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NEW SPIDERS (ARANEAE: MESOTHELAE), FROM THE CARBONIFEROUS OF NEW MEXICO AND ENGLAND, AND A REVIEW OF PALEOZOIC ARANEAE

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Abstract—The fossil record of Paleozoic spiders is sparse. Fifty-two specimens have, at one time or another, been attributed to Araneae, but, herein, the number actually belonging to that arachnid order is reduced to 24. Here, a new specimen of a fossil spider from the Kinney Brick Quarry, New Mexico, is described as *Protolycosa suazoi* **n. sp.**, in the family Arthrolycosidae Harger, 1874. The opportunity is also taken to describe two spider carapaces from the Carboniferous of Britain as *Arthrolycosa* sp., and to review all known Paleozoic spiders. Revisions are presented of species in the Arthrolycosidae: one specimen from the Carboniferous (Moscovian) of Mazon Creek, Illinois, formerly described as *Arthrolycosa antiqua* Harger, 1874, is redescribed as *Palaeothele onoi* **n. sp.**, and placed in the new family Palaeothelidae **n. fam.**; *Arthrolycosa danielsi* Petrunkevitch, 1913, also from Mazon Creek, is referred to *Protolycosa danielsi* **n. comb.** Also, specimens from the Carboniferous (lower Moscovian) of Rakovník, Czech Republic, *Arthrolycosa beecheri* Fritsch, 1904, *A. fortis* Fritsch, 1904, and *Geralycosa fricii* Kušta, 1889 are synonymized under *G. fricii* **n. syn.** and placed in Arthromygalidae Petrunkevitch, 1923, which is shown to be a senior synonym of Parvithelidae Wunderlich, 2017 **n. syn.**; *Eolycosa lorenzi* Kušta 1885 and *Scudderia carbonaria* Kušta 1889 are synonymized under *E. lorenzi* **n. syn.** and placed in Mesothelae *incertae sedis*; *Rakovnicia antiqua* Kušta, 1889 is referred to Tetrapulmonata *incertae sedis*; *Dinopilio gigas* Fritsch, 1904 is considered to be Arachnida *incertae sedis*; and *Eotarbus litoralis* Kušta, 1888 is unidentifiable. From the Carboniferous (upper Moscovian) of Nýřany, Czech Republic: *Eopholcus pedatus* Fritsch, 1904 is synonymized with *Pyritaranea tubifera* Fritsch, 1899 **n. syn.** and referred to Araneae *incertae sedis*, together with *Palaranea borassifoliae* Frič, 1864; *Pleurolycosa prolifera* (Fritsch, 1899) is considered Arthropoda *incertae sedis*. *Arthrolycosa tarda* Fritsch, 1912, from the Carboniferous (Gzhelian) of the Czech Republic, is referred to Arachnida *incertae sedis. Eocteniza silvicola* Pocock, 1911 and *Protocteniza britannica* Petrunkevitch, 1949, from the Carboniferous (Moscovian) of Coseley, UK, are referred to Tetrapulmonata *incertae sedis*.

INTRODUCTION

The fossil record of spiders from the Paleozoic Era is sparse, with about 50 specimens formerly referred to Araneae, of which around half belong to that order (Table 1). The morphology of those which are sufficiently well preserved indicates that they belong to the suborder Mesothelae Pocock, 1892. Here, a new specimen of Carboniferous (Kasimovian) age from the Kinney Brick Quarry, New Mexico, is described, as well as two carapaces from the Carboniferous (Westphalian D, Moscovian) of Writhlington, Avon, UK.

Over the last few decades, all of the known and available Paleozoic spiders have been studied. Most of these are held in major museums in the USA, UK, and Czech Republic, as well as in France and Moscow. One important specimen, *Protolycosa anthracophila* Römer, 1865, was found to be lost when Petrunkevitch (1953) attempted to find it in Wrocław, Poland. However, this specimen was well described by Roemer (1866b), and numerous researchers have studied and figured it since then, so its morphology is quite well known. Similarly, *Arthrolycosa tarda* Frič, 1912, from the Czech Republic, has been lost. In this paper, all of the known Paleozoic spiders are reviewed, concentrating on those that have not been redescribed recently, and their identity as spiders is discussed, as well as how they fit into current hypotheses of early spider evolution.

Since this restudy of the Paleozoic spiders began in the 1990s, several results have been published in the interim. Two supposed spiders from the Devonian, *Palaeocteniza crassipes* Hirst, 1923, from the Rhynie Chert of Aberdeenshire, Scotland, and *Archaeometa*? *devonica* Størmer, 1976 from Alken an der Mosel, Germany, were removed from the order by Selden et al. (1991). The first undoubted mesothele spider was described from the Stephanian of Montceau-les-Mines, France (Selden, 1996a,b, 2000). The supposed giant spider *Megarachne servinei* Hünicken, 1980, from the uppermost Carboniferous of Argentina, was shown to be a large eurypterid by Selden et al. (2005). *Attercopus fimbriunguis* (Shear, Selden and Rolfe 1987), from the Devonian of New York, USA, and *Permarachne novokshonovi* Eskov and Selden, 2005 from the Permian of Russia, were shown to belong to a new order of arachnids, the Uraraneida, by Selden et al. (2008). The supposed araneomorph spiders *Archaeometa nephilina* Pocock, 1911 and *Arachnometa tuberculata* Petrunkevitch, 1949, from the Westphalian of Coseley, England, were determined by Selden et al. (2016) to be Opiliones. Some new spiders were described from Paleozoic strata over this time, preserved only as carapaces. *Arthrolycosa* Harger, 1874 sp. was reported from the upper Permian of Russia by Eskov and Selden (2005); it is the youngest arthrolycosid and the only Permian spider known (Dunlop et al. 2020). Two *Arthrolycosa* sp. carapaces were described in Selden et al. (2014), from the Carboniferous (Kasimovian-Gzhelian) of Chunya, Russia, and the Carboniferous (Bashkirian) of the Donets Basin, Ukraine. The latter occurrence is the oldest fossil spider known.

MATERIAL AND METHODS

The Kinney Brick Quarry Specimen

The new fossil specimen described here was discovered during New Mexico Museum of Natural History and Science (NMMNH) excavations at the Kinney Brick Quarry by Thomas L. Suazo in 2014. It was brought to the author's attention by Amanda Cantrell, formerly of NMMNH, and loaned for study through the kindness of Spencer Lucas, Curator of Paleontology at the NMMNH. The fossil consists of part and counterpart on a gray mudstone with abundant specimens of *Dunbarella*. The

TABLE 1. List of Paleozoic specimens attributed, at some time, to Araneae, with their original name, that used in the most recent version of the World Spider Catalog (Dunlop et al., 2020), and that used herein, together with specimen numbers, type status, repository, locality, age, and identification proposed herein. See the text for more details. Note that the list is unlikely to be exhaustive; other arachnids, such as trigonotarbids, are commonly called spiders by non-specialists.

#	Original name	Author, date/original description	Type	Specimen #	Repository	Locality	Stratigraphy	Other references/notes	Name in Dunlop et al. (2020)	Name in this publication	Higher taxon
1	*Eothele montceauensis*	Selden, 1996	holotype	51961, 51962	Autun, France	Montceau-les-Mines, France	C (Gzhelian)	Selden (2000)	*Palaeothele montceauensis*	*Palaeothele montceauensis*	Palaeothelidae n. fam.
2	*Eothele montceauensis*	Selden, 1996	figured	In.62050	BMNH	Montceau-les-Mines, France	C (Gzhelian)	Selden (2000)	*Palaeothele montceauensis*	*Palaeothele montceauensis*	Palaeothelidae n. fam.
3	*Arthrolycosa antiqua*	Harger, 1874	figured	IP.000162	YPM	Mazon Creek, IL	C (Moscovian)	Petrunkevitch (1913)	*Arthrolycosa antiqua*	*Palaeothele onoi* n. sp.	Palaeothelidae n. fam.
4	*Arthrolycosa antiqua*	Harger, 1874	figured	IP.000163	YPM	Mazon Creek, IL	C (Moscovian)	Petrunkevitch (1913)	*Arthrolycosa antiqua*	*Arthrolycosa antiqua*	Arthrolycosidae
5	*Arthrolycosa antiqua*	Harger, 1874	holotype	IP.000161	YPM	Mazon Creek, IL	C (Moscovian)	Petrunkevitch (1913)	*Arthrolycosa antiqua*	*Arthrolycosa antiqua*	Arthrolycosidae
6	*Arthrolycosa* sp.	Eskov & Selden (2005)	figured	2.78775510204082	Moscow, Russia	Kityak river, Russia	P (Guadalupian)		*Arthrolycosa* sp.	*Arthrolycosa* sp.	Arthrolycosidae
7	*Arthrolycosa* sp.	Selden *et al*. (2014)	figured	3115/294	Moscow, Russia	Chunya, Tunguska Basin	C (Moscovian)		*Arthrolycosa* sp.	*Arthrolycosa* sp.	Arthrolycosidae
8	*Arthrolycosa* sp.	Selden *et al*. (2014)	figured	5431/9	Moscow, Russia	Donets Basin, Russia	C (upper Bashkirian)		*Arthrolycosa* sp.	*Arthrolycosa* sp.	Arthrolycosidae
9	*Arthrolycosa* sp.	this paper	figured	LL11002	MM	Writhlington, Somerset, England	C (Moscovian)			*Arthrolycosa* sp.	Arthrolycosidae
10	*Arthrolycosa* sp.	this paper	figured	LL11001a,b	MM	Writhlington, Somerset, England	C (Moscovian)			*Arthrolycosa* sp.	Arthrolycosidae
11	*Protolycosa anthracophila*	Römer, 1865	holotype	–	Wrocław, Poland	Silesia, Poland	C (upper Bashkirian)	specimen lost	*Protolycosa anthracophila*	*Protolycosa anthracophila*	Arthrolycosidae
12	*Protolycosa cebennensis*	Laurentiaux-Vieira & Laurentiaux, 1963	holotype	MGL 4261	MHNL	Cévennes, France	C (lower Moscovian)		*Protolycosa cebennensis*	*Protolycosa cebennensis*	Arthrolycosidae
13	*Protolycosa suazoi* n. sp.	this paper	holotype	P-71523	NMMNH	Kinney Brick Quarry, NM	C (Kasimovian)			*Protolycosa suazoi* n. sp.	Arthrolycosidae
14	*Arthrolycosa danielsi*	Petrunkevitch, 1913	holotype	UMMP 7219	UMMP	Mazon Creek, IL	C (Moscovian)	Petrunkevitch (1913)	*Arthrolycosa danielsi*	*Protolycosa danielsi* n. comb.	Arthrolycosidae
15	*Geralycosa fricii*	Kušta, 1889	holotype	CGH 1943, 1945	NMP	Rakovník, Czech Republic	C (lower Moscovian)	Petrunkevitch (1953)	*Geralycosa fritschi*	*Geralycosa fricii*	Arthromygalidae
16	*Arthrolycosa fortis*	Fritsch, 1904	holotype	CGH 1937	NMP	Rakovník, Czech Republic	C (lower Moscovian)	Petrunkevitch (1953)	*Arthromygale fortis*	*Geralycosa fricii*	Arthromygalidae
17	*Arthrolycosa beecheri*	Fritsch, 1904	holotype	CGH 1939	NMP	Rakovník, Czech Republic	C (lower Moscovian)	Petrunkevitch (1953)	*Arthromygale fortis*	*Geralycosa fricii*	Arthromygalidae
18	*Eolycosa lorenzi*	Kušta, 1886	holotype	CGH 1941	NMP	Rakovník, Czech Republic	C (lower Moscovian)	Petrunkevitch (1953)	*Eolycosa lorenzi*	*Eolycosa lorenzi*	Mesothelae *incertae sedis*
19	*Scudderia carbonaria*	Kušta, 1889	holotype	CGH 1933	NMP	Rakovník, Czech Republic	C (lower Moscovian)	Petrunkevitch (1953)	*Kustaria carbonaria*	*Eolycosa lorenzi* n. syn.	Mesothelae *incertae sedis*
20	*Scudderia carbonaria*	Kušta, 1890	figured	CGH 1935	NMP	Rakovník, Czech Republic	C (lower Moscovian)	Petrunkevitch (1953)	*Kustaria carbonaria*	*Eolycosa lorenzi* n. syn.	Mesothelae *incertae sedis*
21	*Pyritaranea tubifera*	Fritsch, 1899	holotype	CGH 3170	NMP	Nýřany, Czech Republic	C (upper Moscovian)	Petrunkevitch (1953)	*Pyritaranea tubifera*	*Pyritaranea tubifera*	Araneae *incertae sedis*
22	*Eopholcus pedatus*	Fritsch, 1904	holotype	CGH 3184	NMP	Nýřany, Czech Republic	C (upper Moscovian)	Petrunkevitch (1953)	*Eopholcus pedatus*	*Pyritaranea tubifera* n. syn.	Araneae *incertae sedis*
23	*Palaranea borassifoliae*	Frič, 1864	holotype	E 3491	NMP	Svinná, Czech Republic	C (upper Moscovian)	Petrunkevitch (1953)	*Palaranea borassifoliae*	*Palaranea borassifoliae*	Araneae *incertae sedis*
24	spider	Selden et al. (2014)	figured	3630/1	Moscow, Russia	Kurai (Kurty), Kazakhstan	P (Asselian)		Araneae *incertae sedis*	Araneae *incertae sedis*	Araneae *incertae sedis*
25	*Eocteniza silvicola*	Pocock, 1911	holotype	In.31245	BMNH	Coseley, England	C (lower Moscovian)	Petrunkevitch (1953)	*Eocteniza silvicola*	*Eocteniza silvicola*	Tetrapulmonata *incertae sedis*
26	*Protocteniza brittanica*	Petrunkevitch, 1949	figured	In.22834	BMNH	Coseley, England	C (lower Moscovian)	Petrunkevitch (1953)	*Protocteniza britannica*	*Eocteniza silvicola* n. comb.	Tetrapulmonata *incertae sedis*
27	*Protocteniza britannica*	Petrunkevitch, 1949	holotype	In.14015	BMNH	Coseley, England	C (lower Moscovian)	Petrunkevitch (1953)	*Protocteniza britannica*	*Protocteniza britannica*	Tetrapulmonata *incertae sedis*
28	*Rakovnicia antiqua*	Kušta, 1885	holotype	CGH 610	NMP	Rakovník, Czech Republic	C (lower Moscovian)	Petrunkevitch (1953)	*Rakovnicia antiqua*	*Rakovnicia antiqua*	Tetrapulmonata *incertae sedis*
29	*Gelasinotarbus? fimbriunguis*	Shear, Selden & Rolfe, 1987	type series	43101 + others	AMNH	Gilboa & South Mountain, NY	D (Givetian)	Selden *et al*. (2008)	*Attercopus fimbriunguis*	*Attercopus fimbriunguis*	Uraraneida
30	*Permarachne novokshonovi*	Eskov & Selden, 2005	holotype	PIN 4909/12	Moscow, Russia	Barda River, Matveyevka, Russia	P (Asselian)	Selden *et al*. (2008)	*Permarachne novokshonovi*	*Permarachne novokshonovi*	Uraraneida
31	*Hemiphrynus hofmanni*	Fritsch, 1899	holotype	Me 54	NMP	Nýřany, Czech Republic	C (upper Moscovian)	Harvey & Selden (1995)	*Nyranytarbus hofmanni*	*Nyranytarbus hofmanni*	Trigonotarbida
32	*Hemiphrynus longipes*	Fritsch, 1899	holotype	Me 47	NMP	Nýřany, Czech Republic	C (upper Moscovian)	Harvey & Selden (1995)	*Nyranytarbus longipes*	*Nyranytarbus longipes*	Trigonotarbida
33	*Palaeocteniza crassipes*	Hirst, 1923	holotype	In 24670	BMNH	Rhynie Chert, Scotland	D (Pragian)	Selden *et al*. (1991)	*Palaeocteniza crassipes*	*Palaeocteniza crassipes*	Trigonotarbida
34	*Arthrolycosa? salticoides*	Fritsch, 1899	holotype	Me 57	NMP	Nýřany, Czech Republic	C (upper Moscovian)	Garwood & Dunlop (2011)	*Anthracomartus carcinoides*	*Anthracomartus carcinoides*	Trigonotarbida
35	*Arthrolycosa carcinoides*	Fritsch, 1899	holotype	Me 49	NMP	Nýřany, Czech Republic	C (upper Moscovian)	Garwood & Dunlop (2011)	*Anthracomartus carcinoides*	*Anthracomartus carcinoides*	Trigonotarbida
36	*Promygale bohemica*	Fritsch, 1895	holotype	M 1030	NMP	Nýřany, Czech Republic	C (upper Moscovian)	Garwood & Dunlop (2011)	*Anthracomartus bohemica*	*Anthracomartus bohemica*	Trigonotarbida
37	*Promygale rotundata*	Fritsch, 1899	holotype	Me 48	NMP	Nýřany, Czech Republic	C (upper Moscovian)	Garwood & Dunlop (2011)	*Anthracomartus carcinoides*	*Anthracomartus carcinoides*	Trigonotarbida
38	*Promygale? elegans*	Frič 1901	holotype	M 867	NMP	Nýřany, Czech Republic	C (upper Moscovian)	Garwood & Dunlop (2011)	*Anthracomartus elegans*	*Anthracomartus elegans*	Trigonotarbida
39	*Archaeometa nephilina*	Pocock, 1911	figured	I.15863	BMNH	Coseley, England	C (lower Moscovian)	Petrunkevitch (1953)	*Archaeometa nephilina*	*Archaeometa nephilina*	Opiliones: Archaeometidae
40	*Archaeometa nephilina*	Pocock, 1911	holotype	In.31259	BMNH	Coseley, England	C (lower Moscovian)	Petrunkevitch (1953)	*Archaeometa nephilina*	*Archaeometa nephilina*	Opiliones: Archaeometidae
41	*Arachnometa tuberculata*	Petrunkevitch, 1949	holotype	I.13917	BMNH	Coseley, England	C (lower Moscovian)	Petrunkevitch (1953)	*Arachnometa tuberculata*	*Arachnometa tuberculata*	Opiliones *incertae sedis*
42	*Dinopilio gigas*	Fritsch, 1904	holotype	CGH 1949	NMP	Rakovník, Czech Republic	C (lower Moscovian)	Petrunkevitch (1953)	*Dinopilio gigas*	*Dinopilio gigas*	Arachnida *incertae sedis*
43	*Arthrolycosa tarda*	Fritsch, 1912	holotype	–	NMP	Krsmol near Altpaka, Czech Republic	C (Gzhelian)	specimen lost	*Arthrolycosa tarda*	*Arthrolycosa tarda*	Arachnida *incertae sedis*
44	*Megarachne servinei*	Hünicken, 1980	holotype	CORD-PZ 2110	Córdoba, Argentina	Bajo de Véliz, Argentina	C (Gzhelian)	Selden *et al*. (2005)	*Megarachne servinei*	*Megarachne servinei*	Eurypterida
45	*Megarachne servinei*	Selden *et al*. (2005)	figured	–	Pollini Collection	Bajo de Véliz, Argentina	C (Gzhelian)	Selden *et al*. (2005)	*Megarachne servinei*	*Megarachne servinei*	Eurypterida
46	spider	Poplin & Heyler (1994, p. 165)	figured	5190/1	Paris, France	Montceau-les-Mines, France	C (Gzhelian)		–	*Alanops*?	Xiphosura
47	*Dinopilio parvus*	Petrunkevitch, 1953	holotype	In.37101	BMNH	Chislet Colliery, England	C (Moscovian)	Petrunkevitch (1953)	*Dinopilio parvus*	*Dinopilio parvus*	Arthropoda *incertae sedis*
48	*Arthrolycosa prolifera*	Fritsch, 1899	holotype	CGH 3176	NMP	Nýřany, Czech Republic	C (upper Moscovian)	Petrunkevitch (1953)	*Pleurolycosa prolifera*	*Pleurolycosa prolifera*	Arthropoda *incertae sedis*
49	spider	Poplin & Heyler (1994, p. 166)	figured	6165	Paris, France	Montceau-les-Mines, France	C (Gzhelian)		–	cycloid crustacean?	Arthropoda *incertae sedis*
50	spider	Perrier & Charbonnier (2014, fig. 4G–H)	figured	095184a,b	Autun, France	Montceau-les-Mines, France	C (Gzhelian)		–	*Autunia conferta*?	Plantae
51	*Archaeometa? devonica*	Størmer, 1976	holotype	SMF 30048	Senckenberg, Germany	Alken an der Mosel, Germany	D (Emsian)	Selden *et al*. (1991)	*Archaeometa? devonica*	*Archaeometa? devonica*	unidentifiable
52	*Eotarbus litoralis*	Kušta, 1888	holotype	lost	NMP	Rakovník, Czech Republic	C (lower Moscovian)	Dunlop (1991)	*Eotarbus litoralis*	*Eotarbus litoralis*	unidentifiable

host rock at the Kinney Brick Quarry belongs to the Tinajas Member of the Atrasado Formation, which has been dated to Carboniferous (Missourian, Kasimovian) in age (see Lucas et al., 2011 for further information). The specimen was studied under ethanol using a Leica M205C stereomicroscope. It was photographed using a Canon EOS 5D Mk II camera and 100 mm macro lens in cross-polarized light, both dry and under ethanol, and also under ethanol with the camera mounted on the microscope. Images were captured using DSLR Assistant software (dslrassistant.com) onto an Apple MacBook Pro computer (apple.com), and manipulated in Affinity Photo (affinity.serif.com). Details of photographic methods can be found in Selden (2014). Drawings were made using Autodesk Graphic (graphic.com) from the photographs, with frequent checking back to the specimen. Measurements were made from the drawings using the analysis tools in Graphic.

The Writhlington Specimens

Fossil arachnids are relatively common at Writhlington Geological Nature Reserve, Avon, England, which is an abandoned coal mine tip that has been preserved for fossil collecting because of the abundant and diverse flora and fauna to be found in the rocks there (Jarzembowski, 1989; Palmer et al., 2010). An unusually large number of phalangiotarbids have been collected at Writhlington (Beall, 1991), but this is the first record of a spider from the locality. Two specimens have been found, belonging to the same genus, but only the carapace is preserved in both cases.

The two specimens are preserved in splintery mudstone rich in plant remains. The fauna at Writhlington is probably derived from the roof shales of Nº 10 coal seam, Farrington Member of the Grovesend Formation, Somerset Coal Measures, which is Westphalian D in age (Waters et al., 2009); see Thomas and Cleal (1994) for a summary of the geology. Specimen LL 11001 consists of part (LL 11001a) and counterpart (LL 11001b); specimen LL 11002 consists of one piece only. LL 11001a, an internal mold, occurs on a large slab that bears, in addition to coalified plant axes, two phalangiotarbid carapaces and a blattodean forewing. The distinctly raised pars cephalica of specimen LL 11001a broke away after the photographs and drawings in this paper were made, and part of the detached fragment is now glued onto the matrix adjacent to the remainder of the carapace. Specimen LL 11001b is an external mold with adhering coalified cuticle, which provides more morphological information than LL 11001a. Specimen LL 11002, is preserved as an external mold of the dorsal surface of the carapace with adjacent fragments of legs and opisthosoma. The specimens are deposited in the Manchester Museum, Manchester, England.

Retrodeformation

Material from the Somerset coalfield is characteristically distorted due to tectonic activity (e.g., Ambrose and Romano, 1972; Anderson, 1994). The better preserved of the two phalangiotarbid carapaces on the same slab as specimen LL 11001 is deformed, but the spider carapace is symmetrical. Therefore, the spider carapace must be deformed by extension or compression along its long axis. Since the carapace is longer and narrower than other Carboniferous spider carapaces, it is presumed that extension has occurred in the long axis coupled with lateral compression. Since the direction of elongation is known, and one specimen (the phalangiotarbid) is skewed, it is possible to analyze the strain suffered by the rock and to retrodeform the spider carapace. Various methods can be used to retrodeform fossils (Briggs and Williams, 1981; Cooper, 1990; Williams, 1990; Rushton and Smith, 1993), but care must be taken to understand the nature of the deformation. There are routes by which a strained fossil can form from an original. A scanned image of the deformed fossil can be made symmetrical using a variety of distortions available in image manipulation computer programs, but only one solution correctly retraces the deformation path taken during tectonic activity. For the mudstone enclosing the Carboniferous spiders it is reasonable to assume that the deformation was compressional/extensional rather than pure shearing. Consequently, retrodeformation involves reversal of this process.

Two angles are needed to determine the strain ratio (R, = ratio of long and short axes of strain ellipse): the angular shear (ψ, = deviation from a right angle) and (φ′, = angle between symmetry axis of fossil and greatest extension direction) (see Cooper (1990) for definitions of these terms). The phalangiotarbid carapace on the same slab as specimen LL 11002 (Fig. 1A) is angled at 25° from the long axis of specimen LL 11002 (Fig. 1B) (the greatest extension direction) (i.e. φ′ = 25°), and is skewed 23° from a right angle (i.e. ψ = 23°). Reading these values on the chart of Breddin curves given in figure 9 of Cooper (1990), gives a value of 1.54 for R. Then, the camera lucida drawing of specimen LL 11002 (Fig. 1C) was scanned into the computer and rescaled by shortening the length to 79% and widening the width to 121% (Fig. 1C′) (using Aldus SuperPaint 3.5 on an Apple Macintosh computer). Assuming that the deformation of specimen LL 11001 was the same as that for LL 11002, which is reasonable given that they are from the same lithology and horizon, a similar transformation was done on specimen LL 11001 (Figs 1D,D′). Since φ′ is not known for this specimen, but ψ (14°) and R (1.54) are, the value for φ′ can be read from the Breddin curves graph, giving a value of 11°. There are actually two points on a Breddin curve with the same ψ value but a different value for φ′, one which results from shortening of the animal and one from lengthening (Cooper, 1990, fig. 10; specimen LL 11001 has been lengthened). Rotating the image of LL 11001 by 11°, and then applying the 79% and 121% scaling factors results in the shape shown in Fig. 1D′. Now, both specimens have the same L : W ratio, about 1.

The resultant restorations show how markedly different the carapace appears from what might be expected by simply imagining/restoring the fossil by eye. For example, it might be expected that the carapace was genuinely about 1.5× as long as wide in life, but the computer restoration shows that it was probably closer to being as long as wide. Clearly, there are implications for the interpretation of any fossils that have been deformed, and qualitative restorations made without calculating the amount and direction of compression and extension may be subject to considerable error. For interest, scans were made of the Writhlington phalangiotarbids illustrated by Beall (1991, figs. 2,4; redrawn as Fig. 1E–F in this paper; Fig. 1E was also figured by Jarzembowski 1989, fig. 7). Assuming that these had also been deformed by a factor (R) of 1.54 (the specimens came from the same coal tip and it is assumed that they were from close by within the same mine and that the deformation was similar), and measuring ψ on the drawings (17° for Fig. 1E; 21° for Fig. 1F), values for φ' can be read from the Breddin curves. The φ′ values used for retrodeformation were 55° for Fig. 1E and 19° for Fig. 1F (NB it was assumed that the former was wider than the original and the latter narrower). The resultant retrodeformed shapes (Figs 1E′,F′) are quite similar, although it can be seen that the drawings were not made from perfectly horizontal specimens because the sagittal axes curve (this can be seen in the original drawings). Beall suggested that these two specimens could belong in separate genera, but retrodeformation implies that they are in the same genus.

In a more recent study of Writhlington phalangiotarbids, based on specimens in the collections of the Bristol City Museum and Art Gallery, UK (Pollitt et al., 2004), numerous specimens were illustrated, in various states of deformation. These authors, who identified the phalagiotarbids as *Bornatarbus mayasii* (Haupt in Nindel, 1955), were not concerned with retrodeformation, instead concentrating on the novel morphology revealed by the

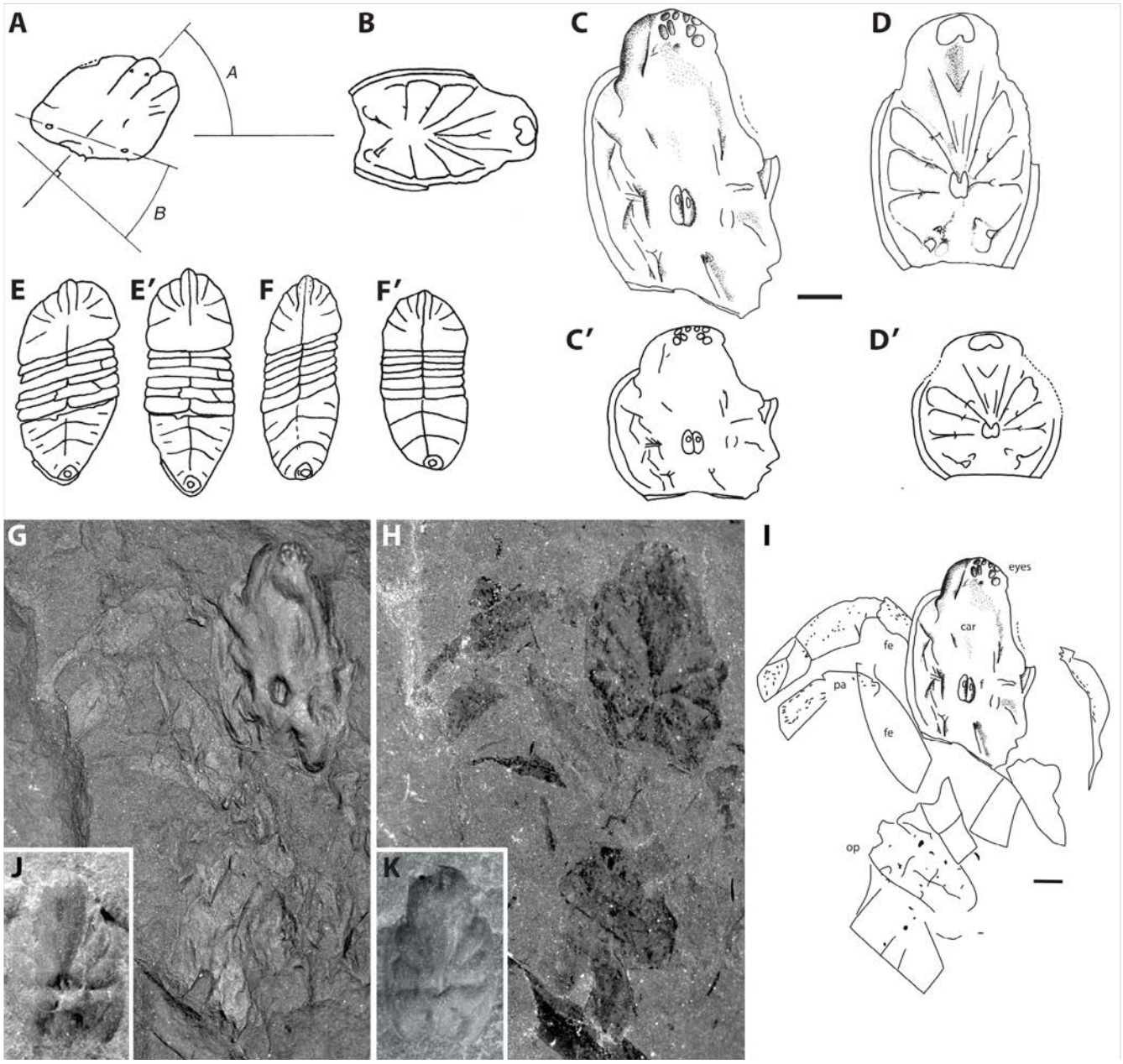

FIGURE 1. *Arthrolycosa* sp. from Writhlington, Avon, England, showing method of retrodeformation using phalangiotarbids on the same slabs (see text for explanation). Specimens in MM. **A**, phalangiotarbid carapace on same slab as LL 11001; **B**, specimen LL 11001 in angular relation to the phalangiotarbid carapace; **C**, camera lucida drawing of the carapace of specimen LL 11002; **C′**, carapace of specimen LL 10002 after retrodeformation; **D**, camera lucida drawing of the carapace of specimen LL 11001; **D′**, carapace of specimen LL 10001 after retrodeformation; **E**, phalangiotarbid specimen figured by Beall (1991, fig. 2) and Jarzembowski (1989, fig. 7); **E′**, phalangiotarbid specimen in E after retrodeformation; **F**, phalangiotarbid specimen figured by Beall (1991, fig. 4); **F′**, phalangiotarbid specimen in F after retrodeformation; **G**, photograph (dry) of whole specimen LL 11002; **H**, photograph (under ethanol) of whole specimen LL 11002; **I**, camera lucida drawing of whole specimen LL 11002; **J**, photograph (dry) of specimen LL 11001a (carapace part); **K**, photograph (dry) of specimen LL 11001b (carapace counterpart). See D for camera lucida drawing of specimen LL 11001. Scale bars = 1 mm.

specimens, and the phylogenetic position of phalangiotarbids within the Arachnida.

Other Specimens

Specimens found in Paleozoic strata and described as spiders are known from numerous localities (listed in Table 1). Those redescribed here come from the Czech Republic, France, England, and Illinois. There are two main localities in the Czech Republic that have yielded fossil spiders: Rakovník and Nýřany. Specimens from Rakovník were collected from the Radnice Coal Seams (Steinkohle) at the Moravia mine in the western part of the Kladno-Rakovník Basin, stratigraphically in the Radnice Member of the Kladno Formation, which is Carboniferous (lower Moscovian, Westphalian C) in age (Kušta, 1885; Štamberg and Zajíc, 2008; Opluštil and Kędzior, 2009; Elicki et al., 2014). These specimens are preserved as carbonized cuticle on a pale grey shale matrix (e.g. Figs. 14–15). Also from the Radnice Coal Seams, but from Svinná, near Radnice, is *Palaranea borassifoliae* Frič, 1864.

The Nýřany specimens come from the Gaskohle at the Humboldt mine, in the western part of the Kladno-Rakovník Basin, stratigraphically in the Nýřany Member of the Kladno Formation, which is Carboniferous (upper Moscovian, Westphalian D) in age (Štamberg and Zajíc, 2008; Opluštil and Kędzior, 2009; Elicki et al., 2014). Specimens from here are preserved as pyritic replacements on a black shale matrix (e.g. Fig. 19); thus, the morphology is difficult to interpret. Another locality, in the Semily Formation, Carboniferous (Gzhelian, Stephanian C) at Krsmol near Altpaka, has produced *Arthrolycosa tarda* Fritsch, 1912, now lost. Štamberg and Zajíc (2008) listed and figured all of the Carboniferous and Permian faunas of the limnic basins of the Czech Republic. Some of the their catalog numbers (Me) differ from those present on the specimens (CGH) and given in, e.g., Petrunkevtch (1953); the Štamberg and Zajíc (2008) numbers are presented alongside the previous catalog numbers.

Localities in France include Montceau-les-Mines, at the northern end of the Massif Central, which has yielded *Palaeothele montceauensis* (Selden, 1996b) in sideritic ironstone nodules, of Carboniferous (late Stephanian) age (Perrier and Charbonnier, 2014). Redescribed here is *Protolycosa cebennensis* Laurentiaux-Vieira and Laurentiaux, 1963, which comes from the Cévennes, southern Massif Central, Le Pin bed, La Grand'Combe coal basin, and is Carboniferous (basal lower Stephanian) in age. Apart from the Writhlington specimens (see above), others from England occur in sideritic ironstone nodules from the 10-foot Ironstone in a former clay pit at Clay Croft open works, Coseley, near Dudley, West Midlands, of Carboniferous (Westphalian B) age (*Eocteniza* Pocock, 1911, *Protocteniza* Petrunkevitch, 1949), and siltstones associated with the Kent No. 7 coal seam, Carboniferous (Moscovian, Westphalian D) from the mine dump of Chislet colliery, Kent coalfield, England (*Dinopilio parvus* Petrunkevitch, 1953). The North American specimens are all from sideritic nodules from the Francis Creek Shale Member of the Carbondale Formation, of Carboniferous (Middle Pennsylvanian, Desmoinesian, Moscovian) age, of Mazon Creek, Grundy County, Illinois (Clements et al., 2019).

Previously described specimens of Carboniferous spiders were loaned from the Yale Peabody Museum of Natural History, the University of Michigan Museum of Paleontology, and the Musée d'Histoire Naturelle, Lille, France, and others studied in the Natural History Museum, London and the National Museum, Prague. Specimens were photographed using a variety of techniques, including black and white film (Ilford FP4, 125 ASA, and Ilford Delta, 100 ASA) using Minolta Dynax 9 and Praktica PLC3 cameras attached to a Wild M7S stereomicroscope or a 50 mm macro lens. Color photographs were taken with Kodachrome 100 ASA film, and then scanned with an Epson Expression 10000XL scanner; some of these are illustrated in grayscale for better comparison. Some photographs were made with a Canon EOS 5D camera and a 50 mm macro lens. Drawings were made using a camera lucida attachment to the microscope, scanned, and then traced using Autodesk Graphic (graphic.com) and Affinity Designer (serif.com). Measurements were made using Graphic.

Abbreviations

Museum repositories are abbreviated as follows: BMNH = Natural History Museum, London; MHNL = Musée d'Histoire Naturelle, Lille; MM = Manchester Museum; NMMNH = New Mexico Museum of Natural History and Science; NMP = National Museum, Prague; UMMP = University of Michigan Museum of Paleontology; YPM = Yale Peabody Museum.

Abbreviations used in descriptions and on the illustrations: 1, 2, 3 … = tergite numbers (note: these are simply counted from the anterior, and do not necessarily relate to somites); I, II, III, IV = walking legs; AME = anterior median eye; car = carapace; ch = chelicera; cx = coxa; d = dorsal; ext mld = external mold; f = fovea; fe = femur; int mld = internal mold; L = length; L/W = length/width ratio; lab = labium; mt = metatarsus; mx = maxilla; op = opisthosoma; pa = patella; Pd = pedipalp; PME = posterior median eye; sp = spinneret; st = sternum; ta = tarsus; ti = tibia; v = ventral; W = width. Arrowheads mark podomere boundaries; arrow flights indicate features descending into the matrix. All measurements are in mm. Leg formula longest to shortest. Body length excludes chelicerae; tarsal length includes claws.

Note: an important author of Paleozoic arachnids was Antonín Frič (1832–1913). In his works published in German, he was also known as Antonin Fritsch, or Anton Johann Fritsch. The surnames used in this article are as printed in the reference. Also, in the synonymy lists, references are listed as they are in the original, following the practice of Štamberg and Zajíc (2008).

SYSTEMATIC PALEONTOLOGY

Order Araneae Clerck, 1757

Diagnosis: Tetrapulmonata with opisthosomal silk glands, silk-spinning spigots (modified setae), and paired abdominal appendages modified as silk-weaving organs; ventral opisthosoma without sternites; dorsal opisthosomal tergites (if present) undivided; anal tubercle lacking flagelliform telson; chelicera with cheliceral gland; cheliceral fang with poison gland opening, without setae; adult male palps modified for sperm transfer; numerous longitudinally oriented lyriform organs present on walking legs in addition to transverse one on distal metatarsus [modified after Selden et al., 1991].

Remarks: This diagnosis, modified from Selden et al. (1991), serves to distinguish crown-group spiders from other tetrapulmonates. However, a number of taxa which could be considered as stem-group proto-spiders have been described in the last few years (Selden et al., 2008; Garwood et al., 2016; Huang et al., 2018; Wang et al., 2018), which prompts the question: what is a spider?

The concept of stem, crown, and total groups was codified by the late Dick Jefferies (Jefferies, 1979), from the original ideas of Hennig (1950, 1966). The crown group (a monophyletic clade including the latest common ancestor and all its descendants) is diagnosed by a number (usually >1) of character states (see Araneae, above). These characters must have accumulated one by one over geological time (see, e.g., text-fig. 2 of Craske and Jefferies, 1989, and figs. 1 of Budd, 1998, and Budd and Jensen, 2000). The stem group is the series of taxa which exhibit some, but not all, of these character states and forms the lineage along which these diagnostic characters were gradually accrued. Hence, Uraraneida Selden et al., 2008, *Idmonarachne* Garwood et al., 2016, and *Chimerarachne* Wang et al., 2018 form the

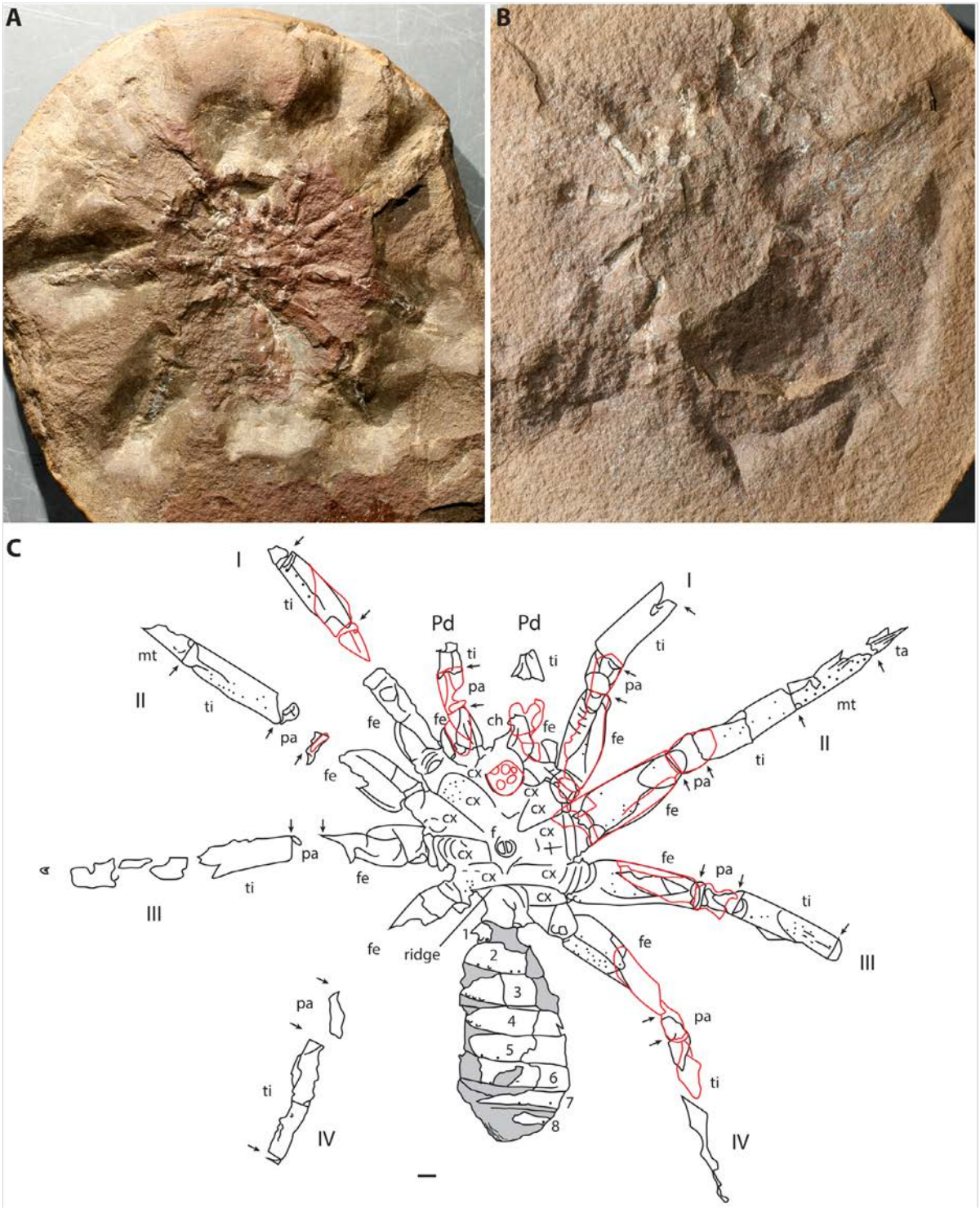

FIGURE 2. *Arthrolycosa antiqua* Harger, 1874, holotype IP.000161 (YPM), Carboniferous (Desmoinesian, Moscovian) of Mazon Creek, IL. **A**, photograph of part; **B**, photograph of counterpart; **C**, explanatory drawing of specimen, mainly the part, with counterpart shown in red. Scale bar = 1 mm.

stem group of Araneae because each possesses one or more spider characters, but not all. For example, uraraneids bear silk spigots but these are not arranged on spinnerets. *Idmonarachne* bears an opisthosoma reminiscent of trigonotarbids, but its leg podomeres are fully differentiated as in a spider and it bears large, forward-directed chelicerae as seen in mesotheles, mygalomorphs, and many araneomorphs. *Chimerarachne* is the most spider-like in many ways of these stem-Araneae in bearing fully functional spinnerets and male pedipalps modified into sperm-transfer organs. However, like uraraneids and uropygids, *Chimerarachne* bears a flagelliform post-anal telson. Apart from this feature *Chimerarachne* could be considered as a spider. This was the conclusion of Wunderlich (2019), who established an order Araneida that included two suborders: Chimerarachnida and Araneae. This grouping would actually constitute a scion (*sensu* Craske and Jefferies, 1989), which is a monophyletic group formed by extending the base of the crown group down into the stem group to incorporate one or more plesions (*sensu* Craske and Jefferies, 1989) (see Budd, 2001, esp. fig. 1, for discussion of these concepts).

Establishing the sequence of accumulation of characters along a stem group is difficult because, first, plesions may exhibit their own suite of apomorphies (indeed, they should if they are to be recognized as anything other than metataxa) and, second, fossils rarely reveal all of the characters required to place them exactly on the stem group. For example, whilst *Chimerarachne* shows character states plesiomorphic for Araneae (post-anal flagellum), it has a unique arrangement of spinnerets (functional anterior lateral, anterior median and posterior lateral spinnerets, vestigial posterior medians), and also a wide sternum, characteristic of opisthothele, but not mesothele, spiders (Wang et al., 2018). None of the fossils described here shows the full complement of spider synapomorphies; however, other features are available which are characteristic, but not diagnostic, of spiders. For example, the carapace of mesothele spiders is quite distinct from that of other Paleozoic arachnids, such as trigonotarbids. It is suboval in dorsal outline, with a fairly straight posterior margin, bears an anterior eye tubercle, and commonly a distinct fovea with radiating grooves; in contrast, trigonotarbid carapaces are subtriangular in outline, with median eyes and, in some families, lateral compound eyes; the carapaces of uropygids and amblypygids are also distinctly different. Nevertheless, spinnerets can be seen in many of the fossil specimens described here, e.g., *Protolycosa anthracophila* Römer, 1865, *P. danielsi* (Petrunkevitch, 1913), *P. suazoi* n. sp., *Palaeothele montceauensis* (Selden, 1996b), *P. onoi* n. sp. Post-anal flagella are not seen in any of these, and were searched for using x-ray CT-scanning in *Palaeothele montceauensis* (Selden et al., 2008). Thus, numerous specimens identified as *Arthrolycosa* sp. (Table 1), which consist essentially of just a carapace, can be identified as members of that genus (and hence as spiders) by comparison with better-preserved arthrolycosids that share similar carapace features but also possess spider synapomorphies, such as spinnerets.

Suborder Mesothelae Pocock, 1892

Included families: Arthrolycosidae Harger, 1874 (Carboniferous–Permian), Arthromygalidae Petrunkevitch, 1923 (Carboniferous-Cretaceous), Burmathelidae Wunderlich, 2017 (Cretaceous), Cretaceothelidae Wunderlich, 2017 (Cretaceous), Eomesothelidae Wunderlich, 2019 (Cretaceous), Liphistiidae Pocock, 1892 (Recent), Palaeothelidae n. fam. (Carboniferous).

Diagnosis: Sternum narrow and elongate, sternite of seventh segment globular, tibial spur present in juveniles and females, spigots of spinnerets almost uniform, lateral four spinnerets large, median four (sometimes fewer) spinnerets much smaller and often not functional (based on Haupt, 2003).

Some distinctive characters of mesotheles are plesiomorphic: opisthosomal tergites and excavation of the coxa of walking leg IV also occur in Amblypygi (Weygoldt, 2000).

Remarks: All true Paleozoic Araneae described here can be referred to Mesothelae. Their carapaces show many similarities with members of this suborder, including an anterior eye tubercle, and the segmented dorsal opisthosoma is also characteristic. However, their familial relationships are open to question because of the poor distinctions between the Paleozoic families, and the creation of four new families by Wunderlich (2017, 2019) for Cretaceous species. Most authors recognize just one family for extant species: Liphistiidae, divided into the subfamilies Liphistiinae and Heptathelinae. However, some authors, beginning with Petrunkevitch (1939), raised these to familial rank (see Xu et al., 2015 for discussion).

Magalhaes et al. (2020) made the point that the extinct families Arthrolycosidae, Arthromygalidae, and Pyritaraneidae could be stem spiders, and so cannot be included in Mesothelae, following their classification as " 'mesotheles' " in Dunlop et al. (2020, p. 133–134). However, in the present work, many of the dubious specimens have been removed from Araneae altogether, and those remaining show spider and, indeed, mesothele characters, such as spinnerets in a forward position on the opisthosoma, tergites on the dorsal opisthosoma, and a narrow sternum. It may be argued that some of these are plesiomorphies within Araneae, and this problem was discussed by Platnick and Gertsch (1976), who searched for synapomorphies of Mesothelae in order to prevent it constituting a metataxon. Since arthrolycosids and arthromygalids are clearly spiders, and show features of Mesothelae, they are included in that suborder here. Moreover, Pyritaraneidae Petrunkevitch, 1953, and superfamily Pyritaraneoidea Petrunevicth, 1955, are not recognized here; the two specimens for which they were erected, *Pyritaranea tubifera* Fritsch, 1899 and *Eopholcus pedatus* Fritsch, 1904, are here synonymized (under *Pyritaranea tubifera*) and placed as Araneae *incertae sedis*. Other Paleozoic spiders previously referred to Arthrolycosidae and Arthromygalidae are here reinterpreted and referred to different higher taxa; see below.

Family Arthrolycosidae Harger, 1874

Included genera: *Arthrolycosa* Harger, 1874, *Protolycosa* Römer, 1865.

Emended diagnosis: Mesothelae in which the opisthosomal tergites occupy the full width of the opisthosoma, and are not set in soft cuticle.

Geological range: Carboniferous (Westphalian B, upper Bashkirian) to Permian (upper Kazanian).

Remarks: Many authors, e.g., Petrunkevitch (1913, 1949, 1955), and Dunlop et al. (2020), attributed the authorship of the family name to Fritsch (1904). However, the name Arthrolycosidae was first proposed by Harger (1874) in his description of the new genus and species *Arthrolycosa antiqua* Harger, 1874, and the family name was considered valid in works by Scudder (1884, 1885), Kušta (1889), Beecher (1889) and, indeed, Fritsch (1904) himself.

Petrunkevitch (1913) referred all Carboniferous spiders to Arthrolycosidae, but, in 1923, he erected Arthromygalidae to accommodate *Arthromygale* Petrunkevitch, 1923, *Eolycosa* Kušta, 1885, *Geralycosa* Kušta, 1889, *Kustaria* Petrunkevitch, 1953, *Palaranea* Frič, 1864, *Protocteniza* Petrunkevitch, 1949, *Protolycosa* Römer, 1865, and *Rakovnicia* Kušta, 1885. He distinguished arthromygales from arthrolycosids by their eye arrangement, and the presence of two smooth claws on their tarsi. Fritsch (1904) had described widely spaced eyes in two rows not borne on an eye tubercle in *Kustaria carbonaria*, *Arthromygale fortis*, and *A. beecheri*. Petrunkevitch (1949) made the point that all spiders he referred to Arthromygalidae were European, while Arthrolycosidae were North American, and used this observation, in part, to refer *Protolycosa* Römer,

1865 from Silesia to Arthromygalidae (Petrunkevitch 1953). In the *Treatise on Invertebrate Paleontology*, Petrunkevitch (1955) distinguished the two families simply on the presence of an eye tubercle (Arthrolycosidae) or its absence (Arthromygalidae), and doubted the presence of eyes in arthromygales.

Arthrolycosids can be distinguished from other mesotheles by their tergites which extend the full width of the dorsal opisthosoma and are not set in soft cuticle. In arthrolycosids (Figs 1–12), although some specimens do not preserve the lateral edges of the opisthosoma, none of them show any trace of soft cuticle beyond the edges of the tergites, which are all as wide as the preserved opisthosoma, with generally parallel anterior and posterior borders, and do not show curved lateral margins. In other mesotheles (Figs 13–18, and Cretaceous and Recent families), the tergites are discrete, elongated elliptical in shape, with rounded lateral edges, and decrease in width from the middle towards the front and the rear of the opisthosoma. Soft cuticle is evident in many fossil specimens (e.g. Fig. 13).

Genus *Arthrolycosa* Harger, 1874

Type species: *Arthrolycosa antiqua* Harger, 1874

Other species: *Arthrolycosa* sp. in Eskov and Selden (2005), from the Permian (upper Kazanian) of the Kirov region, Russia; *Arthrolycosa* sp. A and sp. B in Selden et al. (2014), from the Carboniferous (Bashkirian) of the Donets Basin, Russia, and from the Carboniferous (Kasimovian–Gzhelian) of the Tunguska Basin, Russia; two specimens from Writhlington, Avon, UK, LL11001a,b, LL11002, in Manchester Museum, described herein.

Emended diagnosis: Arthrolycosidae with a relatively equant carapace (L/W < 1.30), bearing a distinct transverse (straight or curved) ridge behind the fovea (a discrete pit with paired depressions within), which demarcates a slope to the posterior margin; leg formula (based on fe–mt) IV>I>III>II (cf. *Protolycosa* IV>III>II>I or IV>II>III>I).

Arthrolycosa antiqua Harger, 1874

Figs. 2–4

1874 *Arthrolycosa antiqua*, gen. et sp. nov.: Harger, p. 219–223.
1884 *Arthrolycosa antiqua* Harger: Scudder, p. 15.
1885 *Arthrolycosa antiqua* Harger: Scudder, p. 734; fig. 909.
1889 *Arthrolycosa antiqua* Harger: Beecher, p. 219–223; figs 1–3.
1889 *Arthrolycosa antiqua* Harger, 1874: Miller, p. 570; fig. 1065.
1890 *Arthrolycosa antiqua*: McCook, p. 455; figs 381–382.
1904 *Arthrolycosa antiqua* Harger: Fritsch, p. 6; fig. 1.
1911 *Arthrolycosa antiqua* Harger: Pocock, p. 4.
1913 *Arthrolycosa antiqua* Harger: Petrunkevitch, p. 86, 89; pl. VIII, fig. 53.
non 1913 *Arthrolycosa antiqua* Harger: Petrunkevitch, p. 91; pl. VIII, fig. 54.
1928 *Arthrolycosa antiqua* Harger, 1874: Savory, p. 268, 283.
1949 *Arthrolycosa antiqua* Harger: Petrunkevitch, p. 276.
1953 *Arthrolycosa antiqua* Harger: Petrunkevitch, p. 101.
1955 *Arthrolycosa antiqua*: Petrunkevitch, p. P133; fig. 98,1.
1993 *Arthrolycosa antiqua* Harger, 1874: Selden, p. 312.
2006 *Arthrolycosa antiqua* Harger, 1874: Penney and Selden, p. 27.
2010 *Arthrolycosa antiqua*: Selden and Penney, p. 188.
2011 *Arthrolycosa antiqua* Harger, 1874: Penney and Selden, p. 52.
2014 *Arthrolycosa antiqua* Harger, 1874: Selden et al., p. 300; fig. 1d.
non 2014 *Arthrolycosa antiqua* Harger, 1874: Selden et al., p. 300; fig. 1e.
2017 *Arthrolycosa antiqua* Harger, 1874: Selden and Penney, p. 116.

Material: Holotype IP.000161, part and counterpart; specimen YPM IP.000163, part and counterpart, both in the collections of Yale Peabody Museum.

Occurrence: Francis Creek Shale Member, Carbondale Formation, Carboniferous (Desmoinesian, Moscovian), Mazon Creek, Grundy County, Illinois.

Remarks: The original description of the type specimen (YPM161) by Harger (1874) was incomplete and erroneous in some respects. Scudder (1884) examined the specimen and pointed out that what Harger had called a chelate pedipalp was, in fact, not chelate. Beecher (1889) cleaned and prepared the specimen, and produced a much more accurate description and illustration. He showed that the so-called chelate pedipalp was actually the first walking leg, and exposed many more leg podomeres. Petrunkevitch (1913) reexamined the holotype and produced a stylized drawing (fig. 53), and pointed out that the distal podomeres of the pedipalps were not preserved, as Beecher had assumed. Here, new photographs (Fig. 2A,B) and an interpretive drawing (Fig. 2C) of the holotype are presented.

The holotype specimen consists of part and counterpart, but the latter shows only a few features that complement those seen on the part. On the drawing (Fig. 2C), they are shown in red. The main part shows dorsal and ventral features superimposed in the anterior half, while the opisthosoma shows dorsal features in positive relief. The major differences in interpretation from previous researchers are as follows. In the central carapace area, previous authors interpreted the fossil to show a carapace with radiating grooves. However, the impressions of coxae dominate, and the transverse line towards the rear of the supposed carapace that could be interpreted as the posterior edge of the carapace, is too far forward to be such, so is here interpreted as a ridge demarcating a posterior slope to the posterior border of the carapace. The fovea is deep and bears twin depressions. The eye tubercle is present at the anterior edge of the carapace, bearing some eye lenses. So, an overall impression of the shape of the carapace can be gleaned, but its lateral edges are not clear. The interpretation of the transverse, slightly recurved, line as the posterior margin suggests that the carapace is rather short and wide, with the fovea towards the rear margin. The opisthosoma shows eight dorsal tergites.

Specimen IP.000163 was dismissed by Petrunkevitch (1913, p. 91) as being badly crushed and was only tentatively referred to *Arthrolycosa antiqua*. It is indeed preserved at an angle to the bedding, so that the chelicerae are preserved to one side, and the carapace is not seen. Since the characters of the genus pertain to the carapace, which this specimen lacks, it cannot be placed here with certainty; nevertheless, it is retained within this species. The anterior part of the specimen shows the ventral surface, whereas the dorsal part of the opisthosoma is preserved, showing the tergites.

Description of holotype (YPM IP.000161): Body L 21.67. Carapace L 9.83, W 7.73, L/W 1.27; lateral border gently curved outwards, with lateral flange, anterior border curved, bearing eye tubercle at anterior edge, posterior border behind transverse furrow. Eye tubercle L 2.14, W 2.17, bearing eye lenses. Deep fovea consisting of 2 semicircular depressions, W 1.1, situated ⅔ of length of carapace from anterior. Gently recurved ridge nearly full width of carapace just posterior to fovea. Pedipalp about ⅓ length of legs. Legs subequal in length, not much longer than body length, formula (based on fe–ti): IV>II>III>I. Podomeres stout, lengths: Pedipalp fe 2.68, pa 2.02; Leg I fe 5.46, pa 2.24, ti 5.23; Leg II fe 5.93, pa 2.07, ti 6.00, mt 4.96; Leg III fe 5.77, pa 2.09, ti 6.05; Leg IV fe 6.69, pa 2.09, ti 7.13. Opisthosoma suboval in outline, L 12.94, W > ~6.5, with 8 visible dorsal tergites, each bearing row of small tubercles along posterior edge. Tergite lengths: 1 ~1.3, tergites 2–6 ~1.6, tergites 7–8 ~1.2. Anal tubercle on ventral side of opisthosoma near

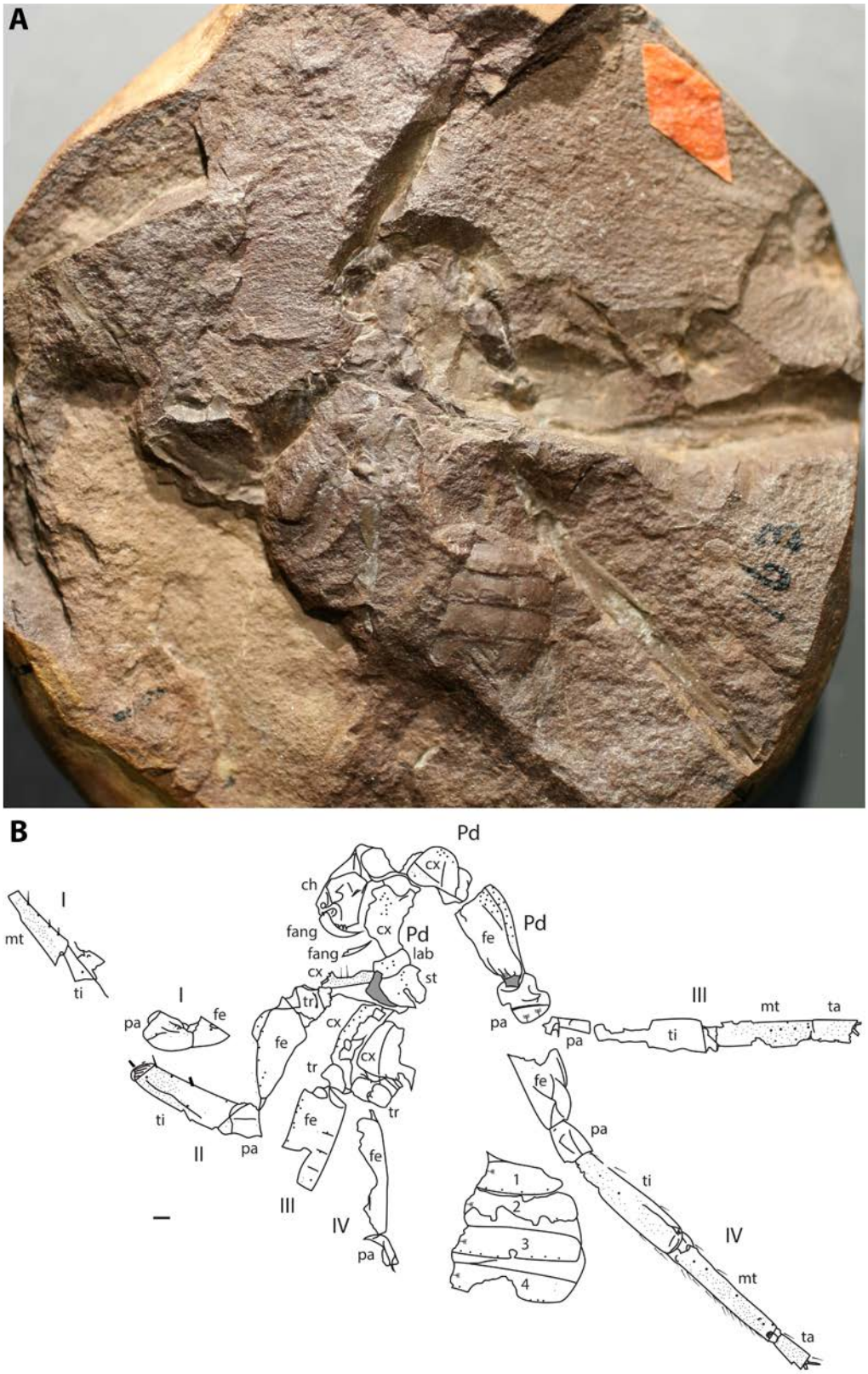

FIGURE 3. *Arthrolycosa antiqua* Harger, 1874, specimen IP.000163 (YPM), Carboniferous (Desmoinesian, Moscovian) of Mazon Creek, IL, part. **A**, photograph (dry); **B**, explanatory drawing. Scale bar = 1 mm.

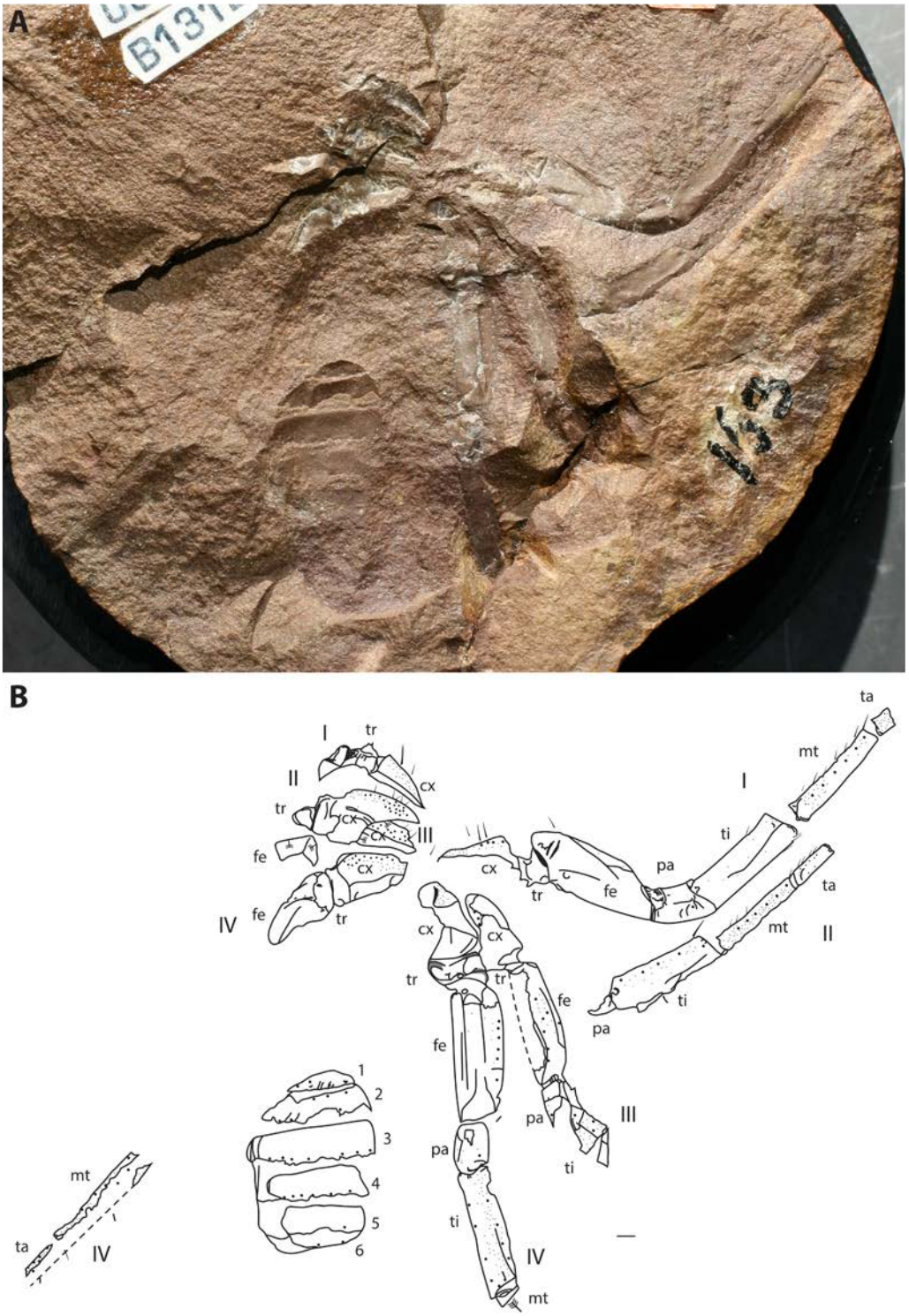

FIGURE 4. *Arthrolycosa antiqua* Harger, 1874, specimen IP.000163 (YPM), Carboniferous (Desmoinesian, Moscovian) of Mazon Creek, IL, counterpart. **A**, photograph (dry); **B**, explanatory drawing. Scale bar = 1 mm.

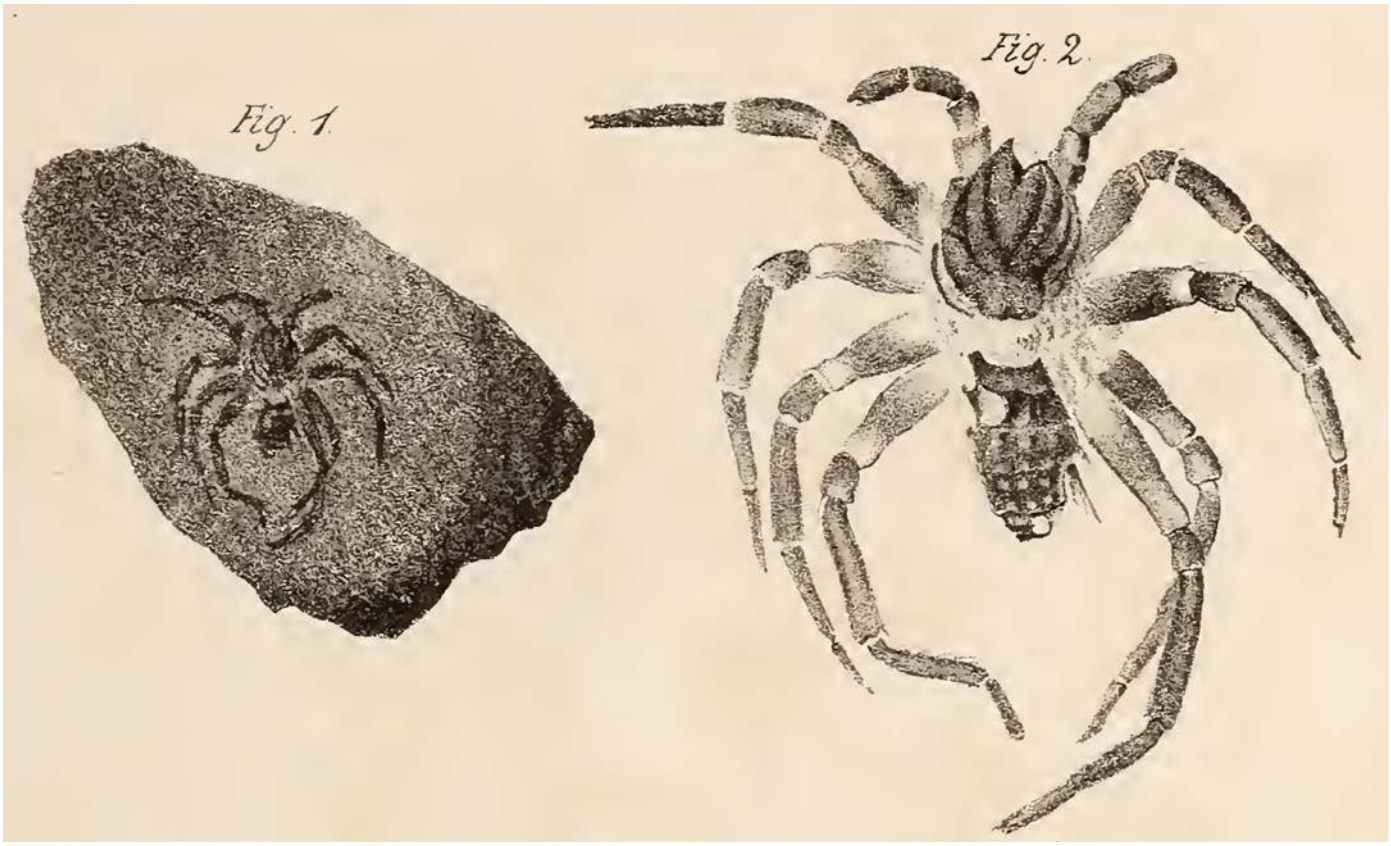

FIGURE 5. *Protolycosa anthracophila* Römer, 1865, holotype and only known specimen (lost), Carboniferous (Westphalian B, Bashkirian), between Mysłowice and Katowice, Upper Silesian Coal Basin, Poland, original illustration by Roemer (1866b, pl. III, figs 1–2). Fig. 1, specimen as it appears in the rock; fig. 2, enlarged drawing of specimen.

posterior border.

Description of specimen YPM IP.000163 (Figs 3–4): Labium L 1.17, W 2.18, L/W 0.53; chelicera L (inc. fang) 4.20, W 3.31, L/W 1.27, fang L 2.67. Legs stout, bearing large setal follicles over exposed surfaces, sub equal in length, formula (based on fe–mt): IV>I>III>II. Lengths of podomeres: Pedipalp cx 3.97, fe 5.50, pa 2.59. Leg I cx 4.04, tr 1.84, fe 7.94, pa 3.35, ti 6.56, mt 6.70; total fe–mt 24.55. Leg II cx 4.19, tr 1.86, fe 6.73, pa 2.27, ti 6.48, mt 5.41, ta 3.02; total fe–mt 20.89. Leg III cx 4.31, tr 1.23, fe 6.81, pa 2.91, ti 7.62, mt 5.67, ta 2.96; total fe–mt 23.01. Leg IV cx 4.05, tr 1.88, fe 7.48, pa 2.77, ti 7.63, mt 7.33, ta 3.03; total fe–mt 25.21. Opisthosoma L 10.43, W 7.13, L/W 1.46. At least 6 opisthosomal tergites with gently recurved posterior margins, bearing tubercles along posterior margin. Measurements (sagittal L, W, L/W) 1: 1.39, >4.40, 0.31; 2: 1.75, >6.45, 0.27; 3: 1.94, >7.49, 0.26; 4: 1.92, >7.01, 0.28; 5: 1.60, >5.94, 0.27; 6: 1.07, >5.12, 0.21.

Arthrolycosa sp.
Fig. 1

Material: LL 11001a and b, part and counterpart, and LL 11002, part only, in the Manchester Museum, Manchester, UK.

Occurrence: Roof shales of Nº 10 coal seam, Farrington Member of the Grovesend Formation, Somerset Coal Measures, Carboniferous (Westphalian D, Moscovian), of Writhlington, Avon, UK.

Remarks: In the following description, the first measurement refers to specimen LL 11001, and the second to LL 11002, as measured from the specimen in the rock. Angles are measured from specimen LL 11002 only [restored angles are given in brackets].

Description: Carapace L 6.75/6.8, W 4.5/4.5, suboval in outline, sharply truncated at W 2.75/2.9 posteriorly, posterior margin slightly recurved. Pars cephalica parallel-sided from anterior border to ⅓ carapace L, ~2.45/2.5 W, tapering to fovea, bounded by first pair of grooves radiating from fovea; posterior half of pars cephalica rising gently forwards from fovea, anterior half domed. Flat carapace rim along lateral margins, maximally 0.3/0.26 W, running from posterolateral corners to start of pars cephalica, (which occurs 1.3/1.47 from anterior border). Fovea prominent, 4.7/4.5 from anterior margin, consisting of pair of longitudinal depressions. Four main pairs of furrows radiating from fovea towards carapace marginal rim; first pair forming posterolateral edges of pars cephalica, subtending an anterior angle of 30° [41°]; second pair subtend an angle of 65° [83°]; third pair an angle of 100° [129°]; fourth pair an angle of 180°. Second to fourth furrows bear slight widening at just < ½ their length from fovea, widening into triangle ~0.25 before marginal rim. Fifth pair of furrows represented by two depressions, corresponding to widened sections of more anterior furrows, subtends an anterior angle of 295° [274°]. Distal triangle of each radiating furrow with slight furrows connecting it to next adjacent distal furrow triangle. Posteriorly bilobed, subcircular break in specimen LL 11002 at anterior edge of the carapace marks where distinct eye cluster projects into matrix; W 1.0, slightly wider than long in plan view, but situated on anteriorly facing slope. Eyes present on LL 10002, forming posteriorly bilobed cluster, or two groups separated by anteriorly narrowed space. Both eye rows recurved, anterior rather gently. Anterior eyes abut anterior margin of carapace with scarcely a clypeus.

Genus *Protolycosa* Römer, 1865

Type species: *Protolycosa anthracophila* Römer, 1865

Other species: *Protolycosa cebennensis* Laurentiaux-Vieira and Laurentiaux, 1963, *P. danielsi* (Petrunkevitch, 1913) n. comb., *P. suazoi*, n. sp.

Emended diagnosis: Arthrolycosidae with carapace distinctly longer than wide, suboval in outline, with recurved posterior margin not nearly full width of carapace; carapace pointed anteriorly, lacking a transverse ridge behind the fovea. Fovea not a deep pit (except *Protolycosa cebennensis*), but paired apodemes shallow towards anterior. Leg I shortest; formula, based on fe–mt: IV>III>II>I or IV>II>III>I (cf. *Arthrolycosa* IV>I>III>II).

Remarks: *Arthrolycosa* and *Protolycosa* are closely related, but the differences in the carapace of *Protolycosa* (distinctly longer than wide, with curved lateral margins, fovea shallowing gently anteriorly) are sufficient to separate it from *Arthrolycosa*. The deep fovea of *P. cebennensis* suggests it is closer to *Arthrolycosa*. It is possible that the matrix surrounding this specimen has suffered distortion, as at Writhlington, which is unnoticed because the carapace appears symmetrical. If so, is possible that retrodeformation would result in this species being referred to *Arthrolycosa*.

Protolycosa anthracophila Römer, 1865

Fig. 5

1865 *Protolycosa anthracophila*: Römer, p. 468.
1866 *Protolycosa anthracophila*: Grube and Römer, p. 33–34.
1866 *Protolykosa anthracophila*: Rose, p. 15–16.
1866a *Protolycosa anthracophila*: Roemer, p. 73.
1866b *Protolycosa anthracophila*: Roemer: p. 136, pl. III.
1866c *Protolycosa anthracophila*: Roemer: p. 428.
1870 *Protolycosa anthracophila* Römer: Thorell, p. 221–222.
1874 *Protolycosa anthracophila* Römer: Harger, p. 221–223.
1882 *Protolycosa anthracophila* Rœm., 1866: Karsch, p. 559.
1884 *Protolycosa anthracophila* Roemer: Scudder, p. 22.
1885 *Protolycosa anthracophila* F. Roem.: Scudder, 742; fig. 941.
1890 *Protolycosa anthracophila* F. Römer: Haase, p. 635.
1890 *Protolycosa anthracophila* Römer, 1866: McCook, p. 453, figs 378–390.
1890 *Protolycosa anthracophila*: Scudder, p. 38.
1891 *Protolycosa anthracophila*: Scudder, p. 29.
1901 *Protolycosa anthracophila*: Fritsch, p. 56.
1904 *Protolycosa anthracophyla* Röm.: Fritsch, p. 12–13, figs. 8–10, pl. XIII, figs. 1–4.
1911 *P. anthracophila*, Roemer: Pocock, p. 4.
1913 *Protolycosa anthracophila* Römer: Petrunkevitch, p. 87.
1928 *Protolycosa anthracophyla* Romer, 1866: Savory, p. 268, 283.
1935 *Protolycosa anthracophyla* F. Roemer 1865: Schwarzbach, p. 87, fig. 3.
1953 *Protolycosa anthracophila* Römer, 1866: Petrunkevitch, p. 102–103.
1955 *Protolycosa anthracophila*: Petrunkevitch, p. P133–P134, fig. 99,1.
1963 *Protolycosa anthracophyla* Römer, 1866: Laurentiaux-Vieira and Laurentiaux, p. 27.
1967 *Protolycosa anthracophyla* Romer: Crowson et al., p. 506.
1992 *P. anthracophyla* Roemer, 1866: Rohdendorf, p. 751.
2001 *Protolycosa anthracophila* Römer, 1866: Penney, p. 999.
2006 *Protolycosa anthracophila* Roemer, 1866: Penney and Selden, p. 27
2010 *Protolycosa anthracophila* Roemer, 1866: Selden and Penney, p. 188.
2011 *Protolycosa anthracophila* Roemer, 1866: Penney and Selden, p. 54.
2017 *Protolycosa anthracophila* Roemer, 1866: Penney and Selden, p. 116.

Diagnosis: *Protolycosa* bearing swellings on opisthosomal tergites.

Material: Holotype only, part only, in the museum in Wrocław (lost).

Occurrence: Coal measures, Carboniferous (Westphalian B, Bashkirian), between Mysłowice and Katowice, Upper Silesian Coal Basin, Poland.

Remarks: Roemer (1866b) described this species, but only after having exhibited it at various meetings around Europe the previous year; hence, the first publication of the spider, including its name, was Römer (1865). Petrunkevitch (1953) was unable to examine this specimen for his study of European fossil Arachnida because it was lost. He presumed this had occurred during World War II, and the holotype (and only known specimen) remains lost. However, Roemer (1866b) gave a very good description and illustration of the specimen, which was supplemented by Fritsch (1904), who also examined the specimen. Laurentiaux-Vieira and Laurentiaux (1963), who described the second species in the genus, pointed out that Petrunkevitch's (1955, fig. 99,1) drawing shows a straight anterior border to the carapace, which is not borne out by looking at the illustrations of Roemer (1866b) and Fritsch (1904). Actually, Fritsch did interpret the carapace differently, considering it almost square in outline, but his interpretation is incorrect.

A copy of Roemer's (1866b) plate is reproduced here (Fig. 5). The carapace of *Protolycosa anthracophila* is broadest just behind its mid-length, tapers anteriorly, and is longer than wide, according to the pictures and description of Roemer (1866b), although Fritsch (1904) interpreted it differently. The fovea lies in the posterior part of the carapace. The anterior edge is pointed and bears a distinct notch. Roemer interpreted the notch as the remains of a pair of maxillae. However, it is more likely that the eye tubercle is missing. This is common in such fossils because the tubercle has enough relief to break off and remain with the counterpart (which is unknown). Roemer measured the whole spider body as 5‴ in length, which is equivalent to about 10.9 mm. On this basis, the carapace measures L 5.02, W 3.79, L/W 1.32.

The pedipalps are simple, not modified. The legs are a little longer than the body, stout, and, according to both Roemer (1866b) and Fritsch (1904) are heavily setose. Fritsch's plate shows numerous macrosetae. The tarsi bear at least paired claws. Leg formula (based on fe–ta): IV>III>II>I. Podomere lengths: Pedipalp pa 0.84, ti 1.59, ta 1.72; Leg I fe 2.77, pa 1.12, ti 2.62, mt 2.41, ta 1.89, total fe–ta 10.80; Leg II fe 3.16, pa 1.34, ti 2.92, mt 2.68, ta 2.13, total fe–ta 12.23; Leg III fe 3.40, pa 1.31, ti 3.64, mt 2.49, ta 2.06, total fe–ta 12.89; Leg IV fe 3.99, pa 1.14, ti 4.12, mt 3.07, ta 2.17, total fe–ta 14.50.

The opisthosoma is longer than wide (L 5.71, W 3.25, L/W 1.76) and bears 8 tergites. Roemer (1866b) drew a row of 3 large tubercles on each tergite, but Fritsch (1904) interpreted them as shallow grooves. Fritsch (1904) described a row of small tubercles along the anterior edge of each tergite, although whether they are actually on the posterior edge of the previous tergite is ambiguous from his figure. Most probably, there may be swellings on the tergites, as shown by Roemer (1866b), in addition to a row of tubercles along the posterior margins. According to Fritsch (1904), the anal tubercle is large and situated subterminally, but this may well be an artifact. Two long, spinose appendages described by Roemer (1866b) were interpreted as spinnerets by Fritsch (1904), and it is difficult to interpret them otherwise.

Protolycosa cebennensis Laurentiaux-Vieira and Laurentiaux, 1963

Fig. 6

1963 *Protolycosa cebennensis* nov. sp.: Laurentiaux-Vieira and Laurentiaux, p. 26–28; pl. III, figs 4–6.

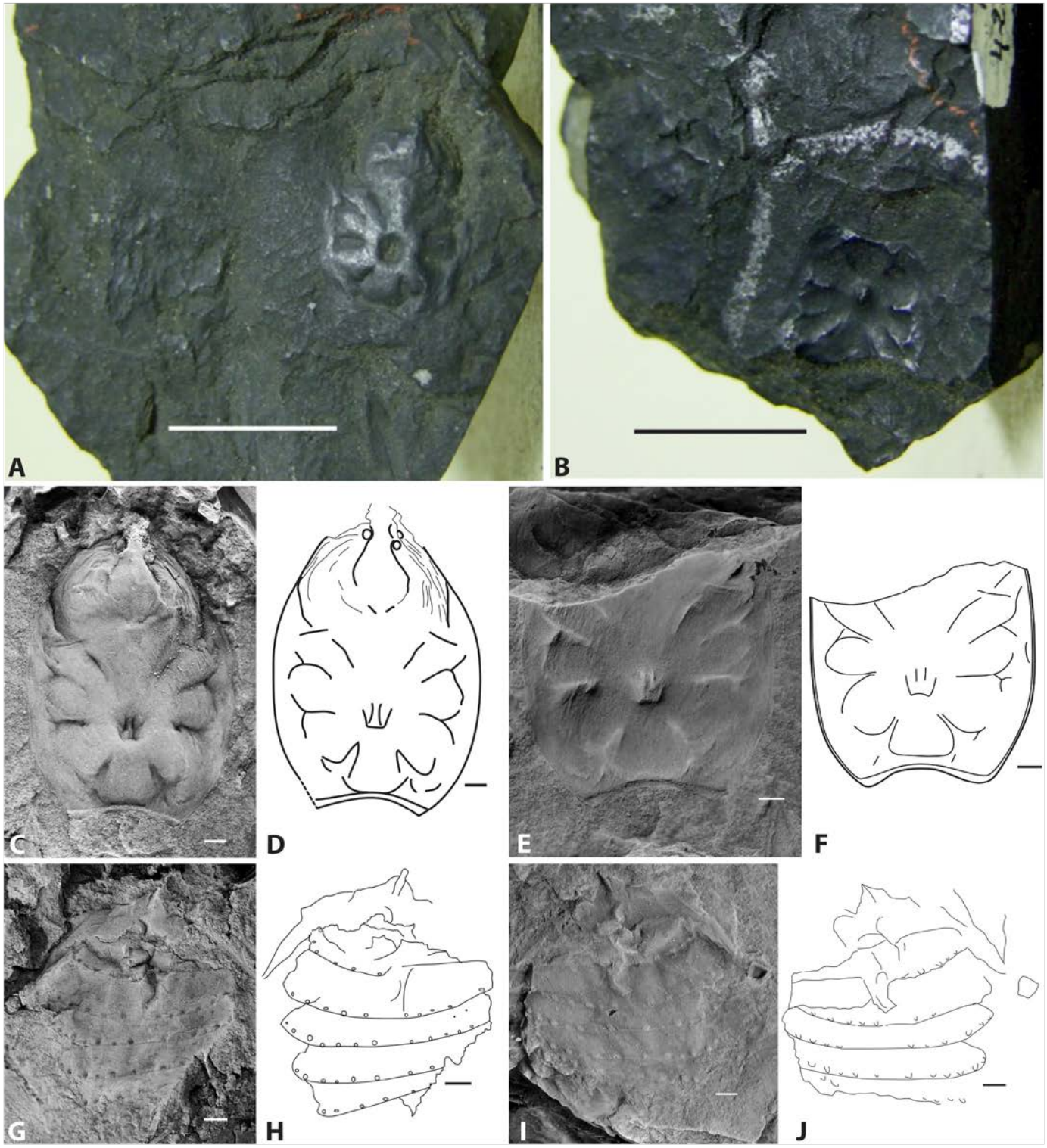

FIGURE 6. *Protolycosa cebennensis* Laurentiaux-Vieira and Laurentiaux, 1963, holotype part and counterpart, MGL 4261 (MHNL), part and counterpart, Carboniferous (basal lower Stephanian, Moscovian), from the Cévennes, Massif Central, France. **A**, photograph of part (dry); **B**, photograph of counterpart (dry); **C**, photograph of carapace of part, whitened with ammonium chloride; **D**, explanatory drawing of C; **E**, photograph of carapace of counterpart, whitened with ammonium chloride; **F**, explanatory drawing of E; **G**, photograph of opisthosoma of part, whitened with ammonium chloride; **H**, explanatory drawing of G; **I**, photograph of opisthosoma of counterpart, whitened with ammonium chloride; **J**, explanatory drawing of I. Scale bars = 10 mm (A–B), 1 mm (C–J).

1993 *Protolycosa cebennensis* Laurentiaux-Vieira and Laurentiaux, 1963: Selden, p. 312.
2006 *Protolycosa cebennensis* Laurentiaux-Vieira and Laurentiaux, 1963: Penney and Selden, p. 27.
2010 *Protolycosa cebennensis* Laurentiaux-Vieira and Laurentiaux, 1963: Selden and Penney, p. 189.
2011 *Protolycosa cebennensis* Laurentiaux-Vieira and Laurentiaux, 1963: Penney and Selden, p. 54.

Material: Holotype, and only known specimen, MGL 4261, part and counterpart, in the collections of Musée d'Histoire Naturelle, Lille (coll. G. Livet).

Occurrence: Le Pin bed, La Grand'Combe coal basin, Carboniferous (basal lower Stephanian, Moscovian), from the Cévennes, Massif Central, France.

Diagnosis: Large *Protolycosa* with piriform anterior cephalic area on carapace, lacking swellings on opisthosomal tergites.

Remarks: This specimen has only been described and figured by Laurentiaux-Vieira and Laurentiaux (1963). The specimen was kindly loaned, and photographs supplied, by Jessie Cuvelier of the Natural History Museum in Lille (Fig. 6). It consists of part and counterpart, the former a complete carapace, the latter with the carapace fractured anteriorly, and both slabs bearing a sequence of opisthosomal tergites about 10 mm removed from the carapace (Fig. 6A–B). The description by Laurentiaux-Vieira and Laurentiaux (1963) is generally accurate (but see measurements below), with the exception that they considered the specimen to lack eyes, and therefore placed it in Arthromygalidae (which was diagnosed by Petrunkevitch (1953) on the basis of lack of eyes). However, the photograph (Fig. 6C) clearly shows a number of spherical structures at the anterior tip of the piriform structure labelled by Laurentiaux-Vieira and Laurentiaux (1963, fig. 4) as "ts, région sommitale." As suggested by Laurentiaux-Vieira and Laurentiaux, the piriform structure cannot be considered as the ocular tubercle, yet the presence of eyes at the anterior end is certain.

Laurentiaux-Vieira and Laurentiaux (1963) did not explicitly define the species, but it can be gleaned from their paper, that they considered the specific differences from *P. anthracophila* to be: *P. cebennensis* exhibits a larger size (the carapace length of *P. anthracophila* is ~5.02, and that of *P. cebennensis* is ~12.04), a more globular opisthosoma, and a greater density of opisthosomal tuberculation.

Description: Carapace subelliptical in outline, lateral sides curved, anterior margin acute, posterior margin recurved and bordered; L 12.04, W 8.15 (max. W slightly more than ½ carapace L, not four-fifths as Laurentiaux-Vieira and Laurentiaux suggested, and which is not borne out by their fig. 4); L/W 1.48. Deep fovea situated ~⅔ length of carapace from anterior margin, bearing pair of deeper apodemes, sloping more gently forward than posteriorly. Furrows radiating from fovea subtending angles of ~60°, ~90°, ~180°, ~250°. At least 5 opisthosomal tergites with gently recurved posterior margins, measuring (sagittal L, W) 1: 1.62, >5.00; 2: 1.71, 7.02; 3: 1.02, 7.02; 4: 1.26, 6.73; 5: 0.93, >4.58. Tergites bear large tubercles along posterior margin, maximally 12 visible per tergite (presumably ~15), ~0.6 between tubercles with larger space (~1.5) between median tubercles; no large swellings or other ornament.

Protolycosa danielsi (Petrunkevitch, 1913)
Fig. 7

1913 *Arthrolycosa danielsi* n. sp.: Petrunkevitch, p. 91; figs 55–56; pl. VIII, figs 45–46.
1928 *Arthrolycosa danielsi* Petrunkevitch, 1913: Savory, p. 268, 283.
1997 *Arthrolycosa danielsi* Petrunkevitch, 1913: Beall, p. 148, fig. 11.17.
2011 *Arthrolycosa danielsi* Petrunkevitch, 1913: Penney and Selden, p. 52.

Diagnosis: *Protolycosa* with triangular projection on anterior tip of carapace; femora only slightly shorter than carapace length.

Material: 7219A,B, part and counterpart, in the collections of Museum of Paleontology, University of Michigan.

Occurrence: Francis Creek Shale Member, Carbondale Formation, Carboniferous (Desmoinesian, Moscovian), Mazon Creek, Grundy County, Illinois.

Remarks: This specimen has a well-preserved carapace, but only the proximal parts of the legs are preserved. Seven tergites of the opisthosoma can be seen. Petrunkevitch (1913, p. 88) distinguished *Arthrolycosa antiqua* from *A. danielsi* on the basis of the former having all femora shorter than the carapace and the eye tubercle not situated at the edge of the carapace, while in the latter the first femur is almost as long as the carapace (the others longer), and the eye tubercle touches the anterior carapace edge. The measurements given here differ somewhat from those of Petrunkevitch, partly because the triangular projection at the front of the carapace of *danielsi* is included here. Nevertheless, the femora of *danielsi* are clearly larger in relation to the carapace length than in the holotype of *A. antiqua*. The ratio of carapace L/femur I L in *danielsi* is 1.11, while in *antiqua* it is 1.80. If all femora are included, these ratios change a little to *danielsi* 1.11, *antiqua* 2.17. However, the eye position is no use in distinguishing the species because the front of the carapace cannot be seen in *antiqua*, while in *danielsi* there is a triangular projection in front of the eye tubercle.

This species is here removed from *Arthrolycosa* and referred to *Protolycosa* on the basis of the carapace shape, which closely matches that of *Protolycosa* in being distinctly longer than wide, and suboval in outline with curved lateral margins. Note that the carapace L/femora L ratio of other *Protolycosa* species approach that of *A. antiqua*: *P. anthracophila* all femora 1.51, feI 1.81; *P. suazoi* all femora 1.80, feI 1.67. They are all relatively longer than in *Arthrolycosa*.

Description: Body L 15.32. Carapace suboval in outline, with recurved, bordered posterior margin, small median triangular projection at anterior tip (L 0.32, W 0.69), L 6.00 (including triangular projection), W 5.08, L/W 1.18; ocular tubercle just inside anterior margin, L 1.03, W 1.16, L/W 0.89; fovea situated ⅔ of carapace length from anterior margin. Chelicera L 2.47, W 1.42, L/W 1.74. Legs robust, long, subequal (based on femora), formula (based on femora) IV>II>III>I . Podomere lengths: Pedipalp cx 1.77. Leg I cx 2.01, fe 5.80, pa 1.28. Leg II cx 2.44, fe 5.87. Leg III cx 2.61, tr 1.13, fe 5.37. Leg IV tr 1.18, fe 6.33. Opisthosoma L >8.78, W >4.99, L/W 1.76; bearing at least 7 tergites, measuring (sagittal L, W, L/W): 1: 0.56, >1.46, 0.39; 2: 0.83, >2.85, 0.29; 3: 1.34, >4.41, 0.33; 4: 1.36, >4.71, 0.30; 5: 1.37, >4.86, 0.28; 6: 1.23, >4.54, 0.27; 7: 0.99, >2.89, 0.34. Row of large tubercles along posterior margin of each tergite.

Protolycosa suazoi n. sp.
Figs. 8–12

Diagnosis: Legs relatively short (ratio feI L : car L 1.80: approaching that of *Arthrolycosa*), which in *Protolycosa anthracophila* is 1.51, and *P. danielsi* 1.11. Difference between lengths (fe–mt) of legs I and IV greater (ratio leg I:leg IV 0.79, than that of *P. anthracophila*, (ratio leg I:leg IV 0.72).

Etymology: In honor of the collector, Thomas L. Suazo.

Material: NMMNH P-71523, part and counterpart, in the collections of the New Mexico Museum of Natural History (Coll. Thomas L. Suazo 2014).

Occurrence: Locality 345, Kinney Brick Quarry, Tinajas Member, Atrasado Formation, Carboniferous (Missourian, Kasimovian), Bernalillo, New Mexico.

Remarks: This specimen clearly belongs in *Protolycosa*

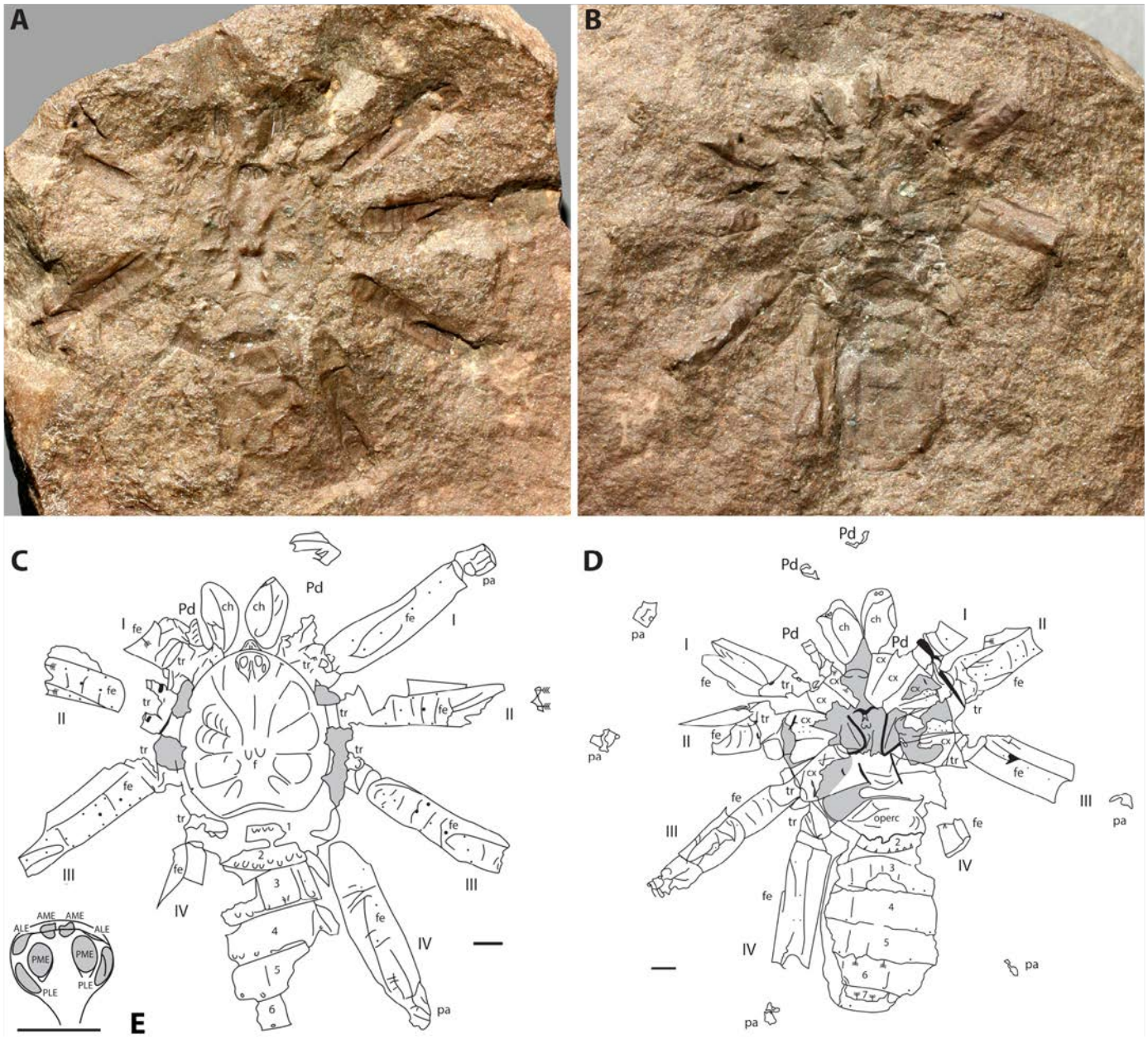

FIGURE 7. *Protolycosa danielsi* (Petrunkevitch, 1913), holotype, 7219A,B (UMMP), part and counterpart, Carboniferous (Desmoinesian, Moscovian) of Mazon Creek, IL. **A**, photograph of part (dry); **B**, photograph of counterpart (dry); **C**, explanatory drawing of A; **D**, explanatory drawing of B. **E**, detailed drawing of ocular tubercle. Scale bars = 1 mm.

on account of its suboval carapace outline, pointed anteriorly, paired foveal apodemes shallowing anteriorly, and lack of a transverse ridge behind the fovea.

Numerous bumps and cavities are present on the opisthosoma, which are probably artifacts of mineralization. The pair of granular areas situated anterolaterally on the opisthosoma (seen as pale patches on Fig. 10) and a pair of knobs on the lateral sides of the opisthosoma (brown knobs on Fig. 10) may be related to the specimen. These features are most probably taphonomic pyritic clots, but could nevertheless be related to the morphology, e.g., marking areas of the book lungs. The ventral side of the opisthosoma is smooth, lacking sternites, which are likely to be preserved on the specimen if they were present; four areas of cuticle extend beyond the central region and represent spinnerets. The anterior edge of each of these is clearly defined, marking the anterior margin of the appendage (sp on Fig. 9B, Fig. 12). Presumably these are anterior and posterior lateral spinnerets; simple spigots are seen at the posterior edge of the right ALS (Fig. 12). The arrangement of these spinnerets, extending laterally beyond the apparent margin of the opisthosoma, is reminiscent of those seen in *Protolycosa anthracophila* (Fig. 5).

Description: Body L ≥11.72. Carapace suboval in dorsal outline, with wider, recurved, posterior margin, more pointed anteriorly, with anteriorly located eye tubercle. Fovea formed of paired depressions, shallowing anteriorly, located centrally on carapace. Shallow depressions radiate posterolaterally, laterally, and anterolaterally from foveal region (Fig. 8, red). Carapace L 5.88, W 4.82, L/W 1.22. Pedipalp shorter than legs, unmodified, lacking claw. Legs subequal in length, leg formula IV>III>II>I

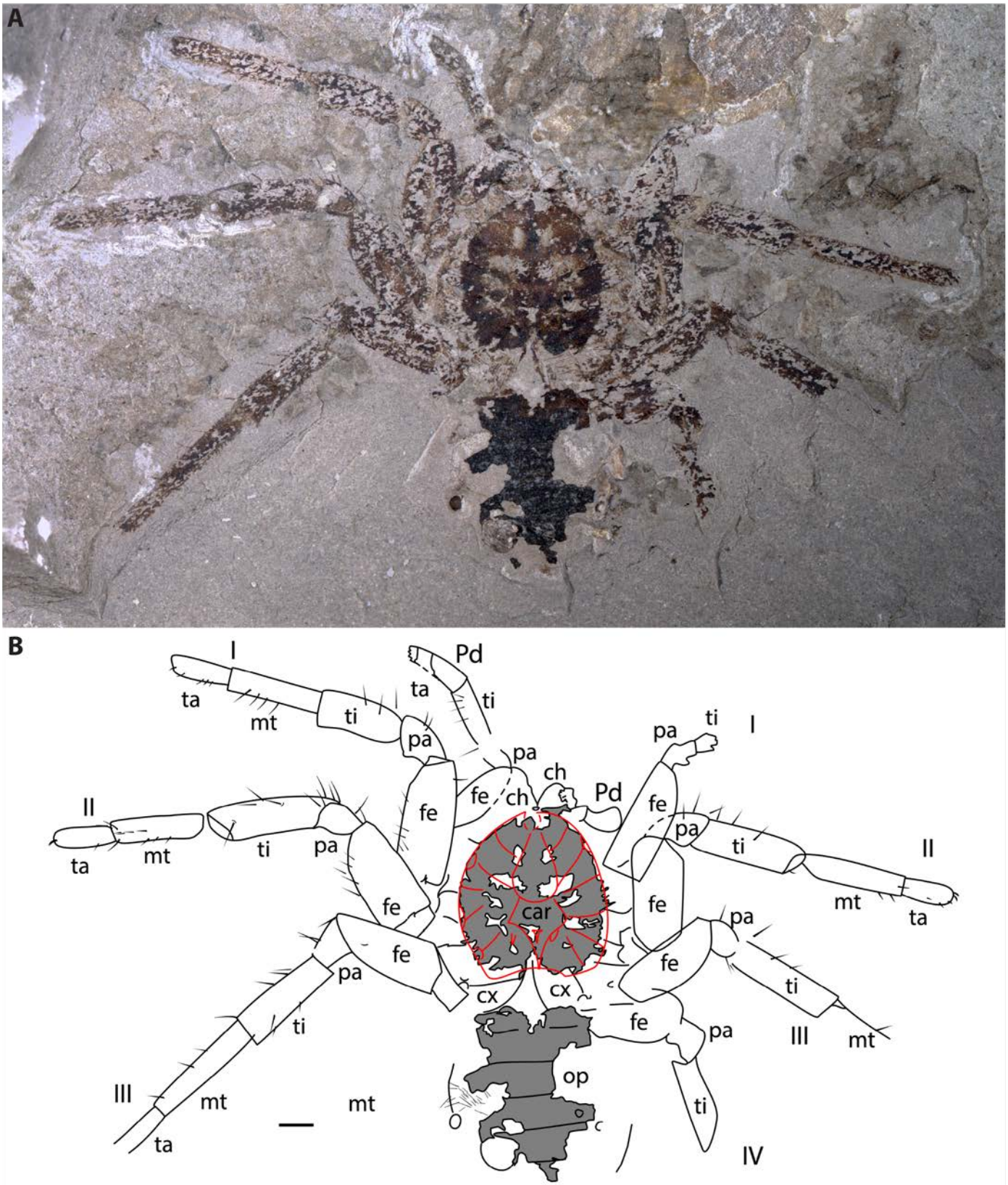

FIGURE 8. *Protolycosa suazoi* n. sp., holotype, P-71523 (NMMNH), part, Carboniferous (Missourian, Kasimovian), Kinney Brick Quarry, Bernalillo, New Mexico. **A**, photograph under ethanol; **B**, explanatory drawing of A; red lines show carapace morphology seen on specimen dry under low-angle light. Scale bar = 1 mm.

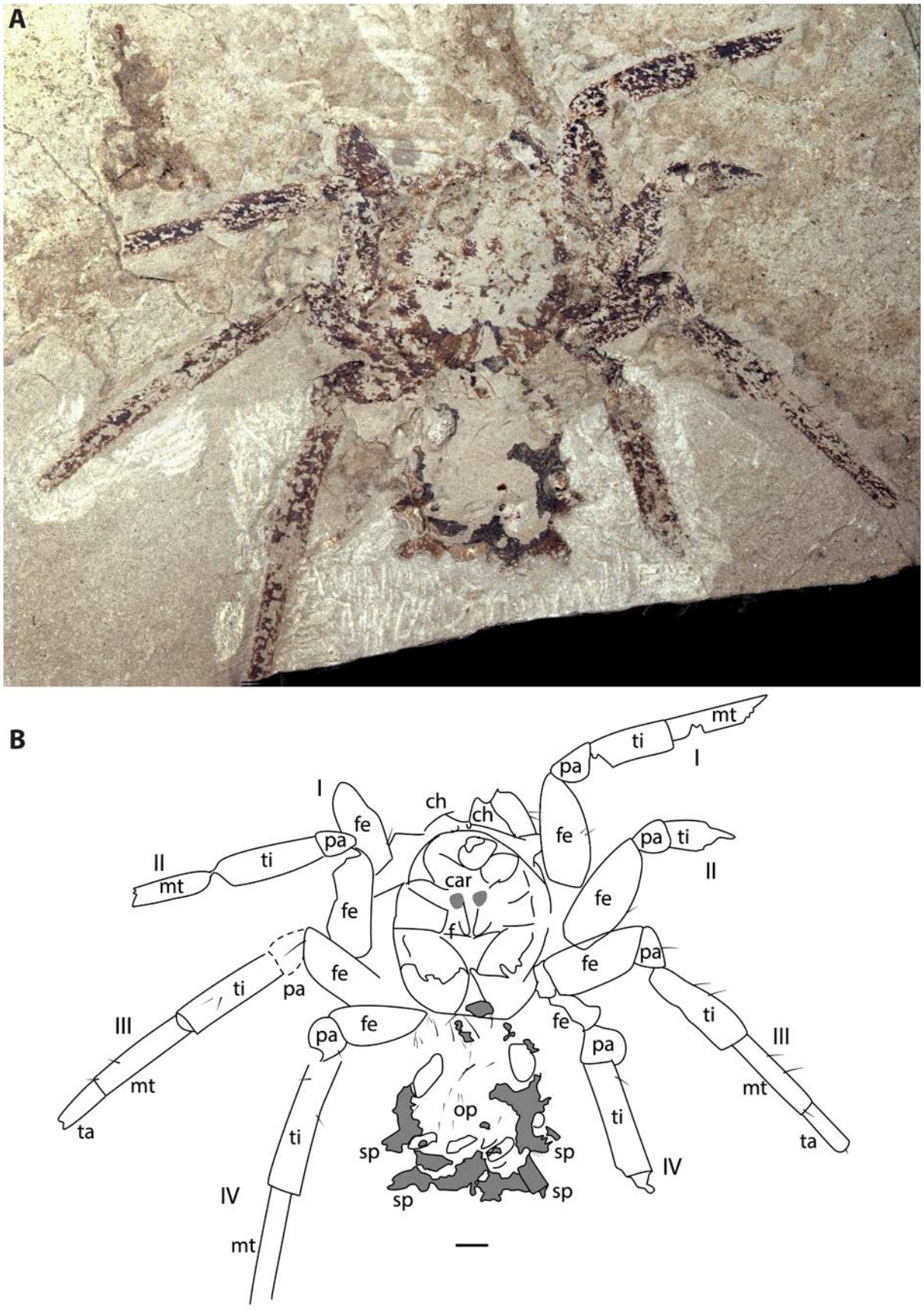

FIGURE 9. *Protolycosa suazoi* n. sp., holotype, P-71523 (NMMNH), counterpart, Carboniferous (Missourian, Kasimovian), Kinney Brick Quarry, Bernalillo, New Mexico. **A**, photograph under ethanol; **B**, explanatory drawing of A. Scale bar = 1 mm.

FIGURE 10. *Protolycosa suazoi* n. sp., holotype, P-71523 (NMMNH), Carboniferous (Missourian, Kasimovian), Kinney Brick Quarry, Bernalillo, New Mexico. Photographs of part and counterpart superimposed, under ethanol. Scale bar = 1 mm.

(based on fe–mt lengths). Tibiae and metatarsi approximately equal in length; tarsi shorter than metatarsi, bearing three short, talon-like claws, paired claws only slightly longer than median claw, and bearing few (≥2) short teeth (Fig. 11). Lengths of podomeres: Pedipalp fe 2.05, pa 0.83, ti 1.94, ta 1.84, total fe–ta 6.66; Leg I fe 3.52, pa 1.30, ti 2.38, mt 2.63, ta 1.82, total fe–mt 9.83, total fe–ta 11.65; Leg II fe 3.19, pa 1.25, ti 3.22, mt 2.94, ta 1.71, total fe–mt 10.61, total fe–ta 12.32; Leg III fe 3.24, pa 1.38, ti 3.12, mt 3.39, ta 1.79, total fe–mt 11.13, total fe–ta 12.92; Leg IV fe 3.10, pa 1.32, ti 3.92, mt 4.08, total fe–mt 12.42. Opisthosoma at least as long as carapace, suboval, dorsal surface with ≥6 tergites, subequal in length, measuring (sagittal L, W, L/W) 1: 0.71, 3.36, 0.21; 2: 0.90, 3.21, 0.28; 3: 1.01, 3.66, 0.28; 4: 0.97, 3.45, 0.28; 5: 0.93, 3.30, 0.28; 6: fragmentary, L >0.65. Ventral opisthosoma lacking segmentation; four spinnerets extend laterally from mid-posterior region of opisthosoma; simple spigots along posterior edge of at least ALS (Fig. 12).

Family Palaeothelidae n. fam.

Included genus: *Palaeothele* Selden, 2000 (= *Eothele* Selden, 1996, preoccupied).

Diagnosis: Mesothelae in which the opisthosomal tergites are distinct, do not extend the full width of the opisthosoma, and are set in soft cuticle (*contra* Arthrolycosidae). Wide anterior–posterior separation of the anterior and posterior spinnerets (*contra* Liphistiidae, see Haupt, 2003, p. 89).

Geological range: Carboniferous (Desmoinesian, Moscovian) to Carboniferous (late Stephanian, Gzhelian).

Remarks: In addition to the characters listed above, the biserially dentate chelicerae seen in *Palaeothele montceauensis* (Selden, 1996) may be a feature of the family but are known only from the type species.

Genus *Palaeothele* Selden, 2000

Type species: *Palaeothele montceauensis* (Selden, 1996b).
Other species: *Palaeothele onoi* n. sp.
Diagnosis: As for the family (monotypic).

Palaeothele onoi n. sp.

Fig. 13

1913 *Arthrolycosa antiqua* Harger: Petrunkevitch, p. 90–91; pl. VIII, fig. 43.
2014 *Arthrolycosa antiqua* Harger, 1874: Selden et al., p. 300; fig. 1e.

Diagnosis: The new species differs from the type species in that the anterior spinnerets lie in the anterior half of the opisthosoma, whereas in the type species, all spinnerets lie in the posterior half.

Etymology: In recognition of the work done by Japanese arachnologist Hirotsugu Ono on mesothele spiders of East Asia.

Material: IP.00162, part and counterpart, in the collections of Yale Peabody Museum (Coll. S. S. Strong).

Occurrence: Francis Creek Shale Member, Carbondale Formation, Carboniferous (Desmoinesian, Moscovian), Mazon Creek, Grundy County, Illinois.

Remarks: This specimen was referred to *Arthrolycosa antiqua* by Petrunkevitch (1913, p. 90–91), who gave little

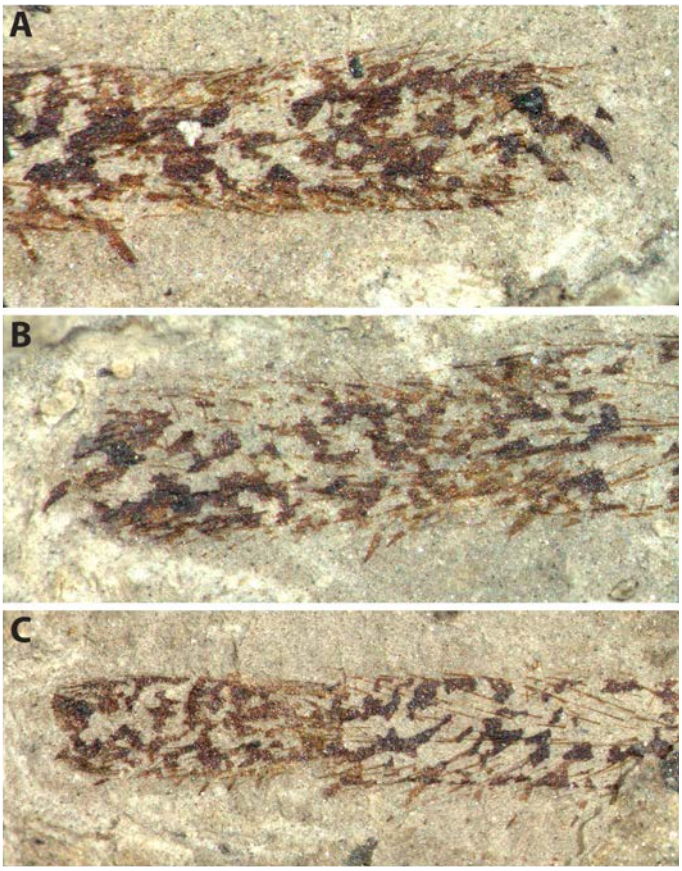

FIGURE 11. *Protolycosa suazoi* n. sp., holotype, P-71523 (NMMNH), part, Carboniferous (Missourian, Kasimovian), Kinney Brick Quarry, Bernalillo, New Mexico, all photographs under ethanol. **A**, tarsus of right leg II, distal to right; **B**, tarsus of left leg II, distal to left; **C**, metatarsus and tarsus of left leg I, distal to left.

description. My restudy has revealed a considerable amount of detail overlooked by Petrunkevitch (Fig. 13). For example, it is one of the few specimens of Paleozoic mesotheles to show the ventral surface of the opisthosoma with book-lung opercula and spinnerets. The opisthosoma is squashed obliquely laterally, appearing as though it has rolled, so that the midlines of the dorsal tergites and the ventral spinnerets appear to the right of the midline of the carapace (Fig. 13); there is no other apparent distortion. Note that, in comparing this specimen to *Palaeothele montceauensis* (e.g., Selden, 1996b, figs 3–4) in the present paper, only the visible tergites are numbered, hence there appears to be a mismatch in tergite numbers, which is probably an artifact of the numbering system. There is little to distinguish this new species from *Palaeothele montceauensis*. They are approximately the same size. However, in the type species, the spinnerets appear to be entirely in the posterior half of the opisthosoma, while in the new species at least the anterior spinnerets are further forward, anterior to the mid-length (Fig. 13).

Description: Body L 14.12. Carapace suboval in outline with nearly straight, bordered posterior margin, ocular area at anterior border, between gently outwardly curved pair of grooves diverging from fovea; fovea a pair of depressions shallowing anteriorly, situated ~⅔ length of carapace from anterior, carapace L 5.05, W 4.40, L/W 1.15. Chelicera L 1.42, W 1.18, L/W 1.21. Legs robust, short. Podomere lengths: Leg I mt 2.13, ta 1.91; Leg II pa 1.22, ti 3.52. Opisthosoma L 8.34, W 5.83, L/W 1.43. Eight dorsal tergites, lengths 1–5 ~1.0, 6 ~0.6, 7–8 ~0.3, with rounded lateral margins, each bearing row of small tubercles along anterior edge. Lateral sides of opisthosoma with wrinkled cuticle (Fig. 13). Ventral opisthosoma bearing two opercular plates anteriorly; 4 anterior spinnerets (2 ALS, 2 small AMS) behind second operculum, situated at nearly ½ length of opisthosoma; 4 posterior spinnerets (2 PLA, 2 PMS) situated at ~⅔ length of opisthosoma (Fig. 13). Anal tubercle of 2 segments situated at posterior tip of opisthosoma.

Family Arthromygalidae Petrunkevitch, 1923

2017 Parvithelidae Wunderlich, p. 95. n. syn.

Included genera: *Geralycosa* Kušta, 1889, *Parvithele* Wunderlich, 2017, *Pulvillothele* Wunderlich, 2017.

Emended diagnosis: Tarsi with elongate paired claws and an apical empodium (pseudopulvillus of Wunderlich, 2017); legs slender; carapace nearly as wide as long, lacking a pronounced ocular tubercle; paracymbial spines apically notched.

Geological range: Carboniferous (early Moscovian) to Cretaceous (earliest Cenomanian).

Remarks: Arthromygalidae was erected by Petrunkevitch (1923, p. 151) thus: "The Arthromygalidae are easily distinguished both from the Liphistiidae and the Arthrolycosidae by the arrangement of their eyes in two rows and by the presence of two smooth claws on their tarsi." Later, Petrunkevitch (1949, p. 276) emended this diagnosis so that the family Arthromygalidae was distinguished from Arthrolycosidae by its lack of an eye tubercle. In the *Treatise*, Petrunkevitch (1955, p. P133), diagnosed Arthromygalidae thus: "Eye tubercle wanting, presence of eyes doubtful." The problem is that in many fossil spiders with an eye tubercle, because the tubercle stands proud of the carapace surface, it is commonly split off when the rock is broken open; see, for example, Figures 5, 8, 10, 14–18. Hence, this character is not suitable to diagnose the family. On the other hand, the characteristic tarsal arrangement (see below) is distinctive.

The tarsal arrangement seen in *Geralycosa fricii* Kušta, 1889 was first described by Fritsch (1904, p. 15) thus: "Die Füsse sind alle sehr lang, behaart und am Ende mit zwei geraden Krallen bewaffnet, zwischen denen noch ein chitinisirter Mittellappen liegt." Thus, he recognized that the paired claws were elongated, and the median structure was likely chitinized. Petrunkevitch (1953, p. 105) likened the Mittellappen to the pulvillus of amblypygids and the arolium of pseudoscorpions. He pointed out that such a structure, which is used for clinging to smooth surfaces such as shiny leaves and rocks, is not found in any modern spiders, and that that it gave evidence that the fossil spider was able to cling to smooth surfaces. However, as pointed out by Fritsch (1904), the Mittellappen is chitinized, whereas the pulvillus or arolium is a soft, pliable structure. A tarsal pulvillus occurs in some amblypygids (the Pulvillata of Quintero, 1985). However, Wolff et al. (2017) pointed out that pulvillus is an erroneous term for this structure, which normally refers to paired lobes beneath the claws in insects, and the term arolium is preferred. Wolff et al. (2017, p. 527) defined the arolium as a median unpaired lobe- or cushion-like attachment organ situated on the pretarsus. This structure in amblypygids and insects is used for clinging to smooth surfaces, and it differs considerably from the structure seen in *Geralycosa*, which is an elongate, triangular structure, rather than a soft pad. The structure in *Geralycosa* is notched distally, giving the impression of a derivation from a paired structure, and is sclerotized. Its position, in place of a median claw, suggests that a better term for it would be empodium (see Wolff, 2015). Its function seems unlikely to have involved clinging to smooth surfaces, and is unknown.

The family Parvithelidae was erected by Wunderlich (2017) for two genera and four species from Burmese amber. The family was diagnosed by the presence of a so-called pseudopulvillus

FIGURE 12. *Protolycosa suazoi* n. sp., P-71523 (NMMNH), counterpart, Carboniferous (Missourian, Kasimovian), Kinney Brick Quarry, Bernalillo, New Mexico. Photograph (under ethanol) of posterior opisthosoma, showing spinnerets.

(Wunderlich, 2017, p. 91), and apically notched paracymbial spines in the male. Wunderlich's pseudopulvillus, at least in *Pulvillothele*, is very similar to the Mittelappen in *Geralycosa*. It is sclerotized and apically notched. The paired claws in *Parvithele* and *Pulvillothele* are elongate, as in *Geralycosa*, but also bear small spines, and there is a small, toothed, median claw as well (Wunderlich, 2017, figs. 21–22). Interestingly, tarsi of the spider-relative *Chimerarachne* Wang et al., 2018 bear elongate, toothed, paired claws, a toothed median claw, and a spatulate structure (called a pulvillus by Wang et al., 2018). Apart from the facts that no teeth can be seen on the paired claws, nor is a median claw visible, the tarsal armature of *Geralycosa* is remarkably similar. The tarsal structures of *Geralycosa*, *Parvithele*, *Pulvillothele*, and *Chimerarachne* are probably homologous and, because of their presence in *Chimerarachne*, are likely plesiomorphic for Araneae. Other characters of *Chimerarachne* (e.g. the anal flagellum) are not present in arthromygalids and parvithelids, which are here synonymized under the older name Arthromygalidae Petrunkevitch, 1923.

Genus *Geralycosa* Kušta, 1889

Type species: *Geralycosa fricii* Kušta, 1889
Other species: None.

Diagnosis: Large arthromygalid (body length ~14–18); shallow, slightly recurved fovea and pair of depressions on carapace posterior to fovea; untoothed paired tarsal claws; empodium (pseudopulvillus) short, triangular, sclerotized and notched.

Remarks: Kušta (1889) gave an overview of the genera he referred to Arthrolycosidae, thus: *Arthrolycosa*: cephalothorax much larger than opisthosoma, *Eolycosa*: cephalothorax larger than opisthosoma, *Scudderia*: cephalothorax about as large as opisthosoma, *Geralycosa*: cephalothorax slightly smaller than opisthosoma, *Rakovnicia*: cephalothorax much smaller than opisthosoma. From this series, he deduced that *Rakovnicia* was the earliest and most primitive, with the smallest cephalothorax, and the lineage extended to *Arthrolycosa*, with the largest cephalothorax, as the most advanced form. It is true that the cephalothorax (carapace) of *Geralycosa* is slightly smaller than the opisthosoma; however, this character is not a good one on which to define the genus. The carapace does have a distinct morphology, however. The fovea is a slightly recurved, shallow depression, and there is a pair of slight depressions towards the posterior part of the carapace, half-way between the fovea and the posterior border. These depressions are arranged at about ⅓ and ⅔ the width of the carapace at that point (Figs. 14–16).

Geralycosa fricii Kušta, 1889
Figs. 14–16

1889 *Geralycosa Fričii* n. gen. n. sp.: Kušta, p. 196; fig. 1.
1890 *Geralycosa Fricii* Kusta: Haase, p. 634.
1891 *Geralycosa fričii* Kušta, 1888: Scudder, p. 26.
1904 *Arthrolycosa Beecheri* Fr.: Fritsch, p. 9–10; fig. 5; pl. 1, figs 3–5. n. syn.
1904 *Arthrolycosa fortis* Fr.: Fritsch, p. 8–9; fig. 4; pl. 1, figs 1–3. n. syn.
1904 *Geralycosa Fritschii* Kušta: Fritsch, p. 14–15; figs 11–13; pl. 3; pl. 12, figs 4–5.
1913 *Arthrolycosa beecheri* Fritsch: Petrunkevitch, p. 87. n. syn.
1913 *Arthrolycosa fortis* Fritsch: Petrunkevitch, p. 87. n. syn.
1913 *Geralycosa fritschii* Kušta: Petrunkevitch, p. 87.
1928 *Arthromygale beecheri* Fritsch, 1904: Savory, p. 268, 283. n. syn.
1928 *Arthromygale fortis* Fritsch, 1904: Savory, p. 268, 283. n. syn.
1928 *Geralycosa fritschii* Kusta, 1888: Savory, p. 268, 283.
1949 *Arthromygale fortis* Fritsch: Petrunkevitch, p. 276. n. syn.

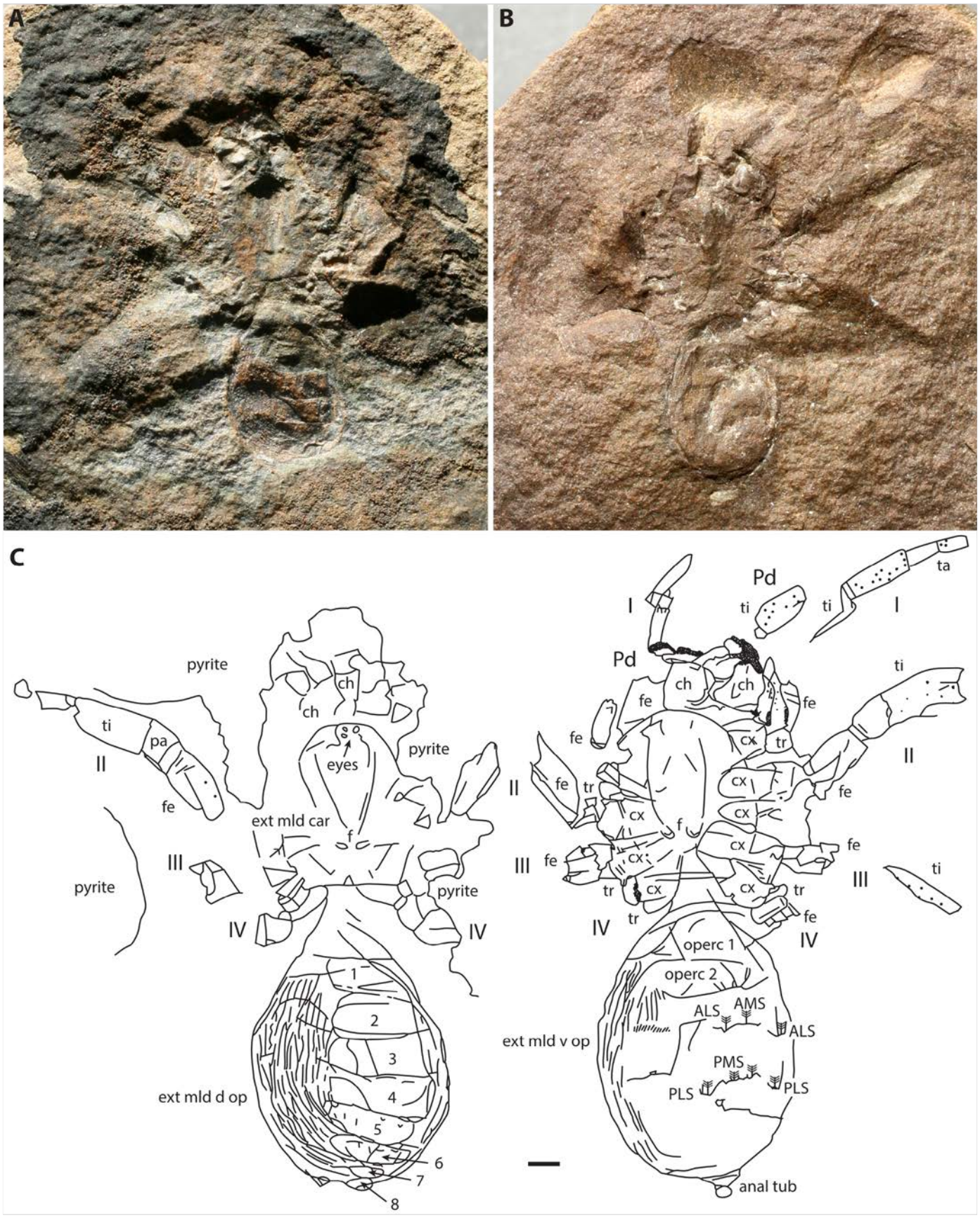

FIGURE 13. *Palaeothele onoi* n. sp., holotype, IP.00162 (YPM), part and counterpart, Carboniferous (Desmoinesian, Moscovian) of Mazon Creek, IL. **A**, photograph of part (dry); **B**, photograph of counterpart (dry); **C**, explanatory drawing of A; **D**, explanatory drawing of B. Scale bar = 1 mm.

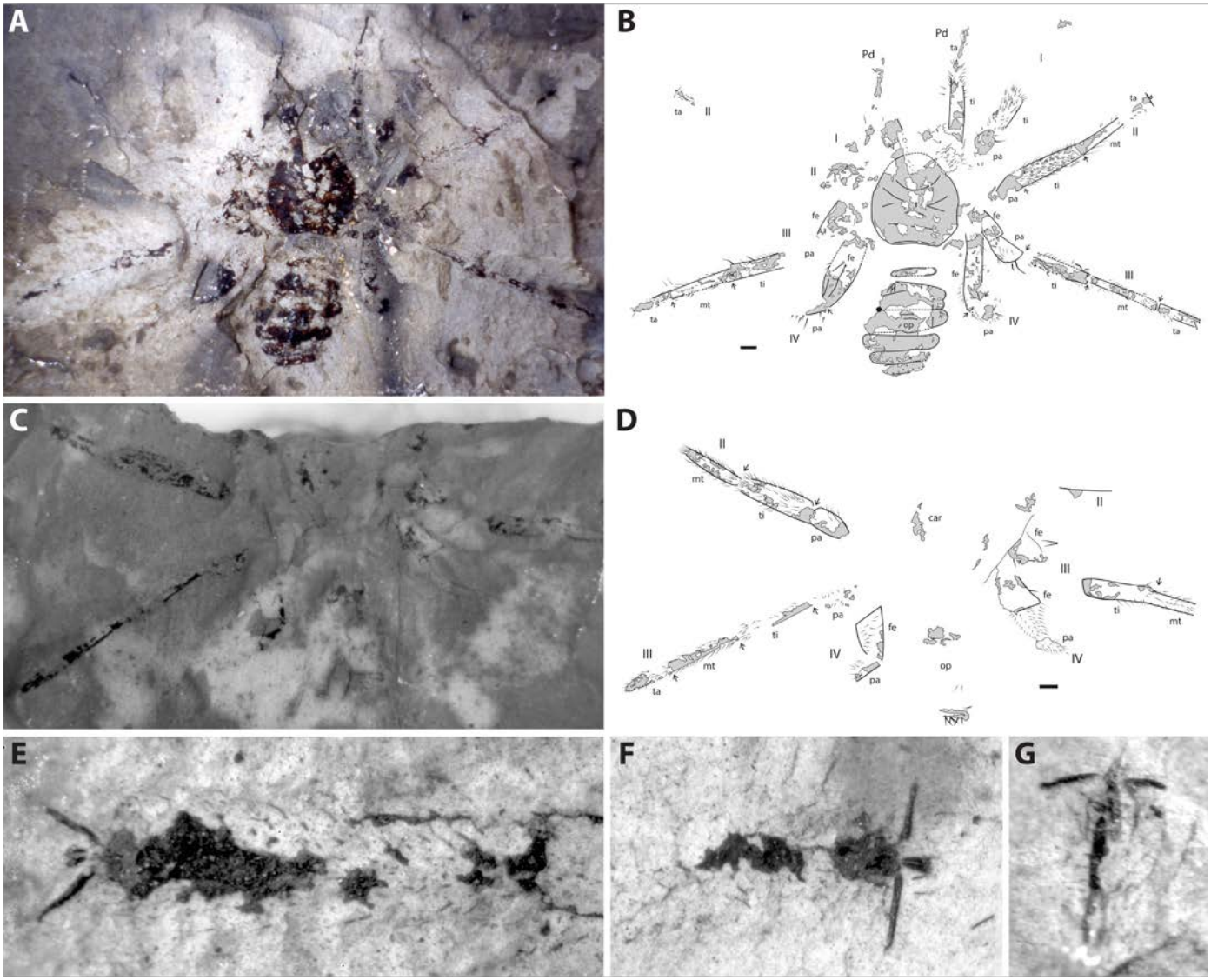

FIGURE 14. *Geralycosa fricii* Kušta, 1889, holotype, CGH 1943 (part) and CGH 1945 (counterpart) (NMP), Carboniferous (lower Moscovian, Westphalian C), Moravia mine, near Rakovník, Czech Republic, photographs under ethanol. **A**, photograph of part; **B**, explanatory drawing of A; **C**, photograph of counterpart; **D**, explanatory drawing of C; **E**, tarsus of left leg III of part, distal to left; **F**, tarsus of right leg II of part, distal to right; **G**, tarsus of left leg II of part, distal to top. Scale bars = 1 mm.

1953 *Arthromygale fortis* (Fritsch): Petrunkevitch, p. 103; pl. 26, fig. 107; pl. 53, fig. 190. n. syn.
1953 *Arthromygale fortis* (Fritsch): Petrunkevitch, p. 103; pl. 26, fig. 108; pl. 54, fig. 195. n. syn.
1953 *Geralycosa fritschi* Kušta: Petrunkevitch, p. 105–106; pl. 27, figs 109–110; pl. 52, figs 185–187.
1955 *Arthromygale fortis* (Frič, 1904): Petrunkevitch, p. P134; fig. 99,3. n. syn.
1955 *Geralycosa fritschi*: Petrunkevitch, p. P135; fig. 99,2.
1986 *Arthromygale fortis* (Frič, 1904): Zajíc and Štamberg, p. 69. n. syn.
1986 *Geralycosa fritschi* Kušta, 1888: Zajíc and Štamberg, p. 69.
1991 *Arthromygale fortis* Fritsch, 1904: Rohdendorf, p. 751; fig. 1414. n. syn.
1991 *Geralycosa fritschi* Kušta, 1888: Rohdendorf, p. 751; fig. 1415.
2006 *Arthromygale beecheri* (Fritsch, 1904): Penney and Selden, p. 27. n. syn.
2006 *Arthromygale fortis* (Fritsch, 1904): Penney and Selden, p. 27. n. syn.
2006 *Geralycosa fritschi* Kušta, 1888: Penney and Selden, p. 27; fig. 3.
2008 *Arthromygale beecheri* (Frič, 1904): Štamberg and Zajíc, p. 53; fig. 27. n. syn.
2008 *Arthromygale fortis* (Frič, 1904): Štamberg and Zajíc, p. 53; fig. 26. n. syn.
2008 *Geralycosa fricii* Kušta, 1888: Štamberg and Zajíc, p. 54; fig. 29.
2011 *Arthromygale beecheri* (Frič, 1904): Penney and Selden, p. 54. n. syn.
2011 *Arthromygale fortis* (Frič, 1904): Penney and Selden, p. 54. n. syn.
2011 *Geralycosa fritschi* Kusta, 1888: Penney and Selden, p. 54; fig. 44.

Material: CGH 1937 (Inv. 804) (Me 60), holotype of *Arthrolycosa fortis* Fritsch, 1904; CGH 1939 (Inv. 811) (Me 59), holotype of *Arthrolycosa beecheri* Fritsch, 1904; and CGH 1943 and 1945 (Me 64), holotype of *Geralycosa fricii* Kušta, 1889, all

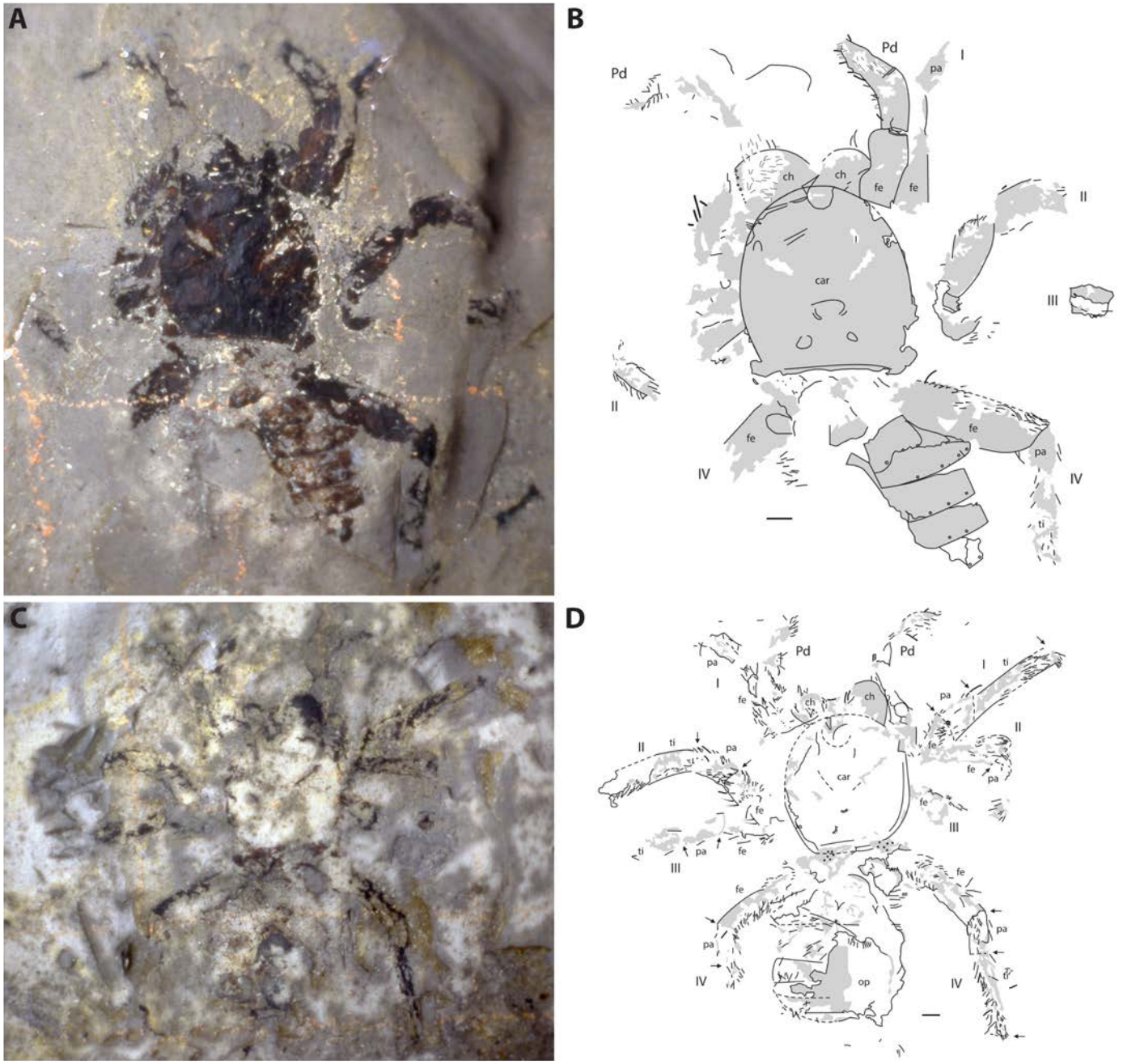

FIGURE 15. *Geralycosa fricii* Kušta, 1889, holotype of *Arthrolycosa beecheri* Fritsch, 1904, CGH 1939 (part) (A–B), and holotype of *Arthrolycosa fortis* Fritsch, 1904 CGH 1937 (counterpart) (NMP), Carboniferous (lower Moscovian, Westphalian C), Moravia mine, near Rakovník, Czech Republic, photographs under ethanol. **A**, photograph of part; **B**, explanatory drawing of A; **C**, photograph of counterpart; **D**, explanatory drawing of C. Scale bars = 1 mm.

in the collections of the National Museum, Prague.

Occurrence: Radnice Member, Kladno Formation, Carboniferous (lower Moscovian, Westphalian C), Moravia mine, near Rakovník, Czech Republic.

Remarks: Petrunkevitch (1953) gave a full redescription of *Geralycosa fricii*, and this study confirms his description (Fig. 14). Petrunkevitch's (1953, figs. 109–110) figures are stylized, and his photographs (1953, figs 185–187) give a better idea of the morphology (but note that these photographs are printed in reverse). The anterior tip of the carapace is lost (see Fritsch, 1904, pl. 3; Petrunkevitch, 1953, fig. 185), so if eyes were present in an anterior cluster they would not be seen on the specimen. Part of the left chelicera is preserved. Leg patellae bear characteristic long, curved spines, seen on right legs I and III and left leg IV (Fig. 14). A characteristic feature of this specimen is the long, paired tarsal claws, which are disposed at a high angle to the tarsus, and the median, bipartite, triangular structure. These are seen clearly on left legs II and III, right leg II, and in a rotated position on right leg III (Fig. 14). As Petrunkevitch (1953, p. 105) suggested, this structure reminds one of the pulvillus of other arachnid orders, but pulvilli are weakly sclerotized, whereas it is likely that in the fossil this structure was sclerotized (see Remarks under Arthromygalidae, above).

Petrunkevitch (1923) erected the genus *Arthromygale* for *Arthrolycosa fortis* Fritsch, 1904, *A. beecheri* Fritsch, 1904 and *Scudderia carbonaria* Kušta, 1889. Later, Petrunkevitch (1949) included *Arthrolycosa tarda* Fritsch, 1912, and probably *Eolycosa lorenzi* Kušta, 1885 and *Palaranea borassifolia* Frič,

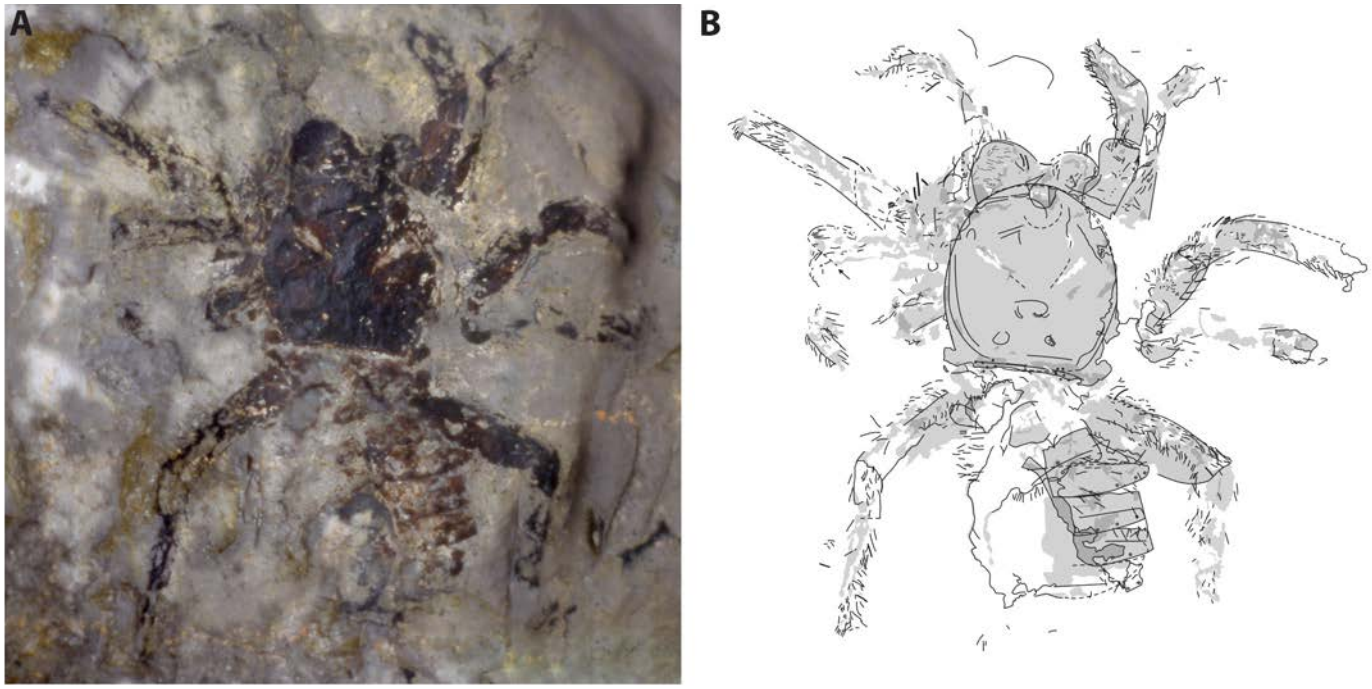

FIGURE 16. *Geralycosa fricii* Kušta, 1889, holotype of *Arthrolycosa beecheri* Fritsch, 1904, CGH 1939 (part) (A–B), and holotype of *Arthrolycosa fortis* Fritsch, 1904 CGH 1937 (counterpart) (NMP), Carboniferous (lower Moscovian, Westphalian C), Moravia mine, near Rakovník, Czech Republic, photographs under ethanol. **A**, photograph of part and counterpart superimposed; **B**, explanatory drawings of part and counterpart superimposed.

1873 in the genus. In 1953, having had a chance to study the specimens, Petrunkevitch retained only the first two of these in *Arthromygale*, synonymizing them into *A. fortis*. Fritsch (1904) described and figured these fossils with eyes, but Petrunkevitch thought the "eyes" were merely granules of matrix. This study of these two specimens shows quite clearly that they are actually part and counterpart of the same specimen! The photographs in Petrunkevitch (1953, Figs 190, 195) are not easily comparable, being in different orientations, at slightly different scales, and on different pages, but notice that the parts of one specimen that have black cuticle preserved match parts of the other where cuticle is missing (see Figs. 15–16). The whole specimen is very flat so that relief, e.g., carapace grooves and raised areas, is determined by the way the cuticle splits across part and counterpart (Fig. 16).

Arthromygale fortis/beecheri and *Geralycosa fricii* are considered to be conspecific based on their similar size; similar length and shape of pedipalps; robust legs of similar proportions; similar carapace shape and pattern of fovea, depressions, and furrows (Figs 14–16); and similar opisthosomas. They occur in the same beds at the same locality

Description of CGH 1943 and 1945 (holotype of *Geralycosa fricii* Kušta, 1889): Body L 13.92. Carapace suboval in outline, with distinct, slightly recurved, bordered, posterior margin; widest ~⅔ of carapace length from anterior margin; distinct, recurved posterior margin to cephalic part, situated ~⅓ of carapace length from anterior margin; transverse, slightly recurved fovea ~⅔ of carapace length from anterior margin. Carapace L 5.77, W 5.32, L/W 1.08. Three grooves radiate from foveal region to lateral margins; pair of slight depressions towards posterior part of carapace. Pedipalps and all walking legs generally setose; patellae, distal tibiae with long, curved spines. Pedipalp pediform, total L (measured from edge of car to tarsal tip 9.53). Legs relatively slender, total L (measured from edge of car to tarsal tip 9.53): Leg II 14.38, Leg III 17.75. Tarsi bearing long, paired claws disposed at high angle to the tarsus, median, bipartite, chitinized triangular structure with apical notch. Podomere measurements: Leg II pa 2.0, ti 4.31, mt 3.49, ta 2.21; Leg III pa 2.13, ti 4.38, mt 4.22, ta 2.81; Leg IV fe 4.79. Opisthosoma L 6.90, W 5.40, L/W 1.28, bearing at least 7 tergites, measuring (sagittal L, W, L/W): 1: 0.55, 2.84, 0.19; 2: 0.95, >4.55, 0.21; 3: 0.90, >4.63, 0.19; 4: 1.37, >5.26, 0.26; 5: 1.06, 4.73, 0.22; 6: 0.76, 3.76, 0.20; 7: 0.59, 2.84, 0.21.

Description of CGH 1937 (holotype of *Arthrolycosa fortis* Fritsch, 1904), and CGH 1939 (holotype of *Arthrolycosa beecheri* Fritsch, 1904): Body L 17.52. Carapace slightly longer than wide, suboval in outline, with slightly recurved, bordered posterior border; ocular tubercle at anterior border; shallow grooves subtending angle of ~80° originating from approximately center of carapace; fovea consisting of bilobed depression ~⅔ carapace length from anterior border; pair of depressions between fovea and posterior border ~⅓ carapace width apart. Carapace L 7.74, W 7.11, L/W 1.09. Chelicera slightly wider than long, L 2.01, W 2.54, L/W 0.79. Pedipalp total L (measured from edge of car) 9.18. Legs robust. Podomere measurements: Leg I pa 2.10, ti 5.38; Leg II pa 2.22, ti 5.58; Leg III pa 2.57; Leg IV fe 5.34, pa 2.10, ti 4.89. Opisthosoma slightly longer than wide, L 9.49, W 7.16, L/W 1.32, bearing 6 tergites, measuring (sagittal L, W, L/W): 1: 1.39, 3.43, 0.40; 2: 1.32, 4.21, 0.31; 3: 1.52, 3.50, 0.43; 4: 1.35, 3.28, 0.41; 5: 0.84, 3.15, 0.27; 6: 0.55, 3.47, 0.16.

Mesothelae *incertae sedis*

Remarks: The small spiders from Rakovník preserved mainly in lateral compression are indistinguishable, and are here synonymized under the older name *Eolycosa* Kušta, 1886. Their segmented opisthosomas indicate that they being to this suborder. While the presence of spinnerets is equivocal, their tergites are set in soft cuticle (no sternites are present), and the leg podomeres are spider-like rather than similar to any other type of arachnid (e.g., see discussion in Garwood et al., 2016). It is possible that they are juveniles of *Geralycosa fricii* found in the same horizon and locality.

Genus *Eolycosa* Kušta, 1886

Type species: *Eolycosa lorenzi* Kušta, 1886.

Other species: None.

Emended diagnosis: Small mesothele spiders (<7.0); bearing discrete, rounded, opisthosomal tergites set in soft cuticle; legs short (~1.3× body L), but not stout.

Remarks: Petrunkevitch's (1955, p. P135) definition stated simply: "Spinnerets terminal," yet the presence of spinnerets is equivocal. There are some structures at the rear of CGH 1948 (Fig. 17A–B), which is presumably what Petrunkevitch was alluding to, but the interpretation of these as spinnerets is optimistic.

Eolycosa lorenzi Kušta, 1886

Figs. 17–18

1886 *Eolycosa lorenzi* Kušta: p. 592; fig. 1.
1889 *Eolycosa lorenzi* Kušta, 1885: Kušta, p. 196.
1889 *Scudderia carbonaria* n. gen. n. sp.: Kušta, p. 196–197; fig. 2. n. syn.
1890 *Eolycosa lorenzi* Kusta: Haase, p. 635.
1890 *Scudderia carbonaria* Kusta: Haase, p. 636. n. syn.
1891 *Eolycosa lorenzi* Kušta, 1885: Scudder, p. 23.
1891 *Scudderia carbonaria* Kušta, 1888: Scudder, p. 30. n. syn.
1904 *Arthrolycosa Lorenzi,* Kušta, sp.: Fritsch, p. 10–11; fig. 6; pl. 2, figs 2–3.
1904 *Arthrolycosa* (*Scudderia*) *carbonaria,* Kušta sp.: Fritsch, p. 6–7; figs 2–3; pl. 1, figs 6–7. n. syn.
1913 *Arthrolycosa carbonaria* (Kušta): Petrunkevitch, p. 87. n. syn.
1913 *Arthrolycosa lorenzi* (Kušta): Petrunkevitch, p. 87.
1928 *Arthromygale carbonaria* Kusta, 1888: Savory, p. 268, 283. n. syn.
1928 *Arthromygale lorenzi* Kusta, 1888: Savory, p. 268, 283.
1949 *Arthromygale carbonaria* Kusta: Petrunkevitch, p. 276. n. syn.
1949 *Arthromygale lorenzi* Kusta: Petrunkevitch, p. 276.
1953 *Eolycosa lorenzi* Kušta: Petrunkevitch, p. 111; pl. 51, fig. 181.
1953 *Kustaria carbonaria* (Kušta): Petrunkevitch, p. 106; pl. 28, fig. 113; pl. 53, figs 188–189. n. syn.
1955 *Eolycosa lorenzi*: Petrunkevitch, p. P135; fig. 99,6.
1955 *Kustaria carbonaria* (Kušta, 1888): Petrunkevitch, p. P135; fig. 99,5. n. syn.
1986 *Eolycosa lorenzi* Kušta, 1885: Zajíc and Štamberg, p. 69.
1986 *Kustaria carbonaria* (Kušta, 1888): Zajíc and Štamberg, p. 69. n. syn.
1991 *Eolycosa lorenzi* Kušta, 1885: Rohdendorf, p. 753.
1991 *Kustaria carbonaria* (Kušta): Rohdendorf, p. 752; fig. 1416. n. syn.
2006 *Eolycosa lorenzi* Kušta, 1885: Penney and Selden, p. 27.
2006 *Kustaria carbonaria* (Kušta, 1888): Penney and Selden, p. 27. n. syn.
2008 *Eolycosa lorenzi* Kušta, 1885: Štamberg and Zajíc, p. 53–54; fig. 28.
2008 *Kustaria carbonaria* (Kušta, 1889): Štamberg and Zajíc, p. 54; fig. 30. n. syn.
2011 *Eolycosa lorenzi* Kusta, 1885: Penney and Selden, p. 54.
2011 *Kustaria carbonaria* (Kusta, 1888): Penney and Selden, p. 54. n. syn.

Material: CGH 1948 (Inv. 809) (part) and CGH 1941 (Inv. 801) (counterpart) (Me 75), holotype of *Eolycosa lorenzi* Kušta, 1886; CGH 1933 (Inv. 806) (Me 63), part and counterpart, holotype of *Scudderia carbonaria* Kušta, 1889; CGH 1935 (Inv. 807) (Me 65), additional specimen of *Scudderia carbonaria*; all held in the collections of the National Museum, Prague.

Occurrence: Radnice Member, Kladno Formation, Carboniferous (lower Moscovian, Westphalian C), Moravia mine, near Rakovník, Czech Republic.

Diagnosis: As for the genus (monotypic).

Remarks: Petrunkevitch (1953) restudied *Eolycosa lorenzi* Kušta, 1886 and considered it as Araneae *incertae sedis* because no diagnostic familial characters could be seen. However, in 1955 he placed it in Arthromygalidae without explanation. The specimen is preserved adjacent to a long plant fragment, in lateral view so that the carapace cannot be seen (Fig. 17). Petrunkevitch counted seven legs and noted that only five could be seen clearly. He surmised that if the blobs present at the front of the spider were swollen male palps, then the spider would be an araneomorph. He noted that the opisthosoma shows clear segmentation, and reckoned that two spinnerets could be seen at its end. In the interpretive drawing here (Fig. 17B), eight appendages can just be made out on the part (CGH 1948), all folded to one side of the specimen. Femora of five appendages lie across the body, the patellae of the two posterior legs can be seen, and tibiae of right and left legs II–IV can be discerned. Metatarsi of right legs II and III and right and left legs IV can be made out, and possibly the tarsus of right leg IV. At the front, parts of distal podomeres of ?right leg I can be seen. The palps may be lost among the mess of hairs around the tibiae of legs I. Only vague outlines of the same appendages can be seen on the counterpart (CGH 1941). The anterior blob probably represents the chelicerae. It is semicircular in shape, with a straight dorsal edge. About five long setae emerge from the curved edges. Posteriorly, a dark, curved area could represent the fang, but it is very unclear. Of the rest of the prosoma, only a vague outline of the ventral side and some small, curved structures at the anterior side can be seen. The opisthosoma of the part consists of an irregular area of dark cuticle with patches missing (but seen adhering to the counterpart) in a regular arrangement that suggests six opisthosomal segments. Further evidence that these are truly opisthosomal segments comes from the large, curved, posteriorly directed setae, which occur along the opisthosoma. Such setae occur at the posterior edge of the tergites in other mesotheles. Seven such setae occur in a presumed mid-dorsal position on CGH 1948, representing the six tergites already mentioned together with one more anterior one (Fig. 17A–B), and a few smaller setae occur on more lateral parts of the segments. On the counterpart (CGH 1941), fragments of four tergites and five setae can be seen (Fig. 17C–D). On the part, some dark patches ventral to the tergites represent cuticle covered by a thin layer of translucent matrix. The two most anterior patches mark the ventral side of the opisthosoma, and the third, most posterior, patch is at the end of the opisthosoma. It is this posterior patch that runs into some elongate blobs with hairs, which Petrunkevitch (1953) thought were two spinnerets. This interpretation is certainly plausible, as is the possibility that the more dorsal blob is an anal tubercle and the lower one is a spinneret, and a third hypothesis that both blobs together represent an anal tubercle or pygidium is also plausible.

Kustaria carbonaria (Kušta, 1889) was removed from *Scudderia* to *Arthrolycosa* by Fritsch (1904), and thence to *Arthromygale* by Petrunkevitch (1923, 1949). Petrunkevitch (1953) pointed out that the name *Scudderia* was preoccupied three times for various insects; *Scudderia* Stål, 1873 is now used for an orthopteran. The genus *Kustaria* was erected by Petrunkevitch (1953) and diagnosed on the concave anterior margin to the carapace, an evenly rounded and convex posterior edge, lack of eyes, long and slender legs and short palps. Two specimens have been described: CGH 1933 (part and counterpart with the same number) and CGH 1935 (single part). Petrunkevitch's (1953, p. 106, pl. 53, figs 188–189) description of the holotype differs from the one presented here. Despite his insistence that the carapace outline is clear, it certainly is not (Fig. 18A–D). The apparent curvature at the front of the carapace

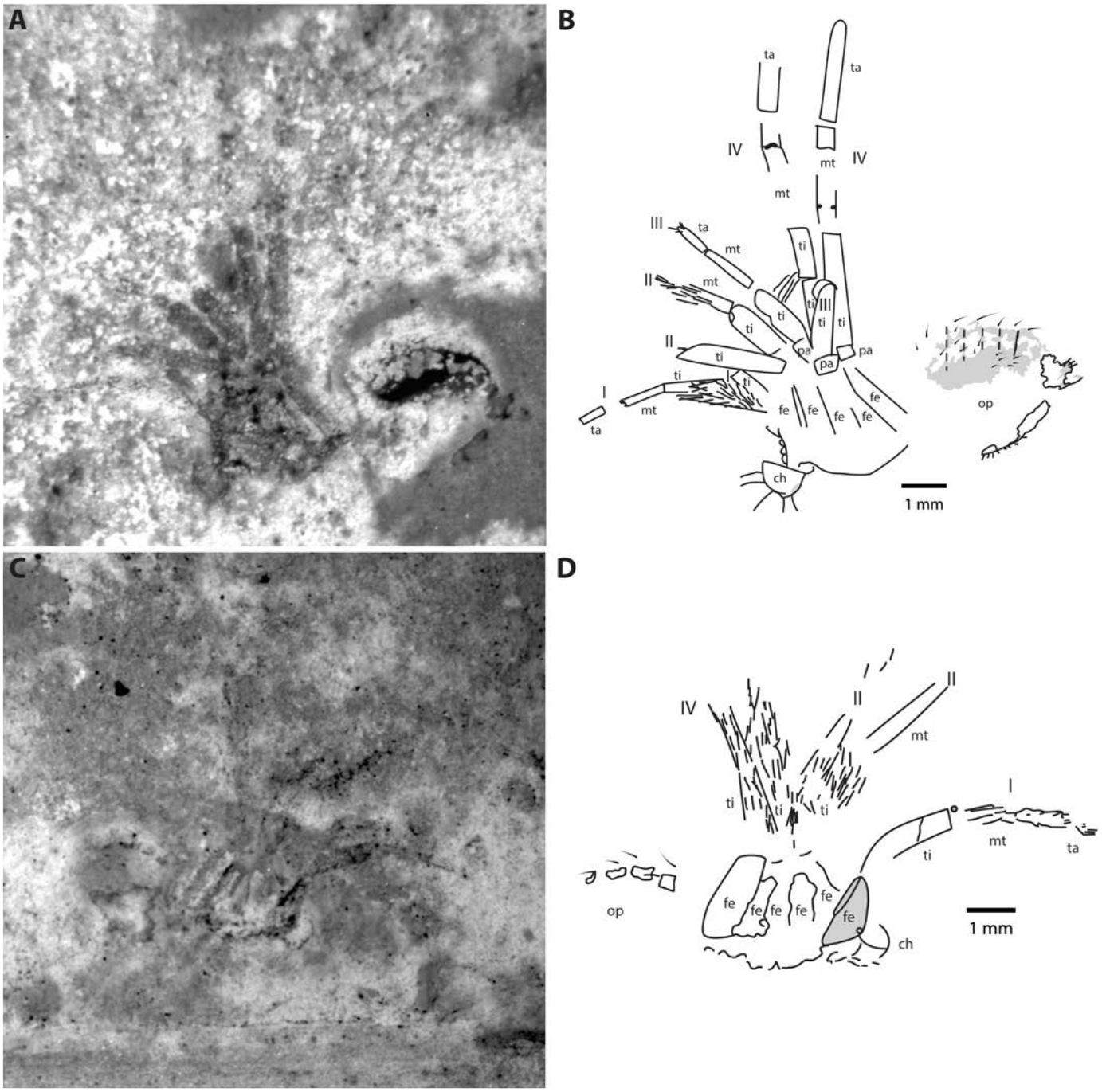

FIGURE 17. *Eolycosa lorenzi* Kušta, 1886, holotype, CGH 1948 (part) and CGH 1941 (counterpart) (NMP), Carboniferous (lower Moscovian, Westphalian C), Moravia mine, near Rakovník, Czech Republic, photographs under ethanol. **A**, photograph of part; **B**, explanatory drawing of A; **C**, photograph of counterpart; **D**, explanatory drawing of C. Scale bars = 1 mm.

is more likely the curved edge of a femur lying across it. Hence, the lack of an eye tubercle or eyes cannot be ascertained. The leg numbering given here is in disagreement with Petrunkevitch. He evidently did not discern that leg III on the left of the part is buried in the matrix. Petrunkevitch (1953, p. 106, fig. 113) pointed out that Fritsch's (1904, fig. 2a,b) reconstructions of specimen 1935 are fictitious, which is true. This specimen does not show much more than can be seen on the type specimen of *Kustaria*. Most legs and pedipalps are visible, but podomeres cannot be demarcated clearly (Fig. 18E–F). The opisthosoma appears to show an elongated first tergite, but this may not be correct; otherwise, seven tergites are visible. Just as in the type of *Eolycosa*, these specimens show discrete, rounded tergites set in soft cuticle of the opisthosoma.

Description of CGH 1948 (part) and CGH 1941 (counterpart) (holotype of *Eolycosa lorenzi* Kušta, 1886) (Fig. 17A–E): Body L (exc. ch, inc. anal tubercle) 6.80; chelicera L 0.96, W 0.72, L/W 1.34. Approximate leg lengths: I: 6.60, II: 6.18, III: 6.43, IV: 9.40. Podomere lengths: Leg I fe1.70, pa 0.42, ti 2.69, mt 2.16, ta 2.23, total fe–ta 9.20; Leg II ti 2.24, mt 2.17; Leg III fe 1.76, pa 0.42, ti 1.57, mt 1.28, ta 0.83, total fe–ta 5.79; Leg IV fe 2.21. Opisthosoma L 3.80, W 2.96, L/W 1.28; visible tergite L: 1: 0.52, 2: 0.48, 3: 0.51, 4: 0.49, 5: 0.42.

Description of CGH 1933, part and counterpart,

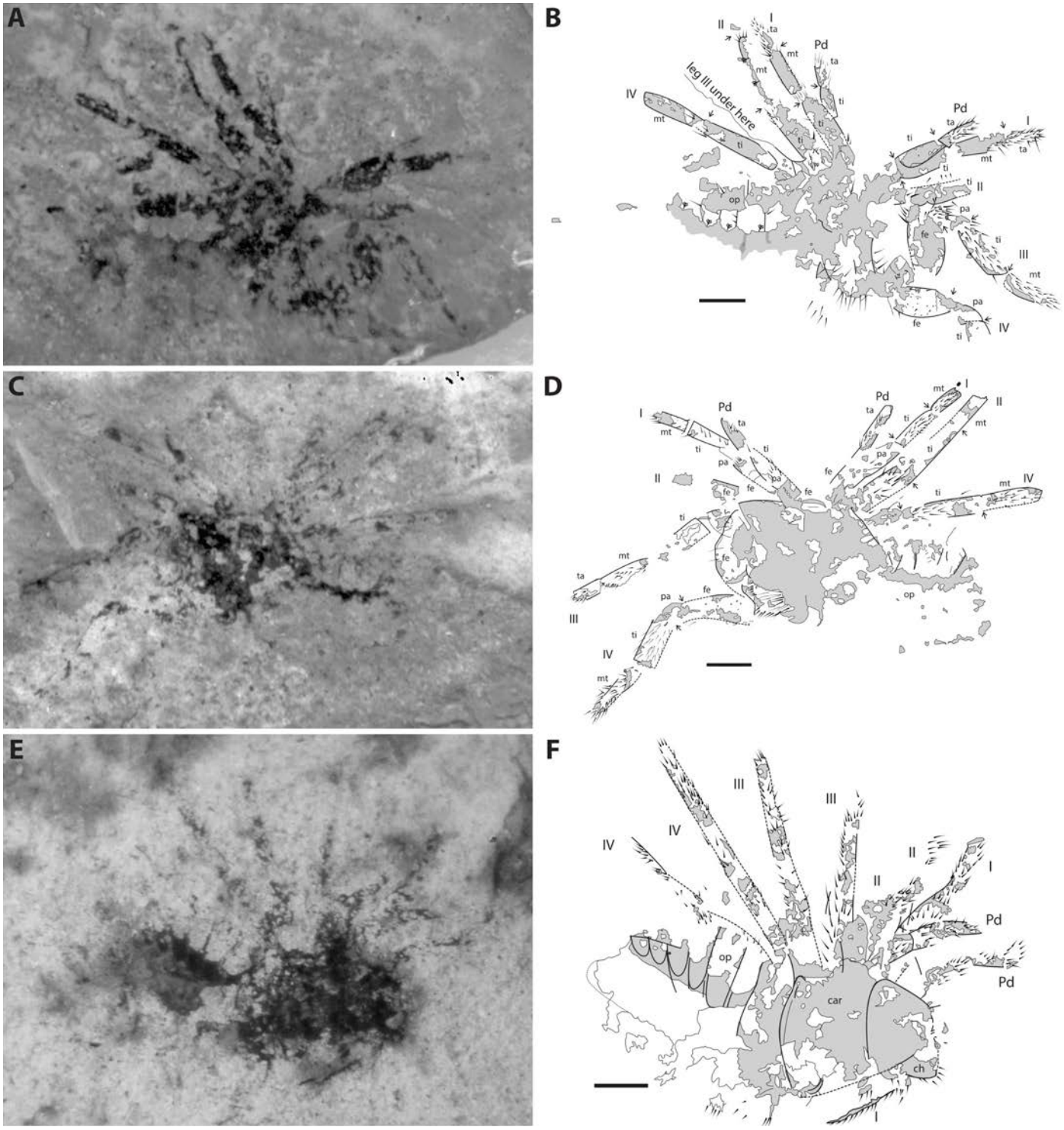

FIGURE 18. *Eolycosa lorenzi* Kušta, 1886, holotype of *Scudderia carbonaria* Kušta, 1889, part and counterpart, CGH 1933 (A–D), and additional specimen of *Scudderia carbonaria*, part only, CGH 1935 (E–F) (NMP), Carboniferous (lower Moscovian, Westphalian C), Moravia mine, near Rakovník, Czech Republic, photographs under ethanol. **A**, photograph of part; **B**, explanatory drawing of A; **C**, photograph of counterpart; **D**, explanatory drawing of C. **E**, photograph of specimen; **F**, explanatory drawing of E. Scale bars = 1 mm.

holotype of *Scudderia carbonaria* Kušta, 1889 (Fig. 18A–D): Body L ~6.47. Carapace L ~2.97, ~W 2.49, ~L/W 1.26. Pedipalp L (measured from edge of car) 2.60. Approximate leg podomere lengths: Leg I ti 1.37, mt 1.13, ta 0.89; Leg II ti 1.81, mt 1.71; Leg III ti 1.45, mt 1.26; Leg IV fe 1.56, pa 0.44, ti 1.53, mt 1.35. Opisthosoma L ~3.33, W ~2.54, L/W ~1.31, visible tergite L: 1: 0.53, 2: 0.63, 3: 0.37, 4: 0.45, 5: 0.51.

Description of CGH 1933, part only, second specimen of *Scudderia carbonaria* Kušta, 1889 (Fig. 18E–F): Body L 6.46. Carapace somewhat piriform in outline, with procurved, bordered posterior margin, lateral sides curving gently to anterior, L 2.87, W 2.58, L/W 1.11. Podomere L (from edge of car) ~2.47. Legs slender, preserved lengths measured from edge of carapace: I ~3.48, II ~3.64, III ~4.24, IV ~5.18. Opisthosoma L 3.83, W 3.22, L/W 1.19, bearing 7 tergites, first tergite longer than others, measuring (sagittal L): 1: 0.80, 2: 0.43, 3: 0.48, 4: 0.40, 5: 0.40, 6: 0.34, 7: 0.34.

Araneae *incertae sedis*
Genus *Pyritaranea* Fritsch, 1899

Type species: *Pyritaranea tubifera* Fritsch, 1899.

Other species: None.

Diagnosis: Spiders with elongate bodies and slender legs, and long, thin metatarsi; elongate spinnerets in a median position on the opisthosoma.

Remarks: Fritsch (1899) described *Pyritaranea tubifera* from the Westphalian of Nýřany as a spider with an elongate opisthosoma. The translation suggests that the opisthosoma was stuck in a tube: "Diese ist eine schmale langbeinige Spinne, die mit dem Hinterleib in einer Röhre steckt" (Frisch, 1899, p. 62), which implies an elongate opisthosoma. Petrunkevitch (1953) cleaned the specimen, redescribed it, and corrected Fritsch's misidentification of a piece of plant material as the tube and opisthosoma. In doing so, the specimen required re-orientation so that it appeared to Petrunkevitch to be laterigrade. Moreover, he considered the opisthosoma, now revealed, to be segmented. Hence, he erected the new family Pyritaraneidae Petrunkevicth, 1953 for laterigrade araneomorphs with segmented opisthosomas. It is shown in Figure 19 here, though it is impossible to discern segmentation of the opisthosoma. Petrunkevitch (1953, p. 108) included in Pyritaraneidae not only *Pyritaranea* but also *Dinopilio* Fritsch, 1904. In the *Treatise*, Petrunkevitch (1955, p. P148) erected the superfamily Pyritaraneidoidea to accommodate the new family.

Eopholcus pedatus was erected by Fritsch (1904) for another pyritized spider from the Nýřany Member. He gave only a stylized drawing of the specimen, and described it as having segmented pedipalps and multisegmented spinnerets surrounding a circular structure (possible anus). Petrunkevitch (1953, p. 108, fig. 112, pl. 54, fig. 194) redescribed the specimen and placed it in Archaeometidae Petrunkevitch, 1949, a family of supposed araneomorph spiders now recognized as Opiliones (Selden et al., 2016).

Eopholcus very much resembles *Pyritaranea* from the same locality, both in its mode of preservation and in the general form of the legs and body. The two specimens are here synonymized under the older name *Pyritaranea tubifera* n. syn. In both specimens, elongate features on the opisthosoma could be interpreted as spinnerets (sp? on Fig. 19). However, similar elongate structures on *Archaeometa nephilina* Pocock, 1911 proved to be taphonomic artifacts (Selden et al., 2016). These specimens cannot be archaeometid opilionids because they lack the extremely elongate femora of those animals.

Pyritaranea tubifera Fritsch, 1899
Fig. 19

1899 *Pyritaranea tubifera* Fr.: Fritsch, p. 62–63; fig. 368.
1904 *Eopholcus pedatus* Fr.: Fritsch, p. 22–23; fig. 28. n. syn.
1904 *Pyritaranea tubifera* Fr.: Fritsch, p. 25; fig. 31.
1913 *Eopholcus pedatus* Fritsch: Petrunkevitch, p. 88. n. syn.
1913 *Pyritaranea tubifera* Fritsch: Petrunkevitch, p. 88.
1949 *Eopholcus pedatus* Fritsch: Petrunkevitch, p. 278. n. syn.
1949 *Pyritaranea tubifera* Fritsch: Petrunkevitch, p. 278.
1953 *Eopholcus pedatus* Fritsch: Petrunkevitch, p. 108; pl. 28, fig. 112; pl. 54, fig. 194. n. syn.
1953 *Pyritaranea tubifera* Fritsch: Petrunkevitch, p. 108–109; pl. 27, fig. 111; pl. 55, fig. 196.
1955 *Eopholcus pedatus*: Petrunkevitch, p. P146; fig. 110,6. n. syn.
1955 *Pyritaranea tubifera*: Petrunkevitch, p. P148; fig. 110/3.
1986 *Eopholcus pedatus* Fritsch, 1904: Zajíc and Štamberg, p. 69. n. syn.
1986 *Pyritaranea tubifera* Fritsch, 1899: Zajíc and Štamberg, p. 69.
1991 *Eopholcus pedatus* Fritsch, 1904: Rohdendorf, p. 754; fig. 1421. n. syn.
1991 *Pyritaranea tubifera* Fritsch, 1899: Rohdendorf, p. 754; fig. 1424.
2006 *Eopholcus pedatus* Fritsch, 1904: Penney and Selden, p. 27. n. syn.
2006 *Pyritaranea tubifera* Fritsch, 1899: Penney and Selden, p. 28.
2008 *Eopholcus pedatus* Frič, 1904: Štamberg and Zajíc, p. 55–56; fig. 33. n. syn.
2008 *Pyritaranea tubifera* Frič, 1899: Štamberg and Zajíc, p. 56–57; fig. 35.
2011 *Eopholcus pedatus* Frič, 1904: Selden and Penney, p. 51. n. syn.

Material: CGH 3170 (Inv. 775) (Me 50), part only, holotype of *Pyritaranea tubifera* Fritsch, 1899; CGH 3184 (Inv. 835) (Me 61), part only, holotype of *Eopholcus pedatus* Fritsch, 1904, both in the National Museum, Prague.

Occurrence: Gaskohle, uppermost part of the Nýřany Member, Kladno Formation (Carboniferous: Westphalian D), Humboldt mine, near Nýřany, western part of the Kladno-Rakovník Basin, Czech Republic.

Diagnosis: As for the genus (monotypic).

Remarks: *Eopholcus* preserves a carapace with a pair of eyes visible anteriorly. The identification of legs and podomeres in both specimens is uncertain.

Description of *Pyritaranea tubifera*: Approximate length of pedipalp: 8.39, Approximate lengths of podomeres: Leg I fe 3.59, pa 1.15, ti 3.80, mt 5.54; Leg II pa 1.70, ti 5.41, mt 6.16; Leg III ti 2.85 4.07, mt 2.71, ta 1.56; 6.37. Approximate leg lengths (fe–mt): Leg I 14.30; Leg II 15.92; Leg III 14.26; Leg IV 14.71. Preserved opisthosoma L 7.30, W 3.53, L/W 2.07.

Description of *Eopholcus pedatus*: Approximate measurements: carapace L 6.13, W 3.70, L/W 1.66. Approximate lengths of podomeres: Leg II fe 6.10, pa 1.32, ti 6.38; Leg III fe 6.26, pa 1.07, ti 5.23, mt ≥5.94; Leg IV fe 5.07, pa 1.85, ti 7.35, mt 10.46. Approximate leg lengths (fe–mt): Leg II 19.11; Leg III 19.39; Leg IV 24.64. Preserved opisthosoma L 9.23, W 4.27, L/W 2.16.

Genus *Palaranea* Frič, 1864
Palaranea borassifoliae Frič, 1864

1864 *Palaranea borassifoliae* Frič: p. 233; fig. 3.
1871 *Palaranea borassifoliae,* Fr.: Frič, p. 8–9; pl. 2, fig. 7.
1873 *Palaranea borassifoliae,* Fr.: Frič, p. 9; pl. 2, fig. 7.
1886 *Palaranea borassifolia* Frič: Feistmantel, p. 48.
1904 *Arthrolycosa*? *Palaranea*, Fr.: Fritsch, p. 11–12; fig. 7.
1928 *Arthromygale palaranea* Fritsch, 1904: Savory, p. 268, 283.
1949 *Arthromygale palaranea* Fritsch: Petrunkevitch, p. 276.
1953 *Palaranea borassifoliae* Fritsch: Petrunkevitch, p. 104; pl. 56, figs 198–199.

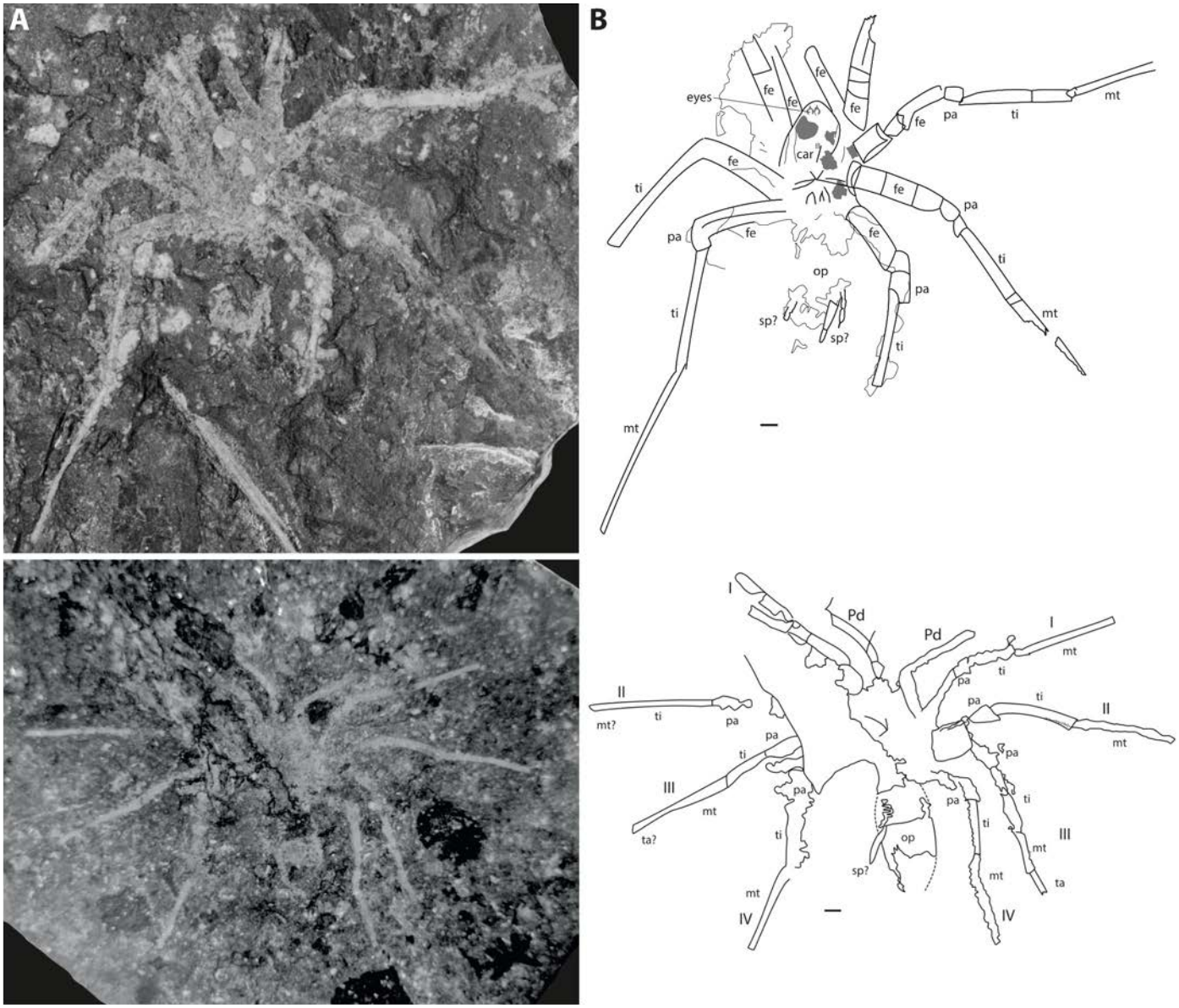

FIGURE 19. *Pyritaranea tubifera* Fritsch, 1899, holotype, part only, CGH 3170 (A–B); holotype of *Eopholcus pedatus* Fritsch, 1904, part only, CGH 3184 (C–D) (NMP). Carboniferous (Westphalian D), Humboldt mine, near Nýřany, Czech Republic, photographs under ethanol. **A**, photograph of specimen; **B**, explanatory drawing of A; **C**, photograph of specimen; **D**, explanatory drawing of C. Scale bars = 1 mm.

1955 *Palaranea borassifoliae*: Petrunkevitch, p. P135; fig. 99,7.
1986 *Palaranea borassifoliae* Fritsch, 1873: Zajíc and Štamberg, p. 69.
2006 *Palaranea borassifoliae* Fritsch, 1873: Penney and Selden, p. 27 .
2008 *Palaranea borassifoliae* Frič, 1864: Štamberg and Zajíc, p. 55; fig. 31.
2011 *Palaranea borassifoliae* Frič, 1873: Penney and Selden, p. 54.

Material: E 3491, part only, in the collections of the National Museum, Prague.

Occurrence: Radnice Coal Seams, Kladno Formation, Carboniferous (Westphalian D), Svinná, near Radnice, Czech Republic.

Remarks: This specimen occurs flattened on a leaf of *Cordaites borassifolius*, and preserves very few morphological details. Numerous authors attributed the name to Frič (1873) (e.g. Dunlop et al., 2020), but the specimen was first described and named in Frič (1864). Petrunkevitch (1953) redescribed the specimen in detail, including spinnerets and claw tufts, none of which are convincingly visible on the specimen. He concluded that its characters were insufficient for identification to a genus but, since Frič (1864) had erected *Palaranea* for it, he retained this name. Petrunkevitch placed it in Arthromygalidae, but since it shows no features consistent with placement in any family, I prefer to consider it as Araneae *incertae sedis*.

Tetrapulmonata *incertae sedis*

Remarks: Together with *Idmonarachne* Garwood et al., 2016, the following genera and species share many characters with Araneae—the carapace bearing an anterior ocular tubercle, simple pedipalps not enlarged into grasping organs (as in Amblypygi or Thelyphonida), for example—but differ either in lacking any evidence for spinnerets (e.g. *Rakovnicia*), or showing the presence of ventral sternites (e.g. *Eocteniza*), which

is not a spider character.

Genus *Eocteniza* Pocock, 1911

Type species: *Eocteniza silvicola* Pocock, 1911
Other species: None.
Diagnosis: Tetrapulmonate with anterior carapace bearing a distinct, compact pars cephalica; posterior carapace with median bilobed structure behind foveal region.

Remarks: Specimen In.22834 was referred by Pocock (1911), with doubt, to *Arthrolycosa* Harger, 1874 (see below). Petrunkevitch (1949) suggested that this specimen belonged in *Protocteniza britannica* and formally synonymized it in Petrunkevitch (1953, p. 104). The carapace pattern of In.22834 is clearly more similar to that of *Eocteniza*, rather than *Protocteniza*, so this specimen is moved to this genus and species. Neither of these specimens can be demonstrated to be a spider; moreover, In.22834, which is placed in this species here, shows characteristics of other tetrapulmonates, e.g., ventral opisthosomal sternites.

Eocteniza silvicola Pocock, 1911
Figs. 20A–H

1911 *Arthrolycosa* Harger, 1874 sp.: Pocock, p. 34, fig. 10.
1911 *Eocteniza silvicola* sp. nov.: Pocock, p. 34; pl. II, fig. 4.
1913 ?*Arthrolycosa* sp. Pocock: Petrunkevitch, p. 87.
1913 *Eocteniza silvicola* Pocock: Petrunkevitch, p. 88.
1928 *Eocteniza silvicola* Pocock, 1911: Savory, p. 268, 282.
1949 *Eocteniza silvicola* Pocock: Petrunkevitch, p. 276.
1949 ?*Protocteniza britannica* Petrunkevitch: p. 277.
1953 *Eocteniza silvicola* Pocock: Petrunkevitch, p. 101–102; pl. 54, fig. 193.
1953 *Protocteniza britannica* Petrunkevitch, 1949: Petrunkevitch, p. 104; fig. 191.
1955 *Eocteniza silvicola*: Petrunkevitch, p. P133; pl. 98,2.
1962 *Eocteniza silvicola* Pocock, 1911: Dubinin, p. 495; pl. 1420.
1967 *Eocteniza silvicola* Pocock: Crowson et al., p. 506.
1991 *Eocteniza silvicola* Pocock, 1911: Rohdendorf, p. 752; fig. 1420.
1980 *Eocteniza silvicola* Pocock, 1911: Morris, p. 37.
1984 *Eocteniza silvicola* Pocock, 1911: Selden, p. 4.
1993 *Eocteniza silvicola* Pocock, 1911: Selden, p. 311.
2006 *Eocteniza silvicola* Pocock, 1911: Penney and Selden, p. 27.
2011 *Eocteniza silvicola* Pocock, 1911: Penney and Selden, p. 52; fig. 42.

Material: In.31245, part and counterpart, and In.22834, part and counterpart, in the BMNH (Wheelton Hind coll.) (coll. W. Egginton).

Occurrence: Nodules in the 10-Foot Ironstone, Lower similis-pulchra Zone, Carboniferous (Moscovian, Westphalian B), Coseley, near Dudley, West Midlands, UK.

Remarks: Pocock (1911) described In.31245, the holotype of *Eocteniza*, as a mesothele, including in the generic diagnosis: narrow, rounded, elevated and convex cephalic area, eyes in a transversely elongated cluster, radiating grooves in the posterior part of the carapace, and an angular fovea. He contrasted *Eocteniza* with previously described Carboniferous genera on the basis that none of them have a differentiated cephalic region. Pocock noted that six tergal plates could be seen on the opisthosoma. Petrunkevitch (1949) commented that the number of visible tergal plates could not be used as a diagnostic character, though it is possible that Pocock did not mean this phrase to be taken as part of the generic diagnosis. Petrunkevitch's (1949) original placement of *Eocteniza* in Arthromygalidae was based on an interpretation of the genus from Pocock's (1911) description that it lacked an eye tubercle. However, when he was able to see the specimen in the BMNH, Petrunkevitch (1953) saw a clear eye tubercle on the specimen and referred it to Arthrolycosidae. Some holes in the matrix adjacent to the carapace margins mark external molds of prosomal appendages (Fig. 20A–D). Little detail can be discerned, but it is evident that the legs were held close to the body during fossilization. Because of the three-dimensional preservation, the anterior (particularly) and posterior tergites disappear at an angle into the matrix.

Specimen In.22834 was first mentioned and figured by Pocock (1911), who referred it, with doubt, to *Arthrolycosa* Harger, 1874. On the basis of the shape of the carapace and opisthosoma, he suggested it was more likely a spider than a thelyphonid. Of particular interest, Pocock mentioned that there are annular segments surrounding the anus (which he suggested showed greater similarity to the Pedipalpi), but the lack of evidence of spinnerets on the ventral opisthosoma hinted at their more anterior position, as in mesotheles. Petrunkevitch (1949, p. 277) suggested that this specimen belonged in *Protocteniza britannica* and, in 1953, he formally synonymized it (Petrunkevitch, 1953, p. 104).

It can be seen from Figure 20E–H that both dorsal and ventral surfaces of the opisthosoma are present, somewhat superimposed on both part and counterpart. Both surfaces consist of plates that appear to extend to the edges of the tagma. This arrangement is unlike any spider (except dorsally in Arthrolycosidae), and more like that of a trigonotarbid (although lateral plates are not present), a thelyphonid, or *Idmonarchne* (Garwood et al., 2016). The carapace appears wide, as Petrunkevitch (1949) mentioned, but its anterior part is missing, so it is actually longer than wide. The anal tubercle consists of three annular segments, which is quite unlike that of a spider. No spinnerets are visible. The first and second tergites have procurved posterior margins, and could represent book-lung opercula. There is a triangular structure on the third tergite, though this might be ventral and showing through to the dorsal side. A similar structure is visible in the holotype, In.31245. This genus is not a spider, but most likely a tetrapulmonate of some kind.

Because of the preservation of these specimens—as a mold within a nodule—their appendages could be revealed using x-ray CT-scanning, as has been done with other arachnid specimens from the same Coseley locality (Garwood et al., 2009) and *Palaeothele montceauensis* from Montceau-les-Mines, France (Selden et al., 2008). However, work by masters student Hannah Ward at the University of Manchester, UK, on the holotype specimen revealed little hidden morphology not seen in hand specimen (Ward, 2017). In this work, the reconstruction of the carapace (Ward, 2017, fig. 4.5) showed it to be rather pentagonal, somewhat reminiscent of the carapace of thelyphonids (see, for comparison, Selden et al., 2014, and Selden et al., 2016). The legs (Ward, 2017, fig. 4.9) are differentiated into well-defined podomeres (a spider characteristic), but the study also revealed the lack of spinnerets or any other opisthosomal appendages.

Description of holotype In.31245: Carapace L 5.0, W 4.35, L/W 1.15, lateral edges gently convex in posterior three-quarters, narrowing abruptly to 2.3 W anteriorly, then sides converging to 1.6 W at anterior border; anterior border gently convex; posterolateral corners rounded, posterior border recurved, middle third particularly so. Pars cephalica demarcated from posterior part of carapace by semicircular furrow, raised, and with bilobed area at anterior edge eye tubercle. On counterpart, two forwardly directed eyes inside deep external mold. Median ridge, of irregular height, runs from cephalic furrow to ⅔ carapace length. Furrow runs from posterior end of median ridge to anterolateral corner of carapace, two furrows run to lateral carapace edges, and two short furrows run from a deep, transverse pit (fovea) posterior to end of median ridge in the direction of the posterolateral corners (but do not meet them). Bilobed structure on median posterior border posterior to foveal region.

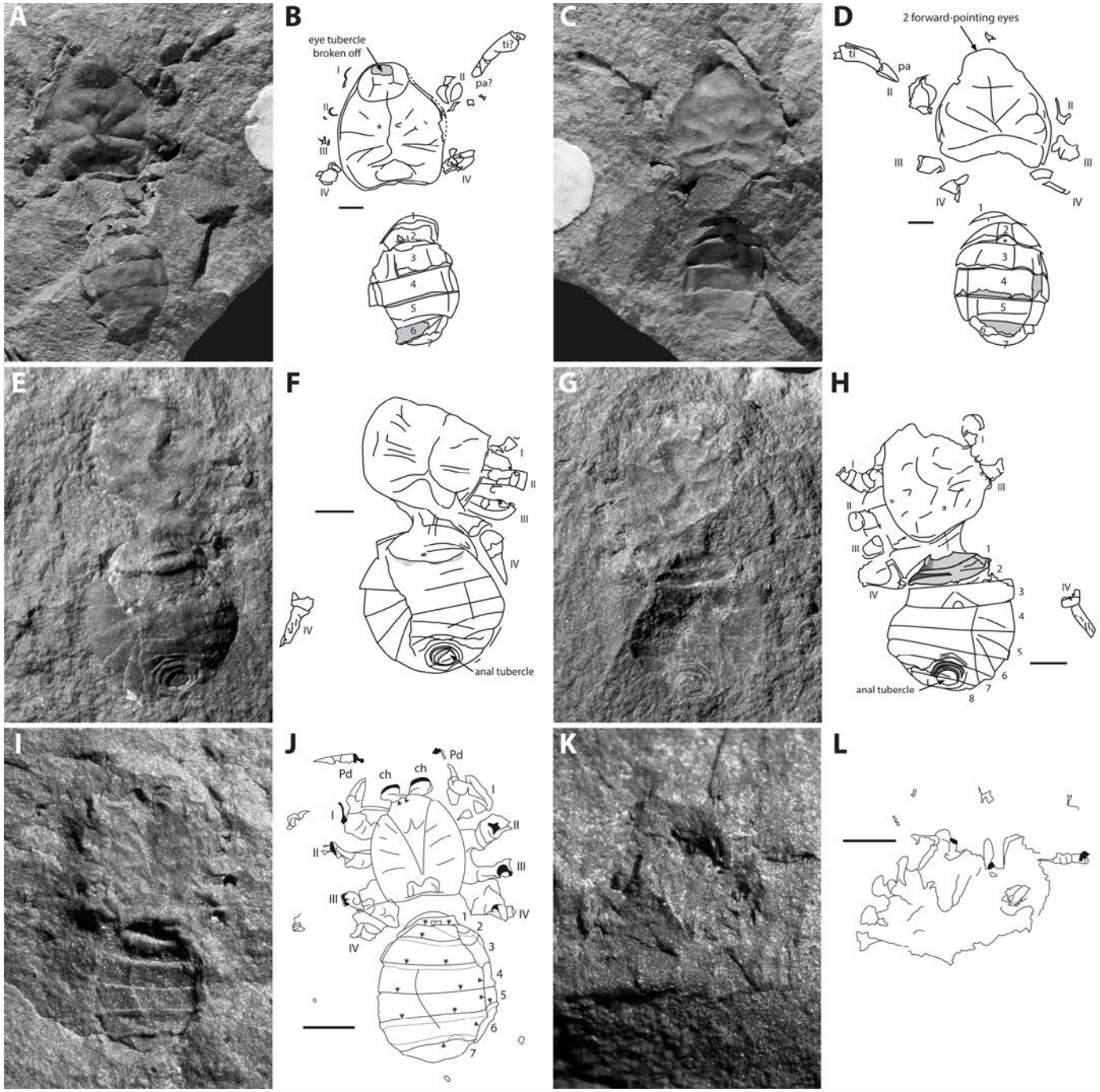

FIGURE 20. *Eocteniza silvicola* Pocock, 1911 (A–H), holotype, In.31245, part and counterpart (A–D), additional specimen In.22834, part and counterpart (E–H), and *Protocteniza britannica* Petrunkevitch, 1949 (I–L), holotype, In.14015, part and counterpart, (all BMNH), Carboniferous (Moscovian, Westphalian B), Coseley, near Dudley, West Midlands, UK, photographs dry. **A**, photograph of holotype of *E. silvicola* part; **B**, explanatory drawing of A; **C**, photograph of holotype of *E. silvicola* counterpart; **D**, explanatory drawing of C. **E**, photograph of additional specimen of *E. silvicola* part; **F**, explanatory drawing of E. **G**, photograph of additional specimen of *E. silvicola* counterpart; **H**, explanatory drawing of G; **I**, photograph of holotype of *P. britannica* part; **J**, explanatory drawing of I; **K**, photograph of holotype of *P. britannica* counterpart; **L**, explanatory drawing of K. Scale bars = 1 mm.

Opisthosoma suboval in outline, L 5.1, W 3.6. At least 7 tergites. Middle tergites (3, 4, 5) L 0.9, 1.0, 0.85, respectively, each tergite bearing prominent longitudinal furrow ~0.5 from lateral edge. Tergite 3 additionally bearing prominent longitudinal furrow on right of midline; tergite 2 bearing similar furrow on left of midline (this asymmetry suggest that they are artefacts of crushing of the tergites). The most posterior tergite bears an irregular scarp across it, and could represent two adpressed tergites (6 and 7).

Description of In.22834: Approximate body L 7.98. Carapace wide, with subparallel lateral margins, narrowing in anterior region, posterior border slightly recurved and bordered; weak median and two pairs of lateral furrows radiating from foveal region (no fovea); L ~3.50, W 3.08, L/W ~1.22. Opisthosoma L 3.76, W 3.56, L/W 1.06, bearing 8 tergites, measuring (sagittal L, W, L/W): 1: 0.43, 1.68, 0.25; 2: 0.53, 2.63, 0.20; 3: 0.64, 2.97, 0.21; 4: 0.84, 3.38, 0.25; 5: 0.75, 3.45, 0.22; 6: 0.43, 3.11, 0.14; 7: 0.43, 2.67, 0.16; 8: 0.30, 1.91, 0.16. Tergites 1 and 2 with procurved posterior margins (book-lung opercula?); anterior and posterior margins of other tergites straight. Sternites curve and lengthen towards lateral margins, lengths of visible sternites at lateral margin: 0.93, 0.73, 0.75, 0.69. Subtriangular ventral? structure in region of third tergite. Anal tubercle of 3 segments.

Genus *Protocteniza* Petrunkevitch, 1949

Type species: *Protocteniza britannica* Petrunkevitch, 1949
Other species: None.

Emended diagnosis: Arachnid with elongate, triangular pars cephalica stretching from in front of foveal region to anterior border, demarcated by anteriorly bifurcating furrows; posterior carapace with median bilobed structure behind foveal region.

Protocteniza britannica Petrunkevitch, 1949

Fig. 20I–L

non 1911 *Arthrolycosa* Harger, 1874 sp.: Pocock, p. 34, fig. 10.
non 1913 ?*Arthrolycosa* sp. Pocock: Petrunkevitch, p. 87.
1949 *Protocteniza britannica* Petrunkevitch, 1949: p. 277, pl. 49 fig. 158.
1953 *Protocteniza britannica* Petrunkevitch: 1949, p. 104.
non 1953 *Protocteniza britannica* Petrunkevitch: 1949, p. 104; fig. 191
1955 *Protocteniza britannica* Petrunkevitch, 1949: Petrunkevitch, p. P134; pl. 99,4.
1962 *Protocteniza britannica* Petrunkevitch, 1949: Dubinin, p. 495, pl. 1418.
1967 *Protocteniza britannica* Petrunkevitch: Crowson et al., p. 506.
1991 *Protocteniza britannica* Petrunkevitch, 1949: Rohdendorf, p. 752; fig. 1418.
1980 *Protocteniza britannica* Petrunkevitch, 1949: Morris, p. 45.
1993 *Protocteniza britannica* Petrunkevitch, 1949: Selden, p. 312.
2006 *Protocteniza britannica* Petrunkevitch, 1949: Penney and Selden, p. 27.
2011 *Protocteniza britannica* Petrunkevitch, 1949: Penney and Selden, p. 54; fig. 43.

Material: Holotype In.14015 in British Museum (Natural History) (Coll. Wheelton Hind). A second specimen, In 22834, was referred to this species by Petrunkevitch (1949, 1953), but does not belong here (see above).

Occurrence: Nodules in the 10-Foot Ironstone, Lower similis-pulchra Zone, Carboniferous (Moscovian, Westphalian B), Coseley, near Dudley, West Midlands, UK.

Remarks: Petrunkevitch (1949) erected the genus *Protocteniza* and placed it in Arthromygalidae Petrunkevitch, 1923. *Protocteniza* has a somewhat oval carapace with a slightly recurved posterior margin, no fovea, and, whereas the pars cephalica is not distinct from the posterior part of the carapace by a constriction of the carapace lateral margin, it is clearly delineated by a pair of furrows diverging from the posterior part of the carapace. At the anterior of the pars cephalica, a small bilobed fracture marks where any eye tubercle, if present, has been broken off, just as in other specimens. A pair of chelicerae can be seen at the anterior edge of the carapace; the other appendages are seen mainly as holes in the matrix. X-ray CT-scanning to discern any hidden parts of this specimen revealed little new information (Ward, 2017). The leg morphology was less clear than that seen in the holotype of *Eocteniza* (see above), but podomeres do seem to be somewhat differentiated (Ward, 2017, fig. 4.20). Traces of the chelicerae were discerned by the CT-scanning, but did not show any useful features (Ward, 2017, figs 4.22–4.23); as in *Eocteniza*, there is no trace of any opisthosomal appendage.

Description: Body L (exc. ch) 5.28. Carapace outline with curved lateral margins, continuing to converge with no abrupt narrowing to rounded anterior border. Posterolateral corners rounded, posterior border recurved, particularly in middle section. Pars cephalica very narrow, bounded by furrows running from anterolateral edge of carapace to ¾ carapace length, with short median furrow in anterior ⅓, not strongly raised. Bilobed structure on median posterior border posterior to foveal region. Carapace L, 2.06, W 1.85, L/W 1.11. Opisthosoma L 2.98, W 2.38, L/W 1.25, bearing 7 tergites measuring (sagittal L, W, L/W): 1: 0.18, 1.01, 0.18; 2: 0.34, 1.56, 0.22; 3: 0.53, 2.14, 0.25; 4: 0.54, 2.32, 0.23; 5: 0.58, 2.38, 0.24; 6: 0.55, 2.34, 0.24; 7: 0.38, 1.52, 0.25.

Genus *Rakovnicia* Kušta, 1885

Type species: *Rakovnicia antiqua* Kušta, 1885.
Other species: None.

Diagnosis: *Rakovnicia* differs from the other small genus from Rakovník, *Eolycosa*, by its longer opisthosomal tergites and stout femora.

Remarks: Despite the difference in orientation—*Eolycosa* specimens are preserved in lateral view, while *Rakovnicia* is a dorsal compression—the opisthosomal tergites in *Rakovnicia* are clearly relatively longer, and the femora are much more robust.

Rakovnicia antiqua Kušta, 1885

Fig. 21

1885 *Rakovnicia antiqua* n. g. et n. sp.: Kušta, 1885, p. 400–401; fig. 3.
1885 *Rakovnicia antiqua* Kušta: Scudder, p. 735.
1886 *Rakovnicia antiqua* Kušta: Scudder, p. 24.
1887 *Rakovnicia antiqua* Kušta: Scudder, p. 735.
1888 *Rakovnicia antiqua* Kušta: Kušta, p. 197.
1890 *Rakovnicia antiqua* Kusta: Haase, p. 631, 634.
1891 *Rakovnicia antiqua* Kušta, 1884: Scudder, p. 29.
1904 *Rakovnicia antiqua* Kušta: Fritsch, p. 15–16; fig. 14; pl. 2, fig. 4.
1913 *Rakovnicia antiqua* Kušta: Petrunkevitch, p. 87.
1928 *Rakovnicia antiqua* Kušta, 1888: Savory, p. 268, 283.
1953 *Rakovnicia antiqua* Kušta: Petrunkevitch, p. 107; pl. 26, fig. fig 106; pl. 51, fig. 182.
1955 *Rakovnicia antiqua* Kušta, 1884: Petrunkevitch, p. P135; fig. 99,8.
1986 *Rakovnicia antiqua* Kušta, 1884: Zajíc and Štamberg, p. 69.
1991 *Rakovnicia antiqua* Kušta, 1884: Rohdendorf, p. 752; fig. 1417.

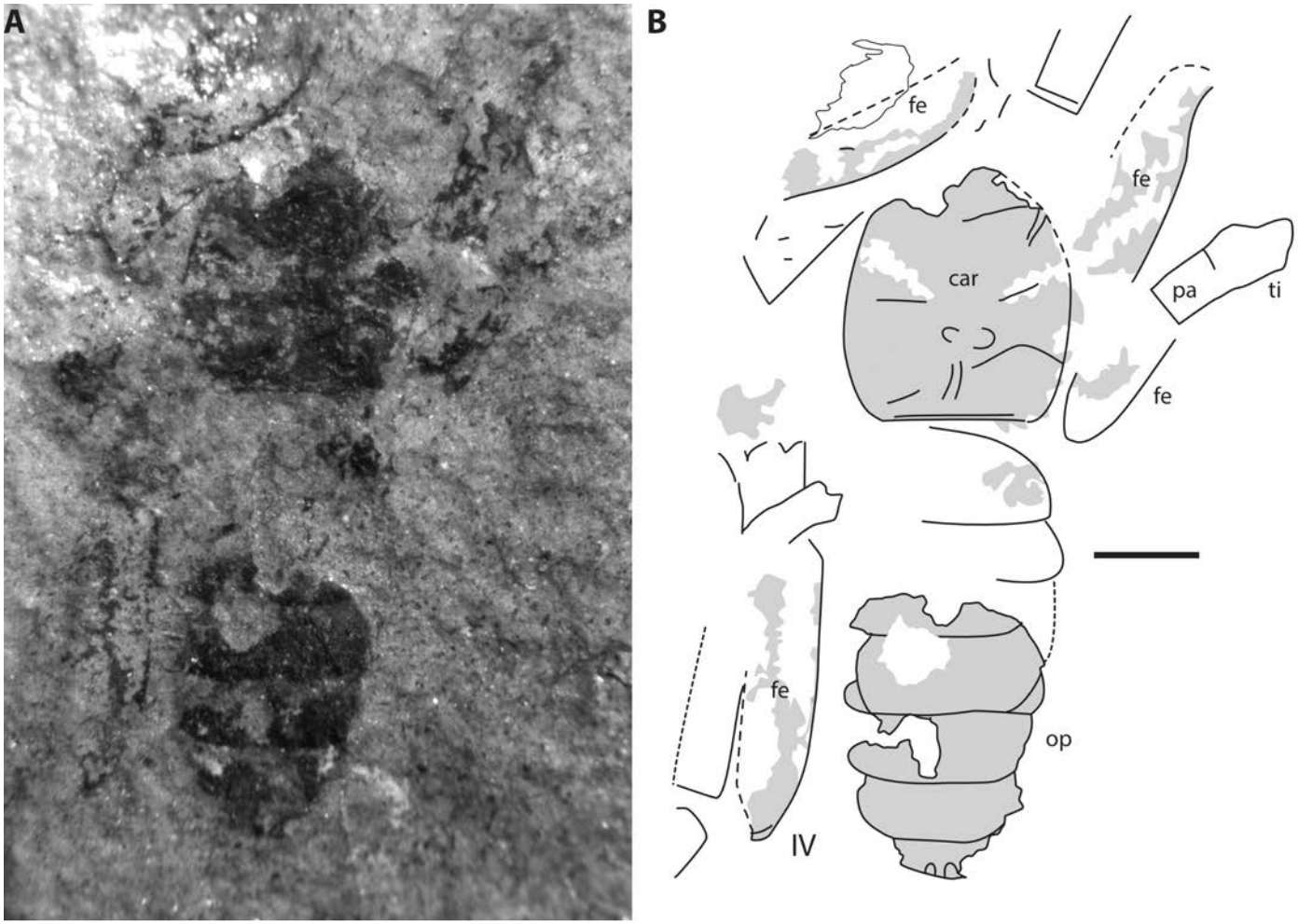

FIGURE 21. *Rakovnicia antiqua* Kušta, 1889, holotype, part only, CGH 610 (NMP). Carboniferous (lower Moscovian, Westphalian C), Moravia mine, near Rakovník, Czech Republic, photographs under ethanol. **A**, photograph of specimen; **B**, explanatory drawing of A. Scale bar = 1 mm.

2006 *Rakovnicia antiqua* Kušta, 1884: Penney and Selden, p. 27.
2008 *Rakovnicia antiqua* Kušta, 1884: Štamberg and Zajíc, p. 55; fig. 32.
2011 *Rakovnicia antiqua* Kusta, 1884: Penney and Selden, p. 54.

Material: CGH 610 (Inv. 810) (Me 73), part only, holotype, in the collections of the National Museum, Prague.

Occurrence: Radnice Member, Kladno Formation, Carboniferous (lower Moscovian, Westphalian C), Moravia mine, near Rakovník, Czech Republic.

Diagnosis: As for the genus.

Remarks: Originally described by Kušta (1885) as a pseudoscorpion, because of the interpretation of the pedipalps as chelate, he also commented that it showed some resemblance to *Arthrolycosa antiqua,* which, in Harger's (1874) original description, was thought to bear forcipulate pedipalps. It was later placed into the order Anthracomarti Karsch, 1882, family Arthrolycosidae, by Scudder (1885, 1886, 1887). Haase (1890) suggested that *Rakovnicia* showed numerous pseudoscorpion-like characters, even if the chelate pedipalps were misinterpreted, and so placed this genus tentatively into the Pseudoscorpiones. *Rakovnicia antiqua* was retained by Petrunkevitch (1953) in a monotypic genus in Arthrolycosidae because its features were insufficient to permit placement in any other known family or genus. Petrunkevitch's (1953, p. 107) description mentioned that the fossil was very flat, the carapace lacked eyes, and that the legs were "evidently slender, but are too poorly preserved to be of service in the identification of the species."

In the present interpretation, there is no evidence whatsoever to support Petrunkevitch's suggestion that the legs were slender in life, since it is mainly just the femora that are preserved. These are distinctly stout and rather long, so the legs may have been quite long in comparison with the body length, though not necessarily slender. The lack of eyes is simply because the ocular region is broken away, which, by itself, may be suggestive of the presence of an ocular tubercle in life.

Description: Body L 6.86. Carapace slightly longer than wide, lateral sides gently outwardly curved, almost subparallel for most of length; posterior margin almost straight–slightly recurved, bordered; anterior border gently recurved; L 2.40, W 2.29, L/W 1.05; fovea a pair of depressions ~⅔ carapace length form anterior; broad, shallow furrows radiating from fovea, subtending angles of ~160° and ~310°. Leg podomere lengths: Leg I 2.26; Leg IV 2.92. Opisthosoma elongate suboval in outline, L 4.34, W 2.12, L/W 2.05, consisting of 7 tergites

measuring (sagittal L, W, L/W): 1: 0.92, 2.02, 0.27; 2: 0.49, 2.11, 0.39; 3: 0.45, 1.68, 0.37; 4: 0.76, 1.92, 0.34; 5: 0.66, 1.77, 0.39; 6: 0.55, 1.65, 0.34; 7: 0.36, 0.94, 0.39.

Arachnida *incertae sedis*
Dinopilio gigas Fritsch, 1904
Fig. 22

1904 *Dinopilio gigas* Fr.: Fritsch, p. 30–31; fig. 35; pl. 5, figs 3–5.
1953 *Dinopilio gigas* Fritsch: Petrunkevitch, p. 109–110; pl. 26, fig. 102; pl. 52, fig. 184.
1955 *Dinopilio gigas*: Petrunkevitch, p. P148; fig. 110,4.
1986 *Dinopilio gigas* Fritsch, 1904: Zajíc and Štamberg, p. 69.
1991 *Dinopilio gigas* Fritsch, 1904: Rohdendorf, p. 754; fig. 1425.
2006 *Dinopilio gigas* Fritsch, 1904: Penney and Selden, p. 28; fig. 2.
2008 *Dinopilio gigas* Frič, 1904: Štamberg and Zajíc, p. 55; fig. 34.
2011 *D. gigas* Frič, 1904: Penney and Selden, p. 55, fig. 45.

Material: CGH 1949 (Inv. 816) (Me 56), part only, holotype of *Dinopilio gigas* Fritsch, 1904, in the collections of the National Museum, Prague.

Occurrence: Gaskohle, uppermost part of the Nýřany Member, Kladno Formation (Carboniferous: Westphalian D), Humboldt mine, near Nýřany, western part of the Kladno-Rakovník Basin, Czech Republic.

Remarks: This large specimen from the Westphalian of Rakovník was described as an opilionid by Fritsch (1904). Petrunkevitch (1953, p. 109–110, fig. 102, pl. 52, fig. 184) developed the specimen further and redescribed it as an araneomorph spider. Petrunkevitch's reasoning for it not being an opilionid was that the opisthosoma was so bent to one side on the fossil that the animal must have had a pedicel, and that its coxosternal region and setation resembled more that of spiders than other tetrapulmonates. On the basis that it seemed to have laterigrade legs, Petrunkevitch (1953) allied the genus with *Pyritaranea* in the new family Pyritaraneidae, defined as araneomorph spiders with segmented abdomens and laterigrade legs. Laterigrade legs are extremely difficult to prove in fossils, especially when there is evidence of distortion of other parts of the body (in this specimen the opisthosoma is turned to one side).

The specimen (Fig. 22) is very large. It is preserved ventral-side up, revealing huge coxae and femora. The coxae of the anteriormost legs meet in the midline, indicating that a sternum is not present, or is smaller and more posterior. Hence, it it is unlikely be a spider. It is placed here as Arachnida *incertae sedis*.

Arthrolycosa tarda Frič, 1912
Fig. 23C

1912 *Arthrolycosa tarda* Fr.: Frič, p. 18, fig. 16.
1949 *Arthromygale tarda* Fritsch: Petrunkevitch, p. 276.

Material: Part only; according to Frič (1912) this specimen was deposited in the collection in Prague. However, it was not listed in the comprehensive catalog of Štamberg and Zajíc (2008), and it was unable to be located in the collections in February 2020. It must be assumed to be lost.

Occurrence: Semily Formation, Gzhelian (Stephanian C) at Krsmol near Altpaka, Czech Republic.

Remarks: The specimen (Fig. 23C) was figured and named by Frič, but not described. His only comment was that it provided evidence that the genus extended into the Permian (at that time, the latest Stephanian rocks of the region were considered to be Permian in age). Petrunkevitch mentioned it only once, in 1949, listing it then under the genus *Arthromygale*. He did not refer to it again. Judging from Frič's (1912, fig. 16) drawing, this specimen could be some sort of poorly preserved arachnid.

Arthropoda *incertae sedis*
Dinopilio parvus Petrunkevitch, 1953
Fig. 23A–B

1953 *Dinopilio parvus* Petrunkevitch: p.110,
1955 *Dinopilio parvus* Petrunkevitch: Petrunkevitch, p. P148.
1967 *Dinopilio parvus* Petrunkevitch: Crowson et al., p. 506.
2006 *Dinopilio parvus* Petrunkevitch, 1953: Penney and Selden, p. 28.
2011 *Dinopilio parvus* Petrunkevitch, 1953, Penney and Selden, p. 55.

Material: In.37101, holotype, part only, in the Natural History Museum, London (Coll. G. Jaffery, Mar. 1938).

Occurrence: Kent No. 7 coal, Grovesend Formation, Warwickshire Group, Carboniferous (Westphalian D), Chislet Colliery tip, near Hersden, Canterbury, Kent, England.

Remarks: Petrunkevitch (1953) examined this specimen, which is trapped on (seemingly under) a cordaitalean leaf. It is very poorly preserved; the outline of 5 pairs of appendages can be seen, extending from an apparent cephalothorax, which appears wider than long. The first three leg pairs appear to be laterigrade, and the last pair is curved unnaturally in a hook-like manner. Petrunkevitch (1953) explained the disposition as possibly due to compression of a dead but still flexible spider carcass. On the basis of its superficial resemblance to a spider, it was identified as an arachnid. Petrunkevitch's (1953, p. 110) referral of the specimen to *Dinopilio* was with reservation: "I did not want to create a new genus on the basis of characters impossible of measurement," but why he chose to place it in this genus (or even name it at all) is unclear.

Fig. 23B gives an interpretive drawing of the specimen. It is clear that, upon closer inspection, the specimen looks much less like a spider. The supposed carapace appears to be a ventral view, with large basal podomeres meeting in the midline, and the podomere disposition is not at all like that of a spider. It is some sort of arthropod, but which phylum is unknown.

Pleurolycosa prolifera (Fritsch, 1899)
Fig. 23C–E

1899 *Arthrolycosa prolifera* Fr.: Fritsch, p. 61; fig. 366; pl. 153, figs 1–3.
1904 *Pleurolycosa prolifera* Fr.: Fritsch, p. 23–24; fig. 29.
1913 *Pleurolycosa prolifera* (Fritsch): Petrunkevitch, p. 96.
1953 *Pleurolycosa prolifera* (Fritsch): Petrunkevitch, p. 111–112; pl. 38, fig. 135.
1991 *Pleurolycosa prolifera* (Fritsch): Rohdendorf, p. 753.
2008 *Pleurolycosa prolifera* (Fritsch, 1899): Štamberg and Zajíc, p. 57; fig. 36.

Material: CGH 3176 (Inv. 626) (Me 77), part (and counterpart?), in the collections of the National Museum, Prague.

Occurrence: Gaskohle, uppermost part of the Nýřany Member, Kladno Formation (Carboniferous: Westphalian D), Humboldt mine, near Nýřany, western part of the Kladno-Rakovník Basin, Czech Republic.

Remarks: *Pleurolycosa prolifera* (Fritsch, 1899) was originally described as an *Arthrolycosa*, the genus *Pleurolycosa* being erected for it by Fritsch (1904). Fritsch (1899) described it as a spider with the remains of an egg sac and juveniles attached at the posterior (Fig. 23D–E), one of the juveniles being figured in his plate 153, fig. 2. Petrunkevitch (1953) figured the specimen, considered the description by Fritsch to be quite erroneous, and concluded that it could not be placed into any arachnid order. The holotype was figured by Štamberg and Zajíc (2008, fig. 36). Petrunkevitch (1953) mentioned a part only; however, during my visit to the National Museum, I photographed a specimen

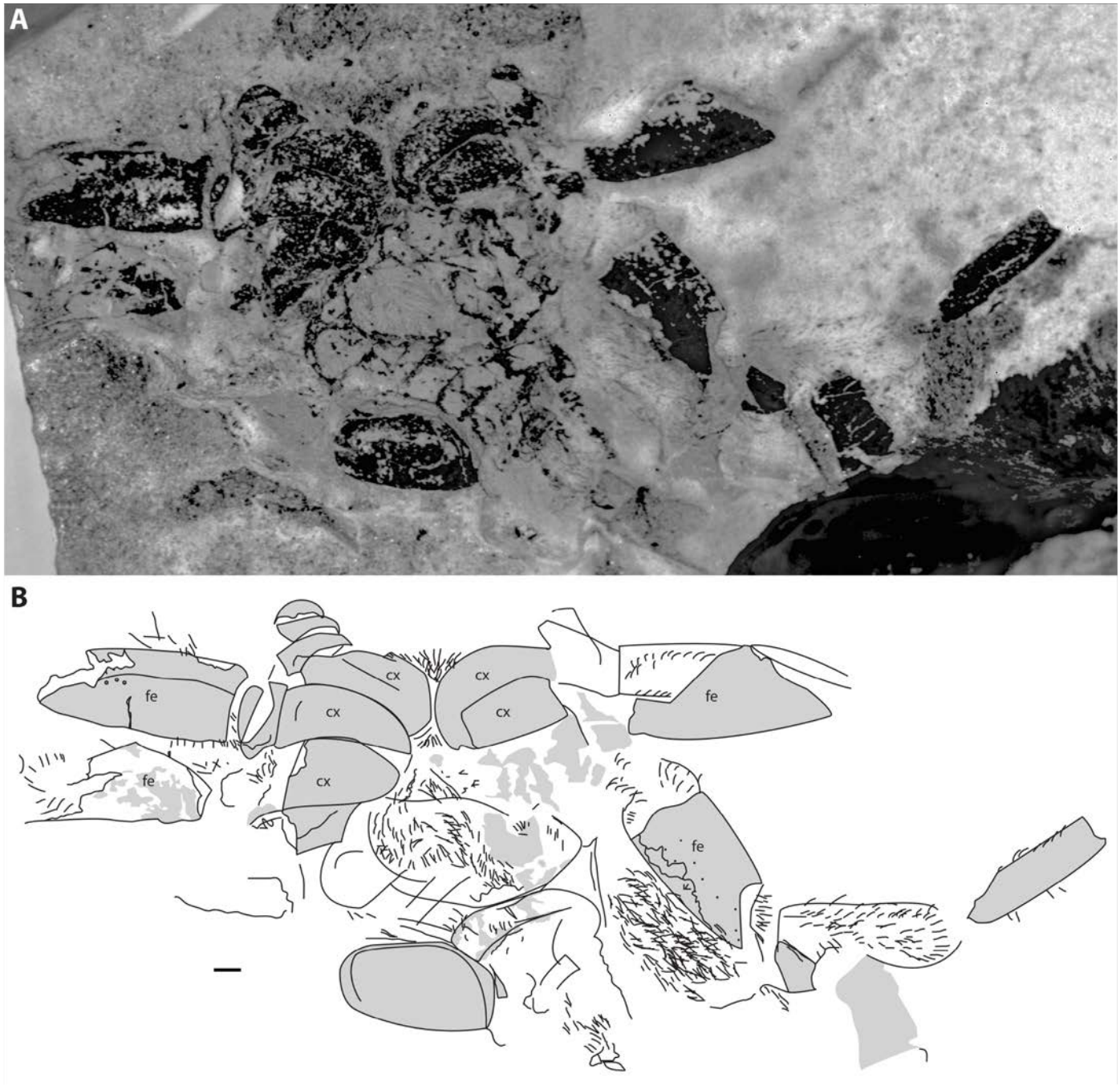

FIGURE 22. *Dinopilio gigas* Fritsch, 1904, holotype, part only, CGH 1949 part only (NMP), Carboniferous (Westphalian D), Humboldt mine, near Nýřany, Czech Republic, photograph under ethanol. **A**, photograph of specimen; **B**, explanatory drawing of A. Scale bar = 1 mm.

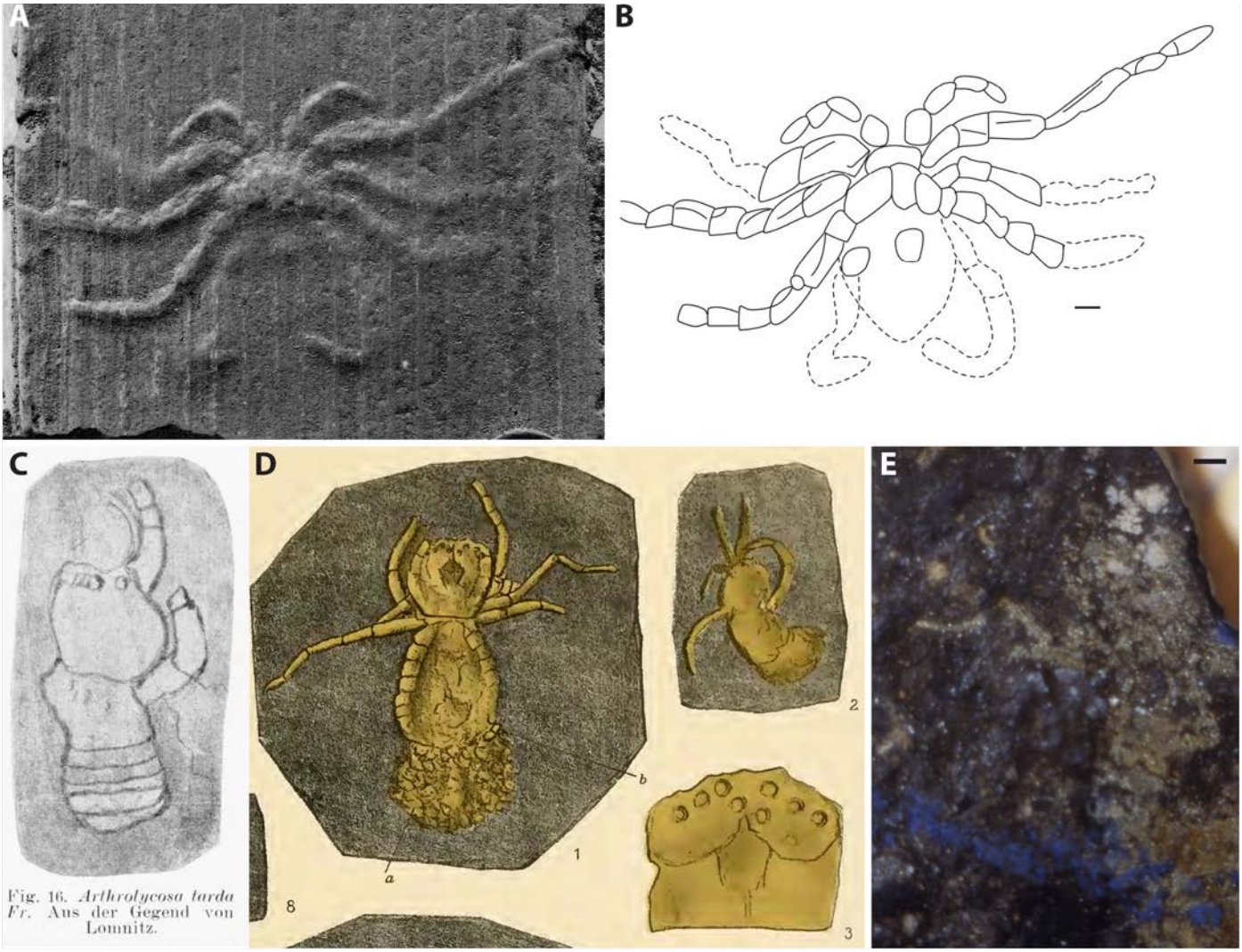

FIGURE 23. *Dinopilio parvus* Petrunkevitch, 1953 (A–B), In.37101, holotype, part only, Carboniferous (Westphalian D), Chislet Colliery tip, near Hersden, Canterbury, England (BMNH); *Arthrolycosa tarda* Frič, 1912 (C), part only, Carboniferous (Gzhelian, Stephanian C), Krsmol near Altpaka, Czech Republic (NMP); *Pleurolycosa prolifera* (Fritsch, 1899) CGH 3176, holotype of *Arthrolycosa prolifera* Fritsch, 1899, part (and counterpart?) (D–E), Carboniferous (Westphalian D), Humboldt mine, near Nýřany, Czech Republic (NMP). **A**, photograph of *Dinopilio parvus*; **B**, explanatory drawing of A; **C**, original illustration of *Arthrolycosa tarda* from Frič (1912); **D**, original illustration of of *Arthrolycosa prolifera* from Fritsch (1899, pl. 153) fig. 1 purports to show the specimen with a cocoon bearing a brood of juveniles, fig. 2 is a single juvenile, and fig. 3 the supposed eye pattern; **E**, counterpart of holotype in the NMP, not previously mentioned or figured. Scale bars = 1 mm.

that appears to be the counterpart (Fig. 23E). It shows no more detail than the part and, following study of this pyritic blob, the conclusion of Petrunkevitch, that it is simply an organic fragment not assignable to Arachnida, is inevitable.

DISCUSSION

The following table summarizes the systematic positions of taxa described here, and some related taxa, with their geological ranges. The classification is based on Garwood and Dunlop (2014) with the addition of Chimerarachnida Wunderlich, 2019, within an expanded Araneida by Wunderlich (2019); † = extinct taxon.

Arthropoda von Siebold, 1848, Cambrian–Recent
- Arthropoda *incertae sedis*
  - †*Dinopilio parvus* Petrunkevitch, 1953, Carboniferous
  - †*Pleurolycosa prolifera* (Fritsch, 1899), Carboniferous
- Arachnida Lamarck, 1801, Silurian–Recent
  - Arachnida *incertae sedis*
    - †*Dinopilio gigas* Fritsch, 1904, Carboniferous
    - †*Arthrolycosa tarda* Frič, 1912, Carboniferous
  - Pantetrapulmonata Shultz, 2007
    - †Trigonotarbida Petrunkevitch, 1949, Silurian–Permian
    - Tetrapulmonata Shultz, 1990, Carboniferous–Recent
      - Tetrapulmonata *incertae sedis*
        - †*Eocteniza* Pocock, 1911, Carboniferous
          - †*E. silvicola* Pocock, 1911
        - †*Protocteniza* Petrunkevitch, 1949, Carboniferous
          - †*P. britannica* Petrunkevitch, 1949
        - †*Rakovnicia* Kušta, 1885, Carboniferous
          - †*R. antiqua* Kušta, 1885
      - Schizotarsata Shultz, 2007, Carboniferous–Recent
        - †Haptopoda Pocock, 1911, Carboniferous
        - Pedipalpi Börner, 1904
          - Amblypygi Thorell, 1882
          - Uropygi Thorell, 1882
            - Thelyphonida Latreille, 1804
            - Schizomida Petrunkevitch, 1945
      - Serikodiastida Garwood and Dunlop, 2014
        - †Uraraneida Selden, Shear and Sutton, 2008, Carboniferous–Permian
        - Araneida Clerck, 1757, Carboniferous–Recent
          - †Chimerarachnida Wunderlich, 2018, Cretaceous
          - Araneae Clerck, 1757, Carboniferous–Recent
            - Araneae *incertae sedis*
              - †*Pyritaranea* Fritsch, 1899, Carboniferous
                - †*P. tubifera* Fritsch, 1899
              - †*Palaranea* Frič, 1864 Carboniferous
                - †*P. borassifoliae* Frič, 1864
            - Mesothelae Pocock, 1892, Carboniferous–Recent
              - Mesothelae *incertae sedis*
                - †*Eolycosa* Kušta, 1886, Carboniferous.
                  - †*E. lorenzi* Kušta, 1886
              - Liphistiidae Pocock, 1892, Recent
                - *Ganthela* Xu and Kuntner, 2015, 7 spp., Recent
                - *Heptathela* Kishida, 1923, 20 spp., Recent
                - *Liphistius* Schiödte, 1849, 56 spp., Recent
                - *Qiongthela* Xu and Kuntner, 2015, 11 spp., Recent
                - *Ryuthela* Haupt, 1983, 15 spp., Recent
                - *Sinothela* Haupt, 2003, 4 spp., Recent
                - *Songthela* Ono, 2000, 14 spp., Recent
                - *Vinathela* Ono, 2000, 8 spp., Recent
              - †Palaeothelidae **n. fam.** Carboniferous
                - †*Palaeothele* (Selden, 1996b), Carboniferous
                  - †*P. montceauensis* (Selden, 1996b)
                  - †*P. onoi* **n. sp.**
              - †Arthrolycosidae Harger, 1874, Carboniferous
                - †*Arthrolycosa* Harger, 1874, Carboniferous
                  - †*A. antiqua* Harger, 1874
                  - †*A.* sp. (numerous)

†*Protolycosa* Römer, 1865, Carboniferous
†*P. anthracophila* Römer, 1865
†*P. cebennensis* Laurentiaux-Vieira and Laurentiaux, 1963
†*P. danielsi* (Petrunkevitch, 1913) **n. comb.**
†*P. suazoi*, **n. sp.**
†Arthromygalidae Petrunkevitch, 1923, Carboniferous–Cretaceous
†*Geralycosa* Kušta, 1889, Carboniferous
†*G. fricii* Kušta, 1889
†*Parvithele* Wunderlich, 2017, 2 sp., Cretaceous
†*Pulvillothele* Wunderlich, 2017, 1 sp., Cretaceous
†Burmathelidae Wunderlich, 2017, Cretaceous
†*Burmathele* Wunderlich, 2017, 1 sp.
†Cretaceothelidae Wunderlich, 2017, Cretaceous
†*Cretaceothele* Wunderlich, 2015, 1 sp.
†Eomesothelidae Wunderlich, 2019, Cretaceous
†*Eomesothele* Wunderlich, 2019, 1 sp.
†*Intermesothele* Wunderlich, 2019, 1 sp.
Opisthothelae Pocock, 1892, Triassic–Recent
Mygalomorphae Pocock, 1892, Triassic–Recent
no Paleozoic examples
Araneomorphae Smith, 1902, Triassic–Recent
no Paleozoic examples

Detailed investigation of the fossils using high-resolution microscopy and different lighting conditions can tease out information overlooked in previous studies or not noticed during cursory investigation. For example, Yale Peabody Museum specimen IP.00162, formerly identified as an *Arthrolycosa antiqua*, shows a great deal of detail when studied under low-angle light, including opisthosomal tergites, opercula, and spinnerets (Fig. 13), such that it has been erected as a new species in *Palaeothele*. The row of spigots seen alongside an opisthosomal appendage on the new species from Kinney Brick Quarry, described here as *Protolycosa suazoi* n. sp., clearly indicates that this, together with the other observable opisthosomal appendages, is a spinneret (Fig. 12). Specimens preserved in three dimensions in nodules, such as *Eocteniza* and *Protocteniza* from the Coal Measures of England and the Mazon Creek nodules, ought to be amenable to CT-scanning; however, this technique has not yet revealed much useful new information (Mark Sutton, pers. comm. 2005; McCoy 2012; Ward, 2017). As such techniques improve, it is to be hoped that future studies may reveal even more important data from these fossils.

From the remarks in the foregoing systematic section, it is apparent that numerous specimens previously referred to Araneae cannot be sustained within that order. Those which remain can be accommodated in Mesothelae. Characters preserved on the fossils indicate that they are spiders (e.g., presence of spinnerets), and the existence of opisthosomal tergites, though a plesiomorphy, places them in that clade. There is no evidence for any opisthothele in the Paleozoic.

It is becoming clear, particularly from the newly described specimens from Burmese amber (Wunderlich, 2017, 2019), that a greater diversity of primitive spiders and spider-like animals exists between Chimerarachnida and Uraraneida, on the one hand, and Mesothelae on the other. For example, while the original mesothele spider from Burmese amber described by Wunderlich (2015), *Cretaceothele*, fits fairly easily into that clade, specimens he described later show characters that differ considerably from extant species. For example, members of the Parvithelidae bear an apically notched median structure on the distal tarsus, as described above (Arthromygalidae). New taxa described in 2019, i.e., the family Eomesothelidae Wunderlich, 2019 containing *Eomesothele* Wunderlich, 2019 and *Intermesothele* Wunderlich, 2019, show spinnerets at the posterior end of the opisthosoma. While these specimens are juveniles, and may not reflect the condition in adults, the posterior position of the spinnerets reflects that seen in Chimerarachnida, as well as more derived spiders of the Opisthothelae.

So, it appears that the simple view of spinnerets moving backwards during evolution to modern spiders, and loss of an anal flagellum seen in the modern sister group of Araneae, the Amblypygi, is not so straightforward after all. Fossils such as *Chimererachne* show a combination of characters (e.g., anal flagellum, posterior spinnerets, broad sternum) seen in more derived Araneae as well as other tetrapulmonates. The curious tarsal structures of the Arthromygalidae mirror those seen in *Chimerarachne* and, to some extent, amblypygids. Some of the fossils described here show a curious combination of characters, e.g., *Eocteniza* looks quite spider-like yet it bears ventral opisthosomal sternites, which are only found in non-spider tetrapulmonates. With the advancement in investigative techniques, and the hope for discovery of new specimens, this diverse array of stem Araneae will become further elucidated in the future.

CONCLUSIONS

- In this paper, two new occurrences of fossil spiders from the Carboniferous Period are described: *Protolycosa suazoi* n. sp., from the Kinney Brick Quarry, New Mexico, and two specimens of *Arthrolycosa* sp. from Writhlington Geological Nature Reserve, Avon, England.
- These two genera, *Arthrolycosa* Harger, 1874 and *Protolycosa* Römer, 1865, are redefined. They are closely related and, together, constitute the family Arthrolycosidae Harger, 1874.
- A specimen in the Yale Peabody Museum formerly attributed to *Arthrolycosa antiqua* Harger, 1874, is shown to belong to a new species of *Palaeothele* (Selden, 1996b): *P. onoi* n. sp., and the new family Palaeothelidae n. fam. is erected for the genus.
- The family Arthromygalidae Petrunkevitch, 1923 is redefined, synonymized with Parvithelidae Wunderlich, 2017, and the genera included are: *Geralycosa* Kušta, 1889, *Parvithele* Wunderlich, 2017, and *Pulvillothele* Wunderlich, 2017.
- *Arthrolycosa beecheri* Fritsch, 1904 and *A. fortis* Fritsch, 1904 are shown to be part and counterpart of the same specimen, and are synonymized with the other large spider from Rakovník: *Geralycosa fričii* Kušta, 1889.
- The small spiders from Rakovník, Czech Republic, preserved mainly in lateral compression, *Eolycosa lorenzi* Kušta, 1886 and *Scudderia carbonaria* Kušta, 1889, are here synonymized under the older name. The presence of spinnerets in these specimens is equivocal, but other features suggest they are mesotheles. They may be juveniles of *Geralycosa* found in

the same beds.

- The spiders preserved by pyritic replacement in the Gaskohle of Nýřany, Czech Republic, *Pyritaranea tubifera* Fritsch, 1899 and *Eopholcus pedatus* Fritsch, 1904, are synonymized under the older name. Though poorly preserved, they appear to be spiders, and are placed as Araneae *incertae sedis* together with *Palaranea borassifoliae* Frič, 1864 from the same horizon.
- A number of specimens previously classified in Araenae are here removed to Tetrapulmonata *incertae sedis* because they either lack spider apomorphies and/or show characters of non-spider arachnids. *Rakovnicia antiqua* Kušta, 1885 differs from the other small spiders from Rakovník by its longer opisthosomal tergites and stout femora; it may belong to Araneae or, equally, another order of tetrapulmonates. *Eocteniza silvicola* Pocock, 1911 and *Protocteniza britannica* Petrunkevitch, 1949, from the British Coal Measures, lack any trace of spinnerets and, in the case of *Eocteniza*, show ventral opisthosomal sternites.
- The large specimen *Dinopilio gigas* Fritsch, 1904 from Nýřany, Czech Republic appears to be an arachnid, but lacks a obvious sternum, hence it is unlikely to be a spider. *Arthrolycosa tarda* Frič, 1912, from Altpaka, Czech Republic, is lost, but a drawing and description suggest it is an arachnid. Both are placed as Arachnida *incertae sedis.*
- *Dinopilio parvus* Petrunkevitch, 1953, from the Kent Coalfield, England, and the very poorly preserved *Pleurolycosa prolifera* (Fritsch, 1899) from Nýřany, Czech Republic, are recognizable only as arthropods, and hence placed as Arthropoda *incertae sedis*.

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