A note published by Provenzano (1962) from his investigations at Miami, further elucidates this matter. By studying the larval life of several species of anomuran crabs and caridean shrimps reared in isolation in the laboratory he found that the moulting to the post larval stage occurred after a variable number of instars. He further found that the occurrence of intermediate forms at the end of the larval series may be connected with the general variability of number of larval instars in these groups. This is to my opinion caused by the fact, that an ecdysis does not take place just because a larva has reached a certain state of development, but because a cuticle can only last a certain time, partly dependent on its thickness, which increases with each instar. Temperature, food, and possibly also certain chemical factors influencing the food available in the surrounding waters may also affect the number of instars. If the larva between two instars has succeeded in being well fed, the new instar will be further advanced in (the larval) development than if the individual larva has just managed to survive or even has been starved.

We therefore see that Brooks' law has to be used with great care, as he also did himself; it was first Fowler (1909) who raised it to a law with Brook's name attached to it. Certain factors have to be constant, what they not always are, like changes in form, in feeding, in living habits, in environment and finally also in internal organs. As an example Przibram and Megusar (1912) found in *Sphodromantis* that the weight doubled from moult to moult, and that the increase in length of the prothorax is, on an average × 1.26. In 1929 Przibram concluded that the doubling of the weight was caused by the doubling of the cells, whose linear dimensions would consequently increase as the cube root of 2. But we have already seen a multiplying of cells together with a shrinking of the body as in the first Nauplius of *Meganyctiphanes* and in the pupal stage of many insects, and we know that in Rotifera, after reaching the adult stage, the number of cells seems to be constant for male or female of one and the same species. But still the animal may grow considerably in size, length and weight, but it is here the single cell which becomes larger.

Finally we can conclude that the larva with all the factors which constantly influence its growth seems to have, as in other invertebrates and fish, a growth-factor which already in the larval life has a tendency of slowly decreasing for finally to reach zero or even be negative about the time of the natural death of the animal.

Data of growth for larvae dealt with in this paper are given on p. 144.

We can therefore see that, as Brooks writes, the growth-factor can be of some help to clear whether an instar of a larval life is missing or not in a certain material, but it has to be used with caution and is best to be relied on for animals living in great abundancy or evenly and commonly distributed through their biotop.

SOLENOCERA

History

Only little is known of the larvae of the *Solenocera*, mostly because the genus is an oceanic Penaeid, of which even the adult is still one of the least known natant genera. This is possibly also caused by the habit of the adult to burrow into the bottom. It is therefore very likely that this shrimp genus is much more common than generally supposed.

The earliest record of the larva in the literature is from 1863 when Fritz Müller describes some larvae from Desterro on the Atlantic coast of Southern Brazil. Müller refers the larvae to the Penaeids or *Cryptopus*. They are all Penaeids, and *Cryptopus*, his Figs. 18–21, is a *Solenocera*. Müller's Figs. 18, 19 is by him referred to "einer dritten Art kurz vor der Verwandlung in die Mysisform". The carapace shows characters of both third Protozoea and first Mysis, the limbs and the body segmentation is as in the third Protozoea. His last two Figures, 20, 21 are clearly details of a larva in the Mysis stage. (See further pp. 45–47).

In 1893 Ortmann describes a larva of the Penaeids with the name of *Opisthocaris muelleri*, new genus, new species. This is also a *Solenocera* larva and in the second Mysis stage. As it also was taken at the coast of Brazil, Ortmann suggests the possibility that his larva is an older stage of the above mentioned larva of Müller. For this reason the species was given the name *muelleri*.

Between these two publications came Bates' "Challenger" Report on the Macrura in 1888, where he on page 363 under the name of *Platysacus crenatus* novum genus, nova species, describes a larva from the Atlantic Ocean off Sierra Leone on the African coast. This larva is also a *Solenocera* and in the third Protozoea stage. Further can be mentioned that it belongs to the same group of *Solenocera* as *Solenocera membranacea* of which the larva first was known much later, but the two are distinctly different species.

In 1904 Lo Bianco gave beautiful, coloured pictures of *Solenocera membranacea* (*S. siphonocera*, Pl. X, Figs. 39–40), and describes them as Zoea and Mysis stages. They represent second Protozoea and first Mysis stage. The morphology of the figures is not correct in detail for *Solenocera membranacea*. The spines on the carapace of the second Protozoea are entirely missing, and the ones placed on the carapace of the first Mysis are not in the correct number or position for that species. Fig. 40 shows a pair of post-cardiac spines which are only found in *Solenocera* larva, but the rest of the spines are not placed in the right position. The two lateral spines on the telson-furca are missing in Lo Bianco's figure. Besides showing the beautiful colour of the living larva Lo Bianco gives the information, that the larvae are found throughout the year at depths down to 300 m. Already in 1902 and in 1903 the same author records the larva from the Napoli plankton and in 1900 he points out together with Monticelli that the *Platysacus crenatus* Bate and the *Oposthocaris muelleri* Ortmann must be *Solenocera* larvae. Lo Bianco's figures were reproduced by Williamson 1915 in "Nordisches Plankton", and Stephensen 1923 recorded the larvae in the Mediterranean and Atlantic Ocean (outside Gibraltar) and in the English Channel.

In 1924 Gurney described some *Solenocera* larval stages from the "Terra Nova" Expedition. Two from the Atlantic Ocean station 43, and a third Protozoea which with few exceptions has the same characters as the third Protozoea of *Solenocera* sp. larva *elongata* described in this paper also from "Terra Nova" St. 43, and which probably is the same specimen. Further from the same station Gurney described a first Mysis larva of *Solenocera* which is the first Mysis stage of the same species. Both are here referred to my *S.* sp. larva *elongata*. From the Pacific Ocean Gurney figures a second and third Protozoea named *Solenocera novaezelandiae* (?) Borr.

In 1938 J. Heldt described the *Solenocera membranacea* larvae at the Oceanografic Station Salammbo on the Mediterranean coast of Tunis, and in 1955 she gave full descriptions of all the larval stages of that species except nauplii from the same locality. Later Kurian has described the same larva from Split in the Adriatic, 1956.

Description

Carapace

In the *Solenocera* larvae the carapace is provided with a varying number of spines and sometimes the whole carapace is covered with longer and shorter hairs. The spines are either smooth or have short hairs or secondary spines covering their surface. The most dominant of the spines is the rostrum. It starts as a thick, hollow rod, which mainly through compressions becomes massive in the first and second mysis, only in the true tropical and oceanic forms much later. Finally ridges and grooves may be found on the carapace. It has therefore been practical to give names to all these characters on the carapace in order to facilitate a distinct description of the species, to provide definite distinctions between the different species making comparisons possible, and finally to arrange the different larvae into groups with certain larval characters being the same for all members inside a group.

Fig. 1 shows a carapace with all the different characters which are found in the larvae. It is of course only a diagram, as no single larva examined possesses all the characters figured.

The carapace (Fig. 1) is often divided into two parts, the carapace proper and a rostral plate (1) (the following numbers in brackets refer to the number given in Fig. 1). The rostral plate is just a curved laminar plate along the anterior margin of the body carrying the rostrum. The rostrum (7) is usually well developed and in the younger stages bent in a semicircular arch pointing ventrally. The rostrum may be smooth on its surface or barbed with short hairs or scales. It is never toothed on its ventral side, but may develop one or two dorsal teeth (8) in the Mysis stages, never in the Protozoea stages. Sometimes the rostrum extends backwards as a dorsal keel on the carapace proper behind the rostral plate. This ridge may also be provided with a single tooth in the Mysis stages, and to distinguish this tooth from the previously mentioned teeth, as not being placed on the rostrum proper on the rostral plate but behind it, I have named this tooth epigastric-rostral tooth (9). From the rostral plate, if present, extends further a pair of strongly developed spines pointing

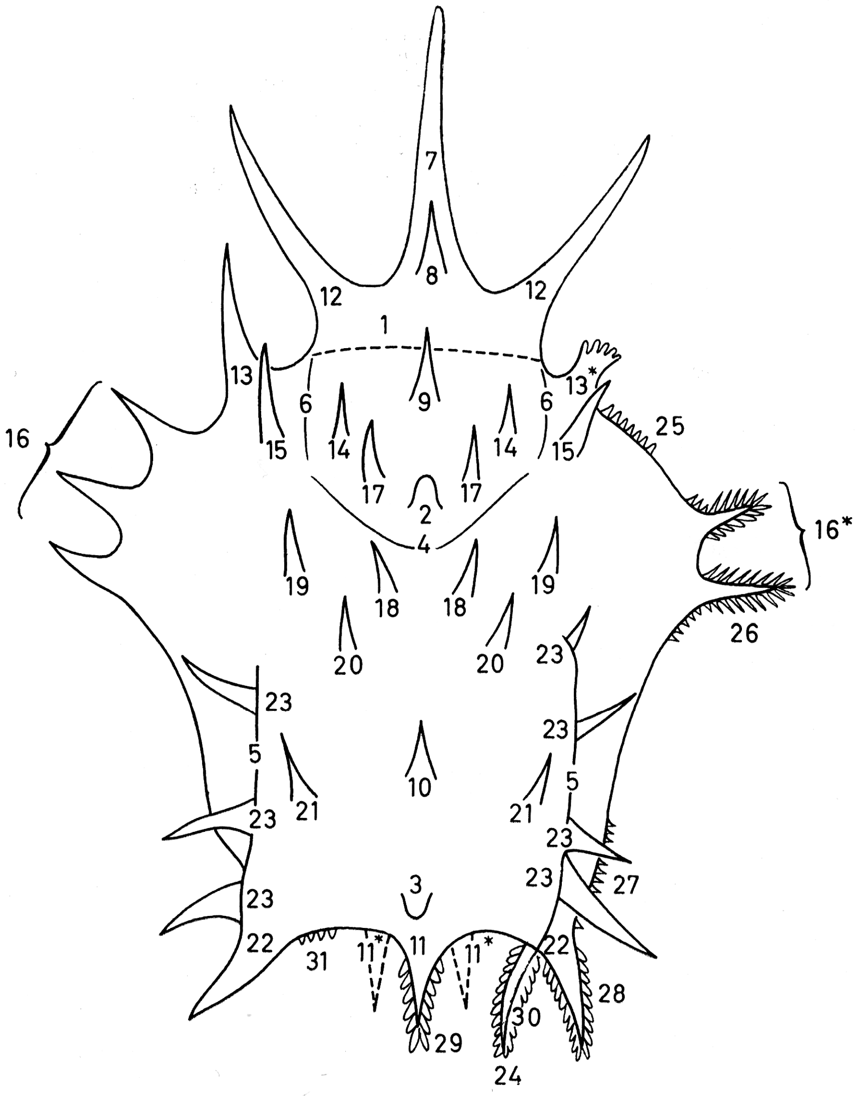


Fig. 1. Diagram of the carapace of *Solenocera*.

1. Rostral plate
2. Anterior dorsal organ
3. Posterior dorsal organ
4. Cervical groove
5. Branchio-cardiac groove
6. Cervico-branchial groove
7. Rostrum
8. Rostral tooth
9. Epigastric rostral tooth
10. Epi-cardiac or *dorsal* spine
11. Medio-posterior marginal spine
11* Medio-posterior marginal spines
12. Supra-orbital spine
13. Antennal spine
13* Antennal process
14. Post-orbital spine
15. Post-antennal spine
16. Branchiostegal spines
16* Branchiostegal process
17. Medio-gastric spine
18. Pre-hepatic spine
19. Latero-hepatic spine
20. Supra-hepatic spine
21. Post-cardiac spine
22. Latero-posterior marginal spine
23. Branchio-cardiac or *lateral* spines
24. Posterio-branchial groove spine
25. Supra-antennal teeth
26. Branchiostegal teeth
27. Branchio-lateral teeth
28. Posterio-marginal teeth
29. Medio-posterior teeth
30. Posterio-branchial teeth
31 Medio-posterior marginal teeth

forwards above the eyes, the supra-orbital spines (12). These are always present on *Solenocera* larvae whether or not a rostral plate is present; they arise from the rostral plate when this is present. Laterally to these and more ventrally is placed a pair of antennal spines (13), named thus because they point forward from the carapace dorso-laterally of the second antenna. This pair of spines is found in the Mysis stages, but not in the Protozoea stages and is always much smaller than the supra-orbital spine. In older Mysis or postlarval stages it may be reduced to a tooth-like process on the antero-lateral corner of the carapace. Characteristic for all *Solenocera* larvae is the presence of two dorsal organs. The anterior dorsal organ (2) is the largest and placed medially on the carapace in front of the cervical groove (4) but behind the rostral ridge and the epigastric-rostral tooth when present. The second dorsal organ (3) is placed posteriorly on the carapace just in front of a medio-posterior marginal spine (11) or when two such spines are present between them. The medio-posterior marginal spine (11) (or spines) is dentated on its surface or at the tip in the Protozoea, but usually smooth in the Mysis. Between the two dorsal organs in the medial line is, with few exceptions, placed a strong, unpaired spine, the epicardial or dorsal spine (10), it is the only unpaired spine found on the carapace except for the posterior marginal spine (11). Finally the latero-posterior corner of the carapace is in many forms projected backwards into a spine, the latero-posterior marginal spine (22). This spine may variate in the different species and stages from being the strongest spine on the whole carapace to only a tiny tooth as in *Solenocera muelleri* or *S.* sp. larva *aequatorialis,* and is even missing in *S.* sp. larva *danae* and *S.* sp. larva *sumatransis.* When the spine is present it is usually in the Protozoea and often even in the Mysis, lined on both sides with the postero-marginal teeth (28). When the spine is absent, the teeth, if present, are placed directly on the margin of the carapace as in *S.* sp. larva *sumatransis.* Between the medio-posterior marginal spine and the latero-posterior marginal spine, the postero-branchial groove spine (24) is placed. This spine is found in all *Solenocera* larvae so far known, but not in any other Penaeid larvae. It could therefore also be called the *Solenocera* spine as characteristic for the *Solenocera* family. In most *Solenocera* larvae, and always in the Protozoea stages, it is covered with a dentated rim (30), which often degenerates with age and may disappear in the oldest larval stages. *Solenocera membranacea* is the only *Solenocera* species of which the first post-larval stage is known, and in this stage the spine is lost. Possibly it disappears in all the *Solenocera* species with the first post-larval stage, because in no adult *Solenocera* any spine is found, which can be traced back to be homologous with it.

These are the spines and organs on the carapace present practically in all *Solenocera* larvae, with only very few exceptions, where one or two of them are missing at the same time, as already mentioned above. However, several other spines, dentations and ridges may be found, all figured together on the diagram, Fig. 1. They are briefly the following: On the carapace behind the supra-orbital spines (12) and in line with them is a pair of small spines, the post-orbital spines (14); similarly placed are the antennal spines (13); behind these and in line with them is a pair of accessory spines, the post-antennal spines (15); finally laterally to the anterior dorsal organ (2) and a little in front of it is very often a pair of small spines, the medio-gastric spines (17). All these spines are found anteriorly of the cervical groove (4) which sometimes is prolonged into a second groove, the cervico-branchial groove (6), running forward on both sides of the carapace reaching its frontal border between the supra-orbital spines (12) and the antennal spines (13); when a rostral plate (1) is present it meets the cervico-branchial groove at its postero-lateral corner.

Behind the cervical groove the following spines may be found. The pre-hepatic spines (18), a little behind and in line with the post-orbital spines. In about the same transverse line on the carapace are the latero-hepatic spines (19), in line with the post-antennal spines (15). A little further back in the area between the last two spines (18–19) a pair of supra-hepatic spines (20) may be found. Finally behind the unpaired dorsal spine (10) may be placed a pair of spines, the post-cardiac spines (21). The dorsal spine as well as the lateral spines (in cases only one lateral spine is present), may be homologous with the spines having the same names in the Brachyuran Zoea. Laterally along the posterior half of the carapace may be found a ridge or groove, the branchio-cardiac groove (5). Along this groove are often placed a number of spines, usually three to four, the branchio-cardiac or lateral spines (23). The branchio-cardiac groove forms posteriorly a long lobe or spine; the spine may have lateral spines as in *Solenocera* sp. larva *elongata,* and the lobe can be developed into an enormous posterior horn as in *S.* sp. larva *danae.* Because of a connection of the spine with the branchio-cardiac groove, the spine is named postero-branchial groove spine (24). Finally on each side of the margin of the carapace a little behind the antennal spine (13) can be found one to three spines, the branchiostegal spines (16). These spines are most strongly developed in the Mysis, but may already be present in the Protozoea, but then they are much smaller and more delicate.

Characteristic for the *Solenocera* is the toothed margin of the carapace. The teeth are more numerous in the Protozoea than in the Mysis, but are often found in limited numbers even on the older Mysis stages. After their placement I have divided them into different groups, which may overlap or be distinctly separated with smooth stretches between them. Further, in most Protozoea the carapace margin is lined by a thin cuticle with marginal teeth. This cuticle may be drawn out into longer or shorter flat or spine-like lobes which then bear the teeth on their whole surfaces or only on their distal margins. These lobes or rims are only found in the Protozoea and disappear with first Mysis. The groups of teeth on the carapace are as follows: anteriorly on the side of the carapace behind the antennal spine are the supra-antennal teeth (25), which reach backwards to the first branchiostegal spine (16) if this is present or to that region; they are in most Protozoea substituted by a short, semicircular lobe with a toothed margin. Posteriorly to these follow the branchiostegal teeth (26) which may be placed on one or two lobes at each side of the carapace. Most latero-posteriorly are the branchio-lateral teeth (27) which may be followed by the postero-marginal teeth (28) placed either along the margin of the carapace proper or lining the two edges of the latero-posterior marginal spine if this is present. Finally the medio-posterior marginal spine or spines (11), if present, are usually tipped or lined with a row of teeth, the medio-posterior marginal teeth (29).

These different groups of marginal teeth on the carapace are very characteristic for the *Solenocera*, and form a clear distinction mark for the larvae in the plankton. Similar teeth, although in a much lower number, are also found in some larvae of Euphausiacea, but here the carapace is always smooth without the many spines present in the *Solenocera*. Spines of this kind are also found on the carapace in the larvae of the near related Sergestidae, where the spines in some of the known Protozoea are even twice as long as in the *Solenocera*, but in the Mysis of Sergestidae the spines are much shorter and fewer in number than in *Solenocera*. The larvae of the two families are, however, easily distinguished because no posterior dorsal organ and no toothed margin of the carapace are known in the larvae of Sergestidae where the spines on the carapace often are branched.

Abdomen and Telson

The abdomen is already divided into six segments plus telson in the second Protozoea, and spines are present on its surface from the third Protozoea. These spines may be placed in five different positions as shown in Fig. 2: An unpaired dorsal spine (1); an unpaired ventral, usually shorter spine (5); further three paired spines with one on each side: a lateral spine (2), a dorso-lateral (3) in front of the dorsal spine and a ventro-lateral (4) pointing backwards from the posterior margin of the segment. The pleura of the abdominal segments are never found in the Protozoea. They usually appear in the second Mysis or later.

In the first Mysis stage a lateral process develops on each side of the first abdominal segment much like the one found in most Zoea of Brachyura, where it, however, is placed on the second abdominal segment. The process is not homologous with the one in the Brachyura which disappears with the Zoea stage. It has been suggested for the Brachyura that this process supports the carapace and keeps it in position. In the *Solenocera* this process develops in the second Mysis into an elongated ridge running in antero-dorsal to ventro-posterior direction (Figs. 4–5). In the adult of which I have only had opportunity to examine *Solenocera membranacea* it seems (Figs. 3–8) to be the same for most members of that genus and for some other Penaeids. On the first abdominal segment the pleuron is by a dorso-ventral line divided into two halves with a flexible suture between. Further on the dorsal side of the segment the cuticle has formed an anterior carina which is placed below a narrow posterior ridge on the same segment. This formation of a lower anterior carina part starts already to develop in the second Mysis with the ridge between the anterior and posterior part running just in front of the dorsal spine. On the second abdominal segment is a similar division of carina into a lower anterior and a higher posterior section (Figs. 7–8), but the pleura are undivided in the second segment

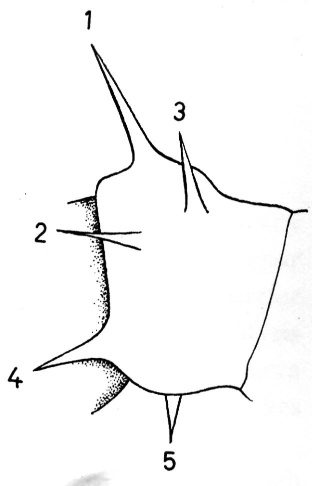


Fig. 2. Diagram of an abdominal segment of *Solenocera* with the following spines:

1. dorsal spine
2. lateral spine
3. dorso-lateral spine
4. ventro-lateral spine
5. ventral spine

as also in the following ones. A comb of stiff hairs is found along the margin of the anterior part of the pleuron on the first segment, beginning close to the dorsal line of the segment. This division of carina on the first and second segments enables the shrimp to bend the abdomen in a dorsal direction until the abdomen forms an angle of 90° with the carapace. With this bending the frontal section of the carina of the first segment disappears under the carapace and the dorsal part of the second segment is placed close to the posterior line of the first segment as shown on Fig. 8. By this procedure which the shrimp undertakes for digging itself into the mud, the posterior part of the carapace reaches backwards underneath the pleuron of the first segment, and the stiff hairs on the margin of the pleuron prevent mud and smaller sand grains from penetrating

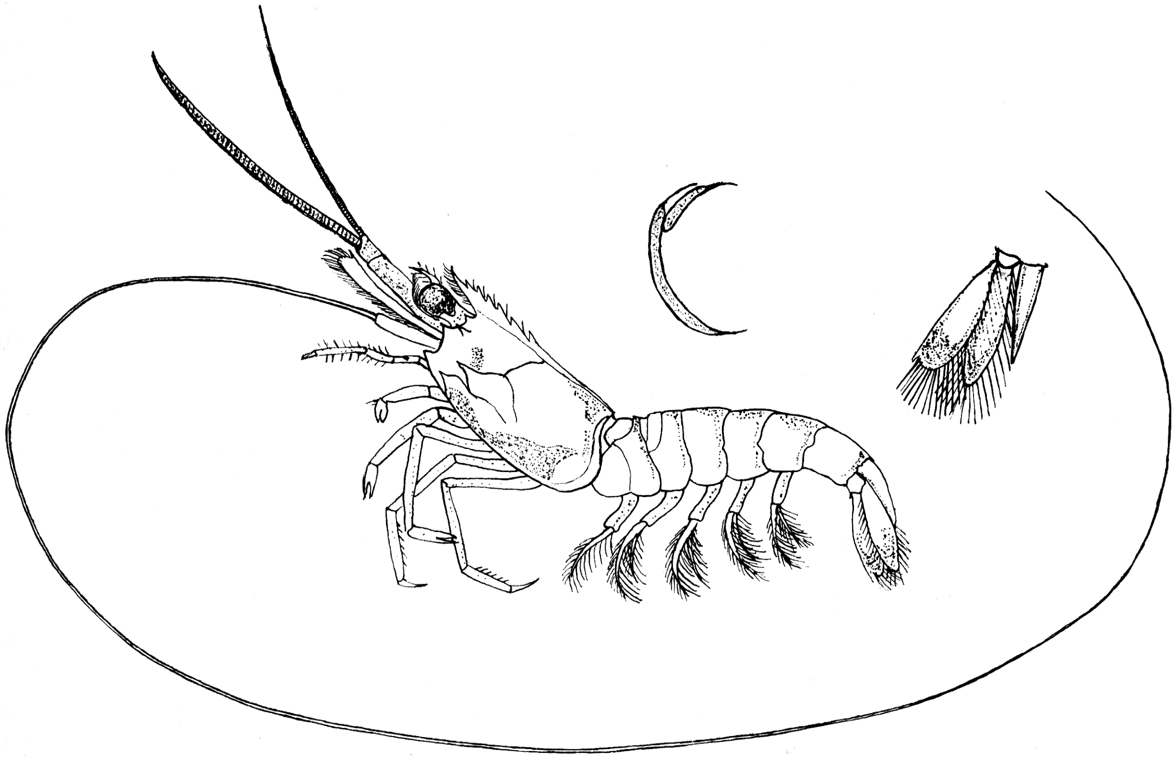
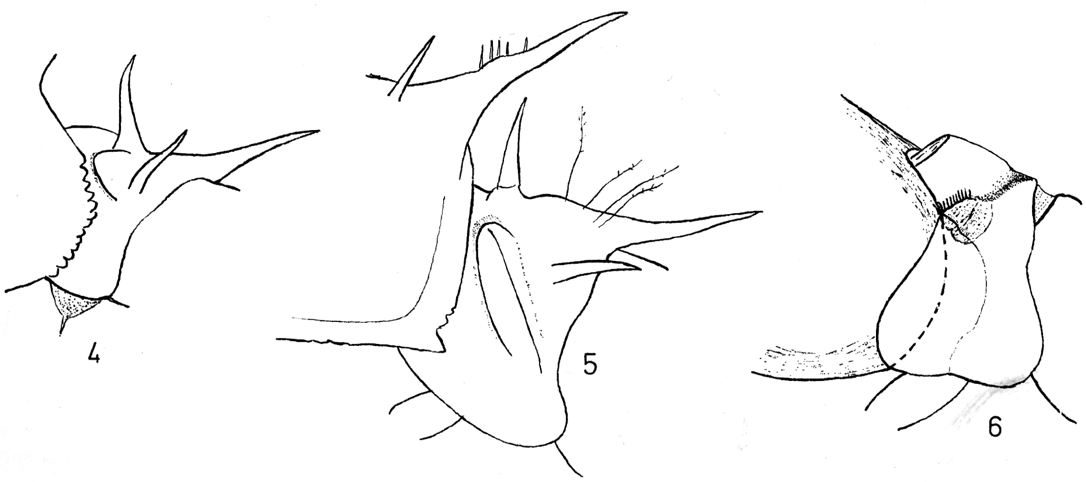


Fig. 3. *Solenocera membranacea* H. MILN.-EDW. Adult female. Separate Figures: above-transverse section of the two flagella of the left first antenna showing one half of the siphon in cross-section, right-telson and the left uropod.



Figs. 4–6. *Solenocera membranacea.* Posterior margin of carapace and first abdominal segment with dorsal spine, lateral spine and dorsolateral spine in first Mysis Fig. 4 and second Mysis Fig. 5. Development of lateral process, Figs. 4, 5, and 6. Division of the lateral pleuron of first segment in the adult, Fig. 6. For further explanation see text.