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## Devonobiomorpha, A New Order of Centipeds (Chilopoda) from the Middle Devonian of Gilboa, New York State, USA, and the Phylogeny of Centiped Orders

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### ABSTRACT

The oldest known centiped fossils are described from Middle Devonian (Catskill Delta) sediments near Gilboa, New York, USA. The new genus and species *Devonobius delta* is represented by numerous specimens, including complete and partial heads and a partial trunk. This species is placed in a new family, Devonobiidae, and a new order, Devonobiomorpha, because of its strikingly dif-

ferent maxilliped coxosternae. The phylogeny of centiped orders is reviewed; the new order is the sister-group of the orders Scolopendromorpha + Geophilomorpha (=Epimorpha). The order Scutigleromorpha, already known from Upper Pennsylvanian sediments, may also occur in the Devonian of Gilboa.

### INTRODUCTION

Centipeds are small terrestrial arthropods lacking mineralized exoskeletons, and for the most part inhabiting the soil and litter environment. They have an extremely low fossilization potential. Only a few modern species are found in littoral or semiaquatic situations where they might be buried in

water-laid, anoxic sediments. Since they cannot fly, they are unlikely to be picked up by the wind and blown into lakes, a fairly common fate for insects and the source of a large percentage of all insect fossils (Carpenter and Burnham, 1985). The delicate exoskeletons of centipeds are also likely quickly to be de-

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graded by soil bacteria and fungi, or eaten by the centipeds themselves after molting. This is particularly significant because a majority of arthropod fossils are probably exuvii (Rolfe and Brett, 1970). Therefore, the fossil record of the class Chilopoda is sparse (Hoffman, 1969).

A few specimens have been reported (there are many more unstudied) from Cenozoic ambers, including the Baltic (Larsson, 1978: 116) and Dominican amber (Shear, in prep.). These fossils, as might be expected, differ little from living forms and usually can be placed in extant genera, or even species. Chamberlin (1949) described *Calciphilus abboti*, a geophilomorph, from a Cenozoic onyx deposit (erroneously cited as Cretaceous in Hoffman, 1969).

Only a few Mesozoic centiped fossils are known, and these only imperfectly. They were described 78 years ago by Fritsch (Hannibal, 1985), and have not been restudied since.

Remains of Paleozoic centipeds have been described definitively only from the famous Upper Pennsylvanian Mazon Creek site (see Nitecki, 1979, for a general review of Mazon Creek fossils). About 60 centiped specimens representing three species have been recovered (Mundel, 1981). *Latzelia primordialis* Scudder (Scudder, 1890) is a scutigermorph. *Mazoscolopendra richardsoni* Mundel and *Palenarthrus impressus* Scudder are scolopendromorphs (Mundel, 1979, 1981), and at least the former seems essentially modern. These fossils are preserved as impressions in ironstone nodules, but frequently color differences in the specimen, or carbon films, provide information of surprising detail. It is essential that this material be restudied. Worthy of further attention, if they can be located, are the specimens described by Matthew (1894) from the Upper Carboniferous Little River Group of New Brunswick, Canada. Matthew named three species of "centipeds," one of which (*Ilyodes attenuata* Matthew) may be a geophilomorph, if it is indeed a centiped at all. Finally, Almond (1985) has referred briefly to possible centiped fossils from the Stephanian B fauna of Montceau-les-Mines, France. Other names listed by Hoffman (1969) as possible Paleozoic centiped fossils cannot, with confidence, be included in the class Chilopoda.

Shear et al. (1984) and Shear (1986) reported the discovery of a new fauna of early terrestrial arthropods of Givetian (Middle Devonian) age from Gilboa, New York, and discussed its geological and paleoecological setting. These fossils are extraordinarily well preserved, and consist of intact cuticles extractable from their matrix by digestion with hydrofluoric acid. They may then be mounted on microscope slides for detailed study. Among the Gilboa fossils are the remains of centipeds, the oldest known fossils of chilopods (Shear and Bonamo, 1988).

The evidence for the presence of scutigermorphs at Gilboa is fragmentary and consists of the frequent presence of podomeres, probably quadrangular in cross section, with characteristic rows of spines on the angles. In one case, a multisegmented tarsus bearing a single claw is attached to the distal end of one of these podomeres. This evidence is equivocal because a few other arthropod groups have legs with similar sculpture, for example, the opilionids (Opiliones, Arachnida) of the family Phalangidae, which were in existence at least by the early Carboniferous (fossil from the Viséan of Scotland; Wood et al., 1985)—and certain insects. A compound eye has also been found (illustrated in Shear et al., 1984: p. 493, fig. 1F), but as it differs greatly from the faceted eye of modern scutigermorphs, it cannot be taken as evidence of their presence and has been provisionally assigned to Insecta (the earliest fossil evidence of that class). For these reasons, a formal description of the animal from which the "sawblade" leg fragments originated is deferred pending the appearance of material which may help us in placing them more definitively.

A centiped belonging to a new order is represented by more than 30 fragmentary specimens (table 3), mostly heads and maxillipeds (poison-claws). Individuals were evidently small, probably no more than 10 mm long. Some preliminary comments concerning this animal have already appeared (Shear and Bonamo, 1988); a detailed description and an analysis of its phylogenetic position follow.

#### ACKNOWLEDGMENTS

We wish to thank Robert Mesibov, Smithsonian, Tasmania, Australia, for generously sup-

plying specimens of *Craterostigma tasmanianus*. Other centipeded specimens used for comparative purposes were loaned by Jonathan Coddington, Smithsonian Institution, Washington, D.C. Our views of centipeded phylogeny were greatly clarified by discussions with Wolfgang Dohle, Berlin. John Almond, Cambridge (UK), was helpful in providing a context in the larger picture of myriapod paleontology. We thank Norman Platnick, Rowland Shelley, Wolfgang Dohle, Jarmila Kukalová-Peck, Stewart Peck, W. D. Ian Rolfe, Paul Selden, John G. E. Lewis, Luis Pereira, and J. Gordon Blower for many helpful comments on the manuscript. At an earlier stage in the project, the centipeded fossils were commented on by Ralph Crabill, Marcus Würmli, John G. E. Lewis, Ted Eason, Otto Kraus, and Edward Laidlaw Smith; however, the authors assume full responsibility for the interpretations and conclusions given here. This study was supported by grants from the National Science Foundation (BSR-82-164-10 and BSR-85-084-42), the Jeffress Memorial Trust (J-31), and the Power Authority of the State of New York.

## PALEOBIOLOGY AND METHODS

The occurrence, taphonomy, preservation, and methods of study of the Gilboa fossils have already been discussed in detail by Shear et al. (1987) in the context of a monograph on the trigonotarbid arachnids of the deposit. These subjects will be reviewed here, briefly.

**OCCURRENCE AND PRESERVATION:** Fossils of plants and animals occur in a gray shale in the upper part of the Panther Mountain Formation, from the west flank of Brown Mountain, near Gilboa, New York (see Banks et al., 1972, for further details; stratigraphic diagram in Shear et al., 1987). The Panther Mountain Formation is part of the Upper Middle Devonian Erian Series, and approximately matches the Middle Givetian of Europe, with an age of 376 to 380 million years. The extraordinary preservation of animal fossils is traditionally ascribed to rapid sorting and burial in fine, anoxic sediment. Shear et al. (1987) have speculated that the mats of plant stems usually present when animal remains are found acted as filters and selectively removed floating bodies and cast exo-

skeletons. The plant stems show a haphazard arrangement in the rock, suggesting that they were probably not transported, and may have been preserved essentially in situ. The decay of the matted stems would also have created the anoxic conditions evidently required for preservation of this kind. Subsequently, the remains, perhaps already disarticulated and folded, were compressed by kilometers of sediment.

However, recent experiments by Allison (1988) have cast doubt on the role played by anoxia in stopping or even slowing decay in buried organisms. Allison found that carcasses of worms and shrimp were "virtually destroyed" within 25 weeks by anaerobic decay, but that there were significant differences in early mineralization between specimens buried in marine waters and fresh water. The latter environment favors methanogenic decay, which in turn promotes the formation of microlayers of iron monosulfide within a few weeks, and this was found to be the most significant factor in preservation. The conclusion is that rapid burial and anoxia are important not as they stop decay, but as they slow it enough for early mineralization to begin (Allison, 1988).

Returning to our material, we have found no evidence of significant mineralization, except that the fossils appear opaque and vaguely metallic under reflected light. Certainly it would seem that there has been no large-scale replacement of organic matter with pyrite. Chemical analyses of cuticle fragments from our collections, now in the planning stages, should help resolve the question.

**METHODS OF STUDY:** Animal fossils are removed from the matrix by acid extraction, using concentrated HF and HCl, followed by a water wash. The cleaned material is mounted in CMC or Clearcol on microscope slides for study. As the accompanying illustrations show, most of the fossils are fragmentary. However, careful study allows detailed restoration, and the rare, nearly complete specimens can be used to check the restorations. Compression, superposition, and fragmentation combine to make the study of these important fossils extremely laborious. The most rewarding technique has been Nomarski interference contrast microscopy, which, at high magnifications, allows optical sec-

tioning and the consequent separation of superimposed parts. Further detail can be obtained by combining reflected and transmitted light, using fiber optics sources.

An Olympus PM-10AD (35 mm format) mounted on an Olympus Vanox II compound microscope was used for photomicrography. Drawings were made by using a drawing tube, by projecting microscope slides directly on paper, and by carefully tracing enlarged photographs. Details were added to the drawings freehand, while examining the slides at high magnifications. Composite drawings have the advantage of showing several focal planes simultaneously, and benefiting from the possibility of systematically varying the intensity of light during observation. More can be seen in the fossils than is possible to show in a photograph, so drawings and photographs of the same specimen may not agree in all details. In making the drawings, we have not attempted to show how various features are superimposed by using dotted or dashed lines, except in a few instances; instead, each visible structure has been clearly outlined. Some details of no anatomical significance have not been rendered, for example, there is no evidence that the distribution of setae on the tergites is regular or symmetrical, so most of them have been omitted.

**TAPHONOMY:** In reflected light, the fossils have a silvery brown to black, reflective, matte surface, probably due to the impressions of tiny individual matrix grains. While generally flat, irregularities in the matrix have caused some parts to be depressed below the level of others. Examined with transmitted light, the fossil range from translucent light brown in color to completely opaque (where many layers of cuticle have been superimposed). It does not appear that any replacement of the original cuticular material has taken place, so this opacity is due to layering of the cuticle rather than to opaque minerals.

While many of the centipeded specimens probably represent actual dead bodies (i.e., fig. 2), a few (i.e., fig. 74) are clearly exuvia. These are characteristically telescoped longitudinally so that the trunk is reduced in length by a factor of as much as 10, the anterior and posterior ends (if both are preserved) being separated by the length of only

two or three intact trunk segments. In these specimens the head shield is often missing.

**PALEOGEOGRAPHY:** Woodrow (1985) has examined the paleogeography<sup>3</sup> and paleoclimate of the Old Red Continent (Laurussia). In Late Devonian time, the continent roughly resembled modern Australia. Most of the western interior was a low altitude, low relief, rolling plain, and the western coastline may have been quite complex. The southwestern quarter of this region (now the central United States west of the Appalachians and east of the northern Rockies) was occupied by the shallow epicontinental Catskill Sea, with a long bay to the north cutting deeply into the plains (into the region of the present Hudson's Bay), and evidently periodically out of connection with the sea. Exchange with the world ocean was limited by islands to the south and west of the opening of the Catskill Sea, which was bounded on its southeastern shore by a tectonic peninsula east of, but parallel to, the present Appalachian Mountains [the tectonic activity was probably produced by the sequential docking of several terranes, especially the Avalon (Ettensohn, 1985)]. The highlands extended northeastward and then west around the northern shore of the continent, encompassing present-day Newfoundland, Scotland, the western Scandinavian peninsula, and Greenland. Wasting of these mountains took place into interior basins in the north, and built extensive coastal deposits on the west and east shores of the southern peninsula. The Catskill Delta was one of these coastal deposits, covering much of eastern North America from Virginia to the St. Lawrence. This alluvial plain may have had a slope of less than 0.2 m/km, and was occupied by several permanent, long-lasting, major river systems as well as shifting, braided streams which alternately built and breached their levees (Woodrow, 1985).

**PALEOECOLOGY:** The climate was tropical; the equator was situated across the base of the Appalachian Peninsula in the Late Devonian. Woodrow (1985) has suggested that the Catskill Delta complex had a seasonal wet/dry climate, controlled by the rain shadow of the mountains to the southeast. While

<sup>3</sup> For a somewhat different interpretation of Devonian paleogeography, see Scotese et al. (1985).

TABLE 1  
Polarity of Characters for Cladistic Analysis of Chilopod Orders

Character	Plesiomorphic	Apomorphic
1. chilopod synapomorphies	absent	present
2. stigmata	dorsal, single	lateral, paired
3. head	domed	flattened
4. eyes	compound	reduced or absent
5. maxilla 2 coxae	separate	fused
6. coxal/anal organs	absent	present
7. maxilliped coxae	separate	fused in midline
8. brood care; epimorphy	fused in midline	suture suppressed
	absent	present; epimorphy suppressed or absent
9. maxilliped podomeres	complete	incomplete
10. Tömösváry organ	present	absent
11. pairs of legs	15	more than 15
12. segments 7–9	3 tergites	1 tergite
13. antennal articles	not annulated	annulated
14. female gonopods	without macroseta	with macrosetae
15. testes	paired	unpaired, median
16. long tergites	undivided	divided
17. anogenital capsule	absent	present
18. segment 16	tergite-sternite	cylindrical
19. maxilliped coxosternae	no ventral apodemes	ventral apodemes
20. maxilliped tergite	separate	fused to succeeding tergite
21. antennal annuli	variable numbers	fixed at 14

this picture describes the situation in the Late Devonian, the Panther Mountain formation is late Middle Devonian. The trend in plate movement was to the north during this interval, but the equator probably was not far from midcontinent by the Middle Devonian. The seasonality (wet/dry) of the climate is shown by the presence of growth rings in woody plant fossils contemporaneous with our animals.

The vegetation of the Catskill Deltas has been summarized by Banks et al. (1985). They hypothesize that the deposit ("Brown Mountain Gilboa") in which the centiped fossils occur "... indicates in situ burial of a dense ground cover of plants [*Leclercqia complexa*]. . . . other abundant remains give evidence of the presence of taller plants of shrubby habit, but without shading leaves" (Banks et al., 1985: 135).

We are unable at present to determine if the centipeds actually lived among the plants or if their remains were washed in and filtered out by the matted axes of *Leclercqia*. The presence of tracheal spiracles in one specimen of *Devonobius delta* confirms that the animals

breathed air, but many geophilomorph centiped species are adapted to periodic flooding of their habitat, are able to spend hours or even days submerged, and some are exclusively intertidal (Lewis, 1981: 382–391). Thus, even if the bases of the *Leclercqia* plants were permanently flooded, it is not inconceivable that the centipeds might have lived there. However, since heterotergy, associated with swift, stable running, is present in this centiped, its style of life was more probably like that of the smaller, litter-inhabiting lithobiomorphs. There is nothing about the morphology of *D. delta* to suggest that it was anything but a predator, like all centipeds. Its prey may have been any animal smaller than itself.

THE PLACE OF THE ORDER  
DEVONOBIO MORPHA IN  
CENTIPED PHYLOGENY

Lewis (1981: 418–424) has given a synopsis of the historical development of ideas on chilopod phylogeny. As Dohle (1985) has stated, much of this past work is simply spec-

TABLE 2

**Character States in Chilopod Orders**

See table 1 for list of characters and polarities. Plesiomorphy is coded by 0, apomorphy by 1, serial transformations by higher digits.

Character	Scutigero- morpha	Lithobio- morpha	Cratero- stigma- morpha	Devono- bio- morpha	Scolo- pendro- morpha	Geophilo- morpha
1	1	1	1	1	1	1
2	0	1	1	1	1	1
3	0	1	1	1	1	1
4	0	1	1	1	1	1
5	0	1	1	1	1	1
6	0	1	1	1	1	1
7	0	1	2	2	2	2
8	0	0	1	?	1	1
9	0	0	0	0	1	1
10	0	0	0	1	1	1
11	0	0	0	1	1	1
12	1	0	0	0	0	0
13	1	0	0	0	0	0
14	0	1	0	0	0	0
15	0	1	0	0	0	0
16	0	0	1	0	0	0
17	0	0	1	0	0	0
18	0	0	1	0	0	0
19	0	0	0	1	0	0
20	0	0	0	0	1	0
21	0	0	0	0	0	1

ulation based on intuition, or on evolutionary "laws" such as tachygenesis, elongation, and the like. Dohle (1985, 1988) has pioneered a cladistic approach, which will be followed here.

The monophyly of the class Chilopoda is well established (Dohle, 1980, 1985). Similarly, with the possible exception of the Craterostigmomorpha, discussed below, and by Dohle (1988), the six orders of chilopods are clearly separable monophyletic entities (Dohle, 1985; Shear and Bonamo, 1988; see following description of order Devonobio-  
morpha). The sister-group of Chilopoda may be Symphyla (Boudreaux, 1979) or Hexapoda; supposed synapomorphies with Symphyla are the partial or complete union with the head of the first trunk segment, which bears appendages, and the suppression of the legs of the last two trunk segments. However, it should be pointed out that this arrangement requires that the terminal genital openings and the fat body of centipeds be regarded as parallelisms to the same characters in Hex-

apoda. Further, when the tergite of the first trunk segment disappears in centipeds it fuses not with the head, but with the tergite of the second trunk segment (Lewis, 1981: 22). In many symphylans the appendages of the first trunk segment are reduced or absent; they never function as part of the feeding complex as do the maxillipeds of centipeds.

Dohle (1980), while hesitating to draw definitive conclusions about myriapods and insects as a whole, has established that Diplopoda and Pauropoda are monophyletic and may be combined as (Superclass?) Dignatha. His evidence also suggests that the sister-group of Dignatha is Symphyla, and that the three orders can be united as Progoneata. Much less certain, but intriguing, is the idea that the sister-group of Progoneata is Hexapoda (or Insecta; see Kukalová-Peck, 1987, for new evidence of the monophyly of Insecta sensu lato). This leaves us with the Chilopoda as the plesiomorphic sister-group of Hexapoda plus Progoneata. If true, this would push the differentiation of all these groups much farther back into the past than previously has been thought. Since Progoneata is the most derived group in the scheme, yet appears earliest in the fossil record (Diplopoda; Upper Silurian), both Chilopoda and Insecta must have been in existence before this time (already suggested for Insecta by Kukalová-Peck, 1987). We find the arguments of Dohle (1980) and Kukalová-Peck (1987) convincing; they may be bolstered by the suggestive evidence of Retallack and Feakes (1987) of possible myriapod burrows in an Ordovician paleosol, and fossils of a potential late-surviving tracheate stem group in marine deposits of the Silurian of Wisconsin (Mickulic et al., 1985).

Competing hypotheses concerning the pathway taken by evolution in the Chilopoda have centered on three important questions: (1) which of two orders, Scutigermorpha or Geophilomorpha, is the most primitive of chilopods? (2) Should the order Lithobio-  
morpha be grouped with scutigermorphs to form a subclass Anamorpha, or with Scolopendromorpha and Geophilomorpha to form a subclass Pleurostigmophora? Finally (3), what is the correct systematic position of *Craterostigmus*?

On the first question, it is now commonly

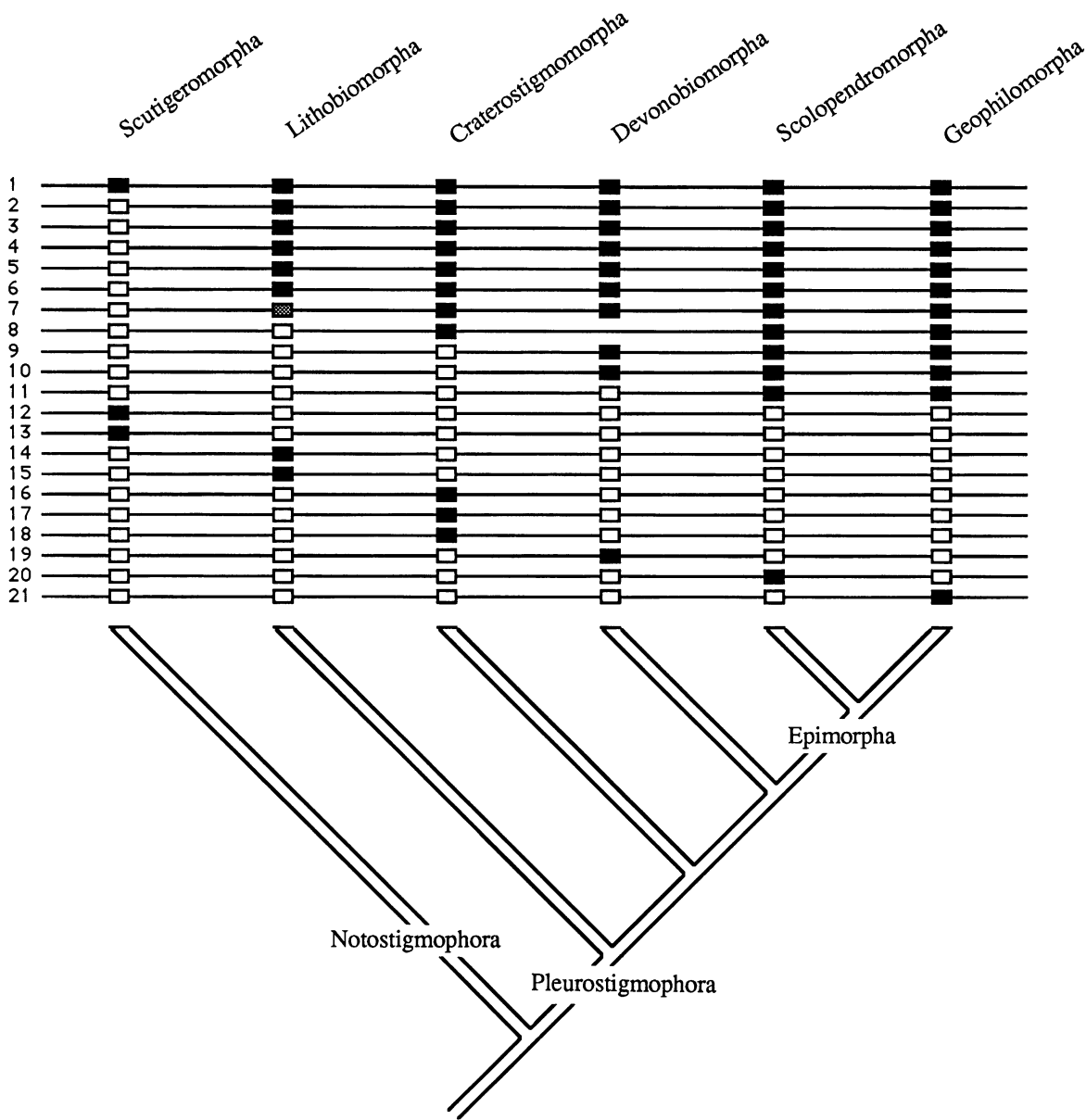


Fig. 1. Cladogram of orders of centipeds. See text for explanation and tables 1 and 2 for character list and states. Character 7 has three states; character 8 cannot be definitely determined for Devonobiomorpha.

accepted that the Scutigermorpha are most similar to the probable common ancestor of all chilopods. The simplified structure of the geophilomorphs is therefore secondary, an adaptation to life in the small spaces of the soil, where burrowing and flexibility are at a premium. Manton (1977) demonstrated this adaptation in detail, but she read her evi-

dence the other way round and emphasized the “advanced” nature of the Scutigermorpha, with their rigid bodies constructed for fast running. Dohle (1985) has described a hypothetical ancestral chilopod in some detail; he gives it many of the plesiomorphic characters of the scutigermorphs.

Manton (1977) is the most recent author

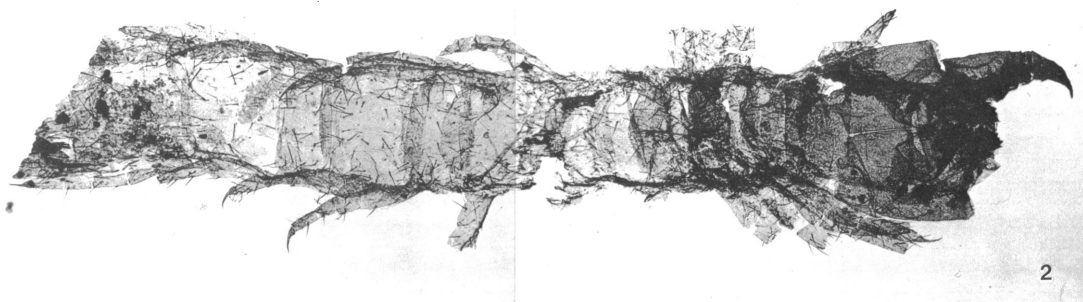


Fig. 2. *Devonobius delta*. Photomosaic of entire specimen 411-15-AR18. See figures 5 and 6 for scale.

attempting to confirm the original hypothesis of Meinert (1868) that the Chilopoda fall naturally into two groups, Anamorpha and Epimorpha, based on ontogenies. In the Anamorpha, containing the orders Scutigermorpha and Lithobiomorpha, the young hatch with 4–7 pairs of legs and add legs in subsequent molts until the adult number of 15 pairs is reached. In the Epimorpha (Scolopendromorpha and Geophilomorpha), the young hatch with the full adult number (21 to more than 100 pairs) and pass through two immobile stages, the peripatoid and foetoid.<sup>4</sup>

PrunESCO (1965) is a later proponent of the alternative hypothesis (first put forward by Brandt in 1841). He argues, on the basis of a number of anatomical features, that the Scutigermorpha stand alone in a subclass Notostigmophora, marked by having masses of fine, unbranched tracheae opening by single large spiracles in the dorsal midline. The other three orders, with paired lateral spiracles, constitute a subclass Pleurostigmophora. Dohle (1985) posed the question in cladistic terms: are those characters shared by Scutigermorpha and Lithobiomorpha plesiomorphic or apomorphic? He then convincingly argued that the former was the case; his phylogeny, supporting Brandt and PrunESCO, has gained wide acceptance.

<sup>4</sup> To avoid multiple citations, it may be taken that all further information on the structure and biology of living centipeds comes from Lewis (1981), unless otherwise indicated.

The 15 pairs of walking legs and the segmental distribution of spiracles suggest that *Craterostigmus* is correctly placed in the Lithobiomorpha (Hoffman, 1982). Manton (1965), however, described many anatomical details which are similar to those in the Scolopendromorpha, and considered *Craterostigmus* to be an aberrant member of that order. In describing the genus, Pocock (1902) called it an “annectant” type, deserving of ordinal status on its own and falling between the Lithobiomorpha and the two epimorph orders. Indeed, Manton (1965), in an often overlooked part of her anatomical monograph on *C. tasmanianus*, stated that the young hatch with 12 pairs of legs, and add the final three pairs in the next molt—anamorphosis is almost, but not quite, absent. Manton also observed parental care of the young in *C. tasmanianus*. Dohle (1988) carried out a detailed study which confirmed Pocock’s original hypothesis; he considered the order Craterostigmomorpha (justified by numerous autapomorphies) as the sister-group, among the living orders, of Scolopendromorpha + Geophilomorpha (=Epimorpha), a conclusion with which observations of our own on *Craterostigmus* had led us to concur. However, we argue below that our new order Devonobiomorpha, erected for the single fossil species *Devonobius delta*, new species, should now be considered the sister-group of the Epimorpha (if not a member of that superorder), while Craterostigmomorpha becomes the sister-group of Devonobiomorpha + Epimorpha.



Shinohara (1970) published a phylogenetic tree of centipeds, which, although it was not argued in cladistic terms, anticipated the successful cladistic analysis of chilopod orders by Dohle (1985, 1988). Dohle's study has given us a framework into which we may attempt to insert our new order. For details of arguments on polarity of characters and synapomorphies of the living order, the reader is referred to Dohle's 1985 paper. Below, we will treat only those characters that can be observed on our fossils (with one exception), or that are autapomorphic for the living orders. Table 1 lists those characters and their polarity (as established by Dohle, 1985), and table 2 gives their distribution among the orders.

1. *Chilopod synapomorphies*. Dohle (1985) has given three of these. The appendages of the first trunk segment have been strongly modified and are equipped with poison glands; often called poison claws or forcipules, they are referred to here as maxillipeds. The second maxillae bear an embryonic egg-tooth, used by at least some species to tear the egg membrane during hatching. The spermatzoa (recently restudied by Jamieson, 1986, and by Beniouri and Descamps, 1985) have numerous peculiarities, among which the most striking is the spirally keeled nucleus.<sup>5</sup>

2. *Stigmata*. Evidence that the dorsal stigmata and the bundles of fine, unbranched tracheae found in the scutigeromorphs (Notostigmophora) are primitive, ground-plan characters for Chilopoda comes from the rather elaborate condition of the circulatory system in the other living orders. If the pleurostigmatate condition were plesiomorphic, the circulation in the Pleurostigmophora should be simple; that it is not indicates that the original condition was to have the blood in the pericardial sinus aerated by a tracheal

"lung." Dohle (1985), in making this argument, points out the wide variation in tracheal arrangements in terrestrial arthropods as evidence by analogy for the plausibility of this sequence.

3. *Head*. The flattened head of the Pleurostigmophora seems to be an adaptation for life in the soil and in small crevices. The head-flattening mechanism is different from that found in symphylans and some hexapods; the head in centipeds is bent posterior to the clypeus, so that this part of it becomes ventral and the mouth is pushed posteriorly. "This is an unusual solution for flattening a head" (Dohle, 1985: 59).

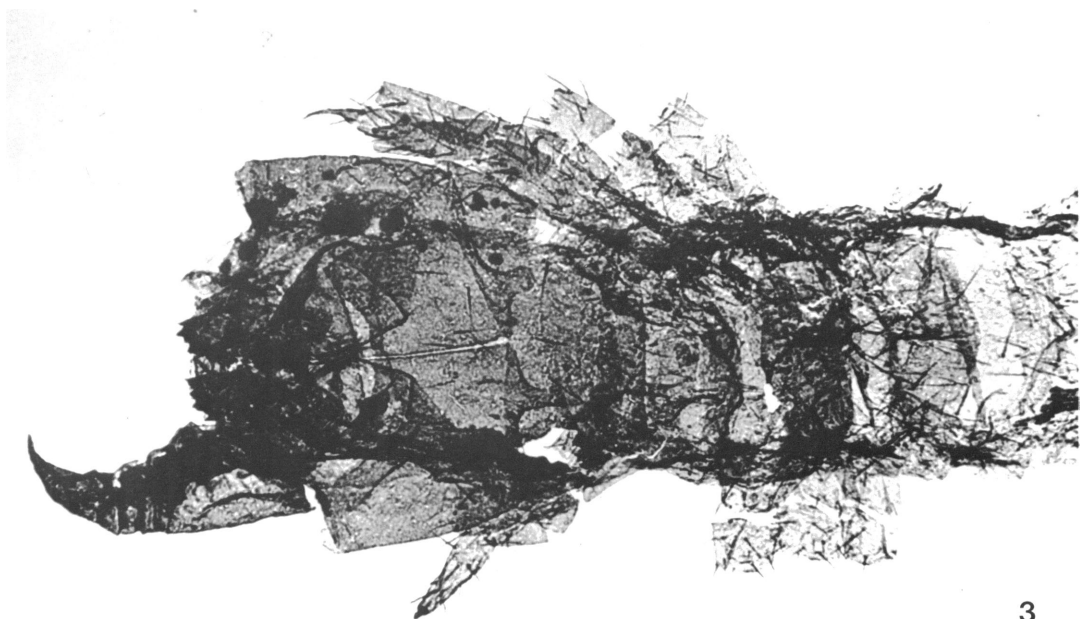
4. *Eyes*. Compound eyes, as found in the scutigeromorphs, are probably plesiomorphic for arthropods in general, so their reduction is apomorphic.

5. *Maxillae 2 coxae*. The fusion of these coxae makes them less like the serially homologous legs and thus is apomorphic.

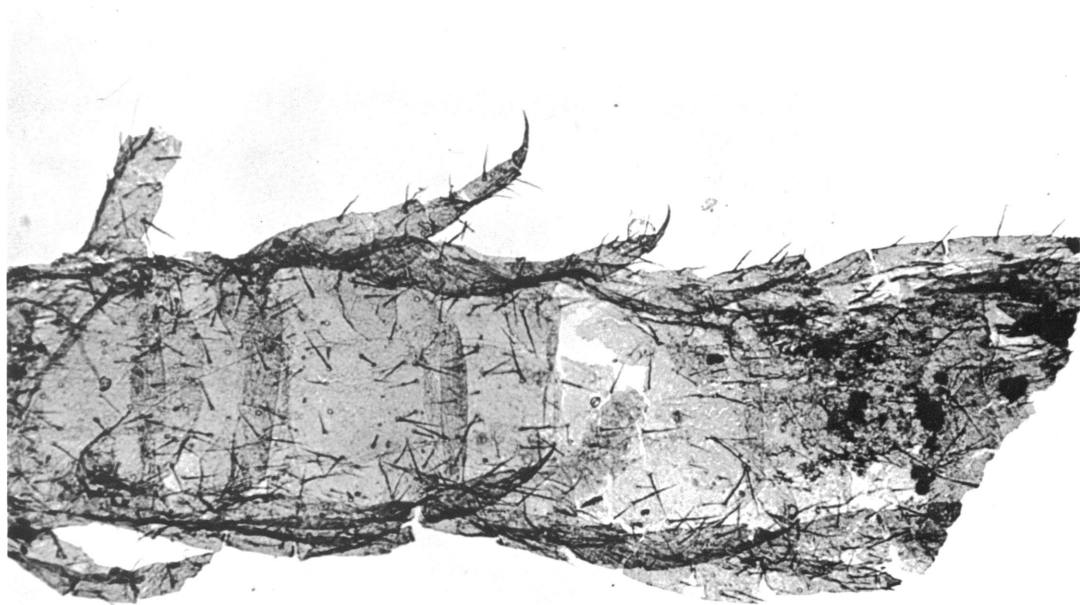
6. *Coxal/anal organs*. Rosenberg (1982, 1983a, 1983b) has shown that these organs, absent in the scutigeromorphs, are very similar at the cellular level in three of the four other living orders. They are assumed to be synapomorphic for Pleurostigmophora, but the function of these organs is the subject of debate, and a resolution could affect polarity. Rosenberg (op. cit.) argues for their use in the uptake of water vapor, while Littlewood (1983) maintains that they produce a pheromone. If the former interpretation is correct, it would be possible to argue that Notostigmophora have apomorphically lost the organs, since (at least superficially) similar structures occur in all myriapod classes and in some primitive hexapods.

7. *Maxilliped coxae*. The fusion of these plates (which may also contain contributions from the embryonic sternum) in the midline is apomorphic because it makes the maxillipeds less like the serially homologous legs. In the lithobiomorphs, some movement is still possible between the plates, but in the other orders (save Devonobiomorpha, where it cannot be checked) the fusion is complete. Some scolopendromorphs have an incomplete suture in the midline; others in the order have no trace of a suture, and the coxae form a single massive plate in geophilomorphs. The loss of any possibility of movement after fu-

<sup>5</sup> Jamieson (1986) argued from spermatozoan ultrastructure alone for a close relationship between lithobiomorphs and geophilomorphs, and between scolopendromorphs and scutigeromorphs. This would contradict the analysis of Dohle (1985), based on anatomy, behavior, etc., and can probably be disregarded. Jamieson also contended, based on the same evidence, that Pauropoda is the sister-group of Chilopoda, a proposition not supported by any other line of evidence.

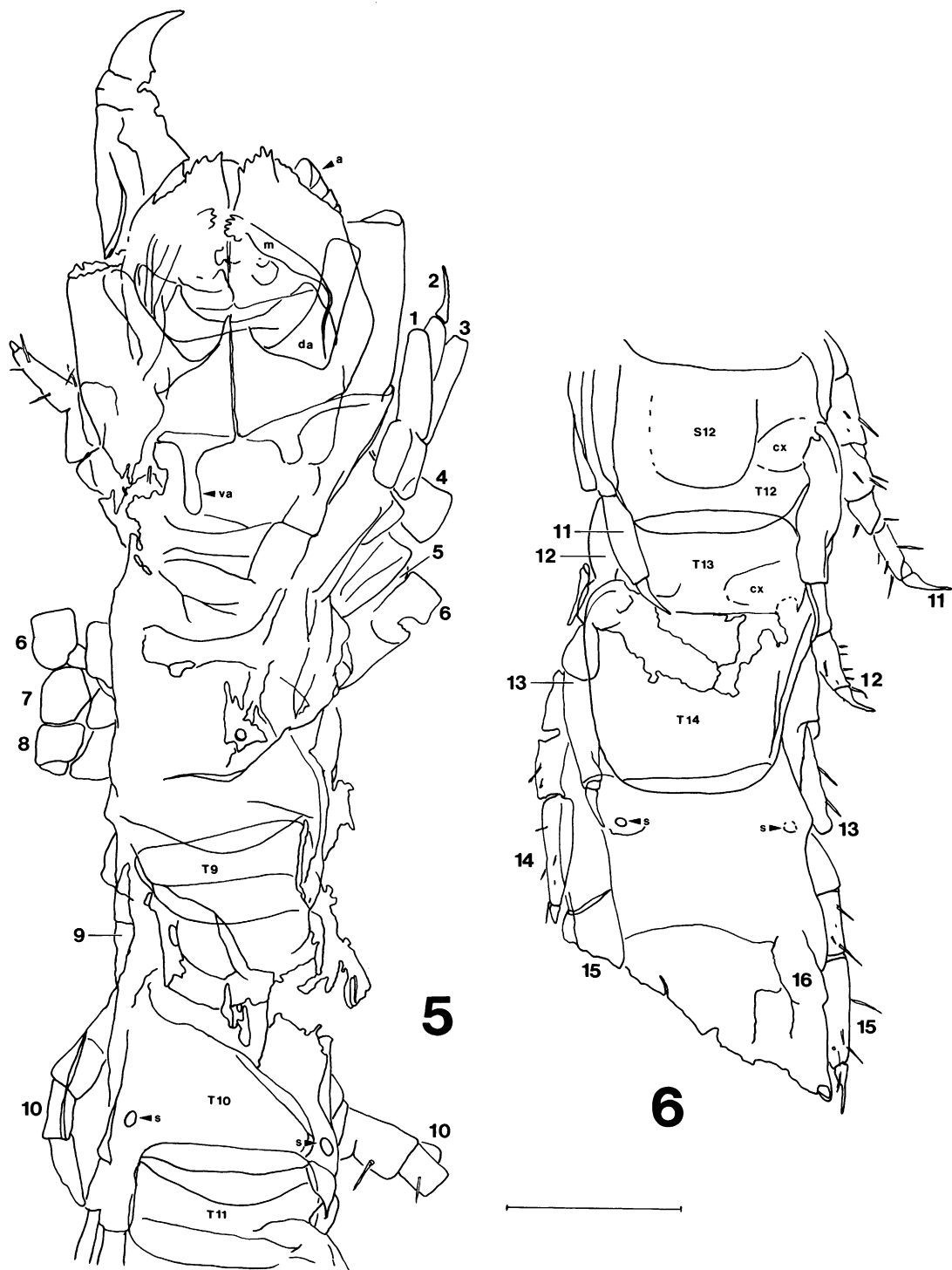


3



4

Figs. 3, 4. *Devonobius delta*, specimen 411-15-AR18. 3. Anterior part. 4. Posterior part. See figures 5 and 6 for scale.



Figs. 5, 6. *Devonobius delta*, specimen 411-15-AR18, interpretive drawings. 5. Anterior part. 6. Posterior part. See table 4 for abbreviations. Scale line = 0.3 mm.



7

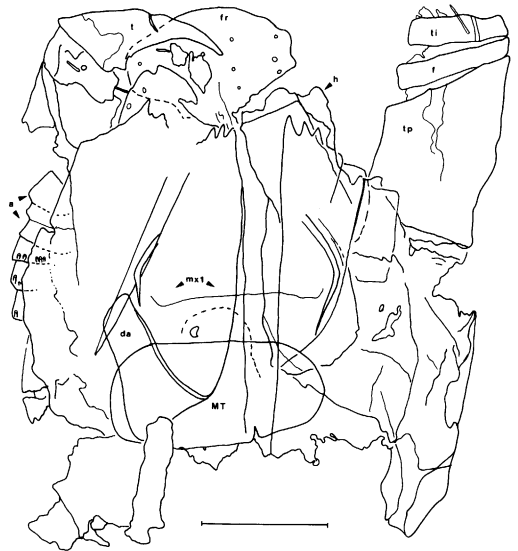


8

Figs. 7, 8. *Devonobius delta*, partial heads. 7. 411-7-AR56. 8. 334-16M-2. See figures 9 and 10 for scale.

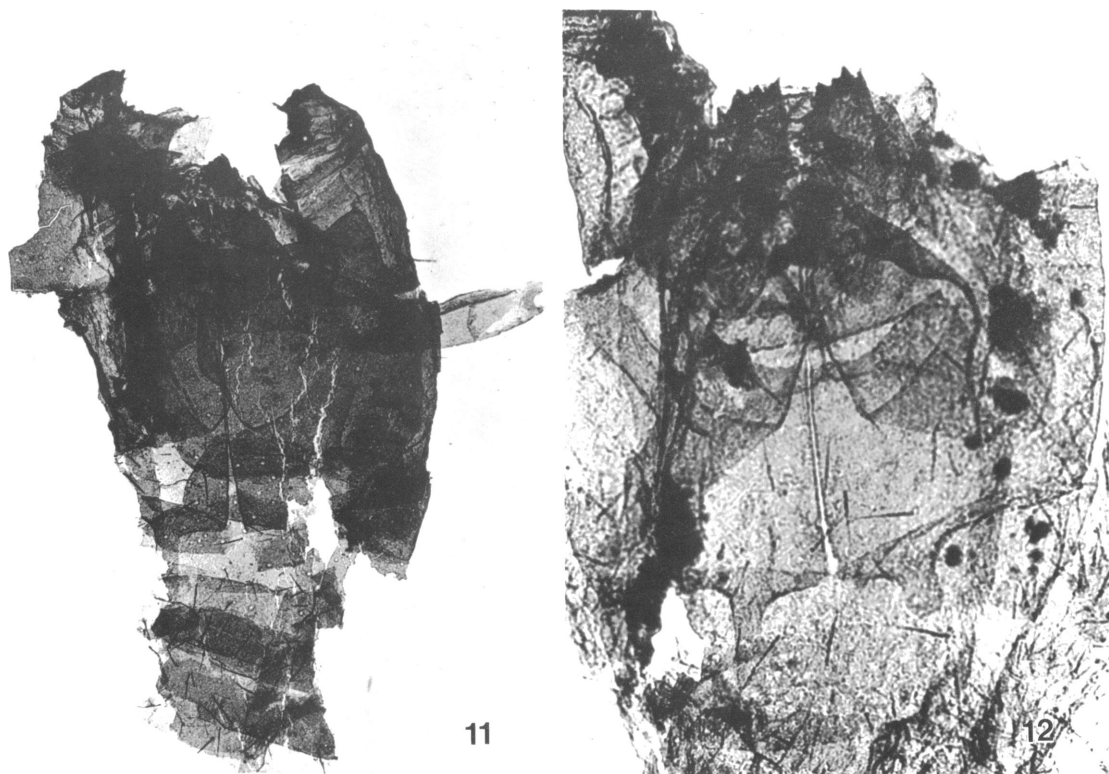


9



10

Figs. 9, 10. *Devonobius delta*, partial heads, interpretive drawings. 9. 411-7-AR56. 10. 334-16M-2. See table 4 for abbreviations. Scale line = 0.3 mm.



Figs. 11, 12. *Devonobius delta*. 11. Partial head 411-7-AR81. See figure 13 for scale. 12. Head of 411-15-AR18; see also figures 3 and 18.

sion is here regarded as the second step in a transformation series.

8. *Brood care and epimorphy*. Regarded as separate adaptations by Dohle (1985), these are combined here because they remain unknown for the extinct devonobiomorphs. Craterostigmomorphs have brood care but only partial epimorphy (Manton, 1965). While brood care is unknown for *Devonobius*, the inferred presence of more than 15 pairs of legs suggests complete epimorphy.

9. *Maxilliped podomeres*. In the scolopendromorphs and geophilomorphs the tibia and tarsus of the maxilliped telopodite are open laterally and the claw is hinged directly to the femuroid. For reasons already stated this is an obvious synapomorphy for the two orders.

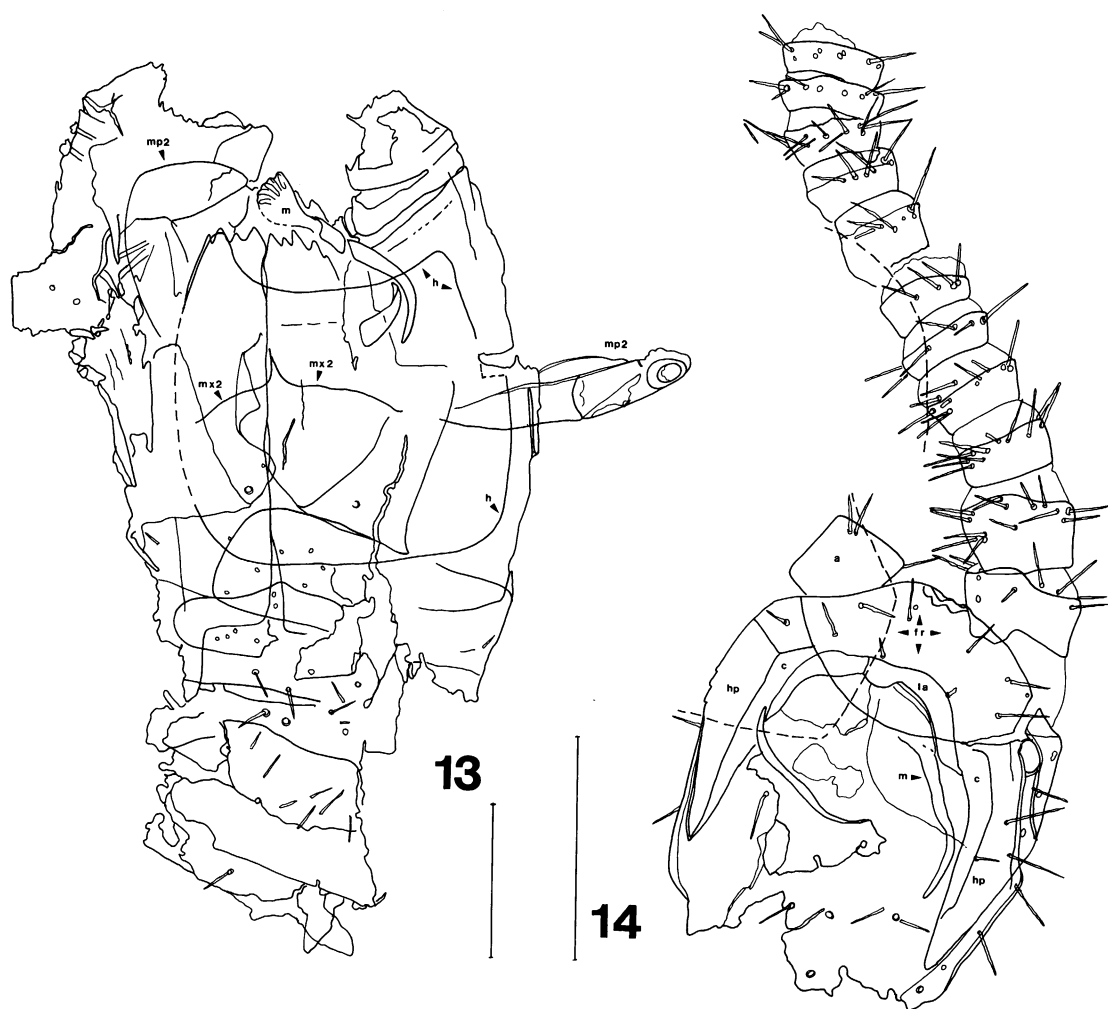
10. *Tömösváry organ*. According to Haupt (1979), these organs are homologous in all *Atelocerata* (=Antennata), and thus their loss is apomorphic. In craterostigmomorphs these organs are partly reduced (fig. 50, To) and may be nonfunctional (Dohle, 1988); they are

not found in devonobiomorphs, scolopendromorphs, and geophilomorphs.

11. *Pairs of legs*. Dohle (1985) argues for the plesiomorphy of 15 pairs of legs, because to regard this number as synapomorphic for the three orders in which it occurs would require considering all the characters which lithobiomorphs and craterostigmomorphs have in common with the epimorph orders as convergences. Simple parsimony argues against this.

12, 13. *Segments 7-9; antennal articles*. Having segments 7-9 covered by a single tergite is an autapomorphy of scutigermorphs, giving greater rigidity to the body and allowing for rapid running (Manton, 1965). By out-group comparison, the multiannulate antennal segments of these animals are also autapomorphic. Several additional autapomorphies for this order are mentioned by Dohle (1985).

14, 15. *Female gonopods; testes*. Terminal gonopods used to hold the eggs before de-



Figs. 13, 14. *Devonobius delta*, interpretive drawings. 13. Partial head 411-7-AR81. 14. Head of 411-7-AR97. See table 4 for abbreviations. Scale lines = 0.3 mm.

positing them are probably part of the chilopodan groundplan (Dohle, 1985). The claws and macrosetae on those of the lithobiomorphs may be an autapomorphy of the order; this is not clear. One argument against it is that retaining the claws makes the gonopods more like legs than they are in the scutigeromorphs; clawed gonopods occur in hexapods as well and may be plesiomorphic for all Atelocerata. The loss of a claw and the reduction of the gonopods in females would have to be a convergence in scutigeromorphs and the other orders, save Lithobiomorpha. More study of this character is required; perhaps it is best to limit the argument for apo-

morphy at the level of Lithobiomorpha to the distinctive macrosetae for the time being. However, the median unpaired testis in male lithobiomorphs is a clear apomorphy because it originates from paired rudiments in the embryo.

16–18. *Long tergites; anogenital capsule; segment 16*. The apomorphic conditions of the latter two of these characters (presence of the capsule, segment 16 a complete cylinder) are unique to *Craterostigma*. The apomorphy of the divided long tergites can be established by outgroup comparison with lithobiomorphs; this is an adaptation to increase trunk flexibility (Manton, 1965).

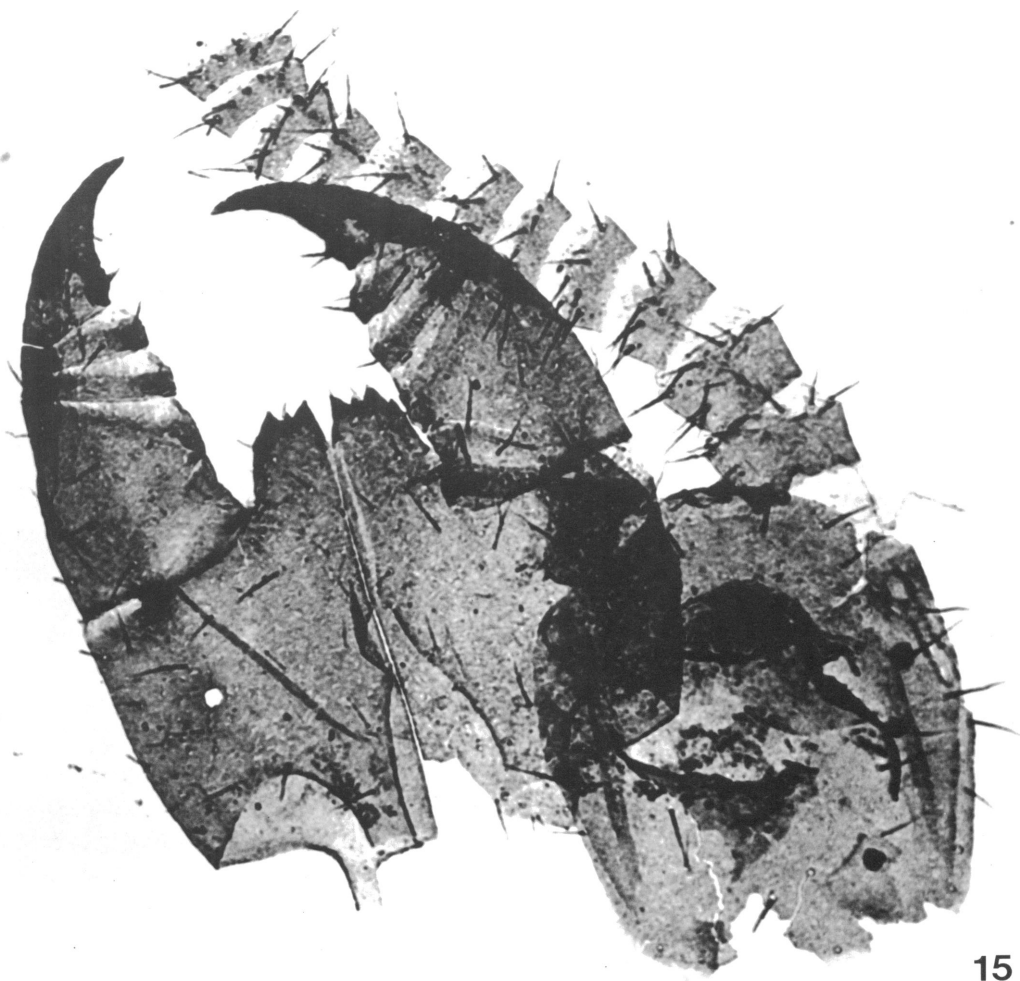


Fig. 15. *Devonobius delta*, head and maxillipeds of 411-7-AR97, in partial organic connection, therefore presumed to be from the same individual. See figure 14 for scale.

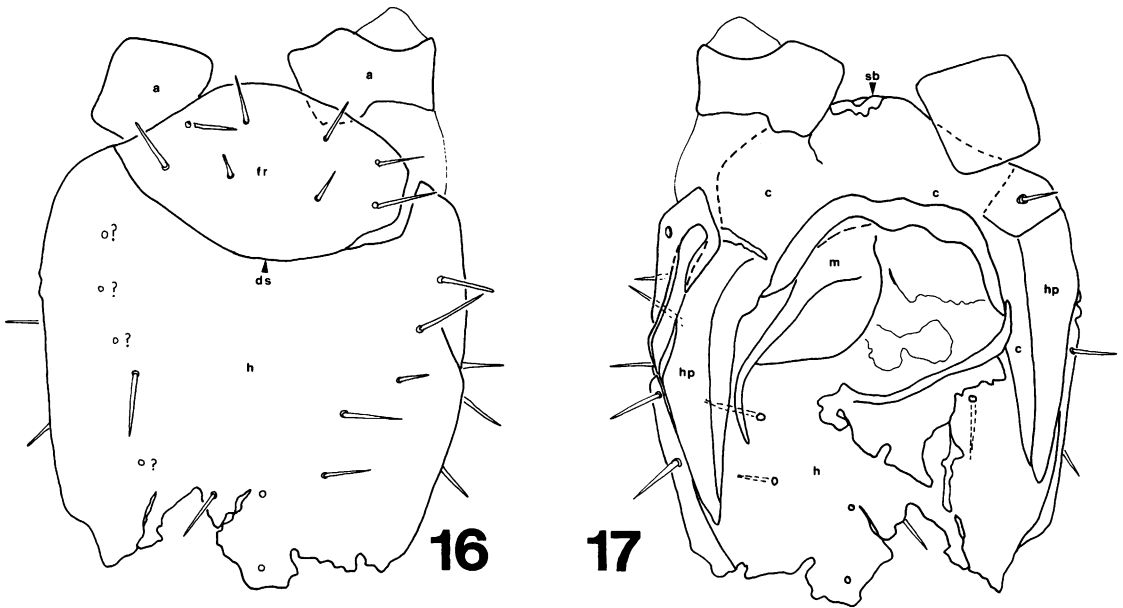
19. *Maxilliped coxosternae*. The presence of long apodemes extending posteriorly from the ventral wall of the maxilliped coxosternae is autapomorphic (by comparison with scutigermorphs and lithobiomorphs) for *Devonobius* alone. The unusual modifications of the maxilliped coxosternae, unlike those found in any other centipeds, provide the main evidence for the proposal of the new order Devonobiomorpha.

20. *Maxilliped tergite*. The fusion of the maxilliped tergite to that of the next posterior

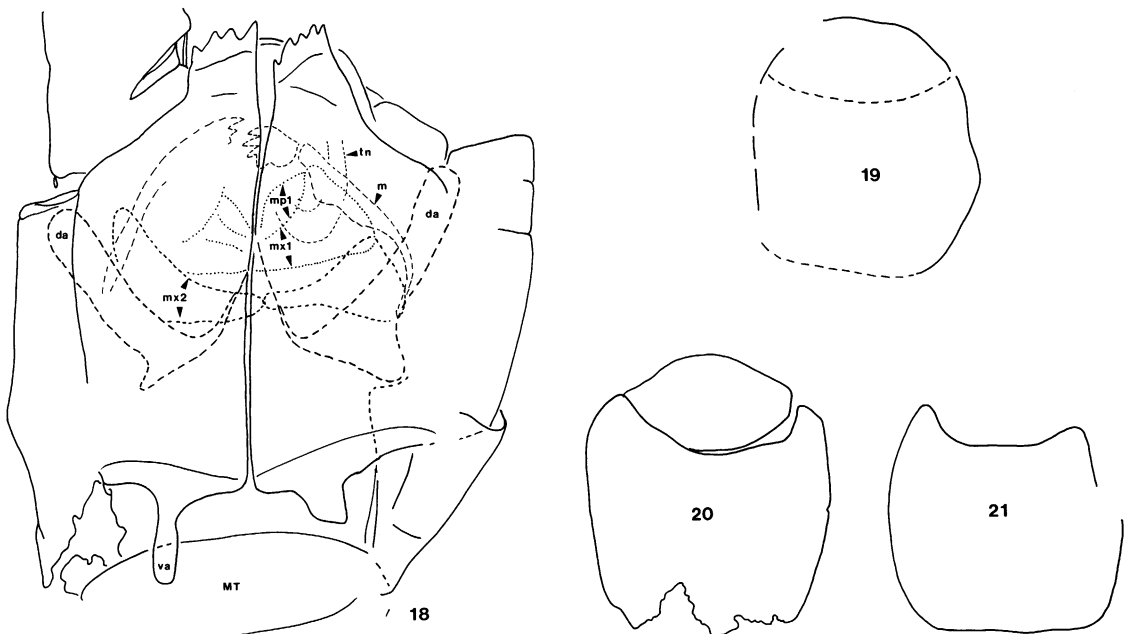
segment in scolopendromorphs is autapomorphic for that order.

21. *Antennal annuli*. A fixed number of annuli (14) in the antenna is apomorphic for Geophilomorpha by outgroup comparison to all other orders (but Dohle [1988] has suggested that the antennomeres of *Craterostigma tasmanianus* are fixed at 18). Other autapomorphies for this order are given by Dohle (1985).

These characters were analyzed using the computer program MacClade 2.1, giving the



Figs. 16, 17. *Devonobius delta*, head of 411-7-AR97. 16. Reconstruction of dorsal surface. 17. Reconstruction of ventral surface. Posterior margin of head torn off and pushed forward ventrally. See table 4 for abbreviations. Scale as in figure 14.



Figs. 18-21. *Devonobius delta*, details of heads. 18. Interpretive drawing of head of 411-15-AR18 (see figs. 3 and 12). Dorsal apodeme of maxilliped coxosternum (da) outlined by heavy, long dashes; maxilla 2 coxosternum (mx2) by heavy, short dashes; maxilla 1 (mx1, mp1) by dotted line, mandibles (m) by light, long dashes; tentorium (tn) by light, short dashes. See table 4 for other abbreviations. 19-21. Outlines of head shields and frons, all to same scale. 19. 411-15-AR18. 20. 411-7-AR97. 21. 411-7-AR81.



TABLE 3  
List of Specimens of *Devonobius delta*

Slide #	AMNH #	Brief description of specimen
329-AR4	43130	Compete maxillipeds, lacking only dorsal apodemes (compound eye fragment associated)
329-AR30	43131	Compete maxillipeds, with parts of first thoracic segment
329-16-AR000	43132	Head fragments, with distal part of antenna
329-16-AR40	43133	Head
329-16-AR48	43134	Very poorly preserved possible basal segments of posterior legs
329-16-AR53	43135	Head and possible maxilliped segment tergite
334-16M-2	43136	Maxillipeds, part of head capsule, and antennal fragment
2002-9-AR13	43137	Head and maxillipeds
2002-9-AR15	43138	Distal part of maxillipeds, antennal fragments ("sawblade" podomere associated)
2002-12-AR74	[NMNH]	Partial head, maxillipeds, 2-3 anterior trunk segments
411-1-AR174	43139	Base of head and first 1-3 trunk segments
411-2-AR1	43140	Telescoped, folded, and compressed molt, including posterior legs and possible pores of anal organs
411-2-AR2	43141	Head and anterior few segments (molt?)
411-2-AR4	43142	Jumble of antennae, legs, and thoracic segments, poorly preserved
411-2-AR13	43143	Few poorly preserved legs
411-2-AR19	43144	Opaque mass with projecting leg
411-7-AR79	43145	Maxilliped coxosternum with complete apodemes
411-7-AR81	43146	Head and maxillipeds
411-7-AR82	43147	Distal 4-5 antennal segments (associated with mite)
411-7-AR97	43150	Head and maxillipeds,

TABLE 3—(Continued)

Slide #	AMNH #	Brief description of specimen
		basal parts of antennae
411-9-AR37	43151	13 antennal segments
411-9-AR56	43152	Head and maxillipeds
411-15-AR18		Head with 14? 15? 16? trunk segments
411-19-AR149	43153	Head folded back over anterior 3 trunk segments
411-19-AR154	43154	Telescoped and distorted molt
411-19-AR160	43155	Possible head fragment
411-19-AR191	43156	Antennal fragment
411-19-AR202	43157	Poorly preserved maxillipeds
411-19-AR212	43158	Head and first trunk segment
411-19-AR229	43159	Fragments with pores of anal or coxal glands?
411-19-AR231	43160	Telescoped and distorted molt
411-19-AR232	43161	Head

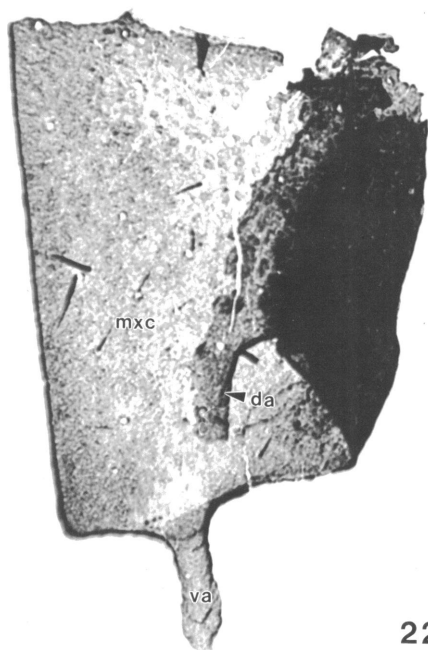
results shown in Figure 1. This tree has a length of 21 and a consistency index of 1.00; a shorter, more consistent tree using these characters is not possible.

From this analysis arises the conclusion that the origins of at least four of the orders of centipeds are to be found earlier than the Middle Devonian. Since the Devonobiomorpha were already present then, so must have been their sister-group, the stem of the Epimorpha (although *Devonobius* was very likely itself epimorphic). The four orders "below" devonobiomorphs in the tree also must have already been in existence. However, as these specimens are the earliest fossils of any centipeds, the origins of the class Chilopoda and the first steps in its differentiation remain unilluminated by fossil evidence.

SYSTEMATICS

CLASS CHILOPODA LATREILLE  
SUBCLASS PLEUROSTIGMOPHORA VERHOEFF  
ORDER DEVONOBIO MORPHA, NEW ORDER

DIAGNOSIS: Differing from all other centipeds in form of maxilliped coxosternae.



22



23

Figs. 22, 23. *Devonobius delta*. 22. 411-7-AR79, maxilliped coxosternum of one side, showing complete ventral apodeme (va). 23. 411-7-AR81, probable telopodite (palp) of maxilla 2. See also figures 11 and 13.

Coxosternae laterally complete, without division into dorsal and ventral parts at dorsal hinge joint between coxal part and trochanteroprefemur of telopodite; with pronounced long ventral apodemes (fig. 54).

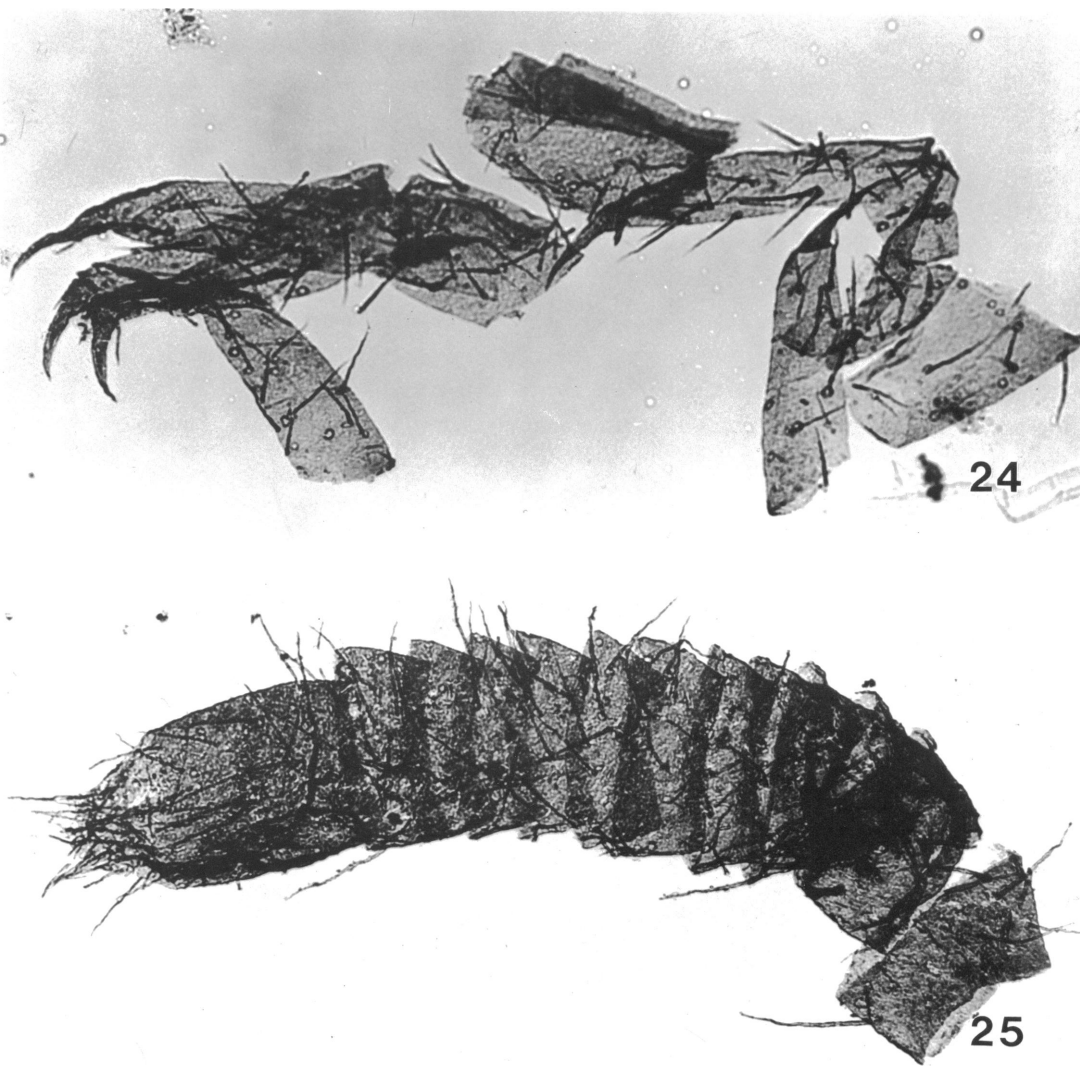
**DESCRIPTION:** Head nearly as wide as long, with transverse frontal suture. Antennal articles more than 14; exact number unknown. Labrum wide, transverse, probably not toothed. Mandibles functional, with dentate processes. Large tentorium present. First maxillary coxosternae fused; palp lobelike. Second maxillary coxosternae fused, shortened in midline; telopodite with long femur, number of telopodite segments unknown, probably three. Maxillipeds with coxosternae completely fused laterally, and with both ventral and dorsal pairs of long apodemes. Mesally, coxosternae bear long toothed processes with 4 or 5 teeth, single enlarged seta (?). Telopodite of maxilliped with 4 segments; trochanteroprefemur with chitin line mesally suggesting fusion of trochanter; femur and tibia complete laterally; tarsus not directly articulated with femuroid, with small me-

sobasal tooth. Nature of poison apparatus unknown.

Number of trunk segments unknown; more than 16. Maxilliped segment with separate tergite. Heterotergy present; at least tergites 9, 11, 13 short tergites, tergites 10, 12, 14, 15 long tergites. Tergites without notches or angular processes, bearing scattered setae. Structure of pleura unknown. Spiracles at least on segments 10, 13. Sterna subquadrate, with anterior lateral angles notched to articulate with leg coxae. Legs moderately long, tarsi undivided, macrosetae lacking. Claw with accessory seta at base. At least some posterior legs enlarged. Coxal organs present. Genitalia unknown.

**NOTES:** Since the new order contains only the fossil species *Devonobius delta*, new species, from the Upper Middle Devonian of New York State, the description given under the species account will serve to provide additional data.

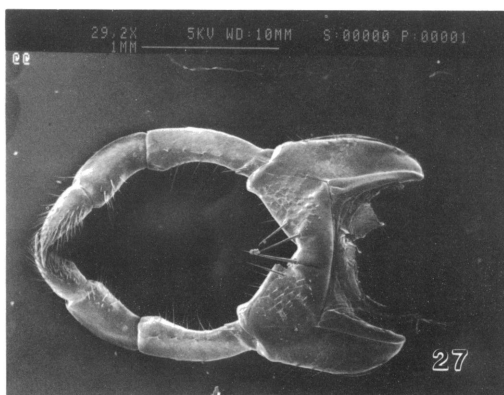
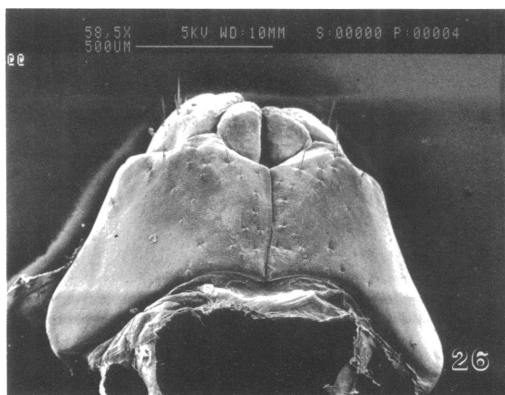
The phylogenetic position of the Devonobiomorpha has already been discussed in the section above.



Figs. 24, 25. *Devonobius delta*. 24. 411-2-AR1. Disarticulated legs. 25. 411-9-AR37. Thirteen antennal segments, including ultimate segment. Size and shape of most proximal segment suggest it is probably not the most proximal segment, and that the antenna has more than 13 segments.

Reluctant at first to establish a new order of centipeds based on a single fossil species (though represented by numerous specimens), we were finally convinced to do so by the studies of centiped morphology and systematics prompted by the requirement to place our material in context. The outstanding preservation of the fossils allows anatomical comparisons with other forms much like those we can make among living centipeds. The comparison of the maxillipeds of *De-*

*vonobius delta* with those of representatives of the other orders (figs. 51–56) provides abundant evidence for its uniqueness. Our cladistic analysis showed that this single species is the sister-group of a taxon encompassing two orders. Precedent exists in the well-accepted treatment of *Craterostigmus tasmanianus* as the sole representative of an order. Therefore, we think we are justified in adding a major taxon at this level to the systematic array.



Figs. 26, 27. *Craterostigma tasmanianus*, scanning electron micrographs. 26. Maxillae 1. 27. Maxillae 2.



Fig. 28. *Devonobius delta*. Maxillipeds, 329-AR4. See figure 30 for scale.

#### FAMILY DEVONOBIIDAE, NEW FAMILY

TYPE GENUS: *Devonobius*, new genus, see below.

DIAGNOSIS AND DESCRIPTION: As for the order Devonobiomorpha.

#### *Devonobius*, new genus

TYPE SPECIES: *Devonobius delta*, new species.

ETYMOLOGY: From the name of the geological period, Devonian, with *-bius*, a combining stem in common use in centiped taxonomy; hence "living in the Devonian." Gender, male.

DIAGNOSIS: As for the order Devonobiomorpha.

DESCRIPTION: As for the type species, see below.

#### *Devonobius delta*, new species

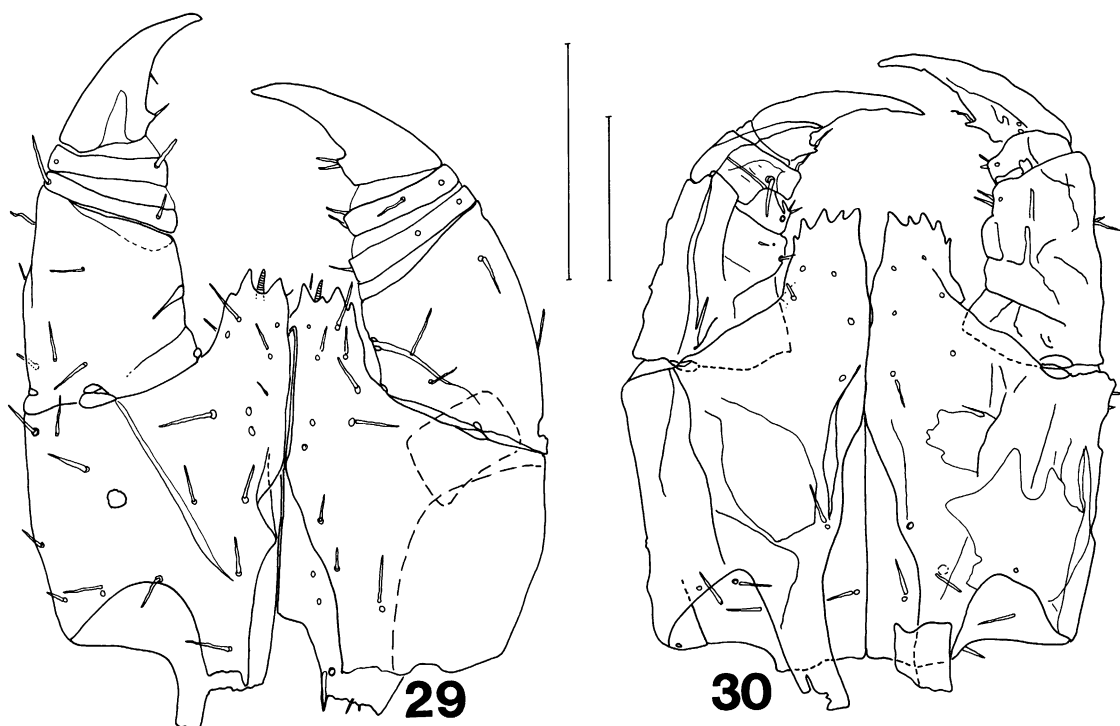
Figures 1–75

TYPES: Holotype specimen slide 411-15-AR18, complete head with 15 or 16 trunk segments; paratypes: slide 41-7-AR97, head with 11 antennal segments, maxillipeds; slide 329-AR4, maxillipeds; slide 411-2-AR1, telescoped, folded, and compressed exuvium including posterior legs. Other material listed in table 3. All material deposited in AMNH, except 2002-12-AR74, deposited in Department of Paleobiology, Smithsonian Institution.

ETYMOLOGY: The specific name, *delta*, a noun in apposition, refers to the Catskill Delta of Devonian time, habitat of the species.

DIAGNOSIS: As for the order Devonobiomorpha.

DESCRIPTION: Head (figs. 7–21) ovoid, slightly longer than wide. Eyes and Tömös-



Figs. 29, 30. *Devonobius delta*, maxillipeds, drawn as dorsal views. 29. 411-7-AR97. See also figure 15. 30. 329-AR4. See also figure 28. Scale line = 0.3 mm.

váry organ absent. Transverse frontal suture (ds, fig. 16) present in anterior third, procurved. Probable dorsal setal pattern as shown in figures 16 and 47. Ventral surface (fig. 17; restored in fig. 46) with sclerotized bridge (sb, figs. 17, 46) between antennal bases; clypeus (c, figs. 17, 46) broad, with long lateral arms extending posteriorly; labrum (la, fig. 46) arcuate, teeth not detected, midpiece not distinct; fulcrum or coclypeus not detected; head pleurite (hp, figs. 17, 46) evidently as anterior and middle piece, middle piece may include posterior section.

Maxilliped tergite present (MT, figs. 10, 47).

Trunk (figs. 2-6, 57) of more than 16 leg-bearing segments, showing heterotergy, tergites 9, 11, 13 short tergites. Tergites oval-polygonal in outline, posterolateral angles not produced. Sternites obscure, probably nearly quadrangular (S12, fig. 6). Protergites and prosternites not detected. Spiracles (s, figs. 5, 6) present on at least segments 10 and 13.

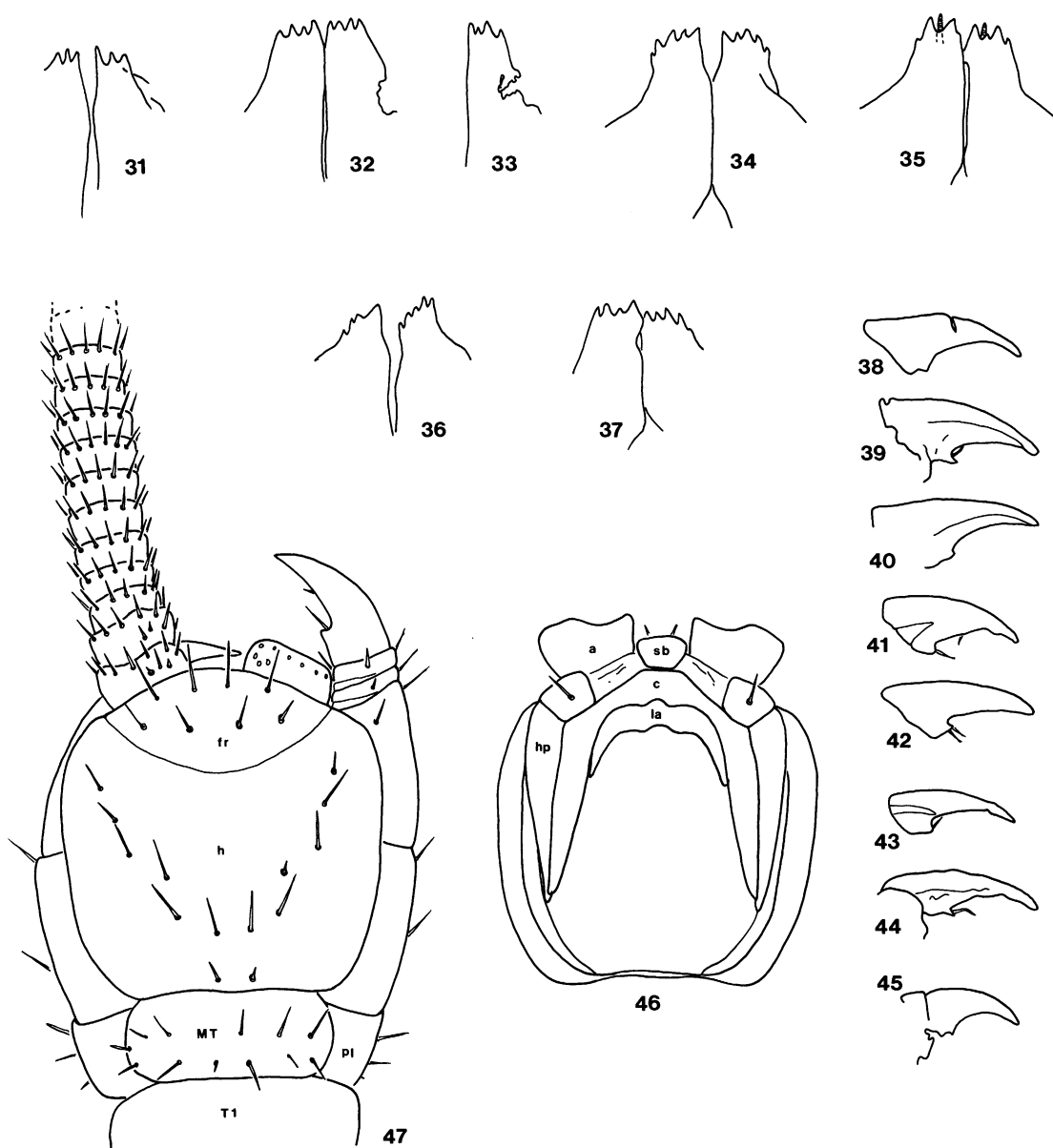
Form and nature of anal and genital segments not known.

Antennae (figs. 14, 15, 25) of undetermined length, composed of more than 13 annuli; antennal annuli much wider than long, with about 10 apical setae in distal ring. Apical antennal annulus (fig. 26) longer than wide, abruptly tapered, distally heavily setose.

Mandibles (m, figs. 9, 13, 18) evidently typical, moderately reduced, with about 5 dentate lamellae; pectinate lamellae not observed. Tentorium partially preserved in one specimen (tn, fig. 18).

First maxillae (mx1, mp1, fig. 18) with coxosterna probably fused; palpus as small, single-segmented lobe. Second maxillae with fused coxosterna (mx2, figs. 9, 18); long palpus of more than two segments (mp2, figs. 11, 13; fig. 23).

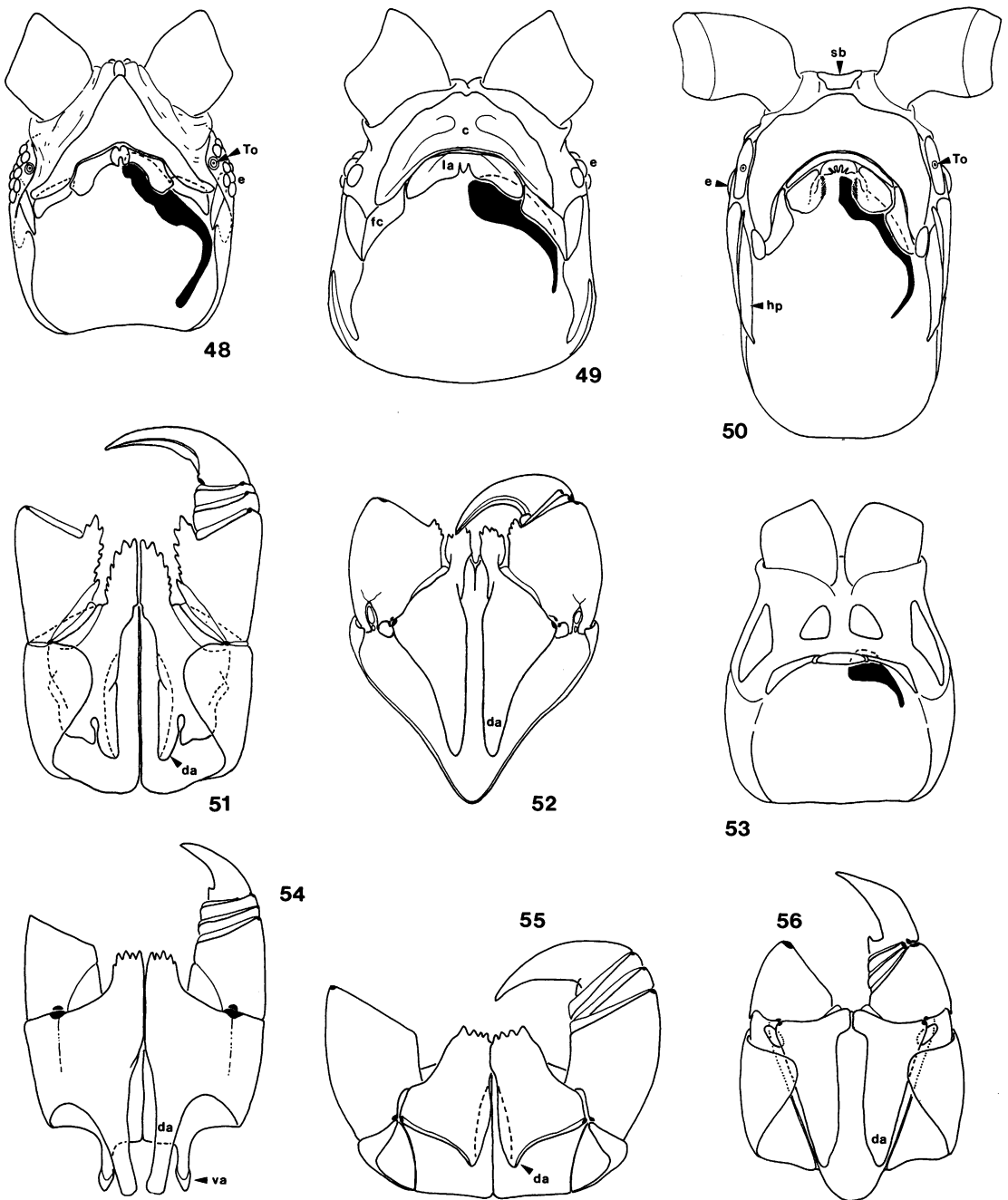
Maxillipeds [figs. 15, 18, 22, 29-47, 54 (restoration)] robust; coxosterna fused in midline with persisting suture, movement probably impossible or very limited; coxo-



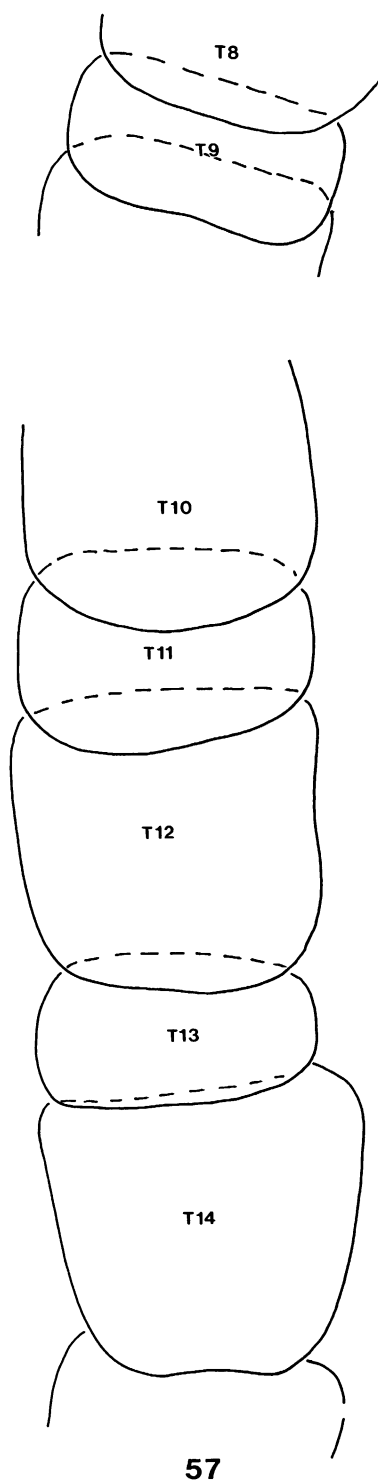
Figs. 31-47. *Devonobius delta*. 31-37. Toothed processes of maxilliped coxosterna, drawn to same scale. 31. 334-16M-2. 32. 411-7-AR56. 33. 411-2-AR1. 34. 329-AR4. 35. 411-7-AR97. 36. 411-15-AR18. 37. 411-7-AR81. 38-45. Tarsi of maxilliped telopodites (poison claws), drawn to same scale. 38. 334-16M-2, left side. 39. 411-7-AR56, left side. 40. 411-7-AR56, right side, drawn reversed. 41. 411-7-AR97, left side. 42. 411-7-AR97, right side, drawn reversed. 43. 329-AR4, left side. 44. 329-AR4, right side, drawn reversed. 45. 411-15-AR18, left side. 46. Restoration of ventral side of head. 47. Restoration of dorsal side of head, maxillipeds, and proximal antennal segments. See table 4 for abbreviations.

pleural suture also complete. Dorsal apodemes (da, figs. 10, 18, 54; figs. 29, 30), relatively broader, shorter than ventral

apodemes (va, figs. 22, 54). Toothed anterior processes long, evidently variable (see figs. 31-37), with 3-5 teeth on each side, in one



Figs. 48–56. Comparisons of heads and maxillipeds of five orders of centipeds, not drawn to same scale. Specimens prepared by digestion in trypsin. Outlines of mandibles shaded. 48. Head of *Lithobius* sp. (Lithobiomorpha), ventral view. 49. Head of *Hemiscolopendra punctiventris* (Scolopendromorpha), ventral view. 50. Head of *Craterostigma tasmanianus* (Craterostigmomorpha), ventral view. 51. Maxillipeds of *C. tasmanianus*, dorsal view. 52. Maxillipeds of *H. punctiventris*, dorsal view. 53. Head of *Strigamia* sp. (Geophilomorpha), ventral view. 54. Restoration of maxillipeds of *Devonobius delta* (Devonobiomorpha), dorsal view. 55. Maxillipeds of *Lithobius* sp., dorsal view. 56. Maxillipeds of *Strigamia* sp., dorsal view. See table 4 for abbreviations.



57

Fig. 57. Reconstruction of tergites of *Devonobius delta*, based on specimen 411-15-AR18. See also figures 2-6. See table 4 for abbreviations.

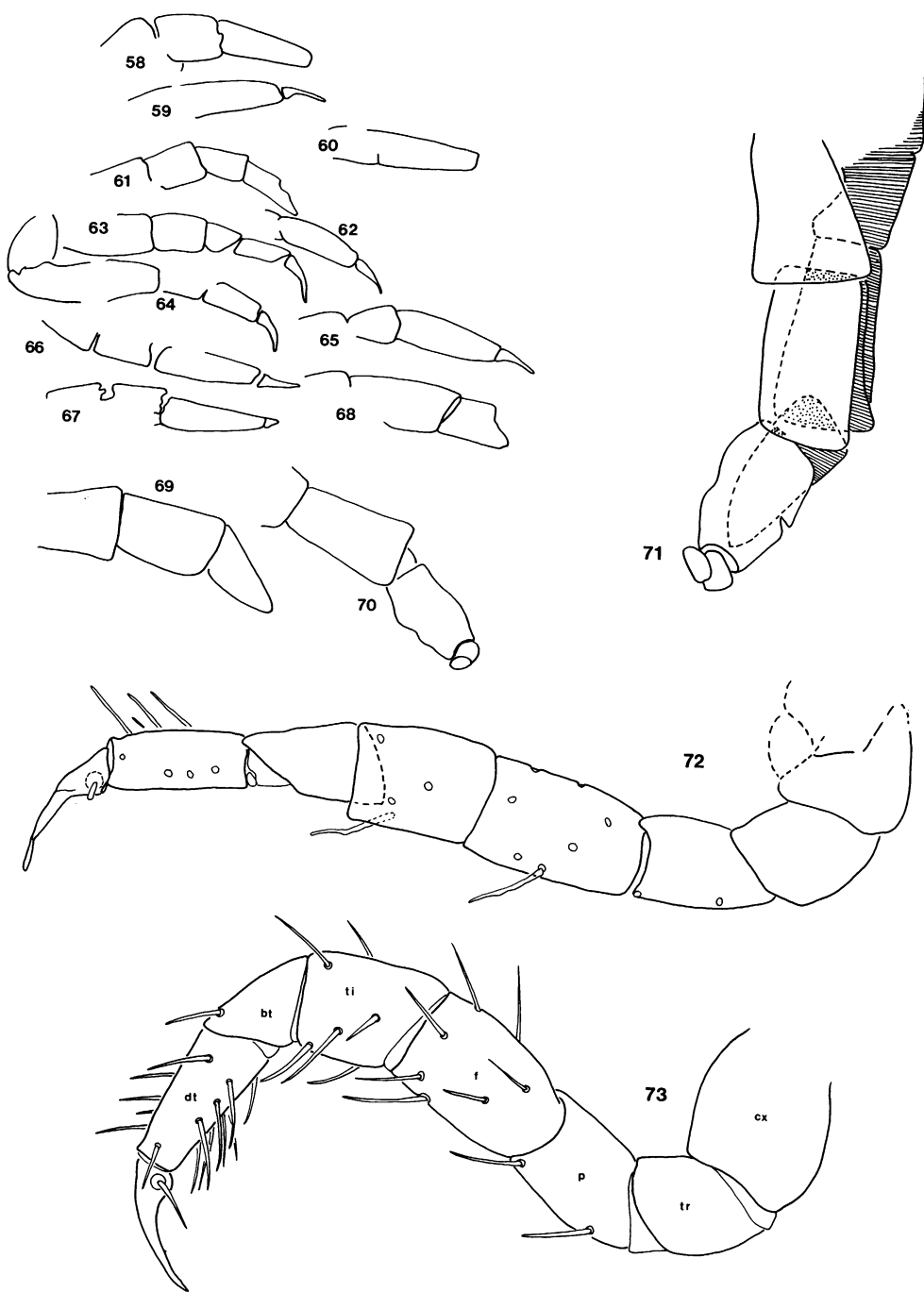
case (fig. 29) with single macroseta. Trochanteroprefemur robust, about 2 to 3 times as long as broad at lateral margin, with persisting trochanteral suture (fig. 29). Femur and tibia articulating laterally, complete, ringlike. Fused tarsus and claw with basal inner tooth (figs. 29, 30, 38-45); poison duct and apparatus not detected, probably not preserved.

Legs (figs. 58-73) relatively long, consisting of coxa, trochanter, prefemur, femur, patelotibia, basitarsus, distitarsus, and posttarsus (claw), relative lengths of segments as shown in figures 72 and 73. Legs without regular pattern of setation, more heavily setose distally. Claw single, large, one-half to one-fourth length of distitarsus, with single anterolateral macroseta articulating in large basal socket. Number of legpairs unknown, probably more than 16. Posterior legpairs (ultimate? penultimate?) enlarged, robust (figs. 69-71, 74), coxae with at least one coxal gland pore (cg, fig. 75).

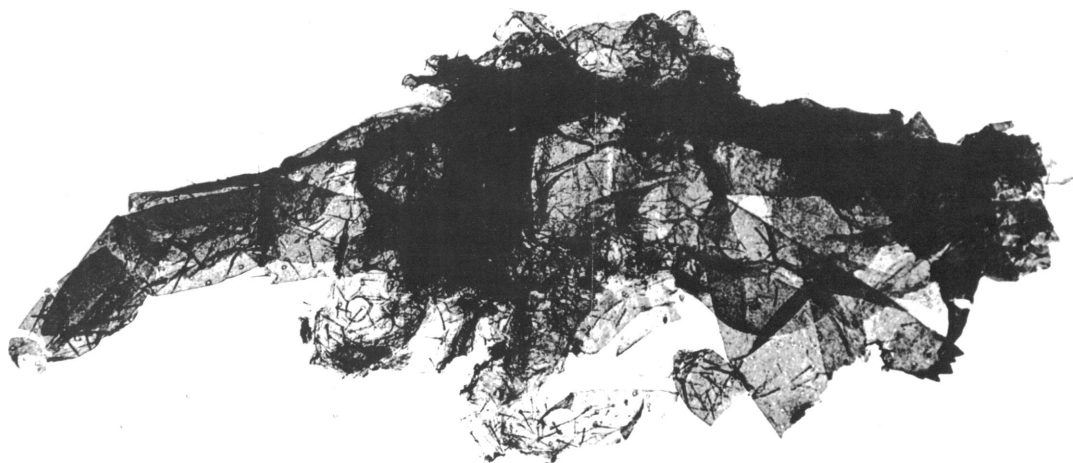
NOTES: As the description is a composite, dimensions are not given except in general, relative terms. The absolute sizes of specimens and individual structures can be estimated from the scale lines accompanying the interpretive drawings. We estimate the largest individuals of which we have a major part to be more than 10 mm in total length, and less than 1 mm in width. In keeping with some conventional usages in centiped systematics, we have considered the first leg-bearing segment (behind the maxilliped tergite) as covered by tergite 1; this maintains a constancy of numbering between the tergites and sternites and the legs (actually the maxilliped tergite, where present, is the first tergite). As far as we can tell, each tergite is associated with a single leg pair and none of the long tergites is divided.

The question naturally arises as to the presence of a single species in our samples. Although size variation exists (see scale lines on various figures), the forms of the poison claws (figs. 38-45) and toothed processes of the maxilliped coxosternae (figs. 31-37) seem to fall within the range of permitted variation. We have no evidence that more than one species of devonobiomorph centiped is to be found among our material, and consider the presence of a single species as our null hypothesis.





Figs. 58–73. Legs of *Devonobius delta*. 58–68. Various legs of specimen 411-15-AR18. 58. Leg 1. 59. Leg 2. 60. Leg 3. 61. Leg 10. 62. Leg 11. 63. Leg 11. 64. Leg 12. 65. Leg 13. 66. Leg 14. 68. Leg 15? 67. Leg 14. 69, 70. Ultimate or penultimate legs of specimen 411-2-AR1. 71. The same, drawn directly from the fossil; leg of one side shaded to aid in separation. See also figures 74 and 75. 72. Reconstruction of midbody leg, based on legs 11 and 12 of 411-15-AR18. 73. Restoration of same, with data from other legs of the same and other specimens.



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Fig. 74. *Devonobius delta*, photomosaic of specimen 411-1-AR1. This specimen is an entire telescoped exuvium. See figure 75 for scale.



Fig. 75. *Devonobius delta*, interpretive drawing of 411-1-AR1. Abbreviations as in table 4. Scale line = 0.3 mm.

Without information on the genital and anal somites we are unable to sex our specimens. However, we have noted that the maxillipeds of specimen 411-7-AR97 (fig. 29) differ in proportion from other well-preserved examples (fig. 30). It is possible that this is an expression of sexual dimorphism, but if it is, we have no way of telling which sex is which. In a lithobiomorph, *Paitobius zinus*, the male

maxillipeds are very much more robust (Cra-  
bill, 1960), so perhaps 411-7-AR97 is a male.

As regards the maxillipeds, the best preserved parts of our specimens, we again draw attention to their structure on two points. The first is the presence of unique ventral apodemes. Figure 22 clearly shows that of the two pairs of apodemes the thinner ones are ventral. These apodemes are unknown in any

other centipeds, as can be seen by a comparison of figure 54 with figures 51, 52, 55, and 56 (because of a mass of other distinctions, scutigeromorphs were omitted from the comparisons). In lithobiomorphs (fig. 55), even the dorsal apodemes are poorly developed. In the other orders (figs. 51, 52, and 56) they are large and nearly completely separated; and in the highly specialized *Craterostigmus* they are complex (fig. 51). The muscles inserting on these dorsal apodemes would obviously adduct the entire maxilliped complex. The ventral apodemes unique to *Devonobius* could be an apparatus by which the maxillipeds could be pulled down and away from the head, possibly to allow the other mouthparts contact with large food items, or to allow for attacks on larger prey. In this respect, the extended but fused posterior ventral maxilliped margins of scolopendromorphs and geophilomorphs, which routinely attack prey items that are large in comparison to their heads, may be a related development, but the complete fusion of the maxilliped coxosternae had evidently taken place first, so that separate apodemes were neither possible nor necessary. Curiously, in all specimens of heads-with-maxillipeds which we have studied (i.e., figs. 9, 10), the dorsal apodemes are folded anteriorly. We do not think that this could have been their position in life, but cannot explain the folding. When maxillipeds are found separated from heads the dorsal apodemes are not folded (figs. 29, 30).

The second distinction is that in devonobiomorphs the coxosterna of the maxillipeds are virtually fused into a ring, rather than there being a distinct gap at the trochanteral condyle. This is clearly apomorphic by comparison with scutigeromorphs and lithobiomorphs. We have no speculations to offer on the functional meaning of this structure.

The other mouthparts, while frequently represented in our material, are difficult to interpret, because they have remained buried in the head capsule, and as they overlie one another, details are obscure (see fig. 18). We are, however, confident in interpreting the coxosterna of the first and second maxillipeds as fused. For comparison we provide SEM photographs of the first (fig. 26) and second (fig. 27) maxillae of *Craterostigmus tasmanianus*; at least the first maxillae, as far as

TABLE 4  
List of Abbreviations

Abbreviation	Meaning
a	antenna
bt	basitarsus
c	clypeus
cg	pore of coxal gland
cx	coxa
dt	distitarsus
da	dorsal apodeme
ds	dorsal head suture
e	eye
f	femur
fr	frons
fc	fulcrum (coclypeus)
h	head capsule
hp	head pleurite
la	labrum
m	mandible
mx1	maxilla 1 coxosternite
mpl	maxilla 1 palpus
mx2	maxilla 2 coxosternite
mp2	maxilla 2 palpus
mx	maxilliped coxosternite
MT	maxilliped tergite
numerals	legs as numbered
p	prefemur
pl	maxilliped pleurite
s	spiracle
sb	sclerotized bridge between antennae
S	sternites as numbered
t	tarsus
tn	tentorium
T	tergites as numbered
ti	tibia
To	Tömösváry organ
tr	trochanter
tp	trochanteroprefemur
va	ventral apodeme

they can be made out (fig. 18) seems to be quite similar in *Devonobius*. The mandibles, heavily sclerotized, are often preserved when the more delicate maxillae have disappeared; they are present in nearly every reasonably complete head. The tendency for the mandibles to be reduced in the more apomorphic orders (figs. 48–50, 53) is reflected in *Devonobius*; the mandibles are about the same proportionally as in *Craterostigmus*. Centiped mandibles are complex, and we have been able to work out only a small amount of the structure from the fossils. The dentate lamellae, again heavily sclerotized, have been

well preserved, but the pectinate lamellae (undoubtedly present) and possible molar surfaces have not survived fossilization in any specimens.

In resolving the ventral surface of the head capsule we were guided by a single, somewhat distorted specimen (411-7-AR97; figs. 14, 15, 17, 46). We are not very confident in the restoration in figure 46, especially as regards the disposition of sclerites, the absence of labral teeth, and the apparent absence of clypeal setation. In addition to the folding, tearing, and distortion of the specimen, obstacles were presented by the overlying maxillipeds and the evidently extreme compression, making dorsal and ventral surfaces very difficult to separate. We are, however, reasonably sure that there are no ocelli and no Tömösváry organs; the apparent circular structure in the photograph (fig. 15) is revealed under high magnification as a misleading artifact resulting from complicated folding of the head pleurite and head capsule margin.

Specimen 411-7-AR97 preserves the basal parts (11 annuli) of the antennae in organic connection with the head (figs. 14, 15), and 411-9-AR37 is a separated distal part. The latter has 13 (or possibly 14) annuli, so we know that the complete antennae had more annuli than this, but how many more cannot be determined. The increase in size toward the basal part of the detached antenna suggests that the antennae were probably short, resembling those of geophilomorphs.

Determining the number of trunk segments in this species is vexing because our single most complete specimen (fig. 2; 411-15-AR18) evidently lacks part of the posterior end. After much study, we have decided that this specimen has parts of 16 trunk segments and their legs. The posteriormost preserved legs are not much enlarged, if at all, yet specimen 411-1-AR1, a complete but telescoped exuvium (fig. 74), shows us that at least one pair of the more posterior legs are very substantially enlarged. Given other characters which place devonobiomorphs between craterostigmomorphs and the two epimorphic orders, we think that the increase in legpairs to 21 or 23 had already taken place in the stem group. Thus the pronounced heterotergy in *D. delta* is primitive for centipeds

and both the divided long tergites of *Craterostigmus* and the suppressed heterotergy of the scolopendromorphs are separate specializations. Heterotergy is correlated with stable running; its suppression and/or the division of long tergites is correlated with flexibility and moving about in confined spaces.

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