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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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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 reveal 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.: it 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.

KEY WORDS: *Campylocephalus*, Drepanopteridae, *Drepanopterus odontospathus*, heterochrony, Hibbertopteroidea, Mycteropoidea, peramorphosis, phylogeny, Stylonurina

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, making the Llandovery *D. pentlandicus* the earliest mycteropoid. 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 present author discovered over 30 well preserved specimens of *Drepanopterus pentlandicus*, much more than

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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 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. *Onychopterella* (?) *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 with *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, the whereabouts of this specimen is unknown 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 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, 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. (See Supplementary Material.)

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).

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 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). Thirteen cm from the base of the bed is a calcareous-rich horizon containing crinoid ossicles, erect bryozoans, monograptids and brachiopods, and there are two thin clay bands, 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 the 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, 1886
(=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
Figs 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 NMS G.1885.26.72.6, part and counterpart (holotype), NMS G.1885.26.72.15 (paratype).

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

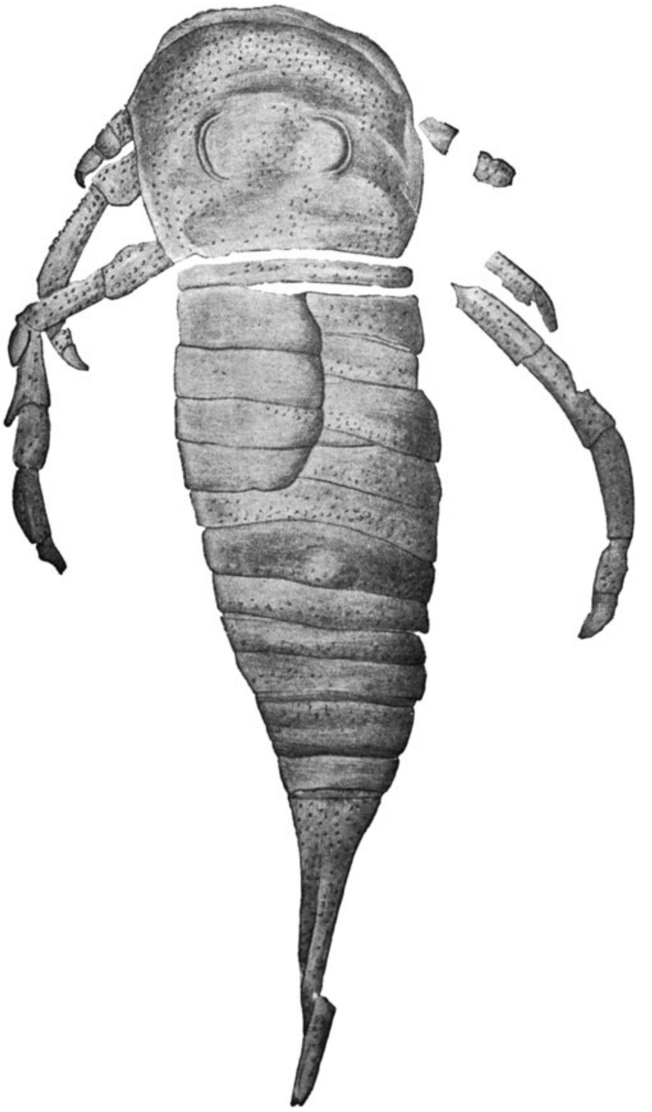

Figure 1 *Drepanopterus pentlandicus* Laurie, 1892. Original figure of a juvenile individual (part to specimen NMS G.1897.32.18?) in Laurie 1899, specimen now considered lost.

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, 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 the 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* were 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 represented by fourteen specimens (Table 1), however in only three (NMS G.1885.26.72.5, Figs 3, 4; NMS G.1897.32.18, Fig. 5c, d; NMS 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, although still

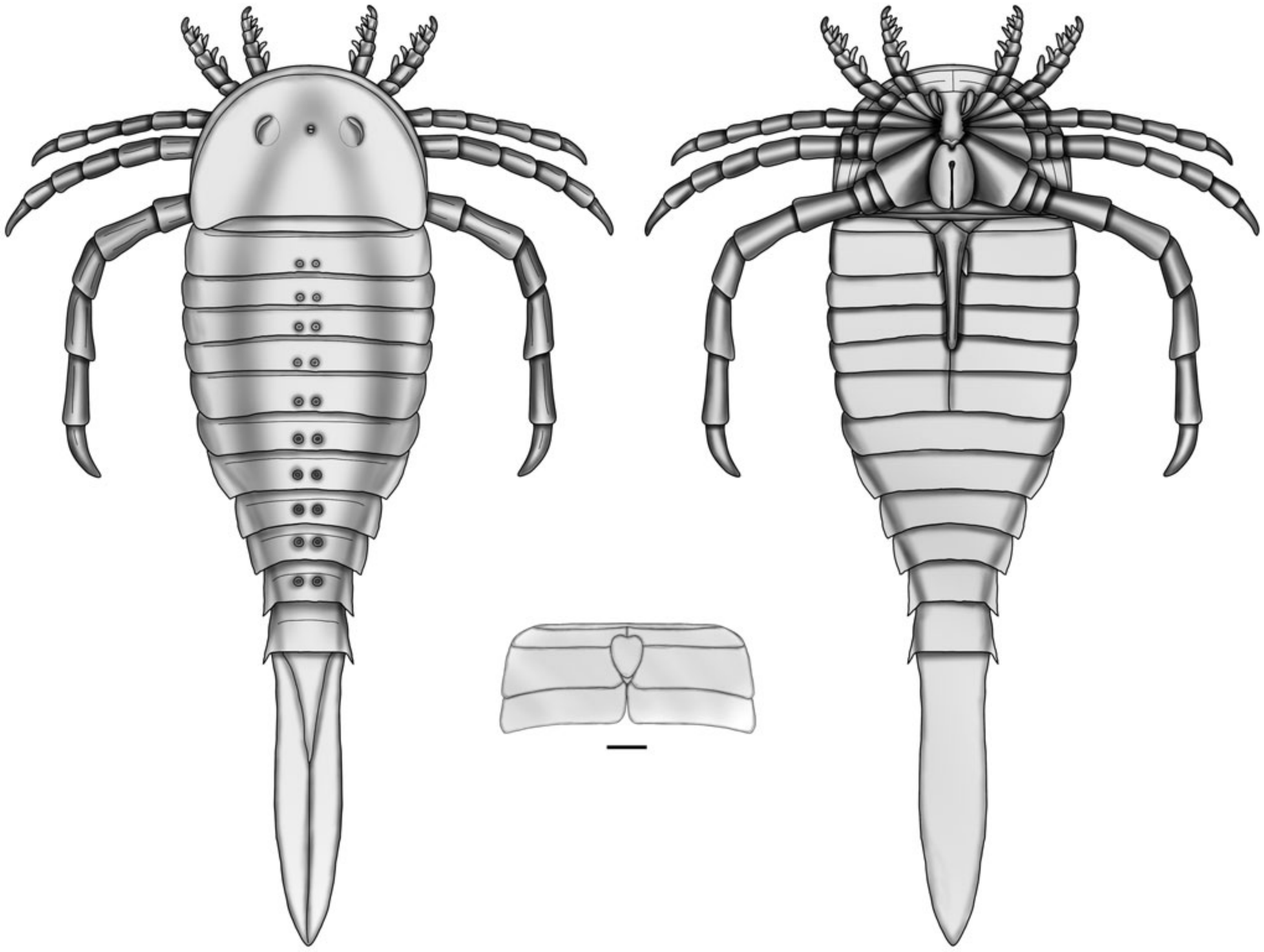

Figure 2 Reconstruction of adult *Drepanopterus pentlandicus* Laurie, 1892. Dorsal and ventral views of a type-A individual are shown either side, while a type-B genital operculum is shown in the centre. Scale bar = 10 mm.

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

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

* = Incomplete.

falling 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 NMS G.1897.32.102) – posterolateral extensions of the carapace are also seen in several specimens of *Drepanopterus abonensis*

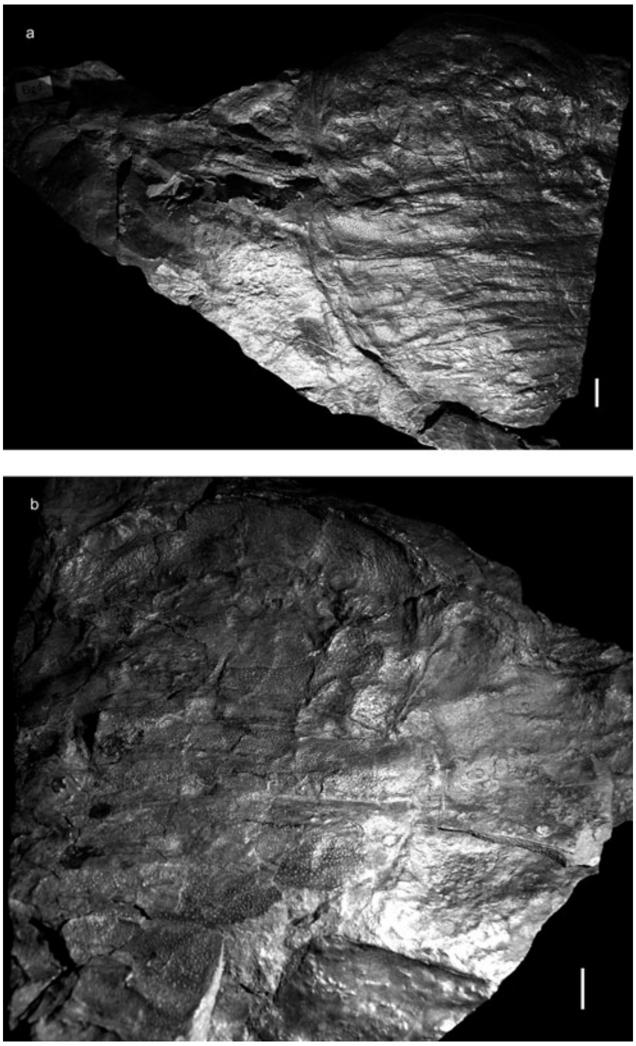

Figure 3 *Drepanopterus pentlandicus* Laurie, 1892: (a) holotype, NMS G.1885.26.72.5, consisting of carapace, mesosomal segments and proximal portions of appendage VI; (b) NMS G.1885.26.72.5, counterpart. Scale bar = 10 mm.

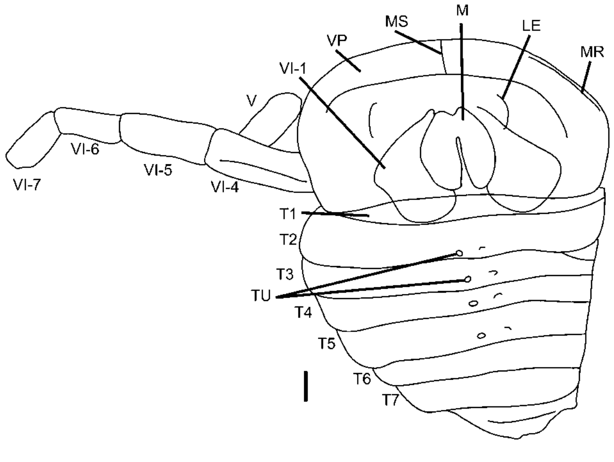

Figure 4 *Drepanopterus pentlandicus* Laurie, 1892, interpretive drawing of holotype NMS G.1885.26.72.5. Abbreviations: LE = lateral eyes; M = metastoma; MR = marginal rim; MS = median suture; TU = tubercles; T1–T12 = tergites 1–12; VP = ventral plate. Prosomal appendages are labelled with Roman numerals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

(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; NMS G.1897.32.97, Figs. 7a, 8; NMS G.1885.26.72.15, Fig. 5b; NMS G.1897.32.868, Fig. 9; NMS 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; NMS G.1897.32.98, Fig. 7b; NMS 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), 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 NMS 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

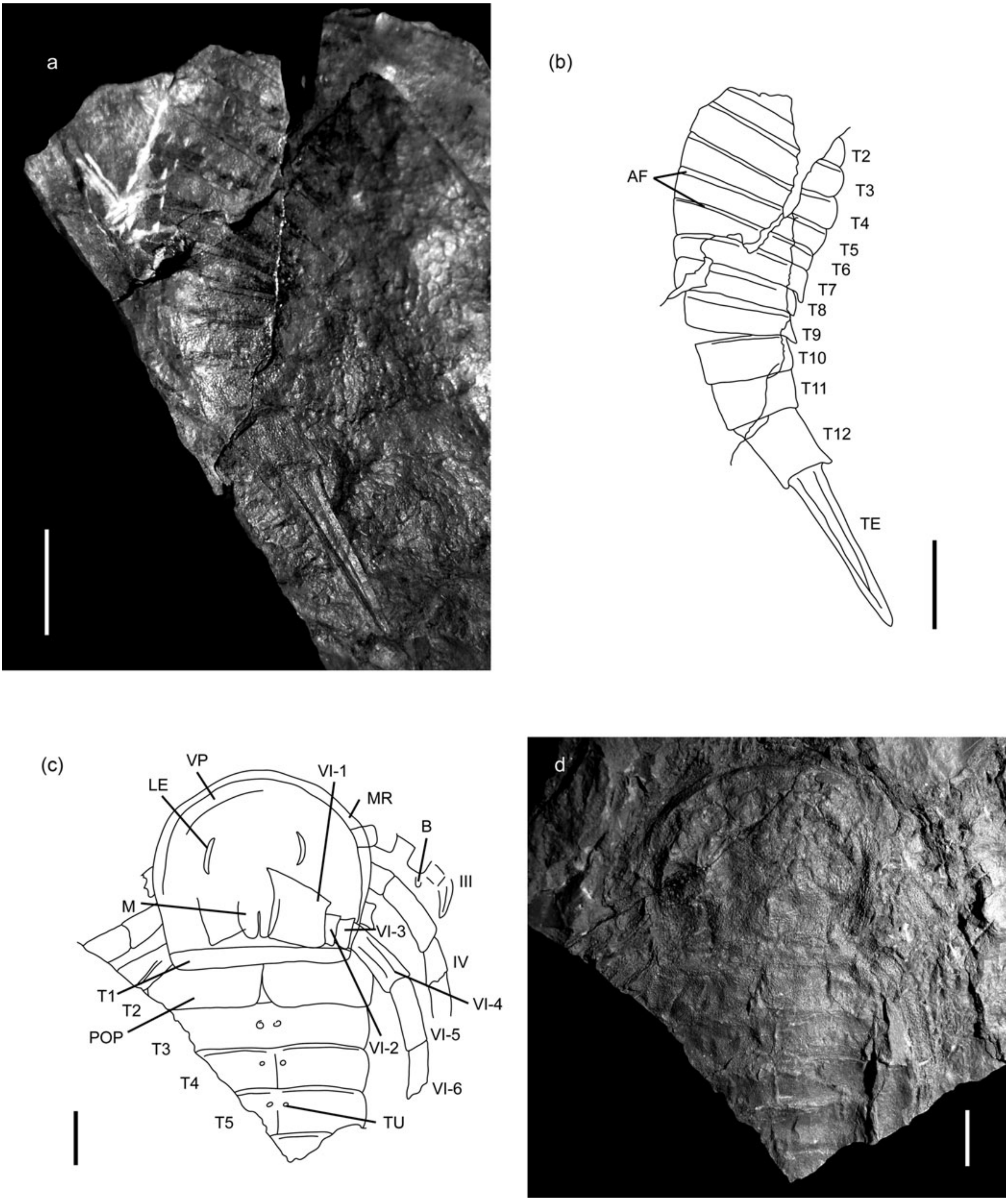

Figure 5 *Drepanopterus pentlandicus* Laurie, 1892: (a) paratype, NMS G.1885.26.72.15, opisthosoma of juvenile individual; (b) interpretive drawing of NMS G.1885.26.72.15; (c) interpretive drawing of NMS G.1897.32.18; (d) NMS G.1897.32.18, juvenile individual consisting of carapace, anterior mesosomal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

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

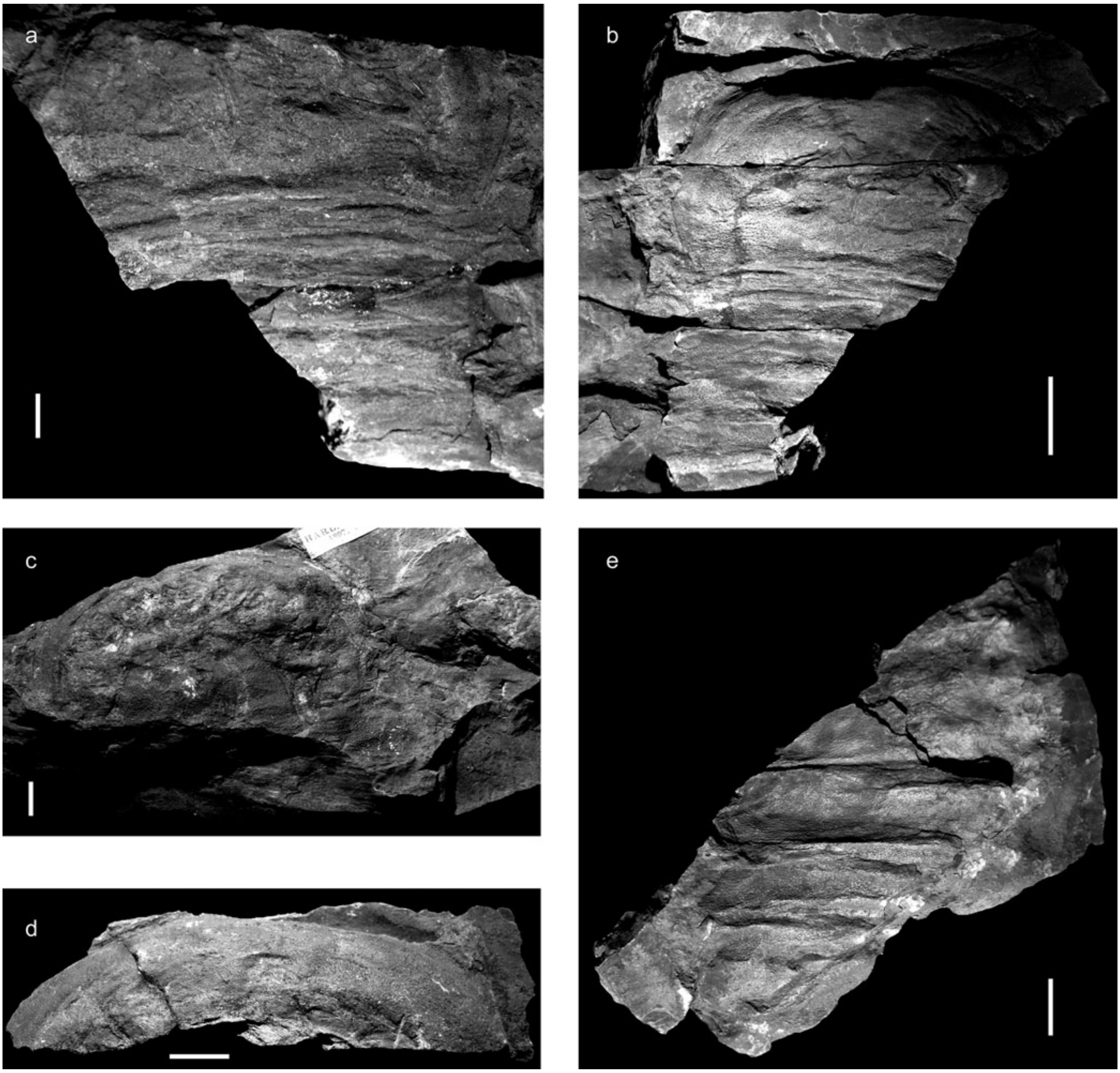

Figure 6 *Drepanopterus pentlandicus* Laurie, 1892: (a) NMS G.1897.32.101, partial carapace and mesosomal segments; (b) NMS G.1897.32.102, counterpart to NMS G.1897.32.101; (c) NMS G.1897.32.107, prosoma showing ventral structures; (d) NMS G.1897.32.105, anterior of prosoma showing ventral plates. (e)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

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

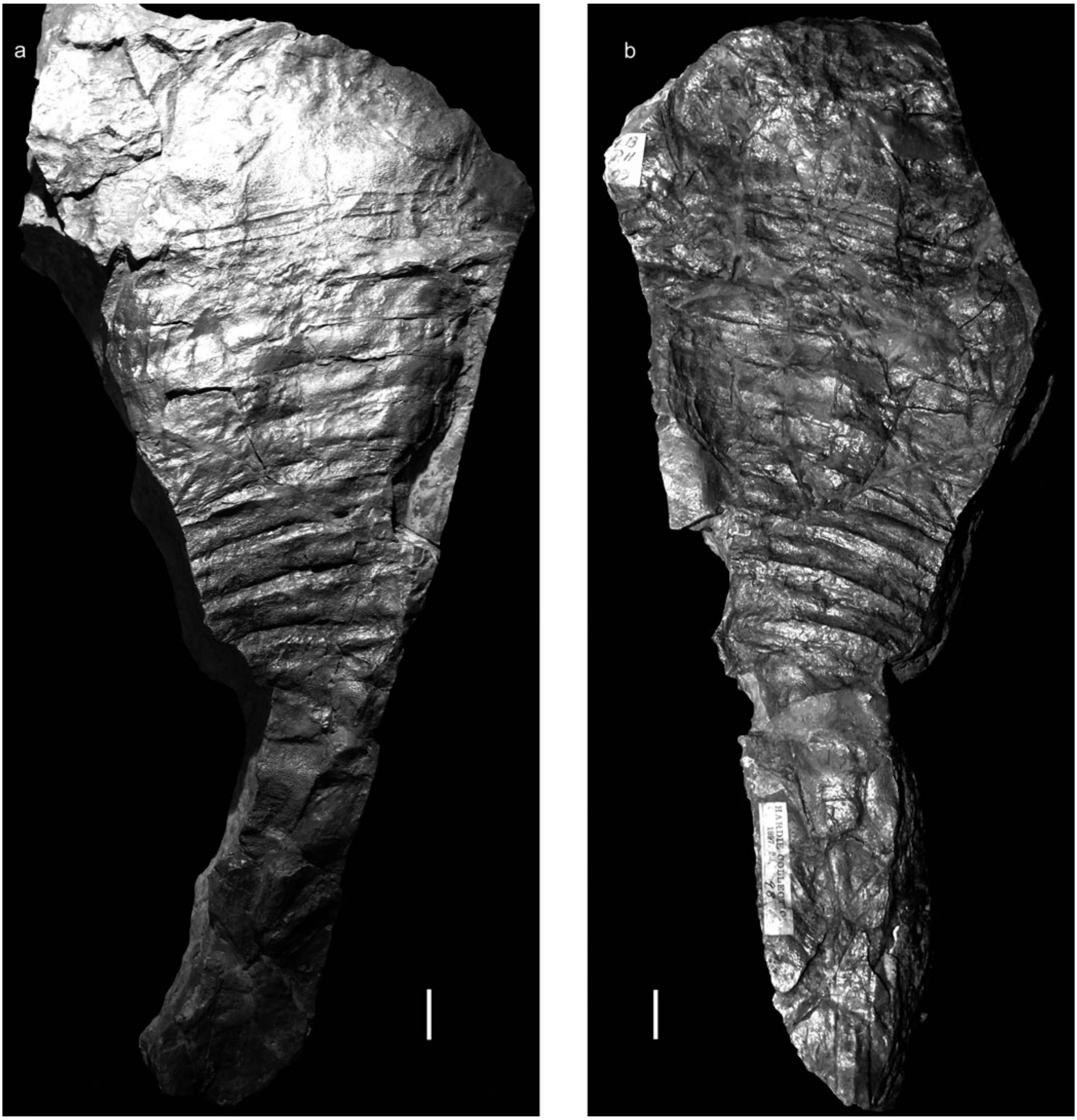

Figure 7 *Drepanopterus pentlandicus* Laurie, 1892: (a) NMS G.1897.32.97, relatively complete individual including carapace, opisthosoma and telson; (b) NMS G.1897.32.98, counterpart to NMS G. 1897.3.97. Scale bars = 10 mm.

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 that of *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); a similar cleft is 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

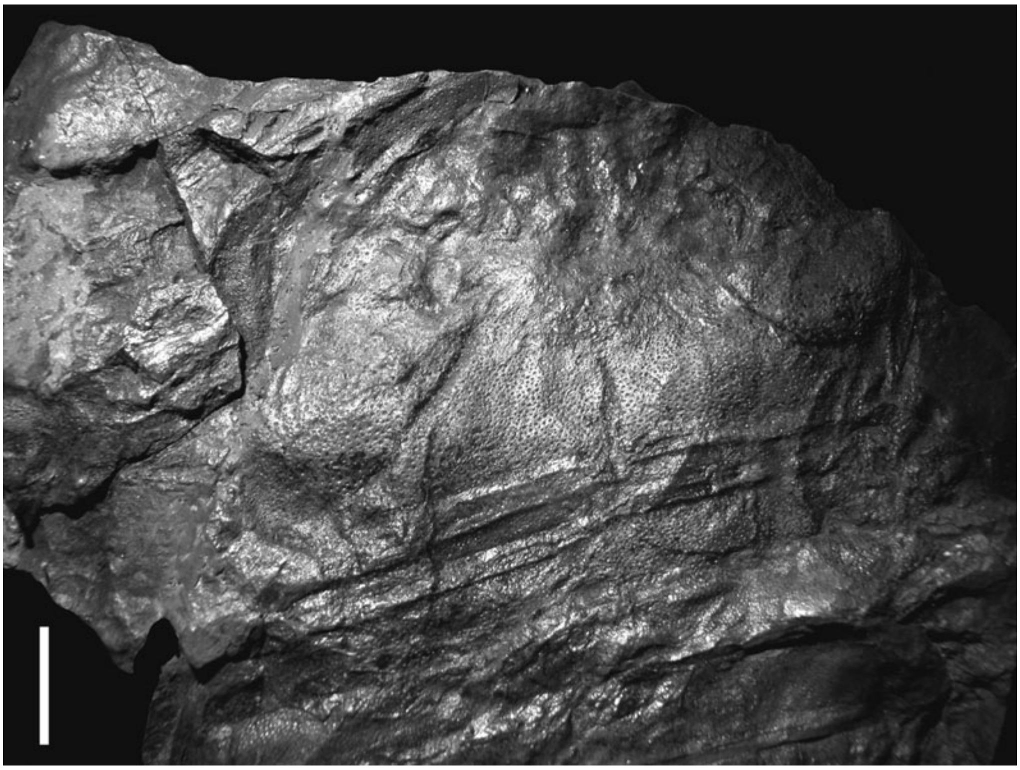

Figure 8 *Drepanopterus pentlandicus* Laurie, 1892, enlarged view of carapace of NMS G.1892. 897.32.97. Scale bar = 10 mm.

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, and 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 and, 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) (note that 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) that 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; NMS G.1897.32.103; NMS 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).

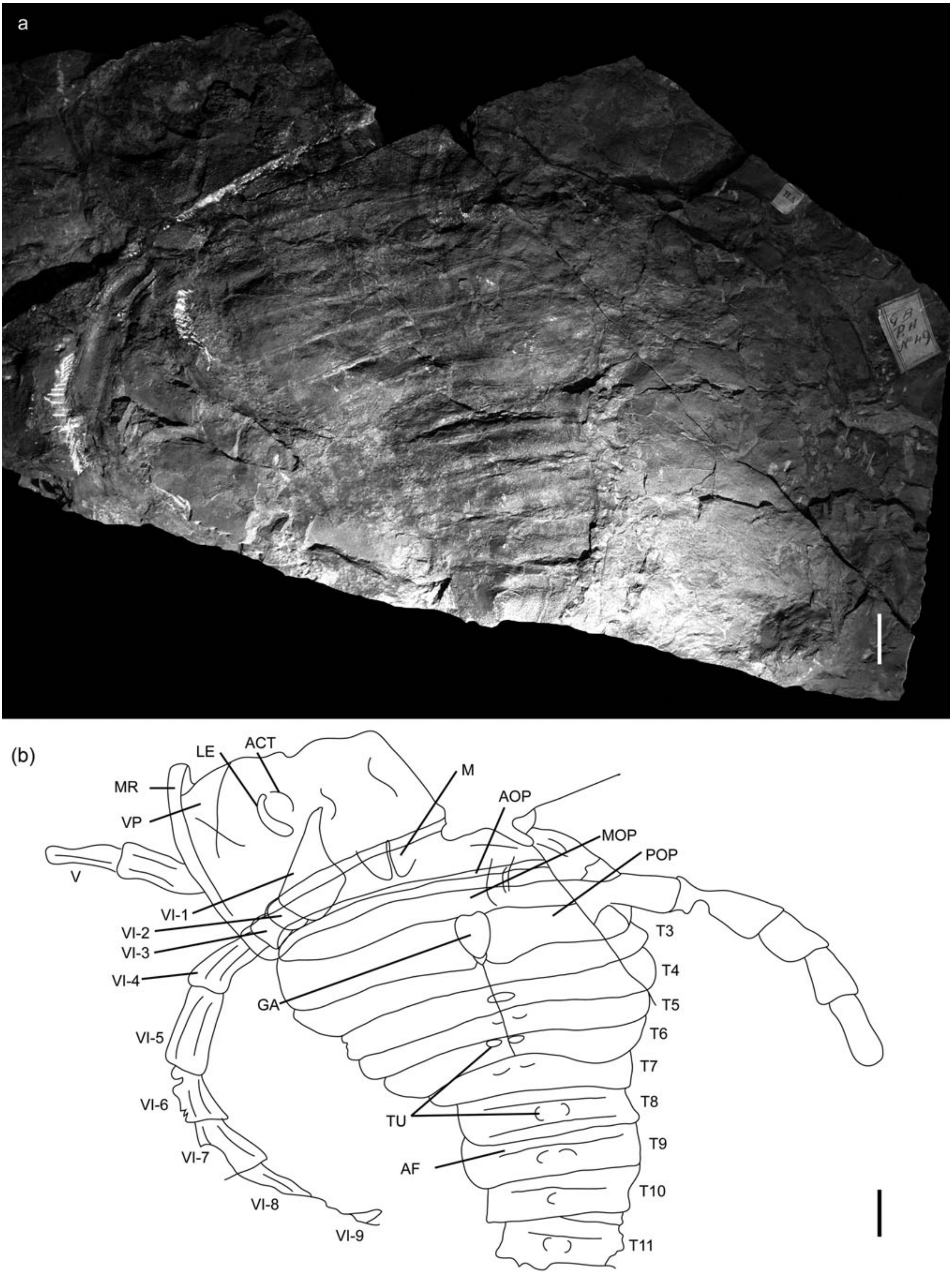

Figure 9 *Drepanopterus pentlandicus* Laurie, 1892: (a) NMS G.1897.32.868, almost complete specimen consisting of carapace and opisthosoma, including appendage VI and type B genital appendage; (b) interpretive drawing of NMS G.1897.32.868. Abbreviations: ACT = annular cuticular thickening; AF = articulating 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.

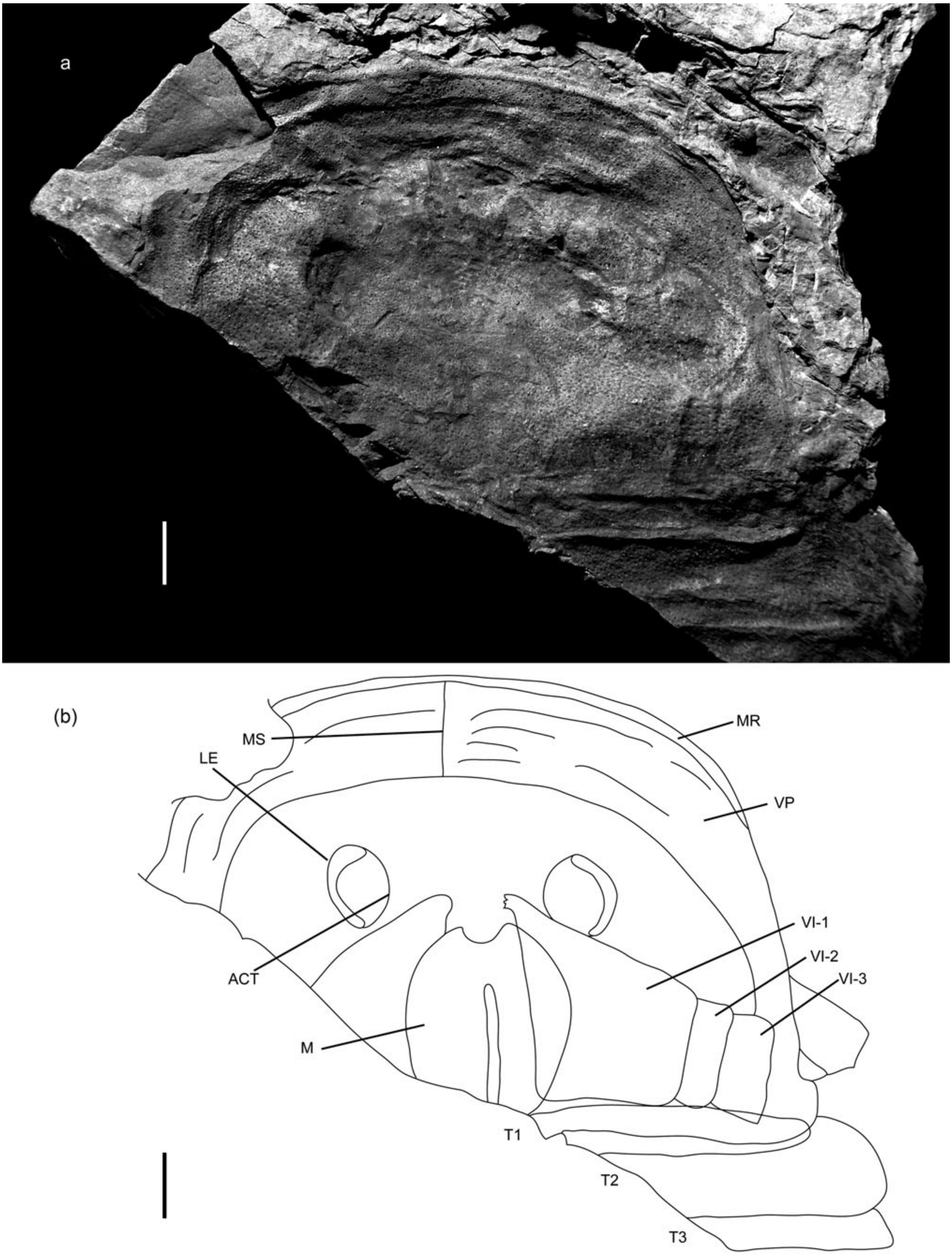

Figure 10 *Drepanopterus pentlandicus* Laurie, 1892: (a) NMS G.1897.32.869, prosoma showing lateral eyes, ventral plates, metastoma and coxa of appendage VI; (b) interpretive drawing of NMS G.1897.32.869. Abbreviations: ACT = annular cuticular thickening; LE = lateral eyes; M = metastoma; MR = marginal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

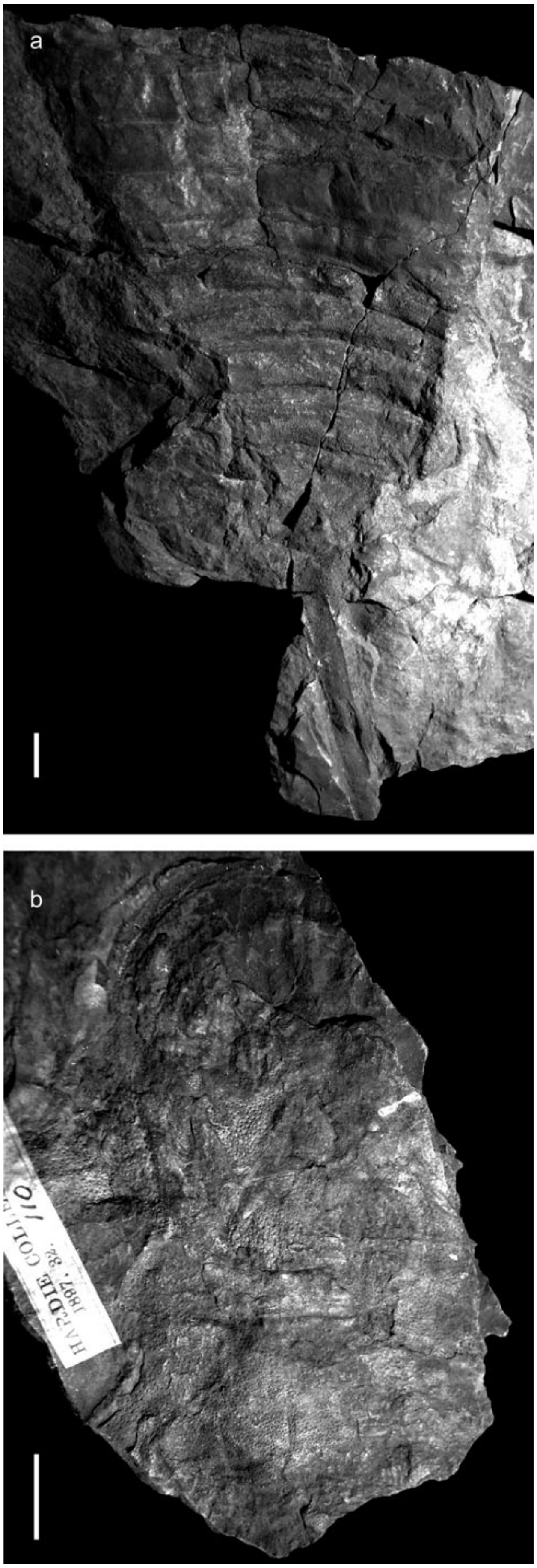

Figure 11 *Drepanopterus pentlandicus* Laurie, 1892: (a) NMS G.1897.32.109, metasoma and telson; (b) NMS G.1897.32.110, carapace with apparently round lateral eye and mesosomal segments. Scale bars = 10 mm.

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* 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 to confirm this.

The telson is clearly clavate in NMS G.1897.32.72 (Fig. 11), NMS G.1897.32.91 (Fig. 12) and NMS 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. *Drepanopterus 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, but 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

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 NMS G.1897.32.18 preserve the full carapace width, allowing for the relative width of the lateral eyes to be calculated. The current data indicate relatively little alteration in lateral eye proportion and position through ontogeny. However, the lateral eyes of the smaller specimens are positioned at the outermost limits of the centrimesial quadrant, whereas in larger specimens they are unquestionably centrimesial.

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	–

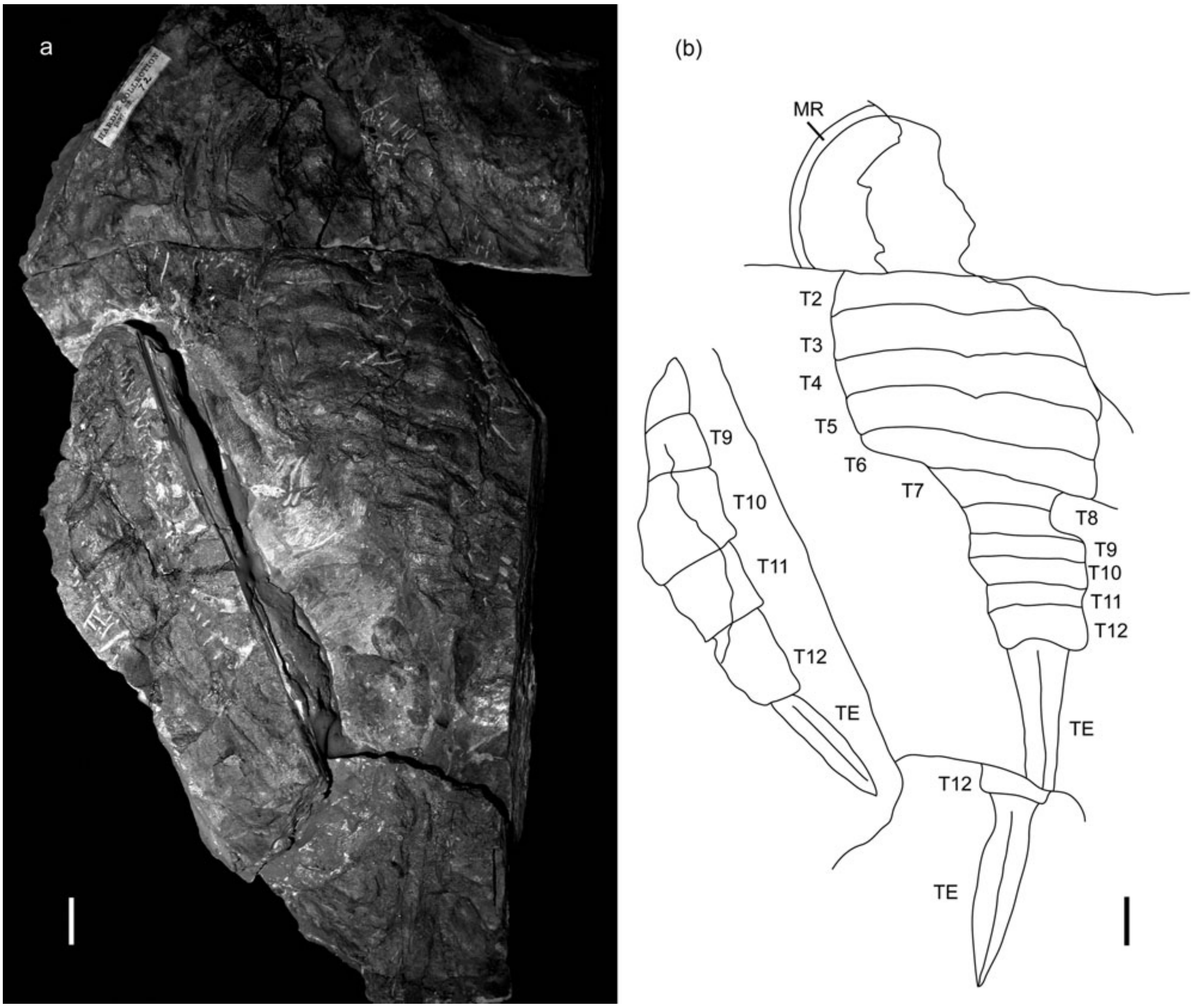

Figure 12 *Drepanopterus pentlandicus* Laurie, 1892: (a) NMS G.1897.32.72, multiple specimens preserved in different levels of sediment on the same slab; (b) interpretive drawing of NMS G.1897.32.72. Abbreviations: MR = marginal rim; T1–T12 = tergites 1–12; TE = telson. Scale bars = 10 mm.

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 on the fact that in ventral view the metastoma overlies the coxae, and so the small plate suggested by Selden *et al.* (2005) to be the metastoma could not be as it would underlie the

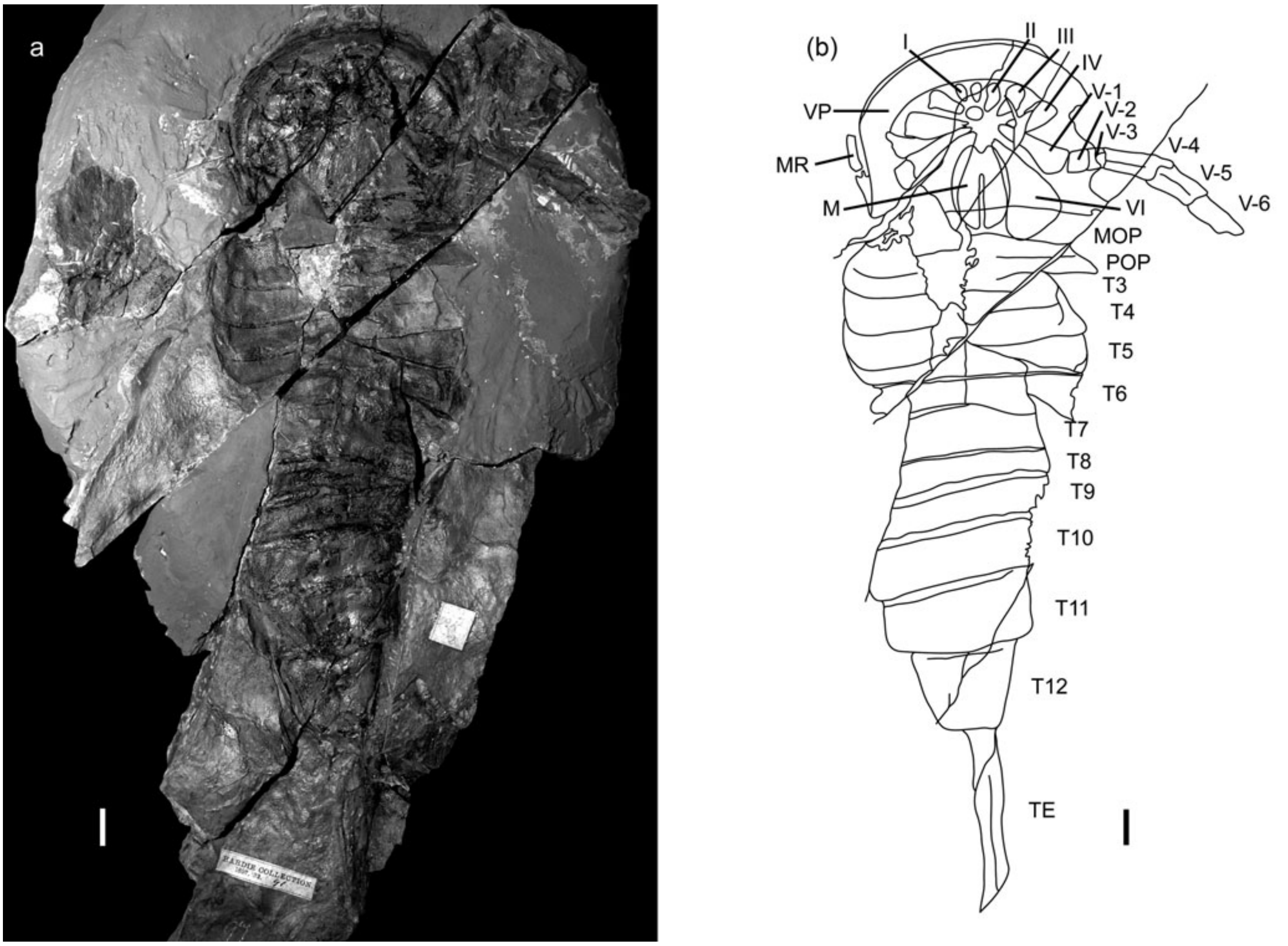

Figure 13 *Drepanopterus pentlandicus* Laurie, 1892: (a) NMS G.1897.32.91, remarkably well preserved specimen showing details of the ventral prosomal structures and the median sutures on the Blattfüsse; (b) interpretive drawing of NMS G.1897.32.91. Abbreviations: M = metastoma; MOP = median opercular 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.

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

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.

coxae. Another similarity is the morphology of the ventral prosomal plates, which until now have not been well known in *Drepanopterus*, 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). 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, but 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 is seen in somite VIII of some synziphosurines (Eldredge 1974; Anderson & Moore 2004; 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

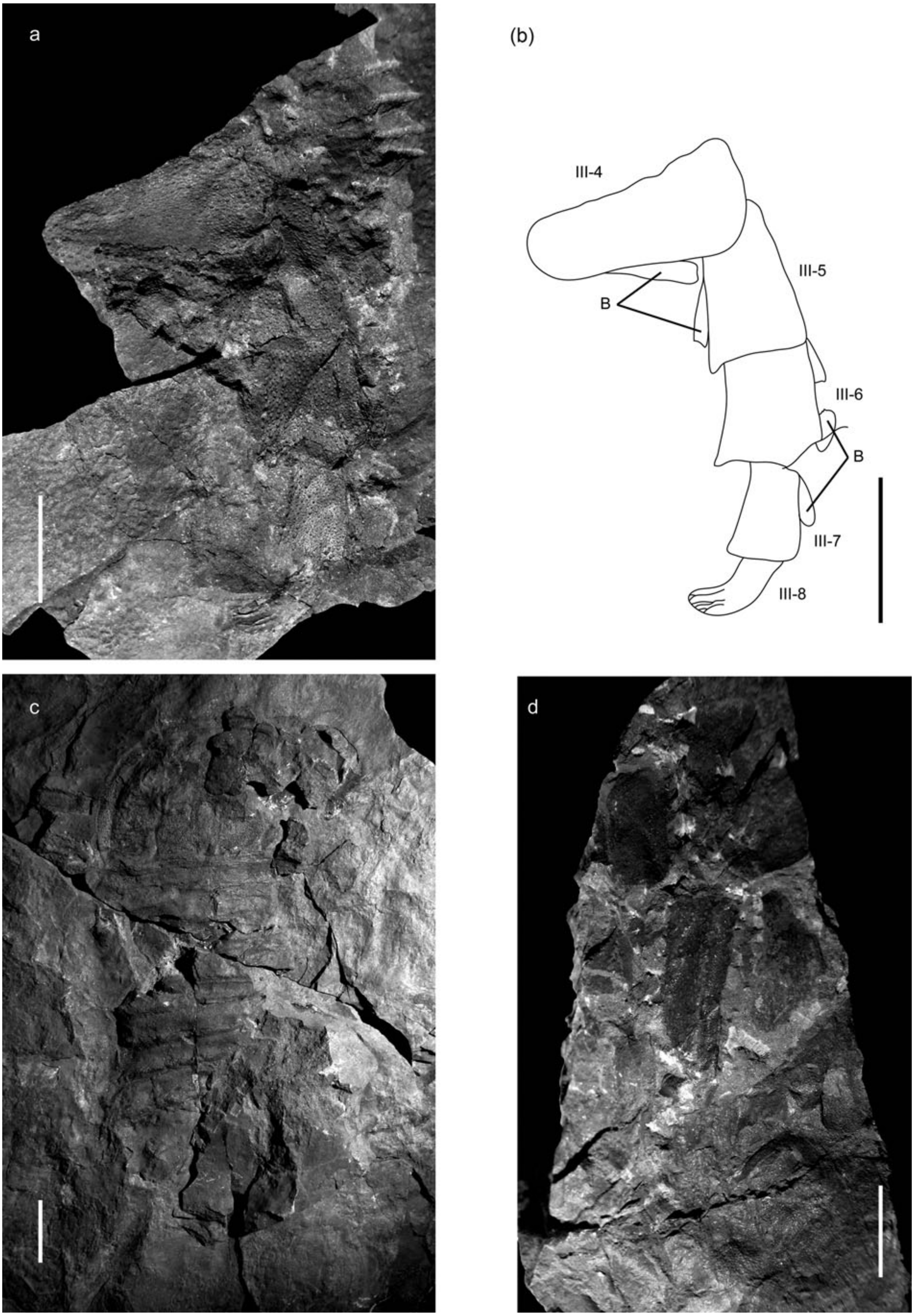

Figure 14 *Drepanopterus pentlandicus* Laurie, 1892: (a) NMS G.1897.32.92, isolated appendage (III?) with blades; (b) interpretive drawing of NMS G.1897.32.92; (c) NMS G.1897.32.94, weathered specimen showing fragments of cuticle; (d) NMS G.1897.32.99, tangle of appendage podomeres. Abbreviations: B = 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.

Table 4 Appendage IV 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.

* = Incomplete.

Table 5 Appendage V 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.

* = Incomplete.

Table 6 Appendage VI 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.

* = Incomplete.

Table 7 Metastoma measurements. Dimensions 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

* = Incomplete.

an enlarged segment, yet neither do the juvenile specimens of *D. pentlandicus* (NMS G.1885.26.72.15, Fig. 5a, b, and NMS 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 or 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 (2009) 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 anteroventral 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 with 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 changes in both 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 metasomal 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

Table 8 Mesosoma (length/width) in mm.

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

* = Incomplete.

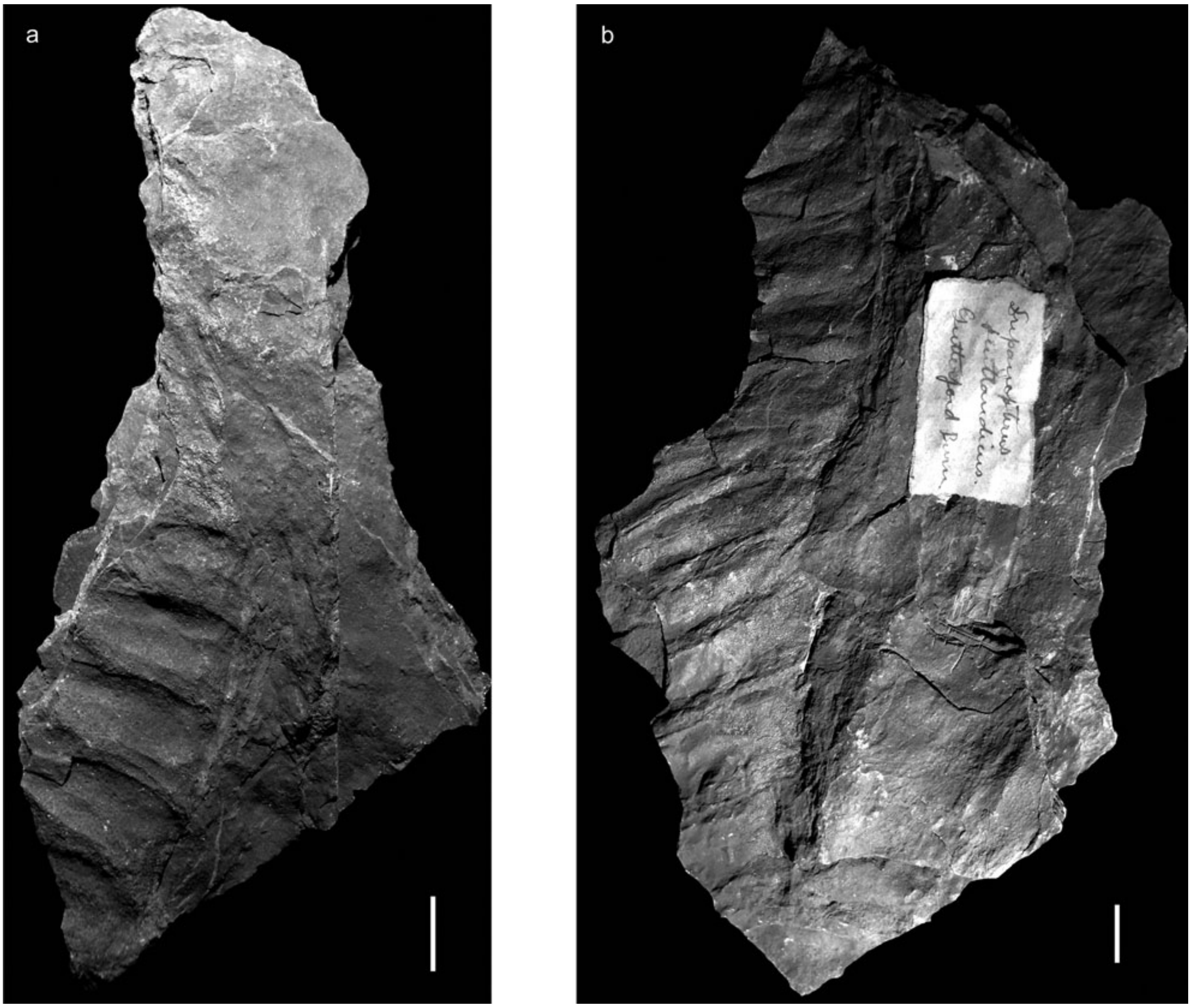

Figure 15 *Drepanopterus pentlandicus* Laurie, 1892: (a) NMS G.1885.26.72.12, lateral portions of mesosomal segments; (b) NMS G.1885.26.72.10, portion of mesosoma and metasoma. Scale bars = 10 mm.

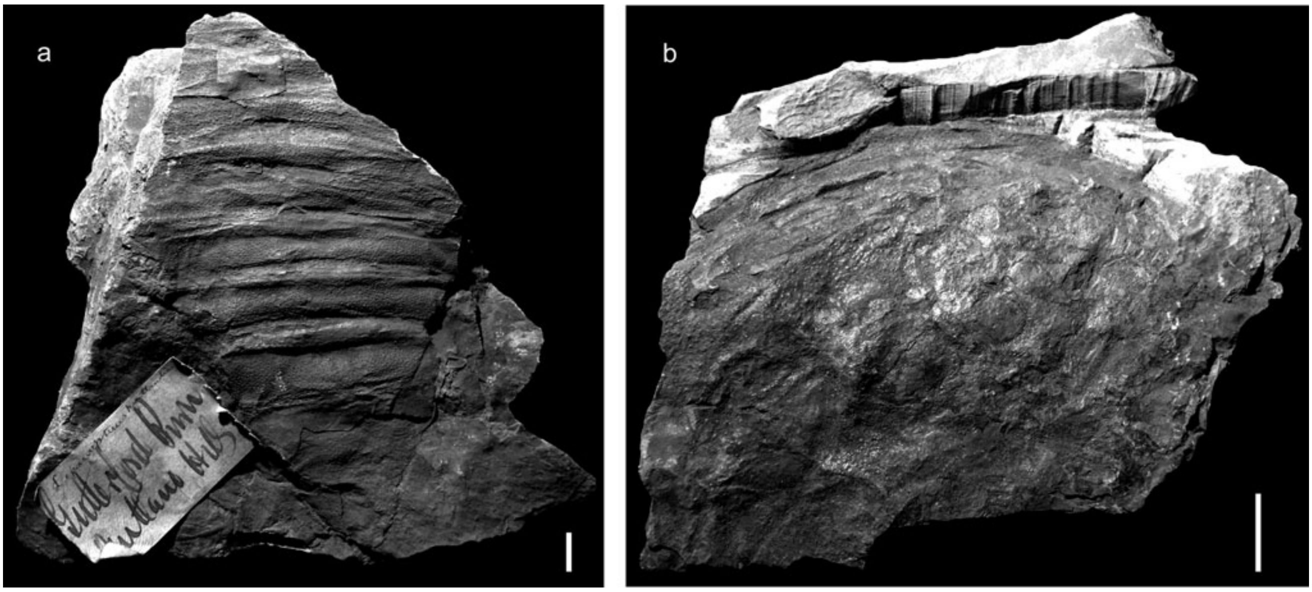

Figure 16 *Drepanopterus pentlandicus* Laurie, 1892: (a) NMS G.1885.26.72.11, opisthosomal segments; (b) NMS G.1885.26.72.3, fragment of large, flattened carapace showing compressed lateral eye and cuticular ornament. Scale bars = 10 mm.

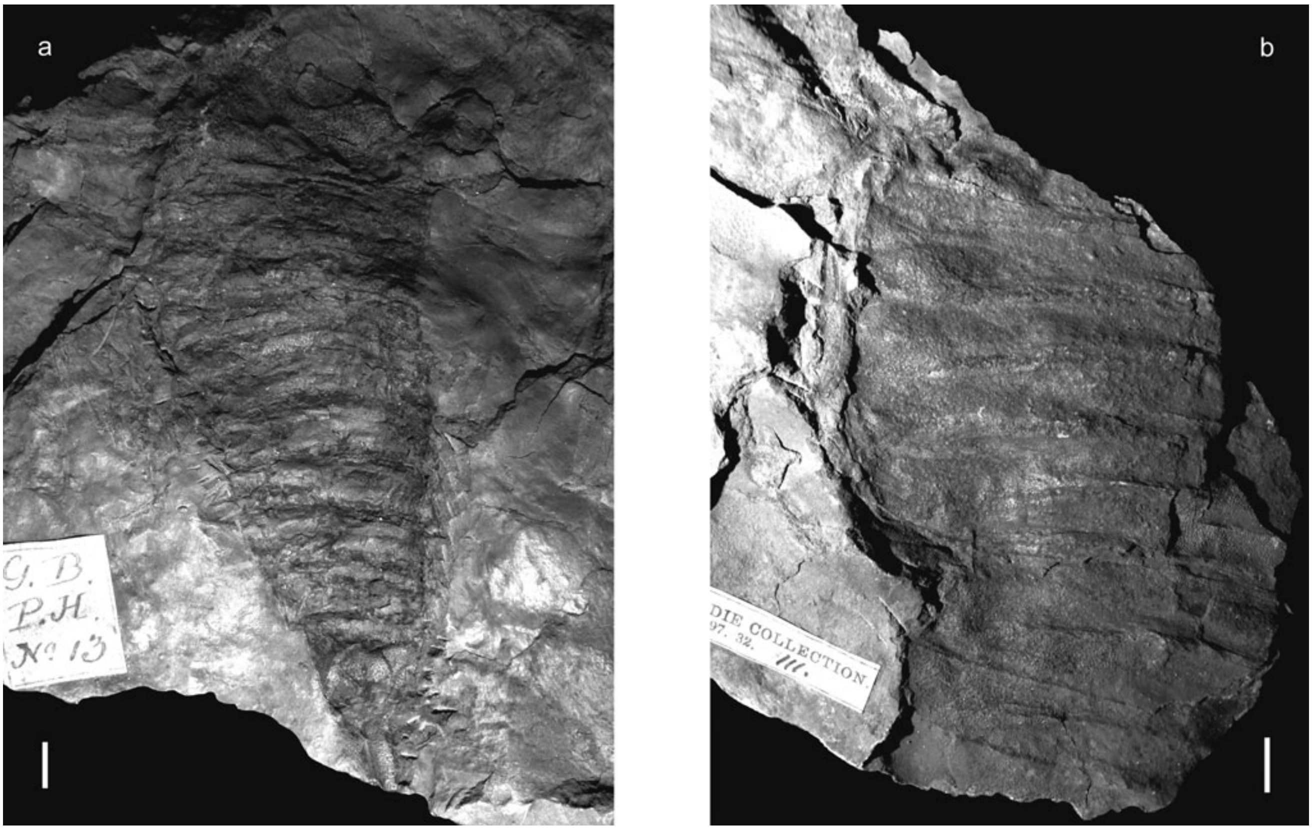

Figure 17 *Drepanopterus pentlandicus* Laurie, 1892: (a) NMS G.1897.32.108, showing opisthosoma and base of telson; (b) NMS G.1897.32.111, lateral portions of opisthosomal segments. Scale bar = 10 mm.

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, lateral eye structure, 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

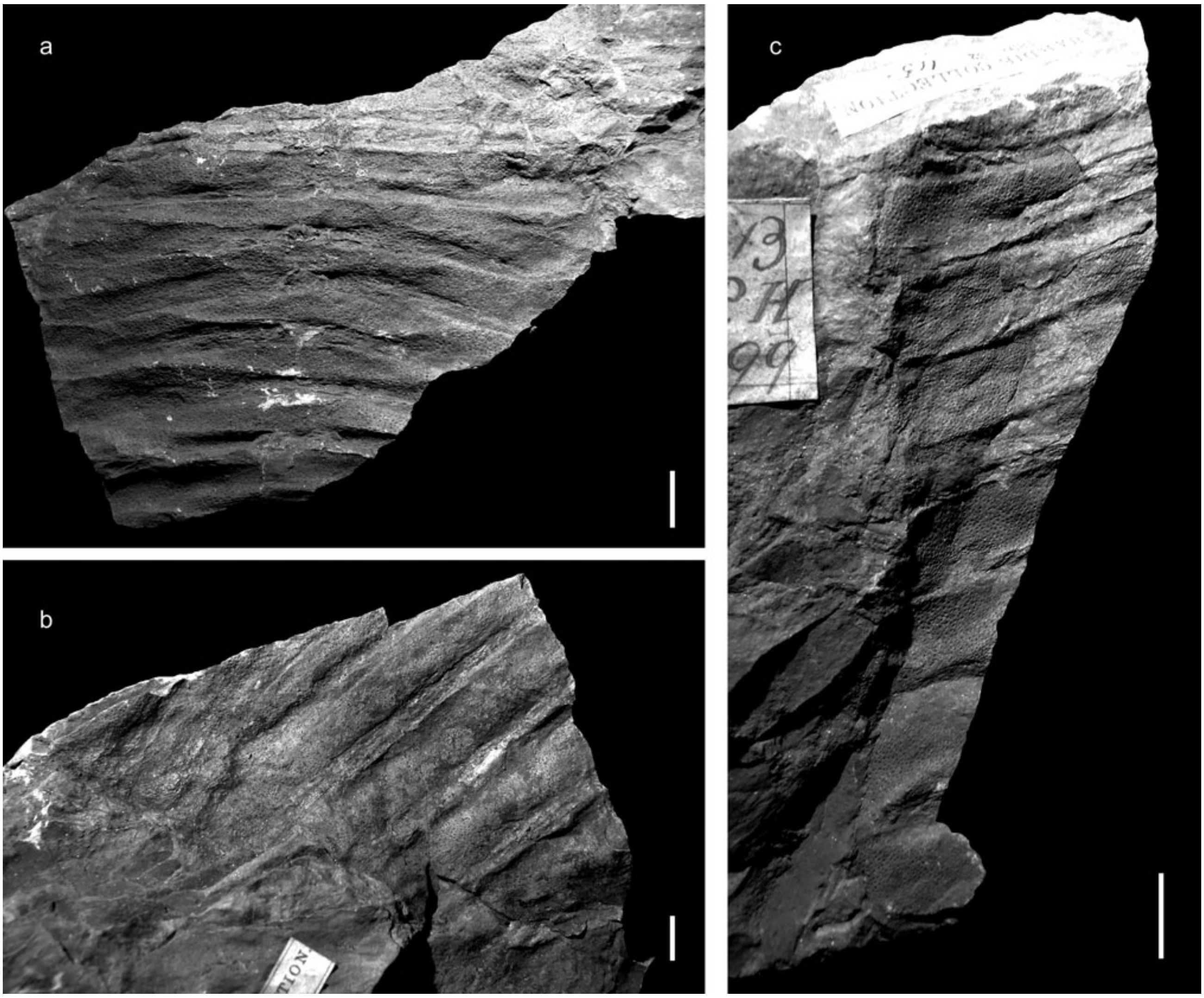

Figure 18 *Drepanopterus pentlandicus* Laurie, 1892: (a) NMS G.1897.32.112, ventral view of tergites showing median tubercles; (b) NMS G.1897.32.113, lateral portions of tergites; (c) NMS G.1897.32.115, tergites showing cuticular sculpture. Scale bars = 10 mm.

material so were not included in the matrix. Analysis of this expanded data matrix as detailed in section 2 (Material and methods) resulted in a single most parsimonious tree (Fig. 22; Supplementary Material) 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. Although *H. whitei* is only known from fragmentary material, its 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*. 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

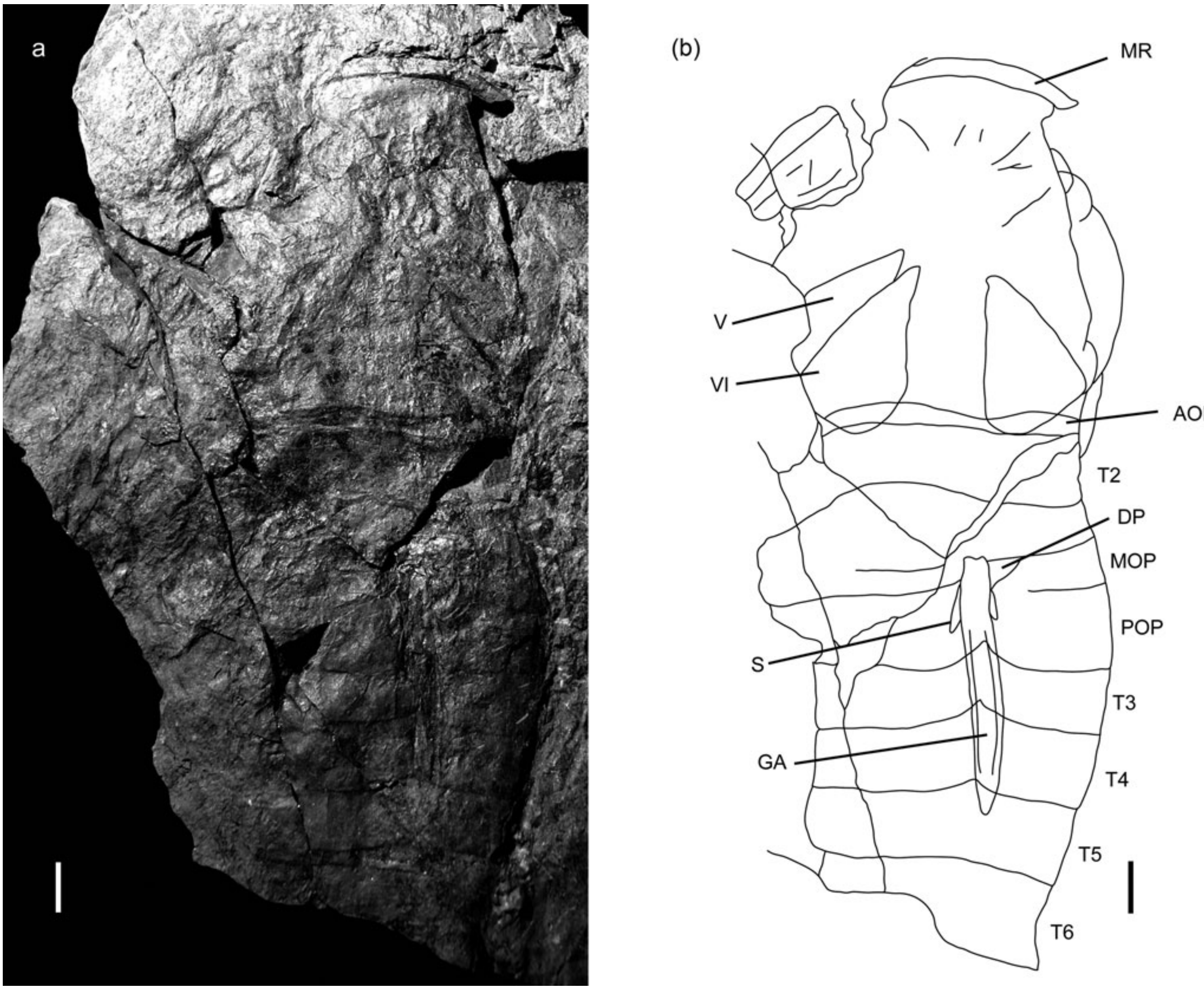

Figure 19 *Drepanopterus pentlandicus* Laurie, 1892: (a) NMS G.1897.32.71, specimen preserving the type A genital appenda; (b) interpretive drawing of NMS G.1897.32.71. Abbreviations: AOP = anterior opercular plate; DP = deltoid plate; GA = genital appendage; MOP = median opercular plate; MR = marginal 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.

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*. However, such a major systematic revision is beyond the scope of the current work.

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

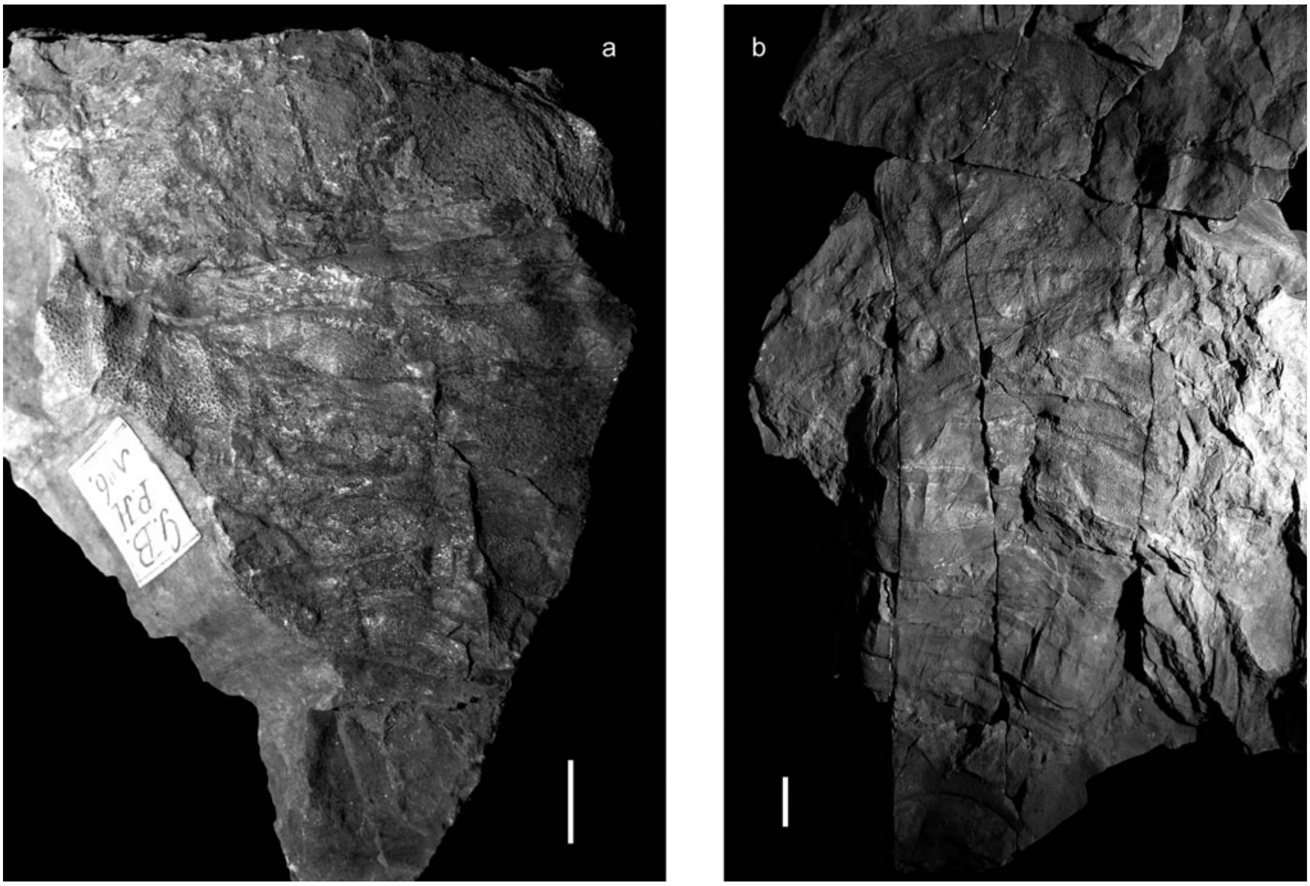

Figure 20 *Drepanopterus pentlandicus* Laurie, 1892; (a) NMS G.1897.32.100, poorly preserved specimen with carapace and mesosomal segments; (b) NMS G.1897.32.103, fractured specimen showing details of carapace structures and anterior opisthosoma. Scale bar = 10 mm.

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

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 (V. P. Tollerton pers. comm. 2010). 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, exhibits 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, shows 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.));

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

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*	–	–

* = Incomplete.

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 (Almond 2002; Whyte 2005), 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, but 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, suggests 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.

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8. Supplementary Material

The morphological character list and character matrix used in the phylogenetic analysis are published as Supplementary Material with the on-line version of this paper. This is hosted by the Cambridge Journals Online Service and can be viewed at http://journals.cambridge.org/tre

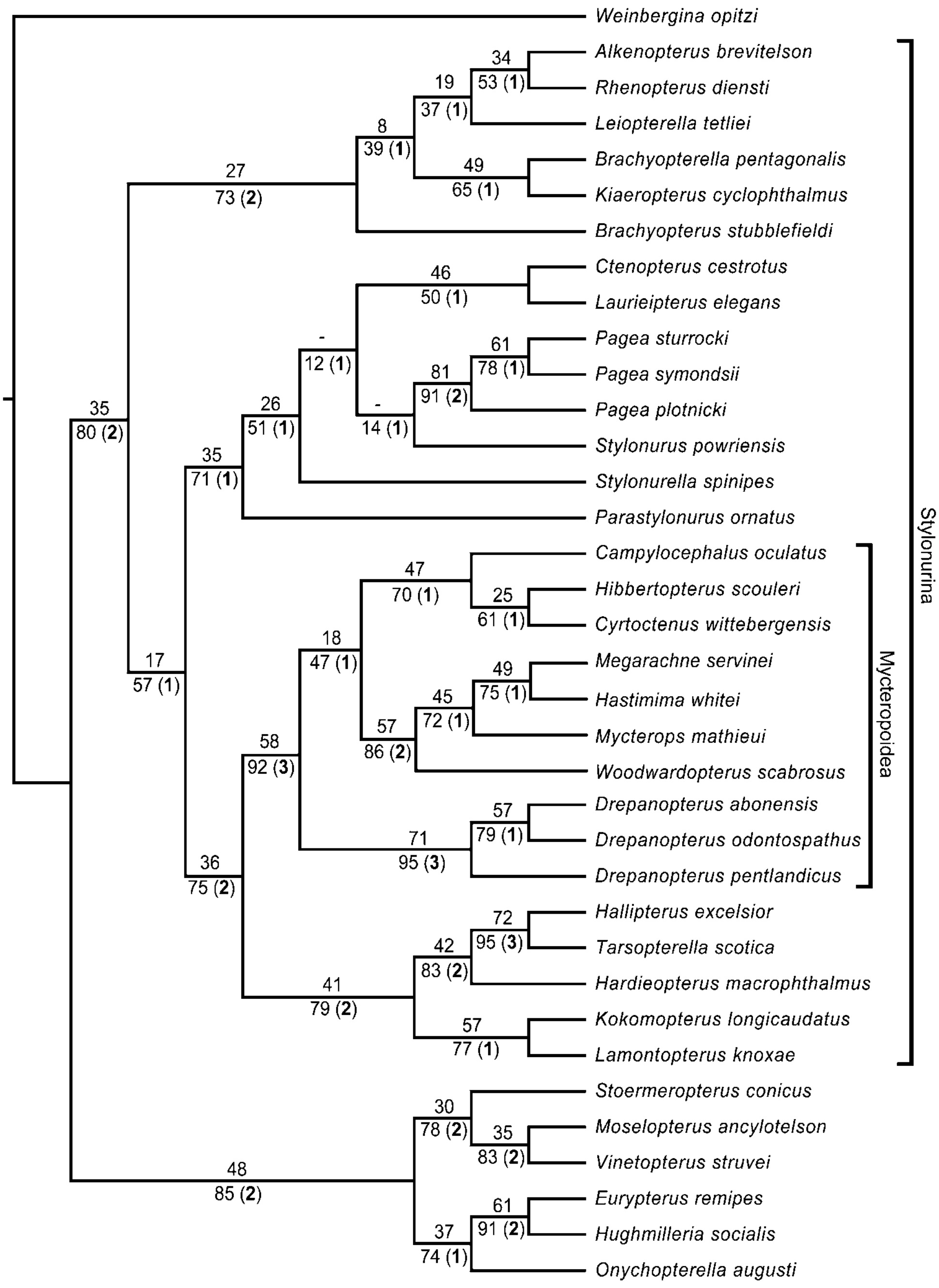

Figure 22 Single most parsimonious tree derived from the matrix shown in the Supplementary Material, analysed as detailed in the Material and methods section (section 2). Bootstrap values are shown above the branches, generated from 50% character resampling with 1000 repetitions, while shown beneath the branches are jackknife values with 20% character resampling with 1000 repetitions, with bremer support values shown in bold within parentheses.

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