

CORAL COLONIES AS MICRO-ENVIRONMENTAL INDICATORS

by J. A. E. B. HUBBARD (*)

(4 figures dans le texte)

RÉSUMÉ

Des observations réalisées sur des coraux vivants, tant sur le récif qu'en aquarium, ont permis d'intégrer les caractéristiques de leur distributions zonéographiques aux propriétés fonctionnelles de leur morphologie squelettique. Les relations existant entre la nature et le taux d'activité des polypes, d'une part, et la morphologie du squelette, d'autre part, sont d'abord discutées; la micromorphologie des septa ainsi que leur angle de divergence, la forme des calices et l'orientation des corallites sont mises en relation avec les paramètres physiques du milieu. De là, l'auteur tire des arguments rendant compte de la distribution spatiale des espèces considérées.

Ces observations sont ensuite transposées dans le passé et servent de fil conducteur à l'interprétation des relations existant entre la distribution de Rugueux paléozoïques et les caractères des sédiments associés.

ABSTRACT

Observations carried on living corals, in reefs as well as in aquarium experiments, made it possible to integrate their distribution patterns with their functional skeletal properties. Relationships between polyps activities and the skeletal morphology are first discussed: such features as septal micromorphology and divergence, calical form and corallite orientation are related to environmental physical factors and from there to distributional limitations.

Some conclusions drawn from the observation of living scleractinians are then tentatively used as a guideline for interpreting the significance of ancient coral-sediment distribution patterns.

Palaeoenvironmental studies of coral-sediment relationships throughout the 100 m. thick Viséan shelf sediments of the Sligo Basin (N.W. Ireland) indicated the potential of coral assemblages as micro-environmental indicators (Hubbard, 1966a, b; 1970a, b). These observations were then compared with analogous rugose and tabulate assemblages in the Lower Palaeozoic of Scandinavia. This enabled the distinction of facies — linked fabrics of environmental origin to be isolated from those resulting from genetic control. In both areas the following facies-linked features were found to be repetitive and therefore were regarded as environmentally significant factors:

- (1) Calical geometry with sediment size.
- (2) Calical diameter with sediment size.

(*) Geology Department, King's College, London University, Strand, London, WC2R 2LS — England.

- (3) Angle of attachment/branching with substrate stability.
- (4) Number of calices per unit area with substrate type.
- (5) Skeletal malformities were most common in beds which show evidence of variations in sediment accumulation rate.
- (6) Skeletal alterations with sediment type.

These observations were then used as a basis for developing comparative laboratory experiments on :

(1) functional morphology; (2) ecological distribution, and (3) preservation of living scleractinian corals from the Caribbean province (Hubbard & Pocock, 1972; Hubbard, 1972; Hubbard, 1973; Hubbard, in press; Hubbard, in preparation).

First ecological distribution patterns were noted in SCUBA dives to 68 m. in as many extreme environments as possible off Bermuda, Puerto Rico, Curaçao, Panama, Yucatan and Florida. Then 28 characteristic species, which had previously proved capable of survival for long periods in an open water circulating aquarium in Miami, were selected for laboratory experiments. These were first subjected to cine-filmed sediment-shedding experiments, in which all the corals were inundated with a 3 cc. sample of sand particles of mixed grain size which had been differentiated by colour painting the size fractions according to Wentworth's scale (Hubbard & Pocock, 1972). Then 21 of these species were subjected to graduated current experiments by constructing a vernier on the inflow control tap and calculating the rate of flow from samples collected in a 100 ml. measuring cylinder over 10 sec. periods. Thereafter all the corals were maintained in the aquarium for periods of up to two years during which their skeletal increments were marked with Alizarin Red S at monthly intervals. Finally they were all fixed in buffered Glutaraldehyde and stained with Eosin and Haematoxylin prior to embedding in epoxy resin. The specimens were sliced for petrographic, histological and ultrastructural distinction of genetic fabrics from diagenetic alteration products. It was then possible to integrate the distribution patterns of these corals with their functional skeletal properties, and with those skeletal fabrics which had developed in the aquarium.

1. *Skeletogenetic — diagenetic fabrics*

Recognition of the intimate relationship of living tissues to skeletal fabrics is fundamental to the understanding of the preservation of coral skeletons as it has a direct bearing on the intraskeletal chemical micro-environments which result in internal precipitation and dissolution. Living scleractinian corals have long been known to be infested with a host of boring and encrusting commensal, symbiotic and saprophytic organisms (Hubbard, 1972) : but their alteration products at petrographic and ultrastructural level are equally complex and could readily result in taxonomically confusing skeletal margins on recrystallisation during fossilisation.

The unnaturally low pH and nutritional deficiencies of Biscayne Bay water used in the aquarium prevented skeletal thickenings from forming, but resulted in many malformational skeletal thinnings e.g. *Cladocora* developed etioliated corallites with a reduced epitheca and pronounced carinae, while internally all the skeletons are heavily infested with filamentous organisms which result in a pseudo-micritisation texture. The inhibition of skeletal growth and concomitant heavy alteration by infestation are attributed to influences resulting from sustaining the corals in an adverse aqueous environment which must have been somewhat alien to the reefal organisms.

2. Behavioural responses

The polyps' behavioural responses appear to be related to a subtle neuroid control over their three intersecting sets of sheet muscle tissues (Hubbard, 1973). This allows the polyps to :

(1) extend as elongated tubes with long sensitive tentacles; (2) partially retract as short squat protrusions with insensitive stubby tentacles; (3) retract the tentacles while the polyp remains distended; (4) to completely retract so their tissues lie flush with the skeleton. On retraction each tentacular unit comes to rest immediately above the oral end of the septum.

All corals are capable of moving fine sand and silt by ciliary action. Coarser grades of material are commonly moved by polypal distension resulting from the stomodeal uptake of water. The amount of extension is variable up to 400 % volume increase : this can be correlated with the calical surface area (Hubbard & Pocock, 1972). Thus calical form can be related to polypal behaviour *viz* those genera which use tentacular action as a further aid to sediment-shedding, e.g. *Porites* have fenestrate or ornate septal structures; whereas the more passive polyps tend to have smoother septa. The angle of diversion of the septa and their ornament can be used as further guides to polypal activity as these symmetrical elements are related to stress directions and the stabilisation of the polyp's muscle tissue sheets. Thus high angle septal divergences are commonly associated with active polyps, e.g. *Diploria*, and flat floored calices tend to contain less active polyps e.g. *Solenastrea*.

The orientation of calices is of fundamental significance to the corals' efficiency as (1) a food catcher and (2) a sediment-shedder (Hubbard, 1973). This is, in turn, reflected in the internal orientation of the skeletal elements developed in the corallites as they reflect former polyp-water interfaces. Thus colonial corals can be ascribed to various degrees of coloniality which are demonstrated by their behavioural responses to grade from (1) pseudo-solitary behaviour in fasciculate corals, through (2) partial integration in cerioids, to (3) complete integration in meandrines. Thus both calical form and corallite orientation may be closely related to sediment-shedding capacities and consequent distributional limitations.

All corals respond to increased current velocities by gradually withdrawing their polyps from being fully distended to completely retracted. On cessation of the current the polyps gradually reverse their retraction sequence until they are fully recuperated and capable of grasping prey. Both rates of retraction and recuperation result from compound behavioural responses which vary irrespective of taxonomic relationship (Table 1). Thus it is possible to group these behavioural responses into nine categories which correspond with the corals' micro-environmental distribution patterns in their common habitats in the Caribbean.

3. Distribution patterns

It is now possible to begin to correlate coral distribution patterns with their hydrodynamic settings and consequent sedimentological regimes in living scleractinian coral communities in the Caribbean (Hubbard, in preparation). Current velocity is one significant factor affecting early colonisation patterns. Thus a polyspecific community initially settles an area in such a manner that each coral obtains its basic requirements. With time the corals themselves influence the local hydrodynamic setting so that those species which thrive in strong currents dominate the topography and result in monospecific mounds. As the community evolves, more tranquil areas develop between the main frame-building corals and these are later occupied by

other species requiring such habitats : this results in the polyspecific mounds commonly defined as patch reefs. Thus it is now possible to relate lateral distribution patterns to vertical sequences in evolving communities.

TABLE I

Synthesis of combined polypal retraction and recuperation rates plotted according to the behavioural responses to graduated calibrated-current experiments.
(HUBBARD, in preparation).

X/X	X/OX	X/—	X/O—
<i>Montastrea annularis</i>	<i>Montastrea cavernosa</i> <i>Oculina</i> <i>Manicina</i> <i>Eusmilina</i>	<i>Acropora cervicornis</i> <i>Solenastrea</i>	<i>Cladocora</i>
REEF FRAME BUILDER	PROTECTED REEF ACCESSORIES	SPECIALISTS	
—/X	—/OX	—/—	—/O—
nil	<i>Porites divaricata</i> <i>Porites furcata</i>	<i>Dichocoenia</i>	nil
	SHELTERED AREAS		
OX/X	OX/OX	OX/—	OX/O
<i>Mycetophyllia</i> <i>Isophyllia</i> <i>Porites astraeoides</i> <i>Diploria labyrinthiformis</i>	<i>Diploria clivosa</i>	nil	<i>Siderastrea siderea</i>
REEF FRAME ACCESSORIES	HIGH ENERGY MARGINS		

The symbols defining each behavioural group are sequentially arranged so that the first pair relates to retraction rates under increasing current velocities, while the second pair refers to recuperation responses under ambient conditions on cessation of current flow, where X = fast, — = slow, and O = pause in polypal response rates. Thus fast retraction before a pause followed by fast recuperation = X/OX; whereas slow retraction before fast recuperation = —/X; and a pause before fast retraction and fast recuperation = OX/X. The chief frame building coral, *Montastrea annularis*, shows consistently rapid responses, whereas pauses in response rate are found in those species which belong to subsidiary habitats such as the more sheltered and specialised areas. Whereas these groupings cut across both taxonomic relationships and generally accepted broad ecological zones they correspond with the micro-environmental strategies outlined in the hydrodynamic-trophic model postulated by Hubbard (in preparation).

4. *Application to the geological record*

In so far as these experiments concerned living scleractinian corals which are found in the Pleistocene of the Caribbean it is possible to apply these findings directly to these communities. But it is also possible to use these findings as a guideline for interpreting the significance of the ancient coral-sediment distribution patterns which were noted previously but barely explained.

The basic parameters which are common to both living and extinct groups are :

- (1) Geometry of the calice.
- (2) Calical surface area.
- (3) Number of septa per calice.
- (4) Number of corallites per unit area.
- (5) Angle of branching.
- (6) Skeletal malformities.
- (7) Destruction of skeletal fabrics by bioerosion, dissolution, precipitation and diagenesis.

Since each corallite records a vertical stacking of fabrics which are in effect superimposed relic calices, an understanding of the three dimensional geometrical reconstruction of the calice is of the utmost importance. Thus each intertabular interval records the micro-environmental influences and subsequent diagenetic consequences of a short period of time. Except where growth has been markedly irregular it is then possible to trace parallel developments in contiguous corallites.

Since the Palaeozoic assemblages comprise soft-bottomed communities the major angular relationships of consequence are those of (i) basal dichotomy (Fig. 2a) which reflects stability relationships with the substrate; and (ii) angle of inclination of the inferred feeding surface area (Fig. 2b). These relationships are summarised in Fig. 1 and were originally reconstructed from observations on the variation in growth forms of lithostrotionid coralla in the Viséan of Cos. Sligo and Leitrim (Hubbard, 1966b, 1970a; Hubbard & Pocock, 1972) whence variation in associated sediment accumulation rates can easily be ascertained from observations on the adjacent trace fossil assemblages (Fig. 2).

The most important angular relationship is α which increases in size approximately in proportion to the grain size and consequent stability of the substrate. As in Pythagoras' theorem α bears a constant relationship with $\gamma + \delta$ in each phase of standardised growth. The second most important angular relationship is β which is the angle of inclination of the feeding surface area and is thus of marked trophic significance. However β 's relationship to the contiguous sediment is more variable as the overlying sediment is even more often of posthumous origin. Nevertheless as with α , β shows a constant relationship to the sum of $\epsilon + \sigma$ in each phase of growth. Angles α and β are independently variable and may even vary within one corallum. Whereas α reflects stability relationships with the substrate, β is a relic of trophic adjustment. The plane χ which unites the two superimposed triangles not only indicates the polyp-water interface, but also approximately parallels the sediment/substrate-water interface. This angular relationship is simpler in soft-bottomed communities, where adjustment is likely to be more gradual, than in the hard-bottomed communities of living reefs where drastic storm damage frequently causes bizarre overgrowths. It is nevertheless possible to use this angular relationship as

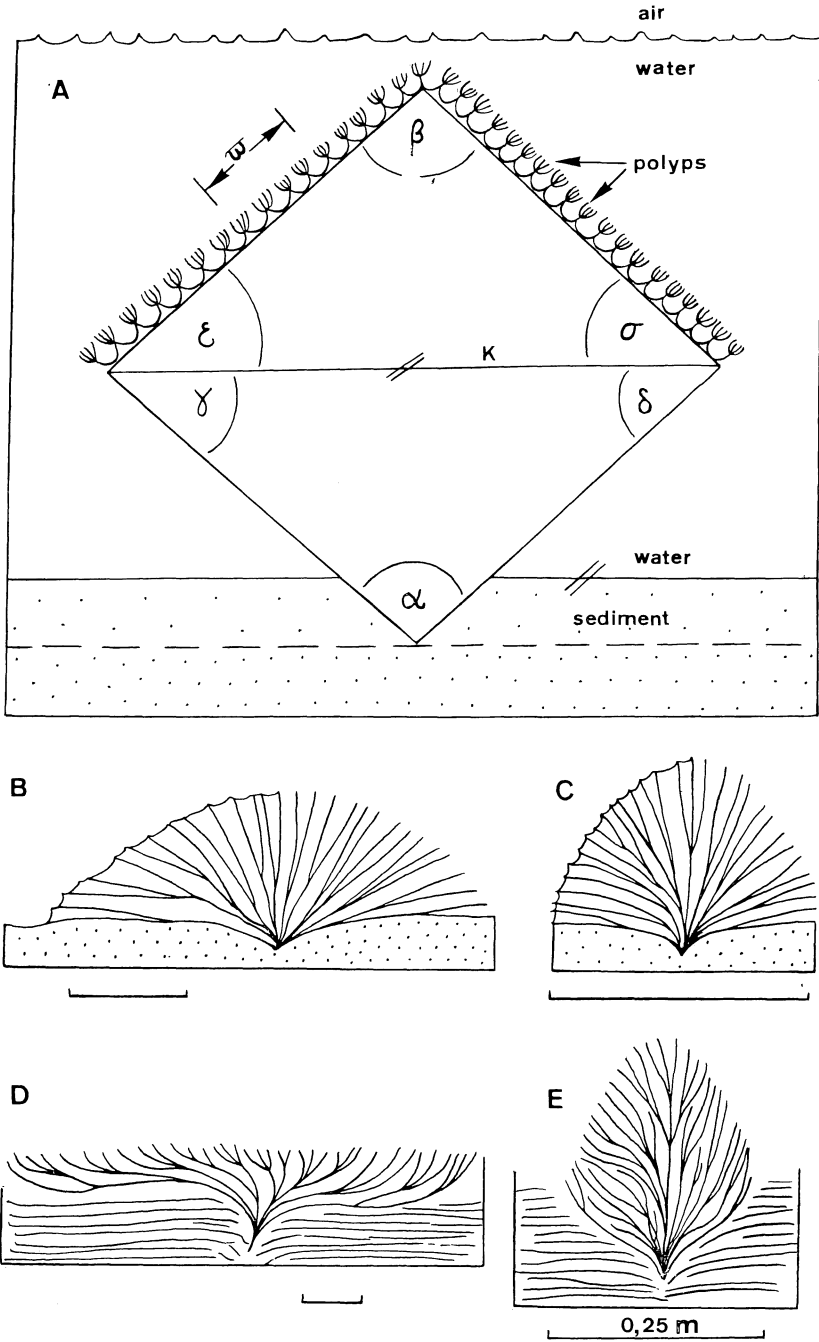


Fig. 1

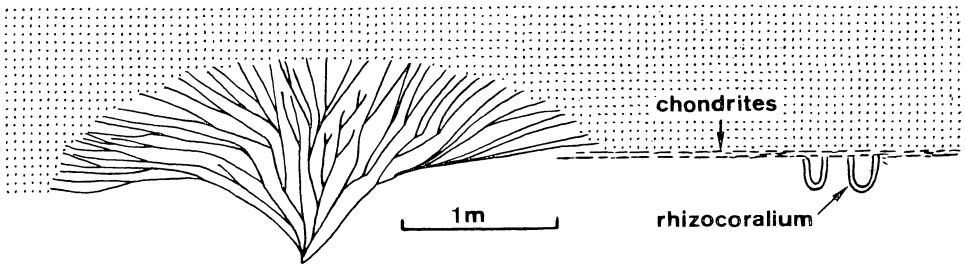


Fig. 2. — Field sketch of the relationships between a fasciculate lithostrotionid colony, the contiguous sediments and associated trace fossils from Serpent Rock. The colony originally grew on a compactable wackestone substrate which was subsequently burrowed by *rhizocoralium*; the rate of accumulation then varied allowing the upper portion of the trace fossil to be eroded prior to the next phase of inundation which in turn became churned by *chondrites* before passing up into a more massive, coarser grained wackestone — packstone. The colony shows a marked change in angle of dichotomy which coincides with the inferred change in micro-environment from more turbid waters with an essentially « squishy » sea bed to clearer conditions in which winnowing predominated over sediment accumulation.

a form of guideline for interpreting hard-bottomed communities as shown in Fig. 3. But the rule is not infallible as there are certain growth habits in which corallites proliferate around dichotomising branches which defy this argument e.g. *Acropora* and *Oculina* (Fig. 3).

The potential of colonial coral colonies as micro-environmental indicators is yet to be realised. The future of such studies lies largely in the understanding of the skeletogenetic-diagenetic variables such as the facies-associated stereozone and amplexoid trends (Fig. 4). Once such phenomena, and many others, are fully understood it should then be possible to differentiate micro-environmental changes within the range of distribution of each species. But, as yet, skeletogenetic-diagenetic studies are at a very preliminary state of investigation.

Fig. 1. — Angular relationships in colonial corals belonging to soft bottomed communities:

A. Schematic diagram of the angular relationships of a typical colonial coral to (1) the sediment-water interface, and (2) the feeding surface area; where α = angle of basal dichotomy, β = angle of feeding-surface area, κ = plane of contact between triangular cross sections made by the superimposition of β on α , ω = section through a typical polypal unit area.

B, C, D & E are characteristic lithostrotionid growth forms found in distinct associations. The bar scale is 0.25 m long in each case.

B, & C occur as both cerioid and fasciculate forms associated with a stable, uncompactable coarse grained wackestone — grainstone substrate. B is common at Streedagh Point, Serpent Rock & Easky; while C occurs in cerioid form at Easky and in fasciculate form on Knocknarae. The cerioid forms are characteristic of grainstone substrates.

D, & E only occur in fasciculate form and are characteristically found on irregularly compacted *chondrites* churned wackestone substrates west of Streedagh Point, at Serpent Rock and in Knocknarae.

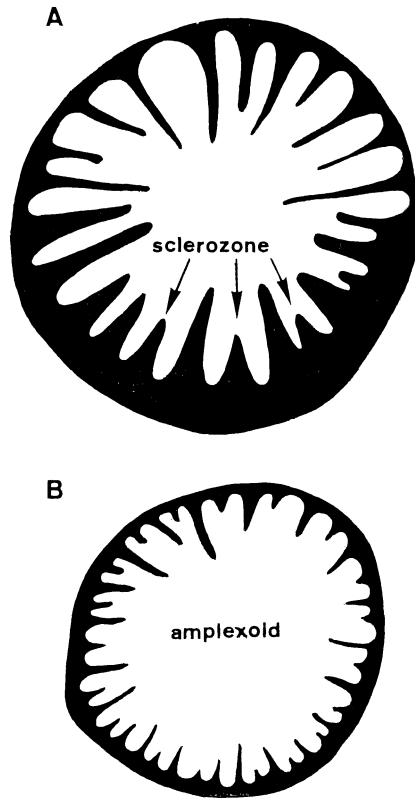


Fig. 3. — Typical cross sections of corallite features commonly illustrated in taxonomic studies of Carboniferous corals which give little indication, if at all, of the diagenetic fabrics as distinct from those of skeletogenetic origin.

- A. shows a well developed sclerozone which occupies the lower two quadrants and is asymmetrically developed in relation to the cardinal fossula.
- B. illustrates the characteristic amplexoid septal trend which commonly results in irregular tapering oral ends to the septa which are suggestive of dissolution phenomena.

Fig. 4. — Schematic section across the axis of a reef to show the relationship between external growth form, internal corallite dichotomies and substrate relationships in reefal/hard bottomed/encrusting communities in a range of micro-environments.

- A. The optimal hemispherical growth form resulting from constant radial increase is limited to the ideal conditions of equal light intensity and nourishment.
- B. Low encrusting asymmetrical growth form resulting from marginal increase in areas of intense wave/current action.
- C. Obtuse isoscele growth characteristic of colonies living near low water spring tide level.
- D. Macro-ellipsoidal hemispherical growth characteristic of deeper waters and areas where there is much competitive crowding.
- E. Obtuse scalene growth characteristic of attachment to high angle slopes and areas with a predominant current direction.
- F. Acute scalene growth characteristic of foliaceous, plocoid and asterioid or stolonal growth forms where polypal proliferation is marginal and asymmetrical. This is characteristic of deep, sheltered, or dark quiet water environments.
- G. Acute isosceles growth characteristic of fasciculate and plocoid forms where there is overcrowding, high sedimentation rates and reduced illumination.
- H. Loosely branching forms with dichotomising within each branch e.g. *Acropora* and *Oculina* which do not fit into this simplified scheme relating corallite dichotomy patterns to substrate types, micro-environmental controls and angles of initial stability.

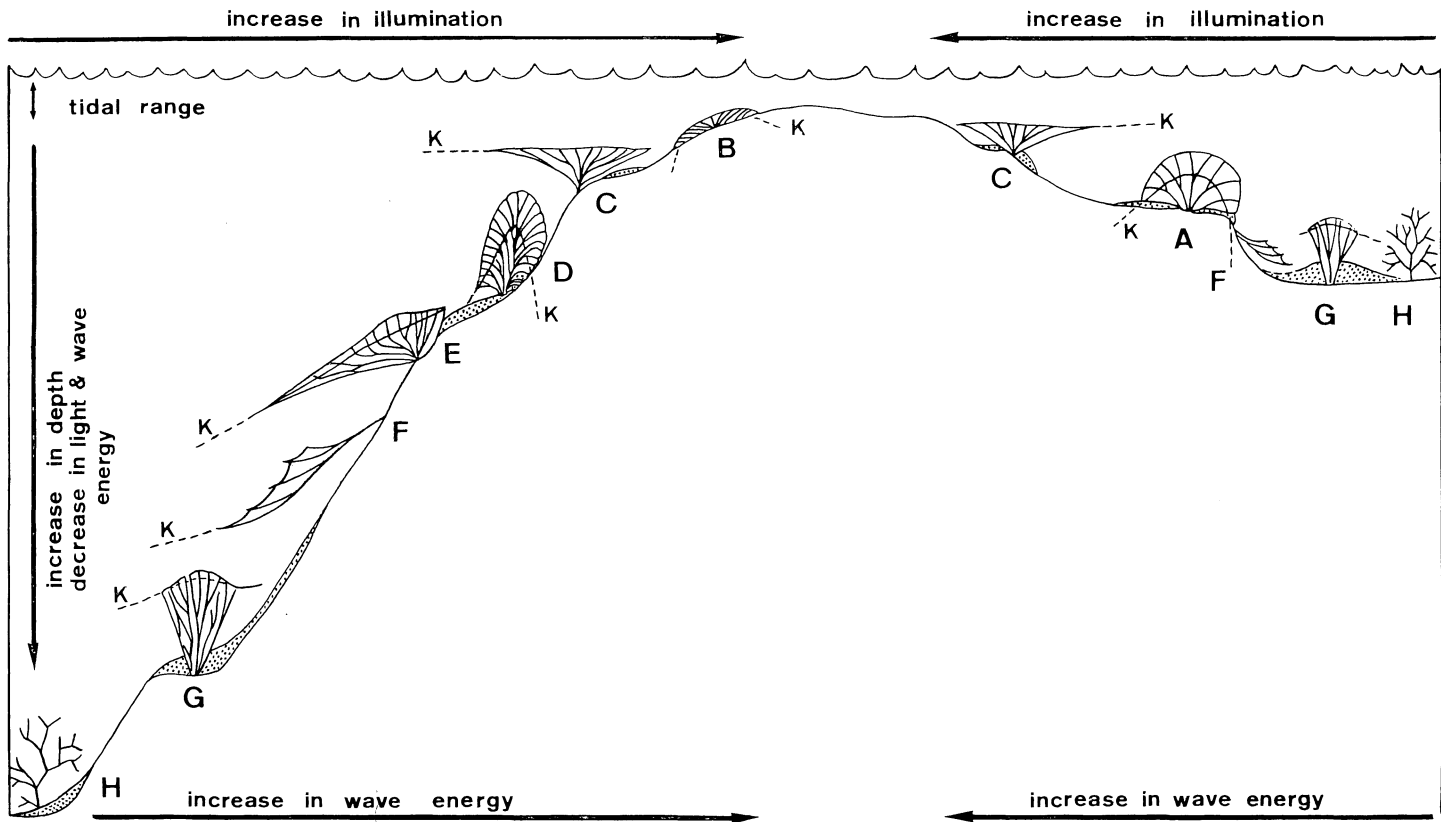


Fig. 4

REFERENCES

- HUBBARD, J. A. E. B., 1966a. — « The Ballyshannon Limestone and Basal Beds » of the Carboniferous of N.W. Ireland, with particular reference to their conditions of deposition. Unpublished Ph. D. thesis. University of London.
- HUBBARD, J. A. E. B., 1966b. — Population studies in the Ballyshannon Limestone, Ballina Limestone and Rinn Point Beds (Viséan) of N.W. Ireland. *Palaeontology*, **9**, 2, 252-269.
- HUBBARD, J. A. E. B., 1970a. — Sedimentological factors affecting the distribution and growth of Viséan caninioid corals in N.W. Ireland. *Palaeontology*, **13**, 2, 191-209.
- HUBBARD, J. A. E. B., 1970b. — Solitary Corals : An Index of Sediment Accumulation Rates. *Abstract Soc. Econ. Paleont. & Mineralogists & Amer. Assoc. Petrol. Geologists Ann. Mtg.*, Calgary.
- HUBBARD, J. A. E. B., 1972. — Cavity formation in living scleractinian reef corals and fossil analogues. *Geol. Rundsch.* **61**, 2, 551-564.
- HUBBARD, J. A. E. B. & Y. P. POCOCK, 1972. — Sediment rejection by scleractinian corals : a key to palaeoenvironmental reconstruction. *Geol. Rundsch.* **61**, 2, 598-626.
- HUBBARD, J. A. E. B. & Y. P. POCOCK, 1973. — Sediment shifting experiments : A guide to Functional Behaviour in Colonial Corals. In *Animal Colonies : Their Development & Function Through Time* (R. S. Boardman, A. H. Cheetham, A. G. Coates, W. A. Oliver Jr. & F. M. Bayer, Editors). *Dowden, Hutchinson & Ross*, Pennsylvania.
- HUBBARD, J. A. E. B. & Y. P. POCOCK, in press. — Barnes' technique amended for analysing cavity development and fabrics in coral reef communities.
- HUBBARD, J. A. E. B. & Y. P. POCOCK, in preparation. — Calibrated-current experiments : an Index to Coral Distribution Patterns. *2nd International Coral Reef Symposium*, Brisbane.