Observations on the fossil resting spore morphogenus *Peripteropsis* gen. nov. of the marine diatom genus *Chaetoceros* (Bacillariophyceae) in the Norwegian Sea

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The morphology and taxonomy of the fossil diatom resting spore morphogenus *Peripteropsis* gen. nov. from the lower Oligocene through middle Miocene sediments of Deep Sea Drilling Project Site 338 in the Norwegian Sea were examined. The new genus *Peripteropsis* is characterized by elongated processes on the shoulder or centre of its valves and contains four species including one new species and three new combinations: *P. tetracornula* sp. nov., *P. trinodis* comb. nov., *P. norwegica* comb. nov. and *P. tetracornusa* comb. nov. *Peripteropsis tetracornula*, the oldest species of the genus, arose in the early Oligocene in the stratigraphic records of the Norwegian Sea, and all *Peripteropsis* species including the last species, *P. tetracornusa*, became extinct by the earliest late Miocene. Some species are biostratigraphically useful in the Norwegian Sea and the North Pacific. Moreover, two similar species which may belong to *Peripteropsis*, ‘*Periptera* schraderi’ and ‘*Periptera* petiolata’, are also described.

**INTRODUCTION**

*Chaetoceros* Ehrenberg 1844 is one of the largest and most diverse of the marine planktonic diatom genera (Van-Landingham 1968; Rines & Hargraves 1988; Hasle & Syvertsen 1996). It plays an important role in marine primary production in nearshore upwelling regions and other coastal areas. Most species of the subgenus *Hyalochaete* Gran are known to form resting spores under various unfavourable conditions, such as nutrient depletion, darkness, and low temperature (e.g. Durbin 1978; Garrison 1981; Hargraves & French 1983; Kuwata & Takahashi 1990; Kuwata et al. 1993; Oku & Kamatani 1995, 1997, 1999; McQuoid & Hobson 1996). On the other hand, resting spores of the other subgenus *Phaeoceros* Gran are reported for only one species, *Chaetoceros eibenii* (Grunow) Meunier. The resting spores of *Chaetoceros* are differentiated from the weakly silicified vegetative frustules by possessing heavily silicified valves, and they occur frequently in nearshore sediments in association with other fossil diatom valves.

In previous studies, many fossil resting spore genera such as *Dictadia* Ehrenberg 1854, *Periptera* Ehrenberg 1854, *Syndendrium* Ehrenberg 1854, *Xanthiopyxis* Ehrenberg 1854, *Liradiscus* Greville 1865 and *Monocladia* Suto 2003a have been described, and diatomists have realized that they may belong to the genus *Chaetoceros*. However, except for studies such as Gersonde (1980), Akiba (1986), Lee (1993) and Suto (2003a, b, 2004), the investigation of the taxonomy and biostratigraphy of fossil resting spores has been limited, because their weakly silicified vegetative valves are not usually preserved as fossils in sediments and the classification of resting spores was thought to be difficult or impossible.

Since *Periptera* was erected by Ehrenberg (1844, 1854), several species have been described (e.g. Abbott & Andrews 1979; Dzinoridze et al. 1979). Recently, Suto (2003b) described *Peripteropsis tetracornusa* from upper lower Miocene to Pleistocene sediments in the North Pacific Ocean and demonstrated its biostratigraphic utility. However, the name ‘*Periptera*’ is invalid because the angiosperm *Periptera* DC 1824 has priority over the diatom resting spore morphogenus ‘*Periptera*’. Therefore, the invalid fossil diatom resting spore morphogenus name ‘*Periptera*’ is renamed as *Peripteropsis* in this study.

Four *Peripteropsis* species, including one new species and three new combinations transferred to new genus from ‘*Periptera*’, are described herein from lower Oligocene through middle Miocene sediments at the Deep Sea Drilling Project (DSDP) Leg 38, Site 338 in the Norwegian Sea (Figs 1, 2) to clarify the systematic taxonomy of this genus, which might appear in the early Oligocene and expanding to the Atlantic and North Pacific.

**MATERIAL AND METHODS**

In this study, 80 samples of a section of middle Eocene through middle Miocene sediments from DSDP Leg 38, Site 338 (67°47.11’N, 05°23.26’E; water depth 400.8 m) were examined (Fig. 1). The diatom biostratigraphy of this site was reported in detail by Schrader & Fenner (1976) and Dzinoridze *et al.* (1978). Most samples investigated in this study include well preserved and abundant resting spore assemblages. The preparation and counting methods of resting spores...
used here follow Koizumi & Tanimura (1985), Akiba (1986) and Suto (2003b).

RESULTS

Peripteropsis species were moderately well preserved in the studied material. The cell/valve counts and stratigraphic distribution of each species are shown in Figs 3, 4 and Table 1. The stratigraphic ranges and ages are described relative to the Neogene north Pacific Diatom Zone (NPD) code of Akiba (1986) and Yanagisawa & Akiba (1998) in the Miocene and the diatom zones of Schrader & Fenner (1976) in the Oligocene and Eocene. The morphogenus name Peripteropsis is used for the fossil resting spores according to Articles 3.3 and 3.4 of the International Code of Botanical Nomenclature (Greuter et al. 2000).

Genus Peripteropsis gen. nov.

GENERIC TYPE: Peripteropsis tetracornusa sp. nov.

DESCRIPTION: Frustule heterovalvate. In girdle view epivalve hyaline and flat to slightly convex, mantle distinct. Epivalve face possesses some elongated processes at the shoulder or the centre of the valve. Mantle of epivalve hyaline and smooth. Hypovalve, hyaline, convex. Mantle of hypovalve with a single ring of puncta at its base. In valve view, valve outline broadly elliptical to subcircular.

REMARKS: This paper describes the taxonomy and stratigraphic occurrences of four species (Fig. 2); Peripteropsis tetracornusa comb. nov., P. tetracladia sp. nov., P. norwegica comb. nov. and P. trinodis comb. nov. Moreover, ‘Periptera petiolaris’ Andrews and ‘Periptera schraderi’ which may belong to Peripteropsis are also described. The description of P. tetracornusa has been presented in detail as the invalid species ‘Periptera tetracornusa’ in Suto (2003b).

ETYMOLOGY: The Latin periperipetra means ‘encircled with pillars’.

Key to species

(1a) Processes at the shoulder of valve ................. 2
(1b) Processes at the centre of valve ................. 4
(2a) Processes with branching processes ............. 3
(2b) Processes without branching processes .......... P. tetracornusa comb. nov.

(3a) Processes three, slender .................. P. trinodis comb. nov.
(3b) Processes four, tricornate .................. P. tetracladia sp. nov.
(3c) Processes numerous, thin and wide ............. P. norwegica comb. nov.
(4a) Central processes with two tricornate ones at the shoulder of epivalve ........... ‘Periptera schraderi’
(4b) Central process on hypovalve ........ ‘Periptera petiolaris’

Peripteropsis tetracornusa (Suto) Suto comb. nov.

Fig. 2A

BASIONYM: Periptera tetracornusa Suto (2003b, p. 2, figs 3, 5–35).

HOLOTYPE: Slide MPC-04054, Micropaleontology Collection (MPC), the National Science Museum, Tokyo. England Finder O44-4N, illustrated in Suto (2003b, figs 11, 12).

TYPE LOCALITY: DSDP Hole 438A-73-5, 9–11 cm, the northwestern Pacific.

SIMILAR TAXA: Peripteropsis tetracornusa is very similar to P. tetracladia because it has four tricornate processes but is distinguished by lacking branched processes. This species differs from P. trinodis, ‘Periptera schraderi’ and ‘Periptera petiolaris’ by possessing no central processes.

STRATIGRAPHIC OCCURRENCE: The species occurs from the early middle Miocene Zone NPD 3A to the upper part of the late middle Miocene Zone NPD 5C (see fig. 2 in Suto 2003b) in the North Pacific Ocean. At DSDP Site 338, rare occurrences of this species are recognized in the middle Miocene (Fig. 3).

ETYMOLOGY: The Latin tetracornusa means ‘four horns’.

Peripteropsis trinodis (Hanna) Suto comb. nov.

Fig. 2B

SYNONYM: Dicladia trinodis Hanna (1927, p. 112, pl. 18, figs 4, 5); Barron & Mahood (1993, p. 38, pl. 3, fig. 10).

DESCRIPTION: Valve ovate in valve view, apical axis 37–52 μm, per-valvar axis 9–11 μm. Epivalve hyaline, convex at the centre, with three slender post-like scarcely dichotomous branching processes, with valve mantle. The slender post-like scarcely dichotomous processes hyaline, located at the conical centre and at each apex of the epivalve. Cross-sectional shape of slender post-like scarcely dichotomous processes circular. Valve mantle hyaline.

TYPE LOCALITY: Location 995 (California Academy of Science), Section 19, T. 18 S., R. 15 E., M.D.M., Fresno County, California, lower Miocene (Hanna 1927).

SIMILAR TAXA: This species is differentiated from other Peripteropsis species by the three slender post-like scarcely dichotomous branching processes.

STRATIGRAPHIC OCCURRENCE: This species was not noted in this study. It is reported from the early Oligocene glacial sediments of Prydz Bay, East Antarctica (Barron & Mahood 1993), and lower Miocene deposits of the Kreyenhagen Shale, California (Hanna 1927).

ETYMOLOGY: The Latin trinodis means ‘three knots’.

REMARKS: Hanna (1927) placed this species in the genus Dicladia, but the species should not be included in Dicladia because it does not possess two conical elevations with dichotomous branching processes at its tips on the epivalve (see Suto 2003a). This species is characterized by the three slender post-like processes and its flat epivalve and belongs to the genus Peripteropsis. Frustule not observed by Hanna (1927) or Barron & Mahood (1993).

Peripteropsis tetracladia sp. nov.

Figs 2C, 5–28, 50

SYNONYM: Periptera tetracladia Ehrenberg (1854, pl. 18, fig. 9); Van Heurck (1885, fig. 8 nec figs 7, 9); Proshkina-Lavrenko &
Fig. 2. Sketches of girdle views of species of *Peripteropsis* which indicate the following morphological characters: (a) pervalvar axis; (b) apical axis; (c) tricornate process; (d) slender post-like scarcely dichotomous branching process; (e) tricornate dichotomous branching process; (f) spiny process; (g) thin and wide dichotomous branching process; (h) slender central process; (i) prominent central process; (j) mantle; (k) a single ring of puncta; (l) epivalve; (m) hypovalve. All sketches were made using LM except for *Peripteropsis trinodis*, which is drawn after illustrations in Barron & Mahood (1993), *P. jouseae* after Dzinoridze *et al.* (1979, fig. 164), and *'Periptera' petiolata* after LM illustrations in Abbott & Andrews (1979).

Sheshukova-Poretzkaya (1949, p. 207, pl. 98, fig. 11a nec fig. 11b); Dzinoridze *et al.* (1978, pl. 17, fig. 8); Dzinoridze *et al.* (1979, p. 62, fig. 162); Schrader & Schuette (1981, p. 1192, figs 9–11 nec figs 9–12); *Dichadia elliptica* Schrader & Fenner (1976, p. 979, pl. 6, fig. 16); *Periptera* sp. 1 of Schrader & Fenner (1976, pl. 39, fig. 7); *Periptera* sp. 2 of Dzinoridze *et al.* (1978, pl. 17, fig. 11); *Periptera schraderi* Jousé in Dzinoridze *et al.* (1979, fig. 163 nec fig. 164).

**DESCRIPTION:** Frustule heterovalvate, apical axis 16.0–26.5 μm, transapical axis 6.5–13.0 μm, pervalvar axis 5.5–9.5 μm. Valve narrowly to broadly elliptical in valve view. Epivalve hyaline, slightly convex in the centre, with four, sometimes several, numbers (see Figs 13, 14), tricornate processes, and with valve mantle. Tricornate processes hyaline, with dichotomous branching processes at their tips, curved near their apices. Mantle of epivalve hyaline, high. Hypovalve hyaline, flat, with two strong spines at the apices. Mantle of hypovalve hyaline, high, with a single ring of puncta along the edge of the mantle.

HOLOTYPE: Slide MPC-03759. Micropaleontology Collection (MPC), the National Science Museum, Tokyo. England Finder P36-4N, illustrated in Figs 5, 6.

TYPE LOCALITY: DSDP Site 338-17-3, 110–111 cm, the Norwegian Sea.

SIMILAR TAXA: This species is differentiated from *P. tetracornusa* and *P. trinodis* by its processes with triangular cross-sectional and dichotomous branching processes at its tips. This species is very similar to *P. norwegica* because it possesses dichotomous branching processes at the edge of the valve, but it is identified by the four tricornate processes on its epivalve. This species differs from *'Periptera' schraderi* and *'P.' petiolata* by lacking central processes.

STRATIGRAPHIC OCCURRENCE: This species is recognized only at DSDP Site 338 and occurs rarely but continuously from the early Oligocene to the middle Miocene.

ETYMOLOGY: The Latin *tetracladia* means ‘four branches’.
**Fig. 3.** Stratigraphic ranges of *Peripteropsis* species in the North Pacific and the Norwegian Sea. Diatom zones and NPD codes for the Miocene are after Yanagisawa & Akiba (1998), and diatom zones after Schrader & Fenner (1976) for the Eocene and Oligocene.

**REMARKS:** *Peripteropsis tetractiadia* was formerly known as *Peripitera tetractiadia* erected by Ehrenberg (1844, 1854). However, the name ‘*Peripitera*’ for diatom resting spore is invalid because the angiosperm *Peripitera* DC 1824 has priority over the diatom resting spore morphgenus ‘*Peripitera*’. Therefore, *Peripteropsis tetractiadia* is invalid in both genus and species names, and the species are renamed as new species belonging to new genus *Peripteropsis*.

*Dicladia elliptica* Schrader & Fenner (1976, p. 979, pl. 6, fig. 16) and *Peripitera* sp. 2 of Dzinoridze et al. (1978, pl. 17, fig. 11) are identified as *Peripteropsis tetractiadia* by the four dichotomous branching processes. The type specimens of *Peripitera schraderi* in Dzinoridze et al. (1978, p. 61, fig. 163 nec fig. 164) belong to *Peripteropsis tetractiadia* because they possess broken tricornate processes on the epivalve; therefore *Peripitera schraderi* is a synonym. *Peripitera tetractiadia sensu* Van Heurck (1880–1885, figs 7, 9), Proshchkina-Lavrenko & Sheshukova-Poretzkaya (1949, p. 127, DSDP 338

**Fig. 4.** Stratigraphic occurrences of species in the genus *Peripteropsis* at DSDP Leg 38 Site 338.
Figs 5–28. *Peripteropsis tetractadiad*, LM. Scale bar = 10 μm for each figure. Figs 5–10, 13, 14: Girdle view of frustule. Figs 11, 12, 15–20: Girdle view of epivalve. Figs 21, 22: Valve view of epivalve. Figs 23–28: Valve view of hypovalve.

**Figs 5, 6.** Holotype (Slide MPC-03759). DSDP Site 338-17-3, 110–111 cm.

**Figs 7–10.** DSDP Site 338-17-1, 100–101 cm.

**Figs 11, 12.** DSDP Site 338-15-4, 100–101 cm.
Peripteropsis norwegica (Schrader) Suto comb. nov.

Figs 2D, 29–40, 51, 52

Basionym: Dicladia norwegica Schrader in Schrader & Fenner (1976, p. 979, pl. 6, figs 13, 14).

SYNONYM: Periptera tetractilus sensu Van Heurck (1885, figs 7, 9 nec fig. 8); Proschkina-Lavrenko & Shushakova-Poretskaya (1949, p. 127, pl. 98, fig. 11b nec fig. 11a); Schrader & Fenner (1976, p. 992, pl. 39, figs 5, 6 nec pl. 6, fig. 12); Schrader & Schuette (1981, pl. 992, figs 9–12 nec figs 9–11).

DESCRIPTION: Frustule heterovalvate, apical axis 6.5–26.5 μm, pervalvar axis 7.0–15.0 μm. Valve narrowly to broadly elliptical in valve view. Epivalve hyaline, slightly convex in the centre, with numerous (6–12) thin and wide processes, with valve mantle. The thin and wide processes hyaline, flatness around the margin of the epivalve, with dichotomous branching processes at their tips, curving near their apices. Epivalve mantle hyaline, high. Hypovalve hyaline, flat, with a single ring of puncta at its base.

HOLOTYPE: Dicladia norwegica sensu Schrader in Schrader & Fenner (1976, p. 979, pl. 6, figs 13, 14).

TYPE LOCALITY: DSDP Site 338-10-2, 55–56 cm, the Norwegian Sea (Schrader & Fenner 1976).

SIMILAR TAXA: This species is distinguished from other Peripteropsis species by the thin and wide dichotomous, branching processes around the margin of the epivalve.

STRATIGRAPHIC OCCURRENCE: The sporadic and rare occurrences of this species are recognized in the upper Oligocene, but this species occurs abundantly and continuously in the lowest Miocene through to the upper middle Miocene sediments at DSDP Site 338.

ETYMOLOGY: The Latin norwegica means ‘Norway’.

REMARKS: Dicladia norwegica Schrader in Schrader & Fenner (1976) belongs to the genus Peripteropsis because it does not possess elevations or domes on its epivalve and has numerous thin and wide processes around the margin of the epivalve. This species has been included with the invalid species Periptera tetractilus for a long time (e.g. Periptera tetractilus sensu Van Heurck 1885, figs 7, 9; Proschkina-Lavrenko & Shushakova-Poretskaya 1949, p. 127, pl. 98, fig. 11b; Schrader & Fenner 1976, p. 992, pl. 39, figs 5, 6; Schrader & Schuette 1981, p. 1192, figs 9–12), but these specimens possess four tricorne processes rather than numerous thin and wide processes. Thus, they do not belong to the renamed species Peripteropsis tetractilus and belong instead to P. norwegica.

Periptera’ schraderi Jousé in Dzinoridze, Jousé & Strelnikova

Fig. 2E

SAME SPECIES: Periptera sp. of Dzinoridze et al. (1978, pl. 17, fig. 7); Periptera schraderi Jousé in Dzinoridze et al. (1979, p. 61, pl. 164 nec fig. 163).

DESCRIPTION: Frustule heterovalvate, apical axis 40–50 μm, pervalvar axis 5.0–9.0 μm. Valve oval in valve view. Epivalve hyaline, slightly convex in the centre, with two tricorne processes at valve shoulder, and two slender central processes, with valve mantle. The tricorne processes hyaline, and curved near their apices. Epivalve mantle hyaline and high. Hypovalve hyaline, flat, with a single ring of puncta at its base.

TYPE LOCALITY: Section 6, core 16, DSDP Site 338, bottom depth 1297 m, Norwegian Sea (Dzinoridze et al. 1978).

SIMILAR TAXA: ‘Periptera’ schraderi differs from other Peripteropsis species by possessing two tricorne processes at valve shoulder and two slender central processes on the epivalve.

STRATIGRAPHIC OCCURRENCE: This species is rarely observed in the middle Miocene at DSDP Site 338. In Dzinoridze et al. (1978, 1979) this species was noted in the upper Oligocene to the lower Miocene in the Norwegian Sea, but in this study it was not recognized in that interval.

REMARKS: Type specimen of Periptera schraderi Jousé in Dzinoridze et al. (1979, fig. 163, holotype) is identified to Peripteropsis tetractilus possessing broken tricorne processes; therefore Periptera schraderi is invalid. Therefore, Periptera schraderi Jousé in Dzinoridze et al. (1979, fig. 164), the other type figure of P. schraderi, must be renamed because it possesses two slender central processes. However, it is not determined whether or not this species belongs to Peripteropsis in this study.

In this study, this type species has not occurred, but very similar species are recognized (‘Periptera’ schraderi?, Figs 41, 42, 49). The specimen in Figs 41, 42 possesses one central slender process, and one in Fig. 49 lacks central slender process, but each specimen possesses two tricorne processes on the valve shoulder and may belong to ‘Periptera’ schraderi.

‘Periptera’ petiolata Andrews in Abbott & Andrews

Figs 2F, 43–48

SAME SPECIES: Periptera sp. (Chaetoceros? sp.) I of Hajas 1968, pl. 137, pl. 38, fig. 8; Periptera sp. (Chaetoceros? sp.) VII of Hajas 1968, pl. 138, pl. 38, fig. 14; Periptera petiolata Andrews in Abbott & Andrews 1979, p. 248, pl. 4, figs 30–34, pl. 8, fig. 1; Periptera sp. of Lee 1993, p. 43, pl. 1, fig. 14, pl. 3, fig. 7.

DESCRIPTION: Frustule heterovalvate, apical axis 45–70 μm, transapical axis 12.0–18.5 μm, pervalvar axis 15–30 μm. Valve narrowly elliptical to elongate rectangular in valve view. Epivalve hyaline, slightly convex, sometimes slightly concave in central area, with distinct mantle, which is hyaline and high. Hypovalve hyaline, with a central prominent process 8–10 μm in height, with a sheath surrounding the hypovalve margin. A prominent process flange is present (Fig. 47) around the margin and its top is flat at the centre. Mantle of hypovalve hyaline, high, with a single ring of puncta at its base.

TYPE LOCALITY: USGS diatom locality 6459, Dawson’s Landing, South Carolina.
Table 1. Occurrence of Peripteropsis species at DSDP Site 338.1

| Diatom zones | NPD | Core Section | Interval (cm) | Log 38 Site 338 | Depth (m) | Peripteropsis tetracladia | Peripteropsis norwegica | Peripteropsis tetracornusa | Peripteropsis petiolata | Peripteropsis cavata | Peripteropsis echinata | Peripteropsis platygona | Peripteropsis pumicosa | Peripteropsis didactyla | Peripteropsis anomala | Peripteropsis aequitrigona | Peripteropsis pacifica |
|--------------|-----|--------------|---------------|-----------------|-----------|------------------------|------------------------|------------------------|------------------------|------------------------|------------------------|------------------------|------------------------|------------------------|------------------------|------------------------|------------------------|
| Phytoderia    | 5B  | 8.1-140-1    | 77.48         | G               | 1 2 + + + 100 |
| Phytoderia    | 9B  | 4.2-140-4    | 77.98         | G               | A         + + + + + 100 |
| C. capillata  | 5A  | 8.3-140-1    | 79.16         | G               | 2         + + + + + 100 |
| Phytoderia    | 6B  | 8.3-80-6     | 80.60         | A               | G         1 2 + + + 100 |
| Phytoderia    | 4B  | 6.4-80-6     | 81.38         | A               | 4         + + + + + 100 |
| Phytoderia    | 4A  | 6.4-50-6     | 80.60         | A               | 4         + + + + + 100 |
| Phytoderia    | 6B  | 9.1-140-10   | 86.98         | G               | A         + + + + + 100 |
| Phytoderia    | 6B  | 9.1-140-10   | 86.98         | G               | A         + + + + + 100 |

1 Numbers indicate individuals encountered during counts of 100 resting spore valves; + indicates epivalves encountered after the count; blank indicates absence of any taxa. Diatom zones and NPD codes in the Oligocene and the middle Eocene after Suto (2003a). Preservation: G, good. Abundance: A, abundant; C, common; R, rare. T, total number of resting spore valves counted.

SIMILAR TAXA: This species is characterized by its prominent central process on the hypovalve.

STRATIGRAPHIC OCCURRENCE: This species occurs rarely and sporadically, only at DSDP Site 338 from the earliest early Miocene through early middle Miocene.

ETYMOLOGY: The Latin petiolata means ‘leafstalk’.

REMARKS: It is not clear whether or not this species belongs to the genus Peripteropsis because it lacks elongated processes on the epivalve. The prominent central process on the hypovalve characterizes this species, but other Peripteropsis species lack processes on their hypovalve. This species may belong to another genus.

Chaetoceros sp. in Harwood (1986, pl. 3, fig. 1) is similar to this species because it possesses a central prominent process on the valve, but it may not belong to Peripteropsis because it connected by slender seta which Peripteropsis species lack. This species may belong to another genus.

DISCUSSION

The morphology, taxonomy and biostratigraphy of the fossil resting spore morphogenus Peripteropsis formerly known as ‘Periptera’ are described in this paper. The genus Peripteropsis is characterized by elongated processes at the valve shoulder. Of the four species in this genus, Peripteropsis tetracladia and P. norwegica are similar to the fossil resting spore genera Monocladia, Dicladia and Syndendrium in possessing dichotomous branching processes on their valves (Suto 2003a), suggesting a close phylogenetic relationship between the four genera. However, Peripteropsis is clearly distinguished by the possession of processes on the valve margin, which are lacking in the other three genera. In addition, Peripteropsis differs from Monocladia, Dicladia and Syndendrium by having a relatively flat valve face in contrast to the strongly domed valve faces of the other three genera. Among the morphogenera of Chaetoceros, no others have such processes on the valve margin, and therefore Peripteropsis is distinct and is clearly characterized by the presence of marginal processes.

The genus Peripteropsis appeared in the early Oligocene and became extinct in the early late Miocene (Fig. 3) in the Norwegian Sea at Site 338. The oldest species P. tetracladia arose in the early Oligocene in the stratigraphic records of the Norwegian Sea and disappeared in the early middle Miocene (Fig. 4). In the late Oligocene, P. norwegica appeared and increased upward in abundance through the early Miocene to middle Miocene (Fig. 5). The last species P. tetracornusa appeared in the earliest middle Miocene and became extinct in the earliest late Miocene. ‘Periptera petiolata’ occurs through the early Miocene to the earliest middle Miocene. ‘Periptera schraderi?’ (see Figs 41, 42, 49) rarely occurs in the early middle Miocene, but its stratigraphic range is not well known because of its rare abundance.

Figs 29–40. Peripteropsis norwegica comb. nov., L.M. Scale bar = 10 μm for each figure. Figs 29–36: Girdle view of frustule. Figs 37–40: Girdle view of epivalve. Figs 29, 30. DSDP Site 338-12-2, 40–41 cm. Figs 31–34, 39, 40. DSDP Site 338-10-2, 80–81 cm. Figs 35, 36. DSDP Site 338-15-4, 100–101 cm. Figs 37, 38. DSDP Site 338-15-1, 30–31 cm.
Suto: Fossil diatom resting spore *Peripteropsis* in the Norwegian Sea
Figs 41–48. LM. Scale bar = 10 μm for each figure. Figs 49–52. SEM. Scale bar = 10 μm for each figure. Figs 41, 42, 50, 51: Girdle view of frustule. Figs 43, 44, 47, 48: Girdle view of hypovalve. Figs 45–46: Valve view of hypovalve. Figs 49, 52: Girdle view of epivalve.

Figs 41, 42. ‘Periptera’ schraderi? DSDP Site 338-8-2, 48–49 cm.
Figs 43–48. ‘Periptera’ petiolata.
Figs 43, 44. DSDP Site 338-14-2, 20–21 cm.
Figs 45, 46. DSDP Site 338-11-4, 70–71 cm.
Figs 47, 48. DSDP Site 338-11-4, 148–149 cm.
Fig. 49. DSDP Site 338-11-4, 148–149 cm.
Fig. 50. Peripteropsis tetracladia. DSDP Site 338-15-2, 100–101 cm.
Figs 51, 52. Peripteropsis norwegica. DSDP Site 338-15-2, 100–101 cm.
Homann (1991) described *Peripteropsis tetracladia* (p. 132, pl. 57, figs 1–3) and *Peripteropsis* sp. (pl. 57, fig. 4) from the Fur Formation, Denmark, in the late Paleocene and early Eocene. These species possess elongated processes at the valve shoulder, but they do not belong to any *Peripteropsis* species described in this study because these are characterized by their central processes, not on the valve shoulder. These taxa occurred from the Paleocene and Eocene deposits; therefore they may be the oldest *Peripteropsis* species. Moreover, Harwood & Gersonde (1990) reported many resting spores, except for *Peripteropsis*, from the lower Cretaceous sediments in the eastern Weddell Sea, east Antarctica.

Each *Peripteropsis* species has its own geographic distribution pattern. *Peripteropsis tetracornus* occurs abundantly in the northwest and northeast Pacific (Suto 2003b) and is also encountered in the Norwegian Sea, although its abundance there is scarce (Table 1). Thus, *P. tetracornus* is probably a cosmopolitan species mainly distributed in the Pacific. *Peripteropsis tetracladia* and *P. norwegica* have been noted only in the North Atlantic, and therefore they may be endemic to this ocean, although available geographic distributional data are very limited at present.

Some species of *Peripteropsis* are biostatigraphically useful in the Norwegian Sea and the North Pacific. Suto (2003b) indicated that the last occurrence of *Peripteropsis tetracornus* (c. 10.3 million years before present) may be a distinct biohorizon and useful for identifying the upper part of the Zone NPD 5C in the North Pacific. *Peripteropsis tetracladia* occurs continuously in the interval from the bottom of the late early Oligocene *Pseudodimerogramma filiformis* Zone through the early middle Miocene Zone NPD 4A, and therefore the species is useful for identifying this interval.

Many detailed descriptions of extant *Chaetoceros* vegetative cells have been published in previous works (e.g. Cupp 1943; Rines & Hargraves 1988; Hasle & Syvertsen 1996). On the other hand, our knowledge on morphologies of their resting spores is limited, mainly because it is difficult to observe in detail in valve view in the case of extant resting spores in their frustule of vegetative cells. Therefore, more detailed studies about extant and fossil resting spores morphology are needed. When the morphologies and combinations between resting spores and vegetative cells are clarified, we can identify the same species of fossil resting spores and extant vegetative cells.

The significant role of *Chaetoceros* in marine primary production and ecology has been known for a very long time (e.g. McQuoid & Hobson 1996; Itakura 2000). The abundance changes of fossil resting spores must be effected by changes in nutrient conditions and/or water-column stratification. Therefore the fossil resting spores abundance changes may indicate the past fluctuations and be used as a paleoecological tool. However, the past ecological influences to resting spores have been neglected because the taxonomies of fossil resting spores are not completed and their ecological information is scant.

It is significant to classify correctly other fossil resting spores in all upwelling regions and several ages and to investigate how old the genus *Chaetoceros* is, in order to understand past productivity and to know the age when circumstances changed to suit initiation and ensuing evolution of this genus. Therefore the establishment of a reliable taxonomy for all fossil resting spores will allow us to detect additional paleoceanographic signals recorded in the fossil resting spore assemblages in upwelling regions.

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