

DESCRIPTION OF A REMARKABLE DEEP-SEA HERMIT CRAB, WITH NOTES ON THE EVOLUTION OF THE PAGURIDEA

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INTRODUCTION

During the Danish *Galathea* Deep-Sea Expedition a haul with a large herring otter trawl was carried through in the East Pacific off Costa Rica, at a depth of 3570 m. This trawling was extremely rich, quantitatively as well as qualitatively (WOLFF 1960), including about 126 species of benthic animals, among which were the large deep-sea angler fish *Galatheathauma axeli*, and the ancient mollusc *Neopilina galatheae* (LEMICHE and WINGSTRAND 1959, p. 63).

Among the 10 species of benthic decapod crustaceans were 18 specimens of a remarkable pagurid which for obvious reasons I regarded as a new genus and species. I consequently selected the largest female as holotype, and the description and illustrations were primarily based on this specimen.

During my work with this interesting crustacean I happened to mention it in a letter to Dr. FENNER A. CHACE, Washington. Fortunately, he drew my attention to the short and very imperfect description given by Miss BOONE (1926 a, b) of an animal which she regarded as a primitive macruran crustacean and referred to a new genus and species, *Probeebei mirabilis*, the only representative of the new family Probeebeidae. It was collected by the American *Arc-*

turus Expedition in 1925. Except for a reference to it in the Zoological Record for 1926 this species has been completely neglected ever since. It was not recognized as a pagurid, and consequently not mentioned by e.g. MELIN in his excellent work on the systematics of the group (1939), in BRONN's Klassen und Ordnungen des Tierreichs (BALSS 1955, 1957 a, 1957 b) or in GORDAN's extensive bibliography of the Paguridea (1956).

On my request Dr. CHACE later furnished me with a photostat copy of BOONE's two papers, which were not obtainable in this country. BOONE's illustration and short description (1926 b) suggested a close relationship between specimens collected by the *Arc-turus* and the *Galathea*. Through the courtesy of Dr. JOCELYN CRANE of the New York Zoological Society I was able to borrow the holotype and only specimen of *Probeebei mirabilis*. A comparison between this juvenile specimen and juveniles of the same stage in the *Galathea* material leaves no doubt that they all belong to one species.

Since the holotype is a juvenile and furthermore is somewhat fragmentary I base the detailed description on the previously selected female and thereupon consider the type specimen.

Probeebei Boone, 1926

Probeebei n. gen., BOONE 1926 b, p. 73.

Diagnosis:

Carapace completely calcified and considerably swollen. Abdomen distinctly segmented and completely calcified dorsally; segments 2-5 asymmetrical in the female, almost quite symmetrical in the male; tail-fan symmetrical in both sexes; segment 2 much larger than the others. Small flagellum on endopodite of maxillula. No flagellum on exopodite of first maxilliped. Chelipeds weak, the right one a little larger than the left. Peraeopods II and III very elongated. Pleopods 2-5 present on the left side of the adult female, both pleopods 1 present in the adult male; no other pleopods found. 11 pairs of phyllobranchiae.

Type species: *P. mirabilis* Boone.

***Probeebei mirabilis* Boone, 1926**

Probeebei mirabilis n. sp., BOONE 1926 a, p. 72; 1926 b, p. 73, fig.

Planopagurus galathea Wolff, 1960, p. 169, fig. p. 177.

Material:

Galathea St. 716, East Pacific off Costa Rica (9°23'N, 89°32'W), 3570 m, 6 May 1952. Gear: herring otter trawl. Bottom: dark, muddy clay. Bottom temp.: 2,0°C. - Four adult females, three adult males, nine juveniles, and fragments of two specimens; in total eighteen specimens.

Description of adult female.

The carapace (Figs. 1 and 2a) is strongly calcified both on the anterior and posterior portion. The length along the median line (excl. of the rostrum) is exactly the same as the maximum width (excl. of the lateral spines).

The anterior portion (the gastric and cardiac regions) is almost circular in general outline. In front it is separated from the vertical, triangular plate between the rostrum and the eye-stalks (see later) by a low, but sharp crest running from the lateral base of the rostrum to the lateral insertion of the antennae and furnished with a single spine beyond the middle of this stretch. Postero-laterally the anterior portion is separated from the posterior one by two almost parallel grooves on each side (Fig. 2d, 1 and 2) which meet dorsally (3), here forming a deeply cut notch (Figs. 1 and 2a). The notch and

one of the two parallel grooves represent the cervical groove (*b* and *c* of BOAS 1880, p. 113). A comparison with BOAS' figs. 16 and 17 (1926 a) of the carapaces of *Paguristes* and *Mixtopagurus* might indicate that the most median of the two parallel grooves (1) should be the cervical one. However, the broadening of the carapace and its macruran- or even crab-like appearance result in a more lateral passing of the *linea anomurica*. In *Probeebei* (Fig. 2a) as well as in the still more carcinized *Porcellanopagurus* (BORRADAILE 1916, fig. 2) and the Lithodidae this line runs longitudinally just below the dorsal, spiny part of the carapace, separating this from the lateral parts which will be described below.

The *linea transversalis* of BOAS (1926 a, fig. 16) is visible as a faint, uncalcified suture (Fig. 2d, l. t.) which runs immediately behind the median part of the cervical groove. Somewhat before the lateral margin it diverges into two branches, one running obliquely forwards immediately behind groove 2 (Fig. 2d) and ending in the *linea anomurica*, and another which curves backwards closely before the lateral margins (when viewed from above) and also ends in the *linea anomurica*.

Returning to the two parallel grooves 1 and 2 and the question which of them is the cervical one, it would seem that the proximity with which the anterior branch of *linea transv.* follows groove 2 might indicate that 2 is a groove in connexion with *l. transv.* and that, accordingly, 1 must be the cervical groove. But a wide separation between the two parallel grooves of the cervical system and the anterior branch of *l. transv.* is clearly visible in *Lomis hirta* (BOUVIER 1895, pl. 13, 7) which resembles a porcellanid crab and is the only species of the family Lomisidae; this family is derived from the symmetrical Pylochelidae, the most primitive pagurids. In *Hapalogaster* which is the most pagurid-like member of the Lithodidae (BOUVIER 1895, p. 166) *l. transv.* is much closer to the cervical groove (l. c., pl. 12, figs. 27 and 29) and the conditions seem to correspond closely with those in *Porcellanopagurus*. For *P. edwardsi* FOREST (1951, p. 87) suggests that the separation between the calcified and the soft part of the carapace must be "ce qui nous semble correspondre à *linea transversalis* de BOAS". This is certainly correct and it must then be the anterior of the branches. The posterior, backwards curved branch found in *Probeebei*, *Lomis*, and *Hapalogaster* is not mentioned in any description of the species of *Porcellanopagurus*.

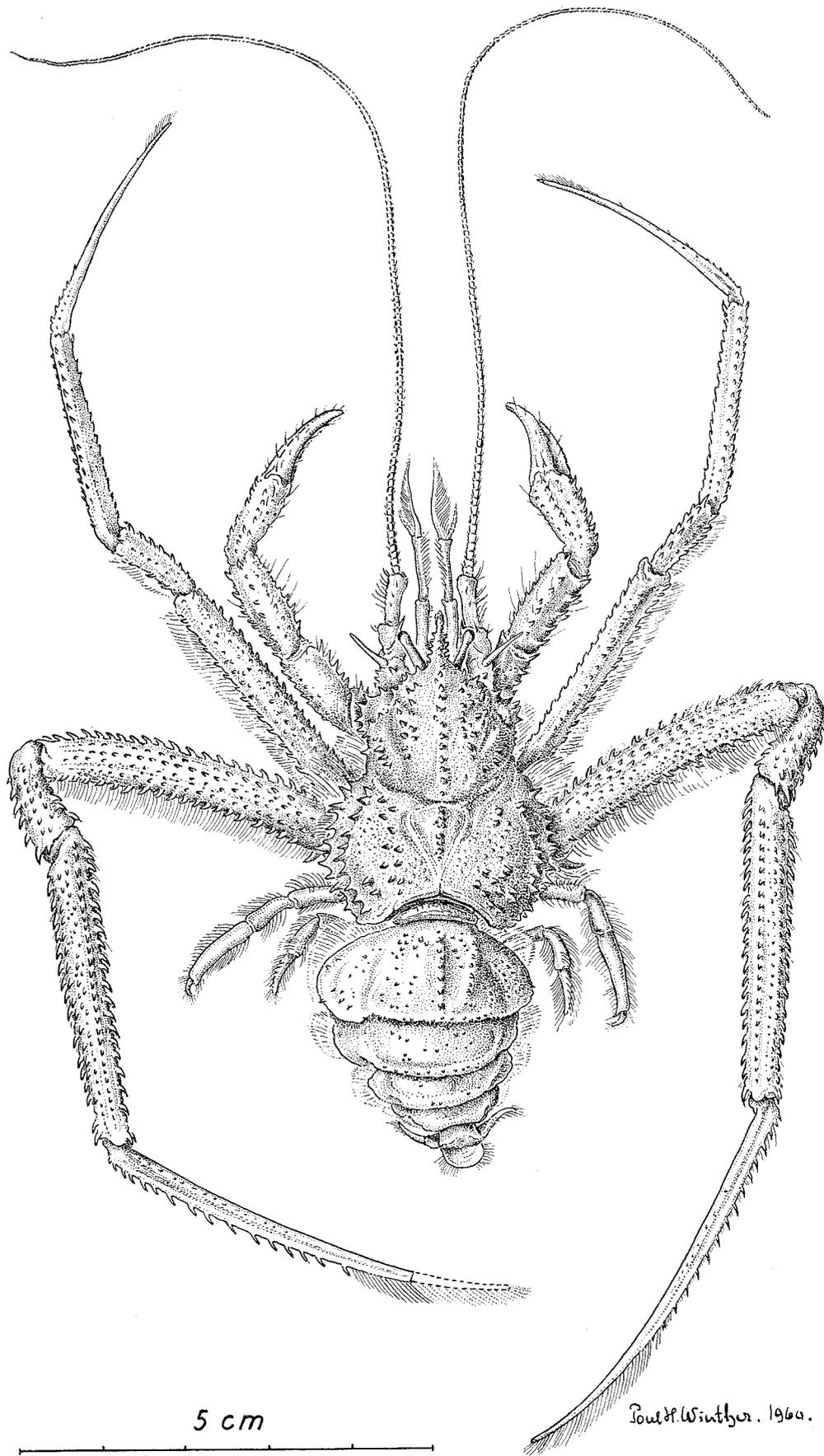


Fig. 1. *Probeebei mirabilis* Boone; described adult ♀, Galathea St. 716.

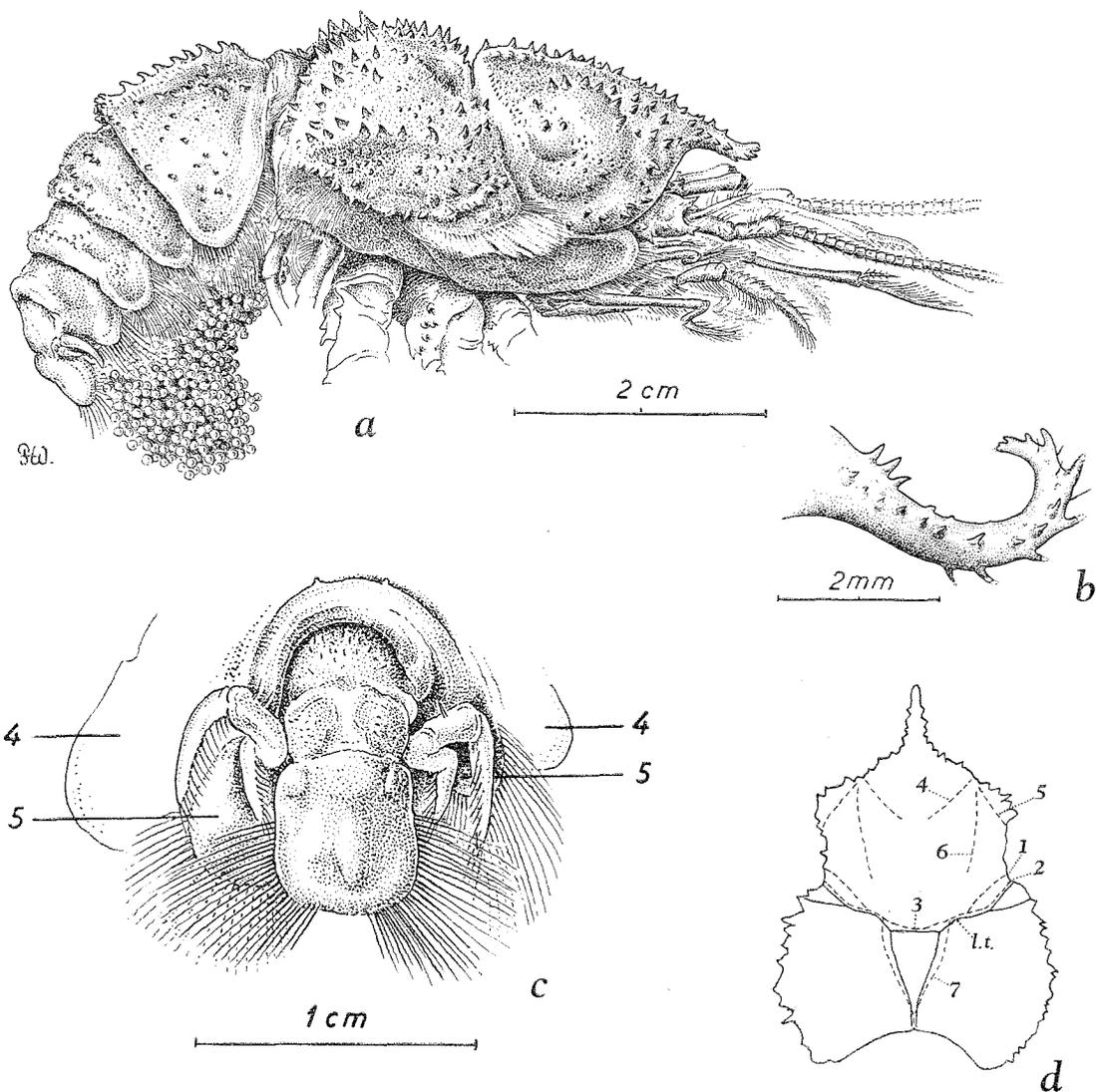


Fig. 2. *Probeebei mirabilis*; a, descr. ♀ from the right side; b, rostrum of juvenile of stage x; c, part of abdominal segment 4, segments 5 and 6, and telson of descr. ♀; d, lines and grooves on the carapace (cf. the text).

By homologizing with these three genera I found it most probable that groove 2 represents the continuation of the cervical groove, and that 1 is a secondarily formed groove, both in *Probeebei* and in *Lomis*. It should be added that in *Pagurus splendescens* (Owen) a system of grooves and lines is found, which, according to the fine illustration in BALSS 1913 (pl. II, 2) is almost exactly like that in *Probeebei*. This species will be further discussed below (p. 26).

Besides these grooves, etc. the anterior portion of the carapace is subdivided by the following grooves: Two faint, oblique ones (Fig. 2d, 4) which almost meet in the median line somewhat in front of the middle and together form a broad V with the opening forwards, two grooves running at right

angles to these and parallel to and not far from the antero-lateral margins (Fig. 2d, 5), and, finally, two obliquely longitudinal grooves which divide the swollen postero-lateral parts of the anterior portion (6).

There are five, more or less distinct, longitudinal rows of short, stout spines which converge posteriorly, and a short, transverse row in a considerably vaulted area close to the antero-lateral margin.

The rostrum is distinctly set off, and its length is about one-fifth of the carapace (excl. of the rostrum), measured along the median line. Dorsally and laterally it is closely covered with spines, and distally it is curved somewhat upwards (Fig. 2a). It is separated from the eye-stalks by a vertical plate which is as high as half the length of the rostrum.

The plate is broadly triangular with a straight lower margin (because eyes, antennulae and antennae are on the same level); it is devoid of spines.

The posterior portion of the carapace (the hepatic and branchial regions) is considerably broader than the anterior and less vaulted medianly. Here two faint grooves are found (Fig. 2 d, 7) which are obviously the cardiobranchial grooves of BOAS (1926 a) and which meet at the posterior margin, forming together a narrow V. A little more medianly are two fine sutures which anteriorly originate from *linea transversalis* and converge posteriorly. They probably correspond to those shown in BOAS' fig. 16 (1926 a) of *Paguristes* and are very conspicuous in *Pagurus splendescens* (BALLS 1913, pl. II, 2).

On the posterior portion are seven longitudinal rows of spines, but the row on each side of the median one is rather indistinct. There are also some scattered spines near the posterior margin.

The entire dorsal surface of the carapace is also covered, besides with spines, with many nodules and scattered hairs which are rather long on the antero-lateral corners of both the anterior and the posterior portion.

The lateral parts of the carapace are considerably less calcified and almost equally broad throughout (Fig. 2 a). They are divided a little before the middle by the line *la'* of BOAS (1880, figs. 141-144) and Figs. 2 a and 9 in this paper. Anteriorly they are broadly rounded and bear a row of long setae. Their surface is furnished with rather long, scattered setae, many small nodules and posteriorly a longitudinal row of small spines.

The abdomen (Figs. 1 and 2 a) has all seven segments well separated. The terga are strongly calcified, except the sixth and the telson which are rather soft. The five first segments have a thick rounded crest also along the dorsal part of the posterior margin, adding to the armour-like appearance of them. All segments have short scattered hairs.

The first segment is much narrower than the following, and when the abdomen is bent upwards as in Fig. 1, only the posterior, thickened part is visible. If held in its supposed natural position (Fig. 2 a), it is a little more than twice as broad as long, with the entire dorsal surface calcified.

Segments 2-5 are asymmetrical, with the left parts somewhat larger than the right so that the abdomen curves to the right side. Laterally the terga are rounded, bent slightly upwards, and with a row of setae. Segment 2 is by far the largest, being as long as segments 3 and 4 and half of 5, measured along

the median line. It has one median row of spines which are distinct and two more indistinct pairs of rows. The posterior crest has many rather small spines. Segments 3-5 gradually become narrower, shorter and with fewer spines, the latter having only two or three very small ones.

Segment 6 (Fig. 2 c) is symmetrical, about as long as broad, and with a transverse, convex suture in front of the insertion of the uropods. The telson is almost rectangular, a little longer than broad, much convex transversely, and somewhat concave longitudinally. There are three low convexities dorsally.

On the ventral side of the abdomen sternal plates are present on segment 1 in much the same way as in the Pylochelidae (cf. fig. 19 of *Mixtopagurus longicaudalis*, BOAS 1926 a), forming a narrow ring, raised as a rounded heel. On segments 2-5 the sterna are shaped as subtriangular plates, almost as in *Lithodes* (BOAS 1924, fig. 27). The pleopods on the left side are inserted close to the interior margin of the plates and on the right side scarlike impressions of the disappeared pleopods are present – as in the male (Fig. 6 b) which has such scars on both sides (cf. p. 19). The vast majority of the ventral side is soft-skinned, with the segments indicated by low, but distinct furrows. The ventral side of the telson is excavated, with a central convexity in front of the anus.

The ocular peduncles are immovably fused with the ophthalmic scales which are very short. The peduncle reaches a little beyond joint 3 of the antennae. It is considerably swollen at the base, the width being here almost twice that of the middle part. It is also somewhat swollen distally. A spine is found on the interior, dorsal part of the scale and on the swollen part of the peduncle, and a third spine dorsally on the peduncle, a little beyond the middle. It has also several long setae dorsally on the distal half. The corneal surface is moderately large, preferably situated on the outer, ventral side of the apex, dark brown, and apparently with well developed ocelli.

The antennulae (Fig. 3 a) of the typical shape. Joint 2 is one-fifth longer than joint 1, joint 3 about twice as long as joint 1. This has a small distal spine on the exterior side and a larger one beyond the middle. Distally on the dorsal side is a double spine. Besides it has many long, feathered setae. The upper (outer) flagellum consists of about 25 joints, the lower (inner) of 6 subequal joints.

The antennae are also typically shaped. Joint 1 hardly visible from above, but ventrally almost as long as broad. On the outer and ventral side is a row

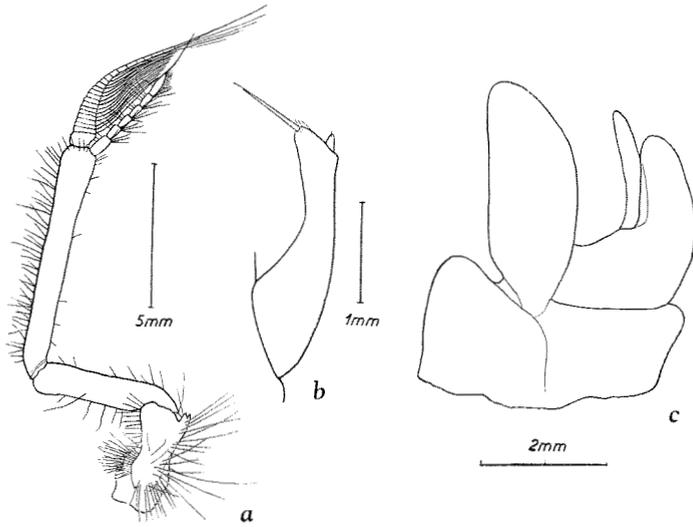


Fig. 3. *Probeebei mirabilis*; a, left antennula of descr. ♀ from inside; b-c, endopodite of maxillula and first maxilliped of dissected ♀ (all setae have been omitted in the maxilliped).

of three spines, and the antennal gland opens on a rounded process on the inner corner. Joint 2 is somewhat broader than long, with one small and three larger spines on the outer margin and a dorsal spine distally. Joint 3 with a strong spine on the inner corner, joint 4 short and unarmed, but with many setae as joint 5. This is almost as long as joints 2-4 combined; it is somewhat widened towards the distal end. The antenna scale is slender, rod-like and furnished with long setae; it is almost as long as joint 5. The flagellum almost twice as

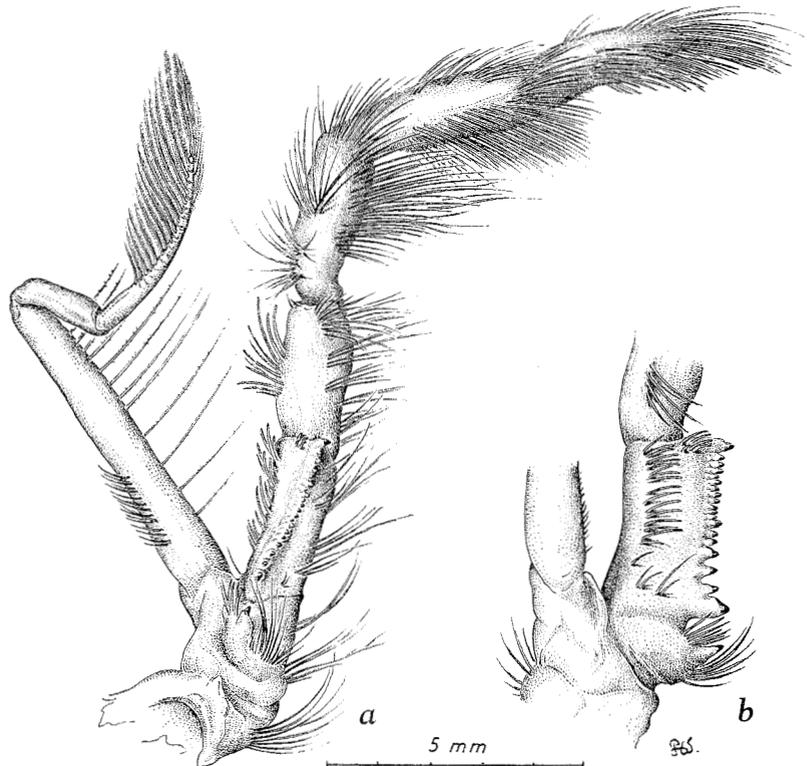
long as the entire body and with short and stout, spine-like setae on the numerous joints (about 140).

The mouthparts. I have compared the mouth appendages with those of *Pagurus bernhardus*¹ and *Parapagurus pilosimanus* and found them fairly equal.

The mandible differs from that of *bernhardus* in having more pronounced teeth on the oral end and joint 3 of the palp relatively smaller. From *pilosima-*

1. The recent, approved nomenclature has been followed (cf. FOREST 1958).

Fig. 4. *Probeebei mirabilis*, dissected ♀; a, left third maxilliped from inside; b, *crista dentata* from in front.



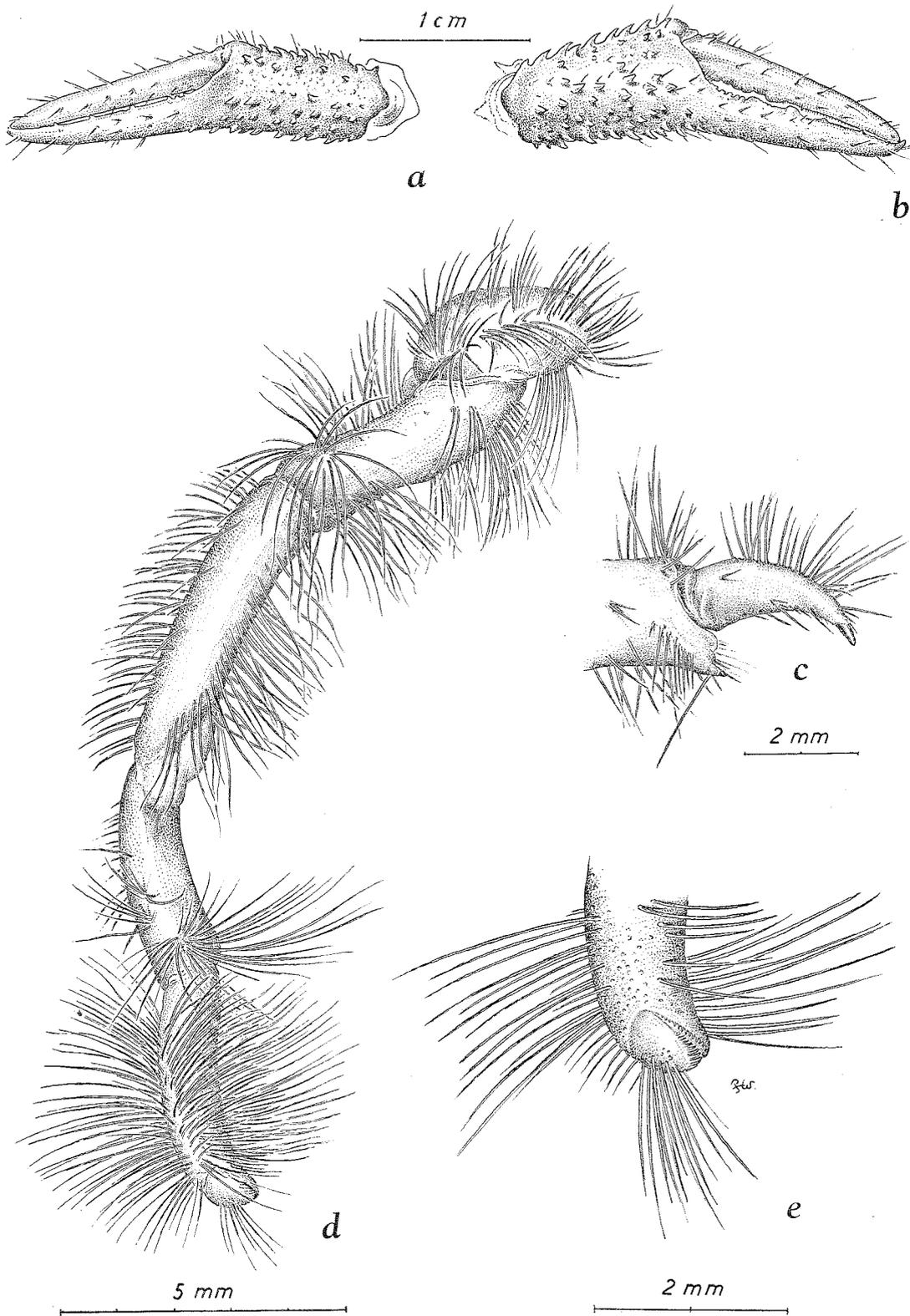


Fig. 5. *Probeebei mirabilis*; a-b, left and right cheliped of descr. ♀; c, distal end of left pereopod IV of descr. ♂, seen from in front; d, left pereopod V of descr. ♂, from behind; e, distal end (some setae left out).

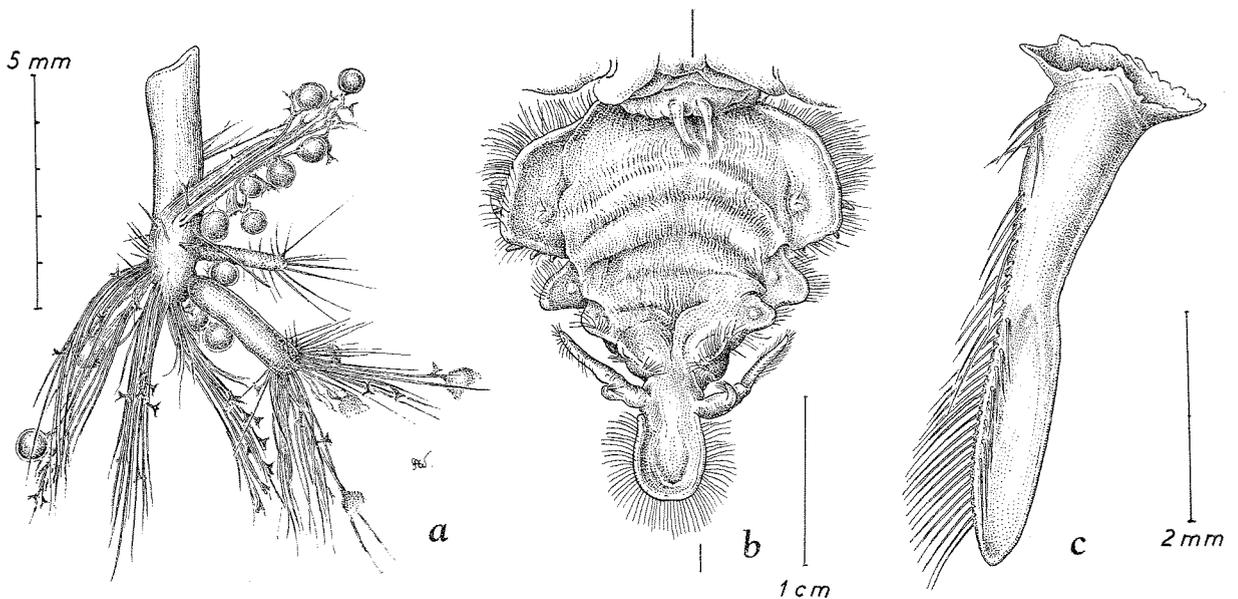


Fig. 6. *Probeebei mirabilis*; a, left pleopod 4 of dissected female from behind (most of the eggs have been removed); b, abdomen of ♂ from below (the short lines above and below the drawing denote the longitudinal axis of the entire animal); c, left pleopod 1 of the same ♂ from inside.

nus it only differs in having a beautiful rosy tinge on the oral part.

The maxillula differs from that of *bernhardus* in having the coxa somewhat more rectangular, the endopodite comparatively narrower (fig. 3b), and the flagellum (appendix) on the latter still smaller, i.e. almost as in *Pylopagurus* (BOAS 1924, fig. 18a). *P. pilosimanus* has no trace of a flagellum.

The maxilla in *mirabilis* and *pilosimanus* differs from that of *bernhardus* in having the endopodite reaching beyond the distal endite and the exopodite considerably narrower, tapering towards the proximal and distal ends, and with a constriction almost midway on the outer margin.

The first maxilliped of *bernhardus* (and *Pylopagurus*) has on the exopodite a well developed flagellum which is completely absent in *pilosimanus* and *mirabilis* (Fig. 3c). The exopodite ends a little more abruptly in the latter.

The second maxillipeds are almost equal, but in *bernhardus* the peduncle of the exopodite is less than twice as long as the longest joint (merus) of the endopodite, while in *pilosimanus* and *mirabilis* it is nearly three times as long.

The third maxilliped of *mirabilis* (Fig. 4) differs in being considerably more slender, the teeth of the *crista dentata* are more numerous (about 20) and of less uniform size (Fig. 4b), and merus is on the whole more compressed. Furthermore, the teeth on the distal half of the inner, dorsal side of merus and the distal spine on carpus, found in *bernhardus*,

are not present. The peduncle of the exopodite does not reach the distal end of carpus in *bernhardus*; it reaches as far as carpus in *pilosimanus*, and somewhat beyond carpus in *mirabilis*.

The chelipeds are unusually weak. Like the carapace they are armed with scattered setae and spines, some of which are placed in rows. On the ventral margin of both ischium and merus are three or four especially long and pointed spines. Both chelae (Fig. 5a-b) are narrow and pointed, dactylus being more than half as long as propodus. The right cheliped is only slightly longer and heavier than the left.

Peraeopods II and III are almost uniform in shape (dactylus of prp. III is relatively a trifle longer than that of II). The total length of prp. III is almost one and a half times that of II. The coxae are cylindrical and very large; they meet almost in the median line. Ventrally they have a row of rather few spines along the proximal and distal margins. One of the spines in the latter row is exceptionally long, and this is also the case with the distal, posterior spine on ischium. Besides the usual scattered setae there is, especially on merus, a dense row of setae, considerably longer on the hind than on the front margin. Only coxa of the *left* prp. III has a sexual opening.

Peraeopod IV is about as long as the greatest width of the carapace. There are two inner, distal spines on coxa and three inner ones on merus. At the end of propodus is a strong spine below dactylus which, however, works in another plane (behind the

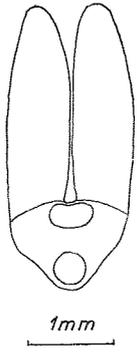


Fig. 7. *Probeebei mirabilis*; section of gill.

spine) so that there is no chela (Fig. 5c). The majority of the many setae on the leg is located along the margins.

Peraeopod V is as shown in Fig. 5d. There are no spines, but a great many setae. Distally is a very tiny, mouth-shaped chela with the "jaws" finely serrated (Fig. 5e).

The pleopods (Fig. 6a) are of equal size. The endopodite is one-sixth longer and twice as broad as the exopodite.

The uropods (Fig. 2c) are practically symmetrical, the right (strangely enough) being perhaps a little bigger than the left. Both the exopodite and the endopodite are sickle-shaped, the former is twice as long and broad as the latter and has along the entire outer margin a narrow band of tiny spines, a rudiment of the file-like surface of other pagurids. The surface of the endopodite is perfectly smooth, except for a row of setae along the inner margin.

Gills. There are 11 gills on each side. The branchial formula is exactly as in *Pagurus* Fabr. (= *Eupagurus* Brandt) and *Lithodes* (CALMAN 1909, p. 280), i.e. with two arthro-branchiae on maxilliped 3 and each of peraeopods I-IV; prp. IV besides with one pleurobranchia. They are of the phyllobranchiate type, with the branches of each pair regularly oval and equally large (Fig. 7).

Ova. Considering the abyssal environment of this species the number of eggs is remarkably large and their size unusually small, the average diameter being 1.0 mm.

Colour. Notes and colour photographs made on freshly caught specimens give the colour of the legs as a bright orange, and that of the carapace and abdomen of a somewhat lighter orange. The juveniles were still lighter. The eggs had a dark red colour.

Size. The described ♀, which is the largest specimen, has a total length of 65 mm (incl. the rostrum). The smallest adult female is 55 mm long. The largest male is 63 mm, the smallest 57 mm long.

Description of male.

The male differs from the female in the following respects:

The abdomen is almost entirely symmetrical, both in dorsal and ventral view (Fig. 6b).

The first pleopods (Fig. 6c) are probably unique in being 1-jointed only. In the other genera in which the males have paired pleopods on the first abdominal segment they have two almost equally long joints (e.g. in *Tomopaguroides* Balss, 1912, fig. 15), whereas their shape is not mentioned in *Tomopagurus* A. M.-Edw. & Bouvier. Also the genera with paired pleopods 1 in females (*Pagurodes*, *Nematopagurus*, *Pylopagurus*, *Pylopaguropsis* and *Ceratopagurus*) have always 2-jointed first pleopods. In *Probeebei* they are furthermore small, less than half as long as the eye stalks, and with the distal half of the inner side slightly excavated. There is a double row of long setae along the posterior margin. — As mentioned above, faint scars of the absent pleopods 2-5 are visible on the small, triangular sternites (Fig. 6b).

The abdomen of a moderately berried female was dissected. The ovary was found to extend into the abdomen. It could not be stated whether a branch of the liver was also present, but it seems unlikely. A male was also dissected, and a pillow-shaped, whitish organ situated immediately inside the soft ventral skin might well be the testes, but the state of preservation was too poor to allow a detailed study. A similar organ was not found in the dissected female.

The gut of the male was filled with a black material. The only identifiable objects seem to be two fragments of tiny crustaceans.

Variation in adults.

The four adult females and three adult males were carefully compared, and besides the variation in size (see above) the following differences were found:

The rostrum is relatively shortest in the described ♀ in which it is a little less than one-fifth of the carapace (excl. of the rostrum), measured along the median line. The longest rostrum (another female) is a little less than one-third of this distance. In a third female it is bent horizontally at an angle of about 30°.

The number of spines on the carapace is somewhat larger in one male and two females which have e.g. a band of irregularly arranged spines along

the median line of the posterior portion of the carapace – instead of one row in the described ♀ (Fig. 1).

The telson may have the hind corners considerably more rounded so that its shape is nearly oval instead of rectangular (Fig. 2c). There may also be setae along the entire hind margin.

The uropods show a slight variation in the width and length of the first joint compared to the length of the exo- and endopodites.

Post-larval development

No larval stages of this species were secured, but a number of juvenile specimens is available, including the holotype. They differ from the adults in having (1) the rostrum much more curved upwards distally (Fig. 2b, p. 14) and considerably longer (if stretched it would be half the length of the carapace (excl. of the rostrum)); (2) the distal end of the telson is bent backwards in the youngest stage (cf. the description of the holotype); (3) the hairs on the carapace are longer; (4) the number of joints in the flagellum of the antennula and the antenna is smaller (cf. the description of the holotype); (5) in particular, in the younger stages the number of pleopods present in both sexes is remarkably different from that of the adult males and females.

In the Paguridae pleopods 2-5 (or 2-4) appear as bilobed formations generally in the fourth zoeal stage (metazoea) which is perfectly symmetrical.¹ In the postzoeal or glaucothoe stage (the fifth) the pleopods are also symmetrical and consist of a peduncle and two rami of which the outer one has long swimming setae. Already during this stage some of the intestines become wholly or in part abdominal, and the pleopods of the right side start degenerating. This procedure is independent of whether a shell is meanwhile occupied or not.

The first adolescent or post-larval stage (or the sixth stage) is characterized by a completely asymmetrical abdomen like that of the adult. Generally the right hand pleopods disappear totally, although rudiments of these are visible on HART's fig. 118 (1937) of an adolescent crab of *Orthopagurus schmitti*, and THOMPSON (1903, p. 189) showed that under normal conditions (in the laboratory) 20 per cent of 107 specimens of *Pagurus annulipes* in the first post-larval (or sixth) stage retained rudiments of

1. A tendency to asymmetry already in this stage may be found occasionally; MACDONALD *et al.* record e. g. (1957, p. 240) that the left of the bud-like pleopods 5 in stage IV of *Anapagurus laevis* is the larger.

the right pleopods. But if he kept crabs of the glaucothoe stage without shell (naked), the average time of metamorphosis was not only postponed one or two days, but as much as 47 per cent (of 221 specimens) had retained rudimentary pleopods on the right side after the moult. In another experiment THOMPSON tried to rear such variants to the adult form. Due to a high mortality only 37 survived, and in no case did any crab preserve the variations beyond the second post-larval (or seventh) stage, and only 16 per cent retained them into that stage. That is, "whenever the moult from the sixth stage failed to give the normal adult pleopod formula, the succeeding ecdysis produced it" (l.c., p. 191).

In other respects juvenile characters are preserved for a considerable time through the first post-larval stages. In *P. annulipes* the full adult colours and the complete specific form are not attained until about the twentieth day from the glaucothoe, and the 9-jointed antennal flagellum of the sixth stage persists till the eighth stage, while crabs forty days from the glaucothoe have only 17 or 27 joints (THOMPSON 1903, p. 158).

Furthermore, FOREST (1954b) has reported on the first three post-larval stages of *Dardanus pectinatus* (Ortmann) and shown that in the first post-larval (or sixth) stage the right pleopods are almost as long as the left, although rudimentary in appearance (l.c., fig. 1A); in the next (seventh) stage they are tiny and bud-like, and in the eighth almost invisible knobs. In this stage the body is 6-7 mm long, whereas the body length of the adult is 23 mm (♂) and 37 mm (♀) (FOREST 1955, p. 100) so that probably several additional post-larval stages are found.

It was therefore surprising to find in the juveniles of *Probeebei mirabilis* that the right hand pleopods were still present in well-sized specimens which, apart from the longer and more upwards curved rostrum and a somewhat reduced number of joints in the flagellum, had attained all the characters of the adult. Three different stages besides the adults can be recognized. Judging from the relatively small increase in size (19-25-35 mm) they probably follow immediately after each other, but it seems likely that another, still unknown stage is found between the largest juvenile stage and the adults, in view of the considerable difference in size between them (35-37 mm and 55-65 mm).

Stage x. Three equally large specimens, 19 mm long, are found, but of one only the carapace is left and one lacks the abdomen. The sex of the third specimen is indeterminable, but it may be a

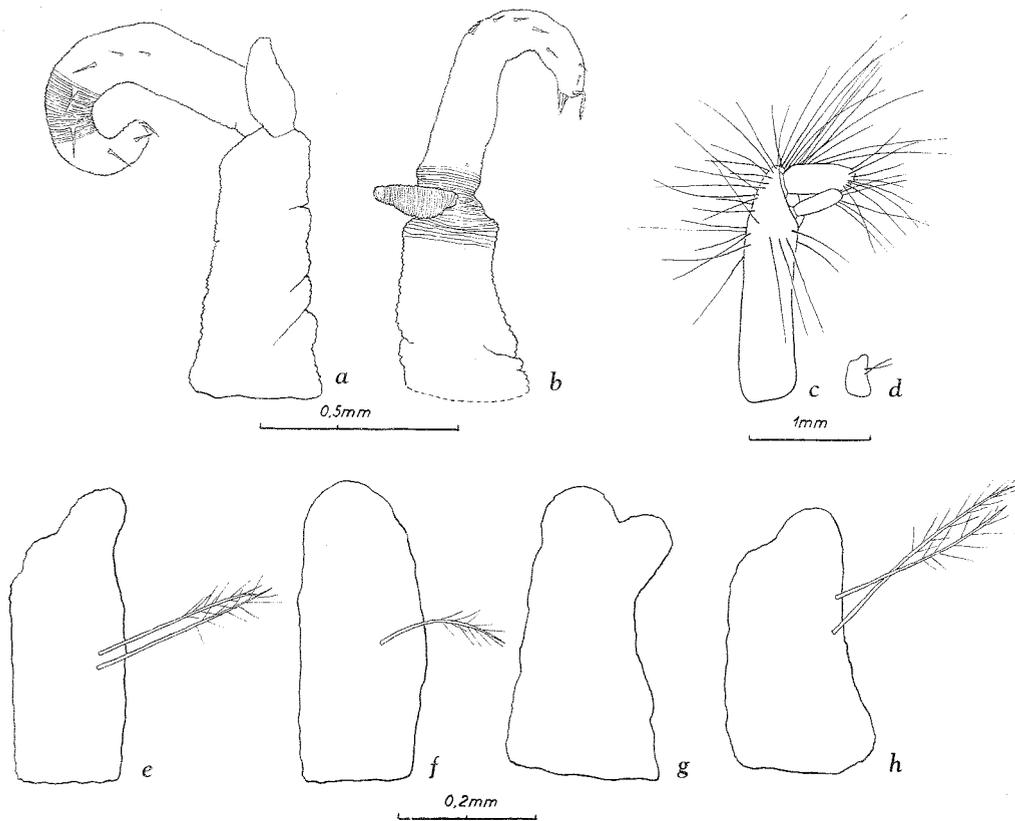


Fig. 8. *Probeebei mirabilis*; pleopods of developmental stages; a-b, left and right pleopod 2 of a ♀ of stage x; c, left plp. 2 of a ♀ of stage y; d and h, right plp. 2 of the same ♀; e-g, right plp. 2, right plp. 3 and left plp. 5 of a ♂ of stage y.

female because of the slightly larger rudimentary pleopods on the left side (see below). There is no trace of pleopods on segment 1. On both sides of the following four segments are rather large, although rudimentary pleopods (Fig. 8a-b). They are about 1.7 and 1.2 mm long, the left ones being slightly larger than the right. They consist of a peduncle, a small, unarmed endopodite and a much longer, curled exopodite with a row of tiny, peculiarly shaped spines towards the distal end. The entire surface is wrinkled with numerous very small folds. Thus, the appendages of this stage have a close resemblance with the *right* pleopods of the first post-larval stage of *Dardanus pectinatus* (FOREST 1954, fig. 1A), but not with the left ones which are without wrinkled surface and have long setae on the exopodite.

Stage y. All four specimens are 25 mm long. In the two females available the left pleopods 2-5 are further developed (Fig. 8c), on the whole differing from that of the adult (Fig. 6a) only in the relatively shorter rami and the less abundant equipment with setae. The right pleopods in the females and the right and left pleopods in the two males available

are all very small (0.4 mm long) and bud-like (Fig. 8d-h); some of them may be faintly bilobed (8g). They may have one or two plumose setae, but these are occasionally absent.

Stage z. The two females available are 35 mm and 37 mm long. The left pleopods 2-5 are now fully developed, although of course smaller than in the adult. The right pleopods have disappeared, but, as in the adult, scars are distinctly visible. The sex opening is still closed. The appearance of the pleopods in juveniles and adults is summarized in table 1.

The holotype (Figs. 9-10)

Material:

Arcturus Oceanographic Expedition St. 74-OT4, 60 miles S. of Cocos Island (4°50'N, 87°00'W), 1145 m, 30 May 1925. Gear: otter trawl. Bottom temp.: about 4,3°C.¹ - 1 juvenile ?female.

1. According to BEEBE (1926, p. 25) the temperatures at the only deep hydrographical station during the *Arcturus* Expedition (St. 50, 2°00'S, 89°30'W) is as follows: 1000 m depth: 4,8°C; 1500 m: 3,17°C. which by interpolation gives 4,3°C. at 1145 m. THOMSEN (1937, p. 11) records for

Table 1. Appearance of the pleopods in juveniles and adults of *Probeebei mirabilis*. 0 = no trace; Sc = scar of disappeared pleopod; Ru÷ = small rudiment, 0.4 mm long; Ru+ = large rudiment, 1.2-1.7 mm long; Pl÷ = almost fully developed pleopod; Pl = fully developed pleopod.

Abd. segment	Stage x Length: 19 mm		Stage y Length: 25 mm				Stage z Length: 35-37 mm		Adult Length: 55-65 mm				
	?Female		Female		Male		Female		Female		Male		
	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right	
1	0	0	0	0	0	0	0	0	0	0	0	Pl	Pl
2	Ru+	Ru+	Pl÷	Ru÷	Ru÷	Ru÷	Pl	Sc	Pl	Sc	Sc	Sc	Sc
3	Ru+	Ru+	Pl÷	Ru÷	Ru÷	Ru÷	Pl	Sc	Pl	Sc	Sc	Sc	Sc
4	Ru+	Ru+	Pl÷	Ru÷	Ru÷	Ru÷	Pl	Sc	Pl	Sc	Sc	Sc	Sc
5	Ru+	Ru+	Pl÷	Ru÷	Ru÷	Ru÷	Pl	Sc	Pl	Sc	Sc	Sc	Sc

Comparison with *Galathea* specimens.

I am much obliged to Dr. JOCELYN CRANE and to the New York Zoological Society for the generous loan of the holotype which enabled me to state with certainty not only the systematic position of this specimen, but also its identity with the *Galathea* specimens.

The holotype is a juvenile ?female and belongs to the above described stage x of which the *Galathea* collected three specimens. A careful comparison revealed an extraordinary similarity in all respects,¹ except the following three:

(1) The total length is 20,6 mm (as against 19 mm) because the carapace is more elongated (Fig. 9), being 1,35 times longer than broad (excl. of the rostrum), but only 1,29 times longer than broad in the *Galathea* specimens. (2) The rostrum is broken before the apex (Fig. 9), but probably did not bend so much backward as in the others (Fig. 2b, p. 14); it also lacks the dorsal spines near the base, of which the three *Galathea* specimens have three (Fig. 2b) and four and four. (3) On pleopods 2-5 the endopodites are still smaller than in the other specimens (Fig. 8a-b), being only about half as large.

Additional description.

The relatively longer and more curved rostrum and the more abundant growth of hairs on the carapace in comparison with that of the adults, as well as the

Dana St. 3556 (2°52'N, 87°38'W), which is very close to *Arcturus* St. 74, at 1000 m: 4,66°C. and at 1200 m: 4,20°; this again points to a temperature of 4,3°C. at 1145 m depth.

1. Even the armament with spines is more equal in the holotype and in one of the *Galathea* specimens, than in the three *Galathea* specimens mutually.

shape of the pleopods were described above. Besides, the holotype and three *Galathea* specimens of stage x differ from the adults in the following features:

(1) The telson has the distal third bent backward in a peculiar way and rounded apically, when seen from behind (Fig. 10a). However, on the upper margin close to the apex two very small, soft, finger-shaped projections emerge, both of which point inward (towards the median line) where they meet (Fig. 10b-c). (2) There are 14 joints in the upper (outer) flagellum of the antennula, 5 in the lower; the flagellum of the antenna has about 70 joints.

Previous description.

The new genus and species was first mentioned in the paper in which BOONE (1926 a) gave an enthusiastic account of the more unusual of the crustaceans from the *Arcturus* Expedition. She claimed (p. 72) that this "shy, small creature" was "the Missing Link", and discussed its systematic position. She rejected it as an aberrant amphipod because of the stalked eyes and macruran-like carapace. The large second abdominal segment reminded her of that of a lithodid crab, but, unfortunately, she abandoned the supposition that it belonged to the Anomura and ended with regarding the animal as a primitive macruran crustacean, although, as she said, it has "the carapace composed of seven articulated plates". This misconception is of course due to the fact that she included the six abdominal segments with the carapace.

In the second paper (1926 b) she gave a reasonably good illustration¹ of the animal in side view

1. Apart from minor inaccuracies (e.g. exaggerated length of the dactylus of pereopod IV) the abdomen has had an extra segment included between segments 5 and 6, and

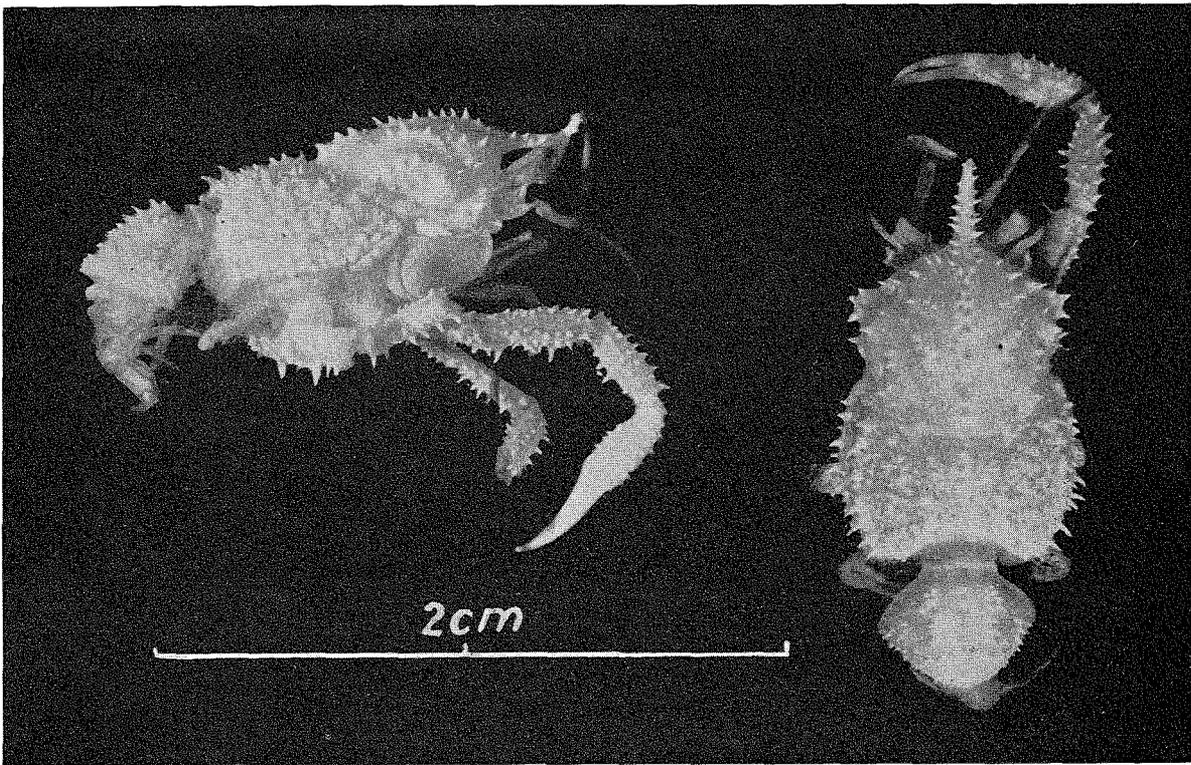


Fig. 9. *Probeebei mirabilis*; holotype.

and the following description (the numbers in brackets refer to the comments given below):

“(1) Family: PROBEEBEIDAE.

Rostrum well developed. (2) Carapace consisting of seven articulated segments. (3) First legs equal, strong, chelate. Outer antennae with scapocerite; flagellum very long. Second antennae long, multi-articulate, biflagellate. Second abdominal segment arched, armoured as the carapace. Rhipidura flexible. Telson transversely divided, distal section reflexed rigidly upon proximal half.

Genus: *Probeebei*, with characters of family. Only genus known. Type: *Probeebei mirabilis* new species.

the pleopods on segment 5 have been left out. According to the illustration both chelipeds were previously present, but later the left chela has been lost.

Probeebei mirabilis, sp. nov.

(4) Rostrum half as long as carapace, upturned. Carapace consisting of seven articulated plates. Eyes prominent. First abdominal segment hingelike, second very prominent, arched. Rostrum, carapace and first two abdominal segments ornamented with rows of prominent spines; (5) third to sixth segments inclusive smooth, subcylindrical, deflected; (6) second, third and fourth segments with degenerate uniramous pleopoda attached at outer lateral margin, resembling side plates. Rhipidura slender, sublnate, outer blade larger. (7) Telson small, transversely segmented, apical part rigidly deflected upon proximal half, tip hooklike, upturned. First legs chelate symmetrical, second and third broken, basal parts are replica of first pair. Third and fourth legs weak. (8) Mouthparts unique.”

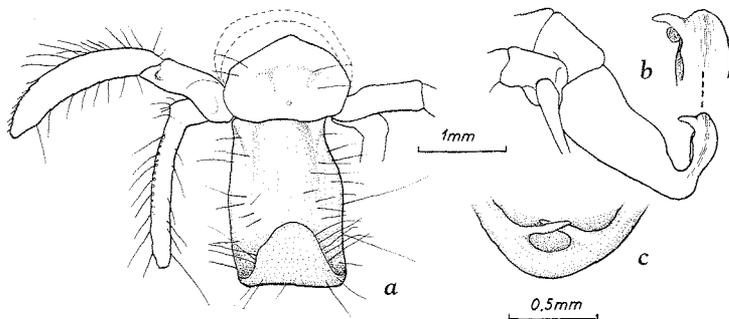


Fig. 10. *Probeebei mirabilis*, holotype; a, abdominal segment 6 and telson from behind; b, the same from the left side; c, the distal part of the backward bent section of telson seen apically.

Comments.

(1) For the reasons given below (p. 26) the family will have to be rejected.

(2) As stated above, this is definitely not the case.

(3) Also in this developmental stage the right cheliped is slightly larger than the left. This is also evident from BOONE's illustration.

(4) Rostrum is half as long as the anterior portion of carapace.

(5) Abdominal segment 3 has a transverse row of many small spines or knobs along the posterior margin and segment 4 a few tiny knobs.

(6) Also segment 5 has pleopods; all pleopods are biramous, but the endopodites are very small and easily overlooked.

(7) Telson is not transversely segmented.

(8) The above description of the mouthparts of the adult shows that they are typically paguridean. They were not dissected by BOONE.

Phylogenetically significant relationships

MELIN (1939, p. 13) pointed out that in the systematic classification of the Paguridae more stress is laid on characters which facilitate a quick identification of the genera than on those which are of real importance for the systematics and phylogeny of the family. Naturally, it is tempting, in a group like hermit crabs which exhibits such a variety of life habits and biological adaptations, to lay too much stress on those characters which are a result of their adjustment to the environment, because they are so easily discernible. The true relationship of the genera should not be based on such easily adaptable and secondary characters, but on those which are not altered by the mode of life and the environment, thus being of a much more conservative nature.

Accordingly, I have tried to base the following considerations on the relationship of *Probeebei* entirely on the latter type, and in the following chapter I shall discuss the other characters of little or no phylogenetic importance.

MELIN (l. c., p. 16) emphasizes the great systematic significance of the number of pleopods which has been so greatly reduced during the evolution of the Paguridea. This character was already pointed out by BOAS (1924, p. 29) who based a new subdivision of "Paguriden" (including the Pylochelidae) on the number of pleopods present. His classification is the following:

1. Pylochelinen: Paired pleopods on abdominal segments 1-6.

2. Paguristinen: Males with a pair of pleopods on the first, sometimes also on the second segment.

3. Pagurinen (including Coenobitidae): Males without paired pleopods; first abdominal segment free, not fused with the last thoracic segment; terga on abdominal segments in one piece; 14 pairs of gills; no spine on joint 3 (ischium) of mxp. 3.

4. Eupagurinen: Males without paired pleopods; first abd. segment free; terga on abd. segments 2-5 paired; 11 pairs of gills; a spine present on joint 3 of mxp. 3 proximal to the *crista dentata*.

Thus, BOAS entirely rejects the ordinary division into Pylochelidae (with paired pleopods on segments 1-6), Paguridae (the flagellum of the antenna pointed; the peduncle rarely as long as the carapace), and Coenobitidae (the flagellum ends bluntly; the peduncle as long as or longer than the carapace). Also the long established division of the Paguridae into Diogeninae Ortm. (= Pagurinae Ortm.) and Pagurinae Latr. (= Eupagurinae Ortm.) by means of the width of the sternum between the third maxillipeds is disregarded.

Unfortunately, MELIN (1939) does not at all refer to the said paper by BOAS which he probably did not know.¹ This is so much more regrettable, since MELIN (p. 14) - in my opinion rightly - chritizises the somewhat arbitrary character (distance between the bases of the third maxillipeds) by means of which the two subfamilies of the Paguridae are divided. Although he bases his excellent key to the genera of this family primarily on the number of pleopods in both sexes, he prefers to retain the old subdivision. This has also been done by all later authors (e. g. FOREST 1955, FIZE & SERÈNE 1955, and BALSS 1957 a). It is beyond the scope of this paper to enter into a detailed discussion of this problem, but I feel convinced that the present, generally accepted classification of the hermit crabs cannot be regarded as the phylogenetically most satisfactory one.

According to BOAS' system *Probeebei* falls within the Paguristinen, since in the males a pair of pleopods is present on the first segment. BOAS divided this subfamily as follows:

(1) Also the female with one pair of pleopods on the first segment; 13-14 pairs of gills: *Paguristes*, *Munidopagurus*, *Paguropsis*.

(2) Female without pleopods on the first segment:

1. MELIN's paper was edited posthumously by BALSS who very regrettably did not include a list of references.

Xylopagurus, *Parapagurus*, *Sympagurus*,¹ *Tomopagurus*, *Tylaspis*.

Of these, *Munidopagurus* can only be included with considerable doubt, since only one female of the monotypic *M. macrocheles* (A.M.-Edw.) is known (MILNE-EDWARDS & BOUVIER 1893, p. 102), so that nothing can be said of the male pleopods.² Moreover, BOAS forgot to include *Tomopaguropsis* Alcock, 1905 and *Tomopaguroides* Balss, 1912, in which the male has one pair of pleopods. Accordingly, a subdivision can be made as follows (with the number of unpaired pleopods in brackets):

- (1) Male with two pairs of pleopods, female with one:

Paguropsis Henderson (♂ 3, ♀ 4)
Paguristes Dana (♂ 3, ♀ 4)
[? *Munidopagurus* A. M.-Edw. & Bouv.
(♂ ?, ♀ 3)]

- (2) Male with two pairs of pleopods, female without paired pleopods:

Xylopagurus A. M.-Edw. (♂ 0, ♀ ?)
Parapagurus Smith (♂ 3, ♀ 4)
Sympagurus Smith (♂ 3, ♀ 4)
Tylaspis Henderson (♂ 3, ♀ ?)³

- (3) Male with one pair of pleopods, female without paired pleopods:⁴

Tomopaguropsis Alcock (♂ 4, ♀ ?)
Tomopaguroides Balss (♂ 3, ♀ ?)³
Tomopagurus A. M.-Edw. & Bouv. (♂ 3, ♀ ?)³
Probeebei Boone (♂ 0, ♀ 4)

Paguropsis and *Paguristes* also differ by having the third maxillipeds close together and therefore belong to the subfamily Diogeninae while all the other genera can be referred to the Pagurinae.

MELIN (l. c.) has also evaluated the systematic importance of the number and type of gills in the Paguridae and considers the number to be very significant, because of its bearing on the phylogeny.

1. This genus is now generally regarded as a synonym of *Parapagurus*.
2. It is more likely that *Munidopagurus* should be ranged with the following genera, the females of which have also one pair of pleopods while the males have exclusively unpaired pleopods: *Pylopaguropsis*, *Pylopagurus*, *Pagurodes*, *Nematopagurus*, and *Ceratopagurus*.
3. The females of *Tylaspis*, *Tomopaguroides* and *Tomopagurus* are unknown.
4. FOREST (1952, p. 8, fig. 8) has described and figured a strange irregularity occurring in *Trizopagurus strigimanus* (White) which belongs to the Diogeninae: Besides the normal left pleopod 2 the males always have also the right second pleopod developed, but it is smaller and with a greater variation in the shape of the exopodite.

On the other hand, the significance of the type of the gills – whether tricho- or phyllobranchiae – has previously been much overestimated. He shows very convincingly that the former cannot be homologized with the trichobranchiae of the Macrura from which the Paguridea have descended. They must in this group probably always be looked upon as phyllobranchiae which secondarily have been split up longitudinally so that they have four branches instead of two.

According to number and type of gills, the genera in question can be arranged in the following way (the gills of *Tylaspis* are unknown):

- (1) With 13 pairs:

Tomopaguroides (trichobr.)
Paguropsis (phyllobr., bifid)
Tomopaguropsis (phyllobr., bifid)
Paguristes (phyllobr.)
Xylopagurus (phyllobr.)
[? *Munidopagurus* (phyllobr.)]

- (2) With 11 pairs:

Parapagurus (trichobr.)
Sympagurus (phyllobr.)
Tomopagurus (phyllobr.)
Probeebei (phyllobr.)

Probeebei has a very small flagellum (appendix) on the endopodite of the maxillula (Fig. 3 b, pag. 16). In most of the above mentioned genera this appendage is not described. The flagellum is absent in *Parapagurus*, *Xylopagurus*, and *Tomopagurus*. It is well developed (2-jointed) in *Paguristes*.

MELIN does not mention the significance of the presence or absence of a flagellum on the exopodite of the first maxillipeds, but in my opinion this must be at least as important as the flagellum of the maxillula. In the above genera it seems to be absent only in *Parapagurus*, *Sympagurus* and *Probeebei* and is at any rate present in *Paguristes*, *Xylopagurus*, *Tomopaguropsis*, and *Tomopagurus*.

Finally, after correctly having denied the morphology of the very adaptable chelipeds any systematic importance, MELIN (l. c.) claims that besides the heterochirality also the plane in which the fingers move is of "rather great systematic value". I have compared two extremes, *Parapagurus* and *Pagurus* (= *Eupagurus*) and found this character so arbitrary that in my opinion little importance should be attached to it. Anyhow, in *Probeebei* the movement is very much as in *Pagurus* and must therefore be in the horizontal plane.

If we primarily consider the number of paired pleopods and of gills, we find that *Probeebei* is closest related to *Tomopaguropsis*, *Tomopaguroides* and first and foremost to *Tomopagurus*; with the latter it does not only agree in number of paired pleopods and in number and type of gills, but also in the horizontal movement of the fingers of the chelipeds.

It differs from *Tomopagurus* in having no unpaired pleopods in the male, in the presence of a small flagellum on the maxillula and the absence of a flagellum on the first maxilliped.

It also agrees with *Parapagurus* (and *Sympagurus*) in several respects: Number of gills, absence of flagellum on the first maxilliped, and lack of right genital opening in the female (see below). It differs in number of male pleopods and presence of a small flagellum on the maxillula.

It is interesting that all the genera listed below, which are most closely related to the bathyal-abyssal *Probeebei* are sublittoral or preferably bathyal or abyssal, thus very rarely occurring at temperatures above 15°C. or there-about.

Tomopagurus rubropunctatus: Barbados, 132 m.

Tomopaguropsis lanata: Off Ceylon, 260-730 m and 668 m.

Tomopaguropsis problematicus: Off Florida and Barbados, 229 and 527 m.

Tomopaguroides valdiviae: Off East Africa, 1079 m.

Xylopagurus rectus: West Indies, 245-267 m.

Xylopagurus cancellarius: Off Colombia, 73 m.

Tylaspis anomala: Central South Pacific, 4343 m.

Parapagurus (about 10 species): Cosmopolitan, bathyal and abyssal (to 4130 m), except two littoral species (18 and 35 m) at high latitudes.

Sympagurus (about 10 species): probably cosmopolitan, bathyal, except one sublittoral species (S. E. Australia, 40-102 m).

Generically, *Probeebei* is well characterized by the calcified abdomen, the presence of a small flagellum on the endopodite of the maxillula, the lack of a flagellum on the exopodite of the first maxilliped, the number of pleopods, and the number and type of gills. However, as demonstrated above, it falls well within the frames of existing families and subfamilies. Consequently, the family Probebeidae (BOONE 1926 b) must be rejected.

Similarities by convergence

Shape and calcification of the carapace and the abdomen. BORRADAILE (1916) pointed

out that Nature's attempts to evolve a crab by convergence result in forms with broadened, mostly flattened carapaces, preferably with spines along the margins and with a distinct rostrum. The abdomen becomes reduced and is eventually bent firmly under the thorax in the way found in Lithodidae, *Lomis*, Porcellanidae, and in true crabs. Less carcinized hermit crabs than *Lomis* and the Lithodidae are the following pagurid genera (Fig. 11): *Porcellanopagurus* (with four Pacific species which hide the short, almost symmetrical abdomen under a bivalve shell), *Tylaspis* (with one Central Pacific, abyssal species with somewhat reduced, probably uncovered abdomen), *Ostraconotus* (with one West Atlantic species with much reduced, uncovered abdomen), and, finally, the Robber Crab *Birgus latro* with a large, almost entirely calcified abdomen. A further example is *Probeebei*. All these five genera have the posterior portion of the carapace larger and more swollen than in the ordinary hermit crabs in gastropod shells. This portion is also as calcified as the anterior one, except in *Porcellanopagurus* where it is covered by the bivalve shell. A distinct rostrum is present in all except *Ostraconotus*. A depression of the carapace similar to that in especially *Porcellanopagurus* and *Ostraconotus* is not found in *Probeebei*.

BORRADAILE (l. c.) already called attention to the extraordinary similarity in shape and calcification of the carapace between the above genera and the N. E. Pacific, littoral species *Pagurus splendescens* (Owen) which also exhibits the same grooves as *Probeebei* (p. 14). However, its abdomen appears to be just as soft and asymmetrical as in other species of *Pagurus* and to be hidden in a snail shell. It seems difficult to understand what has induced this marked carcinization of the thorax in *P. splendescens*. A close study of the morphology and habits of the species might throw light on this point, but, unfortunately, no specimens were available to me.

The abdomen of *Probeebei* is more calcified than in any other representative of the Paguridea, except the Lithodidae and *Lomis*. It is soft-skinned in *Porcellanopagurus*, *Tylaspis* and *Ostraconotus*, but almost fully calcified in the symmetrical Pylocheliidae and in *Birgus*. In the latter the great majority of the outer surface of each abdominal segment is covered by the large, flat tergum and by "small subsidiary platelets (pleura) on either flank" (ALCOCK 1905, p. 149) – cf. HARMS 1932, pl. 8-10. In *Probeebei* the terga not only cover the entire outer surface of the segments, but are also sculptured and furnished

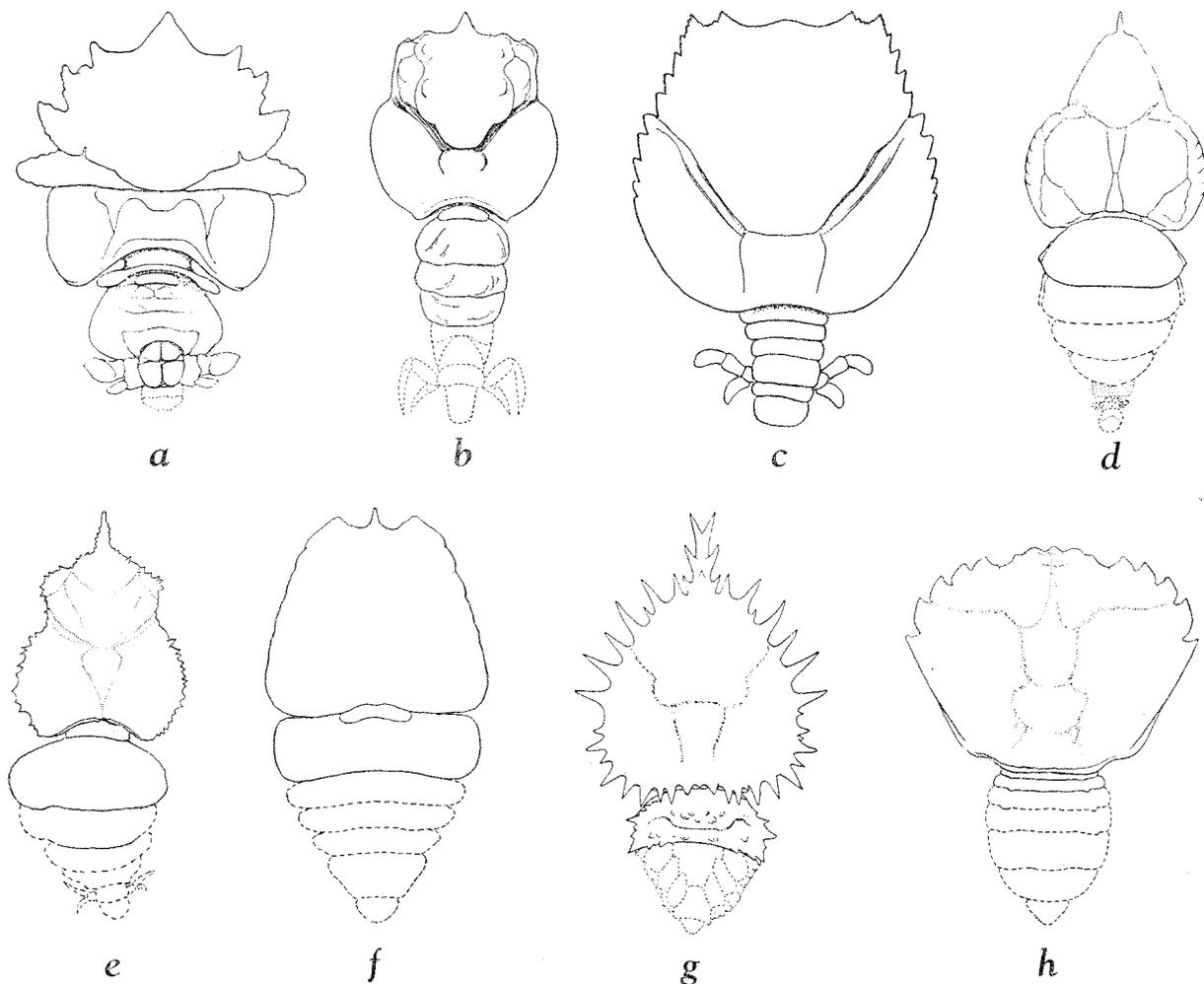


Fig. 11. Carcinization in Paguridea. In each case the part indicated by a dotted line is normally carried under the rest of the body. Not drawn to scale. a, *Porcellanopagurus*; b, *Tylaspis*; c, *Ostraconotus*; d, *Birgus*; e, *Probeebei*; f, *Lomis*; g, *Lithodes*; h, *Carcinus*. (After BORRADAILE 1916, somewhat altered).

with a stabilizing crest along the posterior margin. As in *Lithodes arctica* the second segment is much larger than the others and consists of a single plate without sutures. – A symmetrical or practically symmetrical tail-fan is found not only in the above mentioned genera, but also in species which hide the abdomen in a straight and elongated cavity, e. g. in wood (*Xylopagurus*), in a *Dentalium* shell (*Tomopaguroides*, species of *Parapagurus* and *Pylopagurus*), in straight annelid tubes (*Orthopaguropsis*, species of *Pylopagurus*), in a sack-shaped *Epizoanthus* colony (*Paguropsis*), or in coral rock (*Cancellus*).

Unpaired sexual opening in the female. In females of *Probeebei* only the left genital opening on the coxa of pereopods III is developed – without any trace of the corresponding opening on the right coxa. This peculiar feature was previously

described in a few other genera only: *Parapagurus* (and *Sympagurus*) and *Paguristes*; in the latter it is restricted to nine littoral species along the West-African coast and one species in the Red Sea (FOREST 1954 a, p. 160 and fig. 69). Thus, the unpaired left pleopod is found only in genera in which there are one or two pairs of pleopods in the males. Of the remaining of such genera the openings are paired in all the species of *Paguropsis* which are kept in this Museum. On my request females of the following species were kindly examined by the following colleagues: *Xylopagurus rectus* (A. M.-Edw.) by Dr. J. FOREST (Paris), *Tomopaguropsis problematicus* (A. M.-Edw. & Bouvier) by Dr. E. DEICHMANN (Harvard), and *T. lanata* Alcock by Dr. G. RAMAKRISHNA (Calcutta); in all cases the genital openings were found to be paired. Females of the remaining genera (*Tomopagurus*, *Tomopaguroides*, and *Tylaspis*) are unknown.

In females of one species of the Pylochelidae, *Cheiroplatea laticauda* Boas, the opposite is found: the right genital opening is present, the left absent. I found the similar in an unidentified species of *Diogenes* in this Museum, and Dr. FOREST kindly informed me that this is also the case in three species of *Diogenes*: *D. custos* (F.), *D. miles* (Herbst), and *D. diogenes* (Herbst).

Apparently, it is not possible to ascribe any phylogenetical significance to unpaired female genital openings. Although a left opening occurs exclusively in genera with paired male pleopods, this is not the case in all such genera, and in *Paguristes* it is found only in some of the species; moreover, the genera belong to two different subfamilies. Genera with an unpaired right genital opening (*Cheiroplatea* and *Diogenes*) are still less related, and also in *Diogenes* only some species exhibit this feature.

Appendages. The ocular peduncles and corneae of *Probeebei* do not show any reduction despite the abyssal environment. The ophthalmic scale is, however, unusually small and is apparently absent in the likewise abyssal *Tylaspis anomala* (HENDERSON 1888, p. 81). Both species have also a low number of joints (six) in the lower flagellum of the antennula and peraeopods II and III are considerably elongated (especially the dactylus) and somewhat compressed. This feature is found also in species of the bathyal-abyssal genus *Parapagurus*, and a similar elongation of the walking legs is well known in a great many deep-sea crustaceans. Peraeopods IV of *Probeebei* have lost the function of being pressed against the inner wall of the gastropod shell and of assisting in the movement out of and into a shell (BROCK 1926, p. 437); accordingly, they are without file-like surface and – again as in *Tylaspis* (BORRADAILE 1916, fig. 12) – with a rudimentary chela which cannot function as such. The abundant growth of soft setae, also on this pair of legs, may indicate that they share with peraeopods V the cleaning of the gill chamber and perhaps also of the eggs. Finally, also the outer surface of the uropods has become almost smooth, not file-like.

Conclusions

No other group of crustaceans exhibits such a variety of adaptations to the environment as the hermit crabs. The primitive, still entirely symmetrical Pylochelidae descend almost directly from halassinid ancestors and have primarily survived

at bathyal depths where the possibilities of a partly hidden existence apparently are the best. The evolution of the Paguridae has undoubtedly taken place in shallow water in the tropics on a hard bottom of corals or rock where, however, the feasibility of digging retreats is small. Here the habit of hiding the semi-calcified, exposed abdomen first in natural cavities in the rock (BOAS 1926 a, p. 8) and later in the ever abundant, empty gastropod shells evolved, and the asymmetry and other adaptations to life in a shell were eventually introduced. HARMS (1932, p. 275) claims that the acquisition of the asymmetrical abdomen is not very old, since it is not yet perfectly genotypically induced: MARCHAL (1891), BOUVIER (1892), THOMPSON (1903), and others report on pagurids which with equal readiness accept left coiled as well as the usual right coiled gastropod shells. Another example of this is probably found in *Paguropsis typica* Henderson which protects the almost symmetrical abdomen with a colony of the actinian *Epizoanthus paguropsidis*. Both ALCOCK (1905, p. 27) and BOAS (1926 b, p. 14) report that in both sexes now the left, now the right pleopods are developed. On the other hand, the asymmetry of the hermit crabs is so genotypically fixed that it inevitably appears in the first post-larval stage, independent of whether a snail shell is occupied or not.

In places where gastropod shells were not available in sufficient number (or for other reasons?) the hermit crabs have had the ability to find other means of protecting their abdomen. The furthest advanced adaptation towards this challenge of the environment is undoubtedly found in the Lithodidae or Stone Crabs which are perfectly carcinized, but between this, probably very recent, group (which is unknown as fossils) and the typical, asymmetrical hermit crabs in gastropod shells we find a rich variety of transitional forms. It is characteristic that most of these are met with in the deep-sea, although some (*Cancellus*, *Orthopaguropsis*, *Xylopagurus cancellarius*, *Porcellanopagurus* a. o.) are littoral.

There are several examples of *Dentalium* shells being occupied by Paguridae in the deep-sea: *Parapagurus chuni*, *P. spinimanus*, *Tomopaguroides valdiviae* (BALSS 1912, pls. VIII-XI) and *Pylopagurus discotdalis* A. M.-Edw. (MILNE-EDWARDS & BOUVIER 1893, pl. VI, 7) have attained a totally symmetrical abdomen apart from the lack of right hand pleopods. All these species are bathyal.

A further step has been taken by the above mentioned species *Ostraconotus spatulipes* (A. M.-Edw.)

which lives at 220 m depth in the West Indies and *Tylaspis anomala* Henderson (1888, p. 81) which is the so far deepest recorded hermit crab from a depth of 4343 m in the Central South Pacific. *Tylaspis* has had the abdomen somewhat, *Ostraconotus* the abdomen greatly reduced (Fig. 11). There is no doubt that the abdomen is unprotected in the latter,¹ while the situation in *Tylaspis* is unsettled. HENDERSON and BORRADAILE who are the only ones who have actually studied the male holotype and only specimen both suggest some sort of protection. The former says (l. c.): "The form of the abdomen points to the species having occupied some other dwelling place than the Gastropod shell usually selected by the soft-tailed Pagurids", and BORRADAILE writes (1916, p. 123): "— the soft abdomen is probably somehow protected in life. Perhaps ... it is merely buried in the soft ooze of the sea floor. Certainly in *Ostraconotus* it is not carried under the cephalothorax, and its unarmoured dorsal side makes it unlikely that this is the case in *Tylaspis*." On the other hand, BALSS (1924, p. 763) and MELIN (1939, p. 15) take it for granted that *Tylaspis* lives freely. Without having seen the specimen it is of course difficult to decide this question, but at any rate it seems impossible — judging from the extreme length of the walking legs — to presume that the soft abdomen is buried in the ooze, as suggested by BORRADAILE. The similarity in general appearance with the undoubtedly free-living *Probeebei*, the lack of working chelae on pereopods IV, and the very small size of these and prps. V² make it most probable that the abdomen is unprotected in spite of its soft-skinned nature.

The most advanced evolution along the said line has been achieved by *Probeebei mirabilis* with its fully calcified and well armoured carapace and abdomen. It is difficult to determine how many of the previously mentioned similarities between this species and *Tylaspis* are due to true relationship and how many to convergence in an equal environment, the more so since females of *Tylaspis* are unknown.

Among the asymmetrical pagurids there are three instances of forms with a fully calcified abdomen, viz. the Lithodidae, *Birgus latro* and *Probeebei*, which have arisen from very different stocks within

1. Except BORRADAILE (1916, p. 123) who presumes that it may be buried in the soft sediments on the bottom.
2. MELIN (l.c.) writes that prps. V are monodactylous, but HENDERSON only describes them as "almost rudimentary" without further explanation.

the Paguridae: the Lithodidae from species of Pagurinae close to *Nematopagurus* and *Pylopagurus* of the present day (BOAS 1924, p. 25), *Birgus* (and *Coenobita*) from Diogeninae, and *Probeebei* from the primitive "Paguristinen" of BOAS (1924).

The Lithodidae represent the most advanced, almost crab-shaped stage, while *Birgus* and *Probeebei* are unable to fold the abdomen firmly against the thorax. It is interesting to observe that the two latter, apparently very parallel, lines of evolution have occurred in habitats which must both be considered extremes: dry land and the abyssal depths. It is also characteristic that the genus *Birgus* is definitely and *Probeebei* probably monotypical.

In *Birgus* the calcification of the abdomen is certainly a result of the fact that easy access to very nutritious fruits far inland has led to a giant growth and subsequent lack of sufficiently large shells for protection (HARMS 1932, p. 279). Unlike the species of the also land-dwelling genus *Coenobita* which may take advantage of very large shells of *Turbo*, the Robber Crab never makes use of marine shells (HARMS 1938, p. 21) and is thus restricted to the usually small-sized species of land shells on their native island.

HARMS could postpone the calcification of the abdomen and a considerable number of other characters related to a free-living habit (1938, p. 33) by experimentally offering the young crabs sufficiently large gastropod shells. On Christmas Island the crabs may give up the shell cover already in the first post-larval stages and must invariably do so after a few further moults, at a length of carapace of 6-7 mm. In the Moluccan Islands this occurs at a length of 10-11 mm, but four-year-old crabs from Christmas Island with a carapace length of 21 mm and a soft and perfectly asymmetrical abdomen, hidden in a shell, were still alive in captivity when HARMS' paper was published.

If the interpretation of these experiments is correct, they seem to indicate that the calcification of the abdomen of *Birgus* is not yet genetically fixed and suggests a relatively late evolution of the species. This is supported by the fact that no fossils of *Birgus* are known, in spite of its large size and well calcified exterior.

The recovery in the Lithodidae, *Birgus* and *Probeebei* of a calcified abdomen must, however, have taken place over a long period of time. PRZIBRAM (1907) claimed that experiments with species of *Pagurus* and *Diogenes* without a shell ("enthäust") showed that already after the first moult they would

acquire a distinctly segmented, rather contracted abdomen with a somewhat hardened and pigmented skin. This result is in strong opposition to the findings of THOMPSON (1903): Quite independent of the presence or absence of a shell the young hermit crab will in the glaucothoe and the first of the post-larval stages acquire an asymmetrical abdomen into which certain intestines will move. Later BRINCKMANN (1926) repeated PRZIBRAM's experiments on a much larger scale and very convincingly showed that also in adult hermit crabs the morphology of the abdomen is not the least influenced by the removal of the shell.

Finally, it should be pointed out that in several respects *Birgus*, during the evolution to the habit of a freely roaming animal, has become considerably more changed than *Probeebei*. This cannot be explained by the fact that *Birgus* is restricted to dry land, which must be the most extreme habitat for decapods. A comparison with the closely related Coenobitidae which are also land-dwelling, but use a shell, shows that only *Birgus* has acquired the characters mentioned below.

In one essential respect, calcification of the abdomen, *Probeebei* is further advanced than *Birgus* (p. 26). On the other hand, peraeopod IV of *Probeebei* has still almost the same size as in shell-bearing pagurids, but when *Birgus* leaves the shell and becomes free-living this leg is modified from a short appendage used for holding the shell into a strong leg which, together with the preceding legs, is used for walking.¹ Besides, not only the male, but also the female abdomen of the adult *Birgus* is practically symmetrical, and the uropods have become reduced almost to nothing. Also the eye-stalks, the antennulae, and the antennae are different from those in Coenobitidae, and a pair of lungs is developed.

Probeebei mirabilis shows only one feature which is characteristic of many deep-sea decapods: the elongate walking legs. As in other abyssal pagurids, the eyes are apparently well developed (although the ophthalmic scale, as in *Tylaspis*, is reduced), the size of the eggs is very small, and the colour of the carapace and legs is unusually bright for a bathyal-abyssal animal.

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1. In the Lithodidae peraeopod IV has even become as large as and shaped exactly like the two preceding pairs of legs.

tention to the description of *Probeebei mirabilis*, thereby giving me the fine opportunity to have this species pinned down. Also to Dr. JOCELYN CRANE and the New York Zoological Society for lending me the holotype without which the identity of the material could not have been established. Dr. JACQUES FOREST of the Natural History Museum in Paris furnished me with valuable information about unpaired sexual openings in female pagurids and with a photostat copy. The majority of the illustrations were prepared by Mr. POUL H. WINTHER.

Summary

1. *Probeebei mirabilis* Boone, 1926 is redescribed. It is primarily characterized by the completely calcified carapace and abdomen, the elongated peraeopods II and III, lack of paired pleopods in the female, presence of paired pleopods I in the male, and 11 pairs of phyllobranchiae. The abdomen is very nearly symmetrical in the male, asymmetrical in the female. The adults are 55 mm-65 mm long; they show only slight variation.

2. Three late post-larval stages are available. In view of their considerable size (19-25-37 mm) it is remarkable that the reduction of the right pleopods 2-5 in the female and left and right pleopods 2-5 in the male does not occur till during the youngest of these stages.

3. The holotype is a juvenile, belonging to the youngest of the post-larval stages represented in the *Galathea* material; practically no differences were found. The original description is cited and discussed.

4. The holotype was collected by the *Arcturus* Expedition S. of Cocos Island, Gulf of Panama at 1145 m depth and 4,3°C. The *Galathea* material comprises 18 specimens from the East Pacific off Costa Rica, 3570 m depth, 2,0°C.

5. Phylogenetically, *Probeebei* is most closely related to other genera with paired pleopods in the male and 11 phyllobranchiae: *Tomopagurus*, *Parapagurus* (and *Sympagurus*), and *Tylaspis*. Of these the three last ones are also bathyal or abyssal in distribution.

6. *Probeebei* is another instance of carcinization, i. e. the evolution by convergence of crab-like forms which has occurred in several, systematically unrelated pagurids. Both in carcinized pagurids and in species which protect the abdomen in more or less straight objects such as *Dentalium* shells, worm tubes, pieces of wood, and coral rock, the abdomen has become secondarily symmetrical to a larger or

smaller degree. Such forms are primarily found at bathyal or abyssal depths where sufficient gastropod shell material apparently is not available. The most advanced step was taken by the Lithodidae, the Robber Crab *Birgus latro*, and *Probebebi* which all have a completely calcified, unprotected abdomen. The former and the latter evolved in cold waters, while *Birgus* became a terrestrial form. The evolution of *Birgus* and *Probebebi*, which are only distantly related, has taken place along parallel lines. The abdomen of *Probebebi* is more thoroughly calcified, but in other respects (use also of peraeopods IV as walking legs, almost complete reduction of the uropods, more symmetrical abdomen in the females, etc.) *Birgus* is more adapted to the life as a freely roaming animal.

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