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THE CENOZOIC GONYAULACACEAN DINOFLAGELLATE GENERA *OPERCULODINIUM* WALL, 1967 AND *PROTOCERATIUM* BERGH, 1881 AND THEIR PHYLOGENETIC RELATIONSHIPS

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ABSTRACT—To clarify the systematic positions of the important gonyaulacacean genera *Operculodinium* Wall, 1967 emend. Matsuoka et al., 1997 and *Protoceratium* Bergh, 1881, we present in detail the tabulation of the Oligocene–Pleistocene, thermophilic, cyst-defined species *Operculodinium bahamense* Head *in* Head and Westphal, 1999 emend., and the extant, cosmopolitan, theca-defined species *Protoceratium reticulatum* (Claparède and Lachmann, 1859) Bütschli, 1885. Both species have a sexiform hyposomal tabulation, and L-type (*Protoceratium reticulatum*) or modified L-type (*Operculodinium bahamense*) ventral organization. *Protoceratium reticulatum* has dextral torsion of the hypotheca, requiring assignation of the genus to the subfamily Cribroperidinioideae Fensome et al., 1993, whereas *Operculodinium bahamense* has neutral torsion requiring assignation to the subfamily Leptodinioideae Fensome et al., 1993. The stratigraphic range of this subfamily is now extended upwards to the lower Pleistocene. Paradoxically, *Protoceratium reticulatum* produces a cyst whose morphology is circumscribed by the cyst-defined genus *Operculodinium*, either implying polyphyletic origins for this genus or that combinations of ventral organization and torsion used to subdivide the family Gonyaulacaceae cannot always be applied rigidly. In detail, *Operculodinium bahamense* is shown to have an unusual ventral tabulation in which the first apical plate contacts the apical pore complex but not the sulcus. The new term "episert" is proposed to describe this plate relationship, which appears to have evolved independently in several lineages of the suborder Gonyaulacineae.

INTRODUCTION

Little is known of the tabulation pattern in the cyst-defined dinoflagellate genus *Operculodinium* Wall, 1967 emend. Matsuoka et al., 1997 despite its widespread occurrence in Cenozoic deposits and large number of constituent species. A particular hindrance is that *Operculodinium* is restricted to species with a nontabular to intratabular process distribution, and nearly all of the 57 known species of the genus (Fensome et al., 2008; Marret and Kim, 2009) have at most only subtle and incomplete traces of tabulation beyond the possession of a precingular archeopyle (Matsuoka et al., 1997). Moreover, few extant cyst morphotypes attributable to *Operculodinium* have been linked to a motile stage (Head, 1996a). Of these, a morphotype known as *Operculodinium centrocarpum* sensu Wall and Dale (1966) is known to be a cyst of the theca-defined species *Protoceratium reticulatum* (Claparède and Lachmann, 1859) Bütschli, 1885. Fensome et al. (1993, 2008) assigned the genus *Protoceratium* Bergh, 1881 questionably to their new subfamily Cribroperidinioideae (family Gonyaulacaceae, Lindemann 1928), while treating *Operculodinium* as the cyst stage of *Protoceratium*. The assignation was tentative because Fensome et al. (1993) had been unable to find clear illustrations of the dorsal tabulation of *Protoceratium* in the literature, but they noted that the presence of small first and second postcingular homologs and prominent plate overgrowths are typical of the Cribroperidinioideae. Fensome et al. (2008) explicitly included *Operculodinium* in the Cribroperidinioideae.

The extinct species *Operculodinium bahamense* Head *in* Head and Westphal, 1999 emend., described from the Gelasian (lower Pleistocene) of the Clino Core, Bahamas (Head and Westphal, 1999; Fig. 1), is typical of the genus *Operculodinium* except that its central body bears low sutural ridges that completely express the tabulation aside from some details of the sulcus. It is basically similar also to the cyst of the theca-defined species *Protoceratium reticulatum*. Determining the tabulation in both *Operculodinium bahamense* and *Protoceratium reticulatum* therefore promises to elucidate the phylogenetic relationship between *Operculodinium* and *Protoceratium* and reveal whether these genera indeed belong in the subfamily Cribroperidinioideae.

The aims of this study are therefore to describe in detail the tabulation in *Operculodinium bahamense*, re-evaluate and compare the tabulation in *Protoceratium reticulatum*, and assess the suprageneric positions of their respective genera.

MATERIAL

A total of 68 samples from Ocean Drilling Program (ODP) Site 1007, Bahamas Platform (N 24°30.25′ W 79°19.34′; Figs. 1, 2) were processed for palynology at Brock University, Canada. This site is just 19 km southwest of the Clino Core, which is the type locality of *Operculodinium bahamense*. Samples range from upper Oligocene (Chattian) through upper lower Pleistocene (Calabrian) and consist of gray and white foraminiferal wackestones/packstones, either fully or partially lithified. The lower samples are from ODP Hole 1007C and the upper samples from ODP Hole 1007B (Fig. 2). In addition, the palynological slides containing the type material of *Operculodinium bahamense* from the Clino Core, including specimens originally illustrated by Head and Westphal (1999), were reexamined for morphological consistency with specimens from ODP Site 1007.

Protoceratium reticulatum is redescribed and illustrated exclusively from published information (Paulsen, 1907; Lebour, 1925; Woloszynska, 1929; Schiller, 1936 and references therein; Wailes, 1939; Wall and Dale, 1968; Dodge, 1989; Matsuoka, 1990; Hansen et al., 1997; Hoppenrath et al., 2009; Hernández-

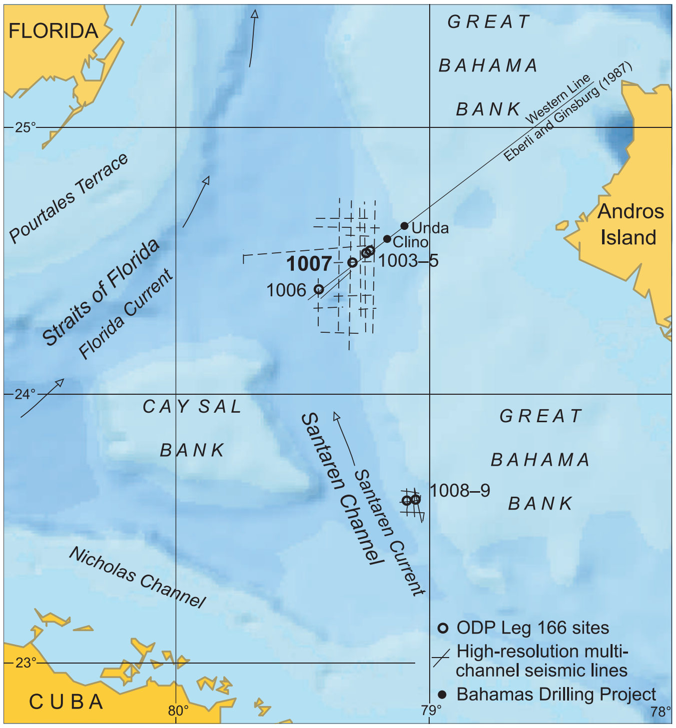

FIGURE 1—Location of Ocean Drilling Program (ODP) Site 1007, at the toe-of-slope of the present Bahamian platform margin, along with other ODP Leg 166 sites, seismic sections, and the Clino Core which is the type locality for *Operculodinium bahamense*. Modified from Anselmetti et al. (2000, fig. 1).

Becerril et al., 2010; Álvarez et al., 2011; Röder et al., 2012; and as *Gonyaulax grindleyei* in Reinecke, 1967; von Stoch, 1969; Balech, 1988).

METHODS

For each palynological sample, between 3.6 and 27 g of rock were dried overnight at 50°C, weighed and then demineralized in cold hydrochloric and hydrofluoric acids in turn, with distilled water washes in between and afterwards. The organic residues were sieved using a 10-µm Nitex nylon screen, transferred to a 15 ml test tube, and placed in an ultrasound bath for 30 seconds, after which two drops of safranin-o were added. The residues were then sieved again prior to strew mounting on microscope slides using Kaiser's glycerine jelly. Where possible, two slides were made from residue sieved at 10 µm, and one from residue sieved at 20 µm. At least 250 dinoflagellate cysts were counted from the 10 µm slides of each sample where possible, and well-preserved specimens of *Operculodinium bahamense* from the 10 µm and 20 µm slides were selected for detailed morphological analysis. Specimens were observed using light microscopy (LM) with a Leica DM 2500 microscope, and photographed using a Leica DMR

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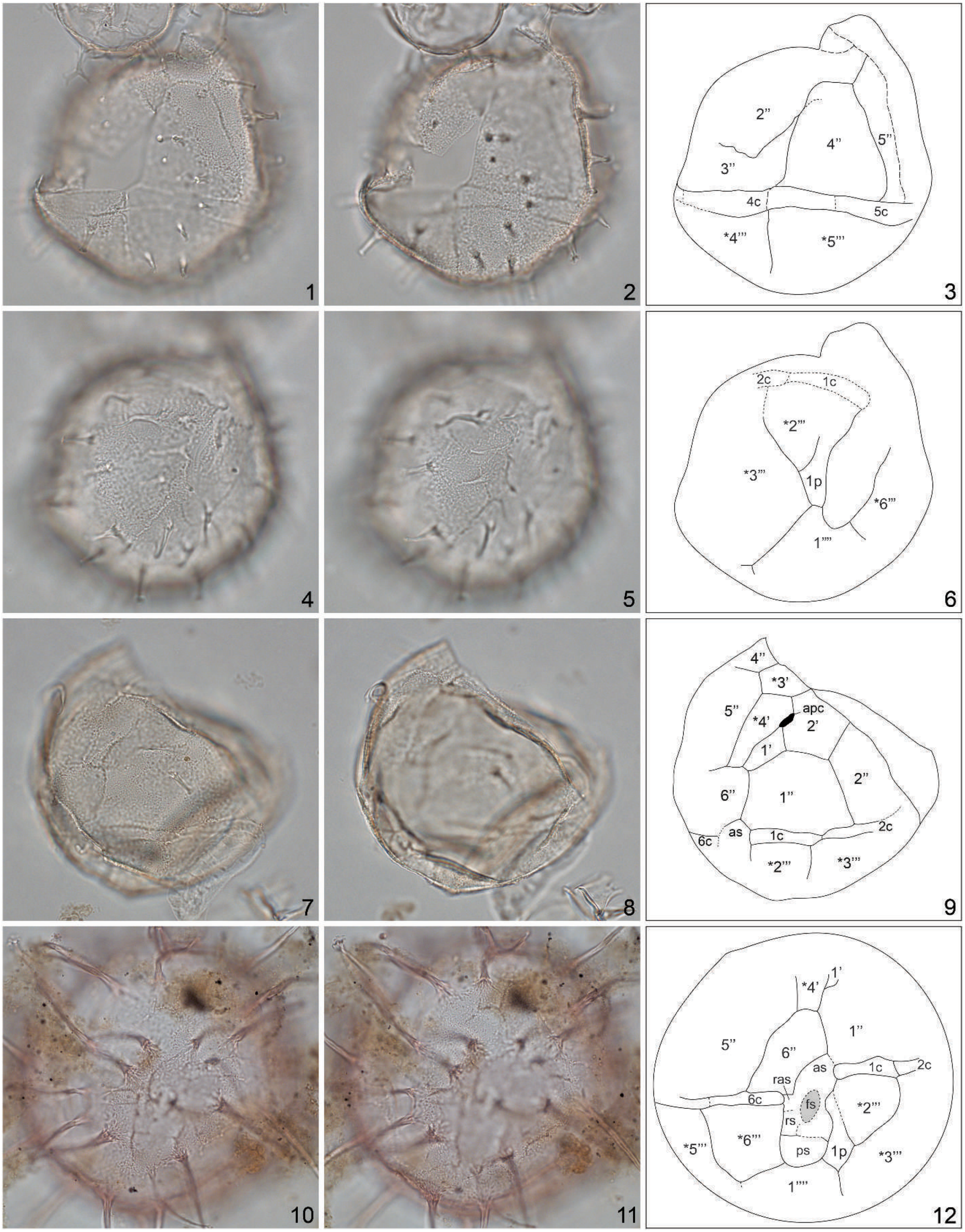
FIGURE 2—Stratigraphic distribution of *Operculodinium bahamense* at ODP Site 1007, showing counts of specimens both with processes and without. The calcareous nannofossil zonation is from the Shipboard Scientific Party (1997), the planktonic foraminiferal zones are from Wright and Kroon (2000), and the series/subseries designations follow Hilgen et al. (2012) except that the Pliocene–Pleistocene boundary follows the international geological time scale (Gibbard and Head, 2010; Gibbard et al., 2010). Boundaries are based on interpolated ages from linear sedimentary plots and age-depth calculations using Wade et al. (2011) for the planktonic foraminiferal datums and Raffi et al. (2006) for the calcareous nannofossils. A "+" indicates specimens recorded outside of the counts.

ODP Site 1007								Raw Counts		
Series / Subseries		Planktonic foraminiferal zone	Calcareous nannofossil zone	Hole 1007B/C	Sample (core, section, interval in cm)	Depth (meters below sea floor)	Age (Ma)	*O. bahamense* (processes)	*O. bahamense* (no processes)	Total in-situ dinoflagellate cysts
PLEISTOCENE	Lower	N22	NN19	B	3H-3, 045–047	22.45	1.399			264
				B	4H-2, 044–046	30.44	1.538	2	1	351
				B	5H-2, 091–093	42.41	1.705	+	2	321
			NN16–NN18	B	6H-1, 115–116.6	50.65	1.869			305
		N21		B	7H-1, 085–087	58.35	2.414			321
				B	8H-1, 097–099	67.97	2.461	1	1	316
				B	9H-5, 085–086	83.35	2.537		1	321
				B	10H-2, 065–068	86.85	2.554	1		358
PLIOCENE	Upper			B	11X-2, 093–095	94.13	2.590	+	3	308
				B	13X-CC, 025–026	110.85	2.672			311
				B	15X-3, 134–135.5	133.84	2.785	+		311
				B	17X-5, 130.5–132	157.40	2.902	2		323
				B	19X-1, 104–106	167.14	2.949			314
				B	20X-CC, 001–002	175.42	2.990			333
				B	21X-CC, 029–031	184.99	3.037			321
	Lower	N19	NN14–NN15	B	23X-4, 095–096	208.55	4.424	14		354
				B	24X-4, 117–118.5	218.07	4.498	16		326
				B	25X-5, 081–082	228.31	4.578	18	+	338
				B	26X-5, 054–055	237.14	4.647	27	+	349
				B	27X-4, 102–103.5	245.32	4.710	23	+	339
				B	28X-3, 130.5–132	253.41	4.774	9	1	344
		N17–N19		B	30X-3, 144–145	272.14	4.919	8	+	382
				B	31X-1, 008–009	276.98	4.957	13	+	417
?			?	B	32X-2, 068–070	288.19	5.055	9	+	391
MIOCENE	Upper		NN11	B	34X-1, 003–005	304.33	5.472	20		297
				C	3R-1, 060.5–062	321.85	5.924	12		338
		N16	NN10	C	4R-2, 005–007	332.10	8.739	7		309
				C	7R-1, 120–123	360.80	9.008	2		378
				C	8R-1, 129–132	370.59	9.100	+		315
				C	9R-1, 001–004	378.91	9.179	6		219
				C	10R-1,108-113	389.60	9.279	10	1	314
				C	11R-1,130-134	399.40	9.371	6		357
				C	12R-2, 010–015	408.70	9.459	1	1	609
				C	13R-1, 043–046	417.83	9.545	3		297
			NN9	C	15R-1, 043–046	437.13	9.760	13	+	358
				C	19R-1, 070–073	475.90	10.440	7	1	163
		N14	NN8							
		N13	NN7	C	25R-2, 145–150	535.80	11.600	2		91
	Middle	N12		C	26R-1, 071–074.5	543.21	11.716	17		311
				C	27R-1, 031–034	552.41	11.791	9		327
				C	28R-1, 087–090	562.67	11.875	2		327
				C	30R-1, 015–018	581.15	12.026	3		298
				C	32R-1, 073–076	600.93	12.187			269
				C	37R-1, 048–051	648.78	12.578	5		330
				C	43R-1, 012–015	706.12	13.046	4		232
				C	45R-1, 016–019	725.36	13.203	5		242
		N11	NN6	C	50R-1, 124–129	774.50	13.402	7		325
			NN5	C	51R-1, 094–097	783.94	13.596	13		351
		N10		C	52R-3, 132–137	793.24	13.895	20		308
		N9								
		N8		C	54R-2, 000–004	813.30	14.618	14		381
				C	57R-1, 012–015	840.82	14.802	4		162
			NN4	C	61R-1, 000–005	879.10	15.514	11		142
	Lower			C	63R-2, 146–149	901.20	16.128			11
		N7								
		N6		C	66R-3, 147–152	931.60	17.604	22		181
				C	68R-2, 000–005	948.00	17.773	5		127
				C	70R-1, 014–019	965.80	17.956	9		288
		N5	NN3							
			NN2	C	76R-2, 003–008	1025.00	19.335	11		62
				C	78R-4, 135–140	1048.70	19.782	19		279
				C	80R-4, 000–005	1065.80	20.105	48		251
				C	82R-2, 005–009	1082.80	20.425	32		175
				C	84R-6, 000–005	1107.60	22.254	3		175
		N4	NN1	C	86R-3, 136–141	1123.80	22.880	15		373
OLIGOCENE	Upper			C	88R-5, 000–005	1144.90	23.080	26		337
				C	90R-1, 128–133	1159.70	23.220	25		362
				C	92R-1, 012–017	1177.80	23.391	21		348
				C	94R-2, 000–005	1198.20	23.583	1		29
				C	95R-1, 049–052	1206.99	23.666			38
		P22	NP25	C	96R-3, 009–013	1218.10	23.771	2		80
				C	97R-1, 080–083	1226.60	23.852			10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microscope with Leica DFC 490 camera at Brock University (Figs. 3–6).

A Zeiss model Evo 40vp scanning electron microscope (SEM) at the Smithsonian Tropical Research Institute, Panama, operating at an acceleration voltage of 8–15 KV, was used to illustrate fine details of the wall surface (Fig. 6.7, 6.10–6.12) and tabulation (Figs. 6.8, 7) in *Operculodinium bahamense*. Samples were sputter coated with a gold/palladium (60/40) layer no thicker than ~50 nm (three to four minutes at 100 μA), using an Anatech Hummer VI-A sputtering system.

The tabulation patterns for both *Operculodinium bahamense* and *Protoceratium reticulatum* were then reconstructed and compared (Figs. 8, 9).

The timescale of Hilgen et al. (2012) is used except that the base of the Gelasian Stage, Pleistocene Series, and Quaternary System are all placed at 2.58 Ma, in accordance with the current international geological time scale (Gibbard and Head, 2010; Gibbard et al., 2010).

All specimens illustrated using LM are housed in the Invertebrate Section of the Department of Palaeobiology, Royal Ontario Museum, Toronto, Ontario, Canada, under the catalogue number ROM 53304 for the holotype of *Operculodinium bahamense*, and ROM 62317–62325A and 62325B for the remainder. For each of these specimens, the sample number, microscope slide designation, England Finder reference, and ROM number are given.

MORPHOLOGICAL TERMINOLOGY

Labeling of tabulation follows a modified Kofoid system that recognizes homologs (Bujak, 1980; Fensome et al., 1993, 1996; de Verteuil and Norris, 1996).

The new term episert is introduced alongside the existing terms insert, metasert, and exsert to describe the relationship between the first apical plate, or its homolog, and the surrounding plates (Evitt, 1985; Fensome et al., 1993; Fensome et al., 1996; Fig. 10). For insert, metasert, and exsert, the first apical plate or its homolog (1’ or *1’) always contacts the sulcus and may (insert), or may not (metasert, exsert), contact the apical pore complex (Fig. 10.1–10.3). Episert describes a different episomal tabulation pattern in which the first apical plate (1’) contacts the apical pore complex, by definition, but does not contact the sulcus (Fig. 10.4–10.6). With respect to the episert condition, which is here recognized in *Operculodinium bahamense*, three specific topologies are presently recognized. Episert type I (Fig. 10.4) is where 1’ is obstructed posteriorly by a contact between the sixth precingular plate or its homolog (6’’ or *6’’) and the first precingular plate (1’’). Episert type II (Fig. 10.5) is where both 6’’ or *6’’ and 4’ or *4’ contact 1’’. Episert type III (Fig. 10.6) is where 4’ or *4’, and possibly Q but not 6’’ or *6’’, contacts 1’’.

SYSTEMATIC PALEONTOLOGY

Abbreviations are as follows: apc=apical pore complex; as=anterior sulcal plate; ras=right accessory sulcal plate; rs=right sulcal plate; ls=left sulcal plate; ps=posterior sulcal plate; fs=flagellar scar.

Division Dinoflagellata (Bütschli, 1885) 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

Remarks.—As noted by Fensome et al. (1993), the family Gonyaulacaceae Lindemann, 1928 has the following characteristics: 1) a sexiform hyposomal tabulation pattern, 2) a sulcus more or less midventrally located, 3) an approximately symmetrical antapical outline, 4) absence of strong dorsoventral compression, and 5) six precingular plates. In an attempt to reflect phylogenetic relationships within this family, Fensome et al. (1993) erected three subfamilies, each distinguished by a combination of two features consistently observed through time, namely ventral organization and torsion of the hyposome. The subfamily Leptodinioideae Fensome et al., 1993, whose type genus is *Leptodinium* Klement, 1960, comprises gonyaulacaceans with an L-type ventral organization and sinistral or neutral torsion of the hyposome; the subfamily Cribroperidinioideae Fensome et al., 1993, whose type genus is *Cribroperidinium* Neale and Sarjeant, 1962, comprises gonyaulacaceans with an L-type ventral organization and dextral torsion of the hyposome; and the subfamily Gonyaulacoideae Fensome et al., 1993, whose type genus is *Gonyaulax* Diesing, 1866, comprises gonyaulacaceans with an S-type ventral organization and neutral torsion of the hyposome (Fensome et al., 1993; Fig. 11). Fensome et al. gave an age range of Middle Jurassic through present day for the Cribroperidinioideae, Late Jurassic through present day for the Gonyaulacoideae, and Middle Jurassic through Miocene for the Leptodinioideae but noted that some extant species presently assigned to *Gonyaulax* might be leptodinioideans.

Subfamily uncertain
Genus Operculodinium (Wall, 1967) emend.
Matsuoka et al., 1997

Type.—The holotype of *Operculodinium centrocarpum* (Deflandre and Cookson, 1955) Wall, 1967 emend. Matsuoka et al., 1997.

Operculodinium bahamense Head *in* Head and Westphal,
1999 emend.
Figures 2–7, 8.1, 9.1–9.5, 10.4, 10.5, 12

1989 *Operculodinium* sp. 3; Manum, Boulter, Gunnarsdottir, Rangnes, and Scholze, p. 13, figs. 5, 6.
1999 *Operculodinium bahamense* Head *in* Head and Westphal, p. 12, 13, figs. 9.9–9.14, 10.1–10.5.

Diagnosis.—Original diagnosis: “A large species of *Operculodinium* with long, sparsely distributed processes; tabulation relatively completely expressed by low sutural ridges that appear as dark narrow lines on surface” (Head *in* Head and Westphal, 1999, p. 13).

Emended diagnosis: a large species of *Operculodinium* with spherical to subspherical central body whose spongy-fibrous luxuria bears sparsely-distributed, solid to fibrous processes with expanded fibrous bases, terminating distally in minute expansions with aculeate margins. Low sutural ridges demarcate

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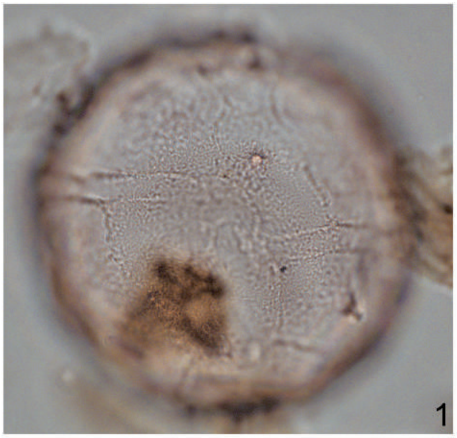
Figure 3—Photomicrographs and tracings of *Operculodinium bahamense* Head *in* Head and Westphal, 1999 emend. *1–6*, holotype, right latero-dorsal view: *1*, upper surface; *2*, slightly lower focus; *4*, ventral surface; *5*, slightly lower focus; with tracings of *3*, dorsal surface showing archeopyle (3’’) and partly broken and overfolded 2’’; *6*, ventral surface, note near alignment of *4’’’/*5’’’ with 3’’/4’’ indicating neutral torsion; central body length, 81 μm; Clino core CUS-K11, slide 3, G18/2; ROM 53433; *7–9*, left latero-apical view: *7*, left latero-apical surface; *8*, slightly lower focus; *9*, tracing of this surface showing narrow contact between 1’ and 6’’ (episert type I), and *3’ separated from the apc; central body maximum diameter, 89 μm; Sample 1007C-15R-1, 43–46 cm, slide 20 μm, N47/1; ROM 62317; *10–12*, ventral view: *10*, ventral surface; *11*, slightly lower focus; *12*, tracing of ventral surface showing details of sulcal tabulation and 1’ separated from 6’’ (episert type II); central body length, 110 μm; Sample 1007C-3R-1, 60.5–62 cm, slide 2 (10 μm), P53/3; ROM 62318.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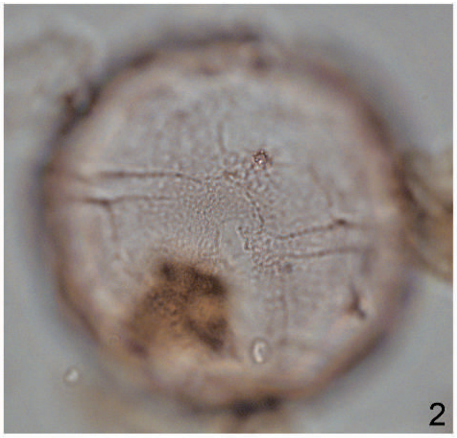
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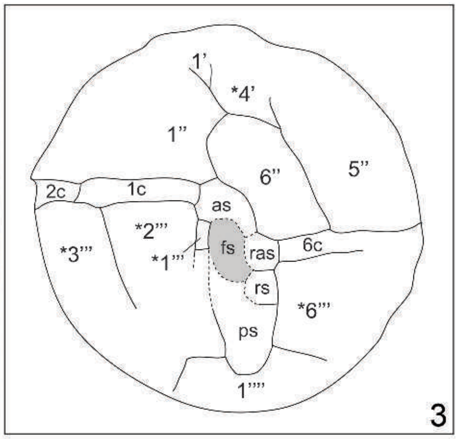
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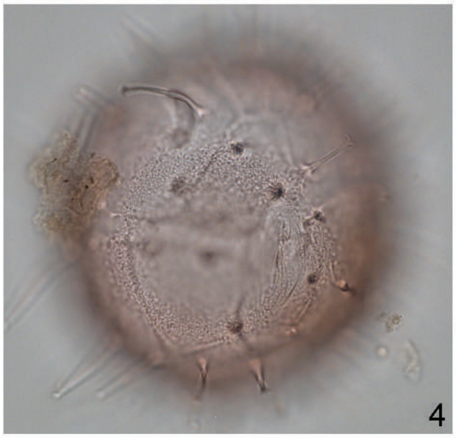
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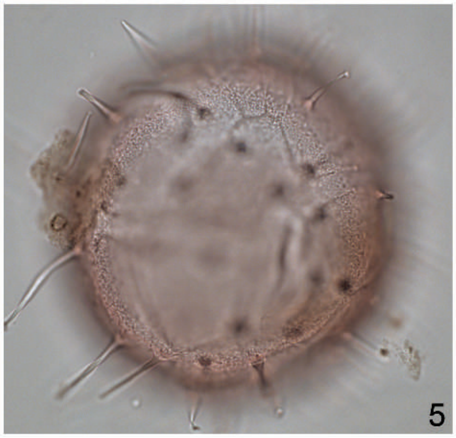
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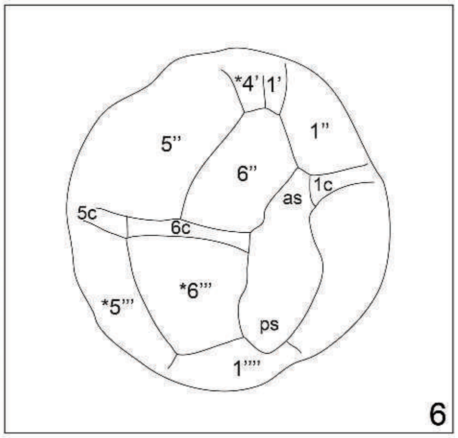
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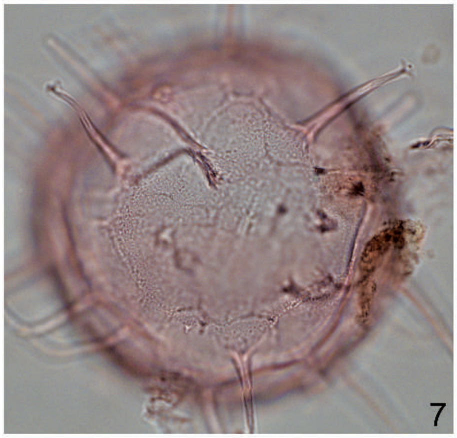
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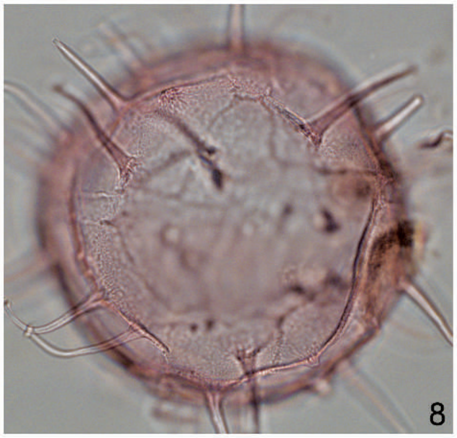
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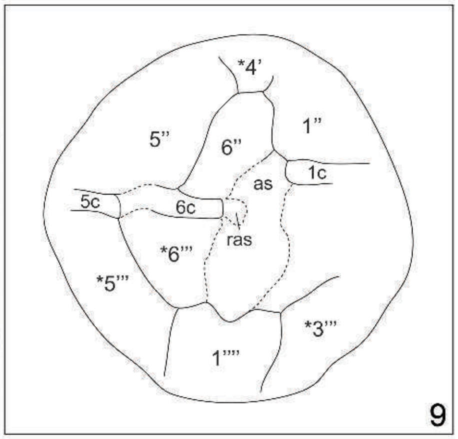
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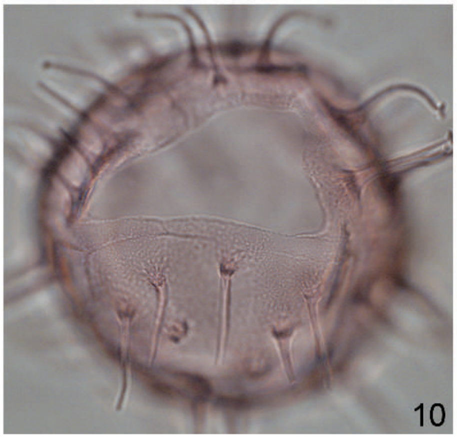
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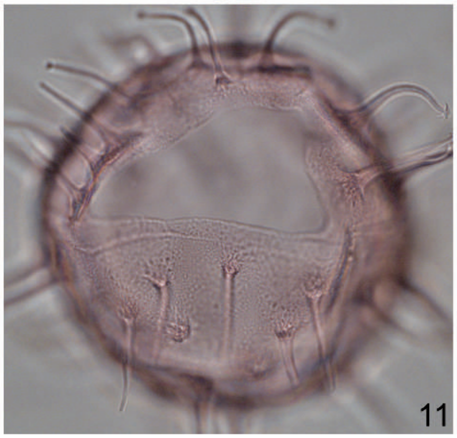
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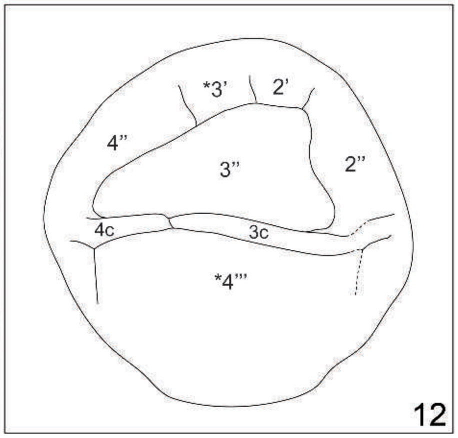
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gonyaulacacean, sexiform tabulation with modified L-type ventral organization, neutrally contorted dorsal tabulation, and episert 1'. Plate formula is 2'+*2', 6'', 6c, 5s, *6''', 1p, 1''''. Archeopyle large, angles rounded, formed by loss of third precingular plate; operculum free.

Description.—Central body spherical to subspherical, wall consisting of thin, solid pedium, and thicker, distally open, spongy-fibrous luxuria. Surface spongy-fibrous to punctate (Fig. 6.7, 6.10–6.12), may become smoother on sulcus (Fig. 6.12). Scattered granules may also occur over surface (Fig. 6.8). Processes slender, solid to fibrous, circular in cross-section, with fibrous expanded bases; terminate distally in minute, flared platforms with recurved, aculeate margins, each bearing up to about eight aculeae. Process distribution sparse, apparently intratabular, with the largest plates bearing up to around seven processes (e.g., seven on plate *4''', Fig. 5.1, 5.2; six on plate 3'', Head and Westphal, 1999, fig. 10.4, 10.5), usually up to four or five processes on other large plates (e.g., 1'' and *3'''), and usually no more than one on smaller plates (e.g., *2'''). Process bases observed to cross plate boundaries only in the midventral region (Fig. 6.8) and occasionally along the cingulum. Process distribution irregular within plate boundaries, adjacent processes may be widely separated or so close as to be fused at base. Processes up to ~35 μm long, with length sometimes variable on individual specimens; some specimens devoid of processes (Figs. 2, 6.1–6.6). Shorter, more slender processes may occur in the sulcal area (Fig. 6.8). Gonyaulacacean tabulation indicated by low (~1.0 μm or less) sutural ridges composed of coalesced fibers or granules, appearing under bright field microscopy as dark narrow lines on surface. Apical pore complex (apc) located at anterior pole, slightly left of sulcal midline; individual constituents of apc not distinguishable under light microscopy (Fig. 5.7–5.9) or SEM (Fig. 6.10). Third apical homologue (*3') does not reach apc owing to narrow 2'/*4' contact (Figs. 5.7–5.9, 9.1, 9.3–9.5). First apical plate (1') either a trapezium reaching 6'' where 1'/6''shorter than 1'/2' (Fig. 9.1, 9.4) representing episert type I topology (Fig. 10.4), or inverted isosceles triangle not reaching 6'' owing to narrow *4'/1'' contact (Fig. 9.5) representing episert type II topology (Fig. 10.5). Plate *4' somewhat larger than plate *3'. Plate 3'', lost in archeopyle formation, directly opposite sulcus. Left margin of plate 6'' curves to left, over anterior sulcal plate (as), causing broad 6''/1'' contact. Plate 1'' always contacts the anterior sulcal plate. Cingulum narrow, equatorial, descending with displacement of about one width. Sulcus broad, aligned, modified L-type (see Remarks); sulcal plates poorly expressed, but anterior sulcal (as), right accessory sulcal (ras), right sulcal (rs), left sulcal (ls), posterior sulcal (ps) plates may all be partially delineated by faint traces, though not necessarily on every cyst; flagellar scar indicated by elongate indentation left of ras; posterior margin of ps convex where contacting first antapical plate (1''''). First postcingular homolog (*1''') small, does not contact cingulum (Fig. 6.12, 9.4, 9.5); labeled as such because occurs within sulcal area; remaining five plates in series obligatorily labeled postcingular homologs. Neutral torsion on dorsal surface indicated by approximate alignment of *4'''/*5''' with 3''/4'' at cingulum, although *4'''/*5''' typically offset slightly to left of 3''/4'' (as for holotype; Fig. 3.1–3.3). Boundary *3'''/*4''' offset conspicuously to left of 2''/3'' at cingulum (e.g., Fig. 5.1–5.3). Sexiform hypocystal tabulation; antapical plate (1'''') six sided but approximately trapezoidal, widening ventrally; 1''''/*6''' longer than 1''''/1p (Fig. 9.2). Archeopyle large, precingular Type 1P (3''), has rounded angles; low sutural crests, where visible, closely follow entire archeopyle margin including rounded angles (Fig. 6.7); operculum free.

Measurements.—Holotype: central body length, 81 μm; process length, 6–11, μm; wall thickness, ~1.7 μm (Head and Westphal, 1999). Upper Pliocene and lower Pleistocene, Great Bahama Bank: central body maximum diameter, 80(89.7)106 μm; average process length, 7(15.0)24 μm; wall thickness, ~0.6(1.1)1.7 μm; 30 specimens measured (Head and Westphal, 1999). ODP Site 1007 (Miocene): central body maximum diameter, 55(84.0)110 μm; average process length, 0(17.2)35.2 μm; wall thickness, ~0.5–1.3 μm; 25 specimens measured. ODP Site 1007 (Pliocene): central body maximum diameter, 68(86.1)106 μm; average process length, 0(10.5)31.8 μm; wall thickness, ~0.8–3.0 μm; 14 specimens measured. ODP Site 1007 (Pleistocene): central body maximum diameter, 74(84.1)96 μm; average process length, 0(6.0)13.6 μm; wall thickness, ~0.8–2.0 μm; seven specimens measured. Overall dimensions: central body maximum diameter, 55(86.1)110 μm; average process length, 0(13.9)35.2 μm; wall thickness, ~0.5–3.0 μm; 76 specimens measured. See Figure 12.

Holotype.—Sample CUS-K 11, slide 3; England Finder reference G18/2. ROM 53304. Clino core, 234.12 m (768.13 ft) below mud pit; lower Pleistocene (Gelasian), ~2.1–2.3 Ma (Head and Westphal, 1999, fig. 9.9–9.12; Fig. 3.1–3.6).

Type locality, Clino Core (N 24°36′07″, W 79°10′41″), western margin of the Great Bahama Bank (Head and Westphal, 1999; Fig. 1).

Comparison.—*Operculodinium giganteum* Wall, 1967, from the upper Pleistocene and Holocene of the Yucatan Basin, Caribbean, may also have sutural lines, but processes are consistently shorter (2–4 μm) and more densely distributed, and the sulcus is narrow and marked by two parallel rows of spines (Wall, 1967). *Operculodinium wallii* Matsuoka, 1983, from the upper Miocene–lower Pleistocene of Japan, lacks sutural lines or ridges. *Operculodinium floridium* Warny and Wrenn, 1997, from the upper Miocene of Morocco, has shorter (2–10 μm), conical processes whose distribution is dense and distinctly intratabular, and lacks sutural lines or ridges.

Occurrence.—*Operculodinium bahamense* is present from the Chattian (upper Oligocene) through Calabrian (lower Pleistocene) at Site 1007, Great Bahama Bank (this study), but its relatively continuous occurrence through the entire studied interval implies that its full stratigraphic range extends above and below the observed occurrence at this site. However, it has a conspicuous highest common occurrence near the lower/upper Pliocene boundary. Head and Westphal (1999, but using the current time scale) recorded it from the Zanclean (lower Pliocene) and Gelasian (lower lower Pleistocene) of the Clino Core, Great Bahama Bank. It has also been recorded from the upper middle Miocene (ODP Hole 642C) and upper Miocene (ODP Hole 643A) of the Norwegian Sea (as *Operculodinium* sp. 3 in Manum et al., 1989; Bleil, 1989).

Remarks.—The present emendation incorporates new details of the tabulation including the recognition of episert type I and type II topologies (Fig. 10.4, 10.5), identification of a modified L-type ventral organization (Fig. 9.4, 9.5), and neutral torsion on the

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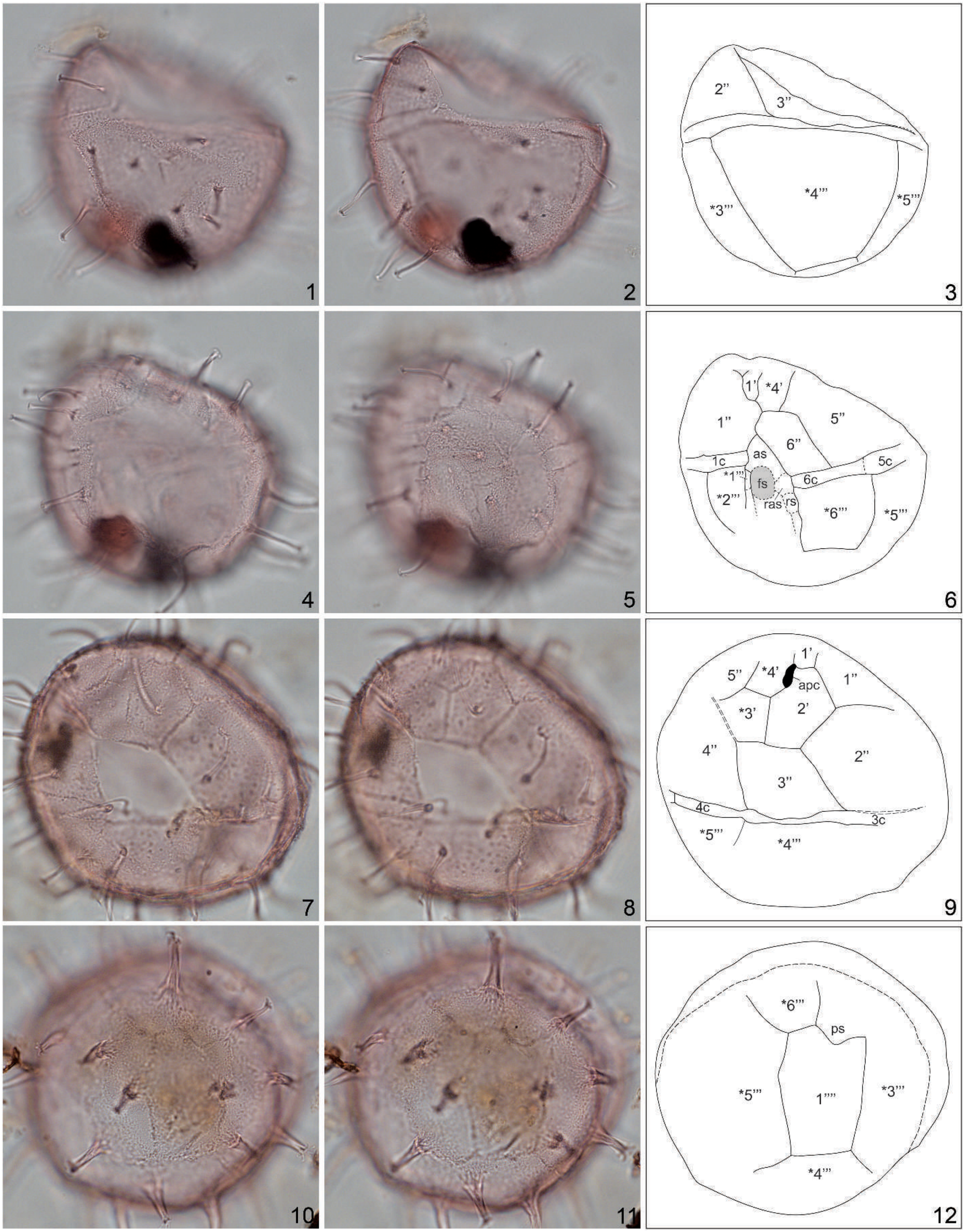
FIGURE *4*—Photomicrographs and tracings of *Operculodinium bahamense* Head *in* Head and Westphal, 1999 emend. *1–3*, dorsal view: *1*, ventral surface; *2*, slightly lower focus on sulcus; *3*, tracing of ventral surface showing details of sulcal tabulation and 1' separated from 6'' (episert type II); central body length, 84 μm; Sample 1007C-7R-1, 120–123 cm, slide 2 (10 μm), L57/1; ROM 62319; *4–6*, ventral view: *4*, ventral surface; *5*, slightly lower focus; *6*, tracing of ventral surface showing narrow contact between 1' and 6'' (episert type I); central body length, 86 μm; Sample 1007C-9R-1, 1–4 cm, slide 1 (10 μm), T33/0; ROM 62320; *7–12*, ventral view: *7*, ventral surface; *8*, slightly lower focus; *9*, tracing of ventral surface showing *4' but not 1' in contact with 6'' (episert type II); *10*, dorsal surface, *11*, slightly lower focus; *12*, tracing of dorsal surface showing alignment of *4'''/*5''' with 3''/4'' indicating neutral torsion; central body length, 83 μm; Sample 1007C-10R-1, 108–113 cm, slide 2 (10 μm), O30/1; ROM 62321.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dorsal surface (Fig. 9.3). The last two features require that this species be assigned to the subfamily Leptodinioideae, although such details are unknown for the type species *Operculodinium centrocarpum*, for which reason the genus is not assigned here to a subfamily. It is acknowledged that the ventral organization is not strictly L-type because plate 6’’ may not always contact 1’ (episert type II topology), and 6’’ has an anterior margin that is dithigmate rectilinear at its contact with *4’ and 1’ (in the case of episert type I topology) rather than the dithigmate geniculate condition that characterizes L-type organization. In other respects, however, the ventral organization has characteristic L-type features including a straight sulcus and a cingulum with ends that are not strongly offset or overhanging (Evitt, 1985, p. 98–100).

The distribution of processes was originally considered nontabular (Head *in* Head and Westphal, 1999) on account of process bases sometimes observed to cross plate boundaries. However, this seems to be restricted to the midventral region and occasionally along the cingulum. Moreover, shorter, more slender processes have been observed in the sulcal area (Fig. 6.8), implying that tabulation has some control over process development. Hence, process distribution appears to be intratabular, although the sparse and irregular distribution of processes makes this difficult to confirm. The genus *Operculodinium* includes species with nontabular and intratabular process distributions (Matsuoka et al., 1997).

The emendation also allows for the wide range in process length seen in our ODP Site 1007 material: specimens with longest processes (average process length up to 35.2 μm) occur in the Miocene and Pliocene, those from the Pleistocene typically have much shorter processes (average process length no more than 13.6 μm), and specimens almost devoid of processes occur throughout (Figs. 2, 12). It has not been determined whether shorter processes are linked to reduced paleosalinity, as for the cysts of *Protoceratium reticulatum* (e.g., Head, 2007; Mertens et al., 2011), but this possibility is being investigated. No statistically significant correlation was found between maximum central body diameter and length of processes.

Subfamily Cribroperidinioideae Fensome et al., 1993
Genus Protoceratium Bergh, 1881

Type.—The holotype of *Protoceratium aceros* Bergh, 1881, this species since considered a taxonomic junior synonym of *Protoceratium reticulatum* (Claparède and Lachmann, 1859) Bütschli, 1885 (Schiller, 1936).

Protoceratium reticulatum (Claparède and Lachmann, 1859) Bütschli, 1885
Figures 8.2, 9.6–9.13

1859 *Peridinium reticulatum* Claparède and Lachmann, p. 405, pl. 20, fig. 3.
1881 *Protoceratium aceros* Bergh, p. 242, pl. 14, fig. 36.
1885 *Protoceratium reticulatum* (Claparède and Lachmann); Bütschli, p. 1007, pl. 52, fig. 2.
1936 *Protoceratium reticulatum* (Claparède and Lachmann); Schiller, p. 322, 323, fig. 338a–338d.
1967 *Gonyaulax grindleyi* Reinecke, p.157–160, pl. 1, fig. 1.
1969 *Gonyaulax grindleyi* Reinecke; von Stoch, p. 563, figs. 6–8.
1982 *Gonyaulax grindleyi* Reinecke; Dodge, p. 210, 211, fig. 25G–25I, pl. VIb.
1986 *Gonyaulax grindleyi* Reinecke; Helenes, p. 96, 98, text-fig. 14.
1988 *Gonyaulax grindleyi* Reinecke; Balech, p.169, pl. 77, figs. 1–5.
1989 *Protoceratium reticulatum* (Claparède and Lachmann); Dodge, p. 294, fig. 39–42.
1996 *Gonyaulax grindleyi* Reinecke; Steidinger and Tangen, p. 506, 507, pls. 4D, 42.
1997 *Protoceratium reticulatum* (Claparède and Lachmann); Hansen et al., figs. 2–23.
2009 *Protoceratium reticulatum* (Claparède and Lachmann); Hoppenrath et al., p. 181–183, figs. k–n.
2011 *Protoceratium reticulatum* (Claparède and Lachmann); Álvarez et al., fig. 5A–5D.
2012 *Protoceratium reticulatum* (Claparède and Lachmann); Röder et al., fig. 1a–1j.

Description.—Theca polyhedral, slightly longer than broad, epitheca conical, shoulders at boundary of apical/precingular plate series, hypotheca rounded, slightly larger than epitheca. Mature thecae strongly reticulated, usually with one trichocyst pore at center of each reticulation. Some cells have broad sutural bands ornamented with longitudinal and transverse ridges. Plate formula typically 4’ (or 2’+*2’), 6’’, 6c, *6’’’, 1p, 1’’’’. First apical plate insert, usually with distinct pore on right anterior margin. Fourth apical plate or homolog of significant size (as large or larger than 3’). Sixth precingular plate five-sided with broadly geniculate anterior margin, does not approach a triangular shape, contacts first apical plate. Cingulum slightly anterior to equator, descending with no overhang, displaced ventrally by about one width, with prominent lists. Sulcus straight, reaching almost to antapex. All features of L-type ventral organization consistently present. First postcingular homolog (*1’’’) small, contained within sulcus. Posterior intercalary plate (1p) long, narrow. Antapical plate (1’’’’) six-sided, trapezoidal, with distinctive arcuate inset at contact with posterior margin of sulcus; contact with 1p shorter than with 6’’’. Sexiform hypothecal tabulation, with antapical tabulation weakly asymmetrical (e.g., von Stosch, 1969; Fig. 9.7) or more strongly asymmetrical (e.g., Reinecke, 1967; Fig. 9.13). Plate 3’’ relatively small, approximately centered on dorsoventral midline. Hypotheca usually dextrally contorted to varying degrees, with *4’’’/*5’’’ boundary displaced to left of 3’’/4’’ boundary at cingulum (Fig. 9.8). Modified from various sources cited herein.

Cyst has spherical, thin-walled (<1.0 μm) central body, with outer surface bearing scattered granules or columellae, often fine and faintly visible, with interconnecting fibrils sometimes discernible. Processes numerous, nontabular, erect, slender, hollow, circular in cross-section, have smooth surface, may broaden slightly at base, distally open with minute distal expansions. Archeopyle precingular, large with rounded angles, formed by release of 3’’; no other indications of tabulation. Central body diameter ~33–48 μm; process length up to ~14 μm. Based on Rochon et al. (1999, as *Operculodinium centrocarpum* sensu Wall and Dale, 1966).

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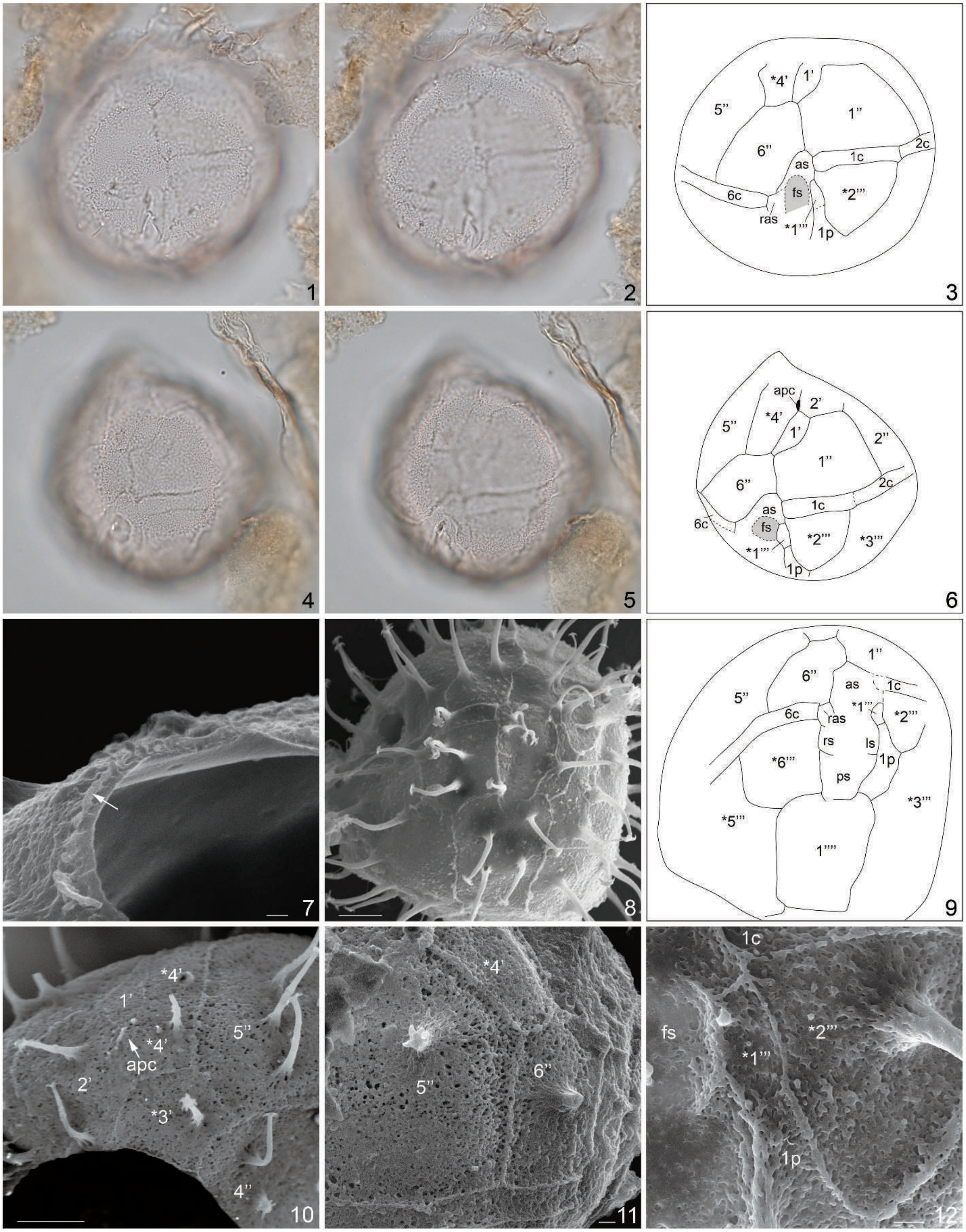
Figure 5—Photomicrographs and tracings of *Operculodinium bahamense* Head *in* Head and Westphal, 1999 emend. *1–6*, dorsal view: *1*, dorsal surface; *2*, slightly lower focus; *3*, tracing of dorsal surface; *4*, ventral surface; *5*, slightly lower focus; *6*, tracing of ventral surface showing 1’ separated from 6’’ (episert type II), and small *1’’’ separated from 1c; central body length, 90 μm; Sample 1007C-10R-1, 108–113 cm, slide 1 (10 μm), P32/3; ROM 62322; *7–9*, ventral view: *7*, dorsal surface; *8*, slightly lower focus; *9*, tracing of dorsal surface showing *3’ not in contact with the apc; central body maximum diameter, 86 μm; Sample 1007C-54R-2, 0–4 cm, slide 2 (10 μm), J43/0; ROM 62323; *10–12*, antapical view: *10*, antapical surface; *11*, slightly lower focus; *12*, tracing of antapical surface; central body maximum diameter, 81 μm; Sample 1007B-24X-4, 117–118.5 cm, slide 2 (10 μm), P66/0; ROM 62324.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Holotype.—Claparède and Lachmann (1859, pl. 20, fig. 3, as *Peridinium reticulatum*).

Type locality, North Sea, collected from modern plankton (Claparède and Lachmann, 1859).

Occurrence.—*Protoceratium reticulatum* is considered a cosmopolitan species and its cysts have a global distribution today (Zonneveld et al., 2013). The cyst has an uncertain stratigraphic range, partly owing to its conflation in the literature with the larger and more robust *Operculodinium centrocarpum* sensu stricto. It extends at least down to the upper Miocene of Belgium (Louwye and De Schepper, 2010, as *Operculodinium centrocarpum* sensu Wall and Dale, 1966).

Remarks.—Considerable variation exists in the geometry and topology of plates, especially the climactals. The third apical plate may (Wall and Dale, 1968; von Stosch, 1969, fig. 7a; Fig. 9.10) or may not (Hansen et al., 1997) contact the apc, and when it does not it has been labeled an anterior intercalary plate (1a; e.g., Dodge, 1989) although we refer to it as the third apical homolog (*3’; Fig. 9.6, 9.8, 9.11). Similarly, the first apical plate may (e.g., von Stosch, 1969; Fig. 9.6, 9.9, 9.10, 9.12) or may not (Balech, 1988; Fig. 9.11) contact the second apical plate. A ventral pore is usually documented on the right anterior margin of the first apical plate (e.g., Hansen et al., 1997; Fig. 9.6, 9.9–9.12) although it was not recorded either by Reinecke (1967) or Hernández-Becerril et al. (2010). Specimens in culture may display anomalous epithecal tabulation with a subdivided *3’ as well as the presence of extra precingular plates (Hansen et al., 1997; Fig. 9.12). Plankton from the North Sea have yielded rare exceptions in which plate 3’’ is divided into two (Fig. 9.12), and the antapical plate similarly divided (von Stosch, 1969).

Torsion in *Protoceratium reticulatum* is often difficult to recognize because of the strong ornament that obscures plate boundaries, and illustrations of the dorsal surface are illusive in the literature (Fensome et al., 1993). However, recent studies by Röder et al. (2012, fig. 1h, 1j) for specimens from the North Sea (the type area for *Protoceratium reticulatum*) and Álvarez et al. (2011, fig. 5A) for specimens from the Pacific off Chile, show pronounced dextral torsion in which the *4’’’/*5’’’ boundary is middorsal. This new evidence, together with L-type ventral organization, small *1’’’ and *2’’’, and plate overgrowths (Fensome et al., 1993), allow *Protoceratium reticulatum* to be assigned unequivocally to the Cribroperidinioideae. However, dextral torsion seems to be a variable feature, as it is weakly expressed judging from reconstructions of the hypotheca (e.g., Wall and Dale, 1968, pl. 3, figs. 7, 8; von Stosch, 1969, fig. 7b), and has even been shown as neutral (Lebour, 1925, pl. 12, fig. 7). Moreover, slight sinistral torsion has been reported by Wailes (1939, fig. 73B, but dextral in fig. 73C) for Pacific specimens off Canada, and Hernández-Becerril et al. (2010) illustrated specimens from the Mexican Pacific that appear slightly sinistrally to neutrally contorted (Hernández-Becerril et al., 2010, figs. 23 and 24, respectively).

TAXONOMIC AND NOMENCLATURAL STATUS OF *PROTOCERATIUM RETICULATUM*

Protoceratium reticulatum was first described, from the North Sea, as *Peridinium reticulatum* by Claparède and Lachmann (1859) and was transferred to the genus *Protoceratium* Bergh, 1881 by Bütschli (1885). It was subsequently accepted that *Protoceratium aceros* Bergh, 1881, described from Danish waters in the Kattegat and serving as the type of the genus *Protoceratium*, was a taxonomic junior synonym of *Protoceratium reticulatum* (Schiller, 1936; Hansen et al., 1997). The type of the genus *Protoceratium* remains the holotype of *Protoceratium aceros* but its correct name is *Protoceratium reticulatum*. The genus *Protoceratium* has itself been considered a junior synonym of *Gonyaulax*, depending upon how broadly authors have treated the circumscription of the latter. Neither original illustrations of *Protoceratium reticulatum* nor *Protoceratium aceros* included analyses of the tabulation, this contributing to confusion between these two species and with the later *Gonyaulax grindleyi* Reinecke, 1967, described from waters off South Africa (Reinecke, 1967).

Balech (1988) accepted the tabulation formula Po, 0a, 3’, 6’’, 6c, 6’’’, 2’’’’, and 6s for *Protoceratium*, based on the tabulation of *Protoceratium spinulosum* (Murray and Whitting, 1899) Schiller, 1936 (Balech, 1988, pl. 73, figs. 1–4). For the genus *Gonyaulax*, Balech (1988) accepted a tabulation formula Po, 0–3a, 3–4’, 6’’, 6c, 6’’’, 2’’’’ (i.e., 1p and 1’’’’), and 7–9s, thus distinguishing *Protoceratium* from *Gonyaulax* on a smaller number of sulcal plates.

Dodge’s (1989) detailed examination of 20 species ascribed to *Gonyaulax* led him to restrict the tabulation of *Gonyaulax* to Po, 3’, 2a, 6’’, 6c, 4–8s, 5’’’, 1p, and 1’’’’, and resurrect *Protoceratium* with the tabulation Po, 3’, 1a, 6’’, 6c, s, 6’’’, 1p, 1’’’’. The presence of two anterior intercalary plates in *Gonyaulax* and only one in *Protoceratium* served as the most notable difference between these genera. Von Stoch (1969) had earlier recognized that *Protoceratium reticulatum* was synonymous with *Gonyaulax grindleyi* Reinecke 1967, but accepted that it belonged in the genus *Gonyaulax*. As the name *Gonyaulax reticulatum* was preoccupied (by *Gonyaulax reticulatum* Kofoid and Michener, 1911), von Stoch maintained *Gonyaulax grindleyi* as the only acceptable name. Dodge (1989) by resurrecting the genus *Protoceratium* allowed this species to be reunited with its earlier name, as *Protoceratium reticulatum*.

Edwards and Andrle (1992) did not accept Dodge’s narrow concept of *Gonyaulax*, and by including forms with 0–3 anterior intercalary plates in this genus, retained the species in *Gonyaulax* as *G. grindleyi*.

Steidinger and Tangen (1996) gave the plate formula for *Gonyaulax* as Po, 3’, 2a, 6’’, 6c, 7s, 6’’’, and 2’’’’ (i.e., 1p and 1’’’’), and noted that details of the apical pore complex might be used to further separate species or groups within the genus. For *Protoceratium*, Steidinger and Tangen accepted the plate formula Po, 3’, 0a, 6’’, 6c, 6s, 6’’’, and 2’’’’ (i.e., 1p and

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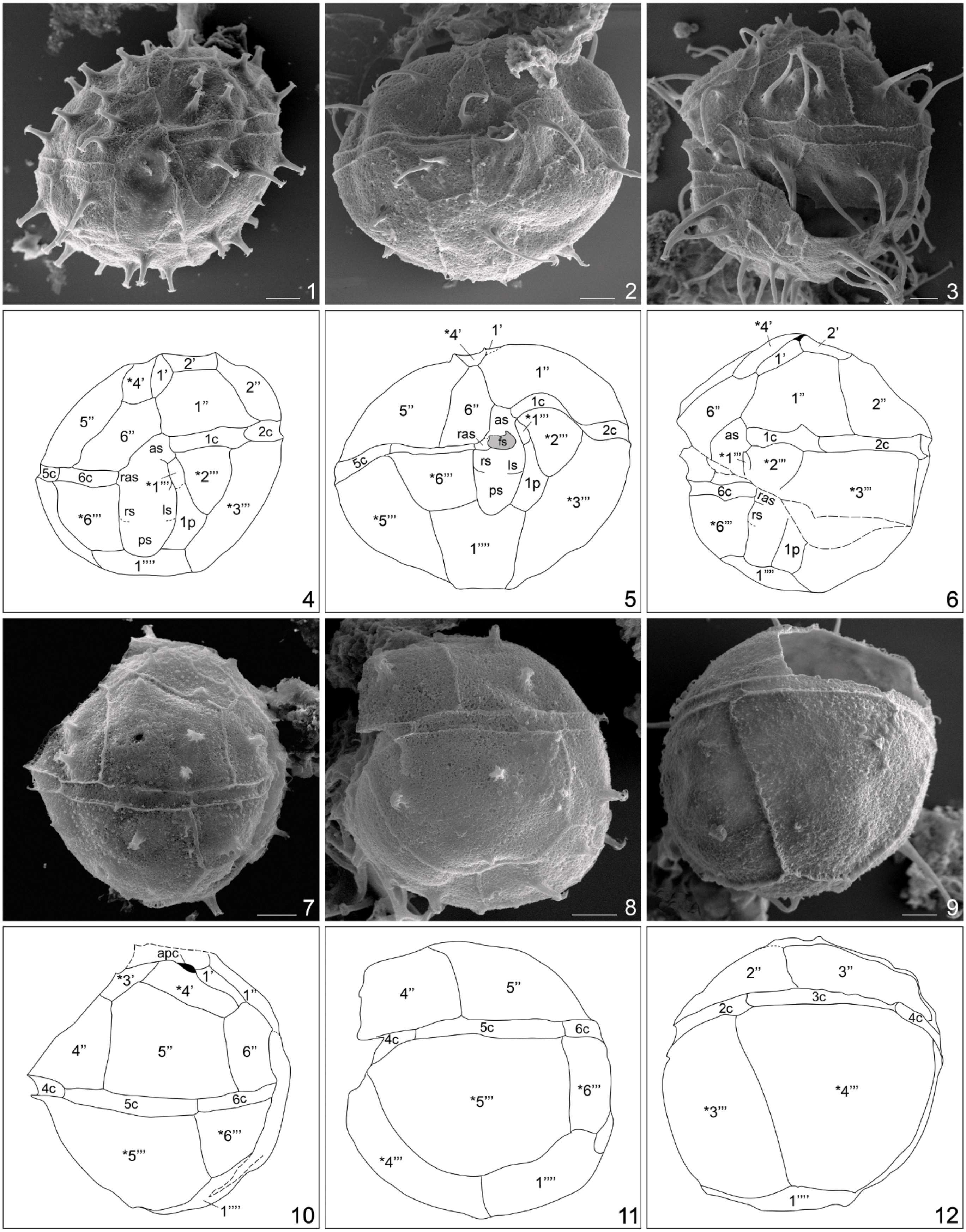
Figure *6*—Photomicrographs and tracings of *Operculodinium bahamense* Head *in* Head and Westphal, 1999 emend. *1–6*, LM photos and tracings of specimens without processes; *7–12*, SEM photos and a tracing; scale bar for *7*=1.0 μm, for *8* and *10*=10 μm, for *11* and *12*=2 μm. *1–3*, ventral view: *1*, ventral surface; *2*, slightly lower focus; *3*, tracing of ventral surface showing details of sulcus, *1’’’ separated from 1c, and 1’ in narrow contact with 6’’ (episert type I); central body length 77 μm; Sample 1007B-31X-1, 8–9 cm, slide 20 μm, H60/4; ROM 62325A; *4–6*, ventral view: *4*, ventral surface; *5*, slightly lower focus; *6*, tracing of ventral surface showing *1’’’ separated from 1c, and 1’ in narrow contact with 6’’ (episert type I); central body length 81 μm; Sample 1007B-31X-1, 8–9 cm, slide 20 μm, T42/0; ROM 62325B; *7*, dorsal view of anterior margin of archeopyle showing sutural crest (arrow) close to margin; Sample 1007C-3R-1, 60.5–62 cm; *8*, *9*, ventral view showing details of ventral tabulation; note in *8*, smaller, more slender processes in sulcal area, and some processes located on plate boundaries, e.g., at *6’’’/1’’’’/ps junction and 5’’/6’’/6c junction; Sample 1007C-54R-2, 0–4 cm; *10*, dorso-apical view showing anterior margin of archeopyle and apical plates including weakly-expressed apical pore complex (apc); Sample 1007C-10R-1, 108–113 cm; *11*, right-lateral view showing spongy-fibrous luxuria and processes with fibrous bases; Sample 1007C-3R-1, 60.5–62 cm; *12*, ventral view showing spongy-fibrous luxuria, surface becoming punctate to smooth within sulcus; note that *1’’’ does not quite contact cingulum (an enlargement of specimen in Fig. 7.1); Sample 1007C-3R-1, 60.5–62 cm.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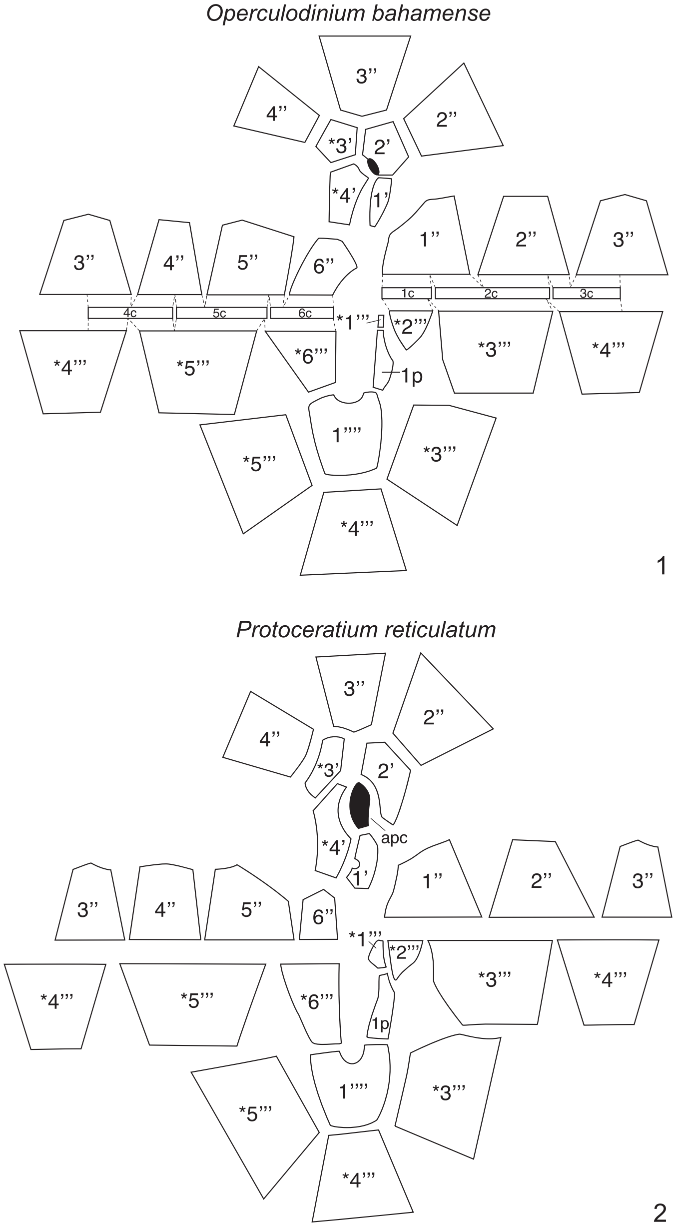
12

1’’’’). However, they considered *G. grindleyi* not to belong to *Protoceratium* on the assumption that the existing 3’ plate is really derived from a 2a intercalary plate, but noted that further interpretation was required. They also observed that the apical pore complex in *G. Grindleyi* is similar to species of *Alexandrium* and not to *Protoceratium*.

Hansen et al. (1997) conducted a detailed morphological study of *Protoceratium reticulatum* from the southern Kattegat, not far from the type locality of *Protoceratium aceros*. They confirmed that *Protoceratium aceros*, *Protoceratium reticulatum*, and *Gonyaulax grindleyi* were all synonymous, with the name *Protoceratium reticulatum* taking priority. They described the tabulation as 3’, 1a, 6’’, 6’’’, 1p, and 1’’’’, but noted that nearly 50% of cells analyzed showed contact between 1a and the apc, so that by strict Kofoidian labeling the tabulation would be 4’, 0a, 6’’, 6’’’, 1p, and 1’’’’ for those cells (Fig. 9.10). They also noted that for cultured cells, the epithecal tabulation was often anomalous, showing a subdivided 1a plate (i.e., plate 3’; Fig. 9.12) and the development of extra precingular plates, as noted above. They cautioned against using tabulation alone to define taxa, and called for cyst type, apc details, plate homology, general cell outline, and cell fine structure all to be used as additional criteria. Hansen et al. (1997) noted that tabulation and fine structure in *Protoceratium reticulatum* indicate a close relationship to the genus *Gonyaulax*, but they sustained the *Protoceratium* pending further knowledge of fine structural diversity within the genus *Gonyaulax*.

We sustain *Protoceratium* as a genus distinct from *Gonyaulax* on a combination of five lines of evidence. Firstly, the epithecal tabulation appears distinct for *Protoceratium*, based on four climactal plates in *Protoceratium* and five in *Gonyaulax* (Dodge, 1989). Secondly, the ventral organization is of L-type in *Protoceratium reticulatum*, whereas in many species of *Gonyaulax*, including the type species *G. spinifera* (Claparède and Lachmann, 1859) Diesing 1866, it is strongly S-type. Thirdly, the resting cyst of *Protoceratium reticulatum* is characterized by numerous unconnected nontabular processes and an absence of tabulation except for the archeopyle, which is a single precingular plate with rounded angles, and hence assignable to the cyst-defined genus *Operculodinium*; whereas all known resting cysts of the genus *Gonyaulax* (Head, 1996a) either have processes and/or crests that are sutural in distribution (e.g., the cyst-defined genera *Achomosphaera*, *Impagidinium*, *Nematosphaeropsis*, and *Spiniferites*) or lack processes but have precingular archeopyles with well-defined angles (e.g., the cyst-defined genera *Ataxiodinium*, *Bitectatodinium*, and *Tectatodinium*). Fourthly, the apical pore in *Protoceratium* is a narrow slit whereas in *Gonyaulax* it is overlain by a lenticular coverplate (Hansen et al., 1997). Fifthly, molecular studies (e.g., Saldarriaga et al., 2004; Kim et al., 2006; Howard et al., 2009; Riccardi et al., 2009; Kudela et al., 2010) together imply that *Protoceratium reticulatum* is not closely related to species presently analyzed within the genus *Gonyaulax* including the type species *Gonyaulax spinifera*.


Operculodinium bahamense

Protoceratium reticulatum

FIGURE 8— “Exploded” schematic representation of the tabulation in typical specimens. *1*, *Operculodinium bahamense* Head *in* Head and Westphal, 1999 emend. (present study); *2*, *Protoceratium reticulatum* (Claparède and Lachmann, 1859) Bütschli, 1885 (after various sources including von Stosch, 1969; Balech, 1988; and Hansen et al., 1997). All tabulation elements are labeled according to modified Kofoid labelling. Note the overall similarity between these two species, other than the broad contact between 6’’ and 1’’ in *O. bahamense* and its resulting episert condition for 1’. Sulcal plates are omitted for simplicity.

The cyst of *Protoceratium reticulatum* was first given a paleontological name by Wall and Dale (1966) who recovered it from the western Atlantic plankton and referred it to the Miocene species *Operculodinium* (then *Baltisphaeridium*) *centrocarpum* (Deflandre and Cookson, 1955) Wall, 1967. It was subsequently realized that the Miocene species was larger and more robust (Head and Wrenn, 1992; Head, 1996a, 1996b; Matsuoka et al., 1997), and the smaller distinctive Quaternary morphotype was accordingly referred either to “*Operculodinium*

←

FIGURE 7—SEM photomicrographs and tracings of *Operculodinium bahamense* Head *in* Head and Westphal, 1999 emend. Scale bars=10 µm. All specimens are from Sample 1007C-3R-1, 60.5–62 cm, and each photomicrograph represents a different specimen. *1*, *2*, ventral views (see *Fig. 6.12* for enlargement of *1*); *3*, left lateral view; *7*, *8*, right lateral views; *9*, left dorso-lateral view. Note in *4*, *6*, and *10* a narrow contact between 1’ and 6’’ (episert type I), and in *5* the absence of such contact (episert type II); and in *4* and *6* the separation of *1’’’ from 1c. Specimen in *9* and *12* shows approximate alignment of *4’’’/*5’’’ with 3’’/4’’ (neutral torsion) and *3’’’/*4’’’ characteristically offset strongly to left of 2’’/3’’.

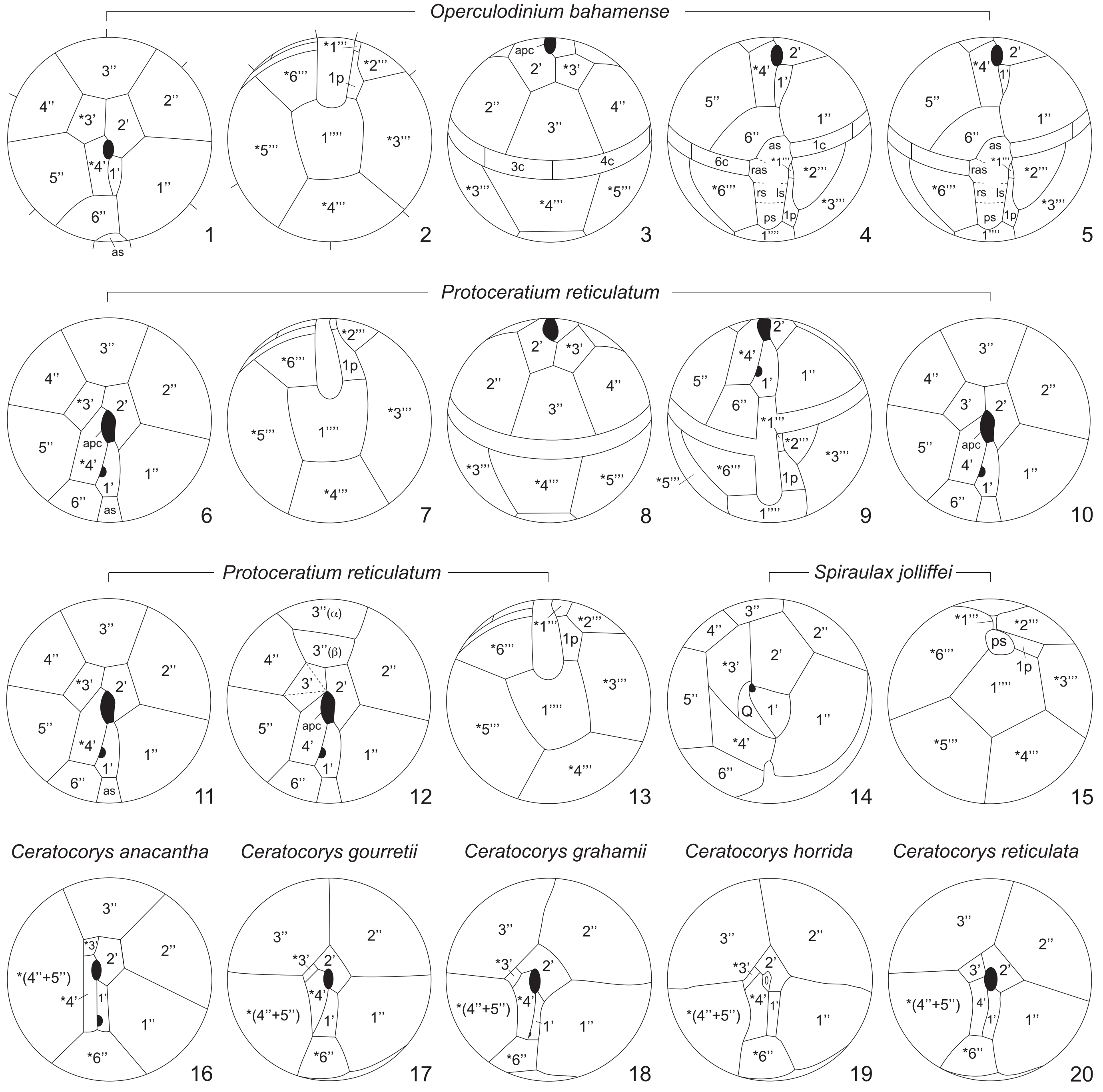


FIGURE 9—Tabulation patterns for *Operculodinium bahamense* Head *in* Head and Westphal, 1999 emend., and for the thecae of *Protoceratium reticulatum* (Claparède and Lachmann, 1859) Bütschli, 1885, *Spiraulax jolliffei* (Murray and Whitting, 1899) Kofoid, 1911b, and selected species of the genus *Ceratocorys* Stein, 1883, as projected onto a sphere. *1–5*, *Operculodinium bahamense*: *1–4*, apical, antapical, dorsal and ventral views, respectively, with *1*, *4* showing the more usual topology (episert type I) in which 1' narrowly contacts 6''; *5*, the alternative topology (episert type II) in which 1' does not contact 6''; short bars projecting from the equators in *1* and *2* represent cingular plate boundaries (this study); *6–13*, *Protoceratium reticulatum*: *6–9*, apical, antapical, dorsal and ventral views, respectively showing the typical tabulation pattern in which *3' is an apical homolog as it does not contact the apex; *8* in this example showing weak dextral torsion (after various sources including von Stosch, 1969; Balech, 1988; and Hansen et al., 1997); *10*, apical view showing the alternative topology in which 3' contacts the apical pore complex, resulting in a true Kofoid third apical plate (adapted from von Stosch, 1969, fig. 7a); *11*, apical view showing 1'' approximately in contact with the apical pore complex (adapted from Balech, 1988, pl. 77, fig. 2); *12*, apical view showing the subdivision of 3' as reported from a cultured cell and indicated by dashed lines (Hansen et al., 1997, fig. 4), and the anomalous division of the third precingular plate (3'') into constituents α and β (adapted from von Stosch, 1969, fig. 7a); *13*, antapical view in which *4''' has an unusually pronounced offset to the left of the dorsoventral midline, resulting in mild dextral torsion (reconstructed from Reinecke, 1967, fig. 1.D1); *14*, *15*, *Spiraulax jolliffei* showing apical and antapical views respectively, in which *4' broadly contacts 1'', resulting in an episert type III topology (modified from Carbonell-Moore, 1996a, fig. 2a, 2d); *16–20*, selected species of the genus *Ceratocorys* showing contact between *6'' and 1'', resulting in an episert type I topology: *16*, *Ceratocorys anacantha* Carbonell-Moore, 1996b (modified from Carbonell-Moore, 1996b, fig. 1b); *17*, *Ceratocorys gourretii* (modified from Balech, 1988, pl. 80, fig. 5) showing a distinctive topology in which *4' does not contact *6''; *18*, *Ceratocorys grahamii* Carbonell-Moore, 1996b (modified from Graham, 1942, fig. 50B as *Ceratocorys horrida*); *19*, *Ceratocorys horrida* Stein, 1883 (modified from Graham, 1942, fig. 44B, see also Balech, 1988, pl. 79, fig. 4); *20*, *Ceratocorys reticulata* Graham, 1942 (modified from Graham, 1942, fig. 55B).

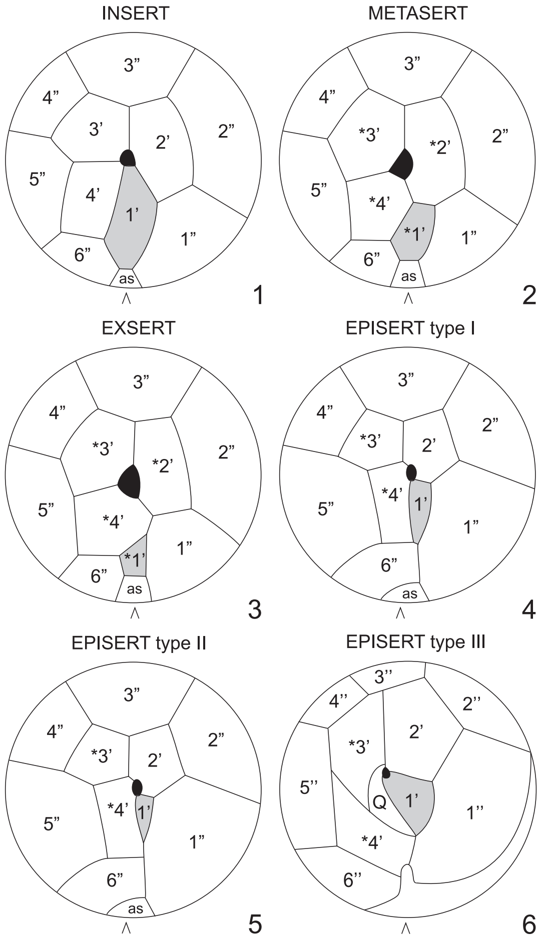


FIGURE *10*—Variations in relationship of the first apical plate or its homolog (shaded in gray) in the order Gonyaulacales. *1–3*, insert, metasert, and exsert conditions, respectively (from Fensome et al., 1996, text-fig. 34); *4–6*, different types of episert topology in which the first apical plate contacts the apical pore complex but not the sulcus: *4*, 5, based on *Operculodinium bahamense* Head *in* Head and Westphal, 1999 emend. (present study); *6*, based on *Spiraulax jolliffei* (Murray and Whitting, 1899) Kofoid, 1911b (modified from Carbonell-Moore, 1996a, fig. 2a). The apical pore complex is shown in black, Q=prepolar plate, and inverted “v” marks the position of the sulcus.

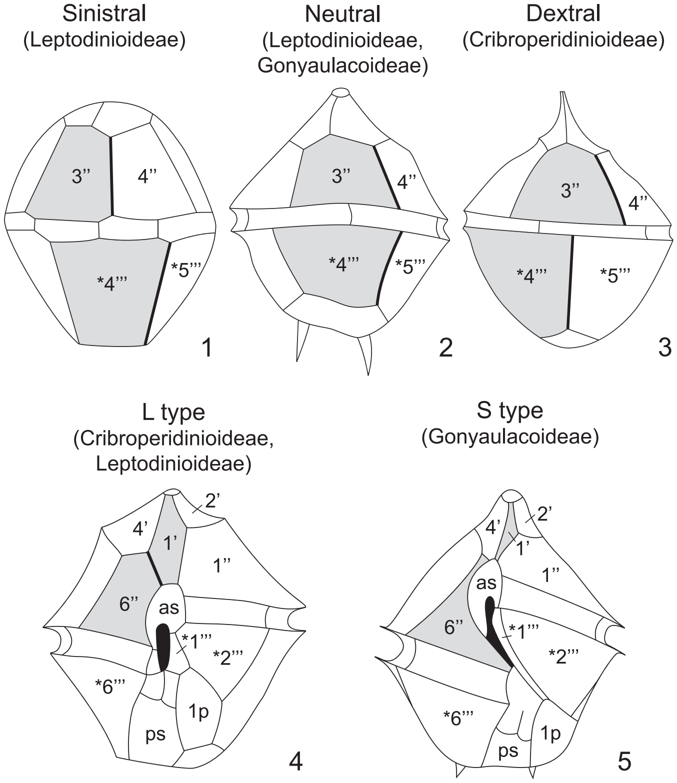


FIGURE *11*—Dorsal and ventral tabulation arrangements used to divide the Gonyaulacaceae into three subfamilies. *1–3*, dorsal surface showing torsional configurations as exemplified by: *1*, *Lithodinia jurassica* (Leptodinioideae); *2*, *Gonyaulax spinifera* (Gonyaulacoideae); *3*, *Cribroperidinium ventriosum* (Cribroperidinioideae); a heavy line emphasizes the relative positions of the 3’’/4’’ and *4’’’/*5’’’ boundaries, where 3’’/4’’ is either shifted to the left (sinistral torsion) or right (dextral torsion), or is aligned (neutral torsion); *4*, *5*, the two main types of ventral organization in the Gonyaulacaceae: *4*, L-type organization as exemplified by *Lingulodinium polyedrum* (Cribroperidinioideae); *5*, S-type organization as illustrated by *Gonyaulax spinifera* (Gonyaulacoideae) although an overhang at ends of the cingulum is not obligatory for S-type ventral organization (Evitt, 1985, fig. 5.12E–H). However, the quasi-triangular shape of 6’’ and its lack of contact with 1’ are characteristic features of S-type organization. The black area represents the flagellar pore. *Operculodinium bahamense* is herein assigned to the Leptodinioideae (L-type ventral organization, neutral torsion) although it has a modified L-type organization because 6’’ always contacts 1’’, and 6’’ may or may not contact 1’. *Protoceratium reticulatum* is here assigned to the Cribroperidinioideae (L-type ventral organization, dextral torsion). Modified from Fensome et al. (1996, text-figs. 39, 40).

centrocarpum sensu Wall and Dale, 1966”, or to “the cyst of *Protoceratium reticulatum*”. Objection to the latter name was based on the fact that four paleontological species have been linked to *Protoceratium reticulatum*, these being *Operculodinium centrocarpum* sensu Wall and Dale, 1966, *Operculodinium psilatum* Wall, 1967 described from the Holocene of the Caribbean, *Operculodinium israelianum* (Rossignol, 1962) Wall, 1967 described from the Quaternary of the Mediterranean, and *Pyxidinopsis psilata* (Wall and Dale *in* Wall et al., 1973) Head, 1994 described from the Quaternary of the Black Sea; as noted by Head (1996a). However, since *Protoceratium reticulatum* was originally described from the North Sea and is abundant there today, whereas *Operculodinium israelianum* and *Operculodinium psilatum* are not found in modern sediments of the North Sea, it seems highly improbable that either of these cyst types is a cyst of *Protoceratium reticulatum*. *Pyxidinopsis psilata* was recorded by Dale (1996, as *Tectatodinium psilatum*) from the Baltic Sea where *Protoceratium reticulatum* is also found. It now appears that these Baltic Sea cysts are not *Pyxidinopsis psilata* but low-salinity morphotypes of *Protoceratium reticulatum* (Mertens et al., 2011). Accordingly, we consider cysts previously labeled as *Operculodinium centrocarpum* sensu Wall and Dale, 1966 as being unambiguous cysts of *Protoceratium reticulatum*, to which they should now be referred.

SIGNIFICANCE OF EPISERT CONDITION

The episert condition, here documented in *Operculodinium bahamense* (Leptodinioideae, Gonyaulacaceae), represents an unusual pattern in which the first apical plate does not contact the sulcus. Two of the three specific episert topologies recognized occur in *Operculodinium bahamense*, these being episert type I (6’’ or *6’’ contacts 1’’; Fig. 9.4) and episert type II (6’’ or *6’’ and 4’ or *4’ contact 1’’; Fig. 9.5). The episert condition has also been reported in several extant species. In *Centrodinium mimeticum* (Balech, 1967) Taylor, 1976 (family uncertain, order Gonyaulacales), 6’’ narrowly contacts 1’’, with

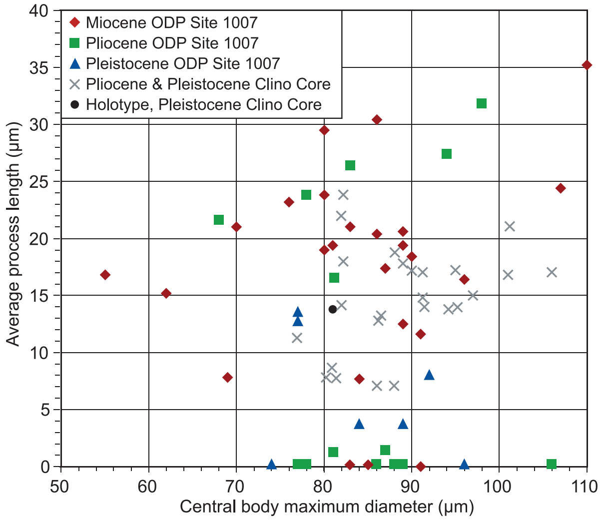


FIGURE 12—Measurements for *Operculodinium bahamense* from ODP Site 1007 (this study) and the Clino Core (Head and Westphal, 1999) showing no statistically significant relationship between the maximum central body diameter and average process length.

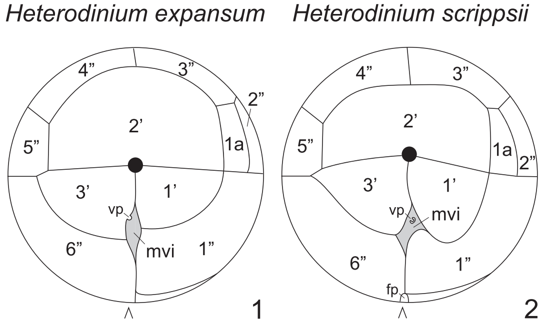


FIGURE 13—Epithecal tabulation in two species of the genus *Heterodinium* Kofoid, 1906 showing the midventral intercalary plate (shaded) which has been suggested to be a first apical homolog, although firm evidence is lacking (see text for discussion). *1*, based on *Heterodinium expansum* Kofoid 1907 (modified from Kofoid and Adamson, 1933, pl. 5, figs. 5–7); *2*, based on *Heterodinium scrippsii* Kofoid, 1906 (modified from Kofoid and Adamson, 1933, pl. 18, figs. 48–51). The apical pore complex is shown in black, vp=ventral pore, mvi=midventral intercalary plate, fp=flagellar pore, inverted “v”=position of sulcus.

1’ tapering to a point just before reaching the sulcus (Balech, 1967, fig. 131, as *Murrayella mimetica*), representing an episert type I topology. A specimen illustrated by Balech (1967, fig. 128) as *Murrayella splendida* also has 1’ tapering to a point close to the sulcus and possibly not touching it. A specimen of *Gonyaulax fragilis* (Schütt, 1895) Kofoid, 1911a (Gonyaulacoideae, Gonyaulacaceae) illustrated by Balech (1962, pl. 22, fig. 351) shows 6’’ in narrow contact, or possibly not in contact, with 1’’. *Spiraulax jolliffei* (Murray and Whitting, 1899) Kofoid, 1911b (Gonyaulacoideae, Gonyaulacaceae) has an extended *4’ that broadly contacts 1’’ (Kofoid, 1911b; Carbonell-Moore, 1996a; Fig. 9.14), representing an episert type III topology.

A characteristic feature of the genus *Ceratocorys* Stein, 1883 (Ceratocoryaceae Lindemann, 1928, Gonyaulacineae) is the broad contact of the sixth precingular homolog (4’’ and 5’’ are presumed fused, or one is missing) with the first precingular plate, resulting in an episert type I topology (Fig. 9.16–9.20). Interestingly, molecular data place the type of the genus, *Ceratocorys horrida*, in very close relationship with *Protoceratium reticulatum* (Saldarriaga et al., 2004) indicating that the Ceratocoryaceae, characterized by five precingular plates, L-type ventral organization and strong dextral torsion, is more closely related to the Gonyaulacaceae than previously thought. The episert condition is therefore presently known only in the gonyaulacinean families Ceratocoryaceae and Gonyaulacaceae, both of which appear closely related, although its rarity in the Gonyaulacaceae acknowledges the possibility that it arose independently in these two families.

Species of the genus *Heterodinium* Kofoid, 1906 (Heterodiniaceae Lindemann, 1928) have a small intercalary plate on the midventral epitheca that contacts neither the apex nor sulcus (Fig. 13). This plate bears a ventral pore that prompted Fensome et al. (1993) to suggest homology with the first apical plate in other gonyaulacaleans. This would result in yet another kind of relationship, in which the first apical homolog neither contacts the apical pore complex nor the sulcus. However, the ventral pore in gonyaulacaleans is not restricted to the first apical plate, and Dodge (1989) showed species of the genus *Gonyaulax*, including the type species *Gonyaulax spinifera*, possessing a ventral pore on the anterior margin of the fourth apical homolog (plate 2a of Dodge, 1989). Furthermore, *Heterodinium* species do not have an epithecal tabulation pattern that closely resembles *Operculodinium bahamense*, and molecular evidence suggests that *Heterodinium* is not a gonyaulacalean (Gomez et al., 2012).

DISCUSSION AND CONCLUSIONS

Reevaluation of the extant, theca-defined species *Protoceratium reticulatum* confirms dextral torsion of the hypotheca and therefore also its placement in the subfamily Cribroperidinioideae, as proposed tentatively by Fensome et al. (1993, 2008). This subfamily therefore contains at least two living species, *Protoceratium reticulatum* and *Lingulodinium polyedrum* (Stein, 1883) Dodge, 1989, in addition to the many fossil genera that extend its history continuously back to the Middle Jurassic (Fensome et al., 1993). However, along with other aspects of its tabulation, the degree of dextral torsion in *Protoceratium reticulatum* is variable, and specimens with neutral torsion (Lebour, 1925, pl. 12, fig. 7) and even slight sinistral torsion (Hernández-Becerril et al., 2010, fig. 23) have been reported. Whether this results from intraspecific variation or the existence of cryptic species will require closer future attention to the dorsal tabulation (often disregarded by biologists) coupled with molecular analysis. Nonetheless, specimens of *Protoceratium reticulatum* possessing all attributes of the subfamily Cribroperidinioideae have been reported from the North Sea (Röder et al., 2012), which is the type locality of this species. As *Protoceratium reticulatum* is the correct name for the type of the genus, the genus itself must be placed in the Cribroperidinioideae.

Restudy of the cyst-defined *Operculodinium bahamense* reveals a modified L-type ventral organization and neutral torsion, allowing this species to be placed in the subfamily Leptodinioideae. This extends upwards the highest known occurrence of this subfamily from the Miocene (Fensome et al., 1993) to upper lower Pleistocene (Fig. 2). Fensome et al. (1993) noted that some species presently assigned to the extant genus *Gonyaulax* might be leptodinioideans, and our observations reduce this stratigraphic gap.

The assignment of *Operculodinium bahamense* to the Leptodinioideae and *Protoceratium* to the Cribroperidinioideae is paradoxical because the cysts of *Protoceratium reticulatum* are fully circumscribed by the genus *Operculodinium*, suggesting a close relationship contrary to that implied by torsion. Moreover, detailed reconstructions of the tabulation in *Operculodinium bahamense* and *Protoceratium reticulatum* reveal strong similarities, even allowing for the episert first apical plate in *Operculodinium bahamense*. The sulcal areas are otherwise similar and characteristically L-type in both species, and the apical and antapical tabulation patterns are also similar. These similarities are more striking considering that comparisons of tabulation patterns are being made between thecae and cysts, and that thecamorphic features are not always reflected fully or indeed precisely on the cyst (see Matsuoka et al., 1998 for an extreme example of discordance). Small differences, such as the absence of a pore on the right anterior margin of the first apical plate in *Operculodinium bahamense*, and the isolation of the first postcingular homolog from the cingulum, are therefore not considered overly significant. Accordingly, it is quite unexpected that these two rather similar species should be separated at subfamily level, and implies either that the genus *Operculodinium* is polyphyletic or that the combinations of ventral organization and torsion used to subdivide the family Gonyaulacaceae cannot always be applied rigidly. A combination of both outcomes is in fact possible.

Helenes and Lucas-Clark (1997) and Helenes (2000) have already reported inconsistencies with the criteria used to distinguish subfamilies of the Gonyaulacaceae, and Fensome et al. (1993) themselves noted that these criteria are gradational in nature and in some instances tendencies only. However, with respect to the L-type and S-type tabulation patterns that form the basis of this subfamilial separation, Evitt (1985, p. 102) had remarked that while intermediate patterns do exist, they are fewer in number than those close to the L-type and S-type extremes. Nonetheless, authors continue to document disparities with the subdivision of Fensome et al. (1993). The modern cyst-defined species *Caspidinium rugosum* Marret et al., 2004 and *Pteridocysta cruciformis* Rochon et al., 2002, for example, exhibit a combination of dextral torsion and S-type ventral organization that hinders assignment at the subfamilial level. *Dimidium* Pearce, 2010, a monospecific genus from the Cretaceous of England, displays a combination of morphologic features characteristic of both the subfamily Leptodinioideae (e.g., L-type ventral organization) and Criboperidiniodeae (e.g., slight dextral organization), further emphasizing the intergradiation of these characters within the family Gonyaulacaceae.

The subfamilial affinity of the genus *Operculodinium* may never be known with certainty because the type species, *Operculodinium centrocarpum* sensu stricto, is extinct and has little reflected tabulation other than the archeopyle. Our results lead us to conclude that it would be premature to assign *Operculodinium* to any of the subfamilies of the Gonyaulacaceae at present, although a thorough revision of the genus is long overdue.

Three additional species could be scrutinized to further our understanding of the genus *Operculodinium. Operculodinium israelianum* (Rossignol, 1962) Wall, 1967 is more similar to *Operculodinium centrocarpum* than probably any other species of the genus, and indeed seems to intergrade with it in the lower Pleistocene (Head, 1996b). It is extant and could therefore be cultured to determine tabulation on the motile cell, and indeed be analyzed directly for molecular phylogeny.

Operculodinium floridium Warny and Wrenn, 1997 is an extinct Miocene–Pliocene species with distinctly intratabular processes that, with careful study, should reveal any dorsal torsion and basic organization of the sulcus. *Operculodinium giganteum* Wall, 1967, from the upper Pleistocene and Holocene of the Caribbean, might be even more profitable, as sutural lines may be present. Moreover, this species is possibly extant given its occurrence in Holocene deposits, although we are not aware of reports of living cysts.

Any future revision of the genus *Operculodinium* would need also to consider the large Cretaceous–Miocene genus *Exochosphaeridium* Davey et al., 1966 emend. Helenes, 2000, which differs from *Operculodinium* primarily in the common, but not obligatory, presence of a weakly developed apical horn. However, the one species of *Exochosphaeridium* for which the tabulation has been elucidated, *Exochosphaeridium alisitosense* Helenes, 2000, has an S-type ventral arrangement in contrast to both *Operculodinium bahamense* and *Protoceratium reticulatum*, but dextral torsion in common with *Protoceratium*. Determining such styles of tabulation represents an important challenge in assessing evolutionary relationships between superficially similar species, and in measuring the significance of criteria presently used to subdivide the Gonyaulacaceae.

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