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THE PROBLEMATIC AQUATIC PALYNOMORPH GENUS *COBRICOSPHAERIDIUM* HARLAND AND SARJEANT, 1970 EMEND., WITH NEW RECORDS FROM THE HOLOCENE OF ARGENTINA

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ABSTRACT—The aquatic palynomorph genus *Cobricosphaeridium* Harland and Sarjeant, 1970 was described from Holocene deposits of Australia. Restudy of the type material shows that these palynomorphs may represent the eggs of crustaceans, and that earlier attributions to the division Dinoflagellata are unsustainable. The genus *Aquadulcum* Harland and Sarjeant, 1970, also first described as a dinoflagellate from the Holocene of Australia, is treated as a synonym of *Cobricosphaeridium*, and the following new combinations are proposed: *C. awendae*, *C. myalupense*, *C. pikeae*, *C. serpens*, *C. yanchepense*, *C.*? *ovatum*, and *C.*? *vermiculatum*. Previous records of the genus are restricted to the Holocene and indicate a freshwater affinity.

Cobricosphaeridium has now been found in Holocene subsurface brackish deposits of Laguna Hinojales in eastern Argentina. This is the first record of this genus from South America and unequivocally extends its ecological range into a brackish environment. Several species are represented, including *Cobricosphaeridium hinojalensis* new species; and their potential as paleoenvironmental indicators is evaluated.

INTRODUCTION

HARLAND AND SARJEANT (1970) described the genera *Cobricosphaeridium* and *Aquadulcum* from Holocene lake sediments of Western Australia and Victoria (Fig. 1) to accommodate what they interpreted as cysts of freshwater dinoflagellates. This work followed an earlier study by Churchill and Sarjeant (1962) of lake sediments from Western Australia that represents the first account of geologically preservable freshwater dinoflagellate cysts from Holocene deposits (see Norris and McAndrews, 1970). Several species erected in these early studies are still accepted as freshwater dinoflagellate cysts, and it is now well known that a number of freshwater dinoflagellate species produce geologically preservable resting cysts (Head, 1996). In contrast, *Cobricosphaeridium* has been regarded either as having questionable biological affinity (McMinn, 1991; Williams et al., 1998), or as possibly representing the eggs of copepods (McMinn et al., 1992).

The genus *Cobricosphaeridium* was erected for forms each bearing two distinctive types of processes, both of variable length and shape, an apical archeopyle, and indications of a sulcus and cingulum. Two species were described, *Cobricosphaeridium hebes* Harland and Sarjeant, 1970, the type, and *Cobricosphaeridium spiniferum* Harland and Sarjeant, 1970 comprising two subspecies, *C. spiniferum* subsp. *spiniferum* and *C. spiniferum* subsp. *elegans* Harland and Sarjeant, 1970. Doubts were first cast on the dinoflagellate affinity of this genus when McMinn (1991) described a new species, *Cobricosphaeridium giganteum*, as an acritarch. Although we now place *Cobricosphaeridium*? *giganteum* questionably in the genus *Cobricosphaeridium*, this species was subsequently demonstrated in incubation experiments to be the egg of a probable copepod (McMinn et al., 1992). Head (1996) retained *Cobricosphaeridium* as a freshwater dinoflagellate genus because the biological affinity of *C. hebes*, the type, had not been disproved. Furthermore, *C. hebes* and *C. spiniferum* have strictly freshwater associations, whereas *C.*? *giganteum* is restricted to brackish environments (McMinn, 1991; McMinn et al., 1992). Williams et al. (1998) nonetheless listed the genus *Cobricosphaeridium* as an acritarch, based in part on the earlier recognition of its problematic morphology (McMinn, 1991; Fensome et al., 1993).

The genus *Aquadulcum* Harland and Sarjeant, 1970 was defined to accommodate forms densely ornamented with vermiculae or very short spines, showing indications of a sulcus and cingulum, and with an uncertain archeopyle possibly in the form of a transapical slit. Harland and Sarjeant (1970) erected four species, including *Aquadulcum serpens*, the type. To these original species, Burden et al. (1986) subsequently added *Aquadulcum awendae* from Holocene freshwater deposits of Ontario, Canada. Burden et al. (1986) interpreted *Aquadulcum awendae* as having a transapical archeopyle and cingulum, and hence considered it a dinoflagellate cyst. Fensome et al. (1993), Head (1996), and Williams et al. (1998) have all accepted *Aquadulcum* as being a dinoflagellate cyst genus.

Our interest in the genera *Aquadulcum* and *Cobricosphaeridium* developed through a paleoecological investigation of Holocene aquatic palynomorphs from Argentina. The palynomorphs are from a 1.10 m-long sediment core in Laguna Hinojales (37°34′S; 57°27′W), Buenos Aires province, Argentina (Fig. 2), the base of this core dating to about 4,500 years B.P. (mid Holocene; Stutz et al., 2002). The specimens show close resemblance to *Aquadulcum* and *Cobricosphaeridium* but lack evidence of dinoflagellate affinity. We have resolved this apparent inconsistency by reexamining the type specimens of *Aquadulcum* and *Cobricosphaeridium*. To shed further light on the problem, the type material of *Aquadulcum awendae* has also been re-studied.

Our paper therefore aims to describe the Argentinean aquatic palynomorphs in light of a review of the genera *Aquadulcum* and *Cobricosphaeridium*, with emphases on morphology, biological affinities, and paleoecology.

MATERIALS AND METHODS

The Laguna Hinojales samples, labelled ''LH,'' are from a 1.10 m long sediment core obtained using a Dachnowsky corer at a site off the eastern shore of Laguna Hinojales, Argentina (37°34′S; 57°27′W; Fig. 2). Two radiocarbon dates were obtained: 4,240 ± 60 years B.P. (Beta-118012) from *Heleobia parchappii*

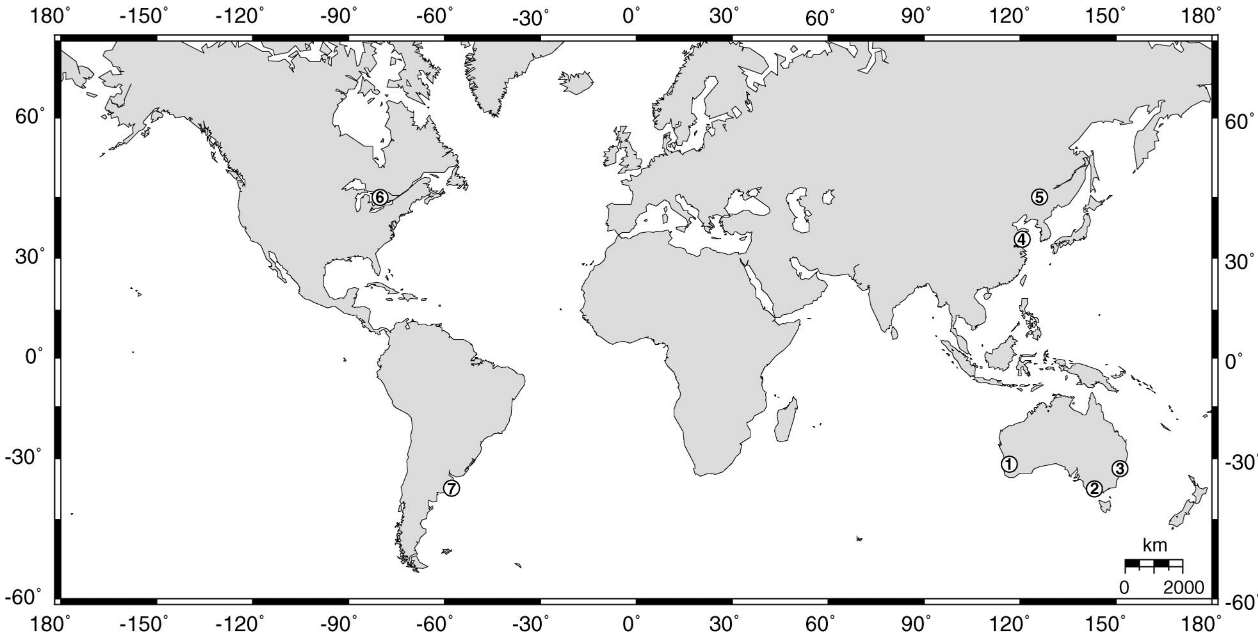
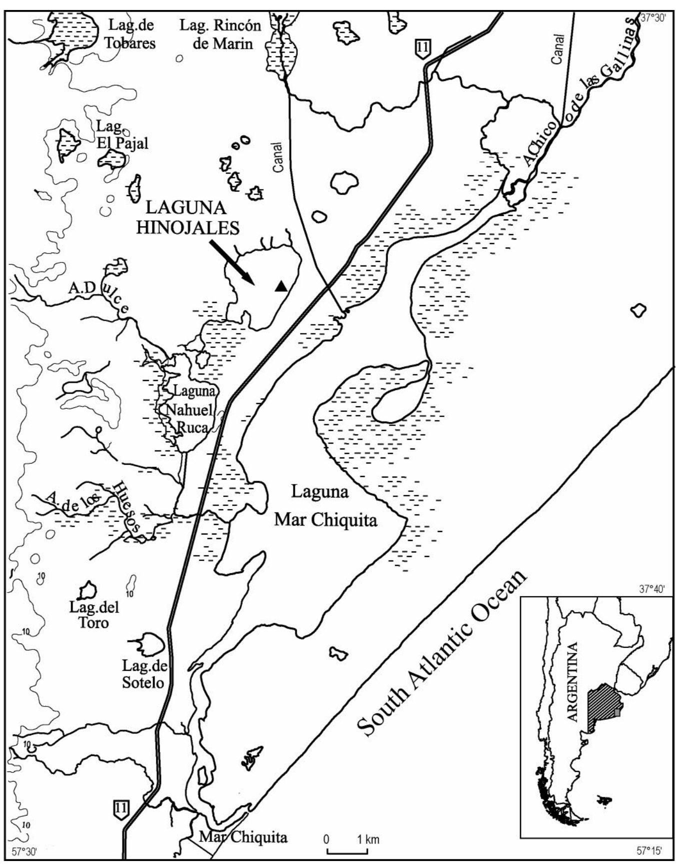


FIGURE *1*—Sites where specimens herein assigned to *Cobricosphaeridium* have been recorded. *1,* Western Australia (Churchill and Sarjeant, 1962; Harland and Sarjeant, 1970); *2,* Victoria, Australia (Harland and Sarjeant, 1970; this study); *3,* New South Wales, Australia (McMinn, 1991; McMinn et al., 1992); *4,* Yellow Sea off Donghai, China (Song et al., 1985); *5,* Songliao Basin, NE China (Gao et al., 1992); *6,* Ontario, Canada (Burden et al., 1986; this study); *7,* Buenos Aires Province, eastern Argentina (this study).



(d'Orbigny, 1835) and *H. australis* (d'Orbigny, 1835) shells between 1.02 and 1.06 m; and 440 ± 50 years B.P. (Beta-114747) from seeds of *Schoenoplectus californicus* (Meyer) Soják, 1972 between 0.58 and 0.62 m. An interpolated age of about 4,500 years B.P. is given for the base of the core (Stutz et al., 2002). The core was sampled for palynological analysis every 1.5–2.0 cm. The 13 samples used in this study are from the lower interval between 0.77 and 1.10 m (Fig. 3).

Sediment samples of 2 to 17 g dry weight were processed at the Laboratorio de Palinología de la Universidad de Mar del Plata, Argentina (Stutz et al., 2002). In order to estimate the concentrations of palynomorphs (specimens per gram dry weight of sediment), five *Lycopodium clavatum* tablets were added to each sample (Stockmarr, 1971). Warm 10 percent KOH was used to dissolve humid acids and to deflocculate clays, cold 10 percent HCl to eliminate carbonates, heavy-liquid separation with $ZnCl_2$ (d = 2.2 g/ml) and concentrated HF to eliminate silicates. Neither acetolysis nor ultrasound treatment were used on material destined for light microscope analysis. Organic residues were sieved at 10 μm using nylon screens, stained with safranin-o and mounted on microscope slides using glycerine jelly. Between two and four slides were made from each sample. All slides were examined under ×1,000 magnification. Additional sieved residues after brief ultrasound treatment were strew mounted and air-dried onto circular cover slips affixed to aluminium stubs, then coated with gold, and analysed using a GEOL JSM-840 SEM (Department of Geology, University of Toronto, Canada).

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FIGURE *2*—The Mar Chiquita region of Buenos Aires province, Argentina, showing the location of Laguna Hinojales. Buenos Aires province is shaded in the inset map. A triangle indicates the position of the studied core, and horizontal dashes indicate marshland. In the vicinity of Laguna Hinojales, Highway 11 marks the position of the relict upper-Pleistocene barrier ridge mentioned in the text.

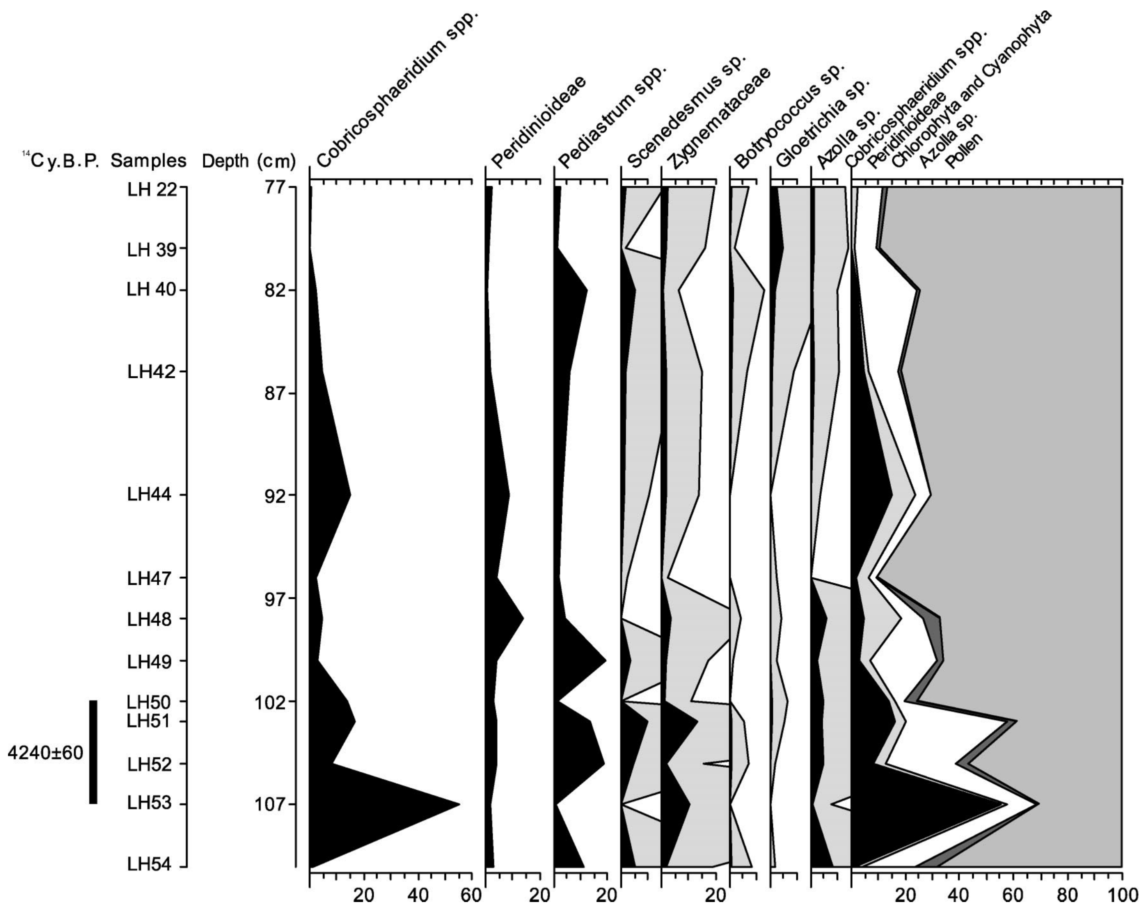


FIGURE 3—Percentage stratigraphic distribution of aquatic palynomorph groups discussed in the text and pollen through the lower part of the Laguna Hinojales core, eastern Argentina. Light shading indicates ×10 exaggeration.

Reexamination of the Harland and Sarjeant (1970) type material from Lake Cobrico, Victoria, Australia (38°18′S, 143°02′E) is based on six original microscope slides representing five samples taken at the following depths: 150 cm (slide LCV/1b), 320 cm (slides LCV/5a and LCV/5b), 340 cm (slide LCV/6b), 350 cm (slide LCV/7a), and 360 cm (slide LCV/8). The slides are still in workable condition despite having been mounted in glycerine jelly more than 30 years ago. The samples are generally dominated either by amorphous organic material (320 cm, 340 cm, and 350 cm) or by structured plant debris (150 cm and 360 cm). *Botryococcus* is common at 320 cm and 350 cm whereas *Pediastrum* is common at 360 cm. Pollen are generally common, and occasional tintiniid loricae were also seen. Specimens of *Cobricosphaeridium* were found to be very rare, with a maximum of nine specimens recorded on one slide. The paucity of specimens has been a hindrance in determining intraspecific variability within this material.

Reassessment of *Aquadulcum* (now *Cobricosphaeridium*) *awendae*, from the Holocene of Ontario, Canada (Burden et al., 1986), is based on a detailed examination of the microscope slide containing the holotype. This slide is in good condition, and is dominated by structured plant debris and pollen. Thirty-three specimens of *A. awendae*, including the holotype, were examined. The material had not been stained, and the thin, colorless nature of the specimens has made their morphology difficult to elucidate.

Specimens are illustrated with a Leica DC300 digital camera attached to a Leica DMR microscope. An England Finder reference follows the sample (and slide) number for each specimen illustrated.

Microscope slides containing the illustrated Argentinean specimens are stored at the Colección Palinológica, Departamento de Geología de la Universidad Nacional del Sur, Bahía Blanca, Argentina. Type specimens from Harland and Sarjeant (1970) and additional illustrated type material are curated at the British Geological Survey, Nottingham, U.K. (specimen numbers MPK 968–973 and MPK 12668–12671 inclusive), and not now in the Department of Geology, University of Alberta as reported in the original paper. The type specimens from Burden et al. (1986) and additional illustrated type material are housed in the Invertebrate Section of the Department of Palaeobiology, Royal Ontario Museum, Toronto, Canada.

BIOLOGICAL AFFINITY OF *COBRICOSPHAERIDIUM*

Earlier reports of an archeopyle, sulcus and cingulum on *Cobricosphaeridium* and *Aquadulcum* species, that began with Churchill and Sarjeant (1962) and continued for 30 years, appear to be unsubstantiated. None of the specimens we have encountered from Australian or Canadian type material, or specimens from Argentina, show morphological evidence of dinoflagellate affinity. Nor can we find any compelling evidence of such affinity from critically appraising the literature. The taxa here assigned to *Cobricosphaeridium* are characterized by an aperture formed by a simple split, and ornament that is extremely variable and heterogeneous (Table 1). These characters are reminiscent of copepod diapause eggs (e.g., Belmonte, 1997, 1998; Castro-Longoria, 2001), including those of calanoid copepods which are well-known free spawners. Moreover, *Cobricosphaeridium*? *giganteum*, which represents a close living analogue to our material, TABLE *1*—Comparison of all species attributed in this paper to the genus *Cobricosphaeridium.* Also included are species in open nomenclature recorded from Argentina during the present study.

	Central body max. dia. (in μm)	Maximum process length (in μm)	Number of specimens measured	Process bases	Process morphology	Surface ornament between processes	Type locality (and reference for morphological information)	Found in the present study of Argentina
C. awendae n. comb. (Figs. 4–6)	40(49.9)67	2.8(7.7)16	33	Convergence of one or more ridges	Membranous, irregularly tapering, distally branched, or digitate to foliate; often scattered spinules	Scabrate ± short low ridges, sparsely scattered spinules, granules	Ontario, Canada (Burden et al., 1986; this study)	No
C. hebes (Figs. 7, 8.1–8.11, 9.2–9.4)	48–64	3–6	6	Convergence of radiating ridges	Short, solid to membranous (occasionally spongy), digitate, bifurcate or foliate when fully developed; usually bearing spinules	Almost smooth, with densely distributed spinules	Victoria, Australia (Harland and Sarjeant, 1970; this study)	No
C. cf. *hebes* (Figs. 7, 8.12–8.16)	52	5	1	Convergence of radiating ridges	Solid to membranous fusion of raised ridges, most bear spinules, and some expand distally as result of projecting spinules	Almost smooth, with low ridges; occasional spinules on ridges	Victoria, Australia (this study)	No
C. hinojalensis n. sp. (Figs. 11.12–11.21, 12.1–12.4, 14.12, 14.14, 14.15)	51(58.9)73	2.5(3.7)5.5	20	Single ridge or convergence of ridges	Solid to membranous, flattened, usually acuminate to evexate; not conspicuously branched	Almost smooth to faintly vermiculate, sometimes sparse spinules or hairs	Argentina (this study)	Yes
C. myalupense n. comb.	48–55	3.5	?	Approximately circular?	Short, solid?, simple or irregularly bifurcate; densely and irregularly distributed	Apparently smooth	Western Australia (Churchill and Sarjeant, 1962; Harland and Sarjeant, 1970)	No
C. pikeae n. comb.	33–37	2	14	Approximately circular?	Densely distributed short spines that bifurcate at constant distance from base	Apparently smooth	Western Australia (Churchill and Sarjeant, 1962; Harland and Sarjeant, 1970)	No
C. serpens n. comb. (Figs. 8.17–8.20, 9.1, 10.7–10.12)	50–62	1	3	Weak convergence of radiating ridges	Incipient processes forming small subcircular areas of more pronounced ornamentation	Low, solid ridges forming vermiculate pattern; some spinules on ridge crests	Victoria, Australia (Harland and Sarjeant, 1970; this study) and Argentina (this study)	Yes
C. spiniferum (Figs. 7, 9.5–9.13, 10.1–10.6)	46–60	6–15	10	Solid/spongy; circular to elongate	Long, solid/spongy, unbranched, bifurcate ± secondary branching, or digitate, often flattened; occasional spinules along main stem	Surface nearly smooth, with densely distributed spinules/hairs	Victoria, Australia (Harland and Sarjeant, 1970; this study)	No
C. cf. *spiniferum* (Figs. 12.5–12.20, 13, 14.1–14.11, 14.13)	51(61.3)70	4(6.8)14	12	Solid; circular, elongate, or convergence of ridges	Long, solid or rarely spongy, unbranched, bifurcate ± secondary branching, or digitate, often flattened; occasional spinules along main stem	Surface nearly smooth, with densely distributed spinules/hairs	Argentina (this study)	Yes
C. yanchepense n. comb.	52	up to 7.5	?	Convergence of radiating ridges	Short, stubby, solid, blunt or distally expanded and branched	Surface granular	Western Australia (Churchill and Sarjeant, 1962; Harland and Sarjeant, 1970)	No
C.? giganteum	66(72)80	18–31	8	Hollow, circular	Hollow, irregularly tapering, complexly branched, stellate, digitate; often scattered spinules	Smooth, with sparsely scattered spinules	New South Wales, Australia (McMinn, 1991; McMinn et al., 1992)	No
C.? ovatum n. comb.	31–34	no processes	?	none	none	Weakly and finely granulorugulate, to incompletely finely reticulate	Songliao Basin, China (Gao et al., 1992)	No

TABLE *1*—Continued

	Central body max. dia. (in µm)	Maximum process length (in µm)	Number of specimens measured	Process bases	Process morphology	Surface ornament between processes	Type locality (and reference for morphological information)	Found in the present study of Argentina
C.? vermiculatum n. comb.	53	?	1	?	"Short stick- or worm-like raised patterns" questionably represents processes	Dense cover of small wrinkles	East China Sea (Song *in* Song et al., 1985)	No
Cobricosphaeridium sp. 1 (Figs. 10.13–10.14, 11.1–11.11)	56–70	2–5	5	Solid; single ridge or convergence of pronounced ridges	Solid, blunt-tipped or tapering, and may be flattened	Smooth surface with low, sinuous ridges; vermiculate to reticulate pattern; scattered granules and spinules	Argentina (this study)	Yes

has been germinated to produce the nauplius stage of an unidentified crustacean, almost certainly a copepod (McMinn et al., 1992, p. 315). We therefore accept that the fossil genus *Cobricosphaeridium* may represent the eggs of unidentified crustaceans such as copepods.

Our reexamination of the type specimen of *Aquadulcum* (the holotype of *Aquadulcum serpens*), shows that it, too, lacks morphological evidence of dinoflagellate affinity. Moreover, *Aquadulcum* lies within the morphological range we have allowed for *Cobricosphaeridium* and so we treat it as a junior synonym. All species formerly belonging to *Aquadulcum* are transferred herein to *Cobricosphaeridium*.

TAXONOMIC APPROACH

Harland and Sarjeant's (1970) species and subspecies of *Cobricosphaeridium* were initially described from observations of relatively few specimens, and our own reexamination is based on even fewer specimens. Because of the limited available material, we have not felt justified in grouping taxa at the present time, even though differences between some taxa seem slight. We expect such consolidation to occur in the future, as more specimens are found, but cannot anticipate exactly how this will happen. Even for living crustaceans, there are presently considerable problems in using egg morphology to identify species (G. Belmonte, personal commun., 2002).

GEOLOGY AND PALEOECOLOGY OF LAGUNA HINOJALES, ARGENTINA

Laguna Hinojales today is a freshwater, shallow, inland lake lacking natural drainage. It is located about 1 km west of Laguna Mar Chiquita, Buenos Aires province, Argentina (Fig. 2). According to Violante (1992), the coastal area north of Laguna Mar Chiquita evolved through the development of a littoral barrier system whose westward advance was controlled by a relict upper Pleistocene barrier ridge. During the Holocene sea-level maximum, this ridge was transgressed via channels, forming a tidal flat between 5,200 and 4,600 years B.P. Following the subsequent fall in sea level, several shallow lakes, disconnected from the sea, became established on the earlier tidal flat.

Our 1.10 m core provides evidence of conditions at Laguna Hinojales only from about 4,500 years B.P. Prieto et al. (1998) have proposed that the Laguna Hinojales area, probably including the Laguna Nahuel Ruca (Fig. 2), underwent an evolution similar to that advanced by Violante (1992) for other lagoons in the region. This implies that the sea had reached the Laguna Hinojales area during the Holocene sea-level maximum, but this seems to have been its farthest western extent. However, our core represents only the regressive phase that followed the Holocene sea-level maximum.

Within our core, specimens of *Cobricosphaeridium* are most abundant between 1.10 and 0.80 m (Fig. 3). This lower interval has already been analysed for pollen, diatoms, ostracods, and gastropods (Prieto et al., 1998). The pollen is characterized by high percentages of Chenopodiineae (up to 65 percent) together with Cyperaceae and Poaceae and traces of *Typha* and *Myriophyllum*, indicating a halophytic vegetation associated with freshwater bodies. Diatoms are mostly represented by the brackish (mesohalobous) taxa *Surirella striatula* Turpin, 1828a and *Campylodiscus clypeus* Ehrenberg, 1840, the slightly brackish (oligohalobous-halophilous) taxa *Rhopalodia gibberula* (Ehrenberg, 1843) O. Müller, 1895 and *Synedra platensis* Frengüelli, 1934, and the freshwater taxa *Cocconeis placentula* Ehrenberg, 1838, *Aulacoseira granulata* (Ehrenberg, 1843) Simonsen, 1979, and *Nitzchia hungarica* Grunow, 1862. Together, these occurrences reflect a mixed-water environment.

Limnocythere staplini Gutentag and Benson, 1962, *Cyprideis* *multidentata* Hartmann, 1955, *Pampacythere multiperforata* Whatley and Cholich, 1974, *P. solum* Whatley and Cholich, 1974, and *Cypridopsis* sp. characterize the ostracod assemblages. Both freshwater and brackish taxa are represented, again pointing to a brackish and mixed-water environment. Calcareous foraminifers include *Ammonia beccarii parkinsoniana* (d'Orbigny, 1839) and *Elphidium* sp., and indicate brackish environments.

Of the gastropods found in the lower part of the Laguna Hinojales Core, specimens of *Heleobia parchappii* (d'Orbigny, 1835) are well preserved and possibly in place, whereas specimens of *Heleobia australis* (d'Orbigny, 1835) show fractures and abrasion, and are thus possibly transported. The former species tolerates wide fluctuations between brackish and freshwater conditions, and the latter prefers brackish water. Well preserved specimens of the terrestrial gastropod *Succinea* sp. and the freshwater species *Biomphalaria peregrina* (d'Orbigny, 1835) are also present. A $\delta^{13}C$ value calculated on a sample of shells (*Heleobia parchappii* and *H. australis*) from 1.02 to 1.07 m depth is $-1.6‰$ PDB, indicating marine conditions (Prieto et al., 1998).

The biota from the lower interval (1.10–0.80 m) can therefore be summarized as consiting of a mixed association of freshwater and brackish taxa (Prieto et al., 1998).

A pollen record for the entire Laguna Hinojales core was recently presented by Stutz et al. (2002), who proposed that a stagnant, nutrient-rich, freshwater body has existed here since at least about 4,500 years B.P. Between 4,500 and 3,300 years B.P. the shallow lake evolved in an environment dominated by a halophytic plant community. These plants were living on soils made saline by the earlier marine transgression. Upsection increases in the percentages of Cyperaceae, *Typha* and *Myriophyllum* suggest a gradual change to a freshwater community.

AUTECOLOGY OF *COBRICOSPHAERIDIUM* FROM THE LAGUNA HINOJALES CORE

Cobricosphaeridium specimens are most abundant in the lower (1.10–0.80 m) interval of the Laguna Hinojales core, reaching 55 percent of the palynological spectrum at 1.07 m. Specimens of *Cobricosphaeridium* above 0.80 m are rare. This lower interval, according to the evidence of pollen, molluscs, foraminifers, diatoms, and ostracods (Prieto et al., 1998; Stutz et al., 2002), represents a coastal environment where freshwater and brackish biotas occur together (see above). In order to refine the ecological interpretation of this lower interval, we examined the distribution of aquatic palynomorphs (Fig. 3). The following typically freshwater palynomorphs were recorded: cenobia of Hydrodictyaceae (*Pediastrum boryanum* (Turpin, 1828b) Meneghini 1840 and *Pediastrum musterii* Tell and Mataloni, 1990) and Scenedesmaceae (*Scenedesmus* sp.), spores of Zygnemataceae (*Spirogyra* spp., *Debarya* sp., *Zygnema* sp., and *Mougeotia* spp.), colonial aggregates of *Botryococcus*, and massulae with spores of the freshwater fern *Azolla*. Of these taxa, *Pediastrum* and *Scenedesmus* are common inhabitants of most of the oligohaline and mesohaline shallow lakes in northern Buenos Aires province (Guarrera et al., 1968), and the Zygnemataceae are restricted to freshwater (rarely brackish) environments and are common in oxygen-rich, shallow, stagnant, moderately nutrient-rich waters (Hoshaw and McCourt, 1988). The chlorococcalean alga *Botryococcus* occurs mainly in freshwater habitats but is also known from brackish environments (Batten and Grenfell, 1996). In addition to these mainly freshwater taxa, sheets of Rivulariaceae (*Gloetrichia* sp.) and cysts of peridinioidean dinoflagellates were also recorded. *Gloetrichia* is a common bloom-forming species of modern lakes (Lee, 1989), and its increase in the upper part of the interval examined may reflect increasing size of the water body. Peridinioidean dinoflagellate cysts were recovered throughout the interval but are more common in the lower part, reaching 15 percent of the total palynomorphs at 0.97 m depth. They exhibit incomplete sutures, thereby preventing a full reconstruction of the tabulation, but resemble cysts of extant freshwater species of *Peridinium*. This genus lives in rivers and shallow lakes of Buenos Aires and other provinces of Argentina (Boltovskoy, 1973a, 1973b, 1975, 1976, 1989). The presence of a single dinoflagellate taxon and a total absence of confirmed marine dinoflagellate cysts indicate freshwater or, at most, a slightly saline paleoenvironment.

Our analysis therefore indicates that while some of the identified algae tolerate brackish conditions, the environment was under considerable freshwater influence. Considering all the evidence, we consider the interval 1.10–0.94 m (4,500–3,300 years B.P.) to represent the deposits of an initially slightly brackish shallow lake that formed on a tidal flat during regression of the sea. This regression immediately followed the mid-Holocene marine transgression. A continuing supply of freshwater from streams entering the lake would have stimulated the growth of algae and other freshwater organisms, resulting in a mix of brackish and freshwater species.

Specimens of *Cobricosphaeridium* are abundant in the lower interval of the core and evidently flourished within this slightly brackish environment. It is difficult to determine conclusively whether they were freshwater or brackish, given both the close juxtaposition of these microhabitats within the area of deposition and the blurring effects of taphonomy and bioturbation. Nevertheless, three lines of evidence suggest a brackish affinity for the *Cobricosphaeridium* species. Firstly, in the lower part of the core where *Cobricosphaeridium* is most common, its abundance is inversely related to that of the common, mostly freshwater algae *Pediastrum* and *Scenedesmus*. Secondly, abundance is reduced in the upper part of the lower interval, where *Gloetrichia* sheets suggest a freshwater influence. Thirdly, only rare specimens occur in the upper interval where conditions are interpreted to have become increasingly freshwater (Stutz et al., 2002; Borel et al., in press). Previous records of the genus *Cobricosphaeridium* show an affinity for freshwater (Harland and Sarjeant, 1970; Burden et al., 1986), although *Cobricosphaeridium*? *giganteum* is restricted to brackish marine conditions (McMinn, 1991; McMinn et al., 1992). Our Argentinean specimens likewise apparently favored a brackish environment.

SYSTEMATIC PALEONTOLOGY

Group Acritarcha Evitt, 1963
Genus Cobricosphaeridium Harland and Sarjeant, 1970 emended

Cobricosphaeridium Harland and Sarjeant, 1970, p. 216, 217.
Aquadulcum Harland and Sarjeant, 1970, p. 220, 221.

Type.—The holotype of *Cobricosphaeridium hebes* Harland and Sarjeant, 1970, pl. 21, figs. 1, 2, text-fig. 2; Figures 7, 8.1–8.7.

Included taxa.—*Cobricosphaeridium awendae* (Burden et al., 1986) n. comb.; *C. hebes* Harland and Sarjeant, 1970 emend.; *C. hinojalensis* n. sp., *C. myalupense* (Churchill and Sarjeant, 1962) n. comb., *C. pikeae* (Churchill and Sarjeant, 1962) n. comb., *C. serpens* (Harland and Sarjeant, 1970) n. comb.; *C. spiniferum* Harland and Sarjeant, 1970 emend., *C. spiniferum* subsp. *elegans* Harland and Sarjeant, 1970 emend., and *C. yanchepense* (Harland and Sarjeant, 1970) n. comb.

Provisionally included taxa.—*Cobricosphaeridium*? *giganteum* McMinn, 1991; *C.*? *ovatum* (Gao et al., 1992) n. comb., and *C.*? *vermiculatum* (Song *in* Song et al., 1985) n. comb.

Original diagnosis for Cobricosphaeridium.—Spherical to subspherical proximochorate cysts, bearing two distinct process

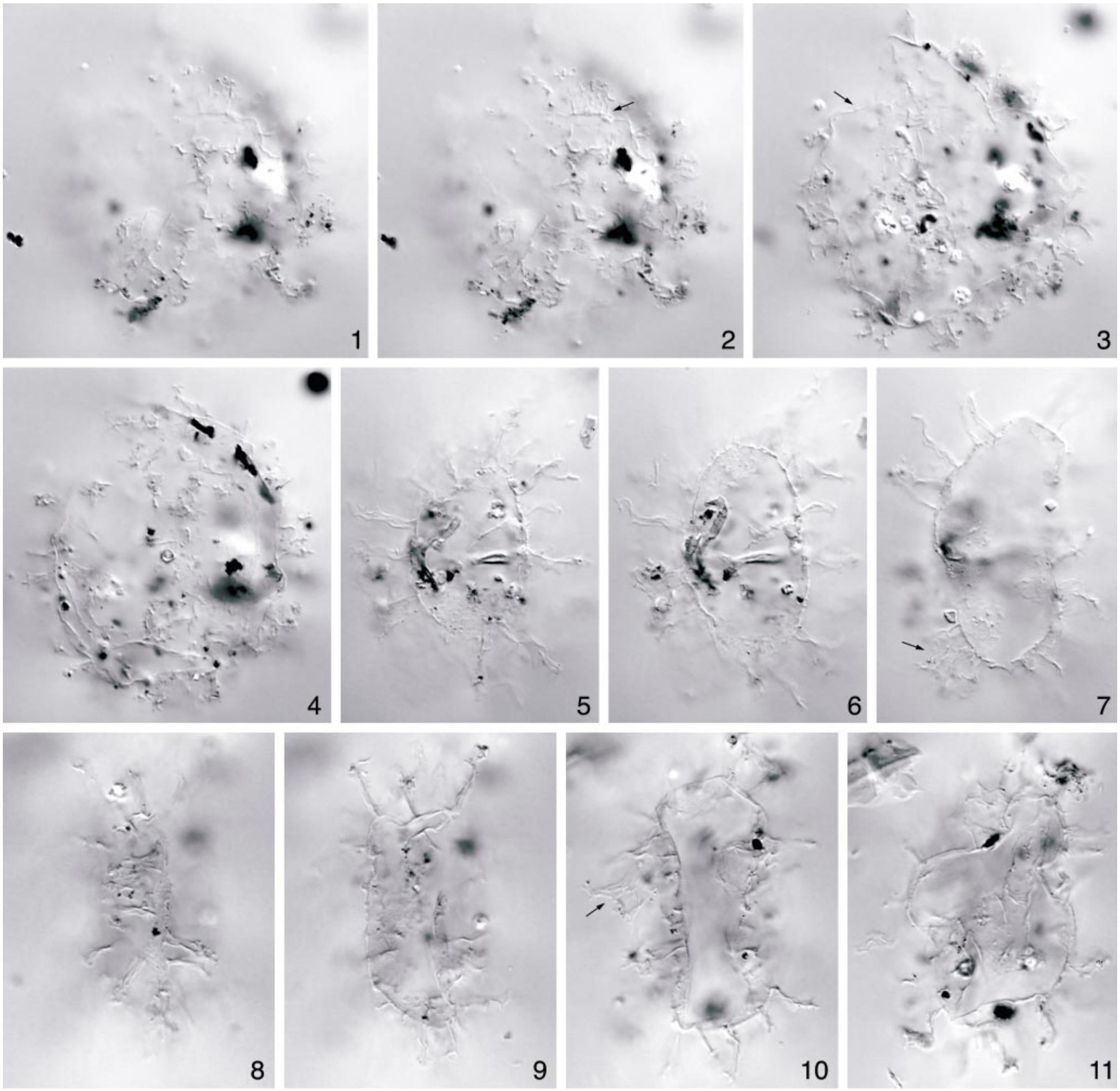
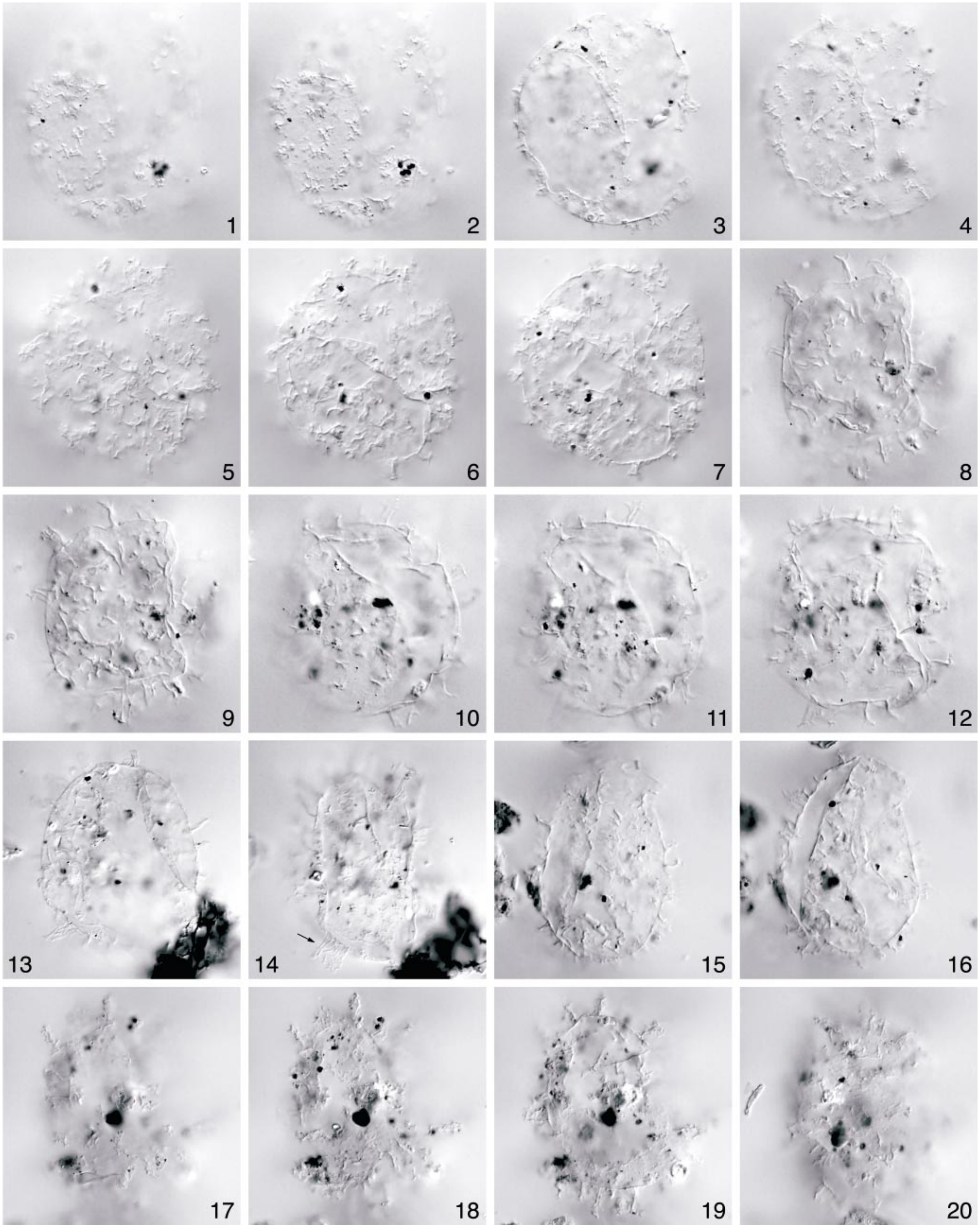


FIGURE 4—Holotype and topotype specimens of *Cobricosphaeridium awendae* (Burden, McAndrews, and Norris, 1986) n. comb. from upper Holocene lake deposits, Second Lake, Awenda Provincial Park, southern Ontario, Canada. All specimens from Core 2, depth 10 cm, slide 1 (ROM 44056). Max. dia. = maximum diameter. *1–4,* Holotype showing *1,* upper surface; *2,* slightly lower focus with arrow indicating membranous linear complex; *3,* mid focus with arrow indicating rupture of central body; *4,* lower surface; central body max. dia., 56 μm; England Finder reference N46/0. *5–7,* Topotype showing *5,* upper surface; *6,* slightly lower focus; *7,* mid focus with arrow indicating membranous linear complex; central body max. dia., 53 μm; England Finder reference N24/0. *8–11,* Topotype showing *8,* upper surface; *9,* slightly lower focus; *10,* mid focus with arrow indicating membranous linear complex; *11,* lower surface; central body max. dia., 50 μm; England Finder reference Q34/4.

types. Processes of the first type are relatively long, up to a quarter of the cyst diameter, of very variable form, slender, tapering to cylindrical, erect or sinuous, wart-like, evexate to digitate and foliate, occasionally forked at their tips; bases of processes usually ornamented with granules. Processes of the second type are short, slender, cylindrical and may also be forked at their distal extremities. These processes are approximately one-half to one-sixth the length of the first type, so that distinguishing between these two process types is always readily possible. Cingulum and sulcus are present, but not often clearly defined: tabulation is otherwise absent. Archaeopyle apical (A in terms of the symbols proposed by Evitt, 1967). (Harland and Sarjeant, 1970, p. 216.)

Original diagnosis for Aquadulcum.—Peridinoid to sub-spherical proximate cysts bearing a dense ornamentation of very short



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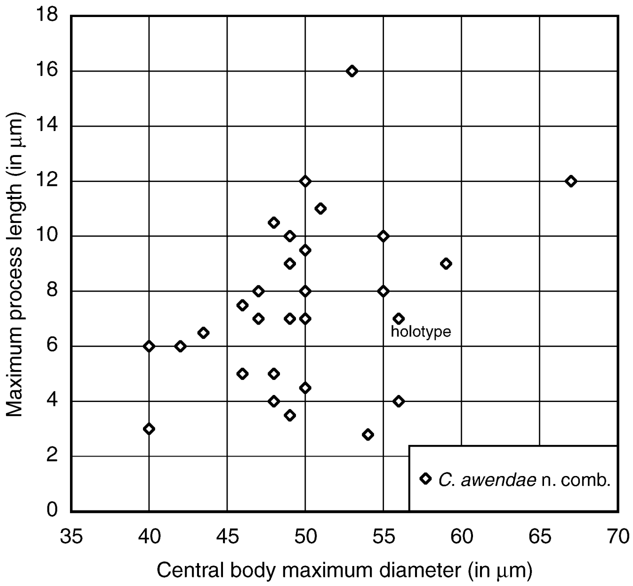

FIGURE 6—Dimensions of *Cobricosphaeridium awendae* (Burden, McAndrews, and Norris) n. comb. specimens from the type slide, all based on measurements from the present study.

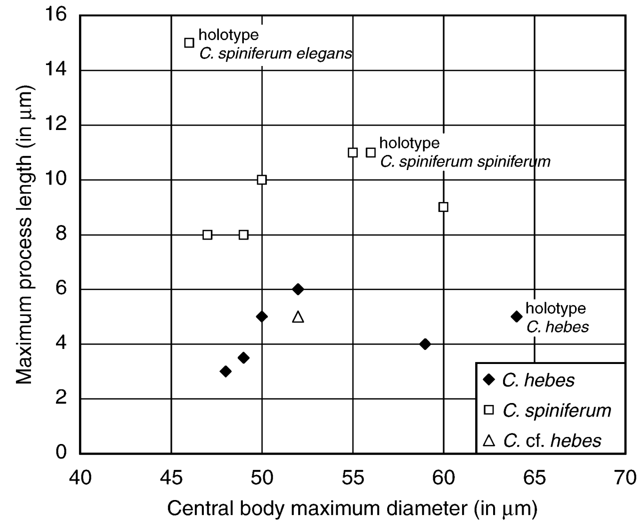

FIGURE 7—Dimensions of *Cobricosphaeridium hebes* Harland and Sarjeant, 1970 emend., *C.* cf. *hebes*, and *C. spiniferum* Harland and Sarjeant, 1970 emend. from the type slides of Cobrico Swamp, Australia, all based on measurements from the present study.

spines or vermiculae. The cingulum and sulcus are clearly differentiated by lack of such ornament. Nature of archaeopyle uncertain, possibly in the form of a transapical slit; no clear opening is normally visible. (Harland and Sarjeant, 1970, p. 220.)

Emended diagnosis.—Spherical or ellipsoidal thin-walled palynomorphs of moderate to large size, bearing solid to spongy or membranous processes of heterogeneous morphology; long, short, or weakly expressed; unbranched or irregularly branched but unconnected distally. Smaller and often more densely distributed elements comprising spinules, hairs, granules, ridges, or combination thereof, usually also present. Processes and ornament distributed over entire surface. No separation of wall layers between processes. Opening is a simple split in wall.

Discussion.—The emendation of this genus is based on new observations of its type, the holotype of *C. hebes*, and other specimens of *Cobricosphaeridium* and *Aquadulcum*. Restudy of these specimens repudiates the presence of dinoflagellate characters (archeopyle, sulcus, cingulum, tabulation) as originally proposed for both *Cobricosphaeridium* and *Aquadulcum*. Harland and Sarjeant (1970, p. 221) based their monospecific genus *Aquadulcum* on just two observed specimens, of which only one (the holotype) was illustrated. *Cobricosphaeridium* has been expanded to include *Aquadulcum* because: 1) the type specimens of *Cobricosphaeridium* and *Aquadulcum* are linked by a morphologically intermediate specimen, recorded as *Cobricosphaeridium* cf. *hebes* in the present study; and 2) the holotype of *Cobricosphaeridium serpens* (=*Aquadulcum serpens*), which is also the type of *Aquadulcum*, has rudimentary structures (referred to as ''weakly expressed'' processes in our emended diagnosis) that resemble processes on *C. hebes*.

The genus is emended to exclude small palynomorphs, because specimens observed in the present study have a central body maximum diameter ranging between 40 and 73 µm. Larger specimens may, however, be accommodated in *Cobricosphaeridium*.

The wall in *Cobricosphaeridium* is thin (about 0.3 µm or less based on our observations) relative to the size of the central body, and this results in frequent crumpling of specimens. The wall is presumed to be colorless, although this could not always be confirmed from Harland and Sarjeant's (1970) heavily stained type material.

COBRICOSPHAERIDIUM AWENDAE (Burden, McAndrews, and Norris, 1986) new combination
Figures 4–6

Aquadulcum awendae BURDEN, MCANDREWS, AND NORRIS, 1986, p. 52–54, pl. 1, figs. 1–15.

Original diagnosis.—Cysts spheroidal, spiniferate, with numerous, nontabular branching processes. Cingulum with narrow pandasutural zones divides cyst unequally, delimiting smaller epitract. Autophragm scabrate. Archeopyle (AIP?). (Burden et al., 1986, p. 52).

Emended diagnosis.—Central body spherical to ovoidal; wall

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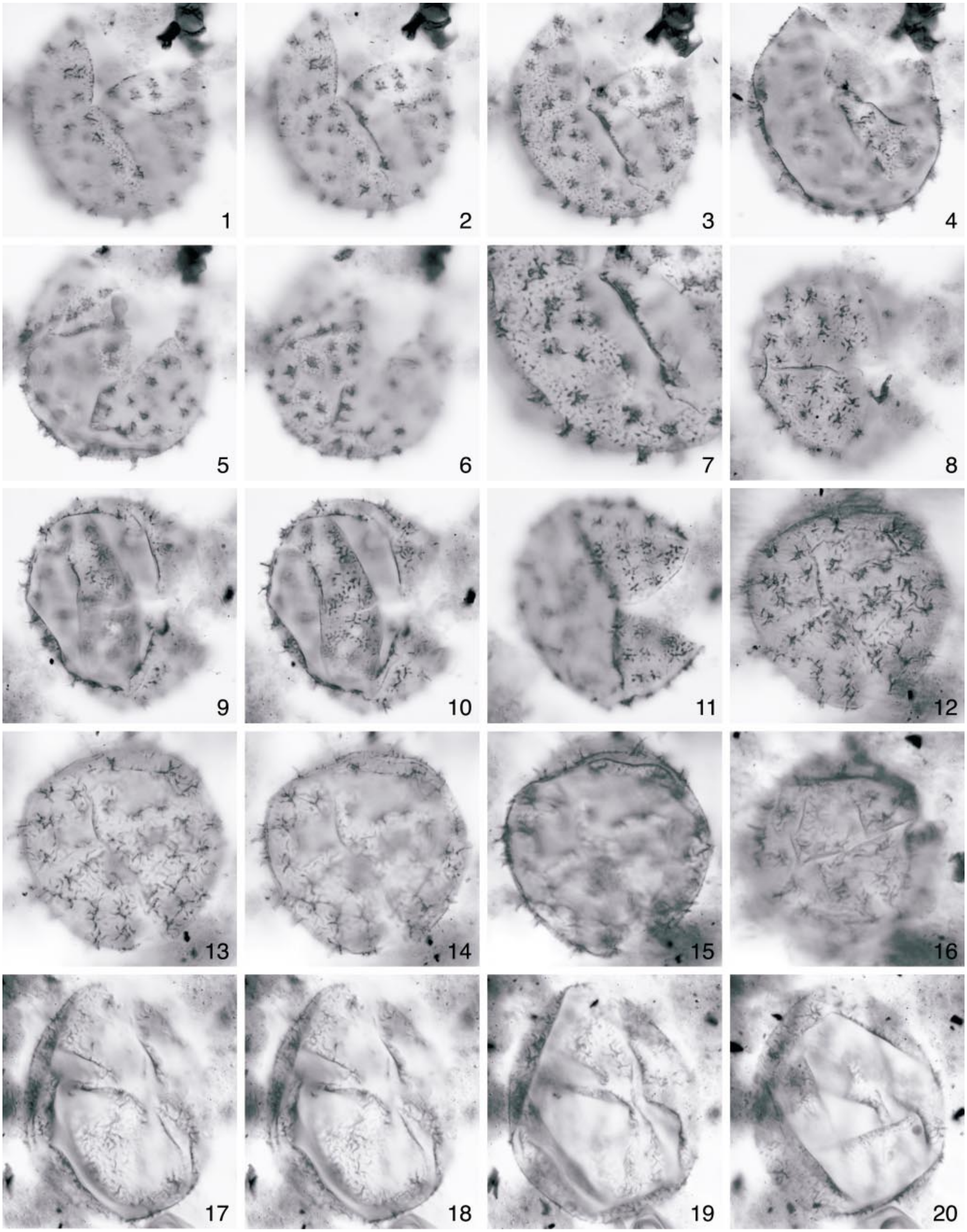
FIGURE 5—Topotype specimens of *Cobricosphaeridium awendae* (Burden, McAndrews, and Norris, 1986) n. comb. from upper Holocene lake deposits, Second Lake, Awenda Provincial Park, southern Ontario, Canada. All specimens from the same microscope slide as the holotype (Core 2, depth 10 cm, slide 1; ROM 44056). Max. dia. = maximum diameter. *1–4*, Specimen showing *1, 2*, upper surface; *3*, mid focus; *4*, lower surface; note unusually short processes; central body max. dia., 56 µm; England Finder reference E38/1. *5–7*, Specimen showing *5*, upper surface; *6*, slightly lower surface; *7*, mid focus; note unusually short processes; central body max. dia., 48 µm; England Finder reference E51/4. *8, 9*, Specimen showing *8*, upper surface; *9*, mid focus; central body max. dia., 40 µm; England Finder reference C37/0. *10–12*, Specimen showing *10*, upper surface; *11*, slightly lower focus; *12*, lower surface; central body max. dia., 42 µm; England Finder reference N41/4. *13, 14*, Specimen showing upper and lower surfaces, respectively; *14*, note membranous linear complex indicated by arrow; central body max. dia., 59 µm; England Finder reference Q28/3. *15, 16*, Specimen showing *15*, upper surface; *16*, slightly lower focus; central body max. dia., 49 µm; England Finder reference Q25/0. *17–20*, Specimen showing *17*, upper surface; *18*, slightly lower focus; *19*, mid focus; *20*, lower surface; central body max. dia., 55 µm; England Finder reference R25/3.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thin, colorless, surface scabrate, bearing long or short processes. Processes membranous, may appear striate for much of length, arising from one or more ridges that converge at base. Process shape irregularly tapering, distally branched, or digitate to foliate; often bearing scattered spinules, but otherwise smooth. Adjoining processes may fuse to form membranous linear complexes. Process distribution irregular but covers entire surface. Between processes, wall surface is scabrate and may include short low ridges and sparsely scattered spinules and granules.

Emended description.—Central body wall less than 0.3 μm thick, colorless, with no visible stratification between processes. Processes formed by thin, erect to suberect membranes that arise from one or more ridges converging at base. Processes not expanded markedly at base, may appear striate for much of length owing to fusion of membranes. Width of processes is variable on individual specimens; range of 2–10 μm on holotype. Process shape very heterogeneous, irregularly tapering, distally branched, or digitate to foliate; often bearing scattered spinules up to about 1.5 μm at distal ends but occasional spinules also project from process stems which are otherwise smooth. Adjoining processes may fuse along much of their length to form long membranous straight or curved linear complexes. One or more of these complexes often appears on each palynomorph (Figs. 4.7, 4.10, 5.14), including the holotype (Fig. 4.2). Process distribution irregular but covers entire palynomorph. Between processes, wall surface is scabrate and may include short (less than 3.0 μm), low (less than 0.5 μm high) ridges which are very faint, and sparsely scattered spinules, pili, coni and granules. Pili up to about 3.0 μm long, usually acuminate but may be minutely bifurcate. Opening is straight or irregular split or tear.

Type.—Holotype: Second Lake, Core 2, depth 10 cm, slide 1; England Finder reference N46/0 (label to right); upper Holocene lake deposits, Awenda Provincial Park, southern Ontario, Canada; Figures 4.1–4.4, 6 (also Burden et al., 1986, pl. 1, figs. 1–3). ROM 44056.

Other material examined.—Thirty-two specimens from the slide containing the holotype.

Measurements.—Holotype: central body, 56 × 48 μm; process length up to 7 μm. Range: central body maximum diameter, 40(49.9)67 μm; standard deviation, 5.6; central body minimum diameter, 33(41.5)50 μm; standard deviation, 4.9; maximum process length, 2.8(7.7)16 μm; standard deviation, 2.9. Thirty-three specimens measured, all from slide containing the holotype. See Figure 6.

Discussion.—The opening in the wall is here interpreted as a simple split, and not a transapical archeopyle as originally diagnosed. A feature originally interpreted on some specimens as a cingulum (Burden et al., 1986) was not identified in the present study of topotype material. It was perhaps misinterpreted from irregularities in process distribution. A small hexagonal platelet figured by Burden et al. (1986, pl. 1, fig. 11) is separate from the underlying specimen and appears not to be a part of it. Burden et al. (1986) assigned this species to the Dinophyceae within the Peridiniales. However, we found no trace of evidence of dinoflagellate affinity in our observations of the type material.

COBRICOSPHAERIDIUM HEBES Harland and Sarjeant, 1970 emended

Figures 7, 8.1–8.11, 9.2–9.4

Cobricosphaeridium hebes HARLAND AND SARJEANT, 1970, p. 217, 218, pl. 21, figs. 1, 2, text-fig. 2.

Original diagnosis.—Spherical to sub-spherical proximate cyst, ornamented with granules and bearing two types of processes. Processes of the first type are relatively short, wart-like, digitate to foliate, sometimes stellate in plan. Processes of the second type are even shorter than the first, slender and not easily seen. Sulcus and cingulum are poorly defined. Archaeopyle apical (A) with a well-marked sulcal notch. (Harland and Sarjeant, 1970, p. 217.)

Emended diagnosis.—Spherical to sub-spherical central body, wall thin, surface almost smooth, bearing short processes and spinules. Processes solid to membranous and digitate, foliate, or bifurcate when fully developed; usually bear spinules, and may appear stellate in plan view. Processes fairly regularly distributed, and usually arise from convergence of radiating ridges at base. Between processes occur densely distributed spinules. Spinules are solid and arise from circular bases or ridges; some fusion may occur between adjacent bases or ridges.

Emended description.—Central body wall less than 0.3 μm thick with no visible stratification between processes. Process morphology variable. Processes when fully developed are digitate, foliate, or bifurcate; arise from convergence of radiating ridges at base. Processes usually bear spinules, and may expand distally as result of projecting spinules. When poorly developed may be reduced to clusters of longer spinules usually mutually fused at base. More fully developed processes essentially membranous to solid in structure, with occasional process stems having fibrous appearance, as on holotype. Longer processes on two specimens (e.g., Fig. 9.2–9.4), but not the holotype, were found to have internally spongy structure. Spinules occur between processes. They are solid and taper to points, and are rather variable in morphology, arising from circular bases or ridges. Adjacent spinules are separated at base by about 0.5–1.0 μm, although some fusion may occur between adjacent bases. Opening is a simple split, on the holotype extending half way around central body and straight to arcuate on upper surface and more irregular on lower surface. Apparently no part of palynomorph is missing.

Type.—Holotype: Specimen MPK 968; slide L.C.V./6b, at depth of 340 cm; England Finder reference V33/2 (IGS label to right); Holocene freshwater peat, Cobrico Swamp, Victoria, Australia. Figures 7, 8.1–8.7.

Other material examined.—Two specimens from slide L.C.V./6b (340 cm) and three from slide L.C.V./8 (360 cm); Holocene freshwater peat, Cobrico Swamp, Victoria, Australia.

Measurements.—Holotype: central body, 64 × 55 μm; process length up to 5 μm; spinules about 1–2 μm long. Range: central

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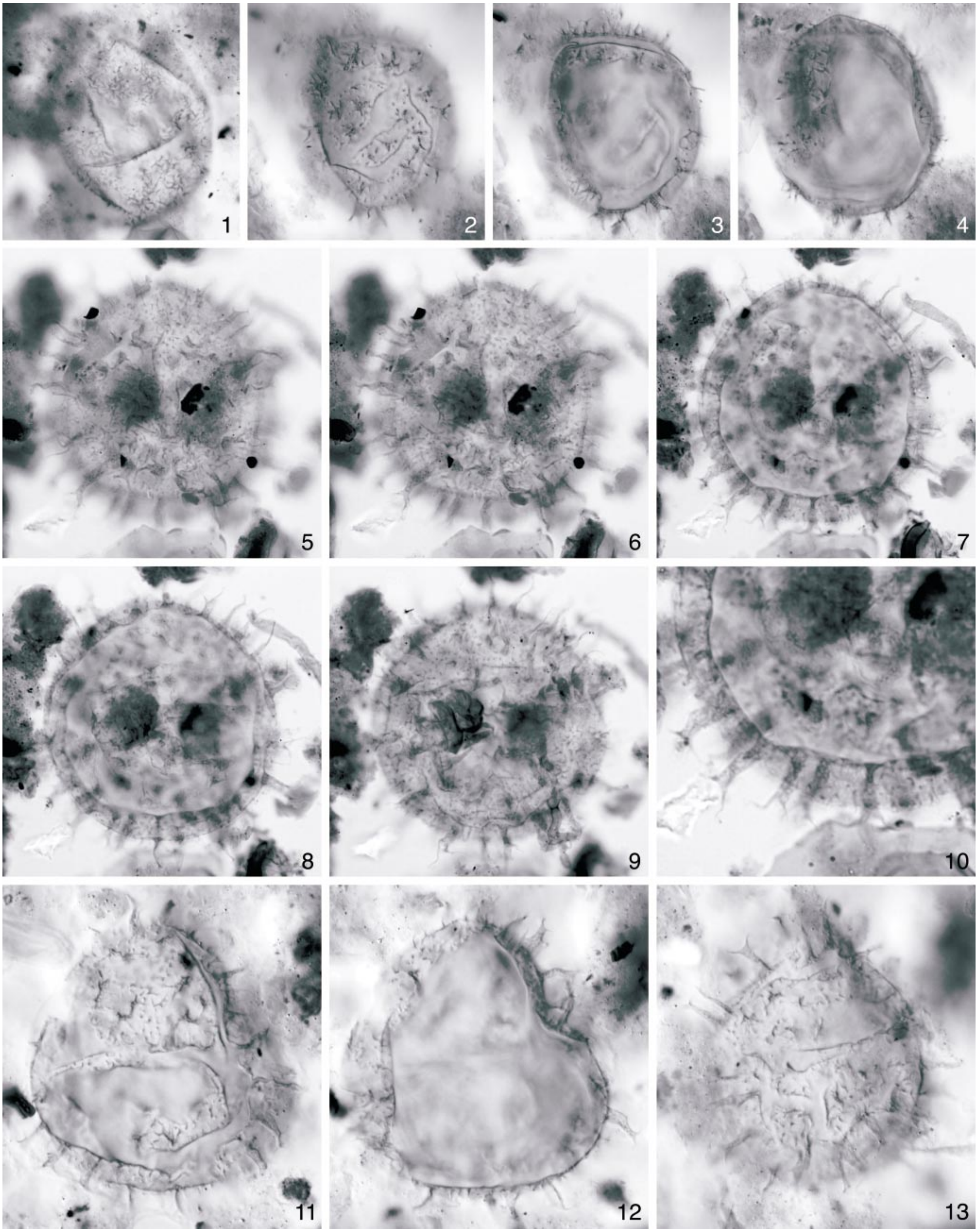
FIGURE *8*—Specimens of *Cobricosphaeridium* from the upper Holocene type locality of Cobrico Swamp, Victoria, Australia. Max. dia. = maximum diameter. *1–7,* Holotype of *Cobricosphaeridium hebes* Harland and Sarjeant, 1970 emend.; *1–6,* showing successively lower foci from upper through lower surface; *7,* an enlarged view of *3*; central body max. dia., 64 μm; MPK 968, slide L.C.V./6b, at depth of 340 cm; England Finder reference V33/2 (IGS label to right). *8–11,* Topotype of *Cobricosphaeridium hebes*; showing successively lower foci from upper through lower surface; central body max. dia., 59 μm; MPK 12668, slide L.C.V./6b, at depth of 340 cm; England Finder reference T31/0 (IGS label to right). *12–16, Cobricosphaeridium* sp. cf. *C. hebes*; showing successively lower foci from upper through lower surface; central body max. dia., 52 μm; MPK 12669, slide L.C.V./6b, at depth of 340 cm; England Finder reference D33/0 (IGS label to right). *17–20,* Holotype of *Cobricosphaeridium serpens* (Harland and Sarjeant, 1970) n. comb.; showing successively lower foci from upper through lower surface (see also Fig. *9.1*); central body max. dia., 57 μm; MPK 971, slide L.C.V./7a, at depth of 350 cm; England Finder reference Q40/0 (IGS label to right).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body maximum diameter, 48(53.5)64 μm; maximum process length, 3(4.4)6 μm; spinule length about 0.5–2.0 μm. Six specimens measured, all from the Cobrico Swamp, Victoria, Australia.

Discussion.—The opening in the wall is interpreted here as a simple split, and not an archeopyle as originally diagnosed. Indeed, no indication of tabulation was seen, and features originally interpreted as a poorly defined sulcus and cingulum (Harland and Sarjeant, 1970) were presumably irregularities in process distribution on some specimens. The central body dimensions of the holotype, at 64 × 55 μm, are substantially larger than those given by Harland and Sarjeant (1970; as 46 × 46 μm).

COBRICOSPHAERIDIUM sp. cf. C. HEBES Harland and Sarjeant, 1970 emended
Figures 7, 8.12–8.16

Description.—Central body spherical to sub-spherical, and has thin wall (less than 0.3 μm) with no visible stratification. Surface almost smooth, bearing processes up to 5 μm high and low ridges. Processes fairly regularly distributed, arise from convergence of radiating ridges at base, most bear spinules, and some expand distally as result of projecting spinules. Low (about 0.5 μm or less), solid ridges occur between process bases. These ridges have width of about 0.5 μm, are straight to slightly sinuous, and most fuse with adjacent ridges to form loosely vermiculate pattern. Occasional spinules up to 1 μm in length occur on ridges.

Dimensions.—Central body 52 × 50 μm, processes up to 5 μm long.

Discussion.—A single specimen was recorded on the type microscope slide of *Cobricosphaeridium hebes*. The specimen differs from *C. hebes* in the extensive development of low ridges rather than spinules between processes, but the nature of the processes is almost identical in both taxa. Furthermore, small, scattered spinules do occur on the low ridges of *C.* cf. *hebes*, and some spinules on *C. hebes* arise from low ridges. *Cobricosphaeridium* cf. *hebes* is considered a possible morphological end member of *C. hebes* and is transitional between the original concepts of the genera *Cobricosphaeridium* and *Aquadulcum*.

COBRICOSPHAERIDIUM HINOJALENSIS new species
Figures 11.12–11.21, 12, 13.1–13.4, 15.12, 15.14, 15.15

Diagnosis.—Central body spherical to ovoid, thin wall, surface nearly smooth to faintly vermiculate, sometimes bearing sparse spinules or hairs. Processes solid to membranous, flattened, usually expanded at base, usually acuminate to evexate, occasionally distally expanded but not conspicuously branched. Process bases elongate, may arise from single ridge or convergence of ridges.

Description.—Central body wall about 0.3 μm thick or less, colourless, no visible stratification between processes; surface nearly smooth, or has low (<0.5 μm) ridges forming coarsely vermiculate pattern, and may have sparsely distributed spinules and/or hairs. Processes always present, solid to membranous, up to about 5.5 μm long, flattened, have heterogeneous but simple morphology, usually expanded at base, and usually acuminate to evexate; some may be distally expanded, but are not conspicuously branched. Process bases elongate, up to 5 μm wide, may arise from single ridge or convergence of ridges. Some adjacent processes may be adjoined at base. Spinules and/or hairs when present are sparsely distributed between processes, up to about 1.5 μm long, have circular to elongate bases; surmount ridges in those specimens bearing vermiculate pattern. Aperture is a simple split extending about half way around body.

Etymology.—From Laguna Hinojales, the type locality.

Type.—Holotype: sample LH44b, at a depth of 92 cm; England Finder reference Z54/3; Laguna Hinojales core of the Mar Chiquita region, Buenos Aires province, eastern Argentina. Figures 11.16–11.19, 12.

Other material examined.—Nineteen specimens from the Holocene of Laguna Hinojales, eastern Argentina.

Measurements.—Holotype: central body maximum diameter, 56 μm; maximum process length, 5.5 μm. Range: central body maximum diameter, 51(58.9)73 μm; maximum process length, 2.5(3.7)5.5 μm. Twenty specimens measured. See also Figure 12.

Discussion.—*Cobricosphaeridium spiniferum* and *C.* cf. *spiniferum* (this study) have more densely distributed spinules, *Cobricosphaeridium* cf. *hebes* (this study) has a more complex and spinulose process morphology, *Cobricosphaeridium awendae* has more complex and membranous processes, and *Cobricosphaeridium*? *giganteum* has long and hollow processes.

COBRICOSPHAERIDIUM MYALUPENSE (Churchill and Sarjeant, 1962) new combination

Palaeohystrichophora myalupensis CHURCHILL AND SARJEANT, 1962, p. 38–40, figs. 5, 22, 23.

Aquadulcum myalupensis (CHURCHILL AND SARJEANT, 1962) HARLAND AND SARJEANT, 1970, p. 221–222.

Discussion.—This species was not observed in the present study, but photographs of the type material in Churchill and Sarjeant (1962) do not show compelling evidence of dinoflagellate affinity, and a reexamination of the holotype by Harland and Sarjeant (1970, p. 222) disclosed no recognizable archeopyle. Accordingly, this species is not considered a dinoflagellate. *Cobricosphaeridium myalupense* has been reported only from upper Holocene freshwater deposits of Myalup Swamp, Western Australia (Churchill and Sarjeant, 1962).

COBRICOSPHAERIDIUM PIKEAE (Churchill and Sarjeant, 1962) new combination

Palaeohystrichophora pikei CHURCHILL AND SARJEANT, 1962, p. 40, 41, figs. 6, 24.

Aquadulcum pikei (CHURCHILL AND SARJEANT, 1962) HARLAND AND SARJEANT, 1970, p. 222.

Discussion.—This species was not observed in the present study, but a photograph of the holotype in Churchill and Sarjeant (1962) shows no compelling evidence of dinoflagellate affinity, and a reexamination of the holotype by Harland and Sarjeant (1970, p. 222) revealed no recognizable archeopyle. Accordingly, this species is not considered a dinoflagellate. This species has been reported only from upper Holocene freshwater deposits of

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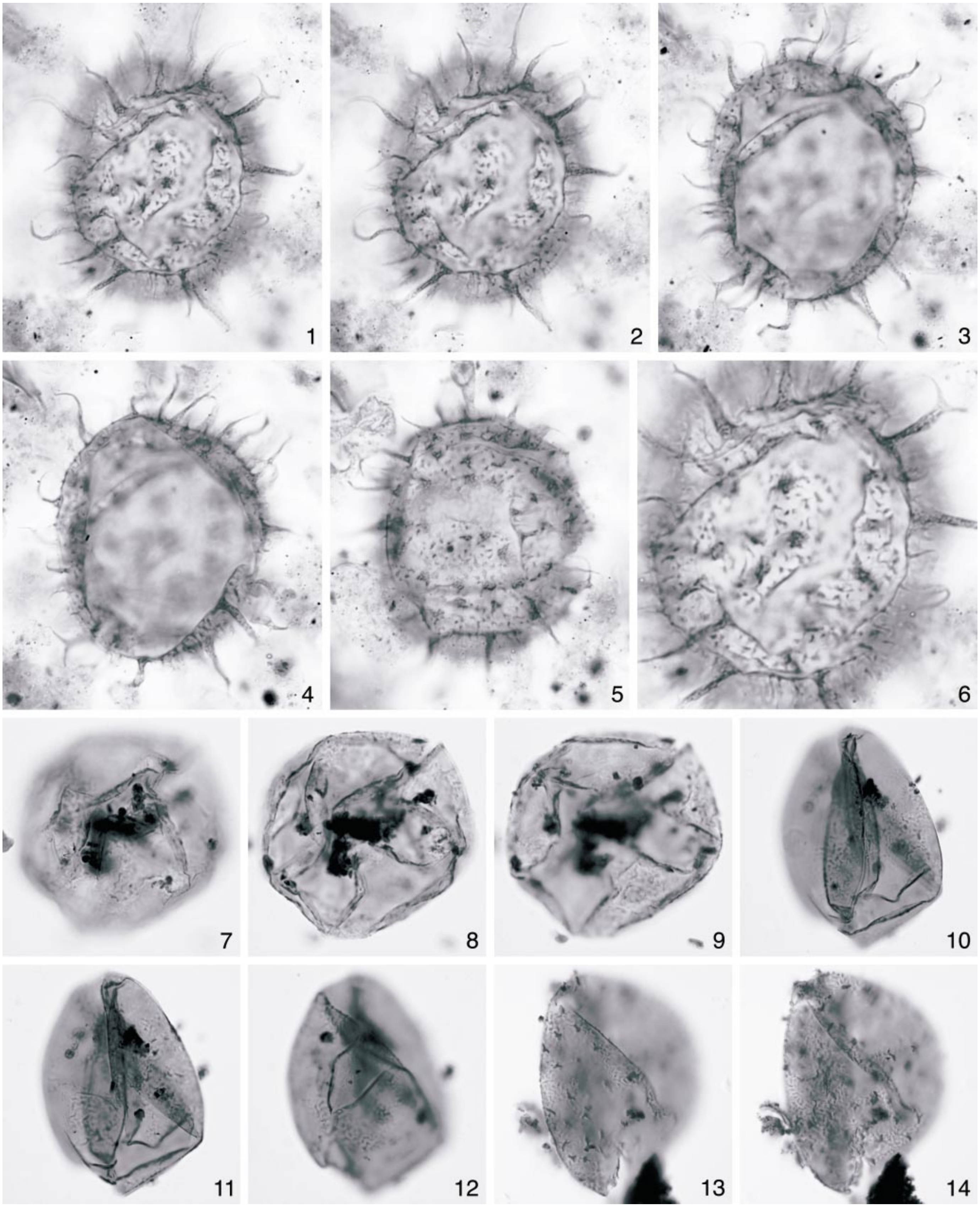
FIGURE 9—Specimens of *Cobricosphaeridium* from the upper Holocene type locality of Cobrico Swamp, Victoria, Australia. Max. dia. = maximum diameter. *1*, Holotype of *Cobricosphaeridium serpens* (Harland and Sarjeant, 1970) n. comb.; focus on lower surface (see also Fig. *8.17–8.20*); central body max. dia., 57 μm; MPK 971, slide L.C.V./7a, at depth of 350 cm; England Finder reference Q40/0 (IGS label to right). *2–4*, *Cobricosphaeridium hebes* Harland and Sarjeant, 1970 emend.; showing successively lower foci from upper through lower surface; central body max. dia., 52 μm; MPK 12670, slide L.C.V./6b, at depth of 340 cm; England Finder reference J31/0 (IGS label to right). *5–10*, Holotype of *Cobricosphaeridium spiniferum* subsp. *spiniferum* Harland and Sarjeant, 1970 emend.; *5–9*, showing successively lower foci from upper through lower surface; *10*, an enlargement of *7*; central body max. dia., 56 μm; MPK 969, slide L.C.V./1b, at depth of 150 cm; England Finder reference P44/0 (IGS label to right). *11–13*, *Cobricosphaeridium spiniferum* subsp. *spiniferum*; showing successively lower foci from upper through lower surface; central body max. dia., 49 μm; MPK 12671, slide L.C.V./5a, at depth of 320 cm; England Finder reference P37/1 (IGS label to right).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Myalup Swamp, Western Australia (Churchill and Sarjeant, 1962).

This species was named for Kathleen McWhae (née Pike), and the ending of the specific epithet has been corrected accordingly.

COBRICOSPHAERIDIUM SERPENS (Harland and Sarjeant, 1970) new combination
Figures 8.17–8.20, 9.1, 10.7–10.12

Aquadulcum serpens HARLAND AND SARJEANT, 1970, p. 221, pl. 21, figs. 7, 8, text-fig. 5.

Original diagnosis.—Peridinioid to sub-spherical central body bearing a dense ornamentation of vermiculae. Sulcus and cingulum clearly defined by lack of ornament. The cingulum is offset by an amount equal to half its own width. The archaeopyle was not seen. (Harland and Sarjeant, 1970, p. 221.)

Emended diagnosis.—Central body spherical to ovoidal; wall thin, colorless; surface smooth, bears low, solid ridges of irregular height fused to form vermiculate pattern. Small subcircular areas of more pronounced ornamentation occur fairly regularly over surface.

Emended description.—Wall colorless (heavily stained on holotype), about 0.3 μm or less in thickness (less than 0.3 μm on holotype), without visible stratification, and has smooth surface bearing low, solid ridges that fuse to form vermiculate pattern. Ridges mostly about 1.0 μm or less in height, and 0.5–1.0 μm wide. Ridges are of uneven height and some ridge crests rise to form small prominences or spinules. Some elements on periphery of specimen are up to 2.0 μm high and represent either ridges or spinules. Occasional isolated spinules occur between ridges. Small subcircular areas of more pronounced ornamentation with vaguely converging ridges occur fairly regularly over surface (see also Harland and Sarjeant, 1970, text-fig. 5). No indications of tabulation; aperture is split of variable length, which when developed opens half way around central body.

Type.—Holotype: MPK 971; L.C.V./7a, at depth of 350 cm; England Finder reference Q40/0 (IGS label to right); Holocene freshwater peat, Cobrico Swamp, Victoria, Australia. Figures 8.17–8.20, 9.1.

Other material examined.—Two specimens from the Holocene of Laguna Hinojales, eastern Argentina. Figure 10.7–10.12.

Measurements.—Holotype: central body, 57 × 48 μm; ridges mostly less than 1 μm high. Argentinean specimens: central body maximum diameter, 50–62 μm; ridge width up to 1 μm; ridge height up to 1 μm. Two specimens measured.

Discussion.—The original description was based on just two specimens (Harland and Sarjeant, 1970). Of these we have re-examined only the holotype. This specimen is the type of the genus *Aquadulcum*, which we synonymize with *Cobricosphaeridium*. *Cobricosphaeridium serpens* is here emended to take account of our interpretation that features originally considered to be a cingulum and sulcus are instead preservational folds of the body wall. The morphology of this species is reminiscent of *Cobricosphaeridium* cf. *hebes* of the present study, except that the latter has pronounced processes and coarser vermiculate ornament. The small areas of pronounced ornamentation on the holotype of *C. serpens*, also noted by Harland and Sarjeant (1970), suggest incipient process formation through localized convergence of ridges (the kind of development found in *C. hebes*). These ‘‘incipient processes’’ support our decision to transfer this species to the genus *Cobricosphaeridium*.

It should be noted that the central body dimensions of 57 × 48 μm are considerably larger than those given by Harland and Sarjeant (1970, as 45 × 37 μm).

The Argentinean specimens compare favorably with the holotype but have less prominent areas of pronounced ornamentation.

COBRICOSPHAERIDIUM SPINIFERUM Harland and Sarjeant, 1970 emended
Figures 7, 9.5–9.13, 10.1–10.6

Cobricosphaeridium spiniferum HARLAND AND SARJEANT, 1970, p. 218–220, pl. 21, figs. 3–6; text figs. 3, 4.

Emended diagnosis.—Central body spherical to broadly ovoidal, surface nearly smooth bearing processes and spinules and/or hairs. Processes unbranched and tapering to slender points, or bifurcate with or without secondary branching, or digitate; may have occasional small branches and/or spinules along main stem. Processes mostly about 4 μm or more in length, have smooth surface, some may have spongy internal structure for part of length; arise from circular to elongate bases. Small solid hairs or spinules occur between process bases.

Emended description.—Central body may be slightly more pointed at one pole, as in holotype. Surface nearly smooth, bearing processes and spinules and/or hairs. Wall thickness about 0.3 μm or less, no visible stratification between processes. Processes have very heterogeneous morphology, arise from circular to elongate bases, often becoming flattened for much of their length, may be unbranched and tapering to slender points, or may be bifurcate with or without secondary branching, or digitate, and may additionally have occasional small or incipient branches (often as spinules) along main stem. All variations are seen on holotype. Branching is typically asymmetrically developed. Surface of processes smooth, possibly with perforations. Nine out of ten specimens examined show spongy internal structure in some or all processes. Spongy structure is confined to base of stem in some specimens, occupies at least proximal half of stem in holotype, and occupies most of stem in another specimen. Processes 4–15 μm in length (mostly 6–11 μm on holotype), have a basal width of about 1.0 to 4.0 μm (about 1.5 to 4.0 μm on holotype), and on holotype are separated from adjacent process bases by about 2–6 μm. Small solid hairs or spinules occur between process bases. They vary in length from 1–5 μm (1.5–3.0 μm on holotype), are about 0.5–1.0 μm in basal diameter, circular to elongate or ridge-like in cross-section (circular on holotype), and are slightly expanded at base. Spinules rather unevenly distributed. On holotype, adjacent spinule bases are separated by about 1.0–2.0 μm.

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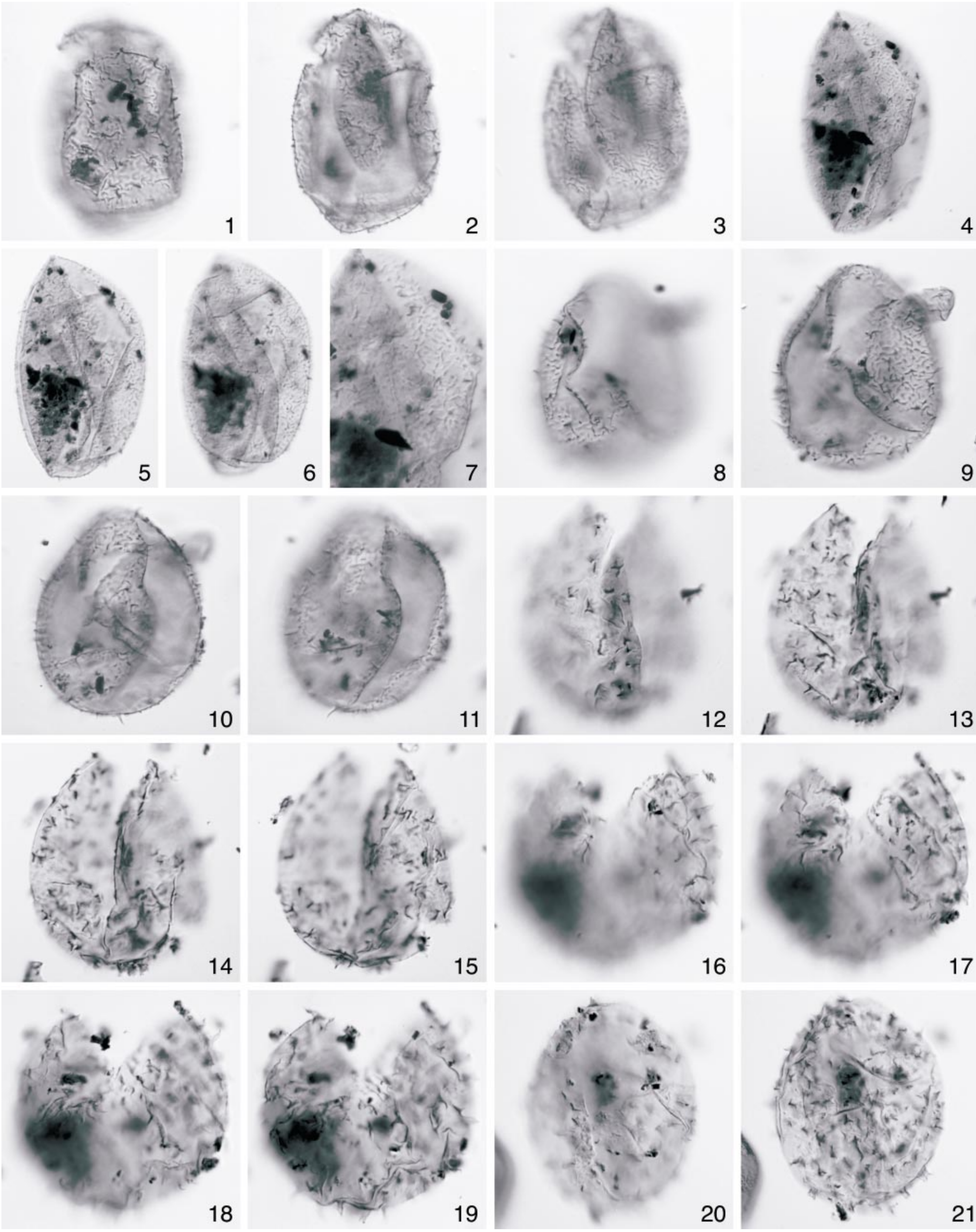
FIGURE *10*—Specimens of *Cobricosphaeridium* from the upper Holocene of Australia and mid Holocene of Argentina. Max. dia. = maximum diameter. *1–6*, Holotype of *Cobricosphaeridium spiniferum* subsp. *elegans* Harland and Sarjeant, 1970 emend. from the Cobrico Swamp, Victoria, Australia; *1–5*, showing successively lower foci from upper through lower surface; *6*, an enlargement of *1*; central body max. dia., 46 μm; MPK 970, slide L.C.V./5a, at depth of 320 cm; England Finder reference J32/0 (IGS label to right). *7–9*, *Cobricosphaeridium serpens* (Harland and Sarjeant, 1970) n. comb. from Laguna Hinojales, Argentina; showing successively lower foci from upper through lower surface; central body max. dia., 50 μm; sample LH44b; England Finder reference F48/4. *10–12*, *Cobricosphaeridium serpens* from Laguna Hinojales, Argentina; showing successively lower foci from upper through lower surface; central body max. dia., 62 μm; sample LH44b; England Finder reference F46/4. *13–14*, *Cobricosphaeridium* sp. 1 from Laguna Hinojales, Argentina; showing successively lower foci of upper and lower surface; central body max. dia., 68 μm; sample LH44d; England Finder reference J21/0.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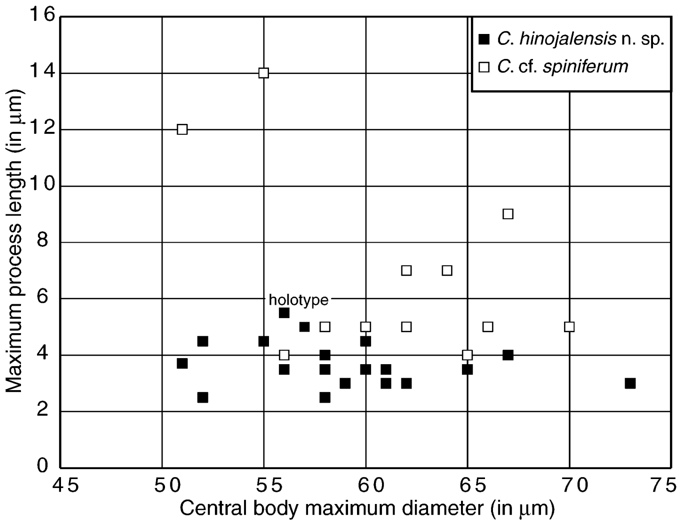

FIGURE 12—Dimensions of *Cobricosphaeridium hinojalensis* n. sp. and *Cobricosphaeridium* sp. cf. *C. spiniferum* Harland and Sarjeant, 1970 emend. from Laguna Hinojales, eastern Argentina.

No indications of tabulation; a short split in wall of holotype represents damage or incipient opening.

Type.—Holotype: MPK 969; L.C.V./1b, at depth of 150 cm; England Finder reference P44/0 (IGS label to right); Holocene freshwater peat, Cobrico Swamp, Victoria, Australia. Figures 7, 9.5–9.10.

Other material examined.—Nine specimens from slides L.C.V./6b (340 cm), L.C.V./5a (320 cm) and L.C.V./8 (360 cm); Holocene freshwater peat, Cobrico Swamp, Victoria, Australia.

Measurements.—Holotype: central body, 56 × 52 μm; process length mostly 6–11 μm. Range: central body maximum diameter, 46(52.0)60 μm; maximum process length, 6–15 μm. Ten specimens measured.

Discussion.—A diagnosis was not given for this species by Harland and Sarjeant (1970), although they provided diagnoses for their two subspecies, *Cobricosphaeridium spiniferum* subsp. *spiniferum* and *Cobricosphaeridium spiniferum* subsp. *elegans*. Both of these subspecies were considered by them to have an apical archeopyle and faint indications of sulcus and cingulum. An archeopyle was not recognized in our reexamination, and indications of sulcus and cingulum are here considered to be folds in the wall.

According to Harland and Sarjeant (1970) these two subspecies could be distinguished readily and consistently on account of their differing process morphology: *C. spiniferum* subsp. *elegans* having longer and more delicate processes than *C. spiniferum* subsp. *spiniferum*. Our own observations are restricted to the holotypes of these subspecies and to eight other specimens on the type slides that broadly resemble them. The two holotypes have clearly different morphologies, but the topotypes were less easy to identify to subspecific level, with two additional specimens appearing transitional between *C. spiniferum* subsp. *spiniferum* and *C. hebes*. Although not mentioned by Harland and Sarjeant (1970), the holotypes of both subspecies have processes whose interiors become spongy towards their base. However, this feature is variably developed on most topotype specimens we observed, and not developed on one of the topotypes. It is clear that more material from the type area needs to be examined in order to clarify the range of morphology exhibited by *Cobricosphaeridium spiniferum*. Pending such a reexamination, we recognize the two subspecies erected by Harland and Sarjeant (1970) and clarify the morphology of their respective holotypes.

COBRICOSPHAERIDIUM SPINIFERUM subsp. SPINIFERUM Harland and Sarjeant, 1970 emended
Figures 7, 9.5–9.13

Cobricosphaeridium spiniferum subsp. *spiniferum* HARLAND AND SARJEANT, 1970, p. 218–219, pl. 21, figs. 3, 6; text fig. 3.

Original diagnosis.—A *Cobricosphaeridium* having a subspherical central body bearing two types of processes. The first are long, approximately one-quarter of the cyst diameter, slender, tapering to cylindrical; they may be erect or curved, with their distal extremities evexate to digitate and foliate, occasionally forked. The base and shank of each process is ornamented with granules. The processes of the second type are short, approximately one-tenth of the cyst diameter, erect, cylindrical, slender and also may be forked at their tips. Cingulum and sulcus are present, delineated by faint upraised sutures and alignment of processes; tabulation not otherwise determinable. Archaeopyle apical. (Harland and Sarjeant, 1970, p. 218.)

Emended diagnosis.—A subspecies of *Cobricosphaeridium spiniferum* with processes mostly about 4–11 μm long and with a basal width of about 1.5 to 4.0 μm.

Type.—As for the species. Figures 7, 9.5–9.10.

Measurements.—Holotype: central body, 56 × 52 μm; process length mostly 6–11 μm.

Discussion.—Harland and Sarjeant (1970) noted that spinules may be forked at their tips. Our observations of the holotype show that most, if not all, spinules are unbranched, although it was not possible to discern whether any have forked tips. The structures interpreted by Harland and Sarjeant (1970) as a cingulum and sulcus are here considered to be folds in the body wall. It should be noted that the central body dimensions of 56 × 52 μm are considerably larger than those given by Harland and Sarjeant (1970, as 49 × 47 μm).

COBRICOSPHAERIDIUM SPINIFERUM subsp. ELEGANS Harland and Sarjeant, 1970 emended
Figures 7, 10.1–10.6

Cobricosphaeridium spiniferum subsp. *elegans* HARLAND AND SARJEANT, 1970, p. 219–220, pl. 21, figs. 4, 5; text fig. 4.

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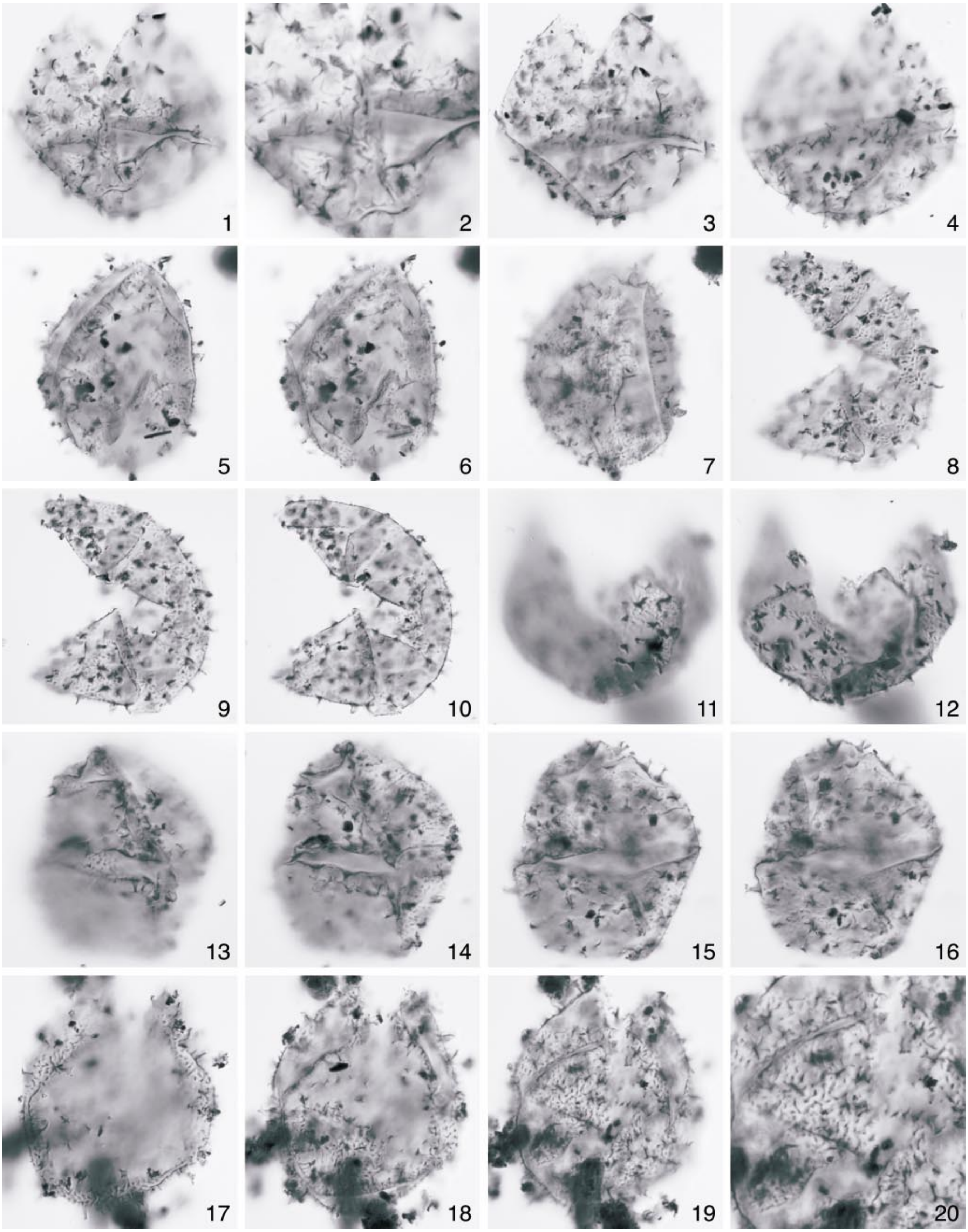
FIGURE *11*—Specimens of *Cobricosphaeridium* from the mid Holocene of Laguna Hinojales, Argentina. Max. dia. = maximum diameter. *1–11, Cobricosphaeridium* sp. 1. *1–3,* Specimen showing successively lower foci from upper through lower surface; central body max. dia., 62 μm; sample LH44b; England Finder reference F47/1. *4–7,* Specimen showing *4–6,* successively lower foci from upper through lower surface; *7,* an enlargement of *4*; central body max. dia., 70 μm; sample LH44d; England Finder reference X47/0. *8–11,* Specimen showing successively lower foci from upper through lower surface; note the presence of sparse, narrow, tapering processes up to 5 μm long; central body max. dia., 56 μm; sample LH44b; England Finder reference S51/1. *12–21, Cobricosphaeridium hinojalensis* n. sp. *12–15,* Specimen showing successively lower foci from upper through lower surface; central body max. dia., 58 μm; sample LH49d; England Finder reference Z49/4. *16–19,* Holotype showing successively lower foci from upper through lower surface; central body max. dia., 56 μm; sample LH44b; England Finder reference Z54/3. *20–21,* Specimen showing upper surface and mid focus respectively; central body max. dia., 56 μm; sample LH49d; England Finder reference Z52/3.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Original diagnosis.—A subspecies of *Cobricosphaeridium spiniferum* in which the conspicuous processes are longer, more flexible and delicate than those of typical specimens of the species. (Harland and Sarjeant, 1970, p. 219.)

Emended diagnosis.—A subspecies of *Cobricosphaeridium spiniferum* in which processes are mostly 9–15 μm in length and about 1.5 to 3.0 μm in basal width.

Emended description.—Central body broadly ovoidal; surface nearly smooth, bears processes and spinules and/or hairs. Wall about 0.3 μm thick or less, no visible stratification between processes. Processes may be unbranched and taper to slender points, or may be bifurcate, and may additionally have occasional small or incipient branches (often as spinules) along main stem. Branching is typically asymmetrically developed. Surface of processes smooth, possibly with perforations, but internal structure of processes is spongy for at least proximal half of stem, and sometimes extending nearly entire length. Processes mostly 9–15 μm in length, have a basal width of about 1.5 to 3.0 μm, and are separated from adjacent process bases by about 2–7 μm. Process bases are subcircular to elongate in cross section. Small solid hairs or spinules occur between process bases. They vary in length from 1 to 5 μm, and most taper to fine points but some may be blunt. Spinule bases are about 1.0 μm or less in diameter, and are circular to elongate or ridge-like. Adjacent bases are separated by about 1.0–2.0 μm and are rather unevenly distributed. No indications of tabulation; a short split in the wall either represents damage or is an incipient opening. Description based on holotype alone.

Type.—Holotype: MPK 970; L.C.V./5a, at depth of 320 cm; England Finder reference J32/0 (IGS label to right); Holocene freshwater peat, Cobrico Swamp, Victoria, Australia. Figures 7, 10.1–10.6.

Measurements.—Holotype: central body, 46 × 41 μm; process length mostly 9–15 μm.

Discussion.—Structures interpreted by Harland and Sarjeant (1970) as a cingulum and sulcus are here considered to be folds in the body wall. The diagrammatic illustration of the holotype in Harland and Sarjeant (1970, fig. 4) shows minute secondary bifurcation on one of the processes. Secondary bifurcation was not definitively seen during reexamination of the holotype. It should be noted that the central body dimensions of 46 × 41 μm are considerably larger than those given by Harland and Sarjeant (1970, as 41 × 35 μm).

COBRICOSPHAERIDIUM sp. cf. C. SPINIFERUM Harland and Sarjeant, 1970

Figures 12, 13.5–13.20, 14, 15.1–15.11, 15.13

Material examined.—Thirteen specimens from the Holocene of Laguna Hinojales, eastern Argentina.

Measurements.—Central body maximum diameter, 51(61.3)70 μm; standard deviation, 5.5; maximum process length, 4(6.8)14 μm; standard deviation, 3.2. Twelve specimens measured.

Discussion.—This form is similar to *Cobricosphaeridium spiniferum* in overall morphology and wide range of variability. Long-processed forms particularly resemble *Cobricosphaeridium spiniferum elegans* (Fig. 14.9–14.14). However, the processes of the Argentinean specimens rarely exhibit a spongy interior, a feature common in the Australian type material. The exception is a single specimen whose long processes show some indications of spongy development (Fig. 14.11). Until the taxonomic significance of spongy process development is better understood, the Argentinean specimens are assigned only tentatively to *Cobricosphaeridium spiniferum*.

COBRICOSPHAERIDIUM YANCHEPENSE (Harland and Sarjeant, 1970) new combination

Organism no. 2. CHURCHILL AND SARJEANT, 1962, p. 50, figs. 8, 35.
Aquadulcum? *yanchepense* (CHURCHILL AND SARJEANT, 1962) HARLAND AND SARJEANT, 1970, p. 222, 223, pl. 22, fig. 3.

Discussion.—This species was not observed in the present study, having been reported only from Holocene freshwater deposits of Western Australia (Churchill and Sarjeant (1962, as Organism no. 2). It was formally described by Harland and Sarjeant (1970) exclusively using Churchill and Sarjeant's (1962) original material. Churchill and Sarjeant (1962) did not find conclusive evidence of dinoflagellate affinity, but Harland and Sarjeant (1970) reported the presence of a sulcus, cingulum, and probable apical archeopyle. Illustrations, which were given only for the holotype (Churchill and Sarjeant, 1962, figs. 8, 35; Harland and Sarjeant, 1970, pl. 22, fig. 3.), show no convincing evidence of dinoflagellate affinity. The heterogeneous process morphology, however, is typical for *Cobricosphaeridium*. Hence, the species is here transferred to this genus.

COBRICOSPHAERIDIUM? GIGANTEUM McMinn, 1991

Cobricosphaeridium giganteum MCMINN, 1991, p. 280, pl. 4, figs. 1–12. MCMINN, BOLCH, AND HALLEGRAEFF, 1992, p. 315, 316, pl. 1, fig. 1.

Discussion.—*Cobricosphaeridium*? *giganteum* was diagnosed as having solid processes (McMinn, 1991, p. 280), but they are hollow judging from McMinn's excellent photomicrographs. Because of this doubt concerning the process morphology, the assignment of this species to *Cobricosphaeridium* is therefore questioned. McMinn's illustrations also suggest that the central body wall is considerably thinner than the 1 μm stated in the original description.

This species was originally described from modern estuarine sediments of New South Wales, Australia, where its distribution shows it to be confined to salinities between 15 and 25 psu (McMinn, 1991). Live specimens were subsequently incubated and found to be the eggs of an unidentified crustacean, almost certainly a copepod species (McMinn et al., 1992). *Cobricosphaeridium*? *giganteum* was not observed in the present study.

COBRICOSPHAERIDIUM? OVATUM (Gao, He, and Qiao, 1992) new combination

Aquadulcum ovatum GAO, HE, AND QIAO, 1992, p. 48, 49, 61, pl. 13, figs. 18–20.

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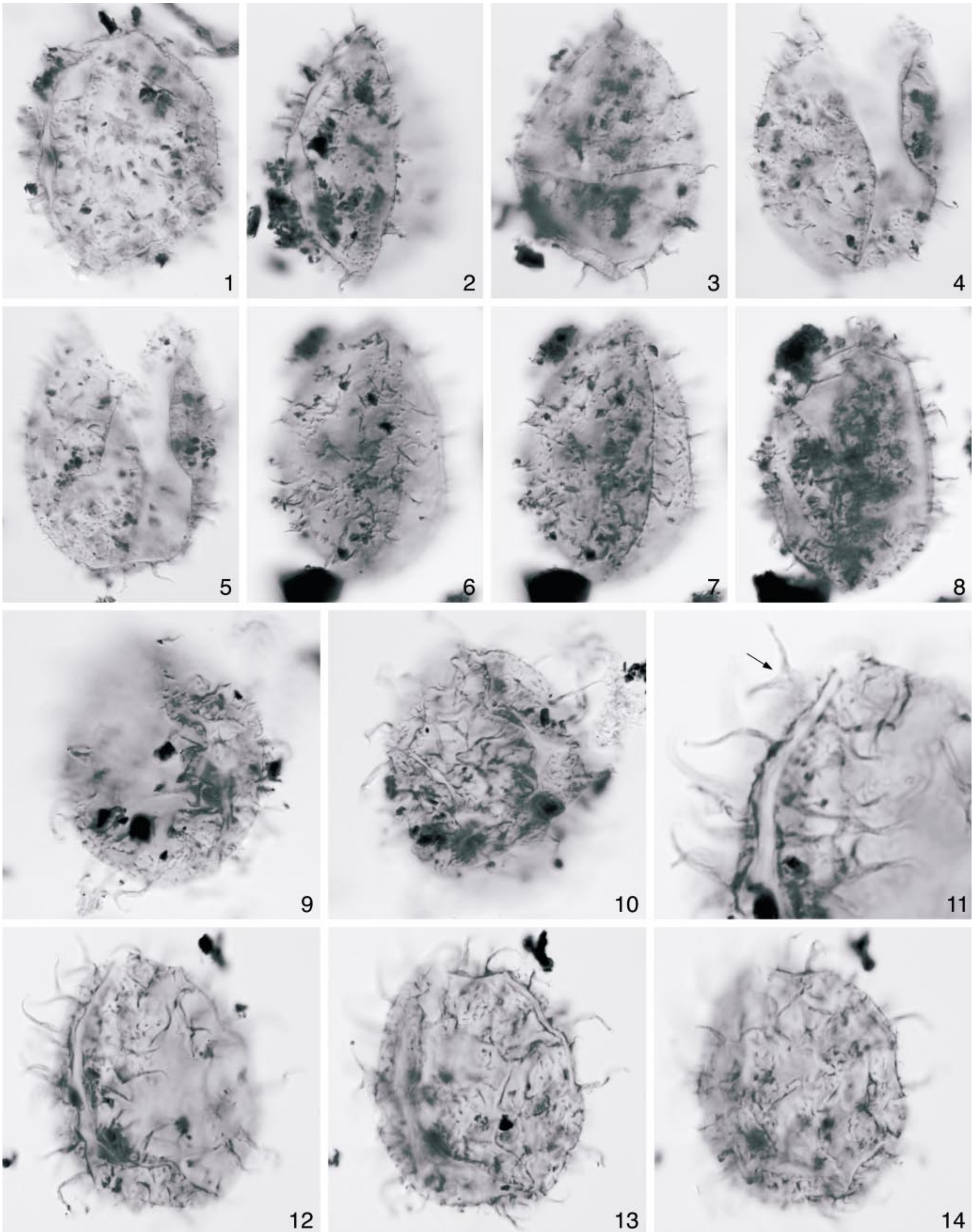
FIGURE *13*—Specimens of *Cobricosphaeridium* from the mid Holocene of Laguna Hinojales, Argentina. Max. dia. = maximum diameter. *1–4*, *Cobricosphaeridium hinojalensis* n. sp., showing successively lower foci from upper through lower surface; *2*, an enlargement of *1*; central body max. dia., 51 μm; sample LH49c; England Finder reference S25/0. *5–20*, *Cobricosphaeridium* sp. cf. *C. spiniferum* Harland and Sarjeant, 1970 emend. *5–7*, Specimen showing successively lower foci from upper through lower surface; central body max. dia., 62 μm; sample LH49d; England Finder reference O60/2. *8–10*, Specimen showing upper surface, slightly lower focus, and mid focus, respectively; central body max. dia., 85 μm; sample LH44d; England Finder reference Y15/0. *11–12*, Specimen showing upper surface and slightly lower focus, respectively; central body max. dia., 70 μm; sample LH44b; England Finder reference W21/3. *13–16*, Specimen showing successively lower foci from upper surface to mid focus; central body max. dia., 56 μm; sample LH44b; England Finder reference Y53/0. *17–20*, Specimen showing successively lower foci from upper through lower surface; *20*, an enlargement of *19*; central body max. dia., 70 μm; sample LH44d; England Finder reference W16/0.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Discussion.—This species, reported from the Maastrichtian (Upper Cretaceous) of China, was not observed in the present study. Although Gao et al. (1992) described it as having a Type (AtI3Pa) archeopyle, their illustrations show no clear evidence of dinoflagellate affinity. This species is transferred provisionally to the genus *Cobricosphaeridium* owing to the apparent absence of processes, and pending re-study of the type material.

COBRICOSPHAERIDIUM? VERMICULATUM (Song *in* Song, Guan, Li, Zheng, Wang, and Hu, 1985) new combination

Aquadulcum? *vermiculatum* SONG *in* SONG, GUAN, LI, ZHENG, WANG, AND HU, 1985, p. 39, 40, pl. 2, figs. 9, 10.

Original description.—Egg-shaped, wall thick and has two layers. Surface of wall is densely covered with small wrinkles, among which are short stick- or worm-like raised patterns, of different size; patterns can be aligned in rows. Focusing down [through specimen], it appears concave. Cingulum and sulcus can be seen. Sulcus is wide and clear from one side to the other; cingulum generally narrower, not as clear as the sulcus. In cingular area there is no wrinkled pattern. At the top there is an opening or archeopyle; if an archeopyle then it is apical in position. The body size is 53×47 μm. The sulcus is as wide as 10 μm.

The wrinkled pattern of this new species is not the same as for others previously described. For example, the wrinkled pattern of *A. serpens* is much finer. The stick-like ornament is aligned only along the cingulum in *A.*? *yanchepense*, and the ornament in *A. pikei* has short thorny wrinkles. (Translated from Song *in* Song et al., 1985, p. 39, 40.)

Discussion.—This species was not observed in the present study, and is known only from Cenozoic deposits of the East China Sea (Song et al., 1985). The single illustrated specimen has a vermiculate ornament and no apparent evidence of dinoflagellate affinity. Our assignment to *Cobricosphaeridium* is questionable because this species does not possess distinct processes, and it is not known if the ''stick- or worm-like raised patterns'' on this species represent discrete or rudimentary processes.

COBRICOSPHAERIDIUM sp. 1
Figures 10.13–10.14, 11.1–11.11

Description.—Central body ovoidal, wall colorless, thickness about 0.3 μm or less, without visible stratification. Smooth surface bears low, sinuous ridges of 0.5–1.0 μm maximum width, and 0.5–1.0 μm maximum height. Ridges have variable width and height; some ridge crests rise to form small prominences or spinules. Ridges fuse to form a vermiculate to irregularly and incompletely reticulate pattern. Granules and spinules are randomly interspersed between ridges, and arise from bases of irregular shape. Also present are short processes 2.0–5.0 μm in length, that arise from single isolated ridges or convergence of pronounced ridges. Processes solid, blunt-tipped or tapering, and may be flattened, and have a scattered distribution separated by 4.0–6.0 μm at base. Aperture is a simple split.

Material examined.—Five specimens from the Holocene of Laguna Hinojales, eastern Argentina.

Dimensions.—Central body maximum diameter 56–70 μm, maximum process length 2.0–5.0 μm. Five specimens measured.

Discussion.—Specimens differ from *C. serpens* in bearing short processes, thereby supporting the synonymy of *Aquadulcum* with *Cobricosphaeridium*. Some specimens (e.g., Fig. 11.4–11.6) have rudimentary acuminate processes arising principally from short, isolated ridges, showing a transitional ornamentation to species without ridges.

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FIGURE *14*—Specimens of *Cobricosphaeridium* from the mid Holocene of Laguna Hinojales, Argentina. Max. dia. = maximum diameter. *1–8, Cobricosphaeridium* sp. cf. *C. spiniferum* Harland and Sarjeant, 1970 emend. *1,* Specimen showing upper surface; central body max. dia., 63 μm; sample LH49d; England Finder reference X59/0. *2–3,* Specimen showing upper and lower surface, respectively; central body max. dia., 64 μm; sample LH49d; England Finder reference E51/4. *4–5,* Specimen showing upper surface and mid focus, respectively; central body max. dia., 67 μm; sample LH49d; England Finder reference T49/2. *6–8,* Specimen showing upper surface, mid focus, and lower surface, respectively; central body max. dia., 62 μm; sample LH44d; England Finder reference X25/4. *9–14, Cobricosphaeridium* sp. cf. *C. spiniferum* subsp. *elegans* Harland and Sarjeant, 1970 emend. *9–10,* Specimen showing upper and surfaces, respectively; central body max. dia., 55 μm; sample LH49d; England Finder reference F59/0. *11–14,* Specimen showing *11–12,* upper surface; *13,* mid focus; *14,* lower surface; *11,* shows wall detail including bifurcate process (arrowed) with spongy internal development; central body max. dia., 51 μm; sample LH49d; England Finder reference G60/0.

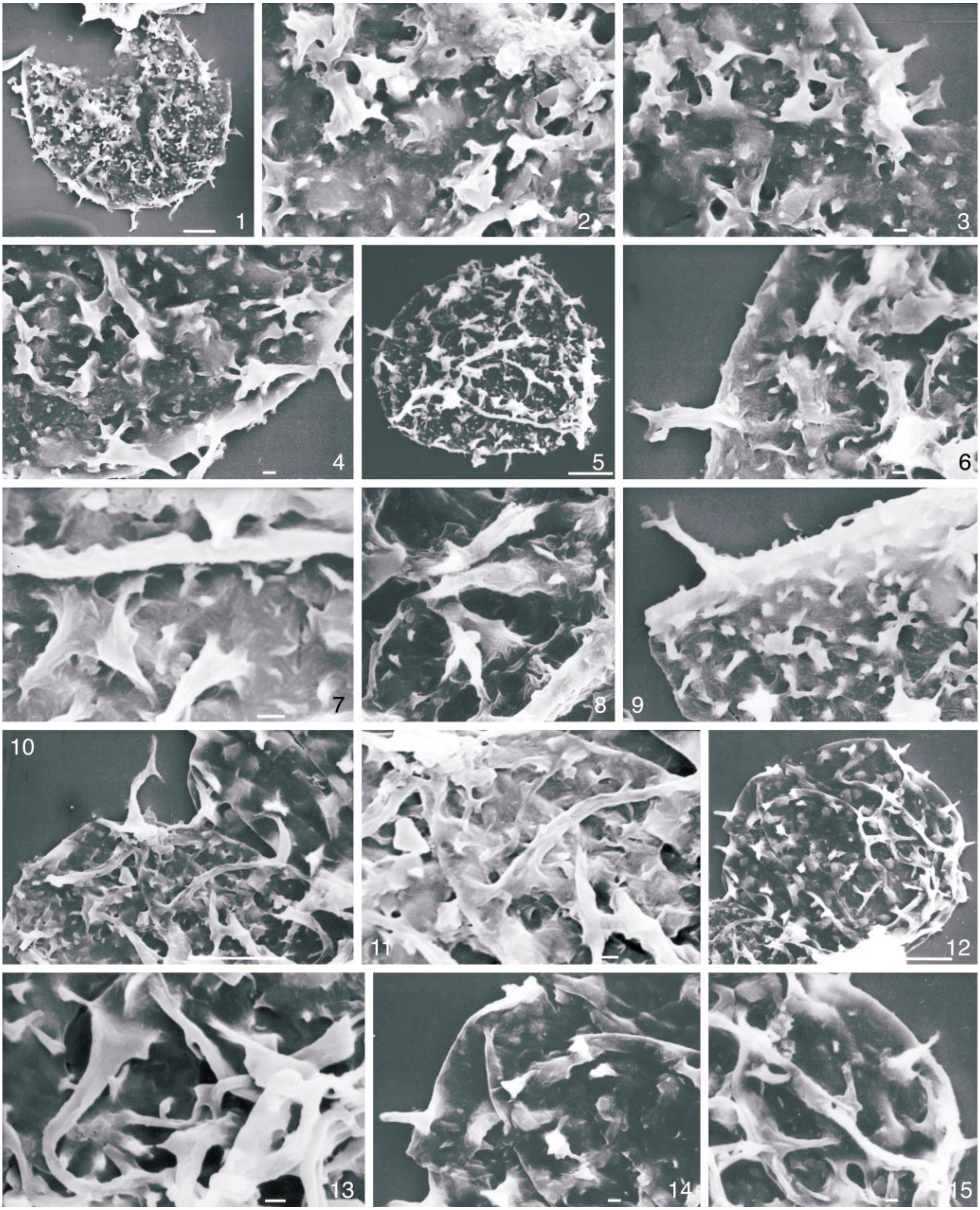
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FIGURE *15*—SEM images of *Cobricosphaeridium* specimens from the mid Holocene of Laguna Hinojales, Argentina. All from sample M49. Scale bars 10 μm for *1, 5, 10, 12*; and scale bars 1 μm for the remainder. *1–11, 13, Cobricosphaeridium* sp. cf. *C. spiniferum* Harland and Sarjeant,1970 emend. *1–4,* Specimen showing *1,* portrait; *2–4,* details of wall surface. *5–8,* Specimen showing *5,* portrait; *6–8,* details of wall surface. *9,* Details of wall surface of a different specimen. *10, 11, 13, Cobricosphaeridium* sp. cf. *C. spiniferum* subsp. *elegans* Harland and Sarjeant, 1970 emend. *10, 11,* Specimen showing portrait and detail of wall surface, respectively. *13,* Details of wall surface of a different specimen. *12, 14, 15, Cobricosphaeridium hinojalensis* n. sp., specimen showing *12,* portrait; *14–15,* details of wall surface.