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REDESCRIPTION OF THE PENNSYLVANIAN TRIGONOTARBID ARACHNID *LISSOMARTUS* PETRUNKEVITCH 1949 FROM MAZON CREEK, ILLINOIS

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ABSTRACT. The holotypes of the trigonotarbids *Lissomartus carbonarius* (Petrunkevitch 1913) and *Lissomartus schucherti* (Petrunkevitch 1913) (Arachnida, Trigonotarbida) from the Pennsylvanian (Westphalian D) of Mazon Creek are redescribed. These forms may be synonymous, representing male/female or juvenile/adult dimorphs, but the two species are retained at present. A new reconstruction of *Lissomartus schucherti* is presented. A new family, Lissomartidae, is proposed for these species based on a combination of their lack of opisthosomal tuberculation and their opisthosomal segmentation pattern of tergites 2 + 3 fused and tergite 9 divided into median and lateral plates. Lissomartidae new family may be intermediate between Trigonotarbidae and Eophrynidae + Aphantomartidae.

Trigonotarbid arachnids ranged from the Upper Silurian (Přídolí) (Jeram et al. 1990) to the Lower Permian (Asselian?) (Scharf 1924). Superficially spider-like animals, they lack silk-producing spinnerets, and are characterized by an opisthosoma with tergites divided into median and lateral plates. Trigonotarbids have been placed in the arachnid taxon Tetrapulmonata Shultz 1990, as the plesiomorphic sister group of the orders Araneae, Amblypygi, Uropygi and Schizomida (Shear et al. 1987). Trigonotarbids are most numerous in the coal deposits of North America and Europe and two specimens from Mazon Creek are redescribed here and interpreted as cursorial predators on other arthropods. These specimens represent two species in a single genus, which is placed in a new family.

PREVIOUS WORK

One of the most productive areas for trigonotarbid fossils is the Pennsylvanian (Westphalian D) locality of Mazon Creek, Illinois. Petrunkevitch (1913) described two new arachnids from Mazon Creek (in what was then the order Anthracomarti): *Trigonotarbus schucherti* and *Trigonotarbus carbonarius*. The genus *Trigonotarbus* Pocock 1911 was rediagnosed by Petrunkevitch (1913) as trigonotarbids having a triangular carapace, lacking ornamentation, with a raised median region. Petrunkevitch (1913) differentiated *T. schucherti* from *T. carbonarius* and Pocock's type species, *T. johnsoni* from the Westphalian B of the British Middle Coal Measures, on account of the coxae touching along the midline in *T. shucherti* and coxae separated by a sternum in the other two species. He differentiated *T. carbonarius* from *T. johnsoni* by the shape of the sternite surrounding the anal operculum (a structure now interpreted as a pygidium, see below).

In 1949 Petrunkevitch created a new genus, *Lissomartus*, for *T. schucherti* and *T. carbonarius*. He created a new family, Trigonotarbidae, for *T. johnsoni*, but placed his new genus *Lissomartus* in the family Trigonomartidae, a substitute name for the family Aphantomartidae, proposed earlier by Petrunkevitch (1945). Petrunkevitch (1949) also created the order Trigonotarbi for some of the anthracomartid material, including *Lissomartus* (see Shear et al. (1987) for a discussion).

Petrunkevitch (1949) diagnosed the family Trigonotarbidae as having an eight-segmented opisthosoma with the terminal tergite not divided into median and lateral plates, while the Trigonomartidae was diagnosed as having an eight-segmented opisthosoma with a terminal tergite which was divided into median and lateral plates. It was on these grounds that *Lissomartus*, with a divided terminal tergite, was placed in the Trigonomartidae. The genus *Lissomartus* was defined by Petrunkevitch (1949) as trigonomartids with a smooth carapace and opisthosoma, the carapace being subtriangular, longer than wide and concave on each side anteriorly. This interpretation and systematic placement was retained by Petrunkevitch (1953, 1955) in his two further major reviews of the Trigonotarbida. The family name Trigonomartidae was rejected in favor of the original name, Aphantomartidae, by Selden & Romano (1983). A reappraisal of *L. carbonarius* and *L. schucherti* was deemed necessary in the light of misinterpretations in Petrunkevitch's morphological and taxonomic work (e. g., Selden & Romano 1983; Shear et al. 1987).

METHODS

The holotypes of *Lissomartus schucherti* (Peabody Museum, Yale University (YPM), specimen no. 169), and *L. carbonarius* (United States National Museum, Washington DC (USNM), specimen no. 37978) were whitened with ammonium chloride and studied under a binocular microscope. Drawings were prepared with the aid of a camera lucida. Both specimens are from Mazon Creek, Illinois, USA, which is dated at Pennsylvanian (Westphalian D) in age (see Nitecki 1979 for a geological interpretation of this locality).

The holotype (British Museum, Natural History (BMNH) In 31239), of *Trigonotarbus johnsoni* and other specimens of this species were studied as the type and only species of the family Trigonotarbidae. The holotypes of *Aphantomartus areolatus* (British Geological Survey (GSM) 25016–7) and *Trigonomartus pustulatus* (USNM 37984), were studied as representatives of the family Aphantomartidae. The holotype of *Eophrynus prestvicii* from the (Lapworth Museum, Birmingham University, UK (BU) 699) was studied as a representative of the Eophrynidae.

MORPHOLOGICAL INTERPRETATION

Both specimens of *Lissomartus* are preserved as external molds in clay-ironstone nodules. YPM 169 (Figs. 1–4) consists of part and counterpart showing the dorsal and ventral surfaces of the animal respectively, while USNM 37978 (Figs. 5, 6) consists of one half of a nodule only, the counterpart being unknown from the time of the original description, and shows the ventral surface.

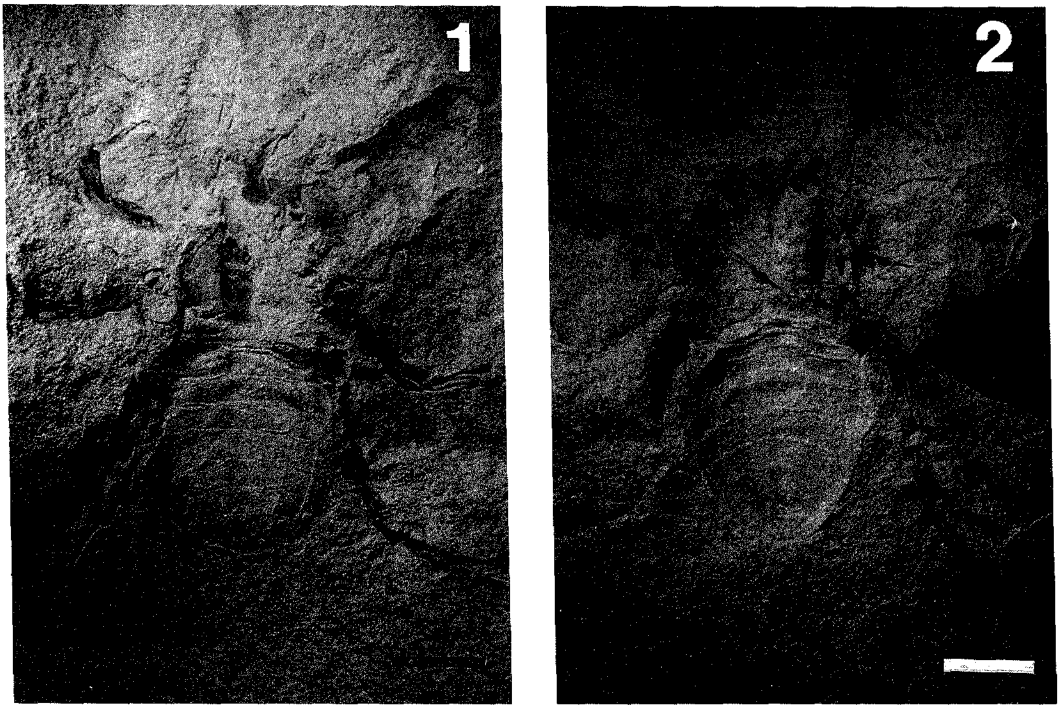
The carapace of YPM 169 (Figs. 1, 3, 7) shows the approximately triangular shape characteristic of many trigonotarbids, with a raised median region bearing a pair of eyes on a single tubercle. Additionally this median region also bears a pair of oval tubercles on this raised median region either side of the eye tubercle, and two less well defined tubercle pairs posterior to the eye tubercle, comprising a round and an elongate tubercle pair respectively.

Some Devonian trigonotarbids show multifaceted lateral eye tubercles in addition to the median eye tubercle (e. g., Shear et al. 1987), and it is conceivable that the oval tubercles either side of the eye tubercle in YPM 169 are lateral eye tubercles, too. However, since lateral eye tubercles are not present in any of the other taxa interpreted as closely related to *Lissomartus* and would represent an uncharacteristically plesiomorphic character in an otherwise rather derived trigonotarbid, I prefer to interpret these, with reservations, as simple tubercles (Fig. 7), as are observed in greater density on the carapaces of the eophrynids and aphantomartids.

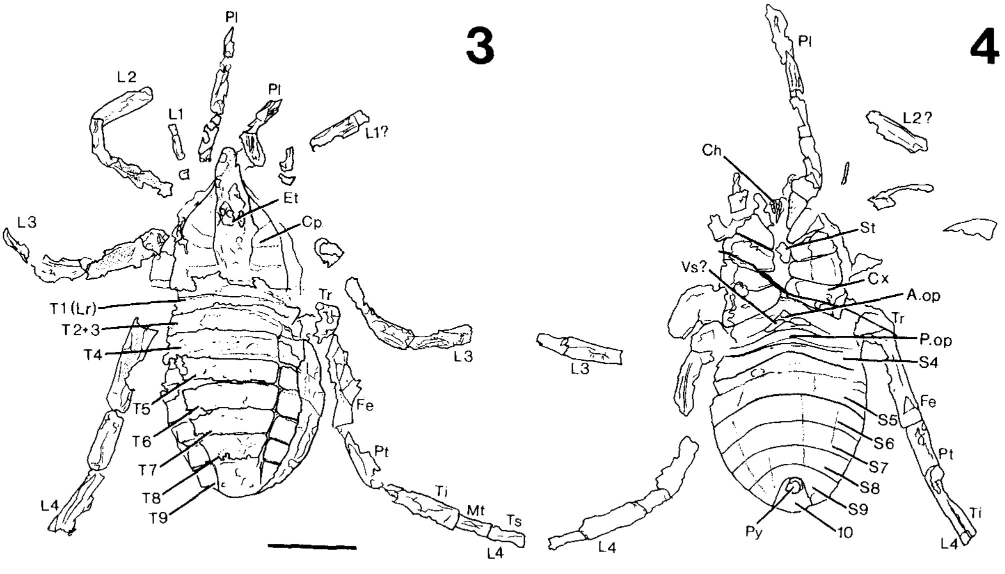
The opisthosomal morphology of the Pennsylvanian trigonotarbids is interpreted in comparison with the superbly preserved Devonian Rhynie chert material (Dunlop 1994). Interpretation of the Rhynie chert material indicates that trigonotarbids have an opisthosoma of 12 segments with 9 dorsal tergites, the first of which is modified into a locking ridge which tucks under the carapace and is often very small (Dunlop 1994). Tergites 2 and 3 are fused into a single macrotergite in most trigonotarbids (Selden & Romano 1983; Shear et al. 1987). The last two segments (11, 12) are ring-like and form a pygidium, with segment 10 forming a plate, not divided into tergites and sternites, surrounding this pygidium (Figs. 4, 7).

Ventrally, sternite 1 is interpreted as being absent in trigonotarbids (Dunlop unpubl. data). In comparison with Recent tetrapulmonate arachnids (Shultz 1993) 'sternites' 2 and 3 (the two anteriormost ventral sclerites in trigonotarbids) probably represent highly derived sutured-on lung-bearing appendages and are termed the anterior and posterior operculae respectively (Shultz 1993). Sternite 4 is therefore the first visible true sternite in trigonotarbids. Applying this interpretation to *Lissomartus*, its dorsal opisthosomal segmentation (Figs. 1, 3, 7) shows a first tergite without lateral plates, interpreted as the locking ridge which would have tucked under the carapace in life, and then subsequent divided tergites indicating a fused macrotergite 2 + 3. Tergite 9 is divided, but the division is not as strong as on the preceding tergites.

Ventrally, in YPM 169 (Figs. 2, 4), there is a raised, bilobed structure apparently on the anterior operculum. This is unusual among trigonotarbids, which normally bear a similar raised structure on the posterior operculum. The bilobed structure is interpreted as being homolo-



Figures 1, 2.—The holotype of *Lissomartus schucherti* (Petrunkevitch 1913) (YPM 169). From the Pennsylvanian (Westphalian D) of Mazon Creek, Illinois, USA. 1, Part showing dorsal surface; 2, Counterpart showing ventral surface. Scale: 5 mm.



Figures 3, 4.—Interpretative drawing of the specimen shown in Figures 1 and 2. 3, Dorsal surface; 4, Ventral surface. Cp = carapace, Et = eye tubercle, T = tergite with number, Lr = locking ridge, S = sternite with number, A. op = anterior operculum, P. op = posterior operculum, Vs? = ventral sacs?, Py= pygidium, Ch = chelicerae, L = walking leg with number, Pl= pedipalp, Cx = coxae, Tr = trochanter, Fe = femur, Pa = patella, Ti = tibia, Mt = metatarsus, Ts = tarsus, St = sternum. Scale: 5 mm.

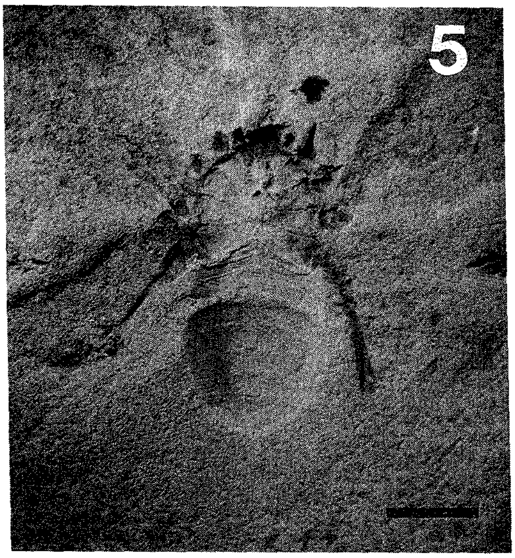


Figure 5.—The holotype of *Lissomartus carbonarius* (Petrunkevitch 1913) (USNM 37978). From the Pennsylvanian of Mazon Creek, Illinois, USA. Ventral surface only. Scale: 5 mm.

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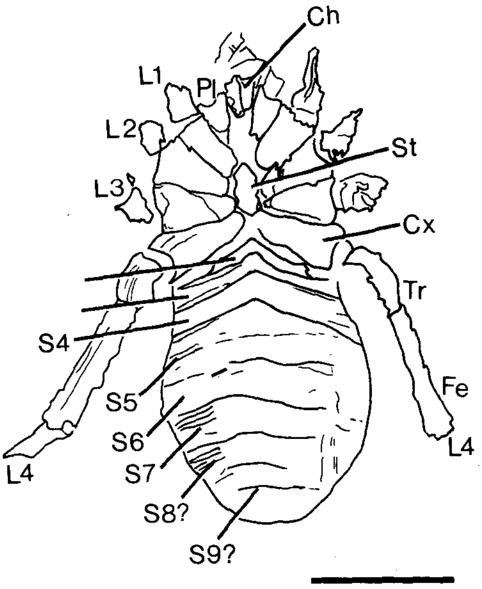

Figure 6.—Interpretative drawing of the specimen shown in Figure 5. Abbreviations as in Figures 3 and 4. Scale: 5 mm.

gous with structures seen in some Recent arachnids called ventral sacs whose function is obscure (Dunlop 1994), rather than a genital organ as Petrunkevitch (1949) suggested. However, it is worth noting that male amblypygids have a pair of gonopodi in this position associated with the genitalia (W. Shear, pers. comm.). The presence of a structure on the anterior operculum raises some doubts about the interpretation of the segmentation in this animal, but there is no visible segment in front of the anterior operculum and the overall segmentation pattern favors interpreting these structures as belonging to the anterior operculum. Whether they are ventral sacs or genitalia is impossible to determine, but since the genitalia of many Recent tetrapulmonates are concealed beneath the anterior operculum I favor their interpretation as ventral sacs.

Both specimens show a distinct deepening of the posterior opisthosoma posteriorly from the middle of sternite 5 (Figs. 2, 4–6). This could give the animal a relatively flat, narrow anterior opisthosoma with a deeper, bowl-like posterior opisthosoma (Fig. 7) in lateral view. The division between the ninth sternite and the tenth segment (not divided into a tergite and sternite) is present but poorly defined. Segment 10 surrounds a two-segmented pygidum. This structure is therefore not an anal operculum as interpreted by Petrunkevitch (1949).

The reconstruction of *Lissomartus schucherti* (Fig. 7) is based on YPM 169, with USNM 37978 (*L. carbonarius*) being used primarily for the coxosternal region. The claws and distribution of setae are hypothetical and based on the well-preserved Devonian trigonotarbids (e. g., Shear et al. 1987) and comparisons with Recent arachnids. The *Lissomartus* species are relatively large trigonotarbids and can be visualized as either ambushing or running down small arthropods on the floor of the coal forests.

SYSTEMATIC PALEONTOLOGY

Order Trigonotarbida Petrunkevitch 1949
Family Lissomartidae new family

Type and only known genus.—*Lissomartus* Petrunkevitch, 1949.

Diagnosis.—Trigonotarbids with a medially raised carapace bearing a pair of eyes on a median tubercle. Carapace relatively smooth, but with slight lateral lobation and medial tuberculation. Opisthosoma smooth with tergite 1 present as a locking ridge, tergites 2 + 3 fused and tergite 9 divided into median and lateral tergites.

Sternite 5 large, with the opisthosoma deepening posteriorly.

Discussion.—*Lissomartus* does not show the deep carapace lobation and heavily tuberculated dorsal surface which characterizes trigonotarbids such as *Aphantomartus* (e. g., Pocock 1911; Petrunkevitch 1953; Selden & Romano 1983). On these grounds I reject Petrunkevitch's (1949) placement of *Lissomartus* in the family Aphantomartidae (his Trigonomartidae).

Lissomartus is clearly related to *Trigonotarbus* (e. g., Pocock 1911; Petrunkevitch 1949) on account of its overall carapace shape and lack of strong tuberculation. However, *Lissomartus* can be differentiated from *Trigonotarbus* by its carapace ornamentation and opisthosomal segmentation. Specifically, *Lissomartus* shows fused tergites 2 + 3, a divided tergite 9 and unfused (barely) sternite 9 and segment 10 whereas *Trigonotarbus* has an unfused 2 + 3, an undivided tergite 9 and sternite 9 fused to segment 10 (unpubl. obs.). On these grounds I also reject Petrunkevitch's (1913) placement of *Lissomartus* in the Trigonotarbidae. Since *Lissomartus* cannot be placed in any existing family I am creating a new, monotypic family, Lissomartidae, to accommodate the genus. This family is known only from the Westphalian D of Mazon Creek.

Opisthosomal segmentation and ornamentation patterns appear to be useful characters, visible in most specimens, on which to base higher taxa in trigonotarbids. The Lissomartidae are clearly related to *T. johnsoni* in terms of their carapace shape and opisthosomal smoothness.

Eophrynidae and Aphantomartidae are probably sister groups, sharing a deeply lobed carapace and a heavily tuberculated dorsal surface. Lissomartidae may represent the plesiomorphic sister group of Eophrynidae + Aphantomartidae (with Trigonotarbidae perhaps the sister group to all three) since they do not have the, presumably derived, heavy tuberculation, but share with Eophrynidae + Aphantomartidae a division of tergite 9 (perhaps not fully complete in *Lissomartus*). There is also the slight lobation of the carapace, reminiscent of that in aphantomartids and eophrynids, and the drawing out of the anterior carapace of *Lissomartus*, similar to the pointed anterior spine of eophrynids.

Genus *Lissomartus* Petrunkevitch 1949

Type species.—*Lissomartus schucherti* (Petrunkevitch 1913).

Included species.—*L. schucherti, L. carbonarius*.

Diagnosis.—As for the family.

Lissomartus schucherti (Petrunkevitch 1913)
Figs. 1–4, 7

Trigonotarbus schucherti Petrunkevitch 1913: 106, 107, figs. 63, 64, Pl. 10, figs. 53, 54.

Lissomartus schucherti (Petrunkevitch). Petrunkevitch 1949: 257.

Lissomartus schucherti (Petrunkevitch). Petrunkevitch 1953: 94.

Lissomartus schucherti (Petrunkevitch). Petrunkevitch 1955: 113, fig. 80 (2a, b).

Type.—Holotype and only known specimen YPM (169), part and counterpart. From the Pennsylvanian (Westphalian D) of Mazon Creek, Illinois.

Diagnosis.—Lissomartids with a raised, bilobed structure of the anterior operculum. Ventrally, anterior sclerites not pointed on the midline.

Description.—Holotype 19.0 mm long; carapace 7.9 mm long, basal width 6.5 mm. Opisthosoma 11.1 mm long with maximum width 9.0 mm. Carapace relatively flat, subtriangular, drawn anteriorly into a long, blunt point. Carapace with medial raised area bearing a pair of eyes on a tubercle, 3.0 mm from the front of the carapace. Slight raised nodes either side of, and posterior to, the eye tubercle, otherwise carapace smooth, but slightly lobed either side of the raised median region.

Sternum present, but slightly displaced and not distinct in the fossil. Coxae subtriangular, becoming progressively larger posteriorly. Trochanters approximately as long as wide. Chelicerae present, but indistinct. Other appendages relatively long and slender with a slight granular texture to the cuticle. Pedipalp shows an oblique articulation to the trochanteraafemur joint. Podomere lengths (in mm): Palp: Fe 2.9, Pa 2.7, Ti 2.0, Ts 2.9. Leg 1: Ti? 3.7. Leg 2: Fe 4.0, Pa 2.8, Ti 3.7. Leg 3: Fe 3.8, Pa 2.9, Ti 3.7. Leg 4: Fe 5.7, Pa 3.4, Ti 4.1, Mt 1.9, Ts 2.1 mm (abbreviations as in Figs. 3, 4).

Prosoma and opisthosoma slightly disarticulated in this fossil. Opisthosoma rounded, left hand margin being absent and the right hand tergites being obscured along their lateral margins by poorly defined, superimposed sternites. With the exception of tergite 1, tergites divided into median and lateral plates, median plates becoming narrower posteriorly. Division of tergite

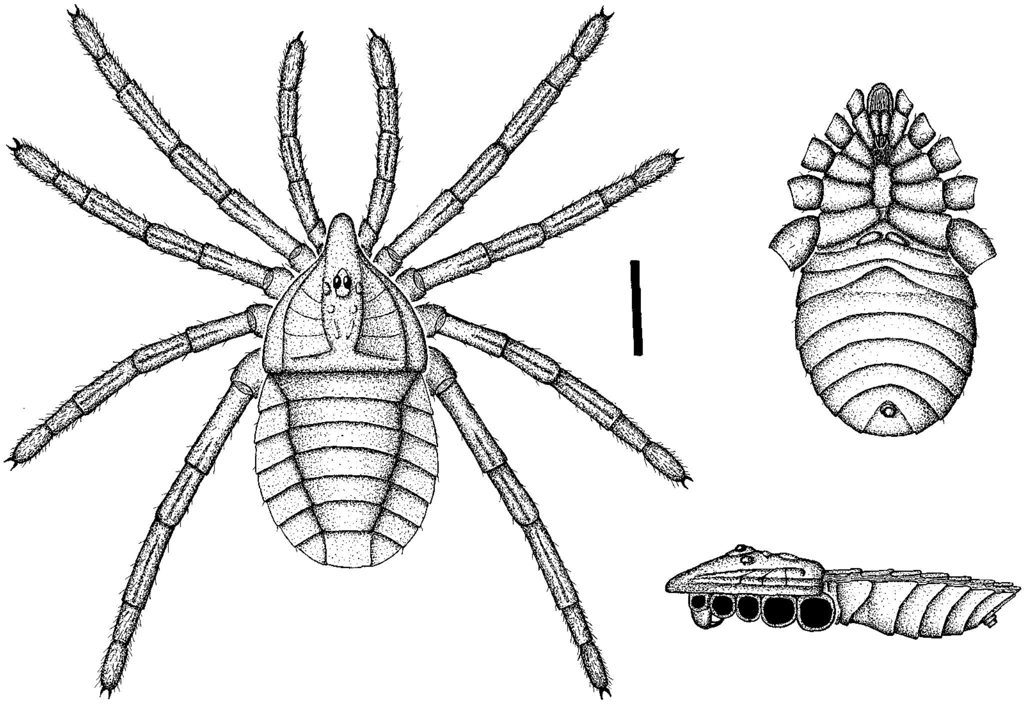

Figure 7.—Reconstruction of *Lissomartus schucherti* in dorsal, ventral and lateral view. Scale: 5 mm.

9 into median and lateral plates weaker than in the preceding tergites. Tergite lengths (in mm): 1: 0.7, 2 +3: 1.2, 4: 1.5, 5: 1.2, 6: 1.5, 7: 1.4, 8: 1.4, 9: 2.2.

Ventrally, anterior sclerites are abbreviated, but are followed by large sternite 5. Anterior operculum bears a raised, bilobed structure on posterior margin. Sternite 5 bears a transverse division (not a segmental division) demarcating a deepening of the opisthosoma posterior to the division. Faint longitudinal folds on the ventral opisthosoma. Ventral sclerites lengths (in mm): anterior operculum: 0.7, posterior operculum: 1.2, sternite 4: 0.4, 5: 2.4, 6: 1.5, 7: 1.3, 8: 1.0, 9: 0.9. Pygidium diameter 0.9 mm.

Lissomartus carbonarius (Petrunkevitch 1913)
Figs. 5, 6

Trigonotarbus carbonarius Petrunkevitch 1913: 107, 8, fig. 65, Pl. 10, fig. 55.

Lissomartus carbonarius (Petrunkevitch). Petrunkevitch 1949: 257.

Lissomartus carbonarius (Petrunkevitch). Petrunkevitch 1953: 94.

Type.—Holotype and only known specimen, USNM 37978, one piece. From the Pennsylvanian (Westphalian D) of Mazon Creek, Illinois.

Diagnosis.—Lissomartids with no raised, bilobed structure on the anterior operculum. Ventrally, anterior sclerites pointed anteriorly on the midline.

Description.—Holotype 16.3 mm long; ventral opisthosoma 9.7 mm long maximum width 7.2 mm. Coxo-sternal region well preserved and shows a sternum, bluntly pointed at either end. Leg 4 coxae attach posterior to sternum, leg coxae 2 and 3 slot into recesses in sternum and leg coxae 1 attach anterior to sternum. Chelicerae present and wedge-shaped in ventral view and with the palpal coxae either side of them they define a small preoral cavity. Femur of leg 4 present and 5.2 mm long. Additional limbs absent.

The prosoma and opisthosoma are slightly disarticulated in this fossil. Anterior segmentation of the opisthosoma clearly shows the abbreviated anterior sclerites pointed anteriorly on the midline and the large 5th sternite behind them. Lengths (in mm): anterior operculum: 0.4, posterior operculum: 0.7, sternite 4: 0.9, 5: 2.1, 6: 1.5, 7: 1.2. Bilobed structure, as in the anterior region of YPM 169, absent, but the deepening of the opisthosoma marked by a transverse division of sternite 5 more pronounced than in

YPM 169. Sternites posterior to this become increasingly poorly defined. Lateral and posterior margins of opisthosoma presumed absent since the pygidium cannot be seen. Lateral margins of the opisthosoma show evidence of folding or wrinkling of the cuticle.

Remarks.—*Lissomartus schucherti* and *Lissomartus carbonarius* are very similar fossils and there is a strong possibility that they are synonymous. In this case *L. carbonarius* would be referred to *L. schucherti* (the first of the two species mentioned by Petrunkevitch (1913)). The minor differences between these fossils could be the result of sexual dimorphism and/or ontogeny, as was suggested by Dunlop (1994) for the trigonotarbid *Pleophrynus verrucosa*. Differences in the anterior opisthosomal (genital) region are recorded within species of Amblypygi and Uropygi (W. Shear, pers. comm.) and there could be a 'straightening' of the anterior sclerites between *L. carbonarius* and *L. schucherti* due to sexual maturation.

However, since there are real morphological differences between the two monotypic species (the lack of a raised bilobed structure and the shape of the anterior ventral sclerites in the smaller *L. carbonarius*) I prefer to retain the species distinction with the reservations noted above; the dimorphic interpretation of *Pleophrynus* above was based on a wide range of specimens. Possibly, future finds of *Lissomartus* will give a clearer picture of intraspecific variation and clarify the position of these species.

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