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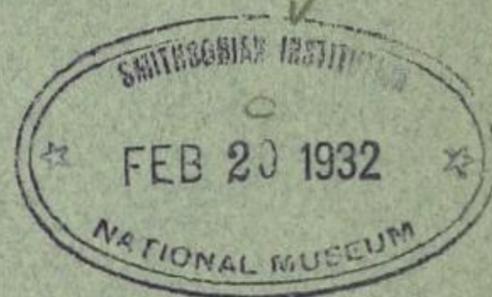
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NEBALIACEA

by

H. Graham Cannon, Sc.D.



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DEC 23 1931

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(Plate XXXII, text-figs. 1-7)

THIS report deals with the Nebaliacea collected by the 'Discovery' during the years 1925-7.

Nebaliopsis typica, G. O. Sars

Nebaliopsis typica was originally described by Sars (1887) from a damaged specimen and a fragment collected by the Challenger Expedition. Thiele (1904) subsequently described the limbs in detail from a crushed specimen collected by the Valdivia Deep Sea Expedition. The Swedish Antarctic Expedition was the first to obtain, in 1902, a complete and undamaged specimen. This was briefly described and figured in a posthumous note by Ohlin (1904), from which it appears that the animal was still alive when it reached the surface. Ohlin merely named the specimen "a new Nebalia", but there is no doubt that it belonged to the genus *Nebaliopsis*. Unfortunately, however, it has been lost. Dr Nils Odhner of the Riksmuseum, Stockholm, in a letter to me says: "It is very likely that it followed the sinking 'Antarctic' to the bottom, when it was wrecked". The Discovery Expedition collected seven specimens during 1925-7, of which six were crushed or fragmentary, but one was complete and undistorted. Enlarged photographs of this specimen are shown in Plate XXXII.

The following list gives details of all the specimens of *Nebaliopsis* which have been found up to the present:

Table I.

Expedition	Locality		Depth	Total length (mm.)	Carapace length (mm.)	Ratio
	Lat.	Long.				
Challenger						
<i>A</i> *	46° 46' S	45° 31' E	1375 fathoms	—	29	—
<i>B</i> †	39° 41' S	131° 23' W	2550 fathoms	22 (+ 3)	16	1.56
Valdivia	0° 20.2' N	6° 45' W	3500 m. vertical net	35	22	1.59
Swedish Antarctic‡	48° 27' S	42° 36' W	2500 m. vertical net	20	14.5	1.38
Discovery 1925-7						
<i>A</i> . St. 81	32° 45' S	8° 47' W	650 (-0) m.	19.5	16	1.22
<i>B</i> . St. 72*	41° 43' 20" S	42° 20' 40" W	2000 (-0) m.	—	19.5	—
<i>C</i> . St. 101	33° 50' S	16° 04' E	2480-2580 m.	30	18	1.67
<i>D</i> . St. 78§	35° 18' S	19° 01' 10" W	1000 (-0) m.	14	8	1.75
<i>E</i> . St. 256§	35° 14' S	6° 49' E	850-1100 (-0) m.	13	—	—
<i>F</i> ₁ . St. 89§	34° 05' 15" S	16° 00' 45" E	1000 (-0) m.	14	—	—
<i>F</i> ₂ . St. 89☐	34° 05' 15" S	16° 00' 45" E	1000 (-0) m.	25	15	1.67

* Carapace and front part of body only.
 † Living when brought to surface—subsequently lost.
 ☐ Complete undamaged specimen (Plate XXXII).

‡ Caudal rami missing.
 § Immature. Carapace crushed.

It has been assumed from the fact that *Nebaliopsis* has only been obtained from deep hauls that it lives at great depths. However, specimen *C* from St. 101 is the first example which has been collected at a known depth. All other specimens were collected by nets which were open on their way up to the surface. Specimen *C* was collected at a depth of approximately $1\frac{1}{2}$ miles.

With regard to localities, the Valdivia specimen is the only representative from tropical waters, the remainder having been collected from sub-tropical to antarctic localities. Of the Challenger specimens, one was collected in the south-west Indian Ocean and the other in the South Pacific. The remainder are all Atlantic specimens.

There is a peculiar mistake in the map published by Thiele (1905, p. 67) in which he records *Nebaliopsis* as having been collected from a point south of Australia. This is presumably the second Challenger specimen from St. 289 in which the longitude has been plotted E instead of W.

From the measurements quoted in Table I, it will be seen that there is considerable variation in the length of the carapace. This is partly only apparent and results from the difficulty of accurate measurement owing to the distortion of most of the specimens, but that there is a real variation can be seen by comparing the ratios taken from Ohlin's figure and that from specimen F_2 , both of which were undamaged.

There is similarly a marked variation in the structure, but not the size, of the anterior limbs. Thiele gave a very complete description of the setation and detailed anatomy of the limbs of his specimen. I have compared the antennules, antennae and mandibles of five of the Discovery specimens with Thiele's description and, while I found a general agreement, there was a very marked variation. It would serve no purpose to record the setation of each limb of the Discovery specimens, but there are several general conclusions which can be stated from the comparison.

The larger specimens are markedly more setose than the smaller. This is seen clearly in the mandibular palp. In specimen *A* (total length 19.5 mm.) the middle joint carries two setae on its median face and the distal joint a row of fifteen, while specimen *C* (total length 30 mm.) bears an irregular row of ten setae on the middle joint and a row of twenty on the distal. A more marked difference is seen by comparing specimen *C* with *D*, but from other characters it is clear that specimen *D* is immature.

The fourth joint of the antennule is produced on its median face into a long pointed process (Thiele, 1904, Pl. 3, fig. 41), which carries a row of marked teeth on its anterior edge. These teeth become obliterated in the larger specimens.

The scale of the antennule, which, according to Thiele, carries a curved row of about fifteen setae, becomes more setose in the larger specimens and loses its characteristic shape (Thiele, 1904, Pl. 3, fig. 40). Thus, in specimen *D*, the scale carries a curved row of seven setae and terminates in a triangular point. In specimen *B* it carries fifteen setae and is an ovoid plate.

Specimens *D*, *E* and F_1 are undoubtedly larval specimens. The flagellum of the antennule is in each case six- instead of twelve-jointed. The most marked difference is in the pleopods. In each case the fourth pleopods consist of a pair of minute knobs, while

the fifth and sixth pairs are fully developed proportionately to the first, second and third pairs. Claus (1889, p. 34, Pl. 1, fig. 3) has recorded an identical condition in *Nebalia geoffroyi*.

Thiele (1904, p. 24) has suggested that his specimen should be distinguished from the typical form as a variety *atlantica*, on the grounds that its rostrum showed a slightly different shape and the exopodites of its pleopods were narrower than those figured by Sars.

I have examined the original specimen from which Sars drew his figures and cannot see any appreciable difference between its rostrum and that figured by Thiele (1904, Pl. 3, fig. 38). In addition, I find that Sars' figure of the third pair of pleopods (1887, Pl. 3, fig. 4) is inaccurate. In his figure the ratio of length to breadth of the exopodite is only 2.3:1, while from actual measurement I found it to be 3.2:1. The form of the pleopods agreed closely with both Thiele's figures and with the Discovery specimens. I consider therefore that there is no evidence to justify the establishment of a new variety for the Valdivia specimen.

With regard to the incomplete Challenger specimen (first on the list, p. 201) it is possible that this may represent a distinct species. The complete animal must have been very large—about half as long again as any other specimen yet found. The carapace is more distinctly corrugated than the normal and is of a pale yellow-brown colour. These characters, however, may well be signs of age, and on them alone it would be unjustifiable to establish a new species or variety.

By studying the undistorted specimen F_2 , I have been able to make out the normal arrangement of the limbs and so to deduce something as to the mode of life of *Nebaliopsis*.

The specimen, as I received it, was extremely transparent. Ohlin's living specimen was described (Ohlin, p. 59) as "in Leben ganz durchsichtig, glashell... Das einzige, was man von ihm... sehen konnte, waren die zwei rotgelblich schimmernden, überaus kleinen Augen". This transparency made it very difficult to study. Whatever illumination was used, the light penetrated the tissues so that individual parts were very difficult to distinguish. In addition, in the centre of the body, there was an opaque orange ovoid mass which obscured everything above and below it. I have not been able to settle the exact nature of this mass. It was probably the remains of the ovary. Eventually I found that by focussing a point source (a 150 C.P. Pointolite) on the edge of the limb I was studying, I was able to light up that part leaving the rest of the animal more or less in the dark. This, for instance, was the only way I could see the edge of the carapace. However, I did not make any real headway until I had the beautiful photographs (Plate XXXII) which I owe entirely to the skill of my colleague, Prof. C. J. Patten. These were taken originally at a magnification of about 1.5, the specimen lying in spirit on a piece of black velvet. The illumination was ordinary north daylight on a fairly dull day. By this method the surface only of the animal has been photographed, as will be seen from the side view where the opaque mass in the centre of the body is practically invisible. Without these photographs I could not have spoken with any certainty as to

the limb arrangement. Figs. 1 and 2 are detailed drawings based on the lateral and ventral photographs.

After as complete a study of the whole specimen as I could make, I embedded it in paraffin wax and sectioned it parasagittally down to the middle plane. The remaining half was dissolved out of the wax by xylol and transferred back to spirit. In this way I have obtained a series of sections from which it will be possible to study, to a certain extent, the internal anatomy. But, more important, in the remaining whole half, I was able to view the limbs from the median aspect, and without this view I maintain that in most Crustacea it would be useless to speculate as to the method of functioning of the limbs. I have not drawn a figure of this view as the overlapping of the setae would have obscured the essential details. In Fig. 4 I have drawn a series of figures showing separately the median aspects of the mouth parts, the first, second and part of the third

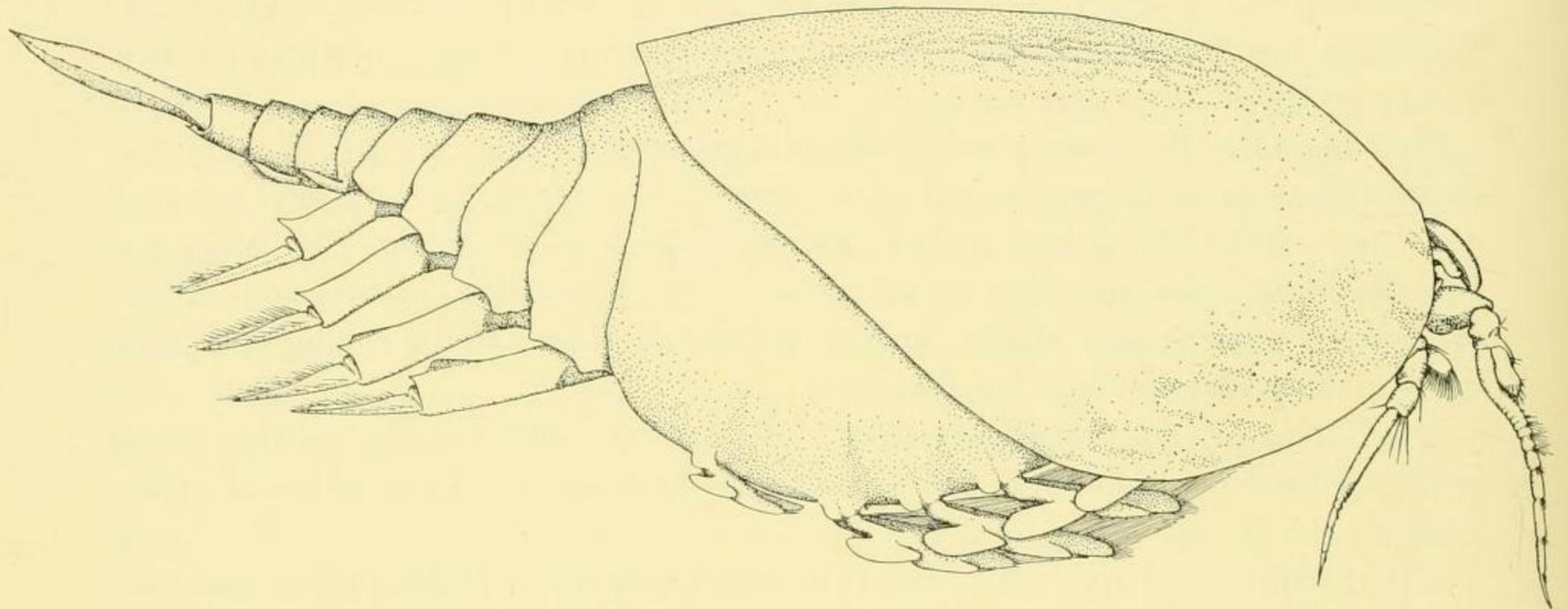


Fig. 1. *Nebaliopsis typica*. Side view.

trunk limbs. This series can be compared with the corresponding figures of *Nebalia* which I have already published (1927, p. 361, Text-fig. 4).

The antennules, antennae and mandibles have been described in sufficient detail by Thiele (1904) and I have nothing further to add beyond what I have already described.

The maxillule, as Thiele states (1904, p. 21), is two-jointed, the palp being reduced to a small stump. This is not, however, blunt as in Thiele's figure (Pl. 3, fig. 48) but terminates in a feathered spine about as long as the palp itself (Fig. 3). The arrangement of the two endites shows a similarity to that of other Malacostraca but has been distorted by the flattening out of the region immediately behind the mouth. In *Nebalia* the lower lip is deeply cleft into two marked paragnaths. The setae of the proximal endite curve round behind the latter and point directly into the mouth as in all the primitive Malacostracan groups. The setae of the distal endites bite together in the middle line immediately underneath the paragnaths (Cannon, 1927, p. 364, Text-fig. 7). In *Nebaliopsis* the paragnaths have become flattened out into two indistinct ridges running parallel to the median plane, and, in so doing, appear to have pushed the maxillules

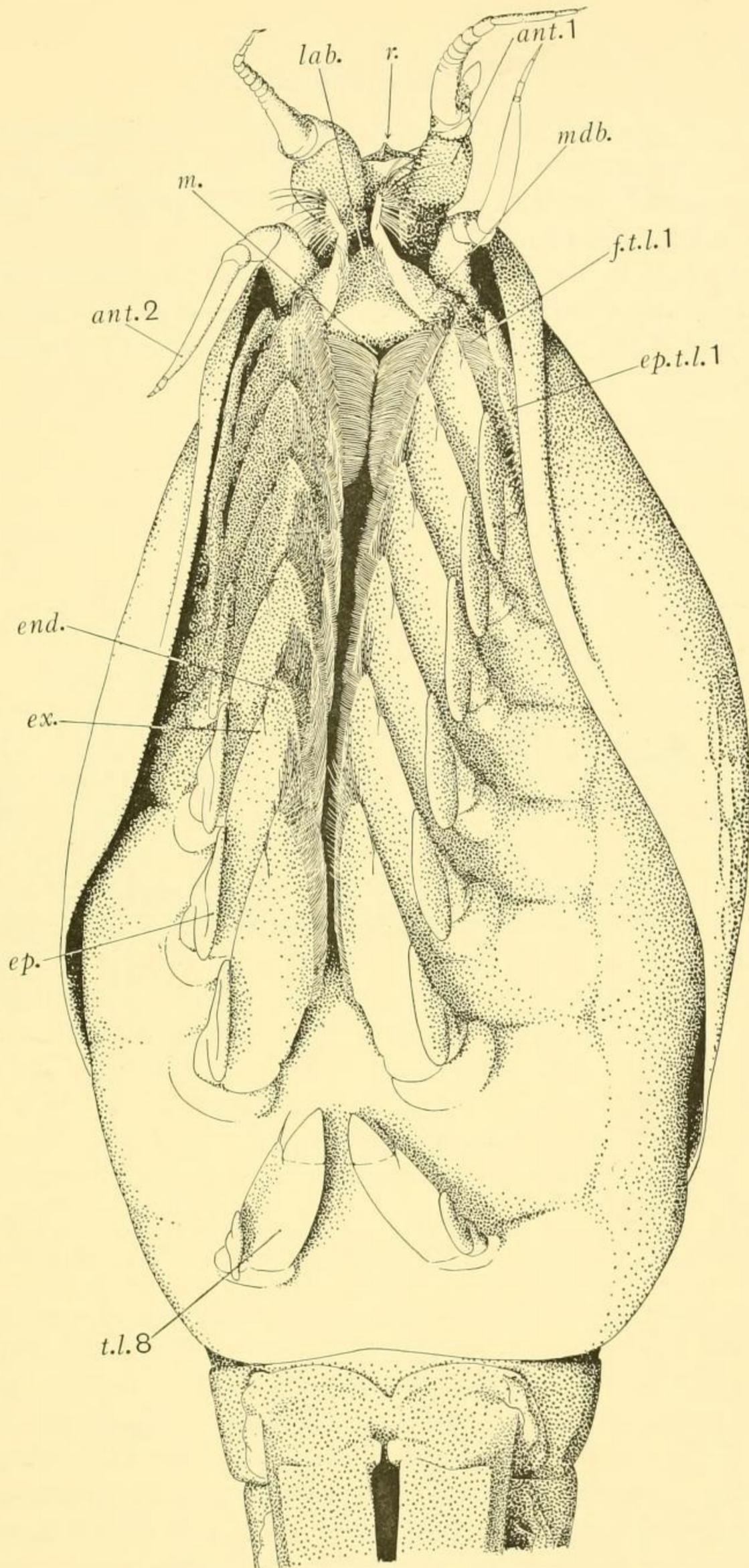


Fig. 2. *Nebaliopsis typica*. Ventral view.

ant. 1, antennule; *ant. 2*, antenna; *end.* endopodite; *ep.* epipodite; *ep.t.l. 1*, epipodite of first trunk limb; *ex.* exopodite; *f.t.l. 1*, filter setae of first trunk limb; *lab.* labrum; *m.* mouth; *mdb.* mandible; *r.* rostrum; *t.l. 8*, eighth trunk limb.

laterally. The three setae borne by the proximal endite of the maxillule still point towards the mouth, but they lie close against the anterior limit of the paragnaths. The distal endites extend forwards on either side of the labrum, the posterior setae recurving towards the mouth (Fig. 4 A).

The maxilla is, in some respects, reduced. Thus the endopodite consists of a small distal lobe while the exopodite is either absent or represented by a group of three or four lateral setae. There are four endites of which the second, third and fourth form a

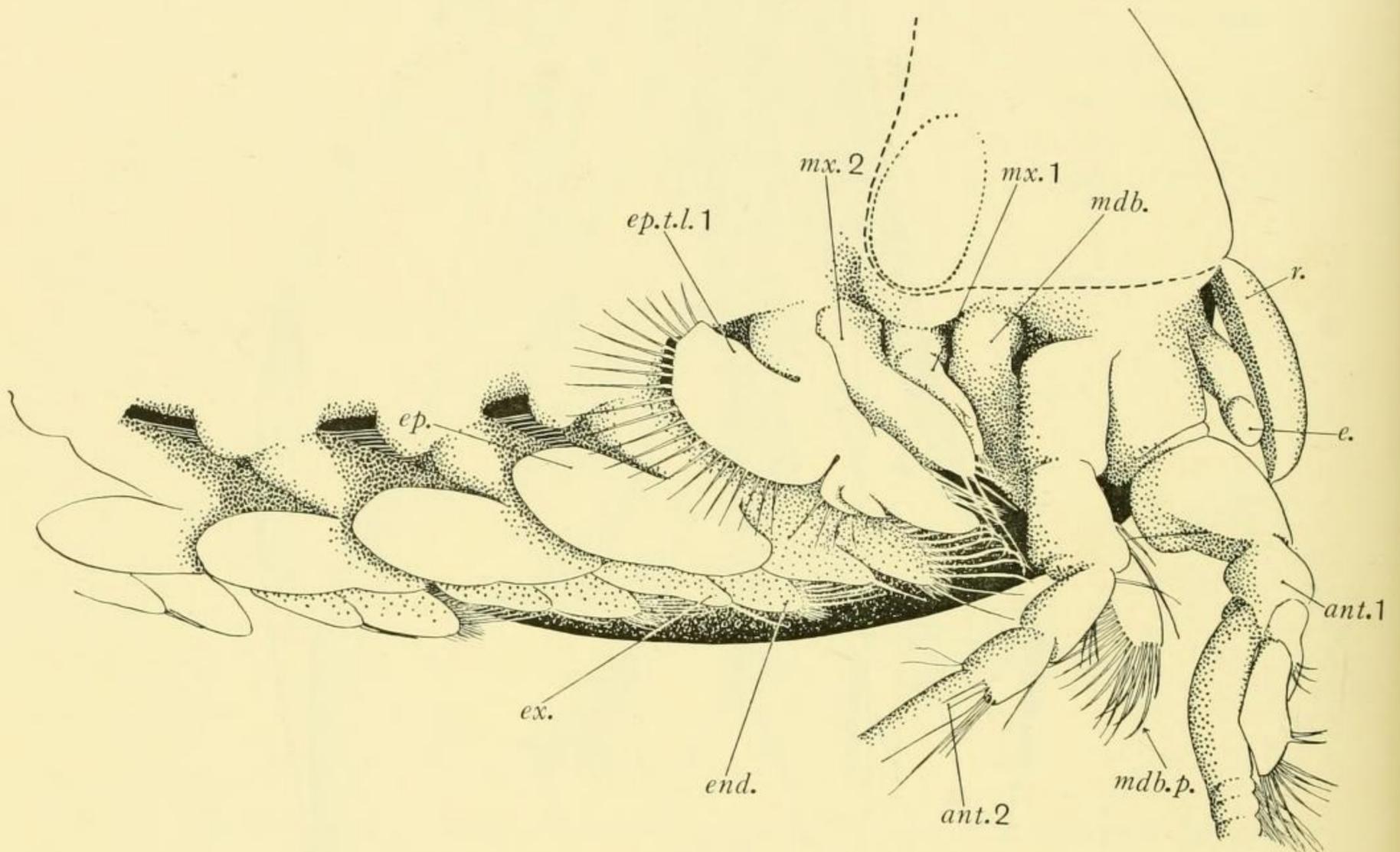


Fig. 3. *Nebaliopsis typica*. Lateral view of front part of body after cutting away the right half of the carapace.

ant. 1, antennule; *ant. 2*, antenna; *e.* eye; *end.* endopodite; *ep.* epipodite; *ep.t.l. 1*, epipodite of first trunk limb; *ex.* exopodite; *mdb.* mandible; *mdb.p.* mandibular palp; *mx. 1*, maxillule; *mx. 2*, maxilla; *r.* rostrum.

small group of three setose lobes at the base of the endopodite. Despite this simplification in structure the maxilla is relatively enormous compared with that of *Nebalia*, and this is due to the development of the first endite, which is approximately twice the length of the rest of the limb. It consists of a curved spoon-shaped plate armed on the inner edge with a row of closely set setae (Fig. 4 A). In *Nebalia* I pointed out (1927, p. 365) that the most anterior setae on this endite curve round the hinder face of the paragnaths just as do the setae of the proximal endite of the maxillule, and, since the limb projects at right angles to the body axis, the tips of these setae lie in one transverse plane. In *Nebaliopsis* the homologous setae occupy a similar position but, owing to the

extension backwards and flattening out of the paragnaths, the limb slopes obliquely forwards and the tips of the setae lie almost in a frontal plane.

Thus the main mass of the maxilla forms a comb of setae lying close against the body wall (the paragnaths) and extending some considerable distance behind the mouth. The morphologically posterior face of the limb is thus ventral and will be referred to as the ventral surface. The remainder of the limb projects forwards on either side of the mouth underneath the maxillules (Fig. 4 A).

The setae are closely set with fine setules on the ventral surfaces, especially so at their bases. Distally the setules are spread out so that the setae appear feathered at the tips (Fig. 4 A). Immediately lateral to the bases of the setae the proximal endite bears a row, or rather a strip, of closely set minute setules which project ventrally across the space between the maxilla and the first trunk limb (Figs. 4 A, 5 A; Thiele, 1904, Pl. 3, fig. 49).

The first trunk limb, which differs markedly from the more posterior limbs, lies close against the maxilla. Its posterior face is thus ventral, and the limb can be said to lie close underneath the maxilla. It bears a proximal endite which corresponds closely in shape and general structure with that of the maxilla. Its setae, however, are armed with setules on their upper and not their lower faces, and at the base of the setae, it carries a strip of closely set minute setules just as in the case of the maxilla, but again these are on the upper and not on the lower surface (Figs. 4 B, 5 A).

The endopodite consists of a lobe bearing a few powerful setae projecting forwards immediately underneath the tips of the maxilla and maxillule (Fig. 4 B). The exopodite projects ventrally, and, in the specimen F_2 , appears to be divided into two parts—an anterior lobe and a posterior flat plate armed at the edges with long setae. Directly behind this posterior part and forming a functional continuity with it, is the large plate which has been homologized with the epipodites of the other trunk limbs. This is a very thin plate from the edge of which project setae of approximately the same length as the width of the plate. It spans completely the lateral gap between the first and second trunk limbs (Fig. 3). The antero-lateral margin of the base of the limb projects forwards and upwards around the side of the maxilla thus tending to close the space between them (Fig. 5 A).

The shape and arrangement of a typical trunk limb can be seen from Figs. 2 and 3. It will be noticed that the limbs are all parallel to the maxilla and first trunk limb, thus sloping obliquely forwards. They are wider apart anteriorly than posteriorly and the inner edges of the limbs are nearer to the body wall than the outer.

Trunk limbs 3 to 7 are closely similar in structure and are referred to as the typical trunk limbs. They are unsegmented, the exopodite being represented by a slight projection ending in a strong spine towards the tip on the outer margin. The endopodite must be considered as the tip of the limb distal to this exopodite lobe. The epipodite is attached at about a third of the way up the limb and projects backwards as a very slightly bilobed structure. It should be called a lobe rather than a plate, as it is comparatively thick and differs markedly in this respect and also in the fact that it bears no

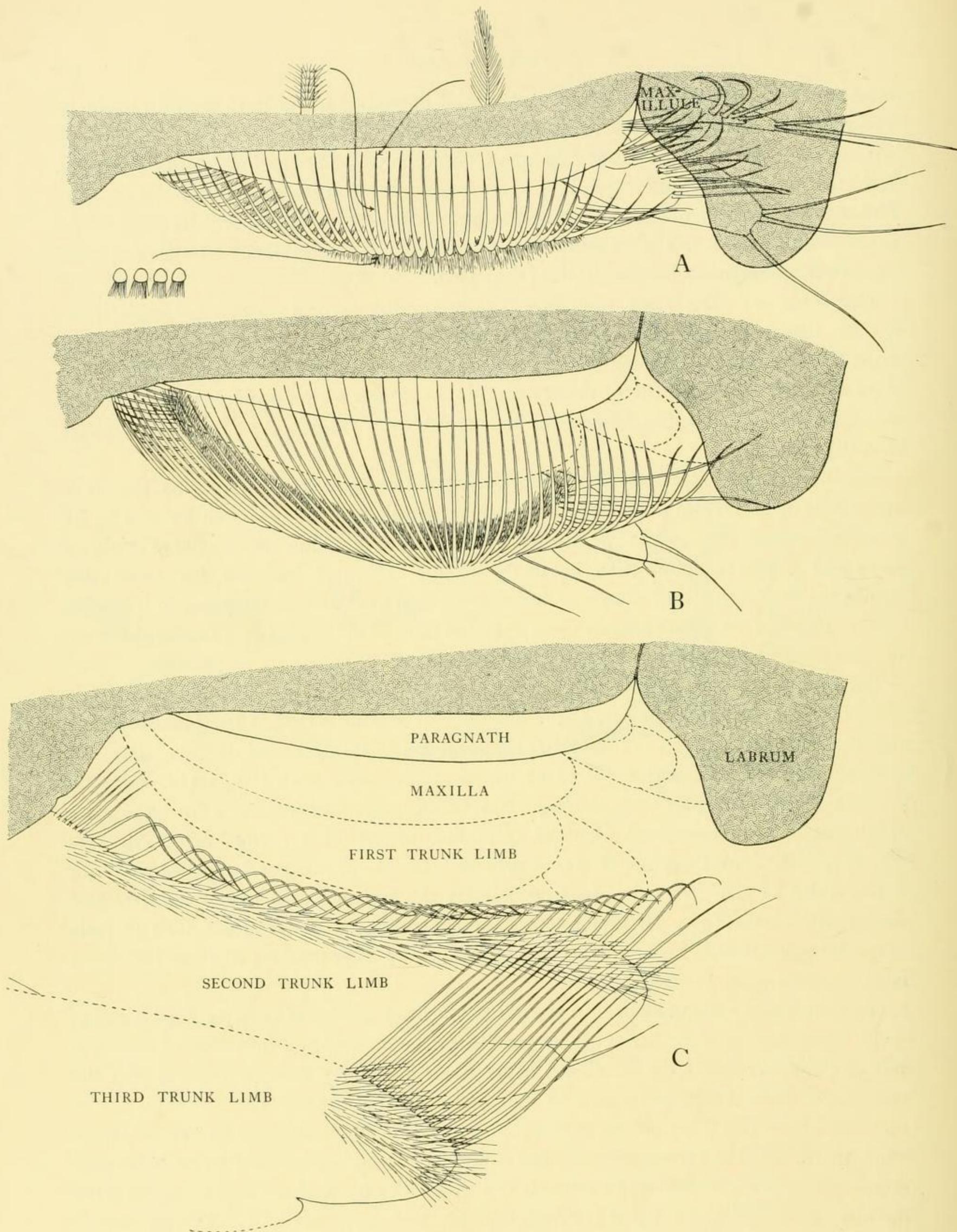


Fig. 4. *Nebaliopsis typica*. Views of maxillule, maxilla, first, second and part of third trunk limbs.
 (For comparison with *Nebalia*, Text-fig. 4, Cannon, 1927, p. 361.)

- A. Maxillule and maxilla. To the left and above are enlarged views showing the setules on a filter seta near its base, in the middle region and at the tip.
- B. First trunk limb.
- C. Second trunk limb and part of third.

marginal setae, from the thin plate-like epipodite of the first trunk limb. A still more important difference is that these epipodites do not nearly cover the lateral gaps between successive trunk limbs (Figs. 1, 3).

It may be conveniently mentioned here that it is a complete puzzle as to how a female *Nebaliopsis* carries its embryos, if indeed they are carried. In all other Nebaliacea the tips of the endopodites of the typical trunk limbs curve inwards and form a basket under the trunk (compare Fig. 6 of *Nebaliella*) but this cannot be possible in *Nebaliopsis*.

The inner margin of these trunk limbs are armed with setae just as are the trunk limbs of *Nebalia*. On each limb there are two distinct sets. One row consists of very long setae which extend forwards as far as the inner margin of the limb in front. The second set is an irregular strip of minute setae which project inwards and touch the tips of the long setae from the limb behind (Fig. 5 A). There is thus a zigzag of setae forming, on each side, the wall of the median space between the limbs, but the setae are not interlocked as in *Nebalia*. The first set are undoubtedly homologous with what I have termed the first row setae of *Nebalia* (1927, p. 359). The second set may represent the fourth row setae of *Nebalia* or may be the fourth and third rows combined.

The second trunk limb differs from the typical trunk limb in that its first row setae, with the exception of the six proximal setae and two or three of the most distal, instead of projecting straight forwards, project obliquely inwards and then curve backwards (Fig. 4 C). The six proximal setae are shorter and project directly forwards. They correspond to the gnathobasic setae of *Nebalia*.

The eighth trunk limbs are very small and bear no setae. The main axis shows a slight segmentation which probably separates off the distal endopodite.

The pleopods and furcal appendages have been sufficiently described by Thiele (1904, p. 23).

From the account I have given of the arrangement of the limbs, it is obvious that the feeding mechanism of *Nebaliopsis* must differ considerably from that of *Nebalia*.

In *Nebalia* all the eight trunk limbs project almost at right angles to the body on either side of a median space—the filter chamber. Their endopodites recurve sharply backwards and slightly inwards so that their tips touch in the middle line. A floor is thus formed to the filter chamber. The eighth trunk limbs interlock in the middle line and so form the hind wall. The lateral walls are formed on either side by a continuous series of interlocked setae borne on the inner margins of the limbs, two sets of setae on each limb (the first and third rows) hooking into the setae of the limbs fore and aft. Thus the only entrance to the filter chamber is anteriorly. Water is sucked in through this opening by the rhythmical movement of the trunk limbs and caused to pass through the filter walls between the trunk limbs to the exterior, the food particles being retained in the filter chamber. The passage of water in one direction through this filter system is made possible by the valvular arrangement of the exopodites and epipodites. On each limb these structures form a complete valve closing the space laterally between that

limb and the limb behind. The whole of the filter apparatus is supported by the carapace which completely covers the trunk limbs.

In *Nebaliopsis* the trunk limbs project obliquely forwards, their endopodites being in a line with the rest of the limb. The limbs are wide apart and the median space between them is open ventrally. The eighth trunk limbs are without setae. The second to seventh trunk limbs bear setae which form a complete wall to the median space but the setae of one limb are not hooked on to those of adjacent limbs. Further, the exopodites are minute and, with the exception of the first trunk limb, the epipodites do not cover the spaces between successive limbs. The carapace, in an average specimen, extends back only to about the fourth trunk limb. In all specimens the lateral margins of the carapace are wide apart and not close together in the middle line as in *Nebalia*.

There are thus very few points of resemblance between the two forms, but I believe it is possible, with a fair degree of certainty, to suggest the mechanism by which *Nebaliopsis* obtains its food.

Nebaliopsis is, I believe, entirely a filter feeder. The molar process of the mandible is represented by a small soft protuberance (Thiele, 1904, p. 21) which must serve as a lateral lip rather than as a masticatory process. The whole mouth armature is extremely soft and quite unsuited for dealing with large food particles. In addition, there is a complicated structure which, in my opinion, must be a filter.

The consideration of the feeding mechanism can be divided into two parts. The action of the second to seventh trunk limbs, and the action of the maxilla and first trunk limbs, which I believe represents the actual filtratory mechanism.

The eighth trunk limbs, from their separation from the more anterior limbs and from the fact that they bear no setae, most probably take no part in the feeding process.

In this analysis I make two assumptions. Firstly, I assume that the typical trunk limbs exhibit a metachronial rhythm in their movement of the type that I have described in detail for *Nebalia* (1927, p. 357) and *Chirocephalus* (1928, p. 816). That is, every limb commences its backstroke just before the limb immediately anterior to it. I have previously suggested (1928, p. 816) that all Crustacea exhibit primitively this type of movement, and I see no reason for assuming that *Nebaliopsis* is, in this respect, different from *Nebalia*. Secondly, I assume that the typical trunk limbs depend to a great extent on their turgidity, that is on their blood-pressure, for rigidity. I believe that this assumption is justified from the fact that the distal two-thirds of each limb is devoid of musculature. Also the cuticle is so thin that it is difficult to imagine any movement being possible in so large a limb without some internal pressure to inflate it. The trunk limb, in these respects, is markedly different from the powerful swimming pleopods which are full of musculature and carry a comparatively thick cuticle.

In Fig. 5 C I have drawn an outline sketch of the seventh pair of trunk limbs seen ventrally and a median aspect of one of these limbs to illustrate the musculature. It will be seen that each limb articulates on a rigid boss or prominence from the body wall (see also Figs. 1, 3). The limb contains two chief muscles. One comparatively powerful muscle is attached in the limb close against the ventral body wall at the base of the first

row setae. It extends backwards and attaches to the body wall at the base of the boss. I call it the flexor muscle. Its contraction must tend to lift the tip of the limb towards the body wall and, at the same time, it must swing the tip round towards the middle line.

The recovery of the limb back to the position shown in Figs. 1 and 2, must be mainly due to the blood-pressure, but it is probably aided by the other muscle in the limb. This, the extensor, is markedly smaller than the flexor. It is attached to the ventral surface of the limb just below the anterior attachment of the flexor, and runs ventro-posteriorly to a point of attachment near the tip of the boss. From Fig. 5 C it will be seen that it also runs postero-laterally. Its contraction must therefore tend to swing the tip of the limb outwards and downwards.

Thus the typical trunk limb oscillates in metachronal rhythm, moving up and down towards the body wall and against the limb in front, the tips of each pair of limbs approaching each other as they move upwards.

The result of this movement is, I believe, a general drift of water away from the limbs. As each limb moves upwards it throws out the water between it and the limb in front. The tip of the limb will be moving fastest, the base not at all. It will touch the limb in front and so occlude completely the inter-limb space in this region. Thus the water towards the tip of the limb will be forced outwards. It will pass out mostly between the ends of the two limbs and the epipodite which stretches between them laterally. The forward drift will obviously be more pronounced anteriorly where the carapace covers the limbs laterally.

A simpler way of considering the limb movement is to look on each limb as an oar used as a scull over the stern of a boat. The oar produces, or tends to produce, a movement of water away from the boat along the length of the oar. The limb, I believe, acts in a similar manner.

To replace the water thrown forwards, water will drift towards the body from all directions in the hinder part of the trunk. Anteriorly the trunk is covered by the carapace so that water cannot pass in laterally and, in addition, the momentum of the moving mass of water passing forwards over the limbs will suck in the surrounding water, but this will be drawn into the stream and not into the inter-limb spaces.

Now this is totally different from the conditions in *Nebalia*. Here, all the water which passes into the inter-limb spaces, is sucked from the mid-ventral chamber through the filter wall. In *Nebaliopsis*, while there are filter walls to this median space, there are no valves on the outer sides of the limbs to cause such a suction. On the contrary, there is a large open space dorsal to the attachment of the epipodite which, as far as I can see, cannot be closed however the limb oscillates, and this must be at least one of the passages for water entering the inter-limb space. There is also a gap distal to the epipodite and there is nothing to hinder water entering here as well.

I have summarized what I believe to be the main water currents around a feeding *Nebaliopsis* in Fig. 5 B. Now the passage forwards of a definite stream over the surface of the limbs must mean that there will be a drift in the same direction between the limbs in the mid-ventral space. I do not mean that there will be a marked anteriorly

directed current towards the mouth as in *Chirocephalus*, but it is impossible to imagine the water moving forwards on either side without the central mass of water moving in the same direction. Of course this would not apply if there were not the wide open space ventrally between the limbs.

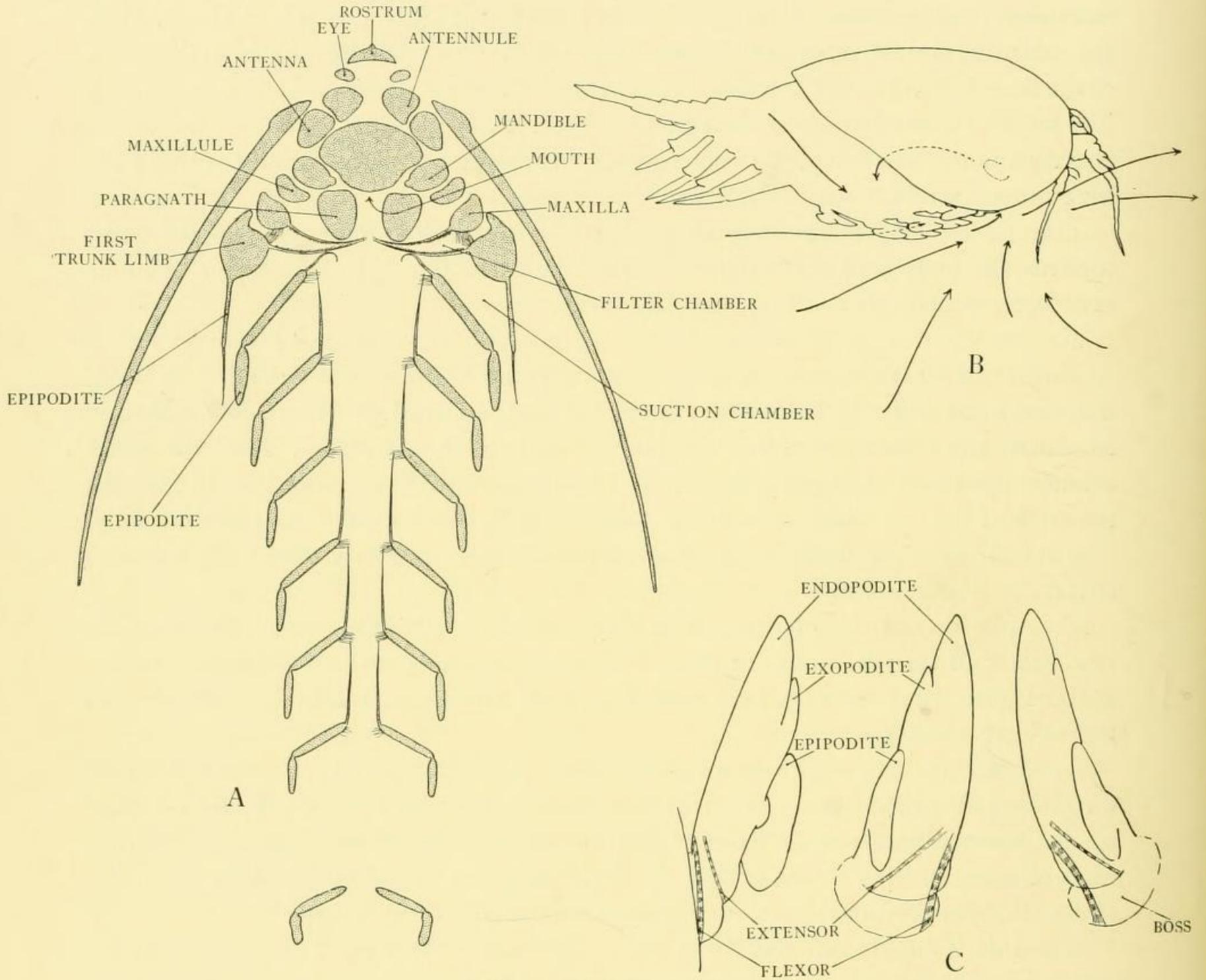


Fig. 5. *Nebaliopsis typica*.

- A. Diagram of hypothetical curved frontal section passing through all the head and trunk limbs, to show the constitution of the filter apparatus and the arrangement of setae on the posterior trunk limbs. (For comparison with *Nebalia*, Text-fig. 1, Cannon, 1927, p. 357.)
- B. Sketch to show suggested water currents.
- C. Median and ventral views of seventh trunk limbs to show musculature.

This current will be greatly increased, as I shall describe below, by the activity of the maxilla and first trunk limb. Any food particle carried on it will be retained in the median space by the filter walls, just as in the case of *Nebalia*. As a limb moves backwards and so increases the inter-limb space in front of it, there must be a slight suction

from the mid-ventral space, although, as I have just stated, most of the water will pass in through the lateral gaps. This will suck particles on to the long filter setae of the limb. They will be swept off again into the mid-ventral space by the strip of short setules of the limb in front (Fig. 5 A) just as, in the case of *Nebalia*, the fourth row setae sweep particles off the first row. It is for this reason that I suggested that the setules immediately behind the long first row setae may be homologous with the fourth row setae of *Nebalia*.

From Fig. 2 it will be seen that the combs of setae on the protopodites of the first trunk limbs are largely exposed ventrally so that, if these setae and the maxillary setae which they cover act as filters, there is this open ventral space from which water can be drawn for filtering. In addition, if what I have argued above is correct, there is a continuous stream from behind and more particularly a forward current in the mid-ventral line which will be laden with food particles kept there by the setae of the trunk limbs.

The structure of the maxilla and first trunk limbs, in my opinion, indicate that they must act as true filters. If this is so, it must be possible to demonstrate an actual filter chamber and a mechanism by means of which water is caused to pass through that chamber, and further, a means by which the filter itself can be cleaned and the residue passed on to the mouth.

The filter chamber is the inter-limb space between maxilla and first trunk limb. It is a thin curved space close against and parallel to the body wall and roofed by the filter comb of the maxilla (Fig. 5 A). The setae of this comb are armed with setules which point downwards into the chamber so that, if water passes through this comb from the chamber, any particles will be retained on the setules. The extent of these setules is shown in Fig. 5 A where three enlarged drawings are shown of the setae near the base, in the middle region and at the tip. These figures were drawn from an isolated maxilla which was viewed from the median plane under a high-power binocular. The arrangement of setules at the base of the setae was confirmed from the series of parasagittal sections.

The floor of the filter chamber is formed by the filter comb of the first trunk limb. Here again, the setae are armed with setules, and they point this time upwards, into the chamber. As before, they would retain any particles carried by water if the latter passed through them out of the filter chamber.

There are no real walls to the filter chamber medianly, anteriorly or posteriorly, as, in these directions, the tips of the setae of the first trunk limb touch the corresponding setae of the maxilla; but laterally, the chamber is bounded by the mats of setules which project downwards from the maxilla and protrude into the similar setules which project upwards from the first trunk limb (Fig. 5 A). This lateral wall must not be looked on as a setal wall through which water could pass. It may be described as a solid mass of setules and I believe it is just as effective as a solid wall would be.

The manner by which water is drawn into this filter chamber is not very precise. When the maxilla and first trunk limbs are lifted up from the body their inter-limb

space, that is, the filter chamber, must enlarge. Water will be sucked in and will pass from the mid-ventral space through the tips of the setal combs. It cannot pass in laterally because of the solid mat of setules. Some of the particles in the stream will be entangled on the tips of the setal combs. The remainder will pass into the chamber and these, as I have explained, cannot get out. They will be caught on the setules of the filter setae.

When the limbs move up again towards the body, this, in itself, will diminish the volume of the filter chamber and so tend to force out its contained water. However, a real suction pump exists which actively sucks water out of the chamber. This is formed by the first and second trunk limbs, and their inter-limb space I call the suction chamber (Fig. 5 A). The valve of the pump is provided by the epipodite of the first trunk limb which, as I have explained, completely covers laterally this inter-limb space. When the second trunk limb moves backwards it will tend to increase the volume of the suction chamber and hence water will be sucked in. Now this cannot pass in laterally as in the case of the more posterior trunk limbs for the epipodite will flap against the second trunk limb and act as a closing valve. Some will pass in from the mid-ventral space and will be filtered on to the setae of the second trunk limb, but the majority will be sucked out of the filter chamber.

From Fig. 2 it can be seen that the suction chamber is roofed by the filter setae of the first trunk limb. This is most clear on the right-hand side of the figure. When the second trunk limb is dragged backwards its tip will probably touch the limb in front. The suction chamber is now closed ventrally and also laterally by the epipodite. Water sucked in must hence pass either from the median space or through the roof of the chamber, that is, from the filter chamber. From Fig. 5 A it can be seen that this roof forms a much greater area than the median wall and so it is probable that the majority of the water passes in through the roof.

Water drawn from the filter chamber into the suction chamber will pass out backwards when the second trunk limb moves forwards relatively to the first. When this happens the space between the two limbs will diminish and so water will be forced out. The epipodite will now flap outwards and allow a free passage posteriorly exactly as in the case of the combined exopodites and epipodites of *Nebalia*.

The peculiar re-curvature of the first row setae of the second trunk limb is difficult to explain. I can only say that if they projected directly forwards in the same direction as the homologous setae of the more posterior trunk limbs, they would project right through the filter apparatus and interfere with its functioning. The direction of the setae of the second trunk limb is, on the whole, at right angles to those of the first trunk limb. The curved setae thus lie across the filter setae, and I suggest that they act as a sort of buffer to the latter preventing them being forced backwards too far when the filter chamber is diminishing. They could not act in this way, even with their re-curvature, if they pointed in the same direction as the filter setae as they would slip in between the latter.

The particles of food filtered off on to the walls of the filter chamber have now to be transferred to the mouth. One of the most striking things about *Nebaliopsis* is the

distance the filter apparatus extends behind the mouth. It is of no use a limb filtering off food particles if there is no means of transferring these to the mouth and hence the posterior part, at least, of the filter would be useless unless a suitable mechanism for the purpose existed. The process of transference is, I believe, carried out entirely by the mandibular palps. The length of these structures is just sufficient to allow them to bend back as far as the hinder limit of the filter chamber. Also, they are jointed in such a way that the tips can be folded back into the mouth entrance and the tips are armed with comparatively stout claw-like setae armed with a brush of setules. I believe they stroke upwards so that their distal setae project through the filter setae into the chamber and then inwards and forwards to the mouth, thus combing the filtered residue to the mouth entrance. Here it is sucked into the mouth by the powerful dilator musculature of the oesophagus.

I have said nothing as to the actual phase differences between the oscillations of the mouth parts. I assume that the trunk limbs behind the first exhibit the typical metachronal rhythm, but exactly how the mouth parts oscillate I think it impossible to say.

To summarize the feeding mechanism as far as I have analysed it—it is suggested that the second to seventh trunk limbs, by their oscillation, produce a drift of water forwards over the mouth parts. This will cause a subsidiary current along the mid-ventral line towards the mouth, and particles in this current will be retained there by the filter setae arming the inner margins of these trunk limbs. Water arriving at the mouth region will be sucked into a filter chamber between the maxilla and first trunk limb when these limbs move downwards from the body wall. It will be sucked out by the backward movement of the second trunk limb, the epipodite of the first trunk limb acting as a valve closing laterally the inter-limb space between the first two trunk limbs. Particles filtered off in this way on to the filter setae of the maxilla and first trunk limb are scraped off and passed forwards by the mandibular palps into the mouth.

Nebaliopsis is without doubt the most specialized of the Nebaliacea (Thiele, 1904, p. 25). Of the other members of the group I have described the feeding mechanism of *Nebalia* from actual observation (1927). In the next part of this report I give evidence that the principle of the feeding process of *Nebaliella* is the same as that of *Nebalia*. Although I have not been able to examine a complete *Paranebalia* I believe, from the published accounts of this genus, that it also feeds in a similar manner. Thus the *Nebalia* mechanism can be taken, in general principle, as representing the primitive feeding mechanism of the Nebaliacea, and it must be assumed that the method of feeding of *Nebaliopsis* has evolved from it.

How this has come about is very difficult to say and will remain so until new forms are found less divergent from other Nebaliacea than *Nebaliopsis*. But, that the change took place in correlation with the planktonic habits of *Nebaliopsis*, is, I think, certain. It is possible to imagine a *Nebalia* adopting a pelagic habit. In fact, certain of the specimens recorded in this report were collected at the surface (p. 221), but I cannot conceive a *Nebaliopsis* living in mud. For this reason I take it that *Nebaliopsis* evolved from a planktonic *Nebalia*.

Such a form, I suggest, developed the maxillary-first trunk limb filter mechanism, at first, to aid its more posterior trunk limb filter, just as I have suggested in the evolution of the primitive Malacostracan the maxillary filter developed to assist the trunk limb feeding mechanism (1928, p. 820). Then, when this became sufficiently advanced, it opened up the carapace—maybe to allow a greater inflow of water on to the maxillary region. At this stage water would enter the mid-ventral space, not only anteriorly, but also ventrally. The maxillary filter now became the chief feeding mechanism and, with further evolution, became greatly enlarged. As it developed so the carapace widened out and water came to be sucked in from all directions. The trunk limb filter was then almost abandoned, the trunk limbs swinging forwards to act as a subsidiary mechanism supplying water to the primary maxillary-first trunk limb filter.

On these arguments *Nebaliopsis* shows an interesting parallel to *Nebalia*. I pointed out (1927, p. 367) that the ancestor of *Nebalia* was a filter feeder and that, in its evolution "the primitive filtering mechanism disappeared, and with the re-establishment of a filtering method of feeding the original mechanism did not return, but an entirely new method was established" (1927, p. 368). Now this filter mechanism of the ancestral Nebaliacean, lost in *Nebalia*, was a maxillary filter (Cannon and Manton, 1929, text-fig. 1) and, in the evolution of *Nebaliopsis*, a maxillary filter has been re-established, but it is an entirely new apparatus—a combination of maxilla and first trunk limb, which is otherwise unknown in the Malacostraca.

Nebaliella extrema, J. Thiele

The genus *Nebaliella* was established by Thiele in 1904 to include two specimens collected by the 'Valdivia' in the neighbourhood of Kerguelen, and a single incomplete specimen collected about 1875 by the 'Gazelle' from the same locality. He described them under the name *Nebaliella antarctica*. He suggested also that a specimen in the Copenhagen Museum, which was collected in Akaroa Harbour, New Zealand, is a young individual of this species. In 1908 he described another species, *N. extrema*, from fifteen specimens collected by the 'Gauss' off the coast of Kaiser Wilhelm II Land. Among the Discovery material there is a single complete and undamaged specimen of this latter species collected in the Palmer Archipelago.

The following list gives details of the localities in which *Nebaliella* has been found:

Table II.

Expedition	Locality	Lat.	Long.	Depth
<i>N. antarctica</i>				
Gazelle, 1875	Kerguelen	48° 30' S	69° 40' E	9 m.
Valdivia, 1898-9	Kerguelen	48° 30' S	69° 40' E	5-10 faden
(Copenhagen Museum)	Akaroa Harbour, N.Z.	43° 50' S	172° 55' E	—
<i>N. extrema</i>				
Gauss, 1902-3	Kaiser Wilhelm II Land	66° 29' S	89° 38' E	380-385 m.
Discovery, 1927. St. 181	Palmer Archipelago	64° 20' S	63° 1' W	160-335 m.

Thiele does not figure or give measurements of *N. extrema* but from his account it is to be presumed that it did not differ markedly in general shape and size from *N. antarctica*. He gives measurements of the latter species but, unfortunately, they do not tally with his drawing. According to his figures the carapace should appear larger proportionately to the rest of the body than in his illustration. If this correction is made the general shape and proportion of the body agree with the Discovery specimen of *N. extrema*.

The chief dimensions of the Discovery specimen are:

Carapace length	5.45 mm.
Carapace depth	3.65 "
Length of rostrum	1.3 "
Length of flange of rostrum	0.65 "
Width of flange of rostrum	0.43 "
Length of eye	1.6 "
Length of caudal furca, excluding terminal spines ...	2.1 "
Total length from tip of rostrum to tip of caudal furca	11.5 "

The three main characteristics of the genus *Nebaliella* are the peculiar form of the rostrum and eyes, the fact that the third and fourth joints of the antenna are separate and armed with stout spines, and the absence of epipodites on the trunk limbs. Of these, the latter distinguishes *Nebaliella* from all other Nebaliacea, but, from a functional standpoint, it is the least important characteristic.

The morphology of the trunk limbs has been described in detail by Thiele (1904, p. 7; 1905, p. 64). Apart from the absence of epipodites they are closely similar to the trunk limbs of *Nebalia*. I have studied their arrangement in the Discovery specimen and find it identical with that of *Nebalia*. As will be seen from Fig. 6, the specimen is an adult female carrying embryos. These were held by the tips of the endopodites curving backwards and inwards to form a complete basket under the trunk and a floor for the filter chamber between the trunk limbs. The walls of the filter chamber are constituted as in *Nebalia*, each trunk limb carrying four rows of setae along its inner margin. The first and third rows are long and form the actual filter wall. The second consists of a few long feathered setae near the base of the limb and the fourth row, of short setae on the hinder face of the inner margin, projecting inwards and backwards through the first row setae of the limb behind. I could not settle whether the first and third rows of successive limbs interlocked as in *Nebalia* as, in removing the embryos in order to study this setation, the setae were naturally displaced. The eighth pair of trunk limbs are close together in the middle line and form the hinder wall to the filter chamber just as in *Nebalia*.

On cutting away the carapace on one side, I found that, although the epipodites were absent, the exopodites were, proportionately to *Nebalia*, much larger, each exopodite completely covering the lateral space between its limb and the limb behind. That is, the exopodite of *Nebaliella* has taken the place of the combined exopodite plus epipodite of *Nebalia* which I showed (1927, p. 358) acted as valves allowing the passage of water from the filter chamber between the limbs to the exterior at the hind end of the carapace.

In *Nebaliella* then, the trunk limbs are arranged in the same way as in *Nebalia*, their

setal armature is the same, and their exopodites take the place of the exopodites and epipodites of *Nebalia*. It is legitimate to deduce that *Nebaliella* is also a filter-feeding organism and that the principle of its filter mechanism is the same as that of *Nebalia*.

Nebaliella, like *Nebalia*, is undoubtedly a mud-living form. In fact, the anterior portion of the Discovery specimen was covered with a layer of mud which had to be removed before its limbs could be studied. The shape of the rostrum and eyes and the armature of the third and fourth joints of the antenna, which, as I have explained, are the other characteristics of the genus, are, I believe, adaptations to this burrowing mode of life. In *Nebalia* I suggested (1927, p. 356) that the rostrum functions in controlling the current entering the filter chamber. This has been carried to extremes in *Nebaliella* and, the animal being apparently blind (Thiele, 1904, p. 4), the eyes have become modi-

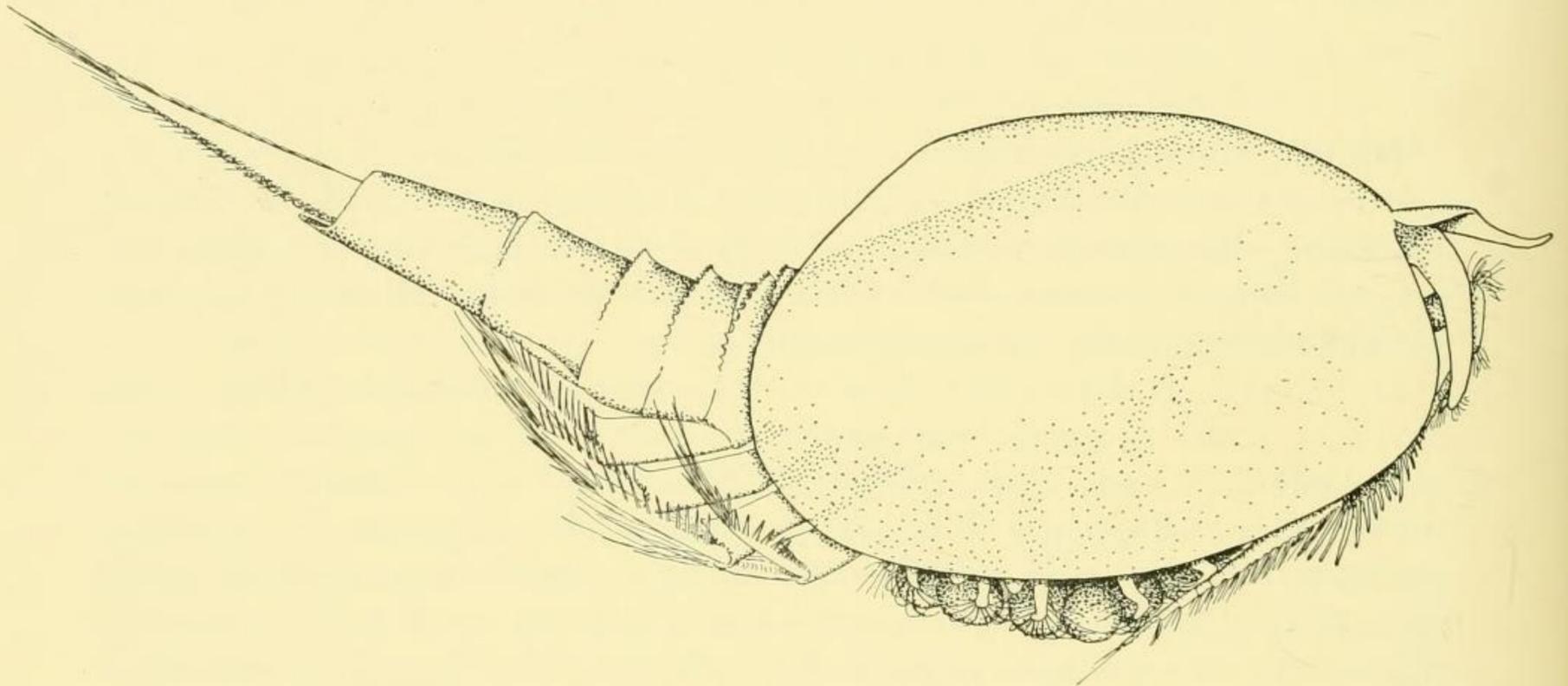


Fig. 6. *Nebaliella extrema*. Side view.

fied in structure and incorporated into this rostral controlling mechanism. Briefly put, the eyes and rostrum together form a plough which forces the mud to the sides and so prevents the filter mechanism becoming choked as the animal forces its way through the mud by means of the powerful claws on the antennae.

The shape of the rostrum and eyes has been described in detail by Thiele (1905, p. 61). They are figured in Fig. 7 in lateral aspect and when viewed obliquely from in front and below. It will be seen that the rostrum consists of a median keel with lateral flanges posteriorly. The eyes are excessively thin scythe-shaped plates. The planes of the eyes are approximately at right angles, each projecting antero-laterally. Thus, in Fig. 7 B, the right eye, which is being viewed in the direction of its plane, shows its thinness, while the left shows its outline. The eyes articulate below the lateral flanges of the rostrum, the convex anterior margin extending up to a point immediately underneath, and slightly median to, the outer edge of the flange. The articulation is thus covered dorsally by the rostral flange.

The concave posterior margin of the eye is produced into a heel near its upper limit

which presses backwards against a knob just above the attachment of the antennule. This knob has been described and figured by Thiele (1905, Pl. 2, fig. 3) but the specimen from which the figure was drawn must have been badly distorted.

Attached to the outer surface of the eye at about the middle of its length and near the lower margin is a muscle which runs backwards and inwards to attach to a median point just below the hinge of the rostrum. By contraction of this muscle the eye would tend to be drawn backwards and inwards. However, its backward movement is re-

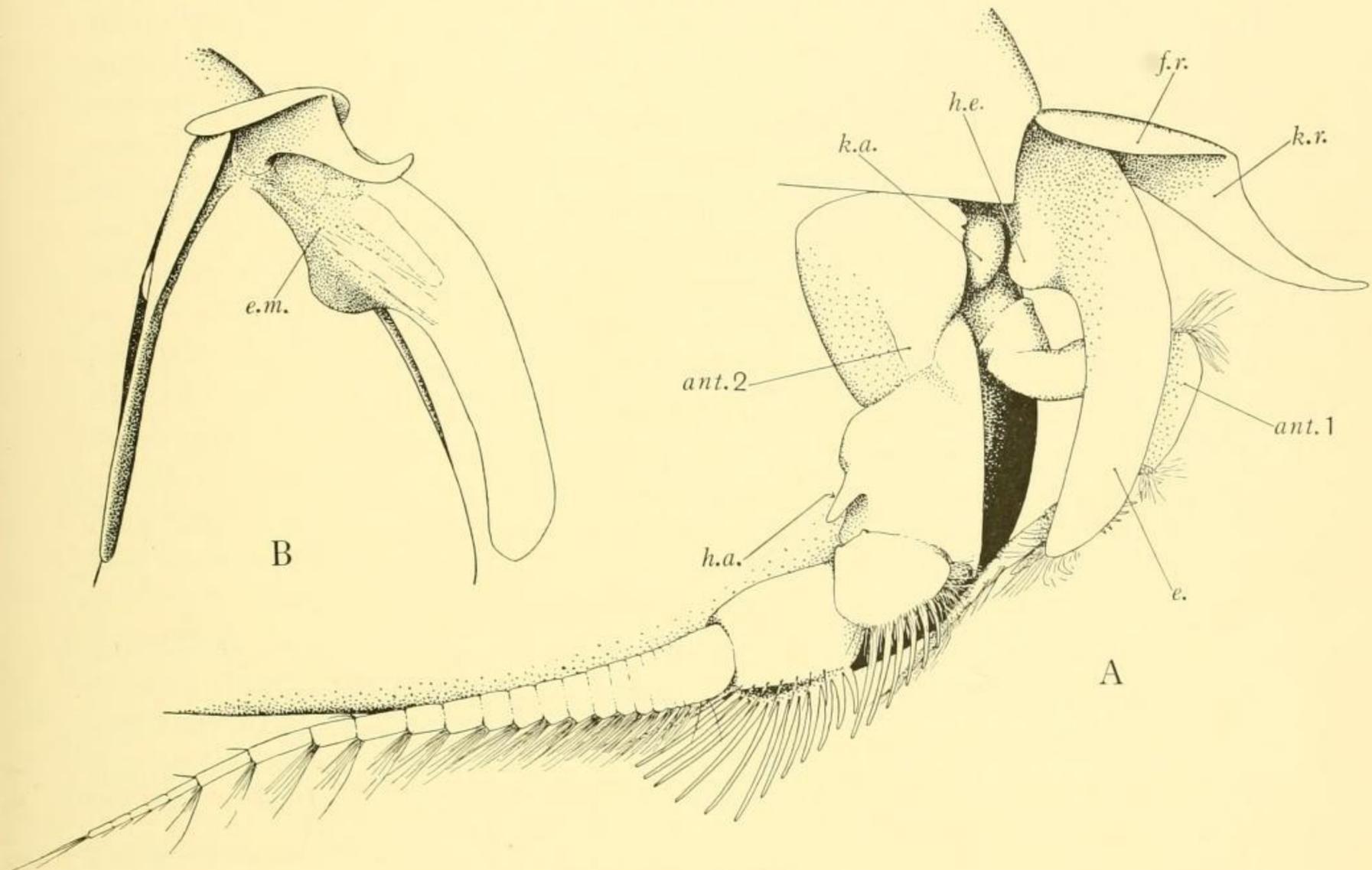


Fig. 7. *Nebaliella extrema*.

A. Side view of rostrum, eyes, antennules and antennae, the right half of the carapace having been partly cut away.
B. Oblique front view of eyes and rostrum.

ant. 1, antennule; *ant. 2*, antenna; *e.* eye; *e.m.* eye muscle; *f.r.* flange of rostrum; *h.a.* hook on second joint of antenna; *h.e.* heel of eye; *k.a.* knob above antennule; *k.r.* keel of rostrum.

stricted by the posterior heel. From the lateral view in Fig. 7 A, it will be seen that this heel is lodged in a gap between the antennular knob and the antennule itself. Contraction of the eye muscle can, therefore, only have one action. It must cause the eye to pivot about this point. This will make the anterior margins of the eyes rotate inwards towards the middle line. Now the eyes form the lateral margins of the anterior entrance to the filter chamber—the only entrance by which food-bearing water is sucked in—and their rotation inwards will diminish the size of this entrance. There is thus in the eyes a mechanism by which the amount of water, and hence the amount of food, entering the carapace can be controlled.

When a *Nebalia* burrows in the mud it depresses its rostrum and partially closes its carapace so that the front end of the carapace will not become swamped with mud and the feeding mechanism choked. I assume that *Nebaliella* behaves in the same way.

Now when the rostrum of *Nebaliella* is depressed the eyes must automatically rotate inwards. In fact, as will be seen from Fig. 7, the rostrum cannot be depressed without the eyes first of all shifting in some way, since the upper limit of the front margin of the eye rests against and appears to support the under surface of the flange of the rostrum. The flange, however, is not flat but concave ventrally (Fig. 7 B). Its ventral surface thus faces downwards and inwards. Pressure of the flange on the upper margin of the eye must therefore force the latter inwards and, since the eye is lodged by its heel against the base of the antennule, this pressure can only have one result, that of rotating the eyes inwards.

As the depression of the rostrum continues the eyes will swing inwards until the upper parts of their anterior margins come to lie alongside the median keel of the rostrum. The latter will then be gripped between the eyes and, together with them, will form a lid tending to close the anterior opening between the valves of the carapace. This lid cannot be further depressed on to the carapace edges unless the eyes can move backwards.

On burrowing, as I have stated above, I assume that *Nebaliella* partially closes its carapace. In order to do this, it must withdraw its antennules or, at least, their upper parts, backwards into the carapace. This will allow the heel of the eye to move slightly backwards, and this, in turn, will allow the rostrum to fold down to its maximum extent until its flanges rest on the anterior edges of the carapace, the tips of the eyes passing just inside the carapace.

Thus when a *Nebaliella* is burrowing the rostrum and eyes together form a lid closing the upper and greater part of the anterior opening of the carapace. It is possible that the distal parts of the antennules will project as sensory feelers through the lower part of this opening just ventral to the tips of the eyes. But for the greater part this gap will be closed by the massive third and fourth joints of the antennae.

From Fig. 7 A it can be seen that the first and second joints of the antennae are of such a length that the powerful spines on the third and fourth joints project just beyond the edges of the carapace (Fig. 6), and I suggest that these are the structures which *Nebaliella* uses to push itself through the mud. They do not occur in any other Nebaliacean and it is possible that they have some other function, but it is because of their strength and arrangement, and from the fact that, in the Discovery specimen they were completely covered with mud, that I suggest that they form the chief burrowing organ. They are situated along the inner lower margins of the two joints and, on the fourth joint along the inner edge of a ridge under which fits closely the edge of the carapace. The latter can thus be almost closed ventrally and yet allow these antennal claws to project.

The separation of the third and fourth joints supports my suggestion, as, separated, they have much greater power for gripping the mud than if they were fused. In the latter case a movement of the whole antenna would be necessary for them to dig into the mud, while as they are, they can do this by rotating about their common joint and about the joint between the third and second segments.

The antennae, during digging, will be drawn forwards as far as possible. This will give the claws a bigger pull and so increase their efficiency for burrowing.

Now the combined action of the eyes, rostrum and antennae will have a further result, and that is, that the tip of the eye must catch on the peculiar hook on the hinder margin of the second joint of the antenna. The hook is so placed that, as far as I can see, the eye cannot rotate backwards without catching on it and, further, it is of just such a shape that the tip of the eye fits into it perfectly. It has been described and figured by Thiele (1904, p. 5) but he does not suggest any function for it. It occurs only in *Nebaliella*.

The eyes are thus depressed by the rostrum and, at the same time they are gripped from behind by the antennal hooks. As a result they are held firmly in position to form with the rostrum a rigid shield covering the anterior opening of the carapace which will guard this entrance against choking by mud during burrowing.

The function of the pleopods is probably to cause a backward current in the burrow which will carry away the mud kicked up by the antennal claws.

The three main differences between the two species of *Nebaliella* are the form of the rostrum, the number of claws on the third and fourth joints of the antenna and the setation on the outer margins of the pleopods. In all these respects the Discovery specimen agreed with the description of *N. extrema*.

The antennal flagellum of *N. extrema* has not been figured, but, from Thiele's description (1905, p. 63) it is to be presumed that it agrees with that of *N. antarctica* (Thiele, 1904, Pl. 1, fig. 8). The Discovery specimen, however, shows a marked difference from Thiele's figure. He describes the flagellum as of thirty-five joints, of which the second to the fourteenth, the sixteenth, the twentieth and the twenty-sixth carry bundles of sensory setae ("Riechschläuchen"). In the Discovery specimen there are about twenty-three segments of which all except the terminal five carry bundles of these setae. If the segments on Thiele's figure are counted as the gaps between successive bundles and the terminal part counted as five segments then there are twenty-two segments, which agrees fairly closely with the Discovery specimen. It will be seen from Fig. 7 A that the proximal segmentation is obscure. The difference is, I believe, due to the fact that Thiele's specimen was probably a male while the Discovery specimen was a female, for Claus (1889, Pl. 2) has shown that in the male of *Nebalia* the true segments of the antennal flagellum show a secondary segmentation which greatly increases the apparent number of segments.

Nebalia longicornis, G. M. Thomson

Specimens of *Nebalia* were collected from three widely separated localities:

Locality	Depth	No. of specimens	
South Georgia, St. 45	233-270 m.	1	<i>N. longicornis magellanica</i>
Falkland Islands, St. 51	105-115 m.	1	<i>N. longicornis magellanica</i>
Simon's Town, S. Africa, St. 90	1-2 m.	6	<i>N. longicornis</i>

As Calman has pointed out (1917, p. 157, and 1927, p. 399) the classification of the forms of *Nebalia* is, at present, very unsatisfactory. The chief characters on which species are diagnosed are: the form of the rostrum, the setal armature of the fourth segment of the antennule and, to a lesser degree, the form of the eye.

If the second of these characters alone is taken into consideration all the Discovery specimens belong to the species *N. longicornis*, since they all carry on the fourth antennular segment one stout spine followed by five or six more slender spines. Also, the single specimens from South Georgia and the Falkland Islands exhibit eyes with the peculiar dorsal tubercle characteristic of the variety *N. longicornis magellanica* (Thiele, 1904, p. 13, and 1905, p. 66).

Considering the rostrum, however, it is not so easy to give a satisfactory name to the specimens. There seems to be some confusion as to the dimensions of the rostrum which characterize the two forms *N. bipes* and *N. longicornis*. From Calman's accounts it appears that he takes a ratio of length to breadth of the rostrum of about 2:1 as being characteristic of *N. longicornis* while he quotes 2.3:1 as being typical of *N. bipes* (1917, p. 156). I have measured the two figures published by Thiele (1904, Pl. 4, figs. 66 and 70) and the ratios are, for *N. longicornis* 1.73:1 and for *N. bipes* 2.61:1.

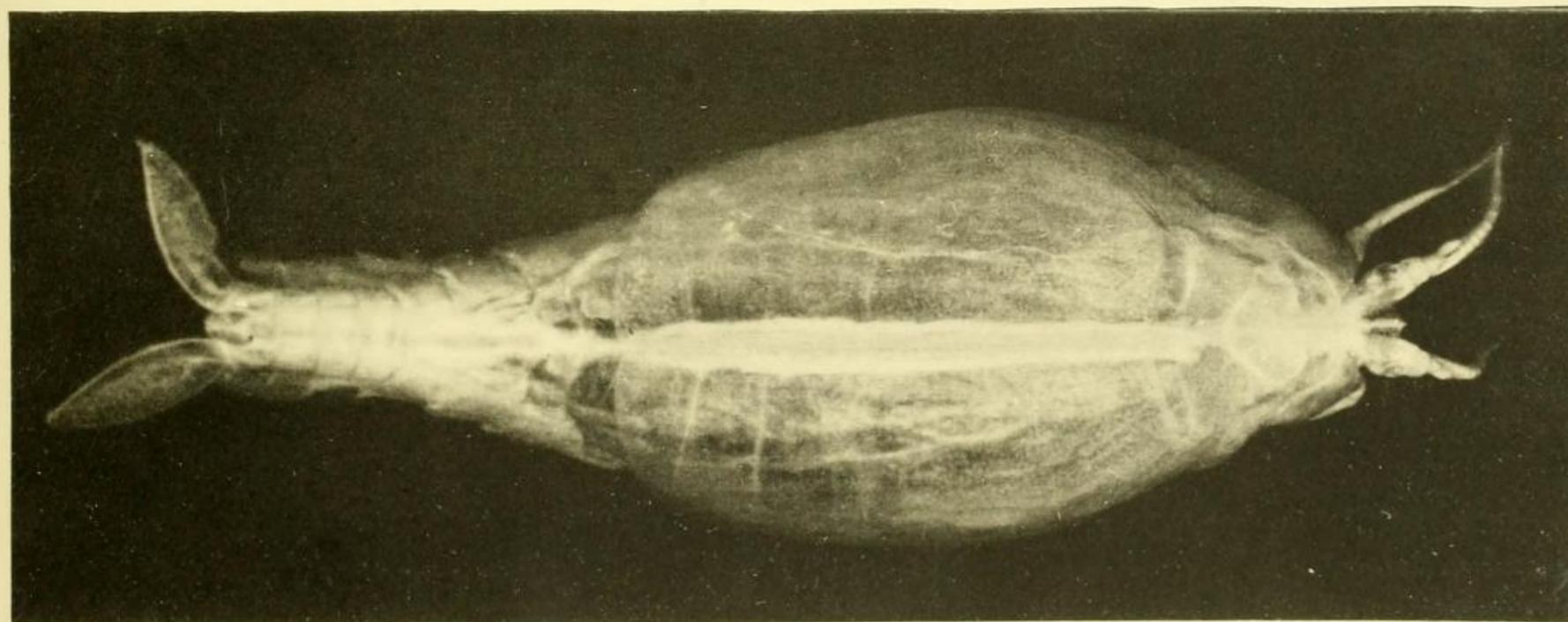
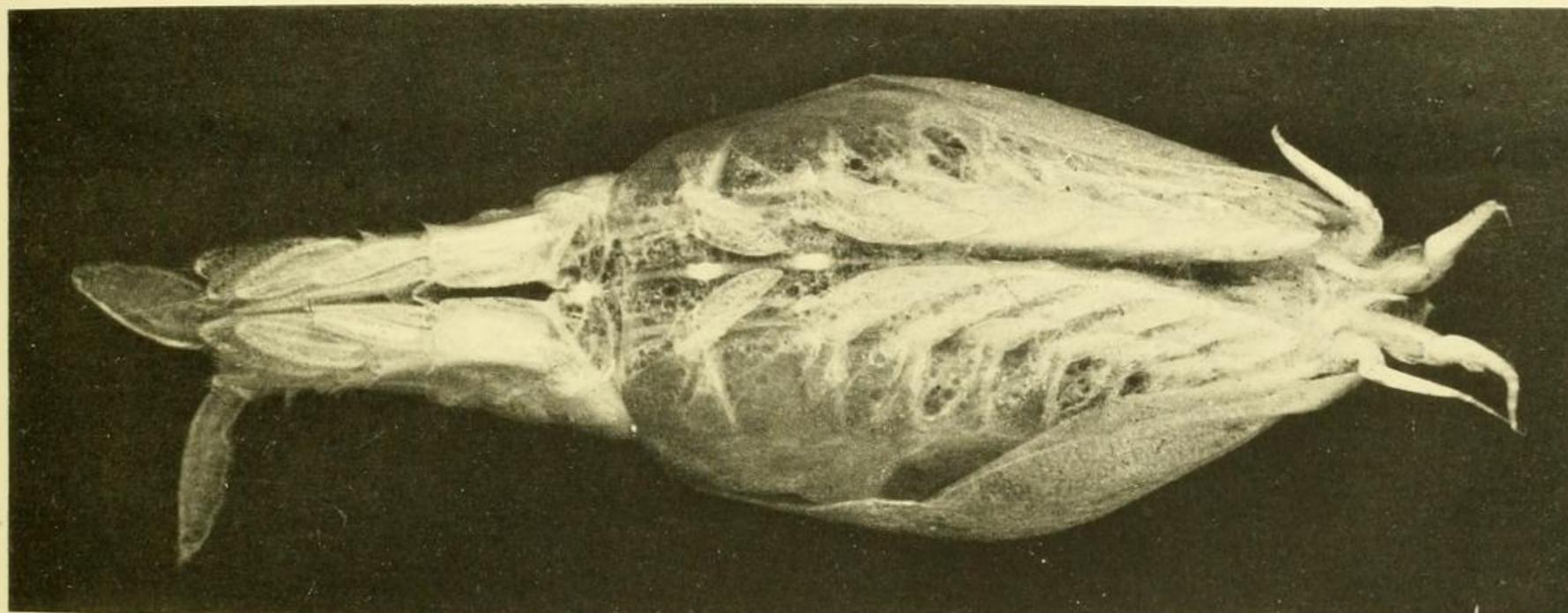
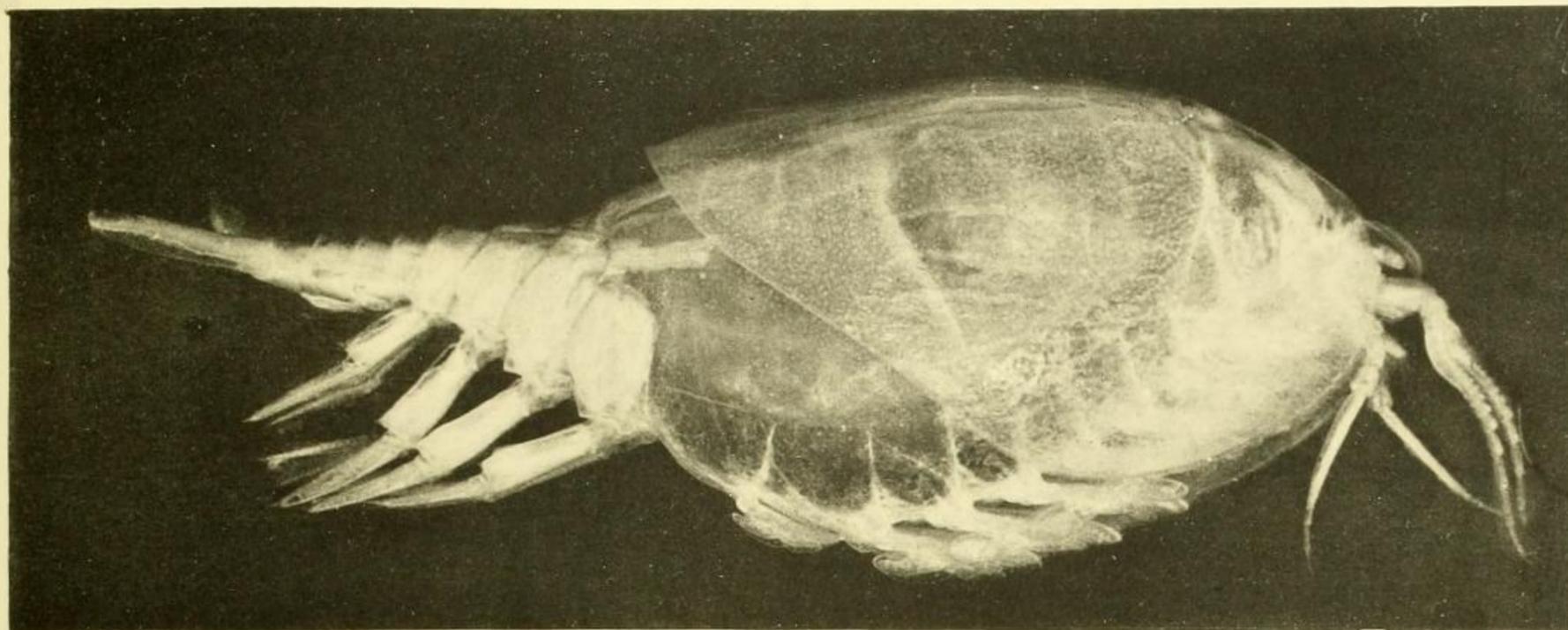
The ratios of the Discovery specimens are: St. 45, 2.07:1; St. 51, 2.37:1; St. 90, 2.52:1, 2.40:1, 2.40:1. Thus they all fall in between Thiele's figures over a wide range. It is obvious that, at least in this collection, it is useless to consider rostral measurements and I have accordingly classified the specimens solely on their antennular armature.

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PLATE XXXII

Nebaliopsis typica, G. O. Sars. Lateral, ventral and dorsal views. (× 6.)



Prof. C. J. Patten photo.

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NEBALIACEA

