A Free-swimming Nauplioid Stage in *Palinurus*.

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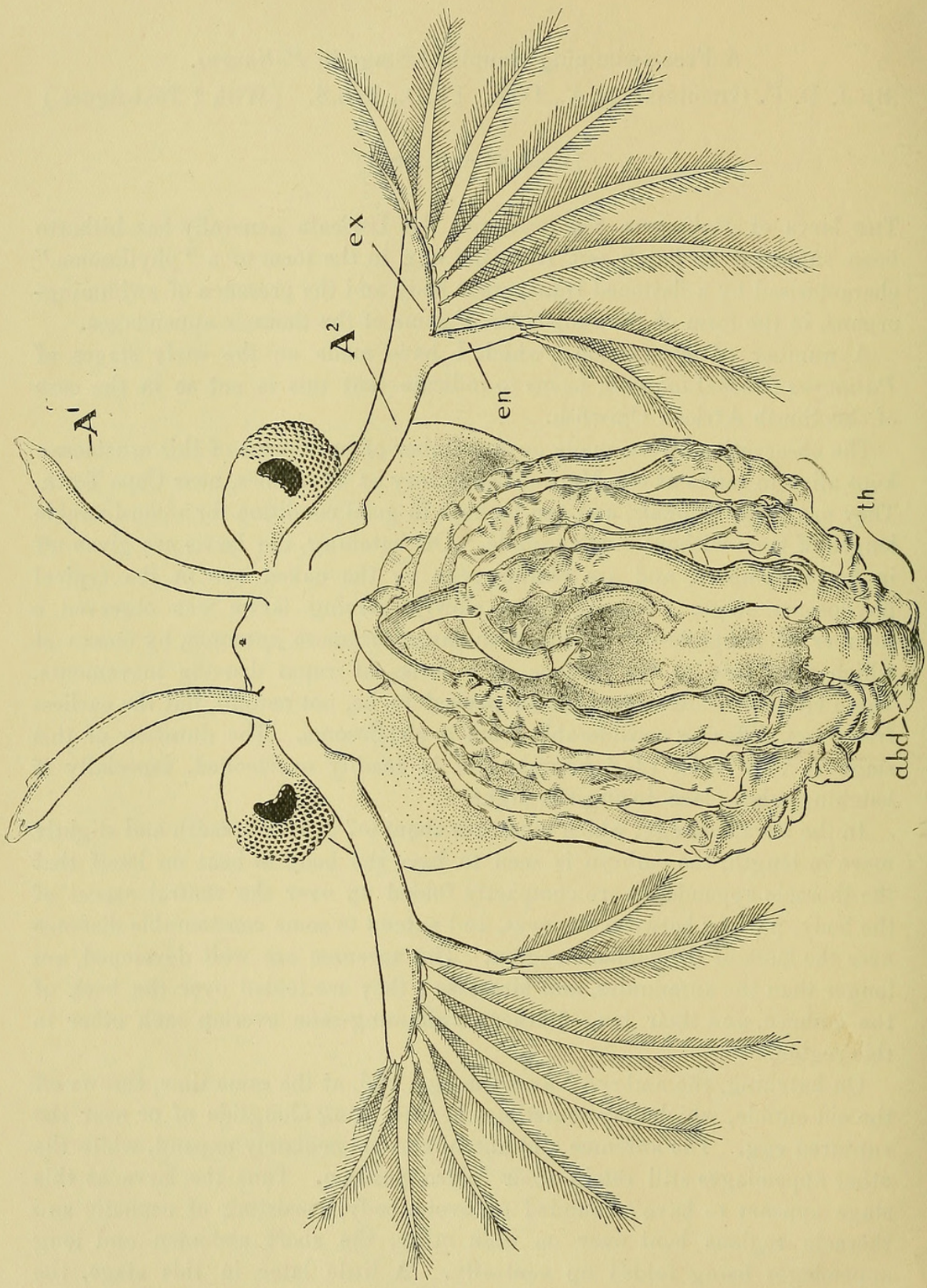
The larva of *Palinurus*, *Scyllarus*, and the Loricata generally has hitherto been supposed to hatch out from the egg in the form of a "phyllosoma," characterised by a flattened transparent body and the presence of swimming-organs, in the form of the exopodites of some of the thoracic appendages.

A number of observations, which I have made on the early stages of *Palinurus* (*Jasus*) *lalandii*, seems to indicate that this is not so in the case of this South African Crawfish.

The observations were made on a number of specimens of this crustacean kept alive in tanks at the Marine Laboratory at St. James, near Cape Town. They are hardy animals, and can be kept in good condition for a considerable length of time without much trouble. On hatching, the larvæ are given off in large numbers, and are readily seen by the naked eye in the typical phyllosoma stage. Among these slowly-moving larvæ was observed a number of nauplius-like forms, with large biramose antennæ, by means of which they rose to the surface in a series of rapid dancing movements. These larvæ on closer examination proved to be, not nauplii, but the earliest free stage, differing considerably from a phyllosoma. The duration of this stage is very brief (4–6 hours), and is readily overlooked, especially if hatching takes place during the night.

In the advanced egg, which measures about 0·7 mm. in breadth and slightly more in length, the embryo is seen to have the body so bent on itself that the thoracic appendages are compactly folded up over the ventral aspect of the body, passing between the eyes, and extend to some considerable distance over the back of the cephalic region. The antennæ are well developed, are longer than the antennules, and biramose; they are folded over the back of the embryo, and their long feathery swimming-setæ overlap each other in this region.

On hatching, the embryo leaves the egg, and, at the same time, throws off the old cuticle, which may sometimes be seen lying alongside of or near the ruptured egg. The antennæ and antennules immediately expand, while the other appendages still retain their folded position. Thus the larva at this stage appears to have a rounded or ovoid body, consisting of cephalic and thoracic regions bent over on each other, the short abdomen and long appendages being folded up ventrally. A little later in this stage, the appendages become somewhat unfolded, and the angle of flexure between the



"Nauplosoma" larva of *Palinurus* (*Jasus*) *lalandii*, ventral aspect, highly magnified.

A¹, antennules. A², antennæ. *ex.*, exopodite, *en.*, endopodite of the antenna. *th.*, thoracic limbs. *abd.*, abdomen.

cephalic and thoracic regions becomes less acute, so as to give the whole body a more elongate appearance. This unfolding also occurs in specimens placed in preserving-fluid at this stage.

The superficial resemblance to a nauplius at this stage is striking, especially in the large biramose swimming-antennæ and apparently ovate body, but a closer examination of the body and appendages indicates that the larva is much more advanced in organization than a nauplius, this latter stage having presumably been passed through much earlier in the development of the egg. For convenience the larva may be called a naupliosoma or described as being in a naupliosoma stage.

The *cephalic region* is broad (0·72 mm.), and is almost circular in outline, the length, from the anterior to the posterior margin of the cephalic shield, being about equal to its breadth. This region is not flat and transparent, as in the succeeding phyllosoma stages, its depth (from the centre of the back to the mouth-appendages) being about four-fifths of its breadth, nor is it transparent, being as yet filled with a considerable amount of yellow yolk-granules. The antennal glands, which appear distinctly in the next stage, were seen in some, and also three large hepatic diverticula on each side. Two powerful muscles, which degenerate at a later stage, were observed attached to the base of each of the antennæ. The cephalic shield is rounded dorsally, and extends backwards over the thoracic region to about the anterior margin of the base of the second maxillipeds (in some cases only to the first maxilliped).

The *thoracic region* is bent forward and under the cephalic region, there being, especially at first, a somewhat abrupt flexure of the body at the junction between the two. This region is characterised also by the presence of a well-marked segment—that to which the first maxilliped belongs—which appendage, it is to be noted, is a mere rudiment. The thoracic region is narrow, resembling the body of a pycnogonid, and, except the part mentioned, shows no distinct traces of segmentation. It is transparent except for the presence of a thin yellow streak—the remains of the yolk in the intestine.

The *abdominal region* or tail is short, and, like the thoracic region, is flexed ventrally. In its anterior two-thirds four distinct segments can be distinguished. It is also narrow, scarcely exceeding the breadth of the first joint of the last appendage (the sixth thoracic). It ends in a pair of furcal processes, provided with setæ, which are not yet free, but covered over by cuticle.

The *pigmentation* of the body is striking; the cephalic region and the intestine are of a faint yellow colour from the presence of the yolk, while on the body and limbs are bright blood-red patches of pigment, usually of a stellate structure in the living animal. These are disposed as follows:

at the tips of the antennules (sometimes absent), at the inner side of their bases, on the lower lips (well marked), at the bases of the third maxilliped, the first, second, and third walking-legs, and at the joints and tips of the walking-legs with the exception of their exopodites which are unpigmented.

The paired *eyes* are well developed, and are situated near the anterior margin of the cephalic shield, to which they are attached by short stout stalks. There is a median eye-spot.

The *antennules* project forward between the eyes. They show no traces of segmentation, and the spines, which appear in the next stage, are still covered by cuticle, though a few short terminal ones and a minute one at a little distance from the free extremity can be made out. The bases of the antennules are visible from the ventral side, and are situated slightly posterior to the bases of the eye-stalks. In length the antennules are about three-fourths of the length of the antennæ.

The *antennæ* are the most conspicuous organs, and are in length about four-fifths of the breadth of the cephalic region. Each consists of a rather long and stout protopodite, the main axis of which is continued into a shorter, but also stout, exopodite, while the smaller endopodite appears as a branch to this main stem, though a little later on (at the third moult) it already exceeds the exopodite in length, and, ultimately, alone survives as the main portion of the antenna. Near the base of the protopodite is a papilla-like projection, apparently a masticatory process. From the posterior border of the exopodite arises a series of long cuticular projections, each resting on a ledge-like indentation of the exopodite. They form broad flat swimming-blades, nearly touching each other at their origin, and bent dorsally at their tips. They are provided with a single series of fine setæ on each side. There are five of them arising from the posterior margin of the exopodite and two from its extremity. In length the inner is a little over three times the length of the exopodite, the terminal one being very much smaller. Into this last and the one next it project two spines which become free at the next stage. The endopodite is also provided with long flat cuticular processes, similar to those of the exopodite, but only two in number. The first, or inner, is shorter than the second. They arise from a common base, and into each projects a spine from the tip of the endopodite.

The *upper lip* is well developed and shows active movement in the living state.

The *mandibles* are short stout organs, with a broad base, and terminate in a short thick spine with about three denticulations. No trace of segmentation nor a biramose condition was seen. Their inner extremities are overlapped by the upper lip.

The *lower lip* consists of two well-marked leaf-like lobes, which also overlap the tips of the mandibles from below, and even the margin of the upper lip to a slight extent.

The *first maxilla* is well developed and shows active movement. It is unsegmented, but biramose, each of the short stout branches being turned inwards and terminated by two or three long sharp spines as yet covered by cuticle and apparently not functional.

The *second maxillæ* lie at some distance from the first maxillæ and other mouth-parts. They are comparatively well developed, but unsegmented, being long blade-like organs projecting forward from their points of attachment on the body. Their outer margins are straight, while their inner is convex, and shows no lobes, though provided with a spine. Their greatest breadth is about one-third of their length. At the free extremity of this appendage are three long spines, not easily made out as they are still covered by cuticle.

The *first maxilliped* appears as a minute knob or projection of the body, about one-quarter of the breadth of the first joint of the succeeding appendage in breadth, and not much over this in length. It is terminated by a sharp spine about its own length. It is situated about midway between the neighbouring appendages and towards the middle line of the body, so that its free end scarcely reaches the margin of the body. It is thus a mere rudiment.

The *second maxilliped* is much longer, and extends forward in a curve to about the middle of the cephalic region. It consists of five distinct segments terminated by spines still in cuticle. It is not provided with an exopodite.

The *third maxilliped* is similar to the second, but is longer. Both are, at this stage, folded inwards under the three succeeding walking-legs. There is no exopodite.

The *first and second walking-legs* are much stouter, being about twice the breadth of the preceding appendage at their bases. They are much shorter than in the next stage, being compressed within the cuticle so that they appear twisted or folded on themselves, a condition specially marked in the third joint of the endopodite. The exopodite is not folded and is not as yet provided with the swimming-setæ so characteristic of their condition in the next stage, though these may be seen indistinctly under the cuticle as well as the segmentation of this appendage. The two powerful muscles with which it is provided for swimming purposes at the next stage are distinctly visible.

The *third walking-leg* differs from the first and second, and though long and folded on itself like them, has only the rudiment of an exopodite.

The *fourth walking-leg* is scarcely to be distinguished as a small swelling, while the fifth is not present even in rudiment.

In comparing this larva with that of other known larvæ of the Loricata we notice some striking differences. The European *Palinurus* and *Scyllarus* have been investigated by Dohrn (1), Claus (2), and Richters (3), and their

development and transition into the phyllostoma stage described. In both cases the form which emerges from the egg is a typical phyllosoma, the body is clear and transparent, the limbs are fully expanded, the various spines and swimming-setæ are fully developed. In the newly-hatched larva of *Palinurus* (*Jasus*) *lalandii*, on the other hand, it is not till the next moult that the typical phyllosoma-form is assumed and in the first free larva the cephalic region is still opaque owing to the presence of yolk, the thoracic limbs with their spines and swimming-setæ are not fully developed. In regard to these points, therefore, the naupliosoma larva corresponds to a stage passed in the egg in the case of *Scyllarus* and the northern *Palinurus*.

Again, in *Palinurus quadricornis* and *Scyllarus* the second antennæ at the time of hatching are shorter than the first, whereas in the form under consideration the first are markedly the shorter, being only about three-fourths of the length of the second antennæ. This new form further differs from the young *P. quadricornis* in having well-marked biramose antennæ, in this respect resembling *Scyllarus*. The presence or absence of marked biramose antennæ cannot therefore be taken as a means of distinguishing the larval forms of the Palinuridæ from other similar forms. This biramose condition persists in the succeeding phyllosoma stages of the Cape *Palinurus*, and is marked in the oldest undoubted phyllosoma belonging to it which I have yet found (4·4 mm. in length).

The hepatic diverticula of the naupliosoma have a much greater resemblance to those of the phyllosoma of *Scyllarus* than to that of *P. quadricornis*, there being three pairs in the first two, while, in the last, they are numerous from the very beginning.

An agreement between the first two is also seen in the absence of an exopodite in the third maxilliped, while it is present in the youngest phyllosoma of the last (taken from the egg just before hatching).

In the newly hatched larva of *Scyllarus* the 4th and 5th ambulatory legs are scarcely to be seen, while in that of *P. quadricornis* they occur as minute buds. In the naupliosoma there is only a slight trace of the 4th, in the form of a minute bud, while no traces at all of the 5th were observed, though they both appear in the stage of 4·4 mm.

Neither in *Scyllarus* nor in *P. quadricornis* are the antennæ at any stage provided with long setose swimming-processes as in the naupliosoma. It is presumed that, at one stage in its phylogeny, *Palinurus* had a free nauplius stage, whose chief organs of locomotion were the biramose antennæ and their swimming cuticular processes. The appearance of such organs at this late stage in the Cape *Palinurus* may be a new acquisition or a belated appearance of an old.

The significance of this stage of so short duration in the life-history of the Crawfish appears to be that it enables the young to ascend more rapidly, and with more certainty, to the surface than in the case with the slowly moving

phyllosoma, which is more adapted to a horizontal mode of progression. The biting and grasping setæ of the mouth-parts and other appendages are not yet developed, and the larva does not appear to feed during this stage. The Cape Crawfish occurs in great abundance on the West Coast of South Africa in marked contrast to the comparative scarcity of the European *Palinurus*. Is it possible that the occurrence of this short stage, which appears to be of a little assistance in the life-history of the animal, may have something to do with this relative abundance? If so, the Cape Crawfish might with profit be introduced into the fisheries of Europe, an undertaking which would be comparatively easy, owing to the hardy nature of this animal.

Bibliography.

1 Dohrn, A.—Untersuchungen, &c. 6. Zur Entwicklungsgeschichte der Panzerkrebse (Decapoda Loricata). Zeitschr. f. Wiss. Zool. Bd. xx., 1870.

2. Claus, C.—Untersuchungen zur Enforschung der genealogischen Grundlage des Crustaceen-Systems. Wien, 1876.

Ueber einige Schizopoden und niedere Malakostraken. Zeit. f. Wiss. Zool. Bd. xiii., 1863.

3 Richters, F.—Die Phyllosomen. Ein Beitrag zur Entwicklungsgeschichte der Loricaten. Zeit. f. Wiss. Zool. Bd. xxiii., 1873.