

A POSSIBLE ONYCHOPHORAN FROM THE MIDDLE PENNSYLVANIAN MAZON CREEK BEDS OF NORTHERN ILLINOIS

IDA THOMPSON AND DOUGLAS S. JONES

Department of Geological and Geophysical Sciences, Princeton University,
Princeton, New Jersey 08544

ABSTRACT—A lobopod animal, *Helenodora inopinata* n.gen., n.sp., is described from two specimens preserved in siderite concretions from the Middle Pennsylvanian Francis Creek Shale, Illinois. The specimens are characterized by a long, vermiform trunk bearing 21 or more pairs of short, lobose limbs ventro-laterally placed. One limb is preserved with two small hook-like claws. Other limbs have suggestions of claws. The body is annulated, with about nine annulations per limb-bearing section. The annulations bear small papillae. The head and posterior end are poorly preserved but there is a suggestion of jaws indicating a ventral mouth in both specimens. All preserved characteristics are compatible with assignment of *H. inopinata* to the subphylum Onychophora. However, because of the poor preservation of the anterior and posterior, assignment is made only to the Phylum Uniramia Manton, 1972. Since the Mazon Creek beds contain a mixture of terrestrial, freshwater, and marine organisms, the habitat of this species remains uncertain.

INTRODUCTION

THE FOSSIL RECORD of onychophorans is very poor or non-existent (Dechaseaux, 1953). The classification of two fossil species assigned in the past to the Onychophora is now uncertain. The most famous "onychophoran," *Aysheaia pedunculata* from the Middle Cambrian Burgess Shale (Walcott, 1911, 1931; Hutchinson, 1930, 1969; Delle Cave and Simonetta, 1975), has recently been thoroughly restudied by Whittington (1978) who concludes that the differences between *Aysheaia* and living onychophorans are extreme. Whittington (1978) prefers not to assign *Aysheaia* to any higher taxon while allowing for the possibility that the group to which *Aysheaia* belonged could have been ancestral to the living uniramians (including onychophorans).

The other possible onychophoran is *Xenusion auerswaldae* (Pompeckj, 1927), recovered from an erratic block found in northern Germany. This block may be from lowermost Cambrian quartzites in southeastern Sweden (Jaeger and Martinsson, 1967). Tarlo (1967) classifies *Xenusion* as a coelenterate of the *Rangea-Charnia* Precambrian type. Whittington considers this "plausible" (Whittington, 1978). However *Xenusion* continues to be discussed as a possible onychophoran (Bergström, 1979, p. 11).

The organism described here as another possible onychophoran is known from two specimens preserved in siderite concretions

from the Mazon Creek beds of Northern Illinois. This extraordinary locality has already yielded many organisms rare or unique in the fossil record. The most famous example is the legendary *Tullimonstrum gregarium* (Richardson and Johnson, 1966), a strange, soft-bodied invertebrate with segmented trunk, clawed proboscis, and eyes on a bar organ. Other unusual finds include a large hydra (Schram and Nitecki, 1975); the earliest fossil squid, complete with tentacles (Johnson and Richardson, 1966); the only fossil echiuran (Jones and Thompson, 1977); a diverse collection of whole-bodied polychaetes (Thompson, 1979); and other worms (Schram, 1973).

SYSTEMATIC PALEONTOLOGY

Phylum UNIRAMIA Manton, 1972
Subphylum ONYCHOPHORA? Grube, 1853
Genus HELENODORA n.gen.

Diagnosis.—Same as for the only species.
Type species.—*Helenodora inopinata*, n.sp.

HELENODORA INOPINATA, n.sp.

Text-fig. 1; Pl. 1; Pl. 2; Pl. 3, figs. 1, 2, 4

Types.—Holotype: FMNH PE 29049 (Text-fig. 1A; Pl. 1; Pl. 3, figs. 1, 2, 4). Paratype: FMNH PE 29050 (Text-fig. 1B; Pl. 2; Pl. 3, fig. 4). Both types are part and counterpart of small siderite concretions in the invertebrate fossil collection of the Field Museum of Natural History, Chicago, Illinois.

Reconstruction.—Text-fig. 2B.

Diagnosis.—Elongated, vermiform fossils with 21 or more pairs of short, tapered legs arranged ventro-laterally and evenly spaced along body; cuticle with fine annulations, approximately nine per segment with the ridges of each annulation bearing tiny papillae spaced about three per mm.

Stratigraphic position and locality.—Middle Pennsylvanian, Desmoinesean (Westphalian D). Carbondale Formation, Francis Creek Shale. Both specimens are from strip mine Pit Eleven, Peabody Coal Company, Will and Kankakee counties, Illinois, U.S.A.

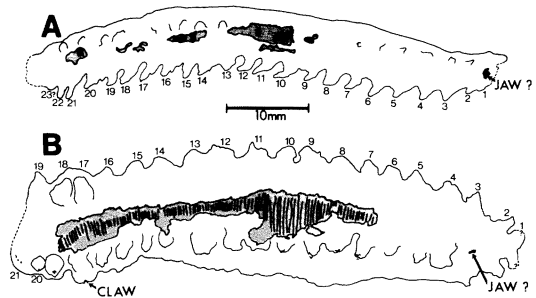
Etymology.—The generic name, *Helenedora*, is Greek for Helen's gift and honors Mrs. Helen Piecko of Chicago, Illinois, who found the only two known specimens of this species and donated them to the Field Museum. *Inopinata* is Latin for unexpected.

Material.—Only two specimens of *Helenedora inopinata* are known. Both are contained in concretions which have split in the plane of the fossils. The fossils are light brown in color and thus stand out against the surrounding dark brown rock matrix, a common mode of preservation in Mazon Creek material.

The fossils show some relief with the legs slightly raised or depressed relative to the plane of the body (Pl. 1, fig. 2; Pl. 2, fig. 2). The texture of the cuticle is accentuated with oblique lighting (Pl. 2, fig. 3). Much of this study was done with the specimens under water to accentuate color differences and minimize surface irregularities.

We are not certain of the orientation of the fossils. In each specimen, one end tapers slightly more than the other end (Text-fig. 1). The more tapered end in each case contains a small dark patch in the approximate position of the jaw in living onychophorans. In addition, in the paratype this tapered end terminates in two paired appendages that look more like stubby antennae or the bases of antennae than they do legs. For these reasons, we will refer to the tapered ends as anterior and designate right and left on this basis, but these designations are not conclusive.

Both specimens are dorso-ventrally flattened with some longitudinal rotation. The holotype shows the dorsal surface and right-lateral side with the right legs outlined; therefore, rotation was to the left (Text-fig. 1A). The obscurity of the left leg row is due to the



TEXT-FIG. 1—Camera lucida line drawings of *Helenedora inopinata* n.gen., n.sp. Appendages are numbered from the anterior (right in both specimens). Shaded areas represent annulated patches of cuticle. A, holotype—FMNH PE 29049. B, paratype—FMNH PE 29050.

presence of the trunk over it. The paratype, however, must have the ventral surface exposed because of the fidelity with which the left row of legs is preserved within the body profile. Rotation was to the right and the right row of legs is outlined (Text-fig. 1B).

Description.—Dimensions.—The trunk of the holotype measures 56 mm in length and 6 mm in width. The slightly larger paratype is 64 mm long and 13 mm wide.

Legs.—There are two rows of paired, ventro-lateral legs. Each leg is preserved as a stubby triangle, tapering distally. The number of pairs of legs is uncertain and may be different in the two specimens. The holotype (Text-fig. 1A) has 22 or 23 pairs of appendages that are most clearly defined on the right (lower) margin. The presumed anterior is incomplete because the concretion failed to split in the exact plane of the head; but because of the pronounced taper, we suspect very little of the head is missing. Appendage 1 (Text-fig. 1A) may be an incomplete leg or the base of an antenna. Posteriorly there may be one or more legs missing. The minimum number of leg pairs for the holotype is 21. The left row of legs is much more obscurely preserved within the body margin (Text-fig. 1A) as slight depressions which show dark outlines when the fossil is wet. Some of the cuticle with transverse annulations lies over the legs, obscuring them.

The paratype (Text-fig. 1B) shows 21 pairs of appendages. If the anterior-most of these are antennae and the second pair are oral papillae, then this specimen has a minimum of

19 pairs of legs. Most of the right (upper) leg row projects from the body margin, as in the holotype, and is clearly defined back to appendage 19. The legs on the left are within the body margin but well-defined. There are one or two additional legs, appendages 20 and 21, which are not exposed on the right.

The legs taper from a wide base to a blunt tip and are approximately 2 mm long in the holotype. Some of the legs in the paratype are longer, up to 3 mm, broader and less pointed. The paratype has one appendage with two small (0.5 mm long) claws at the tip (Pl. 3, fig. 4) and less well-preserved claws on other legs in the left row (Text-fig. 1B). These are on both halves of the concretion. The holotype has no unambiguous claws. One leg has at its tip two small grooves that may be molds of the claws.

Skin.—The cuticle is preserved as brown patches with annuli (Text-fig. 1, A and B; Pl. 2, fig. 3). In the paratype, these patches have a metallic green luster when wet and are in part replaced by pyrite. Most of the patches contain annulations, about 9 per segment. The crests of the annulations on the paratype have small cones spaced evenly 2–3 mm apart. Because of the regularity of the spacing of the cones, these cannot be pyritic growths. Little is seen of the cuticle on the legs. The paratype has a small patch of cuticle over appendage 11 (Text-fig. 1B) but this is poorly preserved and shows no structure.

Head.—The presumed anterior end (see above) is not well-preserved in either specimen. In the holotype, the concretion split with the anterior tip still buried in the matrix. We tried to excavate this matrix without success. The paratype appears to be more complete. The only parts missing may be the tips of the first appendages.

Each specimen has a dark brown patch near the anterior end which we have labeled "jaw?" in Text-fig. 1. This patch in the holotype is shown enlarged in Pl. 3, fig. 2 and exhibits

some lobe-like relief. The patch in the paratype is smaller and pyritized.

In the paratype, the anterior is flattened dorso-ventrally and is complete or almost complete. The first appendages are terminal. The second pair of appendages are smaller than the posterior appendages. The anterior of the holotype is crushed more laterally and is incomplete so we do not know the shape and location of the first appendages.

Discussion.—A vermiform animal like *Helenodora inopinata* with many pairs of appendages and without a skeleton can be assigned to only three existing taxonomic groups: the polychaetes (Annelida), or the tardigrades or onychophorans of the Phylum Uniramia (Manton, 1972, 1977). When all the preserved characteristics of *H. inopinata* are considered, classification is restricted to the onychophorans.

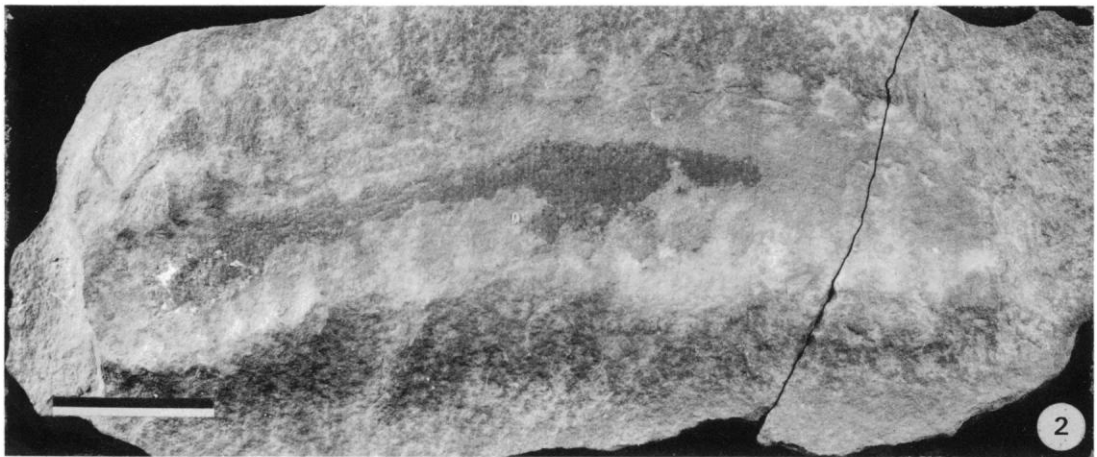
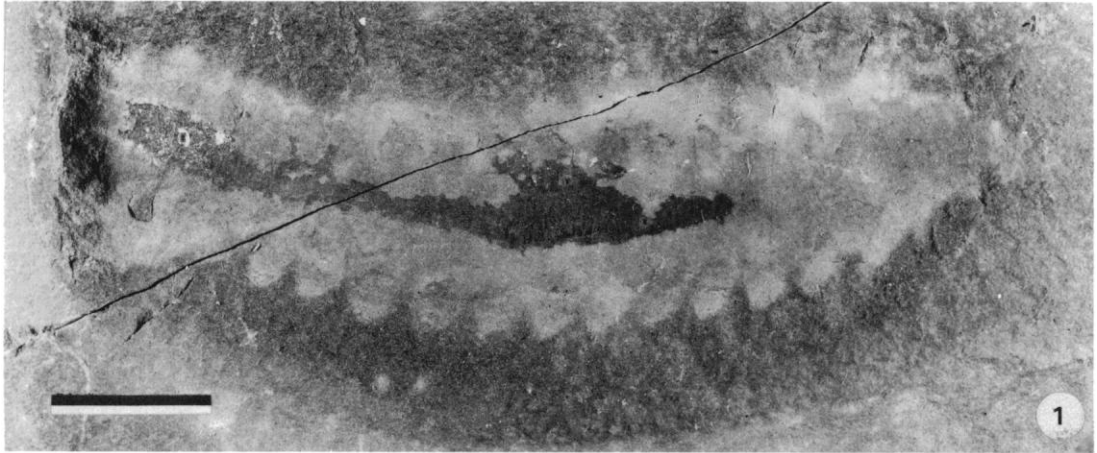
We cannot place *H. inopinata* with the polychaetes because the appendages are not parapodia. The appendages of *H. inopinata* are ventro-laterally placed like lobopodia, not lateral like parapodia. In addition, the parapodia of the Mazon Creek polychaetes are preserved with aciculae and setae and almost never with definite outlines (Thompson and Johnson, 1977; Thompson, 1979). *Helenodora inopinata*, to the contrary, has limbs without aciculae or setae but with very definite outlines. These strong outlines are probably due to the greater thickness of the limbs compared to polychaete parapodia. In the very few cases seen by the senior author where parapodial outlines of Mazon Creek polychaetes are preserved, the preservation of the entire polychaete was extraordinary and the aciculae and setae were also preserved. If *H. inopinata* was a polychaete, the strong outlines of the limbs would indicate exceptional preservation and aciculae and setae would also be preserved. Similarly, when polychaete aciculae and especially setae are not preserved, the faint trace of the worms indicate decay was far advanced

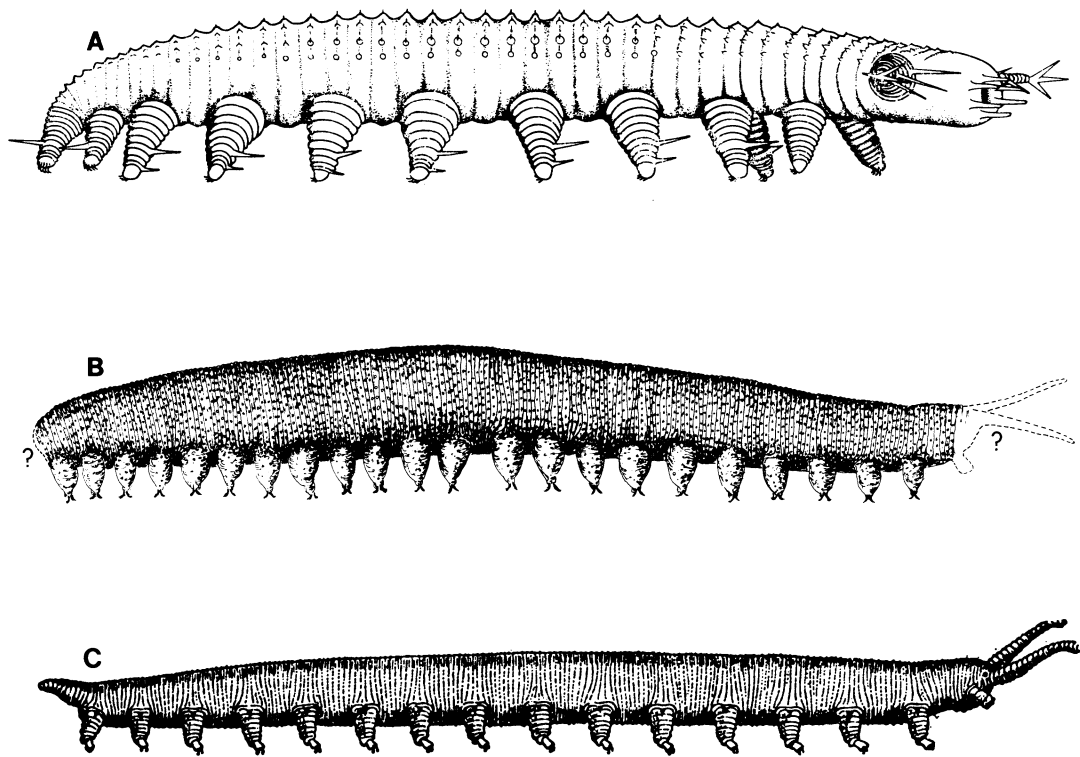
→

EXPLANATION OF PLATE 1

FIGS. 1,2—*Helenodora inopinata* n.gen., n.sp., holotype, FMNH PE 29049, part and counterpart of dorso-ventrally compressed specimen showing dorsal surface and right-lateral side with right legs outlined. 1, anterior is to the right, overhead lighting. 2, anterior is to the left, lighting from left. Bar scale, 10 mm.







TEXT-FIG. 2—Reconstructions of A, *Aysheia pedunculata* Walcott (from: Whittington, 1978). B, *Helenodora inopinata* n.gen., n.sp. C, *Peripatoides novae-zealandiae* (from: Snodgrass, 1958). All three species are enlarged approximately $\times 2$.

before preservation was complete. The specimens of *H. inopinata* are not poorly preserved as the body outlines are clear and the cuticle is preserved in places complete with annulations and papillae. All the evidence indicates the appendages of *H. inopinata* were lobopodia, not parapodia.

Helenodora inopinata cannot be a tardigrade as Delle Cave and Simonetta (1975) have suggested for *Aysheia*. Tardigrades do have lobopodia, but there the similarity ends. Living tardigrades have only eight legs and each terminates in six claws. Tardigrade mouths are terminal. All known tardigrades

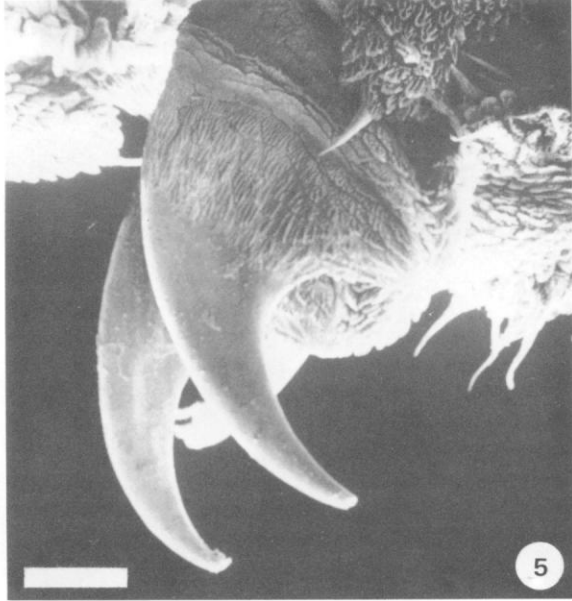
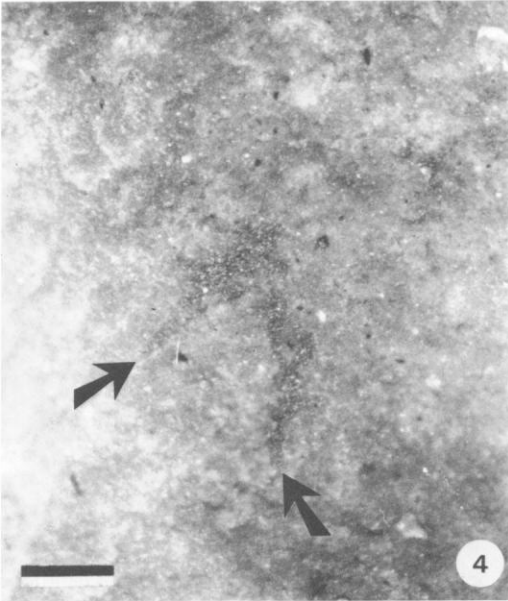
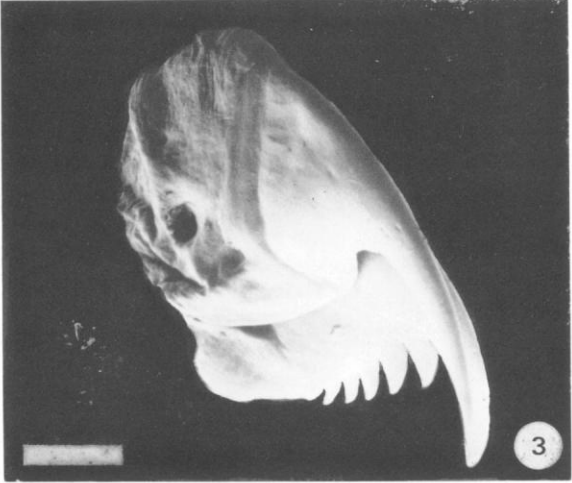
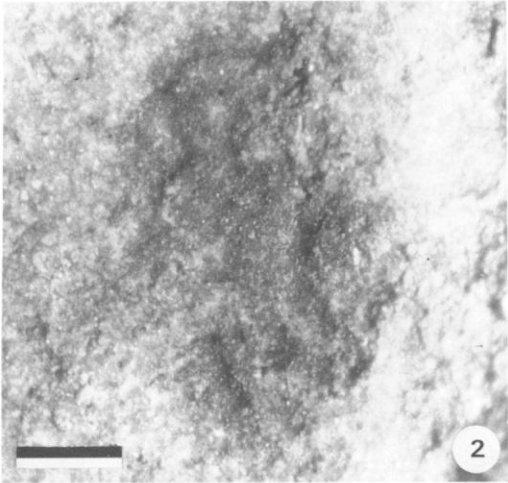
are 1 mm or less in length, clearly different from the macroscopic animal *H. inopinata*.

The classification of *H. inopinata* in the subphylum *Onychophora* is compatible with all preserved characteristics. The limbs are lobose. *Helenodora inopinata* has two terminal claws which are approximately the same size and shape as living onychophoran claws (Pl. 3, figs. 4, 5). The trunk is annulated. When preservation of the cuticle is good, small pumps which may be papillae are visible in rows on the crests of the annulations. The size and shape of *H. inopinata* is similar to recent onychophorans.

←

EXPLANATION OF PLATE 2

FIGS. 1–3—*Helenodora inopinata* n.gen., n.sp., paratype, FMNH PE 29050. 1, 2, part and counterpart of dorso-ventrally compressed specimen showing ventral surface and outlining right legs, anterior is to the left in both figures, bar scales, 10 mm. 3, enlarged view of cuticle impression showing transverse rows which once were papillated (arrows), bar scale, 1 mm.



However, we do not feel that we can firmly place *H. inopinata* with the Onychophora. *Helenodora inopinata* may belong to an extinct group. We are not sure about the details of the head. *Helenodora inopinata* may have had a jaw and ventral mouth, but the dark patches we call "jaw?" in Text-fig. 1 are poorly preserved. The presumed anterior appendages of both specimens are not well enough preserved to know for sure if these were antennae and oral papillae.

Our reconstruction of *H. inopinata* (Text-fig. 2B) reflects our confidence in the morphology of the trunk and limbs, but the anterior and posterior are dashed in to indicate uncertainty. For the reconstruction, we have interpreted the specimens under the assumption that they were onychophorans. The first appendages of the paratype are assumed to be the bases of terminal antennae; the second appendages are assumed to be oral papillae. These assumptions are not inconsistent with the evidence, but we recognize the possibility of other interpretations.

We have included Whittington's (1978) reconstruction of the Burgess Shale lobopod *Aysheaia pedunculata* (Text-fig. 2A) for comparison with *H. inopinata* and a Recent onychophoran (Text-fig. 2C). In contrast to the Recent onychophoran, *A. pedunculata* has fewer limbs, more claws on each limb, spines on the legs, no terminal antennae, no oral papillae, and a terminal mouth. Whittington (1978) has removed *A. pedunculata* from the Onychophora because of these differences. However, he sees as a possibility the descent of both onychophorans and tardigrades from a group including *A. pedunculata*. *Helenodora inopinata* may also be a descendant of this group. Whether or not it had reached the grade of Onychophora we cannot say for sure.

Habitat.—*Aysheaia pedunculata* was almost certainly marine (Whittington, 1978) while all living onychophorans are terrestrial (Clark, 1915; Cuénot, 1949). Unfortunately we do not know the habitat of *H. inopinata*. The Mazon Creek locality contains a mixture of marine, freshwater, and terrestrial organisms (Richardson and Johnson, 1971). The more southerly collecting sites, in particular Pit Eleven of the Peabody Coal Company where both specimens of *H. inopinata* were discovered, contain mostly marine animals. However, an occasional insect, millipede, or amphibian is found here also, along with many terrestrial plants.

The morphology of *H. inopinata*, when compared to the marine *Aysheaia* and the terrestrial *Peripatoides* (Text-fig. 2), may show adaptations for terrestrial life, but this is only speculation. For example, the shorter, more closely spaced legs of *H. inopinata* and *Peripatoides* may be adaptations to terrestrial locomotion. The reduced number of claws may reflect the increased ease with which a terrestrial as opposed to an aquatic organism can grip a horizontal substrate. The slimmer body and legs may facilitate gas exchange in air.

CONCLUSIONS

1) A new genus and species of lobopod metazoan, *Helenodora inopinata*, is described from the Middle Pennsylvanian Mazon Creek beds of Northern Illinois. There are only two known specimens, each preserved in a siderite concretion.

2) The trunk and legs of the specimens are well-preserved, with patches of cuticle showing annulations and papillae. The legs were short cones, terminating in two small claws.

3) Morphology of the head and tail are ambiguous. Both specimens have suggestions of

←

EXPLANATION OF PLATE 3

- FIGS. 1, 2.—*Helenodora inopinata* n.gen., n.sp. 1, Enlargement of anterior of holotype (Pl. 1, fig. 1) with arrow indicating possible jaw, bar scale, 2 mm. 2, enlargement of impression of possible jaw from fig. 1, bar scale, 250 μ m.
- 3—*Peripatus* sp. Two elements which comprise one half of the paired jaw system in a Recent onychophoran, anterior is to the upper right, SEM photomicrograph, bar scale, 100 μ m.
- 4—*Helenodora inopinata* n.gen., n.sp. Arrows indicate tips of paired claws located on the paratype (Pl. 2, fig. 2), bar scale, 250 μ m.
- 5—*Peripatus* sp. Paired claws from Recent onychophoran, anterior is to the left, SEM photomicrograph, bar scale, 50 μ m.

jaws near the tapered end. The paratype has two pairs of terminal appendages that may be parts of antennae and oral papillae.

4) In all preserved characteristics, *H. inopinata* can be classified with the living onychophorans. However, assignment to this group is made only tentatively because of the ambiguity of the details of the head.

5) *Helenodora inopinata* is compared to *Aysheaia pedunculata* and the Recent onychophoran *Peripatoides novae-zealandiae*. Characteristics shared with the terrestrial *P. novae-zealandiae* but not with the marine *A. pedunculata* could indicate *H. inopinata* had adapted to a terrestrial habitat. However, *H. inopinata* comes from beds containing a mixture of marine, freshwater, and terrestrial organisms.

ACKNOWLEDGMENTS

We thank Mrs. Helen Piecko of Chicago, Illinois for her generous donations and enthusiastic cooperation with this study. We also thank H. B. Whittington, S. Conway Morris, and F. R. Schram for comments on an earlier draft of the manuscript. This paper has also benefitted from the critical reviews of D. Baird and A. G. Fischer.

REFERENCES

- Bergström, J. 1979. Morphology of fossil arthropods as a guide to phylogenetic relationships, p. 3-56. *In*, A. P. Gupta (ed.), *Arthropod Phylogeny*, Van Nostrand Reinhold Co., N.Y.
- Clark, A. H. 1915. The present distribution of the onychophora, a group of terrestrial invertebrates. *Smithson. Misc. Collect.* 65:1-25.
- Cuénot, L. 1949. Les onychophores, p. 1-37. *In*, P. Grassé (ed.), *Traité de Zoologie*, 6, Masson et C^{ie}, Paris.
- Dechaseaux, C. 1953. Onychophores, p. 3-7. *In*, J. Piveteau (ed.), *Traité de Paleontologie*, 3, Masson et C^{ie}, Paris.
- Delle Cave, L. and A. M. Simonetta. 1975. Notes on the morphology and taxonomic position of *Aysheaia* (Onychophora?) and of *Skania* (undetermined phylum). *Monit. Zool. Ital. (N.S.)* 9:67-81.
- Hutchinson, G. E. 1930. Restudy of some Burgess Shale fossils. *Proc. U.S. Natl. Mus.* 78:1-24.
- . 1969. *Aysheaia* and the general morphology of the Onychophora. *Am. J. Sci.* 267:1062-1066.
- Jaeger, H. and A. Martinsson. 1967. Remarks on the problematic fossil *Xenusion auerswaldae*. *Geol. For. Stockh. Forh.* 88:435-452.
- Johnson, R. G. and E. S. Richardson, Jr. 1966. A remarkable Pennsylvanian fauna from the Mazon Creek area, Illinois. *J. Geol.* 74:626-631.
- Jones, D. S. and I. Thompson. 1977. Echiura from the Pennsylvanian Essex fauna of northern Illinois. *Lethaia* 10:317-325.
- Manton, S. M. 1972. The evolution of arthropodan locomotory mechanisms. Part 10. Locomotory habits, morphology and evolution of the hexapod classes. *J. Linn. Soc., Zool.* 51:203-400.
- . 1977. The arthropods: habits, functional morphology, and evolution. Clarendon Press, Oxf., 527 p.
- Pompeckj, J. F. 1927. Ein neues Zeugnis uralten Lebens. *Palaontol. Z.* 9:287-313.
- Richardson, E. S., Jr. and R. G. Johnson. 1966. Wormlike fossil from the Pennsylvanian of Illinois. *Science* 151:75-76.
- and ———. 1971. The Mazon Creek faunas. *N. Am. Paleontol. Conv., Chic., 1969, Proc. Part I:*1222-1235.
- Schram, F. R. 1973. Pseudocoelomates and a nemertine from the Illinois Pennsylvanian. *J. Paleontol.* 49:985-989.
- and M. H. Nitecki. 1975. Hydra from the Illinois Pennsylvanian. *J. Paleontol.* 49:549-551.
- Snodgrass, R. E. 1958. Evolution of arthropod mechanisms. *Smithson. Misc. Collect* 138:1-77.
- Tarlo, L. B. H. 1967. *Xenusion*—onychophoran or coelenterate? *Mercian Geol.* 2:97-99.
- Thompson, I. 1979. Errant polychaetes (Annelida) from the Pennsylvanian Essex fauna of northern Illinois. *Palaeontogr., Abt. A.* 163:169-199.
- and R. G. Johnson. 1977. New fossil polychaete from Essex, Illinois. *Fieldiana Geol.* 33:471-487.
- Walcott, C. D. 1911. Cambrian geology and paleontology no. 5, Middle Cambrian annelids. *Smithson. Misc. Collect.* 57:110-144.
- . 1931. With explanatory notes by C. E. Resser. Addenda to descriptions of Burgess Shale fossils. *Smithson. Misc. Collect.* 85:1-46.
- Whittington, H. B. 1978. The lobopod animal *Aysheaia pedunculata* Walcott, Middle Cambrian, Burgess Shale, British Columbia. *Phil. Trans. R. Soc., Lond. B* 284:165-197.

MANUSCRIPT RECEIVED AUGUST 21, 1978

REVISED MANUSCRIPT RECEIVED AUGUST 8, 1979