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PROGRESS IN STUDIES ON MYRIAPODA AND ONYCHOPHORA

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***Hexecontasoma*, a new helminthomorph millipede (Hexecontasomatidae n. fam.)  
from the Mazon Creek, Illinois, fauna (Carboniferous, North America)**

**Abstract:** A new helminthomorph millipede from the Mazon Creek fauna of Illinois has conspicuously keeled pleurotergites and about 60 body segments. It tapers anteriorly and has long legs. Midbody paranota are dentate, resembling those of polydesmids. The metazonite is covered by two transverse rows of longitudinal ornamentation separated by a transverse sulcus. The pleurotergal-sternal arch is rimmed, the sternal area is narrow, and coxae of each legpair are located close to each other. Ornamentation and several other features of this millipede resemble those of Callipodida and, especially, Cambalidea. The millipede is a very rare form; few specimens are known. This species represents a new genus and family. Based on its prominent paranota and anterior tapering, it belongs in the wedge ecomorphological group.

**Key words:** Diplopoda, *Hexecontasoma*, fossil, Carboniferous, Cambalidea

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## INTRODUCTION

There are two major millipede faunas of Carboniferous Age: the fauna preserved in the Gaskohle of Nýřany, the Czech Republic (FRITSCH 1899); and the Mazon Creek fauna of Illinois (BURKE 1979, HANNIBAL 1997, SCUDDER 1882, 1890). During the Late Carboniferous both localities were tropical and located on the same land mass (HANNIBAL & FELDMANN 1981, text-fig. 1). The millipede fauna of both localities includes spinous euphoberiids, spinous and nonspinous oniscomorphs, and "julids." Pleurojulids, long known from the Gaskohle, have also recently been identified in the Mazon Creek fauna (HANNIBAL 1996). Also, MUNDEL (1981) has noted the presence of

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a single specimen of a platydesmid in the Mazon Creek fauna. That specimen has yet to be described formally (P. Mundel, personal communication, 1999).

The purpose of this paper is to describe a new species of helminthomorph millipede discovered during a survey of fossils from the Mazon Creek fauna (SHABICA & HAY 1997) housed in the collections of the Field Museum of Natural History (FMNH), Chicago. This rare form shares a number of characters with extant forms, including eugnath millipedes in the Callipodida, Chordeumatida, Polydesmida, and, especially, the Cambalidea.

#### MATERIAL AND METHODS

Few specimens of the new millipede are known. Each specimen is preserved as the sole megafossil in a concretion. The holotype, FMNH PE 23487 (Figs 1–16), is preserved in lateral view as two parts of a natural mold. One side of the concretion contains a mold of the left side (Fig. 1) of the millipede; the other side contains a mold of the right side (Fig. 2). The specimen is partially coiled in a comma-shaped death position, with the anterior loosely coiled and the posterior third outstretched. This position is similar to the partly flexed death position of modern millipedes described by BLOWER (1985: 41). There is a crack running more or less along the midline of the fossil (Figs 3–5).

The paratype, FMNH PE 13656, is poorly preserved and consists of a partial specimen with only about 35 preserved segments. That specimen is, for the most part, a partially preserved natural mold, laid out in a sinuous curve in lateral view. Much of the concretion is missing.

A third specimen, FMNH PE 32265, may also belong to the new species. It consists of a natural mold with about 50 segments. That specimen, however, is incomplete, very poorly preserved, and more flattened and distorted than the other two specimens studied.

About two-thirds of the holotype (that seen in Fig. 2) was exposed by the initial splitting of the concretion. Preparation of the exposed parts consisted of removing calcite and other materials from the natural mold using needles, mostly insect pins, held in a pin vise. Additional preparation was done using an air-abrasive machine to direct a fine spray of baking soda into deeper crevices. When preparation was complete, extremely dilute hydrochloric acid was used to clear away the residue of baking soda. The specimen was then soaked in moving water, and subsequently still water, to make sure that any acid was removed.

The posterior one-third of the specimen (seen on Fig. 1, but not on Fig. 2) was exposed using an impact tool as well as hand-held needles. Preparation ceased near the edge of the concretion as the concretion both thinned and became softer. A dilute solution of the acetone-soluble glue Butvar (polyvinyl butyral) was used to harden the specimen and to fill in a hole in the matrix.



Fig. 1. *Hexecontasoma carinatum* gen. n., sp. n. from the Carbondale Formation, left side, 3.5x. This and subsequent photos are of latex casts of natural molds of FMNH PE 23487.



Fig. 2. *Hexecontasoma carinatum* gen. n., sp. n., less complete, right side of millipede, 3.7x.



Fig. 3. *Hexecontasoma carinatum* gen. n., sp. n., latex cast of anterior of right side showing presumed collum, a subtriangular plate, at anterior, 10x

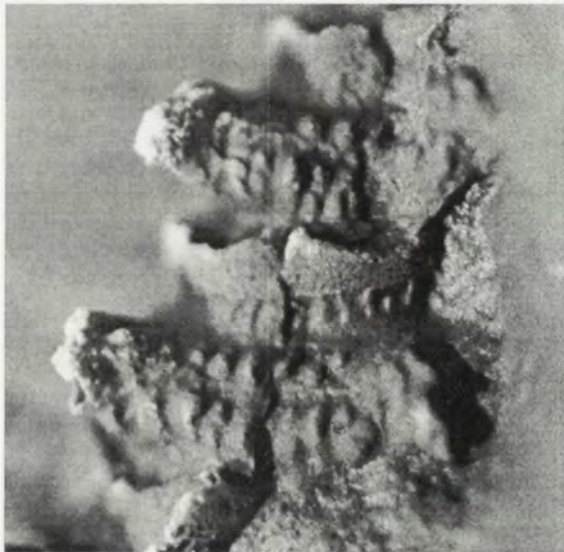


Fig. 4. *Hexecontasoma carinatum* gen. n., sp. n. Dorsal view, showing portions of two anterior segments, an irregular crack (see also Fig. 5) courses through the middle of the segments, 30x

After preparation, both sides of the specimen were cast in latex rubber, using a classic method (PARSLEY 1989) as refined by John Almond (personal communication, 1983). The specimen was first soaked in water. Then, surface water was removed and the specimen rinsed with very dilute dishwater soap. An initial, very dilute layer of latex was applied to the damp specimen. An insect pin was used to advance the front of latex into the natural molds. This procedure was done under a binocular microscope. Several layers of rubber were applied subsequently using a pin for

thinner layers and a brush for thicker layers. The last layers included curtain material to add support. Most photos were taken of latex casts that were whitened using ammonium chloride.

Higher level taxa noted in this paper are used in the sense of HOFFMAN (1979) and ENGHOFF *et al.* (1993).



Fig. 5. *Hexecontasoma carinatum* gen. n., sp. n. Lateral view of segments toward anterior; rough, irregular surface along top of fossil represents plane along which the two sides of the millipede have partially separated along crack, X10.

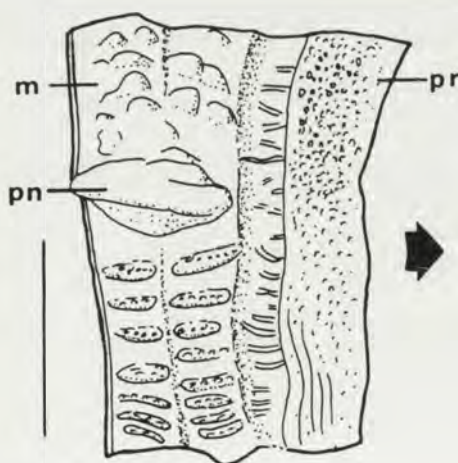


Fig. 6. *Hexecontasoma carinatum* gen. n., sp. n. Camera lucida drawing of a latex cast of single mid-body segment of right side in dorsolateral view. The finely reticulate nature of the prozonite (pr) and the complex ornamentation of the metazonite (m) can be seen. A paranotum (pn) is visible in lateral view. Scale bar equals 1 mm. Arrow points anterior.

## SYSTEMATIC PALEONTOLOGY

## Class Diplopoda BLAINVILLE in GERVAIS, 1844

## Subclass Helminthomorpha POCOCK, 1887

## Order incertae sedis

**Remarks.** *Hexecontasoma* shares a number of characters with several types of extant millipedes. It resembles the colobognath millipedes in the Order Platydesmida in having paranota and many segments. However, the new millipede is not flattened as are platydesmids, the paranota of *Hexecontasoma* are located higher on the metazonites than those of platydesmids, and the longitudinal ornamentation is not like that of platydesmids. *Hexecontasoma* bears a greater number of similarities with eugnath millipedes in the orders Callipodida, Chordeumatida, and Polydesmida, and in the suborder Cambalidea of the order Spirostreptida (Table; see also discussion below).

Table. Chart showing characters of *Hexecontasoma* and four extant orders of millipedes: + = present; - = absent; +/- = present in some species, absent in others; n.a. = not applicable.

Taxa	long body (60 or more segments)	prominent middorsal suture	paranota or paranota-like expansions	paraterga or paranota-like extensions well developed	paranota change with (+/-) fifth segment drastic	longitudinal ridges	longitudinal ridges divided at midlength	pleurotergal-sternal suture	ventral edge of pleurotergal-sternal arch rimmed	coxae close together	coxae contiguous (very close but not touching)	coxal eversible vesicles
<i>Hexecontasoma</i>	+	+(?)	+	+	+	+	+	+	+	+	+(?)	- (?)
Callipodida	+	+	-	n.a.	n.a.	+	-	n.a.	-	+	+	+
Cambalidea (suborder of Spirostreptida)	+	-*	+	-	-**	+	+/-	+/-	+/-	+	+	-
Chordeumatida	-	+	+/-	+/-	-	+/-	-	n.a.	-	+	+	+***
Polydesmida	-	-	+	+/-	-	-	n.a.	-	-	+/-	-	-

\* At least some cambaloids have a midline, but it is subtle, not prominent as in callipodidans and chordeumatidans.

\*\* The paranota-like expansions of cambaloids may show a difference between the 4<sup>th</sup> and 5<sup>th</sup> segment, but the change is not drastic as in *Hexecontasoma*.

\*\*\* On one or two leg pairs of males only.

The ring structure (as interpreted here; see discussion below) and the metazonite ornamentation of *Hexecontasoma* most closely resemble that of cambaloids. In fact, in some respects it is similar to the fossil cambaloid *Protosilvestria* HANDSCHIN, 1944. However, it differs from the cambaloids in at least two certain characters and in one character that is probable, but uncertain. Incomplete information, or lack of information, about the head, collum, sternal details, gonopods, ozopores, and terminal segment, make precise higher-level placement difficult.

#### Hexecontasomatidae new family

**Type genus.** *Hexecontasoma* new genus.

**Diagnosis.** As for the genus.

#### *Hexecontasoma* new genus

**Type species.** *Hexecontasoma carinatum* new species, by original designation and monotypy.

**Diagnosis.** Moderately large millipedes with about 60 body segments and prominent paranota, beginning abruptly on (?)fifth segment. Metazonites covered by two transverse rows of longitudinal ornamentation. Dorsal midline sulcus or suture probably present. Coxae of each leg pair located close to each other. Posterior portion of pleurotergal-sternal arch distinct, with prominent rim.

**Etymology.** The name combines the Greek terms for the number sixty (*hexekonta*) and body (*soma*, n.), to form the word "sixty-body." This is in reference to the body of the millipede having approximately 60 diplosegments.

#### *Hexecontasoma carinatum* new species (Figs 1–16, 18)

**Diagnosis.** As for genus.

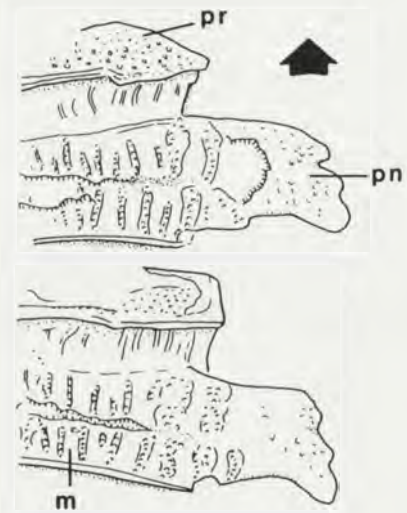
**Description.** Elongate millipede, tapering anteriorly. Outstretched length of holotype about 8.4 cm; maximum height, excluding legs, about 1.5 mm. About 60 body segments. Presumed collum (segment 1; Fig. 3) subtriangular in lateral view. Prozonites very finely reticulate and marked posteroventrally with transverse striae (Figs 5 & 6). Constricted area between prozonite and metazonite marked by fine, sublongitudinal, and frequently downwardly concave, curved ornamentation. Metazonite covered by two transverse rows of longitudinal ornamentation separated by a transverse, medial sulcus (Figs 5 & 6). Areas below paranota, and in center of dorsum, ornamented by rows of elevated longitudinal ridges. Crest of longitudinal ridges beaded with fine tubercles (up to about 12 tubercles per ridge). Lateralmost portions of dorsal side of metazonite tuberculate, with tubercles irregularly and longitudinally arranged. Paranota on (?)fifth to last exposed segment. Paranota broad; midbody paranota with three major teeth (Figs 7–9). Anteriormost tooth less wide, followed by prominent sulcus; following two teeth wider, separated from each other by small sulcus. Anterior edge of paranota ornamented with small, subtle tubercles. Dorsum of midbody paranota tuberculate (Fig. 7); ventral surface very subtly tuberculate (Fig. 8). Posteriormost paranota less complex (Figs 10 & 11). No evidence of setae on pleurotergite. Posterior of pleurotergal-sternal arch convex ventrad. Posterior of pleurotergal-sternal suture prominent, with rimmed margin (Figs 12–14).



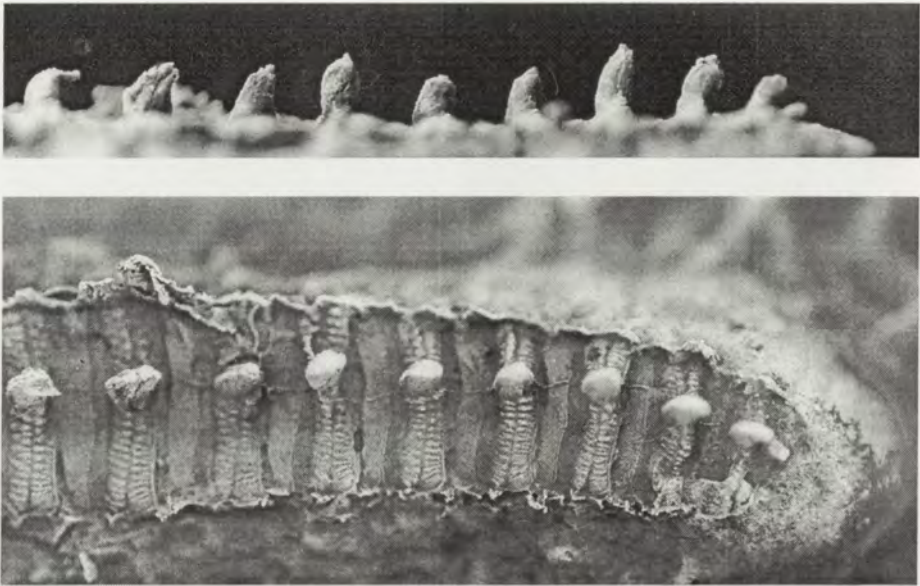
Sternites narrow. Legs closely spaced laterally, long (as in polydesmids), composed of (?)seven segments (Figs 3 & 15). Coxa (Fig. 16) relatively gracile, short to medium in length. Following segment longer, next six segments generally decreasing in length distally.



Fig. 7. *Hexecontasoma carinatum* gen. n., sp. n., paranota of mid-area of right side seen in dorsal view, 10x.



Figs 8–9. *Hexecontasoma carinatum* gen. n., sp. n., left side: 8 (left) – two pleurotergites located towards the anterior; ventral side of paranota and the area beneath paranota are seen. 9 (right) – drawing of these two pleurotergites, showing prozonites (pr), paranota (pn) and metazonites (m). Hachure lines extend from higher to lower planes along cracks and broken areas. Arrow points anteriorly, 25x.



Figs 10–11. *Hexecontasoma carinatum* gen. n., sp. n. **10** (above) – ventral view of paranota of posteriormost segments (the seemingly short paranota in the center of the photo are foreshortened due to problems in producing the latex mold; the simpler, less toothed nature of the posteriormost paranota is real, however, as is the smaller size of the last two paranota); this photo is coordinated with **11** (below) – lateral view of posterior, 10x.

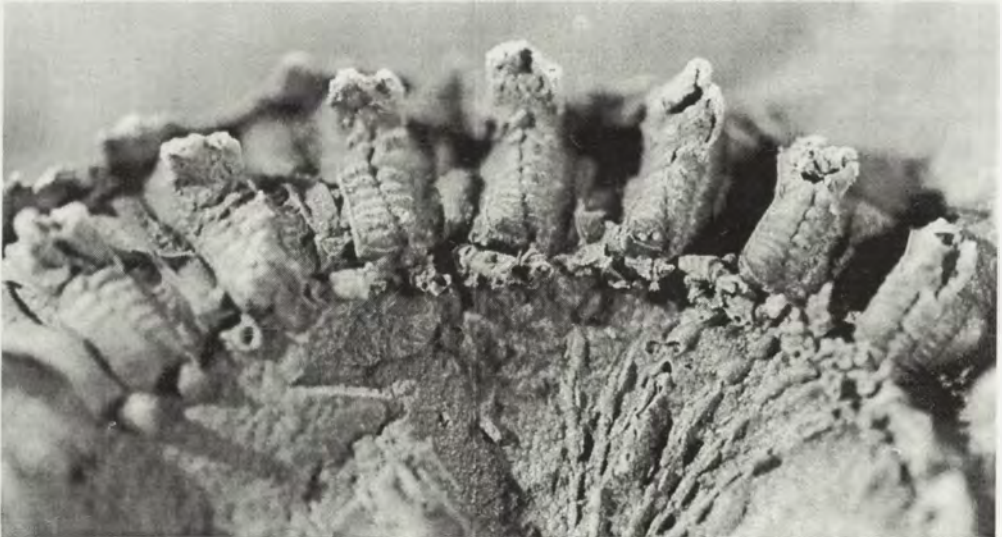


Fig. 12. *Hexecontasoma carinatum* gen. n., sp. n. View of midbody segments showing ventrolateral portions of pleurotergites, parts of sterna, and basal leg segments, 15x.



Fig. 13. *Hexecontasoma carinatum* gen. n., sp. n. View of midbody segments showing ventrolateral portions of pleurotergites, parts of sterna, and basal leg sements, 10x (Unwhitened). Note the rimmed margin of the pleurotergal-sternal suture.

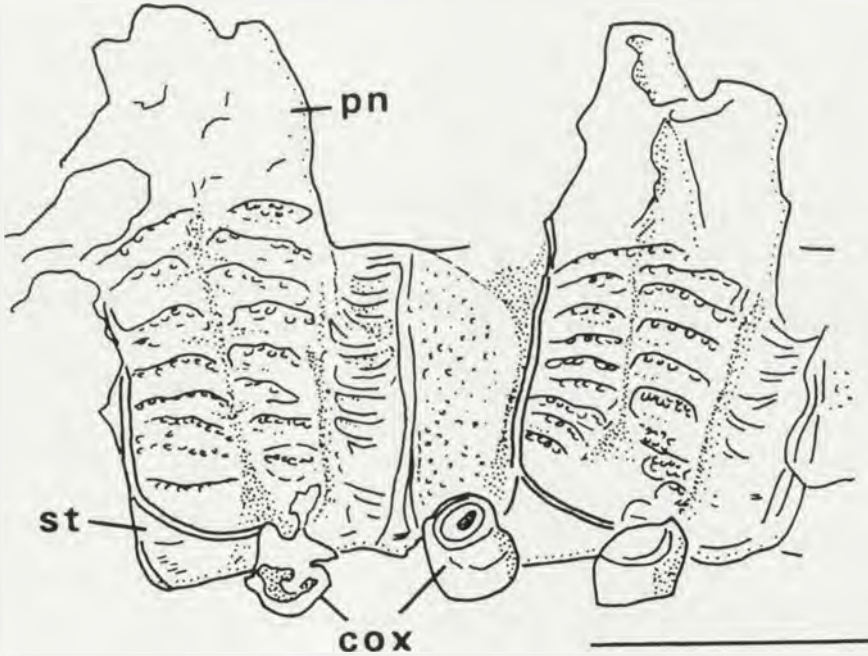
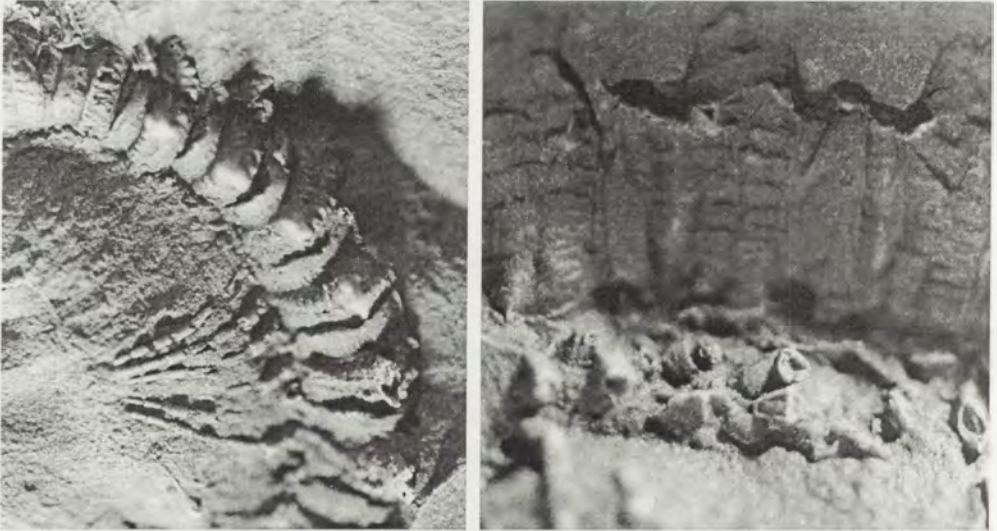


Fig. 14. *Hexecontasoma carinatum* gen. n., sp. n. Carmera lucida drawing of two segments showing ventral side of paranota (pn), exposed parts of sterna (st), and coxa (cox). Scale bar = 1 mm.



Figs 15–16. *Hexecontasoma carinatum* gen. n., sp. n. **15** (left) – view of legs near anterior, showing leg segmentation and breakage; 10x. **16** (right) – view of basal leg segments toward anterior, showing close placement of the coxa, 20x.

**Etymology.** The specific name consists of an adjective derived from the Latin term for keel (*carina*), in reference to the prominent paranota and to the longitudinal ridges on the pleurotergite.

**Material.** Two specimens from the Field Museum of Natural History. Both are from the Francis Creek Shale Member of the Carbondale Formation. The holotype, FMNH PE 23487, was found at Pit 11 of the Peabody Coal Company, in Will County, Illinois, and the paratype, FMNH PE 13656, was found at SE 1/4, SE 1/4, sec. 6, T 31 N, R 9 E, Kankakee County, Illinois (also a Pit 11 locality; see U.S. Geological Survey Essex, Illinois 7.5-minute-quadrangle topographic map). Thus, both specimens are from the marine facies of the Mazonian Delta complex (see BAIRD *et al.* 1985, BAIRD 1997). Millipedes form a very small part of the fauna of this facies (see BAIRD & ANDERSON 1997), but intense collecting has yielded a number of important specimens (see also HANNIBAL & FELDMANN 1981). A third specimen, FMNH PE 32265, which may be referable to this species, was found in Pits 1 or 6 of the Peabody Coal Co. in Will or Grundy County, Illinois. This locality is in the freshwater facies of the Mazonian Delta complex.

**Discussion.** *Hexecontasoma carinatum* has a segment number that is in the range of the callipodidans and cambaloids, with which it shares other features.

Unfortunately, the head and antennae of the new millipede are either not present or are very poorly preserved. The subtriangular plate at the anterior of the left side of the millipede (Fig. 3) probably represents a part of the collum (and here is considered the first segment). It is possible that other anterior elements are preserved on the right side of the millipede.

The holotype is irregularly split along mid-dorsum (Figs 4 & 5). For at least part of the length, the two sides are also slightly offset. Although it is possible that the specimen simply cracked along the dorsum due to the weight of overlying sediment, the mid-dorsum splitting probably indicates that there was a preexisting line of weakness, perhaps a middorsal suture. It might even indicate that the animal had begun to molt before death. The poor preservation of the anteriormost region is additional evidence for molting. The specimen probably does not, however, just represent a molt. A molt would be less likely to be preserved. Millipede molts are usually very thin and are consumed by newly molted millipedes. Also, the C-shape of the specimen is indicative of a carcass, as is the presence of legs. More likely, the specimen represents a molting specimen or a partly crushed carcass. Several of the metazonites of the specimen are also cracked along the transverse sulcus between the two rows of ridged ornamentation (Figs 8 & 9), probably due to the sulcus being a relatively weak zone.

*Hexecontasoma carinatum* has conspicuously keeled diplotergites (Figs 3, 7–10). Because of the difficulty of getting good latex casts of small, deep features, it is difficult to determine the details of all of the paranota of *Hexecontasoma*. The true outline of the paranota can best be seen on paranota preserved along the plane of breakage of the concretion (Fig. 8). I could not detect any certain ozopores on the paranota, but that does not necessarily mean that they were not present. The abrupt appearance of paranota at about the fifth segment of *H. carinatum* is significant as that is the segment on which ozopores appear in some millipedes (ENGHOFF *et al.* 1993, fig. 4). In most of the polydesmidans, ozopores start on the paranota of somite five. This hints at the presence of ozopores in *Hexecontasoma*. The millipede seems to more closely resemble polydesmidans in configuration of the paranota. However, the paranota of *H. carinatum* begin abruptly on the (?) fifth segment, while the paranota of polydesmidans are usually already large on the second segment (the first segment past the collum).

The ridged ornamentation of the tergites of *Hexecontasoma* is like that of callipodidans, for instance that of *Apfelbeckia* VERHOEFF, 1896, cambaloids, and the nemasomatid julidan *Chelojulus* ENGHOFF, 1982 (*cf.* ENGHOFF 1982). Some previously described fossil millipedes also have ridged ornamentation. The metazonites of "*Xyloiulus*" *moniliformis* (WOODWARD, 1905), from the lower Coal Measures of Lancashire, are marked by a single transverse row of ridged ornamentation (WOODWARD 1905). The ridges of that specimen are unlike those of true *Xyloiulus*, however. Woodward's specimen is cambaloid-like in some respects. The question of the presence of cambaloids in the Carboniferous is equivocal (see COOK 1895: 6, HOFFMAN 1969: R595, MAURIÈS 1992: 30), hinging on the identity of very poorly known specimens having longitudinal ornamentation.

While most cambaloids have undivided longitudinal ridges, the cambaloid *Protosilvestria* HANDSCHIN, 1944 (see MAURIÈS 1992), from the Oligocene of Quercy, France has double rows of ridges. The longitudinal ridges of callipodidans are not so divided.

Almost, but not quite all, of the posterior of the holotype of the millipede is preserved. Unfortunately the terminal segment is not seen. I did not think that it

would be possible to safely prepare the terminal segment. In addition the preservation at the very end of the specimen was poor and it was getting to be difficult to tell specimen from matrix.

Sternites (Figs 12–14) are relatively narrow and may have most closely resembled those of the Cambalidea (see below).

Legs (Figs 15 & 16) appear to arise mid ventrally. The coxae of leg pairs are located close to each other, and may have been closely contiguous, although they would not have touched each other. This feature easily distinguishes the new species from most of the Polydesmida (Figs 18 & 21). No coxal eversible vesicles have been located. The legs of the millipede are long, and seem to be composed of seven segments, the usual number. But, as in most fossil millipedes, the legs are broken in various ways and, thus, adjacent legs have what appear to be different segment lengths. The leg segments seem, however, to be of subequal size like those of juliform millipedes.

I have not been able to locate any gonopods.

#### RING STRUCTURE

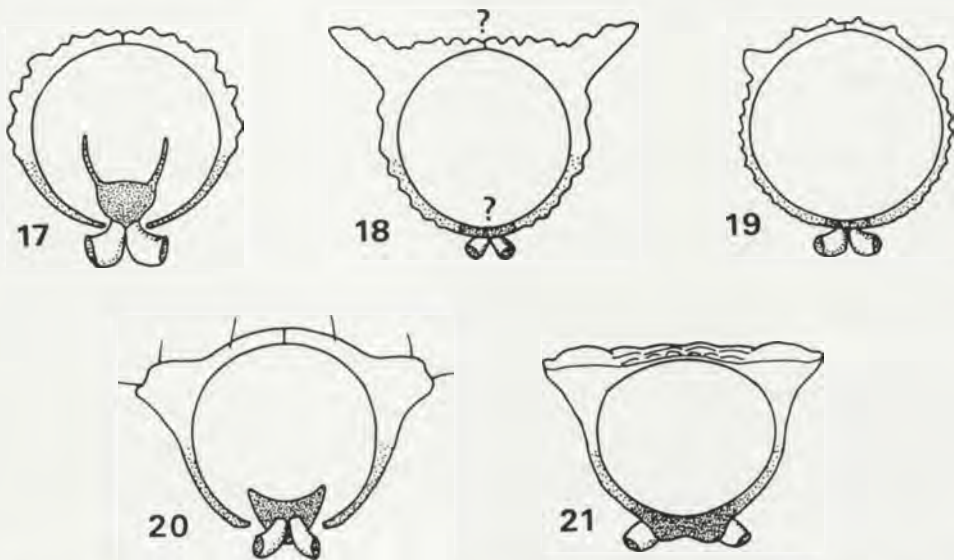
Much of the ring structure of *Hexecontasoma* can be determined, but the exact configuration of the circular or oval nature of the ring cannot be discerned, nor can the medial part of the sternal area be reconstructed with great confidence. However, the structure is more or less as indicated in Fig. 18. If the species was flattened it would be more likely to be preserved in dorsal or ventral view than in side view. In addition, portions of the holotype are rounded. In my interpretation, the ring structure of *Hexecontasoma* would properly be termed a ring *sensu* ENGHOFF *et al.* (1993). The ring structure of *Hexecontasoma* is somewhat similar in some ways to those of callipodidans, cambaloids, chordeumatidans, and polydesmidans (Figs 17–21). *Hexecontasoma* appears to lack spines, such as those found on the pleurotergites of chordeumatidans. The top of the pleurotergites of *Hexecontasoma* may have a prominent dorsal suture (see Discussion, above) as in callipodidans and chordeumatidans. The upper portions of the ring structure resemble that of polydesmidans, while what is known of the sternal region of *Hexecontasoma* seems to resemble that of cambaloids. The legs of *Hexecontasoma* are more closely spaced than those of most polydesmidans. All things considered, the ring architecture of *Hexecontasoma* is closest to that of the Cambalidea (Table).

#### PALEOECOMORPHOLOGY

Based on its prominent, high paranota, and anterior tapering, *Hexecontasoma* belongs to the wedge ecomorphological group. MANTON (1954: 343) has noted that long legs and projecting keels prevent burrowing into compact soil. Also, anterior tapering facilitates wedge pushing (for an extended discussion of morphology that is related to wedge pushing see MANTON (1954, 1961, 1977: 356–364). *Hexecontasoma* is not short, however, as are typical wedge-type millipedes in the sense of HOPKIN &

READ (1992: 38). Instead, the new millipede is longer, as are platydesmidans, a form which MANTON (1961: 394–395) considered to be a wedge pusher.

The more common forms of diplopods, including the euphoberiids and spinose oniscomorphs, found at Mazon Creek and Nýřany have been interpreted as living in more open habitats, leading to a greater likelihood of being swept into a body of water and thus being preserved as fossils (KRAUS 1974: 20, HANNIBAL & FELDMANN 1981: 744, SHEAR & KUKALOVÁ-PECK 1990: 1815). The rarity of *Hexecontasoma* may be related to its presumed habitat, within, rather than above, the leaf litter of the swampy deltaic environment. A layer of leaves would have helped to prevent the millipede from being washed into streams during normal storms. Of course, larger storms could wash away leaf layers, millipedes and all, and transport material far from shore into the marine areas of the delta complex, including the area now known as Pit 11.



Figs 17–21. Inferred ring structure of *Hexecontasoma carinatum* gen. n., sp. n. compared with that of four extant forms. 17 – *Abacion magnum* (LOOMIS) (Callipodida), 18 – *Hexecontasoma carinatum* gen. n., sp. n.; 19 – *Cambala hubrichti* HOFFMAN (Cambalidea); 20 – *Nanogona* COOK, 1895 (Chordeumatida), and 21 – *Polydesmus* LATREILLE, 1802/03 (Polydesmida). Pleurites are lightly stippled and sternites are heavily stippled. Some aspects of the ring structure of *H. carinatum* are incompletely known. The sternal-coxal attachment is incompletely known and it is possible that the ring was open ventrally. The coxae may be oriented more outward than seen here; they may also have been separated from each other slightly more than shown here. Presence of a middorsal suture is uncertain; it is possible that the longitudinal splitting of the holotype is taphonomic. The ring of *H. carinatum* may also be more ovoid or more rounded than shown and the paranota may have tilted upward more than shown. (Fig. 17 modified from HOFFMAN 1990, fig. 26.8; 20 and 21 after BLOWER 1985, fig. 3, with the exception of the addition of a generalized middorsal suture for 20, such as that illustrated by ATTEMS [1926, for example, fig. 184]).

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