inside the carapace damaging the gills, and an opening is kept for the incoming water for respiration, as shown with the arrow on Fig. 7. In the more dorsal part pointing towards the anterior part of the carina the hairs are placed more thickly than on the rest of the margin. The outgoing respiratory water leaves the shrimp through the antennal siphon.

The telson is in the larval forms always bifurcate. In the Protozoea the branches are running almost transversally to the longitudinal line so that the telson is more or less T-shaped. In the Mysis the two branches are moved more towards each other making the telson more Y-shaped. Each branch is normally furnished with four inner setae and one terminal spine. On the lateral margin of the telson are placed three curved



Figs. 7–8. Solenocera membranacea adult. Posterior margin of carapace and first and second abdominal segments in two different positions. For further explanation see text.

spines, which are first present in the Mysis, but often found as plumose setae already in the Protozoea. As in most Penaeid larvae of these stages their mutual placement may vary from species to species.

# **Special Sense Organs**

The dorsal organs are always found in a number of two in the Solenocera larvae, and they are generally very large. The anterior one is placed in front of the cervical groove and is the largest of the two, the posterior and smaller is placed near the hind margin of the carapace either in front of the unpaired medio-posterior marginal spine or if this is paired between the pair. In the Sergestidae, both in the Protozoea and the Mysis (*Mastigopus*), only the anterior organ is present. A dorsal organ can be traced either in the embryo, larva or adult of most groups of Crustacea, but the variation in structure and position and number (1-3) makes it doubtful whether all dorsal organs are homologous.

In Trilobites (RAYMOND 1920, p. 86) there is commonly in the region of the eye a median tubercle which has been related to the dorsal organ of Apus. In some primitive forms this tubercle was developed into a long spine, and RAYMOND suggests that the tubercle is a vestigial organ, and that it "very strongly suggests the zoeal spine of modern Brachyuran Crustacea". RAYMOND, however, later states that there may be even a series of tubercles in Trilobites placed in the median line, and exactly like the anterior dorsal organ. Some facts in the Solenocera speak against this assumption. In the Solenocera the dorsal organ is tubercular, and

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although its function is not yet clear, it can hardly be considered as an only vestigial organ in the larva. Further the dorsal organ may in the decapod larvae be found in a number of up to three unpaired organs placed in the median line, and in most *Solenocera* a dorsal or zoeal spine is found in addition to the dorsal organ; also in the Brachyura a few genera are without the zoeal spine. It appears more likely that the dorsal or zoeal spine and the dorsal organ are two distinctly different developments, but it is probable that a form of a dorsal organ is replaced by a spine, when lost, like an eye may be replaced by a limb-like lobe, but never by a new eye.

An "ocular papilla" is also found in each eye-stalk in the *Solenocera* larva. In the first Protozoea this organ is placed in the region of the developing eye underneath the carapace, but in the second Protozoea, where the eyes are stalked, the papilla is placed on the anterior lower side of each eye-stalk and is usually retained throughout larval life. This papilla is often called the frontal organ, but GURNEY, LEBOUR 1940 (Fig. 16) show that in the larva of *Sergestes crassus* both frontal organ and ocular papilla are present at the same time, which indicates that they are separate organs, and therefore only the ocular papillae will be the right name to use. Also in the first Protozoea of *Parapenaeus longirostris*, HELDT 1938 (Fig. 64,1) is a pair of frontal organs ventrally in front of the carapace which likely are the ocular papilla. This organ is often found in the eyestalk of decapod Crustacea, but as it is placed on the lower side of the eyestalk it is often overlooked. It may be the beginning of the later x-organ which is a hormonal gland in connection with the eye producing a hormon regulating the colour-changing in the chromatophores.

#### **Chromatophores and Coloration**

The chromatophores are not described in the literature except for the two figures of Solenocera membranacea (S. siphonocera) of Lo BIANCO, 1904 (Pl. 10, Figs. 39, 40). They show that the larvae are pigmented with red and orange. After the figures the red is more developed in the Mysis than in the Protozoea, with two pairs of dark red spots on the carapace near the base of the supra-hepatic and the medio-gastric spines. A red line runs through the first five abdominal segments, this is the strongly pigmented intestinal wall, and occasionally a single red spot is found at the basis of telson. The orange is especially found on the hepato-branchial region of the carapace and on the limbs. The material to be dealt with in this paper is all long preserved material with no traces of chromatophores left.

## First Antenna.

#### Appendages

This appendage seems to be jointed throughout the Protozoea stages. After Heldr's figures (1955) of the first Protozoea of S. membranacea the antenna consists of several (5) ringed joints proximally of the two distal joints; in the second Protozoea the number of the rings are still five; in the third Protozoea they are coalesced into two joints proximally of the two distal ones. In the youngest larva from the present material, the third Protozoea, the first antenna is always four-jointed. In the first Mysis the basal joint enlarges and develops the statocyst bulge on its lateral side together with a ventral incavation, which is the beginning statocyst incavation. Further the first and second joints coalesce so that the peduncle of the first antenna in the first Mysis is reduced to three joints. The sutures between the coalesced joints can not be seen, but from the setae placed on the third and fourth joints in the third Protozoea it can safely be concluded that the coalescence occurs between the first and second joints. Further, from the most distal joint, the former fourth joint now the third joint, the two flagella of the first antenna begin to develop and grow rapidly during the following stages after each ecdysis. In the first Mysis the flagella are unjointed, in the second they may in some forms remain unjointed, but have developed groups of olfactory hairs on the surface of the lateral flagella. In other forms they have more than doubled their length and each consists of five to ten joints, but in this case the olfactory hairs remain still undeveloped. The development of the first antenna proceeds in this way through the following stages. The statocyst seems to be fully developed in the fourth Mysis stage in oceanic forms with a slower development, and in the first post-larval stage in the more coastal forms with only two Mysis stages.

## Second Antenna.

This limb is the ambulatory organ of the Protozoea through its three stages and therefore well developed right from the beginning. In the first and possibly the second Protozoea the peduncle seems after HELDT'S (1955) figures to be two-jointed, in the third Protozoea it is only one-jointed. The exopod is the swimmeret and therefore strongly flexible, often ringed into many joints and in all Protozoea stages provided with a series of swimming setae on its tip and median edge. The endopod is usually three-jointed, and even if the lines between the joints are missing the appearance and arrangements of the setae point clearly to a three-jointed endopod. In the Mysis this changes. As in all other Penaeidae the locomotory function is transferred from the second antenna to the pereiopods, and therefore the exopod looses its swimming setae and begins to transform into the unjointed antennal plate. The protopod remains unjointed as in the last protozoea and the endopod is in the first Mysis reduced to an unjointed branch which through the following stages becomes the long, flexible flagellum.

#### Labrum.

The labrum or upper lip is a large semi-globular cup which anteriorly on the median side may continue as a shorter or longer spine. This spine can, as in S. sp. larva *elongata*, be very long and curved into an S-shaped hook (see Fig. 170).

### Mandible.

The mandible is a strong biting-crushing organ with a well developed pars incisor and pars molaris on the corpus mandibulae. In the three Protozoea stages the mandible is without a palp. In the first Mysis stage is a short unjointed palp, and from the second Mysis stage the palp is two-jointed, as in the adult, only not yet furnished with so many setae as in the adult. Also the connection between corpus mandibulae and its palp is not yet so flexible or movable as later, when the cuticle on the corpus mandibulae itself becomes thicker.

## Labium.

The labium or the lower lip is in most of the forms well developed and can be divided into three components: the basal plate or peduncle and two longer or shorter lateral arms, each ending in a disc-shaped plate. The two arms vary very much in length in the different species. In some, e. g. S. sp. larva *danae*, S. sp. larva *braziliensis* or S. sp. larva *sumatransis* they are very short nearly not existing as separate parts. In S. sp. larva *elongata* and in S. sp. larva *aequatorialis* they are well developed, in the latter even to the effect that each labium plate is placed on a long stalk so the plates can be stretched forward, even in front of the mouth. This indicates a direct use of them by the animal when feeding on detritus or small plankton organisms which by the two labium plates with their rows of stiff marginal setae can be filtered and drawn backwards between the mandibles to be masticated before passing into the mouth. In S. sp. larva *nodulosa* the same result is partly, but also only partly, reached through a stalk-like basal plate on the labium moving the rest of the labium forward like a deep, hollow spoon, but without an eventual independence between the right and the left side as is possible in S. sp. larva *aequatorialis*.

## First Maxilla.

The first maxilla is of the usual type with two mastigatory endites. The endopod is two- or three-jointed in the Protozoea and three-jointed in the Mysis. The exopod has the usual bulbous shape with four strong plumose setae. The exopod is lost with the first Mysis stage and does not reappear in the later stages.

#### Second Maxilla.

This limb has also a lobate exopod with four plumose setae in the two first Protozoea stages, and usually five setae in the third Protozoea. With the first Mysis the exopod achieves the shape of the adult as a fanshaped, thin, leaf-shaped organ with a row of plumose marginal setae; the setae are not so thickly plumose

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as in the Protozoea. The protopod is furnished with the usual four endites, two coxa-endites and two basiendites, which are found already in the Protozoea, but first fully developed in the Mysis. The endopod is well developed with up to five joints, but in the younger stages there is often no clear separation between some or all of the joints.

#### First and second Maxillipedes.

In the Protozoea the endopod branch is much better developed than the exopod. This as well as the many setae on the medial margin of the protopod show that it is an organ more for catching and holding the prey than for swimming. The limbs retain partly the same form in the Mysis, but the exopodial branch is here better developed than in the Protozoea.

# Third Maxilliped.

It is only a rudimentory organ throughout the Protozoea and first in the third and last Protozoea it becomes distinctly bifurcated, but it is still too undeveloped to have any real function. In the first Mysis it suddenly starts its proper development and is from now on the longest of the three maxillipedes and can with its endopodial branch reach forward often in front of the eye. It is still more densely provided with setae than the 1st and 2nd maxillipedes.

## Thoracopods.

All the thoracopods start to develop as small limb buds in the Protozoea stages, and in the third Protozoea they can be seen clearly as two rows of five bifurcated limb-rudiments behind the maxillipedes hanging down from the posterior part of the carapace; they are without any segmentation or any function. Also in these limbs a sharp change takes place with the first Mysis stage where they appear as well developed bifurcated appendages which have taken over the locomotory function. At the same time a chela starts to develop on the three first pairs, but the joints of the chela have still long setae, also in the following Mysis stage or stages. They can first function as chelae in the first Postlarval stage. The fourth and fifth periopod are ordinary, bifurcated appendages without chelae. Their function is only locomotory and therefore they have well developed exopods in the Mysis stages; on the fifth pereiopod the exopod is a little better developed in the second than in the first Mysis stage. On the Postlarva the exopod has decreased in size on all these limbs as the swimming function has been taken over by the pleopods.

#### Pleopods.

The five pairs of pleopods start as limb-buds in the Mysis, but although bifurcated they have no function throughout the Mysis life. First in the first postlarval stage they become fully developed and takes over the function of swimming except for the special function and morphological development of the first and second pair as part of the sexual apparatus.

#### Uropods.

The uropods or the sixth pair of pleopods develop in the third Protozoea as a small bifurcated appendage which already in the Mysis takes part in the tailfan, but first in the Postlarva they reach their final shape.

#### Gills

The gills develop from coxa and can possibly be considered as epipodites of this joint. The development starts with the most distal one on coxa and proceeds from there proximally towards the body. Based on their shape and placement the gills are arranged into four groups, of which here no distinction are made for the last two, which I shall return to later. Three of the groups are placed in three parallel lines.

Most distal on each coxa is a mastigobranchia. The mastigobranchia is always lamellar of shape, usually like a thin, membranous leaf, and starts on the first maxillipede as a leaf-shaped lobe much like the exopod

of the second maxilla with both an anterior and a posterior lobe. On the second maxilla the mastigobranchia usually consists of two parts, a proximal leaf-shaped membrane and a distal lobose process. These two parts are united at the base and attached to coxa by one short peduncle. The mastigobranchiae are further found on the limbs from the third maxillipede to the fourth pereiopod both included, but here only their proximal lobes are present, and they are much smaller than on the two previous limbs. In most forms the mastigobranchiae have a smooth margin, but in some forms like *S*. sp. larva *nodulosa* and *S*. sp. larva *sumatransis* a few long, flexible hairs appear on the distal margin of the mastigobranchiae of the five last pairs of thoracopodes but never on the mastigobranchiae of the first and second maxillipede. The fifth pereiopod is without gills or gill-buds in all the examined larvae. This is not the case with the adult, and therefore the gill number may increase in the postlarval stages when the carapace is finally covering the whole thorax. As the gills extend backwards the gills of the fifth thoracapod would not be protected under the short larval carapace and possibly therefore they only develop later.

The next line of gills are the podobranchiae. They are like all the following gills built after two types. In one type they consist of a long stem from which the gill-filaments form small sidebranches dichotomously



Fig. 9. Solenocera. The limbs with basis and coxa provided with full number of gills as developed in the larvae, showing from below the three lines of gills: nearest to basis the mastigobranchiae, in the middle the podobranchiae, and above the pleurobranchiae. For further explanation see text.

to both sides, Fig. 9. This is the case in most of the examined species. The other type is built with a short, wide peduncle with all the gill-filaments extending as long fingers on a hand from the distal end of the peduncle. Finally the gills may be built after a diagram intermediary between these two types. It starts with the finger-shaped type, but the fingers are arranged obliquely slanting in a proximal direction. The peduncle continues as the most proximal finger from which further finger-shaped gill-filaments are branched.

The podobranchiae constitute the first line of the branched gills. They extend from the coxa just proximally of the mastigobranchiae, and the larva has only one on each coxa. They start first on the second maxillipede, and may be found with one gill from the coxa of all the following limbs until the fourth pereiopod where the most posterior one is placed.

Proximally of the podobranchiae are the arthrobranchiae and the pleurobranchiae. They differ as to their placement; the arthrobranchiae extend from the articular membrane between the coxapodite and the body wall, and the pleurobranchiae from the lateral wall of the somite dorsally to the articulation of the appendage. When examining the larvae one gets the impression that both arthrobranchiae and pleurobranchiae start to bud from the most proximal corner of coxa and from there move dorsally over the articular membrane to the limb and further to the lateral wall of the somite. It is possible that all the gills in the *Solenocera* larvae are either podobranchiae or arthrobranchiae and that no proper pleurobranchiae yet have developed, but it seems as if in older stages the gills placed outside on coxa slowly move dorsally. As the material is too small for a more detailed study and especially because not one single postlarva is present in the material or could be obtained for examination, no distinction is made in this paper between arthrobranchiae and pleurobranchiae.

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This most proximal of the three gill-lines starts on the third maxillipede and is found usually also in a single number derived from each limb until the fourth pereioped.

Summing up, the maxima of gills present in the *Solenocera* larvae are as following: One mastigobranchia on each limb from first maxillipede to the fourth pereiopod, one podobranchia from the second maxillipede to the fourth pereiopod and one pleurobranchia from the third maxillipede to the fourth pereiopod. The fifth pereiopod is thus the only thoracopod limb without any gills, when we consider the first and second maxilla as placed on the cephalon. However, the exopod of the second maxilla functions as a gill although it is no gill proper and has no gill-filaments.

Finally, the larval stages in which the gills first occur are the following: In the first Mysis the mastigobranchiae and the podobranchiae start as small buds on the limbs. This, however, with exception of the fourth pereipod, which in the first Mysis only has developed a single gill-bud on coxa for the future mastigobranchia, while all the preceding ones have two gill-buds. In the second Mysis the gills are fully developed, also the podobranchia on the fourth pereiopod plus the pleurobranchia, when present, and the latter not only as a bud, but as a fully developed gill. Only in *S.* sp. larva *danae* small gill buds were found on the first and second maxillipede already in the third Protozoea, but in the four other species in this material with a third Protozoea no traces of gill buds were found. Therefore, in the following first Mysis fully developed mastigobranchiae and podobranchiae and even pleurobranchiae were developed on the third maxillipede. No further numbers of gills developed in the two following Mysis stages of *S.* sp. larva *danae*.

# Larval Stages

All observations so far of the hatching of larvae in the Penaeidae have shown the first larva to be a Nauplius or a Protonauplius followed by two further Nauplius stages and two or more Metanauplius stages, which gives a total of at least five stages belonging to the Nauplius type.

In the Solenocera the youngest known stage is the first Protozoea, and this stage is so far only known from a single species Solenocera membranacea which has been caught and described by HELDT (1938, 1955) from the southern Mediterranean. This first Protozoea is followed by a second and third Protozoea. Dr. HELDT states, that the first Protozoea is very rarely found in the plankton, and first the third Protozoea is frequent in the Mediterranean throughout the year (1955). This seems also in accordance with Lo BIANCO (1904) who does not make clear distinctions between the different stages. He figures the second Protozoea and the first Mysis stage and writes that the larvae are common throughout the year in the Mediterranean at Capri from 300 m to the surface.

The fact that the first and the second Protozoea are so rarely seen, the latter, however, more frequently than the first, shows that the first and partly the second Protozoea must hide in places where they have not yet been regularly found. Further, the fact that no Nauplius has yet been referred to the genus *Solenocera*, although they must have Nauplius stages like the rest of the Penacidac, is likely to be explained by the *Solenocera* spawning their eggs on the bottom in deeper water, where plankton hauls seldom are made. This may explain why the Nauplius has not been caught and still is unknown. Possibly only during the three Protozoea stages the larvae move towards the upper water layers. This gives a reasonable explanation why only the third Protozoea and the following Mysis stages are caught in quantities corresponding to the frequent occurrence of this shrimp in the Mediterranean, where much research has been carried out especially on this group both from Napoli and in later years from Tunis and other places in the Mediterranean Sea.

After the third Protozoea follow the Mysis stages, which by some investigators of decapod larvae also are called Zoea stages. This is not done in this paper because true zoea in the old sense of the word is only referred to Brachyuran and allied larvae. I think there are good reasons for using the term only for the in several points reduced larvae of the Brachyura. Further there is a sharp distinction to be kept between the Protozoea larva in the Penaeids and the following larva, here called the Mysis. Among other things the locomotory function is transferred from the second antenna and partly the mouth appendages in the Protozoea to the pereiopods in the Mysis. The number of Mysis stages seems to be at least two, and in some forms, especially true oceanic forms, several more Mysis stages are added to the first two before the first postlarval stage is reached.

#### Protozoea I

This stage has like other first Protozoea in Penaeidae and Euphausiacea, as far as they are known, sessile eyes, covered by the carapace, and no rostrum is developed. The segmentation of the thorax is beginning, but the abdomen is still unsegmented. The limbs are found back to the third maxillipede, but the latter is not more than a limb bud with a few setae. The first antenna is furnished with several (5) annulated joints proximally of the two distal joints as in the following stage. The first and second maxillae have in this and the following stage a lumpish exopod with four strong, plumose setae. The endopod of both the first and the second maxilla in both first and second Protozoea is well developed, but only the basal joint of it is separated from the rest. The first two maxillipedes are both swimmerets as well as mastigatory in their function. No trace of uropods can be seen.

#### Protozoea II

The eyes are stalked and free of the carapace on which the spines characteristic of the species and a long untoothed rostrum have developed. The margin of the carapace is furnished with a more or less toothed edge. The thorax is now fully segmented, but only its frontal part is covered by the carapace which has not increased in size to the same degree as the rest of the thorax since the previous stage. The abdomen is still unsegmented, without limbs, and no uropods have developed. The third maxillipede is still a limb-bud, but clearly bifurcated.

# Protozoea III

The carapace is now covering from two thirds of the thorax to the full length of the thorax as it is found in *Solenocera* sp. larva *danae*. The rostrum is still without teeth, but the spines on the abdomen have increased in this stage. The abdomen is fully segmented, only the telson may not in all species yet be completely delimited from the sixth abdominal segment. The first antenna is now reduced to four joints in total, which means that the four basal joints have coalesced into one, and the three distal joints remain; the second joint from the base has even enlarged a bit in size from a ring to a proper joint. The second antenna is still the main locomotory organ. The mandible is still without a palp. The first maxilla is unchanged, only the endopod has in most species become three-jointed. In the second maxilla the endites are more developed than in the two preceding stages, and especially many more stiff setae have appeared on their surface so they are now well fitted for serving the feeding of the larva. Also the endopod may have added some joints although its relative length in relation to the rest of the limb is unchanged; the endopod of the two first maxillipedes is now divided into several joints, and the third maxillipede is somewhat enlarged but still unfunctional.

The thoracopods following the maxillipedes are now present, but only as short, bifurcated and unjointed rudiments, without any function or setae except a few embryonic setae on the tip. No abdominal appendages are present apart from the uropods which are developed in their bifurcated shape on the sixth abdominal segment, but they are in this stage so rudimentary that they can only become functionary in the following stage.

# Mysis I

In the first Mysis which follows after the third Protozoea great changes take place which justify the change of name of the larval type. The carapace is much enlarged and has become more squarish, it is now covering the whole thorax. The rostrum has developed one or two dorsal teeth on its upper surface, but none on the ventral, in conformity with the lacking of ventral teeth in the larva as well as in the adult. The shape of the telson has changed from a T-shape to a Y-shape through a changed angle between the two branches and the medial plate of the telson. The branches are placed in a more longitudinal axis to the medial plate. The three lateral spines on each side of the telson which are characteristic for the adult Penaeid are present.

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The antennae and mouth-appendages are no longer swimmerets; this function has now been taken over by the well-developed bifurcated five pairs of thoracopods. The pleopods have started to bud on the abdomen, and the uropods are fully developed and able to be an active part of the tailfan. A small process has developed on the lateral side of the first abdominal segment. In some species this process is in connection with the lateral spine on that segment, but often the process is free, placed ventro-anteriorly of the spines of the segment.

The first antenna has undergone a further reduction to three joints, with the two basal joints coalesced into one joint. The hook on the medial margin of the basal joint for the coming statocyst hollow has started to develop. Finally the two flagella have appeared as two yet unjointed processes from the distal joint of the antenna. The second antenna has also changed, its exopod is no longer a locomotory organ, but is transformed into the unjointed antennal scale which, however, not yet has reached the full size and number of setae. The endopod has coalesced into a single joint, which in the following stages will become the longer flagellum of the second antenna. The protopod is unjointed.

The mandible has in this stage formed a short, unjointed palp always without setae, and the pars-incisiva and the pars-molaris are more clearly differentiated. In the first maxilla the exopod has in some species totally disappeared, in others it is under reduction. The two endites have now reached their full development like in the adult with the distal endite or basi-endite furnished with tooth-like setae for tearing and cutting, while the setae on the coxa-endite are stiff and hair-like as in a broom. The endopod is now in most cases three-jointed.

The second maxilla has no longer a fleshy exopod with setae of the thick type, but a thin leaf-shaped one, with many plumose setae along its margin and with the most posterior setae longer and stronger than the rest. As both an anteriorly pointing and a posteriorly reaching part of the exopod is developed the endopod has grown in size. The numbers of joints have increased and the four medial endites of the protopod are larger and with more setae than in the preceding stages. The maxillipedes are now three in number, all fully developed. The first maxillipede has shortened and is now clearly a feeding organ. The third maxillipede which up to this stage has been rudimentary and without function is from now on the largest of the three. The maxillipedes have well developed exopods functioning as swimmerets together with the exopods of the thoracopods. The two jointed protopod and the endopod have on their medial margins a brim of long setae for filtering water, for catching and holding the prey, and for carrying it to the mouth. It appears that the endopod of the third maxillipede has an additional function as cleaning organ for the mouth appendages.

The first three thoracopods or pereiopods have started to develop a chela and are, together with the two non-chelate, following pairs, the principal locomotory organs, but as the tail-fan now also is functioning the shrimp is able, possible already from the Mysis stage, to jump backwards by clapping the tail-fan and the abdomen against the underside of the body like the adult shrimp. The protopods of the thoracopods are two-jointed and the abdominal appendages or the pleopods are, except for the uropods, only small unfunctional limb-buds.

## **Mysis II**

The toothed edge of the carapace is further reduced although its teeth seldom have completely disappeared. An extra dorsal tooth on the rostrum may have been added. The carapace which already from the first Mysis fully covered the thorax reaches now beyond this and its connection with the free abdomen is supported through the lateral processes on the first abdominal segment. These processes were already present in the first Mysis, but they have enlarged in the second Mysis and are now in most cases shaped as a ridge on both sides of the first abdominal segment running in a dorso-anterior to ventro-posterior direction. The process usually fits in ventrally to the posterior branchio-cardiac spine if this is present, dorsally to the latero-posterior marginal spine if this is present, or between them if both are present as in *Solenocera* sp. larva *elongata* or *S*. sp. larva *aequatorialis*. The pleura have in this stage started to develop from the abdominal segments. The telson is more elongate and slim because the uropods have developed further both in number of setae and in length. The telson and the uropods now form a perfect, functioning tailfan.