Phytotaxa 618 (1): 069–078
https://www.mapress.com/pt/
Copyright © 2023 Magnolia Press

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

https://doi.org/10.11646/phytotaxa.618.1.6

Rhoicosphenia johannessoniae (Bacillariophyceae), a new diatom from the Swedish coast of the Baltic Sea

ADIL Y. AL-HANDAL[1,3], ZLATKO LEVKOV[2,4] & ANGELA WULFF[1,5]
[1]*Department of Biological and Environmental Sciences, Faculty of Science, University of Gothenburg, Sweden*
[2]*Institute of Biology, Faculty of Natural Sciences, Ss. Cyril and Methodius University, Skopje, Macedonia*
[3] *adil.yousif@bioenv.gu.se; https://orcid.org/0000-0003-4703-7823*
[4] *zlevkov@pmf.ukim.mk*
[5] *angela.wulff@bioenv.gu.se; https://orcid.org/0000-0003-0015-7019*

Abstract

Rhoicosphenia is a relatively small diatom genus regarding the number of species and the genus is characterized by its wedge-shaped frustule and heterovalvar structure. It is one of the few genera that is distributed in both marine and freshwater habitats. Few species of *Rhoicosphenia* are known along the stretched Baltic Sea coast of Sweden. The present study describes a new epiphytic species of *Rhoicosphenia* from the brackish water of Grisslehamn in the northern part of the Baltic Sea. *Rhoicosphenia johannessoniae sp. nov*. appears closely related to *R. baltica,* but differs in having more elongated and protracted base pole, densely packed areolae and a central area located below the central part of the valve. Detailed descriptions of the species based on light and electron microscopy, as well as a comparison with related taxa, are provided. The present work is part of a larger project aiming to study the littoral diatoms of Sweden. The finding of this species, together with other species previously described within the project, will add to our knowledge of the diatom assemblages of the Baltic Sea which seems to have a richer flora than earlier anticipated.

Key words: Baltic Sea, epiphytic, heterovalvar, morphology, new species

Introduction

Rhoicosphenia Grunow (1860: 511) although less diverse than many diatom genera, is widely distributed in a variety of habitats stretching from the poles to the equator (Witkowski *et al.* 2000). It may be found as epiphytic on filamentous algae, macrophytes, epilithic, or free-living on the sediment in fresh, brackish and marine environments (Giffen 1970, Medlin & Fryxell 1984, Al-Handal & Wulff 2008a, b, Levkov *et al.* 2010, Harper *et al.* 2012, Ligowski *et al.* 2014, Thomas *et al.* 2015). Not all the *Rhoicosphenia* species, however, are widely distributed, the newly described species are mostly found in a narrow geographic region (Levkov & Navkov 2008, Levkov *et al.* 2010). Only the rather old *Rhoicosphenia abbreviata* (C.Agardh) Lange-Bertalot (1980:586) (widely cited as *Rhoicosphenia curvata* (Kützing) Grunow 1860: 511) is considered cosmopolitan, but this can also be due to misidentification or a more broad species concept (Thomas *et al.* 2016).

Rhoicosphenia can be easily distinguished in light microscopy owing to some characteristic features such as the frustule wedge shape and the heterovalvar structure (Mann 1984, Medlin & Fryxell 1984, Round 1990). The most conspicuous feature of the genus is its dissimilar valve curvature and raphe structure on the two valves (Mann 1982). The valve with a complete raphe system (R-valve) is concave while the other valve is convex and characterized by a reduced raphe system (D-valve) where raphe fissures are confined to the polar parts of the valve. Like several other old diatom genera, *Rhoicosphenia* has been a subject of thorough investigations to reveal its structure and phylogeny (Mann 1982, 1984, Medlin & Fryxell 1984, Thomas *et al.* 2015). Because of its reduced raphe fissures on one valve, *Rhoicosphenia* was originally considered as member of the monoraphid order Achnanthales (Kützing 1844, Grunow 1860, Cleve-Euler 1953). Based on its chloroplast structure, which is similar to that of *Gomphonema* Ehrenberg (1882), Van Heurck (1896) considered the genus as biraphid and placed it in the family Gomphonemaceae. Recent studies on the diatom chloroplasts and valve structure (Cox & Williams 2006) showed that *Rhoicosphenia* has a distinctive

Accepted by Karthick Bala: 12 Sept. 2023; published: 29 Sept. 2023

cladistic position among raphid diatoms, but closely related to *Gomphonema.* Recent molecular analysis of some members of *Rhoicospheinia* suggests that this genus cannot be considered as a sister to *Gomphonema*, as previously hypothesized, but both occupy a lineage in the order Cymbellales (Thomas *et al.* 2016). Currently, *Rhoicosphenia* is placed in the family Rhoicospheniaceae (Chen & Zhu 1983) which also include *Campylopyxis* Medlin (1985:313)*, Cuneolus* Giffin (1979:87)*, Gomphoseptatum* Medlin (1980:212) and *Gomphonemopsis* Medlin (1986:207).

Distribution of *Rhoicosphenia* species in the Swedish freshwater and marine habitats is not well known and only few species have been documented. *Rhoicosphenia abbreviata* is the most reported species of the genus in the west coast of Sweden (Cleve-Euler 1953, Edsbagge 1968, Aleem 1973). This species is also abundant on the Swedish Baltic coast (Snoeijs 1989), which also seems the only *Rhoicosphenia* taxon reported from this region. Other *Rhoicosphenia* species documented from the west coast of Sweden were *R. baltica* (Schumann) Levkov as *Rhoicosphenia curvata* var. *baltica* (Schumann) Cleve-Euler (Cleve-Euler 1953), *R. marina* (Kützing) M.Schmidt (1899: pl. 213: figs 28–39) (Edsbagga 1968, Aleem 1973), and the rarely encountered *R. pullus* M. Schmidt, which has only been reported by Edsbagge (1968) with no details on its description or distribution. In phytoplankton samples collected over the whole Baltic Sea, Hällfors (2004) reported only *R. abbreviata* and *R. marina*.

Our knowledge of the marine diatom flora on the west coast of Sweden remains limited. The reason may be in part due to the short marine coast of Sweden, leaving most of the vast coastal regions as brackish water (Baltic Sea). In the later decades of the 20th century, most algal investigations on the west coast focused on macrophytes rather on microalgae including diatoms (e.g. Kylin 1949, Lundälv *et al.* 1986, Wallentinus 1996). Fresh and brackish water diatoms of Sweden received more attention in the comprehensive work of Cleve-Euler (1951–1955). This work, however, was preceded by two works on the freshwater diatoms of Sarek and Abisko lakes in the northern parts of the country (Hustedt 1924, 1942). More recently, Van de Vijver *et al.* (2008, 2010, 2012) described several new species from some Swedish rivers. Diatoms along the Baltic coast of Sweden were subject of more studies, the most extensive of which was the work of Snoeijs & Vilbaste (1994), Snoeijs & Potapova (1995), Snoeijs & Kasperovichiene (1996) and Snoeijs & Balashova (1998).

In the present work, which is part of an extensive survey of littoral diatoms of Sweden, a new species of *Rhoicosphenia* is described. This species originated from the brackish water environment in Grisslehamn port on the Baltic coast of Sweden, to the north of Stockholm. Light and scanning electron microscopy revealed valve morphological and structural features that are not shared by other taxa of the genus.

Material and Methods

Cells of *Rhocosphenia* sp. were found as epiphytic on the phaeophyte *Ectocarpus siliculosus* (Dillwyn) Lyngbye (1819: 131) collected from the Baltic coast of Sweden at Grisslehamn (60° 46’ 32’’ N, 18° 49’ 51’’ E). Parts of the submerged macrophytes were collected by hand from a depth of 30–50 cm from the water level along the coastal line of the region in May 2019. The sampling area was an archipelago of scattered small isles with clear water. The macroalgal samples were labelled, packed in plastic bags, and stored in cool boxes without any preservation.

After identification of the phaeophytes, parts of the thalli were cut and placed in 50 ml glass jars containing deionized water. The jars were agitated several times to detach epiphytic diatoms. Aliquots were transferred to 100 ml beakers to which adequate volume of 35% hydrogen peroxide was added and boiled for 30 minutes. Before terminating the boiling, few drops of hydrochloric acid were added to remove mineral carbon. After cooling, several rinses with deionized water were made to ensure removal of salts. Few drops of the diatom material were dried on coverslips in ambient temperature and permanent slides from each sample were made using Naphrax as mounting media. Light microscopy (LM) was performed using a Zeiss Axioimager 2 light microscope with differential interference contrast objectives (DIC) and a Canon Powershot 14 camera (Department of Biological and Environmental Sciences, University of Gothenburg, Sweden). For scanning electron microscopy (SEM), a Zeiss Ultra 55 FEG SEM (Chalmers University, Sweden) was used. SEM images were taken while the microscope was operated at 8 KV and 10 mm work distance. Relative abundance of the most frequent species in the samples was estimated for the comparison of species relative abundance.

Terminology for the description of valve morphology and ultrastructure follows Ross *et al.* (1979) and Round *et al.* (1990). Following Mann (1982), the *Rhoicosphenia* concave valve with complete raphe system is referred to as the R-valve, and the convex valve with reduced raphe fissures is referred to as the D-valve.

Results

Division Bacillariophyta Haeckel 1878: 95

Class Bacillariophyceae Haeckel 1878 emend D.G. Mann in Round *et al.* 1990: 651

Order Cymbellales D.G Mann in Round *et al.* 1990: 653

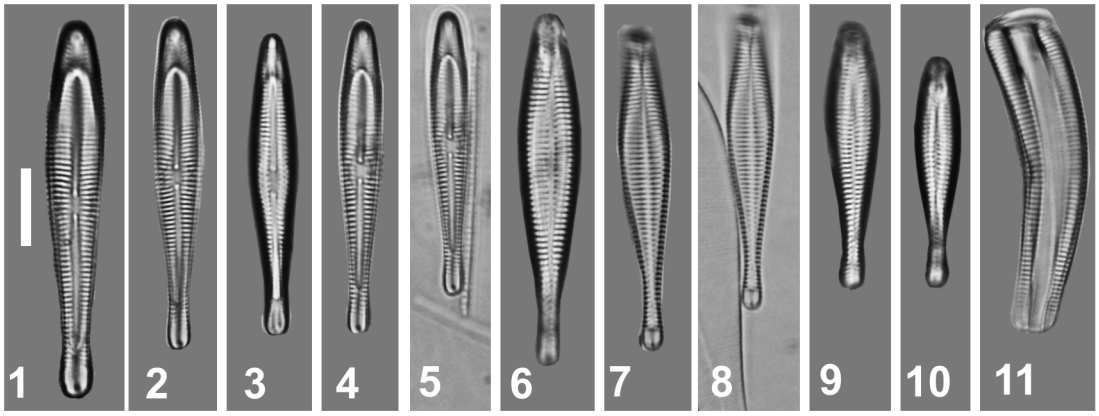
Family Rhoicospheniaceae Chen & Zhu 1983: 453

Genus ***Rhoicosphenia*** Grunow 1860: 511

Rhoicosphenia johannessoniae **Al-Handal, Levkov & Wulff *sp. nov*. (Figs 1–11, 12–25)**

Description

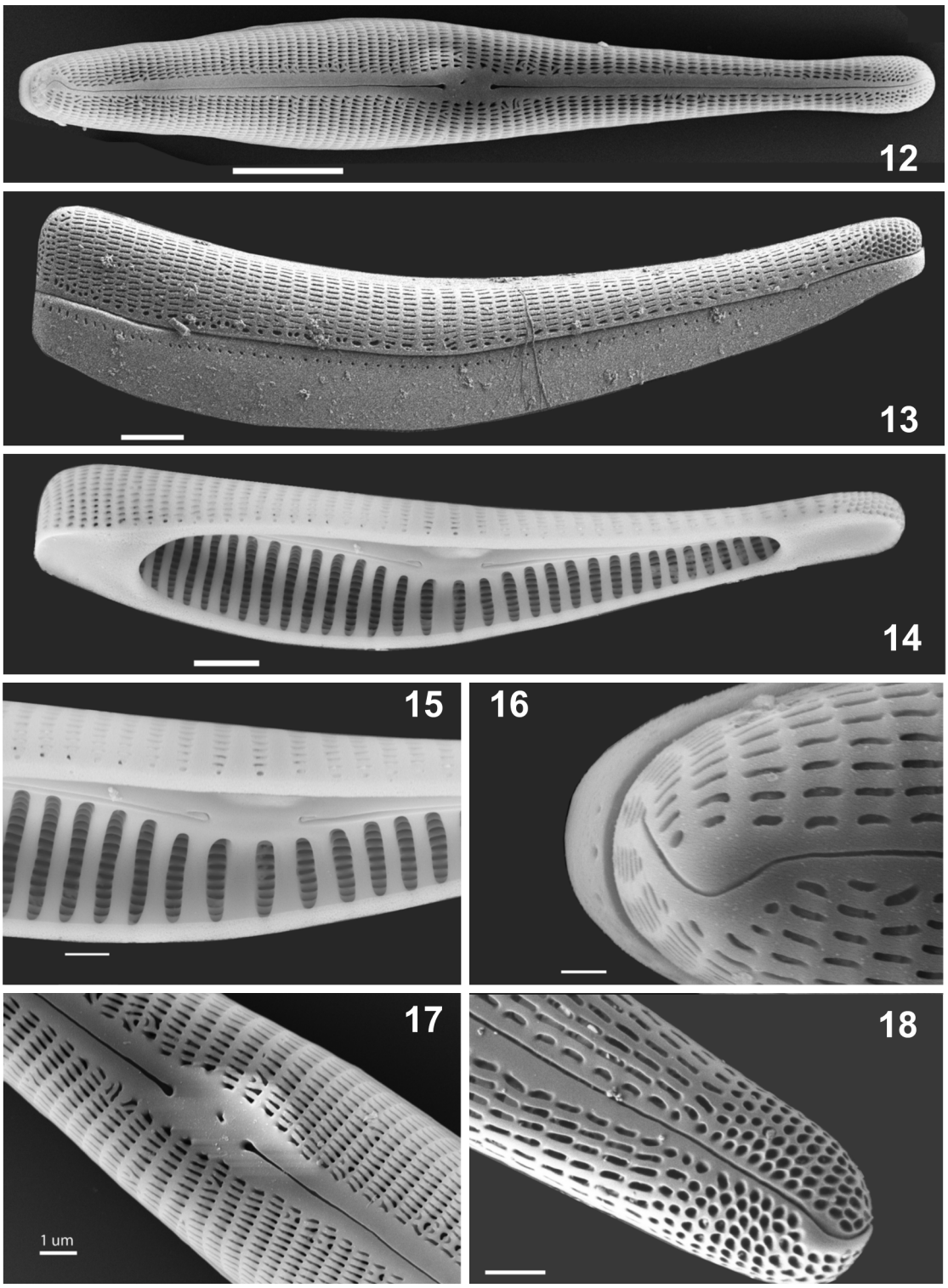
LM observation (Figs 1–11): Valves heteropolar, narrowly clavate, 29–48 µm long and 6.8–8.5 µm wide. Head pole narrowly rounded, base pole protracted to elongated subcapitate with rounded apex. Raphe filiform on the R-valve with distinct proximal endings (Figs 1–5), but not resolvable on the D-valve (Figs 6–10). Axial area linear and very narrow on R-valve with indistinct central area. D-valve axial area narrowly linear lanceolate. Striae on both valves parallel to slightly radiate, 20–22 in 10 µm. Areolae not discernible in LM. Frustules in girdle view bent and wedge shaped (Fig. 11).



FIGURES 1–11. LM images of *Rhoicosphenia johannessoniae sp. nov.*, Figs 1–5. R-valve. Figs 6–10. D-valve (note the narrowly protracted subcapitate base poles), Fig. 11. Whole frustule. Scale bar: 10 µm.

SEM observations (Figs 12–25): R-valves: Valves concave and narrowly clavate with broadly rounded poles (Figs 12, 13). Externally, head poles broadly rounded (Figs 16, 18), base pole narrowly rounded and protracted, with pore field of irregularly arranged poroids, formed of 11–12 rows. Axial area linear and asymmetric, becoming narrower near poles (Fig. 12). Central area slightly wider than axial area, and in some specimens, ornamented with small pore-like depressions that do not penetrate internally (Figs 12, 17). Central area not located in valve centre but positioned below the wider middle part of the valve towards the base pole (Fig. 12). Raphe filiform, proximal endings small, drop-like and distantly spaced (Fig. 17). Distal raphe endings curved and terminate on valve mantle (Fig. 16). Striae parallel to slightly radiate and formed of slit-like, weakly curved areolae (Figs 13, 16). Internally, pseudosepta on both poles large and strongly silicified (Fig. 14). Axial area lanceolate, gradually widens into a large central area. Raphe proximal endings strongly hooked (Fig. 15). Striae weakly radiate in valve centre and separated by well-developed virgae (Fig. 15). D-Valves: Valves concave, narrowly clavate with rounded poles (Figs 19–21). Base pole protracted with 10–12 irregularly arranged rows of poroids which form pore field (Figs 20, 21, 23). Axial area linear, very narrow, slightly widened towards mid- valve (Fig. 20). Raphe system reduced, the upper raphe fissure very short, slightly bent, extends for 4–5 striae and positioned near the head pole (Fig. 24). Raphe fissure at base pole straight, longer than upper fissure with weakly curved distal endings that reach valve margin (Fig. 23). Striae parallel, formed of slit-like areolae, occasionally biseriate stria formed near valve margin (Figs 21, 22). Internally, head pole rounded (Fig. 19), while base

pole rostrate (Fig. 25). Axial area linear-lanceolate. Proximal raphe endings crook-shaped (Fig. 25). Striae parallel, narrow in mid- valve and wider toward poles (Fig. 19). Pseudosepta of base pole interrupted by lacuna which terminate before valve apex with rounded and slightly bent structure (Fig. 25).



FIGURES 12–25. SEM images of the R-valve of *Rhoicosphenia johannessoniae sp. nov.*, Fig. 12. External side of the valve, note the position of the central area towards the base pole, Fig.13. Girdle view of the valve with a cingular band attached, Fig. 14. Tilted view of the valve showing the internal side with the central nodule and the valvocopulae on the poles, Fig.15. The central nodule and raphe proximal endings, Fig. 16. External side of the head pole showing the hooked raphe distal ending which terminate on valve mantle, Fig. 17. External side showing the central area and the isolated areola inside. Fig.18. External side of the base pole with pore field and distal raphe ending. Scale bars: 5 μm (Figs 44–47), 1 μm (Figs 48, 50, 51), 0.4 μm (Fig. 49).

Type: Grisslehamn port, Baltic coast of Sweden, 60° 05' 53'' N, 18° 48' 47'' E, Collectors: Adil Al-Handal and Mikael Hedblom, collection date: May 2019. Permanent slide containing cells of *R. johannessoniae* is deposited at the Macedonian National Diatom collection under accession No. MKNDC 014457. Figures 2 and 7 represent the holotype.

Isotype: Permanent slide containing cells of *R. johannessoniae* is deposited at the University of Gothenburg Herbarium under No. GB-0210437.

Etymology: The epithet is in honour of Professor Kerstin Johannesson of the Tjärnö Marine Laboratory, University of Gothenburg for her contribution and outstanding work on the ecology and phylogeny of some marine benthic invertebrate in Sweden.

Ecology: *Rhoicosphenia johannessoniae* was rather rare and constituted 0.8% of the diatom association in the sample examined. It is a brackish water species found epiphytic on the brown macrophyte *Ectocarpus siliculosus* and did not appear on other macrophytes collected from the same region or in the benthic samples. Water temperature was 12.3 °C and salinity 4.9 psu. Several other species were associated with *R. johannessoniae* including *Licmophora gracilis* (Ehrenberg) Grunow (1867:34, 24.6%), *Licmophora ehrenbergii* (Kützing) Grunow (1867: 36, 10.2%), *Entomoneis paludosa* (W.Smith) Reimer 1975: 4, 5.3%), *Diatoma tenuis* C. Agardh (1812: 15, 3.4%), *Tabularia fasciculata* (C.Agardh) Williams & Round (1986:326, 2.7%), together with small-sized *Navicula* spp. and *Nitzschia* spp.

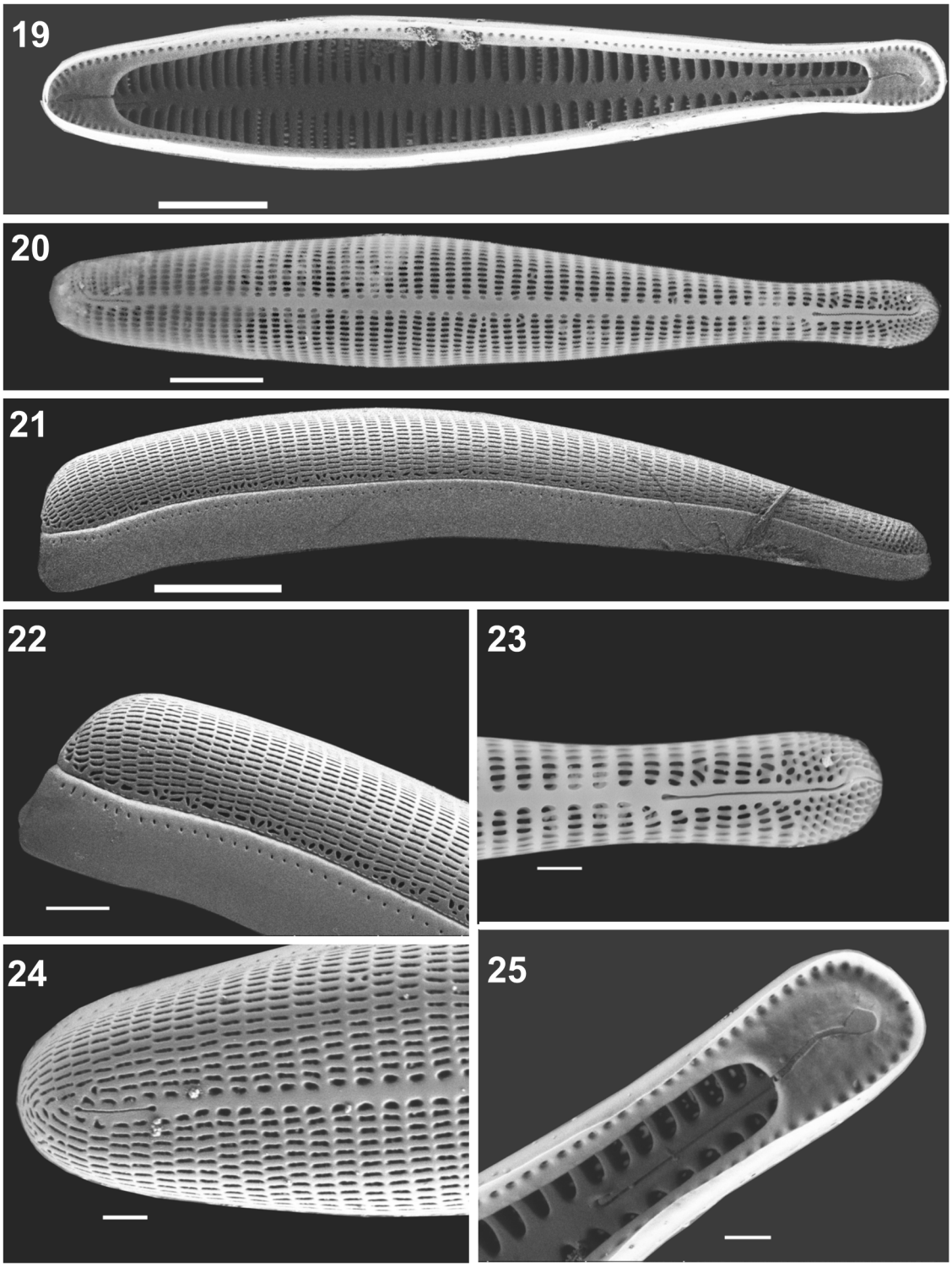
Discussion

Morphologically, *Rhoicosphenia* species may be placed in two groups depending on valve poles shapes and raphe structure. Group 1 encompasses all species that are heteropolar, where the base pole bears apical pore field of poroids that are variable in shape and arrangement. In this group, the majority of the well documented *Rhoicosphenia* species are included. Group 2 includes those species that possess isopolar valves which are with or without a distinct pore field in the base pole. The latter is a small group which only comprises *R. pullus* M.Schmidt (1899: pl. 213: figs 24–27), *R. genuflexa* (Kützing) Medlin (1984: 257) and *R. kloseri* Thomas & Ligowski (Levkov & Nakov 2008, Levkov *et al.* 2010, Thomas & Ligowski 2016: 51). However, representatives of the genus *Rhoicosphenia* exhibit wide variations in valve morphology and structure such as the absence of a pore field (*R. genuflexa*) or the absence of a raphe slit in one valve (*R. michali* Ligowski 2014: 143). According to its morphological features *R. johannessoniae* is a member of group 1.

A comparison of *Rhoicosphenia johannessoniae* with other species of the genus that share similar valve size range is given in Table 1. These include *R. baltica* (Schumann) Levkov (2010:151), *R. macedonica* Levkov & Krstic, *R. lacustris* Levkov (2010:159), *R. tenuis* Levkov & Navkov (2008: 379) and *R. affinis* Levkov (2010: 160). In LM, *R. johannessoniae* is morphologically most similar to *R. baltica* (Levkov *et al.* 2010, p. 151, Figs 4a–v) which both share the protracted capitate base pole (Figs 10–19), a feature that is not seen in the other taxa of the genus. *Rhoicosphenia johannessoniae*, however, has more elongated and protracted base pole, denser striae on both valves, 20–22 in 10 µm, compared to 15–18 in *R. baltica* (Table 1). The areolae of *R. johannessoniae* are more packed, very narrow and slit-like opposed to wider, mostly elliptical on the D-valve of *R. baltica* (Figs 16, 21, 22). The central area of the R-valve of *R. johannessoniae* is not positioned in the wider part of the valve but slightly shifted towards the lower part (Fig. 12), where it is almost central in *R. baltica*.

Rhoicosphenia baltica was first described as *R. fracta* var. *baltica* Schumann (1867:54), but then transferred to *R. curvata* var *baltica* by Cleve-Euler (1953). The illustrations of this taxon in Cleve-Euler (1953, p. 53, figs 601n–p) do not show any protracted base pole, both poles are tapering to narrowly rounded apices and the valves are slightly inflated in the middle. Also, SEM images of both R and D-valves of this species in Levkov *et al.* (2010, figs 5a–g, 6a–g) do not exhibit a protracted base pole, which is the distinguishing feature, and rather resemble *R. abbreviata*, but with denser striae.

Rhoicosphenia macedonica Levkov & S. Krstic (in Levkov *et al*. 2007:117) has been described from Lake Ohrid and represent a typical oligotrophic freshwater species. Differences between *R. johannessoniae* and *R. macedonica* can be noticed in the valve shape, whereas *R. macedonica* has broadly clavate valves with broadly rounded head pole and narrowly rounded and not protracted base pole. *Rhoicosphenia lacustris* has comparable valve size as *R. johannessoniae*, but both species can be easily differentiated by the shape of base pole and stria density (13–15 in 10 µm in *R. lacustris*). *Rhoicosphenia tenuis* Levkov & Nakov (2008:379) has narrow and linear valves without protracted base pole and much coarser striae on R-valve (12–16 in 10 µm). *Rhoicosphenia affinis* is recognized by having pore



FIGURES 19–25. SEM images of the D-valve of *Rhoicosphenia johannessoniae sp. nov.* Fig. 19. Internal side with pseudoseptae on the poles, note the bluntly rounded base valve apex, Fig. 20. External side showing reduced raphe branches, Fig. 21. Girdle view of the valve with a cingular band attached, Fig. 22. External side of the head pole showing slit-like areolae, Fig. 23. External side of the base pole with the reduced raphe branch and pore field, Fig. 24. External side of the head pole with very short raphe branch and slit-like areolae, Fig. 25. Internal side of the base pole with pseudoseptum and raphe branch. Scale bars 5 μm (Figs 52–54), 1 μm (Figs 55–58).

field on base poles of both valves. These features make its differentiation from *R. johannessoniae* simple. Thomas & Kociolek (2015) have described three new *Rhoicosphenia* species from USA., which are characterized by coarsely punctate striae (areolae clearly discernible in LM) with distantly spaced and not protracted head pole. Similarly, *Rhoicosphenia* species described from fossil deposits in India and USA (*R. gandhii* Thomas, Karthick & Kociolek, *R. indica* Thomas, Karthick & Kociolek, *R. reimeri* Thomas & Kociolek and *R. patrickae* Thomas & Kociolek) have much coarser striae, not protracted base pole and different numerical features (Thomas *et al.* 2015).

Rhoicosphenia is an interesting and enigmatic genus and has been a subject of a thorough investigation on its position in the evolutionary tree of diatoms. The heterovalvar structure of the frustule and the heteropolar valves are reasons for uncertainty of taxonomical position of the genus. Kociolek & Stoermer (1986) suggested that *Rhoicosphenia* is more closely related to *Gomphonema*, with *Achnanthes* sensu lato as sister. Later, Cox & Williams (2006), based on 35 characters, suggested that *Rhoicosphenia* is not part of cymbellalean clade, that is opposite to Round *et al.* (1990) and it belongs to the unresolved clade with several naviculoid genera. Recent molecular analyses reveal that *Rhoicosphenia* is sister to a clade of the Cymbellales, but it not closely related to *Gomphonema*. These analyses revealed that both genera are not very close as it was previously supposed, but are placed in the same order Bacillariales (Thomas *et al*. 2016). Bacillariales, however, is an order that include genera so widely apart in terms of habitats, frustule symmetry and structure such the possession of hetrovalves and mode of sexual reproduction. More phylogenetic analyses on the genera in this order may increase our insight of the evolutionary process of diatoms, but also phylogenetic position of *Rhoicosphenia*. Since *Rhoicosphenia* species are distributed in various habitats, starting from oligotrophic ancient lakes, freshwater rivers, eutrophic lakes, brackish water and marine habitats, it will be important to make molecular analyses of different *Rhoicosphenia* species in order to establish a pattern for colonisation of marine to freshwater or vice versa.

TABLE 1. Morphological and morphometric comparison of *Rhoicosphenia johannessoniae* to other similar species.

Features		*Rhoicosphenia baltica*	*R. macedonica*	*R. lacustris*	*R. tenuis*	*R. affinis*	*R. johannessoniae*
Length (µm)		21–57	15–52	25–62	15–60	34–65	29–48
Width (µm)		4.5–8	5.5–8.5	6–9	3–4.5	6.5–8.5	6.8–8.5
Valve	outline	narrowly clavate	clavate	broadly clavate	linear-clavate	broadly lanceolate to subclavate	narrowly clavate
	head pole	narrowly rounded	broadly rounded	obtusely rounded to cuneate	obtuse	subprotracted	rounded in both valves
	foot pole	protracted to subcapitate	narrowly rounded	narrowly rounded	narrowly rounded	narrowly rounded	rounded in the D valve, bluntly rounded in the R valve
Striae	R- valve	slightly radiate	parallel to weakly radiate	radiate throughout	parallel in the middle radiate towards apices	slightly radiate	parallel to weakly radiate
	D- valve	slightly radiate	parallel in the middle, radiate near poles	sub-parallel to slightly radiate	parallel	slightly radiate	parallel
Stria density/ 10 µm	R- valve	15–18	18–22	13–15	12–16	11–14	20–22
	D- valve	15–18	22–24	11–15	13–17	11–14	20–22
Areolae shape	R- valve	elongated to elliptical wide slits	short and broad	long and undulating, very narrow slits	slightly elongated	not discernable	long apical slits, packed
	D-valve	elliptical	short and broad	long and undulating, bvery narrow slits	mostly rounded	very small	short epival slits, packed

...Continued on the next page

TABLE 1. (Continued)

Features		*Rhoicosphenia baltica*	*R. macedonica*	*R. lacustris*	*R. tenuis*	*R. affinis*	*R. johannessoniae*
Axial area	R- valve	narrow, linear	linear, very narrow	narrow, widens in the central area	linear, widens in the central area	naroow, widens towards centre	narrow, tapering towards poles
	D- valve	moderately wide	narrow	wide	narrowly linear		narrow, linear
Central area	R- valve	narrowly elliptical to apically elongated	small ,elliptical to longitudinaly elongated	narrow, lanceolate to elliptical	indistinguished	lanceolate	narrow, longitudinaly elongated
	D- valve	elliptical		wide	indistinguished	lanceolate	absent
Raphe	R- valve	well develved, filliform	filliform with large proximal pores	filliform with large proximal pores	filfiform, slightly unequal ranches	filiform with large endings	filiform with large drop-like proxilal endings
	D- valve	short slits, close to poles	short slits, close to poles	short slits, close to poles	short slits, close to poles	short slits, close poles	short slits, close to poles
Pore field, base pole		areolae of irregular shape and orientation	densly packed areolae	areolae arranged in longitudinal rows	dense areoloae, obliquely oriented	pore field on both valves	rounded, irregularly arranged areolae
Habitat		brackish water, epiphytic or benthic	Freshwater, epiphytic	Fresh to brackish water, epiphytic	freshwater	freshwater	brackish water, epiphytic
Reference		Levkov *et al.* 2010	Levkov *et al.* 2010	Levkov *et al.* 2010	Levkov & Navkov 2008	Levkov *et al.* 2010	present study

Acknowledgements

This work is part of a larger project to investigate the littoral diatom flora of Sweden and is funded by the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (FORMAS, project 2017-00850). Our thanks are to Mr. Mikael Hedblom, Department of Biological and Environmental Sciences, University of Gothenburg, for his help in sampling and transport. The help of CMAL laboratory staff in SEM operation is highly appreciated. Our gratitude to Dr Karthik Balasubramanian, Editor of Phytotaxa, for his critical reading of the manuscript.

References

Agardh, C.A. (1812) *Algarum decas prima*. Litteris Berlingianis, Lundæ, 14 pp.

Aleem, A.A. (1973) Contribution to the study of littoral diatoms on the west coast of Sweden. *Botanica Marina* 16 (4): 193–200. https://doi.org/10.1515/botm.1973.16.4.193

Al-Handal, A.Y. & Wulff, A. (2008a) Marine epiphytic diatoms from the shallow sublittoral zone in Potter Cove, King George Island, Antarctica. *Botanica Marina* 51: 411–435. https://doi.org/10.1515/BOT.2008.053

Al-Handal, A.Y. & Wulff, A. (2008b) Marine benthic diatoms from Potter Cove, King George Island, Antarctica. *Botanica Marina* 51: 51–68. https://doi.org/10.1515/BOT.2008.007

Chen, J.-Y. & Zhu, H.-Z. (1983) Amphiraphidales, a new order of the pennatae, Bacillariophyta. *Acta Phytotaxonomica Sinica* 21: 449–456.

Cleve-Euler, A. (1951–1955) *Die Diatomeen von Sweden und Finnland*. I-V, *Kungliga Svenska Vetenskapsakademiens Handlingar* 4. Stockholm, 950 pp.

Cleve-Euler, A. (1953) *Die Diatomeen von Schweden und Finnland*. Teil III. Monoraphideae, Biraphideae 1. *Kungliga Svenska Vetenskapsakademiens Handlingar* Ser. 4. Stockholm, 255 pp.

Cox, E.J. & Williams, D.M. (2006) Systematics of naviculoid diatoms (Bacillariophyta): a preliminary analysis of protoplast and frustule characters for family and order level classification. *System Biodiversity* 4: 385–399.
https://doi.org/10.1017/S1477200006001940

Edsbagge, H. (1968) Zur ökologie der marinen angehefteten diatomeen. *Botanica Gothoburgensia* 6: 1–139.

Giffen, M.H. (1970) New and interesting marine and littoral diatoms from Sea Point, near Cape Town, South Africa. *Botanica Marina* 13: 87–99.
https://doi.org/10.1515/botm.1970.13.2.81

Grunow, A. (1860) Über neue oder ungenügend gekannte Algen. Erste Folge, Diatomeen, Familie Naviculaceen. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien* 10: 503–582.

Grunow, A. (1867) Diatomeen auf Sargassum von Honduras, gesammelt von Linding. *Hedwigia* 6 (1–3): 1–8, 17-32, 33–37.

Haeckel, E. (1878) *Das Protistenreich. Eine Populäre Uebersicht über das Formengebiet der Niedersten Lebewesen*. Ernst Günther's Verlag, Leipzig, 104 pp.
https://doi.org/10.5962/bhl.title.58542

Harper, M.A., Cassie Cooper, V., Chang, F.H., Nelson, W.A. & Broady, P.A. (2012) Phylum Ochrophyta: brown and golden-brown algae, diatoms, silicoflagellates, and kin. *In*: Gordon, D.P. (Ed.) *New Zealand inventory of biodiversity. Kingdoms Bacteria, Protozoa, Chromista, Plantae, Fungi*. Canterbury University Press, Christchurch, pp. 114–163.

Hällfors, G. (2004) Checklist of Baltic Sea Phytoplankton Species (including some heterotrophic protistan groups). *Baltic Sea Environment Proceedings* 95: 1–210.

Hustedt, F. (1924) Die Bacillariaceen-Vegetation des Sarekgebiets. *Naturwiss. Untersuch. Sareksgeb. Schwedisch Lappland* 3: 525–626.

Hustedt, F. (1942) Diatomeen aus der Umgebung von Abisko in Schwedisch Lappland. – *Archiv Hydrobiologie* 39: 82–174.

Kützing, F.T. (1844) *Die Kieselschaligen. Bacillarien oder Diatomeen*. W. Köhne, Nordhausen, 152 pp.
https://doi.org/10.5962/bhl.title.64360

Kylin, H. (1949) Die Chlorophyceen der schwedischen Westküste. *Lunds Universitets Arsskrift* 45: 1–79.

Lange-Bertalot, H. (1980) Ein beitrag zur revision der Gattungen *Rhoicosphenia* Grun., *Gomphonema* C. Ag., *Gomphoneis* Cl. *Botaniska Notiser* 133: 585–594.

Levkov, Z., Krstic, S., Metzeltin, D. & Nakov, T. (2007) Diatoms of Lakes Prespa and Ohrid, about 500 taxa from ancient lake system. *Iconographia Diatomologica* 16: 1–613.

Levkov, Z. & Nakov, T. (2008) *Rhoicosphenia tenuis*, a new diatom species from Lake Ohrid. *Diatom Research* 23: 377–388.
https://doi.org/10.1080/0269249X.2008.9705764

Levkov, Z., Mihalic, K.C. & Ector, L. (2010) A taxonomical study of *Rhoicosphenia* Grunow (Bacillariophyceae) with a key for identification of selected taxa. *Fottea* 10: 45–200.
https://doi.org/10.5507/fot.2010.010

Ligowski, R., Al-Handal, A.Y., Wulff, A. & Jordan, R.W. (2014) *Rhoicosphenia michali*: a new species of marine diatom (Bacillariophyta) from King George Island, Antarctica. *Phytotaxa* 191 (1): 141–153.
https://doi.org/10.11646/phytotaxa.191.1.9

Lundälv, T., Larsson, C.S. & Axelsson, A. (1986) Long-term trends in algal-dominated rocky subtidal communities on the Swedish west coast - a transitional system. *Hydrobiologia* 142: 81–95.
https://doi.org/10.1007/BF00026749

Lyngbye, H.C. (1819) *Tentamen hydrophytologiae danicae continens omnia hydrophyta cryptogama Daniae, Holsatiae, Faeroae, Islandiae, Groenlandiae hucusque cognita, systematice disposita, descripta et iconibus illustrata, adjectis simul speciebus norvegicis*. Hafniae, Copenhagen, pp. 1–248.
https://doi.org/10.5962/bhl.title.6079

Mann, D.G. (1982) Structure, life history and systematics of *Rhoicosphenia* (Bacillariophyta). I. The vegetative cell of *Rh. curvata*. *Journal of Phycology* 18: 162–176.
https://doi.org/10.1111/j.0022-3646.1982.00162.x

Mann, D.G. (1984) Structure, life history and systematics of *Rhoicosphenia* (Bacillariophyta). V. Initial cell and size reduction in *Rh. curvata* and a description of the Rhoicospheniaceae fam. nov. *Journal of Phycology* 20: 544–555.
https://doi.org/10.1111/j.0022-3646.1984.00544.x

Medlin, L.K. & Fryxell, G.A. (1984) Structure, life history and systematics of *Rhoicosphenia* (Bacillariophyta). III. *Rh. adolfii* and its relationship to *Rhoiconeis*. *In*: Mann, D.G. (Ed.) *Proceedings of the 7th International Diatom Symposium*, Koeltz, Koenigstein, pp. 255–263.

Medlin, L.K. (1985) A reappraisal of the diatom genus *Rhoiconeis* and the description of *Campylopyxis*, gen. nov.. *British Phycological Journal* 20: 313–328.
https://doi.org/10.1080/00071618500650321

Medlin, L.K. & Round, F.E. (1986) Taxonomic studies of marine gomphonemoid diatoms. *Diatom Research* 1 (2): 205–225. https://doi.org/10.1080/0269249X.1986.9704970

Ross, R., Cox, E.J., Karayeva, N.I., Mann, D.G., Paddock, T.B.B., Simonsen. R. & Sims, P.A. (1979) An amended terminology for the siliceous components of the diatom cell. *Nova Hedwigia* 64: 513–533.

Round, F.E., Crawford, R.M. & Mann, D.G. (1990) *The Diatoms, Biology and Morphology of the 358 Genera*. Cambridge University Press, Cambridge, 747 pp.

Schumann, J. (1867) Preussische Diatomeen. Schriften Königl. Phys.–Ökon. Ges. *Königsberg* 8: 37–68.

Schmidt, A. (1899) *Atlas der Diatomaceen-kunde*. Series V: Heft 54. O.R. Reisland, Leipzig, pls. 213–216.

Snoeijs, P.J.M. (1989) A check-list of the benthic diatoms at Forsmark (northern Baltic Sea). 1. Epilithic and epiphytic taxa. *Annales Botanici Fennici* 26: 427–439.

Snoeijs, P. & Vilbaste, S. (1994) Intercalibration and distribution of diatom species in the Baltic Sea. *The Baltic Marine Biologist Publication* 2.16b, Opulus Press. Uppsala, 125 pp.

Snoeijs, P. & Potapov, A, M. (1995) Intercalibration and distribution of diatom species in the Baltic Sea. *The Baltic Marine Biologist Publication* 3.16c. Opulus Press. Uppsala, 129 pp.

Snoeijs, P. & Kasperoviciene, J. (1996) Intercalibration and distribution of diatom species in the Baltic Sea. *The Baltic Marine Biologist Publication* 3.16d. Opulus Press. Uppsala, 126 pp.

Snoeijs, P. & Balashova, N. (1998) Intercalibration and distribution of diatom species in the Baltic Sea. *The Baltic Marine Biologist Publication* 3.16e. Opulus Press. Uppsala, 125 pp.

Thomas, E.W., Kociolek, J.P. & Karthick, B. (2015) Four new *Rhoicosphenia* Grunow species from fossil deposits in India and North America. *Diatom Research* 30: 35–54. https://doi.org/10.1080/0269249X.2014.961554

Thomas, E.W. & Ligowski, R. (2016) *Rhoicosphenia kloseri*, a new isopolar *Rhoicosphenia* (Bacillariophyta) species from the Antarctic with comparison to other isopolar *Rhoicosphenia*. *Phytotaxa* 265 (1): 50–58. https://doi.org/10.11646/phytotaxa.265.1.4

Thomas, E.W., Stepanek, J.G. & Kociolek, J.P. (2016) Historical and Current Perspectives on the Systematics of the 'Enigmatic' Diatom Genus *Rhoicosphenia* (Bacillariophyta), with Single and Multi-Molecular Marker and Morphological Analyses and Discussion on the Monophyly of 'Monoraphid' Diatoms. *Plos One* 11 (4): e0152797. https://doi.org/10.1371/journal.pone.0152797

Van de Vijver, B. & Lange-Bertalot, H. (2008) *Cymbella amelieana sp. nov.* a new large *Cymbella* species from Swedish rivers. *Diatom Research* 23: 511–518. https://doi.org/10.1080/0269249X.2008.9705773

Van de Vijver, B., Jarlman, A. & Lange-Bertalot, H. (2010) Four new *Navicula* species (Bacillariophyta) from Swedish rivers. *Cryptogamie Algologie* 31: 355–367.

Van de Vijver, B., Jarlman, A., Haan, M. & Ector, L. (2012) New and interesting diatom species (Bacillariophyceae) from Swedish rivers. *Nova Hedwigia* 141: 237–254.

Van Heurck, H. (1896) *A treatise on the Diatomaceae*. Translated by Baxter WE. William Wesley & Son, London.

Wallentinus, I. (1996) The Northern Atlantic Coasts (The Swedish West Coast, Norway and Iceland). Marine Benthic Vegetation. Recent Changes and the Effects of Eutrophication. *Ecological Studies* 123: 165–184. https://doi.org/10.1007/978-3-642-61398-2_7

Williams, D.M. & Round, F.E. (1986) Revision of the genus *Synedra* Ehrenb. *Diatom Research* 1 (2): 313–339.

Witkowski, A., Lange-Bertalot, H. & Metzeltin, D. (2000) *Diatom flora of marine coasts I*. *Iconographia Diatomologica* 7: 1–925. https://doi.org/10.1080/0269249X.1986.9704976