RAFFLES BULLETIN OF ZOOLOGY 1993 **41**(1): 119-132

ON THE SYSTEMATICS AND ECOLOGY OF TWO SPECIES OF MIMETIC CRABS BELONGING TO THE FAMILY LEUCOSIIDAE (CRUSTACEA: DECAPODA: BRACHYURA)

Cheryl G. S. Tan and **Bertrand Richer de Forges**

ABSTRACT.- The taxonomy of two leucosiid species - *Dolos petraeus* (Milne Edwards, 1874) (new genus) and *Oreotlos etor*, new species, is discussed. Both mimic dead algae belonging to the genus *Halimeda* Lamouroux, 1812 (Order Caulerpales). Their behavioural and morphological adaptations to this mimicry are discussed.

INTRODUCTION

The resemblance of an animal to another organism (dead or alive), the latter being unpalatable to predators, has been reported in several crustaceans. This phenomenon may be considered as mimicry, and this is the definition used in this paper. Of the Brachyuran crabs reported to be mimetics, majid crabs belonging to the genus *Huenia* de Haan, 1839, are perhaps best known, mimicking the live *Halimeda* in which they live (see Griffin & Tranter, 1986 for review). These crabs are sexually dimorphic and have green carapaces shaped like individual fragments of this algae: "The similarity of the crabs to the algae in colour and shape was really surprising, typically representing the case of the so-called mimicry" (Takeda *et al.*, 1976:103). In the species *H. pacifica* Miers, 1879, very common in the New Caledonian lagoons, only the female exhibits this particular habit (Fig. 3E). Often, the camouflage is enhanced by leaves fixed on the crab's rostrum by special long, hooked setae (Wicksten, 1983).

In contrast, few have remarked about the peculiar camouflage adopted by certain leucosiid genera. Adams & White (1848) and Alcock (1896, 1902) were amongst the first to mention this habit in the genus *Oreophorus* Rüppell, 1830 s. lat. In this paper, two leucosiid species *Dolos petraeus* (Milne Edwards, 1874) and *Oreotlos etor*, new species commonly found in the lagoons of New Caledonia, are reported as mimetics of the algae *Halimeda*. These two species exhibit several features, both morphological and behavioural which allow them to look like individual

Cheryl G. S. Tan - Department of Zoology, National University of Singapore, Kent Ridge, Singapore 0511, Republic of Singapore. **Bertrand Richer de Forges** - Centre ORSTOM de Noumea, B. P. A5 Noumea, New Caledonia.

fragments of the algae. However, unlike species of *Huenia* which are green and mimic live *Halimeda* fragments, these two species mimic the dead, white (decolourised) *Halimeda* fragments.

The specimens examined are deposited in the Museum National d'Histoire Naturelle (MNHN), Paris; the Natural History Museum, London (BMNH), London; and the Zoological Reference Collection (ZRC), Department of Zoology, National University of Singapore. Measurements are of the carapace length and breadth. The male first and second gonopods are here referred to as G1 and G2 respectively.

All specimens were collected by the second author during a dredging program by Office de la Recherche Scientifique et Technique Outre Mer, Institut Francais de Recherche Scientifique pour le Développement en Coopération (ORSTOM), in the lagoons of New Caledonia and the Chesterfield islands.

TAXONOMY

The generic system used in this paper follows the unpublished revision of *Oreophorus* s. lat. by the first author and P. K. L. Ng, in which *Tlos* Adams & White, 1849, *Oreotlos* Ihle, 1918, and *Oreophorus* Rüppell, 1830, are recognised as separate genera (Tan & Ng, in press).

Dolos, new genus

Tlos - Milne Edwards, 1874:51 (part).
Oreophorus (Tlos) – Ihle, 1918:217 (part).
Oreophorus (Tlos) – Serène & Umali, 1972: 53 (part).

Type species.- *Tlos petraeus* Milne Edwards, 1874, designated herein.

Diagnosis.- Carapace distinctly broader than long, dorsal surface finely granulated, granules invisible to naked eye; groove parallel to border of carapace absent; median keel very indistinct/ absent; branchial regions concave; branchiostegite region gently sloping, with distinct small, concave region bearing large mushroom-like granules; front narrow, produced and weakly upturned, strongly bilobed with deep median fissure; granules covering lobes small and flattened; antero- and postero-lateral margins of carapace expanded, lined by small granules, without thick granulated rim; carapace borders with six closed fissures, with only depressions remaining. Antennule folds obliquely into large trapezoidal fossa with dorsally pointed apex, basal segment covered with small granules and occupies all of fossa. Sternum smooth, without large granule-lined excavations. Male abdominal segments without large, prominent granule(s). G1 usually 2-2.5 times longer than G2, distal half straight and may be slightly dilated, distal portion may be covered with short spines or hairs, apex with ovalish opening which may be sparsely rimmed by spines; G2 short with petaloid terminal process.

Remarks.- *Dolos* is allied to the genus *Tlos* by the presence of closed sutures on the margins of the carapace, the concave and plate-like lateral expansions of the carapace and branchial regions, the structure of the basal segment of the antennules (completely occupying fossae) and the presence of two knob-like projections on either side of the cardiac region. It, however, differs from *Tlos* in that the frontal and carapace margins are not strongly upturned, the front is

strongly produced and bilobed, the posterior part of the carapace is not sloping and the sutures on the carapace border are closed, leaving only holes visible. *Dolos,* as recognised at present, consists of only one species, *Dolos petraeus* (Milne Edwards, 1874).

Etymology.- The Greek *Dolos* means "guile or deceit". This alludes to the mimicry of the calcareous algae *Halimeda* by the crabs. The gender is masculine.

Dolos petraeus (Milne Edwards, 1874)
(Figs. 1, 3A, B, 5)

Tlos petraeus Milne Edwards, 1874:51, pl. 3, fig. 4 (New Caledonia).

Material examined.- Neotype male (5.9 mm by 8.3 mm) (MNHN), Stn. DW 905, 50-57 m depth, Lagoon North-West, New Caledonia, 20°59'3"S 164°36'9"E, 26.iv.88. — 1 male (5.0 mm by 6.8 mm) (MNHN), Stn. DW 155, 42 m depth, Chesterfield Islands, 19°49'08"S 158°24'85"E, Corail 2 Expedition, 1.ix.1988. — 1 male (5.0 mm by 6.9 mm) (ZRC), Stn. 702, 37 m depth, Lagoon East, New Caledonia, 21°26'7"S 166°08'2"E, 10.viii.1986. — 1 male (5.2 mm by 6.7 mm) (ZRC), Stn. DW 1174, R. V. Alis, 31.x.1989. — 1 female (5.2 mm by 7.1 mm) (MNHN), Stn. A, 9 m depth, Lagoon, R. V. Dawa, New Caledonia, 23.vii.1985. — 3 females (5.3 mm by 7.3 mm, 6.5 mm by 8.7 mm, 6.6 mm by 9.5 mm) (MNHN), Stn. 83, 22 m depth, "Ile Ouen-Baie du Prony", New Caledonia, 22°31'S 166°30'E. — 1 male (5.4 mm by 7.7 mm) (MNHN), Stn. DW 1072, 20 m depth, Lagoon North, New Caledonia, 19°56'0"S 164°02'4"E, 23.x.1989. — 1 male (5.5 mm by 7.7 mm) (MNHN), Stn. 747, 31-34 m depth, Lagoon East, New Caledonia, 21°14'7"S 165°50'9"E, 6.i.1987. — 1 female (5.7 mm by 8.3 mm) (MNHN), Stn. DW 1157, R. V. Alis, 30.x.1989. — 1 female (5.8 mm by 8.2 mm) (ZRC), Stn. 864, 26 m depth, Lagoon East, New Caledonia, 20°37'8"S 168°08'2"E, 13.i.1987. — 1 female (5.8 mm by 8.3 mm) (ZRC), Stn. 782, 30 m depth, Lagoon East, New Caledonia, 21°06'1"S 165°36'7"E, 8.i.1987. — 1 female (5.8 mm by 8.4 mm) (MNHN), Stn. 781, 36 m depth, Lagoon East, New Caledonia, 21°04'6"S 165°37'8"E, 8.i.1987. — 1 female (6.2 mm by 8.8 mm) (MNHN-MP-B 21300), Stn. 468, 40 m depth, Surprise Atoll, New Caledonia, 18°27'S 163°10'E, 1.iii.1985. — 2 females (6.0 mm by 8.4 mm, 7.0 mm by 9.6 mm) (MNHN MP-B 21298), Stn. 253, Sector Nouméa, New Caledonia, 22°22'S 166°23'E. — 1 female (6.0 mm by 9.0 mm) (MNHN) Stn. DW 1012, 15 m depth, Lagoon North-West, New Caledonia, 20°06'6"S 163°57'0"E. — 2 females (6.3 mm by 8.6 mm, 6.5 mm by 8.9 mm) (MNHN), Stn. DW 122, 32 m depth, Chesterfield Islands, New Caledonia, 19°28'17"S 158°17'06"E, Corail 2 Expedition, 29.viii.1988. — 1 female (6.1 mm by 8.6 mm) (MNHN-MP-B 21227), Stn. 83, 22 m depth, "Ile Ouen-Baie du Prony", New Caledonia, 22°31'S 166°30'E. — 1 female (6.5 mm by 9.4 mm) (MNHN), Stn. DW 1215, New Caledonia 1989, 2.xi.1989. — 1 female (6.6 mm by 9.3 mm) (MNHN), Stn. DW 1004, Lagoon North-West, New Caledonia, 20°10'4"S 163°58'1"E, 2.v.1988. — 1 female (6.7 mm by 9.3 mm) (MNHN), Stn. 2, 14 m depth, Sector Nouméa, New Caledonia, 22°19'S 166°23'E.— 2 females (6.8 mm by 9.5 mm, 6.9 mm by 9.9 mm) (MNHN), Stn. DW 1008, 27 m depth, Lagoon North-West, New Caledonia, 20°11'0"S 163°53'4"E, 2.v.1988. — 1 female (6.8 mm by 9.7 mm) (MNHN), Stn. DW 1009, 18-20 m depth, Lagoon North-West, New Caledonia, 20°09'9"S 163°55'1"E, 2.v.1988. — 1 female (6.8 mm by 9.9 mm) (MNHN), Stn. 1094, Lagoon North, New Caledonia, 19°54'4"S 163°41'2"E, 26 m depth, 24.x.1989. — 1 female (6.8 mm by 10.0 mm) (MNHN), Stn. 894, 12 m depth, Lagoon East, New Caledonia, 20°16'6"S 164°28'0"E, 14.i.1987. — 1 female (6.9 mm by 9.2 mm) (MNHN), Stn. DW 60, 45 m depth, Chesterfield Islands, New Caledonia, 19°14'98"S 158°56'98"E, Corail 2 Expedition, 24.viii.1988. — 1 female (6.9 mm by 9.7 mm) (MNHN-MP-B19160), Stn. 39, 19 m depth, Sector Nouméa, New Caledonia, 22°22'S 166°16'E. — 1 damaged specimen (MNHN), Stn. DW 30, 74 m depth, Chesterfield Islands, New Caledonia, 20°34'37"S 160°51'80"E, Corail 2 Expedition, 22.vii.1988.

Description. (Neotype male) - Carapace 1.4 times broader than long, regions not well-defined; dorsal surface with very small, flat granules invisible to naked eye; branchial regions

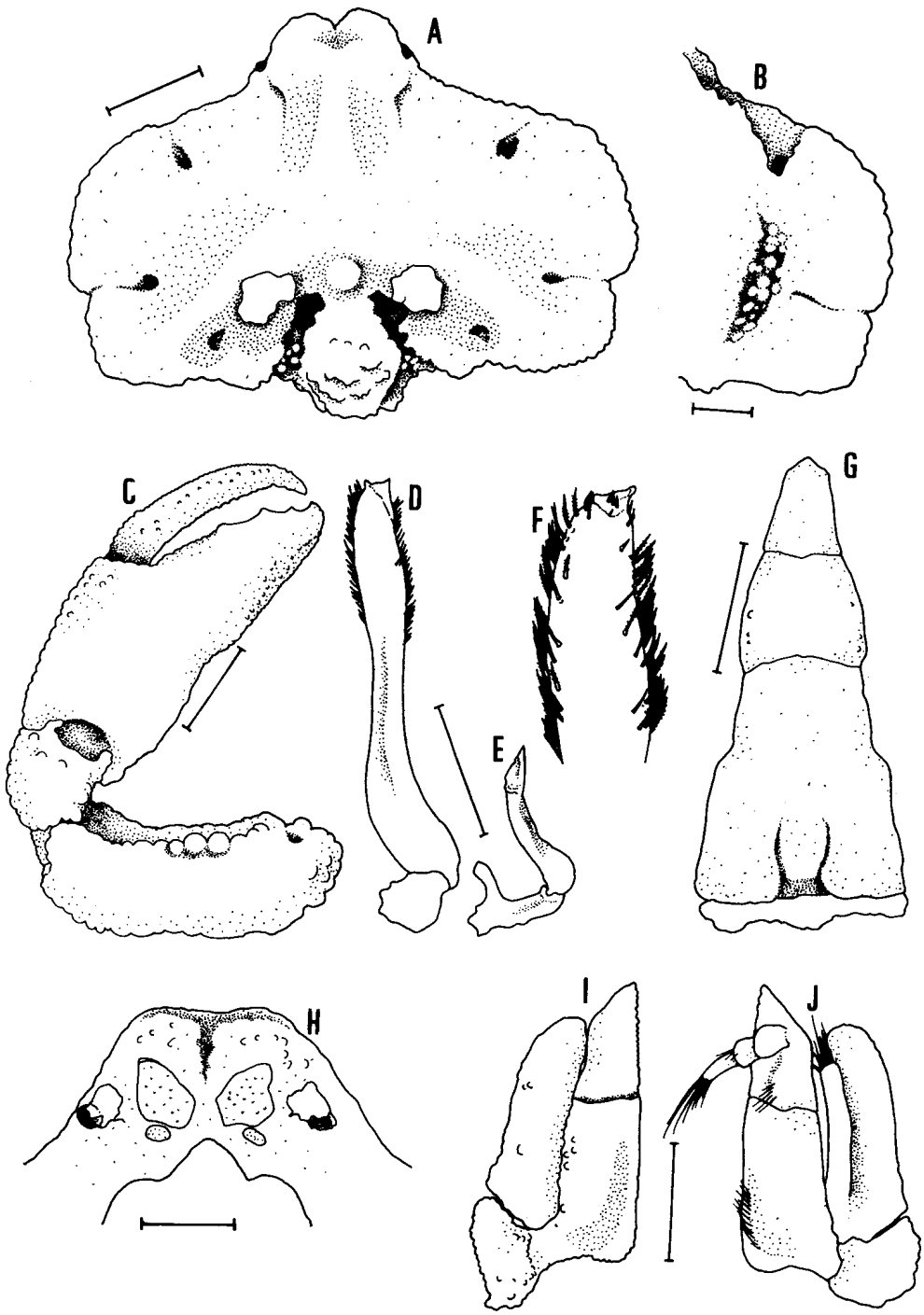


Fig. 1. *Dolos petraeus* (Milne Edwards, 1874), neotype male (MNHN, 5.9 mm by 8.3 mm). A, carapace dorsal surface; B, left branchiostegite region; C, right cheliped outer surface; D, right G1; E, right G2; F, apex right G1; G, abdomen; H, frontal view; I, right third maxilliped outer surface; J, right third maxilliped inner surface. Scales=1.0 mm.

concave, smooth and plate-like, with two irregularly shaped knob-like projections on either side of cardiac region; shallow, irregularly shaped, granule-lined groove on either side of cardiac and intestinal regions, separating cardiac and intestinal regions from rest of carapace, grooves with scattered mushroom-like granules. Front very strongly bilobed, with deep median cleft and triangular groove on dorsal surface; margin of hepatic region not protruded to form angle, sub-hepatic region with small triangular depression; carapace border with 6 closed fissures, with only circular depressions visible: 2 small groove-like depressions (frontal fissures) on frontal margin extending posteriorly on dorsal surface of carapace from orbits, 2 larger rounded depressions (anterior fissures) between frontal and hepatic regions and 2 between hepatic and branchial regions (posterior fissures); posterolateral border beside cardiac region slightly protruded to form rounded angle. Basal segment of antennule occupies entire fossa when closed.

Third maxillipeds finely covered with small granules; merus with pointed apex, outer edge forms rounded angle one-third down from apex, inner surface with median tuft of hair near proximal end; ischium 1.9 times longer than merus along inner margin, outer surface with shallow depression on proximal three-quarters of inner edge.

Fingers shorter than palm, 0.9 times length of palm; distal end of outer surface of immovable finger with short row of small granules; cutting edge of immovable finger with small, far-set teeth on distal half, cutting edge of movable finger lined by small raised granules; inner upper edge of merus lined by large granules, with larger ones proximally, distal third of outer edge also with large granules.

Proximal one-third of posterior edge of merus of last pair of legs with large prominent raised granule followed by 4 large granules distally; carpus and propodus covered by large granules; dactylus thin, longer than propodus, covered by small granules,

Abdomen entirely covered with small flat granules; proximal end of immovable piece made up of segments 3, 4, 5 with two shallow grooves on either side of median line, narrowing suddenly about two-thirds from proximal end; segment 6 with lateral margins slightly convex; segment 7 about as long as segment 6, tapering gradually to triangular apex.

G1 stout, straight, slightly constricted in middle, distal third densely covered with short, branched spines and hairs, rest of G1 glabrous; apex ends in triangular tip surrounded by scattered short spines.

Remarks.- Miers (1884) reported specimens of *"Tlos petraeus* " from Shark Bay, Western Australia but did not present any drawings or figures. His specimens could not be located in BMNH and his record must be regarded as indeterminate for the moment.

Alcock (1896) examined eight specimens of *"T. petraeus"* and provided a description but did not provide any figure. Alcock's description noted the presence of thickened, roughened and upturned lateral margins of the carapace, a median denticle on the male abdomen and a thickening between the branchial node and the postero-lateral angle. This leaves us little doubt that Alcock's specimens are actually *O. havelocki* (Laurie, 1906). In addition, the type locality of *O. havelocki* is the Gulf of Manaar, Ceylon, and Alcock's specimens come from similar locations: Andamans, Ceylon [Sri Lanka] and Pedro Shoal. The type of *O. havelocki* (in the BMNH) has been examined by the first author.

Serène & Umali (1972:55) commented that "... the separation of *muriger* from *petraeus* seems to be based on insufficient differences" as Milne Edwards stated only a few differences between the two: "(1) carapace more triangular; (2) antero-lateral border of carapace less upturned; (3) surface of carapace finely granular; and (4) marginal suture linear and deep. On examination of specimens from New Caledonia, although the species did appear to be related to *T. muriger* Adams & White, 1849, they differed significantly (see remarks for genus *Dolos*). The differences are such that we are dealing not only with a distinct species but a separate genus as well.

D. petraeus is very similar externally to another species, *Oreotlos etor*, new species, and each may be mistaken for the other. Both have smooth, plate-like carapaces whose borders are not upturned, and prominent, bilobed fronts. However, *O. etor* has the antennulary basal segment occupying only half of the fossa when closed (fossa fully occupied in *D. petraeus*) and the immovable piece of the male abdomen has a median denticle very characteristic of *Oreotlos* but absent in *Dolos*. The carapace in *O. etor* is also more rounded at the lateral margins, the latter not bearing any sutures as those found in *D. petraeus*. Due to this roundness, the carapace of *O. etor* has a heart-shaped appearance whilst that of *D. petraeus* appears more rectangular. The two round projections on either side of the cardiac region found in *D. petraeus* are absent in *O. etor* which instead has raised crested ridges on either side of the cardiac region. Also, the branchial regions in *O. etor* are flatter than those in *D. petraeus* . In addition, the triangular frontal groove present in *D. petraeus* is absent in *O. etor* . It is not known whether *O. etor* also exhibits similar mimicry as reported for *D. petraeus*.

The type specimen of *Tlos petraeus* was reported as lost (Guinot, *in litt.* to Serène, in Serène & Umali, 1972) and the second author has not been able to locate it in MNHN as well. Dr Guinot has checked for the specimen again and there is now no doubt that the type specimen of *Tlos petraeus* is indeed missing (*in litt*, 8 May 1993). As noted earlier, Serène & Umali (1972) expressed doubts about the validity of the species and its possible conspecificity with *T. havelocki* (regarded as belonging to *Oreotlos* by Tan & Ng, in press). Due to the state of taxonomy of this group of crabs, the fixing of a neotype will remove any future doubts about the identity of *T. petraeus* Milne Edwards, 1874. A male specimen (5.9 mm by 8.3 mm) from New Caledonia is hereby designated the neotype of *T. petraeus*.

The unusual habit of *Dolos petraeus* in mimicking dead *Halimeda* further distinguishes it from *Tlos muriger* which hides among coral rubble.

Oreotlos etor, new species

(Figs. 2, 3A, B)

Material examined.- Holotype male (5.5 mm by 7.5 mm) (MNHN), paratype female (5.6 mm by 8.1 mm) (MNHN), Stn. DW 70, 54 m depth, Chesterfield Islands, New Caledonia, 19°15'00"S 158°26'60"E, Corail 2 Expedition, 25.viii.1988. — Paratype male (5.0 mm by 6.7 mm), paratype females (6.3 mm by 8.9 mm, 6.4 mm by 8.8 mm) (ZRC), Stn. DW 87, 31 m depth, Chesterfield Islands, New Caledonia, 19°06'14"S, 158°59'94"E, Corail 2 Expedition, 26.viii.1988. — Paratype male (5.3 mm by 7.3 mm) (MNHN), Stn. DW 28, 78 m depth, Chesterfield Islands, New Caledonia, 20°28'07"S 160°56'34"E, Corail 2 Expedition, 22.vii.1988. — Paratype females (5.3 mm by 7.8 mm, 7.2 mm by 10.4 mm) (MNHN), Stn. DW 146, 44 m depth, Chesterfield Islands, New Caledonia, 19°37'00"S 158°16'28"E, Corail 2 Expedition, 30.viii.1988. — Paratype male (5.4 mm by 7.8 mm) (MNHN MP-B 21304), Stn. 484, 35 m depth, Lagoon North, New Caledonia, 19°00'S 163°35'E, 2.iii.1985. — Paratype female (5.9 mm by 9.0 mm)

(MNHN), Stn. DW 144, 50 m depth, Chesterfield Islands, New Caledonia, 19°27'73"S 158°23'28"E, Corail 2 Expedition, 30.viii.1988. — Paratype female (6.0 mm by 8.9 mm) (MNHN), Chesterfield Islands, New Caledonia, Stn. DW 2, 62 m depth, 20°50'48"S 161°37'25"E, Corail 2 Expedition, 20.vii.1988. — Paratype female (6.3 mm by 9.0 mm) (MNHN), Stn. DW 94, 36-53 m, Chesterfield Islands, New Caledonia, 19°06'00"S 158°50'00"E, Corail 2 Expedition, 27.viii.1988. — Paratype female (6.7 mm by 9.4 mm) (MNHN), Stn. DW 94, 36-53 m depth, Chesterfield Islands, New Caledonia, 19°06'00"S 158°50'00"E, Corail 2 Expedition, 27.viii.1988. — Paratype female (7.0 mm by 10.7 mm) (MNHN), Stn. DW 85, 32 m depth, Chesterfield Islands, New Caledonia, 19°12'05"S 158°56'26"E, Corail 2 Expedition. — Paratype female (7.3 mm by 10.9 mm) (MNHN MP-B 21302), Stn. D 61, 50 m depth, Plateau Chesterfield-Bellona, Coral Sea, Chalcal 1984, 21°42'40"S 159°29'00"E.

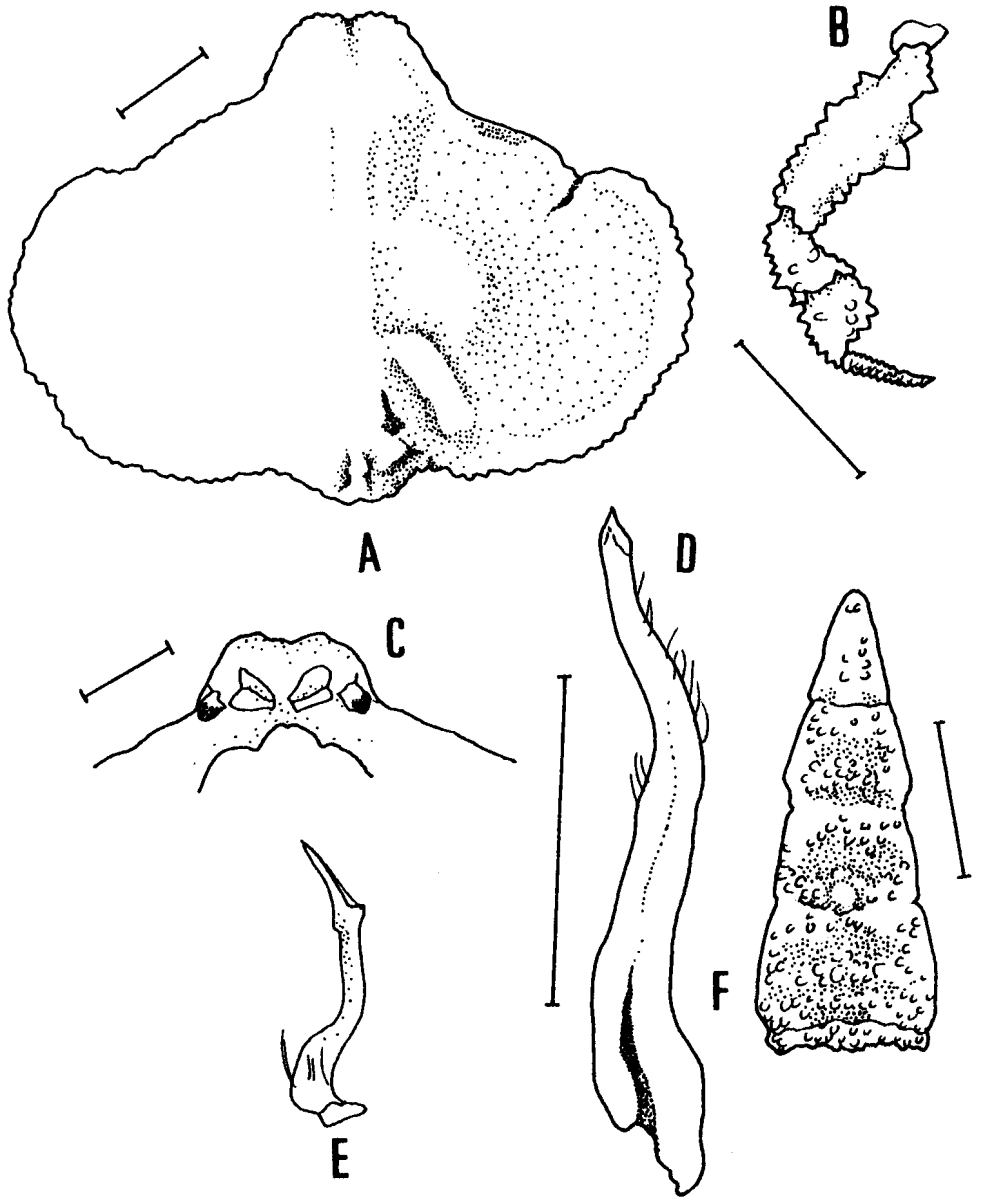


Fig. 2. *Oreotlos etor* sp. nov., holotype male (MNHN, 5.5 mm by 7.5 mm). A, carapace, dorsal surface; B, left last leg, outer surface; C, frontal view; D, right G1; E, right G2; F, abdomen.

Description. - (Holotype female). Carapace 1.4 times broader than long, heart-shaped, regions ill-defined; dorsal surface finely granulated, appearing smooth to the naked eye; depression on region posterior to orbit absent; median keel very wide and indistinct; branchial regions gently convex, surface smooth, posterior region on either side of cardiac region swollen to form crested ridge; very shallow, unexcavated, groove on either side of intestinal and cardiac regions; branchiostegite region finely granulated with no distinct granulated region. Front produced and bilobed with moderately deep median cleft; margins of hepatic and sub-hepatic regions only slightly convex; margin immediately after hepatic region with closed suture. Basal segment of antennule occupies half of fossa when closed, anterior margin of fossa with raised rim.

Third maxillipeds covered with fine granules as on carapace; merus with pointed apex, outer edge with obtuse angle about halfway down from apex; ischium 1.3 times longer than merus along inner margin.

Surfaces of chelipeds granular; fingers 1.4 times longer than palm, dorso-ventrally flattened to form spatulate structure; inner edge of immovable finger and outer edge of movable finger lined by sharp pointed granules; immovable finger slightly dilated in middle; cutting edges of both fingers with denticulate teeth; inner surface of palm with oblique ridge of large granules; edges of merus and carpus lined by sharp pointed granules.

Anterior edge of merus of last pair of legs lined with row of sharp pointed granules, posterior edges also lined with pointed granules, proximal half with larger granules; posterior edge of propodus with clump of large, pointed granules; dactylus long and narrow, covered with small pointed granules.

Borders of abdominal segments lined by larger granules than rest of segments; segment 5 with denticle close to proximal end.

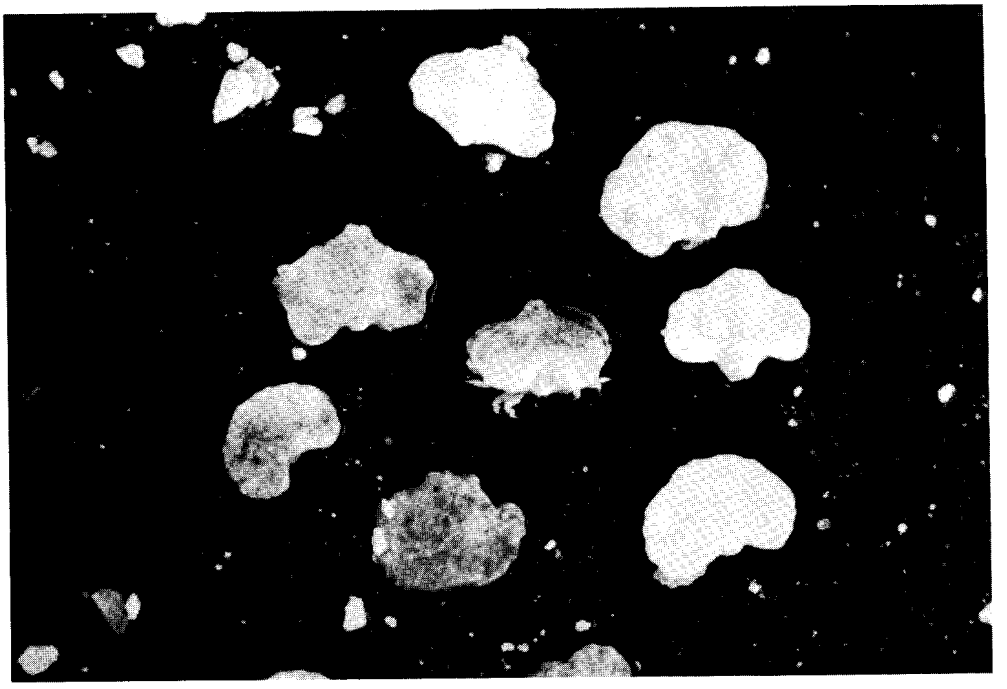
G1 moderately stout and tapering to a point, 2.4 times longer than G2, distal third with sparse hairs, apex simple and pointed; G2 with petaloid terminal process.

Paratype females.— All larger than male holotype; abdomen covered with granules, raised granular patch present on segment 6, immediately posterior to terminal segment; terminal segment triangular; other characters being similar to holotype male.

Remarks.- This species is found in the same locality as *Dolos petraeus* (New Caledonia) and may be confused with *D. petraeus* (see remarks for *D. petraeus*).

DISCUSSION

The two species, *Dolos petraeus* and *Oreotlos etor*, live on soft bottoms, in a very special bioclastic sediment composed mainly of dead and decolourised *Halimeda* fragments which are very common in tropical lagoons where several species of these Caulerpales algae grow. In the Great Barrier Reef lagoon, Drew (1983) estimated that the *Halimeda* segment debris accretion was equivalent to 1 m every 1892 years. For the southwest lagoon of New Caledonia, Garrigue (1991) calculated a carbonate production of 32g/m^2/yr by *Halimeda incrassata*. Sand mixed with *Halimeda* fragments exists in very large areas in the lagoon of Chesterfield atoll, forming bioherms (Richer de Forges *et al.*, 1988). *Halimeda* grows mainly on sandy substrates



A

B

Fig. 3. A, Comparison of live *Oreotlos etor* (centre) with *Halimeda* fragments; B, Appearance of the sediment from the Chesterfield lagoon after washing (Corail 2 expedition). The main components are *Halimeda* fragments. The arrow indicates a specimen of *Dolos petraeus*.

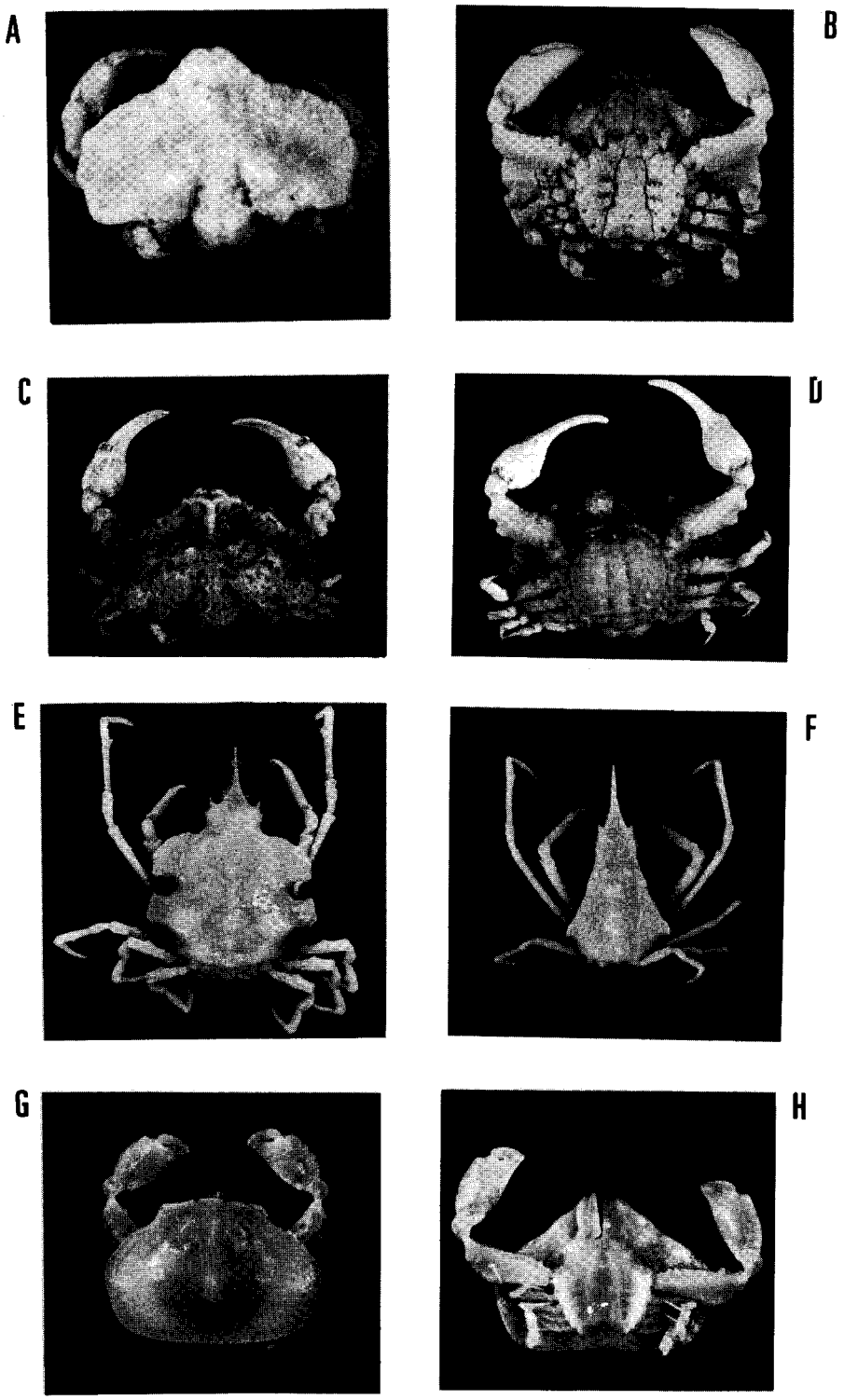


Fig. 4. Mimetic species. A, *Dolos petraeus*, male, dorsal view; B, *Dolos petraeus*, male, ventral view; C, *Oreophorus rugosus*, female, dorsal view; D, *Oreophorus rugosus*, female, ventral view; E, *Huenia pacifica*, female, dorsal view; F, *Huenia pacifica*, male, dorsal view; G, *Cryptocnemus* sp., male, dorsal view; H, *Cryptocnemus* sp., male, ventral view.

in shallow waters. However, several species have been reported in deep waters (to 140 m), growing on rocky bottoms on the outer slopes of reefs (Hillis-Colinvaux, 1986a; 1986b).

According to Alcock (1896), the Indian species of *Oreophorus* s. lat. were found only among dead coral shingle overgrown with *Foraminifera*, etc. The crabs are also often covered with the latter which could perhaps serve as camouflage. Later, Alcock (1902: 92-93) remarked that "Most ... are small, and many combine a lethargic and cataleptic habit with such curious colouring and sculpture that they are hard to distinguish from the bits of dead, worm-eaten coral amid which they live. So perfect in some cases is this protective disguise, that you may find growing on them the same calcareous sea-weed and the same branching Foraminifera (*Polytrema*) with which dead coral is so commonly encrusted. The most perfect disguise of this sort is attained by *Oreophorus reticulatus* ...". Indeed, all specimens of *Oreophorus* s. lat. examined by the authors were no larger than 3 cm in carapace width. Adams & White (1848:ii) mentioned that "... *Tlos*, like *Oreophorus* and *Leucosia*, is apathetic and inert, slow in its progressive movements, relying for security in its stone-like form ...". This inertness is also exhibited by *Dolos petraeus* and *Oreotlos etor*. Such behaviour may be a form of adaptation to avoid predation. The resemblance of *Oreotlos etor* to *Halimeda* fragments is shown in fig. 3A and B.

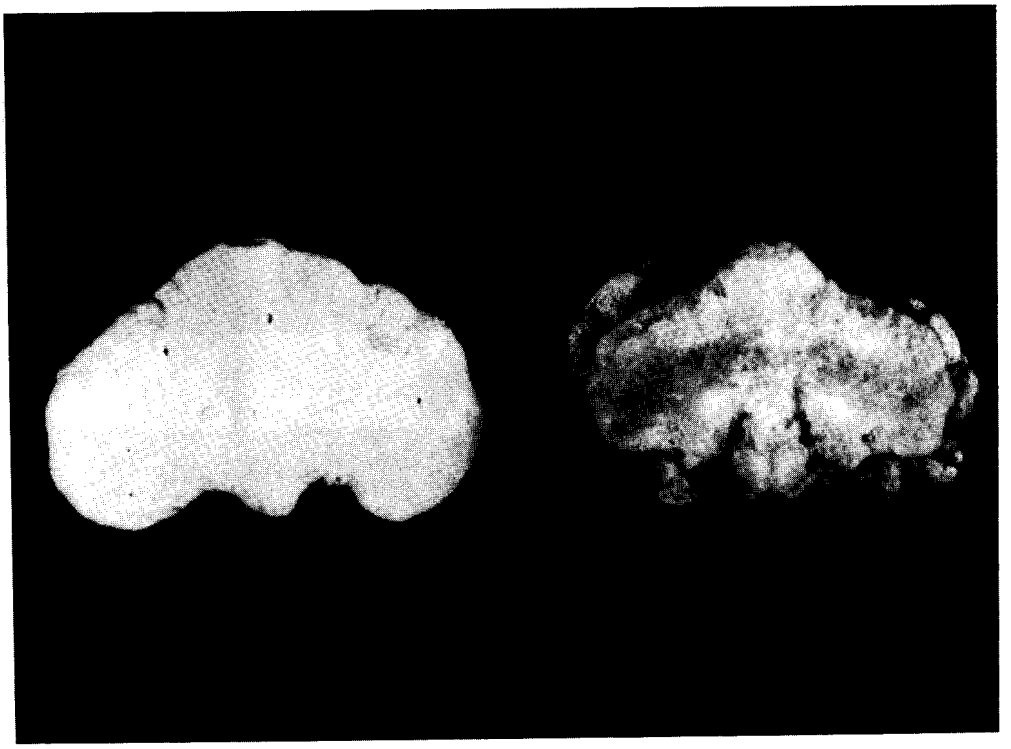


Fig. 5. Comparison of live *Dolos petraeus* (right) with *Halimeda* fragment (left).

The crabs' colouration is similar to that of the surrounding sediment, being generally whitish-grey. The frontal region of their carapaces are produced to resemble the stalks of *Halimeda* fragments (Fig. 3A,B). In addition, the carapace branchial and hepatic regions are flattened and expanded to form leaf-shaped structures and their chelipeds and pereiopods are short and hidden beneath carapace in dorsal view when the animals are stationary. It has been observed that the chelipeds and pereiopods possess sharp spines along the edges and these could perhaps serve to aid the animals in grasping their substrates firmly, in order to flatten themselves more effectively. All these features contribute to their effective mimicry of the algal fragments and render the animals almost invisible to any would be predator.

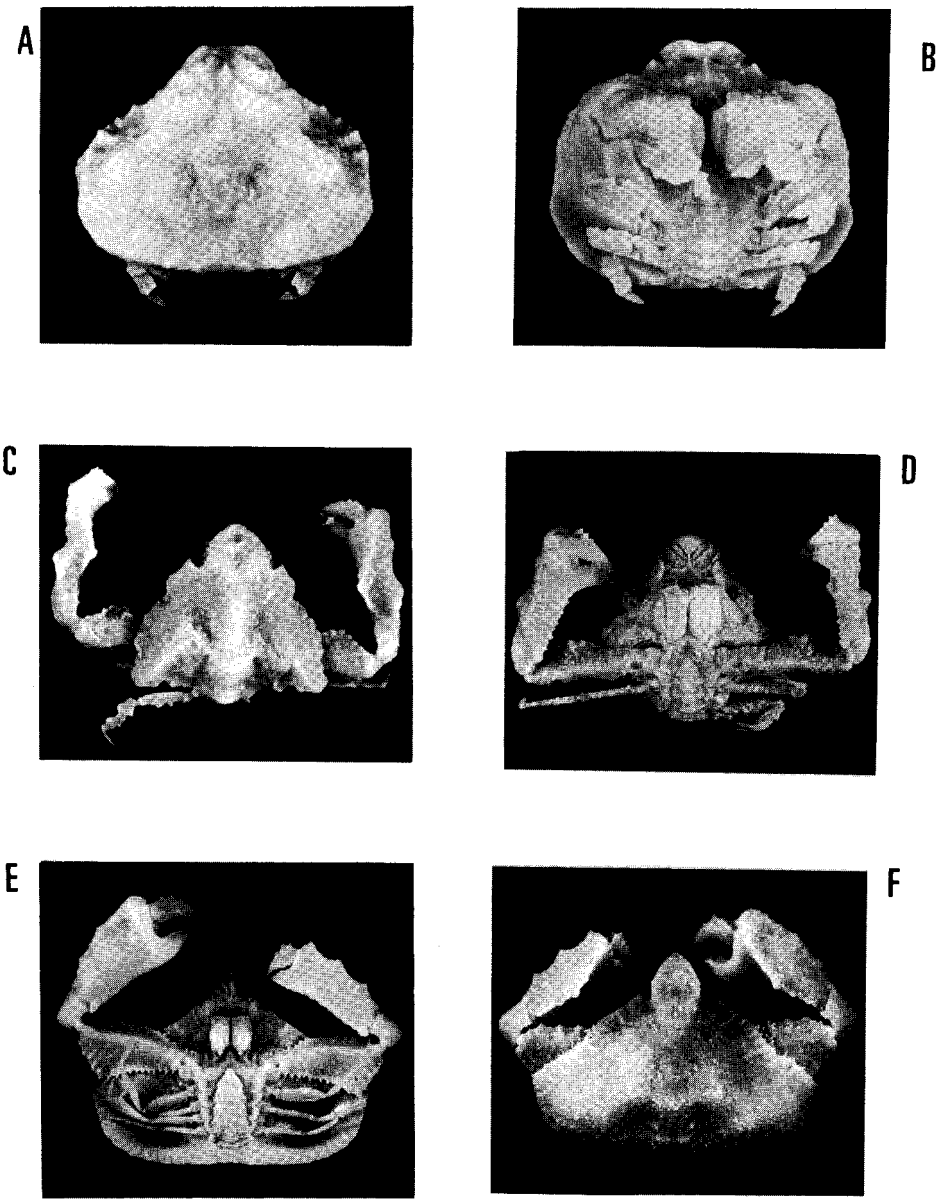


Fig. 6. Mimetic species. A, *Sakaila* sp., dorsal view; B, *Sakaila* sp., ventral view; C, *Pseudolambrus* aff. *harpax*, male, dorsal view; D, *Pseudolambrus* aff. *harpax*, male, ventral view; E, *Cryptopodia pan*, male, dorsal view; F, *Cryptopodia pan*, male, ventral view.

Other genera of Leucosiidae, such as *Oreophorus* Rüppell, 1830, and *Cryptocnemus* Stimpson, 1858, also have adaptations for camouflage. *Oreophorus* (Fig. 4C, D) resembles coral rubble and *Cryptocnemus*, with its flattened carapace, looks like discoid foraminifera (Fig. 4G, H).

It appears that convergence occurs in the mimicry of dead *Halimeda* fragments, as crabs from different families living in the same biotope have similar adaptations to those found in *D. petraeus* and *Oreotlos etor*. In New Caledonia, these include crabs from Parthenopidae such as *Cryptopodia pan* Laurie, 1906, with a very flattened shell that hides the legs completely (Fig. 6E, F), *Pseudolambrus* aff. *harpax* (Adams & White, 1848) which has a very rough, sculptured shell (Fig. 6C, 6D), *Sakaila* sp., with its expanded shell and reduced legs (Fig. 6A, B), and *Aethra scruposa* (Linnaeus, 1764) which has a very flat, expanded shell.

In the Neo-Darwinian theory of evolution, these very modified habits are explained as the result of natural selection under strong predatory pressure. The camouflage (colouration and mimicry) is used by the crabs as defence against visual predators (fishes, cephalopods, etc.) (Mayr, 1971). However, until further work is done on this aspect of crab mimicry, no conclusions can be drawn.

Acknowledgments.- The authors wish to thank Dr Danièle Guinot, Dr Raymond B. Manning and Dr Peter K. L. Ng for reviewing the paper. They also acknowledge Dr Alain Crosnier for the kind loan of a substantial number of specimens. The first author's work was partially supported by a research grant (RP 900360) from the National University of Singapore to P. K. L. Ng.

REFERENCES

Adams, A. & A. White, 1848. Crustacea. In: A. Adams, The Zoology of H. M. S. *Samarang*; under the command of Captain Sir Edward Belcher, C. B., F. R. A. S., F. G. S. During the years 1843-1846 (A. Adams, editor): 1-66, pl. 1-13. Published in two parts: Part I (pp. 1-32, pls. 1-6) is dated on the cover 1848, Part II (pp. 33-66, i-vii, pls. 7-13) has the date 1849 on the front cover.

Alcock, A., 1896. Materials for Carcinological Fauna of India. No.2. The Brachyura Oxystomata. *J. Asiat Soc. Beng.*, **65**(2) : 134-296, pl. 6-8.

Alcock, A., 1902. A Naturalist in Indian Seas (or, Four years with the Royal Indian Marine Survey Ship "Investigator"). London. 328 pp.

Drew, E. A., 1983. *Halimeda* biomass, growth rates and sediment generation on reefs in the Central Great Barrier Reef Province. *Coral Reefs* **2**:101-110.

Garrigue, C., 1991. Biomass and production of two *Halimeda* species into Southwest New Caledonian lagoon. *Oceanol. Acta* **14**(6):581-588.

Griffin, D. J. G. & H. A. Tranter, 1986. The Decapoda Brachyura of the Siboga Expedition. Part VIII-Majidae. *Siboga Exped. Monogr.* **39**, C4:1-333, pls. 1-22.

de Haan, W., 1839. Crustacea. In: P. F. von Siebold, Fauna Japonica: i-ixv, i-xxxi, 1-244, pls. 1-2, A-Q, 1-55. (J. Muller, Amsterdam).

Hillis-Colinvaux, L., 1986a. Historical perspectives on algae and reefs: have reefs been misnamed? *Oceanus* **29**(2):43-48.

Hillis-Colinvaux, L., 1986b. Deep-water populations of *Halimeda* in the economy of an atoll. *Bull. Mar. Sci.* **38**(1):155-169.

Ihle, J. E. W., 1918. Die Decapoda Brachyura der Siboga-Expedition, 3. Oxystomata: Calappidae, Leucosiidae, Raninidae. *Siboga Exped. Monogr.*, **39b²**:159-322.

Laurie, R. D., 1906. Report on the Brachyura collected by Prof. Herdman, at Ceylon, in 1902. In : W. A. Herdman, Report to the Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Manaar. Part V. Supplementary report, **40**:349-432, fig. 1-12, pl. 1-2.

Mayr, E., 1971. Populations, species and evolution. Harvard University Press, Cambridge, Mass. 444 pp.

Miers, E. J., 1879. Descriptions of new or little known species of maioid Crustacea (Oxyrhyncha) in the collection of the British Museum. *Ann. Mag. nat. Hist.*, (5) **4**:1-28, pls. 4-5.

Miers, E. J., 1884. Crustacea. Report of the Zooloogical Collections of H. M. S. *Alert*, London, pp. 178-322, pls. 18-24, pp. 513-575, pls. 46-52.

Milne Edwards, A., 1874. Recherches sur la Faune Carcinologique de la Nouvelle-Calédonie. *Nouv. Arch. Mus. Hist. Nat., Paris*, **10**:39-58, pls. 2-3.

Richer de Forges, B., C. Chevillon, P. Laboute, G. Bargibant, J-L. Menou & P. Tirard, 1988. La campagne Corail 2 sur le plateau des îles Chesterfield (N. O. "Alis", 18 juillet au 6 août 1988). ORSTOM: Nouméa. Rapp. Sc. tech., Sci. mer, Biol. Mar., 50; 68 pp.

Rüppell, 1830. Beschreibung und Abbildung von 24 Arteh kurzschwänzigen Krabben, als Beitrag zur Naturgeschichte des rothen Meeres, Frankfurt, 28 pp.

Serène, R. & Umali, A. F., 1972. The family Raninidae and other new and rare Brachyuran Decapods from the Philippines and adjacent regions. *Philip. J. Sci.* **99**(1-2), 1970(1972):21-105, fig. 1-131, pl. 1-9.

Stimpson, 1858. Prodromus descriptionis animalium vertebratorium, quae in Expeditione ad Oceanum Pacificum Septentrionalem a Republica Federata Missa. *Proc. Acad. Nat. Sci. Philadelphia*, **10**(4):31-163.

Takeda, M., K. Okamoto & T. Fukuda, 1976. *Huenia brevifrons* Ward (Decapoda, Majidae) attached to calcareous green alga, *Halimeda*, from the Ryukyu Islands. *Bull. Natn. Sci Mus.*, Ser. A (Zool.), **2**(2):103-109.

Tan, C. G. S. & P. K. L. Ng, in press. A Revision of the Indo-Pacific genus *Oreophorus* Rüppell, 1830 (Crustacea: Decapoda: Brachyura: Leucosiidae).

Wicksten, M. K., 1983. Camouflage in marine invertebrates. *Oceanogr. Mar. Biol. Ann. Rev.*, **21**: 177-193.