Three species of *Coscinodiscus* Ehrenberg from North Pacific sediments examined in the light and scanning electron microscopes

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ABSTRACT: Specimens of *Coscinodiscus marginatus, C. oculus-iridis,* and *C. radiatus* from Plio-Pleistocene North Pacific sediments were examined in the light microscope and scanning electron microscope, then compared with descriptions and illustrations of various taxa in the literature. *C. marginatus* and *C. oculus-iridis* belong to the group of species characterized by a ring of labiate processes on the mantle, with two larger processes broadened and curled. *C. radiatus,* in contrast, possesses labiate processes upon the valve face as well as in a mantle ring, and the two larger processes have the same shape as others in the ring. *C. marginatus* is distinguished from *C. oculus-iridis* by the possession of a broad hyaline band projecting inward from the valve edge, which looks like a striate margin in light microscopy. The three taxa are otherwise very similar. Based on descriptions and figures in the literature, it is suggested that specimens of *C. marginatus* have occasionally been misidentified as *Endictya* species; *C. oculus-iridis* may be a synonym of *C. argus,* and *C. obscurus* and *C. perforatus* may be junior synonyms of *C. radiatus.* In modern North Pacific sediments, *C. marginatus* and *C. oculus-iridis* are characteristic of the subarctic zone, while *C. radiatus* is restricted to the subtropical and transitional zones. Core records spanning the last 2.6 m.y. (Late Pliocene to Recent) indicate that *C. marginatus* was abundant prior to about 2.4 Ma, and decreased markedly in relative abundance at that time; in the Pleistocene it has only been common during peak interglacial intervals. *C. radiatus* attained its greatest relative abundance in subtropical waters during the late Quaternary (since 0.7 Ma). *C. oculus-iridis* has always been a minor component of the sediment flora.

INTRODUCTION

Coscinodiscus marginatus Ehrenberg, *Coscinodiscus radiatus* Ehrenberg, and *Coscinodiscus oculus-iridis* Ehrenberg are consistent members of modern North Pacific sediment assemblages. During the Plio-Pleistocene interval the two former species experienced pronounced changes of relative abundance at well-defined intervals (Sancetta and Silvestri 1984, 1986). For this reason they may be useful for stratigraphic purposes, as well as for paleoceanographic interpretations. However, the three taxa are very similar, and are easily confused in light microscope (LM) examination, especially if specimens are poorly preserved or lying at an angle on the slide. Descriptions and illustrations in the literature are often incomplete, or emphasize characters which are not reliable for identification. It is therefore desirable to examine the three taxa for specific differences, so that proper and consistent identifications may be made. In the process, some light may be shed upon morphologic variations of the genus.

PREVIOUS WORK

Ehrenberg (1838, 1841, 1843, 1845, 1854) described and illustrated a number of species of *Coscinodiscus,* primarily from fossil material. His descriptions are usually very brief, and were often based upon fragments (Hasle and Sims 1986). Frequently, distinction between taxa was made using nonconservative features such as regularity of areole arrangement, or degree of valve curvature. Subsequent workers adopted different criteria to identify the various taxa, or to justify the naming of new species (e.g. Schmidt 1878; Rattray 1890).

The discovery of submicroscopic valve processes (Ross and Sims 1972; Hasle 1972) has led to major revisions in diatom taxonomy, including the reassignment of many species of "*Coscinodicus*" to other genera. Hasle (1983) has provided a useful summary of the current status of the genus. At present, features considered typical of *Coscinodiscus* include the presence of an external velum, numerous labiate processes, including a marginal ring, and the absence of strutted processes, spines, or pseudonoduli (Fryxell and Hasle 1973).

Of the three taxa of interest here, only one has been examined using modern concepts and methods. Hasle and Sims (1986) studied the type material of *C. radiatus,* and compared it to *C. argus* Ehrenberg, which has been proposed as the type of the genus (Fryxell 1978). The latter species is very similar to *C. oculus-iridis.* The intent of this paper is to compare the three taxa found in North Pacific sediments with those of Ehrenberg, and to determine their validity in the light of recent work.

MATERIAL AND METHODS

Most of the samples examined are from sediment cores from the North Pacific Ocean (table 1 and text-fig. 1). In addition, I had the opportunity to examine Grunow's material from the Richmond, Virginia, deposit, the type locality for *C. marginatus* Ehrenberg. I have not seen the type material of Ehrenberg; identifications are based on careful reading and examination of his published figures.

Although preservation of these robust forms is generally good, there is usually some destruction of fine-scale features, such as the velum and the labiate processes (also noted by Hasle and Sims 1986). Cingula are usually not articulated with the valves, and whole frustules are very rare. In cases where only one large species of *Coscinodiscus* was found in a sample, I have assumed that the associated cingula belong to that

micropaleontology, vol. 33, no. 3, pp. 230–241, pls. 1–3, 1987

TABLE 1
Samples used in this study.

Source	Sample	Species	Preparation	Microscopy
Richmond, Va. (Grunow)	935a	*C. marginatus*	Unknown (probably sieved)	LM
V21-172	151 cm	*C. marginatus*	Settled and sieved	LM, SEM
V20-119	430 cm	*C. marginatus*	Settled	LM
580	3–1, 115 cm	*C. radiatus*	Settled	LM, SEM
RC10-216	145 cm	*C. oculus-iridis*	Sieved	LM, SEM

species; in the case of *C. radiatus* it was not possible to identify the cingula with certainty. Fortunately, Hasle and Sims (1986) have made positive identifications using living material from Oslofjord.

The sediments in the North Pacific consist of diatomaceous silty clays, with diatoms ranging from 10–40% of the sediment by volume. Samples were cleaned using the standard procedure reported by Sancetta and Silvestri (1984), which includes disaggregation in distilled water and repeated settling with decanting of the clay-rich supernatant water. The remaining sample was then stirred briefly, and a drop of suspension added to a cover slip, or to the SEM stub. The water was allowed to evaporate under a heat lamp, so that particles settled to the slip or stub. For LM, the cover slip was heated on a hot plate, with a drop of Permount mounting medium, and mounted on a glass slide. For SEM, the stub was sputter-coated with 60/40 Au–Pd.

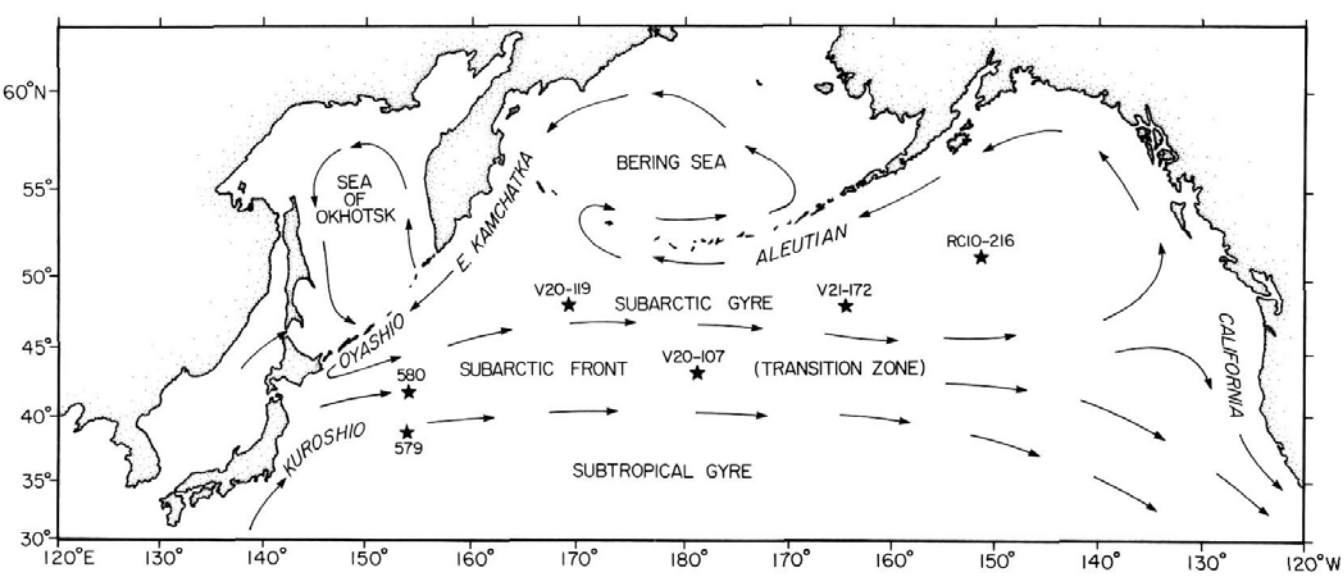
Following examination of these slides, large diatoms in certain samples (table 1) were concentrated by washing the suspension through a 63 μm sieve. The size fraction >63 μm was retained, and slides or stubs prepared following the procedure above. This resulted in cleaner samples, as well as a greater number of specimens for viewing.

The light microscope used was a Zeiss Standard 14, with Nomarski differential interference contrast. Most of the LM photographs are made with Nomarski, using objectives of either 40× or 100×. The scanning electron microscope was a Cambridge Stereoscan 250 Mk 2.

OBSERVATIONS

Coscinodiscus marginatus Ehrenberg

Ehrenberg described (1843) and illustrated (1854, pl. 18, fig. 44) this species from fossil material collected near Richmond, Virginia. His description (Ehrenberg 1843) reads "cellulis subaequalibus, radiatis, majoribus, margine radiatim lineolato." In the caption accompanying the illustration (Ehrenberg 1854) he indicated that he had identified it in Miocene material from Virginia and Maryland, as well as undated samples from Bermuda. The exact locality of the Virginia type material is unknown, but it is probable that it was from either the Calvert or Choptank Formation, of early to middle Miocene age. Numerous subsequent workers (Rattray 1890; Mann 1907; Hustedt 1930; Wornardt 1971) have described and illustrated the species, usually stressing the broad coarsely striate margin and the large polygonal areolae.



TEXT-FIGURE 1
Locations of cores mentioned in this study. Arrows show direction of surface water flow.

Although it was not possible to examine Ehrenberg's type material, I was able to study and photograph Grunow's slide 935a, which was prepared from "Diat.=Erde von Richmond Virginia" (sic). It is very probable that Grunow's sample was obtained from the same locality as that of Ehrenberg. Grunow's notebook lists *C. marginatus* as one of the components of the slide. Specimens on this slide are in all respects similar to those from North Pacific sediments, and a photograph from Grunow's material is included here.

LM observations: Cingula are commonly found in the material from V20-119, which does not contain other species of *Coscinodiscus.* It is presumed that the cingula are those of *C. marginatus.* They are broad, rectangular bands, 12–24 μm wide (average 16 μm), curved in a circular arc. They consist of a thin membrane with thickened rims and ends (pl. 1, fig. 1); the thickened edge is about 3–5 μm wide on the rims, and 5–8 μm wide at the ends. The ends have an asymmetric outline, like that of a canoe viewed from the side. The terminal edge is perpendicular to the dorsal rim and curving toward the ventral. No structure can be seen on the membrane, but there is a ragged appearance where the membrane merges with the thickened rim.

Valves are circular in valve view, with flat or slightly convex surfaces and a steeply-sloping to perpendicular mantle (pl. 1, figs. 2, 3). In very large specimens, the valve face may be slightly depressed in the center. Valves range from 35 to 145 μm in diameter (average of 30 specimens, 86 μm) and are rather uniformly 10 μm high, so that smaller valves have a greater curvature. Polygonal areolae cover the valve surface completely, and are arranged in irregular radial rows (pl. 1, fig. 2). The areolae are loculate, with an internal circular foramen (pl. 1, fig. 2). The external velum is usually dissolved, but regular fine notches around each areola (Hustedt's "ring of faint poroids"?) indicate the original existence of a velum (pl. 1, fig. 4). Areolae are 1½ to 2 in 10 μm in the center, 2½ to 3 in 10 μm at the valve/mantle boundary. Areolae near the valve/mantle boundary are distorted, being elongate toward the mantle (pl. 1, fig. 2). Areolae on the mantle are horizontally directed (in the valve plane). Therefore, in valve view, the walls of mantle areolae appear as coarse radial striae on a marginal band (pl. 1, figs. 3, 5). The "margin" is 4–6 μm wide, corresponding to the thickness of the valve.

Processes are barely visible, and their structure cannot be determined, but in oblique view a ring of small pores can be seen among the mantle areolae. These pores are the outer openings of the processes. A very slight indentation of the outline indicates the position of a larger process (pl. 1, fig. 2).

SEM observations: The edges of the cingulum are robust and hyaline, while the membrane is finely punctate (pl. 1, fig. 6). Puncta are arranged in quincunx rows with the primary alignment in the pervalvar direction (perpendicular to the edges), 35–40 in 10 μm. Viewed internally, the arrangement near the ends becomes less clearly quincunx, and approaches rectilinear (pl. 1, fig. 7).

The valve face may be slightly convex (pl. 1, fig. 8) or concave (pl. 1, fig. 9), with mantle steeply-sloping to vertical. On the outer surface of the valve the areolae are circular with thick walls slightly raised above the opening, producing an effect of low hexagonal ridges and nodes (pl. 1, figs. 8, 9). The remnants of the velum can be seen as fine threads arranged radial to each areola (pl. 1, fig. 8). Mantle areolae are ver-

PLATE 1

Coscinodiscus marginatus Ehrenberg

1 End of cingulum, showing membrane and thickened hyaline rims. V20-119.

2, 3 External view, two focal planes.
2, focus on foramina and elongation of areolae on mantle. Arrow shows indentation corresponding to a larger labiate process; 3, focus on supposed "striate margin" produced by mantle chamber walls. V21-172.

4 Valve face of large specimen, showing remnants of velum around each areole. V20-119.

5 Specimen showing remnants of velum and projection of mantle chamber walls on marginal band. 935a.

6 Portion of cingulum, showing hyaline rim and quincunx puncta. V21-172.

7 End of cingulum, two magnifications, showing transition from quincunx to rectilinear arrangement of puncta. V21-172.

8 Whole valve and detail of valve face, showing remnants of velum. V21-172.

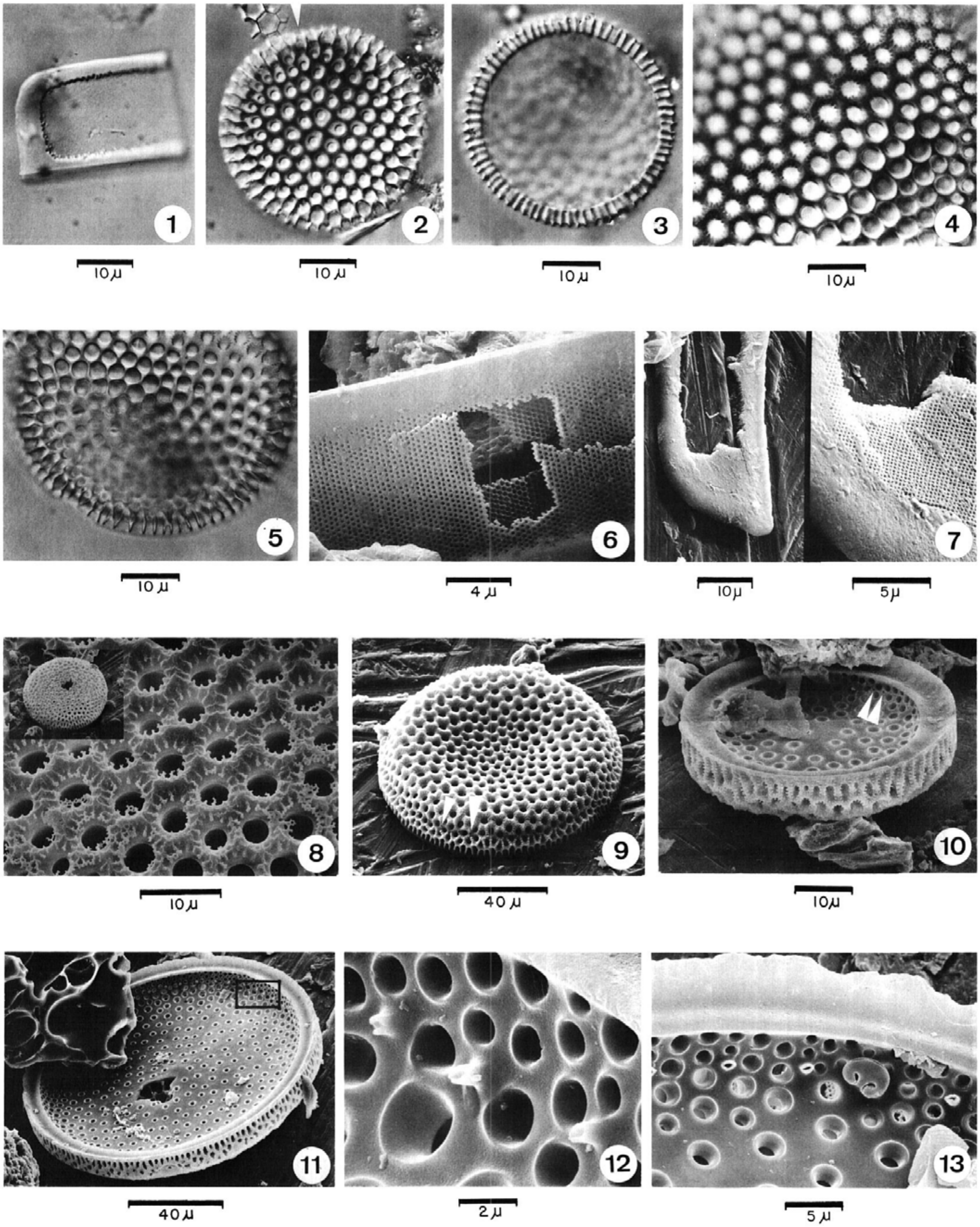
9 Whole valve of large specimen, external view. Note central depression, slight mantle constriction, interareolar nodes, and elongation of mantle areolae. Arrows indicate openings of labiate processes. V21-172.

10 Oblique internal view showing broad hyaline marginal band and elongate mantle areolae. Arrows indicate bases of labiate processes. V21-172.

11 Internal view showing rimmed foramina and external depression corresponding to a larger labiate process. Box shows site of figure 12. V21-172.

12 Detail of figure 11, showing broken bases of labiate processes. V21-172.

13 Inner mantle region showing ring of labiate processes and larger curled process. V21-172.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tically (pervalvar) elongated, about twice as high as they are wide (pl. 1, figs. 9, 10). Internal foramina are circular with slightly thickened rims (pl. 1, fig. 11), arranged in very irregular radial rows.

From an internal view, the "margin" is revealed to be a broad featureless band, projecting 3–6 μm into the cell (pl. 1, figs. 10, 11). The supposed "coarse radial striae" seen in LM are the walls of the mantle areolae projected through the band by transmitted light. The band is slightly curved and is concave from an internal view.

One ring of labiate processes occurs on the mantle, 2–3 in 10 μm (pl. 1, fig. 12). The ends of the processes are often broken. The two larger labiate processes are broad (3 μm), flat, and curled in an exaggerated kidney or mushroom shape (pl. 1, fig. 13). On the outer surface the openings of these larger processes occur in a slight depression (pl. 1, fig. 11).

Comparison with other species: Frequently, *C. marginatus* and its synonyms have been confused in the literature with members of the genus *Endictya* Ehrenberg. Rattray (1890), Mann (1907, 1925), Hustedt (1930), Lohman (1941) and Jousé (1961) have all discussed the problem, drawing different conclusions as to synonymy. It is not always clear whether these authors had actually seen reference material, or were relying upon figures and descriptions in the literature. Most of them refer to the steep areolate mantle as the chief generic character of *Endictya*; *Coscinodiscus* species were believed to be gently convex, without a sharp mantle. Both Hustedt (1930) and Ross and Sims (1974) note the occurrence of an internal velum in *Endictya*. In addition, the illustrations of these authors (Hustedt 1930, fig. 136d, e; Ross and Sims 1974, pl. 1, figs. 2, 5) show a distinctive pattern of concentric rings of areolae on the wide mantle, quite different from that of *C. marginatus*. Sims (personal communication 1986) has noted that *Endictya* possesses a distinct ridge at the valve/mantle boundary, with the labiate processes located along this ridge.

The specimens shown here demonstrate Jousé's point (1961) that the "coarsely striate margin" of *C. marginatus* is actually a steep areolate mantle seen from the internal view in LM, so that the areole walls are projected upon the marginal band. In external view, the steep mantle is more easily recognized, leading some authors to identify their specimens of *C. marginatus* as species of *Endictya*. Probable erroneous identifications include Hanna and Grant's *Endictya robusta* (1926, pl. 16, fig. 2), Lohman's *Endictya oceanica* (1941, pl. 12, fig. 3—a very poorly preserved specimen) and his *Endictya robusta* (1948, pl. 6, fig. 4).

Another synonym is *Coscinodiscus marginatus* forma *fossilis* Jousé. This form is not validly named, as Jousé (1961) did not provide a description or diagnosis clearly related to this taxonomic combination, nor did she designate a holotype. It is not certain from her remarks that she intended to erect a formal subdivision of the species. The distinction of the form rests simply upon the better preservation of the velum. While the velum of ancient specimens may have been more heavily silicified than that of more recent specimens, this is not sufficient to define a separate taxon.

Wornardt's (1971) specimen of *C. marginatus* (his pl. 6, figs. 1–12) possesses a distinct constriction in the mantle zone. Some hints of this morphology can be seen in the Pleistocene North Pacific material (pl. 1, fig. 9), but it is not as well developed. Wornardt may have chosen an abnormal specimen, or his Miocene material may represent an earlier evolutionary stage.

Distribution in North Pacific sediments: In modern day (surface) sediments, *C. marginatus* is rare, averaging less than 5% of the diatom population. It is occasionally more common (15–25%) in the Gulf of Alaska and at about 45°N, between 180° and 150°W. It is very rare in the Sea of Okhotsk (<1%) and absent from samples of the Bering and Okhotsk continental shelves. It does not occur south of 40°N. This may reflect a restriction due to temperature or salinity tolerances; waters of the Sea of Okhotsk and the continental shelves are colder and of lower salinity than those of the open subarctic Pacific, while to the south of 40°N waters become markedly warmer and of higher salinity. Takahashi (1986) reports it as being most common in late fall (October–December) samples collected in sediment traps from the central Gulf of Alaska.

C. marginatus was most common (up to 70% of the flora) in the Late Pliocene, prior to 2.4 Ma (Sancetta and Silvestri 1986). It decreased rapidly to values <20% at 2.4 Ma, coinciding with a major glacial interval on land (Shackleton et al. 1984). During the remainder of the Pliocene and early Pleistocene it was a minor component of the flora (<10%). In the late Pleistocene (since 0.7 Ma) it has been very rare during glacial intervals (<5%), and reached maximum abundance (up to 50%) during interglacials (Sancetta and Silvestri 1984, 1986).

Coscinodiscus radiatus Ehrenberg

Ehrenberg (1841) described this species from Mediterranean fossils and plankton samples from the North Sea, as "testulae magnae cellulis mediocriter amplis, in lineas e centro radiantes dispositis, ad marginem minoribus." He distinguished it from *C. argus* primarily by the smaller size of the areolae. Grunow (1884), Rattray (1890), and Hustedt (1930) have also described or illustrated the species, in some cases defining varieties. The radiating pattern of areolae and absence of interstitial pores were considered to be diagnostic features. Hasle and Sims (1986) have recently examined type material and provided an emended description.

LM observations: Valves are circular and flat, sloping only in the mantle region (pl. 2, figs. 1, 3, 4). Valves range in diameter from 13 to 100 μm (average of 30 specimens, 43 μm). This average is probably skewed toward low values, because large specimens are usually broken. Areolae are loculate, with internal circular foramina (pl. 2, figs. 2, 3). No evidence of the velum can be seen. Outer openings of areolae are irregular hexagons, forming a complete mesh and arranged in more or less regular radial rows (pl. 2, figs. 1–4). The radial arrangement is most obvious in large specimens (pl. 2, figs. 1, 2); the smallest specimens have no regular pattern. On smaller specimens, areolae are equisized across the valve surface and smaller on the mantle. Specimens with more obvious radial arrangement may have areolae slightly increasing in size outward, then decreasing and much smaller in the mantle region (pl. 2, figs. 1, 2). In these large regular specimens there may be a small hyaline central area, which is not seen in smaller forms (pl. 2, fig. 2). Size of areolae varies with size of the valve: on smaller specimens areolae are 4–5 in 10 μm across the valve surface and 6–8 in 10 μm on the mantle; on larger specimens areolae are 3½ to 4 in 10 μm across the valve and 6–8 in 10 μm on the mantle. On the mantle, areolae are slightly elongated toward the margin. The chamber walls of the mantle areolae appear as radial striations on the margin.

Processes are scattered over the valve surface (pl. 2, figs. 1, 2, 4), in no apparent order. Smaller specimens usually have fewer processes, often only one or two. On larger, more regular forms the number of processes is greater (up to 12 or more) and the processes are located at the ends of shorter radial rows.

SEM observations: The valve surface is quite flat, with narrow, steeply sloping mantle (pl. 2, figs. 5, 6). Areolae are circular on the outer valve face (pl. 2, figs. 5, 6), with fine radial ridges, which are probably the remnants of the velum. Areolae are elongated in tear-drop shape at the boundary of the valve face and mantle (pl. 2, figs. 5, 6). From an internal view, areolae are round and separated, with a thickened rim around each foramen (pl. 2, fig. 7). The margin is 1 to 1½ μm wide, flat and featureless. It does not project into the valve interior (pl. 2, fig. 7).

Small labiate processes are scattered over the valve surface (pl. 2, figs. 7, 8) at the ends of some (but by no means all) of the shorter rows of areolae. The outer openings of the processes can be seen among the areolae in external view (pl. 2, figs. 5, 6). There is also a ring of labiate processes around the mantle, about 3 in 10 μm (pl. 2, fig. 9); these are often broken. The two larger asymmetric labiate processes have the same form as others on the mantle, being only slightly larger (pl. 2, fig. 10), in contrast to those of *C. marginatus* and *C. oculus-iridis,* which have a different form. The outer surface of the valve is slightly depressed at the location of the larger processes (pl. 2, fig. 10).

Comparison with the type material: The type-material specimens examined by Hasle and Sims (1986) agree in every respect with the features described here. The central hyaline area is larger in the type material than is observed in the North Pacific, and the plankton samples from Oslofjord have the ends of the larger labiate processes turned slightly away from the valve face, while in the North Pacific samples the processes project straight inward. There is otherwise no difference between the samples. Hasle and Sims (1986) were able to obtain good photographs of the velum and cingula, and the reader is referred to their paper for a description.

The most important feature to note is the presence of the scattered labiate processes on the valve face. Ehrenberg (1841) did not mention them in his description, but his figure can be interpreted as showing the external pores of the processes. Later workers apparently assumed that specimens with such pores represented a different species.

Comparison with other species: C. radiatus is similar to a number of other species, including *C. apiculatus* Ehrenberg, *C. argus, C. obscurus* Schmidt, *C. oculus-iridis,* and *C. perforatus* Ehrenberg. Hasle and Sims (1986) discuss the differences between *C. radiatus* and *C. argus,* the most important being the different structure of the two larger marginal labiate processes and absence of scattered processes on the valve face of *C. argus.* The same distinctions are true for *C. oculus-iridis* as compared to *C. radiatus.*

C. apiculatus has not been examined using modern techniques and concepts. It was described from the Richmond deposit, and is characterized as having separated, circular areolae, a central area, two larger marginal processes, and, according to Hustedt (1930), no scattered pores on the valve face ("Interstitialmaschen"). If this latter statement is true, that feature alone would distinguish *C. apiculatus* from *C. radiatus.* If, as seems probable, the pores were present, but either not seen or not illustrated by Ehrenberg, then the two taxa are probably synonymous, with *C. apiculatus* being the junior synonym. The apparent separation of areolae may be explained as due to an internal view of the specimen (as noted by Hustedt 1930). As Hasle and Sims (1986) have shown, *C. radiatus* does possess a central area, supposed to be characteristic of *C. apiculatus.* In sum, there are no features of the latter species which can separate it from *C. radiatus.*

C. obscurus was described by Schmidt (1878, pl. 61, fig. 16) from the Santa Monica deposit (an outcrop of the Miocene Monterey Formation) and from the Miocene Moron deposit of Spain. It was distinguished by him from *C. radiatus* solely by the possession of small pores at the ends of shorter rows of areolae. As shown by Hasle and Sims (1986), these pores are the outer openings of the labiate processes, and do occur in *C. radiatus.* Therefore, *C. obscurus* is a junior synonym of *C. radiatus.*

Finally, *C. perforatus* was described from the Richmond deposit, and characterized as having radial circular areolae with scattered pores between them (Ehrenberg 1845). Fryxell and Hasle (1974) examined a specimen from plankton of the Persian Gulf identified by them as *C. perforatus,* which possessed labiate processes identical to those of *C. radiatus.* It seems probable that *C. perforatus* is a form of *C. radiatus* in which the areolae are more separated.

Distribution in North Pacific sediments: In the North Pacific *C. radiatus* is only consistently present in surface sediment underlying the subtropical gyre, south of 40°N, where it ranges from 5–10% of the diatom assemblage. It is very rare (1–5%) in sediments underlying the transition zone, and occurs only as individuals in sediments of the subarctic zone; it is absent from the Sea of Okhotsk and Bering Sea. This distribution suggests a preference for waters warmer than those of the subarctic Pacific.

The species is not found in Plio-Pleistocene cores from the subarctic zone. In the western transition zone (Sites 579 and 580) it is present in low numbers throughout the late Pliocene and early Pleistocene (about 10% of the flora), and increases to 20% in the late Pleistocene (after 0.7 Ma).

Coscinodiscus oculus-iridis Ehrenberg

This species was named and illustrated by Ehrenberg (1841, 1854, pl. 19, fig. 2), from a Miocene siliceous marl exposed on the Greek island of Aegina. He also noted its occurrence in modern North Sea plankton (Ehrenberg 1841) and in the Richmond deposit (1854, pl. 18, fig. 42). His description reads: "testulae magnae cellulis majusculis, radiantibus, in externo margine et prope centrum minoribus, mediis nonnullis maximis, stellam centralem efficientibus." Grunow (1884), Rattray (1890), and Hustedt (1930) also provided diagnoses. The most distinctive features are considered to be the central rosette, the depressed central region, and the change in size of the areolae, which increase outward and then decrease again in the outer third of the valve.

LM observations: Cingula are broad rectangular bands, 15–25 μm wide (average 20 μm), and consist of a thin membrane with thickened rims and ends (pl. 2, fig. 11). The thickened rim is usually 4–5 μm wide, while the end may be up to 8 μm wide. The ends are almost rectangular, but have a slight curvature on the ventral side, similar to that of *C. marginatus.* The membrane has a ragged appearance where it joins the rims.

Valves are circular in valve view, with the central half of the valve face depressed (pl. 2, figs. 12, 13). This central region is frequently less silicified than the peripheral part of the valve. The surface slopes up from the depression, rising to about 20 μm above the center, and then curves rapidly downward to form the mantle. Valve diameter ranges from 105–180 μm (average of 30 specimens, 140 μm). Areolae may be enlarged and slightly elongated into a rosette in the center (pl. 2, fig. 12), but this is relatively rare (pl. 2, fig. 14). Areolae are loculate with internal foramina, and consist of more or less regular hexagons, forming radiating rows with secondary spiral rows (pl. 2, figs. 12, 13). The rosette, if present, is about 10 μm wide; next to it the areolae are 2 to 2½ in 10 μm, increasing outward in size until on the crest they are 1 to 1½ in 10 μm. On the mantle they decrease abruptly to 3 in 10 μm, and are arranged in quincunx rows, about 3–4 deep (pl. 3, fig. 1).

Labiate processes cannot be discerned, but in oblique view a ring of small pores can be seen on the mantle, just above the quincunx marginal areolae, about 1 in 10 μm (pl. 3, fig. 2).

SEM observations: At low magnification the cingulum appears to be a featureless hyaline band, with thickened rims and ends (pl. 3, fig. 3). At high magnification, fine pores can be seen, 50 in 10 μm, arranged in quincunx rows, the primary direction being perpendicular to the edges of the cingulum (pl. 3, fig. 4). On the outer surface the pores are simple openings; on the inner surface they have thickened rims (pl. 3, fig. 5). The pore field stops at the thickened edge of the cingulum, which is hyaline.

In external view the valve is depressed in the center, and rises to a concentric crest at the boundary of the valve face and mantle, with the mantle abruptly vertical (pl. 3, figs. 6–8). In internal view the central depression is much less evident (pl. 3, fig. 10), suggesting that the walls of the areolae must be higher in the crest region than in the center.

Areolae are circular in external view, surrounded by thickened ridges with nodes at the junctions of three areolae (pl. 3, figs. 8, 9). Faint radial ridges can be seen around each

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PLATE 2

Figures 1–10: *Coscinodiscus radiatus* Ehrenberg
Figures 11–14: *C. oculus-iridis* Ehrenberg

1 Large specimen showing obvious radial arrangement of areolae. Arrows indicate openings of labiate processes. DSDP 580.

2 Central area of large specimen showing small hyaline area and rosette. Arrows indicate openings of labiate processes. DSDP 580.

3, 4 Small specimen with irregular arrangement of areolae, two focal planes.
3, focus on foramina; 4, focus on outer surface with openings of labiate processes. DSDP 580.

5 External view showing openings of labiate processes and elongate mantle areolae with remnants of velum. DSDP 580.

6 External view of small specimen showing openings of labiate processes on valve face and mantle. DSDP 580.

7 Internal view showing rimmed foramina and labiate processes on valve face and mantle. Box shows site of figure 8. DSDP 580.

8 Detail of figure 7 showing one labiate process on valve face. DSDP 580.

9 Internal view of mantle region, showing intact labiate processes. DSDP 580.

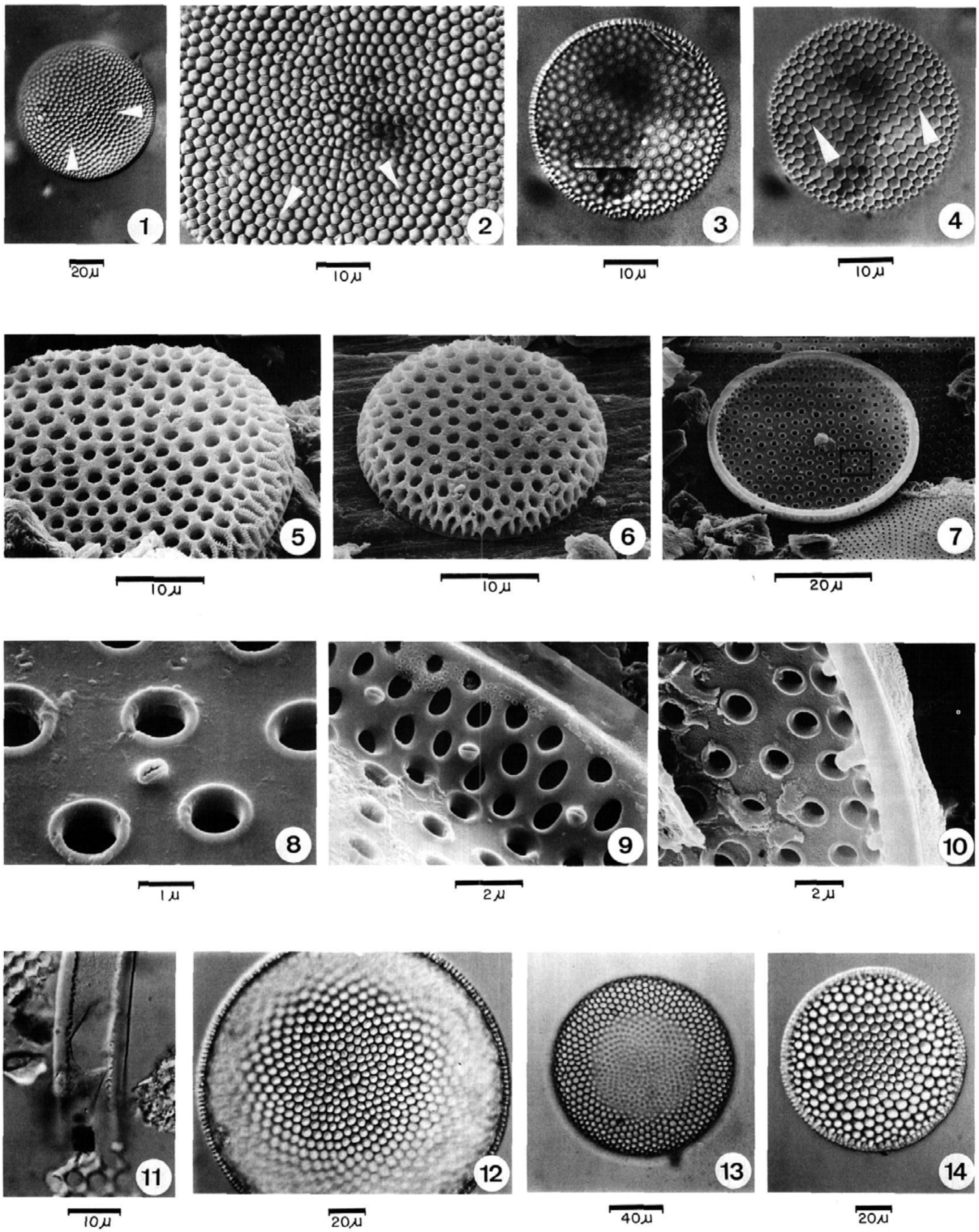
10 View along margin showing one larger labiate process with external depression. Velum preserved on exterior mantle. DSDP 580.

11 Portion of cingulum, showing broken membrane and thickened rims. RC10-216.

12 Central area showing rosette and outward change in size of areolae. RC10-216.

13 Specimen showing central depression with radial and spiral arrangement of areolae. RC10-216.

14 Smaller specimen without central rosette, but with outward change in size of areolae. RC10-216.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areole, especially in the region of the crest. The radial and secondary spiral rows of areolae are clearly seen (pl. 3, figs. 6–8). About halfway down the mantle the pattern of the areolae changes abruptly, forming a marginal zone in which the areolae are smaller, round, and arranged in quincunx (pl. 3, figs. 6–9). Small pores occur at the upper edge of this marginal zone, 1 in 10 μm (pl. 3, fig. 9), representing the external openings of the labiate processes.

The inner membrane, when complete, has rimmed circular openings, the foramina of the areolae (pl. 3, fig. 10). The membrane is usually broken off, revealing the inner walls of the areolae (pl. 3, fig. 11) of which usually only the corners are left. The margin is a smooth hyaline rim, about 5 μm wide; when it is thin the walls of the mantle areolae can be seen through it (pl. 3, figs. 10, 11).

The ring of marginal labiate processes is always broken, so that only the bases of the processes are left. The two larger processes are about 2 μm wide, curled and broadly flattened in a mushroom shape (pl. 3, fig. 12).

Comparison with other species: Most of the features described above have also been seen by Hasle and Sims (1986) in *C. argus* type material, notably the quincunx arrangement of smaller areolae on the mantle, and the shape of the larger labiate processes. The apparent differences (depressed center with rosette and outward change in areole size of *C. oculus-iridis*) may be due to a simple difference in size. As noted above, the rosette is by no means a consistent feature of *C. oculus-iridis*. Structural constraints may dictate that in a very large form the central region must be depressed, the siliceous membrane being too weak to support its own weight. The trend in areole size would therefore represent the projection of equisized circles upon a curved surface. It is probable that *C. oculus-iridis* is simply a large form of *C. argus*, and not a separate species. This suspicion is strengthened by the fact that the type locality for *C. argus* is the Oran deposit in Algeria, one of the many Mediterrean exposures of Miocene material.

It is interesting to note that if the curvature of *C. oculus-iridis* were greatly exaggerated so that the central depression and margin were markedly below the crest, with a very high vertical mantle and very weakened central area, it would bear a striking resemblance to *Craspedodiscus* Ehrenberg, a point noted also by Ross and Sims (1974). Perhaps there is an evolutionary relationship between the two.

It is easy to confuse *C. oculus-iridis* in LM with the other North Pacific taxa discussed above, especially for smaller forms where the central depression is slight and the change in areole size not very marked. In such cases it may be distinguished from *C. radiatus* by the lack of scattered labiate processes on the valve face, and from *C. marginatus* by the lack of the marginal band and the presence of the quincunx areolae along the mantle.

Distribution in North Pacific sediments: C. oculus-iridis is very rare in both modern and Plio-Pleistocene North Pacific sediments, never more than 1% of the diatom assemblage. Specimens are almost always broken. It occurs throughout the subarctic zone and into the deep basin of the Bering Sea, but is absent from the Sea of Okhotsk, the continental shelf, and south of 40°N.

DISCUSSION

The three species of *Coscinodiscus* described here are clearly different from each other, though their synonymy with other species is not established. There are two important characters separating *C. radiatus* on the one hand from *C. marginatus* and *C. oculus-iridis* on the other. These concern the location and shape of the labiate processes. *C. radiatus* has labiate processes scattered over the valve face, and the two large marginal processes are only slightly larger and not differently

PLATE 3

Coscinodiscus oculus-iridis Ehrenberg

1 Fragment of mantle showing marginal zone of quincunx areolae. RC10-216.

2 Fragment of mantle, showing outer openings of labiate processes. RC10-216.

3 Intact cingulum without discernible structure. Boxes show sites of figures 4 and 5. RC10-216.

4 Detail of figure 3 showing quincunx puncta on outer surface. RC10-216.

5 Detail of figure 3 showing rimmed quincunx puncta on inner surface. RC10-216.

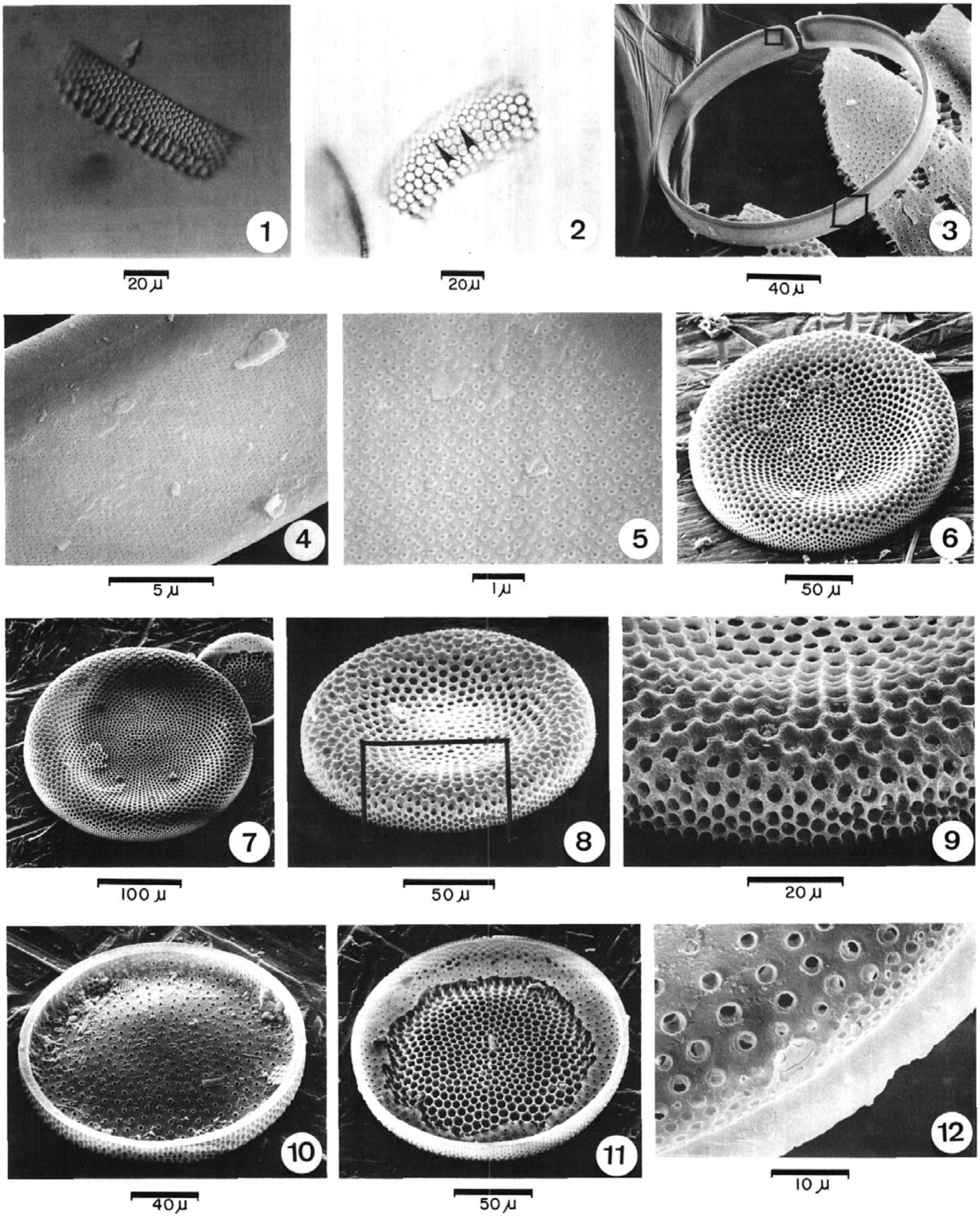
6–8 External views of three specimens showing depressed center, radial and spiral arrangement of areolae, and marginal zone of quincunx areolae. Box on figure 8 shows site of figure 9. RC10-216.

9 Detail of figure 8 showing interareolar nodes, openings of labiate processes, and marginal zone. RC10-216.

10 Internal view of intact specimen showing rimmed foramina and bases of marginal labiate processes. RC10-216.

11 Internal view of broken specimen showing chamber walls preserved only at nodes. RC10-216.

12 Internal view of mantle showing bases of labiate processes and one larger curled process. RC10-216.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shaped than the others in the marginal ring (features shared with the possibly conspecific *C. perforatus*). The other two species have labiate processes only in the marginal ring, and the two larger processes have a distinctly different shape, features they share with *Coscinodiscus granii* Gough and *Coscinodiscus concinnus* Smith (Brooks 1975). Finally, *Coscinodiscus asteromphalus* Ehrenberg and *Coscinodiscus wailesii* Gran and Angst (which may be a junior synonym of *Coscinodiscus gigas* Ehrenberg) possess scattered labiate processes on the valve face, while the two larger marginal labiate processes are broadened and curled (Brooks 1975; Schmid and Volcani 1983). These latter species therefore occupy an intermediate position with respect to variations of the processes. When the type material has been re-examined to establish synonymy, and other species of the genus have been studied in SEM, it may become desirable to subdivide the genus to reflect these differences.

EMENDED DESCRIPTIONS

Coscinodiscus marginatus Ehrenberg **emend.**
Plate 1, figures 1–13

Frustule coin- or drum-shaped. Cingulum broad rectangular with rounded ventral ends, 12–24 μm wide. Cingulum composed of thick hyaline rims 3–4 μm wide and a thinner membrane, with quincunx puncta 35–40 in 10 μm. Valve circular, flat or slightly depressed in center, falling more or less steeply at the mantle which may have a slight constriction about halfway down. Valves 35–145 μm in diameter. Areolae loculate, circular on valve face and elongated on mantle, surrounded on outer surface by ridges and nodes which produce a polygonal effect in LM. Areolae irregularly radially arranged, 1½ to 2 in 10 μm at the center, 2½ to 3 in 10 μm at the margin. Mantle areolae elongated in pervalvar direction, their walls resting on a broad (3–6 μm) hyaline band. One ring of marginal labiate processes, 2–3 in 10 μm, with two larger labiate processes among them, broadened and curled in a mushroom shape. Valve surface slightly depressed at locations of larger labiate processes.

Coscinodiscus oculus-iridis Ehrenberg **emend.**
Plate 2, figures 11–14; plate 3, figures 1–12

Frustule coin-shaped with depressed central regions. Cingulum broad rectangular, 15–25 μm wide. Cingulum composed of thicker hyaline rims 3–5 μm wide and thinner membrane with quincunx puncta, 50 in 10 μm, the inner openings of the puncta with thickened rims. Valves circular with depressed central region and elevated crest dropping steeply to mantle. Valves 105–180 μm in diameter. Areolae loculate, circular, surrounded on outer surface by thickened ridges and nodes, producing hexagonal appearance in LM. Areolae radially arranged, with secondary spirals. Rosette, if present, about 10 μm wide, consisting of 4–7 elongated central areolae. Areolae increase outward in size, 2 to 2½ in 10 μm in center, 1 to 1½ in 10 μm on crest, then decreasing abruptly to 3 in 10 μm on mantle, where they are arranged in quincunx rows. One ring of marginal labiate processes, 2 in 10 μm, with two larger labiate processes among them, broadened and curled in a mushroom shape.

Coscinodiscus radiatus Ehrenberg **emend.**
Plate 2, figures 1–10

Coscinodiscus apiculatus EHRENBERG 1845, p. 77.—EHRENBERG 1854, pl. 18, fig. 43.

Coscinodiscus obscurus SCHMIDT 1878, pl. 61, fig. 16.
Coscinodiscus perforatus EHRENBERG 1845, p. 78.—EHRENBERG 1854, pl. 18, fig. 46.

Frustule coin-shaped. Valve circular, flat, with short vertical mantle. Valves 13–100 μm in diameter. Areolae loculate, circular to polygonal on valve face and elongated on the mantle. Areolae more or less regularly arranged in radial rows, 3½ to 5 in 10 μm on the valve face, 6–8 in 10 μm on the mantle. Labiate processes scattered over valve face at the ends of some shorter radial rows, their number greater in larger and more regularly radial specimens. One ring of marginal labiate processes, 3 in 10 μm, with two slightly larger labiate processes among them, not of different shape. Outer valve surface slightly depressed at location of the larger processes.

ACKNOWLEDGMENTS

I would like to express my deep appreciation to Drs. Riedel and Passauer, of the Botanical Section at the Natural History Museum of Vienna, for allowing me to examine Grunow's slides. Dee Breger was responsible for SEM operation and preparation of the plates, and Paul Bennett provided photographic assistance. I am indebted to Robert Ross for his advice on taxonomic and morphologic interpretations, and to Patricia Sims and Grethe Hasle, who shared their unpublished results with me. The manuscript was reviewed by Lloyd Burckle, Robert Ross, Patricia Sims, John Barron, and Grethe Hasle. Cores from the Lamont-Doherty Repository are curated under NSF Grants OCE 80-22109 and OCE 81-22083. This research was supported by NSF Grant OCE 81-09933. This is Lamont-Doherty Contribution Number 4191.

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Manuscript received July 24, 1986
Revised manuscript accepted November 21, 1986