A DISCUSSION AND PROPOSALS CONCERNING FOSSIL DINOFLAGELLATES, HYSTRICHOSPHERES, AND ACRITARCHS, I

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In 1961 I suggested that many post-Paleozoic organic microfossils that had been called hystrichospheres are really dinoflagellate cysts. Further extensive studies fully support that view. Although new findings and some revisions in details of the interpretations offered in 1961 await future publication, I feel it is appropriate now to propose several nomenclatural changes and taxonomic revisions affecting these fossils. That is the purpose of this paper, which includes (following certain background information): (1) an emendation of the dinoflagellate family Hystrichosphaeraceae, (2) proposal of three new dinoflagellate taxa: Hystrichosphaeridae n. fam., Areoligeraceae n. fam., and Achomosphaera n. gen., (3) a recommendation that the term Hystrichosphaerida no longer be used and that its informal variations, such as hystrichosphere, be used cautiously, and (4) a proposal for a new informal group of microfossils of organic composition and unknown affinity to be known as acritarchs.

Note on Use of Botanical Code.—Downie et al. recently proposed that fossil dinoflagellates and hystrichospheres (including acritarchs in the sense of this paper) be treated nomenclaturally under the Botanical Code. I have adopted this proposal (but without certain of their accessory suggestions regarding the erection of natural genera and form-genera) chiefly on the grounds (1) that, as algae, the dinoflagellates are nomenclaturally botanical entities, and (2) that the acritarchs, whose affinities are unknown (though they, too, probably include many fossil algae), should be treated under the same code as the dinoflagellates for purely practical reasons. However, this paper is not the place to discuss some of the knotty problems raised by transferring genera and families from the realm of the Zoological Code to that of the Botanical Code; for example, problems that devolve from the distinction between natural genera, organ-genera, and form-genera under the Botanical Code and the effect of this distinction on family names proposed originally under the Zoological Code. These and other problems are currently under extensive discussion in correspondence among interested co-workers. Slowly, workable solutions to them will emerge. For the present, I have simply used botanical family names in the same manner as zoological family names have been used in the past. Thus, Hystrichosphaeridae becomes Hystrichosphaeraceae, etc. This may not be the ideal procedure, but it seems at least a temporarily acceptable one that is consistent with stability in nomenclature, which is the spirit and purpose of nomenclatural codes.

Theca, Cyst and Test.—Currently incomplete research suggests that the fossilized remains of dinoflagellates possibly nowhere include the theca, if that term is used to designate only the external cellulose or cellulose-like covering of a motile dinoflagellate cell. Instead, the fossils seem to represent a layer of considerably more resistant material that formed inside the theca. Probably the structure formed by this resistant layer was functionally a cyst, but it will be referred to herein by the
less committal term test. The test appears to have contacted the theca over relatively larger and smaller areas in different genera and species. Tests that formed mainly in contact with or close to the inner surface of thecal plates seem to be represented by such obviously dinoflagellate-like fossils as have been commonly referred to the extant genus Gonyaulax. Tests that also formed within the theca, but that contacted it only by means of pillar-like supporting processes appear to be represented by superficially undinoflagellate-like fossils such as Hystrichosphaera and Hystrichosphaeridium. In genera of the last sort the pattern of thecal plates may not be directly observable, but only reflected by the number and distribution of surficial ridges and projecting processes. In other words, the fidelity with which the fossil test records morphological characteristics of the theca may depend chiefly upon the distance that separated the two structures, the fidelity decreasing with increasing separation. A virtually unbroken series of morphological types that collectively bridge the gap between the extreme examples just mentioned is rapidly being recognized among described genera of fossil dinoflagellates.

A test wall of at least two layers seems typical for fossil dinoflagellates, although it is not universal. The two layers that are discernible in many fossils customarily considered dinoflagellates (Eisenack) are very likely homologous with the two layers noted in fossils like Hystrichosphaera and Hystrichosphaeridium (Klumpp, Evitt) that have traditionally been classified as hystrichospheres, separate from the dinoflagellates.

Hystrichosphaera, Hystrichosphaerida, and Hystrichospheres.—The history of the study of hystrichospheres to 1961 has been ably reviewed by Sarjeant. Only a few details need concern us here.

In 1838, when Ehrenberg illustrated the first fossil dinoflagellates, he also figured some spiny organic microfossils from the Cretaceous of Germany and Poland, which he identified with the modern freshwater genus Xanthidium. He named one of the fossil species Xanthidium furcatum. Subsequent work showed that these objects, although unrelated to Xanthidium, are common fossils, and in 1933, O. Wetzel proposed for them a new genus Hystrichosphaera (type species: Xanthidium furcatum Ehrg.) and a new family, the Hystrichosphaeridae. In 1937 Deflandre emended Hystrichosphaera by separating it from a second genus Hystrichosphaeridium, for whose type species he selected another of Ehrenberg’s forms, Xanthidium tubiferum. In 1938 Eisenack proposed a new order, the Hystrichosphaerida (= Hystrichosphaeridea auct.) for the Hystrichosphaeridae and a second family that he erected at the same time. Subsequent work of many authors (see Sarjeant) has added to this order a complex of genera that have been referred to informally as “hystrichosphaerids,” “hystrichospherids,” or “hystrichospheres.”

Thus, the nomenclatural history and current status of the three formal names, Hystrichosphaera, Hystrichosphaeridae and Hystrichosphaerida, and of their informal derivatives, “hystrichosphere,” etc., are simple and clear. In addition, the morphology of the critical genus Hystrichosphaera is well known, especially through the detailed descriptions of Lejeune and Deflandre, supplemented by more recent observations (e.g., Evitt).

Much uncertainty and conflicting speculation have characterized attempts to determine the biological affinities of hystrichospheres. In conjunction with an extensive review of the evidence, Deflandre concluded that they are not a single
biologic category, but probably a conglomeration of cysts, eggs, and entire shells representing many groups of organisms only remotely related. On the other hand, Eisenack\textsuperscript{12} has argued for the “Einheitlichkeit der HYstrichosphaerideen.” I follow Deflandre in believing that a great variety of biological entities is represented among the fossils that have been called hystrichospheres. Some of these fossils give no indication of being dinoflagellates, whereas many others seem, in fact, to be dinoflagellates, among them the genera *HYstrichosphaera* and *HYstrichosphaeridium*. I propose to consider these genera to be dinoflagellates.

Assignment of *HYstrichosphaera* to the Dinoflagellata means that the family HYstrichosphaeraceae (type genus *HYstrichosphaera* ) is a family of dinoflagellates. Accordingly, the description of the family is emended below in a manner that will exclude those fossils formerly assigned to it which cannot be recognized as dinoflagellates, as well as certain other fossils that are dinoflagellates but which are herein assembled in a new family Areoligeraceae.

I also suggest that use of the name HYstrichosphaerida should be discontinued for two reasons: (1) The name is no longer appropriate for a group of nondinoflagellates, since the taxa upon which it was based (*HYstrichosphaera* and HYstrichosphaeridae) are here considered dinoflagellates. (2) Since the “dinoflagellate hystrichospheres” can be accommodated in the Peridiniales, there is no need for an ordinal grouping within the dinoflagellates to include the HYstrichosphaeraceae and for which the name HYstrichosphaerida (as HYstrichosphaerales) might be used.

By these changes the meaning of the informal term “hystrichosphere” also becomes modified and restricted. In the narrowest sense it now has the scope of a family (HYstrichosphaeraceae) instead of an order (HYstrichosphaerida). Cautionous use of the term in a context that clearly associates it with the dinoflagellates seems advisable in order to avoid confusion with the nondinoflagellate, now “ex” hystrichospheres for which the informal name acritarchs is suggested and defined on a following page.

**Descriptive Terminology.**—The adjectives sutural, intratabular, and nontabular are used in the following pages with reference to contrasting arrangements of surface features (processes, ridges, etc.) on a dinoflagellate test. Sutural features rise from the lines or angles between polygonal fields and correspond in position to the sutures between thecal plates. Intratabular features occupy positions on the test that correspond to more or less of the central portions of thecal plates, rather than to the lines of separation between them. (The “plate-margin processes” and “plate-centered processes” of Evitt\textsuperscript{1} are, respectively, sutural and intratabular.) For example, *HYstrichosphaera* (Fig. 1) possesses both sutural ridges and sutural processes, *Achomosphaera* (Fig. 2) has sutural processes only, and *HYstrichosphaeridium tubiferum* (Fig. 3) has intratabular processes. In *HYstrichosphaera* the simple reticulum of sutural ridges makes obvious the platelike fields that suggest a dinoflagellate tabulation. The arrangements of processes in the other two are not immediately apparent, but are decipherable and distinctive, according well with plausible patterns of thecal plates. Process-groups (i.e., multiple intratabular processes) also occur. The elements of a process-group may be arranged in one or more clusters, or in rows that surround more or less polygonal areas (as in *Areoligeria*, Fig. 4), but these rows are not united in a single reticulum as in *HYstrichosphaera*. 
Projecting surface features that are neither sutural nor intratabular are **nontabular**; that is, they are in random arrangement or the arrangement, if regular, has no apparent relation to a scheme of tabulation.

The term **sulcal notch** is applied to the commonly occurring re-entrant in the outline of an apical archeopyle on the ventral side of the test. The notch records the girdleward extension of the first apical plate in line with the sulcus, and inter-

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**FIG. 1.**—Sutural processes and sutural ridges in camera lucida drawing of *Hystrichosphaera* sp. from the Vincentown Formation (lower Eocene), New Jersey. Dorsal surface, about \( \times 700 \). Note fusion of shafts of alternate pairs of girdle processes. *\( a *\)-precingular archeopyle.

**FIG. 2.**—Sutural processes without sutural ridges in *Achomosphaera ramulifera* (Defl.) n. comb. Holotype, after Deflandre,\(^8\) pl. 11, fig. 6, from the Upper Cretaceous (probably Senonian), Paris; about \( \times 450 \). Note fusion of alternate pairs of girdle processes and some near poles. *\( a *\)-precingular archeopyle.

**FIG. 3.**—Intratabular processes in *Hystrichosphaeridium tubiferum* (Ehrbg.). A, reconstruction of test in ventral view, based on numerous specimens from the Redbank Formation (Maastrichtian), New Jersey; about \( \times 500 \). B, inferred relationship between test and originally surrounding theca. Zigzag line on central body represents suture that forms archeopyle.

**FIG. 4.**—Intratabular process-groups and offset sulcal notch in camera lucida drawings of *Areoligera* cf. *A. senonensis* Lej.-Carp. from the Navesink Formation (Maastrichtian), New Jersey. Ventral views: A, ventral surface; B, dorsal surface par transparence; about \( \times 350 \). Apical archeopyle is open and operculum not shown.

rupts the cycle of precingular plates. In members of the Areoloigeraceae (Fig. 4) this notch is conspicuously offset from the midline.

**Central body** refers to the compact central portion of a test from which the projecting structures (processes, septa, etc.) extend. **Capsule** is restricted to the innermost body formed by a multilayered wall. The capsule may fill all or only part of the central body, depending upon the extent to which their walls are in close contact. **Archeopyle** is used in the sense of Evitt.\(^1\)
Systematics.—Many of the genera in the families discussed below require re-description and revision, but I do not feel this can yet be done effectively. Rather, it should wait until described species can be restudied to search for morphological characters not originally considered, and until additional undescribed forms can be studied and described.

Family HYSTRICHOSPHAERACEAE O. Wetzel 1933 emend.

Type genus: Hystrichosphaera O. Wetzel 1933,7 emend. Deflandre 1937.8

Revised diagnosis: More or less radially or axially symmetrical dinoflagellate tests that consist of a spherical to ellipsoidal central body with basically spinelike sutural processes that may or may not be combined with low sutural ridges, folds, or membranous septa. The tips of processes may be free or interconnected by a network of trabeculae concentric to the central body. Archeopyle exclusively precingular.

Genera referable to the family: Achomosphaera Evitt n. gen., Cannosphaeropsis O. Wetzel 1933 (partim, including the type species C. utinensis), Hystrichosphaera O. Wetzel 1933, emend. Deflandre 1937, Nematosphaeropsis Deflandre & Cookson 1955, Triblastula O. Wetzel, 1933. Hystrichokibotium Klumpp 1953 is probably synonymous with Hystrichosphaera, comprising, I believe, specimens of that genus oriented so that the equatorial band of elongate platelike areas was not visible to the observer.

Discussion: The family is distinguished from Areoligeraceae by the uncompressed spherical to ellipsoidal shape and grossly radial or axial symmetry. It is distinguished from both Areoligeraceae and Hystrichosphaeridaeae by restriction of projecting structures to sutural lines, and by the exclusively precingular archeopyle.

The wall is often distinctly two-layered: a generally thicker inner layer forms a simple spherical to ellipsoidal capsule; the outer layer forms the projecting structures and the external surface between their bases. The two layers may be in close contact over most of the surface (i.e., except under the projecting structures), or separated over large areas. The number of spinelike processes ranges from 2–3 to over 100. They may be solid or hollow, closed at the tips (usually) or open. Cavities of hollow processes do not communicate with the interior of the capsule. No major processes project from the central portions of the polygonal areas.

The distinctively furcate processes typical of Hystrichosphaera (e.g., H. furcata)—trifurcate at the corners of reflected plates, bifurcate along their sides—occur repeatedly in the family. In Achomosphaera the processes stand isolated without sutural septa or ridges connecting their bases; hence, the fact that they are restricted in position to sutural lines is not obvious. In Nematosphaeropsis, the tips of processes are interconnected by trabeculae. In Cannosphaeropsis (as exemplified by the type species and a few others), complete processes may be greatly reduced: many lack bases and shafts and are represented only by characteristic pairs or triplets of short projections corresponding to the furcate tips, which branch from the trabecular network that envelops the central body. (Many species that have been referred to Cannosphaeropsis do not exhibit the basic features of the type species and must ultimately be accommodated elsewhere.) Triblastula lacks the Hystrichosphaera-like processes, but the sutural arrangement of ridges and processes is distinct in the equatorial region.
The tabulation reflected in the arrangement of ridges and processes that is most frequently encountered in the family is 3', 0a, 5–6", 6g, 5", 1p, 1"'.

Genus ACHOMOSPHAERA n. gen.

Type species: Achomosphaera ramulifera (Deflandre) n. comb. = Hystrichosphaeridium ramuliferum Deflandre, 1937, pp. 74–75, pl. 15, figs. 5–6; pl. 17, fig. 10; Upper Cretaceous, France.

Description: Test consists of a spherical to ellipsoidal central body with precingular archeopyle and fureate, spikelike processes like those in Hystrichosphaera in both structure and distribution, but without sutural ridges or septa connecting their bases as in that genus. Tips of processes not interconnected. Wall two-layered; layers typically in close contact between bases of processes.

Discussion: Diagnostic characters are the precingular archeopyle and Hystrichosphaera-like processes, combined with an absence of sutural ridges or septa between process bases and an absence of trabeculae between process tips. Some of the equatorial processes reflecting the girdle are often large and double as in Hystrichosphaera. Processes at the poles may also be larger than ones between polar areas and equator. Hystrichosphaera, the most closely similar genus, and Nematosphaeropsis are distinguished by well-developed sutural ridges or septa, and Nematosphaeropsis has trabecular connections between process tips. Despite the lack of sutural ridges in Achomosphaera, the positional relationship of its processes to other features (e.g., poles, equator, archeopyle) shows that the processes are sutural.

Other species: No others have been described, but undescribed species of the genus have been observed in strata ranging from Alban to Lower Tertiary in age.

Family HYSTRICHOSPHAERIDIACEAE n. fam.

Type genus: Hystrichosphaeridium Deflandre 1937 emend. Eisenack 1958.13

Description: More or less radially or axially symmetrical dinoflagellate tests that consist of a spherical to ellipsoidal central body bearing from a few (but usually more than 15) to more than 50 basically conical to columnar or trumpet-shaped processes. Processes may be intratabular or nontabular, single or in groups. The tips of processes may be free or interconnected by trabeculae concentric to the central body. Archeopyles of several types occur, apical and precingular ones most commonly.

Genera referable to the family: Hystrichokolpoma Klumpp 1953, Hystrichosphaeridium Deflandre 1937 emend. Eisenack 1958, Hystrichosphaerina Alberti 1961, Systematophora Klement, 1960; probably Polystephanephorus Sarjeant 1961. In addition, some species that have been assigned to Cannosphaeropsis (e.g., C. aemula (Deflandre, 1947) and possibly C. caulleryi Deflandre 1938, C. speciosa Alberti 1961, and C. urnaformis Cookson 1953) represent the family.

Discussion: The family is distinguished from the Hystrichosphaeraceae by the intratabular or nontabular distribution of processes, from the Areoligeraceae by the uncompressed spherical to ellipsoidal shape, and from both by the variety of archeopyle types including precingular, apical, and epithecal ones.

The wall may be distinctly two-layered or only one layer may be recognizable. The processes may be solid or hollow and their substance may appear membranous, hyaline, or fibrous. The interiors of hollow processes do not communicate with the
interior of the capsule. Process tips may be open or closed, simple or compoundly divided, free or interconnected by trabeculae. A uniquely large or distinctively constructed process may mark either apical or antapical pole, or both. In species that exhibit a constant and decipherable process arrangement, all processes may be similar or some may be different; for example, the processes reflecting girdle and sulcal plates are often smaller and less complex than the pre- and postcingular processes, or they may be missing entirely.

The following are examples in which major processes or process-groups number less than 40 and are arranged in a constant and decipherable pattern: some species of *Hystrichosphaeridium* (including the type species *H. tubiferum*, Fig. 3), *Hystrichokolpoma, Systematophora, Hystrichosphaerina, Polystephanophorus, and Canno-sphaeropsis* (partim, e.g., *C. aemula* (Deflandre)). The basic tabulation appears to be (1ap), 1–4’, 0a, 6’, 6g, 6s, 5”, 1”, 1”’.

Examples with more numerous, mostly nontabular processes (although alignment of girdle processes may be recognizable) are some species of *Hystrichosphaeridium*, and many species originally assigned to *Hystrichosphaeridium* but excluded from this genus by Eisenack’s 1958 revision. These forms, which have no generic home among the dinoflagellates when *Balitsphaeridium* and *Micrhystridium* are considered acritarchs, include *H. hirsutum* (Ehrenberg), *H. horridum* Deflandre, *H. machaerophorum* Deflandre & Cookson, *H. striolatum* Deflandre, *H. ferox* Deflandre, and *H. flosculus* Deflandre.

New genera are needed here but their erection is beyond the scope of this paper.

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