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REDESCRIPTION OF *DREPANOPTERUS ABONENSIS* (CHELICERATA: EURYPTERIDA: STYLONURINA) FROM THE LATE DEVONIAN OF PORTISHEAD, UK

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Abstract: Stylonurid eurypterids (Arthropoda: Chelicerata) include some of the largest known arthropods – bizarre sweep-feeding hibbertopterids from the Carboniferous to end-Permian. New material of *Drepanopterus abonensis*, a stylonurid from the Late Devonian (Famennian) of Portishead, south-west England, offers key insights into this genus and its affinities. A redescription utilising the new material enables *D. abonensis* to be assigned as basal member of the Superfamily Hibbertopteroidea, the large-sweep-feeding forms, possessing a cleft metastoma and blades (modified blunt spines) on their anterior prosomal appendages. *D. abonensis* also shares characters such as a clavate telson and median ridge on the carapace with the proposed hibbertopteroid sister group the Kokomopteroidea. Hibbertopteroid eurypterids are the most long-ranging stylonurids, surviving the decline and extinction of the other eurypterid families in the Late Devonian, their survival probably because of their sweep-feeding mode of life, which was not in direct competition with their eurypterine relatives and other predators.

Key words: Palaeozoic, Famennian, Drepanopteridae, sweep-feeding, Old Red Sandstone, Hibbertopteroidea, palaeoecology.

EURYPTERIDS are extinct aquatic chelicerates found in Palaeozoic marginal marine, brackish and fresh-water environments. Most species are nektonic predators with their posterior appendages modified into swimming paddles, often found in abundant concentrations of moulted exuviae (Braddy 2001). Stylonurid eurypterids show their posterior appendages adapted for walking and are relatively rare; the Eurypterina (paddled forms) represent around 75 per cent of known eurypterid species, whereas the Stylonurina (walking forms) represent the remaining 25 per cent, although the Eurypterina comprise 95–99 per cent of known specimens (Tetlie 2007). Most stylonurids are known from only one or two specimens. The oldest eurypterid recorded in the fossil record is a stylonurid [*Brachyopterus stubblefield*, from the Late Caradoc (Ordovician) of Wales (Størmer 1951)], as is the youngest [*Hibbertopterus permianus*, from the Late Permian of Russia (Ponomarenko 1985)]; as such, they persist for their entire 210 myr history. Stylonurids are rare throughout the Ordovician and Silurian, although the radiation of the hibbertopteroids (large sweep-feeding forms) in the Late Devonian and Carboniferous represents the last major genus-level radiation of eurypterids (Tetlie 2007).

The hibbertopterids were removed from Eurypterida by Tollerton (1989) based on their possession of a cleft metastoma and laden instead of coxae, a revision previously suggested by Bergström (1980), because of *Cyrtoctenus* originally being described as having pectinate abdominal appendages (Størmer and Waterston 1968). However, many authors have continued to refer the hibbertopterids to the Eurypterida (Dunlop and Selden 1997), and so ascertaining their affinities is an important step in our understanding of stylonurid phylogeny.

New material of *Drepanopterus abonensis*, a stylonurid eurypterid from the Late Devonian Old Red Sandstone (Famennian) of Portishead, south-west England, offers key insights into this genus and its affinities. A full redescription, utilising the new material, allows for *D. abonensis* to be assigned at the familial and superfamilial level and for its relationships with other eurypterids to be explored.

MATERIALS AND METHODS

Specimens were photographed under low-angle light using a Panasonic Lumix DMC-FZ50 digital camera.

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Camera lucida drawings and reconstructions were prepared using Adobe Illustrator 10.

Eurypterid terminology largely follows that of Tollerton (1989). Prosomal appendages are labelled with Roman numerals, and individual podomeres are labelled with Arabic numerals, proximally to distally. Podomere 1 is termed the coxa. Other terminology such as the 'cardiac lobe' and 'median ventral prosomal plate' follows that of Selden (1981). The term 'lade' refers to the plate-like extension that overlies the coxa, as in hibbertopterids (Waterston 1957), while the term 'rachis' refers to the spines modified to comb-like structures, as in *Cyrtoctenus* (Waterston *et al.* 1985). The term 'blade' is used to describe the broad, flattened spines on the anterior prosomal appendages, as in *Hibbertopterus* and *Cyrtoctenus* (Jeram and Selden 1994), although the term was not introduced until similar structures were identified in *Woodwardopterus* and *Megarachne* (Selden *et al.* 2005). Blades are distinct from the flattened spines on appendage II of *Hallipterus* (Kjellesvig-Waering 1963), which lack the lateral expansion and blunt termination.

Institutional abbreviations. BGS, British Geological Society, Keyworth, Nottingham, UK; BMAG, Bristol Museum and Art Galleries, UK; BRSUG, University of Bristol, UK.

GEOLOGICAL SETTING AND PRESERVATION

Drepanopterus abonensis is known from a single locality, a low cliff section 100 m south of Woodhill Bay at Portishead in Somerset, UK. The Upper Old Red Sandstone deposits at Woodhill Bay are suggested to be of Mid-Famennian age (Kellaway and Welch 1993), the sediment derived from the reworked Precambrian Mona Complex (Reynolds and Greenly 1924). These beds disconformably overlie the Lower Old Red Sandstone and dip at an angle of 28 degrees to the south-east (Wallis 1928).

The section was first described by Wallis (1928), although fish remains had previously been reported by Sanders (1863) and Bailey (1865). Wallis divided the *c.* 40 m succession into 18 beds, of which fossils were recorded from beds 7, 8, 10 and 18. The siltstone of beds 8 and 10 preserves the trace fossils *Diplocraterion* and *Cochlichnus*. The siltstone beds contain the majority of the fish scales, while the sandstone beds contain fish scales, arthropod cuticle, including *Drepanopterus*, and plant fragments.

The fossiliferous horizons consist of micaceous siltstones and fine-grained micaceous sandstones. The siltstones are finely laminated, while the sandstones often display trough cross-bedding and cut into underlying beds. Tool marks on the base of the sandstone beds attest to their high energy of deposition. Wallis (1928) suggested that the environment of deposition was a large river system, with lagoons forming along the coast. Pick (1964) further suggested that the beds were deposited on wide alluvial floodplains by rivers constantly altering their flow direction, evidenced by abundant cross-stratification and cross-cutting of channels. As well as the finer sediments deposited on short-lived inter-fluvial lakes and mudflats, coarser deposits were formed by fast-flowing streams (Pick 1964). Measurements of palaeocurrent direction at Portishead show a preferred south-easterly direction of flow, with occasional transitions to a north-westerly flow, thought to be because of the meandering of streams that changed course or joined the main river at different angles (Pick 1964). The eurypterids, found in the finer sandstone layers, are mostly concentrated into one side of a single bed that may represent an oxbow lake.

The eurypterid specimens are predominantly preserved in dorsal aspect; when the ventral portions of the opisthosoma are preserved they are heavily deformed. The exceptions to this are the coxae and metastoma, which are preserved in a manner similar to the dorsal parts of the animal. The cuticle itself is lost in all but a few specimens, although the ornamentation is preserved as a mould. The cuticle is occasionally preserved on the metastoma, detailing fine-scale ornamentation absent on other ventrally preserved specimens. Given that eurypterid cuticle is unmineralised (Gupta *et al.* 2007), it is significant that such well-preserved specimens are preserved in great concentrations. Often concentrations of eurypterids in the fossil record are regarded as mass-moult-mate events (Braddy 2001); however, the presence of dark staining around the joints on some specimens may indicate soft tissue decay, as suggested before in some other eurypterid fossils (Poschmann and Franke 2006, pl. 4, fig. 4), indicating that they are the result of mortalities rather than exuviae. Although some specimens show evidence of warping that could be because of the moulting process, this could also be consistent with the postmortem pliability of the cuticle when left immersed in water, as shown in *Limulus* (Babcock *et al.* 2000). The limbs are generally detached, the telson frequently broken in two and the opisthosoma telescoped or partially disarticulated. The carapace is occasionally found disarticulated, although equally frequently found attached to the first tergite. Tetlie *et al.* (2008) showed that *Eurypterus* specimens with the carapace attached to the first tergite are generally exuviae, with the two ventral plates separated and the rest of the opisthosoma intact; however, the Portishead specimens show the prosomal appendages more disarticulated than would be expected of moults. This could be because of postmortem scavenging, in which case the specimens represent mortalities. The cause of death is unknown; the specimens may

be sourced from further upstream, transported to their current location during a flood event, or have become concentrated within the lake during a drying event.

MORPHOLOGICAL RECONSTRUCTION

Although many of the specimens are fragmentary, their sheer number, coupled with the variety of aspects of anatomy preserved, now makes *Drepanopterus abonensis* one of the most completely known stylonurids, almost rivalling *Parastylonurus ornatus* (Waterston 1979). The only structures for which there is no direct fossil evidence are the chelicerae, type B genital appendage and respiratory structures. Of these, the respiratory structures of eurypterids have been described elsewhere (e.g. Waterston 1975; Selden 1985; Manning and Dunlop 1995; Braddy *et al.* 1999), the chelicerae are well known in several stylonurids (e.g. Waterston 1979), and the type B genital appendage has been described in the Eurypterina (e.g. Waterston 1960; Waterston 1964; Størmer 1973) and Stylonurina (e.g. Kjellesvig-Waering 1966; Waterston 1979).

The morphological reconstruction of *Drepanopterus abonensis* (Text-fig. 1) represents a synthesis of all known fossil data, with the chelicerae reconstructed based on *Parastylonurus*, the most closely related taxon in which these structures are known. It differs from Simpson's (1951, fig. 3) reconstruction in several ways: the opisthosoma is shorter and the prosoma larger (it is possible that Simpson 'attached' a juvenile carapace to an adult opisthosoma to obtain his reconstruction), the morphology of appendage III has altered, a median ridge and oval lens overlying the lateral eyes are present on the carapace and the telson has a more clavate morphology. Most importantly, the metastoma is shown to be cleft posteriorly and setae-bearing blades are identified on the animal's appendages.

The average length of the animal was *c.* 40 cm, with most specimens (e.g. BGS GSM 84698, 84694, 84720; BRSUG 9960, 28610, 28846) indicating a total length of 39.5 cm. Some of the smaller specimens (BGS GSM 84718; BRSUG 28624) indicate an animal *c.* 34 cm long, while the largest (BRSUG 28840) was from an animal *c.* 51 cm long.

The carapace, evident in a number of specimens, is horseshoe-shaped with a broad marginal rim that narrows evenly posteriorly (Pl. 1, fig. 1; Pl. 3, fig. 2; Pl. 5, fig. 4). The marginal rim is devoid of pustules, instead ornamented with parallel striations. Several specimens (BGS GSM 84694, 84718; BMAG Cb4668) display the median ridge located anteriorly on the cardiac lobe (Pl. 1, fig. 1; Pl. 3, fig. 2). The median ocelli are raised on a single node at the anterior termination of this median ridge. The crescentic lateral eyes are positioned on reniform palpebral lobes, positioned on the downward inflection of the cardiac lobe, so that the lateral eyes had a wide lateral field of view. Furthermore, the lateral eyes and palpebral lobes were covered by an oval external lens (Pl. 3, fig. 2). The prosomal ventral plates are often split medially, as would be expected within moults, and appear to be of *Eurypterus* type (Pl. 1, figs 3, 5–6).

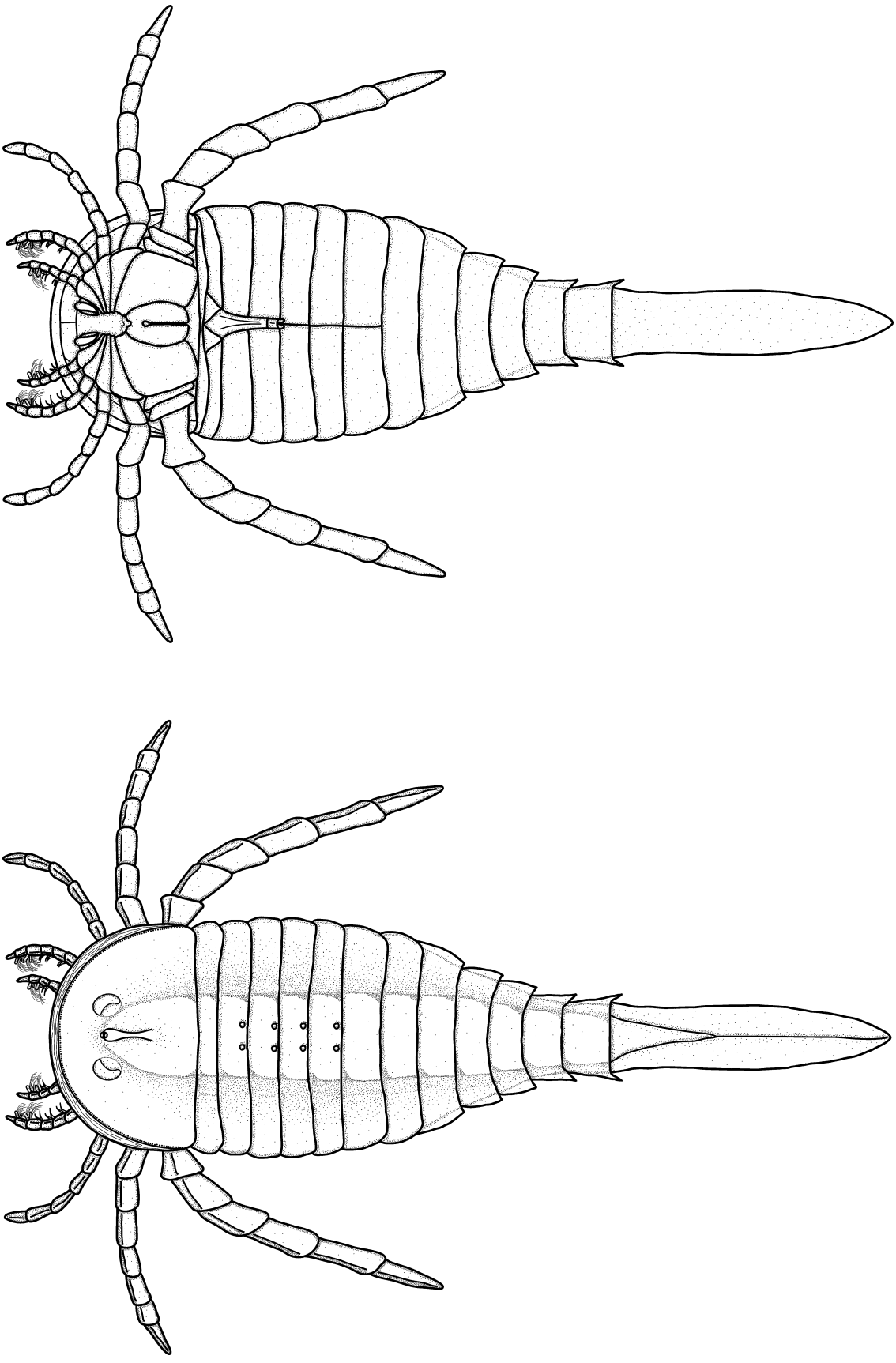
The most commonly preserved prosomal appendages are IV, V and VI. These are nonspiniferous and robust, with each podomere thickening distally. Appendages II and III are only represented by a few specimens; the most completely preserved appendage III (BGS GSM 84701) shows paired spines at the distal joint of podomeres 4–7 (Pl. 1, fig. 9), as in the *Hughmilleria*-type spiniferous appendage. The spines on the two distal podomeres appear to be longer and thicker, lacking the distal curve and end with a blunt termination. Specimen BRSUG 28857 preserves a blade with long setae (Pl. 7, fig. 1), the spine of which is of similar shape and size to those preserved on the appendage. As the distal portions of appendage III are more poorly preserved than the proximal parts, it is likely that these blunt spines represent the remains of blades; where blades are known in other eurypterids (i.e. *Woodwardopterus scabrosus*), they are present only on the distal podomeres.

One specimen (BGS GSM 84700) of the type A genital appendage preserves cuticular strips either side of the appendage on the median opercular plate (Pl. 1, fig. 11). Waterston (1979) described similar structures in *Parastylonurus* as homologous to the spatulae in adelophthalmoids (Størmer 1973).

The animal was deep-bodied down its centre, with the lateral edges flattened. The tergites had a pustule ridge along their anterior margin, lining the posterior edge of a smooth facet (Pl. 3, fig. 7). In life, the tergites would have articulated along this facet, with each tergite overlapping by 4–5 mm. This also accounts for some of the increased opisthosomal length in Simpson's reconstruction.

PALAEOECOLOGY

Drepanopterus abonensis resembles the Carboniferous sweep-feeders in having blades on its anterior appendages. The blades possessed large sensory setae, pits of which are seen on the blades in *Hibbertopterus* (Jeram and Selden 1994). *Drepanopterus*' mode of life was similar to the mycteropids and *Hibbertopterus*; however, the primitive nature of the blades and the lack of coxal laden indicate *Drepanopterus* to be a proto-sweep-feeder, less specialised than its Carboniferous relatives. The trace fossils *Cochlichnus* and *Diplocraterion* in beds 8 and 10 are evidence for an infaunal invertebrate fauna. *Drepanopterus* would have used the blades on its anterior appendages to rake through the substrate, the sensory setae feeling for worm-like invertebrates and phyllocarids or small fish and allowing *Drepanopterus*



TEXT-FIG. 1. Reconstruction of adult *Drepanopterus abonensis* in dorsal and ventral view; ×0.3.

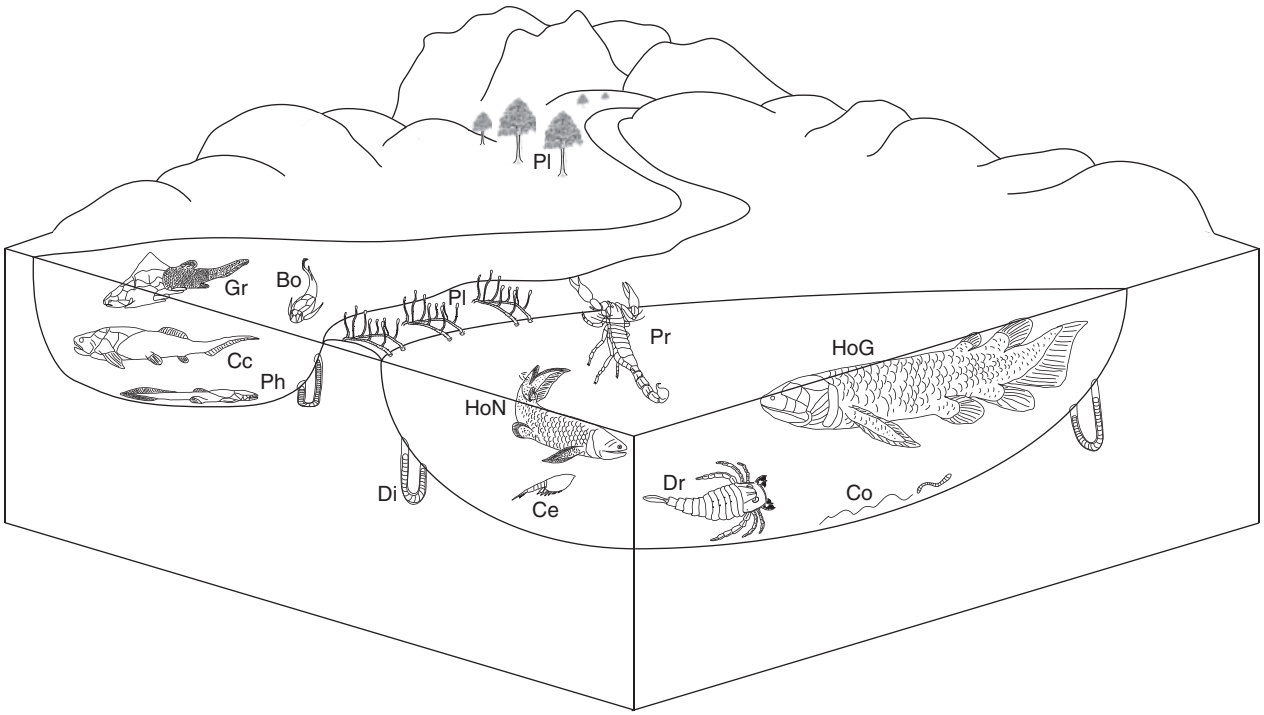
to capture them and drag them towards the chelicerae and coxae for processing. This feeding method is identical to that in *Hibbertopterus* and mycteropids while *Cyrtoctenus*, with its comb-like rachis, could have taken smaller prey such as ostracodes (Waterston *et al.* 1985).

The lateral eyes of *Drepanopterus* are placed on the downward inflection of the carapace, affording a wide lateral field of view. This is not typical of a predator, where an overlapping anterior field of view is advantageous. *Drepanopterus* would have hunted predominantly using the tactile function of its setae, and so the eyes were positioned to watch for predators. *Holoptychius* fish scales indicative of animals up to several metres long are found alongside *Drepanopterus*, and these would easily have taken an adult *Drepanopterus* as prey. Cuticle from the giant scorpion *Praearcturus* has also been found from bed 10, and this too would have been a possible predator on *Drepanopterus* (Text-fig. 2).

Drepanopterus bears paired tubercles on tergites 2–5. The function of these tubercles is unknown, they may have served as sites for sensory setae (Selden 1981) or prevented excessive cuticle abrasion (Braddy 1996). The holotype (BGS GSM 84696) displays tubercles on the tergites and rounded scars corresponding with their position on the sternites, so it is possible that they formed sites for muscle attachments, supporting the opisthosoma or possibly linked in some way to the respiratory system. The book-gills of eurypterids are located on ventral opisthosomal segments 2–5 (Braddy *et al.* 1999), corresponding with the location of the dorsal tubercles on *Drepanopterus*. It is, therefore, likely that these muscle attachment sites assisted the beating of the operculae. The respiratory area of *Limulus* increases drastically with size (Suzuki *et al.* 2008) and so extra muscle attachments may have been required in larger eurypterids, leading to the development of first tubercles and then ridges amongst the other hibbertopterids.

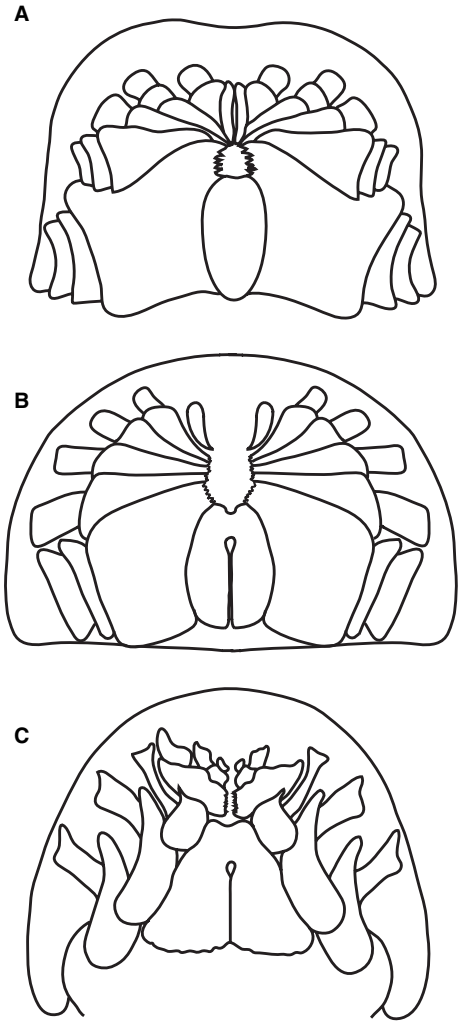
PHYLOGENETIC AFFINITIES

The intrarelationships of the hibbertopterids are contentious, with various genera considered by Jeram and Selden (1994) and Selden *et al.* (2005) to be ontogenetic gradients of others. Tollerton (1989) was mistaken in suggesting that the laden-bearing hibbertopterids lacked



TEXT-FIG. 2. Palaeoenvironmental reconstruction of the Late Devonian of Portishead. The most common fossils found within the river channels are the fish *Holoptychius nobilissimus* (HoN) and *Holoptychius giganteus* (HoG), which are also frequently found in isolated pools. Other fish occasionally present in the channel system include *Bothriolepis* (Bo), *Groenlandaspis* (Gr), *Coccosteus* (Cc) and *Phyllolepis* (Ph). *Drepanopterus abonensis* (Dr) is found alongside *Holoptychius* and cuticle fragments of the scorpion *Praearcturus* (Pr) within the pools. The phyllocarid crustacean *Ceratiocaris* (Ce) has also been reported from the site, along with the trace fossils *Cochlichnus* (Co) and *Diplocraterion* (Di), indicating a burrowing invertebrate fauna. Plant remains (Pl), derived from further upstream, are also found.

coxae, as both structures have been identified on specimens of *Hibbertopterus* (Jeram and Selden 1994, fig. 1) and *Megarachne* (Selden *et al.* 2005, fig. 1C). *Cyrtoctenus* appears to lack laden, although its bizarrely lobed coxae may represent a state whereby the laden have fused onto the coxae, while the state is unknown in other hibbertopterid genera. The laden are probably homologous to the epicoxa on appendages II–V of other Eurypterida (Laurie 1893); this would account for the lack of laden on appendage VI, as the epicoxa fused to form either the endostoma or metastoma (Braddy 1996; Tetlie and Braddy 2004). Laden can be found in some extant arachnid species, such as the scorpion *Heterometrus cyaneus*, where they suture onto the coxa and have a role in food mastication (Kästner 1925).

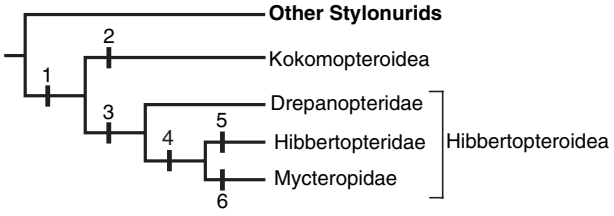


TEXT-FIG. 3. Variation in ventral prosoma structure between three species of eurypterid. A, *Eurypterus remipes*, with its rounded 'consolidated' metastoma. B, *Drepanopterus abonensis*, with its rounded cleft metastoma. C, *Hibbertopterus scouleri*, with its posteriorly expanded cleft metastoma. A and C redrawn from Waterston (1957).

The presence of a cleft metastoma in *Drepanopterus,* albeit with a different morphology to that of *Hibbertopterus* (expanded posteriorly, with an overall triangular outline), indicates that these structures are homologous. In *Drepanopterus*, the metastoma retains its oval outline as a transition between the consolidated rounded metastoma and the triangular cleft metastoma (Text-fig. 3). The hibbertopteroid sister group, the Kokomopteroidea, comprise eurypterids with a posterior notch in their metastoma, and it has been suggested that this notch is the precursor to the cleft metastoma (Tetlie 2008).

The overall morphology of *Drepanopterus abonensis*, therefore, infers a position at the base of the hibbertopterids. *Drepanopterus* shares several characters with the more basal Kokomopteroidea, including the clavate form of the telson and the median ridge on the carapace. Kokomopteroidea and Hibbertopteroidea are united by having podomeres that thicken distally and possibly circular calcareous lenses overlying the lateral eyes; these are present in *Hallipterus* and possibly *Kokomopterus*. If these lenses were present in *Kokomopterus* this indicates that overlying lenses is the plesiomorphic condition in Hibbertopteroidea and Kokomopteroidea, and similar lenses would be expected in *Tarsopterella* and *Hardieopterus*. Both of these taxa have similar shaped lateral eyes, and *Tarsopterella* has slight grooves around the lateral eyes that may infer the presence of overlying lenses. *Drepanopterus* clearly belongs within the hibbertopteroids, however, because of the presence of the cleft metastoma and the modified food capture spines on its anterior prosomal appendages (Text-fig. 4).

As well as sharing characters with the hibbertopteroid sister-group, as would be expected of a basal taxon, *Drepanopterus* also possesses characters found in the two



TEXT-FIG. 4. Cladogram showing the relationships of the Hibbertopteroidea. Numbered nodes denote character transitions. 1, Circular lenses overlying lateral eyes, podomeres thicken distally, median ridge present on carapace, telson clavate. 2, Metastoma notched posteriorly, prosomal appendage V spiniferous. 3, Metastoma cleft posteriorly, blades on anterior prosomal appendages. 4, Telson hastate with paired ventral keels, median ridge on carapace reduced, coxal laden present. 5, Appendage IV used in prey capture. 6, First opisthosomal tergite enlarged, second opisthosomal tergite expanded to form macrotergite.

other hibbertopteroid families, the Mycteropidae and the Hibbertopteridae. In several respects, it appears more closely related to the mycteropids, with a nonspiniferous appendage IV, more gracile prosomal appendages and longer body. The coxae are large and broad, as in *Megarachne*, but *Drepanopterus* appears to lack the laden found in the more derived species, although this could be preservational. The Hibbertopteridae have shortened podomeres and appendage IV is spiniferous and used in food capture. The median ridge on the carapace of both *Drepanopterus* and the mycteropids appears reduced in *Hibbertopterus* and *Cyrtoctenus*. The mycteropids, therefore, are probably a transitional stage between the more primitive *Drepanopterus* and the more derived Hibbertopteridae. However, the mycteropids are clearly separated from the other hibbertopteroids by their enlarged first tergite and parabolic-shaped carapace.

The inclusion of *Drepanopterus* within the Hibbertopteroidea makes this the longest-ranging stylonurid superfamily, including some of the youngest known eurypterid taxa. The Hibbertopteroidea were the only stylonurids to persist past the end-Devonian extinction. The reason for their survival might be linked to their sweep-feeding mode of life, which was not in direct competition with the more nektonic, more predatory Eurypterina and other (e.g. vertebrate and cephalopod) predators. With the amalgamation of Pangaea, the hibbertopteroids gained a more cosmopolitan distribution, representing the last major genus-level radiation within the Eurypterida (Tetlie 2007).

An ecological trend is also apparent throughout hibbertopteroid evolution. The Silurian *Drepanopterus pentlandicus* is known from marine strata (Anderson *et al.* 2007), as is the Early Devonian *Drepanopterus* sp. from Canada (Braddy and Dunlop 2000). *D. abonensis*, however, and the more derived hibbertopteroids, are known from fresh-water sediments (Jeram and Selden 1994), whereas *Megarachne* is from a terrestrial environment (Selden *et al.* 2005). Although most eurypterids are considered to be euryhaline (Braddy 2001), it is likely that there is a genuine trend towards fresh-water environments within this group.

This is reinforced by the dramatic size increase within the group. Chelicerates have haemocoelic solute concentrations very like marine water (Little 1983; Jeram 1989) and would struggle to maintain osmoregulation in fresh water. Large size would lessen these effects, as in living semi-terrestrial crabs, which increase in size towards the littoral environment (Tsai *et al.* 2000). The derived hibbertopterids are far larger than *Drepanopterus abonensis*, while *Drepanopterus pentlandicus* is approximately half this size.

A similar ecological trend is seen in adelophthalmoids (Tetlie and Poschmann 2008). This group also persists past the end-Devonian and is found in increasingly fresh-water environments throughout the late Palaeozoic. They do not show the corresponding size increase evident within the hibbertopteroids however, and this could be due, in part, to their continued predatory life habit, although all localities where adelophthalmoids have been reported to show some evidence of occasional marine influence.

SYSTEMATIC PALAEONTOLOGY

Subphylum CHELICERATA Heymons, 1901
Order EURYPTERIDA Burmeister, 1843
Suborder STYLONURINA Diener, 1924
Superfamily HIBBERTOPTEROIDEA Kjellesvig-Waering, 1959
(nom. trans. Waterston 1968)

Emended diagnosis. Stylonurina with posterior cleft on metastoma, round lenses overlying the lateral eyes and the anterior prosomal appendages II, III and occasionally IV modified for sweep-feeding.

Family DREPANOPTERIDAE Kjellesvig-Waering, 1966

Emended diagnosis. Small to medium Hibbertopteroidea with horseshoe-shaped prosoma and with broad marginal rim; nonspiniferous appendage IV; cuticular ornament pustular.

Remarks. Previous diagnoses of this family (e.g. Kjellesvig-Waering 1966; Poschmann and Tetlie 2004) were based on the appendage morphology and metastoma of '*Drepanopterus*' *bembycoides* [spelt *bembicoides* by Lamont (1955)], which possesses a podomere 7a on appendage VI, and as such belongs within the Eurypterina. The type species of *Drepanopterus*, *D. pentlandicus*, clearly belongs within the Stylonurina. The new diagnosis for Drepanopteridae presented here is, therefore, based solely on *D. pentlandicus* and *D. abonensis*. *Drepanopterus*(?) *lobatus* can only be separated from '*D*'. *bembycoides* by the presence of lobate epimera on the postabdomen, and possibly represents a sexual dimorph. These may both be junior synonyms of *Nanahughmillera*? *conica*, another eurypterid from the same locality in need of redescription but is probably a basal member of the Eurypterina, similar to *Moselopterus* (Tetlie 2000). *Drepanopterus*(?) *nodosus* is a poorly known taxon, which presently defies classification. These taxa should be removed from the genus, pending redescriptions. It is also worth noting that the *Drepanopterus* type of prosomal appendage (Tollerton 1989, fig. 8.4) is not found in either *D. pentlandicus* or *D. abonensis* but is on '*D*'. *bembycoides* and *D.*(?) *lobatus*.

TABLE 1. Taxa previously assigned to the genus *Drepanopterus* and their current assignment.

Taxa	Age and Locality	Assignment and Notes	References
D. abonensis	Devonian, England	*Drepanopterus*	Simpson 1951
D. bembycoides	Silurian, Scotland	Basal Eurypterina; Possible synonym of *Nanahughmilleria* (?) *conica*	Laurie 1899; Tetlie 2004, 2007
D. lobatus	Silurian, Scotland	Sexual dimorph of *D. bembycoides;* Identical to *D. bembycoides* except for the lobate epimera	Laurie 1899; Tetlie 2004
D. longicaudatus	Silurian, USA	*Kokomopterus*	Clarke and Ruedemann 1912; Kjellesvig-Waering 1966
D. nodosus	Silurian, USA	Basal Eurypterina; The holotype and paratype are undiagnostic.	Kjellesvig-Waering and Leutze 1966; Tetlie 2004, 2007
D. pentlandicus	Silurian, Scotland	*Drepanopterus;* Type species	Laurie 1892
D. ruedemanni	Ordovician, USA	Lithic Clast	O'Connell 1916; Tollerton 2004
D. struvei	Devonian, Germany	*Vinetopterus*	Størmer 1974; Poschmann and Tetlie 2004
D. sp.	Devonian, Canada	*Drepanopterus*	Braddy and Dunlop 2000

Genus DREPANOPTERUS Laurie, 1892

Type species. Drepanopterus pentlandicus Laurie, 1892.

Emended diagnosis. Drepanopteridae with crescentic lateral eyes; prosomal appendages II–III spiniferous, modified *Hughmilleria*-type; prosomal appendages IV–VI nonspiniferous *Kokomopterus*-type; cuticle displays pustular ornamentation with paired medial tubercles on tergites 2–5 (emended from Størmer 1974).

Remarks. Eight different species have been assigned to this genus (Table 1). Of these, only the type species *Drepanopterus pentlandicus*, and *Drepanopterus abonensis*, can be assigned to this genus with any confidence.

A specimen assigned to *Drepanopterus* sp., from Arctic Canada (Braddy and Dunlop 2000), consists of an isolated prosoma and telson and shares many characters with *D. abonensis*; however, it differs in having a serrate margin to its telson, suggesting it could be a different species, representing the only *Drepanopterus* outside the UK and spanning the temporal gap between *D. pentlandicus* and *D. abonensis*.

Blades and a posteriorly cleft metastoma bearing an anterior notch have been identified in *D. abonensis*; however, these are currently unknown in *D. pentlandicus*.

Drepanopterus abonensis Simpson, 1951

Material. Holotype: BGS GSM 84694, prosoma and metasoma. Paratypes: BGS GSM 84695-84707, 84718-84720. Additional Material: BMAG Cb3988, Cb4668, BRSUG 9955-9965, 28610-28655, 28830-28866.

Horizon and locality. All specimens were collected from the sole locality; Bed 10, Woodhill Bay Section (cliff 100 m south of Woodhill Bay), Late Devonian (Famennian), Upper Old Red Sandstone, of Portishead, Somerset. Specimens BGS GSM 8694-84707, GSM 84718-84720, BRSUG 9955–9965, 28610–28655 and BMAG Cb3988 and Cb4668 were collected by Fry during the 1950s. BRSUG 28859–28861 were collected by Long during the 1970s, and BRSUG 28830–28858 and 28862–28863 were collected by Tetlie in 2004.

Emended diagnosis. Drepanopterus with a lanceolate, almost clavate telson; crescentic lateral eyes raised on reniform

TABLE 2. Dimensions of all known carapace specimens in mm.

Specimen	Length	Width at base	Margin width	Eye length	Eye width
BGS GSM 84694	76	102	4	12	10
BGS GSM 84695	63*	60*	4	12	10
BGS GSM 84696	40*	57*	4	–	–
BGS GSM 84697	52*	82*	4	12	10
BGS GSM 84698	72	95*	5	–	–
BGS GSM 84699	50*	13*	–	–	–
BGS GSM 84718	61	87	5	12	9
BMAG Cb3988	66	85*	5	12	7
BMAG Cb4668	70	100*	6	12	12
BRSUG 9958	74	107	6	13	12
BRSUG 9961	–	–	4	11	7
BRSUG 28614	59*	77*	5	–	–
BRSUG 28627	–	–	5	12	9
BRSUG 28631	65	44*	4	12	7
BRSUG 28632	65*	82*	6	14	10
BRSUG 28633	68*	54*	5	12	9
BRSUG 28634	54*	70*	4*	12	10
BRSUG 28635	79	93	6	16	12
BRSUG 28636	35*	40*	6	12	9
BRSUG 28830	76	98	6	13	11
BRSUG 28833	–	–	6	12	10
BRSUG 28859	56*	32*	4	7	7

Asterisks indicate incomplete measurements.

palpebral lobes with median ridge running down centre of carapace; metastoma cleft posteriorly with anterior notch; prosomal appendages II and III bearing blades.

Description. Twenty relatively complete carapaces have been described and measured (Table 2) and 40 opisthosomal segments (Table 3). Those specimens that are not well preserved are detailed separately (Table 4).

BGS GSM 84694 (Holotype). Part and counterpart of carapace and preabdomen (Pl. 1, figs 1–2). Marginal rim consists of parallel striations, whereas rest of carapace is covered in pustular ornament. In centre of carapace is raised cardiac lobe, *c.* 26 mm wide, with poorly preserved median ridge. Lateral eyes set on reniform palpebral lobes, positioned centrimesially on carapace, 22 mm apart. Ocellar node present in centre of carapace, 3 mm in diameter, located at anterior of median ridge. Tergites 2 and 3 have paired tubercles 2 mm from posterior margin, 4 mm in diameter, spaced 10 mm apart. A smooth articulating facet is preserved along their anterior margins, 3–4 mm wide, with a pustule ridge along its posterior edge. Tergite 4 is fragmentary, revealing three partial sternites with a

TABLE 3. Dimensions of all known opisthosoma specimens in mm.

Specimen	1	2	3	4	5	6	7	8	9	10	11	12	Telson
BGS GSM 84694	14/105	18/109	22/115*	25/112*	25/120*	22/–	–	–	–	–	–	–	–
BGS GSM 84695	14/–	15/–	–	–	–	–	–	–	–	–	–	–	–
BGS GSM 84698	17/98*	20/–	–	–	–	–	–	–	–	–	–	–	–
BGS GSM 84707	16/120	18/120	22/119	24/117	24/115	25/110	20/103	23/92	24/80	35/68	32/55	32*/46	–
BGS GSM 84718	14/87	16/91	17/–	18/–	–	–	–	–	–	–	–	–	–
BGS GSM 84719	–	22/–	22/–	22/–	20*/–	22/–	20/–	–	–	–	–	–	–
BGS GSM 84720	–	–	–	–	–	–	–	–	–	–	–	34/43	115/23
BMAG Cb4668	12/108	14/117	15/116	15/112	13/108	13/102	14/95	15/–	15/–	16/–	20/52	30/35	36*/30
BRSUG 9955	–	–	–	–	–	–	–	–	–	–	–	26/40	130/31
BRSUG 9960	–	–	–	22/80*	22/72*	18/68*	–	–	–	–	–	–	–
BRSUG 9961	13/67*	16/89*	22/106	21/80*	22/83*	22/113	20/96	16/71	–	–	–	–	–
BRSUG 9963	–	–	–	–	–	–	–	15/42*	20/78	24/68	25/59	30/50	22*/35
BRSUG 28610	–	–	–	–	20/–	20/–	10*/–	18/–	–	–	–	–	–
BRSUG 28611	–	–	25/–	22/–	22/–	20/–	20/–	24/–	20/–	–	–	–	–
BRSUG 28613	–	–	–	–	–	–	–	22*/–	26/–	31/–	32*/–	–	–
BRSUG 28614	14/–	15/86	20/88*	22/98*	22/110	22/–	20/–	20/–	21/–	21/60	22/50	36/45	41*/36
BRSUG 28617	–	–	–	21/–	22/–	21/–	22/–	18/–	22/–	20/–	–	–	–
BRSUG 28620	–	–	–	–	–	–	–	–	23/72	25/64	–	–	–
BRSUG 28623	–	–	–	–	–	–	–	16*/–	20/–	21/–	–	–	–
BRSUG 28624	–	–	–	–	20/–	25/–	22/–	15/–	19/–	–	–	–	–
BRSUG 28630	–	–	–	–	–	–	–	–	–	22/–	32/–	–	–
BRSUG 28633	–	–	–	–	–	–	–	19/–	19/–	19/–	19/–	–	–
BRSUG 28637	–	–	–	–	–	–	17/–	17/–	19/–	18/–	22/–	32/–	–
BRSUG 28641	–	–	–	–	–	–	27/–	22/–	26/–	25/–	30/–	20*/–	–
BRSUG 28642	–	–	–	–	–	–	–	–	–	–	–	–	43*/34*
BRSUG 28644	18/–	22/118	22/120	26/114*	22/118	22/95*	–	–	–	–	–	–	–
BRSUG 28645	–	–	22/127	–	–	–	–	–	16/75	23/70	23/–	36/35	42*/32
BRSUG 28830	12/98	13/110	16/110	–	–	–	–	–	–	–	–	–	–
BRSUG 28831	–	23/89*	24/89*	22/89*	23/89*	–	–	–	–	–	–	–	–
BRSUG 28840	–	–	–	–	–	–	–	–	–	–	–	–/54	–/40
BRSUG 28843	–	–	–	–	–	22/–	22/–	20/–	–	–	–	–	57*/14*
BRSUG 28844	–	–	–	–	–	–	–	–	–	–	–	–	95*/18*
BRSUG 28845	–	–	–	–	–	22/–	26/–	–	–	–	–	–	–
BRSUG 28846	–	–	–	–	–	–	–	–	–	–	–	22/43	46*/33
BRSUG 28850	–	–	–	–	–	–	–	–	–	–	–	–	91*/15*
BRSUG 28853	–	–	–	–	–	–	–	–	–	–	–	–	33*/–
BRSUG 28854	–	22/–	23/–	29/124*	25/128	–/105*	–	–	–	–	–	–	–
BRSUG 28855	–	–	–	–	–	–	–	–	–	–	–	–	92*/10*
BRSUG 28856	–	–	–	–	–	–	–	23/90	79/24	–	–	–	–
BRSUG 28862	–	–	–	–	–	–	–	–	–	–	–	–	69*/17*

Tergite numbers are listed at the top of the columns.
Asterisks indicate incomplete measurements.

TABLE 4. Poorly preserved specimens.

Specimen	Description	Length	Width
BRSUG 9959	Cuticle fragment, warped, rim 3 mm from lateral edge	28	28
BRSUG 9964	Cuticle fragment	33	43*
BRSUG 9965	Cuticle fragment	35	42*
BRSUG 28615	Seven tergites, pustule ridge after each tergite joint	–	–
BRSUG 28616	Partial carapace, marginal rim 5 mm wide	45*	81*
BRSUG 28618	Carapace preserving lateral eye and tergite rims	–	–
BRSUG 28619	Sternite. Ornament granular	22	112*
BRSUG 28622	Fragment of appendage V	72	10
BRSUG 28623	Three postadbominal segments displaying epimera	–	–
BRSUG 28624	Part and counterpart of five tergites	–	–
BRSUG 28625	Sternite	29	98*
BRSUG 28626	Edges of tergites	38	–
BRSUG 28627	Partial carapace, single lateral eye preserved	–	–
BRSUG 28628	Two tergites	15/16	–
BRSUG 28630	Two postabdominal segments, showing epimera, pustular ridge 4 mm from segment anterior	–	–
BRSUG 28632	Partial carapace, pustular ornamentation and single lateral eye	–	–
BRSUG 28636	Partial carapace, ridge of pustules around inner fringe of marginal rim	–	–
BRSUG 28637	Part and counterpart of six postabdominal segments. Epimera present	–	–
BRSUG 28638	Part and counterpart of three tergites	19/17/15	–
BRSUG 28640	Tergite	20	–
BRSUG 28646	Tergite	22	–
BRSUG 28649	Distal portion of prosomal appendage	64	–
BRSUG 28652	Prosomal appendage fragment	32	12
BRSUG 28653	Prosomal appendage fragment, keeled down centre	34	16
BRSUG 28655	Two tergites	24/25	–
BRSUG 28832	Partial carapace, marginal rim 6 mm wide	79*	84*
BRSUG 28833	Partial carapace and single lateral eye	–	–
BRSUG 28834	Partial carapace and single lateral eye	–	–
BRSUG 28835	Partial carapace, marginal rim 4 mm wide	26*	52*
BRSUG 28836	Prosomal appendage fragment, probably IV. Podomeres keeled	38*	7
BRSUG 28837	Partial carapace. Lateral eyes indistinct, marginal rim 4 mm wide	63*	54*
BRSUG 28849	Fragment of podomere, raised along one edge	–	22
BRSUG 28851	Tergite fragments. One edge rounded, indicating preabdominal tergite	35	–
BRSUG 28852	Cuticle fragment. Dappled tuberculate ornament, possibly *Praearcturus*	33	26
BRSUG 28853	Telson fragment.	–	–
BRSUG 28860	Part and counterpart of two preabdominal tergites	15/15	–
BRSUG 28861	Part and counterpart of tergite	23	–
BRSUG 28864	Tergite, warped	22	–
BRSUG 28865	Sternite, no ornamentation	29	55*
BRSUG 28866	Possible tergite	31	–

Dimensions are given in mm.
Asterisks indicate incomplete measurements.

EXPLANATION OF PLATE 1

Figs 1–12. *Drepanopterus abonensis* Simpson, 1951. 1, BGS GSM 84694. Holotype. Carapace, four tergites and three sternites; ×0.35. 2, BGS GSM 84696. Counterpart. Carapace and first two tergites; ×0.35. 3, BGS GSM 84695. Paratype. Carapace showing ventral sutures with parts of two tergites; ×0.7. 4, BGS GSM 84698. Paratype. Carapace with metastoma and coxae faintly preserved; ×0.5. 5, BGS GSM 84696. Paratype. Ventral prosomal plate displaying sutures; ×0.5. 6, BGS GSM 84697. Paratype. Ventral prosomal plate displaying sutures; ×0.65. 7, BGS GSM 84699. Paratype. Ventral prosomal plate displaying sutures; ×0.65. 8, BGS GSM 84699. Counterpart. Ventral prosomal plate displaying sutures; ×0.65. 9, BGS GSM 84701. Paratype. Prosomal appendage III, preserving proximal spines and distal blades; ×0.9. 10, BGS GSM 84703. Paratype. Central podomeres of prosomal appendage; ×0.4. 11, BGS GSM 84700. Paratype. Coxa and proximal podomeres of appendage VI, genital operculum and genital appendage; ×0.5. 12, BGS GSM 84698. Paratype. Pretelson and telson base; ×0.45.

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raised ridge running down the centre; sternites 4 and 5 have paired circular impressions corresponding to tergite tubercle positions.

BGS GSM 84695 (Paratype). Carapace displaying ventral marginal prosomal plate with two sutures and left lateral eye (Pl. 1, fig. 3) located 18 mm from the lateral edge. The outermost suture is 4 mm from lateral edge and curves up to the marginal rim. The inner suture is 9 mm from lateral edge and curves around the anterior of the eye. Two tergite fragments are preserved beneath.

BGS GSM 84696 (Paratype). Ventral marginal prosomal plate displaying two ventral sutures (Pl. 1, fig. 5). One suture meets the lateral margin anteriorly, while the other curves around the front of the carapace; both converge posteriorly 2 mm apart and 5 mm from lateral carapace margin.

BGS GSM 84697 (Paratype). Ventral marginal prosomal plate displaying two ventral sutures (Pl. 1, fig. 6); inner suture 4 mm from posterior margin, upper suture begins 2 mm from lower suture then curves up to meet lateral carapace edge. Almost complete carapace preserved on specimen reverse, pustular ornament well preserved, including pustular ridge around posterior of marginal rim. Lateral eyes poorly preserved, 23 mm apart, 18 mm from anterior margin. Cardiac lobe increases in width to 35 mm posteriorly along carapace. Ocellar node between eyes, 22 mm from anterior margin.

BGS GSM 84698 (Paratype). Prosoma including partially preserved metastoma and coxae, three articulated fragmentary tergites, and a well-preserved pretelson and proximal portion of telson (Pl. 1, figs 4, 12). Carapace marginal rim has a ridge of pustules 1 mm wide posterior to it. Lateral eyes poorly preserved. Metastoma preserved in life position, 46 mm from anterior carapace margin and 40 mm from each lateral edge. Metastoma well-preserved anteriorly, with a 4 mm long and 2 mm wide notch, 20 mm wide at its broadest point around the mid-third and posterior two thirds poorly preserved. Length of metastoma 26 mm, 14 mm wide at its base, cleft 15 mm posteriorly and 1.5 mm wide. Cleft may terminate in rounded hollow, but here preservation is the poorest. Margins of metastoma rounded with a slight 1 mm rim. Coxae of appendage VI preserved alongside, right coxa almost whole, 28 mm long and 20 mm wide. Tergite 1 poorly preserved, lacking tubercles. Tergite 2 incomplete, clearly displays paired tubercles, 3 mm in diameter, 4 mm from posterior margin and with pustular ridge along anterior margin. Tergite 3 incomplete but shows pustulation and pustular ridge along the join with the preceding tergite. Tergite 4 poorly preserved and mostly lost. Telson and pretelson preserved alongside. Telson keeled down centre, width narrows by 2 mm every 10 mm of length and preserved proximal portion indicates a clavate shape.

BGS GSM 84699 (Paratype). Part and counterpart of ventral marginal prosomal plate showing two sutures (Pl. 1, figs 7–8). Sutures converging posteriorly, from 2 mm apart and 3 mm from anterior margin the anterior suture curves up to intersect with the doublure, posterior suture curves in parallel with posterior margin.

BGS GSM 84700 (Paratype). Genital operculum and proximal portions of genital appendage, coxa VI and proximal podomeres of appendage VI (Pl. 1, fig. 11; Text-fig. 5A). Coxa missing gnathobase, 20 mm long and 26 mm wide. Equal-sized structure alongside could be corresponding left coxa, incomplete and dislocated from its life position. VI-2 is 6 mm long, 5 mm wide proximally and 17 mm distally. VI-3 is 4 mm long and 15 mm wide. VI-4 is 39 mm long, 10 mm wide expanding to 13 mm distally and grooved medially 4 mm from posterior margin. Partial VI-5 attached. Genital operculum partially preserved on left side, entirely on right. Right ala of operculum 24 mm long, 52 mm wide and split into two plates; median plate 10 mm long and posterior plate 14 mm long. Anterior of operculum preserves very thin (4 mm) cuticle section hinting at a third plate anterior to the two main plates. Deltoid plates 10 mm long and 8 mm wide on median plate, preserved either side of genital appendage. Genital appendage likely type A, 8 mm wide proximally at posterior plate joint and 14 mm wide distally, with a preserved length of 30 mm. Zipfel divided longitudinally into three segments, outer two 4 mm wide and inner segment 6 mm wide. Alongside genital appendage two structures preserved, each 4 mm wide, running length of posterior opercular plate. Right structure better preserved, however appears to be detached. These probably represent spatulae.

BGS GSM 84701 (Paratype). Appendage III consisting of seven podomeres and associated spines (Pl. 1, fig. 9; Text-fig. 5B). First preserved podomere (probably III-2) 8 mm long and 10 mm wide, with a medial ridge 2 mm from posterior margin. III-3 is 10 mm long and 8 mm wide, again with ridge. III-4 is 6.5 mm long and 8 mm wide with ridge 1 mm from posterior edge. III-4 spine preserved at distal joint, 4 mm long and 1 mm wide, slightly curved and narrowing evenly towards tip. Another disarticulated spine preserved alongside, again 4 mm long and 1 mm wide; probably, represents other spine

EXPLANATION OF PLATE 2

Figs 1–6. *Drepanopterus abonensis* Simpson, 1951. 1, BGS GSM 84704. Paratype. Genital operculum preserving anterior opercula plate; ×0.8. 2, BGS GSM 84705. Paratype. Sternite with central divide; ×0.7. 3, BGS GSM 84707. Paratype. Almost complete opisthosoma. Tergites 4–7 have been partially reconstructed; ×0.4. 4, BGS GSM 84702. Paratype. Carapace with prosomal appendages III-VI; ×0.7. 5, BGS GSM 84706. Paratype. Sternite with central divide; ×0.85. 6, BGS GSM 84707. Counterpart. Three tergites bearing tubercles; ×0.7.

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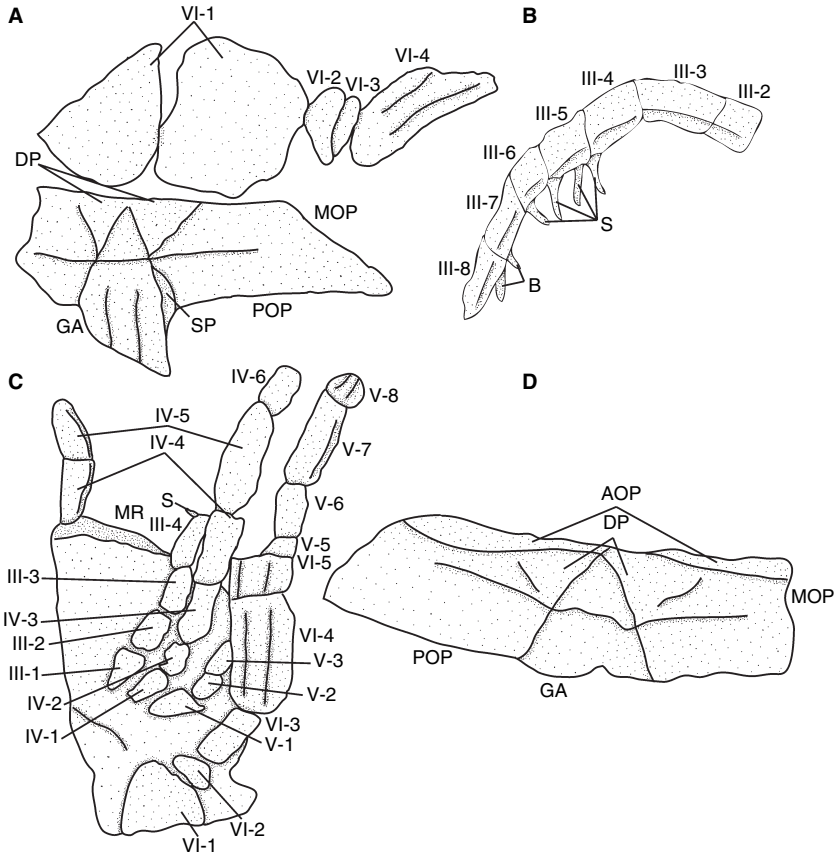

TEXT-FIG. 5. *Camera lucida* drawings of *Drepanopterus* specimens. A, BGS GSM 84700, genital operculum and proximal podomeres of appendage VI; ×0.45. B, BGS GSM 84701, appendage III; ×1. C, BGS GSM 84702, appendages III–VI with partially preserved carapace; ×0.8. D, BGS GSM 84704, genital operculum preserving anterior opercular plate; ×0.65. Abbreviations: DP, Deltoid Plate; AOP, Anterior Opercular Plate; MOP, Median Opercular Plate; POP, Posterior Opercular Plate; GA, Genital Appendage; SP, Spatulae; MR, Marginal Rim; B, Blade and S, Spine.

in pair. III-5 is 8 mm long, 7 mm wide, again with ridge, distal spine 1.5 mm wide and 6.5 mm long, curving distally and narrowing evenly towards tip. III-6 is 5.5 mm long and 5.5 mm wide with a ridge 0.5 mm from posterior margin, distal spine 1.5 mm wide and 5.5 mm long, appears less curved than the others. III-7 is 9.5 mm long and 4 mm wide, distal spine 1.5 mm wide and 5.5 mm long and lacking curvature. Another spine, 2 mm wide and 6 mm long, preserved alongside. III-8 is 3 mm wide and 10 mm long and is narrowing evenly to a blunt termination. The last two pairs of spines are unusual as they are relatively broad and blunt.

BGS GSM 84702 (Paratype). Left prosomal appendage IV and right prosomal appendages III, IV, V and VI, in various stages of completeness (Pl. 2, fig. 4; Text-fig. 5C). Section of deformed carapace preserved, showing pustular ornamentation and a 3 mm wide marginal rim. Appendages projecting anteriorly. On left side of carapace is appendage IV. Two podomeres preserved; proximal podomere 17 mm long before obscured under carapace, 10 mm wide, with ridges 1 mm from either margin. Distal podomere is 15 mm long, 10 mm wide narrowing to 8 mm distally, again with ridges. Third partially preserved podomere is seen. On right side of carapace three appendages are preserved. Appendage III consisting of coxa and four podomeres. Coxa 12 mm long and 8 mm wide narrowing proximally into gnathobase. III-2 is 10 mm long and 8 mm wide. III-3 is 9 mm long and 8 mm wide, as is III-4. III-5 is 8 mm long and 6 mm wide with spine preserved at distal joint; spine 7 mm long and 1 mm wide, narrowing evenly towards tip. Appendage IV consisting of coxa and four podomeres. Coxa 12 mm long and 8 mm wide and is narrowing towards gnathobase. IV-2 fragmented, largest section 13 mm long and 10 mm wide. IV-3 is 17 mm long, 8 mm wide proximally and 9 mm distally, with a ridge along each lateral edge and a central keel. IV-4 is 19 mm long, 7 mm

EXPLANATION OF PLATE 3

Figs 1–8. *Drepanopterus abonensis* Simpson, 1951. 1, BGS GSM 84718. Paratype. Carapace and four tergites; ×0.7. 2, BMAG Cb4668. Relatively complete specimen consisting of carapace with appendages IV and VI and opisthosomal segments 1–12; ×0.5. 3, BMAG Cb3988. Carapace with appendages III, IV and V; ×0.45. 4, BRSUG 9957. Podomeres from appendage VI; ×1.5. 5, BRSUG 9957. Podomeres from appendage V and VI; ×1.5. 6, BRSUG 9957. Counterpart; ×1.5. 7, BGS GSM 84719. Paratype. Opisthosomal segments; ×0.5. 8, BGS GSM 84720. Paratype. Telson and fragments of pretelson; ×0.55.

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wide thickening to 9 mm distally with lateral ridges and a central keel. IV-5 is 14 mm long, 7 mm wide narrowing to 5 mm distally with lateral ridges. Appendage V, consisting of coxa and five podomeres, partially obscured by appendage VI. Coxa V 12 mm long and 10 mm wide, narrowing towards gnathobase. V-2 is 9 mm long and 10 mm wide. V-3 largely obscured by appendage VI. V-4 is 29 mm long and 9 mm wide, with median keel and ridges 1 mm from each lateral edge. V-5 is 24 mm long, 7 mm wide expanding to 9 mm distally, with lateral ridges and a central keel. V-6 preserved length 8 mm long and 6 mm wide. Appendage VI consisting of coxa and five podomeres. Coxa and first three podomeres poorly preserved, lacking shape and often lateral edges. Coxa VI is 40 mm long and 38 mm wide. VI-2 is 5 mm long and 14 mm wide. VI-3 is 5 mm long and 12 mm wide. VI-4 is 12 mm wide expanding to 18 mm distally and 34 mm long. VI-5 is 38 mm long and 16 mm wide, with ridges 2 mm from each lateral edge. VI-6 fragmented with incomplete length, 8 mm long and 16 mm wide.

BGS GSM 84703 (Paratype). Podomeres 3 and 4 from appendage IV (Pl. 1, fig. 10). IV-3 length incomplete, 22 mm long and 8 mm wide expanding to 11 mm distally. IV-4 is 20 mm long, 8 mm wide. IV-5 also present but poorly preserved. All podomeres display pustular ornamentation.

BGS GSM 84704 (Paratype). Genital operculum and proximal section of type A genital appendage (Pl. 2, fig. 1; Text-fig. 5D). Operculum 18 mm long, left ala 52 mm wide and is giving a total width of 104 mm. Divided into three plates; anterior plate 4 mm long, median plate 8 mm long and posterior plate 10 mm long. Grooves separating median and posterior plates not entirely preserved, ceasing on left side after 20 mm. Deltoid plates not preserved, although faint groove rising up from central plate joint may represent this. Type A genital appendage 10 mm wide proximally at median-posterior plate joint, 17 mm wide distally.

BGS GSM 84705 (Paratype). Sternite (Pl. 2, fig. 2), divided down centre, 19 mm long, 54 mm wide from mid-line and is reconstructed total width 108 mm. Sternite surface mostly smooth, sometimes granular.

BGS GSM 84706 (Paratype). Sternite (Pl. 2, fig. 5), divided down centre. 26 mm long, 50 mm wide from central divide, total reconstructed width 100 mm. Edges of sternite rounded. Smooth ornamentation sometimes with granular texture.

BGS GSM 84707 (Paratype). Part and partial counterpart of opisthosoma (Pl. 2, figs 3, 6). First tergite poorly preserved, tergites 4–7 partially preserved and pretelson faintly preserved. Tergites 2–5 bear paired tubercles 3 mm in diameter, centre concave, 9 mm apart and 4 mm from tergite posterior edge. Pustular ornamentation apparent throughout, including ridge 4 mm from anterior margin with smooth anterior articulation facet.

BGS GSM 84718 (Paratype). Carapace and first four tergites of opisthosoma (Pl. 3, fig. 1). Carapace marginal rim narrows evenly posteriorly. Lateral eyes placed centrimesially at either side of median ridge. Cardiac lobe raised with median ocelli on node between lateral eyes. Tergite 1 telescoped into carapace. Tergite 3 telescoped into tergite 4. Tergites 2–5 preserve paired tubercles 3 mm in diameter, 10 mm apart, 4 mm from posterior margin. Pustular ridge also present 3 mm from anterior rim of each tergite.

BGS GSM 84719 (Paratype). Preabdominal tergites 2–7 (Pl. 3, fig. 7) preserved as internal mould. Total tergite widths unknown. Tergites overlap along smooth anterior facet. Tergite 2 displays pustular ornamentation and paired tubercles 3 mm in diameter, separated by 9 and 5 mm from posterior margin. Tergite 3 displays pustular ornamentation and tubercles, with pustular ridge 4 mm from anterior margin, after which ornamentation is smooth. Tergite 4 displays pustular ornamentation and pustular ridge, paired tubercles again present. Tergite 5 broken off anteriorly from pustular ridge. Rest of pustular ornamentation evident, paired tubercles again present. Tergite 6 disarticulated from fifth and lies at 45 degree angle to it. Lacks tubercles and displays pustular ornament with anterior pustular ridge. Tergite 7 partially preserved, has pustular ornamentation and anterior pustular ridge.

BGS GSM 84720 (Paratype). Pretelson and telson (Pl. 3, fig. 8). Pretelson bears epimera. Telson appears clavate, being narrow and keeled. Twenty three millimeters wide at base, narrowing evenly for 50 mm before widening slightly then narrowing to termination. Tergite fragment preserved alongside telson; 23 mm long, pustular ridge 3 mm before anterior edge. Scales preserved, acicular and pointing posteriorly. Scales 1–2 mm in width.

BCM Cb3988. Prosoma and proximal parts of three appendages (Pl. 3, fig. 3). Carapace marginal rim narrowing towards base. Single (left) lateral eye lobe poorly preserved and located centrimesially. Prosoma surface deformed, fossil partially preserved in 3D with hint of cardiac lobe and median ridge. Appendage II faintly present on anterior of carapace. Overall length 25 mm, five podomeres preserved. II-3 is 5 mm wide and 7 mm long. II-4 is 4 mm wide and 5 mm long. II-5 is 4 mm wide, 6 mm long. II-6 is 4 mm wide and 4 mm long. II-7 is 2 mm wide and

EXPLANATION OF PLATE 4

Figs 1–8. *Drepanopterus abonensis* Simpson, 1951. 1, BRSUG 9961. Poorly preserved carapace and opisthosomal segments; ×0.4. 2, BRSUG 9956. Podomeres; ×1.7. 3, BRSUG 28610. Tergites bearing tubercles; ×0.65. 4, BRSUG 9963. Mould of postabdominal segments; ×0.45. 5, BRSUG 9963. Counterpart. Cast of postabdominal segments; ×0.45. 6, BRSUG 28614. Postabdomen and telson; ×0.75. 7, BRSUG 9955. Pretelson and telson; ×0.35. 8, BRSUG 9955. Counterpart; ×0.35.

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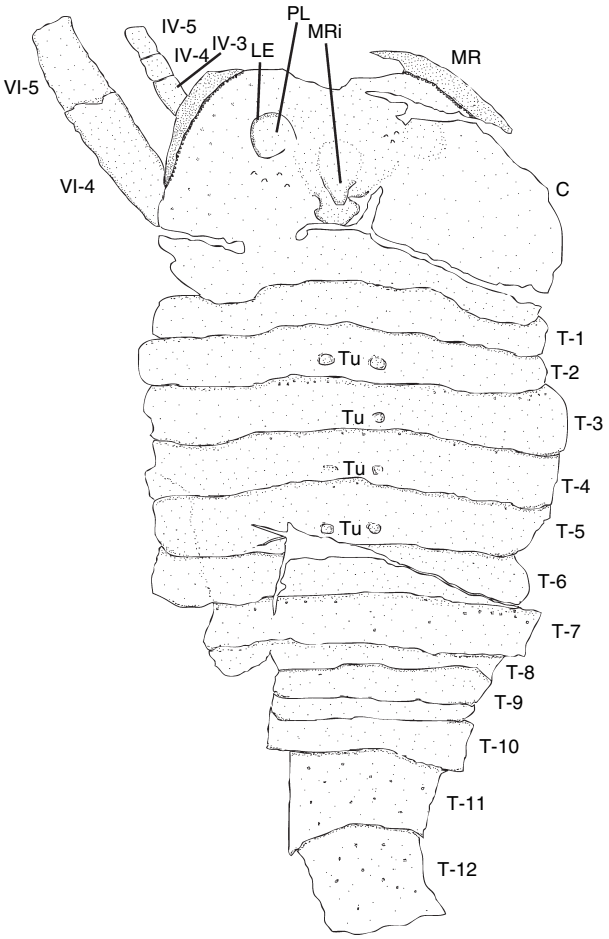
3 mm long. No spines preserved. Three podomeres of appendage IV preserved; IV-3 preserved length 5 mm, 7 mm wide. IV-4 is 16 mm long, 8 mm wide, displaying pustular ornamentation. IV-5 angling down underneath appendage V, 7 mm wide and preserved length 12 mm. Appendage V protrudes from beneath carapace, coxa also faintly preserved. Coxa V is 20 mm long, 10 mm wide narrowing to 2 mm at gnathobase. V-2 is 27 mm long and 6 mm wide, thickening distally to 8 mm. Pustular ornamentation along edge of podomere. V-3 is 8 mm wide and grooved longitudinally, preserved length 15 mm. Single tergite preserved at prosoma base; 13 mm long, pustular ornamentation evident.

BCM Cb4668. Prosoma with two prosomal appendages and articulated opisthosoma missing telson (Pl. 3, fig. 2; Text-fig. 6). Specimen total length 280 mm. Carapace marginal rim narrowing evenly towards base, line of pustules marking inner limit. Semi-lunate and acicular scales preserved around lateral eyes, each scale 1 mm wide. Pustular ornamentation mostly towards carapace margins. Left lateral eye on reniform palpebral lobe centrimesially positioned. Lobe surrounded by faint oval impression indicating overlying lens. Right eye more poorly preserved. Lateral eyes 22 mm apart. Between lateral eyes on anterior of cardiac lobe lies dark-stained median ridge, 22 mm long and 16 mm wide, narrowing posteriorly to 4 mm. Median ocelli probably associated with anterior termination of ridge. Two articulated podomeres of appendage VI on left side of carapace. Intersects with carapace 30 mm from base; VI-4 is 32 mm long, 13 mm wide. VI-5 is 22 mm long, 16 mm wide. Appendage IV consists of three podomeres, 7 mm wide narrowing distally to 5 mm with central ridge. IV-3 is 10 mm long, IV-4 is 15 mm long and IV-5 is incomplete. Opisthosoma includes tergites 1–12 and base of telson. Tergite 3 centre 118 mm wide. Segments 8–10 telescoped. Pustular ornamentation evident on all tergites and telson, epimera faintly preserved on postabdominal segments. Tergites 2–5 faintly preserve paired opisthosomal tubercles, 2 mm in diameter, separated by 12 mm and 4 mm from tergite posterior edge.

BRSUG 9955. Part and counterpart of pretelson and telson (Pl. 4, figs 7–8). On pretelson, epimera and pustular ornament visible. Telson broken in two: first section 47 mm long and second 83 mm. Telson keeled medially and displays pustular ornament.

BRSUG 9956. Part and counterpart of prosomal appendages V and VI (Pl. 4, fig. 2). V consisting of three articulated podomeres, with upper and lowermost obscured by matrix. V-4 preserved length 24 mm and 12 mm wide. V-5 preserved length



TEXT-FIG. 6. *Camera lucida* drawing of BMAG Cb4668; ×0.5. Abbreviations: MR, Marginal Rim; LE, Lateral Eye; MRi, Median Ridge; C, Carapace; Tu, Tubercle; T, Tergite and PL, Palpebral Lobe.

27 mm and 10 mm wide, with two ridges each 3 mm from lateral edge. Podomere appears slightly curved, probably preservational. V-5 is 16 mm long, 10 mm wide and telescoped into V-4. On reverse of specimen two large podomeres from VI seen; VI-5 is 20 mm long, 14 mm wide, VI-6 is 43 mm long and 11 mm wide. Both display pustular ornamentation, possibly serrated along distal joint.

BRSUG 9957. Part and counterpart of two prosomal appendages (Pl. 3, figs 4–6). Part displays three podomeres of a single

EXPLANATION OF PLATE 5

Figs 1–7. *Drepanopterus abonensis* Simpson, 1951. 1, BRSUG 28629. Coxae III-VI; ×1.2. 2, BRSUG 28635. Carapace bearing metastomal imprint; ×0.75. 3, BRSUG 28647. Metastoma with Coxae IV-VI and podomeres 2–4 of appendage VI. Posterior to the metastoma the first sternite is also preserved; ×0.85. 4, BRSUG 28644. Preabdominal segments bearing tubercles; ×0.4. 5, BRSUG 28645. Postabdomen; ×0.35. 6, BRSUG 28641. Opisthosomal mould, dorsal surface; ×0.4. 7, BRSUG 28641. Counterpart. Opisthosomal mould, ventral surface; ×0.4.

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appendage, probably VI, total length 115 mm. VI-4 is 15 mm wide, VI-5 is 12 mm wide. Both pustular with pustular ridges running 4 mm from each lateral edge. VI-6 is 10 mm wide with median keel. Counterpart displays two distal podomeres of appendage VI; VI-7 preserved length 22 mm, VI-8 is 27 mm long. Alongside two podomeres of appendage V preserved; V-3 is 24 mm long and 13 mm wide, V-4 is 24 mm long and 10 mm wide. Ridge 4 mm from anterior edge of first podomere, V-4 with median keel. Both podomeres pustulated. Matrix around podomere joints stained a dark brown/black colour, probably a result of decayed soft tissue.

BRSUG 9958. Part and counterpart of carapace. Length to width ratio 0.69. Lateral angle 87 degrees. Surface ornament pustular, marginal rim ornamentation consists of parallel striations. Single (left) lateral eye preserved centrimesially on carapace. Palpebral lobe reniform. Median ocelli preserved on centre of carapace between lateral eyes, raised on tubercle of 3 mm wide and 2 mm long.

BRSUG 9960. Part and counterpart of opisthosomal segments; four in series on one side of specimen and one isolated on reverse. Pustular ridges 4 mm from anterior of tergites. Paired tubercles present on tergites four and five, 3 mm in diameter and 5 mm apart and located 3 mm from posterior tergite margin. Isolated tergite on reverse of specimen 76 mm wide (incomplete) and 24 mm long.

BRSUG 9961. Partial carapace and opisthosomal tergites (Pl. 4, fig. 1); carapace and nine tergites in series, with two segments disarticulated and adjacent. Carapace preserved and total dimensions unknown. Pustular ornamentation apparent. Oval ocular area preserved. Slight telescoping of tergites 6–8. Pustular ornamentation present throughout, pustular ridge 3 mm from anterior rim on majority of tergites. Disarticulated segments incomplete, anterior-most being 20 mm long. Pustular ornamentation present, ridge of closely spaced pustules before segment joint.

BRSUG 9962. Opisthosomal tergite (one of segments 2–5). 21 mm long and 82 mm preserved width. Paired tubercles 10 mm apart and 2 mm in diameter. Total reconstructed width of tergite 122 mm. Pustular ornament forms ridge along tergite anterior, 5 mm from edge.

BRSUG 9963. Part and counterpart of articulated segments 8–12 and telson base (Pl. 4, figs 4–5). Telson broken midway, keeled medially. Epimera present on all segments, increasing posteriorly. Pustular ornamentation present on all segments including telson, pustule ridge 3 mm from anterior edge present on tergites 8–10.

BRSUG 28610. Three tergites and postabdominal segment (5–8) (Pl. 4, fig. 3). Pustular ornamentation, tergite 5 with paired tubercles.

BRSUG 28611. Five tergites and three postabdominal segments (3–10). Pustular ornamentation evident on all, last four with epimera.

BRSUG 28612. Part and counterpart of podomere. 50 mm long, 16 mm wide narrowing to 5 mm. Ridges 3 mm from each lateral edge. Probably, from appendage VI.

BRSUG 28613. Four postabdominal segments. Pustular ornamentation, forming ridges on anterior of each tergite. Epimera evident.

BRSUG 28614. Part and counterpart of carapace and opisthosoma (Pl. 4, fig. 6). Carapace incomplete and poorly preserved and horseshoe-shaped. Lateral eyes faintly preserved on reniform palpebral lobes either side of a median ridge. Pustular ornamentation obvious throughout. Tergite 1 telescoped under carapace. All segments have pustular ridge 4 mm from anterior edge, tergites 2–5 have tubercles 4 mm from posterior edge. Tubercles 3 mm in diameter and separated by 5 mm. Segments 7–12 have epimera. Counterpart preserves postabdomen and telson.

BRSUG 28617. Two podomeres of prosomal appendage V. Neither podomere is complete; V-5 is 8 mm wide and over 32 mm long. V-6 is 9 mm wide and over 24 mm long. Pustular ornamentation with ridge running down either side.

BRSUG 28620. Three postabdominal segments. Slight 3D preservation with central 40 mm raised. Pustular ornamentation and epimera.

BRSUG 28621. Three prosomal appendages, preserved in parallel. First appendage (III) individual podomeres unidentifiable; 32 mm long, 5 mm wide, with single spine 21 mm along it. Spine 5 mm long and 1 mm wide. Second appendage (IV) width poorly preserved; 70 mm long, at least 7 mm wide, consisting of three podomeres. IV-4 preserved length 28 mm, IV-5 is 22 mm long, IV-6 preserved length 11 mm. Third appendage (V) 53 mm long, consists of two podomeres; V-5 is 21 mm long, 9 mm wide thickening to 14 mm distally. V-6 is 32 mm long,

EXPLANATION OF PLATE 6

Figs 1–10. *Drepanopterus abonensis* Simpson, 1951. 1, BRSUG 28651. Endostoma and terminal podomere of appendage VI; ×1. 2, BRSUG 28830. Carapace with first two tergites; ×0.5. 3, BRSUG 28650. Podomeres; ×3.3. 4, BRSUG 28841. Podomeres from appendage VI; ×1. 5, BRSUG 28839. Podomeres; ×1. 6, BRSUG 28843. Tergites; ×0.85. 7, BRSUG 28840. Pretelson and telson; ×1. 8, BRSUG 28843. Telson; ×1. 9, BRSUG 28844. Telson; ×0.8. 10, BRSUG 28844. Counterpart. Telson; ×0.8.

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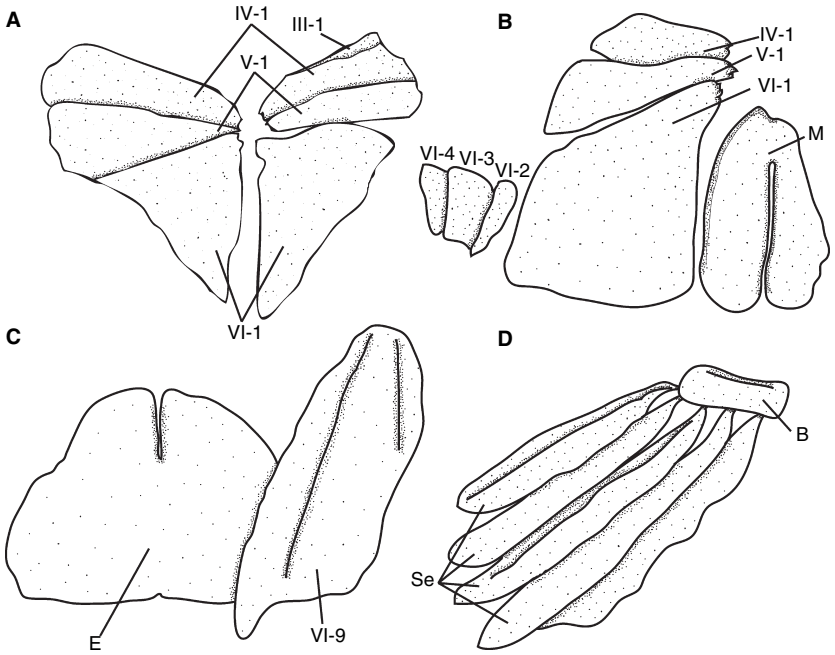

TEXT-FIG. 7. *Camera lucida* drawings of *Drepanopterus* specimens. A, BRSUG 28629, coxae III-VI; ×1.5. B, BRSUG 28647, metastoma, coxa and proximal podomeres of appendage VI; ×0.9. C, BRSUG 28651, endostoma and terminal podomere of appendage VI; ×1.4. D, BRSUG 28857, blade with setae; ×4. Abbreviations: M, Metastoma; E, Endostoma; B, Blade and Se, Seta.

7 mm wide expanding distally to 12 mm. Ridge present either side of podomere.

BRSUG 28629. Coxae of appendages III–VI (Pl. 5, fig. 1; Text-fig. 7A). Coxa III is 17 mm long, 1.5 mm wide at gnathobase expanding to 7 mm distally. Coxa IV is 17 mm long, 1.5 mm wide at gnathobase expanding to 5 mm distally. Coxa V is 16 mm long with 2 mm wide gnathobase expanding to 5 mm distally. Coxae is VI incomplete, 17 mm long and 7 mm wide. Top 4 mm of coxa gnathobasic. Gnathobases darkened.

BRSUG 28631. Part and counterpart of partial carapace. Single eye, apparently ovate but with reniform palpebral lobe located centrimesially. Posterior and to right of eye is median ridge, 15 mm long and 9 mm wide.

BRSUG 28633. Partial carapace, section of postabdomen and isolated tergite. Carapace incomplete. Pustular ornamentation evident throughout. Marginal rim narrows to 3 mm wide at base. Left lateral eye located centrimesially. Right eye poorly preserved and separated from left by 27 mm. Median ocelli present, 3 mm in diameter and is situated centrally between lateral eyes. Isolated tergite 26 mm long. Postabdomen consists of four segments in series. Each segment possesses epimera.

BRSUG 28634. Part and counterpart of partial carapace. Single eye preserved. Ornamentation pustular in places, in others bulbous and warped. Dark, spine-like section of cuticle preserved alongside with furrow running down it. On reverse side of specimen, base of carapace preserved with width of 72 mm.

BRSUG 28635. Carapace imprint (Pl. 5, fig. 2). Lateral angle 85 degrees. Length/width ratio 0.86. Surface pustular and 1–2 mm interspacing between pustules. Marginal rim consisting of parallel striations and is devoid of pustules. Around internal margin of rim is dense pustular ridge, pustules 1 mm in diameter, <0.5 mm interspaced. Lateral eye lobes reniform, positioned centrimesially 27 mm apart. Median ocelli indistinct. Displaced metastoma seen in outline, 28 mm long and 19 mm wide. Section of metastoma cuticle preserved; narrow marginal rim and punctate ornamentation. Anterior margin notched and posterior cleft running through metastoma. Length/width ratio 1.47. Alongside carapace a portion of prosomal appendage is preserved, 15 mm wide and 73 mm long. Pustular ridge 1 mm from anterior edge of podomeres, another 3 mm from posterior edge.

BRSUG 28639. Appendage and three preabdominal tergites. Appendage possibly V, preserved length 74 mm; keeled, 15 mm wide narrowing to 9 mm distally. Tergites incomplete have

EXPLANATION OF PLATE 7

Figs 1–8. *Drepanopterus abonensis* Simpson, 1951. 1, BRSUG 28857. Blade from anterior prosomal appendage bearing setae; ×3. 2, BRSUG 28858. Anterior part of metastoma with taphonomic warping; ×3. 3, BRSUG 28850. Telson; ×0.9. 4, BRSUG 28850. Counterpart. Telson; ×0.9. 5, BRSUG 28854. Opisthosomal tergites; ×0.7. 6, BRSUG 28855. Telson; ×0.85. 7, BRSUG 28862. Telson; ×1. 8, BRSUG 28846. Pretelson and telson; ×0.65.

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pustular ornamentation and rounded edges. One is 14 mm long, the other 30 mm long with evidence of a similar sized one above it.

BRSUG 28641. Opisthosomal section preserving tergites and sternites (Pl. 5, figs 6, 7). Dorsal side with pustular ornamentation. Ventral side with pustular ornamentation less pronounced.

BRSUG 28642. Part and counterpart of incomplete telson and podomeres. Telson section narrowing to 25 mm, keeled down centre with rim around margins. On reverse, a jumble of podomeres are preserved; two easily measurable. First preserved length 35 mm, 7 mm wide, with pustule ridge running down centre. Second podomere 27 mm long, 11 mm wide, with rim to either side. Pustular ornamentation is evident on many of the podomeres.

BRSUG 28644. Part and counterpart of tergites (Pl. 5, fig. 4). Two sections of opisthosomal segments. First section consists of seven preabdominal tergites, some of which have telescoped. Tergites 2–5 with paired tubercles 3 mm in diameter, 4 mm apart and 5 mm from posterior edge. Tergites of second section have telescoped; first tergite 20 mm long, width unknown; second tergite 13 mm long, width 118 mm; third tergite 20 mm long and 90 mm wide.

BRSUG 28645. Postabdomen (segments 7–12) with telson (Pl. 5, fig. 5) and isolated preabdominal tergite (2–5). Preabdominal tergite preserves 3D shape, rising towards centre. Two tubercles located at highest point, 5 mm in diameter and 5 mm apart. Pustular ornamentation abundant and lateral edges rounded. Pustular ornamentation and epimera found on all postabdominal segments. Telson broken midway, ridged along either lateral side.

BRSUG 28647. Metastoma and coxae (Pl. 5, fig. 3; Text-fig. 7B). Coxa IV preserved anteriorly, total dimensions unknown. Coxa V 6 mm wide. Metastoma 39 mm long, preserved width 23 mm (total reconstructed width 27 mm), the widest point within median-third. Notched anteriorly, with thin marginal rim. Posterior margin cleft, 24 mm long, so metastoma almost laterally divided. Coxa VI preserved in position alongside metastoma, 31 mm long, 29 mm wide narrowing to 26 mm anteriorly. Gnathobase 6 mm long. VI-2 and VI-3 are preserved alongside. Rounded with striations, 18 mm long and 15 mm wide.

BRSUG 28648. Arthropod cuticle and two podomeres. First podomere 30 mm long and 8 mm wide. Second podomere hourglass-shaped, 16 mm long and 9 mm wide.

BRSUG 28650. Tergite, sternite and podomeres (Pl. 6, fig. 3). Tergite located on reverse of specimen, width unknown and length 26 mm. Pustular ornamentation, pustular ridge running 4 mm from anterior edge. On opposite side a sternite is preserved. Alongside is a pair of articulated podomeres. First podomere 42 mm long and 12 mm wide, pustular ridge running along either edge and keel running down centre, second incomplete and 8 mm wide with preserved length 17 mm.

BRSUG 28651. Endostoma and podomere (Pl. 6, fig. 1; Text-fig. 7C). Endostoma rounded, 21 mm long, 28 mm wide, notched anteriorly (6 mm long, 1 mm wide), with corresponding notch on posterior. Bears general dimpled appearance; probably, distortion because of preservation. Distal podomere preserved alongside, 35 mm long and 12 mm wide. Pustular, with two ridges of pustules running 2.5 mm from each edge, converging at tip.

BRSUG 28654. Assorted appendages. Concentration of assorted cuticle mostly undiagnostic. Podomere, 6 mm long and 26 mm wide with another podomere mostly obscured beneath. Portion has cuticle preserved, dimpled ornamentation with acicular scales pointing anteriorly. Ridge 3 mm from anterior edge.

BRSUG 28830. Carapace and three tergites (Pl. 6, fig. 2). Carapace pustular, lateral angle 78 degrees. Cardiac lobe 36 mm wide. Pustules on carapace interspaced by 1–2 mm. Marginal rim consisting of parallel striations and devoid of pustules. Median ocelli indistinct, both lateral eyes poorly preserved. Lateral eyes crescentic, positioned on reniform palpebral lobes with slight oval appearance because of external lens. Located centrimesially on carapace, 32 mm apart. First tergite telescoped underneath carapace. Second tergite bears paired tubercles along mid-line. Third tergite displays paired tubercles along mid-line and pustular ridge along anterior joint.

BRSUG 28831. Tergites and leg fragments. Ripples preserved on reverse, each crest 25 mm apart. Two articulated podomeres preserved, first 21 mm long and 10 mm wide, pustular ridge 2 mm from outer edge. Second podomere 15 mm long, 4 mm wide narrowing to termination 2 mm wide. Ridges present along either lateral margin. Five tergites preserved in series. Pustular ornamentation and telescoping evident.

BRSUG 28838. Series of rounded structures, possibly carapaces. Single easily identifiable section, 29 mm long and 36 mm wide. Marginal rim 2 mm wide, acicular scales pointing anteriorly. Possible eyes preserved; 12 mm apart, each 4 mm long and 2 mm wide, positioned antimesially. First tergite also present, length 5 mm.

BRSUG 28839. Prosomal appendage (Pl. 6, fig. 5). 12 mm wide and 104 mm long, consisting of two podomeres. First podomere 6 mm wide thickening distally to 14 mm, 43 mm long with ridge 2 mm from each lateral edge and covered in pustular ornamentation. Second podomere 12 mm wide, narrowing to 11 mm distally and preserved length is 30 mm. Pustular ornamentation and ridge 1 mm from each edge.

BRSUG 28840. Pretelson and telson (Pl. 6, fig. 7), tergites on specimen reverse. Pretelson and telson flattened, telson telescoped slightly into pretelson. Both have pustular ornamentation. Telson narrowing distally, keeled, with dark, black organic-looking material at joint. Tergites 11 mm long.

BRSUG 28841. Prosomal appendage, consisting of three podomeres (Pl. 6, fig. 4). First podomere 42 mm long, 9 mm wide thickening to 11 mm distally. Two ridges present, 3 mm from left edge and 4 mm from right. Second podomere 25 mm long and 8 mm wide. Dark, black organic material around joint. Third podomere incomplete and 5 mm wide. Probably appendage V or VI.

BRSUG 28842. Partial carapace, total dimensions unknown. Marginal rim 4 mm wide. Two fragmented appendages also preserved, first 7 mm wide and 43 mm long, second 8 mm wide and 35 mm long and distal terminations rounded.

BRSUG 28843. Distal portion of telson, plus isolated tergites (Pl. 6, figs 6, 8). Telson keeled down centre. Three well-preserved tergites displaying pustular ornamentation and pustular ridge running along anterior borders 2 mm from edge.

BRSUG 28844. Part and counterpart of telson fragment (Pl. 6, figs 9–10). Proximal and distal sections missing. Keeled with pustular ornamentation, narrowing to 8 mm.

BRSUG 28845. Two tergites. Pustular ornamentation on both sections, with ridges towards anterior margin. Second has small epimera, indicating these are tergites 6 and 7. Neither bears tubercles.

BRSUG 28846. Pretelson and telson (Pl. 7, fig. 8). Pretelson has epimera and pustular ornamentation. Telson keeled medially.

BRSUG 28847. Assorted cuticle. Two segments appear in association, one convex and the other concave, almost appearing to be part and counterpart. Both 24 mm long, 27 mm wide. Ornamentation granular, notched anteriorly. Could be endostoma, but also a similar shape to the coxa. Could represent fragments of *Praearcturus*.

BRSUG 28848. Assorted cuticle. Section of cuticle, 23 mm long, 46 mm wide, displaying tuberculate ornamentation, possibly fragments of *Praearcturus*. On the reverse are more fragments of tuberculate cuticle, 36 mm long and 27 mm wide. Dark staining around cuticle appears similar to the shape of coxa VI of *Drepanopterus*.

BRSUG 28850. Part and counterpart of telson (Pl. 7, figs 3–4). Proximal end missing. Narrows to 4 mm distally. Telson covered in pustular ornamentation with median keel.

BRSUG 28854. Section of opisthosoma (tergites 1–6) (Pl. 7, fig. 5). First tergite partially preserved. Fourth tergite telescopes slightly into third. Paired tubercles present on tergites 2–5, separated by 10 mm and 5 mm from posterior edge. On some tergites, pustular ridge present 5 mm from anterior edge.

BRSUG 28855. Telson and partial carapace (Pl. 7, fig. 6). Telson appears clavate. Keel running down centre, otherwise lacking ornamentation. Total dimensions of carapace unknown, preserved length 33 mm and width 24 mm, displaying pustular ornamentation and 6 mm wide marginal rim.

BRSUG 28856. Opisthosomal tergites, with assorted arthropod cuticle and fish scales. First tergite 90 mm wide and 23 mm long, second 79 mm wide and 24 mm long. Along with pustular ornamentation a ridge of pustules is present after segment joint.

BRSUG 28857. Isolated blade bearing setae (Pl. 7, fig. 1; Textfig. 7D). Dark spine preserving cuticle, setae radiating off it. Spine 6 mm long and 2 mm wide, pustular ridge slightly offset from centre, termination rounded. Setae 19 mm long, each 2 mm wide, consisting of six filaments. Total length of blade including spine and setae 22 mm.

BRSUG 28858. Partial metastoma, distorted, with cuticle still intact (Pl. 7, fig. 2). Anterior of metastoma preserved, ovate with evidence of hollow cleft termination. Taphonomically warped. Edge of metastoma and cleft ridged, with dimpled ornamentation. Anterior edge of metastoma bears notch with rounded shoulders. Preserved length 9 mm and width 15 mm with cleft terminating 6 mm from notch. Notch 4 mm wide and 2 mm long, cleft 1 mm wide, terminating in round hollow 1.5 mm wide and 2 mm long.

BRSUG 28859. Part and counterpart of partial carapace. Single eye preserved centrimesially. Palpebral lobe is reniform. Pustular ornamentation occasionally preserved on carapace.

BRSUG 28862. Fragment of telson (Pl. 7, fig. 7). Tapers to 9 mm wide. Appears clavate in shape, with median keel.

BRSUG 28863. Podomeres. First podomere 26 mm long, 7 mm wide. Second podomere 20 mm long, 7 mm wide.

CONCLUSIONS

Based on new morphological data, including the presence of a posteriorly cleft metastoma and setae-bearing blades on the anterior prosomal appendages, *Drepanopterus abonensis* is redescribed as a basal sweep-feeding hibbertopteroid, using the blades on its appendages to rake through soft sediment for small invertebrates and vertebrates. *D. abonensis* displays a mix of characters shared with the two derived hibbertopteroid families, the Hibbertopteridae and the Mycteropidae, as well as sharing characters with the more basal Superfamily Kokomopteroidea, including a clavate telson and median ridge on the carapace, inferring a sister-group relationship between Hibbertopteroidea and Kokomopteroidea. This firmly places the hibbertopterids within the Eurypterida; the metastoma of *Drepanopterus* is intermediate between the triangular, cleft metastoma found in *Hibbertopterus* and the rounded consolidated metastoma in other eurypterids.

The genus *Drepanopterus* is shown to be polyphyletic, with *D. pentlandicus* and *D. abonensis* retained within the genus and '*D*'. *bembycoides*, '*D*'. *lobatus* and '*D*'. *nodosus* removed pending redescriptions. Hibbertopteroid eurypterids are long-ranging stylonurids that survived the decline and demise of their eurypterine relatives in the Late Devonian. This is most-likely because of their sweep-feeding mode of life, which was not in direct competition with the Eurypterina and other predators.

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