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Bembicosoma re-examined: a xiphosuran from the Silurian of the North Esk Inlier, Pentland Hills, Scotland

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ABSTRACT: The Silurian arthropod *Bembicosoma pomphicus* Laurie, 1899 is re-studied in relation to other Palaeozoic chelicerate taxa. All three known specimens of *Bembicosoma* originate from the Silurian (late Llandovery) Eurypterid Bed of the Gutterford Burn Flagstones, Reservoir Formation, Pentland Hills, Scotland. *Bembicosoma* is removed from its previous tentative assignment to Eurypterida and re-assigned to Xiphosura. A morphological reconstruction of this taxon is presented for the first time. This work continues a reappraisal of the systematics of a number of taxa that belong within the synziphosurines, a loose grouping of early Palaeozoic chelicerate arthropods aligned with the Xiphosura (horseshoe crabs), but which have been mistakenly identified as eurypterids in the past. *Bembicosoma* is significant as it is one of the earliest known synziphosurines.

KEY WORDS: Arthropod, chelicerate, Eurypterid Bed, Gutterford Burn, Llandovery, synziphosurine.

The North Esk Inlier of the Pentland Hills, exposing fossiliferous sediments of Silurian age, is situated to the south-west of Edinburgh, Scotland. The importance of this area as a source of exceptional fossils has been recognised for over 150 years, since Maclaren (1839) published his account of the geology of Fife and the Lothians. In the 1890s, John Henderson and David Hardie made extensive excavations here at a site on the Gutterford Burn (Waterston 1979; Clarkson 2000). This provided Malcolm Laurie with the fossils that he later described in great anatomical detail (Laurie 1892, 1899). The arthropod fauna from the site is dominated by stylonurid eurypterids (see Waterston 1979), but also includes an example of one of the earliest scorpions, *Palaeophonus loudonensis* Laurie, 1899, and fossils identified here as synziphosurines. The site of the excavations on the north bank of the Gutterford Burn produced one of the richest and most varied eurypterid faunas known at the time; the particular productive horizon came to be known as the Eurypterid Bed. The diversity, quality and quantity of fossils collected from this site are of intrinsic interest. However, when one realises that the strata that they were collected from ranged from vertical to overturned in attitude, and explosives are reputed to have been used to liberate the fossiliferous blocks, the truly remarkable history of the collection is revealed.

The Gutterford Burn Flagstones of the Reservoir Formation of the North Esk Inlier (Robertson 1986, 1989) are exposed along the banks of the Gutterford Burn. The Eurypterid Bed was historically cited as belonging within this unit, but until recently, its exact location was only vaguely known. Recent fieldwork undertaken by staff from the National Museums of Scotland (NMS), Edinburgh, and volunteers (July 2003) from the universities of Cambridge, Bristol and Glasgow succeeded in determining the exact location of the Eurypterid Bed and its sedimentary association. The Eurypterid Bed consists of about a 0·5-m thickness of fine green silt intermixed with volcanic ash debris which lends a distinctly greasy feel to the bedding surfaces. Eurypterids, and of course the specimens of *Bembicosoma*, are preserved as carbonised cuticle compressions within this sediment. Associated invertebrate fossils including graptolites, conulariids and crinoid ossicles indicate a marine setting for this deposit (Robertson 1999). The sequence lying stratigraphically below (but physically higher in the actual outcrop) consists of parallel bedded flagstones containing a number of discrete horizons yielding dendroid graptolites. Robertson (1986) reported that the scale of previous excavations was such that the bed in question was no longer exposed, being covered by extensive scree and backfill material. Plotnick (1999) detailed a list of the eurypterid species from the Gutterford site, and also the associated fauna, but omitted to mention *Bembicosoma* amongst these. Based on the interpretation of Waterston (1979), Plotnick (1999) also suggested a marginal marine depositional setting for the Gutterford Burn Flagstones, compatible with but not diagnostic of a tidal flat setting.

Bembicosoma is recognised here for the first time as a synziphosurine arthropod. Synziphosurines are a loose grouping of early members of the Xiphosura, characterised by the possession of unfused dorsal segments in the opisthosoma (Shuster & Anderson 2003). Its reassignment from a possible eurypterid to the Xiphosura makes it one of the earliest recorded representatives of the synziphosurines, and hence, of potential importance in defining certain morphological character polarities, such as opisthosomal segment count.

1. Material and methods

All specimens of *Bembicosoma pomphicus* Laurie, 1899 originate from the Hardie Collection housed in the NMS. The Hardie Collection (NMS G.1897.32) alone contains over 230 chelicerate fossils collected from the Gutterford Burn Eurypterid Bed, the majority of which are eurypterids. This collection formed the basis for the classic study of Scottish Silurian stylonurids by Waterston (1979). Laurie (1899) figured only two specimens of *Bembicosoma* in his original description. The other specimen is illustrated here for the first time.

Camera lucida drawings were prepared using a Leica MZ6 microscope with a drawing tube attachment. Contrast between the enclosing lithology and the fossil remains is generally poor, and so 70% alcohol was used to 'wet' the surface prior to examination and drawing. Specimens of other synziphosurine taxa, including *Bunodes lunula* (Eichwald, 1854) from Saaremaa, Estonia, in the collections of the NMS, and a synziphosurine of equivalent age to *Bembicosoma* from Waukesha, Wisconsin (in the Geology Museum, Department of Geology and Geophysics, University of Wisconsin, Madison, WI, USA), were studied for comparative purposes, in addition to other eurypterids in the Hardie collection (e.g. *Drepanopterus* spp.) from the same horizon as *Bembicosoma.*

2. Taphonomy, preservation and depositional setting of *Bembicosoma*

The host lithology typical of the Eurypterid Bed is a drab, olive-green, fine-grained micaceous siltstone. Fossil remains tend to occur on undulating clay-rich laminae with a characteristic waxy smooth surface within the siltstone associated with abundant amorphous carbonaceous organic material and sheets of *Dictyocaris* Salter, 1860, a distinctively reticulate sculptured 'cuticle' of unknown affinity. Research on graptolite faunas at a lower level within the Reservoir Formation suggests a late Llandovery (Telychian) age for this particular horizon (Bull & Loydell 1995). Specimens of *Bembicosoma* demonstrate variable degrees of compression, in common with the eurypterid fossils from the Eurypterid Bed. Charles Wellman (University of Sheffield, Sheffield, UK) subjected a sample of the Eurypterid Bed to hydrofluoric acid maceration, and although eurypterid fragments were visible on the surface of the sample prior to processing, the residue did not yield any recognisable cuticle fragments. This strongly suggests that the cuticle is predominantly carbonised, rather than retaining original composition and cohesion, as has been demonstrated in other eurypterid fossils (Selden 1981). Silurian eurypterid fossils are most often encountered in sediments akin to finely laminated dolostones typified by the North American 'Bertie Waterlime' deposit. The hummocky nature of the Pentland Hills Eurypterid Bed suggests deposition may have been rapid and chaotic, rather than in quiet lagoonal conditions leading to such finely laminated sediments.

The arthropod remains are frequently draped over the wavy lamellae of the bed and can occupy varying levels within the broken surface of the rock. In some cases, remains are seen to be contorted along with the laminae of the bed. Robertson's (1989) interpretation of the depositional setting of the Reservoir Formation as one in which infrequent debris flows swept down into deeper water from a shallow-water coastline ties in with this observation. In this respect, the preservational dynamics may be similar to those encountered in the Silurian (Ludlow Series) Leintwardine submarine channel deposits of Herefordshire, UK (Anderson 1999). The similarity in the preserved fauna from the two sites supports this suggestion.

3. Systematic Palaeontology

Phylum Chelicerata Heymons, 1901
Class Xiphosura Latreille, 1802
Family Bunodidae Packard, 1886
Genus *Bembicosoma* Laurie, 1899

Remarks. We place *Bembicosoma* within the Xiphosura, recognising that Synziphosurina Packard, 1886 was suggested by Anderson & Selden (1997) to be a paraphyletic assemblage based on a cladistic analysis of the Class.

The presence of a hypertrophied opisthosomal segment 2 in *Bembicosoma* is a character which unites it with *Bunodes*, *Limuloides* and *Pasternakevia* in the Bunodidae. The lack of this structure excludes the unnamed synziphosurine described from the similarly aged Waukesha Lagerstätte by Mikulic *et al.* (1985a, b).

Bembicosoma pomphicus Laurie, 1899
(Figs 1–4)

1899 *Bembicosoma pomphicus* n. gen. et n. sp. Laurie, pp. 588–9, Pl. 5, Figs 30 & 31.
1955 *Bembycosoma pomphicum* Laurie, 1899; Lamont, p. 212.
1979 *Bembycosoma pomphicus* Laurie, 1899; Waterston, p. 316.

Type material. NMS G.1897.32.146 (holotype) and NMS G.1897.32.149 (paratype) (both Hardie Collection) are housed in the Type and Figured collections of the NMS, Department of Geology and Zoology, Chambers Street, Edinburgh.

Additional material. NMS G.1897.32.143 (part) and NMS G.1897.32.144 (counterpart) from the type locality.

Type locality. Silurian (late Llandovery; Telychian) *spiralis* Biozone, Reservoir Formation, Gutterford Burn Flagstones, Eurypterid Bed, Gutterford Burn, North Esk Inlier, Pentland Hills, Scotland, UK.

Emended diagnosis. A small xiphosuran arthropod with an opisthosoma comprising 10 freely articulating segments, a pre-abdomen of seven segments, the first of which is small and reduced, and a post-abdomen of three segments. The pre- and post-abdominal division is not as marked as in other members of the Bunodidae. The second opisthosomal segment is hypertrophied and significantly larger than the other segments. The dorsal surfaces of the prosoma and opisthosoma possess a distinct cuticular sculpture of round, slightly elongate raised tubercles.

4. Morphological observations

General features. All of the specimens are preserved as variably distorted dorso-ventral compressions. In most cases, a thin, black organic residue is present on the surface of the fossils. It is patchily distributed and represents the remains of the original cuticle of the arthropod. The fractured margins of the fossils and the lack of associated appendages suggest that they may represent moulted exoskeletons rather than actual mortalities of the animals. The size and overall dimensions of the three specimens are listed here: NMS G.1897.32.143 and 144 (part and counterpart) with a preserved length of 55 mm (incomplete) and a width of 15 mm, NMS G.1897.32.146 with a length of 35 mm and a width of 17 mm, and NMS G. 1897.32.149 with a length of 45 mm and a width of 20 mm.

Carapace. The carapace is relatively short compared with the pre-abdomen. The width of the posterior edge of the carapace is slightly greater than the first reduced opisthosomal segment. Anteriorly, there is evidence of the development of a narrow marginal rim. Compression of the carapace, to an effectively flat surface, has destroyed much of the other morphological topography. The marginal rim of the carapace curves posteriorly forming genal cornua rather than well-defined genal spines. The holotype (NMS G.1897.32.146), displays a prominent fracture running across the carapace, giving the false impression that the carapace is distinctly foreshortened and an additional opisthosomal segment is present (see Figs 1b, 3). The paratype (NMS G.1897.32.149) retains dark organic traces which form a triangular region with the apex directed anteriorly, towards the anterior of the carapace (Figs 1a, 2). This indicates the position of the cardiac lobe and associated underlying soft tissues. Patchy, ill-defined organic stains towards the right-hand side of the carapace may

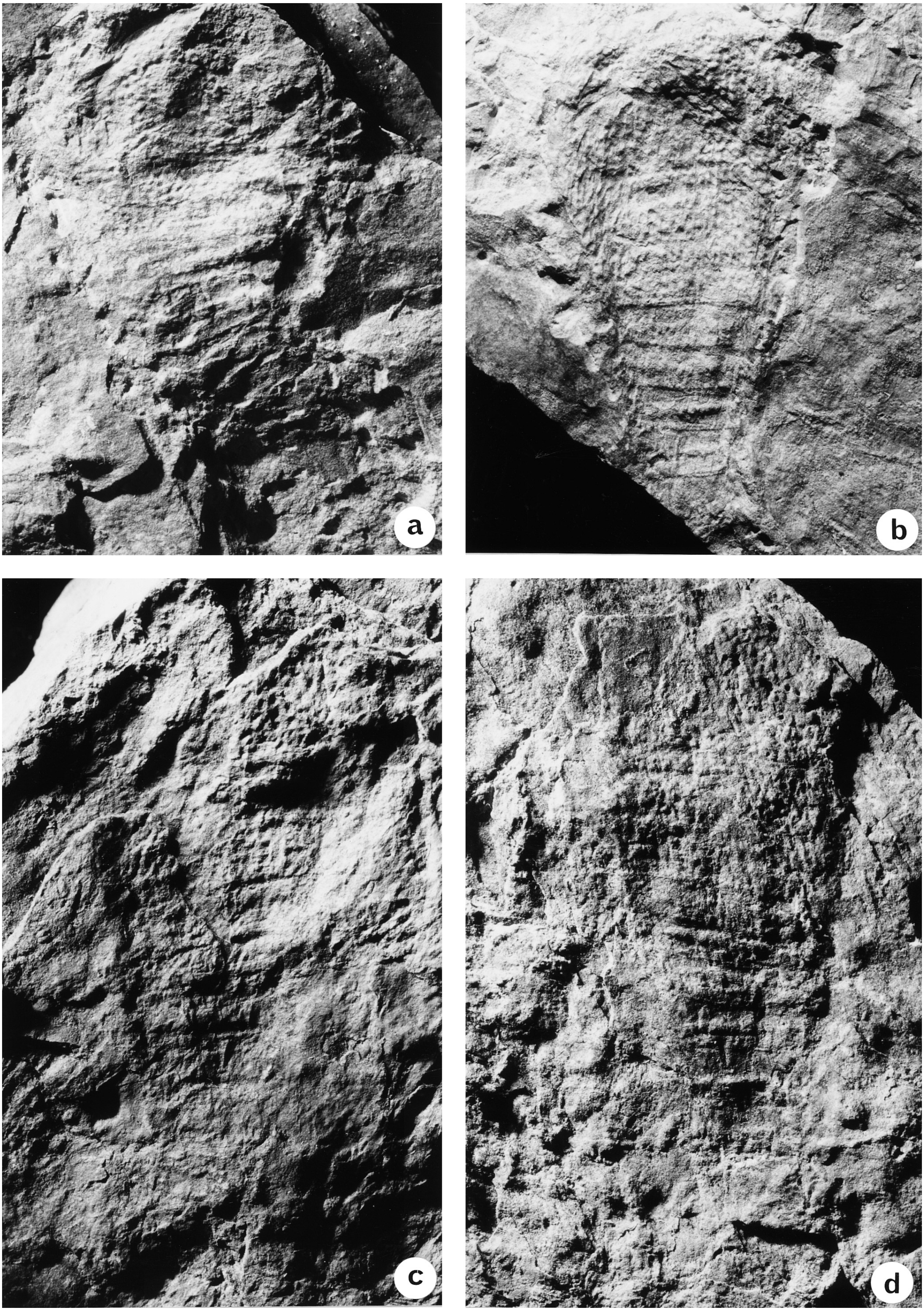

Figure 1 *Bembicosoma pomphicus* Laurie, 1899 from the Late Llandovery, Silurian, Reservoir Formation, North Esk Inlier, Pentland Hills, Scotland: (a) NMS G.1897.32.149 (paratype,) × 2·3; (b) NMS G.1897.32.146 (holotype), × 2·5; (c) NMS G.1897.32.143 (part), × 2·3; and (d) NMS G.1897.32.144 (counterpart), × 2·3.

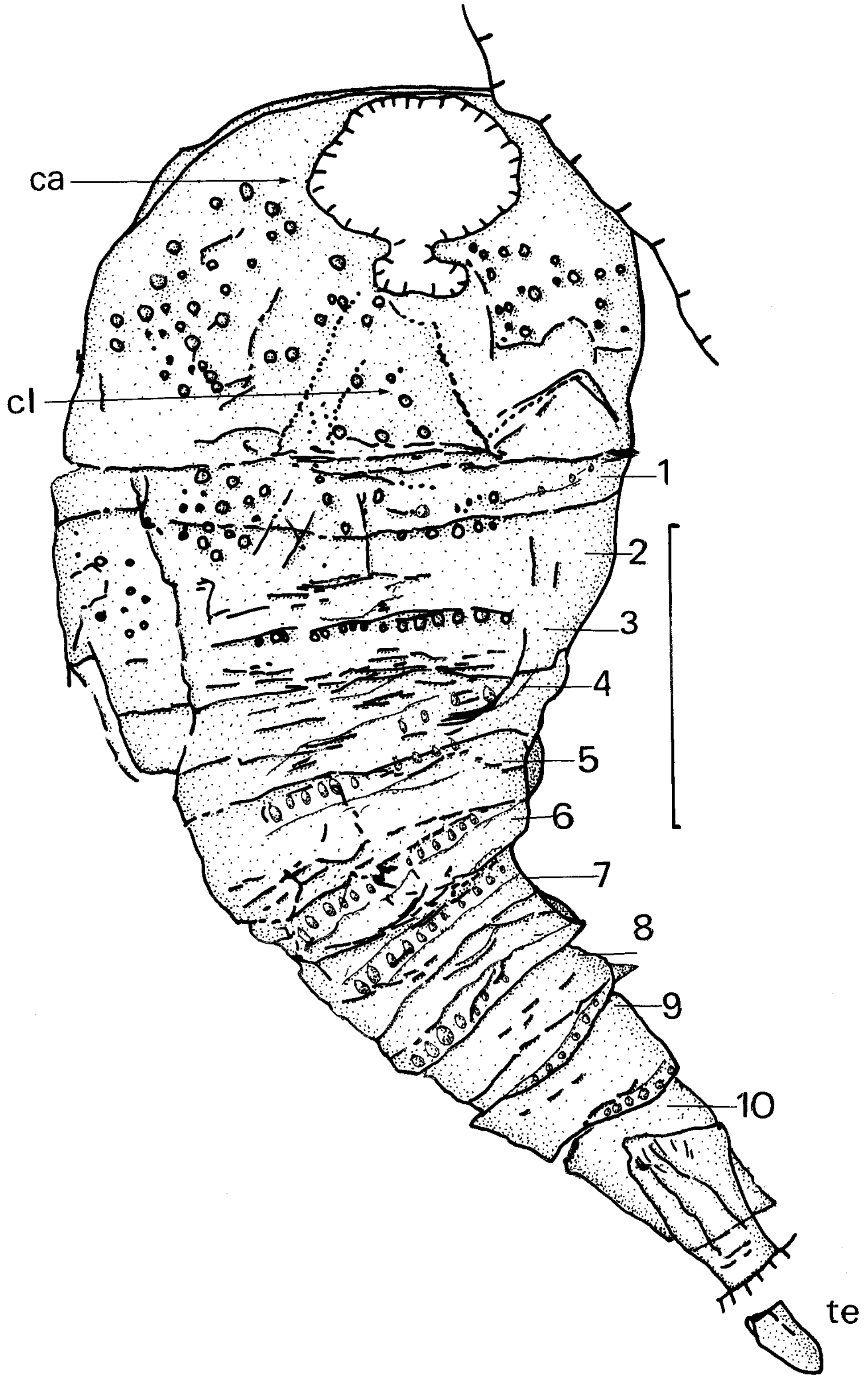

Figure 2 Interpretative drawing of the paratype (NMS G.1897.32.149). Abbreviations as follows: (1–10), opisthosomal segment number; (ca) carapace; (cl) cardiac lobe; and (te) telson. Scale bar = 1 cm.

represent traces of leg appendage musculature, but in the case of discarded moults, they could represent the lightly sclerotised cuticular framework from which the coxal muscles hang. The course of the ophthalmic ridge, presumed to have been originally present by analogy with other bunonids, is not apparent in the available material. The posterior edge of the carapace runs parallel to the first opisthosomal segment, but bulges posteriorly at the base of the cardiac lobe.

Pre-abdomen. The preabdomen is relatively wide and consists of six segments plus the reduced first opisthosomal segment. This segment lies posterior to the carapace margin and is partially obscured by it. It is reduced in axial length and is sub-equal in width to the margin of the carapace (see Fig. 4). The position and size of this segment may explain why its presence was originally missed in the description of Laurie, but it is important in determining an overall opisthosomal segment

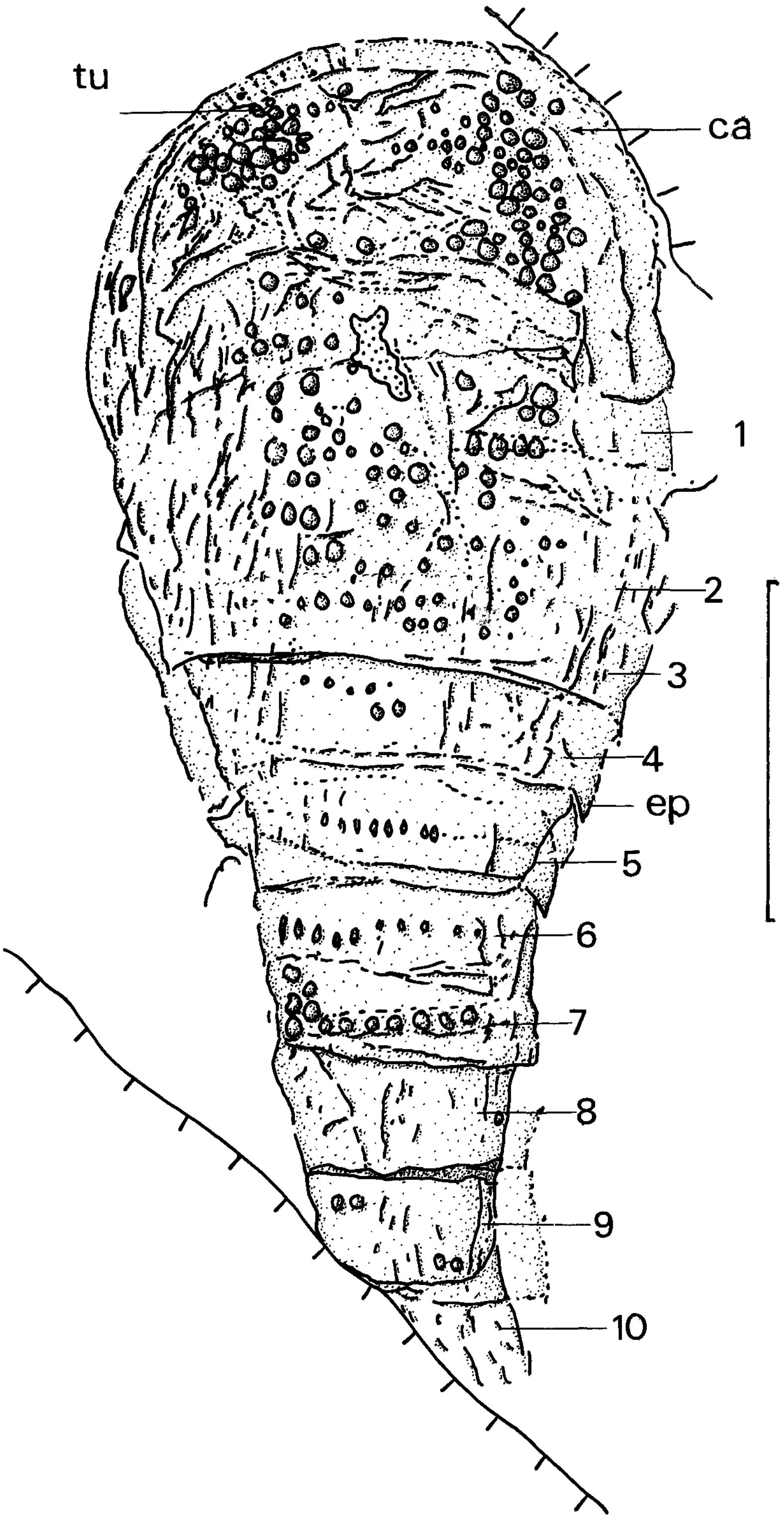

Figure 3 Interpretative drawing of the holotype (NMS G.1897.32.146). Abbreviations as follows: (1–10) opisthosomal segment number; (ca) carapace; (ep) epimeron; and (tu) tubercle. Scale bar = 1 cm.

count of 10. In the holotype (Fig. 1b), the pre-abdomen gives the false impression of a chasmataspid-like buckler region which is in part caused by the presence of a hypertrophied opisthosomal segment 2. An ill-defined lateral flange runs either side of the main raised portion of the pre-abdomen and is homologous to the structure previously recorded in *Bunodes* Eichwald, 1854 and *Limuloides* Woodward, 1865. The curvature apparent in the opisthosoma of NMS G.1897.32.149 (Fig. 1a) demonstrates the unfused nature of these segments.

Post-abdomen. The post-abdomen consists of three annular (ankylosed) segments. The uneven compression of these segments has confused actual segment boundaries in this area. The post-abdomen shows only a slight differentiation from the preabdomen rather than that seen in other synziphosurines such as *B. lunula* Eichwald, 1854. In this respect, the post-abdomen is closer in morphology to that of *Cyamocephalus* (Anderson 1999). The postero-lateral margins of each of these post-abdominal segments are developed into a pair of sharp epimera symmetrical about the axial midline.

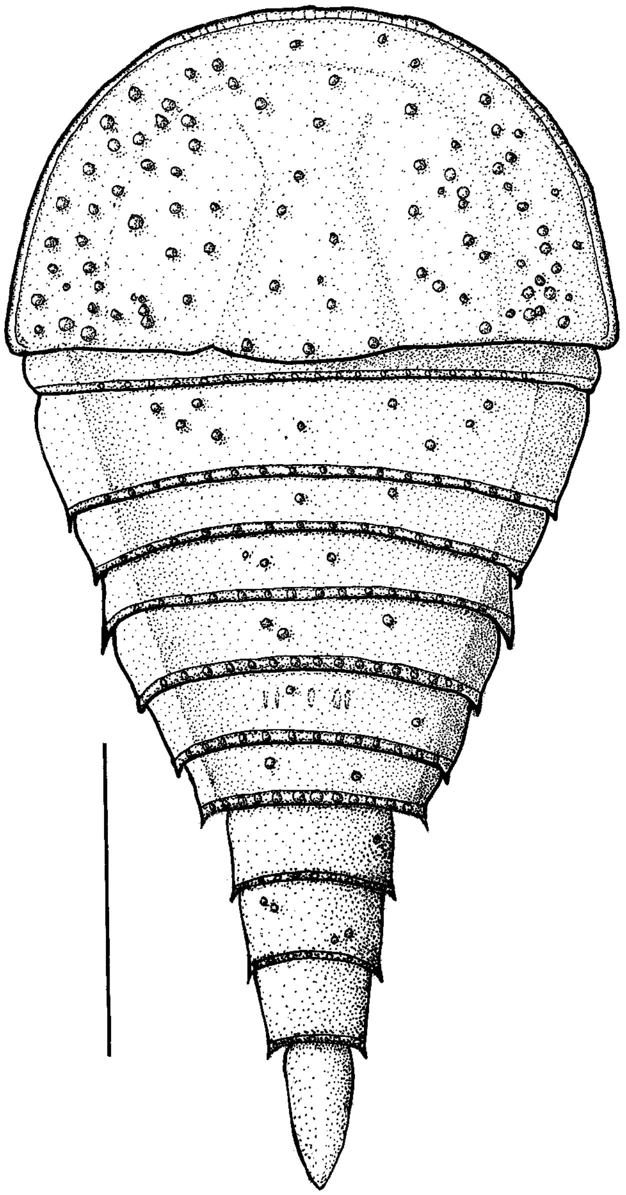

Figure 4 Morphological reconstruction of *Bembicosoma pomphicus* Laurie, 1899. Prosomal (and opisthosomal) appendages are unknown in the specimens and have been omitted from this reconstruction. The course of the ophthalmic ridge is similarly unknown, but is reconstructed by analogy with other known synziphosurines. Scale bar = 1 cm.

Tail spine. The tail spine is only preserved in the paratype, and even here it is damaged and incomplete (Figs 1a, 2). It is short and spearhead-shaped with a proximal region slightly narrower than segment 10. In this specimen, the tail region has fractured to reveal an underlying structure consisting of fine parallel striations.

Cuticular sculpture. A strong cuticular sculpture is present on the carapace and the whole dorsal surface of the pre- and post-abdomen of all specimens of *Bembicosoma*, which Laurie (1899) used as a diagnostic character in his original description. It consists of raised circular or slightly elongate tubercles which become slightly smaller on the carapace rim. In places, a single row of raised, rounded tubercles running across the posterior margin of individual segments in both the pre- and post-abdomen help to define segment boundaries. Laurie defined the genus name *Bembicosoma*, on the basis of these 'peg-shaped' cuticular tubercles.

5. Discussion

Laurie's original description of *Bembicosoma* noted the likely presence of aquatic chelicerate arthropods other than the eurypterids in these beds. In describing *Bembicosoma*, he drew attention to at least nine opisthosomal segments in the most complete specimen (which he cited as the holotype), which does not take into account the much reduced, most anterior first opisthosomal segment recognised here. He stated that, as the segment count was less than 12 (eurypterids consistently possess 12 visible opisthosomal segments), this taxon would have to be removed from Eurypterida and placed within the Xiphosura. Subsequently, Lamont (1955) classified *Bembicosoma* in the Family Stylonuridae within the Order Eurypterida. His opinion was that the coarse sculpture apparent on the cuticle of these fossils indicated that they might be juvenile eurypterids belonging to *Drepanopterus*. Presumably, the justification for this was that Laurie had previously named three species of *Drepanopterus* from the Eurypterid Bed: *D. pentlandicus*, *D. lobatus* and *D. bembycoides*, and most of this material was of adult or sub-adult growth stages. In fact, the cuticle ornament of *Drepanopterus*, is quite distinct from that displayed by *Bembicosoma*. In *Drepanopterus* it is most prominently developed on the dorsal tergites of the pre- and post-abdomen, where it takes the form of widely spaced pits, some with triangular ornament. In *D. pentlandicus*, the ornament is composed of a series of 'V'-shaped scales, which become more rounded towards the lateral margins.

Lamont (1955) reiterated Laurie's original suggestion that this taxon might fit within the Xiphosura, but added that it would have to be a 'primitive form' in view of its Silurian age. The studies of Eldredge (1974) demonstrated the relationship of the early Palaeozoic synziphosurines within the Xiphosura as a whole, and provided just such 'primitive forms'. However, because of the original inclusion of *Bembicosoma* within the Eurypterida, the taxon has not appeared in any systematic treatment of the Xiphosura, a situation analogous to that of the Early Devonian synziphosurine *Willweratbia*, as discussed by Anderson *et al.* (1998).

6. Relationship of *Bembicosoma* with other synziphosurines

Recognising *Bembicosoma* as a synziphosurine chelicerate arthropod has implications for the fossil record of this group as a whole. In the most recent classification of Palaeozoic Xiphosura, Anderson & Selden (1997) recognised the earliest named synziphosurine as *Cyamocephalus loganensis* Currie, 1927 from the Llandovery of the Lesmahagow Inlier, Ayrshire, Scotland. However, palynological evidence from this site suggests it may be early Wenlock in age (Wellman 1995). An as-yet-unnamed synziphosurine from the Brandon Bridge fauna of Wisconsin, USA (Mikulic *et al.* 1985a, b) is of roughly equivalent age (early to mid-Telychian) to *Bembicosoma*. As such, *Bembicosoma* is one of the earliest known synziphosurines. The family Bunodidae Packard, 1886 hitherto contained three genera (Anderson 1996): *Bunodes* Eichwald, 1854 from the late Wenlock '*Eurypterus* dolomite' of Saaremaa, Estonia, several species of *Limuloides* Woodward, 1865 from the Ludlow of Leintwardine in Shropshire, UK, and *Pasternakevia* Selden and Drygant, 1987 from the Ludlow of Podolia, Ukraine. A ghost range for the Bunodidae extending back to the lower Llandovery was proposed by Anderson & Selden (1997) based on the unnamed synziphosurine figured in Mikulic *et al.* (1985a, b). However, further study of this and new specimens from the Waukesha Lagerstätte suggests it is not a member of the Bunodidae, but bears more similarity to the Weinberginidae (Moore *et al.* in press). The late Llandovery age of *Bembicosoma* agrees with the ghost range of Bunodidae and confirms it as the earliest example of this family.

The peg-shaped cuticular sculpture of *Bembicosoma*, as noted by Laurie (1899), is unique amongst synziphosurine fossils. Three-dimensionally preserved material of *Bunodes* from the '*Eurypterus* dolomite' of Saaremaa, Estonia retains some original cuticular material and show a less pronounced sculpture (personal observations). However, a similar cuticular sculpture to that of *B. pomphicus* is also recognised in the chasmataspid chelicerate *Chasmataspis laurencii*, and in an as-yet-undescribed diploaspid chasmataspid from the Lower Devonian of Hombach, Germany (Poschmann *et al.* in press). The exact function of this roughening of the otherwise smooth dorsal cuticular surface remains unknown.

Clarkson *et al.* (2001) demonstrated through careful sampling, collecting and excavation that the Silurian sedimentary succession overlying the Reservoir Formation indicated a predominantly shoreline/shoreface environment, including a suite of lagoonal sediments recognised within the Wether Law Linn Formation. From what the present authors can gather from the ecological constraints of the Xiphosura as a whole, the presence of such sedimentary environments in adjacent or even close proximity to the deeper water setting suggested by the sediments of the Reservoir Formation would provide an ideal habitat for both the synziphosurines and eurypterids. At this time in their geological history, the synziphosurines were strictly marine organisms. Only detailed sedimentary logging, field collection and investigation of the setting of the Eurypterid Bed will lead to a better picture of how this occurrence fits in with the rest of story held within the sediments of the North Esk Inlier.

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