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Source: Paleontological Contributions, 2014(9) : 1-6

Published By: The Paleontological Institute at The University of Kansas

URL: https://doi.org/10.17161/PC.1808.14824

Paleontological Contributions

July 25, 2014 Number 9

A TRIGONOTARBID ARACHNID FROM THE PENNSYLVANIAN ASTRASADO FORMATION OF THE KINNEY BRICK QUARRY, NEW MEXICO

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Abstract.—A new eophrynid trigonotarbid (Arachnida: Trigonotarbida: Eophrynidae) from the Pennsylvanian (Kasimovian) Astrasado Formation of the Kinney Brick Quarry, New Mexico is described. This fossil – the first arachnid to be recorded from the Astrasado Formation – is preserved primarily as a dorsal opisthosoma. *Pleophrynus hawesi* sp. nov. diagnostically preserves evidence for three pairs of posterior opisthosomal spines rather than the two usually seen in other eophrynids. A comparison of opisthosomal tuberculation patterns among the best known eophrynid species is included. At ca. 304.0–306.5 Ma, our new taxon represents one of the youngest records of Eophrynidae, while the Kinney Brick Quarry is only the twelfth site in North America to yield trigonotarbid arachnids; compared to more than 60 such localities in Europe.

INTRODUCTION

Trigonotarbids are an extinct order of spider-like arachnids which have been recorded from the late Silurian through to the early Permian (ca. 419–290 Ma). For a recent overview of their geographical and stratigraphical distribution see Dunlop & Rößler (2013). Trigonotarbid fossils can be recognized by having a dorsal opisthosoma in which the tergites are divided longitudinally into median and lateral plates. This feature they share with some members of the possibly related arachnid order Ricinulei, but in ricinuleids there is further fusion of tergites adjacent to one another such that it is fairly easy to distinguish a trigonotarbid from a fossil ricinuleid. Additionally, some trigonotarbids, including the one described here, are further characterized by having heavily armored cuticle, ornamented on the dorsal surface of the opisthosoma with pustules or tubercles. Some genera also bear short spines projecting backwards from the opisthosomal posterior margin.

Trigonotarbids have been recorded most frequently from the Pennsylvanian Coal Measures of Europe and North America. There is, however, something of a bias towards European localities, particularly regions historically associated with coal mining such as the British Midlands, northern France/southern Belgium, the German Saarland, Bohemia in the Czech Republic, and Silesia in Poland. Of the 77 trigonotarbid-yielding localities recorded by Dunlop and Rößler (2013) sixty-six are European (including Russia), ten are North American and one is from South America (Argentina). Note that four sites from the Lower Devonian of Germany can be added to this list (M. Poschmann, pers. comm.) and that one American locality – recorded in a conference abstract (Easterday, 2001) – was also overlooked here. The American localities, together with their constituent families and genera, are summarized here in Table 1. With three genera in three families, the famous Mazon Creek site in Illinois is the most productive of the North American Coal Measures localities. Given the relative rarity of Trigonotarbida in the USA, any new fossil and/or locality represents a notable discovery. Here, we describe a new trigonotarbid from the Pennsylvanian (Kasimovian) Astrasado Formation at Kinney Brick Quarry, New Mexico. This locality is an important window into the Late Paleozoic non-marine biota of North America (Lucas & others, 2011). To the best of our knowledge, this discovery represents the first fossil arachnid from the Kinney Brick Quarry and the first trigonotarbid for New Mexico in general. Although preserved primarily from an isolated dorsal opisthosoma, its novel pattern of spines and tubercles confirms that it belongs to a new species of the genus *Pleophrynus* Petrunkevitch, 1945 in the family Eophrynidae.

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Table 1. Overview of the trigonotarbid genera found to date in North America (USA and Canada). The eleven localities which have so far yielded trigonotarbids are arranged here from oldest (below) to youngest (above). *In some features, Shear's (2000) genus *Gigantocharinus* resembles an aphantomartid; see remarks in Poschmann & Dunlop (2010).

No.	Locality	Family	Genus	References
1	Lawrence, KS	Anthracomartidae	*Anthracomartus*	Wright & Selden (2011)
2	Kinney Brick Quarry, NM	Eophrynidae	*Pleophrynus*	this study
3	Pawtucket, RI	unknown	*nomen dubium*	Scudder (1893); Rößler (1998)
4	Mazon Creek, IL	Aphantomartidae, Eophrynidae, Lissomartidae	*Aphantomartus, Pleophrynus, Lissomartus*	Scudder (1884); Petrunkevitch (1913, 1945); Dunlop (1995); Rößler (1998)
5	7-11 Mine, OH	Aphantomartidae, Eophrynidae	*Aphantomartus, Pleophrynus*	Easterday (2001)
6	Cotton Hill, WV	unknown	*Areomartus*	Petrunkevitch (1913); Dunlop (2010)
7	Fern Ledges, Saint John, NB	Anthracomartidae	*nomen dubium*	Matthew (1895); Dunlop & Miller (2007)
8	Joggins Fossil Cliffs, NS	Anthracomartidae	*Anthracomartus*	Petrunkevitch (1913)
9	Fayetteville, AK	Anthracomartidae	*Anthracomartus*	Scudder (1884); Petrunkevitch (1913)
10	Alleghany Tunnel, VA	Eophrynidae	*Pocononia*	Ewing (1930); Dunlop (1996)
11	Red Hill, PA	Palaeocharinidae*	*Gigantocharinus*	Shear (2000)
12	Gilboa, NY	Palaeocharinidae	*Aculeatarbus, Gelasinotarbus, Gilboarachne*	Shear & others (1987)

MATERIAL AND METHODS

The new trigonotarbid was discovered in the spring of 2013 by Bill Hawes and other workers at the Kinney Brick Quarry. It is deposited in the Museum of the University of Kansas, Lawrence, USA under the repository number KUMIP 340491. The fossil (Figs 1–2) is preserved with a certain degree of three-dimensional positive relief as dark cuticle, with a red–brown color under alcohol, contrasting against the lighter shale matrix. It consists of a largely complete dorsal opisthosoma, together with some fragments of posterior legs. The anterior tergites are slightly obscured by irregularities in the matrix, but it was not possible to prepare the fossil further. A thin crack runs transversely across the trigonotarbid, but does not disrupt its morphology. The material consists of a single slab (ca. 8 × 9 cm), without a counterpart, with the trigonotarbid preserved adjacent to a fairly large specimen of the bivalve mollusk *Dunbarella*. The specimen was photographed under a combination of 70% alcohol and low-angle lighting using a Canon Eos 400D with a ×1 macro lens. It was drawn on a Leica MZ12 stereomicroscope with a *camera lucida* attachment. All measurements given in the description are in millimeters.

A detailed account of the geological setting and dating of the Kinney Brick Quarry can be found in Kues and Lucas (1992), updated in Lucas and others (2011), and references therein. In overview, the Kinney Brick Quarry is an actively mined brick-clay quarry situated south east of Tijeras, New Mexico, USA within the Manzanita Mountains; see Lucas and others (2011, text-fig. 1) for a map. The locality belongs to the Astrasado Formation – sometimes referred to as the Wild Cow Formation in older literature – and was previously thought to date to the Virgilian stage (ca. 299–305 Ma) of the North American stratigraphic subdivisions. Drawing largely on marine conodonts, Lucas and others (2011) subsequently placed both the marine and non-marine elements at a slightly older (ca. 304.0–306.5 Ma) Kasimovian (=Missourian) age. The specimen comes from the *Dunbarella* layer whereby the Kinney Brick Quarry is thought to represent deposits lain down in an estuarine environment fed by a river system (Feldmann & others, 1992). As well as marine elements such as conodonts, mollusks, brachiopods and crustaceans, this Konservat-Lagerstätte hosts a diverse fauna and flora of terrestrial and/or brackish-water origin. Eurypterids from this site were described by Kues (1985), while Shear, Hannibal, and Kukalová-Peck (1992) reviewed the terrestrial arthropods which, at that time, consisted of insects and myriapods only. Here, we add an arachnid to the fauna.

SYSTEMATIC PALEONTOLOGY

Order TRIGONOTARBIDA Petrunkevitch, 1949
Family EOPHRYNIDAE Karsch, 1882

Diagnosis.— Medium to 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 median and lateral plates. Opisthosoma bears at least two pairs of terminal spines originating from the lateral plates of tergites 8 and 9, and in well preserved material 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 (after Dunlop & Garwood, 2014).

Genus PLEOPHRYNUS Petrunkevitch, 1945

Diagnosis.—Eophrynids in which the opisthosomal tergites are ornamented with numerous small tubercles, plus a discrete pattern of larger tubercles in which the median tergites have four tubercles (two median, two lateral) and each lateral tergite has only a single tubercle; tergite 9 transversely divided. Ventrally (where known) with a pair of ridges along the midline of the opisthosoma (emended from Dunlop, 1994).

Type species.—*Pleophrynus ensifer* Petrunkevitch, 1945 [a junior synonym of *Kreischeria verrucosa* Pocock, 1911].

Figure 1. *Pleophrynus hawesi*, holotype and only known specimen, KUMIP 340491. Dorsal opisthosoma together with limb fragments, photographed under 70% alcohol with low-angle lighting. From the Pennsylvanian (Missourian) Astrasado Formation of the Kinney Brick Quarry, New Mexico, USA. Scale bar equals 5 mm.

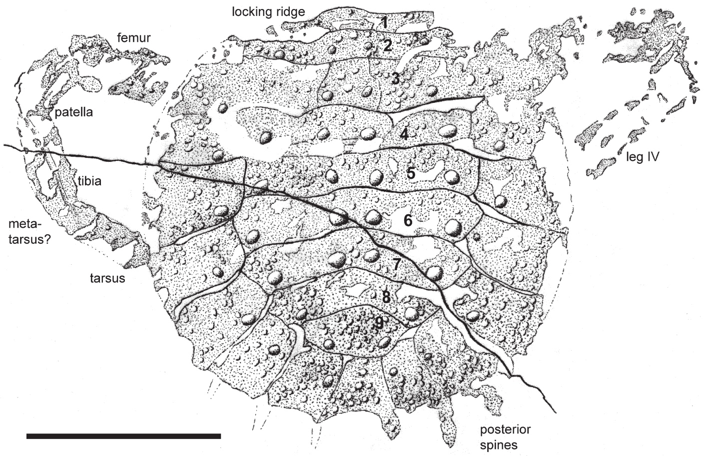

Figure 2. Interpretative *camera lucida* drawing of the specimen shown in Fig. 1. Scale bar equals 5 mm.

PLEOPHRYNUS HAWESI, new species

Figures 1–3

Etymology.—In honor of the collector, Bill Hawes.

Material.—Holotype and only known specimen KUMIP 340491, deposited in the University of Kansas Natural History Museum. From the *Dunbarella* Bed (layer 4 in Kues & Lucas, 1992, fig. 5) in Kinney Brick Quarry, south-east of Tijeras, New Mexico, leg. W. Hawes, spring 2013. Astrasado Formation. Pennsylvanian, Kasimovian (=Missourian).

Diagnosis.—*Pleophrynus* species in which the opisthosoma is almost circular in outline and bears three pairs of posterior opisthosomal spines.

Description.—Dorsal opisthosoma, almost circular in outline, slightly wider than long; length 10.1, maximum width 10.8. Nine opisthosomal tergites visible. Tergite 1 reduced in size, short (length 0.5) and modified into a locking ridge, slightly procurved across the midline. Tergites 2–9 wider, all divided into median and lateral plates (obscured in tergite 2). Most tergites again express slight procurvature across the midline, with the exception of tergite 3 which has a straighter anterior margin. Lengths of individual tergites on the midline 2, 0.8; 3, 1.2; 4, 1.3; 5, 0.8; 6, 1.1; 7, 1.0; 8, 1.0 and 9, 2.7. Tergites with a general background ornament of small, circular tubercles, diameter ca. 0.05–0.07, plus a discrete pattern of larger rounded tubercles, diameters from 0.2–0.6. All tubercles preserved in positive relief. Tergite 1 (the locking ridge) without large tubercles. Median tergites 2–7 with two pairs of tubercles; one pair close to the midline, one pair laterally. Tergites 8–9 lack median tubercles, retaining lateral tubercles only. Lateral plates 3–9 ornamented with single, large tubercle; presence on 2 equivocal due to poor lateral preservation. Median plate of tergite 9 transversely divided; a sulcus running between the antero-median corners of the lateral plates associated with this tergite. Faint lines runs mesal to each lateral tubercle on tergite 9, but do not appear to demarcate separate sclerites. Posterior opisthosomal margin preserves evidence for three pairs of posterior spines (lengths ca. 0.8–1.2); those on left side hinted at by depressions in the matrix only. Spines originate (a) from junction between the median and lateral plates of tergite 9, (b) from the junction between tergites 8 and 9 and (c) from the midpart of the margin of tergite 8.

Incomplete legs preserved on both left and right sides; article width varies between ca. 1.5 proximally to 1.0 distally. Position of the preserved legs in the limb series uncertain, but given their proximity to the opisthosoma could represent the posteriormost leg IV. Four articles (femur, patella, tibia and metatarsus?) identifiable on left leg with measurable lengths of ca. 2.9, 2.0, 3.1 and 1.7. At least proximal leg articles with ornament of small tubercles similar to the tergites. Putative tibia bears an elongate groove along its length. Carapace, pedipalps, sternal region and ventral opisthosoma all equivocal.

Remarks.—The new fossil belongs to the family Eophrynidae. This is evident from, among other characters (see Dunlop & Garwood, 2014), the heavily ornamented dorsal opisthosoma with both a pattern of discrete dorsal tubercles and a series of posterior spines. Eight eophrynid genera are currently recognized in the literature and the known patterns of large opisthosomal dorsal tubercles are summarized for the most complete species in Fig. 3. Our new fossil is similar in size and proportions to the German species *Eophrynus udus* Brauckmann, Koch, & Kemper, 1985 which also has an almost circular opisthosoma. However, our fossil can be excluded from *Eophrynus* Woodward, 1871 because both of its constituent species have four large tubercles along the midline of the median tergites (Fig. 3) rather than the two seen in the new specimen. *Eophrynus* also invariably expresses large median tubercles on tergite 8. These are absent in our material.

Of the other known eophrynid genera, we can also exclude the American genus *Pocononia* Petrunkevitch, 1953 which appears to have a fairly uniform, pustulate dorsal ornament and no clear pattern of discrete tuberculation, although any ornament on the lateral tergites is not well preserved and given these uncertainties we omit the taxon from Fig. 3; see also Ewing (1930), Petrunkvitch (1953) and Dunlop (1996). It does not fit with the Polish/Czech genus *Stenotrogulus* Frič, 1904 nor the German *Somaspidion* Jux, 1982; the latter is based on an isolated opisthosoma. In both of these genera the tubercles on the lateral sides of the median tergites are noticeably larger than the

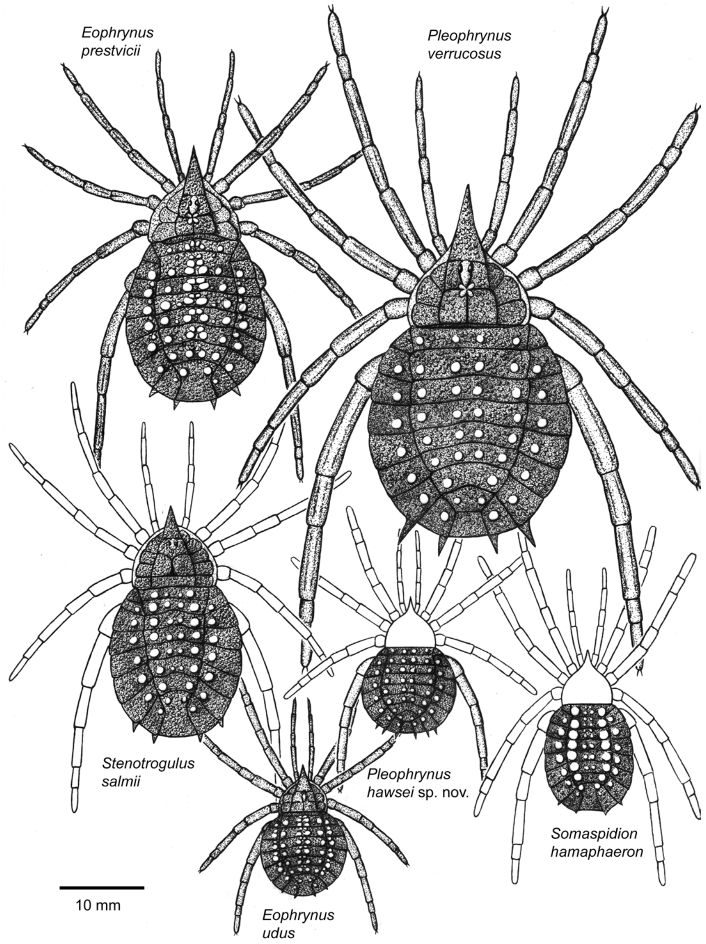

Figure 3. Schematic comparison of dorsal ornamentation patterns – in particular the distribution of large tubercles on the tergites – in those eophrynids which are known from well preserved dorsal surfaces. Reconstructed regions lack shading. Our new fossil from the Kinney Brick Quarry is evidently closest to the *Pleophrynus* condition. All to scale.

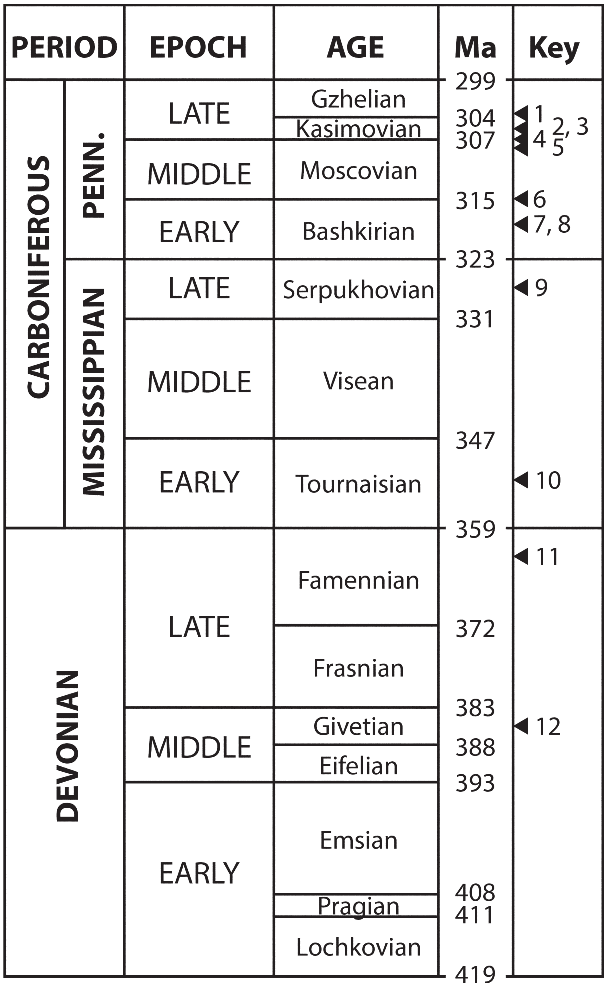

Figure 4. Geologic column of the Devonian and Carboniferous showing the stratigraphic occurrences of North American localities with records of trigonotarbids. See Table 1 for key to localities. Geologic column after Walker & others (2012).

tubercle pair in the middle (Fig. 3). The three Czech genera *Petrovicia* Frič, 1904, *Planomartus* Petrunkevitch, 1953, and *Nyranytarbus* Harvey & Selden, 1995 are problematic. All are based on compressed shale material which was both poorly described (Frič, 1904; Petrunkevitch, 1953) and which appear, at least in *Petrovicia and Nyranytarbus,* to derive in part from material preserved primarily in ventral view. Dorsal tuberculation patterns of these genera are therefore largely equivocal, making it difficult to compare them meaningfully with better preserved eophrynids from which the dorsal surface is known (i.e. those in Fig. 3). From the published photographs (Petrunkevitch, 1953, figs 173–175), *Planomartus* seems to be a composite taxon based on fossils belonging to two different and unrelated families: Anthracomartidae and Aphantomartidae. All three Czech genera may eventually have to be treated as *nomina dubia*.

Our new fossil shows the greatest affinity with *Pleophrynus*. The type species is *Pleophrynus ensifer* Petrunkevitch, 1945 from Mazon Creek, Illinois, which was later synonymized with a British species, *Kreischeria verrucosa* Pocock, 1911, to yield the current combination *Pleophrynus verrucosus* (Pocock, 1911); see Dunlop (1994) for details. Like our fossil, *Pleophrynus* specimens have opisthosomal tergites ornamented with numerous small tubercles, plus a discrete pattern of larger tubercles (Fig. 3) in which the median tergites have four tubercles (two median, two lateral) and each lateral tergite has only a single tubercle. As in our fossil, tergite 8 in *Pleophrynus* is usually, but possibly not invariably, without median tubercles. This is certainly true for the holotype of *P. ensifer* (see Petrunkevitch, 1945, fig. 25, Pl. I(1)). However, Dunlop (1994, fig. 4) recognized otherwise similar-looking morphotypes within the British fauna both with and without this feature, and speculated that the presence/absence of median tubercles on median tergite 8 could be sexually dimorphic rather than explicitly taxonomic. Further well-preserved material may be needed to explore this hypothesis further.

Based on its opisthosomal tuberculation, we are confident in placing the Kinney Brick Quarry trigonotarbid in *Pleophrynus*. Two features of the fossil are particularly interesting and merit its assignment to a new species within this genus. First, the opisthosoma is slightly wider than long, whereas in most eophrynids (Fig. 3) and, indeed, most trigonotarbids, the opisthosoma is usually longer than wider. Although tectonic deformation can distort length–width ratios and we only have one specimen rather than a range of material which could provide data on possible taphonomic effects, it is worth noting that the adjacent *Dunbarella* specimen shows no evidence of distortion. Thus the preserved proportions may indeed reflect the arachnid's appearance in life. The other point of note is that the new fossil preserves three pairs of posterior opisthosomal spines, whereas other eophrynids discovered to date have only two pairs (Fig. 3). Note that the specimen is quite small compared to some of the better known species which hints at the possibility that it may be immature.

DISCUSSION

Although a formal cladistic analysis of the trigonotarbids is lacking, eophrynids are probably a derived group within the order since they express a suite of apomorphic characters, such as their heavily armored bodies. The prominent spines and tubercles were presumably defensive adaptations which increased handling time for predators. A similar morphology can be seen in certain tropical orb-weaving spiders such as *Gasteracantha* which have numerous large spines around the edge of their hardened dorsal opisthosoma. There is evidence that at least wasps are deterred by this structure, since their larvae cannot develop here (Elgar & Jebb, 1999), but it is less certain to what extent other predators (such as birds) are affected. Dunlop and Garwood (2014) also drew ecological comparisons with modern laniatorid harvestmen, unrelated but analogous arachnids, some of which also have similarly tuberculate and spiny bodies. As shown in Fig. 4 and Table 1, the Kinney Brick Quarry specimen represents only the fourth record of Eophrynidae in North America; the others coming from the Pocono Shales of the Alleghany Tunnel, Virginia (Ewing, 1930; Dunlop, 1996) the Francis Creek Shales of Mazon Creek, Illinois (Petrunkevitch, 1945) and from eastern Ohio (Easterday, 2001). Our fossil is also one of the youngest examples of this family recorded so far. In two conference abstracts, Eskov (1998, 1999) mentioned another Kasimovian eophrynid from the Tunguska Basin of Russia, but this material has not yet been formally described. By contrast, most eophrynids are Moscovian in age; equivalent to the Westphalian of more traditional stratigraphic schemes.

Anatomically, the new material preserves some interesting features in addition to the length–width ratio and three posterior spine pairs alluded to above. Historically, interpreting segment count in the eophrynid opisthosoma proved challenging; see Dunlop and Garwood (2014) for a discussion. For example, Petrunkvitch (1945, text-fig. 30) proposed two divergent patterns of segmentation for the obviously similar-looking and closely related *Eophrynus* and *Pleophrynus*. Although the narrow tergite 1 (the locking ridge) was at one stage thought to be absent in eophrynids (e.g. Dunlop, 1994), our new fossil confirms that this element is indeed present in this family. Furthermore, in most trigonotarbids the second and third tergites are normally fused together into a so-called diplotergite. As in our fossil, eophrynids appear to have these elements as separate tergites. It remains unclear whether this is the plesiomorphic state. Putatively basal trigonotarbids, e.g. palaeocharinids and archaeomartids (see Poschmann & Dunlop, 2010), have a diplotergite and, should loss of the diplotergite prove to be a reversal, it may become a potential diagnostic character for Eophrynidae. Finally, the ninth tergite in our material preserves a transverse division defining an anterior and posterior sclerite (Fig. 2). This is an unusual character for trigonotarbids, otherwise only seen in another family: Anthracomartidae (see e.g., Poschmann & Dunlop, 2010). A divided tergite 9 was, however, picked up in *Pleophrynus,* both by Petrunkevitch (1945, fig. 25) and Dunlop (1994, figs 3–4). The presence of this feature in the Kinney Brick Quarry specimen thus confirms that this character can occur in eophrynids too, and further supports our fossil's referral to *Pleophrynus*. Indeed, a transverse division of tergite 9 may prove to be a good diagnostic character for this genus (see Systematics) as it is not seen in the otherwise well-preserved genera, e.g. *Eophrynus*, *Stenotrogulus* and *Somaspidion* (see Fig. 3), with a clear pattern of dorsal segmentation.

In conclusion, the Kinney Brick Quarry is now the twelfth fossil site in North America (Table 1) from which trigonotarbids have been formally described. It should be noted that at least three of these simply record the presence of the order Trigonotarbida. These records are either *incertae sedis* (Dunlop, 2010: Cotton Hill), or so poorly preserved as to effectively render them *nomina dubia* (Rößler, 1998: Pawtucket; Dunlop & Miller, 2007: Saint John). This leaves nine localities in North America – two Devonian, one Mississippian and six Pennsylvanian – with reasonably well-preserved and identifiable trigonotarbids. Compared to the European Coal Measures, trigonotarbids in the Pennsylvanian of America thus remain quite rare, although we are aware of further material, including specimens in both public and private collections from new localities (JAD, unpublished obs.), which will surely offer a better picture of Laurasian trigonotarbid diversity in the coming years.

ACKNOWLEDGEMENTS

We thank Bill Shear and Cary Easterday for literature and helpful comments, as well as Markus Poschmann and Russell Garwood for their reviews of the manuscript.

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