

Morphology and merom gradients in the Ordovician receptaculitid *Fisherites reticulatus*

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The Middle to Late Ordovician receptaculitid *Fisherites reticulatus* (Owen 1844) is the most abundant and widespread receptaculitid known, and yet existing descriptions of its morphology do not reach the level of detail achieved in recent studies of other receptaculitid taxa. We present a redescription of the morphology of individual meroms and of the entire thallus, focusing on gradients in merom number and shape. We document positional information not with distance or angular measurements, but in terms of units of organization of the thallus itself, the number of merom sites from a reference pole. Although more labor intensive, this more accurately portrays thallus symmetry and yields a characterization of form that more directly reflects the developmental program of the organism.

Key words: receptaculitid, morphology, merom, Ordovician.

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Introduction

Toni Hoffman's research in paleontology spanned an unusually broad range of topics, one of which involved the philosophical and methodological issues raised by 'problematic fossil taxa' (Hoffman & Nitecki 1986). Cases in which phylogenetic affinities are obscure highlight the extent to which our understanding of life's history ultimately depends on evaluation of fossil data, with only the most cautious reliance on analogies with living organisms. We intend this contribution to follow in the spirit of his work.

Fisherites reticulatus, previously known as *Receptaculites oweni* Hall (Finney & Nitecki 1979b), is an abundant receptaculitid, best known from the Middle to early Late Ordovician (Mohawkian – lower Cincinnati) Galena Group of the Upper Mississippi Valley region. It is the first receptaculitid formally described and figured from North America (Owen 1844) and the largest receptaculitid known. Given its distinctive form (Fig. 1), its original illustration was adequate for identification; indeed, in terms of recognizability in the field, it is the best-known representative of this group of organisms. Nevertheless, redescription is necessary because neither Owen's (1844) treatment, nor Hall's (1861), nor subsequent references (listed in Nitecki *et al.* 1987), offer the level of detail that has been presented for other taxa in more recent work (e.g., Fisher & Nitecki 1982; Nitecki & Rietschel 1985) and that is required for meaningful comparisons on either an intraspecific or an interspecific level. The abundance of *F. reticulatus* makes it a natural subject for studies of development, paleoecology, and taphonomy that are critical to resolving long-standing controversies over the orientation and mode of growth of receptaculitids (Fisher & Nitecki 1977). However, such studies require a firm foundation in descriptive morphology. In particular, it is essential to describe form in a way that relates to the uncertainties about mode of growth that have helped to make receptaculitids one of the archetypal 'problematic fossil taxa' (Hoffman & Nitecki 1986).

Stratigraphy

The Galena Group is exposed over a large area of northern Illinois, southern Wisconsin, northeastern Iowa, and southeastern Minnesota (Fig. 2; Finney & Nitecki 1979a). Southward of this it dips into the Illinois Basin and then is exposed again in southwestern Illinois and adjacent areas of eastern Missouri. The Galena Group (Templeton & Willman 1963; Willman & Kolata 1978; Ross *et al.* 1982) consists of strata from the base of the Spechts Ferry Formation to the top of the Dubuque Formation (Fig. 3). It overlies the Platteville Group, assigned to the Mohawkian Series, and is overlain by the Maquoketa Group of the Cincinnati Series. In northern Illinois, the rocks of the Galena Group are predominately dolomite, but northward from this, the Galena changes progressively, from the base upward, to a fine-grained limestone. In the opposite direction, the top of the Galena grades into a fine-grained limestone like that to the north, and the lower portion changes to calcarenite.

The maximum thickness of the Galena Group occurs in the vicinity of the type section, near Galena, Illinois. Here its thickest subdivision is the Kimmswick Subgroup, consisting of the Dunleith and Wise Lake Formations (Fig. 3). Of the Galena Group subdivisions, only rather limited parts of the Kimmswick Limestone and the Decorah Formation are present in southern Illinois and adjacent areas of Missouri. The name 'Kimmswick'

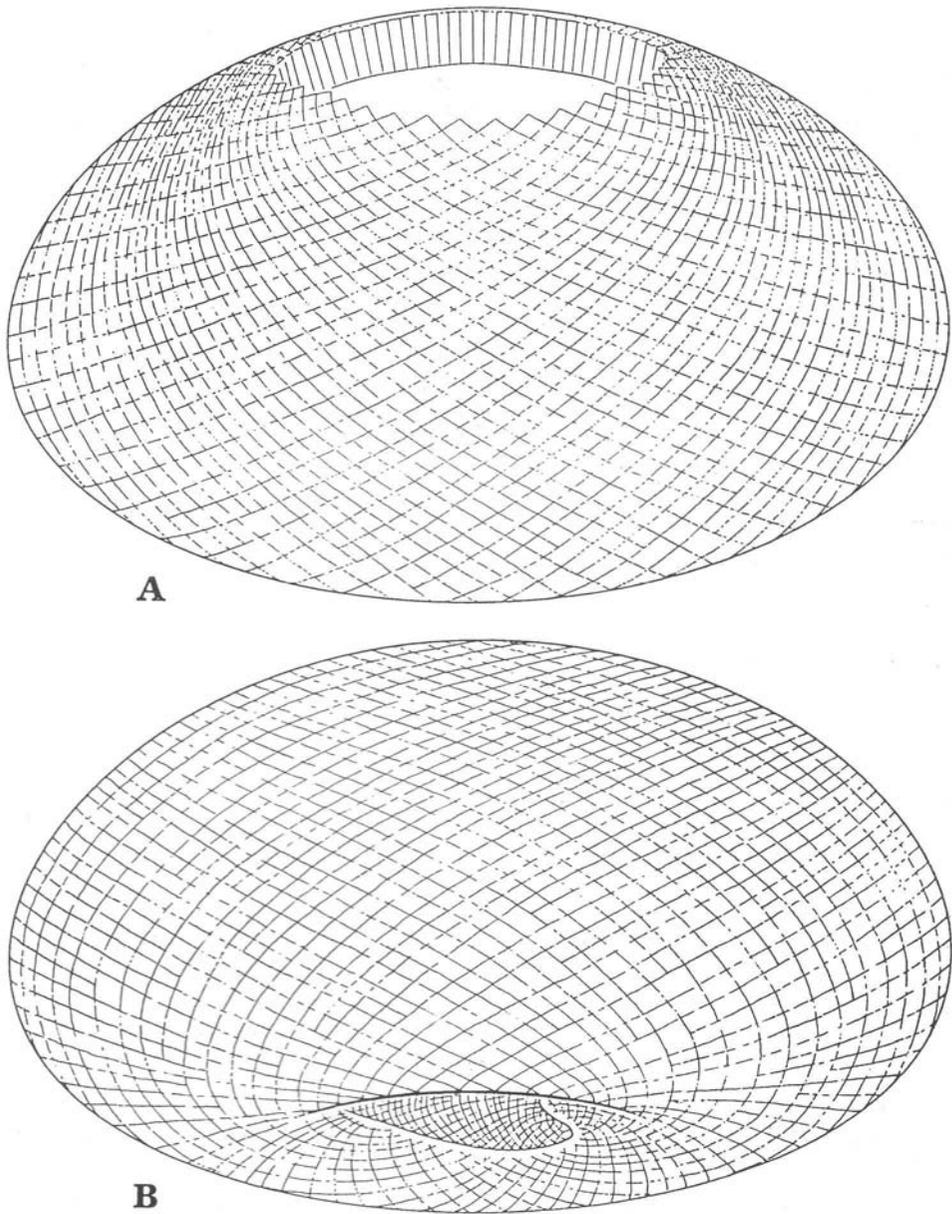


Fig. 1. Diagrammatic reconstruction of the skeletonized portion of the thallus of *Fisherites reticulatus* (Owen 1844) (about two thirds natural size). A. Oblique view from above. B. Oblique view from below.

is used here only with reference to these outcrops in southern Illinois and adjacent Missouri. The terms 'dolomite facies' and 'limestone facies' will be used to refer to outcrops of the Galena Group in northern Illinois, Iowa, Wisconsin, and Minnesota.

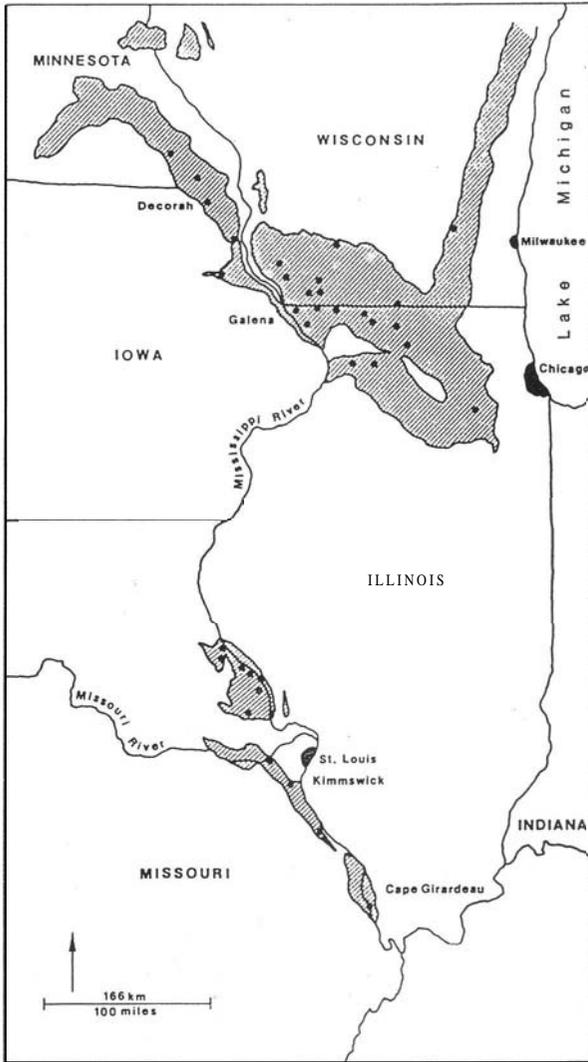


Fig. 2. Map of major outcrop areas of the Galena Group (diagonal lines) and localities of specimens discussed here (dots).

A diverse fauna of brachiopods and bryozoans from the Galena Group has been correlated with faunas of the Trenton Group in New York (Willman & Kolata 1978; Templeton & Willman 1963). On the basis of conodont biostratigraphy (Sweet 1984; Ross *et al.* 1982), the Galena Group ranges upward from the *Phragmodus undulatus* Zone to the *Oulodus robustus* Zone and thus correlates with the middle Mohawkian to middle Cincinnati Series.

Receptaculitids are common throughout the Dunleith and Wise Lake Formations, and throughout the Kimmswick Limestone. Specimens of *F. reticulatus* are especially abundant in three restricted stratigraphic intervals that were previously referred to as the Lower, Middle, and Upper *Receptaculites* zones. The names of these zones are based on the occurrence of '*Receptaculites oweni*', and not on any other receptaculitid found

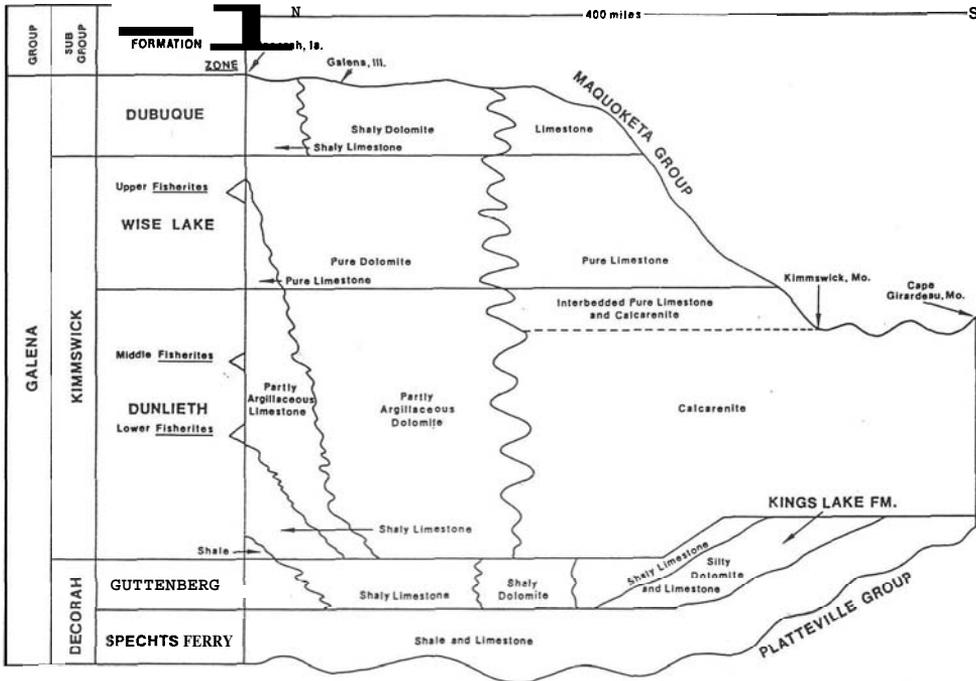


Fig. 3. Stratigraphic chart of the Galena Group showing relationships of the principal rock units discussed in text.

in the Galena Group. Since *Receptaculites oweni* should now be referred to as *Fisherites reticulatus*, the appropriate names would be: Lower, Middle, and Upper *Fisherites* zones (Fig. 3). As restricted by Finney & Nitecki (1979b), *Receptaculites* is a Devonian genus not present in the Ordovician of the Upper Mississippi Valley.

Fisherites is also common in the Bighorn Dolomite of north-central Wyoming, the Fremont Formation of central Colorado, the Upham Formation of the El Paso area, Texas, and the Red River Formation of Manitoba. These formations have been correlated by Sweet & Bergstrom (1976) and Ross *et al.* (1982) with the Edenian and Maysvillian Stages of the Cincinnati Series. Still other occurrences are in Baffin Land (Roy 1941), Greenland (Troedsson 1926), South America (Nitecki & Forney 1978), and Asia (Rietschel & Nitecki 1984; Niko & Ikebe 1988).

The following description is based on examination of over 500 specimens of *F. reticulatus*. About eighty percent of these are from the Kimmiswick Limestone and other units of the Galena Group of the Upper Mississippi Valley region. The remaining specimens are from the Fremont Formation, the Bighorn Dolomite, and the Upham Formation. Collection localities in the Galena Group are shown in Fig. 2. Specimens are deposited in collections of the Field Museum of Natural History (FMNH), the Illinois Geological Survey (IGS), and the American Museum of Natural History (AMNH).

Terminology and orientation

Current anatomical terminology for receptaculitids derives largely from the work of Rauff (1892), Nitecki (1969), and Rietschel (1969), with some additions by Fisher & Nitecki (1978, 1982). We refer to the receptaculitid body as the 'thallus', which was composed of a generally unbranched 'central axis', the surrounding skeletal structures, and associated soft tissues. The skeleton consisted of a large number of calcified elements, 'meroms', that initially interlocked with neighboring elements and often later became fused. In 'double-walled' receptaculitids, such as *F. reticulatus*, each merom was composed of a 'shaft', which expanded proximally to form the 'foot' and distally to form the 'head', made up in turn of the 'plate' and 'stellate structure'. The resulting skeleton resembles the double-walled form of many regular archaeocyathids and radiocyathids, and without necessarily implying homology (though see Zhuravleva 1970; Zhuravleva & Miagkova 1972; Nitecki & Debrenne 1979), we refer to the region spanned by shafts as the 'intervallum', and the regions composed of heads and feet as the 'inner wall' and 'outer wall', respectively.

We regard this redescription of *F. reticulatus* in part as a foundation for evaluating evidence for receptaculitid life orientation and mode of growth. We wish to avoid biasing subsequent analysis, but as noted by Fisher & Nitecki (1982) in the same context, descriptions are greatly simplified by adopting, if only provisionally, *some* orientation and growth scenario. Without claiming to defend our choice in detail at this time, we shall orient receptaculitids following Nitecki (1969, in part), Rietschel (1969), Foster (1973), Gould & Katz (1975, main text), and Fisher & Nitecki (1977, 1978, 1982). This contrasts with the orientation suggested by Byrnes (1968), Nitecki (1969 in part, 1971, 1972), Campbell *et al.* (1974), the 'note added in proof' of Gould & Katz (1975), and Brummer (1979). Our treatment of the order of formation of meroms agrees with Rietschel (1969), Foster (1973), Campbell *et al.* (1974), Gould & Katz (1975), Fisher & Nitecki (1978), and Brummer (1979), but disagrees with Byrnes (1968) and Nitecki (1969, 1971, 1972).

The approximate rotational symmetry of receptaculitids makes it convenient to use geographical terms (e.g., poles, latitude, cardinal directions) to discuss spatial relationships on the thallus. Because of variations in thallus form and degree of recumbency, the exact relation between anatomical polarity and the up-down axis is not fixed, but close association of one pole, the 'nuclear' pole, with the substrate appears to characterize the entire group. Features oriented toward this pole are said to be directed toward the south. East and west have the typical map relation to north and south when the exterior aspect of the thallus is illustrated. On receptaculitids such as *F. reticulatus*, 'hemispheres' are separated by an 'equator' that we define as the locus of points along which a plane tangent to the outer wall would be vertical (or alternatively, parallel to the whole-thallus symmetry axis). Similarly, we define the thallus bottom, sides, and

top as arbitrarily bounded by loci along which tangent planes are oriented at 45° to the horizontal (or to the thallus symmetry axis).

The nuclear pole is closely encircled by meroms and is in some receptaculitids associated with a curved and/or twisted protuberance known as the 'corniculum'. An 'areolar concavity' often surrounds the corniculum, where it merges with the rest of the thallus bottom, or the nuclear pole itself, if no corniculum is developed. Over the opposite pole is a gap in the distribution of skeletal structures, the 'apical lacuna'. Within the highly ordered patterns of merom arrangement typical of receptaculitids, meridional (north-south, hereafter N-S) alignments are referred to as 'orthostichies', southwest-northeast (SW-NE) alignments are 'dextral parastichies', and southeast-northwest (SE-NW) alignments are 'sinistral parastichies'. East-west (E-W) alignments that persist around the thallus and whose members are all located the same distance, measured in number of meroms, from the nuclear pole, are called 'whorls', and all other E-W alignments are 'circlets' (Fisher & Nitecki 1982). New alignments of meroms originate at 'intercalary meroms'.

Preservation

Most specimens of *F. reticulatus* from the dolomite facies of the Galena Group, and a few of the specimens from Wyoming, Colorado, and Texas, are preserved as molds. The original calcified skeleton has been dissolved and is now represented mainly by open pore space. These specimens consist typically of: (1) a mold of the abaxial surface of the outer wall (Fig. 4B); (2) a mold of the adaxial surface of the outer wall, the exterior surfaces of merom shafts, and the abaxial surface of the inner wall, formed by sediment occupying the intervallum (Fig. 4B-E); and (3) a mold of the adaxial surface of the inner wall (Fig. 4D-F). For simplicity, we refer to these three portions of specimens as the outer wall mold, the intervallum cast, and the inner wall mold (equivalent to a cast of the central axis). These three sections often break apart readily, because the outer and inner walls originally separated sediment in each region, leaving a continuous parting after their dissolution. Intervallum casts usually preserve the clearest record of merom morphology and arrangement. Even when other details are obscure, merom positions are represented on intervallum casts by the molds of the merom shafts (Fig. 4C).

Specimens of *F. reticulatus* in limestone (i.e., those from the Kirmmswick Limestone, from the limestone facies of the northern exposures of the Galena Group, and many of the specimens from Wyoming, Colorado, and Texas) typically are preserved as calcite. In some cases, this may represent neomorphic alteration of original skeletal material (Van Iten & Fisher 1983), but in most it is probably diagenetic cement filling spaces left by dissolution of original skeletal material. Such specimens usually cannot be broken from surrounding sediment easily, and finer scale preparation

is only occasionally practical. Rarely, surfaces of considerable extent are exposed by weathering (Fig. 4A), but these surfaces frequently cut across original structure (Fig. 5A–B).

An unusual specimen from the Kimmswick Limestone is silicified and partly exposed by weathering. Only a portion of the corniculum has weathered out fully, but it offers our most complete information on this rarely exposed part of the thallus (Fig. 5A).

Morphology

Thallus shape. — The thallus of *F. reticulatus* is usually a somewhat asymmetrical oblate spheroid. Its axis of approximate rotational symmetry is generally but not always vertical, with a well developed corniculum protruding at the lowermost pole. We have no specimens that preserve all portions of the thallus, from one pole to the other, but there are many that preserve as much as a third or half, and a few, particularly from the dolomitic facies, that are more complete. Preservation seems to be biased against the uppermost portions of the thallus. In *F. reticulatus*, as observed by Rietschel (1969: p. 478) for other receptaculitids, postmortem disarticulation and breakage apparently proceeded from the top downwards, usually leaving only the bottom of the thallus and portions of the sides intact.

Information on thallus shape can be gleaned from almost any specimen, but the type of information varies according to manner of preservation. As noted above, specimens preserved as calcite tend to present cross-sectional views of the thallus, while molds usually offer the most extensive exposure of surfaces. We suspect postmortem deformation has not greatly affected these specimens, but it will be easiest to address this point after discussion of merom morphology and arrangement.

The shape and orientation of the corniculum is variable. It generally resembles a small cone with an apical angle of 30–60°. In a few specimens, it is erect, with an axis of symmetry coincident with that of the thallus as a whole, but more commonly it is recumbent, with a laterally deflected nuclear pole. In these instances, the axis of the corniculum is bent within a more or less vertical plane (i.e., the corniculum is bisected by a plane of mirror symmetry rather than having an axis of rotational symmetry), or twisted in a three-dimensional, helicospiral curve. The sense of this spiral is not constant, for we have observed both dextral and sinistral forms.

The tip of the corniculum is best exposed on the silicified specimen mentioned above (FMNH UC 51619; Fig. 5A) and discussed by Fisher & Nitecki (1982). The heads of the meroms of the nuclear whorl crowd closely around the nuclear pole, leaving only a small gap, about 0.8 mm in diameter, between adjoining corners, directly on the site of the nuclear pole. This gap does not completely perforate the outer wall, but Fisher & Nitecki (1982) suggested that it may represent an occluded nuclear for-

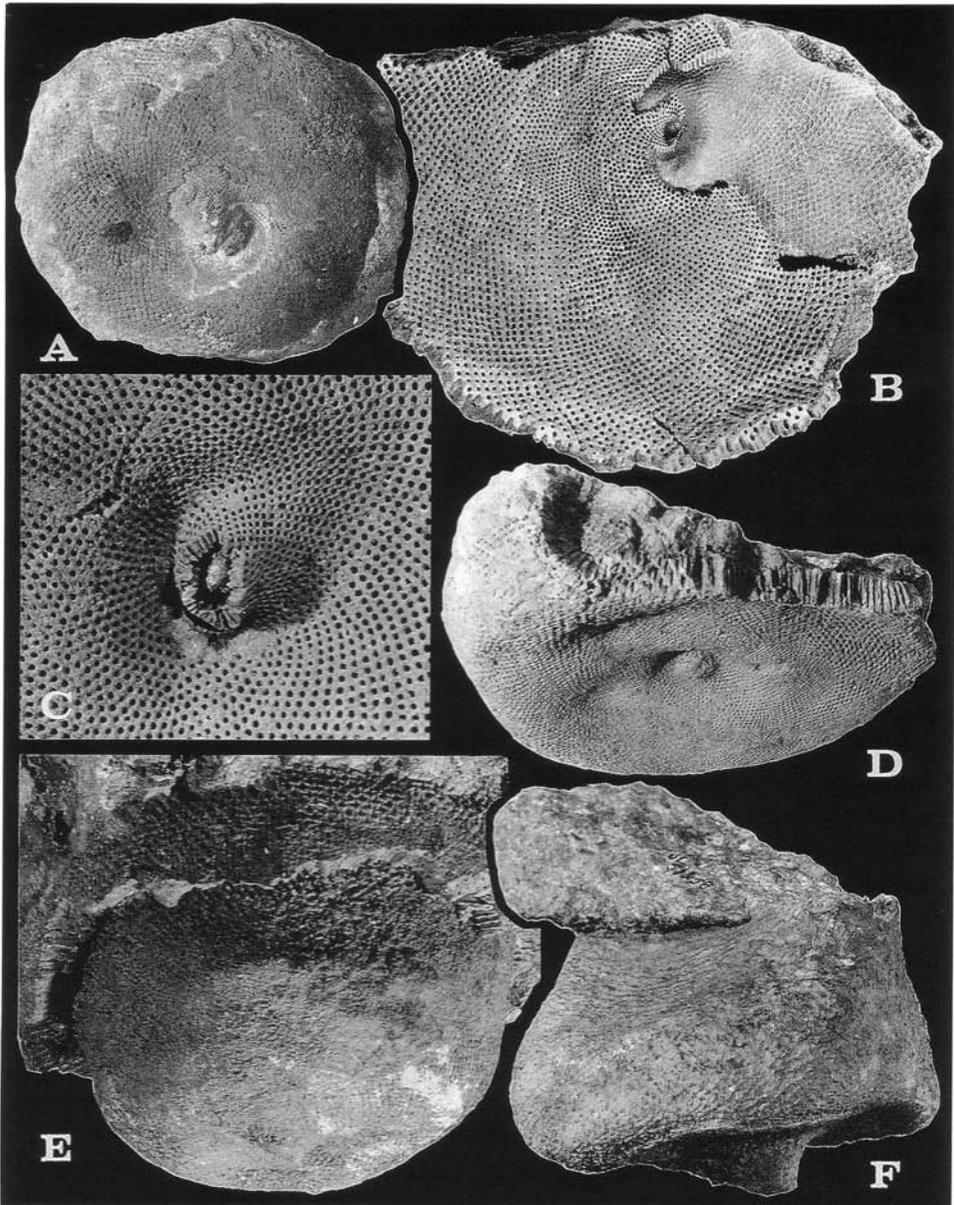


Fig. 4. *Fisherites reticulatus* from the Galena Group, Upper Mississippi Valley region, USA. □A. Neotype specimen (FMNH UC 55024), preserved in limestone, with abaxial surface of outer wall exposed by weathering, $\times 0.3$. OB. Outer wall mold exposed near corniculum and toward upper right; remaining portion of specimen preserved as an intervallum cast (IGS-2), $\times 0.35$. □C. Central region of the thallus bottom (corniculum broken), preserved as an intervallum cast (IGS 100-P9), $\times 0.75$. OD. Most of thallus bottom and sides preserved as an intervallum cast: small region of inner wall mold exposed where the intervallum cast is broken away (FMNH PE 11006), $\times 0.3$. □E. Specimen preserved mostly as an inner wall mold (or central axis cast), with fragmentary intervallum cast (FMNH UC 51628), $\times 0.35$. OF. Inner wall mold (or central axis cast) showing form of a small thallus, bounded above by a circlet of meroms that may represent the margin of an apical lacuna (FMNH UC 51638), $\times 0.95$.

amen. At some earlier developmental stage, this foramen could have been patent, allowing for emergence of a pedicle-like extension of the central axis, as suggested for *Ischadites dixonensis* (Fisher & Nitecki 1978). However, at the stage of development represented by most specimens, the nuclear pole of *F. reticulatus* was almost, if not entirely, 'enclosed'. It is, in this respect, similar to the condition presented by *Receptaculites neptuni* (Rauff 1892), *I. barrandei* (Gould & Katz 1975), *Hexabactron borenorense* (Campbell *et al.* 1974), and many other receptaculitids.

The plates of the nuclear whorl of meroms are unusual in appearing 'folded' along an E-W axis. The southern portions of these plates form a flat surface normal to the nuclear pole. Their northern halves then begin the conical portion of the cornicular surface. With increasing latitude (or distance from the nuclear pole) the apical angle of a tangent cone (i.e., an imaginary cone whose surface would be tangent to the surface of the corniculum at that latitude) may initially increase, but then decreases or remains about constant until near the confluence of the corniculum and the rest of the thallus bottom. Here the apical angle of a tangent cone increases again as the surface of the corniculum flares outward. In general, the corniculum is about 2 cm long and 2 cm in greatest diameter where it joins the rest of the thallus (reference for measurements is given below). However, size and shape of the corniculum are extremely variable (Figs 4, 5A).

The corniculum grades into the rest of the thallus bottom by flaring and then extending outward in all directions. The inner and outer walls show the smallest radius of curvature immediately over the uppermost margin of a recumbent corniculum, where the direction of wall extension swings through about 180° within a narrow latitudinal range. Elsewhere around the corniculum, wall flexure is less pronounced, though it is generally sufficient to produce an areolar concavity completely encircling the corniculum. The topographic effect is as if the rest of the thallus bottom had simply been draped over the recumbent corniculum. However, we have not observed any case where wall flexure brought the surrounding portions of the thallus bottom into contact with the corniculum. For purposes of measurement, the latitude at which the maximum curvature of the outer wall occurs is taken as the boundary between the corniculum and the rest of the thallus.

The shape of the rest of the thallus is illustrated in Figs 4 and 6. Moving outward from the corniculum, the thallus bottom declines to the margin of the areolar concavity, reversing curvature to convex-outward topography. There are occasionally mild undulations in this region, which may reflect either original substrate topography or slight irregularities in growth. This portion of the thallus bottom often approximately coincides in elevation with the lowermost extent of the corniculum. The surface of the thallus then curves upward gently to form the sides and continues around to the top. Only rarely do we have any significant portion of the top of the thallus preserved. One such specimen (FMNH UC 51638; Fig. 4F) is

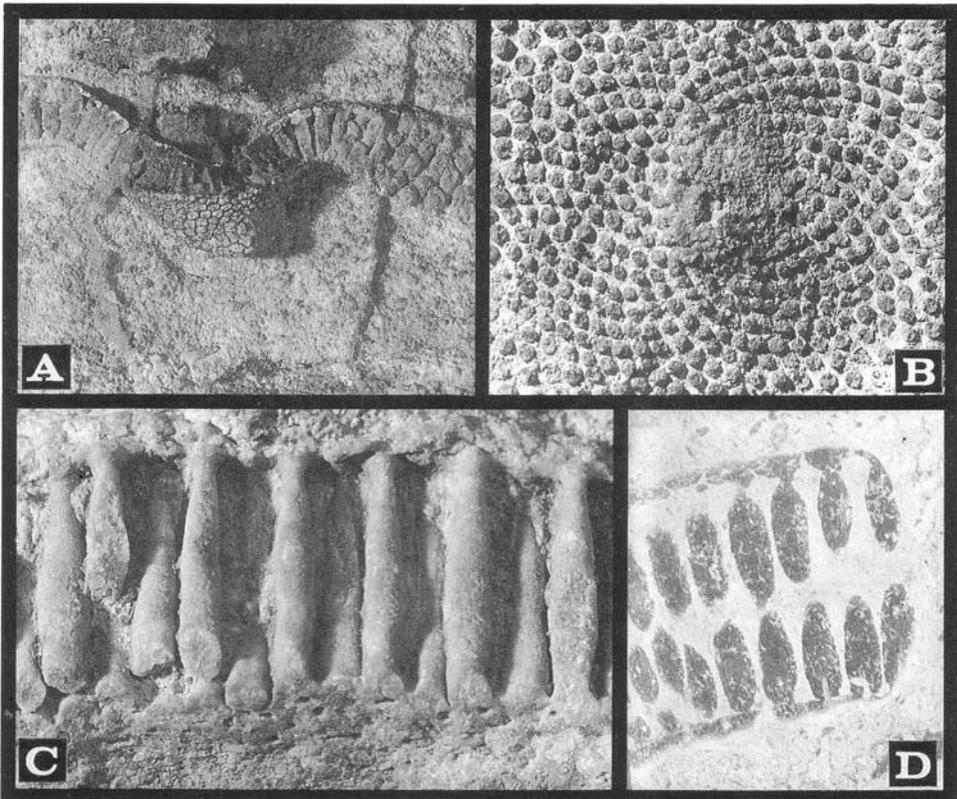


Fig. 5. *Fisherites reticulatus* from the Galena Group, Upper Mississippi Valley region, USA. □A. Silicified specimen from the Kimmswick Limestone (FMNHUC 51619), exposing merom plates in the vicinity of the nuclear pole, x 1.15. □B. Specimen preserved in limestone, with weathered surface cutting obliquely across an array of merom shafts (FMNHPE 14005), x 1.2. OC. Merom heads, shafts, and feet (with pores at vertices) exposed on a specimen in limestone (FMNHUC 26414), x 3. OD. Thin section of a thallus fragment that was broken and abraded prior to burial, strongly suggesting in vivo fusion of meroms (FMNHPE 15250), x 3.

a small thallus showing impressions of meroms extending to within about 2 cm of the lacunar pole. The margin of the preserved array of meroms appears to follow a single circlet for a significant distance around the thallus, but it is not clear whether this represents the edge of an apical lacuna or just strong latitudinal control on disarticulation. No specimen of *F. reticulatus* we have studied preserves a complete, clearly demarcated lacuna such as has been described in *I. koenigi* (Nitecki 1969), *H. bore-norense* (Campbell *et al.* 1974), or *I. dixonensis* (Fisher & Nitecki 1978). Our reconstruction of a smoothly rounded top and an apical lacuna (Fig. 1) on the thallus of *F. reticulatus* is thus based largely on analogy with other well preserved receptaculitids.

The ontogeny of *F. reticulatus* has been reconstructed (Fig. 6) from specimens ranging in thallus size from about 7–34 cm in bottom diameter (BD), assuming these represent stages in a relatively stereotyped onto-

genetic trajectory. Isolated cornicula are extremely rare, but on specimens preserving regions of the thallus bottom peripheral to the corniculum, the size and shape of the corniculum, though variable, show no clear correlation with thallus bottom diameter. This suggests that the corniculum has determinate growth and has already stabilized its size and shape in the smallest of our specimens. A different pattern is shown by the rest of the thallus bottom. Most small thalli (< 20 cm BD) tend to have rounded, bowl-like bottoms, while larger thalli (> 20 cm BD) often have flatter bottoms. This suggests that the topography of the bottom may change, presumably by changes in the latitudinal distribution of rates of marginal plate (and foot) accretion. This trend invites the generalization that smaller thalli are more ovoidal, or globular, and larger thalli, more discoidal (Reitschel 1969: p. 469, makes a similar statement in an interspecific context), but in *F. reticulatus*, this description is only warranted for the bottoms of thalli. We have little direct evidence for the extent of most thalli above the substrate and thus for their overall shape. The preserved height of thallus sides is extremely variable but shows no clear relation to bottom diameter. The growth scenario illustrated in Fig. 6 (and proposed for other receptaculitids by earlier workers; e.g., Rauff 1892; Rietschel 1969; Foster 1973) explains this in terms of a dynamic equilibrium between 'incoming' meroms, recruited from the top of the thallus and 'outgoing' meroms, displaced outward and downward through individual accretionary growth and added to the outwardly extending bottom.

We have also observed a general dependency of bottom topography on grain size of the surrounding sediment, in addition to the effect of thallus size, noted above. Specimens preserved in relatively fine grained matrix tend to have flatter bottoms than similarly sized specimens in coarser grained matrix (which have more rounded, convex bottoms). This difference will be explained below, in the discussion of growth scenarios.

Central axis. — In general, the central axis of receptaculitids is not itself skeletonized, but its form is partly recorded by the proximal ends of meroms. The central axis of *F. reticulatus* is preserved only as the mold of the adaxial surface of the inner wall. Since the inner wall is approximately parallel to the outer wall, the shape of the central axis corresponds closely to the shape of the thallus as a whole (Fig. 6).

On a smaller scale, molds of the adaxial surface of the inner wall show a pattern of shallow dimples and cylindrical protrusions. These features are, respectively, molds of individual merom feet and molds of pores through the inner wall, at the corners of merom feet. On a few specimens, at the centers of molds of merom feet, we have observed slender, tapering protrusions that are molds of the proximal portion of a central canal that runs into the merom shaft.

Merom morphology. — Individual meroms are the fundamental elements of the receptaculitid skeleton (Figs 5C–D, 7). Their shape shows regular, latitudinal variation, but we begin with a general, qualitative treatment.

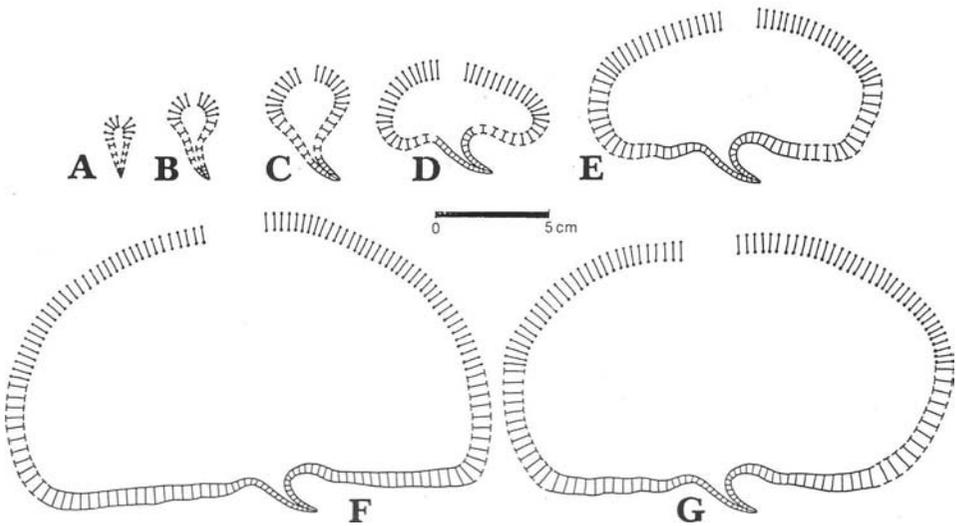


Fig. 6. Ontogeny of thallus shape in *Fisherites reticulatus*. A-G show a series of stages of thallus growth in which regions nearest the nuclear pole stabilize their form and orientation first, followed progressively by regions farther from the nuclear pole. Solid lines along inner and outer walls indicate portions of the thallus that are probably fused; dashed lines indicate portions that are mineralized and finny articulated, but not fused; and dots at merom heads and feet indicate portions of the thallus inferred to have been either loosely articulated, unmineralized, or both.

Merom feet have an approximately equilateral rhombic outline when viewed normal to the surface of the inner wall. The corners of this rhombus are oriented in the cardinal directions. The proximal (adaxial) surface of a merom foot may show a central, conical depression at the opening of the central canal penetrating the merom shaft, but frequently, there is no sign of this opening. In such cases the proximal surface of the foot is gently convex, with a finer scale topography that varies from faint, concentric terracing, roughly parallel to the nearest margin of the foot, to a smooth, granular surface. The abaxial surface of the foot is more nearly flat, but rises centrally to merge with the shaft. At each corner of a merom foot is part of a cylindrical pore whose axis is normal to the inner wall. When neighboring rhombic meroms are viewed in articulation, four corners of four mutually adjacent merom feet are juxtaposed, yielding a single cylindrical pore through the inner wall (Fig. 5C). This arrangement is identical to the pattern described by Billings (1865) for *F. occidentalis* and similar to that described for *H. borenorensis* by Campbell *et al.* (1974), except that the latter species has additional pores along the edges of its feet.

In *F. reticulatus*, adjacent merom feet abut along a planar surface without any indication of imbrication or interdigitation. In early stages of development, their boundaries are demarcated by a sharp groove on both the abaxial and the adaxial surfaces of the inner wall. At this stage, fossil fractures (i.e., ones suffered prior to burial and diagenesis - recognized by

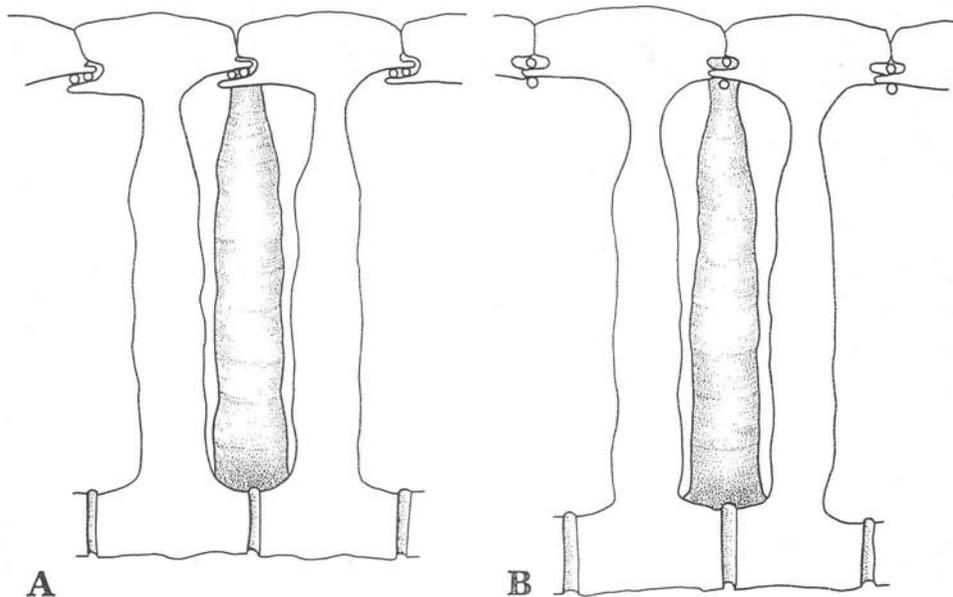


Fig. 7. Morphology of meroms of *Fisherites reticulatus* (based on FMNH PE 14035). □A. Cutaway view showing a meridional cross section (apicallacuna to left; nuclear pole to right) through meroms of one orthostichy, and the shaft (shaded) of one merom immediately to the east. OB. Similar cutaway view of meroms of one circlet (and shaded shaft of a merom to the north or south).

the presence of matrix along the fracture surface) occur exclusively along merom boundaries. At later stages of development, merom feet thicken, eliminating the clear boundaries between them (Fig. 5D). These and other details will be considered below, in the discussion of fusion of adjacent meroms.

Merom shafts are roughly perpendicular to both the inner and outer walls. Adjacent shafts thus diverge abaxially where the thallus has a convex external topography and converge abaxially where the thallus has a concave external topography. Each merom shaft is approximately cylindrical through about the proximal three fourths of its length. It then tapers distally to about one half its basal diameter. Although some shafts (particularly more slender ones) may be quite smooth, many have low, rounded annulations distributed irregularly along the shaft (Fig. 7).

The standard type of merom head in *F. reticulatus* is much like what has been described previously for *R. nephri* (Rietschel 1969) and *I. dixonensis* (Fisher & Nitecki 1978). It consists of a distal, rhombic plate, with comers pointing in the cardinal directions, and situated just proximal to the plate, a four-ribbed stellate structure. The plate has a smooth to somewhat granular, slightly to moderately convex, abaxial surface. There is usually no topographic indication of growth rings, but these may occur, as was illustrated for *R. nephri* by Rauff (1892: Pl. 1: 9–10). In addition, some specimens preserved in limestone show, upon immersion in water or

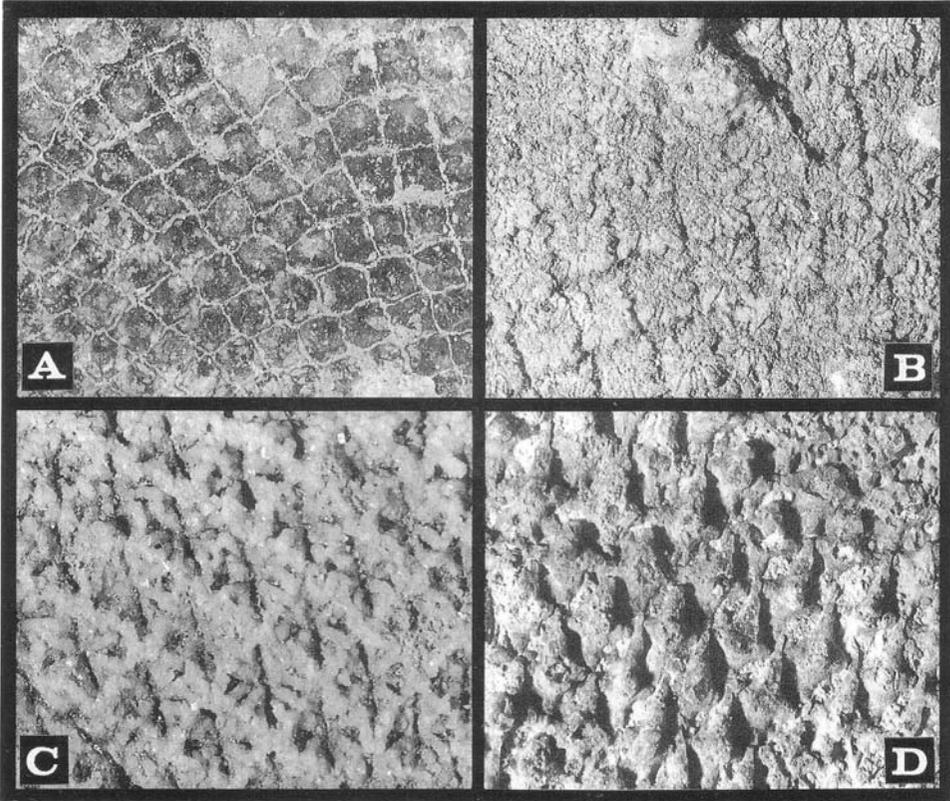


Fig. 8. *Fisherites reticulatus* from the Galena Group. Upper Mississippi Valley region, USA; apical direction (north) is up. □A. Abaxial aspect of merom plates forming outer wall, preserved with little external relief (FMNHUC 25603), x 2.4. □B. Abaxial aspect of merom plates showing radial structures similar to radiocyathid nesasters (FMNH PE 16327; figured by Nitecki & Debrenne 1979), x 2.8. □C. Outer wall mold in dolomitized matrix, showing inverse topography to B, x 3.5. OD. Adaxial aspect of outer wall (merom shafts broken), showing pattern of rib overlap on stellate structures [FMNH PE 14011], x 3.1.

alcohol, concentric light and dark bands, running parallel to plate margins, supporting the idea that individual plates increased in size by marginal accretion, as has been suggested for other species.

There is also evidence of a radially organized structure within the plates (figured by Nitecki & Debrenne 1979), manifested in different ways in different forms of preservation. In specimens that are preserved in limestone and that have relatively smooth abaxial plate surfaces (Fig. 8A), the calcite of the plate is often somewhat translucent. In these cases, light colored radiating features, located within the plate itself, are occasionally visible. The largest four of these extend from the center of the plate to each of its four corners. Between each pair of major rays are located two similar, but less strongly developed rays, running from the center of the plate to its margin. These rays are apparently distinct from the 'spindles' within

each rib of the stellate structure (Rauff 1892), but they are closely comparable to the 'nesasters' of radiocyathids (Nitecki & Debrenne 1979).

In specimens where the abaxial plate surfaces are more rugose and more strongly convex, very little of this structure is visible at all. However, on specimens that are preserved in limestone and that have weathered out extensively, this same radiating structure may be expressed topographically, rendering additional details visible (Fig. 8B). The center of the plate (the intersection of the radiating rays) is occupied by a small rounded prominence, about the diameter of the distal end of the merom shaft. The cross section of individual rays is more or less cylindrical, and they are often inflated slightly near their distal ends. In a few instances, we have observed rays that seemed to have branched distally, so that more than twelve are present at the plate margin. Finally, the rays themselves appear to be formed of more coarsely crystalline calcite than the intervening portions of the plate (this would explain the color difference noted above). When an outer wall showing such detail is traced laterally to where it remains covered by matrix, there is a progressive diminution of the topographic relief of the rays.

In the dolomitic facies, the topography of the abaxial surfaces of merom plates has often been obscured by dolomite crystals on the surface of the mold. Nevertheless, such molds sometimes record an outer wall surface such as that of the weathered specimens described above, showing radial features (Fig. 8C).

These radial features of merom plates are developed consistently enough that it seems likely that they represent original features of plate structure. However, it is not clear whether the rays were initially within the plate or were external structures, nor whether they began as mineralized structures, or as unmineralized regions (occupied first by soft tissue or fluid and later by diagenetic cement) within a mineralized skeleton. The gradient in topographic expression on specimens weathering out of limestone, steepest in a direction normal to the receding front of matrix (which may or may not coincide with the meridional direction), suggests that smooth plates (with the rays internal) represent the least altered condition. On the other hand, radial topographic features on dolomite molds indicate that this topography predates deposition of the surrounding sediment. At the risk of oversimplifying, it seems that either these features were originally internal and were, in some situations, wholly or partly 'exhumed', or else they were originally external and were wholly or partly overgrown by plate accretion. Of these two scenarios, we tentatively prefer the first, for the following reasons: (1) the plates with rays not expressed topographically usually offer the most detailed preservation of other morphologic details (e.g., precise plate boundaries); and (2) the material between and around the rays resembles that of most of the rest of the merom.

It is even harder to determine whether these radial features were originally mineralized or unmineralized. Because the rays were present, as

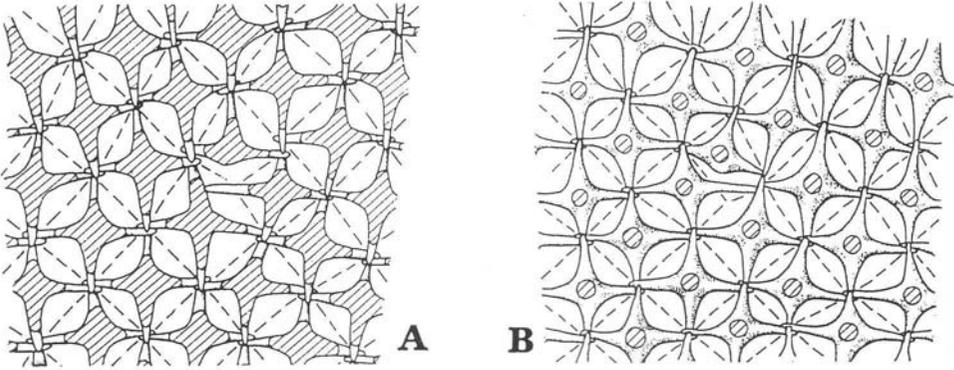


Fig. 9. Pattern of overlap of ribs of stellate structures near a dextral intercalation in *Fisherites reticulatus* (FMNH PE 14011). Apical direction (north) is up. □A. Abaxial aspect; plates removed along areas marked by diagonal lines (positions of plate boundaries indicated by dashed lines), to reveal stellate structures below. □B. Adaxial aspect (shafts removed).

competent structures, by the time of formation of the molds preserved in dolomitic facies, we tentatively regard the radial structures within plates as original, calcareous portions of the plate. However, the possibility remains that they were only secondarily filled by calcite. Petrographic examination of meroms may help to resolve these issues.

Adjacent plates abut one another along somewhat irregular, but mutually complementary margins. The plates are relatively thick at their margins (unlike those of ischaditids), and the surface of contact is either normal to the outer wall, or dips steeply in a southward direction. Throughout much of development, neighboring plates are clearly separate from each other (a small amount of sediment often occurs between them), but many eventually fuse to their neighbors (see below).

Immediately proximal to the merorn plate is the stellate structure, consisting of four ribs, one extending in each cardinal direction (Fig. 9). The latitudinal (eastern and western) ribs are fused to the adaxial surface of their plate from their origin on the merorn shaft, almost to the eastern and western corners of the plate. Distal to this, they are free-standing, and overlap, approximately in the plane of the outer wall, with the western and eastern ribs of their eastern and western neighbors, respectively. The sense of this overlap (i.e., whether an eastern or a western rib of a pair of E-W neighbors lies to the north of the other) is often consistent over small domains on the thallus, but, unlike the situation in *I. dixonensis*, it is not constant over the whole thallus. The northern rib of a given stellate structure, again unlike that of *I. dixonensis*, is fused to its plate almost all the way to the northern corner. It then becomes free-standing and passes below (i.e., adaxial to) the overlapping eastern and western ribs of its NW and NE neighbors, respectively. It ends, however, before encountering the shaft of its northern neighbor. The southern rib has the least topographic expression on the adaxial surface of the plate; it almost seems to emerge from the plate near the southern corner. Extending to the south, it passes

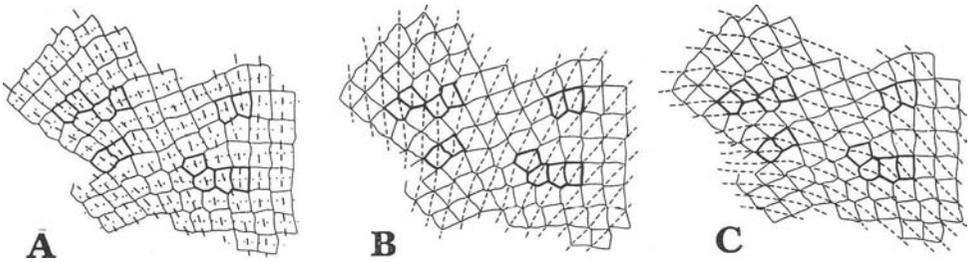


Fig. 10. Merom alignment in the vicinity of dextral and sinistral intercalations (plate pairs in bold outline) in *Fisherites reticulatus* (based on FMNH UC 25603). □A. Dextral parastichies (dotted lines) and sinistral parastichies (dashed lines). OB. Orthostichies (dashed). □C. Circlets (dashed).

above (i.e., abaxial to) the overlapping eastern and western ribs of its SW and SE neighbors, respectively. It then ends by inserting in a small depression located just under the northern corner of its southern neighbor, where the northern rib of that neighbor first becomes free-standing. Although there is some variation in the relative lengths of meridional ribs over the thallus, the sense of their relationship to each other and to latitudinal ribs is constant (Fisher & Nitecki 1982). In this respect, though not in the precise shapes and sizes of ribs, *F. reticulatus* is identical to all other receptaculitids with which we are familiar.

Arrangement of meroms. — Because of the variety of cross-sectional views that may be presented by even a single specimen, merom arrangement must often be interpreted from views of various parts of meroms. However, to simplify discussion, we focus mainly on the outlines of merom plates, as seen on the external surface of the thallus. Within a group of rhombic plates, ignoring minor irregularities of outline, N, S, E, and W neighbors make contact at the corners of their plates, and NW, NE, SW, and SE neighbors meet along an edge. SW-NE neighbors are members of the same dextral parastichy (Fig. 10A, dotted lines); SE-NW neighbors are members of the same sinistral parastichy (Fig. 10A, dashed lines); meridional (N-S) neighbors are members of the same orthostichy (Fig. 10B); and latitudinal (E-W) neighbors are members of the same circlet (Fig. 10C).

The simple, rhombic pattern is modified by intercalation of new alignments of meroms at many points over at least the lower hemisphere of the thallus. These modifications are associated with two varieties of intercalary meroms: (1) asymmetrical intercalary meroms (Figs 10–12), which may be either dextral (where a new dextral parastichy is initiated) or sinistral (new sinistral parastichy); and (2) symmetrical intercalary meroms (both a dextral and a sinistral parastichy are initiated; Fig. 11). Asymmetrical intercalation has been figured by various authors, discussed briefly by Rietschel (1970), and more extensively by Fisher & Nitecki (1982), in their treatment of *F. occidentalis* and *F. reticulatus*. Symmetrical intercalation has been discussed in detail for other receptaculitids by Rauff (1892), Rietschel (1969), Gould & Katz (1975), and Niko

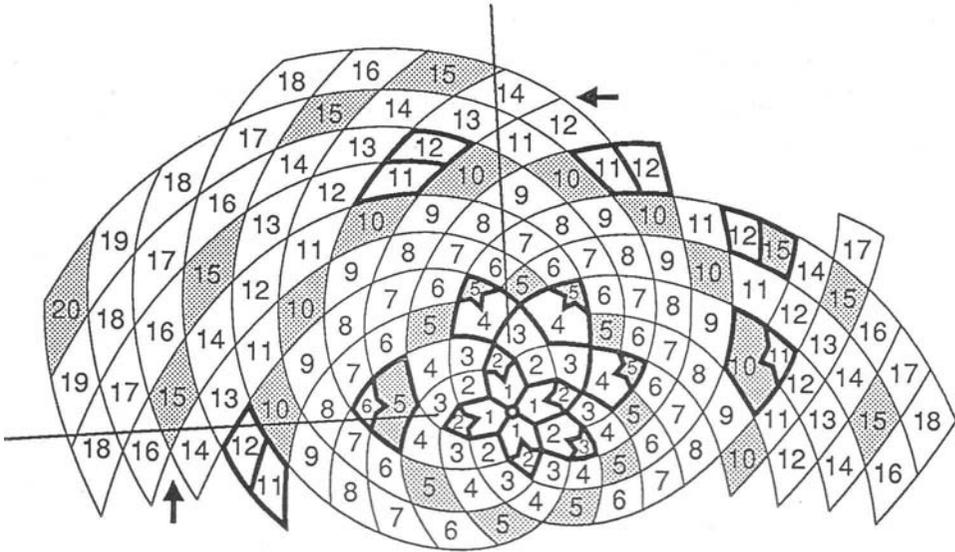


Fig. 11. Map of part of the corniculum of *Fisherites reticulatus* (FMNH UC 51619), after Fisher & Nitecki (1982: Text-fig. 13A). Merom latitude (see text) is indicated by numbers within each plate boundary. This number is incremented by at least one for each plate along a parastichy. The two plates of each asymmetrical intercalation are assigned latitudes that differ by one. This results in increments of two along some parastichies and yields unequal latitudes for some E-W neighbors, but these irregularities cancel when dextral and sinistral intercalations cooccur. New information on plate patterns from these latitudes (e.g., from areas of the specimen not preserved here) could alter certain latitudinal assignments, but not greatly. Bold lines mark plates of intercalary meroms, and a stippled pattern marks the 5th whorl (the last demonstrably complete whorl on this specimen), the preserved portion of the 10th whorl (the last probable whorl on this specimen), and preserved portions of the 15th and 20th surrogate whorls. Radii aligned with the thallus axis (here equivalent to the site of the nuclear pole) bracket a 90° sector within which number of meroms per whorl-equivalent can be counted. Starting with the leftmost merom at latitude 15 [indicated by an arrow at the lower left], and following its circlet clockwise (toward the arrow at the top of the figure), 90° embraces about four meroms on this diagram, which projects the plate pattern onto a plane. In actual practice a comparable procedure is followed on the outer surface of the thallus, here including at least five meroms, suggesting about 20 meroms per whorl-equivalent.

& Hamada (1988), and for *Fisherites* by Fisher & Nitecki (1982) and Niko & Ikebe (1988).

One addition to the qualitative description of asymmetrical intercalations has to do with details of their stellate structures. The northernmost head of an asymmetrical intercalary merom (the NW head of a dextral intercalary merom or the NE head of a sinistral intercalary merom) often has the southern rib of its stellate structure suppressed. If present at all, it is only a short nub near the junction of the plate and shaft (Fig. 9). The SE head of a dextral intercalary merom (or the SW head of a sinistral intercalary merom) has a more nearly normal stellate structure, but because it does not have a neighbor to the west (east), its western (eastern)

rib does not overlap any other latitudinal rib. Rather, it terminates just after crossing the northern rib of its SW (SE) neighbor.

The symmetrical intercalary meroms of *F. reticuhtus* are relatively conventional interpositum-triangulum pairs (Fig. 11), as have been described for many other receptaculitids, including *R. neptuni*, *I. barrandei*, and *I. dixonensis* (Rietschel 1969; Gould & Katz 1975; Fisher & Nitecki 1978). The plate of the interpositum is a symmetrical pentagon, with a vertex pointing to the south and an edge forming its northern boundary. This northern edge has a slight emargination midway along its length. The triangulum lies immediately to the north of the interpositum, and except for a small v-shaped protrusion which fits into the emargination just mentioned, it is an approximately isosceles triangle, with its unique vertex pointing north. Plate alignments in the vicinity of an interpositum-triangulum pair have been described before (Fisher & Nitecki 1978, 1982).

Since we interpret the meroms immediately surrounding the nuclear pole as the oldest, followed in age by those successively farther from it, we begin describing merom organization at the tip of the corniculum. As mentioned previously, a map of plate boundaries on the corniculum of *F. reticulatus* is presently available only for FMNH UC 51619, shown in Fig. 11. This specimen has four symmetrical intercalary meroms immediately surrounding the nuclear pole. Their four interposita form the first whorl of plates, and the second whorl consists of their four triangula and four eastern (or western) neighbors of those triangula – i.e., eight plates in all. Intercalation at symmetrical intercalary meroms occurs in such a way that for each interpositum in one whorl, an additional plate occurs in the succeeding whorl.

One of the non-triangulum plates of the second whorl is itself an interpositum, and thus the third whorl has nine plates. No additional interposita occur in the third whorl, but there are three, immediately adjacent to one another, in the fourth whorl, yielding twelve plates for the fifth whorl. One of these is an interpositum, bringing the total number of plates for the sixth whorl to thirteen. Since the fifth whorl is the last one to be preserved in its entirety on this individual, this is as far as we can go with comprehensive mapping of plate positions. However, a sector is preserved representing at least half of the thallus out to the tenth whorl, and at least a fourth of it for some distance beyond that, allowing some tentative generalizations. Symmetrical intercalary meroms occur as far out as the tenth whorl, but none are known beyond that position, on this or any other specimens of *F. reticuhtus* we have examined. Asymmetrical intercalary meroms, on the other hand, appear to show a complementary pattern, with none occurring closer to the nucleus than the tenth whorl. On FMNH UC 51916, three sinistral intercalary meroms occur immediately outside the tenth whorl, and one more, also sinistral, is located just outside of that. Since no further intercalations occur on this specimen, the latitudinal band on the flanks of the corniculum beyond the tenth whorl must be traversed by at least four circlets spiraling sinistrally to the north

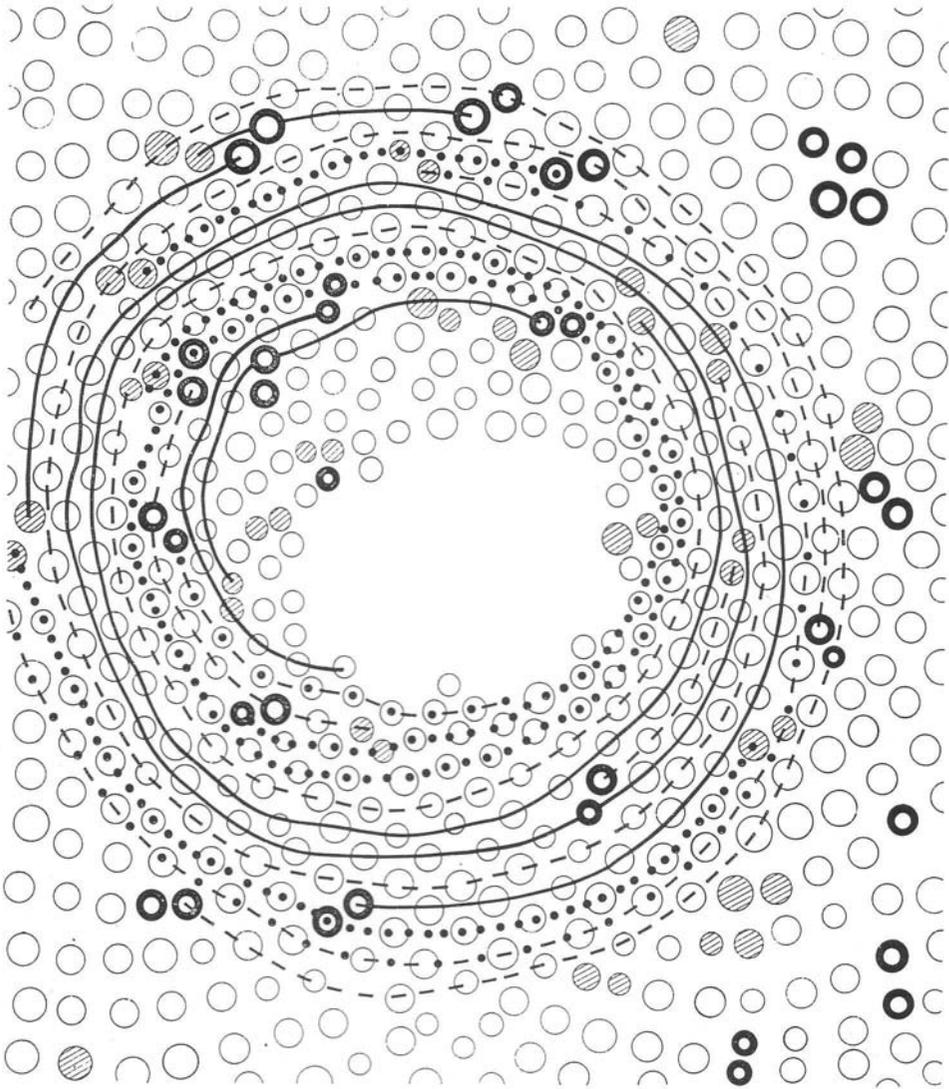


Fig. 12. Map of thallus bottom of *Fisherites reticulatus* [FMNH PE 14005]. Heavy circles mark sinistral intercalations, and diagonal lines mark dextral intercalations. The coraculum and the region immediately surrounding it are not preserved. The pattern of meroms peripheral to this is represented only by the arrangement of merom shafts. Circlets extend for various distances around the thallus, depending on the exact siting of intercalations, and are indicated by a sequence of solid, dotted, and dashed lines.

(this relation between direction of asymmetrical intercalation and number of circlets is illustrated in Text-fig. 24 of Fisher & Nitecki 1982). To proceed further on the coraculum or onto the rest of the thallus bottom, we must shift to other specimens, where we find roughly equal numbers of dextral and sinistral asymmetrical intercalations. In Fig. 12, E-W series of meroms comprise circlets that begin and end at intercalations and extend any-

where from a fraction of the distance around the thallus to multiple revolutions.

It would be only reasonable, given the variation documented for other species (e.g., *H. borenorense*, Campbell *et al.* 1974, or *I. barrandei*, Gould & Katz 1975), to expect certain of these details to vary within *F. reticulatus*. Precise plate positions are not apt to be species-specific characters, but more general features might be. For instance, the presence of four symmetrical intercalary meroms in the nuclear whorl, or the mutually exclusive distribution of symmetrical and asymmetrical intercalary meroms, separated by a latitudinal boundary at about the tenth whorl, might be consistent characters. Although we have not been able to check this on other specimens of this species, maps of well preserved specimens of *F. occidentalis* show similar patterns (Fisher & Nitecki 1982). Somewhat more problematic is the exclusive occurrence of sinistral intercalary meroms among the oldest of the asymmetrical intercalary meroms. We have not been able to confirm this on other specimens and do not know whether it is causally related to the topographic twist (alsosinistral on this specimen) on the corniculum.

Latitudinal position of meroms. — Characterizing merom position by distance or angular measures relative to either pole, though adequate for description of isolated specimens, does not give a stable reference for comparing specimens of different growth stages (Fisher & Nitecki 1982). This is because marginal accretion to merom plates and feet, the one component of thallus growth about which there has been little disagreement, results in displacement of meroms within the frame of reference implied by these measures. We therefore follow Rauff (1892) and Rietschel (1969) in measuring latitudinal position in terms of the number of meroms between a given position and the nuclear pole, and we express this as a positive whole number. There are, however, two factors that make this measure of latitude difficult in *F. reticulatus*. The first is a consequence of asymmetrical intercalation and having meroms organized in circlets rather than whorls. Membership in the same circlet is neither a necessary nor a sufficient condition for having the same latitude, measured in this way. Latitude should therefore be assessed without assuming constancy for all members of an E-W series. An analogue of the whorl-based measure of latitude used on receptaculitids with exclusively symmetrical intercalations can be implemented 'by counting backward [toward the nuclear pole] along a zigzag series of southeastern, southwestern, southeastern, southwestern, ... neighbors of the plate in question. If there exists no southeastern or southwestern neighbor (i.e., if the count runs into a triangulum), the next plate counted should be the southern neighbor (i.e., the interpositum)... If there is an intervening region of non-preservation, an approximate assignment may be made by counting along any other series of parastichies. Since the resulting assignment will be path-dependent, an effort should be made to approach the normal procedure as nearly as possible' (Fisher & Nitecki 1982: pp. 34–35).

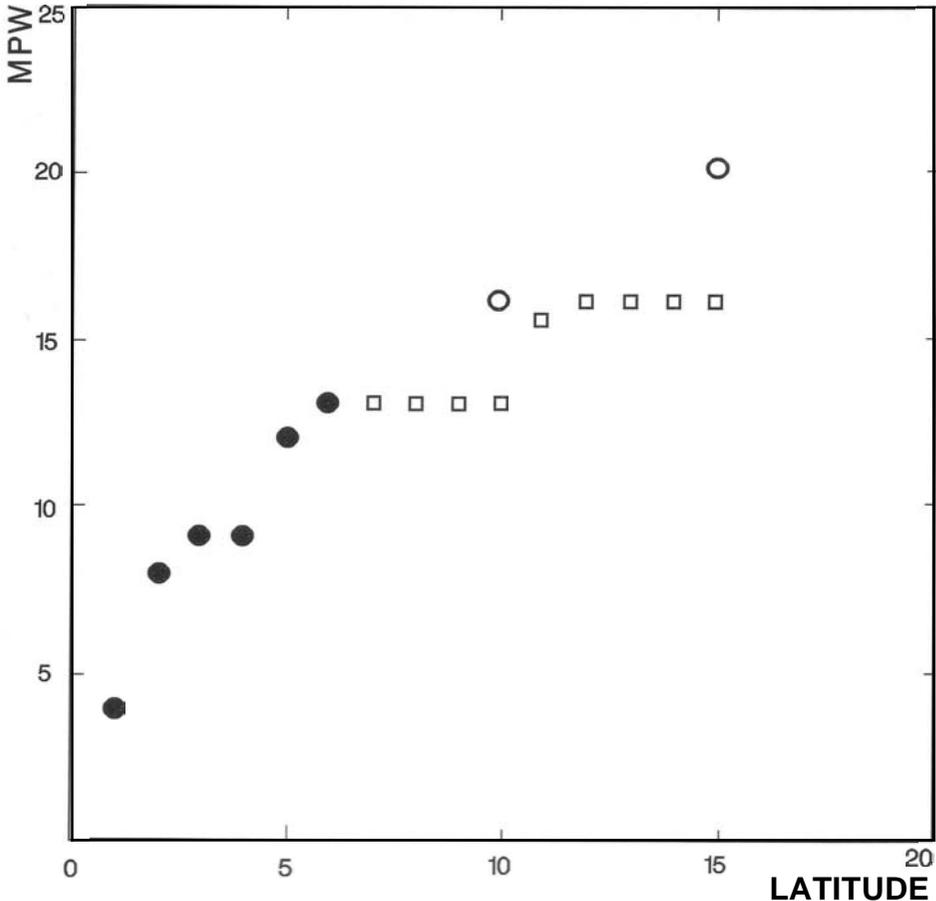


Fig. 13. Graph of number of meroms per whorl or whorl-equivalent (MPW) vs. latitude in *Fisherites reticulatus*, on FMNH UC 51619. Solid dots show values for whorls 1–6, for which we have comprehensive information; open squares represent minimal estimates based on number and latitude of observed intercalations; open circles are probably more accurate estimates for these latitudes, based on counts across a 90° sector.

In practice, to minimize recounting, this procedure can be reversed, determining latitudinal position first for meroms near the nuclear pole and then working outward from these. Auxiliary conventions are noted in the caption to Fig. 11. This, however, brings up the second complicating factor: because of its topographic complexity, the corniculum is frequently fractured and/or covered by matrix so that the nuclear pole and its immediate vicinity are not well exposed. Even intervallum casts may be incomplete in this area because of breakage or incomplete filling of the interstices between closely spaced merom shafts. Therefore, we need an alternative reference for latitudinal estimates.

In response to this second difficulty, we first measured latitude relative to the margin of the corniculum, defined as the latitude at which the

meridional curvature of the outer wall achieves the smallest radius. In the absence of a secure reference for measurement of latitude, the cornicular margin can be traced approximately as the intersection of the thallus surface with a plane normal to the local axis of cornicular symmetry and passing through the point of maximal meridional curvature. Relative invariance in the quantitative attributes of this margin would corroborate a hypothesis that it represents a consistent reference latitude. However, if its attributes vary in a way that suggests correlation with latitude, we would more likely view the cornicular margin as a labile feature, marking a stage in thallus development the timing of which was not fixed. .

Quantitative attributes of the cornicular margin include its diameter and the number of meroms occurring along it. This latter attribute is a specific case of what we refer to as a 'number of meroms per whorl-equivalent', where a whorl-equivalent is a series of complete and/or incomplete circlets that collectively circumscribe the thallus at approximately the same latitude, evaluated topographically, in the absence of a secure reference for direct assignment of 'anatomical latitude' (i.e., latitude measured in merom units from the nuclear pole). A whorl-equivalent is analogous to a whorl (in receptaculitids with exclusively symmetrical intercalation) and to a 'surrogate whorl' (the set of all meroms assigned the same latitude by the convention discussed above for receptaculitids with asymmetrical intercalation). To clarify the difference between these three concepts, a whorl is defined by a combination of neighbor relations (E-W) and anatomical latitude, but avoids reference to topography because it changes with marginal accretion to plates and feet. A surrogate whorl is defined strictly in terms of anatomical latitude, without reference to neighbor relations (because with asymmetrical intercalations, not all meroms assigned the same latitude are E-W neighbors) or topography. In contrast, a whorl-equivalent is defined in terms of neighbor relations (some or all members of one or more circlets) and topography. The concept of whorl-equivalent is useful because neither whorls nor surrogate whorls are clearly identifiable when intercalations are asymmetrical and the nuclear pole is not accessible.

Some of these distinctions are illustrated in Fig. 11. Numbers indicate the latitude of each merom, determined as discussed above and by application of other conventions listed in the caption. The 5th whorl (the last whorl that is completely preserved) and the 10th whorl (the last E-W series that is probably a whorl) are marked by stippled patterns at their respective latitudes. From the nuclear pole through the 10th whorl, whorls, surrogate whorls, and whorl-equivalents all recognize the same sets of meroms, but beyond this latitude, only circlets occur, limiting latitudinally coherent sets of meroms to surrogate whorls and whorl-equivalents. In counting number of meroms per whorl, all meroms are E-W neighbors, and they may be enumerated without ambiguity or loss of continuity. In counting number of meroms per surrogate whorl, gaps may be encountered in the series of meroms assigned to a surrogate whorl (as

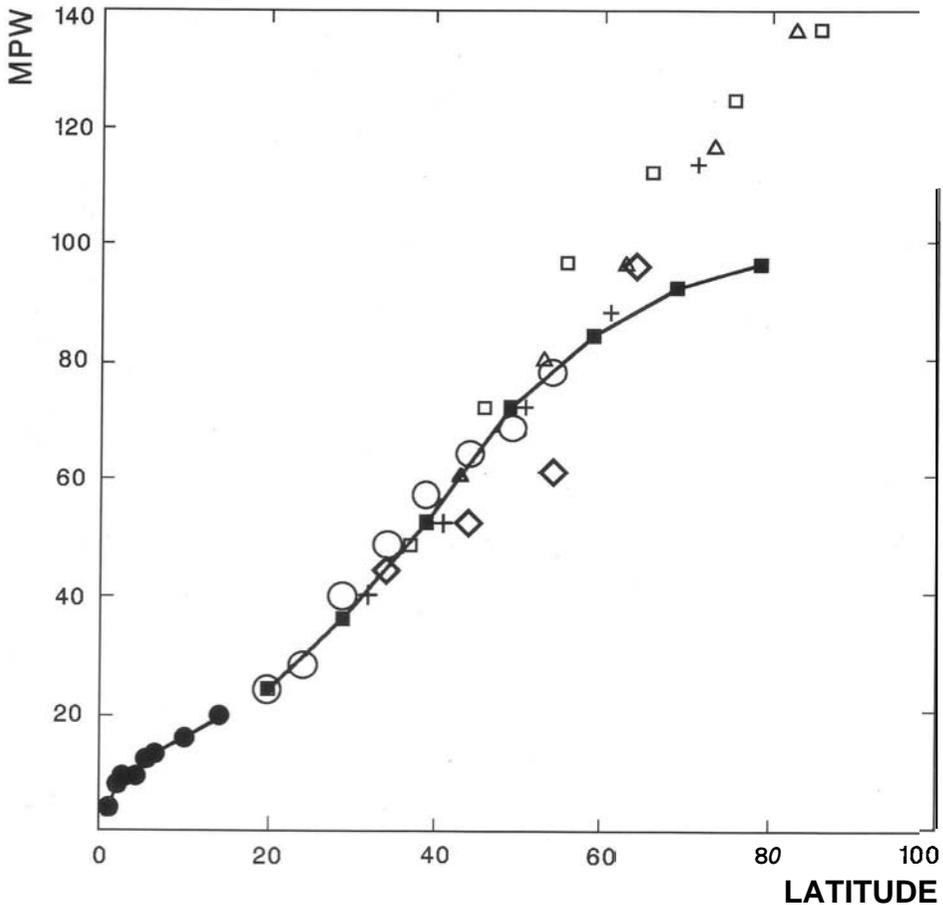


Fig. 14. Graph of number of meroms per whorl-equivalent (MPW) vs. latitude (number of merom positions from nuclear pole) in *Fisherites reticulatus*. FMNH UC 51619 and IGS-1, the two specimens on which latitudinal correlations are based, are represented by solid dots connected by lines and solid squares connected by lines, respectively. Other specimens are: open squares, IGS-2; open circles, FMNH 23778; plus signs, FMNH C-2; open triangles, FMNH 11006; open diamonds, FMNH P61.

shown by stippled plates at latitude 15 in Fig. 11), but individual gaps are never greater than one half merom, and even these close up as dextral and sinistral intercalations occur with similar frequency. In contrast, a whorl-equivalent never includes gaps, but may include overlaps by one half merom, where consecutive meroms are members of the same parastichy. This occurs if a cirlet ends at an intercalation or if it has sufficiently marked latitudinal excursion that shifting along a parastichy is necessary to maintain latitudinal position. A count of number of meroms per whorl-equivalent is incremented by integers as it proceeds along a cirlet, but to avoid overrepresenting the number of meroms, the count is incremented only by one half whenever it proceeds along a parastichy. In cases of

incomplete preservation, the number of meroms counted can be divided by the fraction of 360° (measured relative to a vertex located along the axis of thallus symmetry) over which the transect extends. Some uncertainty attends such a count because of errors in estimating latitudinal position and the position of the thallus axis, but even approximate values record broad features of thallus configuration. Application of these procedures to FMNH UC 51619 results in the profile of number of meroms per whorl (or whorl-equivalent) vs. latitude shown in Fig. 13.

Returning to attributes of the cornicular margin, specimens listed in Tab. 1 vary in cornicular diameter (CD) from 14 mm to 25 mm. It is not immediately clear whether this is because of variation in plate number and/or size at the same latitude or variation in plate number and/or size correlated with latitude, but larger cornicula generally seem to have more meroms per whorl-equivalent along their margin. Although plate widths increase somewhat with latitude (see below), the overall impression of many workers has been that intercalation occurs in receptaculitids in a manner that allows plate widths to remain relatively constant in the face of an expanding thallus diameter (Gould & Katz 1975). Consequently, a conical corniculum would be expected to be encircled by more meroms if it continued expanding to a higher latitude, as seen over the latitudinal range profiled in Fig. 13. The relationship between cornicular diameter and number of meroms along the cornicular margin could thus be attributed simply to cornicula undergoing margin formation at different latitudes, implying that the cornicular margin is not a consistent reference.

Taking a cue from the regular pattern of increase seen in Fig. 13, we might also treat the number of meroms per whorl or whorl-equivalent as an indirect indication of latitude. The resolution of this approach is limited both by the intrinsic discontinuity of increases in number of meroms with latitude (i.e., merom addition is a unitary event and need not occur with every increase in latitude) and by variability in the overall rate of addition. Nonetheless, if thalli of *F. reticulatus* have at least approximately equal numbers of meroms per whorl-equivalent at comparable latitudes, it should be possible to superimpose latitudinal profiles of number of meroms per whorl-equivalent for different specimens and use the optimal superimposition as a basis for latitudinal correlation from specimen to specimen. As a first step in this direction, we have selected a series of specimens on which at least a 90° sector of the thallus bottom is visible, starting with a latitude on the flank of the corniculum or at least near the cornicular margin. We have then counted number of meroms per whorl-equivalent (as above) at regular latitudinal intervals. Profiles compiled from these counts give at least a rough view of the increase in number of meroms with latitude.

In principle, the superimposition of profiles from multiple specimens should be done simultaneously and should consider the full range of available latitudes. However, to simplify the procedure and generate pre-

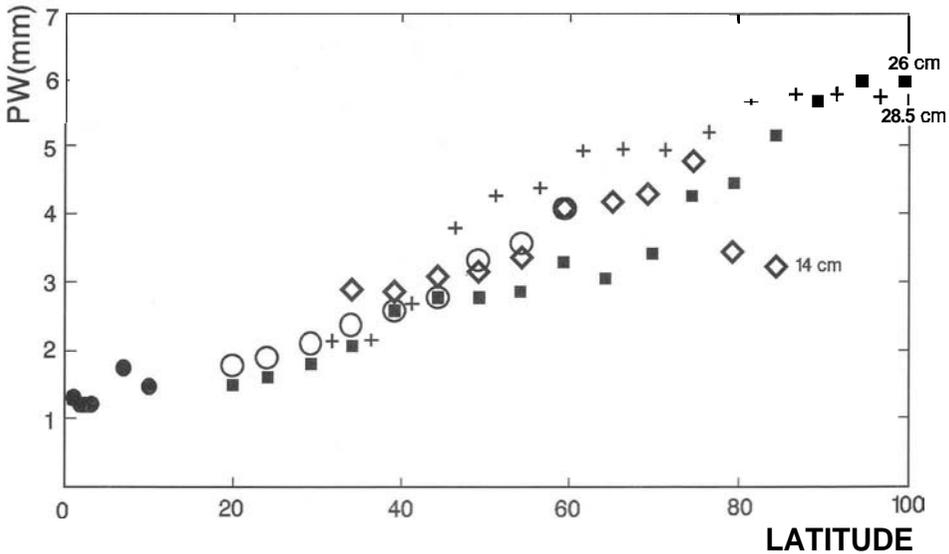


Fig. 15. Graph of merom plate width (PW) vs. latitude (number of merom positions from nuclear pole) in *Fisherites reticulatus* (symbols as in Fig. 14). Thallus bottom diameter (BD) is indicated at the right of each profile for which it is available.

liminary results, we have started with only two specimens, FMNH UC 51619, with the exposed nuclear pole, and IGS-1, on which the preserved array of meroms extends nearer the nuclear pole than on other specimens listed in Tab. 1. We correlate between these two by aligning the value for the southernmost whorl-equivalent of IGS-1 with an extrapolation of the profile for FMNH UC 51619. The 15th whorl-equivalent of FMNH UC 51619, on the flank of the corniculum, contains at least 16 meroms (based on observed intercalations), but our count across a 90° sector suggests a total of at least 20 meroms. The southernmost whorl-equivalent on IGS-1 also occurs on the flank of its corniculum, and contains 24 meroms. Aligning their two profiles as in Fig. 14, we consider the southernmost whorl-equivalent on IGS-1 to have a latitude of 20 merom positions from the nuclear pole. In similar fashion, we use the profile for IGS-1 to assign latitudes to the other specimens, interpolating their southernmost whorl-equivalents into the profile for IGS-1. Although this approach is somewhat arbitrary, the relatively coherent pattern of overlap of profiles in Fig. 14 suggests that these latitudinal correlations may not be far astray.

Latitudinal distribution of intercalations. — Based on the foregoing hypothesis of latitudinal correlation, we resume our description of the distribution of intercalations at latitudes higher than those preserved on FMNH UC 51619. On preserved portions of all specimens listed in Tabs 1 and 2, intercalations are exclusively asymmetrical. Their latitudinal distribution relates to the profiles shown in Fig. 14 in that the number of meroms per whorl-equivalent increases by one for every two asymmetrical

Table 1. Thallus and corniculum measurements for *Fisherites reticulatus*. BD – thallus bottom diameter; CD – corniculum diameter (maximum, at margin of corniculum); MPW @ L_c – meroms per whorl-equivalent at cornicular margin; + – thallus broken at margin.

SPECIMEN	BD (cm)	CD (mm)	MPW @ L _c
IGS-1	26	18.5	50
FMNH P61	14	18	44
IGS-2	25	25	36
C-2	28.5	18.8	32
AMNH 36032	3+	17	25
FMNH P4735	7.5+	14	20

Table 2. Latitudinal distribution of asymmetrical intercalations within 90° sectors on the thallus bottom of *Fisherites reticulatus*. BD – thallus bottom diameter; MPW – meroms per whorl-equivalent; SI – sinistral intercalations; DI – dextral intercalations; + – incomplete preservation. MPW values are for the circllet along the northern margin of the latitudinal band indicated at left.

SPECIMEN (BD):	P61 (14 cm)			IGS-2 (25 cm)			IGS-1 (26 cm)			C-2 (28.5 cm)		
LATITUDE	MPW	SI	DI	MPW	SI	DI	MPW	SI	DI	MPW	SI	DI
x – (x + 10)							36	20	12	40	12	12
(x + 10) – (x + 20)	52	0	12				52	12	12	52	16	16
(x + 20) – (x + 30)	60	4	4	72	20	20	72	20	24	72	24	28
(x + 30) – (x + 40)	86	16	12	96	24	28	84	20	4	88	28	8
(x + 40) – (x + 50)				112	16	32	92	4	8	112	16	24
(x + 50) – (x + 60)				124	24	24	96	4	8	112+	8	4
(x + 60) – (x + 70)				136	12	8	96+	8	4			
(x + 70) – (x + 80)				144+	8	8						

intercalations. The approximately linear increase in number of meroms per whorl-equivalent, through most of the 0–100 latitudinal range, means that intercalations are spaced rather uniformly in a latitudinal direction. However, because the area assignable to a given latitudinal zone increases at higher latitudes, the number of intercalations per unit area must actually decrease with increasing latitude. Above about the 100th whorl-equivalent, intercalations seem to be distributed even more sparsely, but preservation is generally too incomplete to make reliable counts. Intercalations seem to be distributed approximately uniformly in a meridional sense, but we have not tested this statistically. There is no conspicuous clustering of intercalary meroms in general, or dextral and sinistral ones in particular, and we see no evidence of a rigid morphogenetic 'rule' for placement of intercalary meroms. It is more likely that their position is controlled by local rates of growth on the developing apex.

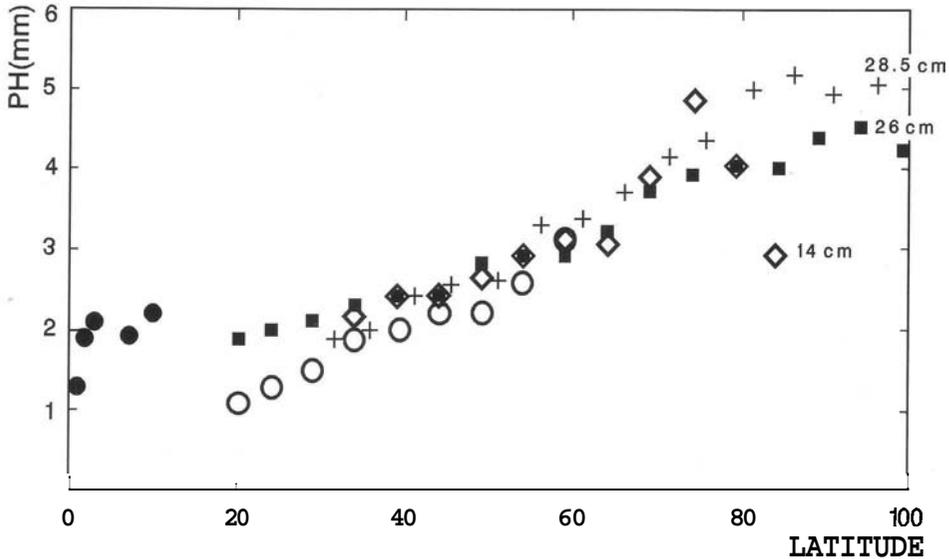


Fig. 16. Graph of merom plate height (PH) vs. latitude (number of merom positions from nuclear pole) in *Fisherites reticulatus* (symbols as in Fig. 14). Thallus bottom diameter (BD) is indicated at the right of each profile for which it is available.

Although the number of dextral and sinistral intercalary meroms is approximately equal, it is likely, given their distribution on specimens we have examined, that most thalli have at least a slight excess of one or the other. Therefore, to the north of the last intercalary merom (if intercalation actually ceases), **all** subsequent meroms must usually be organized into a small number of parallel circlets, spiraling toward the apex in either a dextral or a sinistral direction, depending on the number and sense of the excess intercalations.

Latitudinal position of the margin of the thallus bottom. — The margin of the thallus bottom appears to be located at a significantly higher latitude for larger individuals than for smaller ones. Our growth scenario (discussed below) interprets this as the movement of a labile topographic feature (the margin of the bottom) relative to a stable anatomical reference (whorl-equivalents) through the growth of meroms on the thallus sides and their eventual incorporation into an expanding thallus bottom.

Gradients in merom size and shape. — As might be expected, the only conspicuous meridional gradients in merom size or shape occur on that part of the thallus that departs most from radial symmetry — the corniculum. When the corniculum is bent into a recumbent position, the merom plates on its uppermost (most strongly curved) side are often latitudinally compressed relative to those on the other side. They tend to have normal widths, but much smaller than normal heights.

From any external view of the thallus, the most obvious latitudinal gradient is in the size of merom plates. The smallest plates on preserved

portions of the thallus occur on the corniculum, and the largest ones are usually near the outer edge of the thallus bottom. Intercalary meroms and their SW neighbors (for dextral ones) or SE neighbors (for sinistral ones) are not considered here because of their great size variance. Although plate size may be measured directly when plates themselves, or their molds, are preserved, the geometric similarity of most neighboring plates and their precise tessellation offer other sources for this information. Plate width will differ only insignificantly from the center-to-center distance between E-W neighboring shafts. Similarly, plate height will be about equal to the center-to-center distance between N-S neighboring shafts. Fig. 15 shows plate width (PW, distance from the east to the west corner) vs. latitude. The principal departure from tightly clustered profiles is the decline in PW above latitude 75 (near its thallus bottom margin) for FMNH P61 (open diamonds). This is the smallest specimen of those plotted, and it appears that subsequent accretion to plates above latitude 75 might have brought its profile into conjunction with those of larger thalli. Fig. 16 shows plate height (PH, north to south corner) vs. latitude. Here the divergence of profiles above about latitude 75, with higher latitude portions of the profiles falling out in order of thallus bottom diameter, suggests that growth is still occurring here. Plate shape is shown in Fig. 17 as the ratio of plate width to height. Plates tend to be longitudinally compressed near the tip of the corniculum, equidimensional on the flanks of the corniculum and over the rest of the thallus bottom, and latitudinally compressed on the thallus sides.

The length of merom shafts, or the thickness of the intervallum, can be measured directly along fractures, or, in some instances, by measuring the thickness of an *intervallum* cast. The length of merom shafts (SL; Fig. 18) increases gradually and monotonically (at least through preserved portions of the thallus) away from the nuclear pole. The profile for IGS-2 (open squares) departs notably from those of other specimens, but we interpret this as individual variation, rather than ontogenetic change, because it parallels others, rather than diverging, and because the profiles show no size ordering. It appears that shaft length changes little after meroms attain a position on the thallus bottom. The basal diameter of merom shafts (SD; Fig. 19), measured either on fracture surfaces or the adaxial surface of an *intervallum* cast, initially increases away from the nuclear pole but then decreases, especially near and above the latitude of the thallus bottom margin. The smallest specimen (FMNH P61, open diamonds) has a generally lower profile than the others, above about latitude 45, suggesting that increase in shaft diameter may take place well after shaft length has stabilized.

Thallus shape and merom fusion.— Throughout our description of the morphology of *F. reticulatus*, we have treated the topography of most specimens as an accurate reflection of that of the living organism. Several arguments seem to support this approach. The lack of deformation of other organisms (e.g., brachiopods or gastropods) preserved in the same rocks

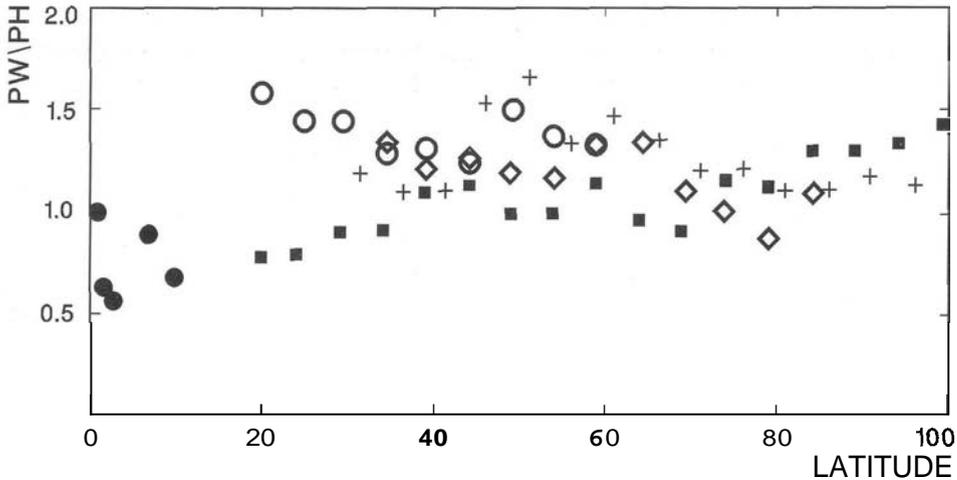


Fig. 17. Graph of merom plate width/height ratio (PW/PH) vs. latitude (number of merom positions from nuclear pole) in *Fisherites reticulatus* (symbols as in Fig. 14).

and the finer scale constancy of shape of receptaculitid meroms, regardless of their orientation, show that these specimens have not experienced significant post-diagenetic shear, or plastic deformation. The more important question, however, is whether or not they were deformed prior to (or during) burial.

This question can be answered by considering geometrical properties of the receptaculitid skeleton. The outer wall consists of a large number of polygonal units that tessellate precisely to form a curved surface. These units, judging from their consistent morphology (whether preserved in articulation or loose in the matrix), were individually rigid. Almost without exception we do not find specimens of *F. reticulatus* in which these units have been deformed or in which articulated assemblages of them have been pulled apart along their boundaries (i.e., without being entirely separated). This indicates that any traumatic (i.e., not growth-related) deformation that has acted on specimens must have been such as to leave distances between points on the surface, measured along the shortest path lying within the surface, unaltered. Is any such style of deformation conceivable? This question can be answered affirmatively, but only for certain types of surfaces. Planar surfaces that are folded about a single axis, or conical or cylindrical surfaces folded about axes parallel to lines that lie completely within them, show such behavior. However, no distance-preserving deformations are possible for ovoidal surfaces (surfaces with the same sense of curvature in all directions) or for sellar (saddle-shaped) surfaces, which together comprise most of the surface of receptaculitid thalli. Therefore, the intact outer wall of a receptaculitid thallus could not have been deformed without producing readily observable distortion, imbrication or separation of meroms. If the inner wall, linked to the outer by merom shafts, is considered in addition, we have still

another constraint on the susceptibility of the thallus to deformation. Any deformation of the outer wall would have involved either extension or compression of the inner wall, and there is no indication that this has occurred.

A final approach to the issue of deformation concerns the issue of merom fusion. This would obviously result in resistance to deformation, but it is important to distinguish fusion during life (which thus characterized the skeleton at death) from diagenetic transformations that mimic fusion. Many observations that seem at first to be *prima facie* evidence of fusion are more ambiguous on second glance. The rigidity discussed above is consistent with merom fusion, but could also have been produced through firm interlocking of stellate structures. At later stages of development, the calcium carbonate of merom feet seems to be continuous from one foot to the next. However, neomorphic alteration, or dissolution followed by precipitation of cement could also produce such an appearance. On larger specimens, the topography of the adaxial surfaces of merom heads, as shown on intervallum casts, becomes subdued, especially near the corniculum. This is suggestive of a secondary deposition of calcareous material along the adaxial surface of the outer wall, and its gradual latitudinal expression argues against its being a postmortem development. However, the same question arises as did at the merom feet. Here again, petrographic analysis may prove helpful.

One way to evaluate the likelihood of merom fusion is through interpretation of the latitudinal gradients in merom morphology discussed above. A necessary (though not sufficient) condition for fusion of adjacent meroms is the complete (local) cessation of growth by accretion to individual meroms. In Figs 15–19, since we have plotted merom variables with respect to whorl-equivalent latitude (rather than simply distance from the nuclear pole), homologous meroms, on thalli of differing size, may be compared directly. The low latitude overlap of plots for thalli of various sizes, even when their plots diverge at higher latitudes, suggests that growth by accretion does indeed cease at the lower latitudes. Once again, this observation suggests progressive development of merom fusion, but it falls just short of actually demonstrating it.

More direct evidence of merom fusion is available through consideration of fossil breaks – i.e., ones that occurred prior to diagenesis. We can, of course, find any number of breaks that have occurred subsequent to diagenesis, and many of these do cut across merom heads and feet rather than along their boundaries (though as frequently in the upper, 'growing' parts of the thallus as in the lower, 'fused' portions). However, the course of these breaks was undoubtedly controlled more by properties of the matrix than by the condition of an enclosed assemblage of meroms. Examination of fossil breaks requires either a fortunate natural exposure or removal of matrix in the laboratory. Most 'margins of incompleteness' that we have been able to study on the scale of individual meroms actually seem to be the results of disarticulation, rather than fracture. However, we

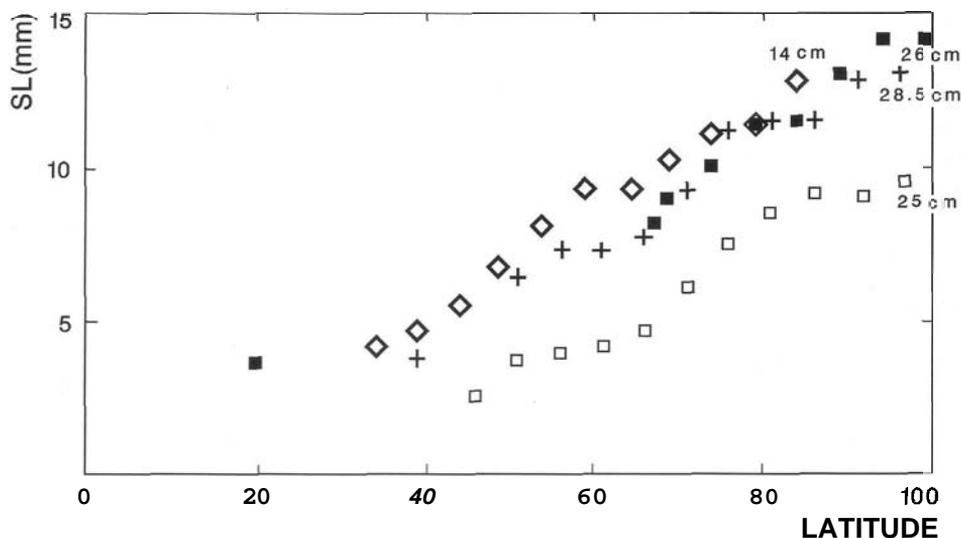


Fig. 18. Graph of merom shaft length (SL) vs. latitude (number of merom positions from nuclear pole) in *Fisherites reticulatus* (symbols as in Fig. 14). Thalassus bottom diameter (BD) is indicated at the right of each profile for which it is available.

have noted a few instances that seem to represent breakage, and sometimes even abrasion (Fig. 5D), across merom heads, and we therefore regard fusion of meroms on the corniculum and bottom of the thallus as an aspect of normal development. Fusion probably developed progressively away from the nuclear pole, as has been described by other workers (e.g., Foster 1973, Campbell *et al.* 1974), but it would take stronger evidence than we have at present to demonstrate this unequivocally.

Growth of receptaculitids

The marked latitudinal variation in merom size and shape and the well ordered array which meroms comprise have been treated by most workers as *prima facie* evidence that meroms were initiated in a particular sequence – i.e., that they neither appeared simultaneously in the development of the organism, nor were added entirely at random, at points dispersed over the thallus. Beyond this, however, there have been two interpretations as to the site of addition of new meroms to the thallus: either at the margin of the array nearest the lacunar pole (which may or may not, according to the interpreted life orientation, be uppermost) or at the nuclear pole, with accessory points of merom addition at, or in close association with, the intercalary meroms. Gould & Katz (1975) argued against the portion of the second interpretation requiring accessory points of initiation. They noted the concordance of growth lines with present plate margins and the approximate equality of numbers of growth lines on

intercalary merom plates and the adjacent plates of intercalated parastichies. Given these observations, intercalary and normal rhombic meroms must retain their identity throughout development of the thallus, and adjacent meroms must not have very dissimilar ages. Thus, new meroms cannot have been inserted into the midst of the array, in the vicinity of intercalary meroms (or at any other non-polar position).

Leaving aside the issue of accessory sites of merom addition, we may consider the relative likelihood of generation of new meroms at either the lacunar or the nuclear pole. As mentioned previously, it is not our goal to resolve this issue here. Nevertheless, our observations provide limited support for the former alternative. One argument, for which we claim no priority, concerns the relative number of meroms per whorl (or whorl-equivalent) occurring near each pole. This is the approach used by Rietschel (1969) for receptaculitids similar to *R. neptuni*, by Foster (1973) for *I. mammillaris*, by Campbell *et al.* (1974) for *H. borenorensis*, and by Gould & Katz (1975) for *I. barrandei* (though all of these authors differ in the weight they give to this argument). It holds that the number of meroms per whorl is more likely to increase during growth than decrease. While this does seem like the most probable scenario, its inverse is obviously not impossible.

A second argument, also used by Rietschel (1969) and Gould & Katz (1975), concerns the consistency (within species) of the small number of meroms surrounding the nuclear pole (Gould & Katz also consider the nature of these meroms - i.e., whether or not they are intercalary meroms). To retain the nuclear pole as the site of addition of new meroms, we would have to assume that merom addition had been completed in all preserved receptaculitids, and that, during development, the number of meroms per whorl typically decreased to some fixed number, after which no further addition occurred. Again, this seems unlikely - though not impossible. Since we have only one adequately exposed corniculum, we cannot yet in fact make this argument for *F. reticulatus*. However, if preparation of additional specimens shows that the number of meroms in the nuclear whorl is as constant here as it is in *I. barrandei*, then this line of reasoning will also be effective.

A third argument, also used by Foster (1973) and Campbell *et al.* (1974), involves the probable fusion of meroms near the nuclear pole. Since the meroms of at least the corniculum show some evidence of fusion on all specimens of *F. reticulatus*, presuming that meroms were added at the nuclear pole would, once again, necessitate the corollary that merom addition had ceased in preserved specimens.

A fourth argument is suggested, though not made explicitly, by Campbell *et al.* (1974). In both *H. borenorensis* and *F. reticulatus* fusion of meroms appears to develop progressively away from the 'enclosed' end of the thallus - i.e., on larger specimens, it seems to have extended to what we recognize as higher latitudes than on smaller specimens. If fusion of meroms is itself considered a developmental process, it seems most likely

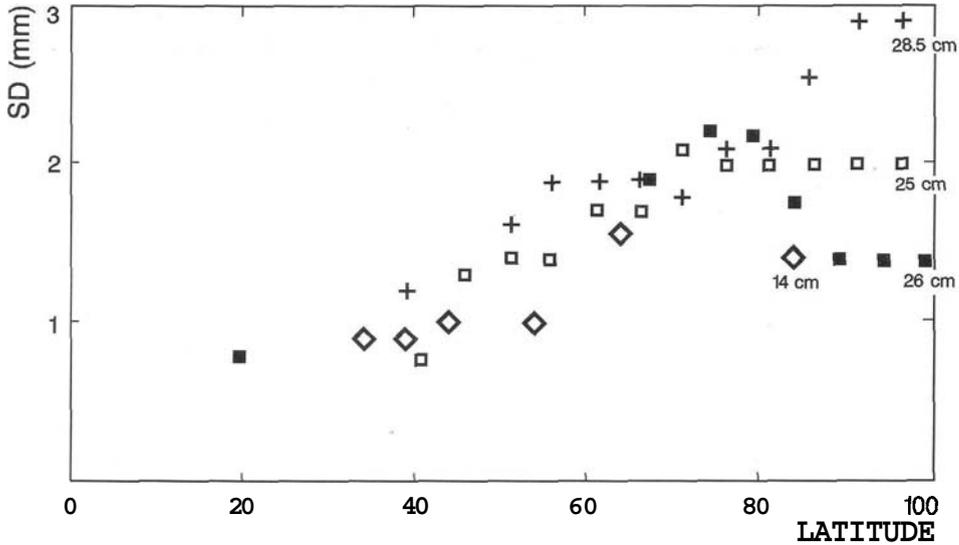


Fig. 19. Graph of merom shaft basal diameter (SD) vs. latitude (number of merom positions from nuclear pole) in *Fisherites reticulatus* (symbols as in Fig. 14). Thallosid bottom diameter (BD) is indicated at the right of each profile for which it is available.

that its polarity would parallel, rather than run counter to, other directional trends in merom development, including the siting of merom initiation. This favors addition of meroms in the vicinity of the lacunar pole.

These four arguments lend tentative support to the present interpretation of receptaculitid growth, though they really do no more than address the relative magnitude of probabilities. In any case, they are part of the basis for a growth scenario (closely paralleling that suggested by Rietschel 1969) for *F. reticulatus*. Skeletal growth would have begun with the initiation of the nuclear whorl of meroms, shortly after attachment of the 'juvenile' to an appropriate substrate (possibly by a pedicle located at the nuclear pole). Meroms continued to be generated at the margin of a lacuna centered over the lacunar pole. Addition of new meroms would tend to shift the relative topographic position of particular meroms to lower portions of the developing thallus, though merom position, measured in whorl-equivalents counted from the nuclear pole would remain constant. During growth, the number of meroms present at the margin of the apical lacuna would increase through the initiation of intercalary meroms. At first the thallus would probably have been an erect conical body. However, gradual or episodic 'toppling' of this cone, and subsequent alteration of the rates of accretion to individual meroms comprising it, would have produced the bent and twisted cornicula that are so common. After a period of growth in a recumbent orientation, rates of merom addition and accretion were altered so that the corniculum flared outward, with subsequent merom addition and accretion acting to 'roll' the top and sides of the thallus down to and across the substrate, forming the gradually expanding bottom.

This scenario allows us to suggest an interpretation of the relationship, noted above, between shape of the thallus bottom and grain size of the surrounding sediment. If the topography of the thallus bottom is controlled at least partly by the topography of the substrate over which it grows, higher rates of substrate aggradation, leading to significant local accumulations of sediment during the lifetime of an individual, should be associated with more convex bottoms. Such rates of aggradation would be more apt to characterize coarser than finer grained sediments. As an additional confirmatory observation, the relatively coarse grained sediments associated with more convex bottoms are often very well winnowed. This is consistent with the rates of sediment movement that would be necessary to cause convexity of thallus bottoms.

A final morphogenetic issue that we can address using this information concerns the question of how new meroms were added to the thallus – one at a time, in a spiral? in large sets that became whorls? or in some other pattern? Almost without exception, receptaculitids have been thought of as having their meroms organized in whorls. Where this is in fact the case, a verticillate mode of merom addition, with all members of a whorl added simultaneously, is probably the most likely, though not the only conceivable, mode of growth. In *F. reticulatus* however, whorls are clearly not the dominant mode of organization over most of the thallus. Moreover, the conspicuous latitudinal excursion of many circlets makes them unlikely candidates for sets of simultaneously generated meroms. We believe that the pattern of merom addition must have changed during growth, from initial addition of whorls, to patterns more characteristic of mature thalli. Although no specimen is sufficiently well preserved to show an undoubted locus of merom addition directly, we can reconstruct aspects of its appearance on the basis of merom arrangement at lower latitudes. Each of the small number of parallel circlets that must usually spiral toward the lacunar pole must end, at the margin of the apical lacuna, with a most-recently-generated member. If addition of meroms to these circlets occurred at regular intervals, these youngest meroms within each such circlet must be nearer in age to each other than any one of them is to an adjacent merom in its own circlet. Thus, these meroms must have been generated almost, if not exactly, simultaneously. At stages of growth when meroms are being formed within the latitudes where intercalary meroms occur, the exact pattern of merom addition must shift slightly whenever new intercalary meroms are generated. At most stages of merom addition, however, a relatively small number of meroms (usually considerably fewer than would occur in a whorl-equivalent at that latitude) must be added, more or less simultaneously, at points dispersed around the margin of the apical lacuna. This pattern of growth suggests that the exact siting and timing of merom addition in receptaculitids such as *F. reticulatus* is much more dependent on local factors on the growing apical region of the central axis than on any circumthallial integrating mechanism.

Systematics

Class Receptaculita (or -phyceae) Weiss 1954

Order Receptaculitida (or -ales) James 1885

Family Receptaculitidae (or -aceae) Eichwald 1855

Genus *Fisherites* Finney & Nitecki 1979

Type species: *Fisherites reticulatus* (Owen 1844).

Remarks. — Diagnosis given in Finney & Nitecki (1979b). The diagnostic features of *Fisherites* include thallus size and shape, quantitative characteristics of latitudinal gradients in merom number and morphology, internal structure of merom plates, and probably the number and arrangement of intercalary meroms on the corniculum.

Species included: *F. arcticus* (Etheridge 1878); *F. burmensis* Rietschel & Nitecki 1984; *F. camacho* (Nitecki & Fomey 1978); *F. coreanicus* Niko & Ikebe 1988; *F. occidentalis* (Salter 1859); *F. orbis* (Eichwald 1840); ?*Fisherites* sp. (Kruse 1989).

Distribution. — Early to Late Ordovician of the United States, Canada, Greenland, and Argentina; Early to Middle Ordovician of Burma and Thailand; Middle Ordovician of North Korea; Middle and Late Ordovician of the Baltic Region.

Fisherites reticulatus (Owen 1844)

Note on synonymy: References to *F. reticulatus* number more than 100 and have been published separately (Nitecki *et al.* 1987). Therefore, they are not included here. An abbreviated synonymy, useful for clarification of nomenclatural issues, is given in Finney & Nitecki (1979b).

Remarks. — Diagnosis given in Finney & Nitecki (1979b). Since the types of *F. arcticus* have never been illustrated, it is difficult to distinguish this species from *F. reticulatus*. Roy's '*Receptaculites* sp.' (1941: Fig. 31C) is probably *F. arcticus*, but neither this specimen nor *F. arcticus* from Greenland (Troedsson 1926: Pls 48–50) show conspicuous differences from *F. reticulatus*. Hinde (1884) argued that *F. arcticus* can be distinguished by its wider plates (7 mm) and generally shorter merom shafts (10–20 mm). However, since each of these characters is dependent on latitude and thallus size, their significance is difficult to evaluate outside the context of more detailed measurements.

F. camacho is distinct from other members of the genus in its greater plate width and merom shaft diameter, and probably in the internal structure of its merom plates (it may not show the radial structure found in all others). Nitecki & Forney (1978) describe it as having a central knob on the abaxial plate surface, but it is possible that this is actually a weathered-out, simple version of the usual internal plate structure.

According to Hinde (1844) and Roy (1941), *F. occidentalis* is difficult to distinguish from *F. reticulatus*; Hinde even considered the two synonymous. However, its maximum observed thallus size is only about half that of *F. reticulatus*, and its bottom is much flatter. Other quantifiable differences involve latitudinal gradients in merom size and shape, and the much smaller size of its corniculum. Several specimens of *F. occidentalis* from its

type locality have extremely well preserved cornicula. Merom arrangement on these shows patterns that are similar to what we have described for *F. reticulatus*, differing mainly in exact numbers and latitudinal bounds (Fisher & Nitecki 1982).

F. orbis occurs stratigraphically lower than *F. reticulatus* and can apparently be distinguished by its smaller thallus and corniculum (holotype illustrated in Nitecki 1986).

Distribution. — Middle to Late Ordovician of Upper Mississippi Valley region; Late Ordovician of Colorado, Wyoming, west Texas, Manitoba, Northwest Territories, and possibly Greenland.

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Streszczenie

Receptaculit *Fisherites reticulatus* (Owen 1844) jest najpospolitszym przedstawicielem tej grupy skamieniałości w środkowym i późnym ordowiku Ameryki Płn. Liczne znaleziska osrodek jego szkieletow pozwalają na szczegółowe odtworzenie przebiegu wzrostu i ułożenia poszczególnych elementów szkieletowych (meromow)