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Fossil marine diatom resting spore morpho-genus *Xanthiopyxis* Ehrenberg in the North Pacific and Norwegian Sea

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**Abstract.** Fossil marine diatom resting spore species in the morpho-genus *Xanthiopyxis* Ehrenberg are described using samples from DSDP Site 338 in the Norwegian Sea, Sites 436 and 438 in the northwest Pacific and from the onland section at Newport Beach, California. *Xanthiopyxis* is characterized by numerous knobs, spines and bristles covering the entire valve face. In this paper eleven species, of which seven are new species, are described and their stratigraphic ranges are presented: *X. polaris* Gran, *X. norwegica* Suto, sp. nov., *X. brevispinosa* Suto, sp. nov., *X. teneropunctata* Suto, sp. nov., *X. lanceolatus* Suto, sp. nov., *X. circulatus* Suto, sp. nov., *X. reticulata* Suto, sp. nov., *X. obesa* Suto, sp. nov., *X. hirsuta* Hanna and Grant, *X. oblonga* Ehrenberg and *X. globosa* Ehrenberg. In addition, resting spores which lack sufficient characteristics to identify easily are assigned to three informal species: *Xanthiopyxis* type A (knobbly type), *X.* type B (short spiny type) and *X.* type C (long spiny type).

**Key words:** *Xanthiopyxis*, fossil resting spore, diatom, ODP, taxonomy

**Introduction**

The marine diatom genus *Chaetoceros* Ehrenberg is one of the most important taxa in the present oceans, especially in upwelling regions (e.g., Hasle and Syvertsen, 1996). When nutrient supplies are depleted, many species form thick-walled resting spores, which sink to the sea floor to await the return of favorable conditions for vegetative growth. Resting spores are therefore preserved in significant quantities in fossil marine diatom assemblages, although their respective vegetative frustules are mostly dissolved. Since *Chaetoceros* is one of the most abundant primary producers in the marine ecosystem in upwelling regions, fossil resting spores may provide useful information for reconstructing paleoproductivity and paleoenvironmental changes in these regions. Nevertheless, few detailed systematic and stratigraphic studies have been carried out on fossil resting spores. As a result, most fossil resting spore species have been left undescribed, or neglected in previous stratigraphic and paleoceanographic studies presumably because of difficulties in identification.

*Xanthiopyxis* is a resting spore morpho-genus. Since *Xanthiopyxis oblonga* was erected by Ehrenberg (1844 (1845)), the genus has come to be regarded as a taxon for fossil resting spores of the genus *Chaetoceros* (Lohman, 1938), and now many *Xanthiopyxis* species have been described (e.g., *X. globosa* Ehrenberg, *X. cingulata* Ehrenberg, *X. umbonatus* Greville, *X. polaris* Gran). The various species of *Xanthiopyxis* are frequently found in sediments, but no systematic study has been completed on the genus, and therefore its taxonomy remains confused.

Suto (2003a, b, 2004a, b) has already described the morphology and stratigraphic ranges of the resting spore morpho-genera *Dicladia* Ehrenberg, *Monocladia* Suto, *Syndendrium* Ehrenberg, *Periptera* Ehrenberg, *Liradiscus* Greville and *Gemellodiscus* Suto. This study examined Paleogene and Neogene sediments in the North Pacific and Norwegian Sea by detailed LM and SEM observations, and describes eleven *Xanthiopyxis* species, including seven new ones, and an additional three forms (Figure 1).

**Samples and methods**

In this study, samples from Deep Sea Drilling Project (DSDP) Site 338 in the Norwegian Sea (67°47.11′N, 05°23.26′E; water depth 400.8 m; Cores...
Figure 1. Sketches of valve and girdle view of *Xantiopyxis* species (A, H, I2, L1, L2, M1, M2, N: girdle view; B, C, D, E, F, G, I1, J, K: valve view). All sketches were made using LM.
Fossil diatom resting spore *Xanthiopyxis*

8–29) and Site 436 in the Northwest Pacific (39°55.96’N, 145°33.47’E; water depth 5,240 m; Cores 1–29), and Holes 438A and 438B in the Northwest Pacific (40°37.79’N, 143°14.15’E; water depth 1,558 m; Hole 438A, Cores 1–85; Hole 438B, Cores 6–16), and from the Capistrano and Monterey Formations at Newport Beach, California, were examined.

Strewn slides were prepared from the samples and counting and identification were carried out following the methods of Akiba (1986) and Suto (2003a).

**Results**

The results of counting and the stratigraphic distribution of each species are shown in Figures 2–6 and Tables 1–4. All values listed in Tables 1–4 indicate numbers of valves. The stratigraphic ranges and ages are described according to the NPD (Neogene North Pacific Diatom Zone) code of Akiba (1986) and Yanagisawa and Akiba (1998) for the Miocene, Pliocene and Pleistocene, and to the diatom zones of Schrader and Fenner (1976) for the Eocene and Oligocene.

*Xanthiopyxis* species are similar to the resting spores of extant *Chaetoceros* species, but the taxonomic relationship between fossil species of *Xanthiopyxis* and resting spores of extant species of *Chaetoceros* cannot be determined because the vegetative valves of *Xanthiopyxis* species were not preserved as fossils. Accordingly, it is appropriate to use the genus name *Xanthiopyxis* as a morpho-genus for the fossil resting spores according to Articles 3.2 and 3.3 of the ICBN (Greuter et al., 2000), as in the case of fossil resting spores of dinoflagellates (Edwards, 1991). The synonym lists in this paper include only fossil spores.

**Systematic paleontology**

Division Bacillariophyta

Subdivision Bacillariophytina

Class Mediophyceae

Order Chaetocerotales

Suborder Biddulphineae

Family Chaetocerotaceae

Genus *Xanthiopyxis* Ehrenberg

*Type species.* — *Xanthiopyxis oblonga* Ehrenberg 1844 (1845).

*Description.* — Epivalve circular, oval or narrowly to broadly elliptical in valve view, valve face convex, covered with numerous knobs, spines, bristles and veins. Mantle of epivalve hyaline or with numerous knobs. Hypovalve face convex or with one hump, hyaline or with numerous spines and knobs. Mantle of hypovalve hyaline with a single ring of puncta at its base.

*Stratigraphic occurrence.* — Middle Eocene to Recent (Figure 2).

*Remarks.* — The genus *Xanthiopyxis* is characterized by numerous knobs, spines, bristles and veins covering the entire valve face. Eleven species of the genus, including seven new ones, are described in this paper: X. polaris Gran, X. norwegica Suto, sp. nov., X. brevispinosa Suto, sp. nov., X. teneropunctata Suto, sp. nov., X. lanceolatus Suto, sp. nov., X. circulatus Suto, sp. nov., X. reticulata Suto, sp. nov., X. obesa Suto, sp. nov., X. hirsuta Hanna & Grant, X. oblonga Ehrenberg and X. globosa Ehrenberg (Figure 1).

*Xanthiopyxis* may represent the fossil resting spores of extant and extinct *Chaetoceros* species, but it is difficult or impossible to classify the spores correctly due to the fact that their respective vegetative stages are not preserved in association with their resting spores. Therefore, in this study, some resting spores which lack characteristics and are therefore difficult to identify easily are assigned to three informal species: *Xanthiopyxis* type A (knobbly type), X. type B (short spiny type) and X. type C (long spiny type).

*Etymology.* — Greek *xanthio-*-, meaning “yellow” but applied as a genus name *Xanthium* to the cockle-burs, hence spiny-textured, + *pyxis*, “box, case.”

**Key to species**

1a. Mantle of epivalve with numerous knobs.............. 2
1b. Mantle of epivalve hyaline................................ 3
2a. Knobs covering the entire epivalve face .................
    .......................................................... *Xanthiopyxis polaris*
2b. Knobs covering the central and marginal epivalve
    face.......................................................... X. norwegica
3a. Valve face covered with knobs.............................. 4
3b. Valve face covered with spines............................ 6
3c. Valve face covered with knobs and spines ......... X. brevispinosa
4a. Knobs are weak .......... X. teneropunctata
4b. Knobs are very small (micro-knobs) ............ X. lanceolatus
4c. Knobs are strong and encircled ..... X. circulatus
4d. Knobs are strong and with veins .................... 5
5a. Knobs covering the entire valve face ................. X. type A (knobbly type)
5b. Knobs encircled by veins ................. X. reticulata
5c. Mantle expanded......................................... X. obesa
6a. Spines are very small (micro-spines) ............ X. hirsuta
6b. Spines are strong and short ......................... X. type B (short spiny type)
Figure 2. Stratigraphic ranges of Xanthiopyxis species. Diatom zones and NPD codes are after Yanagisawa and Akiba (1998) for the Miocene, Pliocene and Pleistocene, and after Schrader and Fenner (1976) for the Eocene and Oligocene.
Figure 3. Stratigraphic occurrences of *Xanthiopyxis* species at DSDP Site 338. Diatom zones are after Schrader and Fenner (1976).
Figure 4. Stratigraphic occurrences of *Xanthiopsis* species at DSDP Holes 438A and B. Diatom zones are after Yanagisawa and Akiba (1998).
6c. Spines are strong and long .................................
6d. Spines are bristly..................................
7a. Valve oval to broadly elliptic ...........X. oblonga
7b. Valve circular .................................. X. globosa

**Xanthiopyxis polaris** Gran
Figures 1.A; 7.1–7.17

*Basionym.*—Xanthiopyxis polaris Gran, 1900, p. 51, pl. 3, figs. 16–19.
*Synonymy.*—Chaetoceros spp. of Shirshov, 1977, pl. 15, fig. 15; Spora of Dzinoridze et al., 1978, pl. 15, fig. 18.

**Description.**—Frustule heterovalvate. Valve circular to oval in valve view, apical axis 4.5–11.5 μm, pervalvar axis 4.5–10 μm. In girdle view, epivalve face strongly vaulted, with numerous short spines and knobs. Mantle of epivalve with numerous short spines and knobs. Hypovalve vaulted or flat, with numerous knobs. Mantle of hypovalve hyaline with a single ring of puncta at its base.

**Type locality.**—Recent Arctic Ocean.

**Similar taxa.**—This species is clearly distinguished from other fossil resting spore species by having an epivalve mantle with numerous short spines and knobs. It differs from *Xanthiopyxis norwegica* by having knobs covering the entire epivalve face.

**Stratigraphic occurrence.**—This species occurs from the latest early Miocene to the Recent in the North Pacific (Figure 2). At DSDP Site 338, the first occurrence of this species is recorded in the bottom of the middle middle Miocene (Figure 3).

**Remarks.**—This species occurs abundantly in the North Pacific and is also encountered in the Norwegian Sea. Thus *X. polaris* is probably a cosmopolitan species.

**Etymology.**—Latin *polaris*, meaning “polar”.

**Xanthiopyxis norwegica** Suto sp. nov.
Figures 1.B; 8.1–8.15

**Description.**—Frustule heterovalvate. Valve circular to oval in valve view, apical axis 21.0–34.5 μm, pervalvar axis 17.0–31.0 μm. In girdle view, epivalve face vaulted, central area vaulted with numerous short spines and knobs, intermediate zone hyaline, marginal zone with numerous knobs and spines. Mantle of epivalve with numerous short spines and knobs. Hypovalve hyaline, nearly flat. Mantle of hypovalve hyaline with a single ring of puncta at its base.
Figure 6. Stratigraphic occurrences of *Xanthiopyxis* species in the Newport Beach Section. Diatom zones are after Yanagisawa and Akiba (1998).
Table 1. Occurrences of *Xanthiopyxis* species at DSDP Site 338. Numbers indicate individuals encountered during counts of 100 resting spore valves; + indicates valves encountered after the count; blank indicates absence of any taxa. Diatom zones and NPD codes in the Miocene are after Yanagisawa and Akiba (1998), and diatom zones in the Oligocene and Eocene after Schrader and Fenner (1976).

Table 2. Occurrences of *Xanthiopyxis* species at DSDP Holes 438A and 438B. Values are for counts of 100 or 200 resting spore valves; + indicates valves encountered after the count; blank indicates absence of any new taxa. Diatom zones and NPD codes are after Yanagisawa and Akiba (1998).

<table>
<thead>
<tr>
<th>Diatom Zones</th>
<th>NPD Codes</th>
<th>Occurrence in Hole 438A</th>
<th>Occurrence in Hole 438B</th>
<th>Depth Interval</th>
<th>Log Size (μm)</th>
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<tr>
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<td>23.4-26.6</td>
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<td>159.7</td>
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<tr>
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<td>NSP 78-84</td>
<td>23.4-26.6</td>
<td>100</td>
<td>3.1</td>
<td>200</td>
</tr>
<tr>
<td>Itsuki Suto292</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tbody>
</table>
Table 3. Occurrences of Xanthiopyxis species at DSDP Site 436. Numbers indicate individuals encountered during counts of 100 resting spore valves; + indicates valves encountered after the count; blank indicates absence of any taxa. Diatom zones and NPD codes are after Yanagisawa and Akiba (1998).

Table 4. Occurrences of Xanthiopyxis species in the Newport Beach Section. Numbers indicate individuals encountered during counts of 100 resting spore valves; + indicates valves encountered after the count; blank indicates absence of any taxa. Diatom zones and NPD codes are after Yanagisawa and Akiba (1998).

Holotype.—Slide MPC-02613 (Micropaleontology Collection, National Science Museum, Tokyo, England Finder O34-2N, illustrated in Figures 8.1, 8.2).

Type locality.—DSDP Site 338-19-4, 10–11 cm, Norwegian Sea.

Similar taxa.—This species differs from Xanthiopyxis polaris by having knobs on the center and margin of the epivalve face.

Stratigraphic occurrences.—This species occurs rarely and sporadically in the interval from the lower Oligocene to the lowermost Miocene at DSDP Site 338 (Figure 3).

Etymology.—Latin norwegica, meaning “Norwegian, of Norway.”

Xanthiopyxis brevispinosa Suto sp. nov.


Description.—Frustule heterovalvate. Valve narrowly elliptical to lanceolate in valve view, apical axis 10.0−20.5 μm, transapical axis 5.5−7.5 μm. In girdle view, epivalve face vaulted, with numerous short strong spines and small knobs. Mantle of epivalve hyaline. Hypovalve vaulted or flat, with numerous short spines and small knobs. Mantle of hypovalve hyaline with a single ring of puncta at its base.

Holotype.—Slide MPC-02615 (Micropaleontology Collection, National Science Museum, Tokyo, England Finder L30-1W, illustrated in Figures 9.33, 9.34).

Type locality.—DSDP Site 338-22-4, 79–80 cm, Norwegian Sea.

Similar taxa.—This species is characterized by having valves with numerous short strong spines and small knobs. Mantle of epivalve hyaline. Hypovalve vaulted or flat, with numerous short spines and small knobs. Mantle of hypovalve hyaline with a single ring of puncta at its base.

Xanthiopyxis brevispinosa Suto sp. nov.


Description.—Frustule heterovalvate. Valve narrowly elliptical to lanceolate in valve view, apical axis 10.0−20.5 μm, transapical axis 5.5−7.5 μm. In girdle
DSDP Site 338 (Figure 3). This species has peaks in abundance in the *Pseudodimerogramma filiformis* Zone, where it comprises over 30% of the resting spore assemblage.

**Etymology.**—The Latin word *brevispinosa* means "short-spined".

*Xanthiopyxis teneropunctata* Suto sp. nov.  
Figures 1.D; 10.41–10.50

**Description.**—Valve oval to broadly elliptical in valve view, apical axis 5.5–11.5 µm, transapical axis 5.5–10.0 µm. In girdle view, epivalve face vaulted, with numerous weak knobs. Mantle of epivalve hyaline. Frustule not observed, and hypovalve unknown.  

**Holotype.**—Slide MPC-02616 (Micropaleontology Collection, National Science Museum, Tokyo, England Finder N43-1S, illustrated in Figures 10.43, 10.44).  

**Type locality.**—DSDP Site 338-8-2, 99–100 cm, Norwegian Sea.  

**Similar taxa.**—This species is characterized by having a broadly elliptical epivalve with numerous weak knobs. This species is very similar to *X. type A* (knobbly type), *X. circulatus*, *X. reticulata* and *X. obesa* in possessing knobs on the epivalve, but differs by having weak knobs on the epivalve. This species is distinguished from *X. lanceolatus* by having an oval to broadly elliptical valve shape.

**Stratigraphic occurrence.**—This species occurs from the lower middle Miocene to the upper Pleistocene in the North Pacific and is also encountered in the Norwegian Sea. Thus *X. teneropunctata* is probably a cosmopolitan species.  

**Etymology.**—Latin *teneropunctata* means "weakly spotted".

*Xanthiopyxis lanceolatus* Suto sp. nov.  
Figures 1.E; 9.1–9.24

**Description.**—Frustule heterovalvate. Valve narrowly elliptical to lanceolate in valve view, apical axis 10.5–42.5 µm, transapical axis 5.5–14.0 µm. In girdle view, epivalve face vaulted, with numerous small weak knobs. Mantle of epivalve hyaline. Hypovalve slightly vaulted or flat, with knobs. Mantle of hypovalve hyaline, with a single ring of puncta at its base.  

**Holotype.**—Slide MPC-02612 (Micropaleontology Collection, National Science Museum, Tokyo, England Finder O40-1C, illustrated in Figures 9.1, 9.2).  

**Type locality.**—DSDP Site 338-20-2, 30–31 cm, Norwegian Sea.  

**Similar taxa.**—This species is characterized by having a narrowly elliptical to lanceolate epivalve with numerous weak knobs. This species is distinguished from *X. teneropunctata* by having a narrowly elliptical to lanceolate valve shape. This species is separable from *X. hirsuta* by its epivalve covered with weak small knobs. This species is similar to *Xanthiopyxis* type A (knobbly type), *X. circulatus*, *X. reticulata* and *X. obesa* in possessing knobs on the epivalve, but differs by having strong rather than weak knobs on the epivalve.

**Stratigraphic occurrence.**—This species occurs very abundantly in the Oligocene at DSDP Site 338 (Figure 3). In the middle Miocene, only rare occurrences of this species are recognized.  

**Etymology.**—Latin *lanceolatus*, “lanceolate, shaped like the head of a lance.”
Figure 8. 1–15. Xanthiopyxis norwegica Suto sp. nov. Scale bar = 10 μm for each figure (LM).
**Xanthiopyxis circulatus** Suto sp. nov.

*Description.*—Frustule heterovalvate. Valve oval to broadly elliptical in valve view, apical axis 4.0–32.5 μm, transapical axis 4.0–14.5 μm. In girdle view, epivalve face vaulted, with numerous knobs. Knobs arranged in a ring in the central area. Inner central part of epivalve hyaline or with some knobs. Mantle of epivalve hyaline. Hypovalve slightly vaulted or flat, with knobs and veins. Mantle of hypovalve hyaline, with a single ring of puncta at its base.

*Holotype.*—Slide MPC-02610 (Micropaleontology Collection, National Science Museum, Tokyo, England Finder N33-1N, illustrated in Figures 7.20, 7.21).

*Type locality.*—DSDP Site 338-12-3, 38–39 cm, Norwegian Sea.

*Similar taxa.*—This species is characterized by veins on the epivalve arranged in a ring.

*Stratigraphic occurrence.*—This species occurs very abundantly from the Oligocene to the lower middle Miocene at DSDP Site 338 (Figure 3).

*Etymology.*—From Latin circulatus, “made round”.

**Xanthiopyxis reticulata** Suto sp. nov.

*Description.*—Valve narrowly to broadly elliptical in valve view, apical axis 10.0–22.5 μm, transapical axis 7.5–10.0 μm. In girdle view, hypovalve face vaulted, with numerous small spines. Veins arranged in a ring in the central area. Inner central part of hypovalve with numerous knobs and veins. Mantle of hypovalve hyaline, with a single ring of puncta at its base. Frustule not observed, and epivalve unknown.

*Holotype.*—Slide MPC-02611 (Micropaleontology Collection, National Science Museum, Tokyo, England Finder P39-3N, illustrated in Figures 10.37, 10.38).

*Type locality.*—DSDP Site 338-14-1, 20–21 cm, Norwegian Sea.

*Similar taxa.*—This species is characterized by the conspicuously expanded valve mantle.

*Stratigraphic occurrence.*—This species occurs in a short interval in the middle lower Miocene at DSDP Site 338 (Figure 3).

*Remarks.*—It is difficult to identify this species in valve view, therefore the valve in valve view may be counted as “*Xanthiopyxis* type A (knobbly type)”.

*Etymology.*—The Latin word *obesa* means “fat”.

**Xanthiopyxis hirsuta** Hanna et Grant

*Description.*—Valve narrowly to broadly elliptical in valve view, apical axis 7.0–10.0 μm, pervalvar axis 6.5–9.5 μm. In girdle view, epivalve face vaulted, with numerous knobs. Mantle of epivalve hyaline, conspicuously expanded. Frustule not observed, and hypovalve unknown.

*Holotype.*—Slide MPC-02614 (Micropaleontology Collection, National Science Museum, Tokyo, England Finder P39-3N, illustrated in Figures 10.37, 10.38).

*Type locality.*—No. 1990, Museum of California Academy of Science, from Arroyo Hondo, Maria Madre Island (Tres Marias Group), Mexico; collected by Hanna and Jordan, May, 1925; Miocene.

*Similar taxa.*—This species is characterized by having an oval valve densely covered with numerous small spines. This species is similar to *X. brevispinosa*, but is differentiated by having a valve possessing micro-spines and lacking knobs. This species is distinguished from *X. lanceolatus* by its oval to broad valve shape. This species differs from *X.* type B (short spiny type) and *X.* type C (long spiny type) by its dense micro-spines on the valve face. This species is very similar to *X. microspinosa* Andrews (1976, p. 18, pl. 6, figs. 1–3) by having a valve covered with numerous micro-spines, but is identified by its oval to...
narrow valve shape. *X. microspinosa* is found in the middle Miocene sediments of the Choptank Formation, Maryland, and characterized by its broadly lanceolate valve shape, but was not observed in this study.

**Stratigraphic occurrence.**—This species is found from the lower Oligocene to the middle Miocene at DSDP Site 338 (Figure 3), but was not recorded at DSDP Site 438 and 436, and the Newport Beach Section.

**Remarks.**—*Xanthiopyxis micro punctatus* Hajós (1968) is synonymized with this species because the valve is densely covered with micro-spines. It is very difficult to tell apart the valve of this species from the epivalve of *Gemellodiscus micronodosus* (Suto, 2004b). It is also difficult to recognize whether or not the valve is an epivalve or hypovalve of this species when it is observed in valve view, because the dense micro-spines make it difficult to recognize the presence of a single ring of puncta at the hypovalve mantle base. Therefore, in this study, valves of this type were counted as “Valve of *X. hirsuta* or epivalve of *G. micronodosus*” when complete frustules of this species did not occur.

**Etymology.**—The Latin word *hirsuta* means “hairy”.

**Xanthiopyxis oblonga** Ehrenberg

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**Description.**—Valve oblong, broadly elliptical in valve view, apical axis 31–70 μm, transapical axis 18–40 μm. In girdle view, valve strongly vaulted, with numerous strong bristles. Mantle unknown. Frustule not observed.

**Similar taxa.**—This species is characterized by its large-sized valve covered with strong bristles. This species is very similar to *X. globosa* in having a valve possessing numerous strong bristles, but is differentiated clearly by its oblong valve shape. This species also resembles *X.* type B and *X.* type C in possessing numerous spines on the valve face, but differs from them by having strong bristles on the valve face.

**Stratigraphic occurrence.**—Abundant occurrences of this species are recognized in the Eocene, after which it becomes rare, and more sporadic from the lower Oligocene to the middle Miocene at DSDP Site 338 (Figure 3).

**Remarks.**—This oblong *Xanthiopyxis* species seems to be one of the most common species from the middle Eocene to the middle Miocene.

The synonymized species *X. acrolopha* was collected from the Miocene Marmorito Formation in
Italy (Forti, 1912), the lower Miocene shales of Phoenix Canyon in California (Hanna, 1927a), the Miocene Oligocene sediments in the Southern Ocean (McCollum, 1975) and the middle Miocene sediments in the Norwegian Sea (Dzinoridze et al., 1978).

*Xanthiopyxis cingulata* of Forti (1913) and *X. hystrix sensu* Forti (1913), Proschkina-Lavrenko and Sheshukova-Poretzkaya (1949), Fenner (1978) and Hajós (1986) are also identified as *X. oblonga* because these specimens possess a large valve covered with strong bristles.

*Xanthiopyxis globosa* Ehrenberg sensu Proschkina-Lavrenko and Sheshukova-Poretzkaya (1949), Shirshov (1977), and Schrader and Schuette (1981), *Stephanopyxis? limbata* Ehrenberg var. crista-galli sensu Kanaya (1959), *Xanthiopyxis oblonga* sensu Fenner (1978) and *Xanthiopyxis* sp. (*X. globosa?*) sensu Dzinoridze et al. (1978) are identified as *X. oblonga* because of their oblong valve covered with strong bristles.

As a result of these studies, it is clear that *X. oblonga* occurs from the Eocene through the middle Miocene and that this species is a cosmopolitan species.

*Xanthiopyxis cf. acrolopha* Forti sensu Hajós (1976, pl. 17, figs. 4, 10, 12), *X. acrolopha sensu* Fenner (1978, pl. 35, figs. 25, 26), *X. oblonga sensu* Fenner (1978, p. 536, pl. 35, fig. 9), and *X. oblonga sensu* Homann (1991, p. 143, pl. 57, figs. 9–12) do not belong to *X. oblonga* because they lack numerous strong bristles on their valve face. *Xanthiopyxis oblonga sensu* Kanaya (1959, p. 121, pl. 11, figs. 9, 10), Gleser et al. (1974, pl. 36, fig. 7) and Lee (1993, pl. 2, fig. 21, pl. 3, figs. 13, 17) are identified as *X. globosa* by their circular valve shape.

**Etymology.**—Latin *oblonga*, meaning “oblong”.

*Xanthiopyxis globosa* Ehrenberg


*Xanthiopyxis globosa* Ehrenberg, 1844 (1845), p. 273; Forti, 1912, p. 1557, pl. 2, figs. 39–49; Hanna, 1932, p. 224, pl. 18, fig. 3; Proschkina-Lavrenko and Sheshukova-Poretzkaya, 1949, p. 87, pl. 84, figs. 12a, b nec pl. 32, figs. 5a, b; Jouseé, 1963, p. 117, fig. 105; McCollum, 1975, p. 536, pl. 15, figs. 6–9; Schrader and Fenner, 1976, pl. 40, figs. 15, 17; Shirshov, 1977, pl. 30, fig. 49, pl. 33, fig. 10 nec figs. 9, 11; Dzinoridze et al., 1978, pl. 17, fig. 2; Fenner, 1978, p. 536, pl. 37, figs. 1, 2; Jouseé in Dzinoridze et al., 1979, p. 62, fig. 159; Hajós, 1986, pl. 16, figs. 12, 13, pl. 43, fig. 7; Homann, 1991, p. 142, pl. 57, figs. 8, 13.

*Synonyms.*—*Xanthiopyxis oblonga sensu* Kanaya, 1959, p. 121, pl. 11, figs. 9, 10; Gleser et al., 1974, pl. 36, fig. 7; Lee, 1993, pl. 2, fig. 21, pl. 3, figs. 13, 17 nec pl. 2, figs. 11, 26, pl. 3, fig. 23.

**Description.**—Valve circular to oval in valve view, apical axis 20–35 μm. In girdle view, valve strongly vaulted, with numerous strong bristles. Mantle unknown. Frustule not observed.

**Similar taxa.**—This species is very similar to *X. oblonga* in having a valve possessing numerous strong bristles, but is clearly differentiated by its oval valve shape.

**Stratigraphic occurrence.**—This species occurs abundantly in the Eocene but it becomes rare and its occurrence more sporadic from the early Oligocene to the middle Miocene (Figure 2).

**Remarks.**—The type specimens of *Xanthiopyxis globosa* were collected from the middle Miocene Marmorito Formation in Italy (Forti, 1912). It has also been reported from the lower Miocene Temblor Formation in California (Hanna, 1932), lower Oligocene sediments in the Southern Ocean (McCullom, 1975), lower Oligocene sediments in the Norwegian Sea.
(Schrader and Fenner, 1976) and middle Miocene sediments in the Norwegian Sea (Dzinoridze et al., 1978). These studies indicate that Xanthiopyxis globosa occur from the early Oligocene through the middle Miocene and is a cosmopolitan species.

Xanthiopyxis globosa sensu Hanna (1970, p. 195, fig. 74) and Hasegawa (1977, p. 100, pl. 23, figs. 15a, b) are identified as X. type C by having long spines on the valve. Xanthiopyxis globosa sensu Lee (1993, p. 45, pl. 3, fig. 22) is assigned to X. type B because it has strong bristles rather than spines. Xanthiopyxis globosa Ehrenberg sensu Proschkina-Lavrenko and Sheshukova-Poretzkaya (1949, p. 87, pl. 32, figs. 5a, b), Shirshov sensu (1981, p. 1192, figs. 9, 10), and Xanthiopyxis sp. (X. globosa?) sensu Dzinoridze et al. (1978) are all identified as X. oblonga because of their oblong valve shape with strong bristles.

Etymology.—Latin globosa, meaning “globose”.

Xanthiopyxis type A (knobbly type)

Figures 1.L1, 1.L2; 7.32–7.35; 10.1–10.28

Synonyms.—Xanthiopyxis sp. 1 of Kanaya, 1959, p. 122, pl. 11, fig. 11; Schrader and Fenner, 1976, p. 1003, pl. 40, figs. 3, 7; Fenner 1978, p. 537, pl. 35, fig. 6; Xanthiopyxis sp. 2 of Kanaya, 1959, p. 122, pl. 11, fig. 12; Chaetoceros sp. of Dzinoridze et al., 1978, pl. 9, fig 14 nec figs. 13, 15; Xanthiopyxis sp. 3 of Fenner, 1978, p. 537, pl. 35, figs. 10–14, pl. 36, fig. 11; Xanthiopyxis mexicana Kanaya, 1957, p. 116, pl. 8, fig. 14; Chaetoceros (?)-Hemiaulus (?) resting spore of Schrader and Fenner, 1976, figs. 12, 13; Xanthiopyxis ovalis Lohman sensu Dzinoridze et al., 1978, pl. 17, fig. 1; Fenner, 1978, p. 536, figs. 20–22; Resting spore C of Barron and Mahood, 1993, p. 44, pl. 5, fig. 18; Chaetoceros spore of Gladenkorn and Barron, 1995, fig. 17.

Description.—Frustule heterovalve. Valve oval to narrowly or broadly elliptical in valve view. In girdle view, epivalve face vaulted, with numerous knobs and short veins. Mantle of epivalve hyaline. Hyalopvalve slightly vaulted or flat, or vaulted in the center, hyaline, with or without knobs and veins. Mantle of hypovalve hyaline, with a single ring of puncta at its base.

Similar taxa.—This species type is characterized by knobs and veins on the epivalve and the hyaline mantle of the epivalve.

Remarks.—This species occurs abundantly in all of the cores and onland sections studied. The valves of these specimens belong to several Xanthiopyxis species, but it is very difficult to determine which ones when their frustules are not observed. Therefore, these valves must be counted as “Xanthiopyxis type A (knobbly type)”, when only epivalve or hypovalve is observed during the counting process.

Xanthiopyxis type B (short spiny type)

Figures 1.M1, 1.M2; 12.1–12.32; 13.1–13.7

Synonyms.—Chaetoceros weissflogii Schütt sensu Brockmann, 1928, p. 57, fig. 3; Omphalotheca sp. of Hanna, 1930, p. 192, pl. 14, fig. 11; Xanthiopyxis ovalis Lohman, 1938, p. 91, pl. 20, fig. 6, pl. 22, fig. 12; Kanaya, 1957, p. 117, pl. 8, fig. 13; Hajós, 1968, p. 116, pl. 28, figs. 3, 5, 6; Hanna, 1970, p. 196, figs. 64, 70; Lohman, 1974, p. 350, pl. 5, fig. 11; Schrader and Fenner, 1976, p. 1003, pl. 40, fig. 1; Hajós, 1986, p. 48, fig. 8; Lee, 1986, pl. 1, fig. 17; Chaeto- ceros sp. of Frenguelli, 1949, fig. 4, pl. 16, 17, 19, 20, 32; Schrader, 1973, pl. 17, figs. 5–7, 9–11; Shirshov, 1977, pl. 5, fig. 23; Chaetoceros tiltilensis Frenguelli, 1949, p. 140, pl. 4, figs. 28–31; Chaetoceros wighamii Brightwell sensu Frenguelli, 1949, p. 142, pl. 4, fig. 13; Makarova, 1962, p. 44, pl. 2, figs. 8–10; Xanthiopyxis sp. 3 of Kanaya, 1959, p. 123, pl. 11, fig. 13; Xanthiopyxis sp. 4 of Kanaya, 1959, p. 123, pl. 11, fig. 14; Xanthiopyxis sp. 5 of Kanaya, 1959, p. 123, pl. 11, fig. 15a, b; Chaetoceros aculeatus Makarova, 1962, p. 54, figs. 5, figs. 30, 31; Jouš, 1963, p. 106, fig. 67; Gleser et al., 1974, pl. 54, fig. 2; Chaetoceros cri nitus Schütt sensu Makarova, 1962, p. 46, pl. 1, fig. 9, pl. 2, fig. 15, pl. 5, figs. 22, 23; Chaetoceros clyno- sporus Makarova, 1962, p. 55, pl. 1, figs. 15, 16, pl. 2, figs. 22–24, pl. 5, figs. 26, 27; Chaetoceros hol saticus Schütt sensu Makarova, 1962, p. 48, pl. 1, fig. 19, pl. 3, figs. 1–3; Hajós, 1968, p. 128, pl. 33, figs. 10, 11, 14, 15; Chaetoceros ingolfianus Ostenfeld sensu Makarova, 1962, p. 46, pl. 1, figs. 10–12; Chaeto- ceros muelleri Lemmermann sensu Makarova, 1962, p. 44, pl. 1, fig. 1, pl. 2, figs. 1–4; Chaetocerotype Aulleniense Ostenfeld sensu Makarova, 1962, p. 46, pl. 1, figs. 4–8, pl. 2, figs. 11–14, pl. 5, figs. 18–21, 28, 29; Chaetoceros rigidus Ostenfeld sensu Makarova, 1962, p. 44, pl. 2, figs. 5–7; Chaetoceros robustus Makarova, 1962, p. 52, pl. 1, figs. 20–22, pl. 5, figs. 6–8; Chaetoceros scab rosus Proschkina-Lavrenko sensu Makarova, 1962, pl. 95, pl. 3, figs. 11, 12; Chaetoceros simplex Ostenfeld sensu Makarova, 1962, p. 44, pl. 1, figs. 2, 3; Chaetoceros subtilis Cleve sensu Makarova, 1962, p. 48, pl. 1, figs. 13, 14, pl. 2, figs. 19–21, pl. 5, figs. 24, 25; Chaetoceros subtortilis Proschkina-Lavrenko sensu Makarova, 1962, p. 52, pl. 2, figs. 16–18; Xanthiopyxis rotund Hajoš, 1975, p. 927, figs. 8a, b; Chaetocerus (?)-Hemiaulus (?) resting spore of Schrader and Fenner, 1976, figs. 19–21;
Figure 12. 1–32. *Xanthiopyxis* type B (short spiny type). Scale bar = 10 μm for each figure (LM).


8. *Xanthiopyxis hirsuta* Hanna and Grant. Scale bar = 5 μm (SEM).


10, 11. *Xanthiopyxis oblonga* Ehrenberg. Scale bar = 5 μm for each figure (SEM).


Figure 13. 1–7. *Xanthiopyxis* type B (short spiny type). Scale bar = 5 μm for each figure (SEM).


8. *Xanthiopyxis hirsuta* Hanna and Grant. Scale bar = 5 μm (SEM).


10, 11. *Xanthiopyxis oblonga* Ehrenberg. Scale bar = 5 μm for each figure (SEM).


22. Girdle view of epivalve, Newport Beach Section, Tm17. 23, 24. Valve view of frustule, Newport Beach Section, N7a. 25, 26. Valve view of frustule, Newport Beach Section, N7a. 27, 28. Oblique valley view of epivalve, Newport Beach Section, N7a. 29, 30. Girdle view of epivalve, Newport Beach Section, N7a. 31, 32. Girdle view of epivalve, DSDP Site 436-5-2, 148–150 cm.

33–40. *Xanthiopyxis* type C (long spiny type). Scale bar = 10 μm for each figure (LM).

Chaetoceros compressus Lauder sensu Shirshov, 1977, pl. 24, figs. 13, 14; Chaetoceros species indet. of Schrader and Ger-sonde, 1978, pl. 2, figs. 5–7; Chaetoceros spore (3) of Fenner, 1978, p. 513, pl. 37, fig. 8; Chaetoceros spore (b) of Fenner, 1978, p. 513, pl. 34, fig. 30; Resting spore of Fenner, 1978, pl. 34, fig. 32, pl. 37, fig. 9; Chaetoceros spore of Schrader, 1978, p. 859, pl. 18, figs. 1, 2, 5–15, 18; Whiting and Schrader, 1985, pl. 5, figs. 9–11; Xanthiopyxis sp. of Hajo´ s, 1986, pl. 22, fig. 14; Xan-thiopyxis sp. 1 of Baldauf and Barron, 1987, p. 8, pl. 4, fig. 6; Xan-thiopyxis type A of Harwood et al., 1989, pl. 4, fig. 5; Chaeto-ceros annanita Cleve-Eider sensu Lee, 1993, p. 32, pl. 1, figs. 7, 9; Chaetoceros coronatus Gran sensu Lee, 1993, p. 33, pl. 1, fig. 6, pl. 3, fig. 15; Chaetoceros costatus Pavillard sensu Lee, 1993, p. 33, pl. 1, figs. 8, 12; Chaetoceros vanheurcki Gran sensu Lee, 1993, p. 36, pl. 3, fig. 11; Chaetoceros lauderi Ralfs in Lauder sensu Lee, 1993, p. 34, pl. 1, fig. 1, pl. 2, figs. 4, 7.

Description.—Frustule heterovalvate. Valve oval to narrowly or broadly elliptical in valve view. In girdle view, epivalve face vaulted, with numerous short strong spines. Mantle of epivalve hyaline. Hypovalve slightly vaulted or flat, or vaulted in the center, hyaline or with numerous strong spines. Mantle of hypovalve hyaline, with a single ring of puncta at its base.

Similar taxa.—These specimens are characterized by short strong spines.

Remarks.—These specimens occur abundantly in all of the cores and onland sections studied. The valves of this type are those of several Xanthiopyxis species, but these valves are difficult or impossible to classify correctly when their frustules are not observed. Therefore these valves must be counted as “Xanthiopyxis type B (short spiny type)”, when only the epivalve or hypovalve is observed during the counting process.

Xanthiopyxis type C (long spiny type)

Figures 1.N; 12.33–12.40

Synonyms.—Chaetoceros sp. of Frenguelli, 1949, pl. 4, fig. 22; Hajós, 1968, p. 131, pl. 33, figs. 13, 16, pl. 34, figs. 8, 9a, b, 17; Chaetoceros longicornis Makarova, 1962, p. 52, pl. 1, figs. 17, 18, pl. 2, figs. 25–30; Chaetoceros seiracanthus Gran sensu Makarova, 1962, p. 48, pl. 3, figs. 4, 5; Chaetoceros spore of Schrader, 1978, p. 859, pl. 18, figs. 3, 4; Chaetoceros sp. I of Hajós, 1968, p. 130, pl. 34, fig. 3; Chaetoceros sp. II of Hajós, 1968, p. 130, pl. 34, fig. 7; Chaetoceros sp. III of Hajós, 1968, p. 130, pl. 34, figs. 4–6, 11; Stephanogonia striolata Pantocsek sensu Fenner, 1978, pl. 34, fig. 34; Periptera sp. (Chaetoceros sp.? ) of Hajós, 1986, pl. 58, fig. 8; Chaetoceros sp. 1 of homann, 1991, p. 75, pl. 9, figs. 2–6; Dicladia sp. of Barron and Mahood, 1993, p. 38, pl. 3, fig. 8.

Description.—Frustule heterovalvate. Valve oval to narrowly or broadly elliptical in valve view. In girdle view, epivalve face vaulted, with numerous long strong spines. Mantle of epivalve hyaline. Hypovalve slightly vaulted or flat, or vaulted in the center, hyaline or with numerous strong spines. Mantle of hypovalve hyaline, with a single ring of puncta at its base.

Similar taxa.—These specimens are characterized by long strong spines.

Remarks.—These specimens occur rarely in all of the cores and onland sections. These valves belong to several Xanthiopyxis species, but it is impossible to identify which ones when their frustules are not observed. Therefore these valves were counted as “Xanthiopyxis type C (long spiny type)”, when only the epivalve or hypovalve is observed during the counting process.

Valve of Xanthiopyxis hirsuta and epivalve of Gemellodiscus micronodosus

Figures 1.11; 11.1–11.24

Description.—Epi- or hypovalve of Xanthiopyxis hirsuta and epivalve of Gemellodiscus micronodosus (Suto, 2004b). In valve view, valve oval to broadly elliptical. In girdle view, valve vaulted, with numerous small spines, and with a mantle.

Remarks.—It is difficult to identify these specimens as either the valve of X. hirsuta or the epivalve of G. micronodosus because these valves are very similar to each other. Therefore, in this study, these valves were counted as “Valve of X. hirsuta or epivalve of G. micronodosus” when the frustule of this type did not occur.

Discussion

Several previously described Xanthiopyxis species were not observed in this study, and therefore are not listed above. It cannot be decided whether these species are fossil resting spores of Chaetoceros or not by the original descriptions and illustrations of these species. Xanthiopyxis granti Hanna is a late Cretaceous diatom characterized by a very slender valve
shape (Hanna, 1927b; Hanna, 1934; Nikolaev et al., 2001). This species may not be a resting spore of Chaetoceros because the valves in the illustrations of Hanna (1927b, 1934) and Nikolaev et al. (2001) possess a porous canal. Xanthiopyxis cingulata Ehrenberg is characterized by having a large valve size (15–40 μm) and valve mantle with spines (Ehrenberg, 1854; Hanna and Grant, 1926; Lohman, 1974). The circular valve of X. umbernatus possesses numerous spines in the valve center and was collected from upper Eocene to upper Miocene sediments (Greville, 1866; Sheshukova-Poretzkaya, 1967; Hanna, 1970; Fenner, 1978). Xanthiopyxis cingulata and X. umbernatus may be resting spores of Chaetoceros, but this cannot be determined in this study because the illustrations do not show the characteristic single ring of puncta on the mantle. Xanthiopyxis microspinosa Andrews has a broadly lanceolate valve with numerous small short spines and was reported from the middle Miocene Choptank Formation in Maryland (Andrews, 1976) and the middle Miocene deposits in the Szurdokpüspöki diatomite quarry, Hungary (Hajós, 1986).

Several extant Chaetoceros species form resting spores possessing numerous spines or knobs over the entire valve face (i.e., C. teres Cleve, C. lauder Ralfs, C. vanheurckii Gran, C. siamensis Ostenfeld, C. hispidum Brightwell, C. affinis Lauder, C. holsaticus Schütt, C. seiracanthus Gran, and C. costatus Pavillard). These resting spores are too similar to distinguish from each other when seen without their vegetative cells. The resting spores of these Chaetoceros species, therefore, may not be identified in fossil records. In this study, these resting spores are informally described as Xanthiopyxis type A, X. type B and X. type C (Figure 1.L-1.N).

Although detailed descriptions of the morphology of extant Chaetoceros vegetative frustules are generally available (e.g., Cupp, 1943; Rines and Hargraves, 1988; Hasle and Syvertsen, 1996), our knowledge of extant resting spore morphologies is poor, because it is difficult to see some of the resting spores in valve view. Therefore, more detailed studies on extant and fossil resting spore morphology are needed in order to clarify the correlation between extant vegetative cells and fossil resting spores. Studying live Chaetoceros species (in culture or wild material) in the act of resting spore production is the only way to identify with certainty the vegetative cell-resting spore pair for each species. Then, fossil resting spores of similar morphology can be assigned to lineages containing extant members.

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**References**


