Modular Growth and Form of Corals: A Matter of Metamers

B. R. Rosen

Modular growth and form of corals: a matter of metamers?

BY B. R. ROSEN

Department of Palaeontology, British Museum (Natural History),
Cromwell Road, London SW7 5BD, U.K.

Following a lead from botanists, this paper offers a re-interpretation of the morphology and growth of scleractinian, rugosan and tabulate corals in terms of iterated morphological units (modules), with an emphasis on the shape and organization of colonies. It presents a new theoretical basis for modules, a new descriptive framework for corals above the zooidal level, a review of practical applications and a comparison of coral modules with other kinds of organic iteration.

Consideration of cloning is a prerequisite and leads to a revival of the hypothesis that colonies have arisen by arrested budding (clonoteny), where zooids are paedomorphic to varying degrees with respect to the primitive state of clonally produced, detached (clonoparous) individuals. A second hypothesis follows, that the mouth structure is universally homologous in all corals. R. Riedl's work (*Order in living organisms.* Chichester: John Wiley (1978)) on morphological organization and hierarchy can therefore be applied to corals to obtain a non-arbitrary theoretical basis for recognizing modules and distinguishing them from other kinds of repetition of parts.

There are five criteria for modularity, four topological and one homological: (i) a modular structure is a three-dimensional tesselation; (ii) modules correspond to homogeneous units of hierarchical subdivision; (iii) an organism is modular if subdivision at the highest (or very high) level reveals homogeneous units; (iv) if homogeneous units occur in an unbroken series of subdivisions, they are all modules at their respective levels (hence modules of modules, that is, cormidia), and the finest unit is the fundamental module; (v) homogeneous units are those which are homologous with each other (homonoms). On this basis, and allowing for interzooidal connective structures, the fundamental module of corals is the zooid (not the polyp alone). Differences between zooids, as suggested by other authors, are of degree, not kind.

Colony form can therefore be specified by using a scheme that starts with zooids, and is based on (i) organization (component morphology and modular arrangement), and (ii) shape, for every modular level present. The basis for higher level modules is reiterative, either homomodular, or heteromodular (subdivided into polymorphic or polystatic). Branching organization and branching shape should be distinguished, and either can occur at any modular level, or even not at all.

Modules bring potentially greater precision to growth studies, statistically and topologically, either heuristically or to test hypotheses about fecundity, senescence, determinate growth, variation and inherited architecture. Higher level modularity has previously been largely ignored. Density banding, dye markers and computer modelling, ideally in combination, are likely to produce the most useful results in the near future, and should lead to advances in taxonomy and phylogenetics, in the understanding of the morphological consequences of the coral–zooxanthellae symbiosis, and in the inference of past conditions from fossil corals.

In a wider phyletic context, zooidal (= fundamental) modules are meristematic and broadly metameric, though it follows from R. B. Clark (*Zool. Jb.* **103**, 169–195 (1980)) that this does not automatically signify a close phylogenetic relationship with annelids,

8-2

or with any other metameric organisms. Coral 'metamers' are probably non-serial and clonal because the coral mode of life is usually vegetative. They exist at a higher organizational level than these other metamers.

'*What is not identically repeated, we do not understand.*' (Riedl 1978)
'*The actinozooid is a living thing which knows no time of youthful vigour, no waxing to a period of adult life, no waning to senility – it knows no age – it practically knows no natural death.*' (Wood-Jones 1907, 1910)

1. Introduction

The purpose of this paper is to adapt and interpret the present body of knowledge of growth and form of corals in terms of modular construction and thereby explore the idea of modules as it applies to corals. This is not a contrived exercise: the modular approach in botany has already proved to be a fertile one, and the same may prove so for corals, too.

There is a long tradition of coral biologists borrowing from botany especially because of the analogous shapes of many plants and corals and their analogous synecology. Crossland (1913) has written of coral gardens, flowers and bushes. Squires (1964) refers to coral thickets and coppices; and stems, buds and branches abound throughout the coral literature. Phytosociology has had a significant influence on coral ecology (see Scheer (1974, 1978) for review of origins of this) and Connell (1978) has made direct comparative observations on the ecology of tropical rain forests and coral reefs. A consequence of the well-known symbiosis between many corals and plants (that is, dinoflagellate algae, or zooxanthellae) is that light is equally important to both plants and zooxanthellate corals, and suggests that coral and plant analogies are not always superficial. In all, the old term zoophytes, which included corals, seems completely appropriate in this context, even though it has long since been rejected nomenclaturally.

The modular idea is not of course botanical in the first place, but its application to organisms has so far been dominated by botanists. As botanists have used the idea in different ways, however (White 1984), I have found it more satisfactory to go back to its more general meaning in design and technology to explore its application to corals. This has proved a better route for making comparisons between coral modules, plant modules and modules of other organisms than trying to apply botanical concepts from the outset (van Valen 1978). For this reason, this paper first considers coral modules in terms of design and topology, then in terms of coral biology, especially homology, function, colony organization and growth, and it concludes with a broader discussion of metamers, meristems, and modules. This exercise is primarily a perceptual one, rather than a practical one based on experiments and new observations. I have tried to provide a balance between detail to satisfy coral specialists, and a broader perspective for other readers.

With the advent of a relatively new concept and term like 'modules', we must ask whether it will help us to advance our understanding of the organisms concerned. Failure to do so will simply ensure that the idea will subside into obscurity as an academic curiosity. For a way forward, however, there is the stimulus of Harper & Bell's (1979) eight-point exposition of the dynamic significance of modularity in organisms in general (see also White 1984). This leads me to suggest five areas for which a modular approach might prove fruitful in coral studies, three of which stem directly from Harper & Bell's points (to which I make cross reference).

(i) Ecology (points 1, 6–8); especially new insights into the basis of 'community' patterns of corals and other associated sessile vegetative organisms, for example, on reefs.

(ii) Evolutionary processes (points **1, 3–5, 7**): see Jackson & Coates (this symposium); hence insights into the origins of coloniality. Also, 'being the right size' (Haldane **1927**) suggests comparisons between sizes of (*a*) colonies, (*b*) solitary corals, and (*c*) polyps within colonies.

(iii) Growth and form (points **2, 4–7**): greater understanding of ecophenotypic and phenotypic form, hence inherited architecture and architectural models as for tropical trees (Hallé *et al.* **1978**).

(iv) Taxonomy and phylogenetics: drawing on (iii), and especially in the scope for more thorough specification of colony morphology.

(v) Symbiosis: in particular, the broad empirical correlation of the colonial habit with the symbiosis with zooxanthellae. Potential insights lie in comparing zooxanthellate and non-zooxanthellate corals in (i)–(iv) above. Form through time (see, for example, Wells **1954**; Coates & Oliver **1973**) may throw light on the age and evolution of the symbiosis.

There are also broader possibilities in the modular approach than for either corals or plants on their own, essentially by using corals to test the general ideas suggested by Harper & Bell (**1979**). The first task, however, is to establish how the diverse array of coral forms and iterative morphology can be placed in a rational modular frame of reference. This should provide the necessary practical basis for further observations and experiments at particular modular levels.

2. Background

(*a*) *Corals*

'Coral' has no formal taxonomic status. I use it here to refer to the anthozoan order Scleractinia (*sensu* Wells **1956**), and the extinct anthozoan subclasses Rugosa and Tabulata (*sensu* Hill **1981**). Emphasis is on Scleractinia because the biology of extinct groups is very much more conjectural. There is nevertheless a surprising amount of relevant work on Rugosa and Tabulata considering the assumptions that have to be made, and the labour-intensive methodology that has been used.

The colonial habit occurs in numerous coelenterates, but in corals it is also allied to the characteristic of an enduring, substantial and often very elaborate calcareous skeleton accumulated throughout a lifetime which may be as long as hundreds, perhaps thousands, of years (Potts *et al.* **1985**; Hughes & Jackson **1985**). Coral polyps are therefore very much attached to their own record of growth history (figure 1), though Sammarco (**1982**) has noted that polyps can occasionally detach themselves from their skeletons and recommence colony growth elsewhere. Although the skeleton is dead, its volume and mass may far exceed the amount of living soft tissue. Thus in a typical domed colony of *Porites*, say 2 m across, the living tissue is virtually a veneer which is, at most, only as deep as about 0.5 % of the colony's radius. In finely branched or sheet-like corals, however, the relative proportion of skeleton is much lower than in massive corals. There are obvious analogies between a coral skeleton and a tree's heartwood.

For appropriate illustrations of the living corals mentioned here, especially of their skeletal morphology, the most comprehensive works are the eastern Australia monographs (Veron & Pichon **1973**, **1980**, **1982**; Veron & Wallace **1984**; Veron *et al.* **1977**). For larger illustrations of living colony form, see more general works like that by Wood (**1983**) and Randall & Myers (**1983**). For fossil forms, see Wells (**1956**) and Hill (**1981**).

(b) Coral colonies

It is conventional to regard a coral consisting of a single polyp as a solitary coral, and those with numerous polyps as colonies (figure 1). The skeletal counterpart to a polyp is the calice, the cavity occupied by the polyp. Over the time that a colony polyp exists (perhaps several years or more: there are no adequate data), it contributes to colony growth in two possible ways: laterally by budding new polyps, and longitudinally by continually renewing its calicinal
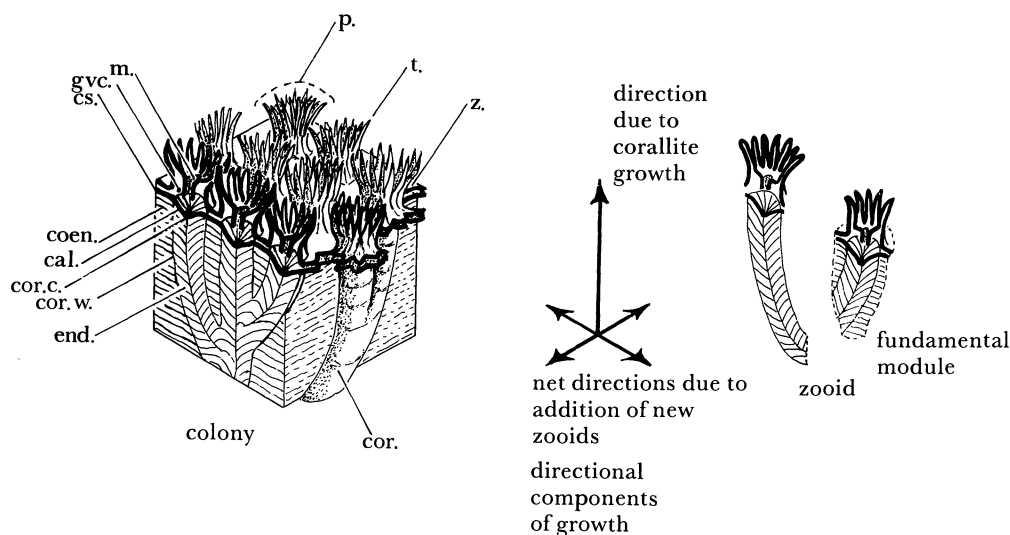

FIGURE 1. General relationships of polyps to skeleton in a plocoid colonial coral (compare with figure 2b). Polyp tissues in bold outline on upper surface and skeletal tissues below. Detailed anatomy is omitted. Representation of skeleton as in figure 2. A zooid (that is, polyp with its calice and corallite) and its share of coenenchymal tissues (if present), represents a fundamental module, and depending on the coral, might be between 1 mm and 20 mm in diameter, typically 2–10 mm. Note continuity of gastrovascular cavity between polyps. In some corals the skeletal components are perforate and the polyp tissues invest the uppermost skeletal layers. Abbreviations: cal., calice; coen., coenosteum; cor., corallite; cor.c., corallite centre; cor.w., corallite wall; cs. (c.e.z.), coenosarc (communal edge zone); end., endotheca; gvc., gastrovascular cavity; m., mouth (=substantive component); p., polyp; t., tentacle; z., zooid.

structure, distally, along its own longitudinal axis, the latter resulting in a tube-like structure, the corallite. It is the combined corallite length and arrangement in a colony that gives a colony its particular form (figures 2 and 3). It is therefore impossible to consider colony form of corals without reference to both polyps and their corallites, even though the bulk of a corallite is dead tissue. In the absence of a suitable term for a polyp with its corallite, and because of its fundamental importance as a unit of colony growth and form, I shall follow bryozoological usage and refer to the two together as a zooid (figure 1).

Unfortunately for the non-specialist or someone seeking to apply a modular approach to corals, this is not the complete picture. Many corals consist of numerous mouths rather than discrete polyps (for example, some of the fungiids), and these corals too are generally regarded as colonies. This may not be rigorous if we follow Wells' (1971) argument that they are 'cerberoid', that is, single-polyp forms with many mouths, but it is convenient to accept that they are colonies at this stage, and return to the problem later (§ 3c). In particular, it is possible to think of these repeated mouths as incomplete polyps or polypoids. Their skeletal counterparts are calicinal or corallite centres without walls defining their limits (figures 2d, h, 3d, h). These

centres consist of distinct structures, or points of convergence of the radial plates (septa) which correspond to the mesenteries of the polyp, or both. In some corals, these skeletal centres are cryptic, and only verifiable by reference to the soft tissue anatomy (for example, *Hydnophora*; figure 3*h*, and see Matthai (1926), figure 16).

(c) Zooidal budding

The development of new zooids in a coral colony is now invariably referred to as budding in the scleractinian literature, and as increase in the rugosan and tabulate literature. Blastogeny has also been used (Fedorowski & Jull 1976) but not widely adopted. One term previously in wide use was asexual reproduction but this has been rejected by some authors (Rosen 1979; Harper & Bell 1979). Various kinds of budding have been defined, but they all belong to one of two major categories, intratentacular and extratentacular (Wells 1956; Oliver 1968; Hill 1981). Both processes amount to expansion of the gastrovascular cavity of the original polyp, with a concomitant opening of a new mouth into this expanded cavity (figure 1), and it would therefore be easy to overstate the biological significance of this distinction. In faviid corals, Matthai (1926) noted that both modes of budding can occur even in a single colony. Corals that differ in their modes of budding can have a similar outward form (for example, *Favia* and *Montastrea*).

Nevertheless, budding modes do have a considerable influence on colony architecture. Figure 2 shows how the combined characters of budding mode and corallite wall development determine whether zooids exhibit a branching pattern, and therefore also whether it is possible to observe zooidal genealogy from skeletal morphology. In corals that have neither a branching relationship between the corallites, nor any other indication of polyp genealogy, it is probably impossible to determine a true polyp-by-polyp growth history other than by direct observations of their growth.

In the Rugosa and Tabulata, we cannot be sure how the various modes of budding inferred from their corallite architecture relate to the presumed polyps, but Oliver (1968) has pointed out their likely correlation with intra- and extratentacular budding in Scleractinia.

It is common to refer to newly budded zooids as daughters. In fact, no sexuality of zooids is meant to be implied, and in living Scleractinia, the zooids of some taxa are hermaphroditic and in other taxa they are specifically male or female (Fadlallah 1983; Harrison 1985). Even the notion of parent and offspring zooids may also be misleading, or difficult to apply. In addition to the reasons shown in figure 2 (compare *a*, *b*, *c*, *f* with *d*, *e*, *g*, *h*), budding in some corals is pseudodichotomous, sometimes making it difficult to distinguish parent zooid from offspring (for example, *Favia* species). (Matthai (1926) insisted that longitudinal division of the mouth, and hence truly dichotomous budding, does not occur in living corals.) In other corals, parenthood is effectively collective among two or more zooids, as within the meander systems of meandroid corals (figure 3*d*) where a new zooid can appear between two pre-existing ones with mesenterial tissues derived from both of them (Matthai 1926; Stephenson & Stephenson 1933).

(d) Growth and form of corals

Growth and form have been studied extensively by coral workers, but only rarely in a way that can be considered relevant to their modularity. The study of growth and form in terms of the repeated units within a colony has been relatively overlooked, whereas the gross outer shapes of corals and the ways in which these grow have always attracted more attention. Closer

to modular considerations is the recent increase in understanding of variation in form between corallites within a colony (see, for example, Oliver 1968; Foster 1983, 1985) and its significance within populations of colonies (see, for example, Best *et al.* 1984; Foster 1984). Even so, much of this is concerned with the components within modules rather than the spatial arrangements and life histories of colony units.

The most relevant and organized body of knowledge of this kind concerns modes of budding in coral colonies, but while this tells us how new zooids arise within a colony and how this affects their arrangment, we have yet to learn about their complete subsequent histories. How often, and when, do they themselves produce offspring zooids, and how long do they survive recognizably within a colony? Wood-Jones (1907, 1910; see quotation at the head of this paper) thought polyps were virtually immortal, but Beklemishev (1969) claimed that they are short lived. Such questions are prompted by Harper's view that colony units can be treated demographically (Harper 1977; Harper & Bell 1979); they constitute a metapopulation (White 1979). In this approach, growth is the net result of the population dynamics of colony units, and form is a synoptic chart or census of the colony units at a particular instant. This raises an old coral question in a new guise: how far can we distinguish the genetic component of colony demography from external influences?

It is useful to distinguish internal and external form in corals because the arrangement of zooids and their interconnecting tissues within a colony is often not evident or deducible from its surface appearance (for example, figure 2*b*, *e*, *f*). Internal form, even of living corals, has to be investigated by preparation of dead material. Similar external forms of corals can have very different internal forms (for example, figure 3*b*) though differences in outward form can usually be related to differences in internal organization.

Somewhat confusingly, 'form' in coral workers' usage often refers to external form, sometimes also called growth form or growth habit, with the added implication that it refers only to those subspecific, plastic, morphological features that are due in part to external influences. In practice, however, it has been a familiar but notorious difficulty to distinguish (i) genotypic form, (ii) phenotypic form, (iii) environmental selection of phenotypic form, and (iv) direct response of growth to external influences (see Foster (1979) for a review of this problem). There is an obvious need to distinguish the form of a particular specimen from more abstract or generalized notions of form based on populations or specimen suites. This allows us to eliminate fortuitous features and progress towards inherited colony architecture, by analogy with tree architecture (Hallé *et al.* 1978).

For growth, too, it follows that there are internal and external aspects, particular and generalized, genetically or externally influenced. Growth is a resultant of lateral and longitudinal directional components, the balance between them differing within colonies, between colonies, and between taxa (figure 1). The use of the modular concept should help us to be more precise in our investigations, by providing standard, specific features to count or observe in a group of animals whose growth and form have otherwise proved elusively complex and irregular to quantify and analyse except at the grossest levels.

3. Cloning, fusion and fission

Remarks on cloning in corals are not only relevant in their own right as a feature of growth, but are essential to an understanding of the different kinds of zooids seen in corals.

Colony growth by budding implies that a colony is a clone (Oliver 1968). In fact, the ambiguities of the word colonial have tempted authors to qualify it by using 'clonal' (Rosen 1979; Ryland 1981), or to give outright preference to clonal, instead (Jackson & Coates, this symposium). We can therefore distinguish cloning in which polyps remain in contact with the rest of the colony, from that in which they become completely detached. The first might be called *clonoteny*, and the second *clonopary*, and each corresponds to Rosen's (1979) continuous and discontinuous categories, respectively. For population studies, the distinction is important, but both phenomena probably have a common origin in being the same process taken to different lengths (Wood-Jones 1907, 1910). The solitary zooidal form is invariably regarded as primitive (see, for example, Wells 1956), and, assuming that clonopary is comparably primitive, coloniality can most simply be regarded as having evolved from solitary forms by paedomorphosis of bud development. Clonoteny is incomplete clonopary. (This is an old idea (see Clark 1964, p. 22), but I exclude from it here the phylogenetic implications with respect to other phyla (that is, the corm theory).)

Taking this point further, this same paedomorphic trend can account for some of the major features of zooidal form and arrangement in colonies, by still further evolutionary suppression of bud development (Wood-Jones 1907, 1910). Zooids without walls, as in thamnasteroid (figure 2d), aphroid and astreoid colonies, are less complete than the free-branching zooids with walls seen in fasciculate colonies (figure 2a). Coates & Oliver (1973) regard the fasciculate (phaceloid) condition as the most primitive kind of coral colony.

There may also be more than one level of bud development within a single colony of a species (*polystatic clonogeny*). I interpret some meandroid corals in this way (figure 3d and §5d); and *Goniopora stokesi* is both clonotenous and clonoparous (Boschma 1923; Rosen & Taylor 1969; Veron & Pichon 1982). Scheer (1959, 1960) on the other hand interpreted the cloned colonies as an unusual development of larval brooding and presumably therefore as a sexually produced phenomenon. There also appears to be some plasticity of clonogenic level in that Sammarco's (1982) observation of polyp detachment in *Seriatopora* may represent an environmentally induced switch from clonoteny to full clonopary.

Clonopary in solitary corals predictably results in solitary offspring (for example, *Fungia*; see Wells 1966), but in colonial corals, the offspring clones might in theory be solitary or colonial. Stoddart (1983) concluded that *Pocillopora damicornis* can produce larvae asexually, but, apart from this, cloning of colonial offspring is more widely documented (see, for example, Hughes & Jackson 1980, 1985; Highsmith 1982). In *G. stokesi* there appears to be specific genetic control of this, though authors differ on the outward details. Thus Boschma (1923) believed that clonoparous zooids are previously attached to their parent colony by a weak skeletal connection, but Veron & Pichon (1982) state that they are held only be extended soft tissue (coenosarc).

Colonies also result from cloning by fragmentation or partial mortality. The genetic element here is less specific, Highsmith (1982) having argued that this kind of cloning is genetic in a broad way, being a susceptibility 'selected for over evolutionary time and incorporated into the life history of many corals'.

The concepts of ramets and genets (as in Harper 1977) can be applied to corals (Rosen 1979;

Heyward & Collins 1985), but because fusion of corals is also widespread, a single colony cannot be assumed to be either a single genet or a single ramet. Fusion of juvenile colonies of the same species has long been known (see, for example, Duerden 1902; Stephenson 1931; Boschma 1929), but more recently there has been increasing recognition of mature colony fusion (see, for example, Hughes & Jackson 1980, 1985). Buddemeier *et al.* (1974, figure 5) reproduced a fine X-ray photograph of a single colony of *Goniastrea retiformis* over 20 cm across with a concordant outline, but with an internal structure showing 'coalescence of two apparently originally independent colonies'.

Conversely, there is also now a substantial body of knowledge of incompatibility reactions between neighbouring corals starting with Lang's (1971) now classic paper on *Scolymia* (a solitary coral). Since such reactions can occur at any taxonomic level, and even between clonally distinct colonies of the same species (see Lang 1984, p. 24, for review), it is clear that the pattern of genetic control of whether fusion or non-fusion takes place is complex, and at the moment we cannot generalize about a possible limiting genetic distance for fusion.

In general, the smallest unit of clonal growth is the zooid, or larval zooid, but in at least some fungiids, the solitary forms can regenerate from broken segments consisting of as little as one-sixth of the original, this being that portion of the original which lies between an adjacent pair of primary septa (Wells 1966).

4. MODULES: THEORY

(a) Generalities

Chapman (1981) has discussed the general history of the use of the word 'module', including its non-biological use. Its biological use has been adapted from architecture and design, this twentieth century use being itself an adaptation of older meanings. Its first botanical use is apparently due to Prévost (1967, in White 1984). Its first zoological use was proposed by Finks (1971), in a very different sense, auspiciously, from the botanical usage. Its rapidly spreading current usage in both botany and zoology, however, is due to Harper (1977), who was the first to suggest that modular organisms included corals.

White (1984) has distinguished the original botanical meaning from Harper's broader application ('any convenient unit'), which according to White corresponds to plant metamerism. Flexibility of choice is the essence of Harper modules, provided that the unit chosen shows (collectively) 'demographic properties' within a plant or colony or genet (Harper & Bell 1979). As White (1984) has pointed out the inconsistency among botanists, which botanical usage is most readily applicable to corals?

The *de facto* notion of a coral module is actually the polyp (Harper 1977; Harper & Bell 1979; Rosen 1979; Ryland 1981; Hughes 1983). Chapman & Stebbing (1980) had evidently also arrived at this independently. Polyps (or zooids) however do not generally correspond to Prévost modules (§7). Few would deny the importance of the polyp as a colony unit, but choice of modules for corals has never been discussed. I have therefore taken an approach derived from Riedl (1978), and first consider the formal analysis of morphological order and repetition, and then the functional and homological significance of the resulting fundamental units.

(b) Topology

The modular idea is essentially a visual and topological one, but the choice of repeated units in corals is wide, including septa, polyps, branches, tentacles, verrucae, mesenteries, mouths and dissepiments (figures 1–3). It is of great importance that many of these repeated elements are parts of other repeated structures, sometimes combined in collective hierarchies. Riedl (1978) has argued that this kind of morphological hierarchy is not an accident of human subjectivity, but an absolute phenomenon. We can start with the whole organism and make successive morphological subdivisions into progressively smaller units. Zooids contain septa, and septa consist of trabecular elements; branches bear polyps and these bear tentacles. I suggest that the following four criteria can be used to find modular order in coral colonies.

(i) A structure is modular if it can be divided completely into a pattern of repeated similar units, without any omitted features. Boundaries of modules should abut and there should be no morphological 'no-man's land' between them (figure 1). In two dimensions, a tesselation is modular, and in corals or plants, *a modular structure is a three-dimensional tesselation* (though the boundaries may have to be drawn in communal tissue or in free space between the visible units). The zooids of a cerioid coral (figure 2 *c*, *g*) are obviously modules, but their mouths alone are not, because this would exclude other repeated units. (For practical purposes of course, key parts like mouths may be used as indicators of zooids (figure 1), but this alone does not make them modules.)

(ii) A second reason why, in this chosen example, mouths and columellae are not modules, is that they occur at the same level of hierarchical subdivision as various other features like tentacles and septa: (zooids (mouth) (columella) (septa) (tentacles) (etc.)). The zooid is the next higher level unit which embraces all these features (figure 1). We can therefore distinguish morphological subdivision which yields only units that are similar (A (B) (B) (B) (B)) from that which yields a variety of different units (A (B) (C) (D) (E)). These are, respectively, homogeneous and heterogeneous subdivisions. *Modules should correspond to homogeneous units of hierarchical subdivision.* The zooids of most kinds of coral obviously fulfil this condition (figure 2), with respect to, say, the whole colony, or, if there are also branches (figure 3 *a*, *e*), to colony branches: (colony (zooids)) or, (colony (branches (zooids))).

(iii) In practice, morphological analysis through successive levels within most organisms reveals that they consist of units of both homogeneous and heterogeneous subdivision at one level or another. Hence, *an organism is modular if subdivision at the highest (or very high) level reveals homogeneous units.* Trees and some corals have a first subdivision which is heterogeneous, consisting of stem and branches, but modular organization is clear thereafter.

(iv) Analysis of some organisms reveals that not only the first subdivision is homogeneous, but that there may be a sequence of two or more further consecutive homogeneous subdivisions, like (colony (branches (zooidal groups (zooids)))), before the sequence is interrupted by heterogeneous subdivision (figure 3).

If homogeneous units occur in an unbroken series of subdivisions, they are all modules at their respective level (hence modules of modules, that is, cormidia), and the finest unit is the fundamental module. From the present point of view, it is of no direct relevance that homogeneous units of some kind may reappear after heterogeneous interruption. In corals, after heterogeneous division of zooids into different parts, homogeneity reappears at the levels of cells, skeletal sclerites, etc., but these are not modules of corals.

With these criteria, a solitary coral (or single zooid: figure 1) is not modular because the first stage of subdivision is heterogeneous, consisting of an array of different zooidal parts. Colonial corals are modular because it is usually easy to show that the above criteria are met, though it is the zooid that is the basis of the fundamental unit, not the polyp on its own (figure 1). A few corals, however, seem to be anomalous. In *Hydnophora*, for example, the finest units of homogeneous subdivision seem to be the monticules (mont. in figure 3*h*), and in *Acropora* (figure 3*a*), the polymorphism of the zooids makes subdivision at the zooidal level seem heterogeneous. These are obviously limitations to purely topological analysis, and recourse must be made to biology (below).

Taking the zooid to be the fundamental module of a coral, notwithstanding the apparent anomalies, we can see that the heterogeneous units found at the next lower level of subdivision always include one mouth and its skeletal counterpart, the corallite centre (figure 1). The various parts that make up a zooid cannot be modules, but can be regarded as components, the mouth or centre being the substantive component of the fundamental module. Completeness of zooidal development can be gauged from the suite of other, accessory, components which are also present in the fundamental module. The notion of a fundamental zooid is similar to that of the unit cell in crystallography, except that it is physically and geometrically less rigid.

(c) *Homology*

Riedl (1978) recognizes seven forms of similarity. Among these the similarity of units found in homogeneous subdivisions constitute homonoms, that is, they are homologous with respect to each other within that particular organism and within their own hierarchical level. Ideally, for present purposes, they should also be homologous from one coral to another, and therefore for the group as a whole. This would be difficult to argue for many higher-level modules, but I do propose this for fundamental modules (zooids).

Wells (1971) has apparently argued the contrary. He states that the repeated units produced by intratentacular budding are not the same as those produced by extratentacular budding, because the first are 'incomplete individuals marked by lack of directive mesenterial couples and often not morphologically individualized', whereas the second are 'complete homomorphic individuals.' Coates & Oliver (1973), in their important contribution to our understanding of coloniality in corals, followed Wells.

Against this, there are three considerations. Firstly the zooids produced by intratentacular budding share an important feature with extratentacular zooids, namely the mouth. This is not a simple structure but a whole functional centre of action within a colony, especially for feeding, reproduction and excretion (Matthai 1926). If the mouth is homologous throughout corals (or Scleractinia, at least), then the zooids must also be homologous, regardless of their budding mode or completeness of development.

Second, if the mouths developed in the zooids of each kind of budding mode are not homologous, we must assume that they have evolved twice, independently, in the two kinds of corals. Moreover, we should expect differences in the anatomy, histology or development of these mouths. It becomes especially difficult to envisage a convincing evolutionary pathway for corals (for example, *Favia* species) which bud both intra- and extratentacularly, even within a single colony (Matthai 1914; Veron *et al.* 1977).

Third, Matthai (1914) also stressed that the symmetry differences referred to by Wells (1971) did not correspond exactly to budding modes.

In all, it is a simpler proposition to regard all mouths as homologous. Thus even if the zooids in some taxa are more complete than in others, they can still be regarded as homologous with each other. Polymorphic zooids within a colony would also be homologous. We therefore have a single conceptual zooid, which is more or less modified, or more or less arrested in its development, and which is sometimes polymorphic, according to the taxon.

Two more general points can be mentioned in support of this homology argument. First, the solitary zooidal state is invariably regarded as primitive with respect to colonial forms (Wells 1956; Coates & Oliver 1973). Second, it is interesting that the mouths within a polystomatous meander (figure 3 d) in *Platygyra sinensis* function reproductively as separate zooids, producing their own egg–sperm bundles during spawning (see photograph by J. Oliver in Talbot (ed.) (1984) p. 115, lower right).

Homology overcomes the limitations of the foregoing topological analysis, not only in the case of polymorphism, but also for corals whose interzooidal, coenosteal or wall modifications dominate the visual pattern of repetition (for example, figure 3 c, h; and the striking, upward extensions of interzooidal tissue in *Pectinia paeonia*). In such cases, homology directs us to the mouth first, to discover the fundamental module. The interzooidal features are secondary. They presumably have an important, if as yet unknown, colony function, and in *M. verrucosa* (figure 3 c) and *H. microconos* (figure 3 h), they are the substantive components of higher level modules consisting also of zooids clustered close to, or around these features. In other corals, such interzooidal features are less regular, as in the collines of *Pachyseris* and *Pavona varians*, or the 'carinae' of frondose *Pavona*, and are less obviously modular. In *Pectinia paeonia, Stylocoeniella* and *Stylocoenia*, there is a single discrete interzooidal structure for each zooid, so it belongs to the same level of modularity as the zooid.

In conclusion, although it is possible to make useful inferences about corals by using Harper modules, I have deliberately tried to qualify convenience with topology and homology in the belief that this will advance our understanding of the morphological comparison (and evolution) of different taxa, and stabilize terminology. The conclusion that the zooid is the primary coral module is not, perhaps, surprising, but it is new in so far as it (i) unites polyp and corallite; (ii) recognizes no fundamental difference between different kinds of zooid; and (iii) provides a fixed point of reference for relating all other kinds of repeated feature to each other.

5. Modular specification of colony form

(a) Colony form = zooidal organization + colony shape

In the previous section, I used morphological analysis to clarify the prime significance of the zooid as a colony unit for corals in general. To specify coral colonies morphologically, we now reverse this approach by starting with the components that make up a zooid and repeating this specification for all the modular levels present in colony. For fossil corals, we have to use the corallite or corallite centre as the fundamental module because polyp tissues are absent.

The need to distinguish internal and external morphology has already been mentioned. Internal morphology concerns the organization of zooids, whereas external morphology includes the expression of this organization at the colony surface together with the colony's outline shape. Colony form can therefore be thought of as the sum of its zooidal organization (internal and external) and its shape. Although shape may be modular too, this is not always

so. If shape is modular it generally reflects an internal modular organization, but shape modules should be specified at the appropriate level of organizational module, because, ordinally, their levels may not correspond.

To date, interest in colony morphology has centred on the fundamental zooid, and generalized shape. Little attention has been paid to higher level modular groupings of zooids. For full colony specification, therefore, I suggest that the procedure might be as follows.

(i) Fundamental module form: (a) components; (b) spatial arrangement of modules; (c) shape of module*.

(ii)* Second-level module form: (a) zooidal complement and other specifically second-level components; (b) spatial arrangement of second-level modules; (c) shape of second-level module*.

(iii)* (and so one, as necessary): (a), (b), and (c) as (ii).

Asterisks indicate features which may not be present or specifiable. Components (figures 1 and 2) include the substantive zooidal components and accessory components; the accessory components are zooidal (endothecal) and coenenchymal (exothecal), the latter being applicable to some corals only. Together, the components, their relationship to each other, and their shape (item (c)) describe the module (figure 1). A module at the first level becomes the substantive component at the second level, and so on for each modular level present (figure 3). Particular components either endothecal or exothecal, may be characteristic of a particular level (for example, figure 3g, h). There may be polymorphism of modules at any level, and these are specified consecutively within each level.

Items (a) and (b) together specify organization. Item (c) refers only to outward shape as it affects the outline of the whole colony. The hierarchy of shape modules (if present at all) may differ from that of the organizational modules in that there may not be a shape module for every organizational level. This approach does not make any assumptions about what is genetic and what is not, but information collected and organized by this scheme may be generalized as coral architecture as a step towards inferring inherited form.

(b) Components of fundamental modules (ia)

The substantive component, the mouth and its skeletal centre, may be difficult to discern on superficial examination, especially in those meandroid corals where in the skeleton, one centre can merge with the next (in contrast to figure 3d). In *Pachyseris*, the mouths are minute and there are no tentacles (Yonge 1930). Exact location of mouths in such corals cannot be inferred from skeleton alone. Accessory zooidal components include septa, tentacles, mesenteries, columella, endothecal dissepiments and various kinds of wall structures (figures 1 and 2). The total complement gives an indication of how complete the zooid is with respect to its notional solitary counterpart. Some wall structures are specialized with parts that project upward from the calicinal surface (*Stylocoeniella*, *Stylocoenia*). It may be necessary to specify more than one kind of fundamental module, as in *Acropora* (figure 3a) and some circumoral corals (figure 2h).

Coenenchymal components are present only in plocoid corals (figures 1, 2b, e, f, 3c), the zooids being spaced from one another and laterally connected by components like costae, exothecal dissepiments and their soft tissue counterpart, communal edge zone. Such interconnections are absent from the Rugosa (Hill 1981). In corals without zooidal walls, however (especially thamnasteroid forms (figure 2d)), the distance between zooidal centres may be so great that the intervening tissue becomes a kind of coenenchyme that merges continuously with zooidal
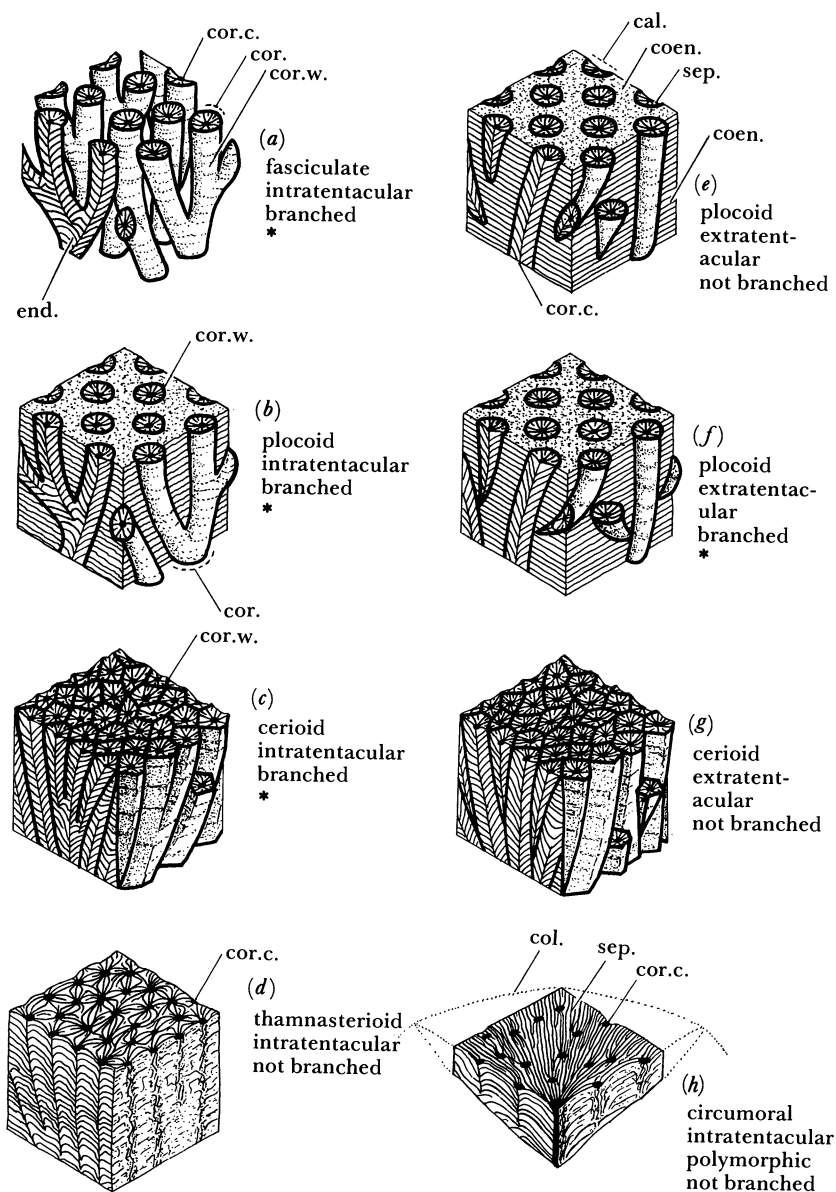
FIGURE 2. Examples of first level (fundamental) modular organization. All examples are schematic, showing only selected components, and are not to scale. Left-hand faces represent cut longitudinal sections, usually sagittal. Right-hand faces represent more or less broken surfaces. Upper faces represent calicinal surfaces without polyp tissues (but compare with figure 1). Polyp tissues are generally continuous between zooids except in (a) where the polyps often become completely separated. Note that left hand faces are idealized and in practice, a cut face would be unlikely to show such consistent alignments and orientation of corallites. In practice, therefore, (b) may appear similar to (e) and (f), and (c) similar to (g). In (b), (c), (e), (f) and (g), walls may be perforate or incomplete and hence transitional in appearance to (d). Abbreviations: col., colony outline; sep., septum; *, genealogy of zooids is directly recorded in the skeleton of these examples, but may be deducible in other examples from other evidence. Other abbreviations as figure 1.

tissues. This tissue may also develop specialized surface structures of its own, especially at higher modular levels.

Topologically, the boundary of the fundamental module takes in the whole zooid down into the skeleton to the point at which corallite growth commenced, and also includes a half-share of any coenenchymal tissue lying between itself and each of its neighbours (figure 1). There

will of course be some modules in many colonies that are not seen at the colony surface at all, having died or degenerated at some earlier point in the colony's history and been obscured by later colony growth.

(c) Spatial arrangement of fundamental modules (ib)

The spatial arrangement of fundamental zooids is primarily controlled by budding modes but is also specified in terms of length, location and angle of budding of zooids. In fasciculate corals, the zooids branch into free space without lateral connecting tissues (figure 2a). In cerioid corals (figure 2c, g), zooids are contiguous, either branched or not branched (but see discussion of intermural budding in Oliver (1968)). In plocoid corals (above), the zooids may be branched (figure 2b, f) or independent, resting proximally on coenosteal components (figure 2e), though their lateral arrangement at the colony surface may be similar in both cases (*Favia* and *Montastrea*, respectively). The first is a consequence of either intra- or extratentacular budding and the second of extratentacular budding.

Many of these standard terms for zooidal arrangement are based on the notion of walls as a single feature, but wall structures are varied and sometimes complex (Wells 1956; Mori et al. 1977; Mori & Minoura 1980; Hill 1981), suggesting that new descriptive terminology is needed, especially for consistency between the major coral groups.

(d) Organization of second level modules (iia) and (iib)

Higher level groupings of zooids, or cormidia, if present, are all reiterations in the broader sense of Harper & Bell (1979), but the Montpellier school use *réiteration* more restrictedly. Thus Dauget (1985) has described regeneration of whole colony growth as *réiteration*, whereas here, this would be just one kind of reiteration which occurs at the highest possible modular level for that particular coral (in response to environmental factors).

The fundamental modules alone may constitute the components at the second modular level, but there is also sometimes a particular feature like a specialized wall or coenosteal structure associated with such zooidal groupings, like the coenosteal verrucae of *Montipora verrucosa* (figure 3c). Some typical arrangements of fundamental modules within second and higher level modules are shown in figure 3.

There are three ways in which these groupings are built up (with or without their own components): (i) homozooidal and (ii) heterozooidal, which are either (iia) polymorphic, or (iib) polystatic. These three categories are not mutually exclusive. They are sometimes clearly genetic (*Hydnophora*) and sometimes environmental (many of the poritids), often with the first modified by the second.

In homozooidal groupings, the zooids are all of the same kind, forming a recognizable discrete structure that results from a particular kind of growth pattern that is sometimes centred around particular points or axes (figure 3b, e). X-ray techniques reveal these groupings very well (and their relation to colony shape), and show how they can vary from being relatively weakly defined (Buddemeier et al. 1974, figure 2: *Porites lobata*) to very definite structures (Buddemeier et al., figure 4: *Psammocora togianensis*).

In heterozooidal groupings, the zooids are not all identical, but are composed of particular combinations of the different kinds of zooid. This is visually obvious in the case of polymorphism (*Acropora*: figure 3a), but not in the polystomatous groupings of some meandroid corals. When they consist of numerous meanders (figure 3d), one kind of zooid is represented by the centres

without complete walls, and the other by the wall that encloses the centres. This may seem nonsense, but is a consequence of growth. The existence of numerous distinct meander systems implies that from time to time during colony grov.th, a new zooid, or an existing zooid within a meander, develops a complete wall (centre of figure 3*d*). The majority of zooids, however, do not do so, so remaining within the walls of those that do. These zooids-within-zooids are, therefore, an example of the idea of paedomorphic clonogeny (§3), but within a single colony, two different stages of arrest occur simultaneously (*polystasis*).

In *Hydnophora* (figure 3*h*) and *Manicina areolata*, there is normally only a single continuous meander system, so there is no polystasis. In some colonies of *Manicina*, however, there are two or three meanders, but these have been interpreted as the result of fusion of different larvae (Boschma 1929; Yonge 1936). Thus fusion can also give rise to higher level modules in the homozooidal category (see also the *Goniastrea retiformis* of Buddemeier *et al.* (1974), mentioned already). *M. areolata* also shows another kind of homozooidal module: its meander system divides into branches (me.br. in figure 3*d*). *Isophyllia sinuosa* shows a five-rayed variant on this theme (Matthai 1926). In corals like the meandroid faviids and mussids where this meander branching is common, the branched sections constitute second level modules, and the distinct meander systems, if present, represent third level modules (by fusion or polystasis).

Second level modules may just be growth aggregations or superimpositions (figure 3*b*, and Buddemeier & Kinzie (1976), figures 1A (*Porites*) and 1B (*Pavona*)), but they can also be categorized as fasciculate, cerioid, plocoid, etc., as for first level modules (see caption to figure 3*d*).

(e) Organization of third and higher level modules (iii a), (iii b), etc.

The zooidal groups of the second level may themselves be grouped (especially figure 3*b*, *d*, *e*,*f*), and the same approach outlined for lower levels can be followed, with suitable modification where necessary. The previous distinction of homozooidal and heterozooidal groups can be generalized for all levels as homomodular and heteromodular. Some examples of three-tier modularity have already been mentioned in connection with meandroid corals whose meanders are branched. Another example of three-tier modularity, based entirely on homomodular groups, is found in verrucose forms of *Pocillopora* whose verrucae represent second level structures (figure 3*g*), and whose flattened, columnar branches represent third level modules. Table *Acropora* consists of polymorphic branches fused or anastomosed into a horizontal plate. Its branches are second level modules, but its plates are sometimes reiterated and therefore represent third level homomodular units. Dauget's (1985) examples of traumatic *réiteration*, already mentioned, also belong here. A number of meandroid corals show a third or higher level organization when the whole colony has the form of a ramose branching or platey system (*Platygyra zelli*, *Merulina ampliata*, *Hydnophora rigida*, and *H. exesa*).

(f) Shape (c)

Each level of modular organization may also contribute directly to shape, so that a shape module usually has a corresponding organizational module, but the reverse is not necessarily true. Similar outward shapes may conceal different modular organizations (Krasnov & Preobrazhenskiy 1972).

The simplest colony shapes are massive (more or less hemispherical), mound-like or encrusting sheets, and are not therefore modular in their shape. Their organization is very varied

ap.z.(f.m.A)
lat.z.(f.m.B)
ram.br.

(a)
acroporoid
(apical ramose-branching)

lat.z.
(f.m.B) coen. ap.z.(f.m.A)

z.(f.m.)*
ram.br.(2 l.m./h.l.m.)

(e)
ramose-branching

z.(f.m.)*

2 l.m./h.l.m.

(b)
multiple–massive

z.(f.m.)* d.b. coen.v.
(coen.u.)

r.(2 l.m.)
z.(f.m.)

(f)
halysitoid
or
cateniform

z.v. lac.(3 l.m.

2 l.m.
z.(f.m.)

(c)
coenosteal–verrucose

z.(f.m.)* me.va. cor.w.
me.br.(2 l.m.) coen. z.c.(f.m.)
sep.
me.sy.
(3 l.m.)

(d)
discontinuous
cerioid–meandroid

cor.
w. end.
z.c.(f.m.)

z.v. z(f.m.)
2 l.m.

(g)
zooidal–verrucose

z.(f.m.) 2 l.m.
mont. sep. me.va.
z.c.(f.m.)

(h)
hydnophoroid
(continuous
cerioid–meandroid)
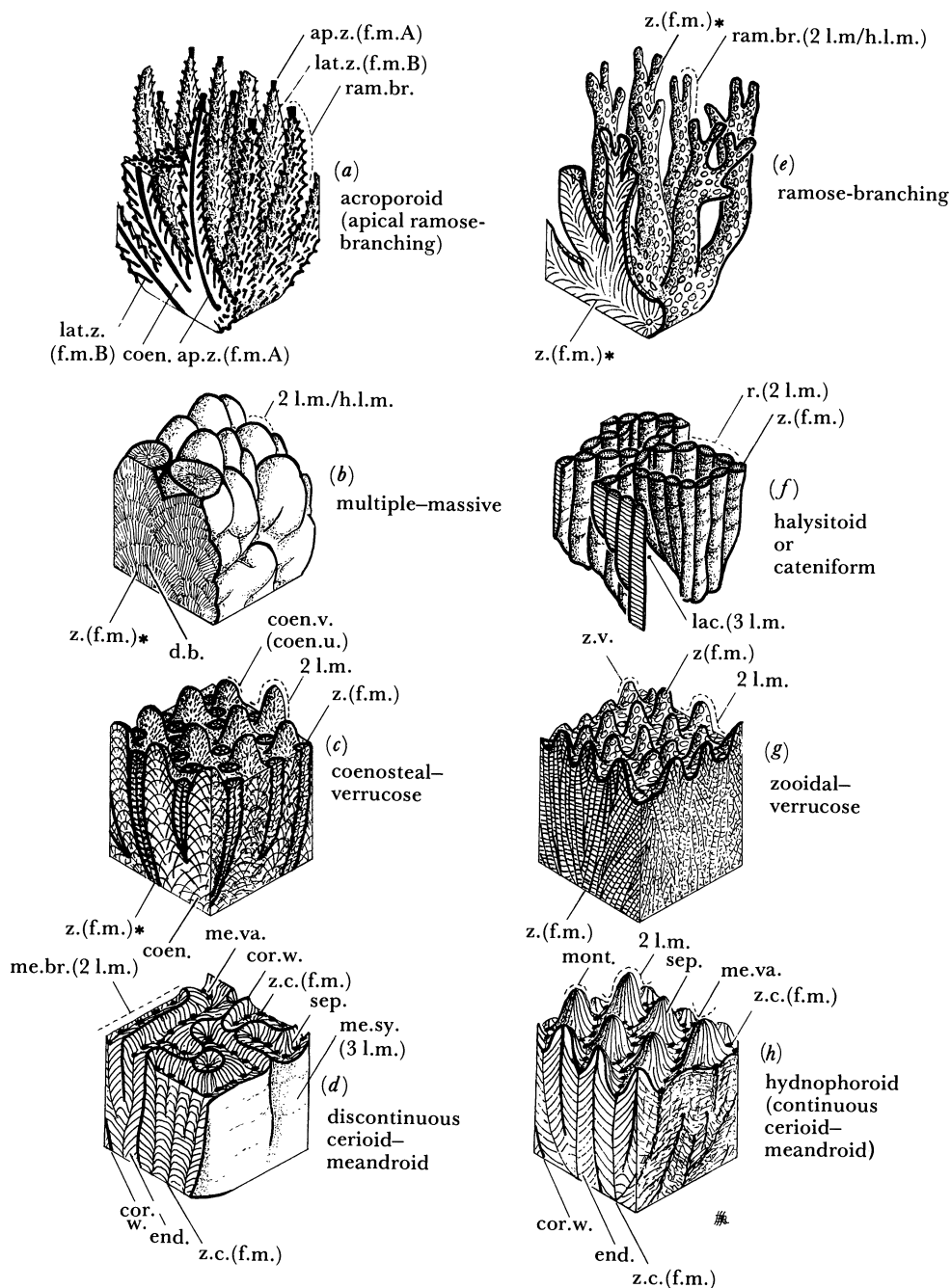
cor.w.
end.
z.c.(f.m.)

FIGURE 3. Examples of second and higher level modular organization. Diagrams on different scales (for zooidal scale, see figure 1) and not to scale. Each example is based on the organization of a particular coral but is not necessarily accurate in other details. Left-hand faces represent cut longitudinal sections, usually sagittal. Right-hand faces represent more or less broken surfaces (except (*a*), (*b*) and (*e*)). Upper faces represent calicinal surfaces without polyp tissues, sometimes with transverse sections through the higher level modules ((*a*), (*b*) and (*e*)). Note modularity of shape as well as organization in all but (*d*).

(*a*) Zooidal organization, a specialized form of figure 2*f*, but second level modules are heterozooidal–polymorphic reiterations of systems of apical and lateral zooids (based on *Acropora*).

(*b*) Homomodular reiteration which can occur at different modular levels in different corals, for example, the second level examples consist of homozooidal reiterations of figure 2*b–g*, and third and higher level examples are reiterations of second or higher level modules like figure 3*c*, *d* or *h*. (Typical of poritids and faviids and common in fossil groups.)

(*c*) Second level modules consisting of homozooidal reiteration of zooids as in figure 2*e*, grouped around coenosteal verrucae (typical of *Montipora verrucosa*).

from single-tier modularity as in some species of *Porites* and *Goniastrea*, to multi-tier modularity in meandroid faviids and mussids. Massive colonies, however, often also bear low to conical protuberances as weak shape modules (figure 3*b*), reflecting second-level homomodular organization. The columns, branches and platey shapes of many corals are, in effect, a further, specialized development of these kinds of protuberances. In this case the branches are described as ramose (figures 3*a*, *e*) to distinguish them from the fasciculate branches in other corals (figure 2*a*). Fasciculate corals are among the most primitive kinds of colony and are especially common in the fossil record. They have only a single modular level, branching zooids, and this corresponds, zooid-for-zooid, with their branching shape-modules (for example, *Siphonodendron*, *Thecosmilia*, *Cladocora*).

The ecological (especially the palaeoecological) literature places an emphasis on shape because corals of particular shapes are broadly associated with particular environmental conditions. Inference of past conditions can, therefore, be made, supposedly, by reference to the shapes of fossil corals, and therefore independently of taxonomic and stratigraphic considerations. Stearn (1982) has discussed some of the problems of this approach, but I would blame some of this on confusion about the modular level at which branching occurs. At the very least, it is necessary to distinguish ramose-branching from fasciculate-branching (Rosen 1971). Hierarchical modular analysis of shape, as outlined here, should also help to provide a finer resolution between shape and environment than exists at present.

Branching is also widely associated with modularity, but in corals this is not universally true. A massive colony of *Montastrea*, for example, has neither branching zooids (figure 2*e*) nor a branching shape (figure 3*b*). Branching at the fundamental organizational level is confined to those forms with zooidal walls as asterisked in figure 2. At higher modular levels, branching can occur within meanders (figure 3*d*), between meanders (figure 3*d*), and between homomodular (figure 3*e*) and polymorphic (figure 3*a*) clusters. Branching organization is not necessarily seen as branching shape: in massive *Favia* it is not (figures 2*b* and 3*b*). In ramose-branching *Acropora* (figure 3*a*) or *Porites* (figure 3*e*) it is; but their branches are first level shape-modules which correspond to second-level organizational modules. Shape, organization and branching in halysitids is particularly unusual (figure 3*f*). In *Porites* (*Synaraea*)

(*d*) Heterozooidal–polystatic reiteration of zooids in linear series (second level modules) often in homomodular branching systems (third level modules), typical of many Faviicae and Eusmiliinae. Note new monocentric corallite, front centre. Intermeander organization is cerioid (compare figure 2*c*), typical of *Platygyra*, but in other meandroid corals may be fasciculate (for example, *Lobophyllia*) or plocoid (for example, *Diploria*).

(*e*) As for (*b*) but ramose-branching, and with third or higher level modules based on reiteration of (for example) figure 3*d*, *g* or *h*. Typical of poritids, pocilloporids and many fossil groups (tabulate and scleractinian). Intergrades with platey-ramose forms.

(*f*) Homozooidal reiteration in ranks (second level modules) grouped in homomodular anastomosing systems enclosing lacunae (third level modules). Typical of halysitid tabulate corals (Ordovician–Silurian).

(*g*) Homozooidal reiteration of (for example) figure 2*e* or *g* grouped into small projections, typical of *Pocillopora*.

(*h*) Homozooidal reiteration of fundamental modules in continuously interlinked meander-rings (second level modules) which surround isolated portions of wall; typical of *Hydnophora*; like cerioid–meandroid forms (figure 3*d*), but not polystatic. (Corallite centres not usually as visible in skeleton as shown.)

Abbreviations: ap.z., apical zooids; coen.u., coenosteal upgrowth; coen.v., coenosteal verruca; dens.b., density band; f.m.A, fundamental module of type A; f.m.B, fundamental module of type B; h.l.m., third or higher level module; lac., lacuna; lat.z., lateral zooid; me.br., meander branch; me.sy., meander system; me.va., meander valley; mont., monticule; r., rank or palisade of zooids; ram.br., ramose branch; z., zooid; z.c., zooidal centre; z.v., zooidal verruca; 2 l.m., second level module; 3 l.m., third level module; *, this repeated unit may be a higher level module than fundamental (see captions). Other abbreviations as figures 1 and 2.

rus, there is polymorphism of shape modules, with horizontal plates and vertical branch-systems (see Randall & Myers 1983, figures 109 and 110).

6. Modular aspects of colony growth

(a) Statistical aspects

The question of senescence has attracted attention especially in connection with fecundity and fitness. Thus, Harper & Bell (1979) generalized that 'the earliest modules developed from a zygote are usually vegetative units and later sexual modules are formed in a possibly infinitely extended phase of sexuality and the production of daughter zygotes.' Babcock's (1984) analysis of fecundity confirms this for *Goniastrea aspera* and *G. favulus*, showing that the proportion of sexually mature polyps in a colony approaches 100% only when the colony radius is greater than 3.51–4.00 cm. This is equivalent to about 220 zooids in *G. aspera* (see also Harriott 1983). Babcock also showed that the frequency of eggs per mesentery is greater in polyps of large colonies than of small ones.

Harper & Bell (1979) have also pointed out that Grigg's (1977) work on gorgonian corals shows that fecundity of colonies continues to increase even though their life expectancy decreases. Gorgonian corals are distinct from those treated here, and may differ especially in not showing colony fusion and fission to the same extent as scleractinians. It is difficult to know what life expectancy means in scleractinians other than for juveniles or as a result of catastrophic events. Hughes & Jackson (1985) give data showing that the probability of post-juvenile colony mortality actually decreases with size (and hence, very broadly, with age), and, in general, colonial scleractinian longevity of both colonies and genets is likely to be well in excess of the 70 years maximum shown by Grigg's gorgonian data. (There might be exceptions to Hughes & Jackson's growth generalizations: *Manicina areolata*, perhaps?) Even the relation between colony size and fecundity can be confused by fission and fusion, as Harriott (1983) has inferred for *Porites lutea* and *P. australiensis*.

A related matter has been that of possible decrease of growth rate of colonies with age. Unfortunately there have been almost as many methods of assessing this as papers on this subject. Buddemeier & Kinzie (1976) provided a useful critique of methods, including those used to assess senescence. They concluded that for many corals, growth rates are faster when colonies are small, but thereafter, there is no change with age. Hamada (1973; not discussed by Buddemeier & Kinzie), reviewed earlier growth data on the massive coral *Goniastrea aspera* which purported to demonstrate senescence, and argued that the data could be better explained in terms of the geometrical properties of hexagonal close packing of zooids. These may be a factor, but there may be a simpler explanation. His calculations use the ratio of new zooids to pre-existing zooids per unit time (I) as a growth measure, and this decreased at various rates in the observed corals. But I is not independent of the original size of a colony (if the number of zooids is assumed to be directly proportional to the area they occupy). For the same value of growth increment, I is less for large colonies than small ones.

In plants, growth and form have been characterized by the relative numbers, positions and ages of the different kinds of modules present (Harper & Bell 1979; White 1984). Although there may be serious practical difficulties in doing the same for corals, similar studies of corals should be of interest. There is also scope for using the proportionality of the number of modules within one particular hierarchical level to those within the next higher level. Such biometric

measures would have taxonomic and ecological value. Wijsman-Best (1974) for instance, counted the number of zooids per meander in some species of *Goniastrea* and *Platygyra* at different depths over about 35 m, and found a decrease of over 80 % with increasing depth. (She concluded that 'this may point to the fact that meandering as such is an adaptation to faster growth, since less skeleton has to be formed per unit of living tissue'.) This particular measurement, incidentally, for meandroid corals, indicates the proportion of zooids that develop walls, to those that remain less developed by not doing so (figure 3 *d*), that is, it amounts to a polystasis ratio.

Other measurements of heuristic interest include the number and position of budding zooids at different times in a growing colony, and the same for the sexuality and reproductive states of polyps. The first of these is complementary to the topological growth studies mentioned below. For reproduction, Hughes & Jackson (1985) have suggested that active polyps may generally be concentrated in central areas of colonies.

(b) Topological aspects: towards architectural models

Few people have recorded observations on colony growth with particular respect to modules and over a long enough period of time to construct architectural models of corals. Most of the information that is available concerns very juvenile stages or a relatively brief interval in the life of mature corals (notably Stephenson 1931; Manton 1932; Stephenson & Stephenson 1933). There are obvious practical difficulties in carrying out this kind of work because colonies grow slowly and zooids are small and numerous in relation to colony size. Here I review some current knowledge which represents the first steps towards the construction of architectural models of corals.

Stephenson's (1931) observations on *Pocillopora bulbosa* (now regarded as a synonym of *P. damicornis*) showed that the first zooid is surrounded by six subsequent zooids, and that this kind of lateral expansion continues until at some, as yet unobserved stage, branches develop by growth from more than one such centre. The iteration of growth centres must arise from, or correlate with, faster longitudinal growth (figure 1) in these areas. With the onset of branch growth, new zooids appear at or around the tips of branches in a broadly axial manner, but without clearly differentiated axial zooids (Manton 1932). This appears to be a common mode of colony growth in ramose branching corals (figure 3 *e*), with the exception of *Acropora* (figure 3 *a*) with its distinct apical zooids (compare Wood-Jones' (1907, 1910) 'groups' 1 and 2, respectively). In young, but postjuvenile dome-shaped colonies of *Favia* the location of new zooids is much less ordered than in *Pocillopora*, with new zooids appearing di- and tristomodaeally almost anywhere in the colony, but with an extratentacular tendency at the colony margins (Stephenson & Stephenson 1933). This can be seen by shading in new zooids in the authors' figures 5–9. The colony in their figure 5, however, shows restriction of new zooids to an annular zone, but this may just have been fortuitous.

A development from simple direct observation has been manipulation of colonies by transplantation, experimental substrates and artificial damage, probably the best known pioneer work of this kind being that of Wood-Jones (1907, 1910). This kind of work has largely been directed to understanding the influence of environment on colony shape, and also, in *Acropora*, environmental effects on polymorphic zooidal organization. Stephenson & Stephenson (1933), Loya (1976) and Kobayashi (1984) showed that coral regenerative growth from damaged surfaces is faster than from undamaged surfaces (a pattern which is familiar in

arboriculture and topiary). Foster (1979) used transplants to analyse variation at the component level of fundamental modules in *Montastrea* and *Siderastrea*. Dauget's (1985) study of *réiteration* has already been mentioned. Although the plasticity of coral morphology is now widely accepted, it was controversial 80 years ago (Wood-Jones 1907, 1910). There is, however, further scope for manipulative studies, especially if, through additional studies of effects on internal as well as external morphology, the plasticity can be specified in modular terms. It is doubtful if there is yet a sufficient body of knowledge to make a synthesis worthwhile.

An alternative approach to making direct observations is to use colony morphology as a growth map. The corallites of many corals are like the petrified wakes of growing polyps (figure 1). Oliver (1968) summarized the generalized growth schemes of a number of extinct corals (see also Krasnov & Preobrazhenskiy 1972) and Randall (1982) has done the same for living *Acropora*. Ideally, there has to be a means of inferring chronology, and, if relevant, the genealogy of zooids. Genealogy is clear in corals whose corallites have a branching organization, but can sometimes be inferred too from mesenterial (hence, sometimes, septal) patterns (figure 2). Matthai's (1914, 1926, 1927, 1948 a,b) fundamental contribution to knowledge of colony growth, especially of budding modes in relation to colony form, was based on mesenterial analysis. Generally, however, this is not sufficient on its own to reconstruct the complete colony history of a particular coral. One reason for this is that the mesenterial relationships between mature zooids are often reciprocal or symmetrical (for example, meandroid mussids and faviids) and leave unanswered a question like that of whether new zooids are added at the ends of meanders, or within their length, or both. The figures 11–14 of *Lobophyllia* given by Stephenson & Stephenson (1933) show that both seem to have occurred, though 'the actual birth of these new mouths was not witnessed by anyone'.

Two rather makeshift ways of inferring time from form are (i) the comparison of differently sized colonies of the same species of the same general shape from the same habitat (see, for example, Stephenson 1931); and (ii) assumption that equal distances along or between zooids represent equal lengths of time. On *a priori* grounds (ramose corals, above), as well as evidence from growth banding (see, for example, Buddemeier & Kinzie 1976) the second method, is at best, a hazardous approximation.

Notwithstanding the above reservations, an architectural model should be possible for *Isophyllia dipsacea* (now *I. sinuosa*) by using a combination of the above approaches, and based on Matthai's work (1926, 1927), supplemented, ideally, by evidence from mature colonies. The relatively flat shape of the colony allows it to be read as a two-dimensional map. With suitable evidence for genealogy of zooids, the growth models of other circumoral, two-dimensional corals (figure 3 h: especially members of the Agariciidae, Fungiidae and Pectiniidae) should also be readily deduced.

In three-dimensional colonies, sectioning or dissection of the skeleton is usually necessary, except for openly branching fasciculate corals (figure 2 a) which are not enclosed by consolidated sediment. An additional assumption that has to be made is that new zooids arise only at or near the living, and therefore outermost, surface of the colony. In fact, this is more likely to have been true of epithecate forms (mostly extinct) than of living scleractinians whose edge-zone usually extends down the exterior of zooidal walls and forms a potential budding site (see Hidaka *et al.* (1982) on the nearly-fasciculate *Galaxea fascicularis*). Fedorowski (1978) illustrated ten examples of growth in the fasciculate, extinct *Heritschioides* sp., but concluded that this coral showed no obvious pattern. Its modular growth model appears to be

opportunistic or at least non-determinate. Two other notable fossil examples are the growth studies of *Halysites* and *Cladochonus* by Hamada (1959, 1973).

In theory, serial transverse sectioning of other kinds of three-dimensional corals should provide modular growth information, but there are geometrical difficulties because successive, equally spaced sections only represent equal distances along corallites for corallites which are perpendicular to the planes of the section. Therefore even if growth was at an equal rate throughout the colony, it would be difficult to reconstruct a sequence of events. One solution is to work with very small colonies (see, for example, Beecher's (1893 a, b) pioneer work). Another is to use corals which maintained a flat living surface as they grew upward (Scrutton 1983). A growth history inferred from Scrutton's work on *Phillipsastrea nevadensis* suggests that its growth pattern is largely indeterminate, like that of *Heritschioides* sp. and possibly of living *Favia* in the examples already mentioned. Computers might be used for reconstruction from serial sections, but the problem of chronology will remain except where there is additional evidence for it.

Such evidence has been well established for over a decade, but is best seen in sections parallel to the general growth trend, and is therefore less useful in serial transverse sectioning methods. This is density banding (figure 3 b), detected by radiography (Knutson *et al.* 1972; see also Buddemeier & Kinzie 1976; Buddemeier 1978 for reviews). These bands represent isochronous surfaces within a colony and reveal very successfully the broad patterns within and between higher level modules. Although the method has been valuable in several respects, its relevance to modular growth has yet to be fully explored. Buddemeier & Kinzie point to this potential in their discussion of Wood-Jones' (1907, 1910) ideas about coral growth. They confirmed that Wood-Jones' three methods of colonial growth were borne out by radiographic work: (i) those in which each polyp is equipotent (for example, *Porites*: figure 3 b); (ii) those in which the active site of growth is associated with the youngest polyps (for example, corals like figure 3 e); and (iii) those in which it is associated with the oldest [apical] polyp in the colony or branch (for example, *Acropora*: figure 3 a). Buddemeier & Kinzie's discussion (pp. 206–207) of this is relevant and stimulating.

Isochronous surfaces within colonies can also be introduced artificially by use of radioisotopes or dyes, and, given enough intervening time between marker bands, can be used to test growth theories (Buddemeier & Kinzie 1976).

A completely different but complementary approach with important potential is computer simulation of growth (Graus 1977). Graus & Macintyre (1976, 1982) showed how colony form of *Montastrea annularis* is related to different patterns of zooidal growth in response to factors of depth and illumination, comparable with their own direct observations of form on reefs, and with Dustan's (1975) experimental results with dye markers. The value of computer simulation in the study of plant growth is well established (Harper & Bell 1979; Bell 1984). There has also been increasing interest in the biomechanical constraints on coral growth with respect to environmental hydrodynamic factors (Graus *et al.* 1977; Schuhmacher & Plewka 1981; Vosburgh 1982; Schuhmacher 1984; and references cited by these authors). Graus *et al.* showed how organization within colonies changes according to hydrodynamic régime. Biomechanical hypotheses, like the illumination hypothesis, above, can also be used in computer simulation.

7. MODULES: MEANS OR MEANING?

The idea of modules has been used in two ways: (i) as a means of understanding growth and form; and (ii) as a concept with postulated biological significance for organisms in general. Evolutionary implications can be derived from each, in the first case for relationships between different taxa in a given monophyletic group, and in the second case for evolutionary processes in general. Many of the other papers in this volume have concentrated on this second theme, that of Jackson & Coates in particular being most relevant to corals. Here, I draw on my previous sections to summarize the prospect for continuing with a modular approach to corals, thereby emphasizing the first theme of morphological methodology. The themes are not of course independent and feedback between them will also be mentioned.

(a) *Taxonomy, morphogenesis of colonies and phylogenetics*

It is essential that modules be not necessarily convenient, but should also have meaning in terms of homology. To relate one coral to another, through modularity, we must use the same *kind* of unit. The branch of a fasciculate coral (figure 2a) is homologous with a zooid in a non-branching coral like *Montastrea* (figure 2e); the branches of a fasciculate coral are not homologous with ramose branches (figure 3a, e). The concept of a single universal coral zooid modified in various ways in different corals and based on homology of mouth structures, gives a unity to colony analysis and morphogenesis. It will, however, be important to establish a proper basis for this suggested homology, or otherwise refute it. In the meantime, it also allows a second suggestion that the developmental basis of much colony form is paedomorphic arrest of budding.

There follow two implications. First, colony form, hitherto very difficult to characterize either verbally or biometrically, should now be specifiable more precisely and on a proper comparative basis. The modular approach draws attention to colonial organization as a source of new taxonomic characters, and promises to fulfil the belief expressed in the convening of an earlier symposium (Larwood & Rosen 1979) that a way forward through some of the taxonomic difficulties that arise from coral coloniality would be generated by a more broadly based exchange among specialists of different groups of organisms (Rosen 1979). The most useful techniques will probably be radiographic study of marker bands, experimental dye marking and computer modelling.

Second, there are possible patterns of colony evolution alternative to those depicted by Wells (1956) or by Coates & Oliver (1973) but still consistent with Beklemishev's (1969) idea that colony evolution shows a tendency towards increasing integration (that is, mainly loss of discreteness of zooids). Progressively earlier paedomorphic arrest of budding is consistent with Beklemishev's view, but there is also a second trend, that of increasing complexity of modular organization (see below). An important incidental to this, however, will be the need to make further studies of wall structures.

(b) *Ecological influences on growth and form*

Improved colony specification should enable us to distinguish more exactly the influence of environmental factors, including hydrodynamic influences, predation, interactions with neighbours and response to damage. Variation might now be analysed not just at the level of zooids and general form, but for each modular level present in a coral, thus expanding on the study framework envisaged by Veron (1982). In this respect Stebbins' (1950) idea, cited by

White (1984), might be tested for corals: 'characters formed by long periods of meristematic activity, being more subject to environmental influences, are likely to be more plastic than those formed rapidly in ontogenesis'. (Concerning meristems, see below.) Foster (1983) has already found evidence that variation patterns at different colony levels are decoupled from each other. Somewhere, between our knowledge of budding modes and the great morphological plasticity of corals, lies the prospect of discovering the inherited architecture of coral colonies.

Conversely, better specification of the effects of environmental variation in corals offers an improved basis for using fossil corals to interpret ancient environments.

(c) Symbiosis with zooxanthellae, and its age and history

It is widely believed that the symbiosis of corals and zooxanthellae has influenced colony growth, form and evolution (Wells 1954; Coates & Oliver 1973; Rosen 1977, 1981). Actual specification of its morphological consequences has, however, proved elusive. There are both primary effects to consider, as well as those consequent upon the kinds of environment that the symbiosis imposes on corals. The kinds of ecological questions considered above can therefore also be formulated with the additional aim of finding differences between zooxanthellate and non-zooxanthellate corals. Two possibilities are higher levels of integration and complexity in zooxanthellates. Integration (in the morphological sense of loss of zooid discreteness) may have its origin in the faster growth rates shown by zooxanthellate corals as part of a broader tendency to have less dense skeletons (Coates & Oliver 1973; Schuhmacher & Plewka 1981; Schuhmacher 1984). Greater modular complexity may result from the greater number of environmental influences affecting zooxanthellate corals than non-zooxanthellate corals.

It is helpful in this respect to think of colony growth and form in vegetative organisms as the equivalent of behaviour in mobile organisms (Bell 1984). What I have previously referred to as spatial strategies (Rosen 1981) become spatial behaviours. Zooxanthellate corals should have a more complex range of behaviours than non-zooxanthellates on at least three counts: their response (i) to light; (ii) to shallow water hydrodynamic factors; and (iii) to a more crowded and heterogeneous habitat. Extensive fission and fusion of colonies is part of this behavioural response (Jackson & Coates, this symposium). Modular complexity may be another. It might be tested by assessing colonies in terms of the quantity of their hierarchical levels of modules, and of their polymorphic and polystatic forms at each modular level, together with the variety of components present in modules above the zooidal level. A theoretical framework for studying complexity is also provided by Lauder (1981).

Clearly, if correlations can be found between modular form and symbiosis, it might also be applied to the fossil record in order to infer the age and history of the symbiosis. Inference of symbiosis in particular fossil corals should help to provide depth, temperature and latitudinal constraints for the formations in which they occur.

(d) Modules, meristems and metamers

To broaden the modular approach to other organisms, we can either attempt to extend the homologous basis of module recognition from corals to other organisms, or concentrate on interpreting the significance of repetition on its own terms (that is, regardless of trying to homologize iterative units across phyletic boundaries). The first option is improbable above the level of cells as modules, except in so far as the coral zooid is presumably homologous with other coelenterate zooids. And yet, the alternative, though it attempts to circumvent the

homology problem, leads us back to it. This is because White (1984) has explained that Harper modules (of plants) are actually plant metamers, and used zoological criteria to argue this.

To many zoologists, however, metamers convey the serial segmentation typical of annelids and arthropods; and to call coral zooids 'metamers' seemingly implies a close phylogenetic connection between coelenterates and metameric organisms: currently, a very unconventional view. Can we call zooids 'meristems' instead? They cannot be in a botanical sense, but they are meristem-like in that zooids are growth points and developmental foci of reproductive tissue and clonogeny. Occasionally, they are even organized apically: non-reiteratively in circumoral corals like *Echinophyllia* (figure 2*h*), and reiteratively in the case of *Acropora* branches (figure 3*a*). *Acropora*, then, has the equivalent of Prévost modules. The other kinds of zooid are not Prévost modules, but as modules they are rather more tightly envisaged (here) than Harper modules.

Fortunately for this dilemma, the problem of homology of metamers is an old one. Clark (1980) has pointed out that there are several different types of metamerism in the Metazoa, notably annelid and chordate, and that they must have evolved independently. He warns that we should not fall into the trap of supposing that because different groups of animals (to which we might also add plants) are metameric, they are phylogenetically related to each other.

If Clark's argument overcomes the phylogenetic objections, it still leaves some purely descriptive difficulties. Coral zooids do not conform to the general notion of metamers because they are only rarely linear (for example, *Teleiophyllia*, *Thysanus*). Colony and genet growth moreover is largely indeterminate, and zooids are clonogenic. Linear arrangement, however, is related to locomotion (Clark 1964, 1980), and would be less likely in vegetative organisms, whose meres are obviously free to grow in sheet-like, multiple runner or three-dimensional systems. When elongation and determinate growth do occur in colonial corals, however (for example, *Herpolitha*, *Manicina*), it is associated with an unattached, sometimes mobile habit. More significantly, the mobile, pelagic relatives of attached colonial organisms are, in fact, linear and determinate (for example, compare graptoloid with dendroid graptolites, and siphonophores with hydroids, respectively).

Coral modules, as meant here, are therefore meristematic and clonogenic metamers. This is acknowledged by Riedl's solution (1978; especially his figures 10 and 14) in which he regards these colony-meres as features at a higher organizational level than annelid-type segmentation. He refers to them as polymers but 'hypermers' might have avoided the coincidence with chemistry while acknowledging Riedl's point. In the end, the appeal of Harper modules (which would include all the features regarded here as modules of corals), is that they transcend the nuances and constraints of meristems and metamers.

References

Babcock, R. C. 1984 Reproduction and distribution of two species of *Goniastrea* (Scleractina) from the Great Barrier Reef province. *Coral Reefs* **2**, 187–195.

Beecher, C. E. 1893*a* The development of a Paleozoic poriferous coral. *Trans. Conn. Acad. Arts Sci.* **8**, 207–214.

Beecher, C. E. 1893*b* Symmetrical cell development in the Favositidae. *Trans. Conn. Acad. Arts Sci.* **8**, 215–219.

Beklemishev, W. N. 1969 *Principles of comparative anatomy of invertebrates*, 2 vols, translated by J. M. MacLennan. Edinburgh: Oliver & Boyd. (Translation of 3rd Russian edition, 1964. Moscow: Nauka.)

Bell, A. D. 1984 Dynamic morphology: a contribution to plant population ecology. In *Perspectives on plant population ecology* (ed. R. Dirzo & J. Sarukhán), pp. 48–65. Sunderland, Massachusetts: Sinauer Associates Inc.

Best, M. B., Boekschoten, G. J. & Oosterbaan, A. 1984 Species concept and ecomorph variation in living and fossil Scleractinia. In *Recent advances in the paleobiology and geology of the Cnidaria* (ed. W. A. Oliver, Jr, *et al.*) *Palaeontogr. am.* **54**, 70–79.

Boschma, H. 1923 Über die Bildung der jungen Kolonien von *Goniopora stokesi* durch ungeschlechtliche Fortpflanzung. *Zool. Anz.* **57**, 284–286.

Boschma, H. 1929 On the postlarval development of the coral *Maeandra areolata* (L.). *Pap. Tortugas Lab. Carnegie Instn* **26**, 129–147.

Buddemeier, R. W. 1978 Coral growth: retrospective analysis. In *Coral reefs: research methods* (ed. D. R. Stoddart & R. E. Johannes), pp. 551–571. Paris: UNESCO.

Buddemeier, R. W. & Kinzie, R., III 1976 Coral growth. *Oceanogr. mar. Biol.* **14**, 183–225.

Buddemeier, R. W., Maragos, J. E. & Knutson, D. W. 1974 Radiographic studies of reef coral exoskeletons: rates and patterns of coral growth. *J. exp. mar. Biol. Ecol.* **14**, 179–200.

Chapman, G. 1981 Individuality and modular animals. *Biol. J. Linn. Soc.* **15**, 177–183.

Chapman, G. & Stebbing, A. R. D. 1980 The modular habit – a recurring strategy. In *Developmental and cellular biology of coelenterates* (ed. P. Tardent & R. Tardent), pp. 157–162. Amsterdam: Elsevier/North Holland Biomedical Press.

Clark, R. B. 1964 *Dynamics in metazoan evolution; the evolution of the coelom and segments.* Oxford: Clarendon Press.

Clark, R. B. 1980 Natur und Entstehungen der metameren Segmentierung. *Zool. Jb. Abt. Zool.* **103**, 169–195

Coates, A. G. & Oliver, W. A. 1973 Coloniality in zoantharian corals. In *Animal colonies: development and function through time* (ed. R. S. Boardman, A. H. Cheetham & W. A. Oliver, Jr), pp. 3–27. Stroudsburg: Dowden, Hutchinson & Ross, Inc.

Connell, J. H. 1978 Diversity in tropical forests and coral reefs. *Science, Wash.* **199**, 1302–1310.

Crossland, C. 1913 *Desert and water gardens of the Red Sea: being an account of the natives and the shore formations of the coast.* Cambridge: University Press.

Dauget, J.-M. 1985 La réaction aux traumatismes: comparaison entre les arbres et les coraux. *Terre Vie* **40**, 113–118.

Duerden, J. E. 1902 West Indian madreporarian polyps. *Mem. natn. Acad. Sci.* **7**, 399–599.

Dustan, P. 1975 Growth and form in the reef-building coral *Montastrea annularis*. *Mar. Biol. Berlin* **33**, 101–107.

Fadlallah, Y. H. 1983 Sexual reproduction, development and larval biology in scleractinian corals. A review. *Coral Reefs* **2**, 129–150.

Fedorowski, J. 1978 Some aspects of coloniality in rugose corals. *Palaeontology* **21**, 177–224.

Fedorowski, J. & Jull, R. K. 1976 Review of blastogeny in Palaeozoic corals and description of lateral increase in some Upper Ordovician rugose corals. *Acta Palaeont. pol.* **21**, 37–78.

Finks, R. M. 1971 Modular structure and organic integration in Sphinctozoa. *Abstr. Progm geol. Soc. Am.* **3**, 764–765. [Abstract.] (Reprinted in *Animal colonies: development and function through time* (ed. R. S. Boardman, A. H. Cheetham & W. A. Oliver, Jr), pp. 585–586. Stroudsburg: Dowden, Hutchinson & Ross. 1973.

Foster, A. B. 1979 Phenotypic plasticity in the reef corals *Montastrea annularis* (Ellis & Solander) and *Siderastrea siderea* (Ellis & Solander). *J. exp. mar. Biol. Ecol.* **39**, 25–54.

Foster, A. B. 1983 The relationship between corallite morphology and colony shape in some massive reef-corals. *Coral Reefs* **2**, 19–25.

Foster, A. B. 1984 The species concept in fossil hermatypic corals: a statistical approach. In *Recent advances in the paleobiology and geology of the Cnidaria* (ed. W. A. Oliver, Jr, *et al.*), *Palaeontogr. am.* **54**, 58–69.

Graus, R. R. 1977 Investigation of coral growth adaptations using computer modelling. In *Proc. 3rd int. Coral Reef Symp.* (ed. D. L. Taylor), vol. 2, pp. 463–469. Miami: Rosenstiel School of Marine and Atmospheric Science, University of Miami.

Graus, R. R., Chamberlain, J. A. & Boker, A. M. 1977 Structural modification of corals in relation to waves and currents. In *Reefs and related carbonates: ecology and geology* (ed. S. H. Frost, M. P. Weiss & J. B. Saunders), *Stud. Geol. am. Ass. Petrol. Geologists* **4**, 135–153. Tulsa: American Association of Petroleum Geologists.

Graus, R. R. & Macintyre, I. G. 1976 Light control of growth form in colonial reef corals: computer simulation. *Science, Wash.* **193**, 895–897.

Graus, R. R. & Macintyre, I. G. 1982 Variation in growth forms of the reef coral *Montastrea annularis* (Ellis & Solander): a quantitative evaluation of growth response to light distribution using computer simulation. *Smithson. Contr. mar. Sci.* **12**, 441–464.

Grigg, R. W. 1977 Population dynamics of two gorgonian corals. *Ecology* **58**, 278–290.

Haldane, J. B. S. 1927 On being the right size. In *Possible worlds*, pp. 18–26. London: Chatto & Windus.

Hallé, F., Oldeman, R. A. A. & Tomlinson, P. B. 1978 *Tropical trees and forests: an architectural analysis*. Berlin: Springer-Verlag.

Hamada, T. 1959 Corallum growth of the Halysitidae. *J. Fac. Sci. Univ. Tokyo Section 2 Geol.* **11**, 273–289.

Hamada, T. 1973 Caliceal increase in massive corals – a geometrical implication. *Scient. Pap. Coll. gen. Educ. Tokyo* **23**, 53–71.

Hamada, T. 1973 '*Cladochonus*' (tabulate coral from the Red Bed of Malaya). *Geol. Paleont. SE Asia* **13**, 23–37.

Harper, J. L. 1977 *Population biology of plants*. London: Academic Press.

Harper, J. L. & Bell, A. D. 1979 Population dynamics of growth form in organisms with modular construction. In *Population dynamics. 20th Symp. Br. ecol. Soc.* (ed. R. M. Anderson, B. D. Turner & L. R. Taylor), pp. 29–52. Oxford: Blackwell.

Harriott, V. J. 1983 Reproductive ecology of four scleractinian species at Lizard Island, Great Barrier Reef. *Coral Reefs* **2**, 9–18.

Harrison, P. L. 1985 Sexual characteristics of scleractinian corals: systematic and evolutionary implications. In *Proc. 5th int. Coral Reef Congr., Tahiti*, vol. 2, pp. 165–170.

Heyward, A. J. & Collins, J. D. 1985 Fragmentation in *Montipora ramosa*: the genet and ramet concept applied to a reef coral. *Coral Reefs* **4**, 35–40.

Hidaka, M., Uechi, A. & Yamazato, K. 1982 Effects of certain factors on budding of isolated polyps of a scleractinian coral, *Galaxea fascicularis*. In *Reef and man. Proc. 4th int. Coral Reef Symp.* (ed. E. D. Gomez *et al.*), vol. 2, pp. 229–231. Quezon City: Marine Sciences Center, University of the Philippines.

Highsmith, R. C. 1982 Reproduction by fragmentation in corals. *Mar. Ecol. Prog. Ser.* **7**, 207–226.

Hill, D. 1981 *Treatise on invertebrate paleontology. Part F. Coelenterata. Supplement 1. Rugosa and Tabulata* (ed. C. Teichert), 2 vols. Kansas: The Geological Society of America and the University of Kansas.

Hughes, R. N. 1983 Evolutionary ecology of colonial reef-organisms, with particular reference to corals. *Biol. J. Linn. Soc.* **20**, 39–58.

Hughes, T. P. & Jackson, J. B. C. 1980 Do corals lie about their age? Some demographic consequences of partial mortality, fission and fusion. *Science, Wash.* **209**, 713–715.

Hughes, T. P. & Jackson, J. B. C. 1985 Population dynamics and life histories of foliaceous corals. *Ecol. Monogr.* **55**, 141–166.

Knutson, D. W., Buddemeier, R. W. & Smith, S. V. 1972 Coral chronometers: seasonal growth bands in reef corals. *Science, Wash.* **177**, 270–272.

Kobayashi, A. 1984 Regeneration and regrowth of fragmented colonies of the hermatypic corals *Acropora formosa* and *Acropora nasuta*. *Galaxea* **3**, 13–23.

Krasnov, Ye. V. & Preobrazhenskiy, B. V. 1972 The nature and significance of life forms in tabulates and colonial scleractinians. *Paleont. J.* **6**, 264–268.

Lang, J. 1971 Interspecific aggression by scleractinian corals. 1. The rediscovery of *Scolymia cubensis* (Milne Edwards & Haime). *Bull. mar. Sci.* **21**, 952–959.

Lang, J. 1984 Whatever works: The variable importance of skeletal and of non-skeletal characters in scleractinian taxonomy. In *Recent advances in the paleobiology and geology of the Cnidaria* (ed. W. A. Oliver, Jr, *et al.*), *Paleontogr. am.* **54**, 18–44.

Larwood, G. P. & Rosen, B. R. (ed.) 1979 *Biology and systematics of colonial organisms. Spec. Vol. Syst. Ass.* **11**. London: Academic Press.

Lauder, G. V. 1981 Form and function: structural complexity in evolutionary morphology. *Paleobiology* **7**, 430–442.

Loya, Y. 1976 Skeletal regeneration in a Red sea scleractinian population. *Nature, Lond.* **261**, 490–491.

Manton, S. M. 1932 On the growth of the adult colony of *Pocillopora bulbosa*. *Sci. Rept. Gt Barrier Reef Exped.* **3**, 157–166.

Matthai, G. 1914 A revision of the Recent colonial Astraeidae possessing distinct corallites. *Trans. Linn. Soc. Lond.* (ser 2) **17**, 1–140.

Matthai, G. 1926 Colony-formation in astraeid corals. *Phil. Trans. R. Soc. Lond.* B **214**, 313–367.

Matthai, G. 1927 *Catalogue of the madreporarian corals in the British Museum (Natural History). Vol. VII. A monograph of the Recent meandroid Astraeidae*. London: Trustees of the British Museum.

Matthai, G. 1948 *a* On the mode of growth of the skeleton in fungid corals and skeletal variation in two large coralla from Tahiti, one of *Pavona varians* (Verrill) and another of *Psammocora haimiana* Milne Edwards and Haime. *Phil. Trans. R. Soc. Lond.* B **233**, 177–199.

Matthai, G. 1948 *b* Colony formation in fungid corals. I. *Pavona, Echinophyllia, Leptoseris* and *Psammocora. Phil. Trans. R. Soc. Lond.* B **233**, 201–231.

Mori, K. & Minoura, K. 1980 Ontogeny of 'epithecal' and septal structures in scleractinian corals. *Lethaia* **13**, 321–326.

Mori, K., Omura, A. & Minoura, K. 1977 Ontogeny of euthecal and metaseptal structures in colonial scleractinian corals. *Lethaia* **10**, 327–336.

Oliver, W. A., Jr 1968 Some aspects of colony development in corals. *J. Paleont.* (*Mem. paleont. Soc.* **2**) **42**, (5 (part II)) 16–34.

Potts, D. C., Done, T. J., Isdale, P. J. & Fisk, D. A. 1985 Dominance of a coral community by the genus *Porites* (Scleractinia). *Mar. Ecol. Progr. Ser.* **23**, 79–84.

Prévost, M. F. 1967 Architecture de quelques Apocynacées ligneuses. *Mém. Soc. bot. Fr.* **114**, 24–36.

Randall, R. H. 1982 Morphologic diversity in the scleractinian genus *Acropora*. In *Reef and man. Proc 4th int. Coral Reef Symp.* (ed. E. D. Gomez *et al.*) vol. 2, pp. 157–164. Quezon City: Marine Sciences Center, University of the Philippines.

Randall, R. H. & Myers, R. F. 1983 *Guide to the coastal resources of Guam. Volume III. The corals.* Guam: University Press.

Riedl, R. 1978 *Order in living organisms*, translated by R. P. S. Jefferies. Chichester: John Wiley & Sons. (German edition: *Die Ordnung des Lebendigen*. Hamburg: Verlag Paul Parey. 1975.)

Rosen, B. R. 1971 Principal features of reef coral ecology in shallow water environments of Mahé, Seychelles. In *Regional variation in Indian Ocean coral reefs* (ed. C. M. Yonge & D. R. Stoddart), *Symp. zool. Soc. Lond.* **28**, 163–183. London: Academic Press.

Rosen, B. R. 1977 The depth distribution of Recent hermatypic corals and its palaeontological significance. *Mém. Bur. Rech. géol. miniér.* **89**, 507–517.

Rosen, B. R. 1979 Modules members and communes: a postscript introduction to social organisms. In *Biology and systematics of colonial organisms* (ed. G. P. Larwood & B. R. Rosen), *Spec. Vol. Syst. Ass.* **11**, xiii–xxxv. London: Academic Press.

Rosen, B. R. 1981 The tropical high diversity enigma – the corals'-eye view. In *Chance, change and challenge; the evolving biosphere* (ed. P. H. Greenwood & P. L. Forey), pp. 103–129. Cambridge University Press and London: British Museum (Natural History).

Rosen, B. R. & Taylor, J. D. 1969 Reef coral from Aldabra: new mode of reproduction. *Science, Wash.* **166**, 119–121.

Ryland, J. S. 1981 Colonies, growth and reproduction. In *Recent and fossil Bryozoa* (ed. G. P. Larwood & C. Nielsen), pp. 221–226. Fredensborg: Olsen & Olsen.

Sammarco, P. W. 1982 Escape response and dispersal in an Indo-Pacific coral under stress: 'polyp bail-out'. [Abstract.] In *The reef and man. Proc. 4th int. Coral Reef Symp.* (ed. E. D. Gomez *et al.*), vol. 2, p. 194. Quezon City: Marine Sciences Center, University of the Philippines.

Scheer, G. 1959 Die Formenvielfalt der Riffkorallen. *Ber. naturw. Ver. Darmstadt* (1959), 50–67.

Scheer, G. 1960 Viviparie bei Steinkorallen. *Naturwissenschaften* **10**, 238–239.

Scheer, G. 1974 Investigation of coral reefs as Rasdu Atoll in the Maldives with the quadrat method according to phytosociology. In *Proc. 2nd int. Coral Reef Symp.* (ed. A. Cameron *et al.*), vol. 2, pp. 655–670. Brisbane: Great Barrier Reef Committee.

Scheer, G. 1978 Application of phytosociologic methods. In *Coral reefs: research methods* (ed. D. R. Stoddart & R. E. Johannes), pp. 175–196. Paris: UNESCO.

Schuhmacher, H. 1984 Reef-building properties of *Tubastraea micranthus* (Scleractinia, Dendrophylliidae), a coral without zooxanthellae. *Mar. Ecol. Prog. Ser.* **20**, 93–99.

Schuhmacher, H. & Plewka, M. 1981 Mechanical resistance of reefbuilders through time. *Oecologia* **49**, 279–282.

Scrutton, C. T. 1983 Astogeny in the Devonian rugose coral *Phillipsastrea nevadensis* from Northern Canada. *Mem. australas. Palaeont.* **1**, 237–259.

Squires, D. F. 1964 Fossil coral thickets in Wairarapa, New Zealand. *J. Paleont.* **38**, 904–915.

Stearn, C. W. 1982 The shapes of Paleozoic and modern reef-builders: a critical review. *Paleobiology* **8**, 228–241.

Stebbins, G. L. 1950 *Variation and evolution in plants*. New York: Columbia University Press.

Stephenson, T. A. 1931 Development and the formation of colonies in *Pocillopora* and *Porites* – Part I. *Sci. Rep. Gt Barrier Reef Exped.* **3**, 113–134.

Stephenson, T. A. & Stephenson, A. 1933 Growth and asexual reproduction in corals. *Sci. Rept Gt Barrier Reef Exped.* **3**, 167–217.

Stoddart, J. A. 1983 Asexual production of planulae in the coral *Pocillopora damicornis*. *Mar. Biol. Berlin* **76**, 279–284.

Talbot, F. H. (ed.) 1984 *Reader's Digest book of the Great Barrier Reef.* Sydney: Reader's Digest.

van Valen, L. 1978 Arborescent animals and other colonoids. *Nature, Lond.* **276**, 318.

Veron, J. E. N. & Pichon, M. 1976 Scleractinia of eastern Australia. Part I. Families Thamnasteriidae, Astrocoeniidae, Pocilloporidae. *Monogr. Ser. Aust. Inst. mar. Sci.* **1**, 1–86.

Veron, J. E. N. & Pichon, M. 1980 Scleractinia of eastern Australia. Part III. Families Agariciidae, Siderastreidae, Fungiidae, Oculinidae, Merulinidae, Mussidae, Pectiniidae, Caryophylliidae, Dendrophylliidae. *Monogr. Ser. Aust. Inst. mar. Sci.* **4**, 1–422.

Veron, J. E. N. & Pichon, M. 1982 Scleractinia of eastern Australia. Part IV. Family Poritidae. *Monogr. Ser. Aust. Inst. mar. Sci.* **5**, 1–159.

Veron, J. E. N., Pichon, M. & Wijsman-Best, M. 1977 Scleractinia of eastern Australia. Part II. Families Faviidae, Trachyphylliidae. *Monogr. Ser. Aust. Inst. Mar. Sci.* **3**, 1–233.

Veron, J. E. N. & Wallace, C. C. 1984 Scleractinia of eastern Australia. Part V. Family Acroporidae. *Monogr. Ser. Aust. Inst. mar. Sci.* **6**, 1–485.

Vosburgh, F. 1982 *Acropora reticulata*: structure, mechanics and ecology of a reef coral. *Proc. R. Soc. Lond.* B **214**, 481–499.

Wells, J. W. 1954 Status of invertebrate paleontology, 1953. III. Coelenterata. *Bull. Mus. comp. Zool. Harv.* **112**, 109–123.

142   B. R. ROSEN

Wells, J. W. 1956 Scleractinia. In *Treatise on invertebrate paleontology. Part F. Coelenterata* (ed. R. C. Moore), pp. F328–F444. Kansas: Geological Society of America, and University of Kansas Press.

Wells, J. W. 1966 Evolutionary development in the scleractinian family Fungiidae. In *The Cnidaria and their evolution* (ed. W. J. Rees), *Symp. zool. Soc. Lond.* **16**, 223–246. London: Academic Press.

Wells, J. W. 1971 What is a colony in anthozoan corals? *Abstr. Progm geol. Soc. Am.* **3** (7), 748. [Abstract.] (Reprinted in *Animal colonies; development through time* (ed. R. S. Boardman, A. H. Cheetham & W. A. Oliver, Jr), 1973, p. 29. Stroudsburg: Dowden, Hutchinson & Ross, Inc.)

White, J. 1979 The plant as a metapopulation. *Ann. Rev. Ecol. Syst.* **10**, 109–145.

White, J. 1984 Plant metamerism. In *Perspectives on plant population ecology* (ed. R. Dirzo & J. Sarukhán), pp. 15–47. Sunderland, Massachusetts: Sinauer Associates Inc.

Wijsman-Best, M. 1974 Habitat-induced modification of reef corals (Faviidae) and its consequences for taxonomy. In *Proc. 2nd int. Symp. Coral Reefs* (ed. A. M. Cameron *et al.*), vol. 2, pp. 217–228. Brisbane: The Great Barrier Reef Committee.

Wood, E. M. 1983 *Reef corals of the world: biology and field guide.* Neptune City: T.F.H. Publications, Inc. Ltd.

Wood Jones, [*sic*], F. 1907 On the growth-forms and supposed species in corals. *Proc. zool. Soc. Lond.* **2**, 518–556.

Wood-Jones, F. 1910 *Coral and atolls; their history, descriptions, theories of their origin both before and since that of Darwin, the influence of winds, tides and ocean currents on their formation and transformation, their present condition, products, fauna and flora.* London: Lovell Reeve & Co. Ltd. (The text of Part II largely corresponds to that of Wood Jones 1907).

Yonge, C. M. 1930 Studies on the physiology of corals. I. Feeding mechanisms and food. *Sci. Rep. Gt Barrier Reef Exped.* **1**, 13–57.

Yonge, C. M. 1936 Studies on the biology of Tortugas corals. I. Observations on *Maeandra areolata. Pap. Tortugas Lab. Carnegie Instn* **29**, 185–198.