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Surface sculpture of the wall in Lower Paleozoic acritarchs

ABSTRACT

Although of unknown exact affinity, acritarchs are probably algal resting cysts, the vesicle wall of which was internally constructed. As the surface sculpture, therefore, would show less environmental influence than does the gross morphology, previous taxonomic neglect or discounting of this feature seems unwarranted. The use of scanning electron microscopy has particularly aided the detailed study of surface sculpture and also allowed better distinction between various types of processes and pylome characters.

A simplified terminology is presented for acritarch wall sculpture that avoids terms for which there are currently conflicting definitions. The sculptural features here defined and illustrated include both those visible with the light microscope and those requiring electron microscopy for recognition or interpretation. Basic terms used include laevigate, granulate, punctate, foveolate, corrugate, echinate, baculate, gemmate, fossulate, rugulate, costate, and cristate. Combined terms may be used to indicate compound wall sculpture, and the prefix micro- is used to indicate features of less than 1 μ in diameter or breadth.

Eleven new acritarch genera and 12 new species are described from the Ordovician and Silurian of Oklahoma and Indiana.

INTRODUCTION

In the pioneering studies of any group of organisms, whether living or fossil, taxa are described with broad limits. As the general knowledge of the group increases, the more stable features may be determined and utilized taxonomically, other characters being recognized as intraspecific, ontogenetic or environmentally induced variations. Data concerning the biology of the particular group of organisms are useful in distinguishing convergent morphologic features from those that better indicate genetic relationships. Thus many benthic organisms show a variety of modifications related to attachment to a hard substrate or the maintenance of stability on a muddy bottom. Planktonic organisms of widely separated groups may have morphologic adaptations that enable them to maintain a favorable position within the water column. Some organisms have modifications that protect them from predation or grazing; others show specialization in ways that increase their efficiency in food gathering. Recognition of the selective value of various modifications, and hence the possibility of their independent evolution in unrelated groups, will allow greater emphasis on those features that may in fact indicate genetic relationships.

Paleozoic acritarchs have not as yet been exhaustively studied and in fact have been known for only a few decades. By definition they include organic-walled microfossils of unknown exact affinity. By analogy with associated microfossils the living organisms probably were holoplanktonic or epiplanktonic. Their capsule-like morphology, with a highly resistant imperforate wall, and the presence of an operculum-closed opening (or evidence of some other terminal means of opening) indicate that these fossils represent a resting cyst stage in the life cycle; various data suggest that they represent unicellular algae.

If the above inferences are correct, various morphologic features of the acritarchs may be assumed to be related to the environmental pressures of a pelagic existence. Schopf (in Tschudy and Scott, 1969, p. 175) stated: "No doubt a great deal of the similarity of appearance reflects a universal biologic application of principles governing size and form and dissemination. It would not be surprising if over a long period of time divergent groups of unicellular organisms did not find a rather similar common pattern that served these functions best. . . . The more obvious functional criteria are less likely to be useful indicators of phyletic alliance than incidental features of ornamentation or composition that do not interfere with the common functional objective and may have no apparent survival value. In ambiguous and difficult material incidental features are more likely to be atavistic and to serve better as indicators of

affinity. For purposes of taxonomic assignment it may be necessary to emphasize and attach more significance to incidental features and minor resemblances than seems, on casual inspection, reasonable."

Current acritarch classifications, whether the "subgroups" proposed by Downie, Evitt and Sarjeant (1963), which lie outside the Code of Botanical Nomenclature (and the Code of Zoological Nomenclature) and to which additional subgroups have been added by others (Staplin, Jansonius and Pocock, 1965; Brito, 1967*b*, 1969; Sinha, 1969), or the Linnean families proposed by Eisenack (1938, 1954, 1969), Klement (1960) and Mädler (1963), all emphasize the general form of the acritarch vesicle, whether spherical, polygonal, or fusiform, for example, and the nature of its periphery, whether simple and smooth or having elongate processes, crests or flanges. Such classifications show a strong parallel to those used until recently for planktonic foraminifera (Bolli, Loeblich and Tappan, 1957; Banner and Blow, 1959). As noted by others (Parker, 1962; Lipps, 1966; Tappan and Lipps, 1966), such features of gross test morphology "appear to be convergent adaptations for a planktonic existence and hence are unreliable for determining natural relations" (Tappan and Lipps, 1966, p. 637). The test wall composition and microstructure, however, "appear not to be environmentally affected and hence probably best reflect relationships" (*ibid.*).

As presently understood, many genera and species of Paleozoic acritarchs have long stratigraphic ranges, but, if one may judge from the variety of forms included, these ranges may be much longer than can be justified. Schopf (in Tschudy and Scott, 1969, p. 179) noted that "Such a long stratigraphic range may signify that general, probably polyphyletic, features of morphology have assumed disproportionate emphasis in classification."

Internally formed morphologic structures are less likely to be environmentally affected than are those in direct contact with the environment, whereas the major morphologic features are most influenced by physical factors. The above-mentioned foraminiferal test is intracellularly deposited, as are the skeletal structures of almost all protistans, for example, the siliceous radiolarians and silicoflagellates, the internally formed and only secondarily external heterococcoliths, or the scales that serve as the base for the later construction of the holococcoliths. Even the latter are deposited inside an outer "organic" skinlike layer. Similarly, the diatom frustule is deposited within a vesicle of the cell, as is the siliceous chrysomonad cyst that is formed within the vegetative cell. Even the cellulosic plates of the armored dinoflagellate theca are internal to a continuous unit membrane in life, each individual plate being enclosed within a thecal vesicle (Loeblich, III, 1970). The dinoflagellate cyst, formed internally to this, was suggested to be in part constructed of the pellicular layer that immediately underlies the thecal plate layer of the complex dinoflagellate wall (Loeblich, III, 1970).

The general morphology of the individual algal cell may be characterized by evolutionary conservatism, but the ultrastructure, because it is not limited by the same environmental restrictions that may affect general morphology, should be taxonomically more useful. The recent development and general application of the scanning electron microscope have been particularly valuable for the study of these very small microfossils of limited gross morphological variability. Although the larger features of the wall sculpture are also recognizable with the light microscope, some are extremely difficult to interpret with this instrument alone.

To date the most detailed review of the larger features of the wall sculpture in acritarchs (visible in the light microscope) is that of Cramer and Cramer (1968) concerning acanthomorphic acritarchs. They stated that, in general, a smooth surface should be regarded as the normal or basic morphology, and any variation or deviation from this should be indicated in taxonomic descriptions. Terms used by Cramer and Cramer (1968) for surface sculpture of acanthomorphic acritarchs include smooth, microscabrate, scabrate, microrugulate, rugulate, striate, spinate, echinate, mammillate and verrucate. They also mentioned walls with hairlike or threadlike processes. Schopf (in Tschudy and Scott, 1969) mentioned smooth, papillate, apiculate and spinose surfaces, as well as those with crests or membranous equatorial flanges. Evitt (in Tschudy and Scott, 1969) used the terms psilate, verrucate, granulate and spinulate. Although in general such sculptural terms have been those applied to the sculpture of spore exines, some variation in the definition results in ambiguity. Thus, some authors use the term psilate for a smooth surface, while others regard this same term as representing a matte finish and use the term shagreen for smooth and glassy. Others regard shagreen as indicative of a faintly roughened, leather-like texture. In addition, most of these terms were originally used in reference to features observed with the light microscope and thus of a much larger scale than the highly characteristic acritarch surface structure commonly visible only with electron microscopy. The descriptive terms may be prefixed with micro- or nano- to indicate such smaller scale features, generally those of less than 1 μ in diameter or width.

SURFACE SCULPTURE TERMINOLOGY

Sculptural elements of acritarch vesicle walls include both those visible with the usual light microscope and other smaller structures that are visible or can be interpreted only at the higher magnifications possible with electron microscopy. Use of the scanning electron microscope has allowed the recognition of these fine details, but modern techniques also allow the later examination and illustration of the same specimens by light microscopy, so that the appearance at various magnifications and with the use of differing instrumentation can be readily correlated. Some of the distinctive features of acritarch wall sculpture have been demonstrated with scanning electron micrographs (for example, in Loeblich, 1970*a*, 1970*b*; Loeblich and Tappan, 1969, 1971, as well as in the present article). Emphasis on such features in the description of new taxa or redescription of older ones for which surface features are inadequately reported will greatly aid a refinement of the present generic categories, making many of these much more useful stratigraphically. Preliminary studies also suggest that, within individual genera, evolutionary lineages may be traceable on the basis of gradual surface textural changes (Loeblich and Tappan, 1971).

Although not exhaustive, many of the more common sculptural types observed to date on acritarchs are shown in the accompanying plates. Variations in the major features of the vesicle, including processes and flanges, are not included here. The sculptural features of the processes may be shown, however, as these may differ from the sculpture of the main vesicle. Some species also show different sculpture in different parts of the vesicle. Because acritarch sculpture is not exactly comparable with that of spore exines, some modifications of previous terminology are proposed here. For all terms the prefix micro- may be used to indicate features of less than 1 μ in diameter or width.

Laevigate. Smooth, unornamented surface, even at high magnification. *Caiacorymbifer waldronensis* (plate 3, figure 8).

Granulate. Tiny granules scattered over the surface. Examples of a microgranulate surface are shown in *Comptaluta pirellum* (plate 4, figures 3, 7), the granules of which are about 0.2 μ in diameter, and in *Ordovicidium elegantulum* (plate 7, figures 1, 5), with granules 0.3 μ in diameter. Some species may have regularly spaced granules, and these may be aligned in definite rows to present a pseudocostate appearance (plate 1, figures 9–10), the parallel narrow ridges resolving into rows of granules, when observed at higher magnification with electron microscopy.

Punctate. Scattered shallow pits. Micropunctate sculpture is visible only with electron microscopy (plate 1, figure 1). An example of compound sculpture (plate 1, figure 2) is microgranulate-micropunctate, with both small pits and granules being visible only with electron microscopy.

Foveolate. Closely arranged pits the diameter of which commonly exceeds that of the interpit areas. A microfoveolate structure has a spongy appearance in electron micrographs (plate 1, figure 3).

Corrugate. Irregular ridges on the surface. A composite sculpture shown in plate 1, figure 4 is termed microcorrugate-microfoveolate, consisting of irregular ridges or corrugations with deep intervening pits.

Fossulate. Closely spaced, high, even granules, leaving irregular grooves between them to give the appearance of a negative or incised reticulum. A microfossulate sculpture is shown in plate 1, figure 7.

Echinate. Surface with small, thornlike spinules, with greatest diameter at their base and tapering rapidly. Example: *Anomaloplaisium lumariacuspis* (plate 2, figure 1); similar features are shown in plate 1, figure 5.

Baculate. Small, cylindrical, rodlike projections of equal diameter throughout their length, terminating bluntly (plate 1, figure 6).

Gemmate. Small, spherical projections, slightly constricted at the base, then enlarging. These range from 0.7 to 1.5 μ in diameter in *Psenotopus chondrocheus* (plate 11, figure 2).

Rugulate. Fine, irregularly wrinkled surface (plate 1, figure 8).

Costate. Parallel, narrow, elongate ridges with wide interridge areas. Two examples are shown (plate 1, figures 11–12). Microcostate sculpture of very fine costae in various arrangements is visible with electron microscopy. These microcostae may be irregularly aligned and discontinuous, producing a vermicular appearance (plate 1, figures 13–14), or regularly arranged, for example, with very fine parallel ridges in varying alignment simulating a pinnate venation; ridges of this sort are 0.05 μ in width in *Rhopaliophora foliatilis* (plate 9, figure 2). The narrow ridges may intersect or anastomose to give a cross-hatched appearance in electron micrographs, as in *Dicommopalla macadamii* Loeblich (1970*a*, fig. 11) and plate 1, figure 15 herein.

Cristate. With simple, low, flangelike surface crests. These may anastomose in a reticulum as in *Melikeriopalla amydra* (plate 6, figures 1–2), or they may form an irregular labyrinthine pattern instead of a regular reticulum (plate 1, figures 16–17).

SYSTEMATIC DESCRIPTIONS

During the writers' continuing studies of Lower Paleozoic Acritarcha, various new taxa were observed, some of which are herein described from Ordovician and Silurian strata. Figured type specimens are deposited in the Helen Tappan Loeblich Collection, Department of Geology, University of California, Los Angeles. Numbers given below for type specimens refer to sample number and slide coordinates, *e.g.*, 69–83(8)31.9–96.1 refers to sample 83 collected in 1969 and slide 8 of the preparation. If no additional numbers follow, the number in parentheses refers to a single-specimen mount. The coordinates, when given, were recorded on a Leitz Orthoplan microscope. A similar system is used for the scanning electron micrographs, *e.g.*, 69–114(SEM 1650) refers to sample 114 collected in 1969, scanning electron micrograph 1650.

Genus ***Anomaloplaisium*** Tappan and Loeblich, **n. gen.**

Type species: Anomaloplaisium lumariacuspis Tappan and Loeblich, n. sp.

Description: Asymmetrically fusiform central body, one side inflated in a broad curve, the other straight or slightly inflated; ends produced into polar spines, one of which is commonly shorter than the other; wall thin; polar spines with echinate surface, the tiny prominent spinules or bulbous projections communicating internally with the hollow polar spines; spinules becoming smaller and rarer at the base of the processes and disappearing, leaving the central body smooth except near the base of the processes where the echinate surface grades into one with rare scattered grana; no excystment opening observed.

PLATE 1

Representative types of surface sculpture found in Acritarcha as seen in scanning electron micrographs. As the figures on Plate 1 merely illustrate sculptural types and include as examples figures of numerous undescribed taxa of various geologic ages, the taxa are not named herein.

1 Micropunctate sculpture. Numerous shallow, scattered pits. ×20,000.

2 Microgranulate-micropunctate. Compound sculpture with interspersed small granules and shallow pits. ×20,000.

3 Microfoveolate. The foveolate structure consists of deeper and more closely arranged pits, resulting in a spongy surface texture. ×20,000.

4 Microcorrugate-microfoveolate. Compound structure, the deep pits of the foveolate surface being separated by acute, irregular corrugations. ×20,000.

5 Echinate. The small, thornlike spinules are widest at the base and taper distally; some may be slightly hooked, others quite symmetrical. ×6,000.

6 Baculate. Surface with small, rodlike spinules of nearly equal diameter throughout, terminating bluntly. ×2,000.

7 Microfossulate. Structurally a granulate surface with very closely packed and elevated granules, the spaces left between the granules giving the general appearance of a negative or incised reticulum. ×20,000.

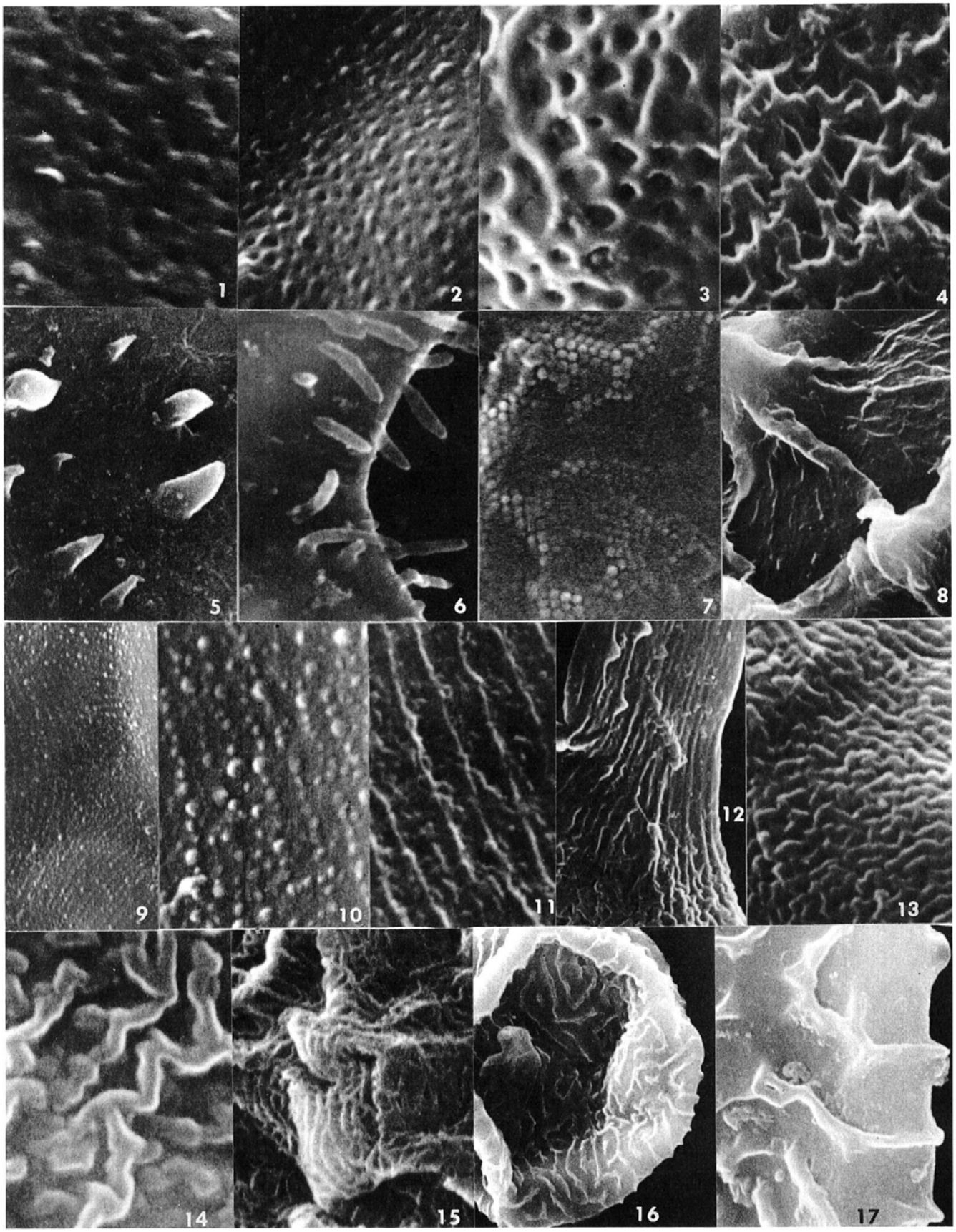
8 Rugulate. Irregular surface wrinkles. ×3,000.

9–10 Microgranulate. 9, a variation of the microgranulate wall in which the microgranules are so regularly aligned that a pseudocostate appearance results, particularly at lower magnifications. ×5,500. 10, a greater enlargement showing the wholly granulate nature of the pseudocostae. ×20,000.

11–12 Costate. Narrow, elongate, parallel costae with wider interridge areas. 11, costate surface with faint, irregular granules in the intercostal areas. ×20,000. 12, more regularly costate example. ×6,000.

13–15 Microcostate. Much finer costae than in figures 11–12. 13–14, a vermicular modification of the more common parallel costae in which the irregularly aligned costae are discontinuous and anastomosing. ×20,000. 15, intersecting microcostae producing a cross-hatched or reticulate appearance. ×15,000.

16–17 Cristate. Low flanges or crests of considerably larger scale than the costae. The crests may be regularly arranged in a reticulum or irregularly arranged and present a labyrinthine appearance as in figure 16. In figure 17 the laevigate intercrest area is displayed. 16, ×1,000. 17, ×5,000.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Remarks: Anomaloplaisium is similar in form to *Disparifusa* Loeblich (1970*b*) but differs in having a smooth central body except for scattered grana near the bases of the polar spines and in having the more prominent spinules confined to the polar spines, resulting in an echinate surface. *Disparifusa* has an echinate surface with small conical spines covering the entire central body.

Derivation of name: Anomaloplaisium from the Greek *anomalos,* uneven, irregular, plus *plaision,* oblong figure or form, latinized to *plaisium.* Gender neuter.

Anomaloplaisium lumariacuspis Tappan and Loeblich, **n. sp.**
Plate 2, figures 1–8

Description: Vesicle asymmetrically fusiform; one side straight or very slightly convex, the other strongly convex; poles projected into elongate, somewhat flexible spinelike processes; one process commonly smaller than the other; wall thin, about 0.3 μ in thickness; polar processes acuminate or, rarely, bifurcate, their surface echinate; the small hollow spinules communicating with the hollow process interior; spinules commonly thin and sharply pointed or, more rarely, bulbous and terminally rounded, becoming smaller and more sparse toward base of process; central body smooth except for small scattered granules toward the two poles; no excystment opening observed.

Dimensions: Maximum length, including processes, ranges from 135 to more than 200 μ; breadth of central body ranges from 23 to 39 μ.

Remarks: Anomaloplaisium lumariacuspis is similar in general outline to *Disparifusa hystricosa* Loeblich (1970*b*) but has more prominent spines on the polar processes. The spines do not grade into granules at the process tips, but are reduced in size as they approach the body, gradually disappearing on the body, whereas in *D. hystricosa* the short conical spines cover the entire body.

Derivation of name: From the Latin *lumaria,* thorny, plus *cuspis,* point, pointed end.

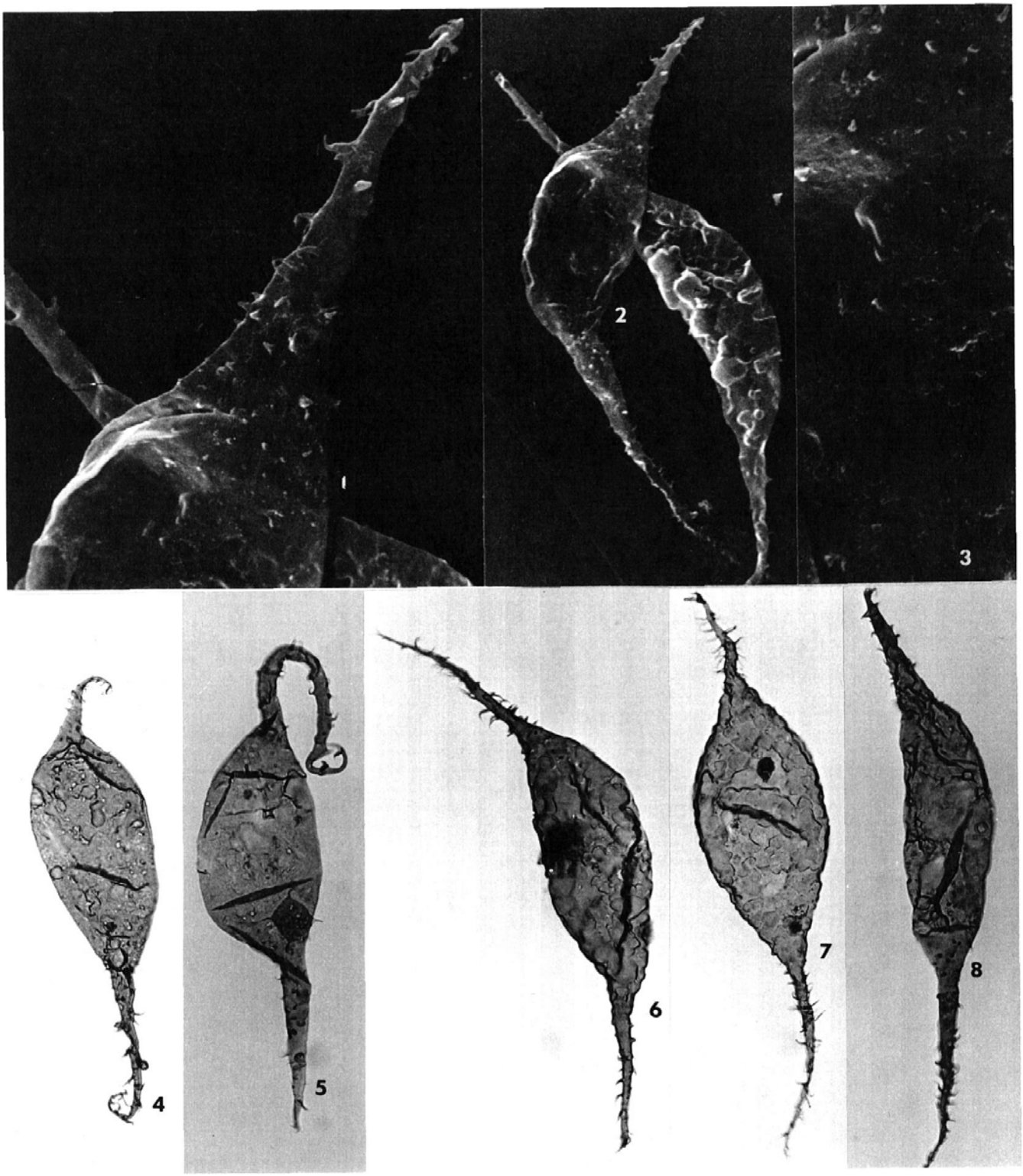
Types and occurrence: Holotype 69–114(1438), isotypes 69–114(1400, 1405, 1407, 1440) and 69–114 (SEM 1650–1652), all from the Upper Ordovician Dillsboro Formation, basal 5½ feet exposed in a road cut on U.S. Highway 50 at the west edge of Aurora, NE¼, NW¼, sec. 6, T4N, R1W, Dearborn County, Indiana. Collected by R. Anstey, T. A. Edison and A. R. Loeblich, Jr.

Genus ***Caiacorymbifer*** Tappan and Loeblich, **n. gen.**

Type species: Caiacorymbifer waldronensis Tappan and Loeblich, n. sp.

PLATE 2

1–8 *Anomaloplaisium lumariacuspis* Tappan and Loeblich, n. sp. 1–3, scanning electron micrographs; 1, isotype, showing the prominent spines producing an echinate surface on the polar processes, the spines grading into granules on the vesicle wall, ×1,700; 2, same specimen as 1, showing the over-all shape, ×600; 3, same specimen as 1, showing the small granules at the polar end of the vesicle which disappear toward the center of the vesicle, ×3,000; 4–8, light microscope photographs, ×518; 4, isotype, showing prominent spines on the asymmetrical polar processes and flexible character of the process tips (both figures 4 and 7 exhibit little of the characteristic arcuate shape, as these specimens are compressed at right angles to the curved axis); 5, isotype, showing a flexible polar process; 6, holotype, showing the typical asymmetrical fusiform vesicle and the prominent spines on the polar processes; 7, isotype, with polar processes of differing lengths; 8, isotype, with a less inflated vesicle and with polar processes of differing lengths. All specimens from the Upper Ordovician Dillsboro Formation of Indiana.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Description: Vesicle ovate to subcircular to circular in outline, ornamented with hollow processes that communicate freely with the vesicle interior; processes distally branched with a variable number of aculeate secondary tips, commonly six, in the type species; wall thin, laevigate in the type species; excystment by simple rupture and splitting of the vesicle wall.

Remarks: Caiacorymbifer differs from *Multiplicisphaeridium* Staplin, 1961, in having only one type of process furcation, a simple distal multifurcation with aculeate branches, instead of having furcations of more than one type or order. However, the number of branches or tips may vary. It differs from *Baltisphaeridium* Eisenack (1958*b*) in that the processes communicate freely with the vesicle and are never plugged. A number of poorly described and illustrated Silurian and Devonian forms probably belong to this genus.

Derivation of name: From the Latin *caia*, cudgel, club, plus *corymbus*, cluster, bunch, plus *fer*, suffix meaning carry, bear, have. Gender masculine.

Caiacorymbifer waldronensis Tappan and Loeblich, **n. sp.**
Plate 3, figures 1–8

Description: Vesicle ovate to subcircular in outline, ornamented with numerous processes, more than 40 visible from one side; processes hollow and communicating freely with the vesicle interior, 5–10 μ in length, rather rigid, up to about 2 μ in diameter at the base, tapering slowly to a furcate tip. With the light microscope the true nature of the termination is barely indicated, but with the scanning electron microscope the distal termination is shown to be a division into six small aculeate branches up to 0.35 μ in length arranged as a rosette. Wall thin, slightly less than 1 μ in thickness; both vesicle and process walls laevigate; excystment by a simple rupture and splitting of the vesicle wall.

Dimensions: Maximum diameter of vesicle, exclusive of processes, ranges from 29 by 34 μ to 32 by 45 μ.

Remarks: Caiacorymbifer waldronensis is similar to *Baltisphaeridium microcladum* Downie, 1963, from the Wenlock Shale, but it has more processes, its process tips consist of aculeate branches, any secondary branching is lacking, and it exhibits no bifurcate, trifurcate, or quadrifurcate variations of branching. It compares closely with the Devonian *Multiplicisphaeridium? sprucegrovensis* Staplin, 1961, in type of branching, but this species is quadrifurcate, and the processes are somewhat longer.

Derivation of name: The specific name refers to the Silurian Waldron Shale in which this species occurs.

Types and occurrence: Holotype 69–63(8)31.9–96.1, isotypes 69–63(13)31.7–109.3, 69–63(13)46.6–98, 69–63(SEM 2966–2967) and 69–63(SEM 2732–2733, 2744), all from the Silurian (late Wenlockian) Waldron Shale at Tunnel Mill, SW¼, sec. 11, T6N, R8E, Jennings County, Indiana. Collected by R. Anstey, T. A. Edison, A. R. Loeblich, Jr., and T. G. Perry.

Genus ***Comptaluta*** Tappan and Loeblich, **n. gen.**

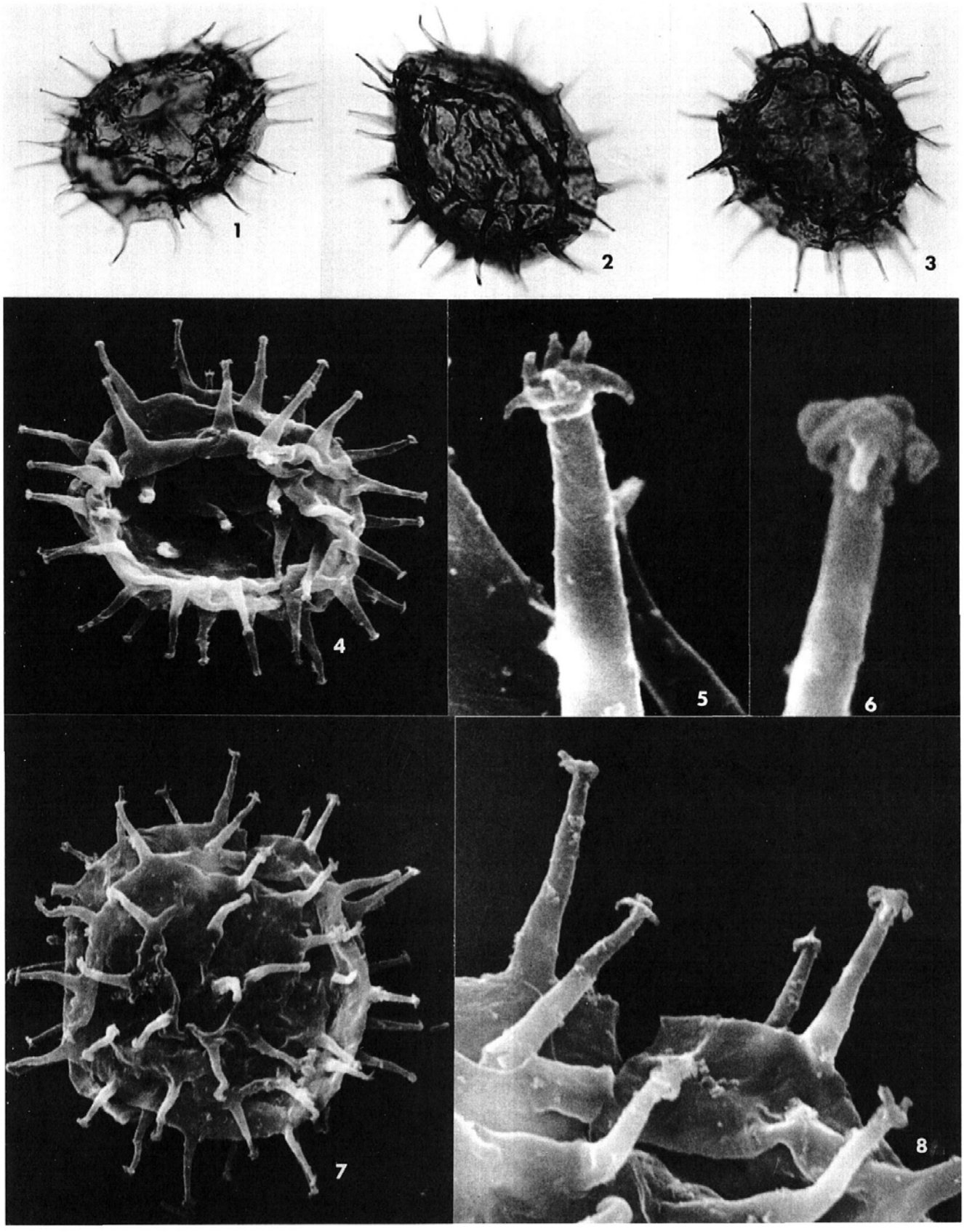
Type species: Comptaluta pirellum Tappan and Loeblich, n. sp.

Description: Vesicle elongate, pear-shaped in outline; apex terminating in two to three long, flexible processes; opposite end with scattered short processes; all processes communicating freely with the vesicle; wall thin, with microgranulate sculpture; no excystment mechanism observed.

Remarks: Comptaluta, new genus, is similar to *Deunffia* Downie, 1960, and *Domasia* Downie, 1960, but differs from the former in having a variable number of processes at each pole rather than a single process at one pole. It

PLATE 3

1–8 *Caiacorymbifer waldronensis* Tappan and Loeblich, n. sp. 1–3, light microscope photographs, ×960; 1, holotype, showing an ovate vesicle and hollow processes that freely communicate with the vesicle, the process tips having a bulbous appearance; 2, isotype, showing an ovate vesicle; 3, isotype, showing a subcircular vesicle; 4–8, scanning electron micrographs; 4, isotype, showing an ovate vesicle and the laevigate wall surface, ×2,000; 5, same specimen as 4, enlargement of a process which shows the distal end to have a rosette of six small projections; as these are barely visible in the optical microscope, the tip commonly appears bulbous, ×20,000; 6, isotype, same specimen as 7, enlargement of the distal end of a process, ×20,000; 7, showing a subcircular vesicle and the distribution of the processes, ×2,000; 8, same specimen as 7, showing the laevigate wall surface, ×6,000. All specimens from the Silurian (late Wenlockian) Waldron Formation of Indiana.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is closest to *Domasia* in having processes at each pole, but *Comptaluta* has two or three long processes at one end and, rather than a single process at the other, has scattered short processes over the vesicle body. It differs from both in having a definitely microgranular surface.

Derivation of name: From the Latin *comptus,* ornamented, plus *aluta,* purse or pouch of soft leather. Gender feminine.

Comptaluta pirellum Tappan and Loeblich, **n. sp.**
Plate 4, figures 1–7

Description: Vesicle elongate, pear-shaped in outline; body grading imperceptibly into two or more long, flexible, pointed processes at the narrow end, or else blunt at the narrow end and with three processes, one arising from the margin at each side and the third, slightly posterior, from the vesicle wall; several shorter processes scattered over broad end; processes communicating freely with the vesicle interior; wall thin, about 1 μ in thickness; surface of vesicle strongly microgranulate; no excystment opening observed.

Dimensions: Length of vesicle, exclusive of small processes, from thickened end to tip of long processes at the opposite end ranges from 97 to 132 μ, and the diameter of the vesicle ranges from 36 to 49 μ.

Remarks: Comptaluta pirellum differs from *Domasia bispinosa* Downie, 1960, in being much larger, distinctly microgranulate in wall sculpture, and more pear-shaped in outline. It has two or three long processes at one end and several shorter ones scattered over the vesicle at the other end, rather than a single small, indistinct spine at one pole and two larger ones at the other.

Derivation of name: From the Latin, *pirum,* pear, plus *-ellum,* diminutive suffix.

Types and occurrence: Holotype 67–94(SEM 2596–2597, 2599) and figured isotype 67–94(SEM 2567, 2569), both from the Middle Ordovician Mountain Lake Member of the Bromide Formation, below the spillway at the northernmost of two small lakes dammed on Spring Creek, NE¼, sec. 17, T2S, R1W, Murray County, Oklahoma. Collected by Helen Tappan and A. R. Loeblich, Jr.

Genus ***Dateriocradus*** Tappan and Loeblich, **n. gen.**

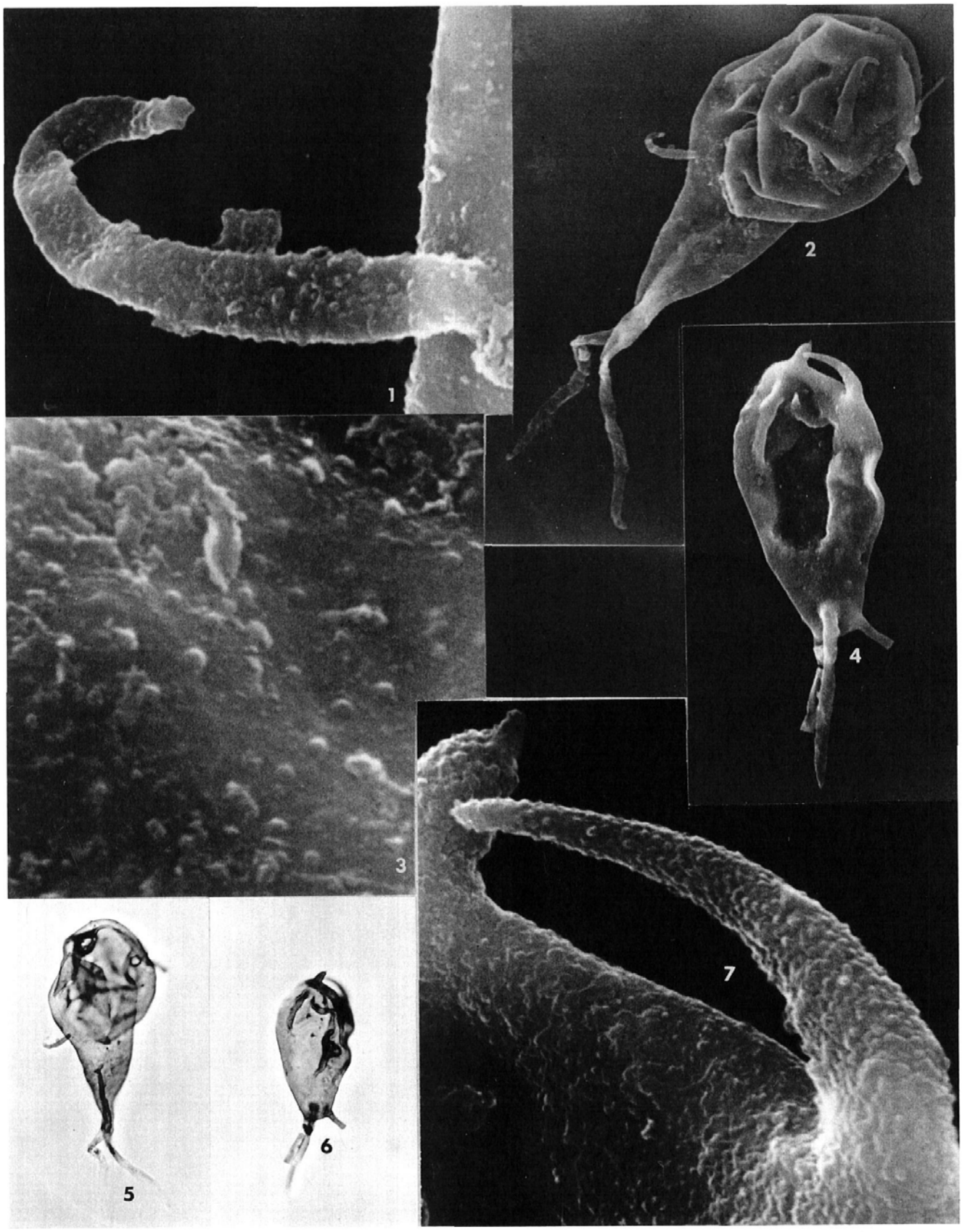
Type species: Dateriocradus polydactylus Tappan and Loeblich, n. sp.

Description: Central vesicle subtriangular in outline, commonly with three long hollow processes in plane of vesicle, rarely a fourth arising from the broad face of the vesicle; processes distally bifurcating up to the fifth or sixth order; wall surface laevigate; excystment by development of an epityche, an arcuate splitting of the wall resulting in a flaplike opening between two processes similar to that in *Veryhachium.*

Remarks: Dateriocradus is similar to *Veryhachium* but differs in having multifurcate processes. Various species of *Veryhachium* may include a rare specimen with a single process that bifurcates, but such specimens are not normal, and the processes are never multifurcate as in *Dateriocradus.* Evitt (in Tschudy and Scott, 1969, figs. 18–10h) figured a species of this genus from the Silurian as *Evittia* sp. *Evittia* Brito (1967*a*) has numerous processes that are terminally bifurcated, but the type species appears to have an inflated vesicle and a microverrucate wall sculpture. Brito (1967*a,* p. 477) also included two species in *Evittia* that may belong here, *Veryhachium sartbernardense* Martin, 1966, from the Ordovician of Belgium, and *V. trispinoramosum* Stockmans and Willière, 1962, from the Devonian of

PLATE 4

1–7 *Comptaluta pirellum* Tappan and Loeblich, n. sp. 1–4, 7, scanning electron micrographs; 1, holotype, enlargement of the small process arising from the left side of the vesicle in figure 2, showing the microgranulate surface sculpture, ×7,000; 2, holotype, showing the pear-shaped vesicle with two long, hollow, flexible processes at the narrow end and the small, hollow processes arising from the vesicle proper, ×750; 3, holotype, showing the microgranulate vesicle wall sculpture, ×20,000; 4, isotype, showing a blunt narrow end with a hollow process arising from the margin at either side and a third arising from the vesicle wall slightly posterior to these two, and the variable length of the processes arising from the broad opposite end of the vesicle, ×750; 5–6, light microscope photographs; 5, holotype, ×384; 6, same specimen as 4, ×384; 7, same specimen as 4, showing the microgranulate sculpture of the short processes arising from the broad end of the vesicle and the similar appearance of the vesicle wall, ×6,000. All from the Middle Ordovician Mountain Lake Member of the Bromide Formation of Oklahoma.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Belgium, but in neither of these species was the wall sculpture described. *Veryhachium furcillatum* Deunff, 1955, from the Devonian of North America should be assigned to this genus.

Derivation of name: From the Greek *daterios,* dividing, plus *krados,* branch, twig, latinized to *cradus*. Gender masculine.

Dateriocradus polydactylus Tappan and Loeblich, **n. sp.**
Plate 5, figures 1–7.

Description: Central vesicle subtriangular in outline, with sides slightly convex; in life vesicle inflated but probably lens-shaped, with three long processes arising in the plane of the central vesicle, rarely a fourth process arising from the face of the vesicle; processes hollow throughout their entire length except for the fine tips, which are probably solid, and communicating freely with the vesicle. Terminally the processes are variously multifurcate, bifurcating up to the sixth order. Wall surface laevigate; excystment by formation of an epityche, resulting from a low, arched, slitlike rupture of the vesicle wall between two processes and the opening out of a broad tonguelike flap.

Dimensions: Diameter of vesicle ranges from 16 to 25 μ, and length of processes ranges from 23 to 45 μ.

Remarks: Dateriocradus polydactylus is similar in size to the Devonian *Veryhachium furcillatum* Deunff, 1955, but differs in that the processes may bifurcate up to the sixth order rather than having simple first-order bifurcations.

This species is rather common in the Silurian Waldron Formation of Indiana.

Derivation of name: From the Greek, *polys,* many, plus *daktylos,* finger, latinized to *dactylus*.

Types and occurrence: Holotype 69–63(19)38.7–104.1, isotypes 69–63(20)18.1–96, 69–63(3)27.4–98.2, 69–63(3)13.2–104.1 and 69–63(SEM 2452–2453, 2964), all from the Silurian (late Wenlockian) Waldron Formation at Tunnel Mill, SW¼, sec. 11, T6N, R8E, Jennings County, Indiana. Collected by R. Anstey, T. A. Edison, A. R. Loeblich, Jr., and T. G. Perry.

Genus ***Melikeriopalla*** Tappan and Loeblich, **n. gen.**

Type species: Melikeriopalla amydra Tappan and Loeblich, n. sp.

Description: Vesicle spherical to subspherical; surface of vesicle cristate, divided into small, irregular, polygonal fields by low, apparently solid ridges or crests; fields may be secondarily subdivided by low and commonly discontinuous ridges; wall thin, ornamented with small, scattered granules and short, discontinuous microridges within the fields; excystment by simple rupture of the vesicle.

Remarks: Melikeriopalla superficially appears to be related to the majority of species placed in *Cymatiosphaera* O. Wetzel ex Deflandre, 1954, because the vesicle surface is divided into polygonal fields by low ridges. From *Cymatiosphaera* it is differentiated by having much lower "lamellae" dividing the sphere into fields, and by the fact that the fields are not smooth, but commonly subdivided by small discontinuous ridges. It differs from *Pterosphaeridia* Mädler, 1963, in having less prominent ridges dividing the vesicle into fields and in the absence of "pore-ducts", whereas from *Cymatiosphaeropsis* Mädler, 1963, it differs in lacking punctae or nodules within the fields. It is doubtful if any of the Paleozoic representatives of "*Cymatiosphaera*" are congeneric with the Mesozoic *Cymatiosphaera* O. Wetzel ex Deflandre, 1954.

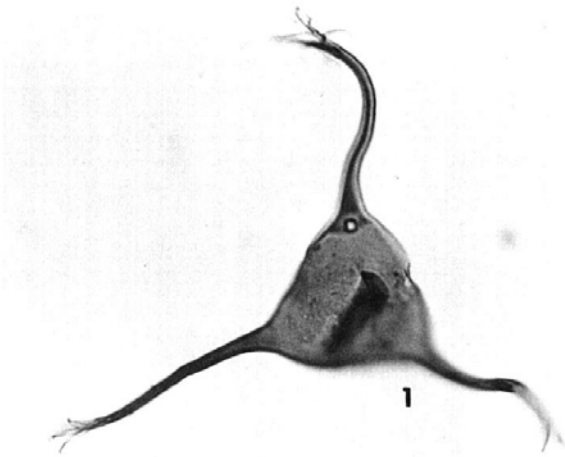
Derivation of name: From the Greek *melikerion,* honeycomb, plus *palla,* ball. Gender feminine.

Melikeriopalla amydra Tappan and Loeblich, **n. sp.**
Plate 6, figures 1–4

Description: Vesicle spherical to subspherical; surface of vesicle reticulocristate, divided by low, apparently solid ridges into small, irregular, polygonal fields, four- to six-sided and commonly 2–3 μ across. Commonly the

PLATE 5

1–7 *Dateriocradus polydactylus* Tappan and Loeblich, n. sp. 1–4, light microscope photographs; 1, holotype, showing the triangular vesicle with slightly inflated sides, and the hollow and terminally multifurcate processes, ×960; 2, isotype, showing the variation in the terminal branching of the processes, ×960; 3, isotype, ×960; 4, isotype, showing the flaplike epityche, ×960; 5–7, scanning electron micrographs; 5, isotype, same specimen as 7, showing details of the multiple branching, ×6,600; 6, isotype, showing a fourth process arising from the surface of the vesicle, ×1,000; 7, isotype, ×1,000. All specimens from the Silurian (late Wenlockian) Waldron Formation of Indiana.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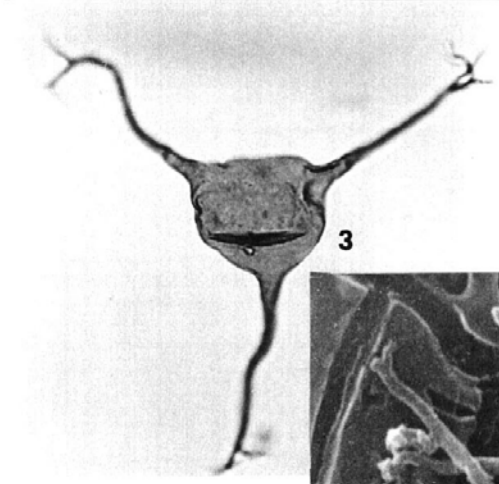
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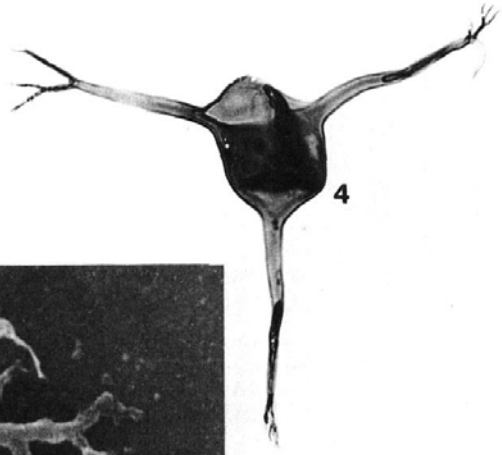
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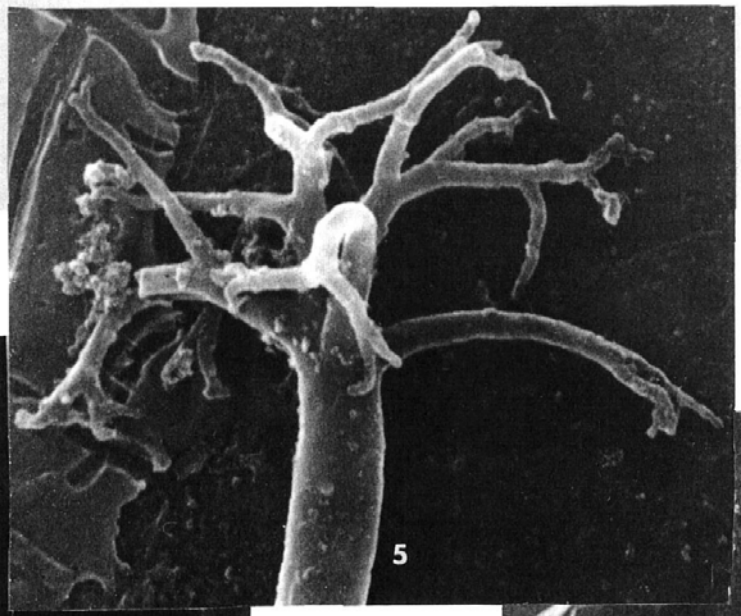
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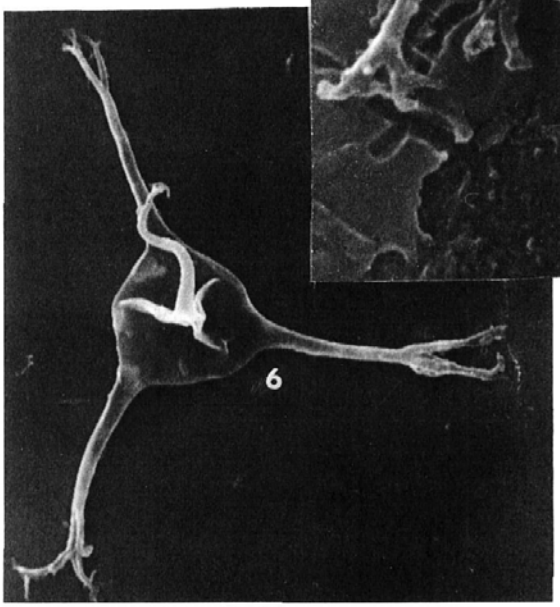
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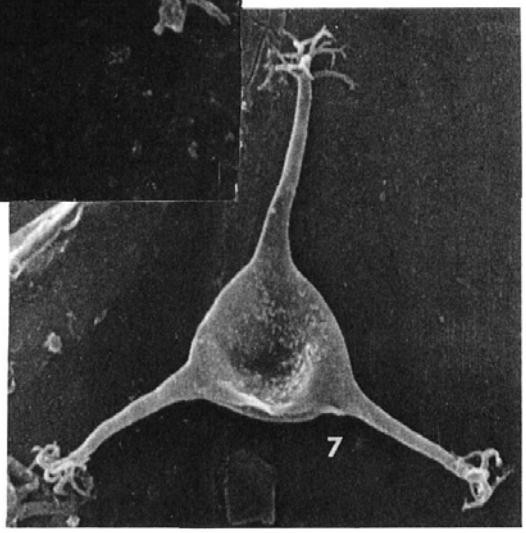
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fields are subdivided by low and discontinuous ridges that give the periphery a serrate appearance. Wall thin, about 1 μ in thickness; surface sculpture cristate, with small, scattered granules and discontinuous microridges within the fields; excystment by a simple rupture of the vesicle.

Dimensions: Diameter of vesicle ranges between 45 and 71 μ.

Remarks: At low magnifications this species may easily be mistaken for *Leiosphaeridia* Eisenack (1958*a*). The fields of this species are smaller than those in any previously described species. It differs from *Cymatiosphaera tecta* (Thiergart) Mädler, 1963, in having fields of smaller size (2–3 μ rather than 4–9 μ) and in having the fields irregularly subdivided into smaller fields by discontinuous microridges.

Derivation of name: From the Greek *amydros*, indistinct, dim, obscure.

Types and occurrence: Holotype 69–63(13)32.9–99.2, isotypes 69–63(8)38.7–100.9 and 69–63(SEM 2883–2884), all from the Silurian (late Wenlockian) Waldron Formation at Tunnel Mill, SW¼, sec. 11, T6N, R8E, Jennings County, Indiana. Collected by R. Anstey, T. A. Edison, A. R. Loeblich, Jr. and T. G. Perry.

Genus ***Ordovicidium*** Tappan and Loeblich, **n. gen.**

Type species: Ordovicidium elegantulum Tappan and Loeblich, n. sp.

Description: Vesicle spherical, having numerous hollow rigid processes that do not communicate with the vesicle, taper very little distally, and are multifurcate; rarely, simple processes occurring with the multifurcate ones; wall double-layered, the processes arising from the outer layer and being easily detached to leave a rimmed scar or hole exposing the inner layer; vesicle wall rather thick, laevigate to microgranulate; inner wall layer in some species also microgranulate; process walls thin, hyaline, smooth or microgranulate; excystment by rupture or splitting of the vesicle wall.

Remarks: Ordovicidium is characteristic of the Middle and Upper Ordovician, where it occurs commonly and abundantly. It differs from *Baltisphaeridium* Eisenack (1958*b*) in having multifurcate rather than simple processes. Typical *Baltisphaeridium* in rare cases has branched processes, but they are bifurcate, not multifurcate. The processes of *Baltisphaeridium* are internally plugged at or a short distance above the junction with the vesicle. *Multiplicisphaeridium* Staplin, 1961, has multifurcate processes, but, unlike the present genus, their cavities communicate freely with that of the vesicle.

Derivation of name: With reference to the Ordovician Period, in which it was particularly abundant.

Ordovicidium elegantulum Tappan and Loeblich, **n. sp.**
Plate 7, figures 1–7

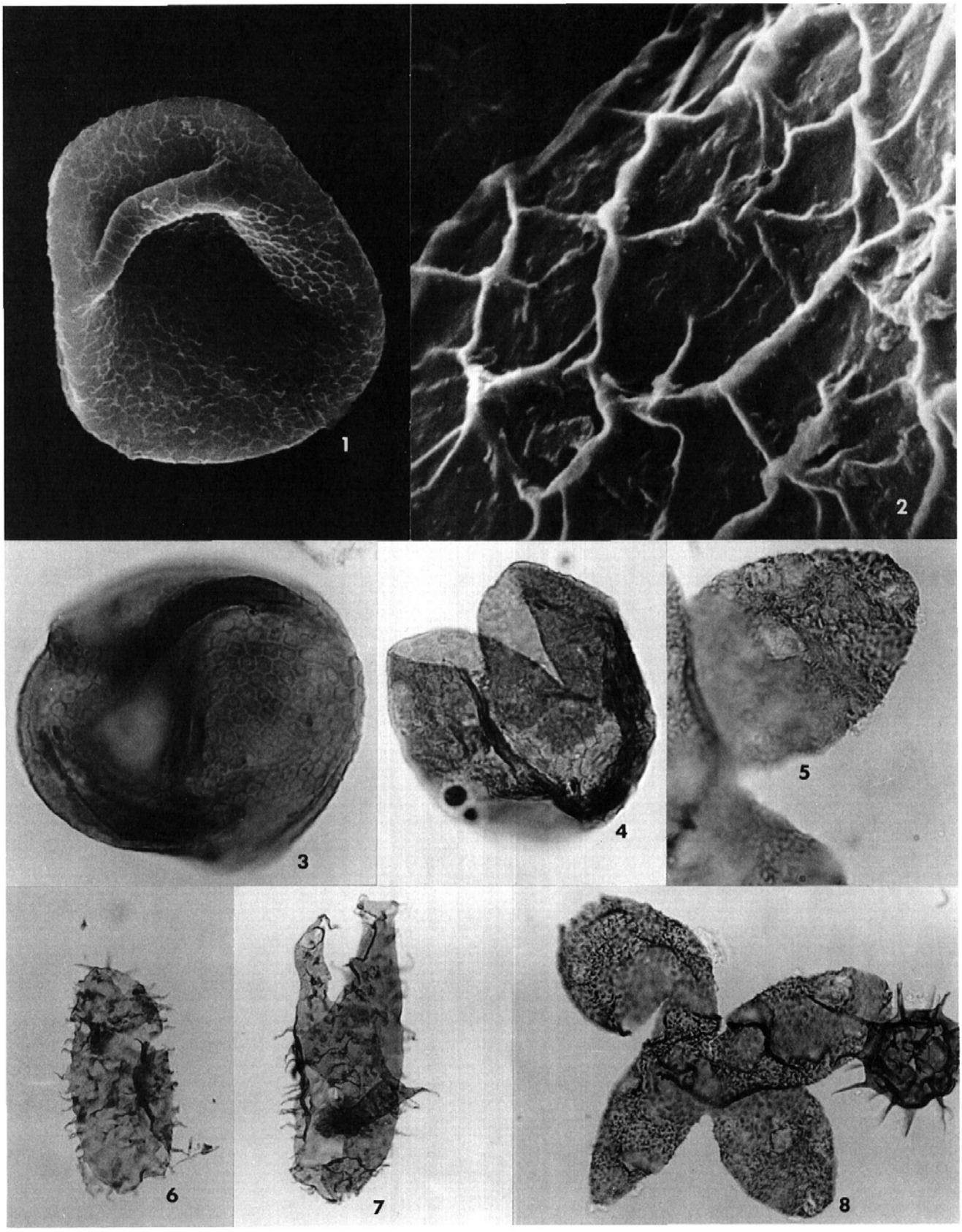
Description: Vesicle spherical, with hollow processes formed from the outer wall layer and thus not communicating with the vesicle interior; processes easily detached, each leaving a rimmed scar that is floored by the inner wall layer; processes tapering slightly distally where they may trifurcate or bifurcate and then bifurcate again; process branches terminating in fine, almost hair-like tips that commonly are broken off. Rarely, one or two of the processes on a specimen are simple, lack any bifurcation, and terminate in a point. Vesicle wall double-layered, rather thick, about 1.5 μ in thickness; hyaline walls of processes thinner, slightly less than 0.5 μ in thickness; both vesicle and process walls

PLATE 6

1–4 *Melikeriopalla amydra* Tappan and Loeblich, n. sp. 1–2, scanning electron micrographs; 1, isotype, showing the honeycomb-like cristate surface sculpture, ×1,000; 2, enlargement of the surface of 1, showing the surface divided into polygonal fields by low ridges, the fields commonly subdivided by lower and somewhat discontinuous ridges and scattered granules on the surface within the fields, ×15,000; 3–4, light microscope photographs; 3, holotype, showing the honeycomb-like surface, ×960; 4, isotype, showing the simple rupture of the wall which is probably the excystment mechanism, ×960. All specimens from the Silurian (late Wenlockian) Waldron Formation of Indiana.

5, 8 *Quadruilobus spinatus* Tappan and Loeblich, n. sp. 5, holotype, showing one broadly rounded lobe and the tiny spinule-like processes, ×960; 8, holotype, showing four broadly rounded lobes merging in the center with no distinct central vesicle, ×518. From the Upper Ordovician Eden Formation of Indiana.

6–7 *Rhachosoarium lappaceum* Tappan and Loeblich, n. sp. 6, holotype, showing the naviform cyst with numerous scattered processes showing no apparent alignment, ×518; 7, paratype, ×518. Both specimens from the Upper Ordovician Eden Formation of Indiana.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microgranulate, with small, scattered granules extending out on the processes and their branches to the beginnings of the hairlike branch tips; excystment by a splitting and rupture of the vesicle wall.

Dimensions: Diameter of vesicle ranges between 55 and 68 μ.

Remarks: Ordovicidium elegantulum is similar to *Baltisphaeridium nudum* (Eisenack) Staplin, Jansonius and Pocock, 1965, but the processes seem to be more massive in the Oklahoma specimens. Eisenack (1959, pl. 17, fig. 4) figured the type as having a fairly large pylome, but this was not mentioned or figured by Staplin, Jansonius and Pocock (1965, p. 190, pl. 20, figs. 2, 6–8; text-fig. 12). The latter authors commented on the granular vesicle wall and the "clear spine wall" in *B. nudum*. In the present species both vesicle and process walls are microgranular. Among the thousands of specimens of this genus that we have observed in the Middle and Upper Ordovician, we have never observed any specimen with a pylome.

Derivation of name: From the Latin *elegans*, choice, elegant; diminutive, *elegantulus*.

Types and occurrence: Holotype 67–107(310), isotypes 67–107(SEM 1166, 1168), paratypes 67–98(727), 67–103(SEM 1120), and 67–103(SEM 1112), all from the Mountain Lake Member of the Bromide Formation, below the spillway at the northernmost of two small lakes dammed on Spring Creek, NE¼, sec. 17, T2S, R1W, Murray County, Oklahoma. Collected by Helen Tappan and A. R. Loeblich, Jr.

Genus ***Pheoclosterium*** Tappan and Loeblich, **n. gen.**

Type species: Pheoclosterium fuscinulaegerum Tappan and Loeblich, n. sp.

Description: Medium-sized cysts, fusiform to ovate in outline, with extremities variable, broadly rounded to acuminate, the acuminate forms commonly terminating in a single simple, bifurcate or multifurcate process; wall thin; surface smooth or microgranulate; scattered capitate, trifurcate, quadrifurcate, or foliate (rarely simple) processes communicating with the central body; no definite excystment opening observed other than a rupture or splitting of the wall.

Remarks: Pheoclosterium is similar to *Dactylofusa* Brito and Santos, 1965, but differs in not having the processes arranged in definite rows. From *Holothuriadeigma* Loeblich (1970*b*) it differs in having an ovate to fusiform rather than a beanlike or reniform outline.

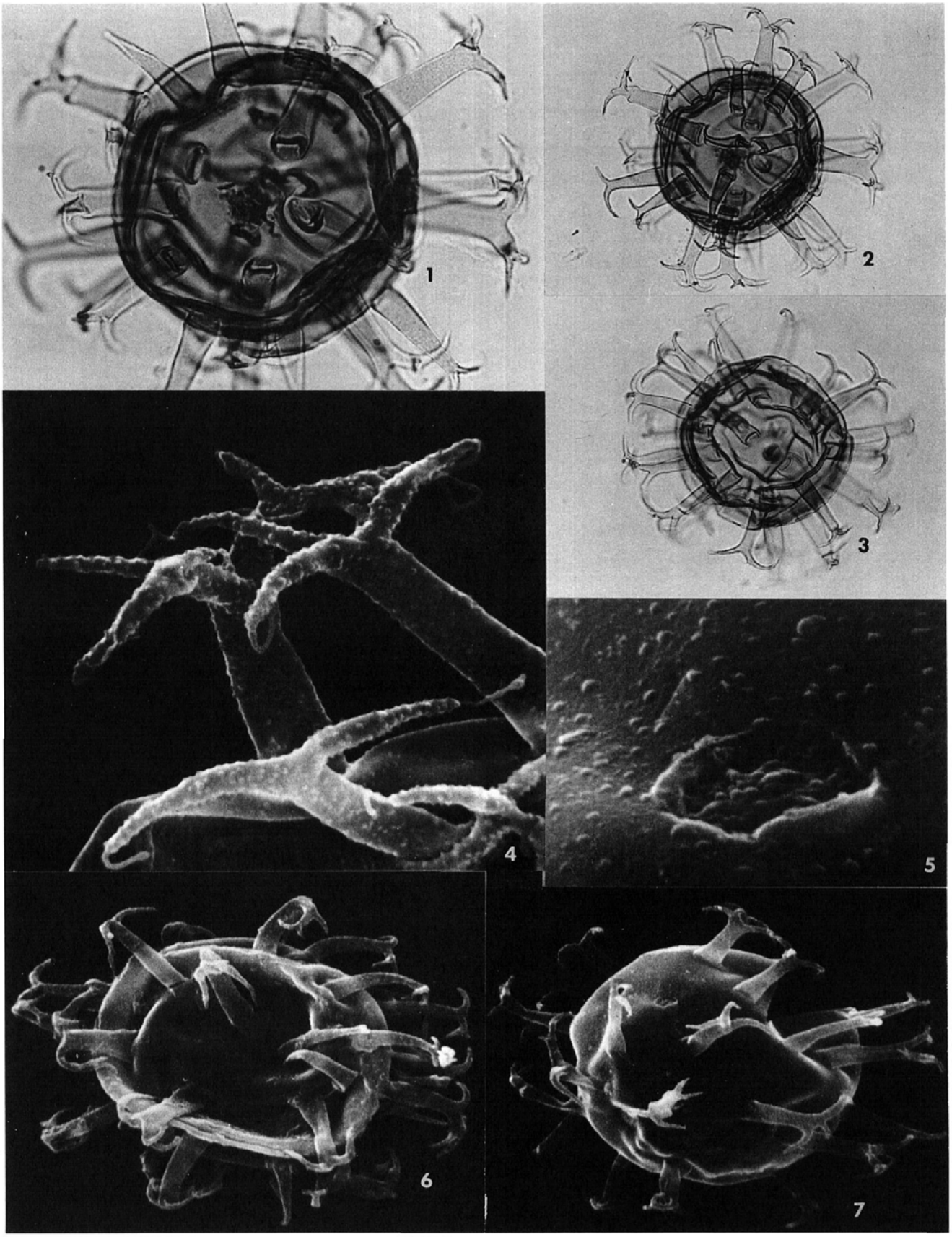
Derivation of name: Pheoclosterium, from Greek *pheos*, spiny plant, plus *kloster*, spindle, *klosterion*, diminutive, latinized to *closterium*. Gender neuter.

Pheoclosterium fuscinulaegerum Tappan and Loeblich, **n. sp.**
Plate 8, figures 1–7

Description: Body of vesicle variable in outline, elongate fusiform to elongate naviform, with extremities acuminate to broadly rounded; acuminate extremities commonly terminating in a pointed projection from the central body or in an elongate process that may have smaller projections on the sides or that may have bifurcate and trifurcate terminations; wall thin, about 0.5 μ in thickness; surface microgranulate; processes numerous, slender, tapering gently to the tips, communicating freely with the central body, scattered rather than arranged in definite rows, terminally trifurcate, although, rarely, a simple process may occur or one that has an inflated termination with five or six spines arising around the edges of the bulbous end; process wall microgranulate, similar in thickness to that of central body; excystment by a simple rupture of the central body.

PLATE 7

1–7 *Ordovicidium elegantulum* Tappan and Loeblich, n. sp. 1–3, light microscope photographs; 1, holotype showing the hollow, thin-walled, microgranulate, multifurcate processes and the rare simple process, neither of which communicates with the vesicle, ×960; 2, same specimen as 1, ×518; 3, paratype, ×518; 4–7, scanning electron micrographs; 4, details of furcation at distal end of processes, showing the branches ending in smooth, flexible, threadlike terminations, and showing the microgranulate process wall sculpture, ×4,000; 5, isotype, enlargement of 7, showing scattered granules on the vesicle wall and a scar where one of the processes has become detached to expose the microgranulate inner wall layer, ×10,000; 6, paratype, ×1,000; 7, isotype, showing the scar in the upper left quadrant which was enlarged in 5, and the simple rupture which probably acts as the excystment mechanism. All specimens from the Middle Ordovician Mountain Lake Member of the Bromide Formation of Oklahoma.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Dimensions: Length, including processes, ranges between 68 and 110 μ; and breadth, including processes, between 42 and 61 μ.

Remarks: Pheoclosterium fuscinulaegerum differs from *Dactylofusa maranhensis* Brito and Santos, 1965, in having scattered, commonly trifurcate processes, rarely simple, rather than claviform processes with five or more digitiform endings arranged in regular rows.

Derivation of name: From the Latin *fuscina,* three-pronged fork, trident, diminutive, *fuscinula,* plus *-ger, -a, -um,* suffix meaning bear, carry, have.

Types and occurrence: Holotype 69–127(4)28.1–93.4, isotypes 69–127(30)21.9–92.1, 69–127(17)26–96.7, 69–127(SEM 1917–1919), and paratype 69–130(1) 17.3–98.3, all from the Upper Ordovician Eden Formation, exposed in a road cut in Pinhook Road adjacent to Interstate Highway 74, on the west bank of the Whitewater River, approximately 7 miles west of West Harrison, Dearborn County, Indiana. Collected by R. Anstey, T. A. Edison, and A. R. Loeblich, Jr.

Genus ***Quadruilobus*** Tappan and Loeblich, **n. gen.**

Type species: Quadruilobus spinatus Tappan and Loeblich, n. sp.

Description: Cyst petaloid, consisting of four relatively large, broadly rounded lobes with no distinct central vesicle but with numerous tiny, apparently simple, spinule-like processes up to 2 μ in length; wall thin; surface appearing granulate-rugulate with the light microscope as a result of the numerous small processes; no excystment opening observed.

Remarks: Quadruilobus does not closely resemble any described genus. Superficially, it recalls *Deflandrastrum* Combaz, 1962, but differs in that its lobes merge proximally into the "central body", and there is no central quadrangular opening.

Derivation of name: From the Latin *quadruus,* fourfold, plus *lobus,* elongate projection or protuberance. Gender masculine.

Quadruilobus spinatus Tappan and Loeblich, **n. sp.**
Plate 6, figures 5, 8

Description: Petaloid cyst consisting of four large, broadly rounded lobes of somewhat variable outline that meet in the center; no distinct central vesicle; processes numerous, spinule-like, tiny, up to 2 μ in length and apparently simple; wall thin, about 0.3 μ in thickness; surface appearing granulate-rugulate in the light microscope, probably owing to compression of the abundant, small, spinule-like processes; no excystment opening observed.

Dimensions: Maximum diameter from tip of one lobe to that of opposite lobe 122 μ, greatest breadth of a lobe 42 μ.

Remarks: Quadruilobus spinatus is a very rare form in the Eden Formation. It is not closely comparable with any described species but differs from *Deflandrastrum colonnae* Combaz, 1962, in not being divided into triangular "cells" and in lacking an open space in the center.

Types and occurrence: Holotype 69–129(2)46.1–92.9, from the Upper Ordovician Eden Formation exposed in a road cut on Pinhook Road, adjacent to Interstate Highway 74, on the west bank of the Whitewater River, approximately 7 miles west of West Harrison, Dearborn County, Indiana. Collected by R. Anstey, T. A. Edison, and A. R. Loeblich, Jr.

Genus ***Rhachosoarium*** Tappan and Loeblich, **n. gen.**

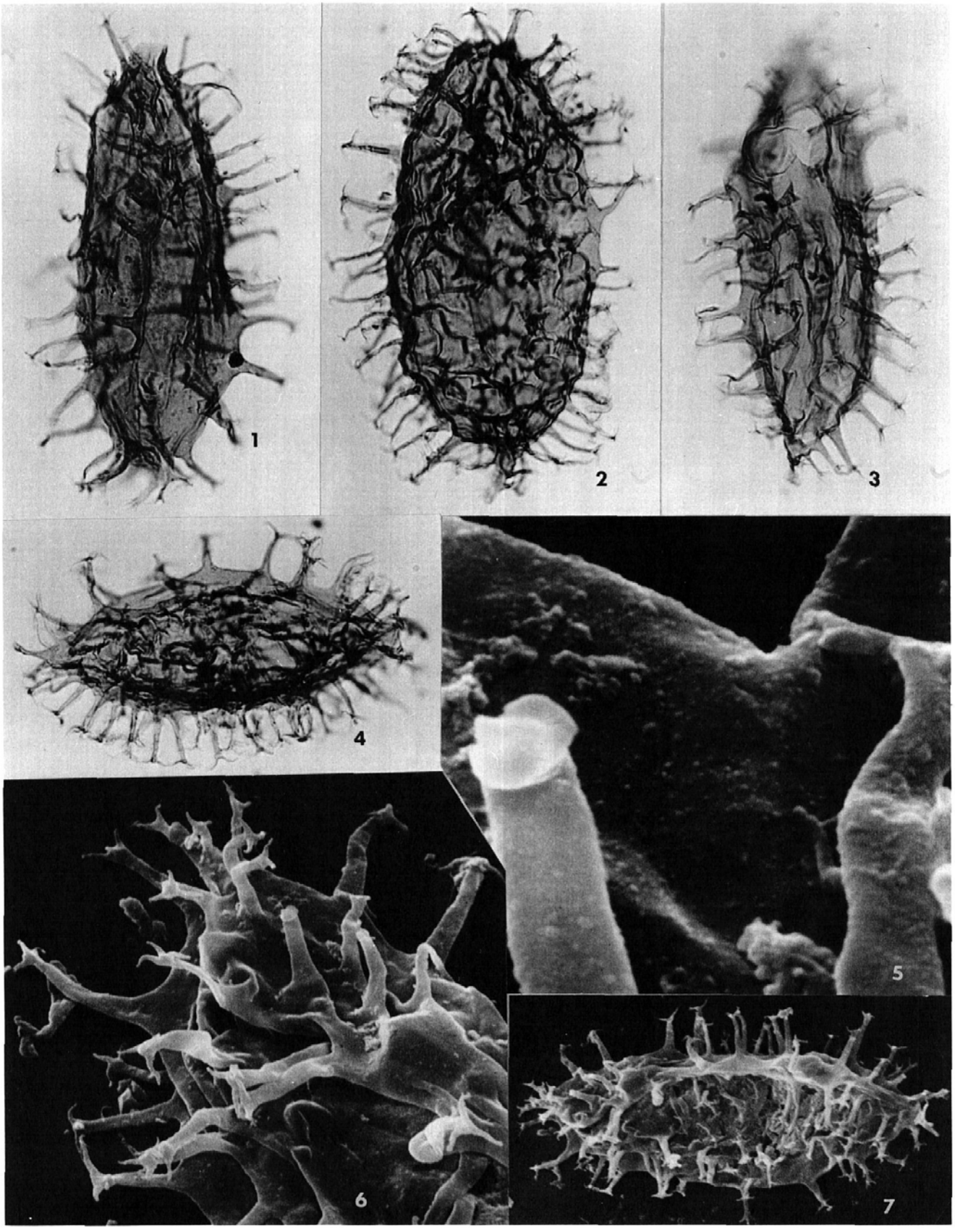
Type species: Rhachosoarium lappaceum Tappan and Loeblich, n. sp.

Description: Vesicle naviform in shape, ornamented with numerous processes that communicate with the vesicle interior; wall thin, scabrate in sculpture; no definite excystment mechanism other than simple rupture of the vesicle.

Remarks: Rhachosoarium is reminiscent in outline and shape of *Navifusa* Combaz, Lange and Pansart, 1967, but differs from that genus in possessing numerous

PLATE 8

1–7 *Pheoclosterium fuscinulaegerum* Tappan and Loeblich, n. sp. 1–4, light microscope photographs; 1, holotype, showing the fusiform or almost naviform shape and the numerous hollow scattered processes which freely communicate with the vesicle and terminate in trifurcations, ×960; 2, isotype, having a more naviform shape, ×960; 3, paratype, clearly showing the trifurcate terminations of the processes, ×960; 4, isotype, showing a more fusiform shape, ×960; 5–7, scanning electron micrographs; 5, isotype, showing the microgranulate process and vesicle walls, ×20,000; 6, same specimen as 5, showing the trifurcate terminations of the processes, ×3,000; 7, same specimen as 5, showing the distribution of the processes, ×1,000. All specimens from the Upper Ordovician Eden Formation of Indiana.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somewhat flexible, scattered processes. It differs from *Dactylofusa* Brito and Santos, 1965, in lacking any tendency for the processes to be aligned in definite rows.

Derivation of name: From the Greek, *rhachos*, thorn bush, brier, plus *öon*, egg, *oarion*, diminutive, latinized to *oarium*. Gender neuter.

Rhachosoarium lappaceum Tappan and Loeblich, **n. sp.**
Plate 6, figures 6–7

Description: Vesicle naviform in shape, with broadly rounded poles, ornamented with numerous scattered processes up to 7 μ in length; processes showing no alignment, about 35–40 visible on the margins of the vesicle; processes opening into the vesicle interior, broad at the base, somewhat flexible, rapidly tapering distally to acuminate tips; wall about 1 μ in thickness, scabrate in surface sculpture; no definite excystment mechanism observed other than simple rupture of the vesicle.

Dimensions: Length of vesicle ranges between 74 and 98 μ, breadth between 33 and 35 μ.

Remarks: Lacking the processes, this species would be placed in the genus *Navifusa*. It is similar in outline to some specimens of the associated *Pheoclosterium fuscinulaegerum*, new genus, new species, but in general it has a more naviform outline, and its processes are simple rather than furcate. It differs from *Dactylofusa maranhensis* Brito and Santos, 1965, in being more naviform in outline, with broadly rounded poles, and in lacking a tendency for the processes to be aligned in rows.

Derivation of name: From the Latin *lappaceus*, burrlike.

Types and occurrence: Holotype 69–127(10)34.5–92.7 and paratype 69–131(13)49.5–99.9 from the Upper Ordovician Eden Formation, exposed in a road cut on Pinhook Road, adjacent to Interstate Highway 74 on the west bank of the Whitewater River, approximately 7 miles west of West Harrison, Dearborn County, Indiana. Collected by R. Anstey, T. A. Edison, and A. R. Loeblich, Jr.

Genus ***Rhopaliophora*** Tappan and Loeblich, **n. gen.**

Type species: Rhopaliophora foliatilis Tappan and Loeblich, n. sp.

Description: Vesicle spherical to subspherical, ornamented with numerous short, stout, hollow processes of various shapes; processes blunt to pointed, commonly with few to many small projections just below or at the summit; processes apparently not communicating with the vesicle; wall thin; surface sculpture microcostate, the parallel ridges of varying alignment simulating a pinnate venation; excystment by means of a circular pylome with operculum and elevated rim.

Remarks: Rhopaliophora differs from *Peteinosphaeridium* Staplin, Jansonius and Pocock, 1965, in possessing short, stout processes of many shapes and forms ranging from simple bulbous to pointed ones, to others that have as many as 14 irregularly shaped projections at or near the process summit; None of the processes has the characteristic buttressed or angular finned structures of *Peteinosphaeridium*. The surface sculpture, a striking pinnately aligned series of ridges, differs from that in *Peteinosphaeridium*.

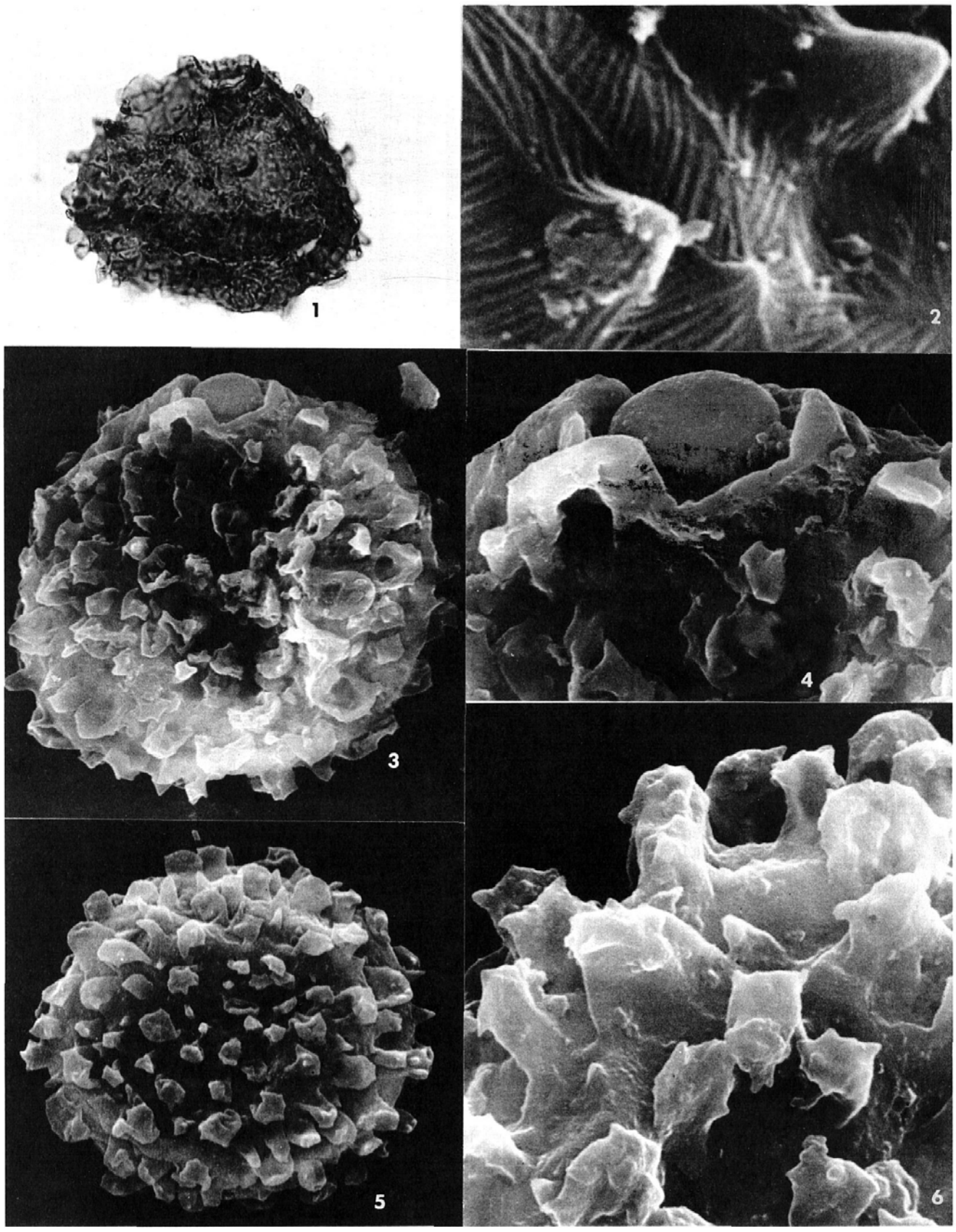
Derivation of name: From Greek *rhopalon*, club, *rhopalion*, diminutive, plus *phor*, suffix, meaning carry, have. Gender feminine.

Rhopaliophora foliatilis Tappan and Loeblich, **n. sp.**
Plate 9, figures 1–6

Description: Vesicle spherical to subspherical, ornamented with numerous short, stout processes that with the light microscope commonly appear to be angular, truncated, or broadly rounded at the summit. With the scanning electron microscope they are clearly shown to be exceedingly variable in size, shape and form, and to range from simple cone-shaped ones to others of nearly equal diameter for their entire length and truncated at the summit, to bulbous ones, some having a number of projections that may be short or equal to the process length. Processes apparently not communicating with the vesicle interior; wall thin, about 0.5 μ in thickness; both process and vesicle walls microcostate,

PLATE 9

1–6 *Rhopaliophora foliatilis* Tappan and Loeblich, n. sp. 1, light microscope photograph of the holotype showing the prominent rim type of pylome and the short, blunt processes, ×960; 2–6, scanning electron micrographs; 2, paratype, showing the characteristic pinnately microcostate sculpture pattern on the process wall, ×30,000; 3, paratype, showing the rim type of pylome with the operculum slightly detached and the distribution of the processes, ×1,300; 4, same specimen as 3, showing details of the pylome and operculum, ×3,000; 5, paratype, showing the varying size of the processes and their distribution, ×1,500; 6, paratype, details of the processes, showing the variation in size and number of the projections on the processes, ×5,000. All specimens from the Upper Ordovician Eden Formation of Indiana.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with a distinctive, strongly pinnate alignment of many tiny costae about 0.05 μ in width; circular pylome 7–10 μ in diameter, with an operculum, a prominent rim, and a produced neck.

Dimensions: Vesicle diameter ranges from 45 to 61 μ.

Remarks: Rhopaliophora foliatilis is similar to *Baltisphaeridium macropylum* Eisenack, 1959, in that both have thick processes, but the present species has much stouter and more variable processes.

Derivation of name: From the Latin *foliatilis,* leafy.

Types and occurrence: Holotype 69–131(11)46.3–110, paratypes 69–127(SEM 1785), 69–127(SEM 1958), 69–129(SEM 2176, 2178) and 69–129(SEM 2129), all from the Upper Ordovician Eden Formation exposed in a road cut on Pinhook Road, adjacent to Interstate Highway 74 on the west bank of the Whitewater River, approximately 7 miles west of West Harrison, Dearborn County, Indiana. Collected by R. Anstey, T. A. Edison, and A. R. Loeblich, Jr.

Rhopaliophora impexa Tappan and Loeblich, **n. sp.**
Plate 10, figures 1–7

Description: Vesicle spherical to subspherical, ornamented with numerous short, stout, hollow processes that vary in size and form, from simple, short low ones to elongate conical ones to those that have as many as 14 projections at or slightly below the summit; these projections commonly attaining almost the length of the process; processes not communicating with the vesicle interior; wall thin, about 0.5 μ or less in thickness; process and vesicle walls with microrugulate surface sculpture; excystment by means of a large, prominent, circular pylome up to 13 μ in diameter, with an operculum; pylome having a thickened rim and prominent elevated neck.

Dimensions: Vesicle diameter ranges from 49 to 87 μ.

Remarks: Rhopaliophora impexa differs from *R. foliatilis,* the type species, in having slightly longer processes that bifurcate profusely, rather than being low and knobby. It is similar to *Baltisphaeridium macropylum* Eisenack, 1959, but the processes branch more, and the branches commonly equal the length of the main process. Eisenack (1959, text-fig. 9a–c) figured the processes of *B. macropylum* as showing only a simple bifurcation distally, with short branches.

Derivation of name: From the Latin *impexus,* uncombed, disheveled.

Types and occurrence: Holotype 69–129(6)32.8–104.6, isotype 69–129(12)20.6–109.5, paratypes 69–127 (SEM 2020–2022) and 69–127(SEM 1967), all from the Upper Ordovician Eden Formation exposed in a road cut on Pinhook Road adjacent to Interstate Highway 74, on the west bank of the Whitewater River, approximately 7 miles west of West Harrison, Dearborn County, Indiana. Collected by R. Anstey, T. A. Edison, and A. R. Loeblich, Jr.

Genus ***Psenotopus*** Tappan and Loeblich, **n. gen.**

Type species: Psenotopus chondrocheus Tappan and Loeblich, n. sp.

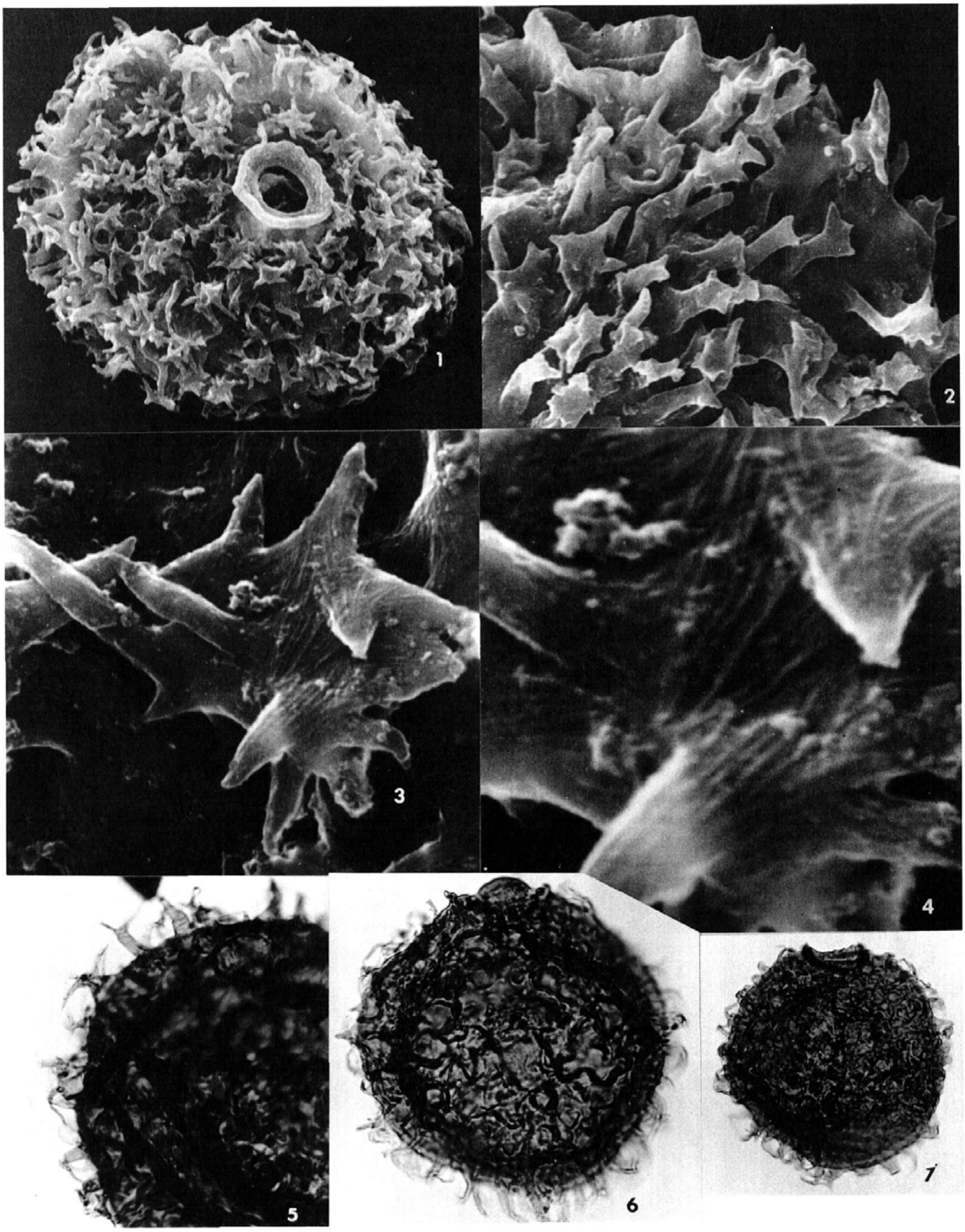
Description: Vesicle spherical, surface gemmate, ornamented with low tubercles or processes arranged in patches or bands separated by bare and laevigate areas; processes apparently solid, low, circular in plan view, varying in size, rounded and smooth to slightly knobby, with a slight tendency to appear aculeate at the tips; wall thin, smooth but commonly with microridges and small, rare, scattered granules; excystment by a simple rupture of the vesicle.

Remarks: Because of the distribution of its tubercles or processes in bands or patches separated by bare areas, *Psenotopus* does not compare closely with any previously described acritarch. It is closest to *Lophosphaeridium* Timofeev ex Downie, 1963, but in that genus the tubercles generally are closely spaced over the entire vesicle wall.

Derivation of name: From the Greek *psenos,* smooth, bald, plus *topos,* place, position, spot.

PLATE 10

1–7 *Rhopaliophora impexa* Tappan and Loeblich, n. sp. 1–4, scanning electron micrographs; 1, paratype, showing the prominent rim type of pylome and a surface ornamented by densely packed processes, ×1,300; 2, paratype, showing the elevated border around the pylome and the varying shape and form of the processes, ×2,600; 3, same specimen as 1, view of a single process from above, showing 12 projections arising from a single process and the characteristic surface sculpture of the processes, ×13,000; 4, enlargement of a portion of 3, ×30,000; 5–7, light microscope photographs; 5, paratype, showing the appearance of the processes as seen in the light microscope, ×960; 6, isotype, showing the prominent pylome at the top with the operculum in place, ×960; 7, holotype, showing the pylome at the top with the operculum dislodged and missing, ×518. All specimens from the Upper Ordovician Eden Formation of Indiana.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Psenotopus chondrocheus Tappan and Loeblich, **n. sp.**
Plate 11, figures 1–6

Description: Vesicle spherical, in compression commonly somewhat angular; surface gemmate, ornamented with low, apparently solid tubercles or processes that occur in patches or bands separated by bare areas; tubercles low, circular in plan view, ranging in size from 0.7 to 1.5 μ, irregularly spaced from 0.6 to 5.3 μ apart, in side view commonly tending to become weakly aculeate, with small projections at the summit; in compression or under high vacuum in an evaporator the areas of bare surface tend to collapse, whereas the bands or patches carrying the tubercles are stronger and stand up owing to the added thickness of the wall; wall thin, about 0.5 μ in thickness, smooth or with minute spherical gemmules and a fine series of irregular ridges; excystment by a simple rupture and splitting of the vesicle wall.

Dimensions: Maximum diameter of vesicle ranges from 67 to 80 μ.

Remarks: Psenotopus chondrocheus does not compare closely with any described acritarch. It differs from the Wenlock *Lophosphaeridium citrinum* Downie, 1963, which possesses capitate processes, in having the tubercles localized in areas separated by bare or bald areas.

Derivation of name: From the Greek *chondros,* grit, grain, plus *ocheo,* bear, carry.

Types and occurrence: Holotype 69–63(SEM 2885), isotypes 69–63(SEM 2465–2466; SEM 2706, 2709) and 69–63(10)49.2–106.1, all from the Silurian Waldron Formation at Tunnel Mill, SW¼, sec. 11, T6N, R8E, Jennings County, Indiana. Collected by R. Anstey, T. A. Edison, A. R. Loeblich, Jr., and T. G. Perry.

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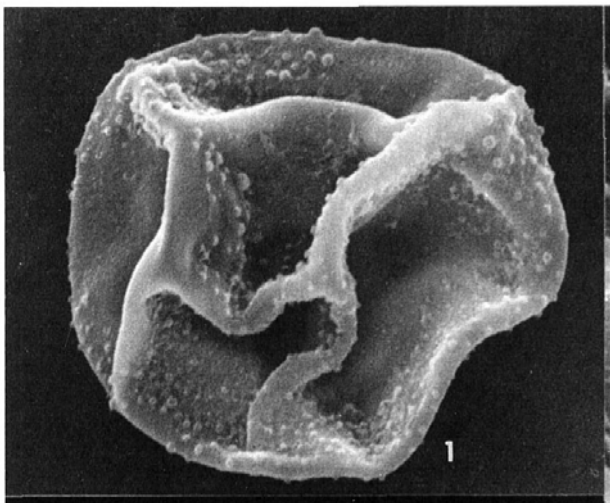
PLATE 11

1–6 *Psenotopus chondrocheus* Tappan and Loeblich, n. sp. 1–5, scanning electron micrographs; 6, light microscope photograph; 1, isotype, showing folds of the vesicle wall and the patchy distribution of the tubercles separated by bare areas, ×1,000; 2, isotype, showing the gemmate sculpture, the bluntly rounded smooth tubercles and the common ones that have short projections at the ends, the small, scattered granules and the fine and commonly discontinuous, low microridges, rarely forming polygonal fields, ×10,000; 3, holotype, showing the polygonal vesicle resulting from folding and compression, and the distribution of the tubercles, ×1,000; 4, an enlargement of the surface of 1, ×3,000; 5, isotype, showing the splitting of the vesicle wall which is probably the excystment mechanism; ×1,000; 6, isotype, showing the appearance of the vesicle in the light microscope, ×960. All specimens from the Silurian (late Wenlockian) Waldron Formation of Indiana.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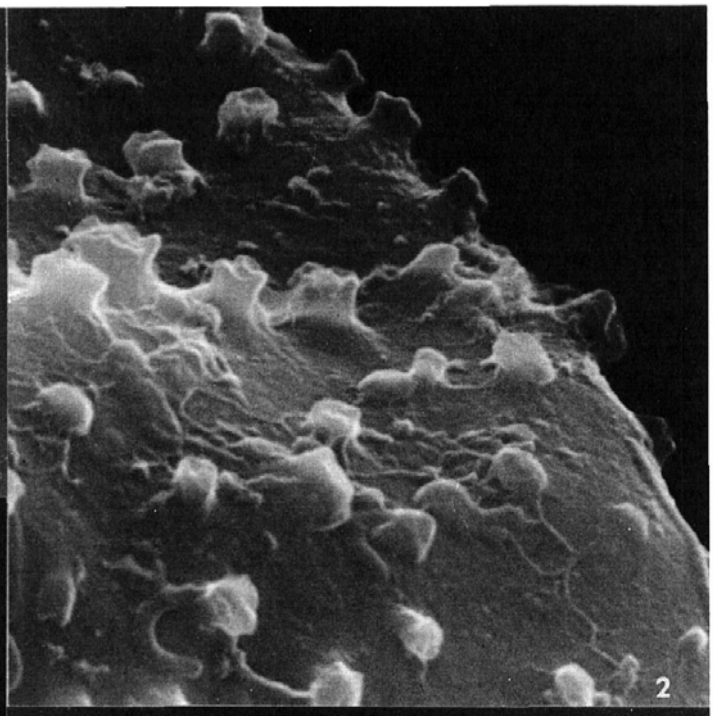
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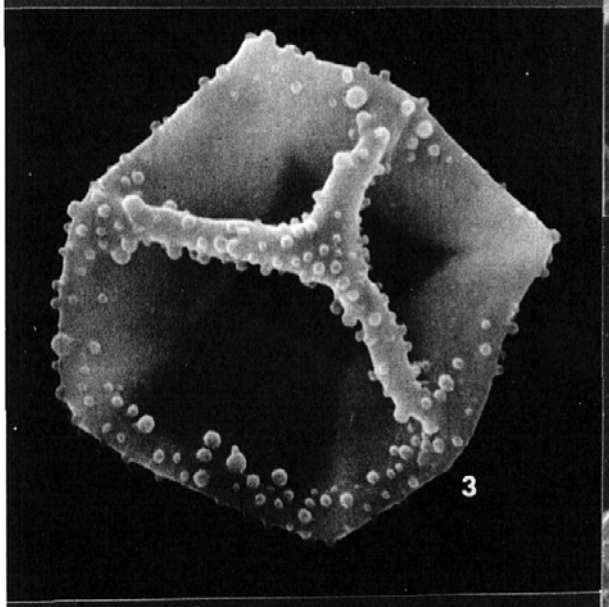
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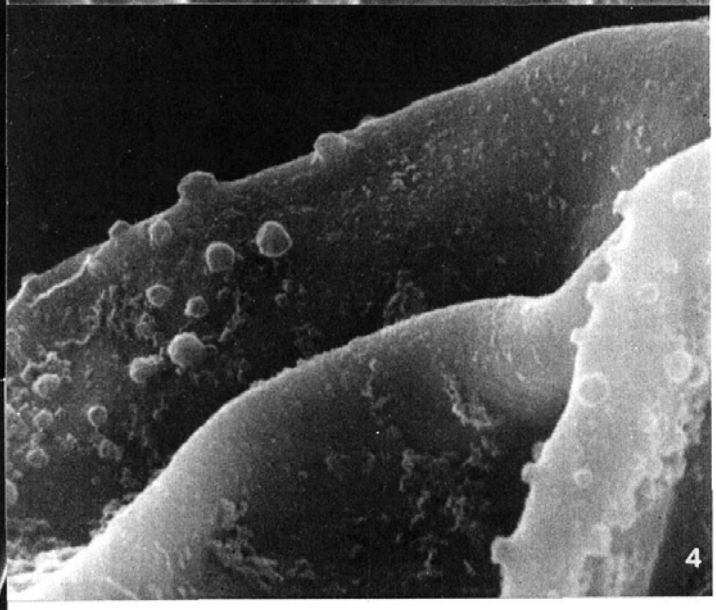
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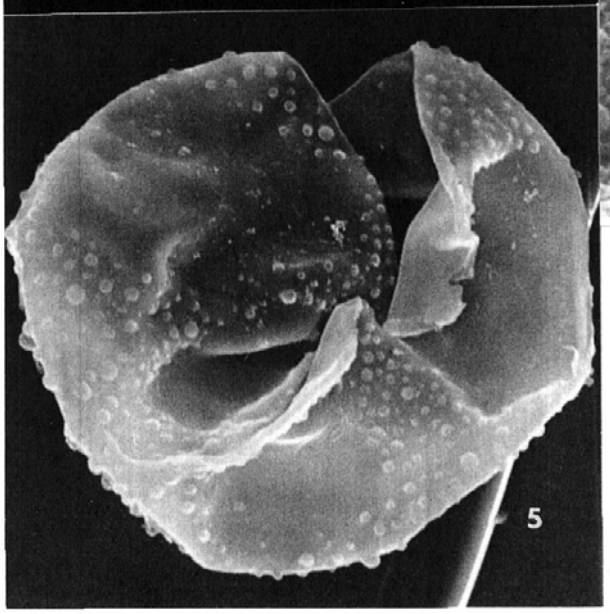
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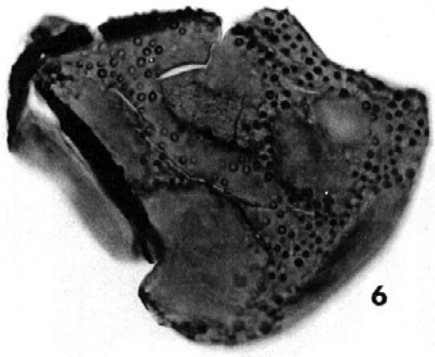
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