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

A. WITKOWSKI1*, C. RIAUX-GOBIN2, G. DANISZEWSKA-KOWALCZYK1

1 Institute of Marine Sciences, University of Szczecin, Mickiewicza 18, PL-70-383 Szczecin, Poland
2 USR 3278 CNRS-EPHE, CRIOBE-Université de Perpignan, FR-66086 Perpignan, France

* Corresponding author: witkowski@univ.szczecin.pl

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 Naviculastum (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 Fragilariaeae 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, Martyna 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), Pseudostaurosiropsis Morales (Morales 2001) and Sarcophagodes Morales (Morales 2002).
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 Cohn 1988, 1999, Lange-Bertalot & Le Cohn 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 indent ed 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 Macrocytis pyriforma (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-cane 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

**Description:**
Frustula aspectu cingulari quadrata ad rectiangula. Valvae minutae, ovales ad subcirculares, 2.1-3.28 (in mediocris 2.6) \( \mu \text{m} \) longae, 1.6-2.3 \( \mu \text{m} \) 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 \( \mu \text{m} \). 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-EPE, CRIOB-Université de Perpignan, slide No. zu7/79 in Friedrich Hustedt Diatom Collection, Alfred Wegener Institute for Polar and Marine Research, Bremerhaven.


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) \( \mu \text{m} \) long; 1.6-2.3 \( \mu \text{m} \) broad; length/breadth ratio 1.3-1.7. Sternum distinct but narrow. Transapical striae uniseriate, alternating at valve middle: 35-50 (mean 40) in 10 \( \mu \text{m} \), 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 \( \mu \text{m} \)) 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 \( \mu \text{m} \)) composed of short well-defined segments (0.6-0.8 \( \mu \text{m} \) 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

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**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.**

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Girdle bands</th>
<th>Length (( \mu \text{m} ))</th>
<th>Width (( \mu \text{m} ))</th>
<th>Sternum shape</th>
<th>Striae in 10 ( \mu \text{m} )</th>
<th>Areolae type</th>
<th>Oclusions type internally</th>
<th>Oclusions type externally</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Nanofrustulum</em></td>
<td>Segmentated</td>
<td>2-1.28</td>
<td>6-7</td>
<td>Narrow linear</td>
<td>11-12</td>
<td>Single rod-like outgrowths</td>
<td>Single rod-like outgrowths</td>
<td>Relatively simple</td>
</tr>
<tr>
<td><em>N. squammatum</em></td>
<td>Segmentated</td>
<td>2-1.28</td>
<td>6-7</td>
<td>Narrow linear</td>
<td>11-12</td>
<td>Single rod-like outgrowths</td>
<td>Single rod-like outgrowths</td>
<td>Relatively simple</td>
</tr>
<tr>
<td><em>N. shiloi</em></td>
<td>Solid</td>
<td>10-15</td>
<td>14-15.5</td>
<td>Narrow linear</td>
<td>9-10</td>
<td>Single rod-like outgrowths</td>
<td>Single rod-like outgrowths</td>
<td>Relatively simple</td>
</tr>
<tr>
<td><em>Pseudostaurosira</em></td>
<td>Segmentated</td>
<td>2.6</td>
<td>1.5-3</td>
<td>Narrow linear</td>
<td>11-12</td>
<td>Single rod-like outgrowths</td>
<td>Single rod-like outgrowths</td>
<td>Relatively simple</td>
</tr>
<tr>
<td><em>P. americanus</em></td>
<td>Solid</td>
<td>6-10</td>
<td>2-3</td>
<td>Narrow linear</td>
<td>11-12</td>
<td>Single rod-like outgrowths</td>
<td>Single rod-like outgrowths</td>
<td>Relatively simple</td>
</tr>
<tr>
<td><em>O. leukenii</em></td>
<td>Solid</td>
<td>7-10</td>
<td>1-5</td>
<td>Narrow linear</td>
<td>6-7</td>
<td>Single rod-like outgrowths</td>
<td>Single rod-like outgrowths</td>
<td>Relatively simple</td>
</tr>
<tr>
<td><em>O. mutabilis</em></td>
<td>Solid</td>
<td>6-10</td>
<td>2-3</td>
<td>Narrow linear</td>
<td>6-7</td>
<td>Single rod-like outgrowths</td>
<td>Single rod-like outgrowths</td>
<td>Relatively simple</td>
</tr>
<tr>
<td><em>O. krumbeinii</em></td>
<td>Solid</td>
<td>6-10</td>
<td>2-3</td>
<td>Narrow linear</td>
<td>6-7</td>
<td>Single rod-like outgrowths</td>
<td>Single rod-like outgrowths</td>
<td>Relatively simple</td>
</tr>
<tr>
<td><em>P. americana</em></td>
<td>Solid</td>
<td>6-10</td>
<td>2-3</td>
<td>Narrow linear</td>
<td>6-7</td>
<td>Single rod-like outgrowths</td>
<td>Single rod-like outgrowths</td>
<td>Relatively simple</td>
</tr>
<tr>
<td><em>Fragilaria flavovirens</em></td>
<td>Solid</td>
<td>6-10</td>
<td>2-3</td>
<td>Narrow linear</td>
<td>6-7</td>
<td>Single rod-like outgrowths</td>
<td>Single rod-like outgrowths</td>
<td>Relatively simple</td>
</tr>
</tbody>
</table>
Figs 1-14. – *Nanofrustulum squammatum* sp. nov. Figs 1-3 LM. Scale bar = 10 µm. 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 *Trachysphaeria*. 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, Wittak & 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 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 *Pseudostraurosira* rather than *Nanofrustulum*. *Pseudostraurosira 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.

**Pseudostraurosira Williams & Round 1987**

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

**Descrip**tio**n**: 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 haec parum visibles 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: *Pseudostraurosira quasielliptica* resembles *Fragilaria flavovirens* Takano, *Pseudostraurosira 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*. *Pseudostraurosira 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.

*Vie Milieu*, 2010, 60 (3)
Fig. 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 µm. 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

**Descrip**

Valvae leniter heteropares, 11-15.5 μm longae, 4-6.5 μm lateae; vertex rotundatus et polus basalis obtusus. Perdistinctum sternum, rectum sed angustum. Striae transapicales parallelæ 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 33). 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, whereas internally they form highly branched volute occlusions typical for *Pseudostaurosira* (Sundbäck 1987).

**Pseudostaurosira later sternum** sp. nov. Figs 40-55

**Descrip**

Valvae heteropoles, claviformes, 10-23 μm longae, 1.9-3.2 μm lateae, cum breviore 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 perpendicularæ, 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)

Frustrules 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 volute occlusions, typical for species of *Pseudostaurosira* (Figs 52-55). Distinct pore fields at both apices, composed of few parallel...
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 similar 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 heteropolares, 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-
HETEROPOLAR SPECIES OF FRAGILARIACEAE FROM KERGUELEN ISLANDS

Institute 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 μm in length, 2-3 μm in width. Sternum usually broad, lanceolate in

Staurosirella poulinii

Figs 68-78. – Staurosirella poulinii sp. nov. Figs 68-72 LM. Scale bar = 10 μm. 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).
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).

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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:*

Heteropolars 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.

*Vie Milieu, 2010, 60 (3)*
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* (Héribaud) Morales & Manoylov (Moraes & 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. olсенii* 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 striae 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*, *Pseudoastaurosira* 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, Sabe & Vyverman 1995, Morales 2002). Included in this group are e.g. *O. mutabilis*, *O. guenter-grassii* (Witkowski & Lange-Bertalot 1999), *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 *Pseudoastaurosira* (Sabe & Vyverman 1995, Morales 2001), *Nanofrustulum* (Round et al. 1999) and *Staurosirella* (e.g. Round & Williams 1987, Morales & Manoylov 2006). With *Pseudoastaurosira* and *Nanofrustulum* the above group of *Opephora* has a similar type of areolae occlusions (Sundbäck 1987, Witkowski 1994, Sabe & 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 *Pseudoastaurosira* 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 *Pseudoastaurosira*. 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 *Pseudoastaurosira* 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, Kramer & Lange-Bertalot 1991, Witkowski 1994, Morales 2005). Regarding the areolae occlusions, in some *Nanofrustulum* and *Pseudoastaurosira* 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. *Pseudoastaurosira 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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