Geol. Mag. **143** (*5*), *2006, pp. 723–735. © 2006 Cambridge University Press*
doi:10.1017/S0016756806002536 *Printed in the United Kingdom*

Eurypterida (Chelicerata) from the Welsh Borderlands, England

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(*Received* 24 March 2005; *accepted* 31 January 2006)

Abstract – Eurypterids from the Welsh Borderlands of England are redescribed from most available material. *Hughmilleria banksii* is here interpreted to represent a new genus. The poorly known *Hughmilleria* (?) *acuminata* (Salter, 1859*a*) is considered a junior synonym of *H. banksii*. Furthermore, *Slimonia*? *stylops* is suspected to be a junior synonym of *Salteropterus abbreviatus*, although they are not formally synonymized as the location of the only known specimen of *S.*? *stylops* is unknown. Morphological differences in carapace shape, eye position, walking leg, genital appendage and telson in *H. banksii* are noted compared to previous descriptions. A prosomal appendage earlier assigned to *H. banksii* is here assigned with caution to *S. abbreviatus* and the reported 'segments' in the posterior part of the telson of *S. abbreviatus* are shown to be cracks. The phylogenetic position of the new genus is inferred to lie between the *Hughmilleria* and the *Slimonia*/*Salteropterus* clades.

Keywords: Hughmilleriids, new genus, Prídolí, *Salteropterus*, *Slimonia*.

1. Introduction

Eurypterids, informally known as sea scorpions, are a diverse group of Palaeozoic, aquatic chelicerates known from the Middle Ordovician to the Upper Permian (Plotnick, 1999), occurring most frequently in the Silurian and Lower Devonian of Europe and North America.

Salter (1856*a*) described a eurypterid from Kington, Herefordshire (Fig. 1) under the name *Himantopterus banksii* Salter, 1856*a*, which he did not figure. The same year, Banks (1856, p. 99) figured three carapaces, two tergites and a telson belonging to this species, and it appears the two authors agreed to place Salter's figures in Banks' paper, although this is not explicitly stated in either. Later, Salter (1859*b*, p. 51) referred to Banks' figures as a part of his (Salter, 1856*a*) original description. *Himantopterus* Salter, 1856*a* was erected for eurypterids with marginal eyes, including species now recognized as *Slimonia acuminata* (Salter, 1856*a*), *Nanahughmilleria lanceolata* (Salter, 1856*a*) and *Erettopterus bilobus* (Salter, 1856*a*). However, *Himantopterus* was preoccupied by a moth (Lepidoptera, Zygaenoidea, Himantopteridae) and Salter (1859*b*, p. 51) synonymized *Himantopterus* with *Pterygotus* Agassiz, 1844 and erected *Erettopterus* as a subgenus for forms with a bilobed telson (e.g. *E. bilobus*), but used the term 'division 1' (of *Pterygotus*) in the text, and the name *Erettopterus* only on the plates. Salter (1859*b*) should have offered *Erettopterus* as a new name to replace the homonym *Himantopterus*, but this was not done.

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Hughmilleria banksii was later also described from Ludlow, Shropshire (Fig. 1) as *Eurypterus acuminatus* Salter, 1859*a* (herein recognized as a junior synonym of *H. banksii*), and *Pterygotus* (*Erettopterus*) *banksii*. The assignment to *Erettopterus* was made when Salter misinterpreted the holotype of *Erettopterus spatulatus* Kjellesvig-Waering, 1961 as being a bilobed telson belonging to *H. banksii*, although he had earlier (in Banks, 1856) figured a styliform telson as belonging to *H. banksii*.

Eurypterids from Perton, Stoke Edith, Herefordshire, England (Fig. 1) were discovered by the Reverend P. B. Brodie, who published a short note of his discovery (Brodie, 1869) where he reported *Stylonurus megalops* Salter, 1859*a* to be the most common form with additional occurrences of *Eurypterus pygmaeus* Salter, 1859*a* (Banks' use of the name in 1856 must be considered a *nomen nudum*) and *Eurypterus acuminatus* Salter, 1859*a*. These specimens were sent to Woodward (1871*a*), who reported that the collection consisted of *Pterygotus banksii* (understandably misidentified as *S. megalops* by Brodie, since Salter at the time assigned telsons of *H. banksii* to *S. megalops* and the bilobed telson of *E. spatulatus* to *H. banksii*), *Eurypterus pygmaeus*, *Eurypterus acuminatus*, *Eurypterus abbreviatus* Salter, 1859*a* and *Eurypterus brodiei* Woodward, 1871*a*. The confusion over the identity of much of this material is related to its very fragmentary nature.

Størmer (1934*a*,*b*) assigned *P.* (*E.*) *banksii* (Salter, 1856*a*) to *Hughmilleria*. The species was later redescribed in more detail by Kjellesvig-Waering (1951), who agreed with Woodward (1871*a*) that the specimens Brodie assigned to *S. megalops* should be assigned to *H. banksii*, but noted that the walking leg assigned by him

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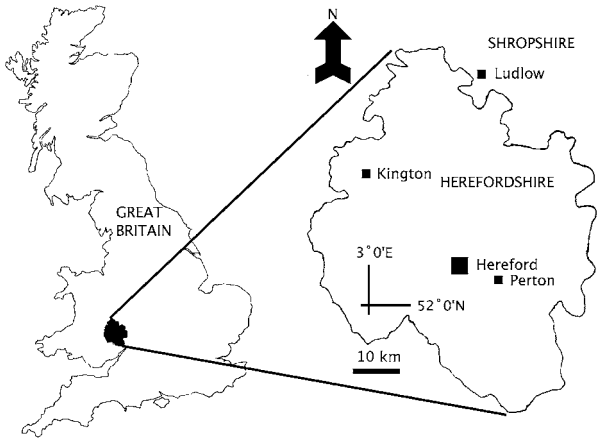


Figure 1. Map of Great Britain showing the outline of Herefordshire and localities where *Herefordopterus banksii* have been found in Herefordshire (Kington and Perton) and Shropshire (Ludlow).

to *H. banksii* (and here to *Salteropterus abbreviatus*) had spines that were 'unusually long compared to other forms of the genus [=*Hughmilleria*]'. Kjellesvig-Waering (1961) briefly discussed the species, but provided no new information. Størmer (1973, pp. 126, 162) suggested that the position of the lateral eyes and the morphology of the paddles in *H. banksii* were suggestive of *Hughmilleria*, while the morphology of the genital appendages (especially type B) was more similar to that of *Parahughmilleria*. He also noted that *H. banksii* might represent a new genus, although the genital appendages are poorly known in other species of *Hughmilleria*. This study shows that Størmer was right in considering this a new genus. Characters previously not recognized as important are the morphology of coxae VI and marginal ornament of the telson.

Earlier descriptions of *H. banksii* are inadequate. The idealized illustrations of the morphology of the carapace, prosomal and genital appendages and telson described by Kjellesvig-Waering (1951) are of little use, no formal diagnosis of the species has previously been given and no type specimen has until now been selected. Here, the systematics of the Herefordshire eurypterids are revised, a new genus is proposed and *H.* (?) *acuminata* is synonymized with *H. banksii*. Previous interpretations of the morphology of *H. banksii* and *S. abbreviatus* are reinterpreted and the phylogenetic positions of these two species are discussed.

2. Material and methods

Most of the specimens are in the British Geological Survey (BGS) collections at Keyworth, Nottingham. The material previously belonged to the Geological Survey Museum (GSM), and proper designation of the specimens is BGS GSM. A few specimens are reposited in the British Museum (Natural History), London (BMNH) and the Field Museum of Natural History, Chicago (FMNH). Two specimens in the Geological Museum, Birmingham University, were not studied. Most of the material is from the Temeside Shale Formation, Perton, Herefordshire (Fig. 1), and the preservation is better at this locality than at the two other localities (see next section). The specimens were studied both dry and immersed in 70 % alcohol solution to prepare the *camera lucida* drawings.

2.a. Stratigraphy, taphonomy and palaeoenvironment

Herefordopterus gen. nov. *banksii* occurs at three different localities: (1) a quarry on Bradnor Hill golf course, Kington, Herefordshire, (2) Perton, Stoke Edith, Herefordshire and (3) Ludlow, Shropshire, all in the Welsh Borderlands, England (Fig. 1) and in two different horizons, the Ludlow Bone Bed Member, Downton Castle Sandstone Formation (Ludlow and Kington) and the overlying Temeside Shales Formation (Ludlow and Perton). The eurypterid bed at the type locality (Kington) is presently inaccessible, the quarry has been disused for around 150 years and the lower beds, from which the eurypterids originated, are now covered by metres of scree. The specimens from the Downton Castle Sandstone Formation generally preserved the original three-dimensionality but details are poor, while specimens in the Temeside Shales Formation are generally flattened but preserve very good details. The following assemblage occurs in the Downton Castle Sandstone Formation (modified from Bassett, Lawson & White, 1982): *Erettopterus brodiei*, *E. spatulatus*, *Eurypterus cephalaspis*, *Nanahughmilleria pygmaea*, *Parahughmilleria salteri*, *Salteropterus abbreviatus*, *Slimonia* (?) *stylops*, *Marsupipterus sculpturatus* and *H. banksii*. The assemblage in the Temeside Shales Formation consists of (modified from Bassett, Lawson & White, 1982): *Dolichopterus bulbosus*, *E. spatulatus*, *Truncatiramus gigas*, *Pterygotus ludensis*, *Eurypterus cephalaspis*, *Nanahughmilleria pygmaea*, *Parahughmilleria salteri*, *Salteropterus abbreviatus*, *Hardieopterus megalops* and *H. banksii*. Plotnick (1999) interpreted the age of both assemblages as Prídolí, and palaeoenvironments to be intertidal sandy shore and intertidal mudflat, respectively (both benthic assemblage 1).

2.b. Abbreviations and terminology

The following abbreviations are used in the figures: c – carapace, dp – deltoid plates, e – eye, ecx – epicoxa, ep – epimeron, m – metastoma, op – operculum, 'pt' – 'post-telson', s – setae, sp – spine, t – telson. Prosomal appendages are numbered I–VI, individual podomeres in prosomal appendages P2–P9 (P1 termed the coxa which are numbered CII–CVI), genital appendage segments of type A and B A1–A3 or B1–B3 respectively and opisthosomal segments 1–12.

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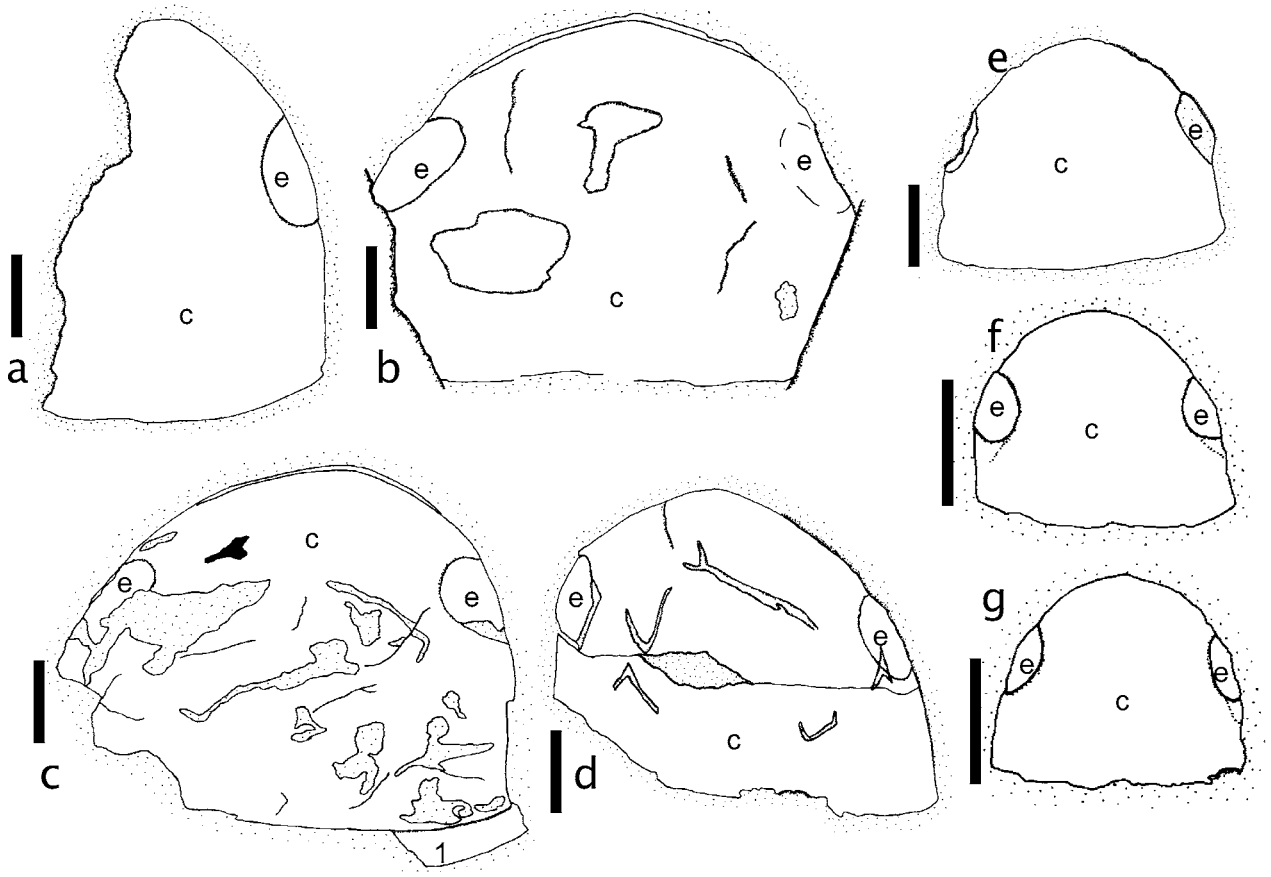


Figure 2. *Herefordopterus banksii*. Carapaces belonging to the species. (a) BGS GSM 89471, Kington; (b) BGS GSM Zf2866, Perton; (c) BGS GSM Zi3949, Perton; (d) BGS GSM 89474, Kington; (e) BGS GSM 89475, Kington; (f) BGS GSM 89479, Kington; (g) the lectotype BGS GSM 89476, Kington. For abbreviations and terminology please see Section 2.b. Scale bars 5 mm.

Morphological terminology follows Tollerton (1989), and higher systematics follows Novojilov (1962) and Størmer (1974).

3. Morphological interpretation

3.a. *Herefordopterus banksii*

Earlier descriptions of *H. banksii* (e.g. Kjellesvig-Waering, 1951) included many erroneous morphological interpretations. Comparisons between the *camera lucida* drawings provided here (Fig. 2a–g), and Kjellesvig-Waering's reconstruction (Kjellesvig-Waering, 1951, fig. 1A) show that he reconstructed a rounded anterior process compared to the more subtriangular carapace identified here. He also reconstructed the eyes slightly too far anteriorly. The single walking leg was confused with that here assigned to *S. abbreviatus*, but also erroneously described (see below). As described here, the prosomal appendages II–V of *H. banksii* are probably standard *Hughmilleria* type spiniferous appendages (Tollerton, 1989).

A coxa of appendage VI of *H. banksii* suggests it had around 12–13 gnathobasic teeth, the same number as pterygotids. This character separates *H. banksii* from other species of *Hughmilleria*, which has 18–20 gnathobasic teeth on VI (Sarle, 1903; Clarke, 1907). The intersegmental membrane and morphology of P5 and P6 in the swimming leg suggest this joint is responsible for the main promotor–remotor motion of the appendage, similar to that seen in *Eurypterus tetragonophthalmus* (Selden, 1981). A particularly wide metastoma with a distinct ornamentation of scales (Fig. 3d) that was assigned to *H. banksii* by Kjellesvig-Waering is here interpreted as a pterygotid (see below). The remaining two types are difficult to assign with certainty, but the more *Slimonia*-like of the two (Fig. 3c) might belong to *S. abbreviatus*. The third and most common type (Fig. 3a, b) is tentatively assigned to *H. banksii*.

Thanks to Kjellesvig-Waering (1951), the genital appendages of *H. banksii* are relatively well known. As with all more derived eurypterids in Eurypterina (*sensu* Novojilov, 1962), with the possible exception of *Megalograptus ohioensis* (see Caster & Kjellesvig-Waering, 1964), the genital operculum in *H. banksii* is composed of the two fused opercular segments posterior to the deltoid plates (Tetlie & Braddy, 2004). Both sexes in *H. banksii* have deltoid plates, although they are generally more clearly expressed in type B

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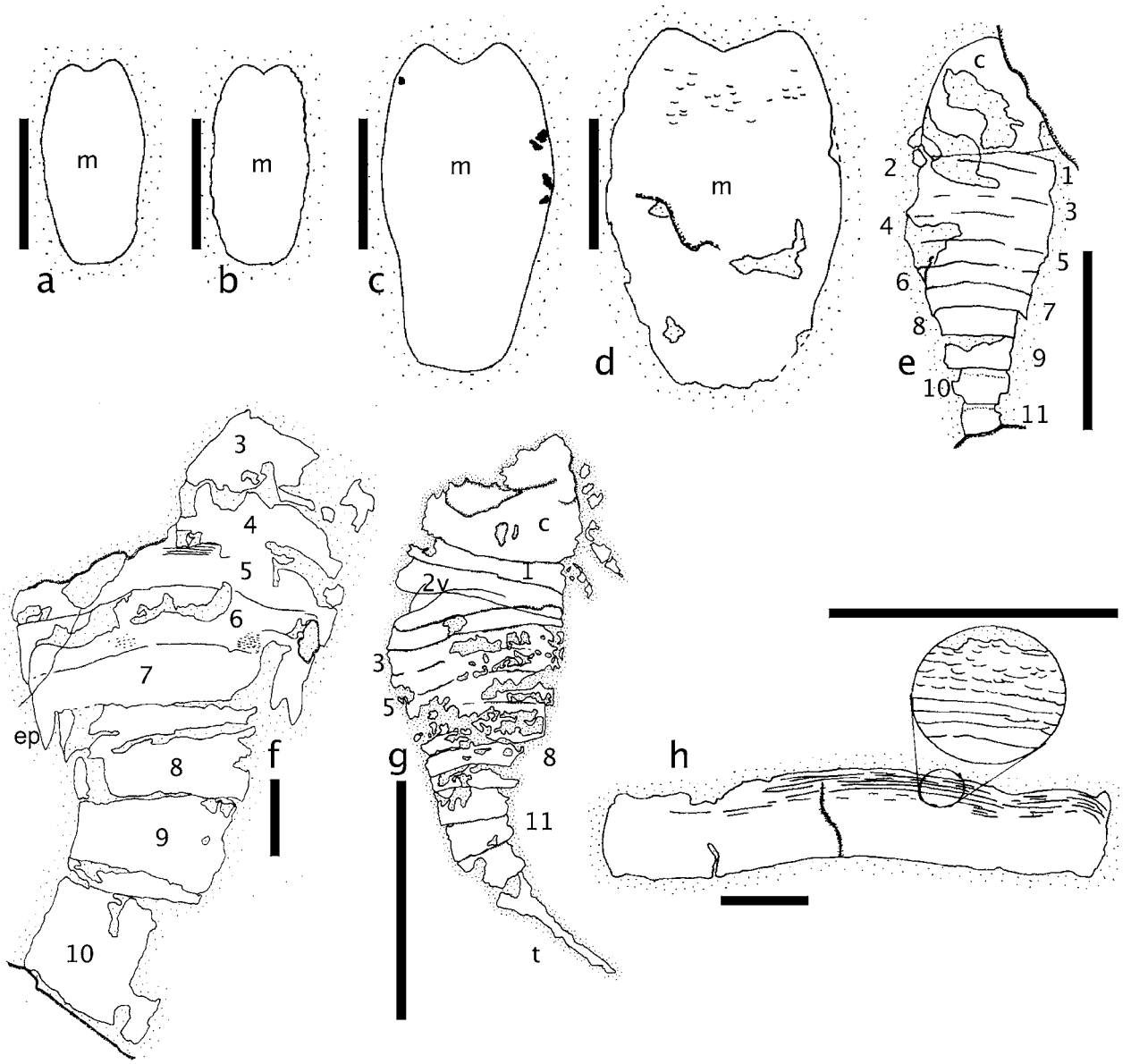


Figure 3. *Herefordopterus banksii*, *Salteropterus abbreviatus* and pterygotid sp. Metastoma and opisthosoma. (a) BGS GSM 89481, metastoma of *H. banksii*, Kington; (b) BGS GSM 89480, metastoma of *H. banksii*, Kington; (c) BGS GSM Zi3965, metastoma possibly belonging to *S. abbreviatus*, Perton; (d) BGS GSM 88907, metastoma possibly belonging to pterygotid sp., Perton; (e) BGS GSM 88912, carapace and opisthosoma of *H. banksii*, Perton; (f) BGS GSM Zi3959, opisthosoma of *H. banksii*, Perton; (g) BGS GSM Zf2871, carapace, opisthosoma and telson of *H. banksii*, Perton; (h) BGS GSM 89472, opisthosomal segment, with a magnified inset showing the anterior ornament, belonging to *Herefordopterus*, *Parahughmilleria* or *Nanahughmilleria*, Perton. For abbreviations and terminology please see Section 2.b. Scale bars 5 mm.

specimens (that is, males *sensu* Braddy & Dunlop, 1997). The posterio-medial margins are produced into long projections on the type A operculum. The ornament of the genital operculae consists of prominent scales, changing postmedially into lines converging towards the distal part of the genital appendages.

Unfortunately, Kjellesvig-Waering (1951) seems to have made a mistake in his observations on the type A appendage. He noted a two-segmented appendage (Kjellesvig-Waering, 1951, fig. 1H), although this would be unusual compared to most eurypterids in Eurypterina (*sensu* Novojilov, 1962) having three-segmented appendages, as described in, for instance, *S. acuminata* by Waterston (1960) and *A. mazonensis* by Wills (1964). The specimen in Figure 4d indicates that there are actually three segments in this appendage. The anterior segment is very long, extending slightly beyond the length of the operculum, showing that it was this segment boundary Kjellesvig-Waering (1951) observed. This segment has several ridges running along its length, suggesting it had a cross-section similar to a step-pyramid. The median segment is one-quarter the length of the first and has a median ridge running along its length. Laterally, it has lines of very

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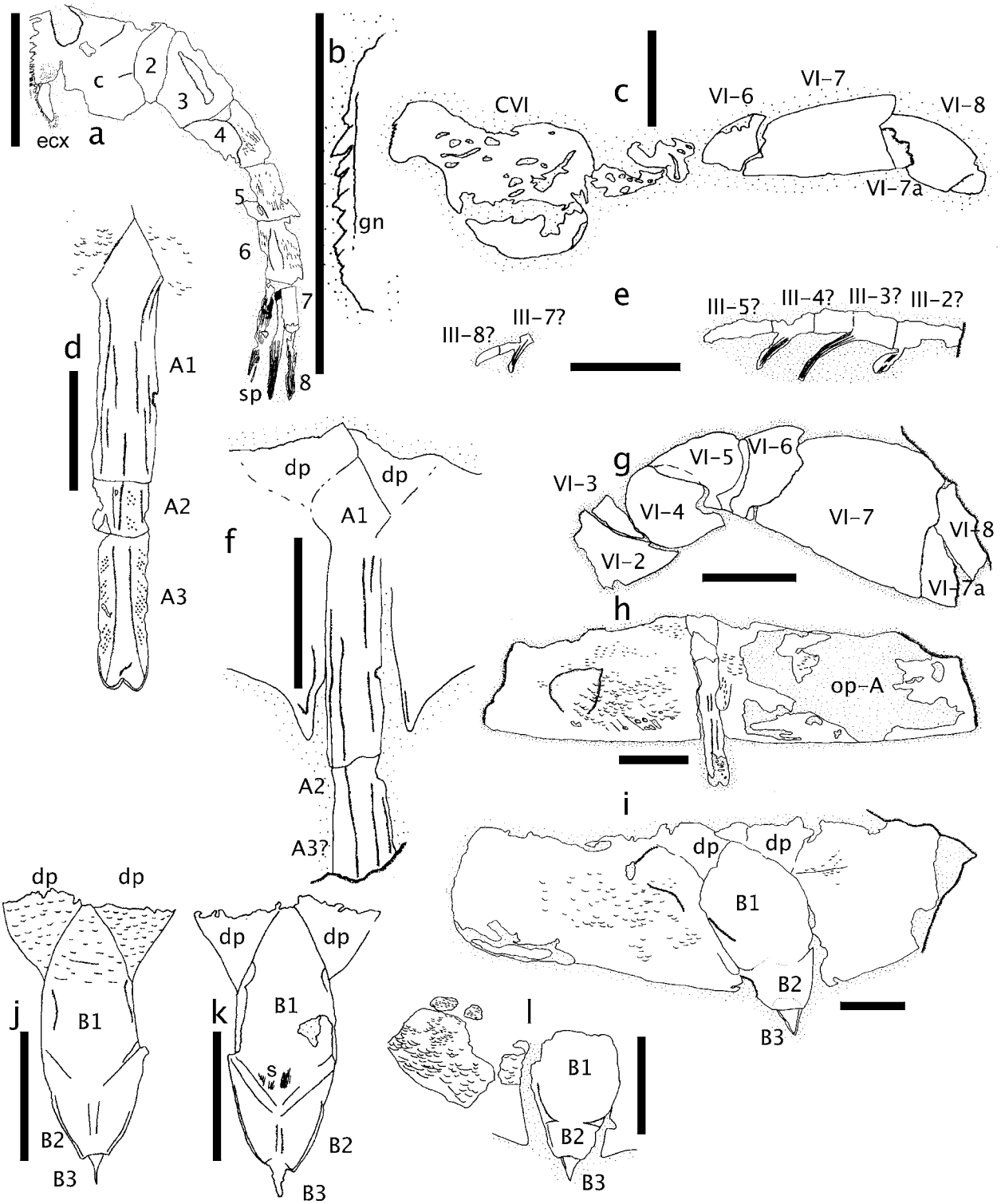


Figure 4. *Herefordopterus banksii*, *Salteropterus abbreviatus* and *Mixopterus* sp. Appendages. (a) BGS GSM 6003, prosomal appendage IV? possibly belonging to *S. abbreviatus*, Perton; (b) gnathobase of specimen in (c); (c) BGS GSM Zf2865, swimming leg probably belonging to *H. banksii*, Perton; (d) BGS GSM Zf2863, genital appendage type A belonging to *H. banksii*, Perton; (e) BGS GSM 88913, spiniferous appendage probably belonging to *Mixopterus* sp., Perton; (f) BGS GSM Zf2861, genital appendage type A belonging to *H. banksii*, Perton; (g) BGS GSM 6001, swimming leg probably belonging to *H. banksii*, Perton; (h) BGS GSM Zf2865, genital appendage type A belonging to *H. banksii*, Perton; (i) BGS GSM 88914, genital appendage type B belonging to *H. banksii*, Perton?; (j) BGS GSM 6004A, genital appendage type B belonging to *H. banksii*, Perton; (k) BGS GSM 6004, genital appendage type B belonging to *H. banksii*, Perton (note setae); (l) BGS GSM 6002, genital appendage type B belonging to *H. banksii*, Perton. For abbreviations and terminology please see Section 2.b. Scale bars 5 mm.

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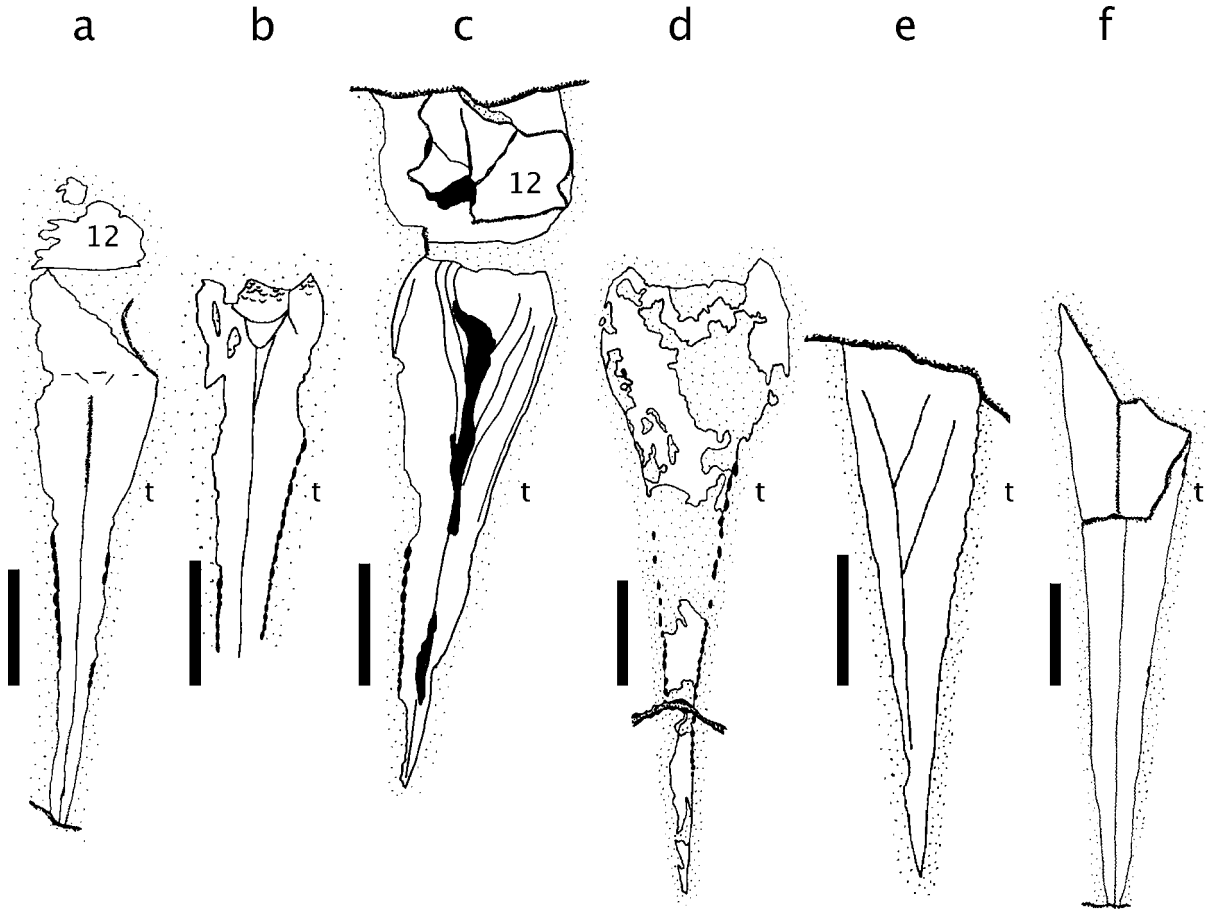


Figure 5. *Herefordopterus banksii*. Telsons belonging to this species. (a) BGS GSM number not known; (b) BGS GSM 5999, Perton; (c) BGS GSM 89400, Perton; (d) BGS GSM 89404, Ludlow; (e) BGS GSM 89405; (f) BGS GSM 89485, Kington. For abbreviations and terminology please see Section 2.b. Scale bars 5 mm.

small triangular scales. Whether these are ornamental or the attachment sites for setae is not known. The posterior segment is approximately half the length of the anterior and twice the length of the median segment. The segment has a broad, raised plateau medially. Towards the lateral margins, small triangular scales form lines similar to those on the median segment. Distally, this segment has a bilobed termination and a narrow rim is present along the bilobed outer margin. However, a more poorly preserved appendage (Fig. 4f) does not show this junction and it is possible that the appendage was composed of two segments, as described by Kjellesvig-Waering (1951), but the preferred interpretation is three segments.

The type B appendage is more or less as Kjellesvig-Waering (1951) described it, consists of three segments, and is teardrop-shaped in overall aspect, again quite similar in shape to pterygotid type B appendages. As in the type A appendage, the diamond-shaped anterior segment is longer than the distal two segments combined. The anterior opercular segment is ornamented anteriorly by scales less dense than on the deltoid plates. Distally, one specimen (Fig. 4k) shows the presence of setae. The arrow-shaped median segment is approximately half the length of the anterior, has a median ridge and a thin marginal rim. The distal triangular segment is half the length of the median and one quarter that of the anterior. It has a narrow marginal rim, but other details cannot be observed.

The two longitudinally most complete telsons in the collections were previously assigned to two taxa (*H. acuminata*, Fig. 5d; *H. banksii*, Fig. 5c). They are also among the most compressed telsons, resulting in having broader anterior regions than uncompressed telsons. Both these telsons show the marginal ornament of scales, and one (Fig. 5c) shows the lines defining the different flat areas of the dorsal side of the telson. The only telson attached to an articulated specimen belongs to a juvenile (Fig. 3g). Although very poorly preserved, this telson is much wider anteriorly than the more or less lanceolate telson reconstructed by Kjellesvig-Waering (1951, fig. 1L), although Kjellesvig-Waering (1951, fig. 2A) also drew this juvenile with a wide telson. Less compressed but anteriorly imperfect specimens include those shown in Figure 5a, b, e and f. All these telsons also indicate the marginal ornament of sclerotized scales. An especially interesting specimen is the telson in Figure 5f, which is three-dimensionally preserved

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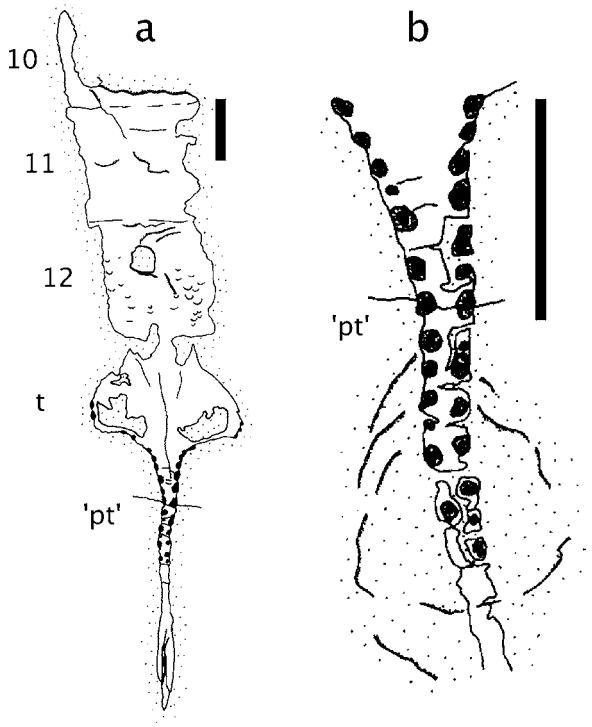


Figure 6. *Salteropterus abbreviatus*. (a) Drawing of Zf2864, segments 10–12 and telson. (b) Close-up of the so-called segmented 'post-telson' reported by Kjellesvig-Waering (1961), showing that it is nothing more than a number of non-linear cracks following deposition of this part of the telson in a depression. For abbreviations and terminology, please see Section 2.b. Scale bars 5 mm.

in sandstone and shows that the ventral side also had a carina only half the height of the dorsal one, and another specimen (Fig. 5b) showing the intricate morphology and scaly ornament of the anterior parts of the dorsal surface of the telson. All telsons are illustrated in Figure 5, indicating their relative longitudinal preservation.

3.b. *Salteropterus abbreviatus*

The most detailed earlier description of this very rare taxon was that of Kjellesvig-Waering (1951). The most interesting feature of *S. abbreviatus* is the posterior elongation of the telson into a bilobed 'rudder' that has earlier been interpreted as segmented, and was termed the 'post-telson'. Kjellesvig-Waering (1951, p. 16) described the preservation of the telson: 'indistinct partings separate the stem into what may be segments, but these are probably due to cracks across the integument'. Later, Kjellesvig-Waering (1958*a*, p. 301) wrote: 'In view of definite segmentation in *C*. [=*Carcinosoma*] *newlini* there seems little doubt that the post-telson of *Salteropterus* is also segmented.' However, the telson in *S. abbreviatus* is not segmented. The observed 'segments' are a series of non-linear cracks developed because this part of the telson was deposited in a depression (see Fig. 6b), and during taphonomy, brittle deformation took place. However, the segmented 'post-telson' might still be present in *C. newlini*, and only a restudy of the Kokomo material can resolve this question.

4. Systematic palaeontology

Class CHELICERATA Heymons, 1901
Order EURYPTERIDA Burmeister, 1843
Suborder EURYPTERINA Burmeister, 1843
Superfamily PTERYGOTOIDEA Clarke & Ruedemann, 1912
Family HUGHMILLERIIDAE Kjellesvig-Waering, 1951
Herefordopterus gen. nov.

Diagnosis. Medium-sized hughmillerid with marginal eyes, parabolic to campanulate A carapace with an angular anterior carapace margin; prosomal appendages II–V (?) of *Hughmilleria* type; 12 or 13 gnathobasic teeth on VI; mid-section second order opisthosomal differentiation; telson lanceolate with bulbous anterior end and with crenulate marginal ornament posteriorly.

Type (and only) species. *Himantopterus banksii* Salter, 1856*a*.

Etymology. After Herefordshire, England, where two of the three localities (both the type locality and the most productive locality) producing the genus are found.

Herefordopterus gen. nov. *banksii* (Salter, 1856*a*)

Himantopterus banksii Salter, 1856*a*, pp. 32–3; Banks, 1856, p. 99, pl. 2, figs 5, 6; Salter, 1856*b*, p. 266, foss. 66, fig. 1.

Pterygotus banksii Salter, 1859*c*, p. 540; Salter, 1867, p. 239; Marston, 1870, p. 409; Woodward, 1871*a*, p. 261; Woodward, 1871*b* (1866–1878), pp. 72–4, pl. 16, figs 2, 3, 5, 6 (not 4); Salter, 1873, p. 189; Woodward, 1877, p. 67; Etheridge, 1888, p. 66; Sarle, 1903, p. 1103; Elles & Slater, 1906, p. 220; King, 1934, p. 563.

Pterygotus (*Erettopterus*) *banksii* Salter, 1859*b*, pp. 51–3, pl. 12, figs 22, 24–29, 31–35, 39, 41–44 (not 23, 30, 36–38, 40, 45, 46); Bigsby, 1859, p. 322; Clarke & Ruedemann, 1912, p. 379; O'Connell, 1916, p. 47; Diener, 1924, p. 10; Størmer, 1936, p. 41.

Eurypterus acuminatus Salter, 1859*a*, pp. 233–6, pl. 10, fig. 17 (not 19); Bigsby, 1859, p. 321; Woodward, 1864, p. 107; Marston, 1870, p. 409; Woodward, 1871*a*, p. 261; Woodward, 1872 (1866–1878), pp. 140, 146–8, pl. 28, fig. 13 (not 15); Woodward, 1877, p. 64; von Zittel, 1885, p. 650; Etheridge, 1888, p. 52; Elles & Slater, 1906, p. 220; O'Connell, 1916, p. 38; Diener, 1924, p. 15; King, 1934, p. 563. Syn. nov.

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Stylonurus megalops (*pars*) Salter, 1859*a*, pl. 10, figs 13, 14; Brodie, 1869, p. 236; Woodward, 1872 (1866–1878), pl. 28, figs 8, 9.
Eurypterus brodiei (*pars*) Woodward, 1871*a*, pp. 262–3, figs 2, 3; Woodward, 1872 (1866–1878), pp. 162–3, fig. 51 (2, 3).
Hughmilleria banksii Størmer, 1934*a*, p. 83; Størmer, 1934*b*, p. 4; Kjellesvig-Waering, 1950, p. 228; Kjellesvig-Waering, 1951, p. 1–14, figs 1A–L, 2A, B, pls 1, 2 (1–5); Kjellesvig-Waering, 1958*b*, p. 1121; Størmer & Kjellesvig-Waering, 1969, p. 210; Kjellesvig-Waering, 1986, p. 12,183; Dunlop, Braddy & Tetlie, 2002, pp. 99–100.
Hughmilleria acuminata Kjellesvig-Waering, 1951, p. 2.
Hughmilleria (*Hughmilleria*) *banksii* Kjellesvig-Waering, 1961, pp. 797–800, pl. 94, fig. 1.
Hughmilleria (*Hughmilleria*) (?) *acuminata* Kjellesvig-Waering, 1961, p. 797, fig. 1 (20), pl. 94, fig. 3, pl. 95, fig. 9.
Hughmilleria ? *banksi* Størmer, 1973, pp. 123, 126–7, 130–2, 141, 162.
Hughmilleria ? *acuminata* Plotnick, 1999, p. 122.
Hughmilleria banksi Kjellesvig-Waering, 1986, fig. 79c; Manning & Dunlop, 1995, p. 288; Plotnick, 1999, p. 122.

Diagnosis. As for the genus.

Lectotype. BGS GSM 89476 (Fig. 2g), a small carapace. No type specimen had previously been designated because it is unknown which specimens were available to Salter. Almost all specimens are from Perton and were collected after the original description (Salter, 1856*a*), and this is one of very few specimens from the type locality, Kington, which presumably Salter had available in his description.

Other material. 5997; 5999; 6001; 6002; 6003; 6004 (counterpart 6004a); 88906; 88907; 88908; 88909; 88912; 88914; 89399; 89400 (counterpart In 44584); 89402; 89404 (previously a type of '*H. acuminata*'); 89405; 89419; 89470; 89471; 89472; 89474; 89475; 89477; 89478; 89479; 89480; 89481; 89485; 89492; 89628; 89629; Zf2861; Zf2863; Zf2865; Zf2866; Zf2867; Zf2868; Zf2869; Zf2871 (counterpart Zf2871a); Zi3940; Zi3949; Zi3959; Zi3965; BU 17; BU 27; In 44566; In 44571; In 44572; PE 4910; PE 4911; PE 4915; PE 4917, PE 4981 (specimens numbered 5997–6004, 88906–89629 and starting with the prefixes Zf or Zi are from the British Geological Survey (BGS GSM), BU 17 and BU 27 from the Geological Museum, Birmingham University, In 44566–In 44584 from the British Museum (Natural History) (BMNH), and PE 4910–4981 are in the Field Museum of Natural History (Chicago)).

Type horizon and locality. Downton Castle Sandstone Formation, quarry on Radnor Hill golf course, Kington, Herefordshire. The eurypterid-bearing strata are in the lower part of the quarry and are now covered by scree.

Additional horizons and localities. Downton Castle Sandstone Formation, Ludlow, Shropshire; Temeside Shales Formation, Ludlow, Shropshire and Perton, Stoke Edith, Herefordshire.

Morphological description. Carapace L/W ratios 0.80 (adults), 0.96 (juveniles); lateral angle 95–100°, close to parabolic and campanulate A shapes (Tollerton, 1989). Lateral margins meet in slightly angular anterior margin. Marginal rim present anterior to eyes, narrowing towards eyes (Fig. 2). Eyes oval and very large (length one-third of carapace length), and placed centrilaterally (Tollerton, 1989). Ocelli (seen on BGS GSM 88910) relatively large, situated between posterior parts of eyes. Ventral doublure not known, but two lines indicating the presence of an epistoma seen on BGS GSM 88910.

One walking leg known (FMNH PE 4917). Four podomeres preserved, two proximal ones without preserved spines, two distal ones with one preserved spine each, that is, the appendage is of the *Hughmilleria* type. The two distal podomeres are rectangular in outline. The preserved lengths and widths (in mm) of these are (proximal to distal): 5.1/2.8; 5.6/3.1. The preserved lengths of both spines are 2.5 mm.

Two specimens preserve appendage VI; BGS GSM Zf2865 (Fig. 4b, c) complete appendage with well-developed coxa and nine preserved (12–13 estimated if complete) gnathobasic teeth. P2 through P5 poorly preserved and boundaries not identified. Triangular P6 5.0 mm long, 3.1 mm wide. P7 long (9.9 mm), slender (5.0 mm); L/W ratio 1.98. P7a poorly preserved. P8 long (7.5 mm), slender (4.2 mm) giving paddle (P7+P8) high L/W ratio of 3.33 (see also Størmer, 1973, fig. 2, who determined L/W ratio to 3.50 based on figures from Kjellesvig-Waering, 1951). P9 not preserved. BGS GSM 6001 (Fig. 4g) well-preserved appendage VI with P2 to P8 preserved. P2 triangular, 5.0 mm long, 4.4 mm wide. P3 very small, triangular (1.2 mm long, 3.0 mm wide). P4 subcircular (4.4 mm long, 4.4 mm wide), partly overlaid by P5 (5.2 mm long and 3.6 mm wide). Intersegmental membrane preserved between P5 and P6. P6 3.2 mm long, 4.9 mm wide, P7 10.2 mm long (but incomplete), 6.7 mm wide. P7a triangular but poorly preserved, also this appendage preserved from posterior. Small fragment of P8 preserved.

No specimens have metastoma preserved *in situ*. Three morphotypes present in material. Most common type (Fig. 3a, b), (L/W = 1.92–2.00) widest centrally, thought to represent *H. banksii*.

Few specimens show significant opisthosomal portions. BGS GSM Zi3959 (Fig. 3f) shows segments 3 to 10, and has a mid-section second order opisthosomal differentiation (Tollerton, 1989). Ornamentation of lines anteriorly and small scales posteriorly on

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pre-abdominal segments. Post-abdominal segments much longer than pre-abdominal and lacking ornament. An isolated opisthosomal segment (BGS GSM 89472; Fig. 3h) has an ornament that gradually turns from broadly lunate scales into lines. Both specimens might possibly belong to *Parahugmilleria salteri* or *Nanahughmilleria pygmaea*, although these taxa have not previously been reported from Perton (Kjellesvig-Waering, 1951, p. 6). However, these two taxa occur in the same formation at Ludlow. Woodward (1871*a*) reported *N. pygmaea* from Perton, but I agree with Kjellesvig-Waering (1951, p. 6) that it is likely that the two juvenile *H. banksii* described below were the basis of Woodward's identification.

Opisthosomal proportions best preserved in two juveniles. BGS GSM 88912 (Fig. 3e) preserved length 12.5 mm, prosoma and anterior 11 opisthosomal segments; eyes not preserved, but prosomal shape indicates *H. banksii*; opisthosoma gently tapering with mid-section second order differentiation. BGS GSM Zf2871 (Fig. 3g) another juvenile, 22.1 mm long; poorly preserved centrilateral eye indicates *H. banksii*. This specimen shows much of the opisthosoma; preservation is poor but suggesting telescoped post-abdomen (post-abdominal segments shorter than in other specimens).

Individual plates (median opercular plate and posterior opercular plate; Tetlie & Braddy, 2004) in genital operculum not identified. Both sexes have deltoid plates which are better expressed in type B specimens. The posterio-medial margins of genital operculum have long projections in type A, shorter in type B; ornament of prominent scales, posterio-medially changing to lines pointing towards distal part of genital appendage.

BGS GSM Zf2863 (Fig. 4d) is a three-segmented type A appendage. Anterior rectangular segment slightly longer than operculum, ridges along length. Median subquadrate segment quarter length of anterior segment; laterally lines of small triangular scales present; ridges along length. Posterior rectangular segment half length of anterior segment; broad raised plateau medially and laterally lines of small triangular scales on lateral slopes; ridges along length; bilobed termination distally with narrow rim.

Type B also three-segmented, teardrop-shaped in overall aspect. Diamond-shaped anterior segment longer than the other two combined; ornamented anteriorly by scales less densely than on deltoid plates; BGS GSM 6004 (Fig. 4k) has setae posteriorly. Arrow-shaped median segment half length of anterior, with median ridge and marginal rim. Distal triangular segment has a marginal rim, and length half of median segment.

Telson wide anteriorly, posteriorly tapering to lanceolate shape. Marginal ornament (crenulate margins) of dark scales on posterior two-thirds. Dorsally, three pairs of ridges define three flat areas anteriorly, the first broadly parabolic, the second parabolic and the third acutely angular, before joining the dorsal keel (Fig. 5b). Keel present dorsally and ventrally; ventral keel half the height of dorsal keel. Anteriorly, small lunate scales ornament telson.

Remarks. The species *Hughmilleria acuminata* (Salter, 1859*a*) was previously known only from telsons, which are perfectly compatible with being anteriorly complete, but flattened telsons of *Herefordopterus banksii* (Salter, 1856*a*) as demonstrated in Figure 5. Luckily, the latter name has priority over the former, as the new genus is interpreted a sister-taxon of (*Slimonia acuminata* + *Salteropterus abbreviatus* (pterygotids)), and two species so close in the phylogeny with the same specific epithet might prove confusing. *H. acuminata* is known from two telsons (only specimen in Fig. 5d figured here) that have a wider anterior portion than usual for *H. banksii*. However, these two specimens are completely flattened, in contrast to the majority of telsons previously assigned to *H. banksii*. Kjellesvig-Waering (1951) noticed the marginal ornament of heavily sclerotized scales in both *H. banksii* and *H. acuminata*, but failed to realize that what he described as the entire telson of *H. banksii* in fact only represented telsons with incomplete antelateral margins or the posterior parts of telsons. Differences in relative widths are easily explained by differing degree of compression, and different degrees of anterior preservation (most specimens earlier assigned to *H. banksii* have a poorly preserved anterior region, laterally or longitudinally). With the inclusion of specimens earlier assigned to *H. acuminata* into *H. banksii*, the entire telson can be described, and is more or less similar to that previously assigned to *H. acuminata*, but somewhat narrower in its uncompressed form. A number of specimens of different ontogenetic stages, different levels of compression and different longitudinal preservation are present, supporting the hypothesis that these two taxa are synonyms (Fig. 5). An idealized reconstruction of *H.* gen. nov. *banksii* is provided in Figure 7.

Family SLIMONIIDAE Novojilov, 1962
Salteropterus Kjellesvig-Waering, 1951
Salteropterus abbreviatus (Salter, 1859*a*)

Diagnosis. Appendage IV (?) with eight podomeres, reduced spinosity with one pair of long spines on podomere six. Telson triangular with marginal ornament of sclerotized scales; long stem-like posterior prolongation, developed distally into three-lobed organ.

Holotype. Specimen figured by Salter (1859*a*, p. 234, fig. 18); repository unknown.

Additional material. BGS GSM 88911 (described by Woodward, 1871*a*, p. 261), BGS GSM Zf2864 (described by Kjellesvig-Waering, 1951, pl. 2, fig. 6).

Type horizon and locality. Downton Castle Sandstone Formation, quarry on Radnor Hill golf course, Kington, Herefordshire.

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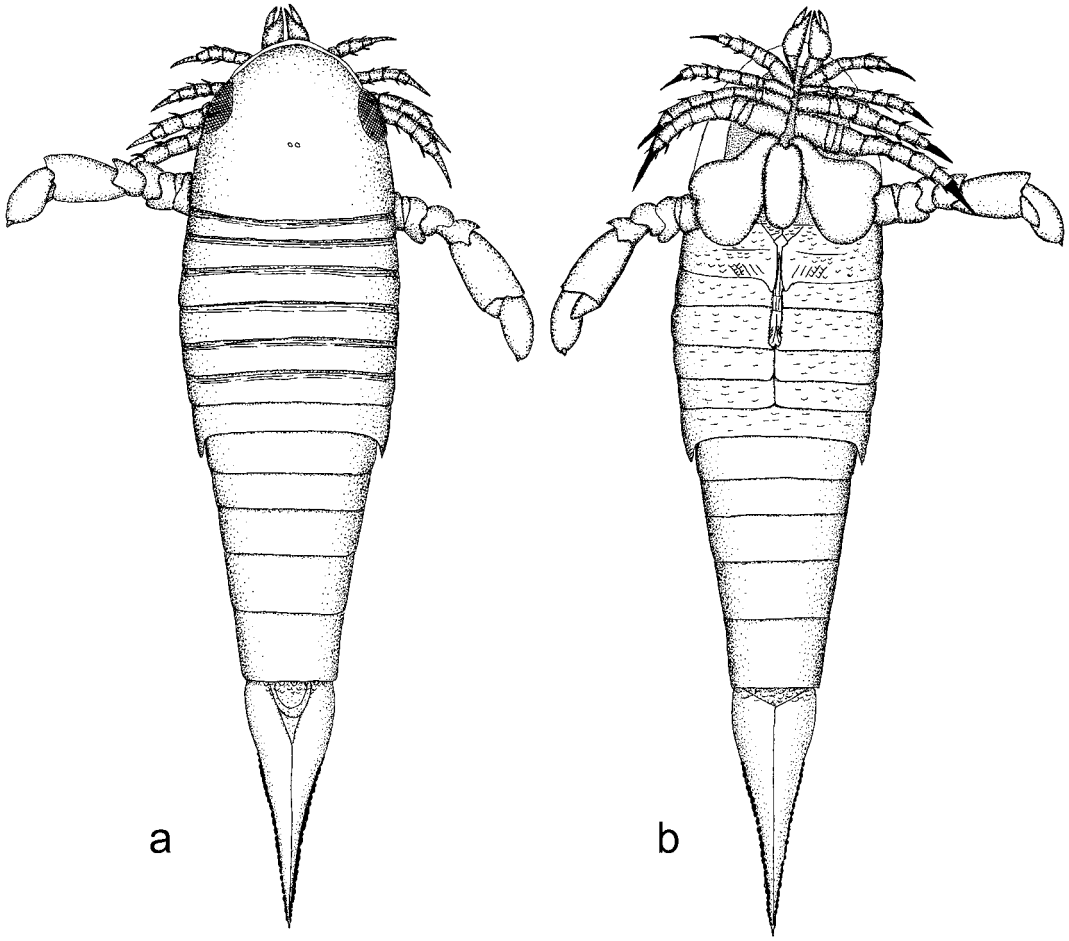


Figure 7. Idealized reconstructions of *Herefordopterus banksii*. (a) Dorsal view; (b) ventral view of specimen with genital appendage type A.

Additional horizon and locality. Temeside Shales Formation, Perton, Stoke Edith, Herefordshire.

Morphological description. One walking leg known (BGS GSM 6003; Fig. 4a) with eight podomeres either representing appendage three or more probably four (see Selden, 1981). Coxa 5.0 mm long, 3.7 mm wide with 15 gnathobasic spines. Posterior spines more slender than anterior ones, although little length difference. Coxa ornamented with small pustules anteriorly and posteriorly. Posterior on coxa a well-preserved epicoxite present (1.5 mm long, 0.5 mm wide), with 30 to 40 small spines or setae. P2 short (1.2 mm) and wide (2.9 mm). P3 3.1 mm long, 2.5 mm wide. P4 2.5 mm long, 2.3 mm wide proximally and distally narrowing. P5 2.1 mm long, 2.0 mm wide with antero-distal projection. P6 2.5 mm long, 1.5 mm wide with a pair of long spines distally; spines as long as P7 and the distal spine (P8) combined, and ornamented with longitudinal striations. P4 to P6 ornamented with lunate scales and striations. P7 very short (1.5 mm), narrow (0.6 mm), with no spines. P8 (distal spine) preserved length 2.4 mm, width 0.2 mm, with longitudinal striations.

A metastoma BGS GSM Zi3965 (L/W = 1.92) widest on the anterior half (Fig. 3c) is interpreted as belonging to *S. abbreviatus* because of similarities to that of *Slimonia acuminata*. Segments 10 to 12 (BGS GSM Zf2864; Fig. 6a) tapering, having semicircular scales. Telson (also BGS GSM Zf2864) anteriorly triangular with marginal ornament of flattened scales and long posterior projection ending in a bilobed rudder.

Remarks. The described prosomal appendage is assigned to this taxon with caution. It was earlier assigned to *H. banksii*, but after the discovery of a *Hughmilleria* type appendage associated with a *H. banksii* specimen (FMNH PE 4917), there is no longer any reason that this unique type of appendage should be assigned to *H. banksii*, as all hughmilleriids, *Slimonia* and pterygotids have undifferentiated walking appendages. The appendage was not only erroneously assigned, but also erroneously described by Kjellesvig-Waering (1951). He described it as showing one spine on P6 and one spine on P7. However, this is not correct, as there is a pair of long spines emerging from the distal margin of P6 (Fig. 4a).

When Kjellesvig-Waering (1951) erected *Salteropterus* he noted (p. 17) that the posterior three opisthosomal segments were tapering and elongated like those of *Slimonia*. Later, Kjellesvig-Waering

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(1961, p. 809) suggested that the fragmentary carapace of *Slimonia* ? *stylops* (Salter, 1859*b*) belonged to *S. abbreviatus*. This was later followed by Caster & Kjellesvig-Waering (1964), Størmer (1974) and Tollerton (1989) placing *Salteropterus* in the family Slimoniidae (but not by Novojilov, 1962, who erected the family). The only known specimen of *S.* ? *stylops* was from Kington, Herefordshire, and was in the collection of R. Banks, Kington, but its repository is now unknown, and the name should possibly be treated as a *nomen dubium*.

Since a segmented posterior part of the telson is not present, the term 'post-telson' is suggested to be abandoned at least for this taxon, since it suggest features posterior to the telson. The elongated structure of *Salteropterus* is a part of the telson.

Family PTERYGOTIDAE Clarke & Ruedemann, 1912
pterygotid sp.

Remarks. BGS GSM 88907, a metastoma (Fig. 3d), was referred to *H. banksii* by Kjellesvig-Waering (1951) but is here interpreted belonging to a pterygotid because of the low L/W ratio and the presence of large semicircular scales ventrally, similar to those described from other pterygotids. It would be no surprise to have identifiable parts of pterygotids present, as several other specimens of *H.* gen. nov. *banksii* (e.g. BGS GSM 88906, BGS GSM 5999, BGS GSM Zf 2863) are associated with fragments of pterygotid cuticle. Additionally, *Erettopterus spatulatus* Kjellesvig-Waering, 1961, *P. ludensis* Salter, 1859*b* and *Truncatiramus gigas* (Salter, 1859*b*) are all described from this horizon, but due to our limited knowledge of these forms, a closer identification of this metastoma is not possible.

Superfamily MIXOPTEROIDEA Størmer, 1955
Mixopterus ? sp.

Remarks. BGS GSM 88913, an appendage (Fig. 4e) belongs to a mixopterid (*Mixopterus*, *Lanarkopterus*, *Carcinosoma*, *Paracarcinosoma* or *Rhinocarcinosoma*). Kjellesvig-Waering (1951, fig. 2c) noted a *Mixopterus* sp. from the locality, which is also the most likely identity also for this specimen, given the long spines on the distal podomeres and the lobe-like spine on the most proximal podomere (see Størmer, 1934*a*).

5. Phylogenetic position of *Herefordopterus* and *Salteropterus*

A character uniting *Herefordopterus* gen. nov., *Hughmilleria*, *Slimonia acuminata* and pterygotids is the presence of marginal eyes, and a character uniting *Herefordopterus* gen. nov., *Hughmilleria* and *Slimonia acuminata* is a marginal rim much broader anterior to than posterior to the eyes. With *H. acuminata* (Salter, 1859*a*) suggested to be a junior synonym of *H.* gen. nov. *banksii*, the only remaining species of *Hughmilleria* are *H. socialis* Sarle, 1903 and *H. shawangunk* Clarke, 1907 from the USA and possibly *H.* (?) *lanceolata* (Salter, 1856*a*) from Scotland. *Hughmilleria chiplonkari* Dubey, 1985 is considered to be a slickenside on a fault plane, vaguely resembling the shape of a eurypterid and is found in a sequence with an age of approximately 870 Ma (P. Kathal, pers. comm. 2003). These three species of *Hughmilleria* (although preservation is poor in *H. shawangunk*) do not have marginal crenulate ornament of the telson, which is present in *Herefordopterus*, *Slimonia*, *Salteropterus* and pterygotids. The three recognized species of *Hughmilleria* also have a greater number of gnathobasic teeth on VI, and all are retained in *Hughmilleria*.

A character uniting *Herefordopterus* and *Hughmilleria* is the mid-section second-order differentiation, but this character is plesiomorphic, as it is present in some species with intramarginal eyes (*Parahughmilleria hefteri* and *Adelophthalmus mazonensis*). A character suggesting that *Salteropterus* occupies a more derived position than *Hughmilleria* and *Herefordopterus* is the partial loss of appendage spinosity in *Salteropterus*. *Hughmilleria* (and probably *Herefordopterus*) has paired spines on the four or five penultimate podomeres (the spines are reduced in the proximal three of these in *H. socialis*) while *Salteropterus*, as described here, retains only one pair of spines on podomere 6 of appendage IV. *Slimonia* and pterygotids have lost all spines on appendages II–V. The characters discussed here suggest the phylogeny of the Pterygotoidea has a topology like this: (*Hughmilleria* (*Herefordopterus* ((*Slimonia* + ? *Salteropterus*) (pterygotids)))).

Acknowledgements. P. Taylor, Dr M. Howe and P. Shepherd (BGS), Dr A. Ross (BMNH) and C. Fricker (FMNH) are thanked for access to and loan of material in their care. V. P. Tollerton Jr (New York State Museum) is thanked for information about the morphology of the genital appendages of *H. socialis*. Dr P. Kathal (Dr Harisingh Gour University) is thanked for information regarding the nature and age of '*Hughmilleria chiplonkari*' Dubey, 1985 and Prof. R. E. Plotnick (University of Chicago) for tracking down this reference. Dr S. J. Braddy (University of Bristol) and Dr R. A. Moore (University of Kansas) are thanked for improving the manuscript, and Prof. D. L. Bruton (Paleontologisk Museum, University of Oslo) for advice on types and taxonomic rules. Dr Jason A. Dunlop (Museum für Naturkunde, Berlin) and one anonymous reviewer suggested valuable improvements to the manuscript. The author acknowledges grants 145565/432 and 166647/V30 from Norges Forskningsråd (NFR) and the University of Bristol for financial support.

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https://doi.org/10.1017/S0016756806002536 Published online by Cambridge University Press