

Tomographic Reconstruction of the Exceptionally Preserved Trigonotarbid Arachnid *Eophrynus prestvicii*

Authors: Dunlop, Jason A., and Garwood, Russell J.

Source: *Acta Palaeontologica Polonica*, 59(2) : 443-454

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: <https://doi.org/10.4202/app.2012.0032>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Tomographic reconstruction of the exceptionally preserved trigonotarbid arachnid *Eophrynus prestvicii*

JASON A. DUNLOP and RUSSELL J. GARWOOD



Dunlop, J.A. and Garwood, R.J. 2014. Tomographic reconstruction of the exceptionally preserved trigonotarbid arachnid *Eophrynus prestvicii*. *Acta Palaeontologica Polonica* 59 (2): 443–454.

An exceptionally preserved specimen of the extinct trigonotarbid arachnid *Eophrynus prestvicii* (Arachnida: Trigonotarbida) from the Late Carboniferous (Duckmantian) British Middle Coal Measures of the UK is redescribed with the help of X-ray micro-tomography (XMT). Previous work is summarised and the correct spelling of the species name confirmed. Reconstruction of the void left by the original specimen within a siderite (ironstone) nodule reveals its three-dimensional structure as well as novel details which are difficult to resolve using traditional methods of study. The pedipalps and legs can now be reconstructed almost in their entirety and we can confirm that the chelicerae hung beneath the prosoma with a backwards-directed fang. Opisthosomal segmentation is clarified: a narrow tergite 1 is followed by eight further tergites (2–9), clearly demarked by their ornamentation. In general, a much more accurate picture of the spines and tuberculation ornamenting the dorsal surface of the body was resolved. Ventrally the opisthosoma bears so-called ventral sacs and terminates in a two-segmented pygidium. Based on the XMT model, a new reconstruction of *E. prestvicii* is presented. Although phylogenetically unrelated, the sometimes similar-looking, spiny and tuberculate lanitorid harvestmen (Opiliones: Lanitores) offer a possible ecological model for these highly ornamented trigonotarbids.

Key words: Arachnida, Trigonotarbida, Eophrynidae, XMT, systematics, harvestmen, Carboniferous, British Middle Coal Measures, United Kingdom.

Jason A. Dunlop [jason.dunlop@mfn-berlin.de], Museum für Naturkunde, Leibniz Institute for Research on Evolution and Biodiversity at the Humboldt University Berlin, D-10115 Berlin, Germany;

Russell J. Garwood [russell.garwood@manchester.ac.uk], Manchester X-ray Imaging Facility, School of Materials, The University of Manchester, Oxford Rd., Manchester, M13 9PL, UK and The Manchester X-ray Imaging Facility, Research Complex at Harwell, Rutherford Appleton Laboratory, Oxon, OX11 0FA, UK.

Received 5 March 2012, accepted 25 May 2012, available online 6 June 2012.

Copyright © 2014 J.A. Dunlop and R.J. Garwood. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

Trigonotarbida is an extinct arachnid order known from the late Silurian to the early Permian (ca. 419–290 Ma). They resolve at the base of the Pantetrapulmonata clade (Shultz 2007), i.e., spiders and their closest relatives, and lack any indication of silk-producing spinnerets. Sixty-seven species are currently recognised in the literature, although some of these are probably based on trivial differences; or even the way the fossils have been preserved. Revisions have invariably reduced their overall alpha diversity (Dunlop 1994; Rössler 1998; Garwood and Dunlop 2011). Trigonotarbid fossils have been recovered most frequently from the Late Carboniferous Coal Measures of Europe and North America (e.g., Frič 1904; Pocock 1911; Petrunkevitch 1913, 1949, 1953; Heide 1951; Brauckmann et al. 1985), together with a further Carboniferous record from Argentina. Eight of the nine described families occur in the late Carboniferous, and the fauna includes

some highly ornamented arachnids with bodies up to a few centimetres long (cf. Rössler and Dunlop 1997).

One of the best known trigonotarbids is the large, spiny and tuberculate species *Eophrynus prestvicii* (Buckland, 1837) from the Coal Measures of the English West Midlands. Frequently mentioned in the literature (see synonymy list) or figured as a general example of a fossil arachnid in both historical (Roemer 1876; Scudder 1885) and modern (e.g., Black 1988) palaeontological textbooks, it is a key species for understanding both the systematics and palaeobiology of the group. Historically, *E. prestvicii* was the first trigonotarbid ever to be described—albeit originally as a beetle—and it is thus the oldest available name. Furthermore, a second specimen (Figs. 1–3) added by Woodward (1871) is exquisitely preserved and offers an unparalleled opportunity to reconstruct the appearance of one of the more anatomically interesting examples of these animals in life. Indeed casts of this important fossil are fairly common in museum displays

and at one stage were even commercially available; often referred to as a fossil “spider”. The Eophrynidae family to which *Eophrynus prestvicii* belongs is probably among the more derived trigonotarbid lineages (cf. Dunlop and Brauckmann 2006). Thus new morphological data from this largely complete fossil should help to clarify both the ground pattern and affinities of the family.

Our chosen study method, X-ray micro-tomography (XMT), has recently emerged as a powerful tool for studying Coal Measures fossils hosted in siderite concretions (e.g., Garwood and Sutton 2010; Garwood et al. 2011). Essentially, the three-dimensional void left by the original organism within the encasing ironstone (siderite) concretion is scanned and reconstructed (Fig. 3). A pilot study, including *E. prestvicii*, was carried out by Garwood et al. (2009). Here, we aim to follow up the results of this work in more detail, complementing Garwood and Dunlop (2011) on another trigonotarbid family Anthracomartidae. Here we offer an assessment of the wider significance of the new morphological data recovered for *E. prestvicii*, supplemented by a detailed historical account, synonymy list and a novel reconstruction (Fig. 4). We also discuss the implications of our results for other eophrynid genera and species (Fig. 5) and—picking up a theme from Loman (1900)—we consider whether the often similarly ornamented laniatorid harvestmen (Opiliones: Laniatores) (Fig. 6) offer a reasonable analogue for the eophrynid mode of life.

Institutional abbreviations.—BU, Lapworth Museum of Birmingham University, Birmingham, UK; NHM, Natural History Museum, London, UK.

Other abbreviations.—XMT, X-ray micro-tomography.

Historical background

Prestwich (1834) mentioned a putative spider [as “Aranea”] from a concretion in the collection of Mr Antice [sic] from Madeley. This fossil was subsequently described by Buckland (1837) as *Curculioides prestvicii* in one of his Bridgewater Treatises “On the Power Wisdom and Goodness of God as Manifested in the Creation Volume IV: Geology and mineralogy considered with reference to natural theology”. The holotype originates from the Carboniferous ironstone of Coalbrookdale, Shropshire, UK and was named in honour of Joseph Prestwich (1812–1896); the local geological historian who first noted the specimen (see above), and who later became a Fellow of the Royal Society. The owner of the holotype was presumably the same William Anstice, who inherited the Madeley Wood Ironworks, and several other mining and ironworking enterprises in the Coalbrookdale area. Although initially noted as an arachnid, this fossil—together with another now recognised as the first ever (fossil or living) ricinuleid (see Selden 1992)—was interpreted by Buckland (1837) as a beetle belonging to the weevil family Curculionidae (Coleoptera). From the annotations on his original

figure it is evident that Buckland (1837) interpreted both the right pedipalp and the right first leg as antennae. This left three limb pairs on the right side contributed towards the misinterpretation as an insect. The projecting anterior part of the carapace was regarded as a proboscis; i.e. the weevil rostrum. Extensive tuberculation on the upper surface of the body—which in this fossil is partly overlain by the smooth sternites—was also noted.

Hollier’s specimen.—Woodward (1871) described a second fossil from the Coal Measures of Coseley, Staffordshire, UK; this time coming from a series of nodules supplied by E. Hollier of Dudley. This may well have been Elliott Hollier (1813–1905, <http://www.hollyer.info/elliott.php>), a chemist based in the Market Place of Dudley who was much involved in local civic affairs and even became the town’s mayor. As of 1862, an E. Hollier from the Market Pace is listed both as Honorary Secretary and Curator of the Dudley and Midland Geological and Scientific Society and Field Club. For a historical account of this organisation see Cutler (1981). A society museum was apparently established as of 1863 but it is unclear whether members’ fossils were habitually deposited there, or remained in private hands (see below).

Woodward (1871: 1) referred to Hollier’s specimen as a “very perfect Arachnide”. The exact circumstances of its discovery are not recorded, but it remains to this day one of the most impressive Carboniferous arthropods (Fig. 2). This specimen fully reveals both the dorsal and ventral surfaces. Woodward (1871) recognised that it was conspecific with Buckland’s (1837) fossil and now correctly identified them as arachnids. His genus name, *Eophrynus* Woodward, 1871, is clearly derived from the modern whip spider (Amblypygi) genus *Phrynus* Lamarck, 1801, to which the fossils were compared. It was, however, explicitly treated by Woodward (1871) as a pseudoscorpion (Arachnida: Pseudoscorpiones). Although these Coal Measures fossils are an order of magnitude larger than all known living pseudoscorpions, Woodward’s (1871) interpretation is easier to understand when the habitus of modern genera like *Cheiridium* Menge, 1855 is taken into account (e.g., Weygoldt 1969: fig. 100). These extant pseudoscorpions also have a triangular prosoma and a rounded, and dorsally highly tuberculate, opisthosoma. Woodward (1871) correctly described numerous morphological details for *E. prestvicii*, including lobes on the carapace and the anteriorly projecting rostrum, as well as the tuberculation pattern on the opisthosoma and the four spines around its posterior margin. Nine opisthosomal tergites, but only seven sternites, were recognised, the sternites supposedly bearing pairs of putative tracheal openings.

Geinitz (1882) described a new (large) species of trigonotarbid from Germany and again interpreted both his fossil and *E. prestvicii* as pseudoscorpions. Karsch (1882) rejected any similarities between *Eophrynus* and whip spiders and in the same paper raised a new, extinct order Anthracomarti. This was divided into two families (spellings as in the original). Architarboidae included his new trigonotarbid genus, *An-*

thracomartus Karsch, 1882, together with fossils belonging to what would later be recognized as another extinct order, Phalangiotarbida. The second family, Eophrynoidea, was restricted to *Eophrynus* and diagnosed on having more tergites than sternites and a tuberculate dorsal surface. Haase (1890) adopted the modern spelling Eophrynidae and redefined the family primarily on the supposedly segmented nature of the carapace, the presence of epimera—i.e., tergites with median and lateral plates—and, oddly, the absence of trochanters. Loman (1900) proposed that trigonotarbids were closely related to various modern groups of harvestmen (Opiliones). *Eophrynus* was explicitly compared to the suborder Laniatores and a drawing of *E. prestvicii* was juxtaposed against the modern Sumatran harvestman *Gnomulus segnipes* (Loman, 1893) which does indeed have a similar overall appearance.

Lost and found.—Pocock (1902) offered the first formal re-description of *E. prestvicii*, although by this time Hollier's fossil was no longer available and Pocock (1902) had to rely on casts and drawings of the original. Pocock (1902) demonstrated that the carapace was lobed rather than truly segmented (contra Haase 1890), but was unable to identify any eyes. Ventrally, a sternum was recognised along with two putative cheliceral articles. The pedipalps were interpreted as long and slender with a short patella barely distinguishable from the tibia. The larger fourth pair of legs was noted, and the legs were described as having a pitted surface and longitudinal grooves, and in one case as supposedly ending in a single claw. The opisthosoma was described as having nine segments—the first short without division into median and lateral plates—with a discussion of possible segmental fusion (see also Discussion). Ventrally the first sternite was thought to be absent, but the tergites and sternites were largely matched to each other, with a discussion of the segmental interpretation of the “anal plate” (the pygidium in modern terminology) and its surrounding sclerites. “Elevations” were described on the posterior border of the third sternite and rows of tubercles (Woodward's [1871] putative tracheal openings) were also highlighted. Eophrynidae was retained in the extinct order Anthracomarti and redefined on, among other things, the presence of spines on the posterior margin of the opisthosoma.

Frič (1904) also received a cast of *E. prestvicii* and offered his own description and illustration. His interpretations largely matched those of Pocock (1902), but Frič (1904) also figured a supposed single tarsal claw of the legs and novel interpretations of the putative genital region on the ventral opisthosoma. Pocock (1911) reproduced his earlier drawings, but could add little to the previous description. However, centrally located eyes were now cited as present and used in the diagnosis of *Eophrynus*. The monographs of Petrunkevitch (1913, 1949) briefly mentioned *E. prestvicii*, but the latter work is of more significance for dividing the old order Anthracomarti into two groups (see Systematic palaeontology). The family Anthracomartidae were retained under the older name, while the other families, including Eophrynidae, were transferred to a new, supposedly unrelated,

order Trigonotarbida. A further putative example of *E. prestvicii* was described by van der Heide (1951) from the Coal Measures of Limbourg in Belgium. Since it is preserved only in ventral view it is difficult to determine its generic affinities unequivocally. Further material from the same locality was assigned to “*Eophrynus* spec. indet”.

Petrunkevitch (1953) incorrectly reported Buckland's (1837) holotype as lost. It is actually in London (see Material and methods). However, Petrunkevitch (1953) did rediscover Woodward's (1871) specimen which, according to his notes, was in private hands until 1945 when it was presented to the University of Birmingham, UK by the Misses Tilley. Note, however, that Strachen (1979)—who was based at Birmingham University—dated this transfer to 1936 and gave the name as “Titley”. How the Titley's (or Tilley's) acquired Hollier's fossil is unfortunately not recorded. Woodward's (1871) specimen was designated the “lectotype” [sic], by Petrunkevitch (1953). In fact he should have treated it as a neotype (Woodward's [1871] specimen was not part of the original type series), but since the holotype still exists this neotype designation is now superfluous. Morphologically, Petrunkevitch (1953) further prepared Hollier's specimen and was able to reveal novel features such as the long anterior spine on the carapace, which Pocock (1902) misinterpreted as a chelicera. Petrunkevitch (1953) confirmed the presence of a pair of median eyes and described pitting on the both lateral lobes of the carapace and, like Pocock (1902), on the limbs. Nine opisthosomal segments were again recognised, but ventrally the raised structures on the third sternites were thought to be associated with the genital opening and were thus assigned to the second opisthosomal segment. While numerous authors have since mentioned *E. prestvicii* (see synonymy list) there have been no new studies of the original material until the provisional XMT results of Garwood et al. (2009); which we expand upon in detail here.

Material and methods

The holotype of *E. prestvicii*, from Coalbrookdale, Shropshire, UK (NHM In 49322) is not particularly well preserved, and given that dorsal and ventral features are partly superimposed it was not considered appropriate for tomography. Much better (Figs. 1–3) is Hollier's more complete specimen BU 699 (cf. Woodward 1871) from the nearby locality of Coseley near Dudley, Staffordshire, UK. Both these examples of *E. prestvicii* come from the British Middle Coal Measures. This can be dated to the Duckmantian substage of the late Carboniferous (ca. 311 Ma); equivalent to the Westphalian B of more traditional stratigraphic terminology. Heide's (1951) specimen is marginally older (Langsettian), but was not examined. As noted above, it is only known in ventral view making its assignment questionable. With respect to related trigonotarbids, the holotype of *Eophrynus udus* Brauckmann, Koch, and Kemper, 1985 is in the private collection of K.H. Hellwig in Hagen, Germany, but a cast

and photographs were kindly provided by Carsten Brauckmann. The original comes from the Hagen-Vorhalle brick pit (Ziegelgrube), North Rhein-Westphalia, Germany and is dated at Marsdenian (= Namurian B; ca. 319 Ma). Comparative material assigned to the eophrynid genera *Pleophrynus* Petrunkevitch, 1945 and *Stenotrogulus* Frič, 1904 was studied by Dunlop (1994, 1995a) respectively. These papers contain further details of localities, stratigraphy and repositories.

Older descriptions of BU 699 can be found in Pocock (1902) and Petrunkevitch (1953). These are expanded here on the basis of the XMT scans (Fig. 3) and examination of the hand specimens. Comparisons with exceptionally preserved Devonian fossils from the Rhynie and Windyfield cherts of Scotland and the Gilboa mudstone of New York (Hirst 1923; Shear et al. 1987; Fayers et al. 2005) yield data on the morphology of presumably basal trigonotarbids and facilitate the interpretation of the larger and more derived Coal Measures species. Comparisons were also drawn with our recent XMT study (Garwood and Dunlop 2011) of the family Anthracomartidae and an overview of trigonotarbid morphology can also be found in Garwood and Dunlop (2010).

X-ray micro-tomography.—BU 699 was scanned on a Nikon HMX-ST (Natural History Museum, London). A tungsten reflection target with 200 mA current and 225 kV voltage was used, and 3142 projections taken with a 1.4 second exposure, and a 1 mm copper filter. A 2000 × 2000 detector panel provided a voxel size of 45 microns. Computer reconstructions were created with the custom software suite SPIERS (Sutton et al. 2012). Images were thresholded, and thresholds manually cleaned, prior to the assigning “masks”. These allowed different morphological features to be rendered as individual isosurfaces, and facilitated the removal from the model of the crack along which the nodule was split. Visualisation and iterative improvement allowed the creation of accurate models which were exported to the open source raytracing application Blender (<http://www.blender.org/>) to create high resolution images (Fig. 3) and films (Supplementary Online Material, SOM at http://app.pan.pl/SOM/app59-Dunlop_Garwood_SOM.pdf). The supplementary data also includes a ZIP archive containing the tomographic model of *E. prestvicii* described herein, using the VAXML interchange format (Sutton et al. 2012). This has a reduced triangle count, and should run on most computers. Free viewing software is available at <http://spiers-software.org/>.

Reconstruction.—In addition to XMT a new, principally hand-drawn, idealised reconstruction is included (Fig. 4). This was constructed in traditional fashion with pen and ink, based on both the XMT model and the hand specimen. Colouration was added digitally—for a justification of the colours see Discussion—using the open source raster graphics editor GIMP. The scanned figure was first quartered to provide manageable image sizes, and then thresholded. The white pixels in the threshold, within the reconstruction were then selected, and coloured with the colouring tool. Textures were

achieved by adding a textured layer above the reconstruction layer and combined using the overlay mode.

Systematic palaeontology

Class Arachnida Lamarck, 1801

Order Trigonotarbida Petrunkevitch, 1949

Remarks.—As noted above, Trigonotarbida was split by Petrunkevitch (1949) into two, supposedly unrelated, groups. This scheme was subsequently questioned (e.g., Shear et al. 1987) and the two names (Anthracomartida and Trigonotarbida) were reunited by Dunlop (1996). A formal synonymy list of trigonotarbid ordinal names can be found in Garwood and Dunlop (2011).

Family Eophrynidae Karsch, 1882

1882 Eophrynoidea fam. nov.; Karsch 1882: 560.

1890 Eophrynidae Karsch, 1882; Haase 1890: 651–652.

Type genus.—*Eophrynus* Woodward, 1871; see below.

Included genera.—*Nyranytarbus* Harvey and Selden, 1995; *Petrovicia* Frič, 1904; *Planomartus* Petrunkevitch, 1953; *Pleophrynus* Petrunkevitch, 1945; *Pocononia* Petrunkevitch, 1953; *Somaspidion* Jux, 1982; *Stenotrogulus* Frič, 1904.

Emended diagnosis.—Large, long-limbed and heavily ornamented trigonotarbids with nine opisthosomal tergites. Tergite 1 highly reduced, forming a locking ridge, tergites 2 and 3 unfused. Tergite 9 divided into medial and lateral plates. Opisthosoma bears two pairs of terminal spines originating from the lateral plates of tergites 8 and 9, and upward facing spines originating from the sternite on all opisthosomal segments anterior to this, except tergite 1. Anterior margin of the carapace drawn out into a long spine. Dorsal surface densely tuberculated, ventral surface sparsely tuberculated (emended from Dunlop 1994).

Remarks.—Petrunkevitch (1955) recognised two eophrynid subfamilies: Eophryninae, characterised by conspicuous large opisthosomal tubercles, and Areomartinae, characterised by a more granular dorsal opisthosoma. These subfamilies were adopted to a certain degree by subsequent authors, although the resurrection of Haase’s (1890) family Kreischeriidae by Rössler and Dunlop (1997) to accommodate the more “granular” eophrynids has rendered Areomartinae largely superfluous. We do not recognise subfamilies here. Some of the genera traditionally assigned to Eophrynidae (cf. Petrunkevitch 1953, 1955) are problematic, being based on incomplete and/or poorly described specimens. Dunlop (2010) excluded two problematic taxa. *Areomartus ovatus* Petrunkevitch, 1913 from West Virginia, USA—which also represents the type genus of Areomartinae—was treated as Trigonotarbida incertae sedis. *Vratislavia silesica* (Römer, 1878) from Poland was transferred to Anthracosironidae. Figures of the (probably lost) type imply eophrynid-like terminal spines, but the rest of the elongate opisthosoma has proportions much more consistent with anthracosironids.

With respect to the remaining genera, Garwood and Dunlop (2011) proposed using XMT-based reconstructions of well-preserved anthracomartids as baseline models for the typical life appearance of members of this family. As noted in the introduction, a general problem with trigonotarbid is that some taxa are based on characters prone to being influenced by taphonomic processes—particularly in specimens hosted in shales—e.g., length/width ratios, absence of eyes, truncated carapaces, etc. We propose that our model here represents a “typical” and almost complete eophryind, and that deviations from this, which may be due to preservational factors represent poor grounds for maintaining separate taxa. Only a few eophrynid genera have been revised in detail, but provisional comments on differences between them and *Eophrynus* can still be made.

Pleophrynus Petrunkevitch, 1945 contains a single species, *Pleophrynus verrucosus* (Pocock, 1911). It is known from the Coal Measures of the UK and North America and was redescribed by Dunlop (1994). It differs from *Eophrynus* in having (i) somewhat isolated rows of large tubercles set against a background of smaller tubercles, and (ii) a distinct pattern of elongate ridges on the sternites close to the ventral midline (Dunlop 1994: figs. 1b, 2c). *Eophrynus*, by contrast, has tubercles formed on the midline in particular into complexes of four larger tubercles, and has as noted above more widely spaced ventral tubercles on the sternites rather than midline ridges. *Stenotrogulus* Frič, 1904 also contains a single species, *Stenotrogulus salmii* (Stur, 1877). It is known from the Coal Measures of the Czech Republic and was redescribed by Dunlop (1995a). It differs from *Eophrynus* (and *Pleophrynus*) in having rather weakly expressed tubercles on the midline of the tergites, such that each tergite primarily reveals four distinct, large tubercles rather than six. The ventral surface of *S. salmii* is not known in detail.

Genus *Eophrynus* Woodward, 1871

1871 *Eophrynus* gen nov.; Woodward 1871: 386.

Type species.—*Curculoides prestvicii* Buckland, 1837; by monotypy; see below.

Included species.—*Eophrynus udus* Brauckmann, Koch, and Kemper, 1985.

Remarks.—A number of trigonotarbid fossils were originally assigned to *Eophrynus* (cf. Stur 1877; Gill 1924; Dix and Pringle 1930; Guthörl 1938; Petrunkevitch 1949; Ambrose and Romano 1972). With the exception of *E. prestvicii* and *E. udus*, all have since been either synonymised or transferred to other genera/families; see e.g., Dunlop (1994, 1995a, 1998) and discussions of the genera above. “*Eophrynus*” *scharfi* Scharf, 1924, from the early Permian Rotliegend of the Ilfeld region of Germany is an incomplete specimen in ventral view. It yields no unequivocal characters of Eophrynidae—or any other trigonotarbid family—and was treated by Rössler et al. (2003) as *Trigonotarbida incertae sedis*. An *Eophrynus* sp. was described from the Coal Measures of Ohio by McComas and Mapes (1988), but is incomplete and mostly preserved in ventral view.

Eophrynus prestvicii (Buckland, 1837)

Figs. 1–4.

1834 “*Aranea*”; Prestwich 1834: 376.

1837 *Curculoides Prestvicii* sp. nov.; Buckland 1837: 77, pl. 46: 2.

1856 *Duma prestvicii* (Buckland); Giebel 1856: 137.

1871 *Eophrynus Prestvicii* (Buckland); Woodward 1871: 386, pl. 11.

1876 *Euphrynus* [sic] *prestvicii* Buckland; Roemer 1876: pl. 47: 12.

1882 *Eophrynus Prestvicii* (Buckland); Geinitz 1882: 241.

1882 *Curculioides Prestvicii* Buckland; Karsch 1882: 560.

1884 *Eophrynus Prestvicii* (Buckland); Scudder 1884: 19.

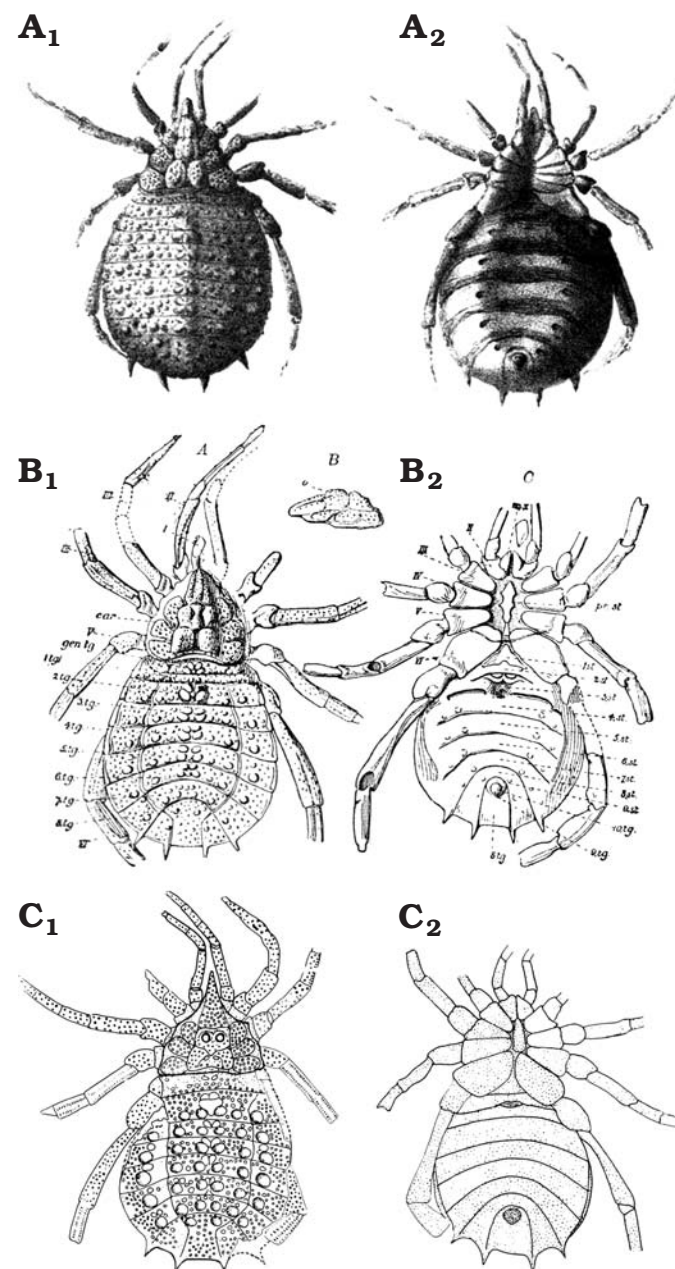


Fig. 1. Historical images of Hollier's specimen of *Eophrynus prestvicii* (Buckland, 1837) from the British Middle Coal Measures (Late Carboniferous, Duckmantian; ca. 311 Ma) of Coseley near Dudley, Staffordshire, UK. Dorsal (A₁–C₁) and ventral (A₂–C₂) views. A, after Woodward (1871: pl. 11); B, after Pocock (1902: fig. 1); C, after Petrunkevitch (1953: text-figs. 82, 83).

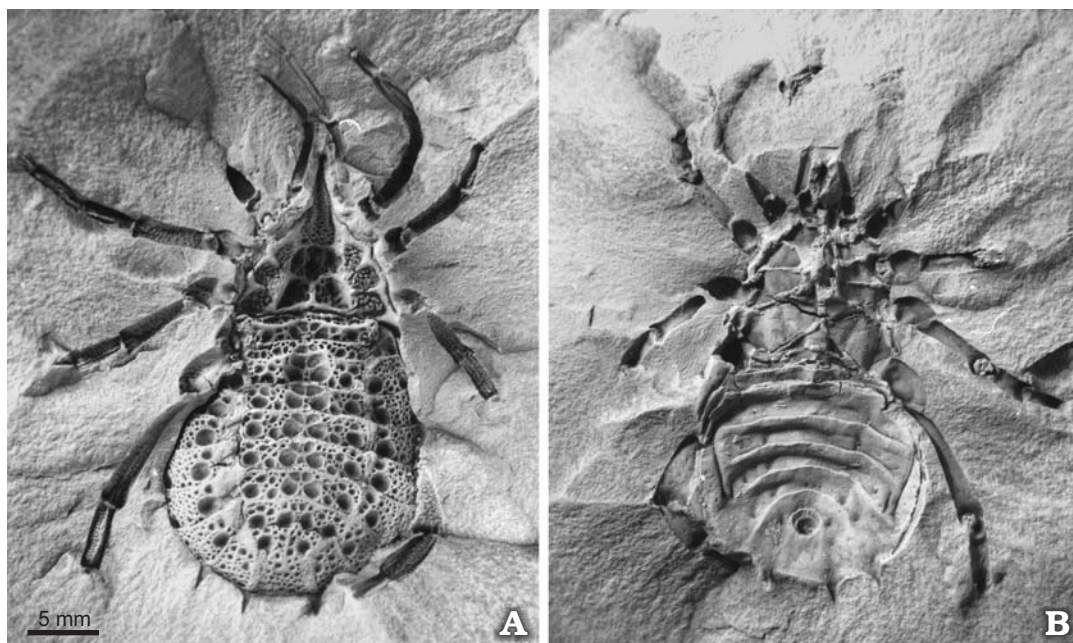


Fig. 2. Photograph of Hollier's specimen (BU 699) of trichotarbid arachnid *Eophrynus prestvicii* (Buckland, 1837), whitened with ammonium chloride to improve contrast. **A.** Dorsal view. **B.** Ventral view.

- 1885 *Eophrynus Prestvicii* (Buckland); Scudder 1885: 737, fig. 913.
 1886 *Eophrynus Prestvicii* (Buckland); Scudder 1886: 25.
 1890 *Eophrynus Prestvicii* (Buckland); Haase 1890: 652.
 1891 *Eophrynus prestvicii* (Buckland); Scudder 1891: 23 (also listed under *Curculoides*, *Duma*, and *Euprynus*).
 1896 *Eophrynus Prestvicii* (Buckland); Howard and Thomas 1896: 53, pl. 1C.
 1900 *Eophrynus prestvichi* [sic] (Buckland); Loman 1900: 82, pl. 10: B, D (also as *prestwichi* in the plate legend).
 1902 *Eophrynus prestvicii* (Buckland); Pocock 1902: 440–448, fig. 1.
 1904 *Eophrynus Prestvicii* [sic] (Buckland); Frič 1904: 46–48, pl. 14: 3, 4, text-figs. 57–61.
 1911 *Eophrynus prestvici* (Buckland); Pocock 1911: 77, text-fig. 39.
 1913 *Eophrynus prestvici* (Buckland); Andrée 1913: 90.
 1913 *Eophrynus prestvici* (Buckland); Petrunkevitch 1913: 97.
 1938 *Eophrynus prestvici* (Buckland); Guthörl 1938: 469–470.
 1949 *Eophrynus prestvici* (Buckland); Petrunkevitch 1949: 246, fig. 122.
 1949 *Eophrynus prestvici* (Buckland); Waterlot 1949: 903, fig. 683.
 1951 *Eophrynus* cf. *prestvici* (Buckland); Heide 1951: 66, pl. 8: 10.
 1953 *Eophrynus prestvici* (Buckland); Petrunkevitch 1953: 76–77.
 1953 *Eophrynus prestvici* (Buckland); Waterlot 1953: 574, fig. 32.
 1955 *Eophrynus prestvici* (Buckland); Petrunkevitch 1955: 112, figs. 32, 78.
 1958 *Eophrynus prestvici* (Buckland); Přibyl 1958: 429–430, 432.
 1972 *Eophrynus prestvici* (Buckland); Ambrose and Romano 1972: 576–577.
 1979 *Eophrynus prestvici* (Buckland); Strachen 1979: 309, 318, fig. 3.
 1982 *Eophrynus prestvici* (Buckland); Jux 1982: 81.
 1985 *Eophrynus prestvici* (Buckland); Brauckmann et al. 1985: 17–18, fig. 5.
 1990 *Eophrynus prestvicii* (Buckland); Shear and Kukulová-Peck 1990: 1811, fig. 4.
 1991 *Eophrynus prestvicii* (Buckland); Brauckmann 1991: 26, fig. 6.
 1994 *Eophrynus prestvicii* (Buckland); Dunlop 1994: 287, 293.
 1995 *Eophrynus prestvicii* (Buckland); Dunlop 1995a: 459.

- 1995 *Eophrynus prestvicii* (Buckland); Dunlop 1995b: 119.
 1996 *Eophrynus prestvicii* (Buckland); Dunlop 1996: 146.
 1997 *Eophrynus prestvicii* (Buckland); Rössler and Dunlop 1997: 238.
 2009 *Eophrynus prestvicii* (Buckland); Garwood et al. 2009: 841–844, figs. 1c–e, 2b.
 2010 *Eophrynus prestvicii* (Buckland); Garwood and Dunlop 2010: 34, fig. 4.

Holotype: NHM In 49322, reasonably well preserved mould of entire specimen, but with supposition of some dorsal and ventral features.

Type locality: British Middle Coal Measures of Coalbrookdale, Shropshire, UK.

Type horizon: Upper Carboniferous, Duckmantian (= Westphalian B).

Material.—BU 699 from the British Middle Coal Measures of Coseley near Dudley, Staffordshire, UK. Upper Carboniferous, Duckmantian (= Westphalian B). Further putative specimen from the “Faisceau de Wilhelmina, Mine Hendrik”, Limbourg, Belgium. Upper Carboniferous, Langsetian (= Westphalian A).

Description.—BU 699 large, total length 30 mm, and heavily ornamented. Carapace lobed—not segmented (cf. Haase 1890)—sub-triangular and with three semicircular lobes on each side (Fig. 3A), abutting a median ridge, drawn into a pointed, anteriorly directed clypeus. Median ridge also lobed, posteriorly splitting into four raised divisions; with a central ocular tubercle bearing a pair of median eyes. Carapace heavily tuberculate; edge marked by three gently curved borders corresponding to lateral lobes. Posterior margin delineated by raised, posteriorly inclined transverse ridge, edges abutting raised lateral margins of first and second opisthosomal tergites.

Ventral prosoma with prominent, almost triangular leg coxae (Fig. 3E), more closely spaced than shown in previ-

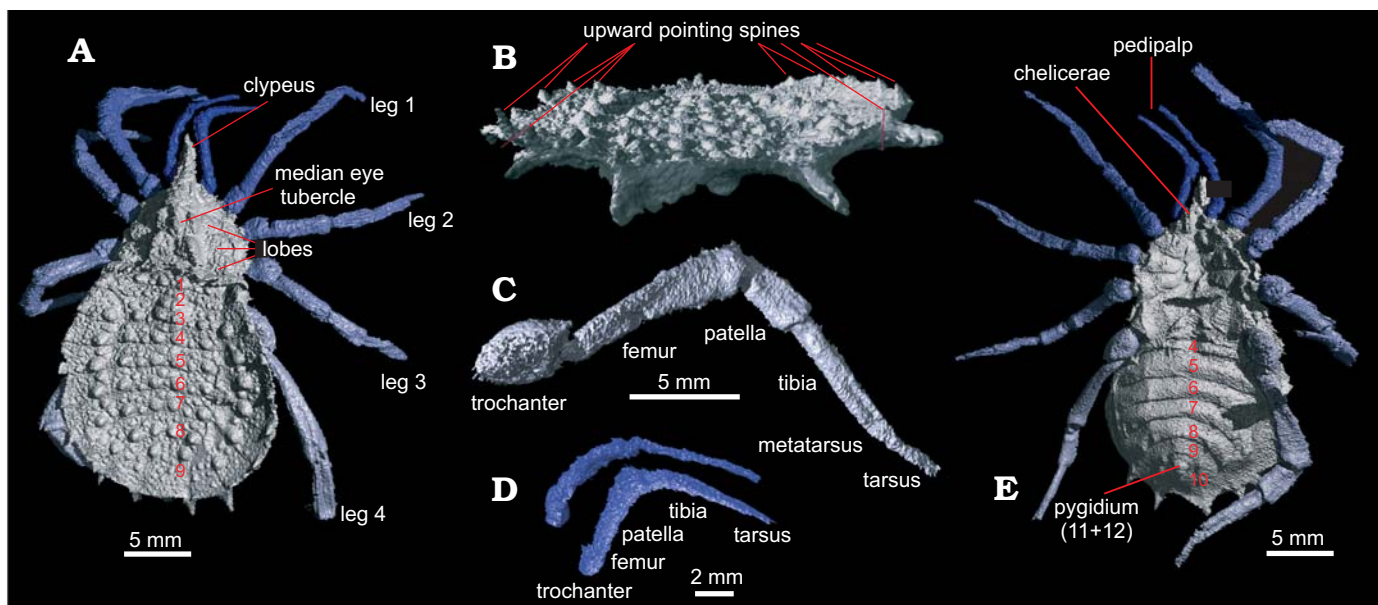


Fig. 3. XMT-based reconstruction trigonotarbid arachnid *Eophrinus prestvicii* (Buckland, 1837), from scans of BU 699. **A**. Dorsal view. **B**. Posterior view, legs removed, to show heavy opisthosomal ornamentation and spines (maximum width 15 mm). **C**. Fourth walking limb with podomeres labelled. **D**. Pedipalps with podomeres labelled. **E**. Ventral view. 1–12, segment numbers.

ous illustrations (e.g., Frič 1904: text-fig. 59). Coxae increase steadily in size posteriorly; those of fourth walking limb occupying posterior third of prosoma. Deeply recessed sternum gives prosoma a thin, concave appearance. Deep but thin transverse ridge of cuticle attaches between coxae of legs three and four. Small, closely-spaced chelicerae tucked between pedipalp coxae, palaeognath in orientation (i.e., hanging downwards with backward-pointing fangs), and lying left of the midline. Basal article (pautron) partially equivocal, but attaches proximally between pedipalp coxae. Well-preserved fangs folded and tucked under the clypeus.

Pedipalps well preserved (Fig. 3D), composed of an almost-spherical trochanter, longer femur, short patella (see Discussion), longer tibia and a tarsus. Legs long and slender (Fig. 3C) composed of a rounded trochanter (contra Haase 1890), femur (the longest article), short patella, long tibia (approaching the femora in length), short metatarsus and slightly longer tarsus. Best preserved limbs display longitudinal medial groove along more proximal articles, with small, regularly spaced depressions on either side of the groove. Distal claws of legs equivocal.

Opisthosomal segmentation best understood via the prominent dorsal ornamentation. First tergite present as a narrow sclerite, bearing a row of small tubercles proximal to posterior margin of carapace. Subsequent segments bear six large tubercles, evenly spaced across opisthosoma, lying towards posterior margin of tergite. Two smaller medial tubercles at anterior margin (clearest in life reconstruction, Fig. 4). Smaller tubercles fill remaining tergite surfaces, creating a highly pustulate dorsal surface. Conical lateral tubercles/dorsally directed spines preserved on postero-lateral margins

of sternites five to seven (Fig. 3B) and outward-pointing spines on segments eight and nine. First visible ventral opisthosomal elements are the anterior and posterior operculae, followed by sternite 4, short and truncated anteriorly by ventral sacs. Sternite 5 longer, but sternites 5–9 (as measured on the midline) decrease in length posteriorly. Degree of posterior recurvature increases posteriorly. Sternites smooth, not heavily ornamented; only visible ornamentation being pairs of small tubercles (Woodward's (1871) putative tracheal openings) on sternites 5–9, situated halfway between midline and lateral margins. These features poorly resolved in the scans. Ventral sacs resolved as a pair of small lobes at posterior margin of posterior operculum (opisthosomal segment 3), immediately anterior to sternite 4. Posteriormost sternite (segment 10) small and almost triangular, housing a pygidium composed of two small, ring-like segments.

Remarks.—Buckland's (1837) original species epithet is "prestvicii" and this spelling was retained by early workers (e.g., Woodward 1871; Pocock 1902), with a lapsus to "prestvichi" in Loman (1900) and "prestvicii" in Frič (1904). The form "prestvici" appears to have first been introduced by Karsch (1882) and again by Pocock (1911). This spelling was adopted by most authors after Pocock (1911), albeit with a reversal to the original -ii form in, e.g., Brauckmann (1991) and Dunlop (1994; 1995a). Following Article 33.4 of the International Code of Zoological Nomenclature a change from an -ii ending to an -i should be regarded as an incorrect subsequent spelling. The valid name is therefore *Eophrinus prestvicii* (Buckland, 1837).

Geographic and stratigraphic range.—Late Carboniferous (?Langsettian–Duckmantian) of ?Belgium and the United Kingdom.

Eophrynus udus Brauckmann, Koch, and Kemper, 1985

1985 *Eophrynus udus* sp. nov.; Brauckmann et al. 1985: 14–18, pls. 1: 1, 2, 2: 1, 2, text-figs. 2, 3.

1991 *Eophrynus udus* Brauckmann, Koch, and Kemper, 1985; Brauckmann 1991: 19–28, pl. 1a, b, text-figs. 3, 4.

2003 *Eophrynus udus* Brauckmann, Koch, and Kemper, 1985; Brauckmann et al. 2003: 51–52, fig. 21.

2006 *Eophrynus udus* Brauckmann, Koch, and Kemper, 1985; Dunlop and Brauckmann 2006: 131.

Holotype: Part and counterpart in the private collection of K.H. Hellwig, Hagen. Cast of the type in the possession of JAD.

Type locality: Hagen-Vorhalle, North Rhine-Westphalia, Germany.

Type horizon: Late Carboniferous, higher Marsdenian (= Namurian B).

Remarks.—Detailed descriptions and figures were provided by Brauckmann et al. (1985) and Brauckmann (1991). This species is slightly smaller (and older) than *E. prestvicii* and has a more rounded opisthosoma. Otherwise, their tuberculation pattern is very similar and it is conceivable that *E. udus* evolved directly into *E. prestvicii* as part of a chronospecies lineage.

Geographic and stratigraphic range.—Late Carboniferous (Marsdenian) of Germany.

Discussion

Chelicerae.—Pocock's (1902) observation of chelicerae in *Eophrynus prestvicii* was challenged by Petrunkevitch (1953) as a misidentification of the clypeus (his "spike of the carapace"). This is corroborated by the XMT results, which show that the true chelicerae are positioned—as might be expected—between the pedipalp coxae, and do not extend in front of the carapace as shown in Pocock's (1902) figures. The chelicerae have two articles, a basal pautron and a backwards-directed fang. The chelicerae in *E. prestvicii* are smaller than those seen in the contemporaneous anthracomartid trigonotarbid and their sinistral position may be a result of post-mortem displacement.

Pedipalps.—Another point of debate was the boundary in the pedipalp between the femur, patella and tibia. Woodward (1871) figured a patella about as long as the femur—implying rather elongate pedipalps verging towards being antenniform structures—while other authors figured a more "typical" short patella (Pocock 1911; Petrunkevitch 1953). The XMT model suggests the latter view is correct and while the resolution of the XMT scan is not optimal as a result of the large nodule in which the specimen is hosted, there does seem to be a bend and a slight swelling at the "knee", which is more consistent with a short patella.

Legs.—On the walking legs Frič (1904) identified single terminal claw. This could not be confirmed in the XMT scans. A single tarsal claw is typical for certain subgroups of harvestmen (Opiliones), and may relate to Frič's (1904) interpreta-

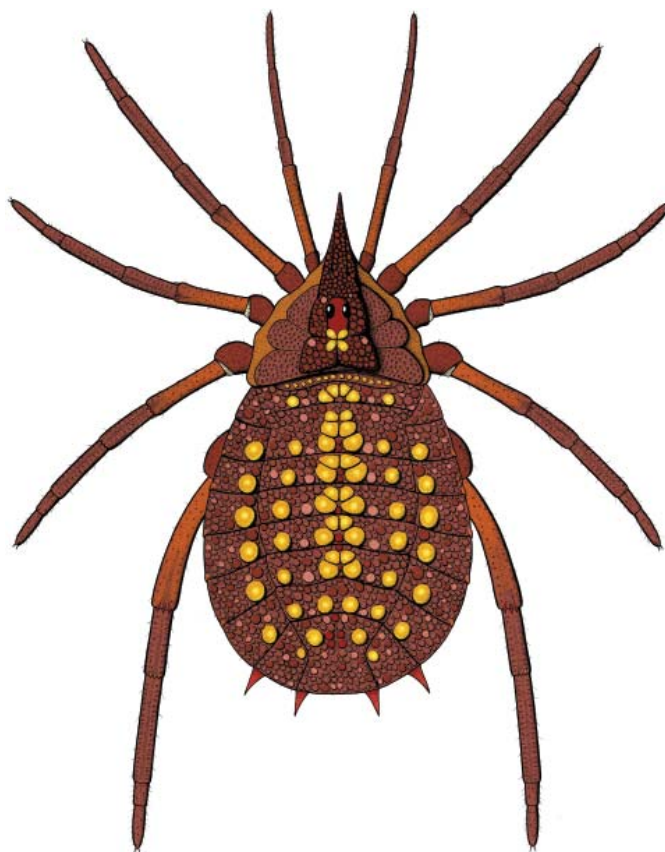


Fig. 4. A new reconstruction of trigonotarbid arachnid *Eophrynus prestvicii* (Buckland, 1837), with colouration based on modern laniatorid harvestmen (Opiliones: Laniatores) (see also Fig. 5). Not to scale.

tion of trigonotarbid as fossil harvestmen suborder. In fact most well-preserved trigonotarbid express a pair of large claws or ungues (e.g., Garwood et al. 2009) at the ends of the legs; sometimes with a smaller medial or empodial claw between the ungues.

Segmentation.—Trigonotarbid opisthosomal segmentation has traditionally proven problematic. For example Petrunkevitch (1955) argued that, across the group as a whole, the total number of opisthosomal segments varies between eight and eleven. The implications of such an inconsistent character state for trigonotarbid monophyly were critically discussed by Shear et al. (1987). Interpretations are complicated by the fact that in many trigonotarbid families the first tergite appears to be reduced in size and/or partially hidden, tucked under the posterior margin of the carapace as a functional "locking ridge" holding the prosoma and opisthosoma together. Dunlop (1994, 1995b) speculated that the locking ridge may be secondarily absent in the Eophrynidae and that a plesiomorphic fused diplotergite (2+3) may have undergone a reversal back to two separate sclerites. The present study demonstrates that this view is incorrect. Tergite one is retained as a very narrow and reduced dorsal element, which has apparently lost the locking function which may be part of the trigonotarbid ground pattern. Similarly there is no evidence of a diplotergite.

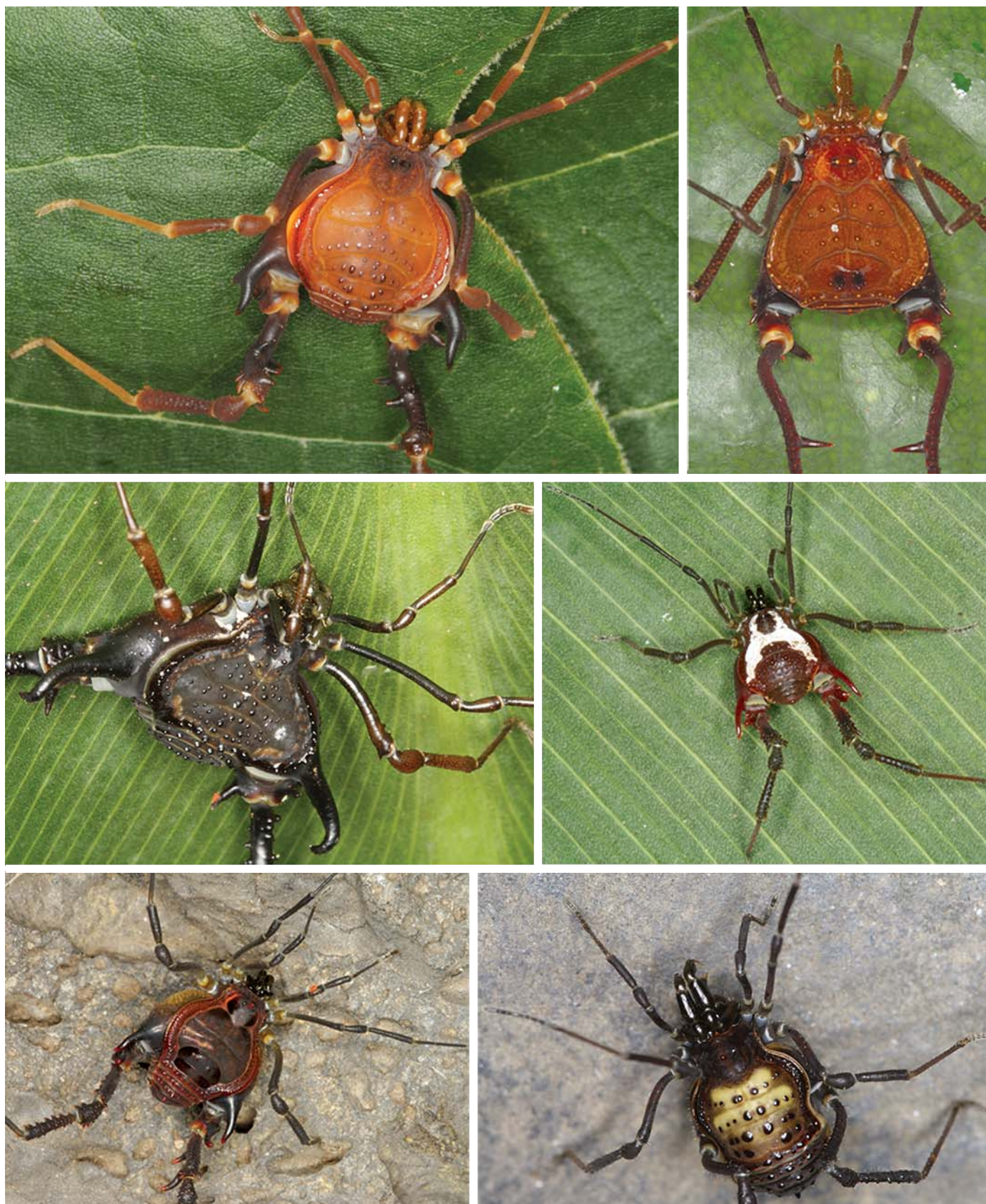


Fig. 5. Comparative images of modern South American laniatorids as potential ecological analogues for Carboniferous eophrynids. Although these harvestmen are not particularly closely related to trigonotarbid, a number of them also express a tuberculate dorsal body surface and marginal spination of the opisthosoma; both of which presumably deter predation by increasing handling time. All images courtesy of Ricardo Pinto da Rocha (São Paulo).

As noted above, trigonotarbids are currently placed in the Pantetrapulmonata group which have a ground pattern character of two pairs of book lungs; later modified in some ingroups such as the more derived spiders. The Devonian Rhynie Chert trigonotarbids in the family Palaeocharinidae clearly preserve the ground pattern condition, with two pairs of book lungs opening on the second and third opisthosomal segments respectively (e.g., Kamenz et al. 2008). For this reason Woodward's (1871) putative tracheal openings on sternites 5–9 of *E. prestvicii*—while poorly resolved in the scans—seem likely to be a misidentification.

Respiratory organs and ventral sacs.—Another controversial feature is a pair of structures on the anterior underside of the opisthosoma, towards the anterior end. First recognised by Pocock (1902), he described them as “arcuate crests” and speculated that they could be associated with respiratory openings. Frič (1904) interpreted them—somewhat speculatively—as openings leading into some sort of a sperm-storage device: a receptacula seminis. Petrunkevitch (1953) preferred to interpret them as part of the second opisthosomal somite and thus explicitly associated with a putative genital opening. Similar raised lobes are seen in the Rhynie chert palaeocharinids (Fayers et al. 2005: fig. 5), and here they clearly occur on the third (i.e., postgenital) segment. These authors suggested that the trigonotarbid structures could be ventral sacs; enigmatic, eversible structures which occur in a topographically homologous position in many whip spiders (Amblypygi) (e.g., Weygoldt 2000: fig. 5). Ventral sacs are conceivably highly modified appendage remnants and are also seen in palpigrades (Palpigradi), albeit here on multiple segments. In whip spiders the ventral sacs are thought to play a role in water balance, but since their physiology is uncertain even among living arachnids further interpretations of the fossil structures would be speculative. Irrespective of their function, our computer model resolves them as a pair of small lobes either side of the midline of the third sternite (or posterior operculum); just anterior to sternite four. Confirmation that they belong to the third opisthosomal segment also argues against them being part of the primary genitalia given that the arachnid gonopore consistently opens on segment two. Unlike Anthracomartidae (images in Garwood and Dunlop 2011), there is no anterior curved transverse ridge associated with these ventral sac structures.

Pygidium.—The almost-triangular posteriormost sternite hosts the pygidium: the anal plate of Pocock (1902) or the anal operculum of Petrunkevitch (1953). The trigonotarbid pygidium (or postabdomen in some terminologies) is not, in fact, plate-like, but consists of two ring-like segments: topographically numbers 11 and 12. This has been adequately demonstrated in other material, including the Rhynie chert palaeocharinids (Hirst 1923; Fayers et al. 2005), and the same ground pattern morphology of a twelve-segmented opisthosoma can be confirmed here for eophrynids too.

Mode of life.—Trigonotarbids and harvestmen clearly resolve at quite different places on the arachnid tree (Shultz 2007), but taking up the theme of Loman (1900) some laniatorid harvestmen appear to offer good modern analogues for eophrynids. Numerous laniatorid species also bear dorso-marginal spines and prominent dorsal tubercles. Some laniatores are also brightly patterned, while others are more conservative in their coloration. It is thus interesting to speculate whether eophrynids employed aposematism (i.e.; warning colouration) or whether they were more cryptic animals, camouflaged against the substrate. For our new reconstruction (Fig. 4) a major consideration was whether Carboniferous predators were largely visual, to appreciate (or avoid) deimatic/aposematic coloration, or whether they used other means or locating prey. The evidence here is inconclusive. It is likely that early tetrapods possessed chromic vision (Bailes et al. 2007; Hart et al. 2008), and there is evidence of other forms of aposematism in some Carboniferous arthropod taxa, such as the ozopores (and thus chemical defences) in euphoberiid millipedes (Shear and Edgecombe 2010). However, there is no evidence for chemical, or any other form of aposematism in any known trigonotarbid, and mimicry is common in Carboniferous arthropod taxa (Scott and Taylor 1983). Furthermore, trigonotarbids were probably habitual predators based on their somewhat spider-like mouthpart structure (Garwood and Dunlop 2010), and excessively bright coloration could have been detrimental to their ability to catch prey. Thus we chose a more conservative model—in keeping with the likely background colours of a Carboniferous forest floors, but with highlighted colour to provide an element of disruptive crypsis (Jarzembowski 2005). As a basis we used a range of colours (yellows and browns) seen in laniatorid harvestmen such as *Acutisoma longipes* (Gonyleptidae, Gonyleptoidea) (e.g., Giribet et al. 2010), with pale appendage membranes in keeping with many modern arachnids.

Anatomical similarities between laniatorid harvestmen and the heavily ornamented eophrynid trigonotarbids may also imply that these extinct arachnids had similar mode of life on the forest floor. In general, the opisthosoma of *E. prestvicii* resolves under XMT as relatively flat and disc-like, similar to the situation in Anthracomartidae (Garwood and Dunlop 2011). While there may have been a certain degree of post-mortem compression we still feel that the XMT results largely reflect the appearance of the animal in life, and that a flattened body may have been advantageous for crawling into narrow spaces and/or living within the detritus. The length of the limbs and lack of apparent raptorial adaptation (such as that seen in the Anthracomartidae) suggests *E. prestvicii* could have been a cursorial predator.

Eophrynus prestvicii is amongst the most heavily ornamented trigonotarbids. The prosomal transverse ridges of cuticle are likely to be an adaptation for strength, but the robust ornamentation of *E. prestvicii*—and other eophrynids—is clearly a defensive adaptation which would have increased the handling time for predators and made these trigonotar-

bids generally less palatable. This is further supported by their high-risk mode of life on the forest floor, and the likely inertial feeding mechanism and lack of differentiated teeth of their likely predators (Reilly and Lauder 1990). The *Eophrynus* ornamentation would also have provided protection against attacks from above and helped prevent crushing. This adaptation is not seen in the Anthracomartidae, which may instead have been ambush predators (Garwood and Dunlop 2011)—a comparatively safe mode of life. Both these adaptations (i.e., defensive ornamentation and ambush predation) could be a response to increasing predation at a time when tetrapod predators were becoming more numerous (Shear and Kukalová-Peck 1990). Ambush predation would allow anthracomartids to spend much of their time in the relative safety of hides, waiting for prey—in contrast to being in a vulnerable position in the leaf litter where *Eophrynus*, with no such behavioural specialisations, would be found. Thus it seems that the Eophrynidae and associated taxa could have responded instead by increasing their defences.

Acknowledgements

We thank Claire Mellish (NHM) and Paul Smith (BU) for the loan of material in their care, Carsten Brauckmann (Clausthal-Zellerfeld, Germany) for material relating to *Eophrynus udus*, Ricardo Pinto da Rocha (University of São Paulo, Brazil) for comparative images of modern arachnids and the reviewers for helpful comments. RG would like to acknowledge the assistance provided by the Manchester X-ray Imaging Facility, which was funded in part by the EPSRC (grants EP/F007906/1, EP/F001452/1, and EP/I02249X/1).

References

- Ambrose, T. and Romano, M. 1972. New Upper Carboniferous Chelicerata from Somerset, England. *Palaeontology* 15: 569–578.
- Andrée, K. 1913. Ueber *Anthracophrynus tuberculatus* nov. gen. nov. spec. aus dem productiven Karbon von Dudweiler im Saar-Revier, nebst einer Liste der bisher im Karbon Deutschland gefundenen Arachnoiden-Reste. *Jahres-Bericht und Mitteilungen der Oberrheinischen Geologischen Vereins* 3: 89–93.
- Bailes, H.J., Davies, W.L., Trezise, A.E.O., and Collin, S.P. 2007. Visual pigments in a living fossil, the Australian lungfish *Neoceratodus forsteri*. *BMC Evolutionary Biology* 7: 200.
- Black, R.M. 1988. *The Elements of Palaeontology*. 2nd Edition. 404 pp. Cambridge University Press, Cambridge.
- Brauckmann, C. 1991. Arachniden und Insekten aus dem Namurium von Hagen-Vorhalle (Ober-Karbon; West-Deutschland). *Veröffentlichungen aus dem Fuhrrott-Museum* 1: 1–275.
- Brauckmann, C., Koch, L., and Kemper, M. 1985. Spinnentiere (Arachnida) and Insekten aus der Vorhalle-Schichten (Namurium B; Ober-Karbon) von Hagen-Vorhalle (West-Deutschland). *Geologie und Paläontologie in Westfalen* 3: 1–132.
- Brauckmann, C., Schöllmann, L., and Sippel, W. 2003. Die fossilen Insekten, Spinnentiere und Eurypteriden von Hagen-Vorhalle. *Geologie und Paläontologie in Westfalen* 59: 1–89.
- Buckland, W. 1837. *The Bridgewater Treatises on the Power Wisdom and Goodness of God as Manifested in the Creation, Volume IV: Geology and Mineralogy Considered with Reference to Natural Theology*. 618 pp. William Pickering, London.
- Cutler, A. 1981. A short history of the Dudley & Midland Geological Societies. *Black Country Geologist* 1: 1–21.
- Dix, E. and Pringle, J. 1930. Some Coal Measures arthropods from the South Wales Coalfield. *Annals and Magazine of Natural History* 6: 136–144.
- Dunlop, J.A. 1994. The palaeobiology of the Writhlington trigonotarbid arachnid. *Proceedings of the Geologists' Association* 105: 287–296.
- Dunlop, J.A. 1995a. A redescription of two eophrynids (Arachnida: Trigonotarbita) from the Coal Measures (Carboniferous) of Ostrava, Czech Republic. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1995 (8): 449–461.
- Dunlop, J.A. 1995b. Redescription of the Pennsylvanian trigonotarbid arachnid *Lissomartus* Petrunkevitch 1949 from Mazon Creek, Illinois. *Journal of Arachnology* 23: 118–124.
- Dunlop, J.A. 1996. A redescription of the trigonotarbid arachnid *Pocononia whitei* (Ewing 1930). *Palaäontologische Zeitschrift* 70: 145–151.
- Dunlop, J.A. 1998. A redescription of the trigonotarbid arachnid *Pseudokreischeria pococki* (Gill, 1924). *Bulletin of the British Arachnological Society* 11: 49–54.
- Dunlop, J.A. 2010. The enigmatic Pennsylvanian arachnids *Areomartus ovatus* Petrunkevitch 1913 and *Vratislavia silesica* (Römer 1878). *Journal of Arachnology* 38: 44–48.
- Dunlop, J.A. and Brauckmann, C. 2006. A new trigonotarbid from the Coal Measures of Hagen Vorhalle, Germany. *Fossil Record* 9: 130–136.
- Fayers, S.R., Dunlop, J.A., and Trewin, N.H. 2005. A new early Devonian trigonotarbid arachnid from the Windyfield chert, Rhynie, Scotland. *Journal of Systematic Palaeontology* 2: 269–284.
- Frič, A. 1904. *Palaeozoische Arachniden*. Privately published by Anton Frič, Prague, 85 pp.
- Garwood, R.J. and Dunlop, J.A. 2010. Fossils explained 58. Trigonotarbitids. *Geology Today* 26: 34–37.
- Garwood, R.J. and Dunlop, J.A. 2011. Morphology and systematics of Anthracomartidae (Arachnida: Trigonotarbita). *Palaeontology* 54: 145–161.
- Garwood, R.J. and Sutton, M.D. 2010. X-ray micro-tomography of Carboniferous stem-Dictyoptera: New insights into early insects. *Biology Letters* 6: 699–702.
- Garwood, R.J., Dunlop, J.A. and Sutton, M.D. 2009. High-fidelity X-ray micro-tomography reconstruction of siderite-hosted Carboniferous arachnids. *Biology Letters* 5: 841–844.
- Garwood, R.J., Dunlop, J.A., Giribet, G., and Sutton, M.D. 2011. Anatomically modern Carboniferous harvestmen demonstrate early cladogenesis and stasis in Opiliones. *Nature Communications* 2: 444.
- Geinitz, H.B. 1882. *Kreischeria wiedeii*, ein Pseudoskorpion aus der Steinkohlenformation von Zwickau. *Zeitschrift der Deutschen geologischen Gesellschaft* 34: 238–242.
- Giebel, C.G. 1856. *Die Insekten und Spinnen der Vorwelt*. xviii + 512 pp. Brockhaus, Leipzig.
- Giribet, G., Vogt, L., Pérez González, A., Sharma, P., and Kury, A.B. 2010. A multilocus approach to harvestman (Arachnida: Opiliones) phylogeny with emphasis on biogeography and the systematics of Laniatores. *Cladistics* 26: 408–437.
- Gill, E.L. 1924. Fossil arthropods from the Tyne Coalfield. *Geological Magazine* 61: 445–471.
- Guthörl, P. 1938. *Eophrynus waechteri* n. sp. (Arach., Anthracom.) aus der Tiefbohrung Stanmgenmühle, Saar-Karbon. *Senckenbergiana* 20: 465–470.
- Haase, E. 1890. Beitrag zur Kenntniss der fossilen Arachniden. *Zeitschrift der Deutsche geologische Gesellschaft* 1890: 629–657.
- Hart, N.S., Balies, H.J., Vorobyev, M., Marschall, N.J., and Collin, S.P. 2008. Visual ecology of the Australian lungfish (*Neoceratodus forsteri*). *BMC Ecology* 2008 8: 21.
- Harvey, M.A. and Selden, P.A. 1995. *Nyranytarbus*, replacement name for *Hemiphrynus* Frič, 1901 (Trigonotarbita: Eophrynidae). *Bulletin of the British Arachnological Society* 10: 74.
- Heide, S. van der 1951. Les arthropodes du terrain houiller du Limbourg méridional (excepté les scorpions et les insectes). *Mededeelingen van de Geologische Stichting, Serie C, IV* (3), (5): 1–84.

- Hirst, S. 1923. On some arachnid remains from the Old Red Sandstone (Rhynie Chert bed, Aberdeenshire). *Annals and Magazine of Natural History, Series 9* 12: 455–474.
- Howard, F.T. and Thomas, T.H. 1896. Note on *Eophrymus*. *Reports and Transactions of the Cardiff Naturalists' Society* 28: 52–54.
- Jarzewowski, E.A. 2005. Colour and behaviour in late Carboniferous terrestrial arthropods. *Zeitschrift der Deutschen Gesellschaft für Geowissenschaften* 156: 381–386.
- Jux, U. 1982. *Somaspidion hammapheron* n. gen. n. sp.—ein Arachnide aus dem Oberkarbon der subvaristischen Saumsenke NW Deutschlands. *Paläontologische Zeitschrift* 56: 77–86.
- Kamenz, C., Dunlop, J.A., Scholtz, G., Kerp, H., and Hass, H. 2008. Microanatomy of Early Devonian book lungs. *Biology Letters* 4: 212–215.
- Karsch, F. 1882. Ueber ein neues Spinnenthier aus der Schlesischen Steinkohle und die Arachnoiden überhaupt. *Zeitschrift der Deutschen geologischen Gesellschaft* 34: 556–561.
- Lamarck, J.B.P.A. 1801. *Système des animaux sans verèbres*. viii + 432 pp. Lamarck and Deterville, Paris.
- Loman, J.C.C. 1893. Opilioniden von Sumatra, Java und Flores. In: M. Weber (ed.), *Zoologische Ergebnisse einer Reise in Niederländisch Ost-Indien*, 1–26. E.J. Brill, Leiden.
- Loman, J.C.C. 1900. Ueber die geographische Verbreitung der Opilioniden. *Zoologischen Jahrbüchern, Systematik* 13: 71–104.
- McComas, G.A. and Mapes, R.H. 1988. Fauna associated with the Pennsylvanian Floral Zones of the 7–11 Mine, Columbiana County, north-eastern Ohio. *Ohio Journal of Science* 88: 53–55.
- Menge, A. 1855. Ueber die Scheerenspinnen, Chernetidae. *Neueste Schriften der Naturforschenden Gesellschaft* 5 (2): 1–43.
- Petrunkévitch, A.I. 1913. A monograph of the terrestrial Palaeozoic Arachnida of North America. *Transactions of the Connecticut Academy of Arts and Sciences* 18: 1–137.
- Petrunkévitch, A.I. 1945. Palaeozoic Arachnida. An inquiry into their evolutionary trends. *Scientific Papers, Illinois State Museum* 3 (2): 176.
- Petrunkévitch, A.I. 1949. A study of Palaeozoic Arachnida. *Transactions of the Connecticut Academy of Arts and Sciences* 37: 69–315.
- Petrunkévitch, A.I. 1953. Palaeozoic and Mesozoic Arachnida of Europe. *Memoirs of the Geological Society of America* 53: 1–128.
- Petrunkévitch, A.I. 1955. Arachnida. 42–162. In: R.C. Moore (ed.), *Treatise on Invertebrate Paleontology, Part P, Arthropoda 2*. xvii + 181 pp. Geological Society of America, Boulder, and University of Kansas Press, Lawrence.
- Pocock, R.I. 1902. *Eophrymus* and allied Carboniferous Arachnida. *Geological Magazine, Decade 4*, 9: 439–448, 487–493.
- Pocock, R.I. 1911. A monograph of the terrestrial Carboniferous Arachnida of Great Britain. *Monographs of the Palaeontographical Society* 64: 1–84.
- Prestwich, J. 1834. On some of the faults which affect the Coal-field of Coalbrookdale. *The London and Edinburgh Philosophical Magazine and Journal of Science* 4: 375–376.
- Příbyl, A. 1958. Nové nálezy arachnidů (Trigonotarbida) z Ostra-Karvinského Karbonu. *Časopis pro Mineralogii a Geologii* 3: 425–434.
- Reilly, S.M. and Lauder, G.V. 1990. Evolution of tetrapod feeding behavior: kinematic homologies in prey transport. *Evolution* 44: 1542–1557.
- Roemer, 1876. *Lethaea geognostica oder Beschreibung und Abbildung der für die Gebirgs-Formationen bezeichnendsten Versteinerungen. I. Theil. Lethaea palaeozoica*. 266 pp. E. Schweizerbart'sche Verlagshandlung, Stuttgart.
- Römer, F. 1878. Auffindung und Vorlegung eines neuen Gliderthieres in dem Steinkohlengebiete der Ferdinandsgrube bei Glatz. *Jahresbericht der Schlesischen Gesellschaft für Vaterländische-Kultur* 1878: 54–55.
- Rössler, R. 1998. Arachniden-Neufunde im mitteleuropäischen Unterkarbon bis Perm—Beitrag zur Revision der Familie Aphantomartidae Petrunkevitch 1945 (Arachnida, Trigonotarbida). *Paläontologische Zeitschrift* 72: 67–88.
- Rössler, R. and Dunlop, J.A. 1997. Redescription of the largest trigonotarbid arachnid—*Kreischeria wiedeii* Geinitz 1882 from the Upper Carboniferous of Zwickau, Germany. *Paläontologische Zeitschrift* 71: 237–245.
- Rössler, R., Dunlop, J.A., and Schneider, J.W. 2003. A redescription of some poorly known Rotliegend arachnids from the Lower Permian (Asselian) of the Ilfeld and Thuringian Forest Basins, Germany. *Paläontologische Zeitschrift* 77: 417–427.
- Scharf, W. 1924. Beitrag zur Geologie des Steinkohlengebietes im Sudharz. *Jahrbuch des Halleschen Verbands für die Erforschung der Mitteldeutschen Bodenschätze und ihrer Verwaltung* 4: 404–437.
- Scott, A.C. and Taylor, T.N. 1983. Plant/animal interactions during the Upper Carboniferous. *Botanical Review* 49: 259–307.
- Scudder, S.H. 1884. A contribution to our knowledge of Paleozoic Arachnida. *Proceedings of the American Academy of Arts and Sciences* 20: 13–22.
- Scudder, S.H. 1885. Arachnoidea. Spinnen. Skorpione. In: K.A. Zittel (ed.), *Handbuch der Palaeontologie, Band II*, 732–746. R. Oldenbourg, München.
- Scudder, S.H. 1886. Systematic review of our present knowledge of the fossil insects myriapods and arachnids. *Bulletin of the U.S. Geological Survey* 31: 1–128.
- Scudder, S.H. 1891. Index of the known fossil insects of the world including myriapods and arachnids. *Reports of the U.S. Geological Survey* 71: 1–744.
- Selden, P.A. 1992. Revision of the fossil ricinuleids. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 83: 595–634.
- Shear, W.A. and Edgecombe, G.D. 2010. The geological record and phylogeny of the Myriapoda. *Arthropod Structure & Development* 39: 174–190.
- Shear, W.A. and Kukalová-Peck, J. 1990. The ecology of Paleozoic terrestrial arthropods: the fossil evidence. *Canadian Journal of Zoology* 86: 1807–1834.
- Shear, W.A., Selden, P.A., Rolfe, W.D.I., Bonamo, P.M., and Grierson, J.D. 1987. New terrestrial arachnids from the Devonian of Gilboa, New York. *American Museum Novitates* 2901: 1–74.
- Shultz, J.W. 2007. A phylogenetic analysis of the arachnid orders based on morphological characters. *Zoological Journal of the Linnean Society* 150: 221–265.
- Strachen, I. 1979. Collections and collectors of note 25. *Birmingham University Geological Museum, Newsletter of the Geological Curators Group* 2 (6): 309–321.
- Stur, D. 1877. Die Culm-Flora der Ostrauer und Waldenburger Schichten. *Abhandlungen der kaiserlich-königlichen geologischen Reichsanstalt* 8: 5.
- Sutton, M.D., Garwood, R.J., Siveter, D.J., and Siveter, D.J. 2012. Spiers and VAXML; A software toolkit for tomographic visualisation, and a format for virtual specimen interchange. *Palaeontologia Electronica* 15 (2): 1–14.
- Waterlot, G. 1949. Les arachnides fossiles. In: P.P. Grasse (ed.), *Traité de Zoologie, Tome 6*, 893–905. Masson et Cie, Paris.
- Waterlot, G. 1953. Classe des Arachnides (Arachnida Cuvier 1812). In: J. Piveteau (ed.), *Traité de paléontologie, Vol. 3*, 555–584. Masson et Cie, Paris.
- Weygoldt, P. 1969. *The Biology of Pseudoscorpions*. xiv + 145 pp. Harvard University Press, Cambridge MA.
- Woodward, H. 1871. On the discovery of a new and very perfect Arachnide from the ironstone of the Dudley Coal-field. *Geological Magazine* 9: 1–4.