New insights on the Paleogene dinoflagellate cyst genera *Enneadocysta* and *Licracysta* gen. nov. based on material from offshore eastern Canada and southern Argentina

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ABSTRACT: *Enneadocysta* is a biostratigraphically important Paleogene dinoflagellate cyst genus. Its original interpretation as a partiform gonyaulacoid (thus belonging to the gonyaulacalean suborder Cladopyxiineae) was based on the presence of two antapical processes. Another Paleogene genus, *Areosphaeridium*, is similar, at least superficially, to *Enneadocysta*, but has a single antapical process, placing it in the sexiform gonyaulacalean suborder Gonyaulacineae. The morphology of a new species of *Enneadocysta* from offshore eastern Canada, *Enneadocysta magna*, shows that the two antapical processes of the genus (unlike processes reflecting other plate series) are penitabular, not mesotabular, and indicates that the genus is gonyaulacinean, not cladopyxiinean. This new interpretation, as well as new material from southern Argentina, confirms the generic assignment of the Southern Hemisphere species *Enneadocysta dictyostila* (emended) and a new species, *Enneadocysta brevistila*. A new genus and species, *Licracysta corymbus*, from offshore eastern Canada is intermediate in morphology between *Enneadocysta* and *Cleistosphaeridium* and strongly suggests an assignment for all three genera to the gonyaulacinean family Areoligeraceae. The new combination *Licracysta*? *semicirculata* is questionably proposed, and the descriptive terms licrate, dolabrate, entire clypeate, ragged clypeate, intratabular, mesotabular, obtabular, contabular and nontabular are either proposed as new or reviewed.

INTRODUCTION

Organic-walled dinoflagellate cysts (dinocysts) of the extinct family Areoligeraceae are distinguished typically by: a sexiform gonyaulacalean tabulation; a sulcus offset to the left with accompanying asymmetry of the antapical outline, the left side being more prominent; and an apical archeopyle (Fensome et al. 1993). They range in age from Late Jurassic to Neogene, but are most diverse from mid Cretaceous to Paleogene: material for the present study is from the Paleogene. In this paper we: 1) re-interpret as areoligeracean the morphology of *Enneadocysta* through a revision of the Southern Hemisphere species *Enneadocysta dictyostila* (= *Enneadocysta partridgei*) and through the introduction of two new species, *Enneadocysta magna* and *Enneadocysta brevistila*; 2) propose another areoligeracean genus, *Licracysta* and the new species *Licracysta corymbus*; and 3) show that these two genera are related to other areoligeracean genera such as *Glaphyrocysta* and *Cleistosphaeridium*. (Full authorships for all generic and specific names cited in this paper are given in Appendix 1.)

MATERIALS AND METHODS

The present investigation involves material derived from the following sources:

1) Conventional core material from the Oligocene interval of shallow corehole 16 (hereafter "Corehole 16"), Jeanne d'Arc Basin, Grand Banks, offshore Newfoundland (text-figure 1), drilled in the 1960s by Pan American Petroleum Corporation (latterly AMOCO) and Imperial Oil Enterprises; this core is now stored at the Canada Newfoundland-Labrador Offshore Petroleum Board in St. John's, Newfoundland, Canada.

2) Cuttings material from Mobil et al. Hibernia B-08 well, also on the Grand Banks (text-figure 1).

3) Type material of *Enneadocysta dictyostila* (Menéndez 1965) from Borehole LSX4, La Sara, Extensión 4, depth 1121-1301m; Estancia La Sara, about 14 km south of Bahía San Sebastián, Tierra del Fuego, Argentina; Eocene-Oligocene (text-figure 2).

4) Middle Eocene samples from the La Despedida section along the Río de la Turba, northern Tierra del Fuego, Argentina (text-figure 2).

5) Samples from the Upper Eocene Cabo Peña Formation in its type area (text-figure 2), northern Tierra del Fuego, Argentina: Section A, Cabo Peña; Section B, Cerro Águila; and Section C, Río Candelaria.

6) Samples from the upper Middle Eocene Lb member of the Leticia Formation, La Despedida Group at Cabo Campo del Medio, southeastern Tierra del Fuego, Argentina. (Olivero and Malumián 1999 – samples provided by E.B. Olivero) (text-figure 2).

7) Original photomicrographs of specimens from Middle to Upper Eocene Río Turbio Formation assemblages, Santa Cruz province, Argentina, provided by S. Archangelsky (text-figure 2).

The Canadian samples and the Argentine samples from Leticia and Cabo Peña formations were processed in the palynology laboratory of the Geological Survey of Canada (Atlantic), Natural Resources Canada, in Dartmouth, Nova Scotia. Treatment included hydrochloric and hydrofluoric acid, mild oxidation (10% nitric acid for one minute) and a 10% ammonia hydroxide
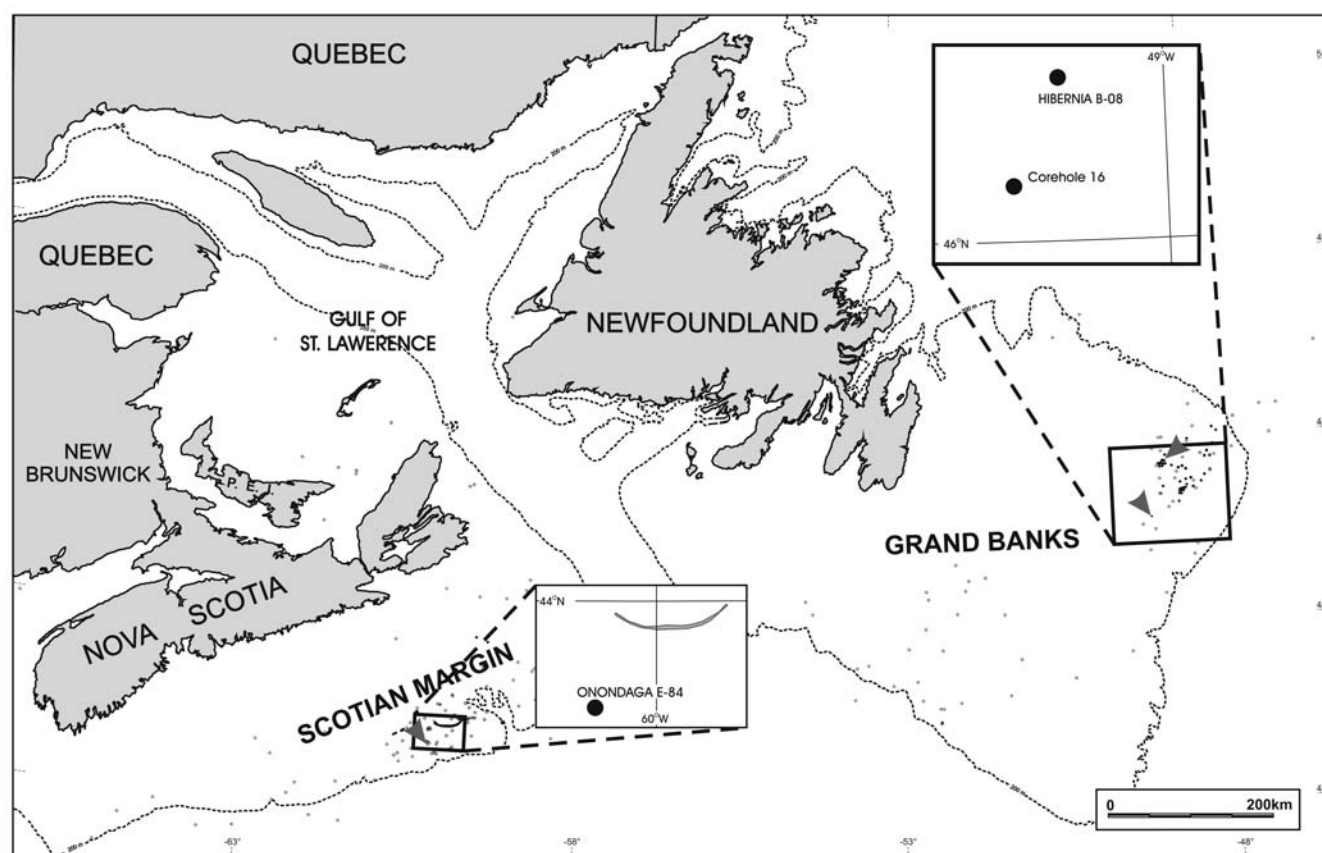
TEXT-FIGURE 1
Map of offshore eastern Canadian localities.

wash for one minute. The organic fraction was concentrated by separation in zinc bromide (specific gravity 2.0). Differential centrifuging was used to remove fine particles and the residues were sieved to concentrate the 10-180μm fraction. The residues were stained using Bismarck C and mounted and dried on coverslips in hydroxyethyl cellulose with ethylene glycol monomethyl ether as a dispersal agent. The coverslips were then glued onto the slides with elvacite. The Argentine samples from La Despedida section were processed at the palynological laboratory at the Centro de Investigaciones en Recursos Geológicos (CIRGEO), Buenos Aires, using the same methods. In this case, the processed material was mounted in glycerine.

Light microscopy of the Canadian material was undertaken using Zeiss photomicroscopes at the Geological Survey of Canada (Atlantic). Microscope co-ordinates quoted are from the Vernier Scale of Zeiss Axioplan 2 microscope, serial no. 310243. Canadian specimens (specimens with GSC numbers) are curated in the National Collection of Type Invertebrate and Plant Fossils, Geological Survey of Canada, 601 Booth Street, Ottawa, Ontario, Canada K1A OE8 (at the time of writing on long-term loan to the GSC Atlantic, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada B2Y 4A2); in captions, these specimens are designated GSC collection numbers. Argentine specimens were studied and are curated (unless otherwise stated) at the Laboratorio Palinológico de la Universidad Nacional del Sur, Bahía Blanca, Argentina; in captions theyare designated by LPUNS collection numbers. Light microscopy of

the Argentine specimens was undertaken using Nikon photomicroscopes at LPUNS; quoted microscopes co-ordinates are from Nikon Eclipse 600 microscope, serial no. 772751. England Finder references are provided for all illustrated specimens. None of the photomicrographs involve image-reversal. The line drawings, other than those of *Enneadocysta dictyostila*, were made using a camera lucida. All drawings show external views.

TERMINOLOGY

Glossaries of the terminology used for dinocysts can be found in Fensome et al. (1993), Williams et al. (2000) and Fensome and Williams (2005), and most if not all terms used in this work are explained in these publications. However, a few new or relatively new terms are critical to the discussion below, so we provide some explanation of these terms here.

The most important group of terms in the present context involves process morphology (text-figure 3). *Enneadocysta* is characterized by solid or closed processes in which the distal endings are drawn out (commonly asymmetrically) into two orthogonal or curved (sickle-shaped) branches that are serrate or denticulate on the outer margin (text-figures 3H-J; Fensome and Williams 2005). This process morphology was termed "licrate" by Sarjeant (1982), after the Greek word *likros*, meaning antler; he cited *Areosphaeridium* (now *Enneadocysta*) *multicornutum* as an example of a species with licrate processes. Previous authors have not emphasized the commonly asymmetrical nature
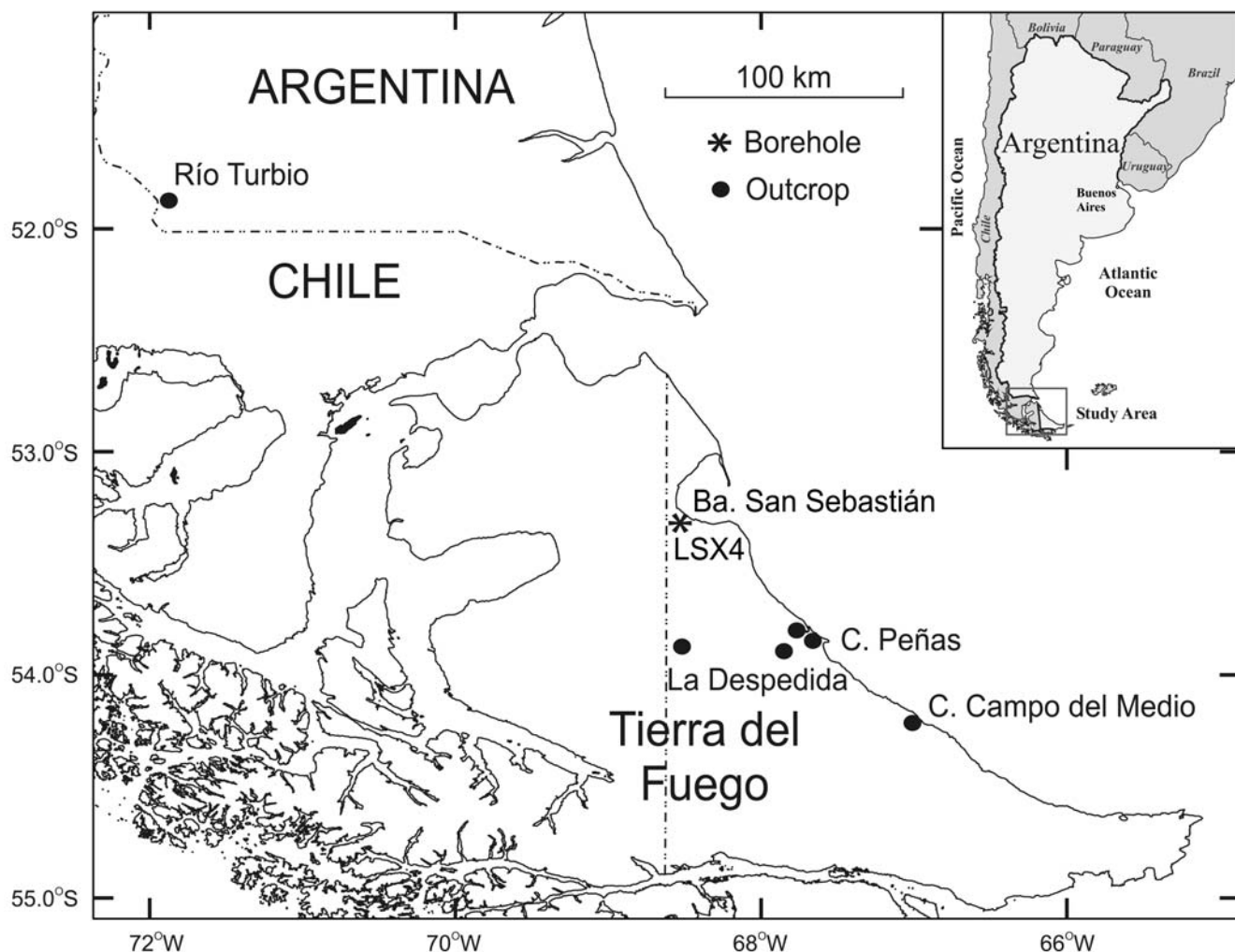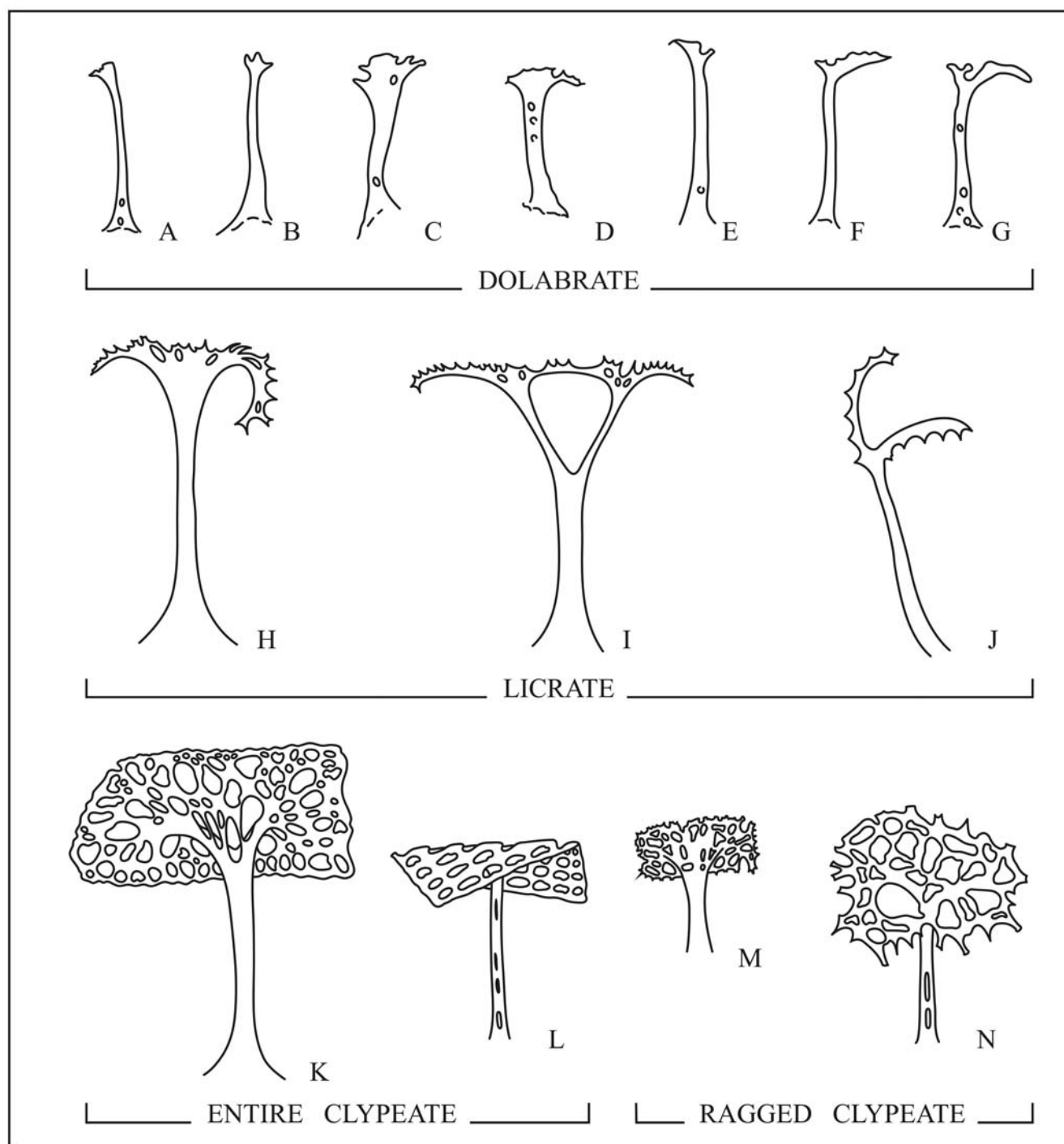
TEXT-FIGURE 2
Map showing Argentine localities.

of the endings of this type of process, but we consider it important in assessing the affinity of *Enneadocysta*.

Eaton et al. (2001) redefined the genus *Cleistosphaeridium* on the basis that specimens are characterized by processes that tend to be asymmetrical – indeed, sickle-shaped, like *Enneadocysta*, but much less pronounced and lacking the distinct serrations that in part define licrate processes. Eaton et al. introduced the term "dolabrate" to describe such processes: this term is from the Latin *dolabra* meaning "pick-axe". Fensome and Williams (2005) defined "dolabrate" as a term "… for a solid process that has an asymmetrical distal bifurcation" (text-figures 3A-G).

A third kind of process ending that is important to the present paper is the "clypeate" type (from the Greek *clypeus*, meaning shield). Like "licrate", the term was introduced by Sarjeant (1982, p. 943), who defined it with the following statement: "Tubular process mouths surrounded by an elaborately perforate, quadrate to polygonal inflation of the periphragm (as in *Areosphaeridium diktyoplokus*)." Fensome and Williams (2005) defined "clypeate" as a term for "… a process bearing a distal perforate, quadrate to polygonal platform." The distal

platform of clypeate processes can be entire, in which the margin is unbroken (text-figures 3 K-L), or ragged (text-figures 3 M-N): hence the terms "entire clypeate" and "ragged clypeate" can be usefully applied to processes.

Evitt (1961) used the term "plate centered" to describe the position of the processes in *Hystrichosphaeridium*. The alternative term "intratabular" was introduced by Evitt (1963) and is generally used to refer to a situation in which there is only one process per plate: but the term is ambiguous both in the sense of position relative to plate boundaries and in the number of processes involved – as in the phrase "intratabular clusters" of processes, for example. Therefore, Fensome and Williams (2005) proposed the term "mesotabular" for a process that is alone on its plate and centrally located. We introduce the term "obtabular" for processes that are alone on their plate but offset toward the plate margin rather than plate-centered. The term is derived from the Latin "*ob*", meaning toward. Another term introduced by Fensome and Williams (2005) and used in this paper is "contabular": this term describes a situation in which ornamental features or process clusters are clearly grouped within (para)plate areas. The widely used term "nontabular" is
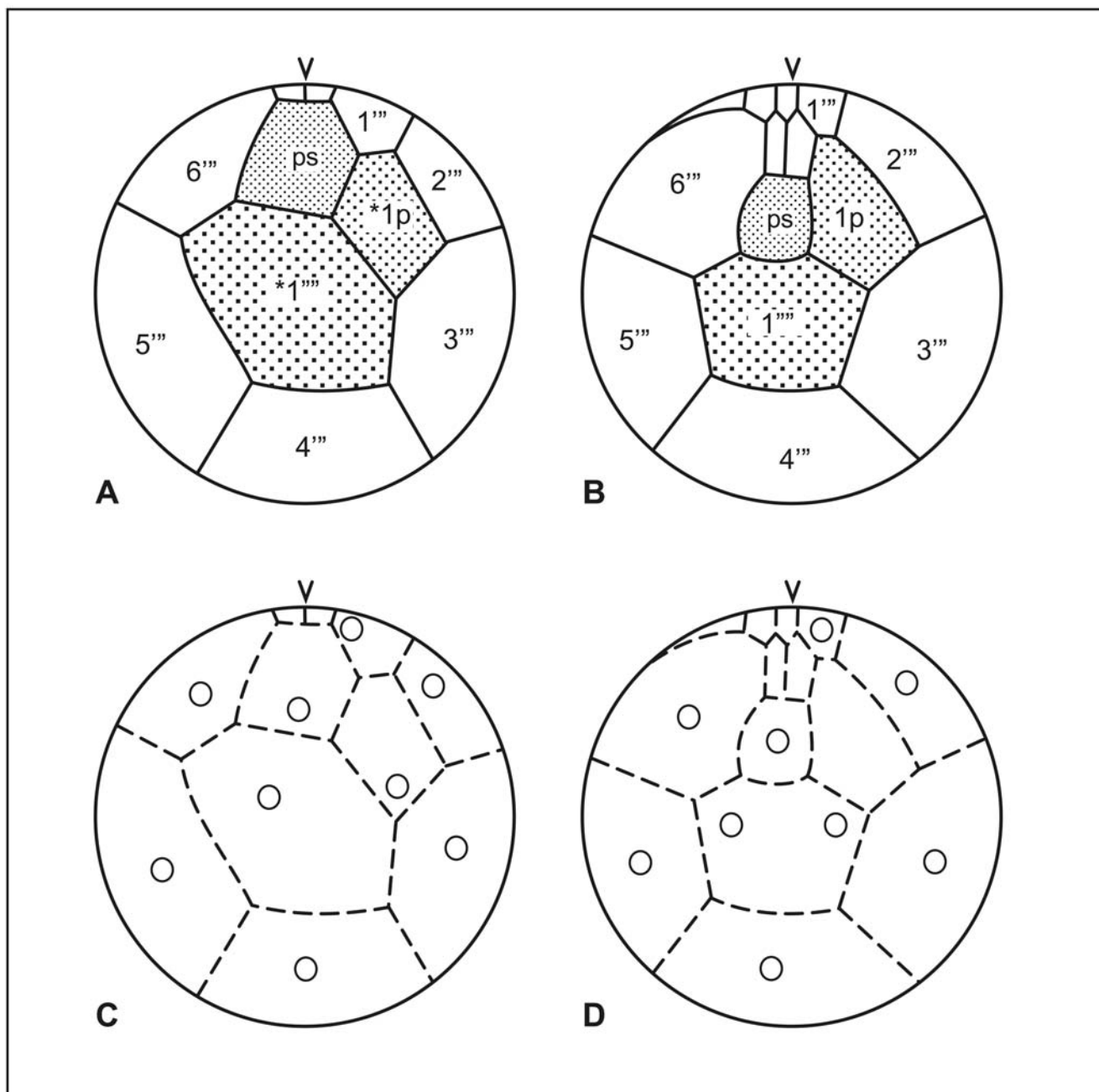
TEXT-FIGURE 3
Line drawings of processes: idealized dolabrate (A-G), licrate (H-J), entire clypeate (K-L) and ragged clypeate (M, N). A-G after Eaton et al. (2001), H-L after Eaton (1971), and M-N after Bujak (1976).

used for processes (or other features) that are not (clearly) related to tabulation.

The terms ambital and marginate have been used to indicate a distribution (e.g. of processes) around the lateral margin, or ambitus of a cyst – usually a dorso-ventrally compressed cyst. Here we prefer ambital.

In this paper we do not use the "para" terminology of Evitt et al. (1977) for reasons of convenience and simplicity rather than philosophy: we consider it understood that we are dealing with cysts that reflect selected (thecamorphic) features of the motile theca, and that we are referring to reflected plates, sutures and so on, rather than the functional features of motile cells.

TEXT-FIGURE 4
Aspects of partiform (cladopyxiinean) and sexiform (gonyaulacinean) tabulation and the interpretation of *Enneadocysta* process distribution. A-B: schematics showing ideal hypocystal tabulation of partiform and sexiform types respectively. C-D: alternative partiform and sexiform interpretations of *Enneadocysta*. Circles indicate process positions; asterisks indicate that plate designation is based on homology with the standard gonyaulacalean pattern rather than on a literal Kofoidian interpretation (see Fensome et al. 1993).

RE-INTERPRETATION OF *ENNEADOCYSTA*

Stover and Williams (1995) proposed the genus *Enneadocysta*, characterized in part by chorate cysts with apparently mesotabular, commonly licrate processes, a spheroidal to lenticular central body and an apical archeopyle. Stover and Williams placed several new species in their genus, including the Southern Hemisphere forms *Enneadocysta partridgei* and (questionably) *Enneadocysta*? *dictyostila*, plus some species

previously assigned to *Areosphaeridium*, including the type of the new genus, *Enneadocysta pectiniformis*.

Areosphaeridium, like *Enneadocysta*, is characterized by chorate cysts with an apical archeopyle, reflecting a gonyaulacalean tabulation. The two genera differ principally in the distribution of processes at the antapex: *Areosphaeridium* has a single, centrally located antapical process that is commonly larger than other processes on the same specimen;

Enneadocysta has two generally licrate processes of more or less equal size at the antapex, neither of which is centrally located or distinctively large (text-figure 4). Most or all of the processes of *Enneadocysta* and *Areosphaeridium* are clearly distributed one per plate, typically mesotabular in the latter genus but commonly obtabular in the former. Stover and Williams (1995) assumed that process distribution in these genera has a simple and direct relationship to the tabulation. The single antapical process of *Areosphaeridium* appears to reflect a sexiform gonyaulacalean tabulation, whereas the pair of off-center antapical processes in *Enneadocysta* was interpreted as reflecting a partiform gonyaulacalean tabulation.

Although Stover and Williams did not classify their taxa above generic rank, their interpretation would necessitate placing *Areosphaeridium* and *Enneadocysta* in separate suborders within the order Gonyaulacales, the Gonyaulacineae and Cladopyxiineae respectively (text-figure 4). (See Fensome et al. 1993 who, following implications in Evitt 1985, strongly emphasized the importance of tabulation at the antapex for determining affinities within the order Gonyaulacales.) Although this interpretation made sense with regard to antapical process distribution, it was remarkable that two dinocyst genera, so similar in overall morphology, should be assignable to separate suborders.

In addition, although the assignment of *Areosphaeridium* to the Gonyaulacineae fits in terms of its general morphology and stratigraphic position, the assignment of *Enneadocysta* to the Cladopyxiineae is not such a comfortable fit. Cladopyxiineans, although represented by a few modern forms such as *Cladopyxis*, were far more diverse in the Mesozoic, and clearly declined in the Cenozoic (Fensome et al. 1996b). Moreover, few cladopyxiinean cysts are chorate. Thus, the occurrence of a chorate cladopyxiinean cyst in the Cenozoic is unexpected. The discovery of a new species of *Enneadocysta*, *Enneadocysta magna* from the Grand Banks, off Newfoundland in Atlantic Canada (text-figure 1), has provided new evidence for solving this dilemma. Some specimens of *Enneadocysta magna* clearly show that the two antapical processes of *Enneadocysta* are penitabular in position (not strictly obtabular because there are two on a single plate). These two processes occur within the area of the antapical plate and thus seem to represent a centrally located antapical plate, as in the Gonyaulacineae (text-figures 5 A-D, 6 E; pl. 1, figs. 4, 8, 17-19). Hence, *Enneadocysta* can be re-interpreted as a gonyaulacinean, rather than a cladopyxiinean, cyst.

If *Enneadocysta* is a gonyaulacinean cyst, what is its family assignment? The two likely candidates are the families Gonyaulacaceae and Areoligeraceae: both are well represented by Paleogene chorate cysts, and an assignment to the Gonyaulacaceae would apparently accord with the morphological similarity between *Enneadocysta* and *Areosphaeridium*. Like typical specimens of *Areosphaeridium*, gonyaulacaceans generally have a spheroidal, symmetrically-shaped central body with a mid-ventral sulcus (reflected as a mid-ventral sulcal notch in forms with an apical archeopyle). In contrast, areoligeraceans, as mentioned above, tend to have a lenticular, asymmetrically-shaped central body and a sulcus that is offset to the left (reflected as an offset sulcal notch along the apical archeopyle margin). However, the lenticular shape of the central body, often with an absence or reduction of mid-ventral processes, and the general asymmetry of some *Enneadocysta*, for example specimens of *Enneadocysta magna* illustrated herein (pl. 1,

figs. 9-12, 15-16) and the holotype of *Enneadocysta arcuata* figured by Eaton 1971, text-fig. 4), are such striking features that we strongly favor an assignment to the Areoligeraceae.

ENNEADOCYSTA AND THE PALEOGENE AREOLIGERACEAN PLEXUS

One of the most distinctive features of *Enneadocysta* is the presence of mesotabular to obtabular licrate processes (text-figure 3 H-J). In their redefinition of *Cleistosphaeridium*, Eaton et al. (2001) emphasized the presence of dolabrate processes that, like some of the processes of *Enneadocysta*, tend to be distally asymmetrical (text-figure 3 A-G). At first impression, the association of *Enneadocysta* and *Cleistosphaeridium* may seem superficial. Both genera involve gonyaulacinean cysts that are proximochorate to chorate with an apical archeopyle: but this description fits many dinocyst genera. Moreover, the processes of *Enneadocysta* are mostly mesotabular to obtabular, whereas those of *Cleistosphaeridium* are nontabular to contabular. However, the overall cyst morphology of both genera show significant features in common, especially the presence of often asymmetrical licrate/dolabrate processes; and the shared traits suggest to us that *Cleistosphaeridium* and *Enneadocysta* are related genera within the Areoligeraceae. (We note here that Eaton et al. 2001 also speculated that *Cleistosphaeridium* may be an areoligeracean.)

The relationship of *Cleistosphaeridium* and *Enneadocysta* is further supported by the recognition of a new genus, *Licracysta*, described herein. *Licracysta* has: 1) dolabrate to licrate processes, reminiscent of both *Cleistosphaeridium* and *Enneadocysta*, but more similar generally to those of *Cleistosphaeridium*; 2) contabular process complexes, as in some forms of *Cleistosphaeridium*; and 3) dorsoventral areas that are process-free, like many *Enneadocysta*. The gradation from forms with a typical areoligeracean morphology (bald dorso-ventral areas, central body compression, antapical asymmetry and sulcal notch offset to the left) to forms more apparently gonyaulacacean-like in appearance (overall cover of ornament, more or less bowl-shaped, uncompressed central body, antapical symmetry and mid-ventral sulcal notch) can also be seen among the specimens of *Areosphaeridium diktyoplokum*, *Areosphaeridium* (now *Enneadocysta*) *arcuatum* and *Areosphaeridium* (now *Enneadocysta*) *multicornutum* illustrated by Eaton (1971; for example compare the specimens shown in his pl. 3, fig. 1 and pl. 3, fig. 9). For a more complete differentiation between *Licracysta* and other similar genera such as *Glaphyrocysta* and *Areoligera*, see the Systematics section below.

Cleistosphaeridium generally has a gonyaulacacean-like appearance, but specimens with an offset sulcal notch and antapical asymmetry do occur (probably more often than might be apparent, since specimen orientation is often difficult).

In summary, we consider that, because of morphological similarities and gradations, the genera *Cleistosphaeridium*, *Licracysta* and *Enneadocysta* form a distinct and morphologically gradational group of genera within the family Areoligeraceae; *Glaphyrocysta* and *Areoligera* appear also to be closely related, especially to *Licracysta* and *Enneadocysta*. Although not all of the genera and species within the group show typical areoligeracean morphology, the tendency to have licrate, dolabrate and clypeate processes, as well as the morphologically gradational nature of members of the group, support a close relationship. Because of the striking similarity of process morphology between some species of *Enneadocysta* and some
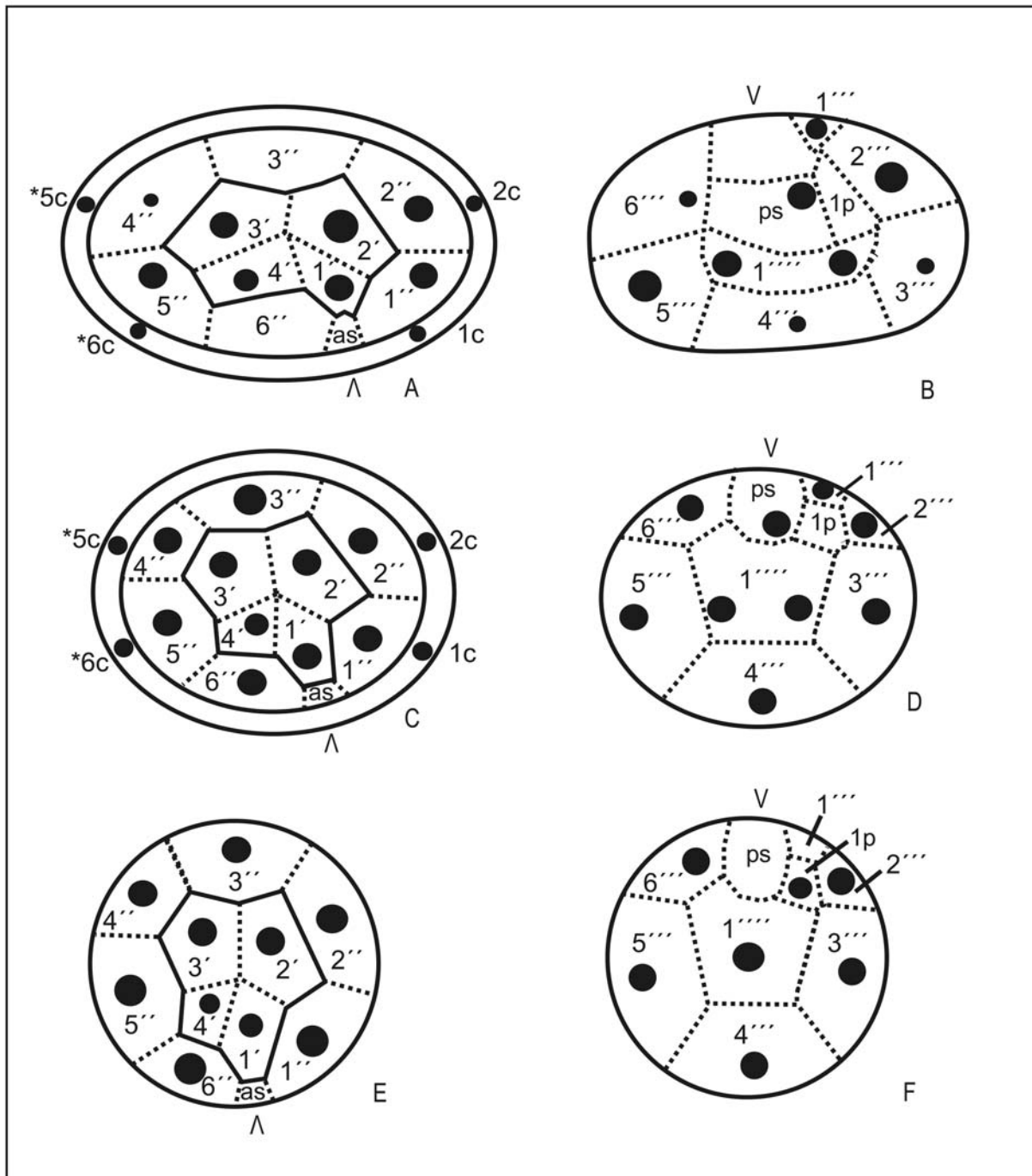
TEXT-FIGURE 5
Schematic showing the distribution of processes (filled circles) relative to interpreted tabulation in species of *Enneadocysta* and *Areosphaeridium*: A-B, *Enneadocysta magna*; C-D *Enneadocysta dictyostila* and *Enneadocysta brevistila*; E-F, *Areosphaeridium diktyoplokum*. Asterisks indicate that plate designation is based on homology with the standard gonyaulacalean pattern rather than on a literal Kofoidian interpretation (see Fensome et al. 1993).

species of *Areosphaeridium*, we speculate that the latter genus may also be an areoligeracean, despite the differences in antapical process distribution. It is interesting to note that Eaton (1971) also closely associated the two morphotypes. However, further development of this idea is beyond the scope of the present study.

Since we are sympathetic to a cladistic approach to evolution and view each of the genera as branches rather than trunks of a phylogenetic tree, we resist the temptation to speculate on an evolutionary lineage accommodating the genera. However, it may be helpful to discuss some of the group's morphological features in general evolutionary terms. For example, we con-

sider that the group evolved probably from a *Glaphyrocysta*-like ancestor in the early Paleogene, its "trademark" innovation (or synapomorphy in cladistic terminology) being the development of licrate/dolabrate/clypeate processes. Whereas the earliest-derived forms would have had typical areoligeracean features (as in *Glaphyrocysta*), there was a tendency to lose some of these features and for a more symmetrical morphology to develop, culminating in the more typically bowl-shaped forms of *Cleistosphaeridium* (and perhaps *Areosphaeridium*). As the group becomes better understood, these morphological trends may be found to be useful biostratigraphically.

ENNEADOCYSTA DICTYOSTILA AND RELATED SPECIES

Menéndez (1965) examined dinocysts from Cretaceous and Paleogene sediments in a borehole from northern Tierra del Fuego, Argentina. One of four new species Menéndez described was *Hystrichosphaeridium dictyostilum,* which he compared with *Hystrichosphaeridium tubiferum*. Pöthe de Baldis (1966) described and illustrated the same species from Paleogene sediments in another borehole from northern Tierra del Fuego but, unaware of Menéndez's work, included her material in *Hystrichosphaeridium diktyoplokum*, a species described by Klumpp (1953) from Germany. Pöthe de Baldis noted that the form was abundant throughout the interval studied.

Both Cranwell (1964) and Wilson (1967) identified the *Hystrichosphaeridium dictyostilum* morphotype as *Cordosphaeridium diktyoplokum* in Paleogene sediments from Antarctica. Cookson and Cranwell (1967, p. 205) found abundant specimens of *Hystrichosphaeridium dictyostilum* in what they considered as Eocene deposits from southernmost Chile. They assigned their specimens to *Cordosphaeridium diktyoplokum*, which they considered to be the senior taxonomic synonym of *Hystrichosphaeridium dictyostilum*. However, even while proposing this synonymy, Cookson and Cranwell noted an "interesting divergence" in the appearance of the process stems between the German and Chilean material. The synonymy was followed by other authors studying deposits from southern Argentina and Chile (Archangelsky 1969a and 1969b; Fasola 1969 and Archangelsky and Fasola 1971), as well as by Eaton (1971, p.359), who transferred Klumpp's species to his new genus, *Areosphaeridium*.

In an abstract, Evitt (1972) highlighted the "regionally persistent differences in the number and arrangement of processes" of specimens of *Cordosphaeridium diktyoplokum* from Lower Tertiary strata in England, Argentina, Chile and Antarctica. It is clear that Evitt was aware of the variability in the number of cingular and antapical processes, a variation that we use here to retain separate species, *Areosphaeridium diktyoplokum* and *Enneadocysta dictyostila*, for Northern and Southern Hemisphere forms respectively.

Hystrichosphaeridium (as *Areosphaeridum*) *dictyostilum* was retained and emended by Sarjeant (1981). According to that author, the type material described by Menéndez contains two morphotypes. One is represented by the holotype (Menéndez 1965, pl.2 fig.6; pl.3 figs.18-20; herein text-figures 7 A-B; pl 3, figs. 1-3), and was considered to be conspecific with *Areosphaeridium arcuatum* and *Cordosphaeridum* (now *Cooksonidium*) *capricornum*, *Areosphaeridium dictyostilum* thus being the senior taxonomic synonym. Sarjeant considered *Enneadocysta dictyostila* to be restricted to the Late Eocene of

both Southern and Northern hemispheres. The second morphotype, represented by the paratype (Menéndez 1965, pl 2, figs. 21-22), was considered to have clypeate processes and thus to be conspecific with *Areosphaeridium diktyoplokum*. In his emended diagnosis for *Enneadocysta* (as *Areosphaeridium*) *dictyostila*, Sarjeant (1981, p.115) stated that there was a single antapical process. He did recognize, however, that the antapical process " … is typically offset to the right of mid-ventral line …" and "… there may be one to occasionally two additional processes.

During the course of palynological investigations of Middle and Upper Eocene strata from southern Argentina (text-figure 2), one of us (GRG) collected samples from Tierra del Fuego, close to the type locality of *Enneadocysta dictyostila*. These samples yielded well preserved specimens of forms that we identify as *Enneadocysta dictyostila* (text-figures 7 C-F; 8 A-R). To confirm this identification, we have restudied the type material and have recognized a uniform morphology, rather than the two morphotypes as interpreted by Sarjeant (1981). That author (p. 115) considered the holotype of *Enneadocysta* (as *Areosphaeridium*) *dictyostila* to be dorso-ventrally orientated, to lack cingular processes, and to have a single antapical process. Based on the location of the archeopyle, we have found that the orientation of the holotype is oblique polar (text-figure 7 A-B). The presence of two penitabular processes on the antapical plate confirms the assignment of this species to *Enneadocysta* without question. We interpret four slender processes between precingular and postcingular processes as cingulars. Process terminations are variable: they may be bifurcate to multifurcate, and have licrate, entire clypeate or ragged clypeate endings (text-figure 8). Other specimens from the type material and from stratigraphically equivalent units at nearby localities conform with this general morphology (text-figures 7 C-F).

Goodman and Ford (1983) recorded specimens of "*Areosphaeridium* sp. cf. *diktyoplokum*" from uppermost Eocene – Lower Oligocene of DSDP corehole 511 from the Falkland Plateau, southwest Atlantic. Apparently unaware of Sarjeant's (1981) paper, Goodman and Ford (1983) differentiated this taxon from *Areosphaeridium diktyoplokum* on the basis of the ragged margins of the distal platforms – i.e. ragged clypeate process terminations as defined herein. Goodman and Ford (1983) stated that "... none of the Southern Hemisphere forms reported to date should be attributed to *A. diktyoplokus* s.s."

Like Cookson and Cranwell (1967), Stover and Williams (1995) noted a difference between Northern and Southern Hemisphere specimens of *Areosphaeridium diktyoplokum*. However, contrary to the treatment of Cookson and Cranwell, Stover and Williams formally distinguished northern and southern forms by erecting a new species, *Enneadocysta partridgei*, to accommodate most Southern Hemisphere specimens previously referred to *Areosphaeridium diktyoplokum*. At the same time, Stover and Williams transferred *Hystrichosphaeridum dictytostilum* to *Enneadocysta*, the new assignment being provisional because they considered that the archeopyle type and the process distribution had not been established

As co-author of a study of ODP Site 1172 on the East Tasman Plateau (Brinkhuis et al. 2003), one of us (GLW) noted numerous specimens of *Enneadocysta partridgei* from close to the Lower/Middle Eocene boundary to uppermost Eocene. The process formula for these specimens is almost invariably 4', 6", 2-4c, 6''', 2'''', with an extra process interpreted as ps. Since the
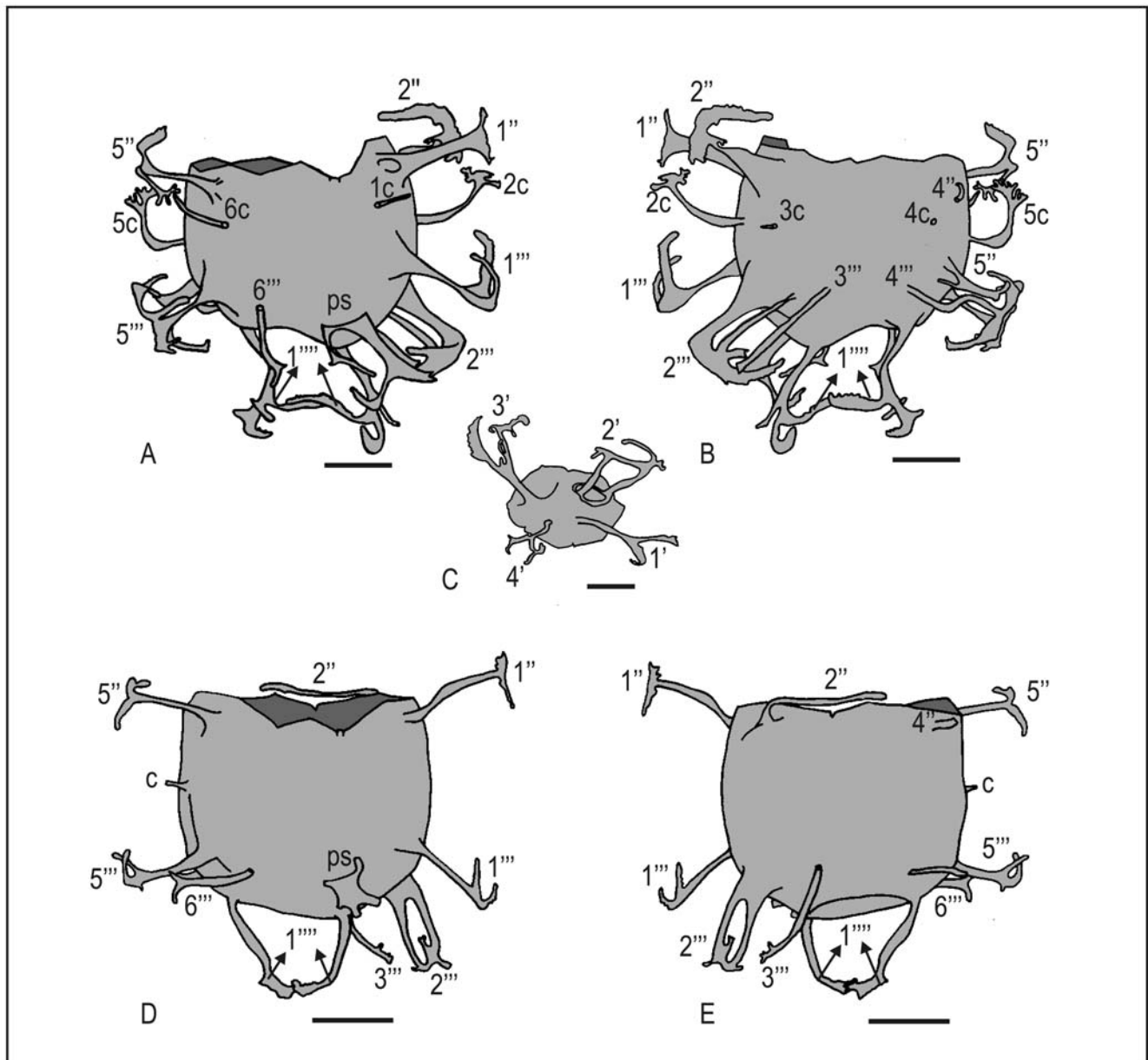
TEXT-FIGURE 6
Sketches of specimens of *Enneadocysta magna* from Corehole 16. A-B: ventral surface and dorsal surface (reversed image) respectively of specimen in ventral view from sample P1435 [depth 88.1 – 91.1m (289-299 feet); composite sample from conventional core], slide 11 (co-ordinates 20.8 x 103.1, England Finder U46/3, GSC type collection no. 128931). C: reversed image of operculum from sample P1436 [depth 116.4-119.5m (382392 feet); composite sample from conventional core], slide 10 (co-ordinates 3.0 x 91.9, England Finder B35/1, GSC type collection no. 128932). D-E: ventral surface and dorsal surface (reversed image) respectively of the specimen figured in pl. 1, figs. 1-3 in ventral view from sample P1435, slide 10 (co-ordinates 20.7 x 93.9, England Finder U37/3, GSC type collection no. 128903). Scale-bar = 20µm

distal terminations of the processes show the same variability as in *Enneadocysta dictyostila*, we conclude that these two species are taxonomic synonyms, the senior name being *Enneadocysta dictyostila*.

A taxon similar to *Enneadocysta dictyostila*, but with very short processes, was illustrated by Cocozza and Clarke (1992, fig 4b, p. 358) and named *Areosphaeridium* sp. A. Levy and Harwood

(2000, pl. 4, figs d-g, p. 209) called the same morphotype *Enneadocysta* sp. 2, and Brinkhuis et al. (2003, figs. 68-69) illustrated it as "*Enneadocysta partridgei* … Short processes (*Areosphaeridium ebdonii*-style)". Brinkhuis et al. considered such variation in process length to be environmentally controlled. In this paper we consider that it would be useful to separate forms with short processes and hence propose a new species, *Enneadocysta brevistila*.

SUMMARY OF OBSERVATIONS

Members of the family Areoligeraceae are important constituents of the Paleogene dinocyst assemblage, significant both biostratigraphically and paleoecologically. Their prominence in this time interval is underlined by the re-interpretation of the characteristic genus *Enneadocysta* as an areoligeracean rather than as a member of the Cladopyxiineae, a suborder sparsely represented in the Paleogene. Our interpretation is promoted by evidence from a new species, *Enneadocysta magna* from the Grand Banks, and from re-evaluation of an existing species, *Enneadocysta dictyostila* from southern Argentina, that we interpret as the senior synonym of the southern ocean species *Enneadocysta partridgei*. A new genus, *Licracysta*, from the Scotian Margin provides a clear morphological link between obviously areoligeracean genera such as *Enneadocysta* (as well as *Glaphyrocysta* and *Areoligera*) and the heretofore-considered-gonyaulacacean genus *Cleistosphaeridium*. Based on this gradation, we thus interpret *Cleistosphaeridium* to be an areoligeracean. The re-evaluation of the relationships between these dinocyst genera helps to clarify the pattern of dinoflagellate evolution in the Paleogene, and promotes more refined biostratigraphic and paleoecologic interpretations.

SYSTEMATIC SECTION

Division DINOFLAGELLATA (Bütschli 1885) Fensome et al. 1993
Class DINOPHYCEAE Pascher 1914
Order GONYAULACALES Taylor 1980
Suborder GONYAULACINEAE (Autonym)
Family AREOLIGERACEAE Evitt 1963

Genus **Enneadocysta** Stover and Williams 1995 **emend nov.**

Enneadocysta STOVER and WILLIAMS 1995, p. 108-109

Type: Gerlach 1961, pl. 28, fig.14, as *Baltisphaeridium pectiniforme.*

Emended diagnosis: Chorate areoligeracean cysts with a subspheroidal to lenticular central body. Processes mostly one per plate, generally mesotabular, but can be obtabular; there are two antapical processes located on or, usually, toward the lateral margin of the antapical plate, rather than a single mesotabular antapical process; occasional plates elsewhere may be represented by two, or rarely more, processes. Process endings generally well developed, commonly licrate and/or entire clypeate to ragged clypeate and usually asymmetrical.

Remarks: The emended diagnosis of *Enneadocysta* is based on a re-interpretation of its tabulation and the observation that, although most of its processes are mesotabular to obtabular, those toward the antapex are not. The two circum-antapical processes, thought by Stover and Williams (1995) to be mesotabular and indicative of a partiform tabulation, actually occur toward the margin of the single antapical plate. Stover and Williams provided the following process formula: 4', 5-6", 0-6c, 6''', 2'''', 0-1as, 1ps.

Based on the reinterpretation of the circum-antapical processes and other new observations, our revised process formula is as follows: 4', 3-6", 0-6c, 6''', 0-1 as, 0-1 ps, 0p, 2''''. This restatement illustrates how misleading such formulae can be, because 2'''' in our formulation represents two penitabular processes on a single antapical plate rather than reflecting, more conventionally, two plate-centered processes on separate plates. Regardless, in light of the re-interpretation of *Enneadocysta* as an

areoligeracean rather than a cladopyxiinean, its reflected tabulation would be standard gonyaulacalean (Fensome et al. 1996a). We consider that all species assigned to *Enneadocysta* by Stover and Williams (1995) can be similarly interpreted.

Comparison: Both *Enneadocysta* and *Areosphaeridium* can have licrate or clypeate processes. *Enneadocysta* differs from *Areosphaeridium* in having two circum-antapical or penitabular processes, rather than a single antapical process (text-figure 5). Moreover, *Areosphaeridium* tends to have a subspherical central body and a symmetrical overall shape, whereas *Enneadocysta* tends to have a lenticular central body and an asymmetrical shape.

Like *Enneadocysta* and other typical areoligeraceans, *Glaphyrocysta* tends to have an asymmetrical, lenticular central body and a sulcal notch offset to the left. However, in *Glaphyrocysta* the processes are generally more irregularly arranged, rarely is there only one per plate, and process endings are not distinctly licrate or clypeate. *Areoligera* has process complexes basally joined by well-developed arcuate to annulate ridges in all major plate series, not just at the antapex. *Ramidinium* has primarily sutural processes that are sometimes joined basally by low, sutural ridges near the cingular area, but not at the antapex.

Smaller, more spheroidal forms of *Enneadocysta*, such as *Enneadocysta multicornuta*, can be distinguished from similar forms of *Cleistosphaeridium* and *Licracysta* by the presence of apparently mesotabular processes. *Cleistosphaeridium* and *Licracysta* have nontabular to contabular processes, and *Cleistosphaeridium* consistently lacks dorso-ventral bald areas. Nevertheless, species such as *Cleistosphaeridium polypetellum* can be difficult to differentiate from specimens of *Enneadocysta multicornuta* that lack dorsoventral bald areas: an assessment has to be made as to whether a specimen bears more than one process per plate. Also, the process endings in *Cleistosphaeridium polypetellum* tend to be more irregular than in *Enneadocysta multicornuta*.

Enneadocysta magna Fensome, Guerstein and Williams, **n. sp.**
Plate 1, figures 1-20; Plate 2, figures 1-19 ; text-figures 5 A-B, 6 A-E

Derivation of name: From the Latin *magnus*, large or great, in reference to the large size of cysts of this species relative to other species of the genus.

Diagnosis: A species of *Enneadocysta* with large cysts (typically 60-70µm wide and 45-50µm long, excluding operculum) and generally slender licrate processes that are commonly highly asymmetrical distally, but may also be nearly symmetrical; there are four precingular processes, and cingular processes sometimes reduced to knob-like projections.

Description
Shape: Cyst chorate with a lenticular central body, dorso-ventrally compressed and with an offset sulcal notch. Antapical outline generally asymmetrical, usually more pronounced on the left side.

Wall relationships: Autophragm only.

Wall features: In cross-section, autophragm surface is slightly rough (scabrate); in plan view the autophragm appears irregularly granulate to pitted, though this may be structural (within the wall) rather than surficial**.** Central body with 19 to 22 pro-
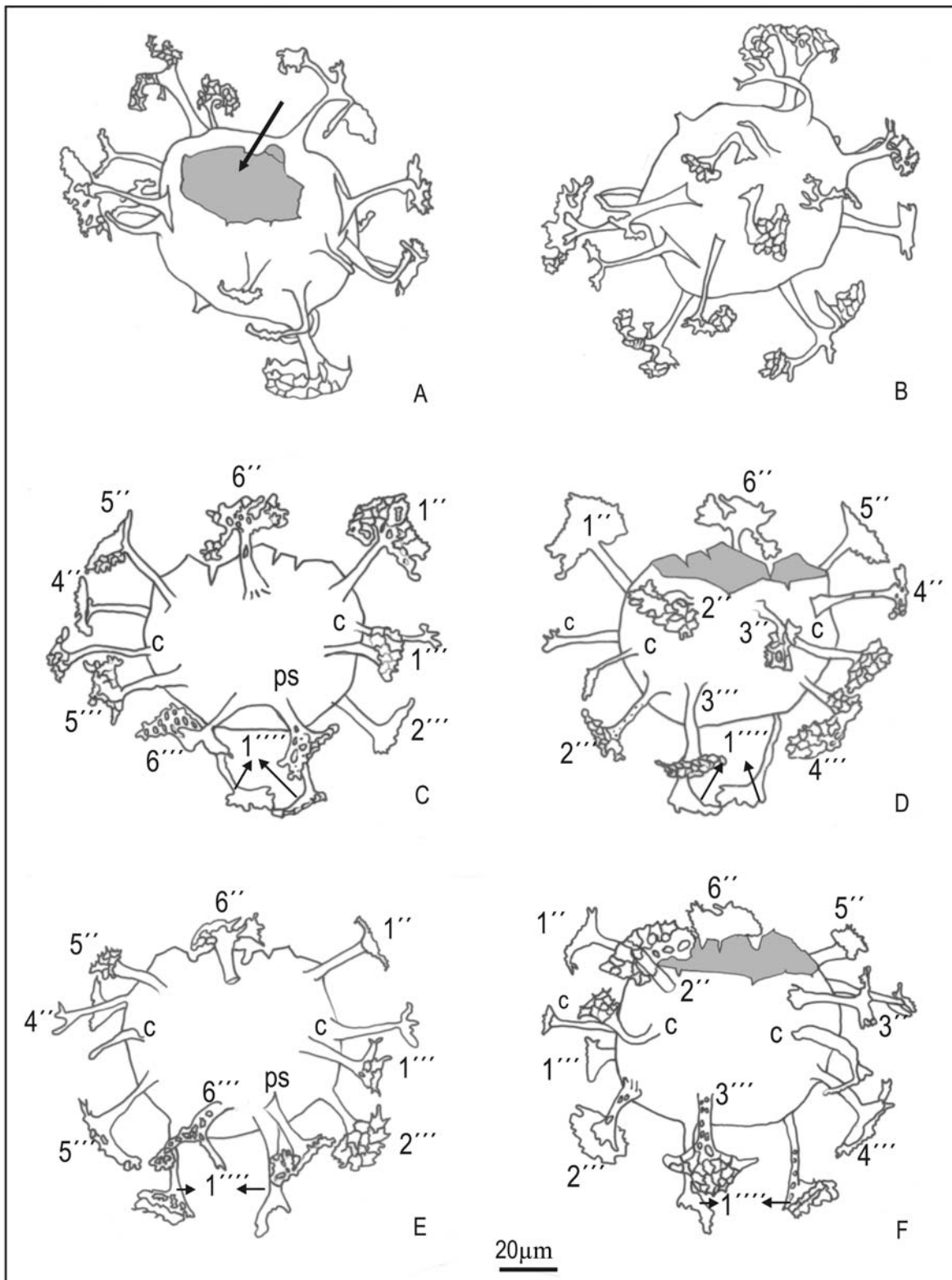
TEXT-FIGURE 7

Sketches of specimens of *Enneadocysta dictyostila*. A-B, holotype, A representing the apical surface (reversed image) and B representing the antapical surface; sample 1301(1) BA PB, co-ordinates 20-89,5 (Watson microscope 90.128), England Finder K38/2; collection of the Laboratorio Palinológico de la División Paleobotánica del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina. C-F, topotype specimens from the Lb member of the Leticia Formation; outcrop sample no. 57, La Despedida Group at Cabo Campo del Medio, southeastern Tierra del Fuego, Argentina; C-D, ventral surface and dorsal surface (reversed image) respectively of a specimen on slide P36632-01, co-ordinates 34.5 x 104.0, England Finder Q42/1 (specimen also shown in plate 3, figs.5-6); E-F, ventral surface (reversed image) and dorsal surface respectively of specimen on same slide, co-ordinates 40.7 x 102.5, England Finder M35/0 (specimen also shown in plate 3, figs. 9-11).

cesses: 8 on the epicyst, 9 or 10 on the hypocyst, and 1 to 4 on the cingulum. Processes usually mesotabular to commonly obtabular, in the latter case generally migrating ambitally toward plate boundaries (pl. 1, figs.17-19; text-figure 6). Process stems smooth, solid to perforate, mostly cylindrical, generally narrow and long (but see specific comments about postcingulars below). Processes may be branched anywhere along their length, and occasionally so deeply that two (rarely more) slender processes result; especially in cases where processes are basally split, but not exclusively so, weakly developed arcuate ridges may connect process bases. Most processes show usually strongly asymmetrical branching or expansion distally. Process tips may be licrate, simply or complexly branched or acuminate. Licrate tips may be strongly asymmetrical with a single branch, or they may be V- to horseshoe-shaped, with smooth inner margins and weakly to moderately denticulate outer margins. The two dorsal apical processes (2' and 3') are larger and more complex than the ventral two. The four precingular processes (1", 2", 4', 5') are more or less equal in size and located toward the ambitus. The cingular processes may be expressed as rounded protuberances or fully developed with branched or licrate terminations. The processes on plates 2''' and 5''' may be wider than the other four postcingular processes. The 3''' process is generally extremely slender. Process 6''' is closely adjacent to the 5''' process. The two antapical processes are laterally located, of equal size, and their licrate tips face each other. The posterior sulcal process is wider than the 1''' process and is usually branched.

Archeopyle: Apical, type (tA); operculum tetratabular, simple, free and generally longer from left to right than dorso-ventrally (text-figure 6 C).

Tabulation: Expressed on epicyst by archeopyle sutures and by location of processes, which tend to be obtabular rather than mesotabular. Plates 3" and 6" never have processes. Cingulum indicated by the presence of one to four processes: we consider that the two cingular plates consistently devoid of processes are 3c and 4c. Processes are generally present on 2c and 5c and also commonly on 1c and 6c. On 2c and 5c the processes appear to have migrated towards the ambitus. All the postcingular plates have processes, and these show a strong tendency to be obtabular. A single antapical plate is indicated by the position of two lateral processes which appear to be penitabular. The position of the sulcus is indicated anteriorly by offset sulcal notch (text-figures 5 A, 6 A, D) and evidently posteriorly by a single, commonly branched process. The posterior intercalary plate appears to be free of processes. (We consistently observed only one plate on the 1p-ps area. As this process is always located directly below the sulcal notch, and considering that it could be obtabular, we consider that it represents the ps plate rather than the 1p plate.) Process formula thus generally: 4', 4", 1-4c, 6''', 1ps, 2''''.

Dimensions: Range of 12 specimens except where noted: central body width 59 (68) 73μm; length (excluding operculum) 41 (55) 63μm; maximum diameter of operculum 38μm (one specimen); process length up to 31 (43) 58μm; maximum process length as percentage of central body width on individual specimen 48 (63) 87 percent.

Holotype: Pl. 1, figs. 5-7. Location: sample P1435, slide 10, co-ordinates 14.7 x 100.5, England Finder O43/4. Repository: GSC type collection no. 128905. Dimensions: central body width 70μm, central body length (without operculum) 57μm, processes up to 44μm long. Geographic occurrence: Corehole 16, Geological Survey of Canada (Atlantic) locality no. D52, Jeanne d'Arc Basin, Grand Banks of Newfoundland, offshore

eastern Canada, sample depth 88.1-91.1 m (289-299 feet; composite sample from conventional core).

Age: Oligocene (Rupelian) based on dinocyst ranges.

Occurrence: Oligocene, here interpreted as Rupelian in Corehole 16 – samples P1435 at 88.1 m (289 feet) and P1436 at 116.4 m (382 feet). The species has also been recorded from several wells on the Grand Banks of Newfoundland, including Hibernia B-08, from which the penitabular nature of the antapical processes was first recognized (pl. 1, figs. 4,8).

Comparison: The other species of *Enneadocysta* with less than 6 precingular processes are *Enneadocysta arcuata*, *Enneadocysta fenestrata* and *Enneadocysta multicornuta*, all of which have five. *Enneadocysta dictyostila* rarely has only five precingular processes but more commonly has six. Two other diagnostic characteristics of *Enneadocysta magna* are the large size and the slender licrate processes with highly asymmetrical distal extremities. *Licracysta*? *semicirculata* appears similar in overall morphology but has more than one process per plate.

Enneadocysta dictyostila (Menéndez 1965) Stover and Williams 1995, **emend. nov.**
Plate 3, figures 1-20; text-figures 7 A-F, 8 A-R

Hystrichosphaeridium dictyostilum MENÉNDEZ 1965, p. 11-12; pl. 2, fig. 6; pl. 3, figs. 18, 22.
Oligosphaeridium? *dictyostilum* (Menéndez) EISENACK and KJELLSTRÖM 1972, p. 845.
Areosphaeridium dictyostilum (Menéndez) emend. SARJEANT 1981, p. 115.
Enneadocysta? *dictyostila* (Menéndez) STOVER and WILLIAMS 1995, p. 109.
Enneadocysta partridgei STOVER and WILLIAMS 1995, p.113-114; pl. 5, figs. 4a-e, 5; pl. 5, figs.1a-c, 2a-c, 3a-c, 4, 5a-b; text-fig. 1, nos. D, J.

Original diagnosis: Body ellipsoidal or oval, membrane almost smooth, with tubular processes (17 or 18), disposed more or less radially and broadening basally; free end(s) infundibuliform with irregular ramification or forming a reticulum. (Translation of Menéndez 1965, p. 11.)

Emended diagnosis: A species of *Enneadocysta* with 6 precingular and 3-5 cingular processes and ragged clypeate to licrate process terminations.

Emended description
Shape: Cyst chorate with a slightly dorsoventrally flattened, subspherical central body that may be symmetrical or slightly asymmetrical in outline.
Wall relationships: Autophragm up to 1.5μm thick.
Wall features: Autophragm smooth to faintly granulate, occasionally pitted. The central body bears 22 to 23 processes, mostly mesotabular but at least three (two antapical and the posterior sulcal) apparently obtabular to penitabular, with 10 epicystal, 9 hypocystal, and 3-5 (usually 4) cingular. Processes predominantly simple, but may occasionally be branched or form a linear complex. Process stems are solid, occasionally faintly fibrous and may be perforate or fenestrate; they vary in width, cingulars being the narrowest. One of the dorsal apical processes (on the operculum) may have a wider stem or may be twinned. Occasionally, cingular processes are minute protuberances without distal expansions. Processes vary distally from bifid to most commonly ragged clypeate (text-figure 8).
Archeopyle: Apical, type (tA), tetratabular, operculum simple, free.
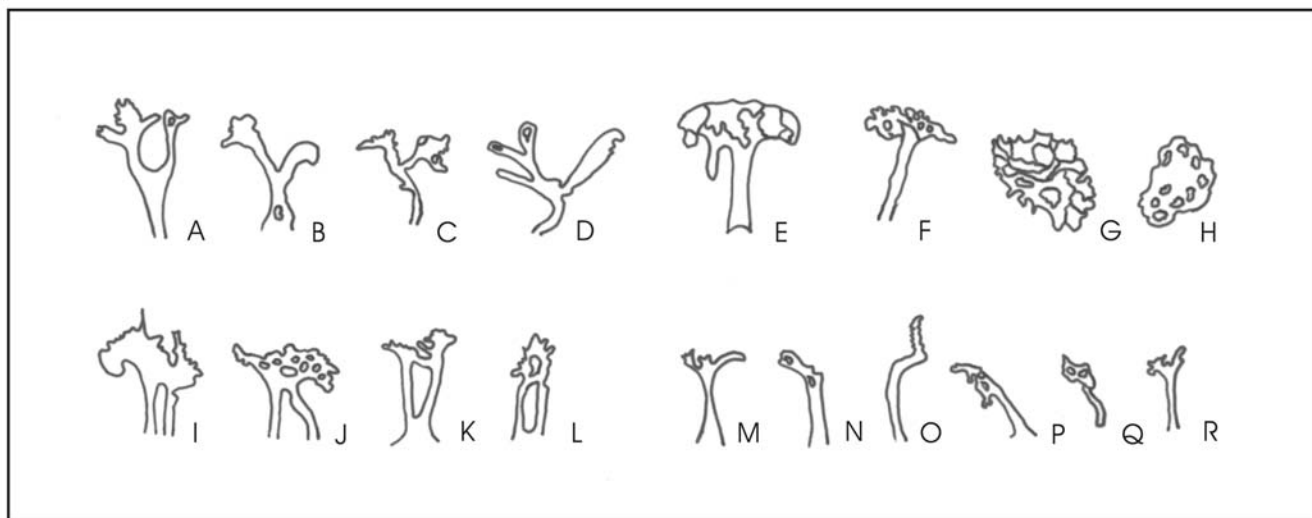
TEXT-FIGURE 8
Process variation in *Enneadocysta dictyostila*.

Tabulation: Indicated by processes and archeopyle margin. Each precingular plate has a mesotabular process, with first and sixth precingular processes and plates being of equal size. The anterior sulcal plate never has a process. Three to four, occasionally five, cingular plates have processes, which are located towards the ambitus. On the hypocyst, there are six postcingular processes, one per plate, a process that we interpret as the postcingular sulcal, and two antapical processes. The two antapical processes are interpreted as penitabular, located close to the lateral boundaries. Process formula: 4', 6'', 3-5c, 6''', ps, 2'''' (interpreted as representing a single 1'''' plate, as discussed above).

Dimensions: Range of 36 specimens except where noted: central body width 50 (54) 67µm; central body length without operculum 40 (44) 58µm (30 specimens); central body length with operculum 57 (66) 75µm (2 specimens); processes length up to 17-30µm; width at midlength of processes stems (excluding cingular processes) 2-5µm; width of distal terminations 14 (22) 32µm.

Holotype: Menéndez 1965, pl. 2, fig. 6; pl. 3, figs. 18-20; herein, pl. 3, figs 1-3; text-figures 3 A-B. Location: slide: 1301(1) BA PB, co-ordinates 20-89,5- (microscope Watson 90.128), England Finder K38/2. Repository: Laboratorio Palinológico de la División Paleobotánica del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina. Dimensions: central body width (in antapical view) 56µm, archeopyle width 30µm, process length 17-22µm, width at mid-length of processes stems (excluding cingular processes) 2.5-3µm, width of distal terminations up to 32µm. Geographic occurrence: Borehole LSX4, La Sara, Extensión 4, Estancia La Sara, about 14km south of Bahía San Sebastián, Tierra del Fuego, Argentina; depth 1121-1301m.

Age: Eocene-Oligocene.

Occurrence: The most definitive age for this species, earliest Mid Eocene to latest Eocene, is based on evidence from ODP Site 1172 (Brinkhuis et al. 2003), for which there is independent biostratigraphic, paleomagnetic and cyclostratigraphic age control. Fossil groups providing biostratigraphic control at Site 1172 include foraminifera, nannofossils, diatoms, radiolarians and dinoflagellates. These data have allowed correlation of the dinocyst events with the geomagnetic polarity timescale (GPTS) and the cyclostratigraphic record (Röhl et al. 2004). Brinkhuis et al. (2003) recorded the first occurrence of this species (as *Enneadocysta partridgei*) within magnetochron C21 (48.5 Ma) and the last occurrence within magnetochron C13 (33.5 Ma).

Comparison: Enneadocysta dictyostila differs from *Enneadocysta fenestrata* in always possessing six rather than five precingular processes and in having processes that are mostly ragged clypeate. *Enneadocysta multicornuta* may have similar process terminations but always has six cingular and only five precingular processes. *Areosphaeridium diktyoplokum*, which also has six precingular processes and no anterior sulcal process, differs in having only one antapical process and predominantly entire clypeate distal terminations.

Enneadocysta brevistila Fensome, Guerstein and Williams, **n. sp.**
Plate 4, figures 1-4, 7-8

Areosphaeridium sp. A of COCOZZA and CLARKE 1992, fig 4b.
Enneadocysta sp. 2 of LEVY and HARWOOD 2000, plate 4, figs d-g.
Enneadocysta partridgei "Short processes (*Areosphaeridium ebdonii*-style)" of BRINKHUIS et al. 2003 figures 68-69.

Derivation of name: From the Latin, *brevis*, short, and *stilus*, stake or pen, in reference to the ragged clypeate processes, similar to those of *Enneadocysta dictyostila*, but considerably shorter.

Diagnosis: A species of *Enneadocysta* with short (up to 15µm) processes, including 6 precingulars and 3-5 cingulars. Processes with ragged clypeate to licrate processes.

Description
Shape: Cyst proximochorate with a slightly dorso-ventrally flattened, subspherical central body that may be symmetrical or slightly asymmetrical in outline.
Wall relationships: Autophragm up to 1.5µm thick

Wall features: Autophragm smooth to faintly granulate, occasionally pitted. Central body bears 22 to 24 processes mostly mesotabular, but at least three (the two antapical and the posterior sulcal) are apparently obtabular to penitabular. Process distribution as follows: 10 on epicyst, 9 on hypocyst and 3-5 (usually 4) indicating cingulum. Processes short, not exceeding 15μm in length, and distally ragged clypeate. Process stems solid, of variable width (up to 12μm, with cingulars thinner), occasionally faintly fibrous, perforate or fenestrate.

Archeopyle: Apical, type (tA), tetratabular; operculum simple, free.

Tabulation: Indicated by processes and archeopyle margin. Each of the precingular plates has a mesotabular process, with the sixth and first precingular processes and plates being of equal size. The anterior sulcal plate never has a process. The three to five cingular processes are obtabular, appearing to have "migrated" toward the ambitus. On the hypocyst, there are six postcingular processes, one per plate, a process that we interpret as the posterior sulcal, and two antapical processes. The two antapical processes are penitabular being near the lateral boundaries. Process formula: 4', 6", 3-5c, 6"', ps, 2"".

Dimensions: Range of 18 specimens except where noted: central body width 50 (52) 67μm; central body length without operculum 37 (46) 55μm (12 specimens); process length up to 5 (11) 15μm; width of processes stems (excluding cingular processes) 3 to 12μm.

Holotype: Pl. 4, figs. 1-2. Location: sample PT 57, slide P36632-1: 32.7 x 105.0, England Finder P44/0. Repository: Laboratory of Palynology, Universidad Nacional del Sur, Bahía Blanca, Argentina. Dimensions: central body width 51μm; central body length 38μm; process length 7-9μm. Stratigraphic and geographic occurrence: Lb member of the Leticia Formation, La Despedida Group (Olivero and Malumián 1999) at Cabo

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PLATE 1
1-20 *Enneadocysta magna* sp. nov. All figures in phase contrast. Scale bar = 20μm.

1-3 Ventral view of specimen from Corehole 16 (GSC Atlantic location no. D 52) on the Grand Banks; Fig. 1 is focused on the ventral surface and Figs. 2 and 3 show progressively lower focal levels. GSC type collection no. 128903, sample P1435, slide 10, co-ordinates 20.7 x 93.9, England Finder U37/3; sample depth in corehole 88.1-91.1m (289-299 feet; composite sample from conventional core).

4,8 Dorsal view of specimen from Hibernia B-08 well (GSC Atlantic location no. D 191) on the Grand Banks, showing penitabular ridge development, especially around the antapical plate, an observation that has led to the present re-interpretation of *Enneadocysta*; specimen tightly compressed so separation of surfaces difficult – Fig. 4 is higher focus and Fig. 5 is lower focus. GSC type collection no. 128904, sample P19043, slide 01, co-ordinates 9.0 x 99.2, England Finder H42/0; sample depth in well 600-610m (cuttings sample).

5-7 Holotype. Ventral view of specimen from Corehole 16 (GSC Atlantic location no. D 52) on the Grand Banks; Fig. 5 is focused on process above the ventral surface and Figs. 6 and 7 show progressively lower focal levels. GSC type collection no. 128905, sample P1435, slide 10, co-ordinates 14.7 x 100.5, England Finder O43/4; sample depth in corehole 88.1-91.1m (289-299 feet; composite sample from conventional core).

9-12, 15-16 Dorsal view of specimen from Corehole 16 (GSC Atlantic location no. D 52) on the Grand Banks; Fig. 9 is focused on process above the dorsal surface and Figs. 10, 11, 12, 15 and 16 show progressively lower focal levels; note the development of a trabeculum linking antapical processes, especially clearly seen in Fig. 12. GSC type collection no. 128906, sample P1435, slide 10, co-ordinates 8.4 x 84.2, England Finder H27/1; sample depth in corehole 88.1-91.1m (289-299 feet; composite sample from conventional core).

13-14 Dorso-ventral view (orientation uncertain) of specimen from Corehole 16 (GSC Atlantic location no. D 52) on the Grand Banks; Figs. 13 and 14 represent progressively lower focal levels; note that the operculum remains attached. GSC type collection no. 128907, sample P1436, slide 10, co-ordinates 19.3 x 97.4, England Finder T40/0; sample depth in corehole 116.4-119.5m (382-392 feet; composite sample from conventional core).

17-19 Dorso-ventral view (orientation uncertain) of specimen from Corehole 16 (GSC Atlantic location no. D 52) on the Grand Banks; Figs. 17, 18 and 19 represent progressively lower focal levels; note that the density of surface ornamentation reflects the tabulation, penitabular bands being less dense than plate centers. GSC type collection no. 128908, sample P1436, slide 10, co-ordinates 21.7 x 91.7, England Finder V34/4; sample depth in corehole 116.4-119.5m (382-392 feet; composite sample from conventional core).

20 Ventral view of ventral surface of specimen from Corehole 16 (GSC Atlantic location no. D 52) on the Grand Banks. GSC type collection no. 128909, sample P1436, slide 10, coordinates 20.5 x 74.8, England Finder U17/O; sample depth in corehole 116.4-119.5m (382-392 feet; composite sample from conventional core).
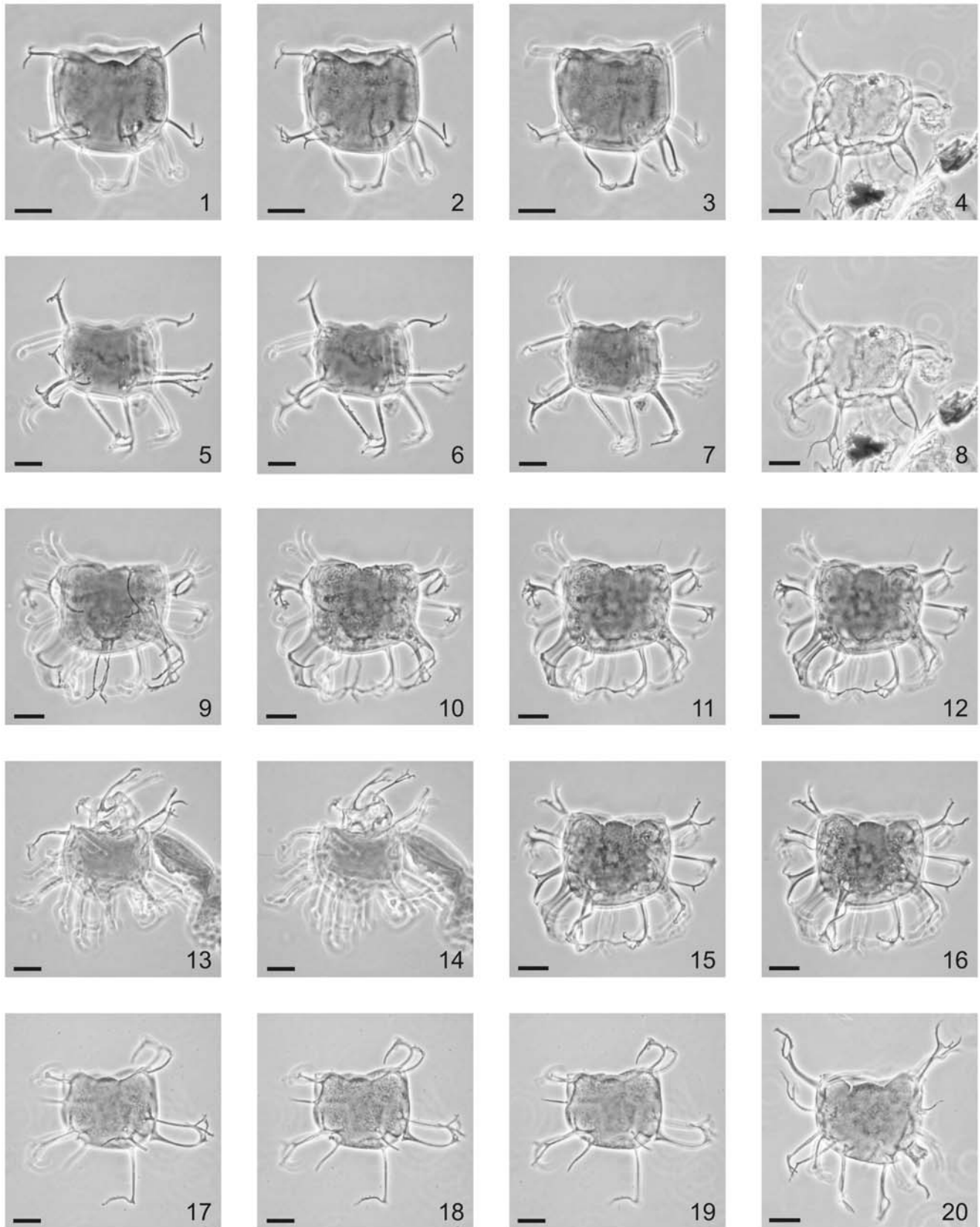
Campo del Medio, southeastern Tierra del Fuego, Argentina. Age: Mid Eocene, based on information in Olivero and Malumián (1999).

Occurrence: Enneadocysta brevistila was recorded by one of us (GLW) from ODP Site 1172 core 40, sections 2, 3 and 4. This interval, according to Brinkhuis et al. (2003), is from magneto-chron 16 r2r, equivalent to 36.4 Ma or early Priabonian.

Comparison: Enneadocysta brevistila differs from *Enneadocysta dictyostila* in having much shorter, wider processes. Like *Enneadocysta brevistila*, *Areosphaeridum ebdonii* has short processes, including six precingulars but no anterior sulcal; it differs, however, in having only five postcingular processes, one antapical process, and usually no cingular processes, al-

though Bujak (1994) stated that there may be one or two cingular processes. *Enneadocysta brevistila* always has at least three cingular processes.

Genus ***Licracysta*** Fensome, Guerstein and Williams, **n. gen.**

Type: Licracysta corymbus sp. nov.

Etymology: From the Greek "*likros*" for "antler", in reference to the dolabrate to licrate (antler-like) processes that are common in this genus.

Diagnosis: Proximochorate to usually chorate areoligeracean cysts with a subspheroidal to lenticular central body. Processes ambitally distributed, generally contabular, but typically varying on a single specimen from rarely mesotabular to loosely


PLATE 2
1-19. *Enneadocysta magna*. All figures in phase contrast. Scale bar = 20µm.

1-3   Dorso-ventral view (orientation uncertain) of specimen from Corehole 16 (GSC Atlantic location no. D 52) on the Grand Banks; Figs. 1, 2 and 3 represent progressively lower focal levels. GSC type collection no. 128910, sample P1436, slide 10, co-ordinates 17.1 x 78.9, England Finder R21/2; sample depth in corehole 116.4-119.5m (382-392 feet; composite sample from conventional core).

4,8   Ventral view of specimen from Corehole 16 (GSC Atlantic location no. D 52) on the Grand Banks; Figs. 4 and 8 represent progressively lower focal levels. GSC type collection no. 128911, sample P1436, slide 10, co-ordinates 9.3 x 77.3, England Finder J19/2; sample depth in corehole 116.4-119.5m (382-392 feet; composite sample from conventional core).

5-7   Dorsal view of specimen from Corehole 16 (GSC Atlantic location no. D 52) on the Grand Banks; Fig. 5 is focused on the dorsal surface and Figs 6 and 7 represent progressively lower focal levels; note in Fig. 6 that the sulcal notch is more or less mid-ventral in this specimen instead of offset to the left. GSC type collection no. 128912, sample P1436, slide 10, co-ordinates 8.8 x 69.2, England Finder H11/0; sample depth in corehole 116.4-119.5m (382-392 feet; composite sample from conventional core).

9-12   Ventral view of specimen from Corehole 16 (GSC Atlantic location no. D 52) on the Grand Banks; Fig. 9 is

focused on the ventral surface and Figs. 10, 11, and 12 represent progressively lower focal levels. GSC type collection no. 128913, sample P1436, slide 10, co-ordinates 7.0 x 91.8, England Finder F34/2; sample depth in corehole 116.4-119.5m (382392 feet; composite sample from conventional core).

13-16   Dorsal view of specimen from Corehole 16 (GSC Atlantic location no. D 52) on the Grand Banks; Fig. 13 is focused on the dorsal surface and Figs 14, 15 and 16 represent progressively lower focal levels; this is an unusual specimen in that many of the processes are deeply split, giving the impression of multiple processes per plate and hence approaching *Licracysta* in morphology. GSC type collection no. 128914, sample P1435, slide 10, coordinates 7.2 x 90.1, England Finder F33/3; sample depth in corehole 88.1-91.1m (289-299 feet; composite sample from conventional core).

17-19   Ventral view of specimen from Corehole 16 (GSC Atlantic location no. D 52) on the Grand Banks; Figs. 17, 18 and 19 represent progressively lower focal levels. GSC type collection no. 128915, sample P1436, slide 10, co-ordinates 8.6 x 106.5, England Finder H50/1; sample depth in corehole 116.4-119.5m (382-392 feet; composite sample from conventional core).

20 – *Cleistosphaeridium diversispinosum* In phase contrast. Scale bar = 20µm.

20   Dorsoventral view (orientation uncertain) of specimen from Onondaga E-84 well (GSC Atlantic location no. D2) on the Scotian Margin. GSC type collection no. 128916, sample P24, slide 10, co-ordi-

nates 17.7 x 95.8, England Finder R39/3; sample depth 949.5–959.2m (3115-3147 feet; cuttings sample).
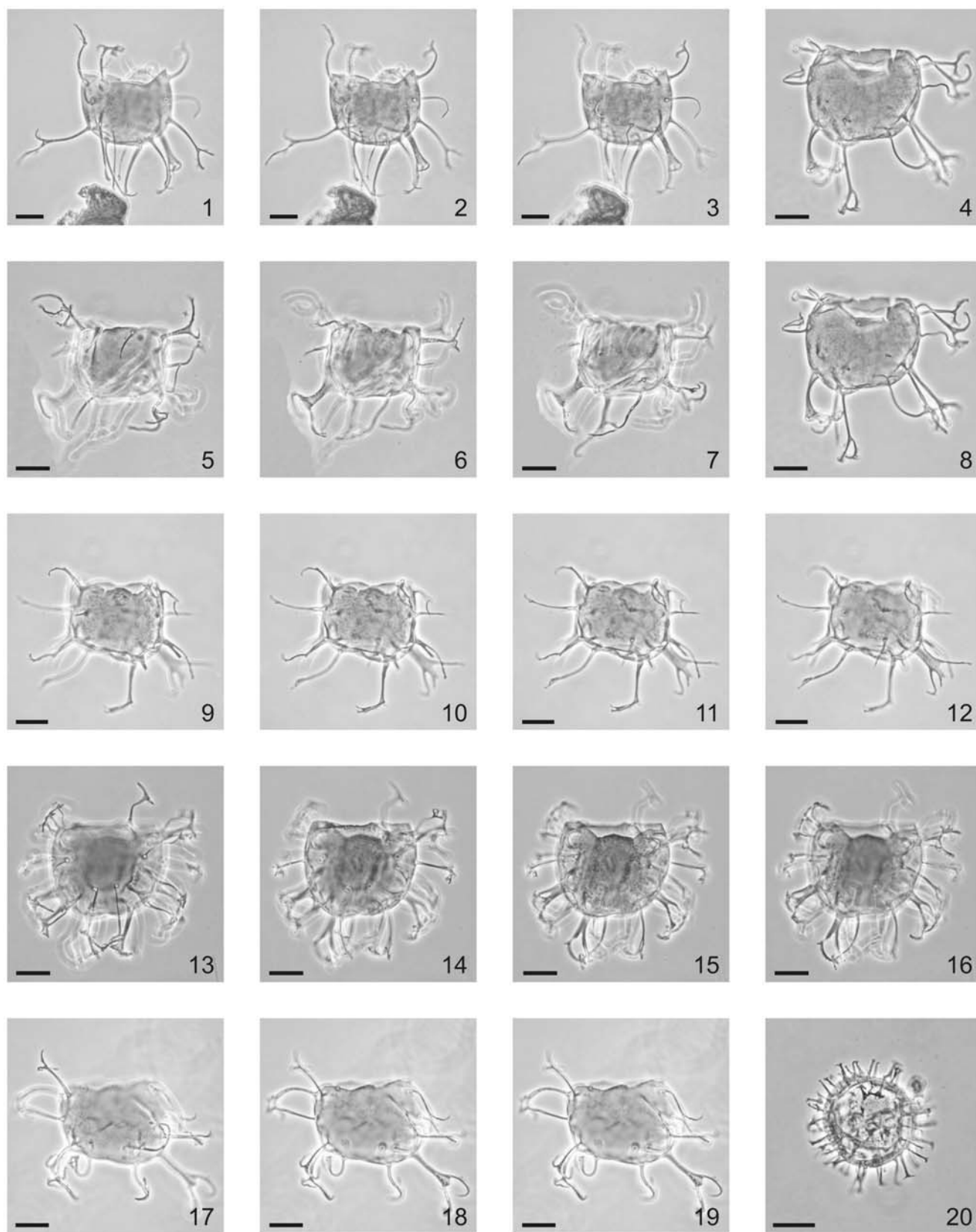
contabular to nontabular. Processes sometimes dolabrate to weakly licrate and individual processes within each complex commonly branched or connected by trabecula or membranes.

Comparison: Enneadocysta has a maximum of one process per paraplate. The process distribution in *Cleistosphaeridium* is overall rather than marginate and adjacent processes are only rarely joined into contabular complexes above their bases (pl. 2, fig. 20; pl. 5, figs. 9-11, 13-15, 17-19). *Glaphyrocysta* does not have dolabrate to licrate processes. In *Licracysta* there is a tendency for processes in complexes to develop connecting arcuate basal ridges, paralleling a similar development in

Cleistosphaeridium. The presence of basal ridges may make it difficult to differentiate *Licracysta* from *Areoligera* in some instances, but the development of dolabrate to licrate processes indicates an affinity to *Licracysta*.

Licracysta corymbus Fensome, Guerstein and Williams, **n. sp.**
Plate 4, figures 5-6, 9-20; plate 5, figures 1-8, 12, 16, 20

Derivation of name: From the Latin *corymbus* (Greek "korymbos") for "bunch of flowers", in reference to the clustered, contabular nature of many of the processes in this species. The epithet is a noun in apposition and its ending should not be changed to agree with the gender of the genus.

PLATE 3

1-20. *Enneadocysta dictyostila*. Figs 1-3 in phase contrast; Figs 4-20 in bright field. Scale bar = 20μm.

1-3 Holotype. Antapical view of specimen from Borehole LSX4, La Sara, Extensión 4, Estancia La Sara, Tierra del Fuego, Argentina; Figs. 1, 2 and 3 represent progressively lower focal levels; Fig 3 is focused on the apical surface and shows the archeopyle margin. Collection of Laboratorio Palinológico de la División Paleobotánica del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; sample 1301, slide 1 BA PB, co-ordinates 20-89,5- (microscope Watson 90.128), England Finder K38/2; sample depth 1121-1301m (cuttings sample).

4 External view of an operculum from the Lb member of the Leticia Formation, La Despedida Group at Cabo Campo del Medio, southeastern Tierra del Fuego, Argentina; LPUNS collection, sample P36632, slide 01, co-ordinates 37.8 x 101.6, England Finder L38/0; outcrop sample no. 57, 220m above the base of the Lb member.

5-6 Ventral view of a specimen (also shown in text-fig. 7C-D) from the Lb member of the Leticia Formation, La Despedida Group at Cabo Campo del Medio, southeastern Tierra del Fuego, Argentina; Fig. 5 is of the highest focal level on the ventral surface, showing the 6''' and the ps processes joined at their bases; Fig. 6 is focused on the ventral surface and shows the sulcal notch and the two processes on the antapical plate. LPUNS collection, sample P36632, slide 01, co-ordinates, 34.5 x 105.5, England Finder Q42/1; outcrop sample no. 57, 220m above the base of the Lb member.

7-8 Ventral view of a specimen from the Lb member of the Leticia Formation, La Despedida Group at Cabo Campo del Medio, southeastern Tierra del Fuego, Argentina; Fig. 7 is at an intermediate focal level on the ventral surface and Fig 8 represents a lower focal level; note that the operculum remains attached. LPUNS collection, sample P36632, slide 01, co-ordinates 31.8 x 99.7, England Finder J44/4; outcrop sample no. 57, 220m above the base of the Lb member.

9-11 Dorsal view of specimen (also shown in text-fig. 7C-D) from the Lb member of the Leticia Formation, La Despedida Group at Cabo Campo del Medio, southeastern Tierra del Fuego, Argentina; Fig. 9 is focused on the dorsal surface and Figs. 10 and 11 represent progressively lower focal levels. LPUNS collection, sample P36632, slide 01, co-ordinates 40.7 x 102.5, England Finder M35/0; outcrop sample no. 57, 220m above the base of the Lb member.

12 Antapical view of specimen from the lower member of the La Despedida Formation at Río de la Turba section, northeastern Tierra del Fuego. LPUNS collection, sample BB 36/99 slide 1, co-ordinates 24.0 x 98.9, England Finder H25/4; outcrop sample no. RT6, 48m above the base of the section.

13-16 Apical oblique view of specimen from the Lb member of the Leticia Formation, La Despedida Group at Cabo Campo del Medio, southeastern Tierra del Fuego, Argentina; Fig. 13 is focused on the archeopyle margin and Figs. 14-16 represent progressively lower focal levels. LPUNS collection, sample P36632, slide 01, co-ordinates 36.4 x 108.0, England Finder S40/1; outcrop sample no. 57, 220m above the base of the Lb member.

17-20 Dorsal view of specimen from the Río Turbio Formation, southwestern Santa Cruz Province, Argentina; Fig. 17 is focused on a dorsal process termination and Figs. 18-20 represent progressively lower focal levels. LPUNS collection sample 230 (+25), slide A, coordinates 33.3 x 104.4, England Finder O43/0; sample no. 230, borehole T-134 (Yacimientos Carboníferos Fiscales), core sample provided by S. Archangelsky from the lower part of the formation (chart I, Archanglesky 1969b).
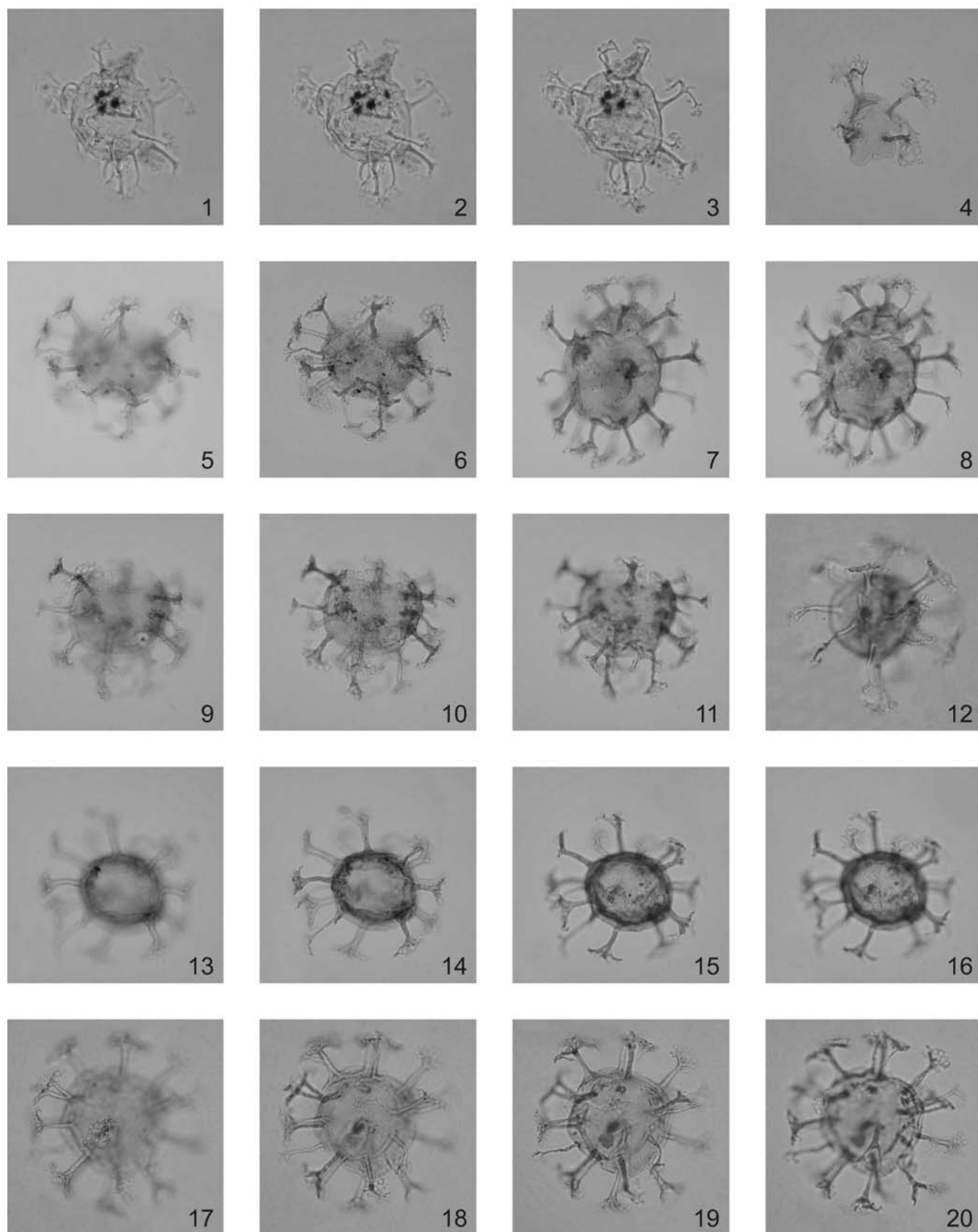
Diagnosis: A species of *Licracysta* with numerous and variable processes, mostly marginately distributed and in contabular complexes, although relatively simple mesotabular processes may occasionally be present. Processes in each contabular complex may be isolated, connected in part by proximal ridges, or connected variably along their length by trabecula or membranes. Each specimen always has at least two contabular complexes with interconnections above the base.

Description

Shape: Cyst proximochorate to chorate with a lenticular central body, dorsoventrally compressed and with a slightly offset sulcal notch. Antapex commonly asymmetrical, more pronounced on the left side.

Wall relationships: Autophragm only.

Wall features: Autophragm scabrate to granular, the granules especially in dorsoventral areas sometimes developed into short irregular rugulae and even an irregular microreticulum. Central body with numerous and variable processes, mostly marginately distributed. Relatively simple mesotabular processes may occasionally be present, but processes are most commonly distributed in contabular complexes. Processes in each complex may be isolated, connected in part by proximal ridges, or connected variably along their length by trabecula or

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PLATE 4

1-4, 7-8 *Enneadocysta brevistila.* All figures in bright field. Scale bar = 20μm.

1-2   Holotype. Right lateral oblique view of a specimen from the Lb member of the Leticia Formation, La Despedida Group at Cabo Campo del Medio, southeastern Tierra del Fuego, Argentina; Fig. 1 is focused on the upper surface and shows the apical margin and precingular processes; Fig. 2 is focused on the lower surface. LPUNS collection, sample P36632, slide 01, co-ordinates 32.7 x 105.0, England Finder P44/0; outcrop sample no. 57, 220m above the base of the Lb member.

3   Apical oblique view of a specimen from the Lb member of the Leticia Formation, La Despedida Group at Cabo Campo del Medio, southeastern Tierra del Fuego, Argentina. LPUNS collection, sample P36632, slide 01, co-ordinates 36.2 x 107.1, England Finder R40/0; outcrop sample no. 57, 220m above the base of the Lb member.

4   Apical – antapical view (orientation uncertain) of a specimen from the Lb member of the Leticia Formation, La Despedida Group at Cabo Campo del Medio, southeastern Tierra del Fuego, Argentina. LPUNS collection, sample P36632, slide 01, co-ordinates 20.0 x 100.5, England Finder K57/3; outcrop sample no. 57, 220m above the base of the Lb member.

7-8   Dorso-ventral view (orientation uncertain) of a specimen from the Lb member of the Leticia Formation, La Despedida Group at Cabo Campo del Medio, southeastern Tierra del Fuego, Argentina; Figs. 7 and 8 represent progressively lower focal levels; note that the operculum remains attached. LPUNS collection, sample P36632, slide 01, co-ordinates 38.5 x 98.4, England Finder H38/3; outcrop sample no. 57, 220m above the base of the Lb member.

5-6, 9-20. *Licracysta corymbus.* All figures in phase contrast. Scale bar = 20μm.

5-6   Ventral view of specimen from Onondaga E-84 well (GSC Atlantic location no. D2) on the Scotian Margin. GSC type collection no. 128917, sample P34, slide 10, co-ordinates 10.2 x 92.4, England Finder J35/3; sample depth 1202.7–1212.2m (3946-3977 feet; cuttings sample).

9-12   Holotype. Dorsal view of specimen from Onondaga E-84 well (GSC Atlantic location no. D2) on the Scotian Margin. GSC type collection no. 128918, sample P25, slide 10, coordinates 16.0 x 94.5, England Finder P37/4; sample depth 978.4–987.9m (3210-3241 feet; cuttings sample).

13-16   Ventral view of specimen from Onondaga E-84 well (GSC Atlantic location no. D2) on the Scotian Margin. GSC type collection no. 128919, sample P25, slide 10, co-ordinates 14.0 x 97.9, England Finder N41/3; sample depth 978.4–987.9m (3210-3241 feet; cuttings sample).

17-19   Dorso-ventral view (orientation uncertain) of specimen from Onondaga E-84 well (GSC Atlantic location no. D2) on the Scotian Margin; Figs. 17, 18 and 19 represent progressively lower focal levels. GSC type collection no. 128920, sample P18, slide 10, co-ordinates 22.2 x 95.0, England Finder W38/1; sample depth 778.8–787.9m (2555 – 2585 feet; cuttings sample).

20   Dorso-ventral view (orientation uncertain) of specimen from Onondaga E-84 well (GSC Atlantic location no. D2) on the Scotian Margin; note in-place operculum. GSC type collection no. 128921, sample P19, slide 10, co-ordinates 17.3 x 86.8, England Finder R29/2; sample depth 797.7–804.7m (2617-2640 feet; cuttings sample).
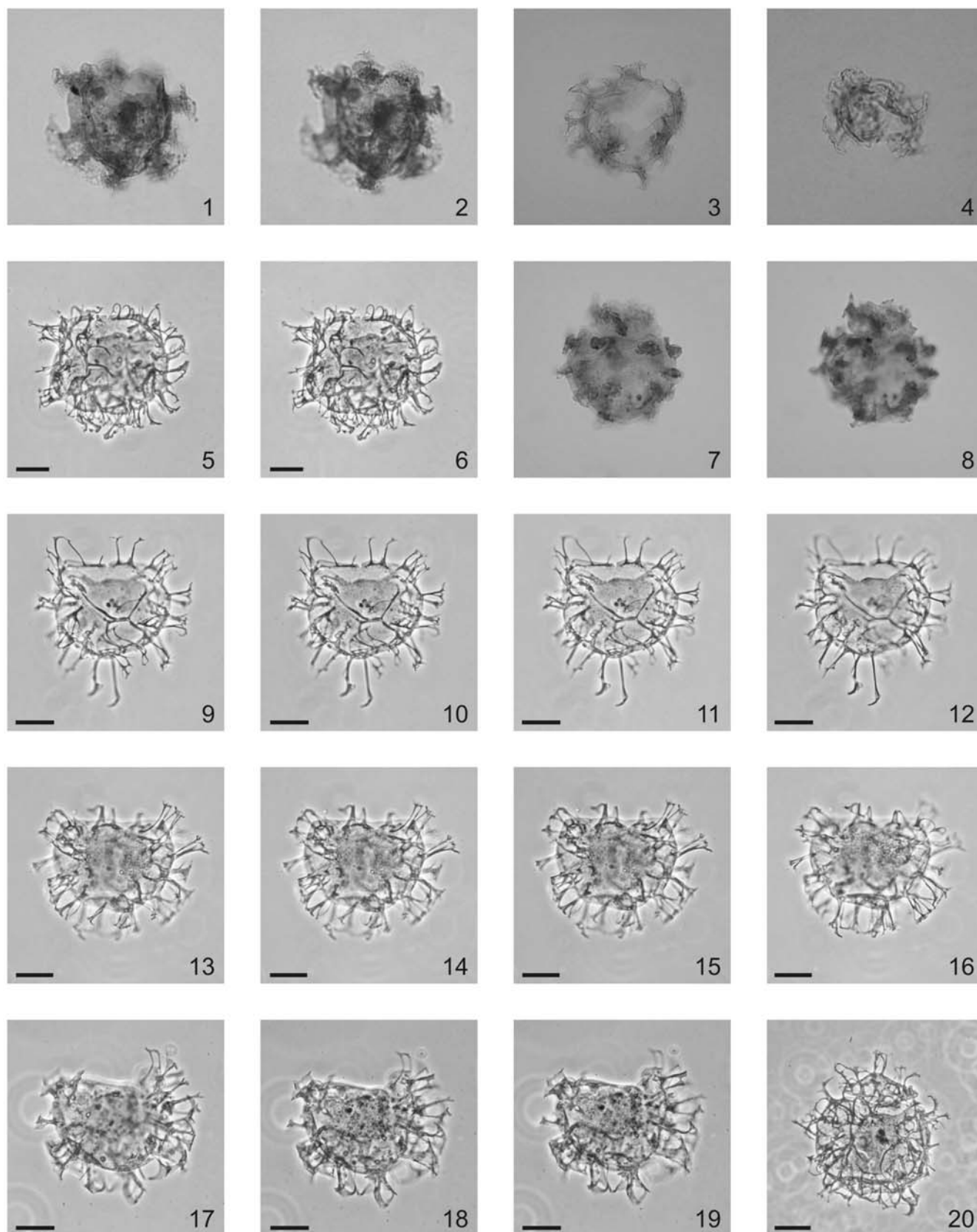
membranes. Each specimen always has at least two contabular complexes with interconnections above the base. The distal terminations of the processes may be acuminate, irregularly branched or, most typically, dolabrate to weakly licrate.

Archeopyle: Apical, type (tA); operculum tetratabular, simple and free.

Tabulation: Expressed anteriorly by archeopyle sutures. Otherwise, isolated processes (especially marking plates 3" and 6") and contabular groups of processes (postcingulars and lateral precingulars) give a general sense of the tabulation. The cingulum can sometimes be distingushed by an equatorial thinning out of processes. The antapical plate is sometimes suggested by a distinctive duo of "inturned" processes and rarely its dorsal anterior boundary appears to be marked by a low ridge that seems to be penitabular. The sulcus is indicated by the offset sulcal notch.

Dimensions: Range of 10 specimens: central body width 59 (64) 73µm; length (excluding operculum) 50 (54) 64µm; process length up to 17 (22) 26µm; maximum process length as a percentage of central body width 23 (34) 42 percent.

Holotype: Plate 4, figures 9-12.

Location: sample P25 [sample depth 978.4-987.9m (3210-3241 feet; cuttings sample)]; slide 10, co-ordinates 16.0 x 94.5, England Finder P37/4.

Repository: GSC type collection no. 128918.

Dimensions: central body width 62µm, central body length 51µm, processes up to 26µm long. Geographic occurrence: Onondaga E-84 well (Geological Survey of Canada, Atlantic locality no. D2), Scotian Margin, offshore eastern Canada.

PLATE 5
1-8, 12, 16, 20. *Licracysta corymbus*. All figures in phase contrast. Scale bar = 20µm.

1-2   Dorsal view of specimen from Onondaga E-84 well (GSC Atlantic location no. D2) on the Scotian Margin; note development of arcuate penitabular basal ridges. GSC type collection no. 128922, sample P27, slide 10, co-ordinates 23.7 x 95.8, England Finder X39/3; sample depth 1040.9–1050.3m (3415-3446 feet; cuttings sample).

3-4   Dorso-ventral view (orientation uncertain) of specimen from Onondaga E-84 well (GSC Atlantic location no. D2) on the Scotian Margin; note incipient development of arcuate penitabular basal ridges. GSC type collection no. 128923, sample P27, slide 10, co-ordinates 8.7 x 98.6, England Finder H41/2; sample depth 1040.9–1050.3m (3415-3446 feet; cuttings sample).

5-7   Dorsal? view of specimen from Onondaga E-84 well (GSC Atlantic location no. D2) on the Scotian Margin. GSC type collection no. 128924, sample P22, slide 10, co-ordinates 17.3 x 96.3, England Finder R39/0; sample depth 892.5–901.9m (2928-2959 feet; cuttings sample).

8, 12, 16, 20   Dorsal view of specimen from Onondaga E-84 well (GSC Atlantic location no. D2) on the Scotian Margin; note that processes on this specimen are more robust (broader) than is typical for this species. GSC type collection no. 128925, sample P34, slide 10, co-ordinates 11.4 x 99.1, England Finder L42/2; sample depth 1202.7–1212.2m (39463977 feet; cuttings sample).

9-11, 13-15, 17-19. *Cleistosphaeridium diversispinosum*. All figures in phase contrast. Scale bar = 20µm.

9-10   Ventral? view of specimen from Onondaga E-84 well (GSC Atlantic location no. D2) on the Scotian Margin. GSC type collection no. 128926, sample P22, slide 10, co-ordinates 19.7 x 89.1, England Finder T32/3; sample depth 892.5–901.9m (2928-2959 feet; cuttings sample).

11, 15   Ventral? view of specimen from Onondaga E-84 well (GSC Atlantic location no. D2) on the Scotian Margin. GSC type collection no. 128927 sample P27, slide 10, co-ordinates 17.6 x 98.2, England Finder R41/0; sample depth 1040.9–1050.3m (3415-3446 feet; cuttings sample).

13-14   Dorsal view of specimen from Onondaga E-84 well (GSC Atlantic location no. D2) on the Scotian Margin. GSC type collection no. 128928 sample P29, slide 10, co-ordinates 14.4 x 102.0, England Finder O45/0; sample depth 1098.2–1107.3m (3603-3633 feet; cuttings sample).

17-18   Dorsoventral view (orientation uncertain) of specimen from Onondaga E-84 well (GSC Atlantic location no. D2) on the Scotian Margin. GSC type collection no. 128929, sample P33, slide 10, co-ordinates 4.0 x 93.1, England Finder C36/0; sample depth 1193.3–1202.7m (3915-3946 feet; cuttings sample).

19   Dorsoventral view (orientation uncertain) of specimen from Onondaga E-84 well (GSC Atlantic location no. D2) on the Scotian Margin. GSC type collection no. 128930, sample P25, slide 10, co-ordinates 3.6 x 107.3, England Finder C50/2; sample depth 978.4–987.9m (3210-3241 feet; cuttings sample).
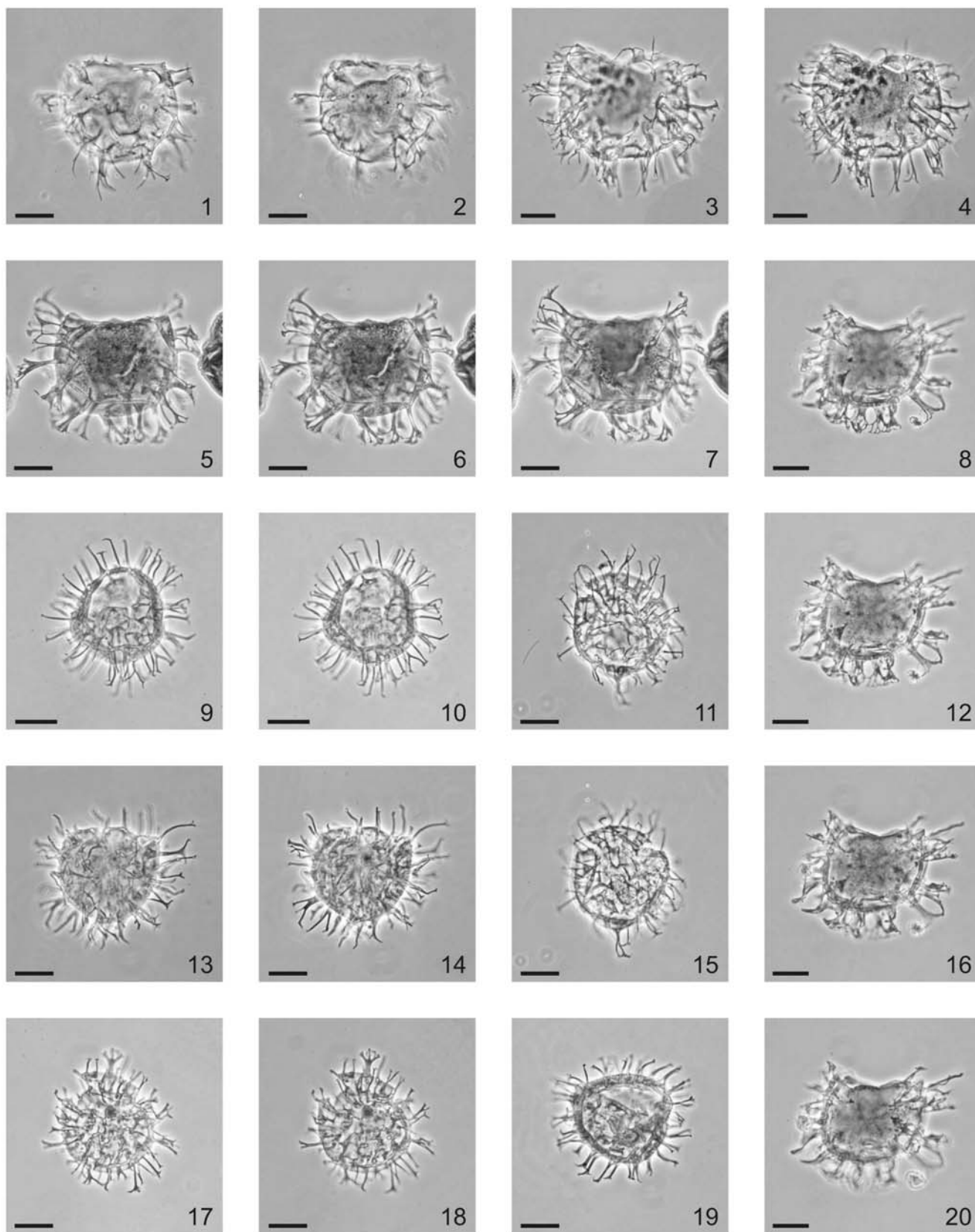
Age: The sample is dated as Early Oligocene (Fensome 2001). Although the holotype is from a cuttings sample and possibly caved, the range top for this species is within the Early Oligocene (RAF, unpublished observations).

Occurrence: The range top of this species is Rupelian (early Oligocene) based on dinocyst assemblages. The base of its range has not been established.

Comparison: Licracysta corymbus differs from species of *Cleistosphaeridium* in having dorsoventral area that are completely devoid or processes or almost so. Forms in the *Cleistosphaeridium diversispinosum/ancyreum* complex have processes that are more uniform in morphology and generally simpler distally.

Other species

Licracysta? semicirculata (Morgenroth 1966) **comb nov.**

Cyclonephelium semicirculatum MORGENROTH 1966, p. 9-10, pl. 2, figs. 3-4.
Areoligera semicirculata (MORGENROTH 1966) STOVER and EVITT 1978, p. 18.

This species is transferred questionably to *Licracysta* because the holotype (Morgenroth 1966, pl. 2, fig. 3; from the north European mid Oligocene) has dolabrate to licrate processes and more than one process per plate. In size and overall morphology (based on Morgenroth's illustration) it resembles *Enneadocysta magna* more closely than *Licracysta corymbus*, differing from the former in its contabular processes. The other specimen illustrated by Morgenroth (his pl. 2, fig. 4) has wider arcuate process complexes akin to those of species of *Areoligera*, and thus may belong to a different species.

Genus **Cleistosphaeridium** Davey et al. 1966 **emend.** Eaton et al. 2001

Cleistosphaeridium DAVEY et al. 1966, p. 166. — EATON et al. 2001, p. 176.

Type: Cleistosphaeridium diversispinosum Davey et al. 1966.

Cleistosphaeridium diversispinosum Davey et al. 1966 emend. Eaton et al. 2001
Plate 2, figure 20; plate 5, figures 9-11, 13-15, 17-19

Remarks: As we visualize *Cleistosphaeridium* as the end member of a morphological series within the family Areoligeraceae, we include several illustrations of specimens of *Cleistosphaeridium diversispinosum* here for comparison. *Cleistosphaeridium* differs from *Licracysta* in having more uniform distribution of processes, thus lacking a bald ventral area, and sometimes a less clear contabular clumping of processes. However, the characteristic asymmetrical process endings of the *Enneadocysta-Licracysta-Cleistosphaeridium* complex are clearly seen in several of the illustrated specimens (for example plate 5, figs. 13-14): in *Cleistosphaeridium*, such processes are typically dolabrate rather than licrate. *Cleistosphaeridium diversispinosum* also tends to be smaller than *Licracysta corymbus*. For the six specimens of *Cleistosphaeridium diversispinosum* illustrated herein, measurements for central body width are 47 (49) 53µm, central body length excluding operculum 41 (46) 53, and maximum length of processes 15 (16) 21µm.

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APPENDIX 1

List of generic and specific names used in text with complete authorships. Further information on the taxonomy and nomenclature of these taxa can be found in Fensome and Williams (2004).

Areoligera Lejeune-Carpentier 1938a
Areoligera semicirculata (Morgenroth1966) Stover and Evitt 1978
Areosphaeridium Eaton 1971
Areosphaeridium arcuatum Eaton 1971
Areosphaeridium dictyostilum (Menéndez 1965) Sarjeant 1981
Areosphaeridium diktyoplokum (Klumpp 1953) Eaton 1971
Areosphaeridium ebdonii Bujak 1994
Areosphaeridium multicornutum Eaton 1971
Baltisphaeridium pectiniforme Gerlach 1961
Cladopyxis Stein 1883
Cleistosphaeridium Davey et al. 1966
Cleistosphaeridium polypetellum (Islam 1983) Stover and Williams 1995
Cooksonidium capricornum (Cookson and Eisenack 1965) Stover and Williams 1995
Cordosphaeridium capricornum Cookson and Eisenack 1965
Cordosphaeridium diktyoplokum (Klumpp 1953) Eisenack 1963
Cyclonephelium semicirculatum Morgenroth 1966
Enneadocysta Stover and Williams 1995
Enneadocysta arcuata (Eaton 1971) Stover and Williams 1995
Enneadocysta brevistila sp. nov. herein
Enneadocysta fenestrata (Bujak 1976) Stover and Williams 1995
Enneadocysta dictyostila (Menéndez 1965) Stover and Williams 1995 emend herein
Enneadocysta magna sp. nov. herein
Enneadocysta multicornuta (Eaton 1971) Stover and Williams 1995
Enneadocysta partridgei Stover and Williams 1995
Enneadocysta pectiniformis (Gerlach 1961) Stover and Williams 1995
Glaphyrocysta Stover and Evitt 1978
Hystrichosphaeridium Deflandre 1937
Hystrichosphaeridium diktyoplokum Klumpp 1953
Hystrichosphaeridium dictyostilum Menéndez 1965
Hystrichosphaeridium tubiferum (Ehrenberg 1838) Deflandre 1937
Licracysta gen. nov. herein
Licracysta corymbus sp. nov. herein
Licracysta? *semicirculata* (Morgenroth, 1966) comb nov. herein
Oligosphaeridium? *dictyostilum* (Menéndez 1965) Eisenack and Kjellström 1972
Ramidinium Guerstein et al. 1998