

Dynomenidae and Dromiidae (Decapoda, Brachyura) from Guam, Philippine Islands, Tonga and Samoa

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ABSTRACT

Five species of Dynomenidae are recorded from Guam, Mariana Islands. Two new species of *Dynomene* are described. Distinctive characters of *D. kroppi* n. sp. are: carapace width/length ratio= 1.1, six small, blunt anterolateral teeth, and five or six spines on inner margins of walking leg dactyli; and for *D. guamensis* n. sp. are: carapace width/length ratio = 1.3, five acute anterolateral teeth, two prominent frontal swellings, two tubercles behind postorbital corner, and seven or eight spines on inner margins of walking leg dactyli. Nine new records and one new dromiid species are reported from Guam; the distinctive characters of *Cryptodromia pitiensis* n.sp. are: carapace width/length ratio= 1.3, a prominent swelling above the anterolateral margin, carapace surface mostly smooth, but areolate and with scattered tubercles. Nine new dromiid records are also reported for Tonga and Samoa. Five new dromiid records are reported, based on material collected by the *Albatross* Expedition, 1907-1910, to the Philippine Islands. A total of 29 dynomenid and dromiid species are reported from the Mariana and Philippine Islands, of which only seven species are shared. New keys are provided to identify species of *Dynomene*, *Sphaerodromia* and *Cryptodromia*. Dynomenids and primitive dromiids share similar gonopod characters. Advanced dromiids have gonopods whose derived structure may be linked to the longer sternal sutures 7/8 in females. The third maxilliped crista dentata, as found in podotreme crabs, is absent from all Eubrachyura. Tooth-like maxilliped marginal tubercles in these crabs should be called the *marginal dentata*. Podotreme crabs show a variety of coxal and sternal abdominal locking mechanisms linked to the presence of uropods.

KEY WORDS

Crustacea,
Decapoda,
Brachyura,
Cryptodromia,
Cryptodromiopsis,
Dromidiopsis,
Dynomene,
Hirsutodynomene,
Lauridromia,
Paradynomene,
Sphaerodromia,
Takedromia,
Indo-Pacific,
gonopods,
new species.

RÉSUMÉ

Dynomenidae et Dromiidae (Decapoda, Brachyura) de Guam, Tonga, Samoa et des Philippines.

Cinq espèces de la famille des Dynomenidae sont signalées de Guam, îles Mariannes. Deux espèces nouvelles de *Dynomene* sont décrites. Les caractères distinctifs de *D. kroppi* n. sp. sont : rapport largeur/longueur de la carapace = 1,1, six dents antéro-latérales petites et émoussées, cinq ou six épines sur le bord interne du dactyle des pattes ambulateires ; et pour *D. guamensis* n. sp. : rapport largeur/longueur de la carapace = 1,3, cinq dents antéro-latérales acérées, deux proéminences frontales saillantes, deux tubercules en arrière de l'angle postorbitaire, et sept ou huit épines sur le bord interne du dactyle des pattes ambulateires. À Guam neuf nouveaux signalements de Dromiidae sont rapportés et une nouvelle espèce de Dromiidae est décrite. Les caractères distinctifs de *C. pitiensis* n. sp. sont : rapport largeur/longueur de la carapace = 1,3, un renflement saillant au-dessus du bord antéro-latéral, surface de la carapace en grande partie lisse, mais aréolée et avec des tubercules épars. Neuf nouveaux signalements de Dromiidae sont également rapportés aux îles Tonga et aux Samoa. Cinq nouveaux signalements de Dromiidae sont rapportés, basés sur du matériel récolté par l'*Albatross Expedition*, 1907-1910 aux Philippines. Au total, 29 espèces de Dynomenidae et de Dromiidae sont signalées des îles Mariannes des Philippines, qui n'ont en commun que sept espèces. De nouvelles clés d'identification sont présentées pour les genres *Dynomene*, *Sphaerodromia* et *Cryptodromia*. Les Dynomenidae et les Dromiidae primitifs partagent des caractères similaires pour les gonopodes. Les Dromiidae avancés ont des gonopodes dont la structure peut être mise en rapport avec les sutures 7/8 des femelles plus longues. Une crista dentata du troisième maxillipède telle qu'on l'observe chez les crabes podotrèmes est absente chez tous les Eubrachiura. Chez ces crabes, les tubercules marginaux du troisième maxillipède pourraient être nommés *marginal dentata*. Les crabes podotrèmes montrent une grande variété de mécanismes coxaux et sternaux pour le maintien de l'abdomen en rapport avec la présence des uropodes.

MOTS CLÉS

Crustacea,
Decapoda,
Brachyura,
Cryptodromia,
Cryptodromiopsis,
Dromidiopsis,
Dynomene,
Hirsutodynomene,
Lawridromia,
Paradynomene,
Sphaerodromia,
Takedromia,
Indo-Pacifique,
gonopodes,
nouvelles espèces.

INTRODUCTION

In this paper, new species and records of the families Dynomenidae Ortmann, 1892 (coral crabs) and Dromiidae De Haan, 1833 (sponge crabs) are reported from Guam, Mariana Islands and the Philippines. The collections of crabs from Guam, that form the basis of this work, were kindly made available by Roy Kropp and Gustav Paulay. The material is especially interesting because it contains two new species of the genus *Dynomene* Desmarest, 1823. In addition, one

new species of *Cryptodromia* Stimpson, 1858 from Guam is reported. New identification keys to species of *Dynomene*, *Cryptodromia* and *Sphaerodromia* are provided. Where appropriate generic diagnoses have been updated and clarified. Some of the dynomenid material in the present collection was briefly reported in a recent review of the family (McLay 1999). These records are repeated here because they were all part of the University of Guam Invertebrate Collection and facilitates a review of the dynomenid fauna of Guam. Other dynomenid records are new.

During 1907-1910 the *Albatross* Expedition to the Philippine Islands collected many specimens of Brachyura. Much of the material was identified by Rathbun (1914a, b, 1916) who published papers on the Goneplacidae, Grapsidae, Ocypodidae, Inachidae and Parthenopidae. However, she did not publish her identifications of the Dromiidae. I have re-identified these specimens and herein report the occurrence of five species previously unknown from the Philippines.

Crabs belonging to the Podotremata Guinot, 1977 have several important characters that are not found in the Eubrachyura Saint Laurent, 1980. Some of these characters may have been retained from a hypothetical, primitive crab-like ancestor while others may be unique to the Podotremata. The features of these animals preserve some of the early stages that lead to the evolution of crab-like body forms. The Dromiidae and Dynomenidae, along with the Homolodromiidae, Alcock, 1900, constitute the Dromiacea De Haan, 1833. McLay (1999) argued that the Dynomenidae and Dromiidae are sister groups and that the Homolodromiidae, in turn, is the sister group to these two families. Using sperm data, these relationships were also supported by Guinot *et al.* (1994, 1998). The opportunity is taken herein, to evaluate this hypothesis using some characteristics of the gonopods, the crista dentata and the abdominal locking mechanisms.

ABBREVIATIONS

The GUM*** registration numbers refer to the original registration numbers of the stations as used in assembling the University of Guam Invertebrate Collection (UGI). Types of the new species of *Dynomene* and *Cryptodromia* have been deposited in the Muséum national d'Histoire naturelle, Paris (MNHN). Some specimens have been deposited in the Zoological Reference Collection (ZRC), National University of Singapore. The rest of the material has been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM). The Siboga Expedition collection is in the Zoologisch Museum, Amsterdam (ZMA). RMNH refers to the Rijks Museum van Natuurlijke Historie, Leiden and TMCD refers to the Taiwan Museum, Taipei. Material from the British Museum of Natural History (The Natural History Museum), London is

labeled BM. Measurements are given as carapace width (cw) \times carapace length (cl). p1 refers to the chelipeds and p2-p5 refer to walking legs, i.e. second to fifth pereopods. The third maxillipeds, that bear the crista dentata, are referred to as mxp3. The cover ratio (cr) is used as a measure of the adequacy of camouflage carried by the dromiid crab: it is the ratio of the area (width \times length) of the piece of camouflage and the cw \times cl as an estimate of the area of the crab to be covered. A cr of 1.0 indicates that the area of the camouflage approximately equals the area of the crab body.

Family DYNOMENIDAE Ortmann, 1892

Genus *Dynomene* Desmarest, 1823

DIAGNOSIS. — Carapace shape wider than long, moderately convex, commonly sub-circular. Surface may be smooth or sparsely granulate, covered with coarse setae, which may short or long, and often arranged in tufts. Lateral carapace margin always well-defined and armed with distinct small teeth or granules. Frontal groove well-marked, splits in two posteriorly, cervical, postcervical and branchial grooves usually evident. Frontal carapace margin broadly triangular, continuous, no rostrum or teeth, eyestalks short, eyes protected by well-defined orbits. Female sternal sutures 7/8 end well-apart on low tubercles behind bases of second walking legs. Antennule can be concealed inside the orbit at the base of the eyestalk. Antennal flagella shorter than carapace width. All segments of antenna moveable, first segment (urinal) always beaked medially and second segment has an exopod firmly fixed. Third maxillipeds opercular, completely covering the buccal cavern, separated at their bases by a plate at the same level as the sternum, basis and ischium of endopod fused but joint always marked by a shallow groove. Crista dentata present. Chelipeds equal, stouter than walking legs, dactyl strongly curved, fingers gaping basally. Last pair of legs very reduced, dactyl rudimentary, forming an obsolete sub-chelate mechanism with an extension of the propodus. Gills usually 19 (including six podobranchs) + seven epipods. Gills variable in shape. Abdomen of six segments and telson, folded loosely under the thorax, uropods large. The lateral movement of the abdomen is restricted by a small sternal tubercle at the base of each of the first walking legs which lies alongside each uropod. Both sexes have five pairs of pleopods, first pair rudimentary in female, last three pairs vestigial in the male. First male gonopods very uniform in structure, consisting of a stout, setose semi-rolled tube with an apical plate, second pair simple, needle-like, with varying numbers of sub-terminal spines (after McLay 1999).

KEY TO THE SPECIES OF *DYNOMENE* DESMAREST, 1823

The following key, modified from McLay (1999), can be used to separate all seven known species of the genus *Dynomene* (species dealt with in this paper are in bold).

1. Anterolateral teeth absent or only represented by two or three small granules not terminated by sharp tooth *Dynomene praedator* A. Milne-Edwards, 1879
— Anterolateral teeth present, well-developed, and sharply pointed 2
2. Carapace tomentum sparse, surface not obscured, long setae not arranged in clumps; chelipeds slender, carpus and propodus smooth, tips of fingers without well-developed teeth 3
— Carapace tomentum dense, surface obscured, long setae may be arranged in clumps; chelipeds stout, carpus and propodus granulated, tips of fingers with well-developed teeth 5
3. Six teeth on anterolateral carapace margin; superior borders of meri, carpi and propodi of p2-p4 armed with small rounded tubercles *Dynomene kroppi* n. sp.
— Five teeth on anterolateral carapace margin; superior borders of meri, carpi and propodi of p2-p4 armed with acute tubercles 4
4. Ratio of carapace width to length > 1.2; lobes behind frontal margin not prominent; no tubercles on carapace posterolateral to corner of orbit; tuberculated subhepatic swelling absent; ten minute spines on inner margins of dactyli of p2-p4 *Dynomene pugnatrix* De Man, 1889
— Ratio of carapace width to length < 1.2; lobes behind frontal carapace margin prominent, elongate; two tubercles on carapace posterolateral to corner of orbit; tuberculated subhepatic swelling present; five or six small spines on inner margins of dactyli of p2-p4 *Dynomene guamensis* n. sp.
5. Carapace tomentum dense, consisting of short setae, bent at right angles, obscuring carapace surface, and 15 to 17 clumps of long (> 0.2 × cw) setae; ratio of length to width of merus of p3 > 2.0 *Dynomene pilumnoides* Alcock, 1900
— Carapace tomentum not dense, consisting of short setae, not bent at right angles, not obscuring carapace surface, and long setae may be arranged in clumps but length < 0.2 × cw; ratio of length to width of merus of p3 < 2.0 6
6. Carapace surface smooth; longer setae arranged in about twenty clumps; ratio of cw to cl approx. 1.2; notch present in supraorbital margin; no spines around postorbital margin; cervical groove branching off subhepatic groove; granules on carpi of p2-p4 not arranged in rows *Dynomene filholi* Bouvier, 1894 (known only from the Atlantic)
— Carapace surface minutely granulated; longer setae not arranged in clumps; ratio of cw to cl approx. 1.3; no notch in supraorbital margin; five small acute spines around postorbital margin; no cervical branch from the subhepatic groove; granules on carpi of p2-p4 arranged in three rows *Dynomene hispida* Guérin-Méneville, 1832

Dynomene kroppi n. sp.

(Figs 1; 3A)

TYPE MATERIAL. — Holotype ♂ 11.9 × 9.7 mm, from Piti Reef, Guam (MNHN-B26474), paratype ♀ 9.5 × 7.5 mm, from GUM300 (MNHN-B26475).

MATERIAL EXAMINED. — **Guam.** Piti Bay, 13°27'N, 144°47'E, 2 m, outer reef flat west of Camel Rock, rubble partially consolidated by sponge, 11.VI.1986, coll. R. Kropp, 1 ♀ 8.6 × 7.7 mm (GUM245B). — Piti Reef, 2 m, among rocks, 24.VII.1993, 1 ♂ 7.3 × 6.2 mm (GUM271). — Piti Reef, 0.5-2 m, among rocks, 4-18.VIII.1993, 1 ♀ (ovig.), 10.7 × 9.4 mm (GUM298). — Piti Reef, 1 m, among rocks, VIII.1993, 3 ♂ 7.0 × 6.0, 8.8 × 7.6, 11.9 × 9.7 (holotype) mm, 1 ♀ 9.5 × 7.5 mm (paratype) (GUM300). — Piti Reef, 1 m, 28.VII.1993, 1 ♂ 6.3 × 5.5 mm (GUM301). — Piti Reef, 1 m, among rocks, 31.VII.1993, coll. H. T. Conley, 1 ♂ 9.0 × 7.7 mm (GUM307).

ETYMOLOGY. — Named after Roy K. Kropp for his contribution to the knowledge of the Decapoda, especially Brachyura, of Guam.

SIZE. — Maximum size for females, 10.7 × 9.4 mm and males, 11.9 × 9.7 mm. The ovigerous female carried around 150 eggs, mean diameter = 0.47 mm (n = 5).

DEPTH AND HABITAT. — All specimens came from coral rubble and rocks in shallow water, 1-2 m.

DISTRIBUTION. — Known only from Guam, North Pacific.

DESCRIPTION

Carapace wider than long, ratio cw/cl = 1.12-1.26, shape sub-oval, frontal and posterior ends truncate, anterolateral margin gently rounded and posterolateral margins convergent. Posterior margin eroded at corners to accommodate last pair of pereopods and medially to accommodate first segment of abdomen. Carapace surface smooth, sparsely covered with short plumose setae, not bent at right angles, and scattered longer filiform setae (long setae five times length of short setae and 0.15 of cw). Setae denser on pereopods. Setae not arranged in clumps and not dense enough to obscure carapace surface.

Carapace surface smooth, frontal groove short, separating pair of low rounded swellings; carapace regions not defined, cervical grooves not marked in male holotype but evident in female paratype. Anterolateral carapace margin begins

just below postorbital corner: bearing six teeth, first four small, blunt and near beginning, last two more distant, larger and more acute. Small blunt posterolateral tooth marks beginning of posterolateral margin.

Frontal margin continuous above orbits that are clearly exposed dorsally, no post-orbital notch; sub-orbital margin not projecting (just visible dorsally) and unarmed. Sub-hepatic area convex, minutely denticulated.

First article of antennule much longer than wide, becoming broader distally and fitting closely beside epistome; second article at almost right angles to first, fitting beneath frontal margin; remaining articles folded into orbital cavity. First article of antenna moveable, beaked medially enclosing urinal aperture; second article longer than wide, surface convex, produced distally at both corners, lateral lobe curves over base of eye-stalk; third article longer than wide; fourth article as long as wide, attached at an angle and bearing flagella 0.65 × cw. Epistome triangular, surface flat, posterior margin eroded to accommodate edges of mxp3.

Subhepatic area convex and minutely granulated. The mxp3 operculiform, bases separated widely by sternum; palp (carpus, propodus, and dactyl) setose along medial margin, two-thirds length of ischium + merus; crista dentata has six very small teeth. Male sternal suture 4/5 complete, others incomplete; in female suture 4/5 faintly marked, complete, suture 7/8 carrying entrances to spermathecae, short, ending apart between bases of fourth pereopods.

Male chelipeds much longer than first pair of walking legs; merus trigonal, superior border armed with row of six small blunt tubercles, inferior border with several scattered tubercles; carpus unarmed except for blunt spur on inner superior border; propodus unarmed except for some very faint tubercles on superior border, fixed finger curved, edentate; moveable finger also curved, bearing single prominent tooth mid-way, fingers only touch at tips, widely gaping. Female chelipeds smaller, about as long as first walking legs; tooth on moveable finger absent.

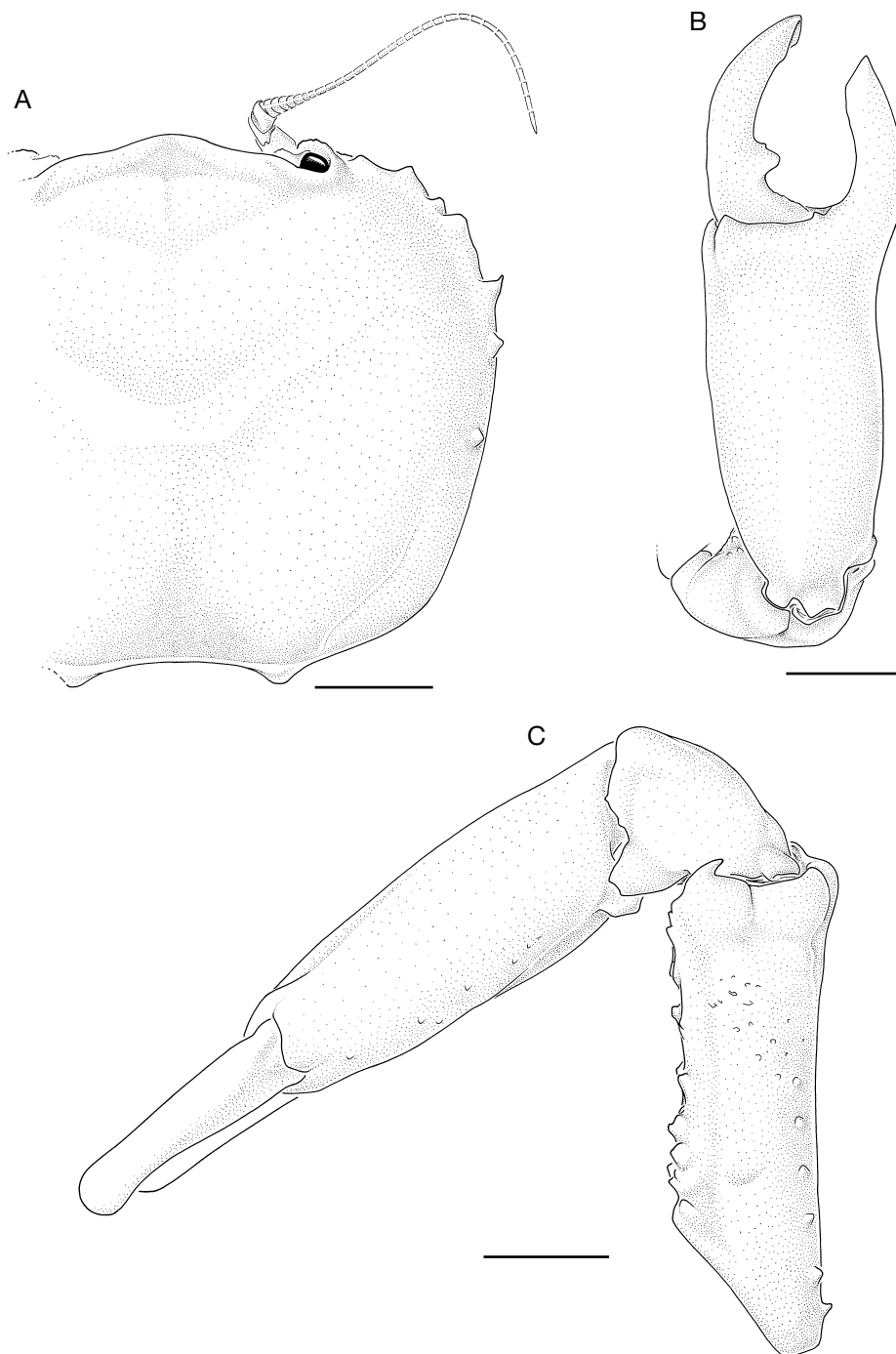


FIG. 1. — *Dynomene kroppi* n. sp., Guam, Piti Reef, 1 m, holotype ♂ 11.9 × 9.7 mm; **A**, dorsal view of right half of carapace; **B**, outer face of right cheliped; **C**, dorsal view of right cheliped (MNHN-B26474). Setae omitted. Scale bars: 2 mm.

P2-p4 decreasing in length posteriorly; meri with row of five or six tiny tubercles along upper border; carpi more densely covered with tubercles; propodi with few scattered tubercles; dactyli curved, inner margins armed with five to six tiny spines increasing in size distally. Length of p3 merus $2.3 \times$ width and about three-quarters of cl. P5 reduced, more so in male: in males length is 26% of preceding limb (female 34%) reaching only 30% along merus of p4 (female 50%). Limb sub-chelate: in males dactylus tiny, claw-like and opposed to propodal extension; in females dactylus longer, flattened; fine structure of dactyl and propodal extension unavailable.

Surface of abdomen smooth, segments increasing in width posteriorly except in female where last segment narrower because uropods totally exclude penultimate abdominal segment from lateral margin (in males uropods make up 30% of lateral margin). Female abdomen totally covers sternum and bases of pereopods, extending anteriorly so that telson covers bases of mxp3. No abdominal locking mechanism and sternal tubercles absent in paratype female. Male abdomen smaller, covering most of sternum, but not bases of pereopods. Male has small sternal tubercles at bases of p2, lying beside uropods when abdomen closed, but no abdominal locking mechanism.

Five pairs of pleopods in both sexes. First pair of female pleopods uniramous, other four pairs biramous. Male first pleopods uniramous, forming semi-rolled tube, with apical sperm aperture beside curved apical lobe, surrounded by setae. Second pleopods, as long as first pair, biramous, exopod rudimentary, gonopod (i.e. endopod) consisting of calcified proximal half and horny, needle-like distal half. Shaft of needle armed with four distal, evenly spaced, inset acute subterminal spines, directed distally, spiraling around shaft over 90° , and ending with single terminal spine. Last three pairs of pleopods rudimentary, uniramous, decreasing in length posteriorly.

DISCUSSION

D. kroppi n. sp. can be distinguished from *D. pugnatrix* by having six anterolateral teeth

(*vs* five in *D. pugnatrix*); the anterolateral teeth smaller and blunter; p2-p4 with small blunt tubercles on the superior borders (*vs* acute tubercles); long setae on carapace which are filiform (*vs* feathered setae); only five or six spines on inner margins of dactyli of walking legs (*vs* 10 spines).

Surface evidence of sternal sutures in male and female *D. kroppi* n. sp. are typical of those found in other species of *Dynomene*: only suture 4/5 is evident, but incomplete, in both sexes and sutures 7/8, which end apart, are marked in females. Only suture 3/4 is deeply incised and complete. A similar situation is found in *Acanthodromia* A. Milne-Edwards, 1880, *Hirsutodynomene* McLay, 1999, *Metadynomene* McLay, 1999 and *Paradynomene* Sakai, 1963. In *Metadynomene*, suture 5/6 is not incised on the surface but is marked by an uncalcified, translucent band across the sternum. The sternal sutures in dynomenids represent a derived condition in that most are not evident on the surface.

In *D. kroppi* n. sp., the uropods are sexually dimorphic, with the female uropods filling all of the abdominal lateral margin and male uropods only about 30%. This is similar to *D. hispida* and *D. praedator* but less than *D. pugnatrix* where male uropods fill about 75% of the lateral margin. In all species of *Dynomene* and *Hirsutodynomene* the uropods are sexually dimorphic with female uropods always being larger. Dynomenids are also unusual in having sexually dimorphic fifth pereopods (see McLay 1999: 449-454, figs 8-10).

D. kroppi n. sp. probably falls into the group of dynomenids that do not grow larger than about 20 mm cw. These species have a brood size ranging from 30 to 900 eggs with a mean diameter of 0.46 mm (McLay 1999: 550). The *D. kroppi* n. sp. ovigerous female carried around 150 eggs, of diameter 0.47 mm, and clearly conforms with this group of small species, which undoubtedly have a planktonic larval stage.

The structure of the second male gonopod of *D. kroppi* n. sp. most closely resembles that of *D. guamensis* n. sp. and only differs in having a

greater number of sub-terminal spines. Unfortunately we do not have the microscopic details of the second gonopod of *D. pugnatrix* which has a similar gross morphology. Otherwise, the closest dynomenids are *D. hispida* and *D. praedator*, both of which have five sub-terminal spines, arranged sinuously around the shaft (see McLay 1999: 456-461). However, *D. hispida* and *D. praedator* have two and three terminal spines respectively, while *D. kroppi* n. sp. has only one. Amongst dynomenids, the species of *Dynomene* tend to have a smaller number of gonopod spines (4 to 15) than is found in other genera (McLay 1999: table 1).

Dynomene guamensis n. sp.

(Figs 2; 3B)

TYPE MATERIAL. — Holotype ♂ 11.0 × 9.7 mm, Piti Lagoon, Guam (MNHN-B26476).

MATERIAL EXAMINED. — **Guam.** Piti Lagoon, 13°27'N, 144°47'E, 1-3.5 m, among dead coral, III.1997, coll. H. T. Conley, 1 ♂ 11.0 × 9.7 mm.

ETYMOLOGY. — The specific name alludes to the island of Guam, the type locality.

SIZE. — Type ♂ 11.0 × 9.7 mm.

DEPTH AND HABITAT. — Type specimen collected from dead coral between 1-3.5 m.

DISTRIBUTION. — Only known from the type locality at Guam, North Pacific Ocean.

DESCRIPTION

Carapace wider than long, ratio of cw/cl= 1.13, shape sub-quadrangular, front gently rounded, anterolateral margins rounded, and posterolateral margins convergent. Posterior corner of carapace margin eroded to accommodate last pair of pereopods, middle of posterior border concave, accommodating first segment of abdomen between two strengthened lobes. Carapace surface and pereopods densely covered with long filiform and short plumose setae bent at right angles near tip (long setae 4.4 × length of short setae, 0.20 × cw). Setae on carapace do not obscure surface and filiform setae, on carapace, are not arranged in clumps but scattered over sur-

face. Filiform setae much denser on pereopods than on carapace.

Carapace surface smooth except for prominent pair of convex laterally elongated swellings near mid-line, behind rostral area, and two small tubercles behind and to the side of each post-orbital corner. Carapace regions not defined, short faint cervical grooves, arising from pits near mid-line, extend anterolaterally but do not reach carapace margins. Anterolateral carapace margin begins below level of postorbital corner, evenly rounded and armed with five equidistant acute teeth directed almost vertically. Preceding first tooth is a group of eight or nine small rounded tubercles that effectively lie below suborbital margin. Single posterolateral tooth, similar to anterolateral teeth, marks beginning of posterolateral margin.

Frontal margin continuous from U-shaped median notch, thickened, initially armed with row of tiny tubercles that continue until about half-way across upper orbital margin where it becomes thinner and largely devoid of tubercles. Postorbital corner not produced, and only a faint notch separates suborbital margin visible in dorsal view.

First article of antennule much longer than wide, broadening distally and fitting closely beside epistome; second article at almost right angles to first, fitting beneath frontal margin; remaining articles folded into orbital cavity. First article of antenna moveable, much wider than long, beaked medially around urinal aperture, both lobes of beak similar in size; second article longer than wide, fitting closely alongside antennule, lateral distal corner produced as a lobe curving over base of eyestalk, medial corner less produced; third article, longer than wide, inserted at an angle between two lobes of preceding article; fourth article as long as wide, carrying flagella. Ratio of length of antennal flagella to cw= 0.5. Epistome triangular, concave, posterior margin with two eroded areas that accommodate distal extremities of operculiform mxp3. Bases of mxp3 widely separated by tip of sternum. The mxp3 palp setose along medial margin, two-thirds the length of ischium + merus; crista dentata composed of

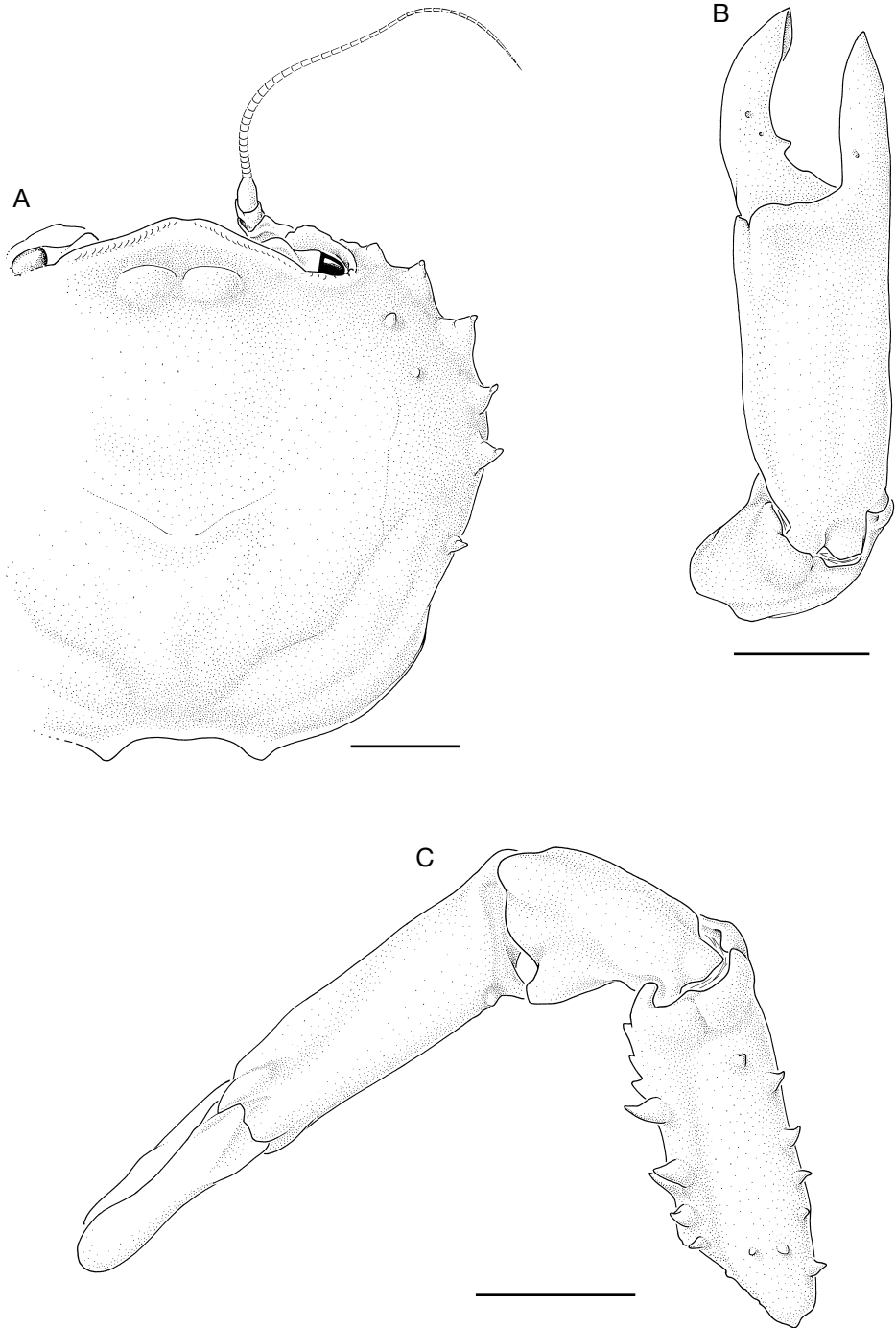


FIG. 2. — *Dynomene guamensis* n. sp., Guam, Piti Lagoon, 1-3.5 m, holotype ♂ 11.0 × 9.7 mm; **A**, dorsal view of right half of carapace; **B**, outer face of right cheliped; **C**, dorsal view of right cheliped (MNHN-B26476). Setae omitted. Scale bars: 2 mm.

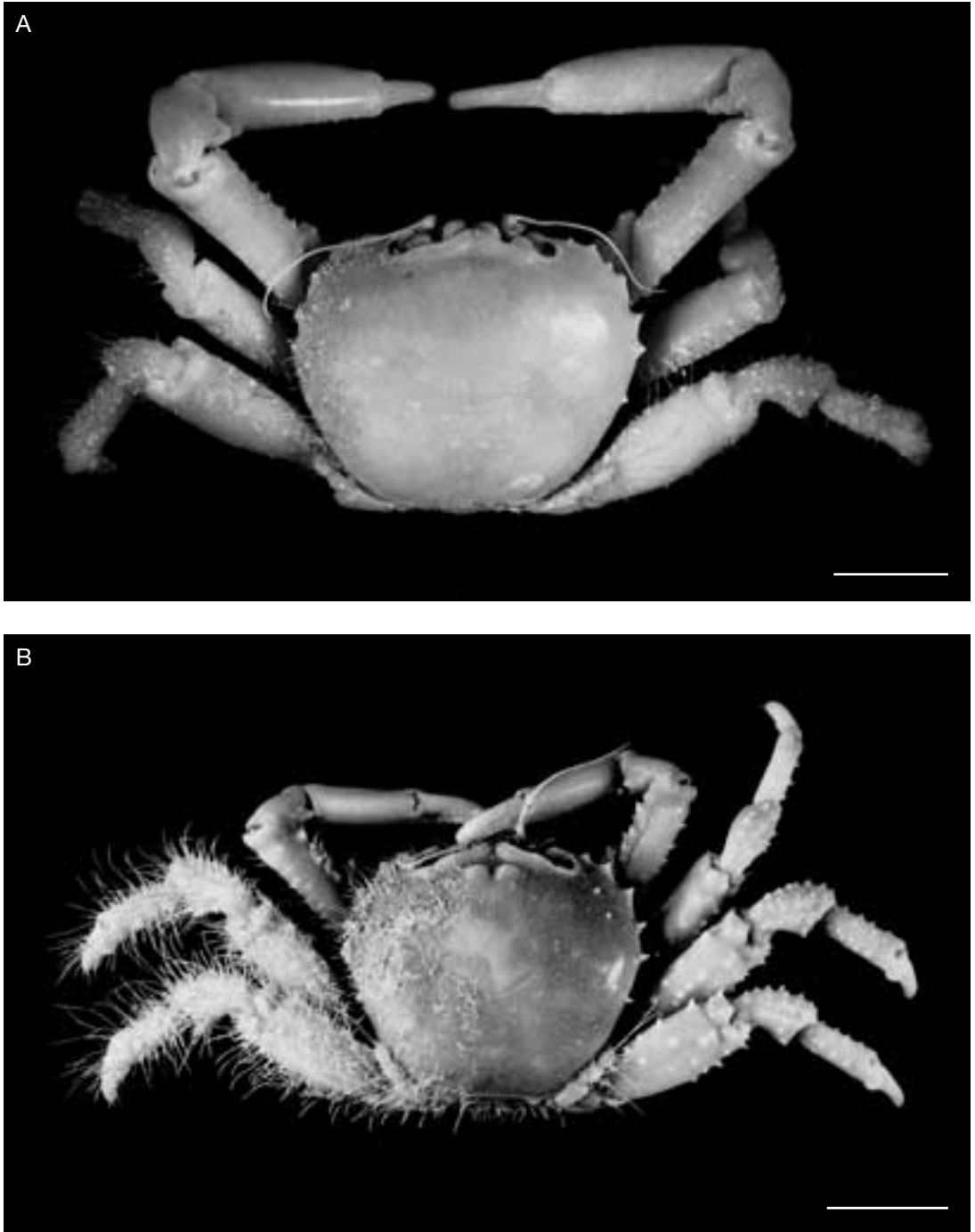


FIG. 3. — **A**, *Dynomene kroppi* n. sp., Guam, Piti Reef, 1 m, holotype ♂ 11.9 × 9.7 mm (MNHN-B26474), dorsal view of whole crab, setae removed from right side of carapace, right third and left fourth leg not shown; **B**, *Dynomene guamensis* n. sp., Guam, Piti Lagoon, 1-3.5 m, holotype ♂ 11.0 × 9.7 mm (MNHN-B26476), dorsal view of whole crab, setae removed from right side of carapace, left second leg not shown. Scale bars: 4 mm.

seven small teeth. Subhepatic area convex, tuberculated, bearing swelling with four or five larger tubercles. Sternal suture 4/5 complete, faintly marked in male. Female sternal sutures unknown. Male cheliped slightly built, scarcely longer than first pair of walking legs; merus triangular in cross section, superior border armed with six small acute tubercles, anterior inferior margin armed with three large acute tubercles paralleled by row of four small blunt granules, posterior inferior margin armed with four similar granules; carpus unarmed except for blunt spur on inner superior border; propodus devoid of granules, inferior margin straight; fixed finger without teeth, moveable finger with single small tooth mid-way, both fingers hollowed out internally, distal margins continuous, meeting only at tips. Two tufts of long setae, inserted mid-way along fingers, extend across gap between fingers.

P2-p4 decreasing in size posteriorly; borders of meri armed with acute tubercles; superior borders of carpi and propodi armed with similar tubercles; dactyli curved, inferior margins armed with seven to eight small spines increasing in size distally. Length of p3 merus about twice merus width and 60% of cl.

P5 reduced (29.3% of length of preceding pereopod), lying alongside posterolateral carapace margin, directed anteriorly, and reaching to about one-third of length of merus of preceding limb. Limb sub-chelate, propodus extended distally, dactyl claw-like as is typical for male dynomenids (McLay 1999: 449). Fine structure of dactyl and propodal extension of male and female not available.

All segments of abdomen freely moveable, width of segments increasing distally, surface smooth. Male telson much wider than long, lateral margins of last abdominal segment occluded to accommodate uropods that occupy almost 66% of lateral margin. Telson extends as far as mid-way between bases of p1. No effective abdominal locking mechanism: one small tubercle on each side of sternum opposite base of p2. When abdomen closed uropods lie beside these tubercles.

Five pairs of pleopods in male: first pair uniramous, forming a semi-rolled tube with dense setae around apical sperm aperture and soft medial lobe. Second pair biramous, endopod (i.e. gonopod) as long as first, basal half stout, calcified, narrowing distally, distal half horny and needle-like; armed with a series of six evenly spaced, tiny acute, inset sub-terminal spines, directed distally and spiraling around the shaft over 180° toward tip which ends with a terminal spine. Exopod well-developed, composed of one article, narrowing distally and reaching almost as far as proximal half of gonopod. Other three pairs of pleopods rudimentary and uniramous, decreasing in length posteriorly. Female characters unknown.

DISCUSSION

D. guamensis n. sp. can be distinguished from *D. kroppi* n. sp. because it has a higher cw/cl ratio 1.3 (*vs* 1.13 in *D. kroppi* n. sp.); five anterolateral acute teeth (*vs* six less acute teeth); two tubercles on the carapace behind the postorbital corner (*vs* none); subhepatic swelling bearing four or five blunt tubercles (*vs* none); superior borders of p2-p4 with acute tubercles (*vs* small blunt granules); and a pair of swellings behind frontal margin much more prominent than in any other species of *Dynomene*.

The structure of the second gonopod of *D. guamensis* n. sp. differs from that of *D. kroppi* n. sp. only in having a greater number of sub-terminal teeth. Apart from *D. kroppi* n. sp. the gonopods of *D. guamensis* n. sp. most closely resemble those of *D. hispida* and *D. praedator*. All dynomenid males have a rudimentary exopod on the second pleopod but in *D. guamensis* n. sp. it is much longer than in any other dynomenid. The exopod is composed of a single article, almost half the length of the endopod (i.e. gonopod) and proximally, it bears a few small setae. It may be that this individual is aberrant, just as we find many female *Metadynomene tanensis* (Yokoya, 1933) with aberrant first pleopods resembling those of males (see McLay 1999: 527-530).

The two new species described here are similar to *Dynomene pugnatrix* De Man, 1889 which is known only from the vicinity of Mauritius and

Madagascar in the Indian Ocean. A distinctive feature of all three of these species is the shape of the chelipeds. They all have chelipeds that are very slender, largely unornamented, fingers gaping widely and not down-curved, and whose margins do not have well-developed teeth, as is usually found in other *Dynomene* species. *D. pugnatrix* is only known from two specimens, one from Mauritius (the type locality) from unknown depth, and the other one nearby from a depth of 90-140 m. However, specimens of both *D. kroppi* n. sp. and *D. guamensis* n. sp. all come from shallow water (1-2 m) where specimens of *D. praedator* were also found. Despite having similar morphology, the two new species appear to differ from *D. pugnatrix* in their habitat, and they are geographically separated by a large distance. It will be interesting to see whether one or other of these species is present in intervening Indo-Pacific areas.

In both *Dynomene kroppi* n. sp. and *D. guamensis* n. sp., the crista dentata is composed of six and seven teeth respectively. The same number is also found in *D. pugnatrix* and is typical for species of the genus *Dynomene* where the number of teeth ranges from five to eight. Species of *Hirsutodynomene* also have a similar number of teeth, but in *Metadynomene* and *Paradynomene* there are around twice this number.

Dynomene praedator A. Milne-Edwards, 1879

Dynomene praedator A. Milne-Edwards, 1879: 8, pl. 14, figs 20-26. — McLay 1999: 481, figs 3b, 8a-b, 11, 12 d, 14 b, 17 b, 19 a-g.

MATERIAL EXAMINED. — **Guam.** Piti Reef, 13°27'N, 144°47'E, among rocks, 1.5 m, 22.VII.1993, 2 ♂♂ 8.5 × 6.5 (GUM268). — Among rocks, 1.5 m, 22.VII.1993, 1 ♂ 13.0 × 10.3 mm (GUM270). — Among rocks, 1 m, 1.VIII.1993, coll. H. T. Conley, 1 ♀ 7.8 × 7.0 mm (GUM300). — Outer reef margin, 1 m under rubble pile, 1-4 m, IV.1998, 1 ♂ 9.5 × 7.5 mm, coll. S. Norby, 1 ♀ (ovig.) 9.7 × 7.1 mm (UGI no registration number, ZRC 2000.0743).

SIZE. — Maximum size for males is 13.5 × 10.7 mm, and for females 12.0 × 9.6 mm. All specimens from Guam are smaller than these sizes. The above oviger-

ous female, with about 160 eggs ready to hatch, was captured during April and so conforms to the reproductive period recorded elsewhere of from January to June.

DEPTH AND HABITAT. — Depth range intertidal to approximately 50 m among coral. All the Guam specimens came from shallow water, 1-4 m.

DISTRIBUTION. — *D. praedator* is a widespread Indo-West Pacific species which has already been recorded from the Mariana Islands (see McLay 1999).

DISCUSSION

Dynomene praedator has been recently re-described and illustrated by McLay (1999) where a full synonymy can also be found. *D. praedator*, along with *D. hispida*, are the two most common shallow water dynomenids throughout the Indo-West Pacific, so it is surprising that *D. hispida* has not yet been found in Guam. *D. hispida* has been collected from the northern Mariana Islands of Maug East and Maug North (Takeda *et al.* 1994) so it is likely to be present in Guam. If it is found, it will mean that Guam will have the richest shallow water dynomenid fauna (four species) in the world.

While all the specimens came from among rocks, one specimen was excavated from 1 m below the rubble surface. This is a much neglected habitat, where we do not usually expect to find crabs.

Genus *Hirsutodynomene* McLay, 1999

DIAGNOSIS. — Carapace much wider than long, moderately convex, commonly sub-circular. Surface sparsely spinous (especially in antero-branchial region), areolate, and covered with coarse setae, which are short and long, and arranged in tufts. Lateral carapace margin always well-defined and armed with distinct teeth. Frontal groove well-marked, splits in two posteriorly, cervical, postcervical and branchial grooves usually evident. Frontal carapace margin broadly triangular, continuous, no rostrum or teeth, eyestalks short, eyes protected by well-defined orbits. Female sternal sutures 7/8 end well-apart on low tubercles behind bases of second walking legs.

Antennule can be concealed inside the orbit at the base of the eyestalk. Antennal flagella shorter than carapace width. All segments of antenna moveable, first segment (urinal) always beaked medially and second seg-

ment has an exopod firmly fixed. Third maxillipeds opercular, completely covering the buccal cavern, separated at their bases by a plate at the same level as the sternum, basis and ischium of endopod fused but joint always marked by a shallow groove. Crista dentata present. Chelipeds equal, stouter than walking legs, dactyl strongly curved, fingers gaping basally. Last pair of legs very reduced, dactyl rudimentary, forming an obsolete sub-chelate mechanism with an extension of the propodus. Gills usually 19 (including six podobranchs) + seven epipods. Gill structure basically phyllobranchiate but the plates are very variable in shape.

Abdomen of six segments and telson, folded loosely under the thorax, uropods large, abdominal locking mechanism absent. Both sexes have five pairs of pleopods, first pair rudimentary in female, last three pairs vestigial in the male. Male gonopods uniform in structure, first pair consist of a stout, setose semi-rolled tube with an apical plate, second pair needle-like with numerous sub-distal spines, some of which overlap, sinuously arranged around the axis (after McLay 1999).

Hirsutodynomene spinosa (Rathbun, 1911)

Dynomene spinosa Rathbun, 1911: 196, pl. 17, fig 1.

Hirsutodynomene spinosa – McLay 1999: 505, figs 3f, 5e-f, 8f, 9c, 11, 13a-b, d, 14d, 17e, 23a-g.

MATERIAL EXAMINED. — **Mariana Islands.** Asuncion Island, 19°40'N, 145°24'E, 1-6 m, along rock wall in holes and corals, 7.VI.1992, coll. P. Schupp, 1 ♀ 24.2 × 18.0 mm (UGI no registration number).

Guam. Piti Lagoon, 13°27'N, 144°47'E, 1.0-2.5 m, among dead coral, 20.IX.1992, 1 ♂ 20.3 × 15.9 mm (GUM287). — 1-2 m, under rubble, IV.1997, coll. H. T. Conley, 1 ♂ 10.2 × 8.1 mm (UGI no registration number). — Tumon Bay, 11 m, on dead finely branched coral, 1.XI.1984, coll. R. K. Kropp & J. H. Dominguez, 1 ♀ 4.4 × 3.9 mm (GUM191B). — Orote Peninsula, southwest end, reef slope, under rock, 20-25 m, 27.II.1998, coll. L. Kirkendale & G. Paulay, 1 ♀ 5.4 × 4.9 mm (UGI no registration number) (ZRC2000.0745). — Orote Point, 18 m, 22.V.1998, 1 ♂ 11.3 × 9.3 mm, coll. L. Kirkendale, 1 ♀ 6.0 × 4.9 mm (UGI no registration number) (ZRC2000.0746). — Luminao Reef, 9 m, rubble, 29.V.1998, coll. L. Kirkendale, 1 ♀ 7.3 × 6.1 mm (UGI no registration number) (ZRC2000.0747). — Cocos Islands, right side, 2-8 m, rubble field, 23.IV.1999, coll. L. Kirkendale, 1 ♀ 8.2 × 6.8 mm (UGI no registration number) (ZRC2000.0749). — Orote Peninsula, 10-22 m, 22.XI.1999, coll. L. Kirkendale, 1 ♂ 13.8 × 10.5 mm (UGI no registration number) (ZRC2000.0748).

SIZE. — Maximum size for females is 32.3 × 29.4 mm, and for males, 28.7 × 21.3 mm. None of the present material exceeds these maximum sizes.

DEPTH AND HABITAT. — *H. spinosa* has been collected from intertidal to around 15 m, on coral. Two of the above specimens came from deeper waters at 18 m and 20-25 m. These specimens extend the lower depth limit to around 25 m.

DISTRIBUTION. — *H. spinosa* is widespread in the Indo-West Pacific, from Madagascar to western Australia and Indonesia, and localities in both the North and South Pacific as far east as the Tuamotu Islands in French Polynesia.

DISCUSSION

Hirsutodynomene spinosa has been described and illustrated by McLay (1999) where a full synonymy can be found. The distinctive features of the species are: a very dense cover of setae, both long filiform setae and short setae bent at right angles near the tip; about 12 spines on the carapace surface; suborbital margin with about five short, acute spines; and a sharp spine on the inner carpal margin of the cheliped. It can be distinguished from the only other species in this genus, *H. ursula* (Stimpson, 1860), which has sparse setae on the carapace, with short setae not bent at right angles; only six spines on the carapace surface; suborbital margin with only a few blunt granules; and a blunt lobe on the inner carpal margin. *H. ursula* is only known from the eastern Pacific.

Genus *Paradynomene* Sakai, 1963

DIAGNOSIS. — Carapace subquadrangular in shape, slightly longer than wide, surface convex, well-areolated, individual areolae each having one or two low conical tubercles. Lateral carapace margins well-defined, sub-parallel and armed with irregular teeth. Narrow frontal groove splits in two posteriorly, cervical, postcervical grooves evident. Frontal carapace margin well-produced anteriorly, cut into three teeth, median tooth small, lateral teeth broad and cristate, eyestalks short, eyes protected by well-defined orbits. Female sternal sutures 7/8 end well-apart on low tubercles behind bases of second walking legs. Antennule can be concealed inside the orbit at the base of the eyestalk. Antennal flagella shorter than half of carapace width. All segments of antenna moveable, first segment (urinal) beaked

medially and second segment has an exopod firmly fixed. Third maxillipeds opercular, completely covering the buccal cavern, separated at their bases by a plate at the same level as the sternum, basis and ischium of endopod fused but joint always marked by a shallow groove. Crista dentata present. Chelipeds robust, equal, stouter than walking legs, last pair of legs very reduced, dactyl rudimentary, forming an obsolete chelate mechanism with an extension of the propodus only in the female. Branchial formula 19 gills + seven epipods. Abdomen of six segments and telson, folded loosely under the thorax, uropods large, abdominal locking mechanism absent. Both sexes have five pairs of pleopods, first pair rudimentary in female, last three pairs vestigial in the male. First pair of male gonopods consist of a stout, setose semi-rolled tube with an apical plate, second pair needle-like bearing a linear row of tiny inset spines along the anterior surface (after McLay 1999).

Paradynomene tuberculata Sakai, 1963

Paradynomene tuberculata Sakai, 1963: 231, fig. 8. — McLay 1999: 543, figs 4e-f, 6e-f, 7c, e, 10b-d, 14a, 25d, 32a-g.

MATERIAL EXAMINED. — **Guam.** 13°27'N, 144°47'E, North West Luminao Reef, 21 m, among dead coral, 29.V.1993, coll. H. T. Conley, ♂ 22.7 × 21.3 mm, 1 ♀ 16.1 × 16.1 mm (GUM 310) (ZRC2000.2122). — Piti Lagoon, 1.2-7.5 m, in dead coral, 26.V.1994, 1 ♂ 21.7 × 20.0 mm. — Piti Lagoon, 4-8 m, among dead coral, 5.VI.1994, 1 ♂ 17.2 × 16.4 mm. — Piti Lagoon, 1.5-5 m, in coral rubble, 12.V.1997, 1 ♀ (ovig.) 20.5 × 19.4 mm. — Luminao Reef, 21-24 m, among coral rubble, 7.V.1998, coll. H. T. Conley, 1 ♀ 8.6 × 8.8 mm (UGI no registration numbers) (ZRC2000.0750).

SIZE. — Maximum size for males is 22.0 × 22.8 mm, and for females 20.6 × 21.4 mm. The largest male from Guam, 22.7 × 21.3 mm, is about the same size as the largest male. The ovigerous female, 20.5 × 19.4 mm, was carrying about 840 small eggs, diameter = 0.5 mm, indicating that *P. tuberculata* has a planktonic larval stage.

DEPTH AND HABITAT. — Before these specimens were collected from Guam, the known depth range was 35-402 m, but it now appears that *P. tuberculata* occurs at shallower depths than previously thought. The depth range is now 1.5-402 m on dead coral and rocky bottoms.

DISTRIBUTION. — *P. tuberculata* is known from the Gulf of Aden in the Indian Ocean, Japan and New Caledonia in the West Pacific and now Guam.

DISCUSSION

Paradynomene tuberculata has been well-described and illustrated by McLay (1999) where a full synonymy can be found. Amongst the dromiids, it is very distinctive in having a strongly calcified, oblong carapace, with an areolate and granulated surface. McLay (1999) noted the similarities of *P. tuberculata* to some dromiids like *Epigodromia* McLay, 1993. These similarities include the carapace surface, the tridentate rostrum and having a front or "face" with a dromiid conformation. These similarities may indicate evolutionary convergence in the two families wherein the species achieve a cryptic appearance by resembling their coral surroundings McLay (1999: 549).

Family DROMIIDAE De Haan, 1833

Genus *Sphaerodromia* Alcock, 1899

DIAGNOSIS. — Carapace sub-globose, as wide or wider than long, surface gradually rounded, tomentose. Front broadly triangular, grooved in midline, rostrum not developed, continuous with supraorbital margin. Distomedial corner of second antennal segment not produced. Coxae of third maxillipeds closely approximated and inserted under tip of sternum. Female sternal sutures 7/8 end wide apart behind genital openings. Cheliped with an epipod and well-developed podobranch, first two pairs of legs also have epipods, with or without podobranchs. Chelipeds longer and stouter than first two pairs of legs, which are not nodose. Usually a small propodal spine on inferior margin overlapping with dactyli of first two pairs of legs. Last two pairs of legs reduced, similar in size, only last pair subdorsal. Three to five propodal spines opposing dactyli, no spines on outer propodal margin, but two to four small spines on inner margin of dactyli. Abdomen of six free segments. Telson rounded, longer than wide in male, wider than long in female. Uropod plates well-developed, visible externally and occluding up to approximately half the sub-terminal abdominal segment from the lateral margins. Abdominal locking mechanism consists of denticulate ridges on coxae of first two legs against lateral margins of telson and last two segments, uropods not used. First male gonopod with a small rounded terminal plate, second gonopod simple, needle-like, with longitudinal row of sub-terminal spines, and an exopod on the basis. Vestigial pleopods present on male segments three to five (modified after McLay 1993).

KEY TO SPECIES OF *SPHAERODROMIA* ALCOCK, 1899

Species dealt with in this paper are in bold.

- Orbit divided horizontally into two chambers
..... *Sphaerodromia brizops* McLay & Crosnier, 1991
- Orbit not divided horizontally, but with incipient vertical division 2
- 2. Carapace approximately as wide as long (ratio cw/cl = 1.0 ± 0.05) 3
- Carapace significantly wider than long (ratio > 1.05) 4
- 3. Carapace surface smooth, anterolateral margin of carapace entire
..... *Sphaerodromia kendalli* (Alcock & Anderson, 1894)
- Carapace surface granulated, anterolateral margin of carapace with a deep notch
about mid-way *Sphaerodromia ducousoi* McLay, 1991
- 4. Anterolateral carapace margin curved upwards like a lamella
..... *Sphaerodromia lamellata* Crosnier, 1994
- Anterolateral carapace margin not curved upwards
..... *Sphaerodromia nux* Alcock, 1899

Sphaerodromia nux Alcock, 1899

Sphaerodromia nux Alcock, 1899: 154; 1901: 40, pl. 4, fig. 19. — Ihle 1913: 92 (list). — Lewinsohn 1984: 115, pls 3B, 4C, D. — McLay 1991: 463; 1993: 127.

MATERIAL EXAMINED. — **Philippine Islands.** Northern Mindanao, *Albatross* Expedition, stn D 5516, 8°46'N, 123°32.30'E, 321 m, 9.VIII.1909, 1 ♀ 30.2 × 28.0 mm (USNM).

SIZE. — Maximum size for females 41.7 × 36.0 mm and for males 67.0 × 58.0 mm. Lewinsohn (1984) noted that larger specimens tend to have a higher cw/cl ratio.

DEPTH AND HABITAT. — Type locality is Gulf of Martaban, 128 m. Previously known depth range of 100-150 m, is greatly extended by the Philippine specimen taken from 321 m. Other species of *Sphaerodromia* also come from deeper water with the maximum depth known being 400-450 m for *S. ducousoi* from the Tuamotu Archipelago.

DISTRIBUTION. — Burma, Seychelles, Madagascar and Reunion. The Philippine specimen represents a considerable eastward range extension.

DESCRIPTION

Carapace wider than long, globose, strongly convex, rising steeply above anterior and lateral margins, covered by short velvety tomentum. Branchio-cardiac grooves distinct, joined by faint groove marking anterior cardiac area border to make H-shape pattern. Anterior to pattern are pair of deep pits. Branchial groove represented by line of pits not reaching lateral margin. Otherwise carapace smooth. Rostrum bilobed, lateral teeth blunt, no frontal groove. Supraorbital margin straight, slightly thickened around postorbital margin. Supraorbital tooth absent. No fissure separating supra- and infraorbital margins. Infraorbital margin triangular, not visible dorsally. Sub-hepatic area slightly concave, bearing many small conical tubercles. Anterolateral margin begins beneath suborbital margin, evenly rounded, without teeth but bearing many small conical tubercles. Posterolateral tooth absent, no division of lateral carapace margin into antero- and posterolateral sections.

Epistome triangular, lateral margins distinct. Crista dentata with 15 large uniform teeth.

Pereopods covered with short setae, margins fringed with longer stiff setae, limbs fitting tightly against carapace. Chelipeds well-developed, merus triangular in cross-section, borders bearing small tubercles. Upper margin of carpus carinate, surface granular. Outer face, upper and lower borders of propodus have small tubercles arranged roughly in longitudinal rows. Fingers long, pearly white, cutting margin armed with five blunt, interlocking teeth as well as five smaller proximal teeth which do not meet.

P2-p3 shorter than chelipeds, smooth, laterally compressed, acute distal spine on propodus. Inner margins of dactyli armed with six or seven short spines all of similar size. Dactyli shorter than propodi, ratio = 0.77. P4-p5 similar, but much shorter than p2-p3, last pair slightly longer. Dactyl of p4 opposed by three or four unequal propodal spines, no spines on outer propodal margin, inner margin of dactyl armed with four short spines. Dactyl of p5 opposed by four short propodal spines, none on outer propodal margin, three small spines on inner margin.

Female sutures 7/8 end apart behind p3. Epipods on p1-p4 and podobranchs on p1-p3. Podobranchs decrease in size posteriorly. Abdominal locking mechanism uses serrated ridges on coxae of p2-p3.

Female telson slightly wider than long, male telson longer than wide. No median abdominal ridge. Uropods large, visible externally, occluding one-third of penultimate abdominal segment from lateral margin in male, but two-thirds in female. Five pairs of pleopods in both sexes, first pair uniramous and reduced, rest biramous in female. Second male gonopod has an exopod, third to fifth pleopods vestigial and bifid.

DISCUSSION

The re-description by Lewinsohn (1984) is amended and details of the mature female from the Philippines are added above. The key provided by McLay (1993), to identify the species of *Sphaerodromia*, is modified herein to include *S. lamellata* Crosnier, 1994 from New Caledonia.

Genus *Dromidiopsis* Borradaile, 1900

DIAGNOSIS. — Carapace as long as wide or longer than wide, surface smooth. Rostrum tridentate, lateral teeth rounded, not prominent. Coxae of third maxillipeds usually separated by a narrow gap and inserted close to the tip of the sternum. Female sternal sutures 7/8 end on tubercles either apart or together, behind chelipeds. Cheliped with an epipod. Legs not knobbed or ridged. Propodi and dactyli of first two pairs of legs equal in length, inner margins of dactyli armed with five or fewer small spines. Dactyl of third leg opposed by one propodal spine with up to two spines on the outer propodal margin. Fourth leg may be as long as second leg, dactyl opposed by up to two propodal spines, usually one spine on the outer propodal margin and another on the outer margin of the dactyl itself. Uropods usually well-developed, visible externally and used in the abdominal locking mechanism by fitting in front of serrated flanges on the bases of the first pair of legs. Last two segments of the abdomen maybe fused or freely movable. First male gonopod a simple semi-rolled tube, sharply tipped and densely setose, second gonopod simple needle-like, no exopod on basis (modified after McLay 1993).

Dromidiopsis lethrinusae (Takeda & Kurata, 1976)

Sphaerodromia lethrinusae Takeda & Kurata, 1976: 118, text fig. 1a-d.

Dromidiopsis lethrinusae – McLay 1993: 139 : fig. 15e-f.

MATERIAL EXAMINED. — **Guam.** Tanguisson Point, on dead *Acropora*, 13°27'N, 144°47'E, 11 m, 30.X.1979, coll. R. K. Kropp, 1 ♀ 3.5 × 4.0 mm (compound ascidian cap) (UGI unregistered) (ZRC2000.2121). — Tanguisson Point, 14 m, on part live part dead *Pocillopora elegans*, 30.X.1979, coll. R. K. Kropp, 1 ♂ 3.6 × 4.1 mm (UGI unregistered) (ZRC2000.2120).

SIZE. — Maximum size for males is cw = 11.9 mm and 17.2 mm for females. Both specimens from Guam are very small.

DEPTH AND HABITAT. — The specimens from Guam came from depths of 11 to 14 m, well within the known depth range of 8 to 45 m. *D. lethrinusae* is an inhabitant of shallow reefs. One of the Guam specimens was found on dead *Acropora* corals and the other was found on a part-live *Pocillopora elegans* colony. Thus far, *D. lethrinusae* is only known to carry compound ascidians as camouflage.

DISTRIBUTION. — *D. lethrinusae* was already known from Japan, New Caledonia and the Philippine Islands and is now known from Guam, Mariana Islands.

DISCUSSION

Dromidiopsis lethrinusae has been re-described and figured by McLay (1993: 139: fig. 15e-f).

Genus *Lauridromia* McLay, 1993

DIAGNOSIS. — Carapace as wide or slightly wider than long. Coxae of third maxillipeds closely approximated and inserted under tip of sternum. Female sternal sutures 7/8 end apart on well-developed tubes behind base of chelipeds. Cheliped with an epipod, superior margin of carpus and propodus armed with two to four large tubercles. Legs not knobbed or ridged. Propodi and dactyli of first two pairs of legs equal in length, inner margin of dactyli typically armed with seven or more small spines. Dactyl of third leg opposed by a single propodal spine, usually two spines on the outer propodal margin. Fourth leg shorter than second, dactyl usually opposed by two propodal spines with up to three spines on the outer margin and usually a spine on the outer margin of the dactyl itself. Uropods well-developed, visible externally, but not used in the locking mechanism. This consists of serrated flange on the base of first and second legs, sometimes on cheliped base, which fit against lateral margins of abdomen. Joint between the last two abdominal segments wholly or at least partially fused. First male gonopod stout semi-rolled tube, tip sharp densely setose, second gonopod simple, needle-like no exopod on basis (after McLay 1993).

Lauridromia indica (Gray, 1831)
(Fig. 4A-F)

Dromia indica Gray, 1831: 40. — Griffith & Pidgeon 1833: 296, crust. pl. 24, fig. 2.

Dromia sp. — White 1847: 55.

Dromia gibbosa H. Milne Edwards, 1837: 175. — Alcock 1901: 75 (list). — Ihle 1913: 89 (list).

Dromia (Dromidia) orientalis Miers, 1880: 370, l. 15, figs 1, 2.

Dromidia cranioides De Man, 1888b: 208, pl. 14, figs 6-8. — Nobili 1903: 22. — Rathbun 1910: 366; 1911: 194.

Dromia cranioides — Alcock 1900: 138; 1901: 46, pl. 2, fig 5.

Dromidia indica — Alcock 1901: 76 (list). — Ihle 1913: 90 (list).

Dromidiopsis cranioides — Borradaile 1903: 299 (list). — Ihle 1913: 26, pl. 1, fig. 4, text figs 8a, 9, 18. — Sakai 1936: 12; 1976: 10, text fig. 1. — Buitendijk 1950: 59. — Serène & Lohavanijaya 1973: 19, figs 8-16, pl. 2, B-D. — Dai *et al.* 1981: 131, text figs 3-4, pl. 1, fig 2. — Dai & Yang 1991: 18, pl. 1 (3), fig. 4 (4-5).

Dromidia orientalis — Ihle 1913: 90 (list).

MATERIAL EXAMINED. — **Indian Ocean.** No exact locality, no depth, no date, 1 ♂ 38.1 × 40.2 mm (holotype of *Dromia indica* Gray, 1831, BM 304a, dried collection, presented by General Thomas Hardwicke.). — Western Indian Ocean, HMS *Sealark*, 7 m, 1905, coll. J. Stanley Gardiner, 1 ♀ 6.7 × 7.2 mm (USNM 41044).

Indo-Malayan Seas. No exact locality, no depth, no date, 1 ♀ 63.6 × 59.4 mm (BM 1880: 6) (holotype of *Dromia (Dromidia) orientalis* Miers, 1880).

Singapore. Johore Strait, off Seletan, 16.IV.1933, coll. M. Tweedie, 2 ♂ ♂ 13.0 × 14.0, 17.0 × 17.2 mm, 2 ♀ ♀ 13.0 × 14.3, 17.1 × 17.7 mm (ZRC 196461115-6). — Siglap, VI.1933, coll. M. Tweedie, 5 ♂ ♂ 14.7 × 15.1-25.8 × 26.4 mm, 5 ♀ ♀ 16.8 × 16.0-40.2 × 40.0 mm (ZRC 196461115-14). — Tuas, 18.VI.1982, coll. W. Lee, 2 ♂ ♂ 38.5 × 38.8, 81.0 × 76.0 mm, 8 ♀ ♀ 52.5 × 53.0 to 63.8 × 63.8 mm, 1 ♀ (ovig.) 63.0 × 62.5 mm (ZRC 1984.5700-5709); 14.VII.1982, coll. W. Lee, 1 ♂ 80.0 × 72.5 mm (ZRC 1984.5643); 8.IX.1982, coll. W. Lee, 1 ♂ 82.5 × 76.5 mm, 1 ♀ (ovig.) 67.0 × 66.4 mm (ZRC 1984.57-11-5717); 1.X.1982, coll. W. Lee, 1 ♂ 79.7 × 72.5 mm (ZRC 1984.5830); 13.X.1982, coll. W. Lee, 3 ♂ ♂ 67.0 × 63.0-78.0 × 69.8 mm, 2 ♀ ♀ 64.5 × 65.0, 69.0 × 69.8 mm (ZRC 1984.6843-6848); 15.II.1984, coll. W. Lee, 7 ♂ ♂ 34.0 × 34.3-80.0 × 72.3 mm, 1 ♀ 35.0 × 35.2 mm (ZRC 1984.5874-5884); 20.III.1984, coll. W. Lee, 1 ♂ 27.0 × 27.8 mm, 1 ♀ 39.4 × 40.5 mm (ZRC unregistered); 5.VIII.1984, coll. W. Lee, 1 ♂ 59.0 × 56.5 mm, 3 ♀ ♀ 52.8 × 51.5-58.0 × 58.2 mm (ZRC 1984.35-38); 16.II.1984, coll. W. Lee, 1 ♂ 55.0 × 52.3 mm (ZRC 1984.5894). — Southern Islands, 1985, coll. P. Ng, 1 ♀ 17.0 × 18.0 mm (ZRC 1985.1726). — Off Singapore, 30.V.1991, coll. P. Ng, 1 ♂ 53.5 × 51.5 mm, 1 ♀ 61.5 × 60.5 mm, 2 ♀ ♀ (ovig.) 54.5 × 54.2, 63.7 × 63.1 mm. — South West Johore, 1992, coll. T. Tan & D. Spiegel, 1 ♂ 45.5 × 44.4 mm, 1 ♀ 44.5 × 45.3 mm; 28.I.1994, coll. R. Teo & M. Sin, 1 ♂ 18.9 × 19.4 mm (sponge cap). — Sultan Shoal, 26.II.1994, coll. R. Teo & M. Sin, 1 ♀ 32.5 × 33.1 mm (sponge cap). — Between P. Tekong & Changi, 26.I.1994, coll. D. Lane, 1 ♀ 30.3 × 30.4 mm (compound ascidian cap). — P. Ubin, east Singapore, 26.XII.1995, coll. A. Wong, 1 ♀ 12.5 × 13.7 mm (compound ascidian cap) (ZRC unregistered).

Thailand. Off Pattaya, 25.XII.1991, coll. P. Ng & L. B. Holthuis, 1 ♀ 32.0 × 33.0 mm (ZRC unregistered).

Philippine Islands. 1 ♂ 30.8 × 31.8 mm (BM 43.6, dry collection, purchased from Mr Cuming). — Sulu Archipelago, Tawi Tawi Group, *Albatross* Expedition, stn D 5163, 4°59.10'N, 119°51.00'E, 51 m, 24.II.1908, 1 ♀ 7.2 × 8.0 mm (USNM 296458).

SIZE. — Maximum size for females is 67.0 × 66.4 mm, and for males 82.5 × 76.5 mm. Females and small

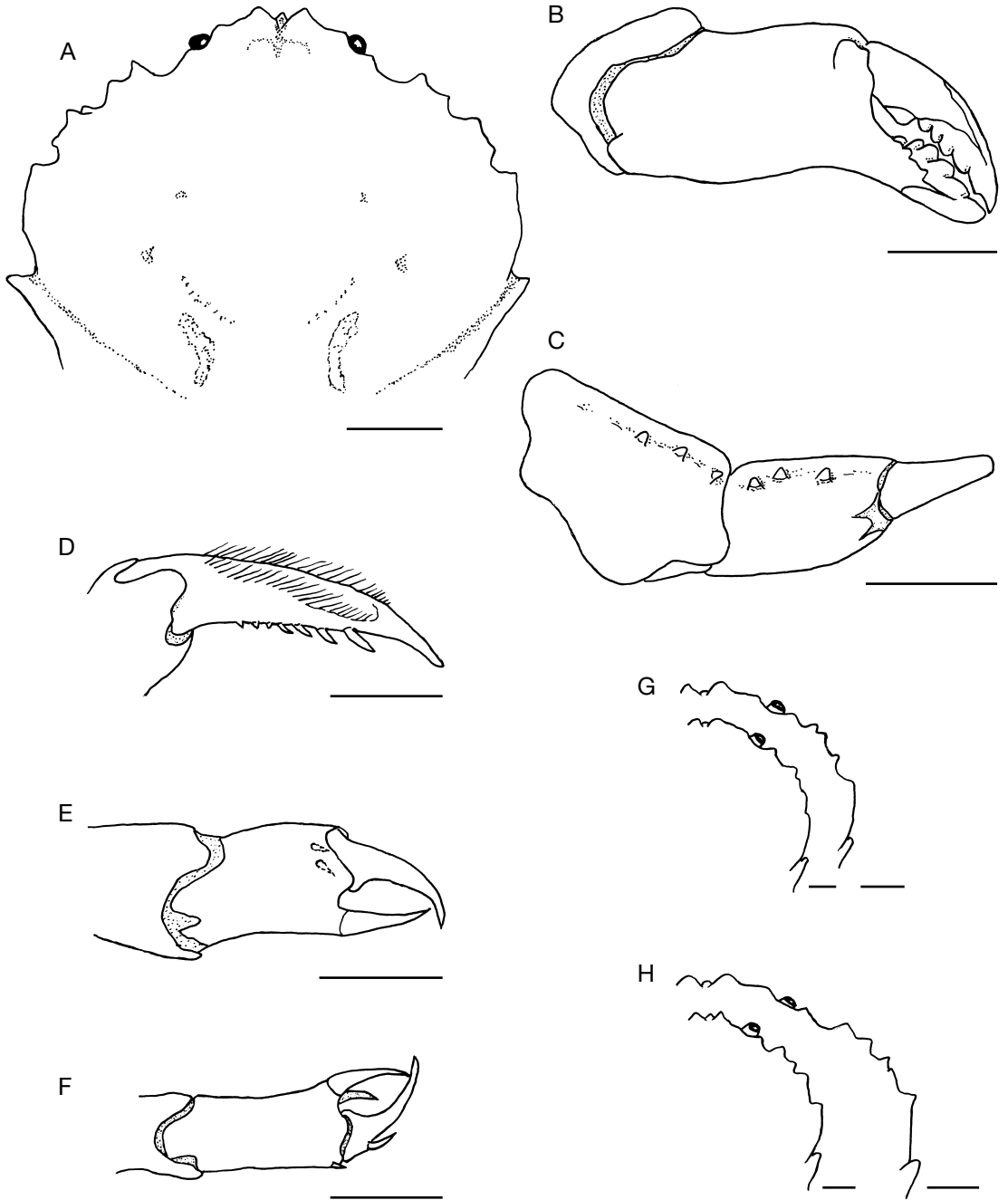


FIG. 4. — *Lauridromia indica* (Gray, 1831), Indo-Malayan Seas, no definite locality, ♀ 63.6 × 59.4 mm; **A**, dorsal view of carapace; **B**, outer face of right cheliped; **C**, dorsal view of right cheliped; **D**, posterior view of right second pereopod, dactyl; **E**, posterior view of left fourth pereopod, propodus and dactyl (the two spines on the outer propodal margin have broken off so they are indicated by dashed lines); **F**, posterior view of left fifth pereopod, propodus and dactyl (holotype of *Dromia (Dromidia) orientalis* Miers, 1880, BM 1880: 6); **G**, Johore Strait, off Seletan, ♂ 13.0 × 14.0, ♂ 17.0 × 17.2 mm (left to right) dorsal view of right side of carapace (ZRC 196461115); **H**, Tuas, Singapore, ♂ 27.0 × 27.8 mm, ♀ 39.4 × 40.5 mm (left to right) dorsal view of right side of carapace (ZRC unregistered). Scale bars: A-C, 10 mm; D-F, 5 mm; G, 2 mm; H, 4 mm (left) & 7 mm (right).

males (less than cw of 50 mm) tend to have cw about the same as cl, but larger males have cw > cl. Females carry a large clutch of eggs: the largest ovigerous female, 67.0 × 66.4 mm, had approximately 13,000 eggs. Egg diameter is 0.75 mm. Near Singapore, ovigerous females have been collected from May to July. The first zoeal stage of *Lauridromia indica* has been described by McLay *et al.* (2001).

DEPTH AND HABITAT. — Depth range is from 7 m to around 90 m. Ihle (1913) provides the deepest record of 61–91 m, but most specimens are found at shallower depths. Habitat is among coral reefs where sponges are found. *L. indica* carries pieces of sponge, usually much larger than itself.

DISTRIBUTION. — Amirante, India, Andaman Sea and Mergui Archipelago (type locality of De Man's species), Singapore, Gulf of Thailand, New Guinea, Java Sea, South China Sea, and China. Now known from the Philippine Islands. Bals (1922: 106) refers to a specimen supposedly from Sagami Bay, Japan, but Sakai (1936, 1976) remarked that he has never found any specimens, even amongst the vast collection of the Emperor of Japan. Thus the occurrence of *L. indica* in Japanese waters remains doubtful.

DESCRIPTION

Carapace as wide as long (wider than long in large males), globose, strongly convex, rising steeply behind rostrum and beside anterolateral margins. Surface smooth, branchial groove shallow, lateral cardiac borders faintly marked, and distinct pit in inner branchial area. Posterior cardiac area with three small protuberances arranged in a triangle. Whole body covered with short velvety tomentum which may be eroded in some places and with tufts elsewhere. Rostrum tridentate, median rostral tooth short, deflexed but visible dorsally, lateral teeth short, blunt and longer than median tooth. Shallow frontal groove runs back between two rounded swellings. Sub-hepatic area smooth, swollen above pleural suture. Anterolateral margin begins at level of infra-orbital margin, evenly convex, with four or five acute teeth. Position and size of anterolateral teeth variable (see below). Posterolateral tooth acute, anterolaterally directed, preceded by pronounced sinus leading to branchial notch. Posterolateral margins slightly convergent.

Supraorbital margin slightly concave, interrupted by small, blunt tooth, no postorbital tooth. Deep fissure at postorbital corner, infraorbital margin

with blunt tooth near inner edge, and slightly visible dorsally. Basal article of antenna wider than long, beaked medially; second article much longer than wide, convex, curving over base of eyestalk, distomedial corner produced, acute; third article inserted at an angle, ratio of length of antenna to cw = 0.35–0.45. Epistome triangular, concave, as long as wide, lateral margin grooved mid-way. Crista dentata with 12 large teeth.

Chelipeds well-developed, massive in male, merus triangular in cross-section, borders tuberculate; outer face of carpus with two large distal tubercles on outer face, upper border with three or four tubercles and inner distal margins with three small tubercles; propodus smooth except for three to five prominent tubercles on inner margin of superior border. Fingers down-curved, maybe pink, outer surface longitudinally grooved, margins bearing six to eight inter-locking teeth with a proximal gape.

P2–p3 shorter than chelipeds, smooth, dactyli as long as propodi, inner margins of dactyli with seven or eight small spines increasing in size distally, outer margins with two divergent rows of stiff setae. P4–p5 shorter than p2–p3, p4 shortest. Dactyl of p4 opposed by large propodal spine with two smaller spines on outer propodal margin. Dactyl of p5 opposed by two unequal propodal spines, with smaller spine on outer propodal margin and a large accessory spine on outer margin of dactyl itself.

Male telson longer than wide, truncate; uropods large, visible externally. Abdominal locking mechanism consist of serrated ridges on coxae of p2–p3, grasping distal telson border and distal notch in penultimate abdominal segment, uropods not involved. Female telson much wider than long, posterior margin rounded, uropods visible externally. Strong abdominal ridge, joint between fifth and sixth segments almost totally fused, suture only evident at margins.

Female sternal sutures 7/8 convergent, parallel anteriorly, diverging slightly before ending on prominent tubercles joined by connecting ridge just behind bases of chelipeds.

DISCUSSION

Serène & Lohavaniyaya (1973) referred their material from the South China Sea and Gulf of

Thailand to *Dromidiopsis cranioides* (De Man, 1888). They listed *Dromia* (*Dromidia*) *orientalis* Miers, 1880 as an uncertain synonym of *Dromidiopsis cranioides*. However, McLay (1993: 145) showed that both of these species are in fact synonyms of *Dromia indica* Gray, 1831. Gray (1831) did not give the sex of the type, but in fact, it is a male. Griffith & Pidgeon (1833: 296) say that their figure of *Dromia indica* is based on “a specimen in the possession of General Hardwick”. This may well be the type specimen, although the figure has no scale bar and they do not give any dimensions.

Dromia gibbosa H. Milne Edwards, 1837 was originally described as follows: “Carapace très fortement bombée et sans bosselures notables en dessus ; dents frontales saillantes et pointues ; la dent orbitaire supérieure et celle formée par l’angle supérieur de la fissure orbitaire externe pointues et saillantes ; la dent orbitaire inférieure petite et obtuse. Bords latéro-antérieurs armés de cinq ou six petites dents coniques ; l’espace entre les deux dernières occupant plus du tiers de la longueur totale de ce bord. Bords latéro-postérieurs beaucoup plus courts que les bords latéro-antérieurs. Pattes antérieures médiocres et à peine bosselées ; bord supérieur de la main armé de cinq ou six pointes ; pattes suivantes médiocres. Abdomen du mâle sans gouttières latérales, bien marquées ; le dernier article triangulaire et presque équilatéral ; pièces latérales rudimentaires”. There are enough details in the above description to confidently say that *D. gibbosa* is almost certainly the same as *D. indica* Gray, 1831. The type specimen of *D. gibbosa*, without locality, has recently been re-discovered in the dry collection of the MNHN (D. Guinot pers. comm.). As a footnote to his description of *D. gibbosa*, Milne Edwards (1837) suggested that his species may be the same as *Dromia aegagrophila* [sic] Fabricius, 1798. However, this is very unlikely and *D. aegagropila* (correct spelling) probably belongs to *Austrodromidia* McLay, 1993.

In *Lauridromia indica*, there is wide variability in the number, shape and arrangement of teeth on the anterolateral margin. Sometimes the teeth on the two sides of the carapace are different. Serène & Lohavanijaya (1973) state that in their two

specimens there were four anterolateral teeth, although on a lower level, there were two accessory teeth on the right, or one on the left, between the first and second anterolateral teeth. The same accessory teeth were noted by Alcock (1900, 1901) and Buitendijk (1950) also found variation in two large males from Singapore, which had up to six teeth. The same variation was noted in the material examined herein (see Fig. 4). In males, the shape of the carapace also changes as they grow larger. Small males and all females have a cw approximately equal to cl, but in large males the cw is significantly larger than cl. This difference is clearly illustrated in the figures of Alcock (1901: pl. 2, fig. 5) and Ihle (1913: pl. 1, fig. 4) which appear to be quite different. Both specimens are males but Ihle’s specimen is much larger. This lead Sakai (1976: 10) to say that Ihle’s material belonged to a species of *Cryptodromia*. But this cannot be true because all species of *Cryptodromia* are quite small whereas the species of *Lauridromia* grow to a much larger size. The variability and growth changes in relative dimensions of the carapace have contributed to the problems of clearly defining the species and to determining the correct name for *L. indica*.

Serène & Lohavanijaya (1973: figs 14, 15) figured the first and second gonopods of *L. indica*. The first gonopod is stout and setose, especially around the tip, forming a partially developed tube. There are no unique features of this appendage which is very similar to that found in most other dromiids except the species of *Sphaerodromia*. The styliform second gonopod is longer than the first and, when inserted, it emerges from the tip of the first. The shaft of the second gonopod is unarmed.

Genus *Cryptodromia* Stimpson, 1858

DIAGNOSIS. — Carapace as wide or wider than long, surface smooth or with a few scattered granules, convex. Rostrum tridentate. Supraorbital tooth small, blunt, usually a small postorbital tooth, and well-developed suborbital tooth. Anterolateral border may bear up to three teeth and subhepatic area may have up to two small tubercles. Antennal exopod well-developed. Coxae of third maxillipeds usually separated by a gap and may be inserted directly under tip of

sternum or well forward and separated by a deep trough. Female sternal sutures 7/8 end apart on small tubercles between or behind bases of first legs. Cheliped usually without an epipod but it may be present, carpal and propodal segments usually nodular. Carpi and propodi of first two pairs of legs may be lobed, nodular or tubercular and inner margins of dactyli have up to six small spines. Last two pairs of legs reduced but still capable of carrying camouflage, fourth pair longer, dactyli opposed by a single propo-

dal spine with up to two spines on the outer propodal margin. Abdomen of six free segments. Uropod plates well-developed and visible externally, employed in the abdominal locking mechanism by fitting in front of flanges of the base of first pair of legs. Telson usually rounded, but may be truncate or even bilobed. Abdominal segments smooth and third to fifth segments may have lateral and/or median tubercles. First male gonopod sharply tipped, setose, second gonopod simple needle-like (after McLay 1993).

KEY TO THE SPECIES OF *CRYPTODROMIA* STIMPSON, 1858

Species dealt with in this paper are in bold.

- 1. Carapace significantly wider than long 2
 - Carapace approximately as wide as long 15
- 2. Single anterolateral tooth 3
 - More than one anterolateral tooth 4
- 3. Anterolateral tooth small, almost concealed under margin
 - *Cryptodromia pentagonalis* Hilgendorf, 1879
 - Anterolateral tooth prominent, laterally directed
 - *Cryptodromia protubera* Dai, Yang, Song & Chen, 1981
- 4. Two anterolateral teeth, carapace surface canaliculated
 - *Cryptodromia fallax* (Lamarck, 1818)
 - Two or more anterolateral teeth, carapace surface not canaliculated 5
- 5. Rostrum bluntly tridentate, small supraorbital tooth 6
 - Rostrum truncate, no supraorbital tooth *Cryptodromia nipponensis* Yokoya, 1933
- 6. Median rostral tooth more prominent than lateral teeth, margins of carpi and propodi of p2 and p3 sharply verrucose *Cryptodromia tuberculata* Stimpson, 1858
 - Median rostral tooth less prominent than lateral teeth, distal margins of carpi and propodi of p2 and p3 lobed, but not sharply verrucose 7
- 7. Carapace surface minutely granular and with two anterolateral teeth, or carapace surface with scattered tubercles, especially behind supraorbital margin, and three anterolateral teeth 8
 - Carapace surface smooth, three anterolateral teeth 9

8. Carapace surface minutely granular, two anterolateral teeth, third and fourth abdominal segments armed with four tubercles *Cryptodromia coronata* Stimpson, 1858
- Carapace surface with scattered tubercles, three anterolateral teeth, third and fourth abdominal segments unarmed *Cryptodromia pitiensis* n. sp.
9. Posterolateral tooth well-developed almost as large as preceding anterolateral teeth ..10
- Posterolateral tooth only weakly developed or absent 12
10. Outer propodal margin of p5 without small spine.....
..... *Cryptodromia marquesas* McLay, 2001
- Outer propodal margin of p5 with small spine 11
11. Prominent, acute tooth-like structure on carapace behind postorbital corner.....
..... *Cryptodromia erioxylon* McLay, 2001
- No tooth-like structure behind postorbital corner
.....*Cryptodromia pileifera* Alcock, 1901
12. Lateral cardiac grooves deeply marked, anterolateral teeth unequal (first largest, third smallest), outer face of cheliped propodus denticulated, superior face tends to have ridge-like margins *Cryptodromia fukuii* (Sakai, 1936)
- Lateral cardiac grooves not marked, anterolateral teeth similar, outer face of cheliped propodus marked by some lines of small granules 13
13. Posterior margin of telson with three spines
..... *Cryptodromia tumida trispinosa* Sakai, 1936
- Posterior margin of telson with two spines or lobes 14
14. Spines on posterior margin of telson short, separated by a broad concavity
..... *Cryptodromia tumida typica* Stimpson, 1858
- Spines on posterior margin of telson long, separated by a narrow concavity.....
..... *Cryptodromia tumida bispinosa* Sakai, 1936
15. Single anterolateral tooth 16
- More than one anterolateral tooth 18
16. Anterolateral tooth well-developed and close to postorbital corner
..... *Cryptodromia hilgendorfi* De Man, 1888
- Anterolateral tooth only weakly developed and separated from postorbital corner by broad concavity 17

17. Sub-hepatic tubercle visible dorsally between postorbital corner and first anterolateral tooth *Cryptodromia laevis* Ihle, 1913
 — No sub-hepatic tubercle visible dorsally *Cryptodromia nierstraszi* Ihle, 1913
18. Two anterolateral teeth 19
 — Three anterolateral teeth 20
19. Small tubercle close to postorbital corner, above level of anterolateral margin
 *Cryptodromia amboinensis* De Man, 1888
 — No tubercle close to postorbital corner *Cryptodromia longipes* McLay, 1993
20. Lateral rostral teeth triangular, anterolateral teeth sharp, not flattened, p2 and p3 very nodular *Cryptodromia mariae* Ihle, 1913
 — Lateral rostral teeth truncate, anterolateral teeth blunt, flattened, p2 and 3 not strongly nodular *Cryptodromia trituberculata* Buitendijk, 1939

Cryptodromia pitiensis n. sp.
 (Figs 5; 6)

TYPE MATERIAL. — Holotype ♀ (ovig.) 17.8 × 14.2 mm, from Piti Reef, Guam (GUM290) (MNHN-B27303); paratype ♂ 13.2 × 11.1 mm, South of Orote Point, Guam (GUM 296) (ZRC2000.2111).

MATERIAL EXAMINED. — **Guam.** South of Orote Point, 13°27'N, 144°47'E, 18-30 m, outer reef slope, 20.XII.1990, coll. G. Nelson & H. T. Conley, 1 ♀ (ovig.) 17.8 × 14.2 mm (GUM290). — South of Orote Point, 18-30 m, among rocks, 15.X.1993, coll. H. T. Conley & C. Thomas, 1 ♂ 13.2 × 11.1 mm (GUM 296) (ZRC2000.2111).

ETYMOLOGY. — The specific name refers to the type locality, Piti Reef, Guam.

SIZE. — Type ovigerous female specimen 17.8 × 14.2 mm. Paratype male 13.2 × 11.1 mm.

DEPTH AND HABITAT. — Type and paratype specimens collected from Piti Reef, 18-30 m.

DISTRIBUTION. — Only known from the type locality on Guam, North Pacific Ocean.

DESCRIPTION

Carapace surface mostly smooth, wider than long, cw/cl= 1.25, convex, areolate, covered with short setae which enhance areolae and subdivi-

sion of carapace into areas. Frontal groove well-marked, posteriorly dividing and surrounding gastric region. Behind gastric region two prominent grooves crossing mid-line: first groove (cervical) begins at small pit near mid-line and curves diagonally across carapace towards second and third anterolateral teeth, while second groove (marking beginning of cardiac region) divides into an anterior branch that meets cervical groove and a posterior branch that runs back to branchial groove. Gastric and cardiac regions swollen. Branchial area with four swellings, two posterior to cervical groove and two smaller swellings anterior to groove. These swellings give carapace a characteristic areolate appearance. Most of carapace surface smooth but some small scattered tubercles, especially just behind supra-orbital margin, where one branchial swelling bears larger tubercle. Rostrum tridentate, teeth prominent, subacute and similar length, median tooth on lower level, deflexed but clearly visible in dorsal view; lateral teeth directed almost vertically and separated by wide U-shaped sinus. Anterolateral margin begins at level of suborbital margin, evenly convex, armed with three well-defined, evenly spaced teeth. Branchial notch

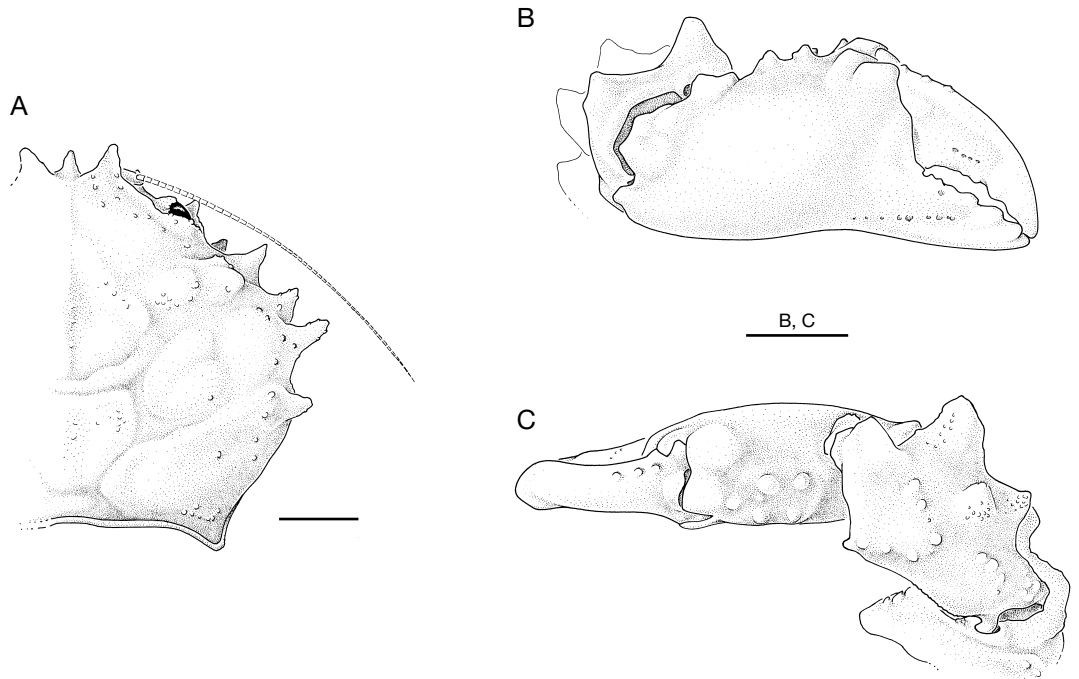


FIG. 5. — *Cryptodromia pitiensis* n. sp., Guam, Piti Reef, 18–30 m, holotype ♀ 17.8 × 14.2 mm; **A**, dorsal view of right half of carapace; **B**, outer face of right cheliped; **C**, dorsal view of right cheliped (MNHN-B27303). Setae omitted. Scale bars: A, 3 mm; B, C, 2 mm.

distinct and followed by posterolateral tooth slightly smaller than anterolateral teeth. Posterolateral carapace margins convergent and posterior margin slightly concave.

Supraorbital margin continues from base of lateral rostral tooth to postorbital corner where it is separated from suborbital margin by deep notch. On left-hand side small tooth interrupts supraorbital margin but this is not present on right-hand side. Eyes exposed dorsally even when retracted. Suborbital margin bears one strong tooth visible dorsally and another smaller tooth at its inner border.

First article of antennae wider than long, beaked medially, upper lobe longer, curved. Second article longer than wide, prominent distal medial tubercle, distomedial margin produced on which third article is inserted at an angle. Exopod fixed, tip bilobed, curving over base of eyestalk forming inner border of orbit. Ratio of flagella length to $cw = 0.55$.

Subhepatic area convex, with large tooth visible dorsally, lying between large suborbital tooth and first anterolateral tooth. Inner margin of third maxilliped merus serrated, palp, setose, exposed, as long as merus plus one-third of basis. Crista dentata on $mxp3$ consists of eight or nine evenly spaced, blunt teeth, increasing in size distally. Female sternal sutures 7/8 end apart just behind bases of first walking legs.

Pereopods covered with short tomentum and fringed with longer setae. Chelipeds without an epipod. In female, chelipeds about as long as first two pairs of walking legs, longer in male. Merus trigonal in section, margins bearing small tubercles, outer distal surface notched. Carpus outer surface has two rounded proximal swellings and two larger swellings near distal end. Several scattered tubercles on superior surface of carpus and row of three tubercles on inner margin. Surface of propodus smooth except for two or three small tubercles on inner superior margin as well as two

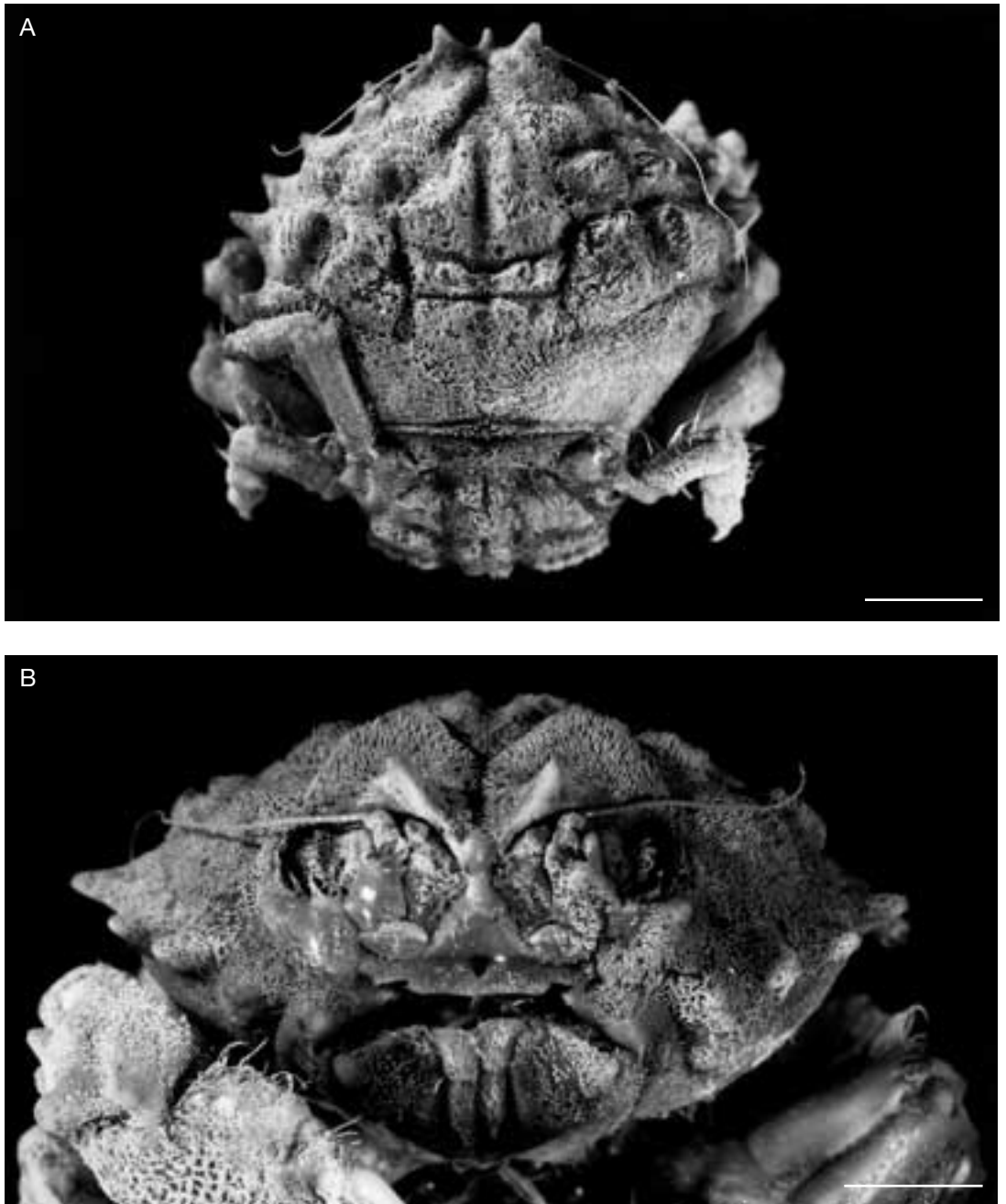


FIG. 6. — *Cryptodromia pitiensis* n. sp., ♀ 17.8 × 14.2 mm, holotype, Guam, Piti Reef, 18-30 m (MNHN-B27303); **A**, dorsal view of whole crab, setae intact, right fourth leg not shown; **B**, frontal view of the crab. Scale bars: A, 4 mm; B, 3 mm.

larger tubercles on superior face of propodus. Fingers straight, gaping, fixed finger with seven teeth increasing in size distally, margin of dactyl with one large proximal tooth (in male) followed by seven teeth as on fixed finger. Last three teeth on both fingers interlocking. Teeth more strongly developed in male.

In female, p2 and p3 about same length as chelipeds, in male shorter than chelipeds. Distal margins of meri, carpi and propodi produced as two lobes, inner margins of dactyli armed with five or six short spines increasing in size distally. P4 and p5 reduced, both about same length, dactyli strongly curved. In female, dactyli opposed by single propodal spines, with p5 having an additional spine on outer propodal margin. P5 subdorsal, when extended forwards almost reaching a line connecting last pair of anterolateral teeth. In male paratype, p4 same as female, but p5 dactyli opposed by two unequal propodal spines.

Abdomen of six free segments, telson much wider than long, posterior margin truncate. Uniramous pleopod on first abdominal segment of female. Uropod plates large, visible externally, in male uropods used in abdominal locking mechanism by fitting in front of serrated flange on coxae of p2.

First male pleopod setose at tip, second pleopod simple, needle-like and as long as first.

DISCUSSION

Using the key to genera in McLay (1993: 123) to identify this new species, the important characters for arriving at the genus *Cryptodromia* are: carapace smooth, as wide or wider than long, rostrum tridentate, female sternal sutures 7/8 end apart, cheliped without an epipod, no spine on outer margin of p5 dactyl, last two abdominal segments not fused, and uropod plates on the abdomen visible externally. In using this generic key it is necessary to make allowance for the presence of scattered tubercles on the carapace of the new species. If the carapace is treated as though it had a granular surface (couplet 16 in the key) the alternative genus would be *Epigodromia* McLay, 1993. The main features, which separate the

species of *Cryptodromia* and *Epigodromia*, are the more granular, often areolate, carapace surface and highly reduced p4 and p5 in *Epigodromia*. The difference between the p4 and p5 is associated with the fact that, while sponges and ascidians are normally carried by species of *Cryptodromia*, none of the species of *Epigodromia* are known to carry camouflage. Thus *C. pitiensis* n. sp. has some features which make it intermediate between these two genera, but the chief reason for placing it in *Cryptodromia* is the fact that the p4 and p5 are comparatively well-developed and clearly equipped for bearing camouflage. The closest species to *C. pitiensis* n. sp. is another new species that has been described from French Polynesia (McLay 2001).

Interesting features of *Cryptodromia pitiensis* n. sp. are the areolate carapace surface and the presence of a pair of well-marked grooves crossing the mid-line anterior to the cardiac region. The areolae are enhanced by setae as in *Dromia wilsoni* (Fulton & Grant, 1902). Similar grooves are usually found among the Dynomenidae, especially in *Dynomene* and *Metadynomene*. Arguments in favour of regarding the Dynomenidae and the Dromiidae as sister groups are given by McLay (1999: 462-467).

The holotype female was carrying about 580 eggs, diameter 0.58 mm. This egg size indicates that we should expect to find that *C. pitiensis* n. sp. has a planktonic larval stage as found in *C. hilgendorfi* (see McLay 1982). The number of eggs and egg diameter of *C. pitiensis* n. sp. is slightly smaller than that found in comparably sized *C. hilgendorfi*.

Cryptodromia fallax (Lamarck, 1818)

Dromia fallax Lamarck, 1818: 264.

Cryptodromia canaliculata Stimpson, 1858: 240. — Ihle 1913: 41. — Ward 1941: 1. — Lewinsohn 1977: 18, text fig. 4a-c; 1979: 8, text fig. 2B; 1984: 108.

Cryptodromia fallax – McLay 1993: 206, fig. 18e. — [Not Ng *et al.* 2000: 159, fig. 1d (= *C. tumida* Stimpson, 1858)].

MATERIAL EXAMINED. — **Guam.** Gun Beach, 13°27'N, 144°47'E, 3-5 m, fore reef, 5.VII.1999, coll. L. Kirkendale, 1 ♀ (ovig.) 7.9 × 6.2 mm (sponge cap) (UGI no registration number) (ZRC2000.0751).

Western Indian Ocean. Salomon, Chagos Archipelago, HMS *Sealark*, 5°20'S, 72°15'E, no depth, 1905, coll. J. Stanley Gardiner, 1 ♀ (ovig.) 10.6 × 9.3 mm (USNM).

SIZE. — Maximum cw for females is 15.0 mm and the smallest ovigerous female had cw = 6.8 mm. Clutch size range is 147–196 eggs. Mean egg diameter = 0.7 mm. The female from Guam had 144 eggs, diameter 0.68 mm, while the female from Salomon had 250 eggs, diameter 0.7 mm.

DEPTH AND HABITAT. — Low intertidal to around 3 m, on sponges. Crabs normally carry pieces of sponge or compound ascidian camouflage.

DISTRIBUTION. — From Red Sea to Philippine Islands and from West Pacific to French Polynesia. Besides the Philippines, *C. fallax* (Lamarck, 1818), is known from Japan and China and has been reported from the northern Mariana Island of Maug East, as *C. canaliculata* Stimpson, 1858, by Takeda *et al.* 1994.

DISCUSSION

For the full synonymy and description of *C. fallax* see McLay (1993: 206). McLay (1993) showed that *C. canaliculata* is a synonym of *C. fallax*, but the status of Ihle's (1913) varieties, "*C. canaliculata* var. *sibogae*" and "*C. canaliculata* var. *obtusifrons*", was not discussed. It is unclear whether these two varieties should be regarded as separated species. Ihle described the first variety as follows: *Cryptodromia canaliculata* var. *sibogae* Ihle, 1913 is: "A species of small size (mature female 6.5 × 6.0 mm), carapace setose, surface slightly convex, sculptured, gastrodurocardiac suture distinct. All three rostral teeth acute, similar in length, narrower and sharper than in the typical form (i.e. *C. canaliculata*). Supraorbital, postorbital and suborbital teeth well-developed and sharp, orbital fissure absent. A single well-developed anterolateral tooth, behind which the carapace margin is convex, representing the rudiment of the second anterolateral tooth, and a small, but clearly visible, posterolateral tooth. There is a well-developed subhepatic tubercle, but the tubercle on the ridge above the pleural suture is absent. The suprasutural ridge bulges, but is not very distinct, which is one reason for regarding this variety as being different from the typical form. In summary, the variety *sibogae* is different because of the smaller size, narrow rostral teeth

and absence of a distinct tooth on the suprasutural ridge" (translated from German). Ihle (1913) notes that it is possible that the specimen of *C. canaliculata*, mentioned by De Man (1888a: 403), belongs to this variety, because it lacked a suprasutural tubercle.

Comparing his other variety, *Cryptodromia canaliculata* var. *obtusifrons* Ihle, 1913, with the typical form Ihle described it as follows: "The general body shape and shape of the carapace are the same as in the typical form, as is the sculpturing on the carapace surface. The gastrodurocardiac suture is very deep. The lateral rostral teeth are more slender, as in the typical form, but the median rostral tooth appears different. This tooth is short, deflexed and ends bluntly (hence the varietal name) so that, in dorsal view, the tooth is only partially visible and the lateral teeth are much longer, projecting further forward than the median tooth. The form of the supra-, infra- and extraorbital (i.e. postorbital corner) teeth, the presence of a subhepatic tubercle, the presence of a groove beside the orbit, the absence of an orbital fissure are all in agreement with the typical form. In contrast to the typical form, the tubercle on the suprasutural ridge is absent in both varieties. In the variety *obtusifrons*, only one well-developed anterolateral tooth is present, behind which there is only a rudiment of the second tooth. The pereopods of this variety are not different" (translated from German). With only one specimen, a small male cl = 7.5 mm, Ihle believed that its systematic position was uncertain, but did not warrant recognition as a different species.

Subsequently, no other authors have referred specimens to these varieties. The main difference between the two varieties is in the shape and size of the rostral and orbital teeth. Ihle (1913) indicated that further specimens are necessary to clearly determine the status of these varieties and this remains true today. Only two specimens were available for the present study and these do not help to resolve this problem. However, it is worth noting that differences in the apparent relative size of the rostral teeth, very much depend upon whether the specimen is viewed exactly

horizontal or not. Tilted forward, the median tooth can appear shorter than the lateral teeth, and *vice versa*. Variation in the shape of the rostral and orbital teeth certainly occur within species and thus it may well be that Ihle's varieties represent no more than intraspecific variations.

Cryptodromia hilgendorfi De Man, 1888

Cryptodromia hilgendorfi De Man, 1888a: 404, pl. 18, fig 3. — Lewinsohn 1984: 109. — McLay 1993: 205, fig 18d; 1998: 347.

MATERIAL EXAMINED. — **Guam.** Calalan Bank, off Glass Breakwater, 13°27'N, 144°47'E, on dead branching coral, 23 m, 23.VIII.1984, coll. R. K. Kropp, 1 ♂ 4.6 × 4.9 mm (compound ascidian cap) (GUM 149) (ZRC2000.2119). — Piti Lagoon, bomb holes, on the sponge *Dysidea granulosa* Bergquist, 1965, 17.IV.1998, coll. V. Paul, 1 ♀ 6.3 × 6.0 mm (UGI no registration number) (ZRC2000.0752). — Tepungan Channel, 3 m, on wall, 15.X.1998, 1 juvenile 2.2 × 2.3 mm (sponge cap) (UGI no registration number, coll. L. Kirkendale) (ZRC2000.0753). — Tepungan Channel, 2 m, 4.XI.1998, coll. L. Kirkendale, 2 ♀ ♀ 3.5 × 3.2, 5.9 × 5.1 mm (sponge caps) (UGI no registration number) (ZRC2000.0754). — No exact locality, 1 m, I.1945, coll. M. Baker, 1 ♂ 4.3 × 4.4 mm (sponge cap) (USNM 170990). — No exact locality, no depth, IV.1945, coll. L. Gressitt, 1 ♀ 6.7 × 6.6 mm (sponge cap) (USNM 172150).

Philippine Islands. Luzon, Grand Island, Subic Bay, X.1907, coll. J. C. Thomson, 1 ♀ 7.8 × 7.6 mm (sponge cap) (USNM 136 ♀ 895). — Sulu Archipelago, Tawi Tawi group, *Albatross*, stn D 5158, 5°11.50'N, 119°54.00'E, 18 m, 21.II.1908, 1 ♂ 6.5 × 6.3 mm (USNM).

SIZE. — Four females ranging in size from 3.5 × 3.2 to 6.7 × 6.6 mm and one juvenile were collected. All of the females had already undergone the pubertal moult and so were sexually mature. For discussion of the size at maturity for *C. hilgendorfi* see McLay (2001). The maximum cw for females is 14.5 mm and for males 16.0 mm.

DEPTH AND HABITAT. — Intertidal to around 100 m. Most of the Guam specimens came from shallow water of only 2-3 m but one specimen came from 23 m. *C. hilgendorfi* is usually associated with sponges and ascidians.

DISTRIBUTION. — *C. hilgendorfi* is a wide-spread Indo-West Pacific species until recently extending as far east as the Gilbert and Ellice Islands, but now known from French Polynesia (see McLay 2001). This a new record for Guam. *C. hilgendorfi* is also known from the Philippines, Xisha Islands, China and the Macclesfield Bank.

Cryptodromia mariae Ihle, 1913

Cryptodromia mariae Ihle, 1913: 38, pl. 1, figs 5, 6. — Buitendijk 1950: 61. — Sakai 1983: 3, pl. 5, fig. A. — McLay 1993: 199 (key).

MATERIAL EXAMINED. — **Western New Guinea.** *Siboga* Expedition, stn 164, 1°42.5'S, 130°47.50'E, 32 m, 1 ♂ 8.0 × 8.7 mm, 1 ♀ (ovig.) 11.4 × 12.1 mm (Syntypes) (ZMA, De 102.952).

Philippine Islands. Sulu Archipelago, *Albatross*, stn D 5146, 5°46.40'N, 120°48.40'E, 44 m, 16.II.1908, 1 ♂ 7.8 × 8.2 mm (USNM).

SIZE. — Only two males and five females are known. The syntypes are the largest known for both sexes: 8.0 × 8.7 mm for males and 11.4 × 12.1 mm for females (Ihle 1913). Sakai (1983) gave measurements of 11.5 × 11.5 mm but not the sex of the specimen. The syntype female is ovigerous, carrying 30 eggs, diameter = 1.1 mm. These relatively large eggs suggest that *C. mariae* may well have abbreviated development.

DEPTH. — The syntypes were collected from 32 m and other specimens have been collected from the intertidal. The Philippine specimen came from 44 m and thus extends the known depth range.

DISTRIBUTION. — New Guinea, Singapore, and Japan. *C. mariae* is a new record for the Philippine Islands.

DESCRIPTION

Carapace longer than wide, evenly convex, smooth, regions not defined, branchial groove not distinct. Transverse groove behind cardiac region marked in female. Body covered with short soft tomentum. Rostrum tridentate, median tooth acute, very small and strongly deflexed, although visible dorsally. Lateral rostral teeth large, projecting, horizontally directed, broadly triangular, separated by U-shaped sinus. Frontal groove not marked. Anterolateral margin begins at level of orbital corner bears two or three small, sub-acute teeth, number can be different on each side, depending upon development of second tooth. Second tooth can be represented by a thin edentate flange. First tooth largest, close to postorbital corner, second tooth smallest (may be absent), mid-way between first and third teeth. Margin between second and third teeth concave. Posterolateral tooth indistinct. Posterolateral margins parallel, posterior margin convex.

Supraorbital margin shallowly concave, interrupted mid-way by small supraorbital tooth. Postorbital corner slightly produced, small orbital fissure separates infraorbital lobe which bears an acute tooth mid-way, only just visible dorsally.

First article of antennule as wide as long in maximum dimensions but narrowed at base and increasing in width distally; second article longer than wide, and along rest of antennule, folded tightly under orbital margin. Basal antennal article wider than long, beaked medially, not gaping; second article much longer than wide, medial corner produced, curved, on which third article is inserted at an angle; third and fourth articles as wide as long. Exopod fixed to second article, tip bilobed, reaching as far as joint between third and fourth article. Sub-hepatic area smooth, concave. Bases of third maxilliped closely approximated. Palp exposed, as long as merus plus one-third of basis. Crista dentata variable: in female syntype eight small teeth on left third maxilliped but on right, five broader distal teeth with proximal border unarmed. In male syntype six small evenly spaced teeth increasing in size distally on right, but on left teeth are grouped distally. Female sternal sutures 7/8 end wide apart on low rounded tubercles joined by narrow ridge just behind chelipeds.

Chelipeds small, carpus with several tubercles on outer surface: superior inner border has small blunt tubercle mid-way and similar larger tubercle at distal corner; inferior border with a larger tubercle and smaller tubercle above it; distal border has two large tubercles. Propodus has one large proximal tubercle, two small tubercles mid-way on outer face and large projecting tubercle at base of dactyl; superior inner margin produced as small blunt lobe. Fingers naked, white, gaping, cutting edges armed with six blunt teeth, only last three interlocking.

P2 and p3 as long as chelipeds, slender, distal borders of articles produced, angular especially carpi. Dactyli long and curved, inner margins have five small spines increasing in size distally.

P4 and p5 reduced, p4 shortest, dactyli short, strongly curved, opposed by single propodal spine, and spine on outer propodal margin. P5 sub-dorsal.

Male and female telsons wider than long, posterior margin rounded. Posterolateral corners of fourth and fifth abdominal segments produced as sub-acute lobes. Median area more strongly convex on fourth to sixth segments with small blunt median distal tubercle, larger on last segment. Uropods well-developed, visible externally, occupying one-third of lateral margin in female. Abdominal locking mechanism in male consists of uropods fitting in front of serrated ridge on coxae of p2. No locking mechanism in mature female.

DISCUSSION

A full re-description, based on the male and female syntypes, is given above because the original has not been brought up to date since Ihle (1913). Present day descriptions of dromiids utilize a greater range of characters than formerly. Besides the two original specimens, only five other specimens have been recorded until now. Buitendijk (1950) reported two females, from the vicinity of Singapore, which she compared with Ihle's syntypes. Variation in anterolateral teeth both within and between specimens was noted. Sakai (1983) reported three specimens from Japan in which the second anterolateral tooth was apparently absent. Distinctive features of *C. mariae* are the carapace, which is longer than wide, the very small median rostral tooth, scarcely visible from above, tubercles on last three abdominal segments, and the long and slender propodi and dactyli of p2 and p3.

Cryptodromia pentagonalis Hilgendorf, 1879

Dromia (Cryptodromia) pentagonalis Hilgendorf, 1879: 814, pl. 2, figs 1, 2.

Cryptodromia pentagonalis – Ives 1891: 218 (list). — Henderson 1893: 406. — Ortmann 1894: 34. — Alcock 1901: 77 (list). — Lenz 1905: 363. — Nobili 1906: 146. — Rathbun 1911: 194. — Ihle 1913: 90 (list). — Balss 1934: 502. — Barnard 1950: 328 (key); 1955: 38. — Guinot 1967: 240 (list). — Lewinsohn 1977: 1; 1979: 6, text fig. 2A.; 1984: 109. — McLay 1993: 198 (key).

MATERIAL EXAMINED. — **Guam**. 13°27'N, 144°47'E, Hospital Point, under rocks at landward edge of erosion beach, intertidal, 15.V.1984, coll. R. K. Kropp, 1 ♀ 5.1 × 4.5 mm (compound ascidian cap) (GUM

124) (ZRC2000.2115). — Asan Point, south of Camel Rock, under stones, intertidal, 16.V.1984, coll. R. K. Kropp, 1 ♀ 5.5 × 5.2 mm (sponge cap) (GUM 125B) (ZRC2000.2116). — Pago Bay, Taogam Point, from edge of erosion beach, intertidal, 5.IX.1984, coll. R. K. Kropp, 1 ♀ (ovig.) 7.7 × 6.4 mm (carrying a thin piece of seaweed) (GUM 156B) (ZRC2000.2117). — Reef flat north of Tanguisson Point, intertidal, 11.III.1992, coll. G. Paulay, 1 ♂ 7.5 × 6.1 mm (sponge cap) (GUM 274) (ZRC2000.2118).

Philippine Islands. MUSORSTOM 2, Cebu Marine Station, intertidal, 9.XII.1980, 1 ♂ 4.8 × 4.6 mm (MNHN unregistered).

Madagascar. Eastern coast, coll. R. Plante, 1 ♀ (ovig.) 10.4 × 10.2 mm (MNHN-B6878). — SW coast, Tuléar, no depth, no date, 1 ♀ (ovig.) 13.5 × 12.9 mm (MNHN-B6931). — Nosy-Be, intertidal, II.1962, coll. A. Crosnier, 1 ♀ (ovig.) 8.0 × 7.7 mm (sponge cap) (MNHN-B6880). — Fort Dauphin, no depth, 1932, 1 ♂ 13.7 × 13.2 mm (sponge cap) (MNHN unregistered).

SIZE. — Maximum male size is 13.7 × 13.2 mm, and for females 13.5 × 12.9 mm. Clutch size ranges from around 100 eggs for a female 8.0 × 7.7 mm, to about 900 eggs for a female 13.5 × 12.0 mm. Average egg diameter = 0.75 mm. This indicates that *C. pentagonalis* has planktonic larvae.

DEPTH AND HABITAT. — Lewinsohn (1984) found many specimens in crevices, and under stones in intertidal pools. Most of the specimens examined herein came from the intertidal. The deepest record for *C. pentagonalis* is 70 m (Rathbun 1911).

DISTRIBUTION. — Previously known only from the Indian Ocean, now known from the Philippines, and Guam.

DESCRIPTION

Carapace pentagonal in shape, wider than long, moderately convex, covered by a long tomentum especially along carapace margins and walking legs. Branchial groove and cardiac border distinct. Rostrum tridentate, teeth prominent, narrow and sub-acute. Median tooth as long as lateral teeth, deflexed, and on a lower level. Supraorbital margin interrupted by small tooth, followed by deeply concave margin preceding a larger postorbital tooth. Infraorbital margin bears a distinct tooth with another at its base. Subhepatic tubercle present scarcely visible dorsally. Infraorbital tooth, tooth at its base and subhepatic tooth arranged as an oblique row. Anterolateral carapace margin convex, sharply

angled like a shoulder and bearing one small tooth slightly below margin at widest point. Area beneath the shoulder slightly excavated. Small posterolateral tooth behind branchial groove. Posterolateral margins convergent, posterior margin slightly convex.

Chelipeds well-developed, carpus bears two strong distal tubercles, propodus smooth. Dactyl strongly curved, fingers gaping.

P2 and p3 shorter than chelipeds, without tubercles, dactyli well-developed, inner margins bearing four or five spines.

P4 and p5 reduced, p4 shortest, p5 sub-dorsal. Dactyli large, strongly curved, opposed by short propodal spines.

Abdomen densely fringed with setae. Uropods well-developed and visible externally. Female sternal sutures 7/8 end apart between bases of p3.

DISCUSSION

Several early authors suggested that *C. pentagonalis* and *C. canaliculata* were synonymous, but Lewinsohn (1979) lists the main differences and clearly shows that *C. pentagonalis* is a valid species.

C. pentagonalis normally carries pieces of camouflage material manufactured from sponges or compound ascidians. However, the female specimen from GUM 156B was carrying a thin, oblong piece of seaweed. Close examination shows that the sheet of seaweed has been cut around all the edges, presumably by the crab. Some sections of the edge are regenerating and the upper surface is approximately half covered with encrusting bryozoans. This suggests that the crab had carried its camouflage for sometime. The crab held the camouflage by inserting the dactyli of p4 and p5 into the under-surface of the seaweed. The cover ratio of the area of the seaweed to $cw \times cl$ was 2.5 indicating that it covered the crab was more than adequately.

Cryptodromia trituberculata Buitendijk, 1939
(Fig. 7)

Cryptodromia trituberculata Buitendijk, 1939: 226, pl. 7, figs 2, 3. — McLay 1993: 199 (key).

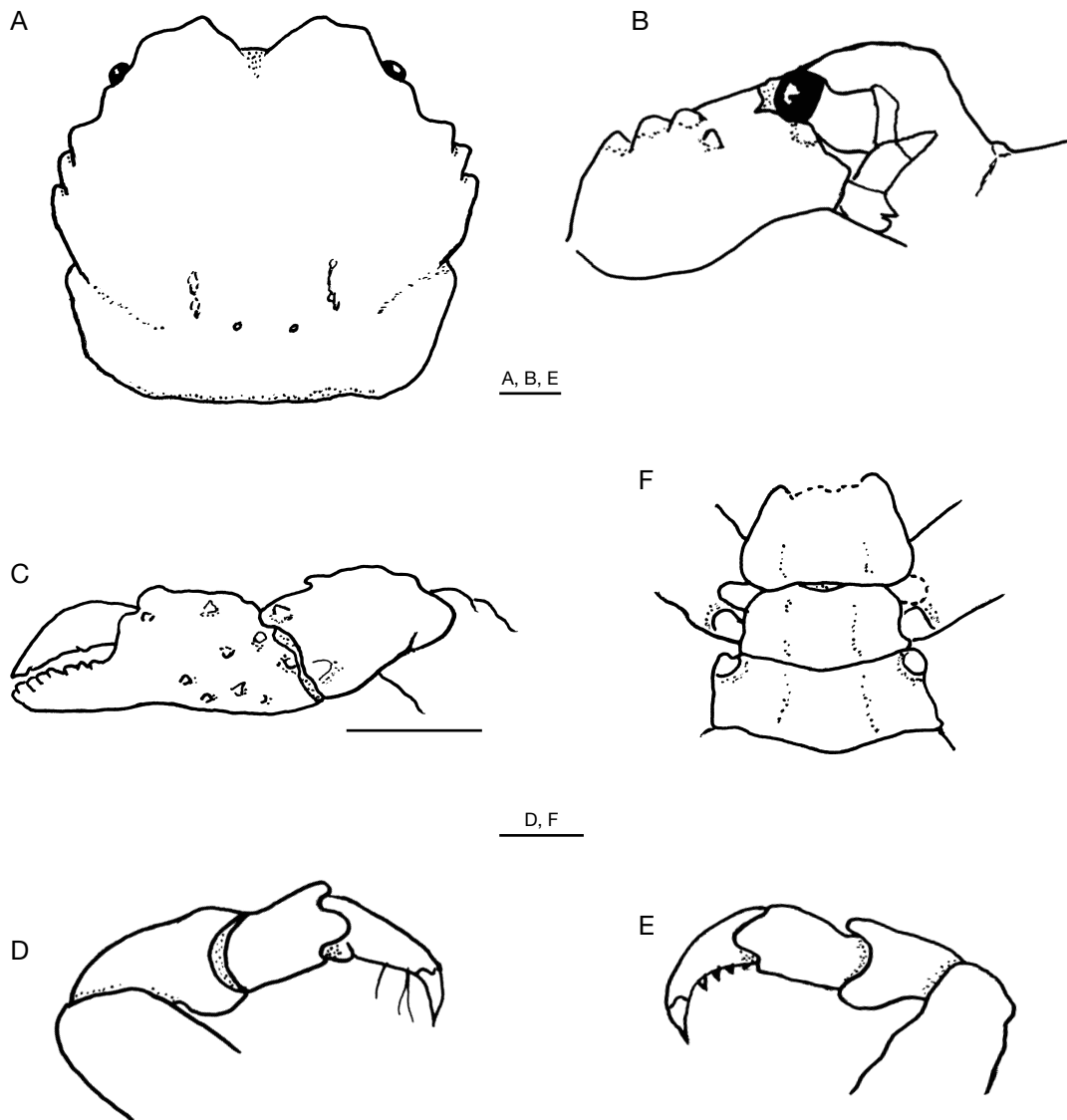


FIG. 7. — *Cryptodromia trituberculata* Buitendijk, 1939, Indonesia, Obi latoe, shore or reef, ♂ 4.4 × 4.1 mm; **A**, dorsal view of carapace; **B**, ventral view right orbital and sub-hepatic area (antenna only shown diagrammatically); **C**, outer face of left cheliped; **D**, posterior view of distal articles of left second pereopod; **E**, posterior view of distal articles of right third pereopod; **F**, dorsal view of posterior abdominal segments and telson (posterior margin damaged and therefore indicated by dashed lines) (holotype, RMNH, Crust. 4198). Scale bars: A, C, 1.0 mm; B, D-F, 0.5 mm.

MATERIAL EXAMINED. — **Indonesia.** Obi Latoe, shore or reef, 23-27.IV.1930, 1 ♂ 4.5 × 4.0 mm (holotype, RMNH, Crust. 4198).

Philippine Islands. *Albatross*, stn D 5145, no depth, 1908, 1 ♂ 4.3 × 4.3 mm (sponge cap) (USNM).

SIZE. — The male holotype, 6.8 × 6.4 mm, is the largest known specimen. The *Albatross* male is small-

er than the type. No *C. trituberculata* females are known.

DEPTH AND HABITAT. — Shallow water. Carries pieces of sponge as camouflage.

DISTRIBUTION. — Previously known from Indonesia. Now known from the Philippine Islands.

DESCRIPTION

Carapace about as wide as long or slightly wider than long, convex and covered with short tomentum, branchial groove distinct. Rostrum tridentate, median tooth strongly deflexed, hardly visible dorsally. Lateral rostral teeth blunt, separated by broad sinus, almost continuous with supraorbital margin which is interrupted by a small supraorbital tooth. Margin concave to small, blunt postorbital tooth. Supraorbital margin fringed with long setae. Fissure separates infraorbital margin, armed with well-developed tooth, not visible dorsally. Sub-hepatic area minutely granulated, with a small tubercle beneath postorbital corner and another suprasutural tubercle lower down. Anterolateral margin begins below level of postorbital corner, convex, armed with three broad, blunt teeth. Carapace widest across third teeth. No posterolateral tooth, posterior carapace margin straight.

First article of antenna wider than long, beaked medially, not gaping. Second article longer than wide, disto-medial corner produced on which third article is inserted, diagonal ridge from lateral proximal margin towards base of third article. Exopod deeply bilobed to accommodate rest of antenna, curving over base of eyestalk.

Chelipeds small, outer face of carpus with two blunt proximal tubercles, and two larger, sharp distal tubercles. Outer face of propodus minutely granular with large proximal tubercle and another at base of dactyl. Fingers long, pearly-white, not gaping widely, fixed finger armed with seven or eight small teeth, margin of moveable finger largely edentate. Legs minutely granulated not verrucose. P2 and p3 similar in size to chelipeds, propodi short, broad, inner margins of dactyli armed with three short spines. Dactyli strongly curved at tips. P4 and p5 shorter, p5 much longer than p4. Dactyli opposed by single propodal spines, with another short spine on outer propodal margin at base of dactyl.

Outer surface of abdomen minutely granular. Posterior telson margin of male truncate. Posterior corners of fifth abdominal segment with strongly produced tubercles. Uropods well-developed, visible externally, utilized in abdomi-

nal locking mechanism by fitting in front of coxal ridges on coxae of p2. Female of this species is unknown.

DISCUSSION

Buitendijk (1939) pointed out that anterolateral teeth in *Cryptodromia trituberculata* may be different on each side of the carapace. On the right side of the type specimen the three broad teeth are of equal size, but on the left the first tooth is smaller than the corresponding one on the other side. This species resembles *C. mariae* in the shortness of the median rostral tooth, but *C. trituberculata* lacks the subhepatic and suprasutural tubercles. Also the second anterolateral tooth in *C. mariae* is very small.

Cryptodromia tuberculata Stimpson, 1858

Cryptodromia tuberculata Stimpson, 1858: 239; 1907: 174, pl. 21, fig. 6. — De Man, 1888a: 401. — Ives 1891: 217 (list). — Cowles 1913: 119. — Ihle 1913: 35. — Balss 1935: 115. — Sakai 1936: 17, text fig. 3, pl. 6, fig. 3; 1976: 13, text fig. 3a, b. — Buitendijk 1939: 225. — McLay 1993: 199 (key).

Cryptodromia tuberculata var. *typica* — Ihle 1913: 35.

Dromia (*Cryptodromia*) *tuberculata* — Estampador 1937: 510.

MATERIAL EXAMINED. — **Philippines.** Saftan Island, *Albatross*, tide pools, 8.XI.1908, 1 ♂ 9.5 × 8.0 mm (sponge cap) (USNM 128564). — Sitandi Island, no depth, 26.II.1908, 1 ♀ 5.3 × 4.5 mm (solitary ascidian cap) (USNM 128566). — Maricaban Island, 13°39.00'N, 120°50.00'E, shoreline, 20.I.1908, 1 ♂ 7.9 × 6.8 mm, 1 ♀ 6.5 × 6.4 mm, 2 ♀ ♀ (ovig.) 6.7 × 6.6, 7.0 × 6.7 mm (sponge caps) (USNM 128565). — Sector G, exact locality not given, MUSORSTOM 2, 128-143 m, 20.XI.1980, 1 ♀ 9.2 × 9.0 mm. — Mactan Marine Station, Olango Reef, 11.XII.1980, 1 ♂ 4.7 × 4.0 mm, 1 ♀ (ovig.) 4.4 × 3.9 mm (sponge cap) (MNHN-B12732).

SIZE. — The type specimen measured 13.0 × 11.0 mm and is the largest known male. The largest known female, 9.2 × 9.0 mm, is reported herein from the Philippines. The two larger ovigerous females reported above carried 25-30 eggs, diameter 0.8 mm. The smallest ovigerous female, 4.4 × 3.9 mm carried only 10 eggs, diameter 1.0 mm. *C. tuberculata* seems to produce small numbers of larger eggs and may well have abbreviated development as found in *C. pileifera* (see Tan *et al.* 1986).

DEPTH AND HABITAT. — Most specimens have been collected from intertidal rocky shores and reefs. Commonly found under stones and among boulders in the middle of the littoral zone. The deepest record is 20 m (Ihle 1913). They always carry pieces of sponge or compound ascidians. Cowles (1913) described how *C. tuberculata* obtains its sponge camouflage. The chelipeds are used to cut out the cover, that is left partially attached to the sponge, and the crab lifts up the edge and pushes itself backwards under the cover grasping it with the p4 and p5. The crab then carries off its new piece of camouflage.

DISTRIBUTION. — Type locality Kikai-shima, Amami Group, Japan, South China Sea, Philippine Islands, Indonesia and Singapore. Balss (1935) reported *Cryptodromia tuberculata* from Cossack, near Port Hedland, western Australia. *C. tuberculata* was first reported from Mindoro and Luzon, Philippines by Estampador (1937).

DESCRIPTION

Carapace wider than long, moderately convex, smooth, covered with a fine tomentum. Branchial grooves faint but branchio-cardiac grooves distinct. Rostrum tridentate, teeth short, blunt, median tooth slightly longer than lateral teeth. Supraorbital eave with blunt tooth, postorbital corner slightly produced. Orbital fissure narrow, infraorbital margin bears strong blunt tooth visible dorsally. Sub-hepatic area with an arched row of tubercles extending from orbital corner to first anterolateral tooth. These tubercles decrease in size posteriorly: first two prominent, nearly as large as anterolateral teeth, and visible dorsally between postorbital corner and first anterolateral tooth. Two or three teeth in transverse row near corner of buccal frame. These tubercles are variable. Anterolateral margin convex, armed with three blunt, sub-equal teeth: first two teeth strong, third smaller and elongated. First anterolateral tooth widely separated from postorbital corner. Posterolateral tooth blunt, following margin convergent, posterior carapace margin straight.

Chelipeds strongly tuberculated. Tubercles conical blunt. Outer carpal surface has about three large and ten small tubercles, distal tubercles more prominent. Propodus has 20 to 25 tubercles of variable size, mostly on outer surface. Tubercles on superior propodal border larger, inner

surface densely pubescent. Fingers compressed, gaping, tips naked and white. Cutting edges armed with six or seven variable teeth, distal three interlocking.

P2 and p3 shorter than chelipeds, strongly nodular or verrucose. Carpi have longitudinal ridges on superior margins and four or five strong tubercles. Inner margins of dactyli armed with four small spines increasing in size distally.

P4 and p5 reduced, p4 shortest, dactyli opposed by single, short propodal spines with another spine on outer propodal margin of the p5.

Third, fourth and fifth abdominal segments each have four tubercles along posterior margin, two in middle and one at each corner. These tubercles are variable in development between individuals. Telson much wider than long, posterior margin sub-truncate, concave. Uropods well-developed, visible externally, used in abdominal locking mechanism by fitting in front of ridge on coxae of p2. Female sternal sutures 7/8 end wide apart on low rounded tubercles between bases of p2.

DISCUSSION

Stimpson (1858) briefly described *Cryptodromia tuberculata* based on specimens collected from Japan. The type specimen is not extant. The species was first illustrated by Stimpson (1907: pl. 21, fig. 6) and subsequently by Sakai (1936: pl. 56, fig. 3). Species of *Cryptodromia* are often distinguished by small differences in the rostrum, anterolateral margin and the abdomen and so these illustrations have largely defined exactly what *C. tuberculata* looks like. The introduction of two varietal names, by Alcock (1899) and Ihle (1913), complicated the taxonomy of *C. tuberculata*.

Alcock (1899) referred his 70 specimens from the Andaman Islands to *Dromia* (*Cryptodromia*) *tuberculata* var. *pileifera*. Although the type specimen of this new variety apparently still exists, in the Indian Museum, its unavailability means that Alcock's (1901: pl. 2, fig. 7) illustration has assumed special significance.

Ihle (1913) separated his specimens from Indonesia into *C. tuberculata* var. *pileifera* and *C. tuberculata* var. *typica* and listed the major

differences: in the *typica* variety there are five sub-hepatic tubercles, arranged in a row, with two being larger, while the *pileifera* variety has only two large tubercles; *typica* has three tubercles above the pleural suture but only one tubercle in *pileifera*. Because he found some specimens with an intermediate numbers of sub-hepatic tubercles, Ihle stated that he considered these two forms to be varieties and not species. Specimens with three larger tubercles were assigned to the *typica* variety while those with only two tubercles were assigned to *pileifera*. Buitendijk (1939) also identified both varieties, from the same localities, among the Snellius Expedition material from Indonesia and noted several specimens which had some features of both varieties. Similarly in a collection from Singapore, Buitendijk (1950) noted some *C. pileifera* specimens which had some features of *C. tuberculata*. Clearly there is a lot of variation in *C. pileifera*. Thus the question arises of whether these two varieties of *C. tuberculata* should be treated as synonyms or as separate species?

Comparison of Sakai's (1936: pl. 56, fig. 3) illustration of *C. tuberculata* with Alcock's (1901: pl. 2, fig. 7) illustration of *C. pileifera* shows additional differences between these two species: lateral rostral teeth very short and blunt in *C. tuberculata* (blunt but larger in *C. pileifera*); median tooth longer than lateral teeth (median tooth shorter); three sub-hepatic teeth visible dorsally (two teeth, one visible dorsally); branchial groove not evident (groove well-marked); chelipeds very tuberculate (not so tuberculate); distal margins of articles of p2 and p3 very tuberculate (not tuberculate). I think that all of these differences indicate that *C. tuberculata* and *C. pileifera* should be treated as valid species.

Cryptodromia tumida Stimpson, 1858

Cryptodromia tumida Stimpson, 1858: 240; 1907: 175. — Ives 1891: 218 (list). — Ortmann 1892: 544. — Bouvier 1899: 176 (list). — De Man 1902: 688. — Ihle 1913: 37, text figs 10-17. — Parisi 1915: 104. — Balss 1922: 107 (list). — Buitendijk 1939: 226. — Ward 1941: 1. — Sakai 1965: 8, pl. 3, fig. 3. — Takeda 1973: 79. — Yamaguchi *et al.*

1987: 6. — McLay 1993: 199 (key). — [Non Montgomery 1931: 413, pl. 29, figs 4, 4a. (= an undescribed species)].

Cryptodromia tumida typica Sakai, 1936: 18, pl. 7, fig. 1, text fig. 4a-b; 1976: 14, text fig. 4a-c.

Cryptodromia fallax — Ng *et al.* 2000: 159, fig. 1d [non *C. fallax* (Lamarck, 1818)].

MATERIAL EXAMINED. — **Guam.** 13°27'N, 144°47'E, Pago Bay, outer reef flat, intertidal at very low tide, 24.V.1986, coll. R. K. Kropp, 1 ♂ 4.4 × 4.3 mm, 1 ♀ 9.0 × 8.1 mm (sponge caps) (GUM 217C) (ZRC2000.2113). — Piti Reef, among rocks, 1 m, 30.VII.1993, coll. H. T. Conley, 1 ♂ 6.8 × 6.1 mm (sponge cap) (GUM 302) (ZRC2000.2114).

Philippine Islands. Sulu Archipelago, *Albatross*, stn D5139, 5°6.00'N, 121°2.30'E, 6 m, 14.II.1908, 1 ♀ 4.2 × 3.9 mm (sponge cap) (USNM 128573). — Stn D5145, 6°4.30'N, 120°59.50'E, 7 m, 15.II.1908, 1 ♂ 4.4 × 4.0 mm (compound ascidian cap) (USHM 128572). — Cataingan Bay, shoreline, 19.IV.1908, 1 ♂ 4.3 × 4.0 mm (compound ascidian cap), 1 ♀ (ovig.) 7.5 × 6.5 mm (sponge cap) (USNM).

Taiwan. Kaohsiung County, Yungan, no date, 1 ♂ 8.0 × 6.8 mm (TMCD 2810) (originally identified as *C. fallax* [Lamarck, 1818] by Ng *et al.* 2000).

Samoa. Tutuila Island, Pago Pago, 14°16.00'S, 170°43.00'W, no depth, no date, 1 ♀ (ovig.) 6.5 × 6.0 mm (sponge cap) (USNM).

SIZE. — Largest known male 10.3 × 9.0 mm (Sakai 1936) and largest female 14.0 × 13.0 mm (Parisi 1915). Smallest ovigerous female, 6.5 × 6.0 mm carried only 17 large eggs diameter 1.0 mm. Another female, 7.5 × 6.5 mm, carried 30 eggs. Evidently, *Cryptodromia tumida* has a reproductive strategy that involves the production of few large eggs with abbreviated development. Buitendijk (1939) recorded ovigerous females in October, November, March and June from Indonesia.

DEPTH AND HABITAT. — All the specimens reported here came either from intertidal or shallow sites. The maximum depth recorded by Sakai (1965) was 10 m. Sakai (1936) gives the habitat as being rocky or stony shorelines. Crabs are normally covered with a mass of sponge or compound ascidians.

DISTRIBUTION. — The type locality of *Cryptodromia tumida* is Foukow Bay, Amami Ohshima, Japan. Subsequently this species has been recorded from several other Japanese localities. It was first recorded from the Philippines by Ward (1941). *C. tumida* is also known from Indonesia and now Guam. Montgomery (1931: 413, pl. 29, figs 4, 4a) recorded *C. tumida* from the Abrolhos Islands, western Australia, but his illustrations suggest that these specimens are not the same as the type specimen and represent an undescribed species. The occurrence of *C. tumida* in Australian

waters remains to be established. *C. tumida* was not previously known from Taiwan and its inclusion brings the total number of dromiid species to 10. It is the only representative of the genus *Cryptodromia* recorded from Taiwan and it can be anticipated that other species in this genus will be found (see Ng *et al.* 2000). Most of the dromiid species known from Taiwan are large crabs, more easily caught by fishermen, and found among the debris landed at fish ports. Shallow water collections should produce several new *Cryptodromia* records. *C. tumida* is also added to the fauna of Samoa. Previously, only *C. coronata* was known from Samoa.

DESCRIPTION

Carapace wider than long, convex, covered by a short tomentum, smooth, rising abruptly behind front, tumid on gastric and hepatic regions. Front broadly rounded, rostrum tridentate, median tooth short, obtuse, deflexed, lateral teeth blunt, more prominent. Supraorbital margin continues back from lateral rostral tooth, interrupted by a stout supraorbital tooth, ending with small post-orbital tooth. Orbital fissure present. Infraorbital tooth stout, obscured from above by supraorbital tooth. One strong sub-hepatic tubercle visible dorsally between postorbital corner and first anterolateral tooth, and one smaller tubercle on ridge above pleural suture. Anterolateral margin with three sub-equal, equidistant, small blunt teeth. First anterolateral tooth largest, second tooth may be obsolete. Posterolateral tooth behind distinct branchial groove. Posterolateral margins convergent, posterior margin slightly concave. Sternal sutures 7/8 end apart on small tubercles between bases of p2. Crista dentata 11 or 12 small teeth.

Chelipeds small, sparsely tuberculate. Carpus with two small central and two strong distal tubercles. Outer surface of propodus smooth, or with longitudinal lines of fine granules. Upper surface of propodus has two elongate proximal ridges and a tubercle at base of dactyl. Male fingers gaping touching only at tips. Dactyl has seven or eight small teeth, but fixed finger only has three or four distal teeth. Female fingers compressed, not gaping. Inner propodal surface densely setose.

P2 and p3 slightly shorter than chelipeds, meri robust, carpi with three distal tubercles, propodi

armed with terminal tubercle on anterior border. Dactyli of both legs with five or six small spines on inner margin.

P4 and p5 reduced, p4 shortest, p5 sub-dorsal. Dactyli of both legs strongly curved and opposed by long straight propodal spines with another shorter spine on outer propodal margin.

Prominent rounded tubercles at posterolateral corners of third and fourth abdominal segments and a pair of median tubercles on fourth segment. Four less distinct tubercles may also be present on fifth segment. Tubercles maybe obsolete in some specimens and less distinct in females. Uropods well-developed and visible externally. Abdominal locking mechanism consists of uropods fitting in front of rounded flanges on coxa of p2. Male telson wider than long, trapeziform, posterior margin truncate or concave. Female telson wider than long, posterior margin bluntly rounded.

DISCUSSION

Several features of *Cryptodromia tumida* are variable. Stimpson (1907) stated that in the female type, which is not extant, the anterolateral teeth were small and equal in size, but De Man (1902) noted that the first anterolateral tooth is usually longest and the third tooth shortest. Ihle (1913) stated that the position of the three anterolateral teeth is variable: the teeth may be evenly spaced, or the distance between the first and second may be slightly larger than between the second and third. However, in De Man's female the distance between the first and second teeth was twice the distance between the second and third. In the type the abdominal tubercles were obsolete. However these tubercles may vary between the sexes. Ihle noted that sometimes there are a pair of less distinct tubercles on the posterior corners of the third as well as on the fourth and fifth abdominal segments. Ihle accepted these variations as being intra-specific, not warranting the designation of additional species or varieties. However, Sakai (1936) dealt with this variation by recognizing three sub-species: *Cryptodromia tumida typica*, *C. tumida bispinosa*, and *C. tumida trispinosa*. These sub-species were defined largely

on the basis of the shape of the telson. In the *trispinosa* sub-species (male type 11.5 × 10.4 mm) the posterior margin of the telson has three unequal spines, and in the *bispinosa* sub-species (male type 11.0 × 9.4 mm) it has two closely spaced, long, acute spines. Sakai assumed that, in the *typica* sub-species (male 10.3 × 9.0 mm and female 11.9 × 9.5 mm), the telson has two blunt posterior projections, separated by a concave margin. The original description of *C. tumida* by Stimpson (1858) did not include any mention of the shape of the telson and, since the type is not available, it is impossible to establish the relationship of Sakai's sub-species to the original form.

Ihle (1913) stated that the posterior margin of the telson in the *Siboga* specimens was bluntly rounded in females but truncate in males. However, after examining some of the same specimens, Buitendijk (1939) declared that some of the males from *Siboga*, station 225, had three spines or lobes on the telson margin, thus indicating that they should belong to the *trispinosa* sub-species.

Besides the telson, Sakai notes differences in the anterolateral teeth, abdominal tubercles and sternal sutures 7/8 of his sub-species. In *C. tumida trispinosa* the second anterolateral tooth is not more prominent than the others, the fourth and fifth (*sic* "fourth to seventh", but his text fig. 5 shows tubercles on segments four and five) abdominal segments of the male have a very low tubercle on each side. In *C. tumida bispinosa* the first anterolateral tooth is nearly as large as the sub-hepatic tubercle, the second tooth is small and indistinct, third is not prominent, abdominal tubercles very low and indistinct, sternal sutures 7/8 very broad but without a terminal process. According to Sakai, *C. tumida typica* has three sub-equal anterolateral teeth (presumably the second tooth can be smaller, although his illustration, pl. 7, fig. 1, shows three similar teeth), abdominal segments four and five have tubercles at the posterolateral corners, and sternal sutures 7/8 end with a terminal process. Clearly, there is some doubt about which of these sub-species may represent the original form, but I have included all three in the above key. The status of these sub-species needs further investigation. Evidently, all

three occur in Japanese waters, but apart from the typical form, *C. tumida trispinosa* is the only one recorded elsewhere, in Indonesian waters.

Genus *Cryptodromiopsis* Borradaile, 1903

DIAGNOSIS. — Carapace as wide or wider than long, surface smooth, short dense tomentum with longer setae on the fringes, frontal groove separating two low rounded protuberances, branchial and cardiac grooves marked. Rostrum tridentate, supraorbital tooth usually present, postorbital tooth blunt or obtuse, a fissure may or may not be present separating the suborbital margin on which there are usually two unequal teeth. Anterolateral margin begins at orbital level, teeth may or may not be present. Subhepatic region usually smooth, without teeth. Coxae of third maxillipeds closely approximated (or separated by a narrow gap) and inserted in front of tip of sternum, separated from it by a trough. Female sternal sutures 7/8 end together or apart between chelipeds, first or second legs, with or without tubercles. No epipod on cheliped, borders of merus may be dentate, no spine on inner superior margin of carpus, up to four tubercles on superior margin of propodus. Distal margins of carpi and propodi of first two pairs of legs lobe-like, two to five spines on inner margins of dactyli. Third leg shorter than fourth, dactyl opposed by one or two propodal spines with one or two spines on the outer propodal margin. Fourth leg shorter than second, dactyl opposed by one or two propodal spines, one to three spines on the outer propodal margin and usually one spine on the outer margin of the dactyl itself. Abdomen of six free segments. Telson rounded or bluntly tipped. Uropod plates well-developed. Abdominal locking mechanism involves a serrated ridge or tooth on the base of the first leg and uropod plates may or may not be involved. First male gonopod stout, two segmented, usually tipped by a sharp tubercle, densely setose. Second gonopod simple, needle-like, tapering, or shorter and tapering only at tip (modified after McLay 1993).

Cryptodromiopsis plumosa (Lewinsohn, 1984)

?*Dromidiopsis plumosa* Lewinsohn, 1984: 104, fig. 3a-g.

Dromidia plumosa – McLay 1991: 470.

Cryptodromiopsis plumosa – McLay 1993: 190, fig. 17f.

MATERIAL EXAMINED. — **Guam.** Apra Harbour, Glass Breakwater, 13°27'N, 144°47'E, 3-6 m, among rocks, 8.XI.1993, coll. H. T. Conley, 1 ♀ 7.2 × 6.8 mm (sponge cap) (GUM 304) (ZRC2000.2112).

SIZE. — Maximum cw for males is 13.3 × 11.7 mm. The specimen from Guam is one of the first females to



FIG. 8. — *Cryptodromiopsis unidentata* (Rüppell, 1830), Guam, Piti Reef, 0.5-2 m, ♂ 7.7 × 7.5 mm, carrying a sponge cap, *Petrosia* sp., frontal view of crab beneath its camouflage cap. Scale bar: 3 mm.

be collected. Another larger female from Hawaii is reported by McLay (2001). Maximum female size is 10.5 × 9.5 mm. *C. plumosa* carries sponge caps.

DEPTH AND HABITAT. — Previously known depth range was 16-55 m. The specimen from Guam, 3-6 m, extends the range to much shallower depths.

DISTRIBUTION. — Recorded from the Seychelle Islands, Chesterfield Islands, New Caledonia and now Guam. *C. plumosa* has also been reported from Hawaii (see McLay 2001). This is clearly a widespread, shallow water, Indo-Pacific species.

DISCUSSION

In his original description of this species Lewinsohn (1984) was uncertain about the genus in which it should be placed. The type specimen is a male and Lewinsohn believed that he needed a female specimen to be sure that it belonged in the genus *Dromidiopsis*. Hence the use of ?*Dromidiopsis*. But he had made an error in stating that there was an epipod on the cheliped, so that the new species should in fact have been placed in the genus *Cryptodromiopsis*. A distinctive feature

of *C. plumosa* is its shaggy appearance, the result of a dense pile of long plumose setae. Also the propodal spines of the legs are distinctive. There is a small distal spine on the inferior margin of the propodi of p2 and p3. On p4 and p5, which are used to carry pieces of camouflage, the spines are numerous and well-developed. The dactyl of p4 is opposed by two or three spines, with one or two spines on the outer propodal margin. On the p5 the dactyl is opposed by two spines with three spines on the outer propodal margin and an accessory spine on the dactyl itself. The presence of large numbers of spines on the p4 and p5 is regarded as being close to the ancestral condition (see McLay 1993). Description of the female characters is given in McLay (2001).

Cryptodromiopsis unidentata (Rüppell, 1830) (Fig. 8)

Dromia unidentata Rüppell, 1830: 16, pl. 4, fig. 2, 2a, pl. 5 fig. 9. — Lewinsohn 1984: 107.

Cryptodromiopsis unidentata – McLay 1993: 192, figs 7a-k, 18a; 1998: 347.

MATERIAL EXAMINED. — **Guam.** Agana Bay, 13°27'N, 144°47'E, reef front, north of boat basin channel, on dead consolidated coral, 12 m, 30.V.1986, coll. R. K. Kropp, 1 ♀ 3.6 × 3.7 mm (unidentified compound ascidian cap) (GUM 229). — Piti Lagoon, among silty dead coral, 2 m, 22.V.1993, coll. H. T. Conley, 1 ♂ 8.3 × 7.9 mm (unidentified sponge cap) (GUM 262). — Piti Reef, 0.5-2 m, among rocks, 4-18.VIII.1993, coll. H. T. Conley, 1 ♂ 7.7 × 7.5 mm (sponge cap, *Petrosia* sp.), 2 ♀ ♀ 5.9 × 6.0 mm (sponge cap belonging to the Desmacellidae, genus could not be determined), 9.4 × 8.9 mm (GUM 298). — Piti Lagoon, 1 m, bomb holes in reef flat, VI.1995, coll. J. Starmer, 1 ♀ 14.2 × 14.0 mm (soft coral cap, *Sinularia* sp.) (UGI no registration number). — Apra Harbour, 20-25 m, American Tanker, 8.IV.1997, coll. T. Leberer, 1 ♂ 10.4 × 10.5 mm (sponge cap, *Istrochota purpurea* (Bowerbank, 1875)) (UGI 6020).

Tonga. Ha'api Group, Lifuka Island, 19°50'S, 174°22'W, 6-10 m, 7.XI.1996, coll. G. Paulay, 1 ♂ 6.9 × 6.8 mm (soft coral cap, *Xenia* sp.) (UGI: BTON-4).

SIZE. — The maximum cw for male *C. unidentata* is 34.0 mm and for females it is 31.0 mm. All the specimens reported here are much smaller than the maximum size.

DEPTH AND HABITAT. — The known depth range for *C. unidentata* is 0-100 m, with most specimens collected from less than 50 m. All the present specimens came from within this range.

DISTRIBUTION. — *C. unidentata* is a widespread Indo-West Pacific species known from the Philippines and as far south as the Kermadec Islands, north of New Zealand, but it has not previously been recorded from Tonga.

DISCUSSION

Cryptodromiopsis unidentata has been described and illustrated by McLay (1993) where a full synonymy can be found. The distinctive features of *C. unidentata* are: a carapace about as wide as long, the lack of any teeth on the anterolateral carapace margin and the dense mat of fine setae on the carapace where they form a "fringe" across the frontal region.

A feature of the camouflage behaviour of *C. unidentata* is the diversity of organisms used to cover itself with. The most common organisms are sponges and ascidians (both solitary and compound), but soft corals and actinians have also

been recorded. Often the crab is deeply embedded in its camouflage so that only the pereopods are visible. The specimens collected from Guam and Tonga were carrying pieces of the sponges *Istrochota purpurea* (Bowerbank, 1875), *Petrosia* sp. and a desmacellid, two soft corals, *Sinularia* sp., and *Xenia* sp. and an unidentified compound ascidian. A notable feature of the present specimens is the size of the pieces of camouflage carried by the crabs. For the crab carrying the soft coral, *Xenia* sp., the cover ratio was 2.81 and for the crab carrying the other soft coral, *Sinularia* sp. the ratio was 2.35. The height of these coral caps was 10 mm and 50 mm respectively. The crab carrying the compound ascidian had a cover ratio of 3.9 but the cap was only 4.0 mm high. The two crabs carrying *Petrosia* sp. and the desmacellid sponge had cover ratios of 3.9 and 4.6 and the height of these caps was 5.8 mm and 3.5 mm respectively. The crab carrying the large piece of dark purple sponge, *Istrochota purpurea*, was dwarfed by its camouflage and had a very strange appearance. The cover ratio was 20.6 and the sponge was around 15 mm high. In this case the crab was not holding the sponge in the middle, but had hollowed out a cavity almost at one end, so that most of the sponge hung over one side in a very asymmetrical way. It was the bizarre appearance of this crab that drew the attention of the divers who collected it. Unless the sponge had some offensive properties it is difficult to conclude that the crab was well-protected beneath its cap. The importance of the ratio of cap area: crab size lies in the fact that it is an indication of the amount of room available for increase in the size of the crab when it next moults. A cover ratio of less than 1.0 indicates that the crab is not well-covered, a ratio of just 1.0 is perhaps the minimum for camouflage, while anything above 1.0 provides room for crab growth. Thus the crabs carrying the soft corals and the sponges, *Petrosia* sp. and a desmacellid, had ratios of 2.35 to 4.6, which probably gave adequate cover. The crab carrying the large piece of *Istrochota purpurea* had a cover more than four times as large as its body. The use of sponges and ascidians by *Cryptodromia hilgendorfi* has been investigated by McLay (1983).

Genus *Takedromia* McLay, 1993

DIAGNOSIS. — Carapace distinctly wider than long, surface moderately to strongly convex, granulated or tuberculated, may be areolated. Rostrum tridentate, projecting, may be truncated, lateral teeth usually thin and eave-like. Anterolateral teeth well-developed, lacinated or tuberculated, posterolateral borders dentate or tuberculated. Coxae of third maxillipeds separated by a wide gap and inserted well forward of tip of sternum on a triangular plate. Female sternal grooves end apart between bases of first legs. Antennal exopod well-developed, prominent median distal spine on second segment, all antennal segments minutely denticulated. Cheliped without an epipod, male chelipeds much larger than those of female. First two pairs of legs tuberculated and granulated, inner margins of dactyls armed with up to five small spines. Last two pairs of legs very small, third pair shortest, dactyli of both pairs opposed by single propodal spines, none on outer propodal margin. Abdomen of six free segments. Uropod plates well-developed, visible externally, used in abdominal locking mechanism by fitting in front of serrated flanges on base of first legs. Male telson rounded or sub-truncate. Abdominal segments adorned with granules and or tubercles. First male gonopod semi-rolled tube, sharply tipped and setose, second gonopod simple, needle-like (after McLay 1993).

Takedromia cristatipes (Sakai, 1969)
(Fig. 9)

Cryptodromia cristatipes Sakai, 1969: 245, pl. 1, fig. 1; 1976: 18, text fig. 10.

Takedromia cristatipes – McLay 1993: 212, figs 9a-b, 19a-b.

MATERIAL EXAMINED. — **Guam.** 13°27'N, 144°47'E, no site details, 13.III.1975, 1 ♂ 22.5 × 18.5 mm (UGI no registration number, ZRC2000.0755).

Philippine Islands. *Albatross* Expedition, Mindanao Island, 7°47.00'N, 123°31.15'E, 333 m, 9.VIII.1909, 1 ♀ 20.0 × 17.5 mm (USNM 128579).

SIZE. — Both of the specimens reported above are the largest known male and female. The male from Guam exceeds the size of the male type, 22.0 × 19.0 mm, from Japan (Sakai 1969). The female, 20.0 × 17.5 mm, from the Philippines is the largest female reported.

DEPTH AND HABITAT. — Known depth range includes 48–430 m. Unfortunately, the exact depth where the Guam specimen was captured was not recorded, but it must be relatively shallow, probably less than 48 m, because it was taken by a diver. The Philippine specimen came from the deeper end of the range, 333 m but did not extend the maximum depth for

T. cristatipes. Like the other members of this genus, *T. cristatipes* is not known to carry pieces of camouflage.

DISTRIBUTION. — Previously known from Japan and New Caledonia. Now recorded from the intermediate localities of Guam and the Philippine Islands.

COMPARISON OF THE FAUNAS OF THE MARIANA AND PHILIPPINE ISLANDS

The dynomenid and dromiid faunas of the Mariana and Philippine Islands are listed in Table 1. *Dynomene pilumnoides* is the only known dynomenid from the Philippines (McLay 1999). *D. hispida*, not dealt with herein, has been collected from the northern Mariana Islands of Maug East and Maug North (Takeda *et al.* 1994) but so far it has not been collected from Guam. Six dynomenid species are known from the Mariana Islands: *D. hispida*, *D. praedator*, *D. guamensis* n. sp., *D. kroppii* n. sp., *Hirsutodynomene spinosa* and *Paradynomene tuberculata* and six species are also known from Indonesia: *D. hispida*, *D. praedator*, *D. pilumnoides*, *H. spinosa*, *Metadynomene tanensis* and *P. tuberculata*. Since Guam and Indonesia, on either side of the Philippines, share four of the eight species it seems reasonable to expect that these will also be found in the Philippines. *Cryptodromia tuberculata* and *C. fallax* were recorded from the Philippines by Cowles (1913) and Ward (1941) respectively. Ward also recorded *Cryptodromiopsis bullifera* from Gulf of Davao, Mindanao, Philippines. Alcalá (1974) reported *Dromia dormia* from coral reefs near Dumaguete City, Philippines where it preyed upon the crown of thorns starfish (*Acanthaster planci*). New dromiid records for the Philippine Islands include *Sphaerodromia nux*, *Lauridromia indica*, *Cryptodromia pentagonalis*, *C. trituberculata* and *Takedromia cristatipes*. In the Philippine Islands a total of 20 dromiid species (in eight genera) and one dynomenid are now known. New dromiids reported for the first time from Guam include *C. hilgendorfi*, *C. fallax*,

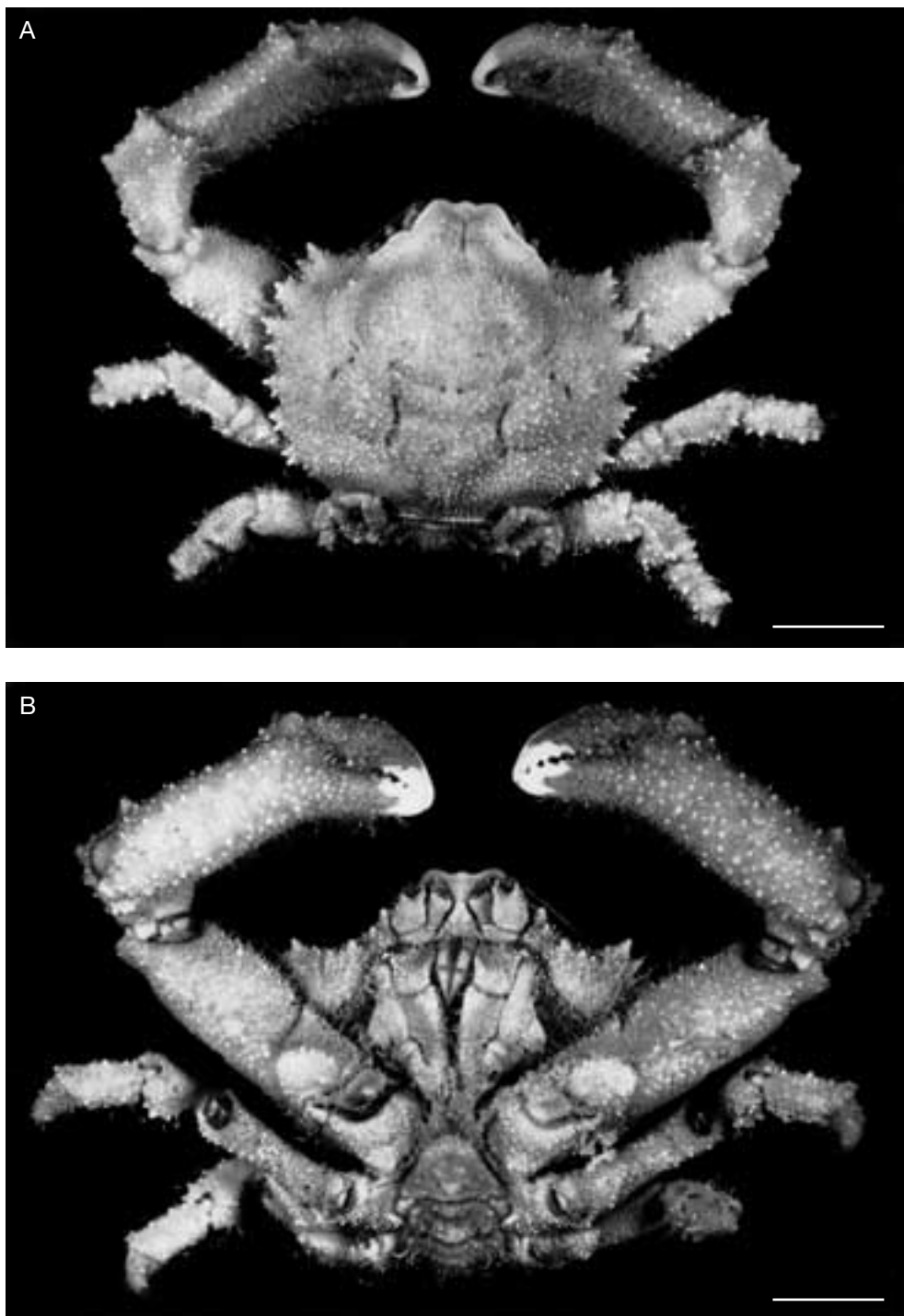


FIG. 9. — *Takedromia cristatipes* (Sakai, 1969) Guam, ♂ 22.5 × 18.5 mm (ZRC2000.0755); **A**, dorsal view of whole crab; **B**, ventral view. Scale bars: 6 mm.

TABLE 1. — Comparison of dynomenid and dromiid faunas of the Philippine and Mariana Islands.

Species	Philippine Islands	Mariana Islands
Dynomeneidae		
<i>Dynomene hispida</i> Guérin-Méneville, 1832	–	+
<i>D. praedator</i> A. Milne-Edwards, 1879	–	+
<i>D. pilumnoides</i> Alcock, 1900	+	–
<i>D. kroppi</i> n. sp.	–	+
<i>D. guamensis</i> n. sp.	–	+
<i>Hirsutodynomene spinosa</i> (Rathbun, 1911)	–	+
<i>Paradynomene tuberculata</i> Sakai, 1963	–	+
Total Number of Dynomeneidae (7 species)	1	6
Dromiidae		
<i>Sphaerodromia kendalli</i> (Alcock & Anderson, 1894)	+	–
<i>S. nux</i> Alcock, 1899	+	–
<i>Dromidiopsis lethrinusae</i> (Takeda & Kurata, 1976)	+	+
<i>Lauridromia indica</i> (Gray, 1831)	+	–
<i>L. intermedia</i> (Laurie, 1906)	+	–
<i>Dromia dormia</i> (Linnaeus, 1763)	+	–
<i>D. wilsoni</i> (Fulton & Grant, 1902)	+	–
<i>Stimdromia angulata</i> (Sakai, 1936)	+	–
<i>Stimdromia</i> sp.	+	–
<i>Cryptodromiopsis bullifera</i> (Alcock, 1900)	+	–
<i>C. plumosa</i> (Lewinsohn, 1984)	–	+
<i>C. unidentata</i> (Rüppell, 1830)	+	+
<i>Cryptodromia amboinensis</i> De Man, 1888	+	–
<i>C. fallax</i> (Lamarck, 1818)	+	+
<i>C. hilgendorfi</i> De Man, 1888	+	+
<i>C. mariae</i> Ihle, 1913	+	–
<i>C. pentagonalis</i> Hilgendorf, 1879	+	+
<i>C. pitiensis</i> n. sp.	–	+
<i>C. trituberculata</i> Buitendijk, 1939	+	–
<i>C. tuberculata</i> Stimpson, 1858	+	–
<i>C. tumida</i> Stimpson, 1858	+	+
<i>Takedromia cristatipes</i> (Sakai, 1969)	+	+
Total Number of Dromiidae (22 species)	20	9
Total Number for both families (29 species)	21	15

Cryptodromiopsis unidentata and *Takedromia cristatipes*. For the Mariana Islands, as a whole, there are now a total of nine dromiid species (in four genera) and six dynomenid species (in three genera) known. A total of 29 dynomenid and dromiid species are reported from the Mariana and Philippine Islands, of which only seven species, all of them dromiids, are shared.

“*Dromia verrucosipes* White, 1847”, a *nomen nudum*, was based on specimens purchased from a Mr H. Cuming who obtained them from the Philippine Islands. Subsequently “*D. verrucosipes*” was synonymised with *Cryptodromia lateralis* (Gray, 1831), from Australia, by Miers (1884)

and Henderson (1888). As a result, Estampador (1937: 510) listed *C. lateralis* in his checklist of Philippine decapods. McLay (1993: 168) transferred *Dromia lateralis* Gray, 1831 to the new genus *Stimdromia* and showed that the Philippine specimens belonged to an undescribed species of *Stimdromia*. This species is listed in Table 1 as *Stimdromia* sp.

Cryptodromiopsis unidentata, reported herein, is the only known dromiid from Tonga. No dynomenids are known from this island. Besides *Cryptodromia tumida*, other dromiids and dynomenids known from Samoa include *C. coronata*, *Dynomene hispida* and *D. praedator* (McLay 1993, 1999).

CRISTA DENTATA AS A BRACHYURAN CHARACTER

Boas (1880) seems to have been the first to use the term "crista dentata" to refer to structures on the inner margin of the mxp3 ischium (or basis-ischium) of decapods. He used the term indiscriminately, in reference to the mxp3 of both natant and reptant decapods, so that its exact original meaning is unclear. Subsequently, the term *crista dentata* has been used to refer to a comb-like row of sharp horny teeth arranged along the *inner* margin of the ischium (McLaughlin 1980). These teeth are used to grasp food passed to the mxp3 by the chelipeds. The outer ischial margin can be setose but often lacks any tubercles.

According to Scholtz & Richter (1995), the *crista dentata* is found among all the Eureptantia Scholtz & Richter, 1995 (that is all Reptantia Boas, 1880, except for the Polychelidae Wood-Mason, 1875) and represents an apomorphy of this group. Within the Brachyura the presence of a *crista dentata* is a plesiomorphic feature of the Dromiacea De Haan, 1833 because it is present in all three families: Homolodromiidae, Dromiidae, and Dynomenidae (although it has been lost in the two species of *Acanthodromia*). Among the remaining podotreme crabs, the *crista dentata* is present only in the Homolidae. The dromiids, dynomenids and some homolids (e.g., *Latreillopsis* Henderson, 1888, *Homolochunia* Doflein, 1904 and *Homolomania* Ihle, 1912) are the only podotremes with operculiform mxp3 armed with a *crista dentata*. The homolodromiids and other homolids (e.g., *Homola* Leach, 1815, *Moloha* Barnard, 1947 and *Dagnaudus* Guinot & Richer de Forges, 1995) have pediforme or sub-pediforme mxp3 (see Guinot 1995 and Guinot & Richer de Forges 1995). If we suppose that the Dromiacea, Homoloidea Guinot & Tavares (2001) and the remaining podotremes (Cyclodorippidae, Cyonomidae, Phyllotymolinidae, Latreilliidae and Raninidae) shared a common ancestor (with pediforme mxp3 and a *crista dentata*) then we must assume that the *crista dentata* has been independently lost several times: among some dynomenids (i.e. *Acanthodromia*), and in latreilliids, cyclodorippids, cyonomids, phyllo-

tymolinids and raninids. The *crista dentata*, as found in podotreme crabs, is absent from all of the Eubrachyura. Among these crabs the grasping role of the mxp3, if it is functional, is performed by teeth-like tubercles on the *outer* margin of the ischium. These teeth-like tubercles, found in the Eubrachyura, are not, as is often assumed, homologous with the *crista dentata*. Since this term has been used for the exterior tubercles of eubrachyurans, another term is required. A suitable descriptive term for them would be *marginal dentata*.

UROPODS AND THE ABDOMINAL LOCKING MECHANISM

In brachyurans, the abdomen is reduced and folded ventrally against the sternum. Its role is mainly protective: forming an incubation chamber in females and covering the gonopods in males. Associated with the change in the role of the abdomen from locomotion to protection, has been the evolution of some kinds of mechanism for securing the abdomen out of the way (Guinot & Bouchard 1998). These authors point out that abdominal locking mechanisms involve some level of coaptation between two independent parts of the body of the crab. They recognized three levels of coaptation: simple juxtaposition, engagement (*engrenage*) and assemblage (*assemblage*). These represent different degrees of specialization and it is clear that, for any structures to be recognized as being part of an abdominal locking or retaining mechanism, there must be some kind of coaptation between the abdomen and another part of the body. Comparison of the abdominal locking mechanisms of brachyurans provides some valuable insights into their phylogenetic relationships. While we find only a single mechanism among eubrachyurans (the *boutonpression*, a coaptation by assemblage that is an apomorphy of this group), the Podotremata show a variety of mechanisms involving structures on either the coxae of p1-p3 or the sternum (coaptations by juxtaposition or engagement). Some podotremes do not seem to have any functional mechanism, not even coaptation by juxtaposition. The variety of mechanisms among

podotremes is linked to the presence of uropods, the size of the abdomen and consequently its proximity to the bases of the pereopods. Another factor is the degree of sexual dimorphism in abdomen size. There is a relatively small difference in size between males and females.

In the Dynomenidae, three conditions are found: there are tubercles on sternite 5 in *Dynomene* and *Hirsutodynomene*; in *Acanthodromia* there are coxal spines on mxp3 and p1-p3 and in *Metadynomene* there is a small ridge or spine on p2-p3 coxae, but no granules on sternite 5; and in *Paradynomene* there are both granules on coxae of p2-p3 and a few granules on sternite 5 (but these do not appear to be effective). Although there are small sternal tubercles at the bases of the p2's in *Dynomene*, *Hirsutodynomene*, and *Paradynomene*, these are not involved in retaining the abdomen. When the abdomen is closed the uropods lie beside these tubercles, but not touching them. There is no locking mechanism so that the abdomen must be held against sternum by muscular tension. At the most, these tubercles can only function to restrict sideways movement of the abdomen. There is no evidence of coaptation of the abdomen, even by juxtaposition, utilizing these tubercles as a holding mechanism. Video-taped aquarium observations of live *D. praedator* from Hawaii, show that during movement the abdomen is not held tightly against the sternum, and periodically "pumping" movements are made by flicking the abdomen. These abdominal movements are also seen when the crab is stationary and feeding. The function of the sternal tubercles is enigmatic. In *Metadynomene* and *Paradynomene* there are small ridges or spines on the coxae of p2-p3, adjacent to the uropods or penultimate segment of the abdomen, but, again there is no evidence of coaptation. In the remaining dynomenid genus, *Acanthodromia*, an abdominal locking mechanism is present and functional. The abdomen fits closely against the bases of the pereopods and is held in place by spinous coxal projections on the mxp3 and first three pereopods. *Acanthodromia* shows coaptation by juxtaposition or engagement.

In dynomenids, sternal tubercles may lie beside the uropods, but since the uropods do not project beyond the lateral abdominal margin they cannot lock in front of these tubercles. In some species there is more than one sternal tubercle present and it may be that they are simply part of the external ornamentation of the body, and their presence near the margins of the abdomen are purely coincidental. Whether they have a role in the live animal needs to be verified, because they certainly do not appear to function in dead specimens. The presence of coxal projections in *Acanthodromia*, *Metadynomene* and *Paradynomene* resembles that found in dromiids. However, since the uropods in dynomenids never project beyond the lateral margins of the abdominal segments they cannot be involved in retaining the abdomen as in dromiids.

Sexual dimorphism of the abdomen, sternal tubercles and the uropods varies between the dynomenid genera. In females the abdomen totally covers the sternum and bases of pereopods, extending anteriorly so that the telson covers the bases of mxp3. The male abdomen is smaller, also covering most of the sternum, but not the bases of the pereopods. The lack of strong sexual dimorphism in abdomen size is a plesiomorphic feature of dynomenids. In males and immature females of *Dynomene*, *Hirsutodynomene*, and *Paradynomene* small tubercles are present at the bases of the p2's, but in mature females these tubercles are usually absent. In all species of *Dynomene* and *Hirsutodynomene* the uropods are sexually dimorphic with female uropods always being larger and occupying a greater proportion of the lateral abdominal margin. In *Metadynomene* the uropods occupy the entire margin between the telson and penultimate abdominal segment while in *Paradynomene* they fill about half the margin. The uropods are not sexually dimorphic in these two genera. The relative size of uropods in male and female *Acanthodromia* is not known. Compared to dromiids, dynomenid uropods are much larger, probably retaining the plesiomorphic condition. The larger size of the loosely held abdomen is also closer to the

presumed ancestral state, wherein it was used in locomotion.

The greatest diversity of abdominal retaining mechanisms is found among the dromiids. We should firstly note that, compared to dynomenids, the dromiids have much stronger sexual dimorphism of the abdomen. This reflects the narrower sternum in dromiid males. In dynomenids the male and female sterna are about the same width. In dromiids the uropods are also strongly sexually dimorphic. In males and immature females they project laterally, whereas in mature females they do not project but simply fill part of the space between the telson and last abdominal segment, as found in dynomenids. In all cases the abdomen retaining mechanism in dromiids involves structures on the coxae of the first three pereopods, which may act singly or in pairs, but never all three together (see Guinot & Bouchard 1998). In some genera uropods are vestigial [V] and/or absent [A]: *Ascidiophilus* Richters, 1880 [A] and *Pseudodromia* Stimpson, 1858 [V] (both of which live tightly enclosed in ascidians), *Tunedromia* McLay, 1993 [A], *Epipedodromia* André, 1932 [A], *Haledromia* McLay, 1993 [V], *Exodromidia* Stebbing, 1905 [V or A], *Eudromidia* Barnard, 1947 [V], *Dromidia* Stimpson, 1858 [V], *Austrodromidia* McLay, 1993 [V or A], *Barnardromia* McLay, 1993 [V], *Speedromia* Barnard, 1947 [V], and *Hypoconcha* Guérin-Méneville, 1854 [V or A]. In species of most of these genera, the abdomen is retained by coxal structures held against the abdominal margins. Vestigial or absent uropods must represent the most derived state. In the remaining dromiid genera the uropods are relatively well-developed and often involved in the abdominal locking mechanism.

Coxal abdominal locking mechanisms occur in all dromiacean families. In the Homolodromiidae a retaining mechanism is normally absent, except in *Dicranodromia felderi* Martin, 1990, where the telson is held by flanges on coxae of p1. Similarly, amongst dynomenids a functional coxal mechanism is only found in *Acanthodromia*. In other species or genera in these two families, a retaining mechanism is absent.

Amongst dromiids coxal mechanisms are widespread. These involve various structures on the coxae of p1 to p3 meshing with the posterior abdominal segments, uropods and sometimes the telson (see Guinot & Bouchard 1998 for a detailed summary). Evidence of the role of the coxal tubercles and ridges can easily be seen in the coaptation of the posterior abdominal segments with these structures. The most derived abdominal retaining mechanism is found where uropods fit tightly in front of coxal structures on the second pereopods as occurs in species of *Dromia*. Guinot & Bouchard (1998) call this condition the “full lock system”. The abdomen can only be released when the second pereopods are moved forwards, thereby moving the coxal tubercles posteriorly and releasing the uropods that are locked in front of the tubercles. This is coaptation by assemblage. McLay (1999: 463) argued that the ancestral dromiacean had no retaining mechanism and that the abdomen was simply retained by muscular tension. The simplest explanation of the evolution of these mechanisms is that coxal retaining mechanisms have evolved independently in each of the three families from an ancestor without such a mechanism. Thus the strong sexual dimorphism of the abdomen seen in dromiids is an apomorphy of this group. Similarly, in the Homoloidea De Haan, 1839, we find coxal mechanisms as well as a unique press-button system on sternite four (termed the “homoloid press-button” by Guinot & Bouchard 1998). Thus it is clear that, amongst the Podotremata, many different abdominal holding mechanisms have evolved independently. The *bouton-pressure* of the Eubrachyura, on sternite 5, is an apomorphy of this group, and presumably evolved from an ancestor lacking an abdomen retaining mechanism.

DYNOMENID AND DROMIID GONOPODS

Some general comments about the variation of dynomenid gonopods and their possible role in species recognition are appropriate here. The first gonopod is a partially rolled tube that forms a tube only distally. At the tip there is an aperture, through which the sperm must pass, with a soft

medial plate on one side and finally a “fence” of filiform setae surrounding the tip. Scanning electron microscope pictures of the tip of the first gonopods of eight species (in four genera) show no consistent variation between species or genera (see McLay 1999: 459, figs 12-14). The second gonopod is long, needle-like and armed with a single row of spines towards the tip. The main sources of variation on the second gonopod are the number of terminal and subterminal spines, their disposition to each other and the direction in which they point. The number of terminal spines ranges from one to three (curved or straight), while the number of subterminal spines ranges from 4 to 24. Species of *Dynomene* tend to have a smaller number of gonopod spines (4 to 15) than is found in other genera. The direction and disposition of the subterminal spines, depends upon their arrangement along the gonopod shaft and whether they follow a sinuous or spiral path.

An important distinction needs to be made between those parts of the gonopods, which come into contact with the female, and those parts that do not. Sexual selection could be expected to operate on the first but not necessarily on the second, unless they are somehow linked to the first. When the second gonopod is inserted inside the first, the only parts that can come into contact with the female are the tips of the first and second gonopods. The tip of the second gonopod can extend out of the aperture of the first but only for a short distance. With the first gonopod closely applied to the spermathecal aperture, the second gonopod can enter the spermathecal opening for a short distance. This means that only the spines near the tip of the gonopod can interact with the female aperture: these are the terminal spines and those subterminal spines nearby. Therefore only variation in these spines can be explained by sexual selection. However, I suggest that in the copulatory position all dynomenid gonopods will appear to be nearly the same. Most of the variation in gonopod structure occurs in parts of the second gonopod that cannot be in contact with the female. Therefore sexual selection cannot be invoked as

an explanation of the variation in dynomenid second gonopods. If the subterminal spines have any function at all it must be in the area of facilitating sperm transfer or cleaning the pathway followed by the sperm. The mechanism of sperm transfer in dynomenids is poorly understood, as it is in all dromiacean crabs (see McLay 2001 for further discussion of this point).

Dromiid males have similar gonopods to dynomenids, supporting the sister group relationship of these two families. The first gonopod is a poorly formed conduit (as in dynomenids) and the second is longer than the first, needle-like and normally lacks a row of spines. An interesting point, overlooked by McLay (1991, 1993), is that the gonopods of the dromiid genus, *Sphaerodromia*, are almost identical to those of dynomenids. In *S. ducousoi* McLay, 1991, for example, the first gonopod has a setose tip with a flexible medial plate, as in dynomenids, but also has a blunt lateral knob on the opposite side. In between these lies the small aperture through which the second gonopod emerges. When the gonopods are brought together with the female spermathecal aperture, the blunt knob engages with a depression on the sternum and the plate fits closely alongside the aperture. The second gonopod has a row of 20 small inset spines similar to that found in *Hirsutodynamene* (see Fig. 10). Similar structures are found in *S. nux* Alcock, 1899 (see 24.0 × 23.3 mm, male specimen MNHN-B6922).

The genus *Sphaerodromia* is regarded, for several other reasons, as being closest to the dromiid ancestral condition (see McLay 1993: 127). All other dromiid genera retain the setose tip, but lack the soft medial plate and lateral knob on the first gonopod, and the shaft of the second gonopod lacks spines. This clearly represents the apomorphic condition amongst the Dromiidae. The Homolodromiidae lack a medial plate on the first gonopod and the second is without spines. It maybe that the medial plate and spinous second gonopod are linked with the very short sternal sutures 7/8 in dynomenids and *Sphaerodromia*. In these animals the angle of the male gonopods, during mating, would have to be greater due to

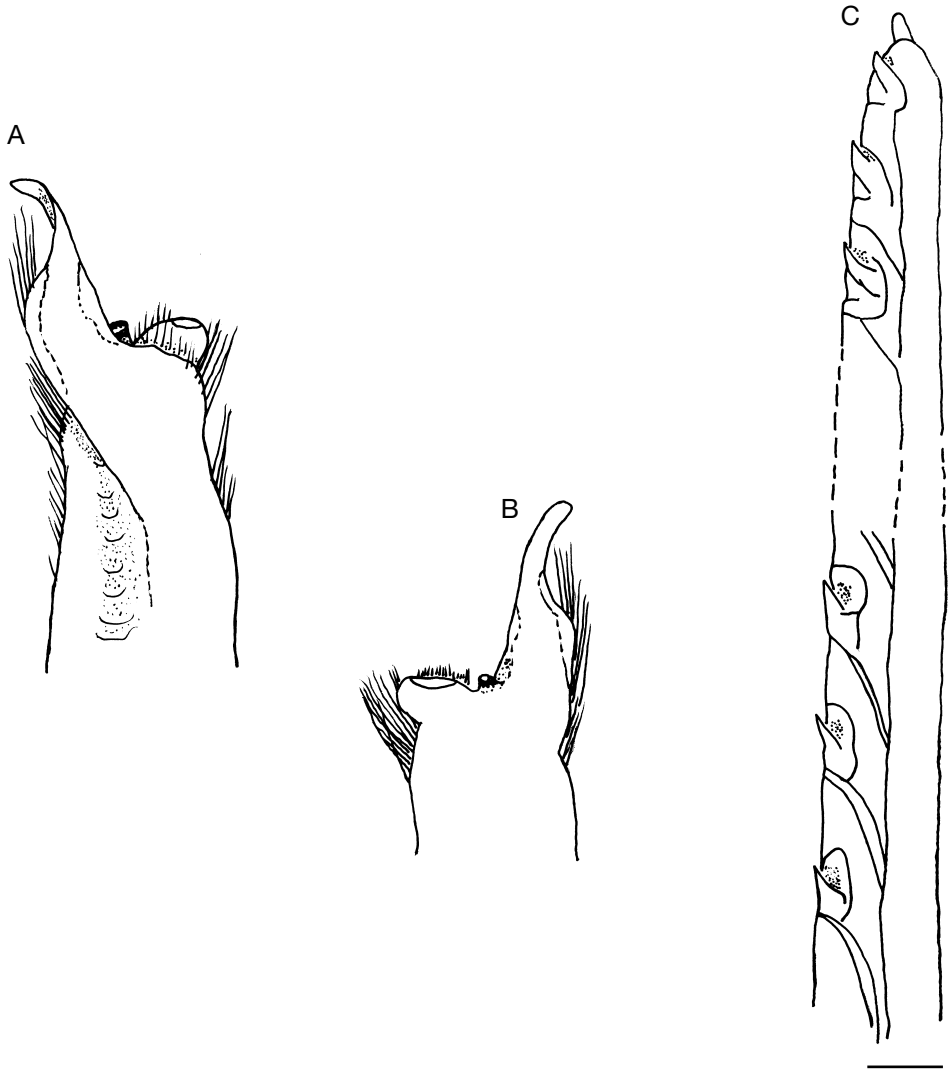


FIG. 10. — *Sphaerodromia ducousoi* McLay, 1991, Tuamotu Archipelago, 450 m, holotype, ♂ 43.0 × 43.2 mm (MNHN-B22172); **A**, distal section of left first gonopod, ventral view; **B**, dorsal view; **C**, two regions of the left second gonopod showing the 13th to 15th inset spines, and the terminal section showing the 19th and 20th inset spines. Scale bar: A, B, 1.0 mm; C, 0.05 mm.

the more posterior placement of the spermathecal openings, and the plate and spines may ensure better sperm transfer by preventing leakage.

What do the gonopods of dromiaceans tell us about their phylogenetic relationships? The homodromiids seem to have retained the ancestral condition (no medial plate on the first gonopod and no spines on the second) while the

ancestor of the dynomenids + dromiids evolved new structures (plate + spinous second gonopod). We have to assume that these new structures were secondarily lost in advanced dromiids, perhaps linked to the evolution of longer sternal sutures 7/8 and more anterior position of the spermathecal openings representing the derived condition. These arguments are not unreasonable and are

consistent with other characters supporting the hypothesis of McLay (1999).

Among the homolodromiids, Guinot (1995) found broken-off tips of the male first gonopods in the spermathecal orifices of some females. For this to occur the second gonopod must be longer than the first and be able to enter the openings. In dynomenids and dromiids the second gonopod can also extend out of the tip of the first, and potentially enter the spermathecal aperture of the female, but broken off pieces have never been found in any species of these families. It is unclear whether these broken pieces of the G2 in homolodromiids are accidental (representing an injury to both parties) or normal and have some role such as dislodging or displacing the sperm of earlier matings. Alternatively they may be some novel kind of "sperm plug".

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