11

Arachnida

Bret S. Beall
Including a Section on the Ricinuleida
by Paul A. Selden

The Mazon Creek region has yielded over 250 arachnid specimens, more than from any other Paleozoic arachnid locality. Only the Cenozoic amber deposits of the Baltic and the Dominican Republic have produced more arachnid fossils. The Mazon Creek arachnids occur with a great variety of other terrestrial animal and plant taxa. This co-occurrence offers an almost unique opportunity to investigate the role of arachnids in a major Pennsylvanian terrestrial biota. Although this sort of investigation is possible at other localities from which arachnids have been collected, the abundance of the Mazon Creek arachnids in association with other taxa necessarily reduces the influence of sampling bias on estimates of relative taxic abundance of the original biota.

The Mazon Creek arachnids are invaluable for studying the evolution (including phylogeny and functional morphology) of the class primarily because of their exquisite preservation. They are usually preserved as relatively uncompressed external molds in siderite concretions, although the entire suite of arachnid fossils actually exhibits a gradient of compression and distortion. The fine texture of the siderite concretions and the minimal distortion of the specimens together preserve a variety of morphological features that either are not visible on specimens from other localities or are possible to interpret only ambiguously. Consequently, the morphology of most of the taxa of Mazon Creek arachnids can be described more accurately. Additionally, the unusual abundance of material permits the comparison of multiple specimens with similar morphology, further reducing the probability that distortion due to taphonomic processes will be interpreted as original morphology. Arachnid fossils are often incomplete, but the presence of multiple specimens aids composite reconstruction at several taxonomic levels. However, such reconstructions involve the risk of underrepresenting actual variation of a particular taxon and so must be made with caution. Certain aspects of the arachnids from Mazon Creek and other localities suggest that many of the extant orders that are also present as fossils at these localities are quite conservative morphologically in spite of the more than 300-million-year histories of their clades. The excellent preservation of the Mazon Creek arachnids reduces influence of distortion-induced measurement error of morphological stasis or bradytelic rates of evolution. The Mazon Creek specimens are capable of providing substantial evidence bearing on the evolutionary history of arachnids, their relationship to other arthropods, and their interactive roles in Late Paleozoic terrestrial biotas.

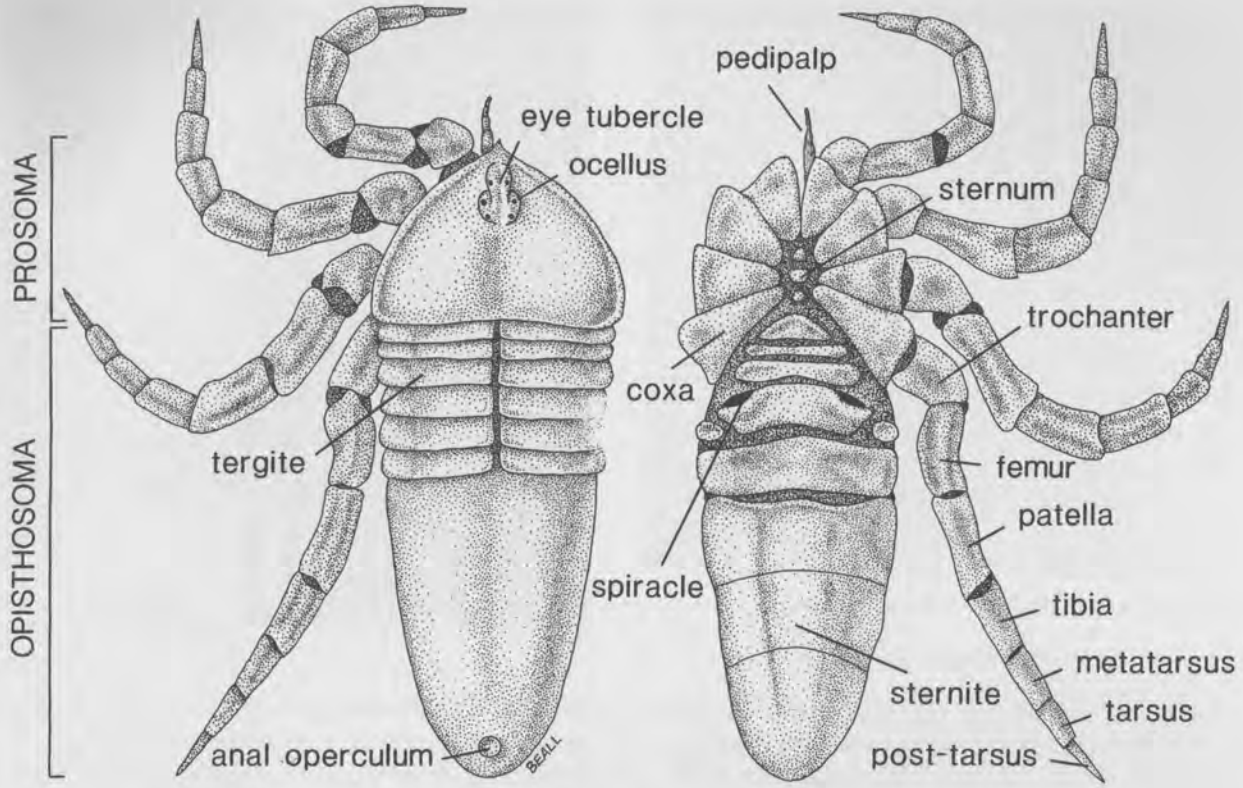

Figure 11.1. General arachnid morphology: *Phalangiotarbus lacoei*, FMNH PE 32197.

Morphology

The general morphology of an arachnid is illustrated in Figure 11.1. The arachnid body consists of distinct anterior and posterior regions called the prosoma (head and thorax) and opisthosoma (abdomen), respectively. The prosoma is composed of the unsegmented acron and the first six somites (segments) and is usually covered dorsally by a single tagma (peltidium or carapace). This tagma may bear up to eight single eyes, or ocelli, some or all of which may be arranged on a tubercle. Each of the six prosomal segments bears a pair of appendages; the chelicerae are the anteriormost pair, followed by the pedipalps and four pairs of legs. In some, the chelicerae have pincerlike claws (chelae). Each appendage is composed of segments (podomeres) that articulate at one or more points (condyles). The segment of the leg that attaches it to the body is the coxa. The segment at the end farthest from the body is the tarsus.

The abdomen (opisthosoma) consists of 12 segments (somites) and a telson at the end. Primitively, each segment has a dorsal tergite and a ventral sternite that are modified in various ways in each order.

Respiration occurs cutaneously, or by means of book lungs, sieve tracheae, or tube tracheae. The openings to these respiratory structures are called spiracles.

Systematic Paleontology

Class Arachnida is in the phylum Chelicerata. Petrunkevitch (1913, 1945, 1949, 1955) recognized 10 orders of the class Arachnida (subphylum Chelicerata), and numerous lower taxa among the Mazon Creek fossils. Subsequently, only Kjellesvig-Waering (1986, in preparation) and Selden (1983, 1984) have reviewed parts of Petrunkevitch's classification. Much work is still necessary to evaluate the validity of many of the genera and species of Mazon Creek arachnids.

A number of problems plague the lower level taxonomy of Paleozoic arachnids from Mazon

Creek and other localities. Both Petrunkevitch and Kjellesvig-Waering developed classification systems in which the limits of the taxa are relatively arbitrary, making their taxonomies quite subjective. Kjellesvig-Waering (1986, in preparation) has emphasized Petrunkevitch's apparent failure to consider taphonomic influences on arachnid morphology; because of this failure, many of Petrunkevitch's taxa are artificial, being distortions of morphology. Finally, because most of the genera and species of extant arachnids have been diagnosed using characters that are rarely preserved in fossils, comparing these extant taxa with extinct taxa of the same rank is extremely difficult. Because of these and other problems at lower taxonomic levels, this chapter focuses on the orders of arachnids known from the Mazon Creek region.

Figure 11.2. *Bicarinitarbus pieckorum*, FMNH PE 107. Scale bar = 5 mm (estimate).

Order Phalangiotarbida

A phalangiotarbid was one of the first arachnids to be described from the Mazon Creek region (Scudder, 1868). At least 150 specimens have been collected, making the Phalangiotarbida the most abundant (61 percent) of Mazon Creek arachnids that can be identified to order.

Morphology. Prosoma semicircular (primitive) to rhomboidal (derived), with pointed anterior projection; eye tubercle trifoliate with three pairs of ocelli along its flanks. Ornamentation consists of the fine pustules (interpreted as setal bases). Ventrally, the basal segment (coxa) of appendages III to VI meet at a sternum composed of up to four sclerites, some of which are medially divided.

Chelicerae unknown. Pedipalps incompletely preserved, but are rather short, antenniform appendages with at least four segments; coxae unknown. Third pair of prosomal appendages raptorial (used for grabbing, based on kinematic analyses of limb structure; Beall, 1984, 1985); corresponding coxae abut medially, with medial margins sometimes slightly spinose. Last three pairs pedal, with leg length increasing posteriorly.

Dorsally, abdomen with six anteroposteriorly narrow, slightly overlapping, medially divided tergites, followed by a large posterior tagma that may bear relics of fusion of tergites; all surfaces finely pustulated. Posterior tagma bears a round anal operculum near posterior margin (Kjellesvig-Waering, 1978, in preparation). Ventral surface with nine sternites connected to tergites by pleated, unsclerotized integument. First three sternites fit between fourth coxae. Fourth sternite as wide as abdomen (opisthosoma), divided into three transverse sections. Fourth through ninth sternites each bearing a pair of transversely arranged, shallow depressions that represent the external expression of entapodemes for dorsoventral musculature.

One or two pairs of spiracles present. One pair of relatively large spiracles always situated along the anterior margin of the median sclerite of the fourth sternite. Another pair of smaller openings sometimes present at lateral edges of anterior margin of second sternite.

Taxonomy. Kjellesvig-Waering (in preparation) assigned all phalangiotarbids to a single family, Phalangiotarbidae, with characteristics of the order. He recognized the following seven genera among the Mazon Creek phalangiotarbids.

Genus *Phalangiotarbus*
Figure 11.1

Posterior margin of prosoma straight to slightly concave anteriorly.

Figure 11.3. *Paratarbus carbonarius,* ISM 14864.
Scale bar = 5 mm (estimate).

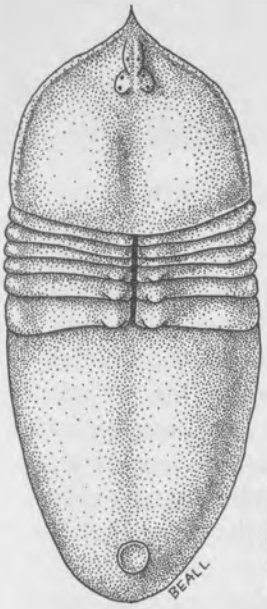

Figure 11.4. *Mesotarbus extraneus,* dorsal reconstruction, FMNH PE 32189.
Scale bar = 5 mm.

Genus *Bicarinitarbus*
Figure 11.2

Posterior margin of prosoma straight; opisthosomal median line flanked by pair of "keels" that extend anteroposteriorly.

Genus *Paratarbus*
Figure 11.3

Posterior margin of prosoma slightly convex; two protuberances occurring at posterior edge of prosoma.

Figure 11.5. *Architarbus rotundatus,* YPM 185.
Scale bar = 5 mm.

Genus *Mesotarbus*
Figure 11.4

Posterior margin of prosoma straight to slightly convex posteriorly; six anterior tergites each with a pair of small protuberances flanking the median sulcus.

Genus *Architarbus*
Figure 11.5

Posterior margin of prosoma strongly convex posteriorly; anterior two tergites similarly curved.

Genus *Mazonitarbus*
Figure 11.6

Posterior margin of prosoma more strongly convex posteriorly that in *Architarbus;* anterior four tergites similarly curved. *Mazonitarbus* probably is a juvenile instar of *Architarbus.*

Genus *Hadrachne*
Figure 11.7

Posterior margin of prosoma slightly convex, with only the first abdominal tergite similarly curved. Known from only a single specimen (largest known phalangiotarbid), this genus may represent an extremely old instar of *Architarbus.*

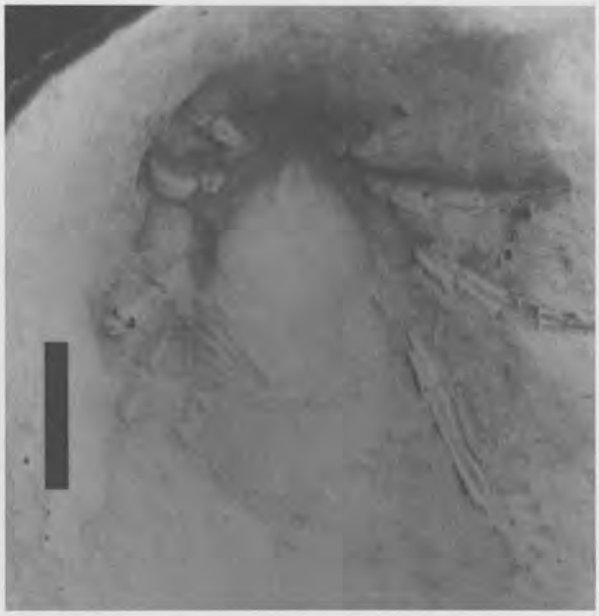

Figure 11.6. *Mazonitarbus minor,* FMNH PE 32155. Scale bar = 5 mm (estimate).

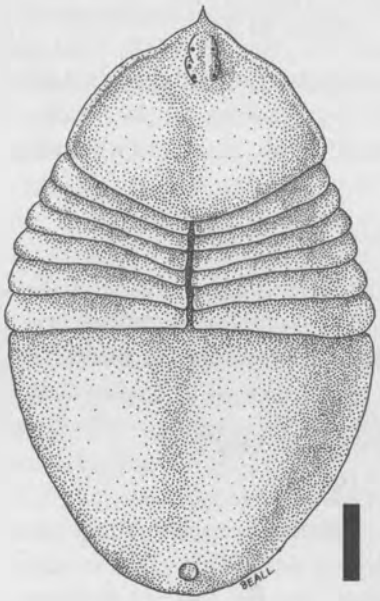

Figure 11.7. *Hadrachne horribilis,* dorsal reconstruction, FMNH OC 9232. Scale bar = 5 mm.

Order Anthracomartida

Originally the trigonotarbids and anthracomartids were placed in the same order, Anthracomarti (Karsch, 1882). Later, Petrunkevitch (1949) placed these arachnids in separate orders. Shear and Selden (1986) have questioned whether these orders are truly distinct, but the

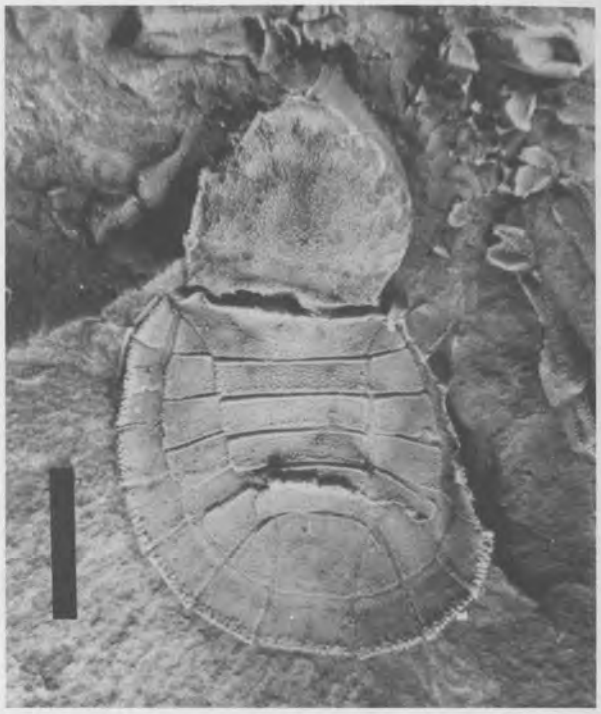

Figure 11.8. Unnamed arthracomartid, FMNH PE 32156. Scale bar = 5 mm (estimate).

trigonotarbids and anthracomartids are treated separately here pending additional analysis.

At least 14 Mazon Creek anthracomartid specimens are known, representing 5.4 percent of the arachnids. Most are too poorly preserved to be described at the generic or specific level but they do provide important data regarding morphological diversity of the order (Figure 11.8).

Morphology. Prosoma subtrapezoidal to subtriangular; convex dorsally. Narrow median ridge sometimes bisects anterior third of prosoma. Pustules form a reticulate pattern. Eyes unknown.

Chelicerae unknown in Mazon Creek forms. Pedipalps antenniform with five segments (podomeres) excluding coxae (Petrunkevitch, 1955). Remaining appendages pedal, with six segments (podomeres) excluding coxae.

First and ninth abdominal tergites undivided; remaining seven tergites divided into five sclerites arranged in five fields. Opisthosomal perimeter smoothly curved or slightly scalloped. Tergites finely pustulose. Ventrally, opisthosoma with 10 undivided, smooth sternites; anal operculum in center of tenth sternite.

Petrunkevitch (1949, 1955) used a series of British anthracomartids to infer aspects of the modes of reproduction and respiration in these arachnids. He interpreted topographic variation of the second, third, and fourth sternites as indicating sexual dimorphism. However, Petrunkevitch does not defend his interpretations of female or male, nor does he argue that the features were not taphonomically induced. Similar structures are absent in North American specimens.

Petrunkevitch (1913, 1949, 1955) also illustrates "lungs" and "pulmonary apodemes" on the second, third, and fourth sternites. Actually, the "lungs" are lung covers, which do not necessarily indicate book lungs (Levi, 1969). Also, Petrunkevitch believed the fossils displayed the internal (rather than external) ventral opisthosomal surface; if he drew the "pulmonary apodemes" accurately, they resemble spiracles.

Taxonomy. No Mazon Creek anthracomartids have been described. As stated above, most of the specimens are too poorly preserved to allow adequate comparison with existing taxa or to justify describing them as new taxa.

Figure 11.9. *Aphantomartus pustulatus,* UMMP 7218. Scale bar = 5 mm (estimate).

Order Trigonotarbida

The trigonotarbids, the last of the three extinct orders from Mazon Creek, constitute 5.8 percent of the arachnids. Selden and Romano (1983) suggest that a taxonomic review may be necessary.

Morphology. Prosoma semicircular to subtriangular, with posterior margin straight; ovoid eye tubercle with two ocelli may be present in center of prosoma. Depression behind eye tubercle may be homologous with foveal depression (external expression of entapodemes for the origination of muscles inserting on the "pumping" stomach) in certain extant orders. Ornamentation often pustulose.

Chelicerae known only in Devonian forms, in which they are clawlike. Pedipalps antenniform, with five segments excluding coxae; coxae abut medially. Remaining appendages pedal with six podomeres, excluding coxae; sternum with independent sclerites or single large tagma.

Opisthosoma with eight tergites and eight to nine sternites; anal operculum terminal or in center of last sternite. Sternites smooth, increasing in curvature (convex anteriorly) toward posterior. Tergites divided into three fields; dorsal surface may be smooth to heavily tuberculate. Posterolateral corners of sixth and seventh tergites may be elongated into spines.

Taxonomy. Trigonotarbid fossils are usually less distorted than specimens of other orders. Although the three genera recognized by Petrunkevitch (1955) are defined in part using primitive characters, each is also distinguished by certain derived characters, and so the taxa can be retained with redescription.

Genus *Aphantomartus* (= *Trigonomartus*) Selden and Romano, 1983
Figure 11.9

Prosoma tuberculate. Sternum wide with sclerites fused into single tagma. Opisthosoma pustulose with many tubercles. Short spines pro-

Figure 11.10. *Pleophrynus ensifer,* ISM 14873. Scale bar = 5 mm.

ject from posterolateral corners of the sixth and seventh tergites, a synapomorphy with several other trigonotarbids (cover).

Genus *Pleophrynus*
Figure 11.10

Prosoma pustulose with sharp anterior process; sternum narrow. Opisthosoma finely pustulose with four pairs of larger tubercles along posterior margins of each tergite. Spines project from posterolateral corners of sixth and seventh tergites.

Genus *Lissomartus*
Figure 11.11

Prosoma with rounded anterior process. Sternum narrow, with three sclerites. Opisthosoma smooth. Fourth sternite with anterior lobe, and corresponding curvature in second and third sternites.

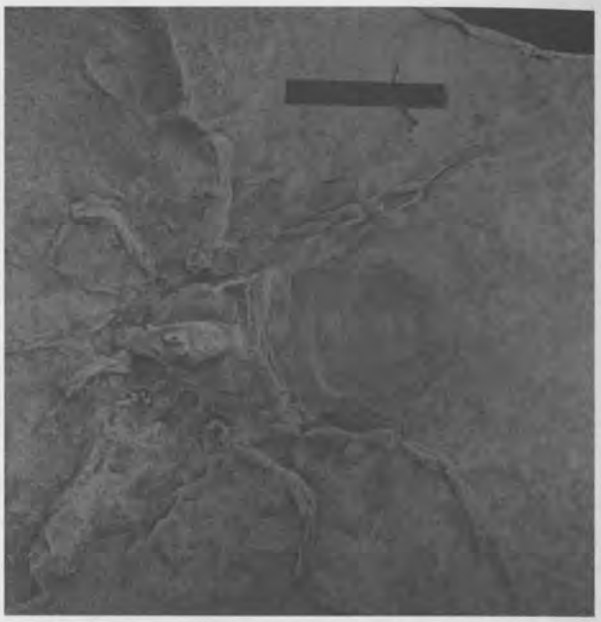

Figure 11.11. *Lissomartus schucherti,* YPM 169. Scale bar = 5 mm (estimate).

Order Uropygida

The uropygids (whip scorpions) represent less than 3 percent of the Mazon Creek arachnids. The whip scorpions are among the most morphologically conservative of all arachnid orders.

Morphology. Prosoma roughly hexagonal, somewhat elongate anteroposteriorly. One pair of medial ocelli and two groups of three closely arranged anterolateral ocelli present. Foveal depression on posterior half of prosoma.

Ventrally, robust coxae flanking sternal sclerites. Chelicerae chelate, bearing two segments. Massive, subchelate pedipalps with five podomeres. Massive, subchelate pedipalps with five podomeres, excluding coxae; coxae abut medially. Third appendages tactilosensory, with slender, elongate podomeres; tarsi subdivided. Remaining appendages pedal, with six podomeres (tarsi subdivided).

Opisthosoma with 12 somites, posterior three reduced to narrow pygidium. Telson "whiplike." Tergites and sternites well sclerotized.

Book lungs present in both second and third opisthosomal somites; spiracles at posterolateral margins of sternites. Anus terminal, immediately below telson.

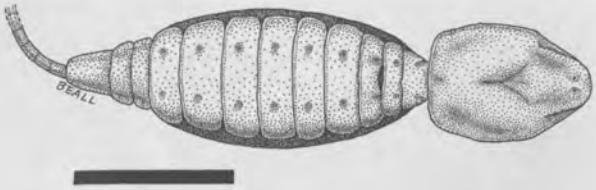

Figure 11.12. *Geralinura carbonaria*, dorsal reconstruction, USNM 37985. Scale bar = 5 mm.

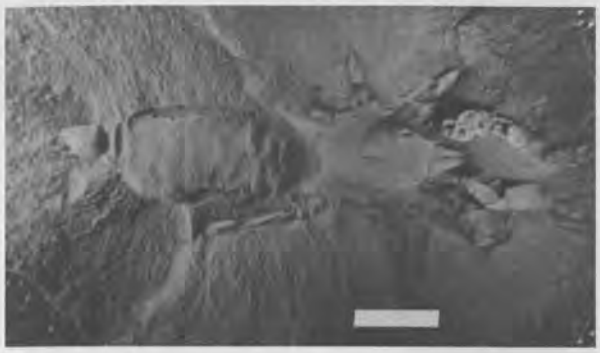

Figure 11.13. *Prothelyphonus* sp., YPM unnumbered specimen. Scale bar = 5 mm (estimate).

Taxonomy. Petrunkevitch (1913, 1949, 1955) recognized two genera of Mazon Creek uropygids. Generic separation may be inappropriate, but additional work is necessary before the genera can be synonymized.

Genus *Geralinura*
Figure 11.12

Prosoma ovate, without eyes; sternum consists of single large sclerite between the first through third pedal coxae.

Genus *Prothelyphonus*
Figure 11.13

Prosoma approximately hexagonal, bearing four pairs of ocelli as described for order.

Order Amblypygida

Like the closely related uropygids, the amblypygids are a rather morphologically conservative order. They constitute only 2.3 percent of the Mazon Creek arachnids.

Morphology. Prosoma slightly heart shaped, with median eye tubercle bearing two ocelli, and two lateral clusters of three ocelli each. Foveal depression on posterior half of prosoma. Ventrally, coxae radiate from four sternal sclerites. Chelicerae with two podomeres, modified into fangs. Pedipalps raptorial, with six podomeres. Third pair of appendages tactile (as in uropygids). Remaining appendages pedal, with six podomeres (tarsi subdivided).

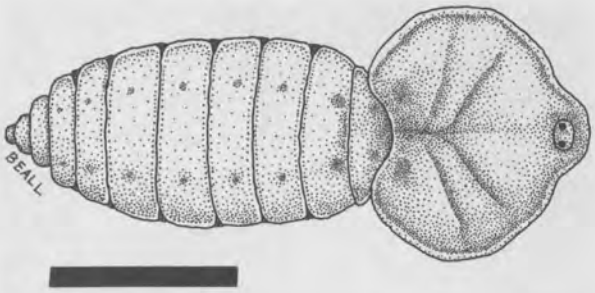

Figure 11.14. *Graeophonus carbonarius*, dorsal reconstruction, USNM 37969. Scale bar = 5 mm.

Opisthosoma with 12 well sclerotized tergites and sternites. First somite forms pedicle; twelfth somite is a reduced pygidium with terminal anus. Book lungs on third opisthosomal somite.

Taxonomy. Petrunkevitch (1955) recognized three genera of Mazon Creek amblypygids. The main differences between the genera (reported number of eyes) is probably due to taphonomic influence.

Genus *Graeophonus*
Figure 11.14

Prosoma with median tubercle bearing single pair of ocelli; groove present in posterior half of carapace.

Genus *Protophrynus*
Figure 11.15

Anterior projection of carapace truncated, with single pair of ocelli; three pairs of lateral ocelli.

Genus *Thelyphrynus*
Figure 11.16

Carapace kidney shaped, without anterior process and without ocelli.

Order Araneida

The araneids (true spiders) represent another minor (2.3 percent) component of the Mazon Creek arachnids. Although poorly preserved, these specimens provide important data regard-

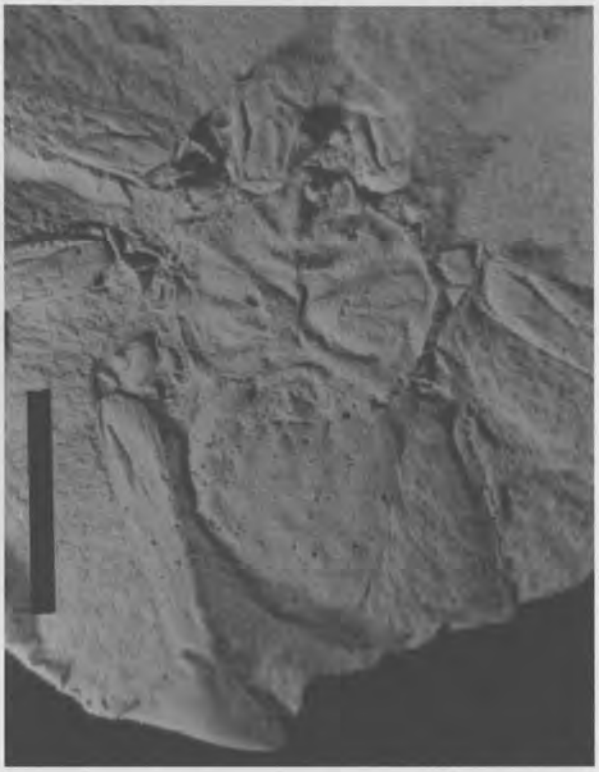

Figure 11.15. *Protophrynus carbonarius,* UMMP 7222. Scale bar = 5 mm (estimate).

Figure 11.16. *Thelyphrynus elongatus,* UMMP 7220. Scale bar = 5 mm (estimate).

ing morphological diversity of the order during the Middle Pennsylvanian.

Morphology. Prosoma ovoid to slightly hexagonal or rectangular, with up to eight ocelli variably arranged on or around an anteromedian tubercle. Foveal depression present. Ventrally, coxae radiate from large sternum.

Chelicerae with two podomeres; terminal podomeres modified as fangs. Pedipalps pediform, with six podomeres. Remaining appendages pedal or raptorial, with seven podomeres.

Opisthosoma with 12 lightly sclerotized tergites, and a variable, smaller number of sternites. First opisthosomal somite forms pedicle. Book lungs or tracheae on second and third opisthosomal somites. Fourth and fifth somites each with up to two pairs of spinnerets, the structures connected to the silk glands and used for spinning webs among other things (a unique trait linking the araneids). Anus terminal.

Taxonomy. All Mazon Creek araneids have segmented opisthosomata, a character state found only in the suborder Mesothelae (= Liphistina) among extant araneids. However, none of these specimens exhibit the shared derived characters described by Plotnick and Gertsch (1976) as necessary to place them within either of the extant suborders. Because the Mazon Creek araneids are so poorly preserved, the absence of shared derived character states in the fossil specimens may be due either to a loss of morphology caused by taphonomic processes or to an original absence of the characters in the specimens. Because neither of these two interpretations can be rejected, the Mazon Creek araneids may be assigned either to the Mesothelae using primitive character states (segmented opisthosoma; medial, rather than terminal, spinnerets) or to Araneida incertae sedis. At the present time I favor the latter option, pending additional work to identify characters in the Mazon Creek specimens that are obligatorily correlated with the shared derived characters of the extant suborders.

The named Mazon Creek araneids are both placed in the genus *Arthrolycosa* (Figure 11.17). Petrunkevitch (1955) stated that this genus possessed two pairs of eyes on a median tubercle, and a carapace with convex sides.

Order Ricinuleida

Ricinuleida is the only extant arachnid order to be described first from a fossil (Cooke and Shadab, 1973). Mazon Creek ricinuleids have provided much information about the extinct

Figure 11.17. *Arthrolycosa danielsi,* UMMP 7219. Scale bar = 5 mm (estimate).

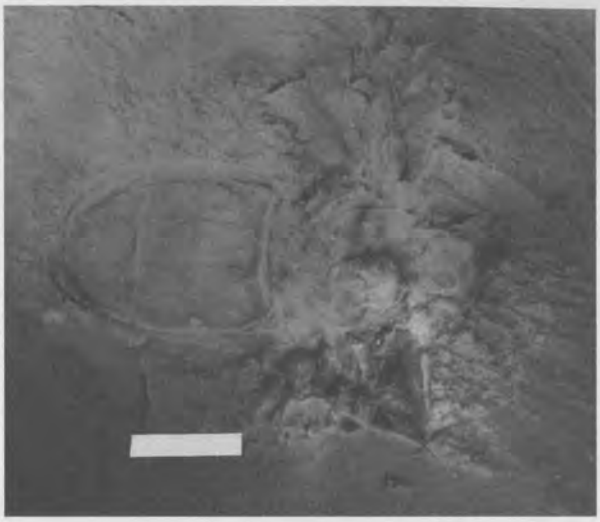

Figure 11.18. *Poliochera glabra,* UMMP 7223. Scale bar = 5 mm.

Figure 11.19. *Curculioides mcluckiei,* FMNH PE 780. Latex mould of dorsal surface. Scale bar = 5 mm.

forms, even though they represent only 3.5 percent of the arachnid specimens.

Morphology. Movable hood (cucullus) hinged to front of carapace and covering chelicerae is diagnostic of the order. Cuticle commonly tuberculate; pair of lateral eyes usually present on fossils at lateral margins of carapace (vestigial in living ricinuleids). Foveal and other depressions on carapace.

Chelicerae chelate, of two podomeres. Pedipalps chelate, of six podomeres with few or no tubercles. Remaining limbs pedal; tarsi (poorly known in fossils) subdivided; third walking leg modified for sperm transfer in males.

Pedicle bearing sexual organs links prosoma and opisthosoma but is commonly hidden by locking of these tagmata. Ventral pouches on anterior opisthosoma receive coxae of walking leg 4 during locking. Transverse tergites in living forms and fossil Poliocheridae (Figures 11.18, 11.20); other fossils without transverse tergites but with longitudinal line or sulcus on dorsal abdomen (Figures 11.19, 11.20). Posterior three somites form a telescopic pygidium.

Taxonomy. A recent revision by Selden (1992) erected two new suborders based on presence or absence of functional eyes and relative sizes of coxae of walking legs 3 and 4. All living ricinuleids are in Neoricinulei, all fossils in Palaeoricinulei. Three of the four genera of Palaeoricinulei occur at Mazon Creek. For species identification see Selden (1992).

Genus *Curculioides*
Figures 11.19, 11.20b, 11.20f

Dorsal abdomen divided by a median line. *Curculioides mcluckiei, C. scaber,* and *C. gigas* occur at Mazon Creek.

Genus *Amarixys*
Figure 11.20d, 11.20e

Dorsal abdomen divided by a median sulcus. *Amarixys sulcata, A. stellaris,* and *A. gracilis* occur at Mazon Creek.

Genus *Poliochera*
Figures 11.18, 11.20a, 11.20c

Dorsal abdomen divided by transverse tergites. *Poliochera punctulata, P. gibbsi,* and *P. glabra* occur at Mazon Creek.

Order Opilionida

Petrunkevitch (1913, 1949, 1955) described two Mazon Creek arachnids as opilionids, or daddy longlegs, *Nemastomoides longipes* (Figure 11.21) and *N. depressus.* The former is an opilionid, but the latter specimen is a phalangiotarbid.

Petrunkevitch (1913) erected the order Kustarachnida to include three Mazon Creek arachnids. However, all of the diagnostic characteristics listed by Petrunkevitch as distinguishing the Kustarachnida either are absent in the fossils or are consistent with reinterpreting the specimens as opilionids (Beall, 1986). When the "kustarachnids" are included with other opilionid fossils, the order represents almost 4 percent of the Mazon Creek arachnids.

Morphology. Prosoma subtriangular to semicircular, with a median eye tubercle bearing two ocelli. Coxae radiate from a central region that may bear a sternum.

Chelicerae chelate, with three podomeres. Pedipalps pediform or raptorial, with six podomeres. Remaining appendages pedal, with seven rather elongate podomeres.

Opisthosoma broadly attached to prosoma; somites difficult to identify externally. A pair of tracheal tubes open ventrally on second opisthosomal somite. Terminal anus operculate.

Taxonomy. The genus *Kustarachne* should be regarded as a nomen nudum. Petrunkevitch (1955) described the family Nemastomoididae as having an oval sternum; the fourth pedal coxae abut, separating the sternum from the first opisthosomal sternite.

Genus *Nemastomoides*
Figure 11.21

Carapace wider than long, with evenly rounded front and sides; eyes on tubercle considerably anterior to center of carapace (Petrunkevitch, 1955).

Order Solpugida

The Solpugida (wind scorpions) are represented in the Mazon Creek biota by a single extremely poorly preserved specimen (YPM 155). Except for rare specimens preserved in Cenozoic amber, no other solpugid fossils are known.

Morphology. Prosoma with large anterior tagma (propeltidium) and three separate posterior sclerites. Propeltidium with median pair of ocelli, and two pairs of lateral ocelli. Pedipalpal coxae large; rostrum projects anteriorly from between the pedipalpal coxae. Remaining coxae arranged in two almost parallel rows; sternum absent.

Chelicerae massive, chelate with two podomeres. Pedipalps tactile and thickly pediform with six podomeres. Third pair of appendages also tactile, antenniform with seven podomeres. Remaining appendages pedal, with eight podomeres. Racket organs (malleoli) situated along coxae and first two podomeres of sixth appendages.

Opisthosoma with 11 somites, each with separate tergites and sternites. Third and fourth sternites with paired tracheal openings, and fifth sternite with a single opening (another pair of openings between third and fourth coxae). Last opisthosomal somite with slitlike anus.

Taxonomy. The holotype and only known specimen of the Mazon Creek solpugid, *Protosolpuga carbonaria,* is severely compressed, and much of the morphology is obscured by irregular sections of carbonized organic material. Although the specimen displays characters that are diagnostic of the order (e.g., massive chelicerae, large pediform pedipalps, rounded posterior margin of anterior prosomal tagma), characters diagnostic of lower taxonomic levels cannot be observed in the specimen (Figure 11.22).

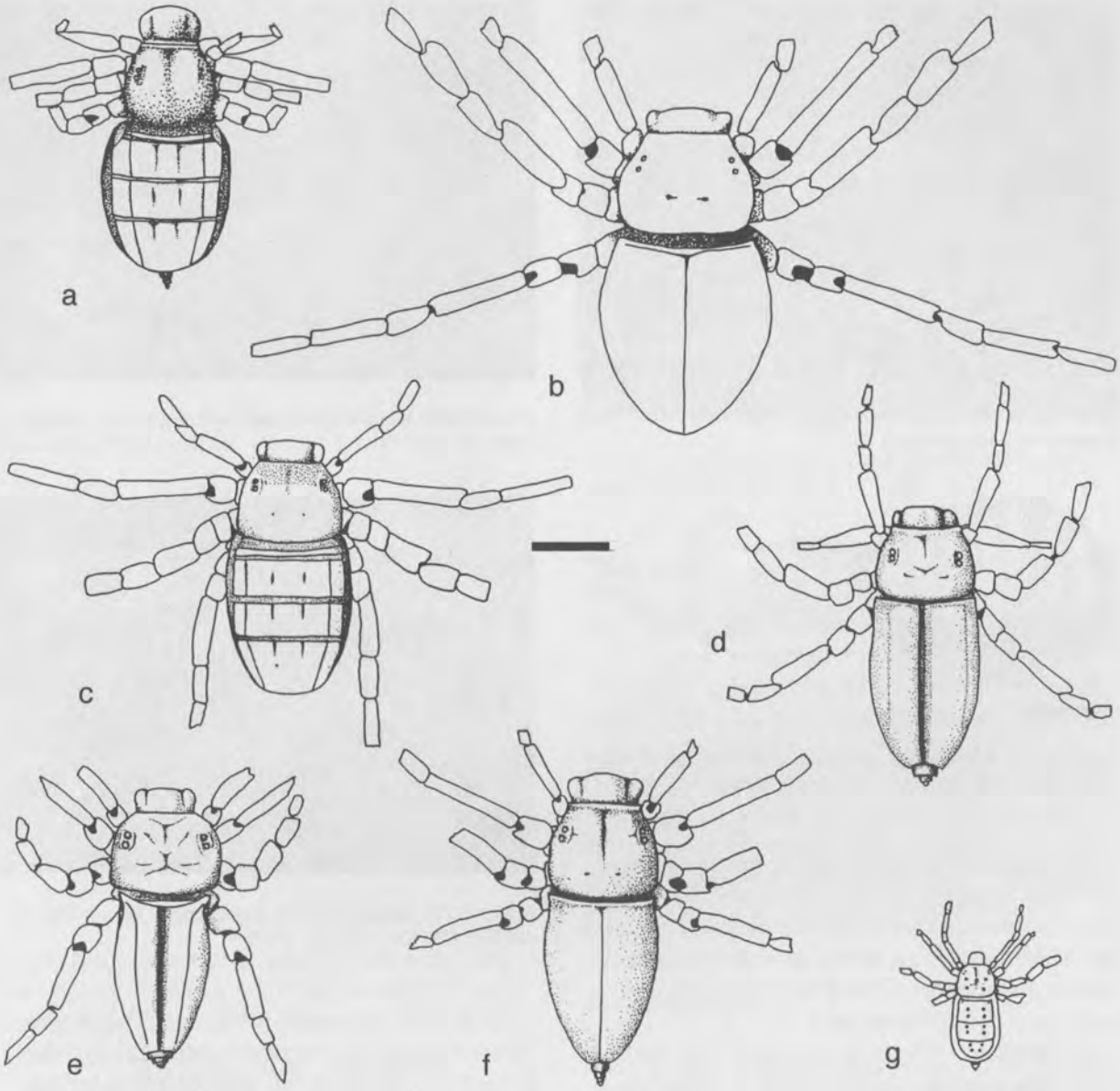

Figure 11.20. Reconstruction of a range of fossil Ricinulei: **a** *Poliochera glabra,* based on UMMP 7223; **b** *Curculioides gigas,* based on FMNH PE 784; **c** *Poliochera punctulata,* based on USNM 37971 and FMNH PE 32206; **d** *Amarixys gracilis,* based on ISM 14862; **e** *Amarixys stellaris,* based on FMNH PE 32184; **f** *Curculioides mcluckiei,* based on USNM 440519; **g** *Terpsicroton alticeps,* based on In 31238, collection of BM (NH).
Scale bar = 5 mm. Reproduced by permission of the Royal Society of Edinburgh from Trans. R. Soc. Edinburgh Earth Sci. 83 (1992): 595–634.

Order Scorpionida

The phylogenetic position of scorpions has been the source of some controversy. Traditionally, workers have referred scorpions to the Arachnida (e.g., Petrunkevitch, 1913, et seq.), but Bergstrom (1980) argued for their merostome (specifically, eurypterid) affinities. Although the latter interpretation deserves serious consideration, I will follow tradition by including the scorpions in this chapter.

Almost 14 percent of the Mazon Creek arachnid fossils that can be assigned to an order are scorpions; only the phalangiotarbids are more abundant. Kjellesvig-Waering (1986) proposed a new classification of the Scorpionida that acknowledged the extreme morphological diversity of the Carboniferous scorpions; his restudy

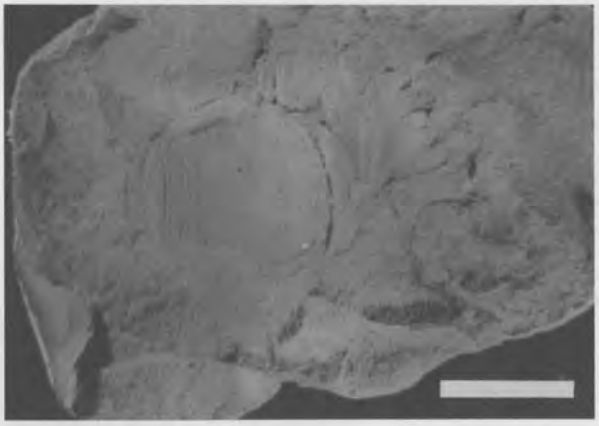

Figure 11.21. *Nemastomoides longipes,* YPM 171. Scale bar = 5 mm (estimate).

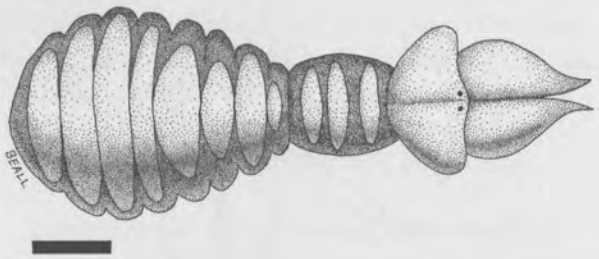

Figure 11.22. *Protosolpuga carbonaria,* preliminary dorsal reconstruction, YPM 155. Scale bar = 5 mm (estimate).

is an excellent summary of the morphology of all fossil scorpions. Although certain aspects of his classification must be questioned, I will use his higher taxa here, using quotation marks to indicate where morphological interpretations may need reconsideration.

Morphology. Prosoma pentagonal or trapezoidal, with anteromedian tubercle bearing two ocelli; single pair of compound eyes or three pairs of ocelli present laterally. Ornamentation pustulose.

Opisthosoma divided into broad mesosoma (seven somites) and narrow metasoma (five somites), with telson modified into sting. Mesosomal tergites and sternites separated by lateral pleural membrane. Kjellesvig-Waering (1986) interpreted the ventral mesosomal sclerites of all but one Mazon Creek scorpion (*Palaeopistho-canthus schucherti;* Figure 11.26) as "abdominal plates"; the homology of the ventral sclerites is a controversial topic that requires more space than is available here.

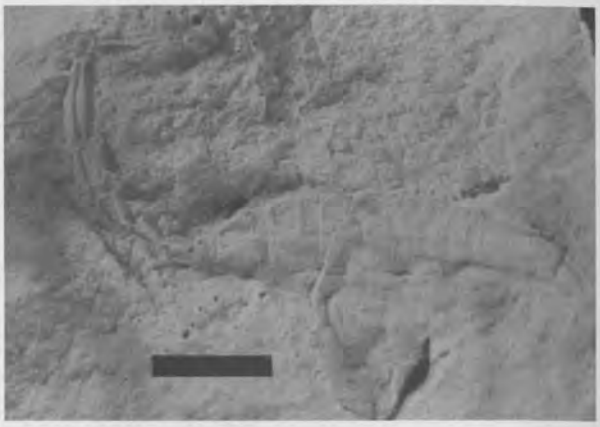

Figure 11.23. Holostern branchioscorpion (*Eoctenus miniatus*), YPM 131. Scale bar = 5 mm.

Figure 11.24. Meristostern branchioscorpion (*Palaeobuthus distinctus*), YPM 133. Scale bar = 5 mm.

Taxonomy. Research addressing the controversies regarding scorpion respiration and the homology of the ventral mesosomal sclerites may modify the following taxa to which Kjellesvig-Waering has assigned all of the Mazon Creek scorpions.

Suborder Branchioscorpionina

Presumed aquatic scorpions respiring by gills. "Gill openings" at intersection of "abdominal plates" and doublure, or on doublure.

Infraorder Holosternina

Branchioscorpions with five rectangular, undivided ventral "abdominal plates" enclosing "gill chamber." Figure 11.23 illustrates *Eoctenus miniatus,* a holostern branchioscorpion.

Figure 11.25. Lobostern branchioscorpion (*Kronoscorpio danielsi*), UMMP 7216. Scale bar = 5 mm.

Figure 11.26. Orthostern neoscorpion (*Palaeopisthocanthus schucherti*), YPM 140. Scale bar = 5 mm.

Infraorder Meristosternina

Branchioscorpions with "abdominal plates" with median suture and enclosing "gill chamber." Figure 11.24 illustrates *Palaeobuthus distinctus*, a meritostern brachioscorpion.

Infraorder Lobosternina

Branchioscorpions with five bilobate "abdominal plates" enclosing "gill chamber." Figure 11.25 illustrates *Kronoscorpio danielsi*, a lobostern branchioscorpion.

Suborder Neoscorpionina

Presumed terrestrial scorpions with sternites, four of which bear a pair of spiracles leading to book lungs

Infraorder Orthosternina

Neoscorpions with rectangular sternites bear spiracles; doublures absent. Figure 11.26 illustrates *Palaeopisthocanthus schucherti*, an orthostern neoscorpion.

Acknowledgments

I wish to thank the editors for inviting me to write this chapter. D. C. Fisher and H. Van Iten commented on early drafts of the manuscript; their comments have improved the text greatly, but all oversights remain my responsibility. The additions by P. Selden subsequent to the completion of the original manuscript are highly appreciated. The following institutions permitted me to examine specimens deposited in their collections: FMNH, USNM, ISM, YPM, NEIU MCP, and UMMP. Many individuals provided information on specimens either directly or indirectly: J. and J. Anderson, C. Berry, P. Caponera, D. Chlipala, J. Dedina, K. Dedina, A. and J. Hay, K. Holm, J. Konecny, S. LeMay, W. Lietz, H. and T. Piecko, J. Pohl, K. and S. Ramsdell, W. Rieger, G. Siwik, M. Smith, T. Testa, and M. Young. I am indebted to these individuals and to the faculty and staff of the above institutions for their gracious and continued assistance.

References

Beall, B. 1984. Functional and autecological analysis of phalangiotarbid arachnids. Geol. Soc. Amer. Abstract with Program, 16:457.

———. 1985. Functional and ecological analyses of phalangiotarbid arachnids (Carboniferous). Unpublished M.S. thesis, University of Michigan, Ann Arbor, 75 pp.

———. 1986. Reinterpretation of the Kustarachnida. Amer. Arachnol., 34:4.

Bergstrom, J. 1980. Arthropod phylogeny and the fossil record, pp. 3–56. *In* A. P. Gupta (ed.), Arthropod Phylogeny. Van Nostrand Rheinhold, New York.

Cooke, J., and M. Shadab. 1973. New and little known ricinuleids of the genus *Cryptocellus* (Arachnida, Ricinulei). Amer. Mus. Novitates, 2530:1–25.

Karsch, F. 1882. Ueber ein neues Spinnenthier aus der schlesischen Steinkohle und die Arachniden der Steinkohlenformation überhaupt. Zeit. Deutsch Geol. Gesell., 34:556–561.

Kjellesvig-Waering, E. 1978. The Phalangiotarbida (Arachnida) of Mazon Creek. Geol. Soc. Amer. Abstract with Program., 10:258–259.
———. 1986. A monograph of the fossil Scorpionida. Palaeontographica Amer., 55:1–287.
———. In preparation. Phalangiotarbid arachnids from the Mazon Creek region of Illinois (Carbondale Formation, Pennsylvanian). Manuscript.
Levi, H. 1969. Adaptations of respiratory systems of spiders. Evolution, 21:571–583.
Petrunkevitch, A. 1913. A monograph of the terrestrial Palaeozoic Arachnida of North America. Trans. Connecticut. Acad. Arts Sci., 18:1–137.
———. 1945. Palaeozoic Arachnida of Illinois: an inquiry into their evolutionary trends. Illinois State Mus. Sci. Papers, 3(2):1–72.
———. 1949. A study of Palaeozoic Arachnida. Trans. Connecticut Acad. Arts Sci., 37:60–315.
———. 1955. Arachnida, pp. P42–P162. *In* R. C. Moore (ed.), Treatise on Invertebrate Paleontology. Part P, Arthropoda 2. Geological Society of America and University of Kansas, Lawrence.
Plotnick, N., and W. Gertsch. 1976. The suborders of spiders: a cladistic analysis (Arachnida, Araneae). Amer. Mus. Novitates, 2605:1–15.
Scudder, S. 1868. Descriptions of fossil insects found on Mazon Creek, and near Morris, Grundy Co., Ill. Illinois State Geol. Surv. Rep., 3:556–561.
Selden, P. A. 1983. The fossil ricinuleids (abstract). 9th Int. Cong. Arachnol., 1983, Panama.
———. 1984. A comparison of the functional morphology of living and fossil ricinuleids (abstract). Symp. "Fossil Arthropods as Living Animals," p. 6.
———. 1992. Revision of the fossil ricinuleids. Trans. R. Soc. Edinburgh Earth Sci., 84:595–634.
Selden, P. A., and M. Romano. 1983. First Paleozoic arachnid from Iberia: *Aphantomartus areolatus* Pocock (basal Stephanian; prov. Leon, N. W. Spain), with remarks on aphantomartid taxonomy. Biol. Geol. Mineral., 94(2):106–112.
Shear, W., and P. Selden. 1986. Phylogenetic relationships of the Trigonotarbida, an extinct order of arachnids. Act. 10th Int. Cong. Arachnol., 1986, Jaca/Espana, 1:393–397.