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RESEARCH PAPER

The first Palaeozoic spider (Arachnida: Araneae) from Germany

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Abstract
The first Palaeozoic spider (Arachnida: Araneae) from Germany is described as *Arthrolycosa wolterbeeki* sp. nov. and comes from the late Carboniferous (Moscovian) strata of Piesberg near Osnabrück in Lower Saxony. Characteristic for the genus, the new fossil reveals a posteriorly tuberculate dorsal opisthosoma, and relatively elongate and setose legs in which the first leg is longer than the second and third legs. Spinnerets are also preserved, confirming its status as a genuine spider rather than being part of an extinct spider-like arachnid lineage. Carboniferous spiders in general are rather rare. While modern spiders are a megadiverse group, the published fossil record suggests they were only moderately diverse in the late Carboniferous compared to other Coal Measures arachnids. Part of the explanation must be that major radiations within Araneae occurred later, probably during the Mesozoic. If the lifestyle of the Carboniferous fossils was similar to that of modern mesothele spiders their rarity as fossils might also relate to them spending much of their lives in burrows, or similar retreats, with limited opportunities for preservation.

Keywords Chelicerata · Mesothelae · Carboniferous · Moscovian · Lower Saxony · Piesberg

Introduction

Spiders (Arachnida: Araneae) are a familiar and ubiquitous group of predatory arthropods found today in most terrestrial ecosystems. More than 51,000 Recent species (WSC 2023) are complemented by a relatively rich fossil record of 1427 extinct ones (Dunlop et al. 2023). For reviews of the spider fossil record, see Selden and Penney (2010) and Magalhaes et al. (2020). In brief, the oldest unequivocal spiders are late Carboniferous in age (Selden et al. 2014; Selden 2021) and can be referred to the suborder Mesothelae (see below). A handful of Triassic species include the first representatives of the suborder Opisthothelae and its two infraorders: Mygalomorphae and Araneomorphae (Selden and Gall 1992; Selden et al. 1999). A few more Jurassic records, including the first evidence of spiders building aerial capture webs, are followed by a substantial increase in recorded diversity in the Cretaceous from which the first spiders in amber, especially Burmese amber from Myanmar (Wunderlich 2015; Wunderlich and Müller 2018), are recorded. The Palaeogene, which includes the highly productive Baltic amber, boasts the largest fossil species assemblage (Penney 2020) and the first appearance of several derived groups, particularly families which apparently abandoned webs for prey capture and adopted free-living hunting strategies instead. Somewhat fewer fossils date from the Neogene, including Dominican and Chiapas amber, and from copal and subfossil records in the Quaternary (e.g. Wunderlich 1988; Scott 2003).

Carboniferous spiders are rare. The revision of Selden (2021) demonstrated that several Coal Measures fossils traditionally assigned to this group lack convincing apomorphies of Araneae and are better placed as *incertae sedis* examples of arachnids, or arthropods in general. They include some intriguing spider-like fossils which potentially lie close to the origins of Araneae; see also Dunlop (2022) for a discussion of their significance. The eleven currently accepted Carboniferous spiders include three species from Bohemia in the Czech Republic. Two are placed as Araneae *incertae sedis*, *Palaranea borassifoliae* Frič, 1864 and *Pyritaranea tubifera* Frič, 1899, and one as Mesothelae *incertae sedis, Eolycosa lorenzi* Kušta, 1886. Three extinct mesothele families were recognised by Selden (2021). Palaeothelidae includes *Palaeothele montceauensis* (Selden 1996) from

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Montceau-les-Mines in France and *P. onoi* Selden, 2021 from Mazon Creek in the USA. Arthrolycosidae includes *Arthrolycosa antiqua* Harger, 1874 from Mazon Creek as well as *Protolycosa anthracophila* Roemer, 1865 from Silesia in Poland, *P. cebennensis* Laurentiaux-Vieira and Laurentiaux, 1963 from Cévennes in France, *P. danielsi* (Petrunkevitch 1913) from Mazon Creek and *P. suazoi* Selden, 2021 from New Mexico in the USA. Finally, Arthromygalidae, which also has Cretaceous records, includes *Geralycosa fricii* Kušta, 1889 from Bohemia.

Here, a new late Carboniferous spider from Piesberg in north-western Germany is described. Leipner et al. (2021) previously mentioned the presence of fossil spiders (as *Arthrolycosa*) here, but the present specimen is the first Piesberg spider to be formally described. This makes it the first named Palaeozoic spider from Germany and at the same time, the oldest formal record of Araneae for this country.

Materials and methods

Material

The new fossil comes from the Piesberg quarry near Wallenhorst, north of Osnabrück in the state of Lower Saxony in Germany. It consists of a part and counterpart collected by Dr Timotheus K. T. Wolterbeek and initially catalogued in his collection under the numbers TKTW0711A/B. It was subsequently deposited in the palaeontological collections of the Museum für Naturkunde Berlin under the repository number MB.A. (Museum Berlin, Arthropoda) 4298. Like most fossils from Piesberg, the specimen is preserved as a thin coating of gümbelite (an illite-group mineral; T. Wolterbeek, pers. comm.), which is mechanically weak and sensitive to flaking. The specimens (particularly the counterpart) are thus fragile and were consolidated in the field using an ethyl 2-cyanoacrylate glue (from Bison) to facilitate their collection and transport. The specimen is best visualised immersed in alcohol, but low-angle lighting is also helpful for resolving surface relief. The new fossil was photographed under alcohol (Figs. 1, 3) using a Canon Eos R. Interpretative drawings (Fig. 2) were made under a Leica M205C stereomicroscope with a *camera lucida* attachment. Comparisons were made to other fossil spiders in the published literature, especially the monograph of Selden (2021). All measurements are in millimetres.

Geological background

The geology and international significance of the Piesberg locality, which was designated a National Geotope in 2019, was recently summarised by Leipner et al. (2021), and references therein. Further geological information can be found

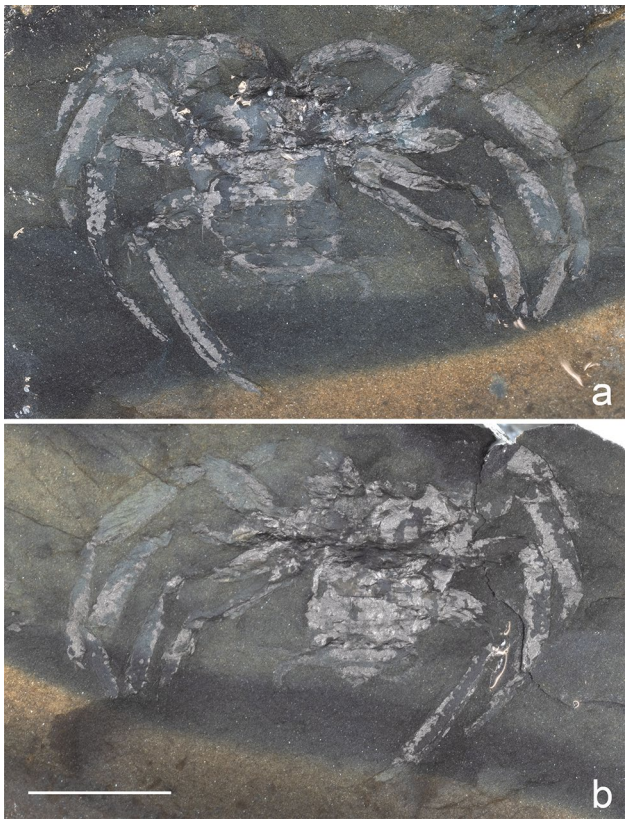

Fig. 1 *Arthrolycosa wolterbeeki* sp. nov., the oldest fossil spider (Arachnida: Araneae) from Germany, from the late Carboniferous of Piesberg near Osnabruck, Lower Saxony. **a** Part. **b** Counterpart. Scale bar equals 5 mm

in, e.g. Brauckmann and Herd (2003) or Köwing and Rabitz (2005). In brief, the Piesberg (and nearby Ibbenbüren) localities are the northernmost outcrops of Coal Measures strata in Germany. The exposed strata at the Piesberg have a total thickness of about 210 m and consist of sandstone, siltstone and shale interspersed with coal seams. Fossils are usually found in shales above the coal seams. The Piesberg fossils belong to the Osnabrück Formation which is dated to the late Carboniferous (Moscovian), with Leipner et al. (2021) noting an absolute age of ca. 315–310 Ma for the Carboniferous of the Osnabrück area.

As well as more than 50 species of Coal Measures plant fossils (Maithy 1972; Josten and van Ameron 1999) and some rare crustaceans and fish (Leipner et al. 2021), the Piesberg quarry has yielded horseshoe crabs (Schultka 2000; Haug et al. 2012) and several examples of terrestrial arthropods. Published records of arachnids and their relatives recorded so far include extinct trigonotarbid arachnids (Rößler 1998) assigned to *Aphantomartus pustulatus* (Scudder, 1884), and a fairly large and well-preserved scorpion (Dunlop et al. 2008) assigned to *Eoscorpius carbonarius* Meek and Worthen, 1868. Further arachnids, including

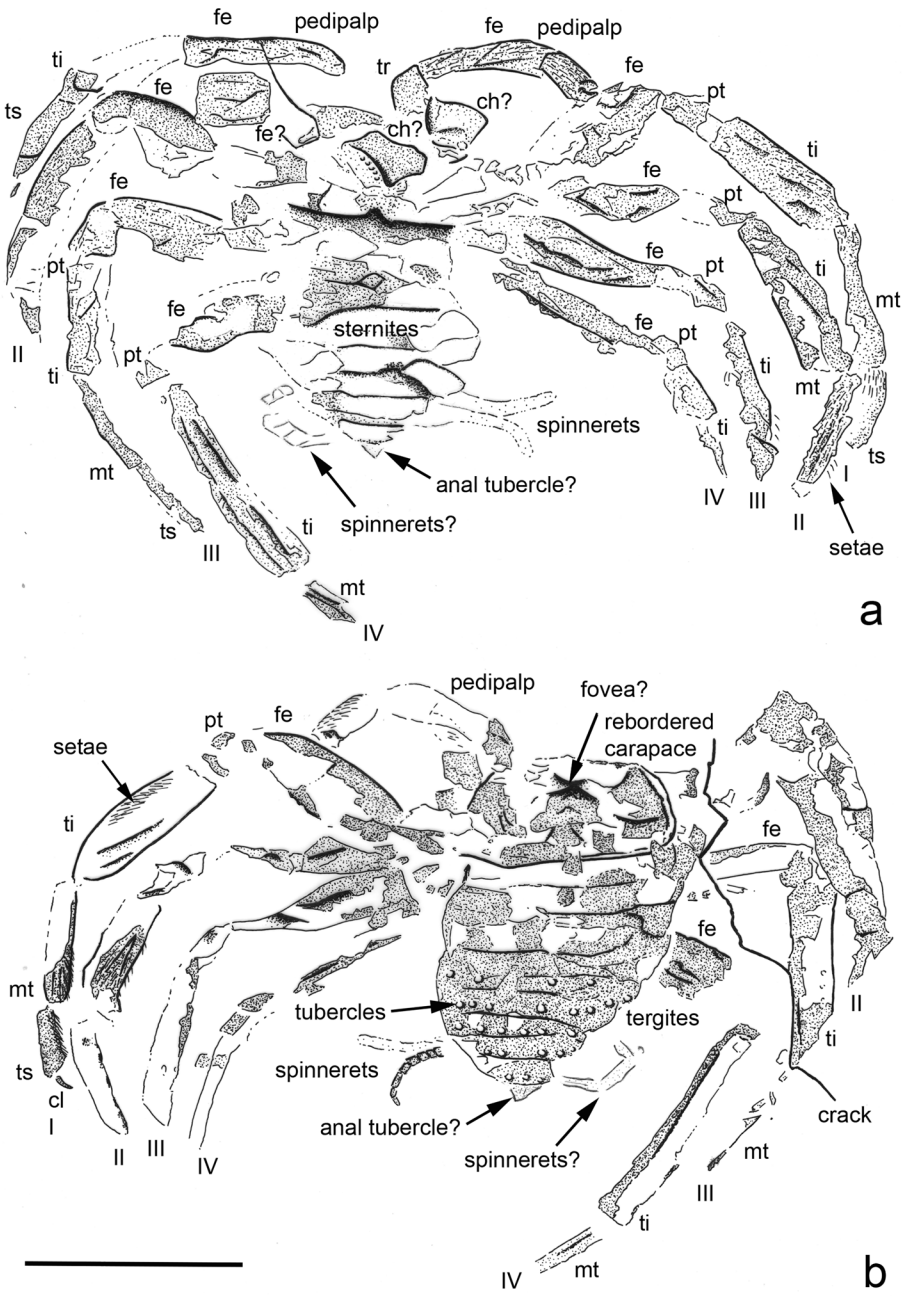

Fig. 2 Interpretative camera lucida drawings of the specimen shown in Fig. 1. Abbreviations: ch? possible chelicera; tr, trochanter; fe, femur; pt, patella; ti, tibia; mt, metatarsus; ts, tarsus; cl, tarsal claw. Legs numbered from I–IV. **a** Part. **b** Counterpart. Scale bar equals 5 mm

members of another extinct order, Phalangiotarbida, have been discovered and await description (Leipner et al. 2021; Angelika Leipner pers. comm.). A diverse insect fauna of more than 25 species has also been documented (e.g. Haug et al. 2013; and references therein), including representatives of Blattodea, Palaeodictyoptera, Megasecoptera, Odonatoptera, and Neoptera. Fragments of large arthropleurid millipedes have also been reported.

Systematic palaeontology

Order **Araneae** Clerck, 1757

Suborder **Mesothelae** Pocock, 1892
Family **Arthrolycosidae** Harger, 1874

Taxonomic remarks. Spinnerets are one of the defining characters of spiders; thus, their presence here in the Piesberg fossil (Fig. 3C) indicates that it belongs to Araneae and is not part of the assemblage of spider-like fossils, which Selden (2021) designated Tetrapulmonata *incertae sedis*; whereby the tetrapulmonates include the spiders and their closest relatives such as whip spiders and whip scorpions. The opisthosoma of the new fossil preserves distinct tergites and sternites (Figs. 1–2). This is a plesiomorphic

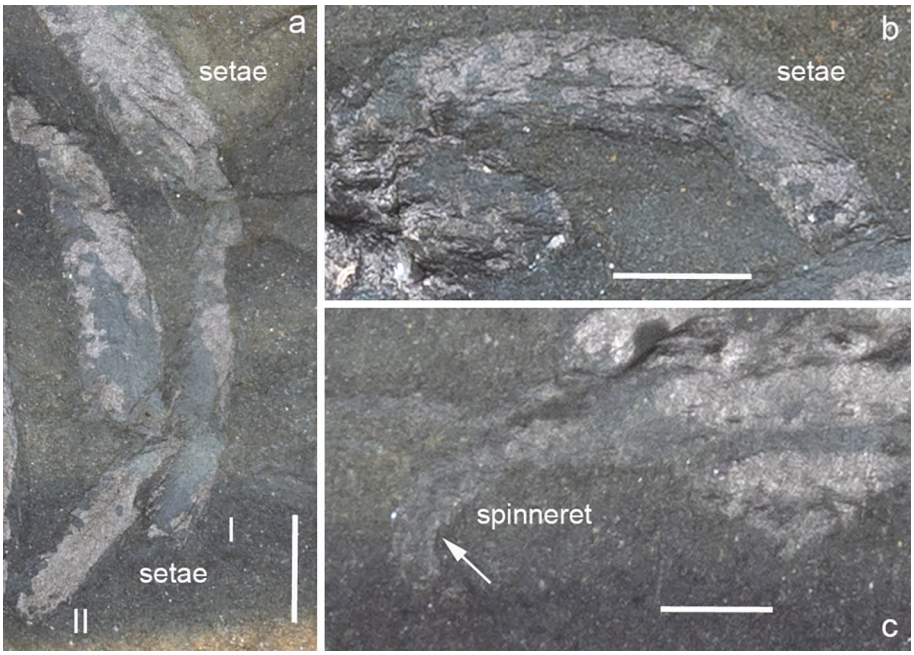

Fig. 3 Details of the specimen shown in Fig. 1. **a** Setose distal ends of walking legs I and II. **b** Setae adorning the pedipalp. **c** Putative spinneret showing evidence of segmentation (arrowed). Scale bars equal 1 mm

character for spiders, but is consistent with it being a member of the suborder Mesothelae, which retains a segmented opisthosoma.

As noted above, three Carboniferous mesothele families were recognised, and re-diagnosed, by Selden (2021). Arthrolycosidae was characterised as Mesothelae in which the opisthosomal tergites occupy the full width of the opisthosoma and are not set in soft cuticle. By contrast, Palaeothelidae comprise mesotheles where the opisthosomal tergites are distinct, but do not extend across the full width of the opisthosoma and are set in soft cuticle. Arthromygalidae were defined as having tarsi with elongate paired claws and an apical empodium (or pseudopulvillus), slender legs and a carapace nearly as wide as long. Based on these criteria, the new fossil is most consistent with Arthrolycosidae as the tergites appear to occupy the full width of the opisthosoma without any surrounding soft cuticle (Figs. 1, 2). The carapace proportions characteristic of Arthromygalidae cannot be easily tested against the new fossil as the carapace is missing the anterior margin, but the legs of the Piesberg spider are fairly robust, and the one well-preserved tarsus (Figs. 1, 2) shows no evidence for an empodium associated with the claws.

Genus ***Arthrolycosa*** Harger, 1874

Type species. *Arthrolycosa antiqua* Harger, 1874

Included species. *A. wolterbeeki* sp. nov.

Taxonomic remarks. Two arthrolycosid genera were recognised by Selden (2021). *Arthrolycosa* Harger, 1874 was redefined as having a carapace about as long as wide, with a distinct ridge behind the fovea (the depression in the centre of the carapace) and legs I and IV being longer than legs II and III. *Protolycosa* Roemer, 1865 was redefined on a carapace longer than wide and somewhat pointed anteriorly with a recurved posterior margin. The fovea may or may not be a deep pit, and leg I is characteristically shorter than the other legs. According to Selden (2021), both genera express rows of tubercles long the posterior margins of the opisthosoma (as does the Piesberg fossil), although earlier workers such as Petrunkevitch (1955) cited this as diagnostic for *Protolycosa* only. Using these criteria, the full proportions of the carapace in the Piesberg fossil are uncertain, but the preserved curvature suggests that it was probably rather short and certainly not longer than wide. Also, the carapace posterior margin is not noticeably recurved. The preserved appendages suggest that leg I was not shorter than the succeeding legs, and a IV > I > II > III leg formula (from longest to shortest) seems likely. For these reasons, the new fossil is most consistent with *Arthrolycosa*, confirming the provisional report of the presence of this genus at Piesberg by Leipner et al. (2021).

Arthrolycosa wolterbeeki sp. nov.

Holotype. MB.A. 4298 (ex. TKTW0711A/B), part and counterpart.

Type locality. From the Piesberg quarry near Wallenhorst, Lower Saxony, Germany.

Age of the type locality. Part of the Osnabrück Formation, late Carboniferous (Moscovian); or Westphalian D in the regional stratigraphy.

Zoobank LSID. 722E7CF1-D026-49EC-91BB-BD28E-C5E36E4.

Diagnosis. *Arthrolycosa* with a relatively compact body, opisthosoma somewhat rounded, nearly as wide as long, thus not noticeably longer than wide and suboval as inferred for *A. antiqua*. Tuberculation along posterior margins of opisthosoma more prominent than in *A. antiqua*. Pedipalp rather long, at least 1/2 the length of the adjacent legs; ca. 1/3 the length in *A. antiqua*.

Etymology. In honour of Dr Tim Wolterbeek, who discovered the holotype and kindly made it available for study.

Description

Almost complete specimen in both dorsal and ventral view. Total preserved length ca. 7.7, but front of carapace missing. Maximum width of carapace 4.8; posterior margin straight to slightly procurved and whole carapace apparently rebordered at least laterally and posteriorly. Anterior region (including any eyes and/or eye tubercles) equivocal, but with a distinct depression (fovea), on the midline and a pair of shallow sulci behind it. Two rectangular to quadratic structures on ventral surface (length 1.2) may be displaced chelicerae, one with evidence for a row of up to five denticles. Coxo-sternal region generally not well preserved. Several subtriangular elements hint at leg coxae, but details largely equivocal.

Pedipalps pediform, long, total length ca. 9.0; lengths of individual articles hard to resolve but femur ca. 3.6, and tarsus at least 2.6. Tarsus ends in a single terminal claw with no evidence for a modified (male) palpal organ. Legs robust and relatively elongate compared to body; femur, patella and tibia quite broad, metatarsus and tarsus more slender; at least leg I terminating in one of a pair(?) of robust claws, but no evidence for an empodium. Right leg 1 largely absent. Left leg I complete, total length ca. 13.4; article lengths: femur ca. 3.7, patella 1.6, tibia 3.6, metatarsus 2.9, tarsus 1.6. Leg II almost complete, total preserved length ca. 11.5; article lengths: femur ca. 3.0, patella 1.6, tibia 4.0, metatarsus 2.9; tarsus missing. Leg III complete, total length 11.9; article lengths: femur ca. 3.4; patella 1.3, tibia 2.7, metatarsus 2.5, tarsus 2.1. Leg IV incomplete, total preserved length ca.13.3; article lengths: femur 4.8, patella 1.4, tibia 5.2; metatarsus incomplete and tarsus missing. Leg formula thus probably IV > I > II > III. Pedipalps and legs with relatively dense setation towards the distal ends, from the tibia onwards, and especially on underside of metatarsus and tarsus of legs.

Opisthosoma compact, oval to shield-shaped in outline with maximum length and width of 5.2. At least eight tergites visible dorsally, all with more or less straight margins, with maximum lengths of ca. 0.9, but shorter towards the posterior end. Five posteriormost tergites each with a row of up to six small tubercles (diameters ca. 0.15), closer to posterior margin. Anterior three tergites show no evidence for tuberculation. Ventrally at least six sternites visible, again with straight margins and lengths up to ca. 0.9, and with shorter sclerites posteriorly. Postanal telson absent; but small posterior element shaped like an inverted triangle could be the anal tubercle. No ventral tuberculation was preserved, but possible diamond-shaped element is present on ventral midline in about the position where the genital opening would be expected (Fig. 2a). Two slender elements (displaced spinnerets), length ca. 2.2, width 0.2, preserved to the left of dorsal opisthosoma with slight curvature. At least one appears articulated, with evidence for up to eight individual elements (Fig. 3c). In ventral view, possibly originating from a rectangular (basal?) element, which would give entire structure a length of ca. 3.7. Less well-defined feature on opposing side of opisthosoma could represent one of a further pair of long spinnerets, but preservation is poor rendering its interpretation equivocal.

Discussion

As noted above, the presence of spinnerets (Fig. 3c) is good evidence for treating the new fossil as a genuine spider and *Arthrolycosa wolterbeeki* sp. nov. is only the twelfth Carboniferous species which can be assigned unequivocally to Araneae. It is also of significance for preserving what appear to at least one pair (and possibly two pairs) of relatively long spinnerets composed of multiple individual elements. The high number of elements is similar to the condition seen in modern members of the Mesothelae (e.g. Haupt 2003; Huber and Haug 2021), although in living mesotheles the spinnerets are shorter and more compact. At least some fossil mesotheles from Cretaceous Burmese amber have annulated spinnerets which are longer and are positioned more posteriorly, such that they are clearly visible beyond the margins of the opisthosoma (Wunderlich 2019: photos 2–3). Somewhat longer spinnerets with multiple elements are also seen in the unusual-tailed spiders from Burmese amber (Wang et al. 2018: Figs. 3, 4) which may be the sister-group of all remaining spiders. The Piesberg fossil could thus be consistent with the hypothesis that fairly long spinnerets with multiple elements are part of the spider ground plan. By contrast, Mygalomorphae and Araneomorphae characteristically have a reduced number of elements, usually four or less, in their spinnerets (Murphy and Roberts 2015; Mariano-Martins et al. 2020), even in those taxa where the spinnerets are

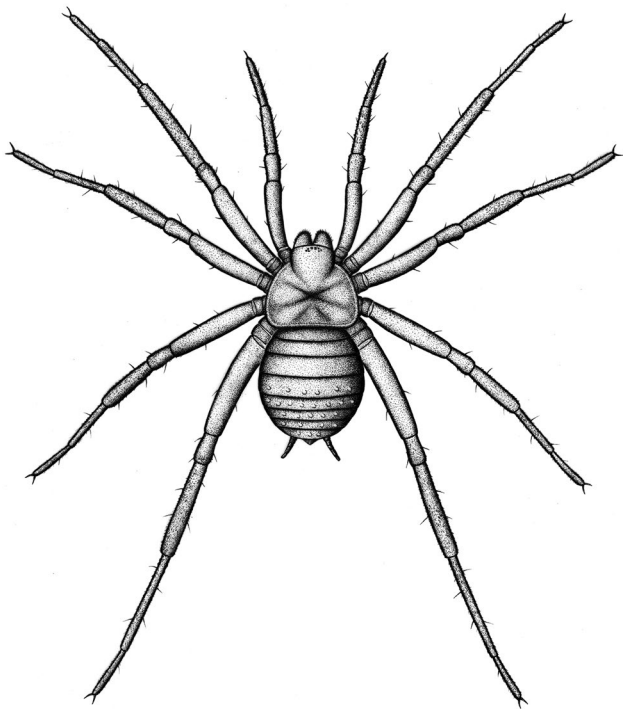

Fig. 4 Reconstruction of the possible appearance of *Arthrolycosa wolterbeeki* sp. nov., in life. Anterior region of carapace based on other *Arthrolycosa* material; leg spination draws on comparisons with modern mesothele spiders

Table 1 Species counts for the eleven arachnid orders known from the Pennsylvanian (data after Dunlop et al. 2023) and updated with records/revisions published since this time, ranked from the most diverse to the least

Order	Common name	Europe	N. America	Other	total
Scorpiones	Scorpions	28	18	–	46
Trigonotarbida†	Trigonotarbids	37	8	1	46
Phalangiotarbida†	Phalangiotarbids	15	15	–	30
Ricinulei	Ricinuleids	6	10	–	16
Araneae	Spiders	9	3	–	12
Opiliones	Harvestmen	6	3	–	9
Thelyphonida	Whip scorpions	6	1	–	7
Amblypygi	Whip spiders	1	3	–	4
incertae sedis†	–	4	–	–	4
Acariformes	Acariform mites	–	–	1	1
Solifugae	Camel spiders	–	1	–	1
Haptopoda†	Haptopodids	1	–	–	1
All Arachnida		113	62	2	177

†Indicates extinct taxa. There are no Palaeozoic records of Palpigradi, Schizomida or the Parasitiformes mite group. There is a Devonian record of Pseudoscorpiones, but no Carboniferous records, and some additional Devonian and Mississippian mites in the Acariformes group. The extinct order Uraraneida is known from the Devonian and Permian, but no Carboniferous species have been identified so far; the spider-like fossils sensu (Selden 2021) are tabulated here as Arachnida *incertae sedis*

more elongated. As noted above, there is no evidence for a post-anal telson in the Piesberg fossil, but there is a small, triangular element at the back of the opisthosoma which probably represents a (large) anal tubercle. A similar structure was observed by Selden (2021: Fig. 13) in at least one of the Carboniferous mesothele spiders and by Wunderlich (2015: photo 13) in a mesothele from Burmese amber.

In a wider context, spiders are one of the more diverse groups of arthropods today. By contrast, when they first appear in the Carboniferous Coal Measures, raw counts of species numbers (Table 1) suggest that they were only moderately diverse in these habitats. More than twice as many species of the extinct phalangiotarbid arachnids have been recorded from the late Carboniferous, and almost four times as many species of trigonotarbids (another extinct group) and scorpions. Following the revision of Selden (2021), plus the new species described here, the number of unequivocal spider species in the Coal Measures (twelve) is less than the number of contemporary ricinuleids (sixteen), one of the rarer and more obscure arachnid orders today. Several factors clearly influence the recorded diversity of Coal Measures arachnids, including a bias towards larger animals. Arachnid groups with small body size, such as palpigrades, pseudoscorpions and mites, are either absent or only rarely recovered from the typical shale or nodule-based preservation. It should be added that the three most species-rich groups of late Carboniferous arachnids (Table 1) may be over-split. Revisions carried out so far have recognised several synonyms (e.g. Rößler 1998; Garwood and Dunlop 2011; Legg et al. 2012), and more may be expected. Thus, the counts for scorpions, trigonotarbids and phalangiotarbids in Table 1 may still be somewhat inflated and overestimate their true diversity.

Despite these caveats, the relative rarity of Coal Measures spiders is noticeable and probably has both an evolutionary and perhaps also a taphonomic explanation. As noted in the Introduction, the oldest unequivocal fossil spiders date to ca. 315 Ma (Pennsylvanian: Bashkirian/Moscovian) with recent phylogenomic data (reviewed by Dunlop 2022) implying spider origins sometime between the Early Devonian and the Mississippian. Molecular datasets also suggest that most of the major lineages within spiders radiated after the Carboniferous (e.g. Fernández et al. 2018: Fig. 2). This is also consistent with the known fossil record (Selden and Penney 2010; Magalhaes et al. 2020), with araneomorph and mygalomorph spiders first appearing in the Triassic, and suggests that only a relatively restricted fauna of spiders belonging to basal (i.e. mesothele) lineages would be expected in the Coal Measures. At the same time, we might

speculate whether these Carboniferous spiders were ecologically similar to modern mesotheles, as this may also have limited their opportunities for fossilisation. Living mesotheles spend most of their lives within a burrow surrounded by radiating silken 'trip wires', emerging occasionally to snatch prey close to the burrow entrance (e.g. Haupt 2003; Sivayyapram et al. 2017). Mature males also have to emerge eventually and search for the largely sedentary females. If Carboniferous spiders had a similar 'sit-and-wait' lifestyle in a burrow, or a similar sort of retreat, it might explain why they rarely came into contact with bodies of water necessary for their preservation as fossils. In this context, it is interesting to consider why neither the present specimen, nor any of the other Carboniferous spiders (Selden 2021), preserve a male palpal organ as we might expect wandering males to be preferentially preserved.

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Data availability The specimen is deposited in the cited collection and institute. Images of the specimen are presented in the text figures. Additional data are available from the author upon reasonable request.

Declarations

Conflict of interest No competing interests.

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