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and *H. tridens tridens* de HAAN (Crustacea, Brachyura)  
Reared in the Laboratory

INVERTEBRAT  
ZOOLOGY  
Crustacea

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**Larval Development of *Helice tridens wuana* RATHBUN  
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This is the second of the series of our studies on the larval development of the estuarine crabs (BABA & MIYATA, 1971). The marsh crab, *Helice tridens tridens* de HAAN is very common in Japan from Aomori Bay and southwards and chiefly inhabits reed marshes along the mouth of the river. Around the estuary of the river Shirakawa, Kumamoto, another subspecies, *Helice tridens wuana* RATHBUN, having a smaller carapace, is also known to us to be there, and seems to prefer the more muddy habitat which it shares with the ocyroid crab, *Macrophthalmus japonicum*, but sometimes occurs mixed with the former subspecies in rather lower level close to the sea.

No information of the first zoeae and further development of both subspecies is procured so far. This paper describes all zoeal stages of the crabs and extensive description is also given to more advanced stage when succeeded in rearing.

Adult crabs were identified by Dr. M. TAKEDA of Kyushu University. For food of the larvae the authors thank the staff members of the Fisheries Research Laboratory of Kumamoto.

### Methods and material

Egg-laden females of *Helice tridens wuana* RATHBUN and *H. tridens tridens* de HAAN were collected from the mouth of the river Shirakawa, Kumamoto and maintained in each a compartment. Immediately after hatching the larvae were transferred into an aquarium with amount of 30 liters containing 60 percent (by volume) of artificially made sea water that was aerated with air stone. Rotifers, *Brachionus plicatilis*, were fed to first zoeae, and *Artemia* nauplii to second and subsequent larvae. The water was renewed once in part a day. The temperature in the aquarium ranges from 22.9 to 24.6°C with a mean of 23.8°C in rearing *H. tridens tridens*, and 17.5 to 25.5°C with a mean of 21.5°C in *H. tridens wuana*.

### Results

A parent female crab of *Helice tridens tridens* released zoeae from her abdomen on 3rd June 1970. The larvae had five zoeal stages and reached the megalopa stage on 18th June, and all died without molting to the crab stage. Zoeae of *Helice tridens wuana* hatched on 25th April 1971 and developed into the first crabs on 29th May, passing through five zoeal and one megalopa stages. The characteristics of the larvae of each stage are described below.

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\* A part of this paper was read at the 41st meeting of the Zoological Society of Japan, held at Fukuoka, Oct. 11, 1970.

## General morphology of the zoeal stages

### FIRST ZOEAL.

*Helice tridens wuana* (Fig. 1). — Age: 1–8 days. Length (a distance between tips of the rostral and dorsal spines): 1.12 mm. The cephalothorax has a slender rostral spine anteriorly extended, which is slightly longer than the dorsal spine. Long and slender lateral spines are present. The eyes are not stalked. The abdomen consists of five segments and the telson. The first abdominal segment is completely covered by the carapace. The second segment bears an anteriorly directed lateral spine on either side, and the third segment likewise has a minute lateral spine. The posterior lateral margin of the abdominal segments 3–5 ends in a short blunt point. The telson is bifurcated in two long processes to make a fork, and is terminally directed dorsally; internally it bears three pairs of well-developed plumose setae. The fork is also internally fringed with very fine setae.

Chromatophores are located on the followings: the base of the rostrum (near the base of the antennule); between the eyes; mandible; labrum; carapacial center; behind the dorsal spine; protopod of the first maxilliped; each abdominal segment.

*H. tridens tridens* (Fig. 6): — Age: 1–4 days. Length: 1.16 mm. Similar to the first zoea of *H. tridens wuana*, also in size. The rostral spine is as long as the dorsal spine. The fourth abdominal segment is additionally provided with a minute spine at the middle of the lateral border, which spine is directed posteriorly.

### SECOND ZOEAL.

*H. tridens wuana* (Fig. 2). — Age: 8–14 days. Length: 1.55 mm. The eyes are stalked and movable. The dorsal spine is longer and stouter than the rostral. The setation of the inner surface of the telson remains unchanged. The chromatophore pattern is as in the preceding stage.

*H. tridens tridens* (Fig. 7). — Age: 4–7 days. Length: 1.34 mm. No differences between these subspecies were observed.

### THIRD ZOEAL.

*H. tridens wuana* (Fig. 3). — Age: 14–17 days. Length: 1.90 mm. The postero-ventral margin of the carapace bears a few setae. The lateral spine becomes somewhat small proportionally. Abdominal segments increase to six. Pleopods appear as small buds. The setation of the telson is 4–4, the innermost pair being short. The chromatophore pattern is equal to that of the second zoea.

*H. tridens tridens* (Fig. 8). — Age: 7–9 days. Length: 1.56 mm. The postero-ventral marginal setae of the carapace are indistinct. The abdominal segments show no signs of pleopods.

### FOURTH ZOEAL.

*H. tridens wuana* (Fig. 4). — Age: 17–20 days. Length: 2.4 mm. About four setae fringe the postero-ventral margin of the carapace. The third maxilliped is simply bifurcated and subsequent thoracic appendages are simple buds; all these are concealed beneath the carapace. The distinct pleopods bear no endopods. The setation of the telson remains unchanged, but the inner pair grows up to the normal size.

*H. tridens tridens* (Fig. 9). — Age: 9–12 days. Length: 2.00 mm. No differences were noted.

## FIFTH ZOEAL.

*H. tridens wuana* (Fig. 5). — Age: 20–24 days. Length: 2.80 mm. The dorsal spine is equal to the rostral in length. The posterior margin of the carapace is fringed with short setae. The third maxilliped and the subsequent thoracic legs are as in the preceding stage but larger. Pleopods are well developed, without setae; each pleopod has a simple endopod. The setation of the telson is 5–5, the innermost pair is very small.

*H. tridens tridens* (Fig. 10). — Age: 12–16 days. Length: 2.51 mm. Similar to the fifth zoea of *H. tridens wuana*.

**Cephalothoracic appendages of the zoeal stages**

## ANTENNULE (Figs. 11–20).

*H. tridens wuana*. — The unsegmented antennule is conical, and ends in a group of setae and aesthetes. In the first zoea it bears three aesthetes and one short seta, the second and the following two stages have four aesthetes and one seta. The base of the antennule in the fifth zoea is inflated and bears about nine aesthetes terminally.

*H. tridens tridens*. — Similar to *H. tridens wuana*. The first zoea has two long aesthetes and a half size seta, the second and third bear each three aesthetes and one seta. The fourth is with four aesthetes and one seta, and the fifth with five aesthetes and one seta.

## ANTENNA (Figs. 21–30).

*H. tridens wuana*. — The antenna of the first zoea is made up of the cylindrical protopod with a spinous process and the exopod. The spinous process terminates at the middle of the rostral spine, with two rows of denticles along the whole length, one row consisting of three denticles and the other of eight. The exopod is slightly less than a half of the spinous process, having a short seta at the distal third. In the second zoea the number of denticles on the process increases to seven and eleven. The third zoea has a slight expansion of the endopod, the spinous process with a row of eight denticles and another of ten denticles. The endopod of the fourth zoea is considerably developed, non-segmented, and fails to reach the tip of the exopod; the spinous process has two rows of nine and twelve denticles, respectively. In the fifth zoea the endopod is well developed but unsegmented, and is slightly shorter than the spinous process of the protopod. The denticles on the process decrease to one and seven.

*H. tridens tridens*. — Similar to the antennae of *H. tridens wuana*, excepting the number of denticles on the spinous process of the protopod. The endopod of the fifth zoeal antenna terminates in the middle of the protopod process.

## MANDIBLE (Figs. 37–44).

*H. tridens wuana*. — The mandible of the first zoea consists of the incisor and molar processes. As the development advances the mandible progressively becomes larger, but the fundamental feature remains constant. The incisor process has three large teeth on one side and without teeth on the opposite side, for instance three teeth on the left mandible and one on the right. The molar process is cylindrical and its masticatory surface is flattened.

*H. tridens tridens*. — No differences were observed between the mandibles of *H. tridens wuana* and *H. tridens tridens*.

## MAXILLULE (Figs. 45–54).

*H. tridens wuana*. — The maxillule consists of two-segmented endopod and basal and coxal endites. These fundamental morphology remains constant throughout the zoeal stages. In the first zoea the endopod has the distal segment with two terminal, two subterminal and one lateral marginal setae, and also the proximal segment with a single seta. This setation is constant in all zoeal stages. The basal endite has five serrated (or plumose) setae or bristles in the first, seven in the second and third, eleven in the fourth and fourteen in the fifth zoea. The coxal setation from the first to fifth zoea is 4, 5, 5, 6, 8. In the second zoea a plumose seta appears on the opposite side of the basal endite or the base of the protopod, and it remains present in the subsequent zoeal stages.

*H. tridens tridens*. — No distinct differences were observed between the zoeal maxillules of both subspecies.

## MAXILLA (Figs. 55–64).

*H. tridens wuana*. — The maxillae of all zoeal stages are composed of an unsegmented endopod, coxal and basal endites and a scaphognathite. The endopod of the first zoea is slightly bifurcated, with two terminal and two long subterminal setae. This remains constant in all zoeal stages. The basal endite is feebly bifurcated and has eight setae in the first two zoeae, nine in the third, ten in the fourth, and fourteen in the terminal zoea. The coxal endite is likewise bifurcated weakly, having five setae in the first zoea, six in the second and third, nine in the following two stages. The scaphognathite of the first zoea possesses four plumose setae, and terminates in a long plumose point. In the second and third zoeae, the apical portion is rounded with the strong plumose setae; the marginal setae increase to eight and nine. In the following stages the fringing setae are completed, with 22 in the fourth and 28 in the terminal zoea.

*H. tridens tridens*. — Very similar to that of *H. tridens wuana*, but the bifurcations of the endites are sometimes indistinct. The setations throughout the zoeal stages are 6, 8, 9, 10, 16 in the basal endite, 5, 6, 6, 8, 8 in the coxal endite, and 4, 10, 11, 21, 30 in the scaphognathite.

## FIRST MAXILLIPED (Figs. 65–69).

*H. tridens wuana*. — The first maxilliped is composed of the protopod, five-segmented endopod and exopod slightly constricted at the middle. In the first zoea, the endopod has the setation of 2, 2, 1, 2, 5. This character remains unchanged in the second stage. The exopod bears four natatory setae in the first stage, and, as the development advances the setae increase to 6 (in second zoea), 8, 10, 12 (fifth zoea). The setation of the endopod is 2, 2, 2, 2, 5 in the third zoea, and 2, 3, 2, 2, 6 in the fourth and fifth.

*H. tridens tridens*. — The setation is completely agreeable with that of *H. tridens wuana*.

## SECOND MAXILLIPED (Figs. 70–74).

*H. tridens wuana*. — The second maxilliped throughout the zoeal stages is composed of the protopod, three-segmented endopod and the exopod similar to that of the first maxilliped. The endopod of the first zoea has the setation of 0, 1, 6, and this remains constant throughout all zoeal stages. Number of the natatory setae on the exopod from the first to fifth zoea is shown as 4, 6, 8, 10, 12.

*H. tridens tridens*. — As in the case of the first maxilliped, no differences were noted between these subspecies.

### THIRD MAXILLIPED.

*H. tridens wuana*. — The third maxilliped is poorly developed in the first three zocal stage. In the fourth stage it appears as a biramous bud, without setae, and it develops to the fifth stage, without morphological change.

*H. tridens tridens*. — Very similar to that of *H. tridens wuana*.

### General morphology of megalopa

*H. tridens wuana* (Figs. 76, 77-86). — Age: 24-36 days. Carapace length: 1.75 mm. The carapace is quadrangular, with a smooth dorsal surface. The rostrum is very short, slightly produced forwards at the middle and curves downwards. Between the eyes the anterior carapace is feebly hollowed. The pereopods are well developed and functional. The last pair is the smallest, having three long setae on the terminal segment. The eyes are large, and placed in a distinct orbit. The abdomen consists of six segments and the telson. The segments 2-3 have each a spine on either side of the posterior lateral border, that of the fifth segment is the strongest, almost reaching the posterior margin of the sixth segment. The telson is longer than the sixth segment, with four plumose short setae on the posterior margin. The second to sixth segment have each a pair of well-developed pleopod for swimming. The setation of these five pleopods is 18, 19-20, 17-18, 16-17, 11-12. Non-setose endopods appear in the second to fifth pleopods, and bear each three small hooks terminally. The sixth pleopod is two-segmented, without endopod.

Chromatophores are located on: eyestalks; center of the carapace; mid-lateral and postero-lateral portions of the carapace; abdominal segments.

*H. tridens tridens*. — Age: more than 16 days. Carapace length: 1.45 mm. Similar to *H. tridens wuana*, but considerably smaller. The telson bears three plumose setae on the middle of the posterior margin. The setation of the pleopods is 12, 12, 12, 14, 10.

### Cephalothoracic appendages of megalopa

*H. tridens wuana* (Figs. 77-84). — The antennule has an enlarged base with three-segmented peduncle. The basal segment of the peduncle bears three short setae terminally, the intermediate segment is with small unsegmented flagellum bearing four short setae apically. Twelve aesthetes are counted on the distal segment. The antenna of ten segments has the setation of 1, 1, 1, 0, 0, 2, 1, 3, 2, 2.

The mandible has the body with sharp cutting edge, and bears two-segmented palp which is furnished with nine simple setae on the anterior margin. The masticatory surface of the molar process disappears. The maxillule consists of unsegmented endopod with three plumose setae and one simple seta, and basal and coxal endites, both with numerous plumose bristles and setae. The maxilla is composed of a simple endopod, bilobed basal and coxal endites and a well-developed scaphognathite. The basal endite bears eleven plumose setae on the distal lobe and six on the proximal. The coxal is likewise equipped with three plumose setae on the distal lobe and eleven on the proximal. The scaphognathite is broadly developed with numerous fringing plumose setae.

The first maxilliped consists of unsegmented endopod with three terminal setae, exopod, epipod, and both endites. The endopod is two-segmented, the proximal segment having two plumose setae distally, and the distal four. The epipod is triangular in shape, with long simple setae marginally. The basal endite is not bilobed, bearing eleven setae, and likewise the coxal endite is with twelve setae.

The endopod of the second maxilliped is four-segmented, having one outer distal

marginal seta on the proximal second segment, five on the outer margin of the penultimate, and nine on the ultimate segment. The exopod of the second maxilliped is well developed, constricted at the middle and has five plumose setae of long size. The epipod is well developed, with about six setae of moderate length.

The third maxilliped is now well developed. The endopod consists of five segments, all segments being setose particularly internally. The exopod is constricted at the middle and bears four plumose setae terminally, its proximal segment having three simple setae marginally. The epipod is well developed, and very setose.

*H. tridens tridens* (Figs. 87-94). —Very similar to *H. tridens wuana*, excepting the setations of the appendages which seem insignificant. For details refer to the illustrations.

### General morphology of first crab

*H. tridens wuana* (Fig. 97). —Age: 36-41 days. Carapace, 1.3 mm wide, 1.4 mm long. The carapace is quadrangular, covered with short fine setae dorsally. The anterior half of the lateral margin bears four teeth, each with small denticles. The cardiac groove is distinct, transversely developed. The frontal region is medially hollowed. The orbit is well developed, its inferior margin is denticulated. Eyes are large, reaching the level of the lateral margin of the carapace. The pereopods are functional. The first is the cheliped, and the followings are ambulatory. The last leg is the smallest. All legs are sparsely setose marginally.

The abdomen is folded beneath the cephalothorax, and is composed of six segments and the telson; all are sparsely furnished with short setae excepting the first segment which bears five short plumose setae on either side. The pleopods are simple, losing swimming function.

Brownish chromatophores are distributed on the whole body, and the yellow chromatophores are limited to the cardiac, gastric, frontal regions and eyestalks.

### Cephalothoracic appendages of first crab

*H. tridens wuana* (Figs. 98-105). —The antennule is composed of a large basal segment and a peduncle of three segments. No fundamental change between megalopa and first crab stages were observed. The antenna is ten-segmented, with the setation of 4, 1, 0, 0, 0, 2, 1, 5, 3, 2; the setae are short. The mandible is similar to that of the megalopa, except for the increased setae on the palp.

The maxillule has the unsegmented endopod with six terminal setae and upper and lower laciniae. The upper bears two rows of setae, one marginal and the other slightly dorsally placed. The lower lacinia is also setose, most of the setae are in two rows in the manner of the upper lacinia.

The maxilla is very similar to that of megalopa.

The first maxilliped is composed of a simple endopod with two lateral marginal setae, the exopod, basal and coxal endites, and the epipod. The exopod is deeply constricted at the middle with two short plumose setae, and terminates in five long plumose setae. The elongated epipod bears long simple setae marginally. The setation of the endites is more complicated than in the megalopa.

The endopod of the second maxilliped is four-segmented and setose excepting the proximal second segment smooth. The exopod is unsegmented, but deeply constricted at the middle; the proximal half of the segment bears six short plumose setae on the distal half of the inner margin, and three plumose on the distal portion of the outer margin and further two simple setae on the proximal of the same. Terminally the exopod has five

plumose setae which are well developed. The epipod is developed, with seven setae. The endopod of the third maxilliped is wider than in the megalopa, and the fringing setae become shorter. The exopod is similar to that of the megalopa excepting that the proximal half has five short plumose setae on the outer border and nine on the inner. Short plumose setae grow dense on the proximal two-fifths margin of the epipod; long plumose setae fringe the remaining part.

### Discussion

Both of *Helice tridens tridens* and *H. tridens wuana* had five zoeal and one megalopa stages in the larval development under laboratory conditions and therefore comparison between these is justified. Through all larval stages *H. tridens wuana* is larger than *H. tridens tridens*, although the adult crabs are quite reverse, as mentioned introductorily. In the first zoeal stage they are different each other in the presence or absence of lateral spines on the fourth abdominal segment; *H. tridens tridens* has a minute spine on either side quite constantly whereas none in *H. tridens wuana*. In the following four zoeal stages no distinct differences between these were noted until the megalopa stage. There are variations in setation of appendages, which, however, seem insignificant for classification. The telson of the megalopa stage has three posterior marginal setae in *H. tridens tridens* instead of four in *H. tridens wuana*. The pleopods of this stage is functional, its setation is 12, 12, 12, 14, 10 in *H. tridens tridens* but 18, 19-20, 17-18, 16-17, 11-12 in *H. tridens wuana*.

A comparison of the zoeae of the two subspecies described in this paper with those of *Sesarma* is made through the papers by YATSUZUKA (1957), COSTLOW & BOOKHOUT (1960, 1962), DIAZ & EWALD (1968) and BABA & MIYATA (1971). Zoeae of all the species of *Sesarma* are reported to have no lateral spine of the carapace. This character is quite reverse in the present *Helice* and therefore seems to be the most useful for distinguishing the two genera. In the megalopa stage the endopod of the pleopod has three hooks in the present *Helice*. As has been pointed out by COSTLOW & BOOKHOUT (I.c.), DIAZ & EWALD (I. c.) and BABA & MIYATA (I. c.) two hooks on the endopod of the pleopod appear in all known megalops of *Sesarma*. And this may also be used to differentiate the megalops of *Helice* and *Sesarma*.

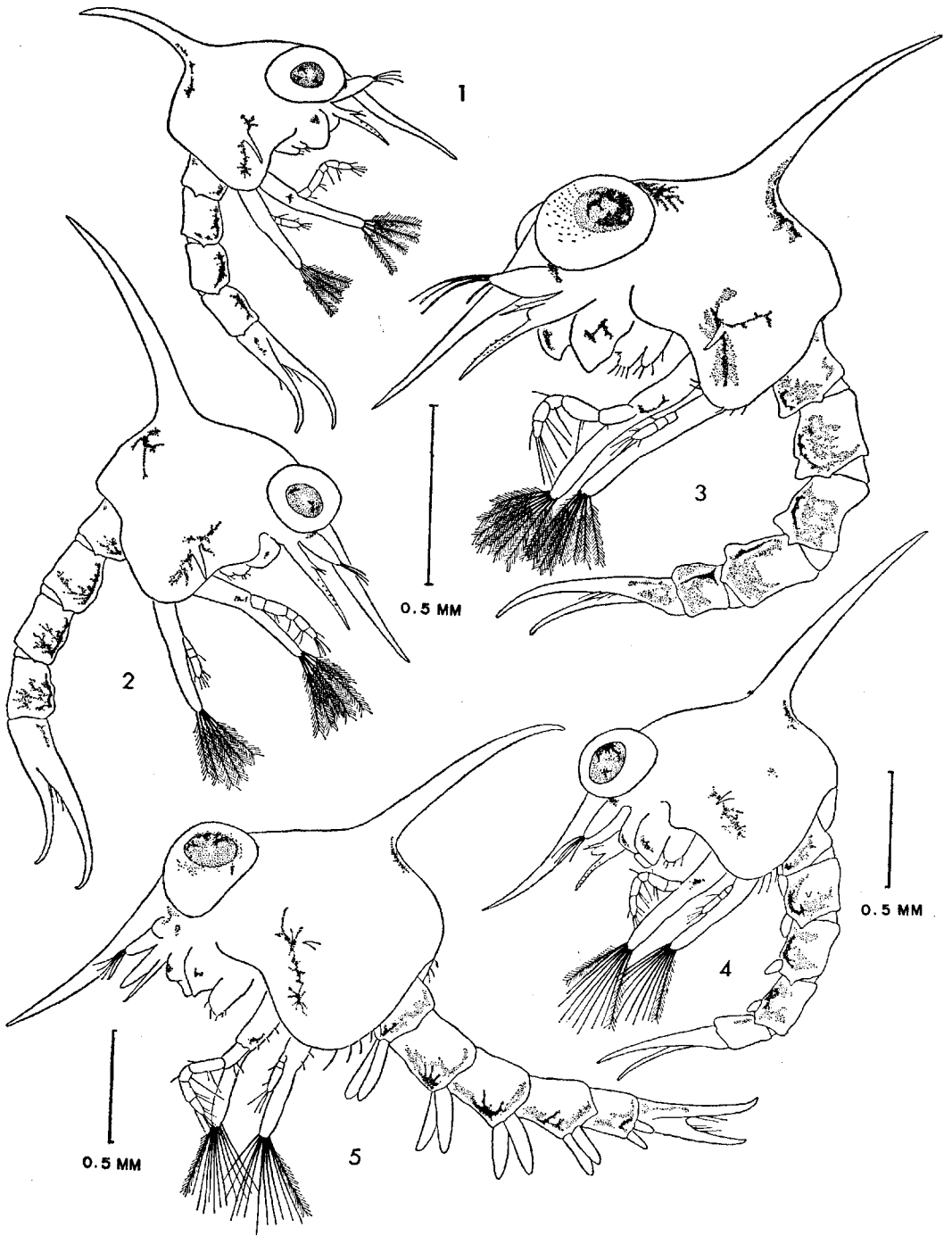
Around the river Shirakawa, Kumamoto, the breeding season of the present two subspecies begins at the latter part of April and ends in the beginning of August, with a peak in June. This period just overlaps that of *Sesarma dehaani*, and therefore comparison of the first crabs of these may be useful. *H. tridens wuana* has distinctly four-toothed lateral margin of the carapace whereas *S. dehaani* bears weak projections only (BABA & MIYATA, I. c.). The mandibular palp is two-segmented in *H. tridens wuana*, but three-segmented in *S. dehaani*. The second maxilliped has a well-developed epipod in *H. tridens wuana*, whereas it is absent in *S. dehaani*.

### References

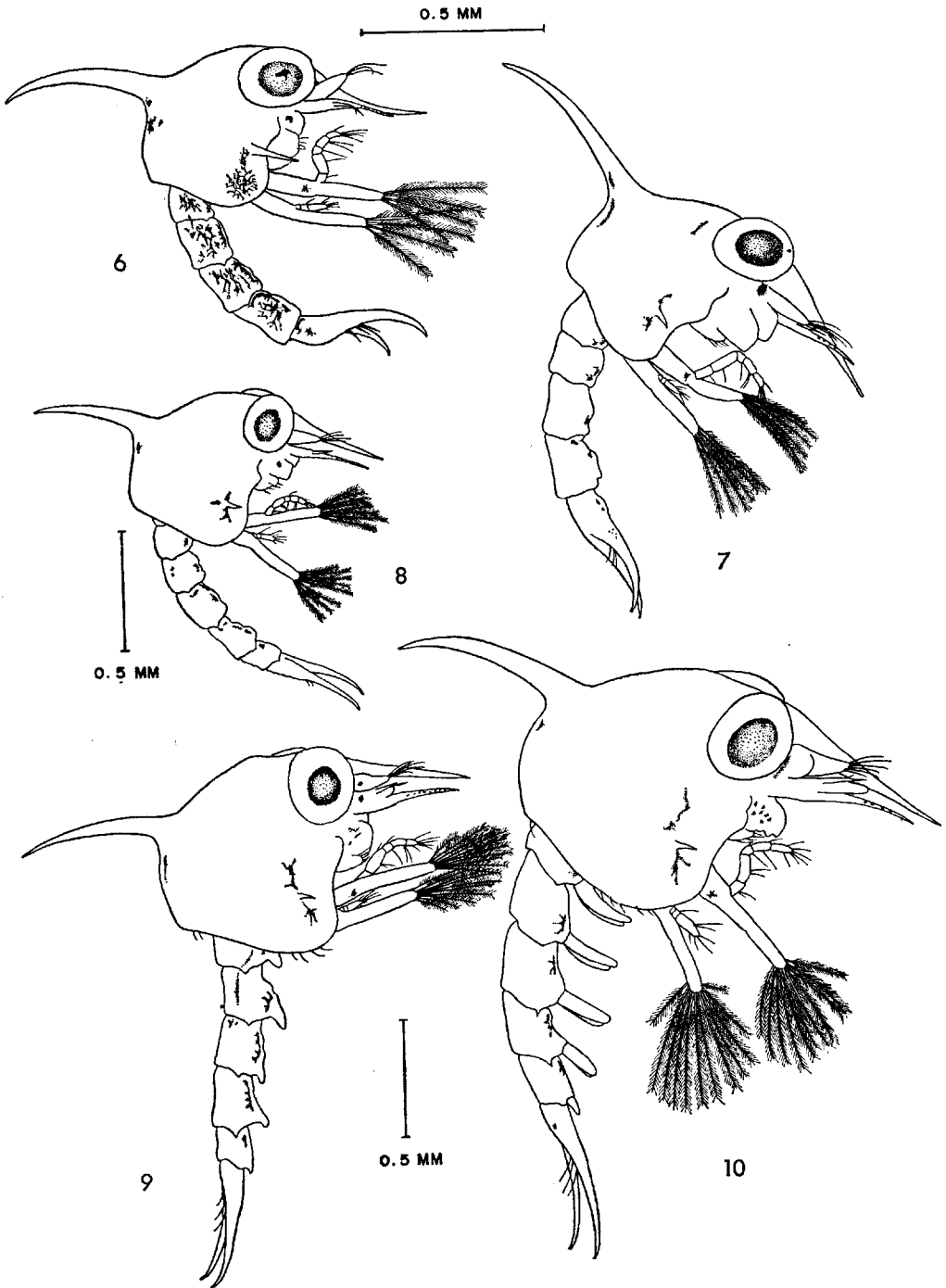
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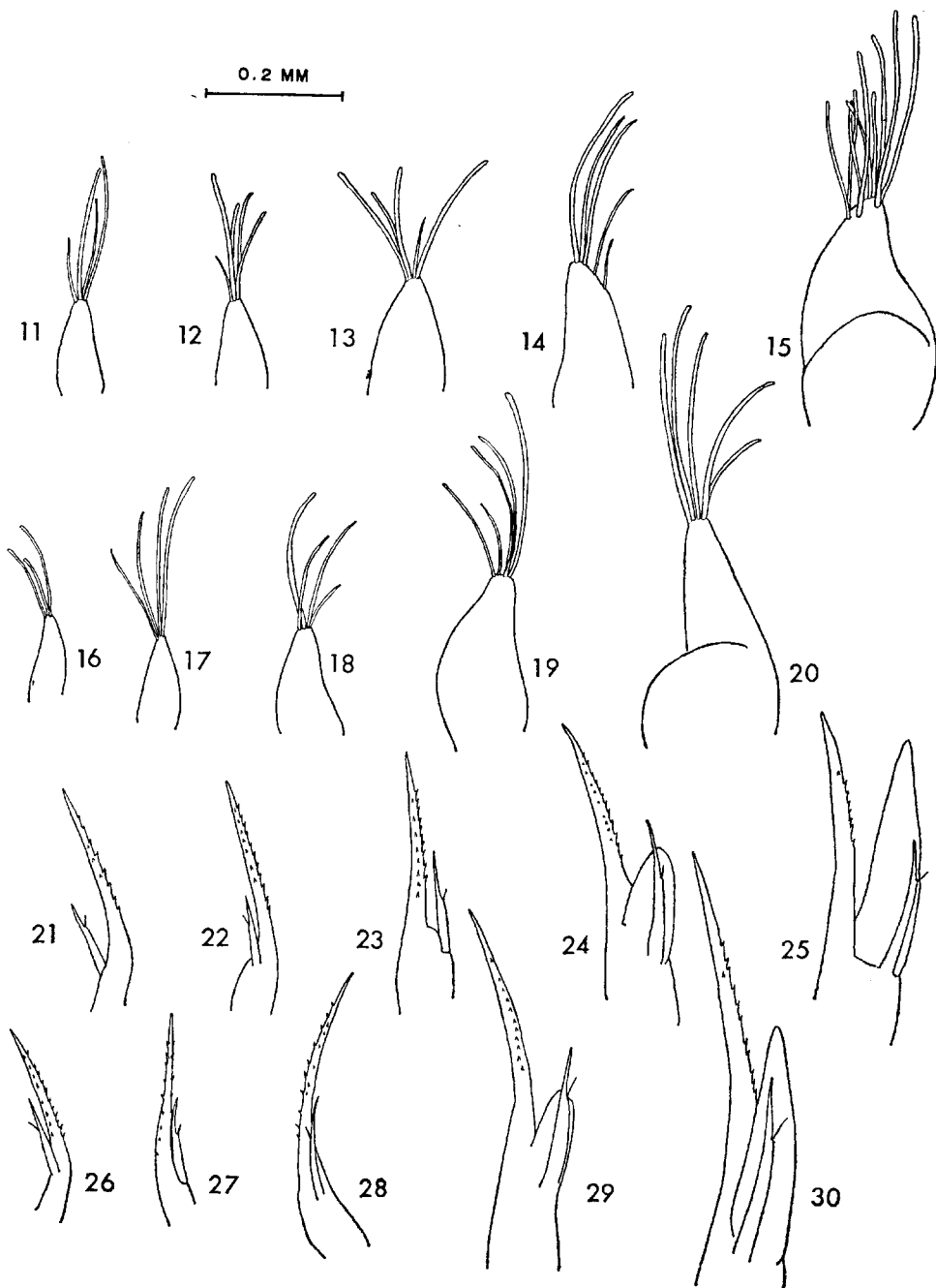
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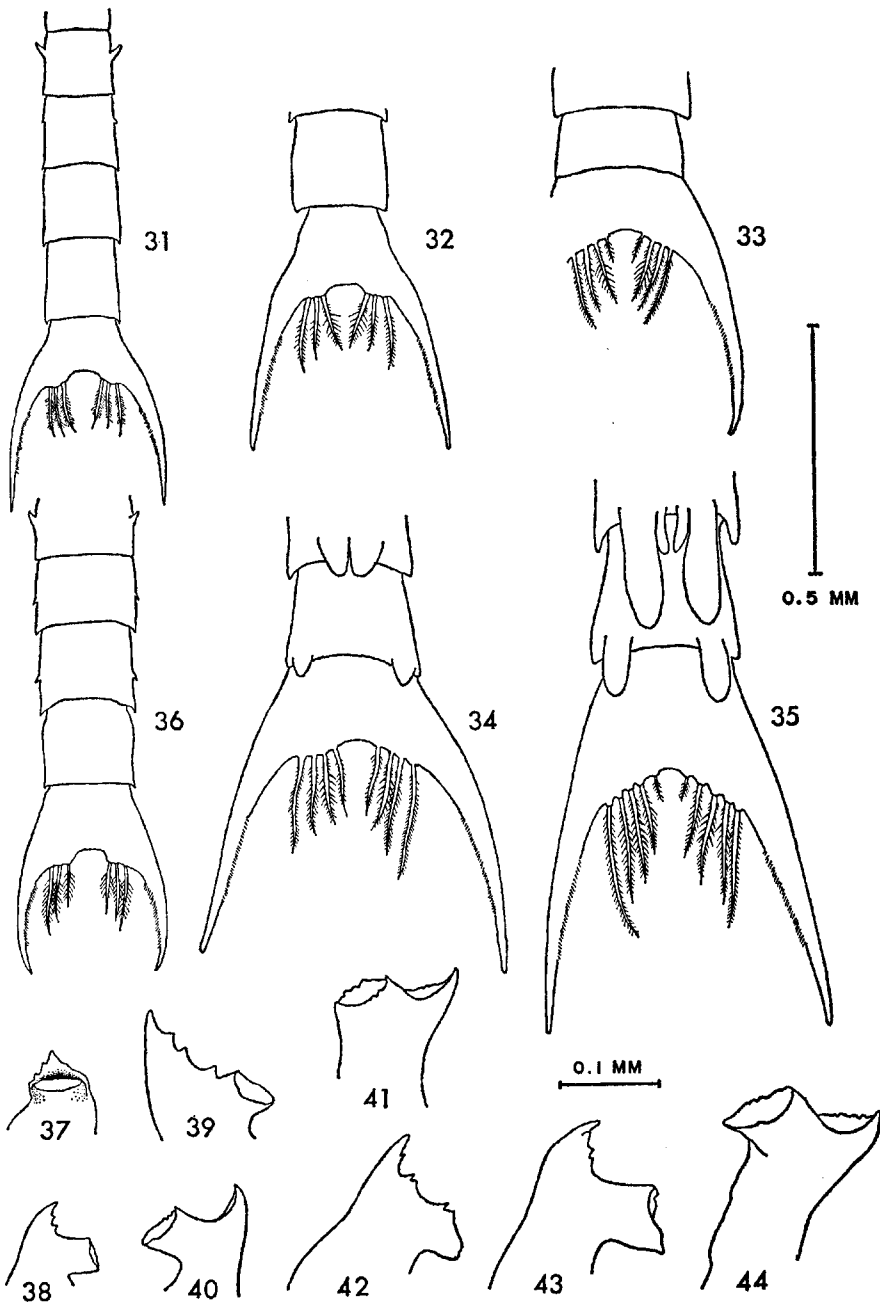
Figs. 1-5. *Helice tridens wuana* RATHBUN, zoea I-V, lateral.



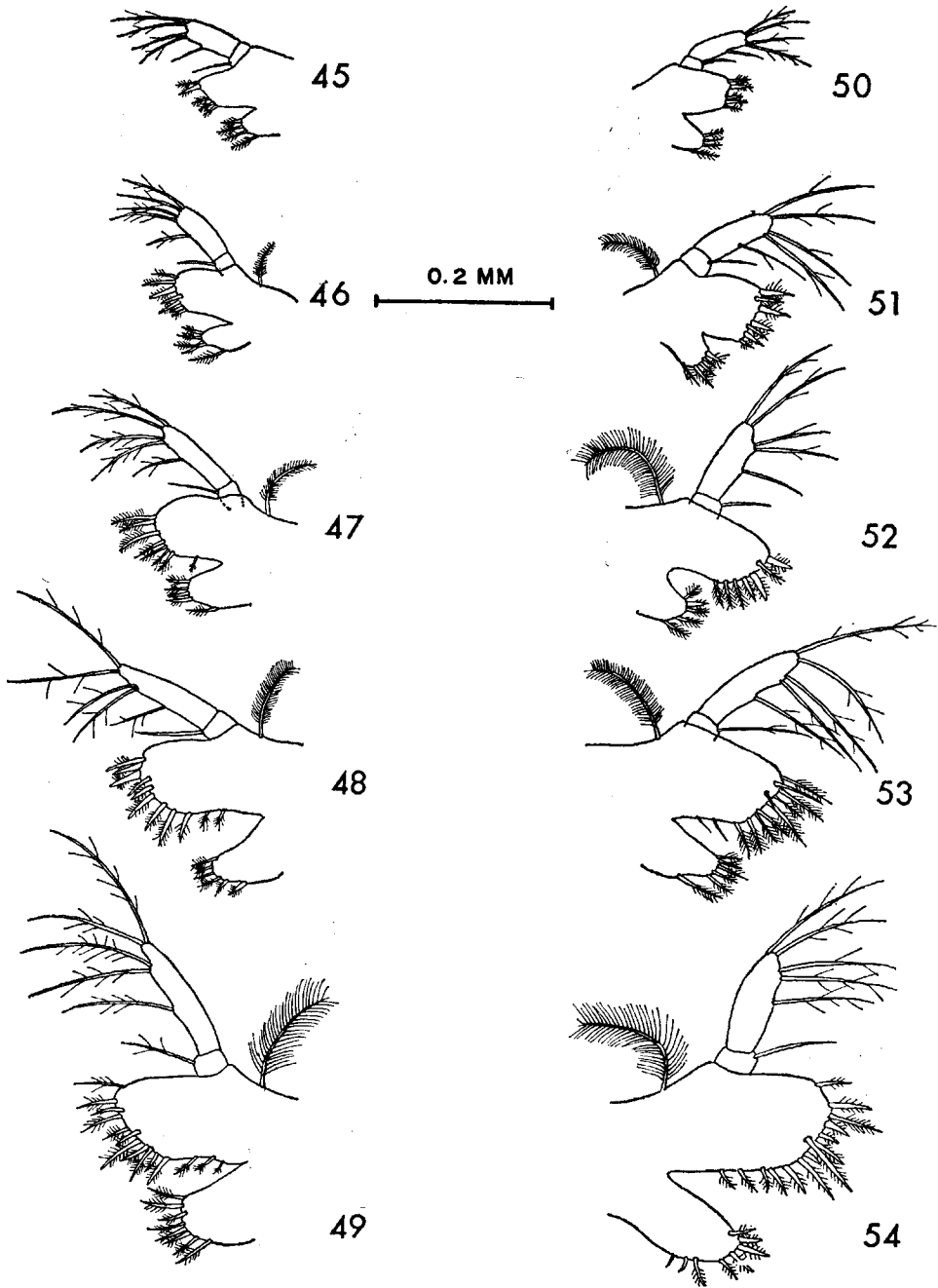
Figs. 6-10. *Helice tridens tridens* de HAAN, zoca I-V, lateral.



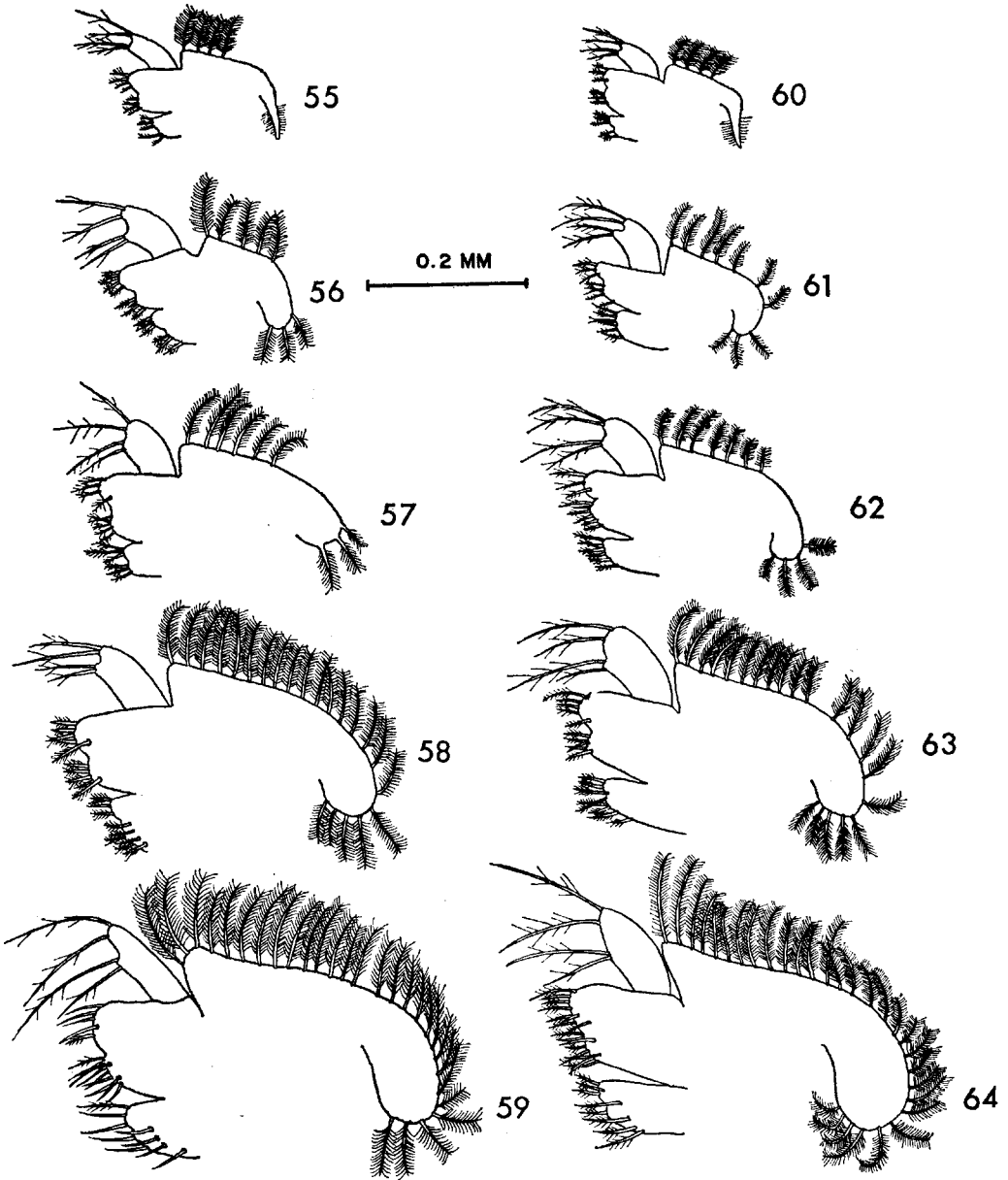
Figs. 11-30. Zoeal antennules and antennae. 11-15, antennules of *Helice tridens wuana* RATHBUN, zoea I-V; 16-20, antennules of *H. tridens tridens* de HAAN, zoea I-V; 21-25, antennae of *H. tridens wuana*, zoea I-V; 26-30, antennae of *H. tridens tridens*, zoea I-V.



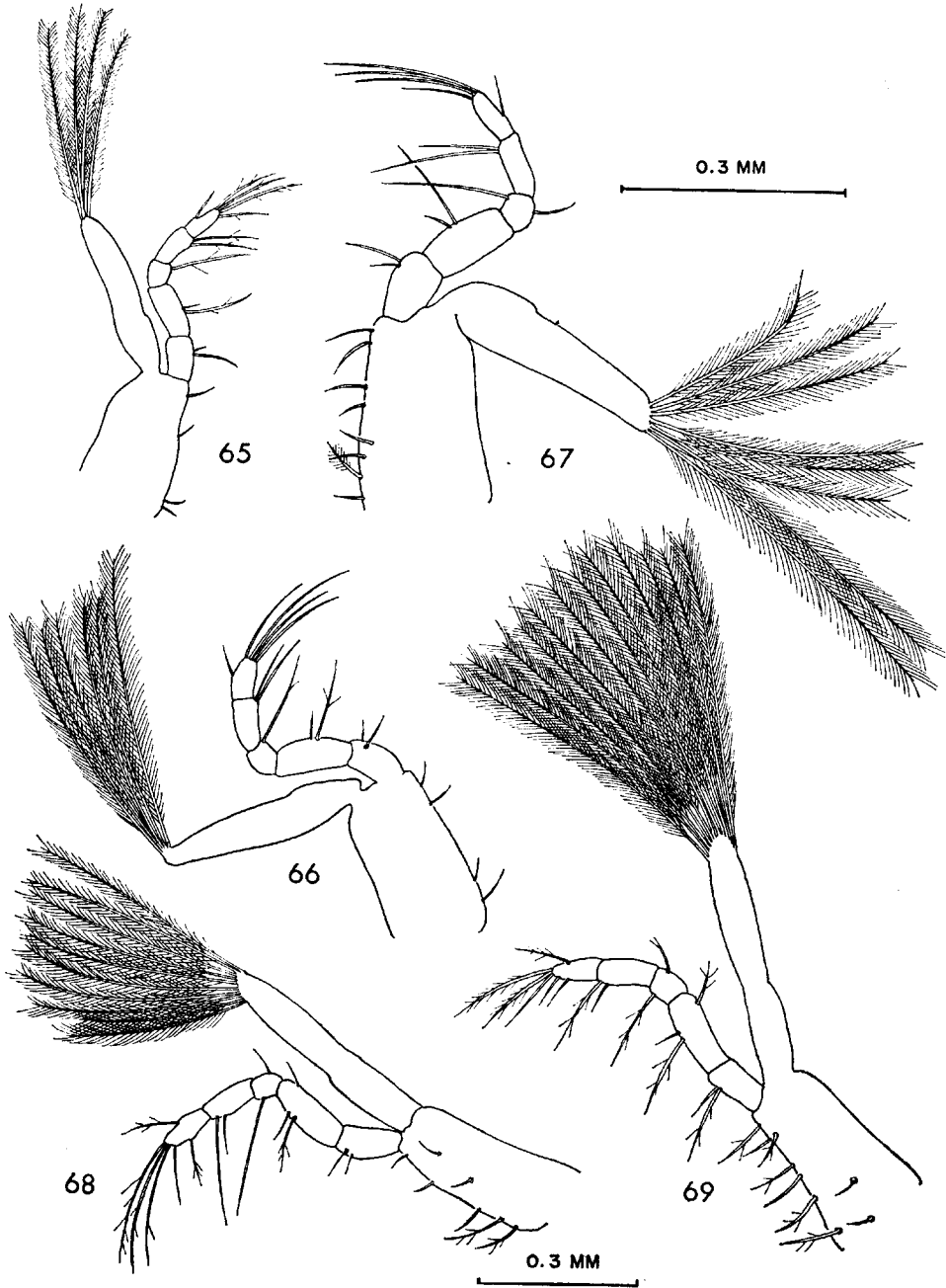
Figs. 31-44. Zoeal abdominal segments and mandibles. 31-35, abdominal segments of *Helice tridens wuana* RATHBUN, zoea I-V; 36, abdominal segments of *H. tridens tridens* de HAAN, zoea I; 37-44, mandibles of *H. tridens wuana*, zoea I-V; 37-38, zoea I; 39-40, zoea II; 41-42, zoea II; 43, zoea IV; 44, zoea V.



Figs. 45-54. Zoeal maxillules. 45-49, *Helice tridens wuana* RATHBUN, zoea I-V; 50-54, *H. tridens tridens* de HAAN, zoea I-V.

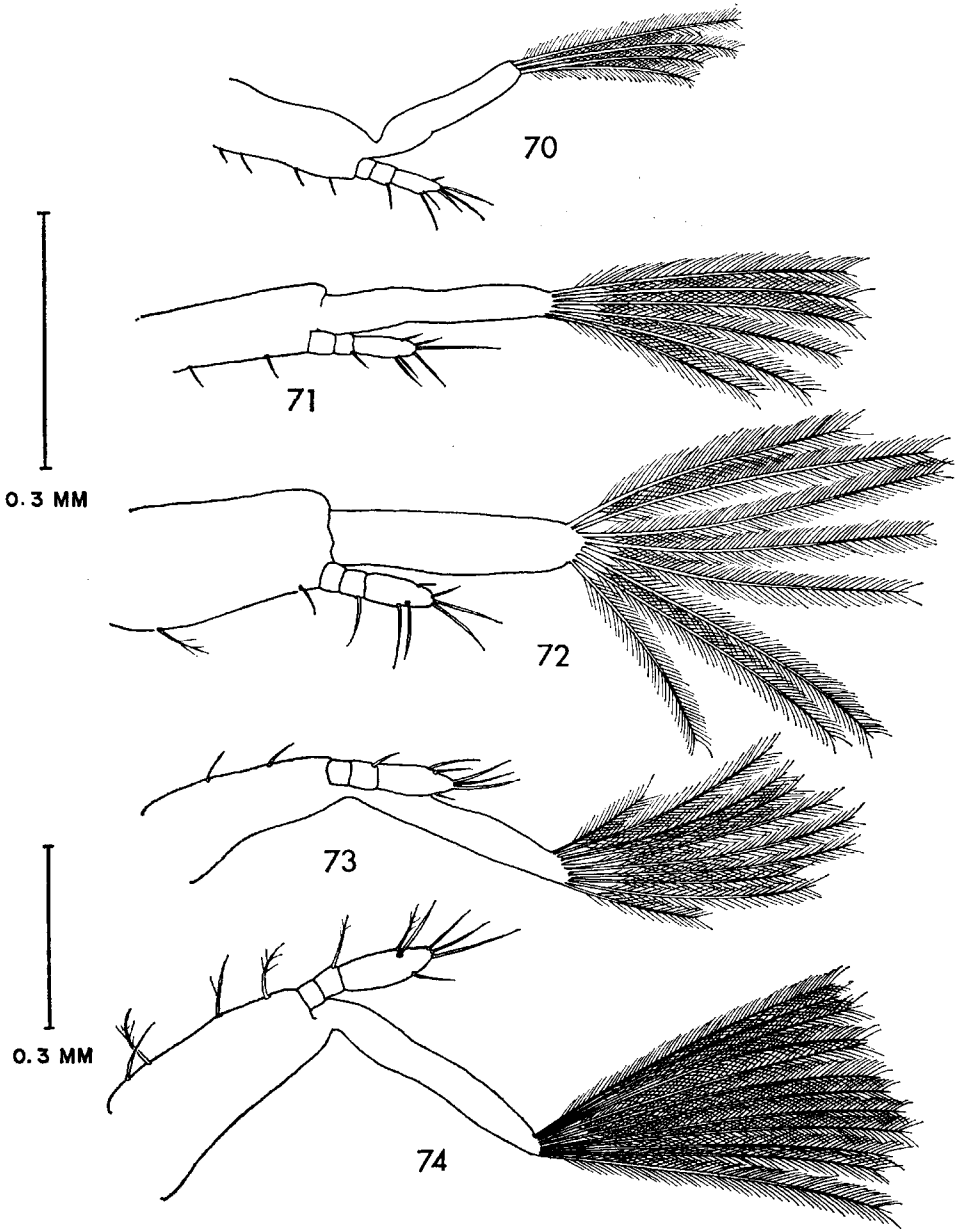


Figs. 55-64. Zoeal maxillae. 55-59, *Helice tridens wuana* RATHBUN, zoeca I-V; 60-64, *H. tridens tridens* de HAAN, zoeca I-V.

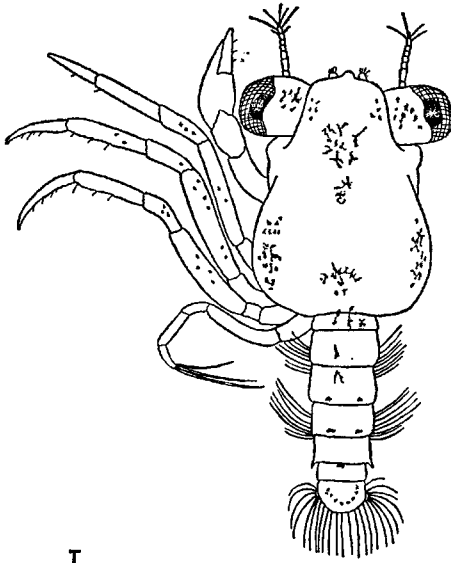


Figs. 65-69. First maxillipeds of *Helice tridens wuana* RATHBUN, zoca I-V.

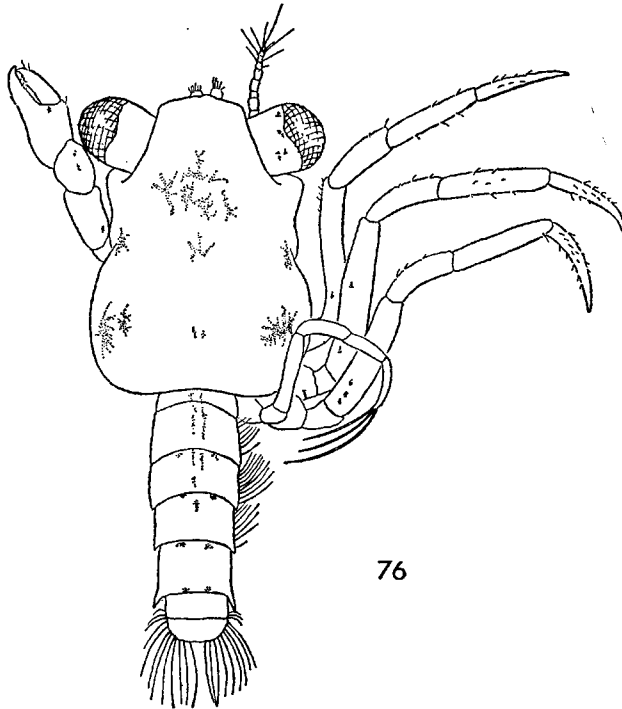




Figs. 70-74. Second maxillipeds of *Helice tridens wuana* RATHBUN, zoea I-V.

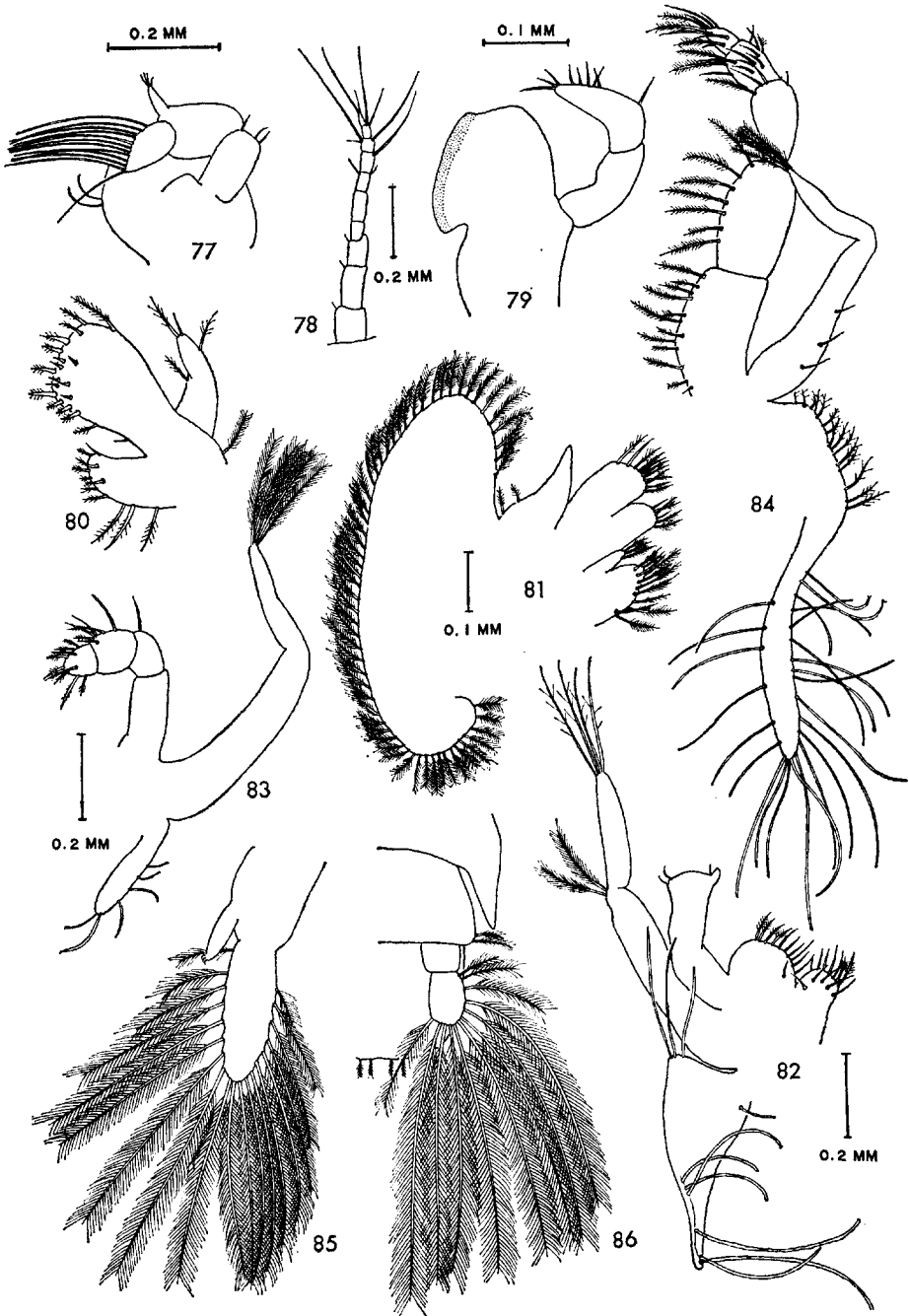


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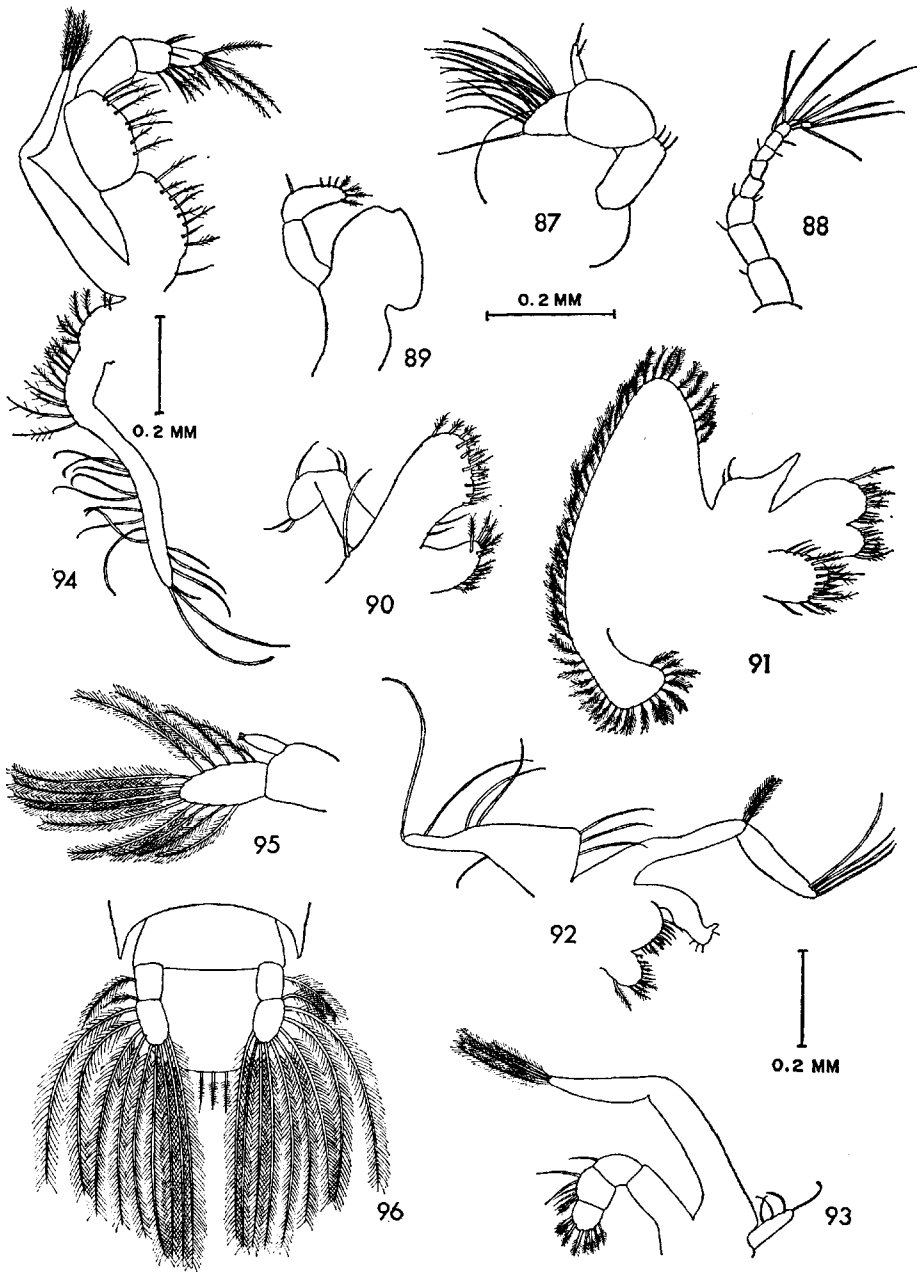


76

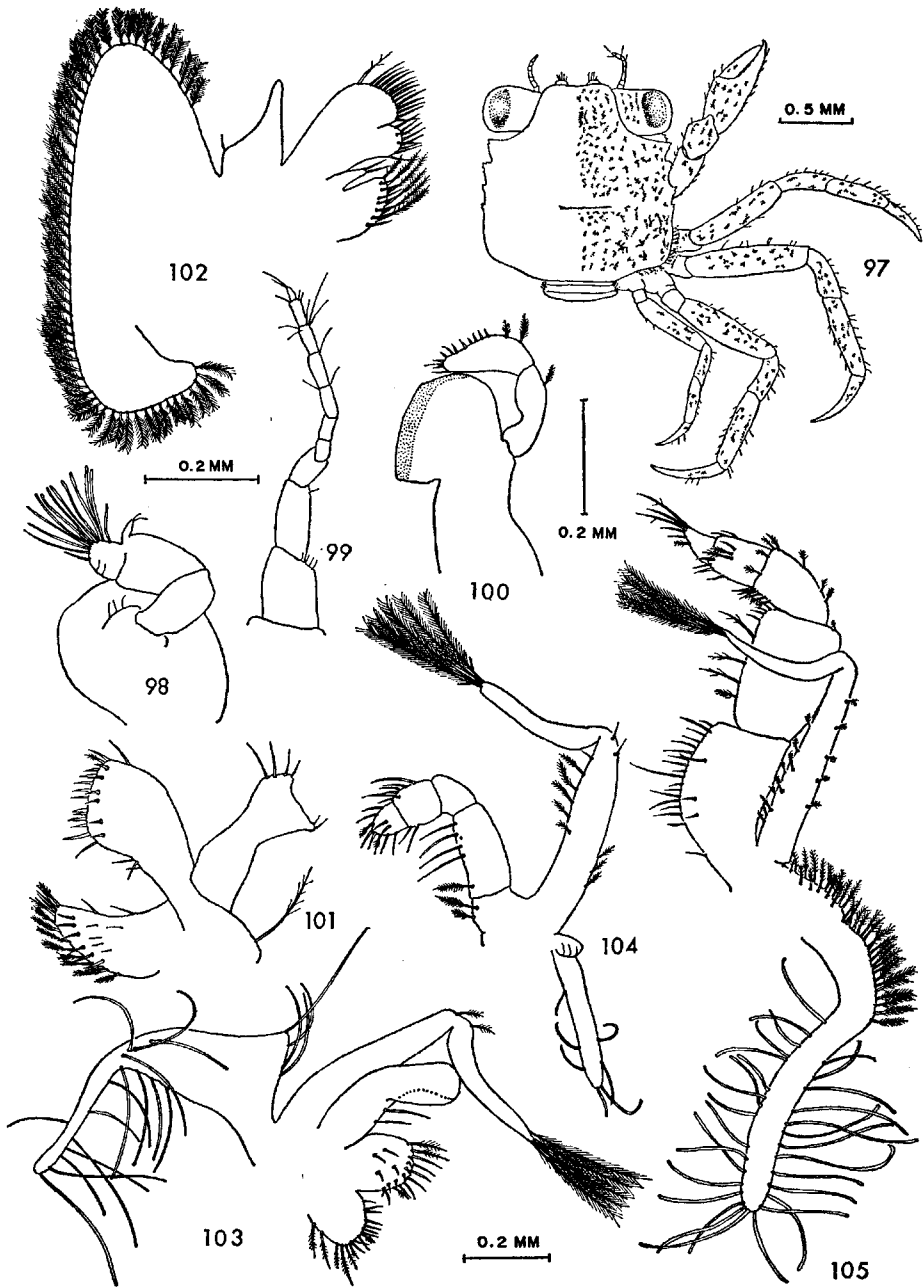
Figs. 75-76. Megalops. 75, *Helice tridens tridens* de HAAN, dorsal; 76, *H. tridens wuana* RATHBUN, dorsal.



Figs. 77-86. *Helice tridens wuana* RATHBUN, megalopa stage. 77, antennule; 78, antenna; 79, mandible; 80, maxillule; 81, maxilla; 82, first maxilliped; 83, second maxilliped; 84, third maxilliped; 85, pleopod of third abdominal segment; 86, left half of terminal segments of abdomen with last pleopod.



Figs. 87-96. *Helice tridens tridens* de HAAN, megalopa stage. 87, antennule; 88, antenna; 89, mandible; 90, maxillule; 91, maxilla; 92, first maxilliped; 93, second maxilliped; 94, third maxilliped; 95, pleopod of fifth abdominal segment; 96 terminal segments of abdomen with pleopods.



Figs. 97-105. *Helice tridens wuana* RATHBUN, first crab stage. 97, animal in dorsal view; 98, antennule; 99, antenna; 100, mandible; 101, maxillule; 102, maxilla; 103, first maxilliped; 104, second maxilliped; 105, third maxilliped.