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NEW DINOFLAGELLATE CYST AND INCERTAE SEDIS TAXA FROM THE PLIOCENE OF NORTHERN BELGIUM, SOUTHERN NORTH SEA BASIN

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ABSTRACT—New dinoflagellate cyst taxa have been recovered from Pliocene deposits in the Antwerp area of Belgium, where a detailed analysis of the Kattendijk and Lillo formations has yielded a diverse dinoflagellate record for the southern margin of the North Sea Basin. Four new species and two new genera of dinoflagellate cysts are recognized: the gonyaulacaceans *Spiniferites coniconcavus* n. sp. and *Pyxidinopsis braboi* n. sp., the goniodomacean *Desotodinium wrennii* n. gen. and sp., and the protoperidiniacean *Scaldecysta doelensis* n. gen. and sp. The protoperidiniacean genus *Barssidinium* Lentin, Fensome, and Williams, 1994 has been emended from new observations on the tabulation of *Barssidinium pliocenicum* (Head, 1993) Head, 1994a emend. The excellent preservation of the Belgian material accounts for these new observations. *Barssidinium wrennii* Lentin, Fensome, and Williams, 1994 is considered a taxonomic junior synonym of *Barssidinium pliocenicum* (Head, 1993) Head, 1994a, which thus becomes the correct name for the type of the genus. The new marine incertae sedis palynomorph *Waaslandia geminifera* n. gen. and sp. is also proposed.

INTRODUCTION

IN BELGIUM, marine deposits of Pliocene age are restricted to the northern part of the country where they represent shallow-water deposition along the southern margin of the North Sea Basin (Fig. 1). These entirely subsurface deposits consist mainly of glauconitic sands with variable clay content. Shells are abundant, usually in distinct layers. Exposures are often temporary and are revealed mostly during major expansion works in Antwerp Harbor. Studies on the Belgian Pliocene by de Heinzelin (1950a, 1950b, 1955) and Laga (1972) have given rise to a robust lithostratigraphy (De Meuter and Laga, 1976; Laga et al., 2002) (Fig. 2). Several paleontological studies have been performed on these deposits, notably mollusks (Janssen and King, 1988) and foraminifers (De Meuter and Laga, 1976). The litho- and biostratigraphy of these units are reviewed in Louwye et al. (in press). Recent construction of the Verrebroek and Deurganck docks, near Doel in the Antwerp Harbor, has exposed two large sections of the Pliocene Kattendijk and Lillo formations. These units were sampled from both exposures for dinoflagellate cyst analysis.

The Kattendijk Formation was defined by de Meuter and Laga (1976, p. 137) as dark-gray to greenish-gray, fine- to medium-grained, glauconitic sands, with shells that are usually dispersed but sometimes concentrated in layers. A gravel of rounded quartz and flints, with sharks' teeth, phosphatic nodules, and rounded bones occurs at the base of the unit. In our sections, the base of the Kattendijk Formation was not exposed, although the deposits otherwise conform to De Meuter and Laga's description. The Kattendijk Formation represents a single depositional sequence and its age is between about 5.0 Ma and 4.7–4.4 Ma (early Early Pliocene) in our sections based on evidence from dinoflagellate cysts (Louwye et al., in press).

The Lillo Formation has been subdivided by De Meuter and Laga (1976, p. 137) into the following members, in ascending order: Luchtbal Sands, Oorderen Sands, Kruisschans Sands, Merksem Sands, and Zandvliet Sands (Fig. 2). The Luchtbal Sands Member is apparently absent from our exposures (Fig. 3). The base of the Lillo Formation is instead represented by the informally designated Basal Shelly Unit of Louwye et al. (in press), which rests unconformably upon the Kattendijk Formation and is overlain conformably by the Oorderen Sands Member. This latter member passes gradually into the clay-rich facies that we assign to the Kruisschans Sands Member. The overlying Merksem Sands and Zandvliet Sands members are not present in our exposures. The Lillo Formation therefore represents a single depositional sequence in our sections, and its age is between about 4.2 and 2.6 Ma (late Early Pliocene and/or early Late Pliocene) based on palynological evidence (Louwye et al., in press).

Reworked dinoflagellate cysts, encountered in Pliocene sediments from the Antwerp area, were illustrated for the first time in a regional pollen study by Hacquaert (1961). Only during the past few years have in situ dinoflagellate cysts been investigated from the Pliocene of Belgium (Louwye and Laga, 1998; Vandenberghe et al., 2000). Dinoflagellate cysts from the Verrebroek Dock and Deurganck Dock exposures in Antwerp Harbor were recently studied in order to resolve sequence stratigraphic questions (Louwye et al., in press). The dinoflagellate cysts were found to be exceptionally well preserved and diverse, with more than 70 taxa recorded. During that study, several new species were encountered. We now formally describe these taxa and assess their taxonomic, stratigraphic, and ecological significance.

MATERIAL AND METHODS

Materials.—Fifteen samples from the Verrebroek Dock exposure and 10 from the Deurganck Dock exposure, near Doel (51°32′N, 4°26′E), were analyzed for marine organic-walled palynomorphs (Fig. 3). Additionally, the holotype of *Barssidinium pliocenicum* (Head, 1993) Head, 1994a from the Upper Pliocene St. Erth Beds of southwestern England was reexamined, as was the illustrated specimen of Gen. et sp. indet. of Head (1998a) from the Upper Pliocene Red Crag Formation of eastern England.

Methods.—For each sample, 75 or 100 grams of dry sediment were processed using hot 10 percent HCl, hot 38 percent HF, ultrasound treatment of the residue for 15 seconds, sieving on a 20 μm Nytal nylon screen, and staining with safranin-O. The residue was mounted on microscope slides using glycerine jelly. Neither oxidation nor alkali treatments were applied. Details are given in Louwye et al. (in press).

Selected duplicate residues containing *Barssidinium pliocenicum* were oxidized for 15 seconds with fuming nitric acid and then washed with KOH before mounting on slides. This treatment served to assess the effects of partial oxidation on the morphology of *Barssidinium pliocenicum*.

Specimens were examined under a Leica DMR microscope and photographed with a Leica DC3 digital camera.

Repository.—Slides containing all illustrated material from Verrebroek Dock and Deurganck Dock, including holotypes, are

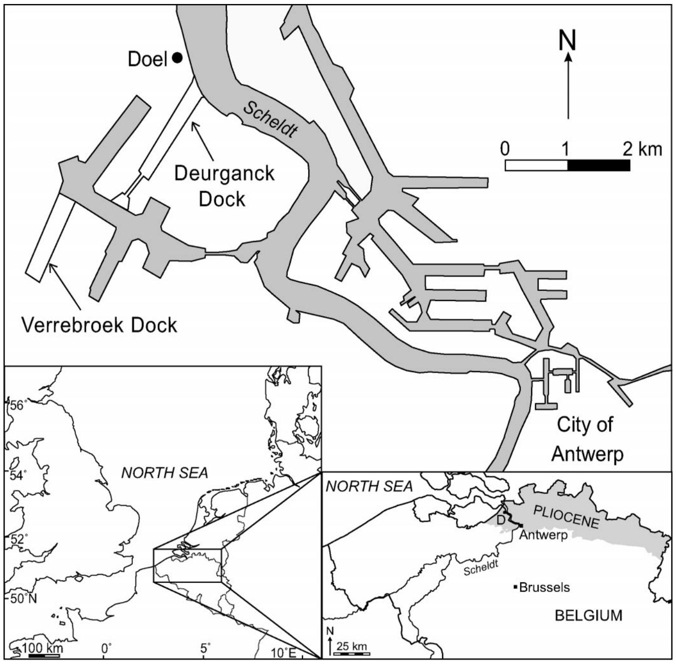

FIGURE 1—Location of the study area in northern Belgium. Lower right box shows distribution of the Pliocene deposits (shaded) in Belgium. D = Doel, village near the studied exposures. Upper box shows Antwerp Harbor, including the Deurganck Dock and Verrebroek Dock localities and the village of Doel.

Lithostratigraphy		Sub-Series
Lillo Formation	Zandvliet Sands Mbr	Upper Pliocene
	Merksem Sands Mbr	
	Kruisschans Sands Mbr	
	Oorderen Sands Mbr	Lower Pliocene
	Luchtbal Sands Mbr	
Kattendijk Formation		

FIGURE 2—Lithostratigraphy of the Pliocene of Belgium, after de Meuter and Laga (1976) and Laga et al. (2002).

stored at the Royal Belgian Institute of Natural Sciences, Brussels under the registration numbers IRScN b4253 to IRScN b4257.

Terminology.—The suprageneric classification of Fensome et al. (1993) is used except where stated. Kofoidian plate labelling is generally used, although modified labelling and terminology for the hypocyst follows Head (1998b), with the exception that we do not use the term ''antapical homologs.'' Strictly, only a single plate that is no longer in first antapical position can be considered as the direct homolog of the first antapical plate (Fensome et al., 1993, p. 254). We use the terms left and right first antapical plates (1$''''$l and 1$''''$r) for two plates in the antapical series that seemingly originate from one ancestral antapical plate. These are equivalent to the left and right first antapical homologs (*1$''''$l and *1$''''$r) of Head (1998b).

Otherwise, plate morphological terminology follows de Verteuil and Norris (1996), except that we have found it necessary to adjust this terminology when describing the hypocyst. The scheme adopted by de Verteuil and Norris (1996) is based on an epicystal perspective, where the poleward margin of a plate lies anterior to the geometry. The terms omega-, theta-, and delta- are inverted when described from the hypocyst in order to maintain plate orientation relative to the pole. However, unlike planate, caroid, fastigiate, and linteloid plates (de Verteuil and Norris, 1996, text-figs. 22, 24–26), this inversion cannot be applied to camerate plates as indicated in de Verteuil and Norris (1996, text-fig. 23). Although plate shape does not change, orientation towards the pole does. Therefore, when describing *Desotodinium* n. gen., we do not use the prefixes omega- and delta- in an inverted epicystal sense when describing a camerate plate on the hypocyst. Instead, we have added the qualifier ''hypocystal'' to indicate the orientation of the plate. Thus, the term ''hypocystal iso-delta-camerate'' describes plates on *Desotodinium wrennii* n. gen. and sp.

This paper follows the timescale of Berggren et al. (1995).

RESULTS AND DISCUSSION

Four new dinoflagellate cyst species are formally described, *Spiniferites coniconcavus* n. sp., *Pyxidinopsis braboi* n. sp., *Desotodinium wrennii* n. gen. and sp., and *Scaldecysta doelensis* n. gen. and sp. The new marine acritarch *Waaslandia geminifera* n. gen. and sp. is also proposed. The excellent preservation of assemblages in both the Kattendijk and Lillo formations is particularly evident among the abundant protoperidiniaceans, which are often only weakly compressed owing to support from sand-sized grains in the sediment. These specimens are usually dark brown in color and show little or no evidence of oxidative damage. This excellent preservation has been critical in elucidating the tabulation on *Barssidinium pliocenicum* (Head, 1993) Head, 1994a emend. The stratigraphic ranges of taxa reported here are based on the stratigraphic interpretation of Louwye et al. (in press) (Fig. 4).

Pyxidinopsis braboi occurs in low abundances (0.4–1.0 percent of the in situ dinoflagellate cyst count) throughout the Lillo Formation and was not found in the Kattendijk Formation (Fig. 4). Its presently established occurrence in Belgium is therefore upper Lower Pliocene and/or lower Upper Pliocene. It has not been recorded elsewhere.

Spiniferites coniconcavus and *Desotodinium wrennii* have comparable stratigraphic ranges with *Pyxidinopsis braboi* in our sections, both having a lowest occurrence in the Basal Shelly Unit below the Oorderen Sands Member and ranging into the Kruisschans Sands Member (Fig. 4). *Spiniferites coniconcavus* occurs infrequently (maximum 0.4 percent of in situ dinoflagellate cyst count) and was recorded only in the Verrebroek Dock. It has not been recorded elsewhere. *Desotodinium wrennii* occurs in similar low abundances (0.3–1.6 percent of the in situ dinoflagellate cyst count) in our sections and is questionably identified from the Upper Pliocene Red Crag Formation of eastern England (as Gen. et sp. indet. in Head, 1998a). Beyond the North Sea Basin, it occurs with continuous but variable abundance from the Lower Pliocene through Upper Pleistocene of the De Soto Canyon, Gulf of Mexico (as Forma D in Wrenn and Kokinos, 1986). *Desotodinium wrennii* is probably the cyst of the extant motile-based species *Pyrophacus horologium* von Stein, 1883 (Wall and Dale, 1971; Head, 1996a); if confirmed, this will extend its stratigraphic range to the present.

Scaldecysta doelensis was recorded only from the upper part of the Oorderen Sands and Kruisschans Sands members of the Lillo Formation (Fig. 4), where it occurs persistently but with abundances not exceeding 1.6 percent of the in situ dinoflagellate cyst count. The lowest occurrence of *Scaldecysta doelensis* coincides with sedimentological evidence for a gradual shallowing of the marine environment. This occurrence suggests a preference for near-shore, shallow-marine environments. *Scaldecysta doelensis* has its lowest occurrence just below the highest occurrence of

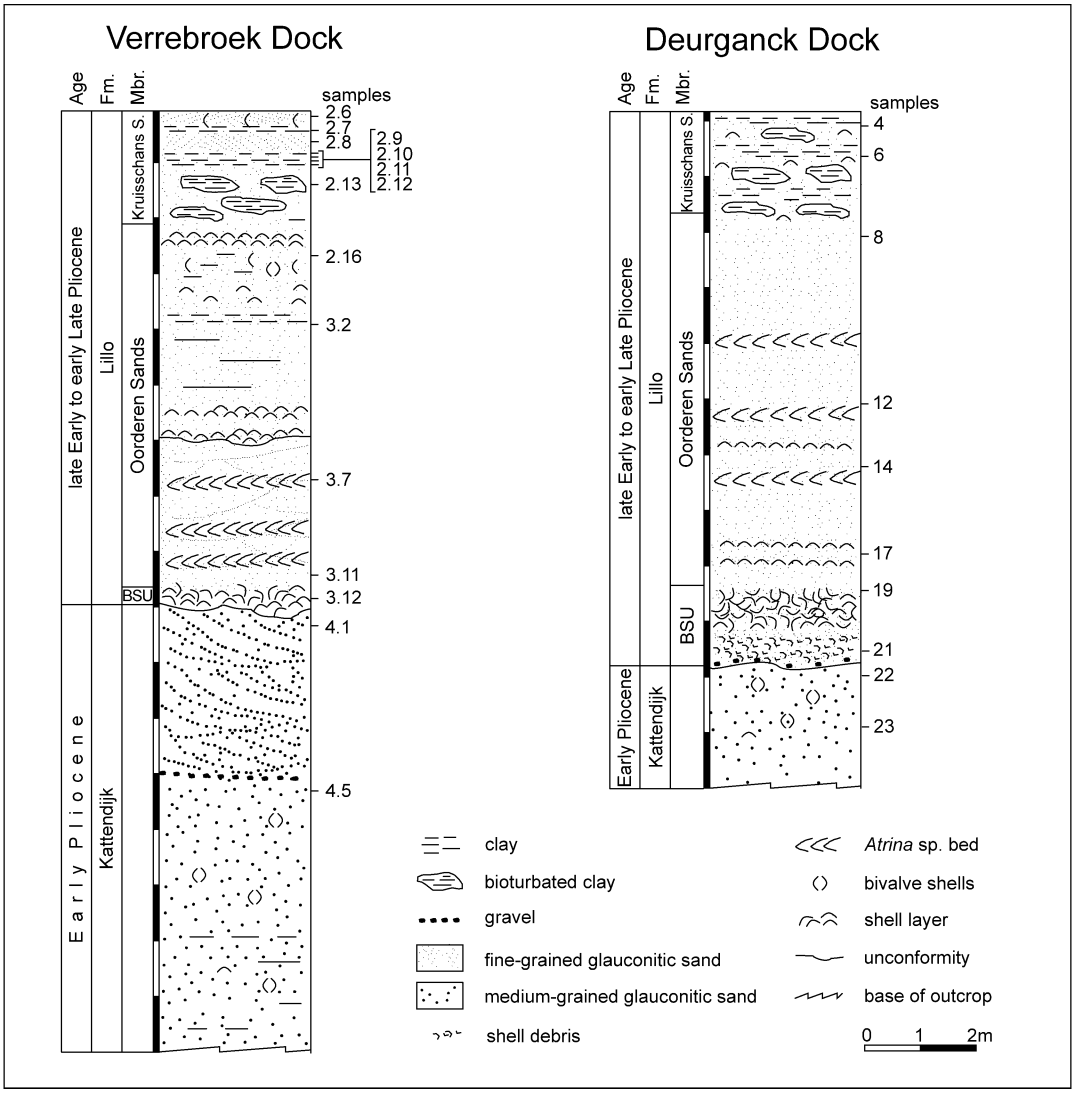

FIGURE 3—Stratigraphy and lithology of the sections in the Deurganck and Verrebroek docks and position of samples. Ages are from Louwye et al. (in press). BSU = Basal Shelly Unit.

Invertocysta lacrymosa Edwards, 1984, a species that disappears at 2.75 Ma (Late Pliocene) in both the Singa section of southern Italy and the central North Atlantic (Versteegh, 1995, 1997), and at 2.74 Ma in the eastern North Atlantic (DSDP Hole 610A, SDS, personal observations). We estimate the first appearance of *Scaldecysta doelensis* at between ca. 4.2 Ma and 2.74 Ma (late Early to early Late Pliocene). Its presence in the Kruisschans Sands Member indicates an age no younger than 2.6 Ma, but its precise stratigraphic top in Belgium is unknown. While environmental control makes the total range of *Scaldecysta doelensis* difficult to estimate, its large size, distinctive morphology, and lack of records beyond our own observations all suggest a short stratigraphic range.

Barssidinium pliocenicum occurs in low to relatively high abundances (0.4–7.6 percent of the in situ dinoflagellate cyst count) throughout the studied sections. Our assessment of this species, based on many specimens from Belgium as well as the re-analysis of type material from southwestern England (Head, 1993), has led us to treat it as a taxonomic senior synonym of *Barssidinium wrennii* Lentin, Fensome, and Williams, 1994 described from the Upper Miocene to Pliocene of offshore eastern Canada. *Barssidinium pliocenicum* extends downwards into the Upper Miocene of Belgium, where it occurs in moderate abundances (as *Barssidinium wrennii* in Louwye, 2002), and it similarly ranges into the Miocene of offshore eastern Canada. The excellent preservation of our Belgian specimens has allowed us to recognize the presence of plate sutures beyond the archeopyle, a feature not previously noted for the genus *Barssidinium* Lentin, Fensome, and Williams, 1994 and requiring its emendation. Selected duplicate residues containing *Barssidinium pliocenicum* were briefly exposed to fuming nitric acid, a strong oxidant, whereupon specimens became pale and showed wall separation (Fig. 10.3–10.6). This confirms earlier suspicions (Head, 1993, 1997; Lentin et al., 1994) that pale specimens of *Barssidinium* may result from specific laboratory processes or partial oxidation of the cysts during their synsedimentary or diagenetic history.

The marine incertae sedis palynomorph *Waaslandia geminifera* occurs in low numbers (0.4–3.3 percent of the in situ dinoflagellate cyst count) in all our lithostratigraphic units. It has a lowest

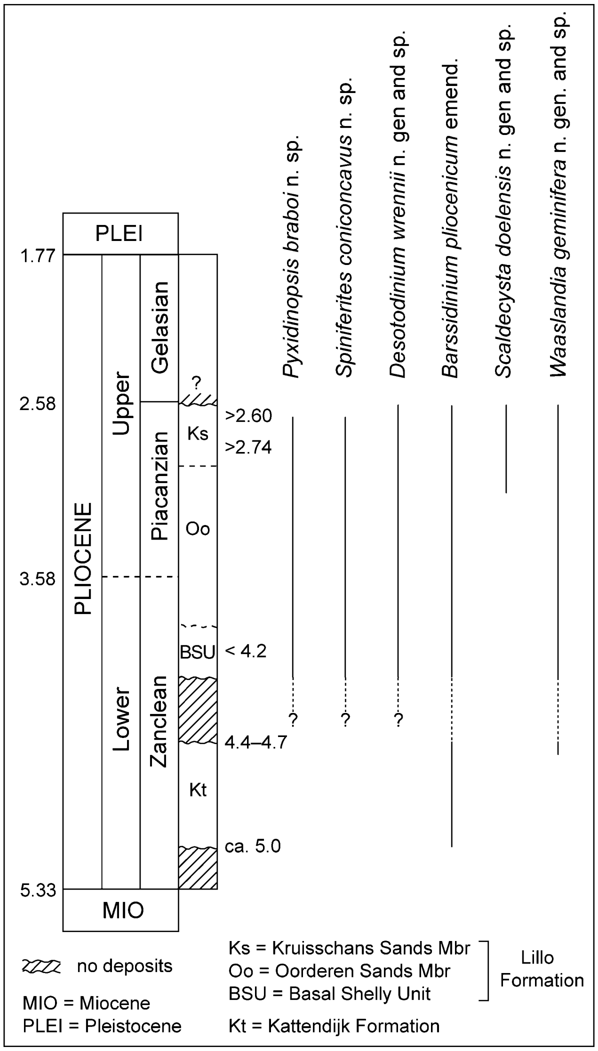

FIGURE 4—Stratigraphic ranges of the new dinoflagellate cyst and marine incertae sedis species from the Deurganck Dock and Verrebroek Dock sections examined in this study. The exact position of the Lower/Upper Pliocene boundary could not be established in this section and is therefore indicated by a dashed line. Ages (Ma) are after Louwye et al. (in press).

occurrence just below the top of the Kattendijk Formation in the lower Lower Pliocene (Louwye et al., in press).

SYSTEMATIC PALEONTOLOGY

Division DINOFLAGELLATA (Bütschli, 1885) Fensome et al., 1993
Subdivision DINOKARYOTA Fensome et al., 1993
Class DINOPHYCEAE Pascher, 1914
Subclass PERIDINIPHYCIDAE Fensome et al., 1993
Order GONYAULACALES Taylor, 1980
Suborder GONYAULACINEAE (Autonym)
Family GONYAULACACEAE Lindemann, 1928
Subfamily GONYAULACOIDEAE (Autonym)
Genus SPINIFERITES Mantell, 1850 emend. Sarjeant, 1970
SPINIFERITES CONICONCAVUS new species
Figure 5.1–5.20

Spiniferites sp. 1 LOUWYE, HEAD, AND DE SCHEPPER, in press, fig. 7r–7t.

Diagnosis.—Broadly ovoidal spiniferate cysts, bearing gonal processes only. Process stems hollow, broad and conical with concave sides near base, distally becoming cylindrical and narrower; closed distally with short and blunt, usually trifurcate endings. Tabulation expressed by low sutural crests and precingular archeopyle (3″). Operculum free.

Description.—Spiniferate cysts with broadly ovoidal central body. Cyst wall thin (<0.3 μm) with shagreenate to faintly scabrate wall surface (best seen using interference contrast optics). Processes gonal, sometimes absent from junctions of cingular plate sutures. Processes broad, hollow, and conical with concave sides near base, distally becoming cylindrical and narrower, with closed, short, and blunt, usually trifurcate endings. Secondary bifurcation absent. Length of conical lower part of process approximately equals length of cylindrical upper part. Flange occurs between bases of two or three antapical processes. Process bases can also be adjoined by flange in apical and cingular area. Tabulation expressed by low sutural crests, sometimes appearing only as dark lines on central body wall. Archeopyle formed by loss of precingular plate 3″. Operculum free.

Etymology.—Latin, *conus* and *concavus*, describing the principal processes, whose bases are cone-shaped with concave sides.

Type.—Holotype, sample VB 3.12, slide p2, England Finder reference M27/0. Basal Shelly Unit, Lillo Formation, Verrebroek Dock; upper Lower or lower Upper Pliocene. Figure 5.1–5.6. Royal Belgian Institute of Natural Sciences, Brussels, registration number IRScN b4253.

Measurements.—Holotype: endoblast length, 40 μm; endoblast equatorial diameter, 36 μm; maximum process length, 11 μm; maximum width of process base, 14 μm. Range: endoblast length, 38(39.9)40 μm; endoblast equatorial diameter, 34(35.0)36 μm; process length, 7(9.8)12.5 μm; width of process base, 4.0(6.8)9.0 μm; width of process top, 1.0(1.7)2.0 μm. Seven specimens measured.

Occurrence.—Basal Shelly Unit and Oorderen Sands Member of the Lillo Formation in the Verrebroek Dock (upper Lower and/or lower Upper Pliocene).

Discussion.—Of the following species, none have the broad conical process bases that characterize *Spiniferites coniconcavus*. *Spiniferites hyperacanthus* (Deflandre and Cookson, 1955) Cookson and Eisenack, 1974 and *Spiniferites mirabilis* (Rossignol, 1964) Sarjeant, 1970 differ additionally in being slightly larger (*Spiniferites mirabilis* endoblast length, 44–58 μm, Reid, 1974; and *Spiniferites hyperacanthus* central body diameter, 53–62 μm, Rochon et al., 1999; compared with *Spiniferites coniconcavus*, endoblast length, 38–40 μm, this study), in having intergonal as well as gonal processes, and in having longer trifurcations on the process tips. *Spiniferites membranaceus* (Rossignol, 1964) Sarjeant, 1970 has longer trifurcations on the process tips and a sutural crest joining the antapical processes along their complete length. *Spiniferites falcipedius* Warny and Wrenn, 1997 differs in its larger size (central body length 51–74 μm) and broader process terminations. *Spiniferites belerius* Reid, 1974 differs in having an apical boss and irregularly shaped processes. The cyst of *Gonyaulax baltica* Ellegaard, Lewis, and Harding, 2002 has trifurcate process terminations that bifurcate distally, in contrast to the blunt and reduced process terminations on *Spiniferites coniconcavus*.

Subfamily UNCERTAIN
Genus PYXIDINOPSIS Habib, 1976
PYXIDINOPSIS BRABOI new species
Figure 6.1–6.12

Pyxidinopsis sp. 1 LOUWYE, HEAD, AND DE SCHEPPER, in press, fig 9h–9j.

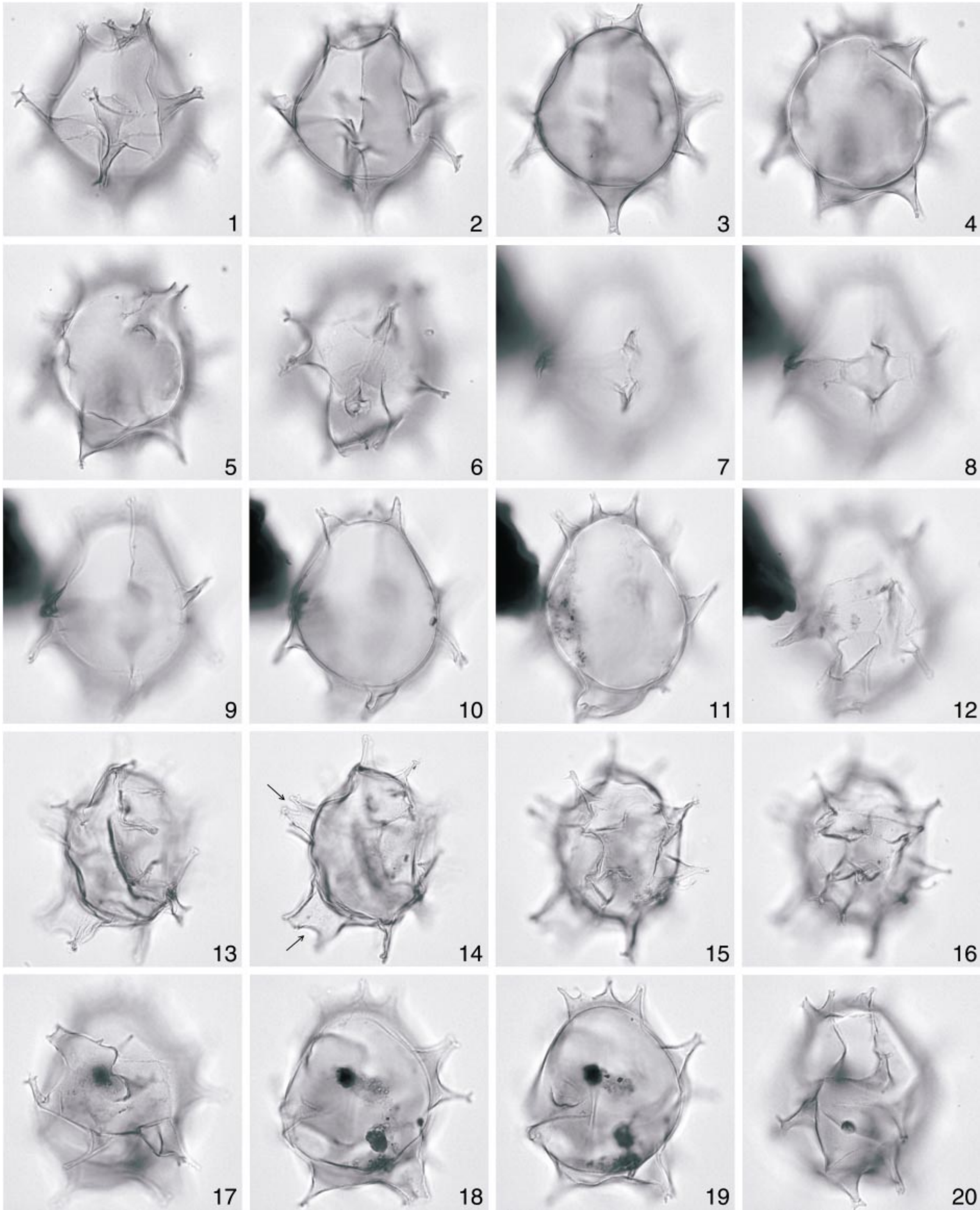

FIGURE 5—*Spiniferites coniconcavus* n. sp. from the Lillo Formation, northern Belgium; upper Lower and/or lower Upper Pliocene. Various magnifications. All images bright field. *1–6,* Holotype, sample VB 3.12, slide p2, M27/0, IRScN 4253. Endoblast length, 40 μm, central body equatorial diameter, 36 μm. Dorsal view of *1, 2,* dorsal surface, showing precingular archeopyle and tabulation, short and blunt process terminations; *3, 4,* mid- and slightly lower foci, process shape conical near base, cylindrical near top; *5, 6,* ventral surface. *7–12,* Sample VB 3.12, slide p2, Q17/0. Endoblast length, 40 μm, central body equatorial diameter, 34 μm. Dorsal view of *7–9,* dorsal surface, showing cingular processes (*7*) and slightly lower foci (*8, 9*) on archeopyle and sutural lineations; *10, 11,* midfoci; *12,* ventral surface. *13–16,* Sample VB 3.12, slide p2, J15/0. Endoblast length, 42 μm, central body equatorial diameter, 34 μm. Right lateral view of *13,* right lateral surface; *14,* midfocus showing flanges between processes, as indicated by arrows; *15, 16,* left lateral surface. *17–20,* Sample VB 3.12, slide p2, C33/0. Endoblast length, 38 μm, central body equatorial diameter, 35 μm. Ventral view of *17,* ventral surface, and *18,* slightly lower focus; *19,* midfocus; *20,* dorsal surface showing archeopyle.

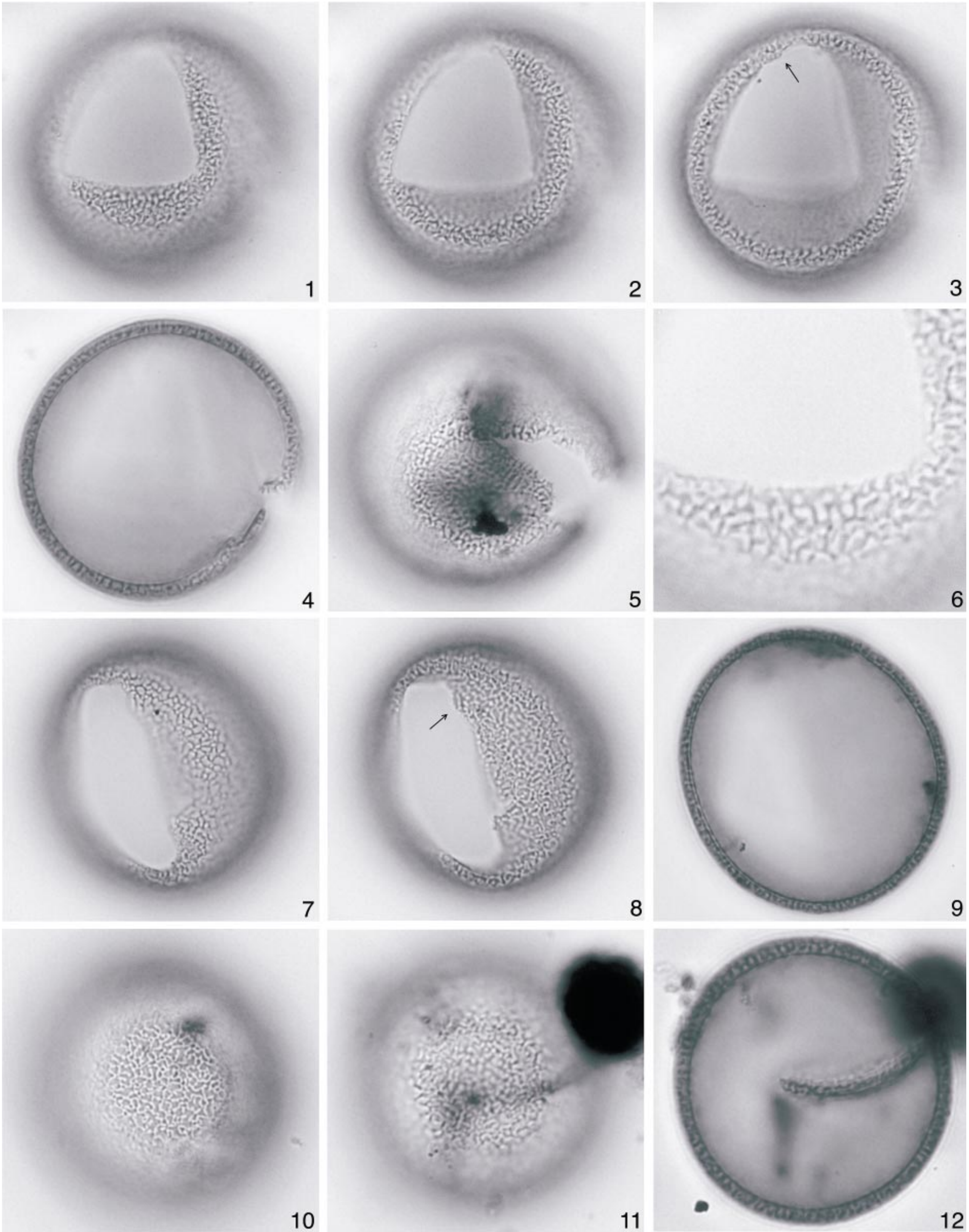

FIGURE 6—*Pyxidinopsis braboi* n. sp. from the Lillo Formation, northern Belgium; upper Lower and/or lower Upper Pliocene. Various magnifications. All images bright field. *1–6,* Holotype, sample DGD 19, slide DGD 19, E53/2, IRScN b4254. Maximum diameter (including luxuria), 40 μm; thickness of luxuria, 2.0 μm. Dorsal view of *1–3,* dorsal surface at successively lower foci, showing precingular archeopyle (3″) with slightly concave archeopyle sides 2–4 (sensu de Verteuil and Norris, 1996; text-fig. 21, p. 100), with arrow indicating reentrant archeopyle side 1 near its midpoint; *4,* midfocus; *5,* ventral surface; *6,* close-up of slightly rounded archeopyle angle 3^4. *7–10,* Sample VB 3.12, slide p2, N19/4. Maximum diameter (including luxuria), 40 μm; thickness of luxuria (or wall), 1.5 μm. Dorsal view of *7,* dorsal surface showing reticulation with

Diagnosis.—A small, spheroidal species of *Pyxidinopsis* Habib, 1976 bearing high (ca. 1.5–2.0 μm), relatively thick (0.3–0.5 μm), straight and sinuous muri that form an evenly distributed, nontabular microreticulation over entire surface. Lumina of microreticulation have small (ca. 0.3–0.5 μm) and large (ca. 0.5–4.0 μm) diameters on same cyst. Surface of muri and lumina smooth. Thickness of pedium ca. 0.3 μm or less. Archeopyle precingular (1P), large; angles 2^3 and 3^4 slightly rounded. Operculum free.

Description.—Small, spheroidal, proximate cysts; wall rigid with characteristic high (ca. 1.5–2.0 μm), irregular, complete or incomplete microreticulation over entire cyst surface. Lumina with small (ca. 0.3–0.5 μm) and large (ca. 0.5–4 μm) diameters occur on same cyst. Larger lumina dominate. Muri are relatively thick (0.3–0.5 μm) and of even height over entire cyst. Surface of muri and lumina smooth. Tabulation not reflected in lumen distribution. Homogeneous and smooth pedium up to about 0.3 μm thick, usually less. Archeopyle precingular (1P), iso-deltacamerate, formed by loss of plate 3″; ornamentation extends to archeopyle borders. Operculum free. Archeopyle sides 2–4 (sensu de Verteuil and Norris, 1996, text-fig. 21, p. 100) are slightly concave. Archeopyle sides 1 or 5 are reentrant near their midpoint (Fig. 6.3, 6.8). Angles 2^3 and 3^4 slightly rounded. No accessory sutures. Small apical protuberance (ca. 1.0 μm), involving both pedium and luxuria, observed on single specimen; not recognized on other specimens possibly due to cyst orientation. No other indications of tabulation. Cysts are susceptible to uptake of safranin-O stain.

Etymology.—Named after the Roman soldier Silvius Brabo who killed the giant Druoon Antigoon, a fierce toll collector on the river Scheldt. He then cut off the giant's hand and threw it into the river. This action, according to legend, gave rise to the name of the city of Antwerp (*ant* = hand; *werp* = throw).

Type.—Holotype, sample DGD 19, slide DGD 19, England Finder reference E53/2. Basal Shelly Unit, Lillo Formation, Deurganck Dock; upper Lower or lower Upper Pliocene. Figure 6.1–6.6. Royal Belgian Institute of Natural Sciences, Brussels, registration number IRScN b4254.

Measurements.—Holotype: maximum diameter, including luxuria, 40 μm; wall thickness, ca. 2.0 μm. Range: maximum diameter, 31(36.1)40 μm; wall thickness, 1.5–2.0 μm. Nine specimens measured.

Occurrence.—Basal Shelly Unit, Oorderen Sands and Kruisschans Sands members of the Lillo Formation at the Deurganck Dock; Basal Shelly Unit and Oorderen Sands Member at the Verrebroek Dock. Upper Lower and/or lower Upper Pliocene.

Discussion.—*Pyxidinopsis delicata* Wilson, 1988 differs from *Pyxidinopsis braboi* n. sp. in having a coarser reticulation with crenulate muri, larger overall size (overall diameter 51–62 μm for *Pyxidinopsis delicata* and maximum diameter 31–40 μm for *Pyxidinopsis braboi*), and thicker wall (ca. 2–4 μm for *Pyxidinopsis delicata* and ca. 1.5–2.0 μm for *Pyxidinopsis braboi*). *Pyxidinopsis waipawaensis* Wilson, 1988 differs in its coarser microreticulation and having a rounded pentagonal to quadrangular archeopyle bordered by a low ridge. *Pyxidinopsis reticulata* McMinn and Sun Xuekun, 1994 has ornamentation within the reticulum. *Cerebrocysta*? *namocensis* Head, Norris, and Mudie, 1989a has a 2P archeopyle. ''*Cerebrocysta powellii*'' Zevenboom and Santarelli (manuscript name in Zevenboom, 1995) is larger in size, has a coarser reticulation, and a thicker wall. ''*Cerebrocysta cassinascoensis*'' Zevenboom and Santarelli (manuscript name in Zevenboom, 1995) has a faintly microgranulate wall and large (5–10 μm) rectangular-shaped lumina.

Filisphaera filifera Bujak, 1984 emend. Head, 1994b differs in having a complete and finer microreticulation consisting of thinner septa (ca. 0.2 μm thick on *Filisphaera filifera*; 0.3–0.5 μm thick on *Pyxidinopsis braboi*), in having smaller lumina (maximum diameter 2.0 μm on *Filisphaera filifera*; up to 4.0 μm on *Pyxidinopsis braboi*), and in being larger (*Filisphaera filifera*, maximum diameter, 48–83 μm, Head, 1996b; *Pyxidinopsis braboi*, maximum diameter, 31–40 μm). Furthermore, *Filisphaera filifera* has an archeopyle with well-defined angles and in optical section the septa reveal a radially striate pattern. *Filisphaera microornata* (Head, Norris, and Mudie, 1989a) Head, 1994b differs in having finer septa, smaller lumina (maximum diameter of 2–2.5 μm, but rarely up to 3.4 μm on *Filisphaera microornata*; up to 4 μm on *Pyxidinopsis braboi*) and in being larger (*Filisphaera microornata*, maximum diameter 49–65 μm; *Pyxidinopsis braboi*, maximum diameter, 31–40 μm).

Suborder GONIODOMINEAE Fensome et al., 1993
Family GONIODOMACEAE Lindemann, 1928
Subfamily HELGOLANDINIOIDEAE Fensome et al., 1993
Genus DESOTODINIUM new genus

Diagnosis.—Discoidal, polar-compressed, proximate, smooth to weakly ornamented cysts, whose compound polyplacoid hypocystal archeopyle is formed of several, but not all, plates of the postcingular series, and one or more fundital plates. Tabulation otherwise weakly or not expressed. Thin equatorial flange sometimes present.

Etymology.—Named after the De Soto Canyon in the Gulf of Mexico, where type was first recorded (as Forma D in Wrenn and Kokinos, 1986); -*dinium* signifies dinoflagellate affinity.

Type.—Holotype of *Desotodinium wrennii* n. sp. Figure 7.1–7.6.

Comparison.—*Capisocysta* Warny and Wrenn, 1997 emend. Head, 1998b differs from *Desotodinium* in having a more complete dissociation of the hypocyst into constituent plates, including all postcingular plates. All known species of *Capisocysta* have a spheroidal rather than discoidal shape, and an equatorial flange is never present. *Tuberculodinium* Wall, 1967 has numerous processes, which are absent from *Desotodinium*. Archeopyle formation in *Geonettia* de Verteuil and Norris, 1996 involves extensive dissociation of plates on both epicyst and hypocyst.

Biological affinity.—Assignment to the subfamily Helgolandinioideae within the Goniodomaceae is based on the following evidence. The archeopyle of *Desotodinium* is restricted to the hypocyst, a rare feature in dinoflagellate cysts. Within the Gonyaulacales, the only previous unambiguous example of such an archeopyle occurs in the goniodomacean genus *Capisocysta* (Head, 1998b). A general characteristic of helgolandinioideans is plate multiplication (Fensome et al., 1993), which is developed extensively on *Tuberculodinium vancampoae* (Rossignol, 1962) Wall, 1967. Plate multiplication on *Desotodinium* is recognized on the type species by the consistent presence of two antapical plates, originating from one ancestral plate. Furthermore, the type of *Desotodinium* bears strong similarity to the cyst of the theca-defined

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small and large lumina; *8,* slightly lower focus showing LO-effect on reticulum, arrow indicates reentrant archeopyle side 5 (s. de Verteuil and Norris, 1996, text-fig. 21, p. 100); *9,* midfocus; *10,* ventral surface showing irregular and incomplete reticulum with straight and sinuous muri (white as LO-effect) enclosing larger and smaller lumina. *11, 12,* Sample DGD 17, slide DGD 17, L52/4. Maximum diameter (including luxuria), 32 μm; thickness of luxuria (or wall), 2.0 μm. Ventral view of *11,* ventral surface; *12,* midfocus showing detached operculum inside cyst.

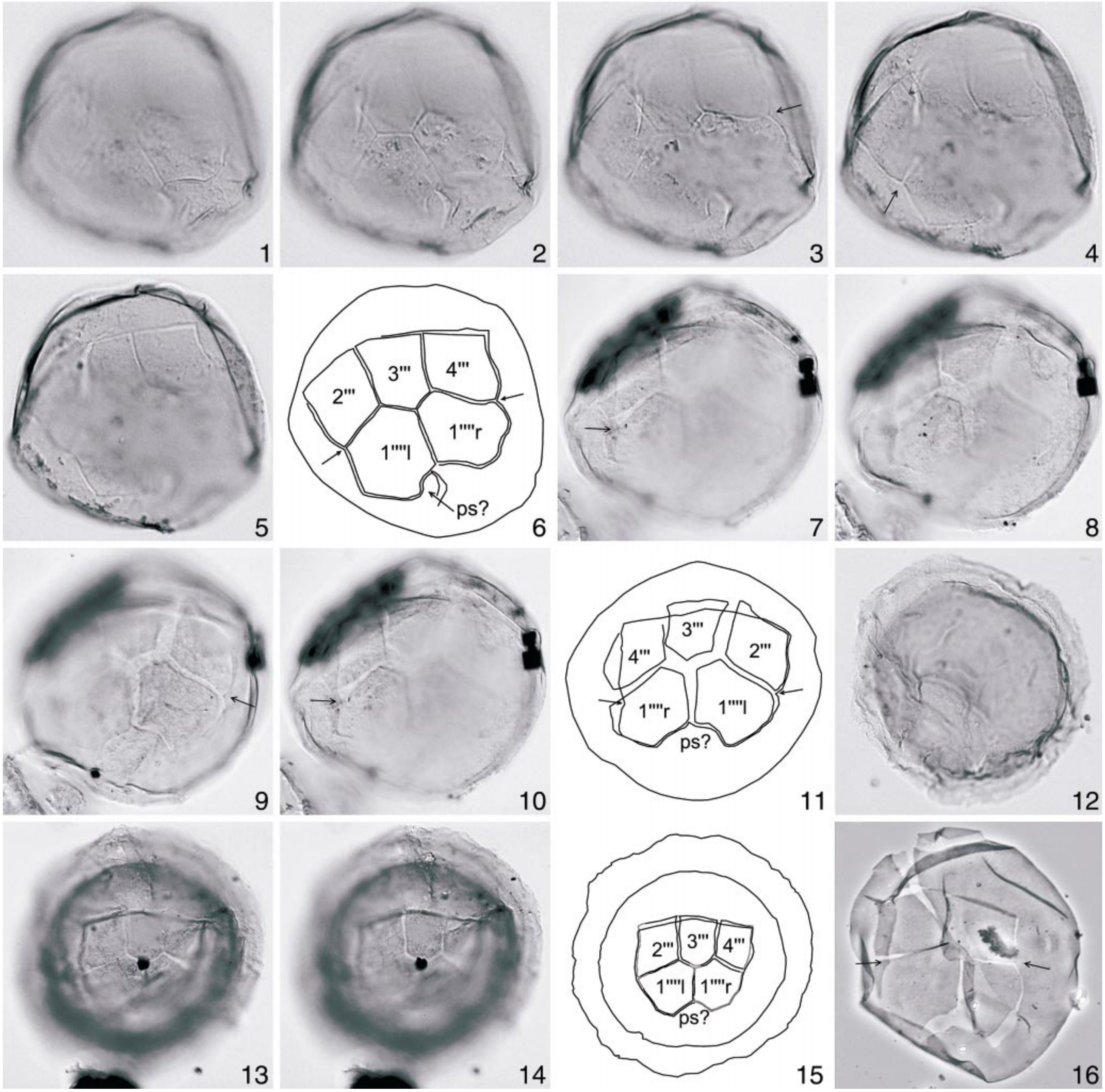

FIGURE 7—*1–15, Desotodinium wrennii* n. gen. and sp. from the Lillo Formation, northern Belgium; upper Lower and/or lower Upper Pliocene. *16,* Gen. et sp. indet. of Head (1998a, fig. 7.16) is questionably assigned to *Desotodinium wrennii*. Various magnifications. *1–5, 7–10, 12–14,* interference contrast; *16,* phase contrast. The label ps? indicates questionable posterior sulcal plate. Arrows in *3, 4, 6, 7, 9–11,* and *16* indicate projections on lateral margins of archeopyle. *1–6,* Holotype, sample VB 3.12, slide p2, W26/1, IRScN b4255. Maximum diameter, 47 μm. *1–6,* Antapical? view showing *1–5,* successively lower foci on archeopyle and adjacent posterior sulcal? plate (*2, 3*); *6,* tracing with opercular plate labeling assumes an antapical view. *7–11,* Sample VB 2.16, slide p3, S37/2. Maximum diameter, 64 μm. *7–11,* Apical view showing *7–10,* successively lower foci on archeopyle; *11,* tracing with opercular plates labeled in conformity with apical view. *12,* Sample VB 2.13, slide VB 2.13A, S29/0. Central body maximum diameter, 62 μm. Flange present. Polar view. *13–15,* Sample DGD4, slide DGD4, L19/3. Central body maximum diameter, 64 μm. *13–15,* Uncertain apical or antapical view of cyst with flange, showing *13,* upper focus, and *14,* slightly lower focus, on archeopyle; *15,* tracing with opercular plate labeling based on antapical view. *16,* Gen. et sp. indet. Head, 1998a from the Late Pliocene Red Crag at Walton-on-the-Naze, Essex, eastern England. Central body maximum diameter, 64 μm. Uncertain apical or antapical view; only four opercular plates are observed, hence questionable assignment to *Desotodinium wrennii*.

helgolandinioidean species *Pyrophacus horologium* von Stein, 1883. See under *Desotodinium wrennii* for discussion.

Discussion.—Some goniodomacean genera show plate multiplication, whereas others do not. Within individual goniodomacean genera, plate multiplication is variable: for example, the pyrodinioidean genus *Capisocysta* contains both a species with a single antapical plate (*Capisocysta lata* Head, 1998b) and a species with two antapical plates (*Capisocysta lyellii* Head, 1998b). Moreover, even within the helgolandinioidean species *Pyrophacus steinii* (Schiller, 1935) Wall and Dale, 1971 (whose cyst-based name is *Tuberculodinium vancampoae*) the degree of plate multiplication is highly variable on the hypotheca. Accordingly, the new genus *Desotodinium* is circumscribed to accommodate species with a single antapical plate as well as those with multiple antapical plates. It is also a feature of some goniodomaceans that more plates may be involved on the hyposome of the motile stage than may be reflected in the cyst. For example, tabulation on the cysts of *Pyrophacus horologium* (Wall and Dale, 1971, fig. 4d–g) incompletely reflects tabulation on the hypotheca (Wall and Dale, 1971, fig. 1a). The same may be true of the new genus *Desotodinium*.

DESOTODINIUM WRENNII new species
Figure 7.1–7.16

Forma D WRENN AND KOKINOS, 1986, p. 205, pl. 10, fig. 5; p. 211, pl. 13, figs. 2, 3.

Forma D of Wrenn and Kokinos, 1986. HEAD, 1996a, p. 1216; LOUWYE, HEAD, AND DE SCHEPPER, in press, fig. 9l.

? Gen. et sp. indet. HEAD, 1998a, p. 812, fig. 4e.

Diagnosis.—A large, thin-walled species of *Desotodinium* n. gen. with smooth to weakly ornamented wall surface, outline circular to subcircular in polar view. Thin, equatorial flange sometimes present. Archeopyle comprises three postcingular plates (interpreted as 2‴–4‴) and two antapical plates; otherwise only weak indications of tabulation on hypocyst, and none on epicyst.

Description.—Large, thin-walled (ca. 0.3 μm or less) cyst, polar-compressed; central body circular to subcircular in outline, nearly colorless to light brown. Wall surface smooth, shagreenate to scabrate. Thin diaphanous flange occasionally present with irregular margin, extends around equator. Tabulation expressed by large hypocystal archeopyle, formed by what we interpret as three postcingular plates (2‴, 3‴, and 4‴), and one left first antapical and one right first antapical plate (respectively 1⁗l and 1⁗l). Archeopyle margin distinctly straight to gently concave on dorsal surface, where delineated by posterior cingular margin. Lateral archeopyle margins usually show small projections between postcingular plates and antapical plates (indicated by arrow on Fig. 7.3, 7.4, 7.6, 7.7, 7.9–7.11). Outward and inward projections along the cingular margin were seen on one specimen: projections of the archeopyle margin towards the cingular series presumably reflect boundaries separating individual cingular plates, whereas projections towards the archeopyle presumably reflect the junction of two postcingular plates with the cingular margin. Postcingular plates 2‴ and 4‴ quadrangular, plate 3‴ typically hypocystal isodelta-camerate to theta-delta-camerate. Irregularly hexagonal antapical plates are approximate mirror images of each other. However, side of plate 1⁗l that contacts ps? plate is inflected inwards on two observed specimens (Fig. 7.2, 7.3, 7.6, 7.9, 7.11), a feature also possibly present on specimen illustrated by Wrenn and Kokinos (1986, fig. 13.2, as Forma D; see their plate 2⁗). Plate adjacent to antapical plates on ventral side questionably posterior sulcal plate (ps?) (see Head, 1998b, p. 800). Opercular plates adherent. No other indications of tabulation.

Etymology.—Named for John H. Wrenn in tribute to his studies on Neogene dinoflagellate cysts from the De Soto Canyon.

Type.—Holotype, sample VB3.12, slide p2, England Finder reference W26/1. Basal Shelly Unit, Lillo Formation, Verrebroek Dock; upper Lower or lower Upper Pliocene. Figure 7.1–7.6. Royal Belgian Institute of Natural Sciences, Brussels, registration number IRScN b4255.

Measurements.—Holotype: maximum diameter, 47 μm; no flange present. Range: central body maximum diameter, 47(59.8)67 μm, nine specimens with and without flange measured; maximum width of flange, 22(23)25 μm, three specimens measured.

Occurrence.—Basal Shelly Unit, Oorderen Sands, and Kruisschans Sands members of the Lillo Formation at the Deurganck Dock and Verrebroek Dock; upper Lower and/or lower Upper Pliocene. Questionable recovery from the Upper Pliocene Red Crag Formation in eastern England (as Gen. et sp. indet. in Head, 1998a). Lower Pliocene through Upper Pleistocene of the De Soto Canyon, Gulf of Mexico (as Forma D in Wrenn and Kokinos, 1986).

Comparison.—See for genus; no other species of *Desotodinium* have yet been identified.

Biological affinity.—Modern cysts of *Pyrophacus horologium* von Stein, 1883 were documented by Wall and Dale (1971, p. 225, fig. 4d–g). Head (1996a) proposed that Forma D of Wrenn and Kokinos (1986), synonymized here with *Desotodinium wrennii*, is probably the cyst of *Pyrophacus horologium*. Our new observations support this likely correlation.

Autecology.—*Pyrophacus horologium* is an extant cosmopolitan species in tropical to cold-temperate waters, and is found in oceanic, neritic, and estuarine settings (Steidinger and Tangen, 1996). Gayoso (2001) reported the motile stage from the Golfo Nuevo (43 degrees south) on the Patagonian coast of Argentina, an environment semi-isolated from shelfal waters of the southern Atlantic Ocean, where low nutrient concentrations and a salinity of about 34 psu occur. Highest abundances were found during summer (January–February), with sea surface temperatures of about 18 degrees Celsius. It has also been recorded in the Gulf of Finland within the Baltic Sea, where it is considered a relatively warm-water species (Edler et al., 1984), and where salinities are around 10 psu or less.

Discussion.—Our interpretation of the tabulation for *Desotodinium wrennii* agrees with the interpretation of Wrenn and Kokinos (1986, as Forma D) for the postcingular plates. However, whereas Wrenn and Kokinos recognized a first and second antapical plate (1⁗ and 2⁗, consistent with the standard peridinialean tabulation pattern), we interpret these plates as left and right first antapical plates (1⁗l and 1⁗r) that originated from a single antapical plate of the standard gonyaulacalean tabulation pattern. Consequently, we classify *Desotodinium wrennii* as a gonyaulacalean dinoflagellate and not as a peridinialean.

The thin equatorial flange, present on a few specimens, probably preserves only under favorable conditions. Wrenn and Kokinos (1986) also illustrated specimens both with and without an equatorial flange.

Gen. et sp. indet. of Head, 1998a (Fig. 7.16) is assigned questionably to *Desotodinium wrennii* because only four plates could be distinguished within the archeopyle: two postcingular plates and two antapical plates. The typical pentagonal plate 3‴ seems to be absent. However, the archeopyle margins show small projections towards the archeopyle between postcingular plates and antapical plates, as for *Desotodinium wrennii*.

Order PERIDINIALES Haeckel, 1894
Suborder PERIDINIINEAE (Autonym)
Family PROTOPERIDINIACEAE Balech (1988) conserved name
Subfamily PROTOPERIDINIOIDEAE Balech (1988)

Discussion.—See Head et al. (2001) for discussion of the validation of the names Protoperidiniaceae and Protoperidinioideae.

Genus BARSSIDINIUM Lentin, Fensome, and Williams, 1994 emended

Original diagnosis.—''Acavate to narrowly circumcavate, dorsoventrally compressed peridinialean cysts with the single or outer wall layer being laevigate to granulate. Processes typically tend to show a strong marginate concentration, but occasionally have a more uniform distribution. Processes generally hollow, tubiform to tapering, sometimes with striae and annular thickenings (or septa) along their length; they are distally open or closed and furcated. The archeopyle usually involves the mid-dorsal intercalary alone, which is large hexa isodeltaform, posteriorly extending almost to the equator of the cyst'' (Lentin et al., 1994, p. 575).

Emended diagnosis.—Dorsoventrally compressed protoperidinialean cysts with subcircular to rounded pentagonal ambitus. Central body brown in color; wall has two closely appressed layers. Wall surface smooth to granulate. Process distribution usually concentrated around ambitus; may reflect tabulation. Processes hollow, tubiform to tapering, usually with annular thickenings along length; distally open or closed. Faint and fine sutural lineations, incompletely reflecting tabulation, variably developed over surface. Archeopyle 2a hexa or penta intercalary, rounded angles, occasional accessory sutures. Operculum free or adherent.

Type.—Holotype of *Barssidinium wrennii* Lentin, Fensome, and Williams, 1994, pl. 2, figs. 2, 5; whose correct name is now *Barssidinium pliocenicum* (Head, 1993) Head, 1994a.

Accepted species.—*Barssidinium evangelineae* Lentin, Fensome, and Williams, 1994; *Barssidinium graminosum* Lentin, Fensome, and Williams, 1994; *Barssidinium olymposum* Warny and Wrenn, 1997; *Barssidinium pliocenicum*; and *Barssidinium taxandrianum* Louwye, 1999.

Occurrence.—Upper Miocene through Upper Pliocene, based on the lowest occurrence of *Barssidinium taxandrianum* (Louwye, 1999) and the highest occurrence of *Barssidinium pliocenicum* (Head, 1993, 1999).

Biological affinity.—Based on the archeopyle shape (penta or hexa intercalary 2a) and the brown color of the central body, we assign *Barssidinium* to the subfamily Protoperidinioideae within the Protoperidiniaceae (as Congruentidiaceae in Fensome et al., 1993). We presume *Barssidinium* to have been a heterotrophic dinoflagellate, based on its inferred biological affinity and the brown color of the wall (Brenner and Biebow, 2001).

Palaeoecology.—Present records suggest a temperate to tropical distribution in neritic, and especially inner neritic, waters.

Discussion.—The genus is emended to account for the nature of the central body wall, as well as new evidence of tabulation including details of the archeopyle. On well-preserved specimens, the central body wall is always brown in color and comprises two closely appressed wall layers that may not be separately resolved under the light microscope except at the base of processes, which are formed only from the outer layer. However, oxidation will induce bleaching of the wall and separation of wall layers (see under *Barssidinium pliocenicum*, below) that sometimes leads to a narrowly circumcavate condition (Lentin et al., 1994) as a preservational artifact. Our Belgian specimens of *B. pliocenicum* reveal extensive traces of tabulation and provide new information on the archeopyle, which is shown to have five or six adjacent plates (not exclusively six, as originally diagnosed by Lentin et al., 1994). Observations on *B. taxandrianum* also reveal tabulation, expressed by faint lines marking the cingulum (SL, personal observations).

The type of *Barssidinium* (the holotype of *B. wrennii*) was stated to have a central body length of 88 μm, a central body width of 57 μm, and a maximum process length of 17 μm (Lentin et al., 1994, p. 578), which is inconsistent with their illustrations. A reevaluation of the holotype by R. A. Fensome (personal commun.) gives the following corrected measurements: body length (measured along apical–antapical axis, excluding antapical horns), 74 μm; body width, 67 μm; maximum process length, 11 μm.

All accepted species have annular thickenings on the processes, with the apparent exception of *B. olymposum*.

Comparison.—*Sumatradinium* (Lentin and Williams, 1976) Lentin, Fensome, and Williams, 1994 has a reticulate to semireticulate wall ornamentation, whereas *Barssidinium* Lentin, Fensome, and Williams, 1994, emended here, has a smooth to granulate surface.

BARSSIDINIUM PLIOCENICUM (Head, 1993) Head, 1994a emended
Figures 8.1–8.12, 9.1–9.9, 10.1–10.9

Sumatradinium pliocenicum HEAD, 1993, p. 40–41, figs. 22.5–22.14, 23, 24 (see also for synonymy); SMELROR, 1999, p. 97, pl. 1, fig. 16.

Barssidinium pliocenicum (Head, 1993) HEAD, 1994a, p. 296; HEAD, 1997, p. 189–190, figs. 13.5–13.9, 14, 17.14; HEAD, 1998a, p. 810, fig. 3a, 3b; HEAD, 1999, p. 91 (unillustrated); VANDENBERGHE et al., 2000, p. 413 (unillustrated); LOUWYE, 2002, p. 60 (unillustrated); LOUWYE, HEAD, AND DE SCHEPPER, in press, fig. 10i–j.

Barssidinium wrennii LENTIN, FENSOME, AND WILLIAMS, 1994, p. 578, pl. 1, fig. 8; pl. 2, figs. 2, 3g, 4–6, 10.

Original diagnosis.—''Skolochorate cysts; central body with weak to moderate dorsoventral compression and rounded pentagonal ambitus. Wall composed of two closely appressed layers and has smooth to shagreenate surface. Periphragm thinner than endophragm and sometimes revealed by wrinkles on wall surface. Processes relatively short for genus, hollow with annular thickenings developed on inner surface of process stems, and distally aculeate. Archeopyle is rounded 2a hexa intercalary, operculum free, occasionally adherent'' (Head, 1993, p. 40).

Emended diagnosis.—A species of *Barssidinium* with rounded pentagonal ambitus. Central body moderately dorsoventrally compressed, composed of two closely appressed layers, outer layer thinner than inner layer. Surface smooth to shagreenate, sometimes marked by low ridges. Processes hollow and distally aculeate, with annular thickenings on inner surface of process stems. Processes not longer than ca. 15 μm. Process distribution concentrated around ambital area, absent or strongly reduced in mid-ventral and mid-dorsal area, reflecting tabulation variably over

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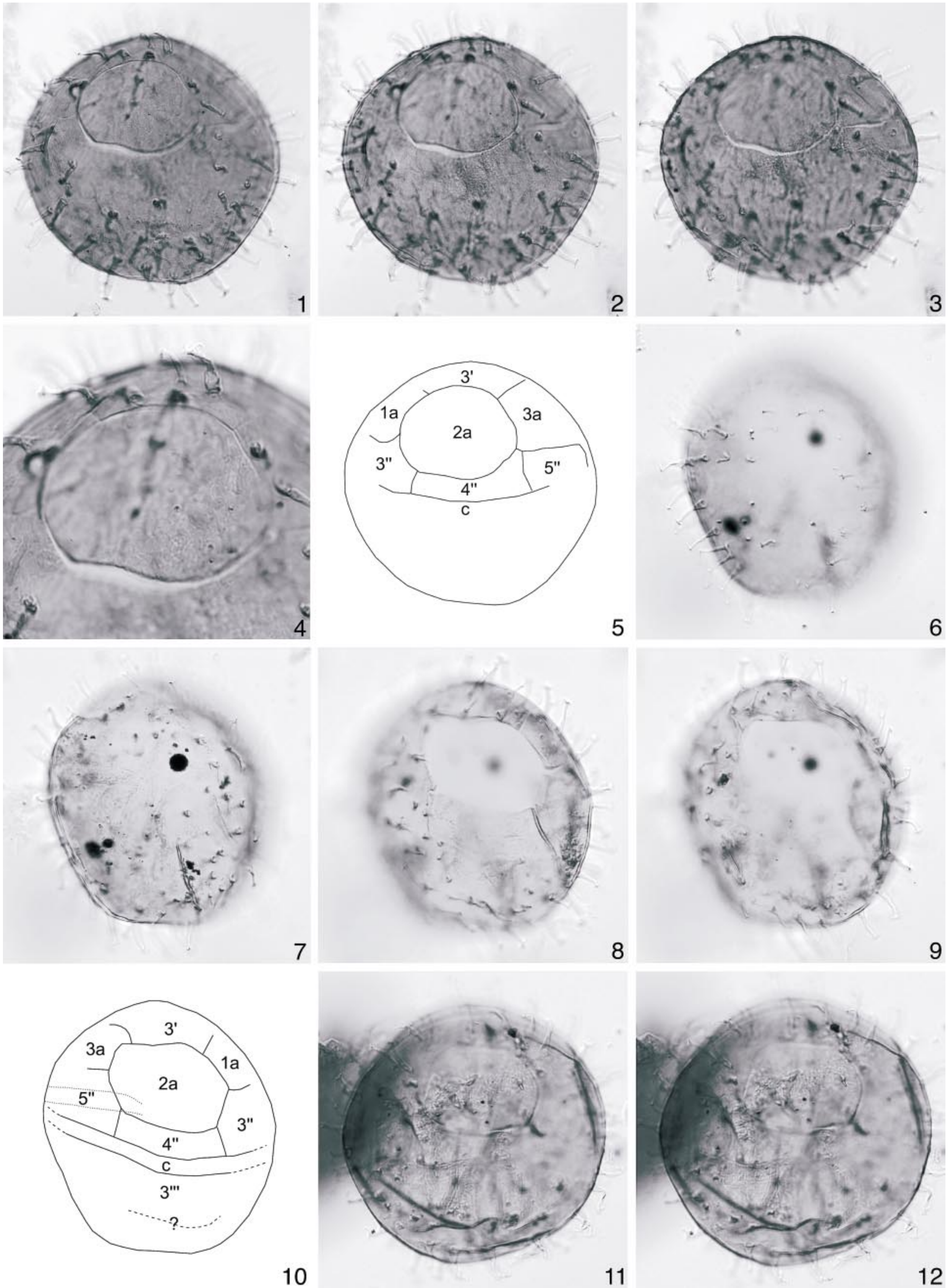
FIGURE 8—*Barssidinium pliocenicum* Head (1993) Head, 1994a emend. from the Lillo Formation, northern Belgium; upper Lower and/or lower Upper Pliocene. Various magnifications. All images interference contrast. Central body length = CBL; central body width = CBW. *1–5*, Sample VB 2.6, slide p1, H22/2. CBL, 83 μm; CBW, 86.5 μm. Dorsal view of dorsal surface at *1–3* successively lower foci; *4*, close-up of archeopyle and tabulation, with operculum in place; *5*, tracing of tabulation on the dorsal surface. *6–10*, Sample VB 2.9, slide p1, G34/2. CBL, 70 μm; CBW, 56 μm. Ventral view of *6*, ventral surface showing process distribution along cingulum; *7*, slightly lower focus showing lineations indicating cingulum on ventral surface; *8, 9*, successively lower foci of dorsal surface showing archeopyle and lineations of tabulation; *10*, tracing of dorsal tabulation, cingulum continues onto ventral surface (dotted lines). *11, 12*, Sample VB 2.9, slide p1, D29/0. CBL, 68 μm; CBW, 68.5 μm. Ventral view of *11*, ventral surface, and *12*, slightly lower focus; see Figure 9.1–9.4 for additional photos.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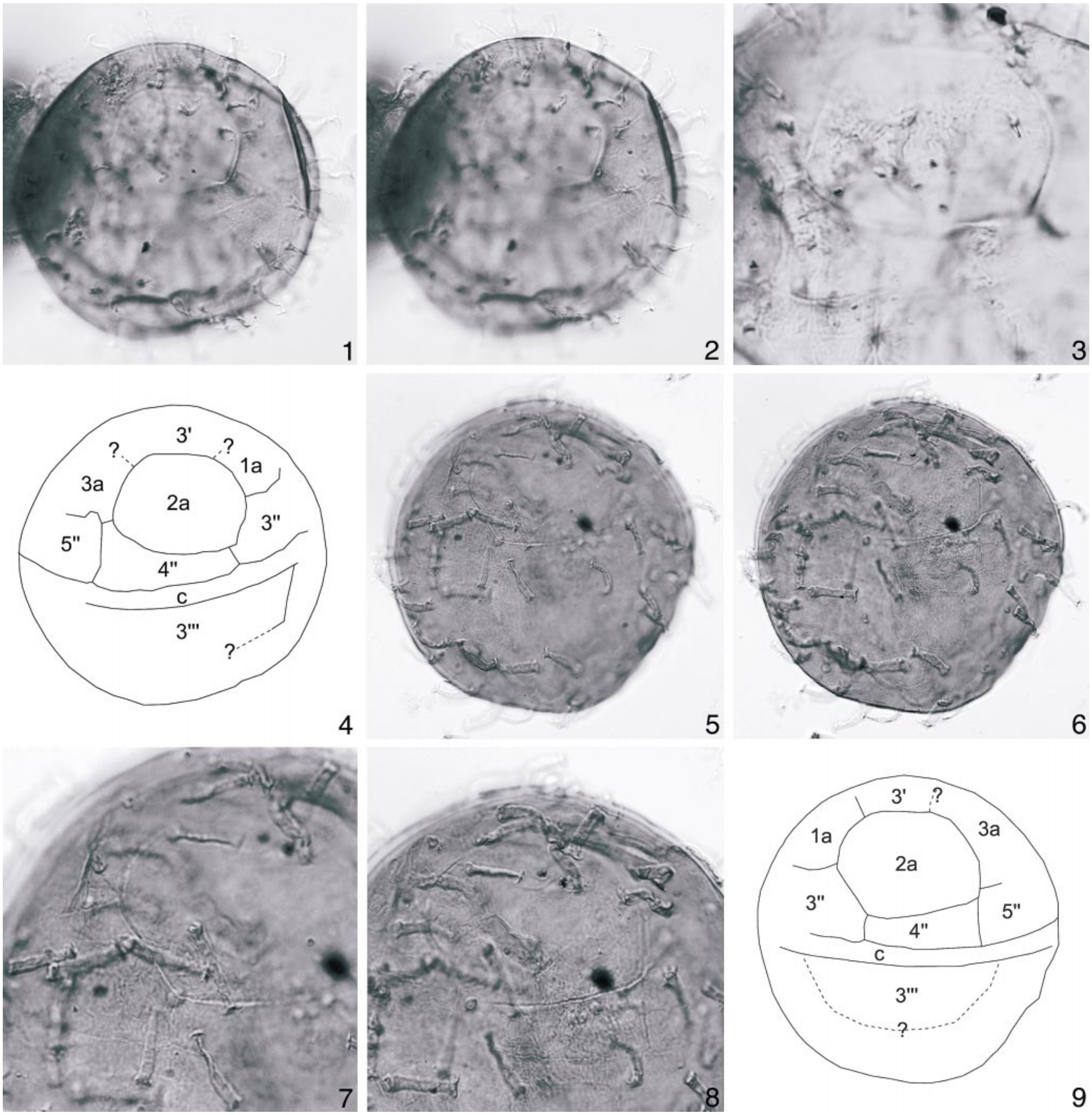


FIGURE 9—*Barssidinium pliocenicum* from the Lillo Formation, northern Belgium; upper Lower and/or lower Upper Pliocene. Various magnifications. All images interference contrast. Central body length = CBL; central body width = CBW. *1–4,* Sample VB 2.9, slide p1, D29/0. CBL, 68 μm; CBW, 68.5 μm. Ventral view of *1,* dorsal surface; *2,* slightly lower focus; *3,* close-up of archeopyle and tabulation, with operculum in place; *4,* tracing of tabulation on dorsal surface. See Figure 8.11, 8.12 for additional photos. *5–9,* Sample VB 2.6, slide p1, M27/0. CBL, 90 μm; CBW, 88 μm. Dorsal view of *5,* dorsal surface; *6,* slightly lower focus; *7,* close-up of archeopyle and tabulation, with operculum in place; *8,* close-up of archeopyle at slightly lower focus; *9,* tracing of tabulation on dorsal surface.

cyst. Faint and fine sutural lineations may occur around archeopyle and cingulum on dorsal surface and may extend to ventral surface. Archeopyle 2a hexa or penta intercalary, rounded angles, occasional accessory sutures. Operculum free or adherent.

Emended description.—Central body light to medium brown, although pale when exposed to oxidation. Wall composed of two closely appressed layers, outer layer thinner than inner layer and may form wrinkles over surface (as in holotype) or show no visible separation (as in the Belgian specimens). Surface smooth to shagreenate, sometimes marked by very low ridges and other

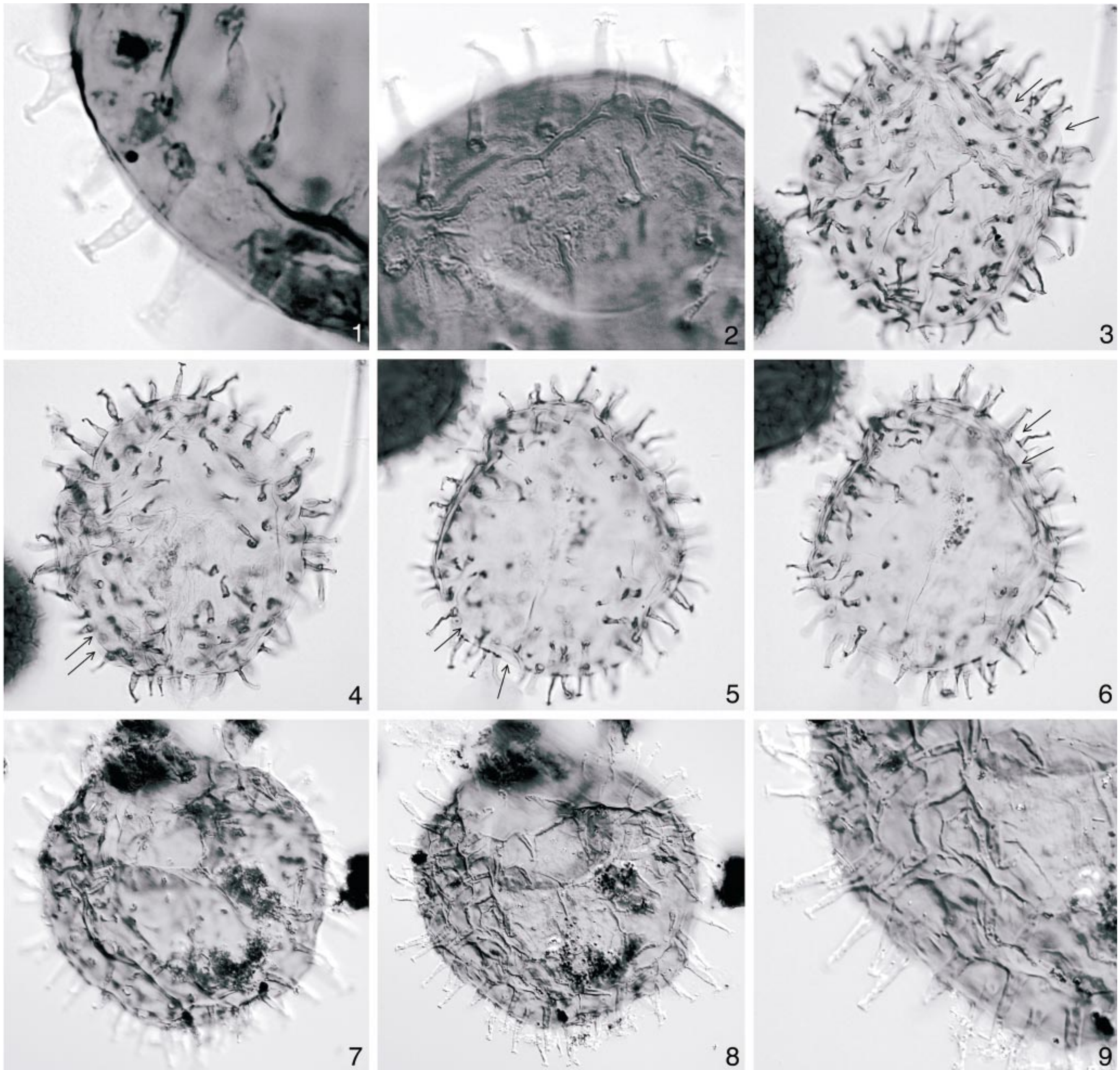


FIGURE 10—*Barssidinium pliocenicum* from *1–6,* the Lillo Formation, northern Belgium; upper Lower and/or lower Upper Pliocene; *7–9,* the holotype from the Upper Pliocene St. Erth Beds, southwestern England. Various magnifications. *1, 3–6,* Bright field; *2, 7–9,* interference contrast. Central body length = CBL; central body width = CBW. *1,* Sample VB 2.9, slide p1, V22/0. Close-up of processes, with annular thickenings, and one bifurcate process; width of photomicrograph, 28 μm. *2,* Sample VB 2.6, slide p1, H22/2. Dorsal view of dorsal surface in close-up showing blotched appearance of the wall surface; width of photomicrograph, 57 μm. *3, 4,* Sample DGD 14, slide DGD 14, N28/0. CBL, 90 μm; CBW, 85 μm. Oxidized specimen, discolored (dark on illustrations due to safranin-O stain) and revealing separation of thin outer wall and inner wall, indicated by arrows. Uncertain view of *3,* upper surface, and *4,* lower surface. *5, 6,* Sample DGD 14, slide DGD 14, O30/4. CBL, 74 μm; CBW, 66 μm. Oxidized specimen, discolored (darker color due to stain) and clearly showing separation of thin outer wall and inner wall, indicated by arrows. Uncertain view of *5,* upper surface, and *6,* lower surface. *7–9,* Holotype of *Barssidinium pliocenicum* Head, 1993 (as *Sumatradinium pliocenicum* in Head, 1993). Sample 1/52 of Head, 1993, slide 2, N27/3, Royal Ontario Museum catalog number ROM49407. CBL, 73 μm; CBW, 74 μm. Ventral view of *7,* dorsal surface; *8,* ventral surface; *9,* close-up of ventral surface showing wrinkled thinner outer wall layer.

irregularities in wall thickness, giving faintly blotched appearance in plan view (e.g., Head, 1993, fig. 22.13, 22.14; Fig. 10.2). Processes, formed from outer wall layer, are hollow and distally aculeate (aculeae about 1.0 μm, and usually less than 2.0 μm, in length; may be recurved or flared, e.g., see SEM in Head, 1997, fig. 17.14). Processes often narrow distally, just below process termination, and on some specimens are constricted also at base and elsewhere along process length. Processes usually closed

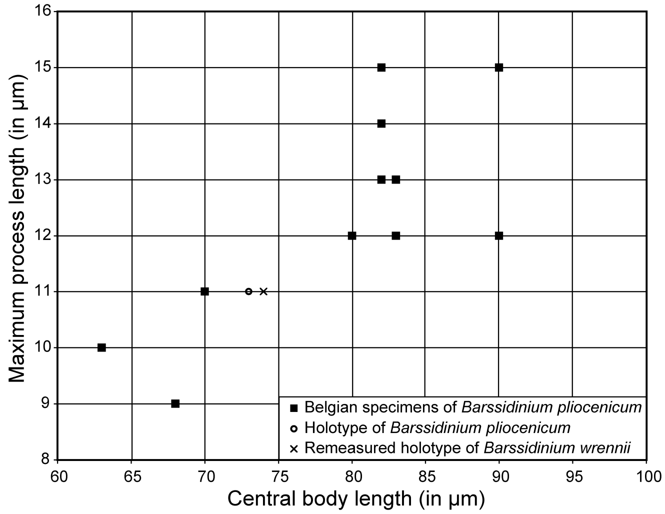


FIGURE *11*—Maximum process length versus central body length for specimens of *Barssidinium pliocenicum* emend. from Belgium, the holotype of *Barssidinium pliocenicum* (Head, 1993) Head, 1994a from southwestern England, and the remeasured holotype of *Barssidinium wrennii* Lentin et al., 1994 from offshore eastern Canada.

distally. Annular thickenings (around two to six, number generally increasing with process length) developed on inner surface of process stems. Processes generally unbranched, but bifurcate processes occasionally developed on one or both lateral margins (Head, 1993, figs. 22.10, 23; Fig. 10.1; but not seen on holotype). Processes usually cover entire cyst but concentrated around ambitus. On Belgian specimens, processes show some alignment on or near plate boundaries, particularly along cingular margins and around third postcingular plate, but also occur randomly. Tabulation also expressed on Belgian specimens by pale, narrow, sutural lines (presumably thinning of wall) developed variably over surface, evident particularly along cingulum and in area around archeopyle. Archeopyle 2a intercalary, rounded outline, variably five-sided camerate, or six-sided linteloid; accessory sutures present. Hexa archeopyle contacts one apical (3′), two intercalary (1a and 3a), and three precingular (3″, 4″, and 5″) plates (Figs. 8.6–8.10, 9.5–9.9). Penta archeopyle contacts plates 3′, 1a, 3a, 3″, and 4″ (Figs. 8.1–8.5, 8.11, 8.12, 9.1–9.4). Hence, the penta geometry involves plate 4″ contacting 3a (Figs. 8.1–8.5, 8.11, 8.12, 9.1–9.4). A penta geometry where plate 4″ contacts plate 1a has not been observed.

Type.—Holotype illustrated as *Sumatradinium pliocenicum* in Head (1993, fig. 22.11). St. Erth Beds, Cornwall, southwestern England; Upper Pliocene. Figure 10.7–10.9.

Measurements.—Belgian specimens (this study): central body length, 63(79.4)90 μm, central body width, 56(76.2)89 μm; archeopyle height (AH), 21.5(28.9)40, archeopyle width (AW), 30(36.4)45 μm, AH/AW, 0.67(0.76)0.81; 11 specimens measured; maximum process length, 9(12.4)15 μm, minimum process length, 6(8.1)10 μm, maximum process width, 1.0(1.7)2.0 μm; 16 specimens measured. See also Figure 11 for dimensions of the Belgian specimens plus those of the holotypes of *Barssidinum pliocenicum* and *Barssidinium wrennii*.

Occurrence.—Lower Pliocene Kattendijk Formation and upper Lower and/or lower upper Pliocene Lillo Formation (this study) and Upper Miocene Diest Formation of Belgium (as *Barssidinium wrennii* in Louwye, 2002). Lower Pliocene (Head, 1997) and Upper Pliocene (as *Sumatradinium pliocenicum* in Head, 1993, 1999) of England. Miocene to Pliocene of offshore eastern Canada (as *Barssidinium wrennii* in Lentin et al., 1994). Restricted to the Upper Pliocene of ODP Site 986, western Svalbard Margin (as *Sumatradinium pliocenicum* in Smelror, 1999). See also discussion of previous records in Head (1993).

Comparison.—*Barssidinium evangelineae* differs from *B. pliocenicum* in having broad, hollow, distally open, aculeate processes. *Barssidinium graminosum* has longer and more slender processes [maximum process length for *B. graminosum*, 13(19)25 μm; maximum process length for *B. pliocenicum*, 9(12.4)15 μm]. *Barssidinium olymposum* has bowl-shaped process terminations. The wall surface of *B. pliocenicum* appears identical to *B. taxandrianum*, but the latter has acuminate and distally closed processes.

Autecology.—The distribution of *Barssidinium pliocenicum* in the Neogene of England (Head, 1993, 1998a) reflects an affinity for warm, neritic waters. Its occurrence in Pliocene deposits of Belgium, which were deposited in a shallow marine environment before the onset of northern hemisphere glaciation at 2.5 Ma, are consistent with this interpretation.

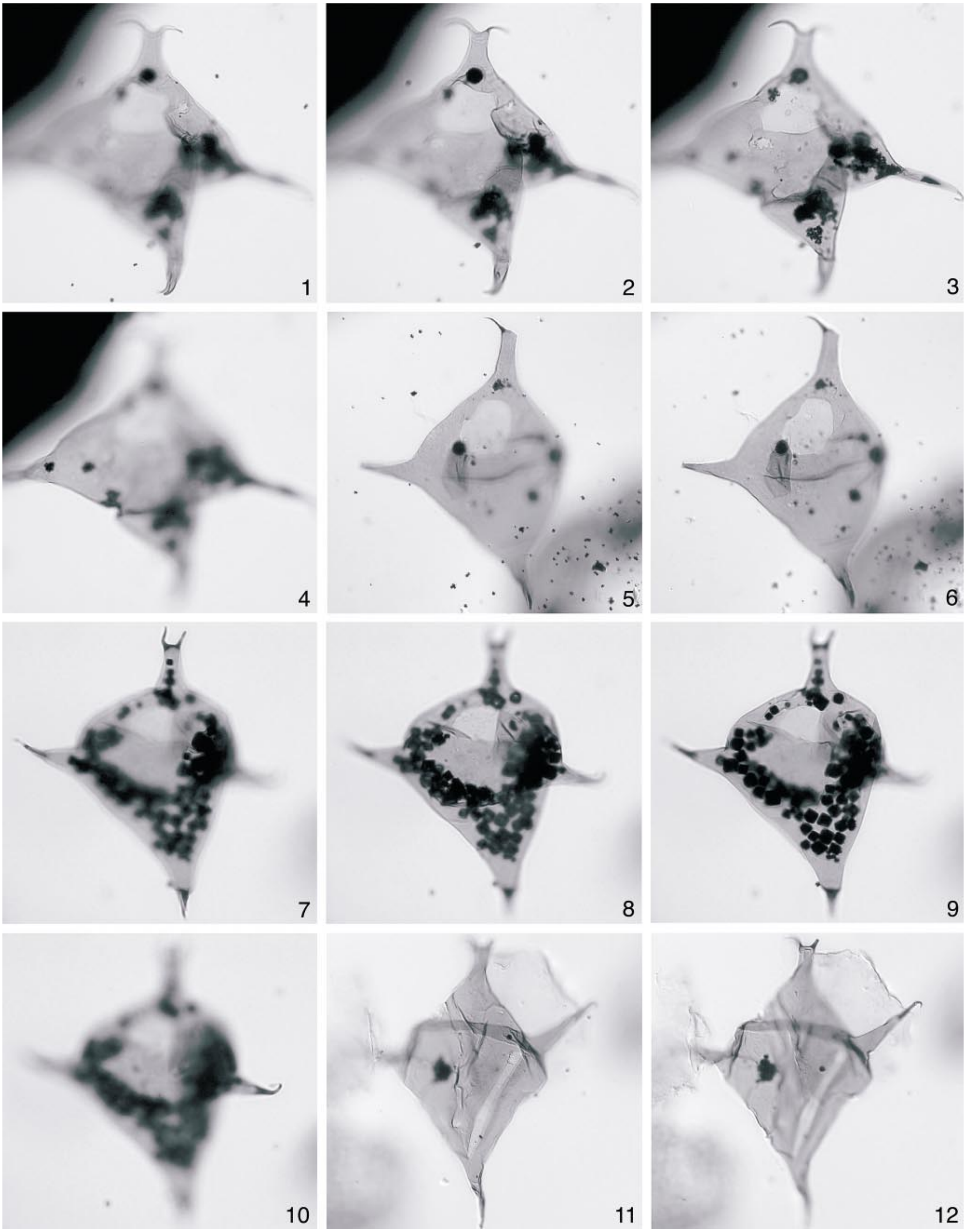
Discussion.—New observations on exceptionally well-preserved specimens from Belgium warrant the emendation of this species. Process distribution is controlled at least partly by tabulation, and hence is not strictly nontabular as suggested by Head (1993). Faint sutural lineations reveal, for the first time in this genus, details of plate geometry and topology, allowing both penta and hexa archeopyles to be observed on *Barssidinium pliocenicum*. Similar faint lines also mark the cingulum on *B. taxandrianum* (SL, personal observation).

We place *Barssidinium wrennii* in synonymy with *B. pliocenicum* based on the new observations of our Belgian specimens, the reexamination of the type material of *B. pliocenicum*, and new information on the holotype of *B. wrennii*.

First, we show that the pale coloration reported for *Barssidinium wrennii* is probably an artifact of laboratory processing caused by oxidation with nitric acid followed by an ammonia treatment (Lentin et al., 1994, p. 568). This treatment has been shown to bleach peridinioid dinoflagellate cysts and cause separation of wall layers (Schrank, 1988). We tested this by exposing our Belgian specimens of *B. pliocenicum* to oxidation and alkali treatment on a set of duplicate residues. Specimens became pale and translucent, and the cyst walls separated into two layers: a slightly thicker inner layer, and a very thin, processes-bearing outer layer (Fig. 10.3–10.6). Similar colorless specimens of *B.*

→

FIGURE *12*—*Scaldecysta doelensis* n. gen. and sp. from the Kruisschans Sands Member of the Lillo Formation, northern Belgium, upper Lower and/or lower Upper Pliocene. Various magnifications. *1–4, 7–10,* Bright field; *5, 6, 11, 12,* interference contrast. *1–4,* Holotype, sample VB 2.9, slide p1B, R48/4, IRScN 4256. Length including horns, 76 μm; width including horns, 96 μm. Dorsal view of *1,* dorsal surface showing two antapical horns; *2, 3,* slightly lower foci on archeopyle and solid tips of apical horn; *4,* lower focus on left lateral horn. *5, 6,* Sample VB 2.9, slide p1, K41/0. Length including horns, 96 μm; right lateral horn is broken off. Dorsal view of *5,* high focus on apical horn, and *6,* slightly lower focus on undistorted archeopyle. *7–10,* Sample VB 2.9, slide p1B, X28/0. Length including horns, 80 μm; width including horns, 78 μm. Cyst filled with pyrite. Dorsal view at *7,* high focus showing long and short antapical horn; *8, 9,* slightly lower foci on archeopyle (shape distorted due to preservational folding); *10,* lower focus on solid tip of right lateral horn. *11, 12,* Sample Verrebroekdok 2.9, slide p1, N24/0. Length including horns, 94 μm. Dorsoventral view of *11,* upper surface, and *12,* lower focus; note tear in wall of hypocyst.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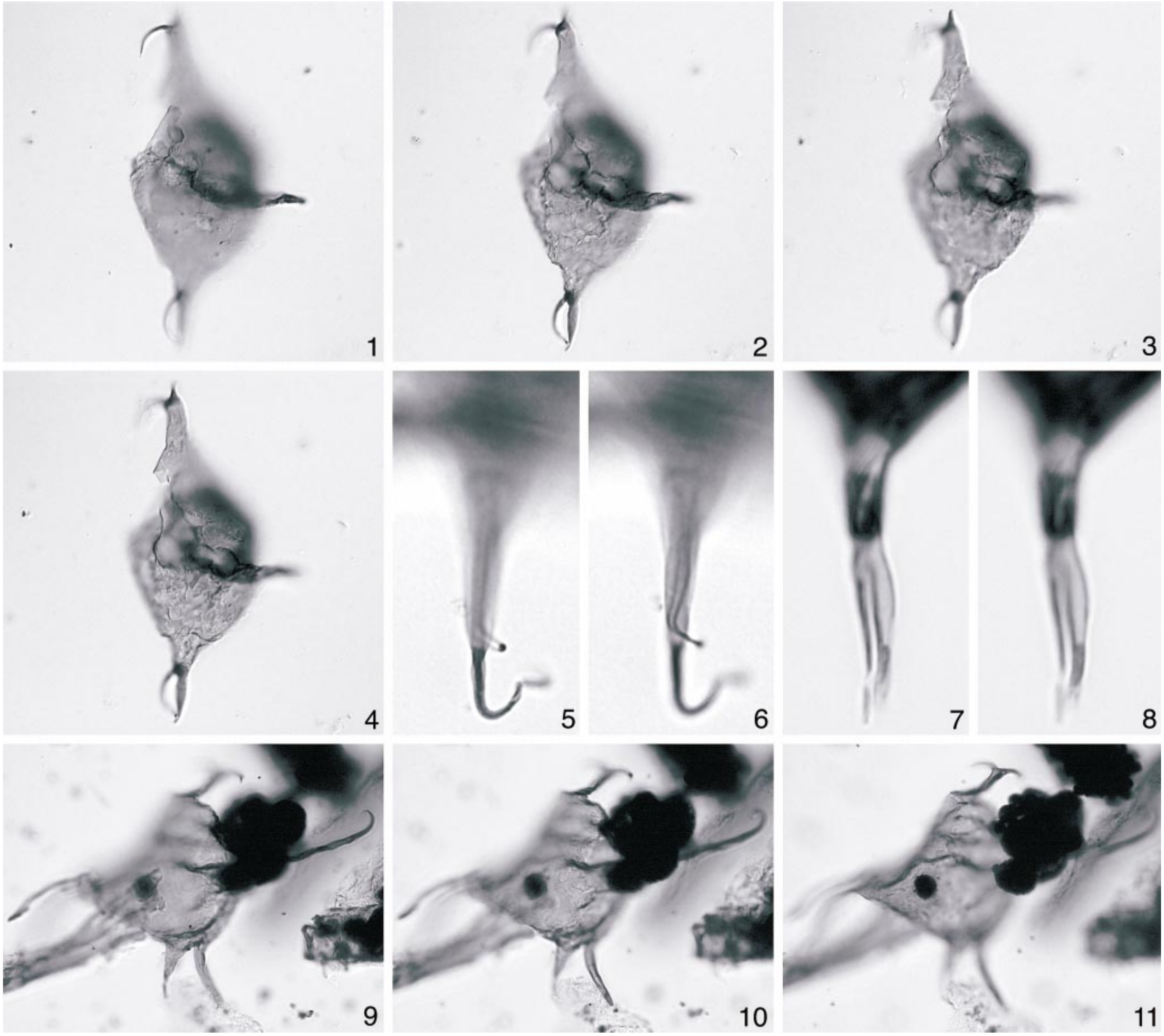

FIGURE 13—*1–8, Scaldecysta doelensis* n. gen. and sp. and *9–11, Scaldecysta* sp. cf. *S. doelensis* n. gen. and sp., both from the Kruisschans Sands Member of the Lillo Formation, northern Belgium, upper Lower and/or lower Upper Pliocene. Various magnifications. *1–4, 9–11,* Interference contrast; *5–8,* bright field. *1–8, Scaldecysta doelensis* n. gen. and sp. *1–4,* Sample Verrebroekdok 2.8, slide p1, X21/1. Length including horns, 84 μm; thickness of central body, 31 μm. Right lateral view at *1,* high focus on right lateral horn; *2–4,* successively lower foci on archeopyle and wall surface. *5, 6,* Sample Verrebroek 2.11, D40/3, close-up of antapical horns showing solid tips and unequal lengths. Height of photomicrograph, 36 μm. Uncertain view at *5,* upper focus, and *6,* lower focus. *7, 8,* Sample VBD 2.13, slide VBD 2.13A, F41/1, close-up of antapical horns showing solid tips and unequal lengths. Height of photomicrograph, 30 μm. Uncertain view at *7,* upper focus, and *8,* lower focus. *9–11, Scaldecysta* sp. cf. *S. doelensis* n. gen. and sp., showing divergent antapical horns and central body approaching pentagonal shape. Sample Verrebroek 2.13, slide Verrebroek 2.13, H29/0. Length including horns, 75 μm; width including horns, ca. 110 μm. Dorsoventral view at *9, 10,* high and slightly lower foci on antapical horns; *11,* lower focus on apical horn.

pliocenicum have been reported from the Coralline Crag Formation of eastern England where natural oxidation of the sediment was suspected (Head, 1997, p. 167). The type specimens of *B. pliocenicum* from the St. Erth Beds of southwestern England have probably undergone some oxidation due to weathering of the sediment, and this would explain the wrinkling of the outer wall layer on these specimens observed by Head (1993). None of these features was seen on our unoxidized Belgian specimens.

Second, the six to eight internal vacuities or tubules interpreted by Head (1993) to occur at a process base on one specimen, interpreted as *Barssidinium pliocenicum*, have not been observed by us on any other specimens. We consider this structure to be a probable artifact of the Cellosize™ mounting medium used by Head (1993).

Finally, *Barssidinium wrennii* and *B. pliocenicum* have also been distinguished on differences in process distribution and size

(Head, 1997). Wrinkling of the outer wall on the type material of *B. pliocenicum* gives the impression that process distribution is denser in mid-dorsal and midventral areas than is really the case, although this is a variable feature in the Belgian specimens. As it stands, this feature cannot be used to separate these two species. Furthermore, remeasurement of the holotype of *B. wrennii* by R. A. Fensome (personal commun., 2003) indicates that the dimensions reported in Lentin et al. (1994) were incorrect (see discussion for the genus *Barssidinium*). New measurements of the holotype of *B. wrennii* plot within the range of *B. pliocenicum* (Fig. 11).

Genus SCALDECYSTA new genus

Diagnosis.—Thin and single-walled protoperidiniacean cysts, smooth or with low ornamentation, brown in color, with rhombic outline in dorsoventral view; sometimes with dorsoventral compression. Five horns present: one apical, two lateral, two antapical. Apical horn ends in two divergent solid tips. Archeopyle formed by loss of single anterior intercalary plate.

Etymology.—Named after the river Scheldt, known as Scaldem during the eighth century, which flows near the type locality; Latin, *cysta,* sac or cell.

Type.—Holotype of *Scaldecysta doelensis* n. gen. and sp. Figure 12.1–12.4.

Comparison.—*Stelladinium* (Bradford, 1975) differs from *Scaldecysta* in its pentagonal rather than rhombic outline and by the presence of a single tip to the apical horn. *Rhombodinium* (Gocht, 1955) differs in having an internal body and a pale or colorless wall.

Biological affinity.—*Scaldecysta* is classified as a protoperidinioidean based on its possession of an intercalary archeopyle, the brown pigmentation of the cyst wall, and its strong resemblance to the genus *Stelladinium*. The close similarity between *Scaldecysta* and *Stelladinium* is revealed through *Scaldecysta* sp. cf. *S. doelensis* n. gen. and sp. (Fig. 13.9–13.11), which has an outline approaching a pentagonal shape and divergent antapical horns as in *Stelladinium*, but an apical horn with two solid tips typical of *Scaldecysta*. Excystment studies of *Stelladinium* link this genus conclusively with the motile-defined genus *Protoperidinium* Bergh, 1881 (see Head, 1996a). *Scaldecysta* is known only from the Pliocene (this study), and we speculate that it represents an evolutionary precursor of *Stelladinium*, a genus not known from deposits older than Pleistocene.

SCALDECYSTA DOELENSIS new species
Figures 12.1–12.12 and 13.1–13.8

Stelladinium? sp. VANDENBERGHE et al., 2000, p. 413.
Stelladinium? sp. 1 LOUWYE, HEAD, AND DE SCHEPPER, in press, fig. 11i–k.

Diagnosis.—A large species of *Scaldecysta* n. gen. with horns ending in solid acuminate tips. Cyst wall thin, brown in color and smooth or faintly ornamented. Apical horn approximately rectangular in outline, ends in two divergent, symmetrically distributed, usually recurved, solid tips. Two closely appressed antapical horns, divergent only near distal end, one horn always longer than other. Two pronounced lateral horns of approximate equal size. Epicyst and hypocyst triangular, largely equidimensional. Large trapezoidal archeopyle, formed by loss of single anterior intercalary plate (presumed 2a). Cingulum and sulcus not expressed. Operculum free.

Description.—Large cyst, rhombic in dorsoventral outline; moderate dorsoventral compression. Wall is thin (<0.3 μm), unstratified under light microscopy, and medium to pale brown in color. Wall surface smooth or shagreenate. Epicyst and hypocyst each triangular, approximately equal in size. Five horns present: one apical, two lateral, and two antapical. Horns are extensions of central cavity and all end in unbranched solid tips. Apical horn is rectangular in dorsoventral outline, ending in two divergent, usually recurved, symmetrically distributed, solid tips. Closely appressed antapical horns diverge only near distal end of hypocyst, with one antapical horn always longer than other (Fig. 13.5–13.8). No other horns or processes observed. Archeopyle large, trapezoidal in shape, formed by loss of single anterior intercalary plate (presumed 2a). Archeopyle height and width of approximately equal dimensions. Cingulum and sulcus not expressed. No accessory sutures. Operculum free.

Etymology.—Named after the village of Doel, which will probably disappear due to expansion of the Antwerp Harbor and particularly with the completion of the Deurganck Dock, where samples for this study were collected.

Type.—Holotype, sample VB 31/10/00 2.9, slide p1B, England Finder reference R48/4. Kruisschans Sands Member, Lillo Formation, Verrebroek Dock; upper Lower or lower Upper Pliocene. Figure 12.1–12.4. Royal Belgian Institute of Natural Sciences, Brussels, registration number IRScN b4256.

Measurements.—Holotype: length (including horns), 76 μm; width (including horns), 96 μm. Range: length (including horns), 60(84.3)104 μm (12 specimens measured); width (including horns), 77(91.3)108 μm (nine specimens measured); thickness, 24(28.8)35 μm (four specimens measured). Measurements are approximate due to frequent cyst folding.

Occurrence.—Restricted to the Lillo Formation (upper Lower and/or lower Upper Pliocene) of both Deurganck Dock and Verrebroek Dock localities, lowest occurrence halfway up Oorderen Sands Member, ranging into the Kruisschans Sands Member. Also observed in the Kruisschans Sands Member at Grobbendonk, Belgium (Vandenberghe et al., 2000), and from Pliocene deposits in the Poederlee borehole, Belgium (SL, personal observation).

Comparison.—See under *Scaldecysta*, since no other species of this genus have yet been identified.

Autecology.—The restricted distribution of *Scaldecysta doelensis* within the shallow marine upper part of the Oorderen Sands and the inner-neritic Kruisschans Sands members (Louwye et al., in press) suggests a preference for shallow marine environments. Temperate climatic conditions prevailed during the deposition of these sequences (Louwye et al., in press).

Discussion.—Cysts of this species are prone to preservational folding and to breakage of the solid tips of the horns. The archeopyle was not observed on most specimens, and when it was visible, the general outline was frequently obscured by folding of the cyst wall. The archeopyle tends to be offset slightly to the left of the apical-antapical axis. Observations on a single undistorted specimen indicate an iso-delta-planate archeopyle with reentrant angles 1^2 and 3^4 (s. de Verteuil and Norris, 1996, text-fig. 21, p. 101; Fig. 12.5, 12.6). It is difficult to ascertain the dorsoventral orientation of the cyst when the archeopyle is absent, as no other indicators of orientation were observed.

SCALDECYSTA sp. cf. S. DOELENSIS new species
Figure 13.9–13.11

Description.—As for *Scaldecysta doelensis* n. gen. and sp., but antapical horns divergent, giving cyst an outline that approaches pentagonal rather than rhombic. No archeopyle observed. Length (including horns), ca. 75 μm; width (including horns), ca. 110 μm; based on one specimen.

Occurrence.—Kruisschans Sands Member of the Lillo Formation (upper Lower and/or lower Upper Pliocene), near the top of the observed range of *Scaldecysta doelensis* in the Antwerp area.

Discussion.—A single specimen was observed that has an apical horn typical of *Scaldecysta* n. gen. However, its hypocystal

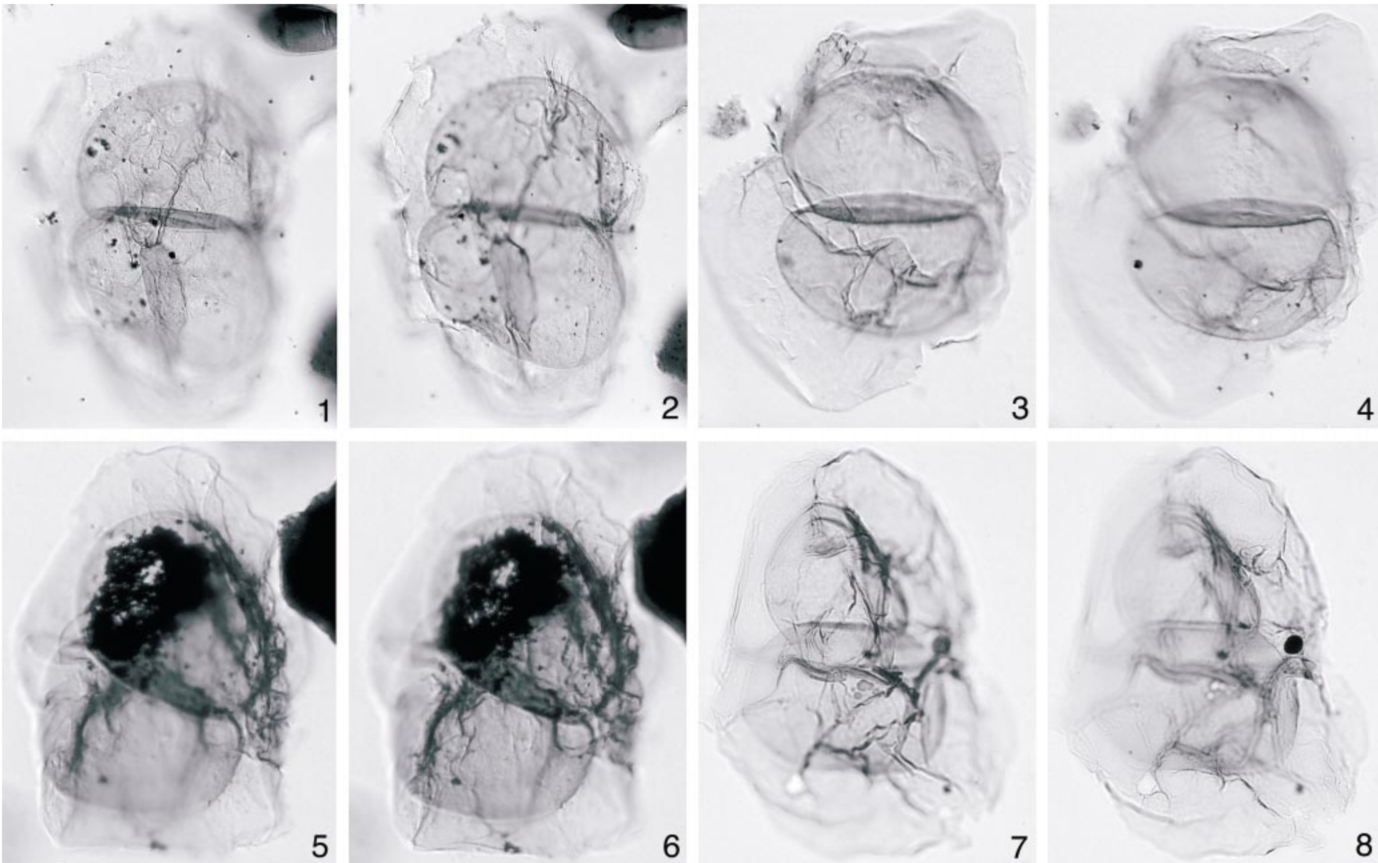

FIGURE *14*—*Waaslandia geminifera* n. gen. and sp. from the Kruisschans Sands and Oorderen Sands members, Lillo Formation, northern Belgium, Pliocene. Various magnifications. *1–6,* Interference contrast; *7, 8,* bright field. *1, 2,* Holotype, sample DGD8, slide DGD 8, V44/2, IRScN 4257. High and low foci, respectively. Maximum outer body length, 123 μm. Note small circular opening in upper half of specimen, not known whether penetrating inner or outer body. *3, 4,* Sample VB 2.10, slide p1, H41/0. Maximum outer body length, 150 μm. High and low foci, respectively. *5, 6,* Sample, DGD 6, slide DGD 6, O52/2. Maximum outer body length, 100 μm. High and low foci, respectively. *7, 8,* Sample VB 2.6, slide p1, X19/2. Maximum outer body length, 167 μm. High and low foci, respectively.

outline recalls that of the genus *Stelladinium*, and supports the view that this genus and *Scaldecysta* are closely related.

MARINE INCERTAE SEDIS
Genus WAASLANDIA new genus

Diagnosis.—Large, cavate, broadly ellipsoidal palynomorph, whose outer body encloses two smaller, hollow thin-walled bodies. Wall surface smooth or weakly ornamented.

Etymology.—Named after the Flemish region *Land van Waas* or *Waasland*, where samples were collected for this study. From the medieval Flemish word *waes*, which referred to the inhospitable clayey soils in the tidal flat environments of the region, which have since been cultivated and are now fertile fields.

Type.—Holotype of *Waaslandia geminifera* n. gen. and sp. Figure 14.1, 14.2.

Discussion.—*Waaslandia* differs from *Cyclopsiella* (Drugg and Loeblich, 1967) Head, Norris, and Mudie, 1989b in having two inner bodies and in lacking a circular pylome with a thickened or raised rim.

WAASLANDIA GEMINIFERA new species
Figure 14.1–14.8

Incertae sedis sp. 1 LOUWYE, HEAD, AND DE SCHEPPER, in press, fig. 12i–k.

Diagnosis.—A species of *Waaslandia* n. gen. with thin-walled outer body, enclosing two smaller, ellipsoidal thin-walled bodies, which contact each other. Wall surface on all bodies is smooth to shagreenate.

Description.—Outer body is large, broadly ellipsoidal in outline, with undulating, irregular ambitus. Wall is thin (less than 0.3 μm), smooth to shagreenate, and folded. Enclosed within outer body are two smaller ellipsoidal, comparably thin-walled (less than 0.3 μm) bodies. Inner bodies contact one another. Longitudinal axis of inner bodies is usually perpendicular to longitudinal axis of outer body (Fig. 14.1–14.6). Both inner bodies have smooth to shagreenate wall surface. Dimensions of both inner bodies approximately equal. No processes observed on inner or outer bodies. Small, circular to ellipsoidal opening visible on two specimens, but unclear whether penetrating inner or outer body.

Etymology.—Latin *geminifera* (adjective) meaning twin-bearing, refers to the two nearly identical inner bodies.

Type.—Holotype, sample DGD 8, slide DGD 8, England Finder reference V44/2. Oorderen Sands Member, Lillo Formation, Deurganck Dock; upper Lower or lower Upper Pliocene. Figure 14.1, 14.2. Royal Belgian Institute of Natural Sciences, Brussels, registration number IRScN b4257.

Measurements.—Holotype: outer body length, 123 μm; outer body width, 80 μm; length of inner body, 44 μm; width of upper inner body, 59 μm; length of lower inner body, 46 μm; width of lower inner body, 60 μm. Range: outer body length, 75(113.2)154 μm; outer body width, 53(77.0)115 μm; length of inner bodies, 42(54.9)79 μm; width of inner bodies, 32(44.8)55 μm. Nine specimens measured.

Occurrence.—Kattendijk Formation at the Deurganck Dock (lower Lower Pliocene); and Basal Shelly Unit, Oorderen Sands, and Kruisschans Sands members of the Lillo Formation (upper Lower and/or lower Upper Pliocene) at both the Deurganck Dock and Verrebroek Dock.

Discussion.—There is no clear means to establish the polarity of our specimens, and their orientation on our illustrations is therefore arbitrary.

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