

Molluscs Associated with Living Tropical Corals¹

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INTRODUCTION

Of the many thousands of molluscan species which are restricted in their distributions to shallow-water, tropical habitats, few can be shown to have a direct or obligatory association with living corals. For the remainder, a coral reef provides a major type of habitat in which the molluscs are living lives comparable to those of molluscs on temperate shores: they are detritivores, herbivores and carnivores, microphagous or macrophagous, whose life cycles are adapted to the temperatures and food webs of tropical reef ecosystems. In this paper I wish to discuss species with direct and obligatory associations with living corals. The purpose of such a survey is to assess the types of interactions which occur between corals and molluscs, to indicate where knowledge is scant, and to recommend directions for future research.

Frequently one encounters molluscan groups which are only generally coelenterate-specific; that is, members of one family will prey on scleractinians, hydrocorals, alcyonaceans, zooanthinarians, gorgonians, and antipatharians. For this reason, the molluscan associates of these non-scleractinians are included in the ensuing discussion. This inclusion leads to some discussion of better studied, non-tropical forms where, due to their distributions nearer the large temperate research laboratories, more and enlightening information is available.

I have been able to find good examples of active mollusc-coral associations in the three molluscan classes, Gastropoda, Lamellibranchia, and Aplacophora. For sake of convenience, and because such a series may indicate evolutionary tendencies, I have divided the associations into four classes. These are: (I) Predatory and parasitic molluscs, all of which presumably survive by eating the flesh of living corals; (II) Molluscs which bore into living coral, using the coral skeleton as a refuge while obtaining their energy from material suspended in sea water which they collect by filtration; (III) Epizoid molluscs which cling to the outer surfaces of living coral and obtain their food by filtration; and, (IV) Molluscs which serve as substrata for corals. As will become apparent, several problems arise in such a classification. Many species fall into the shadows of the outline either because their actual food is unknown, or, as in the case of *Fungiacava* (discussed below), their

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habits overlap the categories. The major problem in classifying the coral-associated molluscs by nature of relationship is that too little knowledge is available. The massive conchological literature is replete with citations of species being "found with," or "associated with," or "on," some cnidarian. Many such citations have entered the literature as verifications of predation. As will be noted in the following discussion, too often the exact habits of many of these molluscs are yet to be learned.

Other reviews relevant to the present topic are those of Graham (1955), Rees (1967), Robertson (1970a), Salvini-Plawen (1972), and Yonge (1974). As indicated by their titles, none of these reviews addresses the topic as I do here and few pose basic questions concerning the biology or evolution of mollusc-coral interactions. All are valuable because of their tabulations, their discussions and their bibliographies.

THE ASSOCIATIONS

(I) Predatory and Parasitic Molluscs.

Except for a few forms (*Fungia*, for example), it is generally very difficult to define what an "individual" is in a coral (see, for instance, papers in Boardman *et al.*, 1973). Thus, a strict distinction between "parasite" and "predator" becomes meaningless. Is an animal which regularly crops some polyps from a coral head, but does not kill the entire head, a parasite or a predator? This debate is best exemplified in studies of the two prosobranch gastropod families Coralliophilidae and Architectonicidae.

Coralliophilids are snails presumably related to the muricids which live either next to or buried in living corals. The precise food and method of feeding are not known for most species. Ward (1965) found mucus, nematocysts and zooxanthellae in the gut of *Coralliophila abbreviata* which, like other members of the genus, lives in permanent sites immediately adjacent to the living portions of scleractinians. Ward maintains that *C. abbreviata* contributes to the weakening and destruction of *Montipora* colonies in Barbados, while Robertson (1970a) suggests that all coralliophilids are, "...well adapted parasites, injuring their hosts slightly." Yonge (1974) says, however, "There is no question of parasitism, feeding is by way of a delicate proboscis which probably seizes animal matter carried by cilia over the surface of the coral."

It should be added at this point that simple analysis of gut contents of coral associated animals may not always indicate what their primary food source is. This is true for a variety of reasons, among which are: (1) coral tissue is generally soft and when masticated by teeth or radulae and partially digested by enzymes it is extremely difficult to identify (see Bosch, 1965, for instance); (2) corals are probably constantly sloughing off moribund zooxanthellae and discharged nematocysts which will likely be carried off in the mucus sheets; and, (3) coral mucus alone may provide a food source for a number of marine organisms (Clausade, 1971; Knudsen,

1967; Patton, 1972; Richman, 1973). A gut filled with unidentified material, nematocysts and zooxanthellae might thus simply result from a coral mucus diet.

Magilus and *Leptoconchus*, two other coralliophilid genera, live embedded in living corals such as *Goniastraea*, *Acropora* and the hydrocoral *Millepora*. Their protoconchs are deeply buried in the coral skeleton and the snails live in tubes extending to the surface of the coral colony. What they eat and how they obtain it are yet unknown.

The Architectonicidae are mesogastropods presumed to be related to the cerithiids. They live among and feed on scleractinians and zoanths, exhibiting a high degree of prey-species specificity. Robertson (1967) and Robertson *et al.* (1970) have summarized most of the available information on interactions between architectonicid snails and their coral hosts. The results indicate that neither *Heliacus*, which feeds on zoanths, nor *Philippia*, different species of which feed on zoanths or the stony coral *Porites*, kill off their host colonies. The motility of the architectonicid snails is sufficient to allow their movement from coral colony to coral colony should they be "complete" predators.

Life cycle studies become particularly interesting in regard to such specialized predators as the coralliophilids and architectonicids. Robertson (1964), Robertson *et al.* (1970) and Scheltema (1971) have established that architectonicids have very long-term pelagic larvae, probably approaching six months for some species. Scheltema (1971) has, in fact, traced potential trans-Atlantic dispersal in *Philippia krebsii*. With such long larval periods and great potential displacement, it would seem critical that such species be able to locate a requisite prey as they near the end of their larval period. Robertson *et al.* (1970), however, claimed that larvae of *Philippia radiata* will settle readily in clean dishes and then quickly attain a state of "arrested growth" which was interpreted as a "searching phase," during which the appropriate prey is found. Contrary indications are present in data obtained in my laboratory in Hawaii by Dale B. Bonar, a former graduate student here. Studying larvae of *P. radiata* taken from near-shore plankton hauls off Oahu, Hawaii, Bonar found that metamorphosis occurred much more readily in the presence of living *Porites*. Nine out of ten larvae placed in bowls with living *Porites lobata* had metamorphosed within two days; not until seven days in culture did larvae without coral begin to metamorphose. Bonar found, in addition, that growth of the teleoconch was strictly dependent on the presence of coral and that culture conditions were strongly influential in determining metamorphosis. Larvae with teleoconch diameters of 1.68–1.70 mm would metamorphose but never grow; larvae with teleoconchs ranging from 1.70 to a maximum 1.77 mm did demonstrate teleoconch growth in the presence of living coral. One animal, reared successfully in the lab, began laying eggs at a shell diameter of 7.2 mm less than three months after it had metamorphosed.

Other common predators of corals and sea anemones include the wentletraps or epitoniid snails. An Hawaiian species, *Epitonium ulu*, lives on and eats the solitary scleractinian *Fungia scutaria*. *E. ulu* was briefly discussed by Bosch (1965),

who reported a very rapid growth rate from settling to reproductive size (1.65 cm) in two to three weeks. Eric Guinther of the Hawaiian Institute of Marine Biology has made other interesting observations on *E. ulu* (personal communication). He notes that the snails apparently never crawl directly on the flesh of the coral, but rather move about the inverted basal area of the coral on a grid of secreted mucous strands which are cemented to the coral skeleton. Small tissue lesions occur on infested *Fungia*, and *E. ulu* guts contain zooxanthellae, nematocysts and pink tissue, indicating that predation (parasitism?) does occur (Bosch, 1965).

Other prosobranch coral predators have been reported among diverse groups, including two species of the muricid genus *Drupa* (subgenus *Drupella*), summarized by Robertson (1970a), and the archaeogastropod *Calliostoma javanicum*. The latter species has been reported to feed on the stony corals *Mussa* and *Agaricia* (Glynn, 1973, cites a Yale University doctoral thesis by J. Lang as a source of this information). This observation provides an interesting example of a trochid gastropod feeding in a carnivorous manner. The group is predominantly herbivorous; could *C. javanicum* be living on the zooxanthellae alone? (See addendum).

A final prosobranch group which lives entirely as predators or symbionts of hard and soft corals is the mesogastropod family Ovulidae. Most of the species in this family feed on octocorals, but some are specialized to live on scleractinians and hydrocorals. The degree to which ovulids utilize the cnidarian substrates for food is variable. Thus, *Simnia spelta* eats away the flesh of its host, the gorgonian *Eunicella stricta*, and incorporates the gorgonian pigment into its own shell (Theodor, 1967). *Neosimnia implicata* apparently harms its host, *Leptogorgia*, very little, eating instead the mucus secreted by the gorgonian and the organic materials trapped in the mucus (Patton, 1972). *Cyphoma gibbosum* is known to eat the flesh of *Plexaura homomalla*, *Gorgonia sp.*, and other gorgonians in the Caribbean (Kinzie, 1970, 1974).

There are fascinating details available in the literature concerning the mimicry of ovulids with their various hosts (Adams, 1968; Fox and Wilkie, 1970; Patton, 1972; Theodor, 1967; Thiriot-Quievreux, 1967).

A very important group of cnidarivores is found in the gastropod subclass Nudibranchia. At least one family, the Tritoniidae, are specialists for preying on Alcyonacea, Gorgonacea, Madreporaria and hydrocorals. *Tritonia hombergi* eats *Alcyonium digitatum* in British waters (Rees, 1967), and *T. bayeri* has been found feeding on *Briareum asbestinum* and *Pseudopterogorgia sp.* in Florida (Marcus and Marcus, 1967). Several aeolid species also eat various reef coelenterates, among them are the Hawaiian *Pteraeolidia ianthina* which lives on, mimics and probably eats the octocoral *Sarcothelia edmondsoni*, and two species of the genus *Phestilla* which feed on Scleractinia. *Phestilla sibogae* which devours *Porites compressa* has been under investigation in my laboratory in Hawaii for the past five years (Hadfield and Karlson, 1969; Hadfield, 1972; Bonar and Hadfield, 1974). This species is highly adapted to life on a specific prey; it lives upon the coral, eats it, and lays its eggs on bared parts of the coral skeleton. Larvae of *P. sibogae* are

induced to settle and complete their metamorphosis into young nudibranchs by a substance released from the coral into sea water.

The only non-gastropod molluscs which are known to live as predators or parasites of hard and soft corals are the neomeniomorph aplacophorans. Salvini-Plawen (1972) has summarized the available knowledge concerning solenogastrenidarian associations. Most such associations involve gorgonians or alcyonaceans, the cnidarians serving as both substratum and prey for the neomeniomorphs. Few of these associations have been reported from shallow tropical waters.

(II) Molluscs Which Bore into Corals.

Members of this group do not, in general, feed on the coral into which they bore. Rather, they use the living coral skeleton as a growing refuge and they take their food by filtration from the overlying sea. Their deleterious effects thus will be restricted to weakening the coral skeleton and competing with the corals for suspended food. Most molluscan representatives in this category are bivalves, although some of the coralliophilid gastropods may have similar habits.

Most boring bivalves are found to belong to the family Mytilidae. Gohar and Soliman (1963a) list three species of the genus *Lithophaga* which they found infesting living madreporarians in the Red Sea. Gerlach (1961) found *Lithodomus* sp. boring into live coral in the Maldiv Islands, and a series of papers by Goreau *et al.* (1969, 1970, 1972) has provided a very comprehensive picture of the biology of *Fungiacava eilatensis*, a mytilid which lives commensally with species of *Fungia*. Gohar and Soliman (1963a, 1963b) and Soliman (1969) have raised the very interesting point that boring bivalves and gastropods which inhabit living coral face a very different problem from those molluscs which bore into non-living substrata; namely, they must continually bore outward, *not* inward, in order to escape being sealed off in their burrows by growth of the coral.

Fungiacava is indeed an interesting animal. Totally committed to its commensal existence, it occupies burrows in living fungiids in only very restricted localities, principally in the northern Gulf of Eilat (Goreau *et al.*, 1969). The relationship between mollusc and coral has been clearly established by the studies mentioned above. The mollusc lives within the coral skeleton and its opening to the outer world is via the coelenteron of the coral. The bivalve extends its siphons into the coelenteron of the coral to collect detrital material, phytoplankton, and exuded zooxanthellae for its own nutrition (Goreau *et al.*, 1970).

Another bivalve which lives in craters which it excavates in living coral is the pectinacean *Pedum spondyloideum*. Yonge (1967) reports that *Pedum* attaches with byssus to living coral when young and becomes progressively encased as the coral grows. *Pedum*, like the *Lithophaga* species mentioned above, is a filter feeder.

The tridacnid clams form a more-or-less continuous series extending from forms which are found lying about on the reef flat (*Hippopus hippus*), to others which nestle amongst living coral (*Tridacna maxima*, *T. fossor*), and finally, to *Tridacna crocea* which is frequently found buried in living heads of *Porites* and other massive corals (Yonge, 1936; Otter, 1937). *T. crocea* bores mechanically by

Table 1. Molluscs Associated with Living Tropical Corals*

Mollusc	"Host"	Nature of Association	Locale	Source
Gastropoda				
Prosobranchia				
Archaeogastropoda				
Trochidae				
1. <i>Calliostoma javanicum</i>	<i>Mussa angulosa</i> (S) & <i>Agaricia</i> spp. (S)	Predatory; produces small lesions on coral	Caribbean	Lang, 1970; cited by Glynn, 1973
Mesogastropoda				
Cerithiacea				
Architectonicidae				
2. <i>Architectonica perspectiva</i>	"zoanths" (Z)	"Probably predatory"	Seychelles	Taylor, 1968
3. <i>Heliacus bicanaliculatus</i>	<i>Zoanthus danai</i> (Z)	"symbiotic"	Gulf of California	Robertson, 1967
4. <i>H. cylindricus</i>	<i>Palythoa caribaeorum</i> (Z) <i>P. mammillosa</i> (Z) <i>Zoanthus pulchellus</i> (Z)	"symbiotic"	Bahamas British Honduras Netherlands Antilles	Robertson, 1967
5. <i>H. discoideus sterkii</i>	<i>Palythoa vestitus</i> (Z)	"symbiotic"	Hawaii	Robertson, 1967
6. <i>H. implexus</i>	<i>Zoanthus confertus</i> (Z)	"symbiotic"	Hawaii	Robertson, 1967
7. <i>H. mighelsi</i>	<i>Zoanthus confertus</i> (Z)	"symbiotic"	Hawaii	Robertson, 1967
8. <i>H. trochoides</i>	<i>Palythoa tuberculosa</i> (Z) <i>P. vestitus</i> (Z)	"symbiotic" "symbiotic"	Maldives Hawaii	Robertson, 1967 Robertson, 1967
9. <i>H. variegatus</i>	<i>Palythoa vestitus</i> (Z) & <i>Zoanthus confertus</i> (Z)	"symbiotic"	Hawaii	Robertson, 1967
10. <i>Philippia radiata</i>	<i>Porites lobata</i> (S)	Predatory	Hawaii	Robertson, 1970b; Robertson, <i>et al</i> , 1970
Ptenoglossa				
Epitoniidae (Scalidae)				
11. <i>Amaea</i> sp.	<i>Tubastraea aurea</i> (S)	"associated"	Maldives	Robertson, 1965
12. <i>Epitonium billeeana</i>	<i>Tubastraea tenuilamellosa</i> (S)	"associated"	Gulf of California	Robertson, 1970a
13. <i>Epitonium costulatum</i>	<i>Fungia</i> sp. (S)	"associated"	S. W. Philippines	Robertson, 1963, 1970a
14. <i>E. ulu</i>	<i>Fungia scutaria</i> (S)	Predatory; produces lesions on coral	Hawaii	Bosch, 1965 Robertson, 1970a
15. <i>Epitonium</i> sp. 1	<i>Palythoa</i> sp. (Z)	"associated"	Ceylon and Maldives	Robertson, 1965
16. <i>Epitonium</i> sp. 2	<i>Tubastraea aurea</i> (S)	"associated"	Maldives	Robertson, 1970a

Table 1. (continued)

Cypraeaacea				
Ovulidae				
17.	<i>Calpurnus lacteus</i>	"soft corals" (A?)	"associated"	S. W. Ceylon Robertson, 1965
18.	<i>C. verrucosus</i>	"soft corals" (A?)	"associated"	S. W. Ceylon Robertson, 1965
19.	<i>Cyphoma gibbosum</i>	gorgonians (G) <i>Plexaura homomalla</i> (G) <i>Briareum asbestinum</i> (G)	Predatory Predatory Predatory	Puerto Rico West Indies Caribbean Ghiselin & Wilson, 1966 Kinzie, 1974 Cierszko <i>et al.</i> , 1974
20.	<i>C. signatum</i>	"branching alcyonarians" (G?)	Predatory	Puerto Rico Ghiselin & Wilson, 1966
21.	<i>Jenneria pustulata</i>	stony corals (S)	Predatory	Tropical Eastern Pacific D'Asaro, 1969
22.	<i>Ovula ovum</i>	<i>Sarcophyton</i> (A)	Predatory	Tropical Pacific Vicente, 1966; Yonge, 1974
23.	<i>Neosimnia implicata</i>	<i>Leptogorgia virgulata</i> (G)	"associated"	North Carolina Field, 1949
24.	<i>Pedicularia californica</i>	<i>Allopora californica</i> (H)	"associated"	California Fox & Wilkie, 1970
25.	<i>Pedicularia decussata</i>	<i>Solenosmilia variabilis</i> (S)	"associated"	N. W. Cuba Dall, 1889; cited by Robertson, 1970a
26.	<i>Pedicularia</i> sp.	Stylasterine hydrocorals (H), gorgonians (G), "madrepores" (S)	"associated"	? Hedley, 1903 and Berry, 1946; cited by Robertson, 1970a
27.	<i>Simnia patula</i>	<i>Alcyonium digitatum</i> (A) & <i>Eunicella verrucosa</i> (G)	"associated"	Britain Rees, 1967
28.	<i>S. spelta</i>	<i>Eunicella stricta</i> (G) & <i>Lophogorgia sarameulosa</i> (G)	Predatory	Mediterranean Theodor, 1967
Neogastropoda				
Muricacea				
Muricidae				
29.	<i>Drupa (Drupella) cornus</i>	<i>Porites</i> sp. (S), <i>Stylophora</i> sp. (S) & <i>Seriatopora</i> sp. (S) <i>Montipora</i> spp. (S) <i>Acropora</i> sp. (S) <i>Pocillopora</i> sp. (S) <i>Pocillopora</i> sp. (S) & <i>Porites compressa</i> (S)	"associated" "on" "on" "on" Predatory	Micronesia Cocos-Keeling Island Cook Islands Maldives Hawaii Demond, 1957 Maes, 1967 Robertson, 1970a Robertson, 1970a Fankboner, cited by Robertson, 1970a

Table 1. (continued)

Mollusc	"Host"	Nature of Association	Locale	Source
30. <i>Drupa (Drupella) rugosa</i> Coralliophilidae	"exclusively stony corals" (S)	"associated"	Micronesia	Demond, 1957
31. <i>Coralliophila abbreviata</i>	<i>Montastrea annularis</i> (S) <i>Acropora palmata</i> (S) <i>Diploria clivosa</i> (S) <i>Favia fragum</i> (S)	Predatory "on" "on" "with"	West Indies Bahamas Bahamas British Honduras	Ward, 1965 Robertson, 1970a Robertson, 1970a Robertson, 1970a
32. <i>C. caribaea</i>	gorgonians (G) <i>Acropora palmata</i> (S) & <i>Diploria clivosa</i> (S)	"associated" "associated"	Bahamas Bahamas	Abbott, 1958 Robertson, 1970a
33. <i>C. erosa</i>	<i>Acropora</i> (S) & <i>Montipora</i> (S)	"lives on"	Cocos-Keeling Islands	Maes, 1967
34. <i>C. sugimotonis</i>	<i>Palythoa</i> sp. (Z)	"associated," presumably predatory	Ceylon & Maldives	Robertson, 1965
35. <i>C. violacea</i>	<i>Porites</i> (S) <i>Porites</i> (S) <i>Porites</i> (S) <i>Porites</i> (S) <i>Porites</i> (S), <i>Pocillopora</i> (S), <i>Stylophora</i> (S), & <i>Seratiopora</i> (S)	"on" "on" "on" "on" "preferred"	Cocos-Keeling Micronesia Clipperton Island Maldiv Islands W. Indian Ocean	Maes, 1967 Demond, 1957 Hertlein & Allison, 1960 Robertson, 1970a Taylor, 1971
36. <i>C. costularis</i>	<i>Porites</i> (S), <i>Pocillopora</i> (S), <i>Stylophora</i> (S), & <i>Seratiopora</i> (S)	"preferred"	W. Indian Ocean	Taylor, 1971
37. <i>Quoyula madreporarum</i>	<i>Seriatopora</i> (S) <i>Pocillopora</i> spp. (S) <i>Pocillopora</i> (S) <i>Pocillopora</i> (S)	"attached" "attached" "embedded in" "on branches and in clefts"	Madagascar Cocos-Keeling Clipperton Island Maldives, New Caledonia, Fiji, Cook Islands, Pacific Mexico & Nicaragua Micronesia	Maes, 1967, cited in Robertson, 1970a Hertlein & Allison, 1960 Robertson, 1970a Demond, 1957
38. <i>Q. monodonta</i>	<i>Montipora</i> (S), <i>Pocillopora</i> (S) & <i>Stylophora</i> (S) <i>Pocillopora</i> , <i>Seriatopora</i> , <i>Stylophora</i> , & <i>Porites</i> (all, S) <i>Porites nigrescens</i> (S)	"with" "with" "with"	Micronesia Seychelles	Demond, 1957 Taylor, 1968
39. <i>Rapa rapa</i>	"large reef Alcyonacea of the western Pacific" (A)	"embedded in, with no communication to outside"	W. Pacific	Bayer, 1961; cited in Rees, 1967

Table 1. (continued)

Opisthobranchia					
Nudibranchia					
Arminacea					
Arminidae					
40.	<i>Armina</i> sp.	"corals" (?)	Predatory	—	Salvini-Plawen, 1972
Phyllididae					
41.	<i>Phyllidia bourgini</i>	<i>Acropora</i> (S) & millipores (H)	Predatory	Madagascar	Vicente, 1966
Dendronotacea					
Tritoniidae					
42.	<i>Tritonia bayeri</i>	<i>Briareum asbestinum</i> (S) & <i>Pseudopterogorgia</i> sp. (S)	Predatory	Biscayne Bay, Florida	Marcus & Marcus, 1967
	Probably <i>T. bayeri</i>	<i>Sarcothelia edmondsoni</i> (A)	Predatory	Hawaii	R. Kinzie, personal communication
43.	<i>T. hombergi</i>	<i>Alcyonium digitatum</i> (A)	Predatory	England	Rees, 1967
44.	<i>T. pickensii</i>	Gorgonacea (G)	"on," probably predatory	Gulf of California	Marcus & Marcus, 1967
45.	<i>T. striata</i>	<i>Paralcyonium elegans</i> (A)	Predatory	?	Salvini-Plawen, 1972
46.	<i>T. wellsii</i>	<i>Leptogorgia virgulata</i> (G)	Predatory	North Carolina	Patton, 1972
Aeolidacea					
Cuthonidae					
47.	<i>Phestilla melanobrachia</i>	<i>Tubeastraea aurea</i> (S) & <i>Dendrophyllia</i> (S)	Predatory	Hawaii, etc.	Harris, 1971
48.	<i>P. sibogae</i>	<i>Porites compressa</i> (S) <i>Porites lobata</i> & <i>P. compressa</i> (S)	Predatory Predatory	Hawaii, etc. Hawaii, etc.	Harris, 1971 personal observation
Pteraeolididae					
49.	<i>Pteraeolidia ianthina</i>	<i>Sarcothelia edmondsoni</i> (A)	Predatory	Hawaii	E. A. Kay, Univ. of Hawaii, personal communication
50.	? "small aeolid"	<i>Porites compressa</i> (S)	Predatory	Hawaii	personal observation
51.	<i>Phyllodesmium xeniae</i>	<i>Xenia umbellata</i> (A) & <i>Heteroxenia fuscescens</i> (A)	Predatory	Red Sea	Gohar & Abul-Ela, 1957
Aplacophora					
Neomeniomorpha					
numerous species					
		octocorals (mainly G?)	Predatory	world wide	see Salvini-Plawen, 1972

Table 1. (continued)

Mollusc	"Host"	Nature of Association	Locale	Source
Lamellibranchia				
Anisomyaria				
Mytilacea				
Mytilidae				
52. <i>Fungiacava eilatensis</i>	<i>Fungia scutaria</i> (S)	Endo-symbiotic	Gulf of Eilat	Goreau <i>et al.</i> , 1969
53. <i>Lithodomus</i> sp.	live coral (S)	Bores into skeleton	Maldive Island	Gerlach, 1961
54. <i>Lithophaga lima</i>	<i>Montipora lanuginosa</i> (S)	Bores into skeleton	Red Sea	Gohar & Soliman, 1963a
55. <i>L. cumingiana</i>	<i>Stylophora flabellata</i> (S)	Bores into skeleton	Red Sea	Gohar & Soliman, 1963a
56. <i>L. hanleyana</i>	<i>Favia stelligera</i> (S) & other spp. (S)	Bores into skeleton	Red Sea	Gohar & Soliman, 1963a
Pteriacea				
Pteriidae				
57. <i>Electroma</i> sp.	<i>Acropora</i> (S)	Externally attached	Fanning Island	Kay & Switzer, 1974
58. <i>Pteria colymbus</i>	<i>Leptogorgia virgulata</i> (S)	Attaches to	North Carolina	Patton, 1972
59. <i>Pteria</i> sp.	antipatharians (Ap)	Attaches to	?	Rees, 1967
Pectinacea				
Pectinidae				
60. <i>Pedum spondyloideum</i>	<i>Porites</i> sp. (S)	Encased by coral growth	New Britain	Yonge, 1967
Ostreacea				
Ostreidae				
61. <i>Ostrea sandvicensis</i>	<i>Acropora</i> (S) & <i>Stylophora</i> (S)	Attaches to	Fanning Island	Kay & Switzer, 1974
Heterodonta				
Cardiacea				
Tridacnidae				
62. <i>Tridacna crocea</i>	<i>Porites</i> (S) & other massive (S) spp.	Boring in living skeleton	Tropical Pacific	Yonge, 1936; personal observations
Taxodonta				
Arcacea				
Arcidae				
63. <i>Barbatia decussata</i>	<i>Porites</i> (S)	Externally attached	Fanning Island	Kay & Switzer, 1974

* Table 1 demonstrates, to the extent currently possible, which molluscs are associated with which cnidarian species or genera. The items listed under "Nature of Association", show most clearly how little is actually known about the nature of these associations. The letters following the named cnidarians in the second column indicate to which cnidarian order each genus or species belongs, as follows: A, Alcyonacea; Ap, Antipatharia; G, Gorgonacea; H, Hydrocorallina; S, Scleratinia; Z, Zoanthinaria.

the grinding action of the thickened shell hinge. Yonge (1936) maintains that this species never settles directly on live coral, but it is frequently seen so surrounded by live coral that this might be questioned.

(III) Molluscs Which Live Epizoically on Coral.

Certain pteriid and ostreid bivalves are frequently found attached by their byssus to the surfaces of living hard or soft corals. Most notable are those species of *Pteria* which are almost invariably found attached to gorgonians and antipatharians (Field, 1949; Rees, 1967; Patton, 1972). Patton reports that the byssal attachment of *Pteria colymbus* to the coenenchyme of *Leptogorgia virgulata* may cause the flesh of the gorgonian to fall away exposing the axial skeleton to fouling by the settlement of sessile organisms.

Kay and Switzer (1974) report on three bivalve species which they found associated with living stony corals at Fanning Island. *Electroma* sp. was associated with *Acropora*, *Ostrea sandvicensis* with *Stylophora*, and *Barbatia decussata* with *Porites*.

Questions arise concerning the nature of these attached filter feeders and their "hosts," such as, are the relationships species-specific? The presumed advantage to the bivalve is that they select settling sites which are raised well above the rubble or sand surrounding the coral, a position assured by the elongate, branching cnidarians upon which they live.

Vermetid gastropods, also filter feeders, are frequently seen growing on Indo-Pacific Scleractinia, but the relationship is not specific (Gerlach, 1961, and personal observations).

(IV) Molluscs Which Serve as Substrata for Corals.

While small coral colonies may be found on the shells of many molluscs, this category was constructed mainly to encompass the abundant vermetid gastropods which are found with their tubes projecting from coral heads throughout the tropical Pacific. The association appears rather non-specific, although in certain locales some species of corals are never seen without vermetids. For instance, most *Porites lobata* heads which I have observed in Hawaii contain the vermetid *Petalococonchus keenae* (Hadfield *et al.*, 1972), and in Palau all of the *Dendropoma maximum* which I saw were buried in living *Porites*. A recent paper by Hughes and Lewis (1974) discusses other aspects of the biology of *D. maximum*. The importance of vermetid shells as settling sites for corals recolonizing areas such as those decimated by *Acanthaster* or pollution is potentially great.

Carried to its logical conclusion, this category must include those symbioses wherein the mollusc serves as requisite host for coral. Such is the situation in the biology of the solitary corals *Heteropsammia* and *Heterocyathus* which always settle on the empty shells of certain snails. The shells of the snails are also used as refuges by the bivalve *Jousseamiella* and the sipunculan *Aspidosiphon* (Bouvier, 1894; Bourne, 1906).

CONCLUSIONS

Altogether, I have summarized data on nearly 80 molluscan species which, in some manner, make their life on or in living corals or by eating them (Table 1). Trends are seen; certain groups are specialized coral carnivores, others use the growing skeleton for a refuge wherein they can grow and feed by filtration. Certain groups remain enigmatic in that their positive association with certain corals is known but the nature of their association is not. The fact that coral mucus and the debris which it collects forms the major food for several species is important in the energy transfers which occur on coral reefs.

Numerous questions arise in any discussion such as this one. Some of the more important ones are the following. How do settling larvae find the specific coral on which they will live and then survive the protective mechanisms of the coral? In fact, life cycle data are absent for nearly all of the species cited in this survey. What are the effects of the unusual and bizarre chemicals synthesized by corals on their molluscan associates (see Ciereszko and Karns, 1973)? Do they orient the molluscs in their specificity toward their prey/hosts? Do they repel certain molluscs from otherwise potential hosts?

C. M. Yonge (1963) noted, "thanks no doubt to the presence of nematocysts, corals are little affected by predators." This seems hardly to be true in light of presently accumulating information. Not only do prosobranchs, nudibranchs and aplacophorans eat corals, but members of several other molluscan groups are capable of residing on the surfaces of coral. Much evidence is also accumulating about predation on corals by fish, echinoderms and polychaete worms. A leading question is, how are the nematocyst toxins avoided, both while the motile animal is crawling on the coral surface and during ingestion of coral flesh? Robertson (1963, 1970a, 1970b, 1970c), Salvini-Plawen (1972) and others suggest two primary answers. First, mucus must play a definite role in defense against nematocysts. It may act simply as a thickened, viscous cushion which the nematocyst threads either cannot penetrate or lose their penetrating velocity in passing through. Mucus may also have a specific neutralizing effect on the chemicals which compose nematocyst toxins. It has also been noted by the above-named authors that cuticular coverings or linings are present about the mouths and anterior digestive tracts of most cnidarians. These cuticular layers no doubt deflect the nematocyst threads and impede their penetration into susceptible tissues. Ward (1965) suggests that a salivary gland secretion "desensitizes" nematocysts ingested by *Coralliophila abbreviata*. As mentioned above, *Epitonium ulu* apparently never crawls directly on the flesh of its host *Fungia scutaria* but moves about it on a grid of mucous threads.

An important and barely touched aspect of mollusc-coral associations is a truly ecological examination of them. Some associations are obviously so well established through long evolutionary time that they exist in all locales where potential hosts can exist; such is true of the gorgonian-ovulid associations. In many instances, however, the host may have a wide range of distribution while the molluscan predator/symbiont will occur with the host in only a few selected areas.

The outstanding example here is the limited range of *Fungiacava eilatensis* as compared to that of its host *Fungia scutaria* (Goreau *et al.*, 1969). Kay and Switzer (1974) have noted discontinuities in the distribution of molluscan species in the lagoon of Fanning Island. Interestingly, they list some of the bivalves which hang onto the branches of live corals as occurring with the corals in less turbid areas of the lagoon and being absent from the still-present "hosts" in the areas of cloudier water.

In summary, I must admit to having barely touched the surface of the fascinating assemblage which can be labelled, "Molluscs Associated with Living Tropical Corals." A major problem exists in assessing the true nature of most such associations. This is partly reflected in confusing use of terms, although I see little value in arguing the meaning of "symbiont" vs. "commensal" vs. "associate" until much more information is available on the biological aspects of these associations. Let us hope that with the appearance of more and better tropical shore marine laboratories, the true nature of these associations will be revealed and that, even more importantly, they will be placed into the larger picture of coral reef ecology, productivity, longevity and geology.

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ADDENDUM

Alan C. Miller [1972. "Observations on the associations and feeding of six species of prosobranch gastropods on anthozoans in Discovery Bay, Jamaica." *The Echo* (Western Malacological Society). 5: 35-36.] reports undigested zooxanthellae in feces of *Calliostoma javanicum* which had been feeding on coral and Frank E. Perron [1975. "Carnivorous *Calliostoma* from the northeastern Pacific." *The Veliger*. 18: 52-54.] notes that several other *Calliostoma* species feed on hydroids. I must agree with Perron that members of this genus are predators.