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Organic-Walled Microphytoplankton of the Sylvan Shale (Richmondian: Upper Ordovician), Arbuckle Mountains, Southern Oklahoma, U.S.A.

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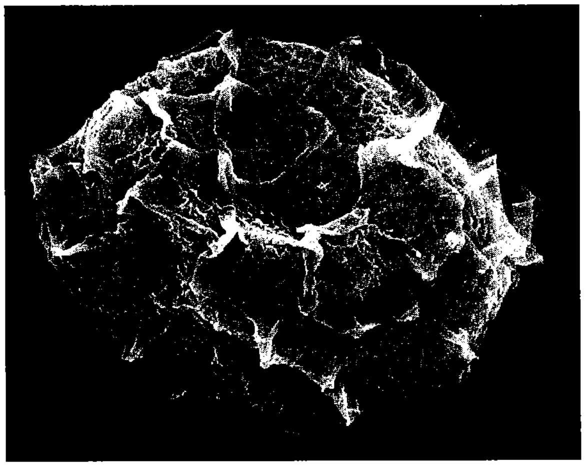

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Cover Illustration

Dictyotidium tappaniae, a new species of prasinophycean green algae from the Upper Ordovician Sylvan Shale, Oklahoma. This specimen measures 46 µm in diameter.

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ABSTRACT.—A diversified and well-preserved suite of organic-walled microphytoplankton (acritarchs and prasinophyte phycomata) is detailed from the Lawrence Quarry section of the Richmondian (Upper Ordovician) Sylvan Shale in the Arbuckle Mountains region of southern Oklahoma, U.S.A. The palynoflora consists of 25 genera and 42 species (including two undifferentiated species-groupings); 23 genera and 40 species of these are acritarchs, and two genera and species are prasinophytes. One new acritarch genus, *Amsdenium*, is established and typified by *A. velatum* Playford and Wicander, new species. The other five newly proposed acritarch species are *Baltisphaeridium curtatum, Caelatosphaera cerebella, Cheleutochroa clandestina, Lophosphaeridium sylvanium,* and *Micrhystridium viriosum. Dictyotidium tappaniae* is the single new prasinophyte species.

The Sylvan palynoflora closely resembles those reported from the Maquoketa Shale of northeastern Missouri and northeastern Kansas and the Vauréal Formation of Anticosti Island, Québec, Canada. Both have been dated as Richmondian from graptolite and conodont evidence. Hence, the Sylvan assemblage has the clear potential for stratigraphic-correlative application within upper Cincinnatian successions of North America. Moreover, the assemblage includes certain acritarch species that occur widely beyond North America, and these serve to reaffirm its Late Ordovician (Ashgill) age.

Paleontologic and sedimentologic data indicate that the Sylvan Shale accumulated in a warm, low-energy, offshore-marine environment with oxygen-deficient bottom conditions. The composition of the palynoflora retrieved from the four composite samples correlates well with models of offshore, open-marine microphytoplankton associations proposed by previous authors and also with a published paradigm linking microphytoplankton diversity trends with paleoenvironment.

The microphytoplankton suites that characterize the coeval Sylvan Shale, Maquoketa Shale, and Vauréal Formation represent a distinct palynostratigraphic assemblage of the low-latitude Laurentian region during the Late Ordovician (Ashgill). Whereas undoubted provincialism existed during the Early and Middle Ordovician, some of the Sylvan-Maquoketa-Vauréal microphytoplankton taxa have been reported from middle- to high-latitude Ashgill localities elsewhere, such as Baltica and the Peri-Gondwana region, thus corroborating a diminished provincialism during this time. Several taxa are known presently only from Laurentia, and these may prove valuable in recognizing low-latitude or warm-water assemblages elsewhere.

INTRODUCTION

The abundance and diversity of organic-walled microphytoplankton in Proterozoic through lower and middle Paleozoic marine sedimentary successions have come to be well-recognized globally in recent decades. Particularly important is their value in local, regional, and international stratigraphic correlations and their contributions to paleoenvironmental and paleogeographic syntheses. Study of these intriguing and morphologically intricate palynologic microfossils presents many rewards and opportunities, most importantly biostratigraphic, and also some tantalizing challenges, especially the determination of their biologic affinities. A relatively small proportion of these microfossils are now accepted as representing cysts (or phycomata) that constitute part of the life cycle of the still-extant prasinophytes. The Prasinophyceae, which is a class of mainly marine green algae, was largely supplanted, from the Late Triassic onward by the cyst remains of another algal group, the dinoflagellates (Tappan, 1980). Most of the pre-Triassic organic-walled microphytoplankton are still unassigned (although not necessarily unassignable) biologically. These are consigned to the informal and undoubtedly polyphyletic taxonomic group, the Acritarcha Evitt, 1963. Recent reviews of Proterozoic–Paleozoic organic-walled microphytoplankton include those by Martin (1993), Wicander (2002), Playford (2003), and Mendelson and Wicander (in press), together with several chapters in the comprehensive palynologic treatise edited by Jansonius and McGregor (1996).

Impressively high levels of microphytoplankton productivity and variety are documented by palynologic assemblages obtained from Ordovician marine strata in many parts of the world. This is particularly true of the Lower Ordovician, which has been more intensively studied palynologically than the Upper Ordovician.

The prime purpose of this study is to provide a detailed taxonomic analysis of acritarchs and prasinophytes retrieved from several samples collected from an Upper Ordovician quarry exposure in southern Oklahoma. Strata at this site were known from prior, essentially reconnaissance studies (Hedlund, 1960; Loeblich and Tappan, 1978) to contain rich assemblages of these palynomorphs. This has facilitated our evaluation of the biostratigraphic, paleoenvironmental, and paleogeographic significance of the microfossils.

GEOLOGIC SETTING

Ordovician rocks are exposed in the Appalachian Mountains as a more or less continuous meridional belt from Québec to Alabama. Smaller, more localized Ordovician exposures occur to the west in the North American Midcontinent region. In southern Oklahoma, three areas include Ordovician outcrops: (1) the Wichita Mountains in the west, (2) the Arbuckle Mountains in the center, and (3) the Ouachita Mountains in the east, which extend into southwestern Arkansas (Goldman and Bergström, 1997, text-fig. 1).

The geologic province traditionally termed the Arbuckle Mountains occupies a nearly triangular area of 2,600 km^2, constituting a substantial inlier of folded and faulted Precambrian and Paleozoic rocks. It is overlapped to the east, north, and west by gently westward-dipping Pennsylvanian and Permian strata and to the south by gently southward-dipping Cretaceous sediments of the Gulf Coastal Plain. As Ham (1969, p. 5) remarked, the term Arbuckle Mountains, as used in a geologic context, is something of a misnomer in that most of the terrane is not mountainous or even hilly. In fact, about 80% of the Arbuckles is topographically subdued, consisting of gently undulating plains.

The geology of the Arbuckles is characterized by outcrops of uplifted, variably deformed Paleozoic carbonates (predominantly) and fine clastics, contrasting with coeval flysch facies prevalent in the Ouachitas to the east. Ham (1969, p. 5) further commented that the approximately 3,400 m of fossiliferous, shallow marine, Upper Cambrian through Devonian strata in the Arbuckle Mountains "constitute the best outcrops and greatest area of exposure of [these strata] in all the Midcontinent region." In structural terms, the Arbuckles are divisible into three areas. From west to east and northeast, these constitute the genuinely mountainous Arbuckle Uplift or Anticline (of the southern Oklahoma aulacogen), the Tishomingo block, and the Hunton Uplift or Arch (Tapp, 1988; Al-Shaieb and others, 1993; Denison, 1997). The three areas, separated respectively by the prominent, high-angle Washita Valley and Reagan Faults, reflect differing tectono-sedimentary styles, with the aulacogen having experienced the greater subsidence and more intense tectonism. The main period of deformation, notably wrench-faulting and uplift, is Late Pennsylvanian; however, lesser deformation, indicated by minor unconformities, may have occurred during the Devonian (Tapp, 1988, p. 179).

Compared with the aulacogen (Arbuckle Uplift), the sediments of the Hunton Uplift (whence the Sylvan Shale samples of this study were collected) are only mildly deformed and generally less well exposed (Denison, 1997, p. 45). Al-Shaieb and others (1993, figs. 3, 4, excursion stops 8–10) provided details of some of the better sections in the Hunton Uplift, including its northern (Lawrence) sector. The wholly marine, Upper Ordovician through Devonian part of the sequence in the Hunton Uplift consists of, in ascending order: (1) Sylvan Shale (Upper Ordovician: Richmondian); (2) Chimneyhill Subgroup (= lower part of Hunton Group), consisting of Keel Limestone or Formation (Upper Ordovician, Gamachian) and Cochrane and Clarita Limestones (Silurian); (3) upper part of the Hunton Group, consisting of the Henryhouse Formation (Silurian) and three Lower Devonian formations (Haragan, Bois d'Arc, and Frisco); and (4) the Woodford Shale (Upper Devonian).

SYLVAN SHALE STRATIGRAPHY

The Sylvan Shale was named by Taff (1904) from exposures near the town of Sylvan, Johnston County, in south-central Oklahoma. The Sylvan Shale is a distinctive lithostratigraphic unit sandwiched between the more resistant and much thicker carbonate strata of the Viola Group (below) and the Chimneyhill Subgroup (above). The Sylvan Shale is developed throughout the Arbuckle Mountains and contiguous southern Oklahoma regions. It forms part of a widespread epicratonic sheet of anoxic, fine-clastic, Upper Ordovician sediments that extends, at the surface and in the subsurface, westward to northwest Texas, eastward to the Ouachita Mountains (where it is mapped as the Polk Creek Shale), and northward (as the Maquoketa Shale) into Kansas, Missouri, and Iowa, and into the Upper Mississippi Valley.

Physical Stratigraphy

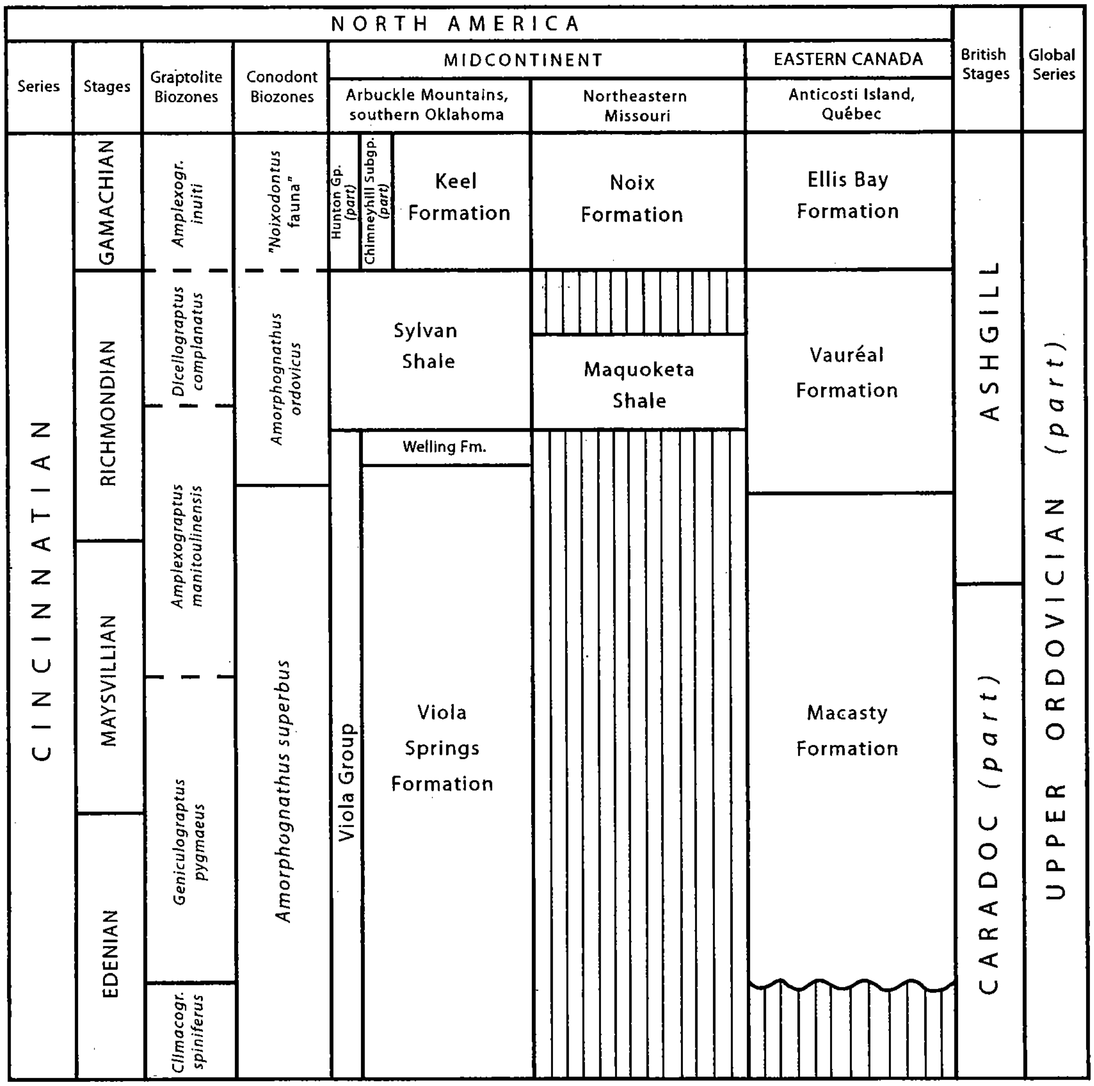
The Sylvan Shale is divisible, characteristically but informally, into two parts in the Arbuckle Mountains (Jenkins, 1970, p. 263; Amsden, 1980, p. 10). The lower part, up to about 40 m thick, consists of somewhat indurated, fissile, brown and medium- to dark-gray shale containing graptolites, especially near the base. The upper portion is up to about 61 m thick (though commonly thinner than the lower part of the Sylvan) and is composed of friable, less-fissile or concretionary, greenish-gray shale with few graptolites. Carbonate content is variable. The formation is typically only slightly calcareous, but locally includes (especially in the upper 30 m) some highly calcareous interbeds. The recessive nature of the formation is expressed by typical gully- or valley-type exposures. The Sylvan exhibits considerable variation in thickness (from about 8 to 130 m), and its greatest thickness occurs in the southern Oklahoma aulacogen (Johnson, 1991, p. 8; Denison, 1997, fig. 6).

Where preserved in cored sections or exposed in the field (albeit uncommonly because of limited outcrop), the upper and lower boundaries of the Sylvan Shale are generally recognizable by their marked lithic contrast with sub- and suprajacent rock units (i.e., the limestone of the Viola Group and the oolitic Keel Limestone, respectively). Such contrasts tend to imply depositional hiatuses, but independent physical evidence is either lacking or inconclusive in that regard. Some authors (e.g., Ham, 1969; Jenkins, 1970, p. 261; Dworian, 1990, p. 14) maintained that the Sylvan is bounded by disconformities. Others (notably Amsden, 1960, 1975, 1980; Amsden and Sweet, 1983; Denison, 1997), however, have been less certain, and it seems likely that the stratigraphic relationships (i.e., depositional breaks, if present) may vary locally and regionally.

Biostratigraphy

The Sylvan Shale is less fossiliferous in its megafossil content than the underlying and overlying rock units (Viola and Hunton Groups, respectively). For instance, Amsden (*in* Amsden and Barrick, 1988, p. 17) pointed to the absence of articulate brachiopods and other invertebrate fossils that might be expected in marine strata of this age. In contrast, graptolites are abundant (if not particularly diverse) in the lower part of the Sylvan, although they are meager, at best, in the upper part of the formation (e.g., Decker 1935; Ham, 1969; Jenkins, 1969; Dworian, 1990). Palynologic microfossils (chitinozoans and acritarchs) have been reported as plentiful and diverse in the Sylvan (Hedlund, 1960; Jenkins, 1970), whereas conodonts have been mentioned only incidentally (e.g., Goldman and Bergström, 1997).

From paleontologic data, the Sylvan Shale is securely dated within the Late Ordovician (Text-fig. 1). Based on chitinozoan assemblages, Jenkins (1970) assigned the formation to the Western European Ashgill Stage. More definitive chronological evidence has been presented by Goldman and Bergström (1997) in their comprehensive survey of Ordovician Midcontinent graptolite faunas. They attributed at least the bulk of the Sylvan to the *Dicellograptus complanatus* graptolite Biozone, with the lowermost part of the Sylvan possibly representing the "very uppermost part" of the *Amplexograptus manitoulinensis* graptolite Biozone. The scant conodont data suggested the equivalence of the Sylvan to the biostratigraphically compatible *Amorphognathus ordovicicus* conodont Biozone. Ac-



Text-figure 1. Chronostratigraphic correlation of Richmondian palyniferous formations (Sylvan Shale, Maquoketa Shale, and Vauréal Formation) within the North American Cincinnatian succession. Based mainly on Goldman and Bergström (1997); also Jacobson and Achab (1985), Amsden and Barrick (1986), and Al-Shaieb and others (1993).

cordingly, Goldman and Bergström (1997, p. 976–978, text-figs. 6, 8, 9) assigned the Sylvan Shale to the Richmondian Stage (within the Cincinnatian Series and correlative in part with the Ashgill; Text-fig. 1), and correlated it with the *Dicellograptus gravis* graptolite Biozone (Ea4; Ashgill) in Victoria, southeastern Australia (Vandenberg and Cooper, 1992).

DEPOSITIONAL ENVIRONMENT

The Sylvan Shale accumulated in a marine environment unfavorable to both sessile and vagrant benthos but clearly conducive to preservation of the organic-walled chitinozoans, scolecodonts, and microphytoplankton, and the delicate rhabdosomes of planktic graptolites. The very fine (mainly clay-sized), moderately carbonaceous, terrigenous clastics that characterize the formation also indicate low-energy, euxinic conditions—evidently lower energy than the immediately sub- and suprajacent carbonate units (Denison, 1997, p. 44, 45).

Water depth in this Sylvan depositional setting is speculative (e.g., Ham, 1969; Dworian, 1990; Denison, 1997), although it was obviously sufficient to establish anaerobism and would appear to signify post-Viola deepening.

PREVIOUS PALYNOLOGIC STUDIES

Palynologic knowledge of marine Ordovician strata in North America is not extensive, although many of the reported palynomorphs are from sections that have been reliably and independently dated by their invertebrate faunas (Wicander and others, 1999; Wicander, 2004). Certainly, ample opportunities exist for the application of studies of organic-walled microphytoplankton (acritarchs, prasinophytes) and chitinozoans, in zoning and correlating North American Ordovician successions and in contributing to paleoenvironmental and paleogeographic reconstructions. Text-figure 2 shows that publications reporting Upper Ordovician microphytoplankton date from 1965, when Staplin and others described four species of acritarchs from the subsurface of Anticosti Island, eastern Canada. Subsequent authors have described or recorded acritarchs and prasinophytes from various Midcontinent locations and elsewhere in North America (Text-fig. 2). However, few of the papers have documented the palynofloras in comprehensive taxonomic detail or recorded the stratigraphic ranges of the taxa. In many instances, the described and illustrated forms consist of a few selected and morphologically distinctive species extracted from spot samples, rather than from systematic collecting of measured and well-documented stratal sections.

Wilson (1958) referred briefly to the occurrence of chitinozoans in the Sylvan Shale, but a master's thesis by Hedlund (1960) was the pioneering palynologic study of the formation. Hedlund documented chitinozoans, acritarchs, and scolecodonts from three exposures of the Sylvan Shale, two of them in the Lawrence Quarry. Hedlund's work remains unpublished, aside from a conference abstract and description of one chitinozoan species (Wilson and Hedlund, 1962, 1964, respectively).

Two monographic studies of Upper Ordovician chitinozoan assemblages of the Arbuckle Mountains region were published by Jenkins (1969, 1970). The latter paper focused on the Sylvan Shale exposed in the Sycamore Creek Anticline (Jenkins, 1970, p. 265, fig. 1), some 55 km south of the Lawrence Quarry (Text-fig. 3). Jenkins (1970) described 12 species (five new) of Chitinozoa. He confirmed a Late Ordovician age (Richmondian; Ashgill) for the Sylvan and effectively laid to rest some earlier suggestions that the formation might be Silurian, at least in part. One portion of Mendelson's (1981) doctoral dissertation concerned acritarchs and prasinophytes from Jenkins's (1970) Sycamore Creek locality, but the work remains unpublished.

Various distinctive acritarch species from the Sylvan Shale of the Lawrence Quarry have been described in commendable detail, along with forms from other pre-Devonian rocks of the Midcontinent (Loeblich, 1970a; Loeblich and Tappan, 1978). However, the latter authors gave only scant attention to the stratigraphic distribution or significance of their described phytoplankton taxa. Furthermore, they did not attempt detailed systematic analysis of the phytoplankton assemblages. Consequently, the current paper is the first to provide a comprehensive systematic coverage, both qualitatively and quantitatively, of organic-walled microphytoplankton from a representatively sampled section of the Sylvan Shale.

Palynologic studies of strata coeval with the Sylvan Shale (Text-fig. 2), especially of the Maquoketa Shale to the north, are particularly relevant, because they record many species present in our samples. The Maquoketa publications are Wright and Meyers (1981; northeastern Kansas), Miller (1991; northeastern Missouri), and Wicander and others (1999; also northeastern Missouri). Also important is Jacobson and Achab's (1985) account of the acritarch flora of the Vauréal Formation (Québec). A brief report by Wicander and Playford (1999) on the acritarch flora of the Bill's Creek Shale and overlying Stonington Formation (both Richmondian) of the Upper Peninsula of Michigan points to affinities with the Sylvan, Maquoketa, and Vauréal assemblages. Our planned additional work on this Michigan material is expected to provide more definitive data in this regard.

MATERIAL AND METHODS

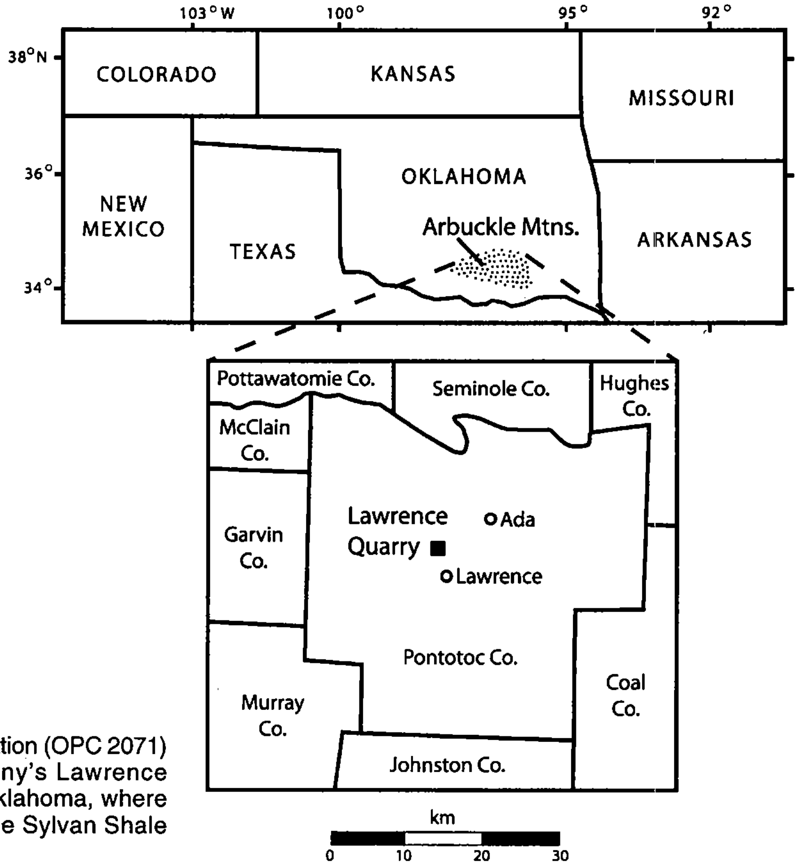
Lawrence Quarry: Description and Samples

Samples for this study were collected from the upper part of the Sylvan Shale from the Ideal Portland Cement Company's Lawrence Quarry in Pontotoc County (SW¼NE¼ sec. 36, T. 3 N., R. 5 E.), Oklahoma, near Lawrence, about 8 km southwest of Ada (Text-fig. 3; locality OPC 2071). This quarry, in the northern (Lawrence) sector of the Hunton Uplift, provides exposures of the following lithostratigraphic units (in ascending order): Sylvan Shale, Keel Formation, and Cochrane Formation (Text-fig. 4).

A total thickness of 15.2 m of the Sylvan Shale is exposed in the Lawrence Quarry from the floor to the contact with the overlying Keel Formation. In this quarry, the Sylvan consists of light-gray to greenish-gray shale and calcareous shale ranging

Author/date	Location	Formation	Age
Staplin and others (1965)**	Québec (Anticosti Island); Jacobson and Achab (1985, p. 167-168, text-fig. 1)	Vauréal Formation (Jacobson and Achab, 1985; Jacobson, 1987)	Richmondian (Ashgill)
Loeblich (1970a)**	Oklahoma; Loeblich and Tappan (1978, text-fig. 1, locality 8 = collecting site of samples analyzed herein, see Figs. 3, 4, this paper)	Sylvan Shale	Richmondian (Ashgill)
Loeblich (1970b)*	Indiana; Loeblich (1970b, p. 43)	Dillsboro Formation	Maysvillian (Caradoc)
Loeblich and Tappan (1971)**	Indiana; Loeblich and Tappan (1978, text-fig. 1, locality 5)	Eden Formation	Edenian (Caradoc)
Tappan and Loeblich (1971)**	Indiana; Loeblich and Tappan (1978, text-fig. 1, locality 5), Tappan and Loeblich (1971, p. 390)	Eden and Dillsboro Formations	Edenian, Maysvillian (Caradoc)
Loeblich and MacAdam (1971)**	Indiana, Oklahoma; Loeblich and Tappan (1978, text-fig. 1, localities 5, 8)	Eden Formation, Sylvan Shale	Edenian, Richmondian (Caradoc, Ashgill)
Cramer (1971)**	Ohio; Cramer (1971, p. 106)	Maysville Formation	Maysvillian (Caradoc)
Loeblich and Tappan (1978)**	Various Midcontinent states and localities; Loeblich and Tappan (1978, text-fig. 1)	various (including Sylvan Shale); Loeblich and Tappan (1978, text-fig. 2)	Edenian-Richmondian (Caradoc-Ashgill)
Jacobson (1978)*	Kentucky; Jacobson (1978, text-fig. 1)	Clays Ferry Formation; Jacobson (1978, text-fig. 2)	Edenian (Caradoc)
Martin (1978)**	Newfoundland; Martin (1978, p. 73, fig. 12.1)	Winterhouse Formation	Caradoc and ?late Ashgill
Jacobson (1979)**	Kentucky, Ohio, New York; Jacobson (1979, text-figs. 1, 2)	various; Jacobson (1979, text-figs. 3-6)	Maysvillian (Caradoc)
Colbath (1979, 1980)*	Indiana; Colbath (1979, p. 2; 1980, text-fig. 1)	Eden Formation	Edenian (Caradoc)
Martin (1980)*	Québec; Martin (1980, fig. 1)	White Head	Caradoc, Ashgill
Wright and Myers (1981)* or **	Kansas; Wright and Myers (1981, p. 4; fig. 1)	Viola Limestone / Maquoketa Shale	late Mohawkian or early Cincinnatian / Richmondian (Caradoc / Ashgill)
Legault (1982)*	Labrador Sea (Orphan Knoll)	unspecified (dredge sample)	late Caradoc-Ashgill
Martin (1983)**	Québec, Ontario; Martin (1983, p. 2-6, figs. 1, 4)	various; Martin (1983, fig. 2)	Edenian (Caradoc)
Jacobson and Achab (1985)*	Québec (Anticosti Island); Jacobson and Achab (1985, p. 167-168, text-fig. 1)	Vauréal Formation	Richmondian (Ashgill)
Miller and Williams (1988)*	Northwest Territories (Hudson Strait); Miller and Williams (1988, p. 121-122, text-fig. 1)	unspecified (cored bedrock samples)	probable Late Ordovician
Martin (1988)**	Québec (Anticosti Island); Martin (1988, p. 306-307)	Ellis Bay Formation	Gamachian (Ashgill)
Miller (1991)*	Missouri; Miller (1991, p. 218, fig. 1)	Maquoketa Shale; Miller (1991, fig. 2)	Richmondian (Ashgill)
Wicander and others (1999)*	Missouri; Wicander and others (1999, p. 3, fig. 2)	Maquoketa Shale; Wicander and others (1999, fig. 3)	Richmondian (Ashgill)
Wicander and Playford (1999)*	Upper Peninsula, northern Michigan; Wicander and Playford (1999, p. 267)	Bill's Creek Shale and Stonington Formation	Richmondian (Ashgill)

Text-figure 2. Published literature concerned exclusively (*) or partly (**) with Cincinnatian (Upper Ordovician) organic-walled microphytoplankton (acritarchs, prasinophyte phycomata) of North America. Chronostratigraphic correlations after Goldman and Bergström (1997) and Davis and Cuffey (1998).



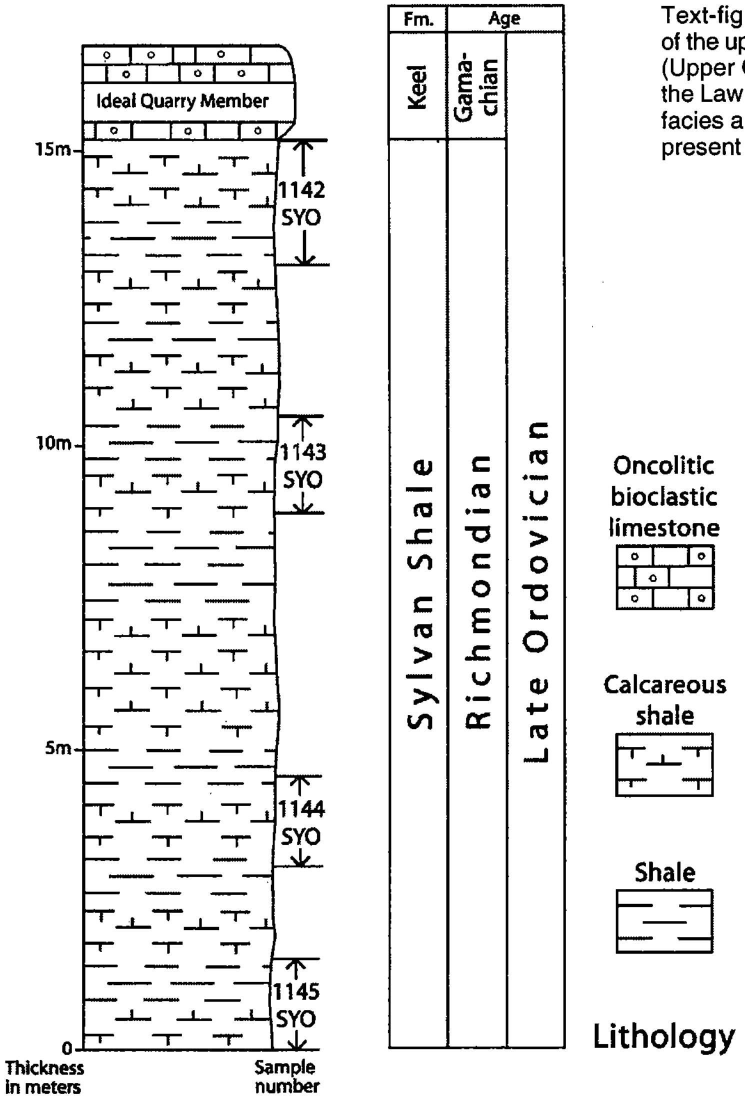
Text-figure 3. Map showing location (OPC 2071) of the Ideal Portland Company's Lawrence Quarry in Pontotoc County, Oklahoma, where the four studied samples of the Sylvan Shale were collected.

from somewhat friable to well-indurated. The contact of the Sylvan Shale with the underlying Viola Group is not exposed here.

Dworian (1990) identified only *Climacograptus tubuliferus* and *Climacograptus* aff. *C. angustus* from the Lawrence Quarry. On that basis, he placed the Sylvan Shale at this locality in the *Climacograptus manitoulinensis* graptolite Biozone of Riva (1974), which is equivalent to the *Amplexograptus manitoulinensis* graptolite Biozone of Goldman and Bergström (1997). However, as stated previously, the latter authors regarded only the lowermost part of the Sylvan Shale in the Arbuckle Mountains as possibly representing the uppermost *Amplexograptus manitoulinensis* graptolite Biozone. Although our Lawrence Quarry samples lacked graptolite megafossils, microscopic sicula and stipe fragments were fairly common in the palynologic residues.

Conformably overlying the upper portion of the Sylvan Shale is the 0.3–1.5 m thick Ideal Quarry Member of the basal Keel Formation (uppermost Ordovician). The member is an oncolitic, bioclastic limestone, consisting of clayey and silty carbonate mud. Ooids are sparse at the base of the member and increase upward toward the boundary with the upper part of the Keel Formation. The Ideal Quarry Member is richly fossiliferous, containing mostly brachiopods, gastropods, and pelmatozoans (Al-Shaieb and others, 1993). The contact between the Ideal Quarry Member and the rest of the Keel Formation is gradational and generally difficult to detect in outcrop. The upper part of the Keel consists of about 1.5–2.1 m of light-colored, cross-bedded, oolitic limestone that is generally unfossiliferous. Unconformably overlying the Keel Formation is the Silurian (Llandovery) Cochrane Formation, a richly fossiliferous, glauconitic limestone that is less than 5.5 m thick and forms the uppermost unit of the Lawrence Quarry exposure. A nodular chert bed at the base of the Cochrane Formation separates it from the underlying Keel Formation.

Four Sylvan Shale samples (suffixed SYO; Text-fig. 4) were collected in the quarry for this study. These are, in ascending order, with strati-



Text-figure 4. Stratigraphic section of the upper part of the Richmondian (Upper Ordovician) Sylvan Shale in the Lawrence Quarry, showing lithofacies and intervals sampled for the present study.

graphic levels measured from below the Sylvan Shale–Ideal Quarry Member contact: 1145 SYO, 15.2 (quarry floor)–13.7 m; 1144 SYO, 12.2–10.7 m; 1143 SYO, 6.1–4.6 m; and 1142 SYO, 2.1 m. They are composite samples intended to provide an overview of the total diversity and abundance of the organic-walled microphytoplankton through the Sylvan exposure at the Lawrence Quarry.

Laboratory Procedure

Laboratory preparation of the four samples followed the standard palynologic technique of successively dissolving 25 g of rock in cold HCl, HF, and HNO_3 to remove carbonates, silicates, and sulfides, respectively, and then neutralizing the residue in distilled water after each acid treatment. The resultant residue from each sample was filtered through 52 μm and 20 μm screens, yielding >52 μm, 20–52 μm, and <20 μm fractions. Slides of each fraction were prepared using either "Eukitt" or "Elvacite" as the mounting medium. At least 12 slides of the >52 μm fraction, at least six slides of the 20–52 μm fraction, and one slide of the <20 μm fraction were prepared from each sample for identification and counting of the acritarchs and prasinophytes. One hundred twenty five specimens in each of the >52 μm and 20–52 μm fractions were counted per sample (i.e., a total of 250 specimens per sample) for determination of relative abundances of taxa and for comparison between the four samples (Text-fig. 5). No counts were conducted on the <20 μm-fraction slides, although

Species Sample nos.→	1142 SYO	1143 SYO	1144 SYO	1145 SYO
Dictyotidium tappaniae	*	*		*
Leiosphaeridia spp.	c	c	a	c
Actipilion druggii	u	u	r	u
Amsdenium velatum	*	*	r	u
Aremoricanium squarrosum	*	*	r	*
Aremoricanium sp. A		*		
Baltisphaeridium adiastaltum	a	a	c	a
Baltisphaeridium aliquigranulum	u	c	u	u
Baltisphaeridium curtatum	a	c	u	u
Baltisphaeridium oligopsakium	a	c	c	c
Baltisphaeridium perclarum	a	a	a	a
Baltisphaeridium sp. A	*		*	
Caelatosphaera cerebella	u	*	r	*
Cheleutochroa clandestina	c	u	r	u
Comasphaeridium lanugiferum			r	*
Dactylofusa ctenista	*	*	r	r
Dorsennidium hamii	u	u	u	r
Dorsennidium undosum	r	r	r	u
Gyalorhethium sp. cf. *G. chondrodes*	r	r		
Gyalorhethium sp. A	*		*	*
Hoegklintia radicosa		*	*	
Lophosphaeridium sylvanium	r	u	u	u
Micrhystridium hirticulum		r	*	r
Micrhystridium prolixum	r	r	r	u
Micrhystridium viriosum	r	r	r	r
Micrhystridium sp. cf. *M. stellatum*	*	r	r	r
Micrhystridium sp. A	r			r
Multiplicisphaeridium bifurcatum	u	u	u	c
Multiplicisphaeridium irregulare	u	u	u	u
Navifusa ancepsipuncta	*	r	*	
Orthosphaeridium insculptum	r	r	r	r
Orthosphaeridium rectangulare	r	u	r	u
Peteinosphaeridium accinctulum	u	r	*	*
Peteinosphaeridium septuosum	r	r	r	r
Poikilofusa sp. A			*	
Polygonium gracile	r	c	c	a
Polygonium polyacanthum	*			*
Sylvanidium paucibrachium	*	*		
Tunisphaeridium eisenackii		*	r	*
Veryhachium oklahomense	u	u	c	c
Veryhachium trispinosum "complex"	a	c	c	u
Villosacapsula setosapellicula	r	*	*	*

Text-figure 5. Occurrence of organic-walled microphytoplankton species in the studied samples of the Sylvan Shale. Relative abundances of individual species, derived from counts of 250 specimens per sample, are specified as follows: v, very abundant (>25% of total acritarch/prasinophyte content); a, abundant (>10–25%); c, common (>5–10%); u, uncommon (1–5%); r, rare (<1%); asterisk (*) signifies presence in sample but not registered in the 250-specimen count.

these were examined to ensure that no small specimens had been excluded in the recovered assemblages.

Additional residues were prepared for picking of single specimens and their examination under the scanning electron microscope (SEM). Residues, in absolute ethanol, from both the >52 μm and 20–52 μm fractions, were allowed to dry on microscope slides. Acritarch and prasinophyte specimens were then picked from each fraction using a micromanipulator (Leffingwell and Hodgkin, 1971) and transferred to circular no. 1 coverslips (diameter 12 mm) pre-coated with a very thin adhesive. Each coverslip was mounted on an aluminum stub and gold-platinum-coated for SEM examination and imaging. Following SEM examination, each coverslip was permanently mounted (via "Eukitt") on a microscope slide, thus preserving the specimens for light-microscopic study.

Conventional light microscopy (LM) and Nomarski differential interference contrast examination were performed using an Olympus BH2 microscope and an Olympus BH microscope equipped with an automatic photomicrographic system. Specimens were photographed with Kodak black and white 35 mm ISO 400 film. A JEOL JSM–840A SEM instrument was utilized for detailed examination and electronic image capture.

Repository

All microphytoplankton specimens illustrated herein (Plates 1–28) are reposited in the Leonard R. Wilson Collection of Micropaleontology and Paleobotany within the Sam Noble Oklahoma Museum of Natural History, The University of Oklahoma, Norman, Oklahoma. The specimens listed in the Appendix are assigned catalog numbers OPC 2071-3819 through OPC 2071-3958.

SYSTEMATIC PALEONTOLOGY

Organic-walled microphytoplankton from the Sylvan Shale samples are predominantly of uncertain or equivocal biologic affinity. They are assigned accordingly to the *incertae sedis* palynomorph group Acritarcha, defined by Evitt (1963), and now widely accepted (e.g., Servais and others, 1997; Wicander, 2002; Playford, 2003). Exceptions in the studied palynoflora are representatives of the genera *Dictyotidium* Eisenack, 1955 emend. Staplin, 1961, and *Leiosphaeridia* Eisenack, 1958. Tappan (1980), among others, attributed both of these genera to the prasinophycean green algae.

Genera and species are treated below as form taxa in accordance with the International Code of Botanical Nomenclature (ICBN: Greuter and others, 2000). Morphologic terminology adopted herein is mainly compatible with that of Williams and others (2000). The prefix "micro" is used to signify morphologic details that are most clearly resolvable with SEM, such as ultra-fine sculpture of the eilyma (e.g., microreticulate). We emphasize our view that, whereas SEM observations commonly are extremely helpful and illuminating, taxonomic circumscriptions and identifications should be based primarily on LM observations and documentation.

Synonymy listings for species include the basionym followed, in temporal order, by citation of any recombinations, synonyms, and diagnostic emendations; or, in some instances, simply by reference to a listing provided in a previous publication. Type-species designations are abbreviated thus: OD, original designation; SD, subsequent designation; and M, monotypy.

Newly established taxa are described in detail and illustrated by LM and SEM photomicrographs. Several informally designated species are also described fully as are the majority of previously named species identified in our samples. Many of the latter species were instituted by Loeblich and Tappan (1978). These are represented herein by specimens that are classed as topotypes, because our samples were collected from the same location (Lawrence Quarry) and stratigraphic section as that of Loeblich and Tappan (1978, fig. 1, locality 8; here designated OPC 2071). Some of the Loeblich and Tappan species were diagnosed on the basis of few specimens (in some instances only one). Hence, a fundamental aim of our study is to circumscribe and illustrate those species more comprehensively—i.e., taking due account of intraspecific variation—from an appreciably larger specimen-base.

Measurements are presented in the following format, 4 (6.5) 10 μm, and represent minimum, mean, and maximum values, respectively.

Prasinophyte Phycomata

Division Chlorophyta Pascher, 1914

Class Prasinophyceae Christensen, 1962

Family Cymatiosphaeraceae Mädler, 1963

Genus **Dictyotidium** Eisenack,
1955 emend. Staplin, 1961

Dictyotidium EISENACK, 1955, p. 179.

Dictyotidium Eisenack, 1955 emend. STAPLIN, 1961, p. 417.

Melikeriopalla TAPPAN and LOEBLICH, 1971, p. 396.

Type species.—Dictyotidium dictyotum (Eisenack, 1938) Eisenack, 1955 [OD].

Discussion.—Dictyotidium Eisenack, 1955 emend. Staplin, 1961, differs from *Cymatiosphaera* O. Wetzel, 1933 ex Deflandre, 1954 in having less conspicuous muri that protrude only slightly from the vesicle margin. The rationale for establishing *Melikeriopalla* Tappan and Loeblich, 1971 and segregating it from other reticulate genera was modification or subdivision of the "fields" (lacunae enclosed by the relatively low muri) with "short, discontinuous micro-ridges" (Tappan and Loeblich, 1971, p. 396). The latter authors compared their genus with *Cymatiosphaera,* although comparison with *Dictyotidium* would have been more apposite because both it and *Melikeriopalla* possess low muri.

Eisenack and others (1979, p. 155) and Cramer and Díez (1979, p. 90) regarded *Melikeriopalla* as a junior taxonomic synonym of *Dictyotidium.* Colbath (1983, p. 257) suggested that the former's type species *M. amydra* Tappan and Loeblich, 1971 (p. 396, 398, pl. 6, figs. 1–4), unlike *Dictyotidium,* might possess "one blind tubular canal or pseudopore extending into the wall from the vesicle interior beneath the center of each polygonal field." However, following a personal communication (G. D. Wood, 1983), Colbath (1987, p. 65) recanted that idea, stating that *M. amydra* is not porate (or pseudoporate). As a corollary, he erected *Orygmahapsis* Colbath, 1987 (p. 66) to embrace three species of prasinophyte phycomata with a well-defined but not strongly projecting, comprehensive reticulum. *Orygmahapsis* was distinguished from *Dictyotidium* by the presence of a single pseudopore centrally located in each polygonal field (but not penetrating the eilyma surface as a puncta). Subsequently, Colbath (1990, p. 104) accepted the view, advanced by some previous authors (as above), that *Melikeriopalla* should be considered a junior synonym of *Dictyotidium,* because "the surface sculpture of the fields" was an insufficient basis for generic differentiation.

Mullins (2001, p. 47, 48) emended the diagnosis of *Melikeriopalla* to include both porate and aporate forms (if the former, the pores not piercing the eilyma surface), and treated *Orygmahapsis* as a junior synonym. This proposal contradicted or failed to take cognizance of Colbath's (1987, p. 65) statement, alluded to above, that "G. D. Wood . . . examined numerous specimens of *Melikeriopalla amydra* Loeblich & Tappan, 1971 (the type species) from Wenlockian strata in the United States, and did not observe psueudopores in any of them." However, the holotype of the type species (Tappan and Loeblich, 1971, pl. 6, fig. 3) was not diagnosed as porate or pseudoporate; indeed Colbath (1987, p. 65) revoked his earlier (1983) suggestion that such could be the case. Furthermore, Mullins's (2001) emendation departed considerably from Tappan and Loeblich's (1971, p. 396) diagnosis by abandoning any reference to a secondary reticulum within the primary lacunae, and by introducing a putative criterion not documented or illustrated by the original authors. Accordingly, we reject Mullins's (2001) version of *Melikeriopalla,* which, in any case, is not satisfactorily substantiated by his own photomicrographs of several specimens he claimed to represent *M. amydra.*

In accepting that *Dictyotidium* and *Melikeriopalla* are congeneric, we emphasize that the original, supposedly discriminative feature of the latter—i.e., finely sculptured-microreticulate lacunae delimited by the primary muri—is generally clearly discernible or demonstrable only via SEM study. This is true of the species newly instituted below, and, as noted by Cramer and Díez (1979, p. 90), may well apply also to some species of *Dictyotidium* defined exclusively or primarily on the basis of LM observations. The closely allied *Cymatiosphaera* likewise includes many species with psilate lacunae as well as those having secondarily reticulate or otherwise minutely sculptured lacunae—e.g., *C. adaiochorata* Wicander, 1974 (p. 12, pl. 7, figs. 6–9), *C. winderi* Deunff, 1967 emend. Playford, 1977 (p. 17, pl. 4, figs. 15–21), and *C. heloderma* Cramer and Díez, 1972 (see Le Hérissé, 1989, p. 73, 74, pl. 1, figs. 1, 5–8, 16, 17).

Dictyotidium tappaniae Playford and Wicander, new species

Plate 1, Figures 1–7

Diagnosis.—Vesicle originally spherical or subspherical; outline circular, subcircular, or oval. Eilyma ca. 0.7–1 µm thick, commonly distorted by compression folds; bearing comprehensive reticulum; muri well-defined, although very narrow (>0.5 µm wide) and low (ca. 0.4–1 µm high), enclosing irregularly polygonal lacunae 4 (6.5) 10 µm in maximum diameter. Lacunae very finely subdivided by secondary microreticulum consisting of very low, rounded muri anastomosing to enclose minute, irregularly polygonal lacunae; 1 or 2 minute, rounded, boss-like elements occurring within some of the lacunae, projecting from muri intersections. The secondary reticulation (i.e., within the primary lacunae) generally evident, if not sharply defined, with ×100 oil-immersion LM objective. SEM of several specimens provides the following dimensional data: width and height of secondary muri, 0.2 µm and 0.1 µm, respectively; maximum diameter of secondary lacunae, 0.2–2 µm; basal diameter and height of boss-like protuberances, 0.5–1 µm. Excystment by simple splitting of eilyma.

Measurements.—Diameter of vesicle 37 (45) 56 µm; based on 28 specimens.

Holotype.—OPC 2071-3819; sample/slide 1142 SYO/20-52 µm/2, field finder S10/3,3; Plate 1, Figure 1. Vesicle outline subcircular, diameter 45 µm; eilyma ca. 1 µm thick, with few compression folds; major (primary) reticulum comprehensively developed with narrow muri (ca. 0.4 µm wide, up to 1 µm high) enclosing variably polygonal lacunae 6–10 µm in maximum diameter; floors of latter modified by ultra-fine secondary reticulum and infrequent minute boss-like elements representative of 1 or 2 thickened intersections of the micro-muri in some lacunae; no excystment structure.

Derivation of name.—Patronymic for Helen Tappan Loeblich (1917–2004), distinguished micropaleontologist, in particular recognition of her innovative research in association with her husband Alfred R. Loeblich, Jr. (1914–1994), on lower Paleozoic microphytoplankton, including those of the Sylvan Shale.

Comparison.—Of the previously established and adequately illustrated species of *Dictyotidium* that are equipped with very fine secondary reticula, the one that bears closest resemblance to *D. tappaniae* Playford and Wicander, new species appears to be the upper Silurian–Lower Devonian species *D. biscutulatum* Kiryanov, 1978 (p. 39, 40, pl. 5, figs. 1, 6), also described by Colbath (1983, p. 258, 259, figs. 31–33), Wicander (1986, p. 339, pl. 3, figs. 1, 2), and Le Hérissé (1989, p. 108, pl. 3, figs. 14, 15, 17). However, *D. tappaniae* differs from *D. biscutulatum* in that its primary reticulum is composed of narrower, more delicate muri, and in having boss-like projections associated with its secondary reticulum. *Dictyotidium tappaniae* is also comparable with *D. perlucidum* Le Hérissé, 1989 (p. 110, pl. 3, figs. 10, 11) but differs in having a larger vesicle and boss-like projections.

Occurrence.—OPC 2071, Sylvan Shale samples 1142, 1143, 1145 SYO (present study).

Family Leiosphaeridiaceae Timofeev, 1956 nom. corr. Mädler, 1963

Genus **Leiosphaeridia** Eisenack, 1958

Type species.—*Leiosphaeridia baltica* Eisenack, 1958 [OD].

Leiosphaeridia spp.

Plate 2, Figures 1–3

Remarks.—Simple, psilate, originally spherical vesicles, with diameters ranging from ca. 40 µm to 130 µm, are fairly common in the study samples. In their strongly compressed preservational state, the eilyma is normally conspicuously folded, resulting in variable (irregularly subcircular) vesicle outlines. All the specimens are attributable to *Leiosphaeridia* Eisenack, 1958 (p. 2–5) but no attempt is made to speciate them.

Acritarchs

Group Acritarcha Evitt, 1963

Genus **Actipilion** Loeblich, 1970

Type species.—*Actipilion druggii* Loeblich, 1970 [OD].

Discussion.—Retention of *Actipilion* Loeblich, 1970 (1970a, p. 710) as a genus separable for instance from *Baltisphaeridium* Eisenack, 1958 ex Eisenack, 1959 emend. Eisenack 1969 (p. 249) is considered justified, mainly by the notably thin, diaphanous wall of its hollow processes that, although lacking internal communication with the vesicle cavity, are devoid of any form of basal plug. In a detailed reappraisal of *Multiplicisphaeridium* Staplin, 1961, Sarjeant and Vavrdová (1997, p. 15) compared that genus with *Actipilion*. They stated that *Actipilion* is distinguishable by "the strong difference in appearance between the dense central body and the filmy, fragile processes, which do not branch distally." Of these distinctions, the most salient is, clearly, the unbranched processes borne by *Actipilion*.

Actipilion druggii Loeblich, 1970

Plate 2, Figures 4–7; Plate 3, Figures 1–5

Actipilion druggii LOEBLICH, 1970a, p. 711, fig. 3A–E.

Description.—Vesicle originally spherical, outline circular or nearly so, distinct from processes. Eilyma relatively thick (1.2–2.1 µm), psilate to scabrate or microrugulate; bearing a variable number (generally 9–22; uncommonly up to 30) of discrete, hollow, spine-like, homomorphic processes, typically curved or sinuous, ranging in length from 21 µm to 60 µm (but fairly uniform on a given specimen, often within range of 30–45 µm). Processes not communicating with vesicle due to continuity of eilyma across their bases; process wall very thin (ca. 0.2–0.3 µm thick), hence of diaphanous appearance and prone to corrosion (irregular pitting); surface scabrate; proximal process contacts angular to slightly curved. Processes tapering uniformly from circular–subcircular bases, 3 (4.5) 8 µm in diameter, to simple acuminate or blunted tip. Excystment structure consisting of a simple split in eilyma.

Measurements.—Diameter of vesicle 40 (54) 73 µm; based on 56 specimens.

Remarks.—Although showing appreciable morphologic variation, *Actipilion druggii* Loeblich, 1970 is readily identifiable as a cohesive specific entity that forms a characteristic although not abundant component of the Sylvan Shale palynoflora. Perhaps its most striking feature is the filminess (and hence fragility) of the hollow processes vis-à-vis the robustness and darker color of the vesicle (Pl. 3, Figs. 1–3). The chief variables are process length, number of processes per vesicle, and the surficial character of the eilyma (cf. Pl. 2, Figs. 5, 7; Pl. 3, Fig. 5). Corroded specimens of *A. druggii* tend to have processes, and to a lesser degree vesicles, that have irregularly pitted walls. In some specimens, the processes may be partly lacking or even entirely removed, with only the circular scars of attachment to the eilyma remaining.

Occurrence.—OPC 2071, Sylvan Shale samples 1142 SYO through 1145 SYO (present study); also Loeblich (1970a). Maquoketa Shale (Richmondian), Kansas and Missouri, U.S.A. (Wright and Meyers, 1981; Miller, 1991). Possibly from the Upper Ordovician of Newfoundland, Canada (Martin, 1978) and Libya (Molyneux, 1988).

Genus **Amsdenium** Playford and Wicander, new genus

Type species.—Amsdenium velatum Playford and Wicander, new species, here designated (the single included species).

Diagnosis.—Vesicle originally spherical; outline circular or subcircular. Eilyma apparently unilayered. One polar or apical region of vesicle extended to form a cylindrical neck-like structure terminating in a circular excystment opening (pylome). Eilyma bearing solid processes of spine-like form. Processes linked by thin membranous muri to form a delicate reticulum.

Derivation of name.—Patronymic for Thomas W. Amsden (1915–2000), formerly of the Oklahoma Geological Survey, in recognition of his outstanding contributions to geologic knowledge of the Arbuckle Mountains and adjacent regions of southern Oklahoma (see Chaplin and Barrick, 1992; Mankin, 2000).

Comparison.—In its general appearance, *Amsdenium* Playford and Wicander, new genus shows some resemblance to *Aremoricanium* Deunff, 1955 (p. 228), but is readily differentiated from the latter by possessing membranous muri connecting and supported by the spine-like processes. That distinction likewise applies, *inter alia*, with respect to *Aryballomorpha* Martin and Yin Leiming, 1988 (p. 112, 113) and *Lua* Martin and Yin Leiming, 1988 (p. 118, 120).

Amsdenium velatum Playford and Wicander, new species

Plate 3, Figures 6, 7; Plate 4, Figures 1–5, 7, 8

Diagnosis.—Vesicle originally spherical, with circular or subcircular outline. Eilyma ca. 0.8–1.5 µm thick, psilate, commonly folded peripherally; bearing solid, psilate, spine-like processes narrowing conspicuously from broad bases (1.5–4 µm in diameter; 3–7 µm apart) to tenuous, thread-like distal portion with acuminate or evexate tip. Processes (if fully intact) ca. 10–16 µm long with curved proximal contacts. Very thin, hyaline membrane interconnecting processes to form a high, delicate reticulum. Relatively squat, hollow, thin-walled, psilate, ± cylindrical protrusion, with circular excystment aperture (pylome), constituting a neck-like, process-free extension of one vesicle polar region; width of neck uniform or slightly diminishing distally; interior freely communicating with vesicle cavity; no operculum observed.

Measurements.—Diameter of vesicle 24 (31) 39 µm; based on 86 specimens. Length and basal diameter of neck 5.5 (8.5) 11 µm and 6 (9) 12.5 µm; based on 50 specimens.

Holotype.—OPC 2071-3835; sample/slide 1144 SYO/20-52 µm/5, field finder T6/2,0; Plate 4, Figure 1. Vesicle outline circular, diameter 31 µm; eilyma ca. 1 µm thick, conspicuously folded peripherally; solid, elongate, spine-like processes 11–15 µm long, with robust bases 2–4 µm wide, tapering rapidly distally; very thin membranous muri, strengthened by processes, forming delicate reticulum (partly preserved); well-developed, hollow, cylindrical, neck-like structure 10 μm wide, 5 μm long.

Derivation of name.—Latin, *velum*, veil, sail, curtain; in reference to the membranous linkages between processes.

Remarks and comparison.—Among the numerous specimens of *Amsdenium velatum* Playford and Wicander, new species, only the best-preserved—serving as the basis for the above diagnosis—retain both an intact neck and at least vestiges of the diaphanous membranous muri supported by the processes. Equally vulnerable to damage or removal are the long, sharply attenuated, and threadlike distal portions of the processes. Most specimens (e.g., Pl. 4, Figs. 4, 8) are degraded to a greater or lesser degree, consisting of a rounded vesicle bearing coarse, blunted, conical projections that are basal remnants of broken processes. Moreover, many specimens possess only an incomplete or fragmented neck.

Amsdenium velatum is somewhat similar to *Aremoricanium rigaudiae* Deunff, 1955 (see Loeblich and MacAdam, 1971, p. 43, pl. 16, figs. 1–8; Kjellström, 1971b, p. 8, fig. 2) in bearing broad-based, elongate, spine-like processes, but differs chiefly in its smaller vesicle, consistent process solidity, and membranous, process-supported reticulum.

Occurrence.—OPC 2071, Sylvan Shale samples 1142 SYO through 1145 SYO (present study).

Genus **Aremoricanium** Deunff, 1955

Type species.—Aremoricanium rigaudiae Deunff, 1955 [OD].

Aremoricanium squarrosum Loeblich and MacAdam, 1971

Plate 5, Figures 1–3

Aremoricanium squarrosum LOEBLICH and MACADAM, 1971, p. 44, pl. 18, figs. 1–8.

Aremoricanium syringosagis LOEBLICH and MACADAM, 1971, p. 44, pl. 18, fig. 9.

Description.—Outline of vesicle (excluding apical projection) ± pentagonal or hexagonal; overall original shape pyriform. Eilyma thin, ca. 0.6–0.8 μm thick, minutely and densely granulate. Prominent cylindrical neck emanating from vesicle apex and with terminal circular aperture (pylome); neck wall thin, essentially psilate; length of neck 22–30 μm, diameter 10–15 μm. Seven to 21 processes regularly spaced elsewhere on vesicle; processes hollow, elongate-cylindrical, relatively slender, very thin walled (ca. 0.2–0.3 μm thick), surface minutely granulate with grana tending to be aligned in barely perceptible, discontinuous, longitudinal rows. Processes tapering slightly from circular, generally slightly constricted base [diameter 3 (7) 11 μm] to closed, obtusely rounded distal end; proximal process contacts angular; process interior and vesicle cavity non-communicative because of eilyma continuity across process base. Operculum not present.

Measurements.—Vesicle diameter 40–65 μm; based on 6 specimens.

Remarks and comparison.—We endorse Loeblich and MacAdam's (1971) statement on the "extreme rarity" in the Sylvan Shale of their species *Aremoricanium* nom. corr. *syringosage*, which is here considered, in agreement with Eisenack and others (1973, p. 42) and Jacobson and Achab (1985, p. 171, 172), conspecific with *A. squarrosum* Loeblich and MacAdam, 1971. Loeblich and MacAdam (1971, p. 44) differentiated the two species primarily on disparate process numbers: *A. squarrosum* bearing "numerous (up to 24)" processes, whereas *A. syringosage* was specified as having only nine processes. However, it seems likely that the latter species was based on only one (holotype) specimen, and our observations on additional Sylvan specimens indicate a range of process numbers per vesicle that effectively encompasses both species. Because of their very thin walls, processes are commonly broken.

Occurrence.—OPC 2071, Sylvan Shale samples 1142 SYO through 1145 SYO (present study); also Loeblich and MacAdam (1971). Edenian of Indiana and Ohio, U.S.A. (Loeblich and MacAdam, 1971). Upper Ordovician (Ashgill) of Québec, Canada (Martin, 1980; Jacobson and Achab, 1985); and from coeval strata in Europe, the Middle East, and North Africa (e.g., see Molyneux and others, 1996, pl. 2, fig. 7; Vavrdová, 1997, fig. 3).

Aremoricanium sp. A

Plate 4, Figure 6

Description.—Vesicle originally spherical, outline subcircular. Eilyma psilate, ca. 1 μm thick, with continuous peripheral compression fold. Neck-like tubular structure projecting from vesicle apex, thin-walled, corroded but evidently ± psilate; diameter 9.5 μm, length at least 10.5

µm (may be incomplete). Processes numerous, tenuous, apparently solid, elongate-cylindrical, curved to sinuous; tapering slightly from circular base (diameter <1 µm) to blunted distal extremity; length 6–8 µm; proximal process contacts curved. No operculum.

Measurements.—Vesicle diameter 48 µm; based on 1 specimen.

Comparison.—This form appears to show no close resemblance to any previously instituted species of *Aremoricanium.*

Occurrence.—OPC 2071, Sylvan Shale sample 1143 SYO (present study).

Genus **Baltisphaeridium** Eisenack, 1958 ex Eisenack, 1959 emend. Eisenack, 1969

Type species.—*Baltisphaeridium longispinosum* (Eisenack, 1931 ex O. Wetzel, 1933) Eisenack, 1959 [OD].

Discussion.—Despite including numerous and diverse species, *Baltisphaeridium* Eisenack, 1958 ex Eisenack, 1959 emend. Eisenack, 1969 presents considerable difficulties in its definitive application because of uncertainties of the morphologic attributes of its type species and others customarily assigned to the genus. This problem has been reviewed by several authors, including Le Hérissé (1989, p. 84, 85), Wicander and others (1999, p. 5), Playford (2003, p. 13), and Tongiorgi and others (2003, p. 52). The last-named authors stated that the "very well preserved" holotype of *B. longispinosum* (Eisenack, 1931 ex O. Wetzel, 1933) Eisenack, 1959 (i.e., the generoholotype) lacks any indication of a pylome; and, furthermore, that "no pylome was observed during our observation of thousands of specimens belonging to *B. longispinosum* and to closely related species. . ." Hence, this substantiates the view that Turner's (1984, p. 101, 102) erection of *Baltisphaerosum* for non-pylomate baltisphaerids was unnecessary (Le Hérissé, 1989; Wicander and others, 1999). Mullins (2001, p. 56–58) quoted an English translation of Eiserhardt's (1989, p. 88, 89) emended diagnosis of *Baltisphaeridium,* which was a circumscription not endorsed either by Wicander and others (1999) or by Tongiorgi and others (2003). Mullins's (2001, p. 58) assertion that "the nature of the excystment opening separates *Baltisphaeridium* (pylome) from *Baltisphaerosum* Turner, 1984 (rupture)" is therefore rejected as unsustainable.

We include in *Baltisphaeridium* forms featuring an originally spherical or near-spherical vesicle; hollow, elongate, spine-like processes clearly set off from the vesicle and not communicating with its interior, commonly because of development of a basal plug; psilate or only minutely sculptured eilyma and process walls; and an excystment structure that, if recognizable, is a simple split in the eilyma. Staplin and others (1965, p. 188) proposed a "restricted" diagnosis of *Baltisphaeridium,* which was accepted by Tongiorgi and others (2003). However, we do not regard that circumscription as satisfactory, mainly because its encompassing suprageneric "subgroup"—Baltisphaeritae—was proposed by Staplin and others (1965) to incorporate forms either lacking any excystment opening or possessing a "simple, circular pylom(e)."

Baltisphaeridium adiastaltum Wicander, Playford, and Robertson, 1999
Plate 6, Figures 3–6

Baltisphaeridium adiastaltum WICANDER, PLAYFORD, and ROBERTSON, 1999, p. 5, 7, fig. 4.6–4.9.

For additional synonymy, see Wicander and others (1999, p. 5).

Measurements.—Diameter of vesicle 42 (56) 70 µm; number of processes 15 (22) 32, length of processes 21 (31) 43 µm; based on 52 specimens.

Remarks.—The present specimens conform to the diagnosis of *Baltisphaeridium adiastaltum* provided by Wicander and others (1999), apart from extending slightly the vesicle size range. Under SEM, some specimens show minute sculptural modification (microgranulate-echinate) of the process wall and, more rarely and irregularly, of the eilyma (Pl. 6, Fig. 6). Under LM, such sculpture may be faintly discerned (e.g., Wicander and others, 1999, fig. 4.9) but is normally imperceptible.

Occurrence.—OPC 2071, Sylvan Shale samples 1142 SYO through 1145 SYO (present study). Upper Ordovician (Richmondian) of Midcontinent U.S.A. (Wright and Meyers, 1981; Wicander and others, 1999) and Anticosti Island, Québec, Canada (Jacobson and Achab, 1985).

Baltisphaeridium aliquigranulum Loeblich and Tappan, 1978
Plate 6, Figures 1, 2

Baltisphaeridium aliquigranulum LOEBLICH and TAPPAN, 1978, p. 1247, pl. 3, figs. 4–8.

Description.—Vesicle originally spherical; outline circular. Eilyma ca. 1.3–2 µm thick, essentially psilate. Six to twelve long, simple, discrete, homomorphic, ± straight, spine-like processes, fairly regularly spaced on eilyma, tapering uniformly to acuminate distal termination. Continuity of eilyma across base of invariably hollow processes precluding internal process-vesicle communication. Length of processes 65–98 µm, circular bases 5–8 µm in diameter; process wall thin (<0.5 µm thick), minutely echinate/granulate, especially in proximal one-half to two-thirds of process length; proximal process contacts slightly curved or almost angular. No excystment structure observed.

Measurements.—Diameter of vesicle 53–63 µm; based on 5 specimens.

Occurrence.—OPC 2071, Sylvan Shale samples 1142 SYO through 1145 SYO (present study); also Loeblich and Tappan (1978). Maquoketa Shale (Richmondian), Missouri, U.S.A. (Miller, 1991). Molyneux and others (1996, text-fig. 8) considered this species "cosmopolitan" and confined to the Ashgill.

Baltisphaeridium curtatum Playford and Wicander, new species

Plate 7, Figures 1–4

Diagnosis.—Vesicle originally spherical; outline circular or subcircular, distinct from processes. Unilayered, psilate to scabrate eilyma, 0.8–1.7 µm thick, bearing 11 to 24 (generally ca. 17–20), evenly distributed, discrete, slender, hollow, homomorphic, spine-like processes tapering uniformly from circular bases (0.8–3 µm broad) to simple acuminate distal termini. Proximal process contacts curved to subangular. Processes straight to curved; length 6 (15) 22 µm; wall ca. 0.4–0.8 µm thick, psilate to scabrate (under SEM); process interior not communicating with vesicle cavity because of eilyma continuing across process base, ± development of short basal process plug. Excystment structure, infrequently evident, consisting of a simple split in eilyma.

Measurements.—Diameter of vesicle 41 (55) 70 µm; based on 43 specimens.

Holotype.—OPC 2071-3853, sample/slide 1143 SYO/20-52 µm/5, field finder Q20/1,5; Plate 7, Figure 2. Vesicle outline circular, diameter 43 µm; eilyma virtually psilate, 0.9 µm thick, with few compression folds; 17 discrete, homomorphic, thin-walled, spine-like processes with hollow interiors lacking communication with vesicle cavity; process length 3–13 µm, basal diameter 1.3–1.9 µm, proximal contacts mostly slightly curved; no positively identifiable excystment structure.

Derivation of name.—Latin, *curtatus*, curtailed, shortened; with reference to the relative shortness of the processes.

Comparison.—*Baltisphaeridium curtatum* Playford and Wicander, new species is separable from co-occurring *B. adiastaltum* (recorded above) mainly in having appreciably shorter processes compared with the vesicle diameter. *Baltisphaeridium curtatum* appears morphologically akin to a Swedish Middle Ordovician species, *B. psilatum* Kjellström, 1971 (1971a, p. 39, pl. 2, fig. 10), but differs in having generally fewer and more narrowly based processes. As noted previously, there are numerous named species of *Baltisphaeridium*, some of which could be closely allied to *B. curtatum*. However, as with *B. adiastaltum* (see comments by Wicander and others, 1999, p. 7), many of these earlier species are insufficiently described or illustrated to permit meaningful comparisons or positive identifications.

Occurrence.—OPC 2071, Sylvan Shale samples 1142 SYO through 1145 SYO (present study).

Baltisphaeridium oligopsakium Loeblich and Tappan, 1978

Plate 7, Figures 5–7

Baltisphaeridium oligopsakium LOEBLICH and TAPPAN, 1978, p. 1252, pl. 5, figs. 4–6.

?*Baltisphaeridium oligopsakium* Loeblich and Tappan, 1978—UUTELA and TYNNI, 1991, p. 44, pl. 6, fig. 58.

Measurements.—Diameter of vesicle 50 (60) 75 µm; number of processes 17 (25) 36, length of processes 23 (31) 38 µm; based on 18 specimens.

Remarks and comparison.—The distinctive morphology of *Baltisphaeridium oligopsakium* Loeblich and Tappan, 1978 has been comprehensively described and illustrated by its original authors and by Wicander and others (1999, p. 7, fig. 5.1–5.10). The present specimens confirm the separation of this species from *B. perclarum* (described below), which has fewer and differently shaped processes, and *B. parvulisidereum* Colbath, 1979, the processes of which appear more slender and lack any basal constriction.

Occurrence.—OPC 2071, Sylvan Shale samples 1142 SYO through 1145 SYO (present study). Aside from a dubious report from the Arenig–Ashgill of Estonia (Uutela and Tynni, 1991), *Baltisphaeridium oligopsakium* has been recorded only from Richmondian strata of the United States Midcontinent (Loeblich and Tappan, 1978; Miller, 1991; Wicander and others, 1999; Wicander and Playford, 1999).

Baltisphaeridium perclarum
Loeblich and Tappan, 1978

Plate 8, Figures 1–3; Plate 9, Figures 3–6

Baltisphaeridium perclarum LOEBLICH and TAPPAN, 1978, p. 1253, pl. 6, figs. 5–7.

For additional synonymy, see Wicander and others (1999, p. 9).

Description.—Vesicle originally spherical; outline circular to subcircular, distinct from processes. Eilyma psilate, evidently unilayered, 1–1.8 µm thick. Processes hollow, elongate (18–75 µm long; commonly 35–60 µm), spine-like, borne discretely and relatively widely spaced on eilyma, numbering 6–14 per vesicle; process wall very thin (ca. 0.2–0.3 µm thick), psilate or minutely sculptured (scabrate to granulate); a basal plug (ca. 1–3 µm thick, uncommonly up to 4.5 µm), with concave to near-flat outer (distal) surface, separating process and vesicle interiors. Processes 18 (60) 95 µm long, broadening from circular, constricted base (3–8 µm in diameter) for ca. one-quarter of total length, then narrowing gradually to acuminate tip. Most specimens equipped with simple, spine-like, homomorphic processes; on other specimens, a few processes possess 1–3 small offshoots from trunk, and/or are clearly bifurcant, the branching (first-order only and equal or unequal) being initiated within the span of ca. 10 µm from process base to the same distance from the distal extremity. No excystment structure observed.

Measurements.—Diameter of vesicle 47 (64) 78 µm; based on 47 specimens.

Remarks.—*Baltisphaeridium perclarum* Loeblich and Tappan, 1978 is one of the most characteristic and distinctive species of the Sylvan Shale's acritarch flora. The above description augments Loeblich and Tappan's (1978) diagnosis and description, in particular extending the lower limit of the vesicle size-range; and concurs also with observations by Wicander and others (1999, p. 9, fig. 4.1–4.4).

Occurrence.—OPC 2071, Sylvan Shale samples 1142 SYO through 1145 SYO (present study); also Loeblich and Tappan (1978). Bill's Creek Shale and Stonington Formation (Richmondian), Michigan, U.S.A. (Wicander and Playford, 1999). See Wicander and others (1999, p. 9) for listing of other prior reports, all from the Cincinnatian of North America and equivalent strata elsewhere. Subsequently, Ghavidel-syooki (2001) reported this taxon from Iranian strata dated within the Llanvirn–Ashgill interval.

Baltisphaeridium sp. A
Plate 9, Figure 2

Description.—Vesicle originally spherical; outline near-circular. Eilyma 1.7 µm thick, essentially psilate; bearing 8 discrete, hollow, straight, spine-like processes tapering ± uniformly from circular bases to simple, acuminate or slightly blunted, distal termini. Proximal process contacts slightly curved or angular; bases circular; process wall thin (ca. 0.4–0.5 µm thick), minutely sculptured with fine echinae/grana <0.4 µm in basal diameter and height. Process interiors not communicating with vesicle cavity because of intervening, slightly thickened eilyma (i.e., incipient plug developed at process base). Processes homomorphic but in two distinct size categories, neither with localized placement: major processes 4 in number, 85–130 µm long, 8.5–12 µm in basal diameter; minor processes numbering 2–4, length 22–48 µm, basal diameter 2.5–6.5 µm. Excystment structure consisting of a simple split in eilyma.

Measurements.—Diameter of vesicle 60, 72 µm; based on 2 specimens.

Comparison.—This form is distinct from other baltisphaerids because of the conspicuous size-differentiation of its processes.

Occurrence.—OPC 2071, Sylvan Shale samples 1142, 1144 SYO (present study).

Genus Caelatosphaera Wicander, Playford, and Robertson, 1999

Type species.—*Caelatosphaera verminosa* Wicander, Playford, and Robertson, 1999 [OD, M].

Caelatosphaera cerebella Playford and Wicander, new species
Plate 9, Figure 1; Plate 10, Figures 1–4

Lophosphaeridium acinatum WICANDER, PLAYFORD, and ROBERTSON, 1999, in part, p. 15, fig. 8.6 only.

Diagnosis.—Vesicle originally spherical; outline circular or nearly so, with ± regularly, although not strongly notched periphery. Eilyma fairly thick (ca. 2.5–3.3 µm, but generally difficult to measure precisely), commonly with relatively coarse compression folds. Surface of eilyma comprehensively incised, to depths of ca. 0.4–1.2 µm, by foveolae and vermiculi that are separated by ca. 1–3 µm of essentially psilate eilyma. Foveolae subcircular or irregularly elongate, up to 2 µm in diameter (generally <0.8 µm); vermiculi consisting of very narrow, short (1–2 µm long), linear or curved, channel-like incisions that may locally branch (bifurcate) or interconnect. Excystment by simple splitting of eilyma.

Measurements.—Diameter of vesicle 41 (61) 78 µm; based on 31 specimens.

Holotype.—OPC 2071-3865, sample/slide 1142 SYO/20-52 µm/4, field finder H14/2,-3; Plate 10, Figure 1. Vesicle diameter 62 µm; outline circular with perceptibly notched periphery revealing depth of eilyma incisement (up to 1.2 µm) by fine foveolae and vermiculi; eilyma ca. 2.5 µm thick; no excystment structure.

Derivation of name.—Latin, *cerebellum* (diminutive), brain-like, cerebral; in reference to the appearance of the vesicle.

Comparison.—*Caelatosphaera cerebella* Playford and Wicander, new species differs from *C. verminosa* Wicander, Playford, and Robertson, 1999 (p. 9, fig. 6.6–6.9) in its coarser, more diverse (foveo-vermiculate vs. vermiculate) surficial modification of the eilyma, manifested in part by the indented vesicle margin.

Occurrence.—OPC 2071, Sylvan Shale samples 1142 SYO through 1145 SYO (present study). Maquoketa Shale (Richmondian), Missouri, U.S.A. (Wicander and others, 1999; as in above synonymy).

Genus **Cheleutochroa** Loeblich and Tappan, 1978 emend. Turner, 1984

Type species.—*Cheleutochroa gymnobrachiata* Loeblich and Tappan, 1978 [OD].

Cheleutochroa clandestina Playford and Wicander, new species

Plate 10, Figures 5, 6; Plate 11, Figures 1–6

Cheleutochroa cf. *C. gymnobrachiata* Loeblich and Tappan, 1978—WRIGHT and MEYERS, 1981, p. 23, pl. 5, figs. E, G–I.

Cheleutochroa diaphorosa auct. non Turner, 1984—MOLYNEUX, 1988, p. 48, pl. 9, figs. 4, 7.

Diagnosis.—Vesicle originally spherical; outline circular or subcircular, ± distinct from processes. Eilyma ca. 0.4–0.6 µm thick; surface very finely and densely sculptured (appearing faintly granulate/punctate under LM, ×100 oil-immersion objective), but distinctly microreticulate under SEM, muri very low and narrow or blade-like (<0.2 µm wide), with variably disposed, rounded, boss-like protuberances or tubercles (<0.4 µm in diameter), and enclosing irregular lacunae (ca. 1 µm or less in diameter). Processes hollow, elongate and spine-like in gross form, mostly 4–10 in number (uncommonly as many as 20), length 11 (21) 35 µm (fairly uniform on given specimen), circular bases 2.5 (5) 8.5 µm in diameter; processes borne discretely and ± regularly on eilyma, heteromorphic due to variable distal termini (simple or, more commonly on same specimen, furcant); proximal process contacts curved, less commonly subangular; process interior opening freely into vesicle cavity; wall, similar in thickness to eilyma, bearing diminutive grana and echinae (<0.5 µm in basal diameter and height), generally more prominent (a) proximally than distally and (b) on 1 or 2 processes (of same vesicle); some processes psilate. SEM revealing microreticulation of eilyma, which dismembers in vicinity of process base to give rise to very narrow parallel striae or minute ridges commonly extending for short distance (ca. 5 µm) along proximal-most portion of process trunk. All or the majority of processes on a given specimen showing variable, equal or unequal branching (bifurcation up to 3rd order; uncommonly trifurcation); branching generally initiated close to distal end of process, less commonly beginning, as first-order bifurcation, up to ca. one-half of distance to process base; simple processes and branches with acuminate or evexate tips. Excystment by simple splitting of eilyma.

Measurements.—Diameter of vesicle 21 (29) 40 µm; based on 72 specimens.

Holotype.—OPC 2071-3869, sample/slide 1142 SYO/20-52 µm/2, field finder J15/-2,-2; Plate 11, Figure 1. Vesicle near-circular, diameter 27 µm; eilyma ca. 0.5 µm thick, marginally folded, very fine sculpture (microreticulate) just discernible; 9 hollow processes, irregularly branching distally, communicating freely with vesicle interior, granulate-echinate sculpture developed on some processes, otherwise process surfaces psilate, proximal contacts curved, bases 4–7 µm wide, length of processes 21–29 µm; no excystment structure.

Derivation of name.—Latin, *clandestinus*, secret, concealed; with reference to the eilyma sculpture.

Comparison.—Under relatively low power LM, *Cheleutochroa clandestina* Playford and Wicander, new species recalls *Diexallophasis* Loeblich, 1970 emend. Sarjeant and Vavrdová, 1997 (p. 18). However, the eilyma of the latter is differently sculptured (i.e., granulate-echinate). *Cheleutochroa clandestina* resembles certain other Upper Ordovician forms assigned to *Cheleutochroa*. These are: (1) the Sylvan Shale type species *C. gymnobrachiata* instituted by Loeblich and Tappan (1978, p. 1254, 1257, pl. 7, figs. 4, 5); (2) an English Caradoc species, *C. diaphorosa* Turner, 1984 (p. 105, 106, pl. 1, fig. 5, pl. 7, fig. 3); (3) *Cheleutochroa* sp. cf. *C. diaphorosa* of Wicander and others (1999, p. 9, 11, fig. 6.3–6.5) from the Maquoketa Shale (Richmondian), Missouri, U.S.A.; and (4) *C. elegans*, as described by Uutela and Tynni (1991, p. 49, pl. VII, fig. 72) from the Ashgill of Estonia. The following are the chief attributes of *C. clandestina* that distinguish it from each of these forms: mostly branched (never exclusively simple) processes [cf. item (1), above]; larger vesicle, sculptured processes [cf. item (2)]; much less conspicuous eilyma sculpture, predominantly furcant and at least partly granulate-echinate processes [cf. item (3)]; and mostly fewer (generally 4–10 vs. 13–28), sculptured processes that are predominantly and commonly more elaborately furcant [cf. item (4)]. Of these four comparative taxa, the last-mentioned, *C. elegans*, seems closest to *C. clandestina*. Indeed, these two species could possibly prove synonymous, with *C. elegans* taking priority, should circumscription of the latter be broadened and expressed more explicitly on the basis of additional material from the Estonian type stratum—the dimensions and presumably the diagnostic data given by Uutela and Tynni (1991) are evidently based on only three specimens and are illustrated by a single SEM image.

A few specimens reported by Wright and Meyers (1981) and one by Molyneux (1988) as, respectively, *Cheleutochroa* cf. *C. gymnobrachiata* and *C. diaphorosa* (see above synonymy list) are clearly conspecific with *C. clandestina*.

Occurrence.—OPC 2071, Sylvan Shale samples 1142 SYO through 1145 SYO (present study). Maquoketa Shale (Richmondian) of Kansas, U.S.A. (Wright and Meyers, 1981). Ashgill of northeast Libya (Hill and Molyneux, 1988; Molyneux, 1988).

Genus **Comasphaeridium** Staplin, Jansonius, and Pocock, 1965 emend. Sarjeant and Stancliffe, 1994

Type species.—*Comasphaeridium cometes* (Valensi, 1949) Staplin, Jansonius, and Pocock, 1965 [OD].

Comasphaeridium lanugiferum
Jacobson and Achab, 1985
Plate 12, Figures 1–9

Comasphaeridium lanugiferum JACOBSON and ACHAB, 1985, p. 176, pl. 5, figs. 6–8.

Description.—Vesicle originally spherical, outline circular or subcircular. Eilyma very thin (<0.5 µm thick); characteristically displaying several, relatively large-scale compression folds mostly marginally and concentrically disposed. Eilyma surface generally ± completely obscured by very dense mesh-like cover of innumerable, fine, crowded and entangled, tendril- or hair-like processes, perceptibly per LM ×100 oil-immersion objective and distinctly per SEM. Processes apparently solid, elongate-subcylindrical, length ca. 0.7 (1.6) 3.3 µm, very slender (ca. 0.1–0.3 µm wide), tips evexate; proximal process contacts slightly curved to angular. Excystment by simple splitting of eilyma.

Measurements.—Diameter of vesicle 30 (36) 44 µm; based on 16 specimens.

Remarks and comparison.—Some specimens of *Comasphaeridium lanugiferum* Jacobson and Achab, 1985 are partly or almost entirely devoid of processes, indicating that these latter are susceptible to post-depositional degradation (e.g., Pl. 12, Figs. 3–5). This species resembles a Swedish lower Silurian species, *C. hirtum* Le Hérissé, 1989 (p. 89, pl. 6, figs. 8–10), but differs in possessing blunted processes lacking bulbous bases.

Occurrence.—OPC 2071, Sylvan Shale samples 1144, 1145 SYO (present study). Vauréal Formation (Richmondian), Anticosti Island, Québec, Canada (Jacobson and Achab, 1985).

Genus **Dactylofusa** Brito and Santos, 1965

Type species.—*Dactylofusa maranhensis* Brito and Santos, 1965 [OD].

Discussion.—Generic categorization of acritarchs with variously sculptured, fusiform vesicles is controversial and confused (e.g., see Fensome and others, 1990, p. 197, 213, 214, 397). This applies to overlapping concepts and application of *Dactylofusa* Brito and Santos, 1965 (p. 12, 20), *Poikilofusa* Staplin, Jansonius, and Pocock, 1965 (p. 185), and *Eupoikilofusa* Cramer, 1971 (p. 83, 84). The latter genus was not legitimately established because Cramer (1971, p. 83) included in its synonymy the other two, previously instituted genera (Fensome and others, 1990, p. 213, 214). Resolution of these problems is beyond the scope of this study, especially as such forms are very minor components of our Sylvan Shale palynoflora. Unquestionably, detailed morphologic studies of the type species are needed to resolve the status of each genus. Such an approach was inherent in Loeblich and Tappan's (1978) usage of *Eupoikilofusa* and *Poikilofusa.* However, for the present, following Fensome and others (1990), the species attributed by Loeblich and Tappan (1978) to the defunct *Eupoikilofusa* are included, by no means satisfactorily, in what can only be regarded as a "ballooned" or uncohesive concept of *Dactylofusa.*

Dactylofusa ctenista (Loeblich and Tappan, 1978) Fensome, Williams, Barss, Freeman, and Hill, 1990

Plate 13, Figures 3, 4

Eupoikilofusa ctenista LOEBLICH and TAPPAN, 1978, p. 1263, pl. 8, figs. 8, 9.

Dactyofusa ctenista (Loeblich and Tappan, 1978) FENSOME, WILLIAMS, BARSS, FREEMAN, and HILL, 1990, p. 180.

Description.—Vesicle elongate-fusiform in outline, attenuating uniformly toward each acute apex and without any clear differentiation of "polar" processes. Eilyma very thin (<0.5 μm thick), hence commonly folded and twisted. Eilyma surface marked by numerous, discontinuous, ± longitudinal, low, straight to sinuous, psilate ridges commonly 0.4–0.8 μm wide, variably spaced (up to ca. 6 μm apart). Ridges discrete or coalescent, tending to become ± imperceptible toward vesicle apices. No excystment structure observed.

Measurements.—Overall length 138 (158) 194 μm, maximum breadth 14 (23) 30 μm; based on 14 specimens.

Remarks and comparison.—Loeblich and Tappan (1978) diagnosed *Eupoikilofusa ctenista* and *E. parvuligranosa* on very few specimens (five and one, respectively) from the Sylvan Shale of the Lawrence Quarry. We confirm the meager representation of acritarchs of this nature in our samples from the same site. Loeblich and Tappan (1978, p. 1263), although conceding close similarity between *ctenista* and *parvuligranosa,* claimed that the latter's sculpture of "small grana that may be aligned in rows" distinguished it from the former (see also Wright and Meyers, 1981, pl. 3, fig. H). Such distinction appears tenable inasmuch as our specimens are consistently non-granulate and thus clearly identifiable as *Dactylofusa ctenista.*

Occurrence.—OPC 2071, Sylvan Shale samples 1142 SYO through 1145 SYO (present study); also Loeblich and Tappan (1978). Upper Ordovician of northeast Libya (Molyneux, 1988).

Genus **Dorsennidium** Wicander, 1974 emend. Sarjeant and Stancliffe, 1994

Type species.—*Dorsennidium patulum* Wicander, 1974 [OD; M].

Dorsennidium hamii (Loeblich, 1970) Sarjeant and Stancliffe, 1994

Plate 13, Figure 2

Veryhachium hamii LOEBLICH, 1970a, p. 741, fig. 35A–F.

Veryhachium hamii Loeblich, 1970—WRIGHT and MEYERS, 1981, in part, p. 29, 30, pl. 6, figs. G, I (non pl. 3, figs. J, N, pl. 8, fig. G).

Dorsennidium? *hamii* (Loeblich, 1970) SARJEANT and STANCLIFFE, 1994, p. 40 ("assignment provisional").

Description.—Vesicle triangular in outline; sides generally slightly convex, or partly convex and partly concave, rarely almost straight; overall appearance typically bell-shaped, 2 sides being equal and longer than the other (generally conspicuously so). Eilyma 0.7–1 μm thick, almost psilate (densely microgranulate under SEM) with 3 co-planar, spine-like, main or "primary" processes, each drawn out from an apex of the vesicle triangle, basal diameter ca. 3–8 μm, length 16 (27) 45 μm (these dimensions highly variable among specimens but fairly consistent on a given specimen). Additionally, "secondary" processes, generally 2 or 1, arising from vesicle face near base of triangle, may be of unequal length on same specimen, nearly equal in length to, or shorter than, main processes. All processes homomorphic, similar surficially and in thickness to eilyma, straight to curved, hollow, internally communicative with vesicle cavity; tapering gradually from base to terminate in simple acuminate tip. Excystment structure (rarely seen) consisting of a simple split extending between 2 primary processes.

Measurements.—Maximum diameter of vesicle 44 (57) 75 μm; based on 24 specimens.

Remarks.—Although morphologically variable, *Dorsennidium hamii* (Loeblich, 1970) Sarjeant and Stancliffe, 1994 is easily recognizable, mainly because of its bell-shaped vesicle. Chief variables are maximum vesicle diameter and length of both process categories. Like Wicander and others (1999, p. 11, figs. 7.5, 7.6), we did not observe any specimens bearing bifurcant or otherwise terminally branching processes (cf. Loeblich, 1970a, p. 741).

Occurrence.—OPC 2071, Sylvan Shale samples 1142 SYO through 1145 SYO (present study); also Loeblich (1970a). Bill's Creek Shale and Stonington Formation (Richmondian), Michigan, U.S.A. (Wicander and Playford, 1999). Numerous reports from Upper Ordovician strata elsewhere in North America and in Europe and North Africa, as summarized by Wicander and others (1999, p. 11). Molyneux and others (1996, text-fig. 8) rightly classed *Dorsennidium hamii* as a cosmopolitan species, but its stratigraphic range evidently extends considerably lower (i.e., into the Caradoc) than the purported Ashgill restriction.

Dorsennidium undosum Wicander, Playford, and Robertson, 1999

Plate 13, Figures 5, 6

Dorsennidium undosum WICANDER, PLAYFORD, and ROBERTSON, 1999, p. 11, 13, fig. 7.1–7.4.

Veryhachium hamii auct. non Loeblich, 1970—WRIGHT and MEYERS, 1981, p. 29, 30, pl. 3, figs. J, N, pl. 8, fig. G only.

Description.—Vesicle polygonal (commonly pentagonal) in outline. Eilyma 0.7–1 μm thick, scabrate. One process drawn out from each vesicle corner, the resultant process number thus concomitant with vesicle outline (i.e., 5 in the case of pentagonal vesicles); additional to these coplanar processes, 4 or 5 processes arising from either or both vesicle faces. Processes spine-like, straight to curved (particularly distally), homomorphic, scabrate, thickness similar to eilyma, hollow, opening freely into vesicle cavity. Processes tapering regularly from base (diameter 3–5.5 μm) to non-furcate, narrowly acuminate distal end; length of processes 15 (23) 31 μm, fairly uniform on given specimen. No excystment structure observed.

Measurements.—Diameter of vesicle 21 (29) 39 μm; based on 16 specimens.

Remarks.—The present specimens are readily accommodated in *Dorsennidium undosum* Wicander, Playford, and Robertson, 1999, but are somewhat less varied morphologically than the type material.

Occurrence.—OPC 2071, Sylvan Shale samples 1142 SYO through 1145 SYO (present study). Maquoketa Shale (Richmondian), Kansas and Missouri, U.S.A. (Wright and Meyers, 1981; Wicander and others, 1999).

Genus **Gyalorhethium** Loeblich and Tappan, 1978

Type species.—*Gyalorhethium spinuliferum* Loeblich and Tappan, 1978 [OD].

Gyalorhethium sp. cf. **G. chondrodes** Loeblich and Tappan, 1978

Plate 14, Figures 1, 2

cf. *Gyalorhethium chondrodes* LOEBLICH and TAPPAN, 1978, p. 1269, pl. 10, figs. 1, 2.

Description.—Vesicle originally spherical, outline circular. Eilyma ca. 0.8 μm thick, with almost psilate (scabrate to faintly granulate) surface and bearing numerous (26–32) discrete, hollow, homomorphic, mostly straight, spine-like processes that taper ± uniformly from circular base (diameter, 1.5–4.5 μm) to acuminate distal tip. Processes 14 (25) 32 μm long, basal separation ca. 5–14 μm; wall <0.5 μm thick, sculpture fine, albeit more conspicuous than that of eilyma, consisting of minute grana and echinae disposed ± regularly along process length. Processes opening directly into vesicle cavity. No excystment structure observed.

Measurements.—Diameter of vesicle 45–56 μm; based on 4 specimens.

Remarks and comparison.—Loeblich and Tappan (1978) recorded *Gyalorhethium chondrodes* from the lower part (Mountain Lake Member) of the Bromide Formation (Mohawkian; Caradoc) of Oklahoma. Unfortunately, the diagnosis is evidently based on only one specimen, thereby providing no perspective on intraspecific variation. Hence, the Sylvan Shale specimens described above could conceivably be accommodated in a less restrictive, multi-specimen definition of *G. chondrodes*. However, *pro tem*, we prefer to adopt only a qualified or provisional ("cf.") specific identification because of the following attributes of our specimens, compared to the *chondrodes* holotype: (1) processes are more numerous; (2) eilyma sculpturing is more subdued in itself and compared to the processes; and (3) sculptural elements are more uniform, in terms of size and distribution, over the extent of the processes.

Occurrence.—OPC 2071, Sylvan Shale samples 1142, 1143 SYO (present study).

Gyalorhethium sp. A

Plate 13, Figure 1

Description.—Vesicle originally spherical, outline subcircular. Eilyma thin (ca. 0.5 µm thick), densely and minutely granulate, with irregular, large-scale compression folds. Eight to eleven, discrete, hollow, homomorphic, curved to straight, spine-like processes spaced ± regularly, their hollow interiors opening freely into vesicle cavity. Length of processes 25–67 µm (but fairly uniform on same specimen), wall thin, like eilyma, and with similarly granulate surface; proximal contacts angular to slightly curved. Processes tapering from circular-subcircular base (5–9 µm in diameter) to simple, acuminate distal tip; attenuation tending to be more pronounced in upper (distal) half of process. Excystment by simple splitting of eilyma.

Measurements.—Diameter of vesicle 43–67 µm; based on 5 specimens.

Remarks and comparison.—Process length in specimens of *Gyalorhethium* sp. A is proportional to vesicle size, with the larger vesicles bearing longer processes. Process length is normally at least two-thirds of vesicle diameter. This form differs from *G. chondrodes* and *Gyalorhethium* sp. cf. *G. chondrodes* (above) mainly in having many fewer and appreciably larger processes and much finer sculpture of both eilyma and processes. *Gyalorhethium* sp. A of Jacobson and Achab (1985, p. 183, pl. 4, fig. 4), from the Richmondian of Québec, Canada, differs from our form in possessing generally more processes that are narrower based and possibly more conspicuously granulate. *Gyalorhethium* sp. of Górka (1987, p. 278, pl. V, fig. 1), from the Swedish Middle Ordovician, has predominantly spinose processes.

Occurrence.—OPC 2071, Sylvan Shale samples 1142, 1144, 1145 SYO (present study).

Genus **Hoegklintia** Dorning, 1981

Hogklintia DORNING, 1981, p. 192.

Hoegklintia Dorning nom. corr. ELEY and LEGAULT, 1988, p. 58, 63.

Type species.—*Hoegklintia visbyensis* (Eisenack, 1959) Dorning, 1981 [OD].

Hoegklintia radicosa (Loeblich, 1970) Jacobson and Achab, 1985

Plate 14, Figure 6

Multiplicisphaeridium radicosum LOEBLICH, 1970a, p. 730, fig. 23A–E.

Hoegklintia radicosa (Loeblich, 1970) JACOBSON and ACHAB, 1985, p. 183, pl. 4, fig. 2.

non *Multiplicisphaeridium radicosum* Loeblich, 1970—UUTELA, 1989, p. 34, pl. VII, fig. 57.

non *Multiplicisphaeridium radicosum* Loeblich, 1970—UUTELA and TYNNI, 1991, p. 95, 96, pl. XXII, fig. 224.

Description.—Vesicle subcircular in outline, not clearly demarcated from processes. Eilyma thin (ca. 0.5 µm thick), psilate or scabrate. Twelve to sixteen, prominent, broadly based, stout, hollow, essentially homomorphic processes drawn out from and communicating internally with vesicle cavity. Process trunks tapering gradually toward blunted extremity that is then divergently digitate (up to third-order furcation); branches ± cylindrical with rounded ends; first-order branches up to ca. 10 µm long and 5 µm broad, higher-order branches progressively smaller; process wall thickness and surface corresponding to eilyma. No excystment structure observed.

Measurements.—Diameter of vesicle 57, 62 µm; length of process trunks ca. 15–40 µm, basal breadth ca. 10–20 µm; based on 2 specimens.

Remarks and comparison.—*Hoegklintia radicosa* (Loeblich, 1970) Jacobson and Achab, 1985 is susceptible to corrosion because of its thin eilyma and process walls. Eisenack and others (1973, p. 573, 574) listed many species, including the present one, as junior taxonomic synonyms of *Multiplicisphaeridium corallinum* (Eisenack, 1959) Eisenack, 1969, which was described originally from the middle Silurian of Gotland (Sweden). However, *M. corallinum* is generally larger than *H. radicosa*, and Loeblich (1970a) noted that the latter has a vesicle outline less clearly delineable from the processes, which are, moreover, stouter and broader based. Specimens recorded from the Finnish and Estonian Ordovician by Uutela (1989) and Uutela and Tynni (1991) are not considered authentic representatives of *H. radicosa*.

Occurrence.—OPC 2071, Sylvan Shale samples 1143, 1144 SYO (present study); also Loeblich (1970a). Upper Ordovician (Cincinnatian, mostly Richmondian) of eastern Canada (Martin, 1980, 1983; Jacobson and Achab, 1985) and Missouri (Miller, 1991).

Genus **Lophosphaeridium** Timofeev, 1959 ex Downie, 1963

Type species.—*Lophosphaeridium rarum* Timofeev, 1959 [SD; Downie, 1963, p. 630].

Discussion.—A very large number of acritarch species (mainly of early to middle Paleozoic age) have been assigned to *Lophosphaeridium* Timofeev, 1959 ex Downie, 1963 (see Fensome and others, 1990, p. 301–306). All are relatively simple morphologically, sharing the following three characteristics: (1) originally spherical or ellipsoidal vesicle; (2) unilayered eilyma bearing small, solid "tubercles" (i.e., in the form of grana, verrucae, bacula, rounded echinae, etc.) that do not project conspicuously from the periphery (as observed per LM); and (3) a simple eilyma split constituting the excystment structure (e.g., Lister, 1970, p. 61, footnote; Playford, 1977, p. 26).

As noted by Colbath (1990, p. 116), but not addressed by Sarjeant and Stancliffe (1994, p. 31) or Sarjeant and Vavrdová (1997, p. 24), some overlap occurs between *Lophosphaeridium* (with particular reference to its inadequately known type species) and *Gorgonisphaeridium* Staplin, Jansonius, and Pocock, 1965 (p. 192, 193). The latter clearly needs more definitive circumscription, with greater emphasis placed on the morphology of the type species *G. winslowiae* Staplin, Jansonius, and Pocock, 1965 (p. 193, pl. 19, figs. 11, 18–20, text-fig. 4; also Playford and McGregor, 1993, p. 15, 16, pl. 5, figs. 8–11, pl. 6, figs. 11, 12, fig. 5). Thus viewed, *Gorgonisphaeridium* is separable from *Lophosphaeridium* in that its processes, typically and originally defined as solid, are more elongate and spine-like in gross form and may branch distally. Colbath (1990, p. 116) has suggested, as a practical if arbitrary measure, that *Lophosphaeridium* "be restricted to species in which the processes are simple, and less than twice their diameter in length." Another problem is that *Lophosphaeridium* and *Buedingiisphaeridium* Schaarschmidt, 1963 (p. 69, 70) may prove synonymous; if so, the former would take priority (Sarjeant and Stancliffe, 1994, p. 32).

Lophosphaeridium sylvanium Playford and Wicander, new species

Plate 14, Figures 3–5, 7; Plate 15, Figures 1–6; Plate 16, Figures 1–6

Diagnosis.—Vesicle originally spherical; outline circular or subcircular. Eilyma 0.5–1 µm thick, psilate or scabrate; typically displaying conspicuous compression folds, and bearing numerous, small, solid, diverse (appreciably heteromorphic) processes, ± uniformly and densely distributed (mostly discrete, 0.5–2 µm apart). Form of processes variable on both a given specimen and among specimens—including grana, coni, acicular spinae, flared elements, and bacula (in varying proportions). Spinae/coni and bacula particularly disparate in shape and distal termini: i.e., simple, with acuminate, evexate, slightly bulbous, or truncate tips; laterally extended/branching (mostly bifid) or tendril-like. Basal diameter of processes 0.1–2 µm, height mostly 0.6–2 µm (uncommonly up to 6 µm); proximal process contacts angular or curved. Excystment structure consisting of a simple split in eilyma.

Measurements.—Diameter of vesicle 32 (41) 54 µm; based on 56 specimens.

Holotype.—OPC 2071-3887, sample/slide 1144 SYO/20-52 µm/1, field finder N19/-5,4; Plate 14, Figure 3. Vesicle subcircular, diameter 41 µm; eilyma 1 µm thick, folded; numerous, minute, solid, heteromorphic processes (in the form of grana, coni, spinae) up to 1 µm in basal diameter, up to 1.2 µm in height, spaced 0.5–2.5 µm apart; simple eilyma split constituting excystment structure.

Derivation of name.—After Sylvan Shale.

Remarks and comparison.—LM and SEM examination of a substantial number of specimens of *Lophosphaeridium sylvanium* Playford and Wicander, new species shows an extensive and continuous range of process morphologies, of the relative proportions of the different process forms, and of process spacing. Under medium- to high-magnification LM (e.g., Pl. 14, Figs. 3–5, 7), it is evident that a single, readily recognizable species is represented. SEM examination (Plates 15, 16) demonstrates the minutae of process-heteromorphy. These variable factors induce something of a dilemma in choosing the appropriate generic assignment. For instance, some specimens, at one extreme of the morpho-continuum, bear a high proportion of elongate spine-like processes (e.g., Pl. 14, Fig. 5; Pl. 15, Figs. 3, 4; Pl. 16, Fig. 6) and could thus be considered compatible with *Gorgonisphaeridium.* However, many specimens within this intergradational plexus—exemplified by the holotype—signify appropriate assignment of the species to *Lophosphaeridium.*

The diverse process character, in particular, segregates *L. sylvanium* from previously described species.

Occurrence.—OPC 2071, Sylvan Shale samples 1142 SYO through 1145 SYO (present study).

Genus **Micrhystridium** Deflandre, 1937

Type species.—Micrhystridium inconspicuum Deflandre, 1937 [OD].

Discussion.—We disagree with Sarjeant and Stancliffe's (1994, p. 12) emendation of *Micrhystridium* Deflandre, 1937 (p. 31, 32), which advocated inclusion of forms with such diverse attributes as a unilayered or bilayered eilyma, process numbers between nine and 35, and processes that may be solid or hollow (in the latter case, communicating or not communicating with the vesicle interior). Hence, the generally accepted and morphologically more cohesive circumscription of *Micrhystridium* is followed herein, as in Wicander and others (1999, p. 17).

Micrhystridium hirticulum Wicander, Playford, and Robertson, 1999

Plate 17, Figures 1–3

Micrhystridium hirticulum WICANDER, PLAYFORD, and ROBERTSON, 1999, p. 17, fig. 9.6–9.8.

Measurements.—Vesicle diameter 22–25 µm; process length 9–16 µm, basal width 1–2 µm, number of processes 33 to 46; based on 4 specimens.

Occurrence.—OPC 2071, Sylvan Shale samples 1143, 1144, 1145 SYO (present study). Maquoketa Shale (Richmondian) of Missouri, U.S.A. (Wicander and others, 1999).

Micrhystridium prolixum Wicander, Playford, and Robertson, 1999

Plate 17, Figures 4–6

Micrhystridium prolixum WICANDER, PLAYFORD, and ROBERTSON, 1999, p. 17, figs. 9.13, 10.7.

Remarks.—The Sylvan Shale specimens average a slightly larger vesicle diameter and longer processes than the type material, and one specimen bears seven processes instead of the typical minimum of nine. Nonetheless, these specimens are all clearly attributable to this species.

Measurements.—Vesicle diameter 17 (22) 25 µm; process length 16 (21) 28 µm, basal width 2–4 µm, distance apart 5–10 µm (as measured mainly along vesicle periphery), number of processes 7–16; based on 11 specimens.

Occurrence.—OPC 2071, Sylvan Shale samples 1142 SYO through 1145 SYO (present study). Maquoketa Shale (Richmondian) of Missouri, U.S.A. (Wicander and others, 1999).

Micrhystridium viriosum Playford and Wicander, new species

Plate 17, Figure 7; Plate 18, Figures 1, 2

Diagnosis.—Vesicle originally spherical or subspherical; outline circular or subcircular. Eilyma thin (ca. 0.5 µm thick), psilate. Four to seven, hollow, psilate, homomorphic, straight to slightly curved, elongate, stout, spine-like processes, distinct but drawn out from vesicle; wall thin (i.e., similar to eilyma thickness); interiors freely communicating with vesicle cavity. Processes 17 (24) 34 µm long, tapering from subcircular base, 3–6 µm in diameter, to acuminate or blunted tip; proximal contacts straight to very slightly curved. Excystment by simple splitting of eilyma.

Measurements.—Vesicle diameter 16 (22) 26 µm; based on 15 specimens.

Holotype.—OPC 2071-3905, sample/slide 1144 SYO/20-52 µm/5, field finder M9/3,-2; Plate 17, Figure 7. Vesicle outline circular, diameter 26 µm; eilyma ca. 0.5 µm thick; 6 prominent, robust, hollow, spine-like processes, 24 µm long, drawn out from and opening freely into vesicle interior, tapering from subcircular base, 4 µm in diameter, to acuminate or blunted tip; proximal process contacts straight or very slightly curved; simple split in eilyma constituting excystment structure.

Derivation of name.—Latin, *viriosus*, robust, strong; in reference to the stout, durable processes.

Comparison.—Micrhystridium viriosum Playford and Wicander, new species differs from *M. prolixum* in having fewer and stouter (less tapering) processes with broader bases; and from *M. irevikenense* Le Hérissé, 1989 (p. 157, 158, pl. 18, figs. 3–5) in possessing a thinner eilyma and process wall and generally fewer processes.

Occurrence.—OPC 2071, Sylvan Shale samples 1142 SYO through 1145 SYO (present study).

Micrhystridium sp. cf. **M. stellatum** Deflandre, 1945

Plate 18, Figure 3

cf. *Micrhystridium stellatum* DEFLANDRE, 1945, p. 65, pl. 3, figs. 16–19.

Remarks.—Morphologically simple specimens with circular-subcircular vesicle outline, not clearly differentiated from the homomorphic, spine-like, psilate, hollow processes, are uncommon in our samples. They are at least comparable to the Mesozoic species *Micrhystridium stellatum* Deflandre, 1945, a binomen that has been applied with varying precision to Paleozoic forms by many authors (e.g., Lister, 1970; Playford, 1977; Colbath, 1990).

Measurements.—Vesicle diameter 23 (27) 31 µm; process length 11 (17) 26 µm, basal width 1.6–2.4 µm, number of processes 12 (18) 25; based on 7 specimens.

Occurrence.—OPC 2071, Sylvan Shale samples 1142 SYO through 1145 SYO (present study). *M. stellatum* has been widely reported *per se* from Ordovician through Jurassic strata (Eisenack and others, 1979, p. 505, 506).

Micrhystridium sp. A
Plate 18, Figure 4

Description.—Vesicle originally spherical, outline subcircular. Eilyma and process wall thin (ca. 0.4 µm thick), hence prone to folding; psilate to minutely and densely sculptured. Processes prominent, distinct from vesicle (proximal contacts angular to slightly curved); homomorphic, spine-like, tapering gently from broad subcircular base to acuminate tip. Processes hollow, communicating directly with vesicle interior. Excystment by simple splitting of eilyma.

Measurements.—Vesicle diameter 60, 62, 75 µm; process length 33–56 µm, width 5–9 µm, number of processes 6, 10, 11; based on 3 specimens.

Comparison.—Too few specimens of this form are available for satisfactory characterization or comparison with published species. However, our specimens show some similarity to *Gyalorhethium chondrodes*, differing chiefly in an appreciably thinner and virtually psilate eilyma and process wall.

Occurrence.—OPC 2071, Sylvan Shale samples 1142, 1145 SYO (present study).

Genus **Multiplicisphaeridium** Staplin, 1961 emend. Sarjeant and Vavrdová, 1997

Type species.—Multiplicisphaeridium ramispinosum Staplin, 1961 emend. Sarjeant and Vavrdová, 1997 [OD].

Discussion.—Sarjeant and Stancliffe (1994, p. 32), following Cramer and Díez (1979, p. 63), considered *Adorfia* Burmann, 1970 (p. 294, 295) a taxonomic junior synonym of *Multiplicisphaeridium* Staplin, 1961. Tongiorgi and others (2003, p. 47) disagreed, based on their study of a Chinese Arenig specimen of *A. firma* Burmann, 1970 (type species). They claimed that, unlike *Multiplicisphaeridium*, the vesicle of *Adorfia* is polyhedral. In any case, Sarjeant and Vavrdová (1997, p. 30) had opted to segregate the two genera and, not unreasonably, to merge *Adorfia* with another (earlier) Burmann genus, *Schizadiacrodium* Burmann, 1968 (p. 42). We follow Sarjeant and Vavrdová (1997).

Multiplicisphaeridium bifurcatum
Staplin, Jansonius, and Pocock, 1965
Plate 18, Figures 5, 6

Multiplicisphaeridium bifurcatum STAPLIN, JANSONIUS, and POCOCK, 1965, p. 182, pl. 18, fig. 13.

?*Multiplicisphaeridium bifurcatum* Staplin, Jansonius, and Pocock, 1965—UUTELA and TYNNI, 1991, p. 88, fig. 193.

Measurements.—Diameter of vesicle 19 (25) 32 µm; number of processes 9 (17) 22, length 9 (15) 21 µm, basal diameter 2–4 µm; based on 34 specimens.

Remarks.—In our material, the processes of *Multiplicisphaeridium bifurcatum* Staplin, Jansonius, and Pocock, 1965 are fairly uniform in length on individual specimens. Furthermore, although the processes are mostly near-homomorphic, showing first-order distal bifurcation, some specimens also possess one or a few simple (unbranched) processes and/or rare processes exhibiting second-order bifurcation. This observation concurs with Loeblich and Tappan's (1978, p. 1276, pl. 14, figs. 1, 2) revised description of the *bifurcatum* holotype and with the description of other North American Richmondian specimens by Wicander and others (1999, p. 17, fig. 10.4). In the present study, as in many prior reports starting with Staplin and others (1965), *M. bifurcatum* is a consistent associate of *M. irregulare* (see below). Given that circumstance, and the possibility or likelihood of morphologic intergradation between the two species, it may be expedient to consider them as taxonomic synonyms. However, we provisionally retain them here as separate taxa (see further remarks below under *M. irregulare*).

Occurrence.—OPC 2071, Sylvan Shale samples 1142 SYO through 1145 SYO (present study). Upper Ordovician elsewhere in North America and in Europe: see Wicander and others (1999, p. 17, 18) for listing of most prior occurrences. Molyneux and others (1996, text-fig. 8) considered this taxon a "cosmopolitan" species in basal Caradoc through upper Ashgill strata.

Multiplicisphaeridium irregulare Staplin, Jansonius, and Pocock, 1965

Plate 19, Figures 1–5

Multiplicisphaeridium irregulare STAPLIN, JANSONIUS, and POCOCK, 1965, p. 183, pl. 18, fig. 18 (non fig. 17).

Measurements.—Diameter of vesicle 17 (26) 33 µm; number of processes 9 (17) 23, length 11 (16) 25 µm, basal diameter 2–4 µm; based on 33 specimens.

Remarks and comparison.—Loeblich and Tappan (1978, p. 1277, pl. 14, fig. 3) redescribed and refigured the holotype of *Multiplicisphaeridium irregulare* Staplin, Jansonius, and Pocock, 1965. Their data and those of later authors (e.g., Turner, 1984, p. 121, pl. 7, fig. 4; Wicander and others, 1999, p. 19, fig. 9.9–9.12) enable reasonably confident identification of this species. Staplin and others (1965, p. 182) separated *M. bifurcatum* from *M. irregulare* because of the former's more uniform processes that are regularly bifurcant (to first order). Our and other workers' observations tend to confirm this distinction, in that most specimens of *M. irregulare* exhibit a much greater degree of process heteromorphy (especially in terms of process length and branching-variation on a given specimen).

Occurrence.—OPC 2071, Sylvan Shale samples 1142 SYO through 1145 SYO (present study). Prior reports essentially as cited for *M. bifurcatum* (above).

Genus **Navifusa** Combaz, Lange, and Pansart, 1967 ex Eisenack, 1976

Type species.—*Navifusa navis* (Eisenack, 1938) Eisenack, 1976 [OD].

Navifusa ancepsipuncta Loeblich, 1970 ex Eisenack, Cramer, and Díez, 1979

Plate 19, Figures 6, 7

Navifusa ancepsipuncta LOEBLICH, 1970a, p. 730, 731, fig. 24D.

Navifusa ancepsipuncta Loeblich, 1970 ex EISENACK, CRAMER, and DÍEZ, 1979, p. 55.

Description.—Vesicle navicular, sides ± straight and parallel, ends broadly rounded. Eilyma thin (ca. 0.5 µm thick), commonly with several small folds; surface psilate to finely punctate, the punctae generally more conspicuous within polar zone extending for some 20–30 µm from each end of vesicle. No excystment structure observed.

Measurements.—Length of vesicle 109 (126) 140 µm, breadth of vesicle 28 (39) 49 µm; based on 8 specimens.

Occurrence.—OPC 2071, Sylvan Shale samples 1142 SYO through 1144 SYO (present study); also Loeblich (1970a), Loeblich and Tappan (1978). Caradoc of Shropshire, England (Turner, 1984). Vauréal Formation (Richmondian), Anticosti Island, Québec, Canada (Jacobson and Achab, 1985). Molyneux and others (1996, text-fig. 8) classified this species as "cosmopolitan" and confined to the middle Caradoc through uppermost Ashgill interval. A subsequent record from Iranian strata is broadly dated as Llanvirn–Ashgill (Ghavidel-syooki, 2001).

Genus **Orthosphaeridium** Eisenack, 1968

Type species.—Orthosphaeridium rectangulare (Eisenack, 1963) Eisenack, 1968 [OD].

Discussion.—Eisenack's (1968, p. 91) diagnosis of *Orthosphaeridium* remains serviceable, despite emendations proposed by Kjellström (1971a, p. 49) and Turner (1984, p. 125). Kjellström (1971a) expanded the generic circumscription to include forms equipped with branching processes (namely, his *O. trabeculatum*, which in that and other respects is not convincingly akin to *Orthosphaeridium*). Turner (1984), although advocating the inclusion of forms with spherical vesicles, did not discuss the tendency for processes to be polar.

Orthosphaeridium insculptum Loeblich, 1970

Plate 20, Figures 1–4; Plate 21, Figures 1–6

Orthosphaeridium insculptum LOEBLICH, 1970a, p. 734, 735, fig. 30A–E.

Description.—Vesicle originally inflated; outline quadrate to subcircular. Single-layered eilyma, 0.9–1.6 µm thick; finely and generally distinctly sculptured with close-spaced grana and minute echinae <1 µm high. Processes discrete, homomorphic, elongate, spine-like, ± straight, distinct from vesicle, numbering 4 to 10 (generally 6 or 7), primarily but not necessarily exclusively borne at corners of quadrate forms or about polar regions of subcircular forms; hollow interior not communicating with vesicle due to presence of plug (<7 µm thick, typically 2–3 µm) located at or ca. 2–4 µm above process base; proximal process contacts curved, bases 3–7.5 µm broad (commonly slightly constricted), distally acuminate; length of processes 40 (62) 90 µm. Process wall ca. 0.3–0.8 µm thick; mostly granulate-finely echinate, but sculpture commonly reduced or absent in distal one-third to one-half of process. Median split constituting excystment structure and resulting in common preservation of half-vesicles.

Measurements.—Diameter of vesicle 48 (62) 76 µm; based on 19 specimens.

Comparison and remarks.—Although generally smaller in vesicle diameter and in maximum process length, our specimens are clearly consonant with the Sylvan Shale specimens diagnosed by Loeblich (1970a) as *Orthosphaeridium insculptum.* Eilyma and process surficial character is somewhat variable (Plate 20), some specimens being more distinctly sculptured than others, especially under LM. Wicander and others (1999, p. 19) noted that *O. insculptum* and *O. vibrissiferum* Loeblich and Tappan, 1971 (p. 186, 188, figs. 7–12) may be conspecific. However, the latter is reputedly constant in process number (four), plug placement at process-eilyma junction, and in process base being sculptured with "small granulose spinules" as well as "fine grana." Because we did not observe any such specimens, we prefer to regard *O. insculptum* and *O. vibrissiferum* as separate species.

Orthosphaeridium densigranosum Kjellström, 1971b (p. 28, 30, fig. 19) has a smaller vesicle than *O. insculptum* and its processes are also shorter with evexate distal termini.

Occurrence.—OPC 2071, Sylvan Shale samples 1142 SYO through 1145 SYO (present study); also Loeblich (1970a). See Wicander and others (1999, p. 19) for listing of other records, all from the Cincinnatian of North America and equivalent strata elsewhere. Martin (1988, fig. 1) and Molyneux and others (1996, text-fig. 8) have provided stratigraphic-range compilations of this cosmopolitan species. More recent reports are from Iranian rocks broadly dated as Llanvirn–Ashgill (Ghavidel-syooki, 2001, 2003).

Orthosphaeridium rectangulare

(Eisenack, 1963) Eisenack, 1968

Plate 22, Figures 1, 2

Baltisphaeridium rectangulare EISENACK, 1963, p. 211, pl. 20, figs. 1–3, 10.

Orthosphaeridium rectangulare (Eisenack, 1963) EISENACK, 1968, p. 92, pl. 25, fig. 1.

For additional synonymy, see Wicander and others (1999, p. 21).

Description.—Vesicle originally inflated; outline quadrate-subquadrate, subcircular, or oval; with 4 prominent, elongate, homomorphic, coplanar, spine-like processes, each based, with curved contact, at a vesicle corner. Eilyma single-layered, 0.8–1.5 µm thick, ± psilate. Processes straight to curved, commonly bent distally, tapering uniformly beyond plugged constricted base to simple acuminate tip; length 47 (88) 120 µm (but subequal on a given specimen), basal diameter 3 (5) 7 µm; hollow process interior precluded from communication with vesicle cavity by proximal plug (4–7.5 µm thick) developed at 0–6 µm above process base; process wall ca. 0.3–0.4 µm thick, essentially psilate. Additionally, although uncommonly, 1 or 2 appreciably smaller, subsidiary processes may occur on vesicle face. Median split in eilyma constituting excystment structure; consequently, half-vesicles bearing 2 of the 4 major processes are commonly encountered.

Measurements.—Diameter of vesicle 39 (64) 87 µm; based on 23 specimens.

Occurrence.—OPC 2071, Sylvan Shale samples 1142 SYO through 1145 SYO (present study); also Loeblich (1970a, as *Orthosphaeridium inflatum* Loeblich, 1970). Numerous other reports include the following: Richmondian–Gamachian of Anticosti Island, Québec, Canada (Jacobson and Achab, 1985; Martin, 1988); Richmondian of Missouri, U.S.A. (Wicander and others, 1999); Llanvirn–Caradoc (Viruan) of Gotland, Sweden (Kjellström, 1971a); Llanvirn–Ashgill of Iran (Ghavidel-syooki, 2001, 2003); Caradoc and Ashgill of Gotland, Sweden (Eisenack, 1968; Eiserhardt, 1985); and Ashgill of Estonia (Uutela and Tynni, 1991), Morocco (Elaouad-Debbaj, 1988), and Jordan (Keegan and others, 1990, as *Orthosphaeridium* cf. *O. inflatum*). Molyneux and others (1996, text-fig. 8) characterized this species as "cosmopolitan" with a range extending from basal Caradoc through upper Ashgill.

Genus **Peteinosphaeridium** Staplin, Jansonius, and Pocock, 1965 emend. Playford, Ribecai, and Tongiorgi, 1995

Type species.—*Peteinosphaeridium bergstroemii* Staplin, Jansonius, and Pocock, 1965 emend. Playford, Ribecai, and Tongiorgi, 1995 [OD].

Discussion.—Peteinoid acritarchs, distinguished by their possession of distinctively laminated processes, are especially characteristic of Ordovician—more particularly of the Lower to Middle Ordovician—strata in many parts of the world. They are represented by three genera: *Peteinosphaeridium* Staplin, Jansonius, and

Pocock, 1965 (the most abundant, diverse, and widespread), *Liliosphaeridium* Uutela and Tynni, 1991, and *Cycloposphaeridium* Uutela and Tynni, 1991, with diagnoses as emended and differentiated by Playford and others (1995).

Peteinosphaeridium accinctulum Wicander, Playford, and Robertson, 1999

Plate 22, Figures 3, 4; Plate 23, Figures 1, 2

Peteinosphaeridium accinctulum WICANDER, PLAYFORD, and ROBERTSON, 1999, p. 21, figs. 10.8–10.10, 11.1–11.4, 12.1.

Description.—Vesicle originally spherical, outline circular or subcircular. Eilyma unilayered, psilate or scabrate, ca. 0.8–2 µm thick, with discrete, prominent, solid, homomorphic, trilaminate processes spaced 2–14 µm apart and attaining lengths of 7 (9.5) 11 µm. Process trunks subcylindrical, tapering slightly to distal extremity, consisting of 3 thin, longitudinally and radially disposed laminae bearing minute echinae (SEM) especially on lamina edges. Width of trunk laminae 1–4 µm, with maximum width at process bases, the latter having angular or slightly curved contacts with vesicle; distally, each trunk lamina forming a fine, minutely echinate lateral branch at process terminus, which is thus trifurcant. Excystment structure consisting of a simple or weakly lipped, circular or subcircular pylome; operculum not observed.

Measurements.—Diameter of vesicle 40 (57) 84 µm; pylome diameter 7 (14) 19 µm; based on 40 and 12 specimens respectively.

Remarks.—Sylvan Shale representatives of *Peteinosphaeridium accinctulum* are compatible with the type material (Wicander and others, 1999), apart from extending the lower limit of the vesicle size range and tending to bear somewhat squatter (generally shorter and stouter) processes.

Occurrence.—OPC 2071, Sylvan Shale samples 1142 SYO through 1145 SYO (present study). Maquoketa Shale (Richmondian), Missouri, U.S.A. (Wicander and others, 1999).

Peteinosphaeridium septuosum Wicander, Playford, and Robertson, 1999

Plate 23, Figures 3–6; Plate 24, Figures 1, 2

Baltisphaeridium sp. b of WRIGHT and MEYERS, 1981, p. 22, pl. 5, figs. A–C.

Peteinosphaeridium septuosum WICANDER, PLAYFORD, and ROBERTSON, 1999, p. 21, 23, figs. 11.5–11.9, 12.2, 12.3.

Description.—Vesicle originally spherical; outline circular or subcircular. Unilayered, psilate or scabrate eilyma, ca. 0.7–1 µm thick; bearing numerous, homomorphic, solid, elongate, spine-like processes with angular or slightly curved proximal contacts, tapering gradually overall from base to ± blunted distal extremity. Processes discrete (basal separation, 2–12 µm), straight to curved, length 4 (7) 10 µm (fairly uniform on given specimen). Processes trilaminate, consisting of 3 longitudinally and radially disposed trunk laminae, 1–3.5 µm wide at base, narrowing ± uniformly to non-furcate distal process extremity. Laminae sculptured, mostly along their edges, with minute blunted echinae commonly extended (in well-preserved specimens, per SEM) as very fine thread-like projections up to 1.5 µm long. Pylome circular-subcircular, generally with flat or slightly elevated, psilate, lip-like modification 2–3.5 µm wide; operculum psilate.

Measurements.—Diameter of vesicle 43 (57) 70 µm; pylome diameter 6 (13) 19 µm; based on 40 and 18 specimens respectively.

Remarks.—Like the Sylvan Shale specimens of *Peteinosphaeridium accinctulum*, those identified here with *P. septuosum* Wicander, Playford, and Robertson, 1999 bear close similarity to the type material. However, the present specimens generally have slightly coarser processes (i.e., incorporating somewhat broader trunk laminae extending distally from process base). The thinness of the eilyma results in its being irregularly pitted or channeled in poorly preserved specimens.

Occurrence.—OPC 2071, Sylvan Shale samples 1142 SYO through 1145 SYO (present study). Maquoketa Shale (Richmondian), Kansas and Missouri, U.S.A. (Wright and Meyers, 1981; Wicander and others, 1999).

Genus **Poikilofusa** Staplin, Jansonius, and Pocock, 1965 *sensu* Loeblich and Tappan, 1978

Type species.—*Poikilofusa spinata* Staplin, Jansonius, and Pocock, 1965 [OD].

Discussion.—As noted above under *Dactylofusa*, a broad concept of that genus includes *Poikilofusa* Staplin, Jansonius, and Pocock, 1965 (p. 185) as a junior synonym. Pending the necessary taxonomic revision of such forms, including the contents of *Eupoikilofusa*, we adopt here informally Loeblich and Tappan's (1978, p. 1281) circumscription of *Poikilofusa*.

Poikilofusa sp. A

Plate 24, Figures 5, 6

Description.—Outline fusiform overall with elliptical vesicle drawn out at each end to form an elongate, conspicuously tapering, spine-like process with obtusely blunted apex. Processes hollow and in unobstructed communication with vesicle cavity. Eilyma and process wall of similar thickness (ca. 0.8 µm) and sculpture; the latter consisting of very evenly and closely spaced, regularly disposed, minute, ± parallel-sided, solid projections with truncate (mainly) or obtusely rounded apices; height and basal breadth of projections both within range of 0.1–0.2 µm, basal separation <0.3 µm (SEM). Projections arranged linearly, near-parallel to sides of vesicle and longitudinally on processes, and also oblique to those directions thus producing an intersecting "criss-cross" pattern. No excystment structure evident.

Measurements.—Overall length 107 µm, breath 43 µm. Length and basal breadth of processes ca. 61–70 µm (the shorter probably incomplete) and ca. 14 µm respectively; based on 1 specimen.

Comparison.—This form differs from *Poikilofusa syrdenospermatella* Loeblich and Tappan, 1978 (p. 1282, 1283, pl. 12, figs. 6, 7) in being less than half as long and in having mainly truncate minute projections that, in part, form intersecting oblique rows as well as longitudinal arrangements.

Occurrence.—OPC 2071, Sylvan Shale sample 1144 SYO (present study).

Genus **Polygonium** Vavrdová, 1966 emend. Sarjeant and Stancliffe, 1994

Type species.—Polygonium gracile Vavrdová, 1966 emend. Sarjeant and Stancliffe, 1996 [OD].

Discussion.—We follow the generic emendation by Sarjeant and Stancliffe (1994, p. 42, 43) in which they reevaluated *Polygonium* Vavrdová, 1966 (p. 412, 413) and reaffirmed the status of *Goniosphaeridium* Eisenack, 1969 (p. 256) and *Celtiberium* Fombella, 1977 (p. 117) as junior synonyms of *Polygonium.*

Polygonium gracile Vavrdová, 1966 emend. Sarjeant and Stancliffe, 1996

Plate 24, Figures 3, 4

Polygonium gracile VAVRDOVÁ, 1966, p. 413, pl. 1, fig. 3, pl. 3, fig. 1.

Polygonium gracile Vavrdová, 1966 emend. SARJEANT and STANCLIFFE, 1996, p. 359, 360.

For complete synonymy, see Sarjeant and Stancliffe (1996, p. 359, 360).

Remarks and comparison.—The Sylvan Shale specimens fit the species emendation of Sarjeant and Stancliffe (1996). However, many of the specimens are somewhat smaller and have fewer processes than those from the Maquoketa Shale of Missouri (Wicander and others, 1999).

Measurements.—Vesicle diameter 17 (27) 39 µm; process length 14 (20) 32 µm, basal width 2–4 µm, distance apart 8–20 µm (as measured around vesicle periphery), number of processes 12–28; based on 57 specimens.

Occurrence.—OPC 2071, Sylvan Shale samples 1142 SYO through 1145 SYO (present study). Richmondian of North America: Maquoketa Shale, Missouri (Wicander and others, 1999); Vauréal Formation, Anticosti Island, Québec, Canada (Jacobson and Achab, 1985). Widely known from Upper Cambrian through Devonian strata (Downie, 1984; Sarjeant and Stancliffe, 1996; Tongiorgi and others, 2003).

Polygonium polyacanthum (Eisenack, 1965) Sarjeant and Stancliffe, 1994

Plate 25, Figures 5, 6

Polygonium polygonale forma *polyacanthum* EISENACK, 1965, p. 137, pl. 13, figs. 3, 4.

Polygonium polyacanthum (Eisenack, 1965) WRIGHT and MEYERS, 1981, p. 27, pl. 3, figs. K, L, pl. 7, figs. A–D. [combination invalid: ICBN, Article 33.2].

Polygonium polyacanthum (Eisenack, 1965) SARJEANT and STANCLIFFE, 1994, p. 44.

Remarks.—Sylvan Shale specimens bear slightly smaller and fewer processes than those described from the Maquoketa Shale of Missouri (Wicander and others, 1999, p. 23, fig. 12.8–12.11), but are clearly attributable to *Polygonium polyacanthum* (Eisenack, 1965) Sarjeant and Stancliffe, 1994.

Measurements.—Vesicle diameter 32 (36) 38 µm; process length 24 (24) 26 µm, basal width 4–5 µm, distance apart 8–12 µm (as measured around vesicle periphery), number of processes 9–15; based on 5 specimens.

Occurrence.—OPC 2071, Sylvan Shale samples 1142, 1145 SYO (present study). Maquoketa

Shale (Richmondian) of Kansas and Missouri, U.S.A. (Wright and Meyers, 1981; Wicander and others, 1999); and Ordovician strata elsewhere (e.g., Eisenack, 1965, Górka, 1969).

Genus **Sylvanidium** Loeblich, 1970

Type species.—Sylvanidium paucibrachium Loeblich, 1970 [OD; M].

Sylvanidium paucibrachium Loeblich, 1970

Plate 25, Figures 1, 2

Acritarchous hystrichosphere—STAPLIN, JANSONIUS, and POCOCK, 1965, p. 185, pl. 19, fig. 15.

Sylvanidium paucibrachium LOEBLICH, 1970a, p. 737, fig. 32A–F.

Remarks.—Loeblich's (1970a, p. 737) comment that his *Sylvanidium paucibrachium* "is not common" in his Sylvan Shale sample agrees with our experience. The few complete specimens we encountered have the following features: vesicle with somewhat irregular bean-shaped outline reflecting original ± ellipsoidal shape; vesicle diameter ca. 65–75 µm; thin eilyma (ca. 0.7–0.9 µm thick); two, simple, spine-like, hollow processes, each sited at opposite "poles" of vesicle; other spine-like but less prominent processes, variable in number, arising elsewhere from eilyma between poles and sometimes congregated in one area or hemisphere. Loeblich (1970a) did not mention the possibility that *S. paucibrachium* and the more common *Dorsennidium hamii* (described previously herein) intergrade morphologically. Our evidence in that regard is inconclusive, and we based our identifications of each species primarily on vesicle shape; i.e., bell-shaped for *D. hamii*, bean-shaped for *S. paucibrachium*. Jacobson and Achab (1985, p. 193) have commented on "superficial resemblance" between the two species and noted that they tend to co-occur.

Occurrence.—OPC 2071, Sylvan Shale samples 1142, 1143 SYO (present study); also Loeblich (1970a). Upper Ordovician (Ashgill) of eastern Canada (Staplin and others, 1965; Martin, 1980; Jacobson and Achab, 1985). According to Molyneux and others (1996, text-fig. 8), *S. paucibrachium* is restricted to the middle Ashgill of Laurentia.

Genus **Tunisphaeridium**
Deunff and Evitt, 1968

Type species.—Tunisphaeridium tentaculaferum (Martin, 1967) Cramer, 1971 [OD as *T. concentricum* Deunff and Evitt, 1968 = taxonomic junior synonym of *T. tentaculaferum* according to Eisenack and others (1973, p. 1057–1059)].

Tunisphaeridium eisenackii
Loeblich and Tappan, 1978

Plate 25, Figures 3, 4

Tunisphaeridium eisenackii LOEBLICH and TAPPAN, 1978, p. 1285, pl. 16, figs. 1–4.

Measurements.—Diameter of vesicle 31–45 µm; overall diameter 40–71 µm; based on 5 specimens.

Remarks.—The delicate, supra-eilyma meshwork extending laterally from the process ends to encompass the entire vesicle was described and well-illustrated by Loeblich and Tappan (1978). However, because of indifferent preservation, the meshwork is incomplete or absent in the few specimens we encountered.

Occurrence.—OPC 2071, Sylvan Shale samples 1143, 1144, 1145 SYO (present study); also Loeblich and Tappan (1978). Maquoketa Shale (Richmondian), Missouri, U.S.A. (Miller, 1991). Vauréal Formation (Richmondian), Anticosti Island, Québec, Canada (Jacobson and Achab, 1985).

Genus **Veryhachium** Deunff, 1954
ex Downie, 1959

Type species.—Veryhachium trisulcum (Deunff, 1951) ex Deunff, 1959 [SD; Downie, 1959, p. 62].

Veryhachium oklahomense Loeblich, 1970

Plate 26, Figures 1–6

Veryhachium oklahomense LOEBLICH, 1970a, p. 742, 743, fig. 36F, G.

Veryhachium lairdii (auct. non Deflandre) Deunff ex Downie, 1958—JACOBSON and ACHAB, 1985, p. 195, pl. 9, fig. 2.

Description.—Vesicle quadrate (rectangular or square) in outline, with ± straight sides. Eilyma <1 µm thick; psilate under both LM and SEM. Four coplanar, homomorphic, spine-like processes, ± straight or curved (particularly toward distal extremity), each drawn out from a vesicle corner and tapering uniformly to simple acuminate tip; hollow interiors in free communication with vesicle cavity, but processes becoming solid in distal portion. Rarely, an additional (fifth), normally smaller process emanates from the vesicle face, at right angles to the plane of the vesicle and of the other processes. Processes psilate, of similar thickness to eilyma, length near-equal on same specimen and ca. 70–110% of vesicle length. Excystment by epityche.

Measurements.—Length of vesicle 17 (22) 28 µm; length of processes 15 (22) 31 µm; based on 31 specimens.

Remarks and comparison.—Wicander and others (1999, p. 25, figs. 13.1, 14.1–14.4) withheld positive specific identification of their specimens, all featuring microgranulate sculpture, preferring a "cf." attribution to *Veryhachium oklahomense* Loeblich, 1970 because of uncertainty as to the latter's sculptural character. The numerous topotypic specimens of the present study, examined via LM (Pl. 26, Figs. 1–4) and SEM (Pl. 26, Figs. 5, 6), consistently confirm Loeblich's (1970a, p. 742) statement (albeit from LM only) that the eilyma is unsculptured. Consequently, the specimens of Wicander and others (1999), although from strata coeval with the Sylvan Shale, are still appropriately termed *Veryhachium* sp. cf. *V. oklahomense.* Specimens from the Ordovician of Western Australia, likewise compared to *V. oklahomense* by Playford and Martin (1984, p. 215, fig. 11E–G), display a finely striate eilyma and process walls. At least some of the English and Libyan Upper Ordovician specimens described and illustrated as *V. oklahomense* by Turner (1984, p. 144, pl. 11, fig. 7) and Molyneux (1988, p. 51, 52, pl. 11, fig. 11), respectively, are almost certainly misidentifications, mainly due to their appreciably greater process length/vesicle diameter ratio (cf. Molyneux, 1988, fig. 2).

Differentiating *Veryhachium oklahomense* from *V. valiente* Cramer, 1964 [p. 311, pl. 12, figs. 3, 4, 6, text-fig. 28 (7–9)], syn. *V. lairdii* Deflandre, 1946 ex Loeblich, 1970, is unclear, but possibly lies mainly in the processes of the latter being more rigid. According to its author (Loeblich, 1970a, p. 739, fig. 34A, B), *V. bromidense* differs from *V. oklahomense* in having a larger, less distinctly quadrate vesicle and is equipped with proportionately shorter, more rigid processes.

Occurrence.—OPC 2071, Sylvan Shale samples 1142 SYO through 1145 SYO (present study); also Loeblich (1970a). Other North American records, all from Upper Ordovician strata, include those by Wright and Meyers (1981), Martin (1983), and Jacobson and Achab (1985). Reports from outside of North America are listed by Wicander and others (1999, p. 25), but some of them require scrunity in view of comments above. More recently, Ghavidel-syooki (2001, 2003) has recorded the species from Iranian strata dated as Llanvirn–Ashgill.

Veryhachium trispinosum (Eisenack, 1938) Stockmans and Willière, 1962 "complex"

Plate 27, Figures 1–4; Plate 28, Figure 1

Hystrichosphaeridium trispinosum EISENACK, 1938, p. 14, 16, text-figs. 2, 3.

Veryhachium trispinosum (Eisenack, 1938) DEUNFF, 1954, p. 306. [combination invalid: ICBN, Article 33.2].

Veryhachium trispinosum (Eisenack, 1938) STOCKMANS and WILLIÈRE, 1962, p. 46, 47, pl. II, figs. 25, 26, text-fig. 1.

Veryhachium trispinosum (Eisenack, 1938) Deunff, 1954 "complex"—WICANDER and WOOD, 1981, p. 67–71.

For additional synonymy, see Wicander and Wood (1981, p. 67–70).

Description.—Vesicle triangular, sides straight to weakly or moderately convex, each corner drawn out to form a hollow, elongate, straight or curved, spine-like process in free communication with vesicle cavity and terminating in simple acuminate tip. Eilyma and process wall <1 µm thick; psilate or very faintly, minutely, and densely granulate (LM), psilate, scabrate, or microgranulate (SEM). Process length near-equal on same specimen and generally approximating or somewhat exceeding vesicle diameter. Excystment by epityche.

Measurements.—Diameter of vesicle 20 (33) 49 µm; length of processes 19 (35) 56 µm; based on 49 specimens.

Remarks.—The Sylvan Shale specimens form a morphologic continuum, expressed in the above description, when examined via LM and SEM. Wicander and Wood (1981, p. 70, 71) discussed taxonomic problems associated with such forms, and these were highlighted by the very extensive synonymy underpinning their pragmatic *Veryhachium trispinosum* (Eisenack, 1938) "complex," a term that is conveniently adopted here.

Occurrence.—OPC 2071, Sylvan Shale samples 1142 SYO through 1145 SYO (present study). Known worldwide, ranging from Ordovician through Permian (Wicander and Wood, 1981, p. 71).

Genus **Villosacapsula** Loeblich and Tappan, 1976

Type species.—Villosacapsula setosapellicula

(Loeblich, 1970) Loeblich and Tappan, 1976 [OD].

Villosacapsula setosapellicula (Loeblich, 1970) Loeblich and Tappan, 1976
Plate 28, Figures 2–6

Veryhachium setosapelliculum LOEBLICH, 1970a, p. 743, figs. 36A, B, 37A, B.

?*Veryhachium calandrae* CRAMER, 1971, p. 106, pl. 6, fig. 99, text-fig. 29a.

Villosacapsula setosapellicula (Loeblich, 1970) LOEBLICH and TAPPAN, 1976, p. 307.

Remarks.—The present specimens are consistent with previously published descriptions of *Villosacapsula setosapellicula* (Loeblich, 1970) Loeblich and Tappan, 1976: see Loeblich (1970a) and Wicander and others (1999, p. 27, fig. 14.5–14.11).

Measurements.—Diameter of vesicle 23 (30) 36 µm; length of processes, equal or unequal on a given specimen, 6 (15) 32 µm; based on 16 specimens.

Occurrence.—OPC 2071, Sylvan Shale samples 1142 SYO through 1145 SYO (present study); also Loeblich (1970a). Known widely from Upper Ordovician sediments of North America and elsewhere in the northern hemisphere (see Molyneux and others, 1996, text-fig. 8; Wicander and others, 1999; Ghavidel-syooki, 2001, 2003).

COMPOSITION OF THE PALYNOFLORA

All four sampled intervals of the Sylvan Shale in the Lawrence Quarry yielded abundant, diverse, and well-preserved palynomorphs. These consist of organic-walled microphytoplankton—acritarchs and prasinophyte phycomata, as detailed in the systematics section—together with chitinozoans and scolecodonts. Graptolite fragments were commonly encountered in the strew slides, but no cryptospores were observed.

In qualitative as well as quantitative terms, the microphytoplankton is represented overwhelmingly by acritarchs, with prasinophytes being a minor component. The acritarchs comprise 34 named species (including six formally established as new, and two "cf." identifications), one species "complex," and five possibly new species that are named informally ("sp. A"). Taxa of prasinophyte phycomata consist of one new cymatiosphaerid species, together with one specifically undifferentiated category attributable to a named leiosphaerid genus.

Qualitative and quantitative data (Text-fig. 5) demonstrate that the microphytoplankton of the sampled intervals has a considerable degree of uniformity. However, not unexpectedly, many of the rarer species—such as *Comasphaeridium lanugiferum, Hoegklintia radicosa, Sylvanidium paucibrachium,* and *Micrhystridium* sp. A—were not recorded in every sample; some (e.g., *Aremoricanium* sp. A and *Polygonium polyacanthum*) are represented by only one or a few specimens in a single sample. By contrast, the majority of the species occur consistently through the section, in proportions fluctuating among "abundant," "common," "uncommon," and even "rare" (Text-fig. 5). Especially prominent are the baltisphaerids: *Baltisphaeridium perclarum* (in particular), also *B. adiastaltum, B. curtatum, B. oligopsakium,* and *B. aliquigranulum.* Persistent, though quantitatively lesser taxa, are *Actipilion druggii, Amsdenium velatum, Aremoricanium squarrosum, Caelatosphaera cerebella, Cheleutochroa clandestina, Dorsennidium hamii, Lophosphaeridium sylvanium, Micrhystridium prolixum, Multiplicisphaeridium bifurcatum, M. irregulare, Orthosphaeridium insculptum, O. rectangulare, Peteinosphaeridium accinctulum, P. septuosum, Polygonium gracile, Villosacapsula setosapellicula, Veryhachium oklahomense,* and representatives of the *V. trispinosum* "complex" and of *Leiosphaeridia.*

CORRELATION AND AGE

Viewed as a whole, and also in terms of their constituent species, the acritarchs of the Sylvan Shale palynoflora have considerable potential for stratigraphic correlation. Furthermore, they provide independent evidence of the age of the formation, confirming inferences previously based on marine faunas and chitinozoans.

Palynostratigraphic Correlation

The present study, together with earlier papers on the Sylvan Shale (Text-fig. 2), indicates its content of 53 subgeneric taxa of organic-walled microphytoplankton, mainly formally named acritarch species (Text-fig. 6). Forty-two of these taxa are described and illustrated herein. Comparison of the species listings in Text-figures 5 and 6 shows that we did not encounter several previously reported Sylvan species. This is not surprising, given that these species are known to be very rare, having been instituted by Loeblich and Tappan (1978) from a very limited database (one or a very few specimens); e.g., *Baltisphaeridium aspersilumiferum, Disparifusa psakadoria,*

Species Formations→	Sylv.Sh.	Maq.Sh.	Vau.Fm.
Dictyotidium tappaniae	+		
Leiosphaeridia spp.	+	+	+
Actipilion druggii	+	+	
Amsdenium velatum	+		
Aremoricanium squarrosum	+		+
Aremoricanium sp. A	+		
Baltisphaeridium adiastaltum	+	+	+
Baltisphaeridium aliquigranulum	+	+	
Baltisphaeridium aspersilumiferum	+		
Baltisphaeridium curtatum	+		
Baltisphaeridium oligopsakium	+	+	
Baltisphaeridium perclarum	+	+	
Baltisphaeridium sp. A	+		
Caelatosphaera cerebella	+	+	
Cheleutochroa clandestina	+	+	
Cheleutochroa gymnobrachiata	+		+
Comasphaeridium lanugiferum	+		+
Dactylofusa anolota	+		
Dactylofusa ctenista	+		
Dactylofusa parvuligranosa	+	+	
Dactylofusa platynetrella	+		
Disparifusa psakadoria	+		
Dorsennidium hamii	+	+	+
Dorsennidium undosum	+	+	
Estiastra oklahomensis	+		
Gyalorhethium spinuliferum	+		
Gyalorhethium sp. cf. *G. chondrodes*	+		
Gyalorhethium sp. A	+		
Hoegklintia radicosa	+	+	+
Leiofusa litotes	+	+	
Leiovalia crassa	+		
Lophosphaeridium sylvanium	+		
Micrhystridium hirticulum	+	+	
Micrhystridium prolixum	+	+	
Micrhystridium viriosum	+		
Micrhystridium sp. cf. *M. stellatum*	+		
Micrhystridium sp. A	+		
Multiplicisphaeridium bifurcatum	+	+	+
Multiplicisphaeridium irregulare	+	+	+
Navifusa ancepsipuncta	+		+
Orthosphaeridium insculptum	+	+	+
Orthosphaeridium rectangulare/inflatum	+	+	+
Peteinosphaeridium accinctulum	+	+	
Peteinosphaeridium septuosum	+	+	
Poikilofusa syrdenospermatella	+		
Poikilofusa sp. A	+		
Polygonium gracile	+	+	+
Polygonium polyacanthum	+	+	
Sylvanidium paucibrachium	+		+
Tunisphaeridium eisenackii	+	+	+
Veryhachium oklahomense	+	+	+
Veryhachium trispinosum "complex"	+		
Villosacapsula setosapellicula	+	+	

Text-figure 6. Checklist of organic-walled microphytoplankton species described from the Sylvan Shale (Sylv. Sh.) by Loeblich (1970a), Loeblich and MacAdam (1971), Loeblich and Tappan (1978), and present authors; and published occurrences of those species in the Maquoketa Shale (Maq. Sh.) of Missouri and Kansas (Wright and Meyers, 1981; Miller, 1991; Wicander and others, 1999) and in the Vauréal Formation (Vau. Fm.) of Anticosti Island, Québec, Canada (Staplin and others, 1965; Jacobson and Achab, 1985).

Estiastra oklahomensis, and *Poikilofusa syrdenospermatella*.

From Text-figure 2, and as discussed previously, it is evident that knowledge of Cincinnatian palynofloras of North America is by no means comprehensive, falling far short of the desirable goal of achieving a detailed palynostratigraphic sequence for that interval. Nevertheless, the extra-Sylvan North American records of many of the 53 taxa are predominantly from two palynologically investigated formations; namely, the Maquoketa Shale of Missouri and Kansas and the Vauréal Formation of Anticosti Island in the eastern Canadian province of Québec. Almost 50% of the known Sylvan taxa are shared with the Maquoketa, 30% with the Vauréal, and 21% occur in all three formations (Text-fig. 6). Although the three units have not received the same degree of palynologic investigation, an appreciable commonality and therefore strong correlation is indicated among their respective palynofloras, as discussed below.

Particularly noteworthy are the following species shared by the Sylvan, Maquoketa, and Vauréal assemblages: *Baltisphaeridium adiastaltum*, *Dorsennidium hamii*, *Hoegklintia radicosa*, *Multiplicisphaeridium bifurcatum*, *M. irregulare*, *Orthosphaeridium insculptum*, *O. rectangulare* (syn. *O. inflatum*), *Tunisphaeridium eisenackii*, and *Veryhachium oklahomense*. Furthermore, *Baltisphaeridium perclarum*, which is a prominent and characteristic component of the Sylvan and Maquoketa palynofloras, has been recorded in the Upper Ordovician Whitehead Formation of Québec, Canada (Martin, 1980) and could reasonably be expected to occur also in the Vauréal Formation (which itself warrants more detailed palynologic study). Other species characterizing the Sylvan assemblage and one or other of the Maquoketa and Vauréal suites include: *Actipilion druggii*, *Aremoricanium squarrosum*, *Baltisphaeridium aliquigranulum*, *B. oligopsakium*, *Caelatosphaera cerebella*, *Cheleutochroa clandestina*, *C. gymnobrachiata*, *Comasphaeridium lanugiferum*, *Dactylofusa parvuligranosa*, *Dorsennidium undosum*, *Leiofusa litotes*, *Micrhrystridium hirticulum*, *M. prolixum*, *Navifusa ancepsipuncta*, *Peteinosphaeridium accinctulum*, *P. septuosum*, and *Villosacapsula setosapellicula*.

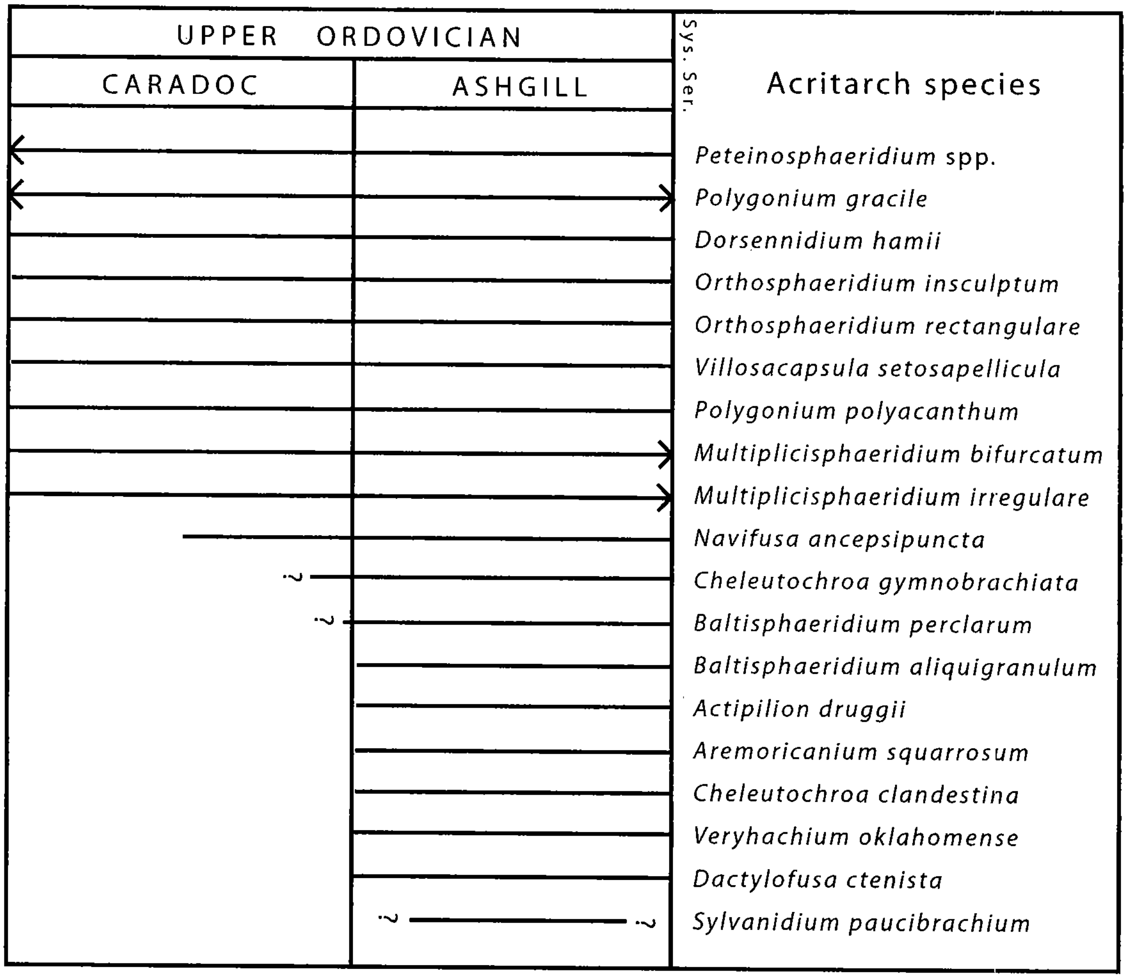
Although palynologic knowledge of immediately pre- and post-Richmondian strata is admittedly sparse, the large majority of species cited above appear collectively to constitute a distinct palynostratigraphic entity, facilitating precise correlation of the Sylvan Shale with both the Maquoketa Shale and the Vauréal Formation. Our further palynological study of the Bill's Creek Shale and overlying Stonington Formation of Michigan's Upper Peninsula is expected to substantiate initial indications (Wicander and Playford, 1999) of acritarch-based correlation of those formations with the Sylvan and Maquoketa Shales and the Vauréal Formation. This likely would corroborate the biostratigraphic data of Goldman and Bergström (1997, p. 971, 972, text-fig. 8).

The following species, although presently unrecorded from sequences other than the Sylvan Shale, are considered likely to prove stratigraphically significant, at least in a regional context: *Dictyotidum tappaniae*, *Amsdenium velatum*, *Dactylofusa ctenista*, and *Lophosphaeridium sylvanium*.

Age of the Palynoflora

An important consequence of the inferred planktic lifestyle of acritarchs is their widespread, more or less facies-independent dissemination, and in some cases virtual cosmopolitanism, through Proterozoic–Paleozoic marine rocks. These features, coupled with their evolutionary development, means that many species are important guide fossils applicable to long-distance correlation and precise age determination.

Marine microphytoplankton provinciality during the Ordovician, especially the earlier part of the period, has been well-documented (e.g., Vavrdová, 1974, 1997; Playford and others, 1995; Tongiorgi and others, 1998; Vecoli, 1999; Servais and others, 2003). Much less is understood concerning global acritarch bioprovincialism during the Late Ordovician, because microphytoplankton of this age have been less studied than those of the earlier Ordovician (e.g., cf. Molyneux and others, 1996, text-figs. 6, 8). However, irrespective of the provinciality factor and possibly suggesting its relative inconsequence or mitigation in the Late Ordovician (Paris and Robardet, 1990, p. 200; Molyneux and others, 1996, p. 504), many Sylvan species do occur outside of Laurentia. These include *Aremoricanium squarrosum*, *Baltisphaeridium aliquigranulum*, *B. perclarum*, *Cheleutochroa clandestina*, *C. gymnobrachiata*, *Dactyofusa ctenista*, *Dorsennidium hamii*, *Multiplicisphaeridium bifurcatum*, *M. irregulare*, *Navifusa ancepsipuncta*, *Orthosphaeridium insculptum*, *O. rectangulare*, *Polygonium gracile*, *P. polyacanthum*, and *Villosacapsula setosapellicula*. Based on this taxonomic association, and considering the reliably known stratigraphic



Text-figure 7. Chronostratigraphic ranges of selected acritarch taxa that occur in the Sylvan Shale and have been reported widely from elsewhere. Selections and ranges based on what are considered authentic identifications. See systematic text for sources of data. Arrows indicate range-extensions into older (Middle Ordovician) or younger (lower Silurian) strata.

ranges of the respective species (Text-fig. 7), the Sylvan palynoflora is clearly of Ashgill age. *Baltisphaeridium aliquigranulum, Cheleutochroa clandestina, C. gymnobrachiata,* and *Dactylofusa ctenista* have been recorded exclusively from the Ashgill; the others listed are known to extend into the Ashgill from older Ordovician strata. It seems likely that *Baltisphaeridium perclarum* is probably confined to the Ashgill, its supposedly older (Caradoc) occurrences requiring confirmation.

Numerous species of *Peteinosphaeridium* occur in Lower and Middle Ordovician successions (e.g., Playford and others, 1995; Tongiorgi and others, 2003), but the diversity of this genus declines considerably higher in the system. For instance, in the Sylvan and Maquoketa Shales only two species (*P. accinctulum* and *P. septuosum*) are represented; and from the Eden Formation of Indiana, Colbath (1979) described two species (*P. indianaense* and *P. spiracula*). *Peteinosphaeridium* disappeared at the close of the Ordovician, as did several other genera including *Orthosphaeridium* (Molyneux and others, 1996, p. 508) and a host of species. Many new taxa appear in the succeeding lower Silurian (Llandovery) acritarch assemblages, which are thus well-differentiated from those of the Upper Ordovician (e.g., Colbath, 1986; Martin, 1988).

The acritarch assemblages clearly confirm the Late Ordovician (Ashgill) dating of the Sylvan Shale, in terms of the international time scale, and agree with accrued evidence from other fossil groups (notably graptolites, conodonts, and chitinozoans).

PALEOENVIRONMENTAL SYNTHESIS

Sedimentologic and paleontologic-palynologic evidence indicates that the Sylvan Shale was deposited in a warm, subtidal, low-energy, offshore-marine environment (Ham, 1969; Amsden and Barrick, 1988; Dworian, 1990; Denison, 1997) with limited bottom circulation promoting anoxic conditions on or near the sea floor. This interpretation is supported by the Sylvan's well-laminated shale and calcareous-shale lithology, its content of graptolites and chitinozoans, and the sparseness of its benthic shelly fauna.

The depositional environment of the underlying carbonate Viola Group changes from a basal, deeper-water facies to a terminal shallower-water facies (Dworian, 1990; Denison, 1997; Wang and Philp, 1997). The Sylvan Shale represents another cycle of initial deeper-water deposition of black, graptolitic shale, followed by gradual shallowing with concomitant deposition of gray and greenish-gray shale and calcareous shale (Dworian, 1990; Pope, 2004).

Overlying the Sylvan Shale is the Ideal Quarry Member of the Keel Formation. This oncolitic bioclastic limestone contains a diverse shelly fauna dominated by disarticulated pelmatozoan plates and abundant brachiopods, and it was clearly deposited in a high-energy marine environment with little terrigenous input during the drop in sealevel associated with the Late Ordovician glaciation (Barrick and others, 1990; Pope, 2004).

The organic-walled microphytoplankton assemblage recovered from the four Sylvan samples provides a further basis for paleoenvironmental interpretation. The two other palynostratigraphically correlative units—the Maquoketa Shale of northeastern Missouri (Miller, 1991; Wicander and others, 1999) and northeastern Kansas (Wright and Meyers, 1981), and the Vauréal Formation of Québec (Jacobson and Achab, 1985)—are lithologically comparable to the Sylvan Shale, i.e., both consist of shales, calcareous shales, and argillaceous limestones.

Various studies have suggested that qualitative changes in organic-walled microphytoplankton morphotypes and fluctuations in species diversity and abundances can be used to determine nearshore to offshore trends (see Wicander and others, 1999; Vecoli, 2000). However, interpreting fluctuations in abundance, diversity, and morphotypes is probably not as simple as has been proposed. Just as for modern microphytoplankton taxa such as dinoflagellates, many interrelated physical and ecological factors are responsible for their distribution patterns (Colbath, 1980; Dale, 1996; Strother, 1996; Vecoli, 2000).

Nevertheless, the composition of the organic-walled microphytoplankton assemblage recovered from the Sylvan Shale indicates a marine, somewhat offshore, shelfal environment with quiescent, anoxic-bottom conditions. As discussed previously, the microphytoplankton assemblage is dominated by acritarchs, with a strictly subordinate prasinophyte content. Furthermore, the four composite samples show a high degree of taxonomic uniformity, albeit with some qualitative fluctuations of the various species (Text-fig. 5).

Jacobson (1979) based his palyno-paleoenvironmental interpretation of Middle and Upper Ordovician marine shales and limestones of Kentucky, Ohio, and New York on the relative abundances of three groupings or "classes" of acritarch species. These were termed the leiosphaerid class, the peteinosphaerid-*Dicommopalla* class, and the baltisphaerid-veryhachid-*Polygonium* class, and were considered to reflect what Jacobson (1979) characterized, respectively, as shallow-nearshore, shoal, and open-sea conditions. Of these groupings, the Sylvan microphytoplankton assemblage is most closely compatible with the baltisphaerid-veryhachid-*Polygonium* class, based on its content of common to abundant *Baltisphaeridium, Multiplicisphaeridium, Aremoricanium* (rare), *Veryhachium,* and *Polygonium.* It thus provides added and independent confirmation of an offshore, open-marine depositional setting for the Sylvan Shale. As shown in Text-figure 5, *Leiosphaeridia* spp. are also prominent (i.e., common to abundant) in the studied samples. Although Jacobson (1979) attributed his leiosphaerid class to nearshore conditions, it is pertinent to note that leiosphaerids are not restricted to shallow-water sediments. They are also known to occur plentifully in offshore and deeper-water sediments that host diverse microphytoplankton assemblages, like that of the Sylvan Shale and the Maquoketa Shale (Wicander and others, 1999, fig. 15).

Dorning (1981) recognized three acritarch assemblages in the Silurian Ludlovian shelf sea of South Wales and the Welsh Borderland, representing, in his view, increasing depth and distance from the paleoshoreline. His offshore shelf assemblage was characterized by high diversity (10–90 species per sample, normally 25–60) and moderate abundance, with no single taxon dominating the assemblage. Common genera, comprising 5–20% of the assemblage, included *Cymatiosphaera, Diexallophasis, Micrhystridium, Multiplicisphaeridium, Protoleiosphaeridium* (= *Leiosphaeridia*), and *Veryhachium.*

Vecoli (2000) reviewed previous studies on the relationship between paleoenvironment and organic-walled microphytoplankton assemblages. He based his paleoenvironmental interpretation of microphytoplankton diversity trends in the Cambrian–Ordovician of the northern Sahara Platform on the following assumptions: (1) thin-walled, simple, spherical acritarchs indicate nearshore, shallow-water conditions; (2) overall acritarch species diversity along a nearshore–offshore transect varies according to the model of Wall and others (1977) for distributional trends of dinocysts in modern environments, i.e., increasing values toward offshore-platform depositional settings; and (3) the spatial distribution of distinctive form classes has paleoenvironmental significance with morphologically complex forms such as *Baltisphaeridium* and *Peteinosphaeridium* being typically more abundant in outer-shelf, deeper-water environments.

The organic-walled microphytoplankton taxa recovered from the Sylvan Shale indicate a marine, offshore-shelf environment with well-oxygenated surface waters (and, from other associated fossil evidence, euxinic bottom conditions). This is corroborated by each of the four samples having a microphytoplankton assemblage that essentially conforms with Jacobson's (1979) offshore, open-marine suite, Dorning's (1981) offshore-shelf assemblage, and Vecoli's (2000) assumptions relating microphytoplankton diversity trends to paleoenvironment.

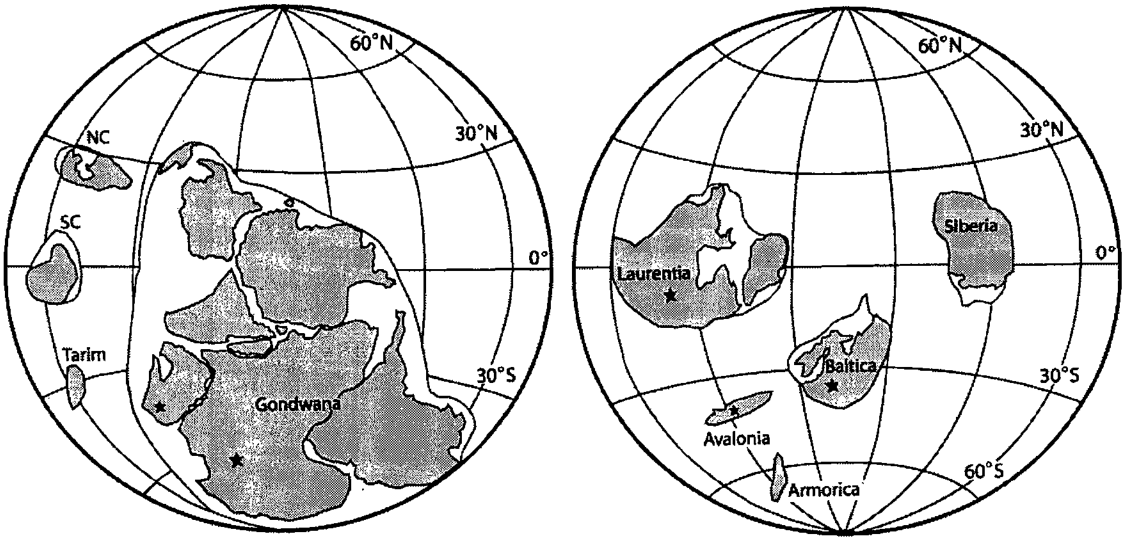
PALEOGEOGRAPHIC IMPLICATIONS

Servais and others (2003, 2004) have reviewed and synthesized what was known about the paleobiogeography of Ordovician marine microphytoplankton. Although little evidence exists of biogeographic differentiation of microphytoplankton assemblages during the Cambrian, provincialism began at the end of that period and continued through the Early Ordovician. The Arenig–Llanvirn was a time when provincialism of the microphytoplankton and other marine fossil groups was especially pronounced (Tongiorgi and others, 1998; Tongiorgi and Di Milia, 1999; Vecoli, 1999; Servais and others, 2003; Servais and others, 2004). It is thus possible to recognize cold-water (high-latitude) and warm-water (low-latitude) microphytoplankton assemblages, as well as taxa that are relatively unrestricted latitudinally during the Early and Middle Ordovician (Li and Servais, 2002). There does not, however, appear to be any significant microphytoplankton provincialism during the Late Ordovician, although this may simply reflect the limited literature dealing with well-documented assemblages of that age (Molyneux and others, 1996; Vavrdová, 1997; Wicander and others, 1999; Servais and others, 2003; Servais and others, 2004; Wicander, 2004).

Laurentia is a well-defined paleocontinent that was equatorially situated approximately between latitudes 25°N. and 20°S. during the Late Ordovician (Li and Powell, 2001; Text-fig. 8). In discussing Late Ordovician microphytoplankton distribution, Wicander and others (1999, fig. 16) plotted North American occurrences of Cincinnatian (= upper Caradoc and Ashgill) assemblages, together with relevant published coeval occurrences elsewhere. They noted that most literature on Upper Ordovician microphytoplankton pertains to occurrences in North America, Europe, and North Africa, an observation echoed by Servais and others (2004). In this paper, we plot the occurrences from well-documented Richmondian and Ashgill equivalents (Text-fig. 8). On that basis, only a handful of papers qualify for inclusion (Wicander and others, 1999, p. 30, fig. 16). As previously discussed, Laurentian microphytoplankton floras of the coeval Sylvan Shale, Maquoketa Shale, and Vauréal Formation show a high degree of similarity, thus constituting a distinct palynostratigraphic entity for Laurentia during the Late Ordovician (Text-fig. 6).

Only limited reports discuss extra-Laurentian Ashgill microphytoplankton assemblages; these are from Libya, Morocco, Belgium, Gotland, Sweden, Estonia, Portugal, and Russia (Text-fig. 8). Virtually nothing is known from Australia, South America, and China.

Whereas unmistakable biogeographic latitudinal provincialism existed during the Early and Middle Ordovician, an appreciable number of Sylvan-Maquoketa-Vauréal microphytoplankton taxa (low-latitude) have been reported from middle- to high-latitude Ashgill locations elsewhere in the world, thus substantiating a lack of provincialism during that time (Text-fig. 8). Discounting stratigraphically long-ranging taxa—such as the *Veryhachium trispinosum* "complex," species of *Micrhystridium* and *Leio-*



Text-figure 8. Geographic occurrences (star symbols) of selected Ashgill organic-walled microphytoplankton assemblages. For published records of Upper Ordovician microphytoplankton assemblages, see Wicander and others (1999, p. 30). Paleogeographic reconstruction (450 Ma) based on Li and Powell (2001). NC = North China Block; SC = South China Block.

sphaeridia, and the four taxa that range into either the Middle Ordovician or lower Silurian—14 of the 15 Upper Ordovician taxa listed in Text-figure 7 occur not only in the low latitudes of Laurentia, but also in the middle and higher latitudes of Baltica and the Peri-Gondwana region (Text-fig. 8).

Distinctive and commonly occurring taxa, however, are known to be restricted both stratigraphically and latitudinally to Laurentia. These include *Baltisphaeridium adiastaltum*, *B. oligopsakium* (excluding a dubious report from Estonia by Uutela and Tynni, 1991), *Comasphaeridium lanugiferum*, *Sylvanidium paucibrachium*, and *Tunisphaeridium eisenackii*. These taxa may prove valuable in recognizing low-latitude or warm-water assemblages elsewhere.

SUMMARY

An abundant, diversified, and well-preserved microphytoplankton assemblage has been recovered from four composite samples of the Upper Ordovician Sylvan Shale exposed in the Lawrence Quarry of the Arbuckle Mountains, southern Oklahoma. The assemblage consists of 42 acritarch and two prasinophyte species associated with scolecodonts, chitinozoans, and fragmented graptolite rhabdosomes. Based on published paleontologic information, the Sylvan Shale is confidently assigned to the North American Richmondian Stage of the Cincinnatian Series and is correlative in part with the international, British-typified Ashgill interval.

The Sylvan Shale microphytoplankton suite consists predominantly of acritarchs with the prasinophytes comprising only a small proportion of the assemblage. Whereas a high degree of taxonomic uniformity exists among the four samples, the majority of species fluctuate quantitatively throughout the sampled section. Especially common are the baltisphaerids: *Baltisphaeridium perclarum*, *B. adiastaltum*, *B. curtatum*, *B. oligopsakium*, and *B. aliquigranulum*. Also persistent, although less plentiful, are *Cheleutochroa clandestina*, *Dorsennidium hamii*, *Lophosphaeridium sylvanium*, *Multiplicisphaeridium bifurcatum*, *M. irregulare*, *Orthosphaeridium insculptum*, *O. rectangulare*, *Peteinosphaeridium septuosum*, *Polygonium gracile*, *Veryhachium oklahomense*, representatives of the *V. trispinosum* "complex," and the prasinophyte *Leiosphaeridia*.

The Sylvan Shale microphytoplankton assemblage shares almost 50% of its species with the Maquoketa Shale of Missouri and Kansas and 30% with the Vauréal Formation of Anticosti Island, Québec, Canada. Twenty-one percent of the Sylvan species are common to all three formations. Hence, this microphytoplankton suite constitutes a distinctively Laurentian Richmondian palynostratigraphic assemblage. Furthermore, certain taxa from these formations have been reported from middle- to high-latitude Ashgill localities in Baltica and Peri-Gondwana. This is indicative of the wide distribution, hence long-distance biostratigraphic potentialities, of such taxa, and also tends to support the view that regional differentiation of marine microphytoplankton assemblages was much less pronounced during the Late Ordovician than in the earlier part of the period.

Paleontologic-palynologic and sedimentologic evidence signifies that the Sylvan Shale was deposited in a warm, subtidal, low-energy, offshore-marine environment with limited circulation and consequential oxygen-deficient–bottom conditions.

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APPENDIX

Inventory of Illustrated Specimens

Catalog numbers (prefixed with the locality number OPC 2071) are those assigned by the Sam Noble Oklahoma Museum of Natural History of The University of Oklahoma (Norman, Oklahoma), where the specimens are reposited within the Leonard R. Wilson Collection of Micropaleontology and Paleobotany.

Field Finder coordinates refer to the Teledyne Gurley Field Finder, which is deposited with the slides (numbered as below), enabling precise location of the individual type specimens. The letter R at the end of the coordinates means the Field Finder is reversed when placed on the microscope stage. For locality and stratigraphic details pertaining to the samples, refer to Text-figures 3 and 4.

Species/type	Pl./Fig.	Sample	Slide	Field Finder	Catalog No.
Dictyotidium tappaniae					
Holotype	1/1	1142SYO	20-52 μm/2	S10/3,3	OPC 2071-3819
Paratype	1/2	1143SYO	20-52 μm/6	R5/-2,-1	OPC 2071-3820
Paratype	1/3	1142SYO	20-52 μm/6	T12/-3,0	OPC 2071-3821
Paratype	1/4, 7	1142SYO	20-52 μm/S8	L16/-4,-2	OPC 2071-3822
Paratype	1/5	1142SYO	20-52 μm/3	D16/3,-3	OPC 2071-3823
Paratype	1/6	1142SYO	20-52 μm/S4	L12/-3,2	OPC 2071-3824
Leiosphaeridia spp.					
Hypotype	2/1	1142SYO	>52 μm/2	W6/4,3	OPC 2071-3825
Hypotype	2/2	1144SYO	>52 μm/1	Q9/0,-5	OPC 2071-3826
Hypotype	2/3	1142SYO	20-52 μm/S4	L11/1,2	OPC 2071-3827
Actipilion druggii					
Topotype	2/4, 5	1144SYO	20-52 μm/S3	P20/-1,-2	OPC 2071-3828
Topotype	2/6, 7	1144SYO	20-52 μm/S2	K10/1,-5	OPC 2071-3829
Topotype	3/1	1145SYO	20-52 μm/6A	J19/1,-2	OPC 2071-3830
Topotype	3/2	1143SYO	>52 μm/1	T10/1,3	OPC 2071-3831
Topotype	3/3	1142SYO	>52 μm/3	C14/-3,2	OPC 2071-3832
Topotype	3/4, 5	1144SYO	>52 μm/S2	J9/3,4	OPC 2071-3833
Amsdenium velatum					
Paratype	3/6, 7	1144SYO	20-52 μm/S8	S12/2,2	OPC 2071-3834
Holotype	4/1	1144SYO	20-52 μm/5	T6/2,0	OPC 2071-3835
Paratype	4/2	1144SYO	20-52 μm/3	H19/4,-3	OPC 2071-3836
Paratype	4/3	1144SYO	20-52 μm/4	L5/5,-4	OPC 2071-3837
Paratype	4/4	1144SYO	20-52 μm/4A	F1/1,5	OPC 2071-3838
Paratype	4/5	1144SYO	20-52 μm/1	N4/-1,1	OPC 2071-3839
Paratype	4/7	1144SYO	20-52 μm/S8	R11/-5,-4	OPC 2071-3840
Paratype	4/8	1144SYO	20-52 μm/S8	S12/2,-3	OPC 2071-3841
Aremoricanium squarrosum					
Topotype	5/1	1144SYO	>52 μm/5	K3/-4,2	OPC 2071-3842
Topotype	5/2	1143SYO	>52 μm/5	H11/-5,-2	OPC 2071-3843
Topotype	5/3	1145SYO	>52 μm/4	M4/-4,-1	OPC 2071-3844

(continued on next page)

Species/type	Pl./Fig.	Sample	Slide	Field Finder	Catalog No.
Aremoricanium sp. A					
Hypotype	4/6	1143SYO	20-52 µm/3	R12/3,2	OPC 2071-3845
Baltisphaeridium adiastaltum					
Hypotype	6/3	1142SYO	>52 µm/3	N8/-1,-1	OPC 2071-3846
Hypotype	6/4	1143SYO	>52 µm/1	E10/-1,-3	OPC 2071-3847
Hypotype	6/5	1142SYO	>52 µm/S1	L9/-5,-2	OPC 2071-3848
Hypotype	6/6	1142SYO	>52 µm/S1	M10/3,1	OPC 2071-3849
Baltisphaeridium aliquigranulum					
Topotype	6/1	1143SYO	>52 µm/5	R12/4,-2	OPC 2071-3850
Topotype	6/2	1143SYO	>52 µm/1	G10/-3,-4	OPC 2071-3851
Baltisphaeridium curtatum					
Paratype	7/1	1142SYO	>52 µm/S1	M7/-4,4	OPC 2071-3852
Holotype	7/2	1143SYO	20-52 µm/5	Q20/1,5	OPC 2071-3853
Paratype	7/3	1143SYO	20-52 µm/6	Q7/1,4	OPC 2071-3854
Paratype	7/4	1142SYO	20-52 µm/S5	N6/-4,4	OPC 2071-3855
Baltisphaeridium oligopsakium					
Topotype	7/5, 6	1144SYO	>52 µm/S2	K9/3,1	OPC 2071-3856
Topotype	7/7	1145SYO	>52 µm/4	S12/-4,1	OPC 2071-3857
Baltisphaeridium perclarum					
Topotype	8/1	1145SYO	>52 µm/1	R2/-4,1	OPC 2071-3858
Topotype	8/2	1145SYO	>52 µm/1	C7/0,3	OPC 2071-3859
Topotype	8/3	1142SYO	>52 µm/2	N15/-3,-2	OPC 2071-3860
Topotype	9/3, 4	1144SYO	>52 µm/S2	J9/-3,1	OPC 2071-3861
Topotype	9/5, 6	1144SYO	>52 µm/S2	K8/-2,0	OPC 2071-3862
Baltisphaeridium sp. A					
Hypotype	9/2	1144SYO	>52 µm/1	C18/3,0	OPC 2071-3863
Caelatosphaera cerebella					
Paratype	9/1	1142SYO	20-52 µm/4	P12/3,-3	OPC 2071-3864
Holotype	10/1	1142SYO	20-52 µm/4	H14/2,-3	OPC 2071-3865
Paratype	10/2	1142SYO	20-52 µm/6	R18/-1,-1	OPC 2071-3866
Paratype	10/3, 4	1142SYO	20-52 µm/S8	L16/-1,0	OPC 2071-3867
Cheleutochroa clandestina					
Paratype	10/5, 6	1142SYO	20-52 µm/S1	M8/1,-1	OPC 2071-3868
Holotype	11/1	1142SYO	20-52 µm/2	J15/-2,-2	OPC 2071-3869
Paratype	11/2	1142SYO	20-52 µm/1	U6/1,-2	OPC 2071-3870
Paratype	11/3, 4	1142SYO	>52 µm/S1	L8/-2,2	OPC 2071-3871
Paratype	11/5, 6	1142SYO	>52 µm/S3	M8/1,2	OPC 2071-3872

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Species/type	Pl./Fig.	Sample	Slide	Field Finder	Catalog No.
Comasphaeridium lanugiferum					
Hypotype	12/1	1144SYO	20-52 µm/1	V16/3,0	OPC 2071-3873
Hypotype	12/2, 3	1144SYO	20-52 µm/S4	M12/-1,4	OPC 2071-3874
Hypotype	12/4, 5	1144SYO	20-52 µm/S5	P6/-2,-2	OPC 2071-3875
Hypotype	12/6, 7	1144SYO	20-52 µm/S4	L13/-1,5	OPC 2071-3876
Hypotype	12/8, 9	1144SYO	20-52 µm/S8	S12/-1,-4	OPC 2071-3877
Dactylofusa ctenista					
Topotype	13/3	1144SYO	20-52 µm/3A	J5/-3,-1	OPC 2071-3878
Topotype	13/4	1142SYO	20-52 µm/5	E5/3,5	OPC 2071-3879
Dorsennidium hamii					
Topotype	13/2	1142SYO	>52 µm/6	T6/1,-3	OPC 2071-3880
Dorsennidium undosum					
Topotype	13/5	1145SYO	20-52 µm/5	H16/4,4	OPC 2071-3881
Topotype	13/6	1145SYO	20-52 µm/5	E15/-3,2	OPC 2071-3882
Gyalorhethium sp. cf. *G. chondrodes*					
Hypotype	14/1	1142SYO	>52 µm/2	W8/-3,2	OPC 2071-3883
Hypotype	14/2	1142SYO	>52 µm/5	G9/-1,-5	OPC 2071-3884
Gyalorhethium sp. A					
Hypotype	13/1	1145SYO	20-52 µm/6A	E13/-1,1	OPC 2071-3885
Hoegklintia radicosa					
Topotype	14/6	1144SYO	>52 µm/S3	N19/-4,-1	OPC 2071-3886
Lophosphaeridium sylvanium					
Holotype	14/3	1144SYO	20-52 µm/1	N19/-5,4	OPC 2071-3887
Paratype	14/4	1142SYO	20-52 µm/4	F6/-4,2	OPC 2071-3888
Paratype	14/5	1144SYO	20-52 µm/3A	F3/-4,0	OPC 2071-3889
Paratype	14/7	1143SYO	20-52 µm/4	D17/-3,-4R	OPC 2071-3890
Paratype	15/1, 2	1142SYO	20-52 µm/S8	L16/0,0	OPC 2071-3891
Paratype	15/3, 4	1144SYO	20-52 µm/S7	R13/1,2	OPC 2071-3892
Paratype	15/5, 6	1144SYO	20-52 µm/S5	P7/2,-2	OPC 2071-3893
Paratype	16/1	1144SYO	20-52 µm/S7	R13/4,2	OPC 2071-3894
Paratype	16/2	1142SYO	20-52 µm/S6	N8/1,2	OPC 2071-3895
Paratype	16/3	1144SYO	20-52 µm/S7	R13/5,-5	OPC 2071-3896
Paratype	16/4	1142SYO	20-52 µm/S4	L12/-5,-1	OPC 2071-3897
Paratype	16/5	1142SYO	20-52 µm/S7	Q12/-1,2	OPC 2071-3898
Paratype	16/6	1144SYO	20-52 µm/S6	M9/2,-2	OPC 2071-3899
Micrhystridium hirticulum					
Hypotype	17/1, 2	1144SYO	20-52 µm/S5	P7/2,1	OPC 2071-3900
Hypotype	17/3	1144SYO	20-52 µm/S6	N9/1,-2	OPC 2071-3901

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Species/type	Pl./Fig.	Sample	Slide	Field Finder	Catalog No.
Micrhystridium prolixum					
Hypotype	17/4	1145SYO	20-52 µm/2	L16/-3,-1	OPC 2071-3902
Hypotype	17/5	1142SYO	20-52 µm/1	B16/-2,-3	OPC 2071-3903
Hypotype	17/6	1145SYO	20-52 µm/5	W15/-4,3	OPC 2071-3904
Micrhystridium viriosum					
Holotype	17/7	1144SYO	20-52 µm/5	M9/3,-2	OPC 2071-3905
Paratype	18/1	1145SYO	20-52 µm/6A	G18/4,-3	OPC 2071-3906
Paratype	18/2	1145SYO	20-52 µm/6A	G11/-3,-4	OPC 2071-3907
Micrhystridium sp. cf. *M. stellatum*					
Hypotype	18/3	1145SYO	20-52 µm/1	J1/-5,-4	OPC 2071-3908
Micrhystridium sp. A					
Hypotype	18/4	1145SYO	>52 µm/4	Q18/3,3	OPC 2071-3909
Multiplicisphaeridium bifurcatum					
Hypotype	18/5	1142SYO	20-52 µm/1	R8/-4,-1	OPC 2071-3910
Hypotype	18/6	1142SYO	20-52 µm/1	M20/2,-2	OPC 2071-3911
Multiplicisphaeridium irregulare					
Hypotype	19/1	1142SYO	20-52 µm/S5	N7/-1,1	OPC 2071-3912
Hypotype	19/2, 3	1144SYO	20-52 µm/S5	P6/-2,1	OPC 2071-3913
Hypotype	19/4	1143SYO	>52 µm/1A	F13/4,-3	OPC 2071-3914
Hypotype	19/5	1144SYO	20-52 µm/2	U5/-4,2	OPC 2071-3915
Navifusa ancepsipuncta					
Topotype	19/6	1144SYO	20-52 µm/5	G14/-4,1	OPC 2071-3916
Topotype	19/7	1143SYO	20-52 µm/2	H18/3,3	OPC 2071-3917
Orthosphaeridium insculptum					
Topotype	20/1	1143SYO	>52 µm/3	V1/6,-2	OPC 2071-3918
Topotype	20/2	1145SYO	>52 µm/5	K2/-4,1	OPC 2071-3919
Topotype	20/3	1145SYO	>52 µm/1	L11/0,-1	OPC 2071-3920
Topotype	20/4	1145SYO	>52 µm/5	C7/3,-2	OPC 2071-3921
Topotype	21/1-3	1144SYO	>52 µm/S2	J9/2,-2	OPC 2071-3922
Topotype	21/4	1144SYO	>52 µm/S2	K10/0,3	OPC 2071-3923
Topotype	21/5, 6	1144SYO	>52 µm/S3	P19/-2,1	OPC 2071-3924
Orthosphaeridium rectangulare					
Hypotype	22/1	1145SYO	>52 µm/5	Q11/0,0	OPC 2071-3925
Hypotype	22/2	1143SYO	>52 µm/6	Q1/-3,-3	OPC 2071-3926
Peteinosphaeridium accinctulum					
Hypotype	22/3	1144SYO	20-52 µm/4	L8/3,-4	OPC 2071-3927
Hypotype	22/4	1142SYO	20-52 µm/5	L13/-4,-3	OPC 2071-3928
Hypotype	23/1	1142SYO	20-52 µm/S6	N8/2,-2	OPC 2071-3929
Hypotype	23/2	1142SYO	>52 µm/S2	N9/-1,-4	OPC 2071-3930

(continued on next page)

Species/type	Pl./Fig.	Sample	Slide	Field Finder	Catalog No.
Peteinosphaeridium septuosum					
Hypotype	23/3	1144SYO	20-52 µm/S8	S12/-3,-4	OPC 2071-3931
Hypotype	23/4	1144SYO	20-52 µm/S6	P9/5,-4	OPC 2071-3932
Hypotype	23/5, 6	1144SYO	20-52 µm/S7	S12/3,-4	OPC 2071-3933
Hypotype	24/1	1143SYO	>52 µm/1A	G7/-4,2	OPC 2071-3934
Hypotype	24/2	1144SYO	20-52 µm/5	V11/5,4	OPC 2071-3935
Poikilofusa sp. A					
Hypotype	24/5, 6	1144SYO	20-52 µm/S8	R11/-4,2	OPC 2071-3936
Polygonium gracile					
Hypotype	24/3	1145SYO	20-52 µm/6B	L3/2,-3	OPC 2071-3937
Hypotype	24/4	1145SYO	20-52 µm/6A	L5/2,1	OPC 2071-3938
Polygonium polyacanthum					
Hypotype	25/5	1142SYO	>52 µm/1	R20/-1,2	OPC 2071-3939
Hypotype	25/6	1145SYO	>52 µm/1	K14/-4,2	OPC 2071-3940
Sylvanidium paucibrachium					
Topotype	25/1	1143SYO	>52 µm/6	L15/2,-4	OPC 2071-3941
Topotype	25/2	1143SYO	20-52 µm/5	K10/2,4	OPC 2071-3942
Tunisphaeridium eisenackii					
Topotype	25/3	1144SYO	20-52 µm/S6	N9/2,-2	OPC 2071-3943
Topotype	25/4	1143SYO	20-52 µm/3A	E7/-1,1	OPC 2071-3944
Veryhachium oklahomense					
Topotype	26/1	1144SYO	20-52 µm/1	R7/5,-4	OPC 2071-3945
Topotype	26/2	1145SYO	20-52 µm/5	F11/-1,1	OPC 2071-3946
Topotype	26/3	1144SYO	20-52 µm/3	D6/3,2	OPC 2071-3947
Topotype	26/4	1145SYO	20-52 µm/5	C7/2,1	OPC 2071-3948
Topotype	26/5	1144SYO	20-52 µm/S6	N9/-1,-2	OPC 2071-3949
Topotype	26/6	1144SYO	20-52 µm/S4	M12/0,2	OPC 2071-3950
Veryhachium trispinosum "complex"					
Hypotype	27/1	1144SYO	20-52 µm/4	G11/-1,-2	OPC 2071-3951
Hypotype	27/2	1143SYO	20-52 µm/5	N17/-5,2	OPC 2071-3952
Hypotype	27/3, 4	1144SYO	20-52 µm/S4	M13/5,-3	OPC 2071-3953
Hypotype	28/1	1144SYO	20-52 µm/4	U18/-5,-3	OPC 2071-3954
Villosacapsula setosapellicula					
Topotype	28/2	1145SYO	20-52 µm/3	F7/4,4	OPC 2071-3955
Topotype	28/3	1143SYO	20-52 µm/5	Q2/3,4	OPC 2071-3956
Topotype	28/4	1145SYO	20-52 µm/5	B5/4,3	OPC 2071-3957
Topotype	28/5, 6	1143SYO	20-52 µm/3A	R13/1,4	OPC 2071-3958

Plates

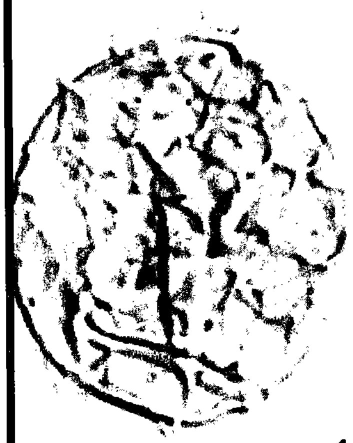
PLATE 1

For locality, stratigraphic, and curatorial details see Text-figures 3 and 4 and Appendix.

Dictyotidium

Figures 1–7.—*Dictyotidium tappaniae* Playford and Wicander, new species. **1**, holotype, ×1150; **2**, **3**, **5**, ×1150; **4**, ×1500, and **7**, part of same specimen, ×3700, showing reticula with boss-like protuberances developed at some muri intersections in the finer reticulum; **6**, ×3700, showing similar detail to Figure 7.

Plate 1



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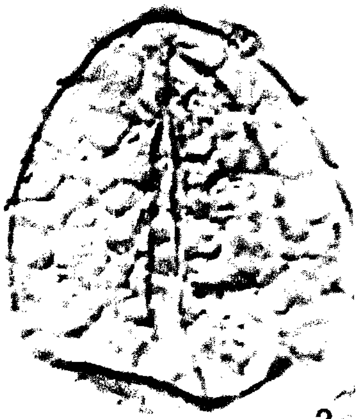

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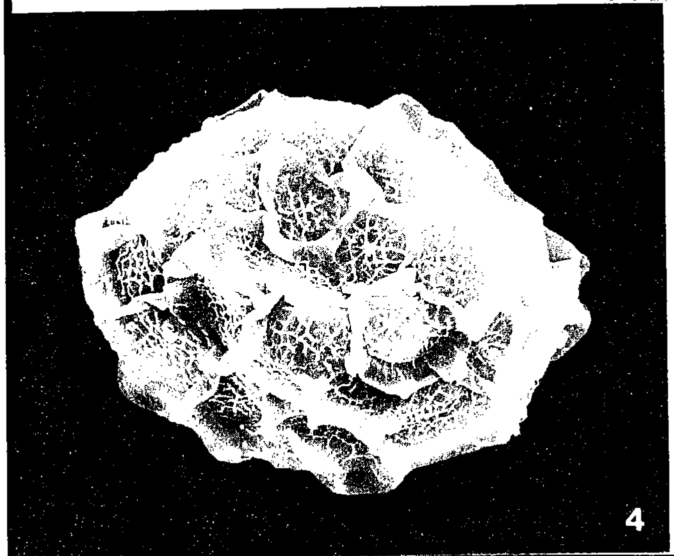

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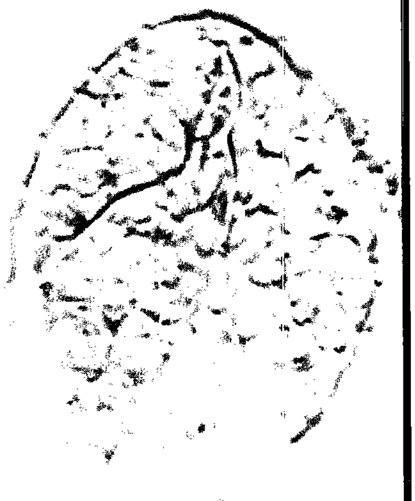

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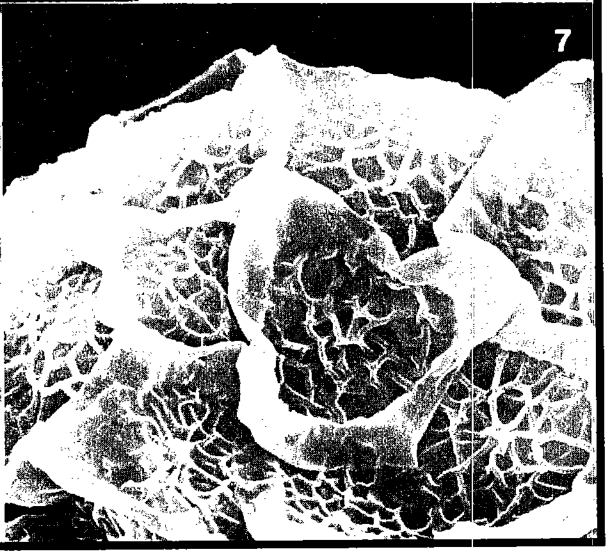

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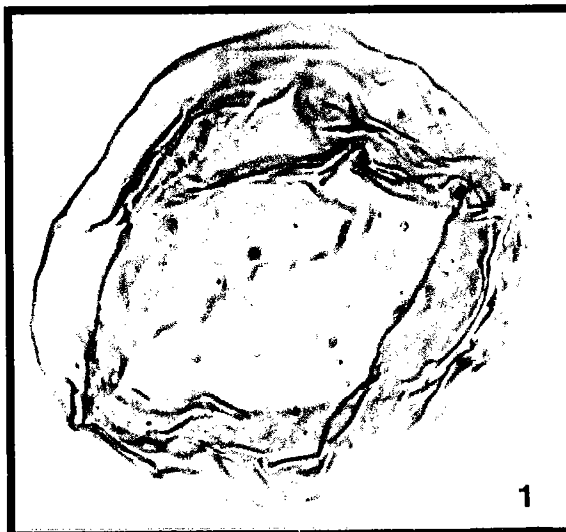
PLATE 2

For locality, stratigraphic, and curatorial details see Text-figures 3 and 4 and Appendix.

Leiosphaeridia and *Actipilion*

Figures 1–3.—*Leiosphaeridia* spp. 1, 2, ×800; 3, ×1100.

Figures 4–7.—*Actipilion druggii* Loeblich, 1970. 4, ×550, and 5, part of same specimen, ×5600, showing surficial detail of eilyma and process; 6, ×670, and 7, part of same specimen, ×3670, showing similar detail to Figure 5.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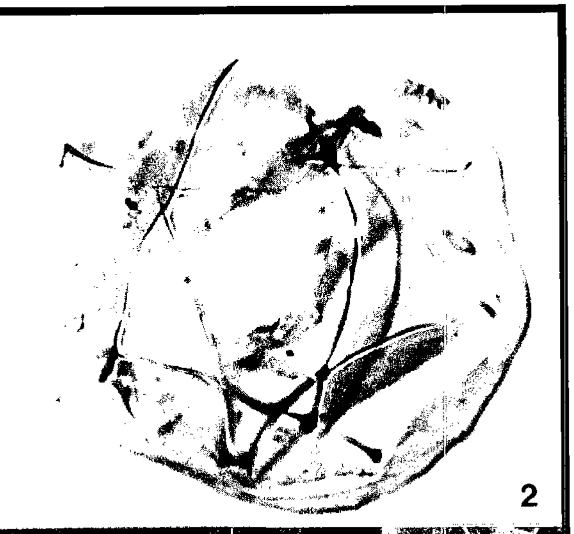
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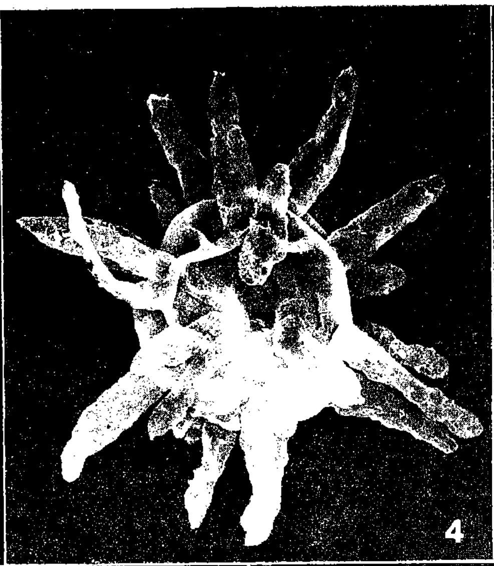
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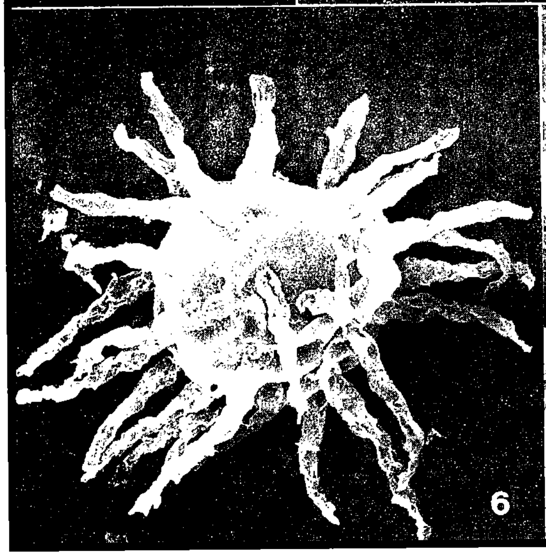
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PLATE 3

For locality, stratigraphic, and curatorial details see Text-figures 3 and 4 and Appendix.

Actipilion and *Amsdenium*

Figures 1–5.—*Actipilion druggii* Loeblich, 1970. 1–3, ×800; 4, ×560, and 5, part of same especimen, ×3670, showing surfical detail of eilyma and processes.

Figures 6, 7.—*Amsdenium velatum* Playford and Wicander, new genus and species. 6, ×1250, and 7, ×1150, SEM and LM photographs, respectively, of opposite sides of same specimen having partly intact membranous reticulum.

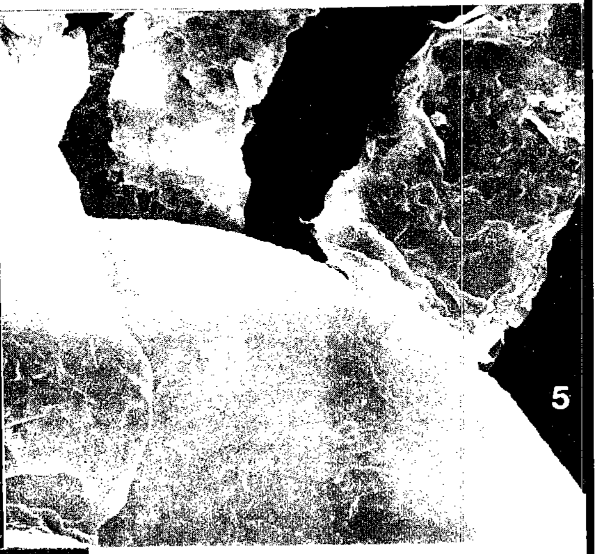
Plate 3


1


2


3


4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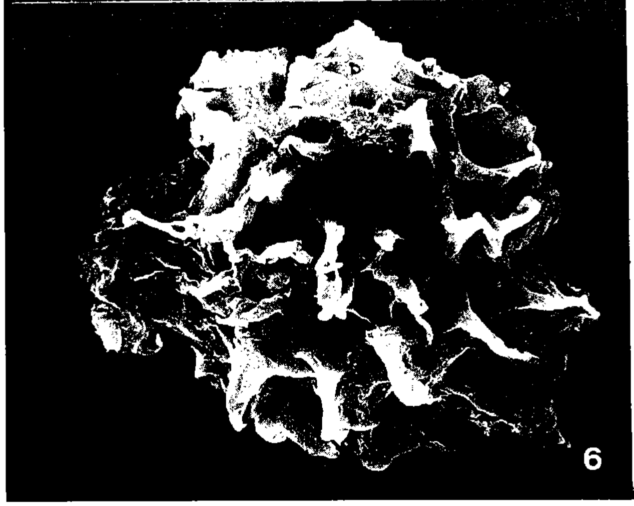
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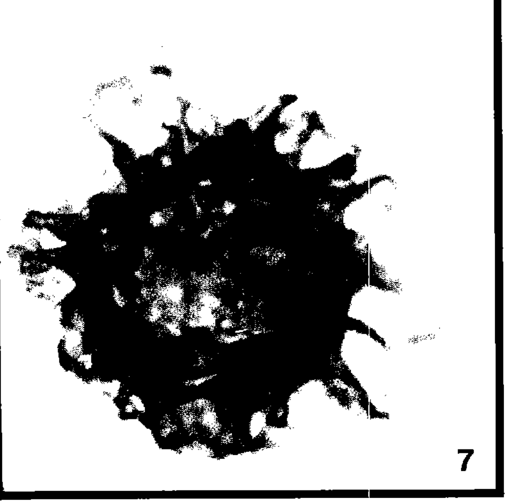
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PLATE 4

For locality, stratigraphic, and curatorial details see Text-figures 3 and 4 and Appendix.

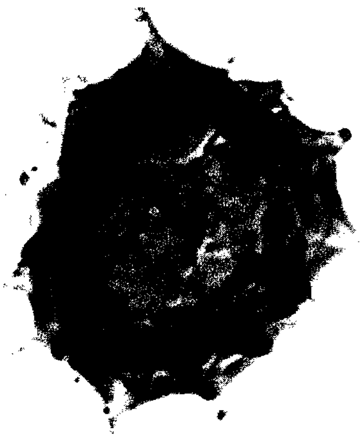
Amsdenium and *Aremoricanium*

Figures 1–5, 7, 8.—*Amsdenium velatum* Playford and Wicander, new genus and species. **1**, holotype, ×1150; **2**, **3**, ×1150; **4**, degraded specimen, ×1150, but with well-developed, near-complete neck; **5**, degraded specimen, ×1150, showing neck orifice; **7**, **8**, variably degraded specimens, ×1900 and ×1650 respectively, neck well-developed (in plan and lateral views respectively).

Figure 6.—*Aremoricanium* sp. A, ×1150.

Plate 4


1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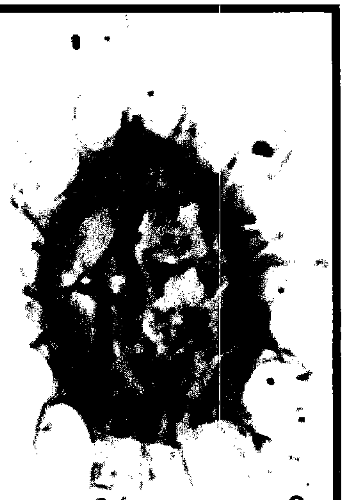
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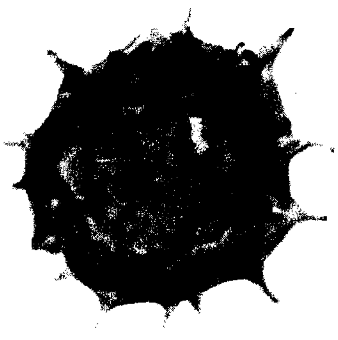
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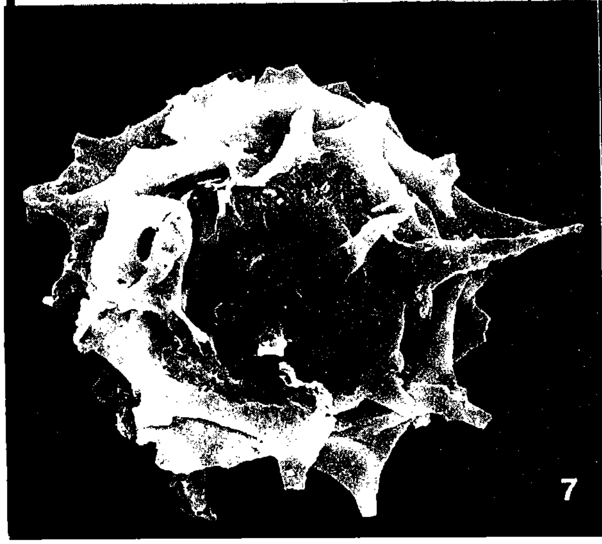
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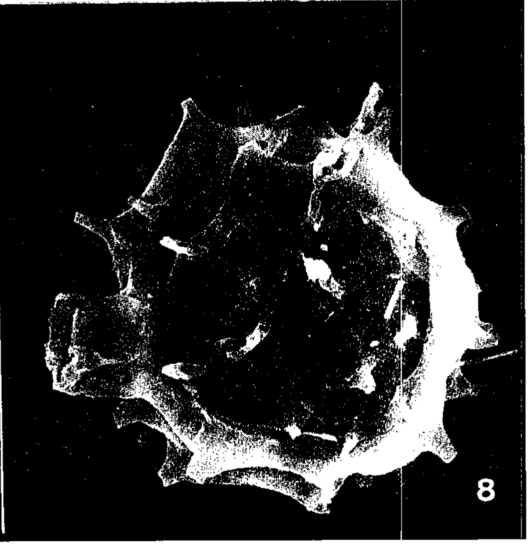

8

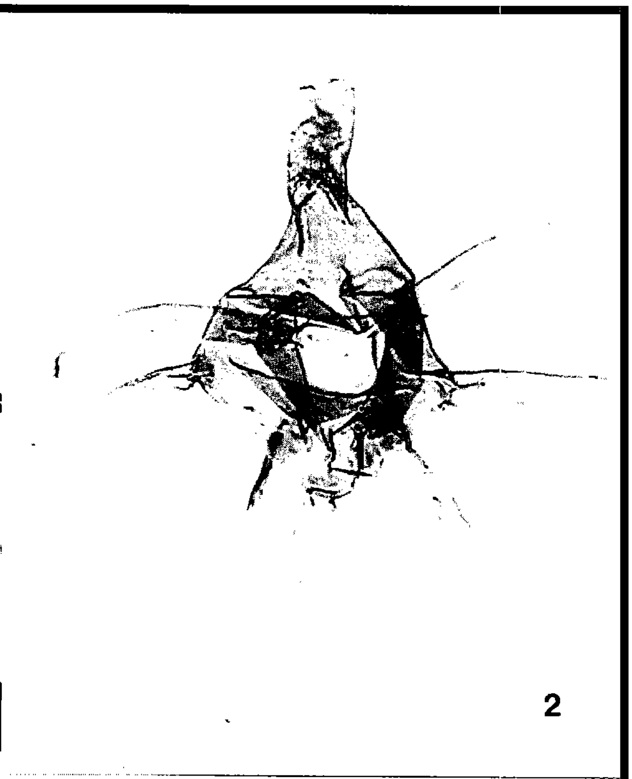
PLATE 5

For locality, stratigraphic, and curatorial details see Text-figures 3 and 4 and Appendix.

Aremoricanium

Figures 1–3.—*Aremoricanium squarrosum* Loeblich and MacAdam, 1971, ×800.

1



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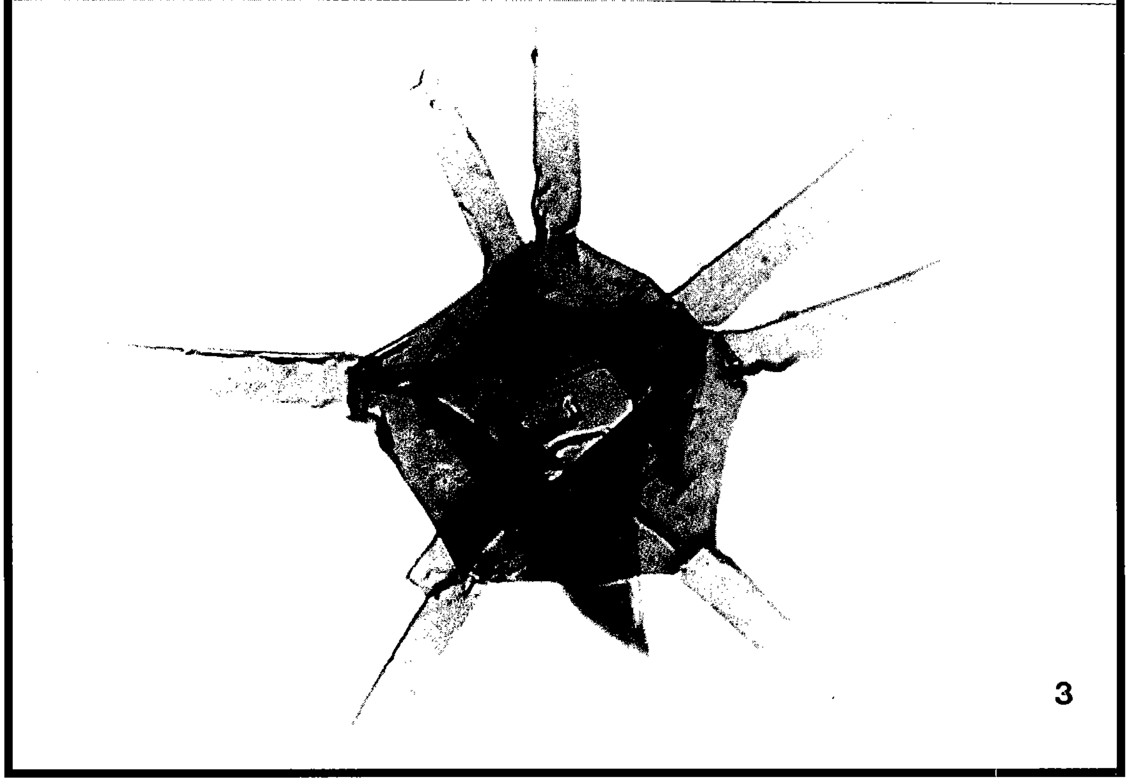


3

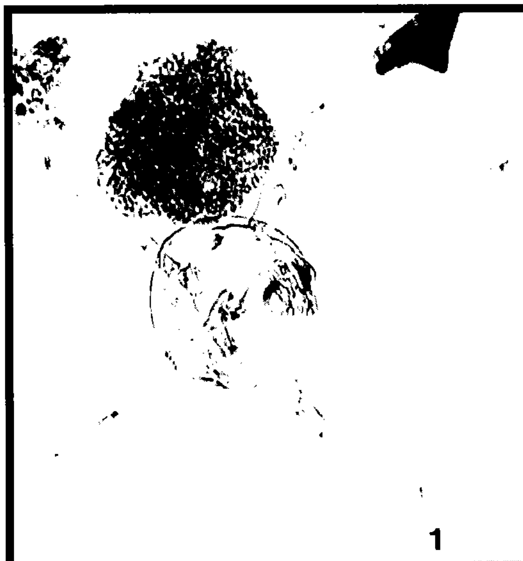
PLATE 6

For locality, stratigraphic, and curatorial details see Text-figures 3 and 4 and Appendix.

Baltisphaeridium

Figures 1, 2.—*Baltisphaeridium aliquigranulum* Loeblich and Tappan, 1978, ×400 and ×800 respectively.

Figures 3–6.—*Baltisphaeridium adiastaltum* Wicander, Playford, and Robertson, 1999. **3**, **4**, ×800; **5**, ×550; **6**, ×3670, showing ultra-fine surficial detail of eilyma and processes.



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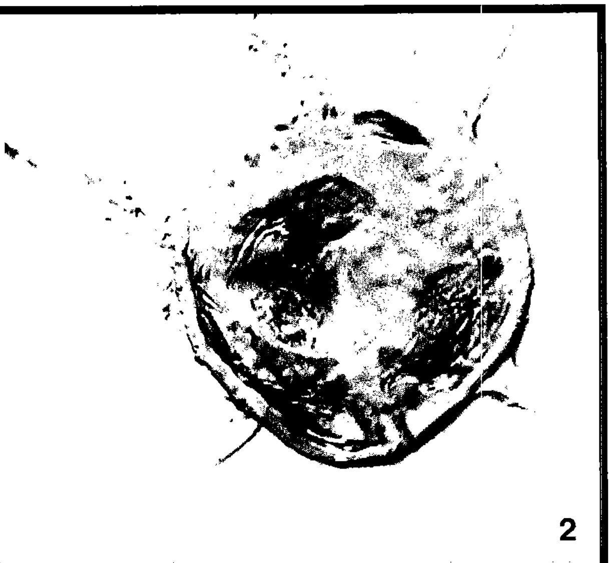

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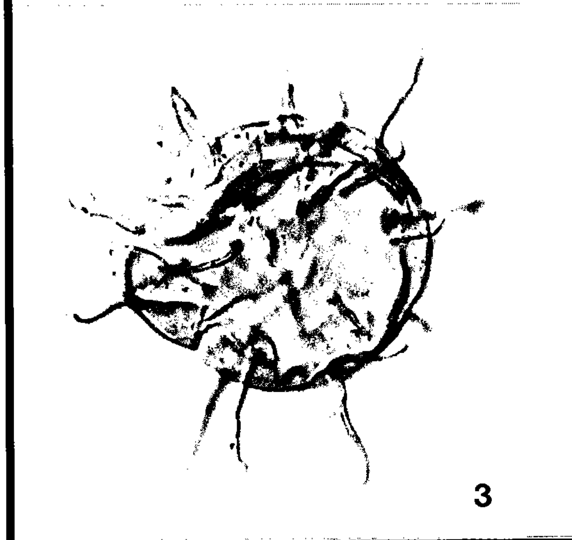

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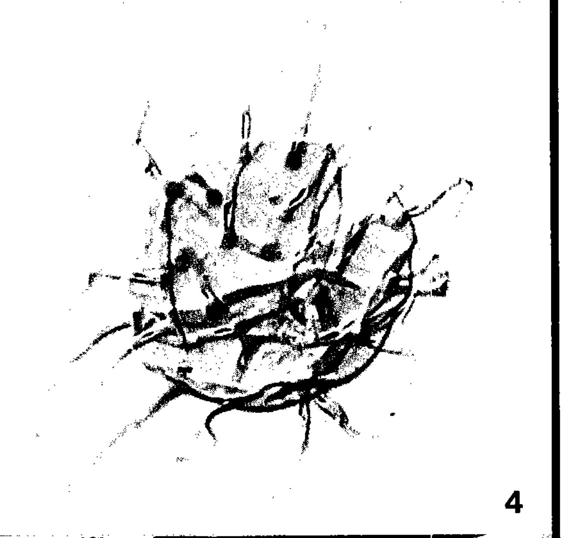

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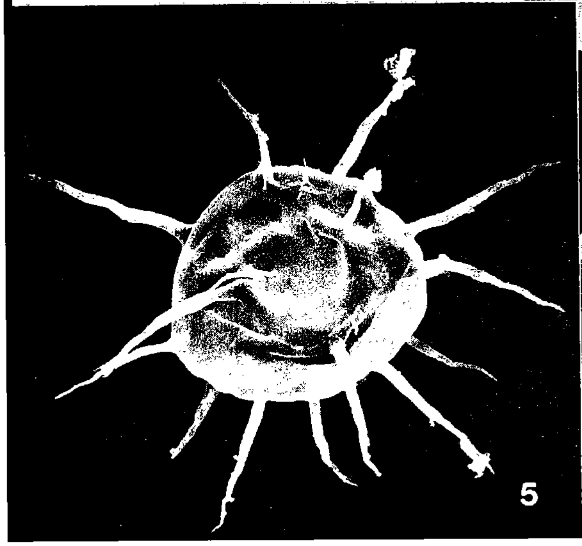

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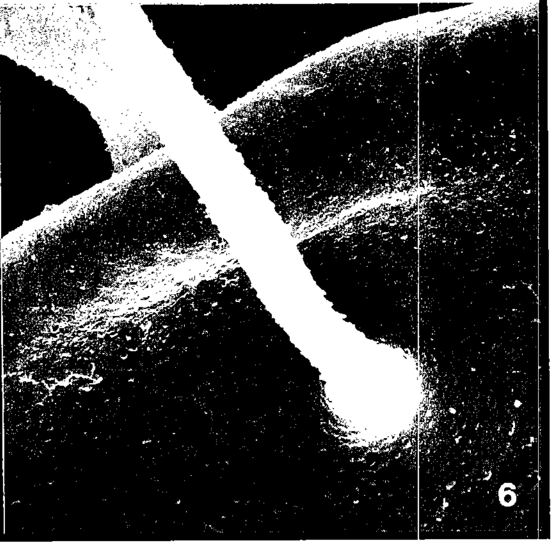

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PLATE 7

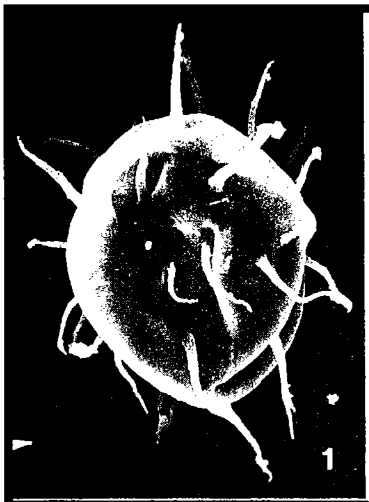
For locality, stratigraphic, and curatorial details see Text-figures 3 and 4 and Appendix.

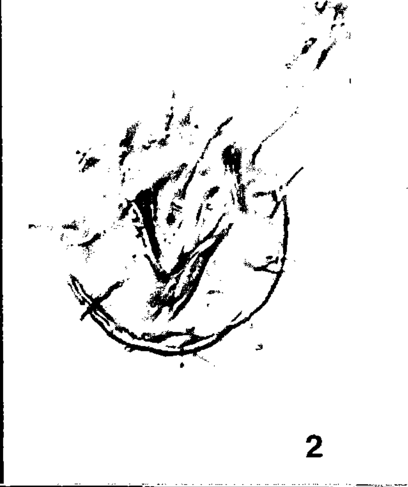
Baltisphaeridium

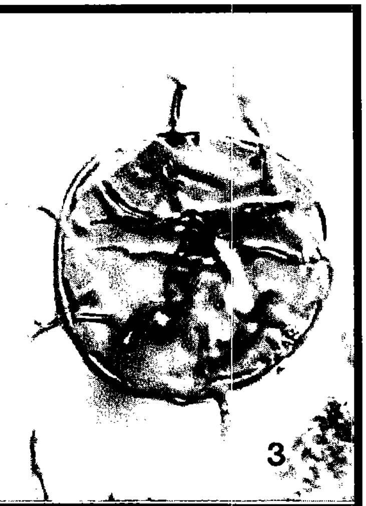
Figures 1–4.—*Baltisphaeridium curtatum* Playford and Wicander, new species. **1**, ×730; **2**, holotype, ×800; **3**, ×800; **4**, ×1100.

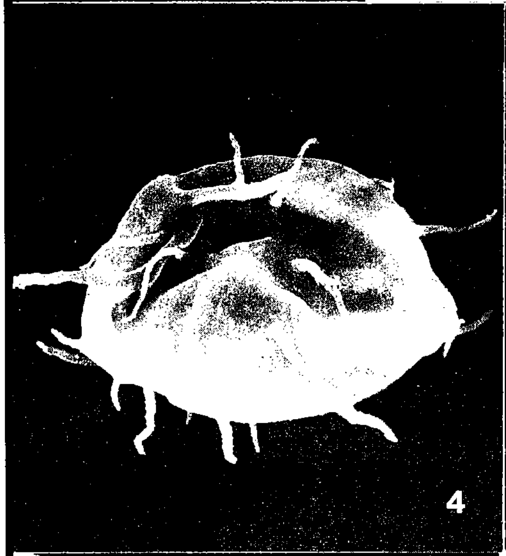
Figures 5–7.—*Baltisphaeridium oligopsakium* Loeblich and Tappan, 1978. **5**, ×600, and **6**, part of same specimen, ×3750, showing surficial detail of eilyma and processes; **7**, ×800.

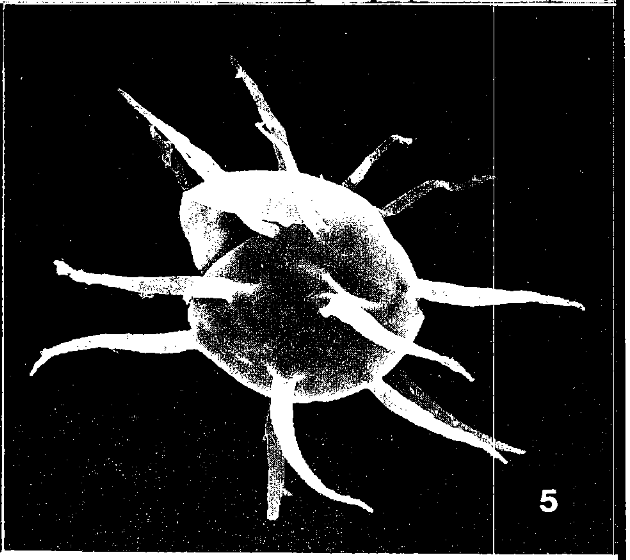
Plate 7

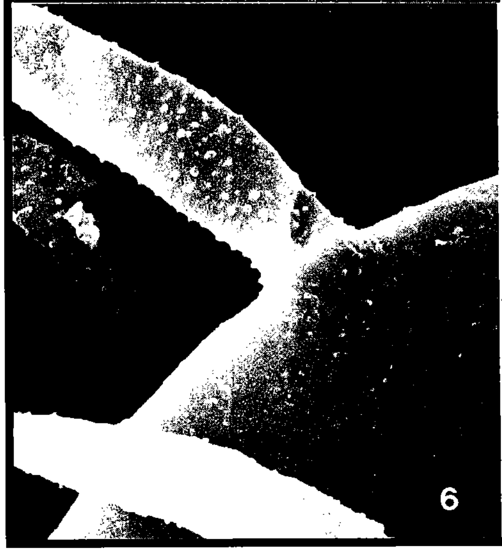












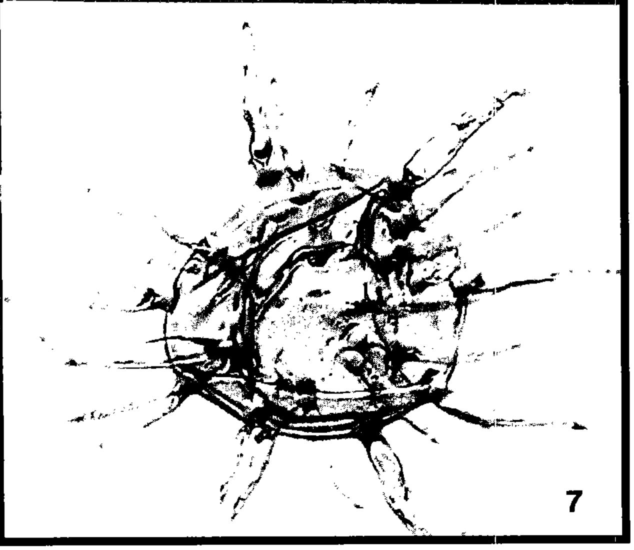


PLATE 8

For locality, stratigraphic, and curatorial details see Text-figures 3 and 4 and Appendix.

Baltisphaeridium

Figures 1–3.—*Baltisphaeridium perclarum* Loeblich and Tappan, 1978, ×800.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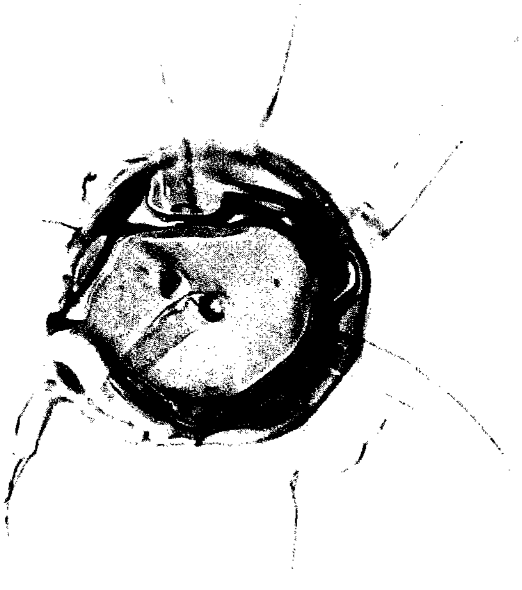
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PLATE 9

For locality, stratigraphic, and curatorial details see Text-figures 3 and 4 and Appendix.

Caelatosphaera and *Baltisphaeridium*

Figure 1.—*Caelatosphaera cerebella* Playford and Wicander, new species, ×1150.

Figure 2.—*Baltisphaeridium* sp. A, ×400.

Figures 3–6.—*Baltisphaeridium perclarum* Loeblich and Tappan, 1978. **3**, ×350, and **4**, part of same specimen, ×1700, showing surficial detail of eilyma and processes (one of which is bifurcant); **5**, ×500, and **6**, part of same specimen, ×3000, showing slightly coarser, but still diminutive, granulate sculpture of eilyma and processes.

Plate 9

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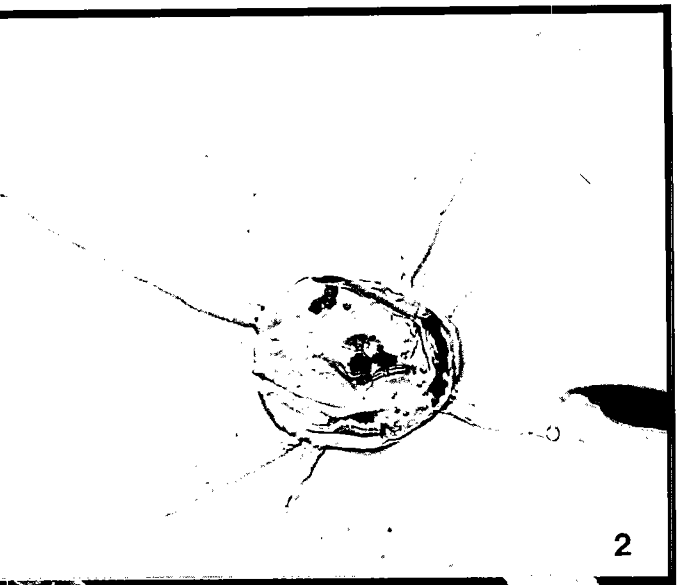

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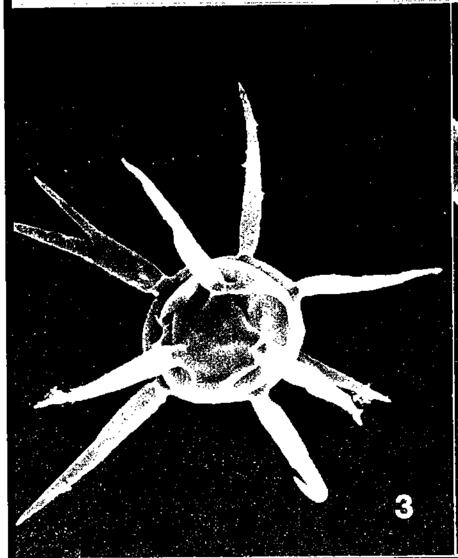

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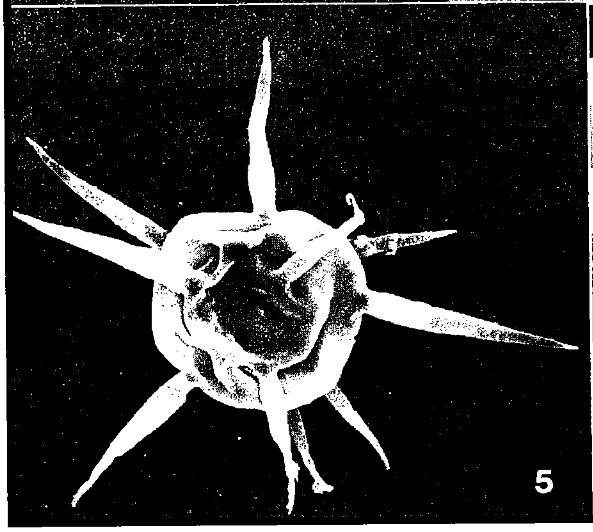

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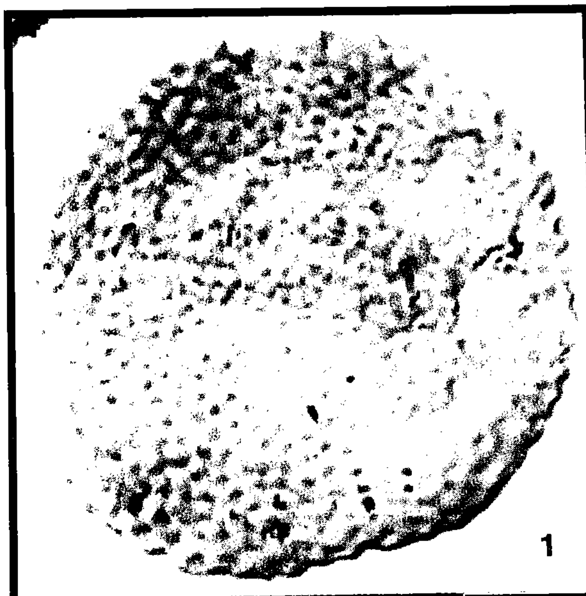
PLATE 10

For locality, stratigraphic, and curatorial details see Text-figures 3 and 4 and Appendix.

Caelatosphaera and *Cheleutochroa*

Figures 1–4.—*Caelatosphaera cerebella* Playford and Wicander, new species. **1**, holotype, ×1150; **2**, ×1150; **3**, ×1150, and **4**, part of same specimen, ×3750, showing detail of vermiculate eilyma.

Figures 5, 6.—*Cheleutochroa clandestina* Playford and Wicander, new species. **5**, ×650, and **6**, part of same specimen, ×6000, showing contrasting sculpture of eilyma (microreticulate) and process base (microstriate).



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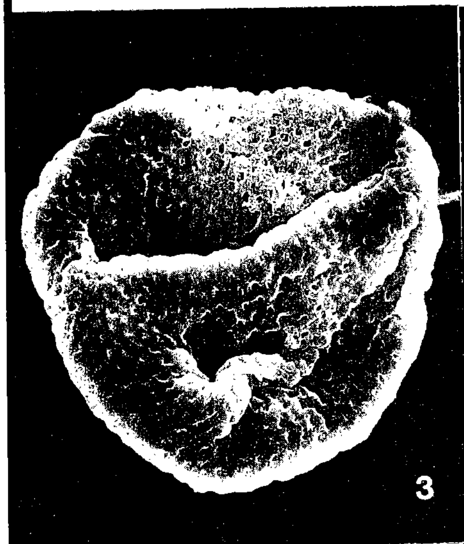

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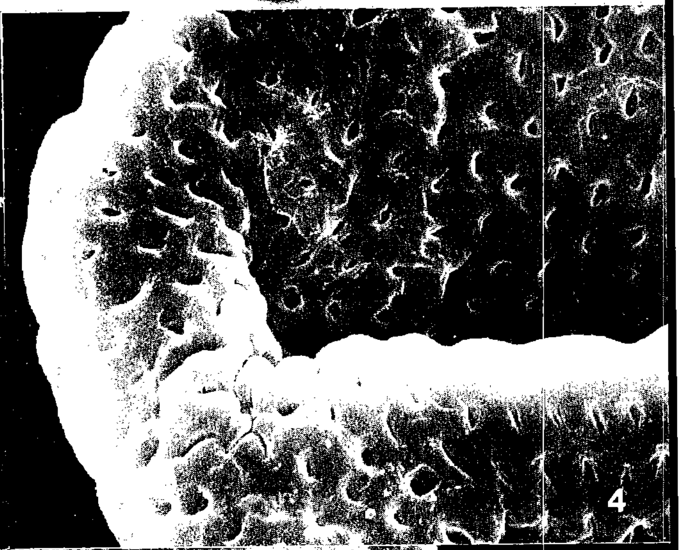

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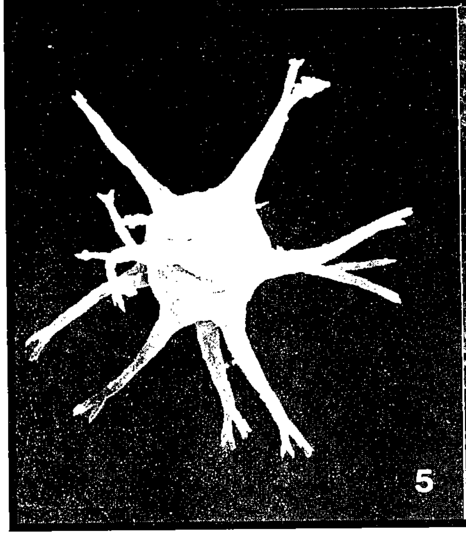

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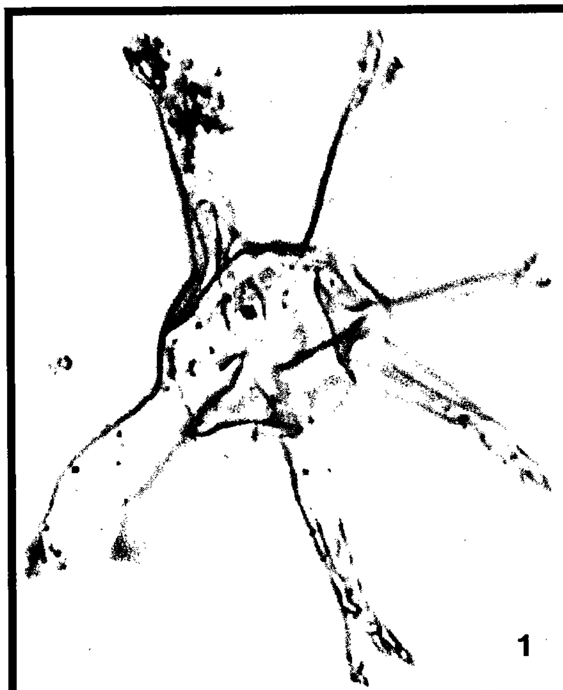
PLATE 11

For locality, stratigraphic, and curatorial details see Text-figures 3 and 4 and Appendix.

Cheleutochroa

Figures 1–6.—*Cheleutochroa clandestina* Playford and Wicander, new species. **1**, holotype, ×1150; **2**, ×1150; **3**, ×750, and **4**, part of same specimen, ×7500, showing microreticulate sculpture of eilyma with minute superposed knob-like elements; **5**, ×900, and **6**, part of same specimen, ×3750, showing eilyma sculpture, microgranulate process sculpture, and hollow interior of a process remnant (broken off near base) opening downwards into vesicle cavity.

Plate 11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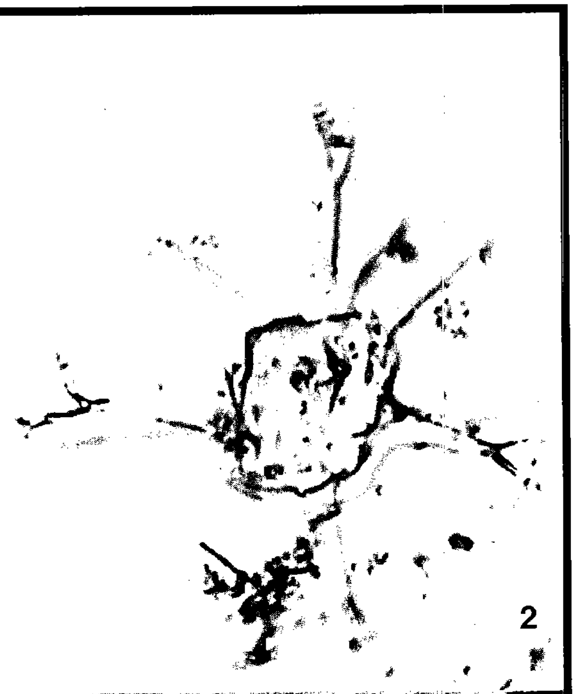
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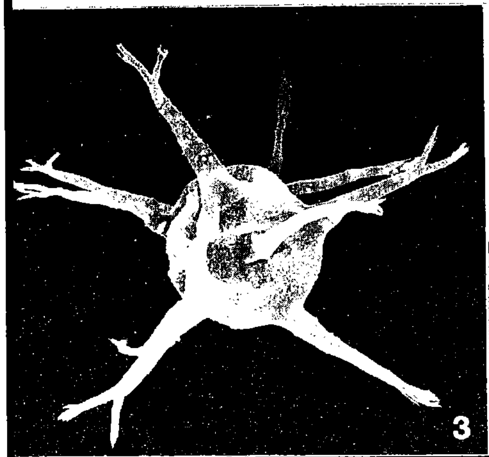
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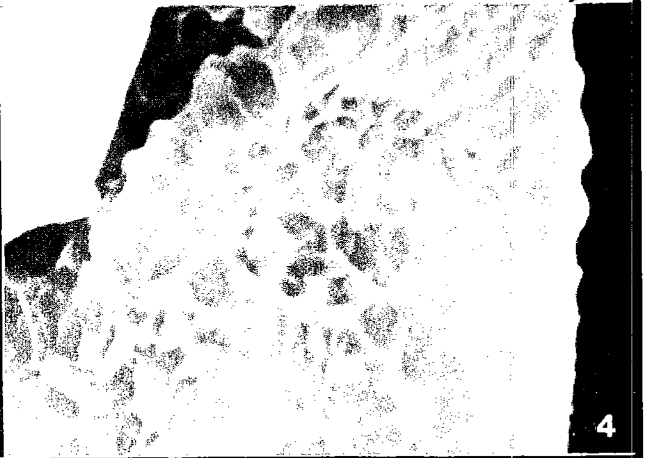
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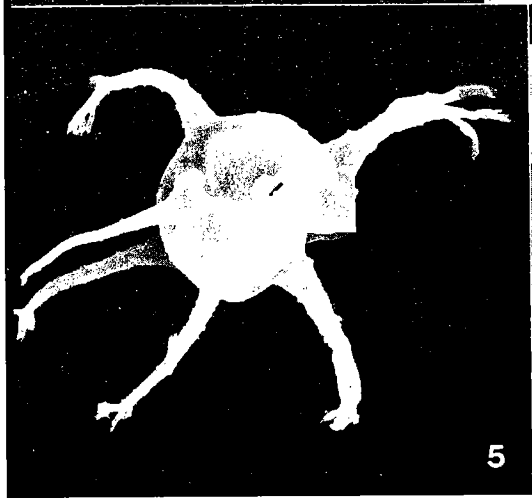
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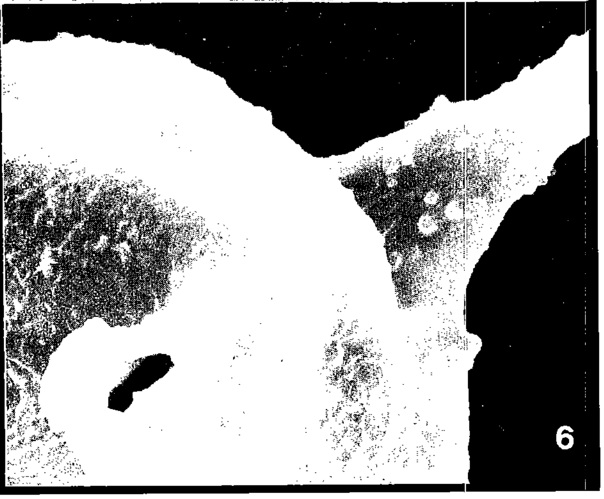
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PLATE 12

For locality, stratigraphic, and curatorial details see Text-figures 3 and 4 and Appendix.

Comasphaeridium

Figures 1–9.—*Comasphaeridium lanugiferum* Jacobson and Achab, 1985. **1**, ×1150; **2**, **3**, LM and SEM photographs of opposite sides of partly degraded specimen, ×1150 and ×1500 respectively; **4**, degraded specimen, ×1500, and **5**, part of same specimen, ×4500; **6**, excysted specimen, ×1500, and **7**, part of same specimen, ×6700, showing detail of processes, excystment structure, and vesicle cavity; **8**, ×1700, and **9**, part of same specimen, ×4000, showing detail of processes and concentric eilyma folds.

Plate 12

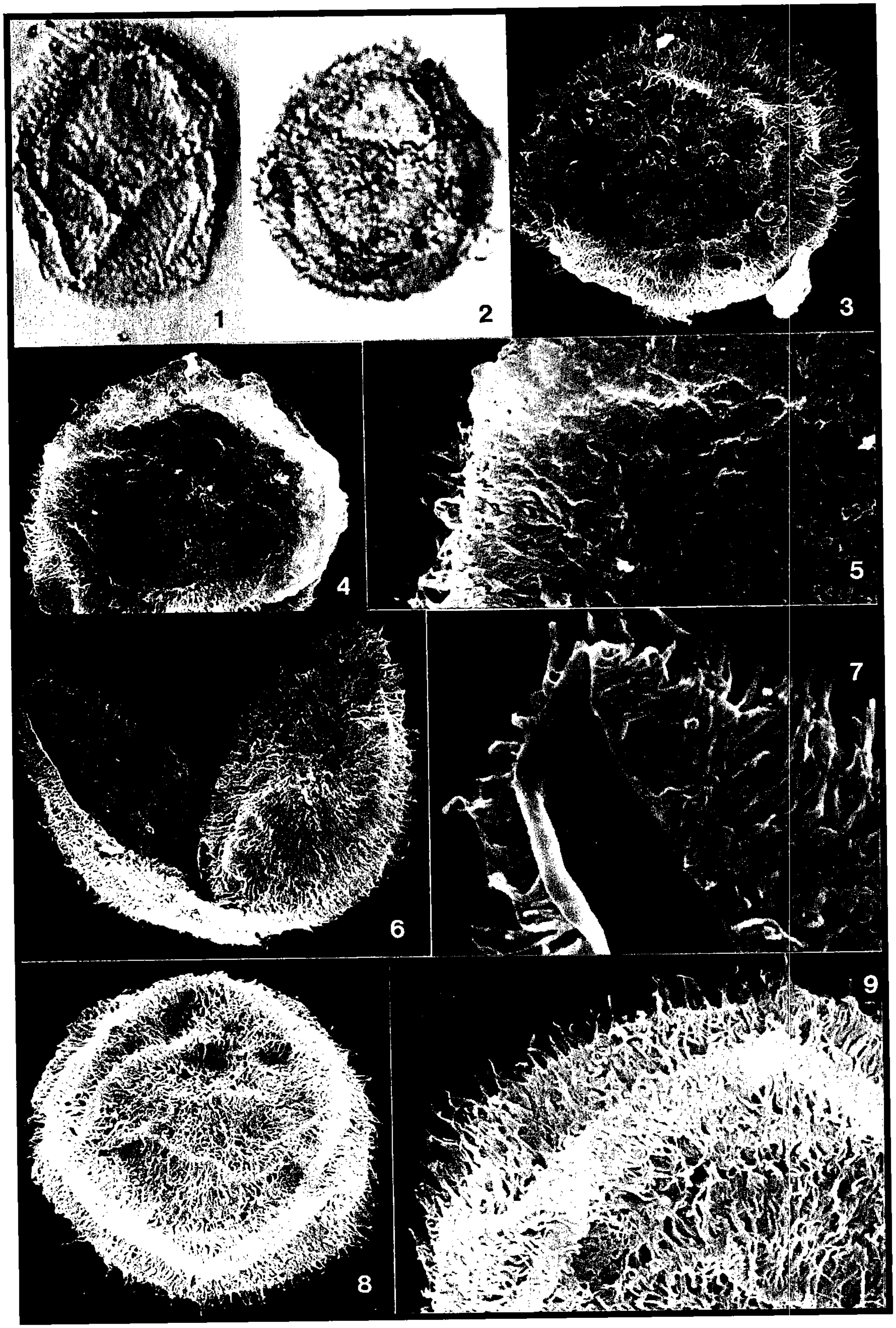

PLATE 13

For locality, stratigraphic, and curatorial details see Text-figures 3 and 4 and Appendix.

Gyalorhethium, Dorsennidium, and *Dactylofusa*

Figure 1.—*Gyalorhethium* sp. A, ×800.

Figure 2.—*Dorsennidium hamii* (Loeblich, 1970) Sarjeant and Stancliffe, 1994, ×800.

Figures 3, 4.—*Dactylofusa ctenista* (Loeblich and Tappan, 1978) Fensome, Williams, Barss, Freeman, and Hill, 1990, ×800.

Figures 5, 6.—*Dorsennidium undosum* Wicander, Playford, and Robertson, 1999, ×1150.

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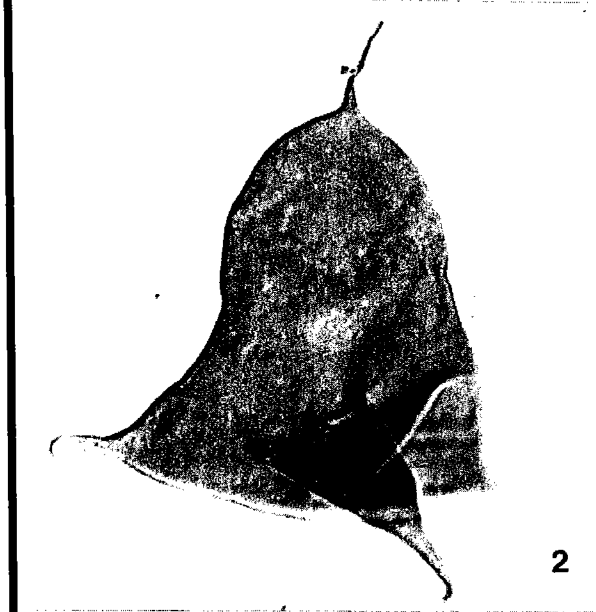

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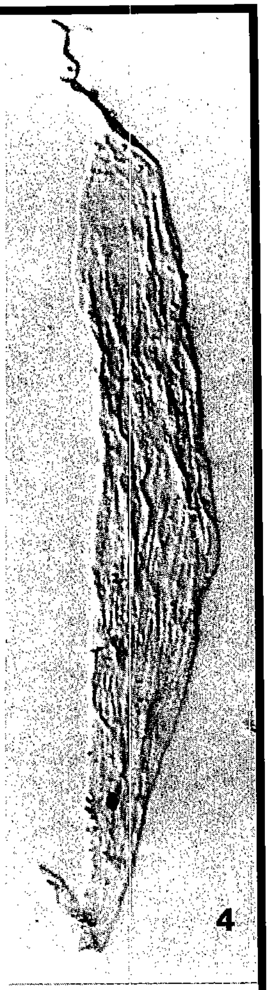

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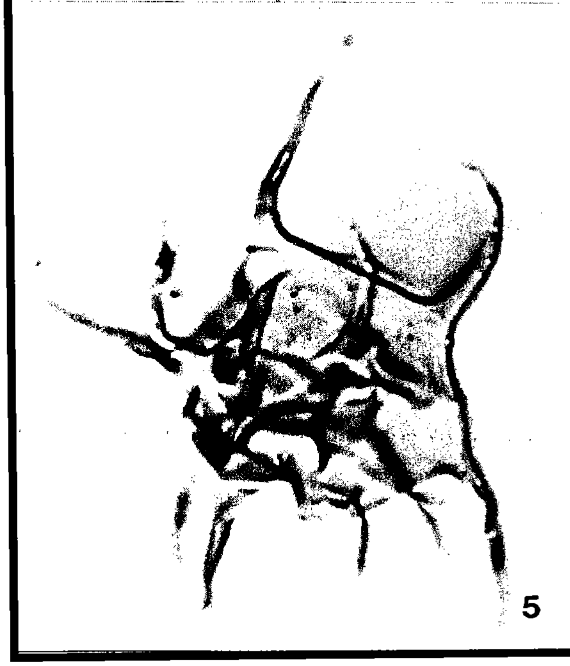

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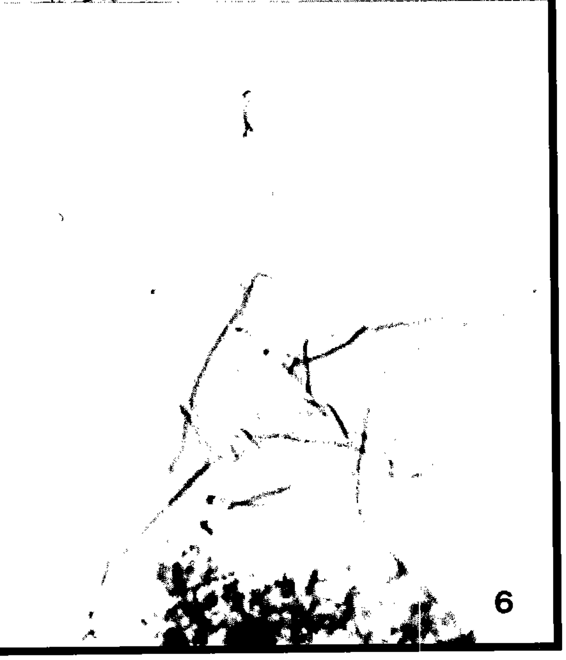

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PLATE 14

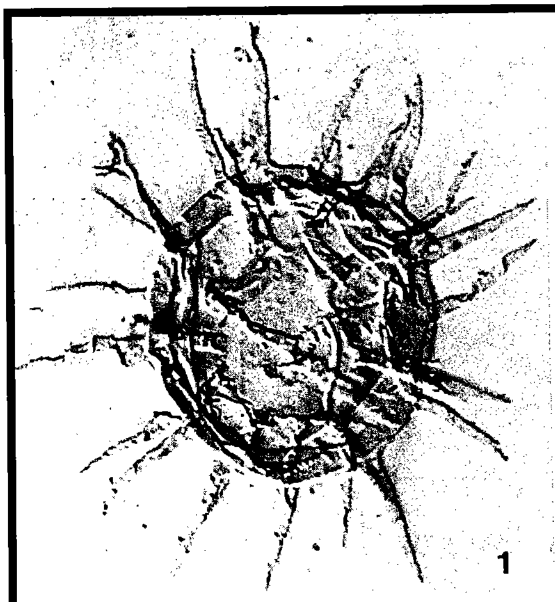
For locality, stratigraphic, and curatorial details see Text-figures 3 and 4 and Appendix.

Gyalorhethium, *Lophosphaeridium*, and *Hoegklintia*

Figures 1, 2.—*Gyalorhethium* sp. cf. *G. chondrodes* Loeblich and Tappan, 1978, ×800.

Figures 3–5, 7.—*Lophosphaeridium sylvanium* Playford and Wicander, new species. 3, holotype, ×1150; 4, 5, ×1150; 7, ×2000.

Figure 6.—*Hoegklintia radicosa* (Loeblich, 1970) Jacobson and Achab, 1985, ×625.



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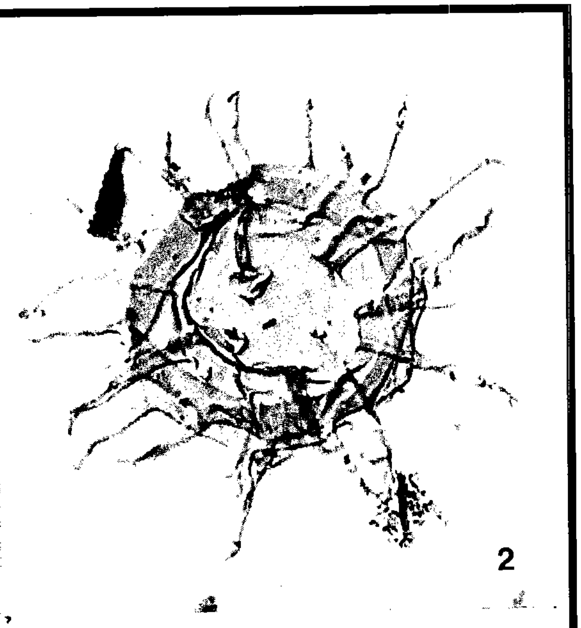

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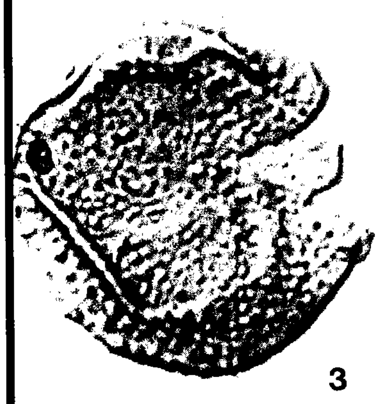

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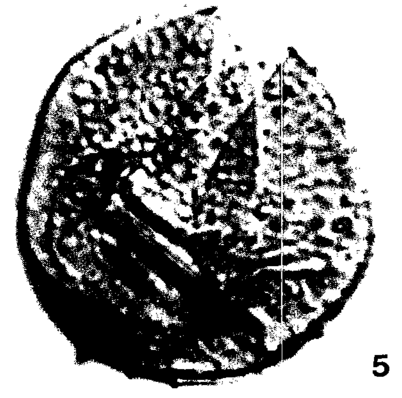

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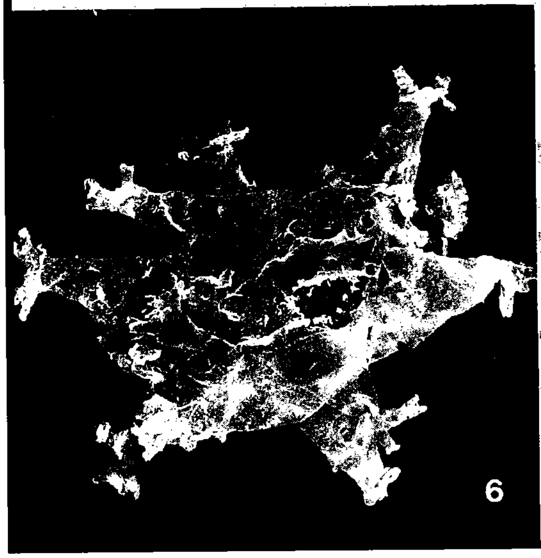

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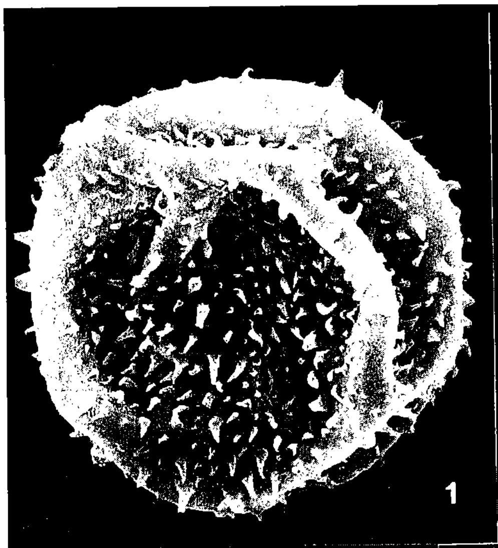
PLATE 15

For locality, stratigraphic, and curatorial details see Text-figures 3 and 4 and Appendix.

Lophosphaeridium

Figures 1–6.—*Lophosphaeridium sylvanium* Playford and Wicander, new species. Complete specimens (1, 3, 5) with highly magnified portions thereof (2, 4, 6, respectively) showing range of process variation. 1, 3, ×1500; 2, 4, 6, ×3750; 5, ×1900.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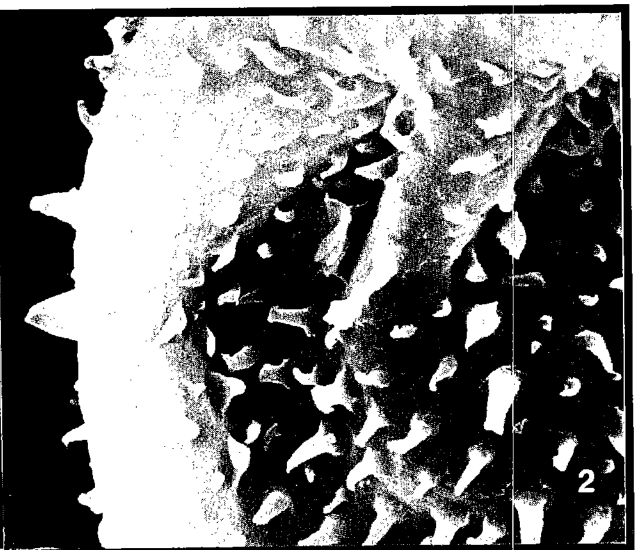
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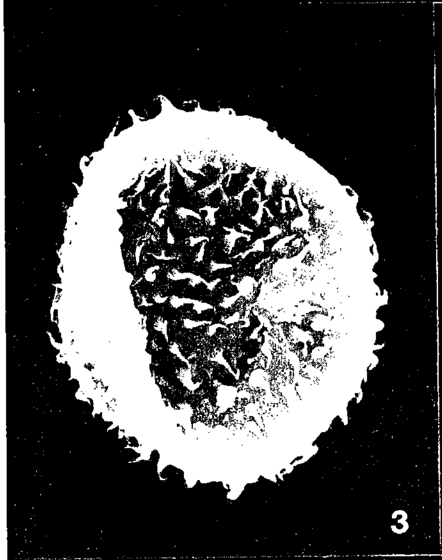
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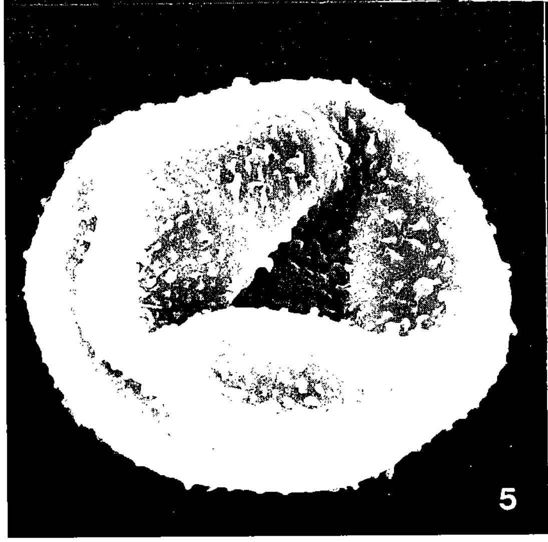
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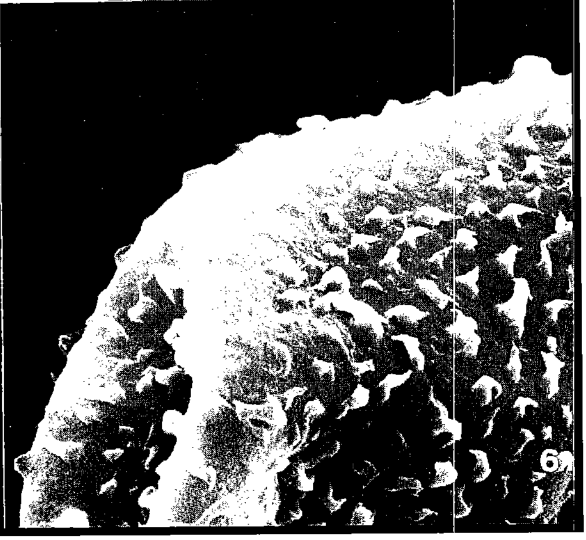
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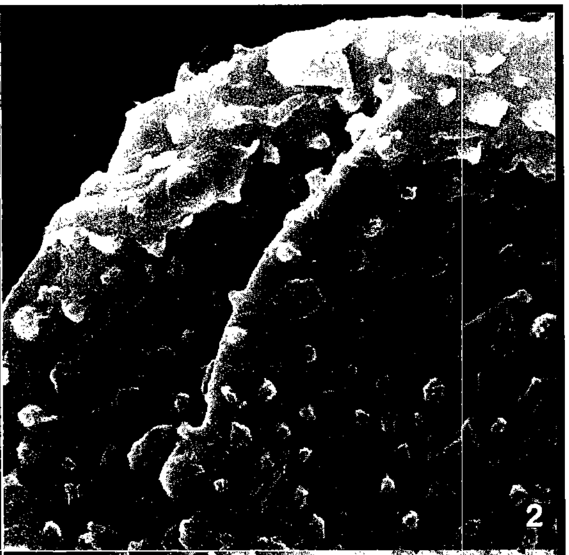
PLATE 16

For locality, stratigraphic, and curatorial details see Text-figures 3 and 4 and Appendix.

Lophosphaeridium

Figures 1–6.—*Lophosphaeridium sylvanium* Playford and Wicander, new species, showing range of process variation. **1–3**, **5**, ×3750; **4**, ×5625; **6**, ×4500, with excystment opening.

1



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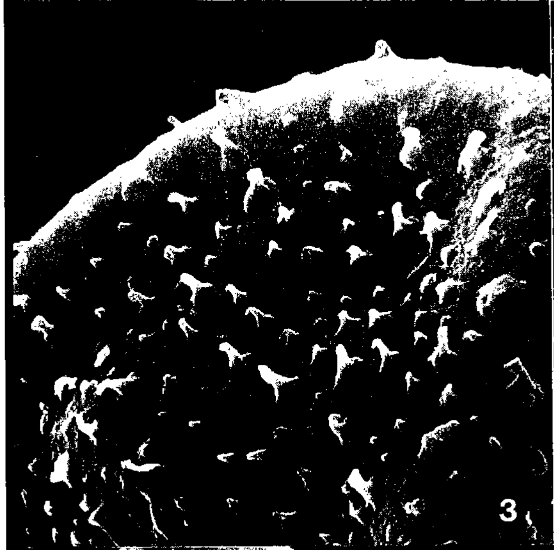

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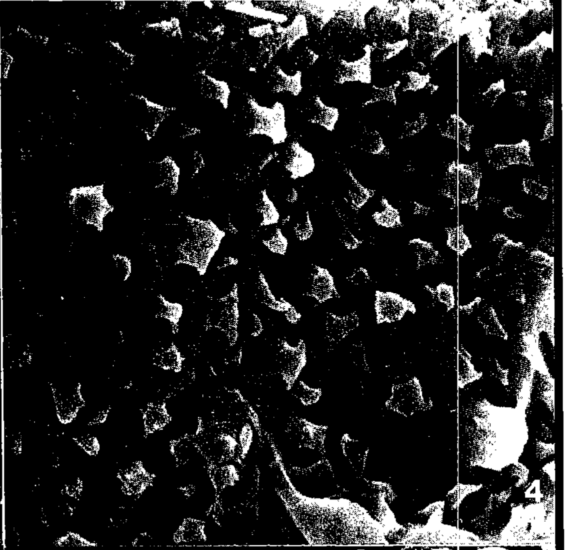

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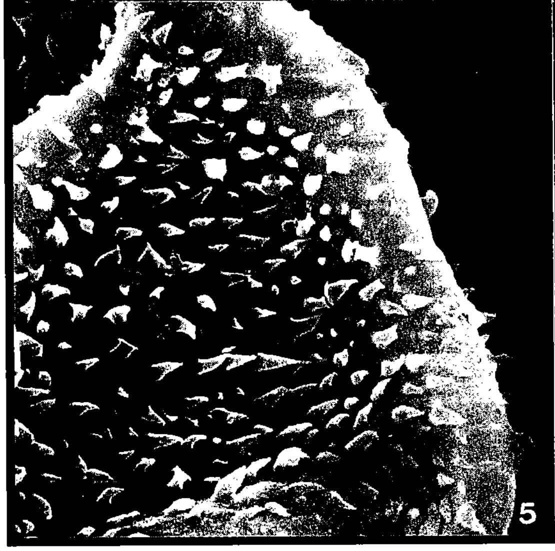

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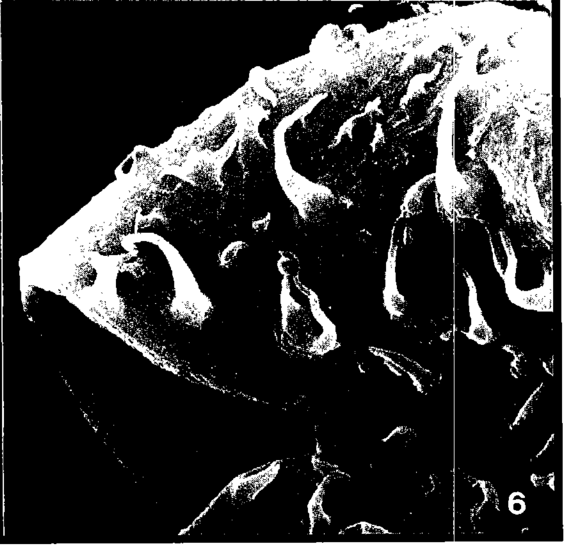

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PLATE 17

For locality, stratigraphic, and curatorial details see Text-figures 3 and 4 and Appendix.

Micrhystridium

Figures 1–3.—*Micrhystridium hirticulum* Wicander, Playford, and Robertson, 1999. **1**, **2**, SEM and LM photographs of opposite sides of same specimen, ×1150 and ×1175 respectively; **3**, ×1150.

Figures 4–6.—*Micrhystridium prolixum* Wicander, Playford, and Robertson, 1999, ×1150.

Figure 7.—*Micrhystridium viriosum* Playford and Wicander, new species, holotype, ×1150.

Plate 17


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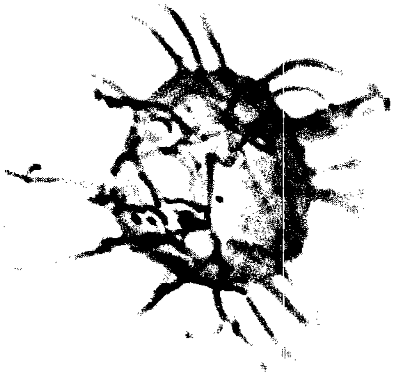
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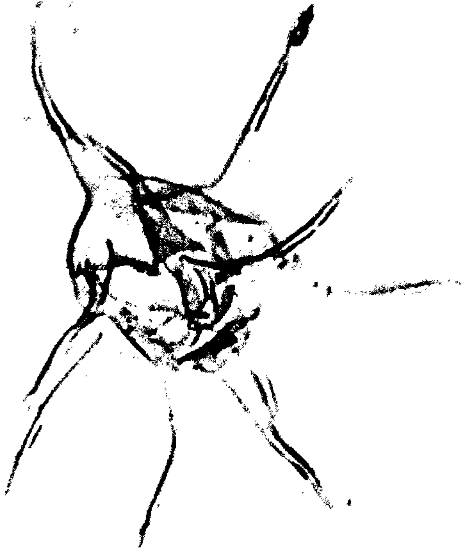
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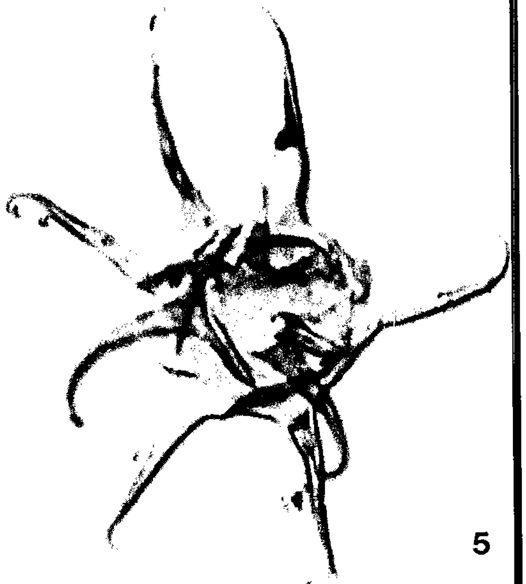
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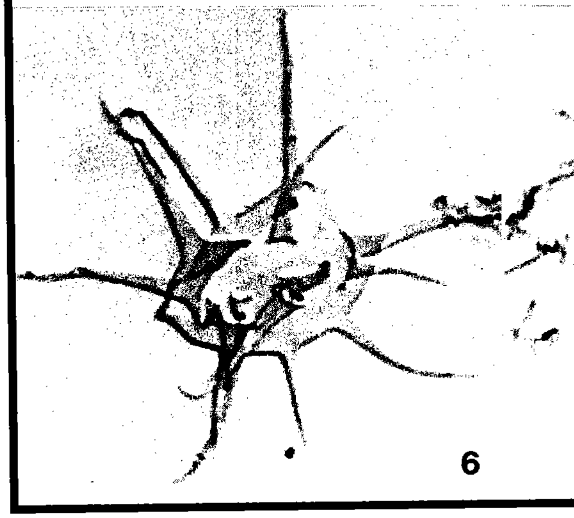
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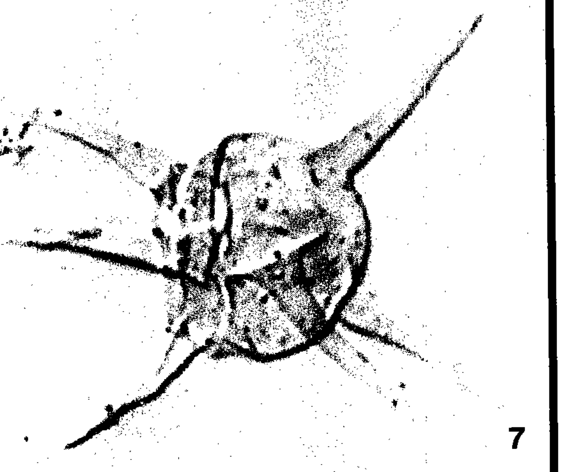
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PLATE 18

For locality, stratigraphic, and curatorial details see Text-figures 3 and 4 and Appendix.

Micrhystridium and *Multiplicisphaeridium*

Figures 1, 2.—*Micrhystridium viriosum* Playford and Wicander, new species, ×1150.

Figure 3.—*Micrhystridium* sp. cf. *M. stellatum* Deflandre, 1945, ×1150.

Figure 4.—*Micrhystridium* sp. A, ×800.

Figures 5, 6.—*Multiplicisphaeridium bifurcatum* Staplin, Jansonius, and Pocock, 1965, ×1150.


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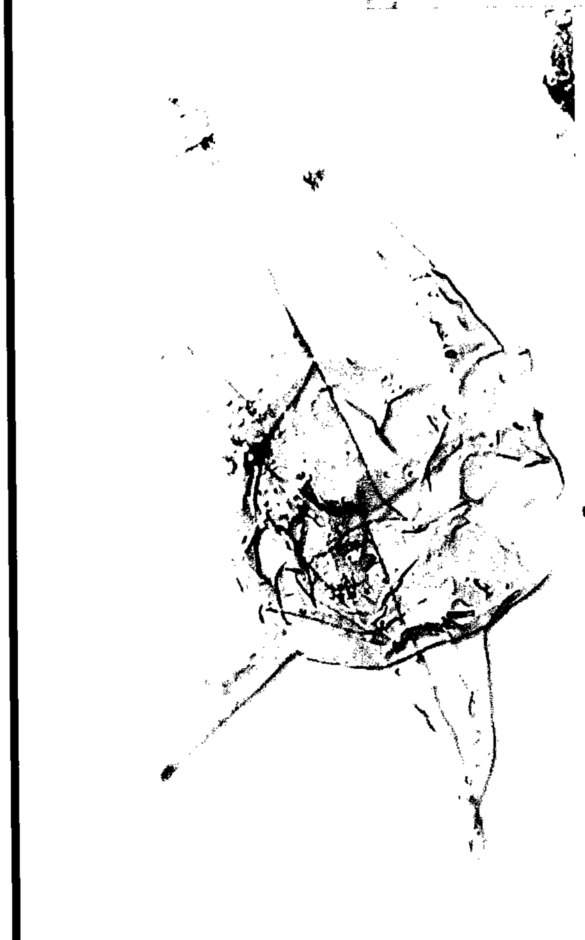
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PLATE 19

For locality, stratigraphic, and curatorial details see Text-figures 3 and 4 and Appendix.

Multiplicisphaeridium and *Navifusa*

Figures 1–5.—*Multiplicisphaeridium irregulare* Staplin, Jansonius, and Pocock, 1965. **1**, ×1275; **2**, ×1275, and **3**, part of same specimen, ×4500, showing detail of irregularly branched processes; **4**, **5**, ×1150.

Figures 6, 7.—*Navifusa ancepsipuncta* Loeblich, 1970 ex Eisenack, Cramer, and Díez, 1979, ×800.


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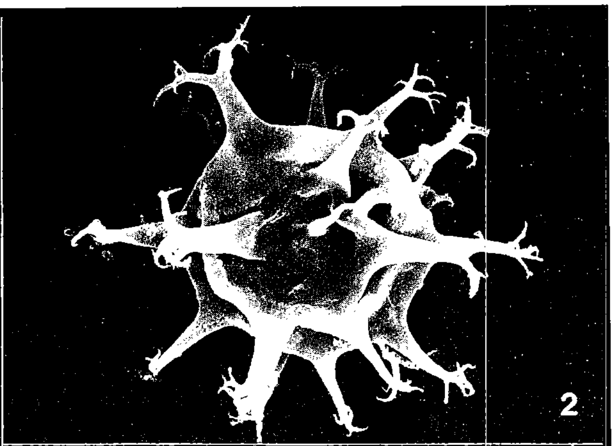
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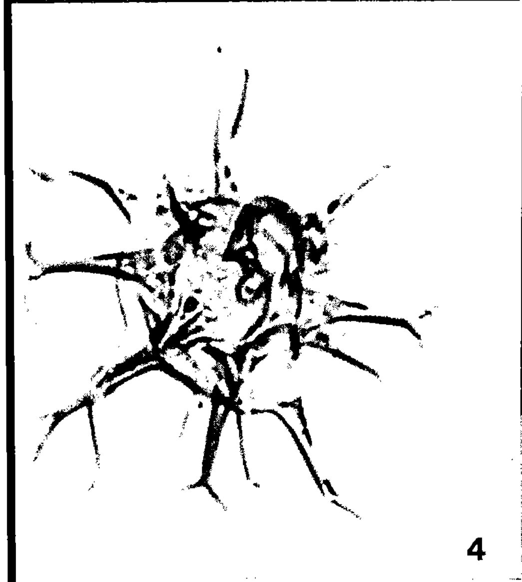
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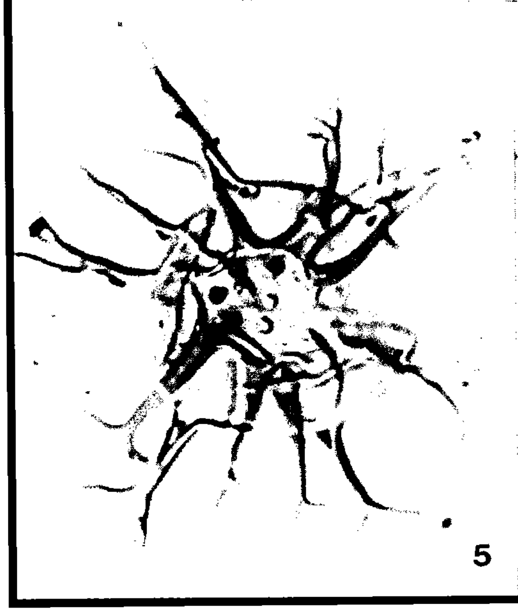
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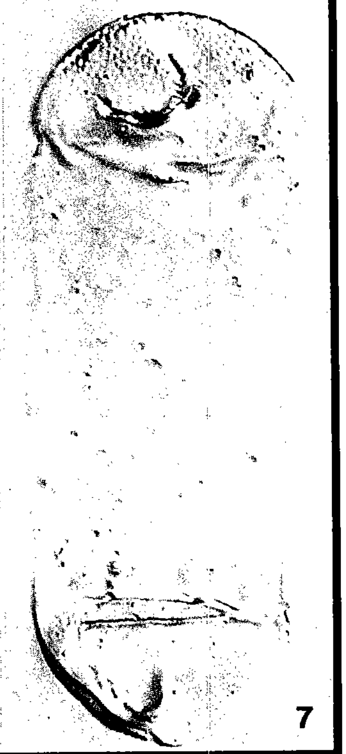
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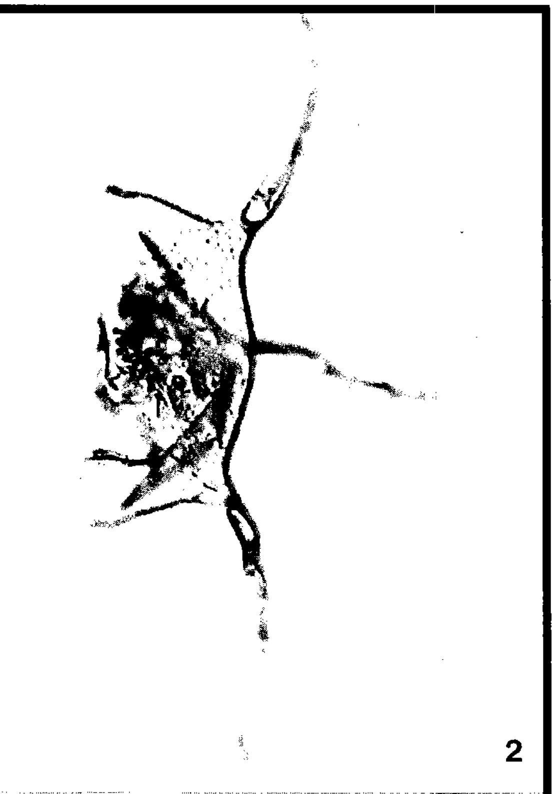
PLATE 20

For locality, stratigraphic, and curatorial details see Text-figures 3 and 4 and Appendix.

Orthosphaeridium

Figures 1–4.—*Orthosphaeridium insculptum* Loeblich, 1970, ×800. Note sculptural variation from relatively coarse (1, 2) to fine (3, 4).

1



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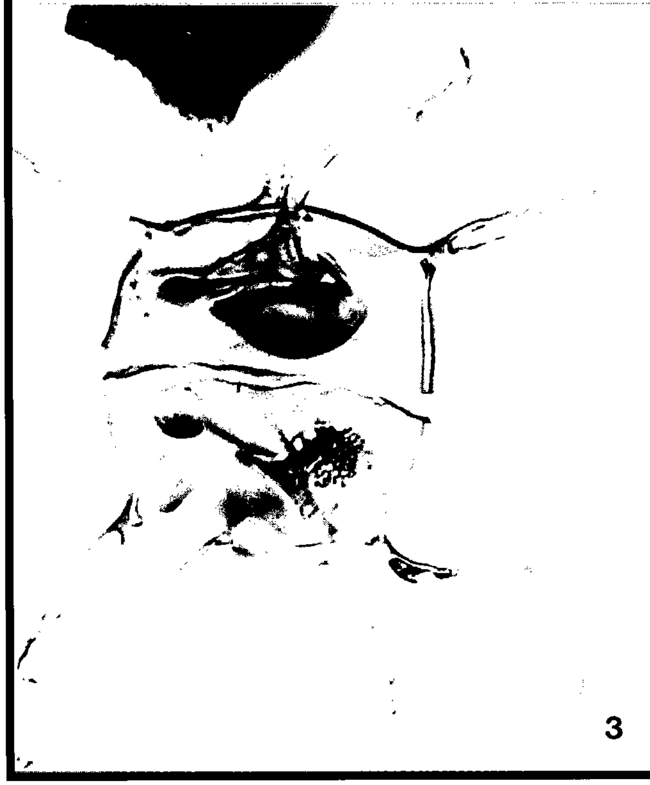

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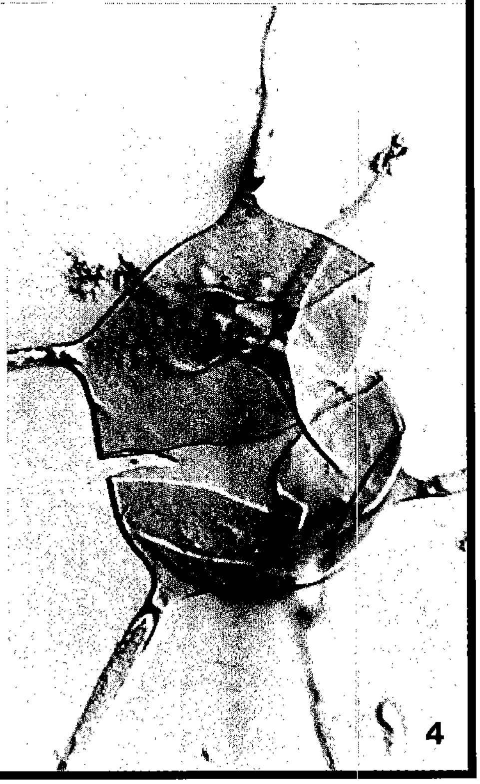


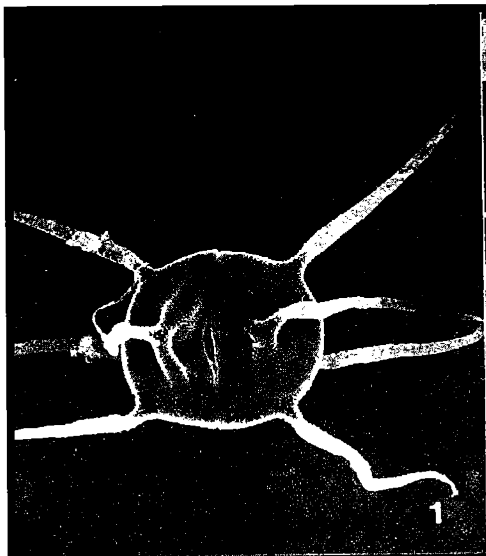
4

PLATE 21

For locality, stratigraphic, and curatorial details see Text-figures 3 and 4 and Appendix.

Orthosphaeridium

Figures 1–6.—*Orthosphaeridium insculptum* Loeblich, 1970. **1**, ×500, and parts of same specimen (**2**, ×1150; **3**, ×3750) showing development of excystment structure; **4**, ×450; **5**, ×340, and **6**, part of same specimen, ×3900.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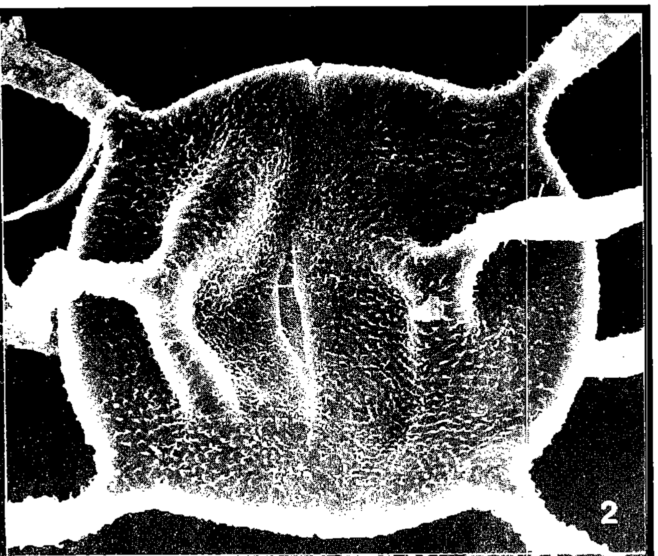
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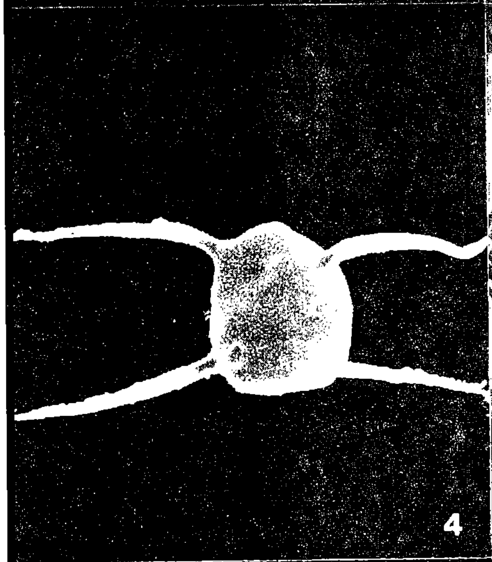
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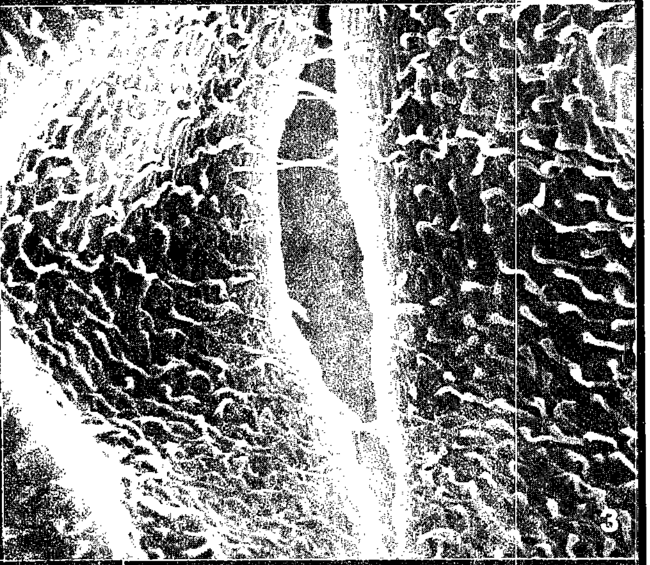
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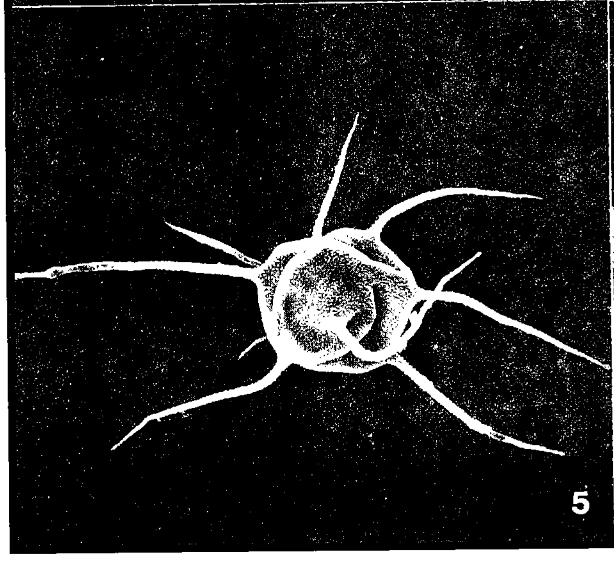
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PLATE 22

For locality, stratigraphic, and curatorial details see Text-figures 3 and 4 and Appendix.

Orthosphaeridium and *Peteinosphaeridium*

Figures 1, 2.—*Orthosphaeridium rectangulare* (Eisenack, 1963) Eisenack, 1968, ×800.

Figures 3, 4.—*Peteinosphaeridium accinctulum* Wicander, Playford, and Robertson, 1999, ×1150.

1

2

3

4

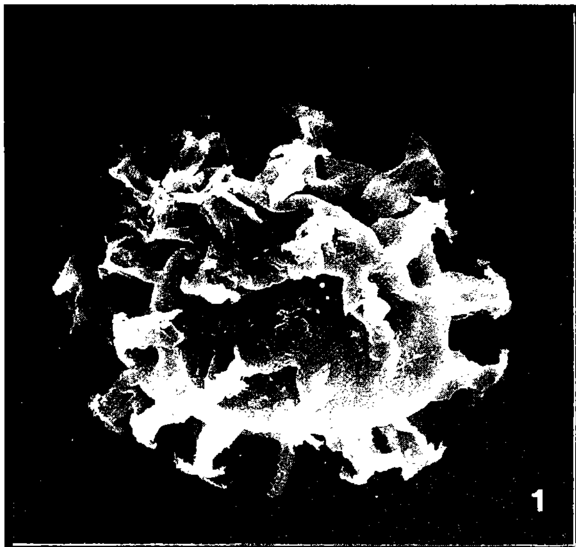
PLATE 23

For locality, stratigraphic, and curatorial details see Text-figures 3 and 4 and Appendix.

Peteinosphaeridium

Figures 1, 2.—*Peteinosphaeridium accinctulum* Wicander, Playford, and Robertson, 1999, ×900.

Figures 3–6.—*Peteinosphaeridium septuosum* Wicander, Playford, and Robertson, 1999. **3**, ×1200; **4**, ×1250; **5**, ×1050, and **6**, part of same specimen, ×3000, showing detail of trilaminate processes.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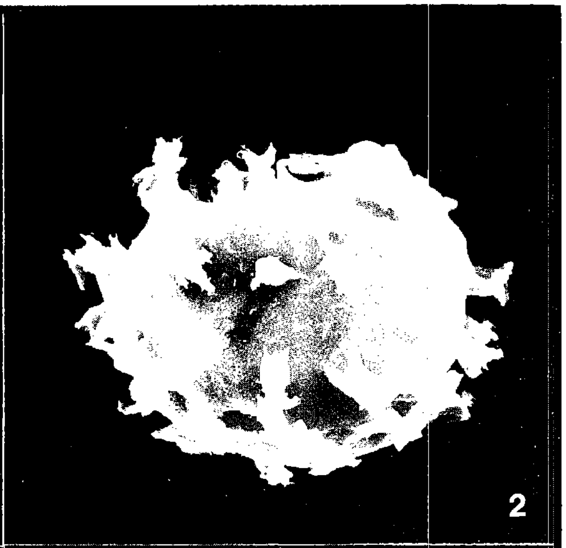
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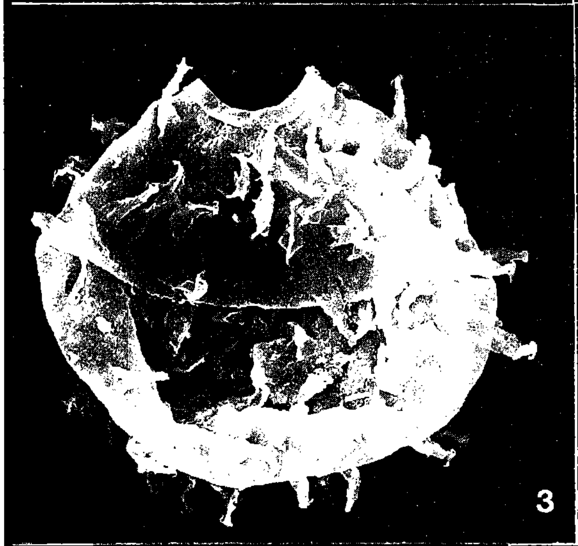
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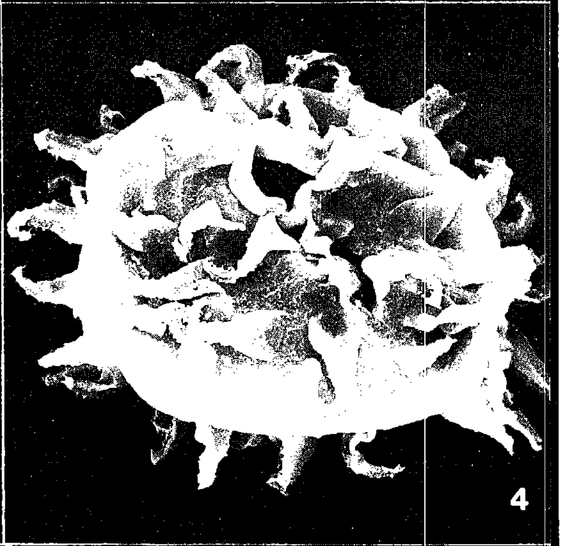
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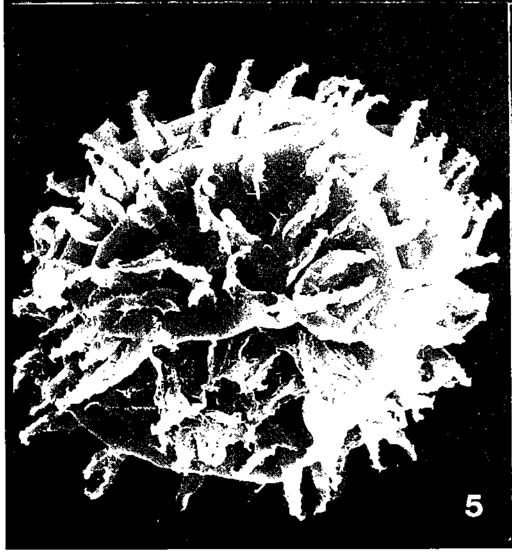
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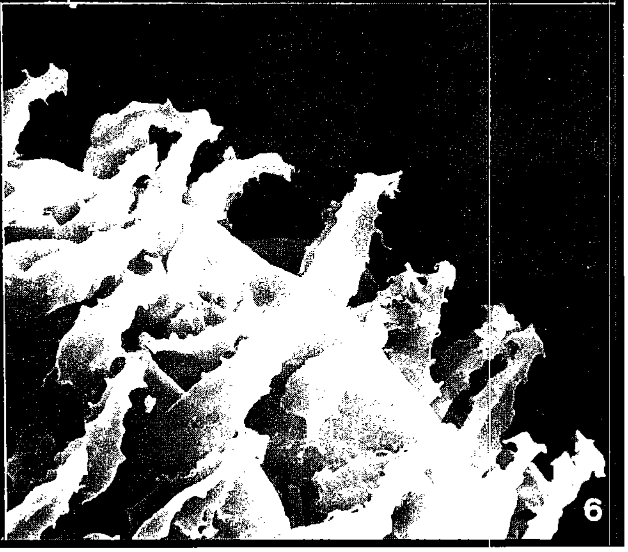
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PLATE 24

For locality, stratigraphic, and curatorial details see Text-figures 3 and 4 and Appendix.

Peteinosphaeridium, *Polygonium*, and *Poikilofusa*

Figures 1, 2.—*Peteinosphaeridium septuosum* Wicander, Playford, and Robertson, 1999, ×1150.

Figures 3, 4.—*Polygonium gracile* Vavrdová, 1966 emend. Sarjeant and Stancliffe, 1996, ×1150.

Figures 5, 6.—*Poikilofusa* sp. A. 5, ×900, and 6, part of same specimen, ×5600, showing surficial detail of eilyma and process.

Plate 24

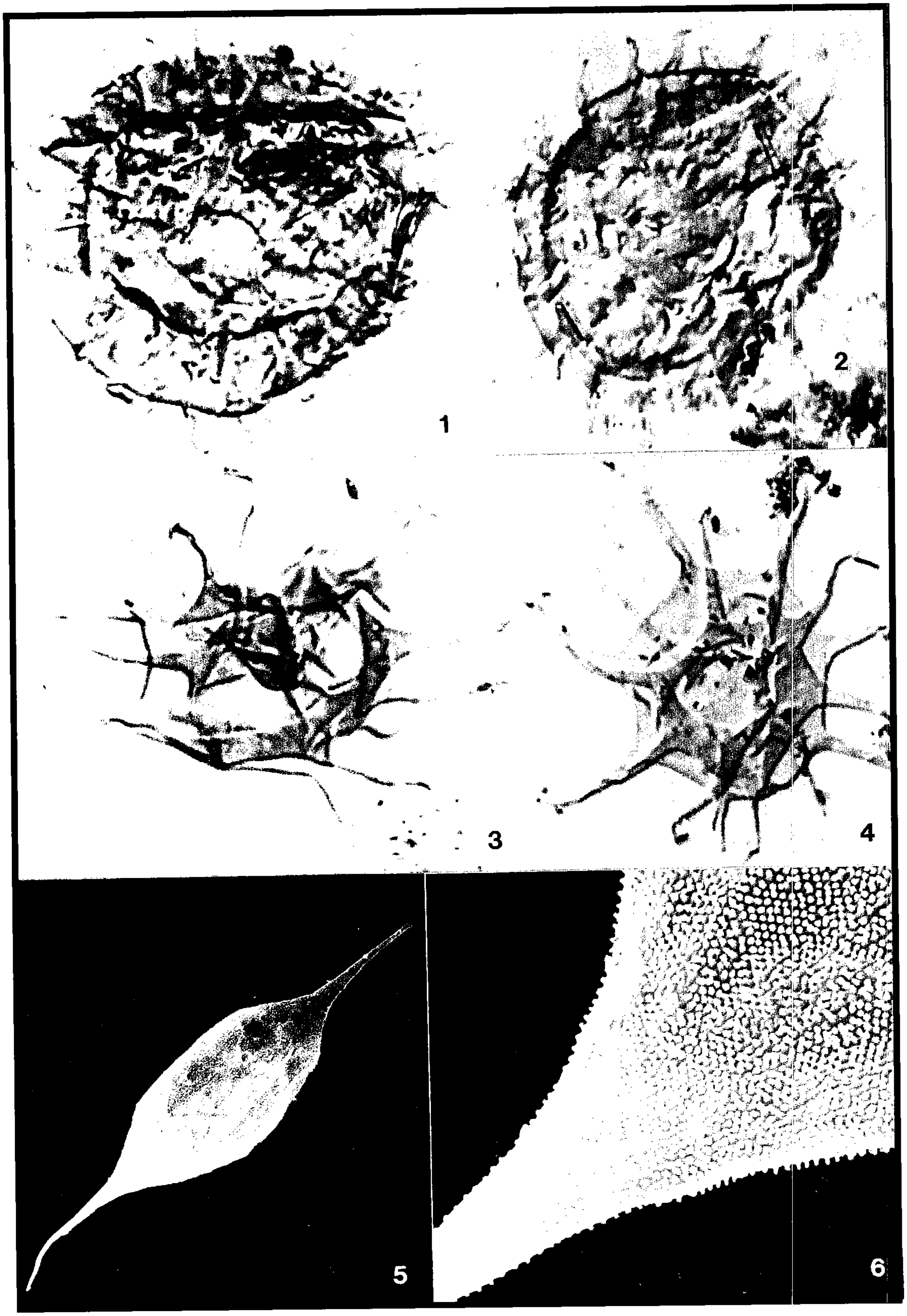


PLATE 25

For locality, stratigraphic, and curatorial details see Text-figures 3 and 4 and Appendix.

Sylvanidium, *Tunisphaeridium*, and *Polygonium*

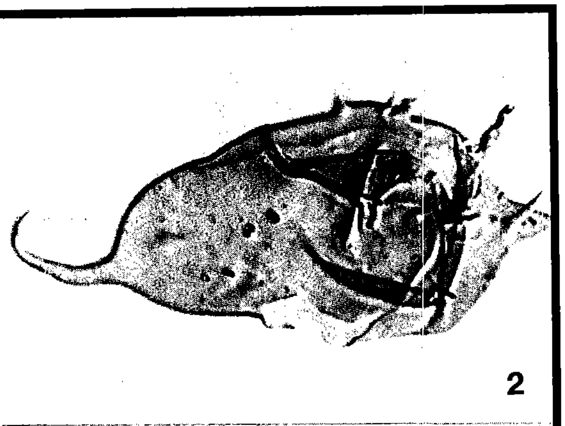
Figures 1, 2.—*Sylvanidium paucibrachium* Loeblich, 1970, ×800.

Figures 3, 4.—*Tunisphaeridium eisenackii* Loeblich and Tappan, 1978. 3, typically degraded specimen, ×1500, showing excystment opening, but devoid of delicate intertwining meshwork linking processes; 4, ×1150.

Figures 5, 6.—*Polygonium polyacanthum* (Eisenack, 1965) Sarjeant and Stancliffe, 1994, ×1150.

Plate 25

1



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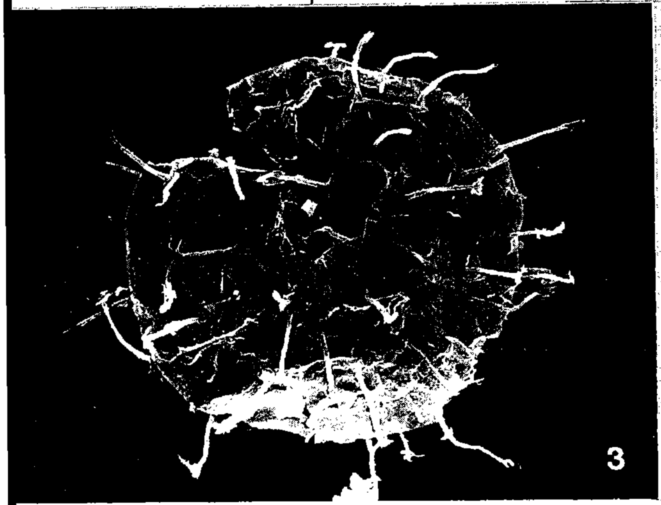

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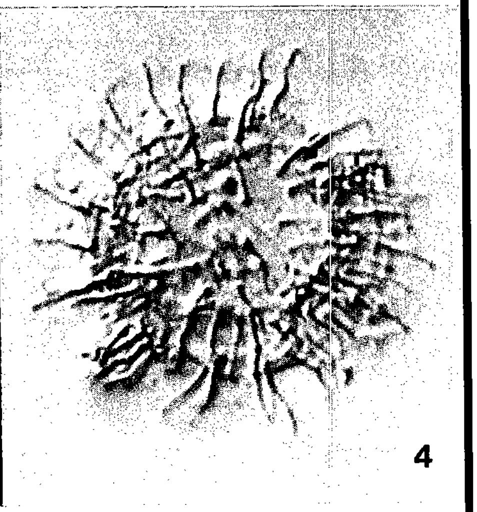

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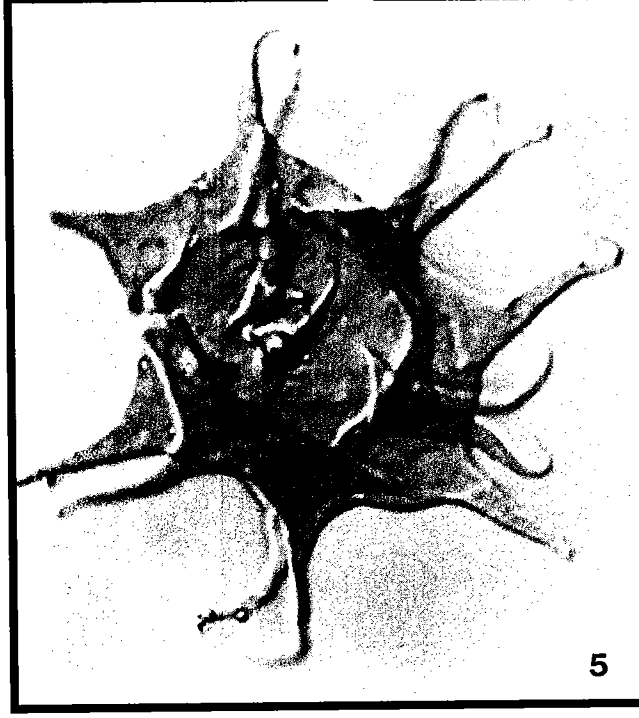

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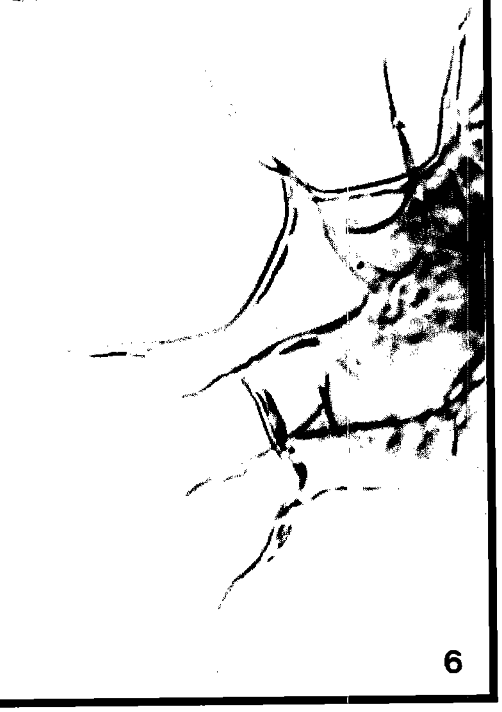

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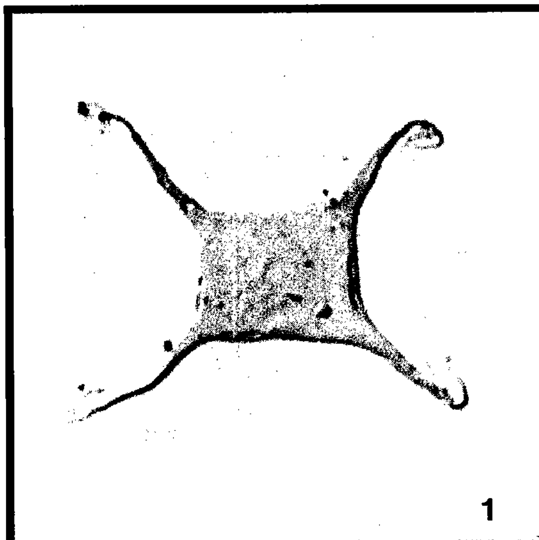
PLATE 26

For locality, stratigraphic, and curatorial details see Text-figures 3 and 4 and Appendix.

Veryhachium

Figures 1–6.—*Veryhachium oklahomense* Loeblich, 1970. **1–4**, ×1150; **5**, ×1125; **6**, ×1275.



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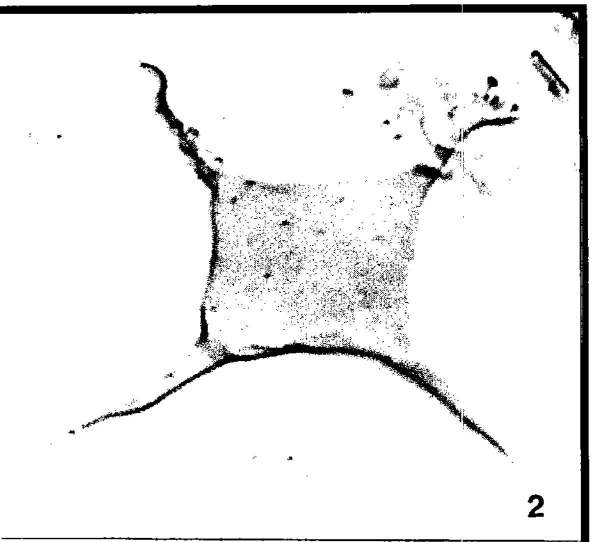

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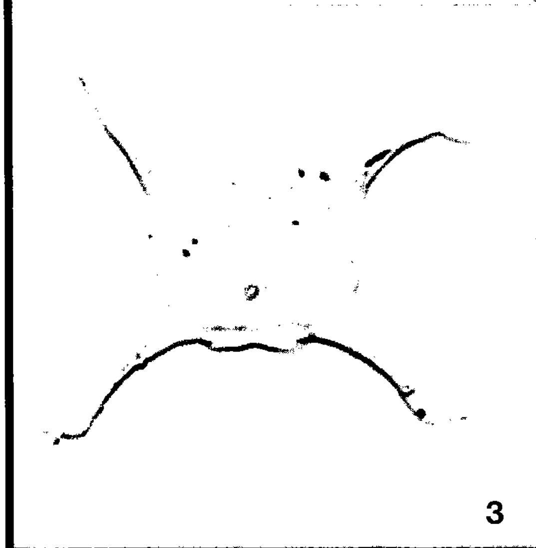

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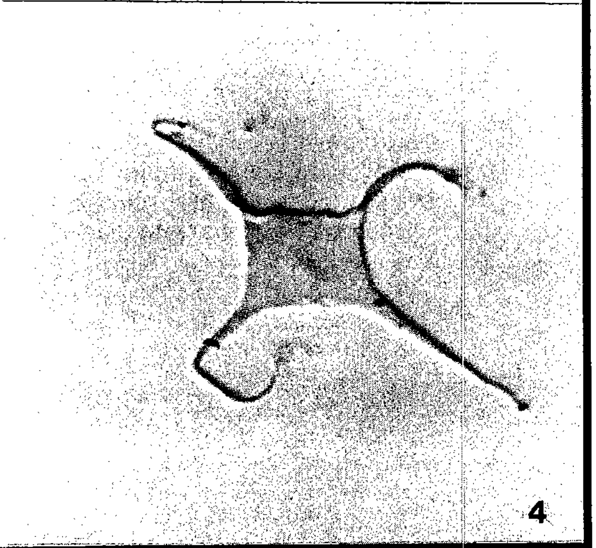

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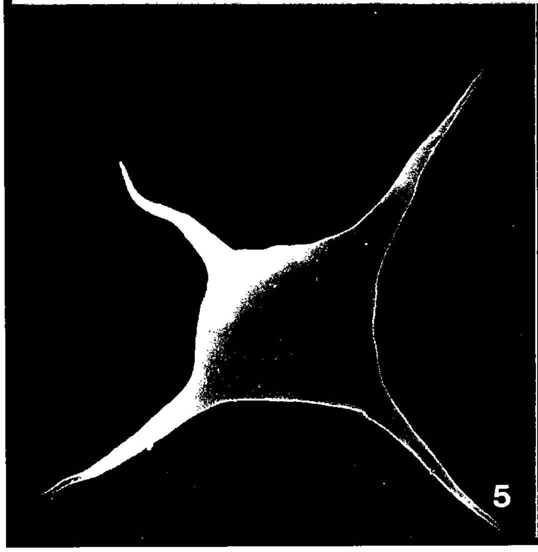

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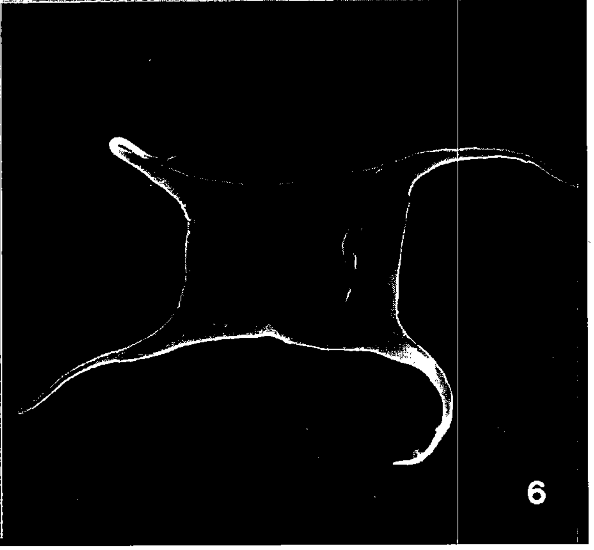

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PLATE 27

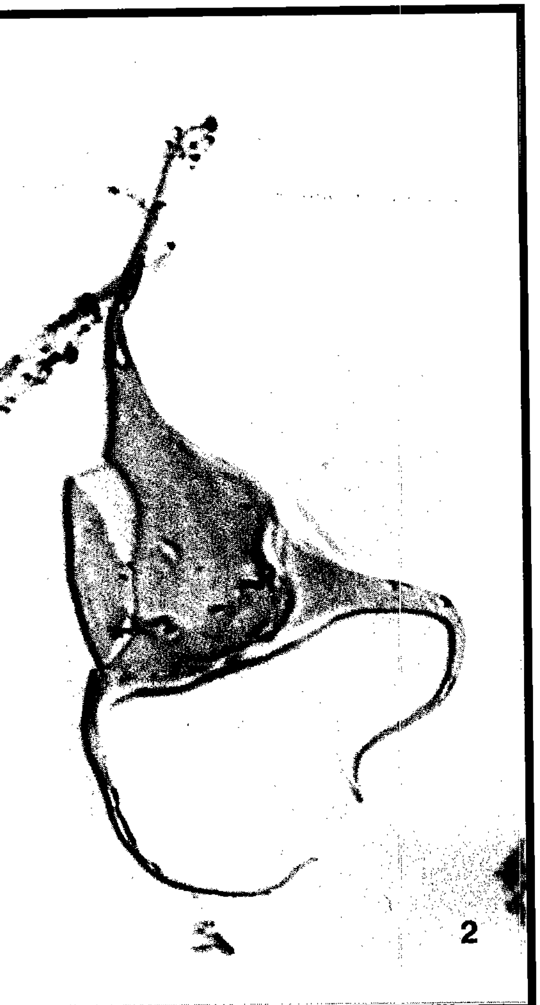
For locality, stratigraphic, and curatorial details see Text-figures 3 and 4 and Appendix.

Veryhachium

Figures 1–4.—*Veryhachium trispinosum* (Eisenack, 1938) Stockmans and Willière, 1962 "complex." **1**, **2**, ×1150, both specimens showing excystment opening (epityche); **3**, ×750, and **4**, part of same specimen, ×5600, showing microgranulate eilyma and process wall.

Plate 27


1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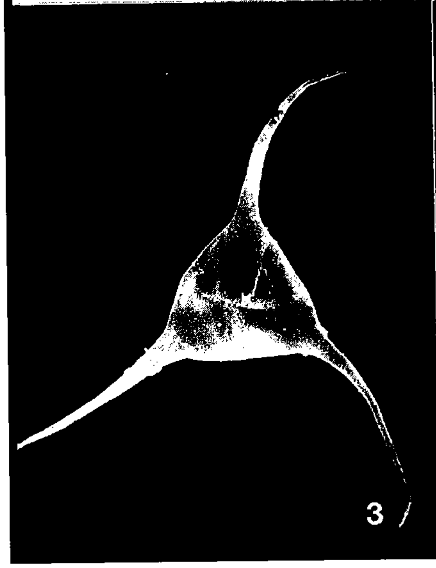
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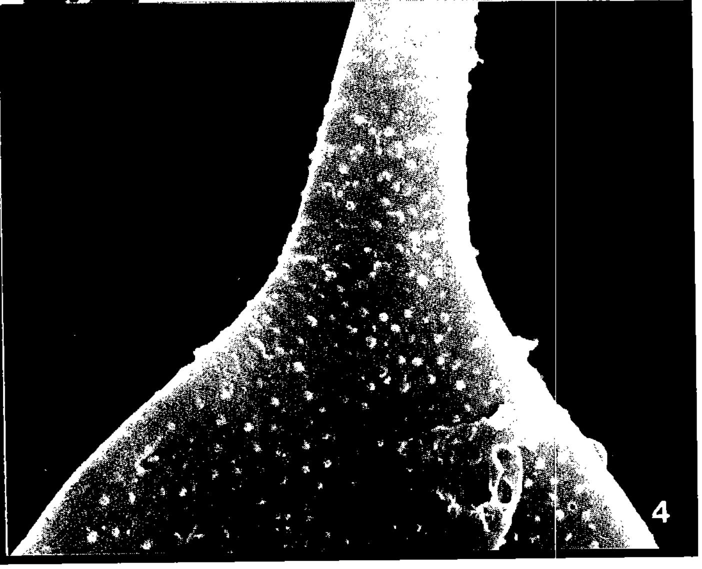
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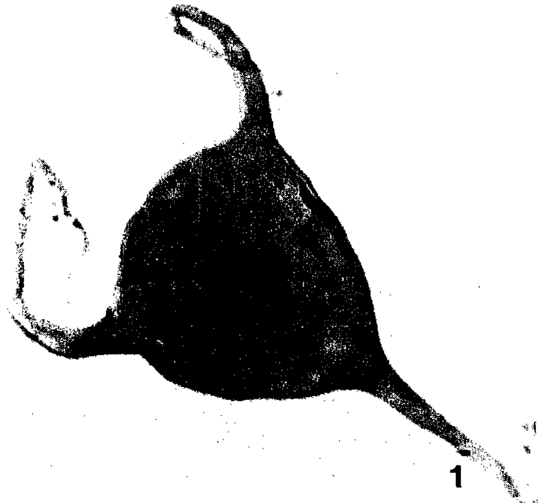
PLATE 28

For locality, stratigraphic, and curatorial details see Text-figures 3 and 4 and Appendix.

Veryhachium and *Villosacapsula*

Figure 1.—*Veryhachium trispinosum* (Eisenack, 1938) Stockmans and Willière, 1962 "complex," ×1150.

Figures 2–6.—*Villosacapsula setosapellicula* (Loeblich, 1970) Loeblich and Tappan, 1976. Four specimens showing finely echinate sculpture of eilyma and processes, and various stages in development of excystment opening (epityche); 2–4, ×1150; 5, 6, ×1500 and ×2000 respectively.



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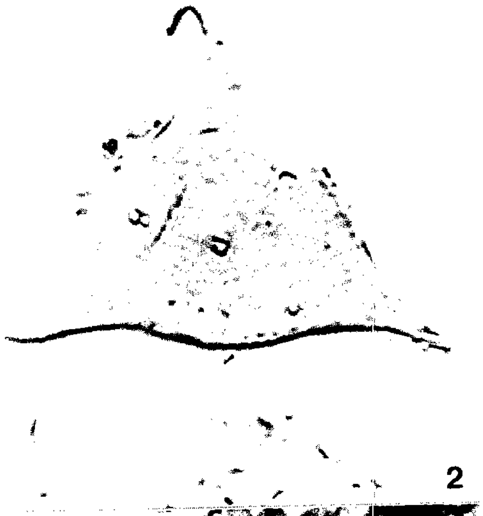

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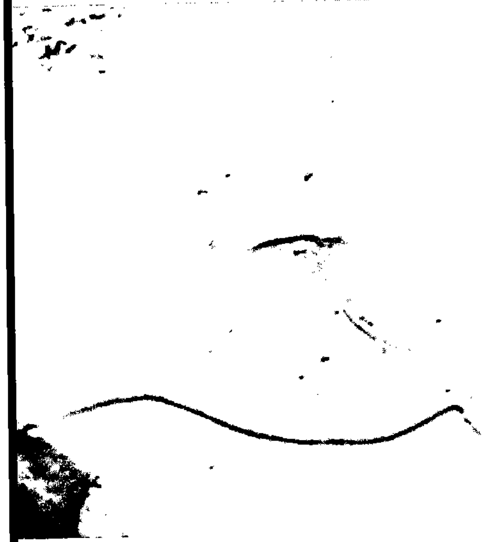

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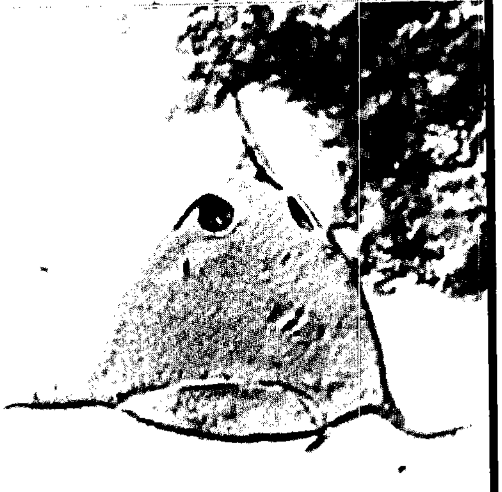

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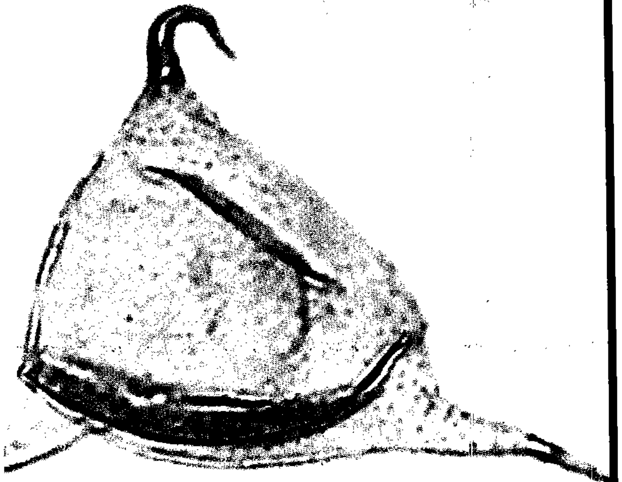

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