

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 103, NUMBER 9

MYSTACOCARIDA, A NEW ORDER OF
CRUSTACEA FROM INTERTIDAL
BEACHES IN MASSACHUSETTS
AND CONNECTICUT

(WITH TWO PLATES)

BY

ROBERT W. PENNAK

Biology Department, University
of Colorado

AND

DONALD J. ZINN

Osborn Zoological Laboratory,
Yale University



(PUBLICATION 3704)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
FEBRUARY 23, 1943



SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 103, NUMBER 9

MYSTACOCARIDA, A NEW ORDER OF
CRUSTACEA FROM INTERTIDAL
BEACHES IN MASSACHUSETTS
AND CONNECTICUT

(WITH TWO PLATES)

BY

ROBERT W. PENNAK

Biology Department, University
of Colorado

AND

DONALD J. ZINN

Osborn Zoological Laboratory,
Yale University



(PUBLICATION 3704)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
FEBRUARY 23, 1943

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

MYSTACOCARIDA, A NEW ORDER OF CRUSTACEA
FROM INTERTIDAL BEACHES IN MASSACHU-
SETTS AND CONNECTICUT

By ROBERT W. PENNAK

Biology Department, University of Colorado

AND

DONALD J. ZINN

*Osborn Zoological Laboratory
Yale University*

(WITH 2 PLATES)

During the course of recent investigations on the ecology of the micrometazoa inhabiting the capillary waters of intertidal beaches in Massachusetts and Connecticut (Pennak, 1942a, 1942b; Zinn, 1942), more than 65 specimens of a small peculiar entomostracan were found. When these organisms were first examined superficially it was thought that they were copepods. In size, in their basic 16-segmented structure, in the general organization of the body into head, thorax, and abdomen, and in the number and arrangement of the appendages (see pl. 1, fig. 3), they appeared to be an aberrant species of Harpacticoida. A more detailed study, however, revealed that in certain fundamental anatomical features they were markedly different from copepods—so different, in fact, as to warrant the erection of a new order, the order *Mystacocarida*. A brief diagnosis of this group is given in the following paragraph.

ORDER MYSTACOCARIDA

The *Mystacocarida* are microscopic Entomostraca inhabiting the interstitial waters of intertidal beaches. Only females are known. The body is colorless, distinctly segmented, cylindrical, vermiform, and elongate; it is divided into a large head, a single-segmented post-cephalosome, a 4-segmented thorax, and a 6-segmented abdomen. The head is elongate, with a cephalic shield, prominent rostrum, and ocelli; it bears two pairs of antennae, a labrum, a pair of mandibles, and two pairs of maxillae. The first antennae are large, elongate, uniramous, and sensory. The second antennae are prominent, biramous, sensory, and elongate. The large labrum is flat, broad, and movable; it is at-

tached to the head between the bases of the antennae and extends posteriorly as far as the postcephalosome. The mandibles are biramous and unmodified, while the first and second maxillae are uniramous and elongate. The postcephalosome bears a pair of flat, broad, irregular mouthparts (ordinarily corresponding to the maxillipeds of other groups). Each thoracic segment has a pair of small, unsegmented lamellar appendages. The terminal (anal) segment bears two large caudal rami which have prominent setae. None of the appendages are prehensile. The dense setation of the median margins of the mouthparts indicates that the Mystacocarida probably feed by straining particles of food from the interstitial water. They move through the capillary spaces by wormlike wriggling movements aided by natatory movements of the second antennae, mandibles, and to some extent the first and second maxillae. Most of the body segments are provided with a pair of lateral, dorsoventral, shallow troughs which have heavily chitinized edges. The indistinct genital aperture is on the first thoracic segment, and the anus is on the last abdominal segment between the bases of the caudal rami. Several larval stages have been found. Only one species is known.

So far as is known, the Mystacocarida are confined to the intertidal zones of marine beaches. They are a part of the complex community of bacteria, protozoa, and microscopic metazoa including harpacticoid copepods, Tardigrada, Nematoda, Oligochaeta, Acarina, and several other groups which inhabit the capillary water between the grains of sand. The Mystacocarida are probably facultative anaerobes since they may occur in portions of the intertidal sand where oxygen may be either absent or present in small quantities.

Superficially, the Copepoda and the Mystacocarida are somewhat similar. The two groups may be most easily distinguished from each other, however, on the basis of the number of segments comprising the head, thorax, and abdomen. In copepods the maxilliped segment is fused with five other anterior segments to form the head, and, in addition, the first thoracic segment is usually fused with the head, the whole thus constituting a cephalothorax. In the Mystacocarida, on the other hand, both the maxilliped segment and the first thoracic segment are distinct and separate from the head. Furthermore, the maxilliped segment is clearly separated from the thorax by a ventral constriction. According to the terminology of Sars (1901, 1903-1911) as clarified by Monk (1941), copepods typically have five thoracic (metasome) segments and five abdominal (urosome) segments. Although there are 10 segments posterior to the maxilliped segment in the Mystacocarida, there is no specialized movable articulation between

thorax and abdomen. The first four segments following the maxilliped segment, however, bear appendages which presumably are comparable with the thoracic appendages of the Copepoda. There are no signs or rudiments of a pair of appendages which would indicate the fifth thoracic segment. The maxilliped segment is so distinctive and unique, and is so sharply set off from the adjacent regions of the body in the Mystacocarida, that it may be conveniently termed a postcephalosome. The body of the Mystacocarida therefore may be divided into a head, a single-segmented postcephalosome, a 4-segmented thorax, and a 6-segmented abdomen.

Except for the first and second antennae, the appendages of the Mystacocarida differ markedly from those of the Copepoda (see pls. 1 and 2). The mandibles are biramous and elongate, the first and second maxillae are uniramous and elongate, and the postcephalosome appendages (maxillipeds) are irregular, broad, and flat. The large size and the dense median setation of the relatively unspecialized and primitive mouthparts indicate that they function in straining food particles out of the interstitial water of sandy beaches. The smaller mouthparts of the Copepoda, on the other hand, are usually composed of relatively few segments and are more or less specialized for the manipulation of food; this is especially true of harpacticoid copepods which inhabit sandy beaches. Not only are the trophic rami of the Mystacocarida large and unspecialized, but also the head is proportionately much longer than it is in the Copepoda. All of the thoracic appendages show a reduction and simplicity found only in the fifth legs of a few copepods. Each leg is a simple, unsegmented lamella which is probably useless in swimming or crawling.

Between the bases of the mouthparts of the Mystacocarida there is an enormous, movable, broad, flat labrum. The labrum of the Copepoda is an insignificant structure.

On the posterior part of the cephalic shield, on the maxilliped segment, on each thoracic segment, and on each of the first five abdominal segments, there is a pair of lateral, dorsoventral, shallow troughs with heavily chitinized, sculptured edges. Structures of a somewhat similar nature are known in only one species of Copepoda (Zinn, 1942). No function can be ascribed to them.

Finally, the Mystacocarida may be differentiated from the Copepoda on the basis of the location of the genital pore; in the former group it is on the first thoracic segment, while in the latter it is on the last thoracic segment.

The peculiar location of the genital pore in the Mystacocarida represents an unusual condition. In the great majority of Crustacea the genital pore is at or near the posterior end of the thorax. Indeed, according to the Calman scheme, the thorax is defined as that region behind the head and in front of, and including, the segment which bears the male genital pore; also, with the exception of the hermaphroditic Cirripedia, the female genital pore is on the last or third-last thoracic segment. Such a definition is arbitrary, to be sure, but it is in striking contrast to the situation in the Mystacocarida.

In spite of the numerous significant morphological differences between the Copepoda and the Mystacocarida, the similar segmentation, the general body organization, and the number and arrangement of the appendages constitute convincing evidence that these two orders are very closely related. Certainly it does not seem possible to demonstrate important phylogenetic affinities between the Mystacocarida and any other order.

Undoubtedly, the Mystacocarida are the most primitive living Crustacea which have thus far been discovered. In addition to the simple body organization, this is clearly indicated by the persistence of larval characters in the head, including the unspecialized primitive morphology of the large mouthparts, the labrum, and the rostral shield. The lamellar structure of the abdominal appendages, on the other hand, is obviously a reduced condition.

DEROCHEILOCARIDAE, new family

Characters as of the type genus, *Derocheilocaris*

DEROCHEILOCARIS, new genus

Body elongate and cylindrical; all segments clearly marked off from each other; thorax and abdomen about the same diameter throughout; head and postcephalosome distinctly narrower than rest of body. Head covered with a cephalic shield which has a large rostral plate bearing a prominent, notched rostrum. Anal segment with a large papilla dorsal to the anus. A pair of lateral, dorsoventral troughs with heavily chitinized edges on the posterior part of the cephalic shield and on all other segments except the last.

First antennae 8-segmented, the terminal segment longest. Second antennae tactile and natatory; both rami elongate. Both rami of mandibles elongate, but endopod distinctly shorter than exopod; gnathobase on basipod. Instead of projecting ventrally, the second antennae and mandibles are flexed so that they extend dorsally and laterally away from the median plane of the body. Labrum very

large and flat; posterior end, between bases of maxillipeds, forming a broad, smooth semicircle at its extremity. First maxillae uniramous, elongate, and composed of seven segments. Second maxillae uniramous, elongate, and 6-segmented; segments not so broad as those of first maxillae. Postcephalosome appendages (maxillipeds) irregular, flat, and broad; not distinctly divisible into exopod and endopod. Each thoracic appendage reduced to a small, simple, unsegmented lamella bearing a few terminal setae. Each caudal ramus prominent and curved dorsally to form a large terminal claw.

Genotype.—*Derocheilocaris typicus*.

DEROCHEILOCARIS TYPICUS, new species

PLATES I AND 2

Head about one-third as long as the rest of the body and separated from postcephalosome by a ventral constriction. Head and postcephalosome distinctly narrower than rest of body. Thoracic and abdominal segments all about the same size. Rostral plate separated from cephalic shield by a well-defined groove, and with three prominent notches at its anterior edge. The median notch is deep and ovoid. The lateroventral notches are also deep but are more nearly circular and are toothed along the ventral margins; it is possible that these may be remnants of chitinous troughs. Near the posterior margin of the median notch are several eyespots. Their number and exact position are variable but typically there are two pairs, one of which is rather small and close to the median line at the posterior end of the notch, while the other two ocelli are larger and more anterior and lateral. The last segment has a prominent median dorsal papilla which bears a single seta and a minute toothed papillule. On each side of the dorsal papilla there is a broadly triangular, flat, short, spinous process. The two caudal rami are slightly longer than the last segment, broad at the base, and are curved dorsally in the form of a large claw. Each ramus bears three large plumose setae, one dorsal and two lateral. The two lateral setae originate at about midlength of the ramus, one being slightly shorter than the ramus and the other about twice as long as the ramus. The dorsal seta originates near the base of the ramus and is slightly longer than the ramus. There are two small papillae on the dorsal surface of each ramus, the anterior one bearing a fine seta. Along the median ventral edge of each ramus are three small equidistant processes each of which bears a spinule.

The lateral chitinous troughs of the head are situated near the posterior margin of the cephalic shield; each of these is roughly

elongate but the dorsal and ventral extremities are irregular in outline; there are six to eight minute chitinous teeth along both the anterior and posterior edges. The troughs of the postcephalosome are irregular in shape but roughly cross-shaped with the vertical axis longer than the horizontal axis; there are four groups of one to four teeth along the inner margin of these two troughs. The troughs of the thorax and abdomen are situated in approximately the middle of the segments. They are all similar, being long and narrow with 10 to 14 triangular interlocking teeth on each side.

The location of the genital pore on the ventral side of the first thoracic segment is indistinctly indicated by the presence of a broadly obtuse chitinous ridge which projects anteriorly and ventrally near the anterior margin of the segment.

The first antennae are long and 8-segmented; the first three segments are short and broad, but the others are elongate, the terminal segment being the longest. The first segment bears one seta; the second has three, two of which are minute; the third has seven, four of which are minute; the fourth through eighth segments bear 3, 4, 4, 5, and 3 to 5 terminal setae, respectively. The first and second segments each have a small dorsal hook, and the terminal segment bears a single delicate aesthetask.

The second antennae are biramous with the 5-segmented endopod being about half again as long as the 9-segmented exopod. The basal endopod segment bears two short median setae while the third segment has a single seta. The terminal endopod segment is long and fingerlike and bears a fringe of fine hairs at its tip. The exopod segments are short; segments one, four, five, and six have a single short seta, while the seventh and eighth have a long plumose seta; the terminal segment is tipped with three long plumose setae. There are five aesthetasks, one on the basipod, one on the first exopod segment, one on the third, and two on the terminal segment. All the aesthetasks project laterally. Because of their delicacy they are often broken off in specimens which have been permanently mounted on slides.

The mandibles are of a generalized larval type. The 2-segmented endopod is about two-thirds as long as the 7-segmented exopod. The basal endopod segment bears a single median seta, while the other has two median and three terminal setae. Exopod segments three, four, five, and six bear a single terminal seta, the last three of which are plumose. The last exopod segment has three terminal plumose setae, two of which are short while the third is slightly more than twice the length of the entire exopod. The basipod bears a single

distal median seta and a prominent, curved, stout, spinelike gnathobase which has several small median spinules. All the segments of the mandibles are beset with small rows of fine hairs.

The seven segments of the uniramous first maxillae are somewhat broad and flat, the third segment being the largest. The basal segment is narrowed at its base where it is attached to the trunk; the second segment is short and is set off from the first and third segments by poorly defined articulations. Except for one small lateral seta on the sixth segment, all of the setae are stout and are arranged along the median margins of the segments (median and terminal margins in the case of the last segment). Beginning with the basal segment the setation of the first maxillae is 3-1-4-2-2-8. All of the setae except those of the terminal segment are borne on small projections.

The uniramous 6-segmented second maxillae are narrower and slightly longer than the first maxillae. The first and second segments are considerably larger than the other four. Like the first maxillae, these appendages are densely setose along the median margins; typically, the setation is 8-8-2-2-2-5. Three of the setae of the basal segment are borne on a prominent process; two setae of the terminal segment and one on the fifth segment are geniculate.

The structure of the postcephalosome appendages (maxillipeds) is unique. They are small, irregular, but somewhat elongate, and usually lie appressed to the trunk. It is likely that several exopod and endopod segments have become fused with the basipod to form the main body of the maxilliped. The remnant of the exopod consists of three small segments, the second and third of which bear two setae. The remaining endopod segments comprise a small bilobed outgrowth which bears five setae. The large basal portion of this appendage has three small lateral and two small median processes all of which bear one or two broad setae.

In studying the first antennae, first maxillae, second maxillae, and maxillipeds of about 20 specimens, it was found that there are occasional variations in the number and precise positions of the setae.

The four pairs of thoracic appendages are small, simple, unsegmented lamellae which lie rather closely appressed to the trunk. They are all about the same size and differ only slightly in shape. The first, second, and fourth appendages are roughly oblong, while the third is tapered slightly, is more ovate, and has a small median notch at about half length. The first abdominal appendages have two terminal setae, while the others have three terminal setae.

From the tip of the rostrum to the posterior end of the caudal rami the length of the adult ranged from 409 to 491 microns; the average length was 458 microns.

Cotypes, U.S.N.M. No. 80450 from Nobska Beach, Mass., have been deposited in the United States National Museum.

Larval stages.—A few specimens of five different larval stages were found. For convenience in making comparisons, these larvae have been arbitrarily numbered 1, 2, 3, 4, and 5 in order of their increasing size, complexity, and maturity. All have two pairs of antennae, mandibles, labrum, second maxillae, and caudal rami. Only the two largest stages have first maxillae and maxillipeds, although all five stages have a maxilliped segment (postcephalosome).

Except for the second antennae and mandibles, all of the larval appendages are strikingly similar to the corresponding appendages of the adult. Attached to the basipod of the second antenna, and more median than the base of the endopod, is an unsegmented biramous quasi palp in all larval stages. The undivided basal portion of this quasi palp is very short while the two rami are about as long as the adjacent endopod (see pl. 2, fig. 8). The distal half of the outer ramus and the distal third of the inner ramus consist of two setae of similar length. In addition, the outer ramus has two small setae near its base. Also, the endopod of the larval second antenna has four segments while that of the adult has five.

The presence of the unique quasi palp on the larval second antennae suggests interesting conjectures. Although the quasi palp is not a very well-developed or robust structure, it is possible that it may function, or at one time did function, as a clasping organ. The possibility then arises as to whether the fifth larval stage may be (or may have been in the past) a functional male phase as is the case in certain other protandrous Crustacea, Mollusca, and Nematoda. In none of the fifth larval stages, however, could any internal reproductive structures be discerned.

The endopod of the larval mandible also differs markedly from that of the adult. In the former it is composed of three broad segments, the terminal segment being much smaller than the other two. In the adult this ramus is composed of two long narrow segments.

The smallest larvae found have a total of only 3 segments posterior to the postcephalosome; the second smallest stage has 5 such segments; the next largest has 7; the other two have 10, the same as the adults. No thoracic appendages are present on the first three larval stages, but the fourth and fifth stages have 3 and 4 thoracic appendages, respectively. In all immature stages the posterior part of the cephalic shield, the postcephalosome, and all posterior segments except the last segment have chitinized troughs.

From the standpoint of morphological characteristics and size (see table 1), it is logical to assume that larval stage 4, larval stage 5, and the adult form a natural sequence. On the other hand, however, it seems very probable that the three earlier stages are an incomplete series and that there are still other early stages which were not discovered during the present investigation. It is particularly likely that there are very early larval stages which are comparable with copepod nauplii in their simplicity. Because of incomplete information concerning the various stages in the development of the Mystacocarida, therefore, no attempt will be made at this time to assign any descriptive, designative names to the five different types of larvae that are known.

TABLE 1.—*Summarized morphological characteristics of larval stages of Derocheilocaris typicus*

Larval stage	Number of segments in endopod of mandible	Quasi palp on basiond of mandibles	First maxillae	Postcephalosome segment	Maxillipeds	Number of thoracic and abdominal segments	Number of pairs of thoracic appendages	Average length, microns
1	3	present	absent	present	absent	3	0	187
2	3	present	absent	present	absent	5	0	203
3	3	present	absent	present	absent	7	0	250
4	3	present	present	present	present	10	3	350
5	3	present	present	present	present	10	4	390
(adult)	2	absent	present	present	present	10	4	458

Internal anatomy.—Although only a superficial study was made of the internal anatomy of *Derocheilocaris typicus*, it might be worth while to indicate a few of the more obvious structural details. In sexually mature individuals the most distinctive feature is a large, elongate, dorsal, granular yolk gland; the posterior end of this yolk gland extends as far as the fourth or fifth abdominal segment; anteriorly, it may not extend beyond the first abdominal segment, or it may extend as far forward as the second thoracic segment. The ovary consists of several immature ova (customarily three to seven); they are rather compactly arranged in the dorsal portion of the third and fourth thoracic segments; often the ovary is partially imbedded in the anterior portion of the yolk gland. A gonoduct could not be definitely distinguished. The digestive tract is tubular and without any pronounced constrictions or diverticula. Neither maxillary nor antennary glands could be discerned. The nervous system, as shown by longitudinal sections, is characterized by a series of extremely large

segmentally arranged ventral ganglia. There is considerably less fusion of the ganglia of the head than in other groups.

Occurrence.—Of five beaches examined in the vicinity of Woods Hole, Mass., *Derocheilocaris typicus* was found only in Nobska Beach near the town of Woods Hole and in a beach 5 km. east of Woods Hole near the town of Falmouth. About 50 mature and 12 immature specimens were collected during June and July, 1939. The great majority of these organisms occurred within a meter of the high-tide line at a depth of 12 to 16 cm. in the damp sand. Although many series of intertidal sand samples were collected at Baxter's Beach, Pine Orchard, Conn., between November 1937, and May 1942, this form was found only during April 1940.

ACKNOWLEDGMENTS

The senior author carried on the field work associated with this study during June and July, 1939, when he was a visiting investigator at the Woods Hole Oceanographic Institution. He wishes to express his gratitude to Prof. H. B. Bigelow, then director of the Institution, for his kindness in providing laboratory facilities. Both authors thank Prof. G. E. Hutchinson, of Yale University, for his many helpful suggestions.

LITERATURE CITED

MONK, C. R.

1941. Marine harpacticoid copepods from California. *Trans. Amer. Microsc. Soc.*, vol. 60, pp. 75-99.

PENNAK, R. W.

- 1942a. Harpacticoid copepods from some intertidal beaches near Woods Hole, Massachusetts. *Trans. Amer. Microsc. Soc.*, vol. 61, pp. 274-285.
1942b. Ecology of some copepods inhabiting intertidal beaches near Woods Hole, Massachusetts. *Ecology*, vol. 23, pp. 446-456.

SARS, G. O.

1901. An account of the Crustacea of Norway, vol. 4, pp. 1-4. Bergen Museum.
1903-1911. An account of the Crustacea of Norway, vol. 5, Copepoda Harpacticoida. 449 pp. Bergen Museum.

ZINN, D. J.

1942. An ecological study of the interstitial microfauna of some marine sandy beaches with special reference to the Copepoda. Dissertation, Yale Univ.

EXPLANATION OF PLATES

PLATE I

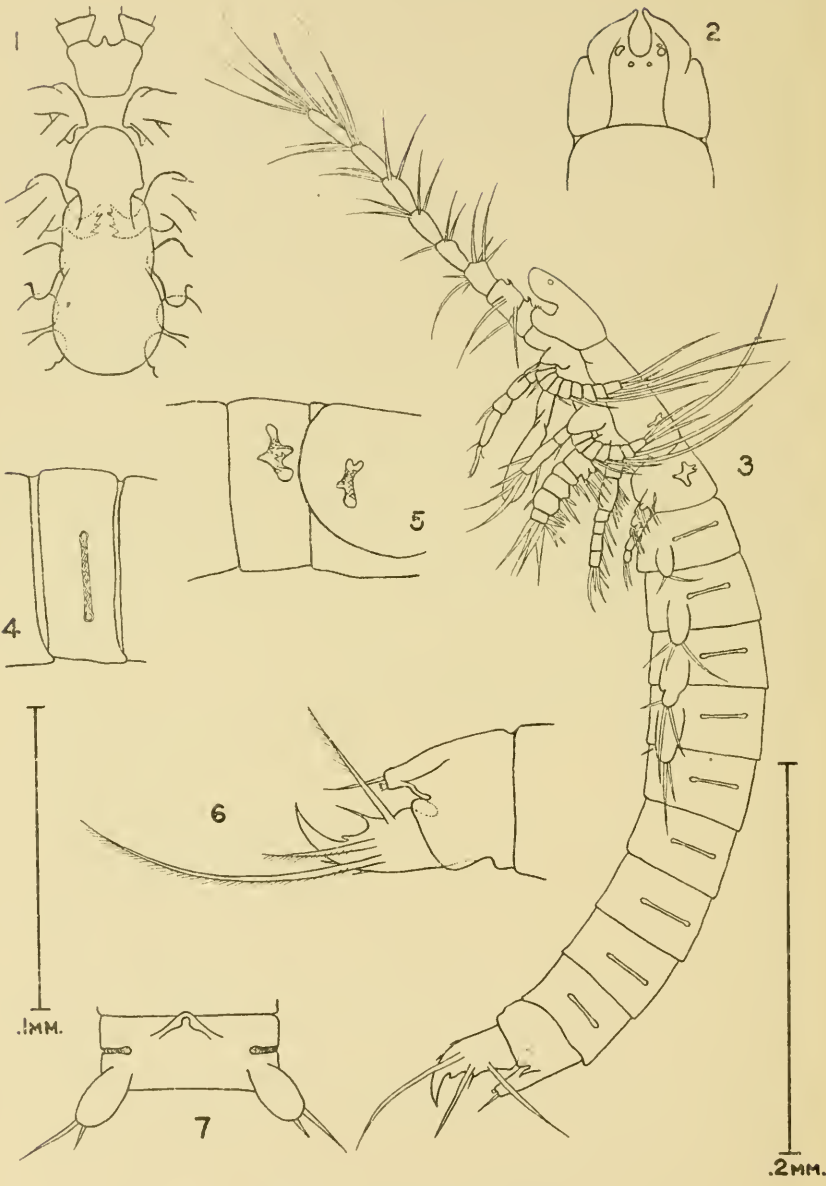
Derocheilocaris typicus

1. Ventral view of head region of adult showing relationships between labrum and basal portions of first antennae through maxillipeds.
2. Dorsal view of cephalic shield, showing notches, sutures, and ocelli.
3. Lateral view of adult.
4. Lateral view of abdominal segment showing detailed structure of a chitinous trough.
5. Lateral view of posterior part of head and postcephalosome showing details of chitinous troughs.
6. Lateral view of posterior end.
7. Ventral view of first thoracic segment showing region of genital opening. (Large scale refers to figure 3; small scale refers to all other figures.)

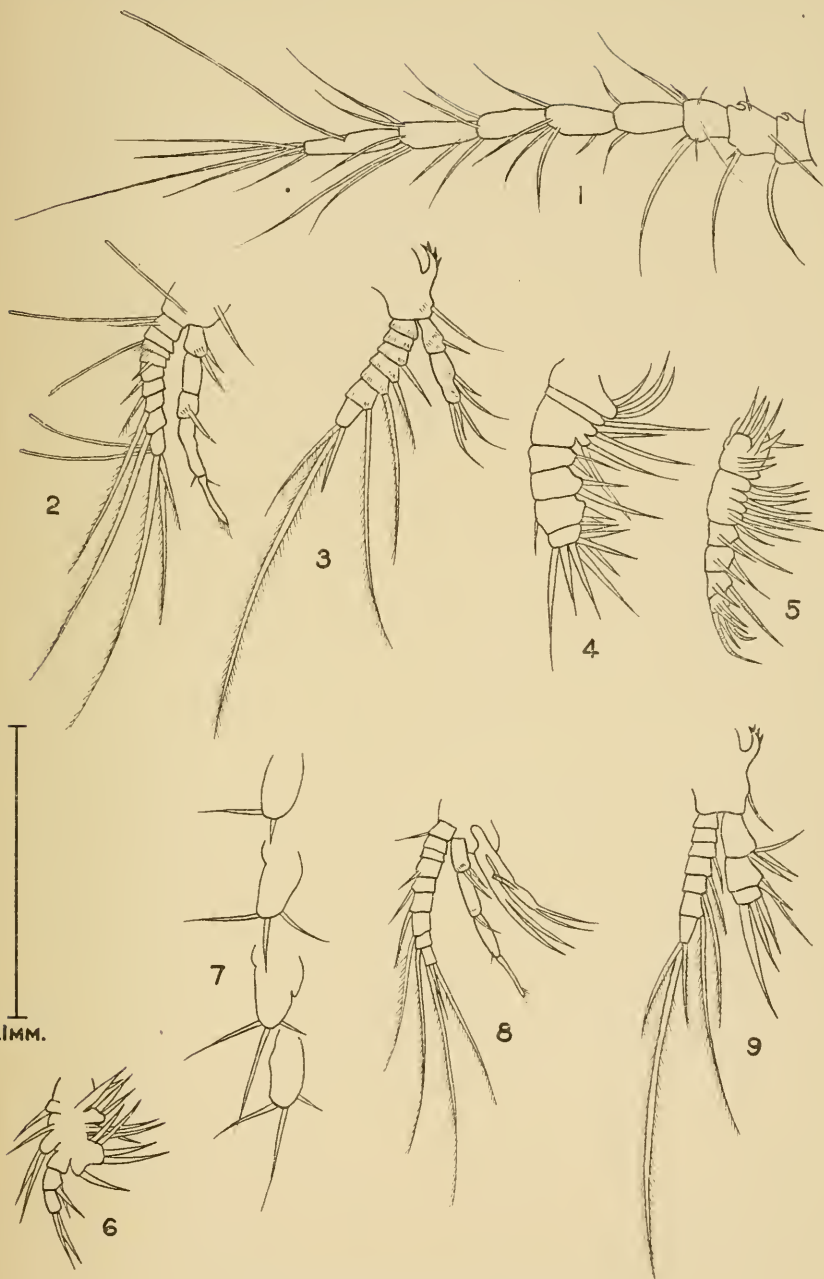
PLATE 2

Derocheilocaris typicus

1. First antenna of adult.
2. Second antenna of adult.
3. Mandible of adult.
4. First maxilla of adult.
5. Second maxilla of adult.
6. Maxilliped of adult.
7. Right thoracic appendages of adult.
8. Second antenna of fifth larval stage.
9. Mandible of fifth larval stage.



DEROCHEILOCARIS TYPICUS
(For explanation, see page 11.)



DEROCHEILOCARIS TYPICUS
(For explanation, see page II.)