The affinities of the Carboniferous whip spider *Graeophonus anglicus* Pocock, 1911 (Arachnida: Amblypygi)

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ABSTRACT: The Late Carboniferous whip spider *Graeophonus anglicus* Pocock, 1911 (Arachnida: Amblypygi), is redescribed on the basis of the holotype and nine other specimens all preserved in sideritic nodules from the British Middle Coal Measures of Coseley, Staffordshire, UK. This species is clearly basal with respect to most living whip spiders, expressing numerous plesiomorphic character states and can be referred to both the suborder Paleoamblypygi and the 'living fossil' family Paracharontidae (with one Recent species), the latter based on an explict character of dorsal spination on the pedipalp femur. This suggests that crown-group Amblypygi originated by at least the mid-Palaeozoic.

KEY WORDS: Arthropoda, Chelicerata, Coseley, Coal Measures, Duckmantian

Whip spiders (Arachnida: Amblypygi), also known as tail-less whipscorpions, are one of the so-called 'minor' orders of arachnids. The catalogue of Harvey (2003) recognised 136 extant species in five families. They occur widely across tropical and sub-tropical ecosystems and are typically nocturnal predators on other arthropods. Weygoldt (2000a) provided an excellent summary of their biology. Whip spiders are distinctive, usually rather delicate-looking arthropods. A detailed account of their skeleto-muscular anatomy can be found in Shultz (1999). They have a flattened body that allows them to crawl into narrow spaces. The body comprises a wide prosomal region covered by a kidney-shaped carapace, narrowly joined via the pedicel to a twelve-segmented opisthosoma in which the posteriormost segments form a small pygidium. The mouthparts comprise so-called 'clasp-knife' chelicerae with two articles, while the pedipalps used for prey capture are large, sub-raptorial and usually rather spiny. The anteriormost legs of whip spiders are elongate, effectively antenniform, and are used to probe ahead of the animal, which walks hexapodously on the remaining three slender leg pairs. Unlike the probably closely-related whip scorpions (Uropygi) (see section 4), whip spiders lack a flagellum (or tail) and/or defensive glands at the back of the opisthosoma.

Fossil whip spiders are poorly known. Selden *et al.* (1991) described some Middle Devonian cuticle fragments from Gilboa, USA including trichobothria on the patella of the leg; a feature consistent only with Amblypygi among extant arachnids. The unequivocal fossil record of whip spiders begins in the late Carboniferous Coal Measures of Europe and North America (see section 1). There are also younger records provisionally assignable to extant families from the Crato Formation of Brazil (Dunlop & Martill 2002; Dunlop & Barov 2005) and as inclusions in amber (e.g. Schawaller 1982). Following Weygoldt (1996), living whip spiders are divided into two suborders: the basal Paleoamblypygi (containing one monotypic family) and the more derived Euamblypygi (i.e. all remaining species). Weygoldt (1996, 2000a, b) suggested that at least one Carboniferous genus resembles the single 'living

fossil' paleoamblypygid, *Paracharon caecus* Hansen, 1921 from Guinea-Bissau in West Africa. Harvey (2003) listed the four known Carboniferous species as members of the Paleoamblypygi, but of uncertain familial affinities. The principal aim of this paper is to re-examine well-preserved members of the British Carboniferous whip spider *Graeophonus anglicus* Pocock, 1911 to see whether testable characters could be resolved which allow this fossil to be integrated more convincingly into Weygoldt's phylogenetic framework.

1. Previous work

The genus *Graeophonus* Scudder, 1890 was erected for two Late Carboniferous Coal Measures fossils. Historically, the older of the two, from Cape Breton in Canada, is an isolated opisthosoma (or abdomen), which was originally interpreted as a dragonfly (Odonata) larva, *Libellula carbonaria* Scudder, 1876. It was thus assigned to a Recent insect genus. The other, more complete fossil, from Mazon Creek, USA, was assumed by Scudder (1890) to be conspecific with the Cape Breton specimen. Both were then interpreted as arachnids and named *Graeophonus carbonarius* (Scudder, 1876). At the end of the nineteenth century, Amblypygi and Uropygi were combined together under the ordinal name Pedipalpi, and Scudder (1890) assigned both *Graeophonus* and a new fossil whip scorpion to a new pedipalp family, Geralinuridae, which was diagnosed by Scudder on a divided carapace. Here, a posterior sclerite was associated with the fourth pair of legs. This actually implies another arachnid order, Schizomida and, if Scudder were correct, *Graeophonus* would be wholly inconsistent with all other whip spiders (living and extinct) in which the carapace forms a single sclerite. Scudder also described the pedipalps as fully chelate and suggested that the first pair of legs were of no significant length. Like the divided carapace, these characteristics are unknown in Recent whip spiders and are presumably misinterpretations based on relatively poor-quality material. In fact *Graeophonus* was effectively referred to Uropygi in its original description, but Scudder's (1890, pl. 40, fig. 3)

figure clearly shows that at least the Mazon Creek example of *G. carbonarius* is a whip spider rather than a whip scorpion or schizomid. Scudder (1895) also recorded this species from the Late Carboniferous Joggins Formation of Nova Scotia, Canada.

Pocock (1911) correctly assigned *Graeophonus* to Amblypygi and, with respect to *G. carbonarius*, noted discrepancies between the abdomen of Scudder's Cape Breton and Mazon Creek examples. Pocock felt that these fossils could not be conspecific, primarily due to differences in the position of the opisthosomal tergal apodemes, and (Pocock 1911, p. 32) proposed a new name for the Mazon Creek whip spider: *Graeophonus scudderi* Pocock, 1911. This name has been overlooked in all subsequent revisions and catalogues (Petrunkevitch 1913, 1949, 1953, 1955; Dubinin 1962; Dunlop 1994; Harvey 2003). Given Petrunkevitch's (1913) decision to assume conspecificity of Scudder's (1876, 1890) fossils, but in not treating the oldest known (Cape Breton) example of *G. carbonarius* as the holotype, further work is clearly needed to resolve the systematics of *Graeophonus* (and two further fossil genera) in North America. The present authors hope to address this in a later paper, and concentrate here on character states in the best known British fossil species.

Graeophonus anglicus Pocock, 1911 was based on a number of rather well-preserved specimens, mostly from Coseley in the English West Midlands (see section 2). Explicit diagnostic characters separating it from the North American species were not elaborated by Pocock (1911), while he proposed that the pedipalps were the main feature distinguishing *Graeophonus* from the then known Recent whip spiders – the extant *Paracharon caecus* was only described ten years later in 1921. Pocock noted that the fossils had relatively short pedipalps compared to extant forms, with a short femur in particular, and with less axial rotation in the horizontal plane. In other words, the pedipalps of the fossils probably still moved up and down to a greater extent – like spider pedipalps for example – rather than from side to side as in most living whip spiders.

Petrunkevitch (1913) described two new Mazon Creek whip spiders, each of which was based on a single specimen assigned, respectively, to a new genus. The supposedly blind *Thelyphrynus elongatus* Petrunkevitch, 1913 was also characterised by non-triangular coxae while the allegedly short-abdomened *Protophrynus carbonarius* Petrunkevitch, 1913 (genus preoccupied, replaced with *Sorellophrynus* Harvey, 2002) was supposed to have only seven opisthosomal segments. *Graeophonus* was rediagnosed by Petrunkevitch on a suite of characters – most of which are potentially influenced by the quality of preservation, or simply apply to whip spiders in general – as well as an explicit character of double trochanters in the legs. Even this character was subsequently withdrawn (Petrunkevitch 1949; see also section 3.4) and Dunlop (1994) questioned whether there was any justification for maintaining three separate Carboniferous whip spider genera.

2. Material and methods

Ten Coseley specimens of *Graeophonus anglicus* (Figs 1–5), originally derived from various private collections (see Pocock 1911 for details), are held in the Natural History Museum, London under the respository abbreviation BMNH. They have the accession numbers: BMNH In 31233 (holotype); In 31234, In 31246, In 31260 (all labelled as paratypes; see also Morris 1980, who mis-cited 31246 as 31248); and I 7892, I 7905, I 13872, I 13877 (previously figured); In 22836 and In 31257 (previously figured). All are in sideritic (ironstone) concretions and, except for I 7905, each nodule consists of both a part and counterpart. The more complete specimens vary in body length from ca. 11–18 mm, suggesting more than one instar was present. All the material redescribed here comes from Coseley near Dudley, Staffordshire, UK. This formerly highly productive locality was extensively collected in the late 19th and early 20th century and has yielded many arachnids among the fauna, but is unfortunately no longer accessible. It is cited in the older literature as belonging to the British Middle Coal Measures, which corresponds to the Westphalian B, or Duckmantian stage using current stratigraphic terminology.

Pocock (1911) assigned a further fossil held in the British Geological Survey to *G. anglicus*. This comes from the stratigraphically slightly younger South Wales coalfield which, being Westphalian D, is about the same age as Mazon Creek. Indeed, Pocock noted that it looked much like the North American *G. scudderi*, except for a longer anterior projection of the carapace. Pruvost (1930) identified a Belgian Coal Measures fossil as *G. carbonarius* (=*scudderi*), which Petrunkevitch (1953) later referred to *G. anglicus* instead. Both the Welsh and Belgian examples are known only from isolated carapaces and were not examined for the present paper.

Photographs were taken digitally and drawings were prepared with the aid of a *camera lucida*. Morphological terminology generally follows Shultz (1999) and fossils were compared to extant material in the Museum für Naturkunde, Berlin and the literature. Interpretations (see section 3) are based on a composite of all available BMNH material. Individual specimens are described in section 4.

3. Morphological interpretation

3.1. Carapace
The prosomal dorsal shield, or carapace, of *Graeophonus anglicus* is shaped somewhat like an inverted heart. It is noticeably pronounced anteriorly, with concave anterior lateral margins and a procurved posterior lateral margin; i.e. the posterior rim of the carapace is not straight (Figs 1a, 2a, 4). BMNH 31260 preserves good surface relief and indicates that in life the carapace had a slight convex profile. As a result of the anterior projection the carapace length:width ratio is somewhat lower than in most living amblypygids, whose carapaces tend to be shorter and broader. At least two pairs of recurved grooves ('valleys' *sensu* Shultz 1999) radiate from near a central carapace depression (Figs 1a, 4d). A further median groove, originating in the same place, runs along the midline in the posterior half of the carapace (e.g. In 31260) (Fig. 4d), and in the holotype (In 31233) a fainter groove is seen on the mid-line behind the ocular tubercle (Fig. 2a). This anteriorly pronounced carapace and its pattern of 'valleys' is quite similar to that of *Paracharon caecus* (cf. Fig. 7). According to Shultz these 'valleys' reflect the underlying musculature. Similarly, a pair of indentations immediately behind the median ocular tubercle (see section 3.1.1) may be the attachment sites (apodemes) of dorsal endosternal suspensor muscles.

3.1.1. Eyes. In *Graeophonus anglicus* a distinct median ocular tubercle is located on the anterior pronouncement of the carapace (Figs 1a, 2a). Unequivocal median eye lenses cannot be resolved on this tubercle in any of the available specimens, although this could simply be an artifact of preservation. More interestingly, lateral eye tubercles and/or their triads of three lenses are also equivocal at their expected position towards the antero-lateral corners of the carapace (Figs 1a, 2a, 4c, d). Given the relative completeness and surface detail (e.g. grooves, apodemes) seen in the better specimens

(BMNH In 31233, In 31260), we may have to entertain the possibility that this is *not* a preservational artifact and that lateral eyes were genuinely reduced or absent in *G. anglicus*.

3.2. Coxo-sternal region

The coxo-sternal region in *Graeophonus anglicus* is commonly quite well preserved (Figs 1d, 2d, 3b, 4a), particularly in BMNH In 31246 and In 31234, or In 31257 for the coxae of legs 2 and 3. Overall, coxae 2–4 (associated with the three pairs of walking legs) are large, subtriangular structures, increasing successively in size posteriorly. They appear slightly splayed in the matrix, probably due to compaction during fossilisation, and commonly overlap each other or meet at a median point. Consequently, the expected small sternal sclerites in the middle of the prosoma between the coxae (cf. Shultz 1999, fig. 1) are obscured in the fossil material. The coxae of the first (antenniform) legs cannot be resolved either. This is unsurprising, as they would be expected to be comparatively slender structures. The pedipalpal coxae in *G. anglicus*, and other mouthpart details, are generally poorly preserved. When visible (Figs 4b, 6), chelicerae can only be seen in outline, whereby several specimens (e.g. In 31234) indicate that they were fairly long and projected forwards as in extant taxa. Cheliceral fangs and/or the taxonomically important dentition of the basal cheliceral article cannot be resolved.

3.3. Pedipalps

The full length of the pedipalp in *Graeophonus anglicus* is never preserved. In the four specimens where palps are present (In 31233, In 31234, In 31246 and In 31257) they invariably project straight forwards (Figs 1–4, 5f). Femora and patellae can be preserved quite well, but the more distal articles are represented at best only in crude outline. As noted by Pocock (1911), the pedipalps appear to have been shorter and less raptorial than is typical for extant whip spiders and, significantly, their femora are slightly raised from the horizontal plane into a more oblique posture (Fig. 1a). This implies that, as in *Paracharon caecus* (Fig. 7), the palps of *G. anglicus* may have been held, and articulated, to some extent vertically in life. In this respect they would be more like a pair of walking legs, or the pedipalps of schizomids and the putative Carboniferous stem-schizomid *Proschizomus petrunkevitchi* Dunlop & Horrocks, 1996. Both the pedipalpal femur and patella are fairly short and stout and this short femur (see also comments in Pocock 1911) could prove diagnostic for the fossil genus (see section 4).

The right pedipalp femur of specimen In 31257 bears two indentations near its proximal margin, adjacent to the trochanter, and a faint border is dicernable just anterior to these indentations. This may represent a dorsal hinge (see section 4) on the anterior surface of the femur where the trochanter attaches. However, this interpretation is made with reservations as the trochanter itself is missing and the actual articulation must be inferred.

3.3.1. Pedipalpal spination. As well as being shorter, the pedipalps of *G. anglicus* appear not to have been as spiny as the pedipalps of most living whip spiders. Spination on the underside of the trochanter (cf. Shultz 1999, fig. 6) was not observed. Of considerable taxonomic importance (see section 4) are one or two small, apparently dorsally positioned, inward-facing spines on the femur of the fossils (Figs 3a, 4b, 6). These spines are not preserved in, for example, the holotype – where femoral spination is hard to resolve due to the orientation of the pedipalps – but they are clearly present in other specimens. BMNH In 31246 (Fig. 6) bears two spines, and is evidently a dorsal view, while In 31257 preserves only one

spine, but the adjacent carapace in this half of the nodule again implies a dorsal position on the femur for this feature. In 31234 also expresses two femoral spines, but in this specimen they are associated with *ventral* features (coxae, etc.), such that they are more likely to be themselves ventral structures. The femur in *G. anglicus* may therefore have borne both dorsal and ventral spination. This would be entirely consistent with living whip spider species. The pedipalpal patella in *G. anglicus* bears two larger, also inwardly-directed, spines (In 31246, In 31257) (Figs 3, 4, 5f, 6), but spination (or lack of it) in the less well-preserved tibiae remains equivocal.

3.4. Legs

The antenniform first pair of legs are very delicate; consequently, their chance of preservation is low. Leg 1 is absent from most *Graeophonus anglicus* specimens, except for a displaced left femur in In 31234 (Figs 1c, 2c), which is extremely slender in comparison to other femora preserved. The remaining walking legs (2–4) seem to have been fairly long and rather slender, but like the pedipalps they are rarely preserved at their full length. The preserved articles tend to increase in length going from anterior to posterior, implying that the more posterior walking legs were slightly longer in life.

The trochanter of the walking legs is typically bell-shaped and widens distally. Only one, undivided, trochanter (Fig. 5f) could be observed in the legs of *G. anglicus*, contradicting Peterunkevitch's (1913) earlier diagnosis of the genus as having two trochanters. In legs 2–4 the femora are quite robust and are typically slightly flattened and distally tapering. The fact that they are preserved on their sides with the anterior (or prolateral) face uppermost probably reflects their life position (Fig. 7a). This torsion of the legs is also seen in extant species (e.g. Shultz 1999; Weygoldt 2000a) and helps the animal lie flat or crawl into narrow spaces. In specimens In 31260 the femur of leg 4 is flattened against the body (Fig. 4c, d). The patella is generally difficult to distinguish as a separate leg article in these fossils (e.g. In 31234, In 31246). This is unsurprising, since in extant taxa the patella is small and the patella–tibia joint is effectively immobile (Shultz 1999) such that these two articles are functionally inseperable.

For the more distal walking leg articles, In 31257 includes an almost complete leg; probably leg 3, but the sequence on this side of the body is incomplete. Here we can identify at least three separate elements beyond the patella: a long one and two successively shorter ones. The distal leg articles of whip spider walking legs are commonly subdivided, although these intratibial and intratarsal joints lack musculature (Shultz 1999). The present authors suggest these elements in the fossil correspond either to three parts of a divided tibia or, perhaps more likely, two tibial elements plus the first (or basitarsal) part of the tarsus; cf. legs 2 and 3 in Shultz (1999, fig. 1) which show exactly this pattern. In the fossil the tip of the leg, and any claws or associated structures, remain equivocal (see section 4). In general, lineations often observed along the length of the leg articles in the BMNH material may be folds associated with compression of the specimens during fossilisation. This folding occurs widely in other arachnid fossils preserved in nodules (JAD pers. obs.).

3.5. Opisthosoma

The opisthosoma in *G. anglicus* is typically oval in outline narrowing both anteriorly (towards the pedicel) and posteriorly (towards the pygidium). Based on the slightly three-dimensional nodular preservation, it gives the impression of having been dorso-ventrally flattened in life. Traces of the arthrodial membrane between the tergites and sternites are
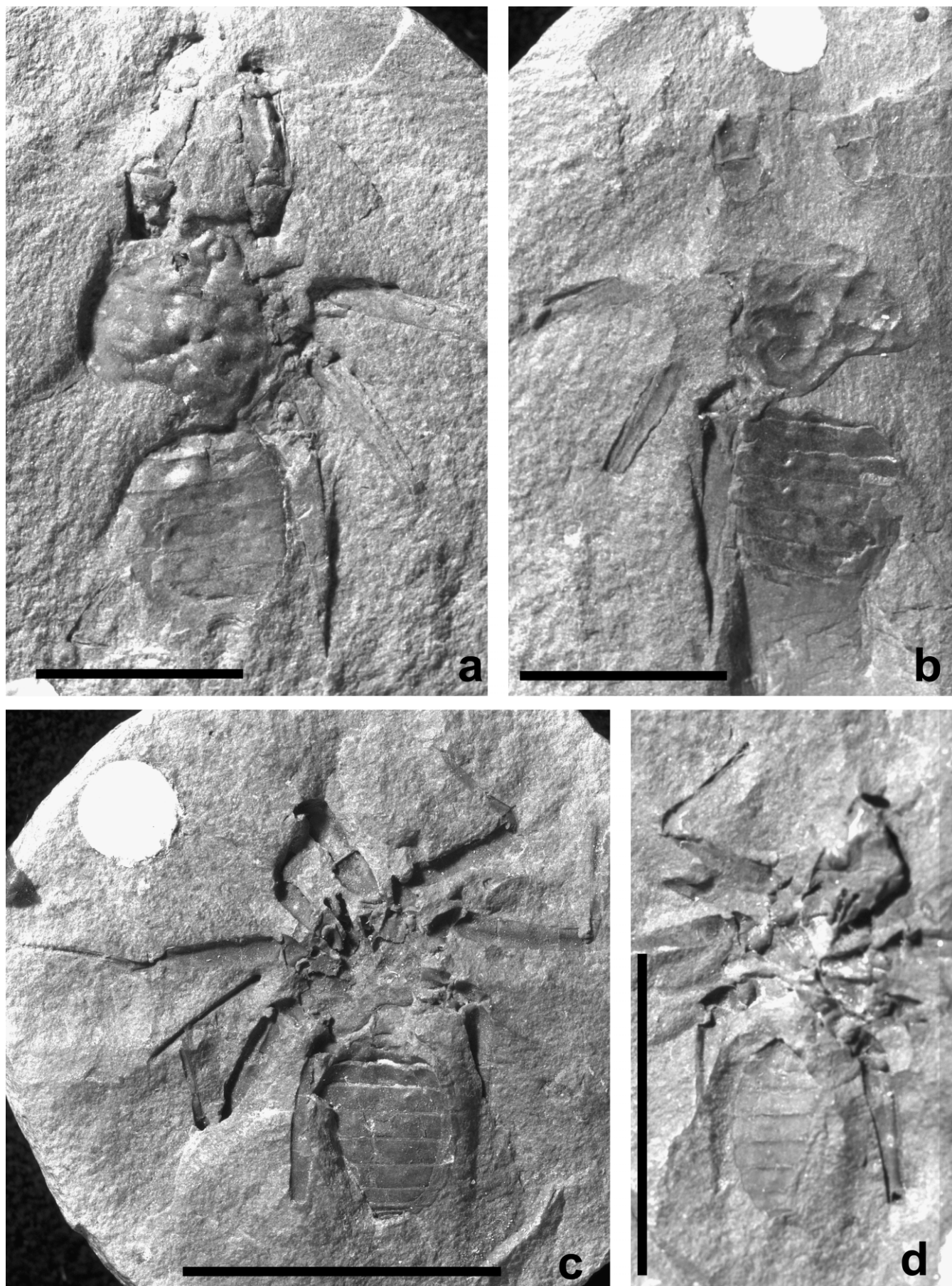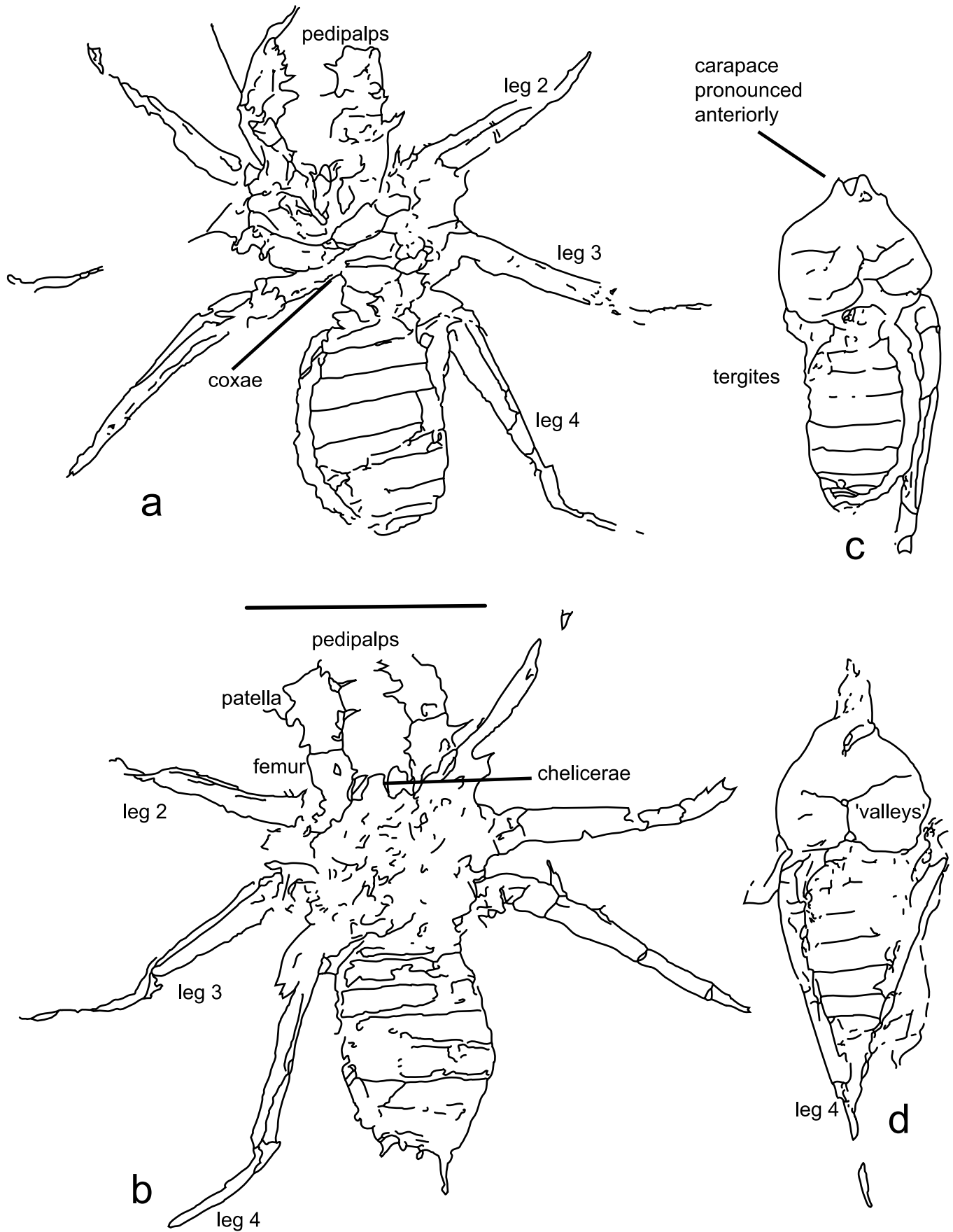
Figure 1 *Graeophonus anglicus* Pocock, 1911, a fossil whip spider (Amblypygi) from the Middle Coal Measures of Coseley near Dudley, Staffordshire, UK. Late Carboniferous, Westphalian B: (a) BMNH In 31233 (holotype, part); (b) In 31233 (holotype, counterpart); (c) In 31234 (paratype, part); (d) In 31234 (paratype, counterpart). Scale bars = 10 mm.
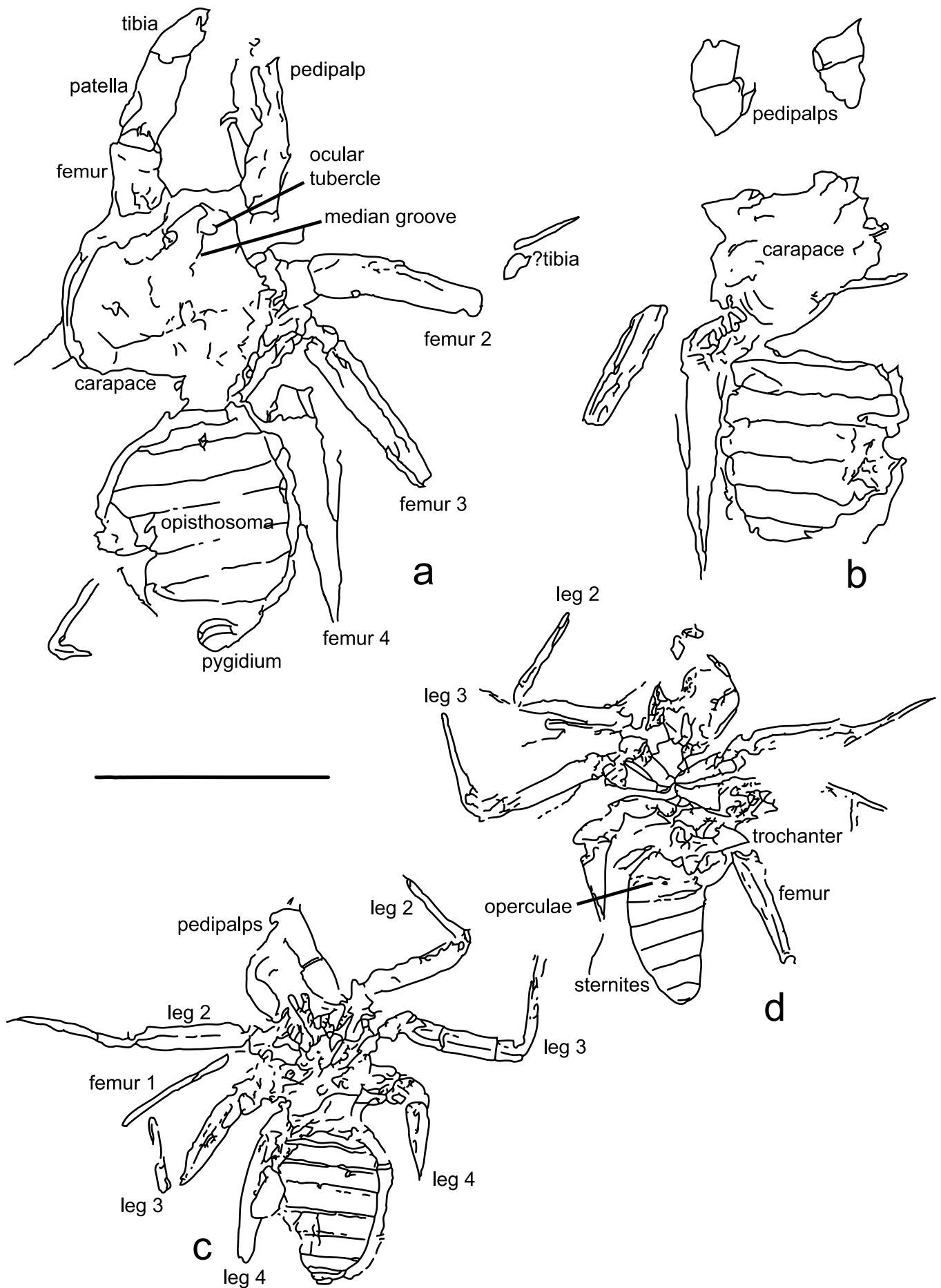
Figure 2 *Graeophonus anglicus* Pocock, 1911, *camera lucida* drawings: (a) BMNH In 31233 (holotype, part); (b) In 31233 (holotype, counterpart); (c) In 31234 (paratype, part); (d) In 31234 (paratype, counterpart). Scale bar = 10 mm.
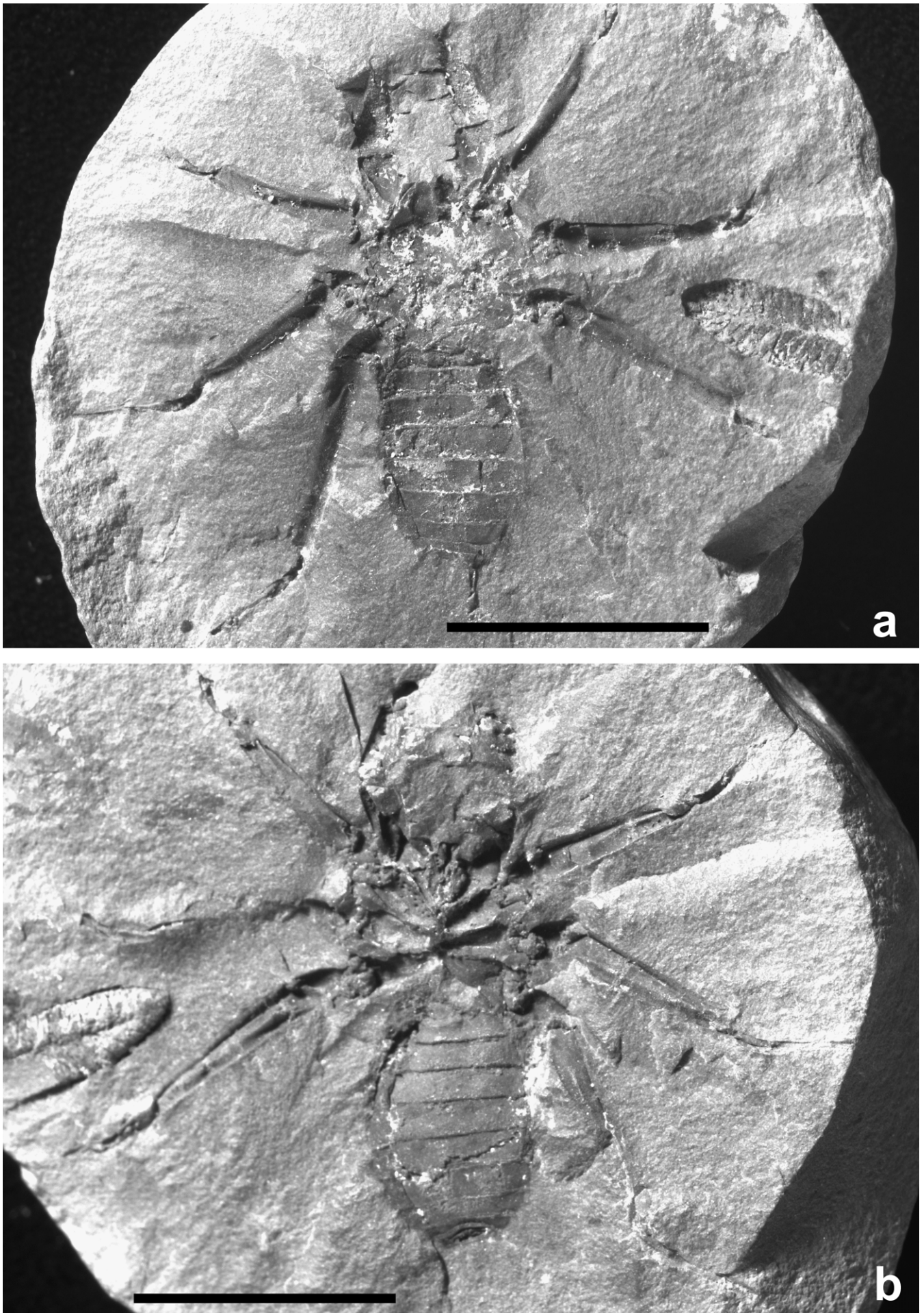
Figure 3 *Graeophonus anglicus* Pocock, 1911: (a) BMNH In 31246 (paratype, part); (b) BMNH 31246 (paratype, counterpart). Scale bars = 10 mm.

Figure 4 *Graeophonus anglicus* Pocock, 1911, *camera lucida* drawings: (a) BMNH In 31246 (paratype, part); (b) In 31246 (paratype, counterpart); (c) In 31260 (paratype, part); (d) In 31620 (paratype, part). Scale bar = 10 mm.

commonly visible, as though squeezed out to the side in a compressed specimen. The quality of preservation varies and determination of the exact number of segments is commonly hampered due to pieces of matrix obscuring surface detail; I 13872 (Fig. 5c) expresses at least ten opisthosomal segments (out of the twelve expected). In outline, there are some subtle

differences between 'fat' (e.g. In 31233) (Figs 1a, b, 2a, b) and 'thin' (e.g. In 31260) (Fig. 4c, d) opisthosomas among the ten specimens, but in the absence of detailed data on ontogeny and/or sexual dimorphism we suspect this is probably of limited taxonomic significance, and in general we see nothing to suggest more than one morphospecies from among this Coseley material.

The tergites of the opisthosoma all express straight posterior margins. Surface contours are generally poorly preserved, although paired indentations along the length of the opistho-soma are sometimes visible (e.g. I 7892, I 13872, In 22836) (Fig. 5a, c, e). These almost certainly represent the apodemes of dorso–ventral muscles (cf. Shultz 1999), which probably compressed the opisthosoma in life. Ventrally, what was traditionally interpreted as the second and third sternites were shown by Shultz (1999) to be highly modified limbs bearing the internalised lungs. These sclerites thus form the anterior and posterior opercula respectively and conceal the vestigial true sternites. In the fossils, I 13872 (Fig. 5c) show these opercula quite clearly. As in extant taxa, the anterior operculum is somewhat larger and both opercula have quite strongly recurved margins. By contrast the subsequent sternites (beginning with somite 4) have straight margins like the tergites.

3.5.1. Ventral sacs? Ventral sacs are small, paired projections on the underside of the opisthosoma associated with the posterior operculum. Like the lung opercula, they are probably highly modified opisthosomal appendages, which in living taxa seem to play some sort of role in water balance (see e.g. Weygoldt 2000a). They occur in some extant whip spiders, whereby Weygoldt (1996) interpreted their absence as apo-morphic. Ventral sacs cannot be resolved in *G. anglicus* – at least there is no evidence for them in specimens like I 13872 (Fig. 5c) in which the ventral surface is preserved quite clearly. The rather soft nature of the ventral sacs in extant whip spiders suggests that the chances of them being preserved are not good, thus their absence in *G. anglicus* may simply be tapho-nomic. However, such sac-like structures were reported by Selden (1996) in a Carboniferous mesothele spider from Montceau-les-Mines, France, and they were also described by Dunlop (1994) in a small (?juvenile) Carboniferous whip spider found at Writhlington, UK. This fossil is incomplete, but was provisionally assigned to *G. carbonarius*, i.e. Scudder's North American species.

4. Systematic palaeontology

Pedipalpi Latreille, 1810

Remarks. There are two main competing ideas about the affinities of Amblypygi: sister-group of Araneae (the Labellata hypothesis) or sister-group of Uropygi+Schizomida (the Pedipalpi hypothesis). Weygoldt & Paulus (1979) supported Labellata based on the very narrow pedicel between the prosoma and opisthosoma and a well-developed sucking stomach within the prosoma. Among recent studies, Wheeler & Hayashi (1998) also recovered this clade, stating that (p. 186) in their analysis 'The Labellata derive their support almost entirely from molecular data . . .'. Genital and sperm characters also seem to favour Labellata (see e.g. Alberti & Michalik 2004, and references therein), but other morphologi-cal data, particularly the slender first pair of legs and the large, sub-raptorial pedipalps, tends to support Pedipalpi. Shultz (1999) offered many further potential synapomorphies for this clade based on detailed skeleto-muscular characters. Pedipalpi was recovered in most trees in Giribet *et al.*'s (2002, figs. 5, 6)

comprehensive analysis, although these authors cautioned that molecular data alone does not always recover this taxon (see their fig. 7). On balance we find Pedipalpi more convincing, although the Palaeozoic Amblypygi are fully formed (i.e. crown-group) whip spiders assignable to an extant clade (see below), and offer little in the way of character states or combinations which could help resolve this conflict.

Order Amblypygi Thorell, 1883

Remarks. Resolving the position of *Graeophonus anglicus* using Weygoldt's (1996) dataset for extant whip spiders is problematic as most of these characters – cheliceral dentition, setal position, genital morphology and spermatophores – are not preserved in the fossils. Thus scoring the fossil into a cladistic analysis would be unsatisfactory (Zhou 2004), given the large amounts of missing data. Yet, as noted by Weygoldt (1996, 2000a, b), there are morphological similarities between the fossils presently studied and the most basal living whip spider. *Graeophonus anglicus* and *Paracharon caecus* share a number of putatively plesiomorphic features: (1) an anteriorly-pronounced carapace; (2) dorso-ventrally articulating pedi-palps (see also Pocock 1911); (3) less than three principal spines on the pedipalp patella (*G. anglicus* has two; section 3.1.1); and, less convincingly, (4) the putative dorsal hinge of the trochanter–femur articulation on the anterior surface of the pedipalp femur. While plesiomorphies cannot be used to define sister-taxa, this suite of characters clearly places *G. anglicus* outside the Euamblypygi *sensu* Weygoldt (1996) and implies that at least one of the Carboniferous species occupies a fairly basal position in the overall tree.

Suborder Paleoamblypygi Weygoldt, 1996
Family Paracharontidae Weygoldt, 1996

Emended diagnosis. Whip spiders with an anteriorly elon-gate prosoma; four internal cheliceral teeth, the uppermost one-cuspidate; pedipalp femur and tibia with very few spines; specifically with only one or two small dorsal spines on the femur. Emended from Weygoldt (1996).

Type genus. *Paracharon* Hansen, 1921 (Recent).

Included genera. *Graeophonus* Scudder, 1890.

Remarks. Is *Graeophonus anglicus* a crown-group whip spider? Petrunkevitch (1913) assigned all the Carboniferous Amblypygi to the extant family Tarantulidae – this name is no longer recognised, see e.g. Weygoldt (1996) – but later, Petrunkevitch (1949, 1953) felt that the fossils could not be referred reliably to living families. However, in the *Treatise on Invertebrate Paleontology* (Petrunkevitch 1955) all the Car-boniferous species were assigned to Phrynichidae based on the putative absence of a pulvillus. This pulvillus is a small, fleshy, adhesive pad occurring between the claws of the walking legs in some extant whip spiders. In older, more typological, schemes (e.g. Millot 1949; Quintero 1986) the presence or absence of this feature was seen as being of fundamental importance and defined 'pulvillate' and 'apulvillate' clades respectively. The analysis of Weygoldt (1996) resolved this character as homoplastic; probably lost multiple times in extant taxa. In any case, few of the Coal Measures whip spiders appear to preserve the ends of the walking legs in sufficient detail (if at all!) to test the presence of a pulvillus reliably (see also section 3.4).

As part of his cladistic classification, Weygoldt (1996) raised the family Paracharontidae for the basal extant genus, *Para-charon* Hansen, 1921; which emerged as sister-group to all remaining Recent whip spiders. Weygoldt diagnosed Para-charontidae largely as outlined above (see Diagnosis), adding
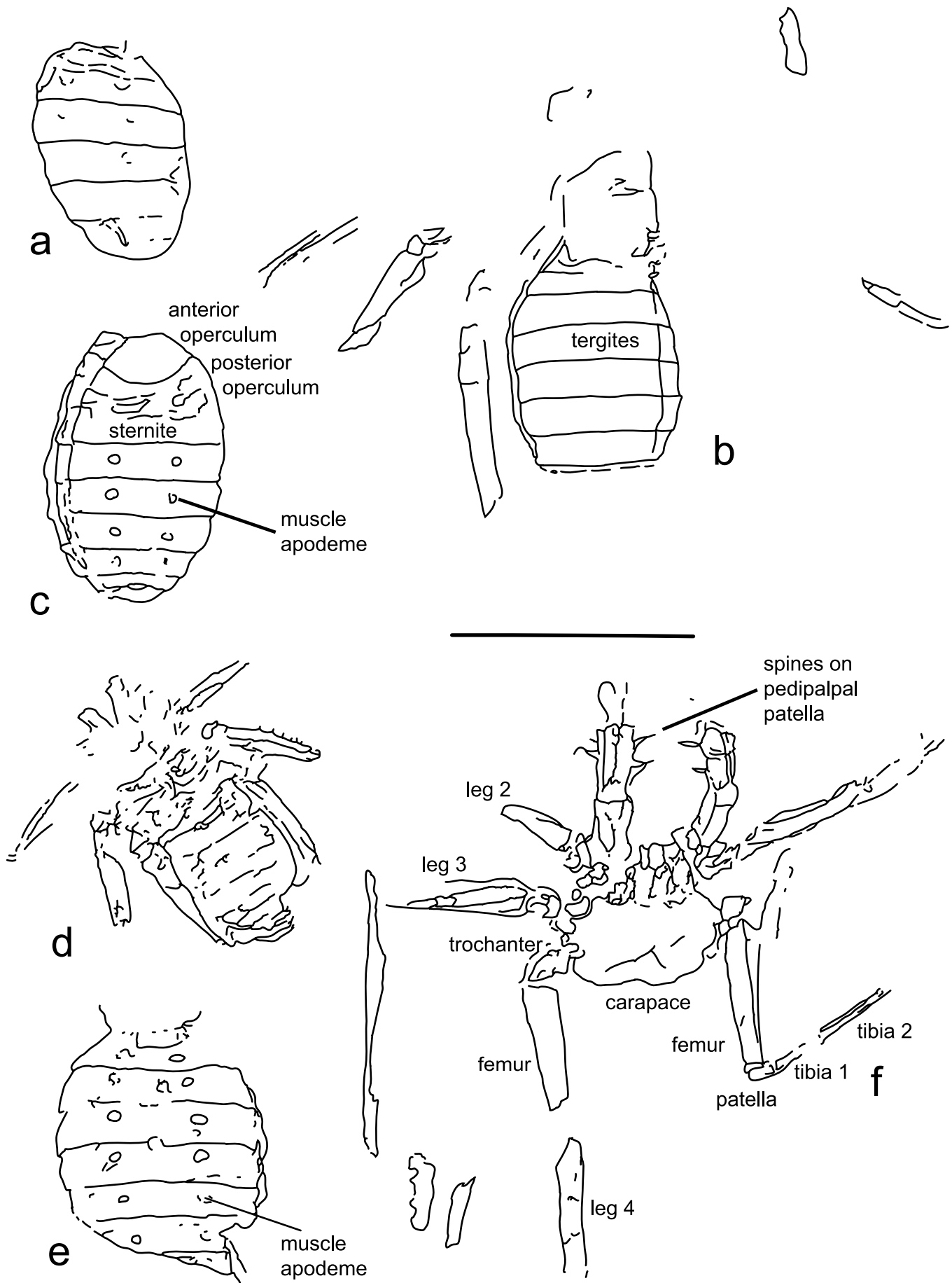
Figure 5 *Graeophonus anglicus* Pocock, 1911, *camera lucida* drawings of additional (non-type) material: (a) BMNH I 7892; (b) I 7905; (c) I 13872; (d) I 13877; (e) In 22836; (f) In 31257. Scale bar = 10 mm.

to this completely reduced eyes and eye tubercles. Blindness in *Paracharon caecus* is presumably related to its unusual and restricted lifestyle within termite mounds. As noted by Weygoldt (1996, 2000a, b) – and specifically taking his 1996 diagnosis – the carapace and pedipalp morphology in *Graeophonus anglicus* closely matches that of Paracharontidae (Fig. 7), the cheliceral dentition is equivocal in the fossil, while the most significant difference between the fossils and the one living species is the absence of a median eye tubercle. *G. anglicus* has a well-preserved median eye tubercle, even though individual lenses cannot be resolved (see section 3.1.1), while lateral eyes remain equivocal in this fossil species. A general problem is that Paleoamblypygi, and its single family Paracharontidae, are largely defined on plesiomorphies with no apomorphic characters available to distinguish between the two higher taxa: i.e. to resolve whether *Graeophonus* is just a paleoamblypygid (as per Harvey 2003) or a *bone fide* paracharontid.

The present authors feel that blindness alone should not justify a separate family and provisionally refer *Graeophonus* to the 'living fossil' family Paracharontidae. This placement still needs to be tested against the North American fossils. However, in support of these conclusions, one paracharontid character which *is* available in *G. anglicus* is the possession of two small spines on the dorsal surface of the pedipalpal femur; i.e. facing inwards when the palp lies horizontal and is viewed from above (see section 3.3.1) (Fig. 6, numbered spines; Fig. 7, arrows). These spines were also picked up in earlier illustrations such as Petrunkevitch (1949, fig. 161) and Waterlot (1953, fig. 39). Similar spines are also present as spinelets in the extant paleoamblypygid *P. caecus* (Fig. 7, arrows), where they were scored as one of a number of alternative apomorphic states for femoral spination (cf. Weygoldt 1996, fig. 12; character 7). By contrast, most euamblypygid families have a more complete row of dorsal femoral spines, except for one highly derived genus where the spines are reduced, but visible as so-called bacilliform processes during development; see Weygoldt (1996) for details. The present authors suggest that this femoral spination represents a scorable, potentially apomorphic character for *G. anglicus* which supports its inclusion in Paracharontidae; the diagnosis of which has been emended accordingly to accommodate the fossil genus. The comparatively small number of dorsal spines could be yet another plesiomorphic character state, but it is noted that the ground pattern of femoral spination in Amblypygi has not yet been resolved. If two dorsal spines are indeed apomorphic, then *G. anglicus* could be resolved as a crown-group whip spider.

Genus *Graeophonus* Scudder, 1890

Emended diagnosis. Amblypygids with a short femur; median eye tubercle present. Emended from Petrunkevitch (1955).

Type species. *Libellula carbonaria* Scudder, 1876.

Included species. *Graeophonus anglicus* Pocock, 1911; *Graeophonus scudderi* Pocock, 1911.

Remarks. The present authors accept that this diagnosis is inapplicable to the isolated opisthosoma used by Scudder to describe the type species. The revised diagnosis draws on Pocock's (1911) recognition of the unusually short femur (Figs 1, 2, 6, 7) compared to living whip spiders, while the reference to eyes distinguishes the fossils from the Recent blind genus *Paracharon* Hansen, 1921. It is not felt possible to offer a better scheme at present for differentiating between the three Carboniferous genera, pending revision of the North American material (see section 1). In the most recent scheme (Petrunkevitch 1955), *Protophrynus* Petrunkevitch, 1913 (now *Sorellophrynus*) was characterised by a truncated anterior projection of the carapace with sessile median eyes and triads of lateral eyes, while *Thelypyhrynus* Petrunkevitch, 1913 was supposed to have an evenly rounded carapace front, lacking eyes altogether. Experience has shown that Petrunkevitch's descriptions and illustrations of Carboniferous arachnids are often unreliable, particularly with respect to eye morphology. Poorly-preserved fossils in which eyes could not be resolved, or in which the relevant part of the body was missing, were invariably interpreted as blind. Published photographs of the Mazon Creek material suggest some potential differences in body shape and proportions which merit further investigation.
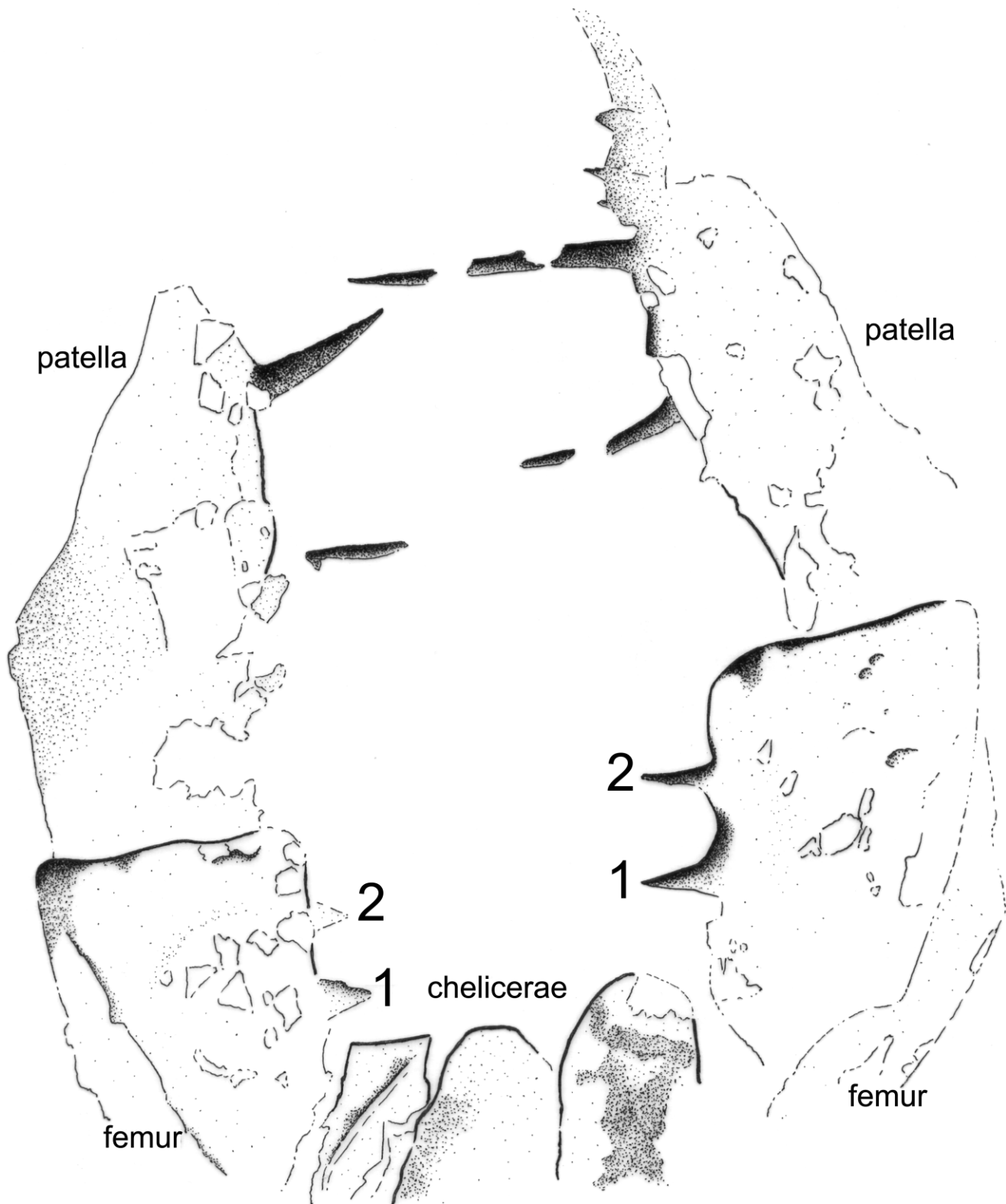
Graeophonus anglicus Pocock, 1911
Figures 1–7

1911 *Graeophonus anglicus* Pocock, pp. 32–33; plate I, figs 4a-d.
1913 *Graeophonus anglicus* Pocock; Petrunkevitch, p. 59.
1930 *Graeophonus anglicus* Pocock; Pruvost, p. 207.
1935 *Graeophonus anglicus* Pocock; Werner, p. 463, fig. 168.
1949 *Graeophonus anglicus* Pocock; Waterlot, figs. 671a–b.
1949 *Graeophonus anglicus* Pocock; Petrunkevitch, pp. 271–273, figs 161–162, 263–264, 268.
1953 *Graeophonus anglicus* Pocock; Petrunkevitch, pp. 99–100; figs 103–105.
1953 *Graeophonus anglicus* Pocock; Waterlot; p. 578, figs 39–40.
1955 *Graeophonus anglicus* Pocock; Petrunkevitch, p. 126, figs 93(2a–c).
1962 *Graeophonus anglicus* Pocock; Dubinin; pp. 435, figs. 1268–1269.
1980 *Graeophonus anglicus* Pocock; Morris, p. 40.
1993 *Graeophonus anglicus* Pocock; Selden, p. 318.
1996 *Graeophonus anglicus* Pocock; Weygoldt, pp. 198, 200.
2000a *Graeophonus anglicus* Pocock; Weygoldt, p. 139, fig. 302.
2000b *Graeophonus anglicus* Pocock; Weygoldt, pp. 340, 348, fig. 3.
2003 *Graeophonus anglicus* Pocock; Harvey, p. 31.

Diagnosis. Pedipalps short with one or two small dorsal femoral, and two larger patella spines.

Type material. BMNH In 31233, from the Middle Coal Measures of Coseley near Dudley, Staffordshire, UK; presumably from the one productive locality here which is well documented: the Claycroft Open Works. Upper Carboniferous, Westphalian B.

Additional material. Paratypes BMNH In 31234, In 31246 and In 31260. Additional specimens BMNH I 7892, I 7905, I 13872, In 13877, In 22836 and In 31257; both sets from the same locality as the holotype. One further Pocock specimen from South Wales (not seen) held in the British Geological Survey (No. JP835), Keyworth, UK, plus Pruvost's (1930) carapace (not seen) reported by Petrunkevitch (1953) to be in the Museum of the University of Louvain (No. 8256), Belgium. An incomplete opisthosoma (BMNH In 39768) from Crowcrook, Ryton on Tyne, UK was tentatively referred to this species by Petrunkevitch (1949), but the present authors cannot confirm or deny this interpretation from such poor material.

Description of holotype (In 31233). Dorsal view (Figs 1a, b, 2a, b), total length ca. 18 mm, but carapace slightly displaced relative to opisthosoma. Carapace broad, anteriorly pronounced, posterior margin slightly procurved; length 7·4 mm, width ca. 9 mm. Median ocular tubercle on carapace forms pear-shaped structure on the anterior pronouncement. Median

Figure 6 *Graeophonus anglicus* Pocock, 1911, detail of the pedipalps in the part (i.e. dorsal view) of BMNH In 31246. Note in particular the two dorsal femoral spines, numbered 1 & 2. Scale bar=2 mm.

eye lenses and/or any lateral lenses on carapace equivocal. Short median groove runs behind median ocular tubercle. Chelicerae not preserved. Pedipalps partially complete, held at an oblique plane of orientation. Palpal trochanters not preserved. Palpal femur short, widening distally, length ca. 3 mm.

Patella 4·4 mm long. Reniform articulation region between femur and patella visible, but spines on pedipalp equivocal. Femora of walking legs 2–4 present, lengths 7·6 mm, 8·0 mm and ca. 9 mm respectively. Fragment of patella 2 preserved. Possible articulated fragment of tibia and tarsus preserved to
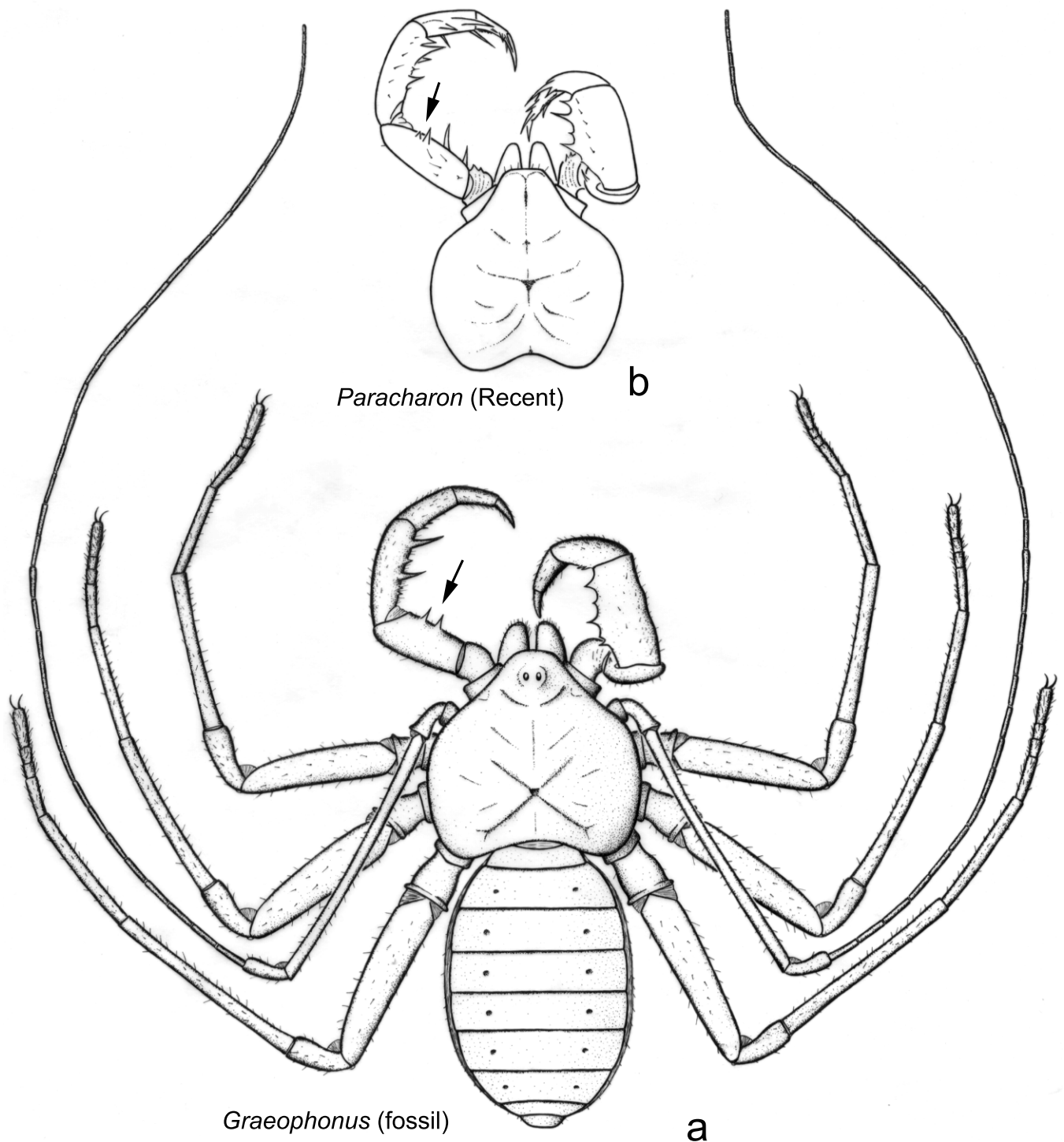
Figure 7   (a) Sketch reconstruction of *Graeophonus anglicus* Pocock, 1911 in dorsal view; distal parts of the limbs based on comparisons with extant species. (b) Comparative drawing of the carapace and pedipalps of the Recent, blind and basal West African species *Paracharon caecus* Hansen, 1921 (Paracharontidae); not to scale. Left pedipalp in both has been deliberately drawn pulled to one side to reveal the femoral spination; the right pedipalp is in both cases in what we assume to be a more natural (life) position. This more or less vertical plane of articulation – probably a plesiomorphic character – differs from that of other living whip spiders, in which the pedipalps articulate in a more horizontal plane. The presence of two dorsal femoral spines (arrowed) in both taxa is a potential synapomorphy for these species and could be used to refer *G. anglicus* to Paracharontidae (see text for details).

the left of opisthosoma. Opisthosoma incomplete, length ca. 11 mm, maximum width 8·6 mm. At least six large tergites can be resolved, all with straight posterior margins. Lateral rim of opisthosoma preserves impressions of arthrodial membrane. Terminal two segments highly abbreviated, forming part of pygidium.

Paratype In 31234. Ventral surface (Figs 1c, d, 2c, d). Total length 11·4 mm, with well-preserved coxo-sternal region;

length 4·6 mm, maximum width 5·2 mm. Chelicerae 1·2 mm long. Pedipalps incomplete, but right pedipalp better preserved on counterpart. Pedipalpal femora and patellae short, lengths 1·8 mm and 3·4 mm respectively. Three pairs of pedal coxae (for legs 2–4), essentially triangular and widening distally. Corresponding legs preserved no further than the tibia and bear traces of longitudinal lineations. Trochanters are distinctly bell-shaped structures, widest proximally and

narrowing distally. Femora 2–4 with lengths of 4·8 mm, 5·0 mm and 5·2 mm respectively. Patellae mostly indistinct, but short, while legs 2 and 3 include proximal parts of long, thin tibiae which bend forwards from the femur–patella joint. Counterpart includes probable slender leg 1 femur, displaced between legs 2 and 3. Opisthosoma 6.8 mm long; right side faint, thus maximum width estimated to be 4·8 mm. Nine opisthosomal sternites with curvature of the anteriormost sclerites in the part implicit of an anterior and posterior operculum respectively.

Paratype In 31246. Dorsal and ventral surface preserved (Figs 3, 4a, b, 6); length 15·4 mm. Prosoma ca. 5 mm long, maximum width 6·0 mm. Chelicerae present in outline on counterpart, ca. 2 mm long. Pedipalps partially complete, stout and held quite straight. Trochanters indistinct, but femora 2·4 mm long; on right side with two short, inward-facing dorsal spines. Patella 3·4 mm long, with two longer, inward-facing spines. Coxae 2–4 well-preserved; sub-triangular in outline, widening distally. Boundaries between trochanters and femora indistinct. Femora 2–4 with lengths of 6·2 mm, 6·6 mm and 7·6 mm respectively. All taper in width distally and show traces of longitudinal lineations. Patellae and proximal parts of basitibia preserved in some limbs. Opisthosoma oval, length 10·4 mm, maximum width 7·2 mm. Nine opisthosomal sternites can be distinguished, the posteriormost reduced as part of the pygidium. Part shows area of arthrodial membrane around the left opisthosomal margin.

Paratype In 31260. Dorsal surface preserved (Fig. 4c, d); length 14·0 mm. Carapace 5·4 mm long, maximum width 6·4 mm. Right leg 4 preserved flattened against the body, but individual articles indistinct. No other appendages preserved. Carapace heart-shaped, pronounced anteriorly, procurved on its posterior margin. Surface relief well preserved in three dimensions and carapace clearly convex in life. Median eye tubercle represented by elliptical structure on anterior pronouncement; lateral eyes equivocal. Two pairs of crescentic, recurved grooves or 'valleys' originate from near the centre of the carapace. A pair of faint indentations (?muscle apodemes) occur in front of the anterior grooves Opisthosoma 8·6 mm long, maximum width 5·4 mm. Eight tergites can be resolved, but terminal end of opisthosoma obscured by matrix.

I 7892. Poor specimen (Fig. 5a). An incomplete opisthosoma, length ca. 10 mm, maximum width ca. 7 mm. Only six segments can clearly resolved, the first four of which express paired muscle apodemes.

I 7905. Part only preserving dorsal surface (Fig. 5b). Outline of carapace faint on right side, left side and surface topology indistinct; maximum carapace width estimated at 7·6 mm. Femora of left legs 3 and 4 preserved, lengths 5·0 mm and ca. 6 mm respectively. Possible fragment of leg 3 tibia preserved to the left of femur. Opisthosoma incomplete, seven tergites only visible, total length ca. 10 mm, maximum width 7·0 mm.

I 13872. Almost complete ventral surface of opisthosoma (Fig. 5c), length 11·0 mm, maximum width 7·2 mm. Opercula and sternites 4–11 preserved. Anterior operculum, curved at both its anterior and posterior posterior boundaries. Adjacent posterior operculum also with curved margins, less obvious on right side. At least four of the subsequent sternites (5–8) preserve paired muscle apodemes.

I 13877. Dorsal surface preserved, total length ca. 11·0 mm. Opisthosoma in counterpart obscured by plant material and specimen generally poor (Fig. 5d). Carapace ca. 4 mm long, maximum width 5·0 mm, with slight anterior pronouncement bearing median ocular tubercle; diameter ca. 0·2 mm. Carapace surface bears two pairs of radiating grooves. Chelicerae ca. 1 mm long. Fragments of proximal pedipalpal articles present, but details poor. Trochanters of legs 3 and 4 preserved in outline as somewhat rounded structures. Femora of legs 2–4 with lengths of 3·8 mm, 4·2 mm and 5·0 mm respectively. All bear weak longitudinal lineations. Opisthosoma 6·8 mm long, maximum width 4·4 mm, but surface details and exact number of tergites poorly resolved.

In 22836. Isolated opisthosoma (Fig. 5e), originally identified as an unfigured paratype of *Plesiosiro madeleyi* Pocock, 1911, but treated as a *G. anglicus* by Petrunkevitch (1949). Length 11·6 mm, maximum width 8·2 mm. Nine segments visible, many with paired apodemes, but boundaries separating posteriormost segments faint. Impressions of arthrodial membrane preserved both on left side of opisthosoma in the part, as well as between some of the sclerites.

In 31257. Dorsal surface of prosoma only preserved (Fig. 5f), length 5·8 mm, maximum width 6·8 mm. Anterior margin of carapace pronounced, but ocular tubercle indistinct. Pair of radiating grooves towards the back of the carapace present in the counterpart. Chelicerae ca. 2 mm long, appearing as a pair of posteriorly rounded nodules. Pedipalps partially complete, with the femora slightly elevated distally. Proximal end of right palpal femur visible on part as a squat structure with a pair of indents at its rounded proximal margin. These also bear an anteriorly curved notch with a faint margin apparently just anterior of the indents. Palpal podomeres short and stout, femur, 1·6 mm long, patella at least 3·4 mm. One small dorsal femoral spine preserved on the left pedipalp. Patella bears two spines. Carapace of part incomplete, revealing underlying triangular leg coxae 2 and 3. Left leg (3?) almost complete, but partly obscured by a large depression in the matrix. Trochanters bell-shaped, widening distally. Lengths of femora 2–4 are 5·6 mm, 6·0 mm and 6·6 mm respectively. Patellae short, ca. 1·2 mm long. Tibiae slender, narrowing in the middle with at least two tibial elements preserved; proximal one up to 5·4 mm long. More distal, tarsal, region preserved as faint outline only in leg 3.

Remarks. Resolving between *G. carbonarius*, *G. anglicus* and *G. scudderi* must be based on study of the types; whereby the next most important step is to clarify whether Scudder's 1876 Cape Breton (*carbonarius*) and 1890 Mazon Creek (*scudderi*, *sensu* Pocock) fossils are conspecific. Peterunkevitch's redescriptions have usually proven inadequate for such tasks and were based on a poor understanding of whether structures were preserved in positive or negative relief. For example Petrunkevitch (1913, text-fig. 29) described a median crest in what would be the type of *G. scudderi* running from the centre of the carapace to its posterior margin, and two pairs of radiating crests. By the time of the diagnosis in Petrunkevitch (1955) this 'crest' had become a groove, while the original photographs (Petrunkevitch 1913; plate V, figs 27–28) imply both dorsal and ventral features whereby radiating crests (or grooves) have to be disentangled from underlying sternal or coxal features. This will be addressed in a subsequent paper.

6. Acknowledgements

7. References

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