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CORAL ASSOCIATIONS AND THEIR VALUE FOR
PALEONTOLOGICAL RESEARCH

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When describing fossil reef facies, one often speaks of coral communities when several species are found in the same layer. The term "organism community" is of a very general nature and embraces co-incident or necessary, permanent or temporary associations of organisms. Lately it is being linked to paleoecological statements more often (Paporte 1977), which gives it a sociological and ecological meaning. This is theoretically justified, because only differentiated ecological factors lead to typical coral communities being formed. However, such coral communities are not co-incident, but regulated by certain laws of environmental conditions, they are not temporary, but permanent phenomena; particularly when environmental conditions are reconstructable and used for a description of the habitats, does it appear advisable to use the well-defined term "association".

Key words: Recent coral associations, reef, ecology.

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WHAT IS MEANT BY ASSOCIATIONS?

The term "association" was taken from plant sociology (Braun-Blanquet 1951) and refers originally to the floristically defined unity of vegetation groups (Tischler 1975). It has been proved that this can be transferred to sessile marine animals and applied to corals (Goreau 1959; Roos 1964; Storr 1964; Kühlmann 1971; Loya 1972) whereby a "coral association" is also determined by its composition of certain species.

Under the influence of varying environmental factors, the hermatypic coral species often change their habitus in a characteristic manner and help to determine the picture of an association (Wells 1973). Therefore, well-defined forms of growth, called ecological forms, are depicted in the associations (Kühlmann 1971, 1974, 1975). One can draw analogous conclusions from examinations of modern reefs (Geister 1980), particularly with well-preserved coral limestone of more recent date, in which the corals are fossilised and preserved in their natural position.

The term association refers to sessile organisms only. This fact excludes the broad spectrum of vagile organisms from our investigation and also limits an

association under systematic aspects from other organism groups. This is also of practical value; for in the paleontological field only the representatives of one or a few large systematic groups are so well fossilized and preserved that they can be evaluated. Thus, one speaks of both coral associations as well as associations of other sessile organism groups, e.g. the crinoid-brachiopod associations.

However, one should avoid speaking of "biocoenosis" in the same connection. This term was defined by K. Möbius (1877) as a "community of living beings, a number of species and individuals selected by the average external conditions which condition each other and are continually reproduced in a limited area" (translated by the author). The term "biocoenosis" refers to all living beings of different systematic groups, both sessile and vagile. These communities can reproduce themselves through similar environmental needs and one-sided or many-sided dependence on the biotope, and form a biocoenological connexion. In a facies with fossils, appearance of genuine biocoenoses is not possible, because a number of ecologically important groups of the biocoenological connexion — e.g. zooxanthelles and other algae, bacteria, some worm-like animals, crustaceans and fishes — are no longer available.

There could probably be hardly any objections to using the advantageous term — association — for well-preserved inclusions in more recent coral limestone which have also maintained their natural state (Weyl 1965; Geister 1975). However, a number of factors often make it difficult to decide whether a genuine association is involved or not.

CRITICAL ASSESSMENT OF CORAL CONGLOMERATES

In a calm water area, even fragile coral skeletons have a good chance of being fossilized, because in an area with much movement in the water they are exposed to much wear and tear. Here, the coral sometimes are torn away from the substrate, carried through the water and deposited elsewhere or pulverised into sand. One can often observe this in recent reef areas (Westermann and Kiel 1961). Corals, torn off from a reef by cyclon waves, were thrown onto the beach in the north of Cuba (Kühlmann 1970). Hills of up to three metres were thus formed. Towards the sea they had shallow slopes of 15° , and towards land, steeper slopes of $40\text{--}45^\circ$. They were like dunes and could be called "gravel dunes". The shallow slopes indicate the intense pushing force of the water. The coral gravel dunes lay 50—100 m inland, because during cyclons the back-flow is so strong that it pulled all coral gravel into the sea. In the coral gravel dunes, the skeletons of the coral colonies were mixed. They were mainly the resistant coralla of *Montastrea annularis*, *Montastrea cavernosa*, *Acropora palmata*, *Dendrogyra cylindrus*, *Diploria strigosa*, *Diploria clivosa*, *Isophyllia multiflora*, *Isophyllastrea rigida*, but also the more fragile types such as *Colpophyllia natans*, *Acropora prolifera* and *Eusmilia fastigiata* (pl. 36: 1). The coral gravel dunes reflected neither the well-zoned coral association of the seaward exposed reef slopes (Kühlmann 1971, 1974) nor the tender colonies such as *Agaricia agaricites* f. *purpurea* and *Helioseris cucullata*.

On the outer slope of the central Pacific atoll Takapoto in the Tuamotu Archi-

pelago in Luv, I was able to note a clear zonation of differing coral associations up to 70 m in depth in June 1978. Characteristic for them were *Pocillopora*, *Acropora*, *Turbinaria*, *Porites*, *Montipora* and *Millepora* species at a depth of 15 to 25 m (pl. 36: 2), and *Porites* and *Leptoseris* species, here in the form of large, overlapping plates in 25 to 55 m depth (pl. 37: 1). Mighty waves had torn a large number of coral colonies from the wide slopes, carried them across the 50—100 m broad reef platform to the shore, to a large wall now about 4 m high and 150—200 m wide (pl. 37: 2). Here, too, the coral gravel consisted of mixed resistants, some of the colonies and pieces being weather worn. These gave only fragmentary information about the coral species on the outer slope. It is noteworthy that also the thick, resistant plate fragments of *Porites* which are often on the lower parts of the outer slope were also present, which points to a strong abrasion through stormy waters down to more than 25 m deep. Pieces of the more fragile *Leptoseris* were not, however, to be found. The material was mixed at the gravel wall which made possible a fragmentary review of the coral species, but not the associations of the outer slope.

If we find similar coral conglomerates in a fossil state, they give us information only about the species forming resistant coral skeletons that once lived there. But they were mostly only a part of the former coral associations, unless one assumes that only resistant colonies could flourish there because of the stormy waters. Judging by the associations of recent reefs, such an assumption is quite unsubstantiated; particularly in the surf area coarsely branched species often flourish, while the hard, semi-spherical *Scleractinia* live in calmer waters together with the more fragile species. All in all one can say that from the coral conglomerates baked into limestone of earlier earth-age one cannot draw conclusions about the complete compositions of the associations, or about the frequency and the degree of coverage of the species.

CRITICAL ASSESSMENT OF SO-CALLED SHALLOW AND DEEP WATER CORALS

When doing paleontological research one now and again yields to the temptation of differentiating between deep-water and shallow-water coral communities, because modern coral associations also appear to show such different characteristics. The question of whether and under what conditions such differentiation is permissible is difficult to answer; even for modern coral reefs it has not been scientifically substantiated. It has often been associated with the sensitivity to light of the hermatypic corals, because of the opinion that the zonation of species depends on the selective absorption of the spectrum in water.

As the symbiosis between corals and zooxanthellae makes the construction of a coral reef possible in the first place, it is almost certain, despite the lack of direct proof up to the present day, that such interaction between animal and plant must have been the physiological precondition for this uniquely successful metabolism in earlier earth-ages. There is no doubt that in general, all hermatypic corals or — more correctly — their plant symbionts, the zooxanthellae, are dependent on light. The

species affiliation of the zooxanthellae was examined a number of times in various modern corals: in all known cases, the species found was the single-cell *Gymnodinium microadriaticum* which belongs to the Dinoflagellata, and there is no reason to assume that *G. microadriaticum* in the coral species "A" flourishes at 1 m and coral "B" only in 30 m depth. Most coral species, like their plant symbionts are obviously euryphotic, as they occur in both shallow water as well as in water over 60 m deep (Goreau and Wells 1967) — i.e. in light milieu which differs in both quantity and quality. Furthermore: if the light were to have a differentiating influence on the depth zonation of the corals, it would also make itself felt in the first few meters, because here the spectrum undergoes the biggest changes due to the filter-effect of the water. But this also differs considerably, depending on the exposition of the coral substrate to the open sea and the main direction of the wind, force of the water movement.

In the West Atlantic reefs, the *Acropora prolifera*-association often occurs immediately below the surface in the calm water of the back reefs. I found them also in the somewhat protected reefs of Cuba in 8–12 m depths, and in July 1977 at 20–30 depth off St. Croix, U. S. Virgin Islands, on the outer slope which is exposed unprotected to the forceful Atlantic swell. In these different depths and habitats, the quality and quantity of the spectrum changes immensely but the environmental hydrodynamic, substratum and sedimentation conditions are very similar.

Table 1

The important ecological forms of *Agaricia agaricites* from Cuban reefs and their dependence on the substrate

Growth form	Description (after Wells 1973)	Substrate
<i>Agaricia agaricites</i> f. <i>purpurea</i>	flat or slightly convex or concave unifacial discs	on steep falls
<i>Agaricia agaricites</i> f. <i>danaei</i>	bifacial lobes	on edges
<i>Agaricia agaricites</i> f. <i>agaricities</i>	submassive, convex	on slightly inclined up to horizontal rock

Agaricia agaricites forms disc-like colonies with one-sided polyp facings directed towards the sea on steep falls. These have been described as f. *purpurea*. On the steep falls of Cuba, they live together with *Helioseris cucullata* in dense clusters and large colonies at a depth of 20–40 m (Kühlmann 1974). I found the same association on the north coast of St. Croix at 20–55 m deep. They also occur in shallow water, however, if they find a suitably steep substrate and calm conditions. Thus, I also found them in the Bay of Arroyo Bermejo, Cuba, at about 5 m.

And finally, I would mention a species of *Napopora*. I discovered this coral—belonging to the Poritidae—in June 1978 on the coral reefs of Moorea, Society Islands. It was the dominating species on an outer slope surrounded by certain currents and clear water at 25–35 m depth. The same species occurred, however, at 1 m of the lagoon under similar hydrographic conditions.

These examples make clear that for the hermatypic coral species and their zooxanthellae, light between 0 m and at least 60 m is sufficient, taking into account the turbidity, and that the coral species cannot be divided in accordance with the different light qualities and intensity at various depths. The analogous conclusion that can be drawn for fossil coral reefs is just as general, i.e. that its builders must once have lived in the trophic zone of the sea. They show, secondly, that the different coral species and associations in general following the movement of the water plus other factors effected by hydrodynamics such as the substrate which changes and inhibits the movement of water, and the sedimentation which is coarser or finer, depend on the strength of the water movement.

It should also be mentioned that some Scleractinia live in Recent reefs and show absolutely light-dependent behaviour in that they clearly prefer darkness. However, these are only a few ahermatypic species which do not live symbiotically with zooxanthellae. They too, cannot be used as yardsticks for depth, for they occur also in shallow water if the light there is subdued.

IMPORTANCE OF GROWTH FORMS

The characteristic ecological forms of growth among various types of corals, caused by certain environmental conditions, in particular through the interaction of hydrodynamic, substrate and sedimentation factors—has been described as the complex of mechanical factors (Kühlmann 1977). As already implied, *Agaricia agaricites* forms such differing ecological growth and those shown in table 1 were particularly conspicuous on the Cuban reefs. *Acropora palmata* (Lamarck) also shows differing ecological forms (Kühlmann 1975): shovel-like branched *A. palmata* f. *palmata* (Duerden, 1902) is to be found wherever there is continuous, moderately moving water; *A. palmata* f. *erecta* Kühlmann stretches a trunk steeply upwards before coming into rougher water and branching out; *A. palmata* f. *retroflexa* Kühlmann forms strong, round branches in rough, one-sidedly directed water movement; and *A. palmata* f. *crustata* Kühlmann simply covers the rock substrate under the influence of environmental factors bordering on the minimum needed for survival. As *Acropora palmata* also often occurs in Pleistocene reefs (Weyl 1965; Geister 1980), these facts are probably not without significance for paleoecological investigations.

Despite the transitional forms which sometimes make it difficult to classify some of the colonies, the typical colonies usually permit conclusions about their ecological conditions to be drawn. In addition, transitional forms are significant in so far as they prove that each case is an ecological form of growth of one and the same

coral species and not various types. In general, here the possibility of assessing the once-existing environmental situation in fossil reefs becomes visible, if the different typical forms of growth of one coral species make an analogous conclusion permissible.

CORAL ASSOCIATIONS

If species emerge under the same environmental conditions, they form typical coral associations. These are particularly valuable for paleoecological statements as they significantly show certain environmental conditions. For example, for the Caribbean region, coral associations were defined as follows:

- The coral association of the wave action zone. Characteristic species: *Acropora palmata* and *Millepora complanta*, probably *Diploria strigosa*. Habitat: horizontal or weakly sloped substrate in moderate surf (Storr 1964).
- The coral association of steep falls. Characteristic species: *Agaricia agaricites* f. *purpurea*, *Agaricia fragilis*, *Agaricia lamarcki*, *Helioseris cucullata*, *Madracis decactis*, the horizontally growing form of *Madracis formosa*, furthermore *Mycetophyllia reesi* and *Dichocoenia stellaris*, perhaps also *Agaricia grahamae* and *Madracis pharensis*, possibly *Astrangia solitaria*, *Phyllangia americana* and *Stylaster roseus*. Habitat: more or less vertical substrate in calm, but not stagnating water (Kühlmann 1974).
- The coral association of sea-grass environments mostly in lagoons. Characteristic species: *Cladocora arbuscula*, *Manicina areolata*, the spheric form of *Siderastrea radians* (Kühlmann 1970) and *Porites divaricata*. Habitat: sandy bottom among sea-grass (Kühlman 1971).

Geister (1975) describes a large number of various zones on the Caribbean reefs which are not so strictly bordered from each other and sometimes overlap. Perhaps this is what makes them more utilisable than exactly defined coral associations for paleoecology, with its many uncertainty factors.

SUMMARY

As only certain organisms groups of earlier biocoenoses are fossilized, it is better to use the term association as recent ecology does. Coral associations are more seldom preserved as fossils than usually assumed. Recent observations show that the corals are often torn off from their substrate by storm waves and carried to the shore. The hills of coral gravel, often meters high, do not reflect the natural associations. One must be careful when classifying reef corals into shallow and deep water species, because, with a few exceptions, they all are euryphotoc. However, forms of growth can lead to conclusions about past environmental factors. Characteristic species of coral associations can indicate habitats.

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EXPLANATION OF THE PLATES 36—37

Plate 36

1. Torn away and shoreward pushed mixed coral skeletons which make it impossible to recognize any association (North coast of Cuba).
2. Outer slope of Takapoto, Tuamotus, between 15 to 25 m deep, densely covered by *Acropora*, *Millepora*, *Pocillopora*, *Porites*, *Montipora* and *Turbinaria*.

Plate 37

1. Outer slope of Takapoto, Tuamotus, between 25 to 55 m deep, partly covered with plate-like overlapping colonies of *Porites* and *Leptoseris*.
 2. Mighty storm waves carried the corals from the slope to the shore of Takapoto Atoll, Tuamotus, where they formed a large wall.
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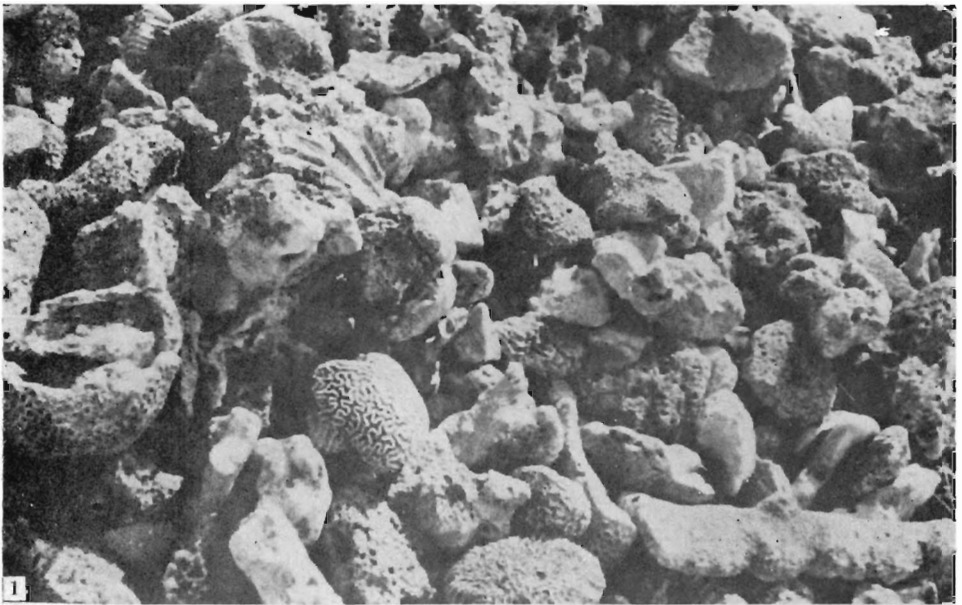


Photo: D. H. H. Kühlmann

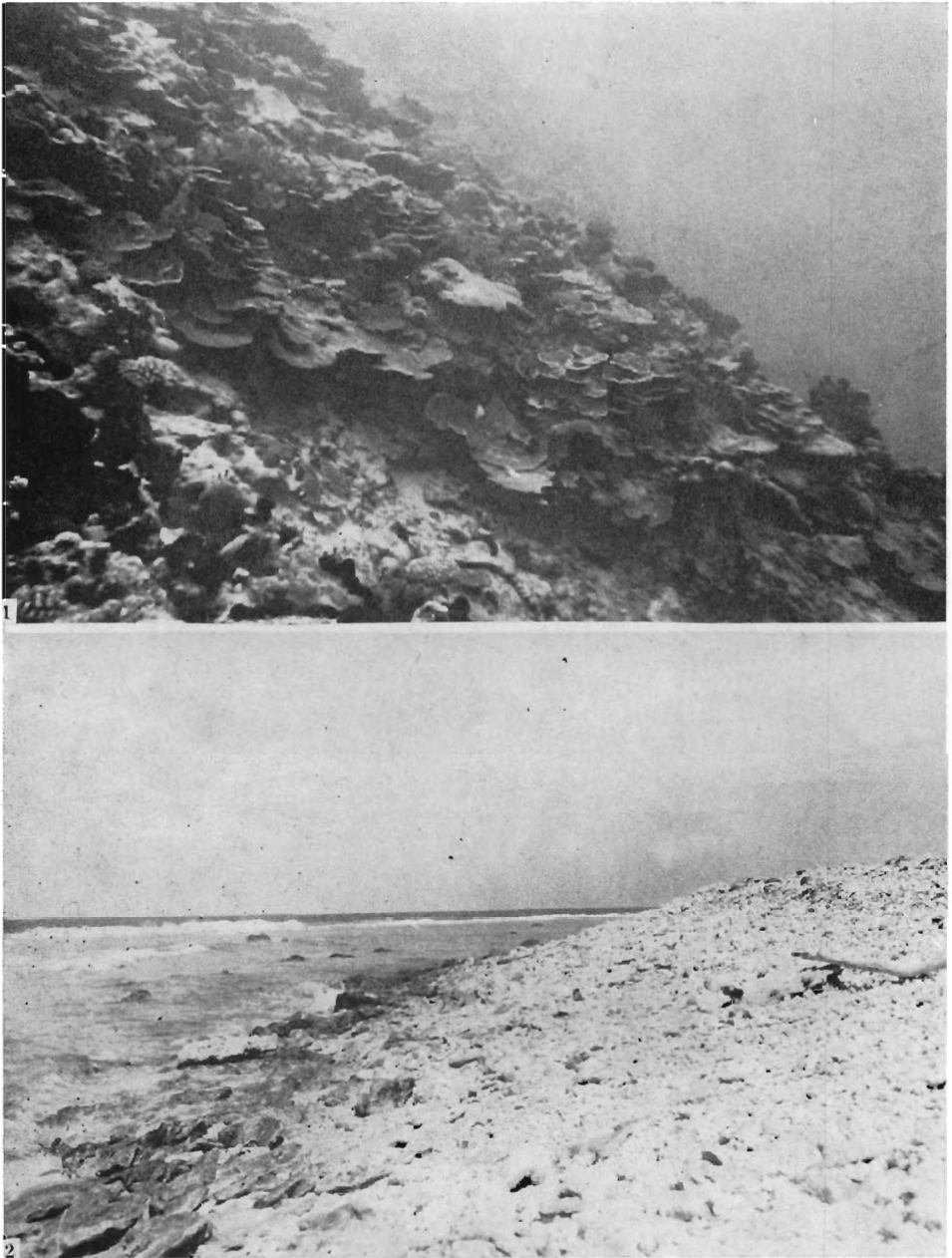


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