

SPICULE PSEUDOMORPHS IN A NEW PALAEOZOIC CHAETETID, AND ITS SCLEROSPONGE AFFINITIES

by DAVID I. GRAY

ABSTRACT. A Palaeozoic chaetetid, bearing intramural spicule pseudomorphs, *Chaetetes (Boswellia) mortoni* sp. nov., is described from the British Dinantian. Spicules are preserved as calcite, pyrite, and silica pseudomorphs. Only silica pseudomorphs retain detail of their tylostyle form. Neomorphism locally obliterates the spicular fabric. A primary mineralogy is suggested consisting of an aragonitic calcareous skeleton, with entrapped opal 'A' spicules. Comparison of morphology and microstructure with extant and fossil sclerosponges indicates a close relationship between this chaetetid and the Ceratoporellida, and supports the sclerosponge nature of some Palaeozoic chaetetids.

THE Class Sclerospongiae Hartman and Goreau, 1972, was proposed following the rediscovery of coralline sponges among the Jamaican coral-reef ahermatypic cryptofauna (Hartman 1969; Hartman and Goreau 1970). Sclerosponges were defined by Hartman and Goreau (1972, p. 144) as 'sponges secreting a compound skeleton of siliceous spicules, proteinaceous fibres and calcium carbonate, the latter laid down as a basal mass in which the siliceous spicules may or may not be entrapped'. The similarity of fossil chaetetids to some sclerosponges (briefly discussed by Kirkpatrick (1909, 1912a, 1912b) along with the monticuliporans), led Hartman and Goreau (1972) to remove the Chaetetida Okulitch, 1936, from the Anthozoa or Hydrozoa to the Sclerospongiae. They also erected the Order Ceratoporellida Hartman and Goreau, 1972, to include four extant sclerosponge genera, and added a third Order, the Tabulospongida Hartman and Goreau, 1975, following the discovery of a tabula-bearing form from the Pacific (Hartman and Goreau 1975), of which two more extant species have subsequently been described (Mori 1976, 1977) and a record traced back into the Mesozoic. Stearn (1972, 1975) discussed the sclerosponge affinities of the stromatoporoids.

The recognition of the Sclerospongiae as a Class has been questioned by a number of authors. Lévi (1973) considered the sclerosponges as a Subclass of the Demospongiae, subsequently followed by Vacelet, Vasseur, and Lévi (1976) and Vacelet (1977). This classification takes into account the organization of living sclerosponge tissue which is 'basically similar to that of the Class Demospongiae except that it is divided into units each of which extends down into the upper layer of the basal calcareous skeleton' (Hartman and Goreau 1972, pp. 144-145).

The variability in spicule form and distribution (see Table 1) suggests that some sclerosponges may be related even more closely to other groups of demosponges. For example, Vacelet (1977, p. 347) mentions that the spicule character of *Tabulospongia wellsii* is similar to that displayed by the Spirastrellidae. Vacelet (1977, p. 347) also states that a basal calcareous skeleton may be a convergent structure in many groups of demosponges. This would account for the great variability of calcareous skeletal morphology and microstructure (see Table 1) observed in those forms classified as sclerosponges, and would imply that 'sclerosponge' is a convenience term for considering groups with a similar homeomorphic tendency.

In this paper the sclerosponges are considered as a Subclass of the Class Demospongiae Sollas, 1875.

The fossil history of sclerosponges that entrap spicules in their calcareous skeleton is represented by a limited assortment of forms including a few ceratoporellids, one species (Każmierczak 1974) of

the Order Muranida Kaźmierczak and Hillmer, 1974, a few problematical records of stromatoporoids and, until now, only two species of Mesozoic chaetetids. Table 1 summarizes their distribution and variation and allows comparisons to be made with extant forms.

Chaetetids are a diverse group with separate Palaeozoic and Mesozoic histories. Differences exist in the skeletal architecture of Palaeozoic and Mesozoic forms (Fischer 1970), and their phylogenetic relationships are not completely understood. Scrutton (1979, p. 169) reviewed briefly their relationships, and whilst supporting their sclerosponge affinities he emphasized the lack of convincing spicules associated with chaetetids as 'a major source of doubt for some workers' to their classification within the Porifera. Dieci, Russo, Russo, and Marchi (1977) were the first to report a spicule-bearing 'chaetetid', *Atrochaetetes medius* Cuif and Fischer, 1974, from the Upper Triassic of Italy, with intramural acanthostyle spicules, replaced by calcite. *Atrochaetetes* Cuif and Fischer, 1974, is characterized by a discontinuous backfill of fascicular fibrous carbonate extending into the lumen (Cuif and Fischer, 1974, p. 8) rather than complete tabulae typical of the chaetetids *s.s.* Continuous fascicular fibrous backfills are typical of ceratoporellids (see below). Since *A. medius* also has a ceratoporellid-like spicular fabric, the genus *Atrochaetetes* should be regarded as an aberrant member of the Ceratoporellida, and removed from the Chaetetida.

Kaźmierczak (1979) reported intramural monaxon spicules, replaced by pyrite, within a Lower Cretaceous (Barremian) chaetetid, *Chaetetopsis favrei* (Deninger 1906) from the Crimea. Like many Mesozoic chaetetids, *C. favrei* increases both by intramural offset and longitudinal (pseudoseptal) fission. The former is not known to occur in Palaeozoic chaetetids (Sokolov 1962, p. 262). The walls of *C. favrei* are anhedral calcite miscospar that is possibly a neomorphic overprint (Kaźmierczak 1979, p. 101), and is dissimilar from the typical fascicular fibrous microstructure of Palaeozoic chaetetids.

This is the first report of convincing intramural spicule pseudomorphs in a Palaeozoic chaetetid, *Chaetetes (Boswellia) mortoni* sp. nov., from the Lower Carboniferous of north Wales, northern England, and southern Scotland. Comparison is made with other chaetetids and sclerosponges, and a model is developed for the mode of spicule preservation. Classification of the Chaetetida within the Sclerospongidea is supported.

OCCURRENCE AND PRESERVATION OF MATERIAL

Eight colonies of this new species have recently been collected from the Lower Asbian (Upper Dinantian), Tynant Limestone (Somerville, 1979) (Lower Brown Limestone of Morton, 1879) of the Llangollen area, north Wales. Although this sclerosponge is a rare element in the brachiopod-dominated macrofauna, it has been collected from a 20-m range of cyclic strata at sites over 4 km of outcrop, and from the underlying scree. It occurs towards minor cycle bases, in subtidally deposited argillaceous algal-foraminiferal packstones and grainstones. The colonies were rolled and some were fragmented prior to burial. One colony has a pronounced micritic (?endolithic algal) rim on part of its

TABLE 1. Table of extant and fossil sclerosponges with associated spicules showing their spicule form and relationship to the basal calcareous skeleton. Mesozoic stromatoporoids of Schnorf (1960) and Yabe and Sugiyama (1935) are omitted owing to their uncertain spicular nature. Species of *Leiospongia* d'Orbigny, 1850, and *Hartmanina* Dieci *et al.* 1974, described by Dieci, Russo, and Russo (1974b) are omitted owing to the absence of associated spicules.

Order symbols, Cer = Ceratoporellida, Tab = Tabulospongida, Unas = Unassigned, Mur = Muranida, Ch = Chaetetida, Stp = Stromatoporoidea; calcareous microstructure symbols, Fascic. fib. = fascicular fibrous, Agg. spher. = aggregated spherules, Microgran. = microgranular; original mineralogy symbols, A = aragonite, Mg-cc. = high magnesian-calcite; spicule distribution symbols, I. = intramural, E. = extramural, m. = subparallel to microstructure fibres, s. = subparallel to growth axis of skeleton, d. = embedded only within the distal portion of the calcareous skeleton, r. = random; spicule type symbols, * = megasclere, ** = microsclere; spicule mineralogy symbols, cc. = calcite, pyr. = pyrite, Fe ox. = iron oxide.

AGE	ORDER	SCLEROSPONGE	SOURCE OF DATA	CALCAREOUS SKELETON		S P I C U L E		PRESENT MINERALOGY	
				MICRO-STRUCTURE	ORIGINAL MINERALOGY	DISTRIBUTION	TYPE		SIZE RANGE Length (µm)
MESOZOIC	Cer	<i>Ceratoporella nicholsoni</i>	Hartman & Goreau 1970	Fascic.fib.	A	I.m.	Acanthostyle*	206 - 298 3.1 - 4.0 Opal 'A'	
		<i>Stromatospongia vermicola</i>	"	"	"	"	"	"	165 - 187 6.2 - 8.0 "
		<i>Stromatospongia norae</i>	"	"	"	"	"	"	195 - 215 5.5 - 6.1 "
		<i>Hispidopetra miniana</i>	"	"	"	"	"	Style*	269 - 301 5.4 - 7.4 "
		<i>Goreauiella auriculata</i>	"	"	"	"	"	Acanthostromylole*	60 - 68 2.3 - 2.7 "
		<i>Tabulospongia wellsi</i>	Hartman & Goreau 1975	Stacked lamellar	Mg-cc	E.	"	Tylostyle* Spiraster**	C.290 C.3.5 Highly variable "
		<i>Tabulospongia horiguchii</i>	Mori 1976	"	"	"	"	Fusiform oxea* Sphaeraster form**	300 - 350 5.7 - 14.0 "
		<i>Tabulospongia japonica</i>	Mori 1977	"	"	"	"	Dichotriaene*	300 - 355 140 - 190 "
		<i>Merlia normani</i>	Kirkpatrick 1909	Fascic.fib.	A	"	"	Tylostyle* Clavidisc** Raphide**	C.140 C.45 C.30 slender "
		<i>Merlia</i> sp.	Hartman & Goreau 1970	"	"	"	"	Tylostyle* Clavidisc**	160 1.8 26 "
PALAEOZOIC	Cer	<i>Astroclera willeyana</i>	Kirkpatrick 1910	Agg.spher.	"	"	Acanthostyle*	C.70 C.8 "	
		<i>Murania lefeldi</i>	Kazmierczak 1974	Microgran. & fib.	?	I.m.	Style or Acanthostyle*	200 30 cc.	
		<i>Chaetopsis favrei</i>	Kazmierczak 1979	Microgran.	?	I.S.	"	C.400 C.28 pyr.	
		<i>Neuropora pustulosa</i>	Kazmierczak & Hillmer 1974	Fibro-normal	?A	"	?Acanthostyle*	128 - 141 6.6 - 7.6 cc.	
		<i>Ptychochaetetes</i> sp.	Termier & Termier 1976	"Lepidoporoïd" (Scaly,porous)	?	I.d.	Monaxon*	?90 ?10 Fe ox.	
		<i>Kericoeelia conica</i>	Dieci et al. 1977	Fascic.fib.	?	I.m.	Style*	190 ± 40 5.2 ± 1.8 cc.	
		<i>Meandripetra zardini</i>	"	"	?	"	"	390 ± 140 27 ± 7 pyr.	
		<i>Scleroeelia hispida</i>	"	"	?	"	Acanthostyle*	61 ± 16 2.3 ± 0.7 cc.	
		<i>Scleroeelia fasciculata</i>	"	"	?	"	"	43 ± 12 2.3 ± 0.7 cc.	
		<i>Atrochaetetes medius</i>	"	"	?	"	"	74 ± 20 3.9 ± 0.9 cc.	
PALAEOZOIC	Dev	<i>Parallelopora mira</i>	Newell 1935	Granular	?	I.S.	?Monaxon* (?Microcleres transverse to megascleres)	C.250 C.10 "	
		<i>Chaetetes (Boswellia) mortoni</i> sp.nov.	This paper	Fascic.fib.	?A	I.m.	Tylostyle* Raphide**	275 ± 50 6.9 ± 0.9 Silica;cc.; C.70 C.3 pyr.	
		<i>Stromatopora centrotrium</i>	Twitchell 1929	?	?	I.r.	"Spinose rod**	C.100 C.7 cc.	

surface (Pl. 102, fig. 6). These colonies are calcitic, with a variable degree of microstructure alteration and compaction distortion. Spicule pseudomorphs have been observed in five of these colonies.

Comparison with material in the British Museum (Natural History) (repository prefix BMNH), Royal Scottish Museum (repository prefix R.S.M.) and Merseyside County Museum (repository prefix LIV.C.M.), led to the discovery of a further five spicule-bearing specimens of the same species. Two of these are partly silicified with intramural spicules locally replaced by silica.

SYSTEMATIC PALAEOLOGY

- Class DEMOSPONGIAE Sollas, 1875
 Sub-Class SCLEROSPONGIDEA Hartman and Goreau, 1972
 Order CHAETETIDA Okulitch, 1936
 Family CHAETETIDAE Milne-Edwards and Haime, 1850
 Subfamily CHAETETINAE Milne-Edwards and Haime, 1850
 Genus CHAETETES Fischer von Waldheim, 1830
 Subgenus BOSWELLIA Sokolov, 1939

Type species. *Chaetetes (Boswellia) boswelli* Heritsch, 1932, 'Upper *Dibunophyllum* Zone (D₂)' of Ivovik, Serbia, U.S.S.R.

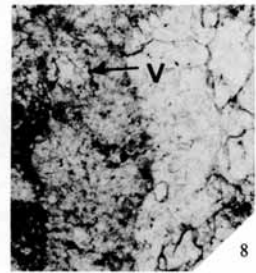
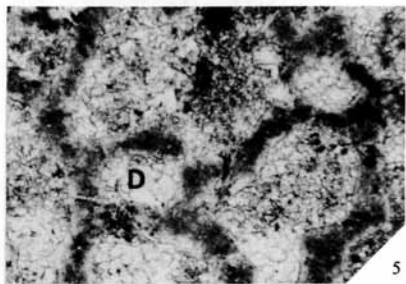
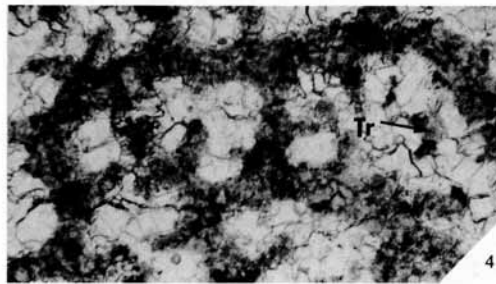
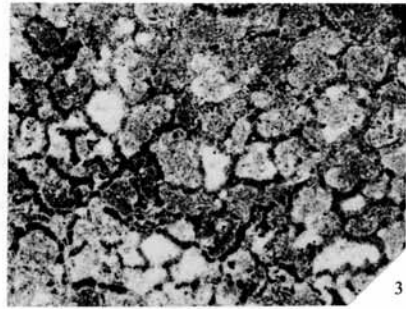
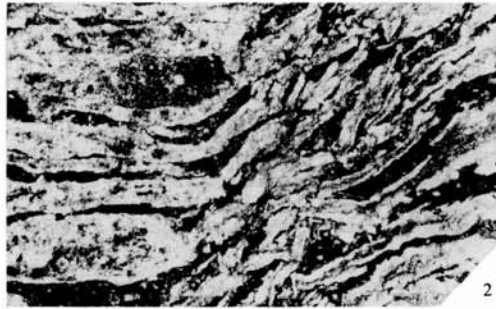
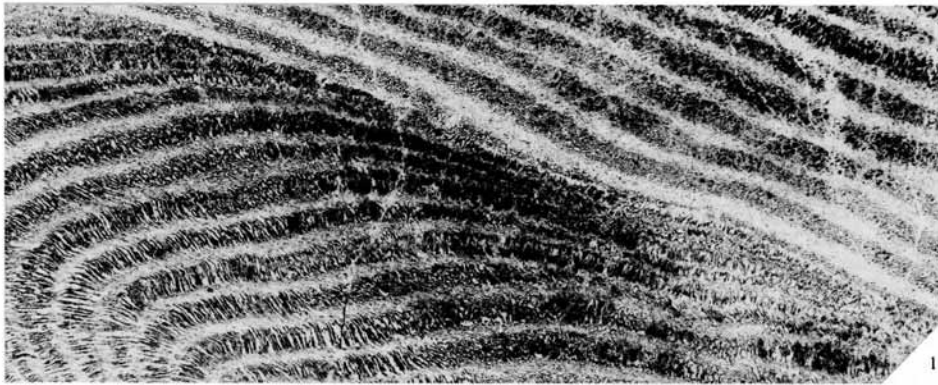
Diagnosis. Chaetetids with thickened irregular walls and rounded corners to lumina that may be either irregular or subpolygonal. Increase by pseudoseptal and basal fission. Incomplete fission and separation of pseudosepta into isolated columns occurs locally. Fascicular fibrous walls. Complete tabulae, variable in distribution. Intramural spicules (originally siliceous) present in some.

Remarks. Palaeozoic chaetetids have been subdivided generically on gross calicle morphology (Sokolov 1939, 1962). Sokolov (1939, p. 411) erected the subgenus *Chaetetes (Boswellia)* to include chaetetids with 'thickened irregular' calicle walls and 'undulate rounded' lumina, also stating that *C. (Boswellia)* 'occupies an intermediate position between . . .' *Chaetetes* and the meandrine genus *Chaetipora* Struve, 1898. Species of *C. (Boswellia)* show this intermediate relationship very clearly, from the more prismatic thick-walled *C. (B.) uniformis*, Spiro 1961, and *C. (B.) heritschi* Sokolov, 1950, to the irregular calicles of *C. (B.) torquis* Spiro, 1961, which is very similar to some of the less meandrine chaetiporinids, e.g. *Chaetipora agonia* Sokolov, 1950. Although this classification is accepted provisionally here the division of the Chaetetidae at a generic level requires further clarification, that must now be based on an understanding of poriferan growth and variation.

EXPLANATION OF PLATE 102

Chaetetes (Boswellia) mortoni sp. nov., Lower Asbian (Lower Carboniferous, Eglwyseg Escarpment, Llangollen (Clwyd, North Wales).

- Fig. 1. Paratype BMNH R49965. Compaction-fractured colony with laminar overgrowth. Negative of longitudinal section, $\times 2.3$.
 Fig. 2. Detail of a compaction-fractured thin-wall growth zone, BMNH R44965. Longitudinal section, $\times 45$.
 Fig. 3. Holotype BMNH R49964. Transverse section illustrating the subpolygonal to slightly irregular calicle pattern, $\times 12$.
 Fig. 4. Transverse section illustrating an irregular calicle pattern, with many pseudosepta, scalloped margins to lumina, and isolated trabecular column (Tr), BMNH R49965, $\times 35$.
 Fig. 5. Transverse section illustrating pseudoseptal fission in the corner of a calicle, BMNH R49964, $\times 40$ (D = Daughter calicle).
 Fig. 6. Transverse section illustrating mosaic neomorphic fabric to calicle walls with a micritic rim. Outer margin of BMNH R49964, $\times 70$.
 Fig. 7. Fractured tabula extending into lumen, longitudinal section, BMNH R49964, $\times 150$.
 Fig. 8. Sub-spherical 'vacuole' (V) within the calicle wall of BMNH R50133, $\times 100$.



GRAY, Palaeozoic chaetetid

Chaetetes (Boswellia) mortoni sp. nov.

Plates 102, 103; text figs. 1–4; Table 2

Derivation of species name. After G. H. Morton who devoted many years of research to the Carboniferous of north Wales in the latter part of the nineteenth century.

Holotype. BMNH R49964, Tynant Limestone (Lower Asbian), quarried face, 400 m north of Tynant Ravine, 4 km north of Llangollen, Clwyd (National Grid Ref. SJ 21964573)

Paratypes. BMNH R4429 (Morton Collection), Lower Brown Limestone (in part equivalent to Tynant Limestone), Llangollen, Clwyd (partly silicified); BMNH R49965, Tynant Limestone (Lower Asbian), quarried face 500 m north of Tynant Ravine (SJ 21974582).

Other material. BMNH R50134, Tynant Limestone (Lower Asbian), World's End, 6 km north of Llangollen, Clwyd (SJ 23314789); BMNH R50133, BMNH R50135, and BMNH R50136 loose on scree slopes near Tynant Ravine, near the base of the Eglwyseg escarpment; BMNH R50188 and BMNH R50189, Tynant Limestone, 300 m north of Llwyn Hên-parc Gulley, Eglwyseg escarpment (SJ 22152638); LIV.C.M. 1974. 57, Eglwyseg Escarpment, Llangollen (in scree, partly silicified); BMNH R45851, Lower Carboniferous, Ravenstonedale, Cumbria; BMNH R46144, J. S. Baker Collection, Carboniferous Limestone (Blue Quarries), Ashfell Edge, Ravenstonedale, Cumbria; R.S.M. 1967.66.86–89 Nicholson Collection (thin sections only; all probably from one colony), Carboniferous Limestone, Archer Beck, Dumfriesshire.

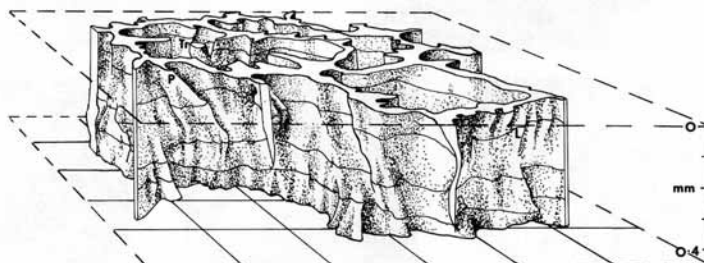
Range. ?Holkierian (BMNH R46144 from ?Ashfell Limestone) to Lower Asbian.

Diagnosis. *Chaetetes (Boswellia)* with irregular to subpolygonal (intracolony variable) calicles. Fascicular fibrous walls with pseudosepta and irregular longitudinal ridges. Isolated pseudoseptal columns locally. Lumen diameter av. c. 500 μm ; wall thickness av. c. 110 μm . Intramural spicules (monaxon tylostyle megascleres) subparallel the fibres, diverging distally, with their pointed (oxeote) ends directed distally. Spicule diameter c. 7 μm ; spicule length variable c. 275 μm in well-preserved specimens. Tabulae well spaced. Basal and pseudoseptal fission only.

Description

Colony form. The colonies are laminar or bulbous, rarely greater than 12 cm diameter by 8 cm high. They display distinct growth bands in rhythms 2 to 5 mm thick, with zones of thinner calicle walls preferentially compaction fractured (Pl. 102, figs. 1, 2). On weathered and polished surfaces the thick-wall bands stand prominent, being a paler shade of brown-grey than the compaction fractured zones. Neither epitheca, astrorhizae, nor surface mamelons have been observed on any colony.

Calicle morphology. The calicles are irregular to subpolygonal (Pl. 102, figs. 3, 4), with the mean diameter of more polygonal lumina between 420 μm and 535 μm (see Table 2). The walls vary greatly in mean thickness, from c. 90 μm to c. 140 μm (measurements taken between ridges and pseudosepta). Pseudosepta are common, occasionally separating from the calicle walls as isolated columns. Both pseudosepta and ridges (undeveloped pseudosepta) longitudinally ornament the calicle walls (text-fig. 1) imparting a scalloped appearance to the lumina in



TEXT-FIG. 1. Block diagram of *Chaetetes (Boswellia) mortoni* sp. nov. to illustrate the development of longitudinal ridges (L), pseudosepta (P), and isolated trabecular columns (Tr) off the calicle walls. Diagram constructed from serial acetate peels of BMNH R50133.

transverse section (Pl. 102, fig. 4). Increase is by both pseudoseptal and basal fission. Pseudoseptal fission commonly occurs in calicle corners (Pl. 102, fig. 5). Incomplete pseudoseptal fission locally forms an irregular calicle pattern. Tabulae are rarely visible, appearing well spaced (≤ 2 per mm), although this may in part be due to the degree of compaction fracture (Pl. 102, fig. 7).

Microstructure. The walls are fascicular fibrous penicillate calcite or chalcedonic silica, with a brown 'dusty' appearance in thin section due to submicroscopic to micrometre-sized inclusions of ?organic material. In the calcitic specimens these inclusions vaguely define the wall fibres and cause a variable pseudopleochroism (between paler and darker brown) cf. Hudson (1962). One specimen, BMNH R50133 has rare subspherical 'vacuoles', c. 50- μm diameter, within the calicle walls, of uncertain origin (Pl. 102, fig. 8). Neomorphism has destroyed details of the microstructure to varying degrees (Pl. 102, fig. 6; text-fig. 5), resulting in inclusion-poor areas lacking spicule relicts (especially the thin-wall growth bands). The walls rarely show a coarser fibrous fabric, with each fibre surrounded by thin brown pellicles that are probably the remnants of the ?organic inclusions.

Spicule form. In the calcitic specimens, spicule pseudomorphs occur within the walls subparallel to the fascicular fibres, diverging distally as straight or slightly curved elongate rods of clearer, inclusion-deficient calcite (Pl. 103, fig. 3) up to 300 μm long. In transverse section they appear as clear calcite circles or ellipses with a range of mean diameters between 6.6 μm and 8.2 μm (Pl. 103, fig. 4). Rarely they may exceed 20 μm diameter. Although surface detail is not visible on these pseudomorphs, their clarity varies from prominent to indistinct, reflecting variation in neomorphism. Rarely the spicules may be preserved as pyrite pseudomorphs with aggregates of pyrite crystals along their length (text-fig. 4c), similar to those described by Kaźmierczak (1979). In contrast some calicles of BMNH R4429 and LIV.C.M. 1974.57 are partially replaced by chalcedonic silica (Pl. 103, figs. 1, 2), with perfect intramural silica spicule pseudomorphs occurring adjacent to more vague calcitic ones. These pseudomorphs are low-relief colourless to high-relief red-brown translucent tylostyles, with circular cross-sections (Pl. 103, fig. 6), distinct bosses at their proximal ends and distally tapering points (Pl. 103, figs. 2, 8, 9, 10). As with the totally calcitic specimens these spicules diverge distally in the calicle walls (Pl. 103, fig. 2), subparalleling the fascicular fibres, but occasionally cross-cutting the wall-fibre trend at a high angle. Fossilized early corrosion features are seen on many spicule pseudomorphs (Pl. 103, figs. 7, 8, 10, 11).

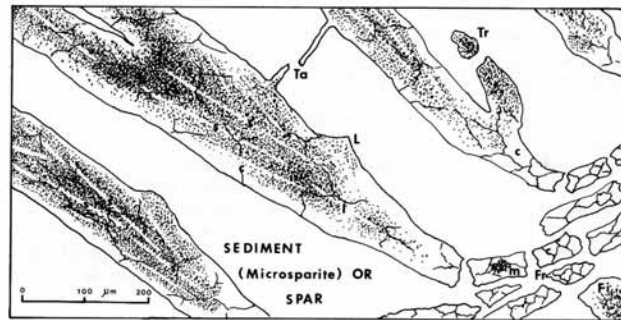
Seldom, and within BMNH R4429 only, ?raphide microsclere pseudomorphs occur (Pl. 103, fig. 7), as thin rods, pointed at both ends, c. 70 μm by 3 μm . These are only discernible in the chalcedonic regions, and would be too small to distinguish within the microstructure of calcitic calicle walls.

Spicule distribution. Spicule pseudomorphs have a variable distribution within the colonies. In the calcitic specimens they are only discernible within some of the ?organic-inclusion-rich areas associated with the less-fractured thick-wall growth bands where neomorphism has most perfectly replaced the primary fabric (see text-fig. 2). Specimens BMNH R4429 and LIV.C.M. 1974.57 also have a variable spicule distribution (see text-fig. 3) dependent on the replacement mineralogy. In BMNH R4429 totally and partly calcitic calicles rarely have visible calcitic spicule pseudomorphs. Here the microstructure is masked by a dense inclusion distribution. Siliceous spicules occur where the outer zone of these calicle walls is silicified. Only two growth bands are completely silicified (text-fig. 3), in which the best examples of a dense spicule distribution are visible (Pl. 103, figs. 1, 2).

TABLE 2. Variation in calicle and spicule size in six specimens of *Chaetetes (Boswellia) mortoni*

SPECIMEN	Average lumen diameter in μm			Average wall thickness in μm			Average spicule length in μm			Average spicule width in μm		
	mean	s.d.	n.	mean	s.d.	n.	mean	s.d.	n.	mean	s.d.	n.
*BMNH R49964	455	130	15	115	35	15	170	70	12	6.6	1.0	20
**BMNH R4429	420	140	10	94	29	10	275	50	10	6.9	0.9	10
**BMNH R49965	485	160	25	130	40	50	155	45	15	7.5	4.0	50
BMNH R50133	520	150	15	117	23	12	154	65	10	7.2	1.8	15
BMNH R50134	423	140	10	141	34	10	207	60	10	8.2	1.1	10
BMNH R50135	535	110	10	116	28	15	(Strongly neomorphosed microstructure)					

* = Holotype; ** = Paratype; s.d. = standard deviation; n. = sample number.



TEXT-FIG. 2. Sketch showing the relationships of the microstructural fabrics in calcitic specimens of *Chaetetes (Boswellia) mortoni* sp. nov. in longitudinal section. Symbols: Ta = fractured tabula; Tr = isolated trabecular column; L = longitudinal ridge or pseudoseptum; s = calcitic spicule pseudomorph; Fr = fracture zone of thin-wall growth bands; I = transition from ?organic-inclusion-dense thick-wall bands to inclusion-poor compaction-fractured zone; c = neomorphic crystal mosaic, with varying degrees of undulose and sweeping extinction often not discernible in the ?organic-inclusion poor regions; m = localized neomorphic fabric of vaguely fibrous microspar-size crystals, with thin brown pelicles.

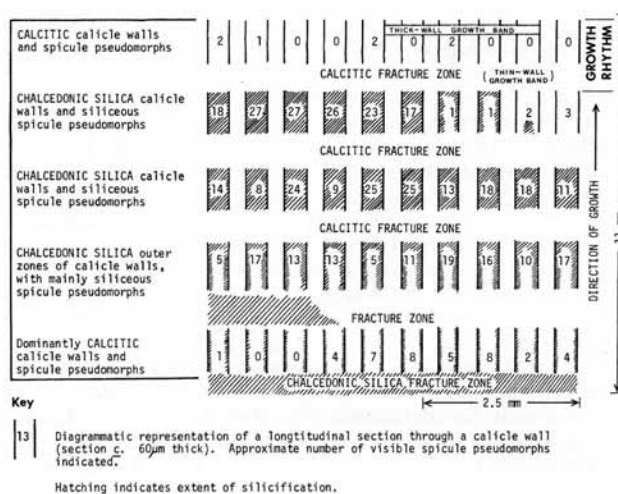
Discussion

The over-all similarity in colony, calicle, and microstructure form confirm that the calcitic and siliceous specimens are conspecific (see Table 2).

Species of *Chaetetes* are poorly defined. The size and degree of variation in calicle form, wall thickness, and tabula density are used as species-dependent characters. Many or all of these characters may, however, be controlled by environmental influences (e.g. Weyer 1967), and therefore where possible care must be taken to sample as large a population as possible. Variation within the specimens of *C. (B.) mortoni* described here is mostly intracolony. Some similarities exist between this and previously described species. The calicle morphology is locally (Pl. 102, fig. 3) similar to *C. (B.) uniformis* Spiro, 1961 from the 'Visean' of the Moscow region, but differs by having a higher density of pseudosepta and slightly smaller calicles. Other closely comparable species are *C. (B.) torquis* Spiro, 1961, a densely tabulate form that displays many ridge swellings on its calicle walls (Spiro 1961, pl. 3, fig. 1a) in a similar manner to *C. (B.) mortoni*, *Chaetetipora agonia* Sokolov, 1950 and the larger-calicled *C. dubjanskyi* Sokolov, 1950. The latter two both show pseudoseptal fission in calicle corners (Sokolov 1950, pl. 15), but differ from *Chaetetes (B.) mortoni* with their indistinctly meandrine form and dense tabula distribution. Compaction-fracture of *C. (B.) mortoni* colonies, however, imparts a superficial meandrine calicle pattern which may obscure the true calicle shape.

Chaetetipora etheridgeii (Thomson, 1881) is a variably meandrine species, characterized by a variable calicle shape, some arranged in 'sub-stellate groups radiating irregularly around a large central . . .' calicle (Thomson 1881, p. 208). It is densely tabulate, with calicles commonly from 0.5 to 2.0 mm diameter, and with thin calicle walls. *Chaetetes (B.) mortoni* may be readily distinguished from this chaetetid by its lack of sub-stellate calicle-groups and its rare tabulae.

Whether the presence of intramural spicule pseudomorphs is a species-dependent factor is open to question. Extant sclerosponges have growth-variable spicule distributions (Hartman and Goreau 1972, p. 213) and Stearn (1972), remarked on a whole population of the extant *Astrosclera* Lister, 1900 (unassigned sclerosponge), from the Pacific without spicules. The problem is further complicated by the variable preservation of the spicules as pseudomorphs. In three calcitic specimens



TEXT-FIG. 3. Schematic diagram illustrating the spicule distribution within the calicle walls of the partly silicified BMNH R4429. Note that the higher numbers of visible spicule pseudomorphs per section of calicle wall occur in the chalcedonic silica zones, which are themselves in part controlled by the growth and fracture banding within the colony.

of *C. (B.) mortoni* they are undetected (BMNH R50135, BMNH R50136, and BMNH R50189). Therefore, although the spicular character is of great significance in understanding the phylogeny and histology of chaetetids, it must only be used with caution as a specific character in fossil forms.

MINERALOGY AND DIAGENESIS OF *C. (B.) MORTONI*

Basal calcareous skeleton. Extant sclerosponges secrete both aragonite (e.g. ceratoporellids) and high-magnesian calcite (e.g. tabulosponges) in their basal skeletons. Both are possible original mineralogies for Palaeozoic chaetetids. Fossil ceratoporellids (Viezer and Wendt 1976), probable sclerosponges (Dieci, Russo, and Russo 1974a), and stromatoporoids (Wendt 1975), that have retained their original aragonitic mineralogy, and have suffered little diagenetic alteration (Scherer 1977), have all been recorded from the Upper Triassic.

The *in situ* transformation of aragonite to calcite (Bathurst 1964; Dodd 1966), observed in Pleistocene scleractinian corals and molluscs (James 1974; Pingitore 1976; Wardlaw, Oldershaw, and Stout 1978), produces a secondary fabric which retains some detail of the primary microstructure. This transformation apparently occurs via a thin solution film less than 15 nm wide (Wardlaw *et al.* 1978, p. 1864) or a chalky solution zone (James 1974; Pingitore 1976). In this polymorphic transformation, relict detail of microstructure is defined by organic, and rarely aragonite, inclusions enclosed within a coarse mosaic of brown neomorphic calcite. Each of these coarse mosaic crystals exhibits straight (James 1974, p. 793) or undulose (Schneidermann, Sandberg, and Wunder, 1972, p. 88) extinction under crossed polars.

The transformation of high to low-magnesian calcite involves a paramorphic incongruent dissolution process (Plummer and Mackenzie 1974, p. 79). Fine detail is preserved in skeletal components during this transformation (e.g. Towe and Hemleben 1976), although ultrastructural changes may be noted (e.g. Sandberg 1975). In comparison, Lohmann and Meyers (1977, p. 1086) described milky skeletal calcite rich in microdolomite inclusions as evidence of an original

high-magnesian calcite mineralogy, apparently caused by an 'incongruent dissolution or solid-stage exsolution' process re-equilibrating the magnesium within coarse crystals that acted as closed or semi-closed systems (Meyers and Lohmann 1978) during the mineralogical transformation. Richter and Fuchtbauer (1978) used the preservation of primary structures by ferroan calcite as a criterion for recognition of primary, high-magnesian calcite.

In calcitic specimens of *C. (B.) mortoni* a relationship between the crystal form and ?organic-inclusion distribution is observed. The paler-brown calicle walls of specimens with less included material comprise 50 μm to 300 μm mosaic crystals with irregular margins, and either straight or slightly undulose extinction under crossed-polars. Most inclusion-rich areas have sweeping or undulose extinction and some lack a crystal mosaic. Often the wall crystals are continuous with the clear lumen-filling spar. No distinct wall-fibre boundaries are visible but vague fibre boundaries are defined by trains of inclusions. Similarly, the margins of calcitic spicule pseudomorphs are indistinct and often masked by these inclusions. Compaction fractured zones lack a dense inclusion distribution and have a neomorphic mosaic which suggests that the transformation to calcite locally destroyed much of the original microstructure. Larger surface areas of fractured calicle walls, exposed to the calcifying pore waters, may have induced a more rapid and destructive mineralogical transformation.

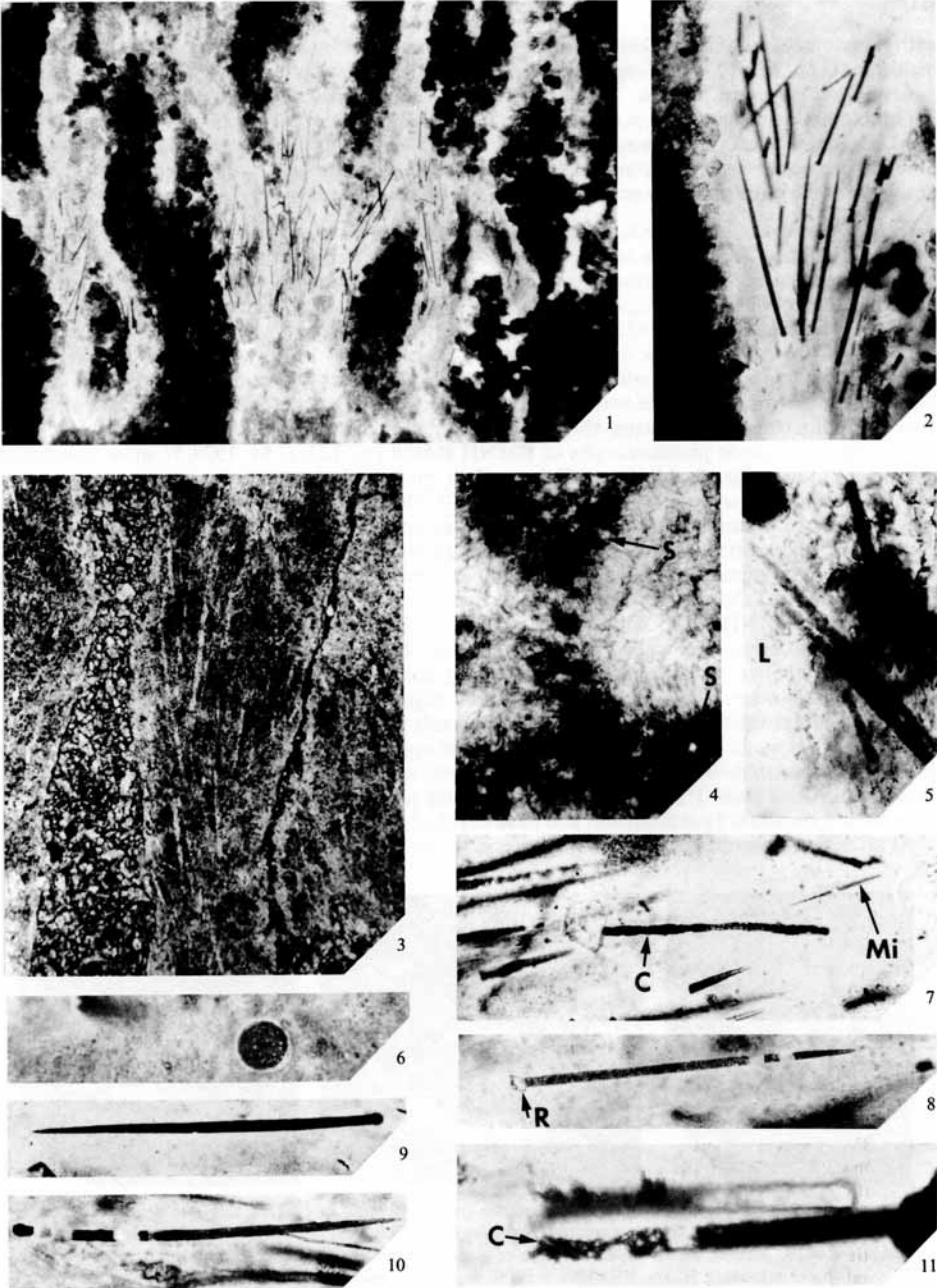
In partly silicified specimens, the chalcedonic silica cementation and replacement occurred after compaction fracture, as indicated by the preferential silicification of their fracture zones. According to Meyers (1977), such compaction fracture could occur as a result of overburden pressure after burial to metres or tens of metres.

The ?organic-inclusions within the calicle walls appear to have provided a template retaining some detail of the original microstructure. The inclusion distribution may be partly related to the diagenetic history of the calicle walls as they are invariably less dense in compaction-fractured zones, and partly primary, caused by a variable secretion of organic matrix within the basal calcareous skeleton. This reliance on inclusions to define the primary microstructure, and the presence of neomorphic crystals with irregular margins, that often continue into the lumina as clear spar suggests an *in situ* transformation from primary aragonite to calcite. Schneidermann *et al.* (1972, p. 89) stated that continuity of neomorphic crystal fabrics from skeletal components into surrounding spar indicated an early aragonite void-cementation that could be 'expected to appear only in association

EXPLANATION OF PLATE 103

Chaetetes (Boswellia) mortoni sp. nov., Lower Asbian (Lower Carboniferous), Eglwyseg Escarpment, Llangollen (Clwyd, North Wales).

- Fig. 1. Paratype BMNH R4429 (Morton Collection). Longitudinal section of calicle walls replaced by chalcedonic (length fast) silica, and zoned dolomite lumen infills. Microgranular silica spicule pseudomorphs visible as dark streaks within the calicle walls, $\times 50$.
- Fig. 2. BMNH R4429. Detail of chalcedonic silica calicle wall in longitudinal section, showing the spicule pseudomorphs diverging distally, $\times 150$.
- Fig. 3. Holotype BMNH R49964. Longitudinal section of calicle wall illustrating well-preserved calcitic spicule pseudomorphs, diverging distally and subparalleling the fascicular fibres, defined by trains of inclusions, $\times 120$.
- Fig. 4. BMNH R50134. Transverse section of calicle, with distinct and vague transverse sections through calcitic spicule pseudomorphs (s), $\times 150$.
- Fig. 5. BMNH R4429. Microgranular silica spicule pseudomorph extending to lumen void (L) calicle wall (w) junction, indicating original extension of distal portion of spicule into the lumen, and its subsequent dissolution, $\times 200$.
- Figs. 6-11. Microgranular silica spicule pseudomorphs of BMNH R4429. 6, transverse section, $\times 1000$. 7, slight surface corrosion on tylostyle (c), with adjacent ?raphide-microsclere (Mi), $\times 200$. 8, tylostyle with discontinuity and replacement by dolomite rhomb (R), $\times 200$. 9, perfect tylostyle pseudomorph. Note proximal boss and distal point, $\times 200$. 10, discontinuous tylostyle pseudomorph (probably a dissolution feature), $\times 200$. 11, detail of a highly corroded tylostyle pseudomorph (c), $\times 600$.



GRAY, Palaeozoic chaetetid

with previously aragonitic skeletons'. Conversely, in silicified specimens rare microdolomite inclusions occur (Pl. 103, fig. 8) within the calicle walls suggesting a high-magnesian calcite original mineralogy. However, intense dolomitization of the lumina of these colonies, the lack of microdolomite inclusions within calcitic specimens, and the common association of dolomite with chert nodules in the Tynant Limestone indicates that the magnesium may have an external source. Staining has not revealed any obviously 'ferroan' calcitic specimens. It would therefore appear that aragonite is the most probable original mineralogy of *C. (B.) mortoni*.

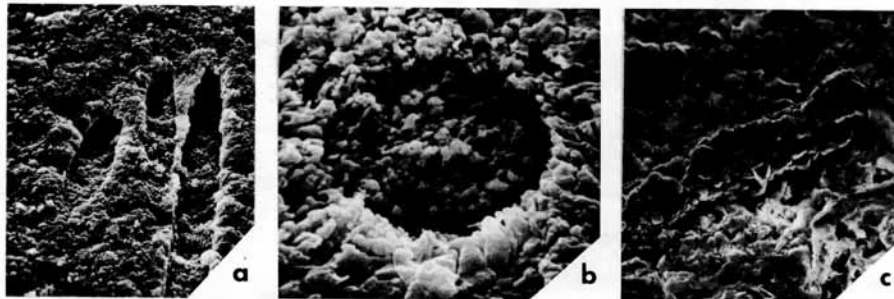
Spicule preservation. There are significant variations in the mode of preservation of the intramural spicules. Extant sclerosponges secrete siliceous spicules of various types (see Table 1) within or external to a calcareous skeleton. Hartman and Goreau (1970, pp. 210, 213) and Land (1976) described live colonies of ceratoporellans in which the opaline silica spicules (Opal 'A' of Jones and Segnit (1971)) were dissolving within the basal calcareous mass.

In *C. (B.) mortoni* spicules are preserved as calcite, silica, and pyrite pseudomorphs. Most specimens contain calcitic pseudomorphs. No spicule pseudomorphs convincingly extend into the lumina, although many spicules would have originally done so, as shown by extrapolation of spicule microstructure where it terminates abruptly against the calicle wall edge (Pl. 103, fig. 5).

The siliceous spicule pseudomorphs of BMNH R4429 and LIV.C.M. 1974.57 show dissolution features (Pl. 103, figs. 7, 11) from slight surface pitting to deep corrosion. Often the spicule pseudomorphs are discontinuous (Pl. 103, figs. 8, 10). The origin of this last feature is uncertain, but may be a severe localized corrosion effect. Dissolved parts of spicules have been replaced by clear chalcedonic silica indicating that a degree of dissolution occurred prior to the silicification of calicle walls. A later diagenetic event is indicated by dolomite rhombs replacing both spicule pseudomorphs (Pl. 103, fig. 8) and chalcedonic-silica walls.

In specimen BMNH R4429 neither axial canals nor axial filaments are visible, even with scanning electron microscopy of HF etched specimens (text-fig. 4*b*) (cf. Schwab and Shore 1971), indicating that an internal alteration of the spicule mineralogy has occurred. This is further confirmed by the presence of sub-microscopic microgranules which impart a red-brown hue and high relief to the spicule pseudomorphs. Deeper coloration corresponds to a more dense microgranule distribution. They give the spicule surface a smooth but frosted appearance in transmitted light. S.E.M. with E.D.A.X. shows that the microgranules are siliceous, and indistinguishable from the surrounding chalcedonic-silica walls. HF etched surfaces reveal the microgranule's form (text-fig. 4*b*). They vary between 0.2 μm and 0.5 μm diameter, and have sharp edges implying an internal structural ordering.

At an early or intermediate stage of diagenesis, biogenic opal 'A' is either converted *in situ* to opal



TEXT-FIG. 4. S.E.M. photomicrographs of spicule pseudomorphs in *C. (B.) mortoni*: 4*a*, longitudinal section of calicle wall with siliceous spicule pseudomorphs preferentially etched (10% HF for 3 minutes), BMNH R4429, $\times 1000$; 4*b*, transverse section of a microgranular silica spicule pseudomorph (etched in 10% HF for 3 minutes), BMNH R4429, $\times 5000$; 4*c*, pyritic spicule pseudomorph, composed of pyrite crystal aggregates (HCl etch), BMNH R46144, $\times 1000$.

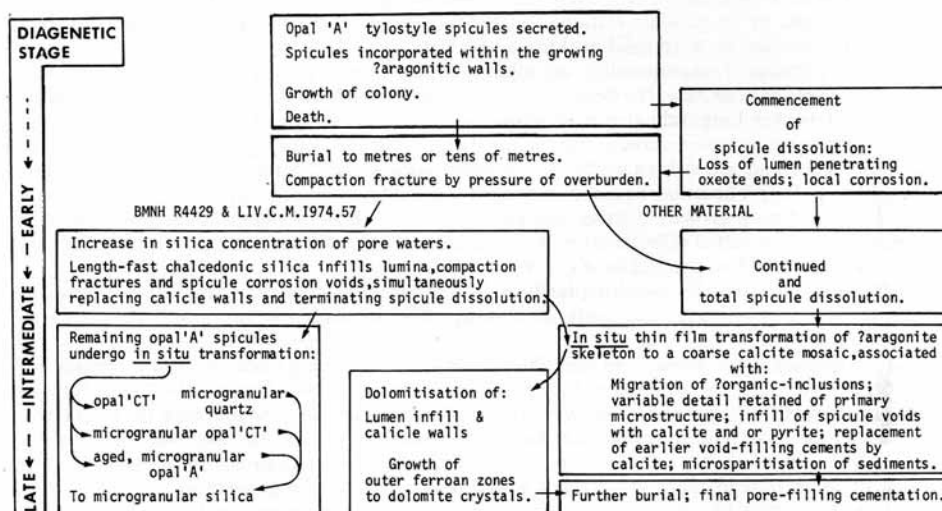
'CT' (Ernst and Calvert 1969; Wise and Weaver 1974, p. 305), a disordered cristobalite-tridymite silica polymorph (Jones and Segnit 1971), or dissolved and subsequently reprecipitated as opal 'CT' or quartz, filling voids and replacing carbonate grains (von Rad, Riech, and Rösch 1978). With increasing diagenetic maturity (depth of burial; time; temperature controls) opal 'CT' is eventually converted to quartz (Reich 1979). There are few records of opal 'CT' from pre-Cretaceous sediments.

The mineralogical composition of the spicule pseudomorphs in *C. (B.) mortoni* invites discussion. Are the spicules not pseudomorphs but diagenetically aged opal 'A' relic spicules? Reich (1979, pp. 754-755, pl. 1, fig. 4) reported Eocene opal 'A' sponge spicules with a pronounced microgranular texture similar to that observed on HF etched spicules in BMNH R4429.

Opal 'CT' normally occurs as bladed microspherules or lepispheres, 3 μm to 15 μm diameter. Siliceous sponge spicules have been recorded replaced by lepispheres that subsequently have been inverted to quartz (Reich 1979, p. 742) leaving visible relics of the precursor lepisphere. Von Rad *et al.* (1978, p. 903, pl. 3, figs. 2, 3) figured lepispheres replaced by microgranular quartz, also with a similar texture to that observed in spicule pseudomorphs of BMNH R4429 (text-fig. 4b). No lepisphere relics are visible in these spicules. Robertson (1978, p. 25) suggested that 'domains' of opal 'CT' would 'presumably appear' within opal 'A' which had escaped early diagenetic dissolution, becoming increasingly numerous as solid state ordering proceeds. These 'domains' may be analogous to the microgranules within the spicule pseudomorphs (i.e. opal 'CT' without a lepisphere stage) or they may be a microgranular quartz replacement of opal 'CT' microgranules.

Opal 'CT' is generally recognized to have a higher relief than opal 'A', but exceptions are known. The high relief of microgranule-dense spicules in BMNH R4429 and LIV.C.M. 1974.57 may be caused by internal reflections on the surfaces of the microgranules. The spicules dissolve in HF far more readily than the surrounding chalcedonic silica (text. fig. 4a). This may be due to their fine granular nature, but Robertson (1978, p. 22) found that opal 'CT' dissolved preferentially in HF with respect to chalcedonic silica.

Thus the origin of the microgranular silica within the spicule pseudomorphs is unclear. It may be diagenetically aged opal 'A'; microgranular quartz replacement of opal 'CT' or relic microgranular opal 'CT' that has not gone through a lepisphere stage (see text-fig. 5). The nature of the silica matrix



TEXT-FIG. 5. Chart illustrating the sequence of events in the diagenetic history of *Chaetetes (Boswellia) mortoni* sp. nov. in relation to the preservation of microstructures and spicule pseudomorphs.

to the microgranules is unknown. In spicule pseudomorphs with few microgranules the matrix is optically similar to the surrounding chalcedonic silica. The occurrence of this microgranular silica fabric within the spicule pseudomorphs and not within the surrounding chalcedonic silica walls, and the retention of delicate spicule corrosion features suggest that the spicules were not originally calcareous, but probably opal 'A', as in extant sponges.

In specimens BMNH R46144, BMNH R50188, and BMNH R45851 pyritic spicule pseudomorphs occur, similar to those described by Kaźmierczak (1979). The pyrite replacement is imperfect, with microcrystalline pyrite (text-fig. 4c) forming discontinuous chains or aggregates of 1 μm to 7 μm crystals along the pseudomorph length. The non-pyritic parts of the pseudomorphs are replaced by calcite. In BMNH R45851 the spicules are pseudomorphed by pyrite only towards the outer edges of calicle walls, where they merge with highly pyritic lumen-filling sediment. In contrast, BMNH R50188 has void-filling spar in the lumina, with pyritic spicule pseudomorphs terminating abruptly at the calicle wall margins, indicating that pyritization occurred after at least partial spicule dissolution. Rickard (1970) suggested that framboidal pyrite may replace organic globules or infill gaseous vacuoles. The calcitic spicule pseudomorphs often contain ?organic-inclusions, which may play a role in the pyrite formation.

AFFINITIES OF *C. (B.) MORTONI* WITH CERATOPORELLIDS

Ceratoporellids secrete a basal calcareous skeleton of fascicular fibrous aragonite calicles. These are subsequently infilled with fibrous aragonite by the upward-growing basal pinacoderm (Hartman and Goreau 1970, 1972). The calicles of *Ceratoporella nicholsoni* are regular, rounded to polygonal, rarely with a meandrine form (Hartman and Goreau 1972, fig. 17) similar to that of *Stromatospongia* Hartman, 1969, another extant ceratoporellid genus. Unlike chaetetids, ceratoporellids do not secrete tabulae. However, as Hartman and Goreau (1972, p. 142) point out, 'the difference is one of degree', with the growth of tabulae representing periodic rather than continuous carbonate secretion from the basal pinacoderm of the sponge animal. *Atrochaetetes*, a Mesozoic ceratoporellid (see above), lacks a continuous calicle infill (Cuif and Fischer 1974) and exhibits intramural spicule pseudomorphs in at least one species (Dieci, Russo, and Russo 1977). Its backfill may have formed by periodic secretion, or by periodic distally directed movement of the living tissues, and may be a character intermediate between solid backfills and tabulae.

The calicle surfaces of ceratoporellids are often ornamented with arborescent processes, rounded knobs, and spines of aragonite. No detailed calicle surface is available on *Chaetetes (B.) mortoni* for comparison; however, longitudinal sections show the distal edges of the calicles as rounded, although pre-burial erosion may have enhanced this. Isolated aragonitic trabeculae grow within the soft tissue of *Ceratoporella*, and are subsequently incorporated within the calcareous walls (Hartman and Goreau 1972, p. 135). These may be compared to the trabecular columns within *C. (B.) mortoni* which remain isolated during growth. Surface mamelons and astrorhizae, evident in some specimens of ceratoporellids as a result of differential growth-rates beneath excurrent canal systems (Stearn 1975), are not present on studied specimens of *C. (B.) mortoni*.

Ceratoporellids increase by pseudoseptal division, and Palaeozoic chaetetids by both pseudoseptal and basal fission. Mesozoic chaetetids in contrast also increase by intramural offset, as do tabulosponges.

Opal 'A' spicules are secreted from scleroblast cells within the living tissue of ceratoporellids and are incorporated within the skeleton as the colony grows. Hartman and Goreau (1972, p. 134) state that the spicules of *Ceratoporella nicholsoni* 'entrapped in the aragonite tend to follow the orientation of the calcareous crystalline units that surround them'. This is very like *C. (B.) mortoni*. The proximal (basal) spicule heads in living ceratoporellids are embedded within an organic matrix (Hartman and Goreau 1970). Although there is no direct evidence for organic fibres surrounding the head of spicules in *Chaetetes (B.) mortoni* the presence of ?organic-inclusions indicates an intimate relationship between the organic, calcareous, and siliceous components of the skeleton. Hartman and Goreau (1970, p. 213) also note that there are regions of the calcareous skeleton of *Ceratoporella*

nicholsoni devoid of siliceous spicules. Although spicule preservation is variable throughout the colonies of *Chaetetes (B.) mortoni*, the local variation in spicule distribution may in part be primary. Ceratoporellids secrete monaxons of various forms, although they are neither known with tylostyles, nor with microscleres. The size of *C. (B.) mortoni* tylostyles does, however, fall within the size range of known ceratoporellid spicules.

The ecology of extant sclerosponges is fundamentally different from that of fossil chaetetids. Extant ceratoporellids are commonly found in a complex association with serpulid worms in submarine caves and at depth on fore-reef slopes (Hartman and Goreau 1970), whereas Palaeozoic chaetetids are common open-shelf dwellers, often associated with shallow-water carbonates.

There are significant similarities between *C. (B.) mortoni* and ceratoporellids in colony, calicle, microstructure form, and spicule character, indicating a close phylogenetic relationship. One notable difference is the presence of true tabulae in *C. (B.) mortoni* and the solid calcareous calicle infill characteristic of extant ceratoporellids.

AFFINITIES OF *C. (B.) MORTONI* WITH OTHER SCLEROSPONGES

Tabulospongids (Hartman and Goreau 1975; Mori 1976, 1977) secrete a calicular basal skeleton of high-magnesian calcite with a lamellar microstructure. The calicles are partitioned by horizontal tabulae, and spiny processes project into the lumina. The distribution of organic fibrils within the skeleton of tabulospongids is documented by Hartman and Goreau (1975, p. 167). These nanometre-sized fibrils act both as a matrix for the calcitic skeleton, and are present within the soft tissues. In *Tabulosporgia horiguchii*, Mori (1976, pl. 3, fig. 3) shows that calicle wall centres are richest in organic matrix, resembling the distribution of probable organic matter now visible in calcitic specimens of *C. (B.) mortoni*. This may be a relict primary texture in the latter.

Tabulospongids secrete siliceous spicules that are not incorporated within their basal calcareous skeleton, but remain within the surface tissues. These spicules have a very low fossilization potential. The spicules are a variety of complex forms, with both megascleres and microscleres secreted by the same colony (see Table 1).

Although the calcareous skeleton is similar in design to many chaetetids, the marked differences in microstructure and spicule form and distribution readily distinguish tabulospongids from such Palaeozoic chaetetids as *C. (B.) mortoni*.

Merlia is an unassigned extant sclerosponge that secretes a prismatic tabular basal aragonitic skeleton, partitioned horizontally by incomplete tabulae. A variety of siliceous spicules are secreted within the living tissue, but not incorporated within the skeleton. Each prismatic calicle is formed by the outgrowth and interlocking of flanges, set at 120°, of stout fibre fascicles which form the calicle corners (see Stearn 1975). The architecture of *Merlia* therefore is subtly different from that of chaetetids. In contrast the types of spicules secreted by *Merlia* are similar to those of *C. (B.) mortoni* (see Table 1) (tylostyles and raphides) indicating some histologic similarities between these sponge animals.

Some Mesozoic stromatoporoids also have similarities with *C. (B.) mortoni*. Schnorf (1960) and Yabe and Sugiyama (1935) described Lower Cretaceous and Upper Jurassic forms with clear areas within the walls which may be sites of intramural spicules (Hartman and Goreau 1970), or part of the primary calcareous microstructure (Fenninger and Flajs 1974). The calcareous skeleton of these sclerosponges resembles chaetetids in as much as they also possess calicles with tabulae and hollow lumina. They are a diverse group, however, and show many characters atypical of Palaeozoic chaetetids.

In addition Table 1 lists the other known forms of spicule-bearing sclerosponges. These are not closely comparable with the present material but indicate the variety of microstructural and morphological patterns thus far encountered within the Sclerospongidea.

CONCLUSIONS

C. (B.) mortoni sp. nov. is a Palaeozoic (Upper Dinantian) chaetetid. The calicle morphology of this chaetetid is variable between slightly irregular (chaetetiporinid) and subpolygonal, having irregularly

thick fascicular fibrous walls, ornamented with longitudinal ridges and pseudosepta. These factors place it within the subgenus *Boswellia* Sokolov, 1949, a typical Palaeozoic chaetetid.

Comparison of the basal calcareous skeleton with extant and fossil sclerosponges, the presence of a neomorphic mosaic, and the dependence on ?organic-inclusions to define the primary microstructure which is variably preserved, suggest that the original calcareous mineralogy was aragonite. Text-fig. 5 summarizes the approximate sequence of diagenetic events related to the preservation of microstructures in the skeletons of *C. (B.) mortoni*.

Spicule pseudomorphs occur within the fascicular fibrous walls as long thin tylostyles, with distally diverging oxeote ends that often would have penetrated the lumen of the sponge animal. They occur now as calcite, pyrite, or silica pseudomorphs, their mineralogy dependent on the diagenetic history of the basal skeleton.

In calcitic specimens, the spicule pseudomorphs are preserved as clear calcite rods in regions of the calicle walls with a dense ?organic-inclusion distribution. They are absent from compaction-fractured zones and are more common in thick-wall zones of growth rhythms. More rarely, the spicules are defined by trains or aggregates of pyrite crystals.

Chalcedonic silica locally replaces the calicle walls, enveloping spicule pseudomorphs that retain detail of their tylostyle form. Early dissolution features are fossilized within these spicules. Voids formed by spicule dissolution are infilled with clear chalcedonic silica. Remaining spicules have undergone alteration to microgranular silica of three possible forms, either diagenetically aged opal 'A', microgranular quartz replacement of opal 'CT', or relic microgranular opal 'CT' that has not gone through a lepisphere stage.

The presence of intramural spicule pseudomorphs within an otherwise typical member of the Palaeozoic Chaetetida further supports the sclerosponge affinities of at least some members of this group. Comparison of this chaetetid with other sclerosponges indicates that the spicular character and calcareous microstructure is very similar to that of the Ceratoporellida. The secretion of tabulae in chaetetids, rather than the backfill of ceratoporellids, remains the distinguishing microstructural feature. Of the two previously described intramural spicule pseudomorph bearing Mesozoic 'chaetetids' *Atrochaetes* Cuif and Fischer, 1974, may be regarded as an aberrant member of the Ceratoporellida rather than a chaetetid *s.s.*, on account of its discontinuous backfill.

Acknowledgements. I would like to thank: Dr. C. T. Scrutton (University of Newcastle upon Tyne) and Dr. M. E. Tucker (University of Newcastle upon Tyne) for their advice and constructive criticism through all the stages of preparation of this paper; Dr. B. R. Rosen, Mr. R. F. Wise, Ms. J. G. Darrell (Department of Palaeontology, British Museum (Natural History)), Dr. C. D. Waterston (Royal Scottish Museum), and Mr. P. Phillips (Merseyside County Museum) who brought fossil material to my attention; and Mr. G. Staines (University of Newcastle upon Tyne) for his technical assistance with the electron microscopy. This research was carried out during the tenure of a N.E.R.C. research studentship.

REFERENCES

- BATHURST, R. G. C. 1964. The replacement of aragonite by calcite in the molluscan shell wall. In IMBRIE, J. and NEWELL, N. (eds.), *Approaches to palaeoecology*. New York, J. Wiley & Sons, Inc., pp. 357-376.
- CUIF, J.-P. and FISCHER, J.-C. 1974. Étude systématique sur les Chaetetida du Trias de Turquie. *Annls Paléont. Invertébrés*, **60**, 3-23, pls. I-IV.
- DIECI, G., RUSSO, A. and RUSSO, F. 1974a. Nota preliminare sulla microstruttura di spugne aragonitiche del Trias medio-superiore. *Boll. Soc. paleont. ital.* **13**, 99-107, pls. 32-37.
- 1974b. Revisione del genere *Leiospongia* d'Orbigny (Sclerospongia triassica). *Ibid.* 135-146, pls. 51-53.
- and MARCHI, M. S. 1977. Occurrence of spicules in Triassic chaetetids and ceratoporellids. *Ibid.* **16**, 229-238, pls. 1-3.
- DODD, J. R. 1966. Processes of conversion of aragonite to calcite with examples from the Cretaceous of Texas. *J. sedim. Petrol.* **36**, 733-741.
- ERNST, W. G. and CALVERT, S. E. 1969. An experimental study of the recrystallization of porcelanite and its bearing on the origin of some bedded cherts. *Am. J. Sci.* **267A**, 114-133.

- FENNINGER, A. and FLAJS, G. 1974. Zur mikrostruktur rezenter und fossiler Hydrozoa. *Biom mineralization*, 7, 69-99.
- FISCHER, J.-C. 1970. Révision et essai de classification des Chaetetida (Cnidaria) post-Paléozoïques. *Annls Paléont. Invertébrés*, 56, 151-220, pls. A-F.
- FISCHER VON WALDHEIM, G. 1830. *Oryctographie du gouvernement de Moscou*, Moscow, 1st edn. 1830, 2nd edn. 1837.
- HARTMAN, W. D. 1969. New genera and species of coralline sponges (Porifera) from Jamaica. *Postilla*, 137, 1-39.
- and GOREAU, T. F. 1970. Jamaican coralline sponges: their morphology, ecology and fossil relatives. *Symp. zool. Soc. Lond.* 25, 205-243.
- 1972. *Ceratoporella* (Porifera: Sclerospongiae) and the chaetetid 'corals'. *Trans. Conn. Acad. Arts Sci.* 44, 133-148.
- 1975. A pacific tabulate sponge, living representative of a new order of sclerosponges. *Postilla*, 167, 1-14.
- HERITSCH, F. 1932. *Chaetetes* und *Caninia* aus dem Karbon von Ivovik bei Krupanj in West-Serbien. *Bull. Serv. Géol. Yougosl.* 1/2, 1-10, pls. I-II.
- HUDSON, J. D. 1962. Pseudopleochroic calcite in recrystallized shell-limestones. *Geol. Mag.* 92, 492-500, pl. XXI.
- JAMES, N. P. 1974. Diagenesis of scleractinian corals in the subaerial vadose environment. *J. Paleont.* 48, 785-799.
- JONES, J. B. and SEGNIT, E. R. 1971. The nature of opal. I. Nomenclature and constituent phases. *J. geol. Soc. Aust.* 18, 57-68.
- KAŹMIERCZAK, J. 1974. Lower Cretaceous sclerosponge from the Slovakian Tatra Mountains. *Palaeontology*, 17, 341-347, pls. 45-46.
- 1979. Sclerosponge nature of chaetetids evidenced by spiculated *Chaetetopsis favrei* (DENINGER 1906) from the Barremian of Crimea. *Neues Jb. Geol. Paläont. Mh.* 1979, 97-108.
- and HILLMER, G. 1974. Sclerosponge nature of the Lower Hauterivian 'bryozoan' *Neuropora pustulosa* (ROEMER 1839) from western Germany. *Acta palaeont. Pol.* 19, 443-453.
- KIRKPATRICK, R. 1909. Notes on *Merlia normani* Kirkp. *Ann. Mag. nat. Hist.* (8) 4, 42-48.
- 1910. On the affinities of *Astrosclera willeyana* Lister. *Ibid.* (8) 5, 380-383.
- 1912a. *Merlia normani* and its relation to certain Palaeozoic fossils. *Nature, London.* 89, 502-503.
- 1912b. On the nature of stromatoporoids. *Ibid.* 607.
- LAND, L. S. 1976. Early dissolution of sponge spicules from reef sediments, North Jamaica. *J. sedim. Petrol.* 46, 967-969.
- LÉVI, C. 1973. Systématique de la classe des Demospongia (Démospouges). In GRASSÉ, P. (ed.). *Traité de Zoologia*, Masson, Paris. Vol. 3, 577-3631.
- LOHMANN, K. C., and MEYERS, W. J. 1977. Microdolomite inclusions in cloudy prismatic calcites: A proposed criterion for former high-magnesium calcites. *J. sedim. Petrol.* 47, 1078-1088.
- MEYERS, W. J. 1977. Chertification in the Mississippian Lake Valley Formation, Sacramento Mountains, New Mexico. *Sedimentology*, 24, 75-105.
- and LOHMANN, K. C. 1978. Microdolomite-rich syntaxial cements: proposed meteoric-marine mixing zone phreatic cements from Mississippian limestones, New Mexico. *J. sedim. Petrol.* 48, 475-488.
- MILNE-EDWARDS, H. A. and HAIME, J. 1850-1854. A monograph of the British fossil corals. *Palaeontogr. Soc. (Monogr.)* Parts 1-5, i-lxxxv, 1-322, pls. I-LXII.
- MORI, K. 1976. A new recent sclerosponge from Ngargol, Palau Islands and its fossil relatives. *Sci. Rep. Tôhoku Univ.*, 2nd ser. (Geol.), 46, 1-9, pls. 1-6.
- 1977. A Calcitic sclerosponge from the Ishigaki-shima coast, Ryukyu Islands, Japan. *Ibid.* 47, 1-5, pls. 1-2.
- MORTON, G. H. 1879. *The Carboniferous Limestone and Cefn-y-Fedw Sandstone of the country between Llanymynech and Minera North Wales*, 140 pp. David Bogue, London.
- NEWELL, N. D. 1935. Some mid-Pennsylvanian invertebrates from Kansas and Oklahoma: II. Stromatoporoidea, Anthozoa and Gastropoda. *J. Paleont.* 9, 341-355, pls. 33-36.
- OKULITCH, V. J. 1936. On the genera *Heliolites*, *Tetradium* and *Chaetetes*. *Am. J. Sci.* 32, 361-379.
- PINGITORE, N. E. JR 1976. Vadose and phreatic diagenesis: Process products and their recognition in corals. *J. sedim. Petrol.* 46, 978-984.
- PLUMMER, L. N. and MACKENZIE, F. T. 1974. Predicting mineral solubility from rate data: application to the dissolution of magnesian calcites. *Am. J. Sci.* 274, 61-83.
- RAD, U. VON, RIECH, V. and RÖSCH, H. 1978. Silica diagenesis in continental margin sediments off Northwest Africa. In LANCELOT, Y., SEIBOLD, E., et al. 1978. *Initial reports of the deep sea drilling project*. Washington (U.S. Government Printing Office), 41, 879-905.
- RIECH, V. 1979. Diagenesis of silica, zeolites, and phyllosilicates at sites 397 and 398. In VON RAD, U., RYAN, W. B. F.,

- et al. 1979. *Initial reports of the deep sea drilling project*. Washington (U.S. Government Printing office), **47**, 741-759.
- RICHTER, D. K. and FUCHTBAUER, H. 1978. Ferroan calcite replacement indicates former magnesian calcite skeletons. *Sedimentology*, **25**, 843-860.
- RICKARD, D. T. 1970. The origin of framboids. *Lithos*, **3**, 269-293.
- ROBERTSON, A. H. F. 1977. The origin and diagenesis of cherts from Cyprus. *Sedimentology*, **24**, 11-30.
- SANDBERG, P. A. 1975. Bryozoan diagenesis: bearing on the nature of the original skeleton of rugose corals. *J. Paleont.* **49**, 587-606.
- SCHERER, M. 1977. Preservation, alteration and multiple cementation of aragonitic skeletons from the Cassian Beds (U. Triassic, Southern Alps): petrographic and geochemical evidence. *Neues Jb. Geol. Paläont. Abh.* **154**, 213-262.
- SCHNEIDERMANN, N., SANDBERG, P. A., and WUNDER, S. J. 1972. Recognition of early cementation of aragonitic skeletal carbonates. *Nature phys. Sci., Lond.* **240**, 88-89.
- SCHNORF, A. 1960. Parastromatoporoidae nouveaux du Jurassique supérieur et du Valanginien inférieur du Jura. *Eclog. geol. Helv.* **53**, 729-732, pls. I-III.
- SCHWAB, D. W. and SHORE, R. E. 1971. Fine structure and composition of a siliceous sponge spicule. *Biol. Bull. mar. biol. Lab., Woods Hole*, **140**, 125-136.
- SCRUTTON, C. T. 1979. Early fossil cnidarians. In HOUSE, M. R. (ed.), *Spec. Vol. Syst. Ass.* **12**, 161-207.
- SOKOLOV, B. S. 1939. Stratigraphical value and types of Chaetetidae of the Carboniferous of the USSR. *C.r. (Dokl.) Acad. Sci. URSS* **23**, 409-412.
- 1950. Khetetidy karbona severo-vostochnoi Ukrainy i sporedel'nykh oblastei (s opisaniem nekotorykh tabulyat). [Carboniferous Chaetetidae of the Northeast Ukraine and adjacent areas.] *Trudy vses. nefi. nauchno-issled. geol.-razv. Inst. n.s.* **27**, 1-101, pls. I-XX. [In Russian.]
- 1962. Gruppya Chaetetida. In ORLOV, Y. A. (ed.), *Osnovy Paleontologii: Porifera, Archaeocyatha, Coelenterata, Vermes*. Moscow [in Russian]. *Fundamentals of Paleontology*, **2**, 259-270. *Israel Prog. sci. Transl.*, Jerusalem 1971 [English translation].
- SOMERVILLE, I. D. 1979. A sedimentary cyclicity in early Asbian (Lower D1) limestones in the Llangollen district of North Wales. *Proc. Yorks. geol. Soc.* **42**, 397-404.
- SPIRO, T. A. 1961. Nekotorie Vizeiskie y Namyurskie chetetidi Podmoskovbya. [Some Viséan and Namurian chaetetids from the Moscow region.] *Paleont. Zh.* **4**, 24-28, pls. II-III. [In Russian.]
- STEARNS, C. W. 1972. The relationship of the stromatoporoids to the sclerosponges. *Lethaia*, **5**, 369-388.
- 1975. The stromatoporoid animal. *Lethaia*, **8**, 89-100.
- TERMIER, H. and TERMIER, G. 1976. Spongiaires hypercalcifiés et ectoproctes sténolèmes fossiles. *C.r. Acad. Sci. Paris*, **282D**, 1269-1272.
- THOMSON, J. 1881. On the genus *Alveolites*, *Amplexus* and *Zaphrentis*, from the Carboniferous System of Scotland. *Proc. Phil. Soc. Glasgow*, **13**, 194-237.
- TOWE, K. M. and HEMLEBEN, C. H. 1976. Diagenesis of magnesian-calcite: evidence from miliolacean foraminifera. *Geology*, **4**, 337-339.
- TWITCHELL, G. B. 1929. The structure and relationships of the true stromatoporoids. *Am. Midl. Nat.* **11**, 270-306, pls. XVIII-XXVI.
- VACELET, J. 1977. Éponges Pharétronides actuelles et Sclérosponges de Polynésie française, de Madagascar et de la Réunion. *Bull. Mus. natn. Hist. nat.* 3^e sér., **444**, Zool. 307, 345-368.
- VASSEUR, P. and LÉVI, C. 1976. Spongiaires de la pente externe des récifs coralliens de Tulear (Sud-Ouest de Madagascar). *Mém. Mus. natn. Hist. nat.* **A44**, 116 pp.
- VEIZER, J. and WENDT, J. 1976. Mineralogy and chemical composition of Recent and fossil skeletons of calcareous sponges. *Neues Jb. Geol. Palaont. Mh.* **1976**, 558-573.
- WARDLAW, N., OLDERSHAW, A. and STOUT, M. 1978. Transformation of aragonite to calcite in a marine gastropod. *Can. J. Earth Sci.* **15**, 1861-1866.
- WENDT, J. 1975. Aragonitische Stromatoporen aus der alpinen Obertrias. *Neues Jb. Geol. Palaont. Abh.* **150**, 111-125.
- WEYER, VON D. 1967. Einige Chaetetidae (Coelenterata) aus dem Unterkarbon des Velberter Sattels (Rheinisches Schiefergebirge). *Geologie*, **16**, 1156-1163, pls. I-II.
- WISE, S. W. and WEAVER, F. W. 1974. Chertification of oceanic sediments. In HSU, K. J. and JENKINS, H. C. (eds.). *Pelagic sediments: on land and under the sea. Spec. Publ. int. Ass. Sediment.* **1**, 301-306.
- YABE, H. and SUGIYAMA, T. 1935. Jurassic stromatoporoids from Japan. *Sci. Rep. Tôhoku imp. Univ.*, ser. 2 (Geol.), **14**, 135-191, pls. XL-LXXI.

DAVID I. GRAY

Department of Geology
University of Newcastle Upon Tyne
Newcastle Upon Tyne, NE1 7RU

Typescript received 12 September 1979

Revised typescript received 21 January 1980