

Polyphyly and homoplastic structures in rhizosolenioid diatom genera: a review

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Background and aims – Traditionally, extant rhizosolenioid diatom genera have been placed in a single family, the Rhizosoleniaceae. However, preliminary molecular data suggested that the family might be polyphyletic. Therefore, a literature review of the morphological, ultrastructural and molecular data of the rhizosolenioid genera was undertaken.

Methods – In addition to the literature survey, the location of the rimoportula in a number of rhizosolenioid genera was investigated by breaking the valves and observing the fragments in the scanning electron microscope.

Key results – The data provides strong support for the previous separation of *Proboscia* and *Rhizosolenia* at the family level (Proboscaceae vs. Rhizosoleniaceae), with the rimoportula being located at the tip of the proboscis in *Proboscia*, or with an internal labia at the base of the hollow tubular rimoportula (= spine or process) in *Rhizosolenia* and *Pseudosolenia*.

Conclusions – The data suggests that a number of rhizosolenioid genera should be transferred to other families, and that gene sequences of two genera (*Dactyliosolen* and *Neocalyptrella*) are needed as their morphological features differ markedly from those of the Rhizosoleniaceae s. str. (*Rhizosolenia*, *Guinardia*, *Pseudosolenia*).

Key words – Bacillariophyta, diatoms, homoplasy, morphology, polyphyly, review, rimoportula, Rhizosoleniaceae.

INTRODUCTION

Traditionally, extant rhizosolenioid diatom genera have been placed in a single family, the Rhizosoleniaceae, because they possess extended girdle regions and a single long spine-like or truncated process on their conical valves. However, it has now become clear that there are fundamental differences within the family with regards to their valve morphology – particularly the position and ultrastructure of the rimoportula. And yet, evidence of this structure in internal view is sparse, likely due to the depth of the conical valve inhibit-

ing easy observation by SEM. Additionally, in nature, valves rarely break at this location further inhibiting EM utility. Details of other valve structures in the rhizosolenioid diatoms are scattered throughout the literature, and only from a few species, making it hard to compare the genera in the family. Preliminary molecular data using 18S rRNA, three-gene analyses, chloroplast markers, and diatom transcriptomes have also suggested that the family might be polyphyletic; however, these analyses have been limited in taxon sampling and by their nature discount the known fossil diversity.

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Plant Ecology and Evolution is published by Meise Botanic Garden and Royal Botanical Society of Belgium
ISSN: 2032-3913 (print) – 2032-3921 (online)

Thus, we have conducted a literature review of the morphological, ultrastructural and molecular data of the rhizosolenioid genera in order to shed light on the apparent polyphyly within the family. We have also examined intentionally broken cultured cells under SEM to examine the variation in ultrastructure of the rimoportula in three genera to determine if characters are present there to describe the molecular clades.

MATERIALS AND METHODS

Material used for the scanning electron microscope (SEM) came from previous DNA extraction efforts outlined in Theriot et al. (2015). The cell pellets to be extracted were placed in 2.0 mL screw-top tubes with the DNA extraction detergent and several 1.0 mm glass beads and placed in a Beadbeater homogeniser for 45 seconds for cell breakage. After breakage, tubes were centrifuged and the supernatant was removed for DNA extraction following QIAGEN Dneasy Plant Mini-kit protocol. The remaining pellet, containing the frustule remains and glass beads were stored at room temperature as cell vouchers for the extraction. For this study, these vouchers were resuspended in distilled water and cleared with a 1:1:1 mixture of 30% hydrogen peroxide: concentrated nitric acid: voucher material. The cleared material was then brought back to neutral pH by centrifugation and dilution, and then dried onto 12 mm diameter glass coverslips. Coverslips were then mounted on aluminium SEM stubs, coated in 15 nm of iridium with a Cressington 208 Benchtop sputter coater and observed with a Zeiss Supra 40 VP field emission SEM.

MORPHOLOGICAL EVIDENCE OF HOMOPLASIC VALVE STRUCTURES

It was known for many decades that rhizosolenioid diatoms possessing truncated tips, like *Rhizosolenia alata* Brightw. (and its varieties) and closely related taxa, were different from the traditional species of *Rhizosolenia* Brightw. that bore ‘spines’ or ‘processes’. Thus, those with truncated tips were often placed in a separate section of the genus – namely, *Alatae* (Gran 1908) or *Inermes* (Pavillard 1925). Some authors recognised that a separate genus was needed for these truncated forms (e.g. Hasle 1975), but it was not until much later that Sundström (1986) in his published doctoral thesis created a monotypic genus with *Proboscia alata* (Brightw.) Sundström as the type species (with its circumscription restricted to North Atlantic type material). However, Sundström (1986) was reluctant to add further species to his new genus until new data became available, and although Priddle et al. (1990) considered some polar *Rhizosolenia* taxa to belong to *Proboscia* Sundström, their book chapter was not the place to make such transfers. This happened over the following years when living species were either transferred to *Proboscia* (Jordan et al. 1991, Hernández-Becerril 1995, Moreno et al. 1996) or were newly described (Takahashi et al. 1994).

Further evidence supporting the separation of *Proboscia* and *Rhizosolenia* concerns the position of the rimoportula and the steps involved in valve morphogenesis. It has

been demonstrated using cultured materials that the spine (or process) in *Rhizosolenia setigera* Brightw. is the external portion of the rimoportula (van de Meene & Pickett-Heaps 2004), while the longitudinal slit is the corresponding feature in *Proboscia alata* (van de Meene & Pickett-Heaps 2002). In short, the proboscis is not a rimoportula. *Pseudosolenia* Sundström also bears a spine-like external portion of the rimoportula (Sundström 1986), and so is similar to *Rhizosolenia*, but the proboscis-like extension in *Urosolenia* Round & Crawford lacks a longitudinal slit, despite bearing small spinulae at the tip (Round et al. 1990). *Guinardia* H. Peragallo also has a recognisable rimoportula, which is often associated with a hollow tubular process that fits into a depression on the valve of the complementary cell (e.g. *G. cylindrus* (Cleve) Hasle – illustrated in Hasle (1975) and Sundström (1986) as “*Rhizosolenia cylindrus* Cleve”). On the other hand, *Dactyliosolen* Castracane appears to be unrelated to the other rhizosolenioid diatoms with regards to its girdle structure (i.e. large pores, internal flanges – illustrated in Hasle 1975).

During valve morphogenesis in *P. alata*, the proboscis increases in length by anti-tip growth (i.e. it grows from the tip backwards), and eventually forms the valve (van de Meene & Pickett-Heaps 2002). The claspers are formed when the expanding (still unsilicified) conical valve comes into contact with the silicified rigid tip of the sibling cell. At first the proboscis presses against the valve, creating an impression of the tip, then the valve produces flanges of silica around it to complete the claspers. This tip-clasper combination allows sibling cells to be loosely filamentous (van de Meene & Pickett-Heaps 2002). The position of the slit (external part of the rimoportula) near the end of the tip suggests that its location on a flattened centric valve would be equivalent to the annulus. During valve morphogenesis in *R. setigera*, growth occurs in two directions; distally to form the hollow, external portion of the rimoportula and backwards to form the conical valve. The extremely long spine-like rimoportula (150–250 µm long) does not appear to touch the opposing valve, and so claspers are not formed and the sibling cells are either solitary or cluster together in parallel (somewhat similar to *Bacillaria* J.F.Gmel.) (van de Meene & Pickett-Heaps 2004). One presumes that those *Rhizosolenia* spp. that possess claspers (and otaria) follow a similar valve morphogenesis pathway to that of *P. alata*, while the valves of the solitary *P. subarctica* K. Takahashi, R. Jordan & Priddle follow that of *R. setigera*.

Thus, the claspers are a direct consequence of the distal ends of valve extensions making an impression on the as yet unsilicified valves of sibling cells, and thus should not be regarded as homologous structures – although their appearance and function may be similar. It is also likely that numerous unrelated genera – e.g. *Pyxilla* Grev., *Skeletonema* Grev., and *Hemiaulus* Heib. (and other hemiauloids) – with long valve extensions use the same mechanism to create impressions or attachment structures on opposing valves. Furthermore, it is assumed that fossil *Proboscia* spp. and *Rhizosolenia* spp. with very long valve extensions (> 100 µm) were solitary because they lacked claspers.

The ultrastructure of the rimoportula also varies considerably within the Rhizosoleniaceae s. lat. Externally, the

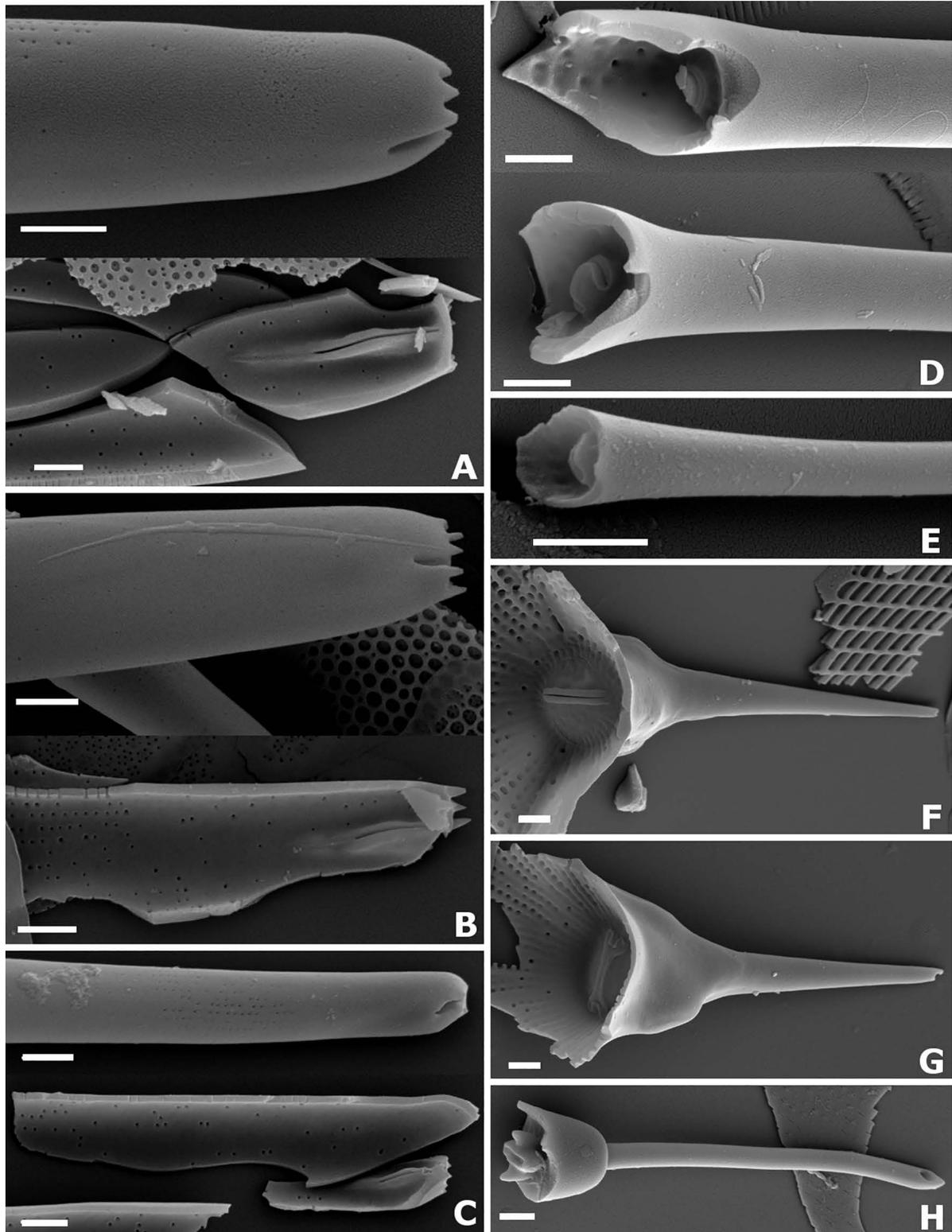


Figure 1 – SEM images of the internal and external rimoportula ultrastructure of selected rhizosolenioid taxa. Images taken with stage tilted to 30° angle and digitally rotated. Voucher numbers indicate DNA extraction associated with each strain, with more material available from author MPA. Material was broken with 1 mm glass bead in Beadbeater per methods in Ashworth et al. (2013) and Theriot et al. (2015); A–C, *Proboscia* spp. (DNA extraction vouchers HK300, HK236 and HK032, respectively); D & E, *Rhizosolenia* cf. *setigera* (DNA extraction vouchers HK032 and HK268, respectively); F, *Rhizosolenia imbricata* HK244; G, *Rhizosolenia formosa* HK354; H, *Neocalyptrella robusta* HK423. Scale bars = 1 μm.

Table 1 – Morphological and cytological features of the genera in the Rhizosoleniaceae s. lat.

¹ Although there is no rimoportula, labiated structures have been observed on the conical part of the valve (Sala et al. 2008). ² See Hernández-Becerril & Meave del Castillo (1996) for definitions. ³ A tube is present in *D. fragilissimus* (Bergon) Hasle and *D. phuketensis* (Sundström) Hasle but not in *D. blavyanus* (H.Peragallo) Hasle (M.P. Ashworth, unpublished observations). ⁴ However, some species (e.g. *R. setigera* and *R. bergonii*) lack them (Sunesen & Sar 2007). ⁵ Claspers, in the true sense, are absent, but the valve does possess a contiguous area into which the opposing valve process fits (see e.g. Yun & Lee 2011). ⁶ The complementary valve process fits into a depression (Yun & Lee 2011), which could be considered analogous to the claspers. ⁷ However, they are absent in *P. subarctica* (Takahashi et al. 1994). ⁸ The valve has an impression of the distal end of the long process (see figures in Tremarin et al. 2015), but does not develop into the pocket-like structure called claspers. However, in terms of valve morphogenesis, the formation of this impression probably occurs in the same way as that of the claspers of *P. alata*. ⁹ Only present in *D. fragilissimus*. ¹⁰ Based on *G. flaccida* (Castracane) H.Peragallo, *G. striata* (Stolterfoth) Hasle and *G. delicatula* (Cleve) Hasle (M.P. Ashworth, unpublished observations). ¹¹ Known at least for the Columbian and Peruvian Amazon (Sala et al. 2008) and Chinese (e.g. Liu et al. 2016) species. ¹² Confirmed only for *D. blavyanus* (round) and *D. fragilissimus* (linear). ¹³ As shown for instance in Cupp (1943) for *R. bergonii* H.Peragallo, and described by Meunier (1915) for *R. shrubsolei* Cleve (= *R. imbricata* Brightwell). ¹⁴ Based on Pavillard (1905). ¹⁵ Reported in Jordan et al. (1991) and Jordan & Ligowski (2004, 2006). ¹⁶ Rott et al. (2006) briefly discussed about auxospores, but did not illustrate them. ¹⁷ Known only for *R. setigera* (van de Meene & Pickett-Heaps 2004). ¹⁸ Known only for *P. alata* (van de Meene & Pickett-Heaps 2002). ¹⁹ Observations by Ferreyra & Ferrario (1983) and R. Ligowski in Jordan et al. (1991). ²⁰ See Priddle et al. (1990) for some discussion on *Rhizosolenia* taxa with multiple rows of copulae. ²¹ Meunier (1910) described resting spores in *R. spyliformis* Brightwell. ²² Edlund & Stoermer (1993) reported resting spores in *Acanthoceras* and *Urosolenia*.

	<i>Rhizosolenia</i>	<i>Pseudosolenia</i>	<i>Guinardia</i>	<i>Proboscia</i>	<i>Urosolenia</i>	<i>Neocahyptrrella</i>	<i>Dactylosolen</i>
rimoportula	tubular (external) flattened labia (internal)	tubular externally, convoluted labia internally (= cornuportula ²)	tubular externally, labia internally	slit-like externally, labia internally	absent ¹	tubular externally, labia or decorated labia internally (= conflatuportula ²)	irregular slit or tube externally ³ , stalked labia internally
claspers	usually present ⁴	absent ⁵	usually present ⁶	usually present ⁷	absent ⁸	absent	usually absent ⁹
otaria	usually present ⁴	absent	absent	absent	absent	absent	absent
pores in velum of copulae	slit-like (single or multiple)	slit-like (single)	rectangular/wide slit (single) ¹⁰	round (single or multiple)	unoccluded round poroids on the bands ¹¹	slit-like (single)	round (multiple) or slit-like ¹²
auxospore	90° to the mother cell, emerging from girdle area ¹³	not known	large bladder forms between broken halves of cell ¹⁴	terminal ¹⁵	reported but not illustrated ¹⁶	not known	not known
valve growth	two-directional; distally to form external rimoportula, proximally to form conical valve ¹⁷	not known	not known	anti-tip; proximally to form proboscis and conical valve ¹⁸	not known	not known	not known
cytoplasmic rotation	observed ¹⁷	not known	not known	not observed ¹⁸	not known	not known	not known
claspers	absent	absent	absent	present, but perhaps only on one valve ¹⁹	absent	absent	absent
otaria	absent	absent	absent	absent	absent	absent	absent
rows of copulae	sometimes > 2 ²⁰	not known	not known	2, as in the vegetative cell	not known	not known	not known
resting spores	sometimes present ²¹	not known	not known	not known	present ²²	not known	not known

rimoportula of *Proboscia* species is a slit near the top of the valve, while internally it is formed of two adjacent thin sheets of silica extending from the interior of the tip, down the proboscis well past the external slit (fig. 1A–C). In the majority of the genera in the Rhizosoleniaceae, the external portion of the rimoportula is a conical tube, usually at the apex of the valve. Internally, the rimoportula of *Rhizosolenia setigera*-like species is a slit across a hemisphere at the base of the external spine, which can be across the side (fig. 1D) or apex (fig. 1E) of the hemisphere. In the otaria-bearing *Rhizosolenia* spp. examined in this study, the rimoportula is a slit across the base of the external spine (fig. 1F & G), with a hyaline thickening around the slit. There appears to be some variation in the morphology of this thickening and the orientation of the slit relative to the otaria among taxa. In *Neocalyptrella robusta* (G.Norman ex Ralfs) Hernández-Becerril & Meave del Castillo, the internal structure of the rimoportula is a laterally-compressed block, with triangular spines perpendicular to the rimoportula slit (fig. 1H).

The morphological and cytological features separating the genera in the Rhizosoleniaceae s. lat. are presented in table 1.

THE RHIZOSOLENIACEAE IS POLYPHYLETIC BY DNA DATA

According to Round et al. (1990) the Rhizosoleniales consists of two families, the Rhizosoleniaceae and the Pyxillaceae, with the former including the following extant genera; *Dactyliosolen*, *Guinardia*, *Proboscia*, *Pseudosolenia*, *Rhizosolenia*, and *Urosolenia*. Since then, only *Neocalyptrella* Hern.-Becerril & Meave has been added (originally named “*Calyptrella*” Hern.-Becerril & Meave, the genus was later changed to *Neocalyptrella* due to the existing occupation of the genus *Calyptrella* Naudin in the botanical nomenclature – see Hernández-Becerril & Meave del Castillo 1997 for further detail). However, the Rhizosoleniaceae is polyphyletic. In early 18S ribosomal RNA phylogenetic studies (Medlin et al. 2000, Medlin & Kaczmarska 2004), *Proboscia* occupies a lone branch among the radial centrics (“Clade 1”), which includes the Coscinodiscales, Aulacoseirales, Melosirales, Leptocylindrales, Corethrales, Paraliales and Rhizosoleniales. However, *Proboscia* and *Rhizosolenia* are not closely related to each other, with the former either sister to the Coscinodiscales, Melosirales and Aulacoseirales (Medlin et al. 2000, Sorhannus 2004) or to “Clade 2” containing the rest of the diatom taxa (Medlin & Kaczmarska 2004), and the latter (plus *Guinardia*) sister to *Corethron* Castracane (Medlin et al. 2000, Medlin & Kaczmarska 2004). Increased taxon sampling and additional DNA markers have failed to bring *Proboscia* and *Rhizosolenia* together into a clade; three-gene analyses (adding the plastid-encoded *rbcL* and *psbC* markers to nuclear ribosomal SSU) place *Proboscia* either sister to all diatoms other than *Corethron* and *Leptocylindrus* Cleve (Ashworth et al. 2013) or sister to the Coscinodiscales (Nakov et al. 2014), while the addition of four more chloroplast markers saw *Proboscia* sister to the Melosirales (Theriot et al. 2015 – reproduced in fig. 2), which was also observed in a more recent 1151 taxon, 11-gene dataset (Nakov et al. 2018) and a phylogenetic analysis of orthologous markers from diatom transcriptomes (Parks et al. 2017). Furthermore, sev-

eral taxa currently in the Rhizosoleniaceae actually come out among the clades of Medlin & Kaczmarska’s (2004) Class Mediophyceae (found within the Subdivision Bacillariophytina Medlin & Kaczmarska in their fig. 1, collapsed here for clarity) in molecular phylogenies. *Dactyliosolen blavyanus* (H.Perag.) Hasle and *Neocalyptrella robusta* have both consistently been found in mediophycean clades; *D. blavyanus* in a clade with the Chaetocerotales and Hemiaulales (Ashworth et al. 2013, Nakov et al. 2014, 2018, Theriot et al. 2015) and *N. robusta* either sister to all other mediophyte diatoms but *Attheya* T.West (Sinninghe Damsté et al. 2004) or in a clade with *Biddulphia* Gray and *Attheya* (Nakov et al. 2018). Sequence data for *Urosolenia* also place it in the clade with the Chaetocerotales and Hemiaulales, sister to *Acanthoceras* Honigsmann (Ashworth et al. 2013, Nakov et al. 2014, 2018, Theriot et al. 2015), which has a frustule morphologically identical to the former genus but with two hollow, open processes (‘setae’) instead of one (Round et al. 1990). Like *Chaetoceros* Ehrenb., both *Urosolenia* and *Acanthoceras* are known to produce resting spores (Edlund & Stoermer 1993).

These differences in the earlier phylogenetic studies, together with key morphological features, led Nikolaev & Harwood (2000) to erect the Probosciceae. However, validation of the new family name was carried out later by Jordan & Ligowski (2004), because there was no formal description in the original paper.

IS *PROBOSCIA ALATA* A SINGLE ENTITY OR A SPECIES COMPLEX?

In the old literature there are at least six forms or varieties of *Rhizosolenia alata* – *R. alata* f. *alata*, *R. alata* var. *corpulenta* Cleve, *R. alata* f. *genuina* Gran, *R. alata* f. *gracillima* (Cleve) Grunow, *R. alata* f. *indica* H.Perag. and *R. alata* f. *curvirostris* Gran. The latter two have since been raised to species level, as *Proboscia indica* (H.Perag.) Hern.-Becerril and *P. subarctica* K.Takahashi, R.Jordan & Priddle, respectively, while the others (except *R. alata* f. *alata*) were synonymised with either the type species (*P. alata*) or with *P. indica*. However, there are small morphological differences in *P. alata* valves from the Arctic, tropical and Southern Ocean that point towards two or more cryptic or pseudocryptic species (compare specimens illustrated in Jordan et al. 1991, Takahashi et al. 1994, Jordan & Ligowski 2004) – notably, the length of the proboscis and degree of proboscis curvature. Furthermore, regarding the copulae, there are several pores in the velum of tropical specimens, but only one in the velum of specimens from polar regions (Sundström 1986). Although there appear to be morphological differences in the winter valve probosces among the three Southern Ocean species (see Jordan et al. 1991), this feature has not been well studied, but might prove to be another good taxonomic character. Finally, the auxospores of *P. alata* s. lat. are known to exhibit some differences, as the Southern Ocean form always has a bifurcated end (Jordan et al. 1991, Jordan & Ligowski 2004), while the one from northern waters seemingly does not (e.g. see Lebour 1930, Cupp 1943). Indeed, the auxospores of other species also show some species-specific characters (compare *P. alata* with *P. truncata* (G.Karst.) Nöthig & Ligowski: Jordan & Ligowski 2004, 2006). Thus,

gene sequences of *P. alata* s. lat. specimens from around the world might help to distinguish these similar-looking forms.

FURTHER STUDIES IN THE RHIZOSOLENIACEAE?

While the ultrastructure of the rimoportula and patterns of valve morphogenesis help us to explain the molecular paraphyly of the Rhizosoleniaceae with regard to *Proboscia* and *Neocalyptrella*, questions remain about rhizosolenioid evolution. There are certainly more data to be collected on rhizosolenioid taxa, though to understand the evolution of *Proboscia* in particular, other non-rhizosolenioid clades should be included in future studies. What ultrastructural and developmental characters, if any, does *Proboscia* share with *Ellerbeckia* R.M.Crawford, *Aulacoseira* Thwaites and *Melosira* C.Agardh, with whom the genus shares a (poorly-supported,

admittedly) molecular clade (fig. 2)? What characters, if any, does the genus share with *Leptocylindrus* Cleve and *Corethron* Castracane, which also have long perivalvar axes, but lack a rimoportula (Round et al. 1990)? What other fossil lineages, such as *Pyxilla* discussed above, should be thoroughly documented by electron microscopy when looking for common ultrastructure?

Details on the ultrastructure of the auxospore and initial cell has been suggested as a source of key characters to understanding the phylogeny of diatoms (Medlin & Kaczmarek 2004, Kaczmarek et al. 2013). However, can we really expect to observe the perizonial bands of the Bacillariophytina clade, where we find *Neocalyptrella*, *Dactyliosolen blavyanus*, *Acanthoceras* and *Urosolenia*, when these taxa do not exhibit an elongation of the valve for which these bands allow? In fact, these “Bacillariophytinan rhizosolenioids”

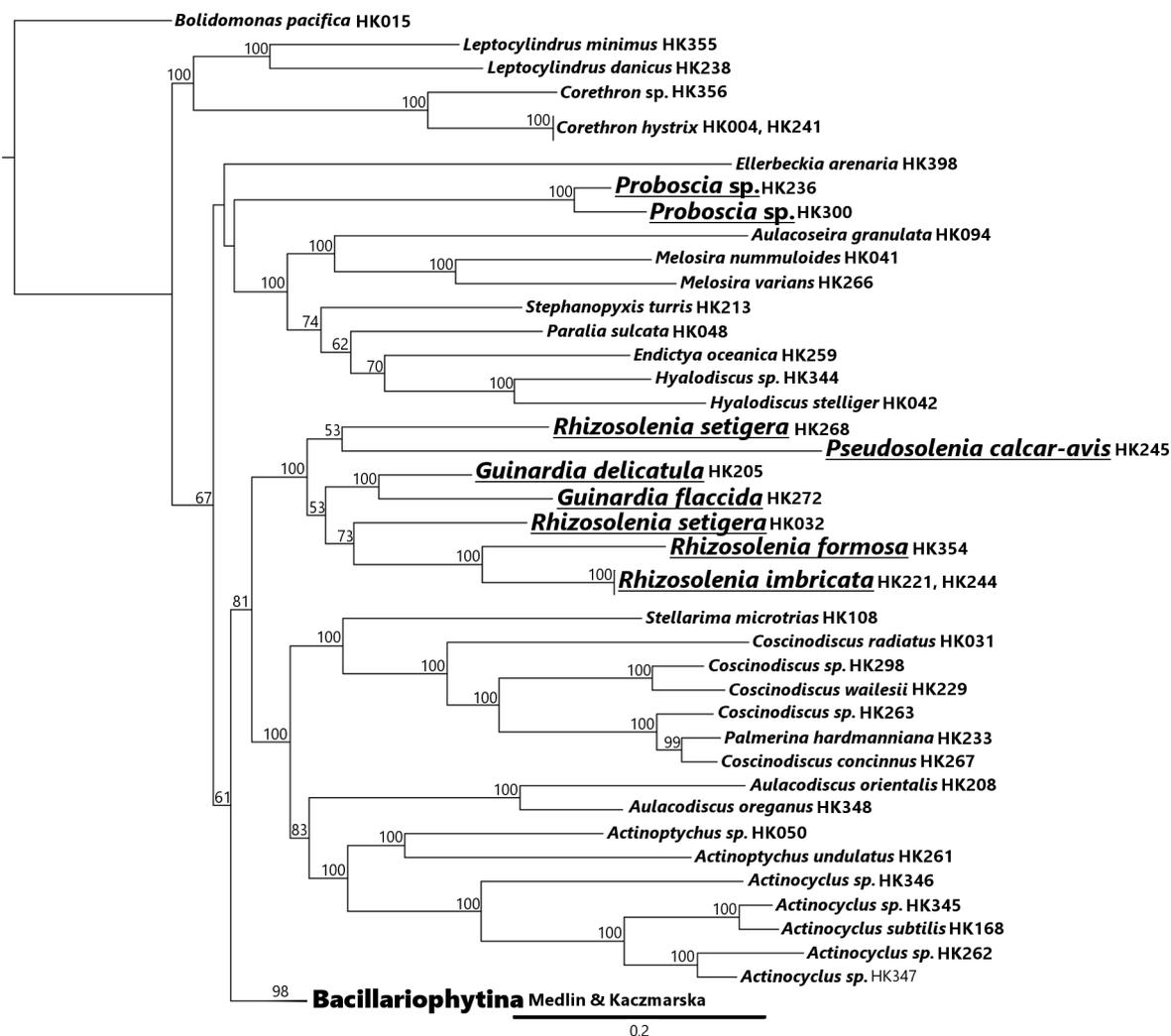


Figure 2 – Phylogenetic tree adapted from NEWICK-formatted trees in Theriot et al. (2015, supplementary files). Maximum likelihood tree based on a 7-gene dataset (nuclear-encoded ribosomal SSU, chloroplast-encoded *rbcL*, *psaA*, *psaB*, *psbA*, *psbC*, *atpB* markers) with bootstrap values from 1000 pseudoreplicates over the appropriate nodes. Rhizosolenioid taxa are highlighted, showing the family is not monophyletic with respect to *Proboscia*. The Bacillariophytina clade is collapsed in this figure for clarity.

could provide a model to explore the molecular basis for initial cell development – closely-related, elongate taxa which do not express perizonial bands will transcribe genes for the development of those bands, while the rhizosolenioids would not. Comparing the transcriptomes of rhizosolenioid and elongate Bacillariophytinan taxa during auxosporulation and initial cell formation could reveal those genes. It would also be interesting to compare those results to other non-elongate Bacillariophytinan clades, such as the Thalassiosirales, to investigate whether the loss of elongate valves was facilitated by the molecular mechanisms in both groups. In this way, we can use the molecular paraphyly of the Rhizosoleniaceae as a map to guide investigations of molecular and genomic mechanisms of all diatoms.

ACKNOWLEDGEMENTS

This manuscript deals with the terminology of valve structures (notably the rimoportula) within rhizosolenioid taxa, and as such is a contribution to the on-going project DIATERM, which is led by Eileen Cox, and to whom this Festschrift is dedicated. Funding for SEM work conducted at UT Austin provided by US Department of Defense grant # W911NF-17-2-0091.

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Managing Editor: David G. Mann

Submission date: 1 Sep. 2018

Acceptance date: 19 Dec. 2018