Taxonomy, morphology and ecology of some widespread representatives of the diatom genus *Opephora*

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Opephora parva, O. pacifica and *O. perminuta* are commonly reported from brackish and marine sediments worldwide, but their true identity is unclear. Therefore, isotype material of these three taxa was examined using light microscopy. In addition, several populations from different localities in Europe, Africa, South America and Australasia were investigated with light and scanning electron microscopy. In the isotype slide of *O. parva* and *O. perminuta*, four different opephoroid taxa could be distinguished; three new combinations are proposed. The correct name of *O. parva* is *O. mutabilis* (Grunow) comb. nov.; this is a distinct, valid species, and is usually reported under the later synonym *O. olsenii. O. perminuta* is transferred to the genus *Pseudostaurosira: P. perminuta* (Grunow) comb. nov. The two other taxa were identified as *O. naveana* Le Cohu and *O. guenter-grassii* (Witkowski & Lange-Bertalot) comb. nov., which is transferred from the genus *Fragilaria*. These four taxa were then compared with isotype material of *O. pacifica* (Grunow) Petit. A detailed description of their taxonomy, morphology and ecology is given. Although *Opephora mutabilis, O. naveana* and *O. guenter-grassii* differ in some respects from *O. pacifica*, the type of the genus, their maintenance in this genus is recommended subject to further research.

Key words: Ecology, morphology, *Opephora, Pseudostaurosira,* taxonomy.

Introduction

Marine and estuarine sediments often harbour dense populations of araphid, opephoroid (i.e. heteropolar) diatoms. In most studies these are referred to as belonging to the genera *Opephora* Petit and *Fragilaria* Lyngbye; some commonly used names and some examples of their use in the literature are listed in Table 1. New taxa (e.g. *Fragilaria gedanensis* Witkowski and *F. guenter-grassii* Witkowski & Lange-Bertalot) have recently been added to this list, while the establishment of new genera (e.g. *Martyana* Round, *Pseudostaurosira* Williams & Round and *Staurosirella* Williams & Round) has augmented the number of synonyms, most of which are still commonly used (cf. Krammer & Lange-Bertalot, 1986–91). However, when comparing descriptions and illustrations it appears that considerable confusion exists over the true nature of these taxa [e.g. compare *O. pacifica sensu* Navarro (1982) and *sensu* Sullivan (1979)]. Moreover, it is suspected (Sundbäck, 1987; Le Cohu, 1988; Lange-Bertalot, 1989) that some of these taxa are synonymous or at least overlapping. This confusion renders detailed ecological and biogeographical comparisons between different areas difficult or even impossible.

While examining intertidal sediment samples from the Westerschelde estuary (The Netherlands), we regularly encountered small, opephoroid diatoms which were provisionally identified as *O. parva* and *O. perminuta.* Although these taxa are commonly reported from diverse marine and brackish habitats, they have, to our knowledge, never been studied in detail. The aim of this study is to establish the identity of *O. parva* and *O. perminuta* and their relationship to the type of the genus (i.e. *O. pacifica*) and other similar, opephoroid taxa.

Materials and methods

In 1992, surface sediment samples were collected at monthly intervals from about 30 intertidal stations in the Westerschelde estuary (The Netherlands). The samples were fixed with formalin (4%). In November 1993, sediment samples were taken in a similar manner at one intertidal station in the Hopkins estuary (Victoria, Australia). The samples were treated with nitric (70%) and sulphuric acid (99%) and gently heated for 30 min. This quite drastic preparation method proved necessary to ensure sufficiently clean material for scanning electron microscopy (SEM). Cleaned material was mounted for light microscopy (LM) in Naphrax and examined using a Leitz Diaplan microscope with differential interference contrast (DIC) optics. SEM examination was performed with a Jeol JSM-840 at 15 kV. Live and fixed material was examined for information on plastid structure, colony formation and micro-habitat.

The herbarium material examined is listed in Table 2. As the holotypes of *O. parva* and *O. perminuta* from the Vienna Herbarium (**W**) were not available for study at the

Table 1. List of the most commonly used names for araphid, opephoroid diatoms from brackish and marine sediments and some examples of their use in the literature

Opephora marina (Gregory) Petit	Frenguelli, 1938; Rincé, 1990
O. marina var. *minuta* Cleve-Euler	Cleve-Euler, 1953; Denys, 1991; Juggins, 1992
O. martyi Héribaud	Sundbäck, 1983; Juggins, 1992
O. olsenii Möller	Hendey, 1964; John, 1983; Poulin *et al.*, 1984; Podzorski & Håkansson, 1987; Sundbäck, 1987; Wendker, 1990; Denys, 1991; Witkowski, 1991; Gätje, 1992
O. pacifica (Grunow) Petit	Hustedt, 1931–59; Cholnoky, 1963; Navarro, 1982; De Jonge, 1985; Rincé, 1990; Vos & De Wolf, 1993
O. parva (Grunow) Krasske	Salah, 1953; Giffen, 1976; Hartley, 1986; Vos, 1986; Denys, 1991; Sabbe & Vyverman, 1991; Vos & De Wolf, 1993
O. perminuta (Grunow) Frenguelli	Frenguelli, 1938; Rincé, 1990; Sabbe, 1993
Fragilaria construens (Ehrenberg) Grunow var. *subsalina* Hustedt	Poulin *et al.*, 1984; Rincé, 1990
F. construens var. *venter* (Ehrenberg) Grunow	Poulin *et al.*, 1984; Rincé, 1990; Vos & De Wolf, 1993
F. elliptica Schumann	Archibald, 1983; Poulin *et al.*, 1984
F. pinnata Ehrenberg	Vyverman & Coppejans, 1987; Rincé, 1990

time of writing, isotype material on the Cleve & Möller slide no. 255 from the Van Heurck Diatom Collection (**AWH**) was studied. Material from the Krasske Collection (**KASSEL**) was unavailable due to temporary closure of the museum where the collection is held.

Frustule dimensions (length, width and stria density) were determined on all material; for comparative reasons all measurements were kept separate for each locality. For each dimension the minimum and maximum values are given, whilst the average value and the standard deviation are given in brackets.

Multivariate analysis techniques (principal components analysis and redundancy analysis: cf. Jongman *et al.*, 1987) were applied to the Westerschelde dataset to assess the environmental preferences of the species studied. This dataset concerns the absolute abundance values of diatom species in 360 sediment samples (30 stations sampled monthly during 1 year) from the Westerschelde estuary.

The use of published data on the biogeography of the described species was restricted to those that providing illustrations which allow unambiguous identification.

Historical background

VanLandingham (1967–79)[and to our knowledge most other authors since Peragallo & Peragallo (1897–1908)] referred to *Sceptroneis marina* var. ?? *parva* Grunow and *S.* ? *marina* var. ?? *perminuta* Grunow (Van Heurck, 1881) as the first records of *O. parva* and *O. perminuta*. The descriptions of these taxa in Van Heurck (1881) consist of some illustrations (pl. XLV, figs 18–20 and 36 respectively) and the accompanying legends, which mention the stria density (9–10 and 15 in 10 μm respectively) of both taxa and the fact that they occur together in the same locality (Hourdel, France). Both taxa were also described in Peragallo & Peragallo (1897–1908), where reference is made to the same locality, Hourdel, and to a slide (no. 155, Cleve & Möller). In the Van Heurck Diatom Collection we found a Cleve & Möller slide labelled Hourdel (no. 255) which contained the two taxa. We consider this slide an isotype, while the corresponding Cleve & Möller slide no. 255 in the Grunow Diatom Collection in Vienna carries the holotypes of both taxa.

However, 2 years before the descriptions in Van Heurck (1881), a list (made by Grunow) of the diatom species on slide no. 255 ('Hourdel, embouchure de la Somme') was published in Cleve & Möller's *Diatoms* (part V (1879), Cleve & Möller, 1877–82). This list contains the following entry: '*Sceptroneis* (*marina* var. ?) *mutabilis* Grunow (*Fragilaria mut.* form. 10 str. in 0·01 mm) common. var. *minuta* Grunow. 15 str. in 0·01 mm'. As the descriptions in Van Heurck (1881) and Cleve & Möller

Table 2. Herbarium slides examined

Material	Herbarium reference
Cleve *et* Möller slide no. 255, Hourdel (France)	**AWH** no. II 9 A12
Frenguelli 379 no. 5, Cabo Guardian, Santa Cruz (Argentina)	**UNLP**
Frenguelli 388 no. 3, Riacho San Blas (Argentina)	**UNLP**
Grunow slide no. 790, Kalkbay, Cape Town (South Africa)	**AWH** no. VI 41 B10
Van Heurck, Types du Synopsis, no. 280, Ile de Mors (Denmark)	**BR**
Salah's material from Blakeney Point, Norfolk (Great Britain)	**BM** 36399–36402 and 36405–36407
Hustedt's material from Miang Besar (Borneo)	**BRM** N 15/51

AWH, Van Heurck Diatom Collection, Antwerp (Belgium); **UNLP**, Collection of the Divisíon Ficología de la Facultad de Ciencias Naturales y Museo de la Universidad Nacional de La Plata (Argentina); **BR**, National Botanical Garden, Meise (Belgium); **BM**, Natural History Museum, London (Great Britain); **BRM**, Friedrich-Hustedt-Arbeidsplatz für Diatomeenkunde,Bremerhaven (Germany).

(1879) correspond to each other and no other opephoroid diatoms were mentioned in the species list of slide no. 255, the entries in both works must refer to the same taxa. However, the entries in Cleve & Möller (1879) represent the oldest legitimate names and therefore have priority. They are also reported in VanLandingham (1978) ['*Sceptroneis mutabilis* Grunow in Cleve & Möller 1881, no. 255 (*marina* var. ?)] and '*S. mutabilis* var. *minuta* Grunow in Cleve & Möller 1881, no. 255 (*marina* var. ?)], though for reasons unknown to the authors their use is not recommended. Moreover, the connection between the descriptions in Cleve & Möller (1879) and Van Heurck (1881) was not made. Peragallo & Peragallo (1897–1908) also mentioned *Sceptroneis mutabilis* Grunow ?? as a possible (note the question marks) synonym of *Grunoviella parva* (Grunow) Peragallo & Peragallo (syn. *Sceptroneis marina* var. *parva*).

In Van Heurck (1881), Grunow placed both taxa as varieties of *Sceptroneis marina* (although with some reserve: notice the question marks in *S. marina* ?? var. *parva* and *S.* ? *marina* var. ?? *perminuta*) because of their resemblance to *S. marina* (Gregory) Lagerstedt (now *Opephora marina* (Gregory) Petit). He also changed the epithet *minuta* to *perminuta*.

Peragallo & Peragallo (1897–1908) transferred *S. marina* var. ?? *parva* and *S.* ? *marina* var. ?? *perminuta* to the genus *Grunoviella* and raised them to specific rank (*G. parva* (Grunow) Peragallo & Peragallo and *G. perminuta* (Grunow) Peragallo & Peragallo). Besides *S. marina* var. ?? *parva*, *Fragilaria mutabilis* var. ? *cuneata* and *S. mutabilis* ?? are given as synonyms.

Finally, Frenguelli (1938) transferred *G. perminuta* to the genus *Opephora* (*O. perminuta* (Grunow) Frenguelli, while Krasske (1939) did the same for *G. parva* (*O. parva* (Grunow) Krasske). VanLandingham (1967–79), however, does not recommend the use of the latter combination.

Observations

Thorough examination of Cleve & Möller slide no. 255 revealed the presence of four different, opephoroid taxa. All four could be related to taxa which have been observed in recent material from the Westerschelde estuary, making SEM examination of these taxa possible. One taxon could easily be identified as *S. mutabilis* var. *minuta* from the description and illustrations by Grunow (Van Heurck, 1881). It has a lanceolate axial area, while the nominate variety has a linear one. LM identification of the other three taxa was more problematic. Due to their small size and overlapping size range and stria density, Grunow seems to have regarded them as one species (*S. mutabilis*). However, differential interference contrast and especially SEM observations made it possible to distinguish three different taxa. One of these, which corresponds most closely to the original description of Grunow, is regarded as good *S. mutabilis*. The other two were recently described as new species, viz. *Fragilaria guenter-grassii* and *Opephora naveana* Le Cohu. Three new combinations are now proposed. In addition, a detailed description of the isotype material of *Opephora pacifica* is provided for comparison.

Pseudostaurosira perminuta **(Grunow) Sabbe & Vyverman comb. nov.**

Basionym: *Sceptroneis* ? *marina* var. ?? *perminuta* Grunow *in* Van Heurck 1881: *Synopsis des Diatomées de Belgique* (1880–5). Atlas, pl. 45, fig. 36.

Type: Holotype, **W**, *non vidi*; isotype, **AWH** slide no. II 9 A12 (Cleve & Möller slide no. 255).

Synonyms: *Sceptroneis mutabilis* var. *minuta* Grunow (*marina* var. ?) *in* Cleve & Möller 1879, fasc. 5:4. *Grunoviella perminuta* (Grunow) Peragallo & Peragallo 1897–1908, p. 327. *Opephora perminuta* (Grunow) Frenguelli 1938, p. 317. *Fragilaria neoelliptica* Witkowski 1994, p. 128. (?) *Fragilaria construens* var. *subsalina* Hustedt 1925, p. 106 (cf. Krammer & Lange-Bertalot 1986–91).

Material examined: **AWH** slide no. II 9 A12 (Cleve & Möller slide no. 255 – Hourdel, Somme estuary), **BM** slides 36399, 36401, 36402, 36405–36407 (Salah's material from Blakeney Point, Norfolk, England), sediment samples from the Westerschelde estuary (The Netherlands).

Type locality: Hourdel (France), 'embouchure de la Somme'.

Other reports: (?) Poulin *et al.* (1984), as *F. elliptica*. (?) Wasell & Håkansson (1992, figs 110–115), as *Fragilaria* spp.

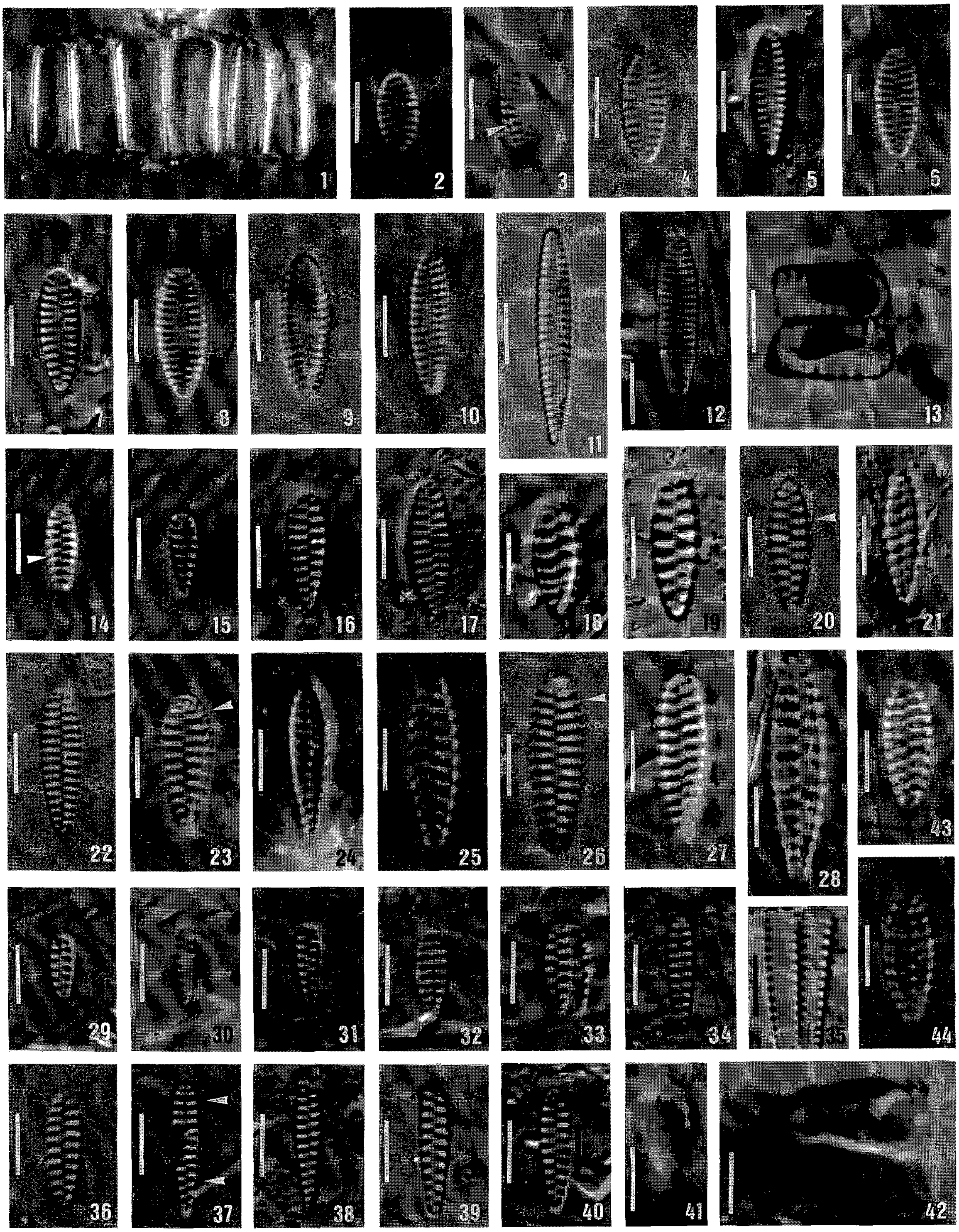
Morphology (dimensions): Westerschelde: L, 6·2–16·2 μm (10·4±2·7); W, 2·2–4·1 μm (3·0±0·5); 14–18 striae/10 μm (16·0±0·8)($n = 30$). Somme (Hourdel): L, 5·6–17·5 μm(10·6±3·1); W, 2·5–4·1 μm (3·6±03); 15–18 striae/10 μm (16·7±0·7)($n = 30$). Blakeney Point: L, 7·2–16·2 μm (11·6±2·4); W, 2·2–4·4 μm (3·2±0·7); 14–17 striae/10μm (15·7±0·9)($n = 10$).

Light microscopy

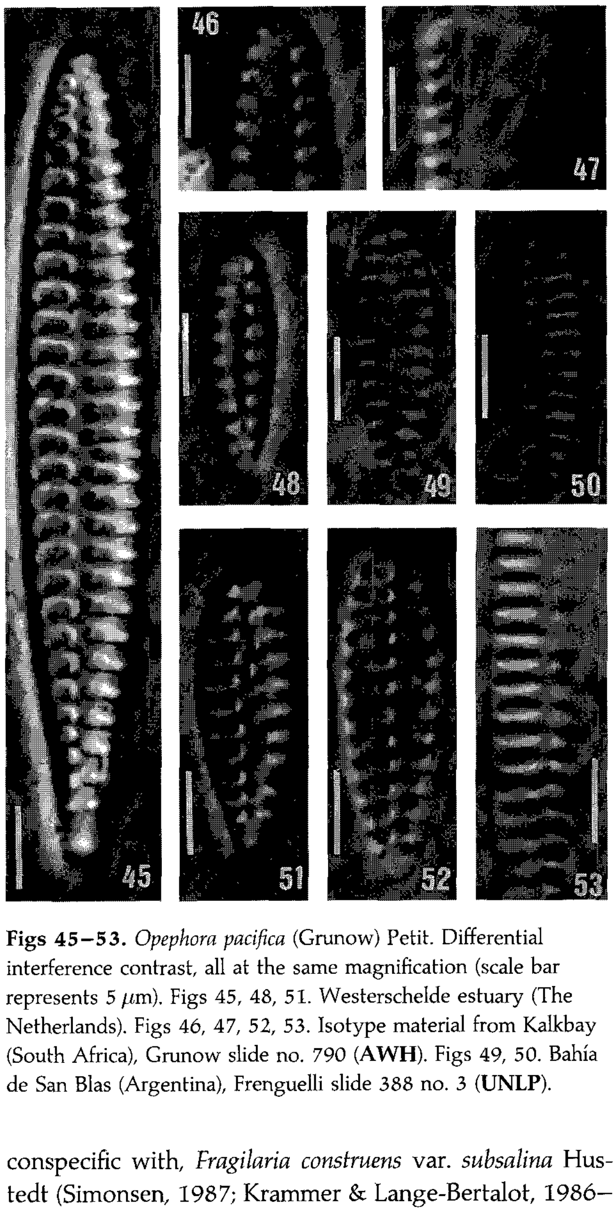
Only solitary valves were found on the type slide. In samples from the Westerschelde estuary, small colonies consisting of 2–6 cells were present (Fig. 1). The plastid structure is unknown. The valves are usually more or less heteropolar (ovate to clavate) (Figs 5–11), rarely isopolar (elliptic) (Figs 2, 4). The valve ends are rounded to cuneate. In girdle view, the frustules are rectangular, 3·1–6·2 μm broad (Fig. 1). The striae are parallel to slightly radiate in the centre, becoming more radiate at the apices; they are usually more or less alternate. The average stria density matches the original description (15 striae/10 μm) in Cleve & Möller (1879) and is almost identical to that in the original illustration of this species in Van Heurck (1881), where 16 striae can be counted in 10 μm. The shape of the axial area is quite variable, narrowly to broadly lanceolate, often occupying almost half the valve width. Moreover, because of the variable length of the striae (within one valve), the axial area is usually irregular (e.g. Figs 8, 10). In some specimens, the striae appear to be interrupted by a prominent, marginal ring of spines (Figs 3, 9, 11). Teratological forms were quite common (Fig. 12).

Scanning electron microscopy

The valve face is flat with a gradual transition to the mantle. In most specimens, a prominent ring of simple spines is present on the margin of the valve face, invariably interrupting the striae [on the vimines (cf.



Cox & Ross, 1980)] (Figs 54–57, 59). They are sometimes more or less spathulate, though shape can be quite variable, even within one frustule (Fig. 55). The spines are accompanied by smaller granules on both sides of the marginal ring of spines (Figs 54–57, 59). The striae comprise circular to elliptical areolae (about 45–60 in 10 μm), which diminish in size away from the valve face margin. The areolae are occluded internally by a velum of the volate type (Figs 58, 60). Externally, a small rib (by which the vola is probably attached to the areolar wall, cf. Fig. 56) is sometimes visible. In most specimens, however, these structures are lost. Apical pore fields are present at both apices. The foot pole field is usually larger and more regular, consisting of a few rows of poroids, often separated by a wavy ridge (Fig. 57). No rimoportulae are present. The cingulum consists of several (up to 10) open, ligulate copulae, which are curved at the apices (Figs 55, 56). The valvocopula is wide.



Figs 45–53. *Opephora pacifica* (Grunow) Petit. Differential interference contrast, all at the same magnification (scale bar represents 5 μm). Figs 45, 48, 51. Westerschelde estuary (The Netherlands). Figs 46, 47, 52, 53. Isotype material from Kalkbay (South Africa), Grunow slide no. 790 (**AWH**). Figs 49, 50. Bahía de San Blas (Argentina), Frenguelli slide 388 no. 3 (**UNLP**).

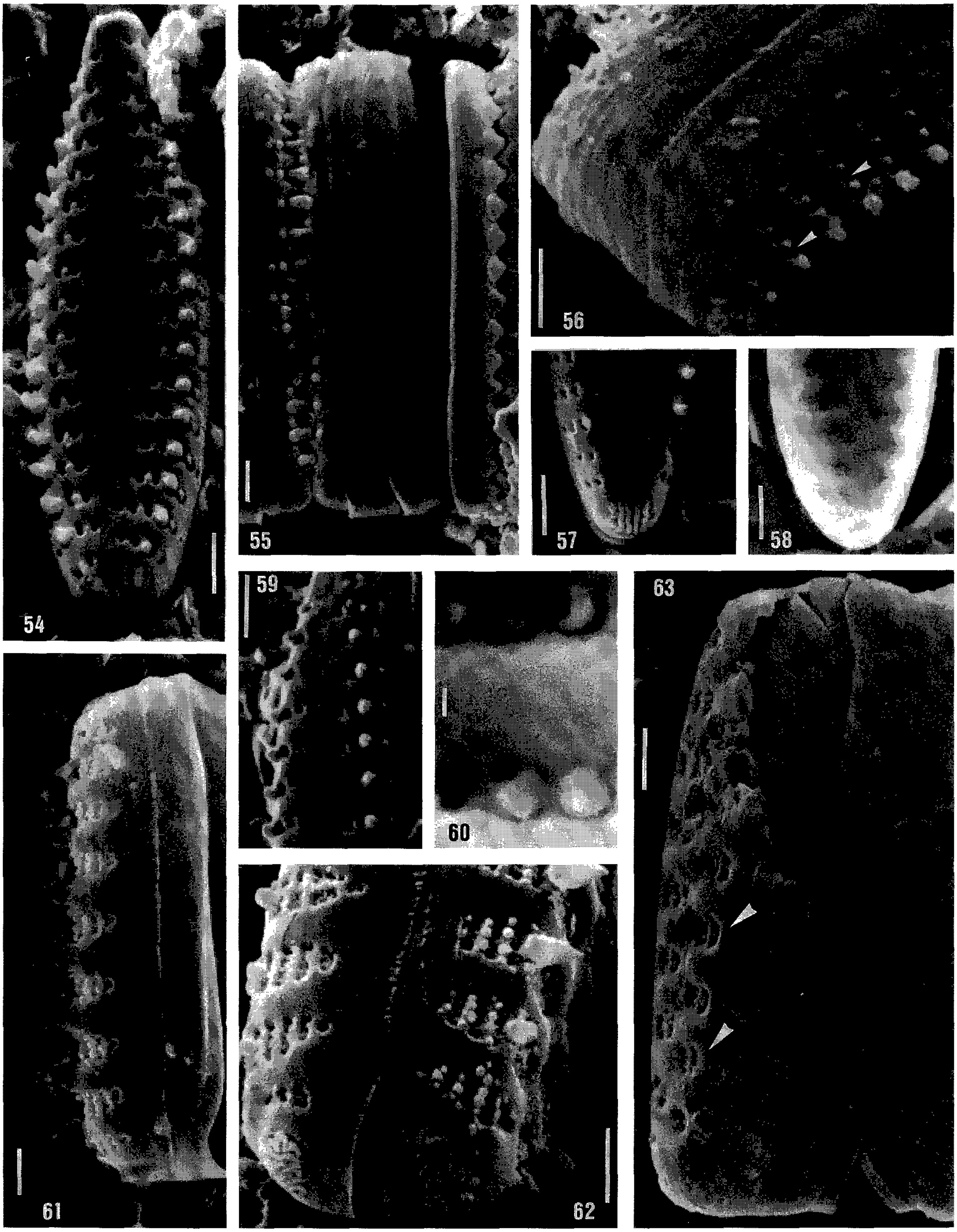
Remarks

Pseudostaurosira perminuta shows some resemblance to *Staurosira elliptica* (Schuman) Williams & Round (syn. *Fragilaria elliptica*). The true identity of the latter is unclear however (Hustedt, 1931–59; Williams & Round, 1987), as SEM examination of the type material has not been done (cf. Krammer & Lange-Bertalot, 1986–91). We agree with Krammer & Lange-Bertalot (1986–91) that specimens of *S. elliptica* described by Haworth (1975) are more closely related to *Staurosira construens* Ehrenberg (syn. *Fragilaria construens* (Ehrenberg) Grunow). They differ from *S. elliptica sensu* Archibald (1983), *sensu* Poulin *et al.* (1984) and *sensu* Krammer & Lange-Bertalot (1986–91). *Pseudostaurosira perminuta* differs from Haworth's specimens in having additional granules, in the constant position of the intercostal spines and the variable shape of the axial area and valve (usually more opephoroid). The main points of difference in the descriptions of Archibald (1983) and Poulin *et al.* (1984) are the granules and the presence of several areolae below the ring of spines. The specimens described by Krammer & Lange-Bertalot (1986–91) have much more coarsely punctate striae.

P. perminuta also resembles, and could possibly be conspecific with, *Fragilaria construens* var. *subsalina* Hustedt (Simonsen, 1987; Krammer & Lange-Bertalot, 1986–91). As no SEM study of the type material of the latter has been done yet (Krammer & Lange-Bertalot, 1986–91) and no data are available on its morphological variability, we prefer to maintain them as two taxa. *S. elliptica sensu* Polin *et al.* (1984) shows a great resemblance to *F. construens* var. *subsalina*.

Finally, *Pseudostaurosira perminuta* shows great affinity

Figs 1–44. *Pseudostaurosira perminuta* (Grunow) Sabbe & Vyverman comb. nov. and *Opephora* spp. from different populations, showing variation in valve outline. Differential interference contrast, all at the same magnification (scale bar represents 5 μm). Figs 1, 3, 5, 13, 16, 17, 19, 24, 31, 34, 35, 37–39, 41–43. Westerschelde estuary (The Netherlands). Figs 2, 4, 6, 8–12, 14, 15, 20, 22, 23, 25, 26, 36, 44. Hourdel (France), Cleve & Möller slide no. 255 (**AWH**). Figs 7, 18, 28, 29, 32, 40. Blakeney Point (England), **BM** slides 36401, 36399 and 36402. Figs 21, 27, 33. Hopkins estuary (Australia). Fig. 30. Bahía de San Blas (Argentina), Frenguelli slide 388 no. 3 (**UNLP**). Figs 1–12. *Pseudostaurosira perminuta* (Grunow) Sabbe & Vyverman comb.nov. (Figs 2, 4, 6 and 8–12 are isotype material). Fig. 1. Ribbon-like colony in girdle view. Figs 2–12. Valve views. Note the arrowhead in Fig. 3 indicating the marginal ring of spines. The valve in Fig. 12 is a teratological form. Figs 13–28. *Opephora mutabilis* (Grunow) Sabbe & Vyverman comb. nov. (Figs 14, 15, 20, 22, 23, 25 and 26 are isotype material). Fig. 13. Bengal rose-stained material; small ribbon-like colony in girdle view. Figs 14–28. Valve views. The arrowheads indicate the marginal ring of spines. Figs 29–42. *Opephora guenter-grassii* (Witkowski & Lange-Bertalot) Sabbe & Vyverman comb. nov. Figs 29–34, 36–40. Valve views. Arrowheads in Fig. 37 show the two different striation patterns (opposite and alternate) within one valve. Fig. 35. Girdle view. Figs 41, 42. Stalked, living cells in valve (Fig. 41) and girdle view (Fig. 42). Note the cuneate shape of the cell in girdle view and the bilobed shape of the plastid in Fig. 42. Figs 43, 44. *Opephora naveana* Le Cohu. Valve views.



Figs 54–60. *Pseudostaurosira perminuta* (Grunow) Sabbe & Vyverman comb. nov. Samples from the Westerschelde estuary (The Netherlands). Scale bar represents 1 μm (except in Fig. 60 where it represents 100 nm). Figs 54, 57, 59. External valve views. Note the prominent ring of spines and the smaller, accompanying spines. Fig. 57 shows the prominent foot pole pore field. Figs 55, 56. Girdle view. Arrowheads indicate a small rib by which the volae are attached to the areolar wall). Note the different spine sizes and shapes within one frustule in Fig. 55. Figs 58, 60. Internal valve views showing the areolar occlusions of the volate type. **Figs 61–63.** *Opephora mutabilis* (Grunow) Sabbe & Vyverman comb.nov. Samples from the Westerschelde estuary (The Netherlands). Scale bar represents 1 μm. External girdle views, showing the marginal ring of spines (missing in Fig. 63) and the prominent marginal crossbar (arrowheads in Fig. 63).

with *P. zeilleri* (Héribaud) Williams & Round (syn. *Fragilaria zeilleri* Héribaud) and its varieties in several respects [cf. type material descriptions in Serieyssol (1988)], viz: the structure of the internal areolar occlusions, the variable shape of the axial area [cf. *F. zeilleri* var. *elliptica* Gasse (Gasse, 1980)], the presence of several areolae below the marginal ring of spines (only *F. zeilleri* var. *nitzschioides* Héribaud; Serieyssol, 1988). The main differences are the presence of the granules and a higher stria density in *P. perminuta.*

Opephora mutabilis (Grunow) Sabbe & Vyverman comb. nov.

Basionym: *Sceptroneis mutabilis* Grunow (*marina* var?) in Cleve & Möller 1879: Diatoms (1877–1882), Part 5, no. 255.

Type: Holotype, **W**, *non vidi*; isotype **AWH** slide no. II 9 A12 (Cleve & Möller slide no. 255).

Synonyms: *Sceptroneis marina* var ?? *parva* Grunow in Van Heurck 1881, pl. 45, fig. 36. *Grunoviella parva* (Grunow) Peragallo & Peragallo 1897–1908, p. 327. *Opephora parva* (Grunow) Krasske 1939, p. 359. *O. olsenii* Møller 1950, p. 197. (?) *O. horstiana* Witkowski 1994, p. 173.

Material examined: **AWH** slide no II 9A12 (Cleve & Möller slide no. 255 – Hourdel, Somme estuary), **BM** slides 36399, 36401, 36405–36407 (Salah's material from Blakeney Point, Norfolk, England), **BRM** slide N 15/51 (Miang Besar, Borneo 4), sediment samples from the Westerschelde (The Netherlands) and Hopkins (Victoria, Australia) estuaries.

Type locality: Hourdel (France), 'embouchure de la Somme'.

Other reports: numerous, mainly as *O. olsenii* (cf. Introduction).

Morphology (dimensions): Westerschelde: L, 3·7–19·4 μm (10·4±3·2); W, 2·5–5·0 μm (3·2±0·6); 8–16 striae/10 μm (10·2±2·1)($n=39$). Somme (Hourdel): L, 7·6–18·1 μm (13·0±2·6); W, 3·1–5·0 μm (4·1±0·6); 9–13 striae/10 μm (10·9±1·0)($n=30$). Blakeney Point: L, 7·0–11·5 μm (9·1±1·9); W, 2·5–5·0 μm (3·6±1·2); 9–14 striae/10 μm (11·2±2·5)($n=4$). Hopkins: L, 7·7–18·1 μm (13·4±2·8); W, 2·5–3·7 μm (3·3±0·4); 9–14 striae/10 μm (11·9±1·8)($n=18$).

Light microscopy

The isotype slide contains only solitary valves whereas small, ribbon-like colonies (of 2 to several cells) were present in the Westerschelde material. In girdle view, the frustules are rectangular (Fig. 13). The plastid structure was not observed. The valves are always heteropolar (ovate to clavate). The axial area is usually very narrow, occasionally slightly lanceolate (Fig. 26). The valvar ends are rounded to cuneate (at the footpole only). The striae are coarse, parallel at the centre, parallel to convergent at the poles, and usually alternate throughout the valve. In larger specimens, the striae appear to be clearly cross-lineolate (Figs 18–21, 23, 25, 28). Most valves have a distinct longitudinal ring of spines along the valve margin (Figs 14, 15, 18, 20, 21, 23–26, 28).

Scanning electron microscopy

A thorough SEM description of this species (as *O. olsenii*), which closely fits the specimens observed in this study, is given by Sundbäck (1987). Some typical specimens from the Westerschelde and Hopkins estuaries are illustrated in Figs 61–65.

Remarks

The average dimensions for each locality compare well and match the description of this species by Sundbäck (1987), except that the maximum stria density values are higher (up to 16 striae in 10 μm) in our measurements. Although different opephoroid taxa were present on the isotype slide, the population illustrated in Figs 14, 15, 20, 22, 23, 25 and 26 was selected as the isotype of *O. mutabilis* because of its close match with the description (9 or 10 striae in 10 μm) and illustrations of *S. marina* var. ?? *parva* in Van Heurck (1881). In original editions of this work, the illustrations show a more or less distinct areolar substructure (cross-lineolation?). However, the marginal ring of spines is not illustrated in the original drawings.

Opephora guenter-grassii (Witkowski & Lange-Bertalot) Sabbe & Vyverman comb. nov.

Basionym: *Fragilaria guenter-grassii* Witkowski & Lange-Bertalot 1993: *Limnologica* 23 (1), p. 65, figs 5a-h.

Type: Holotype slide no. P3 (A, V.92), Institute of Oceanography, University of Gdańsk, Gdynia, Poland.

Material examined: **AWH** slide no. II 9 A12 (Cleve & Möller slide no. 255 – Hourdel, Somme estuary), **BM** slides 36399, 36400–36402, 36405–36407 (Salah's material from Blakeney Point, Norfolk, England), **BRM** slide N 15/51 (Miang Besar, Borneo 4), **UNLP** slide 388 No. 3 (Riacho San Blas, MacDonagh, Argentina), sediment samples from the Westerschelde (The Netherlands) and Hopkins (Victoria, Australia) estuaries.

Type locality: Puck Bay (Zatoka Pucka), Poland.

Other reports: Kuylenstierna (1989–90, fig. 240), as *O.* sp. Navarro (1982, pl. 12, fig. 8), as *O. pacifica*. Rincé (1990, fig. 10), as *O. perminuta*. Salah (1953), as *O. parva.* (?) Frenguelli (1938) as *O. perminuta*.

Morphology (dimensions): Westerschelde: L, 3·7–20 μm (8·7±2·9);W, 1·8–3·1 μm (2·3±0·3); 12–16 striae/10 μm (13·7±1·1)($n=68$). Somme (Hourdel): L, 7·5–13·7 μm (10·6±1·7); W, 2·5–3·7 μm (3·0±0·5); 12–16 striae/10 μm (13·6±1·0)(n = 28). Blakeney Point: L, 4·7–12·5 μm (8·7±2·0); W, 1·6–3·1 μm (2·4±0·3); 12–17 striae/10 μm (13·5±1·5)(n = 32). Hopkins: L, 5·1–8·7 μm (7·3±1·4); B, 1·9–2·5 μm (2·3±0·3); 12-14 striae/10 μm (13·2±0·8)(n = 5).

Light microscopy

In living material, one large plastid, which appears bilobed in girdle view, can be observed (Figs 41, 42). The cells are either solitary or form short radiating or chain-like colonies (in which the cells are attached to each other at their apices). The valves are usually heteropolar, the ends rounded to cuneate (Figs 29–40). In girdle view, the frustules are 2·2–5·9 μm wide and more or less cuneate. The shape of the axial area is variable, ranging from linear (Fig. 40) to narrowly lanceolate (Fig. 36). The striae are parallel at the centre, parallel to convergent at the poles; their arrangement is usually alternate, although valves with opposite striae or a mixed striation pattern could also be observed (Figs 32, 34, 37). They are not visibly cross-lineolate and are not crossed by a marginal longitudinal crossbar.

Scanning electron microscopy

The valve face is flat to rounded, gradually sloping into the mantle. Interlocking spines were never observed (Figs 66, 67, 70, 71). The striae consist of elongated areolae which, both internally (Figs 68, 69) and externally (Figs 70, 71), are crossed by a more or less complex network of narrow ribs (often eroded, cf. Fig. 67) which seem to protrude from the vimines (Figs 67, 69). Apical pore fields are present at both poles, the one at the foot pole usually being more developed (Fig. 67). No rimoportulae are present. The structure of the cingulum is not very clear: it seems to be composed of at least 4 copulae (Fig. 71).

Remarks

Our specimens have a larger size range than the holotype specimens described by Witkowski & Lange-Bertalot (1993)(namely 3·7–20 μm versus 4·5–7 μm respectively) and are usually heteropolar in valve view (cf. Witkowski & Lange-Bertalot (1993), more often elliptic). The latter may be a size-related effect, comparable to those reported by e.g. Geitler (1932), Tropper (1975) and Cox (1993) for other diatom taxa. The 9–12 striae/10 μm given in the type description (Witkowski & Lange-Bertalot, 1993) does not correspond with that of the illustrated type specimens (about 12–14 striae/10 μm), which is closer to our observations.

This species was originally described as a *Fragilaria* species because it does not possess a marginal rib or spines (Witkowski & Lange-Bertalot, 1993). However, these two features are not typical for the genus *Opephora* (as asserted in the type description of *Fragilaria guenter-grassii*), and their absence cannot be a sound basis for the exclusion of *O. guenter-grassii* from *Opephora*.

This species seems to be closely related to *Opephora mutabilis*, from which it differs in size and stria density (although there is a considerable overlap between the two species, the average values for all localities are consistently and distinctly different), in the absence of a longitudinal, marginal crossbar and spines, in the width of the sternum (which tends to be broader in *O. guenter-grassii*), in the arrangement of the striae (sometimes totally or partly opposite: Figs 32, 34, 37) and in habit (no ribbon-like colony-formation, probably due to the lack of spines).

In the LM this species can easily be confused with the recently described species *Fragilaria gedanensis* Witkowski (cf. Witkowski, 1993; Witkowski & Lange-Bertalot, 1993). According to the type description (Witkowski, 1993) this species always has opposite (or slightly alternating) striae. However, the taxonomic value of this feature is uncertain as frustules were found in the Westerschelde material with a mixed striation pattern on a single valve. The ultrastructure of the striae is not clearly defined. In some specimens (cf. Witkowski, 1993, fig. 18) the striae are very like those of *O. guenter-grassii*, while in other specimens the striation pattern resembles that of *F. atomus* Hustedt (syn. *Martyana atomus* Snoeijs), which is sometimes biseriate over part of the valve (cf. Witkowski & Lange-Bertalot, 1993, fig. 2j; Snoeijs *et al.*, 1991, figs 12 and 17). The occurrence of a similar phenomenon (i.e. a locally aberrant striation within one valve) prompted Lange-Bertalot (1989, 1993) to reject the new genus *Punctastriata* Williams & Round. The taxonomic significance of such characteristics clearly needs further investigation.

***Opephora naveana* Le Cohu 1988**

Type: Coll. R. Le Cohu, Kerguelen, Lac des Sternes no. 7 (**PC**).

Synonym: *Fragilaria opephoroides* Takano 1988, p. 36, *nomen nudum* (this entry is not a real synonym as the name was not validly published).

Material examined: **AWH** slide no. II 9 A12 (Cleve & Möller slide no. 255 – Hourdel, Somme estuary), sediment samples from the Westerschelde (The Netherlands) and Hopkins (Victoria, Australia) estuaries.

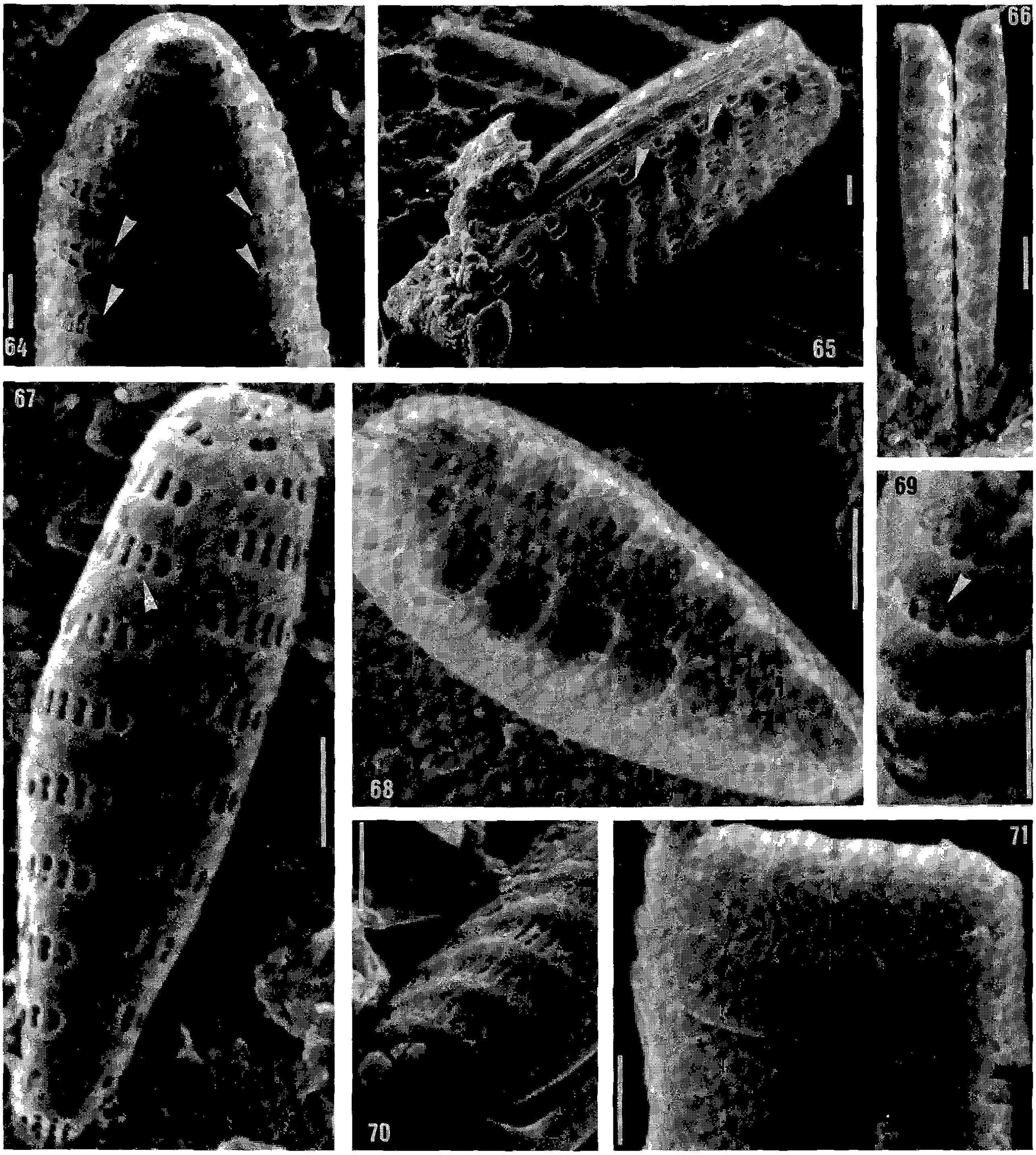
Type locality: Iles Kerguelen, Lac des Sternes.

Other reports: (?) Witkowski (1994, pl. 12, fig. 10), as *Opephora* sp. 1.

Morphology (dimensions): Westerschelde: L, 7·5–12·2 μm (9·5±1·8); W, 2·7–3·7 μm (3·1±0·3); 13–15 striae/10 μm (13·4±0·7)(n = 7).

Light microscopy

The LM features of this species are very similar to those of *Opephora mutabilis*, from which it can be distinguished



Figs 64, 65 *Opephora mutabilis* (Grunow) Sabbe & Vyverman comb. nov. Scale bar represents 1 μm. Fig. 64. Internal valve view, showing the marginal crossbar (arrowheads). Westerschelde estuary (The Netherlands). Fig. 65. External valve view, showing the marginal crossbar (arrowheads). Hopkins estuary (Australia). **Figs 66–71.** *Opephora guenter-grassii* (Witkowski & Lange-Bertalot) Sabbe & Vyverman comb nov. Scale bar represents 1 μm. Westerschelde estuary (The Netherlands). Figs 66, 71. External girdle view. Note the absence of the spines and the marginal crossbar. Figs 67, 70. External valve views. The areolar occlusions in Fig. 67 have probably disappeared because of the acid treatment; the arrowhead indicates the small ribs protruding from the vimines. Figs 68, 69. Internal valve views. Note again the distinct absence of the marginal crossbar. Arrowhead shows the small ribs protruding from the vimines in Fig. 69 (cf. also Fig. 67).

only by its more robust appearance, the number of striae (on average higher in *O. naveana*) and the (often indistinguishable) alveolar nature of the striae (Figs 4, 44).

Scanning electron microscopy

The valve face is flat and clearly separated (often at an angle of almost 90°) from the mantle by a prominent, longitudinal bar (Figs 73, 75–79). Simple spines are present on this bar interrupting the striae (Figs 77–79), though in most specimens they seem to disappear. The striae are composed of at least 2 large alveoli (Figs 73–79), one on the valve face and one (rarely 2, cf. Fig. 75) on the mantle. The striae are sunk below the level of the virgae (cf. Cox & Ross, 1981) externally, internally and are always alternate. The sternum is linear to slightly lanceolate. The alveoli are occluded by a complex, flat cribrum (Figs 73–78) which seems to be composed of densely intertangled volae, sometimes connected to the alveolar wall by a few small ribs (Figs 77, 78). In a specimen from the Braakman (a land-locked creek off the Westerschelde estuary) these ribs are more numerous (Fig. 77). Two apical pore fields are present; that at the foot pole is larger. The pore field at the head pole is often situated on the mantle (Fig. 75). The cingulum is composed of at least 6 open copulae (Fig. 75).

Remarks

Some specimens (Figs 77, 78) clearly belong to *Opephora naveana*. The structure of the cribra with the numerous small ribs protruding from the alveolar walls, bending inwards and ending blindly in the alveoli is an unmistakable feature of this species (cf. Le Cohu, 1988; Takano, 1988). The identity of the majority of the Westerschelde specimens is, however, more problematic. They differ slightly from the type description (Le Cohu, 1988) in the structure of the cribra, which lack the small ribs.

This species is probably closely related to *O. mutabilis*. In the LM, it is often hard to distinguish *O. naveana* from the smaller and more delicate specimens of *O. mutabilis*. The main distinguishing feature between the two species is an electron microscopical one: only the stria structure (no cross-lineolation, different areolar occlusions) can be used to make a positive identification of the two species. Both possess 2 apical pore fields so this feature cannot be used to separate them (cf. Le Cohu, 1988). Further reseach is needed to assess whether two different occlusion types are involved or a variation of the same structure, and whether or not *O. mutabilis* and *O. naveana* are conspecific.

This species was, prior to the description of Le Cohu (1988), also described by Takano (1988) as *Fragilaria opephoroides*. However, only an iconotypus was indicated and therefore, according to articles 8·3, 37·1 and 37·3 of the International Code of Botanical Nomenclature (Greuter *et al.*, 1994), this binomial is invalid.

Opephora pacifica (Grunow) Petit 1888

Basionym: *Fragilaria pacifica* Grunow 1862.

Type: Holotype probably lost (cf. Lange-Bertalot, 1989); neotype, **W**, Grunow slide no. 790 (Flugsand an der Kalkbay, Kap der Guten Hoffnung)(cf. Lange-Bertalot, 1989); isotype, **AWH** slide no. VI 41 B10 (Grunow no. 790 (Flugsand der Kalkbay bei Kapstadt).

Material examined: **AWH** slide no. VI 41 B10 (Grunow slide no. 790, Flugsand an der Kalkbay, Kap der Guten Hoffnung), **UNLP** slide 388 no. 3 (Riacho San Blas, Argentina), sediment samples from the Westerschelde (The Netherlands) estuary.

Type locality: Original type locality 'mari pacifico boreali', neotype locality 'Flugsand an der Kalkbay, Kap der Guten Hoffnung'.

Morphology (dimensions): Westerschelde: L, 13·0–48·5 μm (23·0±12·5); W, 4·0–7·7 μm (5·7±1·5); 6–9 striae/10 μm (7·3±1·0)($n = 7$). Kalkbay: L, 11·2–46·2 μm (23·2±8·5); W, 6·5–8·5 μm (5·6±1·8); 6·5–8·5 striae/10 μm (7·4±0·7)($n = 35$).

Light microscopy

No living material was observed. The valves are usually heteropolar (Figs 45, 48–52), although some isopolar ones were present in the isotype material. The valve apices are broadly rounded to cuneate. The striae are parallel to slightly radiate towards the apices and somewhat alternate. The axial area is narrow. In girdle view, the frustules are more or less rectangular. The cingulum appears to be composed of about 4 copulae which are strongly curved at the apices (Fig. 47). One of these (the valvocopula?) is very wide. Neither a marginal crossbar nor spines were present (cf. Figs 46, 52, 53).

Scanning electron microscopy

This species was rare in the Westerschelde material and only one specimen was observed in the SEM (Fig. 72). Notwithstanding the poor quality of the material, some important features can be distinguished, viz. the wide valvocopula, the absence of a marginal crossbar and spines and the nature of the occlusions, which seem to be composed of small ribs protruding from the alveolar walls and then bending inwards.

Remarks

In Lange-Bertalot (1989) reference is made to two different slides in the Grunow collection [Grunow slides no. 790 (Kap der Guten Hoffnung) and no. 1737 (Samoa)] as containing *Fragilaria pacifica*. It is argued that Grunow's '*Opephora*-Sippen' have spines on the mantle edge and thus do not differ from *O. mutabilis* (cf. Krammer & Lange-Bertalot, 1986–91). However, in the van Heurck Diatom Collection there is a hand-written book ('Grunow – Diatomées', no references) containing a list of Grunow slides (nos. 30–2130). A species list is given for each slide. The list for no. 790 mentions *Fragilaria pacifica* (underlined), whereas the list for no. 1737 does not. Moreover, Grunow (1863) makes no mention of the latter locality in his second description of *F. pacifica*. In other words, the *Opephora* species from Samoa, referred to by Lange-Bertalot (1989) as *O. pacifica*, were not identified as *F. pacifica* by Grunow. Judging from the illustrations in Lange-Bertalot (1989, tafel VII, fig. 14–17), spines occur only in the specimens from Samoa. These actually resemble '*O. pacifica*' valves illustrated in Navarro (1982, pl. 12, figs 5, 6). These possess a marginal crossbar but seem to

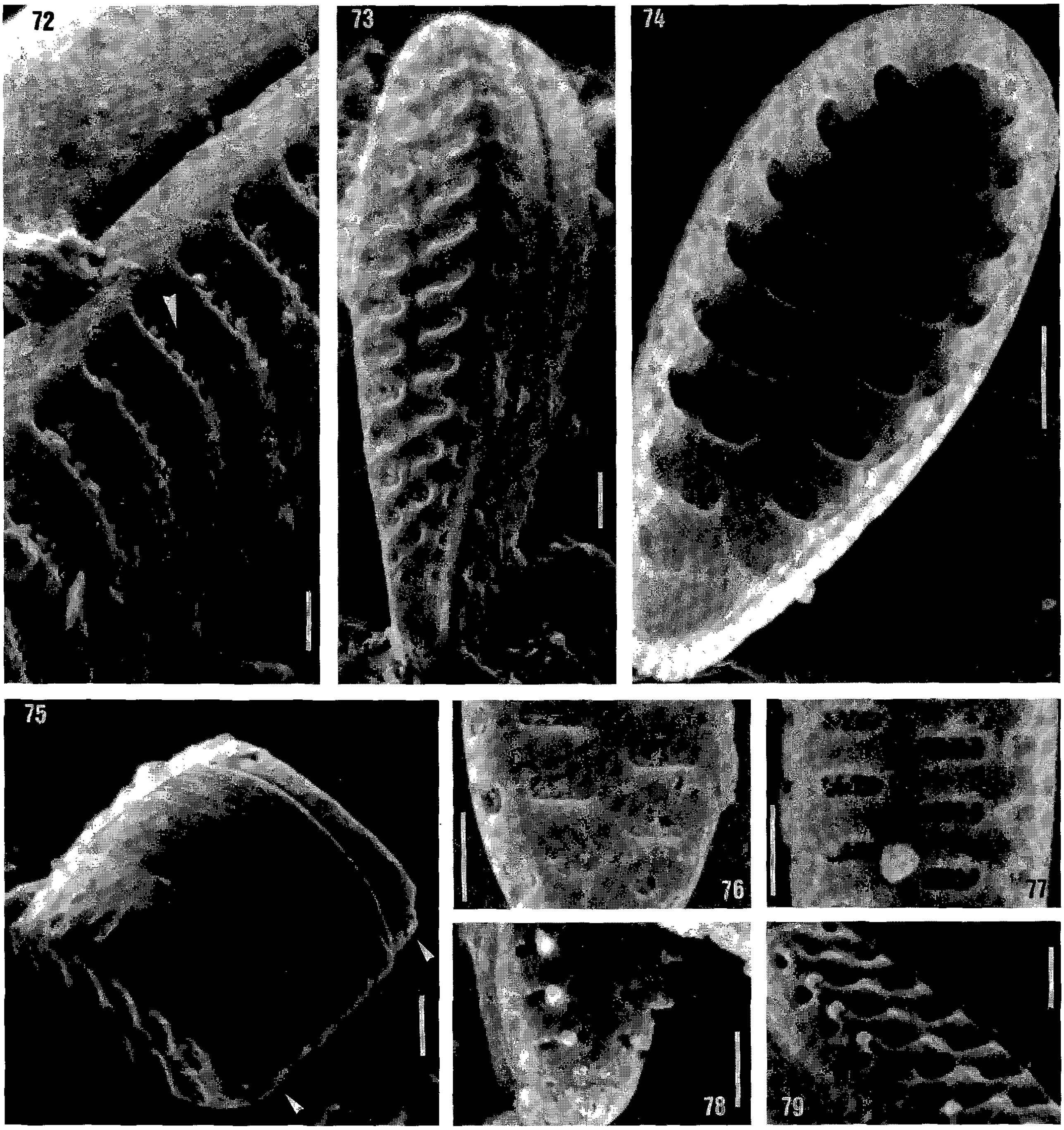


Fig. 72. *Opephora pacifica* (Grunow) Petit. Scale bar represents 1 μm. Westerschelde estuary (The Netherlands). Note the absence of the marginal crossbar and the inwardly bending areolar occlusions (arrowhead). **Figs 73–79.** *Opephora naveana* Le Cohu. Scale bar represents 1 μm. Westerschelde estuary and the Braakman (Fig. 77) (The Netherlands). Figs 73, 76–79. External valve views. Note the prominent marginal crossbar in all specimens and the spines in Figs 77–79. Fig. 74. Internal valve view. Fig. 75. External girdle view. Note the position of the pore field on the valve mantle (arrowheads).

differ from *O. mutabilis* in size and stria density and are therefore probably a different taxon. None of the numerous specimens that we observed on the isotype slide possesses spines.

On the basis of our own observations we therefore believe that *Opephora pacifica* is distinctly different from the above-described *Opephora* species in size, stria density and type of areolar occlusions. In addition, it differs from *O. mutabilis* and *O. naveana* in the absence of a marginal crossbar and spines. The specimens that we observed in the Westerschelde estuary are identical to those illustrated in Sullivan (1979) and Round *et al.* (1990) and probably represent true *O. pacifica.*

Ecology and biogeography

All the species above occur in sandy, intertidal sediments in the Westerschelde estuary (salinity range 5–33‰). *Opephora guenter-grassii* and *O. mutabilis* (and to a certain extent also *Pseudostaurosira perminuta*) usually coexist in the same, predominantly epipsammic assemblages, which are most often dominated by such species as *Achnanthes delicatula* (Kützing) Grunow, *Catenula adhaerens* Mereschkowsky, *Cocconeis peltoides* Hustedt and small taxa related to *Fragilaria atomus* Hustedt (cf. Witkowski & Lange-Bertalot, 1993). Similar assemblages seem to be widespread in brackish-water environments throughout Europe (e.g. Sundbäck, 1983; Juggins, 1992; Sabbe, 1993; Asmus & Bauerfeind, 1994; Witkowski, 1994). *O. guenter-grassii*, in particular, often attains high abundances and can be dominant (up to 16×10^6 cells per gram sediment dry weight (SDW), relative abundance 40%), while *O. mutabilis* is much rarer (up to $1{\cdot}5 \times 10^6$ cells per gram SDW). These two species can be found at all salinity ranges throughout the estuary, while *P. perminuta* seems to prefer higher salinities. Although it occurs at the mesohaline stations (salinity about 10–15‰) it reaches higher abundances (up to $0{\cdot}7 \times 10^6$ cells per gram SDW) in the poly- and euhaline stations (salinity about 20–30‰). *O. pacifica* is very rare (only on one occasion up to $0{\cdot}3 \times 10^6$ cells per gram SDW) in sandy sediments in the mouth of the estuary (salinity about 30‰). Due to the problematic LM identification of *O. naveana*, its ecological preferences are unclear.

All five species are epipsammic, usually attached to the sand grains by short stalks. However, while *O. guenter-grassii* and *O. pacifica* occur as solitary cells or form radiating colonies, *O. mutabilis*, *O. naveana* and *P. perminuta* most often form small ribbon-like colonies, probably due to their interlocking spines. An interesting feature of the spatial distribution of *O. guenter-grassii* (and to a lesser extent *O. mutabilis* and *P. perminuta*) within the Westerschelde estuary is that it seems to be independent of silt content (the sediment fraction < 63 μm) and median grain size of the sediment. *O. guenter-grassii* appeared to be dominant at both a silty (median grain size 70 μm, silt fraction 44%) and a sandy (median grain size 230 μm, silt fraction 3%) station.

O. pacifica is a cosmopolitan, marine, epipsammic and epiphytic species: it has been reported from North America (e.g. Sullivan, 1979), South America, Europe and South Africa (this study). *O. mutabilis* is a cosmopolitan, epipsammic and epiphytic species from predominantly brackish environments in Europe (e.g. Sundbäck, 1987; Kuylenstierna, 1989–90; Wendker, 1990; Gätje, 1992), North America (Poulin *et al.*, 1984), Southeast Asia (Podzorski & Håkansson, 1987), Australia (this study) and Africa (Compère, 1991; as *O. pacifica*). *O. guenter-grassii* has been reported as an epipsammic species from brackish habitats in Europe (e.g. Rincé, 1990, as *O. perminuta*; Sabbe, 1993, as *O. cf. perminuta*; Witkowski & Lange-Bertalot, 1993), North America (Navarro, 1982, as *O. pacifica*), Australia, Southeast Asia and South America (this study) and thus appears to be cosmopolitan. *O. naveana* was described as a freshwater species from the Kerguelen Islands (Le Cohu, 1988) but also appears to occur in brackish and marine sediments in Japan (Takano, 1988), Europe and Australia (this study). Finally, *Pseudostaurosira perminuta* has previously been reported only as a benthic (most probably epipsammic) species from brackish and marine sediments in Europe (Witkowski, 1994).

Discussion

At present, two diatom classification systems exist: a more traditional one (cf. Krammer & Lange-Bertalot, 1986–91) and one recently established by Round *et al.* (1990). Over the fragilarioid diatoms (*Synedra s.l.* and *Fragilaria s.l.*) in particular much controversy exists (Cox, 1993): while Krammer & Lange-Bertalot (1986–91) advocate the maintenance (and amplification) of a large genus *Fragilaria s.l.*, Williams & Round (1986, 1987) and Round *et al.* (1990) have divided *Fragilaria s.l.* into several new or re-established genera. New genera of fragilarioid diatoms have been described since, such as *Desikaneis* (Prasad & Livingston, 1993), *Psammosynedra* (Round, 1993) and *Synedropsis* (Hasle *et al.*, 1994), indicating a general trend towards a more refined classification at the genus level in this group.

In this study we propose three new combinations within the Fragilariales *sensu* Round *et al.* (1990), namely *Pseudostaurosira perminuta*, *Opephora mutabilis* and *O. guenter-grassii*. The past and present generic allocations of these three taxa and of *Opepora naveana* and *O. pacifica* are discussed here in the light of the recent taxonomic changes.

Grunow [in Cleve & Möller (1879) and Van Heurck (1881)] originally placed both *Pseudostaurosira perminuta* and *Opephora mutabilis* in the genus *Sceptroneis* Ehrenberg. However, the characteristics of this genus (e.g. areolar structure and presence of rimoportulae), which indicate a close relationship with the genus *Rhaphoneis* (cf. Round *et al.*, 1990), certainly do not apply to these taxa.

Subsequently, Peragallo & Peragallo (1897–1908) transferred both taxa to *Grunoviella*. This genus was described by Van Heurck (1896) to accommodate *Sceptroneis? gemmata* Grunow and *S. marina* (Gregory) Grunow. On the basis of this description, the LM distinction between *Grunoviella* and *Opephora* seems to be precarious, the only differences, according to Van Heurck (1896), being the shape of the 'marginal beads', ('round' in *Grunoviella*, 'very elongated into the form of button-holes' in *Opephora*) and the shape of the girdle face ('rectangular' in *Grunoviella* and 'cuneate' in *Opephora* – in the original description of *Opephora*; however, Petit (1888) stated that the girdle face is rectangular!). Both Peragallo & Peragallo (1897–1908) and Hustedt (1931–59) argued that the differences between these two genera were not sufficient to justify their separation. Hustedt (1931–59) therefore united them in one genus, *Opephora*. However, we examined a slide (Van Heurck, Types du Synopsis no. 280) which contains several specimens of *Sceptroneis gemmata*, the type of the genus *Grunoviella*, from the type locality ('Isle de Mors' in Jutland, Denmark). All these specimens had a distinct portule (most probably a rimoportula) near the head pole (and possibly a second one near the foot pole), a large, ocellulimbus-like pore field at the head pole and large, marginal alveoli. These features, some of which (the portules) can also be seen on the illustrations of this species in Hustedt (1931–59), suggest a close relationship with *Tabularia* (Kützing) Williams & Round. *Opephora* has neither portules nor ocellulimbus-like pore fields at the head pole and therefore should be kept separate from *Grunoviella*. Further studies using SEM are necessary to determine the proper taxonomic identity of *Grunoviella*. As neither *Pseudostaurosira perminuta* nor *Opephora mutabilis* has portules or large, ocellulimbus-like pore fields, they should not be placed in *Grunoviella*.

The genus *Pseudostaurosira* was established by Williams & Round (1987) to accommodate the species group around *Pseudostaurosira brevistriata* (Grunow) Williams & Round (syn. *Fragilaria brevistriata* Grunow); the same species group is recognised as a 'Sippencomplex' by Krammer & Lange-Bertalot (1986–91). *Pseudostaurosira* is characterised by sparse marginal areolae, a (usually) wide sternum and complex, branched areolar occlusions. It belongs to a group of genera, viz. *Fragilaria s.s.*, *Fragilariforma* (Ralfs) Williams & Round, *Punctastriata* Williams & Round, *Staurosira* Ehrenberg and *Staurosirella*, which replaces the large genus *Fragilaria sensu* Hustedt (1931–59). We agree with Round *et al.* (1990) that, on the basis of the presence of a rimoportula among other characteristics, the genera *Fragilaria s.s.* and *Fragilariforma* are quite distinct from *Staurosira*, *Staurosirella*, *Punctastriata* and *Pseudostaurosira*. However, within the latter group the generic differences are less pronounced and require further investigation.

Examination of isotype material of *Opephora perminuta* reveals that it belongs to *Pseudostaurosira*. It is probably related to *P. zeilleri* and its varieties. These taxa do not completely fit the generic diagnosis of *Pseudostaurosira* (Williams & Round, 1987): the number of areolae on the valve mantle is often higher than 1 or 2 and the shape of the sternum can be quite variable (this study; Serieyssol, 1988; Krammer & Lange-Bertalot, 1986–91). However, they possess similar, complex areolar occlusions and herein differ from *Staurosira*. We therefore placed *O. perminuta* in *Pseudostaurosira*. Wasell & Håkansson (1992) illustrated similar taxa with numerous marginal areolae and also consider that these could belong to *Pseudostaurosira*.

The frustule morphology of *P. perminuta* shows intermediate features between *Staurosira* (number of marginal aeolae) and *Pseudostaurosira* (areolar ultrastructure). Therefore, these genera ought either to be combined or to have their diagnoses reconsidered and modified. The latter is common practice in systematics: for example, the recent discovery of a new species belonging to the genus *Plagiogrammopsis* has prompted Gardner & Crawford (1994) to amend the description of this genus. As all taxa belonging to *Pseudostaurosira* share a similar, complex type of areolar occlusions, which differs from the occlusion type in *Staurosira*, we advocate the maintenance of a separate genus *Pseudostaurosira*. This genus would then also include taxa with more than 2 marginal areolae and a variable sternum shape.

We have transferred *Fragilaria guenter-grassii* to *Opephora*. Recently, some authors have questioned the maintenance of this genus (Krammer & Lange-Bertalot, 1986–91). This is mainly because it was originally established on the basis of LM characteristics which would not justify the creation of a new genus today. However, evidence from our own observations and other studies (Sullivan, 1979; Round *et al.*, 1990) has shown that specimens of *O. pacifica*, the type of the genus, from widely dispersed localities consistently show the same alveolar ultrastructure. Notwithstanding that this *a posteriori* characteristic was not (or rather could not be) recognised by Petit (1888) and has, in recent descriptions, acquired greater taxonomic weight than the original discriminating features given by Petit (1888), it remains characteristic of the *typus generis* and should be treated as such. The same combination of features (the unique areolar ultrastructure plus the other characteristics of the *typus generis*) is, to our knowledge, not known in taxa from any other genus and strongly favours the preservation of the genus *Opephora*.

We believe that *O. mutabilis*, *O. guenter-grassii* and *O. naveana* should be placed in this genus. They share a combination of features (mainly absence of a rimoportula, type of areolar occlusions, brackish and marine habitat) that most closely fit the description of *Opephora sensu* Round *et al.* (1990). All these features can, individually, be found in other genera [(e.g. a similar areolar ultrastructure in *Tabularia investiens* (W. Smith) Williams & Round (Holmes & Croll, 1984)] but the combination only fits *Opephora*.

The distinction between the above-described *Opephora* species is precarious and in LM often problematic. As is usual in the Fragilariaceae (cf. Round & Williams, 1992), it is based largely on a combination of (mainly SEM) characteristics, not on a single or several unique features. These characteristics are described in detail above, where each species is compared with similar taxa. The main argument against distinguishing these taxa is that the characteristics employed can be quite variable, if not in these particular taxa then at least in others (cf. Lange-Bertalot, 1989; Round & Williams, 1992). This complicates the assessment of the taxonomic significance of particular characteristics (viz. striation pattern, alveoli versus areolae, presence/absence of spines, position of spines). However, the decisive criterion for treating these taxa as different species was that they displayed (within certain limits of valve shape, size and stria density) stable frustule morphology. As long as they cannot be shown to be morphological forms along a continuous range, we believe it is better to treat them as separate species, allowing enhanced resolution in ecological research (cf. Mann, 1982).

We are convinced (unlike Krammer & Lange-Bertalot, 1986–91) that *O. pacifica* and *O. mutabilis* are two different species, recognisable at the LM level: *O. pacifica* lacks a marginal crossbar, spines or cross-lineolate areolae and has distinctly fewer striae per 10 μm. The difference between *O. mutabilis* and *O. guenter-grassii* is less obvious: mainly the absence of a marginal crossbar and spines in the latter species. Oddly enough, in nearly all the material studied, these two species occurred together. In combination with the morphological resemblance, this could be an indication of close taxonomic affinity. However, whether we are dealing with two morphological types of one species or with two distinct but closely allied species is hard to assess. The fact that they seem to occupy different micro-habitats (as expressed by the colony-type) and the stability of the distinguishing morphological characteristics support the latter view. Their taxonomic rank (specific or infraspecific) seems to be mainly a subjective matter; as both taxa had already been described, we have not changed it. The distinction between *O. mutabilis* and *O. naveana* has been discussed above. While counting sediment samples of the Westerschelde estuary in the LM, no discrimination was made between these two taxa. Only in the SEM is the difference clear. Until we have more information on the morphological variability and the ecology of *O. naveana*, we will regard them as separate taxa.

Finally, *O. pacifica* shows great resemblance to *Martyana martyi* (syn. *Opephora martyi* Héribaud and *Fragilaria martyi* (Héribaud) Lange-Bertalot) in the LM. However, in the SEM the differences are evident: *M. martyi* has a different areolar structure and a 'step' at the head pole (Round *et al.*, 1990). Moreover, *O. pacifica* is a marine species, while *M. martyi* is common in fresh (and/or brackish?) water (Juggins, 1992).

Conclusion

Notwithstanding the fact that (supposed) representatives of the genus *Opephora* are widespread and often numerous in littoral habitats, little is known about this genus. Unfortunately, the epipsammic habit of many of its representatives does not facilitate the research on living material (cell contents, reproduction, etc.) that is necessary critically to test the conclusions of this study. Much work remains to be done on the morphological variability of frustule characteristics, ecology and affinities with allied taxa, especially the genera *Staurosirella* (e.g. *S. pinnata* (Ehrenberg) Williams & Round) and *Staurosira*.

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