Barker, P. F., Kennett, J. P., et al., 1990
Proceedings of the Ocean Drilling Program, Scientific Results, Vol. 113

26. LOWER CRETACEOUS DIATOMS FROM ODP LEG 113 SITE 693 (WEDDELL SEA). PART 2: RESTING SPORES, CHRYSOPHYCEAN CYSTS, AN ENDOSKELETAL DINOFLAGELLATE, AND NOTES ON THE ORIGIN OF DIATOMS[1]

David M. Harwood[2] and Rainer Gersonde[3]

ABSTRACT

A rich assemblage of Lower Cretaceous (lower Albian) siliceous microfossils was recovered at ODP Site 693 on the Weddell Sea margin of East Antarctica during Leg 113. This assemblage includes marine diatoms, silicoflagellates, radiolarians, Chrysophycean cysts, and endoskeletal dinoflagellates that are extraordinarily well preserved and in most cases, radiolarians excluded, represent the oldest known well-preserved assemblages of these groups. This chapter describes and illustrates Lower Cretaceous diatom resting spores, Chrysophycean cysts, and an endoskeletal dinoflagellate from Holes 693A and 693B. Six new diatom genera and 20 new species of probable diatom resting spores are presented here, in addition to 10 apparently new Chrysophycean cyst taxa and one endoskeletal dinoflagellate species. Diatom assemblages reported here and in the preceding chapter on vegetative forms (Part 1) suggest: (1) that diatoms were a complex, diverse, and widespread group by late Early Cretaceous time; (2) that diversities are high enough to anticipate the construction of a useful biostratigraphic zonation as more data become available; (3) that there is a considerable difference between assemblages in these Albian sediments and younger Senonian diatomites known around the world; (4) that both resting spore formation and the ability to form chains are ancient features of the diatoms; and (5) that diatom distribution in the Early Cretaceous may have been restricted to continental margins and interior seas, areas where resting spore formation is most common. Because these assemblages are the oldest, well-preserved diatom and chrysophycean floras known, this chapter concludes with a brief review and discussion on the origin of the diatoms, addressing both the role of resting spores and postulated links to Chrysophycean flagellates.

INTRODUCTION

ODP Leg 113 recovered a thin (11 m) Lower Cretaceous (lower Albian) diatomaceous horizon (Unit VI, radiolarian diatomite) from the top of an extensive "black shale" sequence (Unit VII) in two holes at Site 693 on a mid-slope bench on the Dronning Maud Land margin, Antarctica, eastern Weddell Sea (Fig. 1) in 2359 m water depth (Barker, Kennett, et al., 1988). The diatomaceous-bearing sediments occur within Sections 113-693A-44R-1 and -44R, CC, and 113-693B-19X-4, and are unconformably overlain by lower Oligocene sediments (Unit V) (Fig. 2).

The lower Albian age is based on associated palynomorphs (Mohr, this volume, chapter 29), and constrained by the dating of underlying sediments as upper Aptian/lower Albian by calcareous nannoplankton (Mutterlose and Wise, this volume), foraminifers (Leckie, this volume) and palynomorphs (Mohr, this volume, chapter 29). Although reports of Aptian-Albian diatoms are few (see review below) and provide little biostratigraphic control, their similarity to diatom assemblages at Site 693 supports the above age.

Exceptionally well preserved assemblages of siliceous microfossils recovered from Site 693 significantly advance our knowledge of the early record of diatoms (this chapter and Gersonde and Harwood, this volume), silicoflagellates (McCartney et al., this volume), and Chrysophycean cysts and endoskeletal dinoflagellates (this chapter), which until this time were either unknown from the Lower Cretaceous, or were represented by poorly preserved and pyritized specimens.

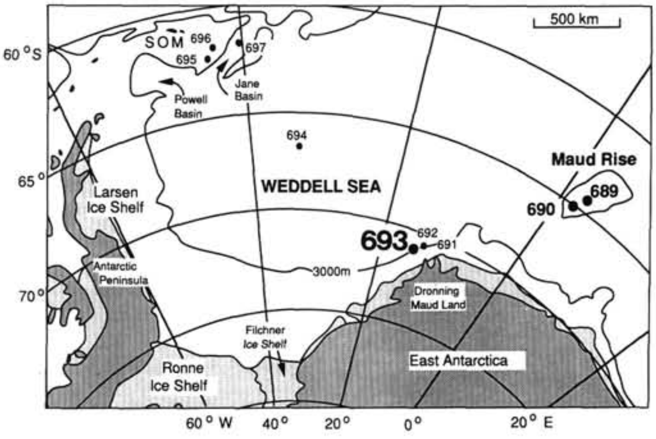

Figure 1. Map showing location of ODP Site 693 on the Dronning Maud Land margin, eastern Weddell Sea where Lower Cretaceous siliceous microfossils reported in this chapter were recovered.

In many phytoplankton groups a resting stage is an adjunct component of their life history strategy. In most cases this involves neritic species (those associated with a continental shelf setting). The function of these resting stages is to render a phytoplankter resistant to environmental stress beyond the tolerance limit of the vegetative cell by enclosing it in a resistant structure and by removing it from the deleterious environment through sinking. Commonly, nutrient limitation following a bloom induces encystment. The resting stage provides the inoculum or refugee assemblage that repopulates the local planktonic environment when favorable conditions appear. In many cases this is a seasonal cycle.

Marine diatoms and some non-marine diatoms produce heavily silicified resting spores in response to environmental stress that in many cases are quite distinct from the vegetative mor-

---

[1] Barker, P. F., Kennett, J. P., et al., 1990. *Proc. ODP, Sci. Results*, 113: College Station, TX (Ocean Drilling Program).

[2] Byrd Polar Research Center, The Ohio State University, Columbus, Ohio 43210. Present Address: Department of Geology, University of Nebraska-Lincoln, NE 68588-0340.

[3] Alfred Wegener Institute for Polar and Marine Research, Columbusstraße, D-2850 Bremerhaven, West Germany.

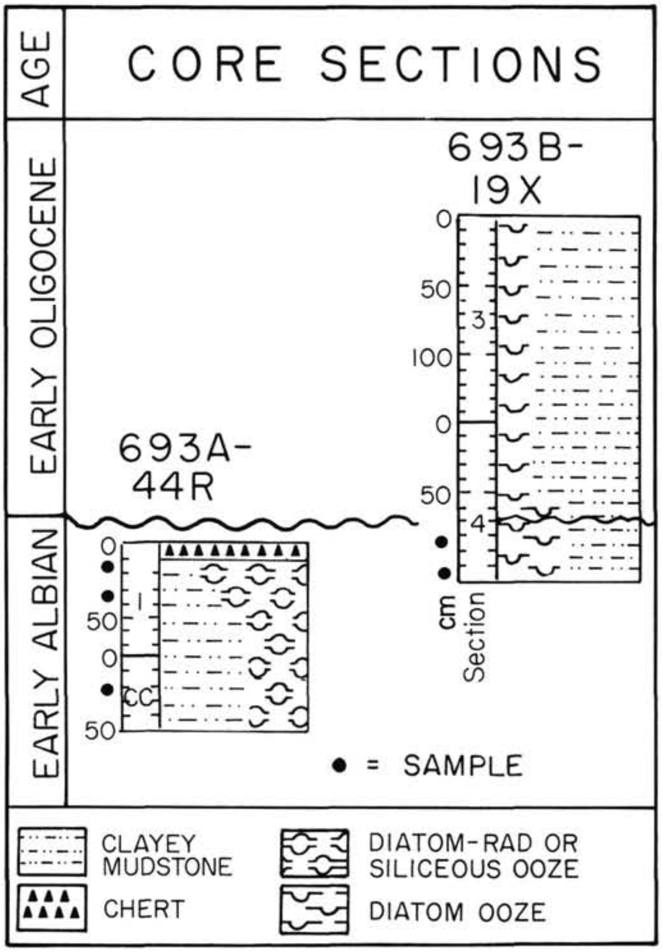

Figure 2. Diagram showing the location of Lower Cretaceous siliceous microfossil-bearing sediments in ODP Hole 693A and Hole 693B, with the location of samples studied.

phology (Hasle and Sims, 1985; Syvertsen, 1985; Sims and Hasle, 1987), although some diatoms produce a physiological resting cell that is morphologically similar to the vegetative cell. Several useful papers that review diatom resting spore formation and other aspects of this adaptation include the works of French and Hargraves (1980), Hargraves and French (1974, 1983), Garrison (1984), Smetacek (1985), Kitchell et al. (1986), and Hargraves (1987).

Chrysophycean flagellates also produce a resistant siliceous stage termed a statospore. Today, most Chrysophycean cysts are found in non-marine environments, however, Chrysophycean cysts are commonly found in fossil marine sediments (Archaeomonads), extending through the Upper Cretaceous (Hajós and Stradner, 1975; Perch-Nielsen, 1975; Harwood, 1988) into the Lower Cretaceous (this chapter). Several useful papers that review the current state of Chrysophycean studies include the works of Tynan (1971), Tappan (1980), Adam and Mahood (1981), Sandgren (1983), and Mitchell and Silver (1986). A useful annotated bibliography on siliceous algal cysts and scales was produced by Adam and Mahood (1979). Cornell (1979) reviews Mesozoic Chrysophycean occurrence.

JURASSIC AND LOWER CRETACEOUS DIATOM OCCURRENCES

Our knowledge of pre-Late Cretaceous diatoms is very limited due in part to the temporal instability of opal-A, and the insufficient search for diatoms in sediments of this age. For this reason, the following review of Jurassic and Lower Cretaceous diatom occurrence is presented to familiarize the reader with the available materials and to emphasize the importance of the assemblages described here and in Gersonde and Harwood (this volume). See Harwood (1988) for a recent review of Upper Cretaceous diatom materials and literature.

The geologic record of diatoms extends back at least to the Early Jurassic as indicated by the recovery of *Pyxidicula bollensis* and *P. liassica* from the Liassic Boll Shales of Wurttemburg (Rothpletz, 1896, 1900). This low diversity assemblage of diatoms is found in abundance among the fibers of the sponge *Phymatoderma*. The diatoms occur as isolated valves (6–14 μm in diameter) and less frequently as whole frustules with one valve smaller than the other. No girdle bands and no apparent overlap of the valves was reported by Rothpletz (1896). From this description, it is likely that these may be resting spores. Although Deflandre (1959) suggested these species belong to the Schizosphaerellidae, it is now generally accepted that these represent the "oldest-known" diatoms (Simonsen, 1979), but it is not known how well they represent the "earliest" diatom.

Other reports of Jurassic diatoms include two species from Western Siberia (Vechina, 1961), and others from the Paris Basin (Cayeux, 1892). Upper Jurassic diatoms reported from the Moscow Basin were later interpreted to be radiolarians (Strel'nikova, 1974).

Reports of pre-Mesozoic diatoms in Precambrian and Paleozoic deposits are believed to be modern contaminants, or, originating locally from younger diatom-bearing deposits (Pia, 1927, 1931; Frenguelli, 1932; Hendey, 1933, Jousé, 1948, Strel'nikova, 1974). The occurrence of diatom-like forms from the Devonian Przeworno Marbles in Poland (Kwiecinska and Sieminska, 1973; Sieminska, 1974; Sieminska and Kwiecinska, 1976) is problematic and Glazek and others (1977) suggest that these fossils are contaminants.

The Lower Cretaceous diatom record is better represented than the Jurassic record, however, only three Lower Cretaceous deposits are known in which diatoms are preserved with the primary skeletal composition of Opal-A (Table 1 of Gersonde and Harwood, this volume). These include sediments from Hannover, Federal Republic of Germany (FRG) (a deposit that can not be located today [Benda, 1982]); Queensland, Australia (moderately well-preserved material that we are currently studying); and ODP Site 693 (this volume).

Geroch (1978) may have described the oldest Cretaceous diatoms in Barremian?-Aptian black-shales recovered from a drill hole in the Polish Carpathians. These diatoms are pyritized, but preserved well enough to recognize poroid structures and processes. All are large centric diatoms that were concentrated in a 64 μm sieve.

Forti and Schulz (1932) reported 11 species and 9 genera from the Albian Gault Phosphorites near Hannover, FRG. Further study of these materials was reported by Schulz (1935). Benda (1982) was unsuccessful in his attempt to relocate this important deposit.

Dun et al. (1901) reported diatoms from calcareous concretions in the Aptian Doncaster Member of the Rolling Downs Group in Queensland, Australia. Harper (1977, unpubl. notes) reopened this study and reported eleven moderately well-preserved diatom morphotypes and six genera. Recently Haig and Barnbaum (1978) illustrated large, pyritized centric diatoms recovered in sieved preparations of the same material.

Jousé (1949) found abundant but poorly preserved and deformed pyritized diatom remains in Albian clays near Vyshi River in the Penza Region of the middle Volga area. Other reports of Albian diatoms include those from lower Albian sediments in the Salzgitter-Goslar area in the northwest Harz Mountains

(Georgi, 1976); those reported from upper Aptian/lower Albian claystones near Hannover, FRG (Kemper et al., 1975); and Lower Cretaceous diatoms from the middle Albian Clearwater and Joli Fou formations of northeastern Alberta (Wall, 1975). Other Lower Cretaceous occurrences are reported by Müller (1912), Strel'nikova and Martirosjan (1981), and Foucault et al. (1986).

It is difficult to compare the ODP Site 693 Lower Cretaceous material with many of the above assemblages due to the poorly preserved state of the latter (Table 1 of Gersonde and Harwood, this volume). Also, many of the smaller diatoms illustrated here and in Gersonde and Harwood (this volume) would not be encountered in >63 μm sieved residues studied by Geroch (1978) and Haig and Barnbaum (1978). Other differences may be due to different stratigraphic levels (we note a greater similarity of the Polish assemblages to Upper Cretaceous floras than to those documented herein); or the differences may reflect a different environmental setting. Lower Cretaceous diatom floras from Site 693 are most similar to the materials from Queensland (Dun et al. 1901; Harper, unpubl. notes and plates) and from the "lost" deposit near Hannover (Forti and Schulz, 1932; Schulz, 1935).

METHODS

Preparation techniques applied to recover siliceous microfossils from Unit VI of Site 693 are outlined below and reported, with slightly varying approaches, in the accompanying chapters by Gersonde and Harwood (this volume) and McCartney et al. (this volume). These authors prepared samples separately and shared residues. Sediment samples were broken into small pieces, dried in an oven, and then soaked in kerosene for several days. A weak, hot solution of Calgon (sodium hexametaphosphate) in distilled water was poured into the sediment mixture, displacing the kerosene by floating it to the surface. The kerosene treatment helps draw the Calgon solution into the sediments, aiding disaggregation (Kummel and Raup, 1965). Kerosene and water were decanted, the sample was dried again and the above process repeated several times before the sediment was sufficiently broken down. The residue was washed repeatedly with distilled water to remove the kerosene and Calgon. A split of the raw sediment residue was taken, and the remaining material was gently washed through a 63 μm and a 38 μm sieve. Materials collected in each of the sieves, as well as the <38 μm size fraction that passed through the finest sieve, were washed into glass vials and slides made from all of the size fractions, including the unsieved residues. Sieving concentrated the rarer diatoms, produced better type specimens, and cleaned the residues for SEM (scanning electron microscope) examination and photography. LM photomicrographs were produced at The Ohio State University using a Leitz Orthoplan microscope (using Nomarski illumination in most cases) with an Orthomat camera. SEM photomicrographs were produced at the Alfred Wegener Institute on a Philips SEM 515. Holotypes and paratypes are deposited in the Friedrich-Hustedt Diatom Collection at the Alfred Wegener Institute, Bremerhaven.

EXPLANATION

This chapter documents the occurrence of 20 new diatom resting spore taxa, 10 Chrysophycean cyst taxa and one endoskeletal dinoflagellate (Table 1) as Part 2 of a three-part survey of Lower Cretaceous siliceous microfossils (the other parts are by Gersonde and Harwood [vegetative diatom valves], and McCartney et al., [silicoflagellates], both this volume). The division between this chapter on diatom resting spores and Part 1 on vegetative forms (Gersonde and Harwood, this volume) is somewhat artificial as we can not be certain that specimens are correctly identified as vegetative or resting morphotypes. In addition, it is likely that species described in this paper are resting spores of species described in Part 1. This is not a new problem to diatom science, and the *International Code of Botanical Nomenclature* is tolerant of several names applied to the same species of fossil organs, such as roots, leaves, palynomorphs, etc. The fact that many diatoms encountered in the Leg 113 Lower Cretaceous material are heterovalvate, resting spores in particular, further complicates the problem, in that different names may be applied to the epivalve and hypovalve. Considerable effort to identify complete frustules reduced this problem associated with heterovalvy. When considering these microfossils one must always bear in mind the selective biases of the fossil record. In some species only one stage of the life cycle may be silicified, thus having the potential for preservation. In the case of diatoms this stage may be the silicified resting spore.

Table 1. Siliceous microfossil taxa proposed in this paper.

Diatoms	
Genus	*Calyptosporium* n. gen. Harwood and Gersonde
Species	*Calyptosporium carinatum* n. sp. Harwood and Gersonde
	Calyptosporium cyclacaenum n. sp. Harwood and Gersonde
	Calyptosporium effalum n. sp. Harwood and Gersonde
	Calyptosporium exasperatum n. sp. Harwood and Gersonde
	Calyptosporium galeolum n. sp. Harwood and Gersonde
	Calyptosporium lentiginosum n. sp. Harwood and Gersonde
	Calyptosporium maximum n. sp. Harwood and Gersonde
	Calyptosporium perexiguum n. sp. Harwood and Gersonde
	Calyptosporium pustulatum n. sp. Harwood and Gersonde
Genus	*Crossophialus* n. gen. Harwood and Gersonde
Species	*Crossophialus paterus* n. sp. Harwood and Gersonde
	Crossophialus glabrus n. sp. Harwood and Gersonde
	Crossophialus gyroscolus n. sp. Harwood and Gersonde
Genus	*Cypellachaetes* n. gen. Harwood and Gersonde
Species	*Cypellachaetes intricatus* n. sp. Harwood and Gersonde
Genus	*Dasyangea* n. gen. Harwood and Gersonde
Species	*Dasyangea dactylethra* n. sp. Harwood and Gersonde
Genus	*Hyalotrochus* n. gen. Harwood and Gersonde
Species	*Hyalotrochus radiatus* n. sp. Harwood and Gersonde
	Hyalotrochus incompositus n. sp. Harwood and Gersonde
	Hyalotrochus sp.
Genus	*Meristosolen* n. gen. Harwood and Gersonde
Species	*Meristosolen cylindratus* n. sp. Harwood and Gersonde
Genus	*Pseudopyxilla* Forti
Species	*Pseudopyxilla systena* n. sp. Harwood and Gersonde
	Pseudopyxilla furcata n. sp. Harwood and Gersonde
Chrysophycean cysts (Archaeomonads)	
Archaeomonas? sp. A	
Archaeomonas sp. B	
Archaeomonas sp. C	
Archaeomonas? sp. D	
Archaeomonas sp. E	
Archaeomonas sp. F	
Archaeomonas sp. G	
Archaeomonas sp. H	
Archaeomonas sp. I	
Archaeomonas sp. J	
Endoskeletal dinoflagellates	
Genus	*Carduifolia* Hovasse
Species	*Carduifolia toxon* n. sp. Harwood and Gersonde

Plates 1–11 illustrate SEM and LM (light microscope) photomicrographs, each of which provide a different perspective to valve morphology. LM was particularly useful in viewing silhouette profiles, which identify structures inside the frustule as well as the shape of the basal poroid layer that is not readily seen in the SEM due to masking by structural ornamentation (Gersonde and Harwood, this volume).

Terminology of resting spores and the identification of primary and secondary spore valves is difficult here. For simplicity, reference is to epivalve and hypovalve only. The position of other valve-like structures such as the infundibulum (Fig. 3; Pl.

6, Fig. 6; Pl. 9, Fig. 4) is unclear within the standard 2-valve model of a frustule. In addition, the differentiation of epivalve mantle and calyptra is artificial at this point, but the genus *Calyptosporium* does not fit well into the standard epivalve-hypovalve format. Whenever possible, descriptive nomenclature proposed by Ross and Sims (1972), Anonymous (1975), Ross et al. (1979), Barber and Haworth (1981) was employed in species description. Several structures are named in this paper for the genus *Calyptosporium* and are described below.

DESCRIPTION OF NEW STRUCTURES

The structures described below are introduced to aid the descriptions for species of *Calyptosporium*. The various structures and a generalized frustule of *Calyptosporium* are illustrated in Figure 3.

Calyptra—derived from kalypter (Gk.), meaning covering, sheath; refers to the cylindrical siliceous envelope that connects the epivalve with the infundibulum and hides the hypovalve (Fig. 3: Pl. 6, Figs. 3, 7; Pl. 7, Fig. 1; Pl. 8, Fig. 3). This covering bears a diverse assortment of ornamentation that appears to be species diagnostic. The calyptra is supported from the inside by mantle costae and fala of the hypovalve. A similar cylindrical sheath is illustrated by Hargraves (1979, figs. 37–40, 48–49) for resting spores of modern diatoms *Chaetoceros curvisetum* and *Chaetoceros sociale* var. *sociale*, and resting spores of *Rhizosolenia setigera* (Hargraves, 1976, figs, 28, 30). In the future, the definition of this structure may include all of the elements now termed the epivalve, calyptra, infundibulum, and lacinia. At the present time their distinction is somewhat artificial as these elements can not be clearly separated.

Confossa zone—derived from confossus (Lat.), meaning pierced full of holes; referring to the distinct zone of perforations (Fig. 3) on the mid-portion of the calyptra (Pl. 6, Figs. 2, 7; Pl. 7, Fig. 1; Pl. 8, Figs. 3, 5). It is present in all species of *Calyptosporium*, although it is absent in some specimens (Pl. 5, Fig. 11). Note that the perforate confossa zones of the calyptra and perforate zone of the hypovalve are at the same level (Pl. 7, Fig. 1, if the hypovalve is reinserted in the calyptra). There is also similar agreement between these two structures and the position of a perforate zone on the infundibulum (Pl. 9, Fig. 6). These three structures may have played a role in regulating contact with the external environment, by developing a double-wall structure (the calyptra/infundibulum-outer wall and the hypovalve-inner wall). The confossa zone may be analogous to the perforate zone present on the epivalve mantle (calyptra?) of many *Pseudopyxilla* species (Pl. 1, Fig. 13; Hajós and Stradner, 1975, pl. 12, fig. 3; Harwood, 1988, fig. 17.26 and 17.27).

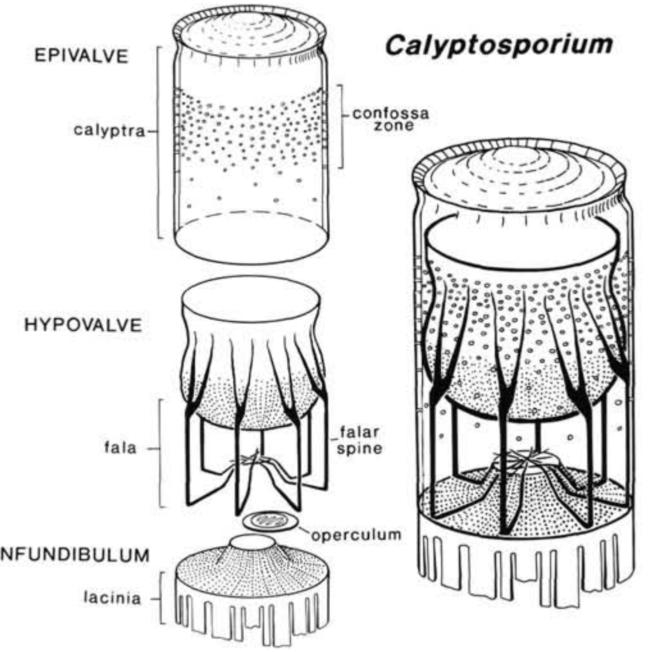

Figure 3. Generalized illustration of *Calyptosporium carinatum* (genotype of *Calyptosporium*) identifying the various structures defined in this paper. Frustule at left in exploded view to clearly identify the various parts that are assembled at right (compare with the diatoms illustrated in Pl. 6, Figs. 1, 2 and Pl. 8, Figs. 1, 2).

Fala—derived from fala (Lat.), meaning scaffold; refers to the collection of buttressed spines that extend vertically from the mantle of the hypovalve of *Calyptosporium* species and lie juxtaposed to the calyptra and infundibulum, which the fala supports (Fig. 3: Pl. 6, Figs. 1, 2; Pl. 9, Figs. 3, 6). Each individual falar spine is shaped like a hook or the letter "J" and originates from the edge of the hypovalve face by the junction of three costae—two that run vertically along the valve mantle (Pl. 2, Fig. 14; Pl. 6, Fig. 2; Pl. 9, Figs. 1, 2) and one that radiates toward the margin from near the center of the valve face (Pl. 5, Fig. 6, 9; Pl. 8, Fig. 7). The form of the falar spines, produced from the junction of the three costae that form a buttressed spine, is a common feature of many Lower Cretaceous diatom resting spores and vegetative cells.

Infundibulum—derived from infundibulum (Lat.), meaning funnel; refers to the broad, funnel-shaped, perforate, inward extension of the calyptra at the opposite end of the frustule from the epivalve face (Pl. 6, Figs. 1, 6; Pl. 9, Figs 4, 6). The infundibulum is supported by the terminal ends of the fala (Pl. 6, Fig. 1; Pl. 9, Fig. 6). The infundibulum appears to attach to the calyptra and the lacinia without overlap or suture (Pl. 6, Figs. 1, 2, 6; Pl. 9, Fig. 4). A circular opening to the interior of the frustule is present at the center of the infundibulum and appears to be covered by a solid siliceous plate (infundibular operculum) of slightly larger diameter than the central opening (Pl. 6, Fig. 6). A different form of the infundibulum may be represented in *Calyptosporium effalum* by the radially perforate sheet(s) of silica that are attached to the radial costae of the epivalve (Pl. 7, Figs. 6, 8).

Infundibular operculum—a circular plate of silica of slightly greater diameter than the central infundibular opening, which it apparently covered. This structure was positively identified in one specimen (Pl. 6, Fig. 6), and possible remnants of this structure on another (Pl. 9, Fig. 6). The operculum does not appear to be connected to the infundibulum and is slightly wider than the infundibular opening. A slight elevation or thickening on the operculum approximates the dimensions of the central infundibular aperture (Pl. 6, Fig. 6). A network consisting of the terminal ends of falar spines (Pl. 6, Fig. 1; Pl. 9, Fig. 4) holds the infundibular operculum in position over the infundibular aperture (Fig. 3; Pl. 6, Fig. 6).

Lacinia—derived from lacinia (Lat.), meaning fringe or lappet on the border of a garment, refers to the elongate, blade-like siliceous extensions that extend downward from the calyptra (Fig. 3), beyond where the infundibulum contacts the calyptra (Pl. 6, Fig. 2; Pl. 7, Fig, 7; Pl. 8, Figs. 2, 3; Pl. 9, Fig. 4). The length of the blades is unknown as they were commonly broken, and the blade width is variable. The lacinia and the infundibulum may represent structures associated with connections to an adjacent "sister"-spore. M. A. Harper (pers. comm.) suggested a union of adjacent spores of *Calyptosporium* similar to that found in paired resting spores of *Melosira hyperborea* Grunow as illustrated in Gran (1897), Müller (1906), and Fritsch (1935; p. 639, fig. 215E), where the lacinia are attached to each cell, and infundibular structures in adjacent cells are juxtaposed, and perhaps connected by mucilage. A structure similar to a lacinia is illustrated by Hargraves (1979, figs. 37–40, 48–49) for resting spores of modern diatoms *Chaetoceros curvisetum* and *Chaetoceros sociale* var. *sociale*, but it is not associated with chain formation.

SYSTEMATIC PALEONTOLOGY

DIATOMS

Genus *CALYPTOSPORIUM* Harwood and Gersonde nov. gen.

Genotype. *Calyptosporium carinatum* Harwood and Gersonde sp. nov.

Derivation of name. kalyptos (Gk.)—covered or hidden; spora (Gk.)—a sowing, seed.

Diagnosis. The genus *Calyptosporium* is proposed for diatoms with a large, cylindrical, frequently heavily silicified frustule consisting of several parts (Fig. 3), including an epivalve with an elongate outer cylindrical mantle-sheath termed a calyptra, which entirely encloses the hypovalve; a funnel shaped, radially perforate inward extension of the distal end of the calyptra called an infundibulum; a hypovalve of variable convexity that is radially perforate on the valve face and bears a spinose apparatus of buttressed spines, termed a fala, that internally supports the calyptra and the infundibulum and holds an infundibular operculum in place over the infundibular aperture (Fig. 3); a lacinia continues distally from the base of the calyptra as an extension of this feature. Radial costae on the hypovalve appear to be a consistent feature of this genus, whereas ornamentation on the epivalve is variable and used as a character for species differentiation. Calyptra usually bear a distinct circumferential band of puncta, referred to as a confossa zone, the upper boundary of which is located at a uniform distance away from the margin of the valve face. Calyptra, epivalve, infundibulum, and lacinia are fused, composing one complex structure; no sutures are visible that divide these elements, although the lacinia and infundibulum do occur as a distinct unit apart from the calyptra (Pl. 2, Fig. 8; Pl. 9, Fig. 4).

Remarks. Species differentiation is based primarily on ornamentation of the epivalve face and hypovalve mantle. Lacinia and infundibulum were not noted in several species of this genus, but this may be an artifact of preservation, as is the absence of the distal end of the calyptra in many specimens. Center of hypovalve is either solid silica (Pl. 5, Fig. 11), or, if perforations continue to the center of the hypovalve, a circular disk with an annular arrangement of puncta (Pl. 5, Fig. 10) may be present. This disk is similar to that seen in some specimens of *Microorbis* (Gersonde and Harwood, this volume). The two species of *Pseudopyxilla* reported here may belong to *Calyptosporium*, but further detail is needed on the hypovalve structure of these and other *Pseudopyxilla* spp. in the SEM, to compare these genera.

Calyptosporium carinatum Harwood and Gersonde sp. nov.
(Fig. 1; Pl. 6, Figs. 1–7; Pl. 9, Fig. 4 ?)

Description. Frustule cylindrical; epivalve broadly domed, smooth without ornament except for a marginal ridge (Pl. 6, Fig. 3); calyptra smooth without ornament, although a narrow confossa zone (~10 μm wide) of randomly distributed puncta is often present near the middle of the calyptra (Pl. 6, Figs. 2, 7); infundibulum (Pl. 6, Fig. 6) radially perforate (10 in 10 μm), gently convex near the calyptra, changing slope and dipping steeply toward the interior of the frustule at ½ radius, and terminating at an opening of diameter generally less than 10 μm that is covered by an infundibular operculum (Pl. 6, Fig. 6); hypovalve strongly convex, slightly constricted at the base, bears a well developed fala (Pl. 6, Figs. 1, 2) and elongate longitudinal costae along much of the length of the hypovalve mantle, assuring a snug fit of the hypovalve against the inside wall of the calyptra; lacinia of broad blades of variable width and unknown length.

Size. Dimension of frustule along pervalvar axis, not including lacinia, ranges between 65 and 45 μm; frustule diameter ranges between 50 and 25 μm.

Holotype. Friedrich-Hustedt Collection No. Zu 3/97-13 (Pl. 6, Figs. 1, 2).

Type locality. Dronning Maud Land margin, Antarctica, eastern Weddell Sea ODP Site 693.

Type level. Lower Albian; ODP Sample 113-693B-19X-4, 77–78 cm.

Derivation of name. carina (Lat.)—keel, referring to the circumferential flange at the epivalve mantle (i.e., marginal ridge).

Calyptosporium cyclacaenum Harwood and Gersonde sp. nov.
(Pl. 6, Figs. 8–12)

Description. Frustule cylindrical; epivalve slopes upward at constant angle, becoming flat or gently convex at the site where a circle of spines is present at ½ to ⅓ radius; central cluster of spines often present; weakly developed marginal ridge; calyptra perforate along much of its length, with a clear boundary at the top of the confossa zone (Pl. 6, Fig. 7); infundibulum and lacinia not observed; hypovalve strongly convex, slightly constricted at the base, bearing a weakly developed fala with longitudinal costae on only the upper portion of the hypovalve mantle.

Size. Dimension of frustule along pervalvar axis ranges between 45 and 30 μm; frustule diameter ranges between 35 and 50 μm.

Holotype. Friedrich-Hustedt Collection No. Zu 3/98-22 (Pl. 6, Fig. 12).

Paratype. Friedrich-Hustedt Collection No. Zu 3/98-23 (Pl. 6, Fig. 9).

Type locality. Dronning Maud Land margin, Antarctica, eastern Weddell Sea, ODP Site 693.

Type level. Lower Albian; ODP Sample 113-693B-19X-4, 77–78 cm.

Derivation of name. kyklos (Gk.)—circle, ring; akaina (Gk.)—thorn, spine.

Calyptosporium effalum Harwood and Gersonde sp. nov.
(Pl. 3, Fig. 8; Pl. 7, Figs. 1–8)

Description. Frustule cylindrical, convex on top, but flattened at base; epivalve broadly domed, bearing between 9 and 30 radial costae that may join with other costae toward the center of the valve, and terminate at a weakly developed marginal ridge (Pl. 7, Figs. 2, 6); calyptra ornamented with short, irregular, and discrete costae that flatten and coalesce distally; upper boundary of confossa zone clearly marked and puncta arranged in longitudinal striae that become disrupted distally; radially perforate siliceous plates, possibly analogous to an infundibulum although not funnel shaped, in contact with the top of the hypovalve (Pl. 7, Figs. 6, 8) in direct contact with falar costae; hypovalve strongly convex, slightly constricted at the base although abundant sublongitudinal costae present a cylindrical form; hypovalve solid except for a radial perforate zone at the valve margin that corresponds in position to confossa zone of calyptra; fala not well developed and represented by reduced spines that lie in the space between adjacent costae (Pl. 7, Figs. 5, 8) and by costae on hypovalve face that continue from the mantle through a marginal ridge and continue to ½ radius (Pl. 7, Figs. 4, 5); lacinia of short regularly spaced spinous extensions (Pl. 7, Fig. 7).

Remarks. The infundibulum-like structure of *Calyptosporium effalum* is not funnel-shaped (Pl. 7, Figs. 6, 8; siliceous plates on the surface of the hypovalve), although this is difficult to discern by the fragments that remain. The absence of a deep funnel in this species agrees with reduced fala, in that the infundibular structure (?) was in direct contact with the hypovalve face.

Size. Dimension of frustule along pervalvar axis ranges between 45 and 30 μm; frustule diameter ranges between 40 and 30 μm.

Holotype. Friedrich-Hustedt Collection No. Zu 3/97-9 (Pl. 7, Fig. 7).

Paratype. Friedrich-Hustedt Collection No. Zu 3/98-6 (Pl. 3, Fig. 8).

Type locality. Dronning Maud Land margin, Antarctica, eastern Weddell Sea, ODP Site 693.

Type level. Lower Albian; ODP sample 113-693B-19X-4, 77–78 cm.

Derivation of name. e—without; fala (Lat.)—scaffold, frame.

Calyptosporium exasperatum Harwood and Gersonde sp. nov.
(Pl. 5, Figs. 1–11)

Description. Frustule cylindrical, convex on top, but flattened at base; epivalve broadly domed, bearing numerous spines (many of which are branching, although they are usually broken) that frequently coalesce to form short costae that are aligned in a semi-annular pattern (Pl. 5, Figs. 4, 5); calyptra ornamented with numerous smaller, short, blunt spines evenly spaced over the calyptra; siliceous band surrounds calyptra (Pl. 5, Figs. 3, 11) at point just beneath confossa zone, which, if present, is represented by a narrow (5 μm) zone of disordered pores; calyptra is weakly silicified beneath this siliceous band, but continues well beyond this as suggested by the length of the falar spines (Pl. 5, Fig. 8); infundibulum not observed; hypovalve face of radial punctate striae (Pl.

5, Figs. 9, 10) or imperforate (Pl. 5, Fig. 11), bears radial costae that continue from near the valve center to the margin of the valve where they join an undulate marginal ridge that "zig-zags" around the margin as part of the falar supporting structure (Pl. 5, Figs. 9. 11); central plate with sub-annular perforations may or may not be present (contrast Pl. 5, Figs. 10 and 11); fala well developed with some very long spines (Pl. 5, Fig, 8); lacinia not observed.

Remarks. Some specimens identified as *Stephanopyxis miriabilis* Forti and Schulz probably belong to *Calyptosporium exasperatum*. The central disk with sub-annular puncta is similar in form to that in species of *Microorbis* in Gersonde and Harwood, this volume). Sub-annular arrangement of spines on epivalve face resembles arrangement in *C. cyclacaenum*.

Size. A wide variation in size is noted in this species. Dimension of frustule along pervalvar axis ranges from 20 to 45 μm; frustule diameter shows less variation, ranging between 30 and 40 μm.

Holotype. Friedrich-Hustedt Collection No. Zu 3/97-18 (Pl. 5, Fig. 1).

Paratype. Friedrich-Hustedt Collection No. Zu 3/92-2 (Pl. 5, Figs. 5, 6)

Type locality. Dronning Maud Land margin, Antarctica, eastern Weddell Sea, ODP Site 693.

Type level. Lower Albian; ODP Sample 113-693B-19X-4, 77–78 cm.

Derivation of name. exasperatus (Lat.)—covered with short hard points.

Calyptosporium galeolum Harwood and Gersonde sp. nov. (Pl. 2, Figs. 11–16)

Description. Frustule cylindrical with a domed top; epivalve (Pl. 2. Figs. 11, 12, at bottom of specimen) highly convex with a shoulder at the valve margin, mantle bears short longitudinal costae that join at the juncture with a radial costa from the valve face to form a spine; hypovalve with similar shape to the epivalve, bearing elongate falar spines (Pl. 2, Fig. 15), and ornamented by radial costae with a form similar to *Cladogramma*.

Remarks. Epivalve is similar in form to *Microorbis* (pl. 17, fig. 10 of Gersonde and Harwood, this volume).

Holotype. Friedrich-Hustedt Collection No. Zu 3/97-1 (Pl. 2, Figs. 11, 12).

Paratype. Friedrich-Hustedt Collection No. Zu 3/98-10 (Pl. 2, Fig. 14).

Type locality. Dronning Maud Land margin, Antarctica, eastern Weddell Sea, ODP Site 693.

Type level. Lower Albian; ODP Sample 113-693B-19X-4, 77–78 cm.

Derivation of name. galea (Lat.)—a vessel or cup shaped like a helmet.

Calyptosporium lentiginosum Harwood and Gersonde sp. nov. (Pl. 4, Figs. 11–13; Pl. 11, Figs. 1–3)

Description. Frustule cylindrical with a hemispherical top and unknown base; epivalve hemispherical and covered with small granules; calyptra similarly covered; infundibulum and lacinia not observed due to fragmentation; hypovalve hemispherical and slightly constricted at the base of smaller specimens and less convex with a flat margin in larger specimens; hypovalve ornamented with a fala consisting of numerous short costae near the valve margin that converge and join with one radial costa to form a vertical spine; suggestion of radial punctate striae on portion of hypovalve face in LM examination.

Size. Dimension of frustule along pervalvar axis ranges between 25 and 50 μm; Frustule diameter ranges between 33 and 90 μm.

Holotype. Friedrich-Hustedt Collection No. Zu 3/97-12 (Pl. 4, Figs. 11, 12).

Type locality. Dronning Maud Land margin, Antarctica, eastern Weddell Sea, ODP Site 693.

Type level. Lower Albian; ODP Sample 113-693B-19X-4, 77–78 cm.

Derivation of name. lentiginosus (Lat.)—full of freckles, spotted.

Calyptosporium maximum Harwood and Gersonde sp. nov. (Pl. 2, Fig. 8; Pl. 8, Figs. 1–8)

Description. Frustule cylindrical, robust, quadrate; epivalve gently convex, bearing scattered, non-linear costae (Pl. 8, Fig. 8) and a circumferential marginal ridge; calyptra smooth without ornamentation, although a broad confossa zone (20–30 μm wide) is present on most specimens near the middle of the calyptra and has a distinct upper (Pl. 8, Fig. 5) and less sharp lower boundary (Pl. 8, Fig. 3); wall of calyptra may be extremely thick (up to 8 μm); infundibulum (Pl. 2, Fig. 8) similar in form to that of *C. carinatum* and *C. pustulatum*, although infundibular opening is larger (up to 20 μm diameter); hypovalve broadly convex with steep mantle, slightly constricted at base, sparsely perforate in discontinuous radial striae and bears a robust fala and radial costae on valve face (not visible in figures); paired longitudinal costae on hypovalve mantle join with radial costae to form falar spines that run vertically along the inside of, and in contact with, the calyptra; lacinia, broad and blade-like, extending vertically downward from the calyptra (Pl. 2, Fig. 8; Pl. 8, Fig. 2).

Size. Dimension of frustule along pervalvar axis ranges between 55 and 65 μm, not including lacinia; frustule diameter ranges between 40 and 80 μm.

Holotype. Friedrich-Hustedt Collection No. Zu 3/93-1 (Pl. 8, Figs. 1, 2).

Paratype. Friedrich-Hustedt Collection No. Zu 3/92-6 (Pl. 8, Figs. 6, 7).

Type locality. Dronning Maud Land margin, Antarctica, eastern Weddell Sea, ODP Site 693.

Type level. Lower Albian; ODP Sample 113-693A-44R-1, 14–18 cm.

Derivation of name. maximus (Lat.)—greatest; referring to the large relative size of this species.

Calyptosporium perexiguum Harwood and Gersonde sp. nov. (Pl. 1, Fig. 5)

Description. Frustule small, cylindrical, broadly rounded at top and flat at base; epivalve hemispherical, apparently smooth, without ornament; calyptra present, of unknown structure; infundibulum and lacinia not observed; hypovalve elongate, with low angle, conical valve face, constricted at base.

Remarks. Species not observed in SEM. May be related to *Calyptosporium lentiginosum*.

Size. Dimension of frustule along pervalvar axis on holotype is 15 μm; frustule diameter of this specimen is 8 μm.

Holotype. Friedrich-Hustedt Collection No. Zu 3/92-3 (Pl. 1, Fig. 5).

Type locality. Dronning Maud Land margin, Antarctica, eastern Weddell Sea, ODP Site 693.

Type level. Lower Albian; ODP Sample 113-693A-44R-1, 14–18 cm.

Derivation of name. perexiguus (Lat.)—very small, meager.

Calyptosporium pustulatum Harwood and Gersonde sp. nov. (Pl. 9, Figs. 1–3, 6)

Description. Frustule cylindrical, robust; epivalve slightly convex, bearing a marginal ridge and ornamented with scattered small pustules; calyptra with similar scattered pustules; confossa zone usually present, consists of scattered pores; infundibulum (Pl. 9, Fig. 6) radially perforate and similar in form to that of *C. carinatum* and *C. maximum*; infundibular aperture is broad (up to 15 μm diameter), no sutures separate infundibulum from lacinia or calyptra; hypovalve highly convex with vertical mantle and slightly constricted at base; hypovalve face radially perforate from the base of the fala toward the valve center, parallel with radial costae; fala structure robust, consisting of paired longitudinal costae on hypovalve mantle that join with radial costae from the valve face to form buttressed falar spines, which run vertically along the inside of the calyptra, in direct contact with it; lacinia not observed due to preservational effects.

Remarks. No infundibular operculum was observed closing the infundibular opening, although weakly silicified fragmented plates resting on the terminal end of the falar spines (Pl. 9, Fig. 6) may be remnants of the infundibular operculum.

Size. Dimension of frustule along pervalvar axis ranges between 55 and 40 μm; frustule diameter ranges between 40 and 32 μm.

Holotype. Friedrich-Hustedt Collection No. Zu 3/92-7 (Pl. 9, Fig. 3).

Type locality. Dronning Maud Land margin, Antarctica, eastern Weddell Sea, ODP Site 693.

Type level. Lower Albian; ODP Sample 113-693A-44R-1, 14–18 cm.

Derivation of name. pustula (Lat.)—blister, pimple.

Genus *CROSSOPHIALUS* Harwood and Gersonde nov. gen.

Genotype. *Crossophialus gyroscolus* Harwood and Gersonde

Derivation of name. krossoi (Gk.)—fringe or tassel; phiale (Gk.)—broad flat vessel, saucer.

Diagnosis. The genus *Crossophialus* is proposed here for discoid diatoms with steep mantles that are often spinose, undulate valve faces, and possess a linking structure produced by silica addition near the margin of the valve in the form of short, radial ridges, reticulate costae, a ring of spines, or a combination of these. Basal siliceous layer of fine radial punctate striae (35 in 10 μm) that are not visible in the LM.

Remarks. Valves illustrated in Plate 3 are clearly incomplete, with a portion of the valve mantle (calyptra?) missing due to preservational effects. The specimens of *Crossophialus* illustrated on Plate 3, Figures 1–7, 9 may be analogous to the calyptra-epivalve of *Calyptosporium* lacking the elongate, cylindrical calyptra due to poor preservation of a highly porous, weakly silicified basal siliceous layer. The effect of expanding the confossa zone of *Calyptosporium* to cover much of the calyptra may yield valves such as *Crossophialus*. In this light, note the similarity of the sharp upper boundary of the confossa zone (Pl. 5, Fig. 11; Pl. 8, Fig. 5) of *Calyptosporium* and the similar boundary in *Crossophialus gyroscolus* (Pl. 3, Fig. 6) from solid silica to perforate silica, where the mantle is broken. Through progressive increase in the number and order of the pores in the confossa zone of *Calyptosporium*, a diatom such as *Crossophialus glabrus* (Pl. 3, Fig. 9) might result.

Crossophialus glabrus Harwood and Gersonde sp. nov.
(Pl. 3, Figs. 7, 9)

Description. Frustule discoid with parallel sides; valve radially perforate, discoid with undulate valve face that is raised in the center; margin of valve face bears a circle of numerous linking spines whose tips connect to the adjacent frustule at the base of a corresponding spine; ring of spines built on marginal hyaline area that is supported on the interior of the valve by slight radial thickenings that extend inward to the point of upward doming of the central region, where punctate striae diffuse and become randomly oriented and fewer in number; valve mantle with longitudinal punctate striae (35 in 10 μm) that continue to the edge of the mantle, which in Plate 3, Figure 9 (upper right margin) does not appear to be broken.

Holotype. Friedrich-Hustedt Collection No. Zu 3/97-25 (Pl. 3, Fig. 7).

Type locality. Dronning Maud Land margin, Antarctica, eastern Weddell Sea, ODP Site 693.

Type level. Lower Albian; ODP Sample 113-693B-19X-4, 77–78 cm.

Derivation of name. glaber (Lat.)—hairless, bald, smooth.

Crossophialus gyroscolus Harwood and Gersonde sp. nov.
(Pl. 3, Figs. 4–6)

Description. Frustule cylindrical(?) (see remarks below); valve discoid, hyaline, with undulate valve face that is raised in the center; margin of valve face bears a loose circle of numerous robust linking spines that are supported by radial thickenings that extend inward to the point of upward doming of the central region, where a ring of greater silicification occurs; mantle imperforate for ~10 μm down from the valve margin to a perforate zone that may be analogous to the upper boundary of the confossa zone of *Calyptosporium*, where the mantle becomes perforate; mantle ornamented with spinose costae (Pl. 3, Fig. 6).

Remarks. Frustule shape and size not determinable due to loss of distal end of what appears to have been a densely perforate valve mantle. Circle of linking spines probably attach to the adjacent frustule in the manner described for *C. glabrus*.

Size. Diameter of valves range between 50 and 60 μm.

Holotype. Friedrich-Hustedt Collection No. Zu 3/98-2 (Pl. 3, Fig. 5).

Paratype. Friedrich-Hustedt Collection No. Zu 3/97-27 (Pl. 3, Fig. 4).

Type locality. Dronning Maud Land margin, Antarctica, eastern Weddell Sea, ODP Site 693.

Type level. Lower Albian; ODP Sample 113-693B-19X-4, 77–78 cm.

Derivation of name. gyros (Gk.)—circle; skolos (Gk.)—thorn/spine.

Crossophialus paterus Harwood and Gersonde sp. nov.
(Pl. 3, Figs. 1–3)

Description. Frustule cylindrical(?); valve with radial punctate striae, discoid with undulate valve face that is raised in the center; margin of valve face bears radial or reticulate costae that extend ⅓ diameter toward center and are separated from adjacent marginal costae by several rows of radial punctate striae; valve center inward from the marginal costae lacks ornamentation other than fine radial punctate striae that lose the radial arrangement at the point of the central doming of the valve; valve mantle (calyptra?) covered with dense spines that may originate from short costae as in *Crossophialus gyroscolus* (Pl. 3, Fig. 6); spines do not extend onto the valve face.

Remarks. The specimen illustrated in Plate 3, Figure 3 may not belong to this species, if the difference between the reticulate or radial costae is a specific character. Species was not observed in the SEM.

Size. Holotype diameter is 55 μm.

Holotype. Friedrich-Hustedt Collection No. Zu 3/97-14 (Pl. 3, Fig. 2).

Paratype. Friedrich-Hustedt Collection No. Zu 3/97-15 (Pl. 3, Fig. 1).

Type locality. Dronning Maud Land margin, Antarctica, eastern Weddell Sea, ODP Site 693.

Type level. Lower Albian; ODP Sample 113-693B-19X-4, 103–104 cm.

Derivation of name. patera (Lat.)—saucer, a broad flat dish.

Genus *CYPELLACHAETES* Harwood and Gersonde nov. gen.

Genotype. *Cypellachaetes intricatus* Harwood and Gersonde

Derivation of name. kypellon (Gk.)—beaker or cup; chaite (Gk.)—long hairs.

Diagnosis. The genus *Cypellachaetes* is proposed here for hemispherical diatom valves that are imperforate, heavily silicified, and possess a linking apparatus of a marginal ring of long gently tapering linking spines.

Remarks. This genus is similar to some *Hemiaulus* spores illustrated in Schmidt et al., 1874–1959, pl. 142, fig. 1, and *Skeletonema penicillis* Grunow in Van Heurck, 1883, pl. 83 ter, fig. 6; Harwood, 1988, figs. 18.17, 18.18. Until thorough SEM documentation of the above diatoms is available, the distinctions between these and *Cypellachaetes*, if any, are not known.

Cypellachaetes intricatus Harwood and Gersonde sp. nov.
(Pl. 1, Figs. 1–4)

Description. Valves hemispherical to conical, constructed of imperforate silica, ornamented with radial costae on the valve face that join with short costae that extend a short distance from the valve mantle to form buttressed linking spines (Pl. 1, Figs. 1, 4) whose tips intertwine to attach adjacent frustules (Pl. 1, Fig. 2); mantle walls are parallel and either smooth or weakly costate; silicification of spines is variable.

Holotype. Friedrich-Hustedt Collection No. Zu 3/98-12 (Pl. 1, Fig. 2).

Type locality. Dronning Maud Land margin, Antarctica, eastern Weddell Sea, ODP Site 693.

Type level. Lower Albian; ODP Sample 113-693B-19X-4, 103–104 cm.

Derivation of name. intricatus (Lat.)—entangled.

Genus *DASYANGEA* Harwood and Gersonde nov. gen.

Genotype. *Dasyangea dactylethra* Harwood and Gersonde sp. nov.

Derivation of name. dasys (Gk.)—hairy, shaggy, tufted, dense; angos (Gk.)—vessel or container, seed-capsule.

Diagnosis. The genus *Dasyangea* is proposed here for diatoms with ovoid frustules and imperforate, parallel sided conical to hemispherical valves that are ornamented with coarse, spinose costae.

Dasyangea dactylethra Harwood and Gersonde sp. nov.
(Pl. 2, Figs. 1–7)

Description. Frustule ovoid with broadly rounded to sub-conical valves; epivalve face covered with rough ornamentation of costae and spines; mantle cylindrical and covered with spinose costae except near the distal edge where a narrow band is free of ornament; hypovalve similar in structure and ornament to epivalve except that the hypovalve mantle is a smooth cylinder, and the base of this valve is slightly constricted.

Holotype. Friedrich-Hustedt Collection No. Zu 3/94-5 (Pl. 2, Fig. 4).

Paratype. Friedrich-Hustedt Collection No. Zu 3/94-2 (Pl. 2, Figs. 5, 6, 7).

Type locality. Dronning Maud Land margin, Antarctica, eastern Weddell Sea, ODP Site 693.

Type level. Lower Albian; ODP Sample 113-693B-19X-4, 103–104 cm.

Derivation of name. daktylethra (Gk.)—finger-sheath, thimble.

Genus *HYALOTROCHUS* Harwood and Gersonde nov. gen.

Genotype. *Hyalotrochus incompositus* Harwood and Gersonde sp. nov.

Derivation of name. hyalos (Gk.)—glass; trochos (Gk.)—wheel.

Diagnosis. The genus *Hyalotrochus* is proposed here for diatoms with one valve that possesses costae on the epivalve face that are irregular near the center, but become organized into radial symmetry before reaching the margin. Hypovalves have an undulate valve face; radial costae on this valve combine at the valve margin to form a "zig-zag" marginal ridge.

Remarks. Epivalves are similar in structure to some species of *Cladogramma*, but hypovalves are distinct from this genus.

Hyalotrochus incompositus Harwood and Gersonde sp. nov.
(Pl. 4, Figs. 5-10)

Description. Frustule discoid; epivalve gently convex, covered by a network of disordered costae, some of which become radial in orientation and continue to the edge of the valve; hypovalve is undulate with a central elevation; short longitudinal costae on the epivalve mantle meet at the valve margin and continue toward the valve center.

Remarks. Species not observed in SEM.

Holotype. Friedrich-Hustedt Collection No. Zu 3/97-8 (Pl. 4, Figs. 5, 6).

Paratype. Friedrich-Hustedt Collection No. Zu 3/98-11 (Pl. 4, Fig. 9).

Type locality. Dronning Maud Land margin, Antarctica, eastern Weddell Sea, ODP Site 693.

Type level. Lower Albian; ODP Sample 113-693B-19X-4, 77-78 cm.

Derivation of name. incompositus (Lat.)—disarranged, confused.

Hyalotrochus radiatus Harwood and Gersonde sp. nov.
(Pl. 4, Figs. 1-4; Pl. 11, Figs. 7, 8)

Description. Epivalve discoid with a steeply elevated, central area that occupies ⅔ radius; radial costae extend from valve edge to a central region where they join with other costae forming an irregular network or central silicified area.

Remarks. The hypovalve of this species in unknown, as is the structure of the epivalve siliceous wall (hyaline, perforate, or striate). Species not observed in SEM.

Size. Holotype and paratype diameters range between 40 and 50 μm.

Holotype. Friedrich-Hustedt Collection No. Zu 3/97-24 (Pl. 4, Figs. 1, 2).

Paratype. Friedrich-Hustedt Collection No. Zu 3/97-21 (Pl. 4, Figs. 3, 4).

Type locality. Dronning Maud Land margin, Antarctica, eastern Weddell Sea, ODP Site 693.

Type level. Lower Albian; ODP Sample 113-693B-19X-4, 77-78 cm.

Derivation of name. radius (Lat.)—ray, rod, spoke.

Hyalotrochus sp.
(Pl. 11, Figs. 4-6)

Genus *MERISTOSOLEN* Harwood and Gersonde nov. gen.

Genotype. *Meristosolen cylindratus* Harwood and Gersonde.

Derivation of name. meristos (Gk.)—divided; solenos (Gk.)—pipe or cylinder.

Diagnosis. The genus *Meristosolen* is proposed here for diatoms with elongate cylindrical frustules comprised of strongly overlapping valves and spinose base and top.

Remarks. Several features suggest an affinity with *Calyptosporium*, including the fact that the epivalve (calyptra) completely envelopes the hypovalve, as well as the presence of what may be a lacinia.

Meristosolen cylindratus Harwood and Gersonde sp. nov.
(Pl. 2, Figs. 9, 10)

Description. Frustule cylindrical with ring of spines at each end; epivalve cylindrical with straight, parallel sides; weakly developed marginal ridge; zone of perforations on epivalve mantle may be analogous to the confossa zone, visible in the upper ⅓ of the cylinder (Pl. 2, Fig. 9); hypovalve cylindrical, constricted near the base, nearly as long as epivalve; both valves extend nearly the length of the frustule.

Remarks. Only one specimen encountered. Species not observed in SEM.

Size. Dimension of frustule along pervalvar axis on holotype is 30 μm; diameter 13 μm.

Holotype. Friedrich-Hustedt Collection No. Zu 3/94-4 (Pl. 2, Figs. 9, 10).

Type locality. Dronning Maud Land margin, Antarctica, eastern Weddell Sea, ODP Site 693.

Type level. Lower Albian; ODP Sample 113-693B-19X-4, 103-104 cm.

Derivation of name. cylindrus (Lat.)—cylinder.

Genus *PSEUDOPYXILLA* Forti, 1909

Discussion. Two species of *Pseudopyxilla* are proposed below. Both bear elongated spines that emanate from the center of the epivalve face. One species bears forked buttressed-spines, the other has a single elongate spine with short barbs that are transverse to the length of the spine. Cylindrical portion of epivalves are hyaline near the spine, becoming perforate at a uniform position toward the base of the valve, resembling a confossa zone of *Calyptosporium*. The hypovalve structure is not known and it is fully enclosed by the elongate cylindrical portion of the epivalve (Pl. 1, Fig. 6); spines at epivalve margin may represent a falar structure, but this is not visible in the LM. With further documentation of these species and other *Pseudopyxilla* spp. in the SEM, *P. furcata* and *P. systena* may eventually be transferred to *Calyptosporium*.

Remarks. If the apical spine is reduced or broken (Pl. 1, Figs. 6, 7) it is not possible to distinguish between *P. systena* and *P. furcata*.

Pseudopyxilla furcata Harwood and Gersonde sp. nov.
(Pl. 1, Figs. 10-15)

Description. Epivalve cylindrical with a conical apex that supports four longitudinal costae that coalesce to form a massive strut, from which the costae diverge to form two buttressed spines in the general shape of a tuning fork; small transverse spines are sometimes present near the terminus of the spines, usually one per spine, if present at all.

Remarks. This species is morphologically similar to *Pseudopyxilla americana* (Ehrenberg) (Forti, 1909, p. 28, pl. 1, fig. 6) and the diatom identified as *P. americana* in Strel'nikova, 1974 (p. 112, pl. 54, figs. 1-15) by the presence of a distinct mantle that frequently bears a ridge, the sub-parallel buttressed spines. It may also have a different stratigraphic range.

Holotype. Friedrich-Hustedt Collection No. Zu 3/97-17 (Pl. 1, Fig. 10).

Paratype. Friedrich-Hustedt Collection No. Zu 3/96-1 (Pl. 1, Fig. 11).

Type locality. Dronning Maud Land margin, Antarctica, eastern Weddell Sea, ODP Site 693.

Type level. Lower Albian; ODP Sample 113-693B-19X-4, 77-78 cm.

Derivation of name. furcatus (Lat.)—forked.

Pseudopyxilla systena Harwood and Gersonde sp. nov.
(Pl. 1, Figs. 8, 9)

Description. Epivalve cylindrical with a conical apex that tapers to an elongate spine that bears a varying number of transverse spines; hypovalve fully enclosed by epivalve mantle (calyptra?).

Holotype. Friedrich-Hustedt Collection No. Zu 3/98-2 (Pl. 1, Fig. 8).

Paratype. Friedrich-Hustedt Collection No. Zu 3/95-5 (Pl. 1, Fig. 9).

Type locality. Dronning Maud Land margin, Antarctica, eastern Weddell Sea, ODP Site 693.

Type level. Lower Albian; ODP Sample 113-693B-19X-4, 103-104 cm.

Derivation of name. systenos (Gk.)—tapering to a point.

CHRYSOPHYCEAN CYSTS

Informal nomenclature is used here for the various forms of Chrysophycean cysts, rather than proposing new names into the literature. This follows the philosophy of Adam and Mahood (1981).

Archaeomonas? sp. A (Pl. 9, Figs. 5, 7)
Archaeomonas sp. B (Pl. 9, Figs. 8, 9)
Archaeomonas sp. C (Pl. 9, Figs. 10, 11, 15)
Archaeomonas ? sp. D (Pl. 9, Figs. 12, 13, 14)
Archaeomonas sp. E (Pl. 10, Figs. 1, 2, 3)
Archaeomonas sp. F (Pl. 10, Figs. 4, 5)
Archaeomonas sp. G (Pl. 10, Figs. 6, 7, 8, 9)
Archaeomonas sp. H (Pl. 10, Figs. 10, 15, 16, 17, 18)
Archaeomonas sp. I (Pl. 10, Figs. 11, 12)
Archaeomonas sp. J (Pl. 10, Figs. 13, 14)

ENDOSKELETAL DINOFLAGELLATE

Genus *CARDUIFOLIA* Hovasse, 1932a, b
Carduifolia toxon Harwood and Gersonde sp. nov.
(Pl. 10, Figs. 19, 20)

Description. Siliceous skeleton shaped like an archer's bow, consisting of a central apical arch that bears multiple branching spines (usually broken) along the convex side; distal ends of the main skeleton bifurcate and trifurcate into short, thin spines.

Remarks. See Dumitrica (1973; p. 824) for a discussion of the genus *Carduifolia*. Species not observed in the SEM.

Holotype. Friedrich-Hustedt Collection No. Zu 3/97-19 (Pl. 10, Fig. 19).

Paratype. Friedrich-Hustedt Collection No. Zu 3/95-6 (Pl. 10, Fig. 20).

Type locality. Dronning Maud Land margin, Antarctica, eastern Weddell Sea, ODP Site 693.

Type level. Lower Albian; ODP Sample 113-693B-19X-4, 77–78 cm.

Derivation of name. toxon (Gk.)—bow.

DISCUSSION

The well-preserved diatom floras and Chrysophycean cyst assemblages reported here and in the accompanying chapter on vegetative forms (Part 1, Gersonde and Harwood, this volume) offer a new perspective on the early history of these groups that was previously not available due to the paucity of material and poor preservation of available materials. A total of 53 diatom taxa in 21 genera are documented in this paper and in Part 1 (Gersonde and Harwood, this volume). Ten Chrysophycean cyst taxa, one endoskeletal dinoflagellate, and three silicoflagellate taxa are also documented here and in McCartney et al. (this volume).

From these numbers it is apparent that marine siliceous phytoplankton were well established by the end of the Early Cretaceous. One must bear in mind, however, the incomplete nature of the fossil record; even though this material is exceptionally well preserved, selective dissolution probably removed numerous floral elements that may be critical to our understanding of phylogeny, spore-vegetative relationships and population structure. Moreover, the limited record of siliceous microfossils of this age (Table 1 of Gersonde and Harwood, this volume) cannot represent the diversity of environments where diatoms and other siliceous microfossils lived. As today, the variety of Early Cretaceous environments (planktonic, benthic, neritic, tropical, polar, etc.) probably contained unique assemblages with morphologic adaptations to the particular setting. Thus, it is unlikely that the known assemblages are representative of the Lower Cretaceous. These limitations, however, do not weaken the significance of the Site 693 siliceous microfossil assemblages, and significant conclusions and comparisons can still be drawn from this unique window into an early stage of diatom development.

Comparing the Site 693 diatom floras to those documented by Forti and Schulz (1932) on German material, we find that 10 of their 14 morphotypes are represented here (this comparison uses our species concepts as applied to their illustrations, and several of our species are referred to by Forti and Schulz as *Stephanopyxis mirabilis*). Similarly, comparison of diatoms illustrated in Harper's unpublished plates shows that 9 of the 11 Queensland diatom morphotypes are also represented in our materials. These statistics agree with Harper's (1977) conclusion that by the Early Cretaceous, diatoms were well established as an algal group and that they were distributed around the globe. We note that most of the Lower Cretaceous and Jurassic occurrences are from sediments deposited in interior seas or on continental margin sites (Fig. 2 of Gersonde and Harwood, this volume). The ecological preference of these assemblages is not known, but Haig and Barnbaum (1978) suggest a slightly hyposaline, shallow sea in the Early Cretaceous Great Artesian Basin of Queensland.

The high number of species and genera present in the Site 693 sediments and the numerous adaptations to chain formation through linking structures suggests that our material is much younger than the time when diatoms originated. There is, however, sufficient commonality of form and structure to suggest that they are close to a common stock. Features common to many "vegetative" diatoms from Site 693 are identified in Part 1 (Gersonde and Harwood, this volume), including a radial poroid primary membrane, a silicified marginal ridge or area that often supports costate linking spines, radial costae on the valve face that unite at the valve margin with paired longitudinal costae from the valve mantle to form varied linking structures and a cylindrical valve with an elongated pervalvar axis (note that all of these features are also known in hypovalves of *Calyptosporium*). Features that are not common to this general plan may represent various stages of evolutionary innovation that are decipherable, given the assumption that the above common structures are more "primitive" features. These discussions all bear on the idea that Jurassic and Early Cretaceous diatom evolution was monophyletic; while this appears to be the case from these assemblages, a potential for polyphyly among the diatoms must also be considered.

It is clear from Site 693 diatom assemblages that resting spore formation and the ability to form chains are ancient features of the diatoms. Much of the silica deposited on Lower Cretaceous diatoms is associated with these two functions and the pseudolocular silica of many vegetative genera is in structural support of the linking spines.

A DISCUSSION ON THE ORIGIN OF THE DIATOMS WITH REFERENCE TO RESTING SPORES AND CHRYSOPHYCEAN CYSTS

Because the Lower Cretaceous diatom assemblages recovered from ODP Leg 113 represent one of the oldest records of diatoms known, a discourse on the origin of diatoms is appropriate here. The commonality of several structures to most diatoms documented here and in Gersonde and Harwood (this volume) and the overall similarity of diatoms recovered from ODP Site 693 to each other and to other Albian/Aptian assemblages, suggests that the Site 693 assemblages are not far removed from an early common stock. Simonsen (1972) speculates that a simple diatom like *Pyxidicula* from the Lower Jurassic (Rothpletz, 1896) may represent the ancestral stock of the diatoms. Given the rapid rate at which pennate diatoms diversified in the late Cenozoic (20 m.y.), it is surprising that Albian diatom assemblages are not much more diverse, because more than 80 m.y. separate Rothpletz's Jurassic diatoms and the Albian assemblages reported in this volume.

The number of diatom species as indicated by the available fossil record has apparently progressed through the Mesozoic; increasing from four species in the Jurassic to almost 25 in the Aptian, to more than 45 in the Albian (see review of Jurassic and Lower Cretaceous occurrences, above), to more than 300 species in 60 genera by the latest Cretaceous (Hanna, 1927, 1934; Strel'nikova, 1974, 1975; Hajós and Stradner, 1975; Harwood, 1988). The limited record in the older sequences may be due to a combination of the following: (1) progressive diversification since the Early Jurassic; (2) a preservational bias against these species due to the temporal instability of Opal-A; (3) insufficient search for diatoms in older sequences; (4) paucity of Jurassic and older marine sequences due to ocean crust subduction; or (5) other factors, including the possibility that many early diatoms were weakly silicified, if at all.

The abrupt(?) appearance of diatoms in the Jurassic and their explosive increase in diversity and abundance (widespread diatomite production) in the Late Cretaceous and early Tertiary has led some workers to suggest a prolonged pre-Jurassic evolutionary history as naked cells, siliceous scale-covered cells, flagellate cells, or weakly silicified cells, or a combination of these forms (Pia, 1931; Simonsen, 1972; Loeblich, 1974; Round and Crawford, 1981; Round, 1981), none of which are preserved as fossils.

Round (1981a, b) and Round and Crawford (1981, 1984) suggest a burst of evolutionary radiation early in the history of diatoms, followed by general evolutionary stasis to the present. These authors, however, suggest a Late Precambrian or early Paleozoic age for this radiation; there is, however, no fossil evidence to support this antiquity. Round and Crawford speculate that diatoms originated from multi-scale-covered photosynthetic cells, basing this on modern diatom morphology, comparative life histories, and on parallels with the Chrysophyceae. They suggest that the scale-covered cells became polarized and two scales developed into the valves and the other scales developed into the cingulum and intercalary bands. Diatom evidence from Albian assemblages of ODP Leg 113 can not support or refute their hypothesis, and cingula are noted on several Lower Cretaceous "vegetative" diatom genera *Basilicostephanus, Gladius, Gladiopsis*, and *Archaeopyrgus* (Gersonde and Harwood, this volume), and *Dactyliosolen priscus* (Forti and Schulz, 1932).

Diatoms cultured or living without a siliceous frustule develop into a globular sub-spherical shape (Richter, 1904; Bachrach and Lefevre, 1929; Hendey, 1945, 1946). This form is what Simonsen (1972) suggests is the forerunner of the diatoms. By covering the protoplasm with two siliceous hemispheres, a morphology ("caged balloons" of Round, 1981a) not unlike Rothpletz's *Pyxidicula* would result. Perhaps their appearance in the Early Jurassic does not mark the origin of the group, but instead may mark the initiation of silicification in the diatoms.

The constancy of form of numerous genera from the Late Cretaceous to the present led Hart (1963) to believe that diatom evolution was already far advanced by the Late Cretaceous and has proceeded slowly to the present. It is clear from comparison of our Albian assemblages to the considerably more diverse Late Cretaceous (Campanian and Maestrichtian) assemblages reported by Strel'nikova (1974), Hajós and Stradner (1975) and Harwood (1988), that a significant amount of evolutionary innovation occurred during the early Late Cretaceous. Many long-ranging genera that continue through the Late Cretaceous and Early Cenozoic originated between the Albian and Campanian (refer to the synthesis of Jousé, 1978).

Simonsen (1979) proposed that diatoms originated in a neritic marine environment because abundant resting spores occur only in shallow-water shelf environments (Ross and Sims, 1974; Jousé, 1978) and because phylogenetic evidence suggests resting spores are characteristic of primitive groups of diatoms (Simonsen, 1972, 1979; Hargraves and French, 1983). Silicification of resting spores would foster a competitive advantage by providing a somewhat impervious barrier, capable of isolating the protoplasm from the perhaps seasonally deleterious environmental changes induced by variation of nutrient and light supply, and perhaps changes in salinity in a nearshore environment. Additionally, the increased weight of the siliceous frustule and compacting of the cell contents through resting spore formation might enhance chances of survival by increasing the sinking rate to deeper nutrient sources. This would remove the diatom from dangerously high light levels, as well as reduce metabolic costs in an environment of lowered light levels and reduced temperatures (French and Hargraves, 1980; Hargraves and French, 1983; Garrison, 1984). Note, however, that the difference in sinking rates between modern vegetative cells and resting spores is not marked (French and Hargraves, 1980; Hargraves and French, 1983). Smetacek (1985) suggests that mass resting spore formation following a nutrient-depleting bloom is a survival mechanism that rapidly propels a population downward into colder, darker waters, where diatom survival is prolonged. Further benefits of resting spore formation include minimal geographic displacement away from fertile environments by oceanic currents (Garrison, 1984) and the dispersal of spores into new, more favorable environments (Smetacek, 1985).

Round (1981a, b), Round and Crawford (1981, 1984) and Smetacek (1985) support the suggestion originally put forward by Pascher (1921) that the diatom vegetative cell was originally an encysted resting stage of a flagellate algae (such as the Chrysophycean flagellates), which through evolution became the dominant phase of the diatom life cycle. They further suggest that a remnant of this ancestry may be reflected in the flagellate male gametes of some centric diatoms. Cavalier-Smith (1986), however, suggests a relationship with flagellates in his Class Synurea (*Synura, Mallomonas, and Mallomonopsis*). The occurrence of siliceous Chrysophycean cysts or statospores (Pls. 9, 10) with the diatoms at Site 693 may strengthen the relationships suggested above, in that both were present at this time. One heavily silicified portion of the Chrysophycean life cycle is the silicified statocyst or statospore (Sandgren, 1983); this plays a role similar to the diatom resting spore. Because the geological record of many phytoplankton groups (Chrysophycean flagellates, dinoflagellates, prasinomonads) is limited to spores or cysts, perhaps the oldest record of silicified diatoms consists only of resting spores. Are the Lower Jurassic diatoms described by Rothpletz (1896, 1900) and Vechina (1961) resting spores of diatoms, or resting spores of another algal group that gave rise to the diatoms? To hypothesize on an early diatom *cell* or a Jurassic "mesotype" (Round, 1981b), we can think about a sphere covered in scales, or a cell with dome shaped valves and simple girdle bands as suggested by Round (1981b), and Round and Crawford (1981). To search for the oldest fossil diatom *valve or frustule*, however, perhaps we should be looking for a solid (or nearly so), highly silicified body, similar to other siliceous algal cysts, such as the Chrysophycean statospore.

Constraint on the above speculation and that of many authors reviewed above, and a better understanding of the early history of diatoms will come only when the fossil record of Jurassic and Lower Cretaceous diatoms and Chrysophycean cysts is better documented. Long intervals with no diatom record exist between the Lower Jurassic and the Aptian, and between the Albian and Santonian. At present we have only glimpses of what appears to be a significant period of diatom evolution, perhaps near the origin of the group. The record of these events has eluded us due to diagenetic loss, limited study, or, perhaps the absence of preservable structures. Analysis of sediments cemented by calcium carbonate at the centers of concretions or from within cemented centers of mollusks, is the direction this research should take in order to advance the early history of the diatoms and Chrysophyceans, because the concretions or shells preserve the temporally unstable opal-A (Blome and Albert, 1985; Harwood, 1988).

Sampling from other Lower Cretaceous and Upper Jurassic localities should attempt to recover assemblages from different environmental settings as well as a range of ages. This is necessary to determine the degree of differentiation into various ecologic facies, and to what extent and at what time the different adaptations to these environments influenced Mesozoic diatom evolution.

ACKNOWLEDGMENTS

We acknowledge the helpful discussions with J. Baldauf, M. Harper, V. Porguen, R. Scherer, and D. Stockwell regarding this material, and thank V. Porguen for his assistance in checking construction of new species and generic names. H. Harper generously provided unpublished plates, notes, and samples of Aptian/Albian diatoms from Queensland for comparison. P. Hargraves and P. Sims reviewed the text. M. Karrer, R. Cordelair, and U. Bock assisted with laboratory preparation; C. Hart and R. Graham provided technical assistance in assembling this manuscript. This work was supported by Byrd Polar Research Center and the Deutsche Forschungsgemeinschaft. This is Byrd Polar Research Center Contribution No. 684 and Alfred Wegener Institute contribution No. 219.

REFERENCES

Adam, D. P., and Mahood, A. D., 1979. A preliminary annotated bibliography on siliceous algal cysts and scales. *U.S. Geol. Surv. Open File Rep.*, 79-1215:1-34.

________, 1981. Chrysophyte cysts as potential environmental indicators. *Geol. Soc. Am. Bull.*, 92:839-844.

Anonymous, 1975. Proposals for a standardization of diatom terminology and diagnosis. *In* Simonsen, R. (Ed.), *Third Symp. Recent and Fossil Marine Diatoms, Kiel.* Nova Hedwigia, Beih., 53:322-354.

Bachrach, E., and Lefevère, M., 1929. Contribution a l'etude du rôle de la silice chez les êtres vivants. *J. Physiol. Path. gen.*, 27:241-249.

Barber, H. G., and Haworth, E. Y., 1981. A guide to the morphology of the diatom frustule, with a key to the British freshwater genera. *Freshwater Biol. Assoc. Sci. Publ.*, 44:1-112.

Barker, P. F., Kennett, J. P., et al., 1988. *Proc. ODP, Init. Repts.*, 113: College Station, TX (Ocean Drilling Program).

Benda, L., 1982. Die diatomeen des späten Apt in Nordwestdeutschland. *Geol. Jahrb.*, A65:405-411.

Blome, C. D., and Albert, N. R., 1985. Carbonate concretions: An ideal sedimentary host for microfossils. *Geology*, 12:212-215.

Cavalier-Smith, T., 1986. The Kingdom Chromista: origins and systematics. *Prog. Phycolog. Res.*, 4:309-347.

Cayeux, L., 1892. Sur la presence de nombreuses Diatomées dans les gaizes Jurassique et Cretacées du Basin de Paris. *Ann. Soc. Geol. Nord.*, 20:57-60.

Cornell, W. C., 1979. Mesozoic silicoflagellates and Archaeomonads. *Am. Assoc. Stratigr. Palynol.*, 5B:31-47.

Deflandre, G., 1959. Sur des nannofossiles calcaires et leur Systematique. *Rev. Micropaleontol.*, 2:127-152.

Dumitrica, P., 1973. Cenozoic endoskeletal dinoflagellates in southwestern Pacific sediments cored during Leg 21 of the Deep Sea Drilling Project. *In* Burns, R. E., Andrews, J. E., et al., *Init. Repts. DSDP*, 21: Washington (U.S. Govt. Printing Office), 819-835.

Dun, W. S., Rands, W. H., and David, T.W.E., 1901. Note on the occurrence of diatoms, radiolaria and infusoria in the Rolling Downs Formation (Lower Cretaceous). Queensland. *Proc. Linn. Soc. N. S. W.*, 26:299-309.

Forti, A., 1909. Studi per una Monographia del genere *Pyxilla* (Diatomee) e dei generi affini. *La Nuova Notarisia*, 20:5-24.

Forti, A., and Schulz, P. 1932. Erste Mitteilung über Diatomeen aus dem Hannoverschen Gault. *Beih. Bot. Zentralbl.*, 50:241-246.

Foucault, A., Servant-Vildary, S., Fang, N., and Powichrowski, L., 1986. Un des plus anciens gisements de diatomées découvert dans l'Albien-Cénomanien inférieur des Alpes ligures (Italie). Remarque sur l'appariation de ces algues. *C. R. Acad. Sci. Paris*, T. 303, Sér. II, no. 5, 397-402.

French, F. W., and Hargraves, P. E., 1980. Physiological characteristics of plankton diatom resting spores. *Mar. Biol. Lett.*, 1:185-195.

Frenguelli, G., 1932. A proposito della diatomee del Paleozoico. *Bol. Soc. Geol. Ital.*, 51:101-114.

Fritsch, F. E., 1935. *The structure and reproduction of the Algae.* Vol. I. Cambridge (Cambridge Univ. Press).

Garrison, D. L., 1984. Planktonic diatoms. *In* Steidinger, K. A., and Walker, L. M. (Eds.), *Marine plankton life cycle strategies*: Boca Raton (CRC Press, Inc.), 2-12.

Georgi, K. H., 1976. Mikrofaunistich-lithologische Untersuchungen der Hilssandstein-Region (Apt/Alb) im Raum Salzgitter-Goslar. *Mitt. Geol. Inst. Tech. Univ. Hannover*, 13:5-112.

Geroch, S., 1978. Lower Cretaceous diatoms in the Polish Carpathians. *Rocz. Pol. Tow. Geol.*, 48:283-295.

Glazek, J., Galewski, K., and Wysoczanski-Minkowicz, T., 1977. Nowe dane o Krasie kopalnym w Przewornie. (New data on fossil karst at Przeworno). *Kras i Speleologia*, 2:81-88.

Gran, H. H., 1897. Protophyta: Diatomaceae, Silicoflagellata and Cilioflagellata. *Norwegian N. Atlantic Expedition*. 1876-78, Vol. 7.

Haig, D. W., and Barnbaum, D., 1978. Early Cretaceous microfossils from the type Wallumbilla Formation, Surat Basin, Queensland. *Alcheringa*, 2:159-178.

Hajós, M., and Stradner, H., 1975. Late Cretaceous Archaeomonadaceae, Diatomaceae, and Silicoflagellatae from the South Pacific Ocean, Deep Sea Drilling Project, Leg 29, Site 275. *In* Kennett, J. P., Houtz, R. E., et al., *Init, Repts. DSDP*, 29: Washington (U.S. Govt. Printing Office), 913-1009.

Hanna, G D., 1927. Cretaceous diatoms from California. *Occas. Pap. Calif. Acad. Sci.*, 13:5-49.

________, 1934. Additional notes on diatoms from the Cretaceous of California. *J. Paleontol.*, 8:352-355.

Hargraves, P. E., 1976. Studies on marine plankton diatoms. II. Resting spore morphology. *J. Phycol.*, 12:118-128.

________, 1979. Studies on marine plankton diatoms. IV. Morphology of *Chaetoceros* resting spores. *Nova Hedwigia, Beih.*, 64:99-120.

________, 1987. The relationship of some fossil diatom genera to resting spores. *In* Ricard, M. (Ed.), *Proceedings of the Eighth International Diatom Symposium*: Koenigstein, 67-80.

Hargraves, P. E., and French, F. W., 1974. Observations on the survival of diatom resting spores. *Nova Hedwigia, Beih.*, 53:229-238.

________, 1983. Diatom resting spores: significance and strategies. *In* Fryxell, G. A. (Ed.), *Survival Strategies of the Algae*: Cambridge (Cambridge Univ. Press), 49-68.

Harper, H. E., 1977. A Lower Cretaceous (Aptian) diatom flora from Queensland, Australia. *Nova Hedwigia, Beih.*, 54:411-412.

Hart, T. J., 1963. Speciation in marine phytoplankton. *In* Speciation in the Sea; *Syst. Assoc., Spec. Vol.*, 5:145-155.

Harwood, D. M., 1988. Upper Cretaceous and lower Paleocene diatoms and silicoflagellate biostratigraphy of Seymour Island, eastern Antarctic Peninsula. *In* Feldmann, R., and Woodburne, M. O. (Eds.), The Geology and Paleontology of Seymour Island. *Geol. Soc. Am. Mem.*, 169:55-129.

Hasle, G. R., and Sims, P. A., 1985. The morphology of the diatom resting spores *Syringidium bicorne* and *Syringidium simplex*. *Br. Phycol. J.*, 20:219-225.

Hendey, N. E., 1933. A preliminary note on the distribution of marine diatoms during the Tertiary Period. *J. Bot. London*, 71:111-118.

________, 1945. Extra-frustular diatoms. *J. Roy. Microscop. Soc.*, 65: 34-39.

________, 1946. Diatoms without siliceous frustules. *Nature*, 158:588.

Hovasse, R., 1932a. Note préliminaire sur les Ebriacées. *Soc. Zool. Fr. Bull.*, 57:118-131.

________, 1932b. Troisieme note sur les Ebriacées. *Soc. Zool. Fr. Bull.*, 57:457-476.

Jousé, A. P., 1948. Dotretichnye diatomovye Vodorosli (Pre-Tertiary diatom algae). *Bot. Zh. SSSR.*, 33:345-356 (in Russian).

________, 1949. Diatoms from Mesozoic deposits. *Diatom Analysis*, 1: 109-114; Leningrad (Gosgeolizdat) (in Russian).

________, 1978. Diatom biostratigraphy on the generic level. *Micropaleontology*, 24:316-326.

Kemper, E., Bertram, H., and Deiters, H., 1975. Zur Biostratigraphie und Palökologie der Schichtfolge Ober-Apt/Unter Alb im Beckenzentrum nördlich und östlich von Hannover. *Ber. Naturhist. Ges., Hannover*, 119:49-85.

Kitchell, J. A., Clark, D. L., and Gombos, A. M., Jr., 1986. Biological selectivity of extinction: a link between background and mass extinction. *Palaios*, 1:504-511.

Kummel, B., and Raup, D., 1965. *Handbook of paleontological techniques:* San Francisco (W. H. Freeman and Co.), 1-852.

Kwiecinska, B., and Sieminska, J., 1973. Diatoms (Bacillariophyceae) in the Przneworno Marbles (Lower Silesia). *Bull. Acad. Pol. Sci. Ser. Sci. Terre*, 20:120-130.

Mitchell, J. G., and Silver, M. W., 1986. Archaeomonad (Chrysophyta) cysts: ecological and paleontological significance. *Biosystems*, 19: 289-298.

Müller, O., 1906. Pleomorphusmus, Auxosporen und Danersporen bei *Melosira-Arten. Jahrb. Wiss. Bot.*, 43:49-88.

________, 1912. Diatomeen aus den Turonschichten der Kreide. *Ber. Deutsch. Bot. Ges.*, 29:661-668.

Pascher, A., 1921. Über die einstimmungen z Wischen den Diatomeen, Heterokonten und Chrysomonaden, *Ber. Deutsch. Bot. Ges.*, 39: 236-240.

Perch-Nielsen, K., 1975. Late Cretaceous to Pleistocene archaeomonads, ebridians, endoskeletal dinoflagellates, and other siliceous microfossils from the subantarctic Southwest Pacific Deep Sea Drilling Project Leg 29. *In* Kennett, J. P., Houtz, R. E., et al., *Init. Repts. DSDP*, 29: Washington (U.S. Govt. Printing Office), 873–907.

Pia, J., 1927. Klasse Diatomeae (Bacillariophyta). *In* Hirmen, M. (Ed.), *Handbuch der Palaobotanik, Bd. 1, Thallophyta, Bryophyta, Pteridophyta*: München und Berlin (Oldenbourg), 44–58.

———, 1931. Vorliassiche Diatomeen? *Neues Jahrb. Mineral. Geol. Palaontol. Abh.*, 3:107–133.

Richter, O., 1904. Über Reinkultuen von Diatomeen und Notwendigkeitder Kieselsame für *Nitzschia palea* (Kützing) W. Smith. *Verh. Ges. Deutsch. Naturf. Atzte*, 2:249.

Ross, R., and Sims, P. A., 1972. The fine structure of the frustule in centric diatoms: a suggested terminology. *Br. Phycol. J.*, 7:139–163.

———, 1974. Observations on family and generic limits in the Centrales. *Nova Hedwigia, Beih.*, 45:97–128.

Ross, R., Cox, E. J., Karayeva, N. I., Mann, D. G., Paddock, T.B.B., Simonsen, R., and Sims, P. A., 1979. An amended terminology for the siliceous components of the diatom cell. *Nova Hedwigia, Beih.*, 64:513–533.

Rothpletz, A., 1896. Über die Flywsch-Fucoiden und einige andere fossile Algen, sowie über Liasische, Diatomeen führende Hornschwämme. *Z. Deutsch. Geol. Ges.*, 48:854–914.

———, 1900. Über einen neuen jurassichen Hornschwamm und die darin eingeschlossenen Diatomeen. *Z. Deutsch. Geol. Ges.*, 52:154–160.

Round, F. E., 1981a. Some aspects of the origin of the diatoms and their subsequent evolution. *Biosystems*, 14:483–486.

———, 1981b. Morphology and phyletic relationships of the silicified algae and the archetypal diatom—monophyly or polyphyly. *In* Simpson, T. L., and Volcani, B. E. (Eds.), *Silicon and siliceous structures in the biological systems*: New York (Springer-Verlag), 97–128.

Round, F. E., and Crawford, R. M., 1981. The lines of evolution of the Bacillariophyta. I. Origin. *Proc. R. Soc. London, B*, 211:237–260.

———, 1984. The lines of evolution of the Bacillariophyta. II. The centric series. *Proc. R. Soc. London, B*, 221:169–188.

Sandgren, C. D., 1983. Survival strategies of chrysophycean flagellates: reproduction and the formation of resistant resting cysts. *In* Fryxell, G. A. (Ed.), *Survival strategies of the algae*: Cambridge (Cambridge Univ. Press), 23–48.

Schmidt, A. 1874-1959. *Atlas der Diatomaceen-Kunde*. Begun by A. Schmidt, continued by M. Schmidt, O. Fricke, H. Müller, and F. Hustedt. Leipzig (Reisland), plates 1–480.

Schulz, P., 1935. Diatomeen aus Senonen Schwammgesteinen der Danziger Bucht. Zugleich ein Beitrag zur Entwicklungsgeschichte der diatomeen. *Bot. Archiv.*, 37:383–413.

Sieminska, J., 1974. Morphological and taxonomic features of the remains of diatom frustules found in the Devonian Marble in Poland. *Intern, Symp. Taxon. Algae (abstracts)*, Univ. Madras: 36–37.

Sieminska, J., and Kwiecinska, B., 1976. The significance of investigations upon diatoms found in the Przeworono Marbles. *Prz. Geol.*, 6: 326–328.

Simonsen, R., 1972. Ideas for a more natural system of the centric diatoms. *Nova Hedwigia, Beih.*, 39:37–54.

———, 1979. The diatom system: ideas on phylogeny. *Bacillaria*, 2: 9–71.

Sims, P. A., and Hasle, G. R., 1987. The Cretaceous *Stellarima* species: *S. steinyi* and *S. distincta*; their morphology, palaeogeography and phylogeny. *Diatom Res.*, 2:229–240.

Smetacek, V. S., 1985. Role of sinking in diatom life-history cycles: ecological, evolutionary and geological significance. *Mar. Biol.*, 84: 239–251.

Strel'nikova, N. I., 1974. *Late Cretaceous diatoms from western Siberia*: Moscow (Akad. Nauka, SSSR), 1–202.

———, 1975. Diatoms of the Cretaceous Period. *Nova Hedwidgia, Beih.*, 53:311–321.

Strel'nikova, N. I., and Martirosjan, G. N., 1981. Lower Cretaceous diatom algae from Stavropol. *Viestnik LGU. Ser. Biologiya*, 3:52–57.

Syvertsen, E. E., 1985. Resting spore formation in the Antarctic diatoms *Coscinodiscus furcatus* Karsten and *Thalassiosira australis* Peragallo. *Polar Biology*, 4:113–119.

Tappan, H. N., 1980. *The paleobiology of plant protists*: San Francisco (W. H. Freeman Co.), 490–534.

Taylor, F.J.R., 1980. Basic biological features of phytoplankton cells. *In* Morris, I. (Ed.), *The physiological ecology of phytoplankton*: Boston (Blackwell Scientific Publications), Studies in Ecology, 7:3–56.

Tynan, E. J., 1971. Geologic occurrences of the Archaeomonads. *In* Farinacci, A. (Ed.), *Proc. 2nd Planktonic Conf.*: Rome (Ed. Tecnoscienza), 1225–1230.

Van Heurck, H. 1880-1885. *Synopsis des diatomées de Belgique*: Antwerp (privately published).

Vechina, V. N., 1961. Novyi rod i novye vidy diatomovykh iz Melovyikh i Paleogenovykh Otlozhenii zapadno-sibirskoi nizmennosti. (New genus and species of the Cretaceous and Paleogene diatoms from the West Siberian Depression. *Tr. Sibir. Nauchno-issledovatel' sk. Inst. Geol. Geofiz. Mineral. Syr'ja*, 15:89–93.

Wall, J. H., 1975. Diatoms and radiolarians from the Cretaceous system of Alberta, a preliminary report. *In* Caldwell, W.G.E. (Ed.), The Cretaceous System in the Western Interior of North America, *Geol. Assoc. Can. Spec. Paper*, 13:391–409.

Date of initial receipt: 1 March 1989
Date of acceptance: 8 August 1989
Ms 113B-201

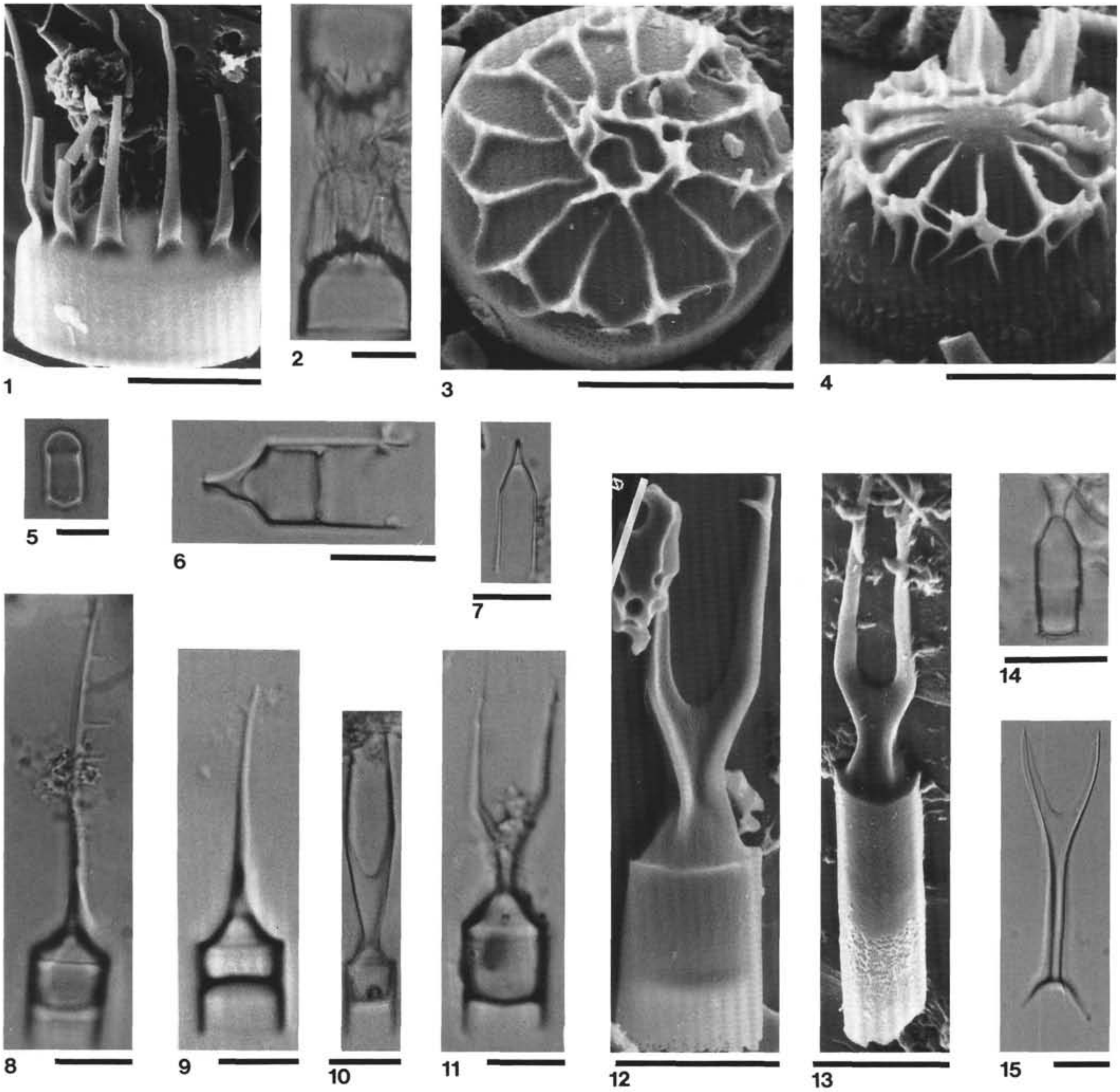

Plate 1. (Scale bars = 10 μm) **1–4.** *Cypellachaetes intricatus* n. sp., (1, 3, 4) Sample 113-693B-19X-4, 77–78 cm; (2) Sample 113-693B-19X-4, 103–104 cm, Holotype. **5.** *Calyptosporium perexiguum* n. sp., Sample 113-693A-44R-1, 14–18 cm, Holotype. **6, 7.** *Pseudopyxilla* spp., (6) girdle view of cylindrical mantle of epivalve (calyptra?) with hypovalve completely enclosed within, Sample 113-693B-19X-4, 103–104 cm; (7) Sample 113-693B-19X-4, 77–78 cm. **8, 9.** *Pseudopyxilla systena* n. sp., (8) Sample 113-693B-19X-4, 103–104 cm, Holotype; (9) Sample 113-693B-19X-4, 77–78 cm, Paratype. **10–15.** *Pseudopyxilla furcata* n. sp., (13) epivalve with structure analogous to calyptra and confossa zone of *Calyptosporium*; (14) hypovalve partly emergent from epivalve showing short spines at hypovalve margin that may be analogous to a fala; (10–13) Sample 113-693B-19X-4, 77–78 cm, (10) Holotype, (11) Paratype; (14,15) Sample 113-693B-19X-4, 103–104 cm. Nomarski illumination in Figures 2, 6–11, 14, 15.

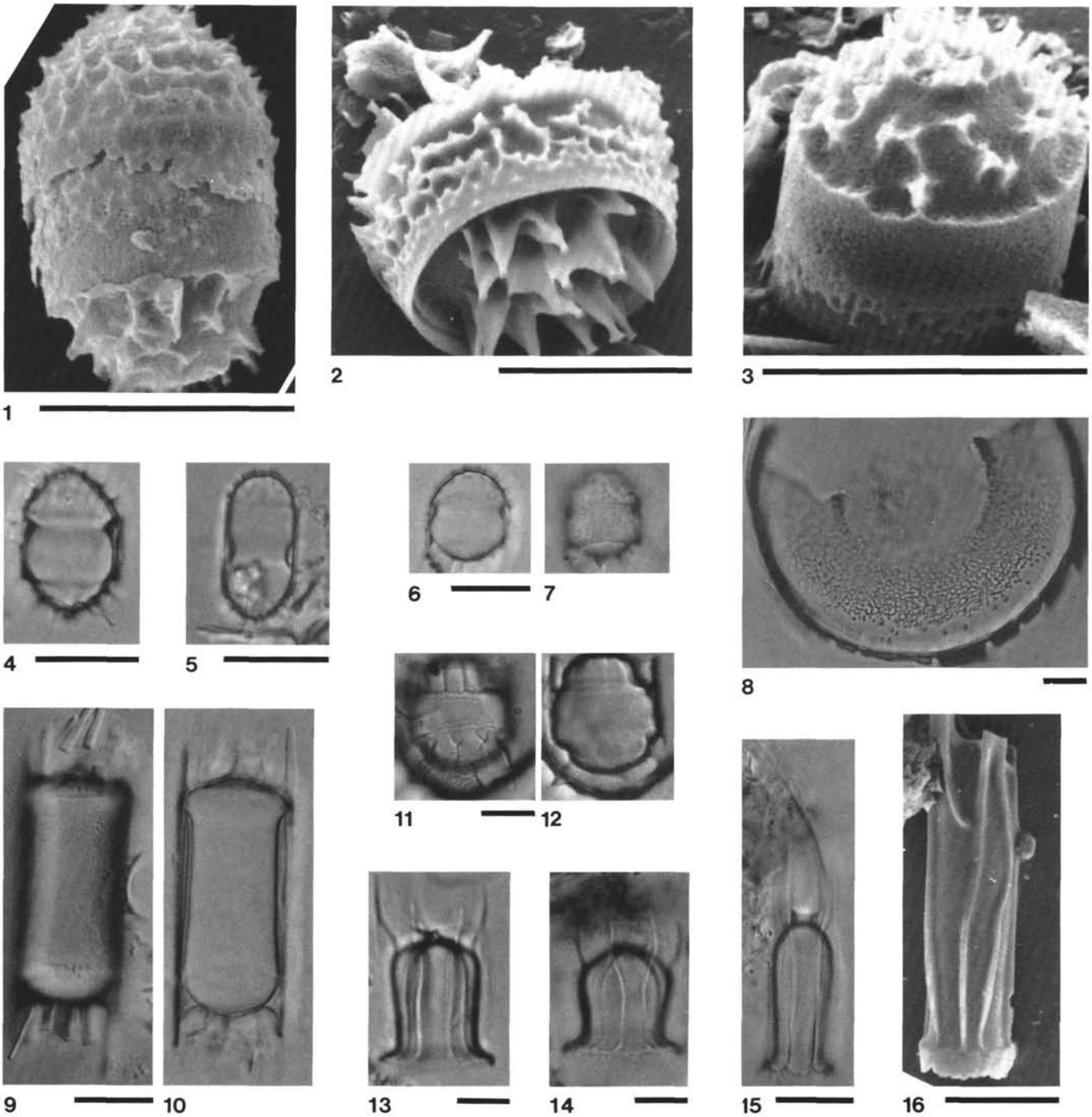

Plate 2. (Scale bars = 10 μm) **1-7.** *Dasyangea dactylethra* n. sp., (1-3) Sample 113-693B-19X-4, 77-78 cm; (4, 6, 7) Sample 113-693B-19X-4, 103-104 cm, (4) Holotype, (6, 7) Paratype; (5) Sample 113-693A-44R-1, 60-63 cm. **8.** *Calyptosporium maximum* n. sp., view looking into infundibular aperture with blades of lacinia visible in lower margin, Sample 113-693B-19X-4, 103-104 cm. **9-10.** *Meristosolen cylindratus* n. sp., Sample 113-693B-19X-4, 103-104 cm, Holotype, high and low focus of same specimen. **11-16.** *Calyptosporium galeolum* n. sp., (11, 12, 16) Sample 113-693B-19X-4, 77-78 cm, (11, 12) girdle view of frustule with epivalve at bottom and hypovalve at top, Holotype, high and low focus of same specimen; (13-15) girdle views of hypovalve, Sample 113-693B-19X-4, 103-104 cm, (14) Paratype. Nomarski illumination in Figures 4-15.

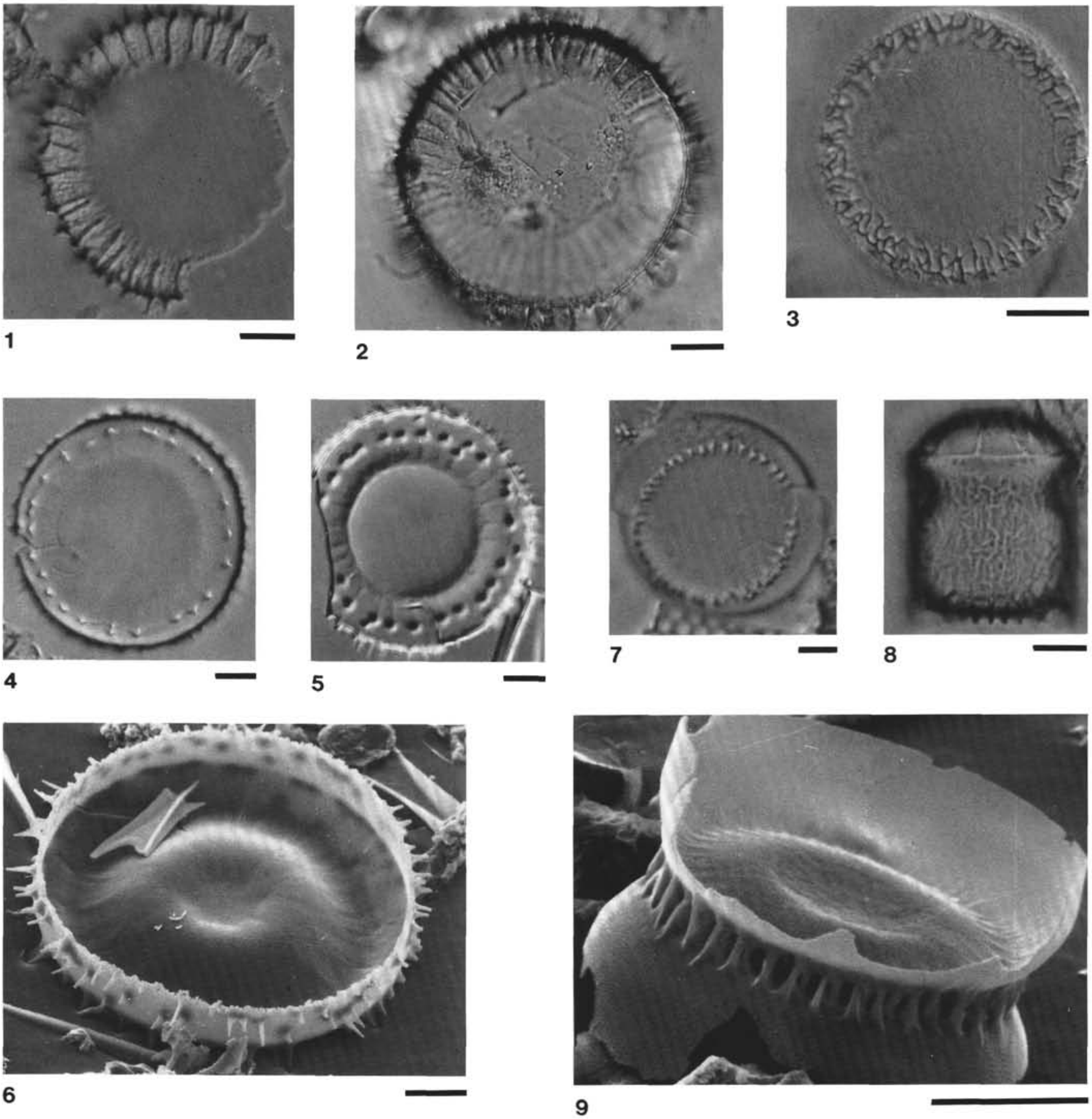

Plate 3. (Scale bars = 10 μm) **1–3.** *Crossophialus paterus* n. sp., (1, 3) Sample 113-693B-19X-4, 77–78 cm, (1) Paratype; (2) Sample 113-693B-19X-4, 103–104 cm, Holotype. **4–6.** *Crossophialus gyroscolus* n. sp., (4, 6) Sample 113-693B-19X-4, 77–78 cm, (4) Paratype; (5) Sample 113-693B-19X-4, 103–104 cm, Holotype. **7, 9.** *Crossophialus glabrus* n. sp., Sample 113-693B-19X-4, 77–78 cm, (7) Holotype. **8.** *Calyptosporium effalum* n. sp., Sample 113-693B-19X-4, 103–104 cm, Paratype. Nomarski illumination in Figures 1–5, 8, 9.

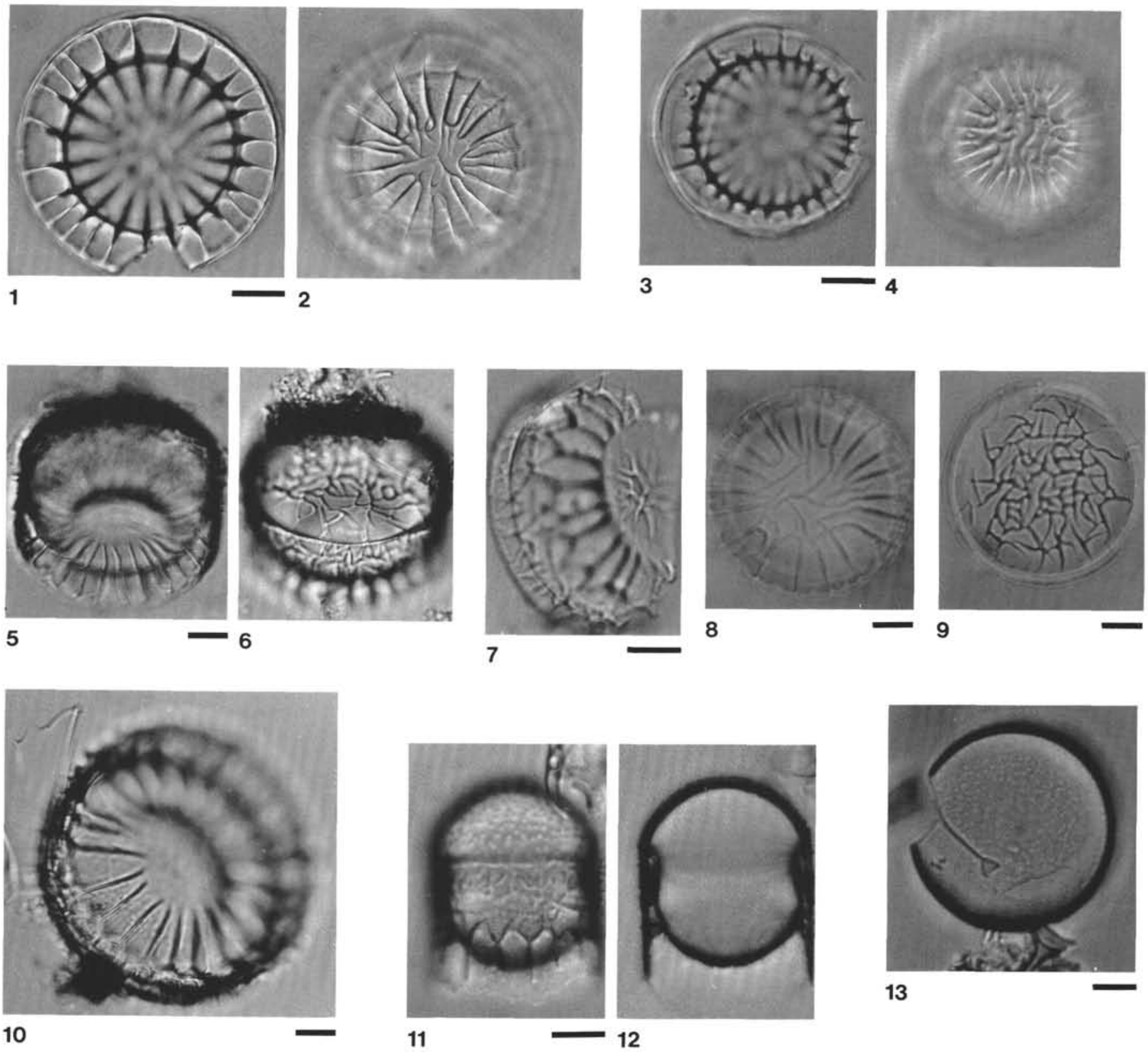

Plate 4. (Scale bars = 10 μm) **1–4.** *Hyalotrochus radiatus* n. sp., Sample 113-693B-19X-4, 77–78 cm, (1, 2) epivalve view of holotype, high and low focus of same specimen; (3, 4) epivalve view of paratype, high and low focus of same specimen. **5–10.** *Hyalotrochus incompositus* n. sp., (5–7) oblique views, Sample 113-693B-19X-4, 77–78 cm, (5, 6) Holotype, high and low focus of same specimen; (8, 10) Sample 113-693B-19X-4, 103–104 cm, (9) Sample 113-693B-19X-4, 77–78 cm, Paratype. **11–13.** *Calyptosporium lentiginosum* n. sp., (11, 12) girdle view of frustule at different focus showing surface ornamentation of hypovalve and epivalve (11) and silhouette at mid-plane focus (12), Sample 113-693B-19X-4, 77–78 cm, Holotype; (13) epivalve face, Sample 113-693A-44R-1, 14–18 cm. Nomarski illumination in Figures 1–12.

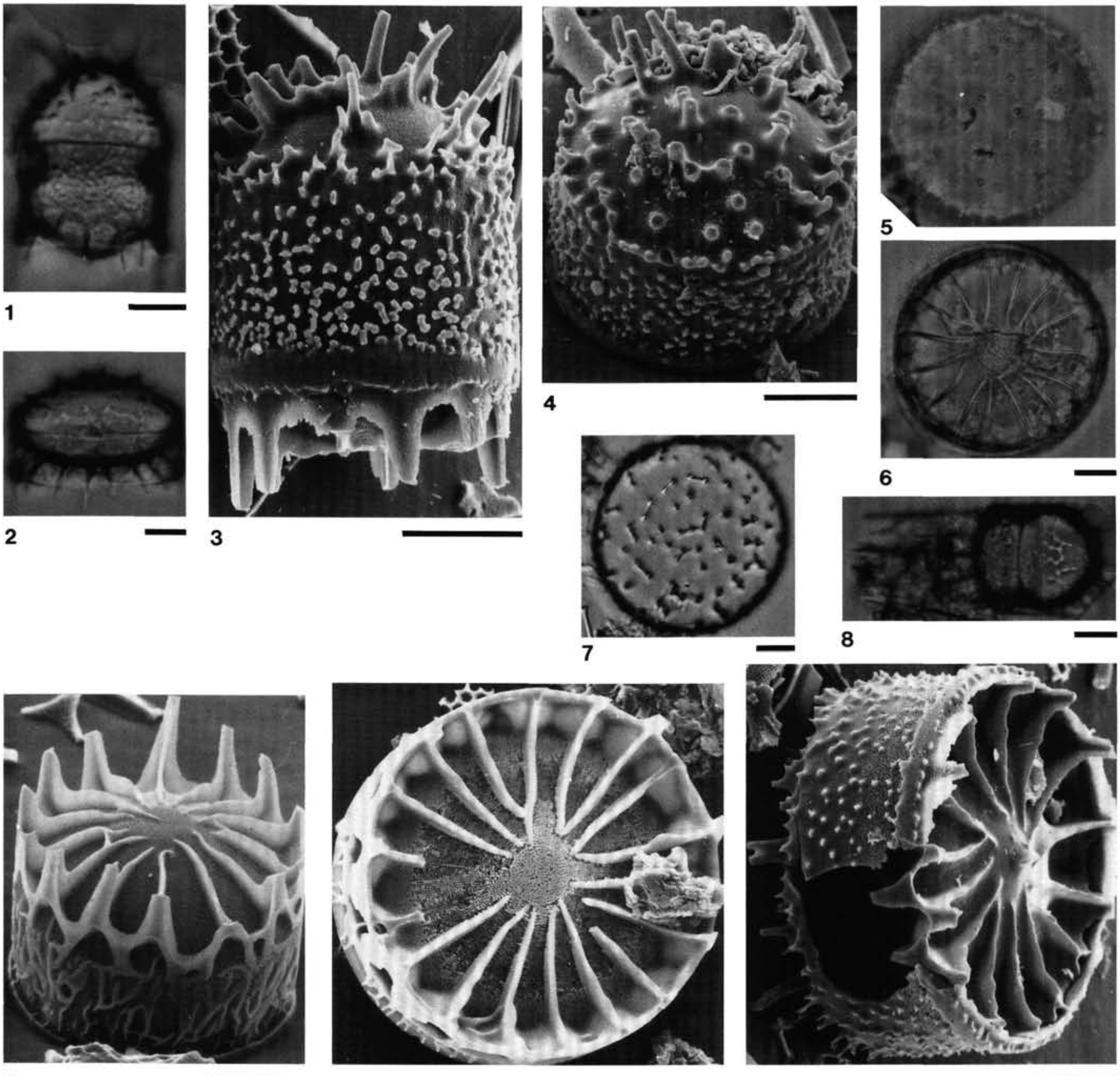

Plate 5. (Scale bars = 10 μm) **1–11.** *Calyptosporium exasperatum* n. sp., (3) girdle view of calyptra with hypovalve face and falar spines visible extending out from base of calyptra; (10) hypovalve in valve view, showing radial costae of the falar structure, radial punctate striae on a portion of the valve face and a distinct central disk with a sub-annular arrangement of puncta; (11) oblique view of calyptra showing confossa zone and hypovalve without perforations (contrast with Fig. 10), note contact of falar spines with calyptra interior; (1, 9, 10) Sample 113-693B-19X-4, 77–78 cm, (1) Holotype; (2, 4–6) Sample 113-693A-44R-1, 14–18 cm, (5, 6) Paratype, high and low focus of same specimen; (3, 11) Sample 113-693A-44R-1, 39–40 cm; (7) Sample 113-693B-19X-4, 77–78 cm; (8) Sample 113-693A-44R-1, 14–18 cm. Nomarski illumination on figures 1, 10, 11.

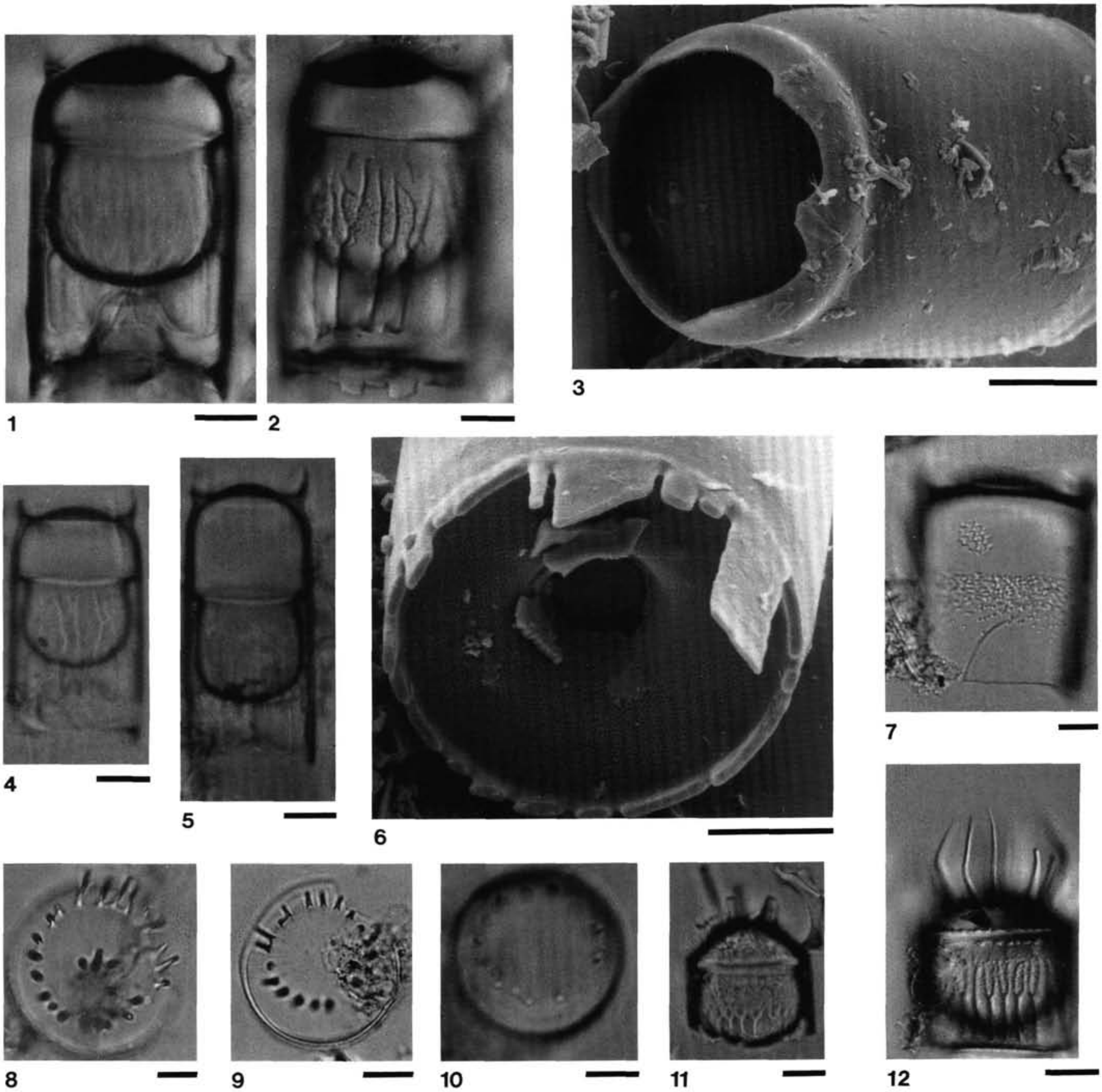

Plate 6. (Scale bars = 10 μm) **1–7.** *Calyptosporium carinatum* n. sp., (1, 2, 7) Sample 113-693B-19X-4, 77–78 cm, (1, 2) Holotype, high and low focus of same specimen showing falar spine network, silhouette of infundibulum, and blades of the lacinia (compare with text Fig. 3); (6) view of lacinia and infundibulum at base of calyptra, note presence of infundibular operculum (center) that is slightly larger than infundibular aperture; (7) girdle view showing confossa zone with distinct upper border; (3–6) Sample 113-693A-44R-1, 14–18 cm. **8–12.** *Calyptosporium cyclacaenum* n. sp., (8) epivalve with circle and central cluster of spines; (8, 9) Sample 113-693B-19X-4, 103–104 cm (9), Paratype; (10, 11) Sample 113-693A-44R-1, 14–18 cm; (12) Sample 113-693B-19X-4, 77–78 cm, Holotype. Nomarski illumination on figures 1, 2, 7–9, 12.

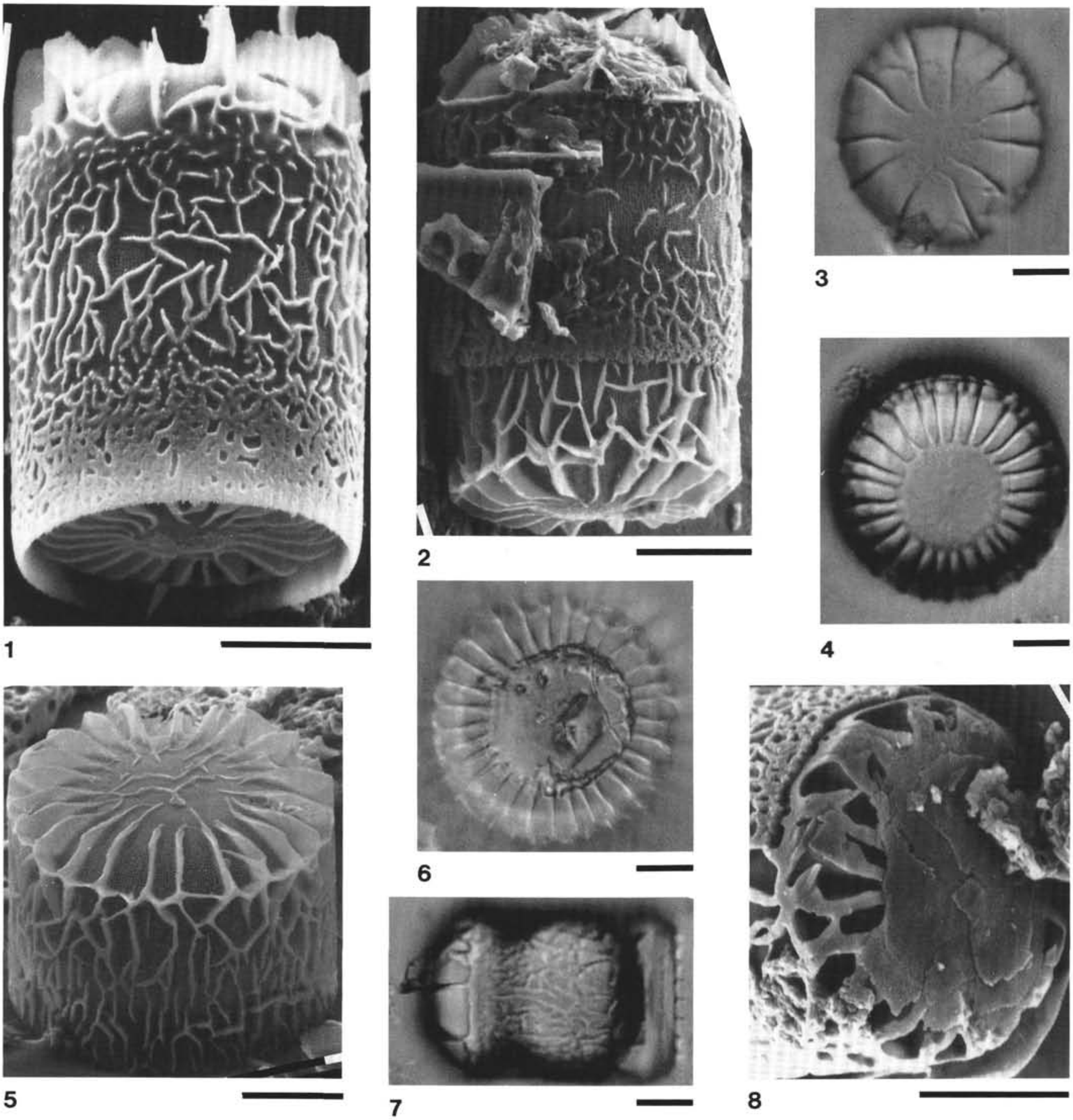

Plate 7. (Scale bars = 10 μm) **1-8.** *Calyptosporium effalum* n. sp., Sample 113-693B-19X-4, 77-78 cm. (1) girdle view showing calyptra with confossa zone of longitudinal punctate striae (arrow) and hypovalve face visible in base of calyptra; (2) girdle view showing hypovalve partly emergent from calyptra, note juxtaposition of perforations on calyptra (confossa zone) with those on hypovalve if re-inserted; (3) hypovalve showing reduced falar structure of costae only, note distinct zone of radial punctate striae near the valve margin at a position that would be adjacent to the confossa zone of the calyptra; (7) Holotype; (8) detail of reduced falar structure with rudimentary spines directed to the left of the radial costae, note sheets of silica with radial punctate striae on top of the costae that may be analogous to an infundibulum. Nomarski illumination on Figures 3, 4, 6, 8.

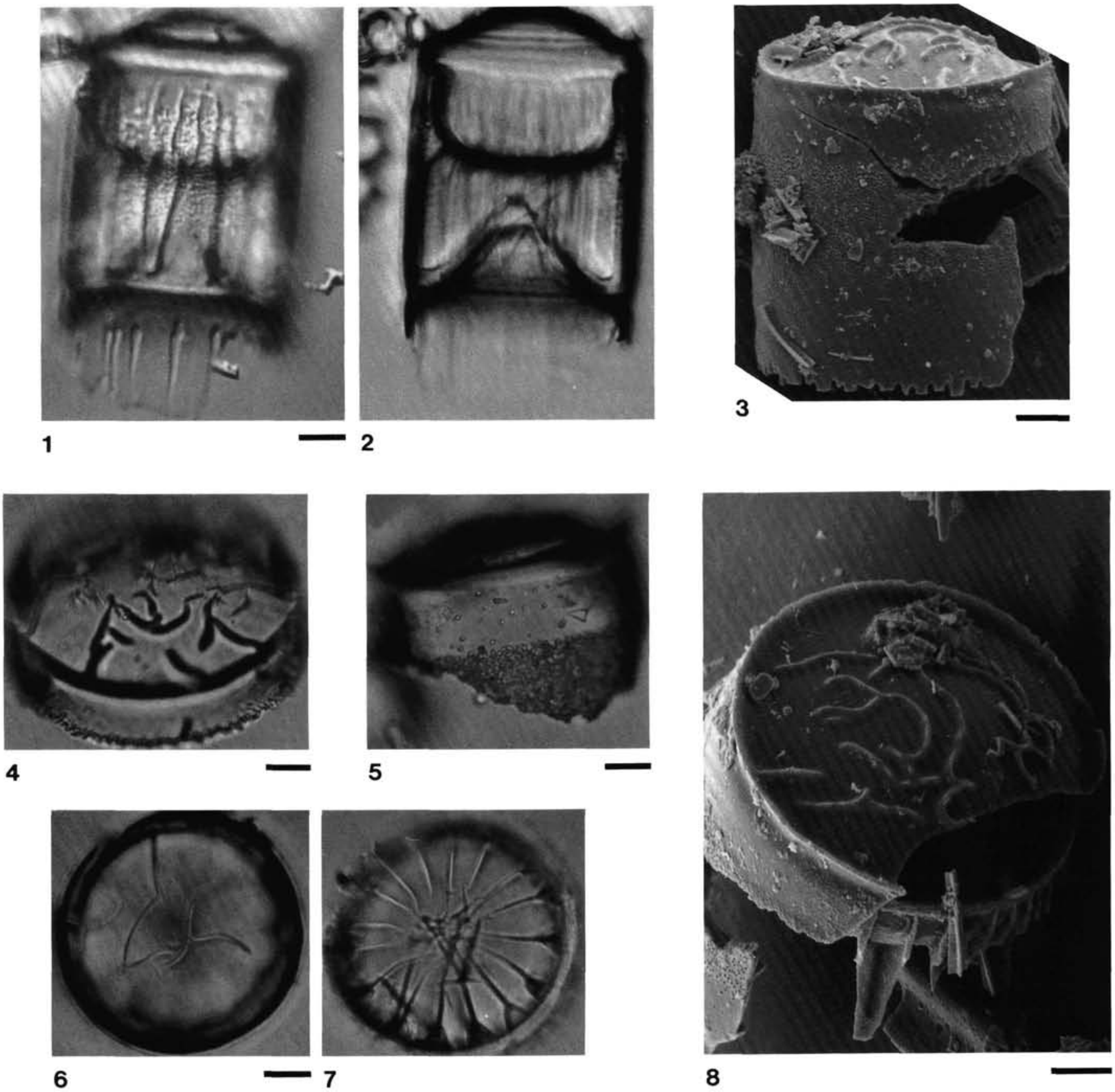

Plate 8. (Scale bars = 10 μm) **1–8.** *Calyptosporium maximum* n. sp., (1) girdle view with silhouette of frustule at mid-section focus showing outline of hypovalve and shadow of the infundibulum (compare with text Fig. 3); (2) girdle view showing paired longitudinal costae on hypovalve that merge to form falar spines, lacinia visible at base; (3) girdle view of frustule showing confossa zone at center of calyptra and broken blades of lacinia at base, hypovalve and one falar spine visible through broken portion of calyptra (see Fig. 8 for another view of this specimen); (5) girdle view of upper portion of calyptra and epivalve, note distinct border between confossa zone and hyaline band above; (6, 7) valve view of epivalve (6) and hypovalve (7) of same specimen showing heterovalvy; (8) oblique view of species shown in Fig. 3, note that some pores of the confossa zone do not continue through the calyptra; (1–5, 8) Sample 113-693A-44R-1, 14–18 cm (1, 2) Holotype, high and low focus of same specimen; (6, 7) Sample 113-693A-44R-1, 14–18 cm, Paratype, high and low focus of same specimen. Nomarski illumination in Figures 6, 7.

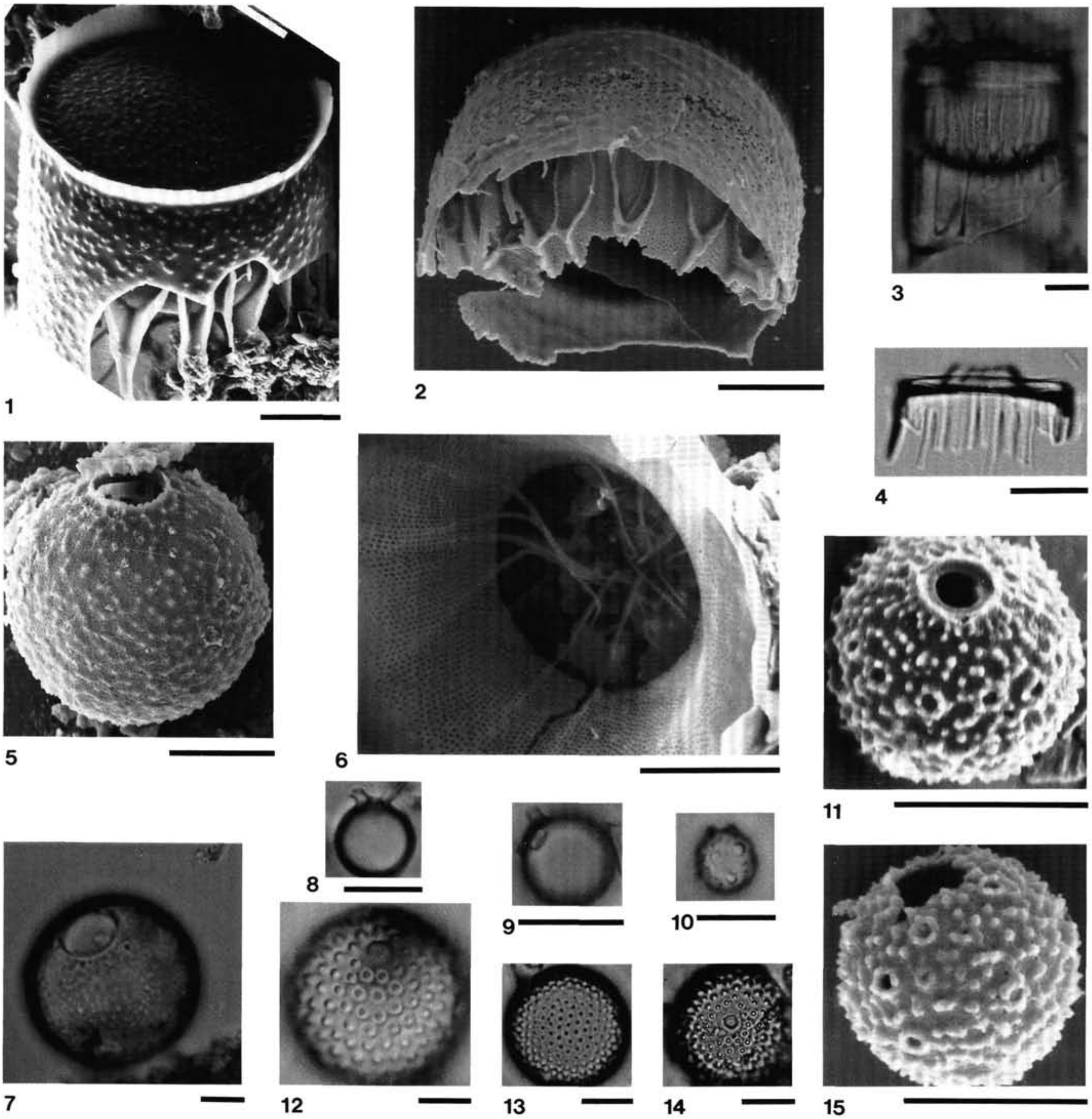

Plate 9. (Scale bars = 10 μm) **1–3, 6.** *Calyptosporium pustulatum* n. sp., (6) infundibulum with large infundibular aperture, terminal ends of falar spines are visible through the infundibulum in contact with it, and covering the infundibular aperture where an infundibular operculum (fragmented siliceous sheets?) was located; (1, 6) different view of same specimen, Sample 113-693B-19X-4, 77–78 cm; (2, 3) Sample 113-693A-44R-1, 14–18 cm, (2) Holotype. **4.** Infundibulum and lacinia structure of *Calyptosporium* spp., probably belonging to *C. carinatum* or *C. pustulatum*, Sample 113-693B-19X-4, 77–78 cm. **5, 7.** *Archaeomonas*? sp. A, (5) Section 113-693A-44R, CC; (7) Sample 113-693A-44R-1, 14–18 cm. **8, 9.** *Archaeomonas* sp. B, (8) Sample 113-693B-19X-4, 77–78 cm; (9) Sample 113-693B-19X-4, 103–104 cm. **10, 11, 15.** *Archaeomonas* sp. C, (10) Section 113-693B-19X, CC; (11) Sample 113-693A-44R-1, 39–40 cm; (15) Sample 113-693B-19X-4, 77–78 cm. **12–14.** *Archaeomonas*? sp. D, (12) Sample 113-693B-19X-4, 77–78 cm; (13) Section 113-693B-19X, CC; (14) Section 113-693A-44R, CC. Nomarski illumination in Figures 5, 8–10, 12–14.

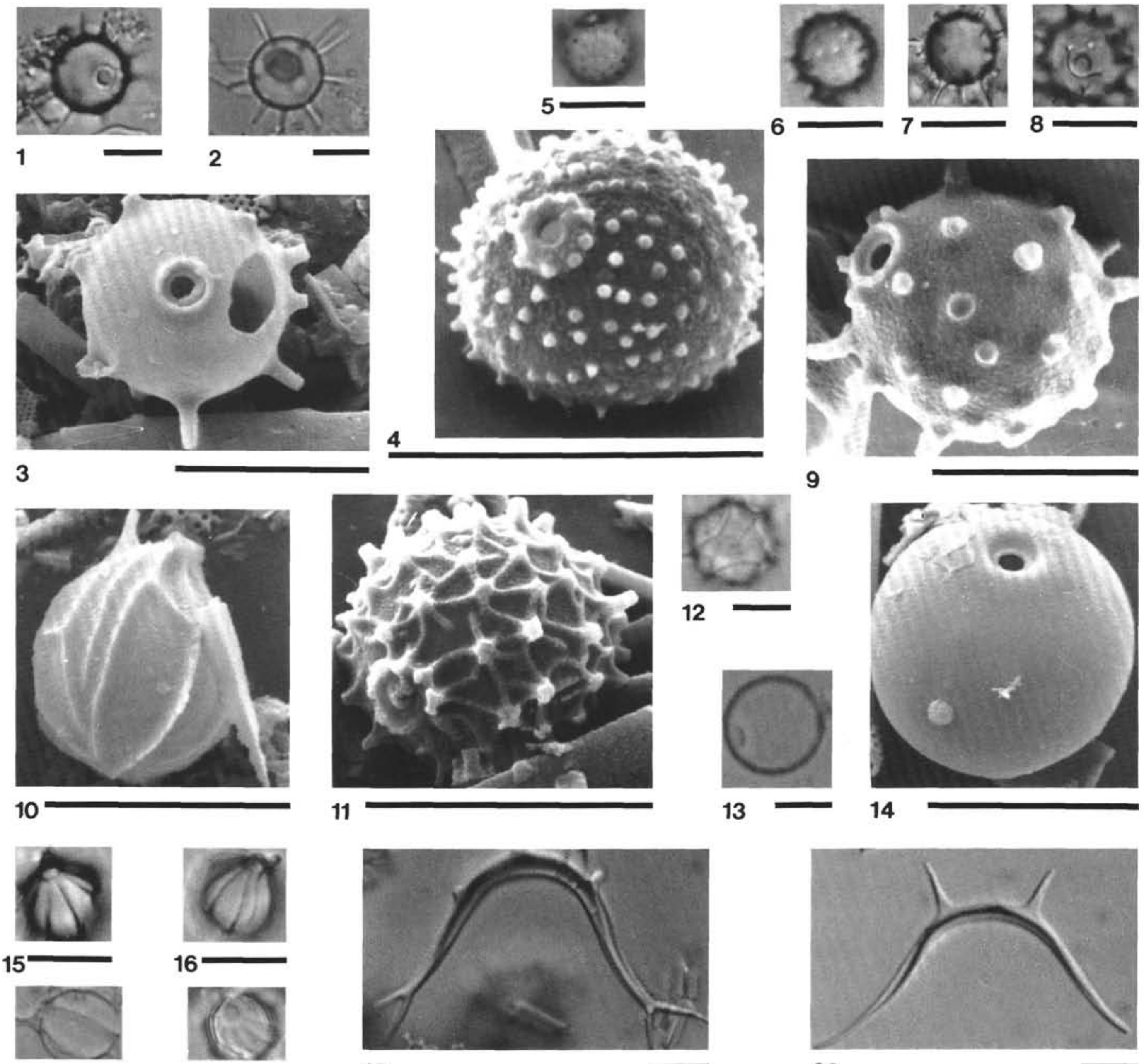

Plate 10. (Scale bars = 10 μm) **1-3.** *Archaeomonas* sp. E, (1) Sample 113-693B-19X-4, 77-78 cm; (2) Sample 113-693B-19X-4, 103-104 cm; (3) Section 113-693B-19X, CC. **4, 5.** *Archaeomonas* sp. F, Section 113-693B-19X, CC. **6-9.** *Archaeomonas* sp. G, (6, 9) Section 113-693B-19X, CC; (7, 8) Sample 113-693B-19X-4, 103-104 cm. **10, 15-18.** *Archaeomonas* sp. H, (10, 15) Sample 113-693B-19X-4, 77-78 cm; (16-18) Sample 113-693B-19X-4, 103-104 cm. **11, 12.** *Archaeomonas* sp. I, (11) Sample 113-693A-44R-1, 39-40 cm; (12) Sample 113-693A-44R-1, 60-63 cm. **13, 14.** *Archaeomonas* sp. J, (13) Sample 113-693A-44R-1, 14-18 cm; (14) Section 113-693A-44R, CC. **19, 20.** *Carduifolia toxon* n. sp., Sample 113-693B-19X-4, 77-78 cm, (19) Holotype, (20) Paratype. Nomarski illumination in Figures 1, 2, 5-8, 12, 15-20.

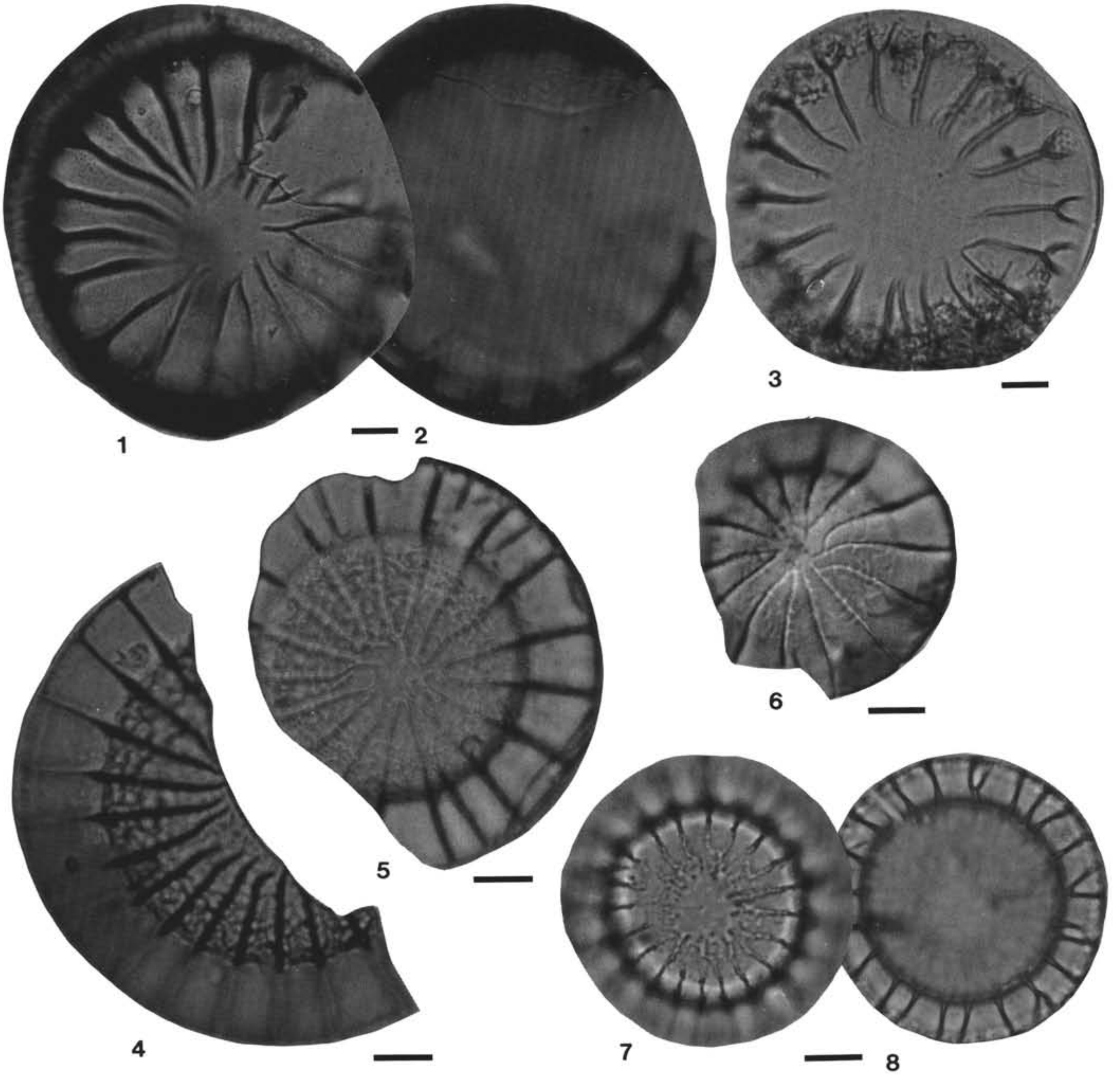

Plate 11. (Scale bars = 10 μm) **1–3.** *Calyptosporium lentiginosum* n. sp., Sample 113-693A-44R-1, 14–18 cm, (1, 2) different view of same specimen, (1) view of hypovalve face with wall of calyptra in upper left, (2) epivalve ornament in fragment at top of photograph. **4–6.** *Hyalotrochus* sp., (4, 5) Sample 113-693A-44R-1, 14–18 cm, (6) Sample 113-693B-19X-4, 77–78 cm. **7, 8.** *Hyalotrochus radiatus* n. sp., epivalve, Sample 113-693B-19X-4, 77–78 cm, same specimen at different focus.