

On the association between the crab *Hapalonotus reticulatus* (Crustacea, Brachyura, Eumedonidae) and the sea cucumber *Holothuria (Metriatyla) scabra* (Echinodermata, Holothuridae) *

by D. VANDENSPIEGEL, A. OVAERE & Cl. MASSIN

Abstract

A study of the fauna associated with holothurians from Hansa Bay (Papua New Guinea) reveals a new symbiotic association between the holothuroid *Holothuria (Metriatyla) scabra* and the crab *Hapalonotus reticulatus*. All the collected holothurians were infested, but with only one crab per holothurian, always in the right respiratory tree near the cloaca. Because of its size, *H. reticulatus* considerably expands the wall of the respiratory tree, forming a membranaceous cyst. This association, therefore, appears to be parasitic. However, the crab does not feed upon host tissue but seems to filter its food from water passing through the respiratory tree of its host.

The description of two males allows to comment upon the taxonomical position of *H. reticulatus*. We classify *H. reticulatus* in the recently re-established family Eumedonidae. This is the first record of a species of Eumedonidae living in association with a holothurian.

Key-words: Symbiosis, taxonomy, crab, holothurian, Papua New Guinea.

Résumé

Des observations réalisées sur la faune associée aux holothuries de la Hansa Bay (Papouasie Nouvelle-Guinée) ont permis de décrire une nouvelle association entre l'holothurie *Holothuria (Metriatyla) scabra* et le crabe *Hapalonotus reticulatus*. Toutes les holothuries récoltées étaient infestées. Il n'y a jamais plus d'un crabe par holothurie. Chaque crabe est logé dans le poumon droit près du cloaque. En raison de sa taille, *H. reticulatus* déforme considérablement la paroi du poumon pour former un kyste membraneux. En conséquence, l'association serait de type parasitaire. Cependant le crabe ne se nourrit pas aux dépens des tissus de son hôte. Il semble plutôt filtrer sa nourriture à partir de l'eau qui circule dans le poumon de son hôte.

L'étude de deux spécimens mâles a permis de préciser la position taxonomique de *H. reticulatus* qui, jusqu'à présent, était incertaine. Nous considérons *H. reticulatus* comme appartenant à la famille des Eumedonidae, récemment rétablie. C'est la première fois qu'un crabe Eumedonidae est trouvé en association avec une holothurie.

Mots-clefs: Symbiose, taxonomie, crabe, holothurie, Papouasie Nouvelle-Guinée.

Introduction

The number of symbiotic associations between crabs and holothurians are not numerous, and consists mainly of crabs belonging to the family Pinnotheridae (genera *Ophistopus*, *Pinnixia*, *Pinnaxoda* and *Pinnotheres*) and

Portunidae (genus *Lissocarcinus*) (for a review see JANGOUX, 1987). The Portunidae are exosymbionts, which live on the integument of the holothurian, while the Pinnotheridae are endosymbionts, which generally live in the gut or in the respiratory trees of their hosts.

Previously *Hapalonotus reticulatus* (DE MAN, 1879) was known from only 3 female specimens (with membranaceous carapaces) from Ambon and Banda. Nothing is mentioned in the literature about the ecology of this crab. Only BALSS (1933) suggested that the body shape of the crab could be the result of a commensal way of life.

The discovery in Papua New Guinea of 6 specimens (2 males and 4 females) of *H. reticulatus* in specimens of *Holothuria (Metriatyla) scabra* JAEGER, 1833, allows us to describe the symbiotic relationship between *H. reticulatus* and *H. (M.) scabra*, and to elucidate the systematic position of *H. reticulatus*.

These findings were briefly reported upon at a colloquium in 1991 (VANDENSPIEGEL & OVAERE, in press), and are now described on full.

Materials and methods

The specimens of *Holothuria (Metriatyla) scabra* were collected at depths of 6 to 11 m, by day, using SCUBA in Hansa Bay (Madang Province, Papua New Guinea) (Fig. 1). The holothurian population lives in a sparse seagrass bed (Fig. 2) of *Halophila* and *Halodule* species (BAY & DEMOULIN, 1989), which extends from 2 to 11 m depth. The substrate is made up of volcanic black sand.

The specimens of *Hapalonotus reticulatus* were removed from holothurians, previously anaesthetized for 2 to 3 hours in a freezer, and immersed in a 2 % marine solution of propylene phenoxetol (Nippa Laboratories, UK; see HILL & REINSCHMID, 1976). The crabs were fixed in formalin and preserved in 70 % alcohol. For

* Publication n° 254 of the King Léopold III Biological Station

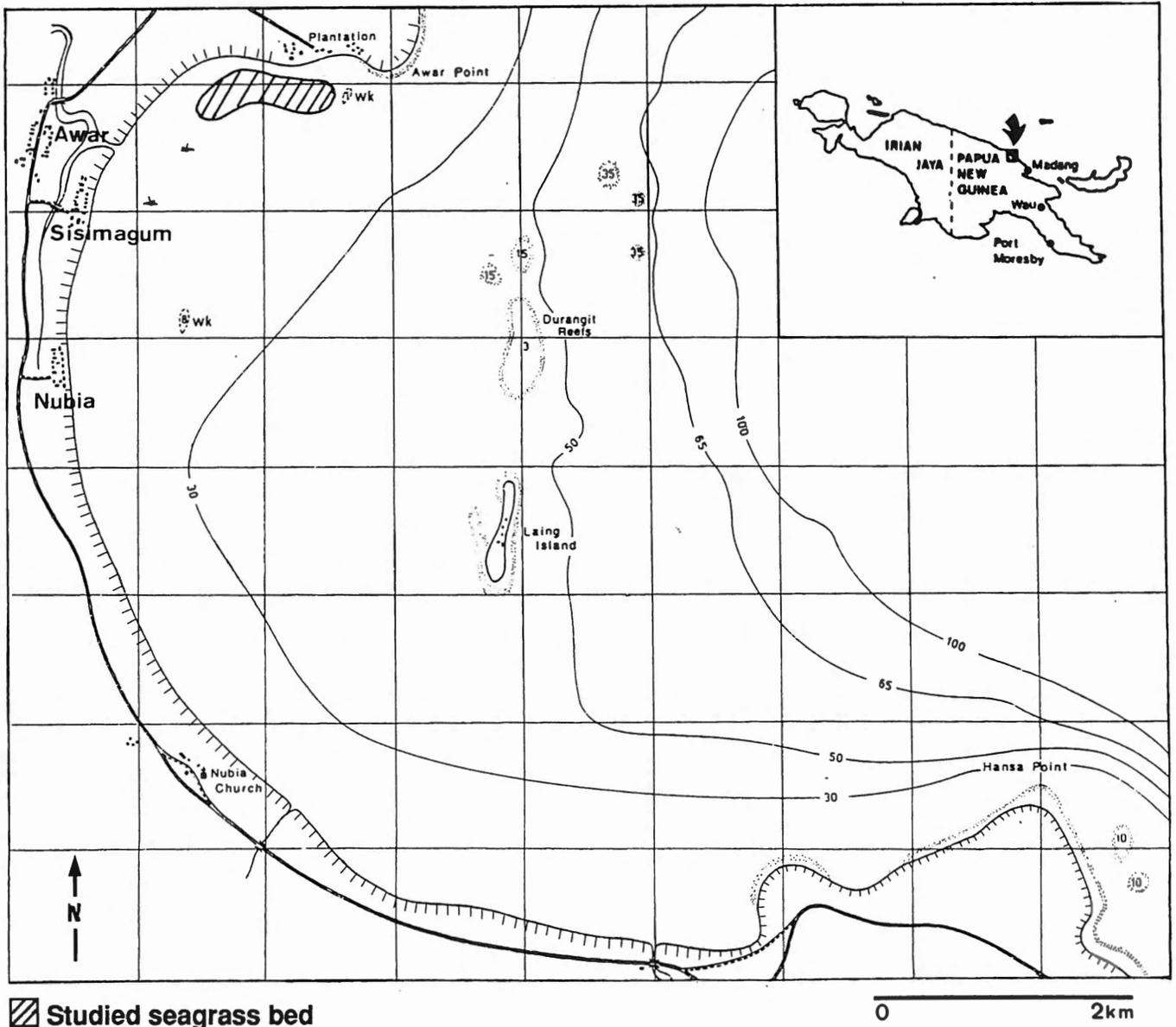


Fig. 1. - Map of Hansa Bay with the studied seagrass bed.

light microscopy, the respiratory tree and the membranaceous cyst of one holothurian were fixed in Bouin's fluid. Pieces of the respiratory tree and membranaceous cyst were cut into 7 μm thick sections. Sections were subsequently treated according to the procedure of GANTER & JOLLES (1969-1970), and used for routine histological examination (MASSON Trichrome).

Taxonomic account

Order ASPIDOCHIROTIDA GRUBE, 1840
 Family HOLOTHURIDAE LUDWIG, 1894
 Genus *Holothuria* LINNEAUS, 1767

Holothuria (Metriatyla) scabra JAEGER, 1833

Among the holothurian species living in the seagrass

beds of Hansa Bay, *Holothuria (M.) scabra* is the only one infested by the crab *Hapalonotus reticulatus*. The holothurian host has the ossicles (Figs. 3, 4), the calcareous ring and the long stone canal (up to 16 cm long for a 21.5 cm long contracted specimen) characteristic of the species. However, the colour of the skin is quite unusual for what has been previously reported for *H. scabra*.

The ossicles present some variation in comparison with other populations. *H. scabra* from the Red Sea (CHERBONNIER, 1955, pl. 32, fig. a, e), Madagascar (CHERBONNIER, 1988, fig. 55 A, B, D, E, H), India (BAI, 1980, fig. 20A), the Philippines Islands (DOMANTAY, 1933, pl. II, fig. 3a, d), Japan (MITSUKURI, 1912, fig. 24b) and New Caledonia (CHERBONNIER, 1980, fig. 16A, H) always possess tables with the edge of the disk being smooth or nodulous. Specimens of *H. scabra* from

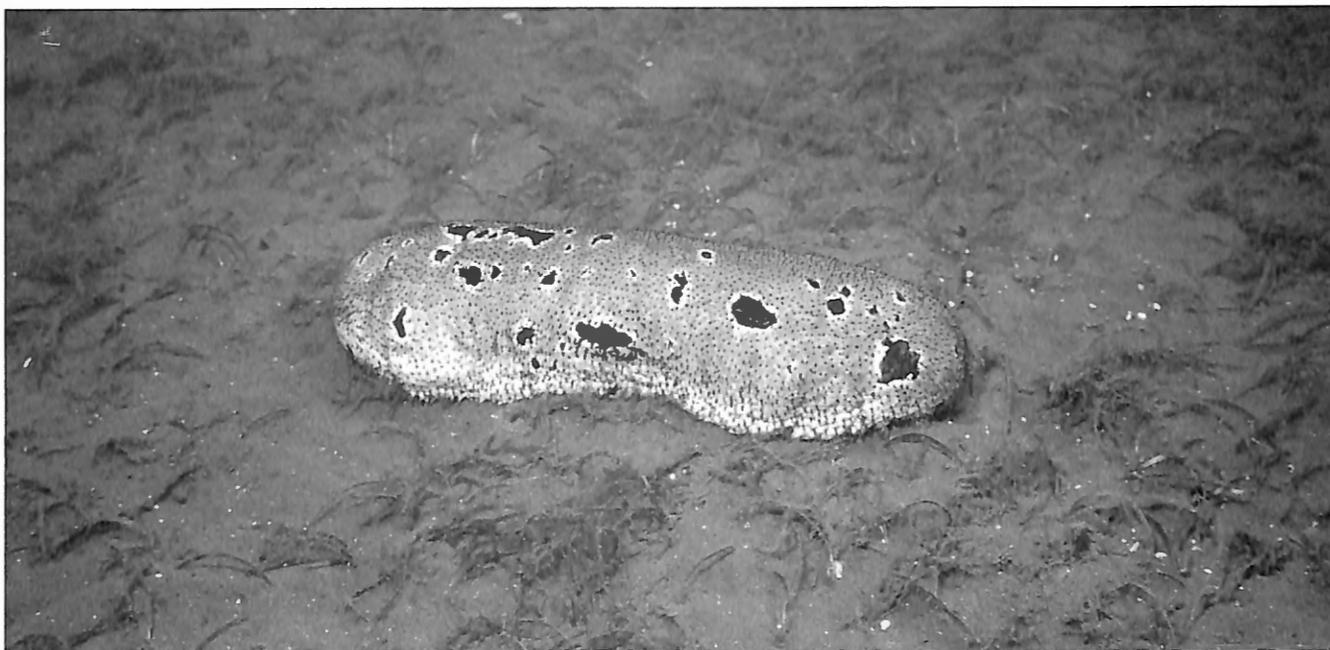


Fig. 2. – *Holothuria (Metriatyla) scabra* from Hansa Bay.

Hansa Bay have tables with the edge of the disk often being spiny (Figs. 3A, 4A). Moreover, the branching rods mentioned by BAI (1980) in the ventral skin and by CHERBONNIER (1988) around the anus have not been observed in our specimens.

The specimens collected in Hansa Bay are pale beige, without dark spots dorsally and almost white ventrally; or dark brown with, dark spots with a white ring around them dorsally (Fig. 2) and white cream with a brown central ridge and some scattered brown spots ventrally. All the intermediate colour patterns between these two extremes have been observed. The ventral tube feet and the dorsal papillae are well developed and give the skin a bristly aspect.

H. scabra is known to have a wide range of possible colour patterns. However, the colour pattern observed in Hansa Bay has never been recorded before. The most frequently observed colour pattern is grey beige to brown, sometimes greenish, dorsally and white beige ventrally (CANNON & SILVER, 1986; FÉRAL & CHERBONNIER, 1986; CONAND, 1989). Some specimens are nearly black with dorsal pale spots or stripes (PEARSON, 1913; BAI, 1980; CHERBONNIER, 1988). The reverse is also known and sometimes dark spots (black or brown) appear on a grey beige background (SLUITER, 1901; H.L. CLARK, 1921, 1946; CHERBONNIER, 1955). CONAND (1989) also described a variety of *H. scabra*, *H. scabra* var. *versicolor*, without transverse ridges, and of pale

beige colour, with dorsally scattered or densely crowded black spots.

Our specimens exhibit a similar colour pattern. However, they can be readily distinguished from *H. scabra* var. *versicolor* by a dark brown dorsal side, and especially by the very characteristic scattered dorsal black spots with a white ring around them. CONAND (1989) noticed ecological differences between *H. scabra* and *H. scabra* var. *versicolor*. If our specimens are closely related to *H. scabra* var. *versicolor* as suggested by their colour pattern, their ecological requirements are, however, typical of *H. scabra* s. str.: all the specimens were observed on a silty seagrass bed between 6 and 11 m depth.

The observed colour pattern seems to be restricted to the population in Hansa Bay (Papua New Guinea). Indeed, the colour pattern with black spots surrounded by white is not mentioned for the populations from Motupore Island near Port Moresby (BROUNS & HEIJS, 1985; SHELLEY, 1985; MASSIN, personal observation) or from Madang (MASSIN, personal observation).

The ossicle variations and the different colour pattern, together with the very high specificity in the relationship between endosymbiont crustaceans and sea cucumbers (HUMES, 1980) could indicate that the name *H. scabra* applies to several species. A detailed study of specimens from a wide range of Indo-Pacific localities would be necessary to elucidate this problem.

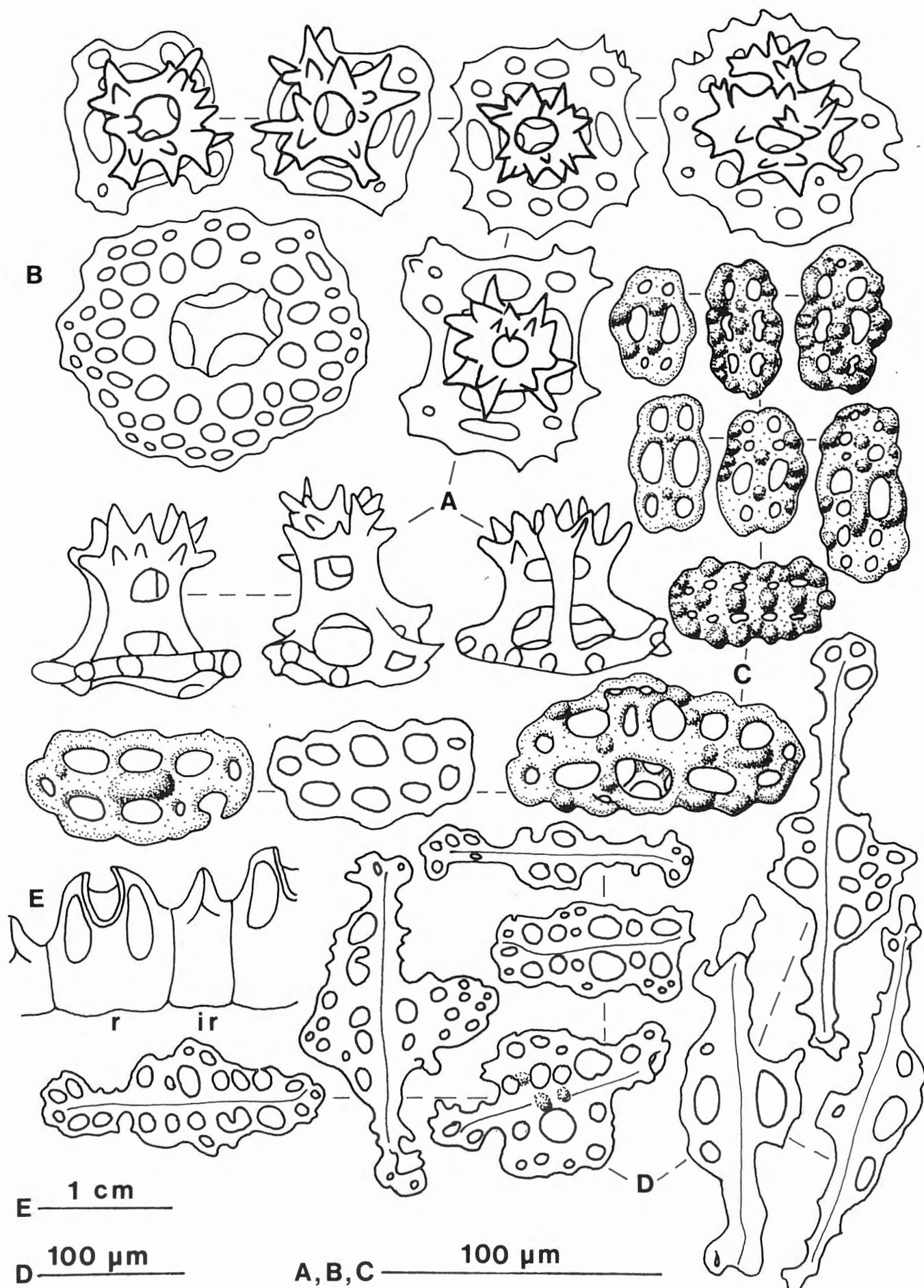


Fig. 3. — *Holothuria (Metriatyla) scabra* ossicles. A : skin tables; B : large skin table (rare); C : skin buttons; D : rods from the dorsal papillae; E : calcareous ring (r : radial piece; ir : interradial piece).

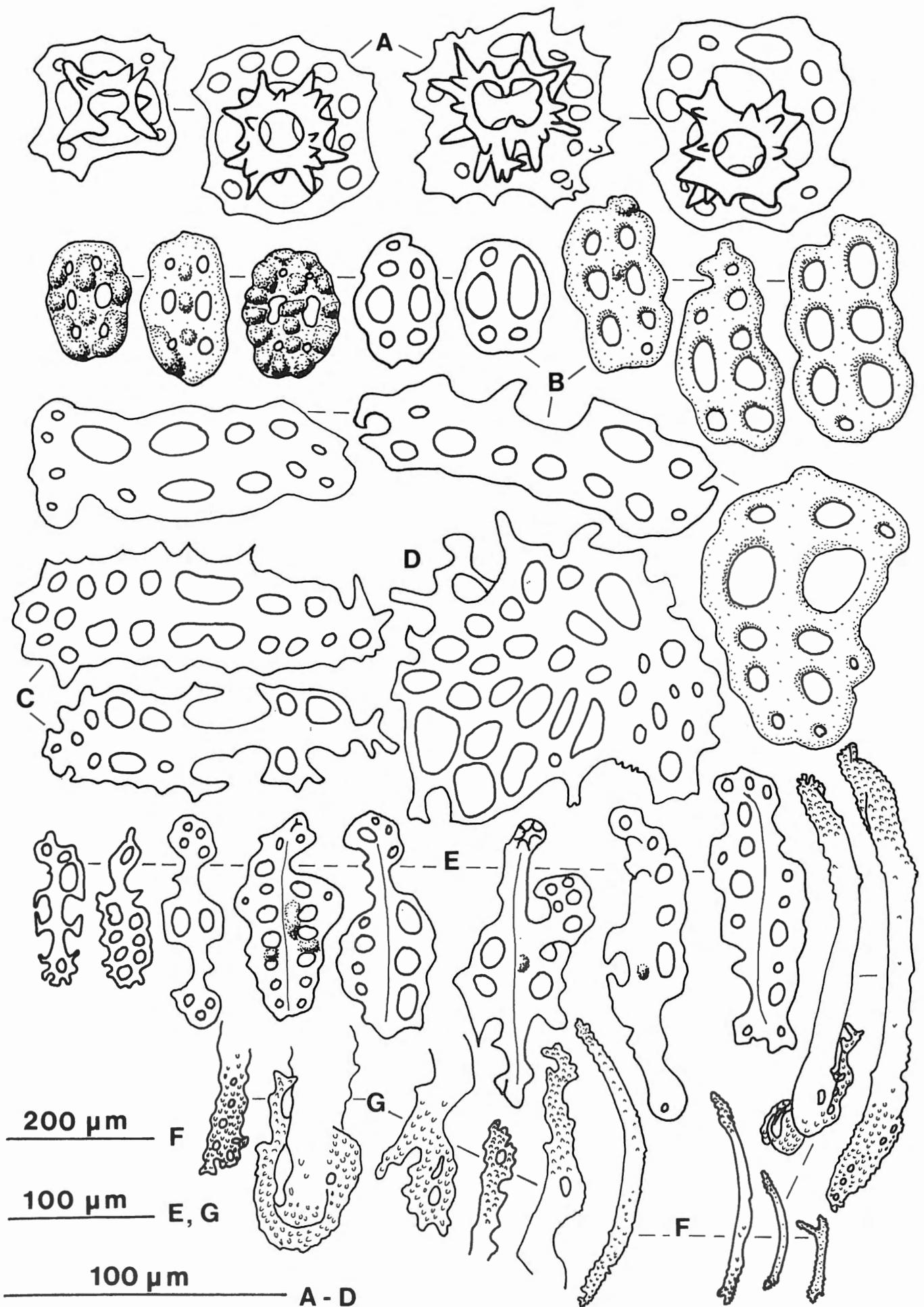


Fig. 4. — *Holothuria (Metriatyla) scabra* ossicles. A : tables from the tube feet; B : buttons from the tube feet; C : plates around the end plate of a tube foot; D : one of the 4 to 5 plates of the tube foot end plate; E : rods from the tube feet; F : rods from the tentacles; G : close-up of the apex of rods from the tentacles.

Order DECAPODA LATREILLE, 1803
 Infraorder BRACHYURA LATREILLE, 1803
 Superfamily XANTHOIDEA MC LEAY, 1838
 (sensu GUINOT, 1978)
 Family EUMEDONIDAE DANA, 1853
 (sensu ŠTEVČIĆ *et al.*, 1988)
 Genus *Hapalonotus* RATHBUN, 1897

***Hapalonotus reticulatus* (DE MAN, 1879)**

Malacosoma reticulata DE MAN, 1879 : p. 67-68.
Hapalonotus reticulatus RATHBUN, 1897 : p. 164. - TESCH,
 1918 : p. 277-279, pl. 18, fig. 3. - BALSS, 1933 : p. 89-
 91, fig. 3, pl. 2, fig. 1. - BALSS, 1957 : p. 1648. - SERENE,
 1968 : p. 74. - GUINOT, 1978 : p. 271. - VANDENSPIEGEL
 & OVAERE, in press.

TYPE-LOCALITY

Amboina, presently known as Ambon (DE MAN, 1879).

MATERIAL EXAMINED

Papua New Guinea, Hansa Bay (Madang Province), sea-
 grass beds off Awar Plantation (4°08'27"S-
 144°51'22"E), in the respiratory tree of the holothurian
Holothuria (Metriatyla) scabra : adult male, B.C. 2001,
 July 1988, I.G. 27.522; adult female, B.C. 2002, July
 1988, I.G. 27.522; ovigerous female, B.C. 2003, at a
 depth of -10 m, 13 October 1989, I.G. 27.598/133; adult
 male, B.C. 2004, at -11 m, 13 October 1989, I.G.
 27.598/135; ovigerous female, B.C. 2005, at -6 m,

1 October 1990, I.G. 27.754/179; female, B.C. 2006, at
 -6 m, 1 October 1990, I.G. 27.754/180.

The material is deposited in the collections of the Royal
 Belgian Institute of Natural Sciences, Brussels.

Our material was compared with the type-specimen at
 the Nationaal Natuurhistorisch Museum, Leiden and
 proved to be conspecific.

DESCRIPTION

The carapace (Table 1) is globular, wider than long,
 antero-lateral margins rounded and inflated, postero-
 lateral margins ill defined and gently curved; proximal
 abdominal segments visible from above; carapace enti-
 rely smooth with the regions poorly indicated if at all;
 gastric pits present; an oblique depression in the anterior
 part of the branchial regions (especially conspicuous in
 the females); front deflexed, frontal margin arched with
 a shallow V-shaped median sinus; orbits somewhat ven-
 tral, shallow, broad; supraorbital margins rounded,
 merging into the rounded lateral margins of the front;
 infraorbital border sinuate with a more or less marked
 inner angle; antennulae robust, folded transversely;
 antennae short; basal (second and third) antennal seg-
 ments quadrate, neither reaching the orbit nor the front;
 the fourth and fifth segments freely moveable in the gap
 between the infraorbital angle and the front, subequal
 in length, but the fourth stouter than the fifth; antennal
 flagellum fine with approximatively 17 segments and
 slightly longer than the major diameter of the eye; eye-
 stalk robust, as long as broad; eye small, cornea pig-
 mented black.

Table I.

Hapalonotus reticulatus : measurements in mm, specimens indicated with their B.C.-numbers.

| | adult males | | adult females | | ovigerous females | |
|-------------------|-------------|------|---------------|------|-------------------|-------|
| | 2001 | 2004 | 2002 | 2006 | 2003 | 2005 |
| carapace | | | | | | |
| length | 15.5 | 16.3 | 18.5 | 22.8 | 20.9 | 20.5 |
| width | 18.8 | 19.6 | 22.4 | 27.2 | 24.5 | 24.9 |
| height (approx.) | 11.5 | 11 | 13 | 20 | 14 | 14 |
| left cheliped | | | | | | |
| propodus length | 13.0 | 13.7 | 15.0 | 15.0 | 14.0 | 10.0* |
| propodus height | 7.5 | 8.0 | 8.4 | 8.7 | 7.5 | 5.1* |
| right cheliped | | | | | | |
| propodus length | 11.5 | 12.5 | 13.0 | 16.5 | 13.0 | 15.0 |
| propodus height | 6.5 | 7.0 | 7.3 | 8.7 | 7.3 | 8.0 |
| abdomen | | | | | | |
| length (extended) | 16.5 | ** | 21.5 | ** | ** | ** |
| width | 7.1 | ** | 12.0 | 15.0 | 14.0 | 13.5 |

* regenerated cheliped;

** extended length or width not measured because of the preservation of the specimen in the membranaceous cyst.

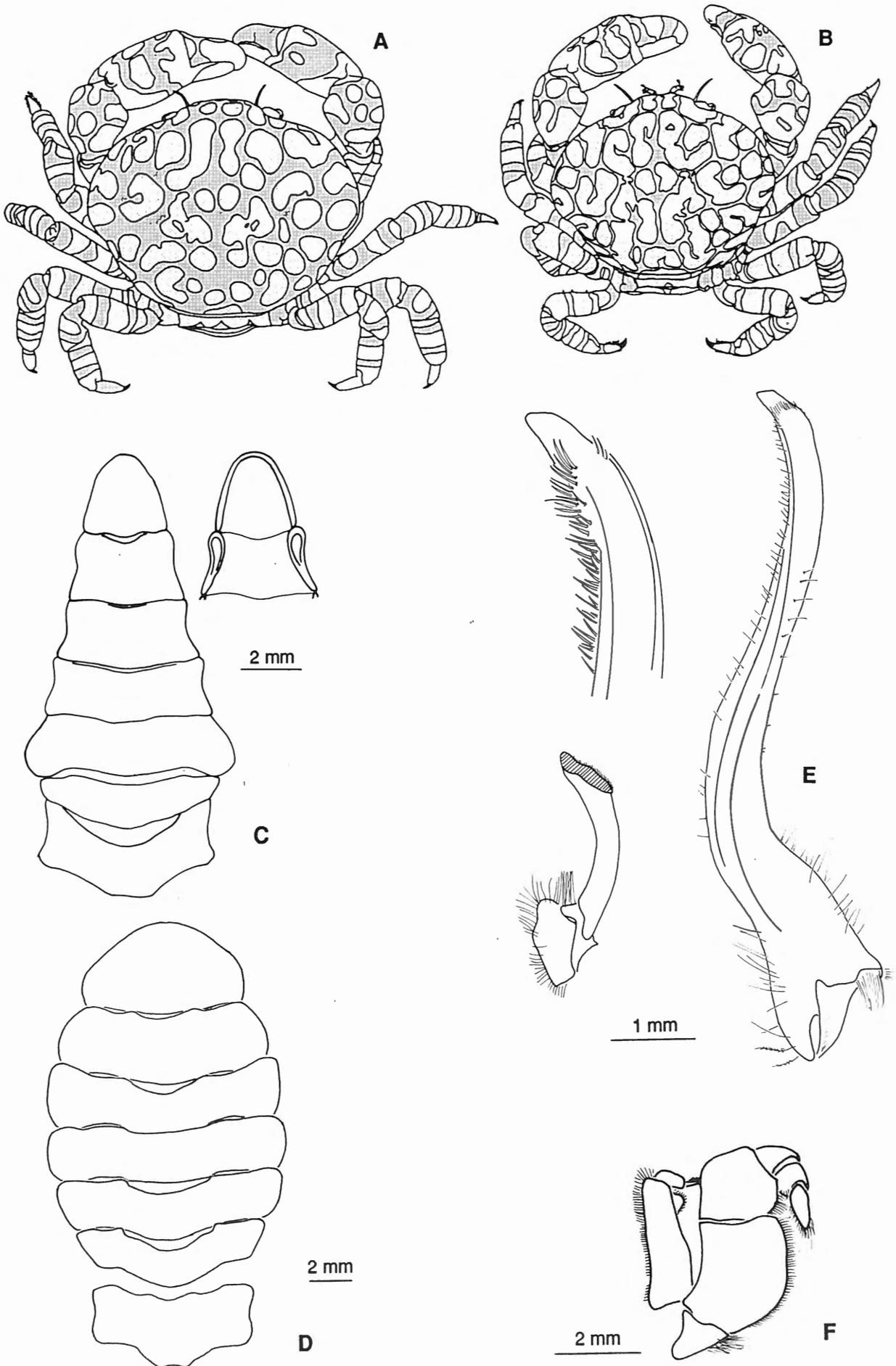


Fig. 5. - *Hapalonotus reticulatus*. A : female; B : male; C : male abdomen; D : female abdomen; E : male pleopods; F : mouthparts.

Buccal cavity quadrate, third maxillipeds (Fig. 5F) parallel, broad, leaving only a narrow gap between them when closed; ischium of 3rd maxillipeds longer than wide with stiff hairs on its inner margin; merus of 3rd maxillipeds little wider than long, external angle rounded; palp robust, articulated at the antero-internal angle of the merus; exognath of 3rd maxillipeds thick, longer than the merus with subparallel lateral margins, totally exposed except for the protuberance on the distal inner margin.

The chelipeds (Table 1) are robust, slightly unequal, one cheliped (usually the left) being stouter; merus slightly projecting beyond the carapace, cross-section triangular, a distal tubercle on the upper margin; ischium and merus not fused, ischio-meral articulation with very limited mobility; carpus swollen, outer surface globular, inner angle produced in a large blunt tooth; propodus with the finger bending downwards; palm very high, rounded dorsally and ventrally, fixed finger and dactylus with 7-8 rounded teeth diminishing in size distally, fingers closing tightly; some macroscopic club-like hairs dispersed on their surface; same reticulated coloration as the carapace.

The walking legs with all segments rounded in cross-section; coxa of last pair elevated above others; thick or clublike hairs more densely distributed on the proximal parts of the dactyli; distinct patches of hair on the proximal inner surfaces of the dactyli of the first and second walking legs, distal part of the dactyli curved, horny and very sharp; dactyli very flexible, resulting in prehensile legs.

The male abdomen (Fig. 5C; Table 1) is divided into seven, moveable segments; third segment widest, filling the gap between the coxae of the last pair of walking legs; telson a little wider than long; locking mechanism of the press-stud type on the 6th segment corresponding with a tubercle on the 5th sternite; thoracic sternum with sutures 4/5 and 5/6 incomplete.

The female abdomen (Fig. 5D; Table 1) is divided into seven broad, moveable segments; 1st segment concealed under the carapace; 4th and 5th segments widest; telson very broad, flattened; long plumose hairs on the external margins of the segments.

Male pleopods (Fig. 5E; Table 1): 1st pleopods relatively slender, sinuous, aperture bordered with a row of subdistal long stiff hairs, tip of pleopod without hairs; 2nd pleopods short and sigmoid. The male genital openings are coxal.

The whole carapace, walking legs and chelipeds are creamy white with brownish red markings forming a banded pattern on the walking legs and a reticulated pattern on the carapace and the chelipeds, the red lines being broader in females (Figs. 5A, B)

The whole body and legs are covered with a barely visible layer of densely packed, very short (30 to 40 μm) translucent hairs, only apparent after rubbing the

carapace with a needle and examining the scrapings under the microscope. This short pubescence makes the crab feel soapy or slimy without the presence of any mucus.

DISTRIBUTION

Ambon (DE MAN, 1879); Banda (BALSS, 1933); Hansa Bay (Papua New Guinea).

DISCUSSION

Malacosoma reticulata was described by DE MAN (1879) on the basis of a single specimen from Ambon, a soft bodied female lacking chelipeds. The generic name *Hapalonotus* was proposed by RATHBUN (1897) as the name *Malacosoma* was preoccupied. DE MAN placed his new genus in the Pinnotheridae though he remarked already on the atypical mouthparts. ALCOCK (1900) assigned *Malacosoma* with some doubts to the subfamily Pinnotherelinae. TESCH (1918) gave a detailed redescription and figures of the holotype. He followed DE MAN in placing the genus in the Asthenognathinae, a heterogeneous subfamily of the Pinnotheridae. BALSS (1933) studied two soft bodied female specimens from Banda, transferred *Hapalonotus* to the family Xanthidae and considered it to be related to *Atergatis* and *Atergatisopsis*. SERENE (1968) (no new record) followed BALSS (1957) in placing *Hapalonotus* in the tribe Zozyimoida, Xanthidae. GUINOT (1978) removed the genus from the Xanthidae sensu BALSS, without assigning it to another family.

Until now only female specimens with a membranaceous carapace were described. This contributed largely to the confusion about the systematic position of the genus. However with the discovery of males (and females) with a calcified body, it is now possible to classify the genus on the basis of a complete set of data. With some caution, we place the genus in the Eumedonidae (sensu ŠTEVČIĆ *et al.*, 1988).

The male pleopods of *H. reticulatus* are of a type present in both the Pilumnidae (sensu GUINOT, 1978) and the Eumedonidae. However the form of the chelipeds, the smooth carapace and chelipeds, the prehensile pereopods and the symbiotic behaviour of *H. reticulatus* are typical for the Eumedonidae. On the other hand some characteristics of *H. reticulatus* are aberrant for the Eumedonidae, i.e. the absence of a well-marked angle between the anterolateral and the postero-lateral margins of the carapace (as in *Rhabdonotus* A. MILNE EDWARDS, 1879), the transversely folded antennulae (as in the Pilumnidae) and the motile ischio-meral articulation of the chelipeds.

Symbiosis *Hapalonotus reticulatus*/*Holothuria scabra*

Each of the six specimens of *Holothuria* (*M.*) *scabra* collected in Hansa Bay was infested by a single individual of *Hapalonotus reticulatus*, either male or female. All crabs were located near the cloaca in the proximal part of the right respiratory tree, being contained within a thick membranaceous cyst (Fig. 6). The occurrence of crabs inside the holothuroid produces a more-or-less noticeable deformation of the right posterior part of the holothuroid when viewed from outside.

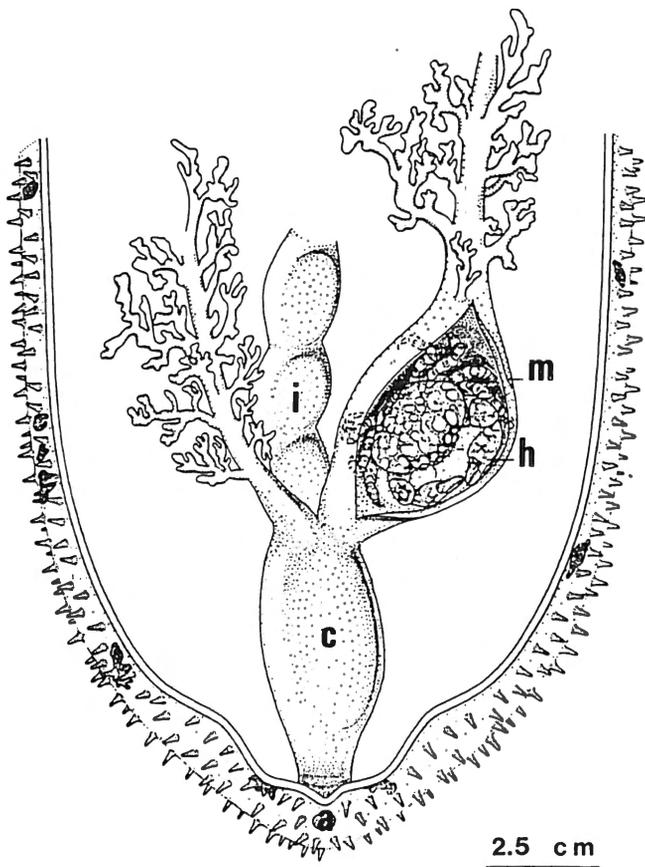


Fig. 6. — *Holothuria* (*M.*) *scabra*. Posterior part showing the position of the crab in the holothurian. a : anus; c : cloaca; i : intestine; h : *Hapalonotus reticulatus* in the right respiratory tree; m : membranaceous cyst.

All collected *H. reticulatus* were adults, two males and four females among which two were ovigerous. No juveniles were observed suggesting that *H. reticulatus* become symbiotic later on in its life cycle.

Given the size of the crab and the crampedness of the cyst in which it is housed, it is unlikely that copulation occurs within the respiratory tree but rather occurs in the cloaca or outside the holothuroid. Aquarium observations showed that the crab can easily pass through the cloacal opening and move quickly on the substrate.

Whatever the place for copulation, males and/or females have to move from one sea cucumber to another for the search of a partner. Owing to the low density of *Holothuria scabra* in Hansa Bay (no more than 3 individuals per 10,000 m²) and as littoral holothuroids do not gather for reproduction, crabs have, most probably, to move over long distances for mating.

Hapalonotus reticulatus presents a vivid, reticulate colour pattern that does not correlate, to human eyes, with the external colour pattern of *Holothuria scabra*. The vivid colour pattern of *H. reticulatus* suggest that it is not a permanent endosymbiont.

The symbiosis between *H. reticulatus* and *Holothuria scabra* is reminiscent of other symbiosis between crabs and holothuroids (WELLS & WELLS, 1961; JONES & MAHADEVAN, 1965; VANDENSPIEGEL & JANGOUX, 1989a). However, this is the first record of the association between an eumedonid crab and a sea cucumber. The exact nature of the relationship between *H. reticulatus* and its host is intriguing. Although *Pinnotheres setnae* CHOPRA, 1931, *Pinnoxodes floridensis* WELLS & WELLS, 1961, *Pinnotheres deccanensis* CHOPRA, 1931, and *Lissocarcinus orbicularis* DANA, 1852 are known to live in holothuroid respiratory trees (CHOPRA, 1931; WELLS & WELLS, 1961; JONES & MAHADEVAN, 1967; TROTT & GARTH, 1970), *H. reticulatus* is the only species, up to now, to induce the formation of a cyst. The cyst, which fits tightly around the crab, suggests long periods of residence and most probably a different relationship than between the above mentioned crabs and their holothuroid host. The relationship is no doubt beneficial to the crab, as shelter and protection is provided. Whether the holothuroids derive any benefit from the crab is doubtful. Even if *H. reticulatus* does not feed upon host tissue, but filters food from water that is passed through the respiratory tree, as described for *Pinnoxodes floridensis* by WELLS & WELLS (1961) and for *Pinnotheres deccanensis* by JONES & MAHADEVAN (1965), it is evident that the crab is detrimental to its host. As stated above, because of its size the crab considerably expands the wall of the respiratory tree, and the holothuroids react to crab presence by forming a membranaceous cyst with a thick wall (thickening due to local accumulation of collagen fibers). This association, therefore, appears to be parasitical.

H. reticulatus co-occurs with other species on holothuroid hosts, which include carapid fishes, other small crabs and shrimps. The most infested host in Hansa Bay was infested by one *H. reticulatus*, one *Carapus* sp., a pair of *Periclimenes imperator* BRUCE, 1967, and a pair of *Lissocarcinus orbicularis*. *Carapus* spp. are endosymbiotic fishes which live in the respiratory tree or occasionally in the coelome of holothuroids (VANDENSPIEGEL & JANGOUX, 1989b), but *P. imperator* and *L. orbicularis* are exosymbiotic, living on the integument of the holothuroid. *L. orbicularis* was observed crawling on the skin of *Holothuria scabra* and usually penetrates the

cloaca of the host when disturbed (VANDENSPIEGEL & MASSIN, personal observation). In other holothuroids, e.g. *Bohadschia argus* JAEGER, 1833, *L. orbicularis* was reported mainly from the respiratory trees (TROTT & GARTH, 1970). Endosymbiotic crab and fish species, occurring together in a single holothuroid host were already reported by TROTT & GARTH (1970) and HABURAY *et al.* (1974).

Acknowledgements

We thank Prof. P.K.L. NG for his very valuable remarks on the content of this article. We thank S. DE GRAVE MSc for critically reading the manuscript and improving upon the English. We thank Prof. J. BOUILLON for providing facilities at the King Léopold III Biological Station of Laing Island (Papua New Guinea) and Mrs. M. KLINKERT for figure 6. Contribution of the "Centre Inter-universitaire de Biologie Marine" (CIBIM). This research was supported by FRFC grants (n° 2.9001.86 and 2.9008.90), the King Léopold III Foundation and the Royal Belgian Institute of Natural Sciences.

References

- ALCOCK, A., 1900. Materials for a carcinological fauna of India. No. 6. Brachyura Catometopa, or Grapsoidea. *Journal of the Asiatic Society of Bengal*, 69 (2) : 280-456.
- BAI, M.M., 1980. Monograph on *Holothuria (Metriatyla) scabra* JAEGER. *Memoirs of the Zoological Survey of India*, 16 (2) : 1-75, 1 pl.
- BALSS, H., 1933. Ueber einige systematisch interessante indopacifische Dekapoden. *Mitteilungen aus dem Zoologischen Museum in Berlin*, 19 : 84-97, pl. 2
- BALSS, H., 1957. Decapoda. 12 Lieferung. VIII Systematik. In *Dr. H.G. BRONNS Klassen und Ordnungen des Tierreichs, 5 Band, I Abteilung, 7 Buch*, GEEST & PORTIG K-G., Leipzig, pp 1505-1672
- BAY, D. & DEMOULIN, V., 1989. The seagrass beds of Hansa Bay (North coast of Papua New Guinea). *Bulletin de la Société Royale Botanique de Belgique*, 122 : 3-17.
- BROUNS, J.J.W.M. & HEIJS, F.M.L., 1985. Tropical seagrass ecosystems in Papua New Guinea. A general account of the environment, marine flora and fauna. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen*, 88 (2) : 145-182.
- CANNON, L.R.G. & SILVER, H., 1986. *Sea cucumbers of Northern Australia*. QLD Museum, Brisbane, i-viii + 60 pp.
- CHERBONNIER, G., 1955. Les holothuries de la mer Rouge. *Annales de l'Institut Oceanographique de Monaco n.s.*, 30 : 129-183, 28 pls.
- CHERBONNIER, G., 1980. Holothuries de Nouvelle-Calédonie. *Bulletin du Muséum national d'Histoire naturelle de Paris, 4e série (2), section A*, 3 : 615-667.
- CHERBONNIER, G., 1988. Echinodermes : holothurides. *Faune de Madagascar*, 70 : 1-292.
- CHOPRA, B., 1931. On some Decapod Crustacea found in the cloaca of holothurians. *Records of the Indian Museum*, 33 : 303-324.
- CLARK, H.L., 1921. The Echinoderm Fauna of Torres Strait. *Publications of the Department of Marine Biology, Carnegie Institution of Washington. Publication*, 214 : 1-223.
- CLARK, H.L., 1946. The Echinoderm Fauna of Australia. *Carnegie Institution of Washington, Publication*, 566 : 1-567.
- CONAND, C., 1989. *Les holothuries aspidochiotes du lagon de Nouvelle-Calédonie : biologie, écologie et exploitation*. Thèse de doctorat, édition ORSTOM : 1-393.
- DE MAN, J.G., 1879. On some new or imperfectly known podophthalmous crustacea of the Leyden Museum. *Notes from the Leyden Museum*, 1 : 53-73.
- DOMANTAY, J.S., 1933. Littoral Holothurioidea of Port Galera Bay and adjacent waters. *Natural and Applied Science Bulletin, the University of the Philippines*, 3 (1) : 41-101, 4 pls.
- FÉRAL, J.P. & CHERBONNIER, G., 1986. Les holothurides. In *Guides des étoiles de mers, oursins et autres échinodermes du lagon de Nouvelle-Calédonie*, Guille, Laboute & Menou (eds.), édition ORSTOM, Collection Faune tropicale, 25 : 55-107.
- GUINOT, D., 1978. Principes d'une classification évolutive des crustacés décapodes brachioures. *Bulletin biologique de la France et de la Belgique*, 112 : 211-292.
- GANTER, P. & JOLLES, G., 1969-1970. *Histochemie normale et pathologique*. 2 volumes, GAUTIER-VILLARS, Paris, 1904 pp.
- HABURAY, K., HASTINGS, R.W., DEVRIES, D. & MASSEY, J., 1974. Tropical marine fishes from Pensacola, Florida. *Quarterly Journal Florida Academy of Sciences*, 37 (2) : 105-109.
- HILL, R.B. & REINSCHMID, D., 1976. Relative importance of propylene phenoxetol in its action as a "preservative" for living holothurians. *Journal of Invertebrates Zoology*, 28 : 131-135.
- HUMES, G., 1980. A review of the copepods associated with holothurians, including new species from Indo-Pacific. *Beaufortia*, 30 (4) : 31-123.
- JANGOUX, M., 1987. Diseases of Echinodermata. III. Agents metazoans (Annelida to Pisces). *Diseases of Aquatic Organisms*, 3 (1) : 59-83.
- JONES, S. & MAHADEVAN, S., 1965. Notes on animals associations. 5. The pea crab *Pinnotheres deccanensis* CHOPRA inside the respiratory tree of the sea cucumber, *Holothuria atra* JAEGER. *Journal of Marine Biology Association of India*, 7 (2) : 377-380.
- MITSUKURI, K., 1912. Studies on Actinopodous Holothurioidea. *Journal of the College of Science, Imperial University of Tokyo*, 29 (2) : 1-284, 8 pls.
- PEARSON, J., 1913. Notes on the Holothuroidea of the Indian Ocean. *Spolia zeylanica*, 9 (34) : 49-101.
- RATHBUN, M., 1897. A revision of the nomenclature of the Brachyura. *Proceedings of the Biological Society Washington*, 11 : 153-167.
- SERENE, R., 1968. The Brachyura of the Indo-West Pacific region. In : *Prodromus for a check list of the non-planctonic marine fauna of South East Asia*. *Singapore National Academy of Science Special Publication*, no. 1 : 33-112.

- SHELLEY, C., 1985. Growth of *Actinopyga echinites* and *Holothuria scabra* (Holothurioidea : Echinodermata) and their fisheries potential (as beche-de-mer) in Papua New Guinea. *Proceedings 5th. International Coral Reef Congress, Tahiti*, 5 : 297-302.
- SLUITER, Ph., 1901. Die Holothurien der Siboga-Expedition. *Siboga-Expeditie*, 44 : 1-142, 10 pls.
- ŠTEVČIĆ, Z., CASTRO, P. & GORE, R.H., 1988. Re-establishment of the Family Eumedonidae DANA, 1853 (Crustacea, Brachyura). *Journal of Natural History*, 22 : 1301-1324.
- TESCH, J., 1918. The Decapoda Brachyura of the Siboga Expedition. II. Goneplacidae and Pinnotheridae. *Siboga-Expeditie*, 39c1 : 149-295, 12 pls.
- TROTT, L.B. & GARTH, J.S., 1970. *Lissocarcinus orbicularis* DANA (Portunidae, Caphyrinae) commensal with *Holothuria argus* JAEGER. A new host record; cohabitation with the pearl-fish *Carapus homei* (RICHARDSON). *Bulletin of marine Science*, 31 : 623-629.
- VANDENSPIEGEL, D. & JANGOUX, M., 1989a. Sur la symbiose entre le pinnothéride *Pinnotheres villosissimus* (Crustacea, Decapoda) et l'holothurie *Actinopyga mauritiana* (Echinodermata). *Vie Marine (hors série)*, 10 : 205-213.
- VANDENSPIEGEL, D. & JANGOUX, M., 1989b. La symbiose entre les poissons Carapidae et les holothuries autour du platier de l'île de Laing (Mer de Bismark, Papouasie Nouvelle-Guinée). *Indo-Malayan Zoology*, 6 : 223-228.
- VANDENSPIEGEL, D. & OVAERE, A., in press. Sur la symbiose entre le crabe *Hapalonotus reticulatus* et l'holothurie *Holothuria (Metriatyla) scabra*. *3rd Colloquium on Echinoderms, Lecce, 9-12 september 1991*.
- WELLS, H.W. & WELLS, M., 1961. Observations on *Pinnaxodes floridensis* a new species of pinnotherid crustacean commensal in holothurians. *Bulletin of Marine Science*, 11 : 267-279.

D. VANDENSPIEGEL
Laboratoire de Biologie Marine
Université de Mons-Hainaut
19, Av. Maistriau
B-7000 MONS, Belgium

A. OVAERE & Cl. MASSIN
Royal Belgian Institute
of Natural Sciences
Department of Invertebrates
29, rue Vautier
B-1040 BRUSSELS, Belgium