Review of the Predators and Parasites of Stony Corals, with Special Reference to Symbiotic Prosobranch Gastropods[1]

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ABSTRACT: Predators and parasites on the living tissues of stony (scleractinian) corals include bony and cartilaginous fishes, asteroids, crustaceans (cyclopoid copepods, cirripedes, and brachyuran crabs), polychaetes, and gastropods (prosobranchs and nudibranchs). These are all facultative predators except the crustaceans and gastropods that are obligately associated (symbiotic) with and feed on their coral hosts. Such symbionts are known in four unrelated families of crustaceans (Xarifiidae, Asterocheridae, Balanidae, and Xanthidae) and four unrelated families of prosobranch gastropods (Architectonicidae, Epitoniidae, Ovulidae, and Coralliophilidae). A fifth prosobranch family includes frequent but not obligate coral associates that are coral- and possibly also mollusk-feeders (Muricidae [*Drupa*, subgenus *Drupella*]). The eolid nudibranch genus *Phestilla* (Tergipedidae) includes the only so far identified opisthobranchs definitely symbiotic with corals. Most of the crustacean and molluscan symbionts live with hermatypic corals in the Indo-Pacific. Specificity to particular genera or families of corals is low, but the bright yellow, orange, or pink phases (species?) of the dendrophylliid ahermatypic coral *Tubastraea* are host to similarly colored prosobranchs (*"Epitonium"*) and a nudibranch (*Phestilla melanobrachia*). Adaptations for feeding on coelenterates are various, but in unrelated gastropod families similar specializations occur (cuticularized esophaguses and proboscises, ptenoglossate-like radular teeth, and total loss of radulae). The most specialized of the coral-dwelling prosobranchs are the coralliophilids (including *Magilus*), parasites without radulae living both on and in coelenterates.

COELENTERATES and in particular stony (scleractinian [madreporarian]) corals have been thought to be nearly immune from predators (Wells, 1957, p. 612) and parasites. Nematocysts presumably are a deterrent. However, it it has been discovered, principally in the last decade, that various animals do feed on the living tissues of coelenterates, and that a few are specialized predators or parasites of stony corals.

FISHES

Bony fishes in twelve families are reported to feed on corals. Many of these fishes either remove the living coral tissues or abrade dead coral skeletons for their attached or contained algae (Cloud, 1959, pp. 398–399, pls. 130–131). The nine families that definitely include frequent to occasional facultative predators on living corals are the Ephippidae (spadefishes), Chaetodontidae (butterflyfishes), Pomacentridae [or Abudefdufidae] (damselfishes), Labridae (wrasses), Scaridae (parrotfishes), Acanthuridae (surgeonfishes), Balistidae [including Monacanthidae] (trigger- and filefishes), Tetraodontidae [including Canthigasteridae, Lagocephalidae, and Colomesidae] (puffers), and Diodontidae (porcupinefishes) [Quoy and Gaimard, 1824–1825, pp. 201–202, 600–601; Al-Hussaini, 1947, pp. 34–39; Gohar and Latif, 1959; Le Danois, 1959; Hiatt and Strasburg, 1960, pp. 91, 101, 113–114, etc.; Talbot, 1965, p. 456; Randall, 1967, pp. 828–830]. The three additional families that possibly include such predators are the Kyphosidae (sea chubs) [Gerlach, 1960, p. 362],

Cheilodactylidae [Squires, 1964], and Ostra-ciidae (trunkfishes) [Hesse, 1924, p. 229; Al-Hussaini, 1947, p. 36]. Several of the occasionally predatory families (e.g., the Acanthuridae) are primarily herbivorous.

A cartilaginous fish feeds on corals in the Red Sea: Gohar and Mazhar (1964*a*, p. 9) found "parts of corals mainly *Stylophora*" in the stomachs of the nurse shark *Nebrius concolor* Rüppell (Orectolobidae). "The teeth are small and adapted for snapping the corals and small sand-living invertebrates" (Gohar and Mazhar, 1964*b*, p. 149). This nurse shark also feeds on fishes and cephalopods.

INVERTEBRATES

Goreau (1964) has described how the large spiny Indo-Pacific asteroid *Acanthaster planci* (Linn.) feeds on coral tissues, and suddenly increased populations of this starfish recently have been devastating corals on the Great Barrier Reef, Australia, and elsewhere in the western Pacific (Barnes, 1966; Chesher, 1969; Paine, 1969; Weber, 1969). Goreau (1964) also reviewed some of the other animals that feed on corals. The invertebrates are now known to include the amphinomid polychaete *Hermodice carunculata* (Pallas) [Marsden, 1962; Glynn, 1963; Marsden, 1963*a*, 1963*b*], the xarifiid cyclopoid copepods (Gerlach, 1960, p. 360, 362; Humes, 1960 and subsequent papers, including Humes and Ho, 1968), the asterocherid cyclopoid copepod *Cholomyzon* (Stock and Humes, 1969), the balanid cirripede *Pyrgoma monticulariae* Gray [Ross and Newman, 1969], the majid crab *Mithraculus sculptus* (Lamarck) [Glynn, 1963], and the xanthid crabs *Trapezia* and *Tetralia* [Knudsen, 1967]. All these invertebrates definitely feed on the living tissues and mucus of corals, either as facultative predators or as obligate parasites (all the crustaceans listed except the *Mithraculus*). The barnacle genus *Pyrgoma*, always associated with stony corals, includes nonparasitic, semiparasitic and wholly parasitic species (Ross and Newman, 1969). Excluded from consideration here are the many other crustaceans associated or "commensal" with corals (Patton, 1966), and the sponges, bivalves, cirripedes, sipunculids, and poly-

chaetes that bore or live in holes in coral skeletons. Other amphinomid polychaetes possibly are like *Hermodice* in feeding on corals (Ebbs, 1966, p. 547).

GASTROPODS

Among the many marine gastropods that consistently are associated (symbiotic) with coelenterates, there are some living with stony corals that definitely feed on the living tissues. Since even the existence of such gastropods is little known among marine ecologists, this paper reviews in detail the kinds of gastropods involved and what little is presently known or can be inferred of their modes of life. Gardiner (1902, p. 338) seems to be the first to have observed that a few (unspecified) gastropods "make a practice of consuming [coral] polyps, leaving dead tracks over the otherwise living colonies."

Many of the eolid nudibranchs, the most renowned gastropods that feed on coelenterates, are able to select and extract undischarged nematocysts from the coelenterate (mainly hydroid) tissues that they swallow, to position these in their own bodies (in their cerata), and to use them for their own defense against predators (Edmunds, 1966, and references therein). Risso-Dominguez (1964, p. 235) avers "that most groups of coelenterates . . . have typical and taxonomically well defined eolid predators." Few eolids symbiotic with stony corals are known so far, and the only two identified are in the tergipedid genus *Phestilla*. The unidentified bright orange eolid discussed and figured by Edmondson ([1933?] 1946, p. 184, fig. 97b) as being associated with and feeding on *Dendrophyllia manni* (Verrill) [=*Tubastraea aurea* (Quoy and Gaimard)] has been shown by Harris (1968), with help from Dr. Kikutaro Baba, to be *Phestilla melanobrachia* Bergh, a species widespread in the tropical western Pacific and obligately associated with *Tubastraea* and other dendrophylliids. This large eolid is polychromatic, individuals being orange, pink, or predominantly greenish-black depending whether they have recently been feeding on orange, pink, or greenish-black *Tubastraea*. (The three differently colored species of *Tubastraea* men-

tioned by Harris are believed by Boschma [1953] all to be phases of *T. aurea*.) Harris suggests that the pigment in the nudibranch is biochemically the same as in the coral, and Harris has observed that this *Phestilla* does not store nematocysts. Edmondson ([1933?] 1946, p. 184) also mentioned a second unidentified eolid with *Porites evermanni* Vaughan, the nudibranch leaving "smooth patches on the coral heads where it has destroyed the polyps." Harris informs me (in litt.) that Edmondson's second species was *Phestilla sibogae* Bergh, which feeds on *Porites* exclusively, and that *Aeolidia edmondsoni* Ostergaard (1955, pp. 133–135, fig. 16, pl. 1), believed by Ostergaard to feed on the polyps of *Porites compressa* Dana, is a synonym. Harris also informs me (in litt.) that he twice has collected a very small, as yet unidentified, eolid that feeds on a *Montipora* at Singapore, and that at the same locality a fourth eolid lives on *Goniopora*.

The only non-eolid nudibranch so far reported to feed on corals is the porostomatous doridoid *Phyllidia bourgini* Risbec, found very commonly on *Acropora* (also millepores) by Vicente (1966, pp. 105, 128) off the southwest coast of Madagascar. The Phyllidiidae have a large muscular pharynx but neither jaws nor a radula. Vicente gave no details, and according to Harris (in litt.) all the phyllidiids with which he is familiar feed on sponges. Vicente's report therefore needs confirmation.

The diversity of shell-bearing prosobranchs symbiotic with coelenterates is reflected in the number of symbiotic genera now known: 26, in eight families (Robertson, 1966, 1967, and new cases reviewed or reported herein). Many of these gastropods are known to feed on their hosts, which besides stony corals include hydroids, stylasterine hydrocorals, discophores, siphonophores, gorgonians, soft corals (alcyonarians), black corals (antipatharians), zoanthids, and actiniarian sea anemones. Four unrelated families and nine genera are definitely known to include species symbiotic with stony (scleractinian) corals. These families and genera are: Architectonicidae (*Philippia*), Epitoniidae (*Epitonium*, s.l.), Ovulidae (*Jenneria* and *Pedicularia*), and Coralliophilidae (*Coralliophila, Quoyula, Leptoconchus, Magilopsis,* and *Magilus*). *Drupella*, a subgenus of *Drupa* (Mu-

ricidae), feeds on corals but is not consistently associated.

Architectonicidae ["Solariidae" + Heliacidae]

In the Hawaiian Islands, *Philippia (Psilaxis) radiata* (Röding) lives near *Porites lobata* Dana and has been seen to feed at night on the polyps (see the following article in this issue: Robertson, Scheltema, and Adams, 1970). Other species of *Philippia* probably have similar habits.

Epitoniidae ["Scalidae" + "Scalariidae"]

Many wentletraps live with or forage for the actiniarian sea anemones on which they feed, but a few have other coelenterate hosts. The following five shallow-water species are known to live with corals: *Epitonium costulatum* (Kiener) under *Fungia* sp. in the southwestern Philippines (Robertson, 1963, pp. 57–58, pl. 5, fig. 4 [the identification is now definite; I since have seen the holotype in Geneva]); *Epitonium ulu* Pilsbry under *Fungia scutaria* Lamarck in the Hawaiian Islands (Bosch, 1965), and the chrome yellow "*Epitonium*" *billeeana* (DuShane and Bratcher, 1965) [DuShane, 1967] with the brilliant orange and yellow phase of the ahermatypic dendrophylliid *Tubastraea tenuilamellosa* (Milne-Edwards and Haime) [a probable synonym of *T. aurea* according to Boschma (1953)] in the Gulf of California. This epitoniid is the prosobranch counterpart of the bright orange phase of the nudibranch *Phestilla melanobrachia* discussed earlier. In the Maldive Islands, a closely related, cryptically colored "*Epitonium*" lives with the same color phase of *Tubastraea aurea* [Harris informs me (in litt.) that he has collected a similar epitoniid with *T. aurea* at Singapore and in the Philippines, and with a pink dendrophylliid at the Great Barrier Reef, Australia], and a species similar to but definitely different from *Epitonium ulu* lives under *Fungia scutaria* [Robertson, 1966, as "*Amaea* sp." and "*Epitonium* sp." and unpublished observations].

There have been no direct observations on the feeding of any of these five species, but

Bosch provides good indirect evidence that in darkness *Epitonium ulu* feeds on the living tissues of *Fungia scutaria*. Bosch saw tissue lesions on the coral and found zooxanthellae and nematocysts in the viscera of the wentletrap; also "wentletraps placed near corals which had been stained with a vital dye (neutral red) soon became suffused with the same color due to the ingestion of dyed coral tissue." Bosch believed that *Epitonium ulu* can grow from a larva to sexual maturity within the remarkable short time of three weeks, and Mr. Eric Guinther (unpublished) recently has confirmed that this can occur even within two weeks.

All the coral-associated wentletraps are likely to feed on the soft tissues of their hosts in the same way as the species that feed on sea anemones: by everting a long acrembolic proboscis and swallowing large pieces of flesh (such as whole tentacles) that are pinched off and pulled into the esophagus with the radula.

Ovulidae ["Amphiperatidae" + "Pediculariidae"]

This fairly small family, allied to the cowries (Cypraeidae), is probably comprised entirely of symbionts that feed on coelenterate hosts. Gorgonians and alcyonarians are the hosts of most of the genera, and only *Jenneria* and *Pedicularia* are known with stony corals.

Jenneria pustulata (Lightfoot), endemic to the tropical eastern Pacific and the only living species in the genus, according to D'Asaro (1969, p. 182) "is a hardy species normally found in association with the stony corals upon which it feeds." Specimens from Panama were taken live to Miami, Florida, and were maintained there in aquaria for three years by D'Asaro. There they fed on the ahermatypic coral *Phyllangia americana* Milne-Edwards and Haime, and the hermatypic corals *Siderastrea siderea* (Ellis and Solander) and *Porites* sp., showing a marked preference for *Phyllangia*. The familial placement of *Jenneria* has been in doubt, but D'Asaro has shown that it belongs here.

Pedicularia decussata Gould was reported by Dall (1889, p. 237) on the ahermatypic and colonial caryophylliid coral *Solenosmilia variabilis* Duncan from 450 fathoms off northwest Cuba. *Pedicularia* is known otherwise only with stylasterine hydrocorals (the commonest hosts), gorgonians and unspecified "madrepores" (Hedley, 1903, p. 343; Berry, 1946).

Muricidae

This is a large family that includes the oyster drills. Tropical species in various muricid genera sometimes occur on living corals. Most such associations are happenstance and temporary except in the case of *Drupella,* a subgenus of *Drupa* restricted to the Indo-Pacific. In Micronesia, *Drupa (Drupella) rugosa* (Born) and *Drupa (Drupella) cornus* Röding both occur "exclusively on living coral," *Drupa cornus* "most frequently on *Porites* sp., but also on *Stylophora* sp. and *Seriatopora* sp." [Demond, 1957, pp. 311–312, as *Morula concatenata* (Lamarck) and *M. elata* (Blainville), respectively]. Likewise at the Cocos-Keeling Islands, Indian Ocean, Maes (1967, p. 130) found *Drupa cornus* "only on living corals," on both "massive and branching corals of several species . . . . A large colony was found on a branching *Montipora* . . . ." In the Cook Islands, *Drupa cornus* has been collected on a branching *Acropora.* In some other areas, *Drupa cornus* occurs on substrates other than live corals (Cernohorsky, 1969, p. 304). In the Maldive Islands, southern India, Ceylon, and Tahiti, I have personally collected the species on and under rocks and dead corals on reefs (even under turfs of green algae), but in the Maldives I also found it in colonies in the clefts of branches of live *Pocillopora.* *Drupa cornus* never is far from live coral and perhaps is associated only for feeding. A third species, *Drupa (Drupella) ochrostoma* (Blainville), less often occurs on corals and lives mainly on and under rocks.

Drupella radulae are unlike those of all other muricids in having long, slender, basally denticulate laterals with hooked and usually bifid tips [Arakawa, 1958, *Drupa rugosa* as *Drupella fragum* (Blainville); 1965, p. 117; Cernohorsky, 1969, pp. 303–307, figs. 8–11]. Cooke (1895, pp. 222–223), Arakawa, and Wu (1965, p. 102) have attributed these struc-

tural adaptations to specialized feeding habits, and have implied that *Drupella* species feed on the living tissues of their coral hosts. Fankboner (personal communication) has studied the feeding and functional morphology of the gut of *Drupa cornus* (or "*Morula elata*"). In Hawaii it consistently lives on *Pocillopora* and *Porites compressa* and feeds nocturnally on the polyps. There is a long pleurembolic proboscis that is cuticularized exteriorly. An enlarged pedal gland secretes mucus masses that during feeding are pushed ahead of the mouth. The cuticularization and mucus presumably prevent injury from nematocysts. Fankboner describes the action of the radula. The coral tissue is liquefied extracorporeally by ejected salivary secretions; thus the food is ingested in a fluid state. Unexploded nematocysts occur in the gut and even the zooxanthellae from the coral tissue are digested. The stomach is atypical of stenoglossans. Fankboner found that *Drupa cornus* would not feed on *Fungia* or dendrophylliid corals.

Drupella possibly also feeds on prey other than corals. As mentioned earlier, the occurrences with corals are inconsistent. There are presumably reliable observations of them feeding on mollusks. *Drupa cornus* was reported by Risbec [1932, as *Ricinula chaidea* (Duclos), a name that has been misapplied to male *Drupa cornus* according to Cernohorsky (1969, pp. 304–305)] to have drilled a small oyster, and a group to have attacked and partly eaten a living *Strombus* without drilling it. According to Taylor (1968, pp. 157, 173), but without details, *Drupa ochrostoma* is also molluscivorous.

Coralliophilidae ["Magilidae" + "Rapidae"]

This fairly small family, supposedly derived from the Muricidae, is reputed invariably to lack jaws and radulae (Carus, 1837, p. 197; Thiele, 1929, p. 300; Abbott, 1958, pp. 65–67; Gohar and Soliman, 1963, p. 106; Ward, 1965, p. 447). Excepting several species of *Coralliophila* living with gorgonians and zoanthids, *Rhizochilus* with antipatharians, *Latiaxis* with gorgonians (and other hosts?) and *Rapa* embedded in alcyonarians, all coralliophilids

on which there is any information as to mode of life occur with stony corals. Various species of *Coralliophila* and the genera *Quoyula, Magilopsis, Leptoconchus,* and *Magilus* are host-specific to stony corals (*Leptoconchus* possibly also to millepores). The four coral-specific genera are restricted to the Indo-Pacific and are derived from *Coralliophila*-like ancestors that lived externally on corals and had regularly coiled shells. *Quoyula* has a limpet-like shell adapting it for external life on corals; *Magilopsis* and *Leptoconchus* are ovoid and bore holes into corals, and *Magilus* becomes uncoiled and is sessile inside corals.

The coral-dwelling species of *Coralliophila* are all external, either on branched corals or in crevices on massive corals (often at the edge of a living colony). The coral substrate beneath them is always scarred (the foot appears to secrete a thin layer of calcium carbonate beneath it), and they appear never to move from their scars as do limpets. Incrusting organisms (vermetids, etc.) occasionally attach them to their coral substrates, and the gastropods still thrive when this happens. *C. violacea* (Kiener),[3] the most abundant Indo-Pacific species, has been reported on *Porites* at the Cocos-Keeling Islands, Indian Ocean (Maes, 1967, p. 133, pl. 2, fig. B), in Micronesia (Demond, 1957, p. 315), and at Clipperton Island in the eastern Pacific (Hertlein and Allison, 1960, p. 16). I have personally collected *Coralliophila violacea* in the Maldive Islands on massive *Porites*. The species is not specific to *Porites,* however. At Tahiti, I collected it on two genera of corals (unfortunately not collected or identified). At the Cocos-Keeling Islands, Indian Ocean, *Coralliophila erosa* (Röding) lives on branching *Acropora* and *Montipora* [Maes, 1967, p. 133, pl. 2, fig. C, as *Coralliophila deformis* (Lamarck), a synonym of *C. erosa* according to Abbott (1958, p. 66)]. At Barbados, West Indies, *Coralliophila abbreviata* (Lamarck) lives on *Montastrea annularis* (Ellis and Solander) [Ward, 1965]. At Great Abaco, Bahama Islands, I have personally collected *Coralliophila abbre-*

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[3] Abbott (1958, p. 66) has suggested that this is a synonym of *Coralliophila erosa* (Röding), but he seems to have lumped at least two species.

viata singly, in pairs, and in colonies on and under *Acropora palmata* [(G. Fischer)?] (Lamarck) and under and near the edge of mats of *Diploria clivosa* (Ellis and Solander). In the collection of the Academy of Natural Sciences of Philadelphia, there are specimens of *Coralliophila abbreviata* from the Florida Keys and Guadeloupe that were also with *Acropora palmata,* and at British Honduras I collected it with *Favia fragum* (Esper). *Coralliophila caribaea* Abbott (1958, pp. 66–67) lives mainly with gorgonians, but at Great Abaco (Bahama Islands) I have also found it on and under live and dead corals (*Acropora palmata* and *Diploria clivosa,* the same hosts as for *Coralliophila abbreviata* in the area).

In mode of life, *Quoyula* is similar to *Coralliophila. Quoyula* substrate scars are smooth peripherally (opposite the shell) and level, and minutely but deeply furrowed under the foot. These numerous furrows bear no relation to the microstructure of the coral skeleton, and they tend to anastomose and parallel one another. The foot appears to be permanently attached. According to Maes (1967, pp. 133–134, pl. 2, fig. D), *Quoyula madreporarum* (Sowerby) "is apparently restricted to corals of the family Pocilloporidae"; she recorded it from Madagascar with *Seriatopora* and at the Cocos-Keeling Islands, Indian Ocean, found it only with two species of *Pocillopora. Quoyula madreporarum* also occurs "imbedded in" *Pocillopora* in the eastern Pacific at Clipperton Island (Hertlein and Allison, 1960, p. 16). I have personally collected it in the Maldive Islands on *Pocillopora* branches and in the clefts between branches. In the Academy collection there are also specimens of *Quoyula madreporarum* collected on *Pocillopora* at New Caledonia, Fiji, the Cook Islands, and the Pacific coasts of Mexico and Nicaragua. However, Demond (1957, p. 316) records *Quoyula madreporarum* in Micronesia with *Montipora* (Acroporidae) as well as *Pocillopora* and *Stylophora* (Pocilloporidae). *Quoyula monodonta* (Blainville) is recorded in Micronesia with *Pocillopora, Seriatopora, Stylophora,* and branching *Porites* (Demond, 1957, p. 316), and in the Seychelles with *Porites nigrescens* Dana (Taylor, 1968, p. 169, as *"Quoyala"*). Maes (1967, pp. 133–134, pl. 11, figs. B–C)

has shown how *Quoyula* develops different growth forms depending on the species of host coral. *Quoyula madreporarum* probably is an ecotypic form of *Q. monodonta* (the sculptural differences mentioned by Demond are inconstant).

The three genera dwelling internally in corals are closely related. *Leptoconchus* has been thought to be juvenile *Magilus,* but Gohar and Soliman (1963) have shown that sexual maturity occurs in both *Leptoconchus* and *Magilopsis.* Adult *Leptoconchus* supposedly always lacks an operculum while both *Magilopsis* and *Magilus* retain an operculum (Carus, 1837, figs. 5–6, a[1]; Gohar and Soliman, 1963, p. 104). The possibility that *Magilus* is a growth form of *Leptoconchus* and/or *Magilopsis* is still not excluded because the *Magilus* form might develop only in fast-growing corals. According to Gohar and Soliman (1963), both *Leptoconchus* and *Magilopsis* bore mechanically into living coral skeletons. A burrow is connected to the exterior only by a small opening opposite the anterior siphon of the gastropod, which is always situated apex down. Professor John W. Wells has observed (in litt.) that *Leptoconchus* burrows are usually at one end of a stomodaeal slit (i.e., near the mouth of a polyp). *Magilopsis lamarckii* (Deshayes) is recorded in *Acropora* at the Tuamotus and in *Goniastrea retiformis* (Lamarck) in the Marianas (Morrison, 1954, p. 14; Demond, 1957, p. 317; Cloud, 1959, pp. 391–392, pl. 129, figs. D–E), and in *Cyphastrea* and rarely *Montipora* in the Red Sea (Gohar and Soliman, 1963). From Madagascar, there are specimens of *Magilopsis lamarckii* in the Academy collection that were found in a massive *Porites. Leptoconchus cumingii* Deshayes is recorded (erroneously?) in *Millepora* at Mauritius (Martens, 1880, p. 238), and in *Favia stelligera* (Dana) and *Goniopora* in the Red Sea (Gohar and Soliman, 1963). *Leptoconchus globulosus* Sowerby is recorded in *Goniastrea* and *Echinopora* in the Red Sea (Gohar and Soliman, 1963, as *Leptoconchus* "*globosus* Deshayes").

In form and habit, *Magilus antiquus* Montfort (the only species in the genus) is the most specialized coral symbiont among prosobranchs. The juvenile shell is coiled and remarkably

variable in size and shape, while the thick adult shell is an uncoiled, irregular tube deeply embedded in a living coral skeleton but with the aperture at the surface. The coiled apex and part of the tube become completely calcified internally, while distally the aperture keeps pace with growth of the surrounding coral (Carus, 1837; Lamy, 1924). *Magilus antiquus* has been collected together with *Magilopsis lamarckii* in *Goniastrea retiformis* in the Marianas (Demond, 1957, pp. 316–317, fig. 25; Cloud, 1959, p. 392, pl. 129, figs. A–B). In the Academy collection there are specimens embedded in *Platygyra* and/or *Leptoria* from Mauritius and the Bismarck Archipelago. Carus mentioned (1837, pp. 195–196) that Rüppell found *Magilus* in the Red Sea only in a coral closely related to *"Maeandrina phrygia"* [*Madrepora phrygia* Ellis and Solander], the type species of *Leptoria*. All these coral hosts are in the family Faviidae, but these records are too few to make it certain that *Magilus* is host-specific.

There are divergent opinions as to the food and mode of feeding of coralliophilids, especially of those living internally in corals. While accepting that the external coralliophilids "feed suctorially on coral tissues," Morton (1958, p. 95) also believed that *Magilus* is "evidently a ciliary feeder." Gerlach has extended this idea to *Leptoconchus* (Gerlach, 1960, p. 360, fig. 4, as *"Leptoconcha"* [wrongly reidentified in the 1961 translation as a *Magilopsis*]), classifying this as a suspension feeder taking zooplankton. These ideas can be traced back to Yonge (1932, p. 274), who stated of a preserved *Magilus*:

It proved impossible to determine the mode of feeding. Radula and jaws are absent, but there is no certain indication of a ciliary feeding mechanism. Examination of the living animal might reveal this. No sign of a style-sac or a gastric shield was found in the alimentary canal (not very well preserved), and this indicates that the animal is probably not a ciliary feeder. As shown later, all the Gastropoda known to feed by ciliary currents possess styles. It is possible that the animal may possess a sucking pharynx and feed on the tissues of the coral, or take zooplankton seized by the tentacles of the polyps. A study of the feeding and other habits of *Magilus* and of the other members of the family Coralliophilidae would be of the greatest interest.

There is still no direct information on the food and feeding of the three genera living internally in corals. In their excellent study of the anatomy and mode of life of *Magilopsis* and *Leptoconchus,* Gohar and Soliman (1963, pp. 106, 108) did not observe feeding, could detect neither animal nor plant remains in the gut, but concluded that these species "are probably not ciliary feeders."

In the best study published to date on the feeding of any prosobranch symbiotic with corals, Ward (1965) concluded that the saliva of *Coralliophila abbreviata* aids in penetration of the coral epidermis, and that the muscular proboscis is used as a pump to ingest the zooxanthellae-containing soft tissues. Earlier, Demond (1957, p. 315) had hinted that *C. violacea* is nutritionally dependent on living corals, and Keen (1958, p. 370) had stated explicitly that *Quoyula madreporarum* feeds upon corals.

In view of the anatomical uniformity of coralliophilids and in the absence of any direct or anatomical evidence of ciliary feeding, I believe that they all feed suctorially on their hosts and the mucus thereon. Even the external coralliophilids are stationary and have a limited number of polyps within reach of their proboscises. Coralliophilid proboscises are greatly extensible, and the hosts show little or no sign of injury other than for the substrate scars and burrows. Coralliophilids thus would seem well adapted parasites, injuring their hosts but slightly. (Ward believes, however, that *Coralliophila abbreviata* contributes to the destruction of *Montastrea annularis* at Barbados.)

In all coralliophilids, the sexes are separate and the males have a penis. According to Gohar and Soliman (1963, p. 112), fertilization in *Magilopsis* and *Leptoconchus* is internal, and (peculiarly) the "spermatozoa are shed in the surrounding water and gain access to the female with the ingoing current." The unattached, saccate egg capsules of coralliophilids are unique among prosobranchs in being retained in or near the mantle cavity. So far as is known, the veligers are all planktotrophic. The only information on settlement is Gohar and Soliman's tantalizing observation (1963, p. 123) that *Leptoconchus* and *Magilopsis* veligers, set free on the surface of a living coral, "remained in their position for some days un-

affected, although directly lying on the flourishing coral polyps. The coral did not kill nor devour the larvae. . . . The polyps tended to close the mouth openings when the larvae came nearby."

DISCUSSION AND CONCLUSIONS

The living tissues of both hermatypic and ahermatypic stony corals are subject to predation and parasitism by a surprising variety of animals, including bony and cartilaginous fishes, asteroids, crustaceans, polychaetes, and gastropods. Most of these are facultative predators, but some of the crustaceans and gastropods consistently live with and feed on the mucus and living tissues of their hosts. These symbionts are all shallow-water, tropical species; many are Indo-Pacific in distribution. There are preferences for suitably shaped coral hosts and for particular genera or families, but outright host-specificity is uncommon. Other possible predators and parasites of corals include turtles, echinoids, pycnogonids, and protozoans.

Among prosobranch gastropods, a few species in the Architectonicidae, Epitoniidae, Ovulidae, Muricidae, and Coralliophilidae are known definitely to feed on corals, and by extrapolation most other species in these families living with corals can be assumed to do so. Among opisthobranch gastropods, a few eolids are coral symbionts (notably the tergipedid genus *Phestilla*); there is also a doubtful report of one doridoid nudibranch (*Phyllidia bourgini*) feeding on corals. These gastropods range from foraging predators that crawl in quest of their coral prey to sedentary or sessile symbionts with corals—notably the coralliophilids, which feed parasitically on coral polyps without seriously injuring them.

Coelenterate-feeding gastropods show a variety of structural modifications of the radula and of the anterior end of the gut. Ovulids and some architectonicids have taenioglossate radulae that are little changed, but other architectonicids, epitoniids, and janthinids have radular teeth each usually with a hooked and 1- to 3-pointed distal end. *Drupella* has a stenoglossan radula with remarkably elongate lateral teeth, likewise hooked distally. Both coralliophilids and phyllidiids lack radulae and jaws, and feed suctorially. Both architectonicids and epitoniids have an elongate, invaginable proboscis and a cuticularized esophagus which may prevent injury from nematocysts (Robertson, 1970). The proboscis of *Drupella* (Muricidae) is cuticularized exteriorly.

Otter believed (1937, p. 348) that a "layer of living [coral] polyps catches and devours as food all free-swimming larvae . . . which happen to come near them." It has been claimed that this is wrong in the case of veligers of the two coralliophilid genera that bore into corals; these larval and postlarval gastropods are said not to be eaten, and neither do they kill the polyps while beginning to bore and to feed. *Philippia* postlarvae, on the other hand, have no immunity to predation by corals (Robertson, Scheltema and Adams, 1970).

ADDENDUM (ADDED IN PRESS)

A tenth family of fishes definitely includes predators on stony coral polyps, the Blenniidae (combtooth blennies). Near Elat, Israel (Gulf of Aqaba), *Cirripectus* sp. and *Meiacanthus* sp. have this habit (*teste* Dr. Lev Fishelson, Tel-Aviv University, August 1969).

The latest literature on the population explosion of the asteroid *Acanthaster planci* includes Chesher (1969) and Fischer (1969).

Although not strictly a predator or parasite, the newly described Indo-Pacific mytilid bivalve *Fungiacava eilatensis* Soot-Ryen (in Goreau et al., 1969) lives in chemically excavated cavities in fungiid corals, and "the long

siphons open into the coelenteron where food, consisting probably to a significant extent of symbiotic zooxanthellae discharged from the tissues of the coral, is collected."

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