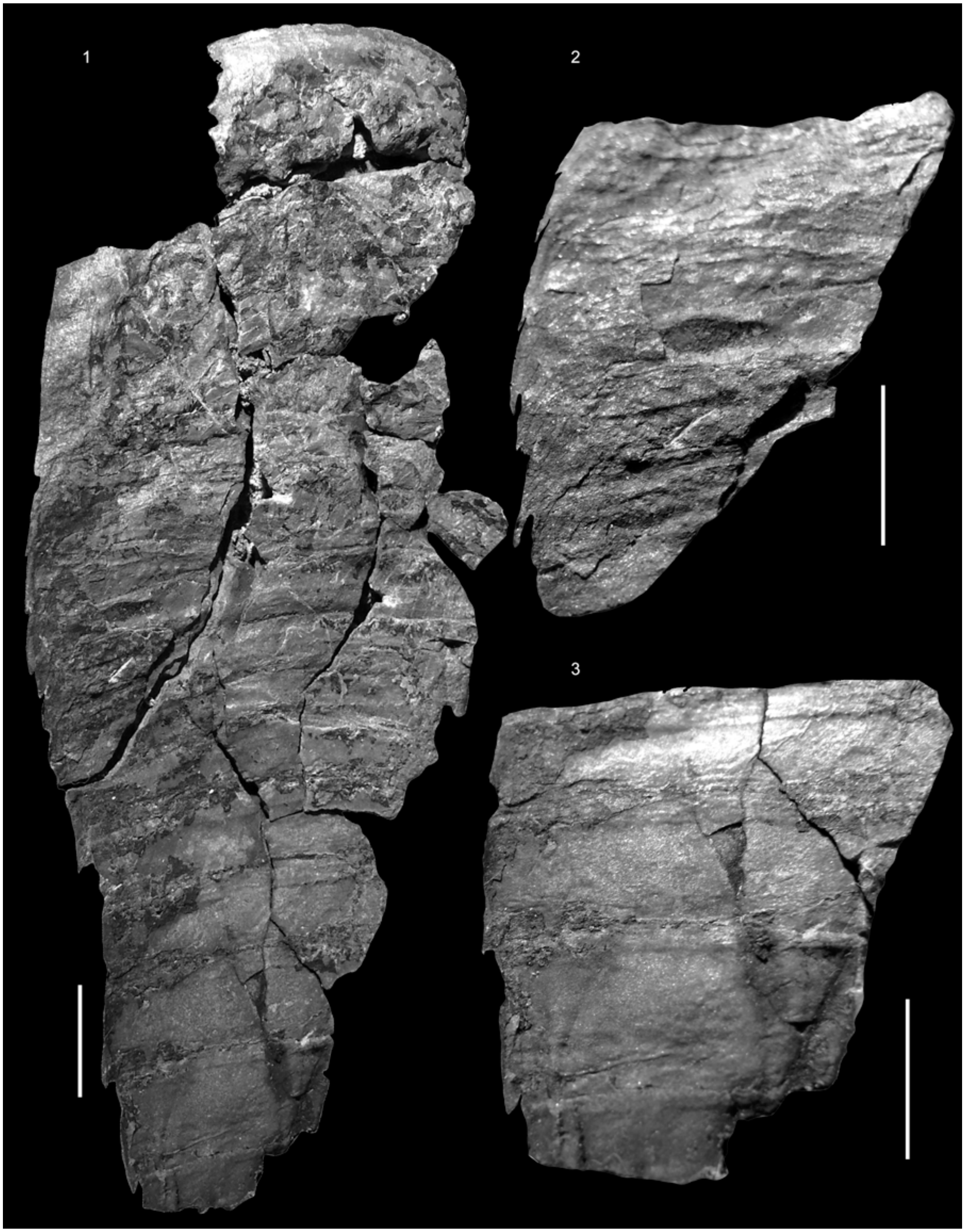
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PLATE 10

Fig.

Stoermeropterus gen. nov. *conicus* (Laurie, 1892)

1 Incomplete carapace and opisthosoma (NMS G.1897.32.139) in ventral view showing the cuticular sculpture of the prosomal ventral plates.

2 Expanded view of mesosoma of specimen in figure 1 (NMS G.1897.32.139) showing the lateral margins of the segments with moveable spines and the ventral cuticular ornament.

3 Expanded view of metasoma of specimen in figure 1 (NMS G.1897.32.139) showing the ventral margins of the segments with epimera.

Scale bars represent 10 mm.

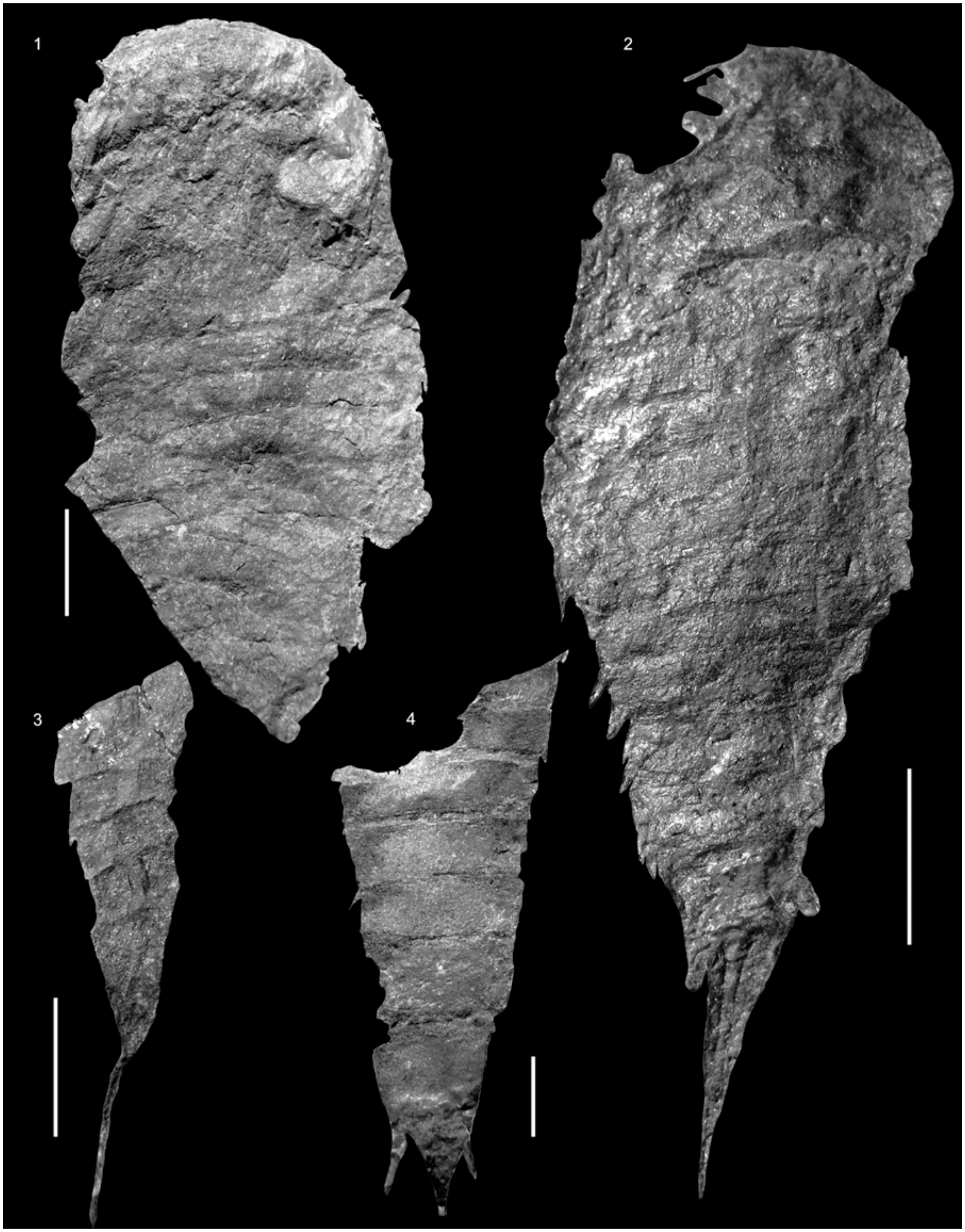
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PLATE 11

Fig.

Stoermeropterus gen. nov. *conicus* (Laurie, 1892)

1 Carapace and mesosoma (NMS G.1897.32.165), probably in dorsal view with the carapace flattened to reveal ventral structures, showing lateral moveable spine on second opisthosomal segment.

2 Paratype of *Drepanopterus lobatus*. Almost complete specimen lacking appendages (NMS G.1897.32.164) in dorsal view showing epimera on the pretelson.

3 Metasoma and telson (NMS G.1897.32.145) showing potential gut trace. Orientation unknown.

4 Metasoma and base of telson (NMS G.1897.32.170) showing pretelsonic epimera. Orientation unknown.

Scale bars represent 10 mm.

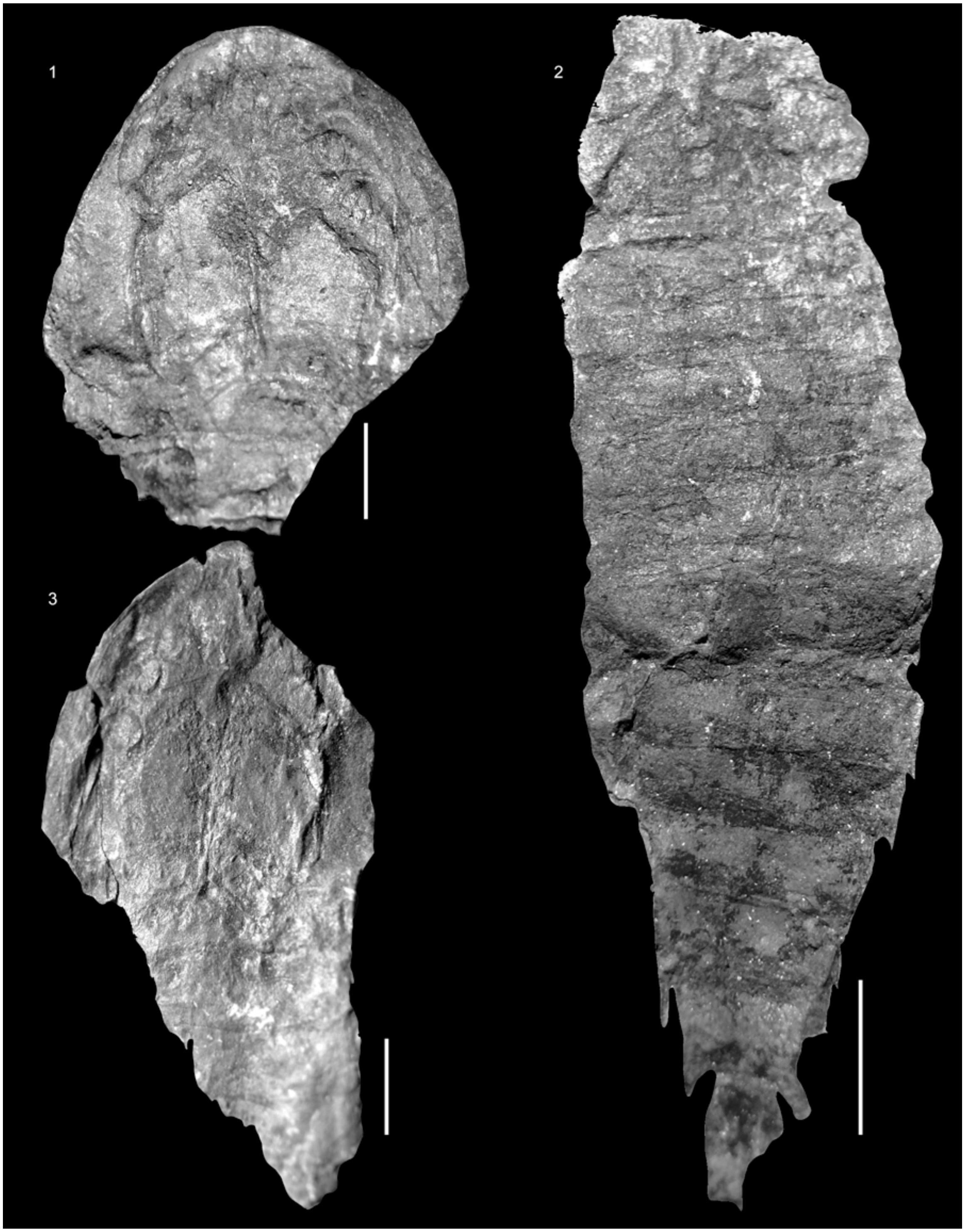
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PLATE 12

Fig.

Stoermeropterus gen. nov. *conicus* (Laurie, 1892)

1 Prosoma and first two opisthosomal segments (NMS G.1897.32.174) in ventral view showing the arrangement of the coxae, including a transverse section through several podomeres.

2 Opisthosoma and partial prosoma (NMS G.1897.32.173) in ventral view.

3 Counterpart to specimen in figure 1 (NMS G.1897.32.174) preserving more mesosomal segments.

Scale bars represent 10 mm.


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PLATE 13

Fig.

Stoermeropterus gen. nov. *conicus* (Laurie, 1892)

1 Partial carapace and opisthosoma (NMS G.1897.32.167) in ventral view.

2 Counterpart to specimen in figure 1 (NMS G.1897.32.167) showing epimera on metasomal segments.

3 Prosoma and opisthosoma (NMS G.1897.32.176) in ventral view with the prosoma expanded laterally due to post-mortem flattening. Cuticular ornamentation visible on the mesosomal segments.

4 Partial carapace showing lateral eye and mesosoma (NMS G.1897.32.172) in dorsal view.

Scale bars represent 10 mm.


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PLATE 14

Fig.

Stoermeropterus gen. nov. *conicus* (Laurie, 1892)

1 Opisthosoma showing crumpling of the mesosoma (NMS G.1897.32.180). Orientation unknown.

2 Opisthosoma and telson (NMS G.1897.32.182) in ventral view showing slight telescoping of the mesosoma and median keel of the telson.

3 Telson and partial pretelson (NMS G.1897.32.192) showing epimeron. Orientation unknown.

4 Carapace showing lateral eyes and mesosoma (NMS G.1897.32.191) in dorsal view.

Scale bars represent 10 mm.

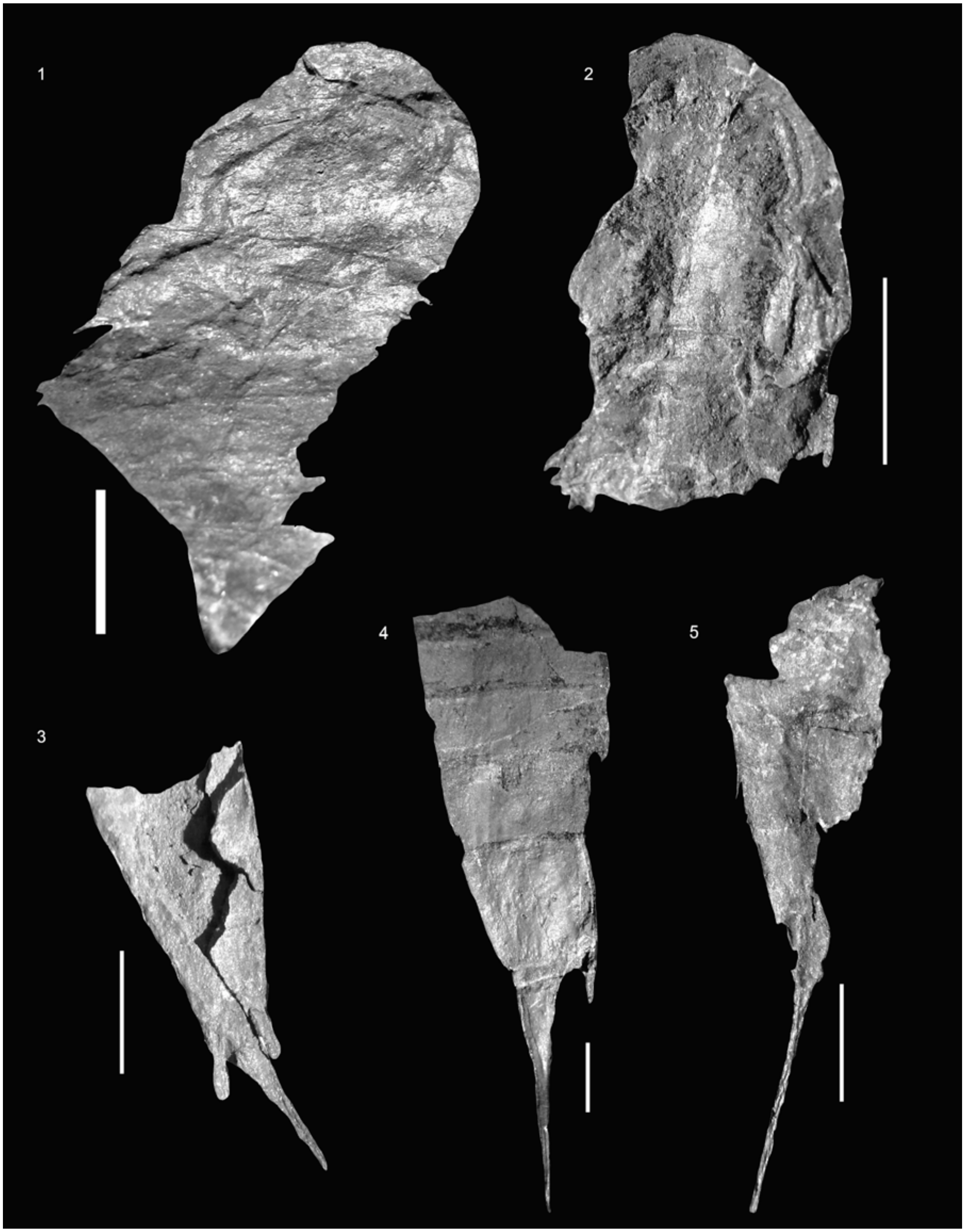
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PLATE 15

Fig.

Stoermeropterus gen. nov. *conicus* (Laurie, 1892)

1 Poorly preserved prosoma and mesosoma (NMS G.1897.32.207) in ventral view.

2 Partial carapace and mesosomal segments (NMS G.1897.32.208) in ventral view showing lateral eye and coxa VI.

3 Metasoma and telson (NMS G.1897.32.197) preserving pretelsonic epimera. Orientation unknown.

4 Metasoma and telson (NMS G.1897.32.198) with pretelsonic epimeron preserved. Orientation unknown.

5 Metasoma and telson (NMS G.1897.32.211) with epimeron preserved. Orientation unknown.

Scale bars represent 10 mm.

Chapter 4

First eurypterid from Italy: a new species of *Adelophthalmus* (Chelicerata: Eurypterida) from the Upper Carboniferous of the Carnic Alps (Friuli, NE Italy)

James C. Lamsdell, Luca Simonetto and Paul A. Selden

(Formatted for submission to *Revista Italiana di Paleontologia e Stratigrafia*)

Abstract: The first eurypterid known from Italy is described, as *Adelophthalmus piussii* sp. nov. It comes from the Upper Carboniferous of the Carnic Alps (Friuli, NE Italy). Relationships with related species are discussed. Adelophthalmids are the commonest eurypterids of the late Palaeozoic, at which time the disparity of the order was waning. The new record enhances our knowledge of adelophthalmid distribution and diversity.

Introduction

Eurypterids form a group of extinct Palaeozoic aquatic chelicerates found in marginal marine, brackish and freshwater environments. Although globally widespread, eurypterids tend to be restricted to Konservat-Lagerstätten due to their unmineralized cuticle (Gupta *et al.* 2007). Despite having a fossil record from every continent with the exception of Antarctica, it is only with the amalgamation of the palaeocontinents in late Devonian and early Carboniferous times that these animals gained a truly cosmopolitan distribution (Tetlie 2007, but see Lamsdell *et al.*

2013), with the radiation of hibbertopterid and adelophthalmid eurypterids following the extinction of every other major eurypterid group (Lamsdell & Braddy 2010).

Of the two eurypterid groups found in the Carboniferous, adelophthalmids are by far the commonest, with over 40 species currently recognized (Tetlie & Poschmann 2008), the majority of which are assigned to the genus *Adelophthalmus* Jordan in Jordan & von Meyer, 1854. *Adelophthalmus* reached its peak diversity in the late Carboniferous, although the earliest known species occurred in the early Devonian (Siegenian and Emsian in terms of Rhenish stratigraphy) of Germany (Poschmann 2006, 2012). Three other Devonian occurrences have been reported: a single specimen from the Frasnian of Australia (Tetlie *et al*. 2004), material from North America that is most likely Famennian in age (Hall & Clarke 1888), and a series of poorly preserved specimens from the Middle Devonian of Russia (Shpinev 2012) which exhibit a number of bizarre characteristics that warrant further investigation and may suggest that their assignment to *Adelophthalmus* is erroneous. There is a dearth of specimens from the early Carboniferous, with a single species described from the Tournaisian of Russia (Shpinev 2006). Any occurrence of the genus is important for reconstructing the biogeography of post-Devonian eurypterids. Here, we report the first eurypterid known from Italy, describe the new species as *Adelophthalmus piussii* sp. nov. from the Upper Carboniferous of the Carnic Alps, and discuss its position within the genus.

Geological Setting

The specimen comes from the debris of a large loose block found in the gravel bank of a small creek, a tributary of Bombaso creek, near to Malga Tratte (Fig. 1). The site is located north of the village of Pontebba, on the main road (SP110) that leads to the mountain border post of Passo Pramollo–Naßfeld between Italy and Austria. It is preserved as a cast in a small slab of thin sandstone. In the block from where the slab originated is a thin level with several fragments of fossil plants, mostly fern-like foliage. A small piece of the slab was sent to Professor Paola Pittau, Dipartimento di Scienze Chimiche e Geologiche, Cagliari University, for palynological analysis, but it was not possible to obtain accurate dating because of the poor preservation of the microfossils; only long-ranging microspores were found. Based on lithological features, and according to the geological setting of the area, it is most likely that the specimen comes from the upper part of the Meledis Formation (upper Moskovian–lower Kasimovian) (Venturini pers. com.), the oldest among the five formations of the Pramollo Group (upper Moskovian-Gzhelian, Upper Carboniferous) (Venturini 1990, Venturini 2002). The whole group is characterized by alternation of transgressive–regressive cycles related to glacio-eustatic control and tectonic activity (Vai &Venturini 1997). The result is a thick sequence of conglomerates and arenites with high quartz content, from a fluvio-deltaic environment, intercalated with marine shallow-water carbonates and pelites. In the lower part of the Meledis Formation, the carbonate levels are intercalated with bioturbated siltstones with abundant ichnofossils and marine fossils, arranged in a transgressive sequence mostly driven by transtensive tectonics which produced several slumping episodes. Alternatively, the deposits of the upper part of the Meledis Formation reflect local transpressive tectonics which were responsible for a fluvio-deltaic environment, testified by channelized quartz-rich conglomerates and shoreface arenites. The specimen seems to be from this upper sequence.

Material and Methods

The single specimen (part only; Fig 2) is preserved as a three-dimensional representation of the dorsal surface in a fine sandstone. It was studied under a Leica MZ605 stereomicroscope, drawn using a camera lucida attachment on the microscope, and photographed dry, in low-angle light, with a Canon 5D MkII digital camera and 50 mm macro lens. Note that, unconventionally, the lighting in Fig. 2 is directed from the SW in order to illuminate the specimen which would otherwise be in the shadow of higher rock matrix. The final drawing and photographs were prepared for publication using the Adobe CS6 software suite. All measurements are in mm; the > symbol indicates an incomplete article and hence a minimum measurement.

Systematic Palaeontology

Subphylum **Chelicerata** Heymons, 1901

Order **Eurypterida** Burmeister, 1843

Suborder **Eurypterina** Burmeister, 1843

Infraorder **Diploperculata** Lamsdell, Hoşgör & Selden, 2013

Superfamily **Adelophthalmoidea** Tollerton, 1989

Family Adelophthalmidae Tollerton, 1989

Genus *Adelophthalmus* Jordan in Jordan & von Meyer, 1854

Adelophthalmus piussii sp. nov.

Fig 2

Material. Holotype and only known specimen, number MFSNgp 31681, Museo Friulano di Storia Naturale, Udine.

Horizon and locality. Upper Moskovian–lower Kasimovian (Upper Carboniferous); from near Malga Tratte, Bombaso valley, Pontebba, Udine.

Etymology. The species is named in honour of the collector, Stefano Piussi of Udine.

Diagnosis. *Adelophthalmus* with median furrow on carapace; carapace lacking expanded posterolateral corners; lateral margins of first opisthosomal tergite angled anteriorly; first opisthosomal tergite maintains constant width at lateral margins.

Description. Body length >37.89. Carapace parabolic (*sensu* Tollerton 1989), 16.98 long, >18.53 wide, bordered by narrow marginal rim. Lateral eyes reniform, 2.88 long, 1.69 wide, located centrimesially 7.96 from carapace posterior border on outer margin of vaulted central portion of carapace. Ocellar mound located between lateral eyes at rear of median furrow 5.82 from carapace posterior border. Four partial prosomal appendages (IV–VI) preserved on left side, but no details discernible. Anterior seven opisthosomal tergites preserved; first reduced, with lateral margins converging slightly forwards. Opisthosomal tergite lengths/widths: 1 = 0.92/>17.36; 2 = 2.06/>19.66; 3 = 3.21/>20.08; 4 = 4.29/>21.24; 5 = 4.61/21.52; 6 = 3.47/>15.76; 7 = >2.35/>8.74. Slight epimera on all opisthosomal tergites. Cuticular ornamentation of lunate scales (preserved as impressions).

Remarks. The specimen is considered to belong to a new, undescribed species on account of its possession of a carapace median furrow combined with its lack of expanded posterolateral corners of the carapace.

Discussion

The genus *Adelophthalmus* is speciose, widespread, long-ranging, taxonomically old (being named in 1854), and the nominate form of a higher taxon (in this case the family Adelophthalmidae); it therefore meets every criterion for the identification of wastebasket taxa as set out by Plotnick & Wagner (2006). The phylogeny of the genus is poorly known; Tetlie & Poschmann (2008) performed an analysis of the Adelophthalmoidea and retrieved *Adelophthalmus* as monophyletic; however, there was a general lack of resolution within the genus, and 18 of the 25 then-known species were excluded from the study. It seems unlikely that the genus is polyphyletic or paraphyletic, though it may suffer simultaneously from under-splitting at the generic level and, paradoxically, over-splitting at the species level. The species now assigned to *Adelophthalmus* have previously been divided into five genera: *Adelophthalmus, Lepidoderma* Reuss, 1855, *Anthraconectes* Meek & Worthen, 1868, *Polyzosterites* Goldenberg, 1873, and *Glyptoscorpius* Peach, 1882. These taxa have all subsequently been synonymized into *Adelophthalmus*, which has priority, for reasons that appear valid for the type species in question (see Tetlie & Dunlop 2005 for a full review). It is possible, however, that *Adelophthalmus* may consist of two or more large clades that could be considered to be distinct genera; it is also uncertain how the Carboniferous genus *Unionopterus* Chernyshev, 1948 resolves in relation to the various *Adelophthalmus* species (Tetlie & Van Roy 2006).

A number of species of *Adelophthalmus* have also been suggested to be synonyms, with Van Oyen (1956) suggesting that as many as 11 species may be junior synonyms of *Adelophthalmus imhofi* (Reuss, 1855). Many of these species are in need of restudy, however, and Van Oyen's proposed synonymies have not been widely accepted, with three of the supposedly synonymous species resolving disparately in the phylogeny of Tetlie & Poschmann (2008). A number of characteristics used to define species are also suspect; the type species, *Adelophthalmus granosus* Jordan in Jordan & von Meyer, 1854, was originally described as lacking lateral eyes, something that is almost certainly a preservational artifact (Tetlie & Dunlop 2005), while *Adelophthalmus luceroensis* Kues & Kietzke, 1981, was described as possessing no median ocelli however they can be clearly seen on two figures (Kues & Kietzke 1981 pl. 1, figs. 5 & 8). Ultimately only a redescription of museum specimens will resolve these issues, however until this is done the true number of true *Adelophthalmus* species currently known will remain uncertain.

The current specimen can clearly be distinguished as a novel species by the autapomorphy of a median carapace furrow and the unique character combination of the carapace lacking expanded posterolateral corners along with the lateral margins of first opisthosomal tergite being angled anteriorly and maintaining a constant width at its lateral margins. The morphology of the first opisthosomal segment also reveals close affinities to some other species of *Adelophthalmus*, with *Adelophthalmus wilsoni* (Woodward, 1888) possessing a first tergite with almost identical morphology (see Owens & Bassett 1976, pl. 29, fig. 5). *Adelophthalmus luceroensis* and *Adelophthalmus dumonti* (Stainier, 1917) also exhibit an anterior curvature of the lateral regions of the first tergite; however, *Adelophthalmus dumonti* also has extended posterolateral regions of the carapace that dorsally overlap the tergite. This configuration is also seen in *Adelophthalmus* *moyseyi* (Woodward, 1907) and *Adelophthalmus granosus* which, together with *Adelophthalmus dumonti,* resolved as a clade in the analysis of Tetlie & Poschmann (2008). *Adelophthalmus piussii* sp. nov. exhibits slight posterolateral extension of the carapace margin but not to the degree seen in *Adelophthalmus dumonti*, with the lateral portions of the first tergite not being completely covered. *Adelophthalmus piussii* thus appears to be an intermediate form between taxa with an anteriorly deflected first tergite such as *Adelophthalmus luceroensis* and the *Adelophthalmus dumonti* clade. It is also possible to polarize these characters, as the earliest known species, *Adelophthalmus sievertsi* (Størmer, 1969), lacks both posterolateral extensions of the carapace and any lateral differentiation of the first tergite. The trend in *Adelophthalmus* thus appears to be one of increasing anterior deflection of the lateral regions of the first opisthosomal tergite followed by an expansion of the posterolateral regions of the carapace eventually resulting in the total dorsal overlap of the lateral regions of the first tergite. *Adelophthalmus piussii*, with its first tergite exhibiting marked lateral deflection, appears to show the onset of posterolateral carapace extension.

Acknowledgments

We thank Stefano Piussi, the collector of the specimen, for kindly presenting it to the Museo Friulano di Storia Naturale for study, Professor Paola Pittau (Dipartimento di Scienze Chimiche e Geologiche, Cagliari University) for palynological investigations, and Professor Corrado Venturini (Dipartimento di Scienze Biologiche, Geologiche e Ambientali, Bologna University) for helpful information on the stratigraphical position of the sample. Jason Dunlop (Museum für Naturkunde) and Markus Poschmann (Generaldirektion Kulturelles Erbe Rheinland-Pfalz) provided valuable comments during the review process that

References

Burmeister H. (1843) - Die Organisation der Trilobiten, aus ihren lebenden Verwandten entwickelt; nebst einer systematischen Uebersicht aller zeither beschriebenen Arten. G. Reimer, Berlin.

Chernyshev B.I. (1948) - New representative of Merostomata from the Lower Carboniferous. *Kievski Gos. Universitet Im T. G. Shevchenko Geoloisheskii Sbornik*, 2: 119-130.

Goldenberg F. (1873) - Fauna Saraepontana Fossilis. Die fossilen Thiere aus der Steinkohlenformation von Saarbrücken. Erstes Heft. 26 pp., Chr. Möllinger Verlag, Saarbrücken.

Gupta N.S., Tetlie O.E., Briggs D.E.G. & Pancost R.D. (2007) - The fossilization of eurypterids: a result of molecular transformation. *Palaios*, 22: 439-447.

Hall J. & Clarke J.M. (1888) - Trilobites and other Crustacea of the Oriskany, Upper Helderberg, Hamilton, Portage, Chemung and Catskill groups. *New York Geological Survey, Paleontology*, 7: 1-236.

Heymons R. (1901) - Die Entwicklungsgeschichte der Scolopender. *Zoologica,* 13: 1-244, Stuttgart.

Jordan H. & von Meyer H. (1854) - Ueber die Crustaceen der Steinkohlenformation von Saarbrücken. *Palaeontographica,* 4: 1-15.

Kues B.S. & Kietzke K.K. (1981) - A large assemblage of a new eurypterid from the Red Tanks Member, Madera Formation (Late Pennsylvanian-Early Permian) of New Mexico: *J. Paleont.*, 55: 709-729.

Lamsdell J.C. & Braddy S.J. (2010) - Cope's rule and Romer's theory: patterns of diversity and gigantism in eurypterids and Palaeozoic vertebrates. *Biol. Lett.*, 6: 265-269.

Lamsdell J.C., Hoşgör İ. & Selden P.A. (2013) - A new Ordovician eurypterid (Arthropoda: Chelicerata) from southeast Turkey: Evidence for a cryptic Ordovician record of Eurypterida. *Gondwana Res.,* 23: 354-366.

Meek F.B. & Worthen A.H. (1868) - Paleontology of Illinois. *Illinois Geological Survey Report*, 3: 544.

Meyer H. von (1853) - Mitteilung an Prof. Bronn. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde*, 1853: 161-165.

Owens R.M. & Bassett M.G. (1976) - A Westphalian eurypterid from South Wales. *Palaeontology*, 19: 185-190.

Peach B.N. (1882) - Further researches among Crustacea and Arachnida. *T. Roy. Soc. Edinb.*, 30: 511-529.

Plotnick R.E. & Wagner P.J. (2006) - Round up the usual suspects: common genera in the fossil record and the nature of wastebasket taxa. *Paleobiology,* 32: 126-146.

Poschmann M. (2006) - The eurypterid *Adelophthalmus sievertsi* (Chelicerata: Eurypterida) from the Lower Devonian (Emsian) Klerf Formation of Willwerath, Germany. *Palaeontology*, 49: 67-82.

Poschmann M. (2012) - Ein neues Vorkommen der „Hachenburger Pflanze“ sowie von Seeskorpionen (Eurypterida) im Unterdevon (Siegenium) des Lahrbachtales (Westerwald, Rheinland-Pfalz, SW-Deutschland). *Mainzer naturwiss. Archiv*, 49: 5-12.

Reuss A.E. (1855) - Palaeontologische Miscellen. III. Über eine neue Krusterspecies aus der Böhmischen Steinkohlenformation. *Denkschriften der königlich-kaiserlichen Akademie der Wissenschaften in Wien*, 10: 81-83.

Shpinev E.S. (2006) - A new species of *Adelophthalmus* (Eurypterida) from the Lower Carboniferous of the Krasnoyarsk Region. *Paleontol. Zh.*, 40: 78-80.

Shpinev E.S. (2012) - New species of the genus *Adelophthalmus* (Eurypterida, Chelicerata) found in the Middle Devonian of Khakassia. *Paleontol. Zh.*, 46: 27–31.

Stainier X. (1917) - On a new eurypterid from the Belgian Coal Measures. *Q. J. Geol. Soc.,* 71: 639-647.

Størmer L. (1969) - Eurypterids from the Lower Devonian of Willwerath, Eifel. *Senck. Leth.*, 50: 21-35.

Tetlie O.E. (2007) - Distribution and dispersal history of Eurypterida (Chelicerata). *Palaeogeogr. Palaeocl. Palaeoecol.*, 252: 557-574.

Tetlie O.E. & Dunlop J.A. (2005) - A redescription of the Late Carboniferous eurypterids *Adelopthalmus granosus* von Meyer, 1853 and *A. zadrai* Přibyl, 1952. *Mitt. Mus. Nat.kd. Geowiss. Reihe*, 8: 3-12.

Tetlie O.E. & Poschmann M. (2008) - Phylogeny and palaeoecology of the Adelophthalmoidea (Arthropoda; Chelicerata; Eurypterida). *J. Syst. Palaeontol.*, 6: 237-249.

Tetlie O.E. & Van Roy P. (2006) - A reappraisal of *Eurypterus dumonti* Stainier, 1917 and its position within the Adelophthalmidae Tollerton, 1989. *Bull. Inst. r. Sci. Nat. Belg.*, 76: 79-90.

Tetlie O.E., Braddy S.J., Butler P.D. & Briggs D.E.G. (2004) - A new eurypterid (Chelicerata: Eurypterida) from the Upper Devonian Gogo Formation of Western Australia, with a review of the Rhenopteridae. *Palaeontology*, 47: 801-809.

Tollerton V.P. (1989) - Morphology, taxonomy, and classification of the order Eurypterida Burmeister, 1843. *J. Paleont.*, 63: 642-657.

Vai G.B. & Venturini C. (1997) - Moskovian and Artinskian rocks in the frame of the cyclic Permo-Carboniferous of the Carnic Alps and related areas. *Geodiversitas,* 19: 173-186.

Van Oyen F.H. (1956) - Contribution a la connaissance du genre *Adelophthalmus* Jordan et Meyer 1854. *Mededelingen van de Geologische Stichting, series C*-IV-3, 7: 4-98.

Venturini C. (1990) - Geologia delle Alpi Carniche centro orientali. *Museo Friulano di Storia Naturale*, 36: 1-222.

Venturini C. (2002) - La sequenza Permo-Carbonifera. In: Vai Gb., Venturini C., Carulli G.B. & Zanferrari, A. (Eds) - Alpi e Prealpi Carniche e Giulie (Friuli Venezia Giulia). *Guide Geol. Reg. SGI,* 9: 31-37.

Woodward H. (1888) - Note on *Eurypterus* from the Carboniferous. *Geol. Mag.*, Decade III, 5: 419-421.

Woodward H. (1907) - Two new species of *Eurypterus* from the Coal-Measures of Ilkeston, Derbyshire. *Geol. Mag.*, Decade V, 4: 277-282.

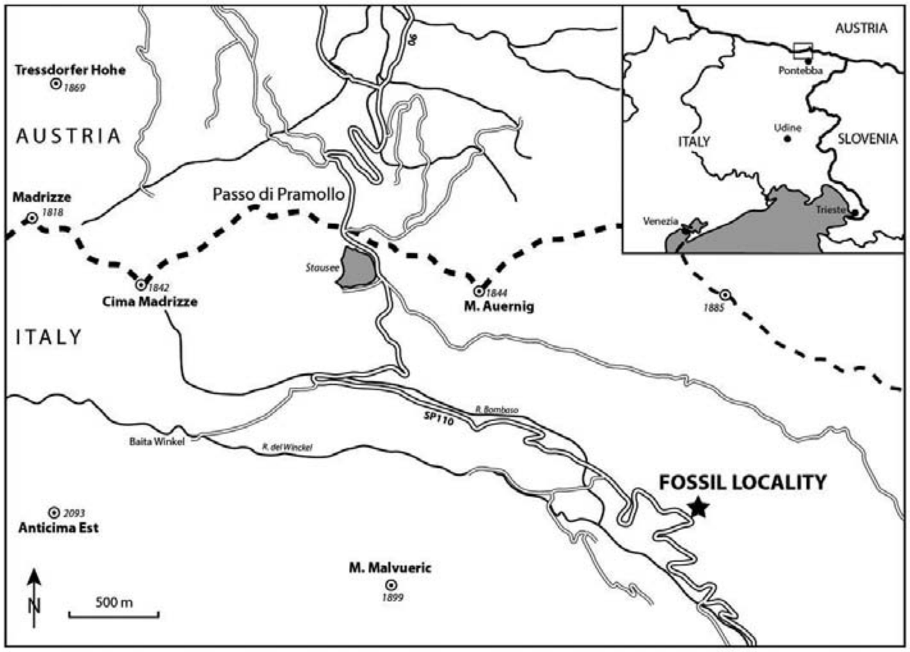

Figure 1. Position of the fossil locality (star) near the road SP110 from Pontebba to Passo Pramollo, which is situated on the Italy–Austria border; spot heights in metres. Inset: location map of the Passo Pramollo area near Pontebba in the north of Friuli.

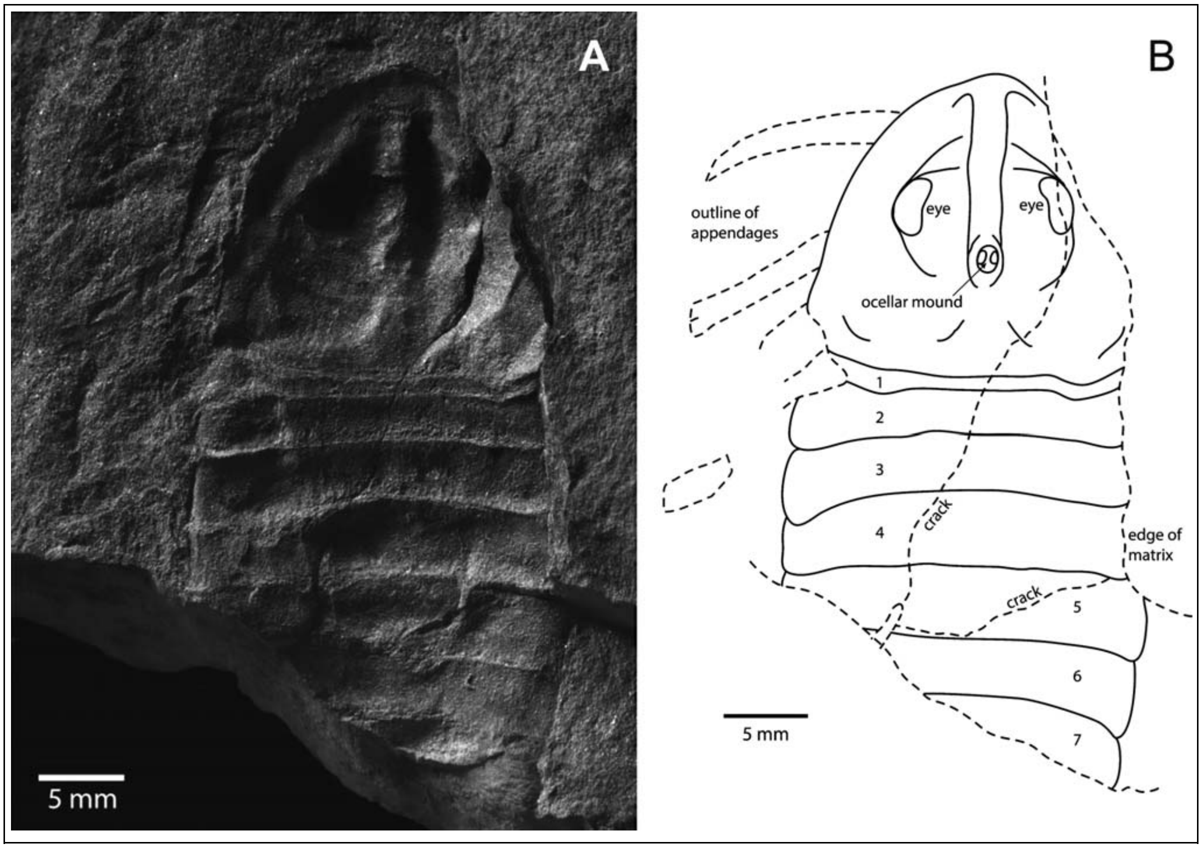

Figure 2. *Adelophthalmus piussii* sp. nov. from the Upper Carboniferous (upper Moskovian–lower Kasimovian) Meledis Formation, Friuli, specimen MFSNgp 31681. A) photographed under low-angle light (illumination from the SW). B) Interpretive drawing for A. Scale bar: 5 mm.

Chapter 5

A new Ordovician eurypterid (Arthropoda: Chelicerata) from southeast Turkey: evidence for a cryptic Ordovician record of Eurypterida

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(Formatted for submission to *Gondwana Research*)

Abstract

A new species of eurypterid, *Paraeurypterus anatoliensis* gen. et sp. nov., is described from the Upper Ordovician (Katian) Şort Tepe Formation of southeast Turkey. The single specimen, preserving the carapace, mesosoma and fragments of appendages, appears morphologically intermediate between the eurypteroid families Dolichopteridae and Eurypteridae. *P. anatoliensis* retains the plesiomorphic conditions of crescentic eyes with enlarged palpebral lobes and a quadrate carapace with ornamentation consisting of small pustules but also displaying the derived characteristics of genal facets and a row of large acicular scales across the posterior of each tergite. Phylogenetic analysis incorporating each of the major eurypterine clades and all Eurypterina having a three-segmented genital operculum (the triploperculate condition) resolves eurypteroids to be an unnatural group, with Dolichopteridae and Eurypteridae forming part of a grade leading to diploperculate Eurypterina. *P. anatoliensis* is intermediate between the two eurypteroid families, as is '*Eurypterus*' *minor* from the Pentland Hills of Scotland, which is shown to be a distinct genus and assigned to *Pentlandopterus* gen. nov. Using the phylogenetic topology to infer ghost ranges for each of the major eurypterid clades reveals that the majority of eurypterid superfamilies must have originated by the Katian, indicating a largely unsampled record of Ordovician eurypterids. The occurrence of poor dispersers such as *Paraeurypterus* in the Ordovician of Gondwana is puzzling, and it has been suggested that they dispersed to the continent during periods of sea level lowstand in the Sandbian and Hirnantian, however this does not explain the lack of Ordovician species in North America and Europe, given the well-sampled nature of these continents, and an alternative is proposed whereby eurypterids originated in Gondwana and radiated out to Laurentia and Baltica in the late Ordovician and early Silurian, thus explaining their sudden appearance in the European and North American rock record.

Key words: Katian, Eurypterina, *Paraeurypterus*, ghost ranges, phylogeny

1. Introduction

Eurypterids are a monophyletic group of Palaeozoic aquatic chelicerates with a distribution largely limited to the palaeocontinents of Avalonia, Armorica, Baltica, Iberia and Laurentia. Of the 246 currently valid eurypterid species only 22 have been reported from outside these palaeocontinents; however, of these, only 13 can be confidently assigned to a eurypterid clade (Table 1). While it has been suggested that the lack of eurypterids other than from Europe and North America is a collecting and research bias (Plotnick, 1999), and a number of further unnamed or fragmentary eurypterids have been reported from outside of these continents (Braddy *et al*., 1995, 2002; Braddy and

Almond, 1999; Tetlie *et al*., 2004), it is the currently held view that the observed distributions represent a true signal, with eurypterids originating in Laurentia and being limited to dispersal along coastlines, with only the pterygotoids being able to cross open oceans (Tetlie 2007a). Any new record of eurypterids from outside North America and Europe is, therefore, of extreme interest, especially if they can be assigned to a group lacking the dispersal capabilities of the pterygotoids, and have a pre-Carboniferous age.

The majority of eurypterid occurrences outside North America and Europe consist of presumably poor dispersers (hibbertopteroids) which occurred during the Carboniferous and Permian, after Gondwana has come into close proximity to Laurentia as a prelude to the amalgamation of Pangaea, or taxa with higher dispersal potential such as pterygotoids or carcinosomatids. *Adelophthalmus* Jordan in Jordan and von Meyer, 1854, another widespread genus, is also known from Gondwanan localities from the Devonian onwards and it is likely that it was able to cross the already narrowing gulf between Gondwana and Laurentia. One occurrence, however, appears to defy explanation: *Onychopterella augusti* Braddy, Aldridge and Theron, 1995, from the Soom Shale of South Africa, which has been dated as latest Hirnantian to earliest Rhuddanian (Vandenbroucke *et al*., 2009). *O. augusti* does not appear to be a good disperser, as its posterior pair of appendages are not overly expanded into a swimming paddle, and its relatively basal phylogenetic position combined with its early occurrence (before the major period of eurypterid radiation during the early Silurian) makes its appearance in Gondwana somewhat problematic.

Here, we report a second Gondwanan Ordovician eurypterid, *Paraeurypterus anatoliensis* gen. et sp. nov., a single specimen from the Şort Tepe Formation (middle

Katian) near Çukurca, southeast Turkey. The new species is placed in a phylogenetic context as intermediate between the families Dolichopteridae and Eurypteridae and forms part of a basal grade of Eurypterina leading to a clade defined by having only two fused plates in the genital operculum. The phylogeny allows for ghost ranges to be estimated for each of the main eurypterid clades which indicate the existence of a diverse record of Ordovician eurypterids and the potential for discovery of further early Palaeozoic eurypterids in Gondwana.

2. Geological Setting

The Border Folds of southeast Turkey represent the northern part of the Arabian Plate dominated by the East Anatolian Fault where it contacts the Anatolian Plate (Fig. 1A), and consists largely of Mesozoic and Cenozoic surface crops with subsurface Palaeozoic formations cropping out in places (e.g. at the Derik, Mardin, Şort Tepe, and Zap areas) that represent an almost complete Cambrian–Ordovician succession (Fig. 1B). The eurypterid specimen was discovered during a geological survey of the most southeastern regions of Anatolia, near the border with Iraq. Here, the early Palaeozoic strata encompass the Derik and the Habur groups which extend from the Amanos-Pazarcık area in the west to Hakkari-Çukurca in the east (Cater and Tunbridge, 1992; Bozdoğan and Ertuğ, 1997) and palaeogeographically belong to the northern margin of the Arabian Plate of Gondwana throughout the Palaeozoic.

Lower Palaeozoic strata were first recognised in southeastern Turkey about 30 km southwest of Hakkari by Altınlı (1963) who reported unnamed, thick, Cambrian limestones overlain by approximately 1000 m of the Giri Formation, comprising Silurian (actually Cambrian and Ordovician) quartzites with subsidiary limestones and siltstones. Some of the latter contained *Cruziana* trace fossils and have been compared to analogous strata in northern Iraq (Dean and Monod, 1990; Dean, 2006). Between Hakkari and Çukurca the River Zap cuts a deep valley to expose two inliers of Cambrian and Ordovician sediments, mostly clastics, that form part of the Arabian Platform (Ghienne *et al*., 2010). Dean *et al*. (1981) recognised that the Giri Formation was equivalent to the shales and sandstones of the Seydişehir Formation, described from the western Taurus Mountains but widespread in the eastern Taurus, southeastern Turkey, and neighbouring parts of Iraq, and of Upper Cambrian and Lower Ordovician age. The strata disconformably overlying the formation, mainly comprising shales and siltstones, were named the Şort Tepe Formation and considered to be of Ashgillian age (Upper Ordovocian, late Katian–Hirnantian). In the Zap Valley, the thick Seydişehir Formation is unconformably overlain by a Lower and Upper Palaeozoic succession that comprises the Upper Ordovician Şort Tepe Formation, the Upper Devonian Yıgınlı Formation and the Lower Carboniferous Köprülü Formation (Fig.2A) (Higgs *et al*., 2002). It is in the Şort Tepe beds of this succession, on the northeast side of the Zap Valley 7.5 km northwest of Çukurca (Fig. 2B), that the eurypterid specimen was discovered. The depositional environment of the Şort Tepe Formation is considered to be that of an outer shelf environment representing the culmination of a period of marine transgression throughout the Seydişehir Formation which it unconformably overlies (Ghienne *et al*., 2010).

In the Hakkari–Çukurca area the Şort Tepe Formation is known for its well-preserved trilobite faunas, with Dean and Zhou (1988) reporting the genera *Lonchodomas* Angelin, 1854, *Dindymene* Hawle and Corda, 1847, *Prionocheilus* Rouault, 1847, *Calymenesun*

Kobayashi, 1951 and *Birmanites* Sheng, 1934, along with fragments of diplograptid graptolites and the brachiopod *Aegiromena* Havlíček, 1961, all located in the grey shale beds within the formation, the same lithology from which the eurypterid was discovered. These macrofossils were used, through comparison with similar faunas elsewhere, to infer a pre-Hirnantian Ashgill age for the formation. Palynological investigations on Ordovician deposits from Turkey are fairly rare and deal principally with the less mature organic-walled microfossils recorded in the Border Folds area where rich and well preserved Upper Ordovician acritarchs, sporomorphs, and chitinozoans have been reported from the Habur Group (Steemans *et al*., 1996). More recently, Paris *et al*., (2007a and 2007b) have determined chitinozoan assemblages in the upper parts of the Şort Tepe Formation dated to the late Caradoc (middle Katian), thus making the new eurypterid older than *Orcanopterus manitoulinensis* Stott, Tetlie, Braddy, Nowlan, Glasser and Devereux, 2005 and *Megalograptus ohioensis* Caster and Kjellesvig-Waering in Størmer, 1955 (both from the late Katian of Laurentia) and *Onychopterella augusti* (from the Hirnantian of Gondwana), but younger than the stylonurine *Brachyopterus stubblefieldi* Størmer, 1951 (from the Sandbian of Avalonia).

3. Materials and Methods

The specimen was recovered from the Upper Ordovician Şort Tepe Formation of southeast Turkey and is deposited in the Natural History Museum of Maden Tetkik ve Arama Genel Müdürlüğü, Ankara (MTANHMSETR). Material of *Eurypterus minor* (Laurie, 1899), studied for comparison, is held at the National Museums of Scotland (NMS), Edinburgh, UK. Eurypterid terminology largely follows Tollerton (1989) for morphology of the carapace, metastoma, lateral eyes, prosomal appendages, genital appendage, opisthosomal differentiation, telson, and patterns of ornamentation; however, the terminology for the ventral plate morphologies follows the revised types of Tetlie *et al.* (2008). Selden (1981) is followed for prosomal structures and cuticular sculpture and the labelling of the appendages. Terminology for the segmentation of the genital operculum follows Waterston (1979). The specimen was studied using a Leica M205 C stereomicroscope and photographs were taken on a Canon EOS 5D Mk II digital camera with a Canon macro MP-E 65 mm 1:2.8 lens with a polarizing filter and a polarized light source with the specimen submerged in alcohol. Image processing was carried out using Adobe Photoshop CS4, and interpretive drawings were prepared for publication using Adobe Illustrator CS4, on a MacBook Pro running OS X.

The specimen consists of parts of the prosoma and mesosoma preserved in a pale grey siltstone with red-brown coloured cuticle preserved in places (Fig. 3), such as on the carapace dorsal surface anterior to the left lateral eye, where it shows a concentric, pustular ornament. Part of the posterior part of the carapace is broken away, revealing the prosoma–opisthosoma junction and the usually hidden, poorly sclerotized, true first tergite. Anteriorly on the right side, the carapace is broken away to reveal the ventral plate (doublure). The median suture of the doublure is not visible, but there is clearly no epistomal plate or transverse suture. Lateral eyes are preserved, but median ocelli seen as pale, circular impressions, and the right one is mostly obscured by a crack. Anterior to the right lateral eye, and posterior to the left lateral eye, are what appear to be worm burrows or grazing traces.

To the right of the carapace, the remains of four appendages can be seen. The most anterior (appendage III) consists of a single podomere that is angled underneath the following appendage and thus lost from view. Appendage IV consists of a single visible podomere and a spine from the preceding podomere that is hidden under the carapace. No details are available of appendage V apart from its existence: it appears from beneath the carapace but is then covered by the overlying, forward-thrust appendage VI.

In the mesosoma, seven fully expressed tergites and the first, usually hidden, true tergite are preserved which, though poorly preserved, can be seen on both lateral margins. On the right side of the specimen, the opercular plates can be seen projecting from beneath the tergites. The exact number of large, acicular scales on each tergite is difficult to ascertain due to damage around the posterior margins; however, it is clear that each tergite bore three sets of large scales for a total of six to nine scales on each segment.

For the phylogenetic analysis, a matrix of 81 characters and 45 taxa was compiled, which can be found in Appendix 2 along with character descriptions. The synziphosurine *Weinbergina opitzi* Richter and Richter, 1929 was specified as the outgroup following Lamsdell *et al*. (2010a,b) as it supposedly represents the most plesiomorphic known xiphosuran (Anderson and Selden, 1997) which are sister group to Eurypterida (Selden and Dunlop, 1998); however, given the unclear nature of synziphosurine intra-relationships (see Lamsdell, 2011) the chasmataspidids *Chasmataspis laurencii* Caster and Brooks, 1956, *Loganamaraspis dunlopi* Tetlie and Braddy, 2004, *Diploaspis casteri* Størmer, 1972 and *Octoberaspis ushakovi* Dunlop, 2002 are included due to the shared synapomorphies of a metastoma and genital appendage. These, however, were left as ingroup taxa to test whether chasmataspidids fall outside Eurypterida or are a clade within Eurypterina, as suggested by Shultz (2007). In order to test the placement of the Turkish specimen among the basal Eurypterina, all the taxa from the analysis of Tetlie and Cuggy (2007) were included, along with taxa from the analysis of Lamsdell (2011). In order to test the ramifications of the ghost ranges for each of the major Eurypterina clades, representatives from each of the more derived groups were also included, each represented by multiple exemplars which more accurately represent the character states and transitions of the group than a single exemplar, such as a single species or a composite taxon (see Brusatte, 2010). *Mixopterus kiaeri* Størmer, 1934a and *Carcinosoma newlini* (Claypole, 1890a) were included to represent the mixopteroids, *Adelophthalmus sievertsi* (Størmer, 1969) and *Nanahughmilleria norvegica* (Kiær, 1911) for the adelophthalmoids, and *Hughmilleria socialis* Sarle, 1903 and *Pterygotus anglicus* Agassiz, 1844 for the pterygotoids. Two other problematic Ordovician taxa were also included: *Megalograptus ohioensis* and *Orcanopterus manitoulinensis*. *O. manitoulinensis* was considered by Tetlie (2007a) and Tetlie and Poschmann (2008) to be part of an unnamed clade consisting of *Orcanopterus* Stott, Tetlie, Braddy, Nowlan, Glasser and Devereux, 2005, *Waeringopterus* Leutze, 1961 and *Grossopterus* Størmer, 1934b which forms the sister-group to adelophthalmoids and pterygotoids, while *M. ohioensis* has traditionally been considered a member of the Mixopteroidea (Caster and Kjellesvig-Waering, 1964), although Tetlie (2007a) considered it to be a basal taxon positioned between *Onychopterella* Størmer, 1951 and Eurypteroidea.

The analysis was performed using TNT (Goloboff *et al*., 2008; made available with the sponsorship of the Willi Hennig Society) employing random addition sequences followed by branch swapping (the *mult* command in TNT) with 100,000 repetitions with all characters unordered and of equal weight. Jackknife (Farris *et al*., 1996) and Bremer support (Bremer, 1994) values were calculated in TNT and the Consistency, Retention and Rescaled Consistency Indices were calculated in Mesquite 2.73 (Maddison and Maddison, 2010). Nonparametric bootstrapping is often difficult with morphological data due to the limited size of the dataset (Zander, 2003) and so was not performed for this analysis. Jackknifing was performed using simple addition sequence and tree bisection-reconnection (TBR) branch swapping, with 100,000 repetitions and 25% character deletion. The matrix and character listing can be found in the Appendix 2 has been deposited in the online MorphoBank database (O'Leary and Kaufman, 2007) under the project code p568 and can be accessed from http://morphobank.org/permalink/?P568.

4. Systematic Palaeontology

Phylum Arthropoda Latreille, 1829

Subphylum Chelicerata Heymons, 1901

Superclass Sclerophorata Kamenz, Staude and Dunlop, 2011

Order Eurypterida Burmeister, 1843

Diagnosis

Chelicerates with the opercula of somites VIII and IX fused into a genital opercular plate.

Remarks

After the identification of a metastoma and genital appendage in two species of chasmataspidid (Dunlop, 2002; Tetlie and Braddy, 2004), Lamsdell (2011) determined the sole eurypterid autapomorphy to be the possession of the fused opercula of somites

VIII and IX forming the genital operculum. The fact that the median and posterior opercular plates were functionally fused had also been recognised by Laurie (1893), Holm (1898) and Wills (1965) but appears to have been missed by subsequent authors.

Suborder Eurypterina Burmeister, 1843

Grade 'Eurypteroidea'

Remarks

Tetlie and Cuggy (2007) retrieved Eurypteroidea as a natural group; however, the analysis herein resolves the group as paraphyletic with a monophyletic Dolichopteridae sister-group to Eurypteridae and the remaining Eurypterina (Mixopteroidea, Adelophthalmoidea and Pterygotoidea). This result was somewhat foreshadowed by Tetlie and Cuggy (2007), who remarked that the Eurypteridae were, in most respects, more derived morphologically than the Dolichopteridae and appears to confirm the results from a less inclusive analysis performed by Lamsdell (2011). Paraphyly invalidates Eurypteroidea as a superfamily; however, the term is currently retained as an identification for the grade of basal Eurypterina that it encompassed. In due course, this may be expanded to also encompass both the Moselopteridae and Onychopterellidae; but these are, for the moment, retained in their own superfamilies.

Genus *Paraeurypterus* gen. nov.

Type species

Paraeurypterus anatoliensis gen. et sp. nov.

Etymology

From the greek παρά (similar) and *Eurypterus* due to its close similarities to the genus *Eurypterus* DeKay, 1825.

Diagnosis

'Eurypteroid' with quadrate carapace possessing genal facets; small, crescentic lateral eyes with large palpebral lobe; carapace ornamentation consists of small pustules, opisthosomal ornamentation consists of scales with a series of large acicular scales across the posterior region of the tergites.

Paraeurypterus anatoliensis gen. et sp. nov. (Figs. 3–4)

Holotype

MTANHMSETR 10-İZ-01-1.

Etymology

Named after the Anatolian Peninsula where the specimen was found.

Locality and Age

The only known specimen is derived from the Upper Ordovician (middle Katian) Şort Tepe Formation, southeast Turkey.

Diagnosis

As for genus.

Description

Preserved body length 84 mm; maximum width (at third tergite) 46 mm. Carapace maximum width 45 mm (at posterior), 32 mm long. Carapace anterior margin relatively straight, very slightly procurved medially; length:width ratio 0.70; genal angle 85°, therefore carapace subquadrate (Tollerton, 1989); posterior margin recurved, angling anteriorly for 2 mm. No epistomal plate or transverse suture (therefore *Eurypterus*- or *Erieopterus*-type); plates ornamented with series of striate terrace lines (Fig. 4A), as seen in *Eurypterus tetragonophthalmus* Fischer, 1839 (Selden, 1981), *Stoermeropterus* *conicus* (Laurie, 1892) (Lamsdell, 2011), *Parahughmilleria hefteri* Størmer, 1973 and *Erieopterus* sp. (Poschmann and Tetlie, 2006). Lateral eyes centrilateral at most anterolateral limit of quadrant (Tollerton, 1989); crescentic, associated with small palpebral lobe giving appearance of circular outline (Fig. 4B; the defunct ovocrescentic of Tollerton, 1989); 6 mm long, 3 mm wide (5 mm including palpebral lobe). Median ocelli central between posteriormost limit of lateral eyes; 1 mm × 1 mm diameter. Carapace marginal rim narrow, extends across entire width of anterior and lateral margins, narrowing very slightly towards posterior, 1.5 mm at widest.

Only small part of one podomere of appendage III preserved. Single preserved podomere of appendage IV 5.5 mm long, 3 mm wide, unornamented; spine from preceding podomere 3.48 mm long, 1.22 mm wide at base, ornamented with series of longitudinal striations; appendage of *Hughmilleria*-type. Only small part of one podomere of appendage V preserved. Visible portions of appendage VI consists of long, slightly curved podomere ornamented with slight scale projections or distally angled serrations on dorsal and ventral (probably podomere 4); longitudinal, parallel grooves run down length of podomere; 15 mm long, 7.5 mm wide; podomere 5 is 7 mm long, flaring distally from 6 mm to 7 mm wide.

True first tergite 1 mm long. Opercular plates project from beneath tergites. First fully expressed tergite (from hereon just 'first tergite') shorter than following tergites; broadest point of body at third tergite (Table 2). Dorsal ornamentation consisting of continuous row of semilunate scales 1–1.5 mm from each tergite anterior border (Fig. 4C). Scale ridges indicate degree of overlap with preceding tergite; portion of tergite before ridge forms smooth articulating facet. Posterior to scale ridge are three discontinuous rows of semilunate scales before ornamentation becomes sparse, still consisting of isolated semilunate scales. Row of acicular scales interspersed with much larger acicular scales across posterior region of each tergite. Large scales, absent from first tergite, increase in size from second to seventh tergite. Each tergite with three sets of large scales (total 6–9 scales), number of scales possibly increasing with size of tergite.

Remarks

In general appearance, *Paraeurypterus anatoliensis* looks very much like a species of *Eurypterus*, drawing initial comparison with *Eurypterus tetragonophthalmus*. A number of features, however, show it to be distinct from that genus: the quadratic carapace, which is trapezoidal in all *Eurypterus* species, the crescentic lateral eyes with an enlarged palpebral lobe (a plesiomorphic state which is lost in the Eurypteridae and the remaining derived Eurypterina), and the carapace ornamentation consisting of small pustules. Pustules are known from the carapace of a number of *Eurypterus* species, including *E. dekayi* Hall, 1859 and *E. tetragonophthalmus*; however, in all of these, the pustules are limited to the margins of the carapace and anterior to the lateral eyes, and not covering the carapace, as appears to be the case in *P. anatoliensis*. The scale ornamentation of the opisthosoma in *P. anatoliensis* also appears different to that of *Eurypterus*, possessing more large acicular scales than in any known *Eurypterus* species, although the number of scales can vary between them. While the species resembles *Eurypterus*, it possesses a number of plesiomorphic characteristics that have already been lost in *Erieopterus* Kjellesvig-Waering, 1958, the sister-taxon of *Eurypterus*, and this is considered justification for its erection as a new genus, a conclusion born out by the phylogenetic analysis presented herein.

Pentlandopterus gen. nov.

Type species

Eurypterus minor (Laurie, 1899)

Etymology

Named after the Pentland Hills, Scotland, from which the only known species is described.

Diagnosis

'Eurypteroid' with a quadrate carapace possessing genal facets; cuticular ornamentation consisting of closely spaced pustules; lateral eyes crescentic with large palpebral lobe.

Pentlandopterus minor (Laurie, 1899)

1899 *Eurypterus minor* Laurie, pp. 587–588, plate V figs 27–29.

1899 *Eurypterus minor* Peach and Horne, pp. 594.

1912 *Eurypterus minor* Clarke and Ruedemann, pp. 132.

1916 *Eurypterus minor* O'Connell, pp. 40.

1955 *Eurypterus minor* Lamont, pp. 200.

1958 *Eurypterus minor* Kjellesvig-Waering, pp. 1123–1124.

1999 *Eurypterus minor* Plotnick, pp. 120.

2006 *Eurypterus minor* Tetlie, pp. 403–405, fig. 4.

2007a '*Eurypterus*' *minor* Tetlie, pp. 560.

Holotype

NMS G.1897.32.120

Additional material

NMS G.1897.32.166 (paratype), G.1897.32.129, G.1897.32.152, G.1897.32.867.

Remarks

The species was given a modern redescription by Tetlie (2006), who considered it to be a *Eurypterus*. Tetlie and Cuggy (2007), however, showed it to be phylogenetically distinct from *Eurypterus* but did not change the taxonomy due to uncertainty as to the exact position of the species. Our analysis confirms that *Pentlandopterus minor* is not a *Eurypterus* and it is here assigned to its own genus. While it shares many characteristics with *Paraeurypterus anatoliensis*, the difference in opisthosomal ornamentation clearly places *P. anatoliensis* phylogenetically closer to the Eurypteridae and the two species are therefore assigned to different genera.

Tetlie (2006) listed NMS G.1897.32.110 as a second paratype, but this specimen number is actually associated with a specimen of *Drepanopterus pentlandicus* Laurie, 1892. The accession number of the *Pentlandopterus* second paratype is at present unknown.

Infraorder Diploperculata nov.

Included groups

Mixopteroidea, Adelophthalmoidea, Pterygotoidea and the ‘waeringopterid’ clade.

Etymology

From the greek *διπλόω* (double) and *operculum*.

Diagnosis

Eurypterina with a genital operculum consisting of two fused segments.

Remarks

Diploperculata represents the clade of ‘derived Eurypterina’ as denoted by Tetlie and Cuggy (2007); those eurypterine groups to which ‘Eurypteroidea’ is sister-taxon, incorporating Mixopteroidea, the unnamed ‘waeringopterid’ clade, Adelophthalmoidea and Pterygotoidea. Two characters potentially define the clade: the first, having a fused genital operculum composed of two segment (the diploperculate condition), gives the clade its name and is used to define the limits of the infraorder. The form of the genital operculum is thought to be an important character, as the possession of a fused genital operculum may be the only eurypterid synapomorphy (Lamsdell, 2011), with the Stylonurina and the basal Eurypterina (Moselopteridae, Onychopterellidae, Dolichopteridae, and Eurypteridae) sharing the plesiomorphic triploperculate (three segmented) condition (Tetlie and Braddy, 2004; Lamsdell, 2011). The other potential characteristic of the clade is having a podomere VI-4 of equal length to podomere VI-3 and VI-5, however *Megalograptus* (which is clearly diploperculate) has a VI-4 longer than VI-3 and VI-5 while the dolichopterid *Strobilopterus* Ruedemann, 1934 also has all three podomeres of equal length and so the character is not included in the diagnosis of the clade.

5. Comparison with other eurypterids

Paraeurypterus is clearly differentiated from the supposedly more primitive suborder Stylonurina, based on the lack of a transverse suture on the prosomal ventral plates and having prosomal appendage VI expanded into a swimming paddle. Although the distal podomeres of the paddle (including those that undergo the characteristic broadening) are not preserved, the fourth, fifth and sixth podomeres are. In eurypterids with a pediform prosomal appendage, the fifth podomere is longer than the fourth, whereas those with a paddle have a fourth podomere that is longer or equal in length to the fifth. *Paraeurypterus* has a VI-4 that is longer than VI-5, and therefore has a swimming paddle. Furthermore, the fact that VI-4 is longer than VI-5 precludes it from comparison with the mixopteroid, adelophthalmoid and pterygotoid clades, which all have a VI-4 equal in length to VI-5. *Paraeurypterus* is therefore most comparable to *Megalograptus* Miller, 1874, Eurypteridae and Dolichopteridae (which with the exception of *Strobilopterus* all have VI-4 longer than VI-5).

Paraeurypterus, along with *Pentlandopterus*, shares several characteristics with dolichopterids, including a dorsal carapace ornamentation consisting of granular pustules, and crescentic lateral eyes associated with enlarged palpebral lobes; however, these are plesiomorphic conditions, also observed in onychopterellids, moselopterids and Stylonurina. Both *Paraeurypterus* and *Pentlandopterus* lack the synapomorphies of either dolichopterid clade, namely a short appendage VI that barely projects from beneath the carapace or an articulating angle between VI-3 and VI-4 of less than 180°. Both genera are separated from *Eurypterus*, however, in lacking a scale ornament on the carapace and having a quadratic rather than trapezoid carapace. *Eurypterus* has also lost the plesiomorphic lateral eye condition, instead having an expanded visual surface with reduced palpebral lobe. One character that separates *Paraeurypterus* from *Pentlandopterus,* but suggests a closer affinity to *Eurypterus* and *Megalograptus,* is its possession of a row of large acicular scales across the posterior margin of each tergite. It is predominantly similarities in opisthosomal ornamentation, along with the morphology of appendage V, that have led to comparison between *Eurypterus* and *Megalograptus* and so encountering a similar morphology in a new taxon may help indicate whether the similarities between the two are synapomorphies, due to convergence or a result of retained plesiomorphic conditions.

Several species of *Eurypterus* (*E. tetragonophthalmus*, *E. dekayi*, *E. ornatus* Leutze, 1958 and *E. hankeni* Tetlie, 2006) have a pustular carapace ornament; however, in all four species the pustules are smaller than in *Paraeurypterus* and *Pentlandopterus*, and in *E. tetragonophthalmus* the pustules are only found around the carapace margin. Most species of *Eurypterus* also have a row of principal scales across the posterior of the carapace which is absent in *Pentlandopterus*, *Paraeurypterus* and *Megalograptus*; however, these are absent in *E. dekayi*, *E. ornatus* and *E. laculatus* Kjellesvig-Waering, 1958. The opisthosomal ornament of *Paraeurypterus* is very similar to that of *E. tetragonophthalmus* (Wills, 1965 pl. 2 fig. 4) with a row of tightly packed semi-lunate scales across the anterior margin, delineating the articulating facet, followed by three discontinuous rows of loosely spaced scales, and a posterior row of larger acicular scales. This type of ornamentation is also seen in *Megalograptus*; however, *Megalograptus* and *Eurypterus* differ from *Paraeurypterus* in having each acicular scale preceded by a longitudinal row of smaller scales. It seems clear that the similarities in ornamentation between the three taxa are not due to convergence, and the age of *Paraeurypterus* and *Megalograptus*, combined with the fact that *Megalograptus* shares several synapomorphies with mixopteroids that are absent from *Eurypterus*, indicates that the rows of acicular scales likely represent a plesiomorphic characteristic for the more derived Eurypterina. This is supported by some other eurypterine species, such as the adelophthalmoid *Adelophthalmus sievertsi*, also having similar rows of scales across the posterior margins of the tergites.

6. Phylogenetic analysis of basal Eurypterina

Analysing the matrix as detailed above yielded two most parsimonious trees with a tree length of 229, an ensemble Consistency Index of 0.498, Retention Index of 0.782, and Rescaled Consistency Index of 0.389, the strict consensus of which is presented here (Fig. 5). The two most parsimonious trees differ solely in the internal topology of the mixopteroid clade, with one tree having *Carcinosoma* Claypole, 1890b as sister taxon to *Megalograptus* and *Mixopterus* Ruedemann, 1921a and the other with *Megalograptus* sister to *Mixopterus* and *Carcinosoma.* The polytomy of *Eurypterus* species is present in both trees.

Eurypterids are resolved as a monophyletic clade with Chasmataspidida forming their monophyletic sister-group. Chasmataspidid monophyly is, in itself, a noteworthy result as they have previously been suggested not to represent a natural group (Tetlie and Braddy, 2004). However, in order to test this fully, all the chasmataspidid species should ideally be included in the analysis with synziphosurines and xiphosurids as in-group taxa to test whether *Chasmataspis* Caster and Brooks, 1956 has closer affinities to xiphosurans. Eurypterida is split into two broad clades: Stylonurina and Eurypterina. Although only a few Stylonurina were included in the analysis, their monophyly was also retrieved in more comprehensive studies of their relationships by Lamsdell *et al*. (2010a, b). This is the first time that representatives of every major eurypterine clade have been included in a published analysis, and it is interesting to compare the topology with the composite tree presented by Tetlie (2007a). Tetlie's composite tree was compiled using the internal topologies of clades retrieved by Tetlie and Cuggy (2007), Tetlie and Poschmann (2008), and Braddy *et al*. (2008), with the relationships between the major clades inferred based on Tetlie's unpublished PhD thesis. The topology retrieved in this analysis broadly correlates with that presented by Tetlie (2007a), with Mixopteroidea as sister-group to a large clade consisting of Pterygotoidea, Adelophthalmoidea and the waeringtopterid clade, within which waeringopterids are sister-group to Adelophthalmoidea and Pterygotoidea. The analysis differs, however, in the treatment of the basal Eurypterina, including the eurypteroids.

The data for the phylogeny of the basal Eurypterina in Tetlie's (2007a) tree predominantly comes from the analysis of Tetlie and Cuggy (2007) which united Dolichopteridae and Eurypteridae as a monophyletic clade, sister-group to the newly named Diploperculata, with *Moselopterus* Størmer, 1974 and *Onychopterella* forming a paraphyletic stem-lineage. The genus *Onychopterella* was resolved as paraphyletic and '*Eurypterus*' *minor* was shown to be phylogenetically separate from *Eurypterus sensu stricto*. *Megalograptus* was excluded from the analysis, however, and in the strict consensus of the eight most parsimonious trees, the dolichopterid clade broke down into a number of smaller clades that formed a polytomy with Eurypteridae. Lamsdell *et al*. (2010a) later added *Vinetopterus* Poschmann and Tetlie, 2004 and '*Drepanopterus*' *bembycoides* Laurie, 1899 to the matrix, resulting in them forming a clade with *Moselopterus* to which they assigned the name Moselopteridae.

Tetlie's (2007a) tree differs in placing *Megalograptus* above *Onychopterella* in the eurypterine stem-lineage and '*Eurypterus*' *minor* well within the dolichopterid clade. The position of *Megalograptus* is based on a single character, the lack of a modified distal margin of the sixth podomere of the swimming leg, but has never been recovered in a phylogenetic analysis. Lamsdell (2011) conducted a more restricted analysis of the basal Eurypterina and retrieved a topology that differed in three ways: *Onychopterella* monophyletic; *Megalograptus* forming a clade with *Mixopterus* rather than the more basal taxa; and eurypteroids paraphyletic, with Eurypteridae phylogenetically closer to Diploperculata than Dolichopteridae. The current analysis supports these results, even with a more inclusive sampling of the dolichopterid and eurypterid clades. Dolichopteridae is shown to be monophyletic and composed of two clades: one comprising *Buffalopterus* Kjellesvig-Waering and Heubusch, 1962, *Strobilopterus* and *Syntomopterella* Tetlie, 2007b, the other *Dolichopterus* Hall, 1859, *Ruedemannipterus* Kjellesvig-Waering, 1966 and *Clarkeipterus* Kjellesvig-Waering, 1966. *Clarkeipterus* has been suggested to be a dolichopterid before (Tetlie *et al*., 2007b) however this is the first time the genus has been given phylogenetic treatment. '*Eurypterus*' *minor* is again distinct from *Eurypterus sensu stricto* but neither is it a dolichopterid, instead resolving as a transitional form between the two clades and elevated to the new genus *Pentlandopterus*. *Paraeurypterus anatoliensis* is also a transitional form, appearing morphologically closer to Eurypteridae but still separated from the clade due to its possession of crescentic lateral eyes with enlarged palpebral lobes and the lack of scales on the carapace. Neither of these two species are assigned to any taxon higher than the level of genus; instead, they are considered members of a grade incorporating the basal members of the Eurypterina of which the Dolichopteridae and Eurypteridae represent radiations of offshoots from the main lineage.

7. Implications for the Ordovician record of eurypterids

Since Tollerton (2004) recognized that the majority of Ordovician eurypterids from New York State (accounting for approximately 75% of Ordovician eurypterid diversity at the time) were either pseudofossils or, in one case, a phyllocarid carapace, Ordovician eurypterids have been considered rare, with the majority of family-level clades originating in the early Silurian. The recent discovery of as yet undescribed eurypterids from the late Ordovician Manitoba biotas (Young *et al*., 2007) and the Middle Ordovician St Peter Formation in Iowa (Liu *et al*., 2006) suggests, however, that Ordovician eurypterids are not as rare as has been assumed, and the discovery of *Paraeurypterus* serves to strengthen this possibility. Furthermore, by combining the deeper-level relationships of eurypterine clades retrieved here with those of Stylonurina recovered by Lamsdell *et al*. (2010a, b), it is possible to estimate ghost ranges of the superfamily-level clades, each of which represent a major species diversification within Eurypterida. Ghost ranges are simply the inferred ranges of clades in time based on sister-group comparison where the sister taxa do not have the same observed temporal point of origination (see Wills, 1999 fig. 1) given a cladogenetic mode of speciation. Furthermore, if the range of the sister taxon to the initial pair temporally predates this ghost range, then a ghost range for their ancestor is inferred. Ghost range inference can drastically affect estimations of speciation rates (Pachut and Anstey, 2007), lineage survival across mass extinctions (Davis *et al*., 2010), and the nature of lineage diversification (Davis *et al*., 2011) and so can have a major impact on our understanding of the evolution of a group and responses to global climatic and tectonic changes. One key condition for inferring ghost ranges is that the sister taxa compared are both monophyletic, something of particular concern at taxonomic levels higher than species. Monophyly of the eurypterid superfamilies is generally well supported; exceptions are the eurypteroids, dealt with herein, and uncertainty over the position of *Megalograptus*. For the purposes of ghost range inference, *Megalograptus* has been considered to be a mixopteroid, probably in a basal position; however, one of the strongest characters uniting *Megalograptus* with the mixopteroids, the enlarged spines on appendage III, show some differences in structure that may suggest that they are convergent. Further study of *Megalograptus* is needed; however, even if it is eventually shown to be distinct from Mixopteroidea and has closer affinities to Eurypteridae this will have little effect on the ghost ranges inferred under the present topology.

After inferring the relationships of the major eurypterid clades, and comparing their temporal ranges (Fig. 6), it is apparent that the majority have extensive ghost ranges. The majority of these stem from the triploperculate Eurypterina such as moselopterids and dolichopterids. The ages of *Paraeurypterus*, *Megalograptus* and *Orcanopterus* suggest that major cladogenesis of eurypterine groups occurred before the Silurian period, during the Katian at the latest. The longest ghost ranges, however, are jointly those of Dolichopteridae and the inferred stylonurine ancestor of the stylonuroid/kokomopteroid/hibbertopteroid clade, each extending for approximately 25 million years, while the ghost range for Eurypteroidea extends some 22 million years. If, indeed, chasmataspidids are monophyletic and sister group to Eurypterida, then the entire order has a ghost range of 7 million years given the estimated age of *Chasmataspis* (Dunlop *et al*. 2004). However, if the Cambrian resting trace is indeed assignable to a *Chasmataspis*-like creature, as suggested by Dunlop *et al*. (2004), then this ghost range would be extended by a further 33 million years. Alternatively, the trace maker could represent a form ancestral to both chasmataspidids and eurypterids; potential support for this stems from the possible identification of a metastoma-like plate on one of the traces, the apparent lack of a genital appendage, and most clearly the possession of six unfused opercula. Where opercula have been identified in chasmataspidids they have only been recognized on the three buckler segments (Tetlie and Braddy, 2004; Dunlop, 2002), while having six unfused opercula is the plesiomorphic condition found in xiphosurids. Another potential ghost range extension would be required if some of the eurypterids from the St Peter Formation are related to *Orcanopterus*, as suggested by Liu *et al*. (2006), resulting in a further inferred gap of 20 million years for all of the triploperculate Eurypterina. Even without this further extension, it is clear that the majority of eurypterid clades must have existed prior to the late Ordovician extinction pulses during the Hirnantian (Brenchley *et al*., 2001) and were, therefore, either largely unaffected by the mass extinction events or were able to rapidly diversify in their aftermath.

Despite the recognition that eurypterids were able to persist through the end-Ordovician mass extinction, with few long-term detrimental effects, it is still unclear where the clade originated geographically, and to what degree their range included Gondwana prior to its collision with Laurussia during the late Devonian and Carboniferous. Tetlie (2007a) considered eurypterids to have originated in Laurentia, with Gondwanan occurrences being the result of isolated transoceanic dispersal, something generally limited to pterygotoids and some mixopteroids. Lamsdell (2011) proposed a method by which the population of *Onychopterella augusti* – which was not likely to have been a strong swimmer – could have become established in what is now

South Africa by traversing the sea floor during periods of sea level lowstand during the Sandbian or Hirnantian (Saltzman and Young, 2005). *Paraeurypterus*, phylogenetically bracketed by dolichopterids and Eurypteridae, was also unlikely to have been a good swimmer and may have crossed to Gondwana during the Sandbian lowstand. It is also possible that the opposite occurred: periods of lowstand allowed Gondwanan eurypterids to cross into Laurentia and then undergo an explosive radiation. Currently, the earliest known eurypterid is a stylonurine from the Sandbian of Avalonia, which was at the time located southwards of Laurentia, and this may, in fact, represent an early stylonurine colonist from Gondwana. This would explain the dearth of Ordovician eurypterids in the well-sampled regions of Europe and North America, and would also go some way to explaining why so many of the earliest encountered species are relatively advanced swimming forms – these would have had a greater dispersal ability than the basal walking forms and so could conceivably appear first in the Laurentian and Baltic fossil record if the group did indeed have its origin in Gondwana. In this scenario, it should still be no surprise that eurypterids are rare in Gondwanan provinces; being a single large continent Gondwana had comparatively less of the shallow marine environments that eurypterids tend to favour, meaning that populations would likely have been smaller and had a more restricted range. Colonizing the shallow seas and island coastlines of Laurentia and Baltica would have lead to a period of explosive radiation, resulting in the relatively sudden appearance of multiple clades in the European and North American fossil record. The fact that the only eurypterids known from the Silurian and Devonian of Gondwana are able swimmers suggests the possibility that the Late Ordovician mass extinction did, indeed, impact the eurypterids, causing them to go extinct on Gondwana while the

Laurentian species were relatively unaffected, with subsequent Gondwanan records representing re-colonization by good dispersers.

The concept that there is an unsampled, early record of chelicerates in Gondwana has been mooted previously by Anderson (1996) who suggested that the sudden appearance of weinberginid synziphosurines during the early Devonian, which retain an extreme number of plesiomorphic morphological features, was due to their radiation from a Gondwanan refuge. The discovery of synziphosurines and xiphosurids (which together probably are not a monophylum – see Lamsdell, 2011) from the Tremadocian and Floian Lower and Upper Fezouata Formations of Morocco (Van Roy *et al*. 2010) shows that these groups certainly had a Gondwanan presence early in their evolution and their dispersal may have followed a pattern similar to that proposed here for eurypterids. Eurypterids and xiphosurans often co-occur throughout the Palaeozoic and eurypterids were probably also present in the Fezouata Formations (Van Roy, pers. comm.); if this is the case it would further strengthen the possibility that the group had a Gondwanan origin.

8. Conclusions

Paraeurypterus anatoliensis gen. et sp. nov., described from a single specimen, is the tenth eurypterid species known from Ordovician strata and is only the second of that age from Gondwana. Morphologically it appears intermediate between the eurypteroid families Dolichopteridae and Eurypteridae, possessing the plesiomorphic conditions of crescentic eyes with enlarged palpebral lobes and a quadrate carapace with ornamentation consisting of small pustules but also displaying the derived characteristics of genal facets and a row of large acicular scales across the posterior of each tergite. These two last characters are therefore plesiomorphic for both *Eurypterus* and *Megalograptus*, an important recognition as they have previously been used to suggest a sister-group relationship between the two taxa. The eurypterine nature of *Paraeurypterus* is further supported by prosomal appendage VI having a fourth podomere that is longer than the fifth and appears to expand distally into a swimming paddle, while a megalograptid affinity can be ruled out because appendage IV is unspecialized, with only a single pair of spines on each podomere. The new species most closely resembles *Pentlandopterus minor*, differing only in size and the possession of the acicular opisthosomal scales.

Phylogenetic analysis incorporating representatives of each of the major eurypterine clades and all triploperculate Eurypterina retrieves a topology similar to that of Tetlie (2007a), with a few differences: *Onychopterella* is retrieved as a monophyletic genus and *Megalograptus* is considered to be part of the mixopteroid clade rather than resolving among the more basal Eurypterina while eurypteroids are shown not to be a natural group but that Dolichopteridae and Eurypteridae are part of a grade leading to diploperculate Eurypterina with *Pentlandopterus* and *Paraeurypterus* being intermediate taxa between the two families. Combining this revised topology of eurypterine relationships with that of Stylonurina retrieved by Lamsdell *et al*. (2010a,b) permits calculation of ghost ranges for each of the major clades of Eurypterida and reveals that the majority of eurypterid superfamilies must have originated by the Katian. The occurrence of *Onychopterella* and *Paraeurypterus* in the Ordovician of Gondwana is puzzling as neither genus was likely to have had a spectacular dispersal ability, however it is possible that they colonized the continent during periods of sea level lowstand in the Sandbian and Hirnantian. One problem with this interpretation is the implication of a large undocumented record of Ordovician eurypterids in the well-sampled regions of North America and Europe. An alternative scenario is proposed whereby eurypterids originated in Gondwana and radiated out to Laurentia and Baltica in the late Ordovician and early Silurian, explaining their sudden appearance in the European and North American rock record and shifting the Ordovician record to the historically understudied Gondwanan continents. It is likely that further study of Gondwanan Ordovician Fossil-Lagerstätten such as the Fezouata formations will reveal more eurypterid species.

Acknowledgments

We thank Sam Ciurca (New York), Peter Van Roy (Ghent University) and Erik Tetlie (Norway) for discussion on the specimen and its possible affinities, Alicia Rosales (University of Kansas) for looking at the potential burrows, and Curtis Congreve (University of Kansas) for general discussion. Wes Gapp (University of Kansas) assisted with the search for some of the more obscure trilobite literature. Úna Farrell (University of Kansas) provided invaluable assistance with interpretation of Turkish antique laws and attempts to accession the specimen. Peter Van Roy provided valuable suggestions and comments during review that greatly improved the manuscript.

References

Agassiz, J.L.R., 1844. Monographie des poissons fossiles du Vieux Grès Rouge, ou Système Devonien (Old Red Sandstone) des Iles Britanniques et de Russie. Neufchatel, folio, 171 pp.

Altınlı, L.E., 1963. Explanatory text of the 1:500 000 geological map of Turkey, cizre sheet. Maden Tetkik ve Arama Enstitüsü (MTA) Publication, Ankara.

Anderson, L.I., 1996. Taphonomy and taxonomy of the Palaeozoic Xiphosura. PhD thesis, University of Manchester.

Anderson, L.I., Selden, P.A., 1997. Opisthosomal fusion and phylogeny of Palaeozoic Xiphosura. Lethaia 30, 19–31.

Angelin, N.P., 1854. Palaeontologica Scandinavica. Pars 1. Crustacea formationis transitionis. Fasc. II– Holmiae. Norstedt & Söner, Stockholm, 92 pp., 41 pls.

Bozdoğan, N., Ertuğ, K., 1997. Geological evolution and paleogeography of the southeast Anatolia in the Paleozoic. In: Göncüoglu, M.C., Derman, A.S. (Eds.), Paleozoic evolution in NW Gondwana. Turkish Association of Petroleum Geologists (Special Publication 3), Ankara, 39–49.

Braddy, S.J., Almond, J., 1999. Eurypterid trackways from the Table Mountain Group (Lower Ordovician) of South Africa. Journal of African Earth Sciences 29, 165–177.

Braddy, S.J., Aldridge, R.J., Theron, J.N., 1995. A new eurypterid from the Late Ordovician Table Mountain Group, South Africa. Palaeontology 38, 563–581.

Braddy, S.J., Selden, P.A., Doan Nhat, T., 2002. A new carcinosomatid eurypterid from the Upper Silurian of Northern Vietnam. Palaeontology 45, 897–915.

Braddy, S.J., Poschmann, M., Tetlie, O.E., 2008. Giant claw reveals the largest ever arthropod. Biology Letters 4, 106–109.

Bremer, K., 1994. Branch support and tree stability. Cladistics 10, 295–304.

Brenchley, P.J., Marshall, J.D., Underwood, C.J., 2001. Do all mass extinctions represent and ecological crisis? Evidence from the Late Ordovician. Geological Journal 36, 329–340.

Brusatte, S.L., 2010. Representing supraspecific taxa in higher-level phylogenetic analyses: guidelines for palaeontologists. Palaeontology 53, 1–9.

Burmeister, H., 1843. Die Organisation der Trilobiten, aus ihren lebenden Verwandten entwickelt; nebst systematische Uebersicht aller Seitherbeschriebenen Arten. G. Reimer, Berlin, 148 pp.

Burrow, C.J., Braddy, S.J., Douglas, J.G., 2002. Pterygotid eurypterid chelicera from the Lower Devonian of Victoria. Alcheringa 25, 263–268.

Chang, A.C., 1957. On the discovery of the Wenlockian *Eurypterus*-fauna from south China. Acta Paleontologica Sinica 5, 446–450.

Chernyshev, B.I., 1933. Arthropoda s Urala I drugikh S.S.S.R. Sbornik Tsentral’nogo Nauchno – Issledovatel’skogo Geolograzvedochogo Instituta, Paleontologiya i Stratigrafiya 1, 15–24.

Caster, K.E., Brooks, H.K., 1956. New fossils from the Canadian-Chazan (Ordovician) hiatus in Tennessee. Bulletin of American Paleontology 36, 157–199.

Caster, K.E., Kjellesvig-Waering, E.N., 1953. *Melbournopterus*, a new Silurian eurypterid from Australia. Journal of Paleontology 27, 153–156.

Caster, K.E., Kjellesvig-Waering, E.N., 1964. Upper Ordovician eurypterids from Ohio. Palaeontographica Americana 4, 300–358.

Cater, J.M., Tunbridge, I.P., 1992. Paleozoic tectonic history of the SE Turkey. Journal of Petroleum Geology 15, 35–50.

Chernyshev, B.F., 1948. New representative of merostomata from the Lower Carboniferous. Kievski Gos., Universitet Insititutim T. G. Shevchenko, Geologicheskii Sbornik 2, 119–130.

Clarke, J.M., 1907. The *Eurypterus* shales of the Shawangunk Mountains in eastern New York. New York State Museum Bulletin 107, 295–310.

Clarke, J.M., Ruedemann, R., 1912. The Eurypterida of New York. New York State Museum Memoirs 14, 1–439, 88 pls.

Claypole, E.W., 1890a. Palaeontological notes from Indianapolis (A. A. A. S.) *Pterichthys – Castoroides – Eurysoma* g. n. American Geologist 6, 255–260.

Claypole, E.W., 1890b. *Carcinosoma newlini.* American Geologist 6, 400.

Davis, R.B., Baldauf, S.L., Mayhew, P.J., 2010. Many hexapod groups originated earlier and withstood extinction events better than previously realized: inferences from supertrees. Proceedings of the Royal Society B 277, 1597–1606.

Davis, R.B., Nicholson, D.B., Saunders, E.L.R., Mayhew, P.J., 2011. Fossil gaps inferred from phylogenies alter the apparent nature of diversification in dragonflies and their relatives. BMC Evolutionary Biology 11, 252, 10 pp.

Dean, W.T., 2006. Cambrian stratigraphy and trilobites of the Samur Dağ area, south of Hakkâri, southeastern Turkey. Turkish Journal of Earth Sciences 15, 225–257.

Dean, W.T., Monod, O., 1990. Revised stratigraphy and relationships of Lower Palaeozoic rocks, eastern Taurus Mountains, south central Turkey. Geological Magazine 127, 333–347.

Dean, W.T., Zhou, Z., 1988. Upper Ordovician trilobites from the Zap Valley, south-east Turkey. Palaeontology 31, 621–649.

Dean, W.T., Monod, O., Perınçek, D., 1981. Correlation of Cambrian and Ordovician rocks in southeastern Turkey. Petroleum activities at the 100th year (100 Yılda Petrol Faaliyeti). Türkiye Cumhuriyet Petrol İşleri Genel Müdürlüğü Dergisi 25, 269–291 [English], 292–300 [Turkish].

De Kay, J.E., 1825. Observations on a fossil crustaceous animal of the order Branchiopoda. Annals of the New York Lyceum of Natural History 1, 375–377.

Delle, N., 1937. Zemgales lidzenuma, Augszemes un Lietuvas devona nogulumi. Acta Universitatis Latviensis, Matematikas un Dabas Zinatnu Fakultates Serija 2, 105–384.

Dunlop, J.A., 2002. Arthropods from the Lower Devonian Severnaya Zemlya Formation of October Revolution Island (Russia). Geodiversitas 24, 349–379.

Dunlop, J.A., Anderson, L.I., Braddy, S.J., 2004. A redescription of *Chasmataspis laurencii* Caster & Brooks, 1956 (Chelicerata: Chasmataspidida) from the Middle Ordovician of Tennessee, USA, with remarks on chasmataspid phylogeny. Transactions of the Royal Society of Edinburgh, Earth Sciences 94, 207–225.

Farris, J.S., Albert, V.A., Källersjö, M., Lipscomb, D., Kluge, A.G., 1996. Parsimony jackknifing outperforms neighbor-joining. Cladistics 12, 99–124.

Fischer de Waldheim, G., 1839. Notes sur un crustacé fossile du genre *Eurypterus* de Podolie. Bulletin de la Société Imperiale des Naturalistes de Moscou 11, 125–128.

Ghienne, G.-F., Monod, O., Kozlu, H., Dean, W.T., 2010. Cambrian-Ordovician depositional sequences in the Middle East: a perspective from Turkey. Earth Science Reviews 101, 101–146.

Goloboff, P.A., Farris, J.S., Nixon, K.C., 2008. TNT, a free program for phylogenetic analysis. Cladistics 24, 774–786.

Grabau, A.W., 1920. A new species of *Eurypterus* from the Permian of China. Bulletin of the Geological Survey of China 2, 61–67.

Hall, J., 1859. Natural History of New York: Palaeontology, III. New York State Museum, 532 pp.

Hall, J., 1884. Note on the Eurypteridæ of the Devonian and Carboniferous Formations of Pennsylvania. Geological Survey of Pennsylvania, Report of Progress 2, 23–39.

Havlíček, V., 1961. Rhynchonelloidea des böhmischen älteren Paläozoikums (Brachiopoda). Rozpravy Ústředního ústavu geologického 27, 1–211.

Hawle, J., Corda, A.J.C., 1847. Prodrom einer Monographie der böhmischen Trilobiten. J. G. Calvé, Prague, 176 pp.

Heymons, R., 1901. Die Entwicklungsgeschichte der Scolopender. Zoologica (Stuttgart) 13, 1–244.

Higgs, K.T., Finucane, D., Tunbridge, I.P., 2002. Late Devonian and early Carboniferous microfloras from the Hakkari Province of southeastern Turkey. Review of Palaeobotany and Palynology 118, 141–156.

Holm, G., 1898. Über die Organisation des *Eurypterus fischeri* Eichw. Mémoires de L'Académie Impériale des Sciences de St.-Pétersbourg 8(2), 1–57.

Hünicken, M.A., 1980. A giant fossil spider (*Megarachne servinei*) from Bajo de Véliz, Upper Carboniferous, Argentina. Boletin de la Academia Nacional de Ciencias, Córdoba, Argentina 53, 317–341.

Jordan, H., von Meyer, H., 1854. Ueber die Crustaceen der Steinkohlenformation von Saarbrücken. Palaeontographica 4, 1–15.

Kamenz, C., Staude, A., Dunlop, J.A., 2011. Sperm carriers in Silurian sea scorpions. Naturwissenschaften 98, 889–896.

Kiær, J., 1911. A new Downtonian fauna in the sandstone series of the Kristiana area: a preliminary report. Skrifter utgitt av Det Norske Videnskaps-Akademi i Oslo I. Matematisk-Naturvidenskapelig Klasse 7, 1–22.

Kjellesvig-Waering, E.N., 1958. The genera, species and subspecies of the Family Eurypteridae, Burmeister, 1845. Journal of Paleontology 32, 1107–1148, 6 pls.

Kjellesvig-Waering, E.N., 1964a. A synopsis of the Family Pterygotidae Clarke & Ruedemann, 1912 (Eurypterida). Journal of Paleontology 38, 331–361, pls. 53–56.

Kjellesvig-Waering, E.N., 1964b. Eurypterida: Notes on the subgenus *Hughmilleria* (*Nanahughmilleria*) from the Silurian of New York. Journal of Paleontology 38, 410–412.

Kjellesvig-Waering, E.N., 1966. A revision of the families and genera of the Stylonuracea (Eurypterida). Fieldiana*,* Geology 14, 169–197.

Kjellesvig-Waering, E.N., 1973. A new Silurian *Slimonia* (Eurypterida) from Bolivia. Journal of Paleontology 47, 549–550.

Kjellesvig-Waering, E.N., 1979. Eurypterids. In: Jaanusson, V., Laufeld, S., Skoglund, R. (Eds.), Lower Wenlock Faunal and Floral Dynamics - Vattenfallet Section, Gotland. Sveriges Geologiska Undersökning, Uppsala.

Kjellesvig-Waering, E.N., Heubusch, C.A., 1962. Some Eurypterida from the Ordovician and Silurian of New York. Journal of Paleontology 36, 211–221, pls. 36–38.

Kobayashi, T., 1951. On the Ordovician trilobites in Central China. Journal of the Faculty of Science, Imperial University of Tokyo (II, Geology, Mineralogy, Geography, Seismology) 8, 1–87.

Kutorga, S., 1838. Beitrag zur Kenntnis der organischen Überreste des Kupfersandsteins. St. Petersburg.

Lamont, A., 1955. Scottish Silurian Chelicerata. Transactions of the Geological Society of Edinburgh 16, 200–216.

Lamsdell, J.C., 2011. The eurypterid *Stoermeropterus conicus* from the lower Silurian of the Pentland Hills, Scotland. Palaeontographical Society Monograph, 1–84, pls 1–15.

Lamsdell, J.C., Braddy, S.J., Tetlie, O.E., 2010a. The systematics and phylogeny of the Stylonurina (Arthropoda: Chelicerata: Eurypterida). Journal of Systematic Palaeontology 8, 49–61.

Lamsdell, J.C., Braddy, S.J., Loeffler, E.J., Dineley, D.L., 2010b. Early Devonian stylonurine eurypterids from Arctic Canada. Canadian Journal of Earth Sciences 47, 1405–1415.

Latreille, P.A., 1829. Les crustacées, arachnides et partie des insectes. In: Couvier, G. (Ed.), Le Règne Animal distribute d'après son organisation, pour servir de base a l'histoire naturelle des animaux et d'introduction a l'anatomie comparée. nouv 4, 339–584. Paris, Déterville & Cochard.

Laurie, M., 1892. On some eurypterid remains from the Upper Silurian rocks of the Pentland Hills. Transactions of the Royal Society of Edinburgh 37, 151–162.

Laurie, M., 1893. The anatomy and relations of the Eurypteridæ. Transactions of the Royal Society of Edinburgh 37, 509–528.

Laurie, M., 1899. On a Silurian scorpion and some additional eurypterid remains from the Pentland Hills. Transactions of the Royal Society of Edinburgh 39, 575–589.

Leutze, W.P., 1958. Eurypterids from the Silurian Tymochtee Dolomite of Ohio. Journal of Paleontology 32, 937–942.

Leutze, W.P., 1961. Arthropods from the Syracuse Formation, Silurian of New York. Journal of Paleontology 35, 49–64.

Liu, H.B., McKay, R.M., Young, J.N., Witzke, B.J., McVey, K.J., Liu, X., 2006. A new Lagerstätte from the Middle Ordovician St. Peter Formation in northeast Iowa, USA. Geology 34, 969–972.

Maddison, W.P., Maddison, D.R., 2010. Mesquite: A modular system for evolutionary analysis. Version 2.73. http://mesquiteproject.org

McCoy, F., 1899. Note on a new Australian *Pterygotus*. Geological Magazine 6, 193–194.

Miller, S.A., 1874. Notes and descriptions of Cincinnatian Group fossils. Cincinnati Quarterly Journal of Science 1, 343–351.

Novojilov, N.J., 1959. Mérostomes du Dévonian inférieur et moyen de Sibérie. Annales de la Société Géologique du Nord 78, 241–258.

O'Connell, M., 1916. The habitat of the Eurypterida. Bulletin of the Buffalo Society of Natural Sciences 11, 1–277.

O'Leary, M.A., Kaufman, S.G., 2007. MorphoBank 2.5: Web application for morphological phylogenetics and taxonomy. http://www.morphobank.org

Pachut, J.F., Anstey, R.L., 2007. Inferring evolutionary order and durations using both stratigraphy and cladistics in a fossil lineage (Bryozoa: *Peronopora*). PALAIOS 22, 476–488.

Paris, F., Le Hérissé, A., Monod, O., Kozlu, H., Ghienne, J.-F., Dean, W.T., Vecoli, M., Günay, Y., 2007a. Ordovician chitinozoans and acritarchs from southern and southeastern Turkey. Revue de Micropaléontologie 50, 81–107.

Paris, F., Boumendjel, K., Dabard, M.P.H., Ghienne, J.-F., Loi, A., Peng, T., Videt, B., Achab, A., 2007b. Chitinozoan-based calibration of Early-Mid Ordovician transgressive events on northern Gondwana. Acta Palaeontologica Sinica 46, 370–375.

Peach, B.N., Horne, J., 1899. The Silurian rocks of Britain, I. Scotland. Memoir of the Geological Survey of the United Kingdom. Hedderwick and Sons, 749 pp.

Pirozhnikov, L.P., 1957. Remains of Gigantostraca from the series of Matakara (Devonian of the North Minusinsk Depression). Vsesoyuznoe Paleontologichesko Obshchestvo Ezegodnik 16, 207–213.

Plotnick, R.E., 1999. Habitat of Llandoverian-Lochkovian eurypterids. In: Boucot, A.J., Lawson, J. (Eds.), Paleocommunities: A case study from the Silurian and Lower Devonian. Cambridge University Press, 106–131.

Poschmann, M., Tetlie, O.E., 2004. On the Emsian (Early Devonian) arthropods of the Rhenish Slate Mountains: 4. The eurypterids *Alkenopterus* and *Vinetopterus* n. gen. (Arthropoda: Chelicerata). Senckenbergiana lethaea 84, 175–196.

Poschmann, M., Tetlie, O.E., 2006. On the Emsian (Lower Devonian) arthropods of the Rhenish Slate Mountains: 5. Rare and poorly known eurypterids from Willwerath, Germany. Paläontologische Zeitschrift 80, 325–343.

Richter, R., Richter, E., 1929. *Weinbergina opitzi* n. g., n. sp., ein Schwertträger (Merost. Xiphos.) aus dem Devon (Rheinland). Senckenbergiana 11, 193–209.

Rouault, M., 1847. Extrait du Mémoire sur les Trilobites du Départment d'Ille-et-Vilaine. Bulletin de la Société géologique de France 4, 309–328.

Ruedemann, R. ,1921a. A recurrent Pittsford (Salina) fauna. New York State Museum Bulletin 219– 220, 205–222.

Ruedemann, R., 1921b. A new eurypterid from the Devonian of New York. New York State Museum Bullet*in* 227–228, 88–92.

Ruedemann, R., 1934. Eurypterids from the Lower Devonian of Beartooth Butte, Wyoming. Proceedings of the American Philosophical Society 73, 163–167.

Saltzman, M.R., Young, S.A., 2005. Long-lived glaciation in the Late Ordovician? Isotopic and sequence-stratigraphic evidence from western Laurentia. Geology 33, 109–112.

Sarle, C.J., 1903. A new eurypterid fauna from the base of the Salina in western New York. New York State Museum Bulletin 69, 1080–1108.

Savage, T.E., 1916. Alexandrian rocks of northeastern Illinois and eastern Wisconsin. Bulletin of the Geological Society of America 27, 305–324.

Selden, P.A., 1981. Functional morphology of the prosoma of *Baltoeurypterus tetragonophthalmus* (Fischer) (Chelicerata : Eurypterida). Transactions of the Royal Society of Edinburgh, Earth Sciences 72, 9–48.

Selden, P.A., Dunlop, J.A., 1998. Fossil taxa and relationships of chelicerates. In: Edgecombe, G.D. (Ed.), Arthropod fossils and phylogeny. Columbia University Press, New York, 303–331.

Sheng, S.F., 1934. Lower Ordovician trilobite fauna of Chekiang. Palæontologia Sinica 3, 1–19.

Shpinev, E.S., 2006. A new species of *Adelophthalmus* (Eurypterida) from the Lower Carboniferous of the Krasnoyarsk Region. Paleontological Journal 40, 431–433.

Shultz, J.W., 2007. A phylogenetic analysis of the arachnid orders based on morphological characters. Zoological Journal of the Linnean Society 150, 221–265.

Steemans, P., Le Hérissé, A., Bozdoğan, N., 1996. Ordovician and Silurian cryptospores and miospores from southeastern Turkey. Review of Palaeobotany and Palynology 91, 35–76.

Størmer, L., 1934a. Merostomata from the Downtonian Sandstone of Ringerike, Norway. *Skrifter utgitt av Det Norske Videnskaps-Akademi i Oslo I. Matematisk-Naturvidenskapelig Klasse* 10, 1–125.

Størmer, L., 1934b. Uber den neuen von W. Gross beschriebenen Eurypteriden aus dem Unterdevon von Overath im Rheinland. Jahrbuch der Preußischen Geologischen Landesanstalt 55, 284–291.

Størmer, L., 1951. A new eurypterid from the Ordovician of Montgomeryshire, Wales. Geological Magazine 88, 409–422.

Størmer, L., 1955. Merostomata. In: Moore, R.C. (Ed.), Treatise on Invertebrate Paleontology Part P. Arthropoda 2: Chelicerata, Pycnogonida and Palaeoisopus. University of Kansas Press, 4–41.

Størmer, L., 1969. Eurypterids from the Lower Devonian of Willwerath, Eifel. Senckenbergiana lethaea 50, 21–35.

Størmer, L., 1972. Arthropods from the Lower Devonian (Lower Emsian) of Alken an der Mosel, Germany. Part 2: Xiphosura. Senckenbergiana lethaea 53, 1–29.

Størmer, L., 1973. Arthropods from the Lower Devonian (Lower Emsian) of Alken an der Mosel, Germany. Part 3: Eurypterida, Hughmilleriidae. Senckenbergiana lethaea 54, 119–205.

Størmer, L., 1974. Arthropods from the Lower Devonian (Lower Emsian) of Alken an der Mosel, Germany. Part 4: Eurypterida, Drepanopteridae, and other groups. Senckenbergiana lethaea 54, 359–451.

Stott, C.A., Tetlie, O.E., Braddy, S.J., Nowlan, G.S., Glasser, P.M., Devereux, N.G., 2005. A new eurypterid (Chelicerata) from the Upper Ordovician of Manitoulin Island, Ontario, Canada. Journal of Paleontology 79, 1166–1174.

Tetlie, O.E., 2006. Two new Silurian species of *Eurypterus* (Chelicerata: Eurypterida) from Norway and Canada and the phylogeny of the genus. Journal of Systematic Palaeontology 4, 397–412.

Tetlie, O.E., 2007a. Distribution and dispersal history of Eurypterida (Chelicerata). Palaeogeography, Palaeoclimatology, Palaeoecology 252, 557–574.

Tetlie, O.E., 2007b. Like father, like son? Not amongst the eurypterids (Chelicerata) from Beartooth Butte, Wyoming. Journal of Paleontology 81, 1423–1431.

Tetlie, O.E., Braddy S.J., 2004. The first Silurian chasmataspid, *Loganamaraspis dunlopi* gen. et sp. nov. (Chelicerata: Chasmataspidida) from Lesmahagow, Scotland, and its implications for eurypterid phylogeny. Transactions of the Royal Society of Edinburgh, Earth Sciences 94, 227–234.

Tetlie, O.E., Cuggy, M.B., 2007. Phylogeny of the basal swimming eurypterids (Chelicerata; Eurypterida; Eurypterina). Journal of Systematic Palaeontology 5, 345–356.

Tetlie, O.E., Poschmann, M., 2008. Phylogeny and palaeoecology of the Adelophthalmoidea (Arthropoda; Chelicerata; Eurypterida). Journal of Systematic Palaeontology 6, 237– 249.

Tetlie, O.E., Braddy, S.J., Butler, P.D., Briggs, D.E.G., 2004. A new eurypterid (Chelicerata: Eurypterida) from the Upper Devonian Gogo Formation of Western Australia, with a review of the Rhenopteridae. Palaeontology 47, 801–809.

Tetlie, O.E., Selden, P.A., Ren, D., 2007a. A new Silurian eurypterid (Arthropoda: Chelicerata) from China. Palaeontology 50, 619–625.

Tetlie, O.E., Anderson, L.I., Poschmann, M., 2007b. *Kiaeropterus* (Eurypterida; Stylonurina) recognized from the Silurian of the Pentland Hills. Scottish Journal of Geology 43, 1–7.

Tetlie, O.E., Brandt, D.S., Briggs, D.E.G., 2008. Ecdysis in sea scorpions (Chelicerata: Eurypterida). Palaeogeography, Palaeoclimatology, Palaeoecology 265, 182–194.

Tollerton, V.P. Jr., 1989. Morphology, taxonomy, and classification of the Order Eurypterida Burmeister, 1843. Journal of Paleontology 63, 642–657.

Tollerton, V.P. Jr., 2004. Summary of a revision of New York State Ordovician eurypterids: implications for eurypterid palaeoecology, diversity and evolution. Transactions of the Royal Society of Edinburgh: Earth Sciences 94, 235–242.

Vandenbroucke, T.R.A., Gabbott, S.E., Paris, F., Aldridge, R.J., Theron, J.N., 2009. Chitinozoans and the age of the Soom Shale, an Ordovician black shale Lagerstätte, South Africa. Journal of Micropalaeontology 28, 53–66.

Van Roy, P., Orr, P.J., Botting, J.P., Muir, L.A., Vinther, J., Lefebvre, B., el Hariri, K., Briggs, D.E.G., 2010. Ordovician faunas of Burgess Shale type. Nature 465, 215–218.

Waterston, C.D., 1979. Problems of functional morphology and classification in stylonuroid eurypterids (Chelicerata, Merostomata), with observations on the Scottish Silurian Stylonuroidea. Transactions of the Royal Society of Edinburgh, Earth Sciences 70, 251–322.

Waterston, C.D., Oelofsen, B.W., Oosthizen, R.D.F., 1985. *Cyrtoctenus wittebergensis* sp. nov. (Chelicerata: Eurypterida), a large sweep-feeder from the Carboniferous of South Africa. Transactions of the Royal Society of Edinburgh, Earth Sciences 76, 339–358.

White, D., 1908. Report on the fossil flora of the coal measures of Brazil. In: White, J.C. (Ed.), Final report on the coal measures and associated rocks of South Brazil. Commissão de Estudos das Minas de Carvão de Pedra Do Brazil, Rio de Janeiro, 377–607.

Wills, L.J., 1965. A supplement to Gerhard Holm's "Über die Organisation des *Eurypterus fischeri* Eichw." with special reference to the organs of sight, respiration and reproduction. Arkiv för Zoologi 2, 93–145.

Wills, M.A., 1999. Congruence between phylogeny and stratigraphy: randomization tests and gap excess ratio. Systematic Biology 48, 559–580.

Young, G.A., Rudkin, D.M., Dobrzanski, E.P., Robson, S.P., Nowlan, G.S., 2007. Exceptionally preserved Late Ordovician biotas from Manitoba, Canada. Geology 35, 883–886.

Zander, R.H., 2003. Reliable phylogenetic resolution of morphological data can be better than that of molecular data. Taxon 52, 109–112.

Eurypterids by period	**Author**	**Age**	**Region**
Ordovician			
Onychopterella augusti	Braddy *et al*., 1995	Hirnantian	South Africa
Silurian			
Hughmilleria wangi	Tetlie *et al*., 2007a	Llandovery	China
Rhinocarcinosoma dosonensis	Braddy *et al*., 2002	Ludlow–Pridoli	Vietnam
Slimonia boliviana	Kjellesvig-Waering, 1973	Ludlow/Pridoli	Bolivia
Devonian			
Acutiramus cf. *bohemicus*	Burrow *et al*., 2002	Pridoli	Australia
Adelophthalmus waterstoni	Tetlie *et al*., 2004	Frasnian	Australia
Pterygotus bolivianus	Kjellesvig-Waering, 1964a	Emsian/Eifelian	Bolivia
Carboniferous			
Adelophthalmus irinae	Shpinev, 2006	Tournaisian	Siberia
Cyrtoctenus wittebergensis	Waterston *et al*., 1985	Tournaisian	South Africa
Megarachne servinei	Hünicken, 1980	Gzhelian–Asselian	Argentina
Unionopterus anastasiae	Chernyshev, 1948	Tournaisian–Visean	Kazakhstan
Permian			
Adelophthalmus chinensis	Grabau, 1920	Asselian	China
Campylocephalus oculatus	Kutorga, 1838	Guadalupian?	Russia
Hastimima whitei	White, 1908	Sakmarian	Brazil

Table 1. Chronological list of undoubted eurypterids from palaeocontinents other than Baltica, Laurentia, Avalonia, Iberia and Armorica. *Stylonurus* (?) *menneri* and *Borchgrevinkium taimyrensis* from the early Devonian of Siberia (Novojilov, 1959) and *Melbournopterus crossotus* from the Silurian of Australia (Caster and Kjellevig-Waering,

1953) are not eurypterids and so have not been included. *Eurypterus loi*, *Eurypterus styliformis* and *Eurypterus yangi* from the Silurian of China (Chang, 1957) are probably based on undiagnostic material and have been excluded pending reevalution of the original material, as have *Nanahughmilleria schiraensis* and *Parahughmilleria matarakensis* from the Devonian of Siberia (Pirozhnikov, 1957), *Adelophthalmus carbonarius* (Chernyshev, 1933) from the Carboniferous of Ukraine, and *Pterygotus* (?) *australis* from the Silurian of Australia (McCoy, 1899). Note however that reports of unnamed or undescribed eurypterids (Braddy *et al*., 1995, Braddy & Almond, 1999, Braddy *et al*., 2002, Tetlie *et al*., 2004) are not listed here.

1	2	3	4	5	6	7
5/44	7/34*	7/46	8/45	8/42	8/40	8/31*

Table 2. Proportions (length/width) of the holotype specimen MTANHMSETR 10-İZ-01-1 of *Paraeurypterus anatoliensis*

*Preserved dimensions.

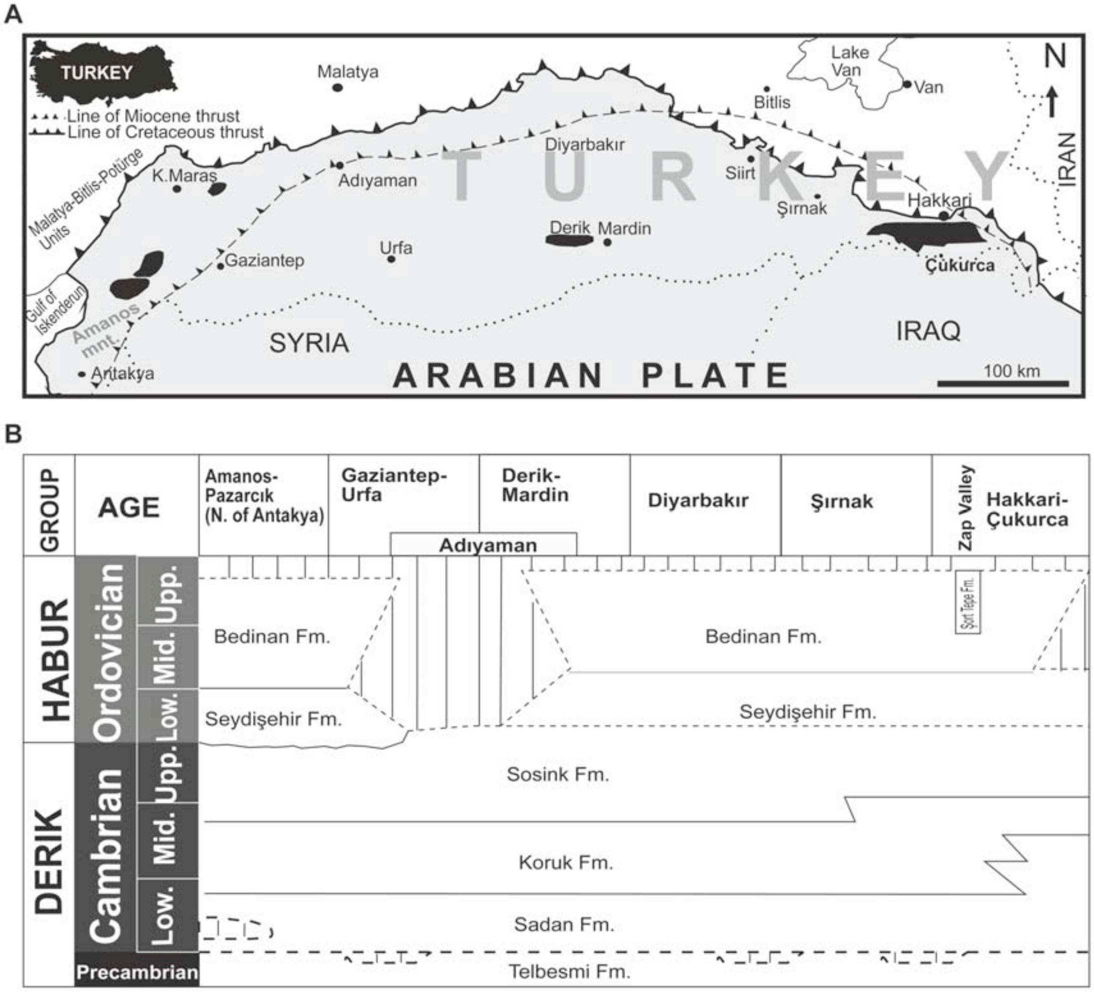

Fig. 1. A, map showing the region surrounding the border between the Arabian and Anatolian plates. Early Palaeozoic outcrops are shown in black. The Zap Valley is located between Hakkari and Çukurca; B, diagram showing the lateral extent of the early Palaeozoic formations between Antakya and Hakkari on the Arabian plate. After Bozdoğan and Ertuğ, 1997.

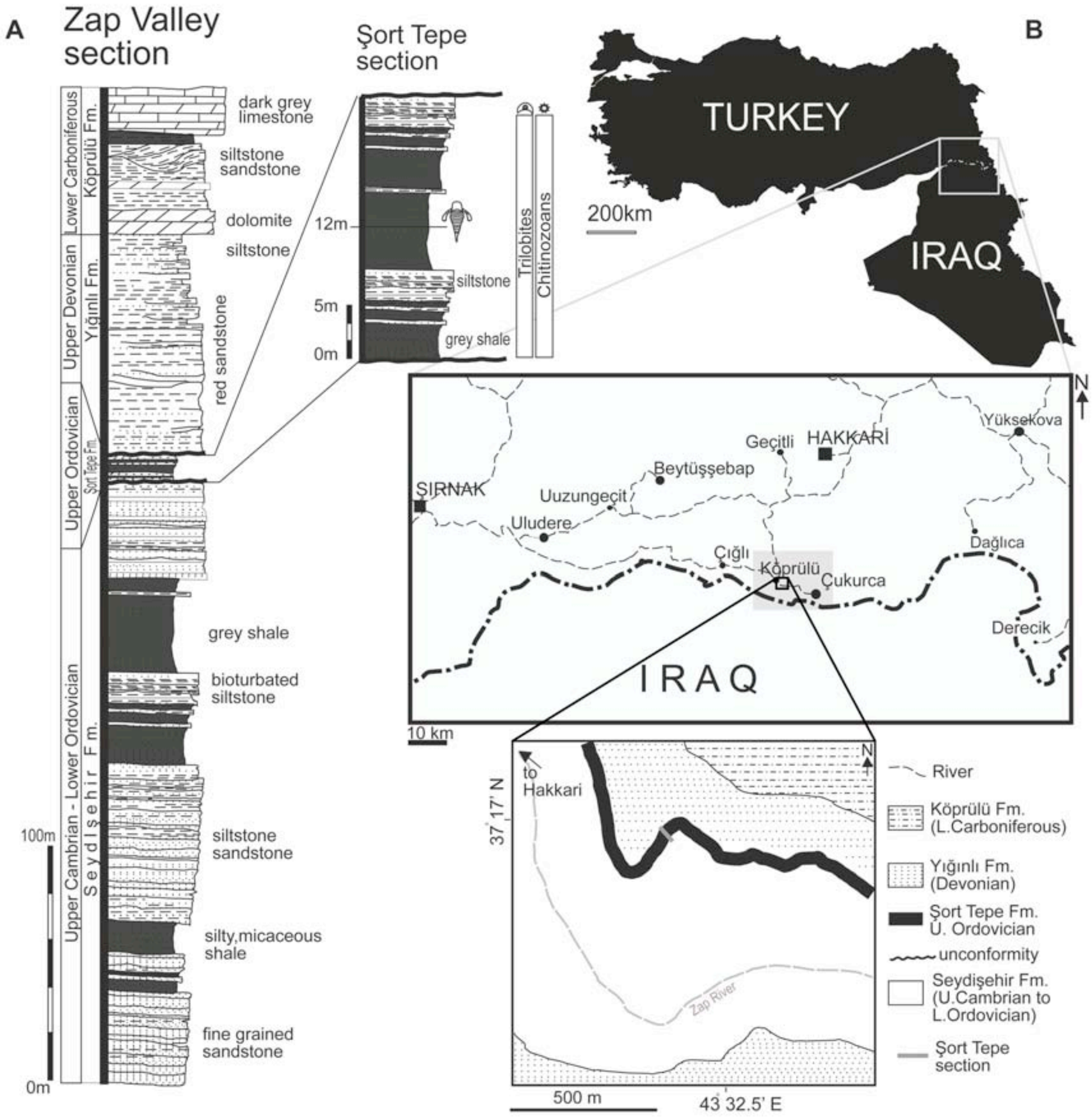

Fig. 2. A, generalized columnar section of the Upper Cambrian-Lower Carboniferous rock units of the Zap Valley section (after Ghienne *et al*., 2010) with the location of the eurypterid shown within the Şort Tepe Formation; B, location and geological maps of the Zap Valley and Şort Tepe section.

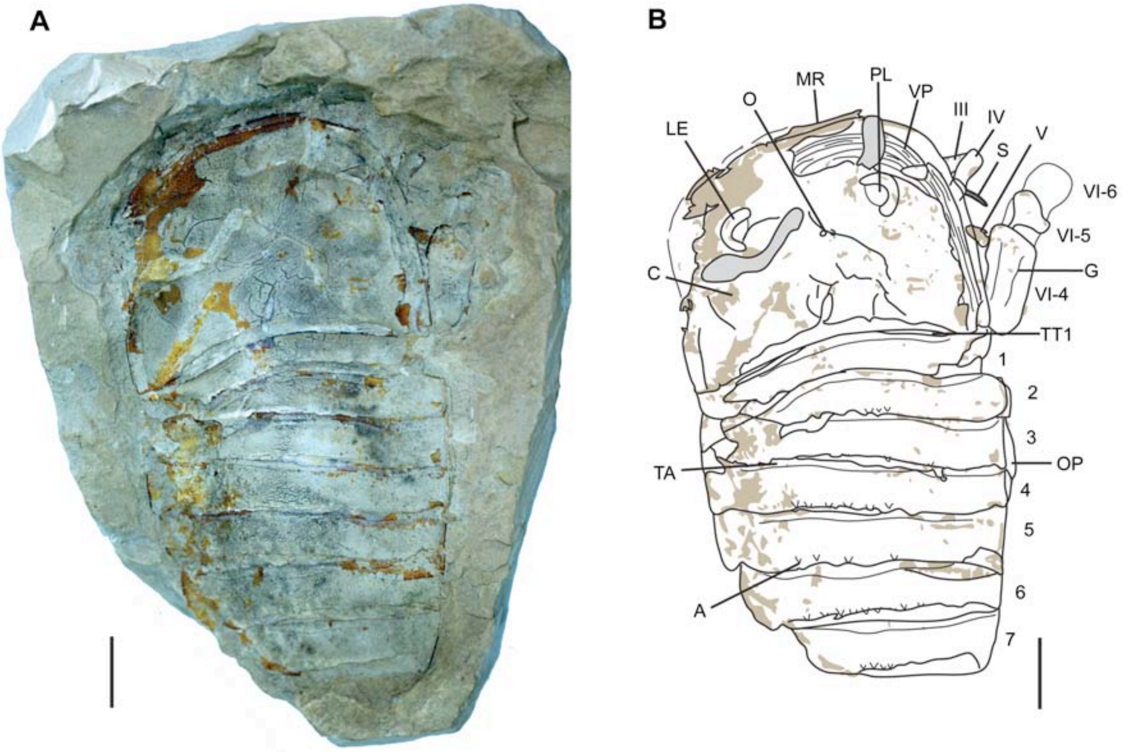

Fig. 3. *Paraeurypterus anatoliensis* gen. et sp. nov. MTANHMSETR 10-İZ-01-1. A, Photograph of holotype and only known specimen; B, Interpretive drawing of holotype. Shaded areas represent preservation of original cuticle. Label abbreviations: A, acicular scales; C, carapace; G, grooves; LE, lateral eye; MR, marginal rim; O, ocelli; OP, opercular plate; PL, palpebral lobe; S, spine; TA; tergite articulation; TT1, true tergite 1; VP, ventral plate; 1–7, tergites; III–VI, prosomal appendages; VI-4–VI-6, podomeres of prosomal appendage VI. Scale bars equal 10 mm.

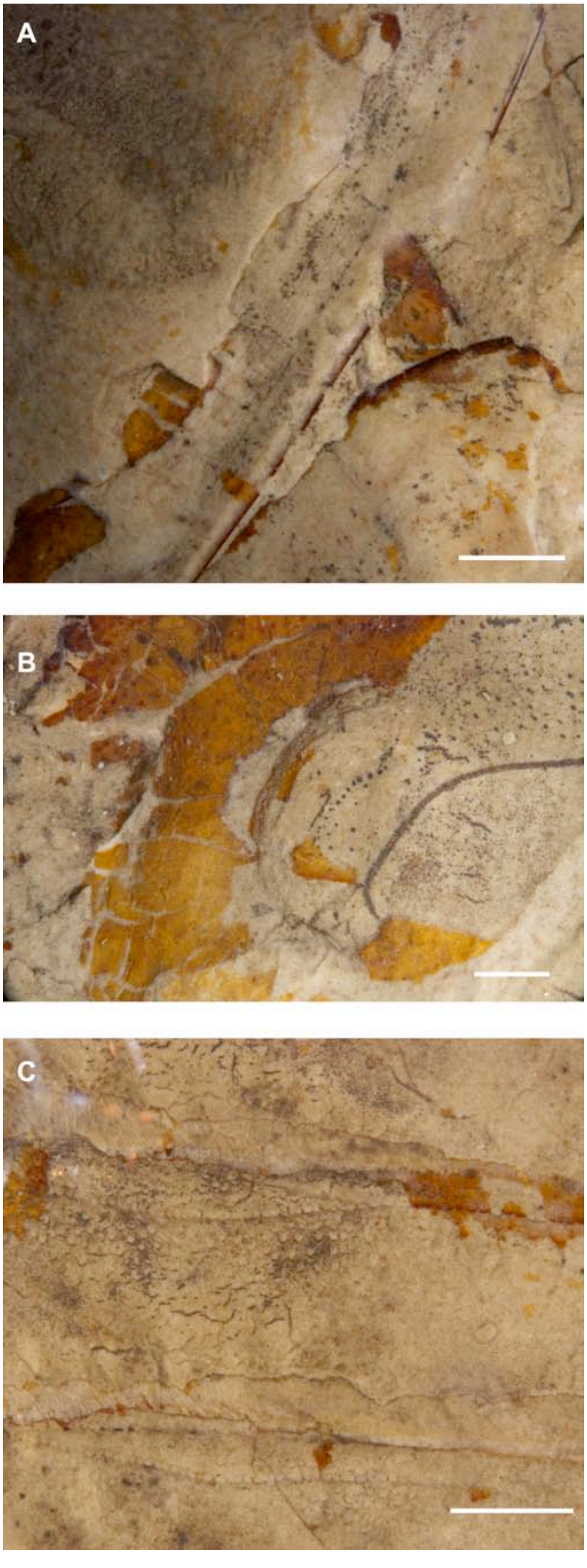
A
B
C

Fig. 4. *Paraeurypterus anatoliensis* gen. et sp. nov. MTANHMSETR 10-İZ-01-1. A, Magnification of exposed ventral plate, showing fine striate 'terrace line' ornament; B, Magnification of crescentic lateral eye with enlarged palpebral lobe; C, Magnification of tergite ornament, showing the row of flattened scales at the posterior of the articulating facet and the large acicular scales towards the rear of the tergite. Scale bars equal 2 mm.

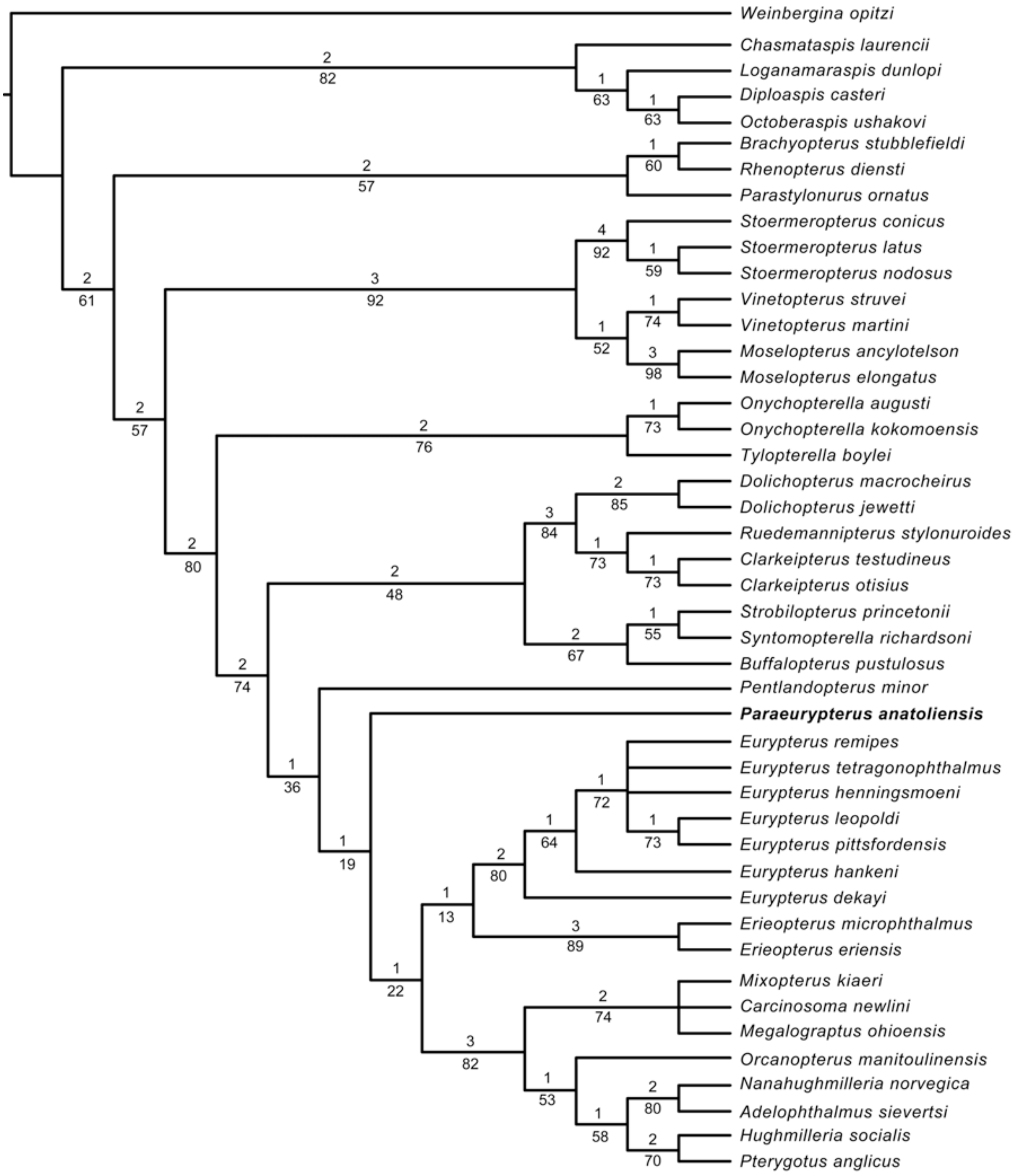

Fig. 5. Strict consensus of phylogenetic analysis consisting of 81 characters coded for 45 taxa, resulting in two most parsimonious trees of 229 steps each. The numbers above the branches are Bremer support values while those beneath each branch are jackknife support values after 100,000 repetitions with 25% deletion. *Paraeurypterus anatoliensis* is highlighted in bold.

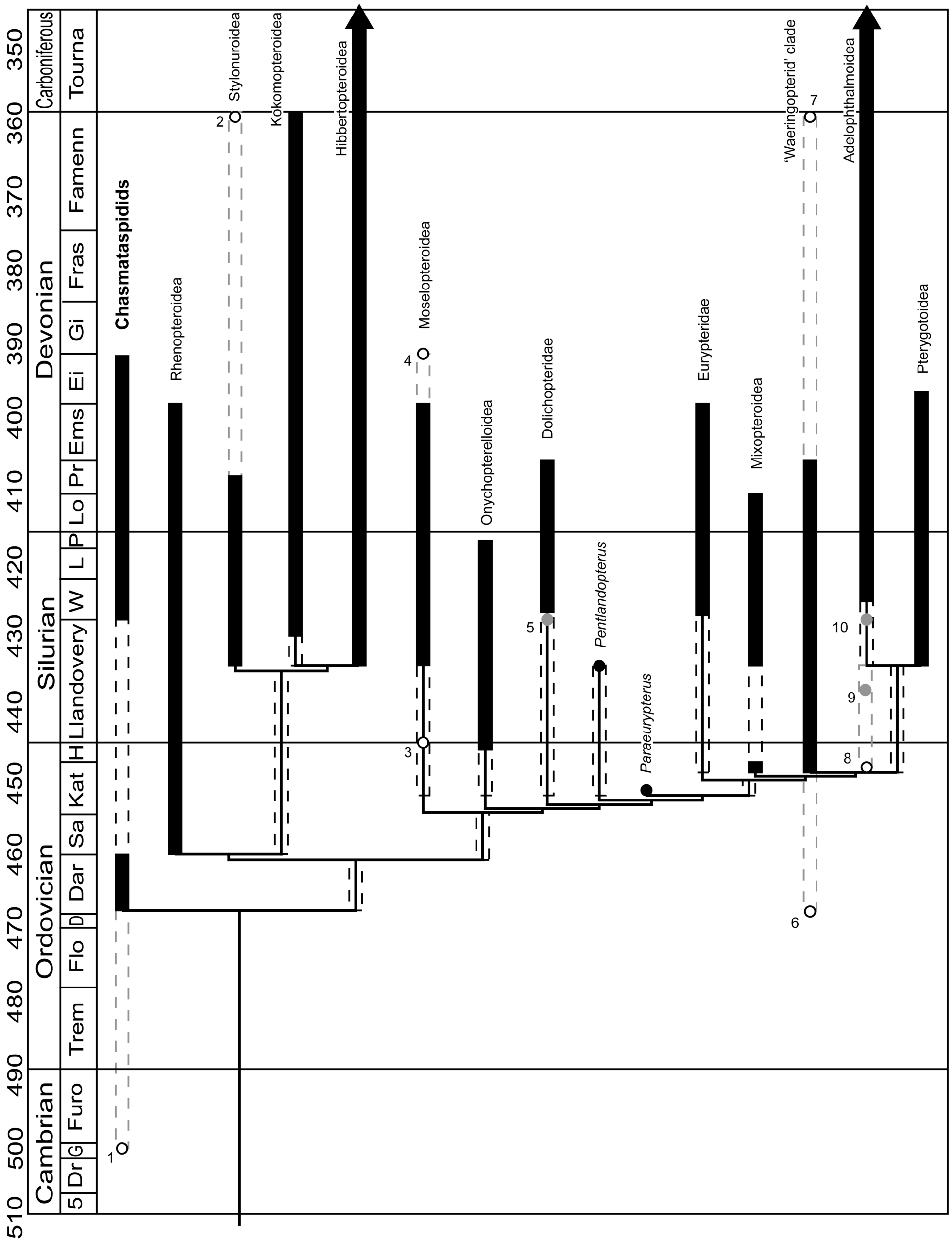

Fig. 6. Composite tree showing the relationships of the major eurypterid clades derived from this analysis and that of Lamsdell *et al*. (2010a,b) with the inferred chasmataspidid sister-group. Solid black bars indicate known ranges, while the black dashed bars show ghost ranges. Grey dashed bars are potential range extensions suggested by fossils in need of further study. The circles indicate single

species occurrences; where these are solid grey the taxonomic assignment is certain but the dating is uncertain, while hollow black circles are species that have a confirmed date but are of uncertain taxonomic assignment. Solid black are of definite age and taxonomic assignment. These single species are as follows: 1, Chasmataspidid-like trace fossil (Dunlop *et al*., 2004); 2, *Stylonurella* (?) *beecheri* (Hall, 1884), which is probably a *Ctenopterus* Clarke and Ruedemann, 1912; 3, *Onychopterella* (?) *pumilus* (Savage, 1916), which is probably a *Stoermeropterus* Lamsdell, 2011; 4, *Moselopterus lancmani* (Delle, 1937); 5, *Dolichopterus gotlandicus* Kjellesvig-Waering, 1979; 6, Undescribed 'waeringopterid' from the St. Peter Formation (Liu *et al*., 2006); 7, *Grossopterus inexpectans* (Ruedemann, 1921b); 8, 'Hughmilleriid' bearing resemblance to *Eysyslopterus* Tetlie and Poschmann, 2008 from the Manitoba formations (Young *et al*., 2007 fig 4f); 9, *Parahughmilleria maria* (Clarke, 1907); 10, *Nanahughmilleria clarkei* Kjellesvig-Waering, 1964b.

Chapter 6

Babes in the wood – a unique window into sea scorpion ontogeny

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(Formatted for submission to *BMC Evolutionary Biology*)

Abstract

Background

Few studies on eurypterids have taken into account morphological changes that occur throughout postembryonic development. Here two species of eurypterid are described from the Pragian Beartooth Butte Formation of Cottonwood Canyon in Wyoming, and included in a phylogenetic analysis. Both species comprise individuals from a number of instars, and this allows for changes that occur throughout their ontogeny to be documented, and how ontogenetically variable characters can influence phylogenetic analysis to be tested.

Results

The two species of eurypterid are described as *Jaekelopterus howelli* (Kjellesvig-Waering and Størmer, 1952) and *Strobilopterus proteus* sp. nov. Phylogenetic analysis places them within the Pterygotidae and Strobilopteridae respectively, both families within the Eurypterina. *Jaekelopterus howelli* shows positive allometry of the cheliceral denticles

throughout ontogeny, while a number of characteristics including prosomal appendage length, carapace shape, lateral eye position, and relative breadth all vary during the growth of *Strobilopterus proteus*.

Conclusions

The ontogeny of *Strobilopterus proteus* shares much in common with that of modern xiphosurans, however certain characteristics including apparent true direct development suggest a closer affinity to arachnids. The ontogenetic development of the genital appendage also supports the hypothesis that the structure is homologous to the endopods of the trunk limbs of other arthropods. Including earlier instars in the phylogenetic analysis is shown to destabilise the retrieved topology. Therefore, coding juveniles as individual taxa in an analysis is shown to be actively detrimental and alternatives ways of coding ontogenetic data into phylogenetic analyses should be explored.

Key words: Palaeozoic, Pragian, Eurypterida, *Strobilopterus*, *Syntomopterella*, *Jaekelopterus*, Cottonwood Canyon, development, instars, phylogeny.

Background

Eurypterids represent a major clade of extinct chelicerate arthropods that probably represent the sister group to arachnids [1, 2]. They are relatively common in Silurian and Devonian Lagerstätten, to which they are generally restricted due to their unmineralized cuticle [3] and have a total range extending from the mid-Ordovician until the end-Permian, throughout which time they exhibited a euryhaline distribution, with an increasing trend towards freshwater habitats apparent through the Carboniferous and

Permian [4]. By the Middle Devonian, eurypterids had become increasingly rare, with the last of the phylogenetically basal swimming forms occurring in the Emsian Beartooth Butte Formation of Wyoming. One of the species described from that locality, *Strobilopterus princetonii* (Ruedemann, 1934), is of particular interest because juvenile specimens have been recognised that show distinct morphological differences from the adults [5].

Here, we describe new eurypterid material from an older section of the Beartooth Butte Formation at Cottonwood Canyon, Wyoming, which is Pragian in age. Two species can be recognised from the locality: the pterygotid *Jaekelopterus howelli* (Kjellesvig-Waering and Størmer, 1952) which is also known from the younger section at Beartooth Butte [6], and *Strobilopterus proteus* sp. nov. Both species are included in a broad phylogenetic analysis of the Eurypterida. Remarkably, multiple instars of both species are also recognisable at the Cottonwood Canyon locality, and these represent a unique opportunity to study the postembryonic development of extinct chelicerate species. There have been few previous studies on eurypterid ontogeny, and these have tended to rely on the same few well-sampled species and focused on changes in the dorsal carapace structures or relative length/width rations of the carapace and opisthosoma [7-9]. *Strobilopterus proteus,* meanwhile, preserves individuals from at least four instars and exhibits previously unrecognised changes in appendage and body segment dimension and structure. Chelicerate palaeontologists have tended to neglect the influence of ontogeny when describing species [10, 11] and it is important to recognise that a number of taxa may be over-split taxonomically. What is largely unknown, however, is what effect including such ontogenetic species into phylogenetic analyses would have, and so the instars of *Strobilopterus proteus* are used in a brief case-study of this possibility.

The current work comprises a complete description of both eurypterid species present at Cottonwood Canyon and a phylogenetic analysis of the Eurypterida. The ontogeny of these species is then analysed using a holomorph approach [10] in order to identify morphological trends that occur during postembryonic development and compared with the known ontogeny of other eurypterid species. Finally, the influence of including juvenile taxa in phylogenetic analysis is tested using the current analysis and material.

Methods

Material

The bulk of the material described herein is the result of fieldwork carried out by Robert H. Denison and Eugene S. Richardson, Jr. in 1962, and accessioned in the Field Museum of Natural History, Chicago. A single specimen was collected during fieldwork led by Hans-Peter Schultze in 1983, and is held in the University of Kansas Museum of Invertebrate Paleontology, Lawrence, Kansas. All specimens are derived from the Pragian Beartooth Butte Formation section at Cottonwood Canyon, Big Horn County, Wyoming. Photographs were taken on a Canon EOS 5D Mk II digital camera with a Canon macro EF 100 mm 1:2.8L IS USM lens with the specimens submerged in ethanol. Image processing was carried out using Adobe Photoshop CS4, and interpretive drawings were prepared for publication using Adobe Illustrator CS4, on a MacBook Pro running OS X.

Geological settings and preservation

The Lower Devonian Beartooth Butte Formation is widespread throughout much of Wyoming and Montana; however, it is the type section in Beartooth Butte and another section in Cottonwood Canyon – both in Wyoming – that are of particular palaeontological interest. The Beartooth Butte section (Park Co., 44°57'N 109°37'W) was discovered by Erling Dorf [12], who interpreted the lithology as one of a non-marine, local channel-fill deposited in quiet, shallow, estuarine conditions, and he undertook preliminary descriptions of the abundant plant material found at the locality [13, 14]. Most attention, however, has focused on the diverse fish fauna, which was described by Bryant [15-18], while low numbers of associated eurypterids were described by Ruedemann [19, 20], Kjellesvig-Waering [21] and Kjellesvig-Waering and Størmer [6, 22]. The eurypterid fauna was recently redescribed [5], with the number of confirmed eurypterid species reduced to just two: *Jaekelopterus howelli* (Kjellesvig-Waering and Størmer, 1952) and *Strobilopterus princetonii* (Ruedemann, 1934). Tetlie also suggested that *Dorfopterus angusticollis* Kjellesvig-Waering, 1955 could represent the telson of *Strobilopterus*; however the style of preservation is different to that of the other arthropods at the locality and the morphology does not bear close comparison to any other eurypterid species. The eurypterid affinities of *Dorfopterus* need to be seriously questioned.

The plant material, representing a rare extensive Lower Devonian assemblage in western North America, is also receiving renewed attention with flora from both Beartooth Butte and neighbouring Cottonwood Canyon being described [23-25]. A fish fauna has also been described from Cottonwood Canyon [26-28] although it is much less diverse than at Beartooth Butte, consisting of two species of *Protaspis* Bryant, 1933, two species of *Cardipeltis* Branson and Mehl, 1931, and a species each of *Cosmaspis* Denison, 1970 and *Lampraspis* Denison, 1970 (all heterostracans), and the dipnoan (lungfish) *Uranolophus* Denison, 1968. Three scorpions from Cottonwood Canyon have also been described, each assigned to its own monospecific genus: *Hydroscorpius denisoni* Kjellesvig-Waering, 1986, *Acanthoscorpio mucronatus* Kjellesvig-Waering, 1986 and *Branchioscorpio richardsoni* Kjellesvig-Waering, 1986. Given Kjellesvig-Waering's propensity for over-splitting scorpion species (see Dunlop *et al*. [29] and Legg *et al*. [11]) it would perhaps be wise to re-evaluate the scorpion material; however, the suggestion that *Acanthoscorpio mucronatus* is a juvenile *Strobilopterus* [30] is not supported by new eurypterid material (unfortunately the scorpion material is not currently available for study and so its true affinities and taxonomic diversity at present remains uncertain). Notwithstanding this body of work, the most abundant component of the Cottonwood Canyon fauna, the eurypterids, have not received a systematic treatment with the exception of an isolated pterygotid ramus [31].

The Cottonwood Canyon (Big Horn Co., 44°52'N 108°02'W) section is situated in the Big Horn Mountains of northern Wyoming [32], roughly 100 km east of the type section in Beartooth Butte. The Beartooth Butte Formation at the Cottonwood Canyon section consists of long, narrow bodies of sediment with lenticular cross-sections comparable to channel fill deposits; is underlain by the Ordovician Bighorn Dolomite and overlain by the Upper Devonian Jefferson Limestone [33]. The formation largely comprises clastic sediments deposited in a carbonate-rich context, with the fossiliferous layers at Cottonwood Canyon consisting predominantly of siltstone and shale, with dolomitised sandstone interbeds rather than the massive dolomitised limestones found at Beartooth Butte. The eurypterids at Cottonwood Canyon are preserved with the original cuticle forming a reddish-brown film over dorso-ventrally flattened impressions, while the plant material is preserved predominantly as carbonaceous compressions with rare occurrences of oxidised preservation [34]. It is possible that the eurypterid material represents moulted exuviae that became entangled with waterlogged uprooted plant material – similar associations can be found in the Lower Devonian of Alken, Germany [35-37]. The eurypterid and plant material lay on the sediment surface for some time before burial, as shown by the encrustation of microconchids on both the plant material [34] and eurypterids. Ostracodes are also present, which may have been feeding on the decaying plant matter and eurypterid cuticle.

Vertebrate biostratigraphy [38, 39] indicates that the Cottonwood Canyon section is late Lochkovian to early Pragian whereas the type section at Beartooth Butte is Emsian in age. Stable oxygen and isotope data [40] indicate that the Beartooth Butte Formation was deposited in an estuarine environment, with the Cottonwood Canyon section being slightly less saline than the type section. It is interesting to note that, whereas eurypterids are common at Cottonwood Canyon where the fish are less prominent, the fauna at Beartooth Butte is clearly dominated by fish, and eurypterids are relatively scarce. This is unlikely to be due to Beartooth Butte representing a more saline environment that the eurypterids could not inhabit because eurypterids were capable of tolerating a wide range of salinities [41], and a third locality for the Beartooth Butte Formation, Half Moon Canyon, is considerably less saline than either of the other localities and appears to be totally devoid of eurypterids. One possibility is that the eurypterid population dwindled in size in the period between the deposition of the Cottonwood Canyon sediments and that of the younger sediments at Beartooth Butte, eventually going extinct before formation of the beds at Half Moon Canyon, which are Givetian in age. Eurypterid diversity did decline throughout the early and mid Devonian with the majority of swimming forms, including the clades including *Strobilopterus* and *Jaekelopterus*, going extinct prior to the Frasnian [4].

Institutional abbreviations

FMNH, Field Museum of Natural History, Chicago, USA; KUMIP, University of Kansas Museum of Invertebrate Paleontology, Kansas, USA; PU, Princeton University Geological Museum, New Jersey, USA; YPM, Peabody Museum, Yale University, New Haven, Connecticut, USA.

Terminology

Eurypterid terminology largely follows Tollerton [42] for morphology of the carapace, metastoma, lateral eyes, prosomal appendages, genital appendage, opisthosomal differentiation, telson, and patterns of ornamentation; however, the terminology for the ventral plate morphologies follows the revised types of Tetlie *et al*. [43]. Selden [44] is followed for prosomal structures and cuticular sculpture, and the labelling of the appendages, with pterygotid cheliceral denticle terminology as used by Miller [45]. Terminology for the segmentation of the genital operculum follows Waterston [46].

Phylogenetic analysis

For the phylogenetic analysis, the matrix of Lamsdell *et al*. [47] was expanded and partially combined with the existing Stylonurina matrix [48-50] and the pterygotoid matrix of Braddy *et al*. [51], resulting in a new matrix consisting of 104 characters and 63 taxa, which can be found in Appendix 3 along with character descriptions. All of the taxa from Lamsdell *et al*. [47] and Braddy *et al*. [51] were included along with the addition of *Laurieipterus elegans* (Laurie, 1899), *Hardieopterus macrophthalmus* (Laurie, 1892), *Kokomopterus longicaudatus* (Clarke and Ruedemann, 1912), *Drepanopterus pentlandicus* (Laurie, 1892), *Megarachne servinei* Hünicken, 1980 and *Hibbertopterus scouleri* (Hibbert, 1836) from the Stylonurina matrix so that each major stylonurine clade was represented by at least two taxa. Finally, *Jakelopterus howelli* (Kjellesvig-Waering and Størmer, 1952), *Strobilopterus proteus* sp. nov. and '*Erieopterus*' *laticeps* (Schmidt, 1883) in order to ascertain the phylogenetic position of the taxa described herein and to resolve the affinities of '*Erieopterus*' *laticeps*, which was considered by Tetlie [52] and Tetlie and Cuggy [53] to represent a dolichopterid.

The analysis was performed using TNT [54] (made available with the sponsorship of the Willi Hennig Society) employing random addition sequences followed by tree bisection-reconnection (TBR) branch swapping (the *mult* command in TNT) with 100,000 repetitions with all characters unordered and of equal weight. Jackknife [55] and Bremer support [56] values were calculated in TNT and the Consistency, Retention and Rescaled Consistency Indices were calculated in Mesquite 2.73 [57]. Nonparametric bootstrapping is often difficult with morphological data due to the limited size of the dataset [58]; however, bootstrapping with 50% resampling was performed. Jackknifing was performed using simple addition sequence and tree bisection-reconnection branch swapping, with 100,000 repetitions and 33% character deletion. The matrix and character listing can be found in Appendix 3 and has been deposited in the online MorphoBank database [59] under the project code p780 and can be accessed from http://morphobank.org/permalink/?P780.

Results

Systematic Palaeontology

Subphylum CHELICERATA Heymons 1901

Order EURYPTERIDA Burmeister 1843

Suborder EURYPTERINA Burmeister 1843

Family STROBILOPTERIDAE fam. nov.

Type genus. *Strobilopterus* Ruedemann, 1935.

Included genera. *Buffalopterus* Kjellesvig-Waering and Heubusch, 1962.

Stratigraphical range and distribution. Middle Silurian (Wenlock) to Lower Devonian (Emsian) of Estonia, Norway and Ohio, New York and Wyoming, USA.

Diagnosis. Eurypterina with semicircular carapace; appendage VI short, barely projecting from beneath carapace; carapace ornamentation radiating out from the lateral eyes and curving around the carapace margins; row of angular scales across the posterior of metasomal tergites.

Genus *Strobilopterus* Ruedemann 1935

v* 1935 *Strobilopterus* Ruedemann, p. 129

v. 1961 *Syntomopterus* Kjellesvig-Waering, p. 91 [preoccupied]

2007 Syntomopterella Tetlie, p. 1424 [replacement name for *Syntomopterus*]

Type species. Pterygotus princetonii Ruedemann, 1934, by original designation.

Included species. Strobilopterus laticeps (Schmidt, 1883) [= *Dolichopterus stoermeri* Caster and Kjellesvig-Waering, 1956], *Strobilopterus richardsoni* (Kjellesvig-Waering, 1961), *Strobilopterus proteus* sp. nov.

Stratigraphical range and distribution. Middle Silurian (Wenlock) to Lower Devonian (Emsian) of Estonia, Norway and Ohio and Wyoming, North America.

Emended diagnosis. Large Strobilopteridae with wide semicircular carapace; lateral eyes lunate to crescentic with palpebral lobe, situated between central and centrimesial sectors; I small, no denticles; II–V small with fixed spines and serrated distal podomere margins; VI short but with powerful serrations on anterior podomere margins; VI-9 larger in later instars; metastoma almost elongate petaloid; type A genital appendage undivided and long; type B genital appendage oval; both genital appendage morphs with angular spatulae; genital operculum striate ornament marked by highly sclerotized, broad lunate scales; tergite of somite VIII reduced; preabdomen short and wide; second order opisthosomal differentiation on segments 2 to 12, especially pronounced on 7; cuticular sculpture of minute pustules, adults with narrow, elongate scales arranged across the posterior of the metasomal tergites in large individuals (emended from Tetlie [5]).

Remarks. The new species of *Strobilopterus* described from Cottonwood Canyon herein shows the characteristic ventral and appendicular morphology of *Strobilopterus* and the diagnostic dorsal carapace structure and ornamentation of *Syntomopterella*. Kjellesvig-

Waering, in a personal communication to Waterston [46], considered the Cottonwood Canyon species to be assignable to *Syntomopterella*; however, the available opisthosomal material corresponds well with the type species of *Strobilopterus*. The discovery of the *Syntomopterella*-type carapace ornamentation in a species of *Strobilopterus* renders *Syntomopterella* without any unique, defining characteristics, and the two genera are therefore synonymised herein, with *Strobilopterus* being the senior synonym. Consequently, the material of *Strobilopterus richardsoni*, and that of the other eurypterids from the Holland Quarry Shale, should be re-evaluated because a number of swimming paddles assigned to *Dolichopterus asperatus* Kjellesvig-Waering, 1961 bear close resemblance to the paddles of *Strobilopterus princetonii* and *Strobilopterus proteus*.

Larger specimens of the Cottonwood Canyon *Strobilopterus* also reveal a number of characteristics that the genus shares with *Buffalopterus*, particularly the elongate scales along the posterior metasomal tergite margins, along with the dorsal carapace ornamentation of scales angled away from the lateral eyes, and cuticular ornamentation of the sternites. The type A genital appendage of *Buffalopterus* is, however, markedly different from that of *Strobilopterus*, consisting of three segments rather than a single fused segment, and so the two genera are retained as distinct entities.

Strobilopterus laticeps (Schmidt, 1883) is based on material described by Schmidt [60], Holm [61] and Størmer [62] and considered by Caster and Kjellesvig-Waering [63] to be two distinct species. The two carapaces figured by Schimdt [60] (his pl. 3, fig. 16, pl. 6, fig. 6), including the holotype, were assigned to *Erieopterus* along with a poorly preserved carapace described by Størmer ([62], fig. 1). Subsequently, a genital operculum figured by Holm ([61], pl. 4, fig. 23) was made the holotype of *Dolichopterus stoermeri*

Caster and Kjellesvig-Waering, 1956, to which a metastoma figured by Holm ([61], pl. 10, fig. 10) and a swimming paddle figured by Schmidt ([60], pl. 7, fig. 9) were also assigned. The carapaces clearly belong to a strobilopterid due to their semicircular shape while the paddle is short and the type A genital operculum is a good match for *Strobilopterus* itself, possessing an elongate appendage that dorsally consists of a single unit, angular spatulae and the striate ornament on the operculum being demarcated by highly sclerotised lunate scales. Given that the dorsal and ventral material both indicates assignment to *Strobilopterus* the two species are synonymised and transferred to the genus herein.

Strobilopterus proteus sp. nov.

Figures 1, 3–15

Etymology. Named for Proteus, a sea-god of Greek mythology and one of several deities referred to by Homer in his *Odyssey* as ‘Old Man of the Sea’, known for his ability to change shape, and origin of the adjective ‘protean’.

Material. Holotype: FMNH PE 28961, relatively complete large individual consisting of articulated carapace, opisthosoma and proximal portion of telson, also preserving part of prosomal appendage VI. Paratypes: FMNH PE 6165–6166, PE 6168, PE 9236, PE 26079, PE 61154–61155, PE 61163, PE 61166, PE 61197–61199. Additional Material: FMNH PE 6167, PE 7077, PE 9242, PE 61150–61151, PE 61162, PE 61165, PE 61168–61172, PE 61179–61180, PE 61185, PE 61187, PE 61191–61192.

Horizon and locality. All specimens were collected from the sole locality, the Pragian Beartooth Butte Formation section at Cottonwood Canyon, Big Horn County, Wyoming, by Robert H. Denison and Eugene S. Richardson, Jr. in 1962.

Diagnosis. *Strobilopterus* with lateral eyes positioned on outer limits of central region; carapace cuticular ornamentation consisting of elongate pustules angling away from the lateral eyes and curving around the carapace margin; podomere VI-9 serrate, enlarged (greater than half the length of VI-8) but not longitudinally drawn-out; podomere VI-7a lacking serrations.

Description. *Strobilopterus proteus* is known from 31 specimens which, between them, provide an almost complete view of the external morphology of the animal. Furthermore, these specimens represent a number of different instars (see discussion below) that allows for some morphological changes that occur throughout the ontogenetic development of the species to be documented.

The carapace is known from 13 specimens (Figs. 1–10), most of which also preserve details of the lateral eyes, median ocelli, and marginal rim. The carapaces range in length from 8–83 mm and from 9–133 mm in width (Table 1), with adult specimens having a length/width ratio of between 0.55 and 0.62 (Figs. 1, 3–6); the length/width ratio increases in the juveniles, up to a maximum of 0.83 (Figs. 7–10). The carapace in juveniles is, therefore, horseshoe-shaped, broadening to semicircular in adults. A marginal rim is present, extending all the way around the front and lateral edges of the carapace, and narrowing towards the posterior. This marginal rim is consistently 0.5 mm wide except in the largest specimens, where it expands in width to 1 mm; the marginal rim is, therefore, comparatively wider in juveniles compared to adults. Lateral eyes are positioned centrally in the largest specimens (e.g. FMNH PE 61151) and are crescentic, surrounding a large, moderately inflated, palpebral lobe. The lateral eyes are equivalent to 14–16% of the carapace length in adults; in the smallest juveniles they correspond to 25–30% of the carapace length and are positioned centrimesially (FMNH PE 6165), while larger adolescents have lateral eyes equal to 19–22% of the carapace length. The median ocelli are located between the lateral eyes at the carapace anteroventral midline and each circular ocellus is consistently around 1 mm in diameter so that, again, they are larger in juveniles relative to carapace size compared to adults. The ocelli in the juveniles are positioned independently on the carapace surface while in larger individuals they are located on a slight inflation (FMNH PE 61154) that appears to be cardioid in shape (FMNH PE 61154) but is not as pronounced as a true ocellar node. The greatest difference between the larger adolescent and adult specimens and the smallest juveniles is the occurrence of elongate genal spines in the latter. These are most clearly seen in FMNH PE 6165 (Fig. 7C) which is dorsally preserved and shows the genal spine projecting from the posterior termination of the carapace marginal rim and extending back as far as the posterior of the second tergite. Genal spines can also be seen in the ventrally preserved specimen FMNH PE 61199 (Fig. 10A) and a posterior flaring of the carapace consistent with the formation of genal spines is present in FMNH PE 61197 (Fig. 9A). In adults, these genal spines are much reduced into genal facets that totally overlap the lateral margins of the first tergite (e.g. FMNH PE 6166). The carapace ornamentation consists of small, closely spaced pustules that evenly cover the dorsal surface. In both juveniles and adults, the ornamentation appears to radiate out from the lateral eyes; however, it is most noticeable in the largest individuals in which a number of pustules are somewhat elongated and clearly angled away from the lateral eyes before curving around the carapace margin (e.g. FMNH PE 61154, PE 61168).

The ventral prosomal structures, including the appendages, are known in detail from a number of specimens, most of which are juveniles. The position of the ventral prosomal plates are visible in FMNH PE 9236 (Fig. 7A), in which the plates have broken away, and FMNH PE 61197 (Fig. 2C). The ventral plates appear to widen towards the posterior of the carapace while the anterior region forms a 'triangular area' *sensu* Størmer [36] and Lamsdell [64]. There is no evidence of a median suture and so the ventral plates are of the *Erieopterus*-type. Deep grooves anterior to the ventral plates in FMNH PE 61197 represent the sutures between the plates and the prosomal body wall that have opened up during ecdysis, as seen also in *Moselopterus* Størmer, 1974; these are distinct from the transverse sutures in Stylonurina, which occur on the ventral plates themselves. The chelicerae, which would insert close to the triangular area, are not preserved in any specimens. Elements of all the postoral prosomal appendages (II–VI) are known (Table 2), although all but appendage VI are known only from juveniles. Appendages II–V are largely homonomous in gross form, possessing an anterior spur at the distal margin of each podomere and an armature of paired, ventral, mediodistal cuticular projections. An ancillary socketed moveable spine, also located on the ventral surface of the appendage, is associated with each pair of cuticular projections. The distal margin of each podomere is denticulate. Each successive appendage increases in length, so that the second appendage is the shortest and the fifth the longest; the appendages in the smallest juveniles are also comparatively longer than in more mature individuals (e.g. FMNH PE 6165), with appendage V extending back as far as the sixth tergite in FMNH PE 61197, while in the slightly larger FMNH PE 9236 appendage II does not extend beyond the carapace margin.

Appendage VI is known from five specimens (Figs. 4, 8–11), three of which are juveniles (FMNH PE 61197–61199) with the remaining two, including the holotype, being adults (FMNH PE 28961, PE 61155). The juvenile specimens preserve the proximal podomeres: the coxa (equivalent to the basipod of non-chelicerate arthropods) is expanded, with a length/width ratio of < 2.0, and has its anterior margin expanded to form an ear, although the exact shape of the ear cannot be ascertained. Podomeres VI-2–VI-5 are equal in dimension and unusually short (FMNH PE 61197), with carapace margin extending over podomere VI-6 which is still short but widens distally compared to the preceding podomeres (FMNH PE 61198). The angle between each of these podomeres is consistently 180°. VI-7 is shown in FMNH PE 61198 (Fig. 8C) to be elongated and laterally expanded, although its full dimensions are not known. Podomeres VI-7–VI-9 are, however, known in detail from the adult specimens and are laterally expanded into a swimming paddle. VI-7 is at least equal in length to VI-8 and can be seen projecting out from underneath the carapace margin in the holotype (FMNH PE 28961), the VI-6/VI-7 joint being located underneath the carapace itself. The dorsal margin of VI-7 bore enlarged serrations as hinted at by the proximal region of FMNH PE 28961 (Figs. 2A, 3) that shows a single serration before the dorsal margin is obscured by overhanging sediment and smaller serrations along its distal margin. The modified spine, so-called podomere 7a, is long and triangular, being about half the length of VI-8 and approximately 50% of its width. Although poorly preserved, there is no evidence on serrations along the anterior margin of VI-7a, nor are there serrations along the posterior margins of VI-7 or VI-7a. VI-8 and VI-9 are best preserved in FMNH PE 61155 (Fig. 11A) which consists of both podomeres in isolation. VI-8 is longer than wide and has its dorsal margin ornamented with a series of alternating large and small serrations, although the ventral margin is devoid of ornamentation. Proximally the posterior margin of VI-8 curves anteriorly into the joint with VI-7 so that at the joint the podomere is only half its total width, which is also the width of VI-7. The gap created by this curvature of the ventral margin is covered by VI-7a. VI-9 is deeply set into VI-8, with VI-8 the ventral margin of VI-8 drawn out into an ancillary lobe, although it is unclear if this lobe articulates with the rest of VI-8 or is simply an extension of the podomere. VI-9 is large and expands distally to maintain the outline of the paddle; however, it is not distally drawn out, instead maintaining a roughly diamond-shaped outline. The antero-distal margins of VI-9 are serrated, bearing six serrations that successively decrease in size.

The metastoma is known from two juvenile specimens (FMNH PE 61197, 61199). Both are markedly wider than long, with length/width ratios of 2.0; the FMNH PE 61197 (Fig. 9) metastoma has a length of 4 mm and a width of 2 mm while the metastoma of FMNH PE 61199 (Fig. 10) has a length of 6 mm and a width of 3 mm. The anterior notch is comparatively deep and the anterior shoulders rounded, while the posterior margin of the metastoma is narrow and appears rounded. In shape it is closest to elliptical (*sensu* Tollerton [42]) and is ornamented by minute scales.

Of the 15 specimens revealing dorsal details of the opisthosoma (Table 3), ten pertain to the six anterior tergites, or mesosoma (Figs. 1, 3, 7–10, 12). The second to sixth tergites are broadly similar, each being approximately equal in length and possessing short epimera (FMNH PE 61192). These epimera are much larger in the smallest juveniles, extending out from the anterior tergite margin into a triangular process (FMNH PE 61197). The third tergite is the broadest, measuring 137 mm in the largest specimen (FMNH PE 28961) and only 10 mm in the smallest juvenile (FMNH PE 6165). The first tergite (that of somite VIII) is however shorter than the succeeding tergites in larger individuals and is laterally reduced, lacking epimera and being overlapped by the genal regions of the carapace. The lateral portions of the second tergite also curve anteriorly, so that the carapace and second tergite occlude either side of the reduced first tergite (FMNH PE 6166, PE 28961). This is not the case in juvenile specimens, however, in which the anteriormost tergite is not differentiated and is fully laterally expressed (FMNH PE 6165, PE 9236). The cuticular ornamentation of the mesosomal tergites consists of the same small pustules as on the carapace; however, these are evenly spaced and show no differentiation in orientation. A smooth articulating facet occurs across the anterior margin of each tergite, demarcated by a row of closely spaced pustules at its posterior.

Of the ventral mesosomal structures, both type A and type B genital appendages are known (Table 4); however, the type A morphology is only seen in juvenile specimens while only the adult type B morphology is preserved (Fig. 13). The type A genital operculum is known from two specimens: FMNH PE 61197 (Figs. 2C, 9) and PE 61199 (Figs. 2B, 10). Neither specimen shows the sutures between the anterior, median, and opercular plates, however the right ala of FMNH PE 61199 displays portions of a striate ornament consisting of highly sclerotised semi-lunate scales alongside a dark circular structure that indicate the position of Kiemenplatten (ancillary respiratory organs; see Selden [65] and Manning and Dunlop [66]). In both specimens the centre of the genital operculum is slightly longer than its lateral portions. The type A genital appendage is long and narrow (length/width ratio ranging from 6.0–7.3), extending as far as the sixth opisthosomal segment, and is undivided with paired carinae proximally which then merge into a larger median carina. Deltoid plates are not preserved; however, angular spatulae can be seen flanking the appendage in FMNH PE 61197. The type B operculum, on the other hand, is also known from two specimens (FMNH PE 26079 and PE 61150), both of which are disarticulated and consist of an isolated type B genital appendage with a single associated ala. The most striking feature of the operculum is the striate ornament of highly sclerotized semi-lunate scales that extends laterally across the ala; these are also seen on the genital operculum of the holotype (FMNH PE 28961), although the genital appendage itself is not preserved. The genital operculum bears a clear suture dividing the median and posterior opercular plates (FMNH PE 26079) which each comprise approximately 50% of the length of the operculum. A strip of lightly coloured cuticle anterior to the main operculum near the genital appendage may represent the remnants of the anterior opercular plate. The type B genital appendage itself is oval and short, having a length/width ratio of around 1.6 and only barely projecting beyond the posterior margins of the operculum. The central portion of the appendage appears more highly sclerotised than the lateral regions, while anteriorly it is hastate where it inserts on the operculum. Triangular deltoid plates are faintly preserved either side of the hastate region. An angular spatula is preserved alongside the genital appendage in FMNH PE 26079 (Fig. 13A) and is covered in short, dense setation. The internal margin of the operculum alongside the appendage also bears short bristles (Fig. 14). These bristles can also be seen preserved in the post-genital opercula (Blattfüsse) of FMNH PE 61197 and

PE 61199, where they from a fringe at the distal margins, and in the holotype FMNH PE 28961 (Figs. 1, 3). The Blattfüsse of these specimens are medially fused with the exception of the first (i.e. that of the third opisthosomal tergite) and are ornamented with fine pustules and small scales (Fig. 15). An isolated Blattfüsse of a larger individual (FMNH PE 61171) shows ornamentation similar to that of the genital operculum consisting of striations formed by highly sclerotised semi-lunate scales, suggesting this ornamentation develops in later instars.

Aspects of the metasoma (comprising the six posterior opisthosomal segments) are known from 12 specimens, representing both the juvenile and adult morphology (Figs. 1, 3, 7–10, 16). The first metasomal segment (the seventh tergite) is differentiated from the rest, being of similar breadth to the mesosomal tergites and possessing large angular epimera (FMNH PE 28961). There is a sudden constriction between the seventh and eighth tergites, marking the differentiation into the preabdominal and postabdominal non-functional pseudotagmata (*sensu* Lamsdell [2]), with segments 8 to 12 narrowing evenly thereafter. These segments also bear short epimera (FMNH PE 61163), as in the mesosomal segments, while in the smallest juveniles these epimera are again enlarged, appearing peg-like and projecting from the segments at a consistent 120° angle (FMNH PE 6165, PE 61197, PE 61199). The length of the first five metasomal segments tends not to vary, while the length of segment 12 (the pretelson) is increased. The degree of pretelson elongation is comparatively greater in the juvenile specimens which have a pretelson length/width ratio of 1.7–2.0 compared to that of 1.0–1.2 in larger, adult specimens. The ornament of these metasomal segments is uniform, however, consisting of small pustules that not only decrease in density towards the posterior of the segment but also increase in size and become asymmetrical, eventually forming narrow lunate scales (FMNH PE 61163, 61170). The anterior margin of the segments comprises a smooth articulating facet with a row of dense pustules along its posterior margin (FMNH PE 61180, PE 61185). The largest specimens also possess an ornamentation of six large, acicular scales across their posterior margin (e.g. FMNH PE 28961) that are themselves covered in the regular cuticular ornamentation (FMNH PE 6168). The telson, however, is not preserved in detail on any specimen, being consistently broken off a few millimetres posterior to its articulation with the pretelson in those specimens where it is visible. A long, strait structure preserved alongside the pretelson of FMNH PE 61197 (Fig. 9) probably represents a portion of the disarticulated telson, however this is still only a fragment and no further details of its morphology are available.

Remarks. *Strobilopterus proteus* exhibits clear characteristics supporting its assignment to the genus *Strobilopterus*, specifically the morphology of the carapace and lateral eyes, the pronounced epimera on the seventh opisthosomal tergite, the cuticular ornament consisting of fine pustules with a striate ornament of highly sclerotised scales on the genital operculum and, particularly, the distinctive morphology of appendage VI. Despite the morphological disparity between the smallest juveniles and the adult specimens, both possess the pustular cuticular ornamentation and pronounced epimera on tergite seven. Furthermore, the type A genital appendage and morphology of prosomal appendages II–V, which are known only from juvenile specimens of *Strobilopterus proteus*, correspond well to those structures in *Strobilopterus princetonii*. The type A genital appendage in FMNH PE 61197 and PE 61199 is identical in morphology to that of the *Strobilopterus princetonii* holotype, YPM 204947, while the anterior prosomal limbs in FMNH PE

61197 strongly resemble those of the juvenile *Strobilopterus princetonii* specimen PU 13854 in both armature and ornamentation, the only difference being their comparative increased length in the *Strobilopterus proteus* specimen.

Strobilopterus proteus can be differentiated from other species of *Strobilopterus* by the position of the lateral eyes on the outer limits of the central region, compared to their fully central position in *Strobilopterus princetonii* and *Strobilopterus richardsoni* and their centrimesial position in *Strobilopterus laticeps*. The carapace cuticular ornamentation consisting of elongate pustules angling away from the lateral eyes and curving around the carapace margin is clearly present in *Strobilopterus proteus* and *Strobilopterus richardsoni* but appears to be absent from *Strobilopterus princetonii*; the presence or absence of this ornamention cannot be ascertained in *Strobilopterus laticeps* but, given its presence in *Buffalopterus pustulosus*, it is most likely the plesiomorphic condition for the genus. Another difference between *Strobilopterus proteus* and *Strobilopterus princetonii* is that the latter possesses serrations on podomere VI-7a and has a longitudinally drawn-out VI-9, both of which are lacking in *Strobilopterus proteus*.

Infraorder DIPLOPERCULATA Lamsdell, Hoşgör & Selden, 2013

Superfamily PTERYGOTOIDEA Clarke and Ruedemann, 1912

Family PTERYGOTIDAE Clarke and Ruedemann, 1912

Genus *Jaekelopterus* Waterston, 1964

Type species. *Pterygotus rhenaniae* Jaekel, 1914, by original designation.

Included species. Jaekelopterus howelli (Kjellesvig-Waering and Størmer, 1952b), *Jaekelopterus marylandicus* (Kjellesvig-Waering, 1964).

Stratigraphical range and distribution. Silurian to Lower Devonian (Wenlock to Emsian) of Maryland and Wyoming, USA, and Alken an der Mosel, Germany.

Emended diagnosis. Pterygotidae with triangular telson; principal denticles on cheliceral ramus inclined (emended from Waterston [67]).

Jaekelopterus howelli (Kjellesvig-Waering and Størmer, 1952)

Figures 17–22

p 1934 *Pterygotus princetonii* Ruedemann, pl. 2 [non pp.163–167, pls. 1 & 3 = *Strobilopterus princetonii* (Ruedemann, 1934)]

* 1952 *Pterygotus (Pterygotus) howelli* Kjellesvig-Waering and Størmer, pp. 997–998, fig. 1

1964 Pterygotus (Pterygotus) howelli Kjellesvig-Waering, tables 1 and 2

v. *1986 Pterygotus mcgrewi* Kjellesvig-Waering and Richardson *in* Kjellesvig-Waering, p. 73 [nomen nudum]

2007 Jaekelopterus (?) *howelli* Tetlie, p. 1430

v. 2010 *Jaekelopterus* cf. *howelli* Lamsdell and Legg, pp. 1206–1207, fig. 1

Material. Holotype: YPM 204946 (originally PU 13740), posterior of telson. Additional Material: YPM 204945 (originally PU 13661), FMNH PE 6177.2, PE 6179–6180, PE 7076, PE 9436, PE 9238–9241, PE 9245–9246, PE 26078, PE 60395, PE 61152–61153,

PE 61156, PE 61161, PE 61164–61165, PE 61169, PE 61175–61176, PE 61181–61184, PE 61186, PE 61189–61190, PE 61193, KUMIP 292563.

Horizon and locality. Specimens YPM 204945 and 204946 were collected by Erling Dorf in 1932 from the type section of the Beartooth Butte Formation at Beartooth Butte, Park County, Wyoming, and are Emsian in age. The remaining Field Museum material originates from excavation of the Beartooth Butte Formation section at Cottonwood Canyon, Big Horn County, Wyoming, by Robert H. Denison and Eugene S. Richardson, Jr. in 1962 and is Pragian in age. The University of Kansas specimen is also from the Cottonwood Canyon locality and was collected during fieldwork led by Hans-Peter Schultze in 1983.

Diagnosis. *Jaekelopterus* with serrated telson margin; second intermediate denticle massively elongate in larger instars; type A genital appendage without median distal indentation.

Description. *Jaekelopterus howelli* is known in total from 33 specimens, which reveal details of the chelicera, appendage VI, metastoma, genital appendage, opisthosomal tergites, and pretelson and telson. The material from Beartooth Butte is scant, consisting of only the holotype YPM 204946 (the posteriormost portions of a telson) and YPM 204945 (isolated trunk tergite). The Beartooth Butte material is not restudied here; instead, see Kjellesvig-Waering and Størmer [6] for a full description of these specimens, and Ruedemann [19] for a photograph of the holotype. Similarly, the cheliceral ramus referred to *Jaekelopterus* cf. *howelli* (FMNH PE 6177.2) by Lamsdell and Legg [31] is not refigured and reference should be made to that paper for a full account of the specimen. The ramus is, however, herein assigned to *Jaekelopterus howelli* without reservation and measurements of the specimen are presented alongside those of the newly described chelicerae.

No details of the dorsal carapace or visual structures are preserved. Of the ventral prosomal structures only the chelicerae, coxa, distal paddle of appendage VI, and the metastoma are preserved. The chelicerae are represented in five specimens, including the one described by Lamsdell and Legg [31]; four of these are isolated free rami, while one is a fully articulated chelicera consisting of the fixed and free rami (Fig. 17). Two of the specimens (FMNH PE 26078 and PE 61161) are from smaller, juvenile individuals, (ramus length < 40 mm) while the complete chelicera (FMNH PE 9436), KUMIP 292563 and FMNH PE 6177.2 are from larger, presumably adult, instars (ramus length 90–110 mm) (Table 5). The free ramus is consistent between the juvenile and adult morphologies in possessing a terminal denticle along with three principal and five intermediate denticles. The terminal denticle is oriented almost at a 90° angle to the ramus, while the principal denticles curve posteriorly along their anterior edge so that they are angled away from the terminal denticle. Paired intermediate denticles are located in front of and behind the anterior principal denticle, with a single intermediate denticle at the posterior of the ramus. In the juvenile specimens, the principal and intermediate denticles are more uniform, being of similar length and morphology; however, in the adult specimens, there is strong differentiation between and within the principal and intermediate denticles. The principal denticles are enlarged compared to the intermediate denticles (with the exception of the second intermediate denticle), with the primary denticle being almost twice as broad as either of the other principal denticles. The intermediate denticles are almost invariably half the size of the principal denticles; however, the second intermediate denticle is drastically elongated, being twice the length of any of the principal denticles but retaining the general intermediate denticle width, making it more of a long stiletto in contrast to the broad, slicing blades of the principal denticles or the short teeth of the other intermediate denticles. The only known fixed ramus is from the adult specimen FMNH PE 9436 (Fig. 17A), in which the denticle morphology broadly parallels that of the free ramus, with three principal denticles and five intermediate denticles arrayed in the same configuration and being of similar dimensions (Table 6). The fixed ramus differs primarily in the morphology of the terminal denticle, which is angular in comparison to the rounded terminal denticle of the free ramus but retains its 90° angle in relation to the ramus, and in the form of the second intermediate denticle which is not elongated as in the free ramus. The positioning of the denticles on the fixed ramus would result in overlap of the principal denticles when the chelicera was closed, while the intermediate denticles would align but fall short of occlusion.

The postoral prosomal appendages are known only from a single coxa of appendage IV or V and a number of fragmentary specimens of appendage VI (Fig. 18). The coxa of IV/V (FMNH PE 61181) has a preserved length of 44 mm, with a width of 28 mm at the gnathobase and a preserved width of 29 mm distally. Twenty teeth are preserved at the gnathobase; these have a uniform long, narrow morphology and are somewhat curved. The coxa narrows markedly after the gnathobases before expanding distally. Eleven coxae of appendage VI are preserved, ranging in length from 8–50 mm (Table 7), representing both juvenile and more mature individuals. The morphology of coxa VI differs from that of coxa IV/V in bearing comparatively broader and having larger, more robust teeth, the most anterior of which is enlarged compared to the succeeding teeth. There are also fewer teeth constituting the gnathobase; the most complete large coxa (FMNH PE 61186) preserves 13 teeth while some of the smaller specimens possess only 10–11 teeth, suggesting that teeth continued to develop later in ontogeny. The smallest coxa (FMNH PE 61176) also differs in the morphology of the teeth, which lack the curved anterior margin seen in larger specimens, while the largest coxae show signs of an ancillary tooth forming alongside the anterior enlarged tooth. Distally, appendage VI is only known from a single specimen (FMNH PE 61156) that preserves the two distal podomeres of a swimming paddle (Fig. 19A, B). The specimen has a preserved length of 51 mm and a maximum width of 25 mm and consists of podomere VI-8 with podomere VI-9 roughly preserved. The anterior margin of VI-8 bears uniform, distally angled serrations while VI-9 is set into a notch located towards the posterior side of the distal margin of VI-8.

The metastoma is represented by four specimens (Table 8), two of which (FMNH PE 61169 and PE 61175) only preserve the anterior portion (Fig. 19). The two complete specimens are oval with their widest point being located at the centre, a rounded posterior margin, and shallow anterior notch flanked by rounded shoulders. The notch in all specimens has a median angle of 120–135°, with the exception of FMNH PE 61175 (Fig. 19D), which is laterally compressed. Of the two complete specimens, FMNH PE 61153 (Fig. 19E) is large, with a length of 57 mm, and FMNH PE 61175 would likely have been of a similar size when complete; however, FMNH PE 61169 (Fig. 19C) would easily have been twice as large. The second complete metastoma, FMNH PE 61165 (Fig. 19G), is smaller (length 20 mm), however, and differs from FMNH PE 61153 (Fig. 19E, F) in being comparatively broader, having a length/width ratio of 1.42 compared to the ratio of 1.46 in FMNH PE 61153.

Three specimens preserve details of the opisthosomal tergites (Fig. 20), all identifiable from the typical pterygotid ornamentation of large scales that grade from being broad or chevron-shaped anteriorly to more elongate semilunate and linguoid scales posteriorly that is also seen on the isolated tergite from Beartooth Butte (YPM 204945). One specimen (FMNH PE 7076) is simply a fragment of cuticle, 40 mm long and 63 mm wide; however, FMNH PE 61189 (Fig. 20C) is a complete tergite and FMNH PE 61190 (Fig. 20A) consists of a number of tergites in series with their lateral margins missing. FMNH PE 61190 is 218 mm long in total, with a maximum preserved width of 211 mm, and preserves four tergites with the following length/width measurements (asterisks indicate incomplete measurements): 47 mm/200 mm*, 40 mm/211 mm*, 54 mm/162 mm*, 47 mm/133 mm*. The first tergite shows the smooth articulating facet across its anterior border with a row of flattened scales delineating the posterior extent of the articulation, while all the tergites also display a cuticular thickening at the posterior margin that can also be seen in FMNH PE 7076 (Fig. 20B). The isolated tergite FMNH PE 61189 has a length of 49 mm and a width of 181 mm and shows strong curvature between the axial and pleural regions, with the lateral margins of the tergite appearing swept back, probably a genuine characteristic in life magnified by the flattening of its three-dimensional shape during the taphonomic process. The lateral margins of the tergite are ornamented with a row of rectangular scales that give it a crenate (*sensu* Tollerton [42]) outline.

The only ventral opisthosomal structures preserved are the genital operculum and genital appendage, with material of both the type A and type B morphologies present (Fig. 21). The type A material is known from two specimens, both of which are fragmentary and relatively poorly preserved. FMNH PE 61193 (Fig. 21A) consists of the medial portions of a genital appendage and one ala (*sensu* Wills [68]) and has a preserved length of 144 mm with a preserved width of 158 mm. The ala is broad, curving smoothly away from the genital appendage distally, and is a single plate lacking the suture that marks the median and posterior opercular plates in some taxa. The lateral and distal margins of the ala show a thickening of the cuticle which narrows towards the base of the genital appendage. The anterior portions of the operculum are not preserved, so it is impossible to see whether deltoid plates were present. The ornamentation of the operculum consists of lunate scales that angle distally while following the curvature of the ala margin away from the genital appendage. The genital appendage itself is long and narrow, having a preserved length of 134 mm and a proximal width of 23 mm, and appears to consist of a single ventral lamella lacking segmentation which extends beyond the posterior margin of the operculum, thickening distally (distal width 33 mm). The other type A genital appendage, FMNH PE 61164 (Fig. 21B, C), is the tip of the ventral lamella of an exceptionally large individual, with a width of 46 mm and a preserved length of 54 mm. The lamella is bordered by a doublure distally that is 5 mm thick and narrows as it curves up the lateral margins of the lamella. The distal termination of the lamella is rounded with no evidence of bilobation; however, the lamella clearly begins to narrow anteriorly, indicating it possessed the typical pterygotid spoon-shape. Another structure possessing doublure or cuticle thickening overlies the lamella partway up its preserved length. This structure is better preserved in the counterpart which shows the cuticle to be ornamented with scales and suggests that the structure is in fact a displaced ala from the genital operculum.

The type B genital appendage is also known from two specimens, both of which preserve a single ala of the genital operculum and the genital appendage itself. Both specimens are large, ranging from 81–175 mm in preserved width with a maximum length of 54–79 mm (Table 9). The ornamentation of the operculum consists of broad scales that become more elongate and linguoid towards the segment posterior; there is no differentiation between median and posterior opercular plates, the operculum appearing to be a single plate lacking any joining suture as in the type A individuals. A cuticular thickening or doublure is present around the distal and inner margin of the operculum, especially prominent where the ala is in contact with the genital appendage. The genital operculum also curves distally around the genital appendage, encompassing the broader upper part of the appendage and abutting the distal lamella. The counterpart specimen of FMNH PE 6179 (Fig. 21E) shows clear indication of triangular deltoid plates flanking the anterior portion of the genital appendage, although the sutures are not clear on the part; the other specimen, FMNH PE 6180 (Fig. 21F) also displays deltoid plates but the sutures are only faintly preserved and identifying the plates is made harder as there is no break or differentiation in cuticular ornamentation. The type B genital appendage at first glance appears to be composed of two units, a proximal dorsal segment and an underlying lamella that comprises the main portion of the appendage; however, closer study reveals that these are, in fact, internal structures, and that the true ventral lamella has broken off near its base in both specimens. The ventral lamella is most obvious in FMNH PE 6179

(Fig. 21D) where its remnants are preserved at the anterior of the appendage, preserving a clear suture where it attached to the operculum with the lamella cuticle being the same colour and bearing similar ornamentation as that of the adjoining ala. The lamellar cuticle is then broken away to reveal the internal structures of the appendage, which are preserved at a different level to the surrounding operculum. The most prominent internal structure, the anterior portion with a broad flange-like termination marked by a distinct thickening, represents the internal doublure or cuticular folding of the operculum which is positioned dorsal to the genital appendage but has been superimposed onto the ventral structures due to compression. The other structure represents the dorsal plate of the genital appendage and consists of a broad triangular plate that narrows drastically posterior to the operculum internal doublure before lengthening distally into a spoon-shaped extension with a bilobed termination. The shape of the true ventral lamella (and hence the genital appendage) is, therefore, uncertain; however, FMNH PE 6179 clearly preserves a hastate proximal portion. The shape of the dorsal plate is a reliable proxy for the distal shape of the ventral lamella, however cuticular fragments around the spoon-shaped portion of the plate in FMNH PE 6180 suggests the ventral lamellar did not narrow as suddenly as the dorsal plate does, instead filling the available space between the two ala of the operculum and forming an uneven diamond.

The telson of *Jaekelopterus howelli* is known from two specimens at Cottonwood Canyon which correspond well to the specimen from Beartooth Butte (Fig. 22). FMNH PE 9246 consists of an articulated telson and pretelson with a total preserved length of 89 mm, the pretelson being 37 mm long and 46 mm wide and the telson 52 mm long with a preserved width of 26 mm. The pretelson is shown to have serrated lateral margins and bears a median carina, while the telson broadens distally and has a flattened posterior margin, hinting at a more triangular shape. The lateral and posterior margin of the telson also bears serrations formed by angular scales. The presence or otherwise of a median carina cannot be ascertained; however, a flattened, ridge-like structure that runs down the centre of the telson may be this feature, although it could also be the result of taphonomic cuticular folding. The second Cottonwood Canyon specimen (FMNH PE 61152) is a relatively complete, isolated telson with a total length of 30 mm (24 mm discounting the terminal spine) and a width of 11 mm at its base, expanding to 23 mm distally. The posterior margin of the telson is almost flat, giving it a definite triangular outline. The lateral and posterior margins are ornamented with angular scales resulting in a serrate margin; these scales reduce in size towards the median posterior spine, which is triangular and 6 mm long, being 4 mm wide at its base. The dorsal surface of the specimen is somewhat worn, and although a structure resembling a median carina is present, it is far from definitive. This specimen, in particular, closely resembles the holotype Beartooth Butte telson (YPM 204946), which is far larger then either of the specimens described here, being 128 mm in width. The holotype also possesses a flattened posterior margin with serrated margins caused by the presence of angular scales that decrease in size towards a triangular posterior spine.

Remarks. *Jaekelopterus howelli* shares an almost identical cheliceral denticulation pattern with *Jaekelopterus rhenaniae* along with a flattened posterior margin to the telson, resulting in an overall triangular shape. The Cottonwood Canyon species is clearly differentiated, however, through its possession of a serrated margin to the telson and the massive elongation of the second intermediate denticle in larger instars. The juvenile chelicerae clearly exhibit the *Jaekelopterus* denticulation pattern and show similar trends to those noted in juvenile chelicerae of *Jaekelopterus rhenaniae* by Poschmann and Tetlie [69]: specifically, a more gracile terminal denticle and less differentiation between the principal and intermediate denticles. The form of the FMNH PE 61152 telson (Fig. 22A), with its flattened posterior, triangular outline and serrated margins, confirms that the Cottonwood Canyon species is the same as the Beartooth Butte pterygotid.

Phylogenetic affinities

Analysis of the phylogenetic matrix as detailed in the methods section yielded two most parsimonious trees with a tree length of 314 steps, an ensemble Consistency Index of 0.455, ensemble Retention Index of 0.811, and Rescaled Consistency Index of 0.369, the strict consensus of which is presented here (Fig. 23). The topology is predominantly congruent with that retrieved by Lamsdell *et al*. [47], while the intrarelationships of the expanded Stylonurina is the same as in earlier analyses [48, 49] and the resolution of the pterygotoids is identical to the analysis of Braddy *et al*. [51]. The result differs from previous hypotheses in splitting the two constituent clades of Dolichopteridae, resulting in the family as presently defined being paraphyletic. The more basal clade consists of *Dolichopterus* Hall, 1859, *Ruedemannipterus* Kjellesvig-Waering, 1966 and *Clarkeipterus* Kjellesvig-Waering, 1966 and comprises the pruned Dolichopteridae, defined by the possession of antelaterally (*sensu* Tollerton [42]) positioned lateral eyes, an angle between podomeres VI-3 and VI-4 other than 180°, an angular projection on the anterior of VI-7, an additional moveable lobe on VI-8, and an expanded VI-9. The second clade constitutes the newly named Strobilopteridae and includes *Strobilopterus* and *Buffalopterus*. The clade is defined by the possession of a semicircular carapace, the first podomere of appendage VI that fully projects beyond the carapace margin being VI-6 (as opposed to VI-4 as in most eurypterids), a distinctive carapace ornament consisting of elongate scales that angle away from the lateral eyes, and an ornamentation of angular scales across the posterior of the tergites. Strobilopterids are a node closer to Diploperculata in relation to dolichopterids due to podomere VI-7a being more than half the width of VI-7 and VI-9 being less than 25% the length of VI-8 (although this characteristic is reversed in adult *Strobilopterus proteus* and *Strobilopterus princetonii*, it is present in earlier ontogenetic stages of *Strobilopterus princetonii* [5]).

All three taxa that are included in the phylogeny for the first time resolve within established clades. *Jaekelopterus howelli* is the sister-taxon to *Jaekelopterus rhenaniae*, united by the possession of a triangular shaped laterally expanded telson. *Strobilopterus proteus* is united with *Strobilopterus princetonii* by a suite of characters including the presence of carapace genal facets, a large podomere VI-9 which is greater than a quarter of the length of podomere VI-8, podomere VI-9 bearing serrations, and possibly the presence of an additional moveable lobe on VI-8. This last character is uncertain, however, as it is possible that the lobe in these taxa is a fixed extension of the podomere lacking the articulation reported in *Dolichopterus*. *Strobilopterus laticeps*, on the other hand, resolves at the base of the *Strobilopterus* clade, united by the presence of angular spatulae associated with the type A genital appendage and the occurrence of broad, sclerotised lunate scales in congruence with the striate opercular ornamentation. The position of *Strobilopterus laticeps* at the base of the clade is important because it suggests that characters that previously grouped strobilopterids with dolichopterids, such as an enlarged podomere VI-9 and serrated podomeres on limb VI, are not part of the

Strobilopterus groundplan, and developed convergently in those species that possess them.

Discussion

Ontogeny

Chelicerates, like all arthropods, mature through a series of static stages called instars punctuated by periods of ecdysis followed by immediate rapid growth. Unlike many crustaceans and insects, however, chelicerates are generally considered to be direct developers that do not undergo extreme metamorphosis after hatching, although some pycnogonids gain body segments with associated limbs during postembryonic development [70] while extant xiphosurans hatch without their full compliment of opisthosomal appendages [71]. This form of hemianamorphic direct development may be the plesiomorphic condition for euarthropods; it is also observed in basal crustaceans, basal myriapods, and trilobites [72], and may be present in megacheirans [73]; the hexapodal larval stage of Acari and Ricinulei is, however, likely to be an independently derived condition [74]. True direct development was therefore thought to be a characteristic of arachnids; however, the veracity of larval eurypterids apparently showing a reduced segment count [75] is uncertain [76], and so it is unclear whether true direct development had already been attained by eurypterids.

There have been few studies of ontogeny in eurypterids, the most widely cited being that of Andrews *et al*. [7], which focused on *Eurypterus remipes* DeKay, 1825; Brower and Veinus [77] and Cuggy [8] also conducted studies on *Eurypterus remipes*, with similar work also having been conducted on *Hardieopterus* (?) *myops* (Clarke,

1907) by Brower and Veinus [76] and *Adelophthalmus luceroensis* Kues and Kietzke, 1981 [9]. The lack of work focusing on eurypterid ontogeny beyond these few examples probably stems from an apparent lack of juveniles in the fossil record. The co-occurrence of different instars at the Cottonwood Canyon locality therefore appears to be a rarity; aside from *Eurypterus remipes*, *Hardieopterus* (?) *myops*, *Adelophthalmus luceroensis*, and the newly described species herein, only juveniles of *Hughmilleria shawangunk* Clarke, 1907 [75] and *Drepanopterus pentlandicus* Laurie, 1892 [50] have also been reported. However, the influence of ontogeny has rarely been considered among chelicerate palaeontologists when describing species as has been shown recently in the case of the xiphosurid genus *Euproops* Meek, 1867 [10], and there remains the strong possibility that a number of eurypterid species are oversplit taxonomically. It has already been suggested that *Pterygotus minor* Woodward, 1864 is a juvenile of *Pterygotus anglicus* Agassiz, 1844 (the two species were synonymised by Braddy [78]), and with *Erieopterus brewsteri* Woodward, 1864 also received the same treatment as a juvenile specimen of *Tarsopterella scotica* (Woodward, 1872). Further probable synonyms remain: *Eusacarna obesa* (Woodward, 1868) is almost certainly a juvenile form of '*Carcinosoma*' *scorpioides* (Woodward, 1868) from the same locality, while *Moselopterus elongatus* Størmer, 1974 and *Parahughmilleria major* Størmer, 1973 are likely adults of the co-occurring *Moselopterus ancylotelson* Størmer, 1974 and *Parahughmilleria hefteri* Størmer, 1973 respectively (JCL personal observations). *Stylonurella* (?) *arnoldi* (Ehlers, 1935) also exhibits signs of representing a juvenile morphology, including enlarged lateral eyes. No adult eurypterids are found in immediate association, although the large hardieopterid *Hallipterus excelsior* (Hall, 1884) is known from the same formation and may yet prove to be conspecific, although it is known only from its carapace and any suggested affinities are extremely tentative. Finally, a eurypterid from Siberia recently described as *Stylonuroides orientalis* Shpinev, 2012 appears to exhibit genal spines and large lateral eyes while having a carapace breadth of less than 10 mm; given the juvenile material described here, it seems certain that '*Stylonuroides*' *orientalis* is an early juvenile form, possibly of one of the other eurypterids present in the fauna.

It is clear that there is still much work needed in order to tease apart the ontogenetic pathways exhibited by eurypterids; by fully describing the ontogenetic changes occurring in species where it can be observed it is possible to propose general trends that will aid in the identification of juveniles in other assemblages, along with providing support for or against homology statements of various morphological features between different taxa. Within this framework, the Cottonwood Canyon species provide a unique and critical insight into eurypterid ontogeny, with multiple instars and multiple specimens of each instar preserved in species that are phylogenetically removed from the well-studied *Eurypterus*.

Ontogeny of *Jaekelopterus howelli*

The fragmentary and incomplete nature of the currently available *Jaekelopterus howelli* material makes it impossible to describe the ontogeny of the species in detail, even though more than one instar is present in the assemblage. Nevertheless, bservations are possible on changes in the chelicerae, metastoma and telson. The chelicerae are known from five specimens, four showing the denticles of the free ramus in some detail, of which two are interpreted as adults and two as juveniles. While both juvenile and adult morphologies clearly correlate well with each other, possessing the same number of denticles in the same arrangement, there are also a number of marked differences (Fig. 24). The principal denticles exhibit positive allometry in relation to the intermediate denticles, being two to three and a half times the size of the intermediate denticles in adult specimens in contrast to juveniles, the principal denticles of which are only one and a half times the size of the intermediate denticles. The terminal denticle shows further positive allometry in comparison to the principal denticles, being larger and more robust in the adult specimens; however, the most extreme example of positive allometry occurs in the second intermediate denticle. This denticle is in no way differentiated from the other intermediate denticles in juvenile specimens, yet in adults it is massively elongate, becoming over twice the length of any of the principal denticles. Positive allometry of the denticles in pterygotid chelicerae has been noted before [79]; however, there has been no published in-depth study on the development of the chelicerae through ontogeny. At present, the extreme elongation of the second intermediate denticle appears unique among eurypterids, although positive allometry of the terminal and principal denticles may be commonplace among pterygotids.

The metastoma also appears to alter its dimensions throughout ontogeny. The juvenile metastoma appears comparatively broader than that of the adult, yet the length/width ratios are not drastically different, being 1.43 as opposed to 1.46. A decrease in relative width of the metastoma through ontogeny has, however, been shown in the related species *Jaekelopterus rhenaniae* [69], and the presence of larger, incomplete metastomae at Cottonwood Canyon means that its final length/width ratios may have been higher still. There may be another change occurring, with the angle of the anterior notch becoming more acute in large specimens, decreasing from 135° in the juvenile metastoma to 120° in the largest specimen. This may, however, simply be another expression of the metastoma getting comparatively narrower through ontogeny, as the angle is defined by the breadth of the flanking shoulders. As the metastomal width decreases, so does that of the shoulders, which makes the notch angle more acute. A decrease in the relative width of the metastoma through ontogeny has also been noted in *Stoermeropterus* Lamsdell, 2011 and *Moselopterus* Størmer, 1974 [64] and, while it appears that the metastoma in *Eurypterus* retains its dimensions throughout ontogeny [80], the new evidence here from *Jaekelopterus* and *Strobilopterus* (below) suggests that the stasis in *Eurypterus* may be the exception rather than the rule.

Ontogeny of *Strobilopterus proteus*

Strobilopterus proteus offers a more complete, although still far from comprehensive, record of post-embryonic development in a eurypterid species. The *Strobilopterus* material at Cottonwood Canyon comprises at least 13 individuals, as derived from a simple carapace count, which encompass a broad range of sizes. Recognising moult stages in eurypterids can be difficult, as like in xiphosurans they are not always clearly discontinuous; however, it has been shown that it is possible to separate instars based on carapace dimensions [7]. In an attempt to differentiate instars of *Strobilopterus proteus*, measurements of carapace length were compared to carapace width (Fig. 25A). The resulting scatterplot suggests a number of groupings that may represent instars, although the smallest individuals fall very close together and are difficult to separate. What the plot does indicate, however, is that the carapace dimensions fall fairly neatly along the regression line, suggesting that any difference in relative dimensions is more likely to be due to an ontogenetic trend rather than taphonomic distortion which produces a more random distribution.

In order to further distinguish the possible instar groupings, comparisons of carapace length and width to the carapace length/width ratio were carried out (Figs. 25B,C). These both revealed the same sets of groupings which are interpreted here as being true instars; a possible larval stage (termed α), a juvenile stage (β), a later juvenile or subadult stage (γ) and a final subadult to adult stage (δ). This final stage can potentially be broken down into a further four stages (δ_1– δ_4), all of which maintain the same adult morphology; however, as each potential instar is represented by only a single *Strobilopterus proteus* specimen, their identification at this time is extremely tentative. If these do represent instars, then this likely indicates that *Strobilopterus* attained its full adult morphology before sexual maturity, as neither modern horseshoe crabs [81] nor scorpions [82] moult again once becoming able to reproduce.

Specimens of two other *Strobilopterus* species were also plotted alongside the *Strobilopterus proteus* distribution in order to test if they easily resolve within any of the recognised instars (Table 10). Three specimens were able to be included, each of which fit within a hypothesised moult stage: the holotype of *Strobilopterus richardsoni*, FMNH PE 5120, correlates to the possible δ_1 stage while *Strobilopterus princetonii* specimen YPM 204949 falls within stage δ_2. The juvenile specimen of *Strobilopterus princetonii* recognised by Tetlie [5] (PU 13854) resolves within stage γ. While each species probably has a somewhat different ontogenetic trajectory, it has been shown that the disparity in three different species of *Adelopthalmus* is not great [9] and so the instars of *Strobilopterus proteus* are considered a good proxy for those of the other *Strobilopterus* species. Furthermore, the juvenile *Strobilopterus princetonii* corresponds in morphology to the specimens of *Strobilopterus proteus* assigned to stage γ with which it is associated. Therefore, these specimens may be useful in corroborating ontogenetic trends observed in the *Strobilopterus proteus* material.

Using the available instars, it is possible to identify a number of trends operating during the postembryonic development of *Strobilopterus proteus*. The most striking, when comparing the α material to the δ specimens, is the presence of large epimera in the former (Fig. 26A). The presence of epimera in these specimens is somewhat inconsistent, with different specimens preserving epimera on the mesosoma, metasoma, or both. It has been noted in other eurypterid species, however, that the lateral epimera tend to break off during collection when the rock is split due to them being positioned on a slightly different plane in the sediment to the main body fossil [83], and this is likely also the case here. The epimera are much reduced in the stage β individuals but are still present as small projections on each of the opisthosomal segments (Fig. 26B), while the available γ material shows the epimera to have been completely reduced on at least the second tergite (Fig. 27A). By stage δ, all the epimera on opisthosomal segments 2–4, are wholly reduced with the epimera on segments 5–12 short and mostly vestigial, with the exception of those of the seventh segment which are retained as relatively large, angular projections (Fig. 27B). Evidence from the juvenile material of *Strobilopterus princetonii* that can be assigned to stage γ suggests that segments 2–4 are already devoid of epimera but that the epimera on the remaining segments are more pronounced than those seen in δ [5]. The observation that epimera may reduce in size throughout ontogeny has also been reported in the stylonurine eurypterid *Drepanopterus pentlandicus* [50], and a reported juvenile specimen of *Hardieopterus* (?) *myops* figured by Clarke and Ruedemann [75] (their pl. 51, fig. 6) exhibits long epimera on the opisthosomal segments that are apparently absent from the adult specimens. A distinct phenomenon has been noted in the ontogenetic development of the xiphosuran *Euproops*, in which the juveniles possess long epimera, the bases of which expand dorsoventrally in each instar so as to increase the apparent width of the opisthosoma and reduce the size of the epimeral projections [10]. A similar situation appears to occur in *Strobilopterus proteus*, with each instar getting comparatively broader as the epimera decrease in size, and may be characteristic of the chelicerate ground plan.

The other immediately obvious trend is the relative reduction in length of the prosomal appendages as the animal matured. The prosomal appendages of the α specimens are long and gracile, with elongate podomeres that result in the appendages projecting from beneath the carapace margin more proximally than in adult specimens, at around the fourth podomere; this results in appendage V curving back as far as the fifth opisthosomal segment. The paddle of appendage VI also possesses comparatively longer podomeres, also appearing to project from under the carapace at the fourth podomere, as is usual for Eurypterida. The appendages have begun to shorten in the β individuals, with appendage IV projecting from beneath the carapace margin at the fifth podomere while appendage VI emerges at the sixth podomere. None of the known *Strobilopterus proteus* γ stage specimens preserve the opisthosomal appendages; however, the apparent γ *Strobilopterus princetonii* shows both appendage IV and VI both appearing at the margin of the sixth and seventh podomeres [5]. In stage δ appendage VI has shortened further still, with the paddle projecting from beneath the carapace at the seventh podomere. The degree of relative shortening of appendage length is extreme in *Strobilopterus proteus*; however, the same general trend has been noted in *Eurypterus remipes* [7] and *Drepanopterus pentlandicus* [50], and can also be observed in the material assignable to '*Carcinosoma*' *scorpioides* [84]. A similar trend can also be seen in the modern xiphosuran *Limulus*, the early free-swimming instars of which have comparatively longer prosomal appendages than the benthically inclined adults [81]. *Strobilopterus princetonii* also indicates that the overall morphology of the paddle changed during ontogeny, with juveniles having podomere VI-9 much smaller in relation to VI-8 than in adults, and the serrations on podomeres VI-7 and VI-8 being less developed [5], although this cannot be confirmed in the currently available material of *Strobilopterus proteus*. The '*Carcinosoma*' *scorpiodes* material also shows this trend [84], and this may be linked to earlier eurypterid instars being more active swimmers.

Another major difference in the earliest α instar of *Strobilopterus proteus* is its development of the posterolateral regions of the carapace being drawn out into long genal spines, a plesiomorphic characteristic that is usually considered absent in Sclerophorata (eurypterids and arachnids) but is present in xiphosurans and chasmataspidids [2]. The genal spines have been reduced to small posterolateral extensions of the carapace by stage β, with the first opisthosomal tergite shown to be fully laterally expressed behind the flattened carapace posterior margin. Similar posterolateral extensions are known a number of other eurypterids, including *Eurypterus* [80], *Drepanopterus* [50], and *Adelophthalmus* [85], and it is possible that these, too, represent the vestigial remnants of genal spines. In the γ and δ instars the lateral portions of the second opisthosomal tergite expand anteriorly until they are overlapped by the carapace posterolateral extensions, the lateral portions of the first tergite apparently having been reduced.

The median ocelli are first observable in stage β specimens and are comparatively large and unpaired, set independently into the carapace cuticle without being positioned on a raised ocellar node. The ocelli are comparatively smaller in γ specimens but still situated independently on the carapace; however, in the δ instars the ocelli are now located together on a raised, cardioid ocellar node. The distinctive carapace cuticular ornamentation also changes throughout ontogeny, with the characteristic orientation of scales pointing away from the lateral eyes and angling around the carapace margins first being recognised in the γ specimens and becoming well-developed in δ individuals, the scales being elongated in the direction of orientation. The final definite trend observable during the ontogeny of *Strobilopterus proteus* is one of comparative shortening of the pretelson which is distinctly elongated in α individuals, the length of the segment being approximately twice the width. The length of the pretelson is gradually reduced through the β and γ stages, until the segment is approximately equal in length and width in δ instars.

The earliest ontogenetic stages of *Strobilopterus proteus* also hint at some trends that are not directly observable within the species. The metastoma is comparatively broad in the α specimens, being almost oval-shaped. The adult morphology of the metastoma in *Strobilopterus*, however, appears to be narrow, as suggested by *Strobilopterus princetonii* Tetlie [5]. As noted above, the metastoma of other eurypterid species has been observed to narrow comparatively as the individual matured, and this could explain the more oval morphology of the structure in the early instars of *Strobilopterus proteus*. These instars also preserve long hairs projecting from the margins of the opisthosomal opercula, with shorter hairs fringing the epimera. Hairs observed on disarticulated opercula of larger individuals are much shorter, often not projecting beyond the margin of the operculum, and it seems that these hairs, too, become comparatively reduced throughout development; a similar trend can be seen in early instars of *Limulus* [86]. Unlike *Limulus*, however, the earliest *Strobilopterus* instars possess the full adult complement of opisthosomal segments and appendages, and this suggests that true direct development may be another characteristic linking eurypterids and arachnids.

Finally, it is unusual that the type A genital appendages of the α instars are so large and well-developed, extending as far as they do to the anterior of the seventh opisthosomal segment. This phenomenon has been reported previously in eurypterids, with juveniles having comparatively enlarged genital appendages [78]. Such development of the sexual organs is generally a sign of sexual maturity, and in males of modern *Limulus* this only occurs in the final moult [81]. The holotype specimen of *Strobilopterus princetonii*, however, possesses a type A genital appendage that only extends down to the fourth opisthosomal segment and, while drawing comparisons between species can be difficult, it is possible that the genital appendage also became relatively shorter throughout ontogeny, a trend most unexpected for a sexual organ. Such a trend is, however, apparent in the prosomal appendages, which represent the endopods of biramous limbs in which the exopod has been reduced. The genital appendage has been suggested to comprise the fused endopods of the genital operculum, with the ala being formed from the exopods [87]. The apparently conflicting ontogenetic trend seen in the genital appendage therefore is due to the appendage not being the sexual organ itself but rather an ancillary structure that follows the development trend of the endopods from which it is derived, while the gonopores, which it overlies, may not fully develop until the final moult, as would be expected. This provides support for the hypothesis that the genital appendage represents a modified endopod of a biramous limb and shows the power of utilising ontogenetic pathways and trends in resolving homology statements.

Implications of ontogenetic data for phylogenetic analyses

Prior to this study, the Cottonwood Canyon material now assigned to *Strobilopterus proteus* had been considered to represent a number of distinct species, with notes held alongside the specimens at the Field Museum even suggesting that one of the juvenile individuals (FMNH PE 6165) was an aglaspidid. As mentioned earlier, chelicerate palaeontologists have traditionally neglected to consider ontogeny when describing species, and so it is fully possible that a number of species actually represent juveniles. Given the increasing application of phylogenetic methodology in chelicerate palaeontology it is important to recognise whether including such ontogenetic species in phylogenetic analyses significantly perturbs the resulting topology relative to that retrieved utilising only adult instars. Often the variations in juvenile morphology appear to reflect primitive character states and, theoretically, juveniles coded as part of an analysis could clade with more primitive groups than their adult counterparts due to an assortment of primitive character states that are lost during later ontogeny – essentially a similar problem to that noted for paedomorphic species [88]. This could then cause further problems with the juvenile taxa introducing derived character states into basal clades and increasing attraction of disparate taxa in different clades, reducing branch support and potentially collapsing the inter-clade topology resulting in deep-level polytomies.

In order to test whether this scenario holds true with the current phylogeny different juvenile ontogenetic stages of *Strobilopterus proteus* (α, β) and *Strobilopterus princetonii* (γ) were coded for the analysis and different permutations run with varying combinations of juvenile instars included, the results of which are shown here (Figs. 28, 29). Performing the analysis with the inclusion of all juvenile instars alongside the original species codings results in a loss of resolution within the Strobilopteridae, with *Buffalopterus pustulosus*, *Strobilopterus richardsoni*, *Strobilopterus laticeps* and *Strobilopterus princetonii* γ forming a polytomy alongside a clade comprising *Strobilopterus proteus* and *Strobilopterus princetonii*. The two earliest instars, *Strobilopterus proteus* α and β, form a polytomy below the main strobilopterid clade. The broad-scale topology of the tree remains unchanged, although Dolichopteridae and Strobilopteridae now form a polytomy rather being fully resolved as part of the paraphyletic grade leading to Diploperculata (Fig. 28A). The ensemble Consistency and Retention Indices are both lower than in the original analysis, being 0.388 and 0.778 respectively, resulting in a Rescaled Consistency Index of 0.302. Removing the original species codings so that only the juvenile instars are included in the analysis results in a widespread loss of resolution, with the entirety of the non-diploperculate forming a large polytomy with a number of smaller clades retained within it (Fig. 28B). Furthermore, the monophyly of Eurypterina is also uncertain as moselopterids are resolved in a polytomy with Stylonurina and the other Eurypterina. Further removing *Strobilopterus princetonii* γ, so that only *Strobilopterus proteus* α and β remained, returns much of the tree to its original topology; however, the strobilopterids instead resolve in a basal polytomy as part of the dolichopterid clade (Fig. 28C), a relationship that is still retained when removing *Strobilopterus proteus* β from the analysis. Including solely *Strobilopterus proteus* β or *Strobilopterus princetonii* γ results in both cases in a similar topology to the first analysis, however the strobilopterid clade is completely broken down and forms a polytomy with Dolichopteridae and the remaining Eurypterina (Fig. 28D). Finally, including each of the earlier instars individually into the analysis results in *Strobilopterus proteus* α resolving at the base of Strobilopteridae, with a loss of resolution between *Strobilopterus laticeps* and *Strobilopterus richardsoni* along with Dolichopteridae and Strobilopteridea (Fig. 29A), while *Strobilopterus proteus* β simply polytomies the entirety of Strobilopteridae while retaining them as a definite clade separate to dolichopterids (Fig. 29B). *Strobilopterus princetonii* γ meanwhile simply resolves as the sister to *Strobilopterus proteus* and *Strobilopterus princetonii* without altering the rest of the tree in any manner (Fig. 29C).

These experiments are instructive in a number of ways. First, it appears that the earlier the instar the more basal within the clade it resolves. Second, the inclusion of instars can destabilise the internal topology of the clade resulting in its ground plan becoming uncertain or different altogether, and this can, in turn, result in loss of resolution over the analysis as a whole. Third, it would also seem that including ontogenetic species alongside more mature instars of the same species goes someway to conserving the tree topology. Even then, the presence of juveniles can be detrimental, interfering with metrics for assessing the completeness of the fossil record; if a group was particularly long-ranging a juvenile found in strata towards the end of its range but resolved at the base of the clade would decrease the values of results calculated using the Relative Completeness Index [89], Stratigraphic Consistency Index [90] and Gap Excess Ratio [91] metrics through an inferred ghost range of the juvenile taxon back to the origin of its group. If the juvenile were to clade at the base of a larger clade, thereby possible affecting several nested clades, the influence on these metrics would be magnified. This, then, leads to incorrect assumptions regarding the completeness of the fossil record and the stratigraphical fit of a phylogenetic topology. Therefore, whenever possible, juvenile specimens should be excluded from phylogenies intending to ascertain inter-clade relationships or be used as part of a broader study; however, a broader analysis looking at taxa in a number of different groups both within and without Eurypterida is needed in order to test whether these observation are valid in a broader context or apply solely given the pattern of development seen in *Strobilopterus*. It should also be noted that ontogenetic data should not be completely excluded from phylogenetic analysis, and that when carefully integrated it has the potential to provide new information that may help resolve competing topologies. As an example, the juvenile specimen of *Strobilopterus princetonii* shows that the terminal podomere of the paddle is reduced in earlier instars in contrast to the larger podomere recognised in the adults. This is an important observation as a reduction of the terminal podomere of appendage VI defines part of the eurypterine tree, and the realisation that strobilopterids do in fact exhibit this reduction is one of the reasons that they have been able to be separated from dolichopterids.

Conclusions

The new species of eurypterid described here from Cottonwood Canyon are a new and important source of data on the postembryological development of an extinct arthropod group. Trends that have been inferred in the few previous studies into eurypterid ontogeny [7-9] are corroborated by the new material, while new developmental phenomena are also described for the first time; the ontogeny of eurypterids appears to broadly parallel that of extant and extinct horseshoe crabs [10, 81, 86] with the major exception that eurypterids may hatch with their full complement of opisthosomal segments and appendages, thus being true direct developers like arachnids, and not hemianamorphic direct developers as in xiphosurans. Ontogenetic data can also be important for informing on homology statements and the observed development of the genital appendage in *Strobilopterus proteus* lends support to the hypothesis that the appendage represents a fused opisthosomal endopod [87].

The inclusion of these taxa into a growing phylogenetic framework provides further resolution of the basal Eurypterina. Previous chelicerate workers have commonly neglected to differentiate between juvenile and adult morphologies, and our experiments using the different *Strobilopterus* instars have shown how including juvenile individuals into an otherwise well-resolved phylogeny can destabilise it. It is integral that future workers account for ontogeny when describing species and selecting taxa for phylogenetic analysis; the preliminary results presented here suggest that coding juveniles as operational units within a phylogenetic analysis will produce unresolved, potentially spurious results. Ontogenetic data should not, however, be excluded without thought; rather, serious attempts should be made to successfully integrate ontogenetic data into phylogenetic analyses without resorting to coding instars as evolutionary individuals. The logical alternative of coding ontogenetic data as separate characters is also problematic, however, as heterochronic perturbations in the timing of development and maturities can make the recognition of homologous developmental stages difficult. Recent studies on trilobites have shown that the protaspid larval phase does not encompass the same developmental stages in all trilobites [92], casting doubt on the validity of the standard direct comparison between final stage protaspides. In order to account for these issues, it has been suggested that comparisons be made only when the entire ontogenetic series is taken into account [92], and recent work has attempted to characterise this both descriptively [93] and quantitatively [94] in a number of trilobite species. In many cases however the entire ontogenetic series will not be available for study, and although instars can be recognised as in the current study it is impossible to correlate these stages with certainty between species. It is possible that in these situations ontogenetic data can still be included in phylogenies through careful character selection and definition, however a definitive procedure is at present lacking. If ontogenetic data could successfully be incorporated into phylogenetic analysis it could potentially have great utility in resolving groups that are at least partially defined by characteristics present only in the larval phases, as in some crustaceans [95, 96]. Furthermore, it is only through accurate handling of ontogenetic data that the affinities of taxa derived through paedomorphosis can be accurately determined phylogenetically. This is key to resolving conflicts in groups where paedomorphically derived species a commonplace, such as amphibians, where paedomorphic species have been shown to behave during analysis in a manner similar to the juvenile ontogenetic stages coded herein [88]. While this study does not present a full solution to the issue, it does suggest that incorporating well-constrained ontogenetic characters in a phylogenetic analysis may be a preferable solution to the potentially destabilising influence of juvenile instars being included as distinct operational units.

Author's contributions

JCL conceived of the study, documented the specimens, undertook the morphological interpretations, processed the images, produced the figures, performed the phylogenetic analysis, and wrote the manuscript. PAS participated in the writing of the manuscript. Both authors have read and approved the final manuscript.

Competing interests

The authors declare they have no competing interests.

Acknowledgements

We grateful to Paul Mayer (FMNH), Stephanie Ware (FMNH) and Scott Lidgard (FMNH) who facilitated access to the Field Museum specimens. Sarah Gibson (University of Kansas: KU) and Hans-Peter Schultze (KU) helped confirm the identity of some of the fish material from the locality and provided information of the existence of eurypterid specimens at Kansas. Úna Farrell (KUMIP) was most helpful in locating the Kansas pterygotid specimen. Curtis Congreve (KU) and Amanda Falk (KU) are thanked for numerous discussion and feedback sessions. Elisabeth Vrba (YPM) gave excellent insights into ontogeny and development during her visit to Kansas. David Legg (Imperial

College London) and an anonymous reviewer are thanked for providing comments on the manuscript. JCL acknowledges a Field Museum Visiting Scholarship and an Association for Women Geoscientists Sean S. Thomson Memorial Service Scholarship that provided funding for museum visits.

References

1. Dunlop JA, Selden PA: **The early history and phylogeny of the chelicerates**. In: *Arthropod Relationships.* Edited by Fortey RA, Thoma RH, Systematics Association Special Volume Series 55. London: Chapman & Hall; 1997: 221–235.
2. Lamsdell JC: **Revised systematics of Palaeozoic 'horseshoe crabs' and the myth of monophyletic Xiphosura**. *Zool J of the Linn Soc* 2013, **167**:1–27.
3. Gupta NS, Tetlie OE, Briggs DEG, Pancost RD: **The fossilization of eurypterids: a result of molecular transformation**. *Palaios* 2007, **22**:439–447.
4. Lamsdell JC, Braddy SJ: **Cope's rule and Romer's theory: patterns of diversity and gigantism in eurypterids and Palaeozoic vertebrates**. *Biol Letters* 2010, **6**:265–269.
5. Tetlie OE: **Like father, like son? Not amongst the eurypterids (Chelicerata) from Beartooth Butte, Wyoming**. *J Paleontol* 2007, **81**:1423–1431.
6. Kjellesvig-Waering EN, Størmer L: **A Lower Devonian *Pterygotus* from Wyoming**. *J Paleontol* 1952, **26**:997–998.
7. Andrews HE, Brower JC, Gould SJ, Reyment RA: **Growth and variation in *Eurypterus remipes* DeKay**. *Bull Geol Inst Univ Uppsala* 1974, **4**:81–114.

8. Cuggy MB: **Ontogenetic variation in Silurian eurypterids from Ontario and New York State**. *Can J Earth Sci* 1994, **31**:728–732.

9. Kues BS, Kietzke KK: **A large assemblage of a new eurypterid from the Red Tanks Member, Madera Formation (late Pennsylvanian–early Permian) of New Mexico**. *J Paleontol* 1981, **55**:709–729.

10. Haug C, Van Roy P, Leipner A, Funch P, Rudkin DM, Schöllman L, Haug J T: **A holomorph approach to xiphosuran evolution–a case study on the ontogeny of *Euproops***. *Dev Genes Evol* 2012, **222**:253–268.

11. Legg DA, Garwood RJ, Dunlop JA, Sutton MD: **A taxonomic revision of orthosternous scorpions from the English Coal Measures aided by x-ray micro-tomography (XMT)**. *Palaeontol Electron* 2012, **15**:1–16.

12. Dorf E: **Stratigraphy and paleontology of a new Devonian formation at Beartooth Butte, Wyoming**. *J Geol* 1934, **42**:720–737.

13. Dorf E: **A new occurence of the oldest known terrestrial vegetation, from Beartooth Butte, Wyoming**. *Bot Gaz* 1933, **95**:240–257.

14. Schultes RE, Dorf E: **A sphenopsid from the Lower Devonian of Wyoming**. *Bot Mus Leaf Harv Univ* 1938, **7**:21–34.

15. Bryant WL: **Lower Devonian fishes of Bear Tooth Butte, Wyoming**. *P Am Philos Soc* 1932, **71**:225–254.

16. Bryant WL: **The fish fauna of Beartooth Butte, Wyoming. Part I**. *P Am Philos Soc* 1933, **72**:285–314.

17. Bryant WL: **The fish fauna of Beartooth Butte, Wyoming. Parts II and III**. *P Am Philos Soc* 1934, **73**:127–162.

18. Bryant WL: ***Cryptaspis* and other Lower Devonian fossil fishes from Beartooth Butte, Wyoming**. *P Am Philos Soc* 1935, **75**:111–128.

19. Ruedemann R: **Eurypterids from the Devonian of Beartooth Butte, Wyoming**. *P Am Philos Soc* 1934, **73**:163–167.

20. Ruedemann R: **The eurypterids of Beartooth Butte, Wyoming**. *P Am Philos Soc* 1935, **75**:129–141.

21. Kjellesvig-Waering EN: ***Dorfopterus*, a new genus of Eurypterida from the Devonian of Wyoming**. *J Paleontol* 1955, **29**:696–697.

22. Kjellesvig-Waering EN, Størmer L: **The *Dolichopterus-Strobilopterus* group in the Eurypterida**. *J Paleontol* 1952, **26**:659–661.

23. Caruso JA, Dattola M, Nauman B, Tomescu AMF: **New observations on the early Devonian floras of the Beartooth Butte Formation (Wyoming)**. In: *Geological Society of America Abstracts with Programs*. 2009: 563.

24. Caruso JA, Barrett-Watson H, Tomescus AMF: **New gametophytes from the Early Devonian Beartooth Butte Formation (Wyoming)**. In: *Botanical Society of America Conference Abstracts and Proceedings: 2011*.

25. Tomescu AMF, Steenbock CM, Caruso JA: **Environments of the Early Devonian Beartooth Butte Formation floras (Wyoming) and the evolution of rooting systems**. In: *Botanical Society of America Conference Abstracts and Proceedings: 2010*.

26. Denison RH: ***Cardipeltis*. An Early Devonian agnathan of th Order Heterostraci**. *Fieldiana Geol* 1966, **16**:89–116.

27. Denison RH: **Early Devonian lungfishes from Wyoming, Utah, and Idaho**. *Fieldiana Geol* 1968, **17**:353–413.

28. Denison RH: **Revised classification of Pteraspididae with description of new forms from Wyoming**. *Fieldiana Geol* 1970, **20**:1–41.

29. Dunlop JA, Tetlie OE, Prendini L: **Reinterpretation of the Silurian scorpion *Proscorpius osborni* (Whitfield): integrating data from Palaeozoic and Recent scorpions**. *Palaeontology* 2008, **51**:303–320.

30. Legg DA, Braddy SJ, Dunlop JA: **The supposed scorpion *Acanthoscorpio mucronatus* Kjellesvig-Waering, recognized as a juvenile eurypterid and its implications for scorpion systematics**. In: *Progressive Palaeontology Programme and Abstracts: 2009*. 19.

31. Lamsdell JC, Legg DA: **An isolated pterygotid ramus (Chelicerata: Eurypterida) from the Devonian Beartooth Butte Formation, Wyoming**. *J Paleontol* 2010, **84**:1206–1208.

32. Sandberg CA: **Widespread Beartooth Butte Formation of Early Devonian age in Montana and Wyoming and its paleogeographic significance**. *Am Assoc Petr Geol B* 1961, **45**:1301–1309.

33. Blackstone DL, McGrew PO: **New occurrence of Devonian rocks in north central Wyoming**. In: *Guidebook Fifth Annual Field Conference.* Edited by Richards PW. Billings: Billings Geological Society; 1954: 38–43.

34. Caruso JA, Tomescu AMF: **Microconchid encrusters colonizing land plants: the earliest North American record from the Early Devonian of Wyoming, USA**. *Lethaia* 2012, **45**:490–494.

35. Størmer L: **Arthropods from the Lower Devonian (Lower Emsian) of Alken an der Mosel, Germany. Part 3: Eurypterida, Hughmilleriidae**. *Senck Leth* 1973, **54**:119–205.

36. Størmer L: **Arthropods from the Lower Devonian (Lower Emsian) of Alken an der Mosel, Germany. Part 4: Eurypterida, Drepanopteridae, and other groups**. *Senck Leth* 1974, **54**:359–451.

37. Dunlop JA, Poschmann M, Anderson LI: **On the Emsian (Early Devonian) arthropods of the Rhenish Slate Mountains: 3. The chasmataspidid *Diploaspis***. *Palaeont Z* 2001, **75**:253–269.

38. Elliott DK, Ilyes RR: **Lower Devonian vertebrate biostratigraphy of the western United States**. *Mod Geol* 1996, **20**:253–262.

39. Elliott DK, Johnson HG: **Use of vertebrates to solve biostratigraphic problems: examples from the Lower and Middle Devonian of western North America**. In: *Paleozoic Sequence Stratigraphy, Biostratigraphy, and Biogeography: Studies in Honor of J Granville ("Jess") Geological Society of America Special Paper 321.* Edited by Klapper G, Murphy A, Talent JA; 1997: 179–188.

40. Fiorillo AR: **The ancient environment of the Beartooth Butte Formation (Devonian) in Wyoming and Montana: Combining paleontological inquiry with federal management needs**. *USDA Forest Service Proceedings RMRS-P-15* 2000, **3**:160–167.

41. Braddy SJ: **Eurypterid palaeoecology: palaeobiological, ichnological and comparative evidence for a 'mass–moult–mate' hypothesis**. *Palaeogeogr Palaeocl Palaeoecol* 2001, **172**:115–132.

42. Tollerton Jr VP: **Morphology, taxonomy, and classification of the order Eurypterida Burmeister, 1843**. *J Paleontol* 1989, **63**:642–657.

43. Tetlie OE, Brandt DS, Briggs DEG: **Ecdysis in sea scorpions (Chelicerata: Eurypterida)**. *Palaeogeogr Palaeocl Palaeoecol* 2008, **265**:182–194.

44. Selden PA: **Functional morphology of the prosoma of *Baltoeurypterus tetragonophthalmus* (Fischer) (Chelicerata: Eurypterida)**. *T Roy Soc Edinb Earth Sci* 1981, **72**:9–48.

45. Miller RF: ***Pterygotus anglicus* Agassiz (Chelicerata: Eurypterida) from Atholville, Lower Devonian Campbellton Formation, New Brunswick, Canada**. *Palaeontology* 2007, **50**:981–999.

46. Waterston CD: **Problems of functional morphology and classification in stylonuroid eurypterids (Chelicerata, Merostomata), with observations on the Scottish Silurian Stylonuroidea**. *T Roy Soc Edinb Earth Sci* 1979, **70**:251–322.

47. Lamsdell JC, Hoşgör İ, Selden PA: **A new Ordovician eurypterid (Arthropoda: Chelicerata) from southeast Turkey: Evidence for a cryptic Ordovician record of Eurypterida**. *Gondwana Res* 2013, **23**(1):354–366.

48. Lamsdell JC, Braddy SJ, Tetlie OE: **The systematics and phylogeny of the Stylonurina (Arthropoda: Chelicerata: Eurypterida)**. *J Syst Palaeontol* 2010, **8**:49–61.

49. Lamsdell JC, Braddy SJ, Loeffler EJ, Dineley DL: **Early Devonian stylonurine eurypterids from Arctic Canada**. *Can J Earth Sci* 2010, **47**:1405–1415.

50. Lamsdell JC: **Redescription of *Drepanopterus pentlandicus* Laurie, 1892, the earliest known mycteropoid (Chelicerata: Eurypterida) from the early Silurian (Llandovery) of the Pentland Hills, Scotland**. *Earth Env Sci Trans R Soc Edinb* in press, **103**:1–27.

51. Braddy SJ, Poschmann M, Tetlie OE: **Giant claw reveals the largest ever arthropod**. *Biol Letters* 2008, **4**:106–109.

52. Tetlie OE: **Distribution and dispersal history of Eurypterida (Chelicerata)**. *Palaeogeogr Palaeocl Palaeoecol* 2007, **252**:557–574.

53. Tetlie OE, Cuggy MB: **Phylogeny of the basal swimming eurypterids (Chelicerata; Eurypterida; Eurypterina)**. *J Syst Palaeontol* 2007, **5**:345–356.

54. Goloboff PA, Farris JA, Nixon KC: **TNT, a free program for phylogenetic analysis**. *Cladistics* 2008, **24**:774–786.

55. Farris JS, Albert VA, Källersjö M, Lipscomb D, Kluge AG: **Parsimony jackknifing outperforms neighbor-joining**. *Cladistics* 1996, **12**:99–124.

56. Bremer K: **Branch support and tree stability**. *Cladistics* 1994, **10**:295–304.

57. Maddison WP, Maddison DR: **Mesquite: A modular system for evolutionary analysis. Version 2.73**. In. http://mesquiteproject.org; 2010.

58. Zander RH: **Reliable phylogenetic resolution of morphological data can be better than that of molecular data**. *Taxon* 2003, **52**:109–112.

59. O'Leary MA, Kaufman SG: **MorphoBank 3.0: Web application for morphological phylogenetics and taxonomy**. In. http://www.morphobank.org; 2012.

60. Schmidt F: **Nachtrag zur Monographie der Rußischen Leperditen II. Die Crustaceenfauna der Euryptereenschichten von Rootziküll auf Oesel. Miscellanea silurica III**. *Mem Acad of Sci St Petersbourg* 1883, **31**:28–84.

61. Holm G: **Über die Organisation des *Eurypterus fischeri* Eichw.** *Mem Acad Imp Sci St-Pétersbourg* 1898, **8**:1–57.

62. Størmer L: **Eurypterid remains from the Ludlow zone 9d of Ringerike**. *Nor Geol Tidsskr* 1933, **14**:119–126.

63. Caster KE, Kjellesvig-Waering EN: **Some notes on the genus *Dolichopterus* Hall**. *J Paleontol* 1956, **30**:19–28.

64. Lamsdell JC: **The eurypterid *Stoermeropterus conicus* from the lower Silurian of the Pentland Hills, Scotland**. *Monogr Palaeontogr Soc* 2011, **165**:1–84.

65. Selden PA: **Eurypterid respiration**. *Philos T Roy Soc Lon B* 1985, **309**:219–226.

66. Manning PL, Dunlop JA: **The respiratory organs of eurypterids**. *Palaeontology* 1995, **38**:287–297.

67. Waterston CD: **Observations on pterygotid eurypterids**. *T Roy Soc Edinb Earth Sci* 1964, **66**:9–33.

68. Wills LJ: **A supplement to Gerhard Holm's "Über die Organisation des *Eurypterus fischeri* Eichw." with special reference to the organs of sight, respiration and reproduction.** *Arkiv Zool* 1965, **2**:93–145.

69. Poschmann M, Tetlie OE: **On the Emsian (Lower Devonian) arthropods of the Rhenish Slate Mountains: 5. Rare and poorly known eurypterids from Willwerath, Germany**. *Palaeontol Z* 2006, **80**:325–343.

70. Vilpoux K, Waloszek D: **Larval development and morphogenesis of the sea spider *Pycnogonum litorale* (Ström, 1762) and the tagmosis of the body of Pantopoda**. *Arthropod Struct Dev* 2003, **32**:349–383.

71. Dunlop JA: **The origins of tetrapulmonate book lungs and their significance for chelicerate phylogeny**. In: *Proceedings of the 17th European Colloquium of Arachnology, Edinburgh, 1997.* Edited by Selden PA. Burnham Beeches: The British Arachnological Society; 1998: 9–16.

72. Hughes NC, Minelli A, Fusco G: **The ontogeny of trilobite segmentation: a comparative approach**. *Paleobiology* 2006, **32**:602–627.

73. Waloszek D, Maas A: **The evolutionary history of crustacean segmentation: a fossil-based perspective**. *Evol Dev* 2005, **7**:515–527.

74. Dunlop JA, Alberti G: **The affinities of mites and ticks: a review**. *J Zool Syst Evol Res* 2007, **46**:1–18.

75. Clarke JM, Ruedemann R: **The Eurypterida of New York**. *N Y State Mus Mem* 1912, **14**:1–439.

76. Brower JC, Veinus J: **The statistical zap versus the shotgun approach**. *Math Geol* 1974, **6**:311–332.

77. Brower JC, Veinus J: **Multivariate analysis of allometry using point coordinates**. *J Paleontol* 1978, **52**:1037–1053.

78. Braddy SJ: **Eurypterids from the Early Devonian of the Midland Valley of Scotland**. *Scot J Geol* 2000, **36**:115–122.

79. Barber J: **Ontogeny in pterygotid eurypterids**. University of Bristol; 2004.

80. Tetlie OE: **Two new Silurian species of *Eurypterus* (Chelicerata: Eurypterida) from Norway and Canada and the phylogeny of the genus**. *J Syst Palaeontol* 2006, **4**:397–412.

81. Shuster Jr CN, Sekiguchi K: **Growing up takes about ten years and eighteen stages**. In: *The American horseshoe crab.* Edited by Shuster Jr CN, Barlow RB, Brockmann HJ. Cambridge, Massachusetts: Harvard University Press; 2003: 103–132.

82. Polis GA, Sissom WD: **Life history**. In: *The Biology of Scorpions.* Edited by Polis GA. Stanford, California: Stanford University Press; 1990: 161–223.

83. Poschmann M: **The eurypterid *Adelophthalmus sievertsi* (Chelicerata: Eurypterida) from the Lower Devonian (Emsian) Klerf Formation of Willwerath, Germany**. *Palaeontology* 2006, **49**:67–82.

84. Woodward H: **On some new species of Crustacea from the Upper Silurian rocks of Lanarkshire &c.; and further observations on the structure of *Pterygotus***. *Q J Geol Soci* 1868, **24**:289–296.

85. Tetlie OE, Van Roy P: **A reappraisal of *Eurypterus dumonti* Stainier, 1917 and its position within the Adelophthalmidae Tollerton, 1989**. *Bull Inst R Sci Nat Belg Sci Terre* 2006, **76**:79–90.

86. Farley RD: **Book gill development in embryos and first and second instars of the horseshoe crab *Limulus polyphemus* L. (Chelicerata, Xiphosura)**. *Arthropod Struct Dev* 2010, **39**:369–381.

87. Størmer L: **Merostomata from the Downtonian sandstone of Ringerike, Norway**. *Skr Norske Vidensk-Akad Oslo Mat-Naturvidensk Kl* 1934, **10**:1–125.

88. Weins JJ, Bonett RM, Chippindale PT: **Ontogeny discombobulates phylogeny: Paedomorphosis and higher-level slamander relationships**. *Syst Biol* 2005, **54**:91–110.

89. Benton MJ, Storrs GW: **Testing the quality of the fossil record: Paleontological knowledge is improving**. *Geology* 1994, **22**:111–114.

90. Huelsenbeck JP: **Comparing the stratigraphic record to estimates of phylogeny**. *Paleobiology* 1994, **20**:470–483.

91. Wills MA: **Congruence between phylogeny and stratigraphy: Randomization tests and the Gap Excess Ratio**. *Syst Biol* 1999, **48**:559–580.

92. Park T-Y, Choi DK: **Constraints on using ontogenetic data for trilobite phylogeny**. *Lethaia* 2011, **44**:250–254.

93. Lerosey-Aubril R, Raimund F: **Late ontogeny and hypostomal condition of a new cyrtosymboline trilobite from the Famennian of Morocco**. *Palaeontology* 2006, **49**:1053–1068.

94. Crônier C: **Morphological disparity and developmental patterning: contribution of phacopid trilobites**. *Palaeontology* in press:1–9.

95. Oleson J: **On the ontogeny of the Branchiopoda (Crustacea): contribution of development to phylogeny and classification**. In: *Evolutionary Developmental*

Biology of Crustacea Crustacean Issues 15. Edited by Scholtz G. Lisse, Abingon, Exton (PA), Tokyo: A. A. Balkema Publishers; 2004:217–269.

96. Oleson J: **Larval development of *Lynceus brachyurus* (Crustacea, Branchiopoda, Laevicaudata): redescription of unusual crustacean nauplii, with special attention to the molt between last nauplius and first juvenile**. *J Morphol* 2005, **264**:131–148.

Specimen	***Length***	***Width at base***	***Margin width***	***Eye length***	***Eye width***
FMNH PE 6165	8	9*	0.5	2	0.5
FMNH PE 6166	18	26*	0.5	4	1
FMNH PE 7077	39*	63*	0.5	6	2
FMNH PE 9236	10	15	0.5	3	0.5
FMNH PE 28961	83	133	1	–	–
FMNH PE 61151	56	62*	1	8	2
FMNH PE 61154	45	68*	1	7	2
FMNH PE 61162	35	51*	0.5	5	2
FMNH PE 61166	21	33*	0.5	4	1
FMNH PE 61168	36*	52*	1	6	2
FMNH PE 61179	27	29*	0.5	4	1
FMNH PE 61197	10	12	0.5	–	–
FMNH PE 61198	15	13*	0.5	–	–

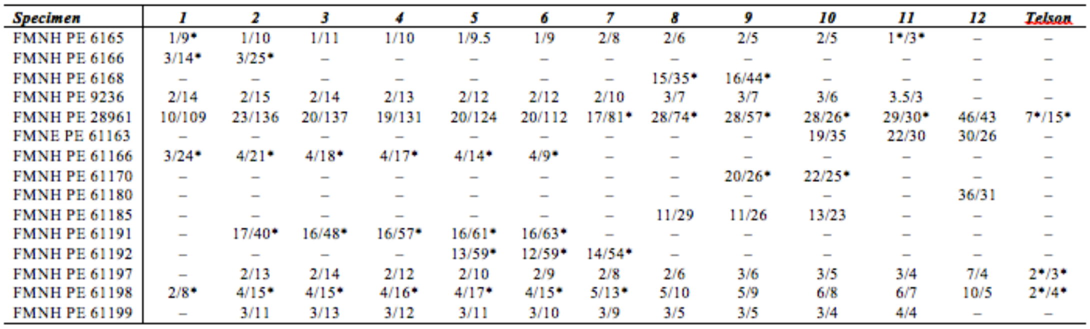
Table 1 - *Strobilopterus proteus* carapace measurements

All measurements in millimetres. Asterisk (*) indicates an incomplete measurement.

Specimen	*Appendage*
FMNH PE 6165	**Appendage III** (podomeres 3 – 5): **3**; 1*/1. **4**; 1/1. **5**; 1*/0.5.
	Appendage IV (podomeres 3 – 6): **3**; 1*/1. **4**; 1/1. **5**; 2/1. **6**; 1*/0.5.
	Appendage V (podomeres 4 – 7): **4**; 2/1.5. **5**; 2/0.5*. **6**; 2/0.5*. **7**; 2/0.5.
FMNH PE 28961	**Appendage VI** (podomeres 7 – 8): **7**; 17*/13. **7a**; 11/8. **8**; 19*/11*.
FMNH PE 61155	**Appendage VI** (podomeres 8 – 9): **7a**; 10/5.**8**; 20/10. **9**; 6/3.
FMNH PE 61197	**Appendage II** (podomeres 5 – 7): **5**; 0.5/0.5. **6**; 0.5/0.5. **7**; 1/0.25.
	Appendage III (podomeres 2 – 5): **2**; 1/1. **3**; 1/1. **4**; 1/1. **5**; 1/1.
	Appendage IV (podomeres 1 – 4): **Coxa**; 2/1. **2**; 1/1. **3**; 1/1. **4**; 0.5*/1.
	Appendage V (podomeres 1 – 9): **Coxa**; 3/1.5. **2**; 1/1.5. **3**; 1/1.5. **4**; 1.5/1. **5**; 3.5/1. **6**; 2.5/1. **7**; 3/1. **8**; 3/1. **9**; 2/0.5.
	Appendage VI (podomeres 1 – 5): **Coxa**; 3/4. **2**; 1/2. **3**; 1/2. **4**; 1/2. **5**; 1/2.
FMNH PE 61198	**Appendage IV** (podomeres 3 – 5): **5**; 4/2. **6**; 3/1.5. **7**; 3/1.
	Appendage VI (podomeres 2 – 7): **2**; 2/4. **3**; 1.5/3. **4**; 2/3. **5**; 2.5/1*. **6**; 2/2*. **7**; 2*/1*.
FMNH PE 61199	**Appendage V** (podomeres 5 – 6): **5**; 3/1. **6**; 2*/1.
	Appendage VI (podomeres 1 – 2): **Coxa**; 3/5. **2**; 1/2.

Table 2 - *Strobilopterus proteus* prosomal appendage measurements

All measurements in millimetres. Asterisk (*) indicates an incomplete measurement.



Specimen	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*Telson*
FMNH PE 6165	1/9*	1/10	1/11	1/10	1/9.5	1/9	2/8	2/6	2/5	2/5	1*/3*	–	–
FMNH PE 6166	3/14*	3/25*	–	–	–	–	–	–	–	–	–	–	–
FMNH PE 6168	–	–	–	–	–	–	–	15/35*	16/44*	–	–	–	–
FMNH PE 9236	2/14	2/15	2/14	2/13	2/12	2/12	2/10	3/7	3/7	3/6	3.5/3	–	–
FMNH PE 28961	10/109	23/136	20/137	19/131	20/124	20/112	17/81*	28/74*	28/57*	28/26*	29/30*	46/43	7*/15*
FMNE PE 61163	–	–	–	–	–	–	–	–	–	19/35	22/30	30/26	–
FMNH PE 61166	3/24*	4/21*	4/18*	4/17*	4/14*	4/9*	–	–	–	–	–	–	–
FMNH PE 61170	–	–	–	–	–	–	–	–	20/26*	22/25*	–	–	–
FMNH PE 61180	–	–	–	–	–	–	–	–	–	–	–	36/31	–
FMNH PE 61185	–	–	–	–	–	–	–	11/29	11/26	13/23	–	–	–
FMNH PE 61191	–	17/40*	16/48*	16/57*	16/61*	16/63*	–	–	–	–	–	–	–
FMNH PE 61192	–	–	–	–	13/59*	12/59*	14/54*	–	–	–	–	–	–
FMNH PE 61197	–	2/13	2/14	2/12	2/10	2/9	2/8	2/6	3/6	3/5	3/4	7/4	2*/3*
FMNH PE 61198	2/8*	4/15*	4/15*	4/16*	4/17*	4/15*	5/13*	5/10	5/9	6/8	6/7	10/5	2*/4*
FMNH PE 61199	–	3/11	3/13	3/12	3/11	3/10	3/9	3/5	3/5	3/4	4/4	–	–

Table 3 - *Strobilopterus proteus* opisthosoma and telson measurements

All measurements in millimetres. Asterisk (*) indicates an incomplete measurement.

Specimen	***Type***	***Length (centre)***	***Length (lateral)***	***Width***	***Appendage Length***	***Appendage Width***
FMNH PE 26079	B	25*	44*	108*	23	14
FMNH PE 61150	B	20*	24*	67*	18*	12
FMNH PE 61197	A	3	2	11.5	9	1.5
FMNH PE 61199	A	3	2	13	11	1.5

Table 4 - *Strobilopterus proteus* genital operculum measurements

All measurements in millimetres. Asterisk (*) indicates an incomplete measurement.

Specimen	*L/W*	*td'*	*d1'*	*d2'*	*d3'*	*i1'*	*i2'*	*i3'*	*i4'*	*i5'*
FMNH	108/24	11*/6*	11/9	10/6	3*/4	2*/2	21/2	5/4	5/4	5/3
PE 9436		–	43	17	62	9	13	30	35	68
FMNH	91/18	10/6	7/5	7/4	2*/3*	2/2	4*/3	2/3	4/4	2/2
PE 6177.2		–	35	14	53	6	9	25	32	69
FMNH	34/8	5/2*	1*/3	3/2	2/1	1/1	1/1	1/1	2/1	1/1
PE 26078		–	14	6	19	3	5	10	12	22
FMNH	24*/7*	–/–	3/3	–/–	3/1	–/–	–/–	2/1*	2/1	–/–
PE 61161		–	–	–	–	–	–	–	–	–
KUMIP	73*/20	–/–	–/–	–/–	–/–	–/–	–/–	–/–	–/–	–/–
292563		–	–	–	–	–	–	–	–	–

Table 5 - *Jaekelopterus howelli* free ramus measurements

All measurements in millimetres. Column headings correspond to the abbreviations listed in figure 23. Values in the second row indicate distance from the terminal denticle. Asterisk (*) indicates an incomplete measurement.

Specimen	***L/W***	***td***	***d1***	***d2***	***d3***	***i1***	***i2***	***i3***	***i4***	***i5***
FMNH PE 9436	110*/32*	10*/7	10/9	8/6	5/4	5/3	3/2	2*/4	4/4	2*/2
		–	46	18	62	8	14	33	38	67

Table 6 - *Jaekelopterus howelli* fixed ramus measurements

All measurements in millimetres. Column headings correspond to the abbreviations listed in figure 23. Values in the second row indicate distance from the terminal denticle. Asterisk (*) indicates an incomplete measurement.

Specimen	***Length***	***Width (gnathobases)***	***Width (distally)***
FMNH PE 9238	32*	20*	30*
FMNH PE 9239	50*	47*	47*
FMNH PE 9240	9*	10*	11*
FMNH PE 9241	24*	37*	11*
FMNH PE 9245	25*	36*	39*
FMNH PE 60395	30*	30*	32*
FMNH PE 61176	9*	6	7*
FMNH PE 61182	37*	43*	52*
FMNH PE 61183	8*	9	9*
FMNH PE 61184	26*	40*	43*
FMNH PE 61186	17*	39*	48*

Table 7 - *Jaekelopterus howelli* coxa measurements

All measurements in millimetres. Asterisk (*) indicates an incomplete measurement.

Specimen	***Length***	***Width (centre)***	***Width (base)***	***Width (shoulders)***	***Notch Depth***	***Notch Angle***
FMNH PE 61153	57	39	16	17	4	130º
FMNH PE 61165	20	14	4	6	1	135º
FMNH PE 61169	45*	60*	–	36	10	120º
FMNH PE 61175	10*	23*	–	10*	5	80º*

Table 8 - *Jaekelopterus howelli* metastoma measurements

All measurements in millimetres. Asterisk (*) indicates an incomplete measurement.

Specimen	***Length (centre)***	***Length (lateral)***	***Width***	***Appendage Length***	***Appendage Width (centre)***	***Appendage Width (distal)***
FMNH PE 6179	54*	–	81*	48	32	11
FMNH PE 6180	79	57	175*	71	45	14

Table 9 - *Jaekelopterus howelli* type B genital operculum measurements

All measurements in millimetres. Asterisk (*) indicates an incomplete measurement.

Specimen	***Length***	***Width***	***L/W ratio***	***Instar***
FMNH PE 6165	8	*10*	0.80	α
FMNH PE 6166	18	*32*	0.56	γ
FMNH PE 9236	10	15	0.67	β
FMNH PE 28961	83	133	0.62	δ_4
FMNH PE 61151	56	*102*	0.55	δ_3
FMNH PE 61154	45	*74*	0.61	δ_2
FMNH PE 61162	35	*59*	0.59	δ_1
FMNH PE 61166	21	*35*	0.60	γ
FMNH PE 61197	10	12	0.83	α
FMNH PE 61198	15	*20*	0.75	β
YPM 204949	38	77	0.49	δ_2
PU 13854	19	37	0.51	γ
FMNH PE 5120	30	53	0.57	δ_1

Table 10 - Carapace data used in instar analysis

Italics represent a carapace width retrieved from extrapolating from half a complete carapace. YPM 204949 and PU 13854 are specimens of *Strobilopterus princetonii*, and FMNH PE 5120 is the holotype of *Strobilopterus richardsoni*. All measurements in millimetres.

Figure 1 - *Strobilopterus proteus*

Holotype FMNH PE 28961. Scale bars = 50 mm.

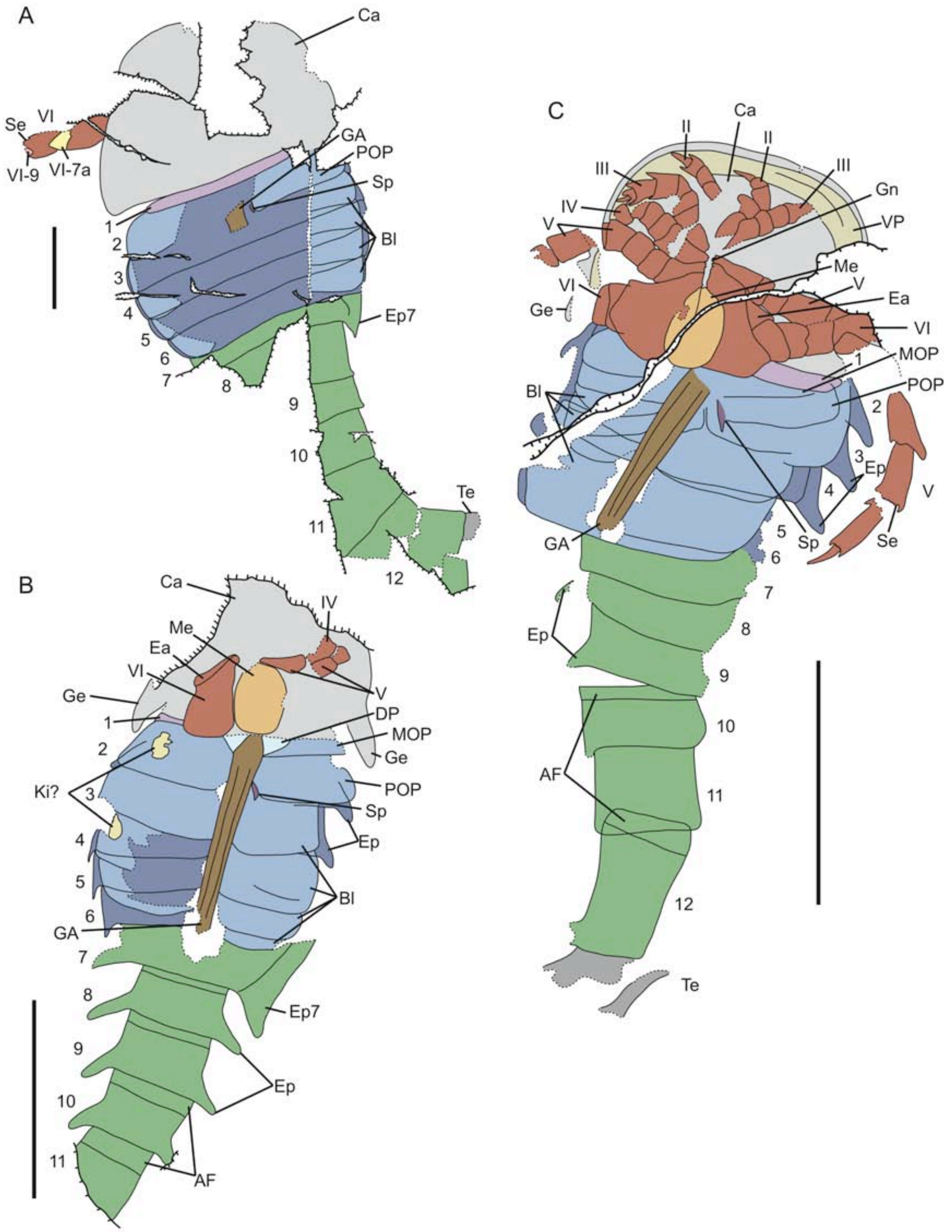


Figure 2 - *Strobilopterus proteus*

Interpretive drawings. A: Holotype, FMNH PE 28961. Scale bar = 50 mm. B: FMNH PE 61197. C: FMNH PE 61166. Scale bars = 10 mm. Specimens are colour-coded, with light grey representing the carapace, red the prosomal appendages, orange the metastoma, blue the mesosoma, green the metasoma, and dark grey the telson. The Blattfüsse are demarcated by a lighter blue, while the first opisthosomal tergite (that of somite VIII) is light purple. The genital appendage is brown, and the spatula dark purple. Dashed lines represent unnatural edges of cuticle preservation, with solid lines delineating the outline of the animal. Thick lines indicated breaks in the matrix. Abbreviations for the labels are as follows: AF, articulating facet; Bl, Blattfüsse; Ca, carapace; DP, deltoid plate; Ea, ear on coxa VI; Ep, epimera; Ep7, enlarged epimeron of opisthosomal segment 7; GA, genital appendage; Ge, carapace genal spine; Gn, gnathobase; Ki?, Kiemenplatten?; Me, metastoma; MOP, median opercular plate; POP, posterior opercular plate; Se, serrations; Sp, spatula; Te, telson; VP, prosomal ventral plates; II–VI, prosomal appendages II–VI; VI-7a, appendage VI podomere 7a; VI-9, appendage VI podomere 9; 1–12, opisthosomal segments 1–12.

Figure 3 - *Strobilopterus proteus*

Counterpart to holotype FMNH PE 28961. Scale bars = 50 mm.

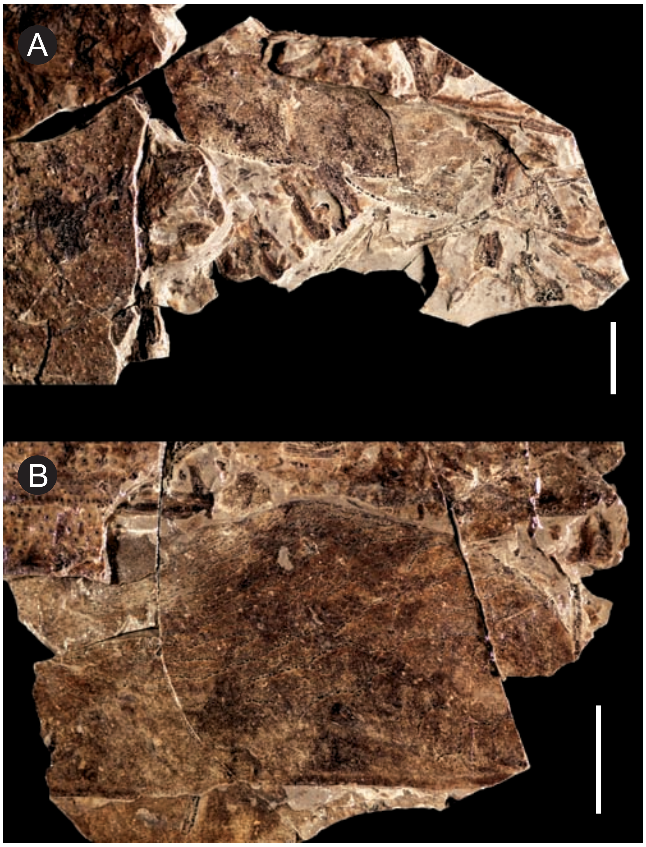


Figure 4 - *Strobilopterus proteus*

Details of counterpart to holotype FMNH PE 28961. A: prosomal appendage VI. B: Blattfüsse. Scale bars = 10 mm.

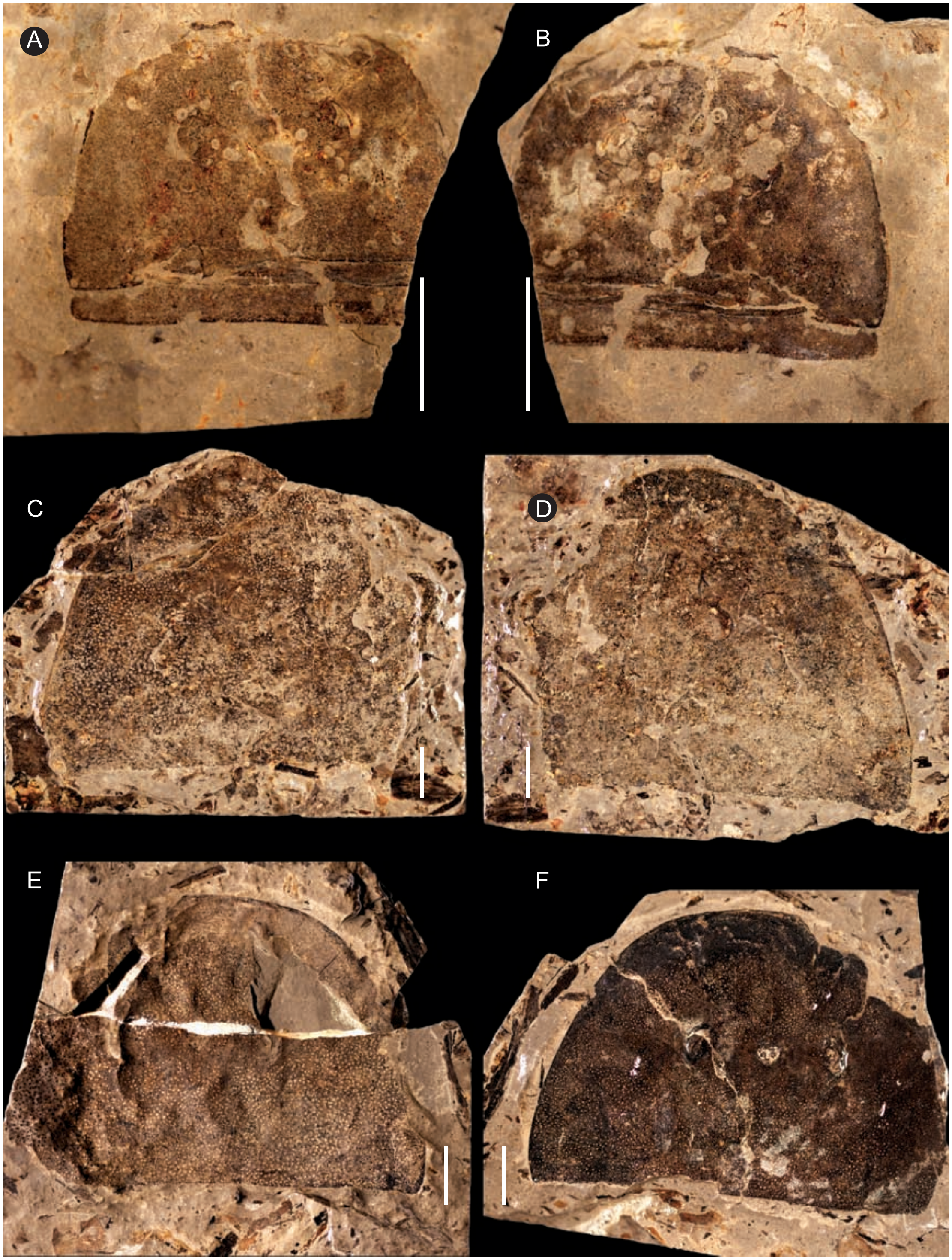

A
B
C
D
E
F

Figure 5 - *Strobilopterus proteus*

Carapace specimens. A: FMNH PE 6166. B: Counterpart to FMNH PE 6166. C: FMNH PE 61151. D: Counterpart to FMNH PE 61151. E: FMNH PE 61154. F: Counterpart to PE 61154. Scale bars = 10 mm.

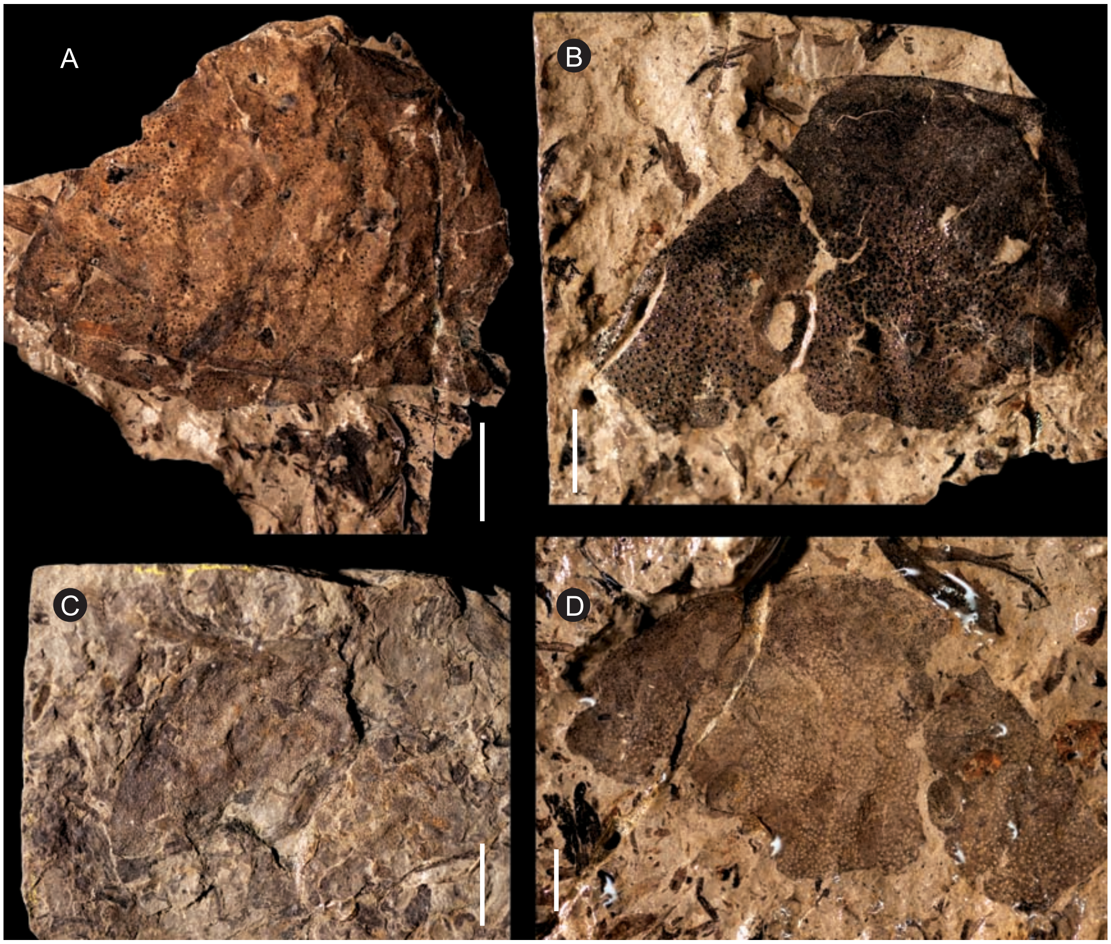


Figure 6 - *Strobilopterus proteus*

Carapace specimens. A: FMNH PE 61162. B: FMNH PE 61168. C: FMNH PE 61179. D: FMNH PE 7077. Scale bars = 10 mm.

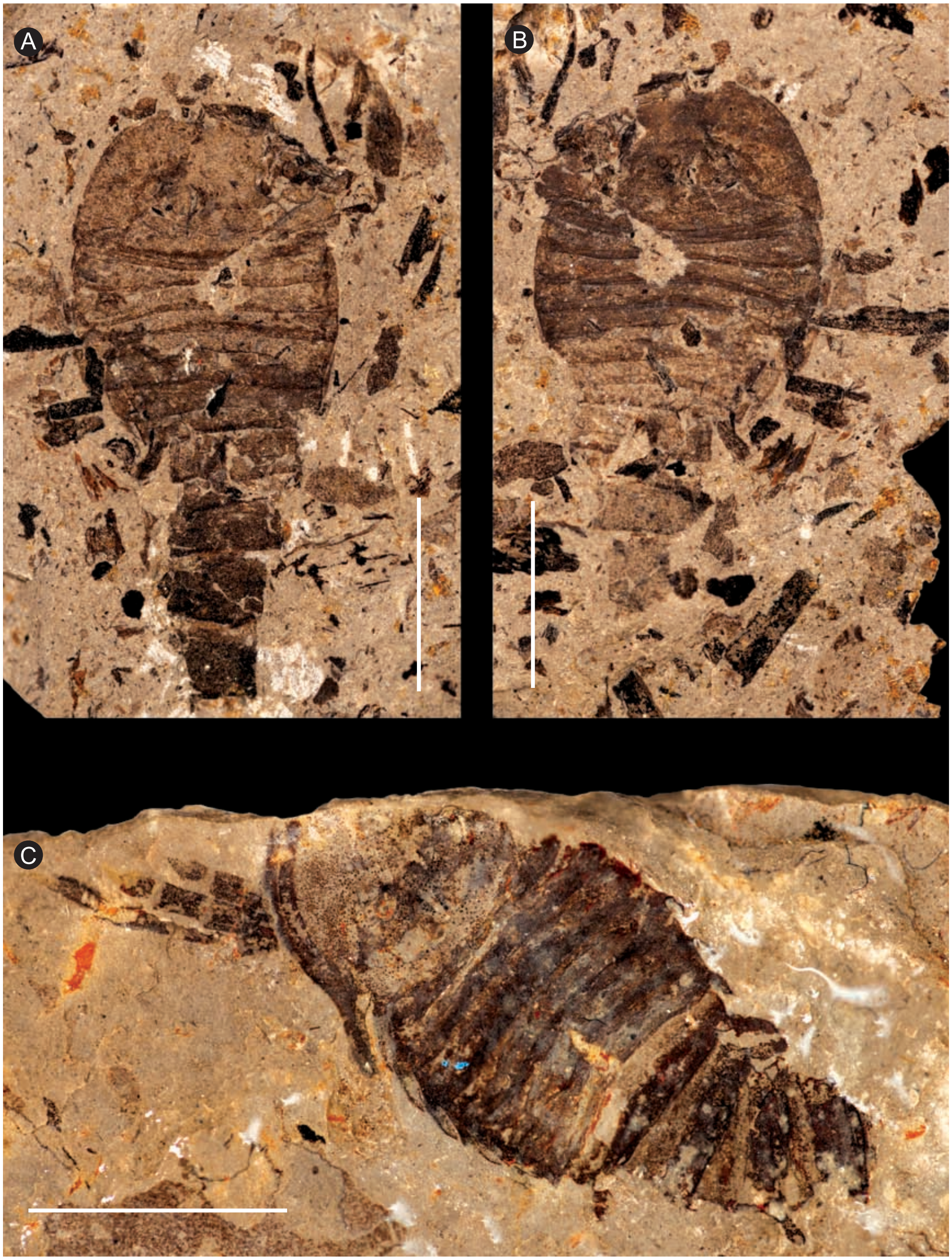

A
B
C

Figure 7 - *Strobilopterus proteus*

Juvenile specimens. A: FMNH PE 9236. B: Counterpart to FMNH PE 9236. C: FMNH PE 6165. Scale bars = 10 mm.

Figure 8 - *Strobilopterus proteus*

Juvenile specimens. A: FMNH PE 61166. B: Counterpart to FMNH PE 61166. C: FMNH PE 61198. D: Partial counterpart to FMNH PE 61198. E: Partial counterpart to FMNH PE 61198. Scale bars = 10 mm.

Figure 9 - ***Strobilopterus proteus***

Juvenile specimens. A: FMNH PE 61197. B: Counterpart to FMNH PE 61197. Scale bars = 10 mm.

Figure 10 - *Strobilopterus proteus*

Juvenile specimens. A: FMNH PE 61199. B: Counterpart to FMNH PE 61199. Scale bars = 10 mm.

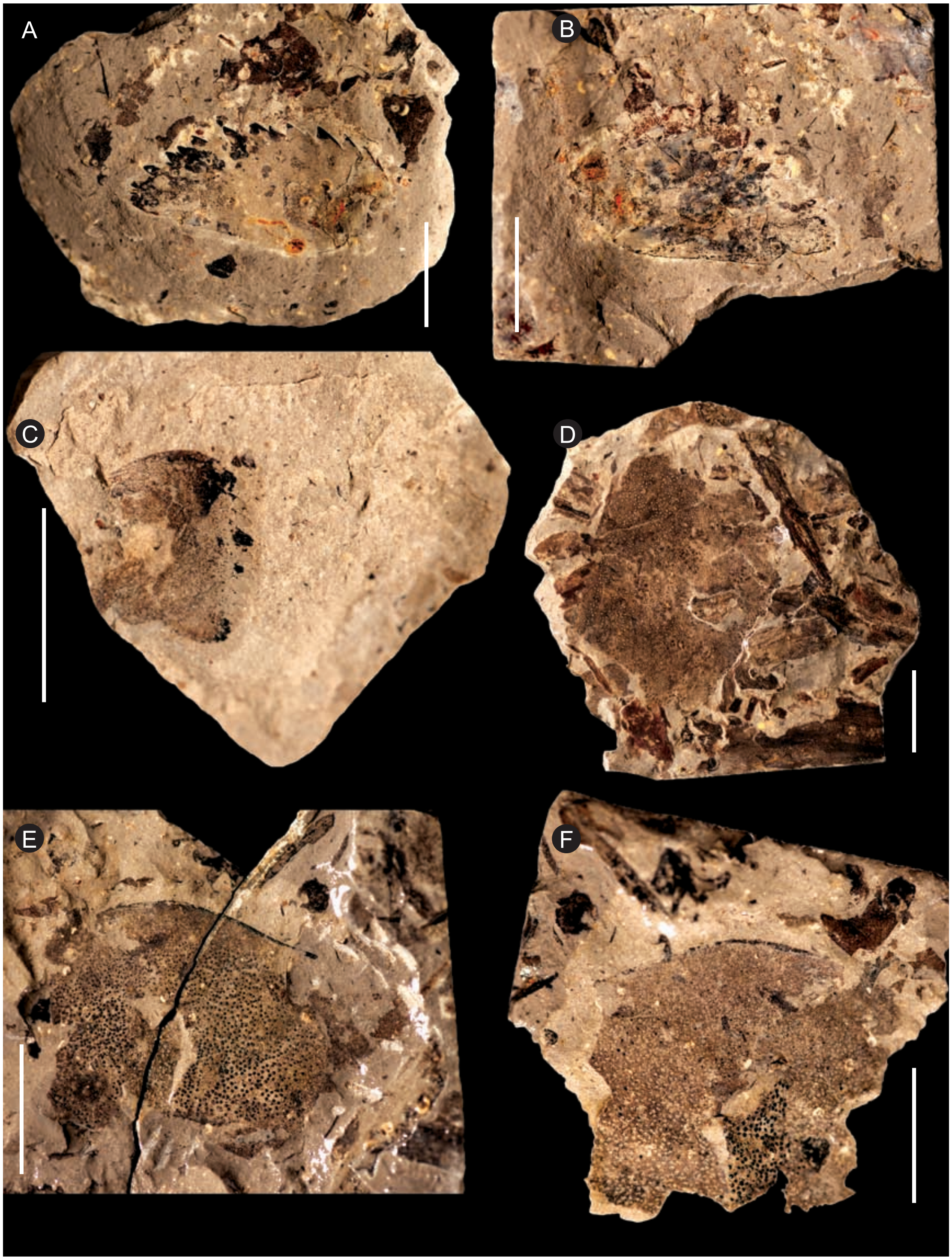


Figure 11 - *Strobilopterus proteus*

Coxa, paddle and carapace cuticle specimens. A: FMNH PE 61155, appendage VI. B: Counterpart to FMNH PE 61155. C: FMNH PE 61172, coxa. D: FMNH PE 61165, carapace cuticle. E: FMNH PE 61187, carapace cuticle showing median ocelli. F: Counterpart to FMNH PE 61187. Scale bars = 10 mm.

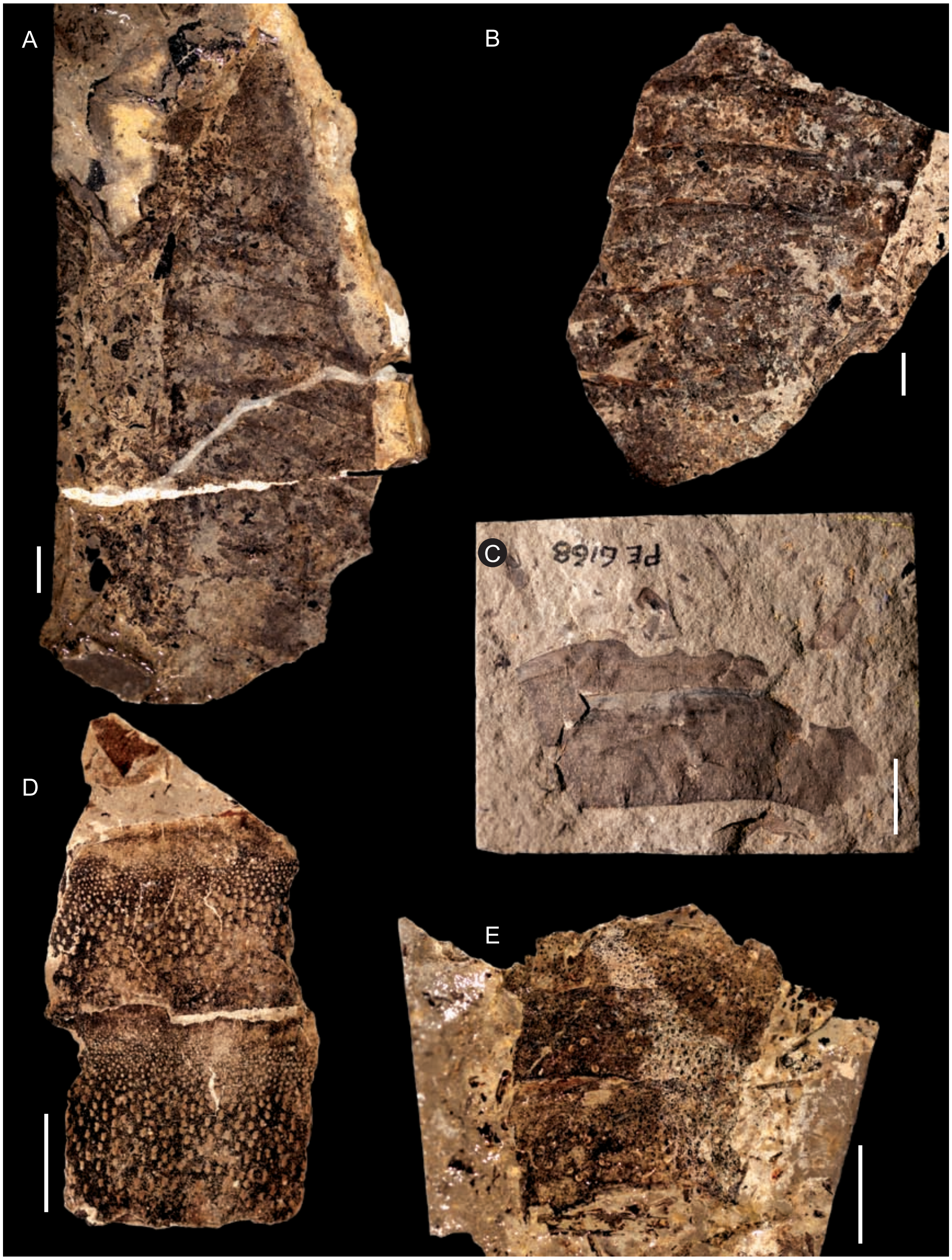


Figure 12 - *Strobilopterus proteus*

Opisthosomal segment specimens. A: FMNH PE 61191. B: FMNH PE 61192. C: FMNH PE 6168. D: FMNH PE 61170. E: FMNH PE 61185. Scale bars = 10 mm.

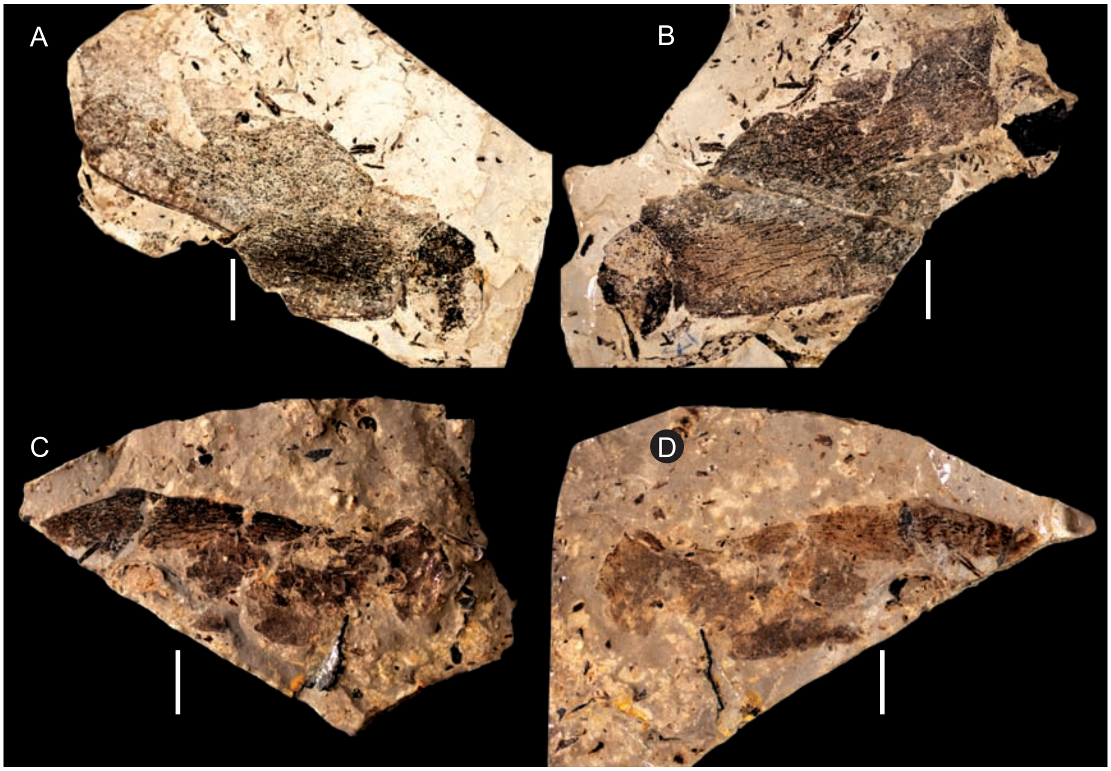


Figure 13 - *Strobilopterus proteus*

Type B genital operculum specimens. A: FMNH PE 26079. B: Counterpart to FMNH PE 26079. C: FMNH PE 61150. D: Counterpart to FMNH PE 61150. Scale bars = 10 mm.

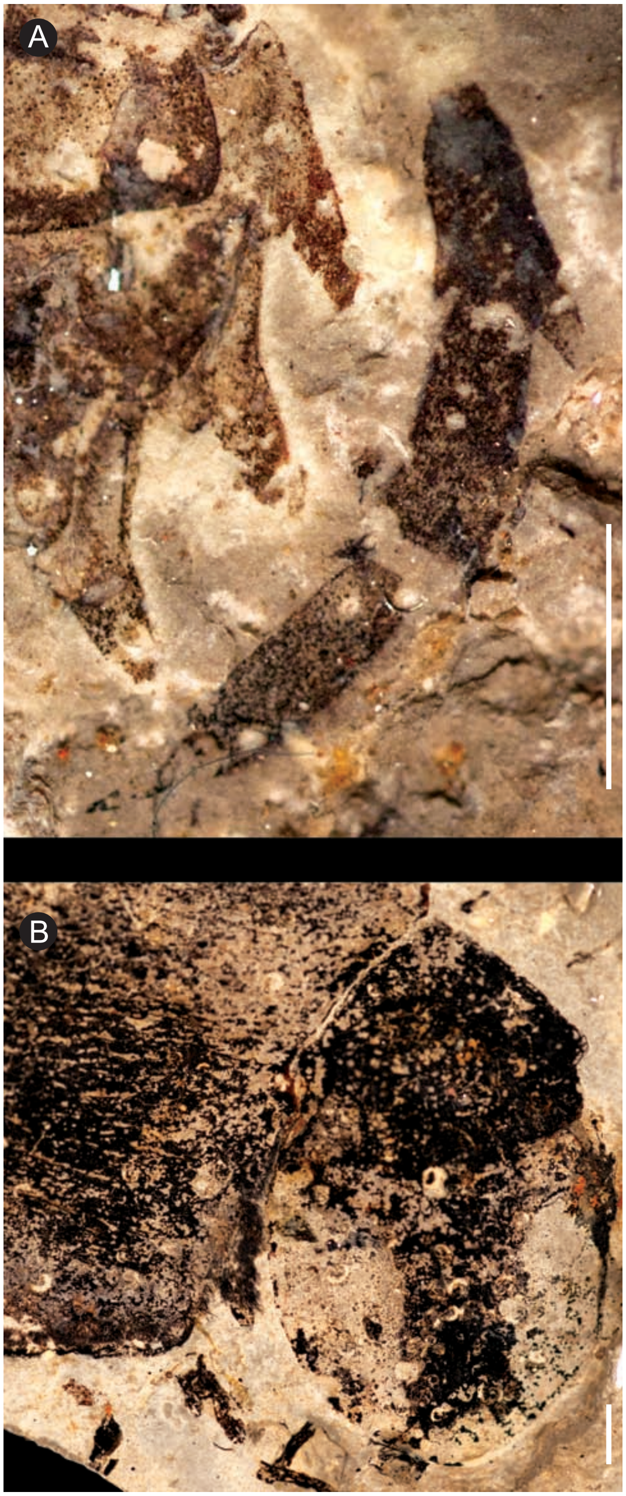

A
B

Figure 14 - *Strobilopterus proteus*

Closeup of opisthosomal appendage setation. A: FMNH PE 61197, ventral view of lateral regions of first three opisthosomal appendages, prosomal appendage V alongside. B: FMNH PE 26079, genital operculum. Scale bars = 2 mm.

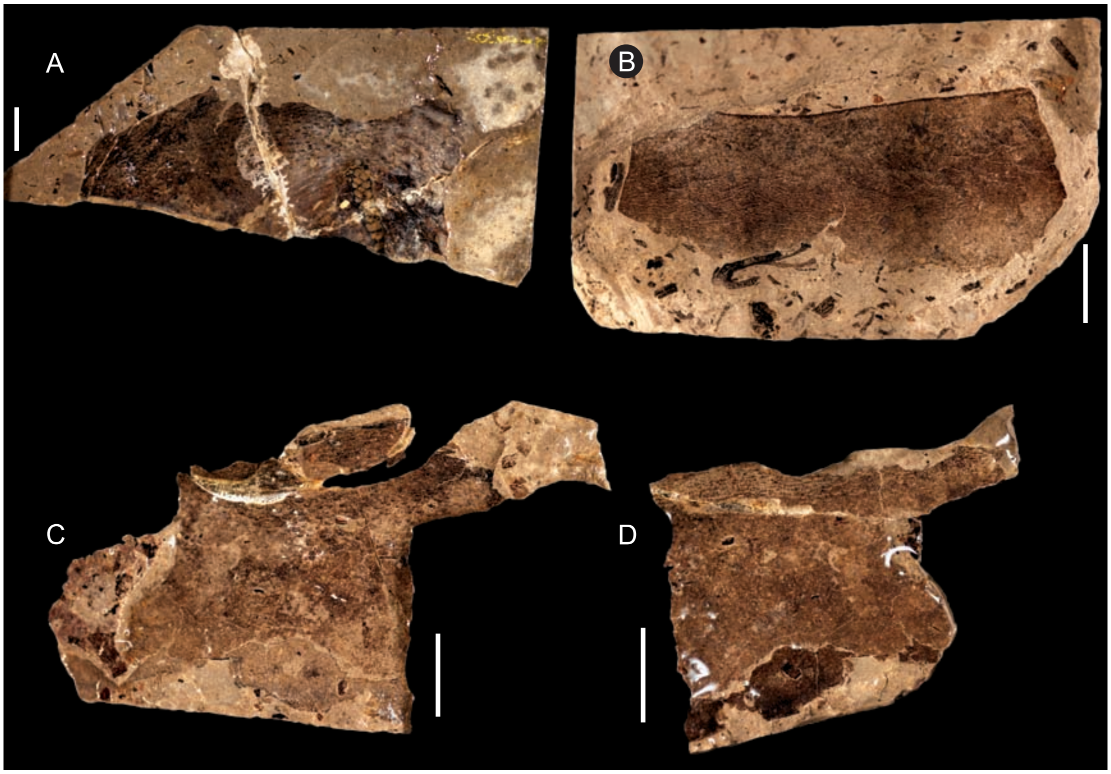


Figure 15 - *Strobilopterus proteus*

Cuticular specimens. A: FMNH PE 6167, possible genital operculum. B: FMNH PE 61171, Blattfüsse. C: FMNH PE 9242, possible Blattfüsse. D: Counterpart to FMNH PE 9242. Scale bars = 10 mm.

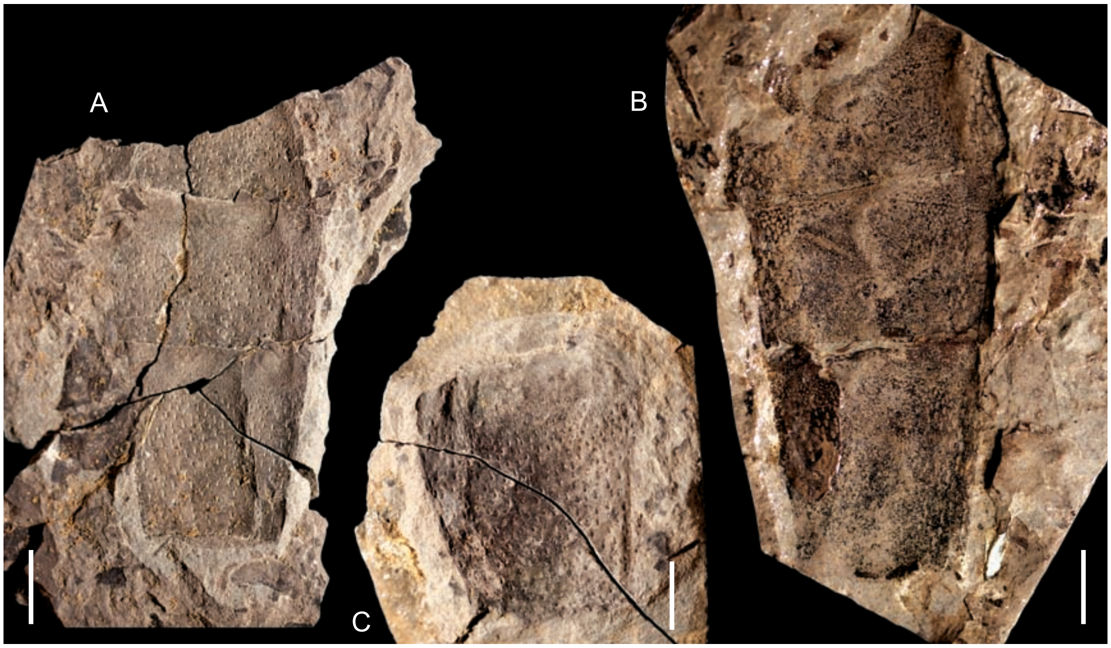


Figure 16 - *Strobilopterus proteus*

Metasomal segment specimens. A: FMNH PE 61163. B: Counterpart to FMNH PE 61163. C: FMNH PE 61180. Scale bars = 10 mm.

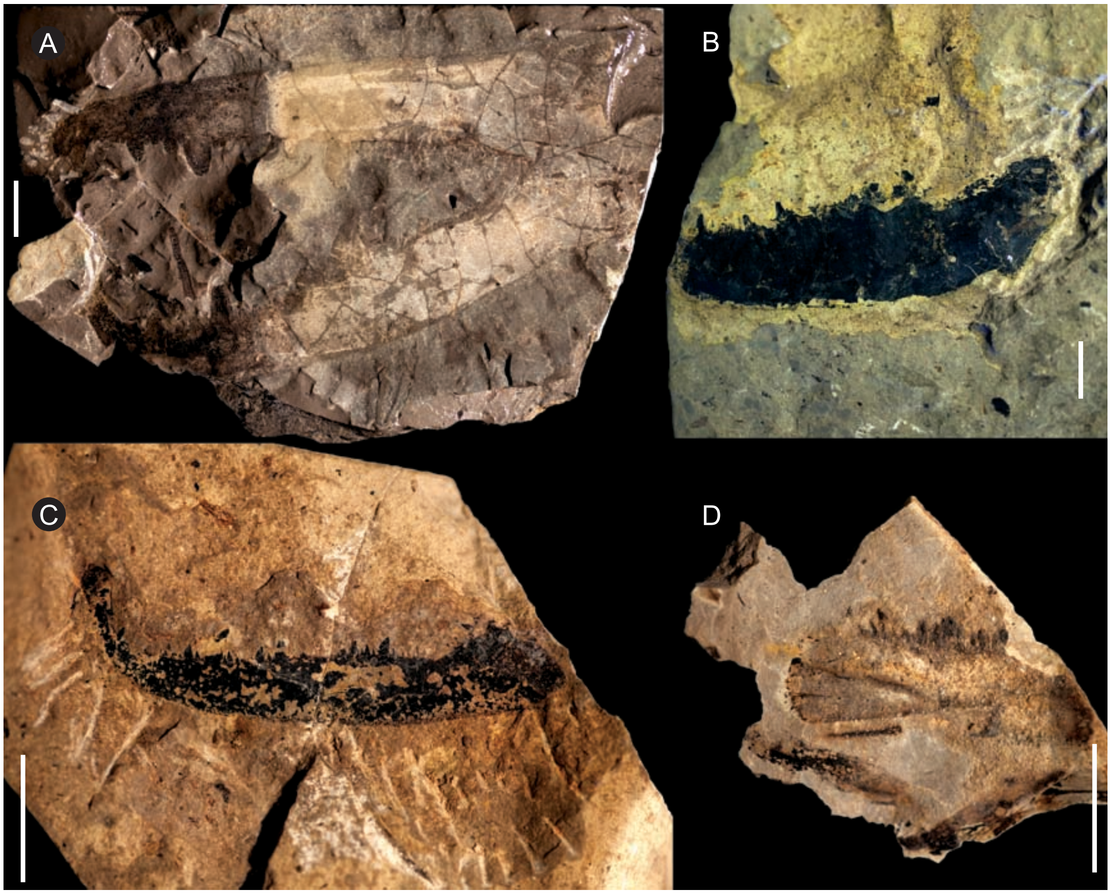


Figure 17 - *Jaekelopterus howelli*

Chelicera specimens. A: FMNH PE 9436. B: KUMIP 292563. C: FMNH PE 26078. D: FMNH PE 61161. Scale bars = 10 mm.

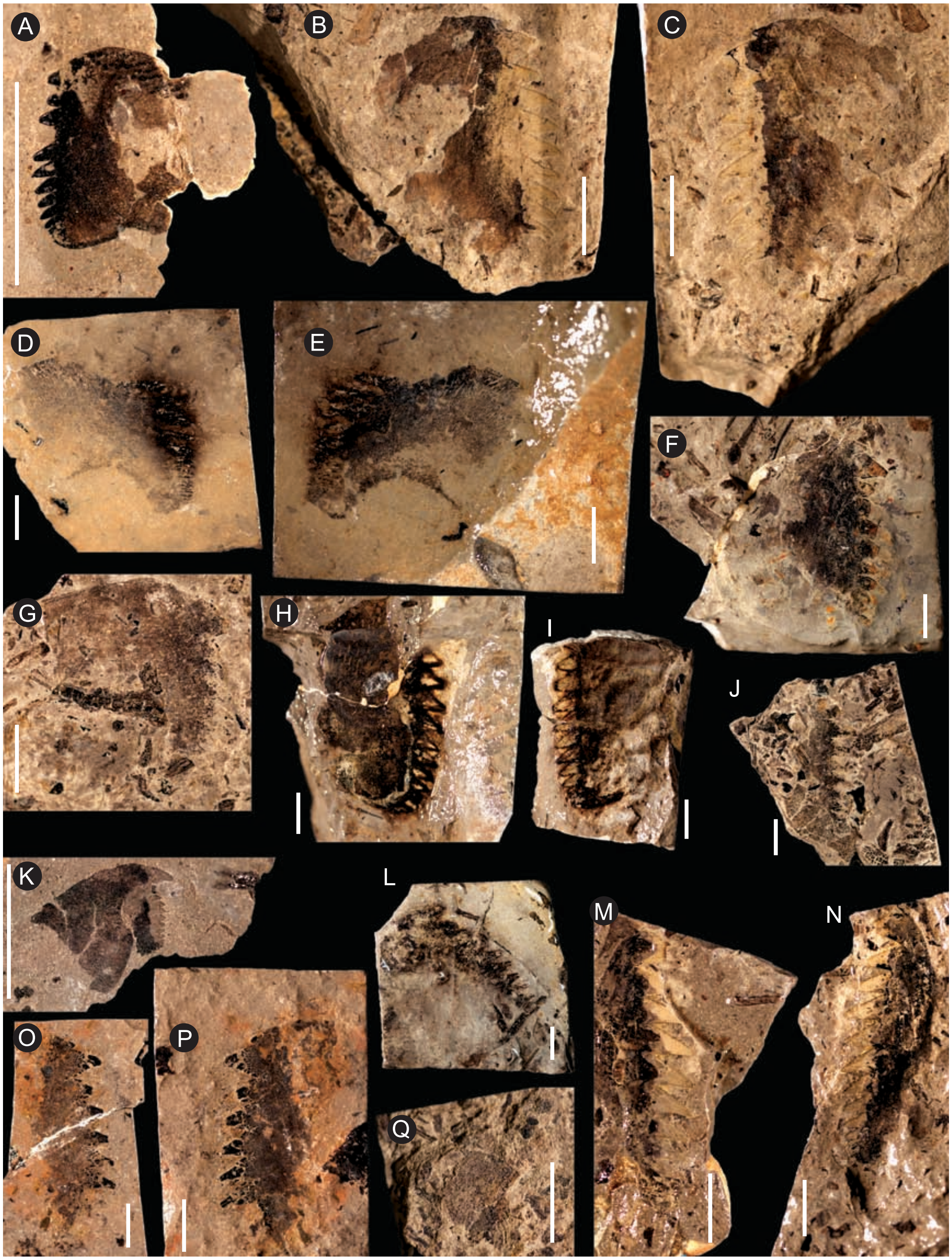


Figure 18 - *Jaekelopterus howelli*

Coxa specimens. A: FMNH PE 61183. B: FMNH PE 60395. C: Counterpart to FMNH PE 60395. D: FMNH PE 61181. E: Counterpart to FMNH PE 61181. F: FMNH PE 9245.

G: FMNH PE 9238. H: FMNH PE 61182. I: Counterpart to FMNH PE 61182. J: FMNH PE 9241. K: FMNH PE 61176. L: FMNH PE 9239. M: FMNH PE 61186. N: Counterpart to FMNH PE 61186. O: FMNH PE 61184. P: Counterpart to FMNH PE 61184. Q: FMNH PE 9240. Scale bars = 10 mm.

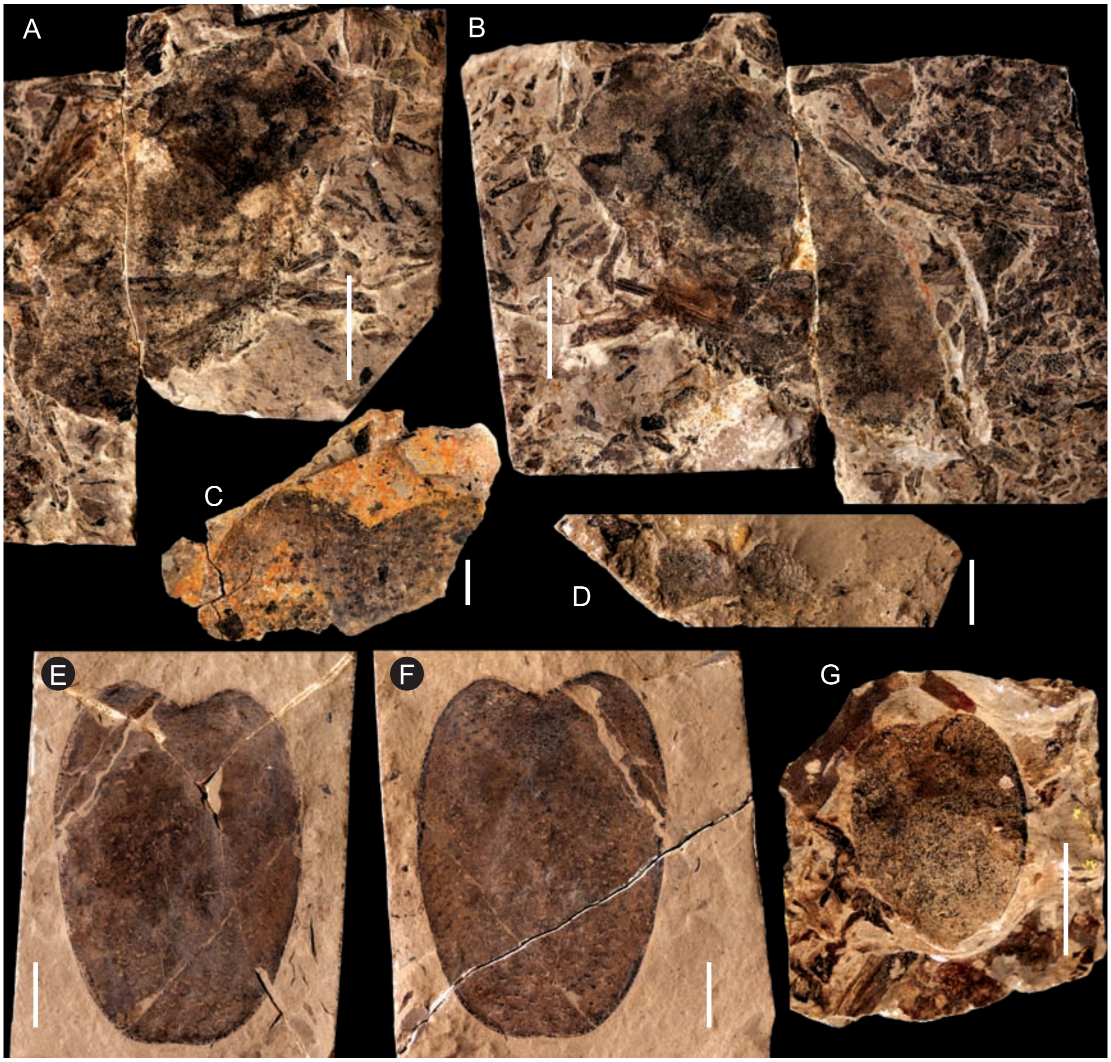


Figure 19 - ***Jaekelopterus howelli***

Appendage VI and metastoma specimens. A: FMNH PE 61156, paddle. B: Counterpart to FMNH PE 61156. C: FMNH PE 61169, anterior of metastoma. D: FMNH PE 61175, anterior of metastoma. E: FMNH PE 61153, metastoma. F: Counterpart to FMNH PE 61153. G: FMNH PE 61165, metastoma. Scale bars = 10 mm.

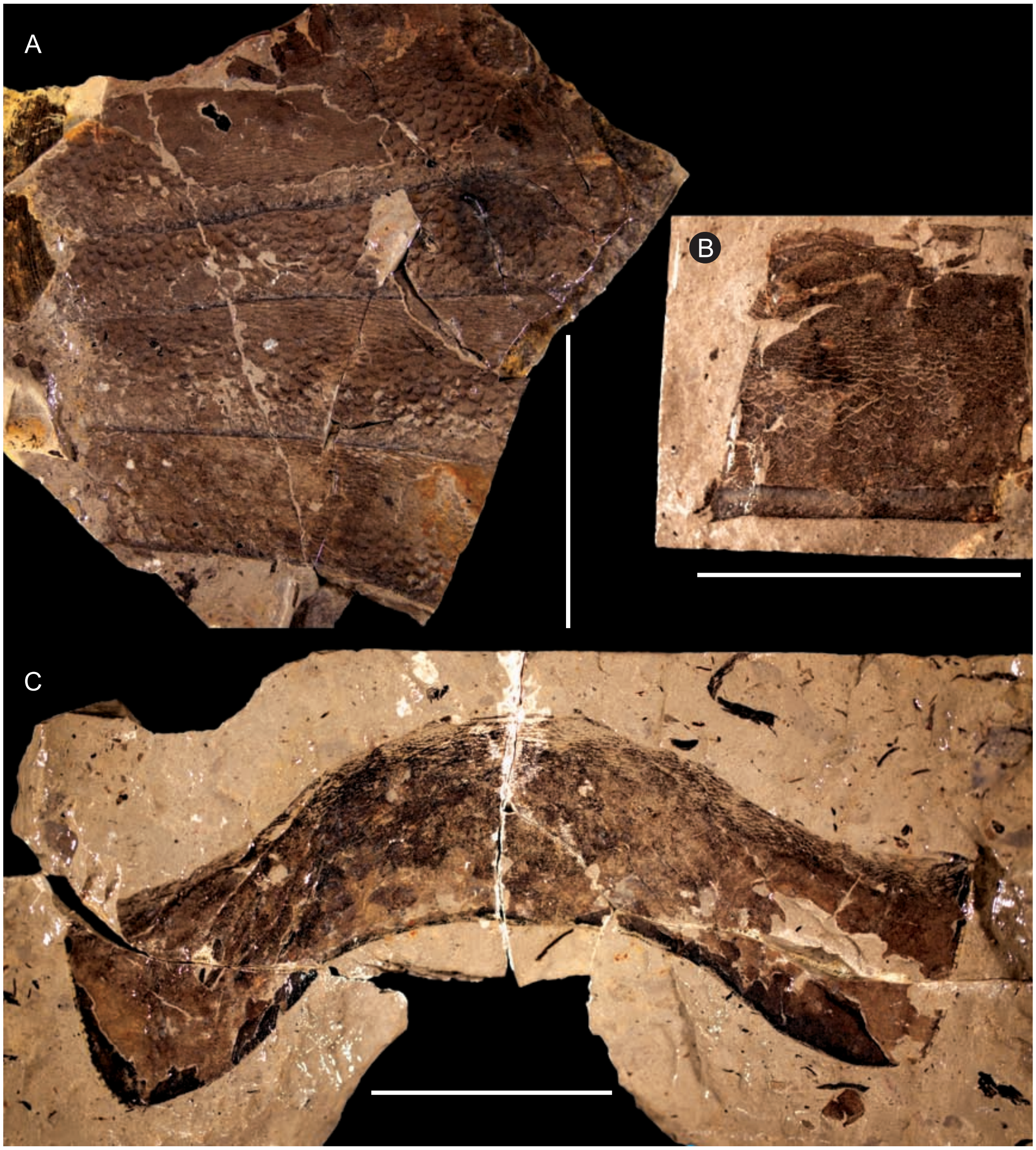


Figure 20 - *Jaekelopterus howelli*

Opisthosomal segment specimens. A: FMNH PE 61190. B: FMNH PE 7076. C: FMNH PE 61189. Scale bars = 50 mm.

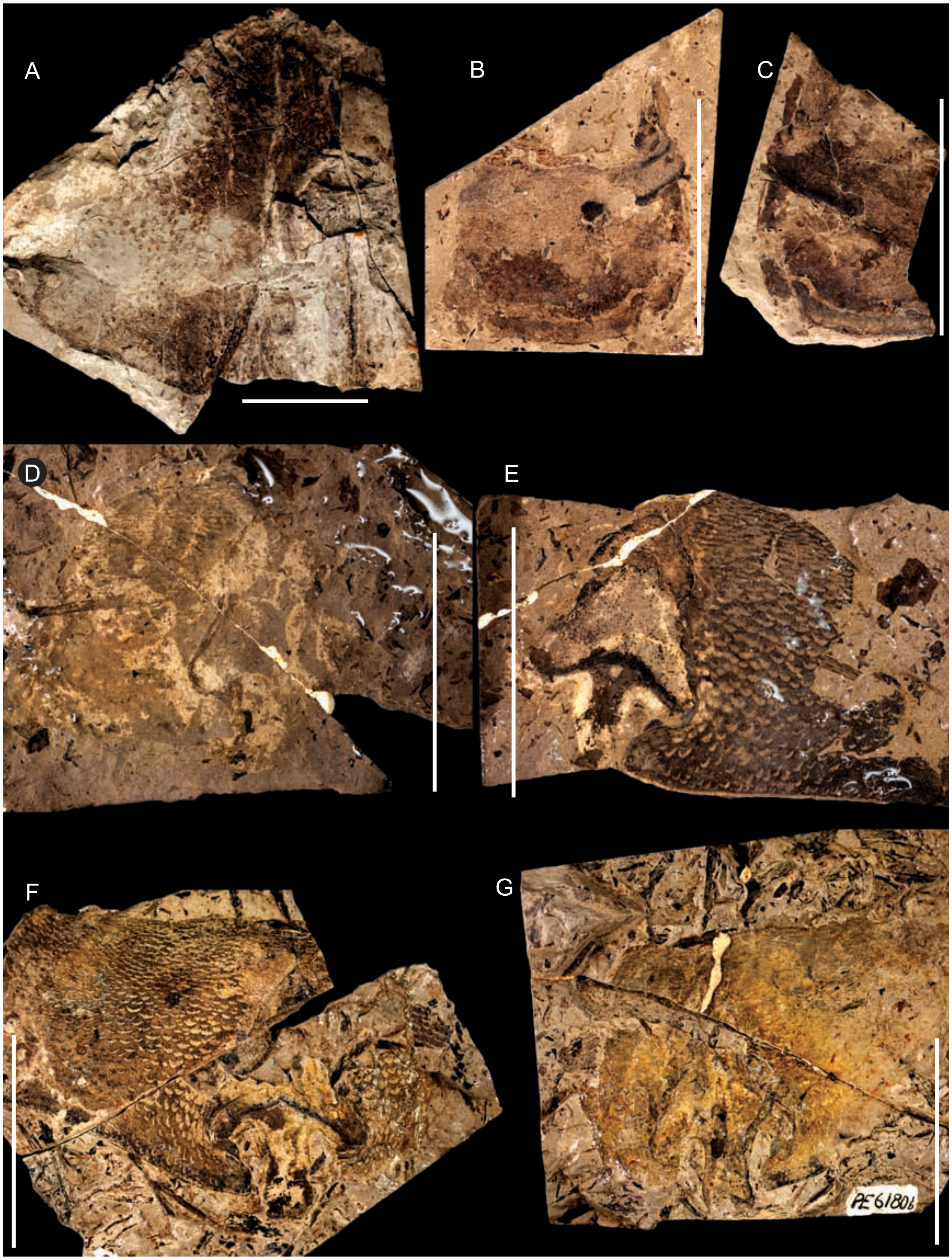


Figure 21 - ***Jaekelopterus howelli***

Genital operculum specimens. A: FMNH PE 61193, type A operculum. B: FMNH PE 61164, tip of type A appendage. C: Counterpart to FMNH PE 61164. D: PE 6179, type B operculum. E: Counterpart to FMNH PE 6179. F: FMNH PE 6180, type B operculum. G: Counterpart to FMNH PE 6180. Scale bars = 50 mm.

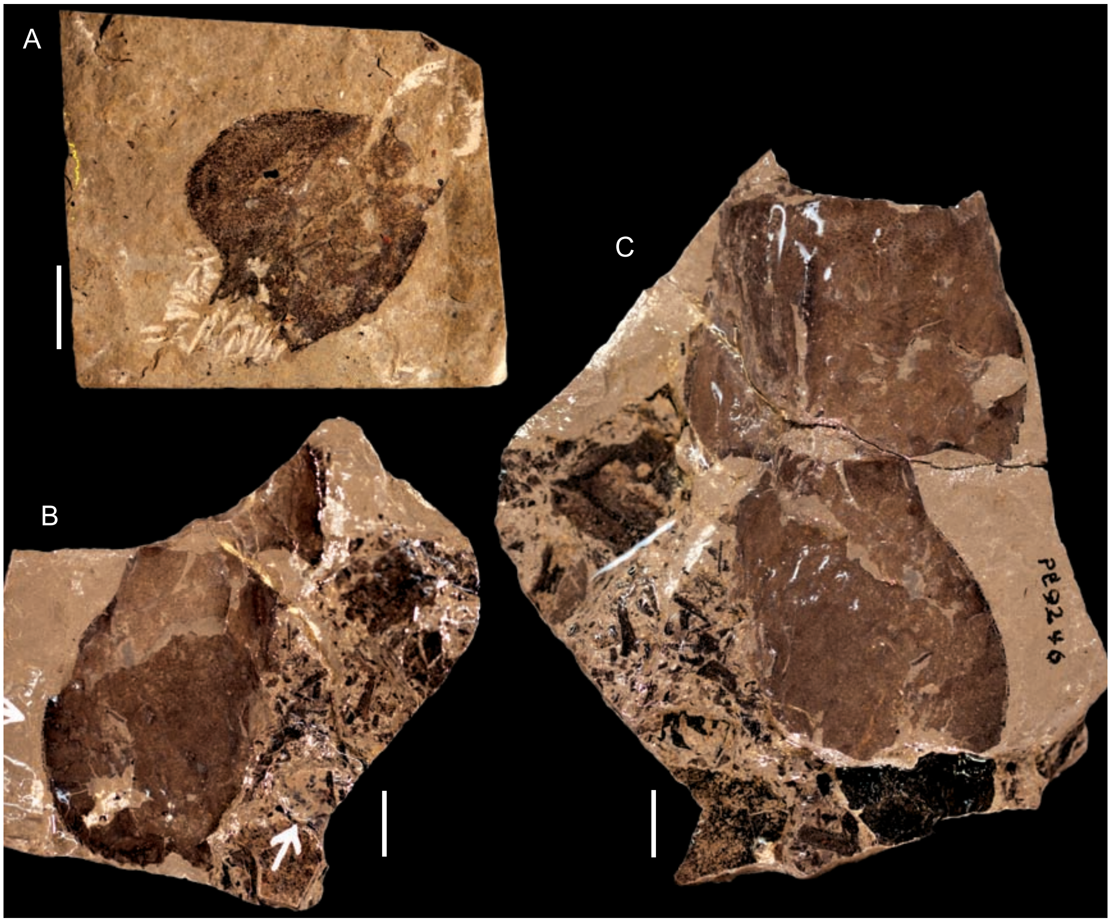


Figure 22 - *Jaekelopterus howelli*

Telson specimens. A: FMNH PE 61152. B: FMNH PE 9246. C: Counterpart to FMNH PE 9246. Scale bars = 10 mm.

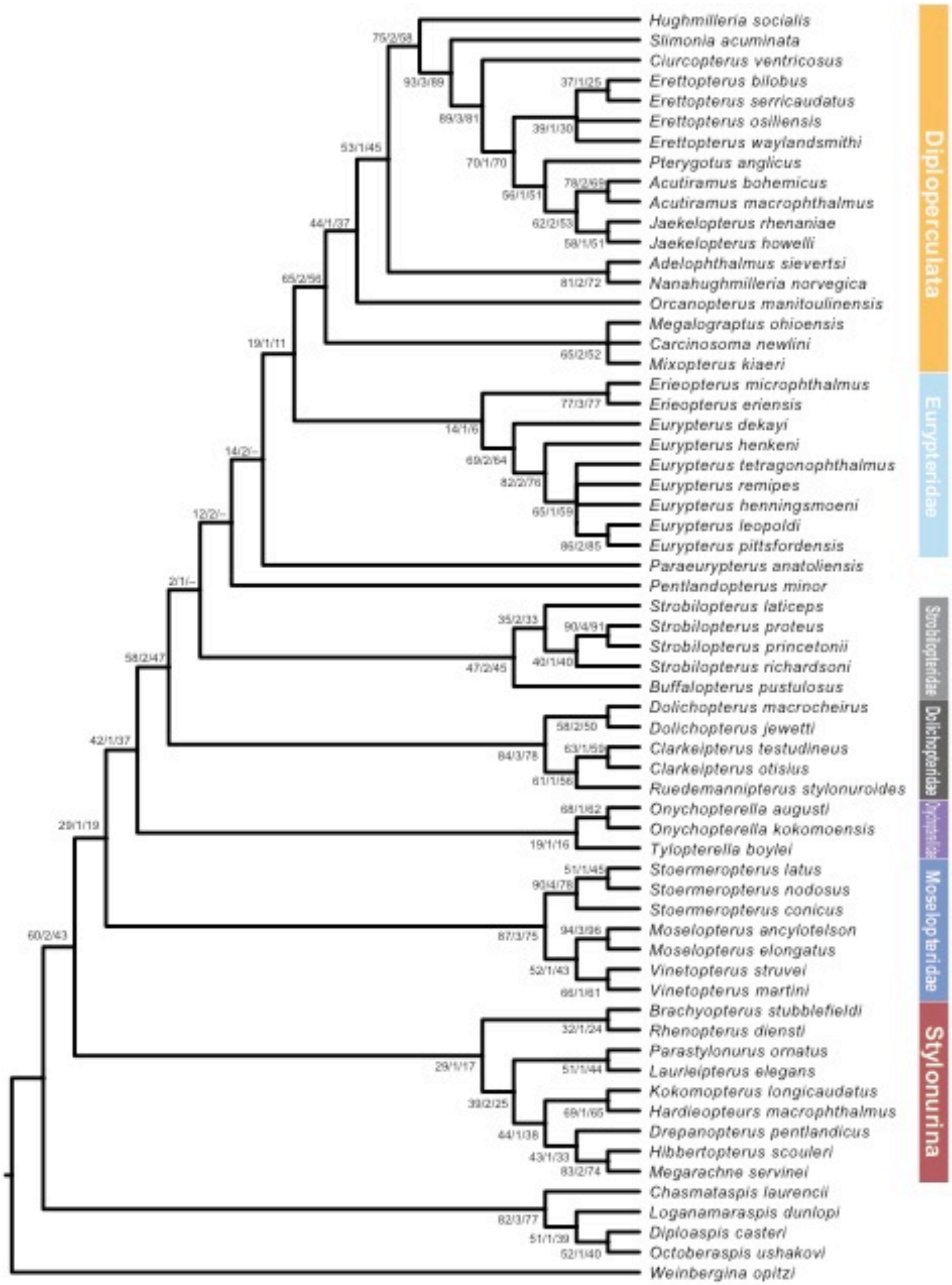


Figure 23 - Result of the phylogenetic analysis.

Strict consensus of 2 MPTs. Clade names are shown to the right of the tree.

Diploperculata comprises the clades Mixopteroidea, Adelophthalmoidea and

Pterygotoidea. Support values are shown by each node in the following format: jackknife support/bremer support/bootstrap support.

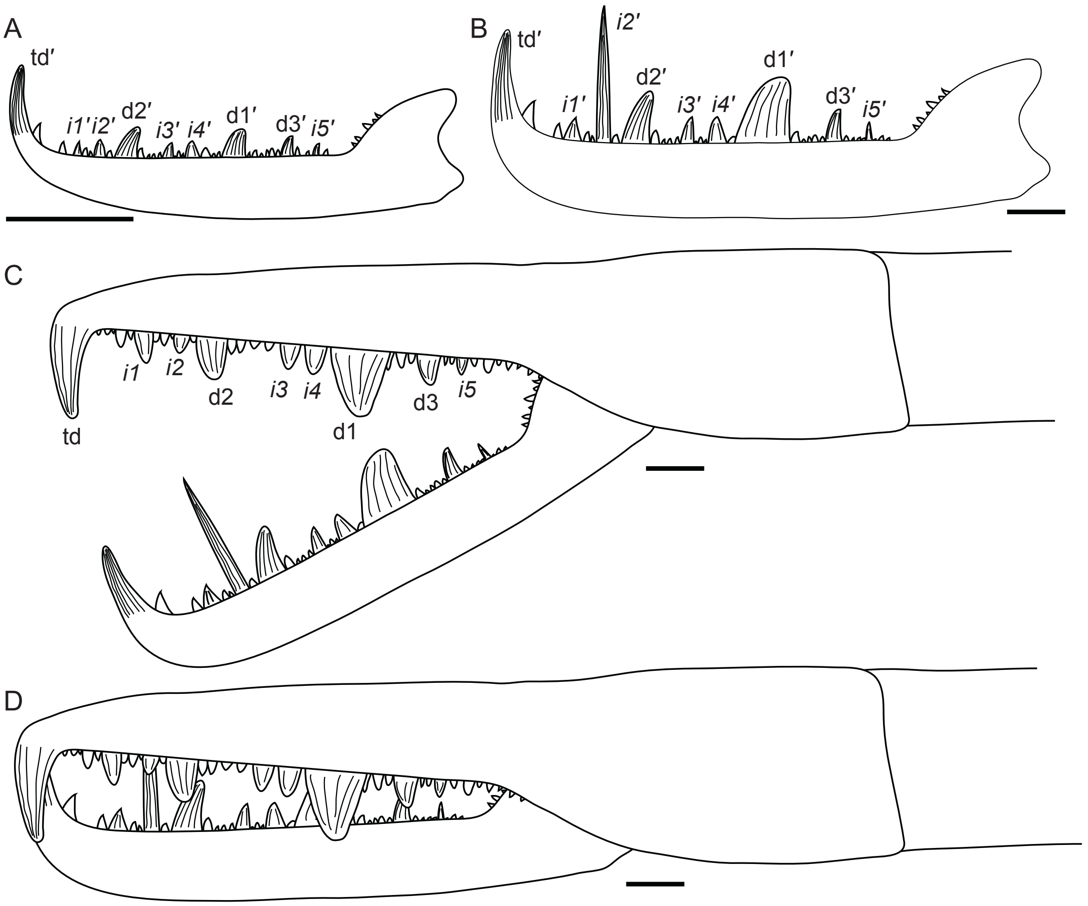


Figure 24 - *Jaekelopterus howelli* chelicera

Reconstruction of the juvenile and adult morphology of the chelicera. A: Juvenile free ramus. B: Adult free ramus. C: Adult articulated fixed and free ramus, agape. D: Adult articulated fixed and free ramus, occluded. Abbreviations: td = terminal denticle of fixed ramus; d1–d3 = principal denticles of the fixed ramus; i1–i5 = intermediate denticles of the fixed ramus; td′ = terminal denticle of the free ramus; d1′–d3′ = principal denticles of the free ramus; i1′–i5′ = intermediate denticles of the free ramus. Scale bars = 10 mm.

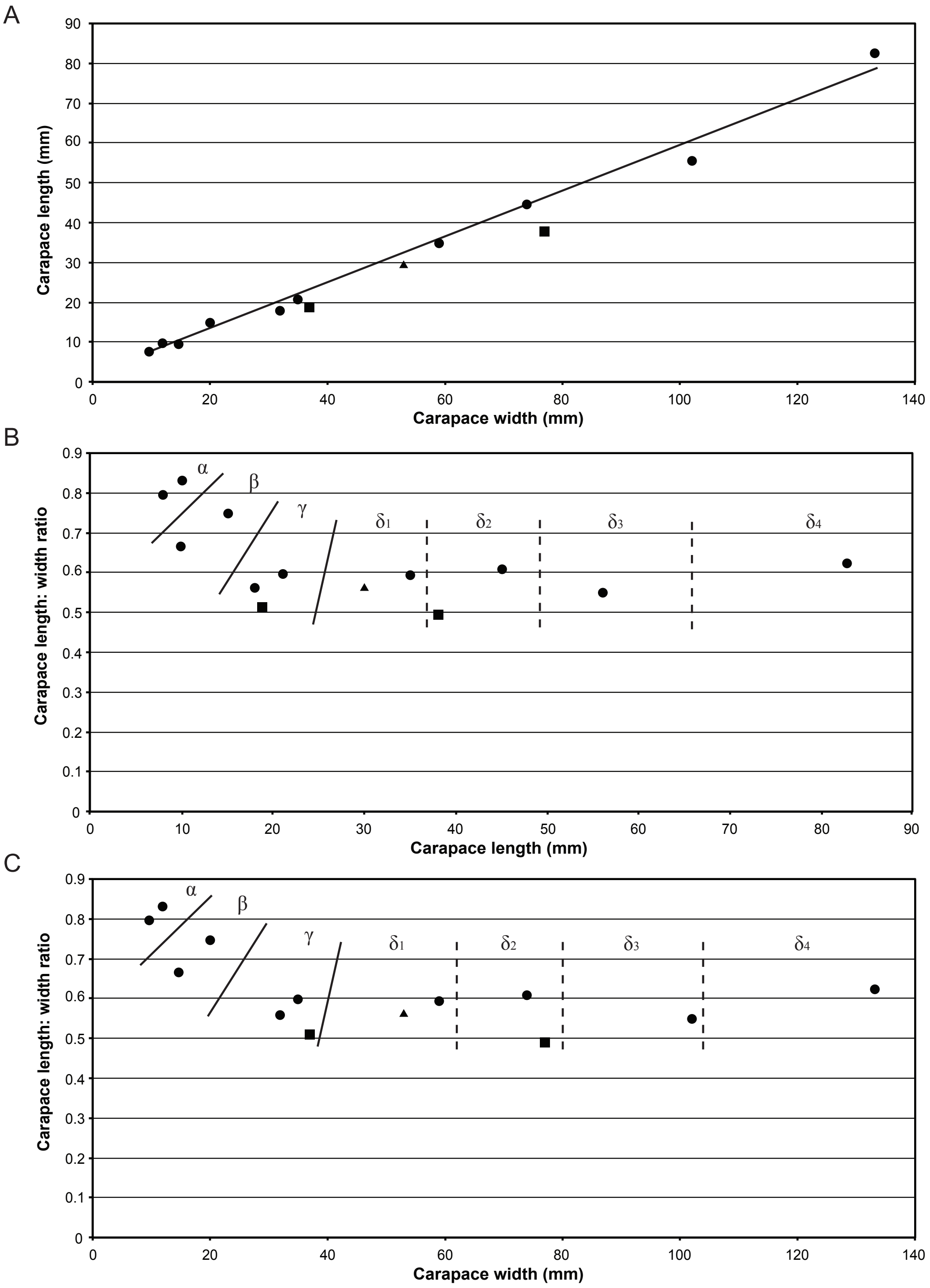

A
Carapace length (mm)
0
10
20
30
40
50
60
70
80
90
Carapace width (mm)
0
20
40
60
80
100
120
140
B
Carapace length: width ratio
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
α
β
γ
δ1
δ2
δ3
δ4
Carapace length (mm)
0
10
20
30
40
50
60
70
80
90
C
Carapace length: width ratio
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
α
β
γ
δ1
δ2
δ3
δ4
Carapace width (mm)
0
20
40
60
80
100
120
140

Figure 25 - Graphs comparing carapace dimensions of instars of *Strobilopterus*

Circles represent specimens of *Strobilopterus proteus*, while triangles represent *Strobilopterus richardsoni* and squares represent *Strobilopterus princetonii*. A: Carapace length vs. carapace width. The regression line is length = 0.5825(width) + 1.4404 and is statistically significant ($r^2 = 0.99034$, 8 degrees of freedom, $p = 2.39\times10^{-9}$) indicating that the relationship between carapace length and carapace width is not random and therefore likely due to ontogeny. B: Carapace length:width ratio vs. carapace length. Instar groupings are shown, with the potential subdivision of the δ specimens shown with dashed lines. C: Carapace length:width ratio vs. carapace width. Instar groupings are shown, with the potential subdivision of the δ specimens shown with dashed lines.

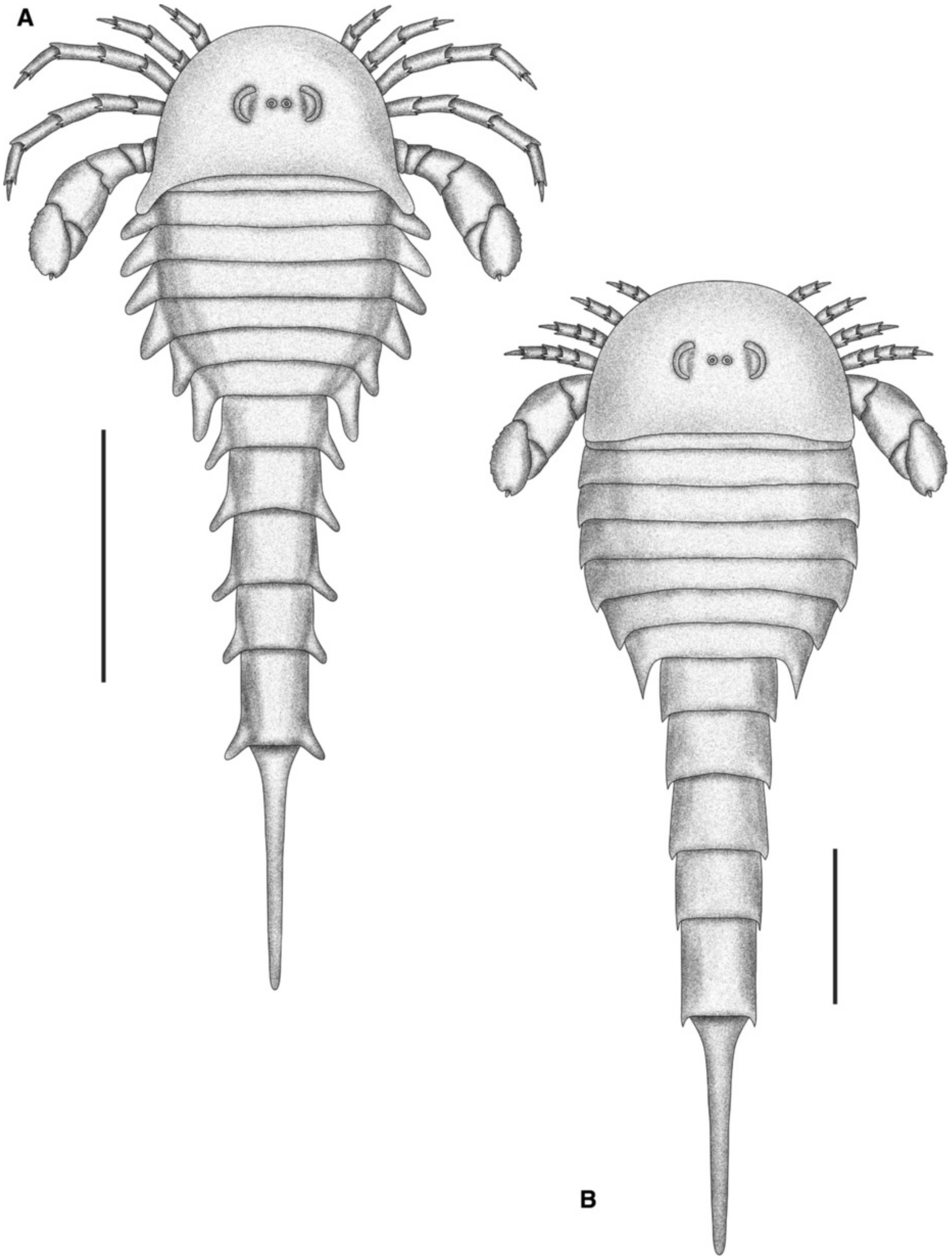


Figure 26 - *Strobilopterus proteus* juvenile instars

Reconstructions of juvenile instars. A: Possible larval instar α. Distal morphology of the paddle is extrapolated from a juvenile individual of *Strobilopterus princetonii*. The telson reconstructed from FMNH PE 61166. B: Juvenile instar β. Details of distal paddle morphology are extrapolated from a juvenile individual of *Strobilopterus princetonii*. The telson is extrapolated from FMNH PE 61166. Scale bars = 10 mm.

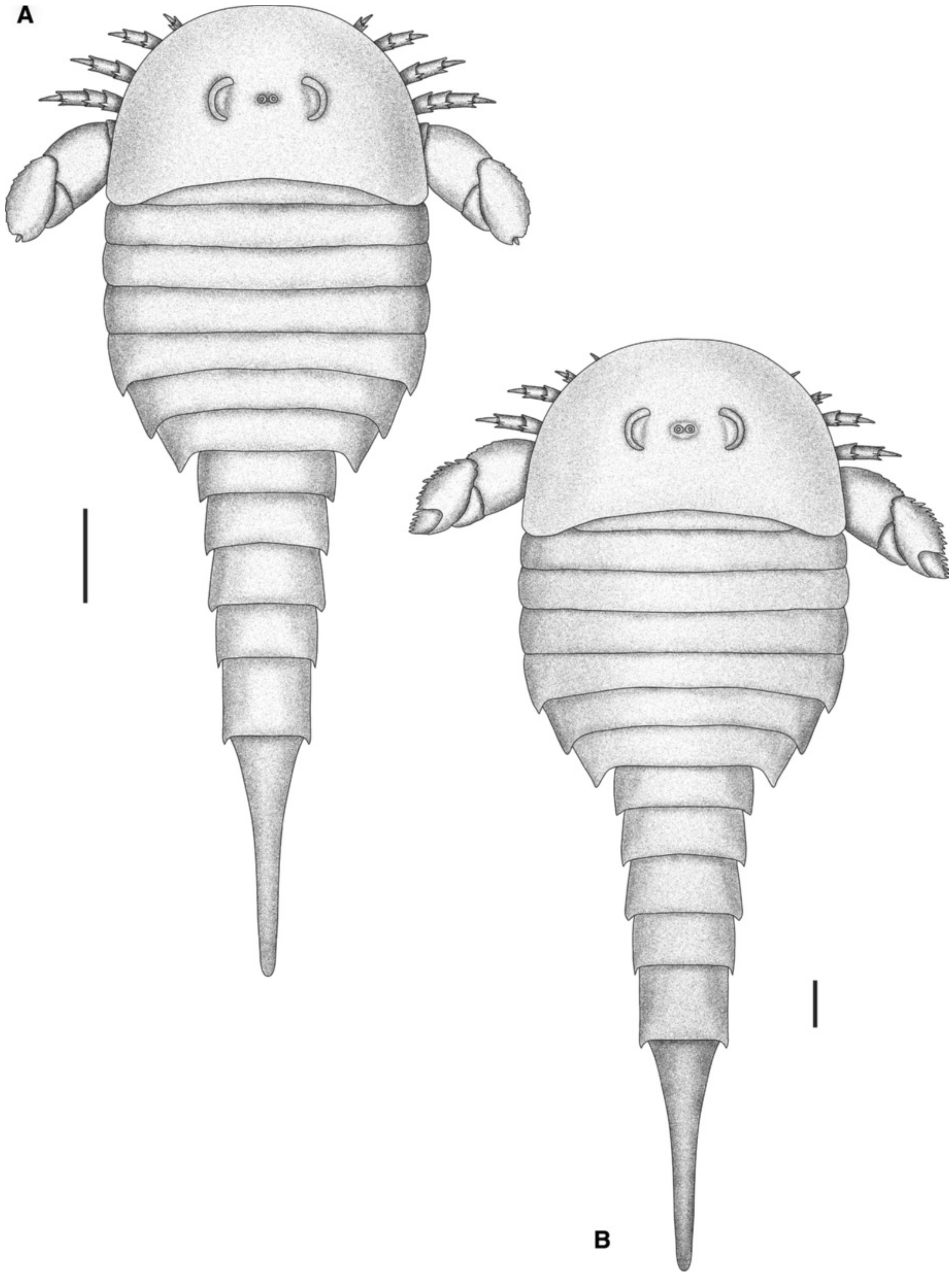


Figure 27 - *Strobilopterus proteus* subadult and adult instars

Reconstructions of subadult and adult instars. A: Juvenile/subadult instar γ. Limbs and posterior opisthosomal segments are extrapolated from a juvenile individual of

Strobilopterus princetonii. The telson is extrapolated from FMNH PE 61166. B: Subadult/adult instar δ. Anterior prosomal limbs are extrapolated from *Strobilopterus princetonii*. The telson is extrapolated from FMNH PE 61166. Scale bars = 10 mm.

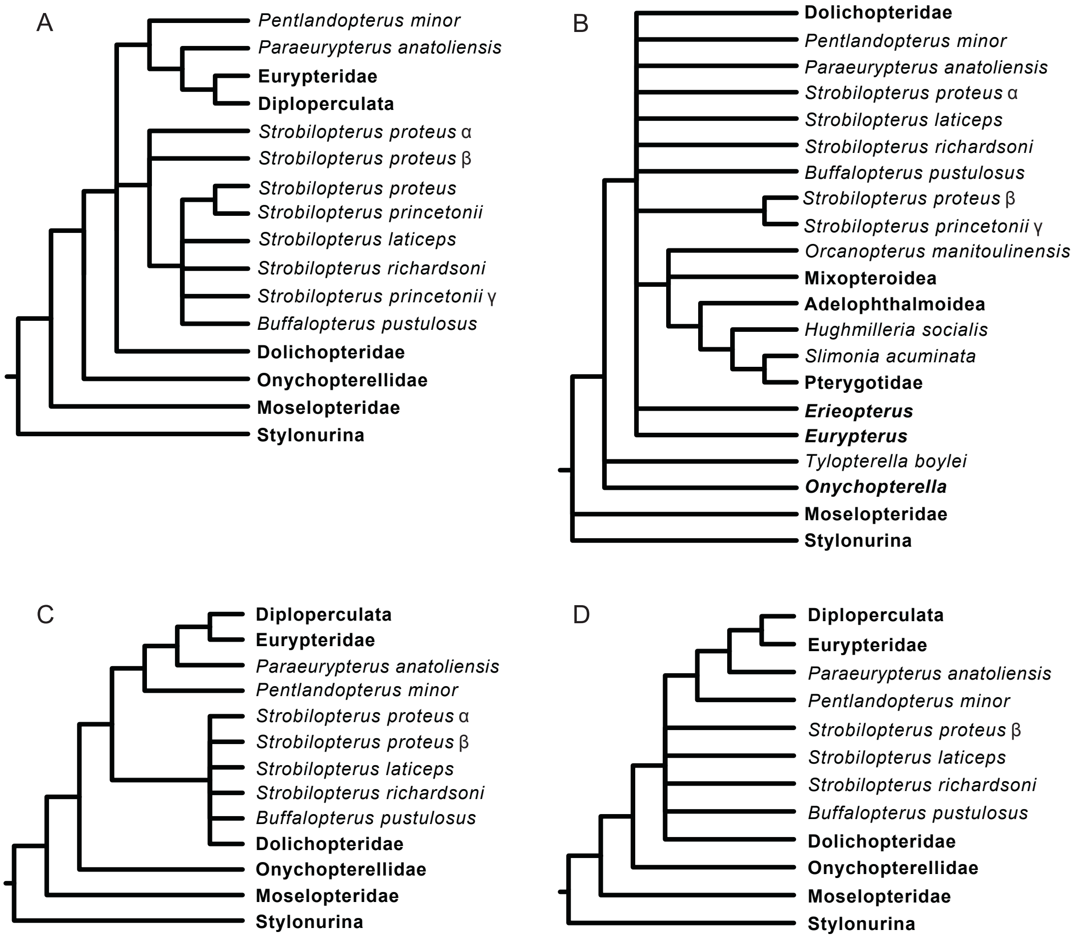


Figure 28 - Results of phylogeny experiments

Strict consensus trees retrieved when including juvenile instars in the phylogenetic analysis. A: All *Strobilopterus proteus* and *Strobilopterus princetonii* instars included. B: Adult *Strobilopterus proteus* and *Strobilopterus princetonii* instars excluded, juvenile instars included. C: Only α and β *Strobilopterus proteus* instars included, all other *Strobilopterus proteus* and *Strobilopterus princetonii* instars excluded. D: Only the *Strobilopterus proteus* β instar included, all other *Strobilopterus proteus* and *Strobilopterus princetonii* instars excluded.

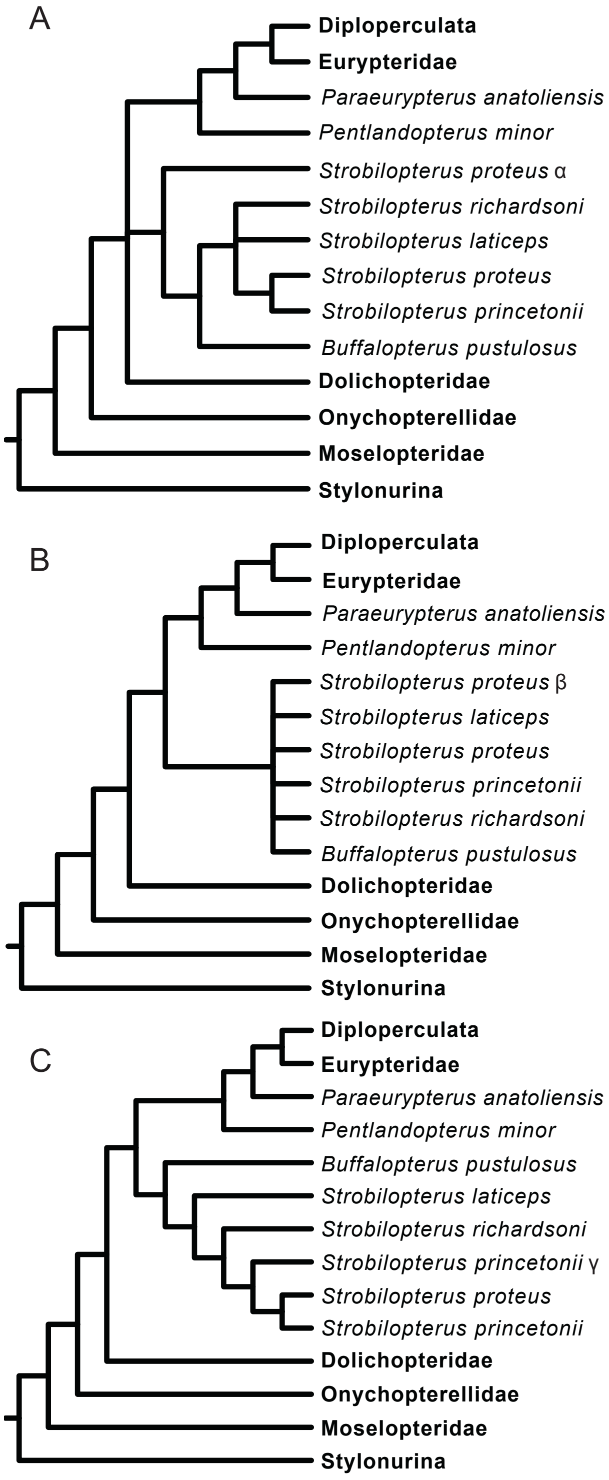

A
Diploperculata
Eurypteridae
Paraeurypterus anatoliensis
Pentlandopterus minor
Strobilopterus proteus α
Strobilopterus richardsoni
Strobilopterus laticeps
Strobilopterus proteus
Strobilopterus princetonii
Buffalopterus pustulosus
Dolichopteridae
Onychopterellidae
Moselopteridae
Stylonurina
B
Diploperculata
Eurypteridae
Paraeurypterus anatoliensis
Pentlandopterus minor
Strobilopterus proteus β
Strobilopterus laticeps
Strobilopterus proteus
Strobilopterus princetonii
Strobilopterus richardsoni
Buffalopterus pustulosus
Dolichopteridae
Onychopterellidae
Moselopteridae
Stylonurina
C
Diploperculata
Eurypteridae
Paraeurypterus anatoliensis
Pentlandopterus minor
Buffalopterus pustulosus
Strobilopterus laticeps
Strobilopterus richardsoni
Strobilopterus princetonii γ
Strobilopterus proteus
Strobilopterus princetonii
Dolichopteridae
Onychopterellidae
Moselopteridae
Stylonurina

Figure 29 - Results of phylogeny experiments

Strict consensus trees retrieved when including juvenile instars in the phylogenetic analysis. A: With the addition of the *Strobilopterus proteus* α instar. B: With the addition of the *Strobilopterus proteus* β instar. C: With the addition of the *Strobilopterus princetonii* γ instar.

Part 2

On trilobite phylogeny

Chapter 7

Phylogenetic support for the monophyly of proetide trilobites

James C. Lamsdell and Paul A. Selden

(Formatted for submission to *Lethaia*)

The monophyly of the order Proetida, the only trilobite group to survive the end-Devonian mass extinction, has been regularly questioned since its erection almost three decades ago. Through analysis of a novel phylogenetic dataset comprising 114 characters coded for 54 taxa, including both traditional members of the Proetida along with a number of other trilobite groups, the monophyly of proetide trilobites is rigorously tested for the first time. Proetida is shown to be monophyletic, united by the initial lateral eye formation in early protaspids occurring at the lateral margin rather than the anterior margin, and the form of the protaspid glabella being tapering with a preglabellar field. A number of adult characters, including the possession of a quadrate or shield-shaped hypostome with angular posterior margins, the hypostome medium body being divided by a deep groove that entirely transverses the median body, the presence of an enlarged thoracic spine on the sixth tergite, and a tergite count of between 7 and 10, also define the basal node. Hystricurid and dimeropygoid trilobites are shown to resolve at the base the group, while the remaining traditional proetide taxa are divided between large proetide and aulacopleuroid clades. Some traditional aulacopleuroid taxa, such as rorringotniids and scharyiids, are retrieved as basal members of the Proetoidea.

Trilobites are a monophyletic group of arthropods (Ramsköld & Edgecombe 1991) and are some of the most iconic Palaeozoic organisms, with some 10,000 species and an evolutionary history stretching some 300 million years from the Cambrian to the Permian (Lieberman & Karim 2010). Trilobite diversity was adversely affected by a number of mass extinction events, including the end-Ordovician (Chatterton & Speyer 1989; Adrain *et al*. 1998), from which trilobite diversity recovered (Adrain *et al*. 2000; Congreve 2013), and the end-Devonian (Feist 1991; McNamara & Feist 2006; Feist & McNamara 2007; McNamara *et al*. 2009) which marked the beginning to the terminal decline of the trilobites until their eventual extinction at the end-Permian (Owens 2003). The youngest known trilobites, and the only group to persist through the Devonian into the Carboniferous, belong to the order Proetida. Proetides were one of the last major trilobite groups to be formally recognised, and were raised to ordinal status by Fortey & Owens (1975). The group has had a checkered taxonomic history, however, with its monophyly challenged a number of times (Bergström 1997; Adrain 2011) resulting in a polyphyletic Proetida being implicitly considered in a number of studies (e.g. Lerosey-Aubril & Feist 2005). Therefore, ascertaining the monophyly or otherwise of proetide trilobites is a key question in trilobite systematics, especially given their distinction of being the only trilobite group to weather the Late Devonian Biodiversity Crisis. The application of paraphyletic or polyphyletic groups in biodiversity studies can have drastic effects on our understanding of mass extinction events, with erroneous patterns of pseudoextinction retrieved when monophyly is not recognized while incorrect assumptions of monophyly can dampen the observed loss of biodiversity, especially when studies are conducted at higher taxonomic levels (Patterson & Smith 1989). Given that the Late Devonian may be potentially unique among the Big Five mass extinctions in being driven primarily by a decrease in endemism and a drop in speciation rate rather than a marked increase in extinction rate (Stigall 2012), and that accurate phylogenetic hypotheses are required in order to assess the mechanisms behind changes in speciation, extinction, and biogeography (Stigall 2010), uncertainty of the monophyly of major groups such as proetides can have serious negative implications for our understanding of the patterns and processes underlying the biotic turnover occurring during this period. Proetides have already been the subject of a number of biodiversity studies focusing on the Late Devonian (Lerosey-Aubril & Feist 2012; Feist & McNamara 2013) and beyond (Owens 2003), with a number of pseudoextinctions amongst Late Devonian proetides having already been hypothesised (Owens 1994). Uncertainty over the order's status serves to only further muddy the waters, and until the issue is resolved the results of such biodiversity studies must be treated with caution.

Taxonomic history of the Proetida

As with many of the major trilobite groups, proetides have had a complicated taxonomic history. The superfamily Proetacea was first diagnosed by Hawle & Corda (1847). For many years trilobite classification hinged on whether authors considered cephalic suture morphology (Beecher 1897) or pygidium size (Gürich 1907) to be of greater importance for defining groups; however, following Swinnerton (1915), a more nuanced hierarchy began to emerge. At this time, proetids comprised part of the Olenina, while bathyurids where included along with illaenids in Ptychoparina; however, Richter (1933) removed illaenids to Bathyuriscidea within Redlichiina, and placed proetids and otarinionids together as part of Ellipscocephalidea within Ptychopariina. By the 1950s, a more modern approach to trilobite systematics began to prevail, encapsulated by Henningsmoen (1951) and Hupé (1955), which discarded the use of single characteristics as the sole criterion for assigning relationships. In the scheme of Hupé (1955), the groups that later became the order Proetida fell broadly into two superfamilies: Holotrachelidae, Proetidae, Tropidocoryphidae, Cyrtosymbolidae, Dechenellidae, Phillipsiidae, and Brachymetopidae comprised the Proetoidea, while Hystricuridae, Toernquistiidae, Dimeropygidae, Bathyuridae, and Otarionideae were included among the Solenopleuroidea. This classification was heavily revised for the *Treatise on Invertebrate Paleontology* (Moore 1959), in which Proetacea was included with the superfamily Illaenacea in the suborder Illaenina within the Ptychopariida (Harrington *et al*. 1959), based on the general lack of glabella furrows, a general lack of eye ridges, and a usual thoracic segment count of between 6 and 10. At the time of the *Treatise*, Proetacea comprised the families Proetidae, Phillipsiidae, Otarionidae, Aulacopleuridae, Brachymetopidae, Phillipsinellidae, Celmidae, Plethopeltidae, and Dimeropygidae, with Holotrachelacea and Bathyuracea being included within Illaenina. Bergström (1973) later transferred the Holotrachelidae and Lecanopygidae (from Bathyuracea) into Proetacea, retaining the superfamily within Illaenida but moving the group out of the ptychopariids. Bathyurids and proetoids, therefore, were considered to be derived independently from illaenids, while hystricurids remained part of the Solenopleuroidea.

Fortey & Owens (1975) raised Proetida to ordinal status, including within it the families Aulacopleuridae, Bathyuridae, Celmidae, Dimeropygidae, Glaphuridae, Otarionidae, Proetidae, and the subfamily Hystricurinae. This new grouping was considered to exhibit a common larval morphology and was further defined based on twelve adult characteristics: (1) a medially transversely narrow rostral plate which generally tapers backwards; (2) a well defined vaulted glabella; (3) poorly expressed anterior glabellar furrows; (4) a well defined occipital ring; (5) well developed (often blade-like) genal spines; (6) semicircular holochroal eyes medially or backwardly positioned; (7) posterior sections of the facial suture diverging at a moderate to high angle, anterior branches usually divergent; (8) doublure of convex species usually recurved steeply beneath the border of the free cheek to form a lateral cephalic 'tube'; (9) thorax usually with 8–10 segments (maybe as few as 6 or as many as 22), width of pleurae equal to or exceeding in width that of the axis, thoracic segments in contact along their length, pleural furrows diagonal; (10) pygidium with strong pleural furrows and margin usually entire, doublure with strong terrace lines; (11) hypostome longer than wide with elongate, oval middle body and one pair of relatively posteriorly situated middle furrows, borders narrow; and (12) preglabellar field variously developed, species with shorter preglabellar field tending to have a granular surface sculpture, those with a longer preglabellar field tending to have a surface sculpture of fine terrace lines. As well as explicitly stating that these taxa formed a natural group – a monophylum – Fortey & Owens (1975) considered there to be no compelling link between Proetida and Illaenida. Bergström (1977) contested that Proetida was an unnatural group, citing the occurrence of two different types of enrollment, and split proetides among three groups; one consisting of the Bathyuridae, Proetidae, and Brachymetopidae, another comprising the Hystricurinae, Dimeropygidae, and Aulacopleuridae, with Glaphuridae and Celmidae forming the third group. Bergström

(1977) considered each of these groups to be independently derived and not closely related to one another, with the hystericurine group forming part of the Solenopleuracea and the glaphurid group being included within the Odontopleurida. Fortey & Owens (1979) refuted Bergström's (1977) contention that enrollment type defined specific groups and maintained the validity of the order. Lütke (1980) provided an in-depth revision of the proetides, which were considered to be a monophyletic suborder of ptychopariid trilobites derived from the Hystricurinae, which had once again been placed within the Solenopleuracea. The group was split into two superfamilies: the Proetacea, incorporating the Proetidae (which included cornuproetids, phillipsiids, cyphoproetids and others as subfamilies) and Tropidocoryphidae, and the Aulacopleuracea, comprising the Aulacopleuridae (including brachymetopids, scharyiids and rorringtoniids), Dimeropygidae, and Cyphaspididae. Glaphuridae and Celmidae where retained within proetides, but were considered of uncertain affinity. This classification became widely adopted (e.g. Owens & Hammann 1990), and in the revision of the *Treatise* was refined to divide Proetida into three superfamies, with Proetoidea including Proetidae and Phillipsiidae, Aulacopleuroidea comprising Aulacopleuridae, Brachymetopidae and Rorringtoniidae, and Bathyuroidea consisting of Bathyuridae, Dimeropygidae, Celmidae, Lecanopgidae, Glaphuridae, Holotrachelidae, and Telephinidae (Fortey 1997).

Recently, however, it has again been suggested that Proetida comprises at least two independently derived groups. Adrain (2011) presented a revised trilobite classification that split aulacopleuroids off into their own order, reducing Proetida to Proetidae and Tropidocoryphidae. Aulacopleurida was also greatly expanded beyond Aulacopleuridae, Brachymetopidae, Dimeropygidae, Rorringtoniidae, and Scharyiidae to include the traditional proetide groups Bathyuridae and Telephinidae, along with Holotrachelidae and Hystricuridae, and the ptychopariid families Alokistocaridae, Crepicephalidae, Ehmaniellidae, Marjumiidae (including Coosellidae), Solenopleuroidae, and Tricrepicephalidae. The rationale for this split hinges upon morphological differences among the larval stages in each group, with Proetida possessing a non-adultlike globular form while Aulacopleurida have adultlike larvae featuring paired spines or tubercles. There are a number of potential flaws with the classification, however, not least that it is presented as a simple list with not clear justification for sweeping taxonomic changes beyond the few lines that appear in footnotes. Furthermore, the apparent separation of 'proetoid' and 'aulacopleuroid' larval type is not as clear-cut as the classification suggests; a globular protaspis is known from both dimeropygids (Chatterton 1994) and aulacopleurids (Yuan *et al*. 2001), while the pattern of paired tubercles considered diagnostic of aulacopleuroids by Adrain (2011) is absent in ehmaniellids (Hu 1998), coosellids (Hu 1978) and crepicephalids (Hu 1971) at least. The supposedly diagnostic paired spines on the posterior of the aulacopleuroid larva are common in trilobites, including redlichiids (Dai & Zhang 2012), olenellids (Webster 2014), olenids (Månson & Clarkson 2012) and cheirurids (Lee & Chatterton 1997), among others. The assertion that there is no clear sister relationship between proetoids and aulacopleuroids also ignores certain characters known to be present in both groups, such as the development of the preglabellar field in the meraspid stage. Given the sudden expansion of the aulacopleuroids with the inclusion of a number of disparate ptychopariid families under the vague characteristic of the possession of a 'flattened, adult-like larvae' there is the possibility that, in Adrain's (2011) classification, the group has become something of a wastebasket taxon for various Cambrian taxa of uncertain affinity, much like Ptychopariida itself had been.

Here, we present a novel phylogenetic analysis comprising both traditional members of the Proetida along with a number of other trilobite groups in order to test the monophyly of proetide trilobites and ascertain the limits of the Aulacopleuroidea. This is the first time that proetide monophyly has been tested phylogenetically, and represents the first rigorous analysis to test the balance of the various criteria used to argue for and against the validity of the order.

Methods

Terminology

Trilobite terminology largely follows Whittington and Kelly (1997); however, an attempt has been made to quantify more accurately the distinctions between the standard pygidial size classifications. The current divisions between the micropygous, isopygous, and macropygous classifications are unclear at best, especially when such mid-tier classifications as subisopygous are included. A new method is set out here that compares the size of the pygidium to the cephalon by overlaying rectangular boxes over the cephalon and pygidium, from which their areas are calculated and compared, giving the size of the pygidium relative to the cephalon as a percentage. Distinctions between micropygous, isopygous and macropygous size ranges were made at major discontinuities of pygidial sizes: micropygous pygidia occupy less than 25% the area of the cephalon, ispopygous pygidia occupy 25–110% the area of the cephalon, and macropygous pygidia occupy greater than 150% the area of the cephalon. Furthermore, micropygous and isopygous pygidia can be further subdivided, with the degree of micropygosity varying from micropygous (10–25%) and extremely micropygous (0.5–5%) and the degree of isopygosity ranging from isopygous (90–105%), subisopygous (35–90%) and extremely subisopygous (25–35%).

Phylogenetic analysis

For the phylogenetic analysis, a matrix of 114 characters and 54 taxa was compiled. Species were coded from figures in the literature, supplemented with observations of specimens where possible. The redlichiid trilobite *Eoredlichia intermedia* (Lu, 1940) was specified as the outgroup, as it represents a well-known member of the group from which ptychopariids likely originated (Lieberman & Karim 2010), and from which both ventral morphological characteristics and earlier ontogenetic stages are known. Ingroup taxa were selected based on morphological completeness and, where possible, the existence of earlier ontogenetic stages assigned to the species. A number of higher-level trilobite groups were included alongside proetide taxa in the analysis, each represented by multiple exemplars where possible, as these more accurately represent the character states and transitions of a group than a single exemplar such as a token species or composite taxon would (see Brusatte 2010), as well as allowing for the potential of para- or polyphyly. A number of ptychopariid groups considered by Adrain (2011) to comprise part of his revised Aulacopleuroidea were included, specifically Alokistocaridea/Ehmaniellidae (represented by *Altiocculus harrisi* (Robison, 1971), *Elrathia kingii* (Meek, 1870), and *Ehmaniella apolabella* Hu, 1998), Crepicephalidae

(*Coosella prolifica* Lochman, 1936; *Crepicephalus buttsi montanaensis* Lochman *in* Lochman & Duncan, 1944), Holotrachelidae (*Holotrachelus punctillosus* (Törnquist, 1884), Marjumiidae (*Marjumia typa* Walcott, 1916; *Modocia kohli* Robison and Babcock, 2011), Solenopleuridae (*Solenopleura canaliculata* (Angelin, 1851); *Parasolenopleura gregaria* (Billings, 1865)), and Tricrepicephalidae (*Tricrepicephalus texanus* (Shumard, 1861)). Alongside these members of the Olenidae (*Olenus wahlenburgi* Westergård, 1922; *Parabolina spinulosa* (Wahlenberg, 1818); *Leptoplastus crassicorne* (Westergård, 1944)) and Ellipsocephalidae (*Lermontovia dzevanovskii* (Lermontova, 1951)) were included as ptychopariids that have not been considered to be allied to the aulacopleuroids. Representatives of the other major trilobite groups hypothesised to be derived from the ptychopariids (Fortey 2001) were included in order to test whether the ptychopariid taxa included in the analysis resolve either as: 1) in-group or stem proetides; 2) as part of a monophyletic Ptychopariida; or 3) as stem-taxa to any of the other included trilobites orders. Asaphida was represented by *Asaphus expansus* (Wahlenberg, 1818), *Isotelus parvirugosus* Chatterton & Ludvigsen, 1976, *Proceratopyge rectispicatus* (Troedsson, 1937), *Proceratopyge promisca* Choi, Kim & Lee, 2008, *Aphelaspis brachyphasis* Palmer, 1962, *Remopleurides caelatus* Whittington, 1959, and *Remopleurides eximius* Whittington, 1959, representing asaphids, aphelaspids, ceratopygids and remopleurids, while Phacopida was represented by *Flexicalymene senaria* (Conrad, 1841), *Calyptaulax annulata* (Raymond, 1905), *Ceraurinella nahanniensis* Chatterton & Ludvigsen, 1976, *Ceraurinella typa* Cooper, 1953, *Parapilekia olesnaensis* (Růžička, 1935), *Anacheirurus frederici* (Salter, 1864), and *Kawina arnoldi* Whittington, 1963 comprising members of Calymenina, Phacopina and

Cheirurina. Harpetida were represented by *Eskoharpes palanasus* McNamara, Feist and Ebach, 2009, *Entomaspis radiatus* Ulrich *in* Bridge, 1930, *Eoharpes benignensis* (Barrande, 1872) and *Harpes macrocephalus* Goldfuss, 1839, with *Harpides atlanticus* Billings, 1865 also being included.

Finally, 19 proetide trilobites were included in the analysis so as to test the monophyly of the group. Hystricurids were represented by *Hintzecurus paragenalatus* (Ross, 1951) and *Politicurus politus* (Ross, 1951), while dimeropygids and toernquistiids were represented by *Dimeropyge speyeri* Chatterton, 1994 and *Toernquistia sanchezae* (Chatterton, Edgecombe, Waisfeld and Vaccari, 1998) respectively. *Tropidocoryphe bassei* Van Viersen, Prescher & Savelsbergh, 2009, *Scharyia micropyga* (Hawle & Corda, 1847) and *Rorringtonia kennedyi* Owens, 1981 represented Tropidocoryphidae, Scharyiidae and Rorringtonidae. *Bathyurus ulu* Ludvigsen, 1979 was included for bathyurids while *Proetus talenti* Chatterton, 1971, *Phillipsia belgica* Osmólska, 1970 and *Gerastos tuberculatus* (Barrande, 1846) where included for proetids. Among the aulacopleurids, *Aulacopleura wulongensis* Wang, 1989, *Aulacopleura longecornuta* (Roemer, 1854), *Aulacopleura konincki* (Barrande, 1846), *Cyphaspis dabrowni* (Chatterton, 1971), *Maurotarion struszi* (Chatterton, 1971), *Maurotarion periergum* (Haas, 1969), *Brachymetopus germanicus* Hahn, 1964, and *Otarion huddyi* Adrain & Chatterton, 1994 were selected for inclusion.

The 114 characters are listed here. The data matrix is shown in Table 1. Characters 1–96 are coded for holaspids only, 97–107 are coded for protaspids only, and 108–114 are coded for meraspids only.

1. Eye angle: *diverging posteriorly (0); equilateral (1); diverging anteriorly (2).*
2. Lateral eye size (as percentage of carapace): *30%+ (0); 20%–29% (1); <15% (2).*
3. Eye shape: *shaded dorsally by palpebral lobe – visual surface with crescentic outline (0); eye expands beyond palpebral lobe – visual surface scimitar-shaped (1).*
4. Eyes sit atop free cheek: *absent [eye visual surface set into free cheek] (0); present, globular [visual surface sits atop free cheek and projects above it with roughly spherical outline] (1); present, turreted [visual surface sits atop free cheek and projects above it with angular outline and flat dorsal surface] (2).*
5. Eye position: *posterior of carapace [0–45%] (0); midline or anterior [48%+] (1); eye encompasses entire carapace length (2).*
6. Eye ridges expressed dorsally on exoskeleton: *present (0); absent (1).*
7. Eye ridges: *angled anteriorly [>110°] (0); equal to eye [90–110°] (1); absent (–).*
8. Ridge insertion on eye: *anterior of eye (0); mid-point of eye (1); ridge absent (–).*
9. Position of palpebral lobe: *main body distant from axial furrow (0); main body abuts axial furrow (1).*
10. Size of palpebral lobe: *equal to or larger than visual surface (0); smaller than visual surface (1).*
11. Carapace shape: *wider than long [≤0.55] (0); equilateral [>0.55] (1).*
12. Posterior suture position: *avoids outer margin (0); cuts through outer margin (1); skirts margin (2); no suture (–).*
13. Suture angle from lateral eye: *30–45° (0); ≥60° (1); ≤0° (2); 10–20° (3); no suture associated with eye (–).*

14. Angle of sutures as they cross the anterior margin: *parallel (0); converging (1); diverging (2); does not cross anterior margin (–).*
15. Cephalic sutures with marked inward curve just prior to cephalic margin: *absent (0); present (1).*
16. Glabella extent: *carapace anterior [>75%] (0); carapace midline or posterior [≤75%] (1).*
17. Effacement of S3: *S3 deeply incised (0); S3 effaced (1).*
18. Effacement of S2: *S2 deeply incised (0); S2 effaced (1).*
19. Positioning of S2 & S3: *well spaced (0); S3 & S2 close together, L3 expanded (1); S3 or S2 effaced (–).*
20. Length of S3/S2: *~50% of glabella width (0); short, ~25% of glabella width (1); S3 an S2 effaced (–).*
21. Relationship of L1 to glabella: *part of glabella [not separated by S1] (0); detached from glabella [S1 extends to occipital ring, separating L1 from glabella] (1); fully merged with glabella [S1 shallow or effaced] (2).*
22. Size of L1: *~25% of glabella (0); reduced, <25% of glabella (1).*
23. Lateral inflation of carapace alongside L1 (ala): *absent (0); present (1).*
24. Anterior narrowing of glabella: *width at anterior <75% width at base (0); width at anterior >75% width at base (1).*
25. Form of broad glabella anterior: *<100% width of base (0); 100% width of base (1); >100% width of base (2); anterior width <75% that of base (–).*
26. Glabella with sudden constriction about 1/3 from anterior: *glabella margins continuous (0); glabella margins with sudden constriction (1).*

27. Anterior portion of cephalic rim broadens into ‘lip’: *width remains unchanged (0); broadened into ‘lip’ (1).*

28. Paired row of spines projecting laterally from marginal rim: *absent (0); present (1).*

29. Cephalic marginal rim demarcated by broad trough: *absent (0); present (1).*

30. Cephalon margin differentiated into broad fringe ornamented with sensorial pits or setae: *absent (0); present (1).*

31. Axial structure on occipital ring: *absent (0); present (1).*

32. Form of occipital axial structure: *raised node (0); enlarged spine (1); absent (–).*

33. Position of genal spine divergence from carapace: *lateral, anterior to carapace posterior margin (0); posterolateral margin, posterior margin of carapace curves down into genal spine (1).*

34. Genal spines purely vestigial: *fully expressed (0); vestigial (1).*

35. Broad genal spines: *width of genal spines ≤15% width of carapace (0); width of genal spines >20% width of carapace (1).*

36. Genal spine curvature: *strong curvature (0); slight curvature (1).*

37. Genal spine angle of divergence: *high [≥30%] (0); moderate [11%–29%] (1); reduced [≤10%] (2).*

38. Length of genal spines: *>100% carapace length (0); 35–100% carapace length (1); ≤30% carapace length (2).*

39. Presence of narrow ridge located in outer field of carapace between the glabella/lateral eyes and the marginal rim: *absent (0); present (1).*

40. Internal pattern of anastomising veins expressed on dorsal cuticle layer: *not expressed, present only as internal structures (0); expressed dorsally (1).*
41. Degree of expression of anastomising veins: *faintly expressed, veins shallow (0); fully expressed, veins deeply incised (1); anastomising veins not expressed dorsally (–).*
42. Ornamentation of free cheek (region outside of lateral eyes but before lateral margin): *granules (0); pustules (1).*
43. Ornamentation of fixed cheek (region between lateral eyes and glabella): *granules (0); pustules (1).*
44. Ornamentation of glabella anterior (region anterior of S1): *granules (0); pustules (1); effaced (2).*
45. Density of anterior glabella pustules: *sparse [and small] (0); dense [and large] (1); pustules not present on glabella (–).*
46. Ornamentation of glabella posterior (region posterior of S1): *granules (0); pustules (1); effaced (2).*
47. Density of posterior glabella pustules: *sparse [and small] (0); dense [and large] (1); pustules not present on glabella (–).*
48. Granular ornamentation punctuated by enlarged pustules: *absent (0); present (1); no granular ornamentation (–).*
49. Extension of carapace ornamentation onto genal spines: *absent (0); present (1).*
50. Extent of carapace ornamentation on genal spines: *entire length of genal spine (0); proximal regions only (1); no carapace ornamentation on genal spines (–).*
51. Fixed and free cheeks of cephalon pitted: *absent (0); present (1).*

52. Hypostome with unsclerotised anterior portion: *absent (0); present, short spinous projections (1); present, posterior margins form enlarged 'forked' morphology (2).*

53. Hypostome with paired posterior projections: *absent (0); present, short spinous projections (1); present, enlarged projections resulting in 'forked' morphology (2).*

54. Breadth of shoulders: *short, not extending beyond maximum width of hypostome body (0); broad, extending beyond maximum width of hypostome body (1).*

55. Form of hypostome median body: *median body extends for entire length of hypostome, undivided (0); median body extends for entire length of hypostome, divided (1).*

56. Form of division of median body: *division formed by lateral grooves that do not meet medially (0); division formed by deep groove that entirely transverses median body (1); posterior median body entirely separated from anterior median body (2); median body undivided (–).*

57. Extent of hypostome doublure/rim: *present along entire lateral and posterior margins (0); present at posterior margin only (1).*

58. Form of hypostome posterior angles: *rounded, so hypostome appears lobate (0); angular, so hypostome appears quadrate/shield-shaped (1).*

59. Position of hypostome constriction: *anterior quarter (0); midpoint (1).*

60. Hypostome dimensions: *elongate [length greater than width, l/w ration >1.30] (0); equilateral [length approximately equal to width, l/w ratio 0.80–1.05] (1).*

61. Free thoracic tergite count: *14–15 (0); 18+ (1); 16 (2); 13 (3); 11–12 (4); 7–10 (5).*
62. Enlarged thoracic spine on sixth tergite: *absent (0); present (1).*
63. Form of epimera on anterior tergites (1–6): *acute, spinous (0); blunt, curved (1).*
64. Form of epimera on posterior tergites (7–n): *acute, spinous (0); blunt, curved (1); blunt, quadrate or lobate (2).*
65. Reduction of epimera on first trunk tergite: *partially reduced, epimeral termination straight, spine small (0); undifferentiated (1).*
66. Reduction of epimera on second trunk tergite: *undifferentiated (0); partially reduced, spine small (1).*
67. Commencement of narrowing of axial rings: *4th axial ring (0); 3rd axial ring (1); terminal pre-pygidial axial ring (2); expanding until mid-ring before narrowing commences, pre-pygidial axial ring same width as first post-cephalic axial ring (3).*
68. Percentage of tergite width occupied by axial region: *36–45% (0); 30–35% (1); 20–25% (2); >45% (3).*
69. Axis with central node on each segment: *present (0); absent (1).*
70. Tubercular swellings in pleural field alongside axis: *absent (0); present (1).*
71. Row of tubercles across the posterior margin of each tergite: *absent (0); present (1).*
72. Ornamentation of dense granules interspersed with larger tubercles: *absent (0); present (1).*
73. Tergites showing marked deflection at fulcrum: *absent (0); present (1).*

74. Pygidium bearing macropleural spines: *absent (0); present (1)*.

75. Pygidial macropleural spines on anteriormost segment, delineated from rest of pygidium by furrow: *absent (0); present (1).*

76. Pygidium with medial posterior indentation: *absent (0); present (1).*

77. Degree of posteromedial pygidial indentation: *gentle [slight indentation] (0); acute [clear indentation] (1); no indentation (–).*

78. Pygidium with tergopleural epimera besides macropleural spines: *absent (0); present (1).*

79. Form of pygidial epimera: *spinous (0); quadrate or lobate (1).*

80. Number of axial rings in pygidium: *4/5 (0); 3 (1); 2 (2); 7/8 (3); 22 (4); 14 (5).*

81. Form of terminal ring in 4/5: *fully expressed (0); suppressed, partially merged with terminal piece (1); pygidium has other than 4 axial rings (–).*

82. Size of pygidium in relation to cephalon (quantified via comparison of boxed area plots): *micropygous [pygidium occupies <25% area of cephalon] (0); isopygous [pygidium occupies 25–110% area of cephalon] (1); macropygous [>150% area of cephalon] (2).*

83. Degree of micropygosity: *extreme micropygosity [0–5%] (0); micropygous [10–25%] (1); pygidium isopygous or macropygous (–).*

84. Degree of isopygosity: *extreme subisopygosity [25–35%] (0); subisopygous [35–90%] (1); isopygous [90–105%] (2); pygidium micropygous or macropygous (–).*

85. Gross pygidial morphology: *simple, paddle-like [broadest at posterior] (0); tail-like [broadest at anterior or mid-point] (1).*

86. Termination of tergopleural grooves: *at pygidial boundary (0); before pygidial boundary (1)*.

87. Pygidial marginal rim (dorsal expression of ventral doublure) demarcated by visible groove: *absent (0); present (1).*

88. Pygidial marginal rim developed into broad pleural fields: *absent (0); present (1); no marginal rim (–).*

89. Pygidial marginal rim overturned onto inflated pygidial lateral margin: *absent (0); present (1); no marginal rim (–).*

90. Tergite furrows encroach onto demarcated marginal rim: *absent (0); present (1); no marginal rim (–).*

91. Dense, unordered ornamentation of scales/pustules: *absent (0); present (1).*

92. Row of four tubercles on each axial ring: *absent (0); present (1).*

93. Axial tubercle row with ancillary tubercles: *present (0); absent (1); no tubercle row (–).*

94. Row of tubercles on lateral ribs of tergopleurae: *absent (0); present (1).*

95. Terminal piece of pygidium composed of axial region and two posteriorly oriented lappets: *absent (0); present (1)*.

96. Form of lappets: *long, produced into spines (0); short, reduced (1); no lappets (–).*

97. Early protaspids with paired posterior spines: *absent (0); present (1).*

98. Fate of posterior spines by end of protaspid stage: *spines retained into meraspid stage (0); spines lost during protaspid stage (1); no spines in protaspid stage (–).*

99. Protaspids with posterior medial indentation: *absent (0); present (1).*

100. Form of glabella in protaspids: *amorphous (0); tapering, with preglabellar field (1).*

101. Protaspid glabellar segmentation: *subdued (0); fully traversing glabella, resembling full body segmentation (1).*

102. Position of initial lateral eye formation in early protaspids: *anterior margin (0); lateral margin (1).*

103. Protaspid eye ridges: *fully expressed (0); suppressed (1).*

104. Late protaspid stages with tubercular swelling on occipital ring: *absent (0); present (1).*

105. Protaspids with median spines: *absent (0); present (1).*

106. Protaspids with anterior spines: *absent (0); present (1).*

107. Protaspid with doublure curved inward resulting in overall globular morphology: *absent (0); present (1).*

108. Meraspid stages with coarse tubercles on the fixed cheek: *absent (0); present (1).*

109. Meraspid stages with a row of tubercles on fixed cheek either side of glabella: *absent (0); present (1).*

110. Meraspid stages with three pairs of tubercles on glabella: *absent (0); present (1).*

111. Spacing of three glabellar tubercle pairs: *equilateral (0); anterior two pairs compressed together (1); no tubercles present (–).*

112. Meraspid stages with row of short spines at pygidium fulcrum: *absent (0); present (1).*

113. Number of tubercles on fixed cheek row: *3 (0); 2 (1)*.

114. Tubercle on eye ridge in meraspid: *absent (0); present (1)*.

Of the 114 characters included in the analysis, 59 code for features of the cephalon, 13 for the thorax, 23 for the pygidium, 16 for cuticular ornamentation, and 19 apply only to juvenile instars. It has long been noted that some trilobite groups, including proetides, may only be united by characteristics evident during juvenile stages (Fortey & Owens 1975; Adrain & Chatterton 1993; Fortey & Chatterton 1998). There has recently been increased discussion surrounding the treatment of ontogenetic characteristics in phylogenetic analyses; while ontogenetic data do improve the accuracy of phylogenetic analyses (Laurin & Germain 2011) it has been shown that incorrect handling of ontogenetic data can negatively impact tree resolution (Lamsdell & Selden 2013) in a manner similar to paedomorphic species (Weins *et al*. 2005). Most analyses to include ontogenetic data do so as discrete characters as part of a broader morphological matrix (Weins *et al*. 2005; Oleson 2009; Haug *et al*. 2010), and this method that has been applied in some previous trilobite analyses (e.g. Fortey & Chatterton 1998), while others have been performed utilising only larval characters (e.g. Chatterton *et al*. 1990) or performed multiple tree searches using separate larval and adult character datasets (e.g. Edgecombe 1992). These latter analyses parallelled an alternative method that seeks to assess the phylogenetic signal of different ontogenetic stages through the use of ontotrees (i.e. performing a number of analyses with the same taxa where each analysis includes data from only a single ontogenetic stage). Such a method has been utilised both phenetically (Michener 1977) and phylogenetically (Steyer 2000); however, while absolute congruence between all the ontotrees would allow a definitive hypothesis of relationships between the included taxa, it is impossible to resolve any incongruence between the different ontotree topologies. A new method was recently proposed by Wolfe & Hegna (2013) that, in a number of ways, represents a progression beyond the ontotree concept; this method also codes individual instars as separate taxonomic units but includes all instars in a single analysis. This method, however. is primarily intended for testing the affinities of larval stages of uncertain taxonomic affinity, a situation most likely to arise where species undergo metamorphic development. Coding ontogenetic data as separate characters is also problematic, however, as heterochronic perturbations in the timing of development and maturities can make the recognition of homologous developmental stages difficult. Recent studies on trilobites have shown that the protaspid larval phase does not encompass the same developmental stages in all trilobites (Park & Choi 2011a), casting doubt on the validity of the standard direct comparison between final stage protaspides. In order to account for these issues, it has been suggested that comparisons be made only when the entire ontogenetic series is taken into account (Park & Choi 2011a), and recent work has attempted to characterise this both descriptively (Lerosey-Aubril & Feist 2006) and quantitatively (Crônier 2013) in a number of trilobite species. In many cases, however, the entire ontogenetic series will not be available for study, and although instars can be recognised as in the current study it is impossible to correlate these stages with certainty between species. Another concern, as noted by Wolfe & Hegna (2013), is that characters that describe the same structure in different ontogenetic stages result in an increased weighting of that characteristic in the phylogenetic analysis. A number of steps have been taken in this analysis in order to circumvent these issues: first, rather than being coded for specific instars, juvenile characters are applied to the relative stages of development (e.g. protaspid, meraspid) rather than the supposed instar; therefore, coding equivalent stages in development rather than focusing on the exact timing of these stages; second, the coding of a morphological characteristic's presence or absence at a juvenile stage was used to define the presence or absence of the characteristic in the species as a whole. In this manner, specific morphological characteristics were not weighted disproportionately in the analysis through being included as multiple characters. For the majority of characteristics used in this analysis, such as the presence of posterior spines on the posterior of the protaspis stage, this treatment is logically consistent with the occurrence of the character during species development as these spines are universally lost after the protaspid stage. The situation is more complicated when a trait is secondarily lost in only some species, or when seemingly homologous structures occasionally develop later in ontogeny in species lacking them during earlier stages. While neither situation occurs in any of the characters utilised for this study, they can conceivably be resolved in the future by having the first case occur as a dependent character (such as spines lost in adult instars) that is coded as inapplicable if spines are not present on the juveniles. If the primary character on which the dependent character relies is unknown, then the dependent character will also be coded as unknown. For the second scenario, the development of homologous structures at a different point in ontogeny could be coded as a second state within the existing character; in this case, when the earlier ontogenetic stages are unknown the character will have to be coded as unknown. Alternatively, the presence or absence of the structures in the species could be coded as a single character and the timing of their development being a separate dependent character. While these protocols should serve to remove the problems of unduly weighting certain morphological traits in the analysis, further work is needed to ascertain how best to implement them across other datasets.

The analysis was performed using TNT (Goloboff *et al*. 2008; made available with the sponsorship of the Willi Hennig Society) employing random addition sequences followed by tree bisection-reconnection (TBR) branch swapping (the *mult* command in TNT) with 100,000 repetitions with all characters unordered and of equal weight. Jackknife (Farris *et al*. 1996) and Bremer support (Bremer 1994) values were calculated in TNT and the Consistency, Retention, and Rescaled Consistency indices were calculated in Mesquite 2.73 (Maddison & Maddison 2010). Nonparametric bootstrapping is often difficult with morphological data due to the limited size of the dataset (Zander 2003), and so was not performed for this analysis. Jackknifing was performed using simple addition sequence and tree bisection–reconnection (TBR) branch swapping, with 100,000 repetitions and 33% character deletion. The matrix and character listing has been deposited in the online MorphoBank database (O'Leary & Kaufman 2012) under the project code p540 and can be accessed from http://morphobank.org/permalink/?P540.

Results

Analysis of the phylogenetic matrix as detailed in the methods section yielded twelve most parsimonious trees with a tree length of 440 steps, an ensemble Consistency Index of 0.321, ensemble Retention Index of 0.671, and Rescaled Consistency Index of 0.215, the strict consensus of which is presented here (fig. 1). A traditional proetide clade is retrieved, comprising Hystricuridae, Dimeropygidae, Toernquiistidae, Rorringtoniidae, Tropidocoryphidae, Scharyiidae, Bathyuridae, Proetidae, Phillipsiidae, Aulacopleuridae, Brachymetopidae, and Otarionidae. Aulacopleurida as defined by Adrain (2011) is shown to be paraphyletic in regard to Proetida, with hystricurids resolving as sister group to all other proetides and dimeropygids and toernquistiids forming a dimeropygoid clade as sister group to the remaining proetides. These form two clades, one consisting of proetids and proetid-like aulacopleuroids while the other comprises Aulacopleuroidea *sensu stricto*. This first clade, comprising Bathyridae, Proetidae, Phillipsiidae, Tropidocoryphidae, Rorringtoniidae, and Scharyiidae, is herein considered to represent the superfamily Proetoidea. There is no logical reason to ascribe ordinal status to the second clade of remaining aulacopleuroids, and so they are also reduced to superfamilial status. As defined herein, the superfamily Aulacopleuroidea therefore consists of the families Aulacopleuridae, Brachymetopidae, and Otarionidae (including at present the Cyphaspidae).

The sister group to Proetida comprises a large clade including various ptychopariids and representatives of two of the other traditional trilobite orders: Phacopida and Asaphida. Phacopida, comprising Phacopina, Cheirurina and Calymenina, is monophyletic, with the relationships of Cheirurina agreeing with other recent phylogenetic analyses (Congreve 2012). Asaphides, however, are revealed to be polyphyletic, forming part of a paraphyletic grade including olenids leading to Phacopida. Remopleurids and aphelaspids, forming Remopleuroidea, resolve as the sister group to Phacopida, while Asaphida *sensu stricto* (here represented by asaphids and ceratopygids – Asaphoidea) are positioned at the base of the clade, separated from the remopleuroids by the olenids.

Evidence of asaphide polyphyly, and some form of relationships with olenids, has been mounting in recent years, with supposed asaphide synapomorphies being shown to have non-homologous developmental origins in asaphoids and remopleuroids (Adrain *et al*. 2009; Park & Choi 2011b) and some hypothesised basal asaphides having olenid-like larval forms (Lee & Chatterton 2005). The topology herein, therefore, corroborates these findings.

The remaining ptychopariids in the analysis resolve as polyphyletic, with ellipsocephalids, solenopleurids, and marjumiids (in part) forming a grade of taxa at the base of the tree, while ehmaniellids form the sister group to the asaphide/phacopide and proetide clades. Harpetids resolve between ehmaniellids and the other ptychopariids, with tricrepicephalids, crepicephalids, coosellids, and some majumiids resolving at the base of the harpetid group. A non-monophyletic Ptychopariida is unsurprising and agrees with previous phylogenetic analyses (Edgecombe 1992). Further work, however, along with a more comprehensive taxonomic sampling, is needed to fully unravel the relationships of the various ptychopariid groups.

Discussion

The recovery of proetide monophyly through phylogenetic analysis confirms that only one major clade of trilobites survived through the Late Devonian into the Carboniferous, as has been assumed in recent studies of trilobite biodiversity over the late Palaeozoic (Owens 2003; Lerosey-Aubril & Feist 2012; Feist & McNamara 2013). Two ontogenetic characteristics define a monophyletic Proetida: the initial lateral eye formation in early protaspids occurring at the lateral margin rather than the anterior margin, and the form of the protaspid glabella – tapering, with a preglabellar field. A number of adult characters also define the base of the clade, although most are subsequently lost or modified in some proetide groups; these include the possession of a quadrate or shield-shaped hypostome with angular posterior margins, the hypostome medium body being divided by a deep groove that entirely transverses the median body, the presence of an enlarged thoracic spine on the sixth tergite, and a tergite count of between 7 and 10. The two major proetide clades, the Aulacopleuroidea and Proetoidea, are further united by the later protaspid stages having a tubercular swelling on the occipital ring. Aulacopleuroids are united by the occurrence of a tubercle on the eye ridge in the meraspid stage, an extension of the carapace ornamentation onto the genal spines, L1 being detached from the glabella (a condition which is achieved convergently in proetids and phillipsiids), and S2 being effaced. Proetoids are defined by the lateral eye being scimitar shaped and expanding beyond the palpebral along, with a number of reversals; the lateral eyes diverge posteriorly as opposed to being equilateral and occupy at least 30% of the carapace length, while the meraspid stages lack a row of tubercles on the fixed cheek either side of the glabella. The division of taxa between the proetoids and aulacopleuroids is different to in previous classifications, with bathyurids, rorringtoniids, and scharyiids being aligned with tropidocoryphids and proetids under Proetoidea. The relationship of rorringtoniids and scharyiids to aulacopleurids and brachymetopids has always been in flux; rorringtoniids were considered sister group to aulacopleurids by Adrain & Chatterton (1993), with scharyiids and brachymetopids positioned at the base of the clade, while Owens & Hammann (1990) included scharyiids within brachymetopids, and placed rorringtoniids at the base of the group. Both scharyiids and rorringtoniids, however, possess the proetoid scimitar-shaped eyes and as well as broad, blade-like genal spines, which they share with both proetids and tropidocoryphids. Scharyiids and tropidocoryphids also share the expression of a sudden constriction of the anterior third of the glabella. The enigmatic genus *Holotrachelus*, meanwhile, resolves within the cheirurids, an assignment suggested previously by Suzuki (2001).

The rearrangement of the proetide familial groups serves to alter the patterns of proetide evolution throughout the Palaeozoic, with a number of proetoid groups going extinct prior to the Carboniferous. The current topology suggests a Cambrian origin for each of the major proetide clades; however, it is possible that both aulacopleuroids and proetoids originated from a paraphyletic Hystricuridae, or some currently unsampled ptychopariid groups, in the Ordovician. Either way, it is clear that both aulacopleuroids and proetoids independently survived the end-Devonian mass extinction and persisted through into the Carboniferous and Permian. This begs the question as to whether there was some inherent property of the group that permitted two of its clades to weather this biotic crisis that resulted in the extinction of all other trilobite groups; however, further studies are needed to ascertain if such a consideration bears any merit of if proetides were simply fortuitous benefactors of contingency. The phylogenetic framework presented here, with its support of proetide monophyly, is a crucial first step towards resolving this issue.

Acknowledgements

Thomas Hegna (Western Illinois University) and Jo Wolfe (American Museum of Natural History) provided a number of useful discussions on the handling of ontogenetic data in phylogenetic analysis that provided a springboard for the ideas presented here. Curtis Congreve (Pennsylvania State University) gave invaluable assistance with trilobite terminology and interesting discussion on the state of trilobite taxonomy. Amanda Falk (University of Kansas) commented on and improved earlier versions of the manuscript.

References

Adrain, J. M. 2011. Class Trilobita Walch, 1771. *In*: Zhang, Z.-Q. (Ed.) Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness. *Zootaxa* **3148**, 104–109.

Adrain, J. M. & Chatterton, B. D. E. 1993. A new rorringtoniid trilobite from the Ludlow of Arctinc Canada. *Canadian Journal of Earth Sciences* **30**, 1634–1643.

Adrain, J. M. & Chatterton, B. D. E. 1994. The aulacopleurid trilobite *Otarion*, with new species from the Silurian of Northwestern Canada. *Journal of Paleontology* **68**, 305–323.

Adrain, J. M., Fortey, R. A. & Westrop, S. R. 1998. Post-Cambrian trilobite diversity and evolutionary faunas. *Science* **280**, 1922–1925.

Adrain, J. M., Peters, S. E. & Westrop, S. R. 2009. The Marjuman trilobite *Cedarina* Lochman: thoracic morphology, systematics, and new species from western Utah and eastern Nevada, USA. *Zootaxa* **2218**, 35–58.

Adrain, J. M., Westrop, S. R., Chatterton, B. D. E. & Ramsköld, L. 2000. Silurian trilobite alpha diversity and the end-Ordovician mass extinction. *Paleobiology* **26**, 625–646.

Angelin, N. P. 1851. *Paleontologia Scandinavica. Pars 1.Crustacea Formationis Transitionis. Fasc. 1.* Paleontologica Suecica, 1–24.

Barrande, J. 1846. *Notice Préliminaire sur le Systême Silurien et les Trilobites de Bohême*. 97 pp. Leipsic.

Barrande, J. 1872. *Systême Silurien du Centre de la Bohême*. Supplement to volume I, Prague and Paris.

Beecher, C. E. 1897. Outline of a natural classification of the trilobites. *American Journal of Science* **3**, 89–106, 181–207.

Bergström, J. 1973. Organization, life, and systematics of trilobites. *Fossils and Strata* **2**, 1–69.

Bergström, J. 1977. Proetida – a disorderly order of trilobites. *Lethaia* **10**, 95–105.

Billings, E. 1865. Paleozoic fossils VI: Containing descriptions of new or little known speices of organic remains from the Silurian rocks. *1861-1865: Geological Society of Canada* **1,** 169–394.

Bremer, K. 1994. Branch support and tree stability. *Cladistics* **10**, 295–304.

Bridge, J. 1930. Geology of the Eminence and Cardareva quadrangles, Missouri. *Bureau of Geology and Mines* **24**, 1–228.

Brusatte, S. L. 2010. Representing supraspecific taxa in higher-level phylogenetic analyses: guidelines for palaeontologists. *Palaeontology* **53**, 1–9.

Chatterton, B. D. E. 1971. Taxonomy and ontogeny of Siluro-Devonian trilobites from near Yass, New South Wales. *Palaeontographica Abteilung A* **137**, 1–108.

Chatterton, B. D. E. 1994. Ordovician proetide trilobite *Dimeropyge*, with a new species from Nortwestern Canada. *Journal of Paleontology* **68**, 541–556.

Chatterton, B. D. E., Edgecombe, G. D., Waisfeld, B. G. & Vaccari, N. E. 1998. Ontogeny and systematics of Toernquistiidae (Trilobita, Proetida) from the Ordovician of the Argentine Precordillera. *Journal of Paleontology* **72**, 273–303.

Chatterton, B. D. E. & Ludvigsen, R. 1976. Silicified Middle Ordovician trilobites from the south Nahanni River area, District of Makenzie, Canada. *Palaeontographica Abteilung A* **154**, 1–106.

Chatterton, B. D. E. & Speyer, S. E. 1989. Larval ecology, life history strategies, and patterns of extinction and survivorship among Ordovician trilobites. *Paleobiology* **15**, 118–132.

Chatterton, B. D. E., Siveter, D. J., Edgecombe, G. D. & Hunt, A. S. 1990. Larvae and relationships of the Calymenina (Trilobita). *Journal of Paleontology* **64**, 255–277.

Choi, D. K., Kim, E.-Y. & Lee, J. G. 2008. Upper Cambrian polymerid trilobites from the Macheri Formation, Yongwol, Korea. *Geobios* **41**, 183–204.

Congreve, C. R. 2012. *Evolutionary patterns of trilobites across the end Ordovician mass extinction*. Unpublished PhD thesis, University of Kanas, 260 p.

Congreve, C. R. 2013. Cladal turnover: the end-Ordovician as a large-scale analogue of species turnover. *Palaeontology* **56**, 1285–1296.

Conrad, T. A. 1841. Fifth annual report on the paleontology of the State of New York. *New York Geological Survey Annual Report* **5**, 25–57.

Cooper, B. N. 1953. Trilobites from the Lower Champlainian formations of the Appalacian Valley. *Geological Society of America Memoirs* **55**, 1–69.

Crônier, C. 2013. Morphological disparity and developmental patterning: contribution of phacopid trilobites. *Palaeontology* **56**, 1263–1271.

Dai, T. & Zhang, X. 2012. Ontogeny of the redlichiid trilobite *Metaredlichia cylindrica* from the Lower Cambrian (Stage 3) of South China. *Journal of Paleontology* **86**, 646–651.

Edgecombe, G. D. 1992. Trilobite phylogeny and the Cambrian-Ordovician 'event': cladistics reappraisal. *In* Novacek, M. J. and Wheeler, Q. D. (eds): *Extinction and Phylogeny*, 144–177. Columbia University Press, New York.

Farris, J. S., Albert, V. A., Källersjö, M., Lipscomb, D. & Kluge, A. G. 1996. Parsimony jackknifing outperforms neighbor-joining. *Cladistics* **12**, 99–124.

Feist, R. 1991. The Late Devonian trilobite crises. *Historical Biology* **5**, 197–214.

Feist, R. & McNamara, K. J. 2007. Biodiversity, distribution and patterns of extinction of the last odontopleuroid trilobites during the Devonian (Givetion, Frasnian). *Geological Magazine* **144**, 777–796.

Feist, R. & McNamara, K. J. 2013. Patterns of evolution and extinction in proetid trilobites during the Late Devonian mass extinction event, Canning Basin, Western Australia. *Palaeontology* **56**, 229–259.

Fortey, R. A. 1997. Classification. pp. 289–302. *In:* Kaesler, R. L. (ed.) *Treatise on Invertebrate Paleontology. Part O, Revised. Arthropoda 1, Trilobita 1 (Introduction, Order Agnostida, Order Redlichiida).* Geological Society of America and University of Kansas Paleontological Institute. Boulder, Colorado and Lawrence, Kansas. 530 p.

Fortey, R. A. 2001. Trilobite systematics: the last 75 years. *Journal of Paleontology* **75**, 1141–1151.

Fortey, R. A. & Chatterton, B. D. E. 1998. Classification of the trilobite suborder Asaphina. *Palaeontology* **31**, 165–222.

Fortey, R. A. & Owens, R. M. 1975. Proetida–a new order of trilobites. *Fossils and Strata* **4**, 227–239.

Fortey, R. A. & Owens, R. M. 1979. Enrollment in the classification of trilobites. *Lethaia* **12**, 219–226.

Goldfuss, G. A. 1839. Beiträge zur Petrefactenkunde. *Verhandlungen* der Kaiserlich *Leopoldinisch-Carolinischen Deutschen Akademie der Naturforscher* **9**, 327–364.

Goloboff, P. A., Farris, J. S. & Nixon, K. C. 2008. TNT, a free program for phylogenetic anaylsis. *Cladistics* **24**, 774–786.

Gürich, G. 1907. Versuch einer Neueinteilung Trilobiten. *Centralbllatt. für Mineralogy,* 129–133.

Haas, W. 1969. Lower Devonian trilobites from central Nevada and northern Mexico. *Journal of Paleontology* **43**, 641–659.

Hahn, G. 1964. Die Gattung *Brachymetopus* McCoy (Trilobita) im Etroeungt und Unter-Karbon Deutschlands. *Senckenbergiana lethaea* **45**, 167–199.

Harrington, H. J., Henningsmoen, G., Howell, B. F., Jaanusson, V., Lochman-Balk, C., Moore, R. C., Poulsen, C., Rasetti, F., Richter, E., Richter, R., Schmidt, H., Sdzuy, K., Struve, W., Tripp, R., Weller, J. M. & Whittington, H. B. 1959. Systematic Descriptions. pp. 171–539. *In:* Moore, R. C. (ed.) *Treatise on Invertebrate Paleontology. Part O. Arthropoda 1 (Arthropoda–General Features, Protarthropoda, Euarthropoda–General Features, Trilobitomorpha).* Geological Society of America and University of Kansas Paleontological Institute. Boulder, Colorado and Lawrence, Kansas. 560 p.

Haug, J. T., Maas, A. & Waloszek, D. †*Henningsmoenicaris scutula*, †*Sandtorpia vestrogothiensis* gen. et. sp. nov. and heterochronic events in early crustacean evolution. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **100**, 311–350.

Hawle, I. & Corda, A. J. C. 1847. *Prodrom einer Monographie der böhmischen Trilobiten*. 176 pp, 7 pls. Prague.

Henningsmoen, G. 1951. Remarks on the classification of trilobites. *Norsk Geologisk Tidsskrift* **29**, 174–217.

Hu, C.-H. 1978. Ontogenies of four Upper Cambrian Trilobites from the Bonneterre Dolomite, Missouri. *Transactions and Proceedings of the Palaeontological Society of Japan* **111**, 348–357.

Hu, C.-H. 1998. Ontogenies of two Middle Cambrian trilobites from the Great Basin of the western United States. *Journal of Taiwan Museum* **51**, 107–117.

Hupé, P. 1955. Classification des trilobites. *Annales de Paléontology* **41**, 91–325.

Lamsdell, J. C. & Selden, P. A. 2013. Babes in the wood – a unique window into sea scorpion ontogeny. *BMC Evolutionary Biology* **13:98**, 1–46.

Laurin, M. & Germain, D. 2011. Developmental characters in phylogenetic inference and their absolute timing information. *Systematic Biology* **60**, 630–644.

Lee, D.-C. & Chatterton, B. D. E. 1997. Ontogenies of trilobites from the Lower Ordovician Garden City Formation of Idaho and their implications for the phylogeny of the Cheirurina. *Journal of Paleontology* **71**, 683–702.

Lee, D.-C. & Chatterton, B. D. E. 2005. Protaspides of Upper Cambrian *Aphelaspis* (Ptychopariida. Trilobita) and related species with their taxonomic implications. *Palaeontology* **48**, 1351–1375.

Lermontova, E. V. 1951. *Nizhnekembriyskiye trilobity i brakhiopody Vostochnoy Sibiri*. Gosgeolizdat, Moskva-Leningrad, 1–222.

Lerosey-Aubril, R. & Feist, R. 2005. First carboniferous protaspid larvae (Trilobita). *Journal of Paleontology* **79**, 702–718.

Lerosey-Aubril, R. & Feist, R. 2006. Late ontogeny and hypostomal condition of a new cyrtosymboline trilobite from the Famennian of Morocco. *Palaeontology* **49**, 1053–1068.

Lerosey-Aubril, R. & Feist, R. 2012. Quantitative approach to diversity and decline in late Palaeozoic trilobites. *In*: Talent, J. A. (Ed.) Earth and Life. P. 535–555.

Lütke, F. 1980. Zur evolution der altpaläozoischen Proetina (Trilobita). *Senckenbergiana lethaea* **61**, 73–144.

Lieberman, B. S. & Karim, T. S. 2010. Tracing the trilobite tree from the root to the tips: a model marriage of fossils and phylogeny. *Arthropod Structure & Development* **39**, 111–123.

Lochman, C. 1936. New trilobite genera from the Bonneterre Dolomite (Upper Cambrian) of Missouri. *Journal of Paleontology* **10**, 35–43.

Lochman, C. & Duncan, D. 1944. Early Upper Cambrian faunas of central Montana. *Geological Society of America Special Paper* **54**, 1–173.

Lu, Y. H. 1940. On the ontogeny and phylogeny of *Eoredlichia intermediate* Lu (sp. nov.). *Bulletin of the Geological Society of China* **3**, 333–342.

Ludvigsen, R. 1979. A trilobite zonation of Middle Ordovician rocks, southwestern district of Mackenzie. *Geological Survey of Canada Bulletin* **312**, 1–99.

Maddison, W. P. & Maddison, D. R. 2010. Mesquite: A modular system for evolutionary analysis. Version 2.73. http://mesquiteproject.org.

Månsson, K. & Clarkson, E. N. K. 2012. Ontogeny of the Upper Cambrian (Furongian) olenid trilobite *Protopeltura aciculata* (Angelin, 1854) from Skåne and Västergötland, Sweden. *Palaeontology* **55**, 887–901.

McNamara, K. J. & Feist, R. 2006. New styginids from the Late Devonian of Western Australia – the last corynexochid trilobites. *Journal of Paleontology* **80**, 981–992.

McNamara, K. J., Feist, R. & Ebach, M. C. 2009. Patterns of evolution and extinction in the last harpetid trilobites during the late Devonian (Frasnian). *Palaeontology* **52**, 11–33.

Meek, F. B. 1870. Descriptions of fossils collected by the U. S. Geological Survey under the charge of Clerence King, Esq. *Proceedings of the Academy of the Natural Sciences of Philadelphia* **22**, 56–64.

Michener, C. D. 1977. Discordant evolution and the classification of allodapine bees. *Systematic Zoology* **26**, 32–56.

Moore, R. C. 1959. *Treatise on Invertebrate Paleontology. Part O. Arthropoda 1 (Arthropoda–General Features, Protarthropoda, Euarthropoda–General Features, Trilobitomorpha).* Geological Society of America and University of Kansas Paleontological Institute. Boulder, Colorado and Lawrence, Kansas. 560 p.

O'Leary, M. A. & Kaufman, S. G. 2012. MorphoBank 3.0: Web application for morphological phylogenies and taxonomy. http://www.morphobank.org.

Olesen, J. 2009. Phylogeny of Branchiopoda (Crustacea) – character evolution and contribution of uniquely preserved fossils. *Arthropod Systematics & Phylogeny* **67**, 3–39.

Osmólska, H. 1970. Revision of non-cyrtosymbolinid trilobites from the Tournasian-Namurian of Eurasia. *Palaeontologia Polonica* **23**, 1–165.

Owens, R. M. 1981. The Ordovician proetacean trilobite *Rorringtonia*. *Geological Magazine* **118**, 89–94.

Owens, R. M. 1994. Pseudoextinctions in Late Devonian proetide trilobites. *Historical Biology* **9**, 207–221.

Owens, R. M. 2003. The stratigraphical distribution and extinctions of Permian trilobites. *Special Papers in Palaeontology* **70**, 377–397.

Owens, R. M. & Hammann, W. 1990. Proetide trilobites from the Cystoid Limestone (Ashgill) of NW Spain, and the suprageneric classification of related forms. *Paläontologische Zeitschrift* **64**, 221–244.

Palmer, A. R. 1962. *Glyptagnostus* and associated trilobites in the United States. *Professional Paper of the United States Geological Survey* **374**, 1–49.

Park, T.-Y. & Choi, D. K. 2011a. Constraints on using ontogenetic data for trilobite phylogeny. *Lethaia* **44**, 250–254.

Park, T.-Y. & Choi, D. K. 2011b. Ontogeny of the Furongian (late Cambrian) remopleuridoid trilobite *Haniwa quadrata* Kobayashi, 1933 from Korea: implications for trilobite taxonomy. *Geological Magazine* **148**, 288–303.

Patterson, C. & Smith, A. B. 1989. Periodicity in extinction: the role of systematics. *Ecology* **70**, 802–811.

Ramsköld, L. & Edgecombe, G. D. 1991. Trilobite monophyly revisited. *Historical Biology* **4**, 267–283.

Raymond, P. E. 1905. The trilobites of the Chazy Limestone. *Annals of the Carnegie Museum* **3**, 328–386.

Richter, R. 1933. Crustacea (Paläontologie). *Handwörterbuch der Naturwissenschaften* **2**, 840–864.

Robison, R. A. 1971. Additional middle Cambrian trilobites from the Wheeler Shale of Utah. *Journal of Paleontology* **45**, 796–804.

Robison, R. A. & Babcock, L. E. 2011. Systematics, paleobiology, and taphonomy of some exceptionally preserved trilobites from Cambrian Lagerstätten of Utah. *Paleontological Contributions* **5**, 1–47.

Roemer, F. A. 1854. Beiträge zur geologischen Kenntnis des nordwestlichen Harzgebirges. *Palaeontolographica* **3**, 1–67.

Ross Jr., R. J. 1951. Stratigraphy of the Garden City Formation in northeastern Utah, and its trilobite faunas. *Bulletin of Peabody Museum of Natural History* **6**, 1–161.

Růžička, R, 1935. Pripevek k pozani trilobite Barrandienu. *Rozpravy Československé Akademickie Věd* **44**, 1–8.

Salter, J. W. 1864. The trilobites of the Cambrian, Silurian, and Devonian Formations, Part 1 (Devonian and Silurain). *Monograph of the Palaeontographical Society* **67**, 1–80.

Shumard, B. F. 1861. The Primordial zone of Texas, with descriptions of new fossils. *American Journal of Science* **32**, 213–221.

Steyer, J.-S. 2000. Ontogeny and phylogeny in temnospondyls: a new method of analysis. *Zoological Journal of the Linnean Society* **130**, 449–467.

Stigall, A. L. 2010. Invasive species and biodiversity crises: testing the link in the Late Devonian. *PLoS One* **5**, e15584, 1–7.

Stigall, A. L. 2012. Speciation collapse and invasive species dynamics during the Late

Devonian “Mass Extinction”. *GSA Today* **22**, 4–9.

Suzuki, Y. 2001. Revision of the late Ordovician trilobite *Holotrachelus punctillosus* (Törnquist, 1884) from Dalarna, Sweden. *Acta Palaeontologica Polonica* **46**, 331–348.

Swinnerton, H. H. 1915. Suggestions for a revised classification of trilobites. *Geological Magazine* **2**, 407–496, 538–545.

Troedsson, G. T. 1937. On the Cambro-Ordovician faunas of western Qurug Tagh, eastern Tien-shan. *Palaeontologia Sinica* **106**, 1–74.

Törnquist, S. L. 1884. Undersökningar öfver SiljansomrÍdets trilobitfauna. *Sveriges Geologiska Undersökning C* **66**, 1–101.

Van Viersen, A. P., Prescher, H. & Savelsbergh, J. 2009. *Bulletin de L’Institut Royal des Sciences Naturelles de Belgique* **79**, 43–53.

Wahlenburg, G. 1818. Petricata telluris Svecanae. *Nova Acta Regiae Societatis Scientarum Upsaliensis* **8**, 116.

Walcott, C. D. 1916. Cambrian geology and palaeontology 3, Cambrian trilobites. *Smithsonian Miscellaneous Collections* **64**, 303–457.

Wang, Q.-Z. 1989. Early Silurian trilobites from Wulong, southeastern Sichuan (China). *Journal of Hebei College of Geology* **12**, 422–440.

Webster, M. 2014. Ontogeny and intraspecific variation of the early Cambrian trilobite *Olenellus gilberti*, with implications for olenelline phylogeny and macroevolutionary trends in phenotypic canalization. *Journal of Systematic Palaeontology*. doi:

10.1080/14772019.2013.852903

Weins, J.J., Bonett, R. M. & Chippindale, P. T. 2005. Ontogeny discombobulates phylogeny: paedomorphosis and higher-level salamander relationships. *Systematic Biology* **54**, 91–110.

Westergård, A. H. 1922. Sveriges Olenidskiffer. *Sveriges Geologiske Undersøkelse Series* **18**, 1–205.

Westergård, A. H. 1944. Borrningar genom Skånes alunskiffer 1941-1942. *Sveriges Geologiske Undersøkelse Series C* **459**, 1–45.

Whittington, H. B. 1959. Silicified Middle Ordovician trilobites: Remoleuridae, Trinucleidae, Raphiophoridae, Endymioniidae. *Bulletin of the Museum of Comparative Zoology* **121**, 371–496.

Whittington, H. B. 1963. Middle Ordovician trilobites from Lower Head, Western Newfoundland. *Bulletin of the Museum of Comparative Zoology* **129**, 1–118.

Whittington, H. B. & Kelly, S. R. A. 1997. Morphological terms applied to Trilobita. pp. 313–329. *In:* Kaesler, R. L. (ed.) *Treatise on Invertebrate Paleontology. Part O, Revised. Arthropoda 1, Trilobita 1 (Introduction, Order Agnostida, Order Redlichiida).* Geological Society of America and University of Kansas Paleontological Institute. Boulder, Colorado and Lawrence, Kansas. 530 p.

Wolfe, J. M. & Hegna, T. A. 2013. Testing the phylogenetic position of Cambrian pancrustacean larval fossils by coding ontogenetic stages. *Cladistics*. doi:

10.1111/cla.12051.

Yuan, W.-W., Li, L.-Z., Zhou, Z.-Y. & Zhang, C.-S. 2001. Ontogeny of the Silurian trilobite *Aulacopleura (Aulacopleura) wulongensis* Wang of Western Hubei and its implications for the phylogeny of the Aulacopleurinae. *Acta Palaeontologica Sinica* **40**, 388–398.

Zander, R. H. 2003. Reliable phylogenetic resolution of morphological data can be better than that of molecular data. *Taxon* **52**, 109–112.

	10	20	30	40	50	60
	70	80	90	100	110	
Eoredlichia intermedia	0000000000	0000000000	0000–00000	1000000000	–000–0–00–	00000–0000
	0000000000	0000–0–0–0	000–000– – –	00–00–????	???????000	–0–0
Elrathia kingii	1100000000	0001010000	0000–00000	1010012200	–000–0–10–	0?????????
	3011101210	0100–100–0	001–111000	00–00–0–10	0000000000	–0–0
Lermontovia dzevanovskii	0000000000	0000010000	0001100000	0–00011111	0000–0–00–	0?????????
	1000000110	0000–0–0–0	000–000– – –	00–00–????	??????????	????
Olenus wahlenbergi	0000101000	0021010000	0001000000	1000011101	1110–0–00–	00000–0000
	2000011010	0000–0–0–0	001–101000	00–00–1000	1000000100	–0–0
Parabolina spinulosa	0100100000	0021000000	0001000000	1000011101	1110–0–00–	00000–0000
	4000011000	0000–0–100	001–100– – –	00–00–1000	1000000100	–0–0
Leptoplastus crassicorne	0100100000	0021000000	0001000000	1000000001	1010–0–00–	00000–0000
	4000001000	0000–0–100	001–100– – –	00–00–1000	1000000000	–0–0
Altiocculus harrisi	1100000000	0001010000	0000–00000	0–10011200	–000–0–10–	0?????????
	1011101210	0100–0–0–2	–00–111000	00–00–????	??????????	????
Crepicephalus buttsi montanaensis	0000100000	0001110001	0000–00010	1010011000	–002–2–00–	0?00100000
	??????????	??10110–1	–1–0111100	00–00–0–10	0000000000	–0–0
Coosella prolifica	0100101000	0031110000	0000–00010	0–10011200	–000–0–00–	0?????????
	??????????	???0–110–1	–1–0111100	00–00–0–10	0000000000	–0–0
Ehmaniella apolabella	0100000000	0001010000	0000–00000	1010011200	–000–0–10–	0?????????
	?0????????	???0–0–0–2	–???111000	00–00–0–10	0000000000	–0–0
Modocia kohli	0100000000	0011010000	0000–00010	0–10012001	0000–0–00–	0?????????
	3000101110	0000–000–0	001–111000	00–00–????	??????????	????
Marjumia typa	0100000000	0000010001	0000–00000	0–10011100	–000–0–00–	0?????????
	0000000010	0000–0–100	01–0100– – –	00–00–????	??????????	????
Solenopleura canaliculata	0100100000	00310110–0	0000–01000	0–??????00	–000–0–1??	0?????????
	??????????	???0–100–3	–???110– – –	00–00–????	??????????	????
Parasolenopleura gregaria	0100100000	00310110–0	0000–01000	10010– – –00	–000–2–00–	0?????????
	0000101010	0000–0–0–0	000–110– – –	00–00–????	??????????	????
Tricrepicephalus texanus	0100000000	0101110000	0000–00010	1010011100	–002–0–00–	0?????????
	4000101110	000100–0–1	–1–0111000	00–00–????	??????????	????
Harpides atlanticus	2200001100	02– – –10011	0010–00001	0–10012?00	–000–0–00–	0?????????
	?0????????	??????????	??????????	??????????	??????????	????
Harpes macrocephalus	1200001100	12– – –10001	0010–00011	1010112100	–000–0–00–	0?????????
	1011101110	0000–0–0–1	–00–111000	00–00–????	??????????	????
Eoharpes benignensis	1200001100	12– – –10001	0010–00011	0–10112100	–000–0–00–	00000–0010
	0011101110	0000–0–0–1	–00–111000	00–00–????	??????????	????
Entomaspis radiatus	2200001100	101– –10001	0001000011	0–10012100	–002–2–00–	00??0–00??
	??????????	???0–0–0–0	01–0111000	00–00–????	??????????	????
Aulacopleura wulongensis	1100001000	00010111– –	1001000000	0–10011200	–111010–10	0?????????
	2011101210	0000–0–0–1	–01–111000	00–00–1101	0101000010	–001
Cyphaspis dabrowni	011101– –01	00010011– –	1101100100	1110011200	–111111–11	0011110111
	??11???110	1000–0–0–0	1???111010	01010–??01	0101000011	1111
Maurotarion struszi	0100000001	?0010111– –	1100–00000	1110011100	–111011010	0?????????
	?1????????	??????????	??????????	????0–??01	0101000011	0101
Brachymetopus germanicus	011101– –01	0– – – –111– –	1101000000	1010012100	–111111–10	0?????????
	5011102110	1000–0–0–5	–1–1111000	01010–????	??????????	????
Rorringtonia kennedyi	1010001011	0031010000	0000–00000	1010011100	–000–0–00–	0?????????
	5011101110	0000–0–0–3	–1–1111001	00–00–????	??????????	????
Bathyurus ulu	10?001– –11	10010010–0	0001200000	0–10012100	–000–1000–	0011100111
	??11???110	0000–0–0–1	–1–1111000	10–00–0–01	010????000	–?–0
Dimeropyge speyeri	010101– –01	00210011– –	2–01100000	0–10011100	–111111–10	010???11??
	5111101111	0010–0–0–1	–1–0111010	10–00–1111	0110000011	01–0
Holotrachelus punctillosus	1100100000	11200011– –	0001000000	10110– – –00	–000–0–00–	0011120010
	5002101310	0000–0–110	01–1100– – –	00–011????	??????????	????
Proetus talenti	101001– –11	10110011– –	1101000000	1010012100	–000–1000–	0011110111
	?011???010	0000–0–0–3	–???111000	01100–0–11	0101000000	–0–0
Phillipsia belgica	101001– –11	1001000011	1101200000	–10012100	–100–1000–	0011110111
	5011102010	1000–0–0–4	–1–2111001	01110–????	??????????	????
Gerastos tuberculatus	101001– –11	1001001011	1101000000	0–10011200	–00101000–	0?????????
	5011101010	0000–0–0–3	–1–1111000	01100–????	??????????	????
Tropidocoryphe bassei	101001– –11	00110111– –	1000–10000	1010011110	–000–0–00–	0?????????
	5000102100	0000–0–0–3	–1–1111001	00–00–????	??????????	????
Scharyia micropyga	1010000001	01110110–0	0000–10000	1010011100	–111010–0–	0?????????
	5011102110	0000–0–0–3	–1–1111000	00–10–0–11	0101000001	01–0
Maurotarion periergum	0100000001	00010111–0	1000–00000	1010011100	–111011–10	0001110111
	3011101110	1000–0–0–0	101–111000	01010–????	??????????	????

Otarion huddyi	011101– –01	00210111– –	1101000100	1110011100	–111111–11	0011110111
	4111101110	0000–0–0–0	11–1111010	01010–????	???????011	1111
Hintzecurus paragenalatus	0101000000	0000010001	0000–00000	0–10001000	–111010–10	0?????????
	5101001010	0000–0–0–0	101–111000	00–00–??11	0100000010	–???
Politicurus politus	0101000000	0030010001	0000–00000	1100000000	–000–0–00–	0?????????
	5101001010	0000–0–0–0	11–1111000	00–00–????	??????????	????
Toernquistia sanchezae	0010100001	0001010000	0000–00000	1010011100	–011010000	010??11??
	5111101111	0010–0–0–1	–01–111010	10–00–1111	0110000011	0100
Aulacopleura konincki	1100001000	00010111– –	1001000000	0–10011200	–111010–10	0000110111
	1011101210	0000–0–0–1	–01–111000	00–00–????	???????010	–001
Kawina arnoldi	110011– –00	1121000000	0001000000	0–110– – –00	–111010–0–	0010100010
	4002101310	0000–0–111	–1–1100– – –	00–011????	??????????	????
Anacheirurus frederici	0100100000	0121000000	0001000000	1010011100	–111010–0–	1000??00?0
	4000101010	0000–0–101	–1–1100– – –	00–010????	??????????	????
Ceraurinella typa	0100100000	0121000001	0001200000	1010011100	–111010–10	1010100000
	4000101310	000100–101	–1–0100– – –	00–010????	??????????	????
Parapilekia olesnaensis	0100100000	0121000000	0000–00000	1000010100	–111010–0–	1001100000
	4000000010	0000–0–100	01–1100– – –	00–01–????	??????????	????
Eskoharpes palanasus	1200001100	12– – –10001	0010–00011	1010112100	–000–0–00–	00000–0010
	???1???10	0000–?????	?00–1?????	?????–??00	0?00???000	–0–0
Aphelaspis brachyphasis	100001– –00	0031010000	0001000000	1000011100	–000–0–00–	00000–0000
	4??????010	0000–0–0–0	001–101000	00–00–1000	1000110100	–0–0
Ceraurinella nahanniensis	0100100000	0121000001	0001200000	1010011100	–111010–10	1010100000
	??0010?310	000100–101	–1–0100– – –	00–0111000	1000110100	–0–0
Aulacopleura longecornuta	0100000000	00010111– –	1001000000	0–10011100	–111010–10	0?????????
	1011101210	0000–0–0–0	101–111000	00–00–????	??????????	????
Calyptaulax annulata	000001– –00	0121000000	0101200000	0–10011200	–111010–0–	00100–0000
	401110?010	0010–0–0–3	–1–1110– – –	00–00–1000	1000110100	–0–0
Flexicalymene senaria	020011– –00	0121000000	0000–00000	0–10011200	–111010–0–	0010100100
	4011100010	0010–0–0–3	–1–0110– – –	00–00–1000	1000110100	–0–0
Isotelus parvirugosus	010201– –00	00010011– –	2–01000000	0–110– – –00	–000–0–00–	00200–0001
	5011003310	0000–0–0– –	–2– –1–0– – –	00–00–1000	– – – –001000	–0–0
Proceratopyge rectispicatus	0100101000	00010011– –	0001000000	0–10011101	1110–0–00–	0?????????
	5011001010	000110–0–3	–1–1111000	00–00–????	??????????	????
Proceratopyge promisca	0100101000	0001000000	0001000000	0–10011101	1110–0–00–	0?????????
	5011001010	000110–0–3	–1–1111000	00–00–????	??????????	????
Remopleurides caelatus	100021– –10	0031000000	0001000000	0–00011100	–010–0–00–	00210–0001
	??10???310	0000–1–1–1	–???101000	00–00–1000	– – – –111000	–0–0
Remopleurides eximius	100021– –10	00310011– –	2–01000000	0–00011100	–010–0–00–	00210–0001
	4010101310	0000–1–1–1	–00–101000	00–00–????	??????????	????
Asaphus expansus	010211– –00	00010011– –	2–01000000	0–110– – –00	–000–0–00–	00200–0001
	5011003310	0000–0–0–3	–1–2110– – –	00–00–????	??????????	????

Table 1. Character matrix for the phylogenetic analysis.

Figure 1. Strict consensus of twelve most parsimonious trees. Numbers above the nodes are jackknife values with 33% deletion, numbers beneath the nodes in bold are bremer support values.

Chapter 8

The systematics and phylogeny of aulacopleuroid trilobites (Arthropoda: Trilobita: Proetida)

James C. Lamsdell and Paul A. Selden

(Formatted for submission to *Journal of Systematic Palaeontology*)

The first phylogenetic analysis of aulacopleuroid trilobites (112 taxa, 136 characters) is presented, prompting a higher-level taxonomic revision of the group. Aulacopleuroidea Angelin, 1854 is shown to consist of six families; Aulacopleuridae Angelin, 1854, Brachymetopidae Prantl & Přibyl, 1951, Chamaeleoaspidae fam. nov., Maurotarinidae fam. nov., Otarionidae Richter & Richter, 1926, and Strasburgaspidae fam. nov. Many of the aulacopleuroid genera are shown to not be monophyletic, with *Brachymetopus* McCoy, 1847, *Harpidella* McCoy, 1849, *Maurotarion* Alberti, 1969, and *Strasburgaspis* Adrain, 2005 being revealed as polyphyletic and *Otarion* Zenker, 1833 as paraphyletic. As such, the genera *Conoparia* Hawle & Corda, 1847, *Otarionella* Weyer, 1965, and *Tricornotarion* Chatterton, 1971, all previously considered to be junior synonyms, are shown to be valid, and the new genus *Adrainops* gen. nov. is named. A number supposed aulacopleuroid taxa are shown to resolve outside of the group, with *Coignops* Gandl, 1980 and *Asiagena* Maksimova, 1975 shown to be phillipsiids and *Proetides* Walter, 1924 and *Pseudotrinodus* Kobayashi & Hamada 1971 resolving as basal proetoids. *Harpidella* McCoy, 1849 and ‘*Strasburgaspis*’ *kielanae* Repina *et al*. 1975 are retrieved

as sister taxa to the proetoid/aulacopleuroid clade. The tree topology suggests that aulacopleuroids and proetoids origanated during the early Ordovician.

Introduction

Aulacopleuroids are a diverse group of proetide trilobites with their earliest records known from the Tremadocian in the early Ordovician (Lu 1975) and one of the last trilobite groups to go extinct in the Permian, with their final representative known from the lowest Changhsingian stage (Diener 1897). While never reaching the diversity of their sister-group, the Proetoidea, aulacopleuroids are an important component of late Palaeozoic ecosystems and have the potential to be an important group for understanding the different processes operating during the various Palaeozoic mass extinctions because the evolutionary history of the group encompasses both the end-Ordovician and end-Devonian events. Aulacopleuroids are also an important trilobite group because they include *Aulacopleura konincki* (Barrande, 1846), the ontogeny of which has been the subject of intense study (Hughes & Chapman 1995; Fusco *et al*. 2004; Fusco *et al*. 2014) resulting in the species being utilised as a model organism of sorts for understanding trilobite development (Hughes 2003a,b; Hughes *et al*. 2006; Hughes 2007).

Proetide monophyly has been questioned a number of times in the past (Bergström 1977; Adrain 2011); however, the concept has recently gained phylogenetic support (Lamsdell & Selden in prep), and is followed herein. Aulacopleuroid taxonomy of recent years has also been in a state of flux; Lütke (1980) considered aulacopeluroids to include aulacopleurids, dimeropygids, and cyphaspidids, with brachymetopids incorporated within aulacopleurids and including scharyiids and rorringtoniids, while Owens & Hammann (1990) considered aulacopleurids and brachymetopids (including scharyiids) to be sister-taxa with rorringtoniids forming a separate clade. Adrain & Chatterton (1993), meanwhile, considered rorringtoniids and aulacopleurids to be sister-taxa, with brachymetopids and scharyiids occurring at the base of the group. Recently, Adrain (2011) greatly expanded the number of taxa assigned to Aulacopleuroidea, including a large number of Cambrian ptychopariid trilobites within the group along with dymeropygids and hystricuriids; however, subsequent phylogenetic analysis has shown that all these taxa fall outside the clade (Lamsdell & Selden in prep). The same analysis removed scharyiids and rorringtoniids from Aulacopleuroidea, aligning them instead with the proetoids.

Here, we present a comprehensive analysis of the aulacopleuroid genera. Alongside Aulacopleuoidae, a number of ingroup proetide taxa are included in order to test aulacopleuroid monophyly, and to ascertain whether further genera should be removed from the group. This is the first time that aulacopleuroid relationships have been tested through phylogenetic analysis and, with 112 taxa and 136 characters, is one of the largest analyses of trilobite taxa to date.

Methods

Trilobite terminology largely follows Whittington and Kelly (1997), with modifications to the pygidial size classifications following Lamsdell & Selden (in prep). Lamsdell & Selden (in prep) should also be consulted for the handling of ontogenetic data in the analysis; for discussion of the various potential pitfalls of including such data in phylogenetic analyses see their discussion and the references therein.

For the phylogenetic analysis, a matrix of 136 characters coded for 112 taxa was compiled, which can be found in Appendix 4 along with character descriptions. *Hintzecurus paragenalatus* (Ross, 1951) was selected to represent hystricurids as outgroup for the analysis, based on their position as the basal most proetides in the analysis of Lamsdell & Selden (in prep). A number of dimeropygid and proetoid taxa was also include alongside aulacopleuroids as ingroup taxa as the affinities of some genera currently assigned to Aulacopleuroidea as uncertain. Aulacopleuroid genera are each represented by multiple exemplars where possible, as these more accurately represent the character states and transitions of a group than would a single exemplar such as a token species or composite taxon (Brusatte 2010), as well as allowing for the potential of para- or polyphyly. Ingroup taxa were selected based on morphological completeness and, where possible, the type species of each genus was also included in the analysis. Species were coded from figures in the literature, supplemented with observations of specimens where possible. The analysis aims to include all currently recognised aulacopleuroid genera; the only genus excluded from the analysis is *Latecephalus* Nan, 1976, for which adequate data is lacking; however, Zhou (1989) considered *Latecephalus* to be a synonym of *Cordania* Clarke, 1892. In total, 33 aulacopleuroid genera are included, represented by 125 species.

The analysis was performed using TNT (Goloboff *et al*. 2008; made available with the sponsorship of the Willi Hennig Society) employing random addition sequences followed by tree bisection-reconnection (TBR) branch swapping (the *mult* command in TNT) with

100,000 repetitions with all characters unordered and of equal weight. Jackknife (Farris *et al*. 1996) and Bremer support (Bremer 1994) values were calculated in TNT and the Consistency, Retention and Rescaled Consistency Indices were calculated in Mesquite 2.73 (Maddison & Maddison 2010). Nonparametric bootstrapping is often difficult with morphological data due to the limited size of the dataset (Zander 2003) and so was not performed for this analysis. Jackknifing was performed using simple addition sequence and tree bisection- reconnection (TBR) branch swapping, with 100,000 repetitions and 33% character deletion. The matrix and character listing has been deposited in the online MorphoBank database (O'Leary & Kaufman 2012) under the project code p852 and can be accessed from http://morphobank.org/permalink/?P852.

Results

Analysis of the phylogenetic matrix, as detailed in the methods section, yielded 48 most parsimonious trees with a tree length of 472 steps, an ensemble Consistency Index of 0.331, ensemble Retention Index of 0.778, and Rescaled Consistency Index of 0.257, the strict consensus of which is presented here (Figs. 1 & 2). The overall topology of Proetida is congruent with that retrieved in the Lamsdell & Selden (in prep) analysis. The contents of Aulacopleuroidea are largely found to be as traditionally defined, with a few exceptions: '*Strasburgaspis*' *kielanae* Repina *et al*., 1975 and a clade including the type species of *Harpidella* McCoy, 1849 resolve as sister taxa to Proetoidea and Aulacopleuroidea, while *Proetides* Walter, 1924 and *Pseudotrinodus* Kobayashi & Hamada, 1971 are aligned with the Proetoidea. Finally, *Coignops* Gandl, 1980 and *Asiagena* Maskimova, 1975, are resolved as phillipsiids. Aulacopleuroidea is shown to consist of four large clades, with two smaller ancillary clades interspersed. These form the basis of six families: Aulacopleuridae, Brachymetopidae, Chamaeleoaspidae, Maurotarionidae, Otarionidae, and Strasburgaspidae. All of these, except the brachymetopids, comprise taxa previously assigned to Aulacopleuridae; however, the aulacopleurids, as previously defined, are shown to be paraphyletic in relation to Brachymetopidae. A number of genera, as currently defined, are shown to be para- or polyphyletic, and a number of genera previously considered to be junior synonyms are here shown to be valid. These include: *Tricornotarion* Chatterton, 1971, *Conoparia* Hawle & Corda, 1847, and *Otarionella* Weyer, 1965.

Systematic Palaeontology

Class **Trilobita** Walch, 1771

Order **Proetida** Fortey & Owens, 1975

(=Aulacopleurida Adrain, 2011)

Diagnosis. Initial lateral eye formation in early protaspids occurring at the lateral margin; protaspid glabella tapering with a preglabellar field; quadrate or shield-shaped hypostome with angular posterior margins; hypostome medium body being divided by a deep groove that entirely transverses the median body.

Included taxa. Aulacopleuroidea Angelin, 1854; Dimeropygoidea Hupé, 1953; *Harpidella* McCoy, 1849; Hystricuroidea Hupé, 1953; Proetoidea Salter, 1864.

Remarks. The validity of the proetide clade has been debated since its inception, however recent phylogenetic analysis has shown Proetida to be monophyletic (Lamsdell & Selden in prep). While the majority of its constituent taxa resolve within either the hystricuroid, dimeropygoid, aulacopleuroid, or proetoid clades, the Ordovician taxa *Harpidella* McCoy, 1849 and '*Strasburgaspis*' *kielanae* Repina *et al*., 1975 fall between the dimeropygoids and the proetoid/aulacopleuroid clade and are currently left unassigned to higher taxa.

Superfamily **Hystricuroidea** Hupé, 1953

Diagnosis. Cranidia with short anterior sections of facial suture; anterior part of cranidium relatively narrow and small; very large eyes and large palpebral lobes; glabella violin-shaped with anterior, waisted constriction; posterior fixigenae extended prominently in transverse direction; pygidium relatively large, with at least three fully developed segments, and often prominent posterior pleural spines (Adrain *et al*. 2003).

Included taxa. Hintzecuridae Adrain *et al*., 2003; Hystricuridae Hupé, 1953.

Remarks. Hystricuridae is here raised to superfamilial status. Its constituent subfamilies, Hintzecurinae and Hystricuridae, are both raised to the rank of family.

Superfamily **Dimeropygoidea** Hupé, 1953

Diagnosis. Hypostome with unsclerotised anterior portion; thorax with tubercular swellings in pleural field alongside axis; tergites showing marked deflection at fulcrum; pygidial marginal rim overturned onto inflated pygidial lateral margin; protaspid eye ridges suppressed.

Included taxa. Dimeropygidae Hupé, 1953 (=Celmidae Jaanusson, 1956); Toernquistiidae Hupé, 1953.

Remarks. Dimeropygoids exhibit a number of similarities with otarionids and cyphaspidids in the expression of fulcral spines on the pygidium during ontogeny and in the pygidial marginal rim being overturned onto the inflated lateral margin of the pygidium, however dimeropygoids lack the posterior medial indentation expressed in protaspids and the expression of the tubercle on the eye ridges in meraspids found in aulacopleuroids. Similar fulcral spines are also known from *Scharyia* Přibyl, 1946a while a number of proetoids exhibit the overturning of the pygidial margins, and it seems that these characteristics, along with others, represent deep-seated parallelisms within the proetide clade.

Superfamily **Proetoidea** Salter, 1864

(=Bathyuroidea Walcott, 1886)

Diagnosis. Lateral eyes scimitar-shaped; thoracic axial rings constant width until the terminal pre-pygidial ring; protaspids lacking ancillary posterior spines; meraspids lacking row of tubercles on fixed cheek either side of the glabella.

Included taxa. Bathyuridae Walcott, 1886; Phillipsiidae Oehlert, 1886; Proetidae Salter, 1864; *Proetides* Walter, 1924; *Pseudotrinodus* Kobayashi & Hamada 1971; Raymondinidae Clark, 1924 (=Glaphuridae Hupé, 1953); Rorringtoniidae Owens & Hammann, 1990; Scharyiidae Osmólska, 1957; Telephinidae Marek. 1952; Tropidocoryphidae Přibyl, 1946b.

Remarks. *Proetides* and *Pseudotrinodus* were traditionally considered brachymetopids; however, their similarities to the group are largely superficial, lacking as they do the vaulted carapace, the broad lateral carapace shelf, and the 14 axial rings in the pygidium.

A number of characteristics, including the form of the lateral eyes and the narrowing of the thoracic axial rings, firmly align both genera with the proetoids. Together with the scharyiids and rorringtoniids, they form a paraphyletic grade of aulacopleuroid-like proetoids that comprise the base of the proetoid clade. *Proetides*, however, is Carboniferous in age, resulting in a large ghost range given the current topology, and it seems likely that increased sampling of proetoid taxa will refine its relationships within the group.

Phillispiids were placed within Proetidae by Jell & Adrain (2003), although subsequent authors have continued to recognize the two groups as distinct families (e.g. Lerosey-Aubril & Feist 2005). The current analysis fails to resolve this issue, and the two families are retained here pending further analysis. Two traditionally aulacopleuroid taxa, *Coignops* Gandl, 1980 and *Asiagena* Maskimova, 1975, are resolved as phillipsiids herein. *Coignops* was considered to be a phillipsiid by Hahn & Brauckmann (1984), and both *Coignops* and *Asiagena* share an almost identical glabella morphology with phillipsiids, and so both are transferred to the family herein.

Superfamily **Aulacopleuroidea** Angelin, 1854

Diagnosis. Converging facial sutures positioned dorsally on carapace; protaspids with posterior medial indentation; tubercle on eye ridges in meraspid.

Included taxa. Aulacopleuridae Angelin, 1854; Brachymetopidae Prantl & Přibyl, 1951; Chamaeleoaspidae fam. nov.; Cyphaspididae Přibyl 1947; Maurotarionidae fam. nov.; Otarionidae Richter & Richter 1926; Strasburgaspidae fam. nov.

Family **Aulacopleuridae** Angelin, 1854

Diagnosis. Carapace flattened, free cheeks broad; palpebral lobe equal to or larger than visual surface; tergite count variable; pygidium extremely subisopygous; pustular ornamentation subdued.

Included taxa. *Aulacopleura* Hawle & Corda, 1847 (=*Arethusa* Barrande, 1846[preoccupied]; =*Arethusina* Barrande, 1852; = *Paraaulacopleura* Chaubet, 1937); *Aulacopleuroides* Zhu & Zhang in Zhu *et al*., 1979; *Songkania* Zhang, 1974.

Remarks. '*Beggaspis*' *elongatum* (Begg, 1939), '*Beggaspis*' *spinicaudatum* Shaw, 1968, and '*Maurotarion*' *megacephalum* Rustan & Vaccari, 2012 resolve as a paraphyletic grade to *Aulacopleura*, and so are transferred to the genus herein.

Family **Brachymetopidae** Prantl & Přibyl, 1951

Diagnosis. Carapace heavily vaulted, height gained largely from free cheeks; carapace lateral margin produced into broad, flattened shelf; lateral eyes globular, with visual surface bulging out beyond palpebral lobe; eye ridges suppressed; S2 effaced; L1 reduced; genal spines with heavily reduced angle of divergence; 9 thoracic tergites; thoracic axial rings expanding until mid-ring before narrowing commences, pre-pygidial axial ring same width as first post-cephalic axial ring; row of tubercles on lateral ribs of tergopleurae; pygidium with 14 axial rings.

Included taxa. *Acutimetopus* Hahn & Hahn, 1985; *Australosutura* Campbell & Goldring in Amos *et al*., 1960 (=*Mystrocephala* Whittington, 1960 [preoccupied]); *Brachymetopella* Kobayashi & Hamada, 1978; *Brachymetopus* McCoy, 1847 (=*Brachymetopina* Reed, 1903); *Cheiropyge* Deiner, 1897 (=*Suturikephalion* Kobayashi

& Hamada, 1982); *Conimetopus* Hahn & Hahn, 1985; *Cordania* Clarke, 1892 (=*Latecephalus* Nan, 1976); *Dixiphopyge* Brezinski, 1988; *Hahnus* Özdikmen, 2009 (=*Eometopus* Hahn & Hahn, 1996 [preoccupied]); *Narinia* Archbold, 1997 (=*Iriania* Archbold, 1981 [preoccupied]); *Loeipyge* Kobayashi & Hamada, 1979; *Radnoria* Owens & Thomas, 1975; *Spinimetopus* Hahn & Hahn, 1985; *Tilsleyia* Hahn & Hahn, 1996.

Remarks. The genus *Brachymetopus*, as currently defined, is polyphyletic. The type species, *Brachymetopus maccoyi* (Portlock, 1843) shares many characteristics with species assigned to *Conimetopus* and sits at the base of a clade including both *Conimetopus* and *Loeipyge*. The remaining *Brachymetopus* species form a paraphyletic grade interrupted by a clade consisting of *Spinimetopus*, *Dixiphopyge* and *Tilsleyia*. As such, splitting *Brachymetopus* as currently defined would reduce it to the type species (unless it were to be synonymized with *Conimetopus* and *Loeipyge*) and result in the erection of at least seven new, mostly monotypic, genera. The alternative, synonymizing *Cheiropyge*, *Conimetopus*, *Dixiphopyge*, *Narinia*, *Loeipyge*, *Spinimetopus*, and *Tilsleyia* into *Brachymetopus*, is equally unsatisfying, as it would result in a single genus exhibiting a massive amount of morphological variation. Pending further revision of the group, the majority of *Brachymetopus* species a herein simply referred to as ‘*Brachymetopus*’.

The genus name *Mystrocephala* Whittington, 1960 is a homonym of *Mystrocephala* Herrich-Schaffer, 1855, which was applied to a moth. *Mystrocephala* Herrich-Schaffer, 1855 was synonymized with *Rhosus* Walker, 1854 by Poole (1989); however, according to article 10.6 of the *International Code of Zoological Nomenclature,* a name remains available irrespective of its invalidity as a junior synonym. *Mystrocephala* Whittington, 1960 is herein synonymized with *Australosutura* Campbell & Goldring in Amos *et al*., 1960; however, while *Mysterocephala* was published in May 1960, and so would have priority over *Australosutura* (published in August), article 23.3.5 of the *Code* states that an unavailable name must be replaced by the next oldest available name from among its synonyms, and so *Australosutura* is the correct, valid name for the genus.

Family **Chamaeleoaspidae** fam. nov.

Diagnosis. Carapace heavily vaulted, height gained largely from free cheeks; carapace marginal rim produced into laterally oriented spines; eye ridges suppressed; S2 effaced; enlarged axial spine on occipital ring; 10 thoracic tergites; axial spine on fourth tergite; row of tubercles on lateral ribs of tergopleurae.

Included taxa. *Chamaeleoaspis* Basse, 2010.

Family **Maurotarionidae** fam. nov.

Diagnosis. Lateral eyes set into free cheek; glabellar anterior narrowing; tergite count variable; row of tubercles on lateral ribs of tergopleurae; meraspid stages with three pairs of equally spaced tubercles on glabella.

Included taxa. *Beggaspis* Přibyl & Vaněk, 1981; *Malimanaspis* Baldis & Longobucco, 1977 (=*Goodsiraspis* Adrain & Chatterton, 1993); *Maurotarion* Alberti, 1969 (=*Branisella* Přibyl & Vaněk, 1981; =*Goniopleura* Hawle & Corda, 1847); *Tricornotarion* Chatterton, 1971.

Remarks. The monophyly of *Maurotarion* is currently uncertain. '*Maurotarion*' *megacephalum* Rustan & Vaccari, 2012 is transferred to *Aulacopleura* and '*Maurotarion*' *thomasi* (Clarkson & Howells, 1981) to *Strasburgaspis* herein. With the exception of reinstating *Tricornotarion* as a valid genus, no further taxonomic changes are enacted until a detailed analysis of the genus can be attempted.

Family **Otarionidae** Richter & Richter, 1926

(=**Cyphaspididae** Přibyl, 1947)

Diagnosis. Carapace heavily vaulted, height gained largely from free cheeks; lateral eyes globular, with visual surface bulging out beyond palpebral lobe; eye ridges suppressed; S2 effaced; carapace ornamentation extending onto proximal region of genal spines; tergite count variable; row of tubercles on lateral ribs of tergopleurae; pygidial marginal rim overturned onto inflated pygidial lateral margin; meraspid stages with three pairs of tubercles on glabella, anterior two pairs closely spaced.

Included taxa. *Adrainops* gen. nov.; *Conoparia* Hawle & Corda, 1847; *Cyphaspis* Burmeister, 1843 (=*Novakaspis* Přibyl, 1946a); *Cyphaspides* Novák, 1890 (=*Protocyphaspides* Přibyl & Vaněk, 1977); *Namuropyge* Richter & Richter, 1939 (=*Coignouina* Reed, 1943); *Otarion* Zenker, 1833; *Otarionella* Weyer, 1965; *Otarionides* Alberti, 1969.

Remarks. The genus *Otarion*, as currently defined, is paraphyletic. To resolve this, the genera *Conoparia* and *Otarionella* are reinstated and the new genus *Adrainops* erected. ‘*Otarion*’ *beukeboomi* is not assigned to a new genus, pending further revision. ‘*Harpidella*’ *spinafrons* (Cooper & Williams, 1935), ‘*Harpidella*’ *triloba* Hu, 1975 and ‘*Harpidella*’ *greggi* Adrain & Chatterton, 1995 resolve within *Cyphaspis* and so are transferred to the genus herein.

Genus ***Adrainops*** gen. nov.

Type species. *Otarion huddyi* Adrain & Chatterton, 1994.

Additional species. *Otarion brauni* Perry & Chatterton, 1979; *Otarion coppinsensis* Adrain & Chatterton, 1994.

Diagnosis. Marginal rim produced into laterally oriented spines; ancillary row of ventral spines projecting laterally from marginal rim; glabella moderately long; free cheek with moderate tubercular ornament interspaced with shallow pits; axial spine on occipital ring.

Derivation of name. Named after Jonathan Adrain, who described the type species along with Brian Chatterton, and has published many taxonomic works on aulacopleuroid trilobites.

Occurrence. Silurian (Wenlock).

Family **Strasburgaspidae** fam. nov.

Diagnosis. Lateral eyes globular, with visual surface bulging out beyond palpebral lobe; row of tubercles on lateral ribs of tergopleurae; meraspid stages with three pairs of equally spaced tubercles on glabella.

Included taxa. *Strasburgaspis* Adrain, 2005.

Remarks. '*Maurotarion*' *thomasi* (Clarkson & Howells, 1981) is transferred to *Strasburgaspis* herein.

Discussion

The existing aulacopleuroid taxonomy is rife with paraphyly and polyphyly, with the analysis showing five genera to be polyphyletic and two paraphyletic. Aulacopleuroidea as traditionally defined is itself paraphyletic in regard to Proetoidea; however, there is a large clade that resolves as sister-group to Proetoidea that comprises the majority of the aulacopleuroid taxa, including *Aulacopleura* itself, and so the superfamily is reduced to consist of this clade alone. Aulacopleuridae too is shown to be a paraphyletic grade leading to Brachymetopidae and so is broken down into its constituent clades. One of these, Otarionidae, is a previously named family that was subsequently synonymized with Aulacopleuridae. This pattern of previously synonymized higher taxa being shown to be valid is repeated in a number of genera. *Otarion* as defined forms a paraphyletic grade to a clade consisting of *Otarionides*, *Cyphaspides* and *Namuropyge*, however parts of the grade include the type species of the previously synonymized genera *Conoparia* and *Otarionella*, which are reinstated. This results in only a single new genus, *Adrainops*, needing to be erected in order to place the various taxa in the analysis assigned to *Otarion* in monophyletic genera.

Both *Strasburgaspis* and *Harpidella* resolve as polyphyletic, split between the base of the proetide clade and ingroup Aulacopleuroidea. In the case of *Harpidella*, the type species falls outside of Aulacopleuroidea while the non-*Harpidella* species resolve within *Cyphaspis* and so are transferred to the genus, while in *Strasburgaspis* it is the type species that resolves within the aulacopleuroids. *Beggaspis* is also polyphyletic, with the type species being the sister-taxon to *Malimanaspis* while the others form a paraphyletic grade leading to *Aulacopleura*. *Maurotarion* is also polyphyletic, with the majority of taxa showing affinity with *Malimanaspis* while some species resolve with *Aulacopleura* and others *Strasburgaspis*. Again, a previously synonymized genus, this time *Tricornotarion*, is shown to be valid. Finally, *Brachymetopus* is also shown to be polyphyletic. This is far from surprising, especially as genera within the group have been specifically considered to be nested within *Brachymetopus* (Hahn & Hahn 1996). The situation is particularly problematic as the type species, *Brachymetopus maccoyi*, shares many characteristics with the genus *Conimetopus*, which is itself part of a small offshoot from the main brachymetopid lineage. While perhaps the most logical course of action, synonymizing the genera *Cheiropyge*, *Conimetopus*, *Dixiphopyge*, *Narinia*, *Loeipyge*, *Spinimetopus*, and *Tilsleyia* into *Brachymetopus* is an unsatisfying solution, as it would result in a single genus showing massive amount of morphological variation (although given that genera are subjective hierarchical constructs have no consistent properties between them this is not a problem *per se*). The alternative, naming a series of monotypic genera, could serve to only clutter the taxonomy. Further, detailed analysis of the brachymetopids is required before major taxonomic revision of the group is undertaken.

Lamsdell & Selden (in prep) considered the timing of proetide evolution, noting that ghost range analysis given the proetide sister-group indicated a Cambrian origin. The lack of a definitive Cambrian proetide record however led them to speculate whether the majority of proetide groups had radiated in the Ordovician, perhaps from a paraphyletic Hystricuridae or some Cambrian lineage. The recovery of *Harpidella* and '*Strasburgaspis*' *kielanae* as a paraphyletic grade leading to proetoids and aulacopleuroids lends strength to the theory that the majority of proetide taxa radiated during the early Ordovician; both are Ordovician taxa themselves, and as such the ghost range for Proetoidea and Aulacopleuroidea extends only as far back as the Tremadocian. While the first proetides, including early hystricuroids and dimeropygoids, most likely originated in the Cambrian, the diverse aulacopleuroid and proetoid clades most likely have Ordovician origins.

Acknowledgements

Curtis Congreve and Martin Stein (trilobites), Amanda Falk (comments), referees.

References

Adrain, J. M. 2005. Aulacopleurid trilobites from the Upper Ordovician of Virginia. *Journal of Paleontology* **79**, 542–563.

Adrain, J. M. 2011. Class Trilobita Walch, 1771. *In*: Zhang, Z.-Q. (Ed.) Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness. *Zootaxa* **3148**, 104–109.

Adrain, J. M. & Chatterton, B. D. E. 1993. A new rorringtoniid trilobite from the Ludlow of Arctinc Canada. *Canadian Journal of Earth Sciences* **30**, 1634–1643.

Adrain, J. M. & Chatterton, B. D. E. 1994. The aulacopleurid trilobite *Otarion*, with new species from the Silurian of Northwestern Canada. *Journal of Paleontology* **68**, 305–323.

Adrain, J. M. & Chatterton, B. D. E. 1995. The otarionine trilobites *Harpidella* and *Maurotarion*, with species from Northwestern Canada, the United States, and Australia. *Journal of Paleontology* **69**, 307–326.

Adrain, J. M., Lee, D.-C., Westrop, S. R., Chatterton, B. D. E. & Landing, E. 2003. Classification of the trilobite subfamilies Hystricurinae and Hintzecurinae subfam. nov., with new genera from the Lower Ordovician (Ibexian) of Idaho and Utah. *Memoirs of the Queensland Museum* **48**, 553–586.

Alberti, G. K. B. 1969. Trilobiten des jüngeren Siluriums sowie des unter- und Mitteldevons. I. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* **520**, 1–692.

Amos A. J., Campbell, K. S. W. & Goldring, R. 1960. *Australosutura* gen. nov. (Trilobita) from the Carboniferous of Australia and Argentina. *Palaeontology* **3**, 227–236.

Angelin, N. P. 1854. Palaeontologica Scandinavica. Pars II, Crustacea formationis transitionis. *Academiae Regiae Scientarum Suecanae (Holmiae)*, 25–92.

Archbold, N. W. 1981. New Permian trilobite from Irian Jaya, Indonesia. *Geological Research and Development Centre, Paleontology Series 2*, 35–41.

Archbold, N. W. 1997. *Narinia*, a new name for the Permian brachymetopid trilobite genus *Irania* Archbold 1981. *Proceedings of the Royal Society of Victoria* **109**, 119.

Baldis, B. A. & Longobucco, M. 1977. Trilobites Devonicos de la precordillera noroccidental (Argentina). *Ameghiniana* **14**, 145–161.

Barrande, J. 1846. *Notice préliminaire sur le systême Silurien et les Trilobites de Bohême*. (Hirschfeld: Leipzig). 97p.

Barrande, J. 1852. *Systême Silurien du centre de la Bohême. 1 ère Partie. Recherches paléontologiques, I: Trilobites.* (Prague and Paris). 935p.

Basse, M. 2010. Neue und wenig bekannte taxa der Scutelluinae, Proetinae und Otarioninae (Trilobita) aus dem Mitteldevon der Blankenheim-, Hillesheim- und Prüm-Mulde (Eifel). *Dortmunder Beiträge zur Landeskunde* **42**, 75–119.

Begg, J. L. 1939. Some new species of Proetidae and Otarionidae from the Ashgillian of Girvan. *Geological Magazine* **76**, 372–382.

Bergström, J. 1977. Proetida – a disorderly order of trilobites. *Lethaia* **10**, 95–105.

Bremer, K. 1994. Branch support and tree stability. *Cladistics* **10**, 295–304.

Brezinski, 1988

Brusatte, S. L. 2010. Representing supraspecific taxa in higher-level phylogenetic analyses: guidelines for palaeontologists. *Palaeontology* **53**, 1–9.

Burmeister, H. 1843. *Die Organisation der Trilobiten aus ihren lebenden Verwandten entwickelt; nebst einer systematischen Uebersicht aller zeither beschriebenen Arten.* (Reimer: Berlin). 147p.

Chatterton, B. D. E. 1971. Taxonomy and ontogeny of Siluro-Devonian trilobites from near Yass, New South Wales. *Palaeontographica Abteilung A* **137**, 1–108.

Chaubet, M. C. 1937. Contribution a l'étude géologique du Gothlandien du versant méridional de la Montagne Noire. *Laboratoire de Géologie de l'Université Montpellier, Faculté des Sciences Mémoire* **1**, 1–223.

Clark, T. H. 1924. The paleontology of the Beekmantown Series at

Levis, Quebec. *Bulletins of American Paleontology* **10**, 1–134.

Clarke, J. M. 1892. On *Cordania*, a proposed new genus of trilobites. *45th Annual Report of New York State Museum 1891*, 440–443.

Clarkson, E. N. K. & Howells, Y. 1981. Upper Llandovery trilobites from the Pentland Hills, Scotland. *Palaeontology* **24**, 507–536.

Cooper, G. A. & Williams, J. S. 1935. Tully Formation of New York. *Bulletin of the Geological Society of America* **46**, 781–868.

Diener, C. 1897. The Permocarboniferous fauna of Chitichun No. 1. *Memoirs of the Geological Survey of India Palaeontologia Indica Series 15, Himalayan fossils* **1**, 1-105, pls 1-13.

Farris, J. S., Albert, V. A., Källersjö, M., Lipscomb, D. & Kluge, A. G. 1996. Parsimony jackknifing outperforms neighbor-joining. *Cladistics* **12**, 99–124.

Fortey, R. A. & Owens, R. M. 1975. Proetida–a new order of trilobites. *Fossils and Strata* **4**, 227–239.

Fusco, G., Hughes, N. C., Websters, M. & Minelli, A. 2004. Exploring developmental modes in a fossil arthropod: growth and trunk segmentation of the trilobite *Aulacopleura konincki*. *The American Naturalist* **163**, 167–183.

Fusco, G., Hong, P. A. & Hughes, N. C. 2014. Positional specification in the segmental growth pattern of an early arthropod. *Proceedings of the Royal Society B* **281**. doi: 10.1098/rspb.2013.3037

Gandl, J. 1980. Trilobiten mit „Kulm-Charakter" aus dem Namur B. *Senckenbergiana lethaea* **60**, 291–351.

Goloboff, P. A., Farris, J. S. & Nixon, K. C. 2008. TNT, a free program for phylogenetic anaylsis. *Cladistics* **24**, 774–786.

Hahn, G. & Brauckmann, C. 1984. Die Anulaspidinae (Trilobita; Karbon-Perm). *Senckenbergiana lethaea* **65**, 165–177.

Hahn, G. & Hahn, R. 1985. Trilobten aus dem hohen Ober-Karbon oder Unter-Perm von Alaska. *Senckenbergiana lethaea* **66**, 445–485.

Hahn, G. & Hahn, R. 1996. Die Trilobiten-taxa des Karbons und Perms. 2. Brachymetopidae. *Courier Forschunginstitut Senckernberg* **195**, 1–242.

Hawle, I. & Corda, A. J. C. 1847. *Prodrom einer Monographie der böhmischen Trilobiten*. 176 pp, 7 pls. Prague.

Herrich-Schaffer, G. 1855. *Systematische Bearbeitung der Schmetterlinge von Europa. Bd. 5: Die Schaben und Federmotten*. Regensburg.

Hu, C.-H. 1975. Ontogenies of four species of silicified Middle Ordovician trilobites from Virginia. *Proceedings of the Geological Society of China* **18**, 115–127.

Hughes, N. C. 2003a. Trilobite tagmosis and body patterning from morphological and developmental perspectives. *Integrative Comparative Biology* **43**, 185–206.

Hughes, N. C. 2003b. Trilobite body patterning and the evolution of arthropod tagmosis. *BioEssays* **25**, 386–395.

Hughes, N. C. 2007. The evolution of trilobite body patterning. *Annual Review of Earth Planetary Sciences* **35**, 401–434.

Hughes, N. C. & Chapman, R. E. 1995. Growth and variation in the Silurian proetide trilobite *Aulacopleura konincki* and its implications for trilobite palaeobiology. *Lethaia* **28**, 333–353.

Hughes, N. C., Minelli, A. & Fusco, G. 2006. The ontogeny of trilobite segmentation: a comparative approach. *Paleobiology* **32**, 602–627.

Hupé, P. 1953. Classification des Trilobites. *Annales de Paléontologie* **39**, 61–168.

Jaanusson, V. 1956. Untersuchungen über baltoskandische Asaph- iden. III. Über die Gattungen *Megistaspis* n. nom. und *Homalopyge* n. gen. *Bulletin of the Geological Institution of Uppsala* **36**, 59–77.

Jell, P. A. & Adrain, J. M. 2003. Available generic names for trilobites. *Memoirs of the Queensland Museum* **48**, 331–553.

Kobayashi, T. & Hamada, T. 1971. Agnostoid trilobites in a Devonian formation in West Malaysia. *Proceedings of the Japan Academy* **47**, 393–400.

Kobayashi, T. & Hamada, T. 1978. Advance reports on the Carboniferous trilobites of Japan. II. One new subgenus and three new species. *Proceedings of the Japan Academy, Series B* **54**, 50–54.

Kobayashi, T. & Hamada, T. 1979. Permo-Carboniferous from Thailand and Malaysia. *Geology and Palaeontology of Southeast Asia* **20**, 1–20.

Kobayashi, T. & Hamada, T. 1982. Advance reports of the Permian trilobites of Japan. II. Cordaniinae, nov. and *Cheiropyge* (*Suturikephalion*), nov. *Proceedings of the Japan Academy, Series B* **58**, 49–51.

Lamsdell, J. C. & Selden, P. A. In prep. Phylogenetic support for the monophyly of proetide trilobites.

Lerosey-Aubril, R. & Feist, R. 2005. First carboniferous protaspid larvae (Trilobita). *Journal of Paleontology* **79**, 702–718.

Lu, Y. 1975. Ordovician trilobite faunas of central and southwestern China.

Palaeontologia Sinica **11**, 1–463.

Lütke, F. 1980. Zur evolution der altpaläozoischen Proetina (Trilobita). *Senckenbergiana lethaea* **61**, 73–144.

Maddison, W. P. & Maddison, D. R. 2010. Mesquite: A modular system for evolutionary analysis. Version 2.73. http://mesquiteproject.org.

Maksimova, Z. A. 1975. [Trilobita]. Pp. 119-133. In: Menner, V.V. (ed) *Kharakteristika fauny pogranichnyckh sloev Silura i Devona tsentral'nago Kazakhstana. Materialy po geologii tsentral'nogo Kazakhstana 12.*

Marek, L. 1952. Contribution to the stratigraphy and fauna of the uppermost part of the Králuv Dvur Shales (Ashgillian). *Sborník Ústøedního Ústavu Geologckého* **19**, 429–455.

McCoy, F. 1847. On the fossil botany and zoology of the rocks associated with the coal of Australia. *Annals and Magazine of Natural History* **20**, 145–157, 226–236, 298–312.

McCoy, F. 1849. On the classification of some British fossil Crustacea with notices of some forms in the University collection at Cambridge. *Annals and Magazine of Natural History* **4**, 161–179, 330–335, 392–414.

Nan, R. 1976. Trilobites. pp. 333-351, pls 195- 201. In: *Palaeontological Atlas of north China, Part 1, Inner Mongolia*, Geological Publishing House: Beijing, 502p.

Novák, O. 1890. Vergleichende Studien an einigen Trilobiten aus dem Hercyn von Bicken, Wildungen, Greifenstein und Böhmen. *Paläontologische Abhandlungen, Berlin* **1**, 1–46.

Oehlert, D. V. 1886. Étude sur quelques trilobites du groupe des Proetidae. *Bulletin de la Société d'Estudes Scientifiques de l'Angers* **15**, 1–23.

O'Leary, M. A. & Kaufman, S. G. 2012. MorphoBank 3.0: Web application for morphological phylogenies and taxonomy. http://www.morphobank.org.

Osmólska, H. 1957. Trilobites from the Couvinian of Wydryszów (Holy Cross Mountains, Poland). *Acta Palaeontologica Polonica* **2**, 53–77.

Owens, R. M. & Hammann, W. 1990. Proetide trilobites from the Cystoid Limestone (Ashgill) of NW Spain, and the suprageneric classification of related forms. *Paläontologische Zeitschrift* **64**, 221–244.

Owens, R. M. & Thomas, A. T. 1975. *Radnoria*, a new Silurian proetacean trilobite, and the origins of the Brachymetopidae. *Palaeontology* **18**, 809–822.

Özdikmen, H. 2009. Nomenclatural changes for twenty trilobites genera. *Munis Entomology & Zoology* **4**, 155–171.

Perry, D. G. & Chatterton, B. D. E. 1979. Wenlock trilobites and brachiopods from the Mackenzie Mountains, north-western Canada. *Palaeontology* **22**, 569–607.

Poole, R. W. 1989. Noctuidae. In: Heppner, J. B. (ed.) *Lepidopterorum catalogus*. New York, Brill. 1314 p.

Portlock, J. E. 1843. *Report on the geology of the County of Londonderry, and parts of Tyrone and Fermanagh*. Dublin and London, 784 p.

Prantl, F. & Přibyl, A. 1951. Revise čeledi Otarionidae R. et E. Richter z českého siluru a devonu (Trilobitae). *Sborník Státního Geologického Ústavu ČSR, oddíl paleontologický* **17**, 353–512.

Přibyl, A. 1946a. O nìkolika novýh trilobitových rodech z èeského siluru a devonu. *Pøíroda, Brno* **38**, 89–95.

Přibyl, A. 1946b. Notes on the recognition of the Bohemian Proetidae (Trilobitae). *Bulletin international, Académie tchèque des sciences* **46**, 1–41.

Přibyl, A. 1947. *Aulacopleura* and the Otarionidae. *Journal of Paleontology* **21**, 537–545.

Přibyl, A. & Vaněk, J. 1977. Einige neue taxa der Trilobiten aus dem Mittel-böhmischen Silur und Devon. Časopis Národního Muzea, oddil Přírodovědný **144**, 83–88.

Přibyl, A. & Vaněk, J. 1981. Studie zur Morphologie und Phylogenie der familie Otarionidae R. & E. Richter (Trilobita). *Palaeontographica Abteilung A* **173**, 160–208.

Reed, F. R. C. 1903. The Lower Palaeozoic trilobites of the Girvan distict, Ayrshire. Part 1. *Monographs of the Palaeontographical Society,* 1–48.

Reed, F. R. C. 1943. The genera of British Carboniferous trilobites. *Annals and Magazine of Natural History* **10**, 54–65.

Repina, L. N., Petrunina, Z. E. & Hajrullin, T. I. 1975. [Trilobites]. In [Stratigraphy and fauna of the Lower Paleozoic of the northern submontane belt of Turkestan and Alai Ridges (southern Tyan-shan)]. *Akademiya Nauk SSSR, Sibirskoe Otdelenie, Instituta Geologii i Geofiziki, Trudy* **278**, 100-248.

Richter, R. & Richter, E. 1926. Die Trilobiten des Oberdevons. Beiträge zur Kenntnis devonsicher Trilobiten IV. *Abhandlungen der Preussischen Geologischen Landesanstalt* **99**, 1–314.

Richter, R. & Richter, E. 1939. Ueber *Namuropyge* n. g. und die basisolution der trilobiten-glatze. *Bulletin du Musée royal d'Histoire naturelle de Belgique* **15**, 1–29.

Ross Jr., R. J. 1951. Stratigraphy of the Garden City Formation in northeastern Utah, and its trilobite faunas. *Bulletin of Peabody Museum of Natural History* **6**, 1–161.

Rustan, J. J. & Vaccari, N. E. 2012. The trilobite *Maurotarion megacephalum* sp. nov. (Aulacopleuridae) in the Lower Devonian of Argentina: phylogenetic and paleobiogeographic remarks. *Revista Mexicana de Ciencias Geológicas* **29**, 346–354.

Salter, J. W. 1864. The trilobites of the Cambrian, Silurian, and Devonian Formations, Part 1 (Devonian and Silurain). *Monograph of the Palaeontographical Society* **67**, 1–80.

Shumard, B. F. 1861. The Primordial zone of Texas, with descriptions of new fossils. *American Journal of Science* **32**, 213–221.

Shaw, F. C. 1968. Early Middle Ordovician Chazy trilobites of New York. *New York State Museum and Science Service Memoir* **17**, 1–163.

Walch, J. E. I. 1771. *Die naturgeschichte der verteinerungen, Dritter Theil. Zur erläuterung der Knorrischen Sammlung von Merkwürdigkeiten der Natur.* P.J. Felstecker: Nürnberg), 235p, 84pl.

Walcott, C. D. 1886. Second contribution to the studies on the Cambrian fauna of North America. *Bulletin of the United States of Geological Survey* **30**, 1–369.

Walker, F. 1854. *Catalogue Lepidoptera Heterocera*. London, 356 p.

Walter, O. T. 1924. Trilobites of Iowa and some related Paleozoic forms. *Iowa Geological Survey Annual Report* **31***,* 167–400.

Weyer, D. 1965. Etroeungt im Morvan (Zentral- frankreich); The Etroeungt in the

Morvan region, central France. *Abhandlungen des Zentralen Geologischen Instituts* **1**, 290–302.

Whittington, H. B. 1960. *Cordania* and other trilobites from the Lower and Middle Devonian. *Journal of Paleontology* **34**, 405–420.

Whittington, H. B. & Kelly, S. R. A. 1997. Morphological terms applied to Trilobita. pp. 313–329. *In:* Kaesler, R. L. (ed.) *Treatise on Invertebrate Paleontology. Part O, Revised. Arthropoda 1, Trilobita 1 (Introduction, Order Agnostida, Order Redlichiida).* Geological Society of America and University of Kansas Paleontological Institute. Boulder, Colorado and Lawrence, Kansas. 530 p.

Zander, R. H. 2003. Reliable phylogenetic resolution of morphological data can be better than that of molecular data. *Taxon* **52**, 109–112.

Zenker, J. C. 1833. *Beiträge zur Naturgesichte der Urwelt. Oragnische Reste (Petrefacten) aus der Altenbruger Braunkohlen-Formation, dem Blankenburger Quadersandstein, Jenaischen bunten Sandstein und Böhmischen Uebergangsgebirge*. (Jena). 67p.

Zhang, W. 1974. [Silurian Trilobita]. Pp. 173-187. In: *Handbook of the stratigraphy and paleontology of southwest China*. Science Press: Beijing.

Zhu, Z., Lin, H. & Zhang, Z. 1979. [Trilobites]. Pp 81-116, pls 35-45. In: *Atlas of the palaeontology of northwestern China, Qinghai,volume 2.* Geological Publishing House: Beijing 219 p.

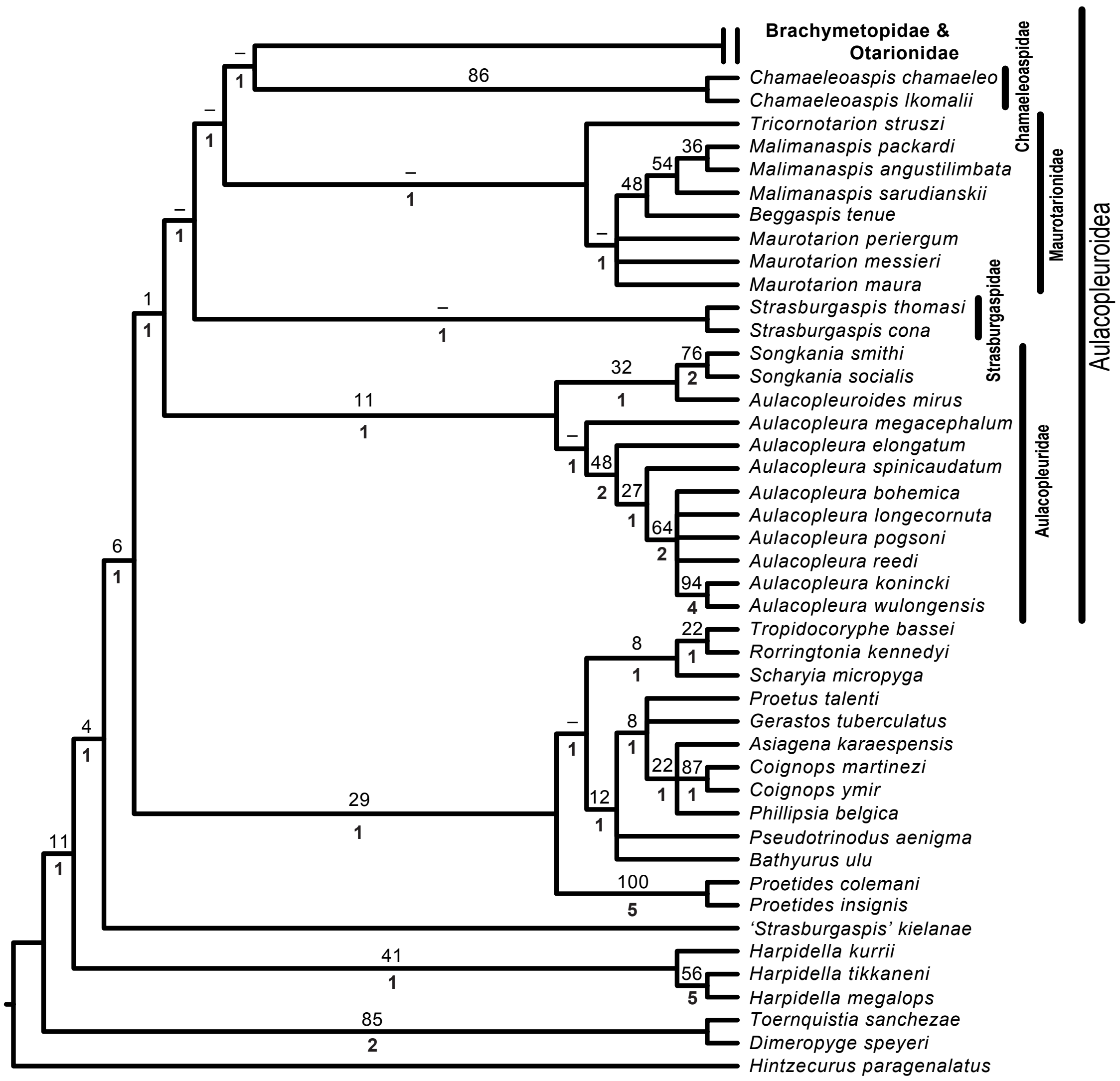


Figure 1. Strict consensus of 48 most parsimonious trees. Numbers above the nodes are jackknife values with 33% deletion, numbers beneath the nodes in bold are bremer support values. Details of the otarionid and brachymetopid clades are shown in figure 2.

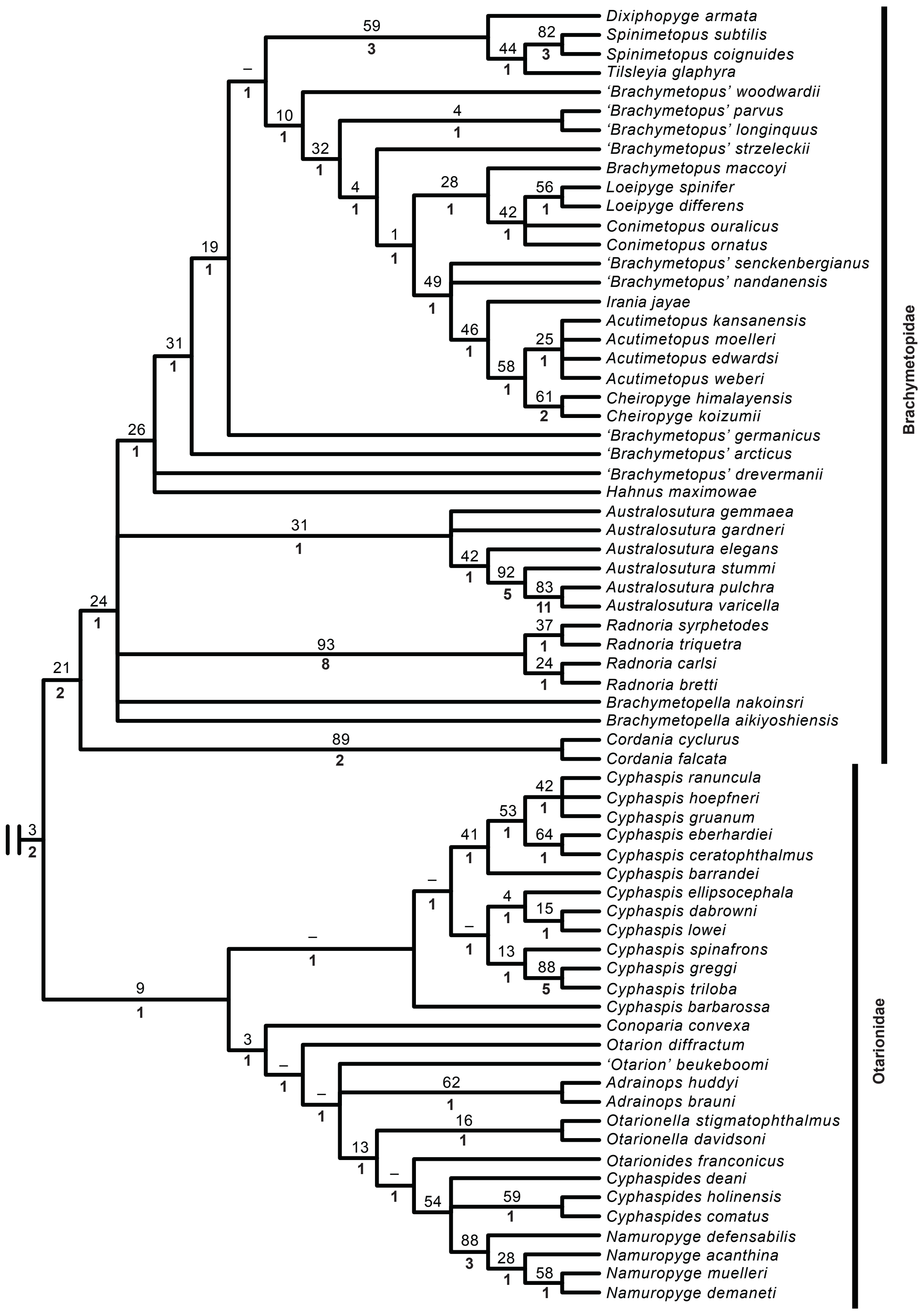

Dixiphopyge armata
Spinimetopus subtilis
Spinimetopus coignuides
Tilsleyia glaphyra
'Brachymetopus' woodwardii
'Brachymetopus' parvus
'Brachymetopus' longinquus
'Brachymetopus' strzeleckii
Brachymetopus maccoyi
Loeipyge spinifer
Loeipyge differens
Conimetopus ouralicus
Conimetopus ornatus
'Brachymetopus' senckenbergianus
'Brachymetopus' nandanensis
Irania jayae
Acutimetopus kansanensis
Acutimetopus moelleri
Acutimetopus edwardsi
Acutimetopus weberi
Cheiropyge himalayensis
Cheiropyge koizumii
'Brachymetopus' germanicus
'Brachymetopus' arcticus
'Brachymetopus' drevermanii
Hahnus maximowae
Australosutura gemmaea
Australosutura gardneri
Australosutura elegans
Australosutura stummi
Australosutura pulchra
Australosutura varicella
Radnoria syrphetodes
Radnoria triquetra
Radnoria carlsi
Radnoria bretti
Brachymetopella nakoinsri
Brachymetopella aikiyoshiensis
Cordania cyclurus
Cordania falcata
Cyphaspis ranuncula
Cyphaspis hoepfneri
Cyphaspis gruanum
Cyphaspis eberhardiei
Cyphaspis ceratophthalmus
Cyphaspis barrandei
Cyphaspis ellipsocephala
Cyphaspis dabrowni
Cyphaspis lowei
Cyphaspis spinafrons
Cyphaspis greggi
Cyphaspis triloba
Cyphaspis barbarossa
Conoparia convexa
Otarion diffractum
'Otarion' beukeboomi
Adrainops huddyi
Adrainops brauni
Otarionella stigmatophthalmus
Otarionella davidsoni
Otarionides franconicus
Cyphaspides deani
Cyphaspides holinensis
Cyphaspides comatus
Namuropyge defensabilis
Namuropyge acanthina
Namuropyge muelleri
Namuropyge demaneti
Brachymetopidae
Otarionidae

Figure 2. Strict consensus of twelve most parsimonious trees, focusing on the otarionid and brachymetopid clades. Numbers above the nodes are jackknife values with 33% deletion, numbers beneath the nodes in bold are bremer support values.

Part 3

On mass extinctions

Chapter 9

Clade history, species ecology and external causal factors influence arthropod survival and recovery during Paleozoic mass extinctions

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(Formatted for submission to *Proceedings of the National Academy of Sciences*)

Abstract

Mass extinctions are known to be extraordinary events during which the normal rules of natural selection do not apply. Evidence points to the operation of a different selective regime, one where clade-level properties are selected upon; however, it is still unclear whether survivorship rules apply across different extinction events, the consequences of differential responses in diversity and disparity during extinction events, and the factors governing subsequent recoveries. Here, we compare variations in diversity and disparity across three arthropod clades for two extinction events: the end-Ordovician (443 Ma) and the late Devonian (385–359 Ma). Our study reveals different patterns of morphospace loss between the two extinctions, with the end-Ordovician characterized by random morphospace loss while a marked migration in morphospace occurs in all three clades during the late Devonian. The nature of these migrations is mediated by species ecology; in one clade, generalists survive and morphospace occupation is reduced to a portion of its original area, while the survivors in the remaining clades are specialists and

morphospace expands into previously unoccupied areas. Variations in diversity between the three clades, with two related groups experiencing major diversity loss during the late Devonian with no subsequent recovery and another undergoing an evolutionary bottleneck before further radiation in the Carboniferous, suggests that inherent properties of the clade can also influence how it responds to mass extinction events. Therefore clade history, species ecology, and external causal factors of individual extinction events all play a role in determining clade survival.

Significance statement

Mass extinctions are important events in earth history that have been instrumental in shaping evolution. During these periods the normal rules of natural selection are suspended and different criteria influence the survival of species. However, it is still unknown whether these criteria are the same for each mass extinction event. We compare changes in taxic diversity and morphological disparity in three clades of Paleozoic arthropods across two mass extinction events, the end-Ordovician and late Devonian, showing that clade history, species ecology, and external factors driving the extinction event all play a role in determining clade survival. These results show the importance of studying clades across multiple extinction events and the importance of individual species in the clade survival during mass extinctions.

Mass extinctions have altered the trajectory of evolution a number of times over the Phanerozoic, with the severe decline of brachiopods at the end of the Permian giving way to the subsequent proliferation of bivalves (1) and the extinction of dinosaurs at the end of the Cretaceous paving the way for the rise to dominance of mammals (2). There is growing consensus that mass extinctions represent a differential selective regime, as factors positively correlated with survivorship under normal extinction intensities are shown to have little effect on survivorship during times of mass extinction, with other factors such as geographic range at the clade level playing a greater role (3). Despite decades of research, there remain a number of issues that require further study, including whether there are general survivorship rules that apply across different extinction events, the consequences of inexact correlations between taxonomic and morphological diversity, and the factors governing the dynamics and outcome of recoveries (3). One way to explore these issues is to study a single clade that experiences multiple extinction events; however, few studies have sought to trace the evolutionary history of a clade in this way, instead focusing on individual mass extinction events. The Paleozoic era includes three of the 'big five' mass extinctions (4), along with a number of smaller extinction events, and so represents the ideal timeframe in which to conduct such a study. The first mass extinction, occurring during the late Ordovician, has been linked to the rapid formation of an unstable icehouse in the middle of otherwise greenhouse conditions (5), with the sudden glaciation and subsequent return to greenhouse conditions resulting in pulsed periods of cladal turnover (6). The final Paleozoic extinction, at the end of the Permian, is also tied to a period of rapid climate change, with the eruption of the Siberian Traps resulting in a global increase in CO_2 levels leading to global warming and ocean acidification, and an associated increase in weathering and nutrient runoff exacerbating already high levels of ocean anoxia (7). Both mass extinctions exhibited heightened rates of extinction mediated by rapid climate change; this, however, is not true of the mass extinction occurring during the late Devonian, which falls temporally between the two. Rather, biodiversity loss during the late Devonian has been linked to a drop in speciation rates due to a decrease in endemism (8), with a shutdown in vicariant speciation attributable to widespread interbasinal species invasions mediated by a global increase in sea level (9–11). Therefore, in this period of time, three mass extinctions with different causal factors occurred, two of which (the end-Ordovician and late Devonian) transpire within 100 million years of one another.

This study utilizes recent advances in the phylogenetic relationships of three Paleozoic arthropod clades, two belonging to the Eurypterida (12, 13) and one to the Trilobita (14), to compare the impact of the end-Ordovician and late Devonian mass extinctions on their evolutionary histories. All three clades originated in the early or mid-Ordovician, experience substantial loss of diversity during the Devonian, and go extinct in the Permian. Mass extinctions have been shown to have varying effects on the clades, in regard to both taxonomic richness (diversity) and morphological variety (disparity). While many clades will disappear completely or pass through the event without suffering any discernible impact, a large number persist beyond the extinction event but experience a decrease in diversity, disparity, or both. These clades may subsequently decline and go extinct (the ‘dead clade walking’ phenomenon (15)), while others persist at a low level of taxic diversity or undergo renewed phases of diversification; those clades that exhibit this last pattern are considered to have passed through an evolutionary bottleneck (16).

Disparity can be negatively impacted in a variety of ways, resulting in either a random, marginal, or directional, loss of morphospace (17). Marginal or directional loss of morphospace can be indicative of a selective force acting on the clade, either in relation to the morphological characteristics themselves or ecological traits for which morphology can act as a proxy (18). Disparity can be assessed from continuous morphological characters or from discrete characters; the latter approach is adopted here, employing the recent detailed cladistics analyses of all three groups.

In this paper, we analyze taxonomic diversity and morphological disparity across the recorded history of the Stylonurina, Eurypterina and Aulacopleuroidea. In doing so, we explore the impact of the end-Ordovician and late Devonian extinctions on the morphospace of each clade, allowing us to examine whether clades respond uniquely to each extinction event or, if not, whether repeated trends manifest as a property of the clade or of the extinction event.

Results

Diversity and disparity through time. Diversity and disparity are decoupled throughout the evolutionary history of all three groups (Fig. 1), with disparity remaining relatively constant irrespective of increases and decreases in diversity. Similar patterns have been shown in vertebrates (19), emphasizing the importance of considering both diversity and disparity in studies of clade history. Eurypterina and Stylonurina exhibit low levels of diversity in the Ordovician before undergoing a massive increase, reaching their peak diversity in the Silurian. Both clades show a marked drop of diversity in the early

Devonian, which increases into the late Devonian. Neither eurypterid clade shows any meaningful recovery of diversity after the late Devonian; both persisted at low levels of diversity until their extinction in the Permian, fitting the pattern of 'dead clades walking' (15). Aulacopleuroid trilobites show a distinctly different pattern, with disparity reaching its acme in the Ordovician and decreasing in the Silurian, remaining relatively stable in the early Devonian before suffering a major reduction in the late Devonian. In contrast to the eurypterid clades, Aulacopleuroidea underwent a major radiation in the Carboniferous, with diversity returning to levels seen in the Silurian and early Devonian before a decline towards the eventual extinction of the clade in the Permian. Aulacopleuroid trilobites therefore experienced an evolutionary bottleneck (16) in the late Devonian.

Both Stylonurina and Aulacopleuroidea attained high levels of disparity in the Ordovician, which they maintained through to the Permian; Eurypterina show a more steady increase of disparity until the early Devonian, after which disparity dropped for the remainder of the Paleozoic. These changes are not significant, however, and so overall disparity did not change drastically in any of the groups throughout the Paleozoic. This pattern of early maximal disparity followed by relatively constant levels is consistent with a clade undergoing explosive radiations, or an unsampled period of cladogenesis (20); as such, it seems likely that Eurypterina radiated later in the Ordovician than Stylonurina and Aulacopleuroidea, although it at present seems likely that all three groups originated after the Cambrian (14, 21).

Despite this, morphospace occupation is shown to change drastically in all three groups (Fig. 2), with each clade experiencing a migration in morphospace throughout the

Devonian. Statistical analysis, however, reveals a difference between these shifts in morphospace occupation. Non-parametric multivariate analysis of variance (NPMANOVA) tests show that, within the Stylonurina and Aulacopleuroidea, Ordovician and Silurian taxa are significantly distinct from Carboniferous and Permian taxa, with the shift in morphospace occupation between the early Devonian and late Devonian for Stylonurina and over the duration of the Devonian for Aulacopleuroidea (Table 1). Eurypterina taxa, meanwhile, exhibit no significant distinction from the Silurian to the Permian; however, Ordovician taxa are shown to be significantly distinct to those in later time periods.

Clade- and extinction-specific trends. The pattern of morphospace loss at the end-Ordovician and during the late Devonian is consistently different across all three clades, with Stylonurina, Eurypterina, and Aulacopleuroidea exhibiting a random loss of morphospace at the end-Ordovician but with no significant difference in morphospace occupation between the Ordovician and Silurian with the exception of Eurypterina (Table 1). The difference in eurypterine morphospace occupation from the Ordovician to the Silurian is likely to be due to the clade continuing its radiation throughout the Ordovician, resulting in a proliferation of new morphotypes in the Silurian. Stylonurina and Aulacopleuroidea, with their earlier originations, have already undergone their initial radiation by the Silurian, resulting in the relative stasis of their occupied morphospace. This pattern of random morphospace loss is consistent with a relatively short-term catastrophe, in which organisms become extinct irrespective of ecology, with survival being ruled by contingency rather than adaptation or selection (17). This is contrasted heavily with the pattern of morphospace loss shown during the late Devonian, with each clade experiencing a migration in morphospace consistent with lateral morphospace reduction, corresponding to an asymmetric, selective extinction event (17). Similar shifts in morphospace have been observed in Ichthyosauria and linked to changes in ecospace occupation (22), and it appears that ecology could, similarly, have been a major selective factor during the late Devonian. It has been suggested that ecological generalists preferentially survived this biotic crisis (8), and this selective pressure could be responsible for the observed migrations in morphospace. Two distinct patterns are apparent, however, with Stylonurina and Aulacopleuroidea expanding into previously unoccupied morphospace, while Eurypterina retreat to a portion of their existing morphospace. This difference can be attributed to differences in ecology; the post-Devonian Eurypterina are considered generalists, however the Stylonurina and Aulacopleuroidea that survive the biodiversity crises are considered specialists, being large sweep-feeders (23) and filter-chamber feeders (24) respectively. It appears that, while one clade followed the expected pattern of weathering the biodiversity crisis due to its ecological generalists, two persisted through species occupying specialist niches that, presumably, did not suffer from the same competitive pressures from biotic invaders as did other clades. Such a pattern is consistent with clade-level sorting (25) mediated by selection occurring at the species or organismal levels, a manifestation of the effect hypothesis (26). It has been suggested that temperature tolerance was also a selective factor during the end Ordovician extinction event (6); however, temperature tolerance may occur independently of morphology and, if survivorship is otherwise independent of ecospace occupation, may result in a seemingly random loss of morphospace. The alternative is that the double-pulsed nature of the extinction has resulted in a seemingly random pattern of morphospace loss from the Ordovician to the Silurian; more detailed analysis of the end Ordovician extinction is required to resolve this issue.

That the closely related eurypteride clades both take on the characteristics of 'dead clades walking' after the late Devonian, failing to recover their diversity, while aulacopleuroid trilobites underwent an evolutionary bottleneck before successfully radiating in the Carboniferous, suggests that some intrinsic cladal properties may also influence how groups respond to mass extinction events and their aftermaths. The evidence shown here suggests that, while mass extinctions themselves can exert different selective pressures due to variations in their underlying causes, how clades respond to these pressures can be influenced by both inherent cladal properties as well as variations in the ecology of their constituent species. This reinforces the importance of examining both diversity and disparity in studies of mass extinction events, as well as the role of individual species in the survival of clades during these periods.

Methods

Phylogenetic Data. For the study, recent phylogenetic matrices for the Stylonurina (12), Eurypterina (13) and Aulacopleuroidea (14) were utilized. The aulacopleuroid analysis was used without modification while the stylonurine and eurypterine analyses were expanded in order to make their sampling of species more comprehensive. Four characters and 11 taxa were added to the stylonurine analysis, while 72 characters and 51 taxa were added to the eurypterine analysis (Appendix 5). For this study, individual species were coded, in order to remove the potential for the inclusion of paraphyletic or polyphyletic groups. The application of paraphyletic or polyphyletic groups in biodiversity studies can have drastic effects on our understanding of mass extinction events, with erroneous patterns of pseudoextinction retrieved when monophyly is not recognized, while incorrect assumptions of monophyly can dampen the observed loss of biodiversity when studies are conducted at higher taxonomic levels (27).

The data matrices were each subjected to cladistic analysis using TNT (28), employing random addition sequences followed by tree bisection-reconnection (TBR) branch swapping with 100,000 repetitions with all characters unordered and of equal weight. The strict consensus tree was constructed for each clade.

Diversity. The phylogenetic trees were plotted against geological time, based on an existing eurypterid database (29), updated for recent discoveries, with aulacopleuroid ranges compiled from the literature. Taxon occurrence was extended according to implied ghost ranges and reconstructed ancestors included as inferred from the tree topology. Three measures of diversity were calculated (observed taxa, sampled taxa, and phylogenetically corrected sampled taxa) for the Ordovician, Silurian, Lower Devonian, Upper Devonian, Carboniferous, and Permian time intervals, with the phylogenetically corrected sampled diversity utilized for the diversity/disparity comparisons.

Disparity. Disparity measures were calculated from the cladistics character data using standard methods (30) and phylogenetically corrected for incomplete sampling through the extension of species ranges and inclusion of reconstructed ancestors as necessitated by tree topology (31). Pairwise (taxon to taxon) Euclidean distance matrices were calculated using Matrix (32) and subjected to PCO using GINGKO (33) from which morphospace plots were produced. Multivariate statistical tests (NPMANOVA) with Bonferroni correction were performed to ascertain the statistical significance of overlap and separation of morphospace between the Ordovician, Silurian, early Devonian (Lochkovian to Eifelian), late Devonian (Givetian to Famennian), Carboniferous, and Permian time periods. The disparity metrics retrieved from the PCO data were subjected to rarefaction analysis using RARE (32) to normalize for sample size.

Acknowledgments

We than M. Benton and S. Brusatte for discussion on disparity analysis, M. Wills for providing software and troubleshooting, and A. Falk and C. Congreve for discussion.

1. Clapham ME, Bottjer DJ (2007) Prolonged Permian-Triassic ecological crisis recorded by molluscan dominance in Late Permian offshore assemblages. *Proc Natl Acad Sci USA* 104: 12971–12975.
2. Smith FA et al. (2010) The evolution of maximum body size of terrestrial mammals. *Science* 330: 1216–1219.
3. Jablonski D (2005) Mass extinctions and macroevolution. *Paleobiology* 31: 192–210.
4. Barnosky AD et al. (2011) Has the Earth's sixth mass extinction already arrived? *Nature* 471: 51–57.

5. Sheehan PM (2001) The Late Ordovician mass extinction. *Annu Rev Earth Planet Sci* 29: 331–364.
6. Congreve CR (2013) Cladal turnover: the end-Ordovician as a large-scale analogue of species turnover. *Palaeontology* 56: 1285–1296.
7. Payne JL, Clapham ME (2012) End-Permian mass extinction in the oceans: an ancient analog for the twenty-first century? *Annu Rev Earth Planet Sci* 40: 89–111.
8. Stigall AL (2012) Speciation collapse and invasive species dynamics during the Late Devonian "Mass Extinction". *GSA Today* 22: 4–9.
9. Rode AL, Lieberman BS (2004) Using GIS to unlock the interactions between biogeography, environment, and evolution in Middle and Late Devonian brachiopods and bivalves. *Palaeogeogr Palaeocl* 211: 345–359.
10. Abe FR, Lieberman BS (2009) The nature of evolutionary radiations: a case study involving Devonian trilobites. *Evol Biol* 36: 225–234.
11. Stigall AL (2010) Invasive species and biodiversity crises: testing the link in the Late Devonian. *PLoS ONE* 5: e15584. (doi: 10.1371/journal.pone.0015584)
12. Lamsdell JC (2013) Redescription of Drepanopterus pentlandicus Laurie, 1892, the earliest known mycteropoid (Chelicerata: Eurypterida) from the early Silurian (Llandovery) of the Pentland Hills, Scotland. *Earth Env Sci T R So* 103: 77–103.
13. Lamsdell JC, Selden PA (2013) Babes in the wood – a unique window into sea scorpion ontogeny. *BMC Evol Biol* 13: 98. (doi: 10.1186/1471-2148-13-98)
14. Lamsdell JC & Selden PA (In prep) The systematics and phylogeny of aulacopleuroid trilobites (Arthropoda: Trilobita: Proetida).

15. Jablonski D (2002) Survival without recovery after mass extinctions. *Proc Natl Acad Sci* USA 99: 8139–8144.
16. Raup DM (1979) Size of the Permo – Triassic bottleneck and its evolutionary implications. *Science* 206: 217–218.
17. Korn D, Hopkins MJ, Walton SA (2013) Extinction space–a method for the quantification and classification of changes in morphospace across extinction boundaries. *Evolution* 67: 2795–2810.
18. Lockwood R (2004) The K/T event and infaunality: morphological and ecological patterns of extinction and recovery in veneroid bivalves. *Paleobiology* 30: 507–521.
19. Ruta M, Angielczyk KD, Fröbisch J, Benton MJ (2013) Decoupling of morphological disparity and taxic diversity during the adaptive radiation of anomodont theraspids. *Proc R Soc, B* 280: 20131071. (doi:10.1098/rspb.2013.1071)
20. Hughes M, Gerber S, Wills MA (2013) Clades reach highest morphological disparity early in their evolution. *Proc Natl Acad Sci USA* (doi: 10/1073/pnas.1302642110)
21. Lamsdell JC, Hoşgör İ, Selden PA (2013) A new Ordovician eurypterid (Arthropoda: Chelicerata) from southeast Turkey: Evidence for a cryptic Ordovician record of Eurypterida. *Gondwana Res* 23: 354–366.
22. Thorne PM, Ruta M, Benton MJ (2011) Resetting the evolution of marine reptiles at the Triassic-Jurassic boundary. *Proc Natl Acad Sci USA* 108: 8339–8344.

23. Lamsdell JC, Braddy SJ, Telie OE (2009) Redescription of *Drepanopterus abonensis* (Chelicerata: Eurypterida: Stylonurina) from the late Devonian of Portishead, UK. *Palaeontology* 52: 1113–1139.
24. Fortey RA, Owens RM (1999) Feeding habits in trilobites. *Palaeontology* 42: 429–465.
25. Vrba ES, Gould SJ (1986) The hierarchical expansion of sorting and selection: sorting and selection cannot be equated. *Paleobiology* 12: 217–228.
26. Vrba ES (1983) Macroevolutionary trends: new perspectives on the roles of adaptation and incidental effect. *Science* 221: 387–389.
27. Patterson C, Smith AB (1989) Periodicity in extinction: the role of systematics. *Ecology* 70: 802–811.
28. Goloboff PA, Farris JS, Nixon KC (2008) TNT, a free program for phylogenetic analysis. *Cladistics* 24: 774–786.
29. Lamsdell JC, Braddy SJ (2010) Cope's rule and Romer's theory: patterns of diversity and gigantism in eurypterids and Palaeozoic vertebrates. *Biol Lett* 6: 265–269.
30. Wills MA, Briggs DEG, Fortey RA (1994) Disparity as an evolutionary index: a comparison of Cambrian and Recent arthropods. *Paleobiology* 20: 93–130.
31. Brusatte, S. L., Montanari, S., Yi, H.-Y., & Norell, M. A. 2011. Phylogenetic corrections for morphological disparity analysis: a new methodology and case studies. *Paleobiology* **37**, 1–22.
32. Wills MA (1998) Crustacean disparity through the Phanerozoic: comparing morphological and stratigraphic data. *Biol J Linn Soc Lond* 65: 455–500.

33. De Cáceres M, Oliva F, Font X, Vives S (2007) GINGKO, a program for non-standard multivariate fuzzy analysis. *Adv Fuzzy Sets Syst* 2:41–56.

	P (same) overall	Pairwise comparisons, Bonferroni-corrected					
			O	S	ED	LD	C
Stylonurina	0***	S	1	▨	▨	▨	▨
		ED	1	1	▨	▨	▨
		LD	0***	0***	0***	▨	▨
		C	0***	0***	0***	1	▨
		P	0.0008***	0.0002***	0.0009***	1	1
Eurypterina	0***	S	0	▨	▨	▨	▨
		ED	0.0033**	1	▨	▨	▨
		LD	0.0005***	1	1	▨	▨
		C	0***	0.3452	0.4555	1	▨
		P	0.0500*	1	1	1	1
Aulacopleuroidea	0***	S	1	▨	▨	▨	▨
		ED	0***	0***	▨	▨	▨
		LD	0***	0***	0.0064*	▨	▨
		C	0***	0***	0***	0.0102*	▨
		P	0***	0***	0***	0.0466*	1

O, Ordovician; S, Silurian; ED, early Devonian; LD, late Devonian; C, Carboniferous; P, Permian.
*$P<0.05$; **$P<0.005$; ***$P<0.0005$.

Table 1. NPMANOVA test for statistical differences between taxa for each of the six time bins based on PCO analyses.

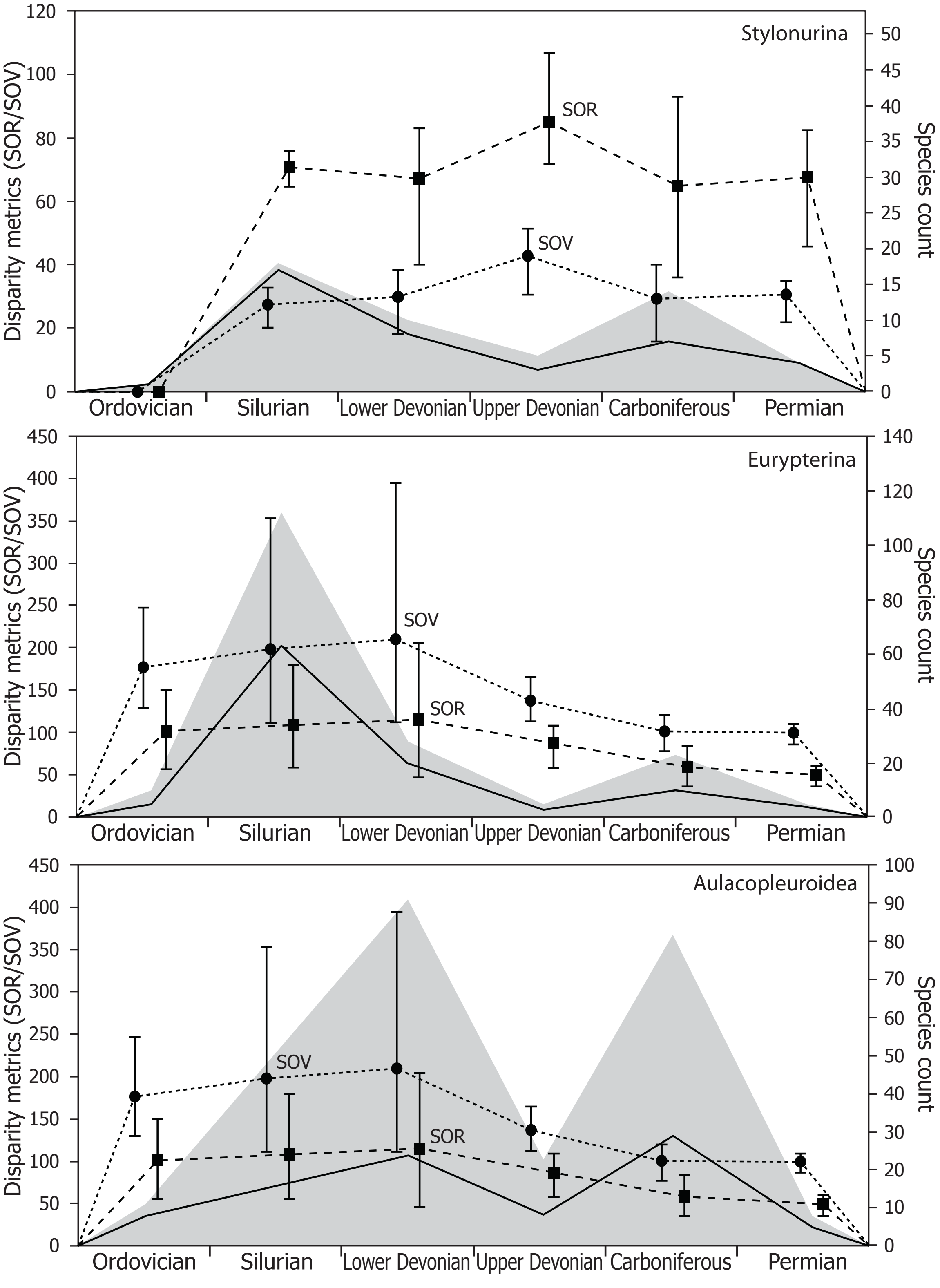

Figure 1. Disparity and diversity of Stylonurina, Eurypterina, and Aulacopleuroidea.

Both the sum of ranges (SOR) and sum of variances (SOV) metrics are shown. Error bars are 95% confidence intervals. Phylogenetically sampled diversity (taxa and implied ancestors included in the analyses) is shown by the solid line. Known disparity (total number of known species) is shown by the shaded area.

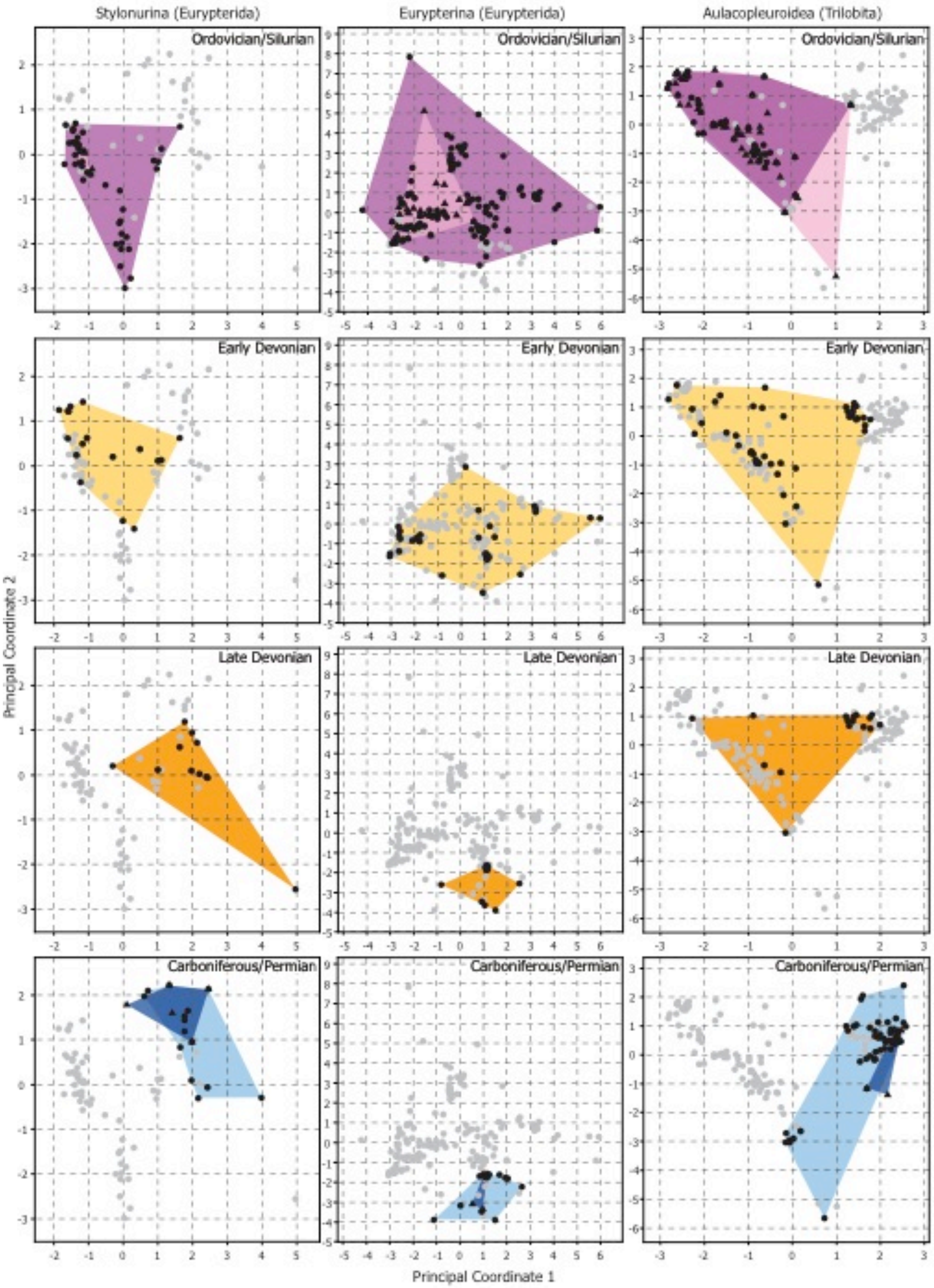

Figure 2. Morphospace occupation by Stylonurina, Eurypterina, and Aulacopleuroidea.

Plots are based on the first two axes from the principal coordinate analysis for each dataset. Black symbols indicate taxa present in the interval, gray symbols indicate taxa present in other intervals. In the Ordovician/Silurian and Carboniferous/Permian time intervals, Ordivician and Permian taxa are indicated by triangles. Minimal morphospace occupations in each time bin are indicated by colored polygons (pink, Ordovician; purple, Silurian; yellow, early Devonian; orange, late Devonian; pale blue, Carboniferous; dark blue, Permian).

Chapter 10

The role of volatility and clade history in arthropod recovery after the late Devonian biotic crisis

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(Formatted for submission to *Proceedings of the Royal Society B*)

Clades that survive mass extinction events are known two exhibit two distinct diversity patterns: either experiencing an evolutionary bottleneck before recovering or remaining at low diversity as a 'dead clade walking'. Volatility and clade history have been considered important factors in contributing to the likelihood of surviving mass extinction events; however, it is unclear how important they are to subsequent recovery. Through comparing rates of character evolution and rates of origination and extinction in three well-studied Palaeozoic arthropod groups it is shown that clades with higher volatility fail to recover after the late Devonian biotic crisis, remaining at low diversity. Differences in ecology appear to be causing the heightened levels of volatility, resulting in fewer surviving species from which to radiate and limiting the possibility for expansion into vacant ecospace. Ecology is, therefore, shown to be an important factor in mediating survival and recovery during the late Devonian. Furthermore it is shown to operate on multiple, sometimes contradictory, levels. It is shown that ecological factors, such as specialization, that influence responses in morphospace act independently of the ecological and historical factors that influence recovery.

1. Introduction

Identifying factors governing the survivorship and recovery of taxa during mass extinctions and their aftermath remains one of the key goals of macroevolutionary studies. Mass extinctions are known to be extraordinary events during which the normal rules of natural selection do not apply, and it has been suggested that a different selective regime acting upon clade-level properties operates during these periods [1]. This suggests that taxonomic survivorship fits the paradigm of 'nonconstructive selectivity' [2], caused by non-random extinction but with survivorship determined by traits that are not otherwise strongly selected for during standard periods of background extinction. Contingency (*sensu* Gould [3]) is a strong factor in such a regime and can result in the removal of otherwise dominant taxa, resulting in sweeping changeovers in faunal composition [4]. As such, clade history can be important for understanding patterns of survival during mass extinctions. Volatility (the measure stability of a clade through time) can also play a role in survivorship over mass extinctions, as highly volatile clades with high background rates of extinction have an increased probability of losing all their species during mass extinction events [5]. Rates of speciation and extinction are not, however, clade-level properties, with the potential of speciation and extinction tied to a number of different characteristics of species and populations [6]. As such, differential survival of low volatility clades represents an example of sorting, and there is a general trend for volatility in all groups to decrease over time [7]. Somewhat paradoxically, origination rates appear to be reset at mass extinctions, resulting in at least temporary increases in volatility [8]. This could in part be due to expansion into new (or previously vacated) ecospace, and similar causes have been suggested for accelerated rates of morphological evolution [9, 10]. It has been shown that the rate at which a group invades available ecological space after mass extinctions can greatly influence its chances of long-term recovery [11]. Therefore, we may expect differences in speciation rate and rates of morphological evolution between groups that successfully radiate out of an evolutionary bottleneck [12] and those that remain at a low diversity as 'dead clades walking' [13]. Alternatively, morphological evolution and speciation could become decoupled, with a clade radiating into new ecospace without any marked increase in speciation.

Here we present an analysis of three Palaeozoic arthropod groups, two clades of Eurypterida and one of Trilobita, studying both rates of speciation and extinction along with morphological character evolution throughout their history from the Ordovician to the Permian. Recent study on changes in diversity and disparity of these clades has shown that all three show drastic changes in morphospace during the late Devonian [14]. While the pattern of morphospace shifting appeared to be mediated by ecology, with Eurypterina retreating to a portion of existing morphospace populated by generalists while Stylonurina and Aulacopleuroidea expanded into new morphospace through the proliferation of specialist taxa, patterns in diversity appeared to be mediated by some clade-specific property. Aulacopleuroidea experienced an evolutionary bottleneck while the closely related Stylonurina and Eurypterina became 'dead clades walking'. This provides a unique opportunity to assess the influence of volatility and clade history on patterns of recovery after mass extinctions.

2. Material and Methods

(a) Arthropod data

The study utilizes phylogenetic matrices of Stylonurina, Eurypterina and Aulacopleuroidea that have recently been the subject of detailed work on diversity and disparity [14]. The stylonurine dataset comprises 84 characters coded for 47 taxa, the eurypterine dataset comprises 176 characters coded for 114 taxa, and the aulacopleuroid dataset comprises 135 characters coded for 112 taxa. Individual species were coded in order to remove the potential for the inclusion of paraphyletic or polyphyletic groups. Such groups have been shown to impact negatively on the accuracy of biodiversity studies performed at higher taxonomic levels [15]. The data matrices were each subjected to cladistic analysis using TNT [16], employing random addition sequences followed by tree bisection-reconnection (TBR) branch swapping with 100,000 repetitions with all characters unordered and of equal weight. The strict consensus tree was constructed for each clade and used to calculate rates of character change and rates of speciation and extinction.

(b) Rates of character change

Rates of character change were described using the patristic dissimilarity of branch of the tree [17]. This method requires the reconstruction of ancestral taxa as dictated by the tree topology. These reconstructed ancestors were assigned temporal ranges as in Ruta *et al*. [18], with the ranges of observed taxa being extended to encompass inferred ghost ranges. Stage duration for all analyses was assigned based on Gradstein *et al*. [19].

Character change can be calculated assuming either punctuated or anagenetic modes of evolution; while there is evidence for both punctuated and anagenetic change in the fossil record [20, 21], here we assume gradualistic change, and so divide each value for patristic dissimilarity by the estimated duration of the associated branch. This assumption allows for the possibility of unsampled species, which could result in larger jumps in character change using a punctuational model, and also accounts for unequal time bin size. Most importantly, these assumptions match those used in calculating rates of speciation and extinction, allowing for relative changes in these rates to be compared directly. In order to test for correlation between rates and time, Kendall's rank correlation test was used to assess whether relatively large and small changes are concentrated at opposite ends of the time-scale; a significant negative correlation would be predicted by elevated rates of early change. Simple regression analysis was performed for the entire time series, as well as for pairs of periods, allowing for particular intervals over which rate shifts occurred to be recognised.

(c) Rates of speciation and extinction

Rates of speciation and extinction were calculated for each clade using modifications to the method of Foote [22, 23] proposed by Rode and Lieberman [24]. The ranges of observed taxa were extended based on inferred ghost ranges as in the character rate analyses, and ancestral taxa were again reconstructed as necessitated by tree topology. Volatility curves were generated for each group by summing the total number of speciation and extinction events in each time period and dividing this value by the total diversity of each period.

3. Results

Rate of character change is shown to have decreased in all three clades from the Ordovician to the Permian (fig. 1, table 1), exhibiting an initial, more rapid decrease before leveling off in the late Palaeozoic. The decrease in rate of character change is accompanied by a decrease in speciation rate. Volatility meanwhile remained relatively constant throughout (fig. 2); while there is a slight decrease in volatility through time, the change is not statistically significant (table 1). Extinction rates, therefore, increased by roughly commensurate levels. The degree of volatility is, however, different between the three clades, with Stylonurina and Eurypterina showing consistently higher volatility than Aulacopleuroidea. Comparing speciation and extinction rates across the three clades reveals further differences (fig. 3), with both eurypterid clades exhibiting elevated levels of extinction during the Silurian while aulacopleuroid extinction levels remain relatively stable throughout. All three clades show suppressed rates of speciation in the mid to late Devonian, mirroring trends observed in other trilobite groups [25], phyllocarid crustaceans [24], and bivalves and brachiopods [26]. Aulacopleuroids show above average rates of speciation in the Tournasian, corresponding to the radiation of brachymetopids following the late Devonian biodiversity crisis, while the speciation rates of Stylonurina and Eurypterina remain relatively low compared to their levels in the Silurian. Both Stylonurina and Eurypterina undergo a peak in extinction during the Kasimovian, while all three clades exhibit high extinction rates at the earliest Permian.

4. Discussion

Through comparing rates of speciation and extinction along with character evolution, a number of clear differences between the eurypterid clades and aulacopleuroid trilobites are apparent. Stylonurina and Eurypterina exhibit higher volatility than Aulacopleuroidea throughout the Palaeozoic, supporting a correlation between clade volatility and recovery after the late Devonian biotic crisis. While it is clearly understood why more volatile clades have an increased likelihood of extinction, as heightened levels of background extinction result in a greater change of heightened extinction levels during mass extinctions resulting in the loss of all species within a clade, it is unclear why increased volatility would result in a group being unable to recover from a mass extinction event. It could be expected that more volatile clades that survived mass extinctions would have an advantage during recovery, as an increased rate of speciation would result in more rapid proliferation once extinction levels dropped. Volatility, however, is not a particular trait of clades but an expression caused by a number of different traits, of which interplay of population structure and ecology, along with rate of genetic mutation, may be the most important. High volatility may, therefore, have a variety of different causes. Stylonurina and Eurypterina have similar evolutionary histories, both exhibiting high rates of extinction throughout the Silurian and a peak in extinction at the Kasimovian, neither of which are apparent in aulacopleuroids. Aulacopleuroids, however, show a marked loss of biodiversity at the end-Ordovician extinction during the Hirnantian, which is not as severe in either eurypterid clade. Differences in ecology appear to be at play; while both aulacopleuroids and the eurypterids are found in a range of marine environments, eurypterids appear to have been limited by the need to moult and potentially reproduce in sheltered, marginal conditions [27]. Eurypterids are known to show a high degree of endemism [28], and this could be due to their needing to return to these marginal conditions; similar population segregation is seen in modern horseshoe crabs, which shows a strong correlation between genetic and geographic distance [29]. The Silurian was marked by a general trend for decreasing sea level [30] punctuated by periods of ocean anoxia [31], and these environmental shifts could have resulted in high species turnover for eurypterids through loss of these marginal environments. By the late Palaeozoic eurypterids had become limited to freshwater environments [32], and so are negatively impacted by the aridification event associated with the rainforest collapse during the Kasimovian [33]. The aulacopleuroids meanwhile remain in the marine realm, and so are not affected by the environmental changes that so negatively impacted the Eurypterida.

There are, therefore, a number of potential reasons for the inability of the eurypterid clades to successfully recover from the late Devonian biotic crisis. The higher rates of extinction among the two clades during the Silurian results in Stylonurina and Eurypterina having a lower pool of species from which to radiate after the Devonian, resulting in a muted recovery compared to the Aulacopleuroidea. The fact that eurypterids were also limited to freshwater environments at this time means that they would have been unable to successfully colonise vacant marine ecospace which the aulacopleuroids could take advantage of. Therefore, while both Stylonurina and Eurypterina are characterized by high volatility in comparison to Aulacopleuroidea, the underlying causes of this difference in volatility is due to differences in ecology between the groups. The inherent clade properties considered by Lamsdell & Selden [14] to be responsible for the recovery of Aulacopleuroidea and the failure of Stylonurina and Eurypterina to regain diversity are, therefore, the results of ecological differences combined with contingency mediated by climatic changes. Interestingly, ecology is shown to exhibit conflicting signals during the late Devonian biotic crisis, with expansion into new morphospace by Stylonurina and Aulacopleuroidea (both specialists) countered in Stylonurina by factors increasing volatility in the group that made them unable to successfully recover their diversity.

The results of this study, combined with the results of previous study of disparity and diversity on these three clades, reveals the importance of comparing changes in disparity, diversity and volatility in order to tease apart the processes influencing the survival and recovery of clades during mass extinction events. Ecology is revealed to be a major factor behind the responses of individual species to the late Devonian biodiversity crisis, and demonstrates the bearing of the evolutionary history of a clade on such studies, along with the importance of having accurate phylogenetic hypotheses. Of the 'big five' mass extinctions, the late Devonian is potentially unique in its causal factors, and so further work is needed to test whether the patterns identify here are typical or atypical for mass extinctions in general.

5. References

1. Jablonski, D. 2005 Mass extinctions and macroevolution. *Paleobiology* **31**, 192–210.

2. Raup, D. M. 1984 Evolutionary radiations and extinctions. In *Patterns of change in Earth evolution*. (eds. H. D. Holland & A. F. Trendall), pp. 5–14. Springer, Berlin.
3. Gould, S. J. 1985 The paradox of the first tier: an agenda for paleobiology. *Paleobiology* **11**, 2–12.
4. Erwin, D. H. 2001 Lessons from the past: evolutionary impacts of mass extinctions. *Proc Natl Acad Sci USA* **98**, 5399–5403.
5. Lieberman, B. S. & Karim, T. S. 2010 Tracing the trilobite tree from the root to the tips: a model marriage of fossils and phylogeny. *Arth. Struct. & Dev.* **39**, 111–123.
6. Vrba E. S. & Gould, S. J. 1986 The hierarchical expansion of sorting and selection: sorting and selection cannot be equated. *Paleobiology* 12: 217–228.
7. Lieberman, B. S. & Melott, A. D. 2013 Declining volatility, a general property of disparate systems: from fossils, to stocks, to the stars. *Palaeontology* **56**, 1297–1304.
8. Krug, A. Z. & Jablonski, D. 2012 Long-term origination rates are reset only at mass extinctions. *Geology* **40**, 731–734.
9. Valentine, J. W. 1969 Patterns of taxonomic and ecological structure of the shelf benthos during Phanerozoic time. *Palaeontology* **12**, 684–709.
10. Valentine, J. W. 1980 Determinants of diversity in higher taxonomic categories. *Paleobiology* **6**, 444–450.

11. Sahney, S., Benton, M. J. & Ferry, P. A. 2010 Links between global taxonomic diversity, ecological diversity and the expansion of vertebrates on land. *Biol. Lett.* **6**, 544–547.
12. Raup, D. M. 1979 Size of the Permo – Triassic bottleneck and its evolutionary implications. *Science* **206**, 217–218.
13. Jablonski, D. 2002 Survival without recovery after mass extinctions. *Proc. Natl. Acad. Sci. USA* **99**, 8139–8144.
14. Lamsdell, J. C. & Selden, P. A. in prep. Clade history, species ecology and external causal factors influence arthropod survival and recovery during Paleozoic mass extinctions. *Proc. Natl. Acad. Sci. USA.*
15. Patterson, C. & Smith, A. B. 1989 Periodicity in extinction: the role of systematics. *Ecology* **70**, 802–811.
16. Goloboff, P. A., Farris, J. S. & Nixon, K. C. 2008 TNT, a free program for phylogenetic analysis. *Cladistics* **24**, 774–786.
17. Wagner, P. J. 1997 Patterns of morphologic diversification among the Rostroconchia. *Paleobiology* **23**, 115–150.
18. Ruta, M., Wagner, P. J. & Coates, M. I. 2006 Evolutionary patterns in early tetrapods. I. Rapid initial diversification followed by decrease in rates of character change. *Proc. R. Soc. B* **273**, 2107–2111.
19. Gradstein, F. M., Ogg, J. G., Schmitz, M. D., Ogg, G. M. 2012 *The geologic timescale 2012*. Boston, USA, Elsevier.
20. Gould, S. J. & Eldredge, N. 1977 Punctuated equilibria: the tempo and mode of evolution reconsidered. *Paleobiology* **3**, 115–151.

21. Sheldon, P. R. 1987 Parallel gradualistic evolution of Ordovician trilobites. *Nature* **330**, 561–563.
22. Foote, M. 2000 Origination and extinction components of taxonomic diversity: general problems. *Paleobiology* **26**, 74–102.
23. Foote, M. 2000 Origination and extinction components of taxonomic diversity: Paleozoic and post-Paleozoic dynamics. *Paleobiology* **26**, 578–604.
24. Rode A. L. & Lieberman, B. S. 2004 Using GIS to unlock the interactions between biogeography, environment, and evolution in Middle and Late Devonian brachiopods and bivalves*.* *Palaeogeogr. Palaeocl.* **211**, 345–359.
25. Abe, F. R. & Lieberman, B. S. 2009 The nature of evolutionary radiations: a case study involving Devonian trilobites. *Evol. Biol.* **36**, 225–234.
26. Stigall, A. L. 2010 Invasive species and biodiversity crises: testing the link in the Late Devonian. *PLoS ONE* **5**, e15584. (doi: 10.1371/journal.pone.0015584)
27. Vrazo, M. B. & Braddy, S. J. 2011 Testing the 'mass-moult-mate' hypothesis of eurypterid palaeoecology. *Palaeogeogr. Palaeocl.* **311**, 63–73.
28. Tetlie, O. E. 2007 Distribution and dispersal history of Eurypterida (Chelicerata). *Palaeogeogr. Palaeocl.* **252**, 557–574.
29. King, T. L., Eackles, M. S., Spidle, A. P. & Brockmann, H. J. 2005 Regional differentiation and sex-biased dispersal among populations of the horseshoe crab *Limulus polyphemus*. *Trans. Am. Fish. Soc.* **134**, 441–465.
30. Haq, B. U. & Schutter, S. R. 2008 A chronology of Paleozoic sea-level changes. *Science* **322**, 64–68.

31. Van Houten, F. B. & Arthur, M. A. 1989 Temporal patterns among Phanerozoic oolitic ironstones and ocean anoxia. *Geol. Soc. Spec. Pub.* **46**, 33–49.

32. Lamsdell, J. C. & Braddy, S. J. 2010 Cope's rule and Romer's theory: patterns of diversity and gigantism in eurypterids and Palaeozoic vertebrates. *Biol. Lett.* **6**, 265–269.

33. Sahney, S., Benton, M. J. & Falcon-Lang, H. J. 2010 Rainforest collapse triggered Carboniferous tetrapod diversification. *Geology* **38**, 1079–1082.

	Stylonurina		Eurypterina		Aulacopleuroidea	
	τ	p	τ	p	τ	p
Character rate change (Ordovician–Permian)	–0.265	0.020	–0.194	9.24×10^{-4}	–0.226	4.92×10^{-4}
Volatility change (Ordovician–Permian)	–0.203	0.121	–0.260	0.090	–0.068	0.638

Table 1. Correlation between time and rate of character change and time and volatility along stylonurine, eurypterine and aulacopleuroid phylogeny. (τ gives Kendall's rank correlation coefficient.)

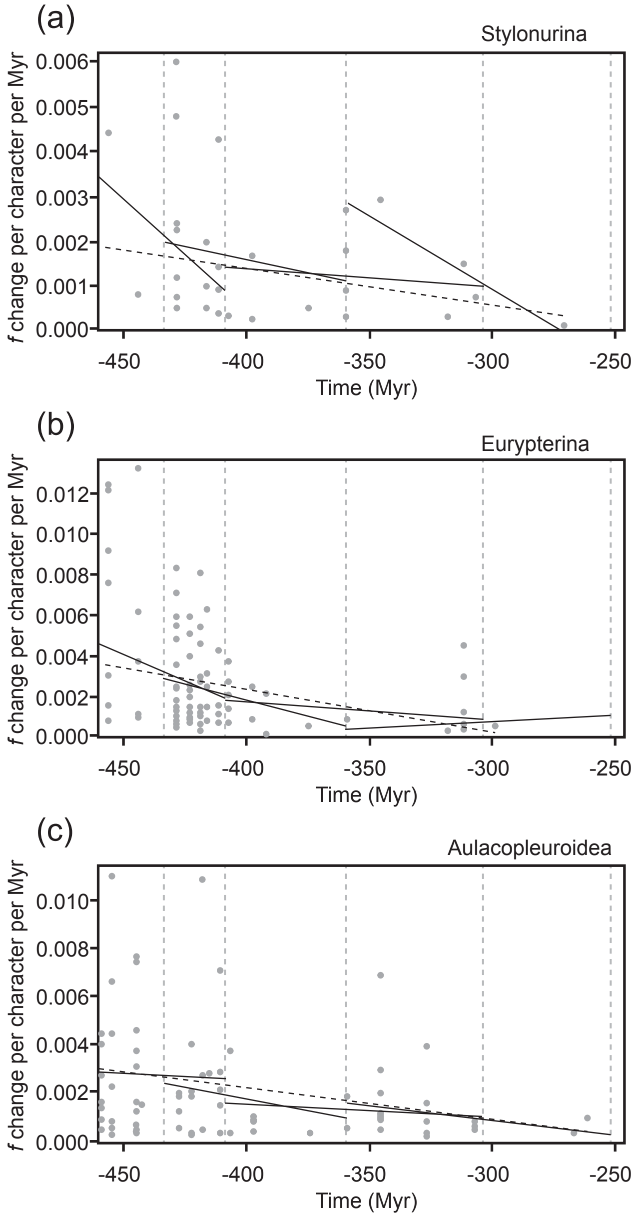

Figure 1. Rates of character change (**Δ**). Partitions separate Ordovician, Silurian, Devonian, Carboniferous, and Permian branches. Dashed regression lines give the relationship between time and change for the entire time period; solid lines give relationships between time and change over adjacent intervals.

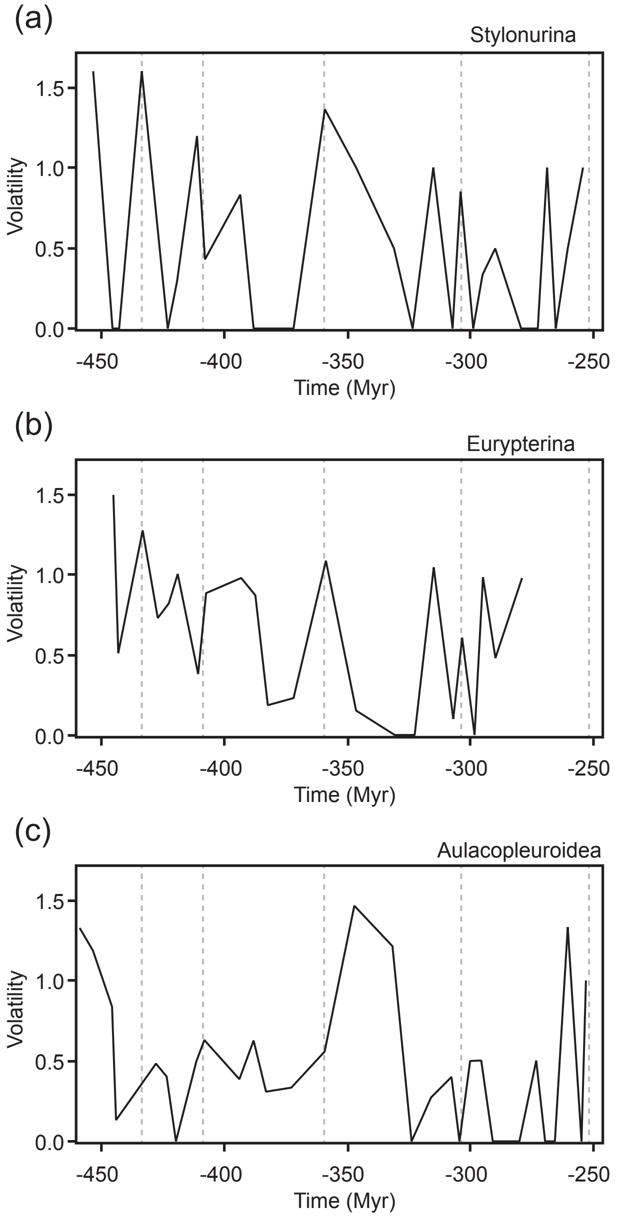

Figure 2. Volatility, given by the fractional rate of origination and extinction of species (the total number of originations and extinctions divided by total diversity), through time. Partitions separate the Ordovician, Silurian, Devonian, Carboniferous, and Permian time periods. (a) Stylonurina, (b) Eurypterina, (c) Aulacopleuroidea.

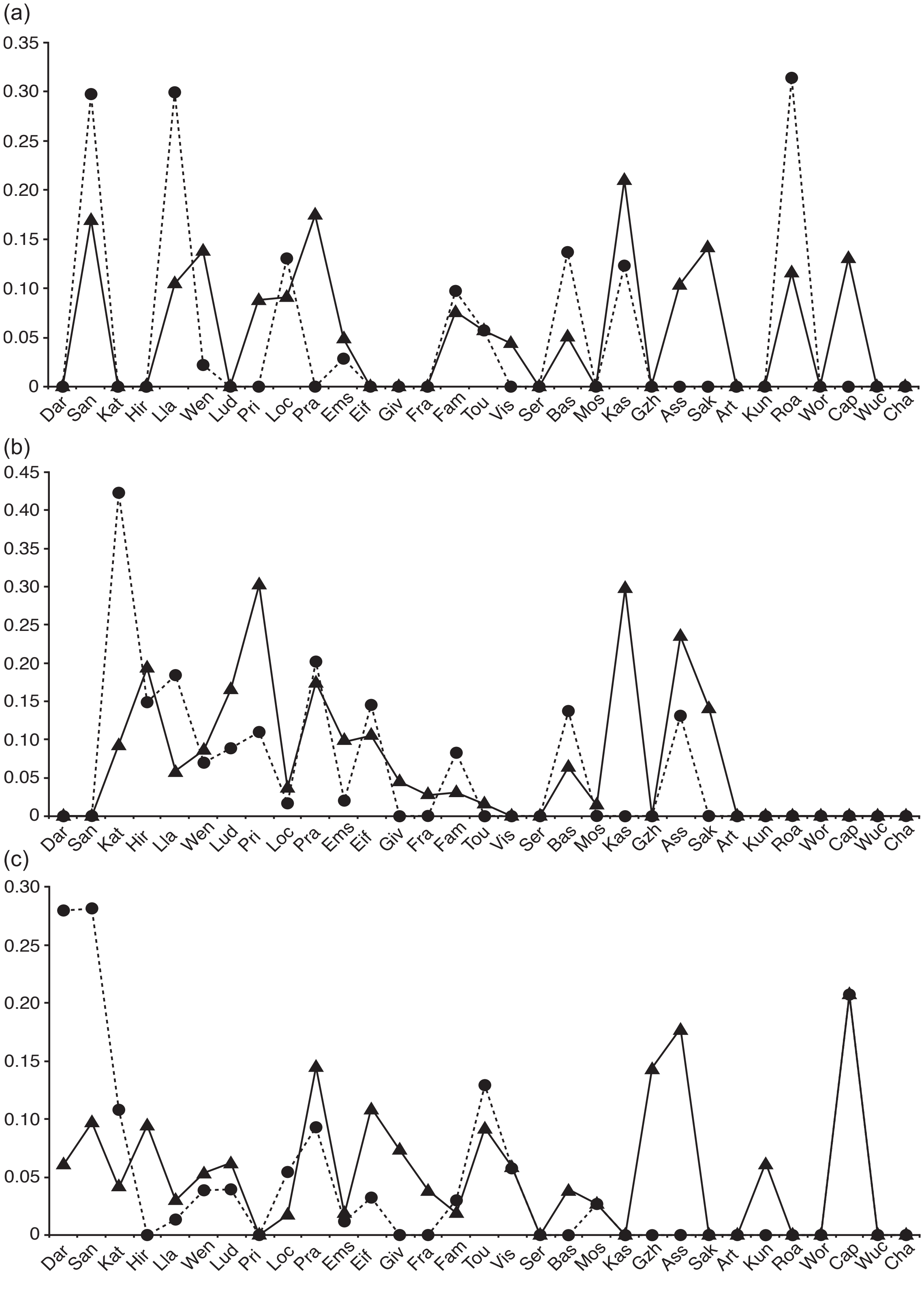
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Figure 3. Speciation and extinction rates for (a) Stylonurina, (b) Eurypterina, and (c) Aulacopleuroidea. Speciation rates are shown by circles and dashed lines, extinction rates by triangles and solid lines.

Conclusion

The results of this dissertation reveal the importance of comparing changes in disparity, diversity, and volatility in order to tease apart the processes influencing the survival and recovery of clades during mass extinction events. The consistent differences in how morphospace occupation changes across the end-Ordovician and late Devonian mass extinction events reveal that the underlying driving factors of individual extinction events can result in very different selective pressures, suggesting that it may not be possible to identify general survivorship rules for all mass extinctions. Ecology is, however, revealed to be a major factor behind the responses of individual species to the late Devonian biodiversity crisis. The somewhat contradictory selective signal exhibited by the studied clades reveals how different aspects of ecology can influence diversity, disparity and volatility in different ways, each influencing aspects of clade survival and recovery in different ways. The results also demonstrate the bearing of the evolutionary history of a clade on such studies. Contingency is an important factor in determining the response of clades to mass extinctions, and only through having a firm understanding of the history of a group can such factors be appropriately accounted for.

One of the overriding conclusions of this study is the importance of having accurate phylogenetic hypotheses. The discovery that Aulacopleuroidea, as traditionally defined, is rife with polyphyletic groups shows that relying on traditional taxonomy has the potential to result in highly spurious data. This also has ramifications for macroevolutionary analyses that rely on higher-level taxa. Higher-level taxa based on polyphyletic or paraphyletic groups can either increase the apparent severity of mass extinctions or dampen their effects; the fact that both an artificial heightening and dampening of extinction rate can occur from the same error only makes it more worrisome. Finally, the fact that most studies have focused at higher taxonomic levels most likely accounts for the supposed occurrence of clade-level selection during mass extinctions. The studies presented here have shown that, when viewed appropriately at the species-level, it is clear that only certain members of clades are surviving mass extinctions. Clade survival is therefore an effect of sorting through and extension of the effect hypothesis; selection is occurring on properties of individuals, not on clades, and it is only through the preferential survival of a subset of individuals within the clade that the clade itself survives. Studies that treat clades as a single taxonomic unit are therefore likely to be overgeneralizing and, as a consequence, mistaking sorting for selection.

Further work is needed to extend these studies beyond the few taxa presented here. A number of clades, including crinoids, phyllocarid crustaceans, and xiphosurans, all have evolutionary histories extending throughout the Paleozoic and it would be interesting to see whether the patterns observed for eurypterids and aulacopleuroid trilobites also occur in these disparate groups. Detailed analysis of disparity and morphospace in late Ordovician trilobite groups could also be a fruitful avenue for further research, in order to test whether there is any morphological signal for the supposed turnover of warm and cold adapted taxa occurring during the mass extinction. Finally, of the ‘big five’ mass extinctions the late Devonian is potentially unique in its causal factors, and so further work is needed to test whether the patterns identify here are typical or atypical for mass extinctions in general.

Appendices

Appendix 1

Redescription of *Drepanopterus pentlandicus* Laurie 1892, the earliest known mycteropoid (Chelicerata: Eurypterida) from the early Silurian (Llandovery) of the Pentland Hills, Scotland

Comprising the morphological character list and character matrix used in the phylogenetic analysis

Character list

1. Antero median carapace protrusion: absent (0); present (1).

2. Carapace anterior: rounded (0); angular (1).

3. Denticulate anterior margin of carapace: absent (0); present (1).

4. Carapace marginal rim broad: absent (0); present (1).

5. Carapace marginal rim with striate ornament: absent (0); present (1).

6. Row of pustules along inside of marginal rim: absent (0); present (1).

7. Lateral carapace margin: continuous (0); stepped (1).

8. Deep carapace with pleural margins curving ventrally: absent (0); present (1).

9. Lateral regions of posterior carapace margins overlapping first opisthosomal tergite: absent (0); present (1).

10. Morphology of genal carapace regions overlapping first opisthosomal tergite: small (0); drawn out into posterolateral lobes (1).

11. Carapace position of greatest width: posterior third (0); median third (1).

12. Prosoma quadrate: absent (0); present (1).

13. Carapace vaulted: absent (0); present (1).

14. Median ridge between lateral eyes: absent (0); present (1).

15. Carapace ornament of large lunate scales surrounding and pointing away from the central area and eyes: absent (0); present (1).

16. Circular plateau ornamentation anterior to median ridge: absent (0); present (1).

17. Position of median eyes on carapace: median third (0); anterior third (1).

18. Ocellar area: absent (0); present (1).

19. Lateral eye shape: crescentic (0); expanded (1).

20. Palpebral lobe: absent (0); circular (1); reniform (2).

21. Lateral eyes converging and placed anteriorly on carapace: absent (0); present (1).

22. Annular cuticular thickening surrounding lateral eyes: absent (0); present (1).

23. Shape of annular cuticular thickening: oval (0); circular (1).

24. Orbital ridges: absent (0); present (1).

25. Median ridge reduced: absent (0); present (1).

26. Transverse suture on ventral plates: absent (0); present (1).

27. Transverse suture curving back at midline: absent (0); present (1).

28. Groove running across doublure: absent (0); present (1).

29. Suture on ventral plates: epistoma absent (0); epistoma present (1).

30. Rostral field: absent (0); present (1).

31. Ventral plates widen anteriorly: absent (0); present (1).

32. Appendage III: spiniferous with paired spines (0); spiniferous with single spines (1).

33. Pairs of spines per podomere on prosomal appendage III: one pair (0); two or more pairs (1).

34. Prosomal appendage IV: spiniferous (0); non spiniferous (1).

35. Pairs of spines per podomere on prosomal appendage IV: one pair (0); two or more pairs (1).

36. Spines on prosomal appendage IV: moveable spines (0); both moveable and fixed spines (1); fixed spines (2).

37. Blade like structures on podomeres of anterior appendages: absent (0); present (1).

38. Blades enlarged and longer than podomere length: absent (0); present (1).

39. Rachis: absent (0); present (1).

40. Coxal laden: absent (0); present (1).

41. Prosomal appendage V: spiniferous (0); non spiniferous (1).

42. Spines on prosomal appendage V reduced: absent (0); present (1).

43. Prosomal appendage VI: walking leg (0); swimming leg (1).

44. Appendage VI reaching to pretelson: absent (0); present (1).

45. Shape of proximal podomere of appendage VI narrow: L/W ≤ 2.0 (0); expanded L/W > 2.0 (1).

46. Podomere VI-5: half the width of VI-4 (0); equal width of VI-4 (1).

47. Distal podomere margin of VI-6 modified: absent (0); present (1).

48. Ear on coxa VI: absent (0); present (1).

49. Appendage VI showing lateral serrations: absent (0); present (1).

50. Podomere 7a on sixth prosomal appendage: absent (0); present (1).

51. Width of VI-7a: narrow [less than 50% of width of VI-7] (0); wide [more than 50%] (1).

52. Shape of VI-7a: oval (0); triangular (1).

53. Longitudinal grooves on podomeres: absent (0); present (1).

54. Podomeres ridged: absent (0); present (1).

55. Podomeres thicken distally: absent (0); present (1).

56. Cleft metastoma: absent (0); present (1).

57. Anterior margin of metastoma: notch absent (0); notch present (1).

58. Posterior margin of metastoma: rounded (0); flattened or recurved (1).

59. Metasoma: bulky (0); gracile (1).

60. Paired tubercles on opisthosomal tergites 2-5: absent (0); present (1).

61. Pustular ornamentation: absent (0); present (1).

62. Acicular scales on opisthosoma: absent (0); present (1).

63. Row of large tongue-shaped scales on posterior margin of opisthosomal segments: absent (0); present (1).

64. Opisthosoma narrower than carapace: absent (0); present (1).

65. Marginal rim on opisthosoma: absent (0); present (1).

66. First tergite with narrow posterior margin: absent (0); present (1).

67. Positive opisthosomal differentiation of third order first segment: absent (0); present (1).

68. Positive opisthosomal differentiation of third order second segment: absent (0); present (1).

69. Second tergite developed into round macrotergite: absent (0); present (1).

70. Preabdominal epimera: absent (0); present (1).

71. Caudal postabdomen: absent (0); present (1).

72. Lateral pleurae: absent (0); present (1).

73. Pretelson elongated: absent (0); present (1).

74. Pretelson postlaterally expanded: absent (0); present (1).

75. Dorsal pretelson lobes: absent (0); present (1).

76. Telson shortened: absent (0); present (1).

77. Telson elongate: absent (0); present (1).

78. Dorsal median keel on telson: absent (0); present (1).

79. Paired broad rounded ventral keels on telson: absent (0); present (1).

80. Telson serrated: absent (0); present (1).

Character matrix

Weinbergina opitzi

00000 0010- 00000 00000 00-00 0000- 00000 00-00 00001 10000 --000 ---00

00000 00001 00000 00000

Alkenopterus brevitelson

00010 0000- 00000 00000 00-00 ????? ????? ???0? 1-00? 10?00 --010 ???10

00000 00000 10000 10000

Brachyopterella pentagonalis

01000 0000- 100?0 ?0100 10-00 11011 ???1- -??0? 1-000 00000 --010 ???1?

00?00 0???0 ????? 0?0?0

Brachyopterus stubblefieldi

00000 0000- 10000 0?100 00-00 ????? ?1-00 00-0? 1-00? 00?00 --000 0?000

00000 00000 00000 00000

Ctenopterus cestrotus

00100 0000- 00000 01?01 00-00 ??011 ?0101 20-0? 1-01? 10?00 --000 ???00

01000 00001 ?0??? 010?0

Cyrtoctenus wittebergensis

10000 00111 00000 00001 01110 ????? ???00 1111? ???00 1?00? ??101 ???00

00100 00000 00010 00010

Drepanopterus abonensis

00011 10010 000?0 00002 01000 1000- 1001- -1000 1-000 10000 --101 11-01

10000 00000 00000 00100

Stoermeropterus conicus

00000 0000- 00000 0?000 00-00 0-010 01000 20-00 1-001 10101 01000 01000

00000 00000 00100 00000

Drepanopterus pentlandicus

00010 00010 00000 0?000 01000 ??0?? ???1- -10?0 1-000 10000 --101 11-01

10000 00100 00000 00100

Hallipterus excelsior

01000 1000- 00011 10?00 01010 10011 ????? ?0-?0 ????? ????? ????? ?????

00??? ????0 ????? ?????

Hardieopterus macrophthalmus

00000 0000- 00011 0?000 00-00 1000- 1???? ???0? 00000 10?00 --001 01100

10101 00000 01001 00??0

Hibbertopterus scouleri

00000 00111 00010 00001 01101 ??0?? 1??00 11101 1-00? 10000 --001 11-00

00100 00000 00000 00010

Kiaeropterus cyclophthalmus

00000 0000- ?0000 00100 10-00 ????? ????? ???0? 1-00? ?0??0 --010 ???10

00000 00000 00??? ???0?

Kokomopterus longicaudatus

00000 0000- 000?0 ???00 00-?? ??0?? 10000 00-0? 0100? 10010 --001 01100

00101 00000 00000 00000

Lamontopterus knoxae

00000 0000- 000?? ????? ????? ????? ????? ???0? 0100? 10?00 --001 ???00

00?01 00000 00000 00000

Laurieipterus elegans

00100 0100- 00000 01001 00-00 11011 10101 20-0? 1-0?0 10000 --000 001?0

00000 00000 ????? 01??0

Megarachne servinei

11000 0000- 00010 00002 010?0 ????? ???1- -1101 1-0?? ??0?? ??101 ?????

0?000 1111? ????? ?????

Moselopterus ancylotelson

01000 0000- 00000 0?000 00-00 ??10- 01000 20-00 1-001 10101 00000 01000

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Mycterops mathieui

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0101? 00000 00110 00100

Parastylonurus ornatus

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00000 00000 00110 00100

Rhenopterus diensti

00000 0000- 00000 00000 00-00 1010- 11-1- -0-00 1-000 10000 --010 01010

11000 00000 10000 10100

Stylonurella spinipes

01000 0100- 01000 0?001 00-00 1000- 1?110 00-00 1-010 10000 --000 ???00

00010 00000 00??? ?????

Stylonurus powriensis

00000 0000- 01010 0?001 00-10 ????? ????? ????? 1-01? 10?00 --000 ???00

01000 00000 00000 01100

Tarsopterella scotica

01000 0000- 00011 1?000 00-10 ????? ????? ????? ????? ????? ???01 ???00

00100 00000 01001 000?0

Vinetopterus struvei

00000 0000- 00000 00000 00-00 ??0?? ????? ???0? ??001 10?01 10?0? ???00

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Woodwardopterus scabrosus

00000 0000- 000?0 ???0? 0???? ????? ???1- -110? 1-00? 10?00 --101 ???0?

00000 01110 00??0 00?10

Eurypterus remipes

00000 0000- 00000 00010 00-00 0-00- 00000 00-00 1-101 11101 11000 01000

00000 00000 00010 00001

Hughmilleria socialis

00000 0000- 00000 00010 00-00 0-010 00000 00-00 00101 11101 11000 01000

00000 00000 00000 00000

Onychopterella augusti

00000 0000- 00000 0?0?0 00-0? ??0?? 0??00 00-00 1-101 10101 01000 ???00

00000 00000 000?0 00?00

Pagea plotnicki

01000 0100- 11010 0?001 00-10 ????? ?11?? ?0-0? 1-0?? 10?0? ??000 ???00

01010 00000 00111 0????

Leiopterella tetliei

0000? 0000- 100?? ????? ????? 1010- 1??10 0???0 1-0?0 1000? ??010 010??

0??10 ?000? ????? ?????

Pagea symondsii

01000 0100- 11110 0?001 00-10 ??00- 1???? ????? ????? 1???? ????? ?????

0?0?? ????? ????? ?????

Drepanopterus odontospathus

00011 000?? 000?0 0?002 01000 ????? ????? ????? ????? ????? ????? ?1???

1???? ????? ????? 00101

Campylocephalus oculatus

00000 00111 10010 00002 01001 ????? ????? ????? ????? ????? ????? ?????

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Hastimima whitei

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Appendix 2

A new Ordovician eurypterid (Arthropoda: Chelicerata) from southeast Turkey: evidence for a cryptic Ordovician record of Eurypterida

Comprising the morphological character list and character matrix used in the phylogenetic analysis

Character list

1. Angular projection on the anterior of the carapace: absent (0); present (1).
2. Anterior margin of carapace: unornamented (0); denticulate (1).
3. Carapace genal spines: present (0); absent (1).
4. Carapace shape: horseshoe or wide-horseshoe (0); semicircular (1); quadrate (2); trapezoidal (3); wide-rectangular (4); subquadrate (5); campanulate (6); parabolic (7); spatulate (8); triangular (9).
5. Carapace genal facets: absent (0); present (1).
6. Angle of genal facets: low angle (0); high angle (1).
7. Lateral eye shape: crescentic (0); expanded (1).
8. Size of palpebral lobe: small (0); large (1); absent (2).
9. Lateral eye position: centrilateral (0); centrimesial (1); antelateral (2); central (3); antemesial (4).
10. Lateral eye abuts carapace margin: absent (0); present (1).
11. Lateral eyes associated with ophthalmic ridge: present (0); absent (1).
12. Suture on ventral plates: *Eurypterus*-type (0); *Hughmilleria*- or *Hallipterus*-type (1); *Megalograptus*-type (2); *Erieopterus*-type (3).
13. Transverse suture on ventral plates: present (0); absent (1).
14. Chelicerae: small (0); able to extend beyond marginal rim (1).
15. Relative lengths of appendages II-V: increasing posteriorly (0); forward appendages enlarged (1).

16. Morphology of spines on prosomal appendages II–IV: reduced [length < width of podomere] (0); regular [length ≈ width of podomere] (1); enlarged [length > width of podomere] (2); absent (3).

17. Mobility of spines on appendages II–IV: fixed (0); moveable (1).

18. Orientation of spines on appendages II–IV: ventral (0); anterior (1).

19. Spines on appendages II–IV thickened and highly sclerotised: absent (0); present (1).

20. Function of appendage V: solely walking or prey-capture (0); adapted to aid in balance during swimming (1).

21. Prosomal appendage VI: walking leg (0); swimming leg (1).

22. Length of prosomal appendage VI: long (0); short [barely projecting from beneath carapace] (1).

23. Shape of proximal podomere of appendage VI: narrow [L/W≥2.0] (0); expanded [L/W<2.0] (1).

24. Anterior margin of coxa VI: undifferentiated (0); expanded to form ‘ear’ (1).

25. Shape of ‘ear’ on coxa VI: triangular (0); rectangular (1); subquadrate/semicircular (2).

26. Angle between VI-3 and VI-4: 180˚ (0); not 180˚ (1).

27. Length of podomeres VI–4 and VI–5: VI–5>VI–4 (0); VI–4≥VI–5 (1).

28. Length of podomeres VI–4 when VI-5 is not longer: >VI–3 and VI-5 (0); VI–3 and VI–5 (1).

29. Podomere VI-5 bordering podomere VI-7: absent (0); present (1).

30. Distal podomere margin of VI–6 modified: absent (0); present (1).

31. VI–7 lateral margins: unornamented (0); serrated (1).

32. Angular projection on the anterior of podomere VI-7: absent (0); present (1).

33. Podomere 7a on appendage VI: absent (0); present on posterior of appendage (1); present on anterior of appendage (2).

34. Width of posterior VI–7a: narrow [less than 50% width of VI–7] (0); wide [more than 50%] (1).

35. Shape of posterior VI–7a: oval (0); triangular (1).

36. VI–8 lateral margins: unornamented (0); small serrations (1); enlarged serrations (2).

37. VI–8 anterior projection: absent (0); present (1).

38. Additional moveable lobe on VI-8: absent (0); present (1).

39. Morphology of VI–8/VI–9 joint: joint flush (0); VI–9 set into VI–8 (1).

40. Length of VI–9 (as ratio of VI–8): large [>50% of VI–8 length] (0); small [<22% of VI–8 length] (1); totally absent (2).

41. Shape of podomere VI–9: spinose (0); triangular, pentagonal or oval (1).

42. VI–9 margin: no ornament (0); serrated (1).

43. VI–9 position: centrally on podomere 8 (0); migrating towards posterior of podomere 8 (1).

44. VI–9 expanded: absent (0); present (1).

45. Podomere cuticular morphology: rounded (0); ridged (1).

46. Metastoma anterior: smooth or shallow notch (0); deeply notched (1).

47. Shape of posterior margin of metastoma: rounded (0); truncated/flattened (1); angular (2); notched (3).

48. Metastoma width: as broad or broader than long (0); narrow (1).

49. First segment expressed dorsally: expressed (0); folded under carapace (1).

50. Microtergite: absent (0); present (1).

51. Genital operculum morphology: consisting of three visible segments (0); consisting of two visible segments (1); unfused (2).

52. Morphology of anterior opercular plate: fully expressed (0); lateral expression only (1); completely supressed (2).

53. Thickness of anterior opercular plate: fully expressed (0); narrow (1).

54. MOP and POP morphology: separate/with clear suture (0); without suture but with ornament differentiation (1); without suture and without ornament differentiation (2).

55. Morphology of type A genital appendage: furca fused (0); unfused (1).

56. Spatulae on type A genital appendage: absent (0); present (1).

57. Morphology of spatulae: angular (0); rounded (1).

58. Moveable preabdominal spines: absent (0); present (1).

59. Postabdominal epimera: present (0); absent (1).

60. Preabdominal/postabdominal boundary: between 7th and 8th segments (0); between 6th and 7th segments (1); between 4th and 5th segments (2).

61. Epimera on segment 7: absent (0); present (1).

62. Number of segments in postabdomen: 3 (0); 5 or 6 (1); 9 (2).

63. Postabdomen: undifferentiated (0); narrowing from preabdomen (1).

64. Caudal postabdomen: absent (0); present (1).

65. Posterior margin of segments 7–9: smooth (0); dentate (1).

66. Posterior margin of segments 10–12: smooth (0); dentate (1).

67. Epimera on pretelson: absent (0); angular (1); rounded (2); sexually dimorphic (3).

68. Telson shape: straight (0); curved (1); paddle-like (2).

69. Telson base: flattened (0); bulbous expansion (1).

70. Telson margin: smooth (0); serrated (1).

71. Opisthosoma lateral division: none (0); trilobed (1).

72. Primary opisthosomal ornamentation: scales (0); closely spaced pustules (1); coarse pustules (2).

73. Primary carapace ornamentation: scales (0); closely spaced pustules (1); coarse pustules (2).

74. Principal scale on carapace: absent (0); present (1).

75. Carapace ornament including elongate pustules that angle away from the lateral eyes and curve around the carapace margin: absent (0); present (1).

76. Row of node-like scales on dorsal opisthosomal segments: absent (0); present (1).

77. Ornamentation of angular scales across posterior of tergite segments: absent (0); present (1).

78. Longitudinal rows of angular scales on tergites: absent (0); present (1).

79. Ornament of chevron scales: absent (0); present (1).

80. Ornament of linguoid scales: absent (0); present (1).

81. Form of posterior margin of articulating facet on tergites: row of pustules (0); row of scales (1); groove (2).

Character matrix

Weinbergina opitzi

00000 -0-?0 03100 11000 0010- 00-00 000-- 00000 00000 ---00 22-0- --000

00000 00000 01100 00000 0

Brachyopterus stubblefieldi

00180 -0010 1?0?0 00000 0000- 00-00 000-- 00000

00001 0??10 ????? ??0?0 01000 00000 0---0 00000 ?

Parastylonurus ornatus

00100 -0000 10000 11000 0000- 00-00 000-- 00000

00000 11110 00000 10000 01100 01000 00000 00000 ?

Stoermeropterus conicus

00100 -0010 11100 00000 00110 00-00 00100 00000 00001 10010 00100 10100

01000 13010 01100 00000 0

Stoermeropterus latus

00100 -0010 1110? ????? 00??? 00-00 00100 00000 00001

???10 0010? 11100 01000 11010 00000 00000 ?

Stoermeropterus nodosus

00100 -0010 1???? ????? ????? ????? ????? ????? ????? 10010 00100 11100

01000 ?2010 01100 10000 ?

Vinetopterus struvei

01100 -0010 13100 00000 00110 00-00 00100 00000 00001

00010 0010? ??000 01101 100?0 01100 10000 0

Vinetopterus martini

01100 -?010 131?? 00000 00??? 00-00 00100 00000 00001 ?0?10 ????? ??000

01101 100?0 01100 10000 ?

Moselopterus ancylotelson

00100 -0010 13100 10000 00110 00-00 00100 00000 00001 00010 0010? 10010

01101 10101 01100 10000 0

Moselopterus elongatus

00100 -0010 13100 10000 00110 00-00 00100 00000

00001 00010 0010? ??010 01101 10101 01100 ?0000 0

Onychopterella augusti

00150 -?010 1???0 1100? 10110 00-00 00101 00010 00000 ??0?0 ????? 0-001

01100 00010 0000? 00000 ?

Onychopterella kokomoensis

00150 -1010 13100 11000 101?? 00-00 00101 00010

00000 00010 0010? 0-001 01100 02010 0000? 00000 ?

Dolichopterus macrocheirus

00120 -0120 10100 21000 10111 11001 11101 20110 11010 11110 01100 10000

01100 01000 00000 00000 0

Eurypterus remipes

00131 01010 10100 11001 10112 01001 00111 10011 10000 00010 01101 0-010

01100 00001 00010 01100 1

Hughmilleria socialis

00170 -1221 11110 11000 10112 01101 00111 00011 10100 010?0 12-20 0-010

11100 00000 00000 00011 ?

Tylopterella boylei

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01100 00000 00000 00000 ?

Megalograptus ohioensis

01121 01040 12101 21111 10112 01001 00111 00012 ----0 03010 12-10 0-011

01100 00000 10000 01100 1

Mixopterus kiaeri

00121 01040 1?101 21110 10112 01111 00111 00011 10000 000?0 12-20 0-010

01110 00100 10000 00000 ?

Strobilopterus princetonii

00110 -0130 1??00 1000? 11111 01101 10101 20110 10000 1?1?0 ???00 10000

01100 00??? 0110? 00000 0

Erieopterus microphthalmus

00141 10010 13100 10001 10112 01001 00111 00011 00000 01010 01101 0-010

01100 01100 00000 00000 ?

Rhenopterus diensti

00170 -0010 10000 00000 0000- 00-00 000-- 00000 00001 00010 00000 0-001

01110 00100 00000 00000 0

Octoberaspis ushakovi

00030 -0000 0???? ????0 10??? ???0? 002-- 00002 ----0 02001 20000 0-002

02100 01000 02200 00000 ?

Loganamaraspis dunlopi

00030 -?0?? ?310? ????? 0000- 0???? ????? ????? ????0 02001 20000 0-012

02100 000?? 0---0 00000 ?

Diploaspis casteri

00030 -1000 01??? 0000? 10??? ???00 002-- 00002 ----0???01 200?? ??002

02100 00201 02200 10000 ?

Paraeurypterus anatoliensis

00121 00110 1?1?? 1100? 10??? 010?? ????? ????? ????0 ???10 ????? ??0?0

0???? ????? 00100 01000 1

Pentlandopterus minor

00121 00110 1???? ????? 10??? 010?? ????? ????? ????? ????0 ????? ??010

01100 00000 01100 00000 ?

Chasmataspis laurencii

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02110 00000 12200 10000 ?

Buffalopterus pustulosus

00110 -0110 131?? ????? 11??? ????? ????? ????? ????? ???10 0110? 0-000

01100 01201 01101 00000 0

Syntomopterella richardsoni

00110 -0130 131?? ????? 1???? ????? 10111 20?1? 1???0 ????? ????? ?????

????? ????? 01101 00000 ?

Dolichopterus jewetti

00120 -0120 ???00 21001 10111 11001 11101 20110 11010 11010 01100 10000

01100 01000 00100 ?0000 0

Ruedemannipterus stylonuroides

10160 -0120 1???? ????? 10??? 11001 ?1101 ?0110 10110 ????0 ????? ??0??

????? ????? 01100 00000 ?

Clarkeipterus testudineus

10020 -0120 1???? ????? 10??? 11001 ?1101 ?0?10 10010 ????? ????? ?????

????? ????? ??100 ?00?? ?

Clarkeipterus otisius

10020 -0120 1???? ????? ????? ????? ????? ????? ????? ????? ????? ?????

????? ????? ??100 ????? ?

Erieopterus eriensis

00111 10010 131?0 1000? 10112 01001 00111 00011 00000 ???10 0110? ??010

01100 0?000 00000 00000 ?

Eurypterus hankeni

00131 01010 101?? 1100? 10112 01001 00111 00011 10000 000?0 ????? 0-010

01100 01001 00010 01100 1

Eurypterus tetragonophalmus

00131 01010 10100 11001 10112 01001 00111 10011 10000 00010 01101 0-010

01100 02001 00010 01100 1

Eurypterus leopoldi

00131 01010 1???? ????? 1???? ????? ?0111 10011 10000 00??? ????? ???0?

???00 02001 ?0010 01100 ?

Eurypterus pittsfordensis

00131 01010 10100 11001 10112 01001 00111 10011 10000 000?0 ????? ??000

01100 02001 00010 01100 1

Eurypterus henningsmoeni

00131 01010 101?0 ????1 10112 01001 00111 10011 10000 000?0 ????? 0-010

01100 02001 00010 01100 1

Orcanopterus manitoulinensis

10170 -1020 1??00 21000 10??? 0??0? 00111 00010 10010 110?0 12-1? ??010

11100 00000 00000 00010 ?

Pterygotus anglicus

00130 -1221 11110 3---0 10112 01101 00111 10011 10100 000?0 12-20 0-000

01100 00201 00000 00011 1

Adelophthalmus sievertsi

00170 -1010 11100 3---0 10112 01101 00111 11011 10100 000?0 12-20 10010

01100 00000 00000 00011 2

Eurypterus dekayi

00131 01010 10100 11001 10112 01001 00111 00011 10000 000?0 01101 0-010 01100 02000 00000 01000 1

Carcinosoma newlini

00190 -1020 1?101 21110 10112 01111 00111 10011 11010 000?0 12-20 0-010 01110 00000 00000 00000 ?

Nanahughmilleria norvegica

00170 -1010 11100 11000 10112 01101 00111 11011 10100 100?0 12-20 10000 11100 00000 00000 00011 1

Appendix 3

Babes in the wood – a unique window into sea scorpion ontogeny

Comprising the morphological character list and character matrix used in the phylogenetic analysis

Character list

1. Angular projection on the anterior of the carapace: absent (0); present (1).
2. Anterior margin of carapace: unornamented (0); denticulate (1).
3. Carapace marginal rim: present (0); absent (1).
4. Carapace genal spines: present (0); absent (1).
5. Carapace shape: horseshoe or wide-horseshoe (0); semicircular (1); quadrate (2); trapezoidal (3); wide-rectangular (4); subquadrate (5); campanulate (6); parabolic (7); spatulate (8); triangular (9); long-rectangular (10).
6. Carapace genal facets: absent (0); present (1).
7. Angle of genal facets: low angle (0); high angle (1).
8. Lateral eye shape: crescentic (0); expanded (1).
9. Size of palpebral lobe: small (0); large (1); absent (2).
10. Lateral eye position: centrilateral (0); centrimesial (1); antelateral (2); central (3); antemesial (4).
11. Lateral eye abuts carapace margin: absent (0); present (1).
12. Lateral eyes associated with ophthalmic ridge: present (0); absent (1).
13. Suture on ventral plates: *Eurypterus*-type (0); *Hughmilleria*- or *Hallipterus*-type (1); *Megalograptus*-type (2); *Erieopterus*-type (3).
14. Transverse suture on ventral plates: present (0); absent (1).
15. Chelicerae: small (0); able to extend beyond marginal rim (1).
16. Form of cheliceral peduncle: approximately equal in length to fixed ramus (0); longer than fixed ramus (1).

17. Denticles on chela: absent (0); present, small, undifferentiated (1); present, large, differentiated (2).
18. Largest denticle medially on fixed ramus: erect (0); inclined (1); acute (2).
19. Angular distal teeth on both rami: absent (0); present (1).
20. Relative lengths of appendages II-V: increasing posteriorly (0); forward appendages enlarged (1).
21. Morphology of spines on prosomal appendages II-IV: reduced [length < width of podomere] (0); regular [length ≈ width of podomere] (1); enlarged [length > width of podomere] (2); absent (3).
22. Mobility of spines on appendages II–V: fixed (0); moveable (1).
23. Orientation of spines on appendages II–V: ventral (0); anterior (1).
24. Spines on appendages II–V: thickened and highly sclerotised absent (0); present (1).
25. Armature of anterior prosomal appendages flattened and laterally expanded into blades: absent (0); present (1).
26. Prosomal appendage podomeres thicken distally: absent (0); present (1).
27. Morphology of appendage V podomeres: undifferentriated and broad (0); podomeres tubular, lacking armature except for penultimate distal podomere (1).
28. Appendage V armature: non-spiniferous (0); spiniferous (1).
29. Coxal laden: absent (0); present (1).
30. Morphology of prosomal appendage VI: equal in width along length (0); distally expanded into swimming leg (1).
31. First podomere of prosomal appendage VI that fully projects beyond carapace margin: Fourth podomere (0); Sixth podomere (1); Third podomere (2).

32. Shape of proximal podomere of appendage VI: narrow [L/W≥2.0] (0); expanded [L/W<2.0] (1).
33. Anterior margin of coxa VI undifferentiated (0); expanded to form ‘ear’ (1).
34. Shape of ‘ear’ on coxa VI: triangular (0); rectangular (1); subquadrate/semicircular (2).
35. Anterior denticle of coxa VI large: absent (0); present (1).
36. Angle between VI-3 and VI-4: 180º (0); not 180º (1).
37. Length of podomeres VI-4 and VI-5: VI-5>VI-4 (0); VI-4≥VI-5 (1).
38. Length of podomeres VI-4 when VI-5 is not longer: >VI-3 and VI-5 (0); equal to VI-3 and VI-5 (1).
39. Podomere VI-5 bordering podomere VI-7: absent (0); present (1).
40. Distal podomere margin of VI-6 modified: absent (0); present (1).
41. VI-7 lateral margins: unornamented (0); enlarged serrations (1); small serrations (2).
42. Angular projection on the anterior of podomere VI-7: absent (0); present (1).
43. Podomere 7a on appendage VI: absent (0); present on posterior of appendage (1); present on anterior of appendage (2).
44. Width of posterior VI-7a: narrow [less than 50% width of VI-7] (0); wide [more than 50%] (1).
45. Shape of posterior VI-7a: oval (0); triangular (1).
46. VI-8 lateral margins: unornamented (0); small serrations (1); enlarged serrations (2).
47. VI-8 anterior projection: absent (0); present (1).
48. Additional moveable lobe on VI-8: absent (0); present (1).
49. Morphology of VI-8/VI-9 joint: joint flush (0); VI-9 set into VI-8 (1).

50. Length of VI-9 (as ratio of VI-8): large [>25% of VI-8 length] (0); small [<25% of VI-8 length] (1); totally absent (2).
51. Shape of podomere VI-9: spinose (0); triangular, pentagonal or oval (1).
52. VI-9 margin: no ornament (0); serrated (1).
53. VI-9 position: centrally on podomere 8 (0); migrating towards posterior of podomere 8 (1).
54. VI-9 expanded: absent (0); present (1).
55. Podomere cuticular morphology: rounded (0); ridged (1).
56. Metastoma anterior: smooth or shallow notch (0); deeply notched (1).
57. Shape of posterior margin of metastoma: rounded (0); truncated/flattened (1); angular (2); notched (3).
58. Metastoma with posterior median cleft: absent (0); present (1).
59. Metastoma shape: broad (0); petaloid, markedly narrower in width (1).
60. First segment expressed dorsally: expressed (0); folded under carapace (1).
61. Microtergite: absent (0); present (1).
62. Genital operculum morphology: consisting of three visible segments (0); consisting of two visible segments (1); unfused (2).
63. Morphology of anterior opercular plate: fully expressed (0); lateral expression only (1); completely supressed (2).
64. Thickness of anterior opercular plate: fully expressed (0); narrow (1).
65. MOP and POP morphology: separate/with clear suture (0); without suture but with ornament differentiation (1); without suture and without ornament differentiation (2).

66. Unsegmented genital appendages: absent (0); present (1).

67. Type-A genital appendage spoon-shaped: absent (0); present (1).

68. Type-A genital appendage with median, distal indentation: absent (0); present (1).

69. Type-B genital appendage oval: absent (0); present (1).

70. Morphology of type A genital appendage furca: fused (0); unfused (1).

71. Spatulae on type A genital appendage: absent (0); present (1).

72. Morphology of spatulae: angular (0); rounded (1).

73. Moveable preabdominal spines: absent (0); present (1).

74. Postabdominal epimera: present (0); absent (1).

75. Preabdominal/postabdominal boundary: between 7th and 8th segments (0); between 6th and 7th segments (1); between 4th and 5th segments (2).

76. Epimera on segment 7: absent (0); present (1).

77. Number of segments in postabdomen: 3 (0); 5 or 6 (1); 9 (2).

78. Postabdomen: undifferentiated (0); narrowing from preabdomen (1).

79. Caudal postabdoment: absent (0); present (1).

80. Posterior margin of all opisthosomal tergites crenulate: absent (0); present (1).

81. Posterior margin of segments 7-9: smooth (0); dentate (1).

82. Posterior margin of segments 10-12: smooth (0); dentate (1).

83. Epimera on pretelson: absent (0); angular (1); rounded (2); quadrate (3).

84. Laterally expanded pretelson: absent (0); present (1).

85. Median carina on pretelson: absent (0); present (1).

86. Telson shape: straight (0); curved (1); laterally expanded (2).

87. Laterally expanded telson shape: rounded (0); triangular (1).

88. Telson base: flattened (0); bulbous expansion (1).

89. Telson bilobed: absent (0); present (1).

90. Median carina on telson: absent (0); low carina (1); vertical rudder (2).

91. Telson laterally ornamented with scales: absent (0); present (1).

92. Telson margin: smooth (0); serrated (1).

93. Opisthosoma lateral division: none (0); trilobed (1).

94. Primary opisthosomal ornamentation: scales (0); closely spaced pustules (1); coarse pustules (2).

95. Primary carapace ornamentation: scales (0); closely spaced pustules (1); coarse pustules (2).

96. Principal scale on carapace: absent (0); present (1).

97. Carapace ornament including elongate pustules that angle away from the lateral eyes and curve around the carapace margin: absent (0); present (1).

98. Row of node-like scales on dorsal opisthosomal segments: absent (0); present (1).

99. Ornamentation of angular scales across posterior of tergite segments: absent (0); present (1).

100. Longitudinal rows of angular scales on tergites: absent (0); present (1).

101. Ornament of chevron scales: absent (0); present (1).

102. Ornament of linguoid scales: absent (0); present (1).

103. Form of posterior margin of articulating facet on tergites: row of pustules (0); row of scales (1); groove (2).

104. Genital operculum striate ornament marked by highly sclerotised, broad lunate scales: ornament independent of sclerotised scales (0); ornament congruent with broad, sclerotised lunate scales (1).

Character matrix (main analysis)

(A = [0,1]; B = [1,2])

Weinbergina opitzi

00100 0-0-? 00310 00--0 11000 00000 010-0 00-00 000-- 00000 00000 ----0

022-0 ----- --000 00000 00000 0-000 00011 00000 0000

Chasmataspis laurencii

00000 0-101 01??? ????? ????? 0???0 ?00-0 00-00 000-- 000-- ----0 ????0

1???? ????? ??002 02110 00000 0-000 00122 00100 00??

Octoberaspis ushakovi

00003 0-000 00??? ????? ????? 000?1 0???? ???0? 002-- 00002 ----0 02000

12000 00010 0-002 02100 00100 0-000 00022 00000 00?0

Diploaspis casteri

00003 0-100 001?? ????? 00000 0???1 0???? ???00 002-- 00002 ----0 ????0

1200? ????? ??002 02100 00000 20000 01022 00100 00??

Loganamaraspis dunlopi

00003 0-?0? ??310 00--? ????? 0??00 000-? 0???? ????? ????? ????0 02000

12000 000?0 0-012 02100 00000 0-?00 0?0-- -0000 00??

Brachyopterus stubblefieldi

00018 0-001 01?0? ????0 00000 000?0 000-? 00-00 000-- 00000 00001 0???1

0???? 0???? ??0?0 01000 00000 0-000 000-- -0000 00??

Rhenopterus diensti

00017 0-001 01000 00--0 00000 00000 000-0 00-00 000-- 00000 00001 00001

00000 0??00 0-001 01110 00000 1-000 00000 00000 0000

Parastylonurus ornatus

00010 0-000 01000 00--0 11000 00000 200-0 00-00 000-- 00000 00000 11011

00000 00000 10000 01101 00100 0-001 00000 00000 00?0

Laurieipterus elegans

01018 0-000 0110? ????0 10000 00000 200-0 00-00 000-- 000?? ????0 1100?

0???? ????? ??0?? ????? ????? ????? ??000 00000 00?0

Kokomopterus longicaudatus

00015 0-001 01??? ????0 11000 10100 000-0 00-00 000-- 00000 00000 1100?

0???? ???0? ??010 01101 00000 0-000 00111 00000 01?0

Hardieopteurs macrophthalmus

00010 0-001 01000 00--0 ????? 10100 000-0 00-00 000-- 00000 00000 1100?

0???? ????? ??000 01101 00300 0-000 00111 00000 01?0

Drepanopterus pentlandicus

00010 10001 01000 00--0 1A001 10000 000-0 00-00 000-- 00000 00000 11101

00000 ?001? 10010 01100 00000 0-000 00011 00000 0000

Hibbertopterus scouleri

00010 11003 01000 00--0 2A001 10010 000-0 00-00 000-- 000?? ????0 1110?

0???? ???1? ??010 01001 00000 0-000 00000 00000 01?0

Megarachne servinei

00013 0-003 01??? ????? 2A001 1001? ?00-0 ????? ????? ????? ????0 ?????

0???? ????? ????? ????? ????? ????? ???00 00??? ????

Stoermeropterus conicus

00010 0-001 01110 00--0 00000 00000 01100 00-00 00100 00000 00001 10001

00010 00010 10100 01000 01B00 0-100 00011 00000 0000

Stoermeropterus latus

00010 0-001 01110 00--? ????? 0???0 0???0 00-00 00100 00000 00001 ????1

00010 000?? 11100 01000 01100 0-100 00000 00000 00?0

Stoermeropterus nodosus

00010 0-001 01??? ????? ????? 0???? ????? ????? ????? ????? ????? 10001

00010 000?0 11100 01000 0?200 0-100 00011 00100 00??

Vinetopterus struvei

01010 0-001 01310 00--0 00000 00000 01100 00-00 00100 00000 00001 00001

00010 0??1? ??000 01100 11000 0-?00 00011 00100 0000

Vinetopterus martini

01010 0-?01 0131? ????? 00000 00000 0???? 00-00 00100 00000 00001 ????1

0???? ????? ??000 01100 11000 0-?00 00011 00100 00??

Moselopterus ancylotelson

00010 0-001 01310 00--0 10000 00000 01100 00-00 00100 00000 00001 00001

00010 0001? 10010 01100 11000 1-000 01011 00100 0000

Moselopterus elongatus

00010 0-001 01310 00--0 10000 00000 01100 00-00 00100 00000 00001 00001

00010 ???1? ??010 01100 11000 1-000 01011 00?00 0000

Onychopterella augusti

00015 0-?01 01??? ????0 11000 0??01 01100 00-00 00101 00010 00000 ???0?

0???? ????? 0-000 01100 00000 0-100 00000 0?000 00??

Onychopterella kokomoensis

00015 0-101 01310 00--0 11000 00101 01??? 00-00 00101 00010 00000 00001

00010 000?1 0-000 01100 00200 0-100 00000 0?000 00?0

Dolichopterus macrocheirus

00012 0-012 01010 00--0 21000 00101 01110 11001 11101 20110 11010 11011

00110 000?0 10000 01100 00100 0-000 00000 00000 0000

Eurypterus remipes

00013 10101 01010 00--0 11000 01101 01120 01001 00111 10011 10000 00001

00110 00001 0-010 01100 00000 0-000 01000 10011 0010

Hughmilleria socialis

00017 0-122 11111 00--0 11000 00101 01120 01101 00111 00011 10100 0100?

012-2 00010 0-010 11100 00000 0-000 00000 00000 11?0

Tylopterella boylei

00015 0-101 01??? ????? ????? ????? ????? ????? ????? ????? ????? ?????

0???? ????? ??001 01100 00000 0-000 00000 00000 00??

Megalograptus ohioensis

01012 10104 01210 00--1 21110 01101 01120 01001 00111 00012 ----0 03001

012-1 00000 0-011 01100 00000 0-000 00100 00011 0010

Mixopterus kiaeri

00012 10104 01?10 00--1 21110 00101 01120 01111 00111 00011 10000 0000?

012-2 000?0 0-010 01110 00000 1-000 00100 00000 00?0

Strobilopterus laticeps

00011 0-011 01??? ????? ????? ????1 1???? 01101 00111 00-11 10000 1101?

?0110 000?0 10??? ????0 ????? ????? ????1 0???? ???1

Strobilopterus princetonii

00011 10013 01??0 00--0 10000 0??01 11120 01101 10111 20110 11000 1?01?

0???0 000?0 10000 11100 00000 ????? ??011 0?0?0 0001

Strobilopterus richardsoni

00011 0-013 0131? ????? ????? ????1 ????? ????? 10111 20011 10000 ?????

????? ????? ????? ????? ????? ????? ??011 010?? 00??

Strobilopterus proteus

00011 10013 0131? ????0 10000 00101 111?0 01101 10111 20110 11000 1001?

0???0 00010 10000 11100 00000 ????? ??011 01010 0001

Buffalopterus pustulosus

00011 0-011 0131? ????? ????? ????1 1???? ????? ????? ????? ????? ????1

00110 000?? 0-000 01100 00100 20000 01011 01010 0000

Erieopterus microphthalmus

00014 11001 01310 00--0 10000 01101 01120 01001 00111 00011 00000 01001

00110 000?1 0-010 01100 00100 1-000 00000 00000 00?0

Paraeurypterus anatoliensis

00012 10011 01?1? ????? 11000 0???1 0???? 010?? ????? ????? ????0 ????1

0???? ????? ??0?0 0???0 ????? ????? ??001 00010 001?

Pentlandopterus minor

00012 10011 01??? ????? ????? ????1 0???? 010?? ????? ????? ????? ?????

0???? ????? ??010 01100 00000 0-000 00011 00000 000?

Dolichopterus jewetti

00012 0-012 0???0 00--0 21000 00101 01110 11001 11101 20110 11010 11001

00110 000?0 10000 01100 00100 0-000 00001 00?00 0000

Ruedemannipterus stylonuroides

10016 0-012 01??? ????? ????? ????1 0???? 11001 ?1101 ?0110 10110 ?????

0???? ????? ??0?? ????? ????? ????? ??011 00000 00??

Clarkeipterus testudineus

10002 0-012 01??? ????? ????? ????1 0???? 11001 ?1101 ?0?10 10010 ?????

????? ????? ????? ????? ????? ????? ????1 00?00 ????

Clarkeipterus otisius

10002 0-012 01??? ????? ????? ????? ????? ????? ????? ????? ????? ?????

????? ????? ????? ????? ????? ????? ????1 00??? ????

Erieopterus eriensis

00011 11001 0131? ????0 10000 0??01 01120 01001 00111 00011 00000 ????1

00110 ????? ??010 01100 00??? 0-000 00000 00000 00??

Eurypterus henkeni

00013 10101 0101? ????? 11000 0??01 01120 01001 00111 00011 10000 0000?

0???? ????? 0-010 01100 00100 0-000 01000 10011 0010

Eurypterus tetragonophthalmus

00013 10101 01010 00--0 11000 01101 01120 01001 00111 10011 10000 00001

00110 00001 0-010 01100 00200 0-000 01000 10011 0010

Eurypterus leopoldi

00013 10101 01??? ????? ????? ????1 ????? ????? ?0111 10011 10000 1000?

????? ????? ???0? ???00 00200 0-000 01?00 10011 00??

Eurypterus pittsfordensis

00013 10101 01010 00--0 11000 01101 01120 01001 00111 10011 10000 1000?

0???? ????? ??000 01100 00200 0-000 01000 10011 001?

Eurypterus henningsmoeni

00013 10101 0101? ????0 ????? ?1101 01120 01001 00111 10011 10000 0000?

0???? ????? 0-010 01100 00200 0-000 01000 10011 001?

Orcanopterus manitoulinensis

10017 0-102 01??0 00--0 21000 001?1 0???? 0??0? 00111 00010 10010 1100?

012-1 0??0? ??010 11100 00000 0-000 00000 00000 10?0

Pterygotus anglicus

00113 0-122 11111 12000 3---- 00101 01121 01101 20111 10011 10100 0000?

012-2 11000 0-000 01100 00011 2000? 11000 00000 1110

Adelophthalmus sievertsi

00017 0-101 01110 00--0 3---- 00101 01120 01101 00111 11011 10100 0000?

012-2 00000 10010 01100 00000 0-000 00000 00000 1120

Eurypterus dekayi

00013 10101 01010 00--0 11000 01101 01120 01001 00111 00011 10000 0000?

00110 000?1 0-010 01100 00200 0-000 00000 00010 0010

Carcinosoma newlini

00019 0-102 01?10 00--1 21110 00101 01120 01111 00111 10011 11010 0000?

012-2 000?0 0-010 01110 00000 0-000 00000 00000 00?0

Slimonia acuminata

00010 0-122 11??1 00--0 01000 00101 01120 01101 00111 00011 10100 1001?

012-2 00000 0-010 01100 00000 20000 11000 00000 11?0

Acutiramus bohemicus

??1?? ????? ????1 1221? 3---- 0??01 01121 01101 ????? ????? ????0 1????

????? 110?? ????? ????? ???11 20001 ?1?0? ????? 11??

Acutiramus macrophthalmus

00115 0-122 11111 12210 3---- 00001 01121 01101 20111 10011 10100 1100?

012-2 1110? 0-000 01100 00011 20001 11000 00000 1110

Erettopterus bilobus

00112 0-122 11111 11000 3---- 0??01 01120 01101 20111 10011 10100 1000?

012-2 1101? 0-000 01100 00011 20012 11000 00000 1110

Erettopterus osiliensis

00112 0-122 11??1 1200? 3---- 0??01 01120 0??01 20111 10011 10100 1000?

012-2 1111? 0-000 01100 00011 20012 11000 00000 11?0

Erettopterus serricaudatus

????? ????? ????1 1100? ????? ????? ????? ????? ????? ????? ????? 1000?

????? 100?? ????? ????? ???1? 20012 11?0? ????? 11??

Erettopterus waylandsmithi

00112 0-122 11??1 1200? ????? ????? ????? ????? ????? ????? ????? ?????

????? ????? ????? ????? ????? 20?1? ???00 00??? 11??

Jaekelopterus rhenaniae

00113 0-122 11??1 1210? 3---- 00001 01121 ????? ????? ????? ????0 1100?

012-2 11100 0-000 01100 00011 21002 10000 00000 1110

Jaekelopterus howelli

????? ????? ????1 1210? ????? ???01 ?1121 ????? ????? 10011 10100 1100?

?12-2 11000 0-??? ???00 ?0011 21002 11?0? ????? 1110

Ciurcopterus ventricosus

00104 0-122 11??? ????0 01000 00101 01??? 01101 00111 ????? ????0 ?????

012-2 100?0 0-000 01100 00010 20000 10000 00000 11?0

Nanahughmilleria norvegica

00?17 0-101 01110 ????0 11000 00101 01120 01101 00111 11011 10100 1000?

012-2 ????0 10000 11100 000?? 0?0?? ?0000 00000 1110

Character matrix addition (juvenile instars)

Strobilopterus proteus α

00001 0-011 0131? ????0 10000 0010? 011?0 0110? ????? ????? ????0 1001? 0???0 000?0 10000 11100 00000 ????? ??011 00000 000?

Strobilopterus proteus β

00011 10013 01??? ????0 10000 0??01 011?? 01101 ????? ????? ????0 ????? 0???? ????? ??000 11100 00000 ????? ??011 00000 000?

Strobilopterus princetonii γ

00011 10013 01??? ????0 10000 0???1 1???? ???01 10111 10011 10000 ????? 0???? ????? ??000 11100 00000 ????? ??011 0?0?0 000?

Appendix 4

The systematics and phylogeny of aulacopleuroid trilobites

(Arthropoda: Trilobita: Proetida)

Comprising the morphological character list and character matrix used in the phylogenetic analysis

Character list

1. Eye ridges: *angled anteriorly [>110°] (0); equal to eye [90–110°] (1); absent (–).*
2. Carapace heavily vaulted, with height gained largely from the free cheeks: *absent, height largely gained from fixed cheeks and glabella (0); present (1).*
3. Carapace shape: *wider than long [≤0.55] (0); equilateral [>0.55] (1).*
4. Carapace with broad surface of free cheek: *absent (0); present (1).*
5. Reduction of lateral eyes: *eyes fully expressed (0); eyes absent (1).*
6. Eye angle: *diverging posteriorly (0); equilateral (1); diverging anteriorly (2).*
7. Free thoracic tergite count: *14–15 (0); 18+ (1); 16 (2); 13 (3); 11–12 (4); 9 (5); 6 (6); 7 (7); 8 (8); 10 (9).*
8. Thoracic tergites postlaterally expanded at fulcrum, forming distal 'oar' shape that increases overlap of succeeding tergite: *absent (0); present (1).*
9. Facial sutures fused: *sutures present, functional (0); sutures absent, headshield fused (1).*
10. Posterior suture position: *avoids outer margin (0); cuts through outer margin (1); skirts margin (2); no suture (–).*
11. Suture angle from lateral eye: *30–45° (0); ≥60° (1); ≤0° (2); 10–20° (3); no suture associated with eye (–).*
12. Angle of sutures as they cross the anterior margin: *parallel (0); converging (1); diverging (2); does not cross anterior margin (–).*
13. Position of converging sutures: *overturned onto margin (0); dorsally on carapace (1).*
14. Lateral eye size (as percentage of carapace): *30%+ (0); 20%–29% (1); <15% (2).*

15. Eye shape: *visual surface with bulbous or crescentic outline (0); visual surface scimitar-shaped (1).*
16. Eye globular, with visual surface bulging out beyond palpebral lobe: *absent (0); present (1)*.
17. Eyes sit atop free cheek: *absent [eye visual surface set into free cheek] (0); present, globular [visual surface sits atop free cheek and projects above it with roughly spherical outline] (1); present, turreted [visual surface sits atop free cheek and projects above it with angular outline and flat dorsal surface] (2).*
18. Eye position: *posterior of carapace [0–45%] (0); midline or anterior [48%+] (1); eye encompasses entire carapace length (2).*
19. Lateral eye kidney-shaped, palpebral lobe recessed: *absent, palpebral lobe partially overlaps eye (0); present (1)*.
20. Visual surface dorsally expanded, palpebral lobe curves upwards behind eye to accommodate: *absent (0); present (1)*.
21. Position of palpebral lobe: *main body distant from axial furrow (0); main body abuts axial furrow (1).*
22. Size of palpebral lobe: *equal to or larger than visual surface (0); smaller than visual surface (1).*
23. Large dorsal spine on palpebral lobe: *absent (0); present (1)*.
24. Large ancillary pustule positioned centrally at lateral eye interior: *absent (0); present (1)*.
25. Eye ridges expressed dorsally on exoskeleton: *present (0); absent (1); inapplicable, eyes abut glabella (–).*

26. Pair of preglabella spines: *absent (0); present (1).*

27. Glabella extent: *carapace anterior [>75%] (0); carapace midline or posterior [≤75%] (1).*

28. Effacement of S3: *S3 deeply incised (0); S3 effaced (1).*

29. Effacement of S2: *S2 deeply incised (0); S2 effaced (1).*

30. Positioning of S2 & S3: *well spaced (0); S3 & S2 close together, L3 expanded (1); S3 or S2 effaced (–).*

31. Length of S3/S2: *~50% of glabella width (0); short, ~25% of glabella width (1); S3 an S2 effaced (–).*

32. Relationship of L1 to glabella: *part of glabella [not separated by S1] (0); detached from glabella [S1 extends to occipital ring, separating L1 from glabella] (1); fully merged with glabella [S1 shallow or effaced] (2).*

33. Size of L1: *>25% of glabella (0); reduced, <25% of glabella (1).*

34. Enlarged L1 when L1 is at least 25% of glabella: *absent, ~25% (0); presents, >40% (1).*

35. Anterior narrowing of glabella: *width at anterior <75% width at base (0); width at anterior >75% width at base (1).*

36. Form of broad glabella anterior: *<100% width of base (0); 100% width of base (1); >100% width of base (2); anterior width <75% that of base (–).*

37. Glabella with sudden constriction about 1/3 from anterior: *glabella margins continuous (0); glabella margins with sudden constriction (1).*

38. Glabella with median node at its anterior: *absent (0); present (1).*

39. Carapace anterior to glabella with median depression: *absent (0); present (1).*

40. Glabella separate from occipital ring by deep trough: *absent (0); present (1)*.

41. L1 teardrop-shaped: *absent (0); present (1)*.

42. L1 separated from glabella by broad, trough-like S1: *absent (0); present (1)*.

43. Glabella anterior lobe diamond-shaped: *absent (0); present (1).*

44. L1 with prominent tubercle pair: *absent (0); present (1)*.

45. Enlarged thoracic spine on sixth tergite: *absent (0); present (1).*

46. Spine on 4th tergite: *absent (0); present (1)*.

47. Axial structure on occipital ring: *absent (0); present (1).*

48. Form of occipital axial structure: *raised node (0); enlarged spine (1); absent (–).*

49. Ancillary axial structures: *absent (0); paired ancillary nodes (1); no primary axial structure (–).*

50. Hypostome with unsclerotised anterior portion: *absent (0); present (1).*

51. Hypostome with paired posterior projections: *absent (0); present, short spinous projections (1); present, enlarged projections resulting in 'forked' morphology (2).*

52. Postlateral corners of carapace expanded into short lappets: *absent (0); present (1)*.

53. Position of genal spine divergence from carapace: *lateral, anterior to carapace posterior margin (0); posterolateral margin, posterior margin of carapace curves down into genal spine (1).*

54. Genal spines purely vestigial: *fully expressed (0); vestigial (1).*

55. Genal spine curvature: *strong curvature (0); slight curvature (1).*

56. Genal spine angle of divergence: *high [≥30%] (0); moderate [11%–29%] (1); reduced [≤10%] (2).*
57. Length of genal spines: *>100% carapace length (0); 35–100% carapace length (1); ≤30% carapace length (2).*
58. Genal spines bow outwards, away from thorax: *absent (0); present (1).*
59. Anterior carapace margin forms angular projection: *absent, carapace margin rounded (0); present (1).*
60. Ancillary row of ventral spines projecting laterally from marginal rim: *absent (0); present (1).*
61. Carapace marginal rim morphology: *smooth (0); produced into laterally oriented spines (1)*.
62. Carapace rim with dorsally projecting row of spines: *absent (0); present (1).*
63. Size of lateral marginal rim spines: *short, approximately same length as rim (0); longer than rim width (1); no spines (–).*
64. Lateral margin produced into broad, flattened 'shelf': *absent (0); present (1)*.
65. Pustular ornamentation present on rim: *absent (0); present (1)*.
66. Shelf ornamentation interrupted by effaced region at shelf commencement: *absent (0); present (1)*.
67. Number of outer rows of pustules in shelf ornamentation: *single row (0); multiple rows (1)*.
68. Ornamentation of pustules on rim oriented so as to appear to be radiating out from carapace: *absent (0); present (1); no ornamentation (–).*

69. Ornamentation of free cheek (region outside of lateral eyes but before lateral margin): *granules (0); pustules (1).*

70. Ornamentation of fixed cheek (region between lateral eyes and glabella): *granules (0); pustules (1).*

71. Ornamentation of glabella anterior (region anterior of S1): *granules (0); pustules (1); effaced (2).*

72. Density of anterior glabella pustules: *sparse (0); dense (1); pustules not present on glabella (–).*

73. Size of anterior glabella pustules: *small, pustular (0); large, tubercular (1); pustules not present on glabella (–).*

74. Ornamentation of glabella posterior (region posterior of S1): *granules (0); pustules (1); effaced (2)*.

75. Density of posterior glabella pustules: *sparse (0); dense (1); pustules not present on glabella (–).*

76. Size of posterior glabella pustules: *small, pustular (0); large, tubercular (1); pustules not present on glabella (–).*

77. Pustular ornamentation subdued: *absent, pustules fully expressed (0); present, pustules short and diffuse (1).*

78. Concentration of pustules between palpebral lobe and glabella: *absent (0); present (1)*.

79. Pustules around lateral eye dense and enlarged: *absent (0); present (1)*.

80. Extension of carapace ornamentation onto genal spines: *absent (0); present (1)*.

81. Extent of carapace ornamentation on genal spines: *entire length of genal spine (0); proximal regions only (1); no carapace ornamentation on genal spines (–).*
82. Breadth of shoulders: *short, not extending beyond maximum width of hypostome body (0); broad, extending beyond maximum width of hypostome body (1).*
83. Form of division of median body: *division formed by lateral grooves that do not meet medially (0); division formed by deep groove that entirely transverses median body (1); posterior median body entirely separated from anterior median body (2); median body undivided (–).*
84. Extent of hypostome doublure/rim: *present along entire lateral and posterior margins (0); present at posterior margin only (1).*
85. Form of hypostome posterior angles: *rounded, so hypostome appears lobate (0); angular, so hypostome appears quadrate/shield-shaped (1).*
86. Pygidium with tergopleural epimera besides macropleural spines: *absent (0); present (1).*
87. Number of axial rings in pygidium: *4/5 (0); 3 (1); 2 (2); 7/8 (3); 22 (4); 14 (5); 9 (6); 10-12 (7).*
88. Size of pygidium in relation to cephalon (quantified via comparison of boxed area plots): *micropygous [pygidium occupies <25% area of cephalon] (0); isopygous [pygidium occupies 25–110% area of cephalon] (1); macropygous [>150% area of cephalon] (2).*
89. Degree of micropygosity: *extreme micropygosity [0–5%] (0); micropygous [10–25%] (1); pygidium isopygous or macropygous (–).*

90. Degree of isopygosity: *extreme subisopygosity [25–35%] (0); subisopygous [35–90%] (1); isopygous [90–105%] (2); pygidium micropygous or macropygous (–).*

91. Pygidial marginal rim overturned onto inflated pygidial lateral margin: *absent (0); present (1); no marginal rim (–).*

92. Dense, unordered ornamentation of scales/pustules: *absent (0); present (1).*

93. Row of four tubercles on each axial ring: *absent (0); present (1).*

94. Ancillary tubercles on pygidial axial ring: *present (0); absent (1); no tubercle row (–).*

95. Row of tubercles on lateral ribs of tergopleurae: *absent (0); present (1).*

96. Thin, lateral spines projecting from tergopleura: *absent (0); present (1).*

97. Form of epimera on anterior tergites (1–6): *acute, spinous (0); blunt, curved (1).*

98. Form of epimera on posterior tergites (7–n): *acute, spinous (0); blunt, curved (1); blunt, quadrate or lobate (2).*

99. Reduction of epimera on first trunk tergite: *partially reduced, epimeral termination straight, spine small (0); undifferentiated (1).*

100. Commencement of narrowing of axial rings: *4th axial ring (0); 3rd axial ring (1); terminal pre-pygidial axial ring (2); expanding until mid-ring before narrowing commences, pre-pygidial axial ring same width as first post-cephalic axial ring (3).*

101. Percentage of tergite width occupied by axial region: *36–45% (0); 30–35% (1); 20–25% (2); >45% (3).*

102. Axis with central node on each segment: *present (0); absent (1).*

103. Tubercular swellings in pleural field alongside axis: *absent (0); present (1)*.

104. Row of tubercles across the posterior margin of each tergite: *absent (0); present (1)*.

105. Tergites showing marked deflection at fulcrum: *absent (0); present (1)*.

106. Prominent row of tubercles present solely on segment axis: *absent (0); present (1)*.

107. Form of pygidial epimera: *broad, extended tergopleura (0); narrow, needlelike (1)*.

108. Inflated node positioned centrally on pygidial axial rings: *absent (0); present (1)*.

109. Occurrence of central node on pygidial axial rings: *every ring (0); alternating rings (1); nodes absent (–)*.

110. Central node on pygidial rings produced into short, posteriorly-inflected conical spine: *absent (0); present (1)*.

111. Length of pygidial epimera: *short (0); long (1); no epimera (–)*.

112. Pygidial epimera broad and blunt, lobe-like: *absent (0); present (1); no epimera (–)*.

113. Pygidial macropleural spines: *absent (0); present (1)*.

114. Paired tubercles running down axis of pygidium: *absent (0); present (1)*.

115. Pygidium with pleurae deflecting posteriorly almost at right angles at fulcrum: *absent (0); present (1)*.

116. Pygidium with paired terminal spines: *absent (0); present (1)*.

117. Pygidium terminating in medial lobe: *absent (0); present (1)*.

118. Axial region of pygidium posteriorly truncated: *absent (0); present (1)*.

119. Fixed cheeks of cephalon pitted: *absent (0); present (1).*

120. Free cheeks of cephalon pitted: *absent (0); present (1).*

121. Pustules enlarged, warty: *absent (0); present (1); no pustules (–).*

122. Anterior carapace pustules oriented as to appear radiating out from glabella: *absent, orientation random (0); present (1); no pustules on fixed or free cheek (–).*

123. Intermediate shelf between glabella and rim: *absent (0); present (1).*

124. Tubercles bordering the lateral eye anteriorly and posteriorly enlarged: *absent (0); present (1)*.

125. Line of three enlarged tubercles position centrally on glabella: *absent (0); present (1)*.

126. Early protaspids with paired posterior spines: *absent (0); present (1).*

127. Protaspids with posterior medial indentation: *absent (0); present (1).*

128. Protaspid eye ridges: *fully expressed (0); suppressed (1).*

129. Late protaspid stages with tubercular swelling on occipital ring: *absent (0); present (1)*.

130. Protaspids with ancillary posterior spines: *absent (0); present (1).*

131. Meraspid stages with a row of tubercles on fixed cheek either side of glabella: *absent (0); present (1).*

132. Meraspid stages with three pairs of tubercles on glabella: *absent (0); present (1).*

133. Spacing of three glabellar tubercle pairs: *equilateral (0); anterior two pairs compressed together (1); no tubercles present (–)*.

134. Meraspid stages with row of short spines at pygidium fulcrum: *absent (0); present (1)*.

135. Number of tubercles on fixed cheek row: *3 (0); 2 (1).*

136. Tubercle on eye ridge in meraspid: *absent (0); present (1)*.

Character matrix

Hintzecurus paragenalatus

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Aulacopleura wulongensis

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Cyphaspis dabrowni

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Maurotarion struszi

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Brachymetopus germanicus

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Rorringtonia kennedyi

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Gerastos tuberculatus

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Scharyia micropyga

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Maurotarion periergum

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Aulacopleura konincki

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Aulacopleura longecornuta

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Aulacopleura bohemica

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Aulacopleura pogsoni

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Aulacopleura reedi

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Aulacopleuroides mirus

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Chamaeleoaspis chamaeleo

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Chamaeleoaspis lkomalii

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Coignops ymir

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Cyphaspides holinensis

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Cyphaspides comatus

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Cyphaspides deani

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Cyphaspis ceratophthalmus

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Cyphaspis barrandei

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Cyphaspis lowei

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Cyphaspis ranuncula

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Cyphaspis barbarossa

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Cyphaspis hoepfneri

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Cyphaspis eberhardiei

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Cyphaspis ellipsocephala

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Cyphaspis gruanum

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Beggaspis tenue

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Beggaspis elongatum

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Beggaspis spinicaudatum

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Dixiphopyge armata

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Harpidella greggi

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Harpidella tikkaneni

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Harpidella megalops

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Harpidella kurrii

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Harpidella spinafrons

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Harpidella triloba

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Malimanaspis sarudianskii

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Malimanaspis packardi

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Malimanaspis angustilimbata

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Maurotarion maura

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Maurotarion thomasi

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Maurotarion megacephalum

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Maurotarion messieri

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Namuropyge demaneti

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Namuropyge acanthina

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Namuropyge muelleri

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Namuropyge defensabilis

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Otarion diffractum

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Otarion beukeboomi

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Otarion brauni

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Otarion convexa

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Otarion stigmatophthalmus

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Otarion davidsoni

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Otarionides franconicus

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Pseudotrinodus aenigma

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Songkania smithi

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Songkania socialis

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Strasburgaspis cona

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Strasburgaspis kielanae

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Acutimetopus kansanensis

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Acutimetopus moelleri

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Acutimetopus weberi

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Tilsleyia glaphyra

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Asiagena karaespensis

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Australosutura gardneri

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Australosutura gemmaea

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Australosutura elegans

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Brachymetopella aikiyoshiensis

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Brachymetopella nakoinsri

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Brachymetopella strzeleckii

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Brachymetopus maccoyi

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Brachymetopus woodwardii

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Brachymetopus drevermanii

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Brachymetopus edwardsi

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Brachymetopus parvus

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Brachymetopus senckenbergianus

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Brachymetopus nandanensis

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Brachymetopus longinquus

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Brachymetopus arcticus

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Spinimetopus coignuides

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Cheiropyge himalayensis

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Cheiropyge koizumii

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Conimetopus ouralicus

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Conimetopus ornatus

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Cordania cyclurus

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Cordania falcata

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Hahnus maximowae

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Loeipyge spinifer ?

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Loeipyge differens

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Mystrocephala pulchra

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Mystrocephala stummi

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Mystrocephala varicella

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Proetides insignis

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Proetides colemani

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Radnoria syrphetodes

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Radnoria bretti

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Radnoria triquetra

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Radnoria carlsi

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Spinimetopus subtilis

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Irania jayae

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Appendix 5

Clade history, species ecology and external causal factors influence arthropod survival and recovery during Paleozoic mass extinctions

Comprising the morphological character lists and character matrices used in the phylogenetic analyses of Stylonurina and Eurypterina

Stylonurina character list

1. Antero median carapace protrusion: absent (0); present (1).
2. Carapace anterior: rounded (0); angular (1).
3. Denticulate anterior margin of carapace: absent (0); present (1).
4. Carapace marginal rim broad: absent (0); present (1).
5. Carapace marginal rim with striate ornament: absent (0); present (1).
6. Row of pustules along inside of marginal rim: absent (0); present (1).
7. Lateral carapace margin: continuous (0); stepped (1).
8. Deep carapace with pleural margins curving ventrally: absent (0); present (1).
9. Lateral regions of posterior carapace margins overlapping first opisthosomal tergite: absent (0); present (1).
10. Morphology of genal carapace regions overlapping first opisthosomal tergite: small (0); drawn out into posterolateral lobes (1).
11. Carapace position of greatest width: posterior third (0); median third (1).
12. Prosoma quadrate: absent (0); present (1).
13. Carapace vaulted: absent (0); present (1).
14. Median ridge between lateral eyes: absent (0); present (1).
15. Carapace ornament of large lunate scales surrounding and pointing away from the central area and eyes: absent (0); present (1).
16. Circular plateau ornamentation anterior to median ridge: absent (0); present (1).
17. Position of median eyes on carapace: median third (0); anterior third (1).
18. Ocellar area: absent (0); present (1).

19. Ocellar area with cardioid shape (ocelli accommodated in paired anterior lobes): absent (0); present (1); no ocellar area (–).
20. Lateral eye shape: crescentic (0); expanded (1).
21. Palpebral lobe: absent (0); circular (1); reniform (2).
22. Lateral eyes converging and placed anteriorly on carapace: absent (0); present (1).
23. Annular cuticular thickening surrounding lateral eyes: absent (0); present (1).
24. Shape of annular cuticular thickening: oval (0); circular (1).
25. Orbital ridges: absent (0); present (1).
26. Median ridge reduced: absent (0); present (1).
27. Transverse suture on ventral plates: absent (0); present (1).
28. Transverse suture curving back at midline: absent (0); present (1).
29. Groove running across doublure: absent (0); present (1).
30. Suture on ventral plates: epistoma absent (0); epistoma present (1).
31. Rostral field: absent (0); present (1).
32. Ventral plates widen anteriorly: absent (0); present (1).
33. Appendage III: spiniferous with paired spines (0); spiniferous with single spines (1).
34. Pairs of spines per podomere on prosomal appendage III: one pair (0); two or more pairs (1).
35. Prosomal appendage IV: spiniferous (0); non spiniferous (1).
36. Pairs of spines per podomere on prosomal appendage IV: one pair (0); two or more pairs (1).
37. Spines on prosomal appendage IV: moveable spines (0); both moveable and fixed spines (1); fixed spines (2).

38. Blade like structures on podomeres of anterior appendages: absent (0); present (1).

39. Blades enlarged and longer than podomere length: absent (0); present (1).

40. Rachis: absent (0); present (1).

41. Coxal laden: absent (0); present (1).

42. Prosomal appendage V: spiniferous (0); non spiniferous (1).

43. Spines on prosomal appendage V reduced: absent (0); present (1).

44. Prosomal appendage VI: walking leg (0); swimming leg (1).

45. Appendage VI reaching to pretelson: absent (0); present (1).

46. Shape of proximal podomere of appendage VI narrow: L/W ≤ 2.0 (0); expanded L/W > 2.0 (1).

47. Podomere VI-5: half the width of VI-4 (0); equal width of VI-4 (1).

48. Distal podomere margin of VI-6 modified: absent (0); present (1).

49. Ear on coxa VI: absent (0); present (1).

50. Appendage VI showing lateral serrations: absent (0); present (1).

51. Podomere 7a on sixth prosomal appendage: absent (0); present (1).

52. Width of VI-7a: narrow [less than 50% of width of VI-7] (0); wide [more

1. than 50%] (1).

53. Shape of VI-7a: oval (0); triangular (1).

54. Longitudinal grooves on podomeres: absent (0); present (1).

55. Podomeres ridged: absent (0); present (1).

56. Podomeres thicken distally: absent (0); present (1).

57. Podomere distal margins crenulate: absent (0); present (1).

58. Cleft metastoma: absent (0); present (1).

59. Anterior margin of metastoma: notch absent (0); notch present (1).
60. Posterior margin of metastoma: rounded (0); flattened or recurved (1).
61. Metasoma: bulky (0); gracile (1).
62. Paired tubercles on opisthosomal tergites 2-5: absent (0); present (1).
63. Pustular ornamentation: absent (0); present (1).
64. Pustules enlarged, resulting in warty appearance to cuticle: absent (0); present (1); no pustules (–).
65. Cuticular ornamentation forms reticulate surface patterns: absent (0); present (1).
66. Acicular scales on opisthosoma: absent (0); present (1).
67. Row of large tongue-shaped scales on posterior margin of opisthosomal segments: absent (0); present (1).
68. Opisthosoma narrower than carapace: absent (0); present (1).
69. Marginal rim on opisthosoma: absent (0); present (1).
70. First tergite with narrow posterior margin: absent (0); present (1).
71. Positive opisthosomal differentiation of third order first segment: absent (0);
    2. present (1).
72. Positive opisthosomal differentiation of third order second segment: absent (0); present (1).
73. Second tergite developed into round macrotergite: absent (0); present (1).
74. Preabdominal epimera: absent (0); present (1).
75. Caudal postabdomen: absent (0); present (1).
76. Lateral pleurae: absent (0); present (1).
77. Pretelson elongated: absent (0); present (1).

78. Pretelson postlaterally expanded: absent (0); present (1).

79. Dorsal pretelson lobes: absent (0); present (1).

80. Telson elongate: absent (0); present (1).

81. Dorsal median keel on telson: absent (0); present (1).

82. Paired broad rounded ventral keels on telson: absent (0); present (1).

83. Telson lateral margins and media keel ornamented with rhomboid scales: absent (0); present (1).

84. Telson serrated: absent (0); present (1).

Stylonurina character matrix

Weinbergina opitzi

0 0 0 0 0 0 0 1 0 – 0 0 0 0 0 0 0 0 – 0 0 0 0 – 0 0 0 0 0 0 – 0 0 0 0 0 0 0 – 0 0 0 0 0 0 1 1 0

0 0 0 – – 0 0 0 0 – – – 0 0 0 – 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0

Alkenopterus brevitelson

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0 1 0 1 0 0 0 0 ? ? ? 1 0 0 – 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0

Brachyopterella pentagonalis

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0 0 0 – – 0 1 0 0 ? ? ? 1 ? 0 – 0 0 ? 0 0 0 ? ? ? 0 ? ? ? ? ? ? ? 0 ? 0 0

Brachyopterella ritchiei

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0 0 – – 0 1 0 0 ? ? ? 1 0 0 – 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0

Brachyopterus stubblefieldi

0 0 0 0 0 0 0 0 0 – 1 0 0 0 0 0 ? 1 0 0 0 0 0 – 0 0 ? ? ? ? ? ? 1 – 0 0 0 0 – 0 ? 1 – 0 0 ? 0 0 ?

0 0 – – 0 0 0 0 0 ? 0 0 0 0 – 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0

Ctenopterus cestrotus

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? 0 0 – – 0 0 0 0 ? ? ? 0 0 0 – 0 1 0 0 0 0 0 0 0 1 ? 0 ? ? ? 1 0 ? 0 0

Cyrtoctenus wittebergensis

1 0 0 0 0 0 0 1 1 1 0 0 0 0 0 0 0 0 – 0 1 0 1 1 1 0 ? ? ? ? ? ? ? ? 0 0 1 1 1 1 ? ? ? ? 0 0 1 ? 0

0 ? ? ? 1 0 1 1 ? ? ? 0 0 0 – 0 0 1 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 0 0

Cyrtoctenus dewalquei

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Drepanopterus abonensis

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0 0 0 – – 1 0 1 0 1 1 – 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0

Stoermeropterus conicus

0 0 0 0 0 0 0 0 0 – 0 0 0 0 0 0 ? 0 – 0 0 0 0 – 0 0 0 – 0 1 0 0 1 0 0 0 2 0 – 0 0 1 – 0 0 1 1 0

1 0 1 0 1 0 0 0 0 0 1 0 0 0 0 – 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0

Drepanopterus pentlandicus

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Hallipterus excelsior

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Hardieopterus macrophthalmus

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Hardieopterus megalops

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Hardieopterus myops

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Hardieopterus lanarkensis

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Hibbertopterus scouleri

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0 0 0 – – 0 0 1 0 1 1 – 0 0 0 – 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0

Kiaeropterus ruedemanni

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Kiaeropterus cyclophthalmus

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Stylonurella spinipes

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Tarsopterella scotica

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Vinetopterus struvei

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Woodwardopterus scabrosus

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Eurypterus remipes

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Hughmilleria socialis

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Onychopterella augusti

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Campylocephalus oculatus

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Campylocephalus permianus

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Eurypterina character list

1. Angular projection on the anterior of the carapace: absent (0); present (1).
2. Anterior projection morphology: rounded (0); quadrate (1). Acute (2).
3. Triangular 'doublure lock' anteriorly on carapace: absent (0); present (1).
4. Carapace anterior: rounded (0); angular (1).
5. Anterior indentation of carapace: absent (0); present, lateral extent independent of lateral eyes (1). Present, lateral extent defined by position of lateral eyes (2).
6. Anterior margin of carapace: unornamented (0); denticulate (1).
7. Carapace marginal rim: present (0); absent (1).
8. Morphology of marginal rim: marginal rim with constant equal width (0); marginal rim narrows evenly posteriorly (1); marginal rim only present anterior to eyes (2).
9. Carapace marginal rim broad: present (0); absent (1).
10. Lateral carapace margin: continuous (0); stepped (1); constrict to form 'waist' (2).
11. Carapace genal spines: present (0); absent (1).
12. Carapace shape: horseshoe or wide-horseshoe (0); semicircular (1); quadrate (2); trapezoidal (3); wide-rectangular (4); subquadrate (5); campanulate (6); parabolic (7); spatulate (8); triangular (9); long-rectangular (10).
13. Carapace flares posteriorly: absent (0); present (1).
14. Carapace genal facets: absent (0); present (1).
15. Angle of genal facets: low angle (0); high angle (1).

16. Genal regions produced into short spurs: absent (0); present (1).

17. Lateral eye shape: crescentic (0); expanded (1).

18. Size of palpebral lobe: small (0); large (1); absent (2).

19. Lateral eye position: centrilateral (0); centrimesial (1); antelateral (2); central (3); antemesial (4).

20. Position of lateral eyes in relation to carapace margin: intramarginal (0); semimarginal (1); marginal (2).

21. Lateral eye abuts carapace margin: absent (0); present (1).

22. Lateral eyes closer to margin than to ocelli: present (0); absent (1).

23. Lateral eye length: short (shorter than a quarter of the carapace length) (0); long (longer than a quarter of the carapace length) (1).

24. Annular cuticular thickening surrounding lateral eyes: absent (0); present (1).

25. Vaulted central portion of carapace: absent (0); present (1).

26. Vaulted central portion of carapace with angular margins, resulting in diamond shape: absent (0); present (1).

27. Lateral eyes associated with ophthalmic ridge: present (0); absent (1).

28. Position of median eyes on carapace: median third (0); anterior third (1).

29. Position of median eyes relative to lateral eyes: median eyes anterior or median to lateral eyes (0); median eyes posterior to lateral eyes (1).

30. Suture on ventral plates: *Eurypterus*-type (0); *Hughmilleria*- or *Hallipterus*-type (1); *Megalograptus*-type (2); *Erieopterus*-type (3).

31. Transverse suture on ventral plates: present (0); absent (1).

32. Ventral plates widen anteriorly: absent (0); present (1).

33. Chelicerae: small (0); able to extend beyond marginal rim (1).

34. Form of cheliceral peduncle: approximately equal in length to fixed ramus (0); longer than fixed ramus (1).

35. Denticles on chela: absent (0); present, small, undifferentiated (1); present, large, differentiated (2).

36. Largest denticle medially on fixed ramus: erect (0); inclined (1); acute (2).

37. Angular distal teeth on both rami: absent (0); present (1).

38. Paired distal teeth on free ramus: absent (0); present (1).

39. Short, raptorial claw on appendage II: absent (0); present (1).

40. Appendage II with clasping organ at base of appendage: absent (0); present (1).

41. Relative lengths of appendages II–V: increasing posteriorly (0); forward appendages enlarged (1).

42. Morphology of spines on prosomal appendage III: reduced [length < width of podomere] (0); regular [length ≈ width of podomere] (1); enlarged [length > width of podomere] (2); absent (3).

43. Morphology of spines on prosomal appendage IV: reduced [length < width of podomere] (0); regular [length ≈ width of podomere] (1); enlarged [length > width of podomere] (2); absent (3).

44. Mobility of spines on appendages II–IV: fixed (0); moveable (1).

45. Terminal spine pair enlarged in relation to previous spine pairs, terminating at a position equal to the terminal podomere: absent (0); present (1).

46. Penultimate podomere appendage III: spiniferous (0); non-spiniferous (1). Appendage non-spiniferous (-).

47. Relative podomere lengths of appendage III: 3 longer than 4 (0); 4 longer than 3 (1).

48. Longest podomere of appendage III: podomere other than 5 (0); podomere 5 (1).

49. Appendage III terminal segment: short, podomere (0); long, modified spine (1).

50. Number of paired spines on appendage III podomere 3: one pair (0); two or more pairs (1). No spines (-).

51. Pairs of spines per podomere on podomeres 4-6 of prosomal appendage III: one pair (0); two or more pairs (1). No spines (-).

52. Pairs of spines per podomere on podomeres 4-6 prosomal appendage IV: one pair (0); two or more pairs (1). No spines (-).

53. Orientation of spines on appendages II–IV: ventral (0); anterior (1). No spines (-).

54. Spines on appendages II–IV broad-based and robust but otherwise undifferentiated from standard *Hughmilleria*-type spines; absent (0); Present (1).

55. Spines on appendages II–IV thickened and highly sclerotised: absent (0); present (1). No spines (-).

56. Prosomal appendage spines showing longitudinal striations: absent (0); present (1). No spines (-).

57. Armature of anterior prosomal appendages flattened and laterally expanded into blades: absent (0); present (1).

58. Prosomal appendage podomeres thicken distally: absent (0); present (1).

59. Morphology of appendage V: podomeres undifferentriated and broad (0); podomeres tubular, lacking armature except for penultimate distal podomere (1).

60. Appendage V armature: non-spiniferous (0); spiniferous (1).

61. Isolated large spine on V–7: absent (0); present (1). No spines (-).

62. Penultimate podomere of appendages II–IV curved: absent (0); present (1).

63. Terminal spine on prosomal appendages: single (0); paired (1).

64. Coxal laden: absent (0); present (1).

65. Morphology of prosomal appendage VI: equal in width along length (0); distally expanded into swimming leg (1).

66. Type of paddle: distal paddle (0); proximal paddle (1).

67. First podomere of prosomal appendage VI that fully projects beyond carapace margin: Fourth podomere (0); Sixth podomere (1); Third podomere (2).

68. Shape of proximal podomere of appendage VI: narrow [L/W greater than or equal to 2.0] (0); expanded [L/W<2.0] (1).

69. Anterior margin of coxa VI: undifferentiated (0); expanded to form "'ear"' (1).

70. Shape of "'ear"' on coxa VI: triangular (0); rectangular (1); subquadrate/semicircular (2).

71. Anterior denticle of coxa VI large: absent (0); present (1).

72. Angle between VI–3 and VI–4: 180° (0); not 180° (1).

73. Length of podomeres VI–4 and VI–5: VI–5>VI–4 (0); VI–4≤VI–5 (1).

74. Length of podomeres VI–4 when VI–5 is not longer: >VI–3 and VI–5 (0); equal to VI–3 and VI–5 (1).

75. Podomere VI–5 bordering podomere VI–7: absent (0); present (1).

76. Distal podomere margin of VI–6 modified: absent (0); present (1).

77. VI–7 lateral margins: unornamented (0); enlarged serrations (1); small serrations (2).

78. Angular projection on the anterior of podomere VI-7: absent (0); present (1).

79. Podomere 7a on appendage VI: absent (0); present on posterior of appendage (1); present on anterior of appendage (2).

80. Width of posterior VI–7a: narrow [less than 50% width of VI–7] (0); wide [more than 50%] (1).

81. Shape of posterior VI,Äì7a: oval (0); triangular (1).

82. VI–8 lateral margins: unornamented (0); small serrations (1); enlarged serrations (2).

83. VI–8 anterior projection: absent (0); present (1).

84. Additional moveable lobe on VI–8: absent (0); present (1).

85. Morphology of VI–8/VI–9 joint: joint flush (0); VI–9 set into VI–8 (1).

86. Morphology of joint when VI–8 is set into VI–9: angular (0); round (1).

87. Length of VI–9 (as ratio of VI–8): large [>25% of VI–8 length] (0); small [<25% of VI–8 length] (1); totally absent (2).

88. Shape of podomere VI–9: spinose (0); triangular, pentagonal or oval (1).

89. VI,Äì9 margin: no ornament (0); serrated (1).

90. VI,Äì9 position: centrally on podomere 8 (0); migrating towards posterior of podomere 8 (1).

91. VI,Äì9 expanded: absent (0); present (1).

92. Podomere cuticular morphology: rounded (0); ridged (1).

93. Walking leg podomeres distally serrated: absent (0); present (1).

94. Metastoma anterior: smooth or shallow notch (0); deeply notched (1).

95. Shape of posterior margin of metastoma: rounded (0); truncated/flattened (1); angular (2); notched (3).

96. Metastoma with posterior median cleft: absent (0); present (1).

97. Metastoma shape: broad (0); petaloid, markedly narrower in width (1).

98. Metastoma widest point: mid or posterior (0); anterior (1).

99. Posterior cordate metastoma extension: absent (0); present (1).

100. First segment expressed dorsally: expressed (0); folded under carapace (1).

101. Microtergite: absent (0); present (1).

102. Laterally reduced anterior opisthosomal segment: absent (0); present (1).

103. Rounded postlateral angles anterior segment: absent (0); present (1).

104. Anterolateral expansion of second tergite: absent (0); present (1).

105. Genital operculum morphology: consisting of three visible segments (0); consisting of two visible segments (1); unfused (2).

106. Morphology of anterior opercular plate: fully expressed (0); lateral expression only (1); completely supressed (2).

107. Thickness of anterior opercular plate: fully expressed (0); narrow (1).

108. MOP and POP morphology: separate/with clear suture (0); without suture but with ornament differentiation (1); without suture and without ornament differentiation (2).

109. Unsegmented genital appendages: absent (0); present (1).

110. Type-A genital appendage spoon-shaped: absent (0); present (1).

111. Number of segments in type A zipfel: 3 (0); 2/1 (1).

112. Type-A genital appendage with median, distal indentation: absent (0); present (1).

113. Type-A genital appendage with complex, trifurcate termination: absent (0); present (1).

114. Type-A genital appendage with lateral flanges: absent (0); present (1).

115. Type-B genital appendage oval: absent (0); present (1).

116. Oval type-B genital appendage with recurved medial groove: absent (0); present (1).

117. Type-B genital appendage with spatulae: absent (0); present (1).

118. Morphology of type A genital appendage furca: fused (0); unfused (1).

119. Spatulae on type A genital appendage: absent (0); present (1).

120. Morphology of spatulae: angular (0); rounded (1).

121. Size of genital spatula: small (0); large (1).

122. Anteriorly inflecting sternites: absent (0); present (1).

123. Preabdomen expanded into 'disc': absent (0); present (1).

124. Opisthosoma lanceolate, with mesosoma not expanding beyond carapace width. Absent (0); present (1).

125. Moveable preabdominal spines: absent (0); present (1).

126. Preabdominal epimera: absent (0); present (1).

127. Morphology of preabdominal epimera: small (0); large (1).

128. Postabdominal epimera: present (0); absent (1).

129. Morphology of postabdominal epimera: small angular cuticular extensions (0); small rounded cuticular extensions (1); large epimera (2).

130. Preabdominal epimera with lateral striations: absent (0); present (1).

131. Preabdominal/postabdominal boundary: between 7th and 8th segments (0); between 6th and 7th segments (1); between 4th and 5th segments (2).

132. Degree of first order differentiation: reduced (0); prominent (1); abrupt (2).

133. Strong curvature of opisthosomal segment 7: absent (0); present (1).

134. Raised median triangle on segment 7: absent (0); present (1).

135. Epimera on segment 7: absent (0); present (1). Midsection second order differentiation.

136. Number of segments in postabdomen: 3 (0); 5 or 6 (1); 9 (2).

137. Postabdomen: undifferentiated (0); narrowing from preabdomen (1).

138. Caudal postabdoment: absent (0); present (1).

139. Caudal postabdomen overlapped by preabdomen: absent (0); present (1).

140. Posterior margin of all opisthosomal tergites crenulate: absent (0); present (1).

141. Posterior margin of segments 7–9: smooth (0); dentate (1).

142. Posterior margin of segments 10–12: smooth (0); dentate (1).

143. Epimera on pretelson: absent (0); angular (1); rounded (2); quadrate (3).

144. Marginal, median notch posteriorly on pretelson: absent (0); present (1).

145. Dorsal paired keels composed of scales on pretelson: absent (0); present (1).

146. Laterally expanded pretelson: absent (0); present (1).

147. Median carina on pretelson: absent (0); present (1).

148. Telson shape: straight (0); curved (1); laterally expanded (2).

149. Straight telson with proximal constriction resulting in clavate or xiphous morphology: absent (0); present (1).

150. Straight telson with rapid proximal narrowing and subsequent needle-like telson morphology: absent (0); present (1).

151. Laterally expanded telson shape: rounded (0); triangular (1).

152. Laterally expanded telson with elongate post-telson spine: absent (0); present (1).

153. Telson with ventral carina terminating proximally in broad plateau: absent (0); present (1).

154. Telson base: flattened (0); bulbous expansion (1).

155. Telson bilobed: absent (0); present (1).

156. Median carina on telson: absent (0); low carina (1); vertical rudder (2).

157. Telson laterally ornamented with scales: absent (0); present (1).

158. Telson margin: smooth (0); serrated (1).

159. Opisthosoma lateral division: none (0); trilobed (1).

160. Primary opisthosomal ornamentation: scales (0); closely spaced pustules (1); coarse pustules (2).

161. Primary carapace ornamentation: scales (0); closely spaced pustules (1); coarse pustules (2).

162. Principal scale on carapace: absent (0); present (1).

163. Carapace ornament including differentiated, directional scales: even, undirected ornamentation (0); carapace ornament including elongate pustules that angle away from the lateral eyes and curve around the carapace margin (1); carapace ornament of large lunate scales surrounding and pointing away from the central area and eyes (2).

164. Dorsal folds on carapace anterior: absent (0); present (1).

165. Dorsal carapace folds concentrated within region between lateral eyes: absent (0); present (1).

166. Row of node-like scales on dorsal opisthosomal segments: absent (0); present (1).

167. Ornamentation of angular scales across posterior of tergite segments: absent (0); present (1).

168. Longitudinal rows of angular scales on tergites: absent (0); present (1).

169. Ornament of chevron scales: absent (0); present (1).

170. Ornament of linguoid scales: absent (0); present (1).

171. Cuticular sculpture of transverse striae on anterior half of mesosomal segments: absent (0); present (1).

172. Ventral metasomal segments with mediolateral striations. Absent (0); present (1).

173. Paired tubercles on opisthosomal tergites 2-5: absent (0); present (1).

174. Isolated central node on each tergite: absent (0); Present (1).

175. Form of posterior margin of articulating facet on tergites: row of pustules (0); row of scales (1); groove (2).

176. Genital operculum striate ornament marked by highly sclerotised, broad lunate scales: ornament independent of sclerotised scales (0); ornament congruent with broad, sclerotised lunate scales (1).

Eurypterina character matrix

Weinbergina opitzi

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Chasmataspis laurencii

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Octoberaspis ushakovi

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Diploaspis casteri

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Loganamaraspis dunlopi

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Brachyopterus stubblefieldi

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Alkenopterus brevitelson

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Alkenopterus burglahrenisis

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Rhenopterus diensti

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Parastylonurus ornatus

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Laurieipterus elegans

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Kokomopterus longicaudatus

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Hardieopterus macrophthalmus

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Drepanopterus pentlandicus

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Hibbertopterus scouleri

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Megarachne servinei

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Stoermeropterus conicus

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Stoermeropterus latus

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Stoermeropterus nodosus

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Vinetopterus struvei

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Vinetopterus martini

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Moselopterus ancylotelson

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Onychopterella augusti

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Onychopterella kokomoensis

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Dolichopterus macrocheirus

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Eurypterus remipes

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Hughmilleria wangi

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Hughmilleria socialis

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Hughmilleria shawangunk

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Herefordopterus banksii

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Tylopterella boylei

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Echinognathus clevelandi

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Megalograptus ohioensis

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Lanarkopterus dolichoschelus

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Mixopterus kiaeri

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Mixopterus multispinosus

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Mixopterus simonsoni

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Strobilopterus laticeps

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Strobilopterus princetonii

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Strobilopterus proteus

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Buffalopterus pustulosus

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Strobilopterus richardsoni

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'Erieopterus' limuloides

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Erieopterus microphthalmus

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Paraeurypterus anatoliensis

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Pentlandopterus minor

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Dolichopterus jewetti

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Ruedemannipterus stylonuroides

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Clarkeipterus testudineus

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Clarkeipterus otisius

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Erieopterus eriensis

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Eurypterus henkeni

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Eurypterus tetragonophthalmus

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Eurypterus leopoldi

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Eurypterus pittsfordensis

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Eurypterus henningsmoeni

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Grossopterus overathi

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Waeringopterus apfeli

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Waeringopterus cumberlandicus

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Orcanopterus manitoulinensis

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Pterygotus anglicus

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Pterygotus monroensis

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Adelophthalmus sievertsi

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Adelophthalmus kamyshtensis

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Adelophthalmus luceroensis

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Adelophthalmus mazonensis

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Adelophthalmus moyseyi

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Adelophthalmus mansfieldi

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Adelophthalmus irinae

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Adelophthalmus imhofi

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Adelophthalmus wilsoni

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Adelophthalmus waterstoni

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Adelophthalmus approximatus

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Adelophthalmus granosus

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Adelophthalmus douvillei

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Adelophthalmus sellardsi

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Adelophthalmus dumonti

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Adelophthalmus zadrai

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Eurypterus dekayi

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Carcinosoma scotica

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Carcinosoma scorpioides

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Carcinosoma newlini

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Carcinosoma libertyi

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Carcinosoma spiniferum

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Rhinocarcinosoma vaningeni

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Rhinocarcinosoma dosonensis

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Rhinocarcinosoma cicerops

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Eusarcana acrocephala

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Eusarcana scorpionis

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Slimonia acuminata

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Salteropterus abbreviatus

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Acutiramus bohemicus

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Acutiramus macrophthalmus

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Acutiramus cummingsi

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Erettopterus bilobus

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Erettopterus osiliensis

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Erettopterus serricaudatus

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Erettopterus waylandsmithi

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Jaekelopterus rhenaniae

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Jaekelopterus howelli

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Ciurcopterus ventricosus

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Eysyslopterus patteni

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Parahughmilleria salteri

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Parahughmilleria bellistriata

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Parahughmilleria maria

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Parahughmilleria matarakensis

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Parahughmilleria hefteri

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Bassipterus virginicus

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Pittsfordipterus phelpsae

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Nanahughmilleria clarkei

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Nanahughmilleria pygmaea

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Nanahughmilleria norvegica

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0 0 0 0 0 0 – – 0 0 0 0 0 0 0 0 0 0 0 ? ? 0 0 0 1 1 1 0 0 0 1 0

Nanahughmilleria notosiberica

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Nanahughmilleria lanceolata

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