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ABBREVIATED LARVAL DEVELOPMENT IN THE ALPHEID SHRIMP

RACILIUS COMPRESSUS PAULSON

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The unusual alpheid shrimp *Racilius compressus* was first described by Paulson in 1875, from specimens from the Red Sea. There were no subsequent reports of the species outside the Red Sea until its rediscovery in Moçambique by Barnard (1955). It has since been reported from Madagascar, East Africa, Thailand, Singapore and Queensland, Australia. It is of widespread occurrence on western Indian Ocean reefs where the normal host coral *Galaxea fasciculatis* L. occurs. No other species have been referred to the genus *Racilius* Paulson. *R. compressus* is note-worthy for its extremely strongly bilaterally compressed body and its association with an oculunid coral, a host not adopted by any other commensal species of the Alpheidae.

Specimens of *Racilius compressus* collected from the coral reefs around Zanzibar Harbour were noted to carry relatively few but large ova, and a female with ova at an advanced stage of development was maintained in sea water until the ova hatched. The first stage was found to hatch with well developed first and second pereiopods and with rudimentary pleopods on all abdominal segments, in a more advanced stage than is typical for the majority of alpheid shrimps. Abbreviated development of larvae has been reported so far in two genera of the Alpheidae, only, *Alpheus* Fabricius and *Synalpheus* Bate, and is an uncommon phenomenon in coral reef Caridea.

DESCRIPTION OF FIRST LARVAL STAGE

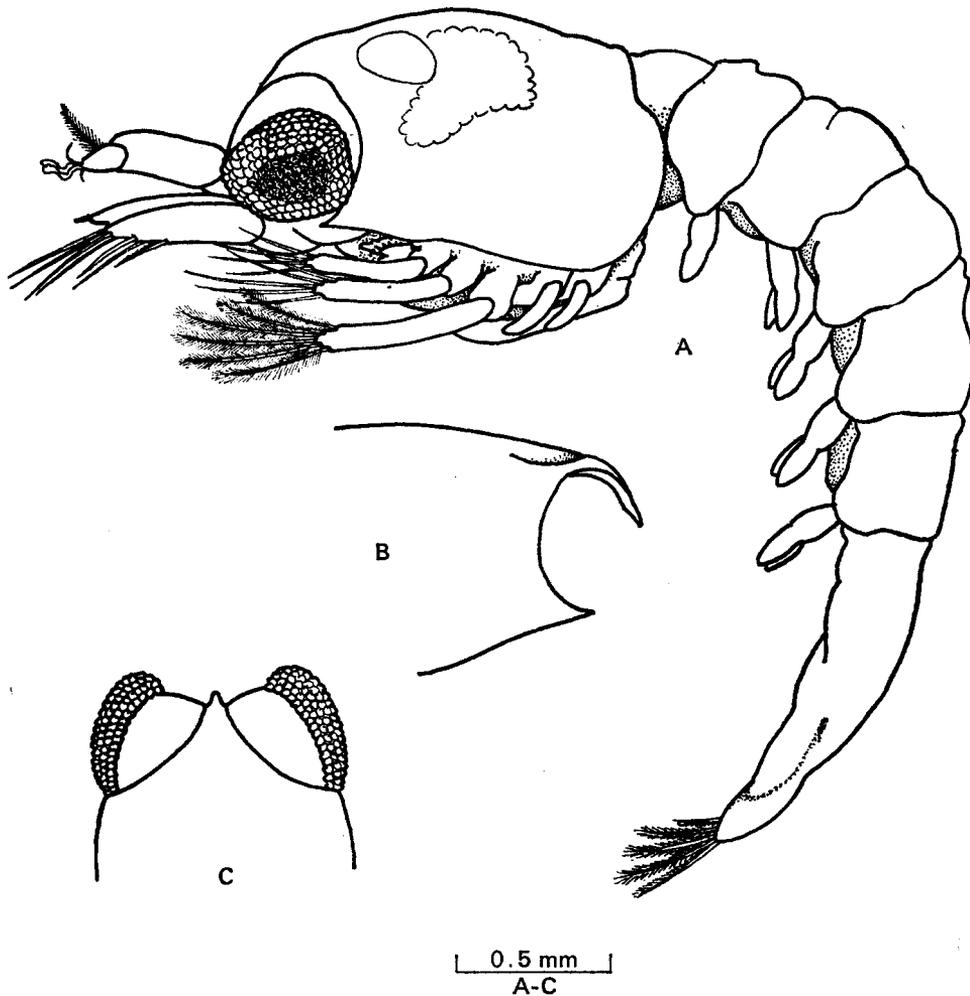
The carapace is smooth and without spines. The rostral process is well developed, slender and strongly curved ventrally. The orbital margin is evenly rounded and the antero-lateral angle of the carapace is acute. There are two large oil globules present in the gastric region and a large mass of yolk immediately posteriorly.

The abdomen consists of five distinct subequal segments with the sixth segment fused with the telson. There are no spinous processes on these segments. Small pleural laminae are present on the first five segments, also lacking in any spines. The sixth abdominal segment and telson are equal to three times the length of the fifth segment. The telson is approximately as broad as long and 1.8 times broader posteriorly than anteriorly. The posterior margin consists of two rounded lobes separated by a shallow median notch. Each side of the posterior border bears well developed setae. The submedian seventh spines are the shortest and the third and fourth, subequal, are the longest. Except for the first, which is setose only on its inner aspect, the posterior marginal setae are densely plumose along their medial and lateral edges. Each seta arises from a distinct marginal tubercle, separated by a deep notch from the adjacent tubercle, and the posterior border of the telson also bears numerous minute setae.

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The antennule consists of three segments, of which the first two are robust, the first being half the length of the second. The dorso-medial end of the second segment is lobular and bears a stoutly based, densely plumose seta. The distal segment is more slender than the proximal segments, tapering distally, and equal to about one third of the length of the second segment. It bears distally two filamentous aesthetascs and two short setae.

The antenna has the protopodite indistinctly subdivided into coxopodite and basipodite, both stout unarmed segments, the basipodite about twice the length of the coxodie. The endopodite consists of a short basal segment and a distal segment, about 3.5 times as long, tapering distally and ending in a small spinous process. The exopod is slightly longer than the endopod and without trace of segmentation. The lateral border



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Fig. 1 *Racilius compressus* Paulson: First larval stage (A) Lateral view. (B) anterior carapace, lateral view. (C) anterior carapace and eyes, dorsal view.

bears two short plumose setae and is without spines. The anteromedial border bears nine long, densely plumose segmented setae.

The mandible has the corpus well developed but both molar and incisor portions are feebly developed, with a few small teeth on the molar portion only, and without a lacinia mobilis.

The maxillula is also poorly developed. The upper and lower laciniae consist of two rounded lobes, the former with a small acute process. The palp is present, rounded, and with a slender terminal seta.

The maxilla has a small elongated unsegmented endopod with a short stout plumose seta distally and with numerous very fine setae along the distal and medial border. The basis has a broad rounded distal endite and a smaller narrower proximal endite. Both endites are without setae. The coxal segment has a feebly bilobed medial border. The distal endite is slender with a short simple seta distally and the proximal endite is represented by a low angular non-setose lobe. The scaphognathite is well developed, broader anteriorly than posteriorly and with ten short, broad, densely plumose setae along the lateral margin.

The first maxilliped bears a short unsegmented endopod. The distal end of the endopod tapers to a point bearing a short robust simple seta. Two short and one longer subterminal setae are also present. The exopod is well developed and is provided distally with four long, densely plumose segmented setae. The basal and coxal segments are distinct, broad, and unarmed along their medial borders, except for a minute simple seta proximally on the basis.

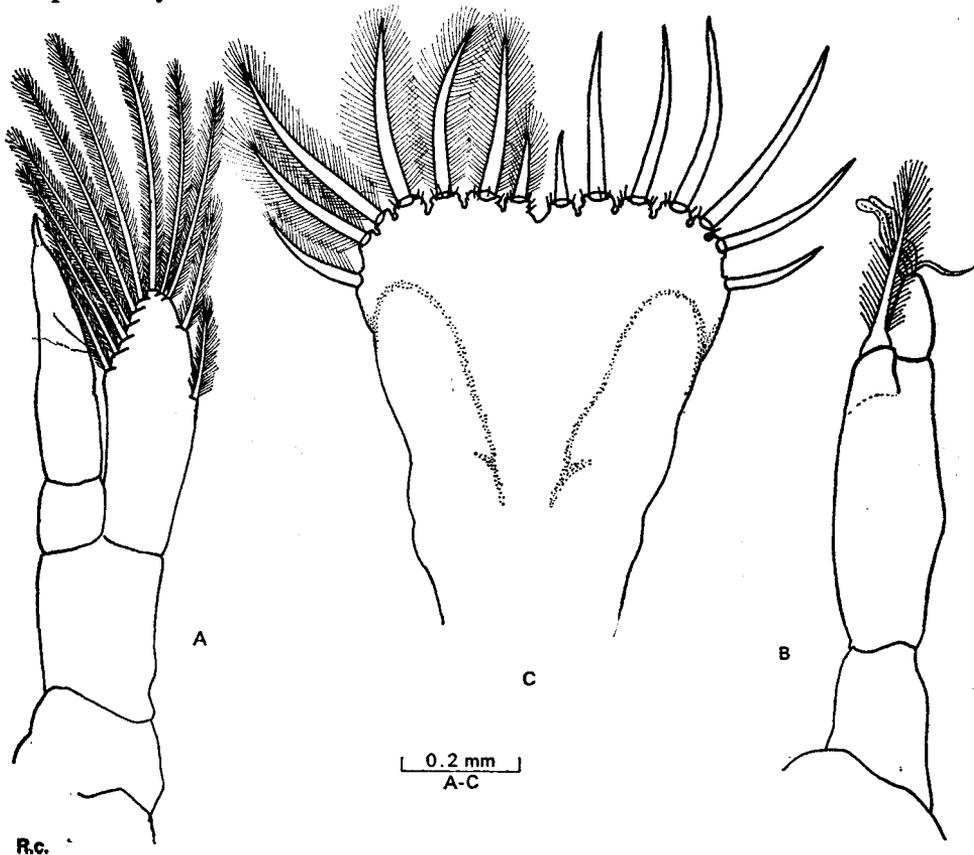


Fig. 2 *Racilius compressus* Paulson: First larval stage. (A) antennule. (B) antenna. (C) telson.

The second maxilliped bears a well developed endopod consisting of four distinct segments. The segments are robust and subcylindrical except for the distal segment, which is tapering and shows indication of division into a small distal dactylar segment and a larger proximal propodal segment. The tip of the dactylar portion bears a stout curved simple seta, with a smaller preterminal seta dorsally. The propodal portion bears a small distoventral seta and a still smaller proximal seta. The carpal segment is the largest segment, about 1.6 times longer than wide, with a strong simple disto-ventral seta. The meral and ischial segments are unarmed, the former being about twice the length of the latter. The exopod is well developed with four long segmented densely plumose setae distally, and with a small simple preterminal seta. The basis and coxa are similar to the first maxilliped.

The third maxilliped has an elongated slender endopod with five distinct sub-cylindrical segments. The carpal segment is the largest and most robust, and the propod and dactylus taper gradually distally, the latter terminating in a hooked simple seta. The endopod, basis and coxa are similar to those of the first maxilliped, the endopod bearing six plumose setae distally.

The first pereopods are well developed with the chelae readily distinguishable. The endopod consists of five distinct segments. The dactylus is relatively slender and equal to the length of the palm. The chela exceeds the combined length of carpus, merus and ischium. A short non-setose exopod, subequal to the length of the chela, is also present. The separation between basis and coxa cannot be discerned.

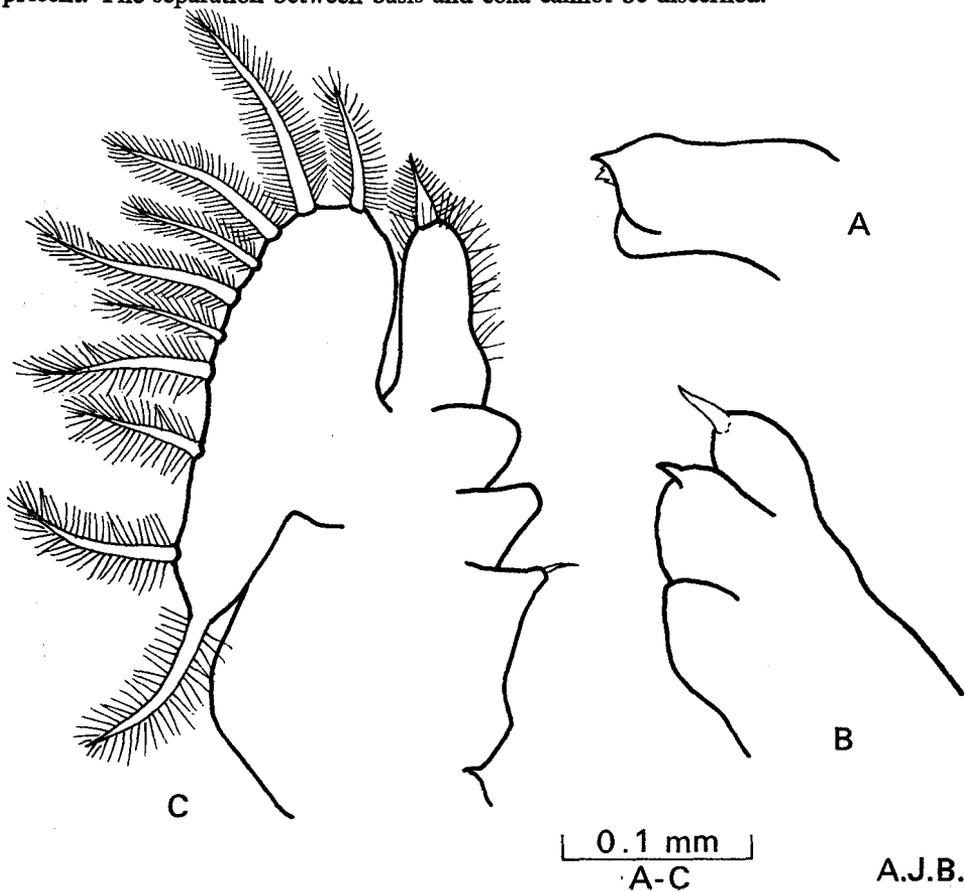


Fig. 3 *Racilius compressus* Paulson: First larval stage. (A) mandible. (B) maxillula. (C) maxilla.

The second pereopod is similarly developed to the first but shorter and much more slender. The chela is distinct and is equal to about 0.9 of the carpus length. A non-setose endopod is also present and an indication of the separation of the basis and the coxa is also apparent.

Rudiments of the third and fourth pereopods are clearly visible but are beneath the cuticle and are not free. The fifth pereopod is well developed and free, and extends forwards along the ventral surface of the body between the second pereopods. The endopod consists of five distinct, unarmed segments and the separation into basal and coxal segments is feebly indicated. There is no exopod.

Pleopods are present on the first five abdominal segments. The peduncles and rami are distinct. All except the first, are biramous and the rami are non-setose.

There are no free uropods but the uropod rudiments are clearly visible beneath the cuticle of the telson.

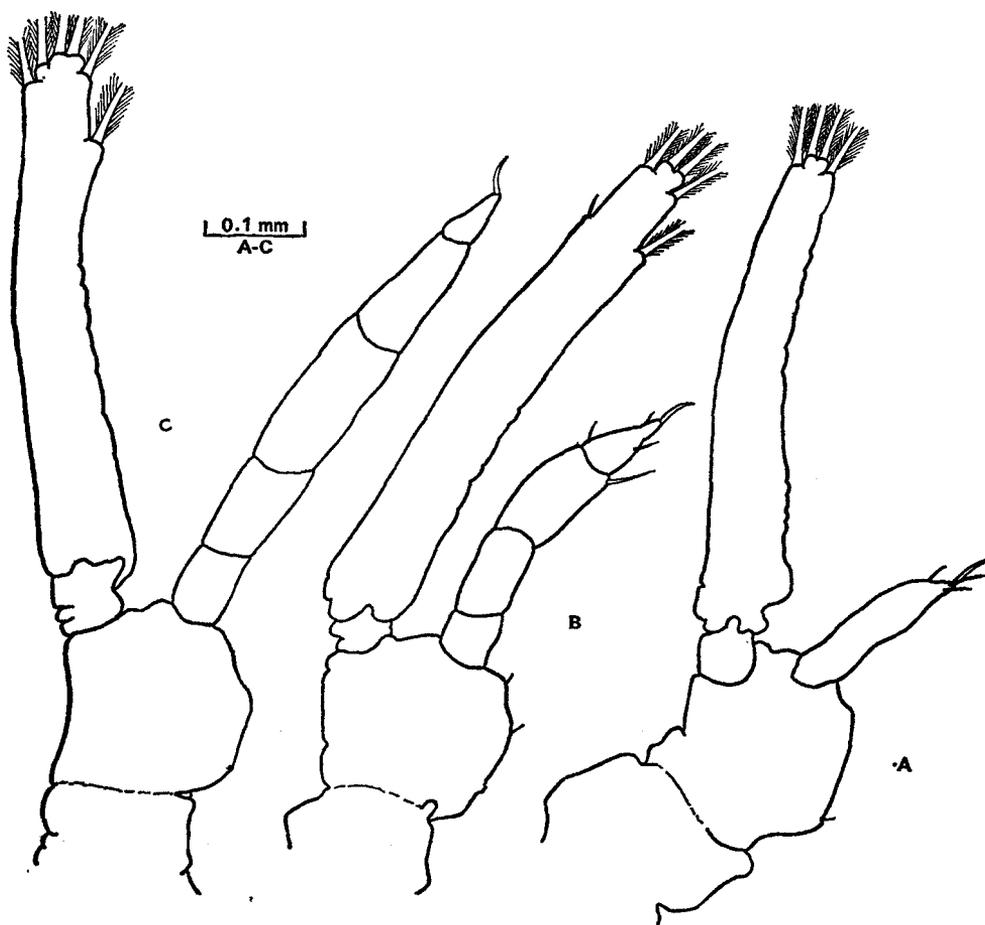


Fig. 4 *Racilius compressus* Paulson: First larval stage. (A) first maxilliped. (B) second maxilliped. (C) third maxilliped.

Measurement: Carapace length, 0.9 mm
Total body length, 3.5 mm

Colouration: Cornea white. Body transparent, with fairly uniformly distributed small yellow-white chromatophores all over, except for the ventral aspect of the abdomen and

the distal halves of the exopods of the maxillipeds. On the abdomen the chromatophores tend to be concentrated into a median dorsal and ventro-lateral longitudinal bands. A few minute red chromatophores were also present around the anterior dorsal region of the carapace, around the base of the rostrum, at the distal median ends of the larger segments of the antennule and antenna, and around the posterior and lateral margins of the telson.

Behaviour: When first hatched the larvae swim actively, head down with the ventral surface of the body uppermost and with the abdomen slightly flexed. Movement is generally by means of the exopods of the maxillipeds, except for sudden backwards escape movements produced by the contraction of the abdominal flexer musculature.

The ovum of *Racilius compressus*

When first laid the ovum is about 1.2 mm, and a typical female will carry about fifteen. When fully developed the ovum measures about 1.4 mm in length.

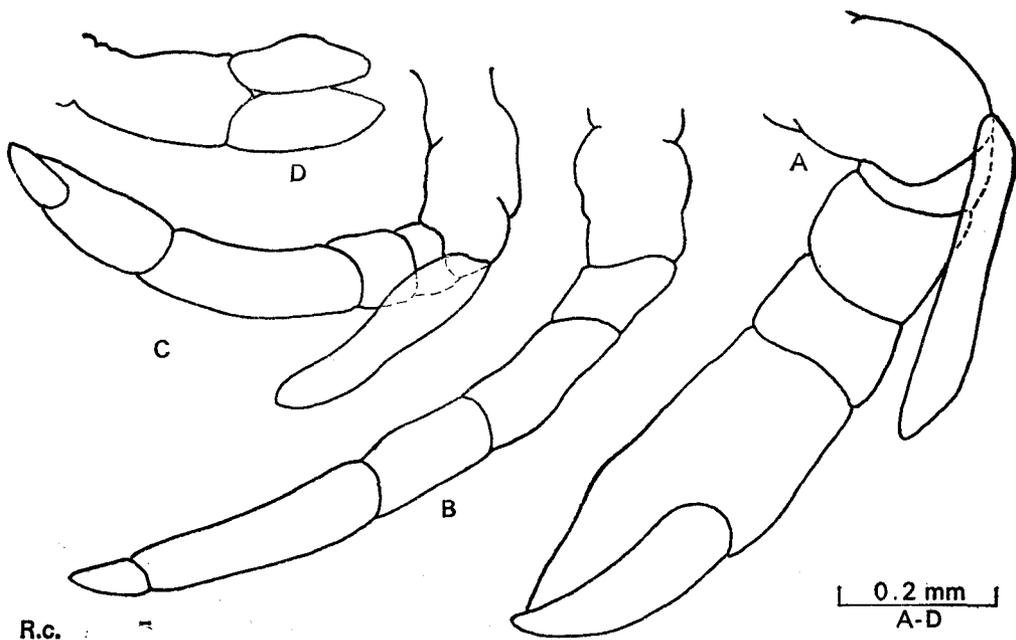


Fig. 5 *Racilius compressus* Paulson: First larval stage. (A) first pereiopod. (B) second pereiopod. (C) fifth pereiopod. (D) third pleopod.

DISCUSSION

Dobkin has proposed the term "pseudo-larvae" for larvae that hatch out into advanced non-planktonic stages. The first larval stage of *Racilius compressus* is not a pseudo-larva, as has been found in *Synalpheus brooksi* Coutière (Dobkin, 1965). The larva of *Racilius compressus* is a typical representative of the family Alpheidae, as described by Gurney (1939), particularly in reference to the presence of a well developed fifth pereiopod preceding that of the third and fourth. It shows a closer resemblance to the stage I larva described by Gurney (1949), for *Synalpheus goodei* Coutière than to *S. brooksi*. In some features the larva of *R. compressus* appears more advanced than that of *S. goodei*, while in others it appears in a relatively earlier state of development. The differences may now be outlined, although the full details of the Stage I larval morphology of *S. goodei* have not been given, preventing a complete comparison.

In the *Racilius compressus* first larva the scaphognathite is provided with ten short densely plumose setae distributed along the entire lateral border, whereas in *S. goodei* the scaphognathite is devoid of setae on its posterior extension, and bears only three on its anterior portion. The first pleopod in the *R. compressus* larva is clearly subdivided into peduncle and ramus, and the second to fifth pleopods are distinctly biramous. In *S. goodei* the pleopods are less well developed. They do not show any indication of peduncle and rami, and do not become biramous until the third larval stage is reached. The fifth pereopod is distinctly segmented. No segmentation is indicated in Gurney's figure for *S. goodei*.

In the *Synalpheus goodei* first larva the antennule has two distal flagellar segments and the development of the three peduncular segments is also clearly indicated in Gurney's figure. The third and fourth pereopods are apparently free and bear rudimentary non-setose exopods, which are lacking in the *R. compressus* larvae, in which these limbs are not free.

The poorly developed state of the mandible, maxillula and maxilla, when compared to these appendages in early larval stages of alpheid species lacking abbreviated development (Gurney, 1938), indicates that they are probably non-functional. As the thorax of the first larval stage contains two large fat globules and a large mass of yolk, the larva could utilize this nutritional source until after a subsequent moult. The first, second and fifth pereopods and pleopods, although free are also clearly non-functional and the larva relies upon the exopods of the three pairs of maxillipeds for propulsion during its planktonic phase, which is probably only of short duration.

In a recent review, Dobkin (1969) has summarized the available information concerning abbreviated larval development in the Caridea. Two genera of the Alpheidae, *Alpheus* Fabricius and *Synalpheus* Bate, are known to have shortened larval histories. Both these genera contain large numbers of species but apparently only one of the former and seven of the latter are so far known to have abbreviated larval development, the vast majority of species having a normal type of caridean larval history. The single species of *Alpheus*, *A. heterochaeles* Say, is apparently free-living, but the species of *Synalpheus* are commensals, many of which are to be found living in association with sponges. Like the species of *Synalpheus*, *Racilius compressus* is also a commensal, but found living in association with the oculinid coral *Galaxea fascicularis* (L.). Despite the apparent advantages of shortened larval life histories in commensal shrimps, which might reduce the chances of larvae being unable to locate their appropriate hosts, through being swept into unsuitable habitats by the prevailing water currents, its occurrence, in commensal shrimps and in tropical marine shallow water shrimps generally, is distinctly rare. In fresh water and deep water Caridea it is comparatively common. The faunas of tropical coral reefs are dominated by the Alpheidae and Pontoniinae, a very large proportion of which are known to live in association with other marine invertebrates but in which abbreviated larval development is known so far in only a very few species. Only a single instance is known in the Pontoniinae. *Pontonia minuta* Baker, the host of which is unknown, has been found to have shortened larval development (Bruce, 1972) and would appear to hatch, at a stage approximately equivalent to that of *Racilius compressus* larvae. It is also noteworthy that three other species of pontoniid shrimp that are to be found with *Racilius compressus* in association with *Galaxea fascicularis*, *Platycaris latirostris* Holthuis, *Ichnopontonia lophos* Bruce and *Anapontonia denticauda* Bruce, all produce relatively large numbers of small ova that hatch into a normal stage I pontoniid larva. Undoubtedly more examples of abbreviated larval development in coral reef Caridea will be discovered but amongst the Caridea that are found in tropical coral reefs, it is distinctly rare.

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RESUMÉ

Le première stage larvaire de la crevette alpheide *Racilius compressus* Paulson a été écolos d'oeufs obtenus d'une femelle recoltée à Zanzibar. Les oeufs sont grands, et ils n'éclosent qu'a un stage avancé, avec trois paires de pereopodes et cinq paires de pleopodes bien developés mais non-fonctionels. La larve ressemble de pres celle de *Synalpheus goodei*, à laquelle elle est comparée. La rareté de development larval abregé chez les Carides des recifs de corail tropicaux est notée.

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