

## Coral-inhabiting swimming crabs (Crustacea, Decapoda, Portunidae) of the Sudanese Red Sea

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### Abstract

Brachyuran crabs show high species richness and constitute one of the most diverse biotic groups in coral reef communities. The present study examines the taxonomy and ecology (occurrence in particular coral habitats) of swimming crabs from the Sanganeb Atoll (Sudan) known for its high diversity of hermatypic corals. During two expeditions in the years 1991 and 1992, eleven species were collected directly from coral colonies or in baited traps in coral habitats: *Carupa tenuipes* Dana, 1852; *Caphyra fulva* Stephenson & Campbell, 1960; *Portunus* aff. *iranjiae* Crosnier, 1962; *Gonioinfradens paucidentata* (A. Milne-Edwards, 1861); *Thalamitoides quadridens* A. Milne-Edwards, 1869; *Thalamitoides spinigera* Nobili, 1905; *Thalamita* cf. *iranica* Stephensen, 1945; *Thalamita murinae* Zarenkov, 1971; *Thalamita prymna* (Herbst, 1803); *Thalamita quadrilobata* Miers, 1884; and *Thalamita savignyi* A. Milne-Edwards, 1861. *Thalamita murinae*, had been recorded only once before and incompletely described; it is redescribed from the holotype. Together with *Thalamita longifrons* (A. Milne-Edwards, 1869) from the Pacific, it forms a distinct group of species living in complex coral habitats. This *Th. longifrons* group is revised; *Th. spinimera* Stephenson & Rees, 1967 and *Th. yoronensis* Sakai, 1969 are considered as new junior synonyms of *Th. longifrons*. The distribution of swimming crabs across the range of sampled habitats showed a characteristic pattern that did not simply reflect the sampling effort. *Thalamitoides spinigera*, a species endemic to the Red Sea and the Gulf of Aden, clearly preferred dead *Stylophora* habitats. Several hypotheses explaining preferences of particular species for *Stylophora* colonies are discussed. Inhabiting various coral habitats (which for many species can be substituted by rock, rubble or mussel clumps) is characteristic for the subfamilies Carupinae and Thalamitinae, whereas Portuninae are found there occasionally only.

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**Keywords:** Coral habitats; Coral-associated brachyuran crabs; Portunid crabs; Thalamitinae; Portuninae; Carupinae

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### Introduction

Brachyuran crabs show high species richness and constitute one of the most diverse biotic groups in coral

reef communities. Sérène (1972) estimated that more than 500 of the Indo-West-Pacific brachyuran species live in coral reefs. Brachyurans occurring as obligate symbionts in living corals are generally limited to a few genera and species in the families Trapeziidae, Tetraliidae, Xanthidae, and Cryptochiridae (Castro 1976; Castro et al. 2004). Studies on these communities have

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focused either on host specificity of particular genera, usually *Trapezia* Latreille, 1828 and *Tetralia* Dana, 1851, living in hermatypic corals of the families Pocilloporidae and Acroporidae (Patton 1966; Knudsen 1967; Abele 1976; Abele and Patton 1976; Galil and Clark 1988; Castro 2000), or on the crustacean fauna associated with various *Pocillopora* species (Patton 1974; Castro 1978; Coles 1980; Kropp and Birkeland 1981). Species living in corals facultatively, i.e. occurring in living as well as dead corals, between stones and coral rubble, have rarely been studied (Coles 1980). Little is known about the association of crustaceans with *Stylophora* species (Edwards and Emberton 1980).

Several species of swimming crabs (Portunidae) have been reported to occur in coral habitats (Borradaile 1903; Tien 1970; Sakai 1976; Garth et al. 1987; Apel and Spiridonov 1998; Spiridonov 1999). With the exception of Monteforte's (1987) paper, however, there were no special studies on portunid occurrence in coral communities. The present study is part of an investigation of

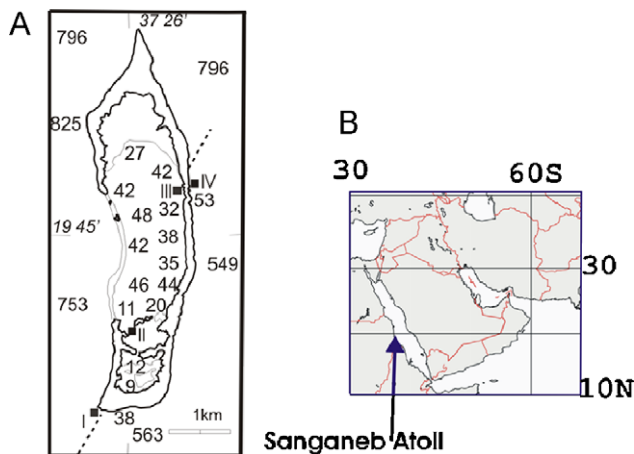
coral-associated brachyurans of the Sanganeb Atoll, which is located off the Sudanese Red Sea coast near Port Sudan (Fig. 1) and known for its high diversity of hermatypic corals (Mergner and Schuhmacher 1985; Schuhmacher and Mergner 1985). Careful collection of crabs from colonies belonging to four coral genera has yielded a variety of brachyurans, including abundant material of swimming crabs. This study examines their taxonomy and occurrence in particular coral habitats.

## Material and methods

During two field expeditions to the Sudanese Red Sea coast in March/April 1991 (Stations 1–54) and September/October 1992 (Stations 100–174), the cryptic decapod fauna was collected in eu- and sublittoral waters using direct hand-collecting, baited traps, and sampling of substrate from different water depths. The substrate types investigated were stones, smaller rocks, live and dead stony corals, and sediment. To facilitate comparisons, almost all localities were chosen close to the transects and test quadrates (TQ I–IV) installed in 1991 for fish census or coral distribution, respectively (Fig. 1A). The distribution of samples among the various habitats is presented in Table 1.

## Collecting of hermatypic coral colonies

Colonies of four of the most abundant branching coral species (*Stylophora pistillata*, *Pocillopora damicornis*, *Seriatothrix hystrix*, *Acropora* sp.) were collected in different localities (outer reef, reef flat, lagoon) and different water depths (1–50 m). Several samples each were taken in five depth intervals: 1–10, 11–20, 21–30, 31–40, and 41–50 m. Living and dead coral colonies of each species were collected separately; for each sample 3–5 living (or dead) colonies of a certain coral species were collected from the substrate and immediately enclosed in plastic containers. Brought to the surface, they were split into small pieces and the Crustacea were sorted out.



**Fig. 1.** Locations of sampling sites and study area. (A) Map of Sanganeb Atoll; Arabic numerals indicate respective depths in m, solid squares with Roman numerals indicate test quadrates, dashed lines indicate transects. (B) Position of Sanganeb Atoll within the Arabian region.

**Table 1.** Distribution of sampling effort (numbers of samples) in various coral and non-coral habitats during German–Sudanese expeditions to the reefs of the Port Sudan area in 1991 and 1992

Depth (m)	Living corals					Dead corals					Rocks, stones	Trap catches
	<i>Stylophora</i>	<i>Pocillopora</i>	<i>Seriatothrix</i>	<i>Acropora</i>	Indet	<i>Stylophora</i>	<i>Pocillopora</i>	<i>Seriatothrix</i>	<i>Acropora</i>	Indet		
00–10	8	9	4	7	1	11	7	1	1	4	9	
11–20	2	3	2	5	1	3	3	0	2	0	2	
21–30	2	0	1	0	0	0	1	0	0	2	0	
31–40	0	0	3	0	0	0	0	0	0	2	0	
41–50	2	0	0	0	0	1	0	0	0	1	0	
Totals	14	12	10	12	2	15	11	1	3	9	11	10

## Direct collecting of Crustacea

Coral-associated crustaceans were collected usually during night dives and picked mostly by hand or forceps.

## Baited traps

In 1992, traps built from plastic tubes by the staff of the Forschungsinstitut Senckenberg (FIS) were baited with fish and set overnight at four different depths (1, 5–10, 30, 50 m) on the reef crest, reef flat, and outer reef.

## Processing of samples and data

All samples were preserved in the field with a 4% solution of formalin and sea water. After the end of the expedition, they were transferred to 70% ethanol and deposited in the collection of the Forschungsinstitut und Museum Senckenberg in Frankfurt on Main (SMF). The portunid specimens were identified and studied morphologically. Scanning electron microscopy was used for investigation of the gonopods of peculiar species. Comparable material from the following museums was also examined: Nationaal Natuurhistorisch Museum, Leiden (RMNH), Zoologisches Museum der Universität Hamburg (ZMH), Zoological Museum of the University of Oslo (ZMO), and Zoological Museum of Moscow University (ZMMU).

The frequency of occurrence of the crabs in each habitat type (e.g. dead and live corals of a particular genus) was statistically compared to the distribution of sampling effort in the same habitat using the  $\chi^2$  test (Zaitsev 1984).

## Presentation of data

The arrangement of genera by subfamily follows [Apel and Spiridonov \(1998\)](#). The synonymies under the species names were restricted to the original descriptions, records from the Red Sea, and references containing the latest synonymy updates. Body size measurements are given in the text as carapace length (CL)  $\times$  maximum carapace width (CW). In listings of general geographic distribution, the author of the first record from the Red Sea is always indicated.

## Abbreviations used

CL = carapace length [mm]

CW = maximum carapace width [mm]

F = frontal width (excluding inner supraorbital lobes) [mm]

FF = female

FO = fronto-orbital width [mm]

Go/1 = gonopod 1 or male pleopod 1

juv = juvenile

MM = male

N-Jetty = northern jetty of the big Port Sudan harbour

ov = ovigerous

P = width of posterior carapace margin [mm]

S-Jetty = southern jetty of the big Port Sudan harbour

Stn = station

T = transect

TQ = test quadrat

## Results

### Family Portunidae Rafinesque, 1815

#### Subfamily Carupinae Paulson, 1875

##### *Carupa tenuipes* Dana, 1852

*Carupa tenuipes* Dana, 1852a: 85. – Dana (1852b, pp. 279–280, pl. 17, figs. 4a–e); Klunzinger (1913, p. 329); Balss (1924, p. 5); Stephenson (1972a, p. 28); Apel and Spiridonov (1998, pp. 172–174, fig. 4, pl. 1): updated synonymy.

*Carupa laeviuscula* Heller, 1862: 520. – Nobili (1906b, p. 189).

#### Material examined

Red Sea, Sanganeb Atoll. 12 juv, Stn 100, no other data; 1 juv, Stn 105, S-Jetty, 1 m, dead *Pocillopora*, 02.10.1992; 1 juv, Stn 110, S-Jetty, 30 m, dead corals, 02.10.1992; 1 juv, Stn 113, S-Jetty, 30 m, dead corals, 27.09.1992; 12 juv, Stn 117, S-Jetty, 14 m, dead *Stylophora*, 27.09.1992; 1 juv, Stn. 133, 1 m, live *Stylophora*, 25.09.1992; 1 juv, Stn 136, no other data; 4 juv, Stn 144, near TQ1, outer reef, 8 m, dead *Pocillopora*, 01.10.92; 2 juv, Stn 152, edge of atoll, 1 m, live *Pocillopora* and *Acropora*, 27.09.1992; 1 FF ov, Stn 159, 1 m, baited trap, night catch, 30.09.1992.

Red Sea, Port Sudan. 2 juv, Stn 172, Wingate Reef, 5 m, dead *Pocillopora*, 20.09.1992; 1 juv, Stn 173, Wingate Reef, Southern Point, 5 m, live *Pocillopora*, 21.09.1992.

#### Size

Juveniles with CL <4 mm. Ovigerous female measures 15.61  $\times$  24.58 mm.

#### Habitat

Shallow subtidal to 80 m, mainly in crevices in coral reefs and rubble ([Monteforte 1987](#); [Apel and Spiridonov 1998](#)). At the Sanganeb Atoll, juvenile specimens occurred at depths between 1 and 30 m on both dead (*Stylophora* and *Pocillopora*) and live coral colonies (*Stylophora*, *Pocillopora* and *Acropora*). Characteristically, they were found in September and October 1992 but not in April and March 1991.

### Distribution

Widespread in the Indo-Pacific, from the Red Sea (Nobili 1906b), East Africa and Madagascar to Japan, Australia, French Polynesia, and Hawaii (Apel and Spiridonov 1998).

### Subfamily Caphyrinae Paulson, 1875

#### *Caphyra fulva* Stephenson & Campbell, 1960

*Caphyra fulva* Stephenson & Campbell, 1960: 97, 104, figs. 1J, 2L, 3I; pl. 4, fig. 2; pl. 5L. – Stephenson (1972a, p. 7, key; p. 25, list); Stephenson (1972b, p. 130); Crosnier (1975, pp. 755–757, figs. 5a–k).

#### Material examined

Red Sea, Sanganeb Atoll. 1 FF ov, Stn 113, S-Jetty, 30 m, dead corals, 27.09.1992; 1 MM, 2 juv, Stn 118, S-Jetty, 18 m, dead *Pocillopora*; 1 MM, 1 FF, 1 juv, Stn 129, N-Jetty, 1 m, dead *Stylophora*, 01.10.1992; 1 MM, Stn 152, edge of atoll, 1 m, live *Pocillopora* and *Acropora*, 27.09.1992.

#### Size

Male 2.44 × 2.62–3.54 × 3.72 mm; female 2.27 × 2.83 mm; female ov 3.78 × 3.87 mm; juvenile 1.46 × 1.64 mm.

#### Habitat

The holotype and the specimens from Madagascar (Crosnier 1975) were collected on alcyonarian hosts, *Xenia umbellifera* and *Heteroxenia fuscescens*. Most *Caphyra* species are thought to be symbionts of Alcyonaria (Crosnier 1975). The present specimens were obtained mostly from dead colonies of *Pocillopora* and *Stylophora* but also from live *Pocillopora* and *Acropora*. These colonies might, however, have had alcyonarian epibionts which in turn hosted *Caphyra*.

#### Distribution

Red Sea (new record), Madagascar, Indonesia (Kei Islands, Sulu Archipelago), Philippines, East Australia (Crosnier 1975).

### Subfamily Portuninae Rafinesque, 1815

#### *Portunus* aff. *iranjae* Crosnier, 1962

*Portunus iranjae* Crosnier, 1962: 61–65, figs. 107, 110–111, 115, 118–119; pl. IV, fig. 2. – Nagai (1981, pp. 30–31, pl. 2D); Dai and Yang (1991, p. 217, pl. 26–4); Spiridonov (1999, pp. 79–80).

#### Material examined

Red Sea, Sanganeb Atoll. Stn 3, 05.04.1991, 1 m, dead *Stylophora*: 1 juv (specimen not extant in the SMF collection).

#### Remarks

The juvenile female resembles *Portunus iranjae* in having seven anterolateral teeth, and in the general pattern of relative tooth sizes. It differs from *P. iranjae*

in the absence of spinuous projections in mesobranchial areas, in this character approaching *P. tenuicaudatus* Stephenson, 1961. The latter species, however, has nine anterolateral teeth and a differently shaped merus of the third maxilliped. With regard to the shape of the front and carapace tubercles the Sanganeb specimen also comes close to *P. guinotae* Stephenson & Rees, 1961 which, however, has six differently patterned anterolateral teeth.

#### Habitat

Mostly coral sand habitats (Spiridonov 1999).

#### Distribution

The species has been described from Madagascar and recorded from the Red Sea (new record), East Africa, Philippines, Japan, off the Chinese coast, Japan, Indonesia, and French Polynesia (Spiridonov 1999).

### Subfamily Thalamitinae Paulson, 1875

#### *Gonioinfradens paucidentata* (A. Milne-Edwards, 1861)

*Goniosoma paucidentatum* A. Milne-Edwards, 1861: 381, pl. 35, fig. 3.

*Thalamita giardi* Nobili, 1905a: 164.

*Goniosoma giardi* (Nobili). – Nobili (1906a, p. 115, pl. 5, fig. 23; pl. 7, fig. 34).

*Charybdis giardi* (Nobili). – Balss (1924, p. 3).

*Charybdis* (*Gonioinfradens*) *paucidentata* (A. Milne-Edwards). – Leene (1938, p. 131, figs. 74–76).

*Gonioinfradens paucidentata* (A. Milne-Edwards). – Apel and Spiridonov (1998, pp. 223–226, figs. 40–41, pl. 7): updated synonymy.

#### Material examined

Red Sea, Sanganeb Atoll. 1 MM, Stn 155, S-jetty, night dive, 10 m, 27.05.92; 1 MM, Stn 161, baited trap, 50 m, night catch, 10.01.92.

#### Size

Male 33.6 × 45.5–43.7 × 57.7 mm.

#### Habitat

Mostly hard substrates from shallow subtidal to 100 m depth (Apel and Spiridonov 1998).

#### Distribution

Red Sea (Balss 1924), Persian (Arabian) Gulf, Gulf of Oman, East African coast, Madagascar, western Indian Ocean islands, Australia, Japan, New Caledonia, and French Polynesia (Apel and Spiridonov 1998).

#### *Thalamitoides quadridens* A. Milne-Edwards, 1869

*Thalamitoides quadridens* A. Milne-Edwards, 1869: 147, pl. 6, figs. 8–15. – Nobili (1906b, p. 212); Stephenson (1972a, p. 52); Sakai (1976, pp. 381–382, pl. 134, fig. 3); Vannini and Innocenti (2000, pp. 286–287, figs. 63, 105): updated synonymy.

### Material examined

Red Sea, Sanganeb Atoll. 2 juv, Stn 26, proximity TQ3, 12 m, live *Acropora*, 09.04.1991; 1 juv, Stn 35, N-Jetty, eastern side, from live *Stylophora pistillata*, 05.04.1991; 1 juv, Stn 45, T3, inner reef, dead *Stylophora pistillata*, 15.03.1991; 2 juv, Stn 52, proximity TQ3, 12 m, dead corals, 01.04.1991; 1 juv, Stn 126, S-Jetty, 20 m, live *Stylophora*, 27.09.1992; 1 juv, Stn 144, TQ1, 8 m, dead *Pocillopora*, 01.10.1992.

### Remarks

Even juveniles (CL about 2 mm) can be distinguished from co-occurring *Thalamitoides spinigera* by presence of the 4th anterolateral tooth and by serration, rather than spines, on the basal segment of the antenna.

### Size

Juveniles  $2.34 \times 3.34\text{--}4.64 \times 7.70$  mm.

### Habitat

In the Sanganeb Atoll area juveniles occurred at depths between 8 and 20 m on both live and dead colonies of *Stylophora*, *Pocillopora* and *Acropora*.

### Distribution

Red Sea (Nobili 1906b), East African coast, Madagascar, Japan, Philippines, Indonesia, Australia, Marshall Islands, Samoa, Fiji, Hawaii (summarised from Stephenson 1972a; Vannini and Innocenti 2000).

### *Thalamitoides spinigera* Nobili, 1905

(Fig. 2)

*Thalamitoides tridens* var. *spinigera* Nobili, 1905b: 403. – Nobili (1906b, p. 213).

*Thalamitoides tridens spinigera* (Nobili). – Balss (1924, p. 5); Zarenkov (1971, pp. 183–184, fig. 82); Neumann and Spiridonov (1999, p. 25).

### Type material

Syntypes: 10 specimens in Museo Regionale di Scienze Naturali, Torino (not seen); Red Sea, western Gulf of Aden (Obock, Djibouti).

### Material examined

Red Sea, Sanganeb Atoll. 3 MM, 1 FF, 1 FF ov, 12 juv, Stn 3, 05.04.1991, N-Jetty, eastern side, 1 m, dead *Stylophora*; 1 FF, 1 FF ov, 18 juv, Stn 8, 06.04.1991, S-Jetty, western side, 1 m, dead *Stylophora*; 5 MM, 1 FF, 10 juv, Stn 12, 04–15.04.1991, S-Jetty, eastern side, 1 m, dead *Stylophora pistillata*; 11 juv, 1 MM, 1 FF, 1 juv, Stn 13, 08.04.1991, N-Jetty, 1 m, dead *Stylophora pistillata*; 1 MM, 1 FF 1 FF ov, Stn 18, lagoon, 13 m, from live *Pocillopora damicornis*, 31.03.1991; 1 MM, 2 FF, 2 juv (SMF 2447 – 1 juv), Stn 46, 25.03.1991, proximity TQ2, 9 m, dead corals; 1 FF, Stn 48, neat TQ 4, 15, dead corals, stones 26.03.1991; 4 MM, 2 FF, 2 FF ov, 2 juv, Stn 51, reef flat, 1 m, dead corals, 30.03.1991; 1 juv, Stn 52, proximity TQ3, 12 m, dead corals, 01.04.1991; 1 FF, Stn 101, S-Jetty, reef crest, 1 m, dead *Stylophora*, 26.09.1992;

1 FF, 4 juv (SMF 24475 – 1 juv), Stn 110, 02.10.1992, S-Jetty, 30 m, dead corals, 02.10.1992; 1 juv, Stn 113, S-Jetty, 30 m, dead corals, 27.09.1992; 2 MM, 3 FF, 10 juv, Stn 115, 1 m, dead *Stylophora*, 26.09.1992; 1 juv, Stn 117, S-Jetty, 14 m, dead *Stylophora*, 27.09.1992; 1 FF, 2 juv, Stn 118, S-Jetty, 12 m, dead *Pocillopora*, 29.09.1992; 1 juv, Stn 124, S-Jetty, 40 m, dead corals, 02.10.1992; 1 MM, 1 FF, 7 juv, Stn 125, TQ1, 14 m, dead *Pocillopora*, 30.09.1992; 7 juv, 3 MM, 1 FF ov, 1 juv, Stn 127, S-Jetty, dead *Stylophora*, 29.09.1992; 7 MM, 2 FF, 1 FF ov, 10 juv, Stn 129, N-Jetty, 1 m, dead *Stylophora*, 01.10.1992; 1 FF, Stn 131, S-Jetty, 4 m, live *Acropora*, 28.09.1992; 1 juv, Stn 136, S-Jetty, 29.09.1992; 1 FF, 1 juv, Stn 138, N-Jetty, edge of lagoon, 1 m, dead *Pocillopora*, 29.09.1992; 1 FF ov, 1 juv, Stn 139, S-Jetty, 30 m, dead *Pocillopora*, 29.09.1992; 6 MM, 3 FF, 6 juv, Stn 154, 1 m, dead *Stylophora*, 25.09.1992; 1 FF, Sanganeb, dead corals; 4 MM, 1 FF, 2 FF ov, 2 juv, Sanganeb, near lighthouse S-Jetty, by E-side, 1 m from dead *Stylophora pistillata*. 1 FF (SMF 21028) Sanganeb Reef, 04.03.1963, I. Eibl-Eibesfeldt coll.

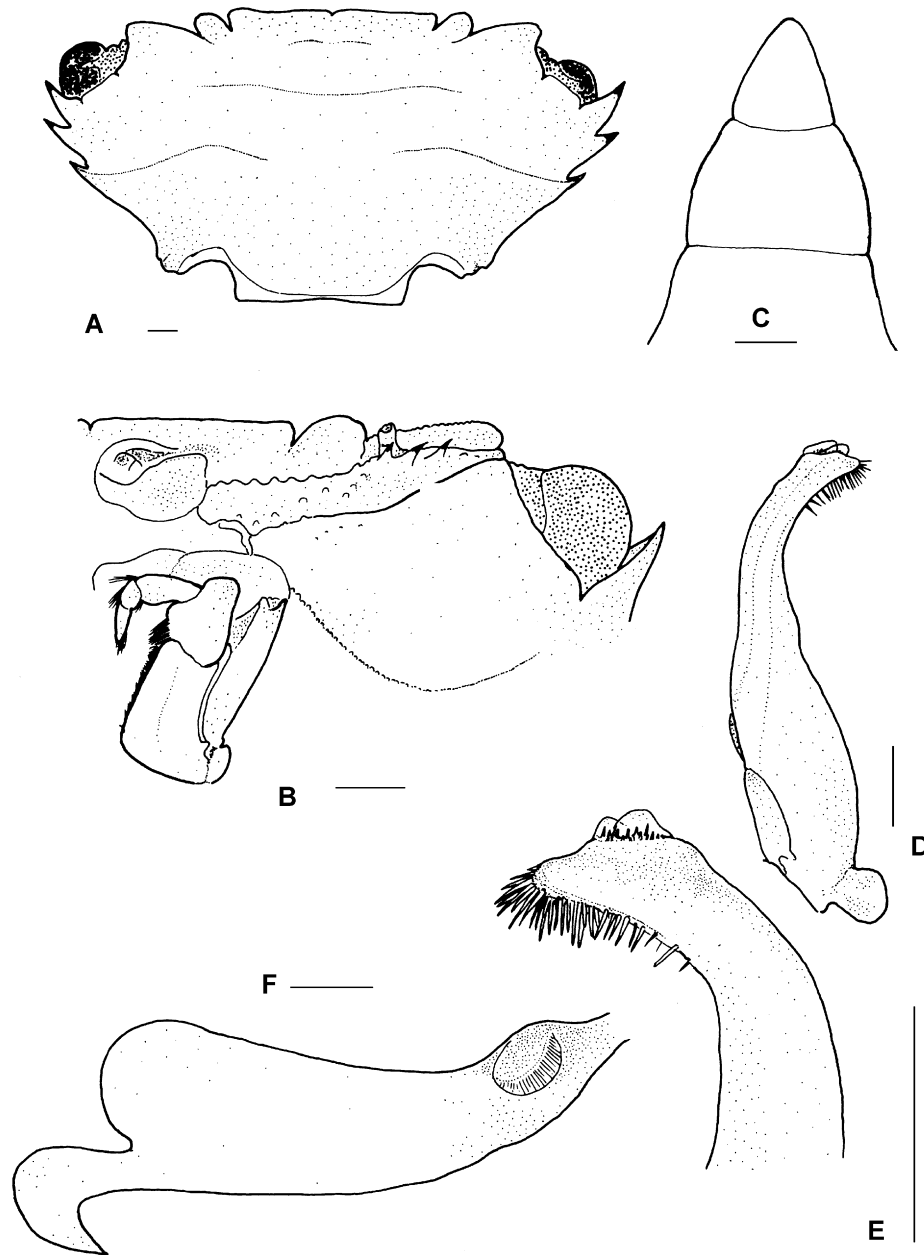
Red Sea, Port Sudan. 8 juv, Stn 166, Wingate Reef, 4 m, dead corals, 21.09.1992; 1 MM, 1 juv, Stn 169, Wingate Reef, inner reef, 5 m, dead *Pocillopora*, 22.09.1992; 1 juv, Stn 171, Wingate Reef, 5 m, live *Pocillopora*, 20.09.1992; 1 MM, 1 juv, Stn 172, Wingate Reef, 5 m, dead *Pocillopora*, 20.09.1992.

Other Red Sea material: 1 FF (SMF 3024), Red Sea, E. Rüppel coll.; 1 MM (SMF 21016), ca. 8 km south of Port Sudan, from *Halimeda*, 11.10.91, H. Salih coll.

Gulf of Aden. 2 MM, 4 FF, 3 FF ov (ZMH K-2366), Djibouti, E. Wache coll.

### Extended diagnosis

Carapace ca. 1.9–2.1 times broader than long, maximum width between second anterolateral teeth, polished. Finely granular carapace ridges present: very closely set, somewhat elevated frontals; uninterrupted mesogastric ridge extending for most of frontal width; sinuous epibranchials. Lateral frontal lobes rounded and clearly separated from medians. Three sharp anterolateral teeth decreasing in size posteriorly, the first (in larger specimens also the second) with serrated outer margin. Rows of granules on subhepatic areas. Basal antennal segment much longer than major diameter of orbit, with a longitudinal line of granules and two to four sharp spines distally. Chelipeds mostly smooth, spines on them sharp and curved; merus with four spines on variably granular anterior margin, subdistal spine largest; carpus with long curved spine on inner face, three spines on outer face, and additional spine on upper face; manus basically smooth, usually with a spine near articulation with carpus and two lateral costae on upper face, each bearing a row of granules and three spines; outer row of spines shifted distally. Meri and propodi of ambulatory legs with



**Fig. 2.** *Thalamitoides spinigera* Nobili, 1905. (A, B, G) Female 10.1 × 20.4 mm, Sanganeb, Stn 125; SMF unregistered. (C–E) Male 12.0 × 22.3 mm, Sanganeb, Stn 125, SMF unregistered. (A) Carapace; dorsal view. (B) Antennular and antennal basal parts, orbit, third maxilliped; ventral view. (C) Abdomen. (D) Right Go/1; abdominal face. (E) Tip of Go/1; sternal face; (F) Female genital sternite. All scale bars = 1 mm.

posterodistal corners forming sharp spines. Natatory legs with propodus nearly as long as merus, armed with five to seven strong spinules on posterior margin. Abdomen of male with segments 2–4 fused; penultimate segment broader than long, its lateral margins strongly converging in distal half. Abdomen of female without keels. Go/1 with distal part rather evenly curved, without clear separation between tip and neck. Female genital opening occupying most of the proximal part of sternite, ovoid, shifted anteriorly.

#### Remarks

*Thalamitoides spinigera* was described by Nobili (1905b) as a variety of *Th. tridens* A. Milne-Edwards, 1869. Stephenson and Rees (1967: 104) synonymised it with *Th. tridens*. Nobili (1906b) had distinguished *Th. tridens* var. *spinigera* from *Th. tridens* by the lateral frontal lobes being rounded (rather than subquadrate) and deeply separated from the medians, and by the basal segment of the antenna bearing strong spines (rather than granules) and serration. In addition, Go/1 in

*Th. spinigera* lacks the clear distinction between the neck and the tip present in *Th. tridens* (compare Fig. 2C with Stephenson and Rees 1967, fig. 38, and with Dai and Yang 1991, fig. 140B-5,4). These differences are constant throughout a large series of specimens, thus necessitating separate species status for the Red Sea form. Larger specimens (CL > 14 mm) show interesting morphological variation, as some of them have a minute tooth between the 2nd and 3rd anterolateral teeth.

#### Size

Male  $6.3 \times 10.74\text{--}14.71 \times 27.59$  mm; female  $5.24 \times 10.01\text{--}15.19 \times 29.56$  mm; female ov  $9.21 \times 17.76\text{--}12.04 \times 23.14$  mm; juveniles  $2.16 \times 2.73\text{--}3.95 \times 7.2$  mm.

#### Habitat

At the Sanganeb Atoll the species occurred at depths between 1 and 40 m; previous records extend the range

down to 55 m. Nearly all specimens (99%) have been collected on dead *Stylophora*, dead *Pocillopora* or other dead corals (Table 2; Fig. 3C); the only previous habitat record indicated occurrence on corals and also on sand with *Lithotamnium* rubble (Zarenkov 1971).

#### Distribution

Red Sea, western Gulf of Aden (Nobili 1905b). The species had been collected in the Red Sea as early as the late 1820ies, but apparently not mentioned in the corresponding account of the Brachyura (Rüppell 1830).

#### *Thalamita cf. iranica* Stephensen, 1945

*Thalamita iranica* Stephensen, 1945: 128–133, figs. 28–30. – Zarenkov (1971, p. 184, 186); Stephenson (1972a, pp. 18–19, key; 48, list); Apel and Spiridonov

**Table 2.** Occurrence of swimming crabs (Portunidae) in various coral habitats sampled at the Sanganeb Atoll and near Port Sudan

Species	Measure	<i>Stylophora</i>		<i>Pocillopora</i>		<i>Acropora</i>	Unidentified	Other samples		Line totals
		Live	Dead	Live	Dead			Stones	Traps	
<i>Thalamitoides spinigera</i>	Ns (f%)	0	10 (67)	2 (16)	5 (45)	1 (8)	8 (89)	0	0	26
	Nsp (p%)	0	211 (79.0)	2 (0.7)	20 (7.5)	1 (0.3)	33 (12.5)	0	0	267
<i>Thalamita savignyi</i>	Ns (f%)	5 (36)	5 (33)	0	1 (9)	0	1 (11)	0	0	12
	Nsp (p%)	11 (38)	16 (55)	0	1 (3.5)	0	1 (3.5)	0	0	29
<i>Carupa tenuipes</i>	Ns (f%)	1 (7)	1 (6.5)	2 (17)	3 (27)	0	2 (22)	0	1 (10)	10
	Nsp (p%)	1 (4.5)	12 (52)	3 (13)	4 (17)	0	2 (9)	0	1 (4.5)	23*
<i>Thalamitoides quadridens</i>	Ns (f%)	2 (14)	1 (7)	0	1 (9)	1 (8)	1 (11)	0	0	6
	Nsp (p%)	2 (25)	1 (12.5)	0	1 (12.5)	2 (25)	2 (25)	0	0	8
<i>Thalamita quadrilobata</i>	Ns (f%)	1 (7)	4 (27)	0	0	0	0	1 (9)	0	6
	Nsp (p%)	1 (17)	4 (66)	0	0	0	0	1 (17)	0	6
<i>Caphyra fulva</i>	Ns (f%)	1 (7)	0	1 (8)	1 (9)	0	1 (9)	0	0	4
	Nsp (p%)	3 (37.5)	0	1 (12.5)	3 (37.5)	0	1 (12.5)	0	0	8
<i>Thalamita prymna</i>	Ns (f%)	0	2 (14)	0	0	0	1 (11)	0	0	4
	Nsp (p%)	0	2 (40)	0	0	0	2 (40)	0	0	5**
<i>Thalamita murinae</i>	Ns (f%)	0	0	0	2*** (18)	0	1 (11)	0	0	3
	Nsp (p%)	0	0	0	2 (66.5)	0	1 (33.5)	0	0	3
<i>Gonioinfradens paucidentata</i>	Ns (f%)	0	0	0	0	0	0	0	2 (20)	2
	Nsp (p%)	0	0	0	0	0	0	0	2 (100)	2
<i>Thalamita iranica</i>	Ns (f%)	0	0	1 (8)	0	0	0	0	0	1
	Nsp (p%)	0	0	1 (100)	0	0	0	0	0	1
<i>Portunus aff. iranjae</i>	Ns (f%)	0	1 (7)	0	0	0	0	0	0	1
	Nsp (p%)	0	1 (100)	0	0	0	0	0	0	1
Column totals		18	247	7	31	3	42	1	3	352

Ns = number of stations at which the species was collected in the respective habitat or traps; f% = frequency of occurrence (in %) in samples from the respective habitat type; Nsp = species-specific number of specimens collected in the respective habitat or traps; p% = species-specific proportion (%) of specimens collected in the respective habitat.

\*Another 12 specimens were collected at Stn. 12, but no habitat data are available for them.

\*\*One specimen collected from live *Acabaria* and *Tubastrea*.

\*\*\*Including one cast molt.

(1998, pp. 249–250, figs. 64, 69–70); Neumann and Spiridonov (1999, p. 23).

#### Material examined

Red Sea, Sanganeb Atoll. 1 juv, Stn 14, reef-plateau, 1 m, live *Pocillopora damicornis*, 29.03.1991.

#### Habitat

Variety of habitats including rocks, coral rubble, *Acropora* and *Pocillopora* corals; shallow subtidal down to 58 m (Apel and Spiridonov 1998).

#### Distribution

Red Sea (Zarenkov 1971), Persian (Arabian) Gulf, Strait of Hormuz, Gulf of Aden, and Red Sea (Apel and Spiridonov 1998).

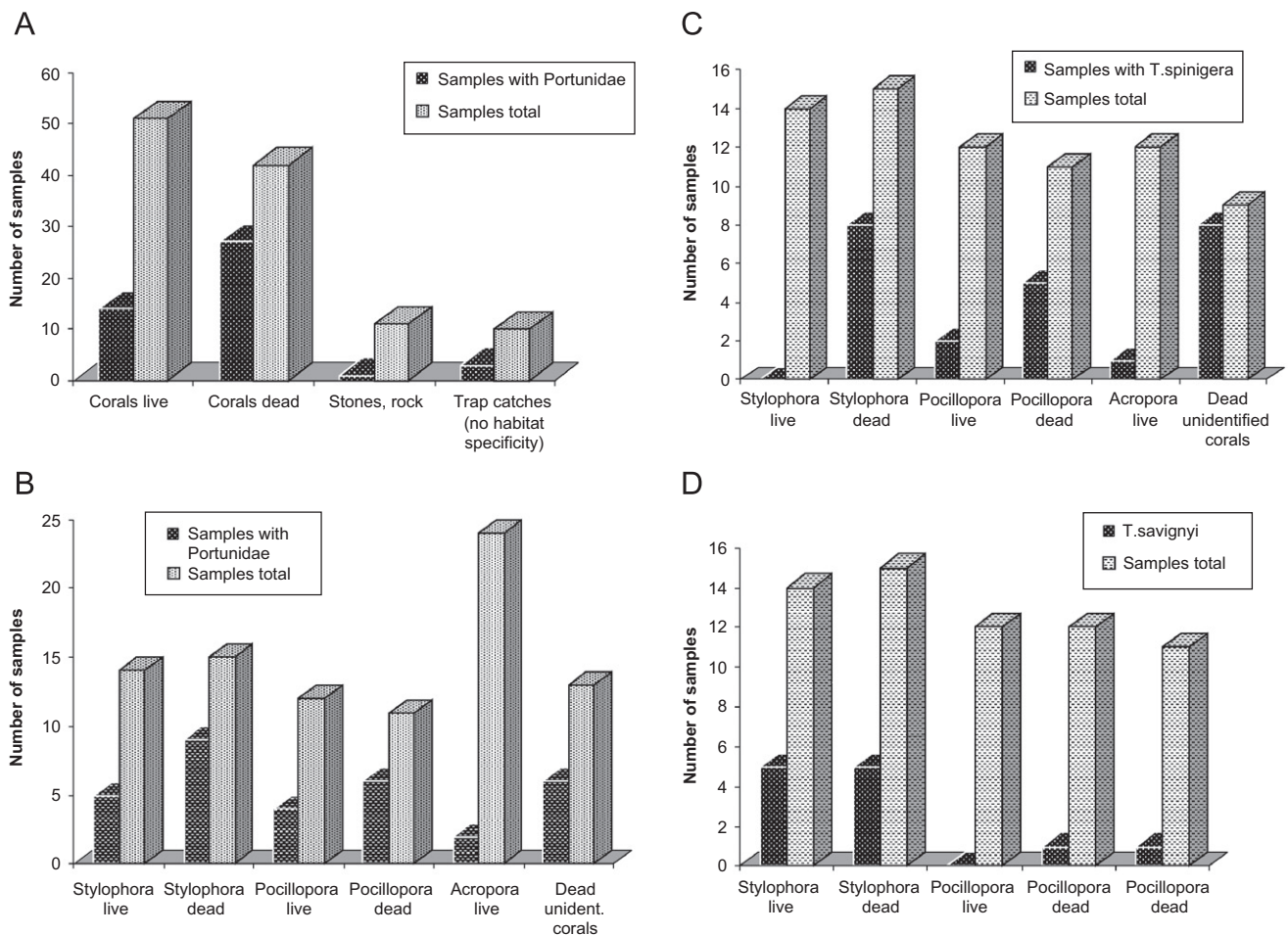
#### *Thalamita prymna* (Herbst, 1803)

*Cancer prymna* Herbst, 1803: 41, pl. 57, fig. 2.

*Thalamita prymna* (Herbst). – H. Milne Edwards (1834, p. 461); A. Milne-Edwards (1861, p. 360); Klunzinger (1913, p. 345, pl. 7, fig. 20); Balss (1924, p. 4); Crosnier (1962, pp. 136–138, figs. 234–236); Wee and Ng (1995, pp. 96–106, figs. 51A–C, 52A–C, 53A–C, 54A–D, 55A, B, 56A–C, 57A–J); Apel and Spiridonov (1998, pp. 257–260, figs. 76, 85); Vannini and Innocenti (2000, p. 285, figs. 62, 67, 104); Poore (2004, p. 429, figs. 136f, 137e).

#### Material examined

Red Sea, Sanganeb Atoll. 1 juv, Stn 3, N-Jetty, east side, 1 m, dead *Stylophora*, 05.04.1991; 1 juv, Stn 12, S-Jetty, eastern side, 1 m, dead *Stylophora pistillata*,



**Fig. 3.** Occurrence of swimming crabs (Portunidae) in samples from various coral habitats. (A) All portunids in various habitats: Frequency of portunid occurrence on dead corals (51.2%) is significantly higher than on live corals (12%; Fisher test value  $F = 16.36$ ,  $p < 0.999$ ). (B) Non-common portunid species (*Carupa tenuipes*, *Thalamitoides quadridens*, *Thalamita quadrilobata*, *Thalamita murinae*, *Thalamita prymna*, *Thalamita iranica*, *Portunus* aff. *iranjae*): Differences between portunid occurrence frequencies on dead *Stylophora* + *Pocillopora* and live *Stylophora* + *Pocillopora* (23.1% and 11.1%, respectively) are non-significant ( $F = 1.39$ ); differences between frequencies on dead + live *Stylophora* and dead + live *Pocillopora* (20.7% and 13.0%, respectively) are also non-significant ( $F = 0.55$ ). (C) *Thalamitoides spinigera*: Occurrence frequency on dead *Stylophora* (53.3%) is significantly higher than on dead *Pocillopora* (18.2%;  $F = 2.75$ ,  $p < 0.095$ ). (D) *Thalamita savignyi*: Differences between occurrence frequencies on live and dead *Stylophora* (28.6% and 26.7%, respectively) are non-significant ( $F = 0.01$ ); differences between occurrence frequencies on dead *Stylophora* and dead *Pocillopora* (26.7% and 9.1%, respectively) are also non-significant ( $F = 1.70$ ).



04–15.04.1991; 2 juv, Stn 50, near lighthouse, 1 m, dead corals, 29.03.1991; 1 juv, Stn 135, S-Jetty, night dive, 10 m, live *Acabaria* and *Tubastrea*, 28.09.1992.

#### Remarks

Although some doubt remains concerning identification of these juvenile specimens, an important diagnostic character, the continuation of the mesogastric ridge up to the anterolateral edge, can be found in specimens as small as the one from Stn 50 ( $5.13 \times 7.71$  mm).

#### Size

Juveniles  $3.54 \times 4.81$ – $5.71 \times 7.34$  mm.

#### Habitat

Mostly rocky shores; frequently recorded from coral-associated habitats (Apel and Spiridonov 1998; Spiridonov 1999).

#### Distribution

Red Sea (Nobili 1906b), and throughout the tropical Indo-Pacific (Wee and Ng 1995; Apel and Spiridonov 1998; Vannini and Innocenti 2000; Poore 2004).

#### *Thalamita quadrilobata* Miers, 1884

*Thalamita quadrilobata* Miers, 1884: 539–540, pl. XLVIII, fig. B. – Alcock (1899, pp. 84–85); Stephenson and Hudson (1957, pp. 349–350, figs. 2G, 3G; pl. 4, fig. 4, pls. 9F, 9M); Stephenson (1972a, p. 18, key; 51, list); Apel and Spiridonov (1998, pp. 260–263, figs. 77–86); Poore (2004, p. 429, figs. 136f, 137e).

*Thalamita admeta* var. *F quadrilobata* Borradaile, 1903: 202–203.

*Thalamita admeta* var. *E intermedia* Borradaile, 1903: 202–203. – Not *Thalamita intermedia* Miers, 1886.

*Thalamita admeta* var. *intermedia* Borradaile. – Nobili (1906b, pp. 208–209): not *Thalamita intermedia* Miers, 1886.

*Thalamita admete intermedia* Borradaile. – Balss (1924, p. 4): not *Thalamita intermedia* Miers, 1886.

*Thalamita borraidailei* Wee & Ng, 1995: 61–62. – Replacement name for *Th. intermedia* Borradaile, 1903.

#### Material examined

Red Sea, Sanganeb Atoll. 1 MM, Stn 3, N-Jetty, eastern side, dead *Stylophora*, 05.04.91; 1 FF, Stn 8, S-Jetty, western side, 1 m, dead *Stylophora*, 06.04.1991; 1 FF, Stn 13, N-Jetty, reef plateau, 1 m, dead *Stylophora pustillata* and stones, 08.04.1991; 1 FF, Stn 38, 08.04.1991, N-jetty, reef-plateau, 1 m, living *Stylophora pistillata*; 1 MM, Stn 54, 16.03.1991.

Red Sea, Port Sudan harbour, in front of Institute of Oceanography, 3–9 m, between stones; 1 MM, Sanganeb, 30.03.1991, near lighthouse, S-jetty, E-side, 1 m from dead *Stylophora pistillata*.

#### Remarks

The species was previously recorded from the Red Sea by Nobili (1906b), under the name *Thalamita admeta*

var. *intermedia* Borradaile (replacement name: *Th. borraidailei* Wee & Ng) which Apel and Spiridonov (1998) have shown to be a junior synonym of *Th. quadrilobata*.

#### Size

Male  $10.0 \times 16.5$  mm; female  $13.38 \times 20.71$ – $15.54 \times ?$  mm (upper end of CW range unknown).

#### Habitat

In the Sanganeb area *Thalamita quadrilobata* is recorded mostly on both dead and live *Stylophora* as well as on rocky substrates, at depths between 1 and 3–9 m. Previous habitat records include rocky shores at depths between 1 and 20 m (Apel and Spiridonov 1998).

#### Distribution

Red Sea (Nobili 1906b), Gulf of Aden, East African coast, Madagascar, Mauritius, Gulf of Oman, Maldives, and Andaman Islands, Philippines, Palau, Australia, French Polynesia (Apel and Spiridonov 1996).

#### *Thalamita savignyi* A. Milne-Edwards, 1861

*Portunus admete* (Herbst). – Savigny (1817, pl. 4, fig. 4); Audouin (1825, p. 83): not *Cancer admete* Herbst, 1803.

*Thalamita admete* (Herbst). – Heller (1861, pp. 355–356); Klunzinger (1913, p. 260, pl. 4, fig. 11); Zarenkov (1971, p. 184): not *Cancer admete* Herbst, 1803.

*Thalamita savignyi* A. Milne Edwards, 1861: 357–358. – Apel and Spiridonov (1998, pp. 267–270, figs. 48, 82–84).

*Thalamita admete* (Herbst). – Paulson (1875, p. 58; partim: description of adults): not *Cancer admete* Herbst, 1803.

*Thalamita admete* var. *savignyi* A. Milne Edwards. – Nobili (1906a, p. 120; 1906b, pp. 20, 206–208).

*Thalamita admete savignyi* A. Milne Edwards. – Balss (1924, p. 4), Stephensen (1945, p. 136; 206, list).

#### Material examined

Red Sea, Sanganeb Atoll. 2 juv, Stn 2, S-Jetty, western side, live *Stylophora*, 06.04.1991; 4 juv, 1 FF, 3 FF ov, Stn 3, N-Jetty, eastern side, 1 m, dead *Stylophora*, 05.04.1991; 1 MM, 1 MM juv, 2 FF, Stn 12, S-Jetty, eastern side, 1 m, dead *Stylophora pistillata*, 04–15.04.1991; 1 MM juv, 3 MM, 1 FF, Stn 13, N-Jetty, 1 m, dead *Stylophora pistillata*, 08.04.1991; 1 MM, 1 FF, Stn 29, near T7, lagoon, 13 m, live *Stylophora*, 31.03.1991; 1 FF ov, Stn 37, S-Jetty, reef flat, east side, live *Stylophora*, 04.04.1991; 1 MM juv., Stn 38, N-Jetty, reef flat, west side, 1 m, live *Stylophora*, 08.04.1991; 1 MM juv, Stn 50, S-Jetty, reef flat, near lighthouse, 1 m, dead corals, 29.03.1991; 1 MM; 1 FF ov, Stn 101, S-Jetty, reef crest, 1 m, dead *Stylophora pustillata*, 26.09.1992; 1 MM, 1 juv, Stn 115, 1 m, dead *Stylophora*,

26.09.1992; 1 MM, Stn 125, 30.09.1992, near TQ1, outer reef, dead *Pocillopora*; 1 FF, 1 juv, Stn 154, 1 m, dead *Stylophora*, 25.09.1992.

#### Remarks

*Thalamita savignyi* is so closely related to *Th. admete* (Herbst) that a number of authors have treated the two names as synonymous. Balss (1924) and Apel and Spiridonov (1998) have presented a set of characters distinguishing the species. It appears, furthermore, that *Th. savignyi* replaces *Th. admete* along both the west and the east coasts of the Arabian Peninsula, as there have not been any reliable records of *Th. savignyi* outside of the Arabian region. Recently we found a collection lot at ZMO containing a large male of this species labeled “Tahiti, 16235 Bonv.?”. According to historical data (M.E. Christiansen, pers. comm. 1999), the person indicated on the label never collected at Tahiti. Therefore, this record from outside the Arabian region must be treated as dubious.

*Thalamita savignyi* differs from *Th. admete* in particular in the development of the 4th anterolateral tooth. Juveniles of *Th. admete* usually lack this tooth. In the present material, a minute but distinguished 4th tooth is present in specimens as small as a juvenile measuring  $4.32 \times 5.96$  mm.

#### Size

Male  $6.0 \times 9.21\text{--}16.94 \times 26.25$  mm; female  $7.09 \times 10.02\text{--}16.52 \times 27.41$  mm; female ov  $10.48 \times 19.63\text{--}16.74 \times 26.09$  mm; juveniles  $2.75 \times 3.52\text{--}5.12 \times 7.56$  mm.

#### Habitat

In the Sanganeb Atoll the species occurred on both live and dead *Stylophora* and sometimes on dead *Pocillopora*, at depths between 1 and 13 m (Table 2, Fig. 3D). Generally, it is known to be associated with hard substrates such as rocks and corals, at depths between 0.5 and 10 m (Apel and Spiridonov 1998).

#### Distribution

Red Sea (Savigny 1817), Gulf of Aden, and Persian (Arabian) Gulf (Apel and Spiridonov 1998).

## Revision of the *Thalamita longifrons* group

### *Thalamita murinae* Zarenkov, 1971

(Figs. 4–7)

*Thalamita murinae* Zarenkov, 1971: 188–187, fig. 85 (carapace, maxilliped III, right cheliped, natatory leg; whereas illustration of basal antennal segment and orbit belongs to another species).

#### Material examined

Holotype: FF (ZMMU Ma 3235), Southern Red Sea, R.V. «Akademik Alexandre Kovalevsky», Stn 575/22A,  $27^{\circ}44'3\text{N}$ ,  $33^{\circ}50.8'E$ , coral reef, 11.11.1963.

Other material: Red Sea, Sanganeb Atoll. 1 MM juv, Stn 107, 50 m, dead corals, 01.10.1992; 1 MM, Stn 118, 12 m, dead *Pocillopora*, 29.09.1992; 1 molt cast, Stn 144, TQ1, 8 m, dead *Pocillopora*, 01.10.1992.

#### Diagnosis

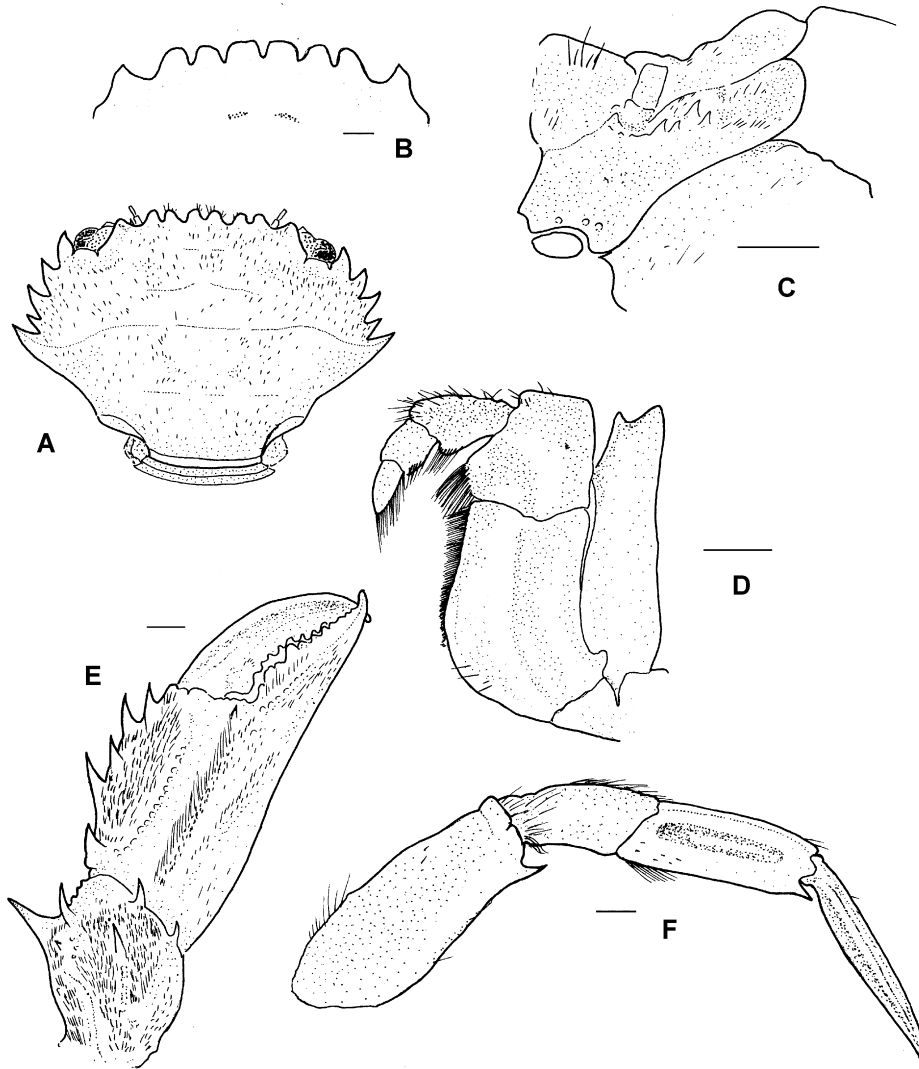
Carapace ca. 1.5 times as broad as long, hairy. Frontal, mesogastric, metagastric, epibranchial, cardiac and mesobranchial carapace ridges present and finely granular; protogastrics inconspicuous. Front (excluding inner supraorbital lobes) about as wide as, or little wider than, posterior margin, somewhat projecting, divided in six lobes, medians and submedians truncated, the former not much produced beyond others. Inner supraorbital lobe of about same width as frontal lobes, truncated. Five anterolateral teeth with sharp tips, fourth smallest but not vestigial, fifth longest but not much longer than others. Basal antennal segment longer than major diameter of orbit, with a short crest bearing three to four spines of different size. Cheliped carpus with an additional spine on upper face; manus with 5 spines on upper face, outer face with upper two costae granular, the uppermost ending in a small spine, inner face with a median granular costa, lower face with squamiform marking. Meri and propodi of ambulatory legs with posterodistal corners forming sharp spines. Propodus of natatory legs broader than dactylus, with posterior margin bearing three spinules, dactylus lanceolate. Lateral margins of male abdomen slightly diverging over proximal two thirds of length, then converging. Abdomen of female with transverse keel on fourth tergite extending for most of segment width. Go/1 rather evenly curved and tapering; a row of 1–12 subterminal spinules beginning shortly behind the tip on lateral face, a row of similar spinules on mesial face starts immediately beneath tip and ends on level of distalmost lateral spinules. Female genital opening located nearly medially, ovoid, bordered laterally by thickened cuticle.

#### Description of holotype

Carapace 1.54 times as broad as long, maximum width between fifth anterolateral teeth, convex. Surface covered with hairs.

Finely granular carapace ridges present, as follows: short, closely set frontals; protogastrics inconspicuous, as groups of sparsely set granules; mesogastric and metagastric slightly sinuous with some interruptions; epibranchials sloping to level of proximal orbital fissure, then straight; a pair of straight cardiac and a pair of mesobranchial ridges.

Front (excluding inner supraorbital lobes) about as wide as posterior margin, somewhat projecting, divided in six lobes, separated by v-shaped incisions: medians broadest, medians and submedians truncated, laterals with antero-lateral corner gently rounded. Inner



**Fig. 4.** *Thalamita murinae* Zarenkov, 1971. (A) Female holotype, ZMMU Ma 3235; modified from Zarenkov (1971). (B) Frontal margin of juvenile male, Sanganeb, Stn 107, SMF unregistered. (C–E) Male, Sanganeb, Stn 118, SMF unregistered. (C) Basal segment of right antenna. (D) Maxilliped 3. (E) Right chela and carpus. (F) Pereopod 3. All scale bars = 1 mm.

supraorbital lobes not wider than frontal lobes, truncated, with distinctly angular antero-mesial corner and rounded antero-lateral corner, supraorbital margin with two fissures, infraorbital border with one fissure, inner infraorbital lobe with broad basis, sharpened at apex, hardly visible in dorsal view.

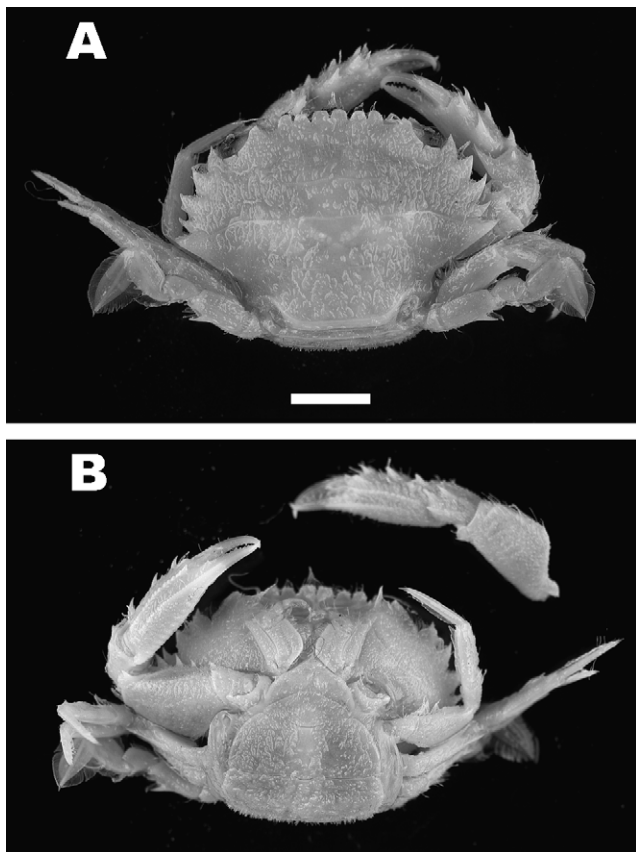
Five anterolateral teeth with sharp tips, first broadest, fourth smallest but not vestigial, fifth longest but not much longer than others. Subhepatic and pterigostomial regions nearly smooth, only few granules near junction with basal antennal segment.

Basal antennal segment (length 2.9 mm) 1.38 times broader than maximum diameter of orbit, ca. 1.75 times wider than maximum diameter of orbit, bearing a group of 3–4 granules along posterior border and a low crest consisting of two large spines and one small spinule between them. Maxilliped III densely granular, endo-

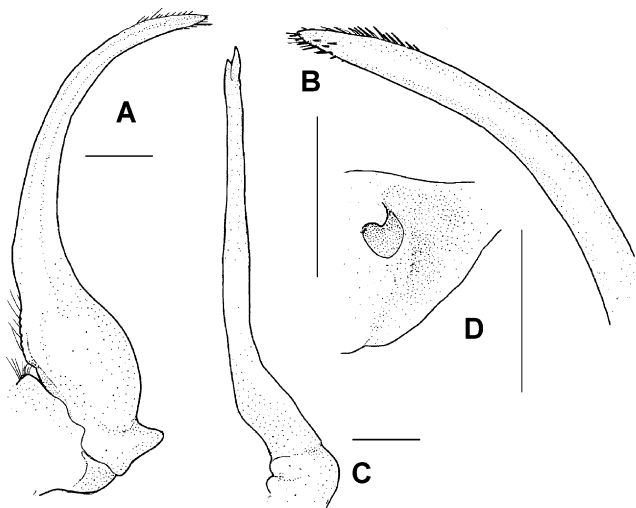
podite with straight anterior edge, subrectangular antero-lateral corner not projecting.

Chelipeds subequal, hairy, ischium with distal spine on anterior margin near articulation with merus; merus short and wide, anterior margin with three typical spines and a distal spinule near articulation with carpus, lower margin with a distant lobule and a spinule near articulation with carpus. Carpus with a granular costa running to a strong curved spine at inner angle; outer face with two costae diverging towards manus and ending in spinules, third (usually outer) spinule is located between them. An additional spine located on upper surface of carpus in mid-line between bases of inner and mesial outer spinule.

Manus with two granular costae on upper surface, each bearing a pair of sharp spines; the usual spine near articulation with carpus. Outer surface with two granular

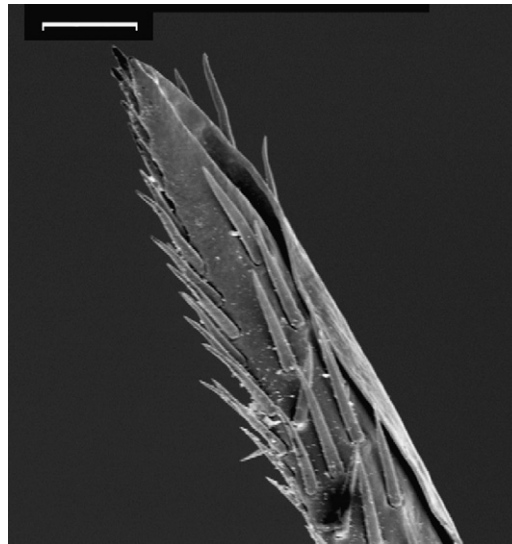


**Fig. 5.** *Thalamita murinae* Zarenkov, 1971; female holotype, ZMMU Ma 3235. (A) Dorsal view. (B) Ventral view. Scale bar = 5 mm.



**Fig. 6.** *Thalamita murinae* Zarenkov, 1971. (A–C) Male, Sanganeb Stn 118, SMF unregistered. (A) Right gonopod 1; abdominal face. (B) Distal part of right Go/1; abdominal face. (C) Right gonopod 2; abdominal face. (D) Female holotype, ZMMU Ma 3235; genital opening. Scale bar = 1 mm.

costae: the upper running to margin between fingers and ending in a spinule, the lower extended along immovable finger.



**Fig. 7.** *Thalamita murinae* Zarenkov, 1971, Sanganeb Stn 118, SMF unregistered; scanning electromicrograph of gonopod 1. Scale bar = 100  $\mu$ m.

Ambulatory legs in general stout, meri ca. 2.5 times as long; at posterodistal corners of legs 2–4 there are stout curved spines, carpi about twice as long as broad, propodi nearly as broad as carpi, their length ca. 2.5 greater than width, with a typical groove along anterior border and a median hollow, posterodistal corner distinctly spiniform; dactyli longer than propodi, with normal grooves, curved at ends.

Meri of natatory legs with a normal spine and a neighbouring spinule at posterior distal corner; propodi of natatory legs broader than dactyli, with three spinules increasing in size distally on posterior border; dactylus lanceolate.

Abdomen hairy, with usual transversal keel on proximal terga, and a keel on fourth tergite extending for more than half of tergite length.

First sternite with angular anterior border of a voluminous sterno-abdominal cavity. Female genital opening located nearly medially on a bend of sternite, ovoid, bordered laterally by thickened cuticle forming a cap that partly covers the opening.

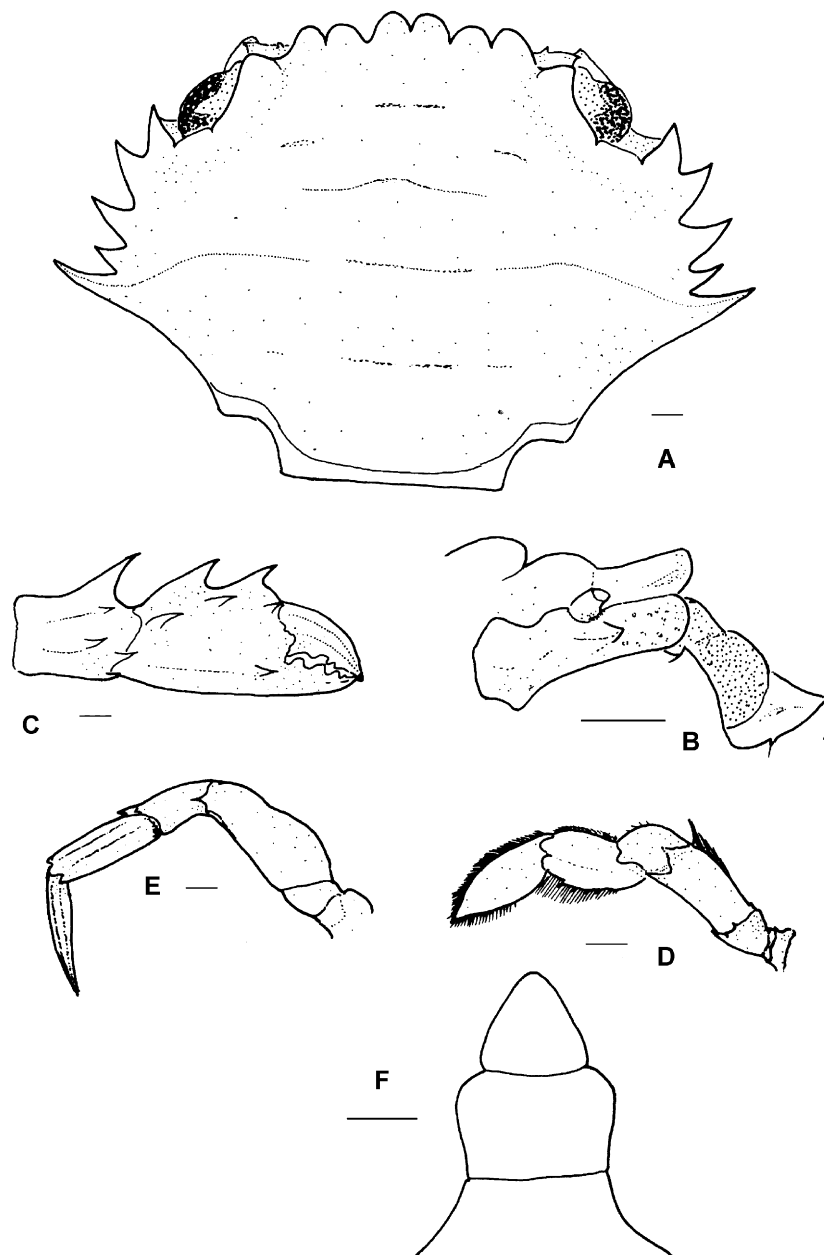
#### Coloration

The holotype (which has been preserved in alcohol for several decades) shows paired brick red spots on meso- and meta-gastric, epibranchial and mesobranchial areas. Debelius (1998) published a photo of a *Thalamita* species (under the name “undetermined species of *Lissocarcinus*”) sitting on a soft coral. This specimen, which may belong to the present species, has a brownish background colour of the carapace, a pair of large bright red spots resembling ink patches which extend to mesogastric, metagastric and epibranchial areas, and a pair of smaller spots on mesobranchial areas.

## Remarks

*Thalamita murinae* was described by Zarenkov (1971) from a female holotype which was later registered in the ZMMU. He named his species after Dr. Galena-Vancetti V. Murina, a benthic biologist who had been working for decades in the Institute for Biology of Southern Seas, Sevastopol, and had been in charge of the benthic collections on board R.V. “Akademik Alexandre Kovalevsky” in the Red Sea in 1961–1964. In the original description some important details were omitted, and Zarenkov’s drawing of the basal antennal

segment shows another species. Therefore, we have provided a redescription of the holotype and a new diagnosis, which includes the characteristics of the male gonopod. The specimens studied show minor morphological variation in the number of spines and spinules on the crest of the basal antennal segment (from two to four; some spinules fused with the large spine), and in the presence of a second additional spine on the upper surface of the larger cheliped carpus in the male. *Thalamita murinae* is most similar to *Thalamita longifrons* (A. Milne-Edwards, 1869).



**Fig. 8.** *Thalamita longifrons* (A. Milne-Edwards, 1869). (A) Female 9.5 × 14.5 mm, RMNH 30208. (B–F) Male holotype 14.0 × 22.0 mm, ZMH K-2573. (B) Basal segment of right antenna, orbit. (C) Left chela and carpus. (D) Right last pereopod; posterior face. (E) Right pereopod 3; posterior face. (F) Abdomen. Scale bar = 1 mm.

### Size

Holotype female 13.0 × 20.0 mm, F 5.5, FO 9.0, P 5.5. Males from Sanganeb 14.0 × 20.5 mm and 4.1 × 6.2 mm, respectively.

### Habitat

In corals between 8 and 50 m depth.

### Distribution

Known from the southern Red Sea only.

### *Thalamita longifrons* (A. Milne-Edwards, 1869), comb. nov.

(Fig. 8)

*Goniosoma longifrons* A. Milne-Edwards, 1869: 155–156, pl. 7, figs. 1–5.

*Thalamita spinimera* Stephenson & Rees, 1967: 95–98, fig. 35, pl.9. – Stephenson (1975, p. 203); Stephenson (1976, p. 24, fig. 1A–E); Chen (1980, pp. 133–134, fig. 16, pl. 4–1).

*Thalamita yoronensis* Sakai, 1969: p. 260, figs. 9a,b. – Sakai (1976, p. 370, fig. 196a, b; pl. 133, fig. 1); Muraoka (1998, p. 36).

### Material examined

Type material. *Thalamita longifrons*: holotype, male, Samoa, Upolu, from the Goddefroy Museum (ZMH K-2573). *Thalamita spinimera*: holotype, male, Mariana Is., Guam, United States National Museum, Washington, DC, # 112/418. *Thalamita yoronensis* (type locality: Amami Islands, Yoron Isld.): It could not be verified where the holotype male had been deposited, but we have seen a specimen collected 3 years prior to publication of the species and donated to the Kanagawa Prefectural Museum by Sakai; this is not labeled as a type, but may be the holotype of *Th. yoronensis*.

Other material. 1 FF juv, Indonesia, Molucca Is., Obi Latoe, Snellius Expedition, 1929–1930 (RMNH 30208, identified as *Thalamita spinimera* by W. Stephenson); 1 FF, Japan (SMF unregistered, T. Sakai collection, on the label only a pencil inscription: “*Thalamita yoronensis*, female S.”).

### Diagnosis

Carapace 1.5–1.6 times as broad as long, sparsely covered with hairs. Granular ridges present on carapace, as follows: closely set frontal; fine protogastrics; mesogastric, metagastric, epibranchial, cardiac and mesobranchial ridges present and finely granular. Front (excluding inner supraorbital lobes) wider than posterior border, projecting, divided in six rounded subequal lobes. Inner supraorbital lobes not wider than frontal lobes, sharpened or rounded. Five anterolateral teeth with sharp tips, fourth smallest but not vestigial, fifth longest. Basal antennal segment longer than major diameter of orbit, with a short crest bearing a single strong spine. Chelipeds finely granular; carpus with an additional spine on upper face; manus with 5 spines on upper face, outer surface

with upper two costae consisting of sharp granules, the uppermost ending in a spine, inner surface with a median granular costa, lower face granular. Meri and propodi of ambulatory legs with posterodistal corners forming sharp spines. Propodus of natatory legs broader than dactylus, with posterior margin bearing three spinules, dactylus lanceolate. Abdomen of male with segments 2–4 fused, penultimate segment broader than long, with lateral margin diverging distally, then rounded. Abdomen of female with a smoothed transverse keel on fourth tergite extending for more than half of segment width. Go/1 rather evenly curved and tapering, markedly narrowing distally; a row of one to twelve subterminal spinules beginning shortly behind tip on lateral face, irregularly set spinules on mesial face located immediately beneath tip, extend to dorsal face. Female genital openings located nearly medially, ovoid, bordered laterally by thickened cuticle.

### Coloration

Carapace has a yellowish-pink background colour with scattered red dots. Granular ridges red. Large, symmetrical red spots on gastric area, epibranchial area (near bases of 4th and 5th anterolateral teeth) and on posterolateral edges; large single red spot in middle of posterior edge; smaller spot on cardiac area (Sakai 1976).

### Remarks

Following the description by A. Milne-Edwards (1869), no additional records of *Goniosoma longifrons* were published for many decades. However, as indicated by the label of USNM lot 48862, cited by Stephenson (1976), the name was sometimes used for identification in museum collections. At the end of the 19th century, *Goniosoma* A. Milne-Edwards, 1861 was made a junior synonym of *Charybdis* de Haan, 1835 (Alcock 1899, p. 47), and *G. longifrons* was thought to belong to *Charybdis*. Moreover, the illustration by Milne-Edwards (1869, pl. 7, fig. 1) is inaccurate in some respects and shows the frontal margin in a form more typical of *Charybdis*. In her revision of *Charybdis*, Leene (1938) recognised that *Charybdis longifrons* resembled *Thalamita* but stated that the only known specimen was no longer in the collection of the MNHN in Paris. From then on, *G.* (or *C.*) *longifrons* A. Milne-Edwards was largely ignored by carcinologists, including Stephenson and Rees (1967) and Sakai (1969) who found ‘unusually’ looking *Thalamita* species and described them as *Th. spinimera* and *Th. yoronensis*, respectively.

Describing species other than *G. longifrons* in the same paper, Milne-Edwards (1869) mentioned that some of his material had been collected in Upolu, Samoa, and lent by Mr. Goddefroy from Hamburg. This note helped us to rediscover the type of *G. longifrons* in the ZMH collection. Comparison of all available type material as well as of the published descriptions and illustrations

has convinced us that *Th. spinimera* and *Th. yoronensis* are junior synonyms of *Th. longifrons*.

The differences between *Th. longifrons* and the most closely related species, *Th. murinae*, are summarised in Table 3.

*Thalamita longifrons* and *Th. murinae* combine to form a very distinct group within the genus *Thalamita*. Their frontal morphology much resembles that of some *Charybdis* species, as does the relative size of the last anterolateral teeth. With regard to gonopod morphology, they have much in common with *Thalamita cooperi* Borradaile, 1903, which belongs to a species group related to *Thalamita woodmasoni* Alcock, 1899 (Vannini 1983). It is also remarkable that *Th. cooperi* has spiniform posterodistal corners of both the meri and propodi of the ambulatory legs. The species of the *Th. woodmasoni* group are similarly characterised by having natatory legs with lanceolate dactyli. Additional spines on the cheliped carpus are known from several *Thalamita* species, in particular *Th. dakini* Montgomery, 1931 (Apel and Spiridonov 1998) and *Th. spinimana* Dana, 1852 (Wee and Ng 1995). Thus, *Th. longifrons* and *Th. murinae* show some rare character states that are scattered within *Thalamita* but share a unique character state in the presence of a distal spine on the outer face of the cheliped manus. Although some other species, e.g. *Th. spinimana*, have a tubercle in place of this spine, it is probably a unique synapomorphy for the *Th. longifrons* species group.

#### Size

*Goniosoma longifrons* holotype male: 14.0 × 22.0 mm (Milne-Edwards 1869 reported 15 × 23 mm); *Thalamita spinimera* holotype male: CL 9 mm; *Th. yoronensis* ?holotype male: 12.7 × 19.0 mm; female (SMF unregistered): CL 9.5, CB 14.5, F 5.0, FO 5.9, P 4.6; female (RMNH 30208): CL 6.4, CB 9.6, F 3.8, FO 4.7, P 3.2. In both females studied by us, the broadened abdomen and the sterno-abdominal cavity are not fully developed.

#### Habitat

The species has been reported from coral reefs and a river mouth (Sakai 1976; Stephenson 1975, 1976); it was also reported to live on alcyonarians (Stephenson and Rees 1967).

#### Distribution

*Thalamita longifrons* is known from the Pacific only: Samoa, Mariana Islands, Xisha Islands, South China Sea, Anamu Islands (Ryukyu), and Maluku (Moluccas) Islands.

#### Habitat preference

The distribution of swimming crabs across the range of sampled habitats shows a characteristic pattern that does not simply reflect the differing sampling efforts. In

spite of intensive sampling of both live and dead corals (Table 1), portunids were never recorded on live *Seriatopora* colonies and were not very common on live colonies of other species. Swimming crabs were present in 64% of all samples from dead coral habitats, whereas only in 27% of samples from live corals (Fig. 3A; Table 2). Portunidae collected from live corals showed some preference to *Stylophora* (Fig. 3A; Table 2), being less frequent on *Pocillopora* and *Acropora*. The most common species, *Thalamitoides spinigera*, clearly preferred dead *Stylophora* habitats where numerous juveniles of this species were found (Fig. 3C; Table 2). Another common species, *Thalamita savignyi*, did not show a clear preference to either living or dead *Stylophora*, but occurred also on dead *Pocillopora* (Fig. 3D). Less common species were rather evenly distributed in various *Stylophora* and *Pocillopora* based habitats (Fig. 3B; Table 2). Direct collection of crabs in stony and rocky habitats brought surprisingly few records of swimming crabs (Fig. 3A), which is probably related to the sampling method. Only specimens visible on the substrate or in crevices can be caught, whereas it is mostly impossible to collect those hidden in crevices of deeper substrate layers such as coral rubble. Crabs caught in baited traps are usually predators and/or large-sized specimens, e.g. *Gonioinfradens paucidentata*, which probably do not show clear preferences to particular habitats.

## Discussion

A peculiar group of swimming crabs belonging to the genus *Caphyra* (subfamily Caphyrinae Paulson) are

**Table 3.** Summary of characters distinguishing *Thalamita longifrons* and *Th. murinae*

Character	<i>Th. longifrons</i>	<i>Th. murinae</i>
Median frontal lobes	Somewhat produced beyond others, rounded	Not produced beyond others, truncated
Submedian frontal lobes	Rounded	Truncated
Inner supra-orbital lobe	Sharpened or rounded	Truncated
Last anterolateral teeth	Markedly longer than others	Somewhat longer than others
Basal antennal segment	With a single spine	With several spines and spinules
Go/1	Tip markedly narrowing, subterminal spinules on lateral and mesial faces merging	Tip not markedly narrowing, subterminal spinules on lateral and mesial faces not merging

known for their symbiotic association with alcyonarian soft corals (Stephenson 1972a; Crosnier 1975). In the present study, *Caphyra fulva* was collected from dead colonies of *Pocillopora* and *Stylophora*. However, with the collecting method used it was not possible to determine whether crabs lived on the stony coral colonies themselves or on the alcyonarians growing on these colonies. Alcyonarians using dead stony coral colonies as a substrate were commonly observed in the Sanganeb area. It is most probable that small *Caphyra* crabs found in the present study used them as hosts.

Swimming crabs of other subfamilies have repeatedly been reported from coral-associated habitats, but few studies have provided further details. Stephenson (1972a), Monteforte (1987), Wee and Ng (1995), Neumann and Spiridonov (1999), and Spiridonov (1999) presented summaries of habitat data for particular species which were based on various sources, including field observations and literature records.

In total, c. 20 species of *Thalamita* and 7 species of *Charybdis* (subfamily Thalamitinae) can be classified as “rock, rubble and reef dwellers” according to the simple ecological classification provided by Galil and Vannini (1990) and Neumann and Spiridonov (1999). These species also occur more or less frequently in coral habitats. *Carupa* (Carupinae) and *Thalamitoides* (Thalamitinae) were reported as mostly reef inhabitants; this is confirmed by the present study. Besides this general characterisation, there are some studies considering portunids in coral habitats which are more regionally focused and based on intensive sampling effort.

When studying crabs along the transect crossing a fringed and a barrier reef at Moorea (French Polynesia), Monteforte (1987) found 73 species only 5 of which belonged to the Portunidae. *Portunus granulatus* (H. Milne Edwards) occurred there occasionally; *Carupa tenuipes* Dana, a cavity species, was found at only one station but quite abundantly; *Thalamita admete* (Herbst) and *Thalamita crenata* Rüppell were relatively uniformly distributed across the reefs; whereas *Thalamita pilumnoides* Borradaile occurred mostly in deeper parts of both the fringing and the barrier reef close to the channel between them (Monteforte 1987, tab. 1, fig. 3).

Amongst the portunids living in the Persian (Arabian) Gulf area, several species show a clear preference to corals (Apel and Spiridonov 1998). The repeatedly mentioned species *Carupa tenuipes* was often recorded in crevices in coral reefs and in the coral rubble. Others included *Gonioinfradens paucidentata* (generally on reefs and rocks); *Thalamita iranica* (*Acropora*, coral rubble and rocky bottom); *Th. prymna* (“in a dense stand of *Acropora*”, seagrass meadow inside the coral reef); *Thalamita rubridens* Apel & Spiridonov, a species with close affinity to *Th. prymna* (generally on reefs and rocks); and *Th. savignyi*, commonly hiding among dead corals. All species except *Th. rubridens* occur in coral

habitats of the Sudanese Red Sea. *Thalamita quadrilobata*, which was rather common among corals in the present study, was found in the Gulf of Oman mainly in rocky habitats (Apel and Spiridonov 1998). It must be noted, however, that the Sudanese waters of the Red Sea are known for their high diversity and dense substrate coverage of stony corals, whereas the Gulf of Oman area is characterised by low diversity and scattered coral growth (Schuhmacher and Mergner 1985; Pilcher and Alsuhaibany 2000; Pilcher et al. 2000).

Thus, observations suggest that most *Thalamita* species are facultative inhabitants of coral reef habitats but also live on rocky bottom or mussel clumps. Monteforte (1987) supposed further that the swimming crabs could be characterised as predaceous/carnivorous but as playing only an inferior role in the trophic network of a high island reef complex. In the Sudanese Red Sea, on the other hand, there appears to be a peculiar assemblage of reef-dwelling portunids partly shared with other areas of the Arabian region. It includes *Thalamitoides spinigera* (endemic to the Red Sea), *Thalamita savignyi* (endemic to the Arabian region), *Carupa tenuipes*, *Thalamitoides quadridens*, and is supplemented by actively moving, large-sized predators, e.g. *Gonioinfradens paucidentata* and *Thalamita prymna*. The present data indicate also that at least the dominant species of this assemblage have certain habitat preferences within the reef environment. They live mostly on dead corals belonging to specific taxa.

The common occurrence of several species of portunids on dead and live *Stylophora* (Fig. 3B–D) is of particular interest. Edwards and Emberton (1980) investigated the crustacean community associated with living *Stylophora* colonies in the Sudanese Red Sea. They found a positive correspondence not only between the living space of a coral and the diversity and abundance of coral-associated crustaceans, but also a negative relationship between the branching index or ‘openness’ (i.e. the living space protected by coral branches) and crustacean diversity and abundance. Their data regarding *Stylophora* colonies suggest that a similar pattern should be found in an interspecific comparison between other coral species. Portunids may prefer *Stylophora* as a micro-habitat, rather than *Pocillopora* and other coral species, because the colonies of the former are less ‘open’ and thus provide greater protected space for their inhabitants. On the contrary, *Seriatopora* and *Acropora* colonies show more open branching, which possibly allows larger predators to penetrate deeper among the branches.

In the case of *Thalamitoides spinigera*, the reasons for exclusive occurrence of crabs on dead *Stylophora* colonies remains unknown, but some explanations can be suggested. Firstly, some extra-metabolites of living corals may be generally poisonous to facultative



crustacean inhabitants. This is supported by the finding that living stony corals are mostly inhabited by a very limited number of specialised crab species such as trapezoids, tetraliids or the xanthid crabs of the genus *Cymo* de Haan.

Secondly, *Th. spinigera* may be excluded from living *Stylophora* by interspecific fighting with other crabs as is often observed in limited space in artificial conditions (Hazlett 1971). The most abundant crabs on living *Stylophora* found in the present study were the species of *Trapezia*, especially *Trapezia guttata* Rüppell, 1830. Usually, a coral colony houses only one pair of adult *Trapezia* (Edwards and Emberton 1980), which indicates that at least intra-specific fighting occurs. On the other hand, there are no data showing agonistic behaviour by these crabs towards other species.

Thirdly, *Th. spinigera* may be attracted to dead *Stylophora* by specific food items. Dead corals provide substrate for a number of marine organisms some of which could be functioning as food source for portunids in general and *Th. spinigera* in particular. *Thalamitoides* species have very long chelae with spoon-shaped dactyli that indicate a feeding mode different from the generalist predaceous habit typical for many of the Portunidae (Schäfer 1954; Monteforte 1987). The above three hypotheses all merit further investigations.

Data on species in the *Thalamita longifrons*/*Th. murinae* group revised in the present study indicate their preference for a coral environment. However, the details of this association are unclear: *Th. longifrons* is known from an array of habitats including alcyonarians, whereas *Th. murinae* was found in particular on dead corals (where there also could be alcyonarian growth) and on dead *Pocillopora*. Infrequent records of these species may be explained by their habit of hiding in corals. It has to be generally noted that the swimming crabs “are active and intelligent, escaping capture with cleverness” (Borradaile 1903, p. 199), so that there are few, if any, effective methods to collect them reliably in complex habitat such as reefs and especially coral rubble.

In contrast to the Thalamitinae and *Carupa*, the species of Portuninae are only occasionally found on corals. Small-sized *Portunus* species probably are not uncommon in the reef areas but occupy a rather specific habitat, e.g. sand flats and canals between reef constructions, burrowing in sand during the daytime and being active at night (M. Apel, pers. comm. 1999; V. Spiridonov, pers. observ. in Egypt 2000). Even though Portunidae is considered as one of the well-studied tropical brachyuran families, symbiotic Caphyrinae, Thalamitinae that hide in complex reef habitats, and Portuninae that burrow in sand may be much more diverse (in terms of species number) than known so far.

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