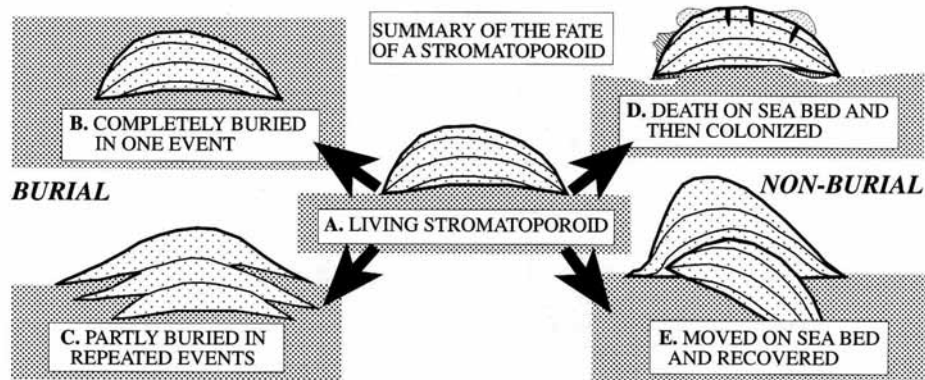


# THE APPLICATIONS OF STROMATOPOROID PALAEOBIOLOGY IN PALAEOENVIRONMENTAL ANALYSIS

by STEPHEN KERSHAW

**ABSTRACT.** Stromatoporoids are epibenthic calcified sponges in many Phanerozoic (especially Palaeozoic) reef, and reef-related environments, and may be used as tools for all scales of palaeoenvironmental analysis. Palaeozoic stromatoporoid classification uses the calcified skeleton, and although higher level taxa may be convergent, genera and species are normally readily identifiable and have palaeobiological utility. A hierarchical growth-form classification of stromatoporoids comprises: Level 1 (outline forms: laminar, tabular, domical, columnar, bulbous, defined with ratio limits; and dendroid, expanding conical, digitate and irregular); Level 2 (ornament, as papillae, mamelons and protuberants, give an increasing degree of disruption of the outline); and Level 3 (growth patterns of smooth and ragged margins, enveloping and non-enveloping laminations, coalescence and anastomosing). Inappropriate growth form terms in current use are rejected, especially *massive* and *encrusting*. Stromatoporoid palaeobiology applied at local scale aids determination of relative degree of contemporaneous turbulence and sedimentation; community scale study of stromatoporoids promotes comparisons between palaeoenvironments in reef and reef-related facies. Palaeozoic stromatoporoids may aid regional and even global event recognition, including changes in ocean states. Major gaps in knowledge are growth rates, and whether stromatoporoids were photosensitive and/or photosymbiotic.

**STROMATOPOROIDS** are benthic, marine macro-organisms composed of a calcium carbonate skeleton accreted in layers (laminae), with vertical elements (pillars) so that a vertical section displays a reticulate structure (Greek *stroma* = a bed/mattress; *poros* = a passage); either vertical or lateral elements of the skeleton may dominate or be equal. Organisms with this architecture were first described from Devonian rocks by Goldfuss (1826), but exist from the Cambrian to Recent; stromatoporoid-like archaeocyaths of Cambrian age (Webby 1979a, 1986, 1993; Debrenne and Zhuravlev 1994 and references therein; Riding and Zhuravlev 1995) precede the first major development of stromatoporoids in the (possibly lower to) middle Ordovician (Kapp and Stearn 1975; Webby 1979a, 1986, 1993; Keller and Flügel 1996) and dominated many Silurian and Devonian reef and reef-related environments. Mehl (1995, p. 49) recorded Late Proterozoic spicules demonstrating that sponges were among the earliest multicellular animals, presumably precursors of Palaeozoic calcified forms. Although stromatoporoids were badly affected by the Frasnian/Famennian extinction and occupied a lesser role in the Mesozoic, some living calcified sponge genera (e.g. *Astrosclera* and *Stromatospongia*) have stromatoporoid skeletons. Despite their abundance in Palaeozoic and Mesozoic rocks, understanding, and hence application of, stromatoporoid palaeobiology and palaeoecology is only partly developed. Widely attributed to the Porifera (e.g. Stearn 1975a), stromatoporoids have great value in palaeoenvironmental analysis (Text-fig. 1). Literature on their palaeobiology began with their use as broad palaeoenvironmental indicators in oil-related work on the Devonian (e.g. Andrichuk 1958; Klovan 1964; Murray 1966; Playford and Lowry 1966; Fischbuch 1968; Jamieson 1969; Noble 1970; Playford 1980). Stearn (1961) recorded variation in growth form within and between taxa, and 27 years have elapsed since the first comprehensive summary of stromatoporoid palaeobiology (St Jean 1971). There have been few attempts to classify and interpret stromatoporoid morphology in detail: studies are available for only a few geographical and stratigraphical settings. This paper reviews current knowledge of



TEXT-FIG. 1. Fossil stromatoporoid skeleton geometries demonstrate events affecting the sea bed during life and in early post-death prior to final burial. A living stromatoporoid (A) may have been completely (B) or partially buried, with flank recovery (C). Death without burial may be suspected for cases with epifauna (D), but may instead have been buried then exhumed. Dislocation during life is recorded in changes of growth attitude (E). For taphonomic aspects, see Text-figure 3.

stromatoporoid palaeobiology and palaeoecology problems, beginning with a discussion of the importance of stromatoporoid affinities in palaeoecology, followed by a revised growth-form classification, and an assessment of the value of stromatoporoids in facies analysis at all scales. The focus is on Palaeozoic stromatoporoids, which are the most abundant and diverse accumulations.

#### STROMATOPOROID AFFINITY

Because of their laminated accretionary growth style, stromatoporoids record environmental changes affecting the sea bed (e.g. Kershaw 1984), particularly in local sedimentation and turbulence. Because this is also true for other organisms with broadly similar lifestyles (e.g. tabulates, bryozoans, chaetetids), affinity is unimportant at this small scale. Affinity is important, however, at the ecosystem scale of interpretation, because of differences in the ecological position of diverse phyla. Hartman and Goreau (1970), Stearn (1972, 1975a) and Wood (1987) have claimed that stromatoporoids have affinities principally with sponges or hydrozoans. Descriptions of living stromatoporoid-like sponges (Hartman and Goreau 1970) led to a preference for poriferan affinities by most authorities. Kazmierczak (1976), Kazmierczak and Krumbein (1983) and Kazmierczak and Kempe (1990) interpreted a cyanophyte affinity for stromatoporoids, but most other workers disagree (e.g. Riding and Kershaw 1977).

Even if stromatoporoids are sponges, at least two further problems exist with their taxonomic status. First, stromatoporoid subgroups contain fossils which lack the typical laminae-and-pillar structure, such as the '*Labechia*'-type (thick pillars and cysts, despite the layered appearance of the entire skeleton), the '*Lophiostroma*'-type (solid laminations with a well-organized system of superimposed tight undulations which form pseudo-pillars, and no galleries; see Mori 1969, 1970), and the recently-erected early Ordovician genus *Zondarella* (Keller and Flügel 1996) has characters which make even stromatoporoid status uncertain. The relationship between these examples and typical stromatoporoids is open to question. Second, Palaeozoic stromatoporoid taxonomy relies on the calcareous skeleton; spicules used in later sponges occur in some Carboniferous stromatoporoids (Wood *et al.* 1989), but Ordovician to Devonian stromatoporoid fossils are aspiculate. A reappraisal of stromatoporoid taxonomy arose from recognition of similarities of

calcareous skeleton in different sponge orders classified by spicule form and composition (Vacelet 1985; Vacelet and Uriz 1991), leading to stromatoporoid structure being regarded as a grade of organization (Vacelet 1985; Wood and Reitner 1988; Wood 1990), and therefore convergent. However, lack of spicules does not empirically negate a classification based on the calcareous skeleton, if there are no other criteria to apply, and such a classification remains the most reasonable for Palaeozoic stromatoporoids.

Studies of stromatoporoid palaeobiology rely partly on the validity of morphospecies based on the calcareous skeleton, allowing comparison between growth forms of the same taxa within and between outcrops. Two features are important. First, there are consistent differences between the skeletons of nearly all calcareous-skeleton-morphospecies in stromatoporoids, at least at genera and species levels. For example, the Palaeozoic skeletal architecture called *Petridiostroma convictum* is distinctive and consistently different from that of *P. simplex*, and *Clathrodictyon mohicanum* is profoundly different from *Plectostroma scaniense* found in the same reef outcrops in late Silurian rocks (Mori 1970; Kershaw 1981; Kano 1989). Nevertheless, Stearn (1989) recognized intraskeletal variations, termed phases, and Prosh and Stearn (1996, p. 13) recommended that the species concept be applied broadly in stromatoporoids, to allow for skeletal variation within taxa, thus avoiding overlap between species. The fact that modern (e.g. *Vaceletia*) and Cambrian (archaeocyathids) aspiculate sponge genera are defined by the form of their calcareous skeletons strongly supports the taxonomic separation, at least at low levels, of stromatoporoids which have persistently different skeletal architecture. Second, because nearly all morphospecies in numerous well-studied outcrops (e.g. Kershaw 1990) generate consistent, distinctly different, growth forms, this provides an ecological reason for accepting their low-level taxonomic distinctness. In contrast, morphospecies of chaetid sponges greatly overlap (West 1994), and some modern corals exhibit intergradations of skeletal structure and careful measurement is required to distinguish species (e.g. Budd *et al.* 1994).

#### STROMATOPOROID RESPONSE AND GROWTH

Stromatoporoid response to sedimentation and turbulence is summarized in Text-figure 1; other responses are less discernible. This section discusses key elements in interpretations of form.

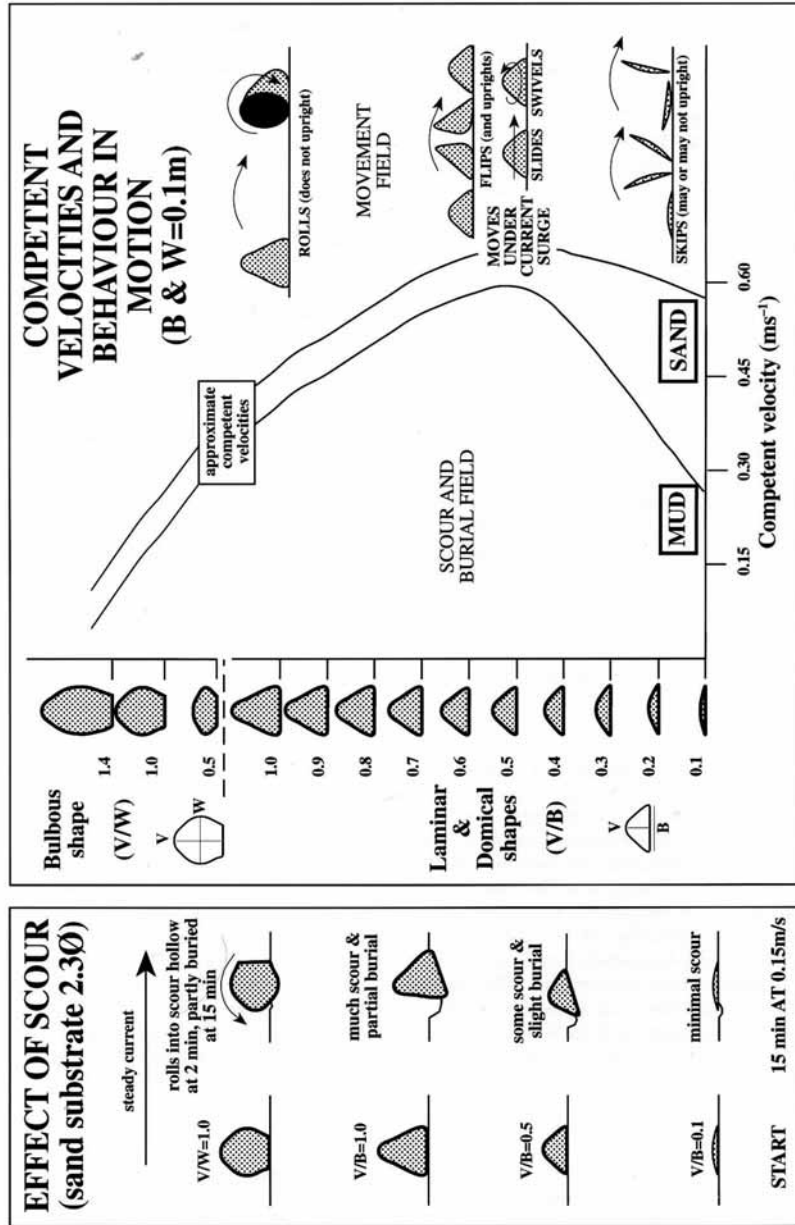
##### *Stromatoporoid taphonomy*

Experiments on model stromatoporoids in a flume (Kershaw 1979) interrelated form and substrate with stromatoporoid stability (Text-fig. 2), and demonstrated variation in stability. Impact damage to stromatoporoids (Text-fig. 3) can be observed both in Palaeozoic events, and in the presently occurring erosion of modern exposures; recently eroded stromatoporoid clasts found in quarries and cliffs on Gotland, for example, are similar in nature to their Silurian counterparts. Breakage is governed by form, degree of fixation to the Palaeozoic sea bed, the degree to which latilaminae are developed, and amount of diagenetic alteration of skeletons, especially along latilaminae. Clasts depicted schematically (Text-fig. 3) are modelled on real examples and occur commonly in stromatoporoid rud- and float-stones and reef debris; skeletal breakage, as well as attitude in exposure may influence form recognition (Text-fig. 4). Stromatoporoid taphonomy is crucial in palaeoenvironmental analyses, and underlies much of the analogy drawn between modern coral reefs and Devonian stromatoporoid reefs. Most studies have been qualitative, but quantitative work (e.g. Kershaw 1990; Kobluk 1974; Kobluk *et al.* 1977), especially where fragments are identified and size-classed, has much potential.

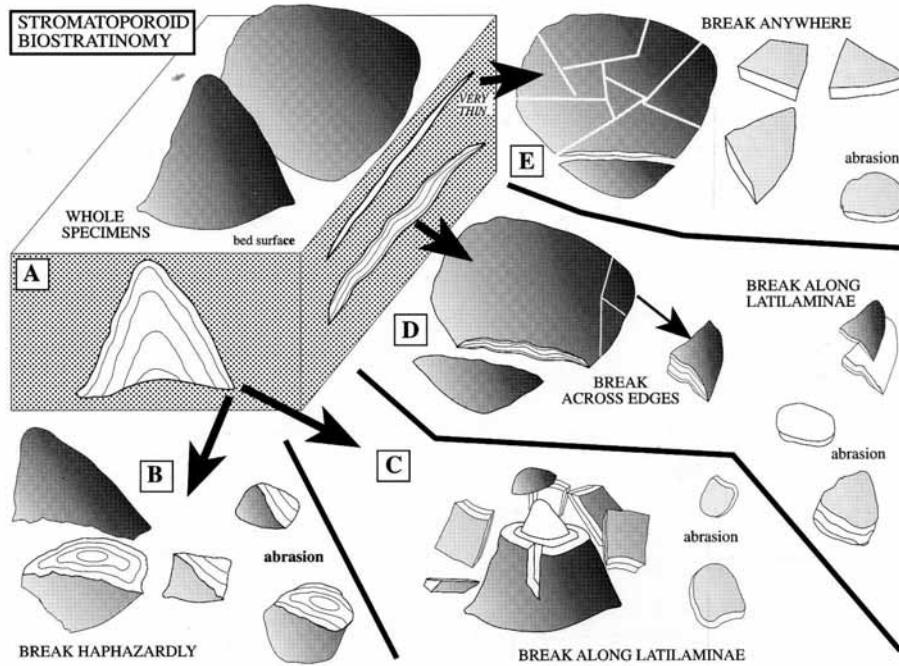
##### *Substrate preference*

Most stromatoporoids lie directly on sediment (clay-rich lime muds to skeletal grains, rarely sands and muds), but are widely assumed to have required a hard surface, such as a shell fragment, for initial settlement (e.g. Jamieson 1969, p. 1330), before spreading across neighbouring areas of soft

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TEXT-FIG. 2. Results of experimental work on model stromatoporoids (Kershaw 1979) illustrating the range of behaviour of simple-shaped forms under steady and surge current influence on sand and mud substrates. Models were not fixed to the substrate, emulating fossil stromatoporoids. The data show that stromatoporoids are more stable on muddy substrates; this is circumstantial evidence to account for their common occurrence on such substrates. Stability is inherent in the common low- to mid-domical shapes, and the slow currents used in these experiments serve to emphasize the important rôle of obstructions which prevented movement of fossil stromatoporoids in reefs in many cases. Responses of more complex forms were not tested, and divergence from this simple pattern is expected.

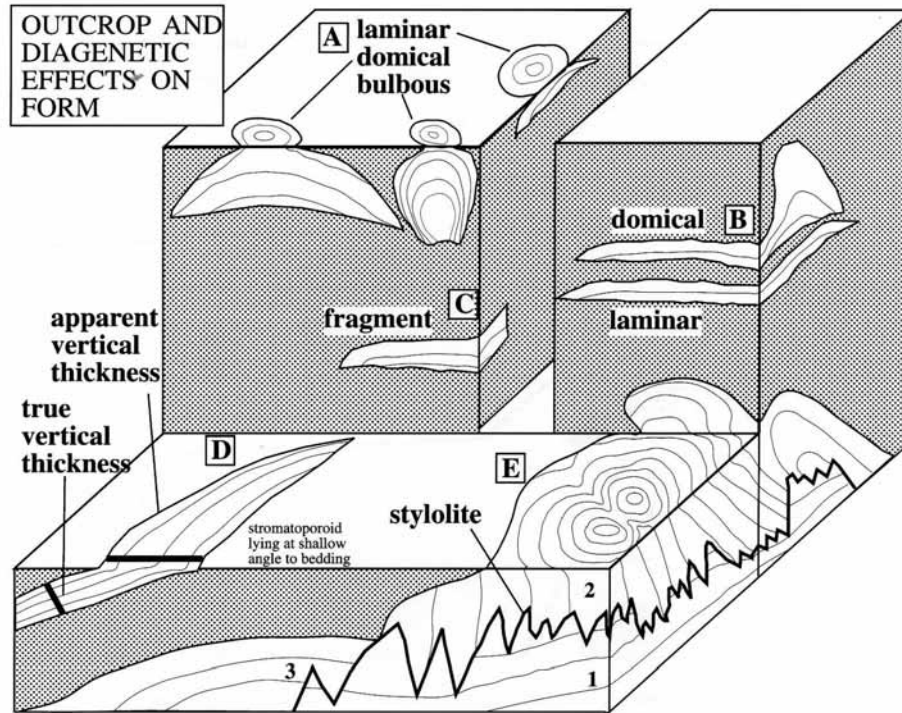


TEXT-FIG. 3. Variation in fracture of complete stromatoporoids (A) relates to morphology (compare B-E). Degree of development, and diagenesis, of latilaminae may affect splitting of stromatoporoids, reflected by differences between B and C.

substrate, a style of growth termed ambitopic by Jaanusson (1979, p. 269). However, many examples show that no hard object underlies initial growth (Text-fig. 5), and published cases from the Ordovician and Silurian suggest growth directly on soft substrates (e.g. Mori 1969, p. 34; Kapp 1974). Stromatoporoids with prominent laminae, and cases where laminae interfinger with sediment e.g. *Simplexodictyon* (formerly *Diplostroma*) *yavorskyi* (Powell 1991) show that laminae grew laterally across adjacent sediment.

Few data are available on detailed substrate selectivity, and its significance in controlling stromatoporoid distribution. Stromatoporoids apparently did not discriminate between specific substrates or substrate features. In the Wenlock of Gotland, Kershaw (1984) noted that one species occurred more commonly on skeletal debris, while others lie more commonly on the calcareous muddy sediment surface itself (Text-fig. 11, discussed below). Stromatoporoid success in reefs is presumed to be due partly to the presence of stable substrates of debris of previous reef builders, as well as the apparent wide tolerance of substrate composition.

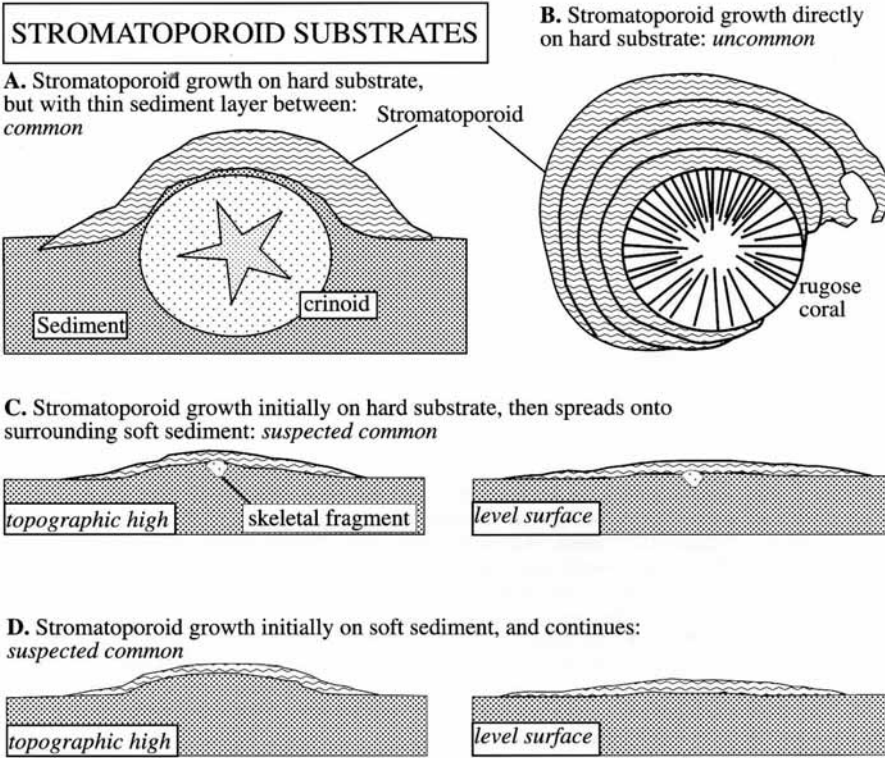
Most stromatoporoids are approximately circular in plan view, so grew unconstrained laterally; others are elongate due to growth on crinoid stems or solitary rugosans, apparently taking advantage of hard/raised settling points, although how much of this is substrate selection, and how much is haphazard settlement is undetermined. That initial growth was on topographic highs in almost all cases is revealed by basal concavities in vertically sectioned samples. Concavities vary in



TEXT-FIG. 4. Schematic illustration of growth form recognition problems in stromatoporoids. A, different forms may appear similar in plan cross section. B, the edge of a domical form may appear laminar. C, fragments may not be recognized in certain planes of section. D, non-perpendicular sections will exaggerate vertical thickness. E, margins may suffer pressure solution and affect form preservation, as in specimens labelled 1, 2 and 3.

depth depending on the height above substrate of the feature they grew on, and tend to be shallow for settlement directly on the sediment. For skeletal debris substrates, a layer of matrix may or may not coat the substrate prior to stromatoporoid settlement. Where stromatoporoids grew directly on hard substrate, they are presumed to have encrusted it, a feature common in Devonian forms (Noble 1970; Kobluk 1975); stromatoporoids could grow on horizontal and vertical surfaces (e.g. up the sides of upstanding solitary corals; Text-fig. 5). It is hard to prove that stromatoporoids grew across the living surfaces of other organisms, but unpublished observations show that they usually tended to avoid competitive interactions with neighbouring organisms, adopting a 'standoff' style of interaction instead (Al Fagerstrom, pers. comm.), and support the view that stromatoporoids normally grew across dead surfaces. Numerous encrusting and boring organisms used hard substrates provided by stromatoporoid upper and lower surfaces, with different distributions; *Trypanites* borings are almost always on upper surfaces, whilst strophomenid brachiopods, spirorbids and encrusting bryozoans occur more on the bases (Mori 1969, 1970; Kershaw 1980; Nield 1984; Pemberton *et al.* 1988). Kershaw (1980) suggested that cavities formed by scouring of sediment from beneath stromatoporoids and/or movement of skeletons on uneven substrates, were used by cryptic organisms. Chaetetids bear similar encrustations (Suchy and West 1988), as do





TEXT-FIG. 5. Stromatoporoids grew on skeletal debris, with or without a sediment interlayer (A-B), and on soft sediment, and may or may not have utilized hard objects such as skeletal particles (C-D). Note that crinoid in A and coral in B are shown in transverse section, overgrowing stromatoporoids are in vertical section.

tabulates found with stromatoporoids, although tabulates usually lack borings. Segars and Liddell (1988, fig. 4) suggested that stromatoporoids perched on topographic highs, forming much cavity space, although substrate consistency would be expected to constrain the amount of cavity space. Primary cavities were apparently rare and are documented in few papers (e.g. Noble 1989, p. 345).

#### *Stromatoporoid basal layers*

Basal surfaces of stromatoporoids which grew on sediment often preserve a wrinkled, thin, compact, layer of skeleton, called peritheca by Galloway (1957), following cnidarian terminology, but *basal layer* is a more neutral term. Galloway noted that basal layers are less than 1 mm thick and of denser skeleton than normal, occasionally showing cystose vesicles. Basal layers are rare in reef stromatoporoids; Parks (1936) noted basal layers at the base of each latilamina in some stromatoporoids, and they are common in stromatoporoids in limestones (Colin Stearn, pers. comm.). Stearn (1983) noted that basal layers may form by lateral growth over the substrate, and they may be irregular, and can be similar to those in tabulate corals, possibly secreted to stop boring organisms penetrating the lower, abandoned parts of the skeleton in contact with the substrate, at

least in argillaceous limestones and calcareous shales. Riding (1974) reinterpreted the algal genus *Keega* as the basal layer of a laminar form of *Stachyodes*, which was then considered by Mistiaen (1991) as representing poor calcification in stromatoporoid early ontogeny.

#### *Growth form development*

Stromatoporoid early growth often formed sheet-like skeletons across the substrate, and subsequent growth was concentrated in central areas, producing a smooth non-enveloping profile (Kershaw and Riding 1978); uncommonly, others are full enveloping (Text-fig. 7). The resulting basal surfaces of skeletons display concentric ridges where successive overlapping layers touch the substrate, enhanced into minor ragged edges if a little sediment collected on the edges as successive layers grew. Form usually changed as individuals grew; change from laminar through domical into bulbous is common, so that determination of growth form should take such changes into account, where they are visible in cross sections; individuals of the same species within an assemblage may display different growth forms if they died before the final form could develop, and low-level taxonomy is crucial in such investigations.

#### *Growth banding and growth rates*

Stromatoporoid growth banding varies from distinct latilaminae (periodic growth interruptions, which may or may not be sharply visible) to unbanded; most is poorly defined and defies objective measurement, so growth rates are poorly constrained. Modern calcified sponges grow 0.1–0.5 mm/yr (Dustan and Sacco 1982; Benavidas and Druffel 1986), but this seems too low for Palaeozoic stromatoporoids, which then would have taken thousands of years for even moderately large individuals. Meyer (1981) claimed that stromatoporoids, competitively intergrown with presumed annually banded favositids, had vertical and lateral rates of 1.3–3 mm/yr and 10–23 mm/yr respectively; Stearn (1989, p. 47) estimated 1–2 mm/yr vertical growth on the basis of minor cyclicity in some samples, these rates are reasonable for reef-builders. Wood *et al.* (1992) suggest that high-integration fossil organisms such as sponges, including stromatoporoids, appear capable of continuous fast growth to large size, while low-integration and aclonal organisms grew more slowly and were less capable of reef-building. Whether stromatoporoids were photosynthetic (Kazmierczak 1976; Kazmierczak and Krumbein 1983), or even bore symbionts (Wood *et al.* 1992) is undetermined, and there is no unequivocal reference point from which to infer that latilaminae are annual, although the growth rates quoted above strengthen the argument that they are. Meyer's (1981) evidence was based on assumed annual growth bands in corals, which may be incorrect; also Fagerstrom's (pers. comm.) extensive field and thin section observations of corals, chaetetids and stromatoporoids show that rarely can both participants in an intergrowth be proved to have been alive simultaneously. Growth rate estimates by Risk *et al.* (1987) depend on assumptions (which they admitted to have problems) of annual cyclicity in microborings interpreted to be algal. Kapp (1975) assumed that Chazy Group (Ordovician) stromatoporoids grew at constant rates, and sediment included resulted from varying sedimentation rate; but there is no current method of testing this.

Stromatoporoid growth rates were presumably a critical part of their palaeoecology. Copper (1988, p. 141, figs 2–3) noted that Holocene coral reef climax stages show characters of *K*-selection, usually being dominated by one taxon, succeeding in its specialization; similarly, most stromatoporoid-dominated assemblages have one species more common than the others, suggestive of *K*-selection. However, in *level-bottom* communities with diverse benthic faunas, one stromatoporoid species is also often more abundant than the others, suggesting that single-species abundance is not simply a feature of climax stage community development. In contrast with corals, neighbouring sponges of the same species will coalesce as they grow into mutual contact, rather than compete, and lead to huge individuals occupying much substrate area, a feature observed in Gotland reef and non-reef stromatoporoids. The frequency of coalescence is unknown because

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stromatoporoid cross sections are two dimensional, and early growth stages are not always in the plane of section. Therefore, application of *r-K* concepts in interpreting stromatoporoid controls is limited; size and growth rate are not necessarily simply linked in stromatoporoids.

#### *Phototropism and depth*

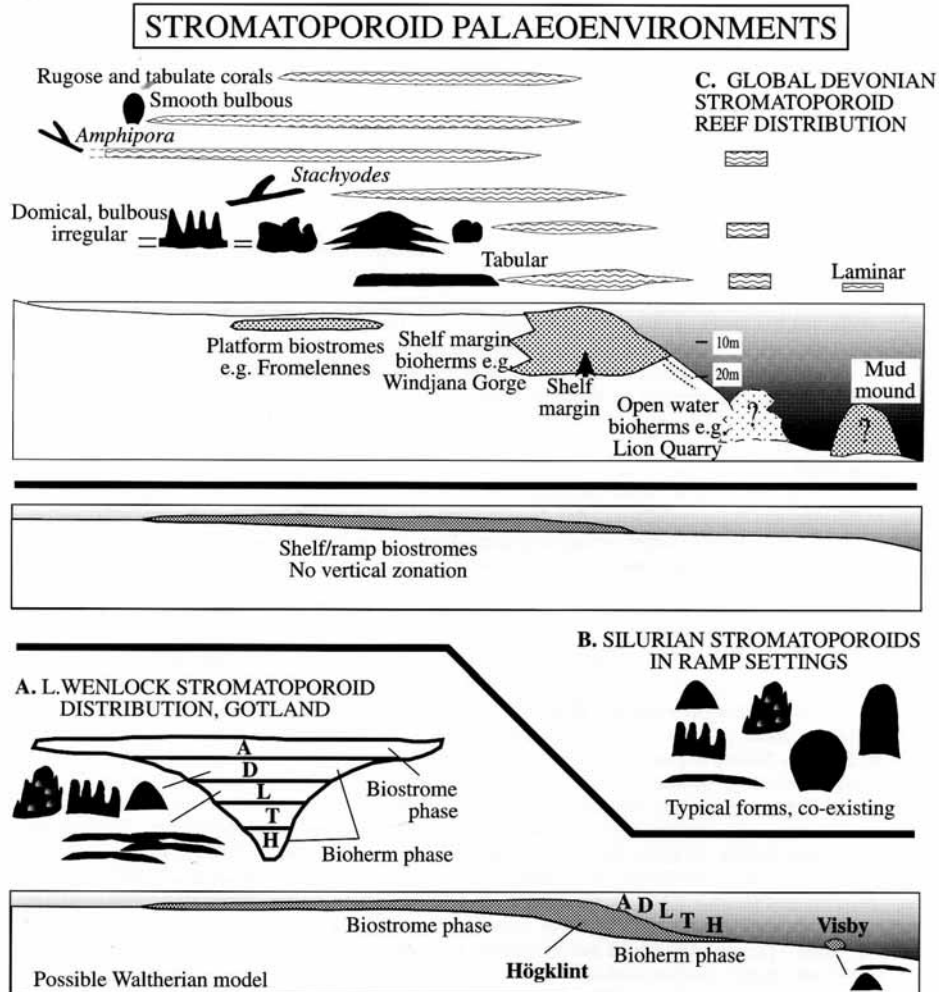
Circumstantial evidence that stromatoporoids were photoresponsive employs size and growth rates in relation to modern coral-dominated reef systems (Baarli *et al.* 1992; Wood *et al.* 1992), morphology (Klovan 1964) and association with algae (e.g. Baarli *et al.* 1992). In contrast, although modern sponge biomass (non-calcified types only) may be 50 per cent. bacteria (Willenz and Hartman 1989), these are not photosensitive. In Devonian stromatoporoid morphotype data, tabular forms are more common in fore-reefs than other large domical/bulbous/irregular forms (Text-fig. 6). Tabular forms grew better in finer sediment, deeper water, facies of the Canadian Leduc reefs, whilst 'massive' and 'subspherical' forms (domical, bulbous and irregular) dominate reef facies and are less common in fore-reefs Klovan (1964). Geopetally constrained fore-reef palaeoslope data in the Canning Basin reef-rimmed shelves (Playford 1980; Playford and Cockbain 1989) imply depths comparable to those of modern reef systems (the earliest deep water laminar stromatoporoids are Ordovician; Bourque and Amyot 1989, p. 255); laminar shape at depth could have collected more light as in some modern corals (Robert Riding, pers. comm.). Arguments favouring algal (= ? microbial) symbiosis (e.g. Cowen 1988) are circumstantial, and papers which record deeper water tabular forms (Klovan 1964, at Redwater; Krebs 1974, in Europe; Kobluk 1975, at Miette; see Wilson 1975, p. 144) do not contain sufficient species-morphotype information to demonstrate flattening at depth within a species. Also, low profile is common in stromatoporoids, and may relate instead to sedimentation rate and substrate type, similarly poorly investigated.

#### *Palaeoenvironmental distribution*

Stromatoporoids with diameters of up to hundreds of millimetres grew in deeper facies, lagoons and small reefs, and up to several metres in larger reefs and mounds (Text-fig. 6), and occupy up to 90 per cent. of reef volume (Machel and Hunter 1994, p. 162). Stromatoporoids were limited in deeper facies, and in mud mounds, occurring uncommonly as small individuals (e.g. Bourque and Raymond 1989). Siliceous sponges played a rôle in deeper water mounds (e.g. Brunton and Dixon 1994), and have been postulated as major elements of stromatoid-rich mud mounds by Bourque and Gignac (1983, 1986), but none of these is the calcified form typified by the stromatoporoid skeleton. In contrast, stromatoporoids may be major elements of framestones, bafflestones, bindstones and debris in both biostromes and bioherms (e.g. Watts 1988a; Sønderholm and Harland 1989; Riding and Watts 1991; James and Bourque 1992; De Freitas *et al.* 1993; Kershaw 1993; Machel and Hunter 1994); absence of a rigid frame is common in stromatoporoid reefs and, except where bound by microbial growth (e.g. Devonian platform-margin reef limestones of the Canning Basin), presumably could not withstand high energy (De Freitas *et al.* 1993). Thus, their ability to create cryptic cavities was limited (Wood 1996) and they usually did not build up high reef profiles; unbound stromatoporoid build-ups are discrete objects (Riding 1981), made of closely juxtaposed fossils, and called cluster reefs by Riding (1990). Opinions about whether biostromes should be regarded as reefs vary, reviewed by Kershaw (1994), who divided biostromes into autochthonous, parautochthonous and allochthonous elements, to emphasize the reefal character of some biostromes.

Stromatoporoids apparently grew best in the shallower, more turbulent waters of Palaeozoic reefs, outcompeting corals and other organisms, and forming low diversity stands in the 'climax' stages of reef development (e.g. Wilson 1975), true in many biohermal reefs (e.g. Devonian reefs in South Devon, UK, Scrutton 1977a, 1977b; the Silurian Höglint reefs of Gotland, Sweden, Riding and Watts 1991); but some exceptionally stromatoporoid-rich assemblages formed as biostromes in lower energy shelf-ramp settings in Silurian and Devonian platforms. Furthermore, Monty *et al.*

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TEXT-FIG. 6. Stromatoporoid growth forms in Silurian and Devonian reef and reef-related environments. A, example of growth form zonation in Lower Wenlock of Gotland, (Watts 1988a; Riding and Watts 1991); H, T, L, D and A refer to halysitid, tabulate, laminar stromatoporoid, domical stromatoporoid and algal phases, respectively, of Watts (1988a). B, Silurian biostromes show diverse growth forms, but lack zonation (Kershaw 1981, 1990; Kershaw and Keeling 1994). C, platform and platform margin distribution of Devonian stromatoporoid growth forms (compiled from global sources, showing a consistent pattern). The depths of open water bioherms and mud mound are speculative; both may be shallow water.

(1982) drew attention to the fact that although stromatoporoids are major reef-builders of the Devonian, they are not abundant in all cases (Text-fig. 12, discussed below). Presumption of shallow water may not be always justified, with an impact on interpretations of sea levels, discussed below.

*Stratigraphical growth form trends*

Ordovician and Silurian stromatoporoid growth forms are conservative but expand with substantial niche exploration in Devonian reef systems, to a 'modern-looking' form distribution (Andrichuk 1958; Fischbuch 1962), but stromatoporoids lack the branching habit of the modern dominant reef coral *Acropora*. Ordovician and Silurian reefs are similar in structure and function and differ mainly in taxa (Copper 1988, p. 137). Many late Silurian reefs resemble Devonian platform margin systems, and include important elements of microbial binding (e.g. Bourque and Amyot 1989), and Devonian (e.g. Gischler 1995) reefs may contain substantial submarine cement.

*Summary*

Stromatoporoid attributes which facilitate their palaeoenvironmental application are: wide substrate tolerance, presumed fast growth, and broad distribution in shallow facies. The application of these attributes needs a common growth form terminology, considered in the next section.

## STROMATOPOROID GROWTH FORM CLASSIFICATION: A HIERARCHICAL APPROACH

Devonian facies patterns revealed by oil exploration of 1950s and 1960s left a huge database on stromatoporoid distribution and growth form, and form classification was developed for general utility, not for palaeobiology. The resulting recurring problems of non-uniformity and imprecision of terminology applied to stromatoporoid growth forms (e.g. Noble 1970; Abbott 1973; Kershaw and Riding 1978) require a standard classification to facilitate useful palaeobiological analysis. Calcified sponges do not correspond to simple geometric forms, and have minor to major form-variations even with specimens, so a terminology describing all variants is cumbersome. Also, although terms such as laminar and bulbous translate easily to other languages, English equivalents are sometimes unclear (e.g. 'wedge' – Dong and Yang 1978; 'clock-like' – Yang and Dong 1980, p. 396). A new approach here, using a three-level hierarchy of common English terms, provides a greater degree of descriptive precision (Text-fig. 7), and inappropriate terms are abandoned (Text-fig. 8).

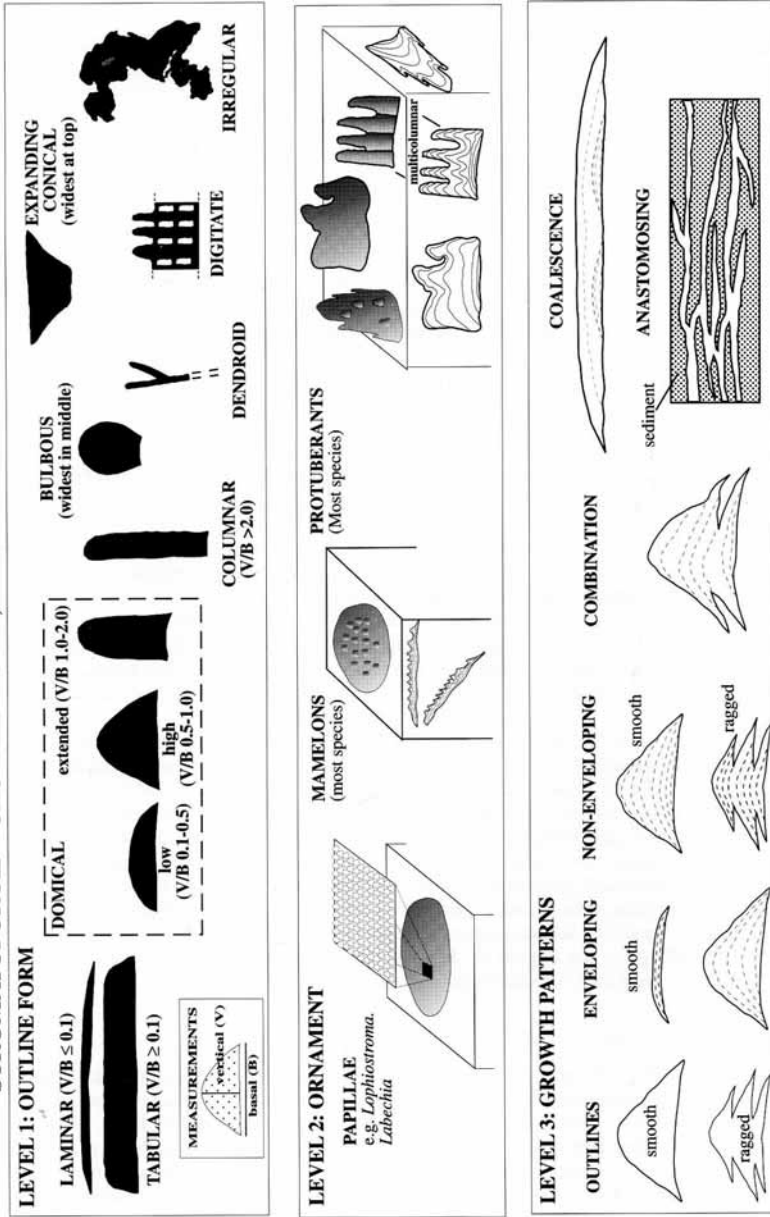
Stromatoporoid form is usually classified from vertical cross sections in quarries and cliffs in solid reef limestones, and imprecision of 2-dimensional views of 3-dimensional objects pervades all form description (Text-fig. 4), clearly illustrated in publications (e.g. Kazmierczak 1971). Simple forms are easier to classify than irregular or disorientated forms and objective classification of many specimens in stromatoporoid assemblages is thwarted. Because stromatoporoids are approximately circular to sub-circular in plan view, random vertical sections give good approximations of the real shape, unless specimens are tilted, overturned or have complex shapes (Kershaw and Riding 1978, 1980); then, the only solution is to remove them from the rock, normally impossible. Complete stromatoporoids can be classified; damaged specimens may or may not reveal sufficient morphology to classify them, depending on the degree of damage. Reef stromatoporoids are also commonly subject to pressure solution which affects shape recognition.

*Hierarchical level 1: form outline*

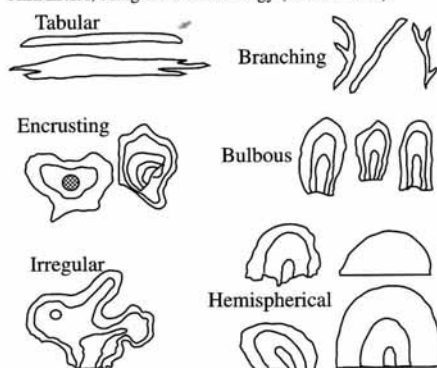
Kershaw and Riding (1978, 1980) selected four terms for basic shapes: laminar, domical, bulbous, dendroid; but many stromatoporoids do not fall into this array, and the parameterization scheme of Kershaw and Riding (1978, 1980) applies in only a few cases (e.g. Kershaw 1981, 1984, 1990). In the following list, italicized terms are intended to evoke unambiguous images of growth form (Text-fig. 7), and terms in brackets are current equivalents, which are abandoned: *laminar* (sheetlike, lamellar, tabular, discoidal); *tabular*; *domical* (hemispherical, massive, conical, domal, tabular); *columnar* (cylindrical); *bulbous* (sub-spherical, massive, globular, nodular, oblate);

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STROMATOPOROID GROWTH FORM, HIERARCHICAL CLASSIFICATION



TEXT-FIG. 7. In Level 1 of this classification, laminar, domical and columnar are a continuum of increasing V/B, with extension to bulbous. Tabular is vertically thickened laminar, different because laminar commonly develops into domical without becoming tabular first. Dendroid forms are always broken fragments, with thin dendroid e.g. *Amphipora*, and thick dendroid e.g. *Stachyodes*. Expanding-conical is rare (e.g. Silurian Sundre Formation, Gotland). Digitate, with vertical elements and small 'bridges' is uncommon (e.g. Silurian Höglint Formation, Gotland; *Ecclimadictyon* of upper Silurian of Quebec; Hughson and Stearn 1989). Levels 2 and 3 are described in the text.

STROMATOPOROID MORPHOLOGY, MIETTE REEF,  
ALBERTA, using older terminology (Kobluk 1975)

TEXT-FIG. 8. Typical stromatoporoids growth form terminology of earlier authors. Note that tabular includes laminar of the scheme in Text-figure 7; bulbous includes extended domical; hemispherical contains both a bulbous and domical form; encrusting and irregular include oblique sections.

*dendroid* (ramose, branching, digitate, foliose, dendritic, twig-like); *expanding-conical* (conical); *digitate*; *irregular* (massive).

Some commonly used terms which are inappropriate or rarely applicable are excluded from this scheme. *Hemispherical* denotes stromatoporoids with rounded upper surfaces, but they are rarely hemispherical (Text-fig. 8), and the edges of laminae nearly always terminate at a shallow angle with the substrate (Text-fig. 7). *Massive* is an adjective with no place in a morphological classification; used to describe large stromatoporoids of any shape, it includes poorly definable forms such as in drill cores where it is of least value (e.g. Fischbuch 1968). *Massive* was abandoned by Kershaw and Riding (1978), but is still in use (e.g. Gischler 1995). Some earlier authors used *massive* correctly in its adjectival sense (e.g. Kobluk 1975, 1978), but it is best avoided. *Encrusting* is a life habit not a growth form, but has become synonymous with thin laminar stromatoporoids which encrusted their substrate. In fact, encrusting stromatoporoids grew into many forms (e.g. Kobluk 1975, p. 248).

*Skeleton size.* Size varies from millimetre scale for examples which died soon after growth began, to large specimens of several metres diameter. Size measurement is problematical; volume is the best measurement and its nearest proxy is area. Area estimates of vertical sections are the most appropriate, best achieved by image processing of orientated sawn samples, but are not given in stromatoporoid papers; in the field, basal diameter of laminar and low to high domical forms, vertical height of extended domical and columnar, and the greater of either vertical or horizontal dimensions of bulbous forms, give broad estimates, but are not fully comparable, and single dimension estimates are not satisfactory because they do not describe the real size.

Basal diameter is usually less than 2 m but large stromatoporoids are found throughout the Palaeozoic. *Pseudostylodictyon lamottense* (Seely) in the mid Ordovician Chazy Group, Vermont, reached 1.1 m across and 1 m high (Kapp 1974); most are ragged non-enveloping high to extended domical forms, including irregular forms and some with a mushroom form as growth exceeded sedimentation. *Stylostroma* (*S. surculum* and *S. mamillatum*) from mid Ordovician reefs in the Mjøsa Limestone at Bergevika, Norway, are up to 1.3 m across and 0.4 m high (Webby 1979b). Late Ordovician columnar *Aulocera* on Anticosti have maximum lengths (presumed height) of 3 m and diameter of 0.3 m (Petryk 1981). Silurian forms from Gotland may exceed 2 m (Mori 1970, p. 137).

#### Hierarchical level 2: ornament

Ornament modifies the profile of the basic shape and falls into three categories (Text-fig. 7).

*Papillae*. These are *c.* 1–2 mm high surface cones, taxonomically constrained in some stromatoporoids, e.g. *Lophiostroma schmidti*, whereas in others they are facultative (e.g. Prosh and Stearn 1996, pl. 3).

*Mamelons*. These are *c.* 2–10 mm high lumps regularly or irregularly distributed on the upper surface, usually facultative. Astrorhizae are located on the apices of some, often with osculum-like openings on the summit and radiating astrorhizal grooves (Nicholson 1892, pl. 15). Mamelons may have aided water flow, by Bernoulli's mechanism (Boyajian and LaBarbera 1987; LaBarbera and Boyajian 1991), because astrorhizae of modern stromatoporoid-like sponges carry the soft tissue exhalant water canal system they most probably had a similar function in fossil stromatoporoids (Stearn 1972, 1975a). Some species lack astrorhizae, so the exhalant system is not preserved and its association with mamelons cannot be demonstrated; in others, astrorhizae do not occur on mamelon apices, so may not have assisted water flow within the system (Stearn 1989; Kershaw 1990). Mamelons may be vertically orientated, even where the stromatoporoid lies *in situ* on a sloping surface (Kershaw 1990), suggesting potential responses to light or current flow, which are poorly investigated. Mamelons occur in stromatoporoids both in argillaceous sediments (Mendez-Bedia *et al.* 1994, p. 168) and mud-free sediments (Kapp 1975, p. 205) so cannot be related reliably to general conditions. Mamelons are commonly present through most of a stromatoporoid skeleton, and impart a wavy appearance to laminae in vertical section; neighbouring specimens of a species may have or lack mamelons (e.g. *Clathrodictyon mohicanum*; Kershaw 1990) and the controlling factors are unclear.

*Protuberants*. These are pointed and rounded surface protrusions with or without a regular pattern, particularly in Devonian stromatoporoids, and may or may not occur through the entire skeleton. Beginning as mamelons, they grew much larger and increase stromatoporoid upper surface area, but whether that was their purpose is unknown; they usually developed in the absence of sedimentation, because no sediment occurs in the low areas. A variant is multicolumnar growth, a series of parallel columnar projections from the upper surface (Text-fig. 7). Some stromatoporoids occur as a mass of multicolumnar growth, similar to the organ-pipe appearance of some modern reef corals; some species are preferentially multicolumnar, e.g. *Actinostroma windjanicum* in the Canning Basin (Cockbain 1984, p. 11).

#### *Hierarchical level 3: internal arrangement of growth lines*

Internal growth patterns visible in almost all stromatoporoids show shape changes with growth, regardless of whether the skeleton is dominated by either lateral or vertical skeletal elements; change in morphology in individuals is recognized by time-equivalent lateral lines (laminae and latilaminae) tracing previous upper surfaces. Growth of smooth-margined stromatoporoids may be *enveloping* or *non-enveloping*, apparently unrelated to sedimentation, while *ragged* margins resulted from episodic flank sedimentation (Text-fig. 7), the italicized adjectives being added to morphotype terms (Kershaw and Riding 1978). Laminar and domical forms are either ragged or smooth, while columnar, bulbous, dendroid and expanding-conical are almost exclusively smooth-margined. Smooth stromatoporoids almost always began with enveloping style, usually changing to non-enveloping as growth progressed. Vertical sections of stromatoporoids show a normally symmetrical outline, and the strong asymmetry of some ragged forms may be due to unidirectional currents, with sediment interpreted as collecting on either the downstream side (Silurian of Norway; Broadhurst 1966), or the upstream side (Ordovician of Vermont; Kapp 1974) of the fossils! Raggedness may be quantified in relation to stromatoporoid size and shape, with potential for sedimentation rate analysis (Text-fig. 11). Anastomosing laminar forms were severely affected by episodic sedimentation resulting in vertically accumulated sheets, with thin sediment layers almost completely separating them (Text-fig. 7). Stromatoporoids with well-developed laminae also show

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that successive laminae may not necessarily form continuous layers across the entire surface and imply that not all the stromatoporoid surface was alive simultaneously.

Study of internal growth patterns may be applied to interpretations of palaeobiology; Kershaw (1984) interpreted stromatoporoids capable of developing a high profile as having been favoured in certain environments, because of their ability to shed sediment so that raggedness did not form, or affected only the lower flanks (Text-fig. 11). Episodic movements leading to abrupt changes in attitude are recorded as changes in growth direction, resulting in complex forms, and emphasize problems of shape classification from two-dimensional faces (Text-fig. 12).

#### *Naming growth forms*

Growth variations can be applied as adjectives to outline forms, e.g. ragged low domical, smooth enveloping extended domical, multiprotuberant tabular, and adequately describe the range of growth forms. Imprecision exists in many papers because of the subjectivity of application of growth form terms (e.g. Text-fig. 8), but much of the problem is due to imperfectly preserved and/or displayed forms.

#### *Other minor features*

*Phases.* In growth of individuals, *phases* (Stearn 1989) result from modification of skeletal tissue vertically and horizontally, and can give the appearance of different species in a single individual, requiring a broad approach to species definitions as discussed by Prosh and Stearn (1996, p. 13). The biological and ecological study of phases is not developed, and their significance is unknown.

*Coalescence.* This occurs between two or more stromatoporoids of the same species which grew near together and merged to produce a larger individual. Coalescing laminar forms thus became large sheets, while high to extended domical forms resulted in multiple columns subsumed within a domical shape. Neighbouring specimens of different species do not show coalescence (Kershaw 1984, 1990).

#### *Modelling stromatoporoid morphology*

Triangular arrays applied by Kershaw and Riding (1978, 1980) for stromatoporoids, and by Young and Scrutton (1991) for corals, quantify morphotypes simply, and are suitable for some field locations, enhanced if taxonomic data are included (Kershaw 1984, 1990). Such schemes are limited in their scope to model fossils, but more comprehensive geometric models (e.g. Hofmann 1994, for stromatolites) have not been attempted for stromatoporoids. Because stromatoporoids grew by accretion of layers (like chaetetids, trepostome bryozoans and tabulate corals; Kershaw and West 1991), it may be possible to model a fundamental growth unit, but different parts of the stromatoporoid surface grew at different rates (not necessarily symmetrically), the upper surface was not always alive at the same time, and parts were killed by sedimentation. Therefore other methods must be used to attempt a satisfactory model.

Computer models of coral growth involve photoresponse (e.g. Graus and Macintyre 1976), unproven in stromatoporoids, and, unlike corals and other clonal organisms (Jackson 1983), stromatoporoids lack subdivisions; although astrorhizae (local drainage systems on stromatoporoid surfaces, giving an impression of subdivisions) tend to be evenly distributed, they are ephemeral and have unclear boundaries (Colin Stearn, pers. comm.), and are missing in many stromatoporoids, where the water transport system was presumably in the soft tissue only. In fact, choanocytes (single aquiferous cells), or possibly choanocyte chambers, are the true poriferan growth units. Stochastic modelling, attempted by Swan and Kershaw (1994), does not make any assumptions about such parameters as light, employing pixels on a computer screen as the unit of growth, emulating choanocytes/choanocyte chambers, and using algorithms which apply rules to pixel distribution. Here there is no need to define growth modules above pixel level, so features such as corallites (for

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corals) or astrorhizae (for sponges) are not considered. The current model generates reasonable approximations to stromatoporoids, allows for episodic sedimentation to create ragged margins, and is likely to be a useful approach to emulating stromatoporoid growth.

#### Summary

The hierarchical growth form approach allows a substantial improvement in precision of form-terminology; it aims to enhance the value of stromatoporoids in palaeobiological and facies analysis, considered in the next section.

### APPLICATION OF STROMATOPOROIDS IN PALAEOENVIRONMENTAL ANALYSIS

#### General relationships

Growth form was controlled by environmental (extrinsic) and genetic (intrinsic) factors (Nicholson 1892, pp. 27–29; Galloway 1957, p. 374; Kissling and Lineback 1967; Fischbuch 1968, fig. 23; Leavitt 1968, p. 323; Mori 1969, 1970; Kapp 1974, 1975; Cornet 1975; Hoggan 1975; Kobluk 1975; Kershaw 1981, 1984, 1990; Cockbain 1984; Kano 1989, 1990). Most species are limited to a narrow morphospace which varies depending on palaeoenvironment-morphospecies interaction. Short-lived events are also recorded, particularly sedimentation and movement effects during life (Text-fig. 1), but since these effects do not influence the basic shape (a domical stromatoporoid reorientated several times in life so that its shape is rounded, is still intrinsically domical) then underlying controls on form, if they can be identified, may provide important data on the overall character of the palaeoenvironment.

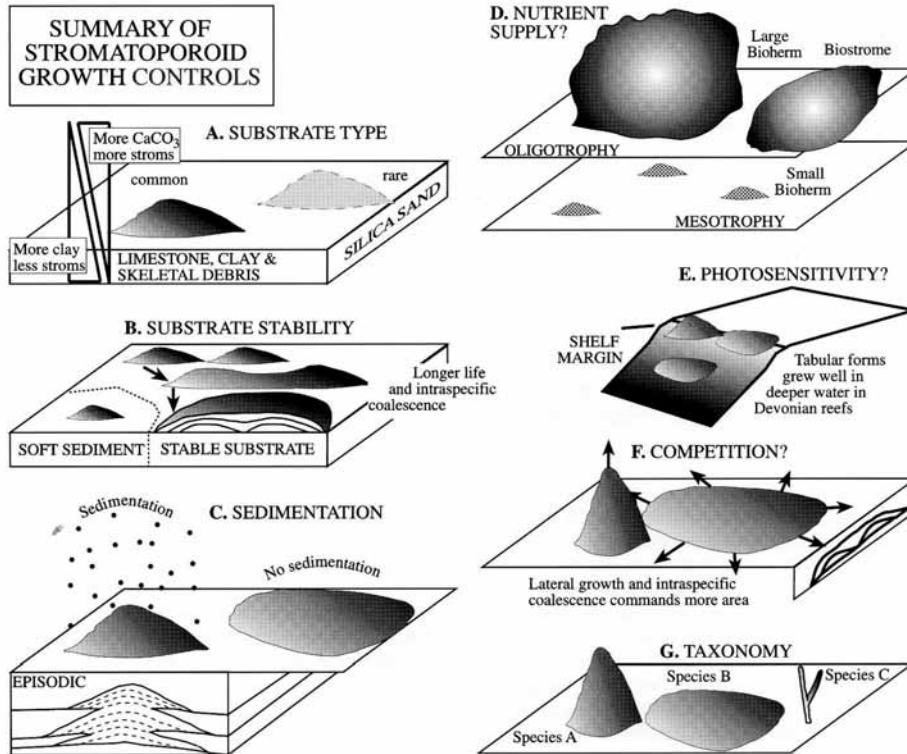
The success of stromatoporoids probably relates to the abundance of hydrodynamically stable low profile forms which could stabilize substrate and facilitate further growth; several studies illustrate the selective advantage of dominantly lateral growth in these fossils (Meyer 1981; Bjerstedt and Feldmann 1985; Harrington 1987; Kano 1990; Kershaw 1990). Stearn's (1982) comparison of stromatoporoid with modern coral growth forms, as a basis for interpreting the nature of ancient reef environments, revealed no parallel patterns; and the forms of modern reef animals are not even useful guides to modern reef environments, thereby emphasizing the care needed for interpretation of stromatoporoids. Nestor (1984) discussed the range of controls on stromatoporoids, and a general summary, derived from many sources, is given in Text-figure 9.

Large stromatoporoids reflect long periods of growth (Wood *et al.* 1992) and highlight their ability to survive events affecting the sea bed. Depending upon the nature of the assemblage, stromatoporoids have the potential to reveal regional and even global processes. Examples of Palaeozoic stromatoporoid assemblages demonstrate the range of process-response relationships in order to emphasize their value in palaeoenvironmental analysis at these different scales.

#### Local scale: autecology

*Mid Ordovician stromatoporoids, Chazy Group, Vermont, USA.* Large stromatoporoids appear in mid Ordovician level-bottom and mound environments, the start of Palaeozoic stromatoporoid dominance in many shallow marine (Webby 1986, 1994) as skeletonized reef metazoa increased (Flügel and Flügel-Kahler 1992, p. 178), although stromatoporoid abundance varies in Ordovician build-ups (Desrochers and James 1989). Stromatoporoid morphology is mostly laminar to domical (e.g. Bolton 1988) except for the unusual tree-trunk shaped aulaccerids, which grew upright (Cameron and Copper 1994), sometimes tapering upwards (Dong 1982, p. 581). Kapp (1974, 1975) and Kapp and Stearn (1975) noted that laminar to high domical forms of abundant stromatoporoids in the mid Ordovician Crown Point Formation, Lake Champlain area, Vermont, have a component of taxonomic control on form; *Pseudostyloclyctyon lamottense* (Seely) grew high domical, whilst *Pachystylostroma* and *Labechia* species were laminar (Kapp 1974, p. 1235). *Pachystylostroma* and

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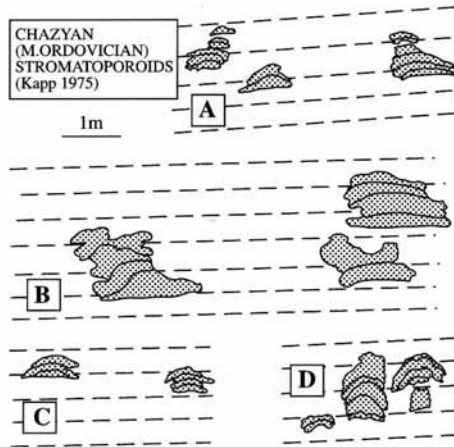


TEXT-FIG. 9. The factors summarized here prescribe the environmental limits of stromatoporoids, and are described in appropriate sections of the text.

*Labechia* are present only in mounds, whilst *Pseudostylodictyon* occurs also in level-bottom sediments. Stromatoporoids occupy the greatest biovolume of mound faunas, but are of low diversity with individual mounds dominated by single stromatoporoid species, different species dominant in different mounds (Kapp 1975, p. 210). Keller and Flügel (1996) described a similar low diversity in Arenig deposits in Argentina, containing the possible stromatoporoid genus *Zondarella*.

Only *P. lamottense* formed large stromatoporoids (Kapp 1974), as stacked ragged domes due to episodic sedimentation, and may have grown rapidly, because it is also the only one in level-bottom facies which was high enough to survive episodic sedimentation. Kapp (1974, p. 1236) noted that individuals began on small substrate irregularities, and although not stated in her papers, the indications are that it could grow on the sediment surface directly, noted also by Kano *et al.* (1994) in middle Ordovician stromatoporoids from Korea. In Vermont, individuals are isolated and grew on several bedding planes (Text-fig. 10); early growth showed lateral expansion with some enveloping latilaminae, then upward growth was apparently stimulated by episodic sedimentation to generate ragged forms.

Individuals may be closely spaced, less than one metre apart (Kapp 1974, text-fig. 3) and commonly asymmetrical (Text-fig. 10), with growth axes of neighbouring stromatoporoids commonly pointing in different directions, interpreted by Kapp as a result of variable local current

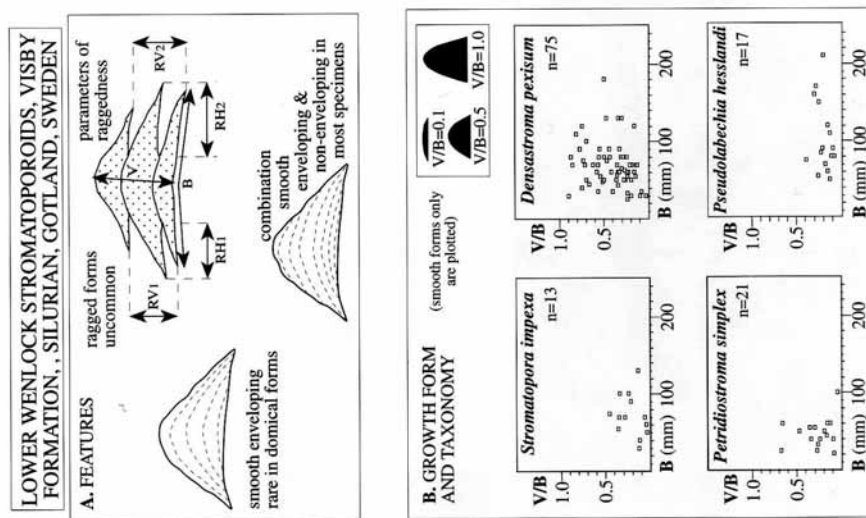
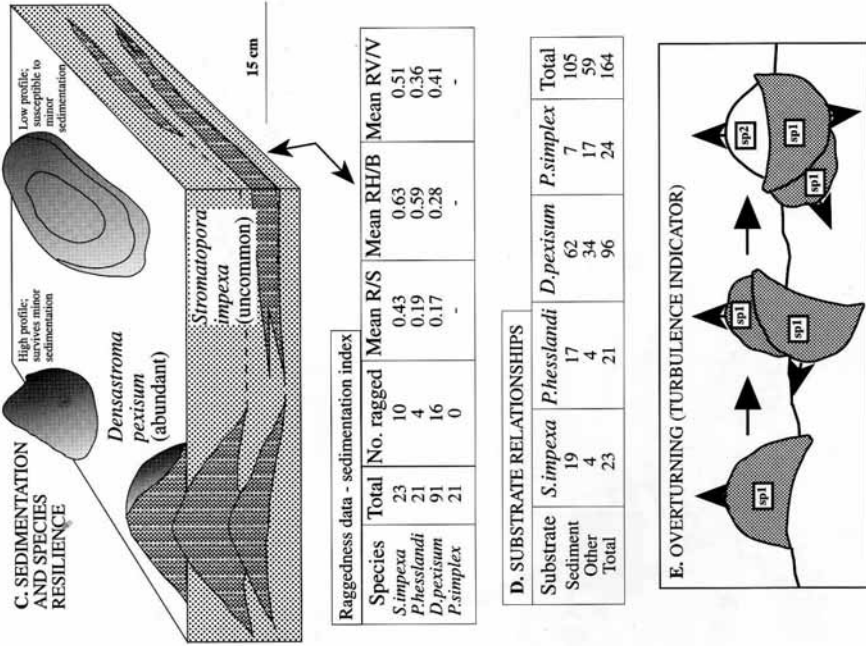


TEXT-FIG. 10. Sketches of stromatoporoid vertical sections drawn from photographs in Kapp (1975). Growth was apparently principally on soft sediment; individuals began growth at different levels, and have ragged margins, suggesting that episodic sedimentation controlled growth initiation and development. Growth is biased in 'left' or 'right' directions. A-C, from Fisk Quarry; D, from Goodsell Quarry.

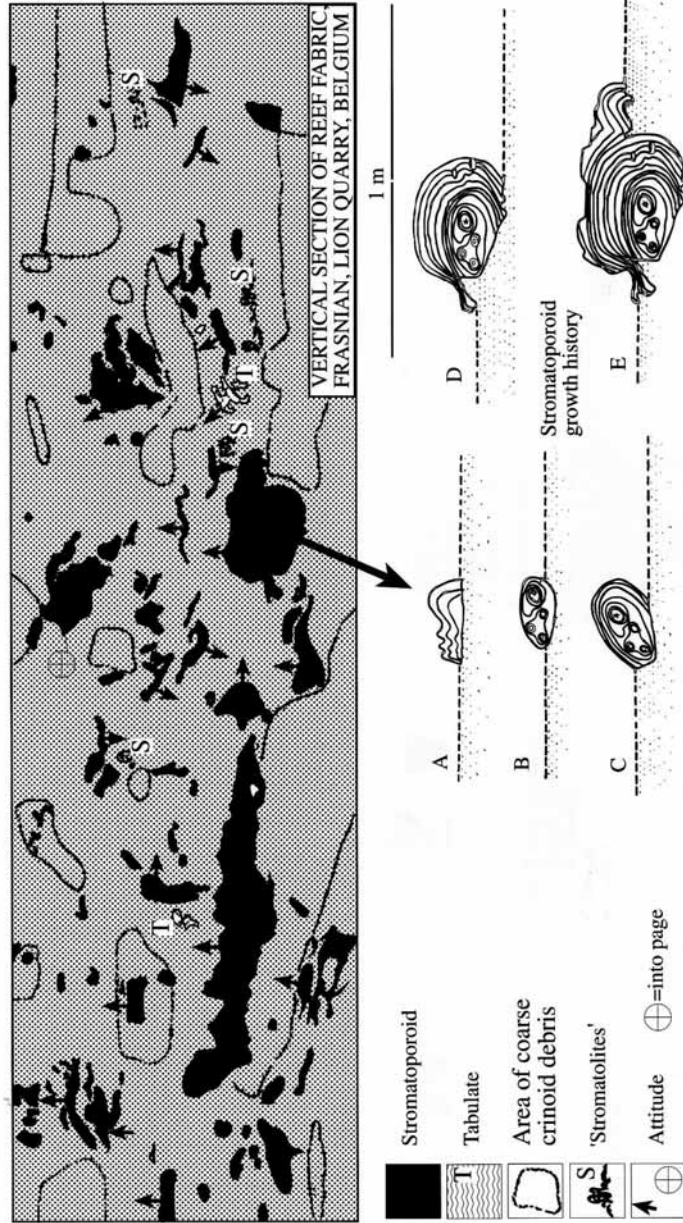
vectors. Asymmetry is maintained through the vertical thickness, so for currents to be the cause, they would have to be peculiar to each stromatoporoid throughout its life, including many episodes of sediment deposition; asymmetry may be better explained by chance growth bias. Kapp (1974) invoked storm-wave erosion to explain truncation of the top of a low domical stromatoporoid; however, this line of truncation is highly unusual because stromatoporoid skeletons are normally weaker in other planes (Text-fig. 3), and is more readily explained if the stromatoporoid and its enclosing rock were fully cemented (Kershaw 1990). Kapp's example might therefore indicate rapid submarine cementation, and possibly even subaerial exposure. Kapp (1975, p. 198) discussed and rejected subaerial processes in the mounds at other levels within the Crown Point Formation, but a reappraisal may be warranted. Submarine dissolution of protruding portions of stromatoporoids is a possible cause, more feasible if stromatoporoids were aragonitic. Kapp (1975, p. 205) recorded (but did not figure) bent mamelons, and interpreted them as soft-tipped, deformed by the overgrowing lamina; although inconsistent with models of the stromatoporoid skeleton secretion, if correctly interpreted this indicates that calcification was not necessarily synchronous with growth in these early stromatoporoids. Overall, the Vermont examples therefore give considerable information about stromatoporoid palaeobiology and autecology, but also raise questions about controls of form.

*Silurian level-bottom stromatoporoids, Visby Formation, Gotland.* Text-figure 11 summarizes autecological features of an assemblage of small stromatoporoids. *Densastroma pexisum* grew taller, and apparently survived episodic sedimentation better, than other species in the assemblage, leading to its higher abundance and lower degrees of raggedness (Kershaw 1984). Some tabulate coral species are likewise better adapted to episodic sedimentation (e.g. Gibson and Broadhead 1989). An environmental energy index, using the proportion of overturned stromatoporoids, could be used only broadly, because domical stromatoporoids are usually upright following disturbance (Text-fig. 2); nearly all Visby Formation stromatoporoids are upright in the muddy limestones, less so in coarser beds interpreted as storm events (Kershaw 1984).

*Late Devonian (Frasnian) bioherm at Lion Quarry, south Belgium.* Text-figure 12 illustrates laminar, tabular and domical stromatoporoids in a Frasnian bioherm, in which large tabular and domical stromatoporoids occur together at particular levels, separated by layers containing small laminar stromatoporoids, and layers with coarse debris. The larger stromatoporoids presumably grew in



TEXT-FIG. 11. Comparative stromatoporoid autecology (data from Kershaw 1984). A, features of stromatoporoids in this assemblage; B, morphological variation between species; C, demonstrates the selective advantage of a high profile form in this environment; D, species selection of substrate type; E, broad indication of frequency of dislocating currents shown by episodic overturning and recovery by species 1, and use of its upturned base by species 2.



TEXT-FIG. 12. Small area of vertical surface of the Frasnian reef in Lion Quarry, near Frasnes, south Belgium. A mixture of whole and fragmented stromatoporoids appears to occur in rhythms separated by coarser debris. The stromatoporoids demonstrate growth on a probable loose substrate, with a prominent lateral growth aspect. The complex form of one specimen is interpreted as episodic reorientation in sequence A-E, temporal energy reduction is indicated by occurrence of thin laminar stromatoporoids associated with microbial heads and mats. This diagram illustrates the problems of growth form classification, with some forms more readily classifiable than others.



episodes of reduced deposition and relative substrate stability, interspersed with energetic events. These features are consistent with the interpretation of Monty *et al.* (1982) that this bioherm lacks a frame, and possibly formed in deeper water.

*Stromatoporoid-coral and stromatoporoid-'worm' intergrowths.* Porifera, Cnidaria and 'worms' intergrew in Ordovician, Silurian and especially Devonian reef- and non-reef settings, and have great potential for stromatoporoid autecological analysis.

Stromatoporoid-syringoporid intergrowths (colloquially called 'caunopores'; Text-fig. 13) may constitute a significant portion of a stromatoporoid assemblage (Mistiaen 1984) and may be stromatoporoid species-specific (Kershaw 1987). Whilst commonly interpreted as a commensal response to protect the delicate coral in high energy environments, in contrast to the separate growth of syringoporids in muddy facies (Mori 1970; Kershaw 1987), Young and Noble (1989) demonstrated the converse in other examples; unpublished observations of intergrowths in a low energy setting at GothemsHAMMAR (?Wenlock, Halla Formation) on Gotland suggest mutualism, because the syringoporids presumably did not need the stromatoporoids' protection. In all intergrowth cases so far reported, parasitism is discounted because there is no adverse effect on the stromatoporoids. Stromatoporoid-rugose coral intergrowths (Text-fig. 13C-E) are less common, but may also be species-specific (Kershaw 1987) and occur in both high and low energy settings.

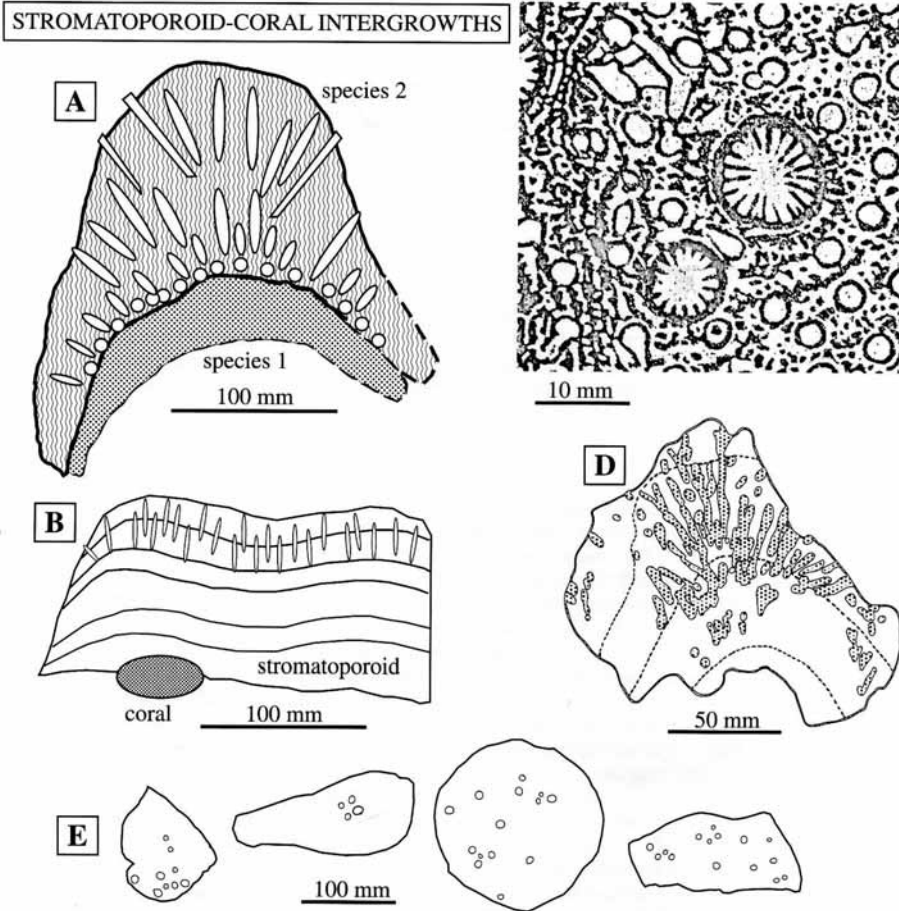
Initiation of coral growth is poorly documented. Stromatoporoids with well-developed laminae favour intergrowths (Mori 1970), possibly facilitating coral larval settling. In some examples from the Ludlow of Gotland (Text-fig. 13A), syringoporids settled at an early stage of the stromatoporoid's growth, from at least one point near the base spreading laterally and vertically as the two grew together. In one case syringoporids began growth across the width of a stromatoporoid at one horizon (Text-fig. 13B), suggesting chance discovery by coral larvae some time after the stromatoporoid had developed. Syringoporids tended to develop throughout the whole stromatoporoid skeleton, whereas rugosans underwent a more restricted branching programme, utilizing only part of the skeleton (Text-fig. 13D). Taxonomy of intergrown syringoporids is influenced by the possibility that corallite walls may be thinned and have different structure from non-intergrowth forms (Mistiaen 1984; Kershaw 1987), whereas rugosans do not seem to show modification. Relative growth rates of intergrown partners were presumably similar, possibly even synchronized, because corals do not normally protrude more than a few millimetres above the stromatoporoid surface, nor were they commonly overgrown by stromatoporoid tissue. It therefore seems that the intergrown partners died together.

Sporadic spiralled tubes intergrown with stromatoporoids (e.g. Stearn 1975a, fig. 2) appear usually to have been overgrown rapidly by the sponge skeleton, also observed for spirorbid worms in Carboniferous chaetetids (Cossey 1983). In these cases, the most reasonable explanation is of larval worms settling accidentally on a living sponge, and being killed quickly. Intergrowths between *Trypanopora* (worms) and stromatoporoids in the Eifelian of Belgium, however, show that *Trypanopora* grew successfully with the stromatoporoid *Habrostroma* (Tourneur *et al.* 1994), the worm tubes orientated normal to stromatoporoid laminae.

#### *Community scale: synecology*

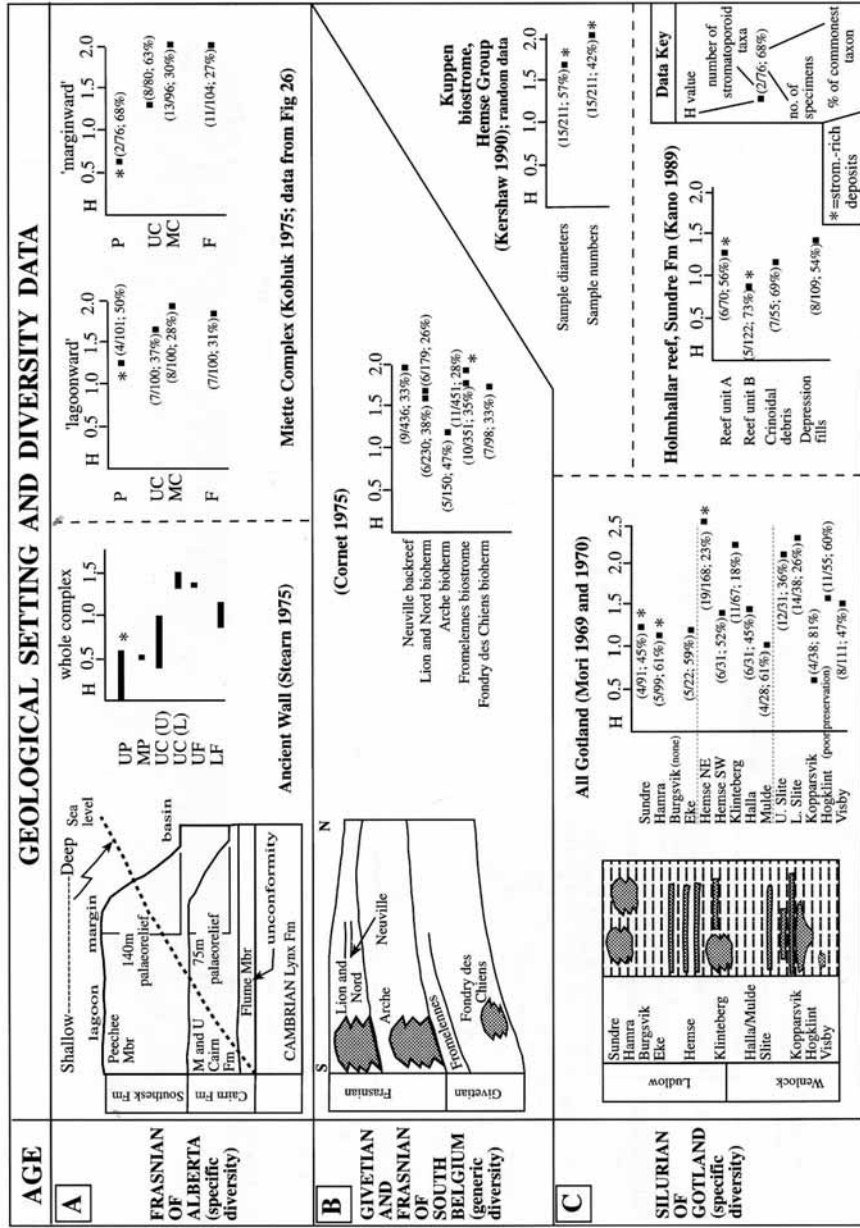
*Stromatoporoid diversity indices as palaeoenvironmental tools.* Quantification of modern organic diversity is achieved using diversity indices (e.g. Pielou 1966), but is problematical in fossils because of problems in precision of species definitions, time-averaging of communities, and taphonomy. Fagerstrom (1983) applied diversity concepts qualitatively to Emsian and Eifelian stromatoporoid assemblages, where diversity in reefs is greater than in level-bottom communities, and Eifelian reef organisms are strongly endemic; also reef environments are likely to have greater origination and extinction rates, and consequently could play an important rôle in the evolution of reef builders. Cockbain (1989) similarly noted higher species numbers in reef (25 taxa) compared with shelf (six taxa) environments in western Australian Mid to Late Devonian successions. In contrast, Devonian reefs in Nevada have lower diversity, with *Hammatostroma* abundant as tabular and bulbous shapes

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TEXT-FIG. 13. Intergrowths of stromatoporoids and corals from the Silurian of Gotland. A–D, from biostromal reefs; E, from muddy facies. A, species 2 directly overgrew species 1; 1 lacks syringoporid coral, but 2 is infested. Syringoporid tubes spread horizontally in the early growth of species 2 and became vertical as the stromatoporoid developed. B, stromatoporoid grew for some time before syringoporid coral colonized the surface, thence developing intergrowth. C, horizontal thin section photograph of *Petridiostroma convictum* infested with both syringoporid and rugose branching corallites. D, vertical section of stromatoporoid showing the rugose coral does not fully infest the stromatoporoid. E, plan view of some low domical stromatoporoids showing location of rugose corals. Corals in A and B enlarged for clarity.

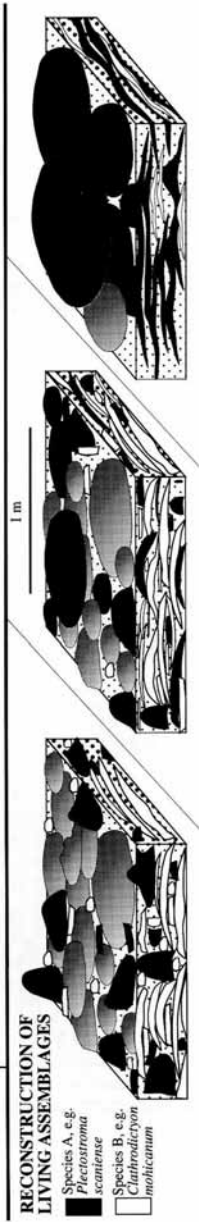
(Hoggan 1975). Brunton and Copper (1994) categorized lower Silurian reef biotas into groups depending on numbers of species, and revealed low diversity in reef cores with up to 70 per cent. of volume being composed of only four species. Copper (1988) drew attention to the lower diversity of modern reef communities in areas under great stress, whereas the rest of a reef complex usually exhibits a higher diversity.



TEXT-FIG. 14. Shannon-Wiener index (H) for stromatoporoid assemblages from published data for Silurian and Devonian locations. See text for explanation.

LUDLOW STROMATOPOROID REEFS OF GOTLAND, SWEDEN

Principal sites	KUPPEN, BIOSTROME (middle Ludlow, Kershaw 1990)	GROGARNSHUVUD, BIOSTROME (middle Ludlow, Kershaw 1997)	HOLMHALLAR, UNCLASSIFIED (upper Ludlow, Kano 1989)
<b>Morphospecies diversity</b>	Low; the 3 most important species (CM, PS, SB), 63% by numbers, are the largest stromatoporoids 	Low; the 3 most important species (PS, SB, SV), 46% by numbers, are the largest stromatoporoids. LS is abundant but small volume 	Low; the 2 most important species (PS and PT), 76% by numbers, dominate the reef 
<b>Growth styles</b>	Two styles, under strong taxonomic control 	Two styles, but species which grew tall at Kuppen, show low to high profile; nearly all low 	Almost all low profile; extensive anastomosing laminar sheets 
<b>Sedimentation rate</b>	Very low; ragged forms are rare	Very low; ragged forms are rare	Very low; stromatoporoids are large laminar forms, anastomosing due to episodic deposition
<b>Biostratigraphy</b>	Species with tall growth forms occur more commonly as fragments. One of those (PS) also has a delicate-looking skeletal architecture	Unknown	Reef is a strong frame; debris lies chiefly between boundstone units
<b>Coalescence</b>	Enhanced competitive ability of low profile forms 	Unknown	As Kuppen
<b>Symbiosis with corals</b>	Intergrown tabulate and rugose corals in 20% of stromatoporoids 		
<b>Reef sediment</b>	Principally micrite, plus crinoidal wackestone	Principally crinoidal and bryozoan grainstone	Principally crinoidal packstone & grainstone
<b>Principal reef features</b>	Low energy allowed tall forms	Higher energy selected for low profile forms	
	Low sedimentation rate allowed abundant growth		
	Coalescence of low profile forms gave competitive advantage		



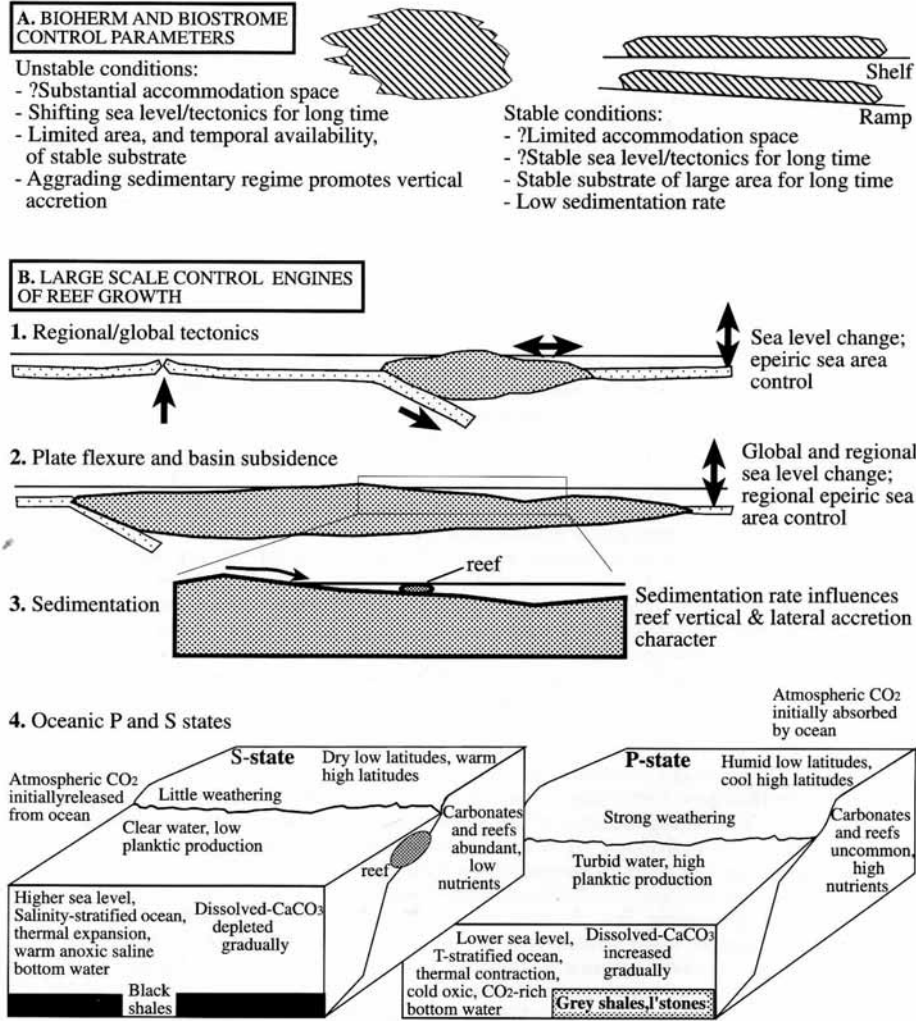
TEXT-FIG. 15. Parameters of stromatoporoid-dominated Ludlow reef communities from Gotland, Sweden, with principal reef features highlighted. The reefs are ideal settings for stromatoporoids because of abundance and diversity of taxa. They formed in ramp/self settings. Together with many Devonian stromatoporoid-rich biostromes, they are platform features not associated with barrier formation at platform margins. Platform margin reefs are much less dominated by stromatoporoids. CM = *Clathrodictyon mohicanum*; LS = *Lophostroma schmidtii*; PS = *Plectostroma scantense*; PT = *Parallelostrom ivoicum*; SB = *Stromatopora? hekkeri*; SV = *Svriueostromella borealis*; LS = *Stromatopora venukovi*.

Although such general observations are valuable, numerical diversity indices, such as the Shannon-Wiener index applied by Stearn (1975b) to the Devonian Ancient Wall stromatoporoid assemblages, provide a better comparative tool for palaeoecological and palaeoenvironmental work. Species diversity indices are calculated from relative abundance of individuals of each species, not just numbers of species, and greatest diversity lies in assemblages with equal numbers of each species. As a preliminary attempt to demonstrate their utility, Text-figure 14 provides diversity indices calculated using the Shannon-Wiener Function (H). Only data for stromatoporoids are given, and total biotic diversity must differ from the indices except in assemblages composed almost entirely of stromatoporoids; such assemblages, although with low total phyla diversity, may have high stromatoporoid diversity. Stearn (1975b, pp. 1637–1639) attributed progressive stromatoporoid diversity reduction at the Ancient Wall to increasing severity of the reef crest environment as relief increased on the reef front, and the same conclusion may be drawn for data given by Kobluk (1975) for both lagoon and reef-margin communities of the Miette Complex (Text-fig. 14A). Similarly, values of H calculated for Devonian stromatoporoids in south Belgium (from Cornet 1975) show that large bioherm complexes, sited in open water, have a slightly lower stromatoporoid diversity than shelf biostromes and backreef settings, and that these biostromes are much richer in stromatoporoids (Text-fig. 14B). In Text-figure 14c, data from Gotland (Mori 1969, 1970) show that stratigraphical units dominated by stromatoporoid-rich platform biostromes (Slite, Klinteberg and Hemse units) have highest diversities of stromatoporoid faunas, whilst lowest values are recorded for very shallow high-stress settings of the Kopparsvik Formation (where salinity may have played a part in diversity control), and deeper muddy environments of the Mulde Formation. Kano's (1989) work on the abundant stromatoporoid faunas of the Upper Ludlow of Holmhällar, Gotland (where facies are only partly exposed and the reef shape indeterminable), shows diversity differs through the reef complex. Ludlow reefs on Gotland (Text-fig. 15) are composed almost completely of stromatoporoids (Kano 1989, 1990; Kershaw 1981, 1990, 1995; Mori 1970); although diversity of phyla is low, stromatoporoid diversity is high (Text-fig. 14). Most are biostromes, implying stable conditions of low sedimentation and possibly sea level stillstands (Kershaw 1994; Kershaw and Keeling 1994) in contrast with bioherms (Text-fig. 16). Stromatoporoid faunas mostly comprise large low profile forms, many coalesced from smaller individuals, and emphasize the competitive advantage of a lateral growth habit, commonly seen in Ordovician to Devonian reef-builders.

The sum of available data serves to corroborate this author's view that platform biostromes (deposited in low stress environments) are the optimum settings for stromatoporoids. In a truly random sample (Kershaw 1990), albeit time-averaged for a single biostrome, stromatoporoid size is emphasized by comparing diversity of the same samples, expressed both as numbers and size ( $\approx$  basal diameter) of individuals; H is lower for basal diameters, emphasizing the competitive ability of large stromatoporoids. In the examples in Text-figure 14, comparisons are only valid *within* and not *between* data sets, because of different data collection methods applied. Diversity index data therefore depend on sampling procedure, but also quality of taxonomy; in the Högklint Formation of Gotland, for example, many stromatoporoids are recrystallized (Mori 1969), reducing utility of the diversity index for that formation in comparison with others. Prosh and Stearn (1996, p. 14) recognized four groups of preservation of increasing degree of recrystallization, and noted that poorly preserved samples may be identifiable when compared with other specimens in a collection; this approach assists diversity measurements in partly altered material.

*Ludlow stromatoporoid reefs of Gotland, Sweden.* Text-figure 15 summarizes data from three well-exposed sites, to compare features of the stromatoporoid assemblages. Environmental and stromatoporoid parameters combined to produce dense accumulations of stromatoporoids in a limited range of growth forms.

*Devonian reef communities and barrier reefs.* Stromatoporoids are very abundant in Devonian reef systems, where *Amphipora* is the most abundant volumetrically (e.g. Cockbain 1984). Although



TEXT-FIG. 16. Parameters of reefs and their controlling factors. A, main features of bioherms and biostromes. B, array of controls on reefs, which interact to varying degrees. B4 relates to Silurian models.

Middle Devonian reefs contain the first interpreted barriers, of which the Canning Basin (Playford and Lowry 1966; Playford 1980) and western Canadian (e.g. Klovan 1964; Jamieson 1969) systems are best known, many lack an identifiable reef core (e.g. the Miette complex of Alberta, Noble 1970, p. 540; the south Belgium bioherms, Monty *et al.* 1982). Devonian reef crests typically contain relatively small numbers of stromatoporoids, with other elements, such as *Renalcis*, being equally or more important reef constructors. In the Canning Basin the crest zone is narrow, 100–200 m wide



(Wilson 1975, p. 137), shows no biozonation, while fore-reef slopes of up to 30° were generated by microbial constructors (Playford and Lowry 1966, p. 71) compared with 5° where reefs are not present on platform margins. Without microbes, stromatoporoids apparently could not resist the destructive energy on reef-crests, and it is likely that few of the Devonian reefs were actually effective barriers (see below).

Sporadic efforts in the integrated application of taxonomic and growth form data illustrate aspects of stromatoporoid community ecology (e.g. Cornet 1975; Hoggan 1975; Kobluk (1975) attempted a community reconstruction using crude statistical measures of association between growth forms and also between species, but his data could not relate species to forms and environments. He noted (p. 243) that some stromatoporoid morphologies occur together and others do not. Kobluk (1975, p. 259) extended life table analysis to stromatoporoids using basal diameter as a proxy for relative age. Data were time-averaged within a bed, growth forms rather crudely classified, and although species/growth form data were not available, the results produced the broad conclusion that most stromatoporoids are small, with a relatively low chance of growing large. This observation is consistent with studies in other sites and ages, presumably largely attributable to fluctuating energy levels and sediment deposition rates. One feature of stromatoporoids influenced by such processes is that because growth form changes as stromatoporoids grew, a form beginning as a laminar shape commonly changed into domical then sometimes bulbous, so it is important to plot growth form against size (e.g. basal diameter; see Kershaw 1990). If this can be related to taxa, then there is a much more useful data set available for the interpretation of controls on stromatoporoid growth form, although little of such information is available for the Devonian.

#### *Regional and global scale synecology and applications*

*Early patterns.* Stromatoporoids were significant marine colonizers even in the early stages of their evolution. Ordovician stromatoporoids were low latitude dwellers, in shallow subtidal platforms and island-arc settings, with migration of stocks along west-flowing currents from their possible North American origin (Webby 1980). Webby suggested the potential value of stromatoporoids in plate reconstructions because of their warm stenothermal character, and this character was retained throughout the Ordovician, Silurian and Devonian, with stromatoporoids subject to secular climatic fluctuations resulting in the late Ordovician and late Devonian declines. The very late Precambrian to late Ordovician warm phase was replaced by cooler global climates from the late Ordovician to Wenlock (Frakes *et al.* 1992), and a return to warm conditions in Wenlock to end-Devonian times facilitated the widespread growth of Silurian and Devonian stromatoporoids. The late Llandovery expansion of stromatoporoid faunas occurred in several sites, such as North America (Colin Stearn, pers. comm.) and South China.

*Silurian oceanography and reefs.* Stromatoporoid faunas and growth forms diversified in the Silurian, with enhanced niche exploration. Silurian palaeocommunities in relation to sea level change have been studied intensively (McKerrow 1979; Johnson *et al.* 1991); oceanographic aspects involve a CO<sub>2</sub>-controlled oceanic stratification model (Text-fig. 16), with reefs in clastic-starved oligotrophic seas (Hallock and Schlager 1986) during warm periods of salinity-stratified oceans with poorly oxygenated bottom waters (Secundo- or S-states of Jeppsson 1990; Aldridge *et al.* 1993; Jeppsson *et al.* 1995; see Text-fig. 16). Stromatoporoid-dominated reefs on Gotland can be related to this oceanic model; some reef chronology and form match both the Silurian eustatic curve of Johnson *et al.* (1991) and Jeppsson's (1990) P and S states (Watts 1988a; Riding and Watts 1991; Kershaw 1993; Kershaw and Keeling 1994).

Regionally and globally controlled changes in reef systems are likely to be environmental rather than ecological, so chronostratigraphical correlation of reefs during global sea level rise should be achievable (Copper 1988, p. 144), supported by the Jeppsson model. A general circulation model (GCM) of the global Wenlock ocean by Moore *et al.* (1993) suggested that the Wenlock was a time of high productivity in a generally stratified ocean, without ice caps. Continent asymmetry (Silurian and Devonian land was mainly in the southern hemisphere), with Gondwana stretching from poles

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to equator, may have prevented polar glaciation (Moore *et al.* 1993), assisting the maintenance of warm global conditions. This model predicts seasonality in the Wenlock, but CO<sub>2</sub>-controlled climatic fluctuation (Jeppsson 1990) was not identified by Moore *et al.*, and Jeppsson's model does not preclude ice caps.

*Stromatoporoids in Devonian global facies patterns.* Although reef facies may be difficult to unravel in tectonically complex terrains (Scrutton 1977b), Devonian reefs formed mostly at platform margins (e.g. Scrutton 1977a in UK; Playford 1980 for Canning basin). Significant build-ups worldwide contain similar fossil assemblages (e.g. Belgium, Eifel of Germany, Alberta, Canning Basin; Wilson 1975, p. 119), although whether this was the cause or result of widespread reef development remains unanswered. Stock (1990) recorded provincialism of earlier Devonian stromatoporoid faunas, changing to cosmopolitanism at genus level through the Frasnian, and restriction in the Famennian; Prosh and Stearn (1996) extended Devonian transgression across epeiric shelves. Rapid widespread migration also promotes the use of stromatoporoids as biostratigraphical tools (Prosh and Stearn 1996), in contrast to the traditional view that they are not sufficiently stratigraphically restricted. The lack of Devonian stromatoporoids in the eastern proto-Pacific ocean (South America) may be due to either adverse flow of the southern subtropical gyre, or higher clastic input from the South American hinterland (Stock 1990), whilst broad shifts of Devonian stromatoporoids in North America relate to climatic change (Stock 1995).

Stromatoporoid growth forms aid recognition of facies patterns in the Devonian Iberg reef in Germany (Gischler 1995); the patterns suggest influence of south-east trade winds, and provide interpretation of the reef as an atoll. Although Gischler (1995, p. 185) suggested that the south-east-facing (windward) portion containing 'massive' stromatoporoids and bulbous corals was wave-resistant, the reef rim itself is hardly preserved. Wave resistance in the constructor organisms of Devonian reefs was relatively low, so early cementation (Burchette 1981; Mountjoy and Riding 1981; Watts 1988b; Gischler 1995) and microbial stabilization were important features. Care is therefore required in interpreting wave resistance in Devonian reef systems; the analogy between modern coral reefs and their Devonian counterparts is not reliable. Kobluk's (1978) application of the Waltherian concept to the Miette reef near Jasper, Alberta, using statistically constrained stromatoporoid assemblages is affected by biostratigraphic disturbance of the reef biota, even locally (e.g. Fischbuch 1970), and reconstruction of the original assemblages is difficult.

*Stromatoporoid reefs and sea level change.* Stromatoporoid reefs are generally assumed to indicate shallow waters. While normally true for rimmed shelves and patch reef bioherms, conflict between ecological upward reef growth and sea level change to generate reef aggradation is not always solved, and controls on biostromes remain problematical. Stromatoporoids in sequence stratigraphical analysis of mid Devonian platform sedimentary rocks of the Great Basin, USA, suggest that biostromes could grow in both transgressive and regressive settings (Elrick 1996, p. 403), which adds to the debate outlined by Brunton and Copper (1994, p. 74) that reefs do not necessarily form in regressive regimes as is normally interpreted, but in transgressive regimes instead (cf. Brett 1995, p. 611). Whether possible third and fourth order cyclicity in the Silurian sedimentary rocks of the Appalachians (Goodman and Brett 1994) can be extended to carbonate sequences with stromatoporoid-dominated reefs in the light of advances in Silurian chronostratigraphy (Kleffner 1995), will depend on future chronostratigraphical refinements.

If stromatoporoid biostromes formed in transgressive (as well as regressive) settings, then water depth (= accommodation space) was presumably not crucial, so substrate was probably the key element in controlling their occurrence (with low sedimentation rate). Availability of suitable substrate also controlled individual stromatoporoid development, and because stromatoporoid substrate tolerance is so broad (discussed earlier), perhaps it is not surprising that biostromes provide the richest stromatoporoid faunas. Some stromatoporoid biostromes are demonstrably shallow, for example the Kopparsvik Formation, Wenlock of Gotland (Riding and Watts 1991); the c. 10 m water depth suggested for many European Devonian examples (Burchette 1981, p. 119);

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the 10–30 m water depth for the Late Llandovery of Michigan (Johnson and McKerrow 1991, p. 156) and the late Ordovician of South China (Johnson *et al.* 1989, p. 47). In contrast, coral-dominated Silurian biostromes formed in deeper water prior to shallowing (Desrochers and Bourque 1989), and stromatoporoids and corals aided stabilization of steep off-reef slopes in the early Silurian biostromes of Greenland during pauses in subsidence (Sønderholm and Harland 1989, p. 361), further illustrating that conditions of stability favoured biostromal growth. Nestor (1995) also noted that stable environments promoted the development of flattened lenticular bioherms and biostromes in Baltica, as in the Devonian biostromes in Belgium (Tsien 1974). There is much work to do here, because although some reefs apparently formed in regressive settings, others present conflicting data. The middle Ludlow biostromes of south-east Gotland have been regarded as exhibiting shallow water characters (low amount of mud, abundant grainstones, abundant syntaxial cement on crinoid grains, eroded biostrome tops, stacked rocky shorelines; Keeling and Kershaw 1994). However, these biostromes contain almost no algae, otherwise common in shallow Silurian facies; that they may have grown in *deepening* water on flooding surfaces, and acquired their shallow water features during later regression, is supported by the recognition of an oceanic S-state during this interval (Lennart Jeppsson, pers. comm.), one feature of which is slightly higher sea level (Text-fig. 16). Clearly, no reliance can be placed on biostromes as general indicators of regressive systems. Whether stromatoporoid-rich deposits can be related to suggestions of orbitally forced sea level change for the Givetian and Frasnian (e.g. Marshall *et al.* 1996, p. 461) awaits further work.

*Effect of the Frasnian/Famennian (F/F) extinction event on stromatoporoids.* To conclude this review, the near-demise of Palaeozoic stromatoporoids is considered. Although Cockbain (1989) noted a reduction from 32 Frasnian genera to 20 in the Famennian, stromatoporoids continued reef-building (Stearn 1987), and the largely Ordovician labechiid group resurged (Stearn 1988), having played only a minor rôle in the Silurian and Devonian. Estimates of taxa reduction are based on species numbers only. Copper (1994a, 1994b) catalogued stress features of reefs and Copper (1986) suggested that cold water was diverted into equatorial regions as Laurussia and Africa sutured, to cause the F/F event. The equatorial position of stromatoporoids is unchanged from the Frasnian to the Famennian. Fagerstrom (1994) noted changes from constructor-binder-baffle guilds in the Frasnian to binder guild facies in the Famennian, because of removal of some growth forms during the F/F event. Wilder (1994) suggested that reefs in the Eifel and Ardennes areas, which grew so well during the clastic-starved episode of Givetian reef-building, declined under high nutrient inputs from the Old Red Continent as humidity and runoff increased later in the Frasnian. He suggested that the dendroid forms survived better than 'massive' stromatoporoids because they could shed sediment more easily, although proof of that will be difficult to obtain. There is recent evidence of an extraterrestrial impact (Warne and Sandberg 1996) early in the Frasnian, but this appears not to have affected the stromatoporoids.

#### SUMMARY

1. Stromatoporoids have been used qualitatively as powerful palaeoenvironmental indicators in numerous studies since the 1950s, but they retain much potential, awaiting more *detailed* studies; systematic data collection has been done in few cases. Studies would be enhanced by a more rigorous data set, promoting use of diversity measurements, using compatible data collection methods. The use of *random* (not haphazard) collection techniques could help to provide comparable data sets, but is rarely possible in exposure.
  2. Integrated studies of growth form, morphospecies and facies will enhance the utility of stromatoporoids; all these aspects are needed to obtain the maximum amount of palaeobiological information.
  3. Currently applied stromatoporoid growth form terminology continues to contain imprecise and inappropriate terms. A hierarchical scheme solves most problems, and is presented for scrutiny.
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4. Application of stromatoporoids in facies analysis draws on their sessile benthic habit, and ability to record processes affecting the sea bed. Their autecology underpins regional and global considerations of stromatoporoid-rich deposits. Work on growth rates and possible photosensitivity of stromatoporoids may enhance understanding of the growth control factors.

5. At regional and global scales of investigation, the traditional view that reefs grew in shallower phases, largely consistent with sea level falls, is being challenged. Stromatoporoid reefs may have responded to oceanic water changes, based on CO<sub>2</sub>-driven climatic changes. There is an exciting opportunity to examine stromatoporoid-rich deposits in the light of these developments, to aid integrated study of regional and global changes, and assist future interpretations of stromatoporoid growth form, and their enclosing facies.

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