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NEW MARINE LITTORAL DIATOM SPECIES (BACILLARIOPHYTA) FROM KERGUELEN ISLANDS. II. HETEROPOLAR SPECIES OF FRAGILARIACEAE

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DIATOMS
BACILLARIOPHYTA
NEW SPECIES
FRAGILARIACEAE
HETEROPOLAR
KERGUELEN ISLANDS

ABSTRACT. – Kerguelen is a Subantarctic archipelago, far from other islands or continents. Its isolation provides an interesting field of investigation concerning species diversity and the emergence of morphological differentiation, particularly in diatoms (Bacillariophyta). Several surveys using light (LM) and scanning electron (SEM) microscopy yielded more than 20 new species and (possibly) two new genera. Most of the new species are from *Navicula* s.s. and were the subject of a separate paper. Here we describe six new species of araphid diatoms. A common feature of these taxa is their various degrees of heteropolarity and the ultrastructure of the transapical striae, typical for species of *Opephora* defined in the broader sense. A detailed analysis of valve ultrastructure reveals data relevant to the classification of these new taxa into the genera *Nanofrustulum* (*N. squammatum*), *Pseudostaurosira* (*P. gersondei*, *P. quasielliptica*, *P. latesternum* and *P. versiformae*) and *Staurosirella* (*S. poulinii*). Their relationships to *Opephora* s.s., as defined by Round *et al.* (1990), are also discussed.

INTRODUCTION

Amongst the araphid diatoms, several genera are characterized by having a heteropolar (clavate) valve shape. In the marine environment the most well known examples of this kind of valve morphology are *Licmophora* C. Agardh, *Opephora* P Petit and *Trachysphenia* P Petit (e.g. Hustedt 1962, Round *et al.* 1990). During the last decades of the 20th century several new heteropolar taxa were described from marine littoral environments, all placed as either species of *Opephora* or *Fragilaria* Lyngbye (e.g. Giffen 1980, Takano 1986, 1988, Le Cohu 1988, Witkowski 1994). The classification of Fragilariaceae has changed radically since the 1980s. First, several new genera were either newly established or re-introduced (e.g. Williams & Round 1987, Round *et al.* 1990, Morales 2001, 2002). Second, Round *et al.* (1990) proposed that the genus *Opephora* be restricted to taxa strictly conforming to the generitype: *O. pacifica* (Grunow) Petit. The latter proposal excluded from *Opephora* most taxa described during the last few decades and, as a consequence, the number of species of *Opephora* has been reduced to a few marine forms. Later, heteropolar forms were either transferred to one of the new genera (e.g. *Staurosirella* Williams & Round 1987, *Martyana* Round in Round *et al.* 1990, *Pseudostaurosira* Sabbe & Vyverman 1995) or described as new (e.g. Morales 2002). Subsequently, many new transfers were proposed, along with additional new genera: *Nanofrustulum* Round, Hallsteinsen & Paasche in Round *et al.* (1999), *Pseudostaurosireopsis* Morales (Morales 2001) and *Sarcophagodes* Morales (Morales 2002).

The study of morphological characteristics with the electron microscope (SEM and TEM) provides crucial evidence for circumscription of old genera or the establishment of new araphid genera with the classic opephoroid shape. However, the most important character appeared to be the structure of the transapical striae. When considering the striae, the associated characters are: number of areolae (solitary versus numerous); the type of areolae (large without further subdivisions, large with subdivisions, small oblong); the type of occlusions (simple rod-like, plate-like, highly sophisticated volate type) (Williams & Round 1987, Round *et al.* 1990, Sabbe & Vyverman 1995, Morales 2001, 2002). The criteria at the genus level, as observed in the electron microscope, have been summarized by Morales (2001). We base the taxonomic decisions presented in this manuscript by following the above criteria.

The problem of mixed diatom assemblages in habitats exposed to strong winds is particularly well illustrated by araphid diatoms. This problem has been discussed by Van de Vijver *et al.* (2002), but examples of these phenomena are numerous. For instance, *Opephora naveana* Le Cohu was described from a Kerguelen island freshwater habitat (Le Cohu 1988). Le Cohu (1999) confirmed that this species occurs in Kerguelen in freshwater and marine coastal environments as shown in this study. Later it was discovered that *Opephora naveana* is widely distributed in brackish-water habitats and has been identified in the Wester Schelde Estuary (Sabbe & Vyverman 1995) and from the Baltic Sea (Witkowski *et al.* 2000). Thus, it seems, *Opephora naveana* is a marine (to brackish-water) species rather than freshwater. Although detailed infor-

mation regarding *O. naveana* is scarce, in general it can be considered a rare species. From our experience we can also outline the problem of appropriate LM identification of this species, which requires specialist knowledge. The newly described *Navicula* species from Kerguelen (Witkowski *et al.* 2010), with the exception of *Navicula irminae*, have not been previously observed in the Subantarctic and Antarctic marine littoral (Witkowski *et al.* 2010). *Navicula irminae* was illustrated by Al-Handal & Wulff (2008, Fig. 67 as *Navicula cf. directa*) from Potter Cove King, George Island. Unlike this species, some of the araphid taxa, as described here, have been observed elsewhere. Information about these taxa comes from either our own observations or published sources (Wassell & Håkansson 1992, Van de Vijver *et al.* 2002). They were published as either unidentified species of *Fragilaria* or erroneously identified (see in species description).

The present paper gives results of our light (LM) and scanning electron microscopic (SEM) studies on a number of araphid, heteropolar diatoms. Unlike the naviculoid diatoms recently described (Witkowski *et al.* 2010), araphid diatoms have been extensively studied in the Antarctic (e.g. Wassell & Håkansson 1992, Sabbe *et al.* 2004), in Austral Islands (e.g. Van de Vijver *et al.* 2002) and in Kerguelen (Le Cohu 1988, 1999, Lange-Bertalot & Le Cohu 1985), though most of these studies deal with freshwater taxa. As shown in our paper, the Kerguelen Islands marine littoral flora is rich in opephoroid species new to science. Here we describe and discuss in detail six new taxa, which represent three genera: *Nanofrustulum*, *Pseudostaurosira* and *Staurosirella*. The ultrastructure of their siliceous cellular exoskeleton is compared to *Opephora cf. marina* (Gregory) Petit, also abundant in the studied area. All of the taxa described herein as new show significant ultrastructural differences when compared to *Opephora s.s.*

ENVIRONMENTAL SETTINGS

The Kerguelen Archipelago (between 49° and 50° S; Indian part of the Southern Ocean), discovered in 1772, of wide ranging area (6993 km²), is located close to the Polar Front system. This Archipelago is composed of ca 300 volcanic islands of complex origin and is located in the northern part of the “Plateau des Kerguelen”, far from continents and other islands (Heard Island is 440 km South). The main island of Kerguelen is deeply indented by numerous fjords and sheltered bays, offering the opportunity for the formation of diverse marine environments. Over several austral summers the microphytobenthos has been studied by C R-G (MicrophytoKer programs), and marine sediments were collected for a diatom survey, particularly several sub-tidal sediments under the *Macrocystis pyrifera* (Linnaeus) C Agardh belt.

MATERIAL AND METHODS

The material for the present study was collected by one of us (C R-G) during several cruises during the period 1985 to 1992. A diversity of sediment samples was taken from sheltered intertidal bays to sub-tidal environments (see Fig. A and Table II in Riaux-Gobin & Romero 2003). Two sites were regularly sampled in 1991 and 1992: Port-aux-Français (49° 20' S, 69° 50' E) and Port-Raymond (49° 21' S, 70° 12' E), located on the Morbihan Bay. Samples were preserved in formalin (final concentration 10 %). Diatom slides were prepared from wet sediments treated overnight at room temperature with 10 % HCl in order to remove calcium carbonate. The samples were then washed several times with distilled water, boiled in 30 % H₂O₂ until the organic matter was completely removed, and washed again several times with distilled water. Permanent slides of cleaned diatom material were mounted using Naphrax®. Permanent slides and raw samples are deposited in the diatom collection of A Witkowski at the University of Szczecin in Poland (SZCZ).

Permanent slides were examined in LM using a Leica DMLB microscope equipped with oil immersion objectives (x100/NA1.4) and Zeiss Axiovert microscope equipped with oil immersion objective (x100/NA1.4, DIC (Differential interference contrast)) and ocular magnification x10. For SEM, a few drops of cleaned material were air-dried on to aluminium stubs, coated with Au and examined at 5 kV in a Hitachi S4500. SEM micrographs were taken by digital camera. The number of specimens measured in each species amounted to ca. 20 in LM and to ca. 12 in SEM. Terminology used in this manuscript follows Anonymous (1975), Round *et al.* (1990) and Krammer & Lange-Bertalot (1991).

OBSERVATIONS

In the sediment samples collected from the marine coastal environment of Kerguelen ca. 300 diatom species have been examined. With respect to species number, *Navicula*, *Amphora*, *Cocconeis*, *Opephora s.l.* and *Planothidium* were dominant. Light microscope analysis of diatom species composition revealed occurrence of numerous taxa which we were unable to identify accurately. These taxa were subject to further investigation using SEM. The SEM images were supplemented by accounts in the literature, including old cruises reports (e.g. Cast-racane 1886, Van Heurck 1909, Peragallo & Peragallo 1897-1908, Heiden & Kolbe 1928, Manguin 1960). This allowed the selection of a group of ca. 24 taxa that could be described as new. The number of unknown species was highest in *Navicula* and in those tentatively assigned to *Opephora*. The common features of the latter group are the heteropolar shape of the valve and the presence of pore fields at both apices. Differences are also found in the fine structure of the striae. Overall, we were able to document 14 taxa among the opephoroid forms, of which

6 to 7 are new to science. Here we describe 6 based on data of their ultrastructure (see Table I).

TAXONOMY

Nanofrustulum Round, Hallsteinsen & Paasche

Nanofrustulum squammatum Riaux-Gobin & Witkowski sp. nov. Figs 1-14

Descriptio :

Frustula aspectu cingulari quadrata ad rectiangulara. Valvae minutae, ovals ad subcirculares, 2.1-3.28 (in mediocris 2.6) μm longae, 1.6-2.3 μm latae. Longitudinis latitudinis ratio : 1.3 ad 1.7. Sternum distinctum sed angustissimum. Striae transapicales uniseriatae, radiantes et alternantes ad mediam valvae partem : 35-50 (in mediocris 40) in 10 μm . Spectabiles squammas prope cingulum.

Holotype: slide no. 7350_8 in Coll. A Witkowski, Institute of Marine Sciences University of Szczecin (SZCZ), leg. Catherine Riaux-Gobin. Holotypus Fig. 4.

Isotypi: slide No. KER11 in Collection C Riaux-Gobin, USR 3278 CNRS-EPHE, CRIOBE-Université de Perpignan, slide No. ZU7/79 in Friedrich Hustedt Diatom Collection, Alfred Wegener Institute for Polar and Marine Research, Bremerhaven.

Type locality: Île Haute, intertidal, Dec. 1991.

Habitat: in littoral sediments of the Kerguelen Islands.

Etymology: the epithet refers to the design of the girdle bands.

LM: (Figs 1-4)

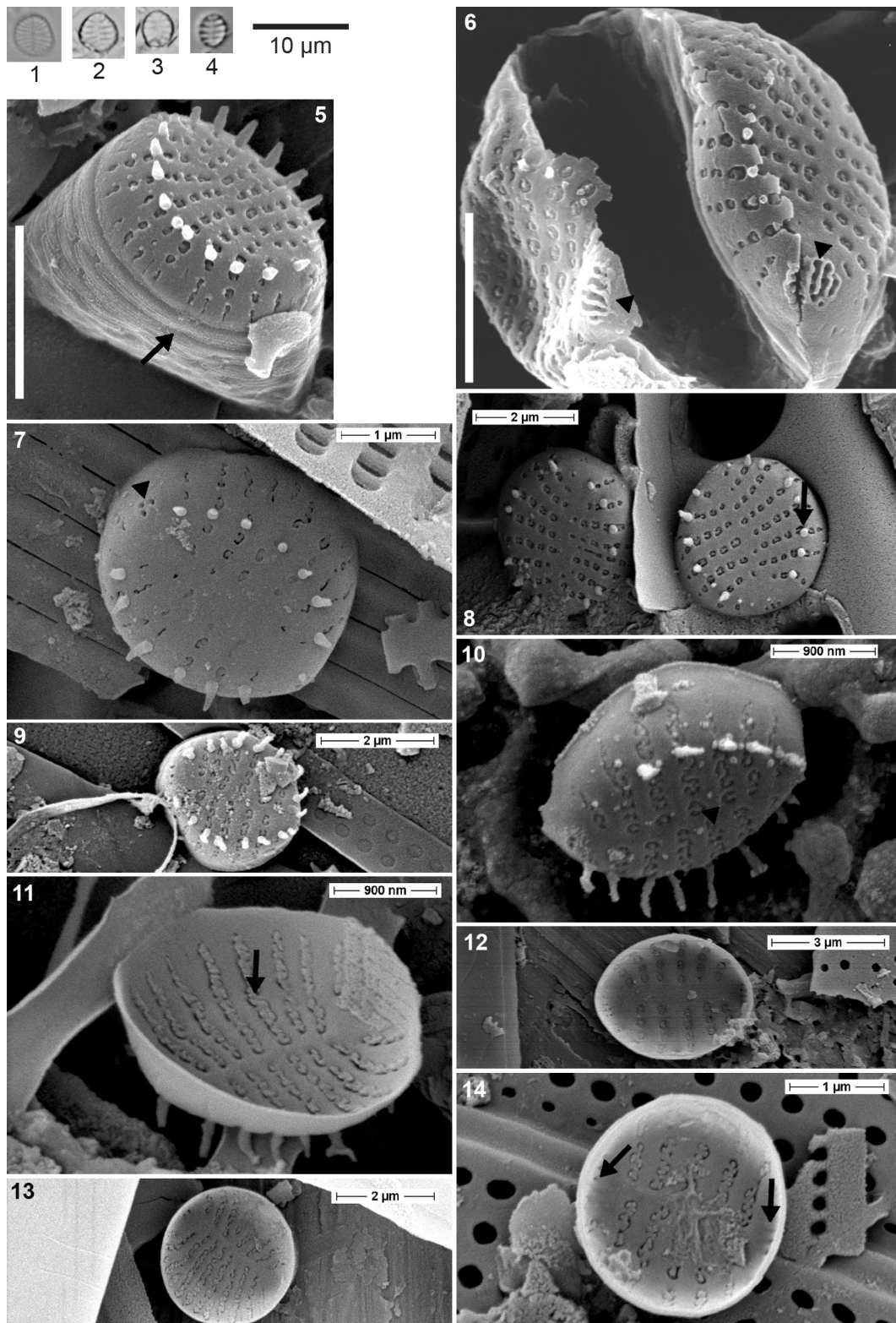
Frustules in girdle view, square to rectangular. Valves small, oval to circular, 2.1-3.28 (mean 2.6) μm long; 1.6-2.3 μm broad; length/breadth ration 1.3-1.7. Sternum distinct but narrow. Transapical striae uniseriate, alternating at valve middle: 35-50 (mean 40) in 10 μm , radiate.

SEM: (Figs 5-14)

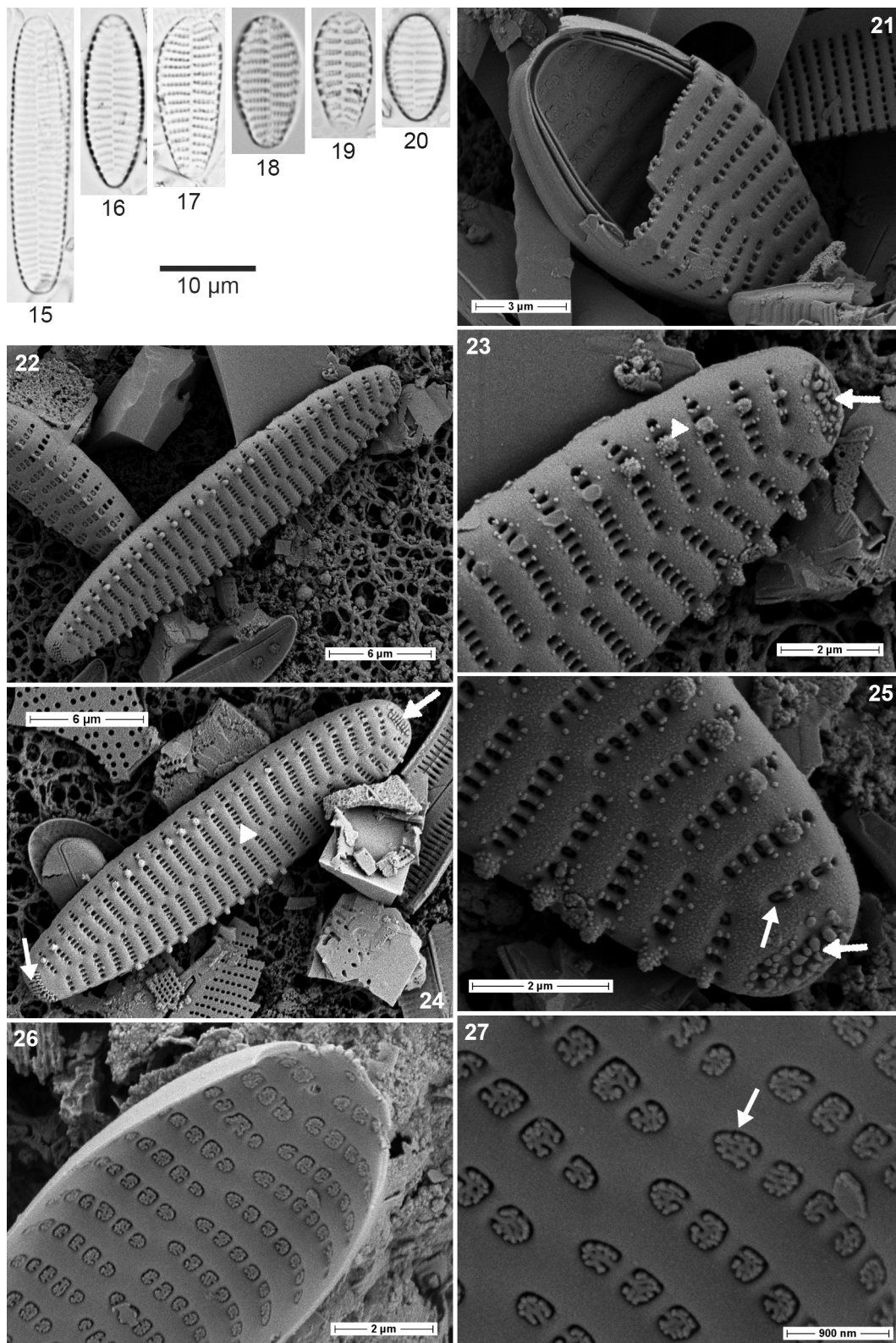
Valve face flat with abrupt transition towards the mantle, mantle relatively deep. Sternum narrow (Figs 5-8). Transapical striae composed of single areolae, prolonged on valve mantle, sometimes one row of marginal short spines with enlarged base (often lacking or reduced to sparse nodules), delineating valve face-mantle junction (Fig. 8). Areolae (4-5 in 1 μm) circular to sub-quadrangular, containing volate occlusions which penetrate deeply into areolar foramina (Figs 8-10). Apical pore fields at one pole, sometimes both, composed of festooned ridges, reduced to small wavy ridge, or few pores on smaller specimens (Figs 6-8). Numerous copulae (girdle width exceeding 8 μm) composed of short well-defined segments (0.6-0.8 μm long, Fig. 5); differ from copulae observed in *Extubocellulus spinifer* that often (but not always) show "quasifract bands" (Riaux-Gobin & Chrétiennot-Dinet 2000). In *N. squammatum* valvocopula is

Table I. – Summary of the data on diatom taxa described as new in this paper and of those compared to newly described ones. Source of data: 1, Takano 1986; 2, Sabbe & Vyverman 1995; 3, Round *et al.* 1999; 4, Witkowski *et al.* 2000; 5, Cejudo-Figueiras *et al.* 2011.

Taxon	<i>Nanofrustulum squammatum</i>	<i>N. shiloi</i> ³	<i>Pseudostaurisira quasielliptica</i>	<i>P. gersondei</i>	<i>P. latesterium</i>	<i>P. versiformae</i>	<i>Staurirella poulinii</i>	<i>Opephora mutabilis</i> ²	<i>O. krumbeyi</i> ⁴	<i>Pseudostaurisira americana</i> ⁵	<i>Fragilaria flavovirens</i> ¹
Girdle bands	Segmented	Segmented	Solid	Solid	Solid	Solid	Solid	Solid	Segmented	Solid	Solid
Length (μm)	2.1-3.28	2-6	11-30	11-15.5	10-23	5-14	24-45	7-60	1.5-4.5	6-22	3-47
Width (μm)	1.6-2.3	2-5	6-7	4-6.5	1.9-3.2	2-3	6-10	2.5-7.0	1.5-4.5	4.5-5.0	2.8-5.0
Sternum shape	Narrow linear	Relatively broad linear to lanceolate	Narrow linear	Narrow linear	Broad lanceolate	Narrow linear to broad lanceolate	Narrow linear	Narrow linear	Zig zag	Narrow linear	Narrow linear
Striae in 10 μm	35-50	15	11-12	9-10	18-20	18-20	5.5-6.5	8-16	18-25	16-18	16-18
Areolae type	Small oblong	Small oblong	Small oblong	Small oblong	Small oblong	Small oblong	Large with secondary apically oriented bars	Large with secondary apically oriented bars	Small oblong	Small oblong	Small oblong
Occlusions type externally	Single rod-like outgrowth	Single rod-like outgrowth	Single rod-like outgrowth	Rod-like outgrowth	Single rod-like outgrowth	Single rod-like outgrowth	A few rod-like outgrowths	A few rod-like outgrowths	Single rod-like	A few rod-like	Two rod-like outgrowths
Occlusions type internally	Relatively simple volate	Single rod-like outgrowth	Volute highly branched	Volute highly branched	Volute highly branched	Volute highly branched	The same as externally	Volute highly branched	Volute highly branched	Volute highly branched	Not illustrated



Figs 1-14. – *Nanofrustulum squammatum* sp. nov. Figs 1-3 LM. Scale bar = 10 μ m. Fig. 4 is of the holotype specimen (DIC). Figs 5-14 SEM. Fig. 5. External view of the valve with part of the girdle, note the presence of numerous, relatively narrow, structureless girdle composed of segments (quasifract; arrow). Fig. 6. Girdle view of a frustule, note the structure of well developed pore fields (arrow heads). Figs 7-10. External view of the valve surface, note poorly developed apical pore field (arrow head in Fig. 7), the presence of the connecting spines on the marginal apically oriented bar (arrow in Fig. 8) and of areolae occlusions (arrow head in Fig. 10). Figs 11-14. Valve internal view showing development of striation, the occlusions of the areolae (arrow in Fig. 11) and the pore field (arrows in Fig. 14).



Figs 15-27. – *Pseudostaurosira quasielliptica* sp. nov. Figs 15-20 LM. Scale bar = 10 µm. Fig. 18 is of the holotype specimen (DIC). Figs 21-27 SEM. Fig. 21. Oblique view of a complete frustule. Figs 22-25. Valve external views, Fig. 23. Close-up of a head pole of specimen illustrated in Fig. 22, note the position of the connecting spines (arrow head) and the head pole pore field (arrow). Fig. 24. Valve with apical pore fields (arrows) and the linear shape of the sternum (arrow head). Fig. 25. Close-up of the foot pole of a valve showing also the presence of relatively simple, bent in areolae occlusions (upper arrow) and foot pole pore field (lower arrow). Figs 26, 27. Internal view of the head pole. Fig. 27. Close-up of a specimen illustrated in Fig. 26, note the complicated shape of areolae occlusions (arrow).

unfragmented (Fig. 5). Areolae occluded externally by volae similar to that in *Trachysphaenia*. There are some similarities with *Staurosira circula* Van de Vijver & Beyens in Van de Vijver *et al.* (2002), but that taxon has fewer striae (20-24 in 10 μm), irregular striation of one or two rows of round areolae, and a different pore field.

Nanofrustulum squammatum shares some similarities to *Fragilaria sopotensis* Witkowski & Lange-Bertalot. However, the latter has fewer striae (13-17 in 10 μm), an abrupt bend towards the mantle and lacks apical pore fields. *Nanofrustulum squammatum* shares some similarities with *Opephora krumbeinii* Witkowski, Witak & Stachura also, but that taxon has fewer striae (28-25) and a different areolae occlusions. Finally, *Nanofrustulum squammatum* can also be compared to "Clone 395" of Round (1992) and Round *et al.* (1999), of which the major difference is the absence of an apical pore field in the latter. Round (1992) referred to "*Fragilaria flavovirens* Takano" which has alternate striae, differs in spine shape and has a lower stria density (16-18 in 10 μm).

The most interesting shared feature of species belonging to *Nanofrustulum* is the girdle. It is composed of a series of fragmented quasifract bands (Hasle *et al.* 1983). Quasifract bands differ from normal bands by giving the impression of being irregularly and artificially broken into smaller or larger units. This kind of girdle was found in several other araphid species and may suggest they belong to the same monophyletic group. One such genus is *Subsilicea*, up until now considered a centric diatom; the girdle structure may suggest a more direct relationship between *Nanofrustulum* and *Subsilicea* (David M. Williams personal information).

Distribution: *Nanofrustulum squammatum* has never been reported outside the Kerguelen Islands nor has anything similar been found in Antarctica or Subantarctica. Wasell & Håkansson (1992) illustrated (Figs 103-106) some similar valves identified as *Fragilaria construens* var. *venter* but these appear to be species of either *Staurosira* or *Pseudostaurosira* rather than *Nanofrustulum*. *Pseudostaurosira trainori* Morales is similar to *Nanofrustulum squammatum* when observed under LM (Morales *et al.* 2010), but the striae occlusion show clearly that the two species belong in two different genera.

***Pseudostaurosira* Williams & Round 1987**

***Pseudostaurosira quasielliptica* sp. nov. Figs 15-27**

Descriptio :

Valvae lineares ellipticae ad heteropolares, cum apicibus rotundatis, claviformes, 11-30 μm longae, 6-7 μm latae, cum obtuso rotundato vertice et rotundato polo basali. Sternum perfecte rectum, angustum et perdistinctum in M.O. Transapicales striae parallelae in media parte et radiantes ad apices, 11-12 in 10 μm . Striae

areolis compositae sed hae parum visibiles in M. O.

Holotype: slide no. 7350_8 in Coll A Witkowski, Institute of Marine Sciences University of Szczecin (SZCZ), leg. Catherine Riaux-Gobin. Holotypus Fig. 18.

Isotypi: slide No. KER12 in Collection C Riaux-Gobin, USR 3278 CNRS-EPHE, CRIOBE-Université de Perpignan, slide No. ZU7/80 in Friedrich Hustedt Diatom Collection, Alfred Wegener Institute for Polar and Marine Research, Bremerhaven.

Type locality: Île Haute, intertidal, Dec. 1991

Habitat: in littoral sediments of the Kerguelen.

Etymology: the epithet refers to the valve outline of the new species, which is only slightly heteropolar, almost elliptic.

LM: (Figs 15-20)

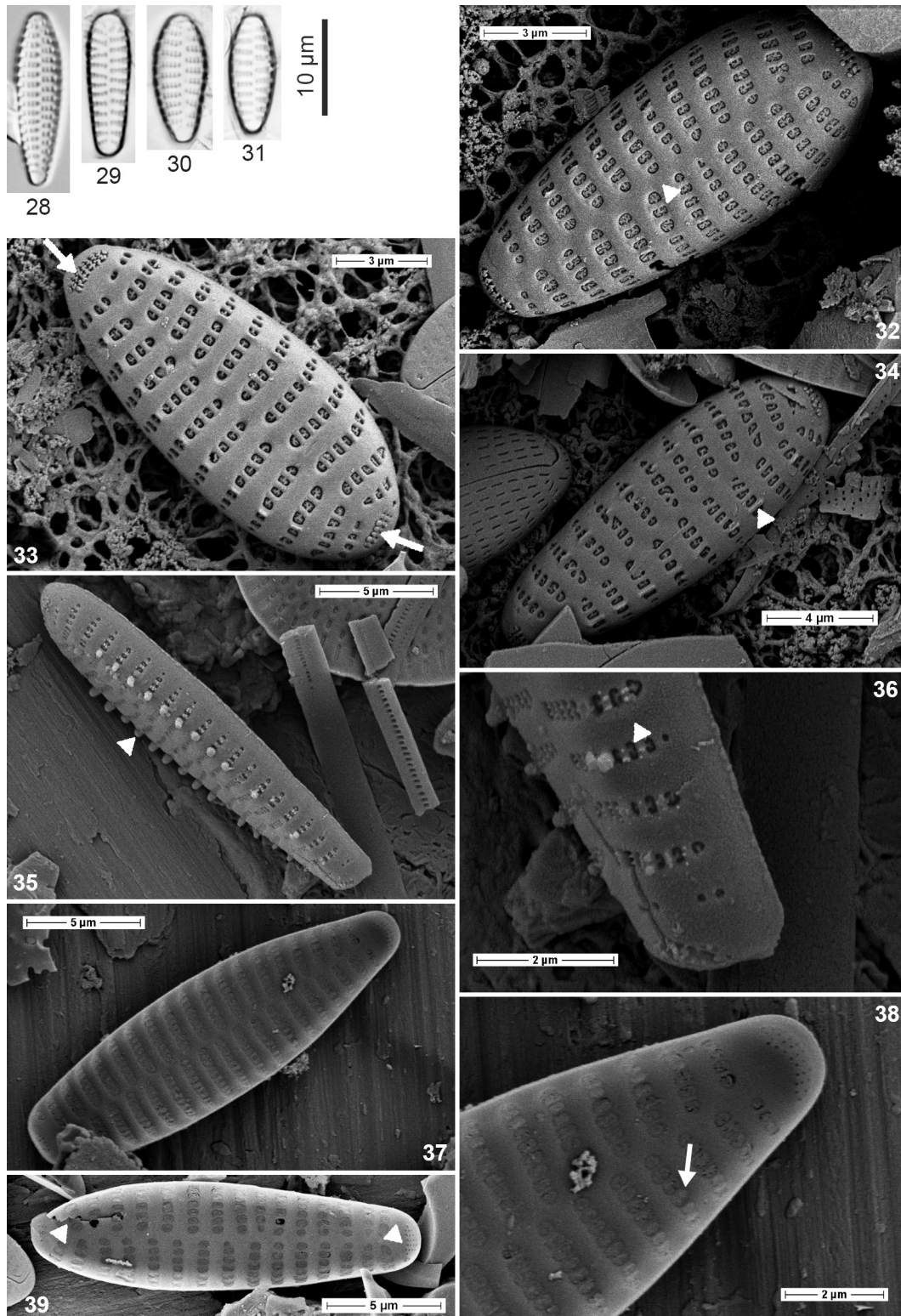
Valves linear elliptic, with broadly rounded apices to heteropolar, clavate with obtusely rounded foot pole and broadly rounded head pole; 11-30 μm in length, 6-7 μm in width. Sternum strictly linear, narrow, distinguishable. Transapical striae parallel in valve middle becoming radiate towards apices, 11-12 in 10 μm . Striae composed of areolae, barely distinguishable.

SEM: (Figs 22-27)

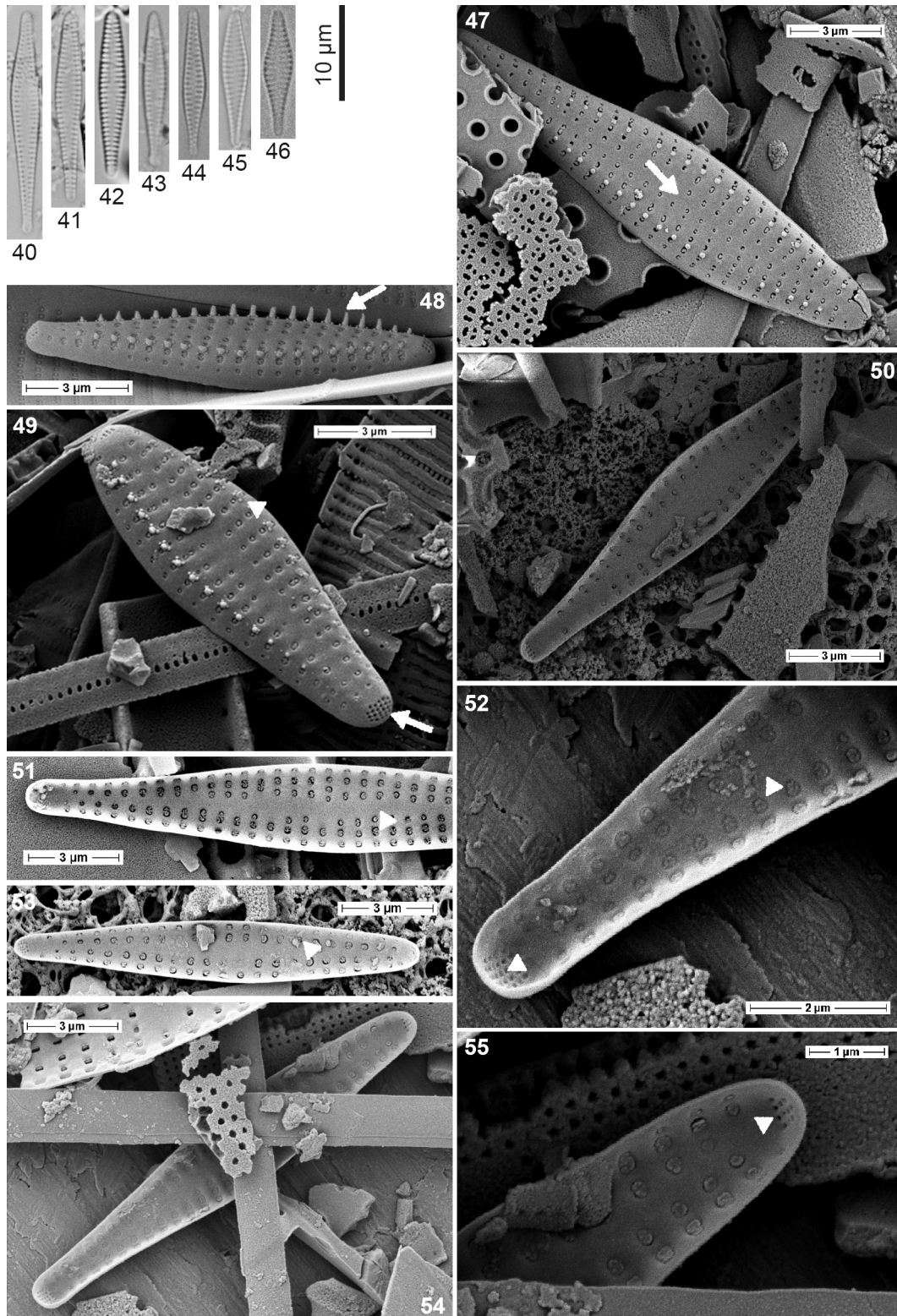
Valve surface flat, gradually turning towards steep mantle. Mantle relatively high, bearing few rows of areolae. Sternum narrow, linear (Figs 21, 22, 24). Connecting spines solid, located at the valve face-mantle junction, on the apical bars crossing the areolae (Figs 22-25). Transapical striae composed of elongate areolae crossed by apically oriented silica bars, resulting in small areolae. Areolae occluded by inwardly bent rods, attached perpendicularly to silica bars crossing areolae (Figs 23-25). Internally pores occluded by complex, highly branched volae (Figs 26, 27). Apical pore fields occur at both valve poles. Each pore field composed of several rows of small pores (Figs 23, 25).

Distribution: this species is so far known only from the Kerguelen Islands marine littoral samples.

Comments: *Pseudostaurosira quasielliptica* resembles *Fragilaria flavovirens* Takano, *Pseudostaurosira americana* Morales in Cejudo-Figueiras *et al.* 2011 (Cejudo-Figueiras *et al.* 2011). *Fragilaria flavovirens* was described from shallow water sandy sediments of Mikawa Bay in Japan (Takano 1986). The two species are similar in terms of their overall morphology but differ with respect to stria density: *F. flavovirens* has slightly narrower valves (2.8-5 versus 6-7 μm) and a distinctly higher stria density, 16-18, as compared to 10-12 in 10 μm for *P. quasielliptica*. *Pseudostaurosira americana* has similar valve outline, though its valves are isopolar and distinctly lanceolate with acutely rounded apices and with a distinct and narrow sternum. However, it differs from *P. quasielliptica* in terms of much denser striation, 16-18 versus 10-12 in 10 μm in *P. americana* and *P. quasielliptica* respectively.



Figs 28-39. – *Pseudostaurosira gersondei* sp. nov. Figs 28-31 LM. Scale bar = 10 µm. Fig. 28 is of the holotype specimen (DIC). Figs 32-39 SEM. Figs 32-36. Valve external view, note the presence of areolae occlusions (arrow head in Fig. 32) and of apical pore fields (arrows in Fig. 33). Fig. 34. Valve view of a specimen showing the shape of the sternum and the apically oriented bars which bear the connecting spines (arrow head). Figs 35, 36. Lateral view of the valve exterior focused on the mantle showing the presence of connecting spines (arrow head in Fig. 35) and the areolae occlusions (arrow head in Fig. 36). Figs 37-39. Valve interior showing the pore fields (arrow heads in Fig. 39) and the areolae occlusions (arrow in Fig. 38). Fig. 38 represents close-up of specimen illustrated in Fig. 39.



Figs 40-55. – *Pseudostaurosira latesternum* sp. nov. Figs 40-46 LM. Scale bar = 10 μ m. Fig. 42 represents the holotype (DIC). Figs 47-55 SEM. Figs 47-49 external valve view, note the sternum shape (arrow in Fig. 47), position of connecting spines (arrow in Fig. 48) and the type of areolae occlusions (arrow head in Fig. 49) and the foot pole pore field (arrow in Fig. 49). Figs 50-55 Valve internal view showing the areolae occlusions (arrow heads in Figs 51-53) and the pore fields (arrow heads in Figs 52 and 55). Figs 52 and 55 illustrate close-up of specimen shown in Fig. 54.

Pseudostaurosira gersondei* sp. nov. Figs 28-39*Descriptio :**

Valvae leniter heteropolaris, 11-15.5 μm longae, 4-6.5 μm latae ; vertex rotundatus et polus basalis obtusus. Perdistinctum sternum, rectum sed angustum. Striae transapicales parallelae per totam valvam, 9-10 in 10 μm .

Holotype: slide no. 7350_8 in Coll A Witkowski, Institute of Marine Sciences University of Szczecin (SZCZ), leg C Riaux-Gobin. Holotypus Fig. 28.

Isotypi: slide No. KER13 in Collection C Riaux-Gobin, USR 3278 CNRS-EPHE, CRIOBE-Université de Perpignan, slide No. ZU7/81 in Friedrich Hustedt Diatom Collection, Alfred Wegener Institute for Polar and Marine Research, Bremerhaven

Type locality: Île Haute, intertidal, Dec. 1991

Habitat: in Kerguelen sediments

Etymology: this species is dedicated to Dr Rainer Gersonde (Alfred Wegener Institute, Bremerhaven, Germany) in recognition of his contribution to the development of diatomology and of diatom based palaeoclimatic and palaeoceanographic reconstructions.

LM: (Figs 28-31)

Valves weakly heteropolar, with broadly rounded head pole and narrower, obtusely rounded foot pole, 11-15.5 μm long, 4-6.5 μm broad. Sternum distinct, linear, but narrow. Transapical striae parallel throughout, 9-10 in 10 μm .

SEM: (Figs 32-39)

Valve face flat with slightly elevated interstriae. Transition between valve face and mantle gradual (Figs 32-34). Apical pore fields at both poles, each composed of few rows of fine puncta (Fig. 33). Transapical striae composed of one large areola crossed by apically oriented bars (Fig. 33); each bar with a single inwardly oriented rod like protrusion to which connects volate, highly branched occlusions; positioned at valve internal surface level (Figs 37-39). Junction at valve face and mantle delineated by robust connecting spines, solid and positioned on apically oriented bars within striae (Figs 35, 36). Bars located at valve face margin (Fig. 36).

Comments: *Pseudostaurosira gersondei* does not resemble any described species of *Pseudostaurosira* or *Opephora* s.l. A single image of a valve face of *Pseudostaurosira gersondei* is illustrated in Van de Vijver *et al.* (2002, Pl. 10: 33), named as *Opephora naveana*. The valve outline of some specimens of *P. gersondei* resemble *O. mutabilis* (Grunow) Sabbe & Vyverman (Sabbe & Vyverman 1995). The two species also overlap in terms of size and striae density: *O. mutabilis* has length of 7-60 μm and width of 2.5-7 μm , whereas *P. gersondei* is 11-15.5 μm long and 4-6.5 μm broad. Striae number in the former species ranges from 6 to 14 in 10 μm , whilst the latter has 9-10 in 10 μm (Sundbäck 1987, Krammer & Lange-Bertalot 1991, Witkowski *et al.* 2000). However,

the striae fine structure differs. In *P. gersondei* the striae forming areolae are consequently occluded with a single rod-like protrusion which terminates in a highly branched occlusion, whereas in *O. mutabilis* externally a few such protrusions are connected to the areolae margins forming a sort of complicated net in the middle of each areolae, whereas internally they form highly branched volate occlusions typical for *Pseudostaurosira* (Sundbäck 1987).

Pseudostaurosira latesternum* sp. nov. Figs 40-55*Descriptio :**

Valvae heteropolaris, claviformes, 10-23 μm longae, 1.9-3.2 μm latae, cum brevior obtuso rotundato vertice et longiore angusto, leviter prolongato ad capitato polo basali. Sternum perdistinctum, angustum, rectum prope apices et amplius, lanceolatum in media parte. Striae transapicales perpendiculares, abbreviatae in media parte, 18-20 in 10 μm .

Holotype: slide no. 7354_1 housed in Coll. A Witkowski at the Marine Sciences Institute, University of Szczecin, Poland (SZCZ). Holotype Fig. 42.

Isotypi: slide No. KER14 in Collection C Riaux-Gobin, USR 3278 CNRS-EPHE, CRIOBE-Université de Perpignan, slide No. ZU7/82 in Friedrich Hustedt Diatom Collection, Alfred Wegener Institute for Polar and Marine Research, Bremerhaven.

Type locality: Port Raymond, subtidal, Nov. 1991.

Habitat: in Kerguelen subtidal sediments.

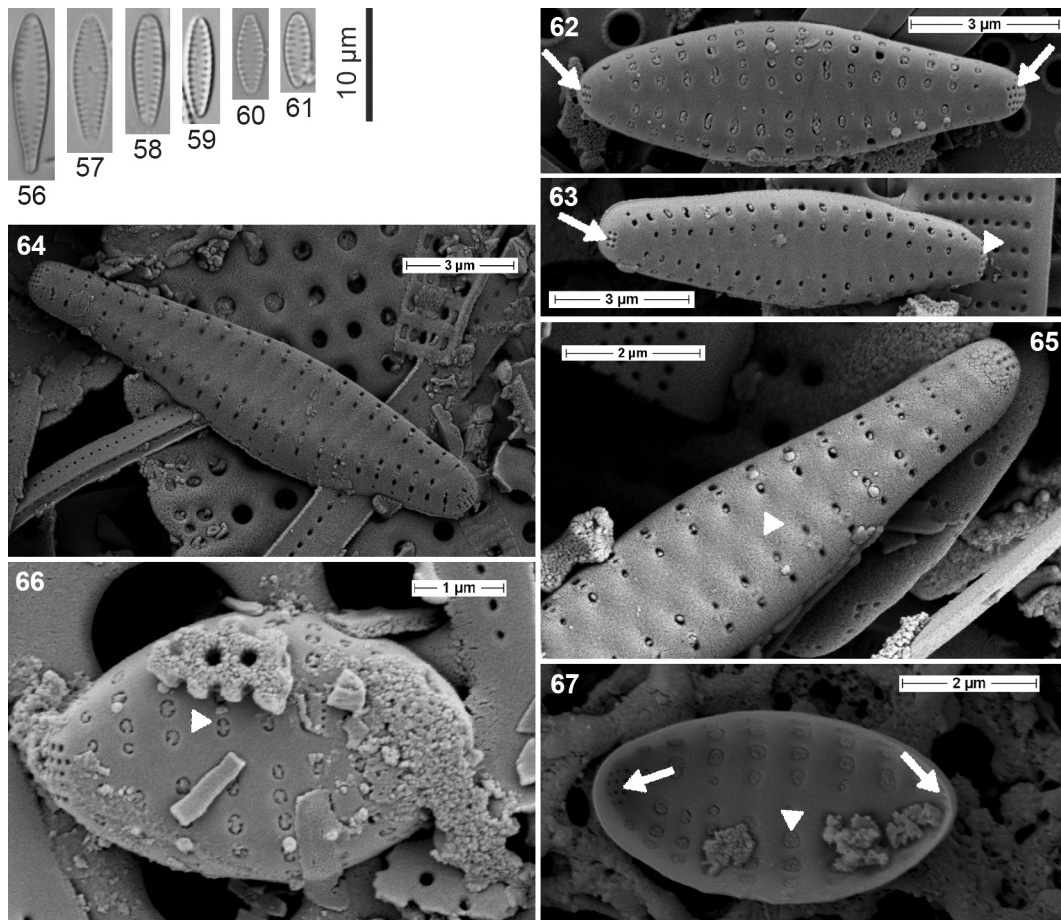
Etymology: the specific epithet refers to a relatively broad, linear-lanceolate sternum.

LM: (Figs 40-46)

Valves heteropolar, club shaped, with shorter, slightly broader obtusely rounded head pole and distinctly longer, narrower, slightly protracted to capitate foot pole, 10-23 μm in length and 1.9-3.2 μm in width. Sternum distinct, narrow, linear at apices becoming broader, lanceolate towards middle. Transapical striae perpendicular, shortened at middle due to broadened sternum, 18-20 in 10 μm .

SEM: (Figs 47-55)

Frustules rectangular in girdle view, valve surface flat turning abruptly towards relatively steep mantle (Figs 47-49). Valve face/mantle transition marked by occurrence of relatively long connecting spines, surrounded by few (2-3) distinctly smaller spines similar to *Opephora mutabilis* (cf. Sundbäck 1987). Larger spines positioned on apically oriented bars, which cross striae (Fig. 49). Sternum broad, linear lanceolate, broadening towards valve middle (Figs 50-53). Transapical striae composed of oblong areolae located along valve margin (Fig. 49). Areolae occluded with complex-shaped volate occlusions, typical for species of *Pseudostaurosira* (Figs 52-55). Distinct pore fields at both apices, composed of few parallel



Figs 56-67. – *Pseudostaurosira versiformae* sp. nov. Figs 56-61 LM. Scale bar = 10 µm. Fig. 59 represents the holotype (DIC). Figs 62-67 SEM. Figs 62-66. External valve views. Fig. 62. Specimen showing the presence of well developed apical pore field (arrows). Figs 63-66. Specimens illustrating the variation in shape and in the transapical striae development. Fig. 63. Specimen with well developed foot pole pore field (arrow head) and poorly developed apical one (arrow). Fig. 65. Close-up of a specimen showing the shape of the sternum (arrow head). Fig. 66. Valve with well preserved areolae occlusions (arrow). Fig. 67. Valve internal view showing the presence of the apical pore fields (arrows) and the ultrastructure of the areolae occlusions (arrow head).

rows of small poroids with head pole smaller than foot pole (Figs 52, 55).

Comments: in terms of valve outline *Pseudostaurosira latesternum* most closely resembles *Trachysphenia acuminata* Peragallo, both possessing similar valve shapes, though valves of *T. acuminata* are somewhat protracted and distinctly more acutely rounded. They differ, however, in sternum shape, which in *T. acuminata* is very narrow and strictly linear. Different is the valve ultrastructure in *P. latesternum*. Unlike in our new species, *Trachysphenia* representatives have domed valves showing no presence of linking spines. The pore fields are differently structured than in *P. latesternum*: those in *Trachysphenia* are composed of a cluster of pores (Round *et al.* 1990) unlike our species which form distinct rows of pores at both apices. The striae ultrastructure of *Pseudostaurosira latesternum* resembles some species of *Opephora*, *O. mutabilis* in particular. However, all valve measurements of *P. latesternum* differ from those of *O. mutabilis*. The most distinct feature of *Pseudostaurosira latesternum* is its broad, linear lanceolate sternum. A simi-

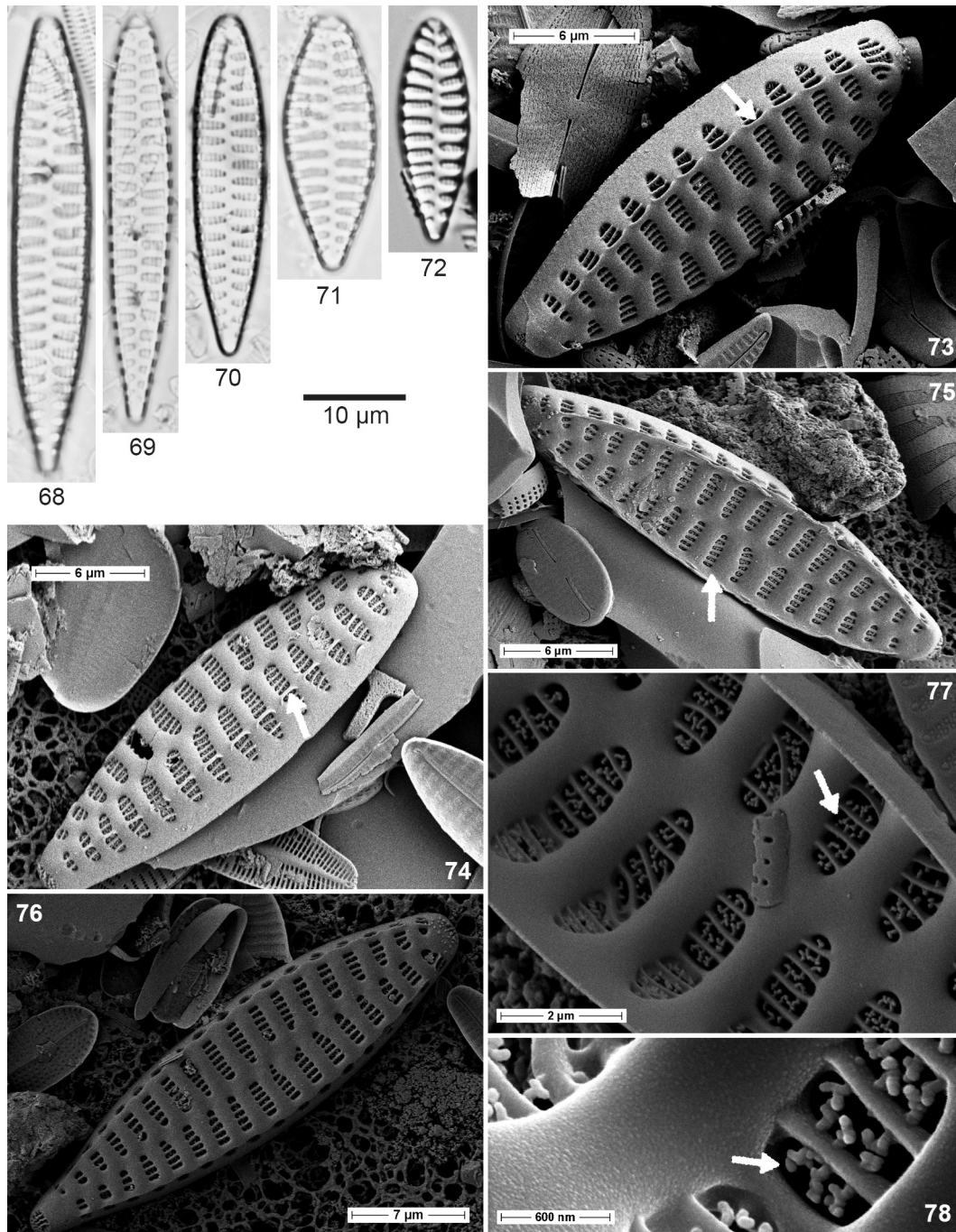
lar sternum occurs in *O. minuta* (Cleve-Euler) Witkowski, Lange-Bertalot & Metzeltin (Witkowski *et al.* 2000) but the latter species differs with respect to the metric characteristics and its valve shape: in *O. minuta* the apices are obtusely rounded and the foot pole is never capitate. Interestingly, the areolae occlusions in *P. latesternum* are typical for *Pseudostaurosira*, but closely resemble those observed in some *Opephora* s.l. and in *Nanofrustulum* and *Trachysphenia* (Round *et al.* 1990, Witkowski 1994, Witkowski *et al.* 2000, this paper).

Pseudostaurosira versiformae sp. nov. Figs 56-67

Descriptio :

Valvae variabili aspectu, paulo ad valde heteropolaris, ellipticae ad lineares, ad apices rotundatae, 5-14 µm longae, 2-3 µm latae. Sternum saepe amplum et lanceolatum. Striae transapicales breves et marginales, parallelae in media parte et radiantes ad apices, 18-20 in 10 µm.

Holotype: slide no. 7354_1 in Coll A Witkowski Insti-



Figs 68-78. – *Staurosirella poulinii* sp. nov. Figs 68-72 LM. Scale bar = 10 μ m. Fig. 72 represents the holotype specimen (DIC). Figs 73-78. SEM. Figs 72-76. Valve external view showing the valve surface and the mantle, note also the presence of peculiar connecting spines (arrow in Figs 73 and 74). Fig. 75. Specimen showing the valve face with slightly depressed striae (arrow). Fig. 76. Valve view of a specimen with well developed apical pore fields (arrow heads). Figs 77, 78. Valve internal views, note the fine structure of the areolae including apical bars crossing the areolae (arrow in Fig. 77) and the occlusions (arrow in Fig. 78).

tute of Marine Sciences University of Szczecin (SZCZ), leg C Riaux-Gobin. Holotypus Fig. 59.

Isotypi: slide No. KER15 in Collection C Riaux-Gobin, USR 3278 CNRS-EPHE, CRIOBE-Université de Perpignan, slide No. ZU7/83 in Friedrich Hustedt Diatom Collection, Alfred Wegener Institute for Polar and Marine Research, Bremerhaven.

Type locality: Port Raymond, subtidal, Nov. 1991.

Habitat: in Kerguelen subtidal sediments.

Etymology: the epithet refers to the highly variable outline of the valve shape.

LM: (Figs 56-61)

Valves highly variable in shape, from strongly heteropolar to slightly heteropolar, almost elliptic to almost linear with broadly rounded apices, 5-14 μ m in length, 2-3 μ m in width. Sternum usually broad, lanceolate in

shape. Transapical striae short, positioned in valve margin, parallel at middle, becoming radiate towards apices, 18-20 in 10 μm .

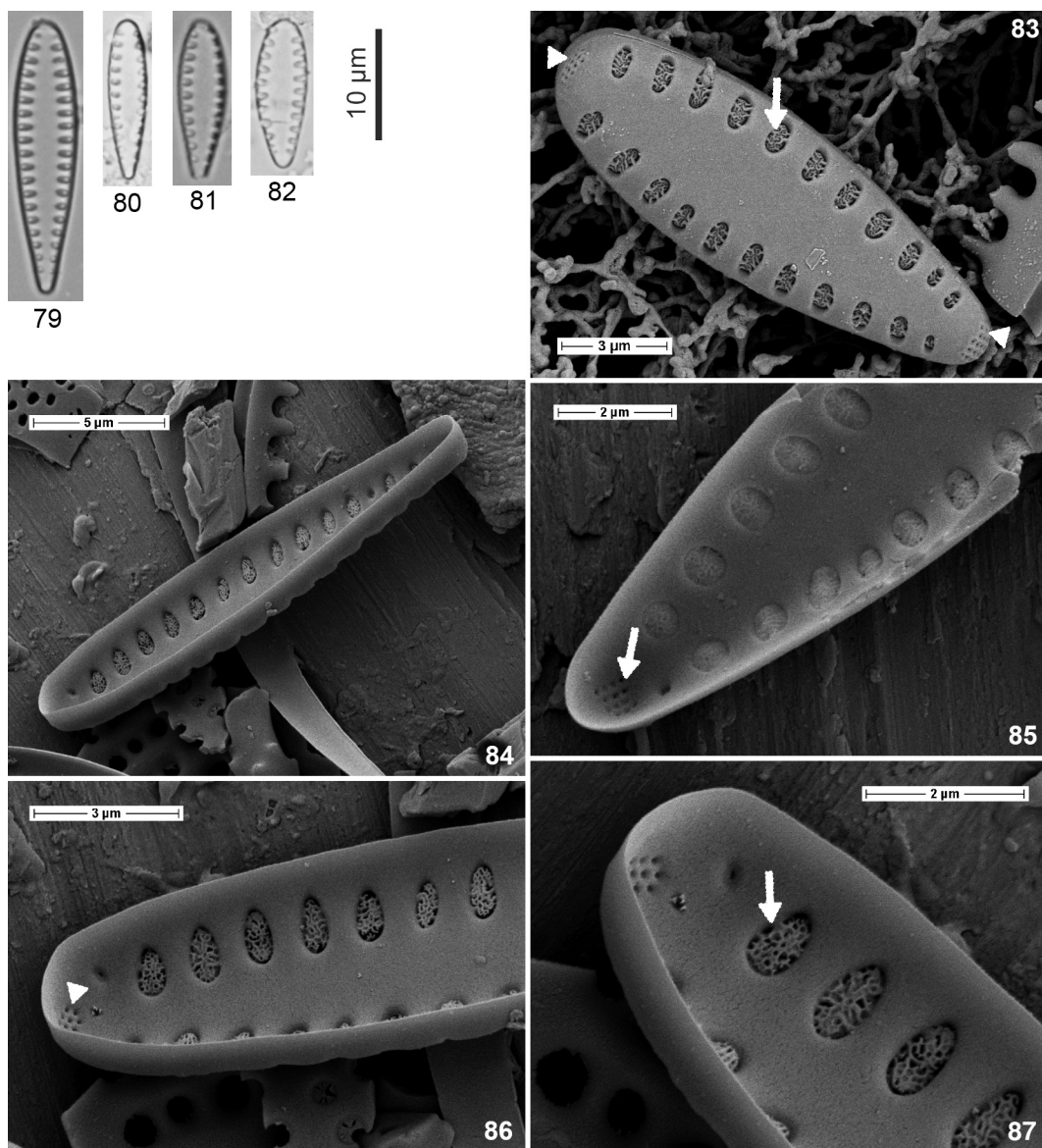
SEM: (Figs 62-67)

Valve face flat in small specimens (approaching linear-elliptical) to slightly arched in longer more heteropolar specimens. Sternum variable in shape, from narrow linear to rather broad linear lanceolate (Figs 62-66). Transapical striae composed of oblong, small areolae. Number of areolae in one stria range from one to few, hence differences in appearance of sternum (Figs 65, 66). Areolae occlusions complicated in shape of volate type, externally and

internally typical of *Pseudostaurosira* (Fig. 66). Valve interior flat, transapical striae positioned in indistinct depressions (Fig. 67). Pore fields at both apices. Foot pole pore field much larger, composed of few rows of small poroids. Head pole very small, usually composed of few poroids (Figs 62, 67).

Comments: *Pseudostaurosira versiformae* has a unique combination of characters unknown in any other species.

Distribution: *Pseudostaurosira versiformae* has also been encountered in samples collected from the South African coast. In Africa it is a common taxon/species (Witkowski unpublished observations).



Figs 79-87. – *Opephora* aff. *marina* (Gregory) Petit. Figs 79-82. LM. Scale bar = 10 μm . Figs 83-87 SEM. Fig. 83. Valve external view showing the ultrastructure of the striae occlusions (arrow) and the apical pore fields (arrow heads). Figs 84-87. Valve internal views. Fig. 84. Specimen showing the position of the striae forming areolae along the transition from the valve face to the mantle. Figs 85-87. Specimens showing the areolae and the apical pore fields, note the ultrastructure of areolae occlusions (arrow in Fig. 87) and the apical pore fields (foot pole - arrow in Fig. 85) and the apical one (arrow head in Fig. 86).

Staurosirella Williams & Round 1987*Staurosirella poulinii* sp. nov. Figs 68-78

Descriptio :

Heteropolaes valvae, claviformes, 24-45 μm longae, 6-10 μm latae, cum late obtuse rotundato vertice et acuto basali polo. Sternum perdistinctum. Robustae transapicales striae, parallelae ad leniter radiantes ad apices, 5.5-6.5 in 10 μm , areola unica formatae, reticulo linearum ad apices directarum munita.

Holotype: slide no. 7350_8 housed in Coll A Witkowski at the Marine Sciences Institute, University of

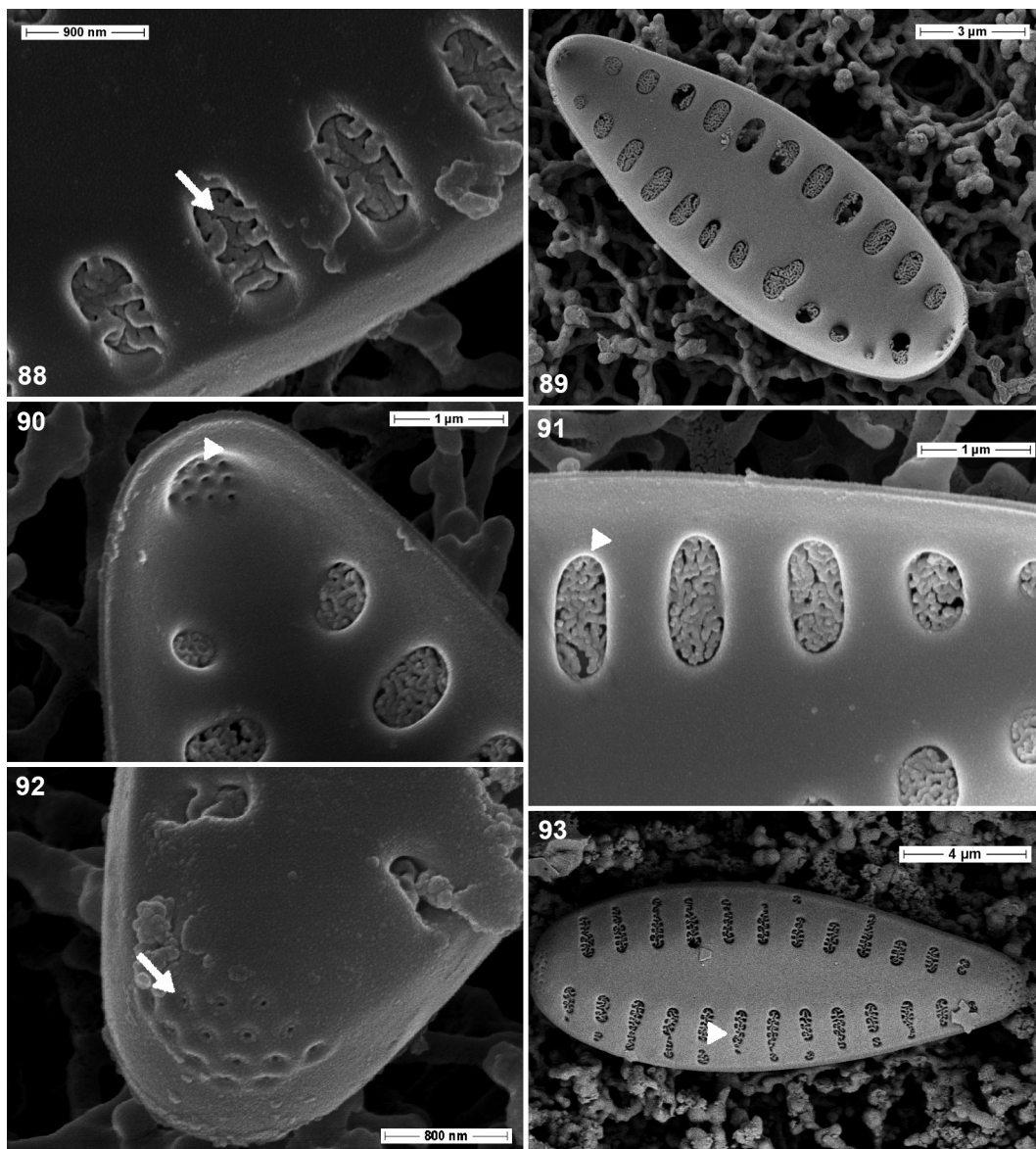
Szczecin, Poland (SZCZ). leg C Riaux-Gobin. Holotypus Fig. 72.

Isotypi: slide No. KER16 in Collection C Riaux-Gobin, USR 3278 CNRS-EPHE, CRIOBE-Université de Perpignan, slide No. ZU7/84 in Friedrich Hustedt Diatom Collection, Alfred Wegener Institute for Polar and Marine Research, Bremerhaven.

Type locality: Île Haute, intertidal, Dec. 1991

Habitat: in Kerguelen sediments

Etymology: this species is dedicated to Dr M Poulin from the Canadian Museum of Nature, Ottawa, Canada in recognition of his contribution to research on the diatom flora of high latitudes of both Hemispheres.



Figs 88-93. – *Opephora* aff. *marina* (Gregory) Petit. Figs 88-92. SEM. Figs 88, 92. Valve external surface, note the fine structure of areolae occlusions (arrow in Fig. 88) and close-up of apical pore field (foot pole, arrow in Fig. 92). Figs 89-91. Valve internal view showing the broad sternum with striae forming areolae along the valve margin. Figs 90, 91. Close-up of the foot pole pore field (arrow head in Fig. 90) and the fine structure of the areolae occlusions (arrow head in Fig. 91). Fig. 93. Valve external view of the specimen originating from South Africa showing some degree of teratological development of striae forming areolae (arrow head), note the size of the areolae which is distinctly larger than in Kerguelen specimens.

LM: (Figs 68-72)

Valves heteropolar, club shaped, with broader, obtusely rounded head pole and narrower, acutely rounded foot pole, 24-45 μm long, 6-10 μm broad. Sternum distinct. Transapical striae robust, parallel becoming slightly radiate towards apices, 5.5-6.5 in 10 μm . Transapical striae composed of one areola, crossed with apically oriented bars, net-like.

SEM: (Figs 73-78)

Valve face flat, with slightly raised interstriae (Figs 73-75). Transition between valve face and mantle abrupt. Contact between valve face and mantle delineated by robust bar (Figs 74, 75). Sternum zig-zag in shape (Figs 74-76). Apical pore field at both poles, composed of few rows of puncta. Head pole apical pore field smaller than that of foot pole (Fig. 76). Transapical striae composed of one large areola crossed by several apically oriented bars. Apical bars occurring at valve margin divide areola in half, each further subdivided by few finer bars. Areolae occlusions, of volate type, as in *Staurosirella* (Figs 77, 78). Internally valve mantle steep and relatively deep. Valve interior flat with elevated interstriae and depressed transapical striae. Striae forming areolae fairly similar to external view. Areolae crossed by apically oriented bars with volate occlusions (Figs 77, 78).

Comments: in LM, *Staurosirella poulinii* resembles *Staurosirella martyi* (Hérubaud) Morales & Manoylov (Morales & Manoylov 2006) but with fewer transapical striae (5.5-6.5 versus 6-10) in 10 μm . *Staurosirella martyi* has a domed valve face unlike *Staurosirella poulinii*, which has a flat valve face. Though the areolae in *S. martyi* also bear apical bars, no apical bar delineating valve face from the mantle was observed. Furthermore, *S. poulinii* appears similar to *Staurosira jolinae* Van de Vijver in LM. However, *Staurosira jolinae* has a completely different fine structure the transapical striae and distinctly denser transapical striae (9-11 in 10 μm).

Opephora aff. *marina* (Gregory) Petit. Figs 79-93

LM: (Figs 79-82)

Valves heteropolar, clavate with broadly rounded head pole and acutely rounded foot pole, 13-25 μm in length, 4-6 μm in width. Sternum relatively broad, linear lanceolate. Transapical striae short confined to valve margin only, parallel in middle becoming slightly radiate towards apices, 8-9 in 10 μm .

SEM: (Figs 83-93)

Valve face flat, gently bent towards valve mantle; mantle rather shallow, steep, devoid of ornamentation. Sternum flat (Figs 83, 89). Pore field at both apices, of almost equal size (Fig. 83); pore fields differ internally from externally: externally composed of several, parallel rows of small pores, apically oriented (Fig. 83, 92); internally, both pore-fields smaller, with oblong shape, forming aggregations of pores without any discernible

distribution pattern (Figs 85-87, 90). Transapical striae composed of one areola (Fig. 84), occluded with complex vela attached to margin of each areola, bending inwards, typical for species of *Opephora* s.s. (Figs 88-91).

Distribution: *Opephora marina* predominantly occurs in the Northern Hemisphere; it has rarely been recorded from the Southern Hemisphere (e.g. Witkowski unpublished observations). However, in the last few decades the specimens illustrated here were identified from the Western Indian Ocean (Giffen 1980, Witkowski unpublished results) and now from Kerguelen.

Comments: *Opephora marina* has been studied in detail by Andrén (1997). Specimens from the western Baltic Sea were observed using LM and SEM whereas original material (Lamlash Bay, Scotland) of *Meridion marinum* Gregory – the basionym of *O. marina* – was examined only in LM. When compared to the illustrations in Andrén (1997), our specimens can be identified as *Opephora* aff. *marina*. In general the only difference between the Kerguelen specimens and those studied by Andrén (1997) is that the specimens from Kerguelen have shorter valves. Specimens from Kerguelen, had valves 13-25 μm long, whereas those from the Baltic Sea were 16-41 μm long and those from Lamlash Bay, Scotland were 25-52 μm long. It is interesting to note that in terms of valve width and stria density specimens from Kerguelen resemble more closely the specimens from the Baltic Sea rather than those from Scotland. The width of the valves was 4-6 μm whereas the stria density ranged 8-9 in 10 μm and 8-11 in 10 μm in Kerguelen and Baltic Sea specimens, respectively. In the specimens from Gregory's material (Scotland), the valve width was slightly lower (4-5 μm), whereas the stria density range was very large, amounting to 5-10 in 10 μm (cf. Andrén 1997).

DISCUSSION

In this paper we have described six new species of diatoms. All are araphid diatoms and belong to the following genera: *Nanofrustulum* (1 species), *Pseudostaurosira* (4) and *Staurosirella* (1). All the new species originate from the marine littoral and sub-littoral habitats of Kerguelen main Island. In addition we present detailed ultrastructural analysis of a species that very closely resembles *Opephora marina* but differs from the type material in some metric characteristics, the most important being valve length. Hence we have decided to refer to it as *O. aff. marina*.

It is not an easy task to find appropriate generic positions for araphid diatoms with heteropolar valves as numerous authors have opted for the genus *Opephora*. As already pointed out by Round *et al.* (1990), the genus delimitation of *Opephora* is too vague, even though the species included have different striae structures (e.g. Sundbäck 1987, Round *et al.* 1990, Witkowski 1994, Sabbe & Vyvermann 1995, Andrén 1997, Morales 2002). Under

the assumption that the genus *Opephora* includes only species that conform to its generitype – *O. pacifica* – then numerous taxa grouped around *O. mutabilis* (= *O. olsenii* Møller) should be excluded. Thus, *Opephora* would have only a few species, including *O. pacifica* and *O. marina*, with the remaining (more than 10) species assigned to a new genus (or genera). Morales (2002) has already made a preliminary survey of taxa belonging to *Opephora* s.l. and for some of them suggested to which genera they need to be transferred. Likewise, in our opinion, if the taxonomy of araphid diatoms is to be clarified, taxa around *O. mutabilis* should be transferred to a new genus, thus separating a group of taxa which have great bioindication potential for assessing water quality in marine littoral zone.

To the best of our knowledge data relevant to *Opephora pacifica* and *O. marina* originates from treated material with no data yet on live cells. For example, it is still unknown whether either of the two form colonies. Hence, generic affinity should rather be based on characteristics which are known with some certainty, such as the stria structure. Therefore we support proposal of Round *et al.* (1990), and later Morales (2002), to include in *Opephora* only taxa that conform to the generitype. In this respect, our study on *O. aff. marina* is a good example of the genus *Opephora*. As this species occurred abundantly in South Africa and Kerguelen we hope to culture it and observe living material. However, the remaining opephoroid taxa we discovered do not conform the genus *Opephora* hence our decision to place them in *Nanofrustulum*, *Pseudostaurosira* and *Staurosirella*.

The aim of our research, besides describing new for science species from the Kerguelen Islands, was to provide a contribution to the species currently classified in *Opephora* but which do not conform to the generitype. Many of these species have been extensively studied but no formal transfers have been made to the appropriate genus (e.g. Round *et al.* 1990, Sabbe & Vyvermann 1995, Morales 2002). Included in this group are e.g. *O. mutabilis*, *O. guenter-grassii* (Witkowski & Lange-Bertalot) Sabbe & Vyverman, *O. horstiana* Witkowski and *O. krumbeinii* Witkowski, Witak & Stachura in Lange-Bertalot & Genkal (1999). Genera with morphology similar to this group of *Opephora* species are *Pseudostaurosira* (Sabbe & Vyvermann 1995, Morales 2001), *Nanofrustulum* (Round *et al.* 1999) and *Staurosirella* (e.g. Round & Williams 1987, Morales & Manoylov 2006). With *Pseudostaurosira* and *Nanofrustulum* the above group of *Opephora* has a similar type of areolae occlusions (Sundbäck 1987, Witkowski 1994, Sabbe & Vyverman 1995, Morales 2001). They differ, however, in the areolae structure. In the species of *Opephora* in question the striae are similar to *Staurosirella*. That is, they have a large areolae subdivided by numerous secondary, apically oriented bars to which the occlusions are bound. In *Pseudostaurosira* and *Nanofrustulum* the striae are composed of a certain number of rather small oblong areolae occluded by vela

(Lange-Bertalot & Genkal 1999, Round *et al.* 1999, Witkowski *et al.* 2000, Morales 2001, Cejudo-Figueiras *et al.* 2011). In *Staurosirella*, the striae are similar to this group of *Opephora* species though the areolae occlusions are less complicated. It is possible that *Nanofrustulum* is the appropriate genus to accommodate *O. krumbeinii*, whereas *Staurosirella* seems appropriate for *O. guenter-grassii*. The latter solution has already been proposed by Morales (2002). However, *O. mutabilis* remains a problem.

In terms of areolae occlusions, *Nanofrustulum* is the genus most similar to *O. guenter-grassii*. As shown by Sato *et al.* (2009), *Nanofrustulum shiloi* and *Opephora guenter-grassii* are sister taxa. Here we describe *N. squammatum*, the second species in genus *Nanofrustulum* represented so far by *Nanofrustulum shiloi* (= *Fragilaria shiloi*). The third possible species in this genus is *Opephora krumbeinii* Witkowski, Witak & Stachura in Lange-Bertalot & Genkal (1999), which requires transfer to *Nanofrustulum* (see above). However, *Nanofrustulum* species have different areolae to *O. guenter-grassii*, the former are small and usually oblong, whereas the latter are large and subdivided by secondary apically oriented bars as observed in *Staurosirella* (e.g. Williams & Round 1987, Morales & Manoylov 2006).

Nanofrustulum taxa share the areolation pattern, and to the certain extent the occlusion type, with representatives of *Pseudostaurosira*. Species representing the two genera differ in respect to the girdle and certain differences in the appearance of areolae occlusions. In *Nanofrustulum* the girdle is peculiar for araphid diatoms and composed of a series of fragmented quasifract bands, whereas in *Pseudostaurosira* the girdle is composed of a few broad, solid bands, common for many araphid genera (cf. illustrations in e.g. Williams & Round 1987, Round *et al.* 1990, Krammer & Lange-Bertalot 1991, Witkowski 1994, Morales 2005). Regarding the areolae occlusions, in some *Nanofrustulum* and *Pseudostaurosira* species they are relatively simple and are composed of rod-like outgrowths bent inwardly and terminating in a relatively simple vela (e.g. *N. Squammatum*, *P. brevistriata*). In other species belonging in these two genera (e.g. in *N. shiloi*, *P. gersondei* sp. nov.) the number of extensions is 1-2, which terminate in a highly branched vela (Lange-Bertalot & Genkal 1999, Round *et al.* 1999, Witkowski *et al.* 2000).

The taxa described here were all observed in samples collected from either intertidal or subtidal zone of the Kerguelen main Island. Although the salinity was not measured, we can estimate it as average oceanic, ranging from 33 to 35 psu. No freshwater sources exist in the neighbourhood of the sampling stations. No counts were made from our slides, but all the new taxa are common; in both LM and SEM preparations, numerous specimens of each were found. Hence, a conclusion is that these are their type habitat, exhibiting optimum living conditions.

All taxa described herein have heteropolar valves. Even if the heteropolarity of a given taxon is difficult to

observe in the LM or at low magnifications in the SEM (cf. *Pseudostaurosira versiformae*), the most convincing evidence of heteropolarity comes from the development of the apical pore fields. The head pole apical pore field is always smaller and composed of only a few poroids.

In summary, the most useful character to differentiate these new taxa is the transapical striae ultrastructure viewed in the electron microscope. In the LM, specimens differ in terms of their shape, size and transapical stria number.

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