

Revisiting *Tylaspis anomala* Henderson, 1885 (Parapaguridae), with comments on its relationships and evolution

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ABSTRACT

The parapagurid hermit crab *Tylaspis anomala* Henderson, 1885, has been discovered living in association with anemones in New Caledonia. Very few specimens were known of this species, previously thought to carry its abdomen unprotected, or perhaps bury it in the soft bottom sediment. The study of all available specimens of this striking hermit crab revealed lack of details and morphological inaccuracies in published accounts. As a result, the monotypic genus *Tylaspis* Henderson, 1885 has been rediagnosed, and *T. anomala* Henderson, 1885 redescribed and illustrated. The genus *Tylaspis* has been found to be more closely related to another monotypic genus, *Probebebi* Boone, 1926, represented by *P. mirabilis* Boone, 1926, than to any other parapagurid genus. A summary of the taxonomy and diagnosis of *P. mirabilis* is presented. The morphological similarities and differences, pleopod development, and habitat of these two species are discussed. Possible evolutionary explanations of their unusual morphology are explored.

KEY WORDS

deep-water hermit crab,
Parapaguridae,
Tylaspis,
Probebebi,
morphology,
pleopod development.

RÉSUMÉ

Réexamen de *Tylaspis anomala* Henderson, 1885 (Parapaguridae) et discussion sur ses affinités et son évolution. *Tylaspis anomala*, un Parapaguridae associé à des actinies, a été découvert en Nouvelle-Calédonie. On ne connaissait que très peu de spécimens de cette espèce et on croyait que son abdomen n'était pas protégé ou bien qu'elle s'enfouissait dans les sédiments meubles. L'étude de tous les spécimens disponibles de ce pagure étonnant a révélé, dans les descriptions précédentes, l'absence de détails morphologiques et des imprécisions. Le genre monotypique *Tylaspis* Henderson, 1885 est redéfini et *T. anomala* est redécrit et figuré. Le genre *Tylaspis* apparaît plus proche d'un autre genre monotypique, *Probeebei* Boone, 1926, représenté par *P. mirabilis* Boone, 1926, que d'aucun autre genre de Parapaguridae. La taxonomie et une diagnose de *P. mirabilis* sont brièvement présentées. Les similitudes et différences morphologiques, le développement des pléopodes et l'habitat de ces deux espèces sont discutés. Des hypothèses explicatives sur l'évolution de leur morphologie inhabituelle sont proposées.

MOTS CLÉS

pagures de profondeur,
Parapaguridae,
Tylaspis anomala,
Probeebei mirabilis,
morphologie,
développement des pléopodes.

INTRODUCTION

The unusual hermit crab *Tylaspis anomala* Henderson, 1885 was described from a male specimen discovered in deep waters (4344 m) of the South Pacific during the British *Challenger* expedition (1872-1876) (Henderson 1885, 1888). According to Henderson (1888), the calcified cephalothorax apparently unprotected by a gastropod shell, alone sufficed to distinguish *T. anomala* from all other hermit crabs. Since the original description, *T. anomala* has been mentioned in faunistic studies and evolutionary discussions of paguroids, or used as one of the prime examples of life in the deep sea (e.g. Alcock 1905; Pzibram 1905; Borradaile 1916; Wolff 1961a, b; Russell 1962; Menzies *et al.* 1973; Marshall 1979; Gage & Tyler 1991). Additional material was reported by de Saint Laurent (1972), including the first known females, based on collections obtained during one of the US *Albatross* expeditions. De Saint Laurent also reinstated and redefined the family Parapaguridae, and placed *T. anomala* in this family based on such characters as presence of labral spine, lack of exopodal flagellum on the

first maxilliped, undivided abdominal tergites, unpaired left gonopore in females, and telson lacking median constriction. This familial arrangement has been followed by subsequent carcinologists (McLaughlin 1983; Lemaitre 1989, 1996).

During studies of the extensive deep-water hermit crab collections obtained during various recent French sampling campaigns in the New Caledonia region, two relatively large, well-preserved male specimens of *Tylaspis anomala* were found, each carrying an anemone as means of protection. Previous specimens of *T. anomala* had been collected without any evidence of protection for their abdomen, leading carcinologists to speculate whether this species was free-living with its abdomen unprotected (Balls 1924; Melin 1939; Wolff 1961a, b), or protected its membranous abdomen by burying it in the soft ooze of the sea floor (Borradaile 1916). The discovery of the New Caledonia specimens suggests an answer to this long-standing question. Also during this study, an additional specimen of *T. anomala* collected in the western Pacific east of Guam, was located in the Zoological Museum of Moscow State University (D. Zhadan, pers.

comm.). This finding extends considerably the distribution of this species from the eastern South Pacific to the western Pacific.

In addition to the apparent absence of shell-carrying behavior, there are also several morphological characteristics of *Tylaspis anomala* that are unusual among hermit crabs. Most striking are: the calcification of the posterior carapace and its partial fusion with the shield; the apparent absence or considerable reduction of the ocular acicles; very long, slender and spinous walking legs (second and third pereopods); the lack of propodal rasp on the fourth pereopod; and symmetrical uropods and telson. Despite the unusual

features found in *T. anomala*, surprisingly few details on these and other important aspects of its morphology are available in published accounts. For example, previous descriptions of *T. anomala* indicate that males have only paired first and second pleopods, and unpaired left third to fifth (Henderson 1888; de Saint Laurent 1972). However, the New Caledonia male specimens have five pairs of pleopods, albeit the third to fifth are asymmetrical (left biramous, right uniramous and short). Detailed examination of other available material of *T. anomala*, revealed additional discrepancies or inaccuracies in published accounts of this taxon. In view of these

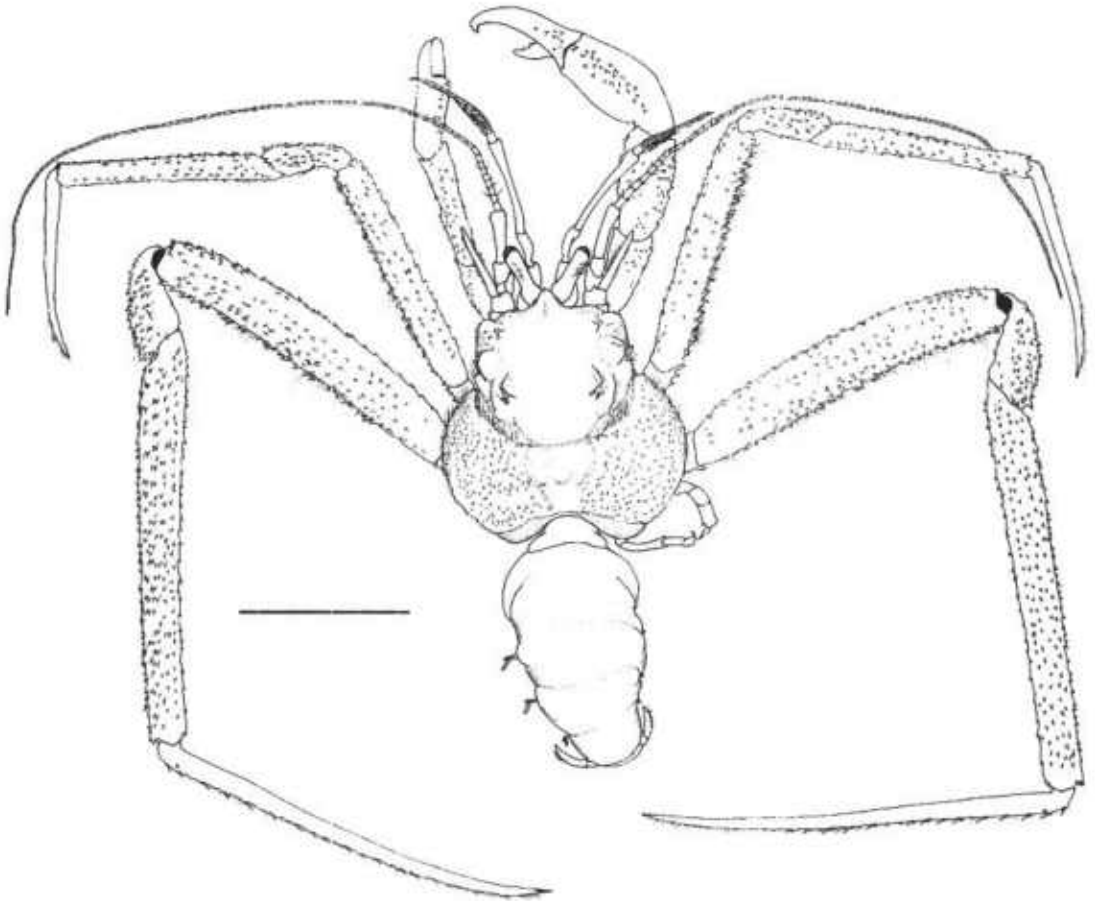


FIG. 1. — *Tylaspis anomala* Henderson, 1885. New Caledonia, BIOCAL stn CP 17, dorsal view of ♂ (SL 8.7 mm) (MNHN-Pg 5533). Scale bar: 10 mm.

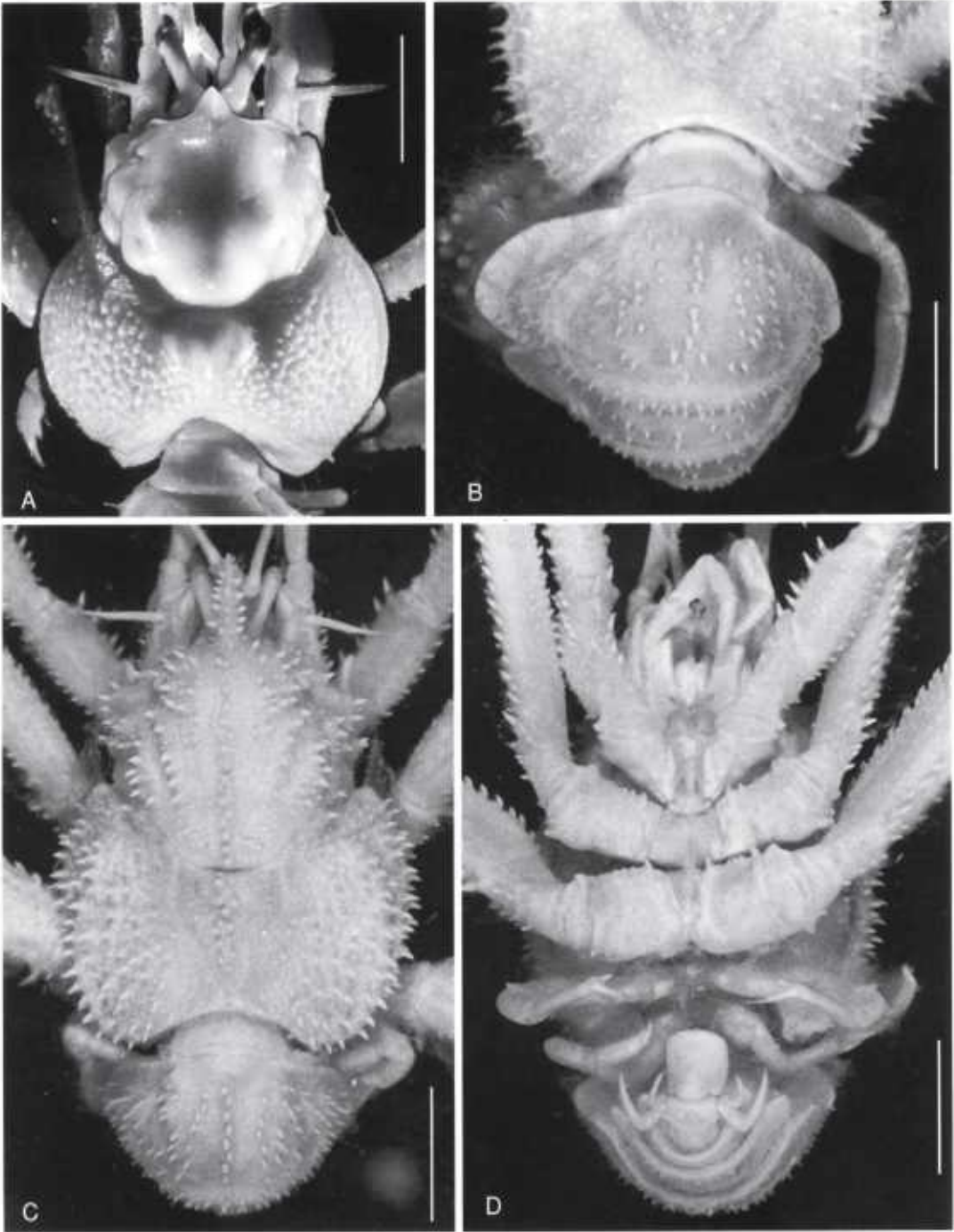


FIG. 2. — **A**, *Tylaspis anomala* Henderson, 1885, New Caledonia, BIOCAL stn CP 17, ♂ (SL 8.7 mm) (MNHN-Pg 5533): cephalic appendages, shield, and posterior carapace (dorsal view); **B-D**, *Probeebei mirabilis* Boone, 1926, eastern Pacific, off Peru, Albatross stn 4647, 04°33'S - 87°42'30"W, 2005 fm, 3667 m, 9.XI.1904 (USNM 267810); **B**, abdomen, posterior portion of cephalothorax and right fourth pereopod (dorsal view) of ovigerous ♀ (SL 20.7 mm); **C**, cephalothorax and abdomen (dorsal view) of ♂ (SL 23.9 mm); **D**, sternum, abdomen, uropods and telson (ventral view) of same ♂. Scale bars: A, 5 mm; B-D, 10 mm.

deficiencies, it is clear that a more detailed and accurate diagnosis of the monotypic genus *Tylaspis* is needed, as well as a redescription of its species *T. anomala*.

While comparing the morphology of *T. anomala* with that of other parapagurids, it was found that many characters are shared with another unique parapagurid, *Probeebei mirabilis* Boone, 1926, to which *T. anomala* is probably most closely related. The morphological similarities and differences of these two species are described in detail, including pleopod development as estimated from a small series of young individuals. The possible evolutionary interpretation of the unusual morphology of the cephalothorax and abdomen of these two species is briefly discussed. Although *P. mirabilis* has been previously described in detail by Wolff (1961b), it is appropriate for comparison purposes to include here a summary of its taxonomy as well as diagnostic characters based on the examination of many specimens in the collections of the National Museum of Natural History, Smithsonian Institution, Washington D. C. (USNM), and Zoologisk Museum, Copenhagen (ZMK).

The New Caledonia material of *T. anomala* is deposited in the Muséum national d'Histoire naturelle, Paris (MNHN); the type is housed in The Natural History Museum, London [formerly British Museum (Natural History)] (NHM); the *Albatross* specimens are part of the collections in the USNM; and an additional specimen is deposited in the Zoological Museum Moscow State University (ZMUM). The type of *Probeebei mirabilis* Boone, 1926 remains deposited in the American Museum of Natural History, New York (AMNH). A single measurement, shield length, indicative of size, is included in parenthesis, as measured (to the nearest 0.1 mm) from the tip of the rostrum to the midpoint of the posterior margin of the shield. General terminology follows McLaughlin (1974) and Lemaitre (1989), except for grooves, lineae, and sulci, used as summarized in Lemaitre (1995: 2, fig. 1); the sulcus verticalis was not included by Lemaitre, and is used as defined by Boas (1926) and Pilgrim (1973). The term "semichelate" is used according to the definition provided by McLaughlin (1997: 435).

SYSTEMATICS

Genus *Tylaspis* Henderson, 1885

Tylaspis Henderson, 1885: 900; 1888: 81. — A. Milne Edwards & Bouvier 1893: 7. — Alcock 1905: 25. — Borradaile 1916: 121, figs 12, 13b. — Balss 1927: 1012. — Melin 1939: 13. — Wolff 1961a: 931; 1961b: 25, fig. 11b. — Gordan 1956: 342. — de Saint Laurent 1972: 120. — Marshall 1979: 304. — Gage & Tyler 1991: 83.

TYPE SPECIES. — *Tylaspis anomala* Henderson, 1885, by monotypy.

DISTRIBUTION. — Pacific Ocean.

DIAGNOSIS

Eleven pairs of phyllobranchiate gills. Shield and

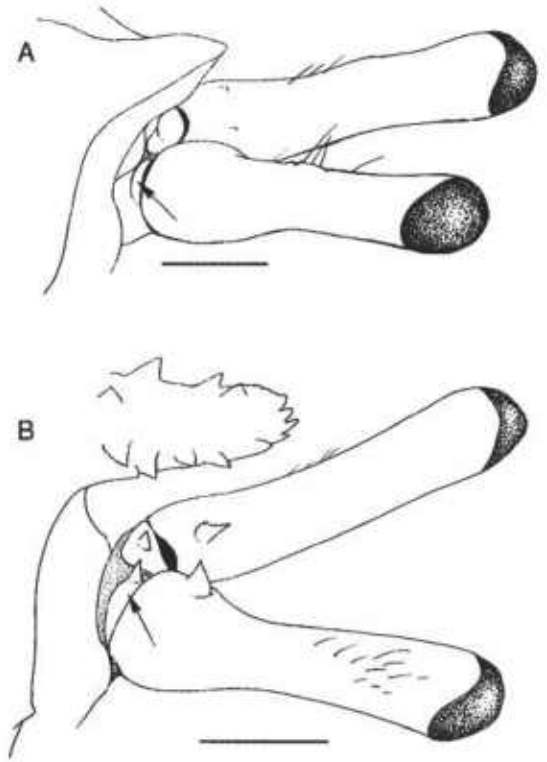


FIG. 3. — Ocular peduncles, acicles (arrows) and rostrum (dorsolateral view): A, *Tylaspis anomala* Henderson, 1885, New Caledonia, BIOCAL stn CP 17, ♂ (8.7 mm) (MNHN-Pg 5533); B, *Probeebei mirabilis* Boone, 1926, eastern Pacific, off Peru, *Albatross* stn 4647, 04°33'S · 87°42'30"W, 2005 fm, 3667 m, 9.XI.1904 (USNM 267810). Scale bars: A, 1 mm; B, 2 mm.

posterior carapace partially fused (Figs 1, 2A), well-calcified. Rostrum well developed. Branchiostegites membranous. Shield marked by deep calcified cervical groove and linea transversalis; dorsal surface strongly convex. Posterior carapace (Fig. 2A) lacking lineae or sulci; lateral margins arciform. Ocular acicles (Fig. 3A) reduced. Antennular and antennal peduncles distinctly overreaching eyestalks. Fourth segment of antennal peduncle (Fig. 4B) unarmed. Thoracic sternite (Fig. 4G) of chelipeds narrow. Sternites of second and third pereopods moderately broadened. Sternites of fourth and fifth pereopods each consisting of transverse rod subdivided in midline, that of fifth very narrow and widely separated from preceding sternite. Ambulatory legs (Fig. 1) very long and slender; second walking leg (third pereopod) distinctly longer than first (second pereopod). Abdomen membranous (Fig. 1), except for moderately calcified tergite of first somite and pleura of second somite. Uropods and telson (Fig. 4H) symmetrical. Males with well-developed paired first and second pleopods modified as gonopods, and asymmetrically paired third to fifth pleopods; left third to fifth pleopods biramous, right third to fifth rudimentary (each consisting of small bud). Females lacking first pleopods; second to fifth pleopods paired (symmetrical or asymmetrical).

Tylaspis anomala Henderson, 1885
(Figs 1, 2A, 3A, 4-7)

Tylaspis anomala Henderson, 1885: 900, fig. 329; 1888: 81, pl. 8, fig. 5. — Alcock 1905: 191. — Pzibram 1905: 198. — Balss 1924: 763, fig. 19. — Melin 1939: 15. — Gordan 1956: 342. — Wolff 1961b: 26. — Russell 1962: 20. — de Saint Laurent 1972: 121. — Menzies *et al.* 1973: 235.

HOLOTYPE. — **South Pacific.** *Challenger*, stn 285, 32°36'S - 137°43'W, 2375 fm (4344 m): 1 ♂, 5.7 mm (NHM 1888: 33).

ADDITIONAL MATERIAL. — **New Caledonia.** NO *Jean Charcot*, BIOCAL stn CP 17, 20°35'S - 167°25'E, 3680 m, 14.VIII.1985: 2 ♂♂, 7.2, 8.7 mm (MNHN-Pg 5533).

Pacific Ocean (other). NE of Easter Island, *Albatross*, stn 4701, 19°11'S - 102°24'W, 2265 fm (4143 m), 26.XII.1904: 2 ♂♂, 6.5, 6.5 mm; 2 ♀♀, 5.9, 8.0 mm (USNM 168482). — E of Guam, *Akademik*

Mstislav Keldysh, 9th cruise, stn 1065, 14°09.5'N - 155°54.04'E, 3800-4270 m, 4-5.XI.1984: 1 ♂, 8.0 mm [not seen] (ZMUM Ma-4831).

DISTRIBUTION. — Pacific Ocean: NE of Easter Island; New Caledonia; and East of Guam (D. Zhadan, pers. comm.). Depth: 3680 to 4344 m.

HABITAT AND SYMBIOTIC ASSOCIATIONS. — The specimens from New Caledonia (MNHN-Pg 5533) were each found carrying an unidentified anemone (removed and under study by D. Doumenc, A. Crosnier, pers. comm.).

REDESCRIPTION

Shield (Figs 1, 2A) approximately as broad as long. Dorsal surface strongly convex, uneven, with scattered short setae; with distinct bulges on lateral region, most bulges with one or more small spines dorsally. Rostrum prominently triangular, well in advance of lateral projections of shield; with distinct mid-dorsal ridge. Anterior margins weakly concave. Lateral projections broadly rounded. Anterolateral region with one to four small spines dorsally. Ventrolateral margin with small spine. Posterior margin broadly rounded. Anterodistal margin of branchiostegite rounded, unarmed, setose.

Posterior carapace (Figs 1, 2A) with numerous small spines on dorsolateral surfaces; dorsomedian or cardiac region somewhat elevated, glabrous, weakly subdivided into three low rounded longitudinal ridges. Branchiostegites (Fig. 4A) divided into anterior and posterior portion by broad, shallow sulcus verticalis.

Ocular peduncles less than half length of shield, inflated basally, and with short dorsal row of long setae. Cornea pigmented, width subequal to distal width of ocular peduncle.

Antennular peduncle long, slender, exceeding distal margin of cornea by half length of penultimate segment; ventral flagellum with six or seven articles. Ultimate segment twice as long as penultimate segment, with scattered setae. Basal segment with strong ventromesial spine; lateral face with distal subrectangular lobe of statocyst armed with two or three small spines, and strong simple or bifid spine proximally.

Antennal peduncle (Fig. 4B) exceeding distal margin of cornea by approximately 0.3 length of fifth segment. Flagellum long, exceeding extended

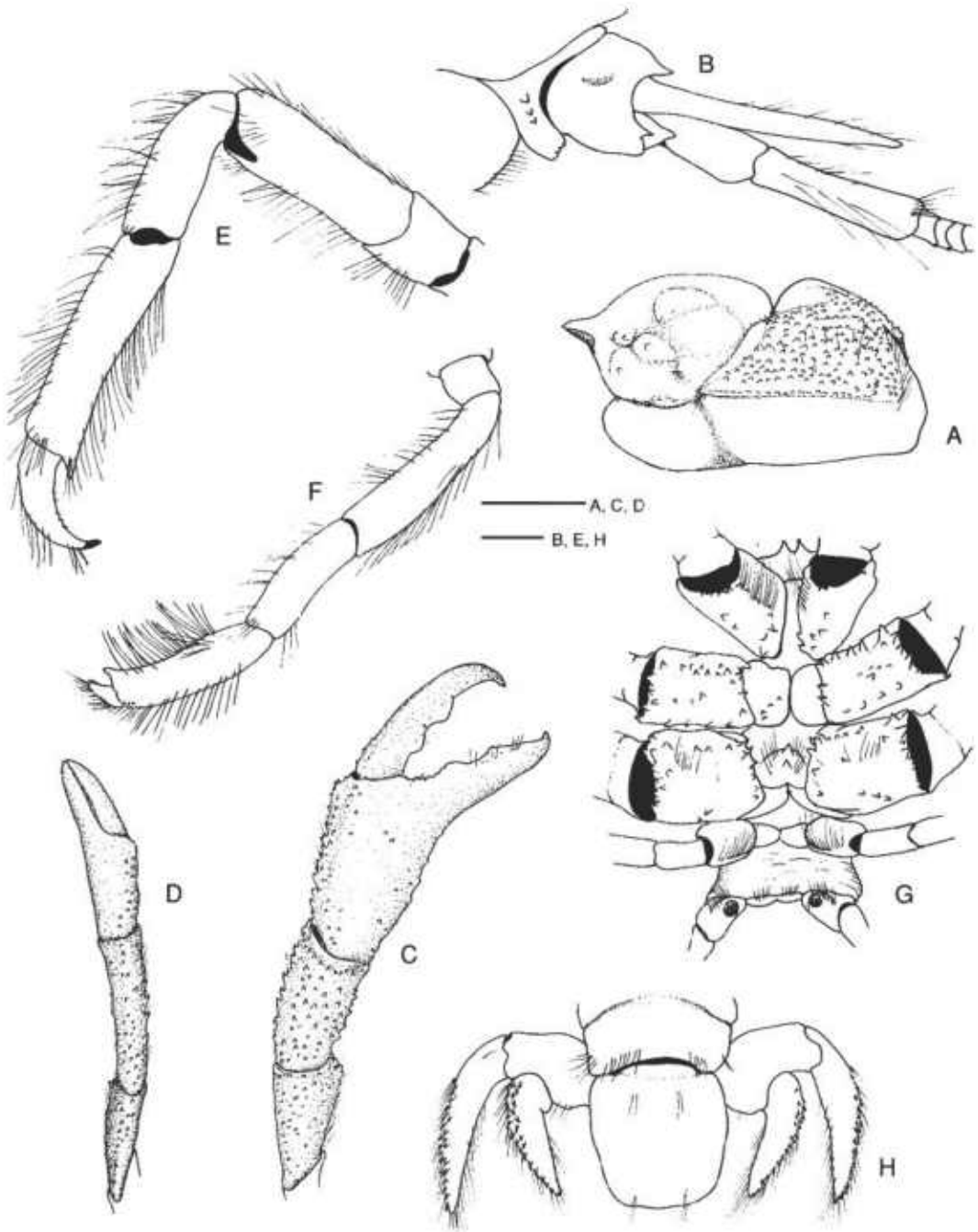


FIG. 4. — *Tylaspis anomala* Henderson, 1885, New Caledonia, BIOCAL stn CP 17, ♂, 8.7 mm (MNHN-Pg 5533); A, shield, posterior carapace, and branchiostegite (lateral view); B, right antennal peduncle (lateral view); C, right cheliped (dorsal view); D, left cheliped (dorsal view); E, left fourth pereopod (lateral view); F, left fifth pereopod (lateral view); G, sternite of third maxilliped, and coxae and sternite of first to fifth pereopods (ventral view); H, telson and uropods (dorsal view). Scale bars: A, C, D, 5 mm; B, E-H, 1 mm.

first ambulatory leg; articles with scattered setae one to two articles in length. Fifth segment unarmed, with long setae laterally and mesially. Fourth segment unarmed; with transverse dorso-distal row of setae. Third segment with strong ventromesial distal spine. Second segment with dorsolateral distal angle weakly produced, terminating in spine; lateral margin with one or two small spines proximally; mesial margin with spine on dorsodistal angle. First segment with two or three small spines on lateral face; ventromesial angle produced, with three or four small spines laterally. Antennal acicles straight, exceeding distal margins of corneae by 0.3 to 0.5 length of acicle, terminating in strong spine; mesial margin unarmed, setose.

Mandible (Fig. 5A) with 3-segmented palp. Maxillule (Fig. 5B, C) with external lobe of endopod weakly developed, internal lobe with two long setae. Maxilla (Fig. 5D) with endopod exceeding distal margin of scaphognathite. First maxilliped (Fig. 5E) with endopod exceeding exopod in distal extension. Second maxilliped (Fig. 5F) without distinguishing characters. Third maxilliped (Fig. 5G) with crista dentata of fourteen corneous-tipped teeth; coxa and basis each with small mesial tooth. Sternite of third maxillipeds with spine on each side of midline. Epistome unarmed.

Chelipeds dissimilar. Right cheliped (Fig. 4C) slender, with scattered short setae. Fingers subequal to length of palm, terminating in small corneous claws; tips strongly curved inwardly, crossed when closed; dorsal and ventral faces unarmed; cutting edges with irregularly sized calcareous teeth, and row of small, fused corneous teeth distally. Palm longer than broad, lateral and mesial faces rounded; dorsal and ventral faces smooth, unarmed or at most with scattered minute spines; mesial face with two or three irregular rows of small spines. Carpus with numerous small spines on dorsal and ventral surfaces, and subdistal row of small spines on dorsal face. Merus with numerous small spines on dorsal and lateral faces, mesial face smooth; ventromesial margin with row of spines. Ischium with spines on dorsal margin and ventral face. Coxa with small spines on ventral face.

Left cheliped (Fig. 4D) well-calcified, slender,

with scattered setae. Fingers terminating in small corneous claws; dorsal and ventral surfaces unarmed; cutting edge of dactyl with row of minute, fused corneous teeth; cutting edge of fixed finger with row of small, regularly spaced teeth interspersed with minute corneous spines. Dactyl subequal to palm in length. Palm with dorsal and ventral surfaces unarmed, except for irregular rows of small spines on dorsomesial face. Carpus with numerous small spines on dorsal surface; ventral face with scattered small spines. Merus with small spines on dorsal and lateral faces, mesial face smooth; with ventromesial and ventrolateral row of spines. Ischium with dorsal spine and several small spines on ventral face. Coxa with small spines on ventral face.

Ambulatory legs (Fig. 1) similar from right to left, very long and slender; second walking leg exceeding first by full length of dactyl, and exceeding extended right cheliped by nearly full length of propodus. Dactyls nearly straight, approximately as long as propodi, with dorsal row of small spines and bristle-like setae, and distal dorsolateral and dorsomesial rows of long setae; ventral margin unarmed. Meri, carpi and propodi each with numerous spines (often in pairs) arranged in irregular rows on all surfaces. Ischia and coxae unarmed. Anterior lobe of sternite of third pereopods (Fig. 4G) sloping, setose, unarmed or with one or two small spines.

Fourth pereopod (Fig. 4E) semichelate. Dactyl subtriangular, strongly curved, terminating in sharp corneous claw, and with three to five minute corneous spinules on ventral margin. Propodus elongate, approximately 3.5 times as long as broad, with strong ventrodistal spine. Merus, carpus, and propodus unarmed but with long setae.

Fifth pereopod (Fig. 4F) chelate, with long setae on merus, carpus, propodus and dactyl. Dactyl and propodus each with weak rasp formed of few minute corneous spines.

Telson (Fig. 4H) lacking transverse suture, subrectangular, slightly longer than broad; posterior margin entire, broadly rounded, unarmed. Uropods (Fig. 4H) elongate, about four times as long as broad; rasps weakly developed, consisting of two or three rows of small corneous spines.

Male paired first gonopods (Fig. 6A) each with

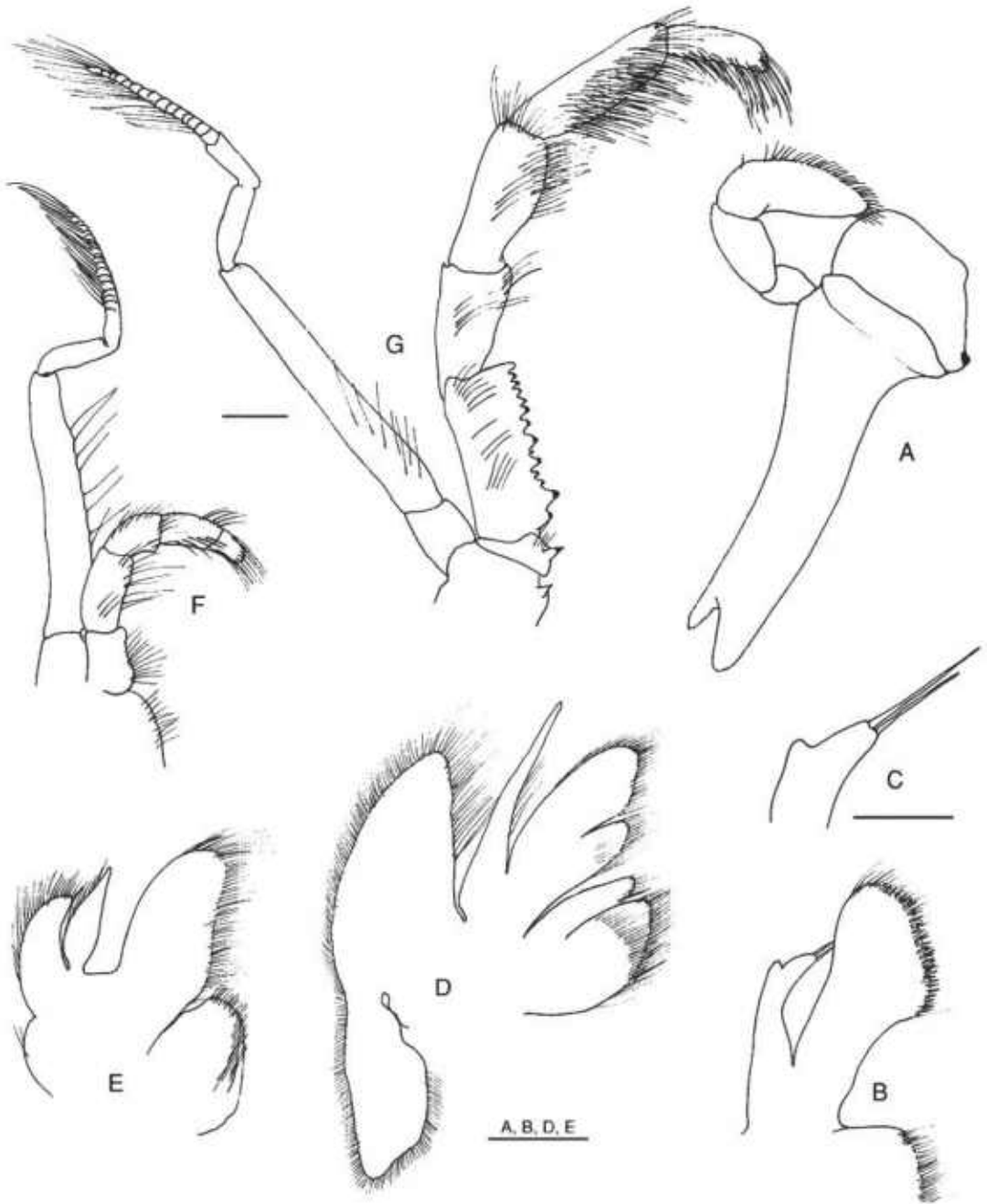


FIG. 5. — *Tylaspis anomala* Henderson, 1885, New Caledonia, BIOCAL stn CP 17, ♂, 8.7 mm, (MNHN-Pg 5533). Left mouthparts (internal view); A, mandible; B, maxillule; C, endopod of same; D, maxilla; E, first maxilliped; F, second maxilliped; G, third maxilliped. Scale bars: A, B, D-G, 1 mm; C, 0.5 mm.

elongate, subconical distal lobe; second paired gonopods (Fig. 6B) each with distal segment twisted distally, distomesial face setose, and with

short bristle-like setae on lateral margin, with short exopod (holotype only). Smaller known female (SL 5.9 mm) with second to fifth pair of pleopods (Fig. 7A-D) symmetrical, biramous, each with short endopod and sparse setae. Largest known female (SL 8.0 mm) with second to fifth pair of pleopods asymmetrical (Fig. 7E-H); left biramous, with subequal rami; right rudimentary, each consisting of small bud.

REMARKS

De Saint Laurent (1972: 121) mistakenly indicated that she examined specimens of *Tylaspis anomala* from US Albatross plankton station 4605. No specimens of this species were obtained at this station.

Several important morphological features of *T. anomala* have been inaccurately or insufficiently reported in previous descriptions of this species. For example, Henderson (1888) and de Saint Laurent (1972) stated that ocular acicles were absent, and this interpretation has been followed by most carcinologists. McLaughlin (1983) did suggest that the acicles in three monotypic parapagurid genera (i.e. *Tylaspis*, *Probeebei* and *Typhlopagurus* de Saint Laurent, 1972) were reduced or lost, but did not specify exactly which was the condition in *Tylaspis*. Although the ocular acicles in *T. anomala* are considerably reduced and indeed not easily discernible, they are present (Fig. 3A). A careful examination of *T. anomala* specimens, and their comparison with those of species from all other parapagurid genera, clearly indicates a continuum from well-developed ocular acicles (*Sympagurus* Smith, 1883, *Oncopagurus* Lemaitre, 1996, *Paragiopagurus* Lemaitre, 1986, *Strobopagurus* Lemaitre, 1989), through stages where they are reduced [*Probeebei mirabilis* Boone, 1926 (Fig. 3B), *Typhlopagurus foresti* de Saint Laurent, 1972] or moderately developed [*Bivalvopagurus sinensis* (de Saint Laurent, 1972), species of *Parapagurus* Smith, 1879], to a condition such as in *T. anomala*, where the acicles are barely discernible.

Although the partial fusion and calcification of the cephalothorax in *T. anomala* is a feature that has been previously documented, the absence of linea or sulci on the posterior carapace has not.

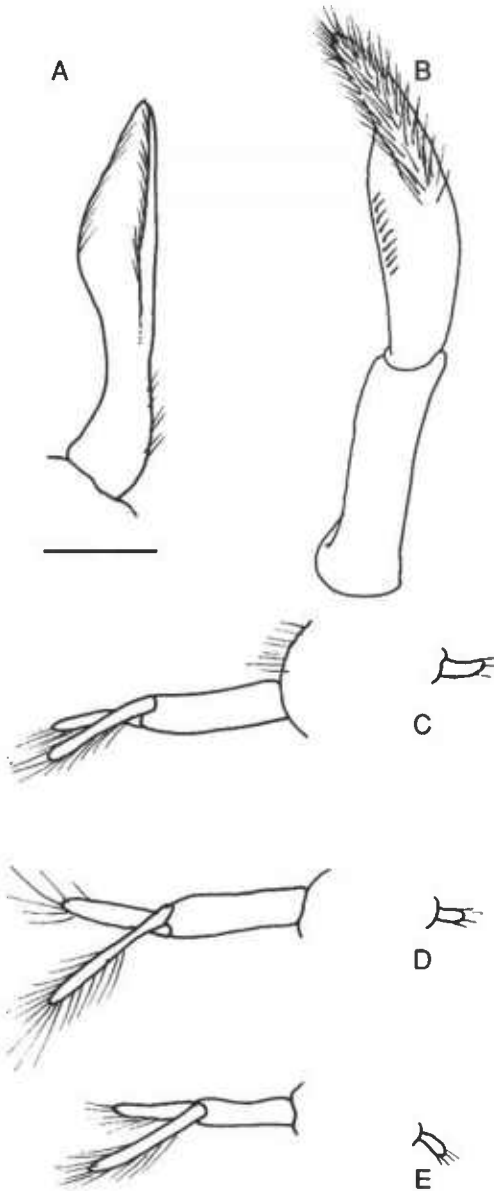


FIG. 6. — *Tylaspis anomala* Henderson, 1885, New Caledonia, BIOCAL stn CP 17, ♂, 8.7 mm (MNHN-Pg 5533); A, B, left first (mesial view) and second (anterior view) gonopods; C-E, third to fifth pair of pleopods (left on left, right on right, lateral view); A, first gonopod; B, second gonopod; C, third pair; D, fourth pair; E, fifth pair. Scale bar: 1 mm.

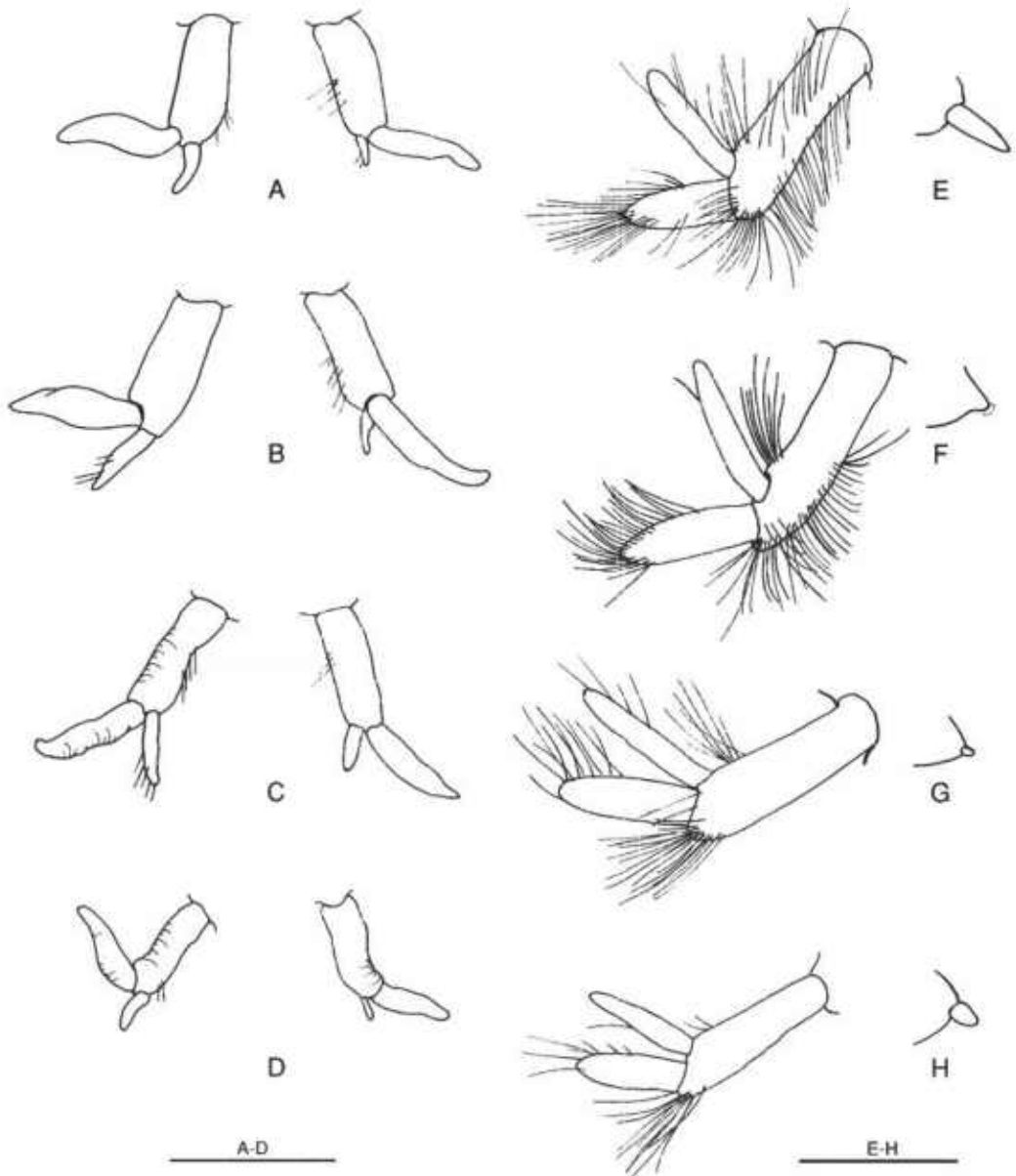


FIG. 7. — *Tylaspis anomala* Henderson, 1885, NE of Easter Island, *Albatross* Stn 4701 (USNM 168482): ♀ pleopods (left on left, right on right, lateral view). A-D, ♀, 5.9 mm: A, second; B, third; C, fourth; D, fifth; E-H, ♀, 8.0 mm: E, second; F, third (scar only on right); G, fourth; H, fifth. Scales bars: A-D, 1 mm; E-H, 2 mm.

The partial fusion of the shield and posterior carapace is marked by a calcified deep cervical groove and lineae transversalis. On the posterior carapace, there is no evidence of lineae or sulci as seen in typical paguroids, although the slightly raised condition of the dorsomedian or cardiac region (as shown in Fig. 2A) might give the appearance that there is at least a sulcus cardio-branchialis on either side of the cardiac region.

The abdomen of *T. anomala* has been described as short, membranous, and without the usual twisting seen in typical shell-inhabiting hermit crabs (Henderson 1888), or simply membranous except for a weak calcification of the second tergite (de Saint Laurent 1972). However, the abdomen is weakly twisted to the right, at least in preserved state (Fig. 1). Examination of all available specimens has shown that in addition to the calcification seen in the pleura of the second somite, the tergite of the first somite is also similarly calcified. As previously mentioned, in the past it has been inaccurately reported that *T. anomala* males have only paired first and second pleopods, and unpaired left third to fifth. Similarly, females have been reported to have unpaired left second to fifth pleopods, with a vestigial right second pleopod (Henderson 1888; de Saint Laurent 1972). In actuality, the holotype as well as both of the New Caledonia male specimens have five pairs of pleopods, albeit the third to fifth pairs are asymmetrical (left biramous, right uniramous and bud-like; Fig. 6C-E). A study of the only two female specimens known (USNM 168482) shows that indeed they lack first pleopods; however, they do have paired second to fifth pleopods. In the smaller female (SL 5.9 mm), the pleopods (Fig. 7A-D) are paired, symmetrical, biramous; in the larger female (SL 8.0 mm), the pleopods (Fig. 7E-H) are also paired, but asymmetrical, with the left biramous and right considerably reduced to minute buds (only a scar is visible on the place of normal development of the right second). In both females, the unpaired left gonopore is clearly developed, suggesting maturity.

The presence of uropodal rasps in *T. anomala* has not been previously reported. Although Henderson (1888, pl. 8, fig. 5a, b) included illustrations of the uropods, he did not depict the

small spines that form the rasps of these appendages (Fig. 4H).

TAXONOMY AND CHARACTERISTICS OF *Probeebei mirabilis* Boone, 1926

The monotypic genus *Probeebei*, and its species *P. mirabilis*, were originally briefly described by Boone (1926a, b) as a primitive macruran, based on a juvenile specimen obtained south of Cocos Island during the *Arcturus* Oceanographic Expedition in 1925 to the eastern Pacific. Unaware of Boone's description, Wolff (1960b) described what he thought to be a new genus and species of pagurid as *Planopagurus galathea*, based on juvenile and adult specimens obtained during the Danish *Galathea* Expedition in 1952 to the eastern Pacific. However, Fenner A. Chace, Jr. (*in litt.*) informed Wolff of Boone's brief description, and shortly thereafter, Wolff (1961a, b) recognized that his taxon actually represented the poorly described *Probeebei mirabilis*, which he then redescribed in considerable detail, showing that it really was a hermit crab which he classified in the Paguridac. *Probeebei* was later placed in the Parapaguridae by de Saint Laurent (1972).

Probeebei mirabilis Boone, 1926 (Figs 2B-D, 3B)

MATERIAL EXAMINED. — For discussion purposes, the following diagnosis of *P. mirabilis* is presented, based on examination of specimens obtained during the US *Albatross* and Danish *Galathea* expeditions, as follows: 18 ♂♂, 20 ♀♀, 7 juveniles (USNM 119893-119897, 267810); 1 ♀, 2 juveniles (ZMK).

DISTRIBUTION. — Eastern Pacific: from south of Cocos Island to off southwest of Galapagos; 1145 to 4775 m.

HABITAT. — Apparently free-living.

REMARKS. — De Saint Laurent (1972) inaccurately indicated that the holotype of this species was from the Indian Ocean. The holotype was actually collected during the *Arcturus* Oceanographic Expedition (stn 74-OT4, 60 miles south of Cocos Island, 04°50'N - 87°00'W, 1145 m, 30.V.1925), and as pre-

viously mentioned is deposited in the American Museum of Natural History, New York (AMNH 12397).

DIAGNOSIS

Eleven pairs of phyllobranchiate gills. Shield and posterior carapace partially fused, well calcified, spinose. Rostrum well-developed, clongate, and spinose; frequently strongly recurved upwardly. Branchiostegite moderately calcified, spinose. Shield marked by deep membranous cervical groove and linea transversalis. Posterior carapace spinose; cardiac sulci extending posteriorly and converging at midpoint of posterior margin; lateral margins broadly rounded.

Ocular peduncles with small dorsal spine proximally. Ocular acicles considerably reduced (Fig. 3B), marked by small spine. Epistome unarmed.

Antennular and antennal peduncles distinctly overreaching eyestalks. Fourth segment of antennal peduncle armed with distolateral and distomesial spines.

Chelipeds dissimilar in size, right not markedly larger than left. Ambulatory legs very long, slender, spinose; second distinctly longer than first. Fourth pereopod (Fig. 2B) semichelate, lacking rasp on propodus. Fifth pereopod chelate. Thoracic sternite of chelipeds narrow (Fig. 2D). Sternites of second and third pereopods moderately broadened. Sternites of fourth and fifth pereopods each consisting of transverse rod subdivided in midline, that of fifth narrow and widely separated from preceding sternite.

Abdomen (Fig. 2B-D) arched under body so ventral surface of telson faces sternite of fifth pereopods; tergites well-calcified, second to fifth spinose and with well-developed pleura. Uropods and telson (Fig. 2D) symmetrical or nearly so. Uropodal exopod and endopod slender, with weakly developed rasp consisting of rows of small corneous spines. Telson subrectangular.

Males with abdominal tergites symmetrical (Fig. 2C, D); with paired first pleopods modified as gonopods; lacking second to fifth pleopods. Females with second to fifth abdominal tergites asymmetrical (Fig. 2B), left pleura larger than right and covering eggs; with unpaired left biramous second to fifth pleopods.

COMPARISON OF *Tylaspis* AND *Probeebei*

SIMILARITIES

Tylaspis anomala and *Probeebei mirabilis* share the following characters: gill structure (phyllobranchia); partially fused and calcified shield and posterior carapace; well-developed rostrum; reduced ocular acicles; unarmed epistome; weakly dissimilar chelipeds; long, spinose ambulatory legs, with second pair distinctly longer than first; fourth pereopod lacking propodal rasp, with strong ventrodistal spine on propodus; symmetrical uropods and telson, with uropodal exopod and endopod having weakly developed rasps; and deep-water habitat. Both species exhibit a similar development of the second to fourth sternites (Figs 2D, 4G), which consists of plates that are broader than in other parapagurids.

DIFFERENCES

Tylaspis anomala and *Probeebei mirabilis* differ in a number of features. No sulci are visible on the posterior carapace of *T. anomala*, although as previously mentioned the raised dorsomedian or cardiac region appears to be marked by a cardiac sulci. The cardiac sulci are clearly defined in *P. mirabilis*. The rostrum is prominent in both *T. anomala* and *P. mirabilis*, but is more so in the latter where it is spinose and often strongly recurved upwards. The ocular acicles are considerably reduced, unarmed, in *T. anomala* (Fig. 3A); the acicles are similarly reduced in *P. mirabilis*, but are marked by a small spine (Fig. 3B). The most striking differences between the two species, however, can be seen in the abdomen. The abdomen in *T. anomala* is slightly twisted to the right (Fig. 1), and membranous except for a moderate calcification of the tergite of the first somite and pleura of the second; adult males have paired first and second gonopods, and paired asymmetrical third to fifth (Fig. 6); adult females lack first and second pleopods, and have paired, asymmetrical third to fifth pleopods (Fig. 7E-H). In contrast, the abdomen of *P. mirabilis* has well-calcified first to fifth tergites; the tergites are symmetrical in males but asymmetrical in females, and armed with spines (Fig. 2B-D); adult males have no pleopods except for paired first, and adult females have unpaired left second to fifth.

PLEOPOD DEVELOPMENT

Pleopod development from larval to adult stages is an aspect that has been insufficiently studied in paguroids in general (see review in Lemaitre & McLaughlin 1992). It is commonly assumed that the megalopal pleopods are the same morphological structures seen in the adult. No anomurans have first pleopods in the megalopa. When juvenile or adult hermit crabs have first pleopods, it has been shown that these arise as new structures modified as gonopods and not from pre-existing pleopods (Provenzano & Rice 1966; Lemaitre & McLaughlin 1992). In the lithodid *Lithodes maja* (Linnaeus, 1758), Sandberg & McLaughlin (1997) have documented the development of paired first and unpaired second to fifth pleopods in females. They observed that in this lithodid, the megalopal pleopods are lost in the transition to the first juvenile stages, followed by gradual development of second to fifth left pleopods from the smaller juveniles (6.6 to 10.5 mm carapace length) to fully grown individuals (65.0 mm carapace length or greater). Paired first pleopods begin to appear relatively late in the juveniles stages when individuals reach about 50.0 mm carapace length.

Unfortunately no larval stages of *T. anomala* or *P. mirabilis* have been found, and only a few young or adult specimens are available. In the male specimens of *T. anomala*, no major differences in pleopods can be seen from the smallest (SL 6.5 mm) to the largest (SL 8.7 mm) specimens (Fig. 6). However, in females, development can be gleaned from differences in pleopod condition between the smallest (SL 5.9 mm; Fig. 7A-D) presumably young, and largest (SL 8.0 mm; Fig. 7E-H) presumably adult specimens. In both females the left second to fifth are similarly biramous, except for a greater development of the rami in the larger female; the right second to fifth pleopods are biramous in the young specimen, and short, uniramous (bud-like) in the adult specimen. Thus, based on the limited material available, it appears that a process of reduction occurs on the right side, whereas increased growth occurs on the left side. Whether or not these pleopods represent appendages that have reappeared after the loss of megalopal pleopods (such as reported for *Lithodes*

maja by Sandberg & McLaughlin 1997), cannot be determined with the limited material available. At least in males, however, development of first and second pleopods does seem to occur secondarily as the individual matures.

Males of *P. mirabilis* develop only paired first pleopods modified as gonopods during the juvenile crab stages. As described by Wolff (1961b: 22, fig. 8, table 1), young males have paired uniramous (bud-like) second to fifth pleopods; adults have only one pair of pleopods, the first. In females of *P. mirabilis* development proceeds on the left second to fifth, from uniramous in the young to biramous in adults; on the right second to fifth, from uniramous in the young to loss or "scars" in adults. Again, the bud-like pleopods observed in juveniles could possibly represent appendages that are reappearing after the loss of megalopal pleopods. Reduction of these appendages continues in males until there is total absence in the adults. Females, however, lose only those on the right side, while those on the left develop into the egg-carrying appendages of the adults. The first pleopods of the male *P. mirabilis* develop as sexual appendages as the animal matures.

HABITAT

Tylaspis anomala and *P. mirabilis* live exclusively in deep waters (typically near 4000 m) of the Pacific. Of benthic decapods, these two species are considered among those that occur the deepest (Wolff 1960a; de Saint Laurent 1972). As previously mentioned, *T. anomala* uses an anemone to protect its abdomen. Although live specimens of *T. anomala* have not been observed, it appears from preserved specimens that, in life, part of the abdomen is bent under the body (see Borradaile 1916: 124, fig. 13; Wolff 1961b: 27, fig. 11). *P. mirabilis* is considered to be free-living, *i.e.* does not use a shell or other means of protecting its abdomen (Wolff 1961a, b), and also carries part of the abdomen bent under the body. A number of lots of *P. mirabilis* have been examined, and none contain evidence of housing or an associated organism as mode of protection. However, the morphology of the fourth pereopod of *P. mirabilis* (Fig. 2B) is virtually identical to that of *T. anomala*. Both exhibit on the propo-

thus of this appendage a strong ventrodorsal spine that, at least in *T. anomala*, is clearly an adaptation for grasping an anemone (Fig. 4E). It is conceivable, therefore, that *P. mirabilis* may similarly use its fourth pereopod to grasp a protective organism or housing yet to be found with specimens of this species.

RELATIONSHIPS AND EVOLUTIONARY COMMENTS

Tylaspis anomala appears to be more closely related to *P. mirabilis* than to any other parapagurid. These two crab-like species exhibit virtually identical morphological developments on the cephalothorax and its appendages, and have similar modes of life. As previously mentioned, the only marked difference between the two can be found in the abdomen (degree of calcification, symmetry, and pleopod arrangement). The two are presumed to represent advanced forms that have evolved as result of the abandonment by their ancestors of shell use or other means of protection (Wolff 1961b). The traditional view used to explain paguroid abdominal modifications (e.g. asymmetry, loss of right pleopods, membranous condition) is based on the assumption that such modifications are the result of hermit crabs occupying dextrally coiled shells (e.g. Boas 1880, 1924; Henderson 1888; Bouvier 1894, 1897; Perez 1934; Russell 1962; Richter & Scholtz 1994). Thus, the premise has been that hermit crabs were first asymmetrical animals that lived in shells. Presumably, in carcinized forms such as *T. anomala* and *P. mirabilis*, abdominal asymmetry was retained from shell-dwelling ancestors, and cephalothoracic and tergite calcification evolved secondarily as a specialization for a free-living existence. The scarcity of calcareous shells at depths where *T. anomala* and *P. mirabilis* live might be cited as a limiting factor that has influenced the evolution of the abdomen in these two forms. However, other parapagurids (*Parapagurus* sp.) with a more conventional hermit crab morphology, live abundantly at similar depths, and do use for housing zoanthids that grow in a dextrally coiled fashion that imitates gastropod shells. Given the morphological cha-

acteristics of the cephalothorax and abdomen, and apparent lack of shell-carrying behavior of *T. anomala*, it is difficult to explain using traditional views of hermit crab evolution, why its abdomen is membranous (except for weak calcification of the first tergite and second pleura) and still has paired pleopods. Equally problematic is to attempt to explain why in *P. mirabilis* only females have asymmetrical tergites (Fig. 2B) and unpaired left pleopods, whereas males have symmetrical tergites (Fig. 2C, D) and pleopods (first). An alternative explanation might be that the asymmetry in abdominal tergites and pleopod condition in females of *P. mirabilis* represent a reproductive modification to egg-carrying, rather than a morphological trait retained from a shell-carrying ancestor.

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