

The Dwelling Cavity of the Coral Crab *Latopilumnus tubicolus* (Crustacea, Pilumnidae) in *Tubastraea micranthus* (Scleractinia, Dendrophylliidae)

HELMUT SCHUHMACHER

Lehrstuhl für Hydrobiologie, Universität GHS Essen
Postfach 10 37 64, D-4300 Essen, Fed. Rep. Germany
Tel. (0201) 183-3777 Telex 8579091 unie d

Received February 13, 1987; Accepted April 5, 1987

Abstract

The recently described crab *Latopilumnus tubicolus* lives exclusively on the azooxanthellate coral *Tubastraea micranthus*, common on Indo-West Pacific coral reefs. At night, crabs collect plankton and detritus from the coral surface; during the day, each crab hides in a tubelike cavity. An advantage to the coral is not known. The dwelling-cavity originates from the central corallite of a branch which has a directive function according to the monopodial growth pattern of *T. micranthus*. After occupation of the central corallite by a young crab, the adjacent polyp takes over the function of elongation of the branch. Subsequently deposited coenosteum and the former side polyp grow past the central corallite, circumvallating the crab. Its dwelling-cavity may elongate to 6 cm due to the growth of the surrounding skeleton. Proliferation of the calcifying tissues (especially near the tube's opening) is suppressed by the crab which moulds the tube's wall with its thick, knobby chelae. *T. micranthus* is considered as a particularly predictable and longevous habitat for a coral crab. A comparison of the presently known modes of coral crab habitation in their hosts reveals three types, characterized by *Latopilumnus*, *Hapalocarcinus* and *Cryptochirus*.

Keywords: dwelling-cavity, coral crab, *Latopilumnus tubicolus*, *Tubastraea micranthus*, monopodial growth, Hapalocarcinidae, coral galls

1. Introduction

Living reef corals accommodate a number of brachyuran associates. Few of these associates have specialized to create pits or cavities in the host coral to hide themselves. Well known in this respect are the numerous hapalocarcinid species (e.g. Fize and Serène, 1957). The xanthids *Domecia acanthophora* and *Cymo* sp. cause growth anomalies which provide shelter in *Acropora* colonies — the first one in the Caribbean (Patton, 1967), the latter in the Indo-West Pacific (Eldredge and Kropp, 1981).

Recently, the pilumnid crab *Latopilumnus tubicolus* was described (Türka and Schuhmacher, 1985). It lives on the azooxanthellate (sensu Schuhmacher and Zibrowius, 1985) coral *Tubastraea micranthus* (Ehrenberg), which is noteworthy for its contribution to the framework of Indo-West Pacific reefs (Schuhmacher, 1984, Wellington and Trench, 1985). The manner in which *Latopilumnus tubicolus* forms its dwelling cavity differs from all known modes of coral endobionts.

2. Location and Methods

In situ observations were made at Sumilon Island (Philippines) near the field station of the Silliman University, Dumaguete, in May 1981. In order to pursue further studies in the laboratory, coral skeletons from this region were obtained from coral traders in Cebu (Philippines) and Germany.

Lapidary saws were used to cut the coral branches in order to lay open the dwelling cavities and to reveal their position in relation to the corallites. The inner surface of the cavities was inspected with the aid of scanning electron microscopy.

3. Observations of the Living Animals

The host coral *T. micranthus* mostly forms two-dimensional arborescent colonies which reach a height of up to 1 m near Sumilon Island (up to 2.5 m at Palau, Wellington and Trench, 1985). The colonies are conspicuous for their black tissue. During the day the crabs hide in cavities (dwelling tubes) the dark openings of which, hardly detectable in the living coral, are 6–12 mm wide. At night the crabs range over the surface of the coral to collect plankton and detritus adhering to mucus on the coral surface (Fig. 1). The vermilion crabs contrast strongly with the black-green or dark brown colour of the expanded polyps when illuminated by a torch. Disturbances cause the crabs to move quickly around the coral stem but not necessarily to retreat into their dwelling tubes.

4. Observations on Dead Coral Colonies

The arborescent colony of *T. micranthus* forms according to a strict monopodial growth pattern. The central corallite of a branch extends at a rate of about 4 cm/yr (Wellington and Trench, 1985), its side-buds, however, are of finite growth and barely rise more than 1 cm above the surrounding coral surface. Due to this different mode of growth the directive polyp is not only slightly larger than the lateral polyps, but, also, its protruding wall forms a particularly deep tube compared to the lateral calices.

The apical part of a branch is formed almost solely by corallites, since, initially, the coenosarc does not deposit more than a thin veneer of a loose, porous calcareous network. It is only after 2–3 years (i.e. 5–10 cm below the tip of the branch) that an appreciable amount of coenosteum forms around the central corallite and between its side-buds. Later on, the continuous deposition of coenosteum thickens the stem and the branches in such a manner that, in basal portions, the core of the corallites constitutes no more than a minor part of the skeleton. The colonization of a coral colony by *L. tubicolus* was not observed directly. The mode of formation of the dwelling tubes is, rather, inferred from the analysis of some 30 tubes of different length of occupancy by a crab. The main features are as follows:

Width of the cavities ranges from 4 to 9 mm and their length from 12 to 60 mm. When crabs were found to lodge at the tip of a branch they had always occupied the central calice (Figs. 4–6). These specimens were all subadult, fitting into the skeletal tube of the directive polyp. With the exception of septal structures which are no longer developed, the corallite appears hardly modified by its inhabitant at this stage.

By way of contrast, the dwelling tubes in the basal region of the colony open laterally from amidst the coenosteum (Fig. 2). These cavities accommodate adult specimens (length of carapace approx. 7 mm). Longitudinal cuttings reveal these tubes also to originate from the central corallite. These tubes pass through coenosteum only, they are mostly bent and can reach a length of 6 cm. Intermediate stages, such as when cavities open at the blunt tip of a short thickened branch (Fig. 5), allow the different forms to be linked in one general scheme (see below).

The insides of recently invaded calices are still covered by remnants of tissue, although the polyp's essentials such as oral disc, column and mesenteries, no longer exist. The exothecal tissue (coenosarc) continues to calcify on what has been before the theca of the calice. Septa and other architectural structures inside of the calice, however, are no longer produced. Lining

tissue is absent from the interior of older dwelling tubes; the bare wall is remarkably smoothed. SEM images show signs of abrasion and a penetration of the skeleton by numerous pores $2\mu\text{m}$ wide. Abraded skeletal dust was found on the outer side of the chelae of the crab (see Fig. 4 in Törka and Schuhmacher, 1985). Homotremid and acervulinid Foraminifera (Fig. 18) and — rarely — calcareous red algae may develop thin crusts on the inner wall. Near the margin of the tube uncommonly structured aragonite layers can be found (Figs. 21–23). They are most likely deposited by appendages of the coenosarc between the coenosteal matrix which, from time to time, expand onto the tube's wall.

In dried coral specimens, only about 30% of the dwelling tubes still contained crabs; the rest had probably escaped. Some of the latter could be found dried up near their cavities. From their positions, it is clear that the crabs enter the tube sideways.

Figure 1. Crab among expanded polyps at night.

Figure 2. Dwelling-cavity ending laterally near the base of a coral stem.

Figure 3. Bifurcation due to the blocking of the former end polyp by *L. tubicolus*.

Figure 4. Two examples of central corallites invaded by *L. tubicolus*.

Figure 5. Longitudinal section through a side branch with exceptionally reduced growth (mainly increment of coenosteum) containing a *Latopilumnus*-tube in the place of the central corallite. Scale=mm.

Figure 6. Recently invaded end polyps with slightly thickened wall. Scale=mm.

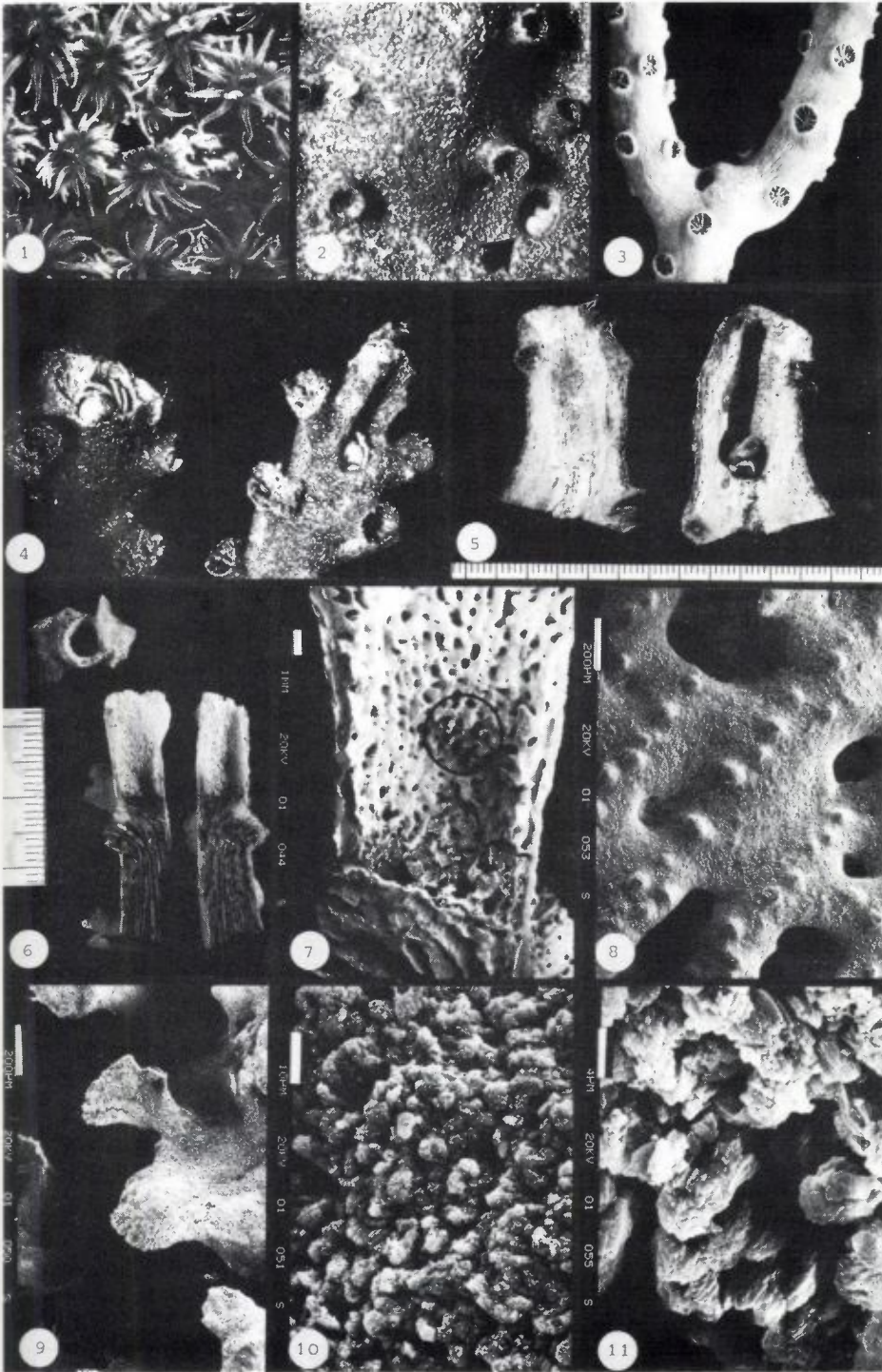
Figure 7. Inner surface of the longitudinally sectioned tube of Fig. 6. Note widening of the tube's base where the crab has nestled in; bar = 1 mm. The following Figures show details of this tube.

Figure 8. Smoothly developed coenosteal network at the distal part of the tube, bar = $200\mu\text{m}$.

Figure 9. Coenosteal protrusions from the encircled area of Fig. 7, moulded by the crab during deposition; bar = $200\mu\text{m}$.

Figure 10. Close-up of the flattened skeleton in the center of Fig. 9; note the lack of erosion marks; bar = $10\mu\text{m}$.

Figure 11. Close-up of the center of Fig. 8; bar = $4\mu\text{m}$.



5. Discussion and Conclusions

It is concluded from the size of the many observed *L. tubicolus* crabs that they settle on the coral well after metamorphosis at a subadult stage. In contrast to *Cryptochirus* and other hapalocarcinid crabs, the young "colonists" do not avoid the polyps, but, rather exclusively settle on them. Since they are within the size range of coral prey, it is likely that a still unknown mechanism or behaviour precludes their capture by polyps.

The different developmental stages of the dwelling tubes allow a reconstruction of the mode by which *L. tubicolus* becomes accommodated on *T. micranthus*. It is crucial for the crab to invade the central polyp of a monopodium; lateral polyps lack the necessary growth potential. It is possible that the crab selects the central polyp because of its size (thereby assuring an ample shelter space). The occupation of a polyp leads to its extinction. When the central polyp is unable to continue its growth and directive function, the next

Figure 12. Subsequent skeletal deposits near the base of a tube which had been used for a longer time than that of Fig. 7; bar = 400 μ m.

Figure 13. Close-up of a skeletal bar from Fig. 12; bar = 40 μ m.

Figure 14. Surface of the bar of Fig. 13 with abraded debris and perforated by boring organisms; bar = 2 μ m.

Figure 15. Longitudinal section through a dwelling-tube, details of which are presented in Figs. 16-23.

Figure 16. Part of the inner wall abraded by the crab; bar = 200 μ m.

Figure 17. Detail of Fig. 16 with abraded debris and marks of bio-corrosion; bar = 4 μ m.

Figure 18. Partly abraded layer of acervulinid foraminifers near the end of the tube; bar = 100 μ m.

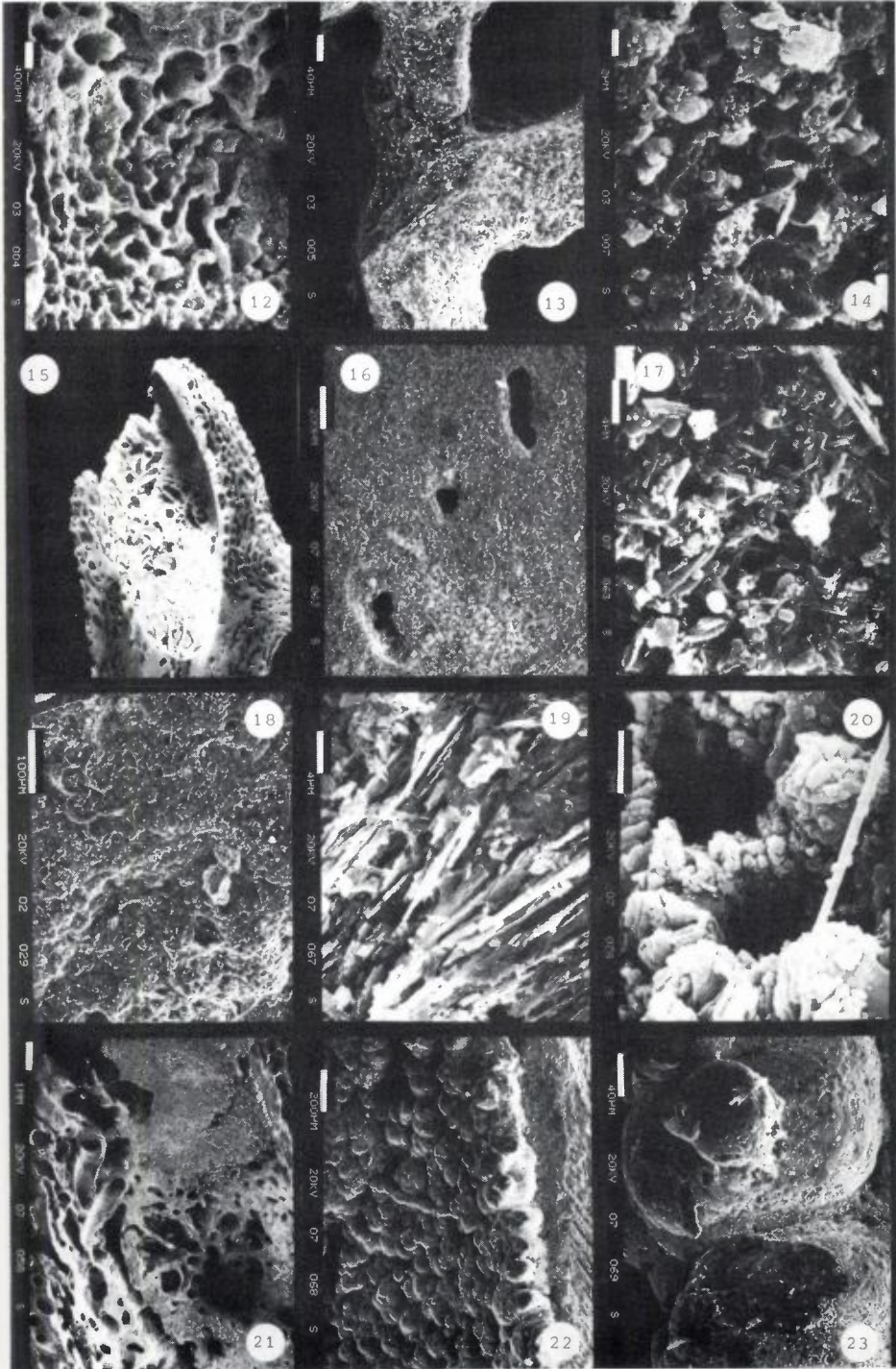
Figure 19. Small area with etched aragonite fibers, probably exposed regularly to the respiratory current of the crab; bar = 4 μ m.

Figure 20. Penetrated and corroded surface of a smooth part, abraded by the crab; bar = 2 μ m.

Figure 21. Section of the tube with an unusual lining of the wall by a layer of sphaerulitic aragonite deposited after erosion by the crab (upper right quarter of the picture); bar = 1 mm.

Figure 22. Subsequently deposited sphaerulitic aragonite near the opening of the tube of Fig. 21; bar = 200 μ m.

Figure 23. Detail of Fig. 22; bar = 40 μ m.



lateral polyp takes over and develops past the crab's lodging (sometimes two side polyps start continuous growth resulting in a bifurcation of the branch — Fig. 3). Simultaneously, the skeletal deposits of the (exo)thecal tissues of the former end polyp become overlain by the coenosteum which thickens the corallum further. In these cases, the opening of the tube is directed to the side of the branch or stem. Sometimes, when the end polyp of a small side branch has been invaded, no other polyp takes over the directive function (unlimited elongation) and the branch extends only slowly by the increment of coenosteum (Fig. 5).

It is characteristic of *T. micranthus* that the coenosarc forms a network several mm deep in the skeleton. The coenosarc gradually fills the primary cavities of the coenosteum with skeletal deposits and is also capable of regenerating tissue injuries at the coral's surface. Thus, the coenosarc tends to recover the inner wall of the dwelling tube, especially at its margin, and to close its opening by the deposition of aragonitic layers (Figs. 9,12,22).

An impending, potentially fatal, reduction of the tube's diameter is counteracted by frequent movements of the crab within the tube and through its opening. The thick chelae, ornamented with numerous pustules and knobs, are instrumental in moulding the tube's wall. Most likely not only proliferation of the calcifying tissue is suppressed by rubbing (Figs. 8,9), but, also, the slight widening of the basal part of the tube is achieved in this manner (as far as it is necessary for the growing crab). Abrasion of the wall is facilitated when its surface is weakened by boring organisms (Figs. 14,17,20). Colonization of old tubes by encrusting organisms, such as foraminifers and serpulids, may probably become a nuisance to the crab.

The few *in situ* observations of the living crabs showed them to collect food from the whole colony. Since most colonies do not accommodate more than one crab (and only rarely two or three), it must be assumed that individuals extend their excursions to neighbouring colonies to meet conspecifics for mating.

The nocturnal activity of *L. tubicolus* corresponds to the general activity pattern of xanthid crabs (including *Trapezia* and other coral-inhabiting species). With regard to the host coral *T. micranthus*, it is particularly advantageous for *L. tubicolus* to evade visual predators, since in the day-light the red crabs could easily be detected among the widely-spaced polyps, which are retracted at that time.

Pilumnid crabs have succeeded in exploiting a variety of niches. The association with *T. micranthus* assures *L. tubicolus* a very stable habitat. The large size of *T. micranthus* colonies warrants a sufficient supply of food. Furthermore, the host coral is superior to many of the common coral species competing for space on the reef, and is not affected by the corallivore *Acanthaster* (Wellington and Trench, 1985). Its skeletal strength ranks it among the most resistant corals with regard to mechanical stress (Schuhmacher, 1984). *T. micranthus* is also a long-lived coral due to the high regeneration potential of its tissue, which minimizes negative consequences of superficial lesions such as necrotic effects and invasions by boring sponges. It is likely that these traits enable the crabs to live on their host colonies for many years. Thus, the growth potential of *T. micranthus* is both advantageous and hazardous to *L. tubicolus*: a continued production of skeletal material is necessary to build up the shelter for the growing crab, simultaneously it bears the risk of imprisoning the latter.

L. tubicolus is now compared with other crabs known to dwell inside living corals. Such dwelling places are not formed by boring. In this respect, three principal modes are distinguished by which crabs (a) create shelter in their host corals, (b) simultaneously avoid being encysted, and (c) maintain continued access to food. The following scheme is drawn from the literature (Fize and Serène, 1957; Patton, 1967; Takeda and Tamura, 1979, 1980; Eldredge and Kropp, 1981). and from personal observations of all mentioned species in their natural habitat:

1. *L. tubicolus* is — besides the anomuran *Paguritta corallicola* (Lewinsohn, 1978) — the only decapod endobiont which settles in a polyp. Due to the fact that it establishes its cavity in a branching coral of monopodial growth an elongated tube arises. The tube is several times the length of its inhabitant and is the largest cavity of all crustacean endobionts. The tube is temporarily vacated during feeding.
2. *Hapalocarcinus* (on Pocilloporidae), *Pseudohapalocarcinus* (on *Pavona*), but also the non-hapalocarcinid *Domecia acanthophora* and *Cymo* sp. (on *Acropora*) induce, upon settlement, a locally and temporarily restricted hypertrophy of the skeleton (which, nonetheless, follows a specific growth pattern). The resulting basket-or pocket-like part of the corallum rapidly encloses the crab as a "gall". In this way,

Hapalocarcinus and *Pseudohapalocarcinus* become totally imprisoned and dependent on a food-source inside. Only the xanthid crabs keep an exit open to feed regularly outside. *Fungicola utinomii* also belongs to this type, although, its hood-like shelter is not the concerted deposit of numerous tiny polyps, but a local excrescence of a *Fungia* disc.

3. The hapalocarcinid *Cryptochirus* spp., *Pseudocryptochirus* spp. and *Favicola* spp. live in small pits at the surface of (mainly) faviid corals. These pits, just fitting the crab in size, form by the growth of the surrounding skeleton. This growth, in contrast to the foregoing types, can be retarded after formation of the pit, resulting in a depression in the colony. Accumulation of detritus and sediments, and even damage to the coral tissue, may result, which, however, can be of nutritional advantage to the crab. Especially in meandroid corals, one small pit is able to influence the groove pattern of the whole colony. Since the coral does not protect the crab from all sides, in crabs under consideration the anterior part of the carapace is developed as an operculum which closes the opening of the pit. Crabs obtain food particles from outside without leaving the retreat.

This rough categorization cannot obscure the fact that most of the biology of the coral crabs, as well as of the nature of their associations, still remains to be investigated. As far as corals are concerned, there is no evidence that they benefit from association with any of the crabs. On the contrary, not infrequently dead areas around the dwelling pits arise and allow boring sponges to enter and algae to settle.

The associations between crabs and corals are conventionally grouped under the heading symbiosis in the broad sense of De Bary: they were specified as a kind of "Karpose" by Matthes (1978) and as inquilinism by Zann (1980). But *L. tubicolus* and other crabs do also exhibit parasitic traits. The terminology does obviously not match the complexity of symbiotic associations.

Acknowledgements

The field studies were supported financially by the Deutsche Forschungsgemeinschaft. Logistic support at the Silliman University, Dumaguete, was generously provided by Prof. Dr. A. Alcalá. The Corallcenter, Wülfrath-Neuiges, kindly supplied *Tubastraea* skeletons for laboratory studies. The subject matter was discussed in its early stage with Prof. Dr. Holthuis and R. Türkay. Y. Paran helped with the English.

REFERENCES

- Eldredge, L.G. and Kropp, R.K. 1981. Decapod crustacean-induced skeletal modification in *Acropora*. Proc. Fourth Int. Coral Reef Symp., Manila 2: 115-119.
- Fize, A. and Serène, R. 1957. Les Hapalocarcinidés du Viet-Nam. *Arch. Mus. Hist. Nat. Paris* 7(5): 1-202.
- Lewinsohn, C. 1978. Bemerkungen zur Taxonomie von *Paguritta harmsi* (Gordon) (Crustacea Decapoda, Anomura) und Beschreibung einer neuen Art der gleichen Gattung aus Australien. *Zoolog. Meded.* 53: 243-252.
- Matthes, D. 1978. Tiersymbiosen und ähnliche Formen der Vergesellschaftung. G. Fischer Verl., Stuttgart, New York, 241 pp.
- Patton, F.K. 1967. Studies on *Domecia acanthophora*, a commensal crab from Puerto Rico, with particular reference to modifications of the coral host and feeding habits. *Biol. Bull.* 132: 56-67.
- Schuhmacher, H. 1984. Reef-building properties of *Tubastraea micranthus* (Scleractinia, Dendrophylliidae), a coral without zooxanthellae. *Mar. Ecol. Prog. Ser.* 20: 93-99.
- Schuhmacher, H. and Zibrowius, H. 1985. What is hermatypic? *Coral Reefs* 4: 1-9.
- Takeda, M. and Tamura, Y. 1979. Coral-inhabiting crabs of the family Hapalocarcinidae from Japan. I. Three species obtained from mushroom coral, *Fungia*. *Bull. Natn. Sci. Mus. Tokyo (A)* 5: 183-194.
- Takeda, M. and Tamura, Y. 1980. Coral-inhabiting crabs of the family Hapalocarcinidae from Japan. II. Genus *Pseudohapalocarcinus*. *Proc. Jap. Soc. Syst. Zool.* 18: 54-59.
- Türkay, M. and Schuhmacher, H. 1985. *Latopilumnus tubicolus* n. gen. n. sp., eine neue korallenassoziierte Krabbe, die Bildung einer Wohnhöhle induziert. (Crustacea: Decapoda: Pilumnidae). *Senckenbergiana marit.* 17: 55-63.
- Wellington, G.M. and Trench, R.K. 1985. Persistence and coexistence of a nonsymbiotic coral in open reef environments. *Proc. Natl. Acad. Sci. USA.* 82: 2432-2436.
- Zann, L.P. 1980. *Living Together in the Sea*. T.F.H. Publ., Neptune, NJ, 416 pp.