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First trigonotarbid arachnids from the Pennsylvanian of Indiana and Oklahoma

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Abstract.—A new specimen of the arachnid order Trigonotarbida is described from the Middle Pennsylvanian (lower Desmoinesian) Shelburn Formation of Indiana, which has previously yielded the remains of a phalangiotarbid. Two new trigonotarbid arachnid specimens are also described from the Middle Pennsylvanian (Desmoinesian) Senora Formation of Oklahoma. These are the first trigonotarbid specimens reported from Indiana and Oklahoma. The Indiana trigonotarbid belongs to the Eophrynidae, as indicated by distinct features such as the large tubercles on the dorsal surface of the opisthosoma and two pairs of terminal opisthosomal spines. This specimen is the first arachnid fossil to be imaged using a Multistripe Laser Triangulation scanner. The heavy dorsal tuberculation, lobed and subtriangular carapace, rounded clypeus, lack of terminal opisthosomal spines, and rounded opisthosoma on Oklahoma specimen FMNH PE 56932 indicate it belongs to the genus *Aphantomartus*, in Aphantomartidae. The other Oklahoma specimen, FMNH PE 56955, possesses opisthosomal tergites that are divided into five plates longitudinally as well as a subquadrate carapace, which identify it as a member of Anthracomartidae; its rounded opisthosomal margin shows it to belong to the genus *Anthracomartus*.

Introduction

The ancient arachnid order Trigonotarbida, recognized from the late Silurian (Dunlop, 1996) to early Permian (Dunlop and Rößler, 2013) (ca. 419–290 Ma), represents some of the earliest terrestrial fauna (Garwood and Dunlop, 2010). This includes the oldest known non-scorpion arachnid, a trigonotarbid, *Palaeotarbus jerami* (Dunlop, 1996), from Ludford Lane, Shropshire, UK (Dunlop, 1996; Selden, 2016). In addition to being present in deposits interpreted as early terrestrial ecosystems, morphological features such as preoral digestion (indicated by plumose setae filters around the mouth region), book lungs (connected to the outside through spiracles), and rounded (plantigrade) leg tips indicate that trigonotarbids were fully terrestrial (Garwood and Dunlop, 2010; Garwood and Edgecombe, 2011). Fanged chelicerae indicate that trigonotarbids were predators, likely feeding on other arthropods, presumably with either an ambush or cursorial predation style (Garwood and Dunlop, 2010).

As the sister group to the Tetrapulmonata clade (which encompasses the extinct arachnid orders Uraraneida and Haptopoda and the extant arachnid orders Araneae, Amblypygi, Schizomida and Uropygi) within Pantetrapulmonata (Dunlop, 1997, 2010; Fayers et al., 2005; Shultz, 2007), trigonotarbids share the apomorphies of two pairs of book lungs and clasp-knife chelicerae (Dunlop et al., 2009). Although outwardly spider-like in appearance, trigonotarbids apparently lack venom glands and silk glands and have a distinctive segmented abdomen featuring tergites that are divided into median and lateral plates (Dunlop and Selden, 2004; Fayers et al., 2005; Selden and Nudds, 2008). Some trigonotarbid families are heavily ornamented with distinct tubercles (raised processes) arranged in patterns on the dorsal surface of their opisthosoma.

Although trigonotarbids have been found throughout Europe from at least 66 localities (Dunlop et al., 2014) and are the most commonly found arachnids in North American Carboniferous deposits (Wright and Selden, 2011), they previously were reported from only 12 North American localities (Dunlop et al., 2014). Because trigonotarbids are largely underrepresented from North America, any new fossil and/or locality is a significant discovery (Dunlop et al., 2014). Here, the first trigonotarbid (an eophrynid) is described from Indiana, from the Middle Pennsylvanian (lower Desmoinesian, equivalent to the Westphalian D in terms of European chronostratigraphy: Peppers and Brady, 2007) shale of the Shelburn Formation near Terre Haute. In addition, the first two trigonotarbid specimens reported from Oklahoma are also described, both from the Middle Pennsylvanian (Desmoinesian) Senora Formation: an *Aphantomartus* from near Morris in Okmulgee County, and an *Anthracomartus* from Sallisaw in Sequoyah County.

Geological setting

Indiana specimen.—The specimen was found in an unnamed bed of shale above Coal IV—part of a cyclothem and likely deposited during infilling of the flooded paleovalley estuaries (King, 1993)—in the Shelburn Formation (McLeansboro Group), Middle Pennsylvanian: lower Desmoinesian

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(Westphalian D), located in Vigo County, Indiana, ~8 miles south of Terre Haute, Indiana. The Shelburn Formation (ranging from 50–250 feet in thickness) contains the Busseron Sandstone; Pirtle Coal; West Franklin Limestone members; unnamed beds of shale, siltstone, and sandstone; and thin discontinuous beds of coal, clay, and limestone (Burger and Wier, 1970). The base of the Shelburn Formation in Indiana overlies the top of the Danville Coal Member (Coal VII) of the Dugger Formation (Tri-State Committee on Correlation of the Pennsylvanian System in the Illinois Basin, 2001) (Fig. 1).

Common species of flora found in associated members of the Shelburn Formation include *Pecopteris miltoni* Brongniart, 1828; *Pecopteris unita* (Brongniart, 1836); and *Neuropteris flexuosa* Sternberg, 1825 (Boneham, 1974), which resembles the Mazon Creek Braidwood Flora (Patrick, 1989). The most common animal is the horseshoe crab *Euproops danae* Meek and Worthen, 1865 (Boneham, 1974). As indicated by the Shelburn Formation flora and fauna (which also includes the phalangiotarbid, *Triangulotarbus terrehautensis* Patrick, 1989), the depositional setting is consistent with that of an emergent swamp/coastal freshwater environment with high turbidity and low salinity levels (Patrick, 1989).

Oklahoma specimens.—Specimen FMNH PE 56932 was found in an unspecified shale unit of the Senora Formation (Middle Pennsylvanian, Desmoinesian) in a strip mine northwest of Morris in Okmulgee County, Oklahoma. Specimen FMNH PE 56955 was found in the shale above the Croweburg Coal (Senora Formation), Sallisaw in Sequoyah County, Oklahoma. Occurring within the Middle Pennsylvanian Liverpool cyclothem (Fig. 2) (Coveney et al., 1987), the depositional environment has been interpreted as an emergent swamp and brackish-water lagoons (Wright, 1975). The Croweburg Coal (in which the Oklahoma spore succession shows a swamp flora consisting of ferns, horsetails, gymnosperms, and lycopods) grades into a unit of thin shale, which was deposited in brackish-water lagoons (Wright, 1975).

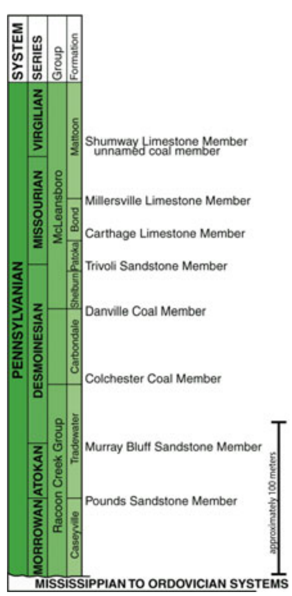

Figure 1. Generalized stratigraphic column of the Pennsylvanian in Illinois (figure and caption modified from Jacobson, 2000).

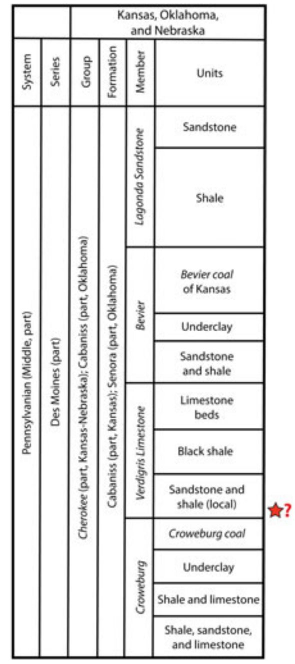

Figure 2. Rock units in the Liverpool cyclothem (modified from Wright, 1975).

Preservation

Indiana specimen.—The specimen is preserved in a siderite concretion with part and counterpart with split/partial external and internal dorsal and ventral molds.

The part shows a concave ventral internal mold of the opisthosoma with superimposition of large dorsal tubercles onto internal ventral sternite surfaces and a partial external dorsal mold along the terminal margin of the opisthosoma (which shows some granular tuberculation). On the prosoma, there are partial external dorsal mold features (granular tubercles on a lobe towards the anterior margin) and internal ventral impressions of the coxae.

The counterpart shows a convex dorsal internal mold of the opisthosoma with superimposition of the ventral pygidium and sternites, as well as a partially dorsal internal mold of the prosoma with superimposition of the ventral coxae. The appendages are not preserved, apart from the trochanter, femur, and partial patella of the right posteriormost leg.

Oklahoma specimens.—Both specimens FMNH PE 56932 and FMNH PE 56955 are preserved primarily as dorsal external molds in siderite concretions, each as part and counterpart. As is the case with other Carboniferous arachnids, both part and counterpart exhibit dorsal opisthosomal surfaces that have become concave, resulting in external molds that misleadingly appear to be a cast or internal mold (Selden and Romano, 1983).

The part of specimen FMNH PE 56932 shows an external mold of most of the prosoma and opisthosoma and the remains of some of the appendages. Sternites 5–8 are visible on the dorsal

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side along the margins of the opisthosoma. Partially visible on the left side are a portion of leg I; the femur, patella, and tibia of leg II; the trochanter, femur, patella, tibia, and metatarsus of leg III; and the femur and patella of leg IV. On the right side, portions of the patella of leg III and femur of leg IV are visible.

The counterpart of specimen FMNH PE 56932 shows most of the prosoma, the far right side of the opisthosoma (corresponding to the far left side of the part) with sternites 5–7 visible on the dorsal side along the margin of the opisthosoma, and the remnants of some of the appendages. On the left side of the specimen (corresponding to the right side of the part), portions of the pedipalp as well as the trochanter and femur of leg II are visible. On the right side (corresponding to the left side of the part), portions of leg I and leg II; the trochanter, femur, patella, and tibia of leg III; and the femur and patella of leg IV are visible.

On both the part and counterpart of specimen FMNH PE 56955, the posterior area of the prosoma, anterior area of opisthosoma, and some portions of unidentified legs are visible.

Materials and methods

These specimens were examined and photographed with Canon EOS 5D Mark II digital camera attached to a Leica M205C microscope with low-angle light to emphasize the surface relief. The stacked photographs were combined using the Photomerge tool in Adobe Photoshop. Illustrations of the specimens were then created in Adobe Illustrator using the composite photographs and the specimen under microscope for reference. For the Indiana specimen (Fig. 3), using a Multistripe Laser Triangulation (MLT) scanner at the University of Kansas, a three-dimensional digital model was created to better show the relief and morphological features of the specimen (Fig. 4). MLT scanning is a low-cost method that previously has been used in the analyses of ichnofossils (see Platt et al., 2010 for scanning settings and methods). All measurements are in millimeters (mm), to the nearest 0.5 mm. Where total lengths or widths are visible, they are given as =; where the total cannot be assessed due to obscurity or lack of preservation, measurements are given as ≥.

Repository and institutional abbreviation.—The specimens are held in the collection of the Field Museum of Natural History with the numbers FMNH PE 9940 (Fig. 3) for the Indiana specimen and FMNH PE 56932 (Fig. 5) for the specimen found near Morris in Okmulgee County, Oklahoma, and FMNH PE 56955 (Fig. 6) for the specimen from Sallisaw in Sequoyah County, Oklahoma.

Systematic paleontology

Class Arachnida Lamarck, 1801
Order Trigonotarbida Petrunkevitch, 1949
Eophrynid assemblage Dunlop and Brauckmann, 2006
Family Eophrynidae Karsch, 1882
Eophrynidae gen. et sp. indet.
Figures 3, 4

Description.—Large trigonotarbid, total preserved length 32.0 mm. Opisthosoma heavily ornamented, posterior margin slightly scalloped. Opisthosoma almost as wide as long (maximum width 18.0 mm, length 19.0 mm). Seven opisthosomal sternites visible (segments 4–10); widths: 4 ≥ 14.0 mm, 5 ≥ 16.0 mm, 6 = 17.0 mm, 7 = 18.0 mm, 8 = 15.0 mm, 9 = 10.0 mm, 10 = 4.0 mm. Degree of sternite curvature increases posteriorly. Two pairs of spines (length 1.0–2.0 mm) on terminal opisthosomal margin, aligned with posterior margins of sternites 8 and 9. Diameter of pygidium: 2.0 mm. Two rows of large tubercles (one located more medially and the other more laterally) superimposed onto sternites 5–9. Large tubercles rounded in shape, diameter 1.5–2.0 mm. Small (0.5–0.75 mm), granular tubercles along terminal margin of opisthosoma and on medial and anterior portions of lobed carapace. Maximum width of carapace 11.0–12.0 mm, length 13.00 mm. Length of partial leg (curved) 16.0 mm total (trochanter = 4.0 mm, femur = 8.0 mm, patella = 4.0 mm).

Materials.—FMNH PE 9940, unnamed bed of shale above Coal IV, Shelburn Formation (McLeansboro Group), Middle Pennsylvanian, lower Desmoinesian (Westphalian D), Vigo County, ∼8 miles south of Terre Haute, Indiana.

Remarks.—The heavy ornamentation of the specimen and two pairs of terminal opisthosomal spines are diagnostic to the families Eophrynidae Karsch, 1882, and Kreischeriidae Haase, 1890, in the monophyletic eophrynid assemblage (which consists of the families Eophrynidae, Kreischeriidae, and Aphantomartidae). The families in this assemblage are characterized by having heavy ornamentation (in the form of tubercles) on the dorsal surface and a deep, laterally lobed carapace with two pairs of terminal opisthosomal spines (found in kreischeriids and eophrynids) (Jones et al., 2014). The particularly large tubercles seen in FMNH PE 9940, which also extend to the lateral tergal regions (Fig. 3), are more similar to those seen in eophrynids than the sparser tubercles confined to the axial region of kreischeriids (Garwood et al., 2009, fig. 1d; Jones et al., 2014, fig. 1H, I).

Family Aphantomartidae Petrunkevitch, 1945

Remarks.—The heavily ornamented dorsal surface and lobed, subtriangular carapace of FMNH PE 56932 are characteristic of the monophyletic eophrynid assemblage, which consists of the families Eophrynidae Karsch, 1882, Kreischeriidae Haase, 1890, and Aphantomartidae Petrunkevitch, 1945. The rounded clypeus and lack of terminal opisthosomal spines denote this specimen as belonging to the family Aphantomartidae (Rössler et al., 2003).

Genus *Aphantomartus* Pocock, 1911

Type species.—*Aphantomartus areolatus* Pocock, 1911, from the upper Carboniferous (Westphalian D) Mynyddislwyn vein, Maes-y-cwmmer, South Wales, U.K.

Aphantomartus sp. indet.
Figure 5

Description.—Relatively small trigonotarbid, total preserved length 8.0 mm. Carapace subtriangular in outline, clypeus

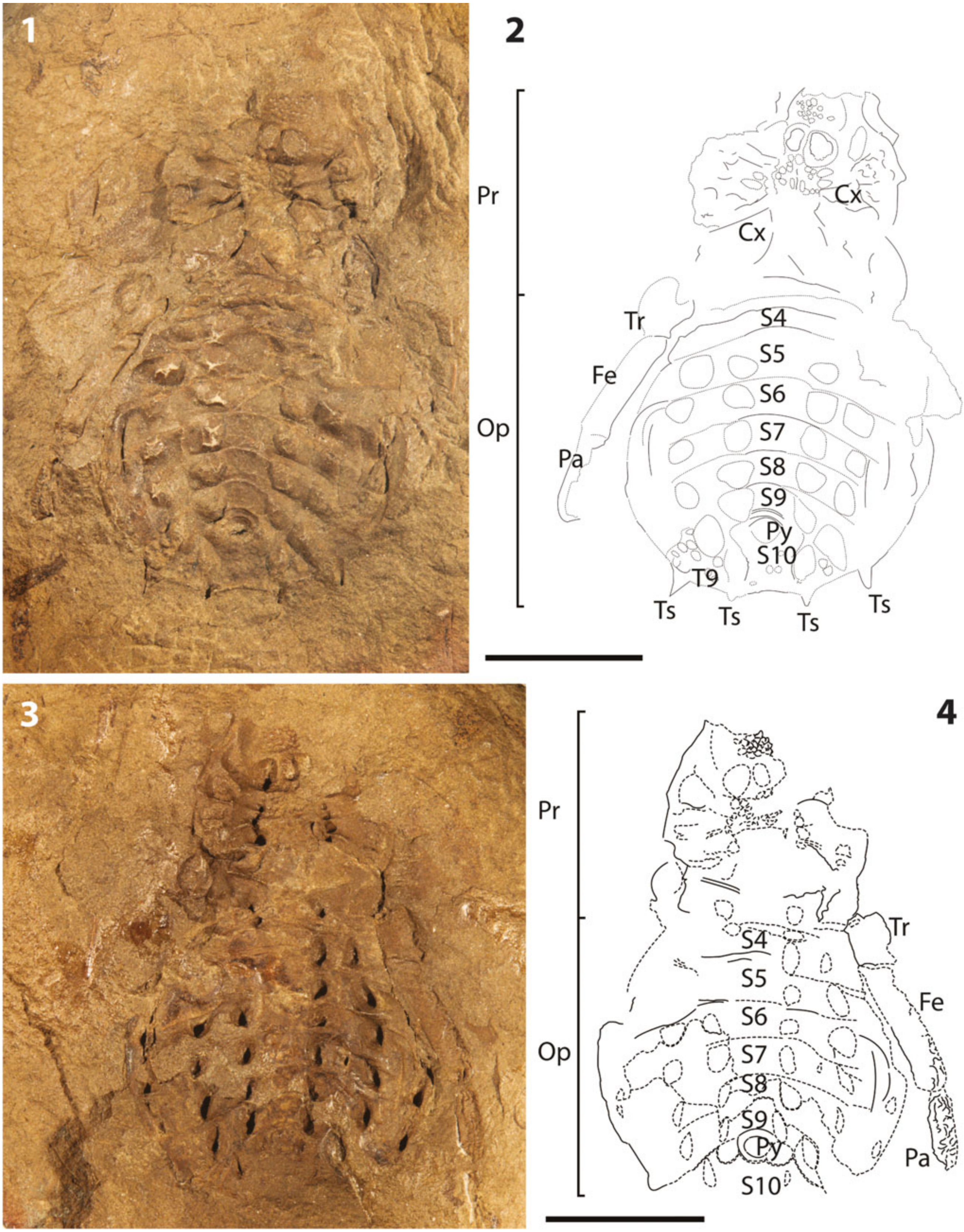

Figure 3. Eophrynid trigonotarbid, FMNH PE 9940, shale above Coal IV, Shelburn Formation (McLeansboro Group), Middle Pennsylvanian, lower Desmoinesian (Westphalian D), Vigo County, 8 miles south of Terre Haute, Indiana. (**1**) Photograph of part; (**2**) explanatory drawing of part; (**3**) photograph of counterpart; (**4**) explanatory drawing of counterpart. Cx = coxa; Fe = femur; Op = opisthosoma; Pa = patella; Pr = prosoma; Py = pygidium; S = sternite; T = tergite; Tr = trochanter; Ts = terminal spine. Scale bars = 5 mm.

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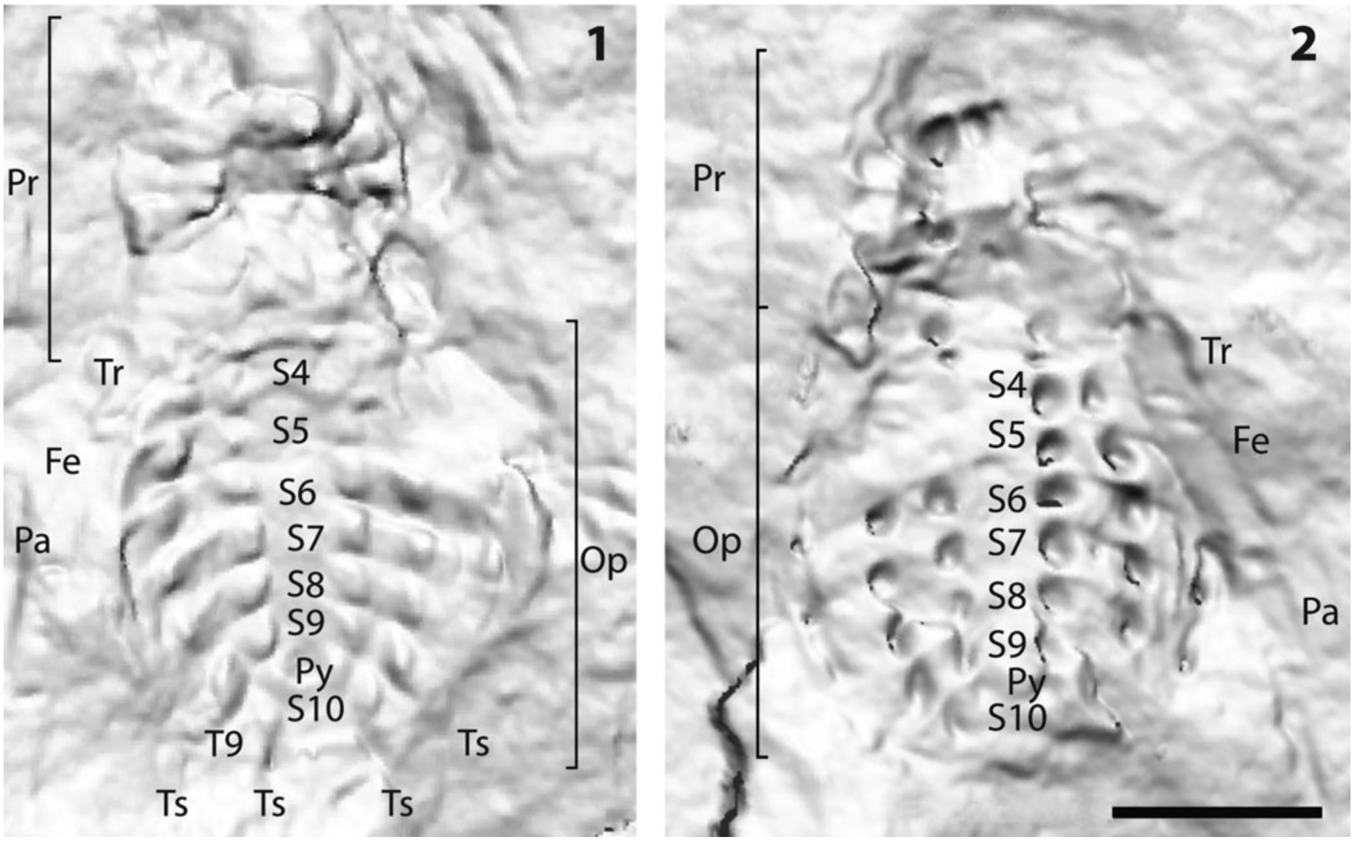

Figure 4. Eophrynid trigonotarbid, FMNH PE 9940, shale above Coal IV, Shelburn Formation (McLeansboro Group), Middle Pennsylvanian, lower Desmoinesian (Westphalian D), Vigo County, 8 miles south of Terre Haute, Indiana, MLT scans. (**1**) Part; (**2**) counterpart. Fe = femur; Op = opisthosoma; Pa = patella; Pr = prosoma; Py = pygidium; S = sternite; T = tergite; Tr = trochanter; Ts = terminal spine. Blue pixels in the MLT images are areas lacking data (the surface in those areas was obscured from the laser by other portions of the surface relief). Scale bar = 5 mm.

rounded; maximum width 5.0 mm, length 4.0 mm. Opisthosoma heavily tuberculated with pattern of larger tubercles along lateral edges of each median tergal area. Opisthosoma elliptical in shape, maximum width 5.0 mm (traversed sternites included 5.5 mm), length 4.0 mm. Tergites 2 and 3 fused into a diplotergite. Tergites 2/3 through 8 visible. Sternites 5–8 partially visible at left and right margins. Tergite widths: 2/3 ≥ 4.5 mm, 4 ≥ 5.0 mm, 5 ≥ 4.25 mm, 6 ≥ 4.0 mm, 7 ≥ 3.5 mm.

Materials.—FMNH PE 56932, unspecified shale unit of Senora Formation (Middle Pennsylvanian, Desmoinesian), strip mine northwest of Morris, Okmulgee County, Oklahoma.

Remarks.—The opisthosoma of specimen FMNH PE 56932 is more rounded in shape, indicating it be *Aphantomartus* sp. rather than the other genus in the family, *Alkenia* Størmer, 1970, which possesses a more elongated opisthosoma (Dunlop and Selden, 2004; Poschmann and Dunlop, 2011).

Family Anthracomartidae Haase, 1890

Remarks.—Specimen FMNH PE 56955 has opisthosomal tergites, with a granular surface texture, divided into five plates laterally, a subquadrate carapace, and tergites 2 and 3 conjoined into a diplotergite. These characteristics refer the specimen to the family Anthracomartidae Haase, 1890 (Garwood and Dunlop, 2011; Wright and Selden, 2011).

Genus *Anthracomartus* Karsch, 1882

Type species.—*Anthracomartus voelkelianus* Karsch, 1882, from the Pennsylvanian (Langsettian) of Nowa Ruda, Poland.

Anthracomartus sp. indet.
Figure 6

Description.—Total preserved length 21.0 mm. Carapace and opisthosomal tergites finely tuberculated. Carapace subquadrate in outline; maximum width 10.0 mm, length 7.0 mm. Opisthosoma divided into five plates laterally, maximum width 14.0 mm, length ≥ 14.0 mm. Locking ridge (segment 1) width ≥ 8.0 mm. Tergites 2 and 3 combined into diplotergite. Tergite widths: 2/3 ≥ 11.0 mm, 4 ≥ 12.0 mm, 5 ≥ 13.0 mm, 6 ≥ 14.0 mm, 7 ≥ 13.5 mm. Opisthosomal posterior margin (segment 7) smoothly rounded.

Materials.—FMNH PE 56955, shale above Croweburg Coal (Senora Formation), Sallisaw, Sequoyah County, Oklahoma.

Remarks.—Specimen FMNH PE 56955 has a smooth opisthosomal margin (as opposed to the scalloped

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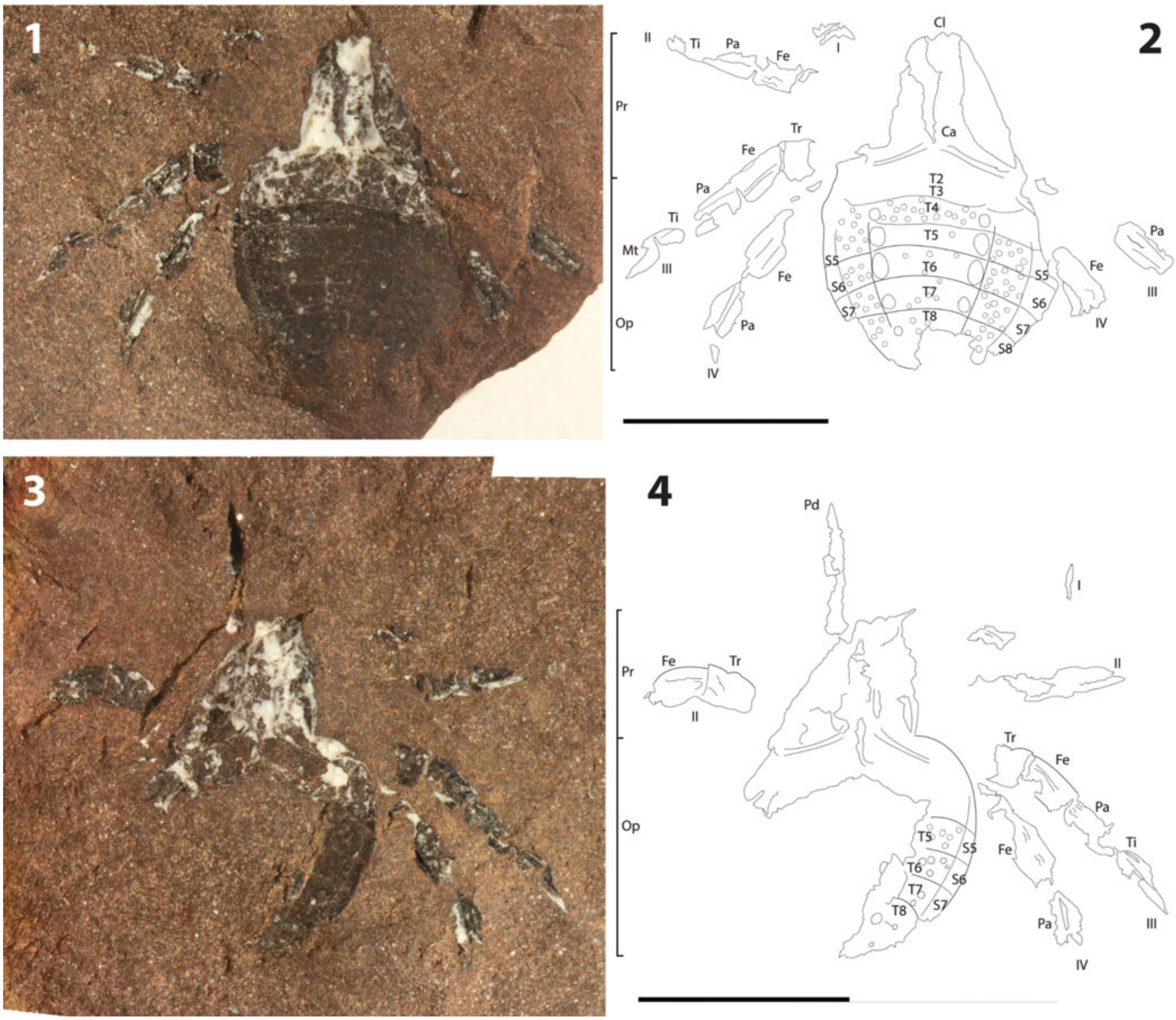

Figure 5. *Aphantomartus* sp. indet., FMNH PE 56932, shale unit of Senora Formation (Middle Pennsylvanian, Desmoinesian), strip mine northwest of Morris, Okmulgee County, Oklahoma. (**1**) Photograph of part; (**2**) explanatory drawing of part; (**3**) photograph of counterpart; (**4**) explanatory drawing of counterpart. I–IV leg numbers; Ca = carapace; Cl = clypeus; Fe = femur; Mt = metatarsus; Op = opisthosoma; Pa = patella; Pd pedipalp; Pr = prosoma; S = sternite; T = tergite; Ti = tibia; Tr = trochanter. Scale bars = 5 mm.

opisthosomal margin of *Brachypyge* Woodward, 1878, and *Maiocercus* Pocock, 1911), which is diagnostic of *Anthracomartus* sp. (Dunlop and Rößler, 2002).

Discussion

The eophrynid assemblage is a monophyletic group composed of the families Eophrynidae, Kreischeriidae, and Aphantomartidae (Dunlop and Brauckmann, 2006). These three families share the synapomorphic traits of heavy ornamentation (numerous large tubercles) on the dorsal surface and deeply lobed carapace margins, often with additional lobation of the median region of the carapace (Hradská and Dunlop, 2013). Two pairs of terminal opisthosomal spines are found in Kreischeriidae and Eophrynidae (Jones et al., 2014). Kreischeriidae and Eophrynidae share other characteristics (generally being large in size compared to other families and having a subtriangular carapace with the clypeus forming an anterior spine [Rößler and Dunlop, 1997]) and at one time were treated as synonyms (Jones et al., 2014). The tuberculation of kreischeriids is a "more uniform, granular pattern" opposed to "discrete large tubercles" found in eophrynids (Dunlop, 1998, p. 52), but the main feature distinguishing these two families is the presence of a diplotergite (formed from the fusion of tergites 2 and 3), which is found in kreischeriids but not in eophrynids (Rößler and Dunlop, 1997). Specimen FMNH PE 9940 does not show whether there is a diplotergite 2–3; however, the particularly large tubercles, which extend to the lateral regions, suggest it is more likely an eophryind than a kreischeriid, so it is referred to that family.

Specimen FMNH PE 9940 is preserved with a substantial amount of relief to its surface features. Because the stacked

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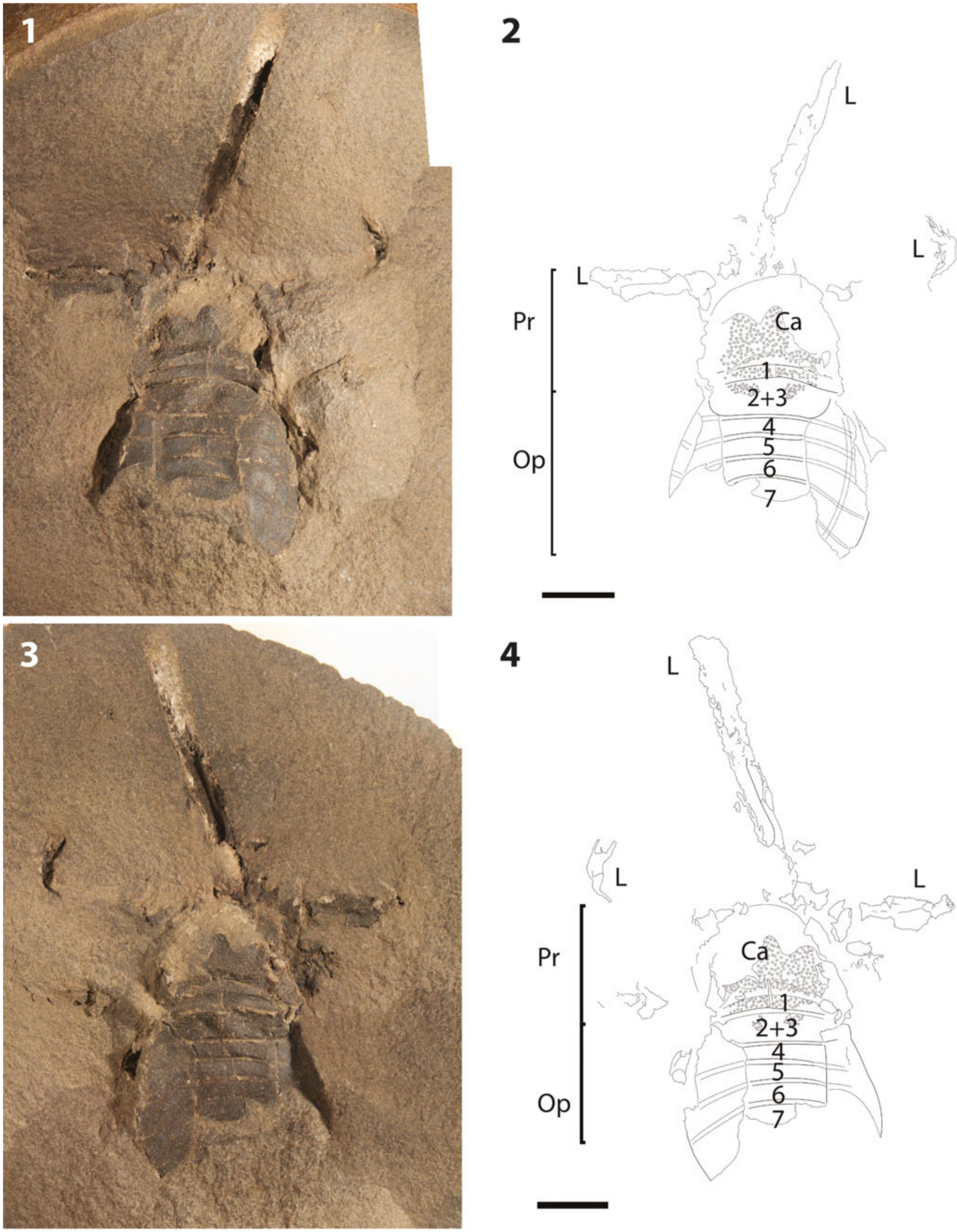

Figure 6. *Anthracomartus* sp. indet., FMNH PE 56955, shale above Croweburg Coal (Senora Formation), Sallisaw, Sequoyah County, Oklahoma. (**1**) Photograph of part; (**2**) explanatory drawing of part; (**3**) photograph of counterpart; (**4**) explanatory drawing of counterpart. 1–7 = tergites, Ca = carapace; L = leg (unidentified); Op = opisthosoma; Pr = prosoma. Scale bars = 5 mm.

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photographs tend to flatten and obscure this relief, Multistripe Laser Triangulation (MLT) scanning was used to create three-dimensional digital models of the specimen. The MLT scanning of FMNH PE 9940 marks the first use of this method on a fossil arachnid.

Aphantomartids (specifically *Aphantomartus pustulatus* [Scudder, 1884]) have been described from three other localities in North America (the 7-11 mine in Ohio, Mazon Creek in Illinois, and Fern Ledges in New Brunswick), but none as far west as Oklahoma (Miller and Forbes, 2001; Dunlop et al., 2014). Specimen FMNH PE 56932 extends the known biogeographic range of the genus, which includes multiple localities in Europe, with *Aphantomartus pustulatus* known from Pas-de-Calais in northern France (Pruvost, 1912) and Halleschen Mulde in Germany (Simon, 1971; Dunlop et al., 2020).

Compared with the specimen of *Aphantomartus pustulatus* from Fern Ledges in New Brunswick (NBMG 4594a/b) (Miller and Forbes, 2001), the opisthosoma of FMNH PE 56932 appears to have a more rounded morphology (but that impression may simply be the result of its preservation in which the lateral margins of the opisthosoma are lined with traversed sternites) (Rössler, 1998). The rounded clypeus of FMNH PE 56932 is similar to that of the specimen of *Aphantomartus* described from the Kent Coalfield of England (Dunlop, 1999) and the specimens of *Aphantomartus pustulatus* described from the Variscan Foreland Basin in the British Isles (Rössler, 1998).

Anthracomartidae is one of the most prevalent trigonotarbid families (Garwood and Dunlop, 2011) with specimens known from many localities across Europe, including multiple *Anthracomartus* taxa known from the Czech Republic (Hradská and Dunlop, 2013). In addition to multiple European localities, anthracomartids are known from Lawrence, Kansas; Mazon Creek, Illinois; Fayetteville, Arkansas; and Joggins Fossil Cliffs, Nova Scotia (Wright and Selden, 2011; Dunlop et al., 2014). Specimen FMNH PE 56955 represents the westernmost known anthracomartid, thus expanding the recognized biogeographic range of Anthracomartidae.

Anthracomartus triangularis Petrunkevitch, 1913, and *Anthracomartus trilobitus* Scudder, 1884, are anthracomartid taxa known only from North America. The granular tuberculation of specimen FMNH PE 56955 bears resemblance to the pustulose nature of *Anthracomartus trilobitus* and *A. hindi* Pocock, 1911 (see Garwood and Dunlop, 2011), but the lack of a complete opisthosoma hinders further comparison with other *Anthracomartus* taxa (Wright and Selden, 2011).

Conclusions

These specimens are the first members of Trigonotarbida reported from Indiana and Oklahoma. Previous research on trigonotarbid occurrences in North America only reported localities at Gilboa, New York; Mazon Creek, Illinois; Red Hill, Pennsylvania; Lawrence, Kansas; Alleghany Tunnel, Virginia; Cotton Hill, West Virginia; Fayetteville, Arkansas; 7-11 mine, Ohio; Pawtucket, Rhode Island; Kinney Brick Quarry, New Mexico; Joggins Fossil Cliffs, Nova Scotia; and Fern Ledges, Saint John, New Brunswick (Dunlop et al., 2014). With trigonotarbids being markedly underrepresented from North America, especially when compared to the >66 localities in which they have been found across Europe, any new fossil or locality is greatly significant (Dunlop et al., 2014). In addition, with a fairly widespread biogeographic distribution across North America, but relatively few recognized localities (Dunlop and Rößler, 2013), other similarly overlooked trigonotarbid specimens from previously unreported localities are likely to exist in museum collections.

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References

Boneham, R.F., 1974, Chieftain No. 20 flora (Middle Pennsylvania) of Vigo County, Indiana: Proceedings of the Indiana Academy of Science, v. 84, p. 89–113.

Brongniart, A., 1828, Prodrome d'une Histoire des Végétaux Fossiles. Paris, F. G. Levrault.

Brongniart, A., 1836, Histoire des Végétaux Fossiles, ou, recherches botaniques et geìologiques sur les veìgeìtaux renfermeìs dans les diverses couches du globe. Paris, G. Dufour et Ed. D'Ocagne, v. 2, p. 337–368.

Burger, A.M., and Wier C.E., 1970, Shelburn Formation, *in* Shaver, R.H., Burger, A.M., Gates, G.R., Gray, H.H., Hutchison, H.C., Keller, S.J., Patton, J.B., Rexroad, C.B., Smith, N.M., Wayne, W.J., and Wier, C.E., Compendium of Rock-unit Stratigraphy in Indiana: Indiana Geological Survey Bulletin, v. 43, p. 164–165.

Coveney, R.M., Leventhal, J.S., Glascock, M.D., and Hatch, J.R., 1987, Origins of metals and organic matter in the Mecca Quarry Shale Member and stratigraphically equivalent beds across the Midwest: Economic Geology, v. 82, p. 915–933.

Dunlop, J.A., 1996, A trigonotarbid arachnid from the upper Silurian of Shropshire: Palaeontology, v. 39, p. 605–614.

Dunlop, J.A., 1997, Palaeozoic arachnids and their significance for arachnid phylogeny: Proceedings of the 16th European Colloquium of Arachnology 1997, p. 65–82.

Dunlop, J.A., 1998, A redescription of the trigonotarbid arachnid *Pseudokreischeria pococki* (Gill, 1924): Bulletin of the British Arachnological Society, v. 11, p. 49–53.

Dunlop, J.A., 1999, A trigonotarbid ('armoured spider') from the Kent Coalfield: Proceedings of the Geologists' Association, v. 110, p. 333–334.

Dunlop, J.A., 2010, Geological history and phylogeny of Chelicerata: Arthropod Structure & Development, v. 39, p. 124–142.

Dunlop, J.A., and Brauckmann, C., 2006, A new trigonotarbid arachnid from the Coal Measures of Hagen-Vorhalle, Germany: Fossil Record, v. 9, p. 130–136.

Dunlop, J.A., and Rößler, R., 2002, The trigonotarbid arachnid *Anthracomartus voelkelianus* (Anthracomartidae): Journal of Arachnology, v. 30, p. 211–218.

Dunlop, J.A., and Rößler, R., 2013, The youngest trigonotarbid *Permotarbus schuberti* n. gen., n. sp. from the Permian Petrified Forest of Chemnitz in Germany: Fossil Record, v. 16, p. 229–243.

Dunlop, J.A., and Selden, P.A., 2004, A trigonotarbid arachnid from the Lower Devonian of Tredomen, Wales: Palaeontology, v. 47, no. 6, p. 1469–1476.

Dunlop, J.A., Kamenz, C., and Talarico, G., 2009, A fossil trigonotarbid arachnid with a ricinuleid-like pedipalpal claw: Zoomorphology, v. 128, p. 305–313.

Dunlop, J.A., Wang, Y., Selden, P.A., and Krautz, P., 2014, A trigonotarbid arachnid from the Pennsylvanian Astrasado Formation of the Kinney Brick Quarry, New Mexico: KU Paleontological Institute, University of Kansas, Paleontological Contributions, v. 9, p. 1–6.

Dunlop, J.A., Penney, D., and Jekel, D., 2020, A summary list of fossil spiders and their relatives, *in* World Spider Catalog: Natural History Museum Bern, online at http://wsc.nmbe.ch, version 20.5 (accessed on 02/19/20).

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, v. 2, p. 269–284.

Garwood, R.J., and Dunlop, J.A., 2010, Fossils explained: Trigonotarbids: Geology Today, v. 26, p. 34–37.

Garwood, R.J., and Dunlop, J.A., 2011, Morphology and systematics of Anthracomartidae (Arachnida: Trigonotarbida): Palaeontology, v. 54, p. 145–161.

Garwood, R.J., and Edgecombe, G.D., 2011, Early terrestrial animals, evolution, and uncertainty: Evolution: Education and Outreach, v. 4, p. 489–501.

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, v. 5, no. 6, p. 841–844.

Haase, E., 1890, Beiträge zur Kenntniss der fossilen Arachniden: Zeitschrift der Deutschen Geologischen Gesellschaft, v. 42, p. 629–657.

Hradská, I., and Dunlop, J.A., 2013, New records of Pennsylvanian trigonotarbid arachnids from West Bohemia, Czech Republic: Journal of Arachnology, v. 41, p. 335–341.

Jacobson, R.J., 2000, Geonote #2—Pennsylvanian Rocks in Illinois: Illinois State Geological Survey, Coal Section. http://isgs.illinois.edu/outreach/geology-resources/pennsylvanian-rocks-illinois (accessed February 2, 2020).

Jones, F.M., Dunlop, J.A., Friedman, M., and Garwood, R.J., 2014, *Trigonotarbus johnsoni* Pocock, 1911, revealed by X-ray computed tomography, with a cladistic analysis of the extinct trigonotarbid arachnids: Zoological Journal of the Linnean Society, v. 172, p. 49–70.

Karsch, F., 1882, Ueber ein neues Spinnenthier aus der Schlesischen Steinkohle und die Arachnoiden überhaupt: Zeitschrift der Deutschen Geologischen Gesellschaft, v. 34, p. 556–561.

King, N.R., 1993, Cyclothems in the Shelburn Formation (Middle and Upper Pennsylvanian) of southwestern Indiana (abstract): Geological Society of America Abstracts with Program, v. 25, no. 3, p. 30.

Lamarck, J.B.P.A., 1801, Systême des Animaux sans Vertèbres: Paris, Lamarck and Deterville, 432 p.

Meek F.B., and Worthen A.H., 1865, Notice of some new types of organic remains, from the Coal Measures of Illinois. Proceedings of the Academy of Natural Sciences of Philadelphia, v. 17, p. 41–48.

Miller, R.F., and Forbes, W.H., 2001, An upper Carboniferous trigonotarbid, *Aphantomartus pustulatus* (Scudder, 1884), from the Maritimes Basin (Euramerican Coal Province), New Brunswick, Canada: Atlantic Geoscience, v. 37(2/3). https://doi.org/10.4138/1979.

Patrick, R.R., 1989, A new phalangiotarbid (Arachnida) from the McLeansboro Group (Pennsylvanian) of Indiana: Journal of Paleontology, v. 63, p. 327–331.

Peppers, R.A., and Brady, L.L., 2007, Palynological correlation of Atokan and lower Desmoinesian (Pennsylvanian) strata between the Illinois Basin and the Forest City Basin in eastern Kansas: Midcontinent Geoscience, v. 253, p. 1–21.

Petrunkevitch, A.I., 1913, A monograph of the terrestrial Palaeozoic Arachnida of North America: Transactions of the Connecticut Academy of Arts and Sciences, v. 18, p. 1–137.

Petrunkevitch, A.I., 1945, Palaeozoic Arachnida. An inquiry into their evolutionary trends: Scientific Papers, Illinois State Museum, v. 3, no. 2, p. 1–76.

Petrunkevitch, A. I., 1949, A study of Palaeozoic Arachnida: Transactions of the Connecticut Academy of Arts and Sciences, v. 37, p. 69–315.

Platt, B.F., Hasiotis, S.T., and Hirmas, D.R., 2010, Use of low-cost multistripe laser triangulation (MLT) scanning technology for three-dimensional, quantitative paleoichnological and neoichnological studies: Journal of Sedimentary Research, v. 80, p. 590–610.

Pocock, R.I., 1911. A monograph of the terrestrial Carboniferous Arachnida of Great Britain: Monographs of the Palaeontographical Society, v. 64, p. 1–84.

Poschmann, M., and Dunlop, J.A., 2011, Trigonotarbid arachnids from the Lower Devonian (Siegenian) of Bürdenbach (Lahrbach Valley, Westerwald area, Rhenish Slate Mountains, Germany): Paläontologische Zeitschrift, v. 85, p. 433–447.

Pruvost, P., 1912, Note sur les Araignées du terrain houiller du Nord de la France: Annales de la Société Géologique du Nord, v. 41, p. 85–100.

Rössler, R., 1998, Arachniden-Neufunde im mitteleuropäischen Unterkarbon bis Perm—Beitrag zur Revision der Familie Aphantomartidae Petrunkevitch 1945 (Arachnida, Trigonotarbida): Paläontologische Zeitschrift, v. 72, p. 67–88.

Rößler, R., and Dunlop, J.A., 1997, Redescription of the largest trigonotarbid arachnid—*Kreischeria wiedei* Geinitz 1882 from the upper Carboniferous of Zwickau, Germany: Paläontologische Zeitschrift, v. 71, no. 3–4, p. 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, v. 77, p. 417–427.

Scudder, S.H., 1884, A contribution to our knowledge of Paleozoic Arachnida: Proceedings of the American Academy of Arts and Sciences, v. 20, p. 13–22.

Selden, P.A., 2016, Land Animals, Origins of: Encyclopedia of Evolutionary Biology, v. 2, p. 288–295. https://doi.org/10.1016/B978-0-12-800049-6.00273-0.

Selden, P.A., and Nudds, J., 2008, Fossil Ecosystems of North America: A Guide to the Sites and their Extraordinary Biotas: Chicago, CRC Press, 106 p.

Selden, P.A. and Romano, M., 1983, First Palaeozoic arachnid from Iberia: *Aphantomartus areolatus* Pocock (basal Stephanian; Prov. León, NW Spain), with remarks on aphantomartid taxonomy: Boletìn del Instituto Geológico y Minero de España, v. 94, p. 106–112.

Shultz, J.W., 2007, A phylogenetic analysis of the arachnid orders based on morphological characters: Zoological Journal of the Linnean Society v. 150, p. 221–265.

Simon, R., 1971, Neue Arthropodenfunde aus dem Stephan der Halleschen Mulde: Bericht der Deutschen Gessellschaft für Geologische Wissenschaft, Reihe A: Geologie/Paläontologie, v. 16, p. 53–62.

Sternberg, K., 1825, Versuch einer Geognostisch-botanischen Darstellung der Flora der Vorwelt. Leipzig and Prague, Kommission im Deutschen Museum, v. 1, pt. 4, p. 1–4.

Størmer, L., 1970, Arthropods from the Lower Devonian (lower Emsian) of Alken an der Mosel, Germany. Part 1: Arachnida. Senckenbergiana Lethaea, v. 51, p. 335–369.

Tri-State Committee on Correlation of the Pennsylvanian System in the Illinois Basin, 2001, Toward a more uniform stratigraphic nomenclature for rock units (formations and groups) of the Pennsylvanian System in the Illinois Basin: Illinois Basin Consortium Study 5, Joint publication of the Illinois State Geological Survey, Indiana Geological Survey, and Kentucky Geological Survey, 26 p.

Woodward, H., 1878, Discovery of the remains of a fossil crab (Decapoda-Bracyura) in the Coal Measures of the environs of Mons, Belgium: Geological Magazine, n. ser., Decade 2, v. 5, p. 433–436.

Wright, C.R., 1975, Environments within a typical Pennsylvanian cyclothem, *in* McKee, E.D., and Crosby, E.J., Paleotectonic investigations of the Pennsylvanian System in the United States, part II: interpretive summary and special features of the Pennsylvanian System: US Geological Survey Professional Paper, v. 853, p. 73–84.

Wright, D.F., and Selden, P.A., 2011, A trigonotarbid arachnid from the Pennsylvanian of Kansas: Journal of Paleontology, v. 85, p. 871–876.

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