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A remarkable spiny arachnid from the Pennsylvanian Mazon Creek Lagerstätte, Illinois

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Non-technical Summary.—The forests of the late Carboniferous period (about 300–320 million years ago) harbored a great variety of arachnids. In addition to the familiar spiders, harvestmen, and scorpions, there were other, stranger kinds of spider-like animals. Here, we describe a large spider-like arachnid with very spiny legs (presumably to deter predators), from the world-famous Mazon Creek fossil localities of Illinois, USA.

Abstract.—A new genus and species of arachnid (Chelicerata: Arachnida), *Douglassarachne acanthopoda* n. gen. n. sp., is described from the late Carboniferous (Moscovian) Coal Measures of the Mazon Creek Lagerstätte, Illinois, USA. This is a unique animal with distinctive large spines on the legs. It has a subovate body, a segmented opisthosoma, and a terminal anal tubercle. The legs are robust and appear to have been similar in construction throughout the limb series, with heavy spination of the preserved proximal podomeres. The mouthparts and coxo-sternal region are equivocal. The preserved character combination does not permit easy referral to any known arachnid order, living or extinct, thus the new fossil in placed as Arachnida/Pantetrapulmonata incertae sedis. It contributes to an emerging pattern of disparate body plans among late Carboniferous arachnids, ranging from anatomically modern members of living orders through to extinct taxa, such as the present fossil, whose phylogenetic position remains unresolved.

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Introduction

The late Carboniferous Coal Measures of North America and Europe offer an important window into the early evolution and diversity of arachnids. As well as hosting groups that are known from older deposits, namely scorpions (Scorpiones) and harvestmen (Opiliones), which have Silurian and Devonian representatives, respectively, the Coal Measures also yield the oldest records of several arachnid orders, namely spiders (Araneae), whip spiders (Amblypygi), whip scorpions (Thelyphonida), tick spiders (Ricinulei), and camel spiders (Solifugae) (for a recent overview of oldest records see Garwood and Dunlop, 2023a, table 1). In addition to living arachnid groups, the Coal Measures also host three extinct orders: Trigonotarbida (known from the Silurian to the Permian), Phalangiotarbida (Devonian–Permian), and the monotypic Haptopoda (Carboniferous). What is also becoming apparent (e.g., Garwood et al., 2016; Selden, 2021) is that there are several Coal Measures fossils of ostensibly spider-like animals that were sometimes initially placed in Araneae, but which lack the key character of silk-producing spinnerets. The impression is that several arachnid fossils of this age belonged to extinct lineages whose position in relation to the established orders has yet to be resolved.

The Mazon Creek Fossil-Lagerstätte is rightly famous for the abundance of marine and non-marine fossil biota found in clay ironstone concretions that are collected from the spoil heaps of the old strip mines around Braidwood in northeastern Illinois (Selden and Nudds, 2012) (Fig. 1.1, 1.2). These localities have yielded fossils of all the extant and extinct arachnid orders listed above (e.g., Meek and Worthen, 1868; Scudder, 1868, 1884, 1890; Melander, 1903; Petrunkevitch, 1913, 1945; Selden, 1992), with the exception of Haptopoda, which has only been found in the British middle Coal Measures. The new fossil from Mazon Creek is evidently something very different from any previously described arachnid from either this or any other Coal Measures locality. It is characterized by its distinctive habitus of an ovate body and robust and very spiny legs. The preserved character combination makes it difficult to place the fossil in any known arachnid order (see below), but it is described and named here with comments on its possible affinities.

Geological setting

The specimen was found at the spoil heap of Pit 15 Northern Mine near Essex, Kankakee County, Illinois, coordinates:

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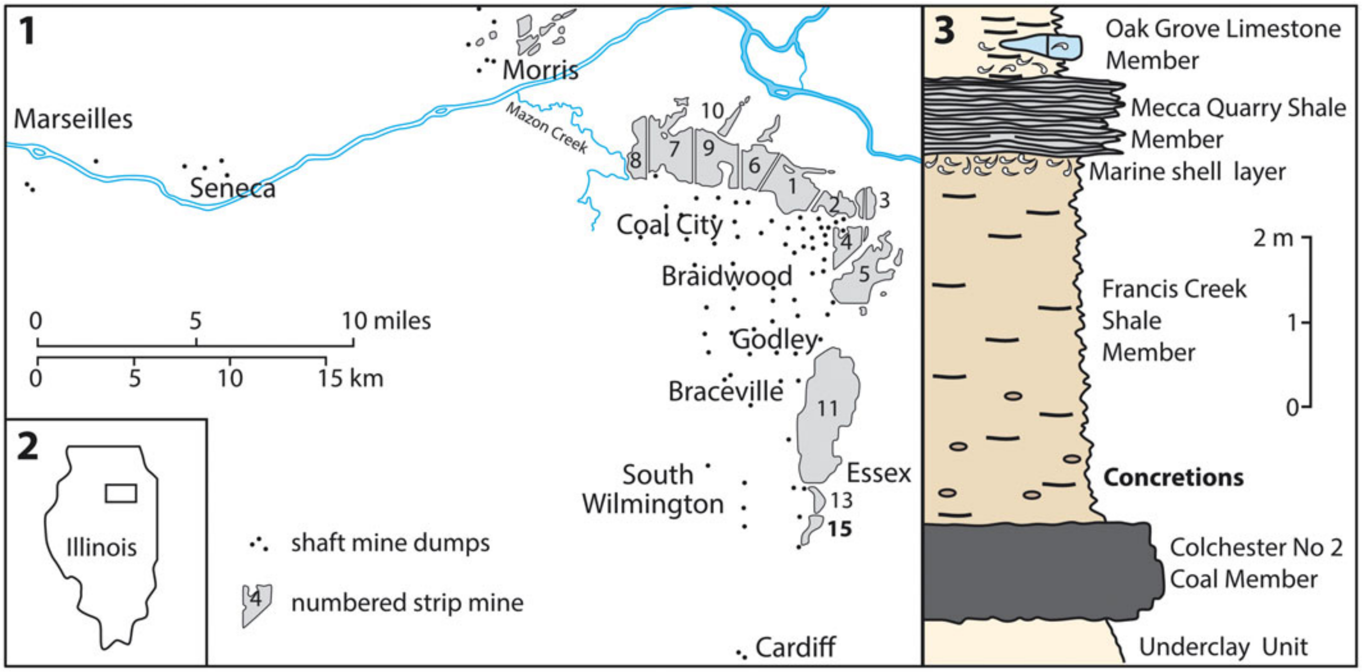

Figure 1. Type locality and stratigraphy for *Douglassarachne acanthopoda* n. gen. n. sp. (**1**) Locations of strip mines and dumps from shafts in the Mazon Creek area; Pit 15 Northern Mine shown in **bold** at bottom right; (**2**) map showing the location of (**1**) in Illinois; (**3**) stratigraphic log of the Francis Creek Shale Member and associated members of the Carbondale Formation, with position of concretions in lower part of Francis Creek Shale Member emphasized in **bold** (map and log based on Baird et al., 1986).

41.1525°N, 88.2275°W (Fig. 1). The fossil-bearing concretions occur in the Francis Creek Shale Member of the Carbondale Formation, which overlies the Colchester No. 2 Coal Member, and is itself overlain by the Mecca Quarry Shale Member (Selden and Nudds, 2012; Clements et al., 2019); the concretions are generally found towards the base of the Francis Creek Shale Member (Fig. 1.3). Based on the Mazon Creek flora containing elements comparable to those in the late Asturian Substage of Western Europe, and the dating of ash beds associated with cyclothems in Europe and North America (Montañez et al., 2016), the age of the coal and overlying shale member of the Mazon Creek area is now established to be between 308.6 and 308.4 million years old.

Materials and methods

Material.—Specimen FMNH PE 91366 (Fig. 2) is preserved in an iron-carbonate concretion, typical of those in the Francis Creek Shale Member. Both part and counterpart are essentially external molds with some adhering pieces of kaolinite, typical of the preservation in the Mazon Creek area. Most of the prosoma and opisthosoma and the proximal parts of all four legs are preserved, but no anterior appendages (palps or chelicerae) are preserved. Only the more proximal parts of the legs are preserved: trochanters, femora, but the more distal podomeres cannot be distinguished. At least patellae and tibiae can be assumed, but no tarsal podomeres are identifiable. The distinctive macrospines are true spines (i.e., cuticle extensions) rather than articulated macrosetae. Each macrospine is about as long as the thickness of the podomere to which it is attached. The macrospines are distinctly curved towards the distal end of the preserved parts of the leg. Rows of spine bases can be seen on the dorsal surfaces of the femora (Fig. 3.1) where the spines disappear into the matrix.

The dorsal shield of the prosoma (carapace) bears a deep depression in the anterior part, which is interpreted as the external mold of an ocular tubercle (Fig. 2). The anterior part of the opisthosoma is superimposed onto the posterior edge of the carapace, as evinced by the posteriormost lines on the carapace being straight, whereas the anterior edge of the opisthosoma is strongly recurved. The disconformity between the posterior edge of the prosoma and the visible anterior parts of the opisthosoma suggests a narrow coupling between these tagmata, rather than a broad junction. Posterior to the anterior edge of the opisthosoma, the tergite anterior and posterior margins are delineated by recurved lines, some rather tuberculated, which then straighten somewhat towards the lateral edges. This gives the impression of the trilobed dorsal surface of the trigonotarbid opisthosoma, but lacking delineation into distinct plates. On the counterpart (the ventral side), the posteriormost segment is sharply delineated from the penultimate segment. At the posterior edge of this segment, in front of the anal tubercle, is a bilobed structure of unknown function. If it is the anus, then the anal tubercle (pygidium) is post-anal (e.g., as in Thelyphonida and Schizomida). These orders also bear paired stink glands in this position (Hansen and Sørensen, 1905).

At the posterior end of the opisthosoma, there is an anal tubercle (pygidium). It is uncertain whether there might be a flagellum attached to this structure buried in the matrix; however, there is no evidence for one.

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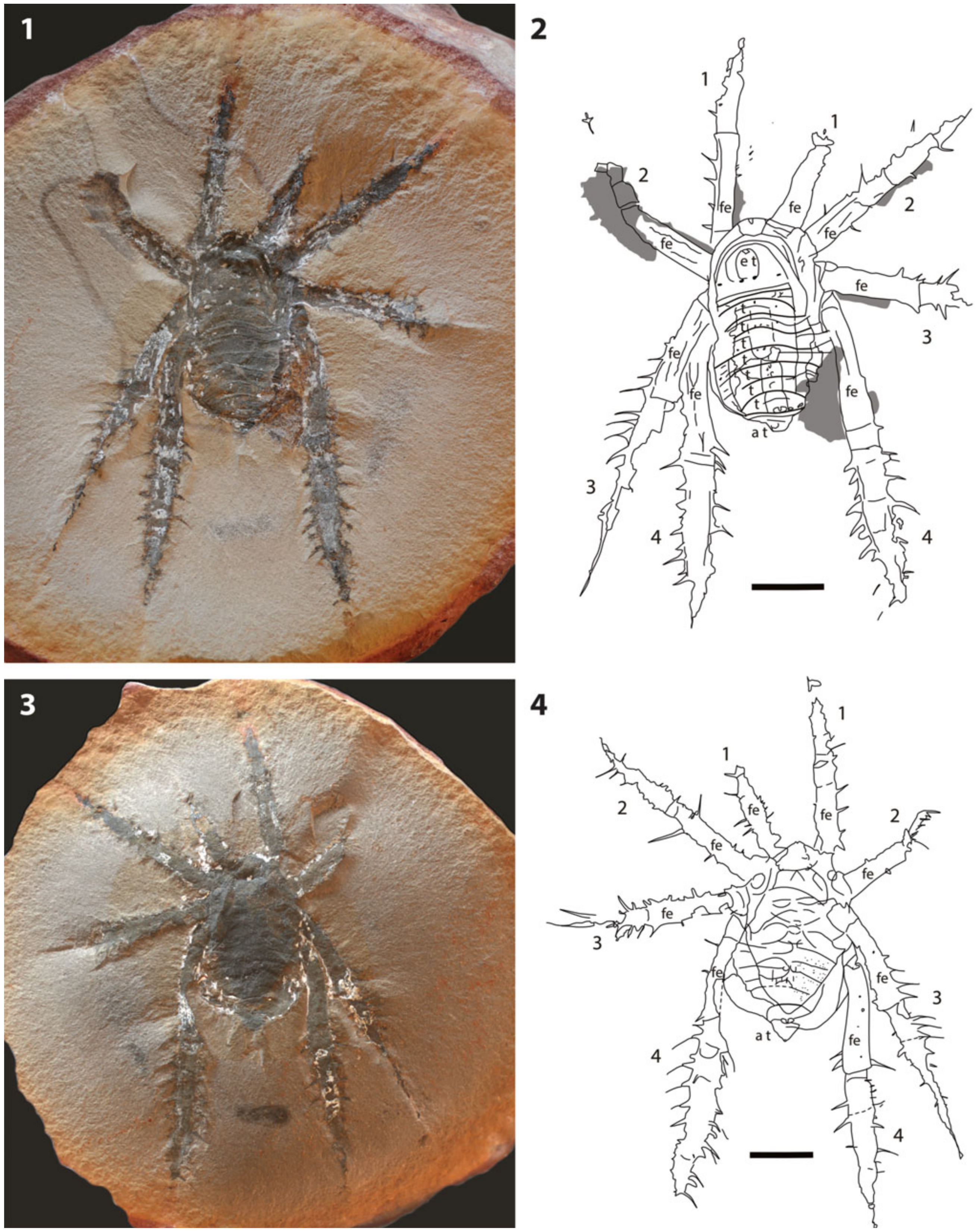

Figure 2. *Douglassarachne acanthopoda* n. gen. n. sp., holotype and only known specimen FMNH PE 91366. (**1**) Photograph of part; (**2**) explanatory drawing of part; (**3**) photograph of counterpart; (**4**) explanatory drawing of counterpart; 1–4 = leg numbers; a t = anal tubercle; e t = eye tubercle; fe = femur; t = tergite. Scale bars = 5 mm.

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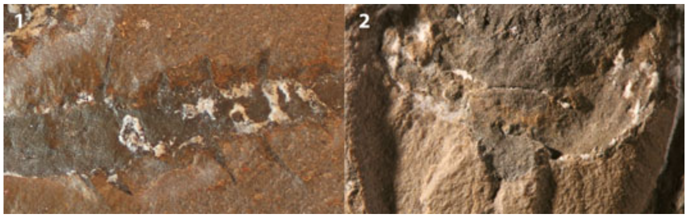

Figure 3. *Douglassarachne acanthopoda* n. gen. n. sp., holotype and only known specimen FMNH PE 91366; for interpretative drawings and scale, see Figure 2. (**1**) Part, detail of distal femur and more-distal podomeres, showing nature of curved macrospines on lateral edge of distal podomeres, bases of macrospines on dorsal surface of femur; (**2**) counterpart, detail of posterior opisthosoma showing bilobed structure at base of anal tubercle.

Methods.—The specimen was found by Bob Masek at the Pit 15 Northern Mine spoil heap (Fig. 1.1) in the 1980s. Bob deployed a common method for splitting a concretion by leaving it outside in water through the winter, so that frost penetrates the natural crack in the concretion along the plane containing the fossil. A sharp hammer blow split the concretion along the plane, revealing the fossil. Around 1990, David Douglass acquired the specimen from Bob, at which time it became part of The David and Sandra Douglass Collection and was displayed in the Douglass family's Prehistoric Life Museum. In 2023, when it became apparent that this specimen represented a new species, David Douglass donated the specimen to The Field Museum of Natural History so it could be researched.

The specimen was examined and photographed with Canon EOS 5DSR digital camera attached to a Leica MZ16 microscope with low-angle light to emphasize the surface relief. Some features, such as the bilobed structure on the last sternite, become clearly visible only in lighting from a particular direction, so lighting needs to be varied in order to comprehend fully the morphology of the specimen. The stacked photographs were combined using the Focus Merge tool in Affinity Photo 2 (affinity.serif.com). Illustrations of the specimens were then created in Affinity Designer 2 (affinity.serif.com) using the composite photographs and the specimen under microscope for reference. Measurements, to the nearest 0.5 mm, were made with Graphic for Mac (graphic.com). Unfortunately, it is known that Mazon Creek concretions are generally not amenable to study by x-ray CT scanning (Saleh et al., 2023), otherwise this technique would have been used on the current specimen.

Repository and institutional abbreviation.—The specimen is deposited in the collections of the Field Museum of Natural History (FMNH) with the number PE 91366.

Systematic paleontology

Class Arachnida Lamarck, 1801
Pantetrapulmonata incertae sedis

Remarks.—The new fossil is evidently an arachnid, having four pairs of legs and a ∼15 mm long body broadly divided into two halves, an anterior prosoma and a posterior segmented opisthosoma. The prosoma is covered with a prosomal dorsal shield, usually referred to in the literature as the carapace, which is subtriangular, apparently undivided, and has a slight anterior projection. The chelicerae (mouthparts) and pedipalps are equivocal and either were very small and/or were lost during preservation. The legs are distinctive, being robust and fairly homogenous; the fourth leg perhaps marginally thicker. Only the proximal articles are preserved, and these are armed with rows of large, slightly curved macrospines, which become more prominent on the articles immediately beyond the femur. The opisthosoma is broadly attached to the prosoma, with a slight narrowing between the two body halves. The opisthosoma has at least eight visible tergites with procurved margins, but no obvious ornament such as spines or large tubercles. The posteriormost segment(s) appear to form a small anal tubercle, but the total number of segments here is hard to resolve.

The preserved morphology is thus distinctive but does not easily match any of the known arachnid orders, living or extinct. Superficial comparisons could be drawn with certain harvestmen, for example some members of the family Podoctidae from the suborder Laniatores or the genus *Lacinius* (Phalangidae) from the suborder Eupnoi. Both include living species with similarly spiny legs (for comparative images, see Zhang et al., 2013, for Podoctidae and Kurt and Erman, 2012, for *Lacinius*). However, we caution that several members of both groups do not have highly spinous legs and that the segmentation pattern of the fossil's opisthosoma differs markedly from at least laniatorean harvestmen in which the carapace and anterior opisthosomal segments are usually fused together to form the scutum magnum condition. Laniatoreans also usually have quite robust, raptorial pedipalps, but these are not visible in the present fossil.

Another key point is that in most harvestmen, except Cyphophthalmi, the second pair of legs are invariably longer and used primarily as tactile appendages. Even the femur of leg 2 is longer and thinner than those of the adjacent legs. By contrast, all legs in the new fossil appear to be of similar build/length, which would be inconsistent with a non-cyphophthalmid harvestman. No known living or fossil cyphophthalmids have such prominently spiny legs.

The overall habitus is also somewhat reminiscent of a mite from the Opilioacarida group (for habitus images of modern species see Oliveira Bernardi et al., 2013; Moraza et al., 2021; and Vázquez et al., 2021). Opilioacarids are fairly large mites, up to ∼3 mm in body length, and one of the few mite lineages that retain external body segmentation. Opilioacarids are also similar to the new fossil in having a broadly oval body, sometimes with a slight projection anteriorly and a partial constriction between the anterior and posterior body regions. In these mites they are referred to as a prodorsum and opisthonotum, which do not correspond exactly in terms of segment number to the prosoma and opisthosoma of other arachnids. These mites also usually express a projecting anal region at the posterior end of the body similar to the pygidium-like structure in the fossil. The legs can have visible spine-like setae along their length (e.g., the tapering and barbed setae or smooth acute setae, sensu Moraza et al., 2021), albeit not as prominent and robust as the leg spines in the new fossil. However, with a body length of 3 mm or less, opilioacarids are still considerably smaller than the new specimen, and the opisthonotum of these mites is rather

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leathery and does not have discrete, plate-like tergites like those in the fossil. Also, the prodorsum should bear two or three pairs of eyes located in groups towards the lateral margins, and in several living opilioacarid species the first pair of legs is distinctly longer and more tactile.

A further possibility is that the new fossil belongs to the wider Pantetrapulmonata lineage, sensu Shultz (2007). These are essentially the spiders and their closest relatives that are characterized by a narrowing of the region between the prosoma and opisthosoma, which is quite extreme in groups such as spiders and whip spiders. The present specimen shows a clear disconformity between the procurved posterior edge of the carapace and straighter opisthosomal tergites, which suggests a relatively distinct, possibly narrow, coupling of the prosoma and opisthosoma, and possibly some telescoping of tergites beneath the rear of the carapace. The relatively undifferentiated series of opisthosomal tergites and a small postabdomen/pygidium at the back of the opisthosoma would also be typical of this arachnid assemblage. If the tergites were divided into median and lateral plates this would be suggestive of the extinct arachnid order Trigonotarbida, although this character is also seen in Ricinulei.

One of the key characters of Pantetrapulomata is unfortunately not preserved. The chelicerae in this group have two articles in a clasp-knife configuration in which the fang folds against the basal element; in harvestmen or opilioacarids, for example, the chelicerae would have three articles, the last two forming a pinching claw.

In summary, we are unable to identify apomorphic characters that would support the placement of the new fossil in any living arachnid order. The overall habitus and distinctive legs are unique among Coal Measures arachnids and would certainly allow the genus to be recognized again. Given the absence of details of the mouthparts, pedipalps, and sternal region, we refer the new species to Arachnida/Pantetrapulmonata incertae sedis.

Genus *Douglassarachne* new genus

Type species.—*Douglassarachne acanthopoda* new species, by monotypy.

Diagnosis.—As for type species, by monotypy.

Etymology.—The genus is named for the Douglass family who kindly donated the specimen to the Field Museum for study.

Remarks.—As for the species.

Douglassarachne acanthopoda new species
Figures 2–4

Holotype.—PE 91366, part and counterpart, donated from The David and Sandra Douglass Collection to The Field Museum of Natural History, Chicago, Illinois; Mazon Creek Lagerstätte, Francis Creek Shale Member of the Carbondale Formation (Desmoinesian), Pit 15 Northern Mine tip, near Essex, Kankakee County, Illinois (41.1525°N, 88.2275°W).

Diagnosis.—Relatively large arachnid (body length >15 mm) with median dorsal ocular tubercle on carapace, abdominal tergites, anal tubercle, legs bearing many long, curved macrospines.

Description.—Large arachnid with subovate body, length including anal tubercle ~15.4 mm. Carapace subtriangular in outline, length 5.2 mm, width 7.2 mm (ratio 0.73). Cephalic area subtrapezoidal, length 2.2 mm, width 3.0 mm (ratio 0.73), with curved anterior–lateral margin, straight posterior edge demarcated by line of tubercles; suboval raised region in median part of cephalic area bearing high point at anterior end (ocular tubercle?). Cephalic area finely tuberculate, lateral areas less so. Transverse line ~0.6 mm behind posterior edge of central area.

Leg lengths (femur length, maximum preserved length): 1: 6.7 mm, 16.1 mm; 2: 6.8 mm, 17.9 mm; 3: 7.0 mm, 22.7 mm; 4: 8.8 mm, 24.6 mm. Leg formula (longest to shortest), based on femora: 4321. Trochanters spineless, femora well demarcated, other podomere joints indistinct. Femur 4 gently curved following lateral edge of abdomen. Macrospines on femora (Fig. 3.1), more distal podomeres, ~2 mm in length, taper distally, curve towards distal end of the leg, arranged in rows of ~4 on lateral and dorsal sides of femora, more numerous and closer spaced on more distal podomeres.

Opisthosoma suboval in outline, length 9.7 mm, width 9.1 mm (ratio 0.56), bearing tergites with variously recurved anterior margins, somewhat straighter margins at lateral parts; sagittal lengths of tergites: 1: 1.4 mm; 2: 1.1 mm; 3: 1.2 mm; 4: 1.2 mm; 5: 1.0 mm; 6: 1.0 mm; 7: 1.2 mm; mean = 1.1 mm. Median and lateral areas distinct but not divided into separate plates. Cuticle finely tuberculate. Few tubercles along posterior edges of tergites. Posteriormost sternite bears bilobed structure postero-medially (Fig. 3.2). Anal tubercle length 1.2 mm, width 2.1 mm (ratio 0.55).

Etymology.—From the Greek αγκάθι, a thorn or prickle, and πόδι, leg, with reference to the very spiny legs of this animal.

Remarks.—Although *Douglassarachne acanthopoda* n. gen. n. sp. lacks synapomorphies that would enable it to be placed more precisely within the Pantetrapulmonata, it shows remarkable macrospines on the legs, which renders that group more diverse than previously known.

Discussion

The spiny legs of *Douglassarachne acanthopoda* n. gen. n. sp. presumably were defensive adaptations, increasing the so-called handling time for predators, but without further information about the mouthparts or the full length of the legs any further ecological inferences would be speculation. In any case, this new species is an interesting addition to the Coal Measures arachnid fauna. Between ca. 318–299 Ma, various arachnid body plans have been preserved, from relatively modern-looking animals through to wholly extinct lineages. At one end of the spectrum there are anatomically modern examples of scorpions (Vogel and Durden 1966), harvestmen (Garwood et al., 2011), and whip scorpions (Garwood and Dunlop, 2023b). The known spiders belong to the extant suborder Mesothelae (revised by Selden, 2021), but more derived clades of spiders

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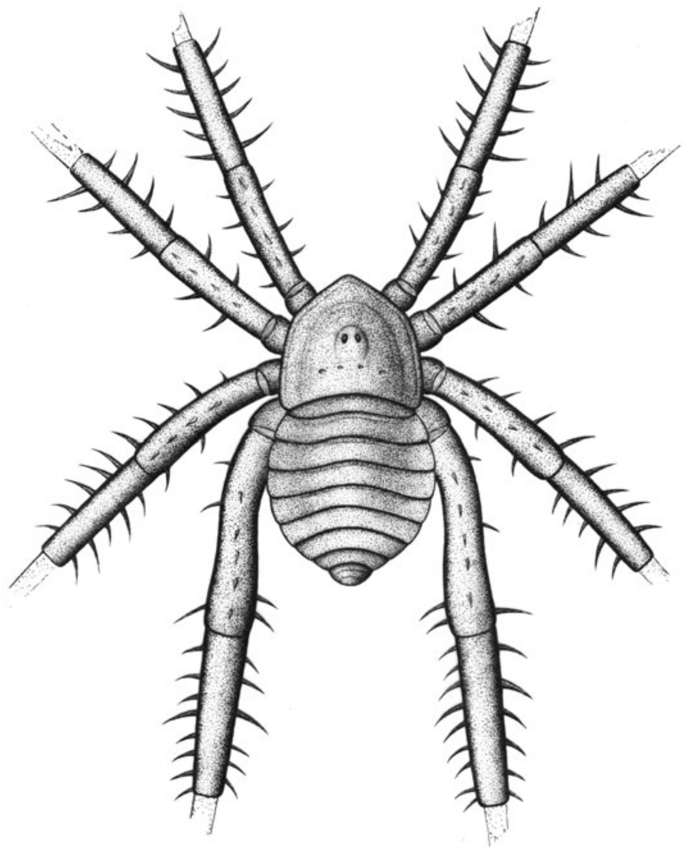

Figure 4. *Douglassarachne acanthopoda* n. gen. n. sp., reconstruction of the possible appearance of the animal in life.

(e.g., mygalomorphs or araneomorphs) have not been discovered so far. At the same time there were ricinuleids, harvestmen, and whip scorpions with distinctive morphologies that are not seen among the modern faunas (e.g., Selden, 1992; Garwood et al., 2014; Garwood and Dunlop, 2023b). Most of the Coal Measures scorpions were also members of now extinct groups.

Other Coal Measures arachnids belonged to completely extinct orders. At least in terms of described species and discovered specimens, the trigonotarbids and phalangiotarbids appear to have been significant faunal components in the Mazon Creek area and several other well-sampled localities of similar age. The order Haptopoda is known only from a single British species, but its morphology is sufficiently well known that its status as a distinct order and its probable affinities to whip scorpions and whip spiders could be tested cladistically (Shultz, 2007; Garwood and Dunlop, 2014). In addition to these fossils, there are several enigmatic taxa that may belong to, as yet unrecognized extinct lineages or may belong to the stem-group of more established clades. For example, the revision of Selden (2021) revealed that several putative spiders in the literature lack spinnerets and are better treated as incertae sedis arachnids. A similar argument could be made for the spider-like *Idmonarachne brasieri* Garwood et al., 2016, and these authors also suggested that bona fide spiders lived alongside grades of arachnids that approached the spider condition.

There is no evidence that *Douglassarachne* n. gen. is a spider, or that it is particularly close to spiders, although it is possible (see above) that its affinities lie with the broader Pantetrapulmonata clade. In any case, its appearance is unique, not only among Coal Measures arthropods, but also among arachnids in general. While a case could be made for erecting a new order (there is a precedence for doing this for a single species with Pocock's (1911) creation of Haptopoda), this is probably unwise so long as certain key morphological characters, and hence its affinities, remain unknown. Irrespective of its phylogenetic position, it still implies a previously underestimated degree of experimentation during the Carboniferous resulting in a wider range of body plans than the twelve arachnid orders that survived the crises of the late Paleozoic. These include the Carboniferous Rainforest Collapse, which may have begun at about 307 Ma (Falcon-Lang et al., 2018), thus more or less contemporary with the Mazon Creek biota, as well as later (ca. 252 Ma) the end-Permian mass extinction event from which a more modern arachnid fauna emerged in the Mesozoic with several fossils assignable to living families.

Mode of life.—The habitus of *Douglassarachne* n. gen., with its very spiny legs, is reminiscent of at least one fossil eupnoid harvestman recently described from Cretaceous Kachin amber (Bartel and Dunlop, 2023), as well as numerous modern species of Opiliones. These include several genera of armored harvestmen (Laniatores), especially in the family Podoctidae (e.g., illustrations in Roewer, 1923), and in certain phalangids such as *Lacinius horridus* (Panzer, 1794) or the European sclerosomatid *Homalenotus quadridentatus* (Cuvier, 1795) (Skinner, 2023) and the nemastomatid hedgehog harvestman, *Centetostoma bacilliferum* Simon, 1879, among many others. In all these cases spines on the legs (and bodies) of harvestmen presumably afford a degree of protection from predators (e.g., Silva et al., 2018). For a general review of spines as defensive adaptations in animals see Crofts and Stankowich (2021).

Numerous late Carboniferous arthropods are armored with large spines. For example, trigonotarbids in the eophrynid assemblage (Dunlop and Garwood, 2014) and millipedes such as *Euphoberia* (Brade-Birks, 1928) and *Myriacantherpestes* (Burke, 1979). Such spininess was absent among their earlier relatives, so its development across different clades in the late Carboniferous possibly reflects the evolution of their predators.

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Declaration of competing interests

The authors declare no competing interests.

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