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 holothurian *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 membraneous 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.

**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 Janouœx, 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 membraneous 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* Jaegér, 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.
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
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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 & HEUS, 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.

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Fig. 2. – Holothuria (Metriatyla) scabra from Hansa Bay.
Fig. 3. — Holothuria (Metriotyla) 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 : table 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
(Family EUMEDONIDAE DANA, 1853)
(Sensu STEVCIC et al., 1988)
Genus HAPALONOTUS RATHBUN, 1897

HAPALONOTUS RETICULATUS (DE MAN, 1879)

Malacosoma reticulatum DE MAN, 1879: p. 67-68.

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 entirely 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 ventral, 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 segments 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 pigmented black.

Table I.

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<th>adult females 2002</th>
<th>ovigerous females 2003</th>
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<td>8.4</td>
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</table>

* 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 quadrates, 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 thicker, 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-merial 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; 3rd 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 to the carapace. 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 rediscription and figures of the holotype. He followed De Man in placing the genus in the Astenognathinae, 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 *Atergatopsis*. Serene (1968) (no new record) followed Balss (1957) in placing *Hapalonotus* in the tribe Zozymoida, 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 Števčič 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. 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.
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.

*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, *Pinnaxodes 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 *Pinnaxodes 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

![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.](image-url)
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 holothroid host were already reported by TROTT & GARTH (1970) and HABURAY et al. (1974).

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