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Schizosphaerella punctulata DEFLANDRE & DANGEARD: Wall ultrastructure and preservation in deeper-water carbonate sediments of the Tethyan Jurassic¹⁾

By OTTO KÄLIN²⁾

ABSTRACT

Schizosphaerella punctulata is a presumably planktonic calcareous nanno-organism of uncertain systematic position occurring widely through most of the Jurassic (Hettangian–Kimmeridgian). It has been described first by DEFLANDRE & DANGEARD more than forty years ago. However, detailed information concerning the test morphology and, in particular, the wall ultrastructure was revealed only by means of the electron microscope. In 1974, an ultrastructural model was proposed for the first time by AUBRY & DÉPÈCHE (cf. Fig. 2 of this paper).

Evidence gathered from an SEM-study of Lower and Middle Jurassic deeper-water sediments from the Southern Alps, the Tuscan and the Umbrian paleogeographic realms, and of some additional samples from the Early Toarcian Schistes Carton of the Causse Basin (southern France), revealed considerable inconsistencies in the reconstruction given by AUBRY & DÉPÈCHE. In the present account, an alternative interpretation of the original wall ultrastructure of *S. punctulata* is thus proposed that would seem to match the main structural features observed with the SEM more accurately (cf. Fig. 12).

It has furthermore been suggested that *Schizosphaerella* was a major sediment contributor in Tethyan Jurassic deeper-water deposits. This view is not confirmed here; rather, schizosphaerellids appear to have been important as sites of nucleation for large amounts of diagenetic calcite, including syntaxial cement deposited in original skeletal voids as well as displacive and/or neomorphic calcite occurring as fringing crusts of radiating prismatic crystals around the valves.

RÉSUMÉ

Schizosphaerella punctulata est un nanno-organisme calcaire, probablement planctonique, de position systématique incertaine, que l'on rencontre fréquemment à travers tout le Jurassique (Hettangien à Kimméridgien). Il a été décrit à l'origine par DEFLANDRE & DANGEARD, il y a plus de quarante ans. Toutefois, les informations détaillées concernant la morphologie du test et, en particulier, l'ultrastructure de la paroi, n'ont pu être mises à jour qu'à l'aide du microscope électronique. En 1974, un modèle d'ultrastructure a été proposé pour la première fois par AUBRY & DÉPÈCHE (cf. fig. 2 de cet article).

Les arguments rassemblés à partir d'une étude au S.E.M. de sédiments carbonatés de mer profonde, d'âge Jurassique inférieur et moyen, provenant des Alpes du Sud, du domaine paléogéographique toscan et ombrien, et de quelques autres échantillons provenant des «schistes-carton», début du Toarcien, du bassin des Causses (sud de la France), révèlent de considérables contradictions dans la reconstruction donnée par AUBRY & DÉPÈCHE.

Dans le présent compte-rendu, une autre interprétation de l'ultrastructure de la paroi originale de *Schizosphaerella punctulata* est donc proposée, tenant compte des principaux traits structuraux que le S.E.M. nous a permis d'observer avec plus de précision (cf. fig. 12).

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Par ailleurs, il avait été suggéré que *Schizosphaerella punctulata* serait un élément majeur de la sédimentation des dépôts profonds de la Téthys au Jurassique. Ce point de vue n'est pas confirmé; *Schizosphaerella punctulata* paraît plutôt avoir joué un rôle important comme sites de nucléation pour de grandes quantités de calcite diagénétique: ciment syntaxial déposé dans les vides du squelette original, et calcite displacive et/ou néoformée dans des croûtes de cristaux prismatiques, disposés radialement autour des valves.

Introduction

In the frame of a sedimentological study on Early and Middle Jurassic deeper-water carbonate sediments from the Southern Alps, the Tuscan and the Umbrian paleogeographic domains, representative samples of the major lithofacies were examined by means of the scanning electron microscope, in order to reveal composition and textural details of the micritic groundmass. As a major result, it appeared that in most of the lithologies investigated, *Schizosphaerella* DEFLANDRE & DANGEARD, a presumably planktonic calcareous nanno-organism of uncertain systematic position, constitutes the only still identifiable biogenic component of matrix that may assume volumetric importance. Coccoliths usually also occur, but other than in post-Jurassic pelagic sediments, they generally can not be demonstrated as contributing significant amounts of carbonate to the rock. The bulk of the fine-grained carbonate is, as a rule, represented by anhedral to subhedral, tightly interlocked calcimicrite and microspar which originated, with progressive lithification, probably both by neomorphic processes and as cement filling interparticle and intrabiotic pore space, and hence does not provide any direct information about the nature of source materials. In cases, e.g. that of the stratigraphically condensed Rosso Ammonitico and related facies, neomorphic calcite and calcite cement might have been derived almost exclusively from truly pelagic sources (cf. JENKYN 1974); but more often the initial sediment most probably was a mixture of pelagic elements and allochthonous, platform-derived carbonate lutum (peri-platform ooze; cf. SCHLAGER & JAMES 1978). In particular, this would apply to even-bedded, relatively rapidly deposited grey to light-coloured basinal limestone formations widespread in the Tethyan Early Jurassic (e.g. the Umbrian Corniola Formation, the Tuscan Calcare Selcifero, the Siniai Limestone of the Ionian Zone and the Medolo or the Domaro Limestone in Lombardy), which on a regional scale can be inferred to be spatially related to sites with persistent shallow-water carbonate deposition, or where alternatively such a link is directly indicated by interbedded mass-flow deposits containing coarser material of obvious shallow-water provenance (e.g. KÄLIN et al. 1979). In contrast to Upper Jurassic and Lower Cretaceous Tethyan lithofacies, such as the Rosso ad Aptici and the Maiolica Formation (cf. BERNOULLI 1972), the deposits examined here invariably lack incompletely lithified, hence diagenetically less altered, counterparts of an equivalent age for a comparison. Thus, both the initial mineralogical and petrographical composition of their lime-mud fraction must largely remain a topic for speculations, as well as the single steps involved in its diagenesis.

The object of the present account is the enigmatic nannofossil *Schizosphaerella* which was obviously one of the most resistant to diagenetic obliteration amongst the components of the fine carbonate fraction of the lithofacies investigated and, as will

be shown, moreover served as a preferred site of deposition for secondary over-growth cement during diagenesis. In case of the coccolithophorids, it has been found that resistivity to dissolution (both with increasing water-depth and progressive burial diagenesis) depends on coccolith architecture, shape and dimensions of the single structural elements and the orientation of the crystallographic axes in the skeletal elements (MCINTYRE & MCINTYRE 1971, ADELSECK et al. 1973, NEUGEBAUER 1974, 1975). As presumably the same factors account for the selective preservation of *Schizosphaerella* in the Early and Middle Jurassic sediments studied, an understanding of its skeletal structure seems to be fundamental. The central theme of this paper is therefore an analysis of the valve ultrastructure of *Schizosphaerella punctulata*. In addition, diagenetic modifications of the primary ultrastructural pattern occurring in Tethyan Jurassic carbonate facies will be described.

Previous work

Representatives of the *incertae sedis* group of the schizosphaerellids were described first in 1938 by DEFLANDRE & DANGEARD. In samples of Lower Oxfordian (Mariae Zone) marls collected at Villers-sur-Mer in Normandy as well as from Bajocian strata at some additional localities in the same region, these authors recognized the presence of abundant tiny (12–30 µm diameter) globular calcareous tests composed of two interlocking subhemispherical valves which, under the light microscope, appear punctate ("... ornémentées de ponctuations ...") in a more or less regular pattern (cf. Fig. 1). With reference to their main morphological features, DEFLANDRE & DANGEARD introduced these nannofossils under the name *Schizosphaerella* n.gen. *punctulata* n.sp. The authors moreover called attention to a striking morphological resemblance of these nannofossils to diatoms, but rejected a close systematic relationship because of the calcareous nature of their skeletons.

In the following twenty years, there were few advances in the understanding of the morphology and the skeletal structure of schizosphaerellids, as well as of their possible systematic position. However, occurrences of *Schizosphaerella* were recognized from additional localities and stratigraphic levels, and its role as an important constituent amongst the nannofossils populating the Jurassic seas became more and

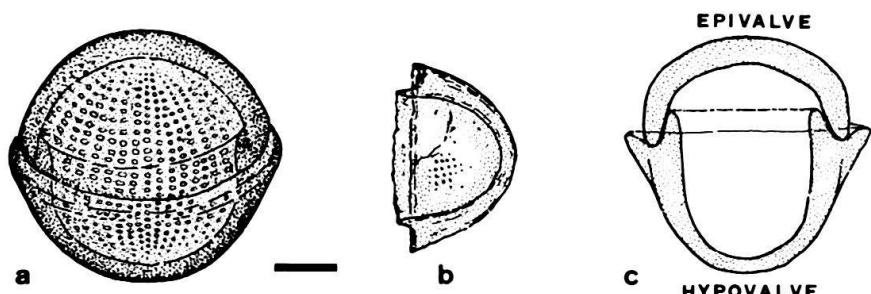


Fig. 1. Morphology and ornamentation of *Schizosphaerella punctulata*, as established by DEFLANDRE & DANGEARD by observation with the light microscope. After DEFLANDRE & DANGEARD (1938, Fig. 1, 2 and 5); scale bar 5 µm approx.

a = Slightly oblique view of an intact specimen of *S. punctulata*. b = Detached hypo valve. c = Axial (longitudinal) section of an intact specimen.

more established amongst French geologists and palaeontologists. In particular, it appeared that the stratigraphic range of these nannofossils extends also into the Liassic. *Schizosphaerella* has been recognized in the Upper Liassic by DANGEARD (1941, 1942) and DEFLANDRE (1954), in the Pliensbachian by URBAIN (1951).

In 1959, in a review on systematics of the calcareous nannofossils, DEFLANDRE proposed the introduction of the family of the Schizosphaerellidae (with *Schizosphaerella* DEFLANDRE & DANGEARD as its type genus), because he felt that further research would reveal a considerable diversity amongst the representatives of this nannofossil group, and at the same time, he suggested the presumed Liassic diatoms of the genus *Pyxidicula* EHRENBERG (cf. ROTHPLETZ 1900) as members of this family.

From the beginning of the sixties, records of the genus *Schizosphaerella* DEFLANDRE & DANGEARD became more frequent and gradually more detailed information concerning the stratigraphic range of schizosphaerellids, the wall ultrastructure and the behaviour during diagenesis became available:

- 1961 STRADNER reported schizosphaerellids from Sinemurian to Bajocian strata in Würtemberg (Germany) and Dorset (England) under the name *Nannopatina* n.gen. *grandaeva* n.sp. In 1963, he placed *N. grandaeva* in synonymy with *Schizosphaerella punctulata* DEFLANDRE & DANGEARD.
- 1964 RIOULT dealt with the mode of preservation of schizosphaerellids included in condensed phosphatic and glauconitic Bajocian deposits (Couche Verte, Conglomérat de Bayeux) from Normandy. He noticed among these specimens forms which, on the basis of overall shape of the valves, valve thickness and nature of the ornamentation, differed from the holotype of *S. punctulata* recovered by DEFLANDRE & DANGEARD from the Marnes de Villers.
- 1965 NOËL, in her monograph about Jurassic coccoliths, published the first electron micrographs of *S. punctulata* (transmission electron micrographs from germanium-shaded carbon replicas of outer valve surfaces; Pl. 27, Fig. 6, 7 and 8 in NOËL 1965). The samples investigated derived from the Toarcian and Pliensbachian of the Yonne area, southeastern border of the Paris Basin. Based on these micrographs, she characterized the ultrastructure of the valve surface as follows: «La coque est faite d'éléments de calcite dont la forme est difficile à définir, mais qui sont organisés de façon telle qu'ils déterminent un réseau assez régulier, à mailles carrées, disposées suivant les parallèles de la coque. Il semble que les éléments de calcite soient des cristaux de section sensiblement rectangulaires, associés par quatre, en croix, dont les bras sont décalés les uns par rapport aux autres.» – She also found that the “ponctuations” on the valve surface, observed by DEFLANDRE & DANGEARD under the light microscope, correspond with voids in the network of the calcitic ultrastructural elements building up the valves; and moreover, she noticed that the above described ultrastructural pattern is often obscured by diagenetic calcite crystals which tend to close the original skeletal voids.
- 1967 LEZAUD described the first occurrence of *S. punctulata* in Early Kimmeridgian sediments (“common” in Baylei Zone, “rare” in Uralensis and Mutabilis Zones) from Baie de Seine.

1970 BERNOUlli & RENZ and BERNOUlli & JENKYNS referred to *Schizosphaerella* DEFLANDRE & DANGEARD (determined by B. Prins) as an important sediment contributor in Early and Middle Jurassic deep-water limestones and marls from Western Greece, the Apennines and the Eastern Alps.

1971 BLACK reported the hitherto earliest reliable stratigraphic occurrence of schizosphaerellids; he found representatives of the species *S. punctulata* in the Hettangian (Angulata Zone) of Pinhay Bay (Dorset). One year later, the presence of this species in Hettangian beds was described also from the Paris Basin (AMEZIEUX 1972).

1974 AUBRY & DÉPÈCHE reexamined the schizosphaerellids from the type-locality Villers-sur-Mer by means of both the light and the scanning electron microscope, and figured a series of SE-micrographs of excellently preserved specimens which they succeeded to free from the argillaceous sediment. Within the population studied, they recognized a considerable variability in the valve morphology: two main groups of valves, i.e. "valves cupuliformes" and "valves en clochette" (bell-shaped) and three types of hingement of the valves were distinguished. The authors furthermore attempted an analysis of the valve ultrastructure and discussed possible ways by which the valve surfaces can be modified during diagenesis. As for the original ultrastructure, they proposed two types of basic structural elements, i.e. tiny calcitic plates ("lames") and rods ("bâtonnets"), arranged together in a regular framework of subcubic cells, each slightly shifted with respect to its neighbours and less than a micron across (cf. Fig. 2a). However, the authors themselves stressed the

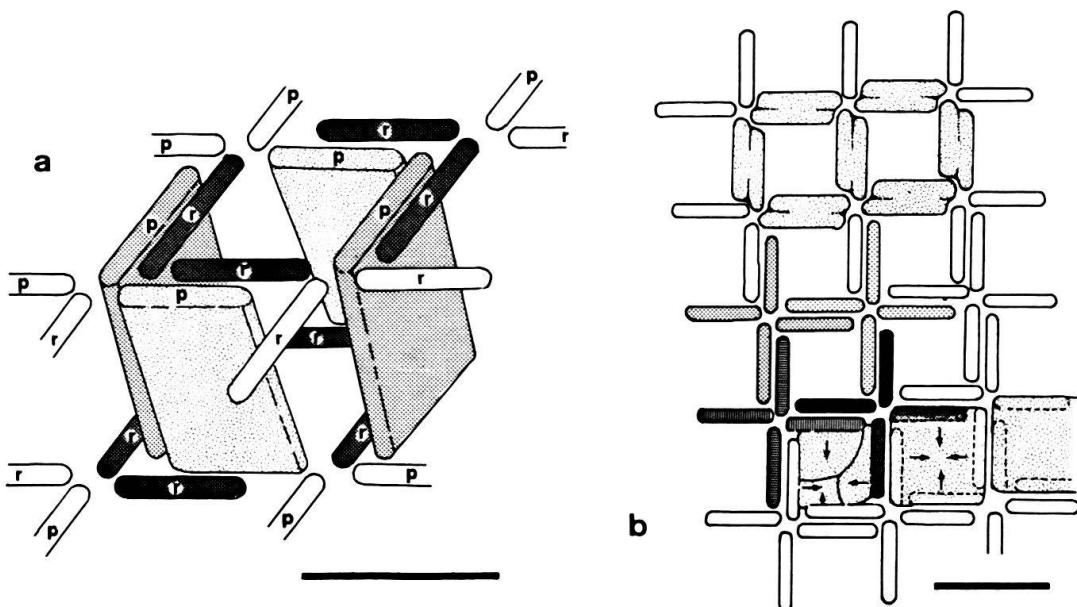


Fig. 2. The ultrastructure of *Schizosphaerella punctulata* DEFLANDRE & DANGEARD according to AUBRY & DÉPÈCHE (1974, Fig. 19 and 23-25); scale bars 1 μ m approx.

a = Diagrammatic representation of a subcubic unit cell of the calcareous framework of a valve; the constituent structural elements are tiny calcite plates (p) and rods (r), with the former being oriented slightly obliquely with respect to the valve surface. b = top view of a portion of a valve surface; juxtaposed rods and terminations of plates define a regular cross-like pattern with square meshes, each of them slightly shifted with respect to its neighbours; in the upper and lower part of the diagram, diagenetic modifications of the original surface pattern are displayed.

provisional character of their reconstruction, as many ultrastructural details observed on SE-micrographs do not allow an unambiguous interpretation and some obviously do not fit the model. Diagenesis in turn tends to modify the regular ultrastructural pattern observed on the surface of well-preserved valve specimens (cf. Fig. 2b, central part), according to AUBRY & DÉPÈCHE, mainly in the following three ways: 1. Coalescence of always two juxtaposed basic structural elements (a plate and a rod according to the structural model proposed by the authors) by which the original surface pattern is reduced to the simple reticulation shown in the upper part of Figure 2b. 2. Cementation of the square original skeletal voids by diagenetic overgrowth on the delimiting basic skeletal elements resulting in a regular mosaic of subcubic calcite crystals, as shown in the lower part of Figure 2b. 3. Transformation of the original mesh-structure into an irregular mosaic of calcite microgranules, with the original wall ultrastructure presumably being partially destroyed during this process. Touching finally on problems related to the systematics of the schizosphaerellids, the authors excluded the possibility of a biological affinity to the diatoms, in spite of an incontestable morphological resemblance. As an argument against this, they quoted not only the different chemical nature of the skeletons, but also the particular ultrastructure, which indeed seems to have no parallels with that of any other organism known to date.

1979 MEDD stated that the entire range of *S. punctulata* established from the British Jurassic material so far examined is from the Planorbis Zone (Early Hettangian) to the Cymodoce Zone (Early Kimmeridgian).

1979 MOSHKOVITZ described, under the name *Schizosphaerella astrea*, a new species of the hitherto monospecific genus *Schizosphaerella*. *S. astrea*, the holotype of which is derived from Early Pliensbachian strata (Ibex Zone) cored in the Stowell Park Borehole, Gloucestershire (England), differs from *S. punctulata* primarily by the ultrastructure of the valves. Instead of the regular pattern with typically cross-like crystallites (cf. Fig. 2b), *S. astrea* reveals on SE-micrographs a random orientation of the basic ultrastructural elements all over its valves, with up to six plate-shaped calcite crystals radiating starlike from the same point. In the Stowell Park Borehole, *S. astrea* ranges from the Early Sinemurian (Bucklandi Zone) to the Early Pliensbachian (Ibex Zone), and it occurs throughout together with representatives of the long-ranging species *S. punctulata*. In his original description of *S. astrea*, MOSHKOVITZ further pointed to a structural resemblance to *Thoracosphaera tesserula* FÜTTERER (1977, Pl. 3, Fig. 1-8, 10 and 11), and – because the genus *Thoracosphaera* KAMPTNER recently has been transferred systematically to the calcareous dinoflagellates (FÜTTERER 1976) – he considered the schizosphaerellids also as possible cysts of calcareous dinoflagellates.

Material studied

The present study, as stated above, grew out of investigations aimed at an environmental and genetic interpretation of Early to Middle Jurassic continental-margin deposits from the Southern Alps and the Northern Apennines. In this

context, *Schizosphaerella* was found to occur with varying frequency in almost all of the lithologies which were examined in detail. I thus shall not attempt to specify individual samples, yet mention here but a number of lithologic units which proved to be particularly rich in schizosphaerellids:

- *Rosso Ammonitico*, lower part; Monte Cetona, southeastern Tuscany. Ammonites collected during a recent survey of the Jurassic sequence outcropping in the area indicate a Lotharingian age (Obtusum Zone) for the respective lithostratigraphic interval (KÄLIN & PATACCA, in prep.). The major lithology is a reddish skeletal wackestone with abundant ammonites ("cephalopod limestone") and crinoid ossicles. In thin-section, the matrix typically reveals a pelleted texture (Fig. 3a) which under the SEM appears as being due to abundant, randomly oriented *Schizosphaerella* valves, 20–30 µm in diameter, set into a mosaic of micrite- to microspar-sized neomorphic calcite and calcite cement. From SEM micrographs of polished and slightly etched sample surfaces, it was found by point-counting that schizosphaerellids occupy around 15% of the total matrix volume.

Interestingly, in this lithology *Schizosphaerella* valves are also frequently found as geopetal fillings of the mouldic cavities of ammonites left after dissolution of the aragonitic shell material (cf. Fig. 3a). Moulds obviously must have been in communication with the overlying water column, and consolidation of the rock as well as subsequent selective leaching of the skeletal aragonite, therefore, are most likely to have occurred very close to or right at the sediment-water interface.

The schizosphaerellids present in this rock-type are invariably globular forms with the two valves joined by simple overlapping. They differ from those encountered within the lithologies that will be mentioned below by markedly larger average dimensions and by the style of preservation. I first tended to relate the latter point to the particular diagenetic history the rock apparently has undergone. However, it now appears more feasible to me that the schizosphaerellids in question belong to the species *S. astrea* most recently described by MOSHKOVITZ (1979), hence the observed diagenetic modification would not be based on the regular ultrastructural pattern characteristic of the species *S. punctulata*.

- *Corso Rosso*; Brescia area, Lombardy. The Corso Formation, part of which is the Corso Rosso, disconformably overlies the massive shallow-water limestones of the Corna Formation in the area east of Brescia and is thought to mark an Early Jurassic structural high near the eastern border of the Lombard Basin. The Corso Formation comprises the Lotharingian and a large part of the Pliensbachian (CASSINIS 1968, 1978; CASSINIS & CANTALUPPI 1967; GAETANI 1975). The Corso Rosso Member, Pliensbachian in age, is a unit of thin-bedded, pink to light-coloured calcilutites containing, besides sponge spicules and occasional crinoid ossicles, chiefly pelagic faunal elements, such as ammonite embryos, fragments of thin-shelled bivalves and radiolarians, the latter preserved as spar-filled moulds. Typically, the rock is strongly bioturbated, and most beds reveal an early diagenetic nodular structure in various stages of development. Lenses of brownish or reddish vitreous replacement chert occasionally occur.
- *Calcare Selcifero*; Monte Cetona, southeastern Tuscany ("Calcare Selcifero B" of KÄLIN & PATACCA, in prep.). In the Monte Cetona area, light grey, chert-bearing basinal limestones ("calcari selciferi") occur in two different stratigraphic positions, below and above the Lotharingian/Early Pliensbachian Rosso Ammonitico Formation, in contrast to the normal Tuscan Jurassic sedimentary

sequence (cf. BERNOLLI et al. 1979; KÄLIN et al. 1979). The younger, Late Pliensbachian, unit referred to here, comprises well-bedded fine calcarenites to calcilutites with sedimentary structures suggesting current-controlled sediment dispersal and deposition. Occasionally, minor slump-sheets and intraformational conglomerates also interfere in the sequence. In this deposit, the volumetric proportion of the fine-grained matrix occupied by *schizospaerellids* has been found to be some 8–10%. Additional biogenic components of the rock include sponge spicules, radiolarians (both commonly preserved as compactively deformed calcite-filled moulds), rare benthonic foraminifera and *Globochaete*.

- *Valmagggiore Formation*; western Lombardy (Monte Nudo Basin, cf. KÄLIN & TRÜMPY 1977). In the Monte Nudo Basin, the Late Liassic and presumably a major part of the Middle Jurassic are represented by a sequence, up to 300 m thick, of interbedded greenish hemipelagic marls and brown-grey or grey-green chert-bearing turbiditic calcarenites to calcisiltites often with associated thick massive marlstones. Paleocurrent indicators, together with the interpretation of the general sedimentary and paleotectonic evolution of the area, yield conclusive evidence that the Gozzano structural high, located some 10–15 km to the west and southwest, was the principal source for the redeposited sediment in the Valmagggiore Formation. The calciturbidites are seen in thin-section to contain, apart from some shell debris of posidoniids and calcite-cemented moulds of fragmented sponge spicules and radiolarians, mainly silt-sized, weakly translucent peloidal lutite aggregates. Sorting during deposition of the turbidites caused these lutite clots to be concentrated in laminae (cf. Fig. 3b), and often they appear as closely packed as to form a supporting framework, with the frame interstices filled by clear (micro)spar. Under the SEM, such particles usually resolve into glomerate clusters of *Schizospaerella* valves and valve fragments with anhedral neomorphic calcimicrite, clay flakes, frequent tiny pyrite fram-boids and occasional coccoliths trapped in between (Fig. 3d).

KÄLIN & TRÜMPY (1977) did not suggest a possible mode of origin for this lutite aggregates; for their data, drawn from thin-sections only, were inconclusive. Based on the lack of obvious shallow-water derived particles as well as of any coarser clastic material over the whole outcrop area of the Valmagggiore Formation and on the available data about the sedimentary evolution of the inferred source area, they however supposed that the gravity-flow deposits would have displaced essentially weakly consolidated, penecontemporaneous deeper-marine sediment. The detailed composition of the lutite clots included within the calciturbidites, now revealed by means of the SEM, largely confirms this view. Furthermore, it suggests that these could have originated as faecal pellets, either by sediment-feeding benthonic organisms populating the source area or possibly also zooplankters feeding on phytoplankton in near-surface waters (cf. ROTH et al. 1975). A pelleted nature of at least parts of the mud fraction of the source material might ultimately also have added to its ability for remobilization and subsequent downslope mass movement, in that cohesion and hence shear strength would be expected to be less in pelleted than in unpelleted muddy sediment.

Silt- and sometimes sand-sized aggregates of *schizospaerellid* skeletons which presumably originated by organic agglutination proved not to be a characteristic of the Valmagggiore Formation only, but were likewise found to represent a major component of current-laid calcarenites and calcisiltites occurring in e.g. the Lombardian *Concesio Formation* (Late Liassic and Middle Jurassic p.p. in the Sebino area, cf. GAETANI 1975) and the Umbrian *Marne del Serrone* (Late Liassic, cf. COLACICCHI et al. 1970, BERNOLLI et al. 1979; Fig. 3c). In addition, a trend towards aggregation of *Schizospaerella* valves has been observed in many, apparently autochthonous Jurassic deeper-water carbonate lithofacies.

In the samples studied from the South-alpine, the Tuscan and the Umbrian Jurassic sedimentary sequence, the skeleton of the schizosphaerellids, however, appeared invariably moderately to strongly altered by secondary calcite overgrowth (e.g. Fig. 4b, d). For the purpose of a reconstruction of the original valve ultrastruc-

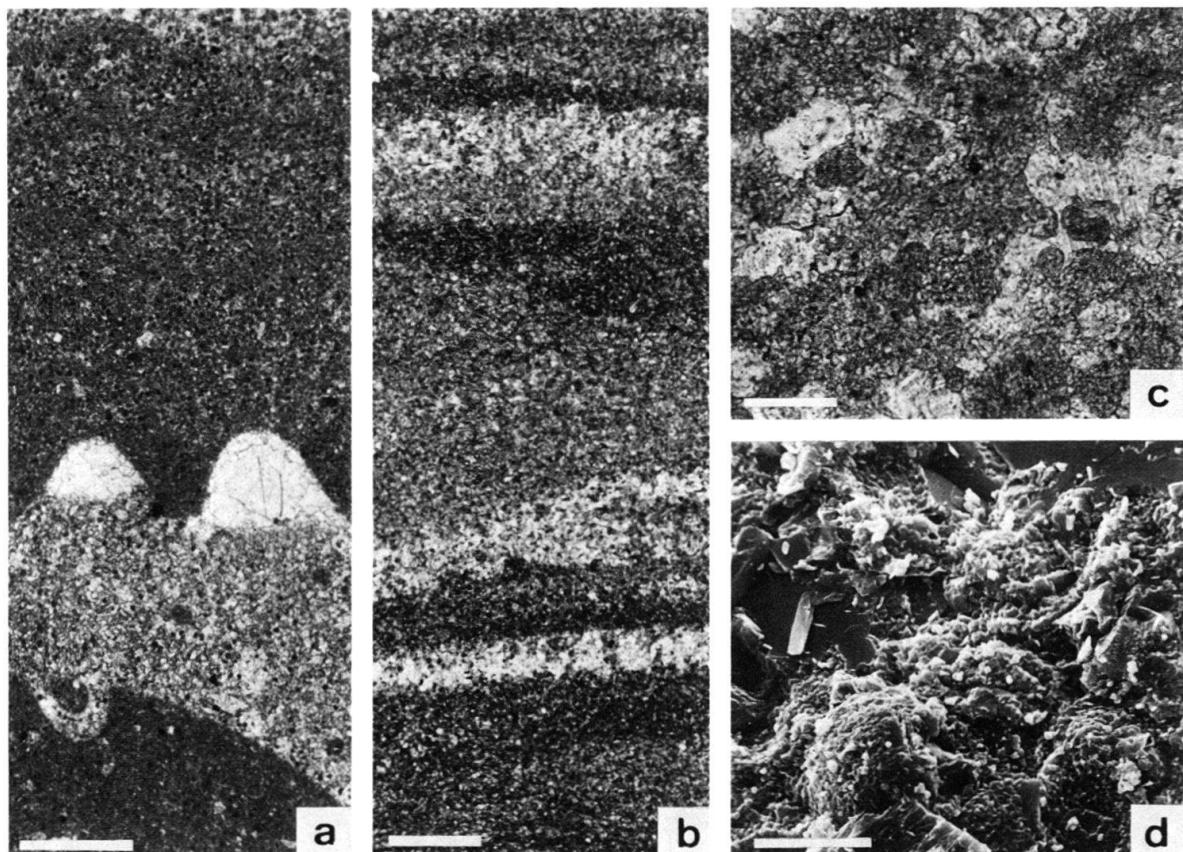


Fig. 3. a = "Pelleted" texture of the matrix of reddish skeletal wackestone (cephalopod limestone). In effect, the dark clots correspond largely with randomly oriented, roughly hemispherical *Schizosphaerella* valves. The lower half of the photograph shows a mould of an ammonite shell filled with geopetal sediment and sparry calcite cement; the infilled sediment likewise contains abundant schizosphaerellid skeletons.

Rosso Ammonitico (lower part); Lotharingian; Monte Cetona (southeastern Tuscany). Thin-section; scale bar 1 mm.

b = Current-laminated fine calcarenite to calcisiltite (turbidite) composed essentially of dark-coloured lutite clots which, with the SEM (cf. Fig. 3d), are clearly seen to be glomerate clusters of *Schizosphaerella* valves and their debris, and are interpreted as redeposited faecal pellets. Light tinge of some of the laminae is due to partial silification.

Valmaggiore Formation; uppermost Liassic; about 1 km northeast of Cittiglio (western Lombardy). Thin-section; scale bar 1 mm.

c = Fabric of fine sand- to silt-sized lutite aggregates of presumed faecal origin with interstitial clear (micro)spar. In places, semicircular sections of the constituent *Schizosphaerella* valves can be discerned. Detail of current-laminated division of a calciturbidite.

Marne del Serrone; Toarcian; Valdorbia (F. Sentino, Umbria). Thin-section; scale bar 50 µm.

d = Clustered schizosphaerellid skeletons and skeletal debris surrounded by (micro)sparitic cement crystals. Fresh broken surface of the same sample as in Figure 3b. Valmaggiore Formation; uppermost Liassic; about 1 km northeast of Cittiglio (western Lombardy). SEM micrograph; scale bar 10 µm.

ture, I therefore had to resort to material derived from outside of the above paleogeographic domains. A number of samples from the Early Toarcian *Schistes Carton* of the Causse Basin (southern France) proved of particular interest. These samples were kindly provided by D. M. Trümpy. As in case of the Oxfordian specimens from Villers-sur-Mer described by AUBRY & DÉPÈCHE (1974), the schizospaerellids contained in the dark-coloured bituminous marls and occasional laminated marly limestones of the *Schistes Carton* often reveal an excellent preservation, presumably with only minor diagenetic modification of the valve ultrastructure (e.g. Fig. 4a, c).

Finally, some 10 samples of presumed Oxfordian–Kimmeridgian marls and limestones from DSDP Site 105 (Cores 37 and 38) in the Western Central Atlantic and Site 367 (Cores 35–37) in the Cape Verde Basin were examined for the presence of schizospaerellids; for there is, strangely enough, no record as yet of *Schizospaerella* from any of the DSDP Sites where Jurassic strata were reached (cf. MOSHKOVITZ 1979). The samples studied here also proved invariably barren and, judging from the preservation of other calcareous micro- and nannofossils, there seems to be no reason to believe that schizospaerellid skeletons were eliminated either by depth-controlled dissolution or during burial diagenesis. The question thus arises, whether such lack is simply due to the fact that the sediments in question actually postdate the stratigraphic range of *Schizospaerella*, hence that they comprise neither the Oxfordian nor the lowermost Kimmeridgian, or whether the occurrence of these nannofossils was for some, possibly ecologic, reasons restricted to the continental-margin areas of the Alpine-Mediterranean Tethys and adjacent epeiric seas. At least in case of Sites 105 and 367, the former possibility might apply, as the Oxfordian has in effect not been reliably documented biostratigraphically. However, also the second point has to be considered until new data become available; in particular, until the systematic position of the schizospaerellids is clarified and then possibly inferences can be drawn about their mode of life.

a = Overview of light-coloured lamina from marly limestone with alternating light- and dark-coloured (rich in organic matter) layers. *Schizospaerella* valves and valve fragments set in a mosaic of blocky (micro)spar which is thought to be largely interstitial cement. Fringes of radially arranged elongated calcite crystals around valves might represent a ?recrystallized first generation cement.

Schistes Carton; Early Toarcian; Tournemire (Aveyron, southern France). SE-micrograph of fresh broken surface; scale bar 25 µm.

b = Groundmass of light-grey basinal lime mudstone: strongly altered (overgrown) schizospaerellid skeletons scattered throughout a mosaic composed of blocky micritic to microsparitic neomorphic calcite and calcite cement.

Calcare Selcifero; Late Pliensbachian; Monte Cetona (southeastern Tuscany). SE-micrograph of fresh broken surface; scale bar 10 µm.

c-d = Morphology of *Schizospaerella punctulata*. c = Relatively thin-walled form with bell-shaped hypoalve (left) and cup-shaped epivalve (right). Part of the epivalve is broken away, such that the proximal terminations of cement crystals grown on the inner surface of the valve are exposed. Terminations of cement crystals perfectly mould the surface morphology of the valve. d = Thick-walled, roughly globular form with the two subhemispherical valves joined by simple overlapping; axial fracture. Original skeletal voids are filled by secondary calcitic overgrowth cement.

c from Schistes Carton; Early Toarcian; Tournemire (Aveyron, southern France); SE-micrograph; scale bar 10 µm. d from Valmaggiora Formation; uppermost Liassic; about 1 km northeast Cittiglio (western Lombardy); SE-micrograph; scale bar 5 µm.

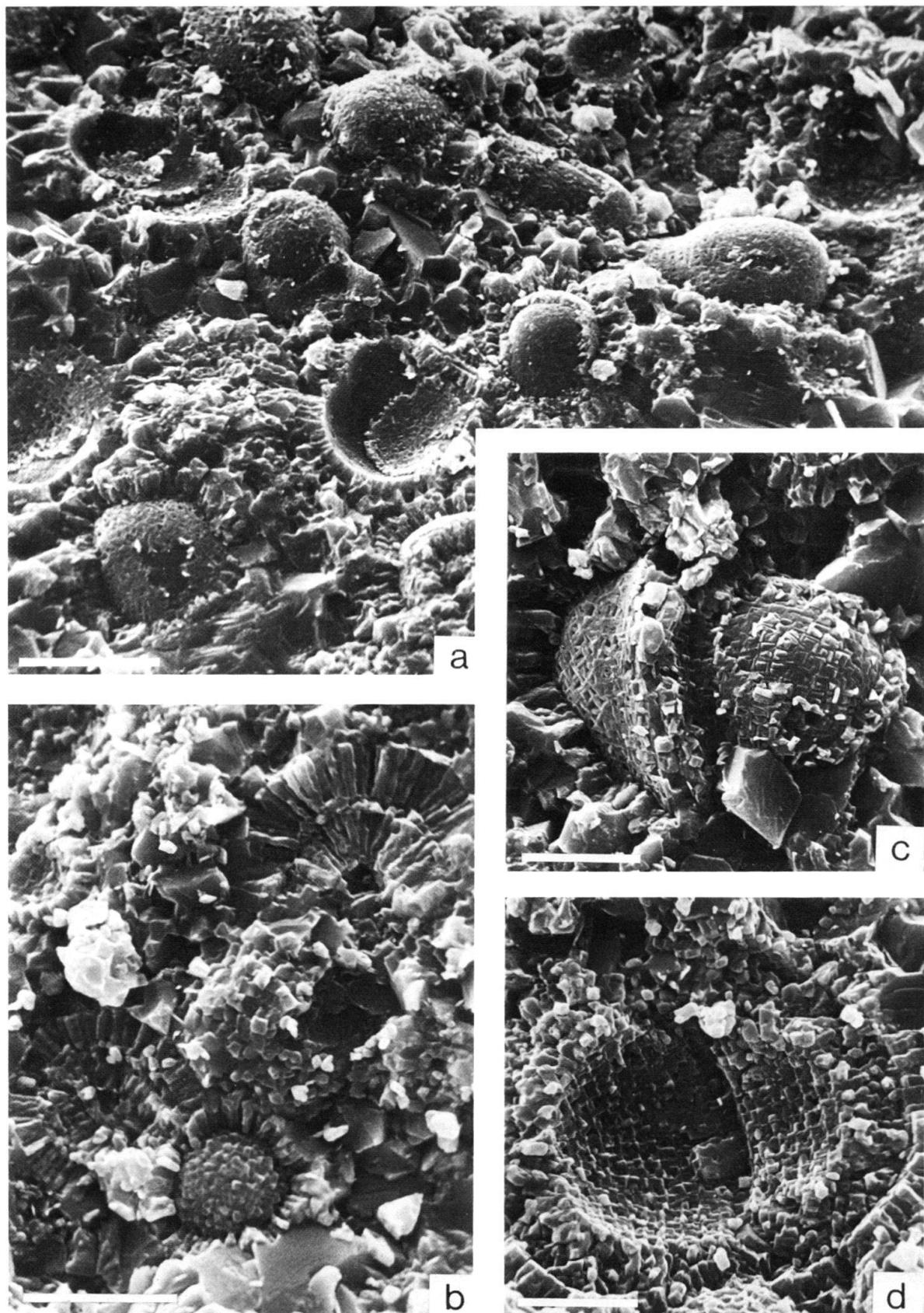


Fig. 4. Ultrastructure of *Schizosphaerella*-bearing sediments and morphology of *Schizosphaerella punctulata*.

The wall ultrastructure of *Schizosphaerella punctulata*
DEFLANDRE & DANGEARD

The evidence gathered during both the investigation of my own material and a revision of already published SE-micrographs on the subject led me to question the accuracy of the model proposed by AUBRY & DÉPÈCHE in 1974 (cf. Fig. 2a) and hence to attempt an alternative interpretation of the original wall ultrastructure of *Schizosphaerella punctulata* that would account for the main structural features observed with the SEM more accurately and would appear more consistent from a geometrical point of view, yet be feasible from a biological one. The results attained will in the following sections be outlined and illustrated with photographs of some carton models which were constructed in order to test feasibility of the structural model.

In contrast to the model suggested by AUBRY & DÉPÈCHE (1974), I think that the wall ultrastructure of *S. punctulata* is based on only one type of fundamental structural element, in spite of its apparent complexity. These are parallelogram-shaped calcite plates, about 0.1 μm thick, some 0.5–0.7 μm wide (cf. Fig. 5a, d; Fig. 6c) and of a length which varies as a function of the wall thickness, as will be seen later. Although an exact determination of interfacial angles of these lamellar calcite crystallites is prevented by their small thickness and, in particular, by their being usually oriented more or less obliquely with respect to the plane of photograph, it seems likely from the available SE-micrographs that the lamellae are actually bounded by rhombohedral crystal faces (cf. Fig. 5c; Fig. 6h), as is frequently found with basic structural elements occurring in coccolithophorids (BLACK 1963, PAUTARD 1970). A basic structural element then could be conceived as an irregularly distorted rhombohedron ($h0\bar{h}1$) elongated to variable extents in the two directions of the edges of one of its faces to assume the form of a thin tabular crystal with parallelogram-shaped outline. In the carton models Figures 7, 9 and 10, as well as in the constructional diagram Figure 12, the rhombohedral symmetry of the fundamental skeletal elements has been left out of consideration in order to facilitate construction, and simple parallelogram-shaped plates with the edges forming angles of 60° (angle a in Fig. 7a) and 120° have instead been used as constructional elements; this point however will be touched on again, when diagenetic modifications of the original wall ultrastructure are discussed.

From SE-micrographs such as reproduced on Figures 5 and 6, it can clearly be seen that the elementary calcite plates are oriented obliquely with respect to the

a-b, e-f = Structure of valve surfaces; fundamental structural elements are parallelogram-shaped lamellar calcite crystallites, oriented obliquely with respect to the valve surfaces (a, f = inner valve surfaces; b, e = outer valve surfaces). In the upper part of e, the calcite lamellae are largely broken away and it appears a more or less regular arrangement of roughly pyramidal forms that correspond with original skeletal voids filled by secondary overgrowth cement (cf. Fig. 11). c-d = Fractured valve specimens revealing the internal structural organization of *S. punctulata*. Arrows in a and d indicate points, where the parallelogram-shaped outline of the basic structural elements is evident (see also Fig. 6c).

Schistes Carton; Early Toarcian; Tournemire (Aveyron, southern France). SE-micrographs; scale bars 1 μm (a, c, d, e, f) and 5 μm (b).

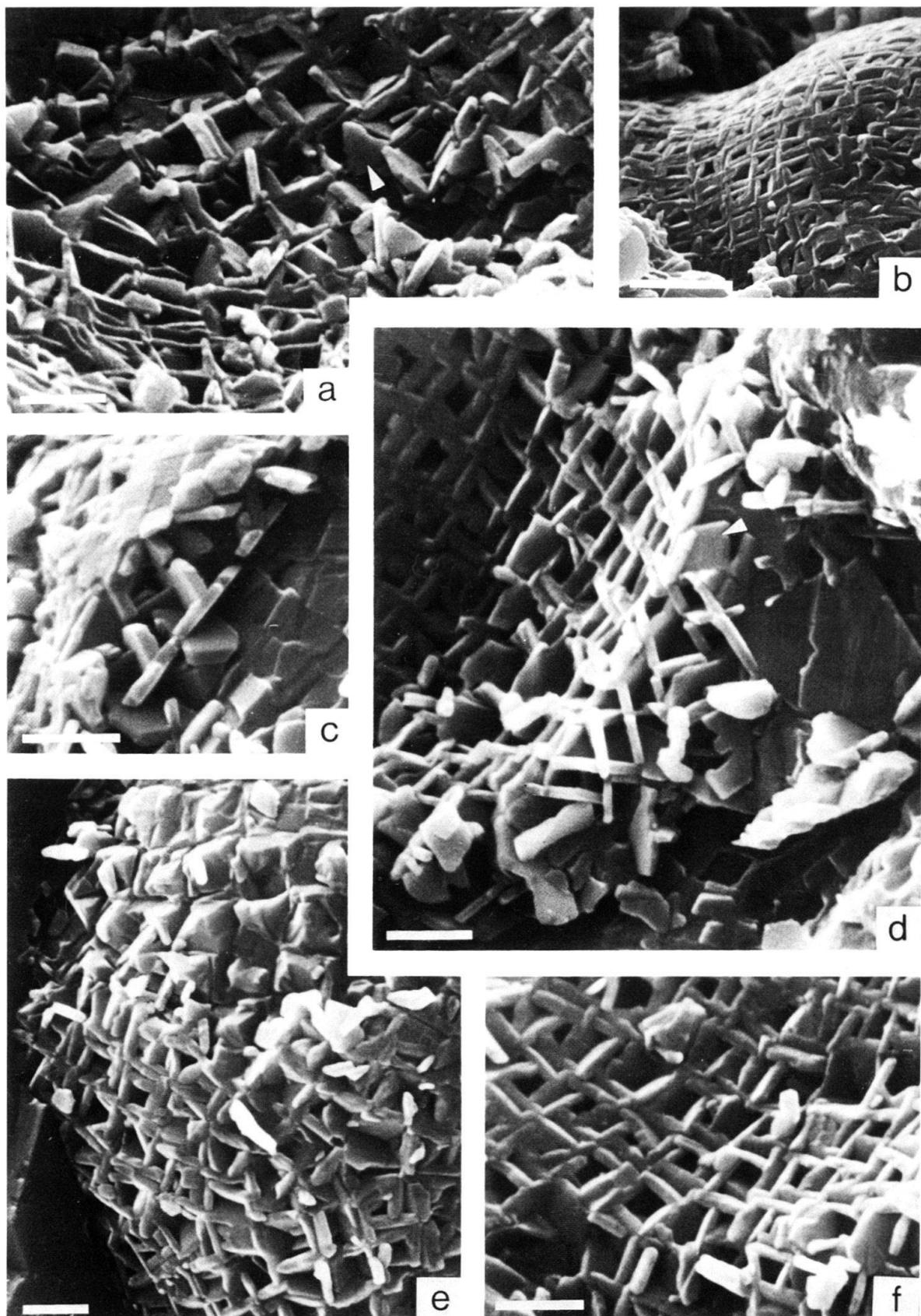


Fig. 5. Wall ultrastructure of *Schizosphaerella punctulata*.

surfaces of the test wall (cf. also Pl. 4, Fig. 12, in AUBRY & DÉPÈCHE 1974 and Pl. 1, Fig. 6, in MOSHKOVITZ 1979); yet from the micrographs the angle of inclination (angle b , or the complement b' in Fig. 7) could again not be accurately established. When looking at a valve surface, it furthermore appears that the lamellae do not always slant in the same direction, but that they may assume different orientations relative to each other and hence mutually intersect. However, orientations do not vary at random; rather, a quite regular surface pattern is normally observed, with the lamellae occupying four distinct positions at right angles to each other (cf. Fig. 6a), which recur systematically. The basic structural elements can then be inferred to be spatially interrelated as illustrated by the models b, c and d in Figure 7.

From the models b and c in Figure 7, two main conclusions can be drawn:

1. Normally, only lamellae that slant in opposite directions may intergrow; hence, no intersections other than parallel to the surfaces of the test wall occur (stages of intergrowth are represented in Fig. 8).
2. The uncertainty about the actual values of both the edge angle a and the angle of inclination b does not raise constraints on the validity of the structural model, because obviously feasibility of the arrangement illustrated by model c does not critically depend on a specific value of either of the angles a or b .

In model d in Figure 7, four couplets of intersecting lamellae are mutually combined in the way displayed in model c, the resulting frame being symmetrical with respect to a central vertical axis of tetragonal symmetry. Viewed from above, the four converging lamellae define a pyramidal cavity, whilst the intersections of pairs of lamellae form a square. Hence, there appear exactly those features which are found in effect to frame the surface morphology in well preserved specimens of *S. punctulata* (e.g. Fig. 5a, 6a, b).

Through systematic iteration of the above frame, finally, a portion of a valve surface has been modelled. The top view of this model, reproduced in Figure 9, reveals an additional characteristic of the surface pattern of *S. punctulata*, namely, a regular slight shifting amongst the juxtaposed tetragonal unit cells (e.g. Fig. 5b). The same feature has already been recognized by NOËL (1965) and then stressed by AUBRY & DÉPÈCHE (1974, p. 9–10 and Pl. 4; see also Fig. 2 in this paper), but no explanation has yet been provided for this point. In the structural model proposed here, such a systematic shift is necessarily implied, because neighbouring isoriented

a, b, c, h = Details of surface pattern of valves (a, h: inner valve surfaces; b, c = outer valve surfaces). Numbers 1–4 in a indicate the four distinct orientations the elementary plates normally occupy (cf. Fig. 7). d, f = Fractured thin-walled specimens; in d, the elementary calcite lamellae are visibly thickened as a result of diagenetic syntaxial overgrowth. e, g = Surface pattern in diagenetically altered valve specimens; the original regular partition into tetragonal unit cells may still be discerned, but the pyramidal cavities are largely closed due to precipitation of syntaxial overgrowth cement on the delimiting skeletal elements (for details cf. Fig. 13).

a, b, c, d, f, h from Schistes Carton; Early Toarcian; Tournemire (Aveyron, southern France); SE-micrographs; scale bars 1 μm . e, g from Valmaggiore Formation; uppermost Liassic; about 1 km northeast Cittiglio (western Lombardy); SE-micrographs; scale bars 5 μm (e) and 2 μm (g).

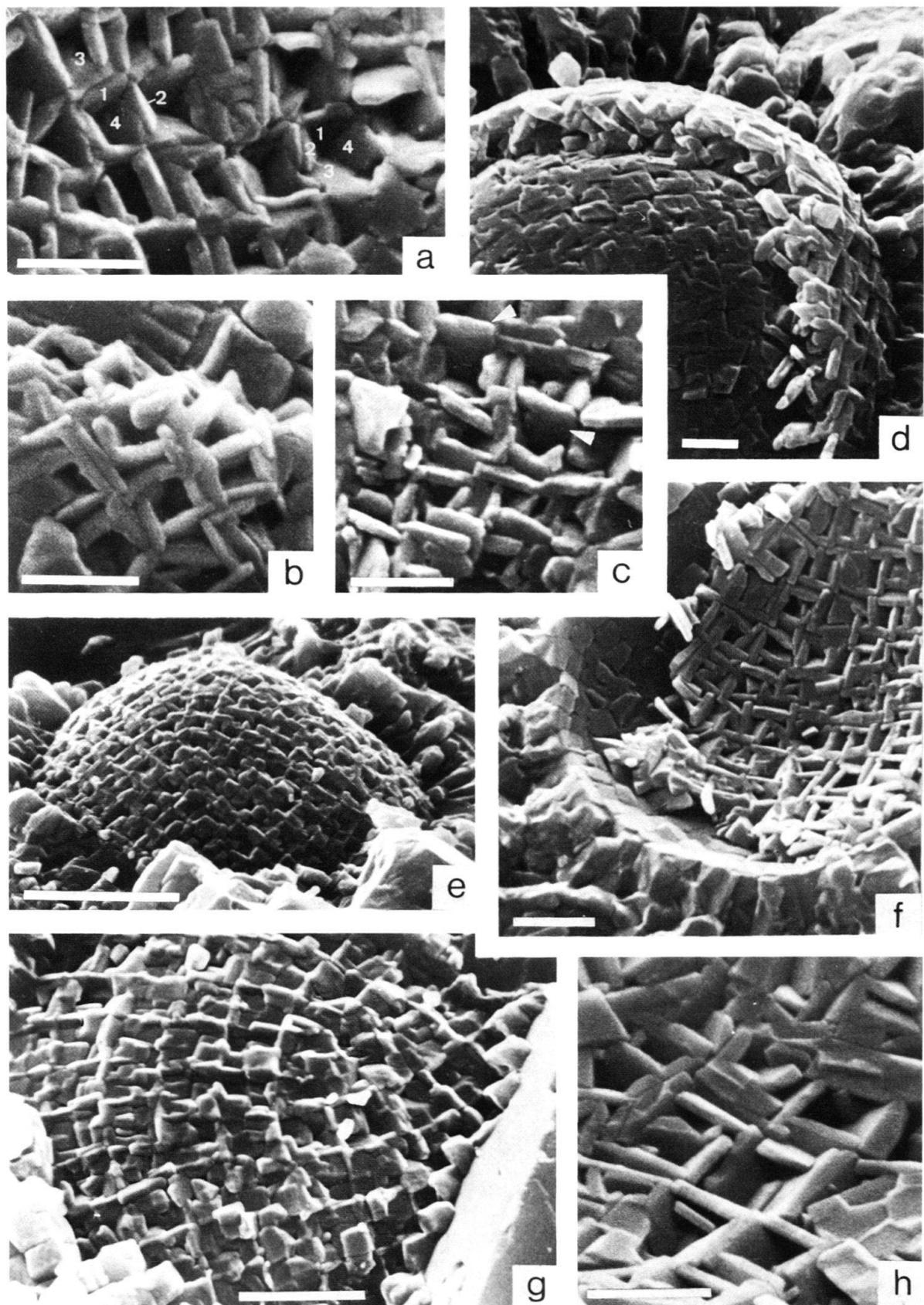


Fig. 6. Wall ultrastructure of *Schizosphaerella punctulata* and its modification by diagenetic overgrowth.

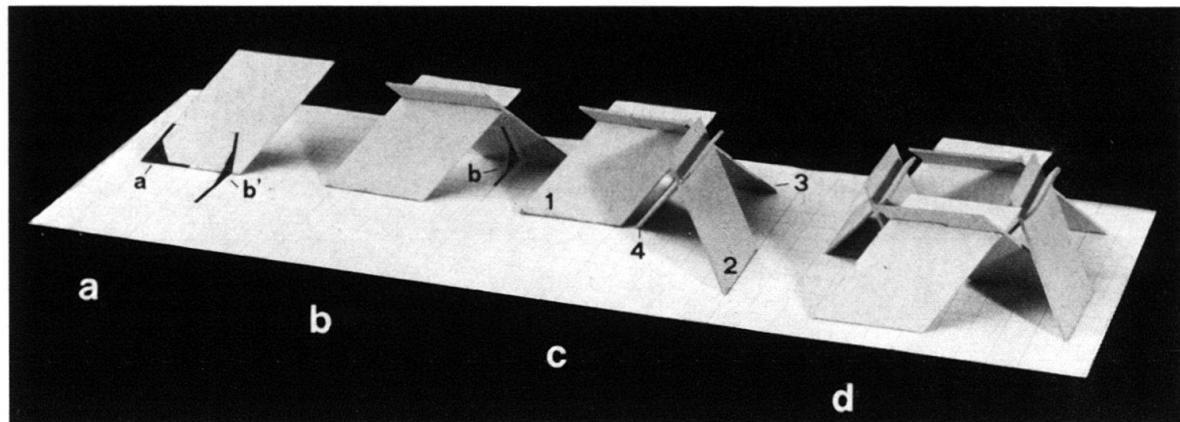


Fig. 7. Inferred spatial orientation of the fundamental structural elements in *S. punctulata*; carton model. a = A single inclined parallelogram-shaped elementary plate (a = edge angle; b, b' = angle of inclination). b = Two intersecting lamellae (cf. Fig. 8). c = Fundamental disposition of two couplets of intersecting lamellae; plates occupy four distinct positions at right angles to one another (cf. Fig. 6a). d = Four couplets of lamellae combined according to model c; the intersections frame a square, whereas the four converging lamellae define a pyramidal cavity (cf. Fig. 5a, 6a).

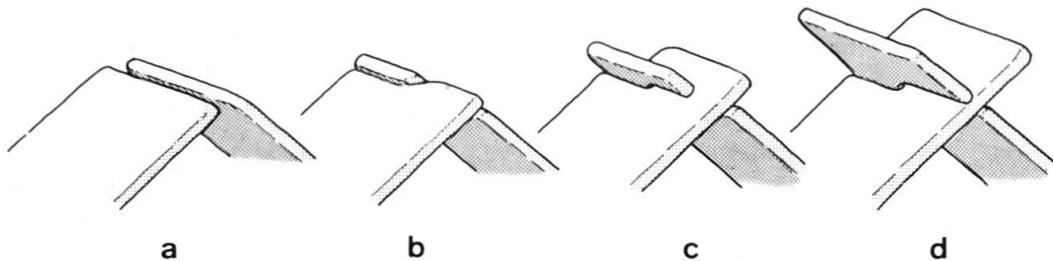


Fig. 8. Mode of intergrowth between two converging lamellae with progressive increase in length. Diagrams are based on data drawn from SE-micrographs, such as Figure 5a, f and Figure 6b, c, h.

lamellae (i.e. for instance 1a, 1b, 1c ... or 4a, 4b, 4c ... in Fig. 9) obviously do not join immediately alongside, but are always interspaced by at least an interval that allows a perpendicularly trending lamella to intervene, yet probably even wider, as the single calcitic skeletal elements were probably coated originally by some organic membrane.

Another point that has not yet been elucidated concerns the internal structural organization of the valves. During SEM-investigation, attention has thus been paid to fractured valve specimens that would permit clarification of the relationship between the internal structure and the regular frame developed both on the outer and the inner surface of a valve. It appeared that the elementary calcite lamellae extend continuously across the full thickness of the test wall (e.g. Fig. 5d). Thus, it can be inferred that increase in thickness of the test wall involves mere lengthwise growth of the fundamental lamellar crystallites, and hence the principles of construction deduced from the surface morphology must apply throughout. The overall skeletal structure of *S. punctulata* then has to be envisaged as it is represented in the constructional model on the Figures 10 and 12.

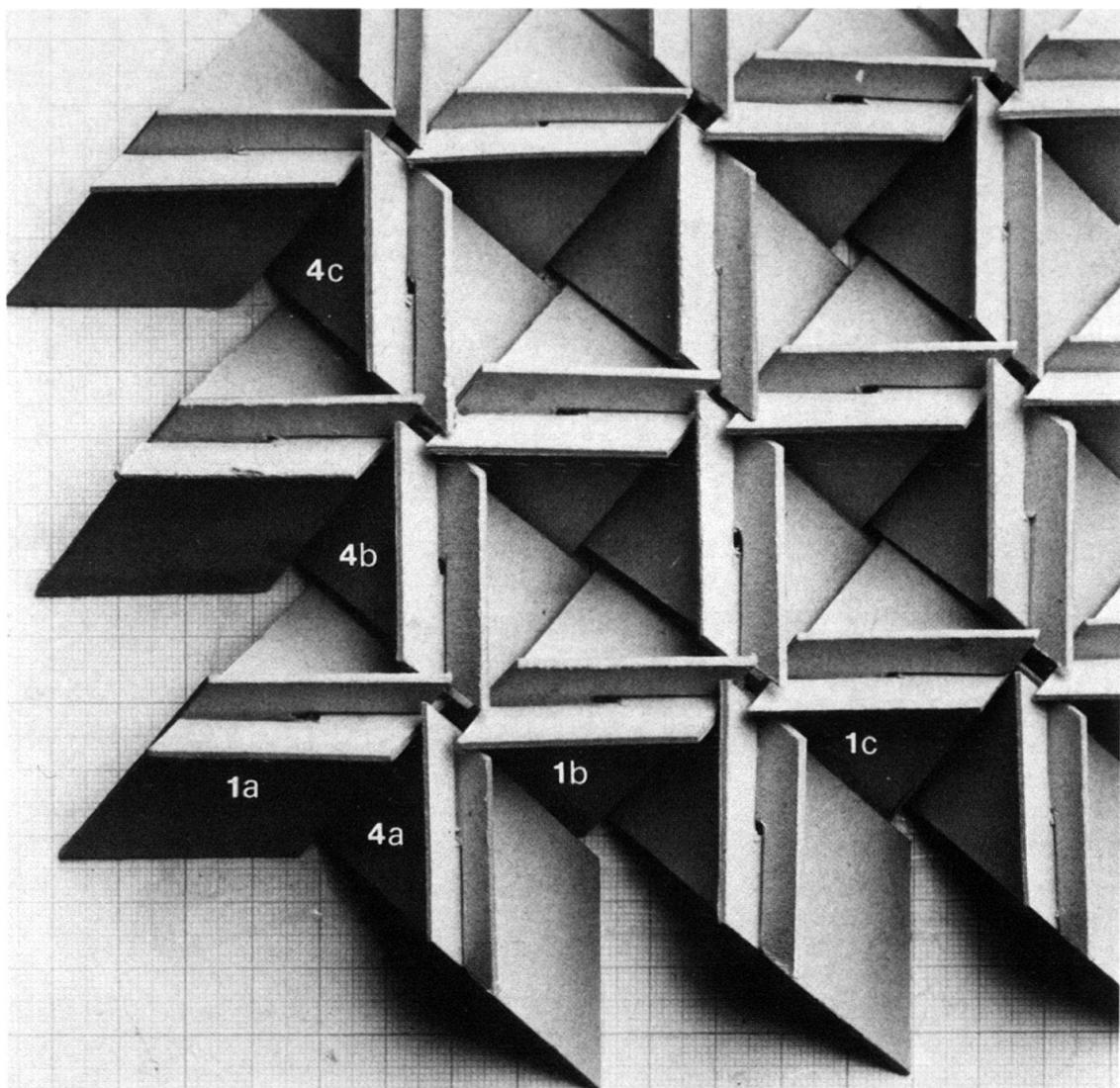


Fig. 9. Ultrastructural pattern of valve surface in *S. punctulata*; carton model.

Some principal features indicated by these figures include:

1. With continued increase in length of the fundamental lamellae, there recurs at regular intervals (h in Fig. 10) the pattern illustrated by Figure 9, with juxtaposed pyramidal cavities, each defined by four converging lamellae. Valves of quite a different overall thickness (e.g. Fig. 4d vs. Fig. 6d or f) may therefore reveal essentially the same surface morphology.
2. Inside the valve, there occur two types of voids, square-bipyramidal and sphenoidal in shape, which are in turn systematically arranged (cf. Fig. 11), consequent upon the regular disposition of the delimiting skeletal elements. Assuming a more realistic width/thickness ratio of the elementary lamellae in the order of 5:1 to 7:1 (cf. p. 994), instead of 35:1 as in the model in Figure 10, the void space can be estimated at some 60–70% of the total volume of a valve.
3. There is, as a consequence of symmetry, no fixed growth direction implied from the architecture of the test wall. Development of the skeleton of *S. punctulata*

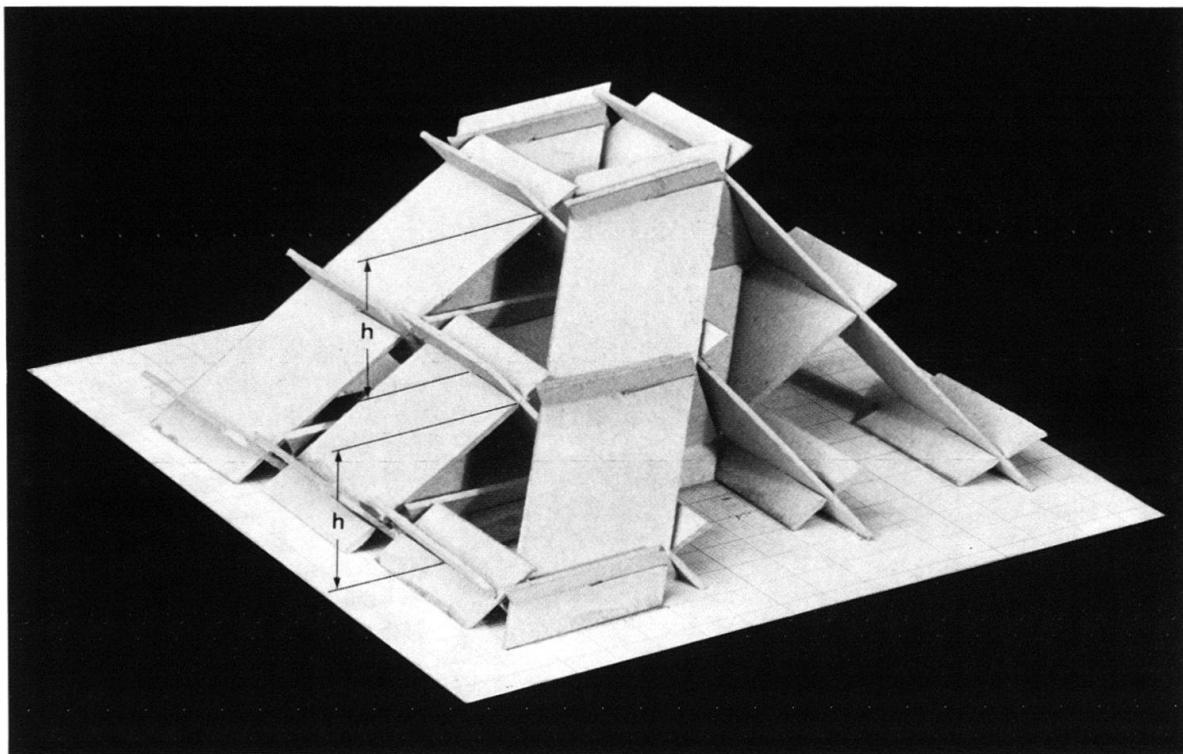


Fig. 10. The wall ultrastructure of *S. punctulata*; carton model. Part of the elementary lamellae are graduated in length in order to indicate systematic recurrence of the pattern illustrated by Figure 9 at regular intervals h . The overall thickness of the model (2 h approx.) is not restricting; wall thicknesses may vary considerably between specimens; in terms of the value h , they usually range from 1 h (e.g. Fig. 6f) to 4 h (e.g. Fig. 4d).

might have proceeded either through centrifugal or through centripetal growth of the fundamental calcite lamellae, i.e. through increment at the convex outer surfaces or instead at the concave inner surfaces of the valves. Likewise a combination of these two possibilities would appear feasible, with accretion of the lamellar crystallites then occurring simultaneously in both directions. Intergrowth amongst lamellae with progressive increase in length, however, strongly suggests that the skeleton developed *in situ*, most likely peripheral to the organic parts of *S. punctulata*. Although apparently trivial, this point might prove of some relevance to the systematic classification of schizosphaerellids; for e.g. in case of coccolithophorids, the single coccoliths do not form *in situ*, but originate within the cell and are, only after having assumed their final shape, extruded to constitute a spherical shell (the coccospHERE) at the cell surface (e.g. WILBUR & WATABE 1963, PAUTARD 1970).

From SE-micrographs of well-preserved specimens of *S. punctulata*, whether those figured in the present paper or those published in previous studies, it is easily seen that the ultrastructural scheme outlined above is not realized uniformly all over the valves, but merges in places into a disorganized pattern. The principal cause accounting for such irregularities in the skeletal structure is curvature of the valves (see also AUBRY & DÉPÈCHE 1974, p. 11), for a perfect development of the drawn structure is possible only on a plane surface (cf. models Fig. 9, 10, 12). Location and

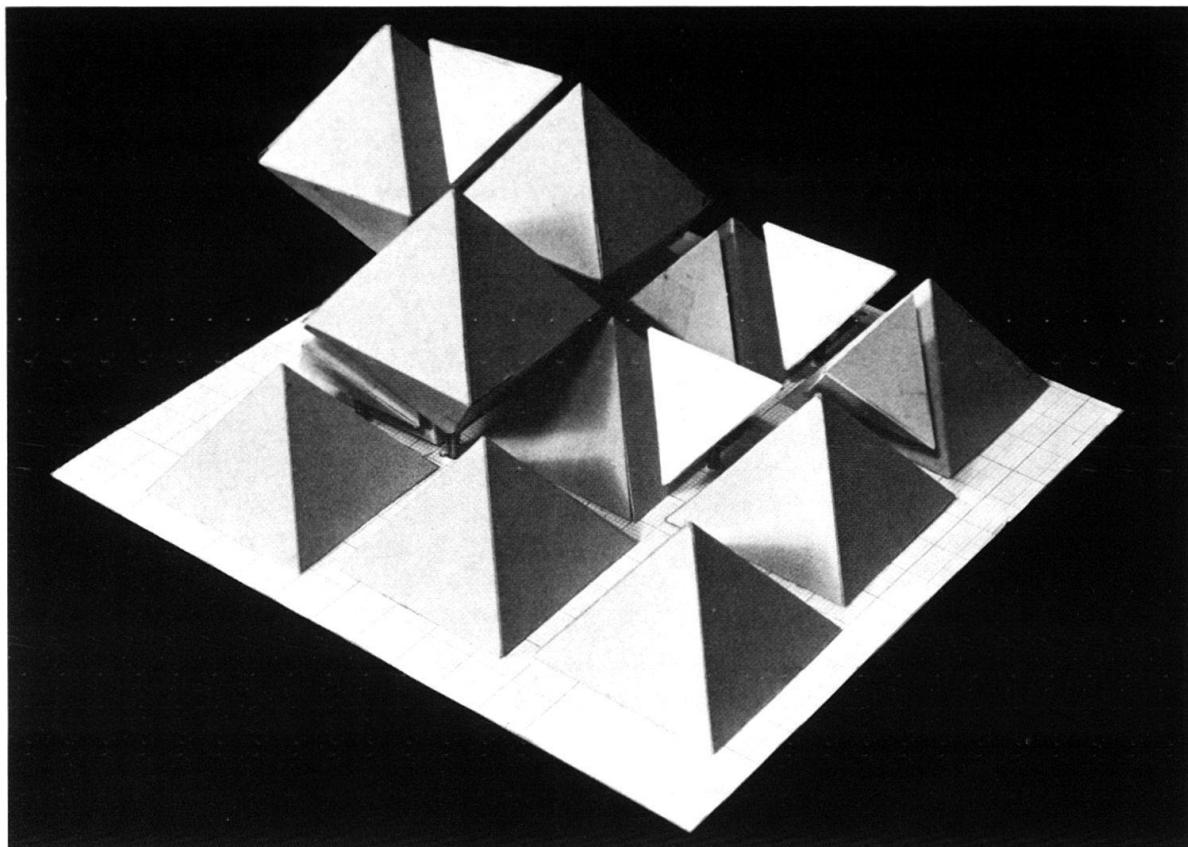


Fig. 11. Types and mutual arrangement of voids defined by the structure shown in Figure 10; carton model.

extent of "disorganized" zones, as well as the degree of disorganization in such zones, may vary considerably among valves. This has, on one hand, to be related to the fact that the valve morphology can be subject to conspicuous intraspecific variation, such that valve curvature may vary greatly among specimens, and in the case of bell-shaped forms even within a single specimen. On the other hand, it must also be relevant in this context that the regular ultrastructural pattern previously described does not always assume the same orientation with respect to the axis of a valve (cf. AUBRY & DÉPÈCHE 1974, e.g. Pl. 1, Fig. 9, vs. Pl. 4, Fig. 1).

Preservation of *Schizosphaerella punctulata* in deeper-water carbonate sediments of the Tethyan Jurassic

In the Jurassic deeper-water deposits examined from the Southern Alps and the Northern Apennines, schizosphaerellids show various modes of preservation, depending on the lithofacies, and its specific diagenetic history. Modifications with respect to the inferred primary skeletal structure (cf. Fig. 12), however, are exclusively due to precipitation of secondary overgrowth cement; in no case definite dissolution features were encountered. Furthermore, it is immediately obvious that deposition of cement on valves did not occur at random, but was largely controlled by the ultrastructural characteristics of the test wall; hence, it would be expected

that diagenetic alteration of the skeleton proceeded in a manner closely similar between various specimens. In fact, all of the different styles of preservation observed in *S. punctulata* can be readily interpreted as stages in a single transformative process, the principal phases of which include the following:

1. *A slight, uniform enlargement of the fundamental skeletal elements by syntaxial overgrowth, upon decay of their presumed (cf. p. 998) organic envelopes.* It is plain that alteration of the skeleton of *S. punctulata* cannot be traced back accurately to the very beginning, as even the best-preserved specimens, such as those reproduced on Plate 4 in AUBRY & DÉPÈCHE (1974), Plate 1, Figures 1, 6, in MOSHKOVITZ (1979) and e.g. Figures 5a, c, d in the present paper, must be expected to have undergone some modification during lithification of the host sediment. However, modification is unlikely to have been significant in these cases. Presumably, it involved merely a slight uniform increase in size of the fundamental calcite lamellae achieved by outward parallel progression of their rhombohedral faces (cf. p. 994), thus causing the lamellae to impinge on one another and hence the inferred original interspaces between them (cf. p. 998) to become largely fastened (compare model, Fig. 12, with SE-micrographs, Fig. 5a, c, d or Fig. 6a, b, c).
2. *Occlusion of the main skeletal voids (cf. Fig. 11) due to continued – yet uneven – syntaxial extension of the delimiting lamellar crystallites.* Once the original skeletal structure is converted in a more or less tight-fitting frame, neither

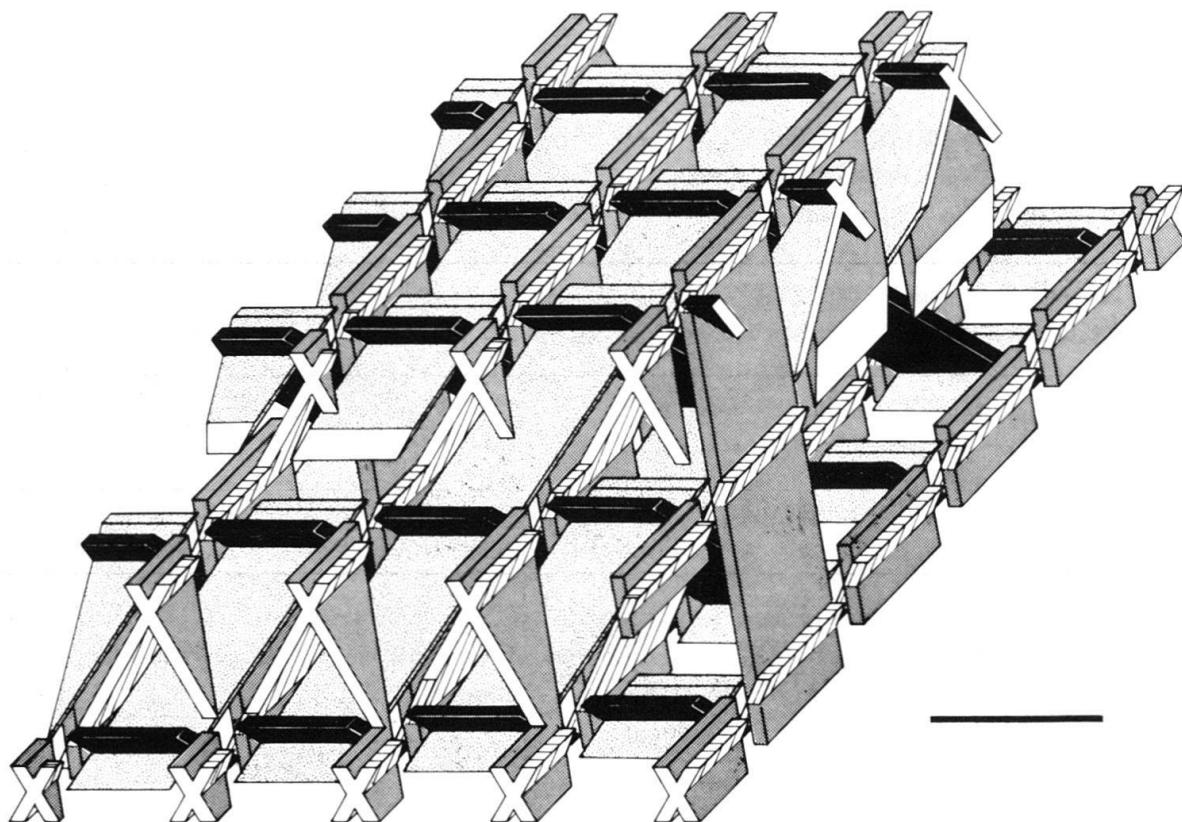


Fig. 12. Constructional model of the test wall of *Schizosphaerella punctulata*; bar is equivalent to 1 μm approx.

widening of the constituent lamellae nor a uniform increase in thickness is logically possible to any greater extent, unless certain lamellae grow at the expense of others. This does not, however, appear to be the normal case. Rather, the lamellar crystallites at this point start to enlarge unevenly through syntaxial growth of cement on the remaining free surfaces. Thus, the (bi)pyramidal and sphenoidal main skeletal voids (Fig. 11) become progressively reduced, inward from their confining 8 and 4 sides respectively, and eventually completely occluded. Advanced stages of cementation of the square-pyramidal cavities at valve surfaces can be seen on Figures 6e, g and, in detail, on Figure 13. The broken specimens on Figure 4d, Figure 5e (upper part) and Figure 14a, on the other hand, illustrate fabrics which originated with the filling of the internal skeletal voids by overgrowth cement. According to the high initial porosity of the valves (cf. p. 999), the volume of cement required for a complete occlusion of the skeletal void space can be assessed as approximately twice that of the original biogenic calcite.

3. *Development of a fringing crust of radially-oriented bladed to fibrous length-fast calcite prisms through displacive precipitation and/or in situ replacement of surrounding carbonate mud.* Particularly in the more calcareous lithologies investigated, a fringe of radiating length-fast calcite prisms is developed around the valves (cf. Fig. 4b and Fig. 14). The thickness of fringes may vary widely between different specimens, and it appears to be related, in a general way, to the overall carbonate content of the host sediment. On a given individual, the fringe usually is of strikingly uniform width (e.g. Fig. 14c, e), a feature which has led previous authors to consider it as part of the original skeleton (cf. BERNOLLI & RENZ 1970, BERNOLLI & JENKYN 1970, MONTANARI 1972) and, consequent-

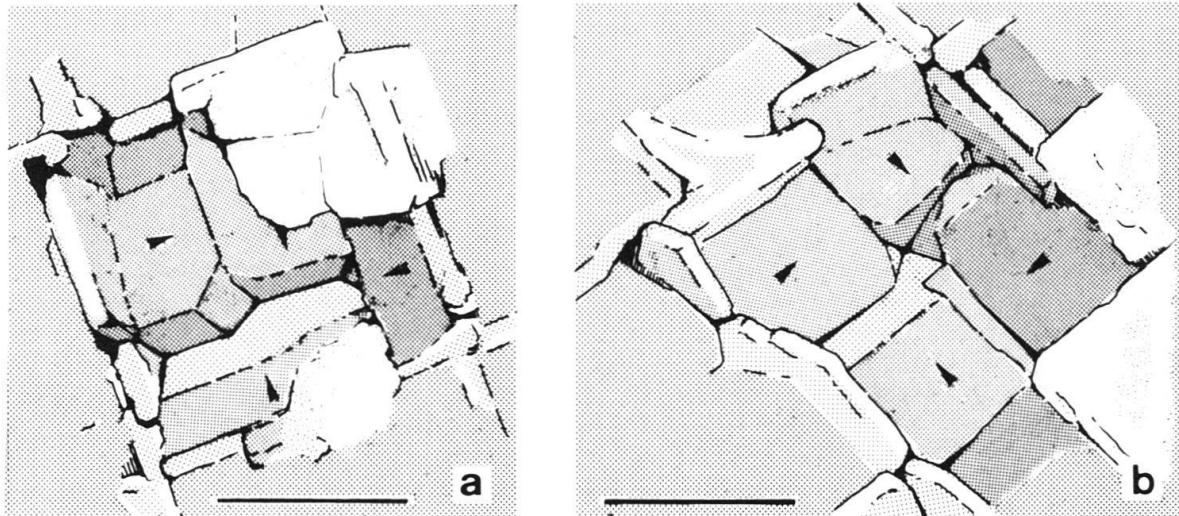


Fig. 13. Advanced stage of occlusion of pyramidal cavities at a valve surface. Occlusion ensues from centripetal syntaxial growth of cement from the confining four lamellar crystallites (arrows), and it may lead to more (b) or less (a) regular patterns, depending on whether or not the cement crystals started growing simultaneously, and whether growth rates were the same. Cement crystals are, at their free surfaces, bounded by plane rhombohedral faces, part of which apparently correspond with those bounding the initial lamellae. Intercrystalline boundaries presumably are plane compromise boundaries.

Both a and b are drawn from SE-micrograph, Fig. 6g; bars are equivalent to 0.5 μm approx.

ly, to over-estimate the volumetric importance of schizosphaerellids in Jurassic pelagic rocks. However, a diagenetic origin of these fringes is clearly demonstrated by the fabrics observed in cases of tightly packed or even interlocking valves, in that a number of clustered valves then may share a single outer fringe (Fig. 14d) or the fringes of adjacent valves are irregularly developed where they interfere with each other (Fig. 14b, h). A uniform development may furthermore be hindered by larger detrital noncarbonate particles, such as mica flakes or quartz grains. Fringes always possess sharp and plane boundaries with their foundation, i.e. the valve surfaces, and they thus have to be designated as "crusts", according to FOLK's (1965) code for description of diagenetic calcite. Likewise, their outer terminations, against the surrounding micrite and microspar, are generally distinct. The single columnar calcite crystals are about 0.3 µm wide at their proximal ends and squarish in cross section (Fig. 14g). Outward, they either enlarge gradually or taper, depending on whether they grow on the convex outer or the concave inner surface of a valve, and at the same time, they tend to assume an irregular polygonal outline. Distal crystal terminations are dominantly planar, but in cases obtuse-rhombohedral (cf. Fig. 14e). Although the calcite prisms are not obviously in lattice continuity with their substrate, their arrangement is systematic and reflects a strong control by the regular surface morphology of the valves; inasmuch as four prisms are normally based on each tetragonal unit cell, with their disposition matching that of the outer faces of the four cement crystals filling the initial square-pyramidal cavities (compare Fig. 6g and Fig. 13b with Fig. 14g). As for the mode of formation of these bladed to fibrous calcitic crusts, evidence is inconclusive, and probably they in fact represent the combined product of different diagenetic processes, including cementation (i.e. passive precipitation into interparticle or intrabiotic pore space), displacive precipitation (cf. FOLK 1965, WATTS 1978, NEUGEBAUER 1979) and neomorphism. Simple pore-space filling clearly must have played a part locally, for instance, in occluding the central void space in the case of intact (double-valved) specimens (cf. Fig. 4c) as well as other larger original open-

a = Fractured valve specimen revealing calcite-cemented former bipyramidal internal skeletal voids (arrow). b, c, d, e (b and c from polished and slightly etched sample surfaces) = diagenetically altered specimens rimmed by crusts of radiating length-fast calcite prisms; b = two adjacent valves (transverse section left, subaxial section right) with their fringing crusts mutually interfering; d = three adjacent valves sharing a single outer fringe of uniform thickness; arrow in e (upper left) points to a calcite prism having obtuse-rhombohedral outer termination (normally, prisms are square-ended). f = Ultra-thin section of finely crystalline basinal limestone showing "encrusted" schizosphaerellids set in a mosaic of neomorphic microspar. g = View of proximal ends of calcite prisms constituting an outer fringe; prisms are squarish in cross section and systematically arranged in groups of four, with each of these groups based on a tetragonal unit cell at the valve surface. h = Detail of mutually interfering fringes between clustered valves.

a, g from Valmaggio Formation; uppermost Liassic; about 1 km northeast Cittiglio (western Lombardy); SE-micrographs; scale bars 2 µm. b, d, h from Calcare Selcifero; Late Pliensbachian; Monte Cetona (southeastern Tuscany); SE-micrographs; scale bars 5 µm (b, h) and 10 µm (d). c from Marne del Serrone; Toarcian; Valdorbia (F. Sentino, Umbria); SE-micrograph; scale bar 5 µm. e from Corso Rosso; Early Domerian; Botticino Mattina (Brescia); SE-micrograph; scale bar 5 µm. f from Calcare Selcifero; Late Pliensbachian; Monte Cetona (southeastern Tuscany); thin-section; scale bar 50 µm.

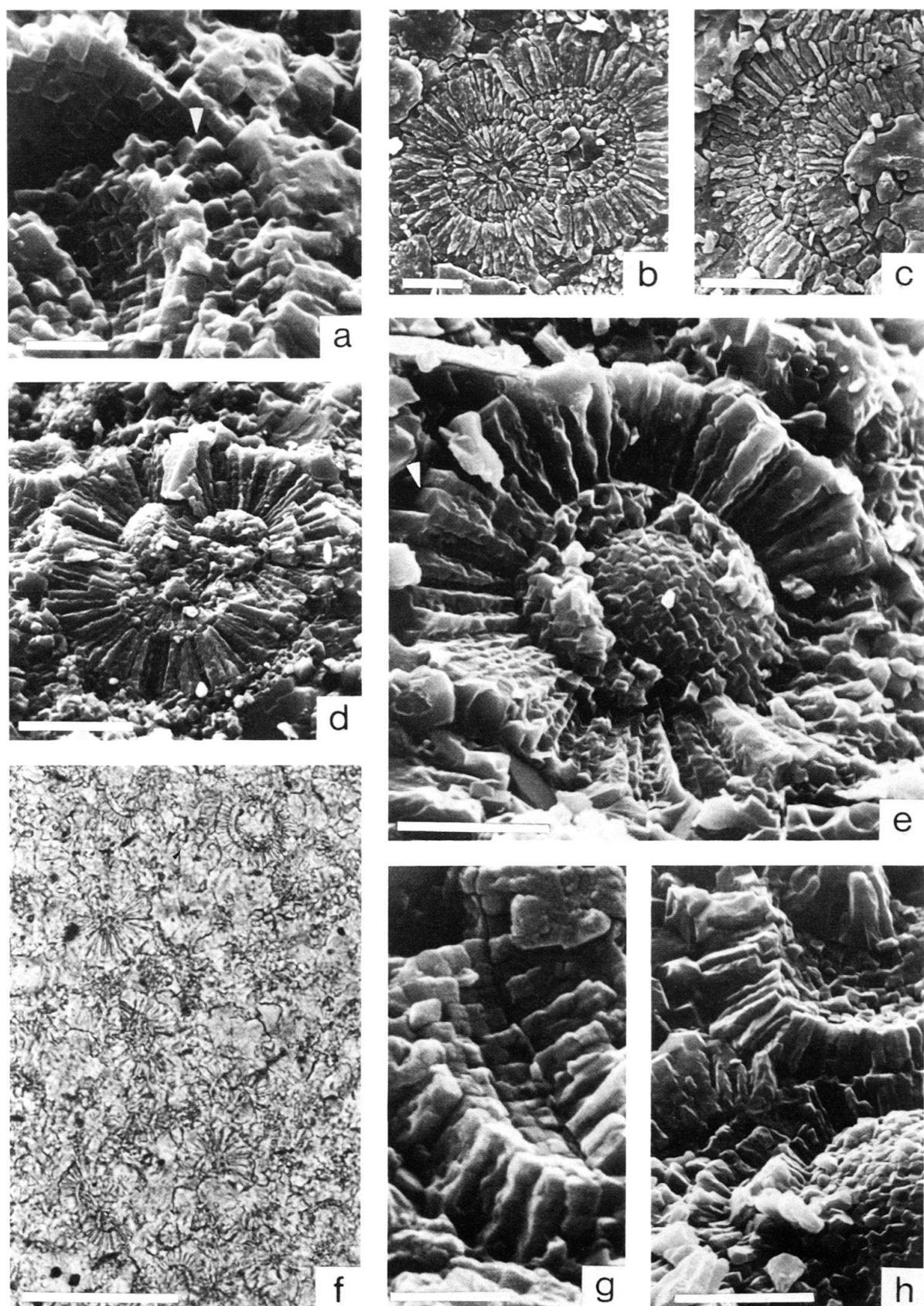


Fig. 14. Mode of preservation of *Schizosphaerella punctulata* in Tethyan Jurassic deeper-water carbonate sediments.

spaces, such as those which might have existed beneath convex-upwards or between tightly packed single-valved specimens. However, it could not have been the principal mechanism operating, because the crusts are not apparently restricted to such possible former open-spaces, but are likewise developed where valves must have been originally in direct contact with the surrounding carbonate mud. This, in turn, would imply that growth of the fabric of radiating bladed to fibrous calcite prisms (... or of a precursor with a metastable mineralogy) proceeded largely by displacive crystallization and/or in situ replacement of carbonate mud via microscale solution-reprecipitation across a film of fluid.

Although the likelihood of displacive crystal growth in carbonate rocks has been seriously doubted by BATHURST (1975), I think that this process cannot be ruled out a priori in the case in question. A full discussion of my arguments will be given elsewhere; yet an essential point is that the crusts described, or their metastable precursors, appear to have formed during a rather early stage of burial lithification, when the development of a rigid framework was not yet completed in the sediment and mud-sized particles thus feasibly could have been displaced to the extent needed. This early date is suggested by the occurrence of *fringed* schizosphaerellids a) as residual carbonate inclusions in cherts, the figuration of which in turn seems to have initiated prior to complete consolidation of the host sediment and b) as undigested inclusions in fabrics of coarse pseudospar, such as syntaxial neomorphic rims on thin-shelled *positoniids*.

The volume occupied by these fringing crusts is considerable; in extreme cases (e.g. Fig. 14b, e), it may exceed that of the encrusted valve by 10–15 times, the total quantity of calcite concentrated diagenetically around and within the skeleton hence amounting to some 30–45 times that of the initial biogenic calcite. Average values obtained by point counting on SE-micrographs of polished and slightly etched sample surfaces are significantly lower. Nevertheless, in the case of the calcilutites of the Pliensbachian Calcare Selcifero exposed in the Monte Cetona area (cf. p. 989 and Fig. 14f), it was found that crusts occupy a volume about twice as large as that of the valves, and that the total of calcite drawn by schizosphaerellids constitutes 25–30% of the rock volume, whereas the contribution of skeletal calcite would be no more than 4–5%. Contrary to what has been suggested by BERNOUILLI & JENKYN (1970), and subsequently has found wide acceptance in literature (e.g. AUBRY & DÉPÈCHE 1974, MOSHKOVITZ 1979), we must conclude therefore that *Schizosphaerella* was not important as a primary sediment contributor in Tethyan Jurassic deeper-water deposits. Rather, its importance lies in providing nucleation sites for large amounts of diagenetic calcite, and in this way it may have played a critical role in influencing the mode and rate of lithification.

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