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The First Paleozoic Pseudoscorpions (Arachnida, Pseudoscorpionida)

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ABSTRACT

The first members of the arachnid order Pseudoscorpionida known from the Paleozoic and from nonamber fossils are described as *Dracochela deprehendor,* new species, and the new genus is made the type of a new family, Dracochelidae. The fossils were recovered from Middle Devonian sediments near Gilboa, New York, USA. The new form has characters of both the Chthonioidea and Neobisioidea; the lack of a firm phylogenetic framework for pseudoscorpion systematics at this time makes it very difficult to determine its evolutionary position, but it is suggested that the fossil is closer to (perhaps even a member of) Chthonioidea. Most of the characteristic and complex adaptations of pseudoscorpions are present in the fossils.

INTRODUCTION

The paleobiology, taphonomy, and stratigraphy of the Gilboa fossils have already been discussed, as have the methods by which the fossils are prepared and studied (Shear et al., 1984, 1987; Shear and Bonamo, 1988). A brief discussion of the evolutionary relationships and paleobiology of Paleozoic pseudoscorpions has also appeared (Shear et al., 1989), but a more extensive treatment follows the systematic part of this paper.

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TABLE 1
Postpaleozoic Fossil Record of Pseudoscorpionida[a]

Superfamily	Family	Number of species[b]							
		A	B	C	D	E	F	G	H
Chthonioidea	Dithidae	–	–	–	–	1	–	–	–
	Chthoniidae	–	–	–	–	2	2	–	–
Feaelloidea	Pseudogarypidae	–	–	–	–	3	–	–	–
Neobisioidea	Neobisiidae	–	1?	–	–	5	–	–	–
Garypoidea	Garypidae	–	1?	–	–	–	–	–	–
	Geogarypidae	–	–	–	–	2	–	–	–
	Olpiidae	–	–	–	–	1	–	–	–
Cheiridioidea	Cheiridiidae	–	–	–	1?	1	1	–	–
Cheliferoidea	Atemnidae	–	–	–	–	1	–	–	–
	Chernetidae	1?	–	–	–	3	2	1	–
	Cheliferidae	–	–	1	–	11	1	–	1?
	Withiidae	–	–	–	–	1	–	–	–

[a] Twelve families in the classification by Muchmore (1982) lack a fossil record and are not listed. Harvey (1986) separated the Geogarypidae from the Garypidae.

[b] Letters code particular deposits and ages as follows: A, Cretaceous Canadian amber (Schawaller, in prep.); B, Eocene Burmese amber (Cockerell, 1917, 1920); C, Eocene Chinese amber (Hong, 1983); D, Oligocene Rumanian amber (Protescu, 1937); E, Oligocene Baltic amber, list in Schawaller (1978); F, Miocene Dominican amber (Schawaller, 1980–1981); G, Miocene Mexican amber (Schawaller, 1982); H, Miocene Saxon amber (Schumann and Wendt, 1989).

Pseudoscorpions are small arachnids which inhabit the soil and litter environment and are found also in rotting wood, under tree bark, in caves and crevices, and in animal nests and human dwellings. About 3000 species are known, but many more await discovery. Important references on the group in general include Beier (1932a, 1932b; systematics), Chamberlin (1931; systematics and morphology), Weygoldt (1969; general biology), and Muchmore (1982; systematics). While some species are robust (to 8 mm long) and heavily sclerotized, most are small (less than 3 mm long) and have a relatively thin cuticle. As small, lightly sclerotized animals living in an environment where biodegradation is rapid, they might be expected rarely to be fossilized. Indeed, up to this time, the only fossil pseudoscorpions appeared to be those caught in sticky tree resins which later became amber.

The previously published fossil record of pseudoscorpions (table 1) extended back only to the Eocene (ca. 45 mya; Cockerell, 1917, 1920; Hong, 1983); however, a single specimen from Cretaceous Canadian amber is presently under study. Although the incomplete nature of many of the amber specimens (or their immaturity) makes it difficult to be certain, there is no evidence which would definitely exclude them from various living families. Even the proverbial pseudoscorpion habit of phoresy has been seen in amber fossils (Müller, 1960; photograph reprinted by Weygoldt, 1969, p. 127; Schawaller, 1981).

The fossils reported on here, parts of two or three individuals of different instars but probably from the same species population, are the first pseudoscorpion fossils from the entire Paleozoic Era, and take the history of the order back to the middle Givetian Age, about 374–380 mya, increasing the documented antiquity of the group nearly by an order of magnitude. These fossils are also the first nonamber specimens reported. They are preserved as unreplaced cuticles which may be extracted from the rock matrix with hydrofluoric acid (Shear et al., 1984, 1987).

Remarkably, the fossils show that all the defining autapomorphies of pseudoscorpions, especially the suite of modifications affecting the chelicerae, were already present at this great age. While the specimens cannot be placed in an extant family, it would not

greatly surprise a modern pseudoscorpion systematist to find a living species with the same combination of characteristics.

Abbreviations (Figures)

a	abdomen
as	abdominal seta
bf	basifemur (femur)
bta	basitarsus
c	chelicera
cff	cheliceral fixed finger
cl	claw
cmf	cheliceral movable finger
cs	coxal spines
cx	coxa
ds	doubled bothrium
et	external bothrium
f	cheliceral flagellum
g	galea
h	hand
L	leg (with numbers)
mt	marginal teeth of chelal finger
p	pedipalp
pff	palpal (chelal) fixed finger
pmf	palpal (chelal) movable finger
ps	preterminal seta
s	ordinary seta
se	serrula exterior
si	serrula interior
t	tibia
tf	telofemur (patella)
tta	telotarsus

Acknowledgments

We are grateful to William B. Muchmore, Mark S. Harvey, and Volker Mahnert for their extensive comments on the manuscript. Each of these authorities presented a unique perspective on the specimens discussed here, and their suggestions much improved the paper. However, the authors are entirely responsible for the present version and whatever errors of description or interpretation it may contain. We also thank Paul A. Selden for his discussion, and for detecting a third specimen among the Gilboa collections. The visit of WS to the USA to study the material was supported in part by the Staatliches Museum für Naturkunde, Stuttgart. This work was supported by National Science Foundation grants BSR 85-084-42 and BSR 88-120-27 to WAS and PMB, and by a grant to PMB from the Power Authority of New York State.

SYSTEMATICS

Because no really satisfactory phylogenetic system of classification exists for pseudoscorpions, and the reexamination of genera often leads to changes in familial compositions and definitions (i.e., Muchmore, 1982; Harvey, 1986, 1988), we have decided not to name any taxa higher than family based on these fossils.

DRACOCHELIDAE, new family

Type Genus: *Dracochela,* new genus.

Diagnosis and Description: See diagnosis and description of genus, below.

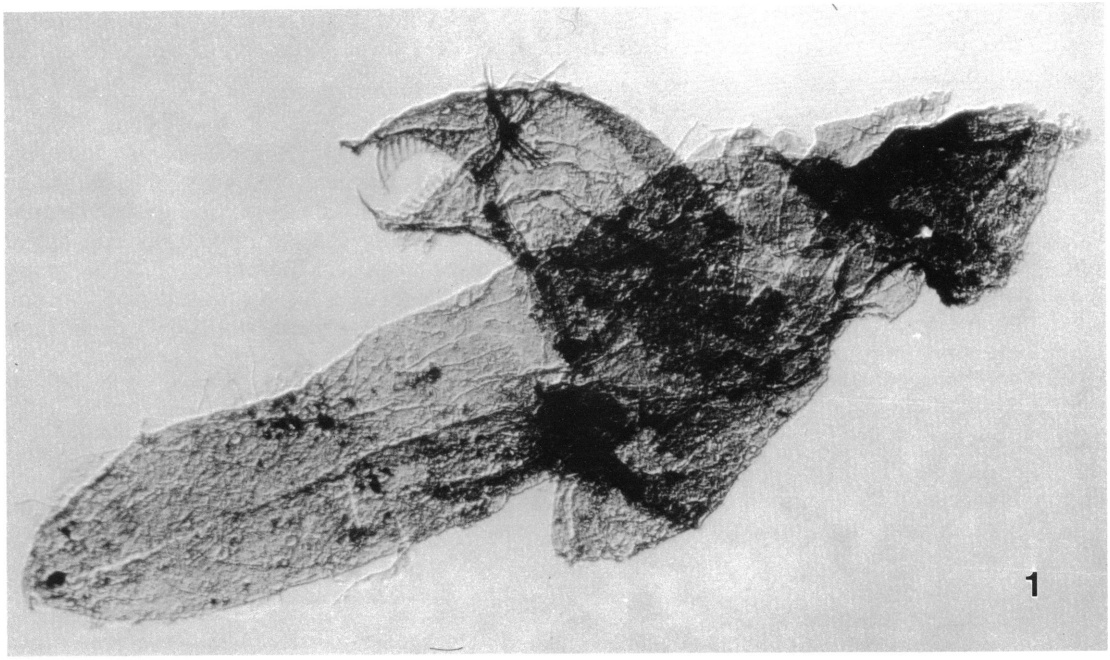
Dracochela, new genus

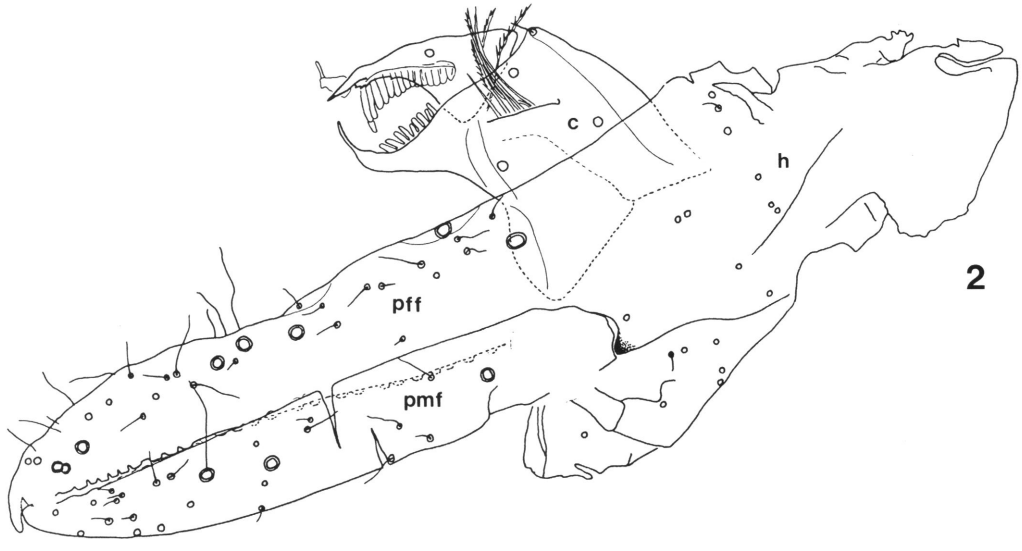
Type Species: *Dracochela deprehendor,* new species, by monotypy and present designation.

Etymology: From Latin *draco,* a dragon, and *chela,* a claw or pincer; hence "dragon claw." When the holotype specimen was first prepared, it was given the laboratory nickname of "the angry dragon" (see fig. 1) before being diagnosed as part of a pseudoscorpion.

Diagnosis: Resembles chthonioids and feaelloids in having a contiguous pair of bothria distal on the fixed chelal finger; differs from chthonioids in having bitarsate first legs and lacking bothria on the chelal hand, from feaelloids in the large chelicerae and smooth cuticle. Resembles neobisioids in having a cheliceral flagllum with a row of feathered setae. Differs from all three superfamilies in having smooth blades in the serrula interior.

Description: Cuticle smooth. Chelicerae proportionally large (one-third to one-half carapace length?). Flagellum with single row of at least 6 partially feathered blades, serrula exterior with about 14 denticulated blades, serrula interior with 9 smooth blades. Galea present. Pedipalp chelae with trichobothria only on fingers, fixed fingers with distal pair of touching bothria; denticulation of fingers even, teeth uniform, inclined. Leg 1(?) bitarsate, lacking trichobothria, preterminal seta unmodified. Coxae with coxal spines (?).

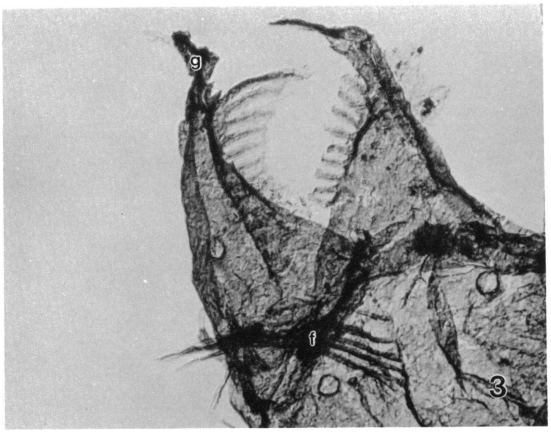


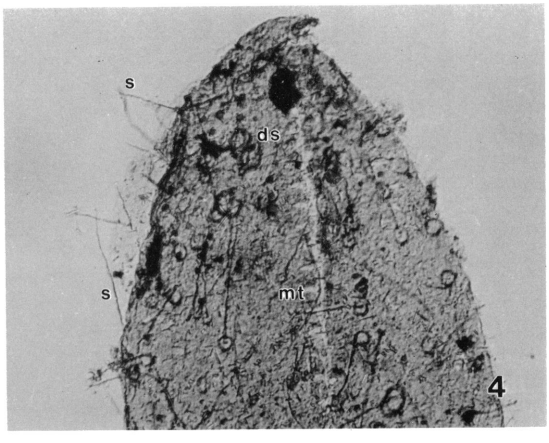


Figs. 1, 2. Holotype specimen (411-19-AR9) of *Dracochela deprehendor*. **1.** Photograph of specimen. **2.** Interpretive drawing. Scale line = 0.1 mm.

Adults not known; description based on tritonymphal and protonymphal characters. Other characters as described for type species, see below.

DISTRIBUTION AND STRATIGRAPHIC RANGE: Known only from the upper part of the Panther Mountain Formation, Middle Devonian (Middle Givetian), site of Blenheim-Gilboa Pumped Storage Reservoir, near Gilboa, New York.





Figs. 3, 4. *Dracochela deprehendor,* specimen 411-19-AR9. **3.** Distal part of chelicera. **4.** Distal part of pedipalp chela.

Dracochela deprehendor, new species
Figures 1–19

TYPES: Holotype specimen slide 411–19-AR9 (AMNH 43162), pedipalp chela and chelicera of probable tritonymph; paratypes slides 411-19-AR17 (AMNH 43163), anterior part of body of probable protonymph, and 411-19-AR2 (AMNH 43164), parts of 3 or 4 legs, abdomen, and possible carapace. No other available material.

ETYMOLOGY: The specific name, *deprehendor,* a Latin noun in apposition, means "one who takes by surprise," in reference to the unexpected nature of this find.

DIAGNOSIS: As for the genus.

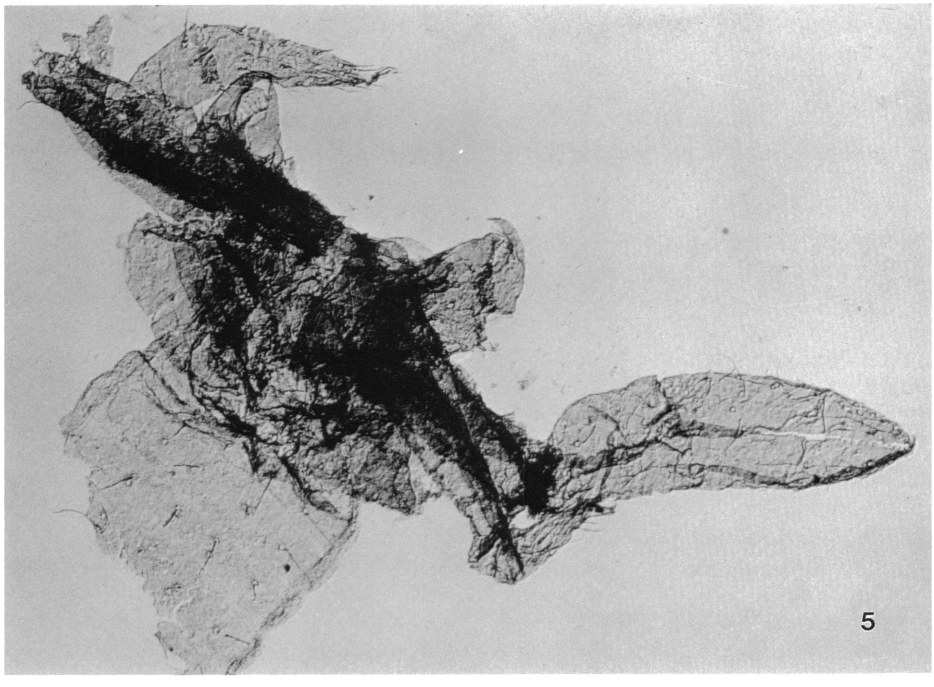
DESCRIPTION OF HOLOTYPE: Probable tritonymph; specimen consists of part of one chelicera, probably seen in ventral view, fingers of one pedipalp chela, probably seen in lateral view, few superimposed unidentifiable pieces of cuticle (figs. 1–4, 11, 15). Cuticle of all parts smooth, without granules, rugae, or tubercles.

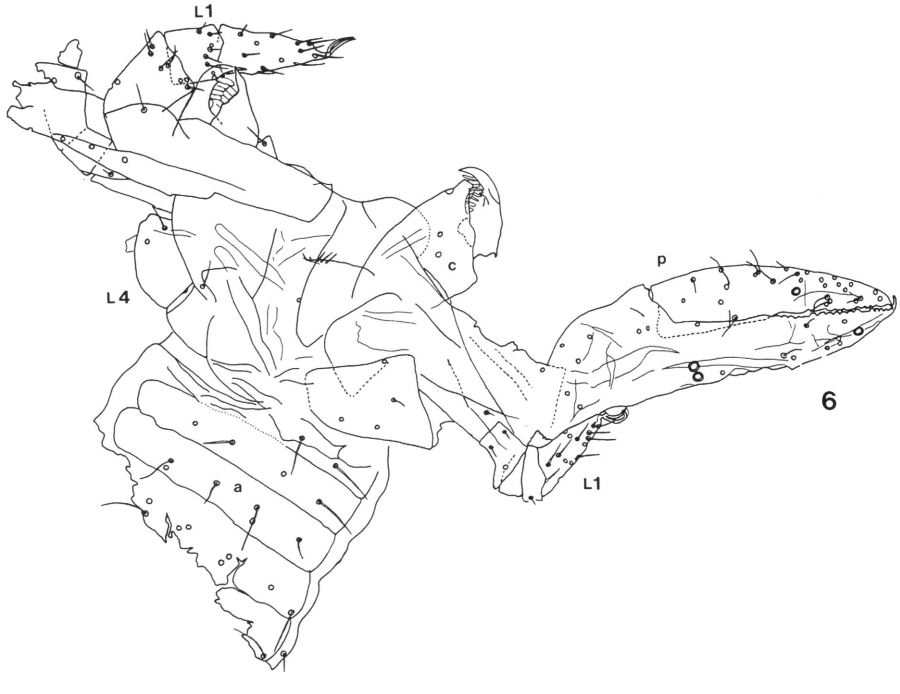
Cheliceral basis with 4 bothria positioned as shown in figure 2. Flagellum (f, fig. 2; fig. 15) of at least 6 blades (probably not completely preserved), first distal blade smooth, other blades distally feathered on one side, all flagellum blades inserted in single oblique row (rather than circle). Serrula exterior (se, fig. 11) with about 14 blades (basal ones overlain by movable finger), distal blade longer than others, all blades denticulated at tips (fig. 14). Serrula interior (si, fig. 11) with 9 blades, all blades evidently smooth. Lamina not observed, lacking? Cheliceral fixed finger with 3 small, acute, undivided teeth near middle of finger, 4 similar teeth distal. Cheliceral movable finger 0.13 mm long, with distinct galea (g, figs. 3, 11), details cannot be seen due to folding, but probably long, tubular, rather than moundlike), single bothrium nearly in middle of finger.

Pedipalp chelal fingers articulated with condylus, as in living species. Movable finger of palpal chela 0.4 mm long, with 3 bothria, positioned as in figure 2; fixed finger with 6 large bothria in addition to pair of small, contiguous bothria near tip (db, figs. 2, 4). Surfaces of both fingers with irregularly distributed setae. Movable finger with indeterminable number of low, subquadrate teeth, fixed finger with about 35 more acute teeth; teeth all subequal, not alternating in size, somewhat inclined, contiguous at their bases (fig. 16). Venom ducts not detected in either finger.

DESCRIPTION OF PARATYPES: Specimen 411-19-AR17, probable protonymph. Specimen (figs. 5–10, 12, 13, 17–19) consists of anterior part, probably mounted ventral side up (carapace not visible), both chelicerae, one pedipalp chela in lateral view, distal parts of 2 legs (probably both legs 1), coxal region (badly folded); anterior half of abdomen with sternites, tergites, pleural membranes.

Cuticle of all parts smooth, lacking granules, tubercles. Chelicerae (figs. 12, 13) with





Figs. 5, 6. *Dracochela deprehendor,* specimen 411-19-AR17 (paratype). **5.** Photograph of specimen. **6.** Interpretive drawing. Scale line = 0.05 mm.

movable fingers 0.09 mm long. Flagellum not seen. Serrula exterior with at least 7 blades (basal ones concealed), distal blade slightly longer than others, all blades finely denticulate at tips; serrula interior with at least 4 blades, not denticulate, lamina absent. Fixed finger with 4 small, acute teeth in middle of finger, one subapical acute tooth. Right movable finger with one bidentate tooth near middle of finger. Left movable finger with 3 small, acute teeth in same position. Galea not seen. Basis of left chelicera with 3 setae; of right chelicera with light area on fixed finger, possibly insertion area for serrula interior.

Movable finger of pedipalp chela 0.21 mm long, with single bothrium, very flat teeth (fig. 6). Fixed finger with 3 bothria, positioned as in figure 6. No additional pair of small bothria visible at tip as in holotype; about 32 teeth, more elevated than on movable finger, somewhat inclined. Surfaces of both fingers with scattered setae. Venom ducts not observed in either finger. Articulation of fingers as in recent species.

Leg (probably leg 1) bitarsate, tarsus 0.09 mm long, basitarsus 0.045, tibia 0.08 (figs. 9, 10, 18). Claws smooth, arolium not seen. Tarsus with scattered acute setae, basitarsal setae more dense on distal part; preterminal tarsal seta acute, not modified.

Coxal region much folded, coxal form and setation obscured; rows of about 5 acute spines in anterior part may be coxal spines (figs. 7, 17).

Compression of fossil makes sternites, tergites difficult to distinguish; neither evidently divided. First abdominal segment folded, with 2 setae on one half; second and third segments complete, each with a row of 4 setae; fourth and fifth segments partially destroyed, setal numbers not ascertainable. All setae smooth, acute (as, fig. 8). Pleural membranes finely striate, not granulated. Spiracles not seen.

Specimen 411-19-AR2 (fig. 19) consists of discernible remains of 3 or 4 legs, parts of abdomen, (unlikely) parts of carapace. Two extended leg tarsi each about 0.20 mm long. Leg a consists of tarsus with distorted claws, distal part of tibia; possible joint between basitarsus, distitarsus marked by transverse rows of small setae; distitarsal setae smooth, acute, scattered more densely distally. Leg b consists of two basal segments, possibly coxa and first femur or first and second femora,[4] both badly damaged, with scattered smooth, acute setae. Leg c consists of femora, tibia, and damaged tarsus; first and second femora together about 0.23 mm long, articulation perpendicular to long axis. Tibia doubly folded but with at least one strong, smooth, acute, proximal seta. Leg d represented only by twisted, folded tarsus, monoarticulate or biarticulate nature not determinable.

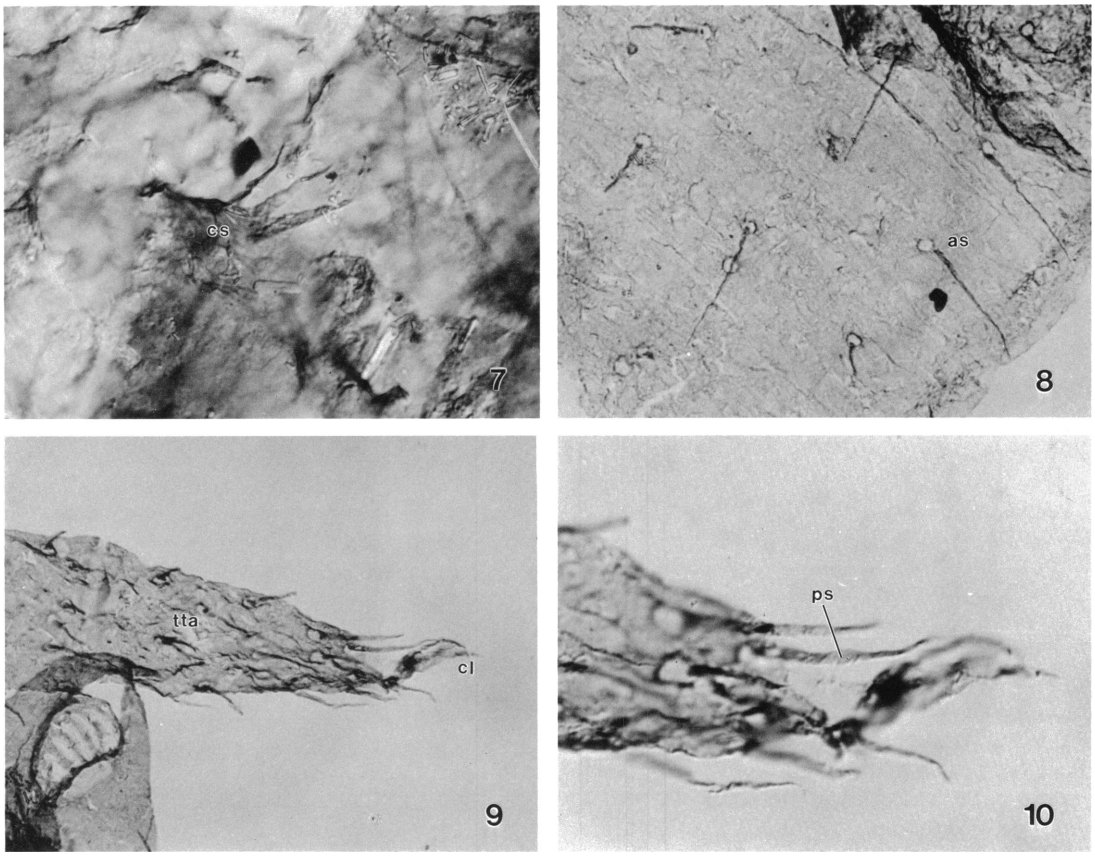
Part of one probable tergite visible, with indications of two rows of setae. Continuous edge can be traced through folded, fragmentary mass which may represent posterior margin of carapace.

DISCUSSION

CONSPECIFICITY: Are the three specimens described above representatives of the same biospecies? For purposes of this discussion, we exclude the second paratype, which is too fragmentary and distorted to provide much information on the question.

All three specimens came from the same small subsample of black shale (#411-19), and therefore are almost certainly exact contemporaries, because the subsample represents (at most) only part of a single depositional event. Thus we may exclude the concepts of chronospecies or paleospecies. Modern soil and litter communities, however, may support several syntopic species of pseudoscorpions. The two more complete specimens are from different instars and there is only some

[4] A pseudoscorpion leg is traditionally described as consisting of coxa, trochanter, first and second femora, tibia, and tarsus (sometimes with distinct basitarsus and distitarsus). Weygoldt and Paulus (1979), however, have argued that the second femur is homologous to the patella in, for example, scorpions. A study of the musculature recently carried out by Schultz (1989) seems to confirm this by listing six points of similarity. Despite these convincing arguments, we use the old terminology here to avoid confusion. Granting the homology of the "second femur" and patella, pseudoscorpion and solpugid legs still remain unique among arachnid legs in having the "knee" (main dorsoventral flexure) between the patella and tibia rather than between the femur and patella (or "first" and "second" femora).



Figs. 7–10. *Dracochela deprehendor,* specimen 411-19-AR17 (paratype). **7.** Suspected coxal spines. **8.** Abdomen and abdominal setae. **9.** Telotarsus, probably of leg 1. **10.** Same, greater magnification to show preterminal seta (ps).

overlap between what is preserved on one and what is preserved on the other.

Arguing for conspecificity on the basis of the information available, we may adduce the following. The pedipalp chelae closely correspond in general shape, and the dentition is identical. The bothria of the fingers are similarly placed (a basal pair and a single distal bothrium on the fixed finger, a distal bothrium on the movable finger). The serrulae exterior and interior are similar, respectively, in both specimens, and so is the denticulation of the cheliceral fingers.

Against this we can only draw attention to the fact that no galeae can be observed on the protonymphal chelicerae. However, the galeae, a delicate structure, may have been lost in the fossilization process on this tiny, poorly sclerotized specimen. There is also the fact that some instars of living pseudoscorpions have galeae and others, from the same species, do not.

The preponderance of evidence available leads us to the conclusion (obvious from our Description) that both more complete fossils are different instars of the same biospecies.

PALEOBIOLOGY: In addition to the more general accounts already published concerning the Gilboa fauna (see Shear et al., 1984; Shear et al., 1987; Norton et al., 1988; Shear and Bonamo, 1988; Shear et al., 1989a; Kethley et al., 1989) we expand here on our earlier remarks (Shear et al., 1989b) concerning inferences on the habits of *Dracochela depre-*

hendor. Unless otherwise attributed, all information below on the structure and habits of living pseudoscorpions comes from Weygoldt (1969).

The chelicerae of pseudoscorpions, with their characteristic suite of modifications, are a multipurpose tool for the organism (figs. 3, 21, 22). Their chelate design and array of denticles function in grasping and holding prey. In species with large chelicerae (mostly Chthonioidea and Neobisioidea), the prey is vigorously masticated by alternating movement of the chelicerae, as digestive enzymes are regurgitated over the resultant mass. The galea, when present, is the outlet of a prosomal silk gland; the silk is used for the construction of molting and hibernation chambers. The serrulae are used to groom and clean the appendages, and probably also aid in closing the preoral cavity to facilitate external digestion. The flagellum, trichobothria and setae, and lyriform organs of the chelicerae are sensory organs, though the exact function of the flagellum remains unclear.

All of these functions can be transferred to the Devonian fossils, because the resemblance of their chelicerae to those of living forms is exact. Of special significance is the presence of the galea, because it establishes that pseudoscorpions were using silk at this early date. together with the spider spinneret from Gilboa (Shear et al., 1989a) this is the earliest evidence in the fossil record for silk production by animals. Though we were not able to detect lyriform organs anywhere on our specimens, their presence in the animals, when alive, is certain.

The pedipalp chelae of pseudoscorpions are also used for grasping and manipulating prey, as well as for climbing, arranging bits of debris for nests, grasping larger animals during phoresy, and for several social functions, such as fighting with conspecifics and in courtship and mating. They are richly supplied with trichobothria (usually 12 or 14 in adults, rarely more, on each chela) and are probably the main source of sensory information. Some pseudoscorpions have venomous palpi, with the venom apparatus in both fingers or in either one alone.

We found no trace of a venom apparatus in our specimens; the ducts are usually clearly visible in prepared material analogous to the fossils. Aside from this, we can also assume the full complement of functions for the palps of *D. deprehendor.*

The legs of our Devonian fossils appear as robust and functional as those of modern species, but we observed only equivocal evidence for an arolium between the claws, a structure which in living forms aids in climbing smooth surfaces.

While four well-corneated eyes are present in some pseudoscorpions, many have two poorly formed ones, or are entirely blind. Vision is not at a premium in the habitat of most pseudoscorpions. We currently have no information on the eyes of *D. deprehendor,* if present, but this would be most interesting since earlier work on trigonotarbids from the Devonian has shown clear indications of the degeneration of the original lateral compound eyes of arachnids (Shear et al., 1987). And, of course, the immaturity and state of preservation of our specimens allows us to say nothing about the genitalia or reproductive habits.

We were unable to observe any spiracles on the abdomen of the paratype, but these may not have been preserved if they occurred in the flimsy intersternal membranes. The presence of abundant trichobothria, however, which cannot function under water, assures us that these animals were fully terrestrial. It has been observed that pseudoscorpions with smooth or only faintly sculptured cuticles inhabit moist biotopes (soil, litter, caves, intertidal zones) and those with a more or less granulated cuticle are found in drier places (under bark, in bird and mammal nests, in buildings). The Devonian fossils obviously belong to the first group.

Analogy with living pseudoscorpions has allowed us to suggest that the holotype is a tritonymph and the first paratype a protonymph. The number of bothria on the movable chelal finger conveniently corresponds to the number of posthatching instars—protonymphs have 1, deutonymphs two, tritonymphs three, and adults four bothria. It is possible that Devonian pseudoscorpions had more instars, but unlikely that they had fewer. Numerous other characters may change with instar as well. In *Ideoroncus setosus*

(Neobisioidea), for example, the serrula exterior has 18–22 blades in adults, 16 in tritonymphs, 14 in deutonymphs, and about 11 in protonymphs (Mahnert, 1984). The number of blades in the serrula interior is also different in successive instars of several chthonioids and neobisioids (W. Schawaller, personal obs.). A similar increase in the number of blades occurs in *Dracochela* from protonymph to tritonymph. However, the denticulation of the blades is the same in all instars. Adults of *Roncocreagris cambridgei* (Neobisioidea) have eight serrula interior blades, tritonymphs seven, deutonymphs six, and protonymphs five (Gabbutt and Vachon, 1968). Adults of *Verrucadithella dilatimana* (Chthonioidea) have no galea, tritonymphs have a five-forked galea, and deutonymphs a four-forked one (Mahnert, 1983). Legs are stouter in nymphs than in adults. Similar changes are at least possible in the fossil species.

Therefore, the general picture that emerges is that of a small but powerful predator with large chelicerae, which it used to chew up prey. *Dracochela* likely inhabited a moist but aerial biotope, and may have been a resident of the matted lower stems of the *Leclercqia* plants from among which its remains were extracted. The life history consisted of at least three preadult instars.

Again, as in previous studies of the Gilboa fossils, we are confronted with the remains of animals which, while clearly somewhat archaic for their inclusive taxon, are extraordinarily modern in general appearance and already superbly adapted for life on land. This speaks to either a long, undetected period of evolution for most major taxa of terrestrial arthropods, or to a very rapid development of the anatomical and physiological equipment required to live on land. In addition, the generally primitive nature of vascular plant life contemporaneous with these advanced animals leads to the counterintuitive inference that well-adapted arthropods colonized terrestrial habitats before the vascular plant life that now forms the basis for primary productivity on land. These and other paleoecological issues will be addressed at greater length in the future (Shear and Kukalová-Peck, 1990; Shear, in press).

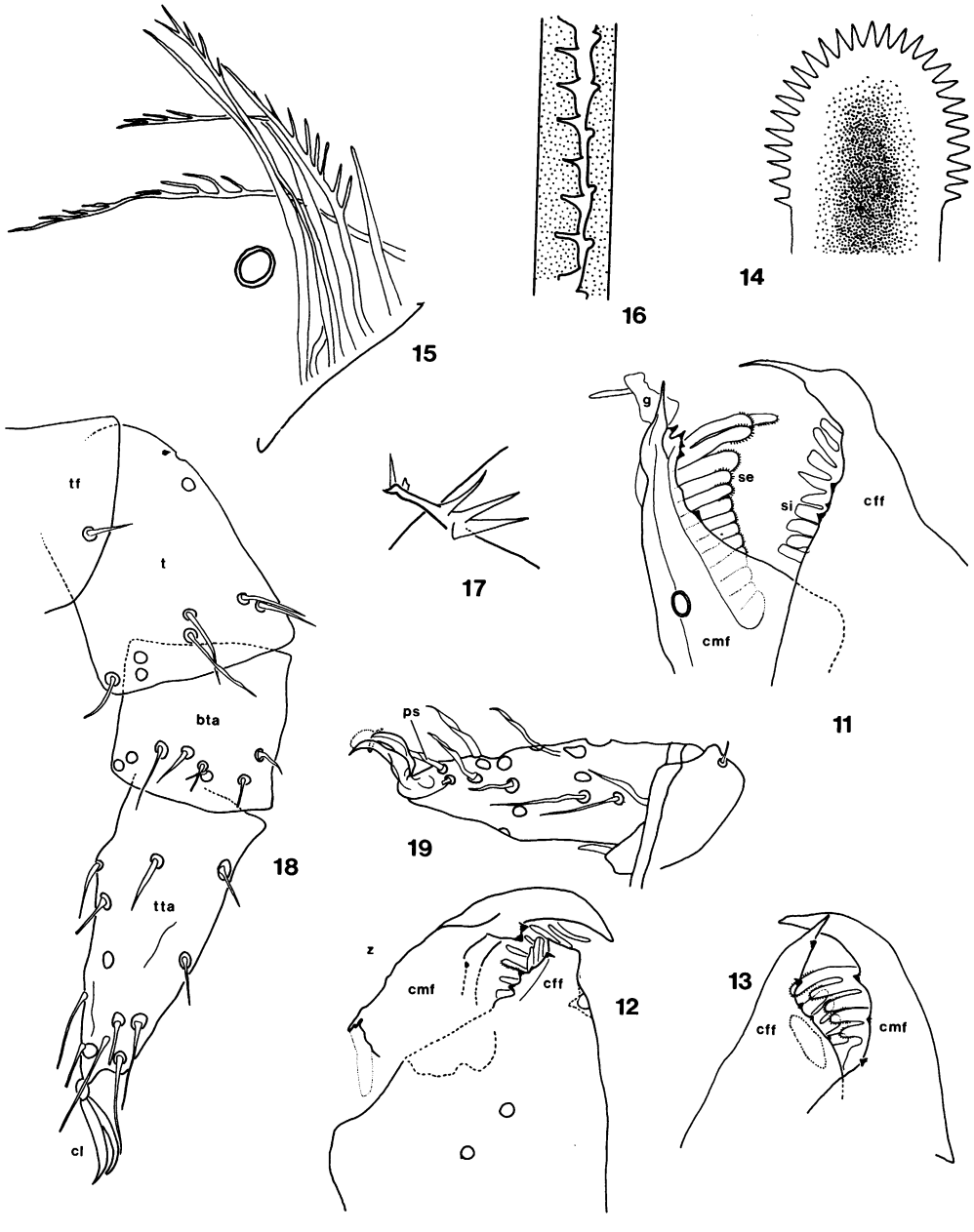
PHYLOGENETIC RELATIONSHIPS: Our remarks here are based on the assumption that at least the two most complete of the three fossils are conspecific. The different morphology of different instars (see above) and the preservation of different parts on each fossil allow a marginally satisfactory discussion of relationships. Furthermore, synapomorphic characters for only a few pseudoscorpion families have been established and there is no available phylogenetic analysis of the order. As mentioned above, the present classification is clearly not very reflective of real affinities, since revisionary studies tend to reveal the presence of new families, genera, and relationships previously unrecognized. For these reasons, and because we cannot clearly assign the fossil species to a living family based on its combination of characteristics, we have not named any new taxa higher than family. In the following discussion, information on the characters of recent pseudoscorpion families is from Muchmore (1982) unless otherwise attributed.

Dracochela is similar to members of the superfamilies Chthonioidea and Neobisioidea because of the large chelicerae relative to body size and the smooth cuticle; a third superfamily, Feaelloidea, recently shown by Harvey (1986) to be the sister group of Chthonioidea, has small chelicerae and granulate cuticle. Table 2 compares selected characters of *Dracochela* with these three superfamilies, and these characters are further discussed below.

1. Cheliceral flagellum. The single (incomplete?) row of flagellar blades in the fossils is very similar to those of recent Neobisiidae (compare figs. 15 and 21). The number of blades, their length, and feathering are characteristic features of recent genera in this family. In the holotype, the first distal blade is shorter (taphonomic change?) and smooth; all the other blades are feathered. In recent genera, the last basal blade is often shorter, and sometimes the basal blades are not feathered. A few chthoniid genera (i.e., *Lechytia*; Muchmore, 1975) possess a row of setae, but they are at best only weakly serrate.

2. Galea. Present in several genera of Neobisioidea, a distinct galea (g, fig. 21) is absent from many chthonioids. However, the galea is of low systematic value because it correlates with spinning activity, which differs in different instars and between the sexes.

3. Serrulae. In the fossils, the serrula in-



Figs. 11–19. *Dracochela deprehendor*. **11.** Chelicera of 411-19-AR9; compare with figure 3. **12.** Right? chelicera of 411-19-AR17. **13.** Left? chelicera of same. **14.** Reconstruction of serrated serrula externa blade. **15.** Cheliceral flagellum of 411-19-AR9. **16.** Pedipalp chelal teeth of 411-19-AR9, representative group. Distal above, movable finger on left. **17.** Coxal spines of 411-19-AR9; compare with figure 7. **18.** Probable leg 1 of 411-19-AR17; compare with figures 3, 4, 9, 10. **19.** Telotarsus of anther legs of 411-19-AR17.

terior has smooth blades and those of the serrula exterior are denticulate or serrulate. In Chthonioidea, Feaelloidea, and Neobisioidea, the serrular blades are nearly all alike and denticulated. Thus, the smooth serrula interior blades, if not taphonomically altered, may provide a synapomorphy for a distinct clade of Devonian pseudoscorpions. Unfor-

TABLE 2
Comparison of Fossils with Three Recent Superfamilies

Character	Fossils	Chthonioidea	Neobisioidea	Feaelloidea
Cheliceral flagellum	row of setae	cluster of setae, rarely a row	row of setae	1–2 setae
Distinct galea	present	absent in most	present in many	present
Blades of serrula interior	smooth	denticulate	denticulate	denticulate
Seta of movable cheliceral finger	in middle	usually subbasal	usually subdistal	subdistal
Number of bothria on palpal fixed finger	6 + 2[a]	6 + 2 (adults and tritonymphs)	8 (adults) 7 (tritonymphs)	8 + 2 (adults) 7 + 2 (tritonymphs)
Number of bothria on palpal hand	0[b]	2 (adults) 1 (tritonymphs)	0	0
Teeth of palpal chela	narrow, inclined	mostly acute, well-separated	mostly narrow, inclined	slightly acute, separated
Venom ducts	absent?	absent	present	absent
Tarsus of leg 1	biarticulate[c]	monoarticulate	biarticulate	monoarticulate
Femoral articulation of leg ?4	perpendicular	usually oblique	usually perpendicular	perpendicular
Preterminal tarsal seta	acute[c]	acute	modified	acute
Coxal spines	present[c]	present	absent	present
Pleural cuticle	finely granulate[c]	variable	granulate, often in rows	wrinkled, plicate

[a] Count from suspected tritonymph; "6 + 2" refers to 6 bothria distributed along the finger and two adjacent ones close to the tip.
[b] Palpal hand damaged.
[c] Observable only on suspected protonymph.

tunately, we cannot see if the cheliceral serrulae of the fossils are attached to the fingers just at one end, or along the entire length.

4. Trichobothriotaxy of the cheliceral finger. The galeal trichobothrium on the movable cheliceral finger in the fossil is placed nearly in the middle of the finger. In Chthonioidea this trichobothrium usually has a subbasal position; in Neobisioidea and Feaelloidea its position is usually subdistal.

5. Trichobothriotaxy of the palpal chela. The contiguous apical bothria of the holotype's fixed finger are probably important, and are found among modern Chthonioidea (fig. 23) and Feaelloidea. The fossil tritonymph (assuming that inference to be correct) has as many bothria (6 + 2) on the fixed finger as are found in tritonymphs and adults of nearly all recent species of chthonioids, and differs in that no bothria can be detected on the damaged chelal hand. In early instars of some neobisiids, the hand has no bothria, but in adults, there is often at least one bothrium situated below the base of the fixed finger. In the Ideoroncidae, another neobisioid family, the number of trichobothria is greatly multiplied, but three or four large ones are to be seen on the dorsum of the hand. The compression of the fossil does not allow us to tell if individual bothria are on the lateral or medial side of the chela. Since we are uncertain of the homologies between the fossil's bothria and those in modern families (or even, for other reasons, from one modern family to another), we cannot name them using the usual terminology. The question of polarity of trichobothriotaxic characters also arises. Is having all the bothria on the finger primitive or advanced? Is having more or fewer than the standard number primitive or advanced? Is the contiguous pair apical on the fixed finger of the fossil and in chthonioids and feaelloids a synapomorphy or a symplesiomorphy? Harvey (in litt.) regards this character as a clear synapomorphy.

6. Teeth of the palpal chela. The uniform

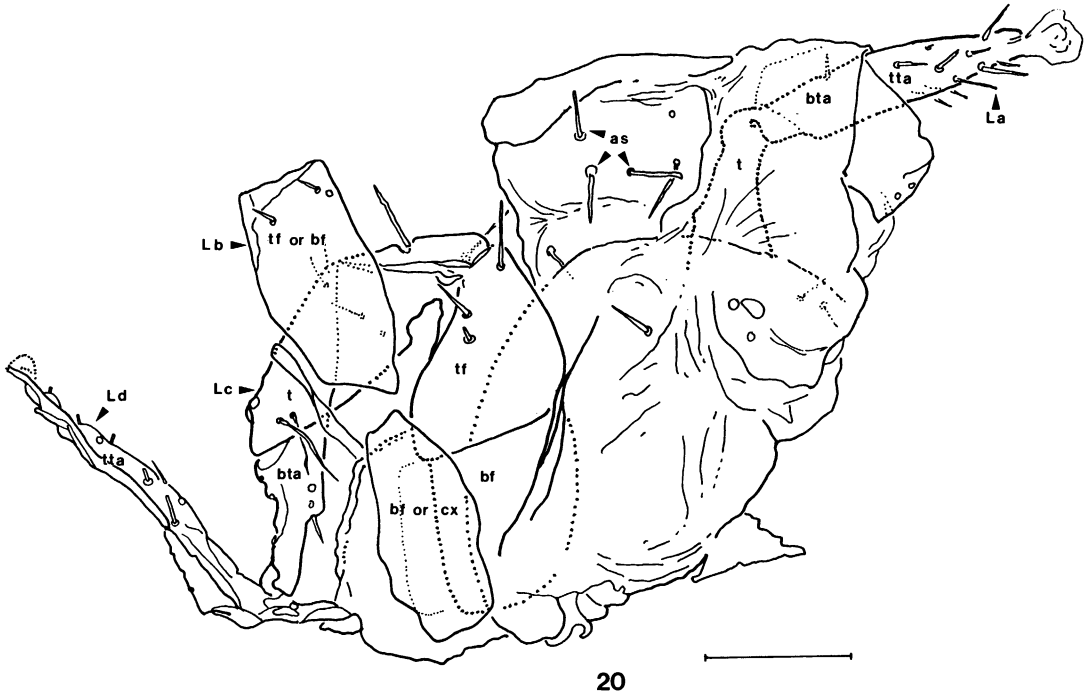


Fig. 20. *Dracochela deprehendor,* specimen 411-19-AR 2 (paratype). Scale line = 0.1 mm.

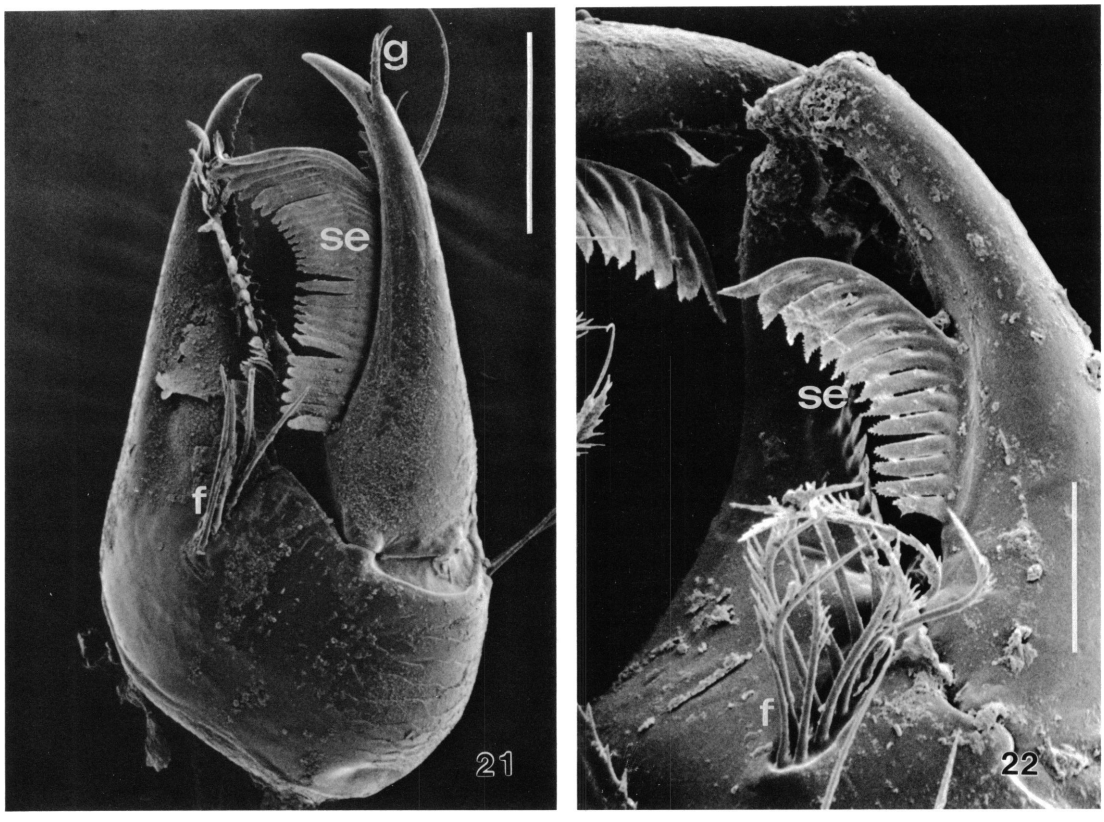
and slightly inclined teeth, larger on the fixed and smaller on the movable finger, are similar to those found in recent Neobisioidea. Many chthonioids, however, have regular, inclined teeth (i.e., *Mundochthonius rossi* Hoff; Hoff, 1949: 437).

7. Venom apparatus. No venom ducts could be observed in the palpal chela of either fossil. All Chthonioidea (and Feaelloidea) lack venom ducts. In the Neobisioidea, the Hyidae and Ideoroncidae have them in both fingers, and the Neobisiidae and Syarinidae have them in the fixed finger only. Chamberlin (1931) considered the chthonioids the most generalized of pseudoscorpions, but was puzzled by the lack of a venom apparatus, finally concluding that the primitive condition was to have venom ducts in each finger, and that the various patterns of loss were derived. Although this seems somewhat contradictory, it is not unusual to find primitive and advanced characters in the same taxon; absence of a venom apparatus may be synapomorphic for the fossils, chthonioids, and feaelloids. If the absence of the venom apparatus is plesiomorphic, it tells us nothing about the affinities of the fossil species.

8. Tarsus of leg 1. The first (or possibly second) leg tarsus of the paratype is biarticulate. In recent Chthonioidea both anterior leg pairs have monoarticulate tarsi, and the posterior tarsi are biarticulate; in Feaelloidea all legs have monoarticulate tarsi. In Neobisioidea (and Garypoidea) all legs have biarticulate tarsi. Once used at the highest taxonomic level to define suborders of pseudoscorpions, this character is now thought to be of little value.

9. Femoral articulation. In most Neobisiidae, the articulation between the two femora (see above) is perpendicular to the long axis of the leg, or nearly so, and this is the case in the second paratype fossil (411-19-AR2). Most chthonioids have this articulation oblique. However, this is a character that has not been recorded for many species in both superfamilies, and we do not know that the leg observed in the fossil specimen was a fourth leg.

10. Preterminal tarsal seta. All (?) Neobi-



Figs. 21, 22. Scanning electron micrographs of chelicerae of extant pseudoscorpions. **21.** Adult of *Tuberocreagris rufula* (Banks) (Neobisiidae). Scale line = 0.1 mm. **22.** Adult of *Mundochthonius basarukini* Schawaller (Chthoniidae). Scale line = 0.03 mm.

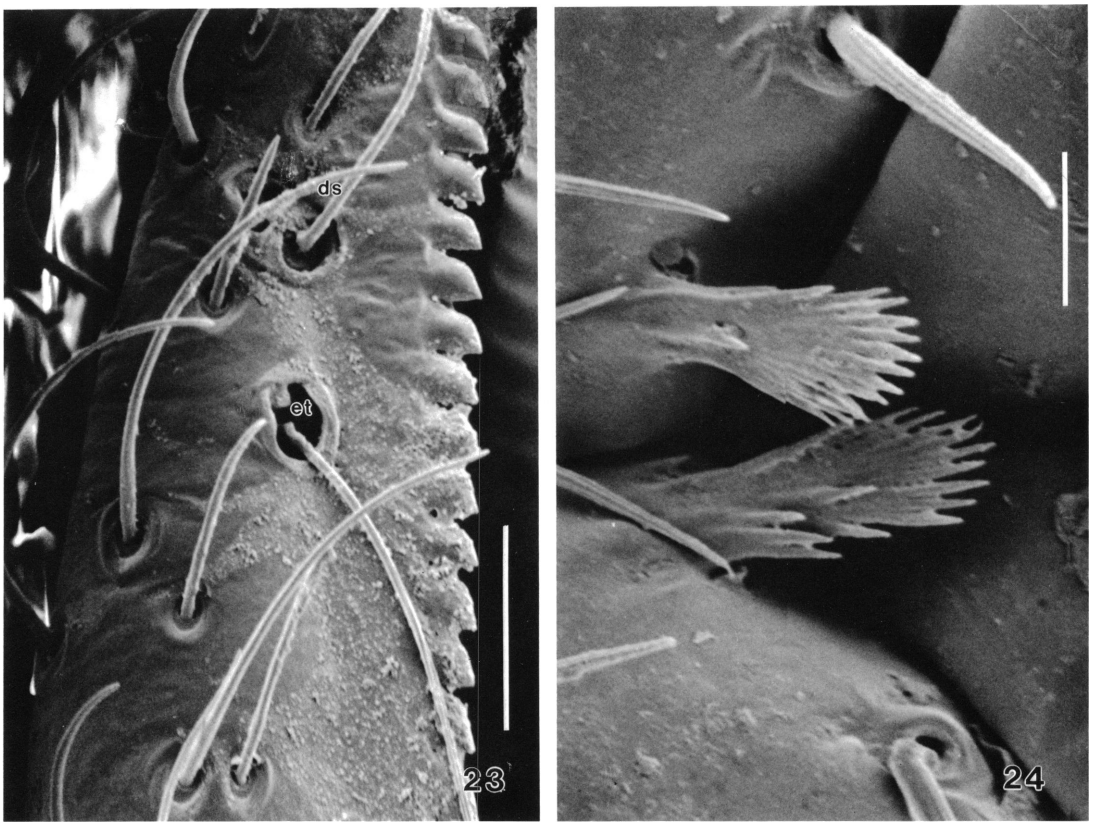
sioidea have modified preterminal tarsal setae, even in early instars. In both the fossil species and in living chthonioids and feaelloids, the seta is smooth, acute, and unmodified. This is very likely the plesiomorphic condition.

11. Coxal spines. A single row of acute spines (fig. 7) appears in the coxal region of the fossil protonymph; we interpret these as coxal spines. These are present, differing in form and number from genus to genus, in chthonioids and feaelloids, and are always absent in all other superfamilies of pseudoscorpions. While the spines in recent species of Chthonioidea are mostly denticulated or feathered (fig. 24) and are acute in only a few genera, those of some species of *Feaella* are simple, acute, and even have sockets (Harvey, 1989).

12. Pleural cuticle. The preserved pleural regions of the protonymph abdomen have a minute, uniform granulation, and are not striate. The nature of the pleural cuticle is probably of use in the higher classification of recent families, but not enough is known to make it useful for comparative purposes.

Of the 12 characters listed here and the 13 summarized in table 2, *Dracochela* is unique in a single character, the smooth blades of the serrula interior, which might possibly be due to taphonomic processes (though it is hard to see why the serrula interior blades should have been made smooth and the serrula exterior blades left denticulate).

Unfortunately it is difficult to know what to make of this data in the absence of any phylogenetic analysis of pseudoscorpion families. Polarities and weights of characters cannot be assessed in isolation. If all characters are given the same weight and assumed



Figs. 23, 24. Scanning electron micrographs of structures of *Mundochthonius basarukini* Schawaller (Chthoniidae). **23.** Distal part of movable finger of pedipalp chela, showing doubled trichobothrial socket (ds). Scale line = 0.02 mm. **24.** Coxal spines of coxae 2. Scale line = 0.01 mm.

to be apomorphic as expressed, the fossil is closest to Neobisioidea. However, after our initial report on the fossils appeared (Shear et al., 1989b), Dr. Mark Harvey of the Western Australian Museum, Perth, wrote us to comment on the systematic placement of *Dracochela.* Harvey places Feaelloidea as the sister group of Chthonioidea, based on the presence in both superfamilies (and no others) of the contiguous bothria also found in *Dracochela* (Harvey, 1988). All feaelloids have a distal seta on the movable finger of the chelicera, but in chthonioids the seta is subdistal (Harvey, personal commun.), as it is in our fossil species. The coxal spines of *Dracochela,* like those in some species of *Feaella,* are simple and perhaps socketed, but this is undoubtedly plesiomorphic.

If the contiguous distal bothria, coxal spines, and absence of a venom apparatus are regarded as important synapomorphies, *Dracochela* seems closer to Chthonioidea. While explicit argumentation is lacking, most pseudoscorpionologists have considered the chthonioids as the most plesiomorphic group in the order. Thus it would be reasonable to find a chthonioid-like pseudoscorpion as the earliest representative of the group. The hypothesis of chthonioid affinities for a Devonian pseudoscorpion, based on the three characters given above, has obvious consequences in suggesting polarities for other character transformations. Absence of a galea, for example, would appear to be apomorphic. Modified coxal spines are synapomorphic for chthonioids. Biarticulate anterior tarsi are primitive.

Most useful in the study of pseudoscorpion evolution at this point would be an exhaustive phylogenetic analysis of the extant fam-

ilies, similar to the work of Raven (1985) on mygalomorph spiders. Only a small beginning has been made on this work (Harvey, 1986, 1988).

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