

This item is the archived peer-reviewed author-version of:
--

Analysis of type material of Opephora pacifica and emendation of the genus Opephora (Bacillariophyta)

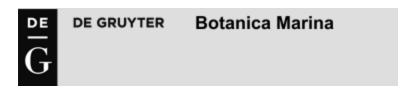
Reference:

Morales Eduardo A., Wetzel Carlos E., Ector Luc, Van de Vijver Bart.- Analysis of type material of Opephora pacifica and emendation of the genus Opephora (Bacillariophyta)

Botanica marina - ISSN 0006-8055 - 64:1(2021), p. 55-69

Full text (Publisher's DOI): https://doi.org/10.1515/BOT-2020-0033

To cite this reference: https://hdl.handle.net/10067/1767550151162165141



Analysis of type material of *Opephora pacifica* (Grunow) P.Petit and emendation of the genus *Opephora* P.Petit (Bacillariophyta)

Journal:	Botanica Marina
Manuscript ID	Draft
Manuscript Type:	Research article
Date Submitted by the Author:	n/a
Complete List of Authors:	Morales Luizaga, Eduardo Antonio; University of Evora School of Science and Technology, Biology; University of Evora School of Science and Technology, Institute of Earth Sciences Wetzel, Carlos; Luxembourg Institute of Science and Technology, Environmental Research and Innovation Department (ERIN) Van de Vijver, Bart; Botanic Garden Meise, Department of Bryophyta & Thallophyta Ector, Luc; Luxembourg Institute of Science and Technology, Environmental Research and Innovation Department (ERIN)
Classifications:	5 Algal systematics/floristics/biogeography
Keywords:	brackish, diatoms, marine, taxonomic revision, taxonomy

SCHOLARONE™ Manuscripts Analysis of type material of *Opephora pacifica* (Grunow) P.Petit and emendation of the genus *Opephora* P.Petit (Bacillariophyta)

Eduardo A. Morales, Carlos E. Wetzel, Bart Van de Vijver and Luc Ector

*Corresponding author: Eduardo A. Morales, Water Laboratory, University of Évora, P.I.T.E. Rua da Barba Rala No. 1, 7005–345 Évora, Portugal; and Institute of Earth Sciences - ICT, University of Évora, Rua Romão Ramalho 59, 7000–671 Évora, Portugal, e-mail: edu_mora123@outlook.com

Carlos E. Wetzel: Environmental Research and Innovation Department (ERIN), Luxembourg Institute of Science and Technology (LIST), 41 rue du Brill, L-4422 Belvaux, Luxembourg

Bart Van de Vijver: Meise Botanic Garden, Research Department, Nieuwelaan 38, B-1860 Meise, Belgium; and University of Antwerp, Department of Biology, ECOBE, Universiteitsplein 1, B-2610 Wilrijk, Antwerpen, Belgium

Luc Ector: Environmental Research and Innovation Department (ERIN), Luxembourg Institute of Science and Technology (LIST), 41 rue du Brill, L-4422 Belvaux, Luxembourg

Running title: Emendation of Opephora

Abstract

The genus *Opephora* currently contains 37 species and 27 infraspecific taxa. However, the existing literature reveals a wide morphological diversity and the need to establish defining characters to circumscribe the genus as a cohesive and, perhaps, monophyletic group. The type material of *Opephora pacifica*, the generitype, is analysed. We emend the description of both the species and the genus, the latter also based on published light and scanning electron microscopy observations of closely related species. After review of the available literature, we determined that currently only two species can be ascribed with 100% certainty to the genus *Opephora*: *O. pacifica* and *O. marina*. Based on available literature information, it is highly likely that *O. fragilarioides* also belongs to this genus. We present a table with all known species and infraspecific taxa and make comments regarding their recent transfer to other genera, their current accepted nomenclature, and the genus to which they should probably be ascribed pending the collection of further information.

Keywords: brackish; diatoms; marine; taxonomic revision; taxonomy.

Introduction

Over decades, the correct taxonomy of the genus *Opephora* P.Petit has been the subject of much controversy. One of the reasons is that the genus was traditionally composed of a heterogeneous mixture of small-sized araphid diatoms, difficult to identify using light microscopy (LM). The advent of scanning electron microscopy (SEM) confirmed a complex morphological variability, but despite some nomenclatural arrangements (e.g. Sabbe and Vyverman 1995) and guiding suggestions (Round et al. 1990, Morales 2002), the taxonomic boundaries of the genus have remained undefined.

The circumscription of *Opephora* through well-established distinguishing characters that clearly separate it from other, small-celled araphid diatoms lacking a rimoportula is important. The genus *Opephora* contains at present 37 species, 20 varieties and 7 forms (Guiry and Guiry 2020, Kociolek et al. 2020), many of them relatively common in brackish and marine habitats and appearing as frequent citations in floristic, taxonomic and ecological studies (e.g. Witkowski 1994, Ferreira et al. 2010, Witkowski et al. 2010, Koutsodendris et al. 2017, Siqueiros-Beltrones et al. 2017). Additionally, this genus appears represented in molecular phylogenies, but without clear definition of its identity at the morphological level, making it difficult to interpret its evolutionary associations with other taxa (Li et al. 2015, 2016, 2018).

Opephora was described in 1888 by Petit as having rectangular frustules, cuneiform valves, striae in the shape of buttonholes more or less elongated and located at the edge of the valves, and presenting a wide axial area. Petit (1888), however, did not describe any new species but transferred three taxa from other genera and placed them in his new genus: Opephora pacifica (Grunow) P.Petit (=Sceptroneis pacifica Grunow), O. pinnata (Ehrenberg) P.Petit (=Fragilaria pinnata Ehrenberg pro parte) and O. marina (W.Gregory) P.Petit (=Meridion marinum W.Gregory pro parte), but

without the designation of a generitype. Patrick in Patrick and Reimer (1966) designated a type for the genus choosing *O. pacifica* since the other two species had been erected based on parts of previously described species. The same authors also noted that Boyer's (1927) designation of *Opephora schwartzii* (Grunow) P.Petit ex Pelletan (=*Fragilaria schwartzii* Grunow) is incorrect since this taxon did not form part of the species originally considered by Petit (1888).

The original description of *O. pacifica* by Grunow (1862), as *Fragilaria pacifica*, was based on material collected from 'mari pacifico boreali'. Lange-Bertalot (1989) noted that the holotype slide is lost (see also Guiry and Guiry 2020), as is apparently also the case of the type material from the Pacific Ocean. To solve such a loss, Lange-Bertalot (1989, p. 95, pl. 7, figs 14 and 15) erected a neotype based on slide 790 of the Grunow Collection, W (Naturhistorisches Museum Wien, Austria, 790 Grunow, Flugsand der Kalkbai am Cap d.g. Hoff. Expedition Novara). A replica of slide 790 was deposited as slide VI-41-B10 in the Van Heurck Collection, at that time housed at AWH (Antwerp Scientific Collection, Belgium). This replica was studied in 1995 by Sabbe and Vyverman (1995, p. 239, figs 47, 52, 53), who referred to the slide as the "isotype". Since 2006, the entire Van Heurck diatom collection is part of Meise Botanic Garden (BR, Belgium). The above discussed slide, VI-41-B10, mentions on its label the "Kalkbay" locality and the Grunow number 790. Unmounted material used to prepare the slide was also found in the BR collection and is processed in this paper for further analysis.

Herein, we present the results of the LM and SEM analysis of slide VI-41-B10 and its unmounted material. With the aid of published information, we adjusted the differentiating features of *O. pacifica* and the genus *Opephora*, delimiting the number of

species contained in it through analysis of published information and making corresponding nomenclatural changes.

Materials and methods

For LM, slide VI-41-B10 of the Van Heurck Collection at BR (Figure 1) was analyzed using an Olympus® BX53 microscope (Olympus, Anvers, Belgique), equipped with Differential Interference Contrast (Nomarski) and an Olympus® UC30 digital camera (Olympus, Anvers, Belgique), and with a Leica® DMRX (Leica Microsystems AG, Wetzlar, Germany) with bright field equipped with a Leica® DC500 camera (Leica Camera AG, Wetzlar, Germany). For SEM analysis, a subsample of the Kalk Bay material (Grunow sample 790) from the BR collection was oxidized using 37% H₂O₂ and heating to 80°C for approximately 1h and subsequently rinsed with distilled water until neutrality. An aliquot of the material was rinsed with deionized water over 3 µm pore glass fiber filters. A subsample of the resulting cleaned material was coated with platinum using a BAL-TEC MED 020 Modular High Vacuum Coating System (Leica Camera AG, Wetzlar, Germany) for 30 s at 100 mA. The stub was analysed using a Hitachi SU-70 electron microscope (Hitachi High-Tech Corporation, Tokyo, Japan), operated at 5 kV and 10 mm working distance. All micrographs were digitally manipulated and plates containing LM and SEM pictures were mounted using CorelDraw X8® (Corel Corporation, Ottawa, Canada).

Morphological terminology follows Barber and Haworth (1981) for valve shape and stria pattern, Cox and Ross (1981) and Cox (2012) for lateral extensions (virgae) and cross bars (vimines and viminules), Williams and Round (1987) and Round et al. (1990) for areolar substructures, spines features, apical pore fields and girdle bands.

Results

The observed diatom flora in slide VI-41-B10 is rather diverse and composed of many species belonging to the genera *Biddulphia* and *Achnanthes*, *Eunotogramma frauenfeldii* (Grunow) Grunow, *Terpsinoë americana* (Bailey) Ralfs and *Fragilaria capensis* Grunow. The population of *Fragilaria pacifica* is rather small and represents less than 5% of the total diatom flora.

Redefinition of the genus Opephora

Opephora P.Petit emend. E.Morales, C.E.Wetzel, Van de Vijver et Ector

GENERITYPE: Opephora pacifica (Grunow) P.Petit

DESCRIPTION: Frustules rectangular in girdle view (Fig. 11), attached by mucilage stalks. Valves clavate in various degrees. Sternum of variable width and shape. Transition from valve face to mantle varying from abrupt (90°) to the formation of a transition zone. Striae composed of a single oval to elliptical areola running uninterruptedly from valve face to mantle. Internally, areolae opening into a single depression, running from valve face to mantle, occasionally becoming a chamber-like structure. Volae highly branched, usually in a dichotomous manner, arising from the virgae at different depths. Virgae flared at proximal and distal stria ends. Apical pore fields more or less developed, of the ocellulimbus type and composed of round poroids, present on both valve ends and internally sunken into apical depressions. Siliceous plaques present in the form of minute depositions arranged along the abvalvar edge of the valvocopula. Cingulum composed of a very large valvocopula, and few to many copulae. All girdle elements open, ligulated and lacking perforations.

Redefinition of Opephora pacifica

Opephora pacifica (Grunow) P.Petit emend. E.Morales, C.E.Wetzel, Van de Vijver et Ector

Basionym: *Fragilaria pacifica* Grunow 1862, Verh. K.K. Zool.-Bot. Ges. Wien 12: 373, pl. VIII: fig. 19.

Homotypic synonyms: *Sceptroneis pacifica* (Grunow) Elmore 1921, Univ. Stud. Univ. Nebraska 21: 47. *Grunoviella pacifica* (Grunow) Mills 1934, An index to the genera and species of the Diatomaceae and their synonyms, Wheldon & Wesley Ltd. London, p. 822.

Microscopical study of Kalk Bay material: This manuscript, Figs 2–11 (LM); 12–25 (SEM).

Description: Frustules rectangular in girdle view (Figs 11, 13), attached by mucilage stalks. Valves clavate with broadly rounded apical pole and cuneate, acutely rounded foot pole (Figs 2–10). Valve dimensions (n=45): length 11–46 μm, width 6.5–8.5 μm, stria density 6–9 in 10 μm. Sternum narrow, linear, fusing without interruption with both valve poles (Figs 2–10, 12). Valve face convex and transition from valve face to mantle abrupt (Figs 12, 13, 18). Each stria composed of a single oval areola, bending and running without interruption from valve face to mantle (Figs 12–24). Internally, areolae opening into a single, unchambered depression (Figs 21–25). Volae robust and dichotomously anastomosing into a net-like occluding structure (Figs 12, 15–18, 21–25). Virgae flared at proximal and distal stria ends (Figs 12, 21). Apical pore fields composed of round pores, well-developed on both valves ends (Figs 12, 16, 17, 21), having approximately the same size, and internally sunken into apical and foot pole depressions (Figs 21, 22). Pores in apical pore field located at the valve apex rather simple and located on a more or less transapically elliptical pore plate (Figs 15, 17). Pores in foot-pole apical pore field lying in neatly arranged grooves, parallel to apical

valve axis, all within a transapically elliptical pore plate (Figs 13, 15). Cingulum composed of a very large and thick valvocopula (Figs 13, 14), and few to many slender, less silicified copulae (Fig. 14). All girdle elements open, ligulated, lacking perforations. Small silica plaques present along the abvalvar edge of the valvocopula, having the shape of blisters disorderly arranged in a single row (Figs 13, 14).

Discussion

The measurements presented in the description of *O. pacifica* originated from Sabbe and Vyverman (1995), who analyzed slide VI-41-B10 from the Van Heurck collection (AWH, Belgium). A re-analysis of the same slide confirmed these data indicating that all observations made at the LM level agree well with those made by Sabbe and Vyverman (1995). The latter authors refer to slide VI-41-B10 as the "isotype", but there is no historical record of any type from the 'mari pacifico boreali' material used originally by Grunow (1862) to describe the species. Therefore, and since Lange-Bertalot (1989) erected a neotype based on Grunow 790 with slide VI-41-B10 being a replica of it, the latter should be considered as the isotype.

Populations of *Opephora pacifica* have been reported and illustrated several times in the past (Witkowski et al. 2000, 2010, Li et al. 2018). Using the current (new) morphological knowledge gathered in the present study, it is clear that most of these records actually belong to other (most likely undescribed) species. The *O. pacifica* population shown by Li et al. (2018, figs 324–329, SEM) differs from the *O. pacifica* type material by size (Li et al. 2018: length 4.5–10.5 μm, width 2.5–3.0 μm having a stria density of 11–14 in 10 μm), virgae being broader than the striae (contrary to the type that has virgae barely wider than the striae) and a smaller apical pore field at the head pole composed of only a few pores contrary to the type that presents a much larger

apical pore field. Witkowski et al. (2000, pl. 25, fig. 26, SEM) presented one specimen with slender striae, different from any other *Opephora* seen during our literature review. The authors identified this taxon as *O. pacifica*, but the structure and shape of the striae, much wider in the type specimens of *O. pacifica*, actually suggest that the taxon in Witkowski et al. (2000) is new and requires a proper description. Probably only some of the LM figures presented by Witkowski et al. (2000, pl. 25, figs 18–25) might belong to this new taxon (e.g. figs 22 and 23) and the remaining seem to belong to *O. pacifica*, but SEM analysis will be necessary to confirm this.

Based on the observations made in the current study, we now can indicate both exclusive, distinguishing morphological features of the genus *Opephora* and several other, typical but not exclusive characters.

Distinguishing characters of *Opephora*: Striae composed of one single, transapically elliptical areola. Volae arising from the virgae, forming intricate, intertwined, net-like structures and plaques located on the distal edge of the valvocopula. If it is considered that loss of characters can potentially be used as synapomorphies (D.G. Mann, pers. com.), then the complete lack of vimines, viminules, spines and flaps, all present in the morphologically closely related genus *Pseudostaurosira* D.M.Williams *et* Round (Morales et al. 2019), could be used as distinguishing features of *Opephora*.

Other salient but not unique features: Girdle composed of a much wider valvocopula and slender copulae. All girdle elements open, ligulate, the latter feature also observed in *Staurosirella* D.M.Williams *et* Round (Morales and Manoylov 2006), but in this latter genus the valvocopula is always fimbriate, and mantle plaques always absent. *Pseudostaurosira* also has a well-developed valvocopula and slender copulae (Morales

et al. 2012, 2015), but the valvocopula in the latter is much less developed than in *Opephora* and mantle plaques are absent from the girdle elements.

Internally, the areolae open up into depressions, a feature also present in *Pseudostaurosira*. However, in *Pseudostaurosira*, the striae are composed of more than one areola (Morales et al. 2015) and occasionally, if only a single areola is present (as in *Pseudostaurosira varisterna* (Chunlian Li, Ashworth *et* Witkowski) E.Morales (Morales et al. 2019), spines develop along the stria at the valve face-mantle transition. As stated before, spines are always lacking in all *Opephora* species.

In the past a fairly large number of species have been included within the genus Opephora since the exact morphology of the generitype was not fully known. Table 1 contains all the names currently associated to *Opephora*, including varieties and forms. Most of them were already transferred to other genera. Witkowski et al. (2010) already indicated this based on the description and illustration in Round et al. (1990) stating that the actual number of true *Opephora* taxa has been reduced to a few marine forms whereas most other taxa were transferred to other araphid genera. Only two taxa can currently be ascribed with certainty to this genus, *Opephora marina* (type material studied by Andrén in 1997) and *Opephora pacifica* (neotype material studied herein). A third taxon, Opephora fragilarioides H.Kobayasi, is most likely also a member of the genus *Opephora* considering the morphological details given by Kobayasi et al. (1977), showing single-slit striae, absence of vimines and spines, and the interpretation given by Witkowski et al. (2000) based on SEM observations. However, until the type population of O. fragilarioides is studied in detail, the transfer cannot be made with certainty. A complete revision of all *Opephora* names falls beyond the scope of the present paper and should be the focus of a thorough morphological study based on type analysis of all

species, preferably with the underlying support of molecular results. However, based on information and illustrations available in the literature, the following new combinations can be presented.

Neofragilaria burchardtiae (Witkowski, Metzeltin et Lange-Bertalot) E.Morales comb. nov.

Basionym: *Opephora burchardtiae* Witkowski, Metzeltin *et* Lange-Bertalot in Moser, Lange-Bertalot and Metzeltin 1998. Bibliotheca Diatomologica 38: 355–356, pl. 71, fig. 2, pl. 78, figs 1–13.

This species should be placed within the genus *Neofragilaria* based on the presence of vimines at the valve face/mantle junction and the presence of spines (Desikachary and Prema 1987, Li et al. 2015). The virgae are doubly flared and the areolae are very wide, approximately rectangular to square in shape. The striae open internally into depressions. The volae originate from inner areolar perimeter and intertwine to form a complex, flat, net-like pattern covering the entire areolar opening. This latter feature distinguishes the genus from *Pseudostaurosira* in which the volae are not as complex, and there are also flaps as additional areolar coverings.

Pseudostaurosira minuta (Cleve-Euler) E.Morales, C.E.Wetzel, Van de Vijver et Ector stat. nov. comb. nov.

Basionym: *Opephora marina* var. *minuta* Cleve-Euler 1953, Kongl. Svenska Vetensk.-Akad. Handl., ser. 4, p. 16, fig. 314e.

This taxon, as presented in Witkowski et al. (2000) is a member of *Pseudostaurosira* since it has wide and short vimines (Morales et al. 2019). Additionally, spines interrupting the striae are present. The latter are composed of two areolae, one on the

valve face and another on the valve mantle. The virgae are doubly flared. The small size of the valve face areolae leaves a wide, lanceolate sternum. Apical pore fields are present on both valve ends.

Acknowledgements

This work was co-funded by the European Union through the European Regional Development Fund, framed within the Operational Programme Competitiveness and Internationalization, COMPETE 2020 through the ICT project (UID/GEO/04683/2013) with reference POCI-01-0145-FEDER-007690 and the Agencia Portuguesa do Ambiente, APA-000004DFIN.AALP/2017 integrated within the Operational Program for Sustainability and Efficiency in the Use of Resources 2014-20, POSEUR-03-2013-FC-000001. Funding for this research was also partly provided in the framework of the DIATOMS project (LIST-Luxembourg Institute of Science and Technology).

References

Andrén, E. 1997. A study of the diatom *Opephora marina* (Gregory) Petit. *Diatom Res*. 12: 199–205.

Barber, H.G. and E.Y. Haworth. 1981. *A guide to the morphology of the diatom frustule. With a key to the British freshwater genera*. Scientific Publication No. 44. Freshwater Biological Association, Ambleside. pp 112.

Boyer, C.S. 1927. Synopsis of North American Diatomaceae. Part I.—Coscinodiscatae, Rhizoselenatae, Biddulphiatae, Fragilariatae. *Proc. Acad. Nat. Sci. Phila.* 78 (Supplement): 1–228.

Cleve-Euler, A. 1953. Die Diatomeen von Schweden und Finnland. Teil II.

Arraphideae, Brachyraphideae. *Kongl. Svenska Vetensk.-Akad. Handl.*, ser. 4, 4(1): 1–158, figs 292–483.

Cox, E.J. 2012. Ontogeny, homology, and terminology–wall morphogenesis as an aid to character recognition and character state definition for pennate diatom systematics. *J. Phycol.* 48: 1–31.

Cox, E.J. and R. Ross. 1981. The striae of pennate diatoms. *In*: (R. Ross, ed.) *Proceedings of the Sixth Symposium on Recent and Fossil Diatoms. Budapest, September 1-5, 1980. Taxonomy. Morphology. Ecology. Biology.* Otto Koeltz Science Publishers, Koenigstein. pp. 267–278.

Desikachary, T.V. and P. Prema. 1987. Diatoms from the Bay of Bengal. *In*: (T.V. Desikachary, ed.) *Atlas of Diatoms. Fasc. III*. Madras Science Foundation, Madras. pp. 1–10, pls 222–331.

Elmore, C.J. 1921. The diatoms (Bacillarioideae) of Nebraska. *Univ. Stud. Univ. Nebraska* 21: 22–215.

Ferreira, T., M.C. Freitas, R. Bao and C. Andrade. 2010. Associações de diatomáceas em lagunas – Lagoas de Albufeira e de Santo André (SW Portugal): resultados preliminares [Diatom assemblages in lagoons - Lagoa de Albufeira and Santo André (SW of Portugal): preliminary results]. *e-Terra. Revista Electrónica de Ciências da Terra. Geosciences On-line Journal* 12 (19): 1–4.

Gogorev, R.M. and E.K. Lange. 2014. Центрические и бесшовные пеннатные диатомовые (*Bacillariophyta*) водной толщи реликтового озера Могильное (остров Кильдин, Баренцево море) [Centric and araphid diatoms (*Bacillariophyta*) in water column of the relict Lake Mogilnoye (Kildin Island, Barents Sea)]. *Nov. Sist. Nizsh. Rast. [Novitates Systematicae Plantarum non Vascularium]* 48: 66–80, 11 pls [in Russian].

Grunow, A. 1862. Die österreichischen Diatomaceen nebst Anschluss einiger neuen Arten von andern Lokalitäten und einer kritischen Uebersicht der bisher bekannten Gattungen und Arten. Erste Folge. Epithemieae, Meridioneae, Diatomeae, Entopyleae, Surirelleae, Amphipleureae. Zweite Folge. Familie Nitschieae. *Verh. K. K. Zool.-Bot. Ges. Wien* 12: 315–472, 545–588, 7 pls.

Guiry, M.D. and G.M. Guiry. 2020. *AlgaeBase*. World-wide electronic publication, National University of Ireland, Galway. http://www.algaebase.org; searched on 07 May 2020.

Kobayasi, H., K. Kato and T. Nan-un. 1977. Lake Hachino Gata: A very small lake with many things that influence the preparation of the land when it dries up and in turn influences many other things. Report from the Hachino Gata Investigation Association, March 1977 [in Japanese].

Kociolek, J.P., K. Balasubramanian, S. Blanco, M. Coste, L. Ector, Y. Liu, M. Kulikovskiy, N. Lundholm, T. Ludwig, M. Potapova, F. Rimet, K. Sabbe, S. Sala, E.

Sar, J. Taylor, B. Van de Vijver, C.E. Wetzel, D.M. Williams, A. Witkowski and J. Witkowski, J. 2020. DiatomBase. Accessed at http://www.diatombase.org on 2020-05-07.

Koutsodendris, A., A. Brauer, J.M. Reed, B. Plessen, O. Friedrich, B. Hennrich, I. Zacharias and J. Pross. 2017. Climate variability in SE Europe since 1450 AD based on a varved sediment record from Etoliko Lagoon (Western Greece). *Quaternary Sci. Rev.* 159: 63–76.

Lange-Bertalot, H. 1989. Können *Staurosirella*, *Punctastriata* und weitere Taxa sensu Williams & Round als Gattungen del Fragilariaceae kritischer Prüfung standhalten?

Generic rank for *Punctastriata*, *Staurosirella* and other taxa sensu Williams & Round? *Nova Hedwigia* 49: 79–106.

Li, C.L., M.P. Ashworth, A. Witkowski, P. Dąbek, L.K. Medlin, W.H.C.F. Kooistra, S. Sato, I. Zgłobicka, K.J. Kurzydłowski, E.C. Theriot, J.S.M. Sabir, M.A. Khiyami, M.H.Z Mutwakil, M.J. Sabir, N.S. Alharbi, N.H. Hajarah, S. Qing and R.K. Jansen. 2015. New insights into Plagiogrammaceae (Bacillariophyta) based on multigene phylogenies and morphological characteristics with the description of a new genus and three new species. *PLoS ONE* 10: e0139300.

Li, C.L., M.P. Ashworth, A. Witkowski, C.S. Lobban, I. Zgłobicka, K.J. Kurzydłowski and S. Qin. 2016. Ultrastructural and molecular characterization of diversity among small araphid diatoms all lacking rimoportulae. I. Five new genera, eight new species. *J. Phycol.* 52: 1018–1036.

Li, C.L., A. Witkowski, M.P. Ashworth, P. Dąbek, S. Sato, I. Zgłobicka, M. Witak, J.S. Khim and C.-J. Kwon. 2018. The morphology and molecular phylogenetics of some marine diatom taxa within the Fragilariaceae, including twenty undescribed species and

their relationship to *Nanofrustulum*, *Opephora* and *Pseudostaurosira*. *Phytotaxa* 355: 1–104.

Mills, F.W. 1934. *An index to the genera and species of the Diatomaceae and their synonyms. 1816-1932. Part 11 (Ga-He)*. Wheldon & Wesley, Limited, London. pp. 822. Morales, E.A. 2002. Studies in selected fragilarioid diatoms of potential indicator value from Florida (USA) with notes on the genus *Opephora* Petit (Bacillariophyceae). *Limnologica* 32: 102–113.

Morales, E.A. and M.B. Edlund. 2003. Studies in selected fragilarioid diatoms (Bacillariophyceae) from Lake Hovsgol, Mongolia. *Phycol. Res.* 51: 225–239.

Morales, E.A. and K.M. Manoylov. 2006. Morphological studies on selected taxa in the genus *Staurosirella* Williams et Round (Bacillariophyceae) from rivers in North America. *Diatom Res.* 21: 343–364.

Morales, E.A., M.H. Novais, G. Chávez, L. Hoffmann and L. Ector. 2012. Diatoms (Bacillariophyceae) from the Bolivian Altiplano: three new araphid species from the Desaguadero River draining Lake Titicaca. *Fottea* 12: 41–58.

Morales, E.A., C.E. Wetzel, B. Van de Vijver and L. Ector. 2015. Morphological studies on type material of widely cited araphid diatoms (Bacillariophyta). *Phycologia* 54: 455–470.

Morales, E.A., C.E. Wetzel, M.H. Novais, K. Buczkó, M.M. Morais and L. Ector. 2019. Morphological reconsideration of the araphid genus *Pseudostaurosira* (Bacillariophyceae), a revision of *Gedaniella*, *Popovskayella* and *Serratifera*, and a description of a new *Nanofrustulum* species. *Plant Ecol. Evol.* 152: 262–284. Moser, G., H. Lange-Bertalot and D. Metzeltin. 1998. Insel der Endemiten. Geobotanisches Phänomen Neukaledonien [Island of endemics. New Caledonia – a

goebotanical phenomenon]. Bibl. Diatomol. 38: 1–464.

Ognjanova-Rumenova, N., D. Temniskova-Topalova and M. Valeva. 1994.

Sciences, San Francisco, California. Mem. Calif. Acad. Sci. 17: 291–300.

Ultrastructure of *Fragilaria* Lyngbye species (Bacillariophyta) from Neogene sediments in Bulgaria. *In*: (J.P. Kociolek, ed.) *Proceedings of the 11th International Diatom Symposium. San Francisco, California. 12–17 August 1990.* California Academy of

Patrick, R. and C.W. Reimer. 1966. The diatoms of the United States. Exclusive of Alaska and Hawaii. Volume 1. Fragilariaceae, Eunotiaceae, Achnanthaceae, Naviculaceae. *Monogr. Acad. Nat. Sci. Phila.* 13: 1–688.

Petit, P. 1888. Diatomacées récoltées dans le voisinage du Cap Horn. In: (P. Hariot, P.

Petit, J. Muller d'Argovie, E. Bescherelle, C. Massalongo and A. Franchet, eds) *Mission Scientifique du Cap Horn 1882-1883. Tome V, Botanique*. Gauthier-Villars et Fils, Imprimeurs-Libraires, Paris. pp. 111–140, pl. 10.

Round, F.E., R.M. Crawford and D.G. Mann. 1990. *The diatoms. Biology and morphology of the genera*. Cambridge University Press, Cambridge. pp. 747.

Round, F.E., H. Hallsteinsen and E. Paasche. 1999. On a previously controversial "fragilarioid" diatom now placed in a new genus *Nanofrustulum*. *Diatom Res.* 14: 343–356.

Sabbe, K. and W. Vyverman. 1995. Taxonomy, morphology and ecology of some widespread representatives of the diatom genus *Opephora*. *Eur. J. Phycol*. 30: 235–249. Siqueiros-Beltrones, D.A., U. Argumedo-Hernández and F.O. López-Fuerte. 2017. Diversity of benthic diatoms in the Guerrero Negro Lagoon (El Vizcaíno Biosfere Reserve), Baja California Peninsula, Mexico. *Rev. Mex. Biodivers*. 88: 21–35. Williams, D.M. and F.E. Round. 1987. Revision of the genus *Fragilaria*. *Diatom Res*. 2: 267–288.

Witkowski, A. 1994. Recent and fossil diatom flora of the Gulf of Gdańsk, Southern Baltic Sea. Origin, composition and changes of diatom assemblages during the Holocene. *Bibl. Diatomol.* 28: 1–313.

Witkowski, A., H. Lange-Bertalot and D. Metzeltin. 2000. Diatom flora of marine coasts I. *Iconogr. Diatomol.* 7: 1–925.

Witkowski, A., C. Riaux-Gobin and G. Daniszewska-Kowalczyk. 2010. New marine littoral diatom species (Bacillariophyta) from Kerguelen Islands. II. Heteropolar species of Fragilariaceae. *Vie Milieu* 60: 265–281.

Figures 1–12. *Opephora pacifica* from Kal Bay (isotype).

(1) Grunow slide no. 790 containing material collected from Flugsand an der Kalkbai, Kap der Guten Hoffnung. (2–11) LM photographs. (11) Girdle view. (12). SEM image showing the external features of the valve: single-slit striae bearing well-developed, dichotomously-branched volae and well-developed apical pore fields.

Figures 13–20. SEM images of external features of *Opephora pacifica* from Kalk Bay (isotype) material. (13, 14) Girdle views showing relatively shallow valves, wide valvocopulae bearing small depositions on their distal edge, and the much slender copulae. (15–17) Detail of the valve apices showing the apical pore fields, sometimes occluded by extra siliceous material as in (15). (18) Detail in girdle view showing the single-slit areolae and the degree of development of the volae. (19–20) Two other specimens found in Kalk Bay (isotype) material depicted in valve view, showing variability in valve outline.

Figures 21–25. SEM images of internal features of *Opephora pacifica* from Kalk Bay (isotype) material. (21) Internal view of whole valve. Notice lack of chambered areolae and the degree of entanglement of the volae. The internal side of the apical pore field can be seen in the upper left side of the image. (22–25) Various shots depicting the high degree of entanglement of the volae, anastomosed and forming a net-like pattern.

Table 1. Taxa ascribed to *Opephora* and taxonomic status after the present revision. Rows in gray depict confirmed or possible true members of *Opephora*.

Taxon	Current taxonomic	Reference	Comments
	position		
Opephora americana Peragallo	Unknown		
Opephora angusta Cholnoky	Unknown		Probably
			conspecific with
			Neofragilaria stylus
			Krzywda,
O ₂			Witkowski et
			Chunlian Li in Li et
7			al. (2015)
Opephora anomala Giffen	Unknown		Probably a
			Neofragilaria
	4		Desikachary,
			A.K.S.Prasad et
			Prema in
			Desikachary &
		7	Prema (1987)
Opephora ansata M.H.Hohn et	Unknown		Probably a
Hellerman			Staurosirella
			following the
			drawing in Patrick
			and Reimer (1966)
Opephora bituminosa (Pantocsek)	Unknown	This manuscript	Probably a
Cleve-Euler			Pseudostaurosira
			following the

			interpretation of
			Ognjanova-
			Rumenova et al.
			(1994)
Opephora burchardtiae Witkowski	Neofragilaria	This manuscript	
	burchardtiae		
	(Witkowski)		
	E.Morales comb.		
	nov.		
Opephora cantalense Héribaud	Unknown		
	T.1.1		
Opephora cantalense var. capitata	Unknown		
Héribaud			
Opephora cantalense var. obesa	Unknown		
Héribaud	(0)		
Opephora cantalense var. obesa	Unknown		
Tempère <i>et</i> H.Peragallo			
Opephora cantalense var. obtusa	Unknown		
Tempère <i>et</i> H.Peragallo		_	
Opephora fragilarioides H.Kobayasi	Unknown		Probably a true
			Opephora following
			the original drawing
			by Kobayasi et al.
			(1977), and SEM
			illustration in
			Witkowski et al.
			(2000, pl. 25, fig. 26

			as O. pacifica)
Opephora gemmata (Grunow)	Unknown		
	Chikhowh		
Hustedt			
Opephora gemmata f. minor Jurilj	Unknown		
Opephora giffenii Schoeman	Unknown		Probably a
			Neofragilaria
Opephora glangeaudii Héribaud	Unknown		
On only one or out on out of	Staurosirella	Manalas at al	
Opephora guenter-grassii		Morales et al.	
(Witkowski et Lange-Bertalot) Sabbe	guenter-grassii	(2019)	
et Vyverman	(Witkowski et		
7	Lange-Bertalot)		
	E.Morales,		
	C.E.Wetzel et Ector		
Opephora hachiroensis H.Kobayasi	Unknown		Original pictures not
	7		clear, but probably a
			Stauroforma
Opephora horstiana Witkowski	Sarcophagodes	Morales et al.	
	mutabilis (Grunow)	(2019)	
	E.Morales		
Opephora kittonii Cleve-Euler	Unknown		Probably a
			Neofragilaria
Opephora krumbeinii Witkowski,	Nanofrustulum	Morales et al.	
Witak et Stachura apud Lange-	krumbeinii	(2019)	
Bertalot et Genkal	(Witkowski, Witak		
	et Stachura)		
	E.Morales		

Opephora lanceolata Lohman	Unknown		
Opephora linearis J.W.Sherman et	Unknown		
R.M.Patrick			
Opephora lineata Edsbagge	Unknown		
Opephora lineata Giffen	Unknown		Probably a
			Pseudostaurosira
Opephora marina (W.Gregory)	Current	Andrén (1997)	Type analyzed
P.Petit			
Opephora marina var. genuina	Unknown		
Cleve-Euler			
Opephora marina var. minuta Cleve-	Pseudostaurosira	This manuscript	Witkowski et al.
Euler	minuta (Cleve-Euler)		(2000) present LM
	E.Morales,		and SEM images of
	C.E.Wetzel, Van de		this taxon as
	Vijver <i>et</i> Ector stat.		Opephora minuta
	nov. comb. nov.		
Opephora marina var. perminuta	Pseudostaurosira	Sabbe and	
(Grunow) Proschkina-Lavrenko	perminuta (Grunow)	Vyverman (1995)	
	Sabbe et Wyverman		
Opephora marina var. pontica	Unknown		
Tarnavschi et Oltean			
Opephora martyi Héribaud	Staurosirella martyi	Morales and	
	(Héribaud)	Manoylov (2006)	
	E.Morales <i>et</i>		
	Manoylov		

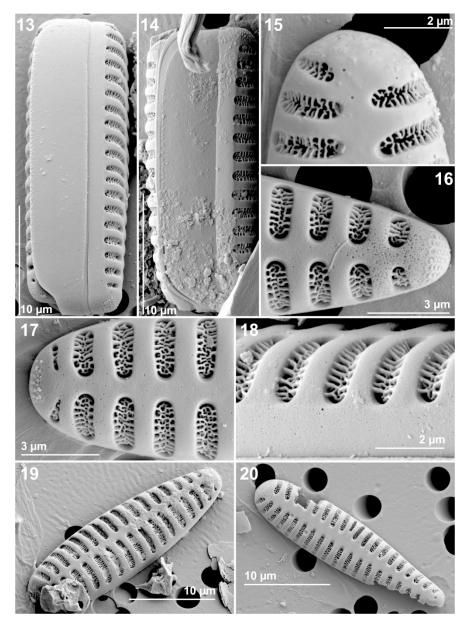
Opephora martyi f. anomala	Unknown	Opephora martyi is
Héribaud		now in
		Staurosirella, this
		forma should be
		revised
Opephora martyi f. elliptica	Unknown	Opephora martyi is
Komarenko		now in
		Staurosirella, this
		forma should be
		revised
O,		
Opephora martyi f. intermedia	Unknown	Opephora martyi is
Komarenko		now in
(Staurosirella, this
	_ .	forma should be
		revised
	4	
Opephora martyi f. semirostrata	Unknown	Opephora martyi is
Tinny		now in
		Staurosirella, this
		forma should be
		revised
Opephora martyi f. vinaninkarenae	Unknown	Opephora martyi is
Manguin		now in
		Staurosirella, this
		forma should be
		revised
Opephora martyi var. amphioxys	Unknown	Opephora martyi is
V.S.Poretzky		now in
		Staurosirella, this

		variety should be
		revised
Opephora martyi var. baicalensis	Unknown	Opephora martyi is
Skvortzov		now in
		Staurosirella, this
		variety should be
		revised
Opephora martyi var. capitata	Unknown	Opephora martyi is
Héribaud		now in
		Staurosirella, this
		variety should be
		revised
Opephora martyi var. elongata	Unknown	Opephora martyi is
Skvortzow	Chkhowh	now in
Skvortzow		
	4	Staurosirella, this
		variety should be
		revised
Opephora martyi var. minor	Unknown	Opephora martyi is
Héribaud		now in
		Staurosirella, this
		variety should be
		revised
Opephora martyi var. okadae	Unknown	Opephora martyi is
(Skvortzow) Okuno		now in
		Staurosirella, this
		variety should be
		revised

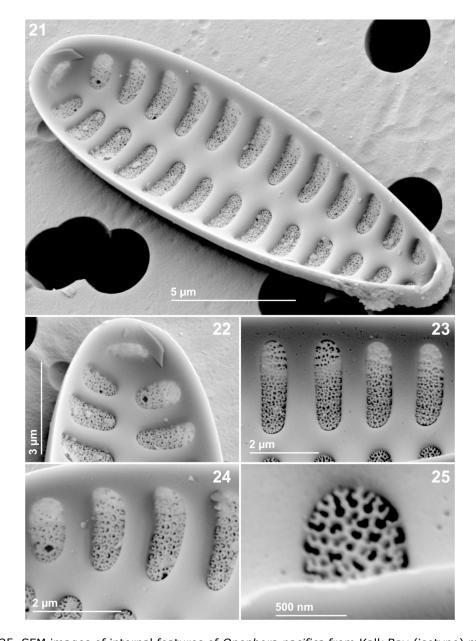
Opephora martyi var. polymorpha	Unknown		Opephora martyi is
(Jouravleva) Proschkina-Lavrenko			now in
			Staurosirella, this
			variety should be
			revised
Opephora martyi var. robusta	Unknown		Opephora martyi is
Héribaud			now in
			Staurosirella, this
			variety should be
			revised
Opephora martyi var. robusta	Unknown		Opephora martyi is
Skvortzow			now in
			Staurosirella, this
	L .		variety should be
	0		revised
Opephora minuta (Cleve-Euler)	Pseudostaurosira	This manuscript	Witkowski et al.
Witkowski, Lange-Bertalot et	minuta (Cleve-Euler)		(2000) present LM
Metzeltin	E.Morales,		and SEM images of
	C.E.Wetzel, Van de		this taxon
	Vijver et Ector stat		
	nov. & comb. nov.		
Opephora mutabilis (Grunow) Sabbe	Sarcophagodes	Morales et al.	
et Wyverman	mutabilis (Grunow)	(2019)	
	E.Morales		
Opephora naveana Le Cohu	Pseudostaurosira	Morales and	
	naveana (Le Cohu)	Edlund (2003)	
	E.Morales <i>et</i> Edlund		

Opephora neoelliptica (Witkowski)	Pseudostaurosira	Morales (2002)	
Witkowski, Metzeltin et Lange-	neoelliptica		
Bertalot	(Witkowski)		
	E.Morales		
Opephora okadae Skvortzow	Unknown		Syn.: Opephora
			martyi var. okadae
			(Skvortzow) Okuno.
			Placement in
			Staurosirella should
			be assessed.
Opephora olsenii M.Møller	Pseudostaurosira	Sabbe and	
	perminuta (Grunow)	Vyverman (1995)	
	Sabbe et Wyverman		
	4.		
Opephora pacifica (Grunow) P.Petit	Current	This manuscript	Isotype material
			analyzed in this
			manuscript
Opephora pacifica f. parva	Unknown		
Mereschkowski			
Opephora pacifica var. trigona	Unknown		
Héribaud			
Opephora parva (Grunow) Krasske	Unknown		Probably a member
			of Sarcophagodes
			following SEM
			illustrations in
			Witkowski (1994)
Opephora perlonga Giffen	Unknown		

Opephora perlonga var. clavata	Unknown		
Giffen			
Opephora perminuta (Grunow)	Pseudostaurosira	Sabbe and	
Frenguelli	perminuta (Grunow)	Vyverman (1995)	
	Sabbe <i>et</i> Wyverman		
Opephora pinnata (Ehrenberg)	Nanofrustulum shiloi	Round et al.	
P.Petit	Round, Hallsteinsen	(1999)	
	et Paasche		
Opephora pinnata var. lanceolata	Unknown		
C.S.Boyer			
Opephora polymorpha Jouravleva	Unknown		
Opephora schulzii (C.Brockmann)	Stauroforma schulzii	Gogorev and	
,			
Simonsen	(C.Brockmann)	Lange (2014)	
	Gogorev		
Opephora schwartzii (Grunow)	Unknown		
	Clikilowii		
P.Petit ex Pelletan			
Opephora taiaensis J.R.Carter et	Unknown		
Denny			



Figures 13–20. SEM images of external features of *Opephora pacifica* from Kalk Bay (isotype) material. (13, 14) Girdle views showing relatively shallow valves, wide valvocopulae bearing small depositions on their distal edge, and the much slender copulae. (15–17) Detail of the valve apices showing the apical pore fields, sometimes occluded by extra siliceous material as in (15). (18) Detail in girdle view showing the single-slit areolae and the degree of development of the volae. (19–20) Two other specimens found in Kalk Bay (isotype) material depicted in valve view, showing variability in valve outline.



Figures 21–25. SEM images of internal features of *Opephora pacifica* from Kalk Bay (isotype) material. (21) Internal view of whole valve. Notice lack of chambered areolae and the degree of entanglement of the volae. The internal side of the apical pore field can be seen in the upper left side of the image. (22–25) Various shots depicting the high degree of entanglement of the volae, anastomosed and forming a net-like pattern.

BIONOTE

Eduardo A. Morales

Water Laboratory, University of Évora, P.I.T.E. Rua da Barba Rala No. 1, 7005–345 Évora, Portugal; and Institute of Earth Sciences - ICT, University of Évora, Rua Romão Ramalho 59, 7000–671 Évora, Portugal,

edu mora123@outlook.com

Eduardo A. Morales is an expert on diatom taxonomy and ecology. He worked at several U.S.A, Bolivian, Brazilian and Argentinian institutions as Researcher, Adjunct Professor, Taxonomy Coordinator, Instructor and Invited Lecturer. He was also Curator of the Cryptogams Herbarium, Bolivian Catholic University in Cochabamba, Bolivia. He is currently a visiting Researcher at the University of Évora in Portugal. His research focuses on taxonomy and diversity of araphid diatoms of freshwater, brackish and marine environments.



863x1151mm (72 x 72 DPI)