

The Adaptive Functional Structure of Mucus-Gathering Setae in Trapezid Crabs Symbiotic with Corals

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Abstract

Coral-inhabiting trapezid crabs feed on the lipid-rich coral mucus. The mucus may have acted as an important element in selection effecting coral-crustacean symbiosis, which prompted specialized feeding mechanisms. These mucus-gathering structures are described, illustrated and compared with similar structures in other coral symbiont decapods.

Keywords: coral-crustacean symbiosis, Trapeziidae, mucus-feeding, dactylar setae

1. Introduction

Among the environmental accommodations of Crustacea, symbiosis plays a very significant role, evident from the fact that this group has more symbioses with members of other phyla and with each other than any other major group of invertebrates. Among the symbiotic crabs, Trapeziidae, one of three brachyuran families that are obligatory symbiotic, are associated with corals. Species of the genus *Trapezia* Latreille, are obligate symbionts of pocilloporid corals, the closely allied *Tetralia* Dana, and *Tetraloides* Galil, are symbionts of *Acropora*, whereas *Quadrella* Dana, and *Calocarcinus* Calman, occur typically on octocorallians. *Hexagonalia* Galil, was reported from Stylasteridae — the first record of symbiosis between a trapezid crab and an hydrozoan (Galil, 1986c).

The Trapeziidae range from the Red Sea and the east coast of Africa across the Indo Pacific to the west coast of North America. Some species are nearly as widely distributed as the family as a whole.

Borradaile (1902) reported on the association of members of the Trapeziidae with madreporarian corals and alcyonarians and was the first to remark on some of the modifications in their structure in correspondence to their habitat. Recently, more punctilious collection and observation procedures have made possible the gathering of precise data, and the specificity of the obligate association has been clarified (Garth, 1964; Knudsen, 1967). Recent work has added new genera and species (Takeda and Galil, 1980; Galil and Lewinsohn, 1983; Galil, 1983, 1986a,b,c). As a result, this family of small and obscure crustaceans is now acknowledged as one of the most successful and ubiquitous components of the tropical marine fauna.

Corals secrete mucus as protection against sedimentation or drying (Patton, 1976; Pascal and Vacelet, 1981). These secretions are believed to play a part in the food chain: mucus may serve as a means of trapping detritus and phytoplankton, mucus can also directly serve as a source of food, as it contains amounts of lipids, ranging from 20–90% of dry weight (Benson and Muscatine, 1974; Ducklow and Mitchell, 1979; Daumas and Thomassin, 1977; Daumas et al., 1982; Stimson, 1986).

The feeding behaviour of *Trapezia* was first described by Knudsen (1967) and corroborated by Patton (1974) and Castro (1976). The crabs' actions consist of scratching and poking the coral polyps with the dactyls of the walking legs to stimulate mucus production. The mucus extruded by the polyp is gathered on specialized dactylar setae by brushing the coral tissues and transferred to the mouth. Examinations of stomach contents (Barry, 1965; Knudsen, 1967; Preston, 1971; Patton, 1974; Stimson, 1986) indicated that the studied *Trapezia* and *Tetralia* species fed on coral mucus and on detritus settling on it. Wolodarsky (1979) reported that *Trapezia* incorporated material from radioactively labelled coral mucus and tissues. Stimson (1986) wrote that the crabs' presence induces the host corals to produce and release fat-filled packets on which the crabs feed. Odinetz-Collart and Forges (1985), working in Polynesia, wrote that the predominance of symbionts can be related to the inducement of hypersecretion of coral mucus due to physical disturbance.

According to Coles (1980), the number and biomass of symbionts are proportional to the area of the host living tissue. A decline in the symbiotic crustaceans' reproductive activity in damaged corals, a pronounced decrease in their lipid reserves (Glynn et al., 1985) followed by their immigration, attest to the crabs' dependence on the host mucus as principal food source.

2. Materials and Methods

Examination of extensive collections representing the entire Indo-Pacific region, provided opportunities to study large series of trapezid specimens. The specimens upon which this study is based are deposited in the following museums: Allan Hancock Foundation, University of Southern California (AH), American Museum of Natural History (AMNH), British Museum (Natural History) (BM), Bernice P. Bishop Museum (BPBM), Naturhistorisches Museum Wien (NHMW), National Museum Singapore (NMS), National Science Museum, Tokyo (NSMT), Northern Territory Museum, Darwin (NTM), Museum National d'Histoire Naturelle, Paris (PM), Rijksmuseum van Natuurlijke Historie, Leiden (RMNH), Natur-Museum Senckenberg, Frankfurt (Senck. M.), Tel Aviv University Zoological Collections (TAU), National Museum of Natural History, Smithsonian Institution (USNM), Western Australian Museum (WAM).

The taxa examined were chosen to represent as wide a range as possible of dactylar structural diversity.

Specimens examined with scanning electron microscope (SEM) were mounted on stubs with double-sided sticky tape, dried (critical point method) and then coated with carbon and gold-paladium.

3. Mucus-Gathering Structures in Trapezid Crabs

In *Trapezia* (Fig. 1), the ambulatory dactylis are highly setose. The distal end of dactyl is spoon-shaped posteriorly and the upper surface is composed of several rounded ridges, distally bevelled thus forming a corrugate surface. A dense tuft of setae encircles the tip. The posterior margin of the dactyl is set with transverse rows of short comb-like spinules proximally (Fig. 2), and with stout spines arranged in two parallel rows distally. Lateral margin of dactyl bears a row of long, plumose setae. The shape and number of spines and setae are species specific. Two species of *Trapezia*: *T. cymodoce* (Herbst) and *T. intermedia* Miers, have their chelipeds covered with a dense tomentum.

In *Tetralia* (Fig. 3), the ambulatory dactyls are short and stocky, with a cornute tip. The posterior distal surface of the dactyl bears plain setae arranged distally in discontinuous transverse rows. The superior distal surface, just behind the tip is furnished with three curved spines and with more spines distributed proximally. The large chela bears at its upper proximal surface a setae-filled pit. The propods and dactyls of the fifth pereopods are medially fringed with long setae.

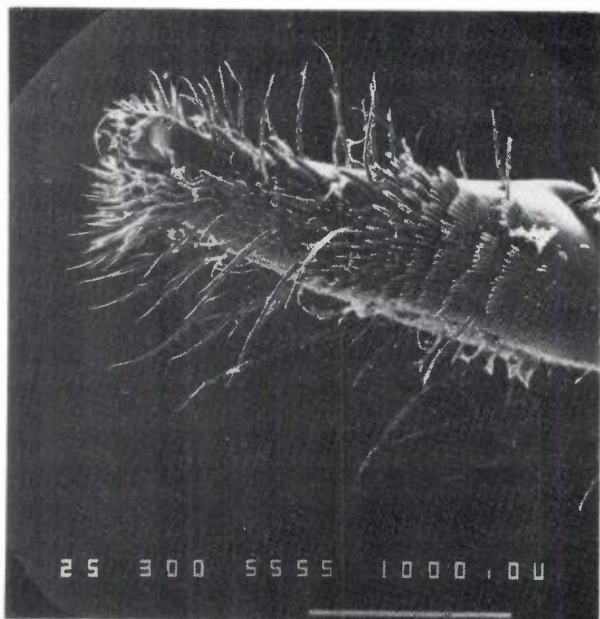


Figure 1. *Trapezia ferruginea* (Latreille), male, Red Sea; dactylar tip of fifth pereopod. Bar = 1 mm.

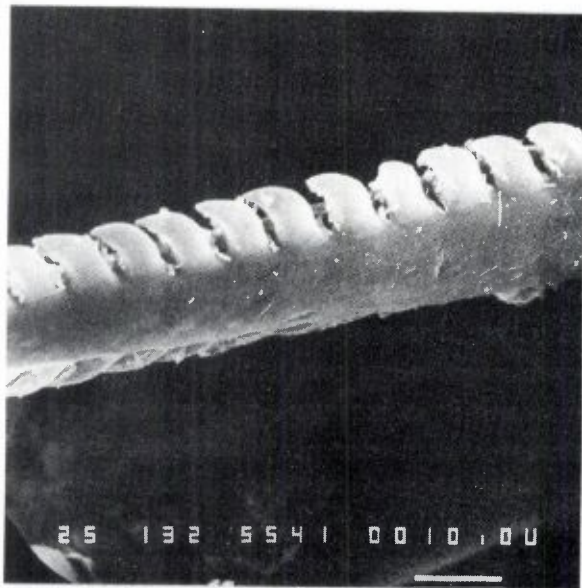


Figure 2. *Trapezia cymodoce* (Herbst.), male, Red Sea; serrated spinule of dactyl of first pereopod. Bar = 10 μ m.

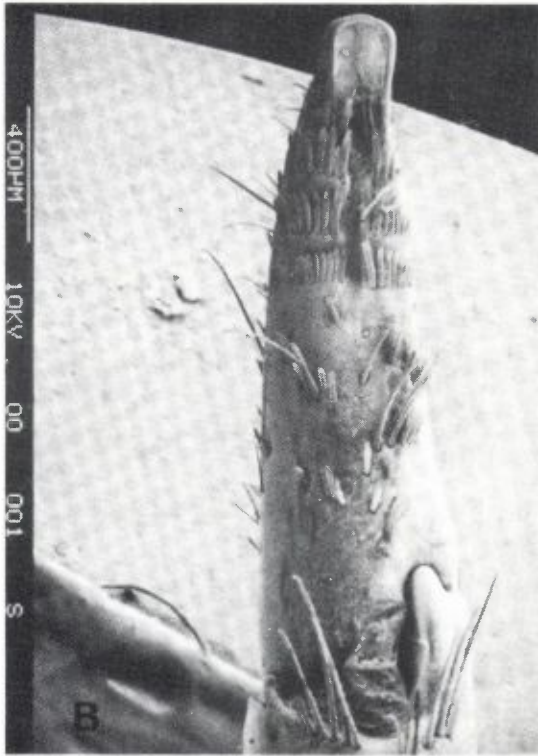


Figure 3. *Tetralia cincipes* Paulson, male, Seychelles; dactylar tip of fifth pereopod. Bar = 400 μ m.

In *Tetraloides* (Fig. 4), the ambulatory dactyls are sparsely setose, with some plumose setae. The hoof-like cornute tip is medially grooved. The posterior distal surface bears three transverse rows of plain spines. The dactylar superior surface is set with three stout spines distally behind the tip and one or two spines proximally.

In *Quadrella* (Fig. 5), the ambulatory dactyls are long, slender and setose. The posterior margin of the dactyl is furnished with a row of triangular teeth, diminishing in size proximally and is basally spinose. Additional spines are found at the base of the dactylar teeth. Short irregular rows of spinules are set anteriorly and laterally on the dactyl. The apical tooth is strong, curved and cornute. The superior distal surface is set with a cluster of small, curved preapical spines.

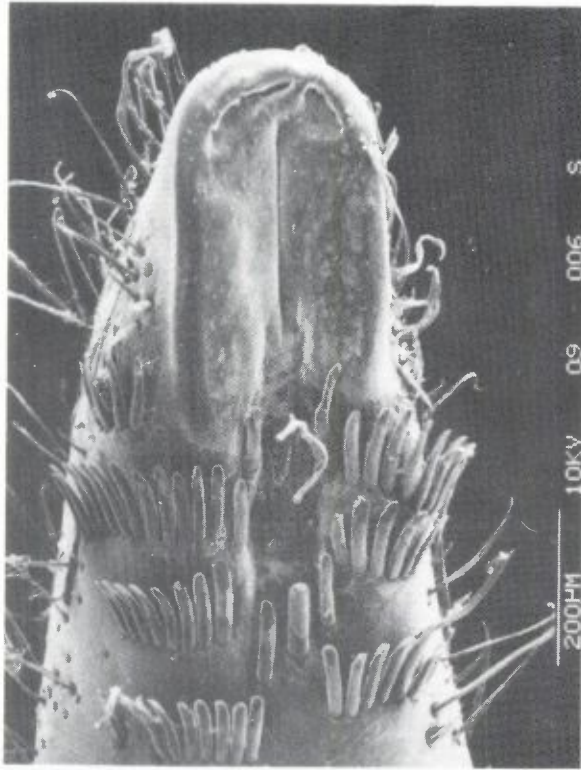


Figure 4. *Tetraloides nigrifrons* (Dana), male, Red Sea; dactylar tip of fifth pereopod. Bar = 200µm.

In *Hexagonalia*, the ambulatory dactyls are sickle-shaped and slender. The dactylar posterior margin is set with a double row of triangular-teeth, which have curved and cornute spines at their distal bases. The dactylar tip bears a large, cornute tooth. The interior surface of the dactyl is furnished with short transverse rows of spinules proximally; the exterior surface has a single transverse row. Curved spines are set distally on the anterior surface.

In *Calocarcinus*, the stocky ambulatory dactyls bear plumose setae. The posterior margin is set with a double row of stout spines, with smaller spines interiorly. The anterior surface is set with curved spines distally. The dactylar tip is curved and cornute.

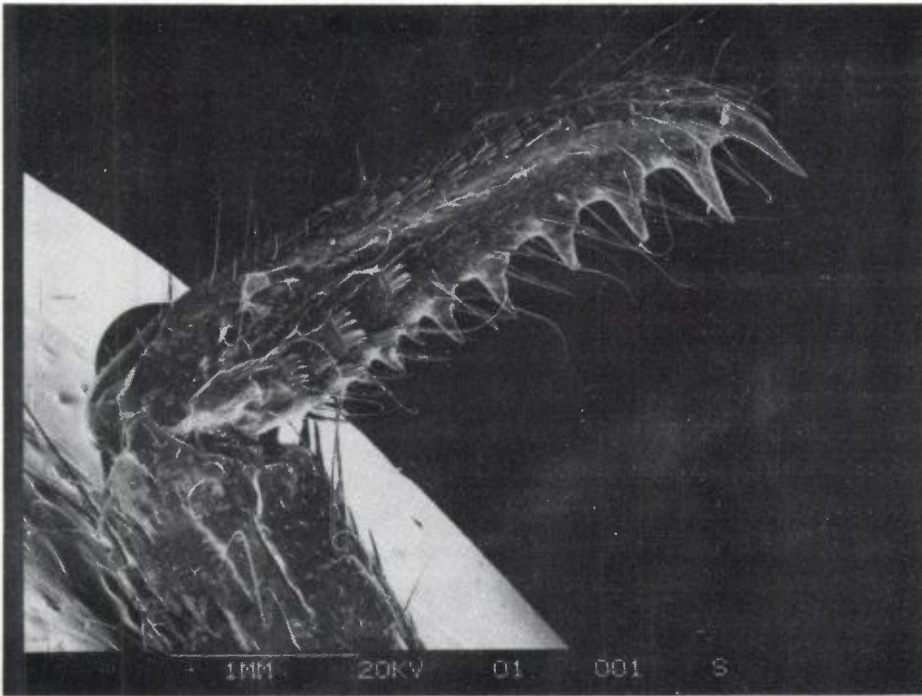


Figure 5. *Quadrella coronata* Dana, male, Moluccas Islands; dactyl of fifth pereiopod. Bar = 1 mm.

4. Mucus-Gathering Structures: Comparison with Other Coral-Inhabiting Decapods

Only a limited number of decapods are adapted for coral mucus feeding. Trapezid crabs display a variety of morphological modifications, many of which have counterparts in other coral-symbiotic decapods.

The subfamily Pontiinae comprises many coral associated species that vary from facultative associates to host specific obligate symbionts, among which modifications are found, paralleled in the trapezids, and ordinarily not found in free-living taxons. These can possibly be regarded as accommodations to life as mucus-feeding coral associates (Bruce, 1976).

Harpiliopsis beaupressi (Audouin), *Periclimenes amymone* De Man, and *P. spiniferus* De Man are the most abundant pontoniids on pocilloporid

corals. All three have on the ventral margin of the chela of first pereiopods well developed clusters of anteriorly curving setae. In another coral associated pontoniid genus, *Coralliocoris* Stimpson (Bruce, 1976), the proximal ventral region of the chela of the first pereiopod bears transverse rows of long, curved, comb-like setae in addition to a well developed subterminal brush. Likewise, one of the most familiar of coral symbionts, *Alpheus lottini* Guerin, common on pocilloporid corals throughout the Indo Pacific ocean, bears a prominent cluster of setae on the fingers of the second pereiopodal chela (Patton, 1974). According to Bruce (1971) these structures are associated either with feeding or cleaning the shrimps from the host-coral mucus. Patton (1974) suggested that as these setae are often entwined with amorphous mucal material similar to that found in the specimens' stomach, the setae are an adaptation for collecting the sediment and coral mucus on which they feed.

In *Anchistus custos* (Forsk.) a pontoniid associated with *Pinna*, that feeds on mucus produced by its bivalve host, the dorsal and ventral edges of the palm of the chela are expanded, curved medially and fringed with long setae, forming a deep channel along the palm (Bruce, 1976). Johnson and Liang (1966) have reported that the chela is used to sweep up mucus and food from the host's gills, so that it accumulates in the palmar groove. A similar structure — a setae filled pit at the upper proximal surface of the large chela — is found in members of the *Acropora*-associated genus *Tetralia*, while two species of the pocilloporid-associated genus *Trapezia* have the entire upper and outer surface of chela covered with fine down-like setae. *Trapezia cymodoce* and *Tetralia cavimana* Heller were observed sweeping the coral surfaces with the chela, brushing the mucus-laden tomentum with pereiopodal dactyls and transferring it to the mouthparts.

5. Discussion

The induction of adaptive interactions is a significant strategy for survival in the extremely competitive environment of the coral reef. The evolutionary course by which the multifarious adaptation may have developed in the trapezids may have begun as a simple relationship with its coral host, where the crabs sought shelter among the branches, occasionally feeding on detrital material settling on the coral, and on mucus, secreted by the coral to remove the detritus. From this incidental association, selective pressures of the environment may have furthered progressively more integrant relationships, evolving to where, in the absence of sedimentation, the crabs stimulate

the coral to actuate the production of mucus (Bruce, 1976; Knudsen, 1967; Stimson, 1986). Though it is not certain if the development of mucus gathering activities was originally necessary for survival, the nutrient-rich coral mucus may have served as an important component in selection inducing coral-crustacean symbioses (Stimson, 1986); a selection that produced a set of feeding mechanisms and behavioral responses that may be said to show adaptive aspects (Ross, 1983).

Although our understanding of the mucus-gathering structures in the Trapeziidae is still limited, some generalizations can be made. Based on setal type, number and pattern, the variation is towards increase in structure complexity that may serve to maximize feeding and optimal fitness. This is most conspicuous in the dactyl, where a wide range of modifications is found to occur. It is apparent that the madreporarian-inhabiting genera — *Trapezia*, *Tetralia*, *Tetraloides*, living in the more competitive and heterogeneous environment of the shallow reef, have the more highly specialized mucus gathering modifications. In *Tetraloides* we find plumose setae, plain setae arranged in transverse rows and subapical spines. In *Tetralia*, in addition to the aforementioned structures, we find a setae-filled pit on the chela and a setal fringe on fifth pereopods serving to sweep the coral surface and collect mucal matter. *Trapezia* crabs, inhabiting the mucus-poor pocilloporid corals (Castro, 1976) have more evolved modifications: a subterminal brush which encircles periopodal dactyls; a dactylar posterior margin with stout spines distally and transverse rows of comb-like setae proximally; plumose setae on the interior margin and in some species tomentose chelipeds.

The mucus-gathering mechanisms vary from the simple, unspecialized to the highly modified. However, many examples of similar modifications are found in unrelated coral symbiotic groups such as Pontoniinae and Alpheidae — a testimony to the great functional adaptability of the decapod crustaceans.

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