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OBSERVATIONS ON THE HABITS OF THE
CRUSTACEAN EMERITA ANALOGA

WITH ONE PLATE

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OBSERVATIONS ON THE HABITS OF THE CRUSTACEAN
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During June and July, while attending the 1910 session of the Marine Biological Laboratory of Stanford University at Pacific Grove, California, the writers had an opportunity of observing certain phases of the life history of *Emerita*, which, as they do not appear to have been mentioned in literature, seem worthy of recording, particularly as they furnish some extremely fine examples of the correlation of structure and habits. Garstang, in several admirable papers pointing out the close correlation in various Crustacea between structures not commonly considered useful and the habits of the animals possessing them, very justly claims that while morphology and embryology have received a vast amount of attention, "bionomics" has been neglected and as a result the significance of many structures is entirely missed, while even their morphology is often incorrectly interpreted because their function is ignored or merely inferred from their form.

The aphorism of Jeffries Wyman: "The isolated study of anything in Natural History is a fruitful source of error", is strikingly illustrated in the morphological views that have been advanced for the significance of some of the structures in *Emerita*, as well as the numerous cases cited by Garstang. It seems curious that so many investigators shrink from the often trivial expenditure of time and energy involved in the experimental method of checking and completing their morphological work, when this almost invariably brings such a large return. It is as a slight contribution toward interpreting some of the well-known features of *Emerita*, that the following observations are offered.

The genus *Emerita*—the better known name *Hippa* has been transferred to *Remipes*—is represented on the Pacific Coast of North America by two species of wide distribution. One, *Emerita emerita*

(Linn.), ranges, according to Miss Rathbun,¹ from Lower California to Chili and is also found on the east coast of Brazil; the other, with which we have to do in the present paper, *Emerita analoga* (Stimp.), is found on sandy beaches from Oregon to Chili.² Neither of these differs widely from the well-known *Emerita talpoida* (Say), in fact some authors include all three in a single species, and it is probable that their habits are essentially similar.

The related family Albuneidæ is represented by two species, *Blepharipoda occidentalis* Randall, and *Lepidopa myops* Stimpson, both from Southern and Lower California, but these are less abundant and no opportunity has presented itself of observing their habits.

Emerita analoga, locally known as the "sand crab", or sometimes as the "sand flea", appears to be present in California on all sandy beaches exposed to the surf. We have had the opportunity of examining them in the vicinity of Swanton, Santa Cruz County, near Pacific Grove, Monterey County, and at Alamitos Bay, Los Angeles County, and have handled material from several other localities on the California coast.

In Southern California the "soft shelled", or newly molted individuals, which are looked upon as a different kind, are extensively used for bait in surf fishing. According to Miss Rathbun³ they are not only used for bait, but as an article of food on the coast of Peru, where they are known as "Mui-muis".

Though the structure and development of *Emerita* are well known, little work seems to have been done on their habits. S. I. Smith has given the most complete account of the habits of *Emerita talpoida*, in connection with a full study of the larval stages,⁴ but even this is rather meager, and, moreover, as he was unable to observe certain points, he has incorrectly interpreted them. Benedict gives a few observations concerning *Lepidopa*,⁵ and Garstang⁶ some features in the respiration of a European species of *Albunea*. These views will be considered in their appropriate connection.

It will be convenient to consider the habits and the structural features involved in the following order: habitat, burrowing, food-getting, and respiration.

¹ Proc. U. S. Nat. Mus., Vol. 38, p. 554. 1910.

² Rathbun, *loc. cit.*; Holmes, Occas. Papers Calif. Acad. Sci., Vol. 7, p. 103. 1900.

³ Proc. U. S. Nat. Mus., Vol. 38, p. 554. 1910.

⁴ Trans. Conn. Acad., Vol. 3, p. 311. 1877.

⁵ Proc. U. S. Nat. Mus., Vol. 26, p. 889. 1903.

⁶ Quart. Journ. Micr. Sci., Vol. 40, p. 224. 1897.

HABITAT

The sand crab inhabits a strip of beach in or near the wash of the waves. Here it is distributed from the high-tide limit, for a given tide, to a short distance beyond the point where the waves strike the sand, but the center of abundance is that portion washed by each wave. During a very low tide at Alamitos Bay, the crabs did not follow the wave wash out to its lower limit, but stopped at an intermediate point. Further observations at Swanton confirmed this.

Although occasionally found singly, *Emerita* is essentially a gregarious animal. It occurs in large "beds", which are marked by small V-shaped ripples in the sand. Here, as Leidy has said of the eastern form, they are as thick as currants in plum pudding. If one turns over the sand of one of these beds he will find the sand crab in incredible numbers lying within a few inches of the surface. In these places adults and young of both sexes may be found associated. Generally mature females and males are at once distinguished by the difference in size (see figs. 1 and 2, pl. 1). For this reason collections often consist of females only, the smaller males being regarded as young. Measurements of the carapace of 27 specimens (length from rostrum to median posterior dorsal margin) of each sex collected at Pacific Grove give the following: average of males (all with enlarged genital papillæ) 12.4 mm., range 10.5 to 14.5 mm.; average of females (all egg-bearing) 21.4 mm., range 17 to 25.5 mm. The males are without pleopods, while the second, third and fourth segments of the abdomen of the females are provided with them. The telson of the adult female is more heavily ciliated along its lateral margin and is somewhat wider than that of the male. The following are measurements of two typical specimens: female, length of carapace 20.3 mm., length of telson 13 mm., width of telson 6.9 mm., width 53 per cent of length; male, length of carapace 11 mm., length of telson 7.6 mm., width of telson 3.3 mm., width 43 per cent of length.

The following brief data on the period of egg-bearing in *Emerita analoga* have been gathered from the material at hand, and, although incomplete, may throw some light on its duration. Of 45 females collected at Swanton on January 5, 1911, none were carrying eggs, although many young females were present. Out of four females taken at Alamitos Bay on January 4, 1911, one carried small eggs in which the eye pigment had not appeared. A single adult female from Humboldt Bay, May 28, 1911, was not egg-bearing. During June, 1910, females carrying eggs of all stages from those ready to hatch to those in which the eye pigment had not yet formed were abundant

at Pacific Grove. Many of the maturer eggs hatched in the laboratory. A number of female specimens collected on July 11, 1906, at the same place, carried eggs without eye spots. In a lot of eight females from Little River near Trinidad, collected August 28, 1911, seven carried eggs, those from one specimen only showing the eye pigment. A series of 35 females, from San Diego (date unknown), included 14 egg-bearing individuals, the smallest of which had a carapace length of 11 mm.; four others were of practically the same dimensions. This is apparently the limit of egg-bearing size.

BURROWING

While there are many burrowing species among the Crustacea, *Emerita* and its allies show a degree of adaptation to this kind of life far more complete than found elsewhere. To understand this we must consider their peculiar habitat. Many burrowing forms live in mud or sand in still water or at least in sheltered positions—*Callianassa* and *Upogebia*—where a permanent hole is formed. Others, as the Cancridæ, cover themselves in the loose sand or gravel in shallow water or along sheltered shores. In *Emerita*, however, the method of food-getting, to be described later, requires that they occupy exposed sandy beaches exactly within the action of the waves. In this position they maintain themselves near the surface. It is not easy to realize the ceaseless activity necessary to keep this position. With every wave the top layer of the sand is converted into a fluid which is swept by the current with surprising rapidity. Any solid object in or on this surface layer is at the same time undermined and shifted by the force of the water. Every bather knows what insecure footing is furnished by the sand in shallow water where the action of the waves is strong. If the beach is carefully examined for several days in succession, it will also be seen that the sand has been shifted, the movement often affecting a layer several feet thick in a single day. As a result the animal dislodged or uncovered by each wave must reestablish itself to be in readiness for the receding wave from which its food is obtained.

As pointed out by Smith,⁷ their peculiar oval shape is well adapted for burrowing in the sand. It is interesting to note that a shape superficially very similar to that of the Hippidæ appears in a very different group, the Raninidæ among the true crabs, which are also burrowing forms.

⁷ Trans. Conn. Acad., Vol. 3, p. 312. 1877.

While the wave is in, *Emerita* may often be seen swimming about close to the surface of the sand, but as the wave recedes they bury themselves. This behavior suggested to us that they might follow the movements of the tide up and down the beach so as always to be within the wash of the waves, but as already stated observations failed to show that this took place to any marked degree.

If they are turned out with a spade, they burrow into the water-saturated sand with astonishing rapidity. They are unable to burrow readily in the dryer sand farther up the beach and when placed upon it cover themselves only after several attempts. Their method of burrowing may best be observed by placing them in a dish containing a shallow layer of wet sand. By reference to figs. 1, 2 and 3, pl. 1, it will be seen that the general form of the body is ovoid, and that the dactyls of all the legs are flattened and expanded to serve as digging organs. In burrowing, *Emerita* invariably moves backwards,⁸ stirring up the sand with some of the appendages while pushing and swimming backwards with others until it is covered. The detailed action of the parts involved is somewhat as follows: the uropods, which appear to be the most important, strike upwards and forwards in unison tending to throw the loose sand upon the back, or, where the sand is firmer, to force the body downward and backward. The four large pereopods take part in the process in varying degrees, apparently in each case acting alternately. The last pair, which, it will be noted, are directed backward along the sides of the body (fig. 3, pl. 1), move laterally, pushing the sand to each side. The two middle pairs act much as in walking, that is, in such a way as to thrust the body backwards, the broad trowel-like dactyls serving to catch in the sand. The flattened first pair of pereopods corresponding to the chelipeds of allied forms, which are held forward, are used to scull the body backward, so that under the combined action of all these appendages the animal is carried diagonally downward and backward until the anterior end of the carapace is just covered. *Emerita* seldom goes more than a few millimeters below the surface except when trying to escape or under unnatural conditions, and usually remains with some of the appendages exposed in a manner soon to be described. When burrowing they always work against the current and consequently, as the wave runs off, are left facing the sea—a position of some importance in connection with their feeding habits.

⁸ "This species [*Emerita talpoida*] burrows like a mole, head first, instead of backwards." Verrill, Report U. S. Fish Commission for 1871-72, p. 338. 1873.

FOOD-GETTING

The investigation of the method by which *Emerita* obtains its food forms the main part of the present work and has furnished the most important results. As far as the literature examined by the writers is concerned, there appears to be little mention of food, and the speculations concerning the organs which are used in feeding show how far pure morphology may go astray. In the paper of Smith's already mentioned, he says, "The mouth parts of the adult are not adapted for ordinary prehension or mastication, but I am unable to make any positive statement in regard to the food of these animals. In all specimens examined the alimentary canal was filled with fine sand which seemed to be nearly free from animal or vegetable matter. The material from the stomach, however, shew, under the microscope, a small quantity of vegetable matter, and it seems probable that the sand is swallowed for the nutritive matter it may contain".⁹ In regard to the antennæ, the chief organs in feeding, he says, "Judging from the peculiarly armed setæ of the flagella, one of the principal offices of the antennæ is the removal of parasitic growths and all other foreign substances from the appendages of the anterior portion of the animal".¹⁰ These meager notes are all the data that we have been able to find.

Under normal conditions, on the part of the beach left uncovered by the receding wave, the animals will often be found, if they have not been disturbed by the observer's footsteps, facing the sea with the rostrum just below the surface of the sand, while the stalked eyes and the antennules project slightly. If one stands in the midst of a bed while the wave sweeps over it, he will see little change at first, but as soon as the water begins to run down the beach, the crustaceans will thrust out their antennæ, normally hidden beneath the external mouth parts, and hold them directed forward and laterally with the tips curved outward. Here the antennæ remain, except for one or two momentary infoldings, until the last film of water has drained off, when they are again coiled beneath the mouth parts.

The water running past the antennæ forms, on the beach, the characteristic V-shaped marks, already mentioned, by means of which the presence and extent of a bed may often be clearly made out at a considerable distance.

⁹ Trans. Conn. Acad., Vol. 3, p. 313. 1877.

¹⁰ *Loc. cit.*

It requires only an examination of the structure of the antennæ and of the contents of the stomach to make clear the process of feeding. The stomach is found to contain not only "vegetable matter" as noted by Smith, but also microscopic animals. We have, in the antennæ and mouth parts, structures admirably adapted for straining such organisms from the waves, and the use, just mentioned, of the antennæ is not intelligible on any other assumption. There can be little doubt, therefore, that the food, instead of being swallowed with the sand, is strained from the water and transferred to the mouth. To understand the process more clearly let us consider, first, the structure of the antennæ and mouth parts and, second, the stomach contents.

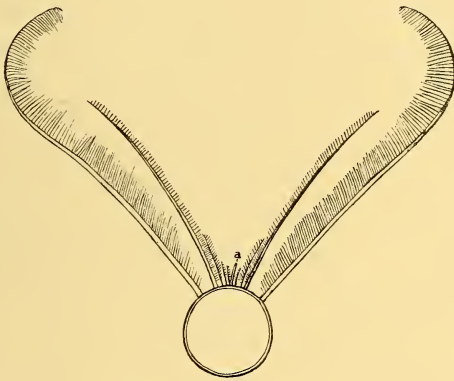


FIG. 1.—Cross section of antenna of adult female *Emerita* taken near base, showing arrangement of setæ.

The form of the antennæ has been accurately described by Smith.¹¹ The concave side is provided with four rows of large diverging setæ armed with secondary setæ directed inward (fig. 1 and pl. 1, fig. 5). In addition there are 5 or 6 smaller setæ lying nearer the median line (8 to 12 are described by Smith for *E. talpoida*). One of these, rather thicker than the rest and lacking the secondary setæ, occupies a median position and exhibits a pit in the tip suggestive of a sensory organ (a, fig. 1). The antennæ thus present to the water flowing against the concave side a very efficient straining apparatus.

Attempts were made to seize the extended antennæ, and by examination, to determine what was being captured, but the animals proved too active and the few taken in this manner showed only sand grains. The antennæ of a preserved specimen from Little River near Trini-

¹¹ Trans. Conn. Acad., Vol. 3, p. 325. 1877.

dad, California, were examined and a few diatoms were found entangled in the hairs together with sand grains and unrecognizable debris, similar to that obtained from the stomach.

The mouth parts are admirably adapted for the manipulation of these minute organisms which the antennæ have strained from the waves. In the normal position of the parts one is struck by the great development of the external (third) maxillipeds (fig. 4, pl. 1), which like double doors cover the entire buccal region of this remarkable animal. Along the median line they meet closely at the base; near the distal end they diverge slightly, but the longer hairs in this region still serve to close the cavern. Posteriorly the closely approximated bases of the first pair of pereopods curve forward and overlap slightly the posterior edge of the external maxillipeds, completely closing the cavern in that direction. A small diamond-shaped hole which would otherwise be left in the median line between their bases and the proximal ends of the third maxillipeds is closed by the tips of the palps. Laterally, the external border of the operculiform ischial joint, which is also ciliated, comes accurately in contact with the pterygostomial plate for rather more than half its length. Anterior to this, it fits against the basal portion of the antennæ, so as to completely close the cavity at this point. The cavern is least complete in front. Immediately below the antennules and eyes lie the crossed distal portions of the antennal peduncles, and against these the tips of the third maxillipeds rest. Crannies which might otherwise remain open are stopped by the greater development of hairs in this region (fig. 7, pl. 1). When the antennæ have been folded, they are thus inclosed in a cavity in which the food they have caught may be removed and transferred to the mouth without loss. For this use the other mouth parts are well adapted. The relation of the parts is well shown by fig. 7, pl. 1, which represents the buccal region exposed by turning back the external maxillipeds.

Careful observation shows that when *Emerita* is undisturbed it folds in the antennæ separately as the wave runs off the beach. Each flagellum is allowed to trail out nearly parallel with the body, and then is folded up and withdrawn under cover of the third maxillipeds with such a rapid motion as to escape analysis. Inside the buccal cavern each antenna is coiled loosely with the food-laden bristles pointing toward the center (fig. 7, pl. 1). From the anterior portion of the cavern the two palps of the second maxillipeds, armed with bristles arranged like those of a tube brush, project down into the coil of the antennæ. These are apparently used to scrape the food toward the

slit-like mouth. Portions of the first maxilliped and of the first and second maxillæ flank the elongate mouth and are provided with long stiff setæ, which are curved over the margin and directed upward into the gullet. These three comb-like structures apparently serve as valves to prevent the escape of the minute food and to work it into the mouth. The mandibles, which correspond closely with Smith's description¹² of those in *E. talpoida*, are very much reduced, and are so soft as to be of no use in mastication, thus illustrating in a striking fashion the degree of adaptation to the peculiar form of food which has taken place in this animal.

The contents of a considerable number of stomachs were examined at different times and were always found to consist of the same kind of material; chiefly shells of various diatoms, masses of brownish oily matter apparently derived from the diatoms, radiolarians, foraminifera, spicules of unrecognized origin, what were probably one-celled algæ, and considerable amounts of sand—about what would be obtained by unselective straining of the water along shore. No food has been seen which appeared to come from the breaking up of larger animals, and indeed it is difficult to see how *Emerita* could do this, in view of the complete absence of chelæ or other grasping organs, and of hard grinding surfaces on any of the mouth parts.

A striking contrast is presented by *Blepharipoda*, where well-developed chelæ are present together with a spiny merus on the third maxillipeds and heavy and well-calcified mandibles of the common type. The antennæ are also much smaller than those of *Emerita*. Unfortunately no fresh specimens were available for the examination of the stomach contents.

RESPIRATION

A number of devices are found in burrowing crabs for the removal from the respiratory stream of particles of sand or mud, which might be harmful to the gills. In some the water is inhaled between the chelipeds and the ciliated pterygostomian region, thus straining out the sediment (*Calappa*,¹³ *Bathynectes*¹⁴). Others, however, have the antennules (*Albunea*¹⁵) or the antennæ (*Corystes*¹⁶) modified to form a tube through which water may be drawn from above the

¹² Trans. Conn. Acad., Vol. 3, p. 338. 1877.

¹³ Garstang, Quart. Journ. Micr. Sci., Vol. 40, p. 212. 1897.

¹⁴ Garstang, Journ. Mar. Biol. Asso., Vol. 4, p. 396. 1897.

¹⁵ Garstang, Quart. Journ. Micr. Sci., Vol. 40, p. 224. 1897.

¹⁶ Garstang, Journ. Mar. Biol. Asso., Vol. 4, p. 224. 1896.

surface of the sand. Garstang (*loc. cit.*) says, "It seems to me not unlikely that further observation of the habits of *Hippa talpoida* [= *Emerita talpoida*] of the American coasts will reveal an essentially similar sieve-like function for the curiously bent and setose second antennæ of that animal". *Emerita*, however, as might be expected, shows a very close correspondence with its congener *Albunea*, the antennules and not the antennæ forming the respiratory tube.

Before considering in detail the mechanism of respiration in *Emerita*, it will be well to describe the animal's normal position in the sand. If a specimen of *Emerita analoga* is placed in a dish containing sand and water it will usually bury itself at once until the rostrum is just below the surface of the sand. Here while the body is concealed, the antennules and slender eye-stalks may be seen projecting above the surface. Occasionally it buries itself more deeply at first, but usually comes to rest in the position described. If the antennules are carefully examined it will be seen that they extend vertically from the sand, the four flagella making the angles of a square prism, while the space between them forms a sort of canal free from sand which is excluded by the interlocking hairs which each flagellum sends out toward its neighbor (figs. 3 and 6, pl. 1). If some powdered carmine or India ink suspended in sea water is allowed to flow from a pipette near the antennular tube, it will usually be drawn down the tube showing an inhalant current. Occasionally the current will be found to set in the opposite direction, and if an animal resting upon the surface of the sand is examined, this will be found to be the normal direction. Here the water is drawn in at the sides of the carapace, as may readily be shown by experiment.

A closer examination shows the presence of very complete channels for the conduction of water to the gills. The single respiratory channel inclosed by the four branches of the antennules turns, at the bases of the latter, ventrally into a chamber inclosed between the bases of the antennæ laterally, the bases of the antennules dorsally, and the expanded ciliated tips of the exognaths of the first and second maxillipeds ventrally. Passing back, the channel is divided by the raised and overhanging apex of the triangular labrum, and now lies to either side, enclosed laterally by the pterygostomial plate and ventrally by the exognath of the first maxilliped. In this canal is found the leaf-like scaphognathite.

The use of such a respiratory apparatus is obvious. While the animal is buried, an adequate supply of water free from sediment may be obtained from above the surface of the sand when the wave

is in, by means of the antennular tube, and then forced out into the surrounding sand. When swimming about or resting on the surface of the sand, the water is taken in at the sides of the carapace and forced out through the antennular tube, the direction of the current thus being that common to most crabs. At other times, possibly when the sand is uncovered, this may also prove to be the more serviceable method. Reversal of current took place in the animals observed in the aquarium at times apparently because of irritation due to the carmine or to stimulation with a pencil point and again without visible cause.

Reversal of current has been described by Garstang in *Corystes*¹⁷ and *Portunus*¹⁸ and the same thing has recently been observed by us in the case of *Cancer magister*, the common edible crab of the Pacific Coast. It is apparently a much more common phenomenon than is ordinarily supposed.

SUMMARY

The present paper treats of the habits of *Emerita analoga* [= *Hippa analoga*] of the western United States, particularly in regard to burrowing, feeding and respiration.

1. The food of *Emerita analoga* consists of microscopic organisms strained from the waves, to which it is constantly exposed, by means of the greatly developed antennæ. This is shown by examination of stomach contents and observation of living animals under natural conditions.

2. The structure of the peculiar antennæ, the uses of which have hitherto been incorrectly inferred, of the greatly reduced mandibles, and the remainder of the greatly modified mouth parts are remarkably adapted to this form of feeding, and unfitted for any other.

3. The burrowing habits necessitated by their peculiar habitat in the shifting sand within the wash of the waves is accompanied by a large number of adaptive structures, among which are the oval form of the body, the expanded dactyls of the ambulatory legs, and the form and position of the uropods.

4. Respiration, in accordance with their burrowing habits, is carried out by a specialized apparatus similar to that described by Garstang for *Albunea*. Water may be drawn from above the surface of the sand

¹⁷ Journ. Mar. Biol. Asso., Vol. 4, p. 228. 1896.

¹⁸ *Op. cit.*, p. 405.

by a tube formed of the ciliated antennules, and forced out of the gill chamber at the sides of the body, or under other conditions the current may be reversed.

5. There is a constant difference in the size of the male and female; in twenty-seven specimens of each the former averaged 12.4 mm. and the latter 21.4 mm.

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EXPLANATION OF PLATE 1

Emerita analoga (Stimpson)

All figures are from photographs made by the authors of specimens taken at Pacific Grove, California.

FIG. 1. Adult female.

FIG. 2. Adult male. Figures 1 and 2 are from the same negative and show the relative sizes of the two sexes. Slightly less than natural size.

FIG. 3. Adult female, lateral view.

FIG. 4. Adult female, ventral view.

FIG. 5. Antenna from adult female.

FIG. 6. Frontal region of adult female.

FIG. 7. Partially dissected adult female from ventral side.

The operculiform third maxillipeds are turned aside to show the position of the coiled antennæ. Compare with fig. 4. The second and third pereopods have been removed.

ABBREVIATIONS

a1 = first antennæ or antennules.

a2 = second antennæ or antennæ.

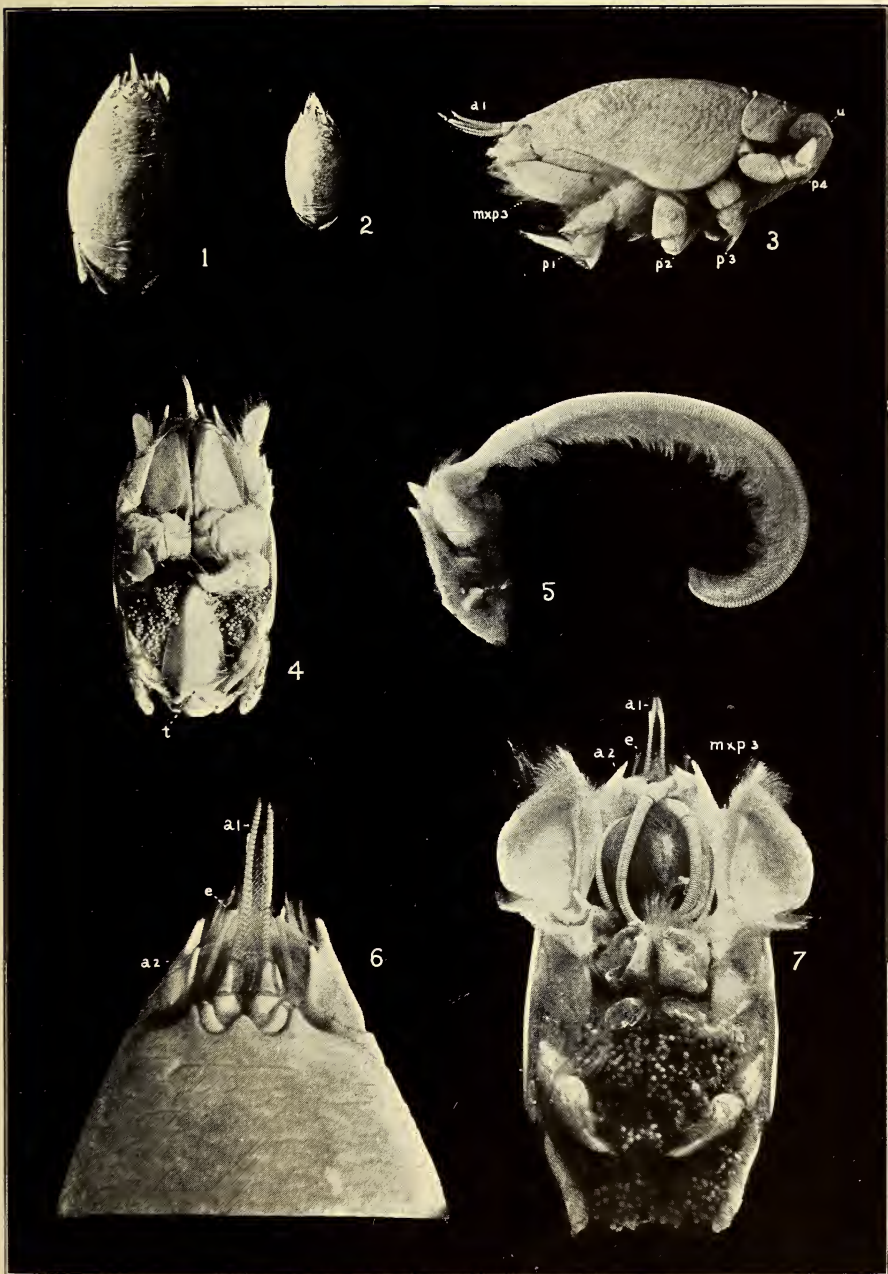
e = eyes.

mxp3 = third maxillipeds.

p1, p2, p3, p4 = first pereopod, etc.

t = telson.

u = uropods.



EMERITA ANALOGA (Stimpson)