

REVIEW

Chemical adaptations in the Octocorallia: evolutionary considerations

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ABSTRACT: The Octocorallia are a highly diverse group, rich in secondary compounds which serve several ecological functions, including predator defense, interspecific competition for space, anti-fouling, and reproduction. The Alcyonacea are characterized by high frequencies of ichthyotoxicity and feeding deterrence which are not generally correlated with each other. This may be due to the multiple functions these compounds perform, masking correlations which would otherwise be apparent. Correlations between ichthyotoxicity and physical defense exist, but only at higher levels of taxonomic resolution. One resultant selective advantage of variance in ichthyotoxicity and feeding deterrence may be Diffuse Batesian Mimicry, whereby the toxic or feeding-deterrent characteristics of a majority of species help to protect a taxon with a small number of general morphological types and small variance in coloration from generalist predators. Surface-brooded planulae of Indo-Pacific coral species, similar in appearance but not possessing toxic or feeding deterrent attributes, may be similarly protected. The chemical characters of octocorals may serve the same functions which morphological characters in scleractinian corals serve, particularly in predator defense and competition for space. Most octocorals lack a rigid skeleton possessed by scleractinians, which can protect polyps from predation. Octocorals also lack toxic stinging nematocysts common to scleractinians, but possess allelopathic capabilities. In some octocorals, 'non-toxic' nematocysts on sweeper tentacles may still be effective in competition for space; in others, aggressive interactions can be avoided through re-orientation or movement, resulting in directed growth. Octocoral orders are distributed inequitably between the tropical Atlantic and Indo-Pacific. The Gorgonacea dominate the former; the Alcyonacea, the latter. Octocoral species diversity is higher in the western Indo-Pacific, as is the abundance and diversity of secondary metabolites and their functions. This may be a result of differential levels of extinction between the 2 regions during the early Miocene and the late Pliocene/early Pleistocene, with high extinction rates having been experienced in the Caribbean. These extinctions may also have affected radiation in the secondary metabolites produced by those species and the functions which those metabolites serve. Secondary metabolites appear to have contributed to the evolutionary success of the Indo-Pacific Alcyonacea. In accordance with the Time-Stability hypothesis, we believe that this high abundance and diversity evolved in the Indo-Pacific under conditions of reduced climatic change and lower extinction levels, when compared to the Caribbean.

INTRODUCTION

Coral reefs are among the most ancient structures on earth built by living organisms. Although many people associate coral reefs with hard or scleractinian corals, in the Indo-West Pacific, soft corals or octocorals can dominate many reefs (Benayahu & Loya 1977, Nishihira 1981, Dinesen 1983). Most of these

octocorals belong to the order Alcyonacea, a highly diverse group of benthic colonial invertebrates. In the Caribbean, a similar co-dominance can occur between scleractinians and octocorals, but the major octocoral representatives there are the Gorgonacea, including the sea fans and sea whips – highly flexible, often branched sessile epifauna (Bayer 1957, Wells 1957).

One of the reasons for the evolutionary success of alcyonaceans in the Indo-West Pacific is considered to be the high levels of secondary metabolites commonly found in their tissues (Tursch et al. 1978, Coll 1981). The types and concentrations of these compounds vary greatly between species (Faulkner 1977, 1984, 1986, 1987, 1988, 1990, 1991). These compounds are now known to play a number of ecological roles in these organisms (Bakus et al. 1986, Sammarco & Coll 1988).

Here, we review and discuss some aspects of the chemical ecology of the Octocorallia, particularly the Alcyonacea and Gorgonacea, and how it has contributed to the evolutionary success of this taxon. The primary factors we will cover fall into 4 categories: (1) the role of secondary compounds in defense against predation, competition for space, anti-fouling, and enhancement of reproduction; (2) mimicry as a broad predator defense mechanism, assisting in protection of the order Alcyonacea as a whole; (3) secondary compounds in the Alcyonacea as functional equivalents to certain defense characters in the Scleractinia; and (4) high species diversity in the Alcyonacea as it relates to the high diversity of alcyonacean toxins, the variety of their functions, and their biogeographic distribution.

FUNCTIONS OF SECONDARY METABOLITES IN OCTOCORALS

The Alcyonacea

Predator defense

A high proportion (ca 60 %) of the soft corals on the Great Barrier Reef are ichthyotoxic (Coll et al. 1982b, Coll & Sammarco 1983, authors' unpubl. data). Here, ichthyotoxicity is defined as toxic to standard test fish (*Gambusia affinis*) exposed to crude aqueous extracts of a soft coral (sensu Yamanouchi 1955). Effects noted in test fish range from respiratory stress through disorientation to mortality. This is admittedly a simple test but has served well as an indicator of the presence of cytotoxic or other bio-active molecules.

The soft coral *Sinularia flexibilis* contains a range of diterpenes, which vary in concentration from collection to collection. With this species, only 11,12-deoxyflexibilide (Fig. 1,1) is ichthyotoxic to any appreciable extent (Y. Uchio et al. pers. comm.). (We will refer back to other compounds from *S. flexibilis* later in the review.)

Further tests with *Gambusia affinis* and these aqueous soft coral extracts have demonstrated that ca 75 % of these extracts possess feeding deterrent characteristics. Strangely enough, this deterrence, whether via taste, olfaction or gustatory cues, does not appear to be correlated with ichthyotoxicity as assessed by these

naive predators (La Barre et al. 1986a). Thus, we believe that there are a number of synergistic factors which may be acting to alter the perception of taste in the test fish.

Sinularia flexibilis possesses significant feeding deterrence, and a second metabolite derived from it, dihydroflexibilide (Fig. 1,2), has been recently identified as being responsible for this character (T. Aceret pers. comm.). In the case of *Sinularia maxima*, Wylie & Paul (1989) identified diterpene (Fig. 1,3) as an ichthyodeterrent.

Some toxic secondary compounds produced by alcyonacean soft corals are actually sequestered and stored by specialist predators and used for their defense. One example is the molluscan predator, *Phyllodesmium longicirra* (Coll et al. 1985). These and other selective predators may possibly be attracted to soft coral colonies by their toxic terpenoids (Hadfield & Ciereszko 1978), which may also stimulate egg-laying in certain molluscs such as *Ovula ovum*. This mollusk consumes (Coll et al. 1983) and lays eggs on (K. Muzik pers. comm.) toxic soft corals of the genus *Sarcophyton*.

Ichthyotoxicity in the Alcyonacea is negatively correlated with the occurrence of certain physical morphological attributes specifically associated with anti-predator defense (Sammarco et al. 1987); that is, the presence of toxicity may be associated with the absence of physical defense against predators. This relationship only becomes clear, however, at high levels of taxonomic resolution (at the genus level, or within selected families). Such physical characters include polypary armament, micro-armament of the individual polyp, and mineralization of the coenenchyme.

Competition for space

Terpenoid secondary metabolites function as allelopathic agents in interspecific competition for space in certain alcyonaceans (Sammarco et al. 1983). They can cause tissue necrosis and growth inhibition in scleractinian corals both through direct tissue-to-tissue contact or through the water column in the absence of contact (Coll et al. 1982a). In the case of *Sinularia flexibilis*, the active allelopathic agents are dihydroflexibilide (Fig. 1,2), and the more potent flexibilide (Fig. 1,4). The effectiveness of the allelopathic compounds responsible for these deleterious responses varies greatly between species. The susceptibility of the competing species to the released toxins is also highly species-specific, whether the competitor for space is a scleractinian or another alcyonacean coral (Sammarco et al. 1985, La Barre et al. 1986b). These important chemically mediated competitive abilities in the Alcyonacea

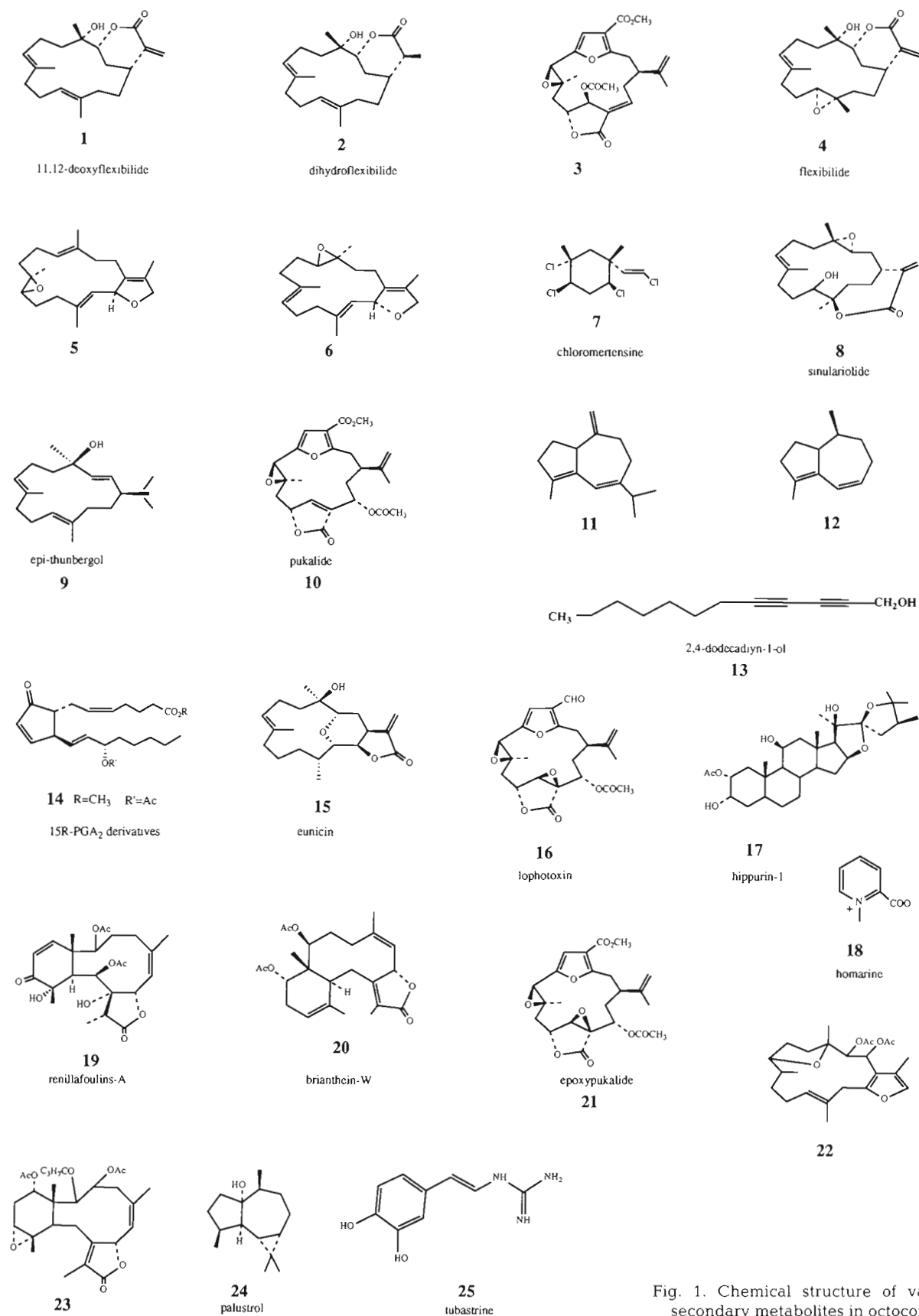


Fig. 1. Chemical structure of various secondary metabolites in octocorals

may be enhanced by various behavioural and physiological adaptations. Such adaptations may include: (1) alteration of internal hydrostatic pressure to cause bending of the organism away from its competitor; (2) the secretion of a polysaccharide cuticle to protect itself against its competitors' offensive or defensive mechanisms; (3) redirected growth away from and sometimes over its competitor (La Barre & Coll 1984, La Barre et al. 1986b), and (4) sweeper tentacles in some Caribbean (Sebens & Miles 1988) and Indo-Pacific (Alino 1989) gorgonaceans.

In addition, predation and environmental factors such as food, light, and turbidity may exert control over competitive balance between certain species of octocorals and scleractinians, whether chemically mediated or not. In the central region of the Great Barrier Reef, it appears that higher nutrient concentrations in inshore waters may have created a situation where environmental conditions slightly enhance growth rates and competitive advantage in the octocoral *Clavularia inflata* over even the fastest growing scleractinian corals, such as *Acropora longicyathus*. This competitive trend can be reversed between certain species if the competing pair is transplanted to mid-shelf waters where nutrient concentrations and related conditions (turbidity, zooplankton, density, etc.) are reduced. Thus, competition for space in octocorals is also subject to variance depending upon environmental factors (Alino et al. 1992).

Anti-fouling

A range of cembranoid diterpenes, including Structures 5 and 6 (Fig. 1), has been shown to inhibit growth of the common filamentous alga *Ceramium codii*, observed in the field to attach to the polypary of alcyonacean soft corals (Coll et al. 1987). This process, however, is not entirely one way. Recent investigations of associations between soft corals and the red alga *Plocamium hamatum* have revealed that the chlorinated monoterpene, chloromertensine (Fig. 1,7) present in this alga can kill the soft coral *Sinularia cruciata* (Coll et al. 1988, De Nys et al. 1991). This same compound also exhibits anti-feedant and anti-fouling properties (Hay et al. 1989).

In *Sinularia flexibilis*, sinulariolide (Fig. 1,8) is capable of inhibiting algal overgrowth, as shown by laboratory experiments (Tursch et al. 1978).

Reproduction

A range of secondary metabolites also appears to play an important role in reproduction in the alcyonaceans. Certain diterpenes (e.g. *epi-thunbergol* and *pukalide*,

9 & 10 respectively of Fig. 1) are present in the eggs of the alcyonaceans *Lobophytum compactum* and *Sinularia abrupta*, respectively; yet they cannot be detected in the tissue of the parent colony (Bowden et al. 1985, Coll et al. 1989). These egg-specific terpenes do not appear to be effective anti-feedants against reef fish, as fish consume large amounts of the eggs; nor are they effective antibiotics against marine bacteria (Alino 1989).

Recent evidence suggests that they play a role in spawning. Both *epi-thunbergol* and *pukalide* stimulate polyp contraction and thus egg release (Pass et al. 1989). Additional recent experimentation has demonstrated that *epi-thunbergol* is the active vector in sperm chemotaxis within *Lobophytum compactum* (Coll pers. comm.). In other cases (e.g. *Clavularia inflata*), sesquiterpenes and their degradation products, such as Structures 11 and 12 (Fig. 1), have been implicated as anti-feedants in protecting externally brooded eggs (Coll et al. 1988). Preliminary investigations have also identified a lipid-derived molecule, 2,4-dodecadiyn-1-ol (Fig. 1,13), as the principal sperm attractant in the scleractinian coral *Montipora digitata* (Coll et al. 1990).

The multiplicity of functions identified for secondary metabolites in the Alcyonacea make it nearly impossible to predict their function in any given species (Sammarco & Coll 1990).

The Gorgonacea

Predator defense

Toxicity has been well documented in the Gorgonacea. Data on the frequency and distribution of this character in this group, however, have not yet been collated; thus, a complete, direct comparison between the Alcyonacea and Gorgonacea in this regard would be difficult.

Studies of gorgonacean octocorals have implicated toxic secondary metabolites in defense against predators (Ciereszko & Karns 1973, Pawlik et al. 1987). Prostaglandins (e.g. Fig. 1,14) have been shown to be effective feeding deterrents against a range of reef fish (Gerhart 1984), while toxic cembranolides (e.g. Fig. 1,15) have been postulated to play an anti-predatory role in other gorgonians (Lee et al. 1981). Lophotoxin (Fig. 1,16), a highly toxic terpenoid, is derived from the aposymbiotic sea whip *Lophogorgia chilensis*, and has been implicated in defense against predators in this species (Fenical et al. 1981). Novel steroidal metabolites, such as hippurin-1 (Fig. 1,17), have been isolated from *Isis hippuris*, a gorgonian from the Great Barrier Reef (Kazlauskas et al. 1977). Their ecological and/or physiological functions within the organism, however, are not known.

Toxic terpenoids are distributed within a single gorgonian colony unevenly. Concentrations are apparently higher in those portions of the colony which receive higher intensities of predation, particularly the thin, polyp-rich, terminal branchlets (Harvell et al. 1988, Harvell & Fenical 1989).

Competition for space

Competition in gorgonaceans has not been studied extensively. Encrusting morphs, such as some of the *Erythropodium* spp., can dominate certain habitats on Caribbean reefs and can readily overgrow scleractinian corals and other sessile epibenthic organisms (Karlson 1980). The majority of gorgonians, however, are erect in form, greatly reducing the need for expansion in 2-dimensional space – a common requirement in encrusting forms.

With respect to the erect forms, whip corals or holaxonians can cause tissue necrosis upon contact with their hetero-specific neighbours (Theodor 1966, 1971, 1975). It has not been confirmed, however, that this response is caused by allelochemical agents. The Gorgonacea are known to be rich in secondary compounds (Faulkner 1977, 1984, 1986, 1987, 1988, 1990, 1991) which, based upon the data available to date, appear to function primarily as anti-predator or anti-fouling (see below) agents.

Encrusting gorgonians, like *Briareum* and *Erythropodium* species (Karlson 1980), utilize rapid growth rates and possibly specially adapted tentacles, similar to the sweeper tentacles of certain scleractinians, to expand their living space (Sebens & Miles 1988, Alino 1989, Alino et al. 1992).

Anti-fouling

Various Caribbean gorgonians have exhibited anti-fouling characteristics, and these have often been associated with novel metabolites. These compounds can inhibit successful settlement and survival of algae [homarine (Fig. 1,18), Targett et al. 1983] and sessile epifauna [Ritschoff et al. 1985; renillafoulins (Fig. 1,19), Keifer et al. 1986; pukalide (Fig. 1,10), Gerhart et al. 1988] on these octocorals. Certain metabolites including brianthein-W (Fig. 1,20), found within *Briareum* sp., have been shown to have insecticidal properties (Cardellina et al. 1984).

Some diterpenes involved in anti-fouling are effective against both adult and larval forms of marine organisms (Ritschoff et al. 1985, Keifer et al. 1986, Gerhart et al. 1988).

Reproduction

The chemical aspects of gorgonian reproduction have not been studied in detail thus far. A review of compounds found within these organisms, however, has revealed the presence of pukalide (Fig. 1,10) (Gerhart et al. 1988) and epoxy-pukalide (Fig. 1,21) (Ksebati et al. 1984). These compounds have been found to occur within the eggs, but not the tissue, of the alcyonacean genus *Sinularia* (Coll et al. 1989). It is possible that they play a similar role within the Gorgonacea, although this remains to be experimentally confirmed.

Chemotaxonomy

Secondary metabolites in the Gorgonacea have been used to establish phylogenetic relationships between various members of the order (Gerhart 1983). This has resulted in a cladistically deduced chemotaxonomic phylogeny, which agrees well with relationships established using conventional taxonomic techniques (Bayer 1981). This was accomplished despite some of the potential drawbacks associated with chemotaxonomy (Sammarco & Coll 1988, p. 108–109). These include: (1) the publication of only novel compounds in the chemical literature by investigators, rather than details of all secondary metabolites found in an organism; and (2) the increase in resolution of analytical chemistry over the past 20 years, implying that in organisms analysed years ago with older technology, many compounds may have been missed.

CO-EVOLUTION

The Alcyonacea

Mimicry

Mimicry is defined as the close resemblance of one organism (the mimic) to another (the model) by which a third organism (the operator) is deceived (see Brower 1969, Pianka 1983). Usually the mimic is a prey organism, heavily preyed upon by one species of predator, which resembles a second morphologically similar model species which is toxic, distasteful, or possesses some degree of protection from the predator which the mimic does not have.

Batesian mimicry is specifically the close resemblance of a palatable or harmless mimic to an unpalatable or venomous model in order to deceive a predator (see Lincoln et al. 1982, Pianka 1983, also see Brower 1960, and McNaughton & Wolf 1979 for general discussion). The mimic gains protection by association or

similarity. The predator generally learns the morphological (or other) patterns of the model toxic prey, associates a negative feeding response with it, and in turn transfers this association to the mimic.

Here we define Diffuse Batesian Mimicry (Sammarco & Coll 1988) as the close resemblance of a very large number of unpalatable or toxic models belonging to a single taxon and a similar number of palatable or harmless mimics, thereby affording protection to the taxon as a whole by association or similarity.

Toxicity, palatability, and physical attributes associated with predator defense vary considerably across the Alcyonacea. The trade-off between chemical and physical defense discussed earlier is not as obvious as one might suspect. One reason for this could be that these compounds play a number of roles other than predator defense (see Sammarco & Coll 1990). We also believe, however, that a second mechanism, not exclusive of the first, may also be operating. That is, this clouded association between morphology and ichthyotoxicity may represent a form of protection by association: Diffuse Batesian Mimicry.

A large proportion of alcyonaceans possess toxins. These species fall into only a few general morphological types (e.g. branching, encrusting or massive upright). Within each category, there are probably as many toxic as non-toxic examples. In addition, many species across genera are similar in appearance, and the variance in toxicity within genera is often as high as that between genera (Coll et al. 1982b, Coll & Sammarco 1983). This combination of traits may well serve as a blanket deterrent to generalist predators for the order as a whole, because of the difficulties associated with a predator learning to identify acceptable food choices by visual cue alone.

Co-evolved feeding relationships

In some cases, specialist soft coral predators such as *Chaetodon melannotus* feed upon some of the most ichthyotoxic octocoral species with impunity (Randall 1967, Anderson et al. 1981, Motta 1988, Alino 1989).

Chaetodon melannotus, a specialist predator, identifies its soft coral prey via visual cues (Alino et al. 1989, Alino 1989). It further modifies its food choice on the basis of the chemistry (Alino et al. in press). This predator is most likely co-adapted to detoxify the secondary metabolites present in its food, much like *Ovula ovum* (Coll et al. 1983) and *Cyphoma gibbosum* (Gerhart 1986). Alino (1989) and Alino et al. (in press) demonstrated that none of the original diterpenes known to be present in the soft coral could be found in the fecal pellets of fish feeding on this soft coral. The fish appears to be capable of metabolizing these compounds.

Toxicity and reproduction

Two major forms of sexual reproduction in the Octocorallia are brooding and spawning with external fertilization. Although spawned eggs of many species have been shown to contain significant amounts of terpenoid metabolites, they do not appear to possess effective feeding deterrents (Bowden et al. 1985). The survival of reproductive propagules in this group appears to arise not from chemical defense but from predator satiation. Eggs are often released in a multi-species mass spawning event, encompassing both scleractinian and octocoral species alike (Harrison et al. 1984, Babcock et al. 1986, Alino & Coll 1989).

Many of the non-spawning species, including *Clavularia inflata*, *Pachyclavularia violacea*, and *Briareum stechei*, brood their developing larvae on the surface of the parent colony where they are openly exposed to predators. It has now been shown that the planulae of *C. inflata* possess significant feeding deterrent properties, as determined through studies of the highly specialized octocoral predator *Chaetodon melannotus*. The planulae of *P. violacea* and *B. stechei* both have bright brownish-red coloring, similar morphology, and are also surface-brooded. The planulae have not, however, been assessed for feeding deterrent properties (Alino 1989).

Colonies of *Pachyclavularia violacea* are well defended chemically and possess diterpenoid compounds related to Structure 22 (Fig. 1). As assessed by *Gambusia affinis* bioassays, the aqueous extracts are ichthyotoxic and confer significant feeding deterrent properties on regular fish food. By contrast, *Briareum stechei*, which also contains diterpenes like Structure 23 (Fig. 1), is almost totally benign under both assay systems (Alino 1989). Because of the common co-occurrence of these species, *B. stechei* planulae may be protected from predation by association with toxic *P. violacea* planulae through Diffuse Batesian Mimicry. *Clavularia inflata* spawns 2 wk later than *P. violacea* and *B. stechei*, does not have similar morphology to the other brooding planulae, and so, possesses its own suite of feeding deterrents including Structures 11 and 12 (Fig. 1). This represents an interesting area for continued research.

The Gorgonacea

Several studies have examined the co-adapted associations between gorgonians and selected predators. In particular, Gerhart (1986) has demonstrated that the gastropod *Cyphoma gibbosum* is immune to prosta-glandins found within its prey – *Plexaura homomalla* – in the Caribbean.

The same gorgonacean is also known to release chemicals which act as kairomones. In this case, the hydrozoan *Millepora complanata* responds to the presence of these compounds by directed growth towards, and eventual overgrowth of, the gorgonian to enhance its colony size and vertical growth rate (Wahle 1980).

Where secondary metabolites of organisms interact with marine larvae or adults, the ultimate effect may not necessarily be negative for the affected organism. For example, cembranolides [including eunicin (Fig. 1,15)] derived from gorgonian octocorals are known to immobilize veliger larvae of the nudibranch *Phestilla sibogae*. This nudibranch is a natural, co-adapted predator of these gorgonians. It has been proposed that this is a mechanism by which settlement of this veliger on the gorgonian is enhanced, allowing it to mature on its natural prey. In this way, the probability of the offspring locating a suitable and ample supply of food is increased (Hadfield & Ciereszko 1978).

COMPARISON OF SOME ADAPTATIONS IN THE OCTOCORALLIA AND THE SCLERACTINIA

Evolutionary background

Grasshoff (1984) claims both that the Octocorallia and the Hexacorallia (to which the Scleractinia belong) were derived from a primitive Anthozoan ancestor with a multi-mesenterial polyp [but see Schmidt (1974) for alternate hypothesis]. According to Grasshoff, the split between these 2 major taxa occurred during the early Triassic (245 million years ago). During this period, the Hexacorallia apparently split into a number of groups, one of which was the Scleractinia. This point in geological time represented a point of great radiation for both the Octocorallia and the Scleractinia.

Nematocysts

One difference between the 2 groups involves evolution of the cnidoblast or stinging cell, a unique coelenterate feature. In the Scleractinia, stinging nematocysts perform at least 2 functions: food capture (Barnes 1974) and aggression or defense against sessile neighbors in competition for space [see Lang & Chornesky (1990) for review].

Highly potent toxins are often associated with specific types of coelenterate nematocysts. The specialized cells assist in prey capture (usually zooplankton) using proteinaceous toxins and assist competition for space by effecting extracoelenteric digestion of other sessile benthic organisms. Nematocysts may be associated with specialized morphological structures,

such as extruded mesenterial filaments or sweeper tentacles.

By contrast, the Octocorallia generally lack stinging nematocysts (e.g. mastigophores) and therefore do not use proteinaceous toxins for prey capture. Instead they possess rhabdoidic heteronemes (β -rhabdoids; Schmidt 1974) and utilize atrichous isorhizas or glutinants to entangle their prey (Meglitsch 1972). Recent evidence has demonstrated, however, that some species, including the Indo-Pacific *Briareum stechei* (Alino 1989) and the Caribbean *B. asbestinum* (Sebens & Miles 1988) are indeed capable of producing sweeper tentacles and killing their neighbors. The frequency of occurrence of this defence mechanism within the Gorgonacea is not yet known.

The role of secondary metabolites in prey capture by octocorals remains to be investigated. To date, there is no evidence for it.

Toxins and refuge

Branching scleractinian corals provide structural refuge for associated organisms such as fish. Octocorals, although lacking these structural attributes, can provide a chemically mediated refuge for some fish. In the case of *Abudefduf leucogaster* (Pisces) in Papua, New Guinea, this is effected through the release of toxic sesquiterpenes including palustrol (Fig. 1,24) by the soft coral *Litophyton viridis* (Coelenterata, Anthozoa), stimulated by direct contact with the fish (Tursch 1982).

The Octocorallia are generally characterized by an abundance of secondary metabolites with varying functions. The Scleractinia have not been studied as thoroughly for secondary compounds. Evidence is now emerging which demonstrates that bioactive secondary compounds are present in the Scleractinia as well. Sakai & Higa (1987) have found a compound, tubastrene (Fig. 1,25), with anti-viral activity in the scleractinian coral *Tubastrea aurea*. Further evidence of secondary metabolites from within the Scleractinia, however, remains scant. This area is only now opening up and deserves further investigation.

BIOGEOGRAPHY: CARIBBEAN VERSUS INDO-PACIFIC OCTOCORALS

Distribution in the Recent

Both the Octocorallia and the Scleractinia have pan-tropical distributions (Levinton 1981). Not all orders within each, however, are equitably distributed between the Caribbean and the Western Pacific. In the

Indo-Pacific, the Alcyonacea are the most conspicuous and abundant group of octocorals – particularly the families Nephtheidae, Siphonogorgiidae, and the Alcyoniidae (Wells 1957). The orders Stolonifera and Telestacea may also be commonly found there. In the shallow waters of the Caribbean, the Gorgonacea are the best represented – particularly the families Gorgonidae, Plexauridae, and Muriceidae (Bayer 1957). The Alcyonacea are all but absent in the Caribbean.

As is the case with many benthic marine organisms (Stehli & Wells 1971, Goldman & Talbot 1976, Vermeij 1978, Stanley 1979, Briggs 1987), the family, generic, and species diversity of corals, both soft and hard, is much higher in the Indo-Pacific than in the Caribbean (Bayer 1957). With respect to the Scleractinia, there are at least 80 genera and 700 species in the Indo-Pacific, but only 26 genera and ≥ 60 species in the Atlantic (Wells 1957, 1973, Goreau & Wells 1967). For example, the scleractinian *Acropora* alone has about 70 species in the Indo-Pacific, but only 3 in the Caribbean. With respect to alcyonacean octocorals, there are > 90 species of the Indo-Pacific genus *Sinularia* alone; in the Caribbean, there are 3 alcyonacean species. As with the scleractinians, there is little if any overlap in species between Indo-Pacific and Caribbean octocorals.

Links between species diversity and chemical diversity

The question arises as to whether the selective advantage conferred upon the Alcyonacea by their chemistry has contributed to their differential evolutionary success in the Indo-Pacific when compared to the Gorgonacea in the Atlantic. The answer may well be 'yes', but 'contributed to' would be the appropriate phrase, rather than 'responsible for'. The question must be considered in the context of other important influencing factors – particularly historical ones.

The benthic marine fauna of the tropical Western Atlantic have experienced several major perturbations and extinctions within the past 25 million years. During the pre-Miocene (> 25 million years ago), the Scleractinia were known to have a pan-Tethyan distribution, and the fauna of the western Pacific and the western Atlantic were apparently quite similar (Rosen 1978, Stanley 1979, Veron 1986). Two sets of extinctions occurred since that time in the Caribbean. The first occurred in the early Miocene with the closing of the Isthmus of Panama; this separated the Indo-Pacific from the newly formed Atlantic (Rosen 1978, Stanley 1979, 1984, Veron 1986). The second was associated with the late Pliocene/early Pleistocene, accompanying the onset of the last major glaciation (Stanley 1979, 1981, 1984, 1985, 1986). Both

events were associated with major climatic and oceanic cooling.

Many scleractinian species suffered extinction through both the first (Wells 1956) and second (Dana 1975, Frost 1977) events in the Caribbean but not in the Indo-Pacific. Kuhlmann (1985) explains that the generally north-south orientation of the Rocky Mountains allowed the southerly advance of continental ice without significant obstacle. The generally east-west orientation of the Eurasian mountain ranges – from the Pyrenees through the Himalayas to the Aleutians – are believed to have deterred southerly migration of the glaciers in that part of the world. Parts of the Atlantic apparently cooled considerably in comparison to the Indo-Pacific, causing extinction of various genera of corals (e.g. *Fungia*, *Pocillopora*, *Stylophora*, *Montipora*, etc.). In addition, the Indo-Pacific Ocean covers one third of the Earth, and the tropical Indo-Pacific is an order of magnitude larger than the tropical Atlantic. The differential thermal capacities of these 2 bodies of water must have also contributed to the differential cooling. Atlantic locations farther south near Brazil served as refuges, and corals are believed to have reinvaded the Caribbean from there after this last glacial epoch.

Such extinctions represent a significant phyletic bottleneck for the Caribbean, leaving fewer species behind from which further radiation could continue. We believe that major extinctions experienced by the scleractinians in the Caribbean were also experienced by the octocorals. This, of course, is difficult to document, because the Octocorallia generally do not fossilize well (Tasch 1973), with several exceptions (Bayer 1957, Konishi 1982).

The reasons for the differential evolutionary success of the major octocoral groups in the 2 regions are complex. Based upon the geological history of the 2 regions, ecological requirements for the taxon, and paleontological evidence drawn from sister taxa, we propose that these differences are closely linked to concepts which led Sanders (1969) to propose the Time-Stability Hypothesis (also see Klopfer 1959, Klopfer & MacArthur 1960, 1961, Slobodkin & Sanders 1969). Over long periods of geological time, the Alcyonacea experienced broad taxonomic radiation in the Indo-Pacific. The reduced climatic perturbations experienced in this geographic region facilitated this radiation in many benthic marine taxa.

The Alcyonacea may have experienced a higher degree of extinction in the Caribbean than the Gorgonacea. The Gorgonacea have a broader latitudinal distribution than the Alcyonacea and, as a group, would appear to be more tolerant of lowered temperatures than the Alcyonacea.

The same processes which allowed the Alcyonacea to radiate taxonomically in the Indo-Pacific also

allowed them to radiate chemically with respect to their secondary chemistry. The intraspecific diversity of compounds can be quite high in this group, let alone interspecific or intergeneric (Faulkner 1984, 1986, 1987, 1988, 1990, 1991, Hochlowski et al. 1984). The total gene pool available to the taxon for producing a wide range of secondary metabolites in the Caribbean would have been more limited.

Links between chemical diversity and functional diversity of secondary metabolites

We propose that the same process which has permitted radiation in the diversity of secondary metabolites in the Indo-Pacific has also permitted radiation in their function (Sammarco & Coll 1988, 1990). At the moment, the only functions defined in the Caribbean Gorgonacea thus far are ecological – feeding deterrence and anti-fouling. It is possible that the relative brevity of this list is due to a more limited number of studies on the Gorgonacea in this region; but we believe that this is only part of the answer.

A latitudinal cline in species diversity, with higher species diversity occurring in the tropics, is certainly as well documented as the longitudinal one discussed above (Fischer 1960, Stehli 1968, Stehli et al. 1969). A similar latitudinal cline in the frequency of occurrence in toxicity was originally suggested by Bakus (1974), and Bakus & Green (1974), based on work on sponges and holothurians. Although this suggestion has more recently come into question (McClintock 1987), data derived from the Octocorallia confirms that the diversity of the secondary metabolites is higher in the tropics than in the temperate regions (Faulkner 1977, 1984, 1986, 1987, 1988, 1990, 1991). It is not known whether a longitudinal cline in toxicity also exists, for the question has not yet been directly addressed.

AREAS FOR FUTURE RESEARCH

Although our knowledge of the chemical ecology of octocorals has increased in recent years, there are still numerous unanswered questions to be addressed. We have identified several general areas requiring attention, including:

- (1) The possible use of secondary metabolites by octocorals as a mechanism for food capture;
- (2) The possible use of secondary metabolites in the Gorgonacea as allelopathic agents;
- (3) The possible use of secondary metabolites in the Gorgonacea in reproduction, particularly as sperm attractants;
- (4) The separation of function in various secondary metabolites found within a single octocoral species, and in different tissues within a colony;
- (5) The possible function of octocoral secondary metabolites as anti-microbial agents (bacteria, virus, and fungus – marine and other);
- (6) The chemotaxonomy of Indo-Pacific Alcyonacea, beginning with individual families;
- (7) The testing of hypotheses concerning Diffuse Batesian Mimicry in octocorals and their brooded planulae;
- (8) The mechanisms by which octocoral terpenes act on scleractinian cells and tissue at the cytological and biochemical levels and their target sites; and
- (9) An analysis of molecular structure and stereochemistry in octocoral secondary metabolites as they relate to known ecological and physiological functions.

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