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Geology

JAN 23 1975

University of Illinois
at Urbana-Champaign

Published by Field Museum of Natural History

Volume 33, No. 6

November 29, 1974

 This volume is dedicated to Dr. Rainer Zangerl

Paleozoic Peracarida of North America

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INTRODUCTION

Schram (1970) described, from the middle Pennsylvanian Essex fauna of northeastern Illinois, the earliest isopod peracarid, *Hesslerella shermani*. This phraetoicidean isopod extended the range of the isopods back some 50 million years from the late Permian to the Middle Pennsylvanian. A detailed description of *H. shermani* can now be offered.

Another new species of peracarid has been found in the Essex fauna and is assigned to the order Tanaidacea Dana, 1853.

The only other previously suspected Paleozoic peracarids were the problematic order Anthracocaridacea Brooks, 1962. This order was erected to accommodate two Lower Carboniferous species which had originally been mistakenly assigned to the syncarid genus *Palaeocaris*. Restudy of the original material by this author of the anthracocaridacean, *Acadiocaris novascotica* (Copeland) 1957, indicates this crustacean is in fact a spelaeogriphacean. *A. novascotica* is redescribed herein. The spelaeogriphaceans were previously known from one species occurring in pools in Bat Cave, in Table Mountain, outside Cape Town, South Africa.

The Pygocephalomorpha Brooks, 1962 have been reassigned as a suborder of the mysidaceans (Schram, 1974). Probably some of what remains of the Eocaridacea Brooks, 1962 are also peracarids. As a result, it becomes evident that the superorder Peracarida was a major element in the Late Paleozoic radiation of eumalacostracans and constituted the principal caridoid types of that time.

Library of Congress Catalog Card Number: 74-22954

Specimens in various collections have been used in this study. They are denoted by the following prefixes:

- PE and P—Field Museum of Natural History fossil invertebrate collections.
- GSC—Geological Survey of Canada, Ottawa.
- A—Collection of Mr. and Mrs. Charles Asher, Peoria, Illinois.
- B—Collection of Mr. and Mrs. Jerry Bietz, Peoria, Illinois.
- EX—Collection of Mr. Dan Damrow, Norridge, Illinois.
- CG—Collection of the Calvin George family, Naperville, Illinois.
- SLM—Collection of Mr. Stephen LeMay, Chicago, Illinois.
- MDS—Collection of Ms. Mildred Sheffle, Peoria, Illinois.
- LS—Collection of Mr. Levi Sherman, DesPlaines, Illinois.
- BW—Collection of Mr. and Mrs. Berkeley Wickkizer, Peoria, Illinois.

SYSTEMATICS

Superorder PERACARIDA Calman, 1904

Order ISOPODA Latrielle, 1817

Suborder PHREATOICIDEA Stebbing, 1893

Family PALAEOPHREATOICIDAE Birshtein, 1962

Hesslerella Schram, 1970

Diagnosis.—Head short with prominent cervical furrow; eyes sessile and protrude beyond front of head; anterior thoracic coxae apparently fused to pleura; bases of thoracopods greatly elongate and inflated than coxae; no subchela on second thoracopod; fifth abdominal segment inflated; pleotelson large and pointed posteriorly.

Type of genus.—*Hesslerella shermani* Schram, 1970.

Hesslerella shermani Schram, 1970

Hesslerella shermani Schram, 1970, Science, 169 pp. 854-855, fig. 1.

Description.—The cephalon is short with a prominent cervical groove (PE16527, PE21821), with the sessile eyes protruding out beyond the anterior surface of the cephalon. The peduncle of the first antenna has three subequal segments (A 00700, B 514P, EX1881) and the flagella is moderately developed (fig. 1a). The second antenna has five segments in its peduncle (EX1881, PE16527), the two proximal segments being shorter than each of the distal segments. The flagella of the second antenna are quite long. The maxilliped is formed from three segments (PE16527) (fig. 2).



FIG. 1. *Hesslerella shermani*. EX1881. A, Cephalon and anterior thorax. $\times 16$. B, Abdomen displaying a pleopod and pleotelson with uropods. $\times 33$.

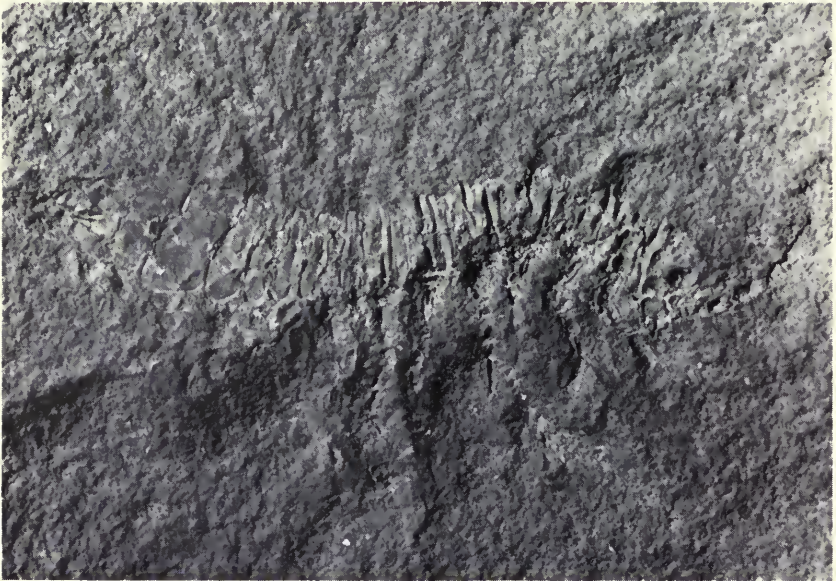


FIG. 2. *H. shermani*. PE16527. Holotype.

The thoracomeres 2 through 8 are prominently decorated with two ridges, with the thoracomere margins marked off by doublures. The pereiopods are all similarly developed, and the first pereiopod is not subchelate. The coxa is small (PE 16527, CG 11-244, B 443W) and appears to be almost fused to the pleura of the anterior thoracomeres. The bases of all the thoracopods are greatly expanded and elongate. The rest of the segments of the leg are short and subequal. Pereiopods 2 through 4 are anteriorly directed, and 5 through 8 are directed posteriorly (PE 16527, EX 1881).

Pleomeres 1 through 4 are about the size of any of the thoracic segments (fig. 1b). The fifth abdominal segment is greatly inflated and almost twice as long as any of the anterior pleomeres (PE 16527, EX 1881, B 443W). Natatory pleopods have been seen on only the first and second abdominal segments. The pleotelson is large and posteriorly pointed. The uropods are short with a protopod of one segment and the styliform exopods and endopods each with two small segments (PE 16527).

A reconstruction of *Hesslerella shermani* is offered in Figure 3.

Remarks.—*Hesslerella* occupies an intermediate position anatomically between the families Amphisopidae (which has two fossil representatives, the Triassic *Protamphisopus wianamatensis* (Chilton) 1918 and the

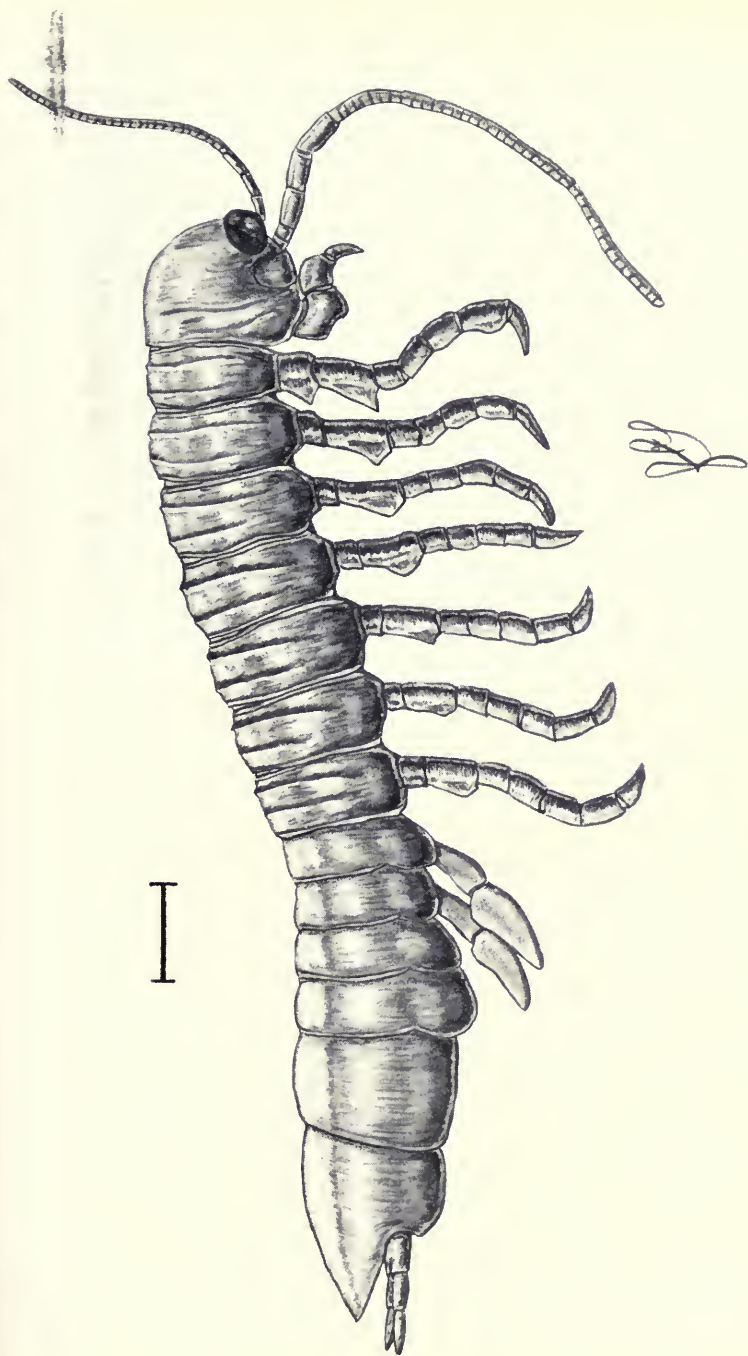


FIG. 3. *H. shermani*. Reconstruction. Scale denotes 2 mm.

Permian *P. reichelti* Glaessner, 1962) and Palaeophreatoicidae (with two Permian species, *Palaeophreatoicus sojanensis* Birshtein, 1962, and *Palaeocrangon problematicus* (von Schlotheim) 1820). In common with the amphisopids, *Hesslerella* has a short cephalon, an inflated basis on the thoracopods, possibly coxae fused to the pleurites on the anteriormost thoracomeres, and a moderately posteriorly projected telson. In common with the palaeophreatoicids, *Hesslerella* possesses eyes protruding beyond the anteriormost surface of the cephalon, coxae free on most of the thoracopods, an enlarged fifth pleomere, and a non-subchelate first thoracopod. This last character is not preserved on any of the other palaeophreatoicids but is a primitive condition and could be present on the other species.

H. shermani consequently occupies an intermediate position between the two families. Although it possesses advanced characteristics, especially in terms of thoracopodal anatomy, it has more characteristics in common with *Palaeocrangon* and *Palaeophreatoicus* and is here classified with them.

Holotype.—PE16527 in the fossil invertebrate collection of Field Museum of Natural History.

Order TANAIIDACEA Dana, 1853

Suborder MONOKONOPHORA Lang, 1956

Family INCERTA SEDIS

Cryptocaris, new genus

Diagnosis.—Since only one species is known, the diagnosis of the genus is the same as that of the species.

Type of genus.—*Cryptocaris hootchi* Schram, n. sp.

Remarks.—This animal is very rare and has only come to notice since 1972 in collections from Peabody Coal Co. Pit. 11. Except for appendages, the material is usually well preserved, however, and although only a few specimens are known most of the anatomy of the creature can be discerned from these.

Cryptocaris hootchi, new species

Diagnosis.—Carapace with prominent rostrum, optic notches, and branchiostegal development; paired longitudinal ridges on thoracomeres on either side of dorsal midline; thoracic pleura greatly developed, each with three longitudinal ridges; marked pleura on the abdomen; uropods



FIG. 4. *Cryptocaris hootchi*. B509G. With arrows pointing to peduncles of first and second antennae (photographed by reflected light off a gold-plated specimen). $\times 5$.

greatly elongated; telson small and spatulate; uropods and telson with long terminal spines.

Description.—First antenna is biramous with three subequal segments in the peduncle (MDS 3999) and the second antenna has two subequal segments in the peduncle (B 509G) (fig. 4). The carapace has a broad triangular rostrum with prominent optic notches (EX 1882, BW 100). EX 1882 indicates the eyes were spherical, moderate in size, and stalked (fig. 5). The first two thoracomeres are covered by the carapace and are apparently fused to it.

Thoracomeres 3 through 8 have the pleura developed as large lappets. Each pleuron has three longitudinal ridges on it and each thoracomere has two longitudinal ridges on each side of the dorsal midline (BW100).

Regretably, little can be learned about the appendages (figs. 6, 7). LS 1366 has a classic tanaidacean silhouette, but the fossil is largely a color difference in the rock, and very little can be discerned of the actual anatomy. This specimen does have the terminal portion of a pleopod which is somewhat serrated and the serrations marked with large spines.



FIG. 5. *C. hootchi*. EX1882. Latex mold of a natural cast. $\times 6.5$.

LS1995 has the distal two segments of some of the anterior pereiopods but nothing else can be determined about these appendages. P32053 also has thoracic appendages present, but the preservation of the fossil is poor and no actual anatomy is determinable (fig. 7).

The abdominal segments are smaller and shorter than the thoracic segments and have well-developed pleura (EX1882, BW 100). The telson appears to be small and spade-like with long, posteriorly directed cerci or spines (BW100, SLM 6) (fig. 8). The uropods are very large with a protopod and two long blade-like segments on both the exopod and endopod (MDS 3999) and these further decorated, apparently, with long terminal spines (fig. 9). A reconstruction of *Cryptocaris hootchi* is presented in Figure 10.

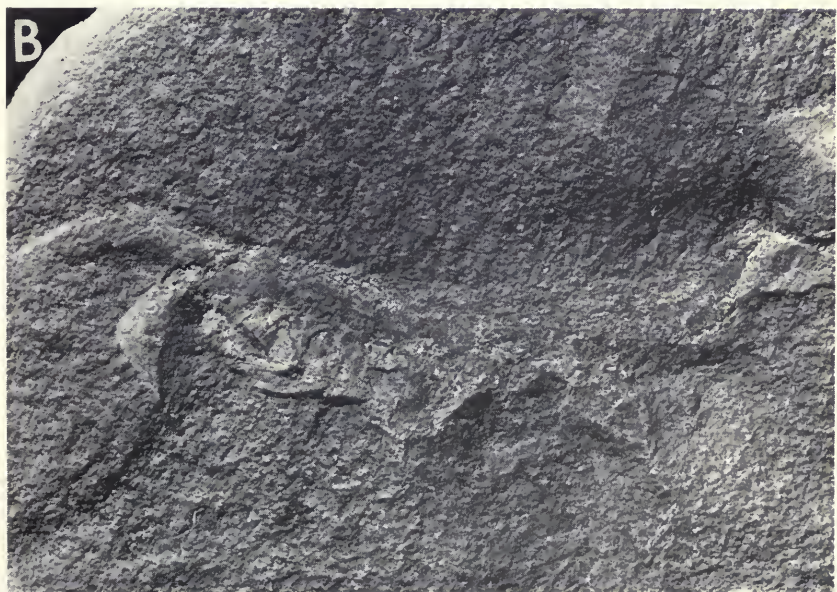


FIG. 6. *C. hootchi*. A. LS1995 \times 4.3. B. LS1366. With ghost-like preservation of thoracopods. \times 2.7.



FIG. 7. *C. hootchi*. P32053. Holotype, preservation in lateral aspect of a very large individual. $\times 1.7$.

Remarks.—As is usually the case, the presence or absence of oostegites on the fossils can not be effectively used as proof of peracarid affinities of *Cryptocaris hootchi*. The general body plan, however, especially the reduced abdomen, form of the carapace, and the fusion of the carapace with the first two thoracomeres, suggests a monokonophoran tanaidacean.

Appendage structure, especially of the anterior thoracopods, could substantiate a tanaidacean assignment if they were present. Unfortunately, the only specimen to preserve a complete lateral view with all structures, LS 1366, is poorly preserved, but, again, the outline certainly suggests a tanaidacean.

Assignment to the order Monokonophora is based on similarity to the fossil *Ophthalmapseudes rhenanus* (Malzahn) 1957 and recent forms. Placement in a family must remain uncertain since familial taxonomy in tanaidaceans is based on fine structure of mouthparts (Lang, 1970; Gardiner, 1973).

Tanaidaceans are noted for a reduced abdomen. The abdomen of *C. hootchi* is reduced in length as compared to the length of the exposed

segments of the thorax (table 1), although the abdomen is not as reduced as in modern tanaidaceans, and the telson and sixth pleomere are separate. In these characters, *C. hootchi* is primitive. The reduced size of the abdomen exceeds what one would expect in other types of peracarids or caridoid malacostracans, with the exception of isopods or certain brachyuran decapods.

The measurements in Table I indicate that *Cryptocaris* has a wide range of variation, carapace length extending from 1.4 to 7.2 mm. in the specimens at hand. This wide variation might at first cast some doubt on whether there is only one species present. In addition, with increasing size, there is a tendency to decrease the pereon-pleon ratio and to increase the



FIG. 8. *C. hootchi*. BW100. Photographed under water showing the uropodal spines or cerci. $\times 4$.



FIG. 9. *C. hootchi*. SLM6. A, General overview. $\times 2$.

number and length of the spines or cerci in the tail region. All of this is consistent, however, with what one would find in tanaidaceans, which typically have a succession of manca stages and an array of primary and secondary copulatory males and copulatory females, all with significant size and morphological differences from each other. The nature of the variation in *C. hootchi* morphology thus does not necessarily indicate a multiplicity of taxa, but rather more strongly argues for its tanaidacean affinities.

Anthracocharis scoticus (Peach) 1882 was placed by Brooks (1962) in his order Anthracocaridacea. From illustrations in the literature this animal bears marked similarity to *Crytocaris* and *Ophthalmapseudes*. Definite reassignment of *A. scoticus* to the tanaiids must await study of the original material.



FIG. 9. **B**, Close-up of tail region demonstrating the maximum development of spines or cerci seen in specimens of this species. $\times 5$.

Holotype.—P32053 in the fossil invertebrate collections of Field Museum of Natural History.

Order SPELAEGRIPHACEA Gordon, 1957

Family ACADIOCARIDIDAE, new family

No optic notch on carapace; thoracopodal endopods well developed; natatory pleopods on the first five pleomeres (*M. Miss.*)

Acadiocaris Brooks 1962

Diagnosis.—Since there is only one species, the diagnosis of the genus is the same as that of the species.

Type of genus.—*Acadiocaris novascotica* (Copeland) 1957

Remarks.—Brooks (1962) recognized both *Acadiocaris* and *Anthracocaris* Calman, 1933 as being distinctive crustaceans and placed them in a separate order, Anthracocaridacea, tentatively assigned to the Peracarida. Hessler (1969) suggested possible affinities of this order to

TABLE 1. Measurements of specimens of *Cryptocaris hootchi* in millimeters.

*denotes holotype.

Specimen	Carapace Length	Length of thoracomeres 3-8	Length of abdomen (-telson)
EX1882	3.4	7.6	
BW100	3.0	7.0	4.8
B 509G	2.7	4.5	
MDS 3999	1.4	3.0	3.6
SLM6	7.2	14.3	9.7
LS 1995	5.0	8.4	7.0
P 32053*	7.0	11.5	9.6

spelaegriphaceans, tanaidaceans, or thermosbaenaceans. Several features suggest spelaegriphacean affinities for *Acadiocaris*: The second antennal peduncle with four segments, the carapace covering but not fused to the second thoracomere, natatory pleopods, and the nature of the telson and uropods.

Copeland (1957) originally presented a short description of this species with some good photographs. His description is substantially correct except for some inconsistencies which probably arose from Copeland's unfamiliarity with possible modern analogs of this beast, and the very poor nature of the preservation. Brooks (1962) based his "redescription" of this animal solely on Copeland's pictures, perhaps overcriticized Copeland's work, and made some unwarranted assumptions in his own right. Brooks never saw the original material. It was thus necessary to examine the type material myself, which I did with the gracious assistance of Dr. Copeland. A redescription and illustration is presented below.

Acadiocaris novascotica (Copeland) 1957

Palaecaris novascoticus Copeland, 1957, Jour. Paleontol., p. 596; Rolfe, 1962, Paleontology, p. 549.

Acadiocaris novascotica Brooks, 1962, Bull. Amer. Paleontol., 44, p. 217; Hessler, 1969, Treatise Invert. Paleontol., Part R, p. R393; Schram, 1969, Fieldiana: Geol., 12, p. 218.

Diagnosis.—Carapace without rostrum; telson spatulate with few terminal spines; uropods with lobate, leaflike rami fringed with setae.

Description.—The first antenna has two flagella (GSC 13320, GSC 13322) and a peduncle of three segments (GSC 13319). The second antenna has a long flagellum and a peduncle with four segments (GSC 13319), however, no scaphocerite has been detected on any of the specimens (fig. 11). The carapace is rectangular in outline and apparently had no rostrum.

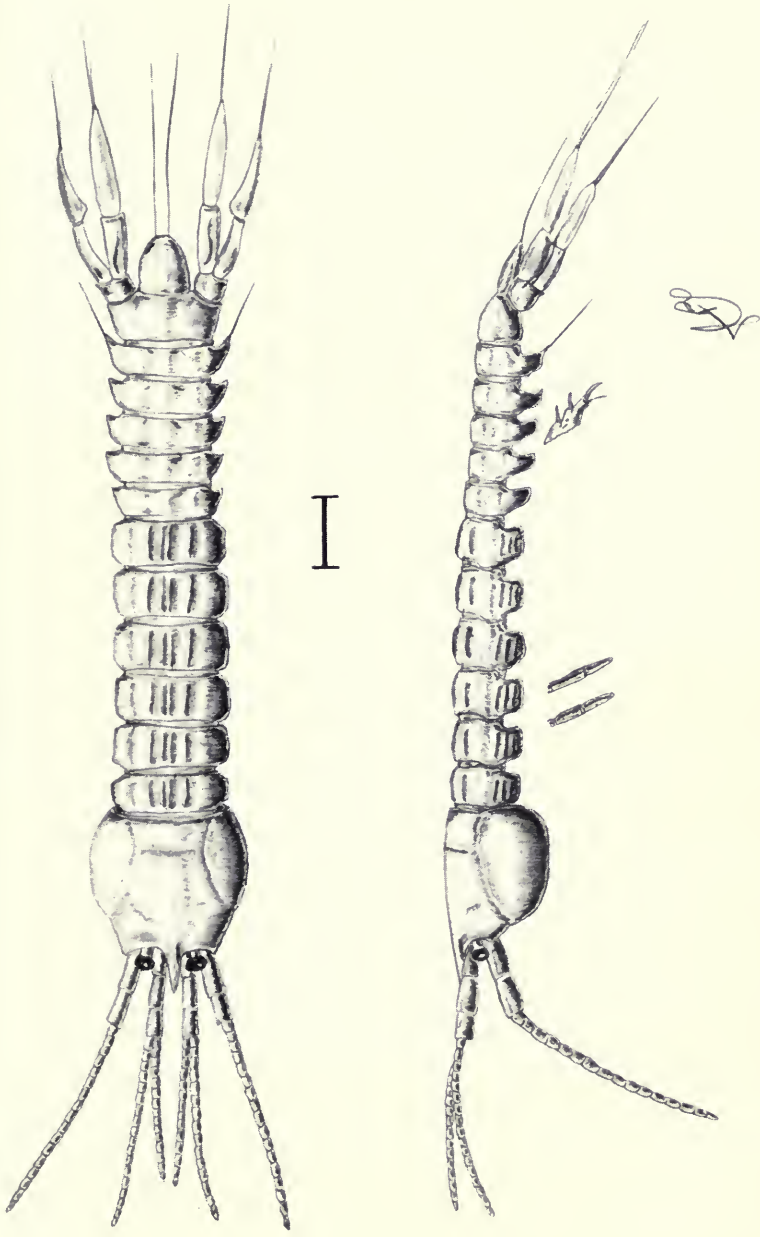
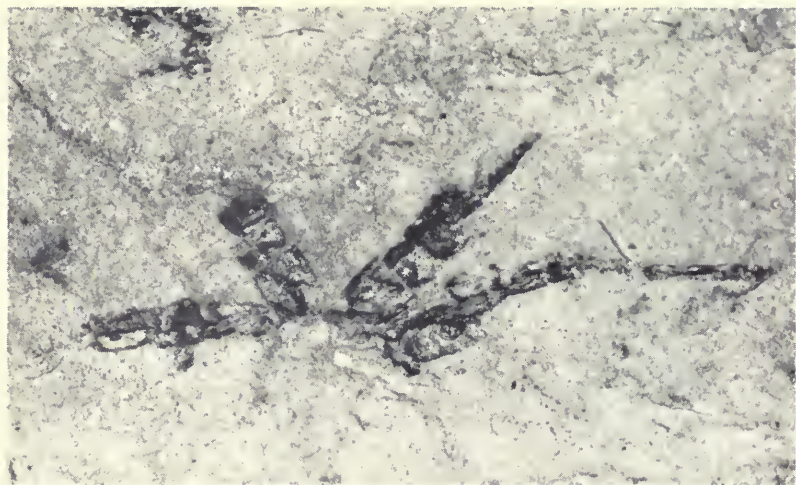
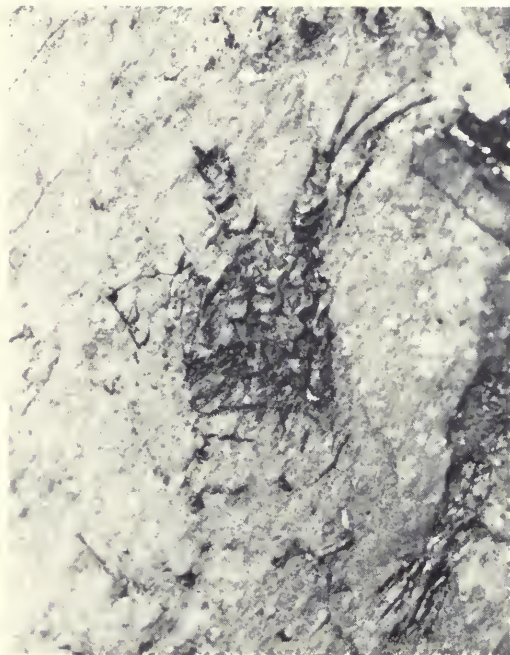


FIG. 10. *C. hootchi*. Reconstruction. Scale represents 2 mm.



A



B

FIG. 11. *Acadiocaris novascotica*. A, GSC13319. Displaying antennal peduncles. Note four segments on second antenna. $\times 18$. B, GSC13320. With antennal flagella. $\times 16$.

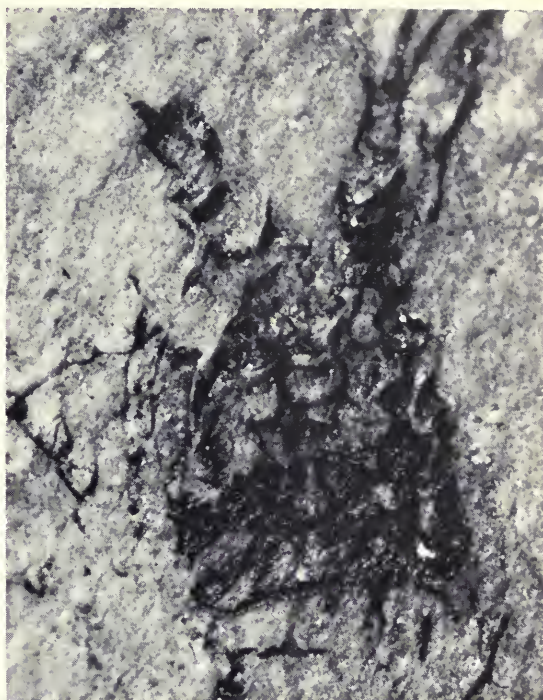


FIG. 12. *A. novascotica*. GSC13320. Close-up with carapace partially covering and unfused to second thoracomere. $\times 32$.

The carapace covers but is not fused to the second thoracomere (GSC 13320, GSC 13316) (fig. 12).

The thoracic pleura were only slightly developed (GSC 13316, GSC 32785) (fig. 13). Thoracopods 2 through 8 are poorly preserved but appear to have the following structure: There was a protopod of two short segments, the coxa and basis. The endopod had five subequal segments, each about as long as the protopod, with the knee occurring between the carpus and propodus. No exopods were preserved. The structure of the first thoracopod is not determinable, only 2 through 8 can be verified (GSC 13322) (fig. 14).

The abdominal pleura were well developed, becoming more pointed posteriorly as one proceeds caudad (GSC 13316, GSC 13320). The five pairs of pleopods were well developed and apparently biramous (GSC 13323). The telson was spatulate with prominent spines (GSC 13321). The uropods were lobate (GSC 13321, GSC 32785). The endopod had a single setose element. The exopod had a proximal element with a thick lateral



FIG. 13. *A. novascotica*. GSC13316. Holotype. $\times 10.6$.



FIG. 14. *A. novascotica*. GSC13322. Exposing the ventral surface of the thorax. $\times 18$.

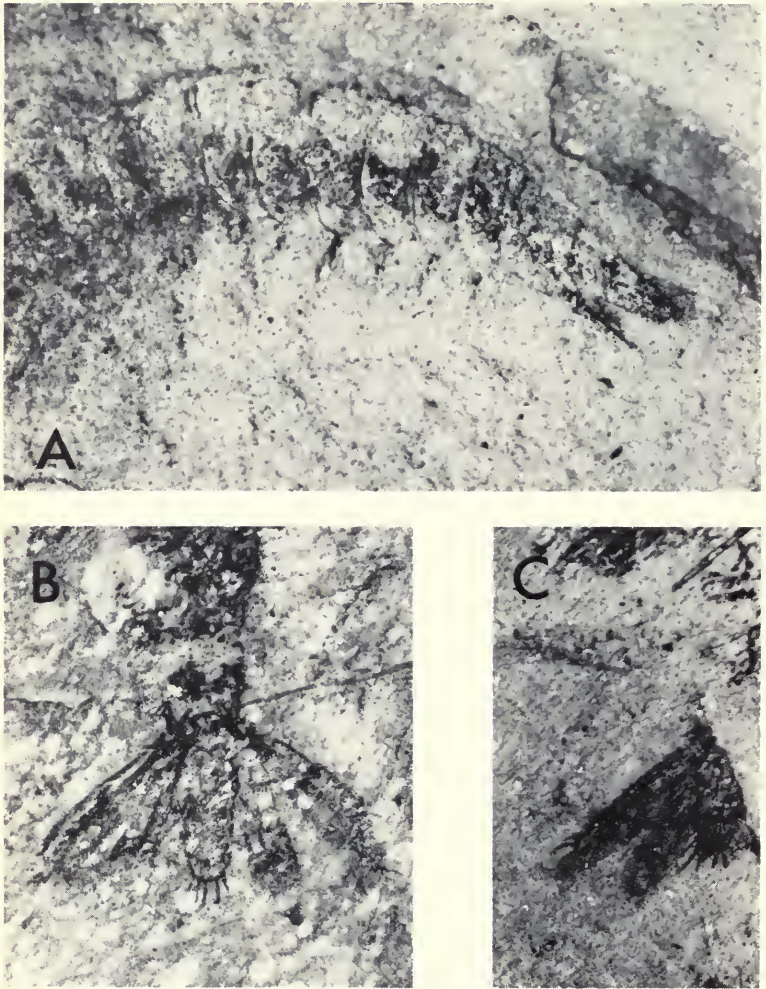


FIG. 15. *A. novascotica*. A, GSC13323. With pleopods. $\times 15.5$. B, GSC13321. With telson and uropods. $\times 15$. C, GSC13317. With part of telson and uropods. $\times 15$.

border, with spines located distally; and a smaller distal setose element (fig. 15). A reconstruction of *Acadiocaris novascotica* is offered in Figure 16.

Remarks.—The material for *Acadiocaris novascotica* is of poor quality. It consists of black carbonaceous, pyritized films on a black shale. The matrix is crumbling. The material has to be studied under xylene or glycerol to see details. The fossils appear to be disintegrating with time as the pyrite in them is oxidizing. (All photos of this animal were taken under xylene.)

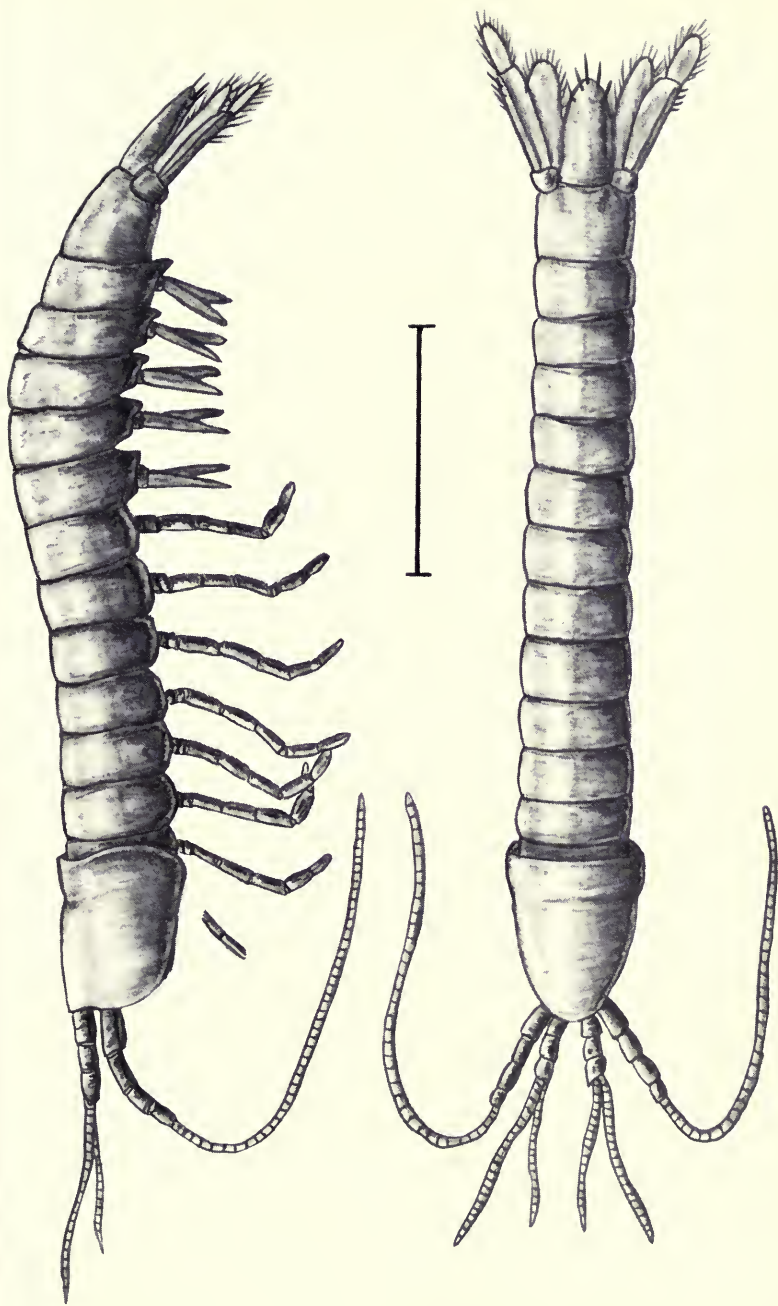


FIG. 16. *A. novascotica*. Reconstruction. Scale denotes 2 mm.

TABLE 2. Measurements of specimens of *Acadiocaris novascotica* in millimeters (* denotes holotype.)

Specimen	Length from head to base of telson	Length of cephalothorax	Length of abdomen (without telson)	Length of telson	Length of carapace	Antennal peduncles
GSC 13316*	9.4 (?)	5.8 (?)	3.7			{ 1st antenna—1.2 2nd antenna—1.5
GSC 13319						
GSC 13320	7.5	4.4	3.1	1.3	1.3	
GSC 13321				1.0		
GSC 13323		3.7	3.1			

Oöstegites, the prime peracaridan character, were not observed. But oöstegites are typically lost in modern peracarids after breeding. Only one specimen (GSC 13322) preserved features, though very poorly, of the ventral surface (fig. 14). Despite these deficiencies, *Acadiocaris* is most probably a spelaeogriphacean since so many characters combined to indicate such, viz., the four segments in the second antenna peduncles, the carapace covering but not fused to the second thoracic segment, the knee of the thoracic endopods between the carpus and propodus, and features of the telson and uropods.

No thoracic exopods were noted. These structures are important features (Grindley and Hessler, 1971) on the modern spelaeogriphacean, *Spelaeogriphus lepidops*. The absence of exopods on these fossils should not be taken as evidence that they were never present, especially in view of the poor state of preservation.

In comparing *Acadiocaris* to *Spelaeogriphus*, the differences encountered would seem to separate these two genera at a level to warrant separate families. *Acadiocaris* has features that would be of a more primitive nature when compared to *Spelaeogriphus*. The carapace, rectangular in outline, lacks any optic notch. The thoracopodal endopods seem to be well developed, relatively large, with marked segments as compared to *S. lepidops*. The pleopods are natatory in form and are present on the first five pleomeres. Since no formal diagnosis has been previously written for the Spelaeogriphidae, one is presented here.

Family SPELAEOGRIPHIDAE Gordon, 1957

Carapace with prominent optic notch; thoracopods present but somewhat reduced in size and modified, exopods two to four natatory in structure and five to seven (or eight) branchial; natatory pleopods well developed and present on first four pleomeres, fifth pair of pleopods vestigial. (*Recent*)

DISCUSSION

With the recognition of a diverse array of Peracarida in the late Paleozoic the Peracarida are now known to be among the most ancient of eumalacostracans. The Mississippian saw the specialized pygocephalomorph mysidaceans, spelaeogriphaceans, and possibly tanaidaceans. By Pennsylvanian time there were definitely tanaidaceans and isopods. The existence so early of such an assemblage with advanced peracarid forms indicate that the peracarid radiation was probably initiated in Devonian time when it is generally thought caridoid eumalacostracans were taking origin.

The predominant aspect of this peracarid Paleozoic radiation was in a specialization of the primitive mysidaceans, the pygocephalomorphs. These caridoid forms are perhaps the most distinctive of the Paleozoic groups. The significance of the pygocephalomorphs has already been discussed (Schram, 1974).

Of the remaining groups known in the Paleozoic, it is noteworthy that two of them, the spelaegriphaceans and phreatoicidean isopods, occupied marine habitats. Today, however, these groups are exclusively freshwater forms.

The spelaegriphaceans were previously known from one species, *Spelaegriphus lepidops*. No other living species have been found, though if others exist they should probably be sought in the Gondwana areas (Australia, India, Africa, South America, and Antarctica). This Gondwana distribution is a pattern which has been displayed in many other groups in various phyla; among them the crustacean groups of phreatoicidean isopods and anaspidae and stygocaridacean syncarids. *Acadiocaris novascotica* preserved certain primitive anatomical conditions, such as lack of optic notches, well-developed thoracic endopods, and five pair of functioning pleopods. But *Acadiocaris* is of additional significance because of its location, on a Laurasian northern continent, and its near-shore marine habitat.

This is a repetition of what has become a classical situation for many crustacean groups: origin in a marine habitat (possibly in Laurasian waters), and later dispersal into Gondwanaland and freshwater refugia.

An identical and more complete pattern of this Laurasia-Gondwana history is seen in the phreatoicidean isopods. *Hesslerella shermani*, the earliest of these forms, is marine, and as indicated above, is anatomically intermediate between the Palaeophreatoicidae and the Amphisopidae. Is *Hesslerella* an advanced paleophreatoicid linking the more primitive members of the family to other phreatoicideans (indicating an even earlier and as yet undiscovered history of isopods)? Or is *Hesslerella* a primitive form which in turn gave rise to the two families? This dilemma is perhaps insoluble for the time being since so little is known anatomically about the other palaeophreatoicids, especially the structures of the appendages.

The Permian palaeophreatoicid genera, *Palaeophreatoicus* and *Palaeocrangon*, are both found in marine habitats. The former is found in the Soviet Union near Archangel on the Arctic coast east of Finland. *Palaeocrangon* is found in northern Germany and England. Combining these with the Illinois location of *Hesslerella*, an Appalachian-Caledonian affiliation is noted for the Late Paleozoic. The earliest amphisopid is

Protamphisopus reichelti Glaessner, 1962 of the Zechstein of Germany, beds equivalent in age to those containing *Palaeocrangon*. *P. reichelti* is associated with a marine fauna containing, among other things, the only fossil cumacean (mistakenly described as a carapace of a phyllocarid, *Nebalia bentzi* Malzahn, 1958) and *Ophthalmapseudes rhenanus* (Malzahn) 1957, a tanaidacean. In Triassic time *Protamphisopus wianamatensis* (Chilton) 1918 is known from freshwater deposits in Australia. The transition of phreatoicideans from marine to freshwater habitats thus seems to have been effected in early Triassic time.

It is now evident that the Permo-Triassic was a time of profound change within the Peracarida. As stated above, there is evidence that the phreatoicidean isopods had undergone an expansion in marine waters of the Permian and that by the close of the Triassic they had already occupied the southern continent refugia they are known in today. This "marine Laurasia to freshwater Gondwana" change is a duplicate of a pattern seen in the Syncarida (Schram and Schram, 1974). It is also probable that the spelaeogriphaceans (marine in the Mississippi and freshwater today) underwent a similar transition in the Permo-Triassic, conforming to the above pattern, though there is still no definite evidence for such a transition in the Permo-Triassic fossil record.

There has been some difference of opinion on evolution within the Isopoda regarding the relation of the Phreatoicidea to the other suborders. Chilton (1894) and Barnard (1927) placed the phreatoicideans close to the Asellota, a group which is generally considered to have several primitive characters. Nicholls (1943, 1944), in his monographic review of the phreatoicideans, argued for their derivation from the Flabellifera. Hessler (pers. comm.) believes the phreatoicideans to be very specialized.

In an attempt to arrive at a judgement of which organisms and characters are primitive in the Isopoda, an analysis of characters within the various suborders and possible isopod precursors was attempted (table 3). A series of characters was arrived at that were felt to reflect an archetypal isopod condition—an "isopodan facies." These characters are: *Normal mouthparts*, which refers to all oral appendages and parts being present and at least relatively unmodified or not lost as adaptations toward special feeding types such as sucking; *Thoracic coxae small and free*: where the coxal joints are not enlarged, specialized, or fused into the thoracic pleura, i.e., they are functional, freely moving joints; *Pereiopods isopodous or relatively so*: refers to a condition where the appendages are similar except for the typical slight changes in orientation that occur between anterior and posterior groups; *Abdominal segments free*: with none of the anterior

pleomeres fused to form a solid unit (this does not refer to the pleotelson involving the sixth pleomere which seems to have been formed independently in various groups); *Pleopods primarily natatory*: reflecting a primitive function of pleopods seen in lower peracarid groups which was abandoned in favor of a strictly respiratory role in isopods; *Body rounded*: or perhaps somewhat laterally flattened as it is in most of the lower peracarids. In addition to the characters just enumerated, there are two features whose exact status and condition is somewhat obscure: *Number of antennal peduncular segments*: six is the largest number with five being most common; *Uropods biramous, subterminal, and styliiform*: the opposing case being uropods lateral and broad, a condition which might be equally considered primitive depending upon one's viewpoint.

In scoring the isopod suborders on the above characters, the phreatoicideans emerge as the most primitive. The ambiguity evidenced in Table 3 in the Flabellifera is due to the specialization of some families toward a parasitic mode of life. The Cirolanidae, however, come closest to a primitive condition and differ from phreatoicideans only in having a dorso-ventrally flattened body and great epimeral development on the pereiomeres. I consider both these features more advanced. The Asellota differ significantly from phreatoicideans in having the dorso-ventral flattening, fused pleomeres, and a distinct dicotomy of structure between anterior and posterior pereiopods.

Dahl (1954) investigated embryos and brood pouch young of *Mesamphisopus capensis* and found similarities in the uropods, pleon shape, and gnathopods to cirolanid and valviferan types. He took these similarities as almost positive proof of Nicholls' (1943-1944) contention that phreatoicideans are derived from cirolanid flabelliferans. It would seem, however, that one can make the opposite claim with equal validity, that flabelliferans and valviferans arose from phreatoicideans by, at least in part, neotenus processes.

The Paleozoic fossil record now is known to have an extensive phreatoicidean history on several continents in differing habitats antedating the appearance of the flabelliferans, *Isopidites* and *Ankelacephalon*, in the Triassic of Europe. This predating, of course, cannot be used as positive evidence that phreatoicideans came first, but certainly must be considered.

I feel it is a mistake to insist that one group, as we now understand them based largely on Recent forms, gave rise to the other. I believe that phreatoicideans, especially with the evidence of *Hesslerella*, stand closest to the isopodan archetype described above, an archetype that can, in turn, be easily derived from isopod precursors among the known peracarids.

TABLE 3. Analysis of supposed archetypal isopod characters in the known suborders of Isopoda. + denotes character as stated present; - denotes some more derived condition present, ± denotes some members with primitive condition and some with a derived state.

Suborders of Isopoda	Normal mouthparts	Body rounded	Thoracic coxae small and free	Pereiopods isopodous or relatively so	Abdominal segments free	Uropods		Antennal peduncle, No. of segments
						Pleopods primarily natatory	biramous, subterminal, and styliform	
Asellota	+	-	+	-	-	+	+	6
Phreatoicoidea	+	+	+	+	+	+	+	5
Flabellifera	±	-	±	+	±	-	-	6 & 5
Gnathidea	-	-	±	+	+	-	-	4
Anthuridea	-	+	±	+	±	-	-	5
Valvifera	+	-	-	+	-	-	-	5
	(-)							
Oniscoidea	+	-	-	+	±	-	+	5
	(-)							
Epicaridea	-	-	-	+	+	-	-	

The major thrust of the Paleozoic peracaridan radiation occurs in the primitive groups, in the form of the epibenthic pygocephalomorph mysidaceans. This group had a radiation reaching a peak in the Pennsylvanian and then became extinct in the Permian. The last pygocephalomorphs seem to have at least partially conformed to the Gondwana pattern, with the Permian family Notocarididae being restricted to Gondwanaland (*Paulocaris* of Brazil and *Notocaris* of South Africa).

Only two peracaridan groups reported from the Paleozoic, the tanaidaceans and cumaceans, have not experienced the Gondwana pattern. Both these groups are present in the seas of the world today virtually unchanged.

The peracarids underwent some significant evolutionary events in the Permo-Triassic. Peracarids, however, are major elements in the modern fauna, and, indeed, with recent discoveries in the deep sea, are probably the largest group of eumalacostracans today. The Paleozoic constituents of the peracarids are different from those of today. Mysidaceans are now represented by the predominantly pelagic suborder Mysida. The isopods are now composed of the more advanced, dorso-ventrally flattened types with most of the non-parasitic forms being benthic. The cumaceans, which have some freshwater species, and tanaidaceans are both predominantly marine, benthic, infaunal, detritus feeders. Apparently, the only peracarids to appear since the opening of the Mesozoic, the Amphipoda, is another predominantly benthic group.

What seems to have occurred is this: with the development of schizopodous caridoids in the Devonian, there was a rapid diversification of the basic peracarid orders (with the possible exception of the amphipods). The functional emphasis in the Paleozoic peracarids was on the epibenthic types such as pygocephalomorphs. At the close of the Permian, with the development of decapods and advanced peracarids, the primitive peracarids either occupied refugia or became extinct. The new wave of peracarids are adapted to benthic modes of life and also radiated in the deep sea where today they are the dominant crustacean forms. This specialization is in contrast to the Eucarida which effectively occupy pelagic and epibenthic habitats.

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