

AHERMATYPIC CORAL BANKS: LIVING AND FOSSIL COUNTERPARTS

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ABSTRACT

Reef-like structures referred to as banks are produced by framework-building ahermatypic scleractinians in cool water at various depths, usually below those of hermatypic shallow-water reef corals. The distribution of Holocene banks is closely related to the ecological requirements of the ahermatypic corals. Fifteen major regions of bank development are known today in the Atlantic and Pacific and these banks vary widely in composition and ecological structure. Newly discovered living banks come from the Subantarctic South Pacific and off the coast of Chile. Emphasis is given to the high faunal content but low coral species diversity as well as the potentially high predation pressures which can exist on these banks.

Only eight widely scattered fossil examples are known. These range from Triassic to Tertiary in age and, like living examples, each varies in composition and structure. It is suggested that the earliest scleractinian corals of the Triassic were ahermatypic and that the development of extensive shallow-water coral reefs in post-Triassic time was related to the acquisition of symbiotic algae (zooxanthellae).

Caution is urged in the interpretation of all ancient reef-like coral accumulations since deep-water banks can superficially resemble shallow-water reefs. Increasing amounts of new information of Holocene examples can yield considerable insight into recognition of ancient counterparts.

INTRODUCTION

The mention of rich deposits of scleractinian corals almost invariably brings to mind the visual image of a tropical shallow water reef environment dominated by massive hermatypic Scleractinia. However, not all coral-dominated assemblages are necessarily tropical or shallow water. Reef-life structures constructed by colonial ahermatypic corals also occur in cold (4°-20°C), deep (60-1500m) water.

Whereas hermatypic corals are severely restricted geographically and bathymetrically by the ecological requirements imposed by their algal symbionts (zooxanthellae), ahermatypes are not limited by these requirements and are much more widely distributed (Fig. 1). Hermatypes are relegated to shallow (0-70 m), tropical waters; ahermatypes occur from 0-6200 m, -1° to 29°C, and from the Norwegian Sea (70° N) to the Ross Sea, Antarctica (78° 24'S).

Ahermatypic species form a significant component of the Holocene Scleractinia both in species diversity and abundance. Ninety of the approximately 190 Holocene genera (47%) and about 560 of the approximately 1500 Holocene species (37%) are primarily ahermatypic. Although most coral species are either hermatypic or ahermatypic — and 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, oftentimes families, genera and even species have hermatypic and ahermatypic components: *Madracis pharensis pharensis* is ahermatypic and *M. p. luciphila* is hermatypic; *Oculina varicosa* occurs naturally in both the hermatypic and ahermatypic conditions.

HOLOCENE CORAL BANKS

Ahermatypic corals are often incorrectly referred to as "deep-water" or "solitary" corals. As indicated above, ahermatypes 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 continental slope depths, large, robust colonial species do occur. For instance, *Lophelia prolifera* (Pallas 1766) (= *L. pertusa*), most common between 500-800 m (Cairns 1979), forms colonies up to 1 m tall and has a growth rate of about 5-7 mm/year (Wilson 1979). (In contrast, growth rates of 100 mm/year are not uncommon for branching hermatypic corals). Furthermore, when environmental conditions are favorable these large, arborescent corals produce an extensive reef life framework, trap sediment, and provide niches for other benthic organisms. Such deep water associations are referred to as coral banks. They are usually very diverse assemblages of

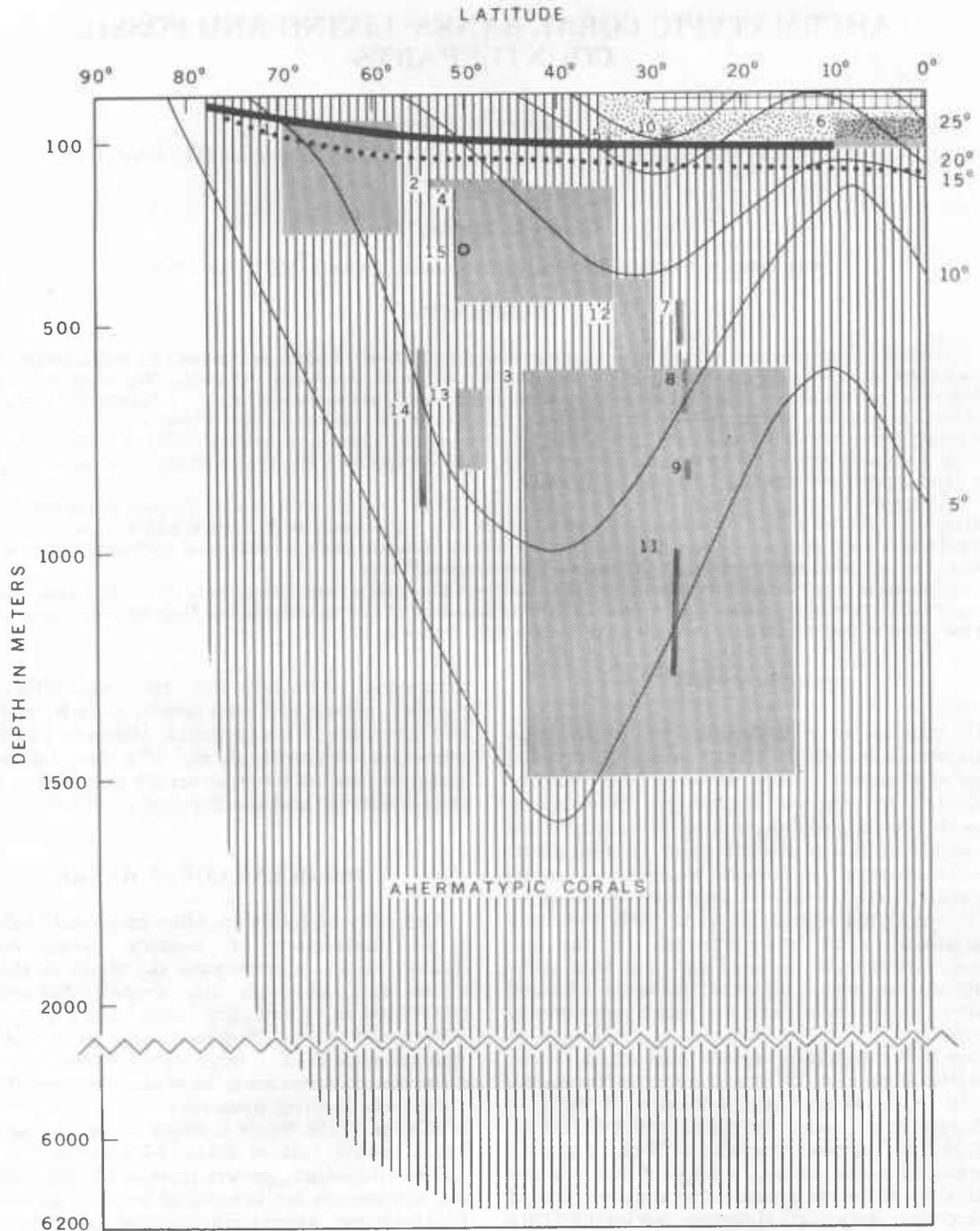


Figure 1. Distribution of modern hermatypic and ahermatypic corals. Modified after Teichert (1958) and Squires (1963).
 ▨ Tropical coral reefs. ▩ Hermatypic corals. ▭ Depth and geographic limit for ahermatypic corals.
 — Effective depth and geographic limit for calcareous algae. ··· Extreme depth and geographic limit for calcareous algae. Numbered rectangles correspond to deep-water coral structures listed in Table 1. Isotherms are

species and can become massive structures with great relief above the sea floor. Squires (1964) introduced the genetic classification scheme of: colony → thicket → coppice → bank, for such deep-water coral structures, and this terminology has been generally accepted.

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, Table 1). Reviews of all or some of these structures are included in LeDanois (1948), Teichert (1958), Allen and Wells (1962), Stetson, Squires, and Pratt (1962), and Squires (1963, 1964, 1965). Deep-water coral structures are reported herein for the first time from a Subantarctic South Pacific seamount (?bank) (54°49'S, 129°48'W, 549-915 m) and from two Chilean fjords (48°09'S, 74°36'W, 821 m, 8.3°C and 51°52'S, 73°41'W, 636 m, 10°C). 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.

Environmental limitations imposed on all deep-water coral banks are: 1) location on a hard substrate usually below the general depth of hermatypic reef-building activity, 2) association with

vigorous current activity and nutrient supply, such as in an area of upwelling, the axis of a current or gyre, or at the mouth of a fjord which is receiving a rapid exchange of nutrient-rich water, and 3) cool water temperatures. 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 framework structure of deep-water banks is produced by one or only a few species of corals so the total coral diversity is usually low. These framework-building scleractinian species are slightly different for the coral banks of each geographic area. Some cosmopolitan species, such as *Desmophyllum cristagalli* and *Solenosmilia variabilis*, are present on most banks, whereas other framework species are endemic to particular ocean basins. The Subantarctic South Pacific structure is dominated by *Solenosmilia variabilis*, usually a minor component of other coral banks. The Chilean coral structure appears to be based on pseudocolonial *Desmophyllum cristagalli*, a large, robust solitary

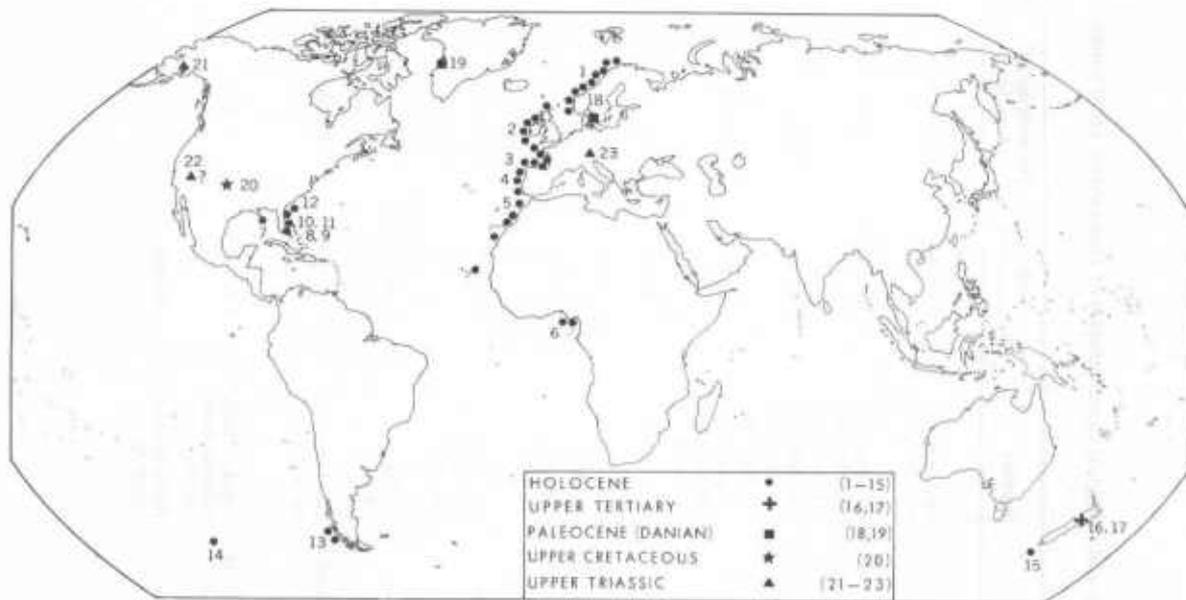


Figure 2. Distribution of known deep-water ahermatypic coral banks. Numbers refer to structures given in Table 1.

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 ahermatypic coral banks.

	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 Danaois (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>	?
3. "European" Le Danaois (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 Danaois (1948)	Ireland to northeast Africa (51-34°N)	200-450	up to 13	?	thickets	3-4	<i>D. cornigero</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. asperulo</i> <i>D. sp. cf. D. rameo</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 (1979)	off Little Bahama Bank (26.5°N)	600-700	5.5-10	?	"lithoherm"	7	<i>E. profundo</i> <i>L. prolifera</i>	at least 20 benthic groups from 7 phyla**
9. Straits of Florida Neumann & Ball (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 varicosa</i>	well over 400 species from 25 groups in 10 phyla***
11. Little Bahama Bank H. T. Mullins et al. (in press)	North of Little Bahama Bank (27.5°N)	1000-1300	(4-6)	5-40	banks	16	<i>S. verticillata</i>	at least 14 benthic groups in 7 phyla****
12. Blake Plateau Steinson et al. (1962)	Blake Plateau (30-34°N)	400-800	6-10	?	?	about 10	<i>E. profundo</i> <i>L. prolifera</i>	?

(Table 1, continued)

13. Chilean fjords	48°S, 51°S	636,821	8.3-10	?	?	3-4	pseudocolonial <i>Desmophyllium</i> <i>crisitagalli</i>	?
14. Subantarctic South Pacific	Seamont (55°S, 130°W) off Auckland Is. (50.5°S)	549-915	?	?	?	5	<i>Solenosmita variabilis</i>	32 benthic groups from 13 phyla
15. New Zealand Squires (1965)	Hinakura, New Zealand (upper Miocene)	334	(2-3)	40	coppice	3	<i>Goniocorella dumosa</i>	low — few species mollusks
16. New Zealand Squires (1964)	Lake Ferry, New Zealand (Lower Pliocene)	(150-600)	(6-10)	4.5	thicket	1	<i>Lophelia parvisepta</i>	low — few species mollusks and brachiopods
17. New Zealand Squires (1964)	Faske Sjael-land, Paleocene (Danian)	(50)	(18)	20	bank	35	<i>Dendrophyllia Faksephyllia</i>	diverse — about 90 species
18. Denmark Floris (1979)	Nugssuaq Paleocene (Danian)	(750-80)	? cool	5	thickets	15 approx.	<i>Oculina</i>	moderate
19. West Greenland Floris (1972)	Lamy, New Mexico (Upper Cretaceous Turonian)	(150-2850)	cool	1.13-1.79	thicket	1	<i>Faksephyllia</i> <i>Dendrophyllia</i>	low — rare oysters, ?crustaceans, ?worms, ?fish
20. U.S.A. Coates & Kauffman (1973)	Iliamna, Alaska (Upper Triassic)	(200)	cool	35.5	bank	11 approx.	<i>Archohelia dartoni</i>	about 30 species
21. U.S.A. Stanley (1979)	Pilot Mts. Nevada (Upper Triassic)	?shallow-moderate	?cool-moderate	1.5-9.0	bank	12 approx.	<i>Thecosmita Montlivaltia</i>	about 64 species
22. U.S.A. Stanley (1979)	Northern Alps (Late Triassic)	(30-100)	moderate	10	bank	few 1-5	<i>Thamasteria Actinastrea</i> <i>Thecosmita</i>	low-moderate mollusks, brachiopods, foraminifera, hydrozoans

* Burdon-Jones & Tembis-Lyche (1960).
 ** J.L. Lang, pers. comm.
 *** J. Reed, pers. comm.
 **** Mullins et al., in press.

species which attaches to individuals of the same species, forming long pseudocolonial chains.

In contrast to the relatively low coral diversity in a deep-water bank, the total faunistic diversity is usually high. Burdon-Jones and Tambs-Lyche (1960) recorded 300 species from a Norwegian bank, and 32 benthic invertebrate groups representing 13 phyla were collected from the Subantarctic South Pacific structure. Obviously then, intricate ecologic relationships exist and high predation pressures can be expected. As a possible consequence of this high predation pressure, one South Pacific stylasterine hydrocoral has developed freely hinged opercula to protect its gastrozooids (Cairns, in press).

FOSSIL DEEP-WATER CORAL BANKS

Unlike Holocene examples, fossil counterparts of deep-water scleractinian banks are extremely rare. Only eight occurrences from Triassic to Tertiary age are known for the world (Fig. 2, Table 1). Some of these appear strikingly similar to better-known Holocene banks and thickets.

The oldest suspected examples are of Triassic age and are known from western North America (Stanley 1979a) and Europe (Zankl 1971). These were constructed by some of the earliest scleractinians and occur as thin, biostromal to biohermal carbonate masses. They developed on hard substrates in basinal settings, usually on molluscan shell debris. Examples in Europe bordered shallow-water carbonate banks. They were constructed primarily by *Thecosmilia*, 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 ahermatypic banks off Florida (Table 1).

Examples representing relatively shallow banks and thickets at higher latitudes come from the Early Tertiary of Greenland and Denmark (Floris 1972, 1979). They are constructed by slender, branching species of *Oculina* and *Dendrophyllia*, as well as other corals, producing distinctive mounds in outcrop.

Finally, Late Tertiary banks constructed by *Lophelia* were reported from two localities in New Zealand by Squires (1964). These are directly comparable to Holocene examples in composition and shape (Table 1).

The first scleractinian corals of the Triassic did not build reefs or contribute extensively to reef limestone (Wells 1956, Newell 1978). It has been suggested that most, if not all, of these early scleractinians were ahermatypic, with many of the same

species living in shallow as well as occasionally deeper water environments (Stanley 1979b). Changes in diversity patterns and the appearance of true reefs later in the Mesozoic suggest that abundant hermatypic corals may not have existed until some time after the Triassic. This was a major turning point in the evolution of scleractinian corals as well as shallow and deep-water reef-like structures.

Besides the advent of shallow-water reef building on a large scale, the impact of this event was the sharp differentiation of corals along two ecologic lines. Most hermatypic reef corals today are colonial while the majority of ahermatypes are solitary. A clear differentiation became apparent in the Jurassic with the evolution of the deep-water caryophylliids. During their evolution, ahermatypic corals have been subjected to intense and long-term competitive pressures by their faster-growing hermatypic counterparts, relegating most ahermatypes to deep-water environments. It may be difficult therefore, to make direct comparisons in size and growth forms between ahermatypes of ancient deep water banks and those of the Holocene. Still, however, there are many colonial ahermatypic corals, including those which construct deep-water banks, that are difficult to distinguish from hermatypic species on morphologic lines alone.

PROBLEMS OF RECOGNITION AND INTERPRETATION

A major question that arises is why there are not more examples of deep-water coral banks in the rock record. There is some evidence of the existence of deep water scleractinian structures 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.

As was pointed out by Teichert (1958), if preserved in a stratigraphic sequence, many of the Holocene deep water coral banks and thickets could easily 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 stem from the type of circular reasoning that unilaterally associates colonial coral reef struc-

tures with tropical, shallow-water settings. Caution is urged in the designation of shallow-water environments based simply on the presence of corals or reef structures.

CRITERIA FOR RECOGNITION OF ANCIENT DEEP-WATER CORAL BANKS.

Some criteria have already been proposed by Teichert (1958) to aid in the recognition of ancient deep water coral banks, including: 1) absence or paucity of algae, 2) lack of extensive, laterally contiguous shallow-water facies, 3) breakdown of coral framework predominantly by bioerosion rather than wave erosion (Wilbur 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, 6) occurrences at high paleolatitudes, and 7) lenticular or mound-like shapes and geometries. It is apparent that ahermatypic corals produce reef-like banks of different compositions in a variety of latitudes, physical settings, and depths, including some overlap with shallow-water reefs (Fig. 1, Table 10) so that no single criterion can serve to interpret a deposit as a deep-water bank.

Other criteria that may be helpful 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.

Designation of the corals from a bank as ahermatypic solely on the basis of external morphology may be difficult, as has been expressed by Rosen (1977), but possibilities for indirect inferences may come from studies of colony integration (Coates and Oliver 1973). Also, if the fossil corals are still preserved in original aragonite, the use of stable isotopes of oxygen and carbon may help to distinguish ahermatypic corals (Weber 1973). However, because of the instability of aragonite, this method is useful only under exceptional instances of preservation and therefore not widely applicable to fossil occurrences (Scherer 1977).

SUMMARY

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, growth of coral framework produces structures of impressive size. Such extensive, porous carbonate banks are frequently aligned along the edge of continents, and these may have potential as hydrocarbon reservoirs. Their value as

rich fishing grounds is also known, and some are a source of precious corals (i.e., *Corallium*, antipatharians, gold and bamboo corals) (Center for Natural Areas 1979). Recent discoveries of banks on Pacific seamounts and guyots show that these banks may act as staging areas for the migration and dispersal of the coral larvae.

The general paucity of ancient examples, which nevertheless extend back to the Triassic, leads us to suspect that many occurrences in the rock record may go undetected. This could be because of their close resemblance to shallow-water counterparts and the circular reasoning frequently attached to the occurrence of coral-rich deposits as being solely from shallow-water habitats. Increasing awareness of deep-water Holocene banks and the application of multiple criteria can aid in the recognition of ancient deep-water examples.

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