Palaeobiology of *Tetragonis sulcata* d'Eichwald, 1860, an Ordovician receptaculite in erratics from the northern Netherlands

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A study has been made of the receptaculite *Tetragonis sulcata* d'Eichwald, 1860 in Upper Ordovician erratics from the northern Netherlands. D'Eichwald's original description is reviewed, giving a wider conception of the morphological diversity of receptaculites. *Tetragonis sulcata* is placed in the family Tetragonaceae Rietschel, 1969 (nomen correctum), together with *Lepidolites dickhauti* Ulrich, 1879.

The aim of this study was to reconstruct the living receptaculite organism by documenting homologies between *Tetragonis sulcata* and receptaculites described in the literature. Through analysis of a diverse set of morphological features which thus were obtained, an attempt could be made to determine the pattern of receptaculite morphogenesis. This study therefore concentrates on the functional morphology, growth, and calcification of meroms which are extensively reviewed, particularly with respect to receptaculite growth. The geometry of merom distribution as a result of polar growth of receptaculites has been studied. A description is given of a merom arrangement not yet considered before, the *Tetragonis* type, which is compared with the normal, *Receptaculites,* type. Controversial issues, such as the position of soft parts in receptaculites as well as their life orientation, are discussed with regard to their palaeobiological significance. This approach produced some arguments against an apex-down orientation, as proposed by Campbell et al. (1974).

Based on these data, the systematic position of receptaculites is analysed. Consequently, it is inferred that they should be regarded as calcareous algae. Comparison with representatives of the chlorophyte order Dasycladales provides sufficient arguments to establish the separate order Receptaculitales within the Thallophyta.

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Introduction

The motivation to make this report were recent finds of yet unrecorded receptaculites in Dutch limestone erratics. During a study of the 23 specimens involved, new morphological data were recovered which led to a review of d'Eichwald's (1860) *Tetragonis sulcata,* a poorly known receptaculite. Homologies, arising from a comparison with other receptaculites through study of the extensive literature, are incorporated into a palaeobiological interpretation of receptaculites in general.

STORAGE OF MATERIAL

The 12 specimens collected by the author as well as all acetate peels are stored in the Rijksmuseum van Geologie en Mineralogie, Leiden, The Netherlands, catalogued under the numbers RGM 243 780 - 243 791. Two specimens, J 305 and J 2756, are in the Jonker collection housed in the Geologisch Instituut der Rijksuniversiteit Groningen. One specimen, I 50, is in the Huisman collection in the Natuurhistorisch Museum, Groningen. The other 8 specimens are in private amateur collections and are numbered I 51 (collection of Mr W. F. Anderson, Losser), I 52 to I 54 (collection of Mr and Mrs J. J. Peters, Norg), I 55A and I 55B (separately found but belonging to the same specimen, both in the collection of Mr F. Smeenge, Hoogezand), I 56 (collection of Mr P. Beersma, de Punt), I 57 (collection of Mr S. van der Veer, Groningen).

ACKNOWLEDGEMENTS

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PREPARATION

Two methods of preparation have been applied. One consisted of taking serial acetate peels, the other of cutting away the matrix to the critical level and polishing the surface with emery paper, taking photographs or peels whenever necessary.

The strong cementation of the matrix made it almost impossible to prepare the specimens free. Hence it was very difficult to observe details such a growth-lines on the surface of the fossil.

THE OSTSEEKALK MATRIX

The receptaculites are preserved in a compact, organodetritic, rather hard, yellow-brown to grey-white coloured micrite, with a conchoidal fracture. Microcrystalline pyrite, or small aggregates of pyrite or related minerals are abundant, often lining the fossils.

Associated with the receptaculites is an abundant flora consisting of the algae *Vermiporella* Stolley and, less common, of *Coelosphaeridium* Roemer and a poor fauna of unidentified sponges, the brachiopod *Strophomena* Sowerby, ectoprocts, the trilobites *Encrinurus* Emmrich and *Remopleurides* Portlock, small ostracodes, gastropods, fragments of orthoconic cephalopods, and crinoid ossicles. Trace fossils preserved as colour differences and as calcite or pyrite filled cavities are common, often mottling the matrix.

Erratics with such a composition are frequently found in the Groningen area. Jonker (1904) was the first to relate these to the Upper Ordovician 'Ostseekalk' (= Baltic Sea Limestone).

Descriptions of the Ostseekalk are presented by Wiman (1894, 1907) Hucke & Voigt (1967) and Neben & Krueger (1973): 'The Ostseekalk is a very compact, fine grained limestone, whitish-grey to brown, often with red mottles or flames, with a conchoidal fracture and similar to the Solnhofen Lithographic Limestone. Fossils are rare but excellently preserved. They are often lined with haematite, which also occurs as veins or cavity fillings. Fissures and cavities filled with calcite are common throughout the matrix'.

Wiman (1907), in the most important paper on this subject, describes seven different types of Ostseekalk erratics. The Groningen erratics would be more or less identical with three of Wiman's types. The 'red flamed' and the 'greyish' type contain *Vermiporella* Stolley, *Coelosphaeridium* Roemer and unidentified sponges. From the 'greyish' type Wiman reports the receptaculite *Tetragonis murchisoni* (d'Eichwald). The 'Sund' type is petrographically characterized by fossils covered with haematite (obviously pyrite and its oxidation products).

The generic name Ostseekalk is used to indicate a type of limestone with the characteristics mentioned above and has been applied only to erratics. According to Stolley (1896a, 1896b), Jonker (1904) and Wiman (1907) the Ostseekalk is identical to the solid rock of the Wesenberg and Lower Lyckholm Limestones of Estonia in both petrographical and palaeontological respect. Consequently the source area of the Ostseekalk erratics is believed to be Estonia and the adjoining part of the Baltic Sea between Estonia, Gotland and the Åland Islands as well as the southern part of the Gulf of Bothnia (Stolley, 1896a, 1896b; Jonker, 1904; Wiman, 1907; Kruizinga, 1918).

The Ostseekalk is assigned to the Rakvere (Wesenberg) and Nabala (Saunja) Stages, E and F1a respectively (Stolley, 1896b, 1897; Wiman, 1907) ranging from Middle to Late Caradoc (Hucke & Voigt, 1967).

Wiman's (1907) listing of *T. murchisoni* d'Eichwald in Ostseekalk erratics of the 'greyish' type is important in stratigraphic respect, since Schmidt (1881) states that this fossil is restricted to the Lower Lyckholm Limestone of Estonia. It might well be that in both cases *T. sulcata* is meant.

Other limestones with *T. sulcata* in the collections of the Rijksmuseet Stockholm were collected at Tapa (Taps) and Uuemoisa, Estonia, both from the Lower Lyckholm Limestone of the Nabala (Saunja, F1a) Stage. In all respects, the matrix, as well as the receptaculites within, are identical to those of the Groningen area.

These data are consistent with an assignment of Ostseekalk erratics containing *Tetragonis sulcata* d'Eichwald, 1860 to the Wesenberg Limestone of the Rakvere (E) Stage, more probably though to the Lower Lyckholm Limestone of the Nabala (F1a) Stage, of Middle to Late Caradoc age.

Morphological descriptions

TERMINOLOGY

The terminology used in the present paper is mainly that proposed by Rietschel (1969), to which a few new morphological terms are added.

In conformity with the spelling of the order Receptaculitales, the English spelling 'receptaculite' is used instead of 'receptaculitid'.

Terminology of the merom

Apicad arm: arm directed towards the apex, = adapertural arm (Campbell et al.), distal ray (Foster), proximale Arm (Rauff).

Arms: three or four needle like structures, perpendicular to each other and parallel to the outer wall (Figs. 4, 8), = rays (Foster), stellate structure (Nitecki).

Axial canal: space inside the merom.

Cap: rhombic or hexagonal plate-like structures at the extremity of the meroms, together forming the outer surface of the fossil (Figs. 3, 4, 8), = outer plate (Foster), facet (Nitecki), Täfelchen (Rauff, Rietschel).

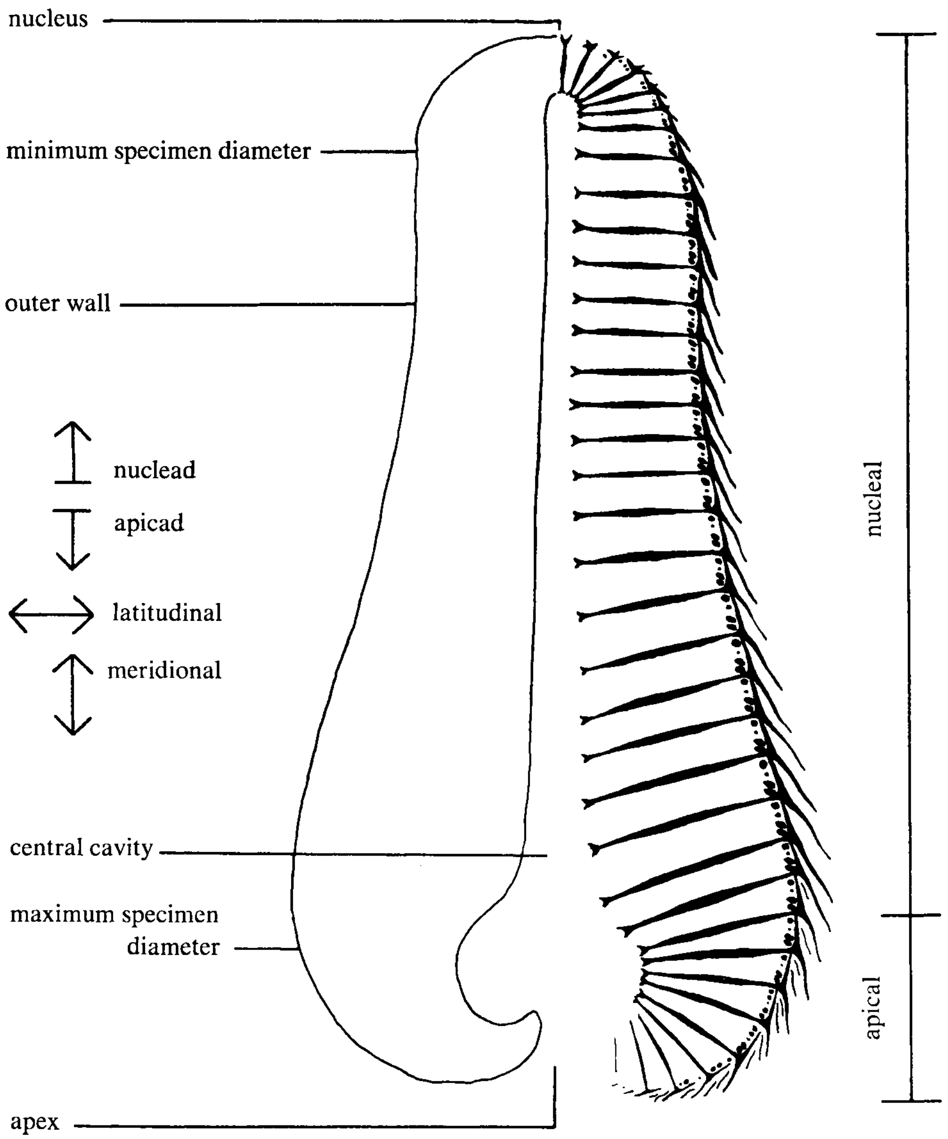


Fig. 1. Diagrammatic representation of a longitudinal section of *T. sulcata,* illustrating the terminology.

Column: cylindrical structure connecting the arms and the foot (Fig. 3), = radial arm (Foster), lateral shaft (Nitecki), Säulchen (Rauff, Rietschel).
Distal offshoots: rib-like structures at the inner part of the cap, radiating from the base of the cap (Fig. 8).
Enveloping layer: thin outer layer covering the whole merom, = Hüllschicht (Rietschel).
Foot: funnel-shaped termination of the column, opposite the cap (Fig. 3).
Head: the cap and the arms together.
Intermeromal: between the meroms.
Intrameromal: inside the meroms.
Latitudinal arms: two lateral arms, arranged according to the latitudes (Figs. 4, 8), = lateral rays (Foster), horizontal rays (Nitecki), laterale Arme (Rauff).
Meridional arms: two transversal arms, arranged according to the meridians (Fig. 15 B), = vertical rays (Nitecki).
Merom: each individual structural unit of the fossil (Fig. 3), = element (Foster), lateral or lateral branch (Nitecki).
Merom core: interior of the merom.
Meromal: of the merom.
Nuclead arm: meridional arm directed towards the nucleus (Figs. 3, 4, 8), = abapertural arm (Campbell et al.), proximal ray (Foster), distale Arm (Rauff).

Terminology of the receptaculite body (Fig. 1)

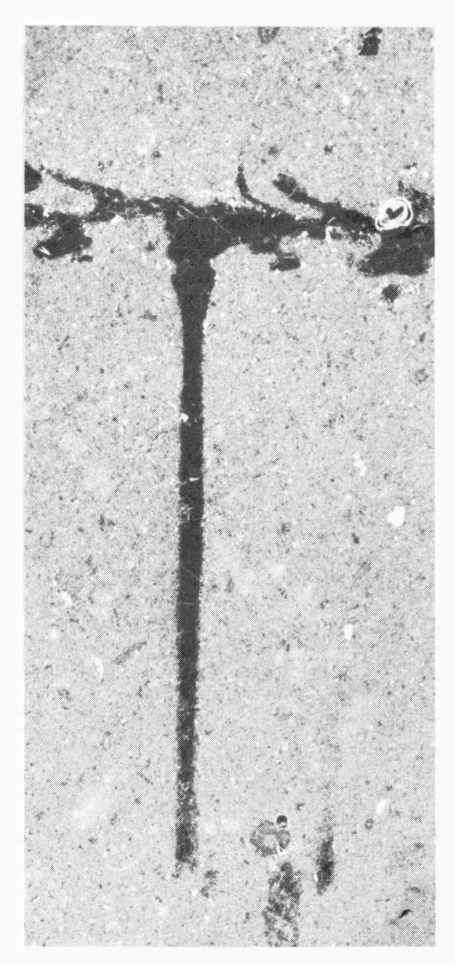
Apex: broad open pole of the fossil, = apertural end (Campbell et al.).
Apicad: in the direction of the apex, = adapertural (Campbell et al.), distal (Foster), proximal (Rauff).
Apical: the region between apex and maximum specimen diameter.
Central cavity: the open space at the centre of the fossil, = inner space (Campbell et al.), main axis (Nitecki), innere Hohlraum (Rauff, Rietschel).
Latitudinal: the direction perpendicular to the meridians, = lateral (Foster, Rauff).
Maximum specimen diameter: the region where the fossil reaches its maximum diameter.
Meridional: the direction parallel to both poles.
Minimum specimen diameter: the region at the top where the spherical shape of the nucleal part of the receptaculite body changes into a conical shape.
Nuclead: in the direction of the nucleus, = abapertural (Campbell et al.), proximal (Foster), distal (Rauff).
Nucleal: the region between nucleus and maximum specimen diameter.
Nucleus: acute closed pole of the fossil, = enclosed end (Campbell et al.).
Orthostichies: the meridians and latitudes together (Fig. 16).
Outer wall: the continuous outer surface of the fossil, formed by interlocking of merom heads.
Parastichies: the intersecting dextral and sinistral whorls (Fig. 16).

PRESERVATION

All specimens are practically complete, except for those parts which were eroded during glacial transport.

After death of the organism, the connection between the meroms was severed, starting at both apex and nucleus. This phenomenon seems to be related to turbulency in the depositional environment. All other morphological features are well preserved except where recrystallization or silicification took place, both occurring to a minor degree.

In the merom two generations of cement are seen. The outermost parts are of a very thin, sometimes red coloured layer of tiny cement crystals of the first generation. The interior of the merom consists of uncoloured blocky calcite of the second generation (Fig. 2). This feature is universal in various types of meroms and was described by Rietschel (1969). He regarded the thin outer layer to be a



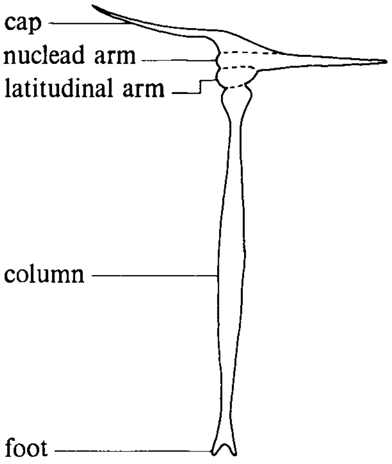


Fig. 2. Acetate peel of a complete merom of *T. sulcata* I 55A (10), showing the two cement generations, × 25. Collection of Mr F. Smeenge.

Fig. 3. Schematic lateral view of a complete merom, drawn from Fig. 2, illustrating merom terminology; × 30.

primary structure, but in the present material it must be regarded as a secondary structure caused by diagenesis. Observations supporting this view are:

A) The thickness of the outer layer is variable within the merom itself, within the meroms of one and the same specimen as well as between different specimens. This variation in thickness does not follow any regular pattern as should be expected were this layer a 'Hüllschicht' indeed (see Rietschel, 1969).

B) The frequent fissures and cavities in the matrix are filled with blocky calcite of the second generation and often have a similar coating of fine cement crystals. This applies also to the (originally aragonite but completely recrystallized) gastropod fossils. However, the original texture of trilobite, ostracode and crinoid fossils is well preserved.

C) When neighbouring meroms are in contact (for instance caps and latitudinal arms) no double layered partition wall can be distinguished: the large calcite crystals of the second generation merge into the neighbouring meromal elements. The same phenomenon is also met with when gastropod fossils are in contact with the receptaculite meroms.

D) When the central cavity and intermeromal space are filled with faecal pellets cemented by blocky calcite, the meroms are not preserved at all or they are deformed and intergrowth is seen with this anorganic calcite (specimens RGM

243 781 and RGM 243 786, Fig. 5). Specimen J 305 shows blocky calcite filling the inside of the fossil. This filling is identical with that observed in other cavities in the Ostseekalk. Only the outer caps of the meroms could be observed; the arms, columns and feet were dissolved leaving the open space inside the outer wall to be filled with blocky calcite during diagenesis.

E) Broken meroms show a continuous outer layer of fine cement crystals, also covering the broken parts. Rauff (1892a) observed the same feature on *Receptaculites neptuni* Defrance.

These arguments point to a different primary skeletal matter of the meroms, that dissolved during diagenesis whereupon secondary calcite filled the voids, resulting in the casts described above.

MORPHOLOGY OF THE MEROM

Meroms are the structural units of which the receptaculite body is built up. The meroms of *T. sulcata* show the same basic structures as have been described by Rietschel (1969): they consist of a head, a column and a foot (Figs. 2, 3).

Measurements of meromal elements are given below in the respective sections. Because all parts of the meroms increase in size from the nucleus towards the maximum specimen diameter and from the apex towards the maximum specimen diameter, only values for these regions are given. A realistic statistical treatment of the measurements could not be carried out since the construction of the meroms, the preservation of the specimens and their incompleteness due to glacial erosion prevented the measuring of all meromal parts and their progressive change in size. For these reasons the values given are only statistical means of the relevant measurements.

The head

The head consists of a cap, the peripheral part, and three perpendicular arms.

The cap is formed by a rhomboidal, undulated plate-like outgrowth of the merom, arising from the place where the arms meet. The nuclead part of the cap is attached to the arms where the latter meet, supported by a thickening of the basal part of the nuclead arm. It is bilaterally symmetric, the plane of symmetry being directed meridionally, having a nuclead concave and an apicad convex part, the extremity being tipped up (Figs. 3, 4). Cross-sections reveal that on the nuclead part a proximal concave and a distal convex section are super-

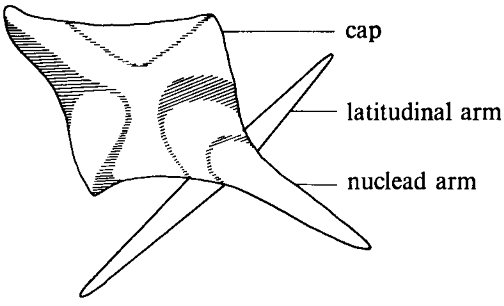


Fig. 4. Diagram of the merom head, showing the undulation of the cap; × 40.

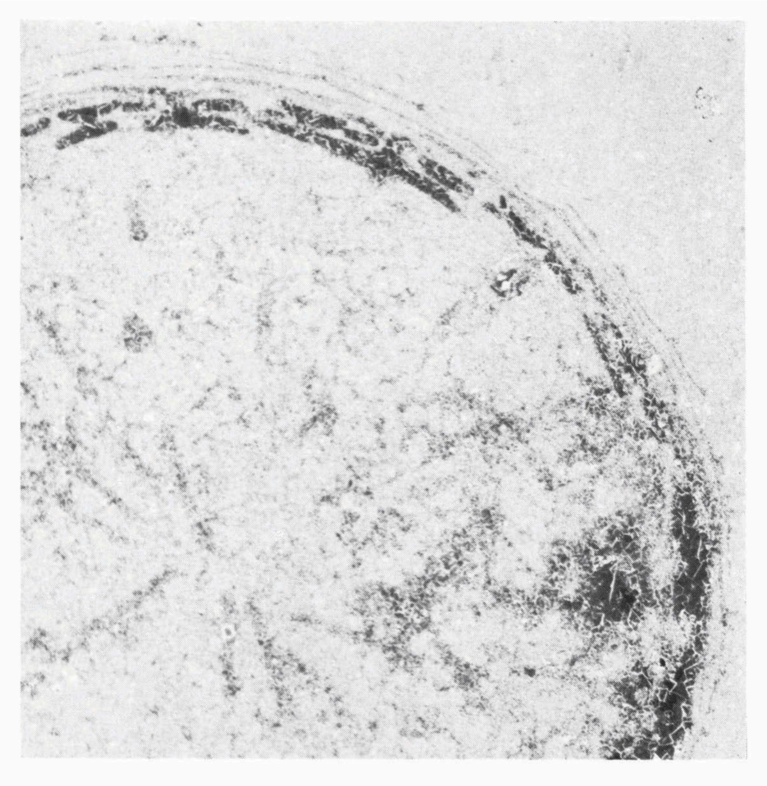


Fig. 5a. Acetate peel of the cross-sectioned body of *T. sulcata* RGM 243 781 (4). Note the change in shape of the cross-sectioned caps at increasing distance from the outer wall. Note also the cross-sectioned elliptical nuclead arms and the laterally sectioned latitudinal arms. The intermeromal space is filled with faecal pellets cemented by blocky calcite deforming the columns and feet; × 24.

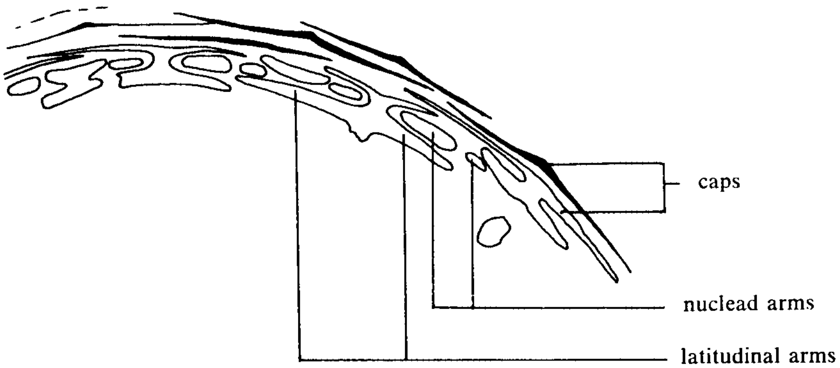


Fig. 5b. Schematic drawing of Fig. 5a.

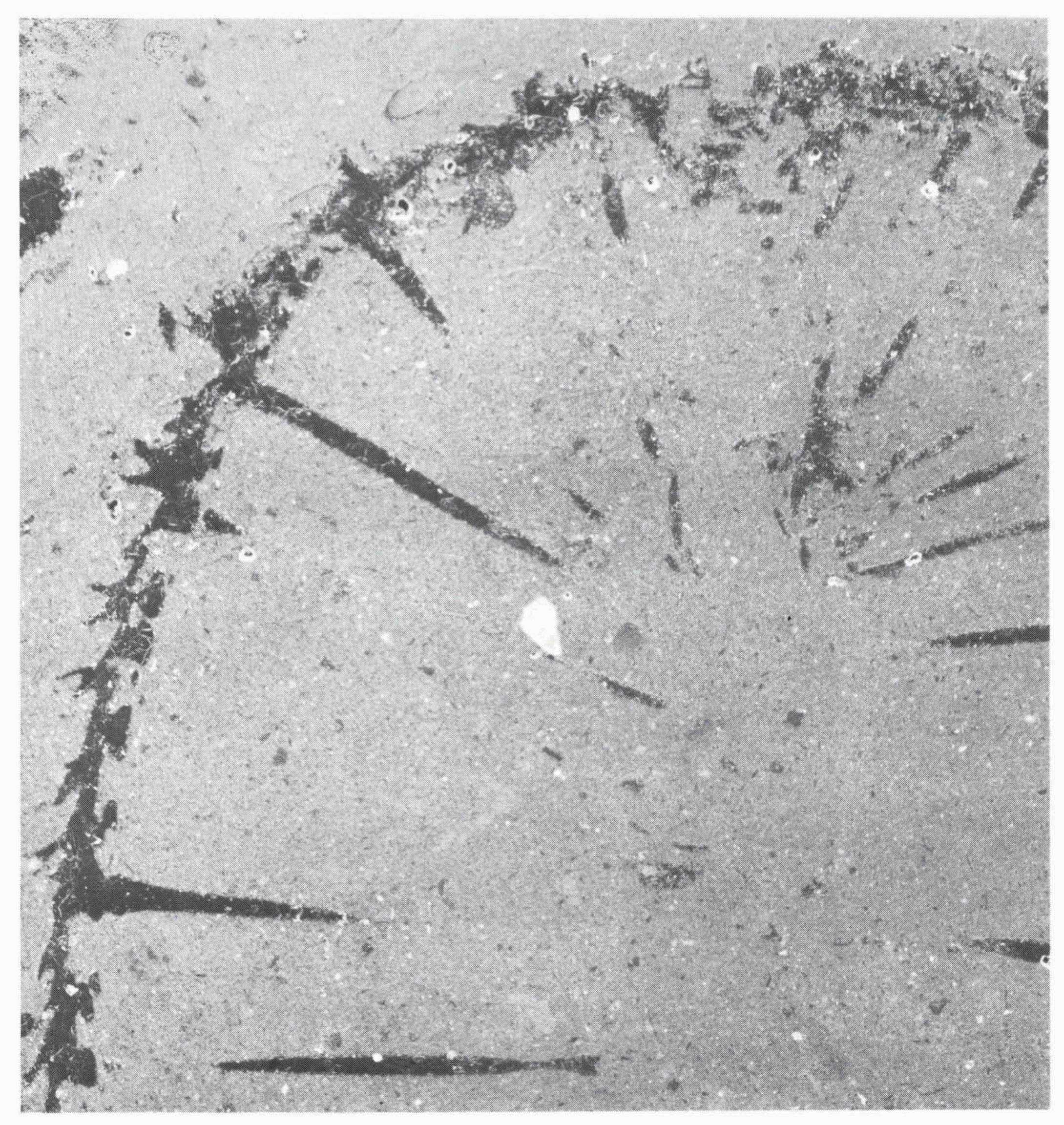


Fig. 6. Acetate peel of the nucleus of *T. sulcata* I 55A (2), showing the cup-shaped caps at the nucleus, which itself is collapsed, and their apicad transition into normally defined caps, × 22. Collection of Mr F. Smeenge.

Table 1. Measurements of the cap in mm.

cap	length	width	thickness	diameter
nucleus	—	—	0.08	0.30
minimum specimen diameter	0.9	1.0	0.10	—
maximum specimen diameter	4.0	3.5	0.18	—
apex	1.4	1.2	0.10	—

Fig. 7. Inner surface of a cap of *T. sulcata* RGM 243 791, exhibiting distal offshoots. Note the smooth outer surface, the rhomboidal shape and the meridional, latitudinal and diagonal overlap of the caps; × 16.

imposed, whereas on the apicad part a proximal convex and a distal concave section are superimposed (Figs. 4, 5). At the nucleus the caps are not undulated but are irregularly cup-shaped (Fig. 6). Their shape changes apicadly, the apicad part becoming the actual undulated cap whereas the nuclead part becomes reduced and eventually disappears. This change of shapes is already completed before the minimum specimen diameter is reached. From there downward the concave part of the cap becomes shorter with respect to the convex part.

The outer surface of the cap is generally smooth, except for some very small ridges which might be interpreted as growth lines in analogy with the observations of Rauff (1892a) and Rietschel (1969) (Figs. 5, 7).

The inner surface of the cap usually shows a number of well defined irregular ribs radiating from the basal part of the cap while increasing in number and diameter (Figs. 7, 8). Byrnes (1968) referred to these structures as 'distal offshoots' a term which will be used here. At the base of the cap the distal offshoots appear as small ridges but halfway the whole cap is distinctly ribbed whereas at the margins only the loose termini are seen lying next to each other (Fig. 8). The number of distal offshoots varies from 10 to 15, the diameter from 0.20 to 0.35 mm. At their extremity each is about 0.30 mm in diameter.

No caps of the above type have been described before, although caps of some *Ischadites* and *Receptaculites* species, as described by Rauff (1892a), are

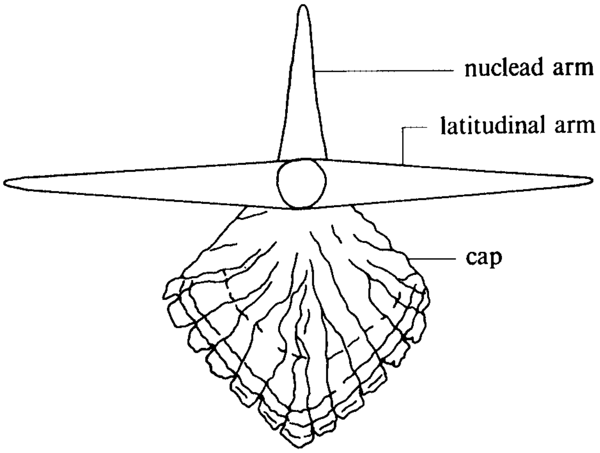


Fig. 8. Schematic diagram of the merom head, partly drawn from Fig. 7, seen from the underside, showing the distal offshoots with growth-lines; × 20.

similar. As far as is known, the nuclead part of these caps is still present. The latter have a different symmetry, caused by the absence of undulation of the caps. From the observations of Nitecki (1970) it can be concluded that the caps of *Lepidolites* are similar to those of *T. sulcata.*

The presence of distal offshoots seems to be a feature generally to be encountered in merom morphology. Byrnes (1968, pp. 371-372, figs. 1, 2) figured and described these of *Ischadites struszi* Byrnes. Distal offshoots are also present in *Receptaculites neptuni* Defrance, *R. orbis* d'Eichwald, *Ischadites koenigi* Murchison as figured by Rauff (1892a, Pl. 1, fig. 8 and Pl. 4, figs. 2 - 5, respectively) and Rietschel (1969, Pl. 3, fig. 15) and in *Ischadites dixonensis* (Miller & Gurley) as figured by Fisher & Nitecki (1978, fig. 2). Nitecki (1971, figs. 2 - 3) believed similar structures in *Ischadites stellatus* (Fagerstrom) to be additional arms of the merom head.

Nitecki & Debrenne (1979, pl. 3, fig. 5) compared the distal offshoots of *Receptaculites oweni* Hall with nesasters of radiocyathids. The fine meshwork on the caps of *Hexabactron borenorense* Campbell, Holloway & Smith observed by Campbell et al. (1974, pl. 15, fig. 4; pl. 16, fig. 1) might also be interpreted as distal offshoots (compare Rauff, 1892a, pl. 4, figs. 3, 5).

The arms

The arms are all slender structures, at their base attached to both cap and column. Usually they are perpendicular to the column, but slight deviations occur.

Although in all receptaculites, except *Ischadites struszi,* the lower part of the head comprises four arms, *T. sulcata* only possesses three arms, the apicad arm being absent (Figs. 4, 8). The nuclead arm as well as the two latitudinal arms are well defined, long, acute structures. They are perpendicular to each other and run parallel to the outer wall and hence are slightly bent (Figs. 5, 9). In cross-section they all appear to be distinctly elliptical at their basal part, gradually becoming circular towards the end (Fig. 5). The latitudinal arms are attached to the merom head at a lower position than are the nuclead arms (Fig. 2).

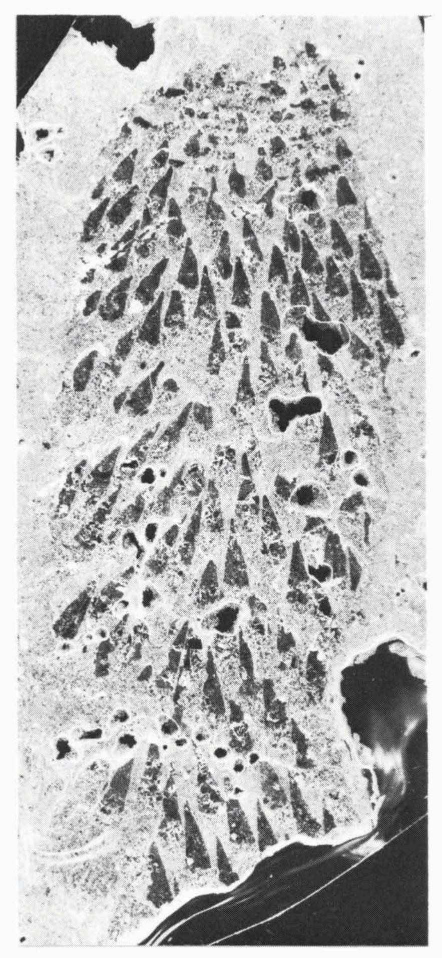


Fig. 9. Acetate peel of the surface of RGM 243 791 (1) after removal of the caps. Note the nuclead arms, the basal parts of the caps (lower left) and the distinct bilateral arrangement of the meroms; × 6.

Table 2. Measurements of nuclead arms in mm.

nuclead arm	length	width	thickness
nucleus	0.45	0.12	0.09
maximum specimen diameter	2.30	1.10	0.15
apex	0.30	0.18	0.10

Table 3. Measurements of latitudinal arms in mm.

latitudinal arm	length	width	thickness
nucleus	0.8	0.11	0.10
maximum specimen diameter	4.4	0.7	0.23
apex	1.0	0.07	0.07

Fig. 10. Latitudinal arms of *T. sulcata* RGM 243 788 after removal of the nuclead arms and caps. Notice the continuous layer of latitudinal arms, their dextracclive position and the arrangement of the meroms; × 12.5.

The column

The column ranges in shape from that of a spindle to that of a funnel. It shows an incision followed by a knob-like thickening directly below the centre of the merom head (Figs. 2, 3). Mostly the column is perpendicular to the outer wall, but at the nucleal part of the receptaculite body near the maximum specimen diameter it usually deviates a little towards the nucleus. From the nucleus to the

Table 4. Measurements of the column in mm; diameter values taken half-way the length of the column.

column	length	diameter
nucleus	2.8	0.15
minimum specimen diameter	3.2	0.23
maximum specimen diameter	7.3	0.28
apex	1.2	0.14

maximum specimen diameter the angle between the column and the cap decreases from about 60° to 15°. From the minimum specimen diameter to the maximum specimen diameter it increases from 15° to 30°, up to 80° at the apex (Fig. 13).

At places where the columns lie close to each other, traces of irregular junctions can be observed; these might be identical to the 'interlocking rays', as noticed by Foster (1973), but might just as well be due to diagenetical phenomena.

The foot

The foot consists of a small and ill-developed funnel-shaped expansion of the basal part of the column (Fig. 2). It is best defined at the nucleal part of the body decreasing in size towards the nucleus and the apex, being absent at the lower apical part of the receptaculite body.

On the inner surface of the relatively huge feet of specimen RGM 243 783 several large irregular outgrowths can be observed. Campbell et al. (1974, pl. 13, fig. 4) figured similar structures and refer to them as 'proximal offshoots'. This term was originally proposed by Byrnes (1968, p. 371, fig. 5) to indicate radial structures on the foot which are similar to the distal offshoots on the cap (see also Campbell et al., 1974, pl. 16, figs. 3, 4).

Table 5. Measurements of the foot in mm. Minimum diameter values taken at the transition between column and foot, maximum diameter values at the free extremity of the foot. The aberrant values of RGM 243 783 are not included; their minimum and maximum diameter values amount to 0.19 and 0.70 mm, respectively.

foot	minimum diameter	maximum diameter
nucleus	0.08	0.13
maximum specimen diameter	0.16	0.21
apex	0.07	0.12

FINE STRUCTURE OF THE MEROMS

According to Rietschel (1969) the merom consists of three parts. The first is a thin layer covering the whole merom, referred to as the enveloping layer (= Hüllschicht; Rietschel, 1969). The second and the third part, together referred to as merom core (= Merom-Kern; Rietschel (1969), consists of A) a thick layer of blocky calcite or (rarely) of calcite having a pinnate texture and B) an axial canal preserved as axially arranged dirty parts of calcite crystals or as calcite of a different texture.

The enveloping layer occupies up to 10% of the merom diameter of the column directly below the arms and diminishes down to 1% of the merom diameter towards both the cap and foot (Rietschel, 1969).

When the axial canal in each of the arms is preserved, it consists of a conspicuous large spindle-shaped structure. The axial canal in the column is mostly inconspicuous and often merges into the blocky calcite forming the rest of the merom core.

It appears that when meroms are filled with detritus, only the enveloping layer is present (see Rietschel, 1969, pl. 4, figs. 16, 17). Therefore the meroms

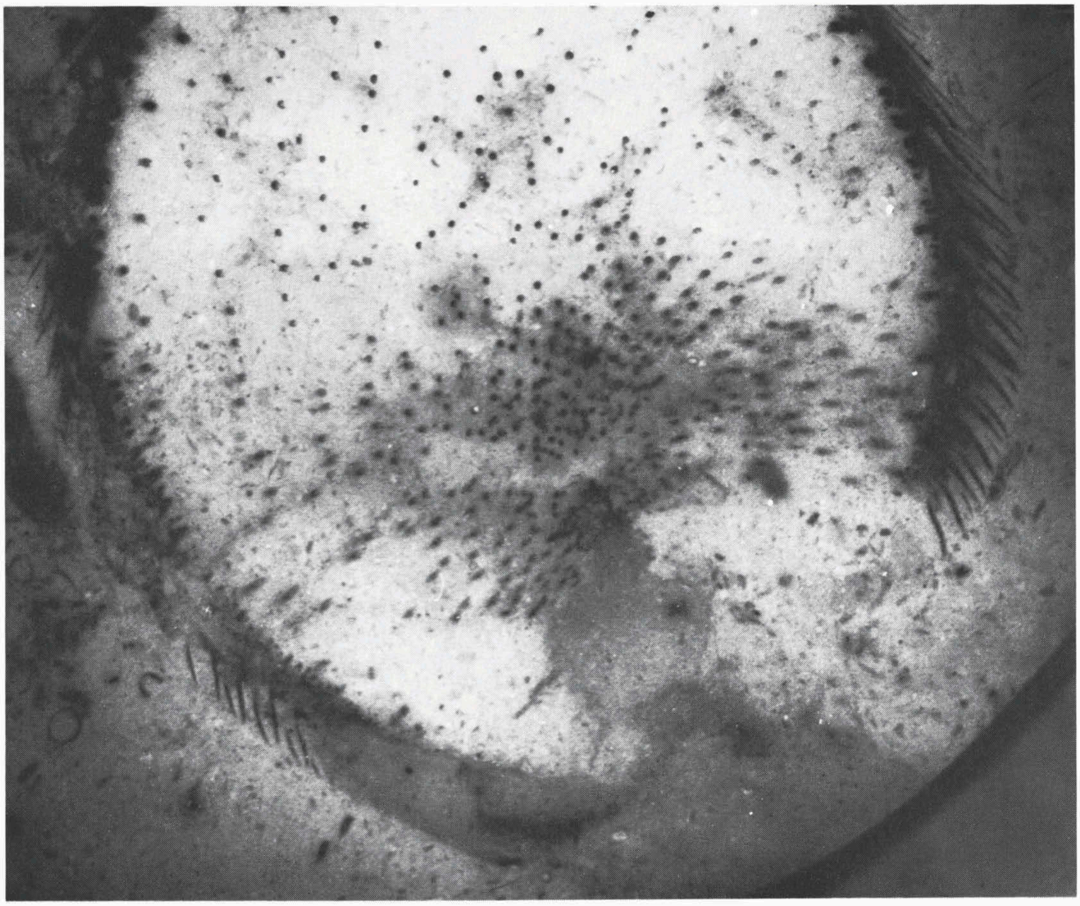


Fig. 11. Diagonal section of the apex of *T. sulcata* RGM 243 780, showing the apical part of the central cavity and the uncalcified meroms (below left), both preserved as colour differences. Note the oxidized pyrite representing the apical merom wall (at the bottom) and its upward curvature near the apex, forming an aperture-like structure; × 7.5.

initially must have been hollow structures consisting only of the enveloping layer covered by the cap. The space within the enveloping layer became gradually filled with carbonate afterwards, clogging the small opening in the merom foot and thus preventing any detritus to enter.

The carbonate filling the enveloping layer, at least in meroms with a pinnate texture, is of organic origin. The infilling of the remaining space, the axial canal, is of anorganic origin and took place after or even during lifetime of the receptaculite organisms.

The three-layered built up of the merom is usually obscured by diagenesis, such as is the case in the meroms of *T. sulcata* in which the original meromal matter has completely been replaced (see p. 6). For that reason the original meromal matter is believed to be aragonitic rather than calcitic, although no conclusive evidence can be presented.

A remarkable fine structure is to be seen on the outside of a merom of *T. sulcata* (specimen I 55A). It consists of very small aggregates of oxidized pyrite with a density of about 6000/mm^2, arranged in circlets on the surface of the merom. On parts where no aggregates are present, light reflections can be seen which correspond to the circlets of aggregates, together forming one surficial pattern. However, this feature can only clearly be seen on the upper part of the column of one single merom, situated somewhat below the maximum specimen diameter. Less distinctly it has been observed on other merom columns as well as on some merom heads, also of specimen RGM 243 780.

It is a usual but rather remarkable phenomenon to observe relatively large amounts of (oxidized) pyrite in *T. sulcata.* It is interesting to notice here that Nitecki (1970) observed a similar feature in *Lepidolites dickhauti.* In his specimens the merom caps were preserved as sulphides whereas associated fossils do not show this preservational condition. The occurrence of pyrite is by no means restricted to these species. Rietschel (1969) states that often the inner surface of the caps and the outer surface of the feet are covered with a thin layer of pyrite, whereas the meromal carbonate has been dissolved. Often meroms, in which the skeletal carbonate is replaced by sedimentary material, show an enveloping layer preserved as pyrite; also the merom core of calcareous meroms may completely be replaced by pyrite.

The remarkable mode of preservation by pyrite described above indicates that at least part of the pyrite is related to decay of organical matter belonging to the receptaculite itself.

MORPHOLOGY OF THE RECEPTACULITE BODY

Shape and size

T. sulcata is club-shaped to almost cylindrical. The outer wall near the nucleus is flattened, merging into a cone at the minimum specimen diameter. The body retains this shape up to about half-way the apex, from there expanding towards the maximum specimen diameter which is situated close to the apex (Fig. 12).

Of specimen RGM 243 780 the apical region itself is preserved. It consists of a thin but dense layer of minute aggregates of oxidized pyrite as well as of texture and colour differences. The layer of pyrite aggregates forms a flat bottom representing the uncalcified part of the merom wall, merging into its calcified counterpart somewhat below the maximum specimen diameter (Fig. 13). Close to the apex this layer curves inward forming an 'apical lacuna' (Fig. 11). At the apex some sort of small plug is present which expands towards the central cavity into which it gradually merges. Near the apex the columns of uncalcified meroms are preserved as colour differences (Fig. 11).

The nucleus is relatively acute compared with the apex, whereas both poles are slightly indented (Figs. 6, 11). A reconstruction of the original shape is shown in Fig. 1. The shape of *T. sulcata* from the northern Netherlands is identical to those from the Lower Lyckholm Limestone of Estonia, one of which is figured by Rietschel (1969, p. 470, fig. 1e; note that in his opinion the apex is erroneously orientated downward). The body shape of *T. sulcata* shows little variation, although some specimens show indentations in the outer wall similar to those described and figured by d'Eichwald (1860).

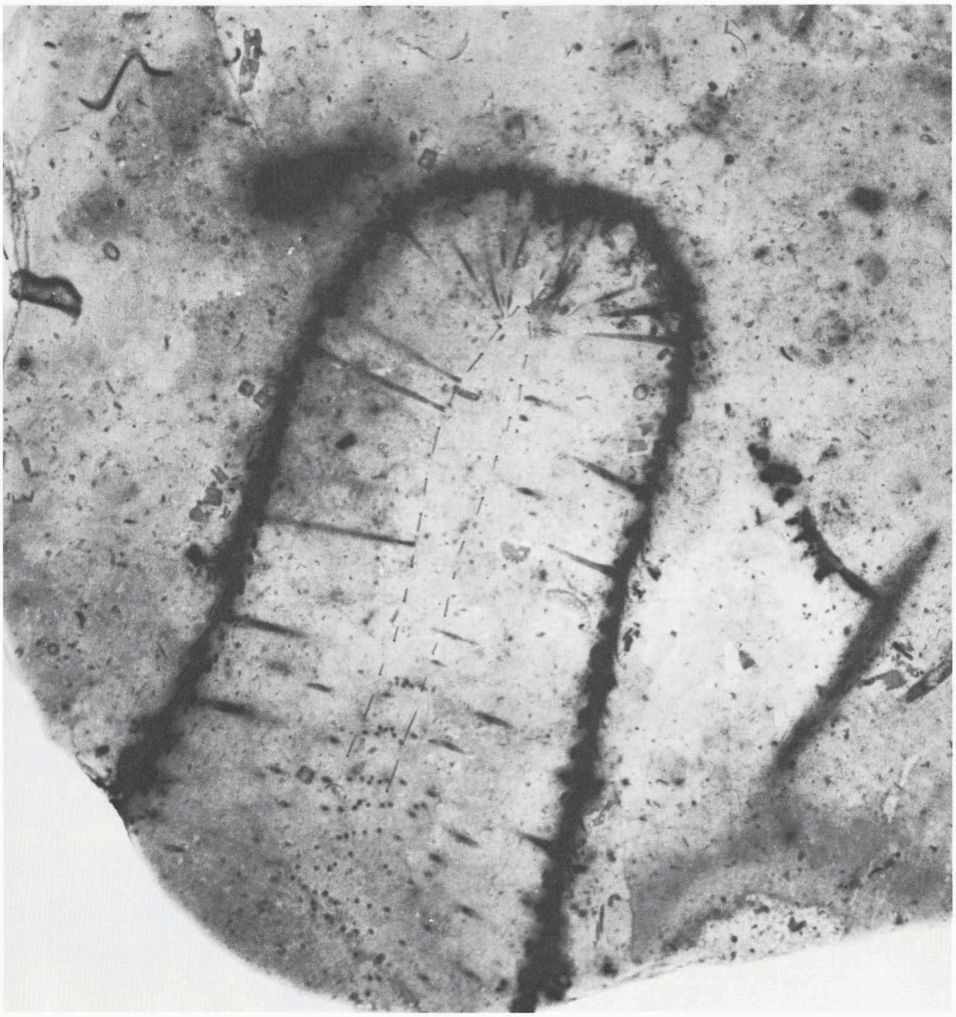


Fig. 12. Meridional section of the nucleal part of the body of *T. sulcata* (I 55A) within the matrix, showing the general shape, columns and feet of the meroms and the reconstructed central cavity, × 5 (photographed under water; overexposed to emphasize the basal parts of the meroms). Collection of Mr F. Smeenge.

Table 6. Measurements of the body size in mm.

body length			distance from apex	distance from nucleus
35 - 65	minimum specimen diameter	7 - 13	35 - 55	3 - 6
	maximum specimen diameter	18 - 23	6 - 11	35 - 50

The central cavity

The central cavity is formed by the feet lying next to each other. However, it is often difficult to distinguish the intermeromal space from the central cavity, be-

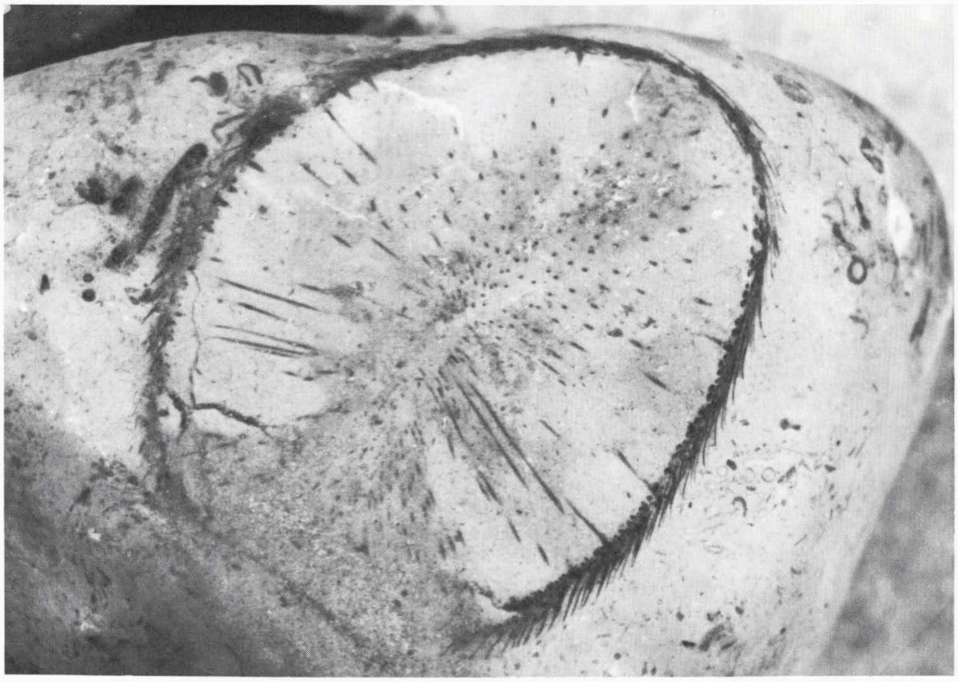


Fig. 13. Diagonal section of the apical part of *T. sulcata* RGM 243 780 within the matrix, showing part of the small central cavity and the layer of oxidized pyrite forming a flat bottom below the apex. Note the outer wall, the decrease in size of the cross-sectioned pairs of latitudinal arms and the increasing angle between cap and column; × 3.

cause no 'closed' inner wall is present. The central cavity communicates with the intermeromal space as well as with the axial canals originally present in the meroms. The central cavity, of which a reconstruction can be seen in Fig. 1, generally is very small, occupying about 8% to 15% of the total body volume. It starts about 3 mm below the nucleus (Fig. 12). In apicad direction it slightly increases in diameter until the maximum specimen diameter is reached. A little below the maximum specimen diameter it expands rapidly reaching its maximum diameter, whereafter it gradually decreases towards the apex (Figs. 1, 11).

CONNECTION BETWEEN THE MEROMS

The caps are imbricated like shingles on a roof and overlap each other in meridional, latitudinal and diagonal direction (Figs. 5, 11, 14). The degree of overlap in meridional and latitudinal direction is usually very small and amounts to 1/10 of the total surface area of the cap, in both directions to the same extent. About 3/4 of the surface area of the cap are covered by four neighbouring caps in diagonal direction. This leaves less than 1/4 of the cap surface which is not covered by neighbouring caps (Fig. 14). The degree of overlap of the caps increases apicadly from the maximum specimen diameter.

The nuclead arms of *T. sulcata* lie end to end following the meridians exactly (Fig. 9). The latitudinal arms lie side by side following the lattitudes. They extend beyond the tips of both neighbouring arms at the same latitude. The right

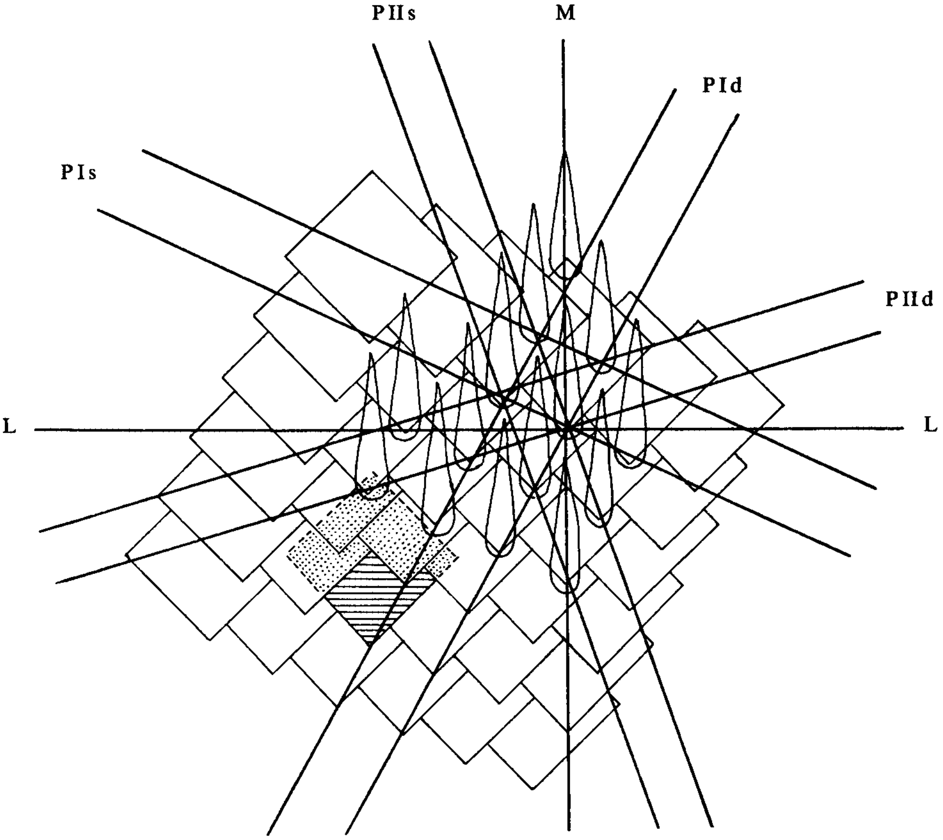


Fig. 14. Schematic representation of the arrangement of caps and nuclead arms of *T. sulcata.* in sinistracclive position.

M = meridian } orthostichies
L = latitude } (first geometrical system)
P I = first set of parastichies (second geometrical system)
P II = second set of parastichies (third geometrical system)
d = dextral; s = sinistral

latitudinal arm lies now at the nuclead, then at the apicad side of the left latitudinal arm of the neighbouring merom and so dextracclive and sinistracclive arrangements (Rauff, 1892a) are present. The latitudinal arms are closely packed which gives the impression of a striated continuous layer as shown by Fig. 10 (compare d'Eichwald, 1860, pl. 27, fig. 5b).

The caps always overly the arms, columns and feet of the neighbouring meroms. The nuclead arms lie directly below the caps but always above the latitudinal arms. Due to the arrangement of meroms the nuclead arms always overly several latitudes instead of one in other receptaculites and thus several pairs of latitudinal arms are covered by only one nuclead arm (Figs. 14, 15).

Due to the imbrication of the caps, they do not lie against each other, as is usual in receptaculites, nor are they fused and hence no 'closed' outer wall is present. The same applies to the feet, which means that the intermeromal space is free to communicate with the central cavity, not being separated by a 'closed' inner wall.

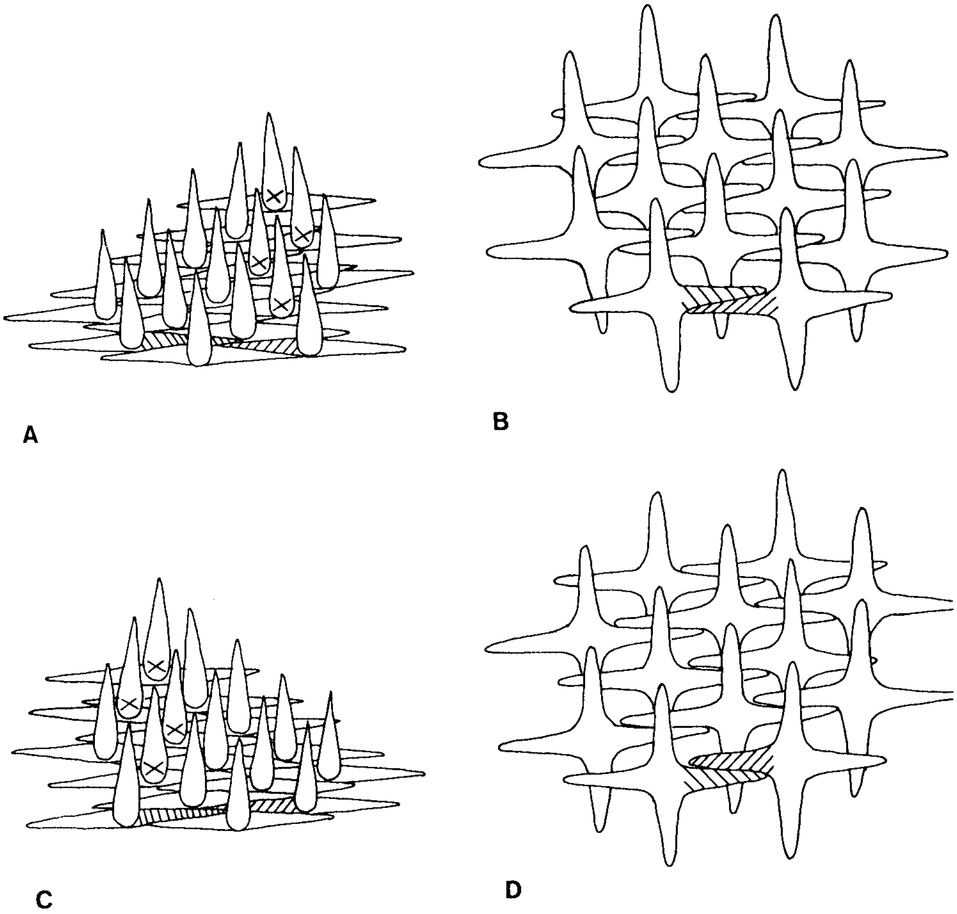


Fig. 15. Interlocking and arrangement of merom arms. Note the difference in packing of the arms between the two types. A: *Tetragonis* type, dextracclive, drawn from *T. sulcata* RGM 243 788; B: *Receptaculites* type, dextracclive, after Byrnes (1968) and Rietschel (1969); C: *Tetragonis* type, sinistracclive, drawn from *T. sulcata* RGM 243 788; D: *Receptaculites* type, sinistracclive, after Byrnes (1968) and Rietschel (1969).

In areas where the curvature of the receptaculite body is pronounced, the columns and feet lie close sometimes even against each other. Generally, however, ample space between these meromal elements is present (Fig. 12).

ARRANGEMENT OF MEROMS

Receptaculites show a regular configuration of meroms according to two geometrical systems. One comprises a set of meridians and latitudes, the orthostichies, the outer consists of a set of intersecting dextral and sinistral whorls, the parastichies. As will be demonstrated in the following chapter, receptaculite growth implies meroms which alternate in position on the latitudes. This alternating arrangement produces all other geometrical patterns, i.e. the meridians as well as

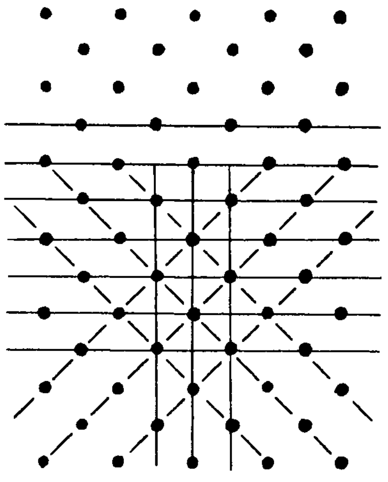


Fig. 16. Geometry of the *Receptaculites* type of merom arrangement produced by the alternating position of meroms on the latitudes.
Dots = merom position; horizontal lines = latitudes; vertical lines = meridians; dashed lines = parastichies.

the dextral and sinistral whorls (Fig. 16). Since this type of merom arrangement has been extensively studied on *Receptaculites neptuni* (Gümbel, 1876; Rauff, 1892a; Rietschel, 1969, 1970), it will be referred to as the *Receptaculites* type.

Compared with the *Receptaculites* type the arrangement of meroms of *T. sulcata,* referred to as the *Tetragonis* type, exhibits a shift in the alternation of meroms on the latitudes. As a result of this shift the 4th instead of the 3rd latitude is in the same position as the 1st one. The meroms on the 2nd and 3rd latitude lie lower left and upper right respectively in dextracclive position and lower right and upper left in sinistracclive position, as shown in Fig. 15 by the arms marked (×). In fact, instead of meroms alternating on two succeeding latitudes (in the *Receptaculites* type) the position of meroms on the latitudes of the *Tetragonis* type is repeated every three latitudes. This arrangement implies the creation of an additional, third, geometrical system of yet another set of dextral and sinistral parastichies (Fig. 14). Actually, this additional system is derived from the *Receptaculites* type system of orthostichies by a slight rotation. The 'new' set of meridians of the *Tetragonis* type is obtained by connecting the nuclead arms which are in direct line with each other; the 'new' set of latitudes is obtained by connecting the centres of meroms at right angles to the meridians.

With regard to the position of the different meromal elements to each other, the *Tetragonis* type shows important differences when compared with the *Receptaculites* type:

a) the degree of imbrication of the caps increases strongly in diagonal directions (one cap is diagonally covered by four neighbouring caps instead of two),

b) the nuclead arm overlies three pairs of latitudinal arms instead of only one pair,

c) the mutual space between nuclead arms and latitudinal arms is reduced and thus they are more tightly packed into an almost continuous layer.

Within one specimen the *Tetragonis* type of merom arrangement is present in a dextracclive and a sinistracclive modification: the tip of the nuclead arm lies either to the right or to the left of the closest neighbouring nuclead arm respectively (Fig. 15). Each of two modifications is restricted to one half of the receptaculite in meridional direction, separated by a small transition area (Fig. 9). Foster (1973) described a similar bilateral symmetry in the arrangement of meroms of *Ischadites mammilaris.*

The number of meroms at the nucleal pole is limited, although the exact number could not be determined due to the post-mortem collapse of this pole. Estimates run from 4 to 12, whereas in receptaculites in general 8 is the normal number (Rietschel, 1969). From the nucleus towards the maximum specimen diameter the number of meroms increases to approximately 30 at about the 20th latitude; then only occasionally an increase occurs. This increase of the number of meroms is achieved by consistently adding one merom per latitude thus creating a new merom parastichy integrated in the surrounding pattern of older ones. In *T. sulcata* the insertion of new parastichies runs according to the SM 3/1 type (Rietschel, 1970, text-fig. 4). It consists of a division of either a dextral or a sinistral parastichy respectively. In this type the last merom of the original parastichy forms a unit together with the first meroms of both newly created parastichies.

Near the nucleus of *T. sulcata* the latitudes form circlets around the nucleus. The remaining part of the body shows latitudes which coincide with a compressed slowly-winding dextral spiral rather than a set of circlets and thus are not true latitudes in the meaning of the word.

Biological interpretation of receptaculites

GROWTH AND CALCIFICATION

The geometrical arrangement of meroms as well as the morphological development of meroms from nucleus to apex imply that receptaculites increased in size by polar growth (Rietschel, 1969, 1977; Gould & Katz, 1975; and others). Rietschel (1969), Foster (1973), Campbell et al. (1974), Gould & Katz (1975), and Fisher & Nitecki (1978) contra Byrnes (1968) and Nitecki (1971, 1972) inferred that the apex must have been the growing pole. They base their views on the pattern of insertion of new merom parastichies, on the growth lines of merom caps and/or on the progressive fusion of merom caps and feet towards the nucleus. The presence of not yet fully grown and uncalcified meroms near the apex of *T. sulcata* clearly supports this view.

Growth and calcification of the meroms

Only the cap and foot of a merom exhibit growth lines, in contrast to the arms and column, therefore it must be postulated that two different modes of growth must have been present. During merom growth both the cap and foot were subjected to an increase in surface area, whereas the rest of the merom is subjected to an increase in volume.

Surface increase of the cap was achieved by marginal growth, as is indicated by the growth lines. The presence of distal offshoots and few but coarse and pronounced growth lines on the inner part of the cap demonstrate that marginal growth was different from that of the outer part of the cap, the latter having many but very fine growth lines and no distal offshoots at all.

It must be assumed that distal offshoots initiated growth of the inner part of the cap, the space in between gradually becoming filled afterwards thus producing growth lines. One argument supporting this view is that distal offshoots not connected with each other are present on the edges of caps of *T. sulcata* and in the form of crenated edges on caps of other receptaculites. Another argument is that distal offshoots progressively become more pronounced towards the apex, the growing pole, a phenomenon already observed by Byrnes (1968) in *Ischadites struszi.*

Growth of the outer part of the cap was preceded by growth of its inner part as is demonstrated by the presence of distal offshoots not connected with each other on the edges of the caps. For these reasons it might very well be that the outer part of the cap is a separate plate-like structure based on the inner part of the cap. Also Byrnes (1968) noticed that the merom caps of *Ischadites struszi* consist of two different parts, an outer plate and an inner layer of distal offshoots. Rauf (1892a) arrived at the same conclusion because of the matrix-filled seams he observed between the outer and inner part of the caps of *Receptaculites neptuni.*

The same mode of growth of the cap might also have been that of the foot, which according tot Byrnes (1968) shows 'proximal offshoots' similar to the distal offshoots of the cap; also here growth lines may be observed (Byrnes, 1968; Rietschel, 1969).

Growth lines among other morphological features show that merom growth was accompanied by merom calcification. Observations on *T. sulcata* support Rietschel's (1969) conclusion that merom calcification proceeded from cap towards foot with increasing distance from the apex.

The base of the cap, the arms, the column, and the upper part of the foot have grown in yet another way. It has been concluded (p. 16) that in early ontogenetic stages the meroms consisted only of an enveloping layer. Meroms increased in length as well as in diameter from apex to maximum specimen diameter, but meanwhile the enveloping layer retained its thickness. In this respect Rietschel's (1969) view is adopted that the enveloping layer expanded during merom growth. Therefore, merom calcification did not take place by simply adding carbonate to the merom, as otherwise the enveloping layer should have been much thicker than it is at present. Because it seems difficult to imagine the calcified enveloping layer to expand during merom growth, it must be assumed that meroms calcified by deposition of carbonate on the outer surface of the enveloping layer, meanwhile resorbing carbonate from the inner surface. Also Campbell et all. (1974) suggest that during merom growth some carbonate resorption must have been necessary, for *Hexabactron borenorense* paradoxically has its thickest caps near the apex.

Since meroms apparently were required to cover the surface of the receptaculite completely, they had to adapt their size and proportion constantly while changing their position from apex to maximum specimen diameter. This adaptation is reflected by the pattern of growth lines on the merom caps: while increasing in size the meridional axis of the rhomboidal merom cap decreased with respect to the latitudinal axis (see Rietschel, 1969), obviously to keep up with the increasing space between the merom caps latitudinally. In order to fit in the interstices between previously generated caps, a particular shape and size was needed for merom caps initiating new merom parastichies ('interpositum' and 'triangulum'; Fisher & Nitecki, 1978). These observations indicate that meroms were able to adapt their size and proportions through individual growth and calcification.

The absence of apicad arms in *T. sulcata,* their presence in only three out of numerous meroms in *Ischadites struszi* (Byrnes, 1968) as well as the absence of columns and feet in *Sphaerospongia tessellata* Philips (Hinde, 1884) endorse the view that to a certain extent the receptaculite organism must have controlled merom calcification.

Growth of the receptaculite body

Receptaculites grew by generating new meroms at the apex, by intercalating new merom parastichies and by (individual) increase in size of the meroms. At the apex meroms were generated either in circlets (Rietschel, 1969; Gould & Katz, 1975) or in spirals (Nitecki, 1969, 1971; see Gould & Katz, 1975). In both generative modes previously formed meroms were constantly 'pushed' away from the aperture by newly inserted ones. This mechanism forced the older meroms to change their position gradually from the apex via the maximum specimen diameter to the nucleal part of the receptaculite body. Since from the apex to the maximum specimen diameter the intermeromal distance increased in latitudinal direction, the meroms had to adapt their size and proportion individually in order to cover the surface of the receptaculite completely and not to loose contact with each other. However, merom size was apparently limited and thus additional meroms had to be intercalated between the existing number of meroms, which gave rise to new merom parastichies. After the maximum specimen diameter was reached, the intermeromal distance remained constant and so merom growth and calcification ceased. Because meroms arriving at the maximum specimen diameter were slightly larger than previously arrived ones, merom size decreases from there towards the nucleus.

This particular mode of growth produced meroms which only vary in size and proportion in meridional direction and are identical in latitudinal direction.

In *T. sulcata* the collapse of the nucleus, which is also frequently observed in other receptaculites, can be due to the not yet fully grown meroms at this place. Due to the small size of the receptaculite in the earliest ontogenetic stages (see Rietschel, 1969), the nucleus moved relatively rapidly out of the zone of growth, thus producing incomplete meroms near the nucleus. Also the absence of the apical part of the body of many receptaculites (for instance all *Receptaculites* species) may be due to incompletely calcified or uncalcified meroms near the apex. Certainly the apical aperture, if present, has been widened after death of the organism due to decay of organic matter and washing away of incomplete meroms, though its primary presence has been demonstrated by Campbell et al. (1974).

Receptaculite geometry and receptaculite growth

A number of geometrical arrangements of meroms can be recognised on the receptaculite body. Meroms are generated at the apex either in circlets (Rietschel, 1969; Gould & Katz, 1975), in a double dextral spiral (Nitecki, 1969), or in a not specified spiral way (Rietschel, 1969; Nitecki, 1971; this paper). The *Tetragonis* and *Receptaculites* types of merom arrangements have been described in the former chapters. Latitudinal arms (in a *Tetragonis* type of arrangement also the nuclead arms) show either a dextracclive arrangement, a sinistracclive arrangement, or bilateral symmetry when both arrangements are present. Rietschel (1969, 1970) described three types of insertion of new merom parastichies: the first one consists of a unit of two meroms initiating two parastichies (a dextral and a sinistral one; the SM 2/2 type), the second differs from the first in having a unit of three meroms initiating two parastichies (the SM 3/2 type), whereas the third type includes a unit of three meroms asymmetrically initiating either a dextral or a sinistral parastichy (the SM 3/1 type).

All receptaculites show the pattern of orthostichies and parastichies in a greater or less degree no matter which one of the above mentioned merom arrangements is present. It has been demonstrated (p. 21) that this pattern forms a geometrical unit produced by the alternating position of meroms on the latitudes. According to Gould & Katz (1975), receptaculite geometry developed only by placing new meroms in the interstices between previous ones. It is obvious that this mode if inserting new meroms in its turn produced the alternating position of meroms on the latitudes and consequently also the pattern of orthostichies and parastichies. Therefore, generation of meroms in circlets or in spirals, a merom arrangement according to the *Tetragonis* or *Receptaculites* type as well as a dextracclive or a sinistracclive arrangement of merom arms, only seem to be different manners in which newly formed meroms can be fitted into the largest space available. Bilateral symmetry in the arrangement of merom arms, however, cannot adequately be explained in this way.

Although at least in some receptaculites (for instance *Ischadites koenigii;* Nitecki, 1969) the apical meroms are arranged in spirals, all receptaculites which yet have been reported show nucleal meroms arranged in circlets. Fisher & Nitecki (1978, p. 20) state that *Ischadites dixonensis* '... shows subtle indication, especially near the summit of the thallus, of the helical surface topography which is so typical of *Ischadites koenigii.*' (the 'summit of the thallus' is here referred to as 'apex'). According to their fig. 4, the nucleal part of the same specimen shows meroms arranged in circlets. For these reasons both generative modes may have been present during receptaculite growth: in early ontogenetic stages meroms were inserted in circlets starting from the initial circlet of 8 meroms (rarely 4 or 7; Rietschel, 1969) around the nucleus, whereas in later ontogenetic stages they were inserted one at a time in a spiral way. At least both modes of generating meroms seem to be present in *T. sulcata.*

The presence either of a *Receptaculites* or a *Tetragonis* type of merom arrangement may have been determined by functional requirements. Since in the *Tetragonis* type the imbrication of caps increased strongly and the packing of merom arms is much tighter, this arrangement offers a more solid connection compared with the *Receptaculites* type.

Rauff (1892a) stated that a dextracclive arrangement of latitudinal arms is far more frequently present than a sinistracclive arrangement. It seems possible that this conspicuous preference is related to the mode of generation of meroms. It is obvious that generation of meroms according to a double dextral spiral, as has been observed by Nitecki (1969) on *Ischadites koenigii,* implies a dextracclive arrangement of merom arms. Because Rietschel (1969), Nitecki (1971) as well as the present author did not specify spiral insertion of meroms, its relationship to a dextracclive arrangement remains uncertain.

According to Gould & Katz (1975), the seemingly random intercalation of new merom parastichies is actually governed by the tightness of the old parastichies. It seems likely that also the three types of intercalation of new merom parastichies described by Rietschel (1969, 1970) are different manners in which the space arising between the old parastichies can be filled.

It is still to be solved which relationships exist between the different modes of merom arrangements mutually and between receptaculite growth and merom arrangement. In *T. sulcata* the following arrangements are present: 1) generation of meroms in circlets at the nucleal pole and in a dextral spiral in the remaining part of the body; 2) *Tetragonis* type of merom arrangement; 3) bilateral symmetry in the arrangement of merom arms (i.e. both dextracclive and sinistracclive arrangements); 4) intercalation of new merom parastichies according to the SM 3/1 type. Probably the presence of one of the arrangements of meroms mentioned above or a combination of these is of systematic importance.

ORIENTATION OF RECEPTACULITES DURING LIFE

Relatively little attention has been paid to receptaculites preserved in growth position in order to determine their life orientation. According to Nitecki (1971, 1972), the common *Calathium egerodae* Nitecki and *Ischadites koenigii* as well as *Ischadites abbottae* Nitecki and *I. stellatus* (Fagerstrom) were found in growth position with their apex obviously orientated downward (note that due to differences in the interpretation of the terms 'apex' and 'apically', which in this paper have a specific meaning, they must be replaced by 'nucleus' and 'nucleally'). Nitecki (in Gould & Katz, 1975, Note Added in Proof) assured that the apex is down in receptaculites preserved in growth position. Without commenting on Nitecki's earlier observations, Fisher & Nitecki (1978) inverted this orientation in assuming the nucleus to have been downward in life position. Other statements were probably based on preconceived ideas on the nature of receptaculites: a sponge interpretation as well as an algal interpretation require the apex to be orientated upward; the first to interpret the apical aperture as an 'osculum', the second because in 'related' algae the growing pole is upward. Campbell et al. (1974) adduced strong sedimentological arguments to demonstrate that the apex of *Hexabactron borenorense* and, consequently, that of other receptaculites, was the lower pole in life position. The present author can only agree with this view, at least as far as *Hexabactron borenorense* is concerned, for many observations on *T. sulcata* can be interpreted in different ways. However, an algal interpretation of receptaculites (assimilation, calcification) provide important arguments against the possibility of an apex-down life orientation, as will be discussed on p. 34.

The apical aperture

A major aspect regarding an apex-down life orientation is the presence of an aperture in the centre of the apex. The presence of such primary apical aperture has been much disputed in the past. Rauff (1892a) and Rietschel (1969) assumed the receptaculite body to be completely closed and regarded the presence of an apical opening frequently found in receptaculite fossils to be due to post-mortem decay and removal of the weakly or not calcified apical meroms. Hinde (1884), Byrnes (1968), Nitecki (1972), Fisher & Nitecki (1978), and Foster (1973) were convinced of the primary presence of an apical aperture. Campbell et al. (1974)

at last furnished clear proof that a well defined primary apical aperture is present in *Hexabactron borenorense.*

An apex-down orientation would solve the problem of how receptaculites were attached to the substrate if it is assumed that rhizoids projected from the apical aperture. For it seems unlikely that large receptaculites with an acute nucleus and a blunt apex (for instance *Ischadites mammilaris,* up to 20 cm long) could retain a nucleus-down upright position other than being attached to the substrate. Since the nucleus definitely is a closed pole and no structures have been found which could have supported the body, a nucleus-down position seems to be unlikely in view of its attachment to the substrate. If the apex is considered to be part of a supporting structure, the definition or even the presence of an apical aperture would probably have been controlled by the energy of the environment, the body shape and the body size of the receptaculite.

The well preserved apex of *T. sulcata* RGM 243 780 shows a structure which can be interpreted as an apical aperture (Fig. 11). It consists of a kind of plug in the centre of the apex, which differs in colour and texture from the wall formed by the apical meroms surrounding it. The diameter of this plug measures 0.7 mm. As a matter of fact Nitecki (1970, p. 22, fig. 14) observed a 'scar of pedicle attachment' at the apex of *Lepidolites dickhauti,* a receptaculite closely related to *T. sulcata.*

FUNCTIONAL ASPECTS OF THE MEROM

A major functional aspect of meroms seems to be that they simply had to fill space (see Gould & Katz, 1975). There are various arguments which support this view. For instance, individual growth of meroms, especially that of the merom caps, seems to be an ability entirely required to fill the intermeromal space which progressively increased from the apex up to the maximum specimen diameter. For the same reason intercalation of new merom parastichies was needed since the size of meroms was limited. However, meroms seem to have performed yet another function.

As has been described in this paper and in previous studies, all meromal parts are in some way connected with the corresponding parts of neighbouring meroms:
caps: imbricate arrangement, toothing of crenated edges, formation of a continuous wall, fusion;
arms: complex interlocking resulting into a rigid outer wall;
columns: interlocking of 'interlocking rays' into an 'interlocking zone';
feet: formation of a continuous wall, fusion.
These morphological features reveal that meroms also must have had a supporting function. Other observations, such as insertion of new meroms next to incomplete ones after a period of ceasing growth (a phenomenon described by Rietschel, 1969) agree with this view.

In the light of a supporting function of meroms some other morphological and organisational features may be understood. Since *Hexabactron borenorense* has its thickest caps near the apex (Campbell et al., 1974), apparently to support its large body, the lighter weight of meroms as hollow structures offers quite an advantage, as hollow structures may offer the same mechanical resistance as solid ones. Calcification of meroms long before they reached their final size and proportion, does not seem to be difficult to understand if one assumes an apex-down growth orientation, since the apical meroms had to prevent a collapse of the weak and vital growing pole. For these reasons the depositional-resorptional mode of merom calcification may have been a functional requirement considering the presence of meroms as hollow structures as well as their increase in volume. Those meromal parts which only required an increase in surface area did not demand for such a mode of calcification and thus were enlarged by marginal calcification. Furthermore it seems obvious that the enveloping layer is thickest at the incision between merom head and column, since that seems to be the most vulnerable part of the merom.

The remarkable undulation of the cap can be understood by considering their imbrication. From the manner of undulation and imbrication it is concluded that the caps form a dense outer layer by covering a convex part of a cap with a convex part of the neighbouring cap and vice versa. Probably the imbrication of undulated caps contributed to the solidity of the receptaculite body.

As has been demonstrated above on p. 24, the merom cap seems to consist of two separate parts. The thin plate-like outer part seems to have served as a covering of the outer surface of the receptaculite body and probably also as that of the space inside the merom. The rest of the cap, in some meroms fused with part of the arms (nuclead and/or latitudinal arms), in others being a separate, probably hollow structure, seems to have functioned as the bearer of the outer plate-like covering and may also have contained organic tissue, as will be discussed in the next section. Moreover, it contributed to the solidity of the merom skeleton by means of toothing of crenated edges.

The arms are considered to have functioned as supporting structures but probably also carried organic tissue inside their axial canals.

The columns may have had the same function as the arms; their spindle shape suggests that they had to withstand pressure. Tight packing of columns, as has been observed in several receptaculite species, may have contributed considerably to the solidity of the merom skeleton.

The frequently ill-developed feet of several receptaculite species suggest that their supporting function was of minor importance; any other function does not seem to have been present.

Merom caps almost always have a rhomboidal shape (the hexagonal caps of *Hexabactron borenorense* and *Sphaerospongia tessellata* being the only exceptions) even when lying apart from each other as in early stages of growth or in imbricative arrangements. However, merom feet are circular in outline whereas those lying against each other generally have a hexagonal shape rather than a rhomboidal one (Rietschel, 1969, pl. 2, fig. 6). The function of the rhomboidal shape of the merom caps remains uncertain; would the caps merely have functioned to form a continuous outer wall, then a hexagonal shape as shown by the feet would have been more obvious.

SOFT PARTS OF RECEPTACULITES

From the mode of calcification it becomes clear that the meromal carbonate must have been deposited in the cell wall or within the cell itself. Calcification by extracellular or surficial deposition of carbonate would result in completely different meroms:

a) meroms would be preserved as negatives instead of positives (Rietschel, 1969);
b) all parts of the meroms in contact with each other, i.e. caps, arms and feet, would be fused.

Rietschel (1969) argued that no soft tissue could have existed between the meroms, for it would have to be present in an increasingly more confined space during merom growth. Moreover, in receptaculites having a closed inner wall (for instance all *Receptaculites* species) this intermeromal tissue could only have communicated with soft tissue inside the central cavity near the apex of the receptaculite body. Campbell et al. (1974) inferred that in *Hexabactron borenorense* the intermeromal tissue would communicate with that inside the central cavity through the pores in the inner wall. However, this could not have been the case in those receptaculites possessing a closed inner wall. Moreover, the merom arms of *T. sulcata,* especially the latitudinal arms, form an almost impenetrable layer, a feature also observed in some other receptaculite species, and thus would have prevented any intermeromal soft tissue to perform its function. Campbell et al. (1974) further assumed that intermeromal soft tissue communicated with a tissue outside the merom wall. Since the major part of receptaculite species do have a closed outer wall, the presence of the latter tissue is rather hypothetical. For these reasons it seems unlikely that the intermeromal space was completely filled with soft tissue, although a thin covering might have been present. However, it seems very unlikely that any tissue could have been present outside the merom wall, as has been postulated by Campbell et al. (1974).

Merom growth and calcification imply that intrameromal soft tissue must have been present between the apex and the maximum specimen diameter. It also may have been situated in the meroms at the nucleal part of the receptaculite body, although there are indications that in some receptaculite species the intrameromal space became closed there during receptaculite growth (Rietschel, 1969). The axial canal in the merom columns, if preserved, is usually present as axially arranged fine particles of pyrite or unidentified organic matter which provide direct evidence that soft tissue must have been present inside the meroms.

It seems likely that soft tissue communicating with the intrameromal soft tissue was present in the central cavity. Whether this space was completely filled with this tissue, or that it only covered the outside (= inner wall), could not be determined.

In case of an apex-down life position, rhizoids would probably have been present, projecting from the apical aperture, to retain the upright position of the receptaculite body.

ECOLOGY OF RECEPTACULITES

T. sulcata is only known from the Ostseekalk and the Lower Lyckholm Limestone, both being organodetritic micrites. The well-preserved almost complete fossils indicate that they became fossilised in their natural environment. Associated fossils, which mainly consist of small and delicate benthonic organisms, are found in the same state of preservation indicating a low-energy environment. The abundance of dasyclad algae *(Vermiporella* and *Coelosphaeridium)* shows that *T. sulcata* must have lived in the photic zone. During the Late Devonian *Vermiporella* appears to have been restricted to lagoon or back-reef environment (Wray, 1977).

Lepidolites dickhauti has been reported from carbonate rocks in which faunal elements, the same as are associated with *T. sulcata,* are predominant (Nitecki, 1970). However, no dasyclad algae were mentioned.

From these observations it can be concluded that *T. sulcata,* as well as *Lepidolites dickhauti,* inhabited low-energy, shallow marine environments restricted to a carbonate facies.

Receptaculites in general seem to have inhabited a diversity of environments. They have been found associated with reefs ranging from extremely high-energy to inter-reef environments as well as in non-reef environments. They also do not seem to have been restricted to a specific lithofacies as they are encountered in carbonate, marly as well as shaly rocks (Rietschel, 1969; Nitecki, 1970, 1972).

Systematics

Ordo RECEPTACULITALES Sushkin, 1962
Familia TETRAGONACEAE Rietschel, 1969 (nomen correctum)
Genus *Tetragonis* (d'Eichwald, 1842)

Tetragonis sulcata d'Eichwald, 1860

The genus *Tettragonis* was described by d'Eichwald in 1842, but in 1845 Lonsdale changed its name into *Tetragonis* because of the etymology of the generic name, a compound of the Greek tetra = four and gonos = corner. D'Eichwald adopted this change in 1860, the generic name *Tettragonis* thus becoming invalid. Consequently the family name Tettragonaceae Rietschel, 1969 must be replaced by Tetragonaceae Rietschel, 1969 (nomen correctum).

Tetragonis as conceived by d'Eichwald in 1842 comprised *T. murchisoni* only. D'Eichwald's *Tetragonis* (1860, pp. 433 - 434, pl. 27, fig. 55) includes his new species *sulcata,* based on one incomplete specimen. It was described from the 'dolomitic limestone' of Kirna, Estonia, but obviously the Lower Lyckholm Limestone is meant here.

The classification of *T. sulcata* will be discussed in detail below and also the assignment of *T. sulcata* and the closely related *Lepidolites dickhauti* Ulrich, 1879 to the family Tetragonaceae within the Thallophyta.

SYSTEMATIC POSITION OF RECEPTACULITES

Hardly any group of fossils has such a comprehensive record with respect to its affinities as receptaculites. Earlier discussions, however, narrowed down their assignments to either calcareous algae or sponges. Hinde (1884), Waterlot (1932), de Laubenfels (1955), and Foster (1973) regarded receptaculites as sponges or as related to sponges. Kesling & Graham (1962), Nitecki (1967 and subsequent papers), Byrnes (1968), Rietschel (1969, 1977), Campbell et al. (1974), and Gould & Katz (1975) on the other hand favoured an algal affinity. A third possibility, namely that they should be regarded as an extinct group of organisms which cannot be assigned to any of the extant phyla, has only briefly been considered (see Foster, 1973).

Comparison with sponges

Those authors who regarded receptaculites as sponges, based their views mainly on morphological similarities between the spicules of sponges and the meroms of receptaculites, leaving the organisational aspects out of consideration. Rauff (1892), Rietschel (1969), Foster (1973), and Campbell et al. (1974) extensively compared receptaculites with sponges. All but Foster concluded that an assignment to sponges could not be maintained, especially in view of their organisation.

Besides the arguments adduced by Rauff (1892a), Rietschel (1969) and Campbell et al. (1974), there are some additional arguments against a sponge affinity of receptaculites:

The spicules of hexactinellid sponges, to which meroms should belong according to their morphology, are formed by concentric deposition of silica resulting into concentrically layered spicules. The cap as well as the foot were formed by marginal deposition of carbonate, the rest of the merom by a depositional-resorptional mode of calcification. The distinct build-up of the merom consisting of an enveloping layer and a merom core with an axial canal is not known of any sponge spicules. Moreover the non-calcification of the apicad arm in *T. sulcata* and *Ischadites struszi* and the column and foot in *Sphaerospongia tessellata* is a phenomenon difficult to reconcile with a spicule nature of meroms. The complex connections between single meroms by means of caps (through imbrication, toothing or fusion), arms (interlocking), columns ('interlocking zone'), and feet (fusion) are unknown in sponge organisation.

Of decisive importance against a sponge affinity of receptaculites are the differences in the mode of growth between receptaculites and sponges as well as the absence of any incurrent and outcurrent canals in the merom skeleton which would support water transport.

The deficiency of an analysis of receptaculite geometry and its relationship to receptaculite growth, seems to have obscured the essential differences between the mode of growth of receptaculites and that of sponges. Sponge spicules may be arranged geometrically and may also show a regular variation in size (see Foster, 1973) but these are certainly not produced by polar growth, let alone in a receptaculite manner (insertion of meroms in the interstices between previous ones and intercalation of new merom parastichies because of the limited size of meroms). In fact, the similarities between the arrangement of meroms and the arrangement of spicules are the same as those between meroms and the zooecia of bryozoans. Bryozoan colonies show a geometrical arrangement of zooecia similar or even identical to that of meroms but the former were produced by peripheral growth, which could not have been more different.

No ostia nor any incurrent or outcurrent canals which would make up a sponge-like water transporting system are present in the merom wall and consequently receptaculites could not have fed in a sponge-like way. Although *Hexabactron borenorense* as well as *Calathium egerodae* show intermeromal pores, these cannot be interpreted as having been part of a water transporting system (Campbell et al., 1974), the more because most receptaculite species do have a closed outer wall and often also a closed inner wall. In case of an apex-down life position of receptaculites, the apical aperture, which in the sponge hypothesis is interpreted as an osculum, would also have been oriented downward, thus making a sponge-like way of feeding very unlikely.

Receptaculites and sponges differ in the morphology, build-up, and calcification of their skeletal elements but especially in their mode of growth and feeding. From the evidence provided it is concluded that previous assignments of receptaculites to the Porifera cannot be maintained.

Receptaculites as plants

Rietschel (1969, 1977) concluded that the essential features of the mode of growth of receptaculites are more typical of plants than of animals. His arguments include that:

A) The meroms of a single specimen are of the same shape but vary in size and proportion with regard to their position to the growing pole.

B) Meroms had the ability to grow individually accompanied by increasing calcification.

C) The receptaculite organism controlled merom calcification which only took place in the cell wall.

D) New meroms were added to the merom skeleton by polar growth of the receptaculite.

E) Receptaculites never reached a fixed number of meroms and thus were able to grow unlimited.

F) Growth of mature receptaculites decelerated but reinforcement of growth was possible.

The first four features are intrinsically the same as those which in this paper are considered to characterize receptaculite growth. Therefore Rietschel's argumentation is here accepted and consequently receptaculites are regarded as a group of plants thus belonging to the Thallophyta.

When receptaculites are regarded as plants, the position of an assimilating tissue provides a general problem. Rietschel (1969) assumed an intrameromal tissue capable of assimilation to be present in the meroms near the apex, which in his view was the uppermost pole. In the apex-down orientation an assimilating tissue must have been present in the nucleal part of the receptaculite body. Campbell et al. (1974) inferred that from the nucleal part of *Hexabactron borenorense* assimilation hairs may have projected through the pores between the caps. This possibility, however, implies the existence of soft tissue on the outside of the merom wall. As has been demonstrated above (p. 30), this cannot have been the case in the majority of receptaculites. Any other interpretation would necessitate assimilation through a calcified wall which, indeed, is not an uncommon practice. If the assimilating tissue would be situated inside the meroms, it would be present in the arms, as Rietschel (1969) stated. Nevertheless, several receptaculite species show meroms in which the cap is attached to the arms by means of a 'connecting neck' (see Foster, 1973), and thus the arms would be too far from the outer surface to enable assimilation through the calcified walls of the cap and the arms. In this interpretation it might well be supposed that an assimilating tissue could have been present inside the caps of these receptaculites, obviously the best position for such a tissue since it was only covered by the thin outer plate of the cap through which it was also protected. Anyway, in receptaculites with imbricated caps, this seems to be the most likely place for an assimilating tissue. However, some receptaculites show meroms of which the entrance to the axial canal in the foot has become closed by increasing calcification, especially at the nucleal part of the body; only there an assimilating tissue could have been present in an apex-down orientation. Nevertheless, its presence is postulated in imbricated caps as well as in caps attached to the arms by a 'connecting neck', although it also may have been present inside the merom arms. The interpretation of Campbell et al. (1974), though very attractive when considering the function of intermeromal pores in *Hexabactron borenorense,* cannot apply to the majority of receptaculites.

A problem related to the position of assimilating tissue, is the calcification of meroms. Because calcification in plants is mainly, but not totally, due to assimilating phenomena, the site at which assimilation would have to take place in the apex-down orientation seems to be rather illogical. Calcification decelerated as soon as the apical meroms reached the maximum specimen diameter, and only from there upward to the nucleus assimilation could have taken place. Therefore soft tissue at the apical part of the receptaculite body, required for the generation, individual growth and calcification of meroms, could not have had an assimilational function. In this view the apex-up orientation of Rauff (1892a) and Rietschel (1969) is far more likely to be expected with regard to assimilation and calcification. However, the apex-down orientation as advocated by Campbell et al. (1974) and Nitecki (1971, 1972), which has been discussed on p. 27, seems to be rather incontestable.

Systematic position within the Thallophyta

The present author agrees with Rietschel (1969, 1977), Campbell et al. (1974), Gould & Katz (1975), Nitecki & de Lapparent (1976), and Fisher & Nitecki (1978) contra Kesling & Graham (1962), Nitecki (1967-1976), and Byrnes (1968) that receptaculites cannot be assigned to the order Dasycladales. Although the Recent genera *Neomeris* Solms-Laubach and *Bornetella* Solms-Laubach, but especially fossil cyclocrinitids, show striking similarities to receptaculites, basic differences in morphology and growth persist:

The skeletal elements of dasyclads, the laterals, are morphologically similar to the meroms of receptaculites. The lateral heads, which only consist of a cup-shaped cap-like structure, are united into an outer cortex and thus assume a hexagonal shape, which provides a major difference when compared with the essentially rhomboidal caps. Another important difference is the lack of any arm-like structures on the lateral heads. Heavy calcification of the edges of the lower part of the lateral head may produce structures resembling merom arms, but these always follow the symmetry of the lateral head and hence are never perpendicular to each other. Consequently no axial canals are present nor do they show the characteristic interlocking of merom arms.

Dasyclad laterals are calcified by uncontrolled deposition of carbonate in an extracellular mucus, and thus fuse together when lying against each other i.e. in the outer cortex.

The growing pole of dasyclad algae is situated at the top of the thallus, opposite an attachment structure at the base consisting of an extension of the central stem (the central cavity in receptaculites). Receptaculites probably had their growing pole at the base of the body, the very same pole where an attachment structure, similar to that of dasyclads, might have been located. In case of a nucleus-down orientation, an attachment structure consisting of rhizoids as an extension of the central cavity could not have been present.

Dasyclads are unicellular algae. As Campbell et al. (1974) already concluded, in view of their size receptaculites must have been multicellular organisms.

Receptaculites oweni, the largest receptaculite known, reached a diameter of at least 30 cm, the volume of the central cavity being about 1000 cm^3. Especially in physiological respect, it is difficult to imagine even a multinucleate unicellular organism to be of that size.

Calcification in dasyclad algae may be due to passive deposition of carbonate caused by assimilational phenomena. Since Recent dasyclads include calcareous as well as non-calcareous forms, a supporting function as a main cause of calcification can be excluded. This also provides evidence against an assignment of receptaculites to the order Dasycladales, since meroms were obviously supporting structures.

The evidence provided favours a plant nature of receptaculites, although the apex-down orientation provides serious difficulties. Substantial differences in morphology and organisation do not permit an assignment of receptaculites to the order Dasycladales. Several receptaculite characteristics, such as the mode of merom growth and calcification as well as a supporting function of meroms, are unknown in the division Chlorophyta. Only because the order Dasycladales includes calcareous forms similar to receptaculites, the latter are assigned to the division Chlorophyta as a separate order, Receptaculitales, as proposed by Rietschel (1969). Future study, however, may prove that receptaculites should be attributed to an even higher new taxon within the Thallophyta (see Note).

DEFINITION AND RELATIONSHIPS OF RECEPTACULITES

The present study on the palaeobiology of receptaculites involves only those receptaculites with the following properties:

1) The receptaculite thallus is built up of calcareous meroms distributed around a central cavity according to a geometrical arrangement consisting of orthostichies (meridians and latitudes) and parastichies (dextral and sinistral whorls). On the thallus two morphologically distinct poles can be recognised, the closed vegetative pole, called the nucleus, and the growing pole, which may show a central aperture, called the apex.

2) The merom consists of a head, a column and a foot; the head comprises a terminal cap and four perpendicular arms: two latitudinal, one nuclead and one apicad arm. The merom is composed of an outer enveloping layer and an axial canal with or without an intermediate layer.

3) Meroms interlock in a complex way by means of caps, arms, columns, and feet, functioning as a supporting skeleton. Caps form an outer wall by lying against each other, by fusion, or by imbrication. The nuclead arms are situated below the layer formed by the caps, whereas the latitudinal arms lie side by side below the layer of nuclead arms but on top of the layer of apicad arms.

4) Meroms were calcified by deposition of carbonate in the cell wall or inside the cell itself, a process controlled by the receptaculite alga. Merom calcification is variable and genetically controlled non-calcification of meromal parts may occur.

5) The receptaculite thallus increased in size by polar growth according to which new meroms were added to the merom skeleton. By inserting new meroms in the interstices between previous ones their geometrical arrangement arose. Because merom size was limited, new merom parastichies were intercalated at the apex and integrated in the surrounding pattern of older ones. At the nucleus the num-

ber of meroms was limited, increasing towards the apex by intercalation of new merom parastichies.

6) The size and the shape of meroms vary with regard to their position to the apex. At the apex meroms are smallest, increasing in size towards the maximum specimen diameter, where they reach their maximum and final size. From the maximum specimen diameter onwards, the meroms decrease in size until the nucleus is reached.

This conception of the order Receptaculitales does not allow the inclusion of cyclocrinitids or other dasyclad algae such as *Anomaloides* Ulrich (Nitecki, 1972). For the same reasons also a close relationship between receptaculites and the Early Cambrian radiocyathids, as has been assumed by Nitecki & Debrenne (1979), cannot be supported. In the first place radiocyathids do not seem to have had a polar mode of growth: the skeletal elements are arranged in a random manner and not according to any pattern, nor do the size and proportion of these vary with their position to the poles. In the second place, the morphology of the skeletal elements differs substantially from that of meroms: Nitecki & Debrenne (1979) compare the 'nesasters' with the distal offshoots of caps of *Receptaculites oweni* (which are considered to be additional arms), but no other structures comparable to the merom head (the plate-like outer part and the arms) are present. Even if the nesasters are interpretated as 'merom' arms, their variable number and the absence of interlocking of these structures set them apart from any known receptaculite meroms. Also their morphogenesis seems to have been different according to the description of nesasters given by Nitecki & Debrenne (1979). Consequently, it seems that the resemblance between receptaculites and radiocyathids is only superficial and does not imply a close relationship between these groups.

Definition and classification of *Tetragonis sulcata* d'Eichwald, 1860

Tetragonis sulcata d'Eichwald, 1860 is characterized by: 1) imbricated rhomboidal sheet-like caps of which the nuclead part is absent; 2) well defined nuclead arms underlying the neighbouring caps and absence of apicad arms; 3) presence of an outer wall formed by the imbricated caps and absence of an inner wall; 4) arrangement of meroms according to the *Tetragonis* type; 5) bilateral symmetry in the arrangement of merom arms; 6) intercalation of new merom parastichies according to the SM 3/1 type.

From this definition it can be concluded that the genus *Tetragonis,* as far as the species *sulcata* is concerned, cannot be identical with the genus *Ischadites* Murchison, 1839 (as redefined by Nitecki, 1969), as proposed by Hinde (1884), Rauff (1892a), Laubenfels (1895), and Byrnes (1968). According to the description of *T. murchisoni* d'Eichwald, 1842, which is the type of the genus *Tetragonis,* there are substantial specific differences between *T. sulcata* and *T. murchisoni* (see also d'Eichwald, 1860; Rauff, 1892a). Therefore it may be necessary to define a new genus based on *T. sulcata.* Since no study on the morphology and organisation of *T. murchisoni* is available, no new genus will be established here.

From Nitecki's (1970) redescription of *Lepidolites dickhauti* Ulrich, 1879, it may be concluded that it is closely related to *T. sulcata.* The shape and the size of the thallus as well as the dimension of the central cavity are identical. Also the morphology of the merom is similar to that of *T. sulcata;* a merom head consisting of a sheet-like cap ('lateral head') and four arms ('stellate structure') is present as well as a column. Feet ('calcification of the main axis') are absent and they are poorly developed in *T. sulcata.* According to Nitecki's figures (for the measurements do not correspond with these) the size of the meroms (cap and columns) is but slightly larger. *Lepidolites dickhauti* exhibits imbricated caps which are arranged in a receptaculite manner, though it could not be determined whether a *Receptaculites* or a *Tetragonis* type of merom arrangement is present. Rietschel's (1969) classification is therefore supported in placing *Tetragonis* together with *Lepidolites* in the family Tetragonacea Rietschel, 1969 (nomen correctum). Dependent upon further studies on the morphology, organisation and relationships of *Lepidolites dickhauti,* the *Tetragonis* species *T. murchisoni* and *T. parvipora,* as well as the genera *Palaeospongia* d'Orbigny, 1849 and *Selenoides* Owen, 1852, which Rietschel (1969) also included in the family Tetragonaceae, the classification proposed by Rietschel will be adopted.

ALGAL INTERPRETATION OF RECEPTACULITES

According to the conclusions drawn in preceding chapters, the algal nature of receptaculites can be interpreted as follows:

The order Receptaculitales comprises multicellular marine calcareous algae of which the thallus is composed of meroms regularly distributed around the central cavity. Two distinct and morphological different poles are to be recognised: the closed vegetative pole (the nucleus) and the growing pole (the apex) which may show a central aperture of variable definition. Meroms were generated at the apex, whereafter they were forced to change their position towards the maximum specimen diameter by new merom generations which were constantly inserted. During their displacement, meroms increased in size until the maximum specimen diameter was reached whereupon merom growth ceased. Merom calcification, which took place in the cell wall or within the cell, was controlled by the receptaculite organism and apparently accompanied merom growth. Merom caps increased in size by marginal growth of the outer plate, preceded by growth of the inner part which was initiated by the distal offshoots. Probably the feet grew in the same way. The other meromal parts grew by expansion of the enveloping layer and calcified by deposition of carbonate on the outer surface of the enveloping layer whereas carbonate resorption took place from the inner surface.

The receptaculite thallus grew by adding meroms to the merom skeleton, by merom growth and by intercalation of new merom parastichies at the apex, which were integrated in the pattern of older ones. The geometrical arrangement of meroms is produced by their alternating position on the latitudes caused by inserting new meroms in the interstices between previous ones. Merom growth was required to keep up with the increasing intermeromal space during their displacement from apex to maximum specimen diameter. For the same reason and because the size of meroms was limited, new merom parastichies had to be intercalated. From the nucleus, at which the number of meroms is limited, the rate of intercalation of parastichies decreases towards the apex, where numerous meroms are present.

In growth position, the apex probably was the lower pole, attached to the substrate by rhizoids projecting from the apical aperture as an extension of the soft tissue originally present in the central cavity. The meroms, together forming the supporting skeleton of the thallus, were also filled with soft tissue, which at the nucleal part of the thallus was capable of assimilation in the caps and/or arms.

In case of a nucleus-down life position, which with respect to assimilation and calcification would be more likely, intrameromal tissue would have assimilated near the apex accompanied by merom growth and calcification. However, it is unknown how the receptaculite thallus would have retained its upright position during life in this orientation.

Notes

After this study had been completed, a specimen of *T. sulcata* was recognised from Upper Ordovician (Caradocian) limestone of Balclatchie, Ayrshire, Scotland. It is stored in the British Museum (Natural History), Mrs Robert Gray collection, reg. no. V. 15445a, and was described and figured by Elliott (1972) as *Ischadites* sp. I gratefully acknowledge Dr G. F. Elliott for kindly providing the fossil for study.

Apart from a bilateral symmetry in the arrangement of meroms and the mode of intercalation of new merom parastichies, both of which could not be determined due to the preservational condition of the fossil, the receptaculites answers to the definition of the species given in the present paper. Ecology as well as stratigraphical position are similar to that of *T. sulcata* from the Baltic region. The known geographical distribution of the species is now extended to the Caradocian of Scotland.

A recent paper by Nitecki & Toomey could not be included in the present study. I am indebted to Dr M. H. Nitecki for providing a copy of this yet unpublished paper.

In the first part of the study it is concluded that receptaculites are algae, based mainly on the same evidence provided in the present paper. In the second part, an alternative classification is proposed by erecting the new class Receptaculitaphyceae within the division Chlorophyta, including the orders Receptaculitales James, 1885, Radiocyatales Debrenne, Termier & Termier and the new order Cyclocrinales. The order Receptaculitales comprises, among others, the family Tetragonaceae. Nitecki's previously proposed classification therefore seems to have been abandoned. Nitecki & Toomey retain the assignment of cyclocrinitids to receptaculites (s.l.), but remove both from the order Dasycladales. According to the present author's view (p. 34) a detailed comparison between receptaculites (s.s.) and dasyclads produces essential differences in organisation, which therefore do not allow such an assignment. The relationships between receptaculites (s.s.) and radiocyathids, as inferred by Nitecki & Debrenne (1979) and Nitecki & Toomey, are also questioned in the present paper. Furthermore, Nitecki & Toomey suggest a relationship between receptaculites and archaeocyathids, though no eleborate argumentation has yet been presented.

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