

Decapod Crustacea from the International Indian Ocean Expedition: the larval development of *Heterocarpus* (Caridea)

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(With 11 figures in the text)

The larval species *Atlantocaris gigas* Ortmann is shown to be conspecific with *Heterocarpus ensifer* A. Milne Edwards, while *Procletes biangulatus* Bate is the larva of *Heterocarpus levicarina* (Bate). Each species passes through 13–15 zoeal stages and 3–4 megalopal stages. The later zoeal stages are large, have a long toothed rostrum, a carinated carapace and dorsal abdominal spines. The carinae on the carapace are retained in the adult; the rostrum becomes shortened and the abdominal spines modified at metamorphosis. Larval characters support the retention of *Heterocarpus* in the Pandalidae.

New information on the distribution of both species is included.

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Introduction

The marine crustacean fauna is so rich in species, most of which pass through a long series of planktonic larval stages, that it has always been difficult to relate some of the planktonic larvae to their respective adults. This is particularly so when the sampling is inadequate and of a general nature, as of several major expeditions. The result is that taxonomists have had to create new genera or species based on larvae alone. It is quite common to find cases of this sort in crustacean taxonomy, and the larval genus *Procletes* is among them. The aim of the present work is to establish the adult species which give rise to *Procletes* larvae.

Material and methods

Most of the material for this work was derived from the International Indian Ocean Expedition (1960–65). Of 1927 plankton samples collected from different parts of the Indian Ocean, 76 provided larvae or juveniles of one or other of the species involved. This material includes 120

specimens of the larval species *Procletes biangulatus* Bate, 1888 and 4 specimens of the larva first described as *Atalantocaris gigas* by Ortmann (1893). Throughout, the sampling was carried out by vertical hauls with the Indian Ocean Standard Net (Curry, 1963), from 200 m to the surface, in the open sea and from near the bottom to the surface in shallow waters. The mesh size of 0.33 mm may have been too large to retain the smallest larvae; no larvae in the first stage and very few in the second and third stages were caught. The material is in good condition except for the loss of some of the long appendages in many cases.

In addition to material from the IIOE, I was fortunate in being able to study Bate's type material of *Procletes biangulatus*, specimens of "*Procletes gigas*" originally described by Gurney and an adult specimen of "*Heterocarpoides*" *levicarina* (Bate) from the British Museum (Natural History), London.

The later larval stages of the two species studied are very distinctive. The early larval stages lack some of the more distinctive features but possess sufficient characters to link them with the later stages. In many cases the larvae were moulting and hence the identification of the following one or two stages was possible. The changes from stage to stage take place very gradually.

Larvae of *P. biangulatus* were allotted to different stages firstly from their state of development, particularly of the appendages. Later, these stages were tested for their dependability by plotting the carapace lengths of the pre-exuvial stages against those of post-exuvial stages, following "Hiatt's graphic method" (Hiatt, 1948; Kurata, 1962). These points fall on a straight line, and correspond to a growth factor of 1.268 between successive stages. While this confirms that most individuals are likely to pass through each of the assumed 13 zoeal and 3 megalopal stages, it does not preclude the possibility of some individuals developing with rather more or rather fewer stages. Only four specimens of *Procletes gigas* were obtained; these were compared with larvae of *P. biangulatus* of the same carapace length.

The terms "zoea", "megalopa" and "juvenile" are used in this paper as defined by Williamson (1969). The term "carapace length" (C.L.) means the length from the posterior orbital margin to the mid-dorsal end of the posterior carapace margin. "Rostral length" (R.L.) is the length between the posterior orbital margin and the tip of the rostrum. The numbering of spines on the telson always starts from the anterior dorso-lateral margin. The abbreviations R.T., A₁, A₂, A₂S are often used for rostral teeth, first antenna, second antenna and antennal scale respectively.

Identification of the larvae

During his work on the "Challenger" material, Bate (1888) created the genus *Procletes* to accommodate his new species *P. biangulatus* and *P. elliotti*. The latter is almost certainly a younger stage of the former (see below). Ortmann (1893), working on Atlantic material, erected the genus *Atlantocaris* to include his new species *A. gigas* and *A. longirostris*; the latter is however almost certainly an oplophorid. *P. biangulatus* and *A. gigas* show some common features but also some important differences. Coutière (1907) suggested for the first time that *Procletes* and *Atlantocaris* are synonyms. Lenz & Strunck (1914) also considered *Atlantocaris* to be a synonym of *Procletes* and described a new species *Procletes atlanticus*, which is, as pointed out by Gurney (in Gurney & Lebour, 1941), nothing other than *P. gigas*.

Gurney (in Gurney & Lebour, 1941) revised the genus *Procletes*, including *Atlantocaris*. He confirmed that only two species are really known and suggested that "the two species, *P. biangulatus* and *A. gigas* may be accepted as belonging to the same genus or to two very closely allied genera". Gurney mentioned *P. elliotti*, which Bate had inadequately described and had not figured. Bate (1888) observed that "it resembles *P. biangulatus*, but differs from it in having the lateral walls of the carapace free from carinae, the supra-

orbital teeth not so long, the flagellum of the second pair of antennae shorter than the rostrum, and the telson longer than the sixth pair of pleopoda", and the present study shows that it is almost certainly an early zoeal stage of *P. biangulatus*.

Different authors have suggested different parentage for these larvae, Ortmann (1893) suggested the Acanthephyridae, though he noted that the absence of an exopod on the fifth leg is not consistent with this. Coutière (1907) thought they were related to *Thalassocaris*; Lenz & Strunck (1914) agreed with Coutière, but pointed out that all the described larvae may not belong to this genus. Gurney (in Gurney & Lebour, 1941) eliminated all these propositions by adequate arguments and suggested that "if *Thalassocaris* is excluded, the only other genus which can be considered is *Heterocarpus*", and that *P. gigas* is probably the larva of *H. ensifer* A. Milne Edwards. On another occasion in his paper he also stated "no suggestion can be made as to the exact position of *P. biangulatus*", but suggested that it may provisionally be accepted as also belonging to *Heterocarpus*, though there are a lot of differences.

Holthuis (1952, 1955) included *P. gigas* in the synonymy of *H. ensifer*, but in the earlier paper he raised the point that in a series of collections from West Africa, the largest larval specimens (= *P. gigas*) were 53 mm long whereas the smallest metamorphosed specimens (= *H. ensifer*) were only 45 mm long. It is known that in several species of Decapoda metamorphosis may take place over a wide range of size, and in both *Rhynchocinetes rigens* Gordon and *Stenopus hispidus* (Olivier) the smallest larvae capable of metamorphosis at the next moult are only about half the length of the largest (Gurney & Lebour, 1941). It appears that in such species some larvae, apparently in the last zoeal stage, may moult to produce very similar but slightly larger larvae, while others moult to produce post-larvae. It seems likely that the same phenomenon of delayed metamorphosis may take place in *H. ensifer* and related species. The West African record (Holthuis, 1952) is important in linking *H. ensifer* and *P. gigas* at a specific level because no other species of *Heterocarpus* has been recorded from this area.

Recent work on the larvae of *Thalassocaris* (Gopala Menon & Williamson, 1971) confirms that *Procletes* (including *Atlantocaris*) does not belong to this genus. The latest available stage of *P. gigas* is that from Discovery Station 281, described by Gurney (in Gurney & Lebour, 1941). Re-examination of this specimen and comparison with the youngest juvenile of *H. ensifer* in the IIOE collections not only confirms the similarity of the carinae on the carapace (stressed by Gurney) but also reveals additional points of similarity not previously noted. These include the spines on the anterior carapace margin, protuberances on the 1st abdominal somite and asymmetry of the 2nd legs. These points are described in detail in the descriptive part of the present paper.

The almost complete series of developmental stages of *P. biangulatus* in the present collection show that the larvae develop into a form which can be identified beyond doubt as that originally described as *Dorodotes levicarina* by Bate (1888). The nature of the carapace and its carinae, the rostrum and its dentition, the abdominal somites and their spines, all point to such an identification (see "Descriptions of larvae and juveniles").

The genus *Heterocarpus* is here regarded as consisting of two subgenera, as suggested by De Man (1917, 1920), although acceptance of the parentage of the larvae as outlined above affects the name of the second subgenus. It may be noted that some authors, notably Holthuis (1955), have recognized a generic rather than a subgeneric distinction in this case. The synonymies of the genus and its two subgenera are as follows:

Genus *Heterocarpus* A. Milne Edwards, 1881

- Heterocarpus* A. Milne Edwards, 1881, *Annls Sci. nat. (Zool.)* (6) 11 (4): 8. Type species, by original designation: *Heterocarpus ensifer* A. Milne Edwards, 1881, *Annls Sci. nat. (Zool.)* (6) 11 (4): 8. Gender: masculine.
- Procleles* Bate, 1888, *Rep. Voy. Challenger (Zool.)* 24: 883. Type species, by selection by Holthuis (1955): *Procleles biangulatus* Bate, 1888, *Rep. Voy. Challenger (Zool.)* 24: 884. Gender: masculine.
- Dorodotes* Bate (part), 1888, *Rep. Voy. Challenger (Zool.)* 24: 627, 677. Type species, by selection by Holthuis (1955): *Dorodotes reflexus* Bate, 1888, *Rep. Voy. Challenger (Zool.)* 24: 678. Gender: masculine.
- Atlantocaris* Ortmann, 1893, *Ergebn. Plankton-Exped. 2 (Gb)*: 73, 79. Type species, by selection by Holthuis (1955): *Atlantocaris gigas* Ortmann, 1893, *Ergebn. Plankton-Exped. 2 (Gb)*: 80. Gender: feminine.
- Heterocarpoides* De Man, 1917, *Zool. Meded. Leiden* 3: 284 (as subgenus). Type species, by monotypy: *Dorodotes levicarina* Bate, 1888, *Rep. Voy. Challenger (Zool.)* 24: 680. Gender: masculine.

Subgenus *Heterocarpus* A. Milne Edwards, 1881

- Heterocarpus* A. Milne Edwards, 1881 (see generic synonymy).
- Atlantocaris* Ortmann, 1893 (see generic synonymy).

Subgenus *Procleles* Bate, 1888

- Procleles* Bate, 1888 (see generic synonymy).
- Dorodotes* Bate (part), 1888 (see generic synonymy).
- Heterocarpoides* De Man, 1917 (see generic synonymy).

The two species, whose development is described in the next section of the paper, belong to different subgenera and have the following synonymies:

Heterocarpus (Heterocarpus) ensifer A. Milne Edwards, 1881

- Heterocarpus ensifer* A. Milne Edwards, 1881, *Annls Sci. nat. (Zool.)* (6) 11 (4): 8.
- Atlantocaris gigas* Ortmann, 1893, *Ergebn. Plankton-Exped. 2 (Gb)*: 80.
- Procleles atlanticus* Lenz & Strunck, 1914, *Dr. Südpol. Exped. 15 (Zool. 7)*: 334.
- Procleles gigas* (Ortmann) Gurney, 1941 (in Gurney & Lebour), *J. Linn. Soc. Lond. (Zool.)* 41: 130.

Heterocarpus (Procleles) levicarina (Bate, 1888)

- Dorodotes levicarina* Bate, 1888, *Rep. Voy. Challenger (Zool.)* 24: 680.
- Procleles biangulatus* Bate, 1888, *Rep. Voy. Challenger (Zool.)* 24: 884.
- Heterocarpoides levicarina* (Bate) De Man, 1917, *Zool. Meded., Leiden* 3: 284.

The subjective synonyms *Dorodotes levicarina* and *Procleles biangulatus* originated in the same publication (Bate, 1888) and therefore have equal priority. The genus-group name *Dorodotes* is not available for the subgenus concerned, as the type species of *Dorodotes* (namely *D. reflexus*) is no longer considered to be congeneric with the present species (see De Man, 1920). The subgeneric name *Procleles* must therefore be used, as it has priority over *Heterocarpoides*. The validity of the name *Procleles* is not affected by the fact that it was originally applied to a larval stage. The specific epithets *levicarina* and *biangulatus* are both available, and, as first reviser, I have selected the former, taking the view that it is preferable to use the name originally applied to the adult form; *levicarina* also has page priority over *biangulatus*.

Descriptions of larvae and juveniles

Heterocarpus (Heterocarpus) ensifer A. Milne Edwards

(Figs 1 to 3)

Material examined. IIOE: 5 specimens, from Stations Anton Bruun 325, Pioneer 27, Meteor 161, Diamantina 1/63—29 and 2/63—71. British Museum: 2 specimens, from Discovery stations 281 and 701 (east and west Atlantic).

The larvae of *H. ensifer* described by Ortmann (1893) and by Lenz & Stunck (1914) and that from Discovery station 281 (Atlantic), previously described by Gurney (in Gurney & Lebour, 1941), are all late megalopae in almost the same stage of development. Gurney also described two zoeal stages, the youngest being that from Discovery Station 701 (Atlantic). One of the specimens from the IIOE collection is in the same stage as Gurney's youngest, one is still younger and the other three are older zoeae. The larval series for this species is not complete, but comparison with the development of *H. levicarina* and the application of a similar growth factor suggest that *H. ensifer* probably passes through 18–19 larval stages of which three or four are megalopae. Five developmental stages are described separately below.

Zoeal stage ?IX, C.L. 1.5 mm: IIOE Anton Bruun Station 325 (Fig. 1(a)).

Rostrum 2.3 mm; 18/9 teeth, 3 dorsal teeth on carapace, 4th just above posterior orbital margin. Carapace dorsally slightly concave in lateral view; very small anterior and comparatively large posterior papilla; large supra-orbital, antennal and pterygostomian spines, prominent lateral spine at about half length of carapace, level with supra-orbital spine; ventral margin without spines or serrations. Five carinae on each side of carapace, 1st–3rd longitudinal and almost as long as carapace, 4th and 5th oblique: 1st from base of supra-orbital spine to lateral spine, then curving up as faint ridge to upper posterior margin; 2nd at level of antennal spine and 3rd from lower base of pterygostomian spine, both running parallel to ventral margin of carapace; 4th faint, from just above lateral spine to just in front of posterior dorsal papilla; 5th running postero-dorsally from 2nd to lateral spine then posteriorly to margin; 3rd and 5th more prominent than others. Abdominal somites 3 and 4 with long posterior dorsal spines, that of 3rd somite an extension of dorsal ridge arising near anterior end of somite; small prominence just anterior to spine of 4th somite; 6th somite 6.5 times as long as deep, with pair of postero-lateral pointed processes. Abdominal pleura 1–3 rounded, those of somites 4 and 5 with very blunt postero-ventral spines. Well developed anal spine. Telson 1.3 mm long, excluding posterior spines; four times as long as maximum width, tapering to half maximum width; four pairs dorso-lateral spines and five pairs terminal spines: 4th pair (last of dorso-laterals) just in front of posterior margin and overlying 5th (largest) pair; posterior spines, in order of size: 5th, 7th, 6th, 8th, 9th (9th very small). Uropods well developed, exopod with external terminal spine and few setae at proximal end.

Eyes well developed, with slender tapering stalk. Antennules long, fairly well separated and curving apart towards distal end; 3-segmented peduncle reaches $\frac{3}{4}$ length of A_2S , first segment largest and bearing long ventral spine, stylocerite small and blunt; flagella unsegmented. A_2S (Fig. 1(d)) about 4.6 times as long as broad, narrowing distally; large apical spine and series of ten small teeth of different sizes on outer margin; proximal ventral seta near external margin; two dorsal ridges parallel to outer margin, inner ridge not reaching tip; flagellum probably long but broken; large ventral spine on basis at base of

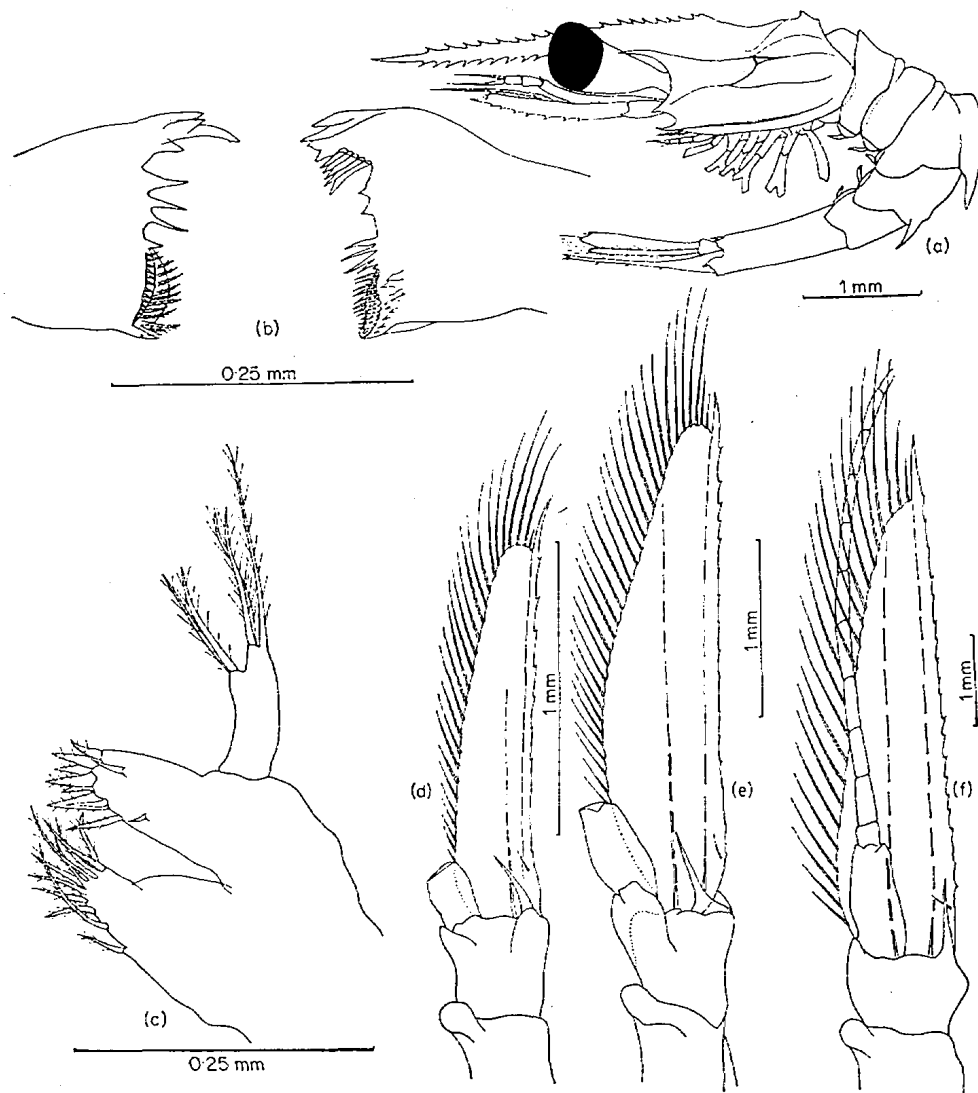


FIG. 1. *Heterocarpus (Heterocarpus) ensifer* A. Milne Edwards. (a)–(d) larval stage ?IX (zoea), C.L. 1.5 mm: (a) lateral view; (b) mandibles; (c) maxillule; (d) antenna, ventral; (e) antenna of larval stage ?XIV (zoea), C.L. 3.5 mm; (f) antenna of larval stage ?XVII (=megalopa ?II), C.L. 7.5 mm (Discovery St. 281, Atlantic).

A₂S. Mandibles (Fig. 1(b)) asymmetrical, without palp, with well developed incisor and molar processes. Maxillule (Fig. 1(c)) with unsegmented endopod and no trace of exopod. Maxilla (figured in Gurney & Lebour, 1941) with undivided endopod, four well-marked inner lobes and large exopod which is broad distally and comparatively narrow proximally. Maxilliped 1 with large bilobed epipod, 4-segmented endopod, exopod slightly expanded at base and bearing many setae. Maxilliped 2 with 5-segmented endopod, long setose exopod and comparatively small bilobed epipod. Legs 1–4 with exopods bearing setae. Five pairs of pleopod buds.

Zoeal stage ?XI, C.L. 2 mm: IIOE Pioneer St. 27. (Same stage as that from Discovery St. 701, mentioned by Gurney, in Gurney & Lebour, 1941.) IIOE specimen: R.L. 3.5 mm, R.T. 21/10; Gurney's specimen: R.L. 3.65 mm, R.T. 19/9.

A re-examination of Gurney's specimen shows it to agree well with that from the present collection, but there are some errors and omissions in Gurney's description. Gurney did not mention all the carinae on the carapace, and stated that "These carinae, which are so conspicuous in *P. gigas*, are not found in the younger stages and are evidently adult rather than larval characters". While these carinae are more prominent in the adults, I find them to be present on the carapace of all zoeae, including the youngest, from the present collection, as well as Gurney's own specimen from the Station 701. They can be seen by illuminating or observing the carapace from different angles. In addition to those carinae previously mentioned, there is an indication of a 6th, just above and parallel to the ventral margin of the carapace, extending the full length. Gurney did not mention the antennal spine on the carapace of his specimen.

Dorsal posterior spines on abdominal somites 3 and 4 (not 2 and 3 as mentioned by Gurney). Pleura of somites 4 and 5 rather more pointed than in stage IX; that of somite 3, said to be pointed by Gurney, is rounded in all stages. Sixth somite relatively shorter in this stage.

The telson of Gurney's specimen has four pairs of lateral and four pairs of terminal spines, as against "2 pairs of lateral and 5+5 terminal spines" mentioned by him. The discrepancy is partly explained by assuming that Gurney regarded the 4th pair as terminal, rather than dorso-lateral, but he must have overlooked one pair of dorso-laterals. The small median pair of terminal spines, present in stage IX, is not represented. The telson of the IIOE specimen is lost and so a comparison is not possible. The exopod of the uropod has a terminal spine on the outer margin.

A₂S with ridges and setae as in stage IX. Pleopods present on abdominal somites 1-5, and some bear one or two small setae.

Zoeal stage ?XIII, C.L. 3.0 mm, R.L. 4.6 mm, R.T. 18/9: IIOE Diamantina 1/63-St. 29.

The carapace shows no additional characters but the carinae are more developed, particularly the 6th which runs parallel to the lateral carapace margin, curves up at the posterior end and runs close to the posterior carapace margin.

Pleura of abdominal somites 4 and 5 with small postero-ventral spines. Sixth somite 2.2 times as long as broad. Telson about 2.2 mm long, maximum width 0.5 mm tapering to about 0.2 mm, with five pairs dorso-lateral and five pairs terminal spines; size order of terminal spines remains as in earlier stages; median pair remains very small.

It will be seen that this stage has acquired an additional pair of dorso-lateral telson spines (between the original 3rd and 4th), and all the spines previously present are retained. The median pair on the posterior margin are, however, lost at about this stage, and apparently may disappear before the additional pair of dorso-laterals appear. This seems to be the case in the specimen in stage XI (Gurney's material), mentioned above. The difference may be related to the different localities of the specimens, Gurney's specimen being from the North Atlantic, but there is insufficient material to confirm this suggestion.

Antenna with segmented flagellum, almost as long as body. A₂S narrowing to distal end, long spine at tip, maximum width 0.5 mm, five times as long as wide; ten small spines on external margin; dorsal surface with two well developed ridges; proximal sub-marginal seta on ventral side.

Legs 1-4 with long setose exopods; no trace of chela. Pleopods biramous and setose. Uropods shorter than telson, exopod with outer terminal spine and a few proximal outer setae.

Zoeal stage ?XIV, C.L. 3.5 mm, R.L. 6.2 mm, R.T. 17/10: IIOE Diamantina 2/63-St. 71.

Carapace with minute anterior dorsal papilla, large posterior papilla; carinae well marked, lateral spine relatively small, supra-orbital and pterygostomian spines reduced, antennal spine well developed. Abdominal somites 3 and 4 with long dorsal spines, pleura of 4th and 5th with pointed spines, 6th somite twice as long as maximum width, with two postero-lateral pointed processes; anal spine well developed. Telson 2.6 mm long, excluding spines; maximum width 0.7 mm, tapering to about 0.2 mm; five pairs dorso-lateral and four pairs terminal spines.

Eye-stalk much more reduced than in stage IX. A_1 reaching almost to tip of A_2S , with large ventral spine and large but still blunt stylocerite; both flagella segmented but broken. A_2S (Fig. 1(e)) narrowing distally, about 3 mm long including terminal spine, maximum width 0.7 mm; 16 lateral spines, larger and smaller spines generally alternating; two well marked dorsal ridges, proximal ventral submarginal seta; basis bears long ventral spine; flagellum broken off. Legs 1-4 with large setose exopods, no trace of chela. Pleopods biramous and setose; 1st pair with very small endopod, 2nd-5th pairs with rudimentary *appendix interna*. Uropods shorter than telson; exopod with lateral terminal spine and few proximal setae.

Stage ?XVII or XVIII (megalopa), C.L. 7.5 mm, R.L. 14 mm, R.T. 18/11: Discovery St. 281, south-eastern Atlantic (see Gurney, in Gurney & Lebour, 1941) (Figs 2(a) and 3(a)-(c)).

Gurney's specimen is estimated to be in the XVII or XVIII stage, which may correspond to the 2nd or 3rd megalopa. There is no need to redescribe this specimen in detail, but the following notes cover errors in the description given by Gurney and some additional characters which he overlooked.

Carapace with minute anterior and small posterior papilla; supra-orbital spine still large; Gurney's description of the carinae states "there are three well marked carinae, the two ventral ending in front in a large marginal spine; the dorsal carina ends in a large lateral spine, but is continued to the supra-orbital spine as a less marked line". This overlooks the prominent carina near the ventral margin of the carapace and does not mention the less prominent ridges both above and below the lateral spine, although these latter are shown in his figure. There is little difference in the carapace carination from that of the stage IX zoea, except that the first carina joins the posterior end of the carapace more dorsally and the 4th extends anteriorly to the base of the rostrum and posteriorly to join the 1st (Fig. 3(a)). The 2nd, 3rd, 5th and 6th carinae are more prominent and the others have become less distinct. Gurney probably meant the antennal and pterygostomian spines when he wrote "the two ventral ending in front in a large marginal spine". There is also a very small spine just above the antennal spine which may be called the infra-orbital spine.

Abdominal somites 3 and 4 with large posterior dorsal spines (not somites 2 and 4 as mentioned by Gurney), small "step" just in front of spine on 4th somite. Pair of faint tubercles, one below the other, on dorso-lateral aspect of 1st abdominal somite (Fig. 3(b)). Telson with five pairs dorso-lateral and four pairs terminal spines (Fig. 2(a)). Gurney's observation is erroneous in this case also, as he again overlooked a pair of spines.

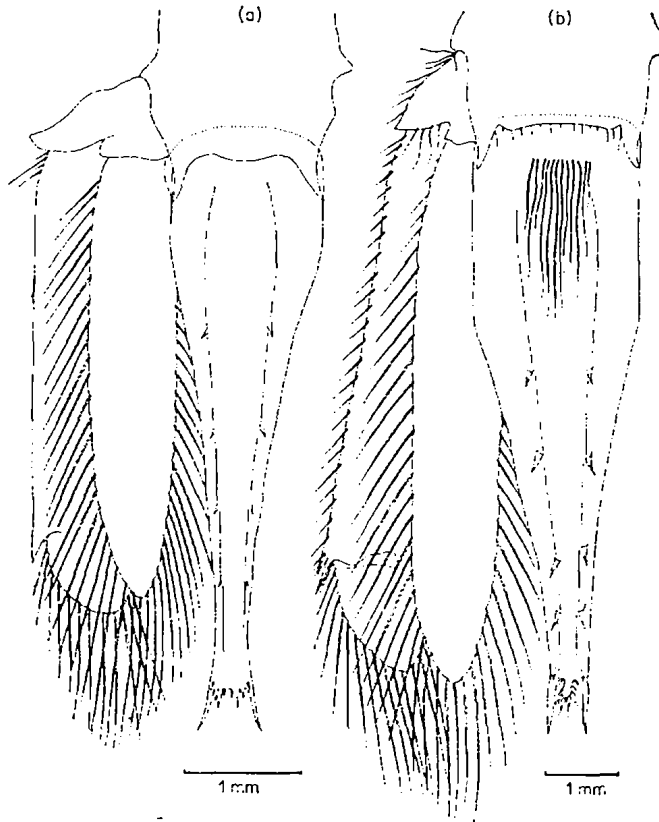


FIG. 2. *Heterocarpus (Heterocarpus) ensifer* A. Milne Edwards. (a) telson and left uropod of larval stage ?XVII (=megalopa ?II), C.L. 7.5 mm (Discovery St. 281, Atlantic); (b) telson and left uropod of juvenile, C.L. 14.5 mm.

A_2S (Fig. 1(f)) 4.5 times as long as maximum width of 1.3 mm, narrowing distally; large terminal spine; two well-defined ridges dorsally, running whole length; proximal ventral submarginal seta present; outer margin with 20 rather irregular small spines. Flagellum segmented, four times as long as A_2S and reaching beyond rostrum. Leg 1 without chela, but leg 2 with small chela (Fig. 3(e)). Gurney apparently failed to notice that the 2nd legs are unequal: the left has a larger carpus (1.44 mm c.f. 0.9 mm) and a smaller chela (0.8 mm c.f. 1.1 mm). Pleopods functional, first with small endopod, 2nd–5th with well developed endopod and *appendix interna*. Exopod of uropod with small protuberance on inner side of base of terminal spine (Fig. 2(a)). The specimen is about to moult and it appears that in the next megalopa the exopod of the uropod will have two terminal spines, caused by the splitting of the large single spine. The protuberance at the base of the large spine observed in this stage covers the tip of the second spine beneath the cuticle.

Juvenile, C.L. 14.5 mm, R.L. 1.7 mm, R.T. 18/11: IIOE Meteor St. 161 (Figs 2(b) and 3(d), (e)).

I have illustrated different parts of the specimen for comparison with the oldest megalopa (Gurney's specimen), to establish they are conspecific. The points of similarity are summarized as follows:—

(1) Rostrum (Fig. 3(a), (c)). Both have the rostrum longer than the carapace with the same tooth formula. Four of the dorsal teeth are on the carapace and the 5th just above the posterior margin of the orbit. It can be seen that the megalopa would show no change in the number of rostral teeth at the next moult.

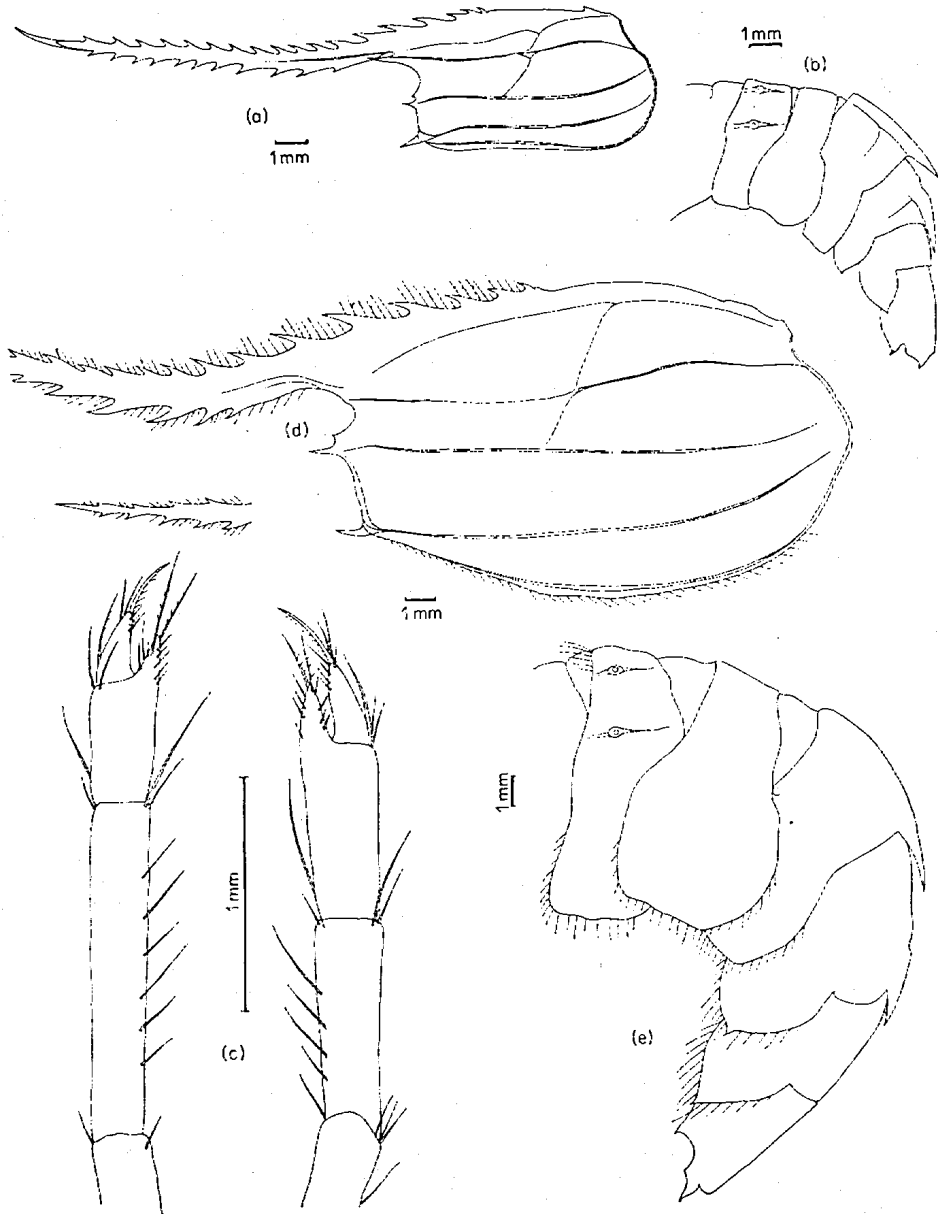


FIG. 3. *Heterocarpus (Heterocarpus) ensifer* A. Milne Edwards. (a)–(c) larval stage ?XVII (=megalopa ?II), C.L. 7.5 mm (Discovery St. 281, Atlantic); (d), (e) juvenile, C.L. 14.5 mm: (d) carapace and rostrum; (e) abdomen.

(2) Carapace (Fig. 3(a), (c)). In both cases there are anterior and posterior papillae, though these are very much reduced in the juvenile. Pterygostomian, antennal and infra-orbital spines are present in both. The supra-orbital spine in the megalopa is a larval character and has disappeared in the juvenile, but still a minute projection can be seen in that position. The pattern of the carinae is similar, some of them reduced, but the four main ones well marked. The lateral spine on the carapace of the megalopa is again a larval feature and has disappeared in the juvenile, but a scar or ridge can be recognized in that position.

(3) Telson (Fig. 2(a), (b)). The posterior margin of the telson is altered in the juvenile by the development of a central lobe, and a group of long dorsal setae are added near the anterior end. These changes are, however, quite consistent with regarding both stages as belonging to the same species, and the good agreement in the number and arrangement of dorso-lateral spines supports this conclusion.

(4) A₂S. There is good agreement in shape, the presence of a long terminal spine and of two dorsal ridges. The outer spines on the scale of the megalopa is a larval character.

(5) Second paraeopods (Fig. 3(e)). The juvenile *H. ensifer* has very unequal second paraeopods, each with a multi-segmented carpus. The carpus is still undivided in the megalopa but the legs are already unequal. The much longer carpus on the left side is particularly noticeable.

(6) Abdominal somites (Fig. 3(b), (d)). In both stages the first and second somites are devoid of any dorsal carina. A pair of round dorso-lateral tubercles, one below the other, occur on the 1st segment. These tubercles are fairly easily identifiable in the juveniles and adults, but rather difficult to see in the megalopa. This seems to be an "adult" character. The 3rd somite has an elevated dorsal carina produced into a long posterior spine in both cases; in the megalopa the dorsal carina is more pronounced. The 4th somite again has a carina produced posteriorly into a spine, but both the carina and spine are somewhat reduced in the juvenile; a "step"-like formation is quite noticeable in both cases just before the origin of the spine. The pleura of the 4th and 5th somites are produced into a pointed spine in both cases. The 6th somite is not unusually long, has no carina, but has two pointed lateral processes distally.

Remarks. While there is no room for doubt as to the relation of *Atlantocaris gigas* to *H. ensifer*, the presence of the lateral carapace spine and the increasing number of spinules on the outer margin of the A₂S in the larval stages are confusing features. In both cases they appear to be larval characters, without parallel in any other group. Examples are, however, known in which outer spines are present on the antennal scale of the adult but not the larva (e.g. *Oplophorus*, *Thalassocaris*).

The carinae on the carapace provide another example of a larval character not found in any other group, but in this case the character is not confined to the larvae alone, as the main carinae are also well developed in the adult. The carina just above the ventral margin of the carapace has seldom been mentioned or figured by previous workers. The same is true of the infra-orbital tooth which first appears in the megalopa, although this was mentioned by Bate (1888) as the "first antennal tooth", and by Figueira (1957) as an "acute tooth-shaped process".

It is interesting to note that in the juvenile, examined under low power, the whole body is decorated with minute pits from which very slender setae arise.

Now that most stages in the development of *H. ensifer* are known, we may re-examine

the status of var. *parvispina* De Man (1920) and of *H. sibogae* De Man (1917). The variety was differentiated from the typical form solely on the reduction of the spine on the 4th abdominal somite. It has been noted, however, that this spine tends to be reduced during development, particularly between the megalopa and the juvenile, and it seems doubtful whether the degree of reduction represents a sound basis for a taxonomic distinction. This appears to agree with the view of Figueira (1957) and Hayashi & Miyake (1969), who synonymized the variety with *H. ensifer*.

H. sibogae was separated from *H. ensifer* chiefly by the presence of a sharp dorsal carina on the first and second abdominal somites. The Indian Ocean specimens in the present collection, like Rathbun's (1906) samples from the Hawaiian Islands, show no trace of a carina on these somites in any stage of development, but there are no fully mature specimens. No carina was mentioned or figured by A. Milne Edwards (1881) in his original description of *H. ensifer*, but Rathbun (1906) showed that specimens from the Caribbean (the type locality) had a small carina. She also showed that there was considerable variation in the size of the carina in specimens from different localities. De Man (1917, 1920) grouped together those forms with a small carina and with no carina as *H. ensifer* and separated those with a sharp carina as *H. sibogae*. While it is not at present possible to make a final decision on the validity of *H. sibogae* as a separate species, it would seem more satisfactory to distinguish between forms with and without a carina, rather than to use De Man's grouping based on the size of the carina.

Whatever the status of *H. sibogae* and *H. ensifer* var. *parvispina*, their larvae are likely to be very similar to "*Atlantocaris gigas*" and probably difficult to differentiate.

The distribution of the species is discussed towards the end of this paper (Fig. 11).

Heterocarpus (Procletes) levicarina (Bate, 1888)

(Figs 4 to 9)

Material examined IIOE: about 80 specimens from 62 stations. British Museum: Bate's (1888) type specimen of *Procletes biangulatus* from the Aru Is., Pacific Ocean; an ovigerous female from Martaban, recorded by Henderson (1893).

Bate (1888), under the name *Procletes biangulatus*, described a larva which is apparently in the first megalopa stage. The two specimens recorded by Gurney in Gurney & Lebour (1941) are in early zoeal stages. The material from the IIOE agrees well with Bate's and Gurney's descriptions. It contains representatives of nearly all larval stages, except the first zoea and the last megalopa. No juvenile or adult specimens are included.

As is usual with collections of this type, larvae can be assigned to stages with certainty only up to the stage IV zoea. The larval development appears to be very gradual, as in the case of *H. ensifer*, and it has been estimated that there are 13 zoeal and 3 megalopal stages before the first juvenile stage is attained (see Material and methods). It is to be noted that a number of characters of both the carapace and abdomen gradually develop during the zoeal stages and then become reduced during the megalopal stages.

As it is difficult to measure the total length of the larvae due to their shape, carapace length (C.L.) has been used. The average C.L. for each of the assumed zoeal stages II–XIII is 0.5, 0.6, 0.7, 0.8, 0.9, 1.0, 1.2, 1.4, 1.6, 1.8, 2.2 and 2.7 mm, and for megalopal stages I–III it is 3.6, 4.4 and 5.6 mm. These stages probably represent a fairly typical pattern of development, but variations between individuals are to be expected.

Carapace not very broad or very shallow in any larval stage; length (excluding rostrum) about twice breadth, with small anterior and fairly large posterior dorsal papilla in all stages. Rostrum increasing in length throughout zoeal stages, probably less than half C.L. in stage I, about half C.L. in stage II (Figs 4(a) and 8(a)), almost equal to C.L. in stage V (Fig. 4(b)), at least twice C.L. in late zoeal stages (Figs 4(c), (d), (e)); R.L. progressively

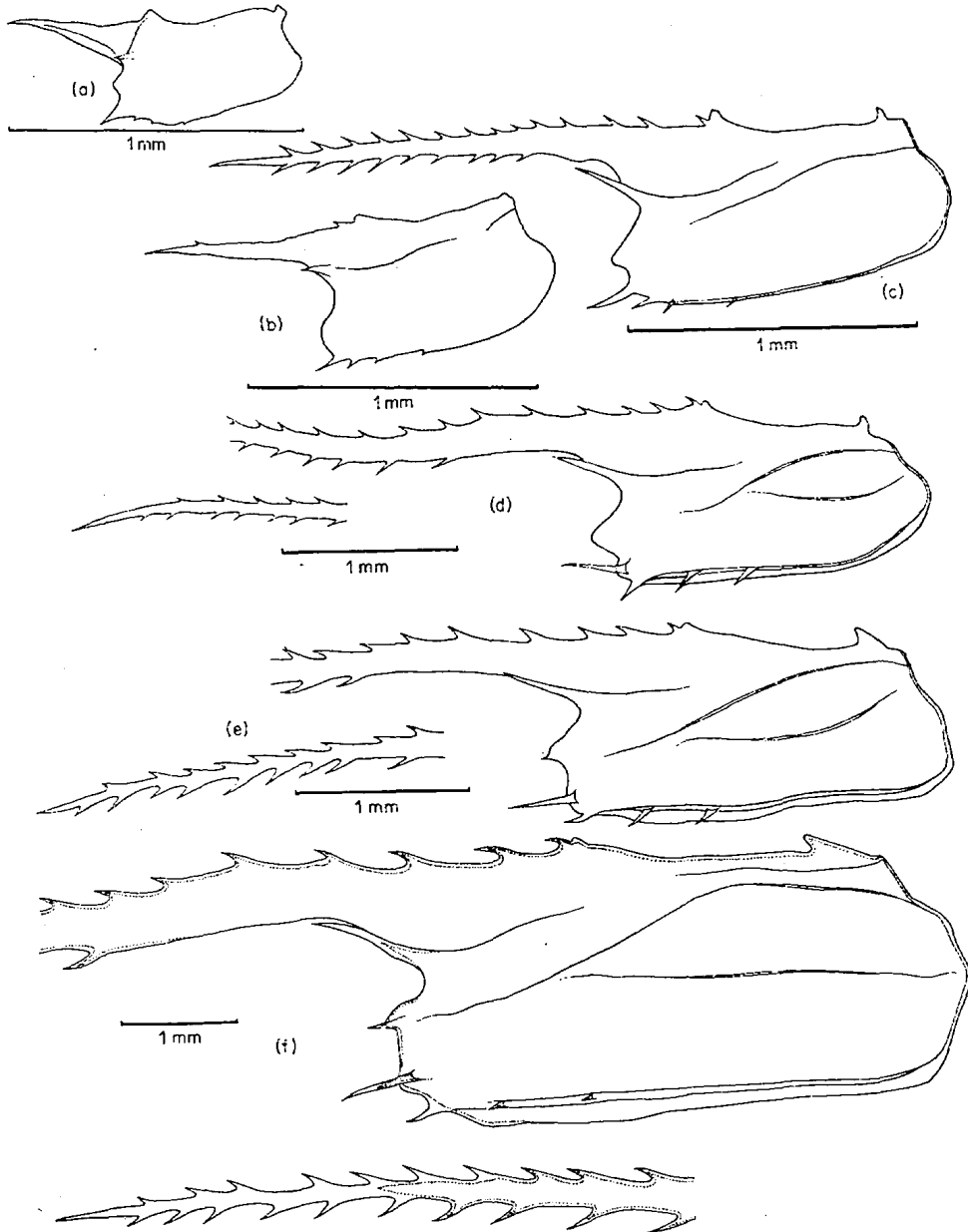


FIG. 4. *Heterocarpus (Procletes) levicarina* (Bate). (a)–(f) carapace and rostrum in larval stages III, V, VII, X, XI and XV (=megalopa II).

reduced in megalopal stages, about 1.7 times C.L. in penultimate megalopa (Fig. 4(f)). R.T. minute in stage V (Fig. 4(b)), distinct in all subsequent stages; 5/0 in stage V increasing to 17-20/11-15 in last two or three zoeal stages (occasional specimens with larger number of teeth considered in Discussion); 18/11 in penultimate megalopa, apparently 11/5 in last megalopa (from moulting megalopa II: Fig. 4(f)); usually 3 R.T. on carapace in later zoeal stages, 4th just above or slightly behind posterior orbital margin. Supra-orbital spine probably absent in stage I, small in stage II (Fig. 8(a), (b)), increasing in subsequent stages until last zoea (Fig. 4(a)-(e)), apparently decreasing rapidly in megalopal stages (Fig. 4(f)). Infra-orbital tooth probably develops in last megalopal stage, present in adult. Antennal spine first appears as lobe on anterior carapace margin, increasing in size in successive stages to stage X (Figs 4(a)-(d) and 8(a), (b)), ending in spine in stage XI (Fig. 4(e)), spine larger in following stages. Two spines on ventral margin, behind pterygostomial spine, in stage II (Fig. 8(a), (b)), third spine appears in stage III (Fig. 4(a)); all persist until penultimate megalopa, absent in juvenile stages. There is some migration of spines during development: by stage VII the two posterior "marginal" spines have become submarginal; the original pterygostomial spine becomes submarginal in stage VIII or IX and moves dorsally in subsequent moults to occupy a branchiostegal-hepatic position in the late zoeal and megalopal stages; the 1st marginal spine becomes quite large and occupies the pterygostomial position in the late zoeal stages; it persists until megalopa II but is apparently lost at the next moult (Fig. 4(f)).

No carinae on carapace in stages I-IV. In stage V first carina represented by faint line from upper base of supra-orbital spine to middle of carapace, second carina a short curved ridge just ventral to posterior dorsal papilla (Fig. 4(b)); first carina of constant length in zoeal stages but probably absent in juvenile stages, as in *H. ensifer*; second carina becoming progressively longer, curving downwards at about middle of carapace then running towards antennal spine: about 3/4 length of carapace in stage VII, almost reaching base of antennal spine in megalopal stages (Fig. 4(c)-(f)). Third ridge appears in stage VII, running close to carapace margin from "2nd pterygostomial spine" to just behind posterior dorsal papilla, two antero-ventral teeth on ridge. Fourth carina appears in stage VIII or IX, occupying mid-lateral position from near second carina (under anterior dorsal papilla) almost to posterior margin. All carinae conspicuous in late larval stages. In penultimate megalopa (Fig. 4(f)), second carina joins antennal spine and fourth joins second, as in adult. Other authors have ignored what is here regarded as the third carina and have not shown it as distinct from the ventral carapace margin. It is, however, well developed and quite distinct from the margin in all later larval stages and in juveniles and adults, although the margin is often folded under in preserved specimens.

Abdominal somite I smooth in stage II (Fig. 5(b)); small antero-lateral projection appears in stage VI (Fig. 5(c)), long and pointed in all later zoeal stages, reduced in megalopal stages but persists in vestigial form in adult. A similar protuberance has been reported in several decapod groups and it may help to support the carapace (Heegaard, 1966). Second abdominal somite smooth in stage II, dorsally slightly carinate in stage VI, carina rather more elevated in stage VII, forms well-developed slightly pro-curved spine in stage VIII (Fig. 5(e)), spine prominent in late zoeal stages (Fig. 5(f), (g)), progressively reduced in megalopal stages (Fig. 5(h), (i)); moulting specimen suggests spine absent and carina feeble in last (3rd) megalopa. Third abdominal somite with beak-like carina ending in small posterior spine in stage II, spine larger in subsequent stages; carina slightly



FIG. 5. *Heterocarpus (Procletes) levicarina* (Bate). (a) 2nd legs of megalopa I. (b)–(i) armature of abdominal somites in larval stages II, VI, VII, VIII, XI, XIII (=last zoea), XIV (=megalopa I) and XV (=megalopa II). (h) and (i) show outlines of following stage, visible through cuticle.

pointed anteriorly in stage VI, anterior point larger in stage VII, produced into long point in stage VIII and all later zoeal stages (Fig. 5(b)–(g)); anterior spine procurved and longer than posterior in last zoeal stage, very much shortened in 1st megalopa (Fig. 5(h)), reduced to a step in last megalopa; posterior spine remains large. Fourth somite with posterior carina ending in small spine in stage II, small protuberance just in front of spine; spine and protuberance better developed in later stages and present in adult; spine about half as long as posterior spine on 3rd somite in late larvae, juveniles and adults. Fifth somite bears posterior spine from stage II to adult, similar in size to that on 4th somite. Sixth somite much the longest, three to four times as long as its maximum width in zoeal stages, without dorsal carina, with two lateral pointed projections from stage IV. Abdominal pleura 1–3 never pointed in any stage; 4th pleuron pointed in zoea XI (Fig. 5(f)), produced into tooth in remaining zoeal stages, tooth much reduced in megalopa II, absent in adult; 5th pleuron produced into tooth in stage XI and all subsequent stages including adult. Anal spine first appears in zoeal stage IV, long and pointed in subsequent larval stages, very short in adult.

Telson (Fig. 6(a)–(i)) in stage II with 8+8 long spines, 1st pair lateral, 8th pair small. Almost as long as maximum width and articulates with 6th somite in stage III; 1st pair spines much shortened. More than twice as long as maximum width in stage IV, rather broader posteriorly than anteriorly, with three pairs lateral spines. About 3.75 times as long as maximum width in stage VI, almost parallel sided. Becoming progressively longer and narrower posteriorly in subsequent stages. Telson about 1.5 mm long in stage VIII, the three pairs lateral spines well separated, 8th pair minute, 4th pair longest followed by 6th, 5th and 7th. Almost same length in stage IX, but 1st and 2nd spines further forward and additional small pair present between former 2nd and 3rd pairs: total 9+9 spines, including 4+4 lateral. Telson about 2.7 mm long in last zoeal stage (XIII), about 0.6 mm wide anteriorly tapering to about 0.2 mm posteriorly; 9+9 spines, first four pairs (previously lateral) now dorso-lateral, 5th pair robust and long, 6th–9th pairs very small. Ninth pair spines absent in megalopal stages, dorso-laterals and outermost pair on posterior margin well developed; little change in telson shape compared with late zoeal stages.

Eyes stalked in stage II; stalk never very long; eyes comparatively small in later stages. Antennules (Figs 8(b) and 9(c)) widely separated at base, curved, with unsegmented peduncle bearing outer segment and inner long seta in stage II; two-segmented peduncle with ventral spine on basal segment in stage III; three-segmented peduncle with stylocerite and long ventral spine on 1st segment in following stages; stylocerite long and pointed and peduncle bearing two-segmented flagella from late zoeal stages.

Protopod of antenna (Fig. 7(a)–(h)) bearing inner spine at base of endopod in stages II–VII, blunt and vestigial in later stages; ventral spine at base of scale from stage IV onwards; small inner dorsal tubercle on protopod in last zoeal stage, large and pointed in megalopal stages. Endopod ending in spine and seta in stage II, simple rod in stages III–VI, longer and with proximal segment formed in stage VIII, two setae at tip in stage X, fully segmented and twice length of scale in last zoea. A_2S segmented at tip in stages II and III, with three setae on outer margin in stage II and two in stage III, distal seta replaced by small spine in stage IV, proximal seta present until last zoeal stage and absent in megalopal stages; outer margin of A_2S with four small notches in stages VIII–X (Fig. 7(e), (f)); distal lobe of scale progressively narrower from stage XII, terminal spine long and pointed; length of scale (excluding terminal spine) five times maximum width in last zoeal stage,

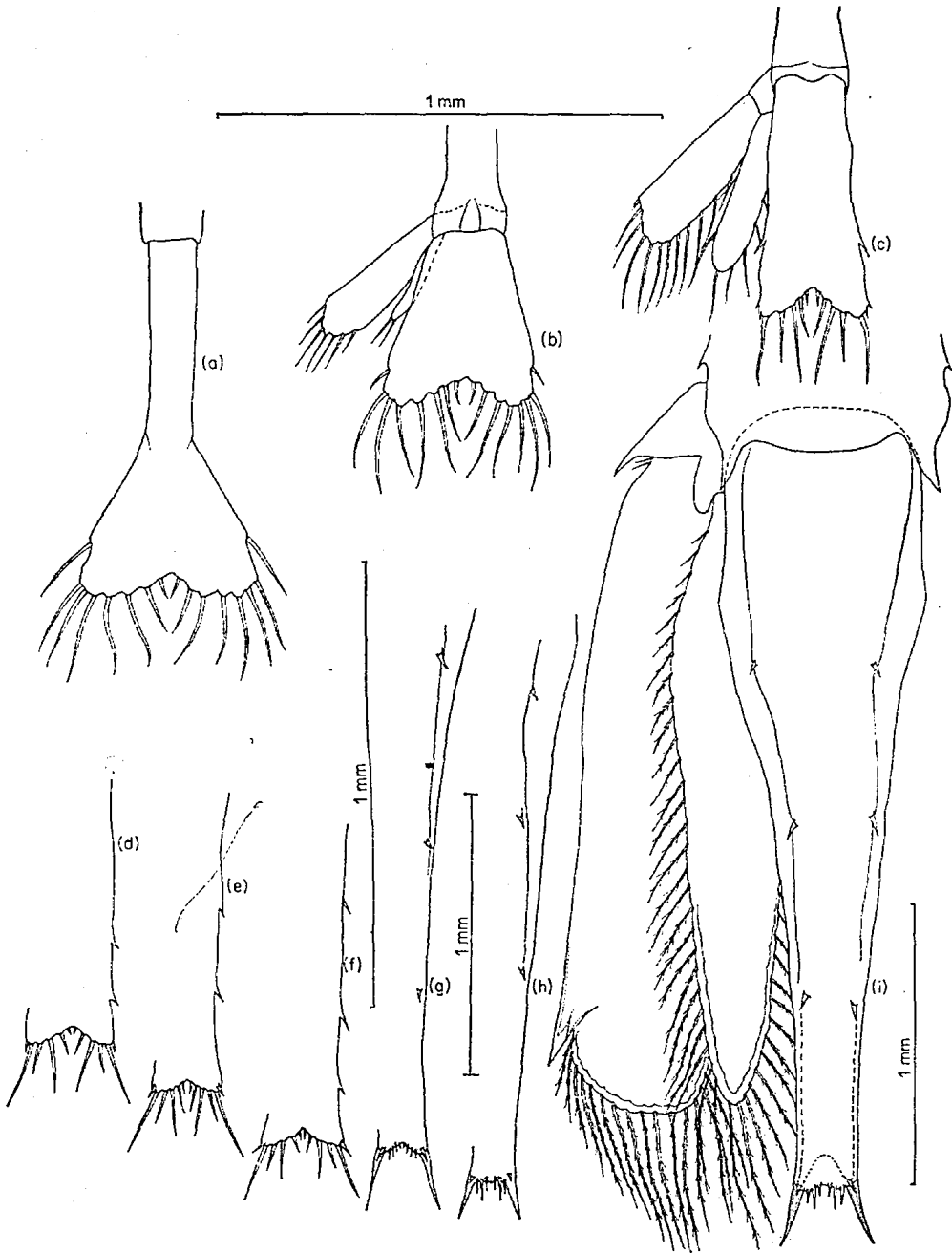


FIG. 6. *Heterocarpus (Procletes) levicarina* (Bate). (a)–(i) telson etc. in larval stages II, III, IV, VI, VIII, X, XIII (=last zoea), XIV (=megalopa I) and XV (=megalopa II).

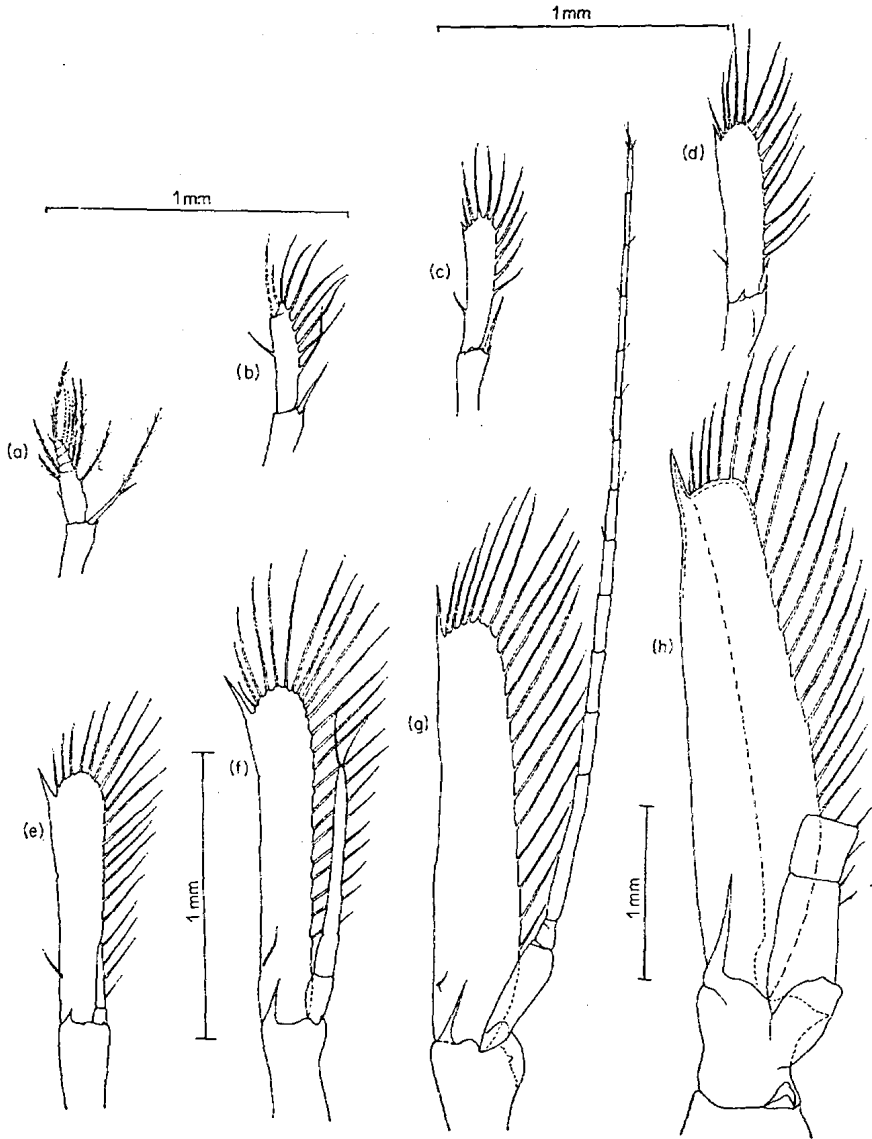


FIG. 7. *Heterocarpus (Procletes) levicarina* (Bate). (a)–(h) antenna (ventral) in larval stages II, III, IV, VI, VII, X, XIII (=last zoea) and XV (=megalopa II).

terminal spine about 0.3 mm long; dorsal ridge from base of scale to base of distal spin present in megalopal stages.

Mandibles (Figs 8(c) and 9(b)) asymmetrical, incisor and molar processes well marked megalopa II still without palp. Maxillule (Figs 8(d) and 9(d)) with unsegmented palp i zoeal and first two megalopal stages; swelling on outer margin in stage II may represer exopod, not present in later stages. Maxilla (Figs 8(e) and 9(e)) with broad unsegmente endopod narrowing to tip in all zoeal and megalopal stages; four well marked endites i

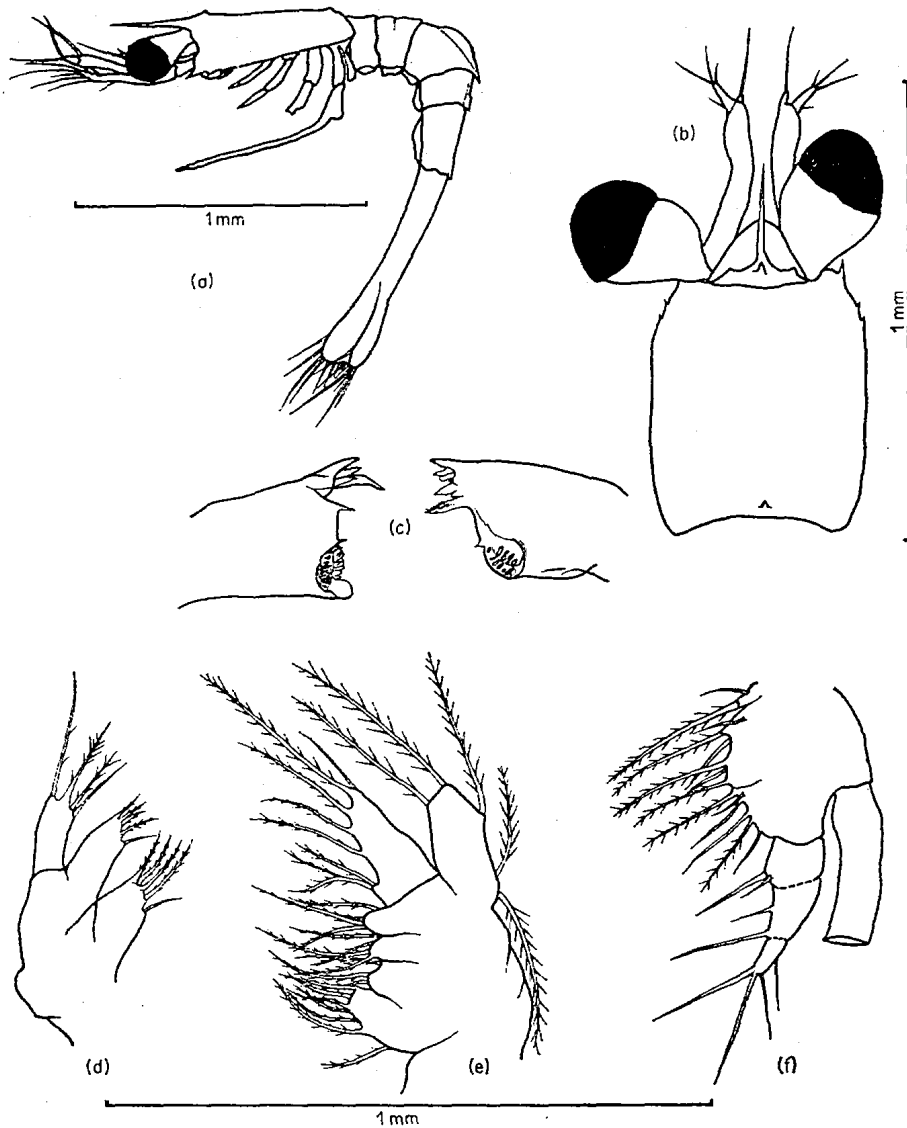


FIG. 8. *Heterocarpus (Procletes) levicarina* (Bate). (a)–(e) zoeal stage II: (a) lateral view; (b) carapace, eyes and antennules, dorsal; (c) mandibles; (d) maxillule; (e) maxilla. (f) zoeal stage III, 1st maxilliped.

zoeal stages, third much reduced in megalopa II and probably fused with fourth in last megalopa; exopod comparatively small in zoea II but large and ear-shaped in later stages.

Maxillipeds 1–3 (Figs 8(f) and 9(f), (g)) with setose exopods from zoea II; maxilliped 1 with 3-segmented endopod in all stages; maxilliped 2 with 5-segmented endopod, 4th segment unusually large and bulbous; all with large bilobed epipods from later zoeal stages. Leg 1 biramous in stage II, endopod rod-like; leg 2 a small bud, other legs not represented in this stage. Leg 1 without any trace of chela in any stage. Leg 2 with rudimentary chela in last zoea and megalopae (Figs 5(a) and 9(h)); left and right equal in all proportions in

megalopa I; left missing in specimen of megalopa II, carpus not yet segmented. Megalopae with row of spines on outer margin of ischium of leg 3; propodus about twice as long as carpus, with row of spines on inner margin; dactylus nearly half as long as propodus, very slender and slightly curved; other legs similar to 3rd. Functional exopods on legs 1-3 in stage VII, on legs 1-4 in stage IX; no exopod on leg 5 in any stage; exopods on legs 1-4 reduced in megalopae.

Pleopods first appear in stage X as small buds; large and with one or two setae in stage XII; fully setose and with *appendix interna* in megalopa I. Uropods present from zoea III: endopod in stage III about $\frac{3}{4}$ length of exopod, with two terminal setae, exopod without distal spine; rami articulate with protopod from stage IV onwards; rami subequal and exopod with outer terminal spine from stage VI onwards; small swelling at inner side of base of terminal spine in megalopa II (Fig. 6(i)), second spine (visible through cuticle of megalopa II) will appear in this position in megalopa III. Exopod without diaeresis and outer margin without setae in zoeal and megalopal stages; diaeresis but no outer setae present in adult.

Remarks. Comparison of the second megalopal stage from the present collection (Fig. 9(a)) with an adult of *H. levicarina* provides overwhelming evidence that they are the same species. The similarity of the carinae on the carapace, the posterior spines on the 3rd, 4th and 5th abdominal somites, the "step" before the spine on the 4th somite, the shape of the 5th pleuron, the armature of the telson and uropods, the shape of the scaphognathite, and the symmetry of the 2nd legs may be particularly mentioned. The anteriorly directed abdominal spines, which are so conspicuous in the late zoeal stages, are already vestigial by megalopa II and will probably disappear almost completely at the next moult (Fig. 5(i)), to approach the adult condition. The rostrum of the megalopa is about twice as long as the carapace, with 18/11 teeth, whereas in the adult of *H. levicarina*, R.L. is about $\frac{3}{4}$ C.L. and there are 10-14/4-6 teeth. In the majority of Caridea the rostrum increases in length and number of teeth in the megalopal and juvenile stages, but the moulting megalopa II in the present collection (Fig. 4(f)) shows that the rostrum of the following stage will be considerably reduced in length with only 11/5 teeth, the adult number. The only other species which seem to merit consideration in relation to the parentage of the present larvae are *H. dorsalis* Bate and *H. affinis* De Man, both of which have abdominal spines similar to those of *H. levicarina*. These two species, however, must be eliminated from such consideration because their pattern of carapacial carinae does not agree with that of the larvae and their second legs are markedly asymmetrical. It was noted in the development of *H. ensifer* that the asymmetry of the second legs was already apparent in the megalopal stages, whereas the symmetry of these legs in the megalopal stages of the present species has previously been mentioned as a link with *H. levicarina*.

From the point of view of geographical distribution and abundance of adults, *H. wood-masoni* Alcock should also be considered, but the lack of dorsal abdominal spines on the 4th and 5th somites, the differences in the carapacial carinae and the marked asymmetry of the second legs of this species preclude it from the parentage of the present larvae. It is, however, surprising that these larvae have a wide distribution along both the east and west coasts of India, while no adults of *H. levicarina* have been recorded from that region. On the other hand, *H. wood-masoni* has been recorded in large numbers in exploratory fishing in the deep waters off the west coast of India, but no larva that could be referred to it has been recorded.



FIG. 9. *Heterocarpus (Procletes) levicarina* (Bate). (a)–(h) megalopa II: (a) lateral view; (b) mandibles; (c) antennule (ventral); (d) maxillule; (e) maxilla; (f) 1st maxilliped; (g) 2nd maxilliped; (h) 2nd leg.

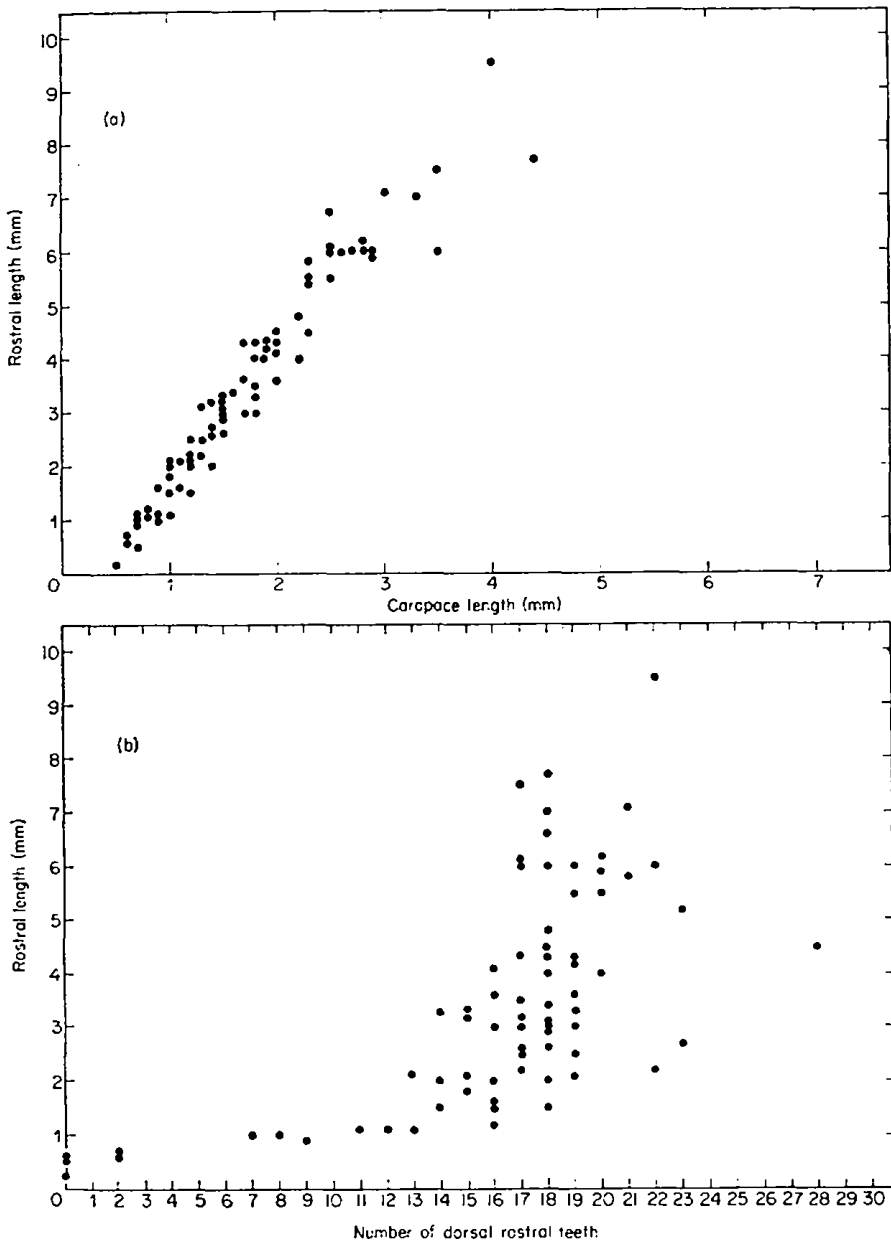


FIG. 10. *Heterocarpus (Proclates) levicarina* (Bate). (a) Relation between rostral length and carapace length. (b) Relation between rostral length and number of dorsal rostral teeth.

De Man (1920) suggested that the development of the rostrum in one juvenile of *H. levicarina* which he examined probably merited its separation as "var. *longirostris*". The larval material from the IIOE can not be satisfactorily subdivided on the basis of rostral length (Fig. 10(a)), but in a few specimens the number of dorsal rostral teeth is much greater than in others of the same R.L. or C.L. (Fig. 10(b)). It is not possible to say whether these larvae would have developed into juveniles of "var. *longirostris*", but they tend to

give some support to the suggestion that an infraspecific division based on rostral characters may be valid. Such larvae were not confined to one region of the Indian Ocean.

De Man (1917) differentiated his new subgenus *Heterocarpoides* (= *Procletes* Bate) from the subgenus *Heterocarpus* on the absence of certain carinae on the carapace and the symmetry of the second pair of legs. To these points of adult morphology may be added the presence of an additional pair of dorso-lateral spines on the telson and the absence of external setae on the exopod of the uropod. The differences in the carination of the carapace may also be used to separate the two subgenera in the late larval stages, in which *Procletes* also possesses anteriorly-directed dorsal spines on the abdomen. In all zoeal stages *Procletes* has spines on or near the ventral carapace margin, whereas there are none in the larvae of *Heterocarpus ensifer*. As larvae are known for only one of the 21 species of *Heterocarpus* s.s., no consideration of larval variation within the subgenus is possible. This limits the value of larval characters in assessing whether *Procletes* merits generic or only subgeneric separation. As stated by Gurney (in Gurney & Lebour, 1941) "The two species, *P. biangulatus* and *A. gigas*, may be accepted as belonging to the same genus, or to two very closely allied genera". A subgeneric distinction seems to express this situation satisfactorily.

Distribution

Figure 11 shows the distribution of juveniles and larvae of *H. ensifer* and larvae of *H. levicarina* in the Indian Ocean with regard to the present collection. Only the presence or absence of the species in samples from each 5° square is marked; the symbols do not represent the exact position of the samples, and give no indication of the number of samples taken within each square or the number of larvae captured. The plankton samples were restricted to the upper 200 m and the adults are probably more common in deeper water. The patterns of distribution shown by the planktonic larvae are, however, probably also relevant to the adults.

Only four larvae of *H. ensifer* are represented in the present collection: two from south of Java, near 110°E, and two from the central Indian Ocean, just north of the Equator. The sonic depths for these sampling areas are between 1280 and 5596 m. One juvenile was collected off Mombassa, East Africa, in a sonic depth of only 243 m. The only other published records of this species from the Indian Ocean are both recent: off Quilon, south-west India (C.M.F.R.I., 1969) and off north-west Sumatra (Hayashi & Miyake, 1969). The former of these records is from just within the Arabian Sea and the latter from the south of the Bay of Bengal. The absence of specimens of *H. ensifer* from IIOE samples from the Arabian Sea and the Bay of Bengal, in spite of thorough and repeated coverage of both areas, probably means that the species does not penetrate an appreciable distance into either area. The new records from the Indian Ocean are all from further south than the two previous records and include both the extreme east and extreme west as well as the centre of the equatorial part of the area.

This species has been recorded by different workers from the North Atlantic: different localities in the Caribbean Sea, the Gulf of Mexico, off North Carolina, off the coast of Morocco and off Banana; from the South Atlantic: off the west coast of Africa; from the Pacific: between the Phillipines and Borneo, New Britain, Hawai and Sagami Bay, Japan,

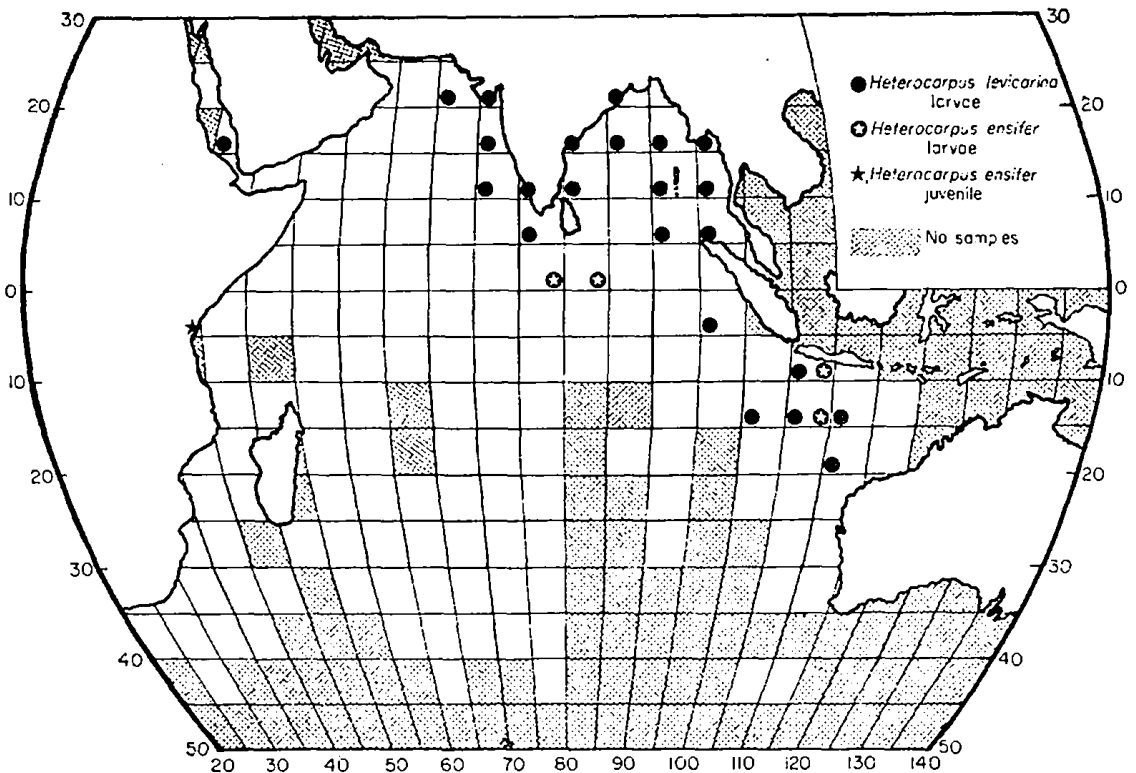


FIG. 11. Distribution of *Heterocarpus (Heterocarpus) ensifer* A. Milne Edwards and *Heterocarpus (Proclates) levicarina* (Bate) in samples collected by the International Indian Ocean Expedition.

at depths between 55 and 850 m. De Man's variety *parvispina* has been recorded only from the Bali Sea, north of the Sulu Is. and off the Kei Is., all in the west Pacific, at depths between 275 and 521 m.

The distribution map of *H. levicarina* is based on 62 samples, each comprising one to six larvae, collected during 1963-65. Of these, 40 samples were collected in 1963, 18 in 1964 and four in 1965. An attempt was made to study the seasonal distribution of the larvae for the year 1963, when areas where the species was most commonly taken were sampled each month. No larvae were taken in January, February, June, October and November, and only a few late zoeae in July, August and December. There were two peak periods, in May and September, when almost all larval stages were obtained. Both these peaks occurred within the period of the south-west monsoon.

Zoogeographically, *H. levicarina* shows a wide distribution in the north-eastern half of the Indian Ocean with no records from the south-western half. Most records were from near coast-lines but some were from the open ocean and sonic depths ranged from 43-5943 m. The distribution forms an almost continuous belt from north of North-West Cape, Australia, to north-west India, including the south-west coasts of Java and Sumatra, the entire Bay of Bengal and the west coast of India. The species also occurred at one station in the Red Sea.

Adults had previously been collected from the Gulf of Martaban, Burma (Henderson, 1893), off the Irrawady delta and the Mergui Archipelago, Burma (Kemp, 1925), the Gulf

of Oman (Calman, 1939) and the Red Sea (Balss, 1915). The record from the Gulf of Oman indicates a rather greater range in the northern Arabian Sea than that shown in Fig. 11; the other earlier records are all within the range covered by the IIOE records. The distribution of *H. levicarina* is now seen to be much more extensive and more continuous than previously indicated. The species also extends eastwards from the Indian Ocean, through Indonesia to the Coral Sea; the records are from the Bay of Bima, between Misool and Salawatti, Lebetobi Strait and Saleh Bay (De Man, 1920), Straits of Macassar (Lenz & Strunck, 1914), Arafura Sea (Bate, 1888), the northern end of the Great Barrier Reef (Gurney, in Gurney & Lebour, 1941) and off Cairns, north-eastern Australia (McNeill, 1968). Its penetration into the western Pacific therefore seems to be very limited. The known depth range is 13–274 m.

Taxonomic affinities

A. Milne Edwards (1881), while creating the new genus *Heterocarpus* from the species he named *H. ensifer*, stressed its similarity to the Oplophoridae. Smith (1882), unaware of Milne Edwards' paper, gave the name *Pandalus carinatus* to the same species; later (1884) he recognized the genus *Heterocarpus* but drew attention to its pandalid characters. Nearly all subsequent authors have followed Smith (1884) in placing *Heterocarpus* in the Pandalidae, but a notable exception is Thompson (1967) who recommended the erection of a new superfamily, the Heterocarpodoidea (sic), to include the Heterocarpodidae (sic), Rhynchocinetidae and Campylonotidae.

The larvae of *Heterocarpus* (including *Procletes*), described in the present paper, give considerable support to the inclusion of the genus in the Pandalidae, and the following larval characters are shared with such genera as *Pandalus* Leach, *Pandalina* Calman and *Plesionika* Bate: the cephalothorax is neither expanded nor compressed; a long toothed rostrum is developed early in the zoeal stages; the antennules are long, well separated and curved; the antennal endopod is short until the late zoeal stages; the maxillule in the early zoeal stages bears a vestigial exopod (although without setae in *Heterocarpus*); there is no fusion or reduction of the coxal endites of the maxilla. The characters of the maxillule and maxilla contrast with those of the Oplophoridae, Campylonotidae, Thalassocarididae and Palaemonidae while the late development of the antennal endopod contrasts with the condition in the Rhynchocinetidae. Larval characters thus give support neither to the inclusion of *Heterocarpus* in the Oplophoridae, as suggested by Milne Edwards (1881), nor to the erection of the superfamily Heterocarpodoidea, said by Thompson (1967) to occupy "a taxonomic niche between the Oplophoroidea and Palaemonoidea".

The only larval character found in both *H. ensifer* and *H. levicarina* which distinguishes them from all other members of the Pandalidae is the early development of carinae on the carapace. Although this feature may appear as early as zoeal stage V in *H. levicarina*, it is probably best regarded as an adult character which develops precociously. Development of comparable carapace ridges in the zoeal stages is not recorded for any other genus, but nothing is known of the development of *Eugonatonotus* Schmitt. The presence of spines on the outer margin of the antennal scale in the zoeal stages of *H. ensifer* and the development of anteriorly directed dorsal processes on the abdominal somites of larvae of *H. levicarina*, although striking diagnostic characters, can only be regarded as of subgeneric or specific value from the point of view of classification.

Summary

Samples taken during the International Indian Ocean Expedition contain a few specimens of the larval species *Atlantocaris gigas* Ortmann (= *Procletes gigas* auct.) and many specimens of *Procletes biangulatus* Bate. The material is used to supplement earlier descriptions of these larvae, to establish their parentage, describe their distribution and discuss their taxonomic affinities.

Atlantocaris gigas is shown to be the larva of *Heterocarpus ensifer* A. Milne Edwards, and both the generic and specific names of the larva become junior synonyms of those of the adult.

The adult form of *Procletes biangulatus* is that previously known as *Heterocarpus* (*Heterocarpoides*) *levicarina* (Bate). The subgeneric name *Heterocarpoides* is a junior synonym of *Procletes*, and the specific epithet *levicarina* is selected rather than *biangulatus*, although both are of equal priority.

H. ensifer is estimated to pass through 15 zoeal and 3 or 4 megalopal stages; the corresponding number of stages for *H. levicarina* is 13 and 3. Both species develop carapace ridges at about zoeal stage V, the larval rostrum is very long and toothed and there are large median backwardly-directed spines on the abdomen. Forwardly-directed spines on somites 2 and 3 are also present in the later zoeal stages of *H. levicarina*.

Specimens of *H. ensifer* were taken in the eastern, central and western parts of the equatorial Indian Ocean; the species also occurs in the Atlantic and Pacific Oceans. *H. levicarina* appears to be fairly common in the north-eastern half of the Indian Ocean and penetrates eastwards as far as the northern end of the Great Barrier Reef; it is not recorded from any other area.

The larval characters of *Heterocarpus* (including *Procletes*) are fully consistent with its inclusion in the Pandalidae and do not support the recent suggestion that it should be removed to a new superfamily.

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