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Centiped Legs (Arthropoda, Chilopoda, Scutigeromorpha) from the Silurian and Devonian of Britain and the Devonian of North America

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ABSTRACT

Remains of arthropod legs with a pentagonal cross section and serrate margins, found at three Silurian and Devonian sites (Ludford Lane, Wales; Rhynie, Scotland; and Gilboa, New York, USA), are herein attributed to terrestrial scutigeromorph centipeds. The Silurian and Devonian legs are distinct from each other, from previously described Carboniferous remains, and from modern scutigeromorphs, but the general pattern and many of the details of leg construction in these centipeds seems to have been conserved over a 415 million year history. The legs are attributed to a new scutigeromorph genus, *Crussolum,* placed in a new monobasic family Crussolidae; fairly complete remains from the Devonian of Gilboa, New York, are assigned to the new species *Crussolum crusserratum* Shear. The Silurian (Ludford Lane) and Rhynie legs are too poorly known to be given a species epithet, but more than one taxon may be present.

INTRODUCTION

One of the most distinctive isolated exoskeletal elements found by hydrofluoric acid maceration in the intensively studied Middle Devonian (Givetian) Gilboa fauna of terrestrial arthropods is the "sawblade" or serrate podomere, initially attributed to a scutigeromorph centiped (Shear et al., 1984). These podomeres are characterized by a pentangular cross section, with each of the angles ridged and set with distally pointing cuticular teeth, which on better preserved examples subtend small setal sockets. Arthropod po-

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TABLE 1
Specimens Studied

Slide no.	Accession no.[a]	Figure	Brief description
Crussolum crusserratum			
329/AR35	AMNH 43162	17	tibia
334/1a/AR16	AMNH 43163		prefemur
334/1b/AR1	AMNH 43164	16	femur
334/1b/AR78	AMNH 43165	11–13, 19	tarsus
411/2/AR20a	AMNH 43166		prefemur
411/7/AR14[b]		18	tibia + tarsus
411/7/AR44	AMNH 43167		tibia
411/15/AR8	AMNH 43168		tibia
411/15/AR15	AMNH 43169		tibia
2002/12/AR12	AMNH 43170	8, 14	prefemur
2002/12/AR15	AMNH 43171		prefemur
2002/12/AR20	AMNH 43172		tibia
2002/12/AR21	AMNH 43173	9	tibia
Crussolum sp. from Ludford Lane			
DE 1.4.2/50	UM K25082	21, 22	femur + tibia
DE 1.4.12/60	UM K25083	23	femur
DE 3.1.1/88A	UM K25084		femur + tibia
DE 3.1.18/105	UM K25085		tibia
DE 3.2.32.141	UM K25086		tibia
DE 4.1.9/48	UM K25087	25	tibia
DE M.2.8/181	UM K25088		tibia
LE 1.6/15/76	UM K25089		tibia
LL 1.6/15/76	UM K25090		tibia
LL/S10/1/6	UM K25091		tibia
LL Orig "cent tibia"	UM K25092		tibia
Rhynie specimen	UM K25093		tibiae?

[a] AMNH: American Museum of Natural History, UM: Ulster Museum.
[b] Unfortunately this important slide was destroyed in a laboratory accident.

domeres have been recovered from the Upper Silurian (Pridoli) Ludford Lane deposit (Jeram et al., 1990), characterized by the serrate margins of at least some of the podomeres, strikingly similar to the Gilboa "sawblade" leg segments. The best articulated examples from Ludford Lane, however, cannot with certainty be attributed to the same taxon as the serrate podomeres. Careful searching of Rhynie Chert thin sections by one of us (AJJ) has revealed small sections of nearly identical podomeres.

All the fossils discussed here, with the exception of the single Rhynie example, were obtained by hydrofluoric acid maceration of shales, mounted on microscope slides and studied and photographed using Nomarski Differential Interference contrast optics. The Ludford Lane and Rhynie specimens are deposited in the Ulster Museum, Belfast, and the Gilboa specimens in the American Museum of Natural History, New York. Table 1 provides the slide numbers engraved on each slide and the corresponding museum accession number.

Acknowledgments

P. M. Bonamo, of SUNY Binghamton, oversaw the preparation of specimens from Gilboa, and was responsible, with the late J. D. Grierson, for the original discovery of that fauna; the Hudwick Dingle slides were prepared in the Cardiff laboratory of D. Edwards, who also provided bulk samples for preparation in Manchester. P. Manning gave technical assistance in Manchester. We also thank J. Hannibal of the Cleveland Museum of Natural History and G. Buckley of the Field Museum of Natural History, Chicago, for the loan of specimens of *Latzelia primordialis,* and Hannibal for the photograph of that species. We wish to thank E. L. Smith, San Francisco, and the late R. Crabill for suggestions on the identity of the Gilboa specimens, early in the work on that fauna, and H. Borucki, University of Hamburg, Germany, for his comments at a later stage. This research was supported by National Science Foundation Grants BSR-8216410, DEB-9112487, and DEB-9508573 to W. A. Shear, and NERC Grant GR3/7882 to P. A. Selden.

ATELOCERATE LEGS

We briefly considered an arachnid identity for the legs discussed here, but the presence of prefemora and the single claw of the tarsus do not support this hypothesis, and leave the various classes of Atelocerata for consideration.

Homologies of leg podomeres among the Arthropoda have been the subject of extensive debate. Difficulties have arisen in part because the same names have been used for podomeres that may not be homologous, and different names have been used for clearly homologous podomeres, even within taxa that are relatively uniform in leg structure. Kukalová-Peck (1978, 1983, 1986, 1990) has attempted to integrate information obtained by careful study of fossil insects with the results of modern insect morphology. The details of her work are beyond the scope of this article, but fundamentally she suggests that the primitive arthropod leg was multiramous (neither biramous nor uniramous) and that its "stem" consisted of 11 segments. In the course of evolution, the number of stem segments and rami has been reduced in all extant arthropod groups. (In the following discussion, the podomere names sensu Kukalová-Peck are preceded by the letters KP.) In the Atelocerata (Chilopoda, Hexapoda, Symphyla, Diplopoda, and Pauropoda), according to Kukalová-Peck (1978, 1990) the two basal podomeres, epicoxa and subcoxa, have been subsumed into the lateral body wall. The coxae of all Atelocerata are evidently homologous as such. However, the trochanter is hypothesized to be a synthetic podomere resulting from the fusion of the KPtrochanter and the KPprefemur; in some Paleozoic insects, and possibly in the extinct Euphoberiida, the line of fusion can still be detected (Kukalová-Peck, 1978). Thus the KPfemur is the insect femur, but is called the prefemur in myriapodous atelocerates. The KPpatella has fused to the KPtibia in all living insects (but remains partially free in some Paleozoic ones), while in the myriapodous classes, the KPpatella is called the femur and remains a distinct segment. For both insects and myriapodous classes the KPtibia is the same as the tibia sensu auctorum. The KPbasitarsus and KPdistitarsus are regarded as distinct segments, and may be subject to either extensive fusion or subdivision; some authors recognize a basitarsus in hexapods, but in such groups as Diplura the tarsus is unitary and evidently a fused basitarsus + distitarsus. Among myriapods, millipeds have a unitary tarsus (where a divided tarsus occurs, as in some species of the order Callipodida, it is clearly secondary) and centipeds frequently retain the distinction between basitarsus and distitarsus. The postarsus is uniformly recognized in all groups, but is often simply called a claw in myriapods. Thus the fundamental difference between the insect leg and the myriapod leg is the plesiomorphic presence of two segments (femur [KPpatella] and tibia) between the prefemur (KPfemur) and the tarsus in the latter; only the tibia and tarsus are distal to the knee in hexapod legs. Additionally, all pterygote insect thoracic legs bear two articulated claws on the tarsus, while those of myriapodous arthropods have at most a single accessory claw, the functional claw being the postarsus.

The presence of a free prefemur and a single tarsal claw strongly indicates that the legs discussed below are not from insects, and a similar argument, based on the presence of two articles preceding the "knee" podomere, excludes arachnids. No known fossil or extant diplopods have multiarticulate tarsi. The strongly apomorphic legs of symphylans and pauropods have reduced numbers of podomeres, with strikingly different proportions;

symphyla have two tarsal claws. Thus we have concluded that the legs are from a chilopod. Among chilopods, only scutigeromorphs have legs pentagonal in cross section and having marginal spines on the angles subtending small setae. Likewise, multiarticulate tarsi are found only in this group. The evidence therefore strongly points to a scutigeromorph centiped identity for these isolated legs.

The following section demonstrates even more detailed similarities between the legs of extant scutigeromorphs and the fossil legs.

SCUTIGEROMORPH CENTIPEDS

Scutigeromorph centipeds are perhaps the most familiar members of the Class Chilopoda because of the frequent occurrence of *Scutigera coleoptrata* L., the House Centiped, in centrally heated homes of the north temperate zone. Its original habitat is the Mediterranean region, where it occurs out of doors in sunny places, hiding under stones. This large, fleet centiped often elicits fear when it makes an appearance in a home in Europe or America, but is probably quite effective in helping to control household insects. The order Scutigeromorpha is of low diversity worldwide compared to other orders of centipeds; recent systematic treatments have significantly reduced the numbers of species recognized (Würmli, 1973a, 1973b, 1974a, 1974b, 1975, 1977; Würmli and Negrea, 1977). Scutigeromorph species tend to resemble one another closely, varying in size and in details of the mouthparts, cuticular microsculpture, and genitalia. Most species are tropical in distribution. General information on scutigeromorph anatomy and biology is summarized in Lewis (1981).

Scutigeromorphs are now generally recognized as the earliest surviving offshoot of the atelocerate line and the sister group to all other centipeds. However, with their many specializations for a cursorial life, they are probably far from the ground plan of the ancestral centiped (Dohle, 1980, 1985; Kraus and Kraus, 1994; Borucki, 1996).

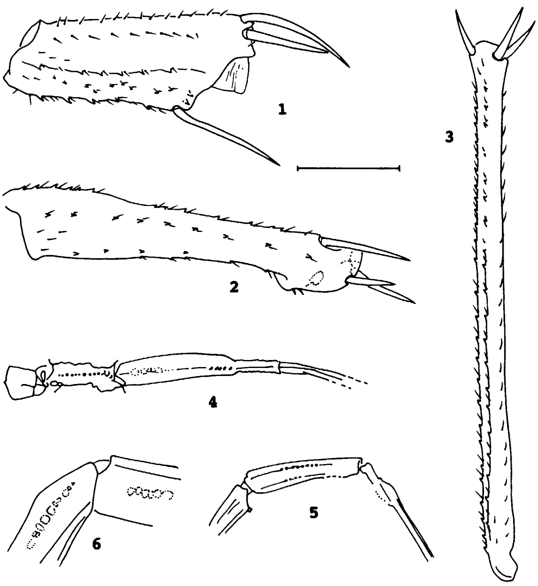
A single Paleozoic fossil species is known, *Latzelia primordialis* Scudder, 1890, of the Westphalian D Francis Creek Shale at Mazon Creek, Illinois, USA (Scudder, 1890a, 1890b; Mundel, 1979). Although more detailed work on this fossil is required, its general appearance is remarkably similar to that of living scutigeromorphs.

The scutigeromorphs are recognized as primitive centipeds (Dohle 1980, 1985) and as such are the most primitive living atelocerates. Thus the extension of their fossil record back to the Devonian and Silurian, demonstrated below, is of considerable evolutionary significance.

For purposes of comparison, we examined the legs of a range of taxa of living scutigeromorphs, including the species *Scutigera coleoptrata* L., *S. rugosa* Newport, *S. nigrovittata* Pocock, *Thereuonema tuberculata* (Wood), *Parascutigera mjoebergi* (Verhoeff), and *Thereuopodina queenslandica* (Verhoeff). The legs of all these species are remarkably similar and thus the following description was prepared, based primarily on the fifth leg of *Scutigera coleoptrata,* the best known species.

The leg (fig. 27) consists of seven podomeres: coxa, trochanter (KPtrochanter + KPprefemur), prefemur (KPfemur), femur (KPpatella), tibia, tarsus, and postarsus (claw). The coxae and trochanters are not preserved in our fossil material and so will not be described. The prefemur (fig. 1) is the bulkiest of the podomeres and generally about three times as long as wide. Seen in lateral view, the proximal end is obliquely truncate, with the ventral margin somewhat swollen. The distal articulation with the femur is likewise oblique, with the dorsal surface more extended distally. Two large macrosetae are present dorsally at the articulation; ventrally a single large macroseta, projecting straight downward, is inserted about a fourth of the podomere's length back from the distal articulation. These macrosetae have a distinctive scaly microsculpture. Though the prefemur is somewhat oval (anteroposteriorly compressed) in cross section, there are also five to seven distinct angles, each of which is marked by a row of small setae, and ventrally with cuticular teeth in more posterior legs.

The femur (fig. 2) is more slender, four to five times as wide as long, but its general shape is similar to that of the prefemur. Distally there is a single large dorsal macroseta and two ventrolateral macrosetae. The five-



Figs. 1–6. Podomeres of scutigeromorph centipeds. Figs. 1–3. *Scutigera coleoptrata,* leg 11. **1.** Prefemur. **2.** Femur. **3.** Tibia. Figs. 4–6. *Latzelia primordialis.* The exact identity of these legs is not clear; compare fig. 7. **4.** Left leg 14(?), coxa, trochanter, prefemur, femur and proximal part of tibia. Femur is narrowed distally by obscuring matrix. **5.** Right leg 13(?), distal part of prefemur, femur, proximal part of tibia. Note broken ventrodistal spine on prefemur; compare with fig. 1. **6.** Right leg 11(?), joint between prefemur and femur.

angled appearance of the prefemur is accentuated on the femur, and unarticulated spines (teeth) appear on the dorsal setal rows that mark the angles; they are formed from extensions of the proximal side of the setal sockets and point distally at a low angle, giving a serrate appearance. On the anterior and posterior surfaces, scattered setae also appear. In cross section, the femur resembles a pentagon with three angles dorsally and two ventrally. The distodorsal macroseta is at the end of the dorsalmost row of teeth, the two laterodorsal rows lack a terminal macroseta, and the ventrodistal macrosetae are set at the ends of the two ventral rows. We refer to the angles that end with a macroseta as major angles, and those that lack a macroseta as minor angles. There is some variation in angulation. In the giant scutigeromorph *Thereuonema tuberculata* (Wood), two additional minor angles appear vaguely on the prefemur and more distinctly on the femur, for a total of seven. These additional angles never have terminating macrosetae.

The knee-joint of the leg, the point where maximum flexion occurs, is between the femur and the tibia. The tibia (fig. 3) is a long, slender podomere typically ten times or more longer than wide and only about half the diameter of the femur. The pentangular cross section is so pronounced that the surfaces of the podomere between the angles may actually be slightly concave. The angles are reinforced with stronger cuticle and marked with rows of setae, each subtended proximally by a prominent acute tooth usually about the same length at the seta itself. On the ventral angles, these spines may be somewhat separated from the setal base and there are often two or three of them per seta, large single spines separating linear series of smaller ones. On some legs, the two ventral rows are represented only by the setae. The "sawblade" appearance is most distinctive in the tibia. At the distal end of the tibia, close to the articulation with the tarsus, there are three macrosetae terminating the major angles, as described for the femur. Again, some variation in angulation occurs in larger species; in *Thereuonema tuberculata,* the posteriolateral minor angle is suppressed in the midlength of the segment and the others are accentuated to give the segment an almost rectangular cross section. The suppressed angles appear again distally, near the articulation.

The tarsus is clearly divided into two parts, a basitarsus and telotarsus. The telotarsus is further subdivided into pseudosegments (so called because they are not independently musculated). In Scutigera coleoptrata, the basitarsus begins with a long segment and up to nine short segments follow; the last of these segments bears a pair of strong lateral macrosetae, and thus marks the division between the basitarsus and telotarsus. The distitarsus may have 25 or more pseudosegments; the last one is the longest and bears the postarsus or claw. The setation and sculpture of the tarsal pseudosegments are complex. The basitarsal segments have a dense cover of microspinules, with a few short, small setae. Distoventrally there are two large spines, and the ventral surface is set with fine hairs and setae, some of which

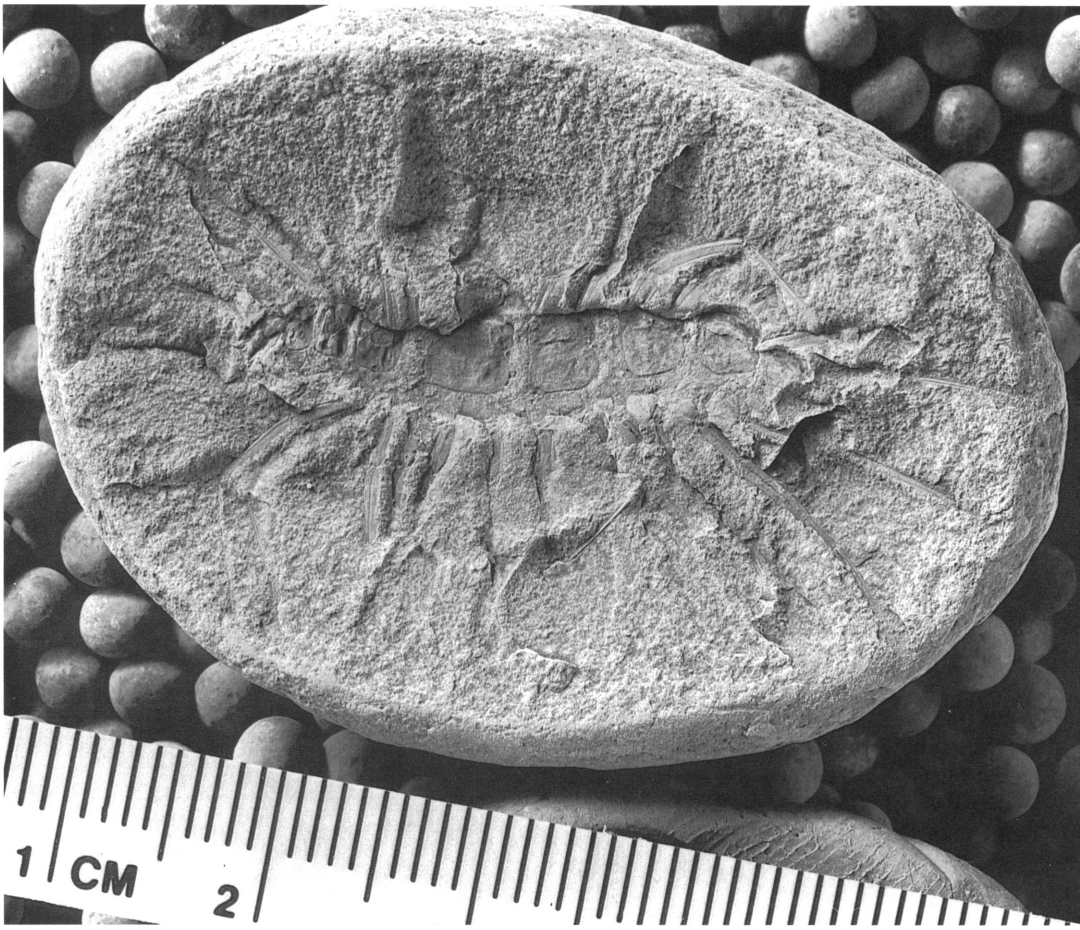


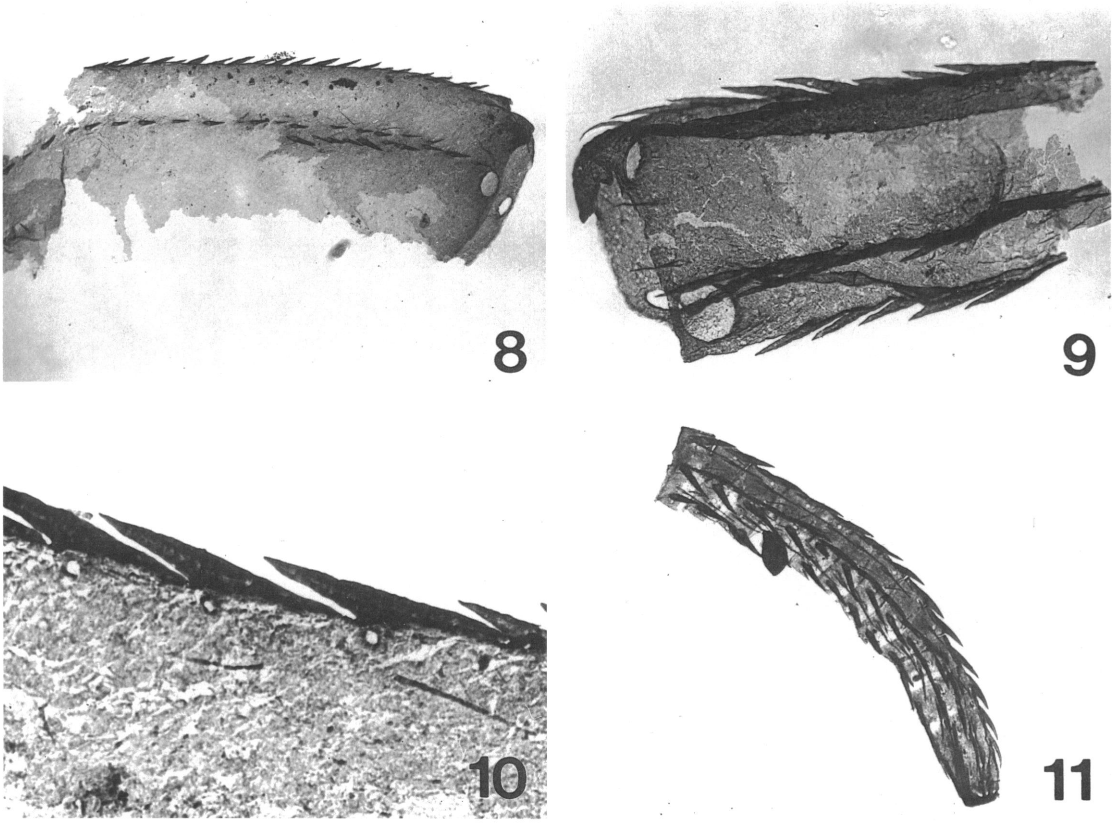
Fig. 7. *Latzelia primordialis,* CMNH 008672, Cleveland Museum of Natural History. Photograph courtesy of Dr. J. Hannibal.

are bent proximally and some of which extend straight ventrally. The distitarsal segments are separated by poorly sclerotized cuticle ventrally but overlap dorsally, and are well covered in spinules. There is a large dorsal seta subtended by a spine on each segment. Ventrally, there are three socketed setae, one of them sharply bent and pointing distally, or modified to a clublike shape. Interestingly, these two types of modifications occur on alternating pseudosegments. On the last segment, the postarsal claw is subtended by a small, blunt, clawlike seta.

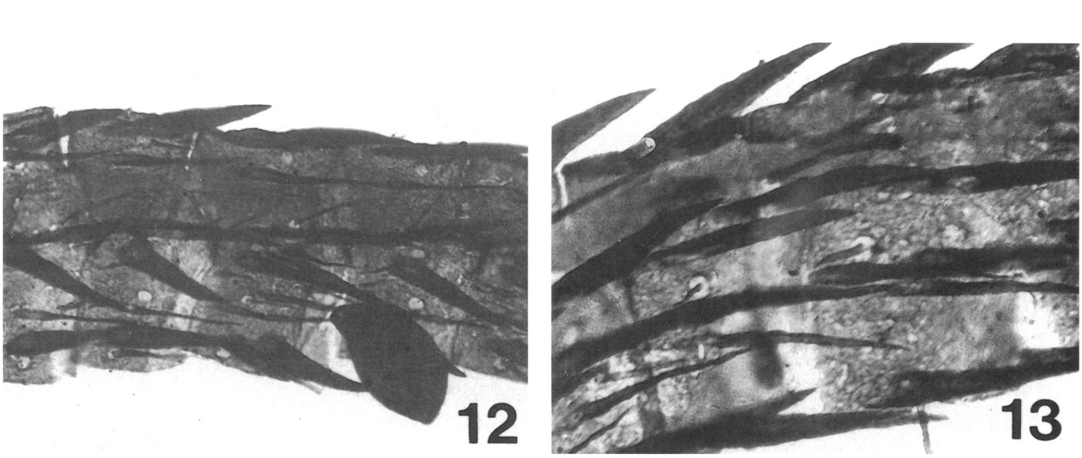
All of the 15 pairs of legs follow this basic pattern of segmentation and ornament, differing in a single animal mostly in length (the length difference has the functional significance of overlap in stride, thus allowing greater stride length and running speed); much of this length difference is made up in somewhat longer tibiae and much longer tarsi with more pseudosegments; the last pair of legs is extremely long and antenniform and is used as a sense organ.

In addition to the socketed setae and the strong spines referred to above as teeth, fine hairlike spines also occur on the legs. While these superficially resemble setae, they are not socketed. These were described by Würmli (1974a, 1974b) as spiculae (Haarspitzen). The spines of the tarsi verge on this type, but are often rather flattened and broader.

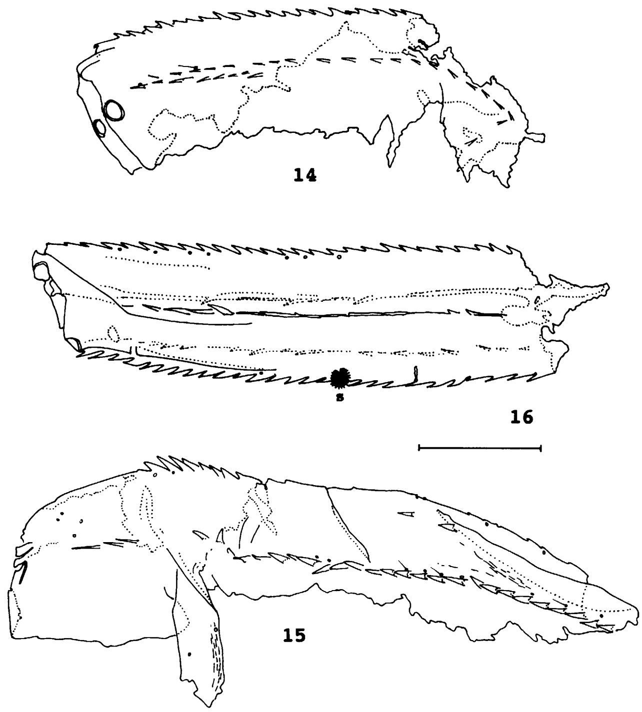
The fact that such a detailed composite description could be made up provides some clear guidelines in recognizing isolated po-



Figs. 8–11. Podomeres of *Crussolum crusserratum.* **8.** Specimen 2002.12.AR12 (see also fig. 14), prefemur; ventral surface missing. 40×. **9.** Specimen 2002.12.AR12, distal end of tibia. 100×. **10.** Specimen 2002.9.AR15, showing marginal serrations subtending setal sockets. 400×. **11.** Specimen 334.1b.AR78, tarsus, probably incomplete proximally and lacking claw (see also fig. 19). 100×.



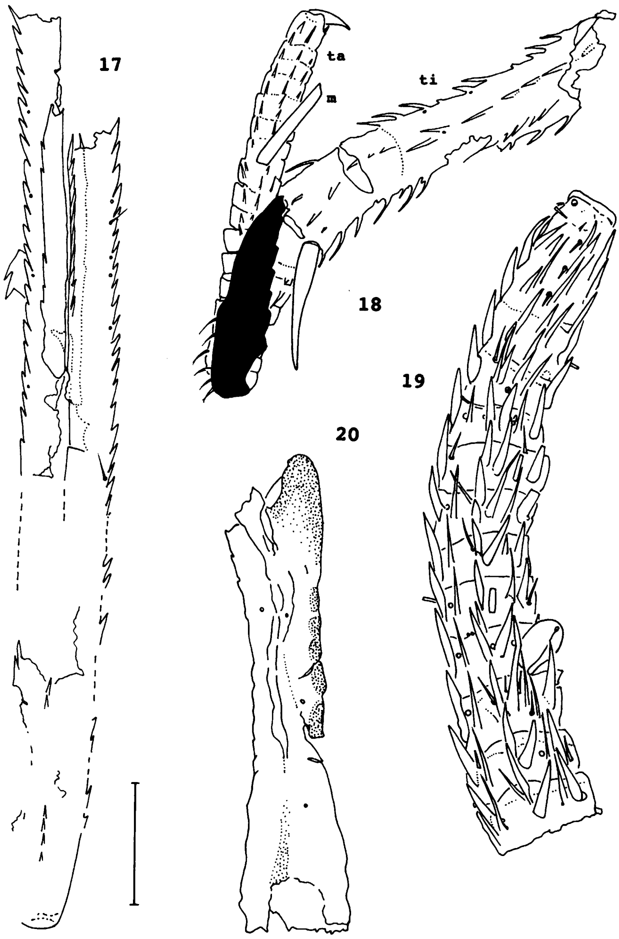
Figs. 12, 13. Specimen 334.1b.AR78, tarsus of *C. crusserratum.* **12.** Segments from midregion; large, dark, oval object is a plant spore. **13.** More distal segments, showing spinules and setae.



Figs. 14–16. Podomeres of *Crussolum crusserratum*. Distal to the left in all figures. **14.** Specimen 2002/12/AR12, prefemur (see also fig. 8; orientation reversed in drawing). **15.** Specimen 2002/9/AR15, prefemur. **16.** Specimen 334/1b/AR1, femur. Scale line = 0.43 mm.

domeres, which make up the bulk of our fossil material.

We also studied specimens of the Carboniferous fossil species *Latzelia primordialis* Scudder, but because of the means of preservation (in siderite nodules) no legs were preserved distal to the basal half of the tibia. Only a small number of specimens were available; most of those referred to by Mundel (1979) can no longer be located in the Field Museum (Chicago) collections. The best available specimen for legs therefore came from the Cleveland Museum of Natural History, Cleveland, Ohio (CMNH 8672; fig. 7). As with all known specimens, it came from the Westphalian D Francis Creek Shale of the Mazon Creek, Illinois, area. No further data were available. The specimen consists of part and counterpart of an ironstone nodule, showing the dorsal surface of a more or less complete individual (head and eight tergites). Two or three of the legs are reasonably well preserved. Figure 4 shows a probably penultimate leg (leg 14), and includes part of the coxa, trochanter, prefemur, femur, and the basal section of the tibia. While no macrosetae are visible on this leg, it is clear that the podomeres in life had an angular cross section and that along the edges of the angles were small protuberances, probably like the small spines found in living scutigeromorphs. Another leg from the other side of the body (fig. 5), which appears to be leg 13, has the distal part of the prefemur, the entire femur, and the basal part of the tibia preserved. The prefemur clearly shows an indication of the single large ventrodistal macroseta found in *Scutigera* legs, and the angular cross section with acute projections can be seen on the femur. In both of these legs, the proportions are similar to those of extant forms. Only one major difference between the legs of this Carboniferous scutigeromorph and the living species could be found. On the illustrated 13th leg, a series of large, well-defined quadrangular to oval depressions occurs in a row along one of the leg angles on both the prefemur and femur. The



Figs. 17–20. Podomeres of *Crussolum crusserratum* and Ludford Lane specimen. Figs. 17–19. Podomeres of *C. crusserratum.* **17.** Specimen 329/AR35, tibia, distal above, distal part incomplete; proximal end possibly present; dashed sections obscured by overlying material. **18.** Specimen 411/7/AR14, distal end of tibia and complete tarsus; dark object is overlying piece of coalified plant material; ti, tibia; ta, tarsus; m, macroseta displaced from distal end of tarsus. **19.** Specimen 334/1b/AR78, partial tarsus (see also figs. 11–13); proximal end incomplete, missing at least 10 segments. **20.** Specimen DE.3.1.18/105, distal end of tibia of Ludford Lane *Crussolum* with preserved articulating surface. Scale line = 0.43 mm for fig. 17, 0.3 mm for figs. 19, 20, 0.6 mm for fig. 18.

same situation occurs on the prefemur and femur of another leg on the counterpart (fig. 6). These depressions would have appeared on the leg as rounded bosses, if they are not artifacts of preservation. We were not able to verify the appearance of this detail on the three available Field Museum specimens because they were not as well preserved.

DESCRIPTIONS OF FOSSILS

The serrate edges, pentagonal cross section, subsegmented tarsi with characteristic ventral ornamentation including spiculae, knee articulation between femur and tibia, and single claws of the fossil podomeres described below, by comparison with living and already-known fossil forms, support the hypothesis that they belonged to scutigeromorph centipeds. In addition, the single articulated example from Ludford Lane appears to preserve the femuro-tibial joint as the knee, or point of maximum flexion of the leg, typical of scutigeromorph centipeds. By means of this comparison, it has been possible to tenatively identify isolated podomeres, and these have then been observed to carry features, such as macrosetal sockets, consistent with a scutigeromorph identity.

THE GILBOA LEGS

LOCALITY AND HORIZON: Near Gilboa, Schoharie County, New York State, in the upper part of the Panther Mountain Formation on the west flank of Brown Mountain. The Panther Mountain Formation belongs to the Tioughniogan Stage of the Erian Series and has been thought to be roughly equivalent in age to the middle Givetian of Europe (Shear et al., 1984; where more details on stratigraphy can be found). Richardson et al. (1993) considered the formation to be possibly older, based on palynological evidence. Spores from the deposit conform to those high in the devonicus-naumovae Zone, suggesting an age no older than late Eifelian, but more likely early to middle Givetian.

PRESERVATION: The fossils are preserved as small fragments of more or less unaltered cuticle, with infrequent articulated specimens. The level of preservation is uniformly much higher than at the earlier Ludford Lane locality. For further details on preservation, see Shear et al. (1987). The appearance of the cuticle of the "sawblade" legs from this deposit, as well as the presence of fragments in organic connection, suggest that only a single species of scutigeromorph centiped was present. Therefore, we will discuss the material not specimen by specimen, but by podomere, and provide a formal name for the species.

CHILOPODA LATREILLE, 1802
ORDER SCUTIGEROMORPHA LEACH, 1814
FAMILY CRUSSOLIDAE SHEAR, NEW FAMILY

TYPE GENUS: Monobasic on *Crussolum* Shear, new genus.

DIAGNOSIS: as for *Crussolum,* new genus (see below).

Genus *Crussolum* Shear, new genus

TYPE SPECIES: *Crussolum crusserratum* Shear, new species.

ETYMOLOGY: From the Latin crus, a leg, and solum, only; neuter. "Only legs," and refers to the fact that no other body parts can unequivocably be attributed to this species.

DIAGNOSIS: A genus of scutigeromorph centiped in which the leg tarsi are not clearly divided into basitarsi and distitarsi and have a characteristic pattern of ventral spination and setation (see below, and figs. 11–13, 19 and 26; these characters are not known for *Latzelia,* which preserves only the body and the proximal portions of the legs). Presently known only from the Silurian and Devonian of Britain and the United States.

Crussolum crusseratum Shear, new species
Figures 8-19, 26, 28

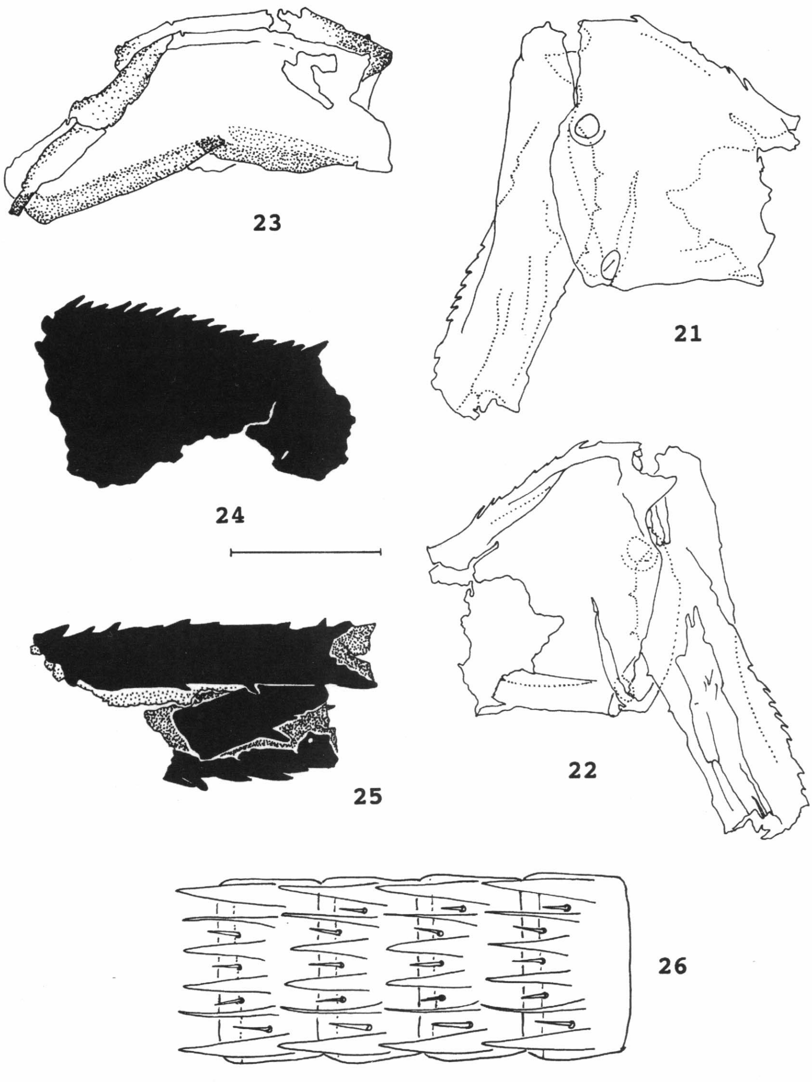
TYPES: Holotype, specimen 334/1b/AR78, deposited in the American Museum of Natural History. The other specimens named and discussed below and listed in table 1 are paratypes.

DIAGNOSIS: as for the genus (see above).

DESCRIPTION: *Prefemur*: Based on size, general shape, and the presence of macrosetal sockets in one case, specimens 2002/12/AR12 (figs. 8, 14), 2002/9/AR15 (fig. 10, 15), 334/1a/AR16, and 411/2/AR20A are prefemora. This podomere is characterized by two dorsal rows of small serrations, scattered spinules on the lateral surface (411/1/AR20A), and two dorsal macrosetae (2002/12/AR12; figs. 8, 14). The largest specimen, 2002/9/AR15 (fig. 15), seems relatively complete except for the ventral surface and is 2.56 mm long. As in this specimen, 334/1a/AR16 shows small spinules on the lateral surface, below the dorsal serrated ridges.

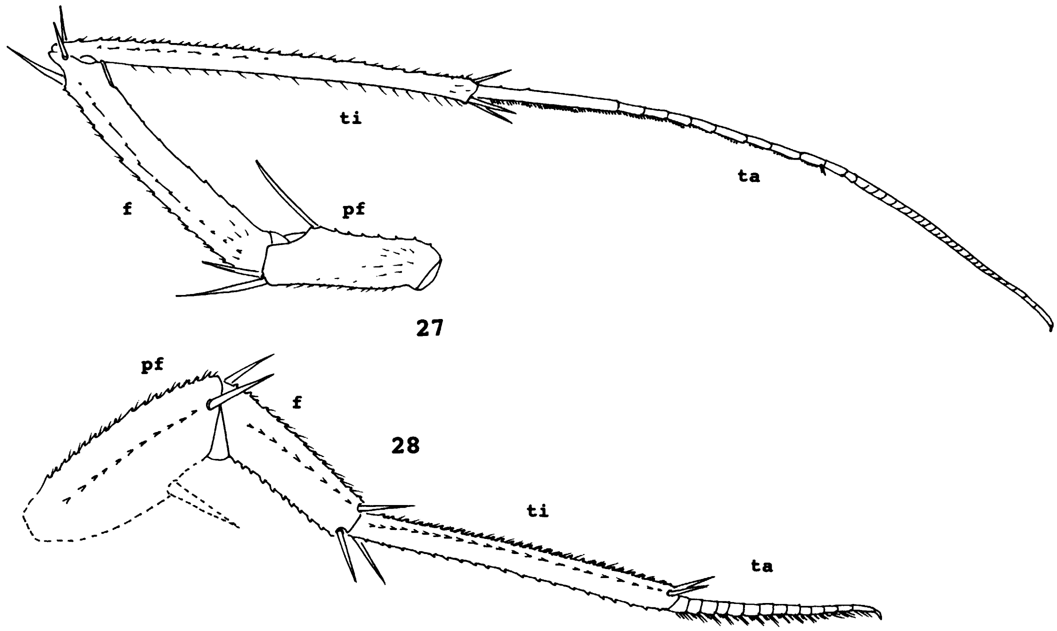
Femur: Only a single specimen, 334/1b/AR1 (fig. 16), can unequivocally be assigned to this podomere. This specimen preserves the distal one-half to two-thirds of the segment; the proximal articulation is missing. Five longitudinal angles, each bearing typical serrations (spines) subtending setae can be detected. At the distal end are three macrosetal sockets, as in *Scutigera coleoptrata.*

Tibia: Tibiae may be recognized by their narrowness and long rows of well preserved serrations, five rows on more completely preserved specimens. Two macrosetae occur at the distal end near the articulation with the tarsus. The longest specimen is 329/AR35 (fig. 17), about 3.63 mm long and 0.35 mm wide. Five angular ridges with serrations can



Figs. 21–26. Podomeres of Ludford Lane *Crussolum,* Hudwick Dingle specimen, and partial reconstruction of *C. crusserratum.* **21.** Specimen DE 1.4.2/50, femur and tibia in articulation. **22.** Same, reverse (drawn from other side of slide). **23.** Specimen DE 1.4.12/60, probable femur. **24.** Specimen HD2/2/1, example of Hudwick Dingle type of serrate fragment; specimen completely opaque and coalified. **25.** Specimen DE 4.1.9/48, fragment of tibia from Ludford Lane. **26.** Diagrammatic reconstruction of tarsal subsegments of *C. crusserratum,* ventral view; compare fig. 19. Scale line = 0.3 mm; fig. 26 not to scale.

be seen; the distal end is broken but the proximal end may be present, though obscured by overlying pieces of cuticle. This specimen is associated with an unusual type of cuticle ornamented with elongated setal sockets in short, arcuate rows. This cuticle is found in living archaeognath insects, where the sockets bear broad scales. The cuticle and the serrate tibia are not in organic connnection and their association on this slide is taken as fortuitous; the legs of living archaeognaths do not resemble those of scutigeromorph centipeds. Isolated distal ends of tibiae are found on 2002/12/AR21, marked by two large macrosetal sockets (fig. 9). Specimen 2002/12/AR20 preserves the proximal end of a tibia, perhaps the same tibia as the distal end of 2002/12/AR21, since the slides are sequen-



Figs. 27, 28. Legs of scutigeromorph centipeds. **27.** Leg 10 of *Scutigera coleoptrata*. **28.** Reconstruction of generalized leg of *Crussolum crusserratum*. pf, prefemur; f, femur; ti, tibia; ta, tarsus.

tial. Specimen 411/15/AR15 is a fragment of a large tibia in which the setal sockets distal to each spine of the serrate ridges can be easily seen. Specimen 411/7/AR14 preserves the distal end of a tibia in connection with a tarsus (fig. 18). Specimen 411/20/AR22 is the distal end of a tibia.

Tarsus: Two specimens preserve tarsi: 334/1b/AR78 (figs. 11–13, 19) consists of 12 pseudosegments from near the end of a tarsus, and 411/7/AR44 (fig. 18) preserves an entire tarsus and postarsal claw in connection with the distal end of a tibia. Unfortunately this specimen was subsequently destroyed in a laboratory accident. There appear to be about 25 pseudosegments in the complete tarsus. Specimen 334/1b/AR78 is mounted ventral side up on the slide and has the setation and spination of each pseudosegment nearly perfectly preserved, and allows a tentative reconstruction (fig. 26). Each pseudosegment is cylindrical, about one-fourth as long as wide; There are four major spicules, two lateral and two more closely set near the midline. Between the lateral spicule of each side and the central pair occur single, thin minor spicules. Spines subtend setal sockets; about half of these contain long, thin, presumably tactile setae. Near the distal end of the tarsus this pattern becomes congested and confused and the pseudosegments loose their distinctiveness. The distal taper of the last pseudosegment suggests that it is indeed the most distal and that only the claw is missing. This pseudospination is exactly matched on specimen 411/7/AR14, the complete tarsus. In this specimen there is no indication of subdivision of the tarsus into basitarsus and telotarsus (though part of the tarsus is folded over and concealed by a bit of coalified plant material) and all of the pseudosegments are very similar. The claw is about three times longer than broad, very slightly curved, and acutely pointed.

Discussion: Although a complete leg is not known from this deposit, the shape and cuticular ornamentation of the fragments available suggest that they come from a single species. Based on the serrate angular ridges of the femur and tibia, with the spines subtending setae, the macrosetation at the distal end of the prefemur, the pseudosegmentation of the tarsi, and the single claw, we interpret these legs as coming from a scutigeromorph centiped. It is also possible that isolated segments from a single sample of matrix (for example, 334/1b or 2002/12) are from the same individual animal or even the same leg, but this cannot be definitively established.

OTHER GILBOA SPECIMENS: Scutigeromorph centipeds have enormous eyes that appear compound but are actually of the pseudofacetted type (Paulus, 1979). This type of eye, while appearing compound, is in fact built up again from the remains of a degenerate compound eye and has a very different microstructure. A large, many-faceted eye is known from Gilboa (Shear et al. 1984) from at least two specimens. We re-examined a large, complete eye (specimen 329-AR4) and a smaller, fragmentary one (411-20-AR1) for this study. The lenses of both eyes are obviously hexagonal, while those of scutigeromorph centiped eyes are round. The cuticle to which the eye of 329-AR4 is attached bears sculpture which is unlike that of the Gilboa "sawblade legs" as well as living scutigeromorph centipeds. In our judgment it is not assignable to the Gilboa scutigeromorph, nor are other specimens of collections of ringlike segments at Gilboa, based on the characteristic complicated setation of the tarsal pseudosegments of the scutigeromorph.

THE LUDFORD LANE LEGS

LOCALITY AND HORIZON: The Ludford Lane site comprises the Ludlow Bone Bed Member of Downton Castle Sandstone Formation, 0.15 to 0.20 m above the Ludlow Bone Bed, Ludford Lane, Ludlow, Shropshire, England (National Grid Reference SO 5116 7413). The Ludlow Bone Bed marks the base of the Pridoli Series of the Silurian System and has an approximate age of 414 million years. Further details are given in Jeram et al. (1990).

PRESERVATION: The preservation quality of the Ludford Lane terrestrial arthropod cuticular fragments is quite variable, but nowhere equal to that at the later Gilboa site. In contrast, associated eurypterid and scorpion cuticle is much better preserved. Most centiped specimens are very small fragments, flattened, often coalified to opacity, and badly eroded. The erosion and reduction to small size probably occurred during transport and before fossilization. Subsequently, cracking of the matrix may further have reduced the size of the pieces, and the impressions of matrix grains further obscured detail. Thus the specimens are best studied under both incident and transmitted light.

Jeram et al. (1990) illustrated three leg fragments (DE 3.1.2.87, figs. 1J, 1K; DE.1.2.16/47, figs. 1H, 1I; DE M.2.11/185, figs. 1M, 1O) which they attributed to a scutigeromorph centiped and restored as part of a whole leg, along with DE 1.4.2.50. As detailed below, only this latter specimen and some others subsequently obtained are indeed scutigeromorph, but the three former specimens are not. The discovery of the arthropleurid *Eoarthropleura* at Ludford Lane (Shear and Selden 1995), and the additional finding of beautifully preserved legs of this animal from a Frasnian site in New York, have combined to convince us that these three fragments are in fact *Eoarthropleura* legs. These, and the *Eoarthropleura* legs from New York, will be treated separately in a later publication.

Scraps and fragments of cuticle, including multiarticulate structures, probable tergites and coxae, and other structures, may also be attributable to centipeds, but are too fragmentary and too poorly preserved to be certain.

SYSTEMATIC ASSIGNMENT: Because of their similarity to the legs described above as *Crussolum crusserratum,* the following specimens are referred to *Crussolum* spp. We have no evidence that all the fragments came from the legs of a single species, and even the generic assignment may have to be revised later.

Specimen DE 1.4.2/50
Figures 21, 22

Illustrated in Jeram et al. (1990), p. 660, fig. 1N.

DESCRIPTION: This specimen, less coalified than the others but with considerably eroded cuticle, consists of the distal end of a femur and the proximal end of a tibia in articulation. It is referred to hereafter as LL50. Little detail can be seen of the cuticle of the femur, which is 0.63 mm wide and bears a row of serrations on the dorsal edge. Laterally, near the articulation, there is a large round hole which is likely to be a macrosetal socket. A heavily sclerotized triangular process projects from the rim just dorsal to the hole, and below it part of the rim margin has peeled off and has been displaced proximally. The short piece of tibia is 0.24 mm wide. There are indications of three or four angular margins, two of them preserving serrations.

INTERPRETATION: This is the prefemur and tibia of a scutigeromorph centiped, based on the marginal serrations of both segments and the shape of the tibia. The broken tibia may be assumed to have been significantly longer (see below).

Specimen DE 3.1.1/88

Illustrated in Jeram et al. (1990), p. 660, fig. 1P.

DESCRIPTION: This poorly preserved specimen (hereafter called LL88A and LL88B) consists of two pieces originally in organic connection but broken apart during mounting. Part A is a badly folded fragment of the distal end of a femur; part B is a mostly complete tibia. The tibia has a single distal macroseta and preserves a few marginal serrations. Based on the curvature of the preserved dorsal surface of the femur, the tibia was about three times longer than the femur, and about ten times as wide as long.

INTERPRETATION: The femur and tibia of a scutigeromorph centiped, probably the same species as LL50, discussed above.

ADDITIONAL SPECIMENS FROM LUDFORD LANE

The following specimens are very small, fragmentary remains, all probably part of individuals of the same scutigeromorph species from which the last two specimens came.

DE 3.1.18/105 is a proximal end of a tibia, with an articulating surface preserved.

DE 1.4.12/60 (fig. 23), poorly preserved, is nonetheless clearly a femur.

LL 1.6/10/2 is a long, isolated angular ridge with many serrations. It is one-third again as long as the complete tibia of DE 3.1.1/88 and thus came from a much larger leg.

Small pieces of serrate tibiae are found on slides DE 3.2.32/141, DE M.2.8/181, LL 1.6/15/76, LL Orig "cent tibia," DE 4.1.9/48 (fig. 25), and LL/S10/1/6. Tibial fragments on DEF 1.5.5/61 show an unusual form of sculpture between the angular ridges, with scattered nodules of thicker cuticle. This may be caused by real sculpture or random differential erosion. Such sculpture does not occur on modern scutigeromorph legs.

SPECIMENS FROM HUDWICK DINGLE

Specimens HD 2/2/1 (fig. 24) and HD 0/0/1 were obtained from a different location, Hudwick Dingle, about 20 km northeast of Ludlow, Shropshire, from the Lower Devonian (Gedinnian) Ditton Series (see Dineley, 1978, for details). They are serrated podomere margins, entirely opaque, significantly larger than the Ludford Lane specimens, and with much stouter serrations. They may or may not be pieces of "sawblade" legs.

THE RHYNIE FRAGMENT

A sawed slab of Siegenian age Rhynie Chert (see Trewin, 1994, for a review of the Rhynie paleoenvironment and depositional conditions) from the Ulster Museum was found to contain a small fragment of "sawblade" leg, probably part of a tibia of a *Crussolum.* Impossible to photograph, the specimen adds only an earlier Devonian occurrence to the record, but also represents the first new animal to be discovered in the Rhynie Chert since the 1920s.

COMPARISONS

As is obvious from an examination of the photographs and drawings, the leg of *Crussolum crusserratum* bears a strong resemblance to that of modern scutigeromorph centipeds. A tenative reconstruction of the leg of *C. crusserratum* is presented in figure 28. This reconstruction is admittedly highly speculative, since it is not known if the available specimens represent parts of the same or even similar legs; the legs of living scutigeromorphs are known to vary along the length of the body. There is also the possibility that more than one species is represented, or even that we are in error is assigning these fragments to the Scutigeromorpha.

Points of similarity with *Scutigera coleoptrata* (fig. 27) include the tibia, strongly pentangular in cross section, bearing prominent serrations on the angles, each of which probably subtends a seta, and the multiarticulate tarsus with complex ventral setation and spination, including spiculae. Details, however, differ. The ventral surface of the prefemur is missing in all specimens. Thus the typical macrosetation pattern on that podomere of modern scutigeromorphs cannot be verified for this species, but at the end of the prefemur and tibia we can clearly see three macrosetal sockets, as in the living forms. Although most of the legs of *Scutigera coleoptrata* have three apical tibial macrosetae, two setae occur on some anterior legs, and specimen 411.7.AR14 has only two visible sockets on the distal end of the tibia. However, the apex of the tibia is poorly oriented and partly concealed by an opaque fragment of plant material; it is possible that three sockets are present. While both *C. crusseratum* and the living species have multiarticulate tarsi, modern scutigeromorph centipeds have the tarsus divided into basitarsal and telotarsal regions, and have a different (and more complex) ventral spination of the tarsal pseudosegments. The undivided tarsus would have to be regarded as an autapomorphy of *Crussolum crusserratum.*

The Ludford legs represented by LL50 and LL88 are also likely to be from a scutigeromorph centiped similar (at least in leg design) to the Gilboa form and to modern scutigeromorph centipeds. The evidence, however, is scanty: the tibiae are ten times longer than broad and have serrate angles. Tarsi are not known, so we cannot say if they were subsegmented. Multisegmented structures have been found in Ludford Lane residues, but are poorly preserved and cannot with certainty be assigned to a taxon.

None of the leg types described here can be closely compared to the legs of the other known Gilboa centiped, *Devonobius delta* Shear and Bonamo. Entire legs are well known for that animal, and the differently shaped podomeres lack macrosetae, having a moderate vestiture of ordinary setae (Shear and Bonamo, 1988).

Nonetheless an important point is supported by this fragmentary material: scutigeromorph centipeds, with their distinctive legs, may have already evolved by the Late Silurian, and by the Middle Devonian may have been approaching their modern form, which was obviously fully achieved by the Upper Pennsylvanian, attested to by the fossils of Latzelia primordialis. The discovery of an extinct order of centipeds, Devonobiomorpha (Shear and Bonamo, 1988), at Gilboa, indicates that there may have been a greater diversity of centipeds at the ordinal level in the middle Paleozoic than exists today.[4] As yet we know very little about Carboniferous centipeds, with two Mazon Creek species, *L. primordialis,* and a scolopendromorph, being the only adequately described forms (Mundel, 1979).

[4] Borucki (1996), in a detailed and exemplary review of centiped phylogeny, has placed *Devonobius* in the order Craterostigmatomorpha (recte pro 'Craterostigmomorpha'), but by implication as a plesion within that taxon. Additional fossil evidence bearing on this question has recently been discovered and will be reported on by one of us (WS) in a later publication.

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