

# Constructional Azooxanthellate Coral Communities: An Overview with Implications for the Fossil Record

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*As evidenced by the success of zooxanthellate coral species today, symbiosis with algae confers great advantages to organisms inhabiting the reef environment. Although not as well known as their zooxanthellate counterparts, azooxanthellate coral communities, dominated by so-called "deep-water corals," can and do build constructional framework, harboring a variety of associated vertebrate and invertebrate fauna.*

*As has long been noted, when it comes to reefs and constructional roles, zooxanthellate and azooxanthellate corals exhibit mutually exclusive relationships. This is traditionally explained in terms of competition. When zooxanthellate species are absent due to restrictive environmental conditions, azooxanthellate species may inhabit relatively shallow water, even building limited constructional framework. In some non-reef settings where zooxanthellate corals are not living under optimal conditions, azooxanthellate species can be found living alongside them. On the shallow-water reef as a rule, azooxanthellate corals are relegated to cryptic habitats not colonizable by the overwhelmingly dominant zooxanthellate species.*

*A review of 16 well-documented examples of modern constructional azooxanthellate coral communities and their physical and biological characteristics reveals a wide variety of latitudinal and depth ranges, temperatures, species composition, thicknesses, and species diversity. In all major oceans, they are best developed in cold and relatively deep water, as deep as 1500 m, and from the equator to latitudes of over 70°. Besides having a predominantly coral composition, some deep-water, azooxanthellate coral communities with extensive constructional framework have unexpected faunal diversity and presumably also complex interactions. The paleobiogeography and evolution of some of these deeper-water, coral-dominated azooxanthellate communities, known to have inhabited atolls and oceanic seamounts, may have been influenced by plate tectonic seafloor movements.*

*While we are becoming increasingly cognizant of Holocene examples, counterparts in the geologic record are much more poorly known. The apparent paucity of ancient analogs may stem from difficulties in their interpretation and recognition in the geologic record. Judging from the size, facies relationships, faunal content, and diversity of Holocene examples, ancient deep-water coral structures, when preserved in the rock record, could be easily misconstrued as features of shallow-water origin. More careful analysis of deep-water Holocene examples can greatly expand our awareness of ancient analogs. In some cases, depending on the amount and thickness of construction, they could hold potential as hydrocarbon reservoirs.*

*Azooxanthellate scleractinian communities are common in today's oceans and examples of them extend back to the Middle Triassic period. Fossil examples, unfortunately, are rare and sporadic in stratigraphic distribution, with the most notable reports from the Tertiary. Our view of the relative abundance of ancient counterparts may be hampered by poor preservation and problems of recognition.*

## INTRODUCTION

In the fossil record, the mere mention of rich deposits of scleractinian corals usually elicits the visual image of palm trees lining coral sand islands, tropical breezes, and the crash of the surf on an exposed reef flat. Needless to say, not all coral-dominated communities with constructional framework are necessarily tropical or of shallow-water origin. Unlike the geologists' stereotype mentioned above, many coral communities dominated by colonial, framework-building corals are growing today in cold (4°–20°C) and deep (60–1500 m) water. Some grow very slowly and their reeflike coral structures reach the Arctic Circle (Maksimova, 1972). Such structures and their associated communities are variously referred to as

deep-water reefs, buildups, banks, and mounds. Because they have not been studied as well as tropical shallow-water reefs, their importance to geology may be substantially underrated. The purpose of this paper is to review current knowledge of Holocene examples including their physical and biological characteristics and to compare these with ancient examples whose occurrences hold implications for other ancient reef communities.

Zooxanthellate corals are severely restricted both geographically and bathymetrically by their algal symbionts, and therefore are relegated to shallow (0–70 m), tropical waters. Azooxanthellates on the other hand, are not limited by these requirements and attain wider distributions both with respect to depth and geography (Figs. 1 and 2). They occur from 0–6200 m,  $-1^{\circ}$  to  $29^{\circ}\text{C}$ , and from the Norwegian Sea ( $70^{\circ}\text{N}$  to the Ross Sea, Antarctica ( $78^{\circ}24'\text{S}$ )).

Wells' (1933) original terms, "hermatypic" and "ahermatypic," have gained wide usage and may appear to most casual readers as rather straightforward and unequivocal in application. Because the originally defined terms inextricably associate presence and absence of symbiotic zooxanthellate algae with the ability to construct reefs and because deeper-water corals construct framework, a degree of confusion has ensued (Rosen, 1981; Stanley, 1981). Particular corals, however, may or may not have zooxanthellae inhabiting their tissues. Some corals with zooxanthellae do build reefs; that is, they actually contribute to the framework. Other zooxanthellate species (?potentially reef-building) do not build reefs. Some corals without benefit of zooxanthellae erect mounds or buildups of constructional framework in deep water, while still other species without zooxanthellae live in the niches, interstices, or cryptic habitats on or in the framework of shallow-water reefs.

To solve the problem, a useful redefinition of terms was proposed by Schuhmacher and Zibrowius (1985), which we follow here. In this new scheme, the terms hermatypic and ahermatypic denote the contribution to framework in classic shallow-water reefs. Two new terms, "constructional" and "non-constructional," denote forming or not forming elevated, durable structures in either shallow or deep water. Finally, zooxanthellate and azooxanthellate are applied to corals living with or without benefit of algal symbionts. We urge adoption of this tripartite system because it solves much of the dilemma inherent in Wells' original definition, allowing more flexibility in discussions about modern and ancient corals and reefs. All corals contributing to deep-water mounds or thickets are azooxanthellate; some are constructional, and some non-constructional. None are hermatypic although some have the potential to produce substantial constructional framework.

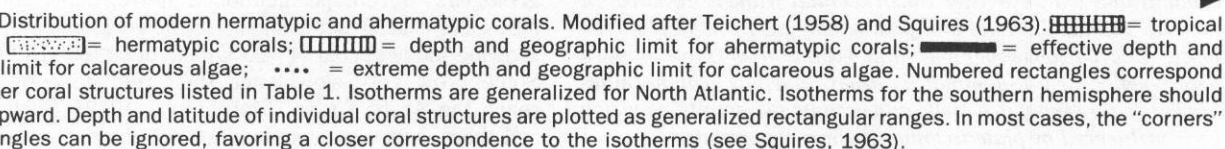
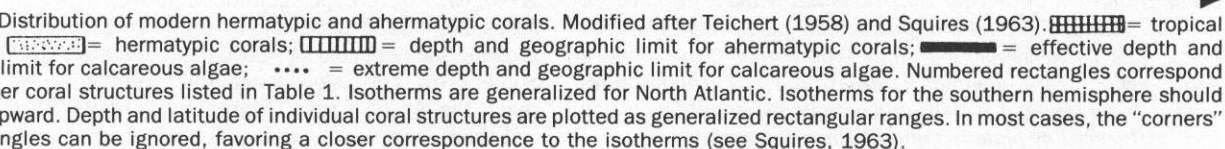
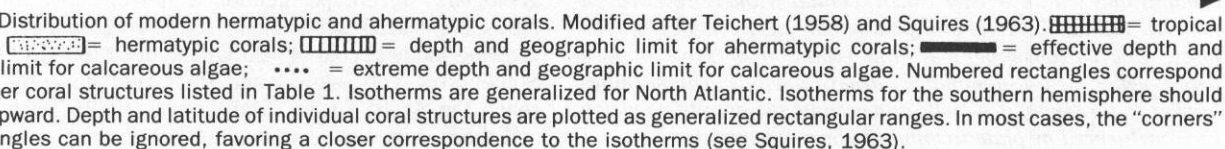
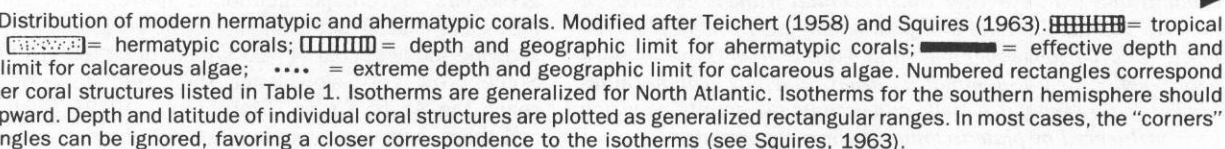
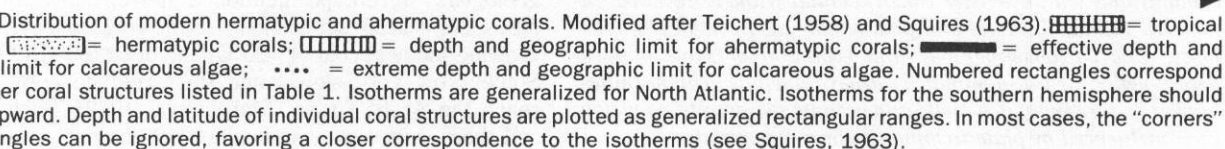
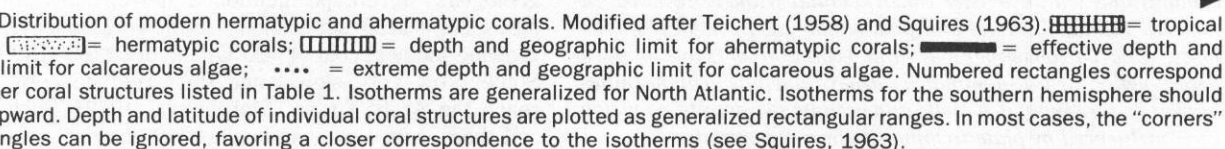
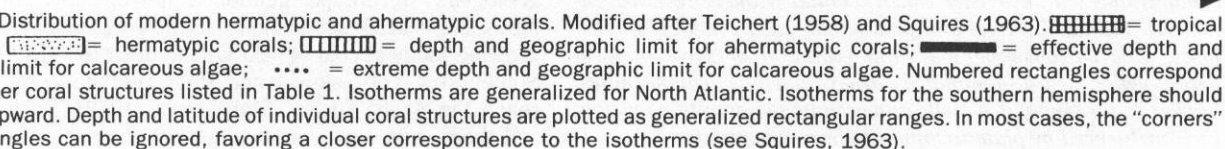
Azooxanthellate species form a significant component of the

Holocene Scleractinia both in species diversity and abundance. In today's oceans 90 of the approximately 190 Holocene genera (47%) and about 560 of the approximately 1500 Holocene species (37%) are, strictly speaking, azooxanthellate. Although some coral species occur in both conditions—often the higher taxa are exclusively one or the other—it is stressed that this character is ecologically influenced and therefore not a good conservative taxonomic character. For instance, often families, genera, and even species may exist in either condition (apozooxanthellate). *Madracis pharensis pharensis*, for example, is azooxanthellate, while *M. p. luciphila* exists in the zooxanthellate state. Another example, *Oculina varicosa*, also occurs naturally in both conditions. Thus the ecologic condition in at least a few corals is not rigidly fixed. In addition, zooxanthellate and nonzooxanthellate species do not always follow strict phylogenetic lines as reflected in their classification into higher taxonomic groups.

#### AZOOXANTHELLATE CORALS IN DEEP-WATER SETTINGS

Azooxanthellate corals are often incorrectly referred to as "deep-water" or "solitary" corals. As indicated above, azooxanthellates do occur in shallow water and, although the deepest Scleractinia (2000–6200 m, i.e., *Fungiacyathus* and *Leptopenus*) are invariably small, fragile, solitary species, at shallower depths, large, robust colonial species do occur. *Lophelia proliifera* (Pallas, 1766) (= *L. pertusa*), for instance, is most common between 500–800 m (Cairns, 1979) and forms colonies reaching up to 1 m in height. It has growth rates of about 5–7 mm/year (Wilson, 1979), in contrast to growth rates of 100 mm/year or more for branching zooxanthellate constructional reef corals. Furthermore, given favorable environmental conditions, these large, arborescent corals produce an extensive reef framework, trap sediment, and provide niches for a variety of other organisms. Such deep-water associations with constructional framework have been referred to as coral banks, thickets, or mounds. They can be very rich in species (Table 1) and produce structures with significant relief above the sea floor. Unfortunately, few have been drilled to confirm suspicions about their origins. Squires (1964) introduced the now-frequently used genetic classification scheme of: "colony—thicket—coppice—bank" for such deep-water coral structures, and the utility of this terminology in classifying reef structures of various types has been borne out.

Deep-water coral banks and coppices were first discovered in 1865 (Sars) off the coast of Norway and they are now known to be widely distributed (Fig. 2). Reviews of all or some of these structures are included in: LeDenois (1948); Teichert

**FIGURE 1**—Distribution of modern hermatypic and ahermatypic corals. Modified after Teichert (1958) and Squires (1963).    = tropical coral reefs;  = hermatypic corals;  = depth and geographic limit for ahermatypic corals;  = effective depth and geographic limit for calcareous algae;  = extreme depth and geographic limit for calcareous algae. Numbered rectangles correspond to deep-water coral structures listed in Table 1. Isotherms are generalized for North Atlantic. Isotherms for the southern hemisphere should be shifted upward. Depth and latitude of individual coral structures are plotted as generalized rectangular ranges. In most cases, the "corners" of the rectangles can be ignored, favoring a closer correspondence to the isotherms (see Squires, 1963).

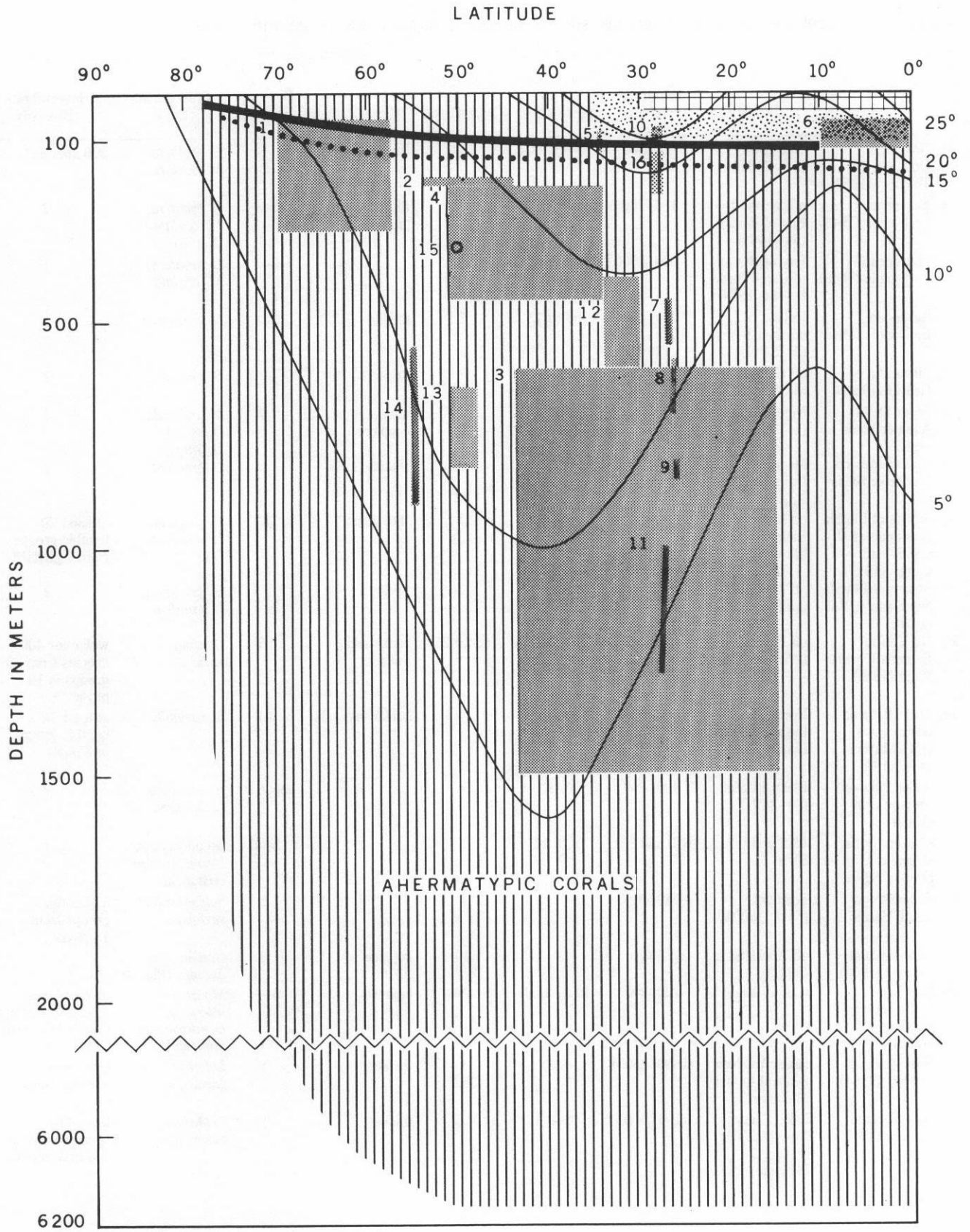


TABLE 1.—Physical and biological characteristics of azooxanthellate coral banks and thickets.

	Locality	Depth (m) (estimated)	Temperature (°C) (estimated)	Thickness of Deposit (m)	Classification	Coral Diversity (species)	Predominant Coral	Invertebrate Diversity
1. Norwegian Dons (1944) Teichert (1958)	off Norway (57°–70°N)	57–300	4–6.5–8.4	60	banks, coppices		<i>L. prolifera</i> , <i>M. oculata</i>	300 species*
2. European Le Danois (1948)	off Ireland to Bay of Biscay (54–44°N)	180–200	9–12	?	thickets, “massifs”	3–4	<i>L. prolifera</i> , <i>M. oculata</i> (Fig. 3)	?
3. “European” Le Danois (1948)	Bay of Biscay to Cape Verde Is. (44–15°N)	600–1500	up to 11	?		3–4	<i>L. prolifera</i> , <i>M. oculata</i>	?
4. European Le Danois (1948)	Ireland to northeast Africa (51–34°N)	200–450	up to 13	?	thickets	3–4	<i>D. cornigera</i>	?
5. Moroccan Gravel (1923)	off Casablanca (34°N)	80–110	15–16	?	thickets		<i>D. ramea</i>	?
6. Niger Delta Allen & Wells (1962)	Niger Delta (1–7°N)	50–120	15–16	2–17	thickets coppices	7	<i>M. asperula</i> , <i>D. sp. cf.</i> <i>D. ramea</i> , <i>L. prolifera</i>	?
7. Gulf of Mexico Moore & Bullis (1960)	Mississippi Delta (27°N)	450–550	10.4	55	?banks	2	<i>L. prolifera</i>	?
8. Straits of Florida Neumann et al. (1977) and Cairns (1977)	off Little Bahama Bank (25.6°N)	600–700	5.5–10	?	“lithoherm”	7	<i>E. profunda</i> <i>L. prolifera</i> (Fig. 3)	at least 20 benthic groups from 7 phyla**
9. Straits of Florida Neumann & Bell (1970)	off Miami (26°N)	825	?	?	thickets		<i>E. profunda</i> , <i>L. prolifera</i>	?
10. Off Central Eastern Florida Reed (1980)	off Florida (27.5–28.5°N)	70–100	7.5–15–26.5	about 25	banks and thickets	6	<i>Oculina</i> <i>varicosa</i>	well over 400 species from 25 groups in 10 phyla***
11. Little Bahama Bank H. T. Mullins et al. (1981)	North of Little Bahama Bank (27.5°N)	1000–1300	(4–6)	5–40	banks, mounds	16	<i>S. variabilis</i>	at least 14 benthic groups in 7 phyla
12. Blake Plateau Stetson et al (1962)	Blake Plateau (30–34°N)	400–800	6–10	?	?	about 10	<i>E. profunda</i> , <i>L. prolifera</i>	?
13. Chilean fjords Cairns & Stanley (1982)	48°S and 51°S	636 and 821	8.3–10	?	?	3–4	pseudocolonial <i>Desmophyllum</i> <i>crisagalli</i>	?
14. Subantarctic South Pacific	Seamont (55°S, 130°W)	549–915	?	?	?	5	<i>Solenosmilia</i> <i>variabilis</i>	32 benthic groups from 13 phyla
15. New Zealand Squires (1965)	off Auckland Is. (50.5°S)	334	?	40	coppice	3	<i>Goniocorella</i> <i>dumosa</i> (Fig. 3)	
16. Red Sea Fricke & Hottinger (1983)	Gulf of Aqaba	120–200	21.7–21.8	?	bioherm	6–7	<i>Madracis</i> <i>interjecta</i> , <i>Dendrophyllia</i> <i>minuscula</i>	diverse—see Fricke & Hottinger (1983; 115–116)
17. New Zealand Squires (1964)	Hinakura, New Zealand (upper Miocene)	(1500–2500)	(2.3)	3.4 36.6	thicket	1	<i>Lophelia</i> <i>parvisepta</i>	low—few species molluscs
18. New Zealand Squires (1964)	Lake Ferry, New Zealand (Lower Pliocene)	(150–600)	(6–10)	4.5	thicket	1	<i>Lophelia</i> <i>parvisepta</i>	low—few species molluscs and brachiopods

TABLE 1—(Continued)

	Locality	Depth (m) (estimated)	Temperature (°C) (estimated)	Thickness of Deposit (m)	Classification	Coral Diversity (species)	Predominant Coral	Invertebrate Diversity	
19.	U.S.A. Bailey & Tedesco (1986)	North Carolina (Pliocene)	Shallow: <30?	cool, temperate	1	thicket	1	<i>Septastrea crassa</i>	high—76 molluscs and other taxa
20.	Denmark Fløris (1979)	Faske Sjaelland, Paleocene (Danian)	(50)	(18)	20	bank	35	<i>Dendrophyllia, Faksephyllia, Oculina</i>	diverse—about 90 species
21.	West Greenland Fløris (1972)	Nugssuaq Paleocene (Danian)	(?50–80)	?cool	5	thickets	15 approx.	<i>Oculina, Lophelia?</i> , <i>Faksephyllia, Dendrophyllia</i>	moderate
22.	U.S.A. Coates & Kauffman (1973)	Lamy, New Mexico (Upper Cretaceous Turonian)	(450–2850)	cool	1.13–1.79	thicket	1	<i>Archohelia dartoni</i>	low—rare oysters, ?crustaceans, ?worms, ?fish
23.	U.S.A. Stanley (1979)	Iliamna, Alaska (Upper Triassic)	(~200)	cool	35.5	bank	11 approx.	<i>Retiophyllia Distichophyllia</i>	about 30 species
24.	U.S.A. Stanley (1979)	Pilot Mts. Nevada (Upper Triassic)	?shallow– moderate	?cool– moderate	1.5–9.0	bank	12 approx.	<i>Retiophyllia Pamiroseris</i>	about 64 species
25.	Central Europe Zankl (1971)	Northern Alps (Late Triassic)	(30–400)	moderate	10	bioherms	few 1–5	<i>Retiophyllia</i>	low—moderate molluscs, brachio- pods, foraminifers, hydrozoans
	Čar et al., 1981	Yugoslavia (Late Triassic)	?moderate	?cool— moderate	25–140	bioherms	8	<i>Margarosmilina</i> ,  branching colonial and solitary forms	moderate—hydrozoans,  molluscs, echino- derms, planktonic foraminifers

\*Burdon-Jones & Tambs-Lyche (1960).

\*\*J.L. Lang, pers. comm.

\*\*\*J. Reed, pers. comm.

(1958); Allen and Wells (1962); Stetson, Squires, and Pratt (1962); Squires (1963, 1964, 1965); Cairns and Stanley (1982); and Mullins et al. (1981). Deep-water coral structures are also reported from a Subantarctic South Pacific seamount (?bank) (54°49'S, 129°48'W, 549–915 m) and from two fjords (48°09'S, 74°36'W, 821 m, 8.3°C and 51°52'S, 73°41'W, 636 m, 10°C), located off Chile (Cairns, 1982a; 1982b; Cairns and Stanley, 1982). The South Pacific and Chilean records have not been verified by observation or seismic profile but are strongly indicated by the abundance of typical framework coral species and the diversity of the associated fauna.

The occurrences of Holocene examples are governed by: 1) location on a hard substrate with sufficient submarine topography usually below the general depth of zooxanthellate, reef-building activity, 2) association with vigorous current activity and the abundance of organics and nutrients carried in the current, such as in an area of upwelling, an axis of a current or gyre, or at the mouths of fjords which are facilitating a rapid exchange of nutrient-rich water, and 3) cool water temperatures. Unlike shallow-water reefs which flourish in clear, nutrient-deficient water (Hallock and Schlager, 1986), euphotic, deeper-water coral communities without benefit of algal

symbionts may require more nutrient availability. The South Pacific structure is suspected to be in an area of current divergence and therefore of upwelling. Houtman (1967) has shown that such a divergence occurs between the Subantarctic and subtropical Convergence Zones on the New Zealand Plateau and a similar divergence may also occur between the closely spaced convergences in the vicinity of the Subantarctic seamount coral structure.

The constructional framework of azooxanthellate coral banks or mounds is slow-growing and is produced by one or only a few species of corals. It may nevertheless harbor a community of organisms much richer than that expected at such depths. The composition and relative abundance of framework-building scleractinians vary somewhat for coral banks of different geographic localities (Table 1). Those of the eastern north Atlantic and western Atlantic show similarities in dominant corals while those from other ocean basins, like Chile, the Subantarctic, New Zealand, and the Red Sea have different corals in the constructional role. *Lophelia prolifera*, a cosmopolitan species, is a prime colonial constructor of framework off Norway and in the western Atlantic (Cairns and Stanley, 1982). Other species, such as *Desmophyllum cristagalli* (Fig. 3A) and

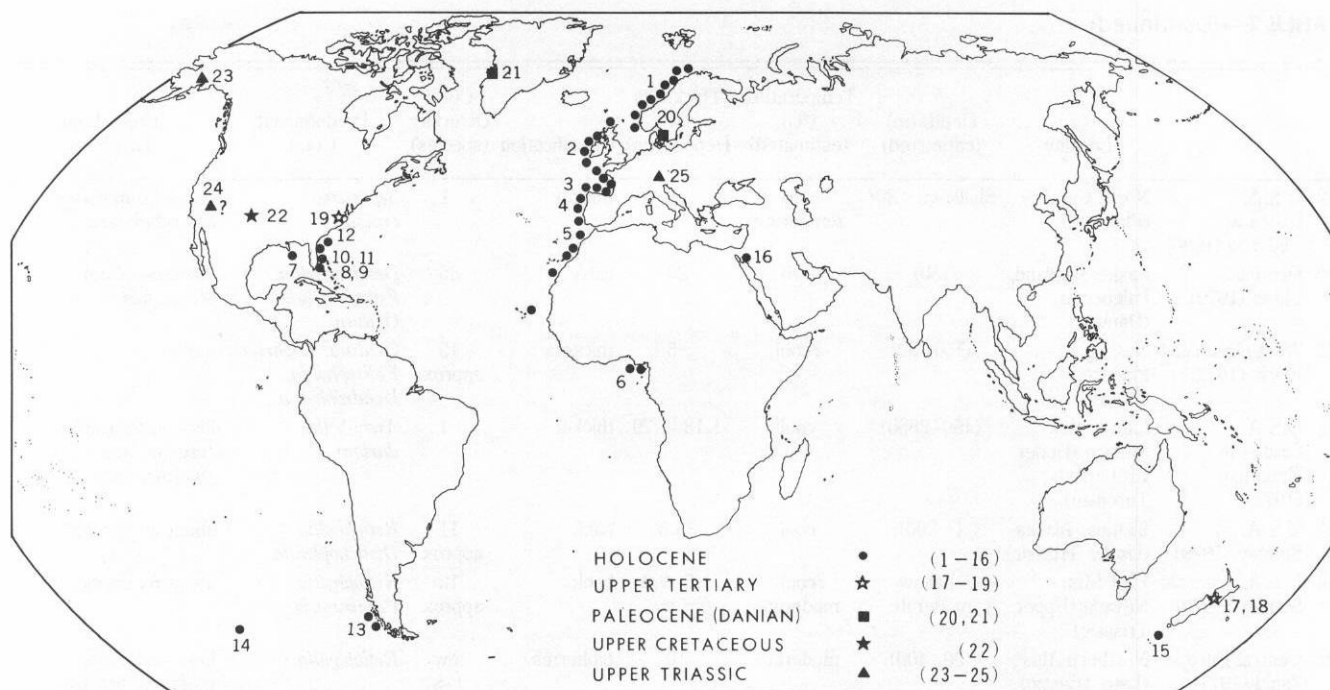


FIGURE 2—Distribution of known deep-water azooxanthellate coral banks. Numbers refer to structures given in Table 1.

*Solenosmilia variabilis* (Fig. 3D) appear fairly cosmopolitan. The colonial *Madracis interjecta* is distinctive in characterizing deep bioherms of the Red Sea (Fricke and Hottinger, 1983). The Subantarctic South Pacific structure is dominated by *Solenosmilia variabilis* (Cairns, 1982b), usually a minor component of coral banks elsewhere. The Chilean coral structure appears to be based on *Desmophyllum cristagalli*, a large, robust solitary species which, rather than budding, attaches to individuals of the same species, forming long pseudocolonial chains (Fig. 3A).

Most coral thickets and deeper-water banks produce pronounced topographic features with relatively low coral diversity. One or two species usually predominate as framework-builders. In contrast to the corals, the diversity of other invertebrates and fish is usually high. For example, Burdon-Jones and Tambs-Lyche (1960) recorded 300 species from a bank off the fjord coastline of Norway. Approximately 32 benthic invertebrate groups, representing 13 phyla, were collected from the Subantarctic South Pacific locality. With this kind of diversity, intricate ecologic relationships can exist. As a consequence of predation pressure in one deep-water locality in the South Pacific, stylasterine hydrocorals have developed freely hinged opercula to protect their gastrozooids (Cairns, 1981; 1982a). If fossilized, some examples of deeper-water banks could lead to possible confusion with shallow-water counterparts.

#### FOSSIL COUNTERPARTS

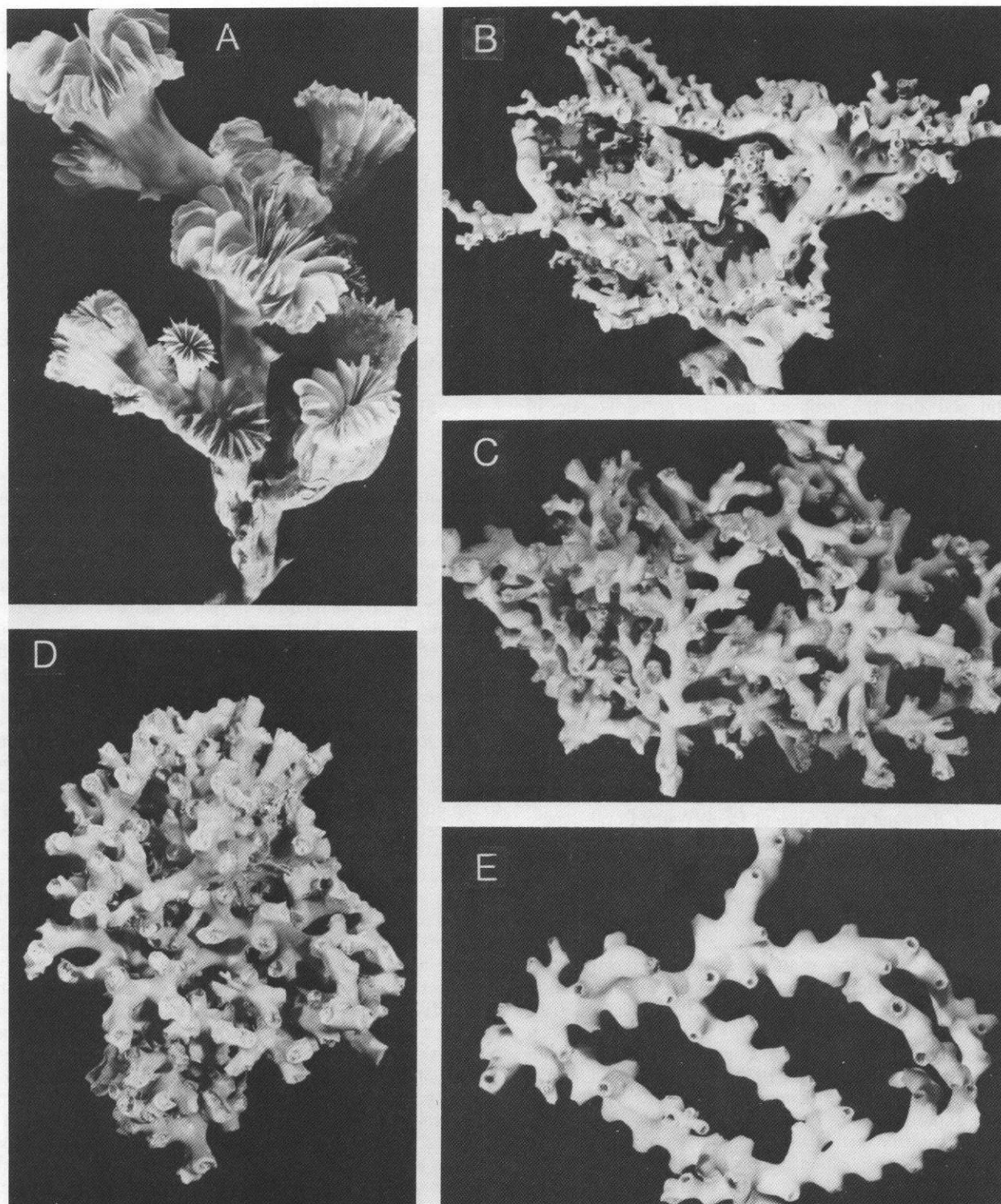
Unlike Holocene examples, fossil counterparts of deep-water scleractinian banks are extremely rare (Table 1). Only

ten occurrences representing all ages from Triassic to Tertiary age are known (Fig. 2). Some of these appear strikingly similar to Holocene banks and thickets described above.

The oldest suspected examples are of Triassic age and are known from western North America (Stanley, 1979a) and Europe (Stanley, 1981; Zankl, 1971). These were constructed by some of the earliest scleractinians and while some occur as stratigraphically thin, biostromal deposits, other are biohermal carbonate masses, reaching 140 m in thickness (Čar et al., 1981). Most developed on hard substrates in basinal settings, usually on molluscan shell debris. Examples in Europe bordered shallow-water carbonate banks. They developed in extensive lagoons or basins and were constructed primarily by *Retiophyllia*, a branching colonial, framework-building coral similar to *Lophelia* in growth form.

A small Cretaceous thicket was reported from the western interior of the United States (Coates and Kauffman, 1973). Its framework was produced by *Archohelia*, a colonial branching coral closely related to *Oculina*, a genus known to produce banks off Florida (Table 1). Examples representing relatively shallow banks and thickets at higher latitudes come from the Early Tertiary of Greenland and Denmark (Fløris, 1972, 1979). They are constructed by slender, branching species of *Oculina* and *Dendrophyllia*, as well as other corals, producing distinctive mounds in outcrop.

Late Tertiary coral thickets constructed by *Lophelia* colonies were reported from two localities in New Zealand by Squires (1964). Although these are comparable to Holocene examples in composition, they are of much smaller size (Table 1). Similarly, a small Pliocene thicket, dominated by *Septastraea*,



**FIGURE 3**—Modern constructional azooxanthellate corals. **A)** Pseudocolonial *Desmophyllum cristagalli*, Albatross sta. 2781, 51°52' W, 73°41' S, 637 m, 4 February 1888, USNM 19167,  $\times 0.50$ . **B)** *Madrepora oculata*, Albatross sta. 2669, 31°09' N, 79°34' W, 644 m, 5 May 1886, USNM 14496,  $\times 0.46$ . **C)** *Lophelia prolifera*, Albatross sta. 2662, 29°25' N, 79°43' W, 793 m, 4 May 1886, USNM 16154,  $\times 0.40$ . **D)** *Solenosmilia variabilis*, Eltanin sta. 1346, 54°49' S, 129°48' W (seamount in Subantarctic South Pacific), 548 m, 7 November 1964, USNM 47426,  $\times 0.60$ . **E)** *Enallopsammia profunda*, Albatross sta. 2415, 30°44' N, 79°26' W, 805 m, 1 April 1885, USNM 10679,  $\times 0.05$ .

has been reported by Bailey and Tedesco (1986) from North Carolina. Newton et al. (1987) reported late Pleistocene mounds 10–15 m high from the west Florida carbonate slope (which are not listed in Table 1 or Figure 2). With a pervasive framework of *Lophelia prolifera*, the mounds appear to be extensive and can be traced over a 20 km zone parallel to the slope.

#### Problems of Recognition and Interpretation

A major question arising is why so few examples of deep-water coral banks are known from the rock record. With evidence of deep-water scleractinian associations as far back as the early Mesozoic, and considering the abundance and wide distribution of these features along the margins of continents today, one would expect them to be much more common than the spotty geographic and stratigraphic distributions reflected in Figure 2. We suspect that they may very well be more common and that the problem may be primarily one of recognition and interpretation.

The possibility of confusing ancient coral banks with true shallow-water reefs was suggested by Teichert (1958). If preserved in a stratigraphic sequence, many of the Holocene deep-water coral banks and thickets have potential to be misinterpreted as tropical, shallow-water structures. Especially significant in Holocene examples is the extent of framework and debris produced by scleractinian corals and the abundance and high diversity of the preservable organisms. Such relationships are not those normally associated with deeper-water deposits and it is conceivable that many ancient occurrences go undetected simply because they are misinterpreted. This may also stem from the type of circular reasoning that unilaterally associates rich coral deposits with warm, shallow-water hermatypic settings. Caution is therefore urged in interpretations of such environments based simply on the presence of corals or even reef-like structures.

#### Criteria for Recognition of Ancient Deep-Water Coral Banks

Some criteria proposed by Teichert (1958) have been subsequently expanded by other authors (Mullins et al., 1981; Cairns and Stanley, 1982) to aid in the recognition of ancient deep-water coral banks. They include: 1) absence or paucity of algae including algal-induced boring, 2) lack of extensive, laterally contiguous shallow-water facies, 3) breakdown of coral framework predominantly by bioerosion (including microfungus boring) rather than wave erosion (Wilber, 1976; Wilson, 1979), 4) low diversity of the coral fauna, 5) an admixture of open ocean (planktonic) and deep-water constituents together with coral faunas (Vella, 1964; Eade, 1970), 6) occurrences at high paleolatitudes, 7) lenticular or mound-like shapes and geometries, and 8) predominance of fungal instead of algal borings. It is apparent that azooxanthellate corals today produce reef-like banks of different composition in a variety of latitudes, physical settings, and depths, including some overlap with shallow-water reefs (Table 1), so that no single criterion alone can serve to interpret a deposit as a deep-water bank. Other potentially helpful criteria include the successional development in composition and shape of the banks as outlined by Squires (1964) and Wilson (1979), which appears to be different from shallow-reef succession.

Fossil corals do not contain zooxanthellae preserved in their skeletal remains. Therefore, designation of ancient corals from a suspected deep-water bank as azooxanthellate solely on the basis of external morphology may be difficult, as has been expressed by Rosen (1977). Yet, possibilities for indirect inferences may come from studies of colony integration (Coates and Oliver, 1973; Coates and Jackson, 1987). Also, as previously mentioned, if the fossil corals are still preserved in original aragonite as in the case of some Triassic ones, the use of stable isotopes of oxygen and carbon may help to distinguish zooxanthellate from azooxanthellate corals (Stanley and Swart, 1984). Unfortunately, because of the instability of aragonite precipitated by the coral in equilibrium with sea water, this method is useful only under exceptional instances because the original aragonite of most fossil corals is easily susceptible to early diagenesis.

#### SUMMARY AND IMPLICATIONS FOR THE FOSSIL RECORD

Today, with continued exploration of the sea, Holocene deep-water ahermatypic coral banks are becoming increasingly well known. They occur in a variety of physical and biological settings and, in some cases, slow, uninterrupted growth of coral framework has produced structures of impressive size. The ecology and taxonomic composition of the dominant corals may vary widely, as do other physical features of the banks or bioherms. While not hermatypic in the sense of true shallow-water reefs, many such examples contain constructive framework produced by corals. Their value as rich fishing grounds is of course well known and some are a source of precious corals (i.e., *Corallium*, antipatharians, gold and bamboo corals; see Center for Natural Areas, 1979). Extensive, deeper-water, porous carbonate banks may result from the growth of azooxanthellate corals. Some of these are aligned up-slope parallel to the edge of continents, and such relationships could present unrealized opportunities for hydrocarbon reservoirs. Recent surveys have revealed that azooxanthellate corals inhabit thickets on Pacific seamounts and guyots. Unlike banks and thickets occurring on continental slopes, these are rather isolated on prominences within vast ocean basins. The composition of corals and other organisms of these communities deserve careful study and comparison. Some of the similarities and differences observed may be attributable to the relative proximity of seamounts to each other and the abilities of the deeper water organisms to disperse. Utilizing these subsea features as staging areas, some benthic organisms may be capable of breaching portions of the Pacific which ordinarily act as filter barriers to shallow-water counterparts. Add to this the geological perspectives, including the dynamic process of sea-floor spreading which integrates and conveys subsea features like seamounts across ocean basins, and some of the complex patterns of biogeography and evolution presently unaccountable by conventional models may be resolved.

All successful reef-builders and some reef-inhabiting organisms throughout the Phanerozoic appear to have fostered a symbiosis with algae (Cowen, 1983; this volume). The geological history of scleractinian communities is admittedly spotty but evidence for azooxanthellate ecology appears in the earliest



scleractinian associations of the Triassic (Stanley, 1979b; 1981; Flügel and Stanley, 1984). An analysis of zoantharian corallite morphology through time (Coates and Jackson, 1987) yielded decidedly anomalous results for these corals. Because much of the early Mesozoic reveals little evidence of shallow-water reef-building by corals (see Stanley, this volume), it is suggested that the first strong bonds between corals and symbiotic algae, prerequisites for true reef-building, began shortly after this time, following a profound mass extinction event (Benton, 1986). This would mark the start of the strong ecologic differentiation of the two groups of corals. The fossil record of Jurassic corals (Wells, 1956; Roniewicz, 1984) reveals this differentiation, and succeeding geologic periods contain examples of deeper-water coral communities of thickets, mounds, and banks distinctly separated from shallow-reef examples. Preliminary testing of this idea by quantitative geochemical methods (Stanley and Swart, 1984) yielded positive results and more in-depth research now underway is expected to provide conclusive data. While the taxonomic composition of deeper-water constructional corals varies through time for these communities, their paleoecologic roles including shape and growth forms appear similar.

Many examples of deep-water coral banks in the fossil record may simply go unrecognized by many field geologists due to the type of circular reasoning frequently inspired by rich deposits of corals. Investigators should use caution when interpreting rich coral communities in the fossil record, particularly those in anomalous paleogeographic positions. The use of multiple criteria in conjunction with common sense can help resolve potential errors in interpretation.

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We must never forget that ideas devoid of a clear meaning frequently gave the strongest impulse to the further development of science. The idea of an elixir of life or of the transmutation of base metals gave rise to the science of chemistry; that of perpetual motion to an intelligent comprehension of energy; the idea of the absolute velocity of the earth gave rise to the theory of relativity, and the idea that the electronic movement resembled that of the planets was the origin of atomic physics. These are indisputable facts, and they give rise to thought, for they show clearly that in science as elsewhere fortune favors the brave.

—Max Planck