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Carboniferous araneomorph spiders reinterpreted as long-bodied harvestmen

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Archaeometa nephilina Pocock, 1911 from the Late Carboniferous (Bashkirian/Moscovian: Duckmantian, *c.*315 Ma) Coal Measures of Coseley in the English West Midlands was originally interpreted as an araneomorph spider (Arachnida: Araneae). It is, in fact, a harvestman (Arachnida: Opiliones), albeit one with an unusual, long-bodied morphology. Another Coseley fossil, *Arachnometa tuberculata* Petrunkevitch, 1949, was also interpreted as an araneomorph spider, but it is not well preserved, and is regarded as Opiliones *incertae sedis*. Interestingly, the *Archaeometa* Pocock, 1911 body plan, here also revealed through computed microtomography (μCT), has morphological parallels with some modern laniatorid harvestmen in the family Assammidae. However, the Coal Measures fossils do not preserve unequivocal laniatorid apomorphies, and so are referred to an uncertain position within Phalangida (transferred herein from Araneae). The *Archaeometa* specimens are further examples of Carboniferous Opiliones, which were originally misidentified, and contribute to a picture of an increasingly diverse Coal Measures harvestman fauna.

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Keywords: Araneae; Coal Measures; fossil; Opiliones; systematics

Introduction

The Late Carboniferous Coal Measures of Europe and North America are a vital source of information about early arachnid evolution. Numerous monographs have documented these fossil faunas in some detail (Frič 1904; Pocock 1911; Petrunkevitch 1913, 1949, 1953), although key to interpreting these data is the correct assignment of specimens to their higher groups or orders. Misidentifications of individual fossils can create a misleading picture of the stratigraphical ranges of the animals involved. Here, we focus on a case study involving some putative spiders (Arachnida: Araneae) described by Pocock (1911) and Petrunkevitch (1949) from the Coal Measures of Coseley in the English West Midlands (Figs 1–5). The work of these authors implied a Palaeozoic record of spiders belonging to the derived infraorder Araneomorphae: the fossils were likened to modern orb-weaving spider genera such as *Nephila, Tetragnatha* or *Deinopis*. With the help of computed microtomography (μCT), we demonstrate that at least one of these fossils is an unusual, long-bodied harvestman (Arachnida: Opiliones). Thus, the species of Pocock and Petrunkevitch can be formally excluded from the spider fossil record. There is now no convincing evidence for Palaeozoic araneomorphs; the oldest unequivocal araneomorph spiders are the Triassic fossils documented by Selden *et al*. (1999, 2009).

Placing these results in a wider context, this is not the first time that a Carboniferous harvestman was originally misidentified (see Discussion). Indeed, recent and ongoing studies of Coal Measures Opiliones have begun to reveal a wide range of both modern and extinct body plans (Garwood *et al.* 2011, 2014; and references therein). The long-bodied morphology documented here adds to the recorded Palaeozoic diversity (and disparity) of Coal Measures harvestmen. Interestingly, it shows remarkable parallels to some modern laniatorid harvestmen in the family Assamiidae (Fig. 6). The fossils cannot be placed unequivocally in this suborder, however, because the key laniatorid feature of raptorial pedipalps cannot be observed due to lack of preservation.

Historical background

Archaeometa nephilina Pocock, 1911 was raised for a fossil from the famous Coal Measures deposit of Coseley near Dudley in the English West Midlands. The holotype,

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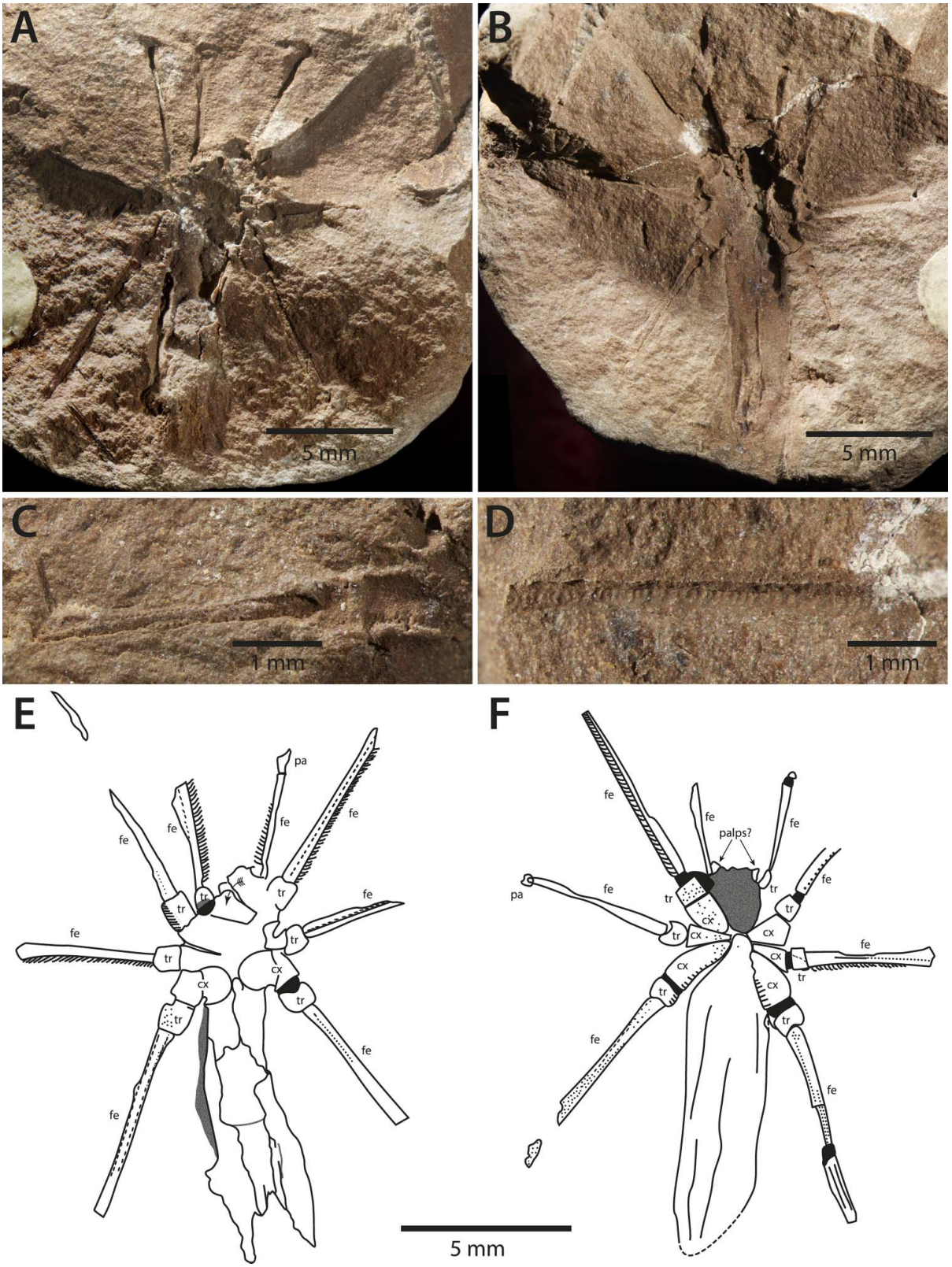

Figure 1. *Archaeometa nephilina* Pocock, 1911. Holotype (NHMUK In 31259; ex W. Egginton Collection) from the Late Carboniferous of Coseley near Dudley, UK. Originally interpreted as a Palaeozoic orb-weaving spider (Araneae), but here shown to be an unusual, long-bodied harvestman (Opiliones). **A**, photograph of part; **B**, photograph of counterpart; **C**, detail of left leg 4 (coxa to femur) of counterpart; **D**, detail of left leg 2 femur of counterpart, showing distinctive ornament; **E**, interpretative drawing of part; **F**, interpretative drawing of counterpart.

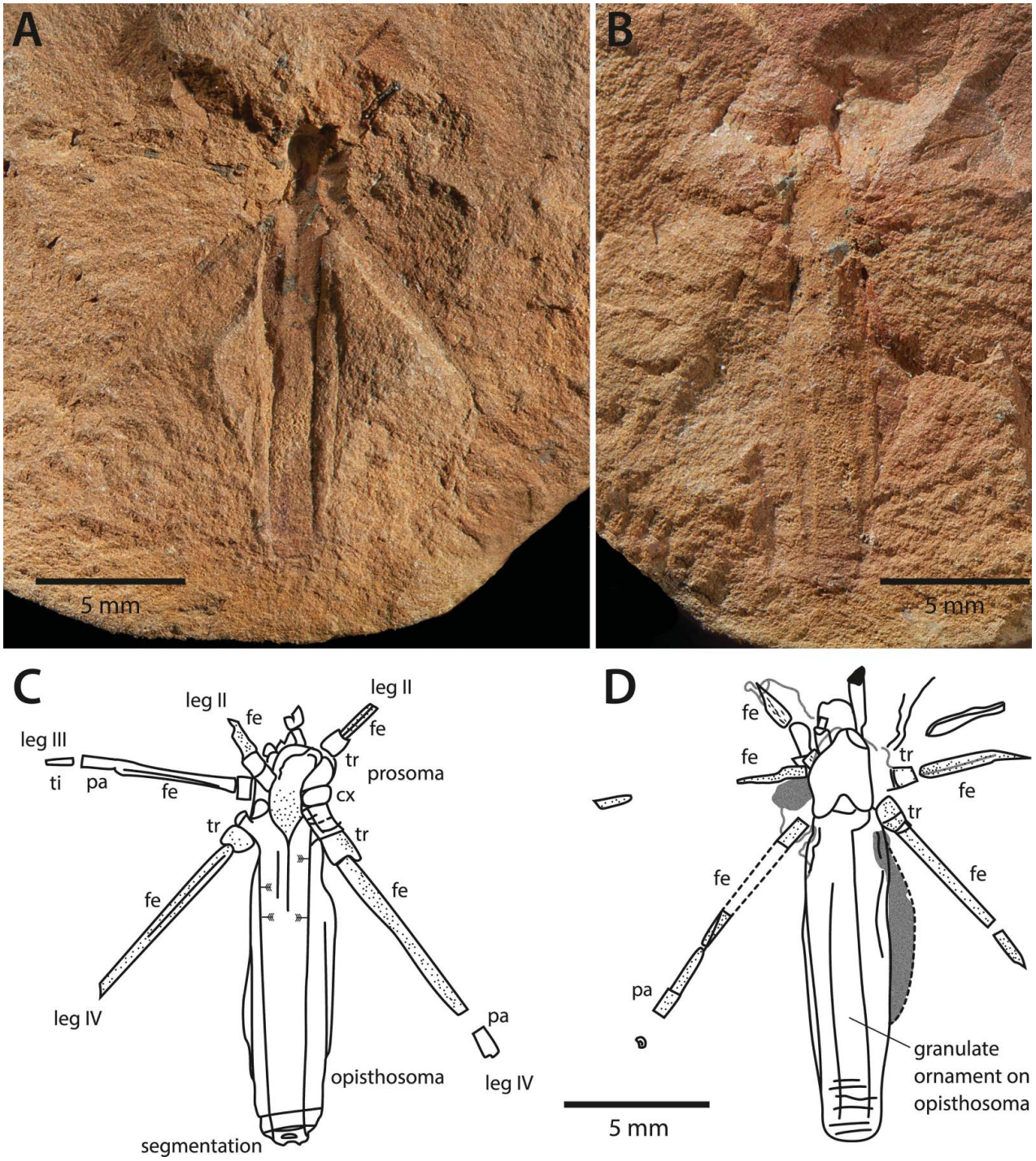

Figure 2. *Archaeometa nephilina* Pocock, 1911. Additional specimen (NHMUK 1.5863 ex J. R. Gregory Collection), also from the Late Carboniferous of Coseley. **A**, photograph of part; **B**, photograph of counterpart; **C**, interpretative drawing of part; **D**, interpretative drawing of counterpart.

deposited in the Natural History Museum, London (NHMUK In 31259), was originally part of the Walter Egginton Collection. Pocock's description and nomenclature clearly indicate that he believed it to be a fossil spider, closely related to living orb-weavers. *Meta* in the genus name derives from a modern spider genus. He even hypothesized that his fossil could belong to the extant family Argiopidae; this is an older systematic concept and the two extant genera he explicitly compared his fossil to (*Tetragnatha* and *Nephila*) would now be placed in the families Tetragnathidae and Nephilidae, respectively. Pocock (1911) described the fossil as having a long,

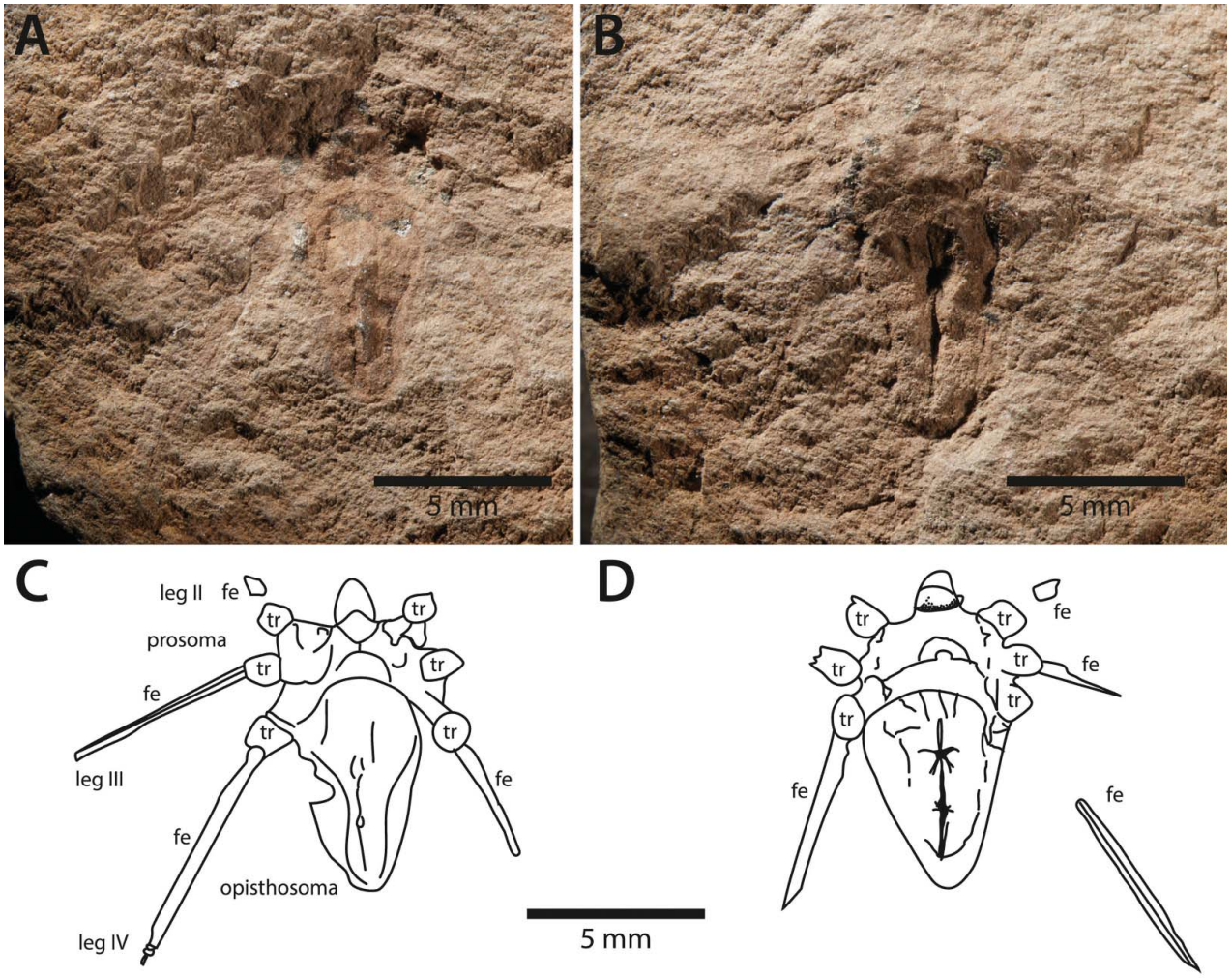

Figure 3. *Arachnometa tuberculata* Petrunkevitch, 1949. Holotype and only known specimen (NHMUK I. 13917; ex J. S. Neil Collection), also from the Late Carboniferous of Coseley. **A**, photograph of part; **B**, photograph of counterpart; **C**, interpretative drawing of part; **D**, interpretative drawing of counterpart.

cylindrical body, without any segmentation, and long, slender limbs in which the second pair of legs appeared longest. Note that an elongate second leg pair would be a highly unusual feature for a spider.

Archaeometa nephilina was listed as a fossil spider by Petrunkevitch (1913), who was later able to study the material in person. Petrunkevitch (1949) largely accepted Pocock's description of the holotype, and assigned a further Coseley fossil from the Natural History Museum (NHMUK I. 15863), originating from the J. R. Gregory Collection, to the same species. Petrunkevitch (1949) regarded this second specimen of *A. nephilina* as better preserved. Based on this, he expanded the description to include a flat carapace and at least four segments towards the posterior end of the elongate opisthosoma. Again, he noted the long legs and commented on the stout trochanters which, significantly, reminded him of a harvestman. No mention of spinnerets was made in this, or Pocock's, description. Petrunkevitch (1949), nevertheless, maintained that *A. nephilina* was a derived (in his scheme: arachnomorph) spider, and expanded the comparisons to modern long-bodied spider genera such as *Hypochilus* (Hypochilidae) and especially *Deinopis* (Deinopidae).

In the same monograph, Petrunkevitch (1949) proposed a new spider family, Archaeometidae, to accommodate the Coseley fossils. He also described another species, *Arachnometa tuberculata* Petrunkevitch, 1949, as an archaeometid. This fossil also comes from Coseley and is held in the Natural History Museum (NHMUK I. 13917); originally in the J. S. Neil Collection. Petrunkevitch (1949, p. 280) himself regarded it as "A rather poorly preserved specimen" and differentiated *Archaeometa* Pocock, 1911 from *Arachnometa* Petrunkevitch, 1949 primarily on the presence of a shorter, anteriorly wider opisthosoma in the latter. Petrunkevitch (1953, p. 107) listed both species and, in this publication, explicitly defined

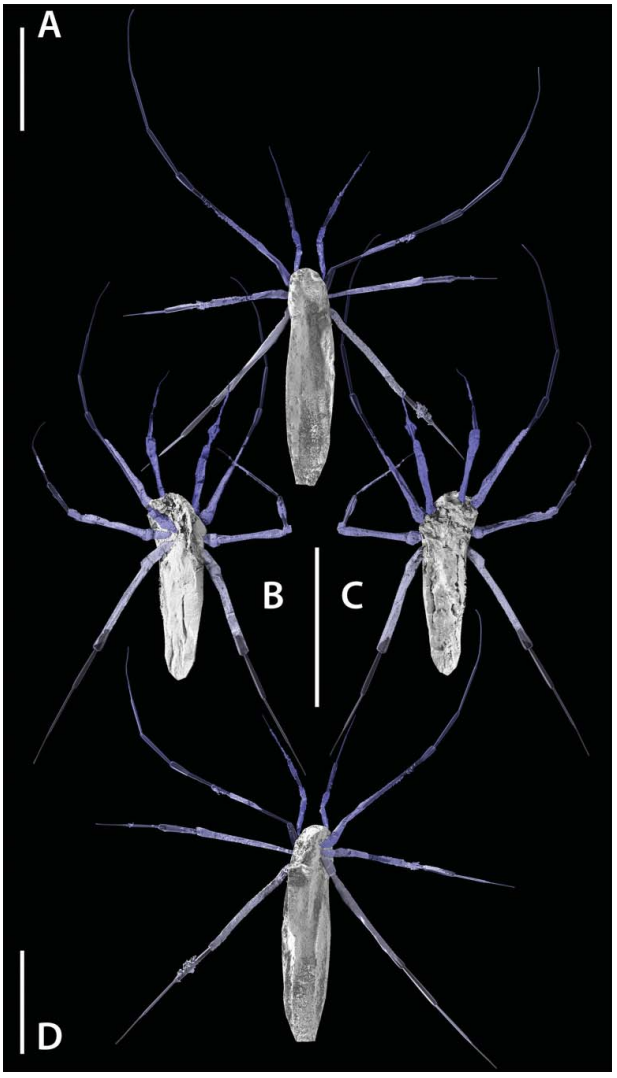

Figure 4. Tomographic reconstructions of *Archaeometa nephilina* Pocock, 1911, with inferred anatomical elements rendered semi-transparent. **A**, NHMUK 1.5863 ex J. R. Gregory Collection, in dorsal view; **B**, holotype NHMUK In 31259 ex W. Egginton Collection in ventral view; **C**, holotype NHMUK In 31259 in dorsal view; **D**, NHMUK 1.5863 in ventral view. Scale bars 10 mm.

Archaeometidae as "Arachnomorph spiders with prograde legs, and segmented abdomen." A problematic Czech Coal Measures genus, *Eopholcus* Frič, 1904, was now also included in Archaeometidae. Essentially the same scheme was maintained by Petrunkevitch (1955) in the *Treatise on Invertebrate Palaeontology*. Archaeometids were treated as a fairly derived (i.e. araneomorph) lineage of spiders and, in the same work, they were also raised to their own fossil superfamily: Archaeometoidea.

A considerably older fossil from the Early Devonian of Alken an der Mosel in Germany was later assigned to Archaeometidae as ?*Archaeometa devonica* Størmer, 1976. This highly dubious record would potentially extend the fossil record of araneomorph spiders back to more than 400 million years, but Størmer's (1976) material is poor and his interpretation unconvincing. Selden *et al*. (1991) rejected ?*A. devonica* as a spider, or even an arachnid, and further questioned whether Pocock's *A. nephilina* was a spider as well. They noted that the original specimens have a tuberculate cuticle and longitudinal folds, features never seen in more convincing Coal Measures spiders. Subsequently, Penney & Selden (2006) critically reviewed the fossil spider families. They concluded that Archaeometidae is not a valid family of extinct spiders and stated that the fossils assigned to it do not belong to Araneae; see also Selden & Penney (2010) and Penney & Selden (2011). In a similar vein, Selden in Dunlop (2007, p. 256) suggested that the *Archaeometa* fossils could be harvestmen, given that the second pair of legs is longest. This is a typical feature of at least the derived harvestman suborders (see Discussion). In this paper, we confirm this supposition, based on detailed photographic and tomographic restudy of the type material. We formally transfer *Archaeometa nephilina* to the Phalangida clade of the Opiliones, and treat *Arachnometa tuberculata* as Opiliones *incertae sedis*.

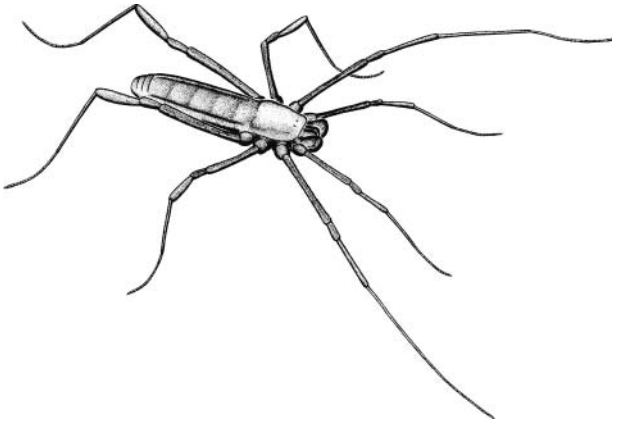

Figure 5. Reconstruction of the likely appearance in life of *Archaeometa nephilina* Pocock, 1911 as a long-bodied harvestman.

Material and methods

Material deposited in the Natural History Museum, London (**NHMUK**), including Pocock's holotype of *Archaeometa nephilina* (NHMUK In 31259), the second specimen described by Petrunkevitch (NHMUK I. 15863), and Petrunkevitch's holotype of *Arachnometa tuberculata* (NHMUK I. 13917), was examined. All three fossils are preserved in clay-ironstone (siderite) concretions from the productive locality of Coseley near Dudley, Staffordshire, UK. This is conventionally dated to the

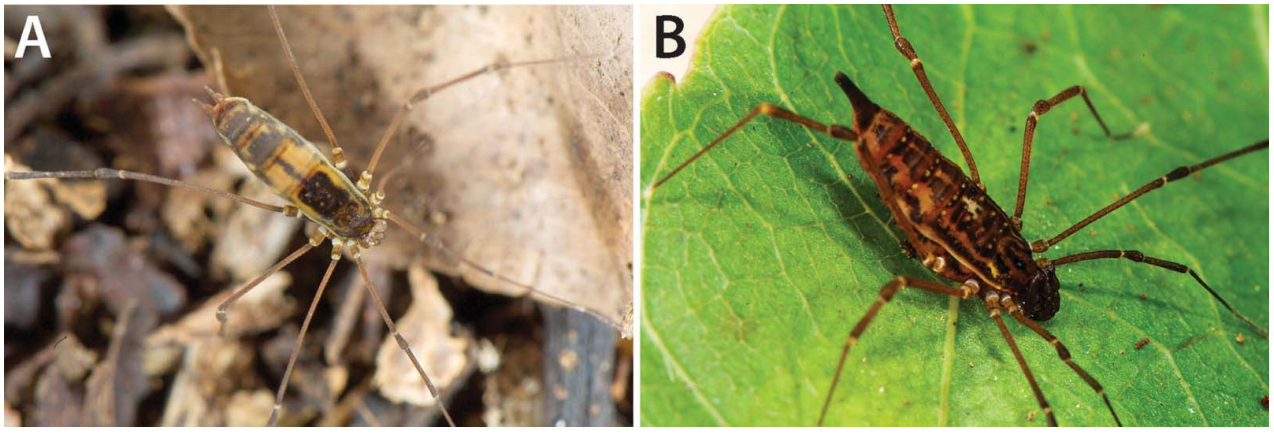

Figure 6. Comparative photographs of modern long-bodied harvestmen belonging to the extant family Assamiidae (Opiliones: Laniatores: Grassatores). Both species have yet to be formally described. **A**, unnamed Assamiidae; **B**, *Montalenia* sp. Images courtesy of Gonzalo Giribet.

Late Carboniferous (Bashkirian/Moscovian: Duckmantian), equivalent to the Westphalian B of traditional terminologies. Pointon *et al*. (2012) have dated the Duckmantian of Western Europe as straddling the Bashkirian/Moscovian boundary at around 315 Ma.

All specimens were photographed with Canon EOS 5D cameras mounted on a Leica MZ16 stereomicroscope, dry, in cross-polarized light. A mosaic of photographs was taken across each specimen at several levels of focus, which were later merged (using Adobe Photoshop CS6) to produce a composite, high-resolution photograph with a large depth of field. Drawings were made both with a camera lucida attachment on the microscope and by tracing the photographs using iDraw (www.indeeo.com).

Given the significance of limb proportions for correctly placing these fossils – i.e. many harvestmen have leg II longer than leg I – investigation of *A. nephilina* was undertaken using computed tomography, with the specific aim of revealing any distal leg podomeres, which are preserved but otherwise hidden deep in the nodule (Figs 1, 2). Both the *Archaeometa nephilina* holotype (NHMUK In 31259) and second specimen (NHMUK I. 15863) were scanned on a Nikon HMX-ST 225 scanner at the NHMUK with a tungsten reflection target. NHMUK In 31259 was scanned with 3142 projections at 500 ms exposure and a current and voltage of 200 μA and 180 kV, with no filtration. This provided a reconstructed dataset with a 15.4 μm voxel size. Double the number of projections (6284) were employed for NHMUK I. 15863 to improve the signal to noise ratio. This scan used a current and voltage of 190 μA and 195 kV, a 0.5 mm copper filter, and an exposure of 354 ms. The resulting dataset has a 14.0 μm voxel size.

Digital visualizations were created with the SPIERS software suite (www.spiers-software.org), following the methods of Garwood *et al*. (2012). Models were exported as VAXML datasets (Sutton *et al.* 2012), and included as Supplemental Material to the current publication. STLs from these models were then imported into the open source raytracer Blender (www.blender.org). Missing elements of the anatomy were created following the methods of Garwood & Dunlop (2014) and rendered transparent: missing podomere proportions are tentatively based on extant laniatorid harvestmen of the family Assamiidae since, amongst living harvestmen, some of these offer the closest match to the fossils in terms of body shape and general habitus (see Discussion).

Microtomography proved to be particularly useful for resolving legs I and III of the holotype almost in their entirety, and legs I and III of the second specimen (Fig. 4; Supplemental video). Scans also confirmed that the femoral length of leg II exceeded that in all other limbs, although distal elements of legs II and IV are not resolved. Limb article measurements derived from the scans were incorporated into the sketch reconstruction (Fig. 5), and combined with details from extant harvestmen as previously outlined, to yield what we hope is a more accurate impression of the appearance of the animal in life. Fossils were compared to summary works on living harvestmen, particularly habitus images in Roewer (1923), as well as more recent publications specifically documenting extant taxa with more elongate body plans (e.g. Santos & Prieto 2010). Comparative images of modern, long-bodied harvestmen (Fig. 6) were kindly provided by Gonzalo Giribet (Harvard).

Measurements (in mm) were made from a combination of hand specimen and μCT scan data. Because the whole of each leg is not preserved, femur length was used as a proxy for leg length to express leg formula (longest to shortest)

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Order ***Opiliones*** Sundevall, 1833
Clade ***Phalangida*** Bristowe, 1949
Family ***Archaeometidae*** Petrunkevitch, 1949 (transferred herein from Araneae Clerck, 1757)

Emended diagnosis. Opiliones with an elongate body, about five times longer than wide. Opisthosoma not strongly differentiated dorsally from carapace, and with longitudinal striations and segmentation restricted to the posterior end, effectively representing the scutum magnum condition. Legs slender with tubercular micro-ornament. (Emended from Petrunkevitch 1955).

Genus ***Archaeometa*** Pocock, 1911

Type and only species. *Archaeometa nephilina* Pocock, 1911, by original designation.

Diagnosis. As for the family.

Archaeometa nephilina Pocock, 1911 (Figs 1, 2, 4, 5)

1911 *Archaeometa nephilina* Pocock: 37, text-fig. 11.
1913 *Archaeometa nephilina* Pocock; Petrunkevitch: 88.
1949 *Archaeometa nephilina* Pocock; Petrunkevitch: 279, figs 159, 260.
1953 *Archaeometa nephilina* Pocock; Petrunkevitch: 107, fig. 192.
1955 *Archaeometa nephilina* Pocock; Petrunkevitch: 146, fig. 110(2).
1962 *Archaeometa nephilina* Pocock; Dubinin: 497, figs 1422A, B.
1980 *Archaeometa nephilina* Pocock; Morris: 27.
1991 *Archaeometa nephilina* Pocock; Selden *et al*.: 244.
2006 *Archaeometa nephilina* Pocock; Penney & Selden: 26, fig. 1.
2010 *Archaeometa nephilina* Pocock; Selden & Penney: 188.
2011 *Archaeometa nephilina* Pocock; Penney & Selden: 51, fig. 41.

Material. NHMUK In 31259 (holotype; ex W. Egginton Collection). NHMUK 1.5863 (ex J. R. Gregory Collection). From Coseley near Dudley, Staffordshire, UK. Late Carboniferous (Duckmantian).

Diagnosis. As for the family.

Description. NHMUK In 31259 (holotype; Figs 1, 4; see video and data in Supplemental Material), near complete specimen. Body cylindrical, total length *c.*12.0, maximum width 2.5. Chelicerae and carapace/eyes not seen; basal elements of pedipalps present, total length and details not known. Coxa I not seen, coxae II–IV subtriangular; anterior portion of opisthosoma extended between coxae III–IV. Trochanters robust, quadratic elements. Legs (where preserved) elongate, slender; femora II and IV noticeably longer than I and III. Leg articles subquadrate in cross section (at least for proximal articles), femur, patella and tibia slightly expanded distally. Tibia of at least leg III fairly broad, laterally compressed element. Metatarsus and tarsus (where preserved) very thin. Leg article lengths: leg I: femur 3.5, patella 0.9, tibia 1.8, metatarsus 2.6, tarsus ≥ 0.8; leg II: femur 5.7; leg III: femur 4.5, patella 1.3, tibia 2.2, metatarsus 3.7, tarsus ≥ *c.* 1.0; leg IV: femur 6.3. Other leg articles not measurable. At least femora with distinct ornament of at least two rows of tubercles along their length, each row set onto slightly raised ridge. Opisthosoma elongate, bluntly rounded posteriorly. Details poorly preserved, but with three or four longitudinal folds on the ventral surface, unpaired and not extending along the entire length of the opisthosoma.

NHMUK 1.5863 near complete and larger specimen (Figs 2, 4; see video and data in Supplemental Material). Body cylindrical, total length 21.5, maximum width 4.6. Carapace flat, mostly featureless, possible small pair of median eyes towards anterior margin of carapace. Chelicerae and pedipalps not seen. Trochanters robust; legs elongate, slender. Leg formula II, IV, III, I. Leg article lengths: leg I: femur 5.4, patella 1.8, tibia 3.7, metatarsus ≥4.3; leg II: femur *c.* 13.0; leg III: femur 6.1, patella 2.0, tibia 3.9, metatarsus *c.*8.0; leg IV: femur 10.5. Other leg articles not measurable. Opisthosoma elongate, bluntly rounded posteriorly, with two distinct longitudinal grooves running dorsally along the entire length (represented ventrally as long ridges). Hints of broad segmental areas along length of opisthosoma, which terminates in four short (*c.*1 mm), distinct segments.

Opiliones *incertae sedis*
Genus ***Arachnometa*** Petrunkevitch, 1949 (transferred herein from Araneae Clerck, 1757)

Emended diagnosis. Fossil harvestman with a kite-shaped opisthosoma bearing a median ridge with two tubercles; the anterior tubercle slightly larger than the posterior tubercle. (Emended from Petrunkevitch 1955).

Type and only species. *Arachnometa tuberculata* Petrunkevitch, 1949, by original designation.

Arachnometa tuberculata Petrunkevitch, 1949 (Fig. 3)

1949 *Arachnometa tuberculata* Petrunkevitch: 280, figs 160, 261.
1953 *Arachnometa tuberculata* Petrunkevitch; Petrunkevitch: 107.

1955 *Arachnometa tuberculata* Petrunkevitch; Petrunkevitch: 146, fig. 110(2).
1962 *Arachnometa tuberculata* Petrunkevitch; Dubinin: 497, fig. 1423.
1980 *Arachnometa tuberculata* Petrunkevitch; Morris: 27.
2006 *Arachnometa tuberculata* Petrunkevitch; Penney & Selden: 27
2010 *Arachnometa tuberculata* Petrunkevitch; Selden & Penney: 189.
2011 *Arachnometa tuberculata* Petrunkevitch; Penney & Selden: 51.

Material. NHMUK I. 13917 (holotype, ex J. S. Neil Collection). From Coseley near Dudley, Staffordshire, UK. Late Carboniferous (Duckmantian).

Description. Incomplete specimen, both part and counterpart reveal dorsal surface (Fig. 3). Total body length 13.4, maximum width 5.6. Chelicerae, pedipalps, leg I and details of carapace/eyes not seen in detail; carapace possibly with anteriorly projecting region. Leg II preserved as robust, rounded trochanter with fragment of femur. Legs III–IV preserved as robust, rounded trochanters with long, slender femora; preserved femur lengths 8.3 (III), 10.0 (IV). Opisthosoma kite- or shield-shaped in outline; length 9.2, widest in anterior third, tapering and bluntly rounded posteriorly. Opisthosoma without obvious segmentation, with narrow marginal region and distinct median ridge (length *c*.6 mm) bearing two raised, blunt tubercles 2.4 apart; anterior tubercle slightly larger than posterior.

Remarks. As noted above, even the original description (Petrunkevitch 1949, p. 280) remarked on the poor preservation of this specimen. While it is clearly an arachnid of some description, it shows no diagnostic features of spiders, such as the presence of opisthosomal spinnerets. The trochanters of the legs are quite robust and the legs themselves (where preserved) are long and slender. For this reason it may well be a further example of a harvestman, but leg II is missing and it is impossible to say if this was longest, whilst somatic details such as eyes or a clear opisthosomal segmentation pattern are equivocal. The opisthosoma is shorter and wider than in *Archaeometa*, while the dorsal ridge and tubercle ornament in *Arachnometa tuberculata* offers a reasonable character (see Diagnosis) by which the species could be recognized in future. However, in lieu of better-preserved material we find it difficult to make meaningful comparisons with other Coal Measures (or living) arachnid taxa, and therefore propose that *A. tuberculata* is best treated as Opiliones *incertae sedis*.

Discussion

Four suborders of harvestman, Cyphophthalmi, Eupnoi, Dyspnoi and Laniatores, have been recognized traditionally. An extinct suborder (Tetrophthalmi) was added recently by Garwood *et al*. (2014). Three of these principal clades are represented by Carboniferous species; one can be assigned to Tetrophthalmi, three to Eupnoi, and five to Dyspnoi. It should be stressed that only the tetrophthalmid, one of the eupnoids, and one of the dyspnoids have had their placement tested cladistically. All three taxa derive from exceptionally preserved fossils from Montceau-les-Mines in France and were reconstructed using computed tomography to create three-dimensional models of the nodule-hosted specimens (Garwood *et al.* 2011, 2014). These studies demonstrate that a long-legged eupnoid and a spiny dyspnoid harvestman, both with essentially modern body plans, coexisted alongside the extinct, four-eyed (tetrophthalmid) lineage which had a combination of characters quite unlike that of any living species.

Other Coal Measures harvestmen are more ambiguous and merit further study. For example, a putative trogulid (Dyspnoi) from Commentry in France was described by Thevenin (1901). Petrunkevitch (1913) described an extinct family (Nematostomoididae) from Mazon Creek, which he assigned to Dyspnoi; however, this subordinal placement should be treated with caution because the family diagnosis includes characters which should not be part of the harvestman ground plan. *Kustarachne* Scudder, 1890 from Mazon Creek is an interesting case: Petrunkevitch (1913) placed these fossils in a new, extinct arachnid order which he also named Kustarachne, subsequently emended to Kustarachnida. Only later were these specimens correctly recognized as misidentified harvestmen (Beall 1986). In fact, *Kustarachne* has a body plan quite similar to living sclerosomatids (Eupnoi: Sclerosomatidae), with what appears to be a *scutum parvum* plate covering most of the dorsal opisthosoma; see Dunlop (2004) for a redescription. Further unpublished fossil harvestmen from Mazon Creek await description.

Archaeometa nephilina can be added to a lengthy list of Coal Measures harvestmen which were originally misidentified. Its correct assignment here brings the total number of Carboniferous taxa to 10. Harvestmen today are the third most diverse group of arachnids, after the mites and spiders, but remain rather poorly represented palaeontologically, with only 40 valid species in the entire fossil record. Even if the exact affinities of *Archaeometa* cannot be resolved (see below), these specimens are definitely not spiders, and they contribute instead to a growing picture of a taxonomically and morphologically diverse Opiliones fauna in the coal swamps towards the end of the Carboniferous. Part of the problem with interpreting *Archaeometa* in the past may have been that a long, cylindrical body is not typical for Opiliones: a compact and somewhat rounded or subtriangular shape is typical (e.g. figures in Roewer 1923). An elongate second leg pair and harvestman-like trochanters were noted in the literature on *Archaeometa*, but both Pocock and Petrunkevitch

seem to have been misled by the superficially spider-like appearance of these fossils (Figs 1, 2).

Assigning *Archaeometa* further within Opiliones is problematic. The long legs, with an elongate second pair, and the fairly large (12 mm) body length, argue against the basal harvestman suborder Cyphophthalmi. The general body shape and lack of an anteriorly projecting ocularium does not resemble the two known examples of Tetrophthalmi. This suggests placement in the more derived Phalangida clade, i.e. Eupnoi, Dyspnoi and Laniatores. Explicit assignment to one of these suborders is more difficult, since this requires key diagnostic pedipalp characters that remain equivocal in *Archaeometa*. For example, a terminal pedipalpal claw would imply a eupnoid, a reduced claw a dyspnoid, while a distinctly spiny and/or raptorial pedipalp would be characteristic for laniatorids, none of which can be seen in the fossils, even with the application of computed tomography (Fig. 4). We should add that the apparent presence of a *scutum magnum*, i.e. the carapace plus most tergites fused into a single dorsal plate, would be more consistent with laniatorid affinities.

Modern comparisons

Despite their unusual shape, comparisons can be drawn between *Archaeometa* and certain dyspnoid harvestmen, particularly those in the family Trogulidae. Trogulids typically have a rather elongate, flattened, albeit somewhat kite-shaped, body, see e.g. Schönhofer & Martens (2008) and Schönhofer *et al*. (2013) for recent accounts. As in the Carboniferous fossils, there can, in some *Trogulus* species, be distinct longitudinal lines running lengthways down the opisthosoma. However, trogulids are characterized by the presence of a 'hood' – a prominent bifurcating anterior projection from the carapace originating in front of the eyes – and there is no indication for such a hood in either of the *Archaeometa* specimens. Furthermore, the body and limbs of trogulids are covered with a rough, granular ornament, not seen in the fossils, while the legs of trogulids are generally more robust and less elongate than those preserved in *Archaeometa*.

There are also notable similarities between *Archaeometa* and some living laniatorids in the Old World family Assamiidae. Certain assamiid species also exhibit an elongate, somewhat cylindrical body and long, slender legs. Examples include currently undescribed members of the family Assamiidae (an unnamed assamiid and a member of the genus *Montalenia* Santos & Prieto, 2010; Fig. 6). These authors' illustrations of the female of the type species of their new genus, *Montalenia forficula* Santos & Prieto, 2010 (figs 11, 21) from Equatorial Guinea, also show a fairly long-bodied harvestman. Similar to Archaeometa, it has four segments more clearly expressed towards the back of the opisthosoma, although the segments in the fossil are shorter and less separated than those in *M. forficula*. We should further note that widely separated tergites – where the intersegmental membranes are clearly visible – are often indicative of the swollen opisthosoma in a pregnant female. Thus we should bear in mind that both gender and the presence of eggs can affect the overall appearance of a harvestman. The implication from the compact posterior tergites of the fossils is that they were probably not gravid females. *Montalenia forficula* also has a series of projections from the posterior margin of the opisthosoma which, if this were to be preserved as a fossil, might even be mistaken for spider spinnerets. We should caution, however, that *M. forficula* shows sexual dimorphism, in which the male is notably shorter than the female. Furthermore, most assamiid harvestmen have a more typical, compact body, and thus these elongate morphotypes are not characteristic for the whole family. Rather they are restricted to particular genera or species, and perhaps even particular genders within species.

It is tempting to refer *Archaeometa* to Laniatores based on the resemblance of the fossils to the long-bodied assamiids noted above. This would make these specimens the oldest known laniatorids, and extend the range of the suborder back more than 250 million years from the previous oldest examples in Eocene (*c*.45–49 Ma) Baltic amber described by Koch & Berendt (1854) and revised by Ubick & Dunlop (2005). Time-calibrated estimates of phylogeny (Giribet *et al.* 2010; Sharma & Giribet 2011, 2014; Hedin *et al*. 2012) strongly imply that laniatorids should have been present in some form during the Carboniferous; the latest estimates for the origins of Laniatores range between *c*.355.5 Ma (Garwood *et al.* 2014, fig. 3B) and 410.3 Ma (Sharma & Giribet 2014), which corresponds to somewhere in the early Devonian–early Carboniferous. However, as noted above, we lack explicit laniatorid and/or assamiid apomorphies such as a distinctly raptorial pedipalp in these fossils.

Because different groups of harvestman can appear superficially similar, we cannot rule out the additional possibility that these fossils belong to a Palaeozoic group with an extinct body plan – for example, one belonging to the stem-lineage of a living suborder, as was the case with the recent discovery of Tetrophthalmi. Furthermore, Assamiidae does not resolve as an especially basal laniatorid family (Sharma & Giribet 2011, fig. 18, 2014, fig. 1), being part of the more derived Grassatores clade. Again, in the absence of preserved apomorphies, it would be premature to try and date Grassatores on the basis of these *Archaeometa* fossils alone. The data of Sharma & Giribet (2011) suggested that Grassatores may have radiated *c*.254 Ma, i.e. after the end Permian mass extinction event, although Sharma & Giribet (2014) noted that the use of total-evidence techniques could result in a much older date for this radiation. These authors also commented that the absence of Mesozoic fossils of this group

makes testing this hypothesis difficult. An older calibration point remains unavailable, so the search for an unequivocal Palaeozoic laniatorid continues.

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Supplemental material

Supplemental material for this article can be accessed at http://dx.doi.org/10.1080/14772019.2015.1018969

Supplemental video: A video showing the tomographic reconstructions of *Archaeometa nephilina* Pocock, 1911; Holotype NHMUK In 31259, and NHMUK 15863.

Supplemental data: VAXML models of *Archaeometa nephilina* Pocock, 1911; Holotype NHMUK In 31259, and NHMUK 15863, combined into a single .zip file.

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