Systematic placement of the necklace-chain genera *Bleakeleya*, *Koernerella* and *Perideraion* (*Koernerellaceae fam. nov., Koernerellales ord. nov., Bacillariophyta*)

Christopher S. Lobban, *Division of Natural Sciences, University of Guam, Mangilao, GU 96923, USA*

Matt P. Ashworth, *UTEX Culture Collection of Algae, University of Texas at Austin, Austin, TX, USA*

Bleakeleya Round (in Round & al. 1990: 394), type *Bleakeleya notata* (Grunow) Round (≡ *Asterionella bleakeleyi* var. *notata* Grunow, 1867) and suggested that *A. bleakeleyi* var. *recticostata* Körner, 1970 "…should be a species and not a variety of *B. notata*". Round & al. (1990: 394) further commented that, "*B. notata* cannot be included in either *Asterionella* or *Asterionellopsis* without over-widening the circumscription of these and making imprecise genera". Lobban & al. (2011) found these two taxa and several similar species in Micronesia and, based upon ultrastructure and gene sequences described two new genera, including *Koernerella* Ashworth, Lobban & E.C.Theriot for *Asterionella notata* var. *recticostata* and *Perideraion* Lobban & R.W.Jordan for three previously undescribed species. A second species of *Koernerella, K. grunowii* Lobban & C.O.Pérez, was subsequently discovered in Grunow's Honduras material (Lobban & Pérez 2016) growing on *Sargassum* along with *B. notata*.

When we described *Perideraion* and *Koernerella*, there was insufficient taxon sampling to place them within the *Fragilariophyceae* and sequence analysis showed a clade encompassing *Asterionellopsis*, *Asteroplanus*, *Delphoneis*, *Rhaphoneis* and a separate *Bleakeleya* clade (Lobban & al. 2011: fig. 47). That has changed considerably in the last ten years, particularly because of work on the *Plagiogrammales* (e.g. Sato & al. 2008, Li & al. 2015, 2020). Meanwhile, *Bleakeleya* was placed in the "*Ulnariaceae*" E.J.Cox, *nom. inval.*[*] (*Licmophorales, Fragilariophycidae*) by Cox (2015: 87) but was found by Medlin & Desdevises (2016) to pair with *Asterionellopsis* in the *Asterionellopsidaceae* Medlin (*Rhaphoneidales, Urneidophycidae*). *Perideraion* and *Koernerella* remained in the *Fragilariaceae* by default, not considered by either Cox (2015) or Medlin & Desdevises (2016). The analysis by Medlin & Desdevises (2016: fig. 1, "clade 7, Asterionellopaceae [sic], fam. nov.") showed a clade comprising *Asterionellopsis* and *Asteroplanus* and they added *Bleakeleya* only under "expected/predicted genera to be included in this clade…". (Medlin & Desdevises 2016: 138) citing morphology described in Round & al. (1990). Despite this, they concluded by describing the new family specifically to include *Bleakeleya*.

Our recently published diatom trees (Ashworth & Lam in Lobban & al. 2022) show the *Bleakeleya–Perideraion–Koernerella* clade in a clade with the *Rhaphoneidales* and *Plagiogrammales*, two well-defined orders. The relationship between these clades and to *Asterionellopsis* shifts somewhat with the analytical method used to construct the tree; Fig. 1 is a strict consensus tree of the three supplemental trees in Lobban & al. (2022). Although there is a general morphological similarity in frustule and colony form between *Asterionellopsis* and *Bleakeleya*, namely tapered cells attached by ocelli or basal pore fields, respectively, the two genera are widely separated in our trees. *Asterionellopsis* was shown to have several species separable on molecular data but with very few morphological differences (Kaczmarska & al. 2014), but is easily distinguished from *Bleakeleya, Perideraion* and *Koernerella* by the strongly spathulate valve, with a broad basal part (bearing a small, rimmed basal pore field) tapering abruptly to a narrow, linear apical part. In addition, the basal and apical fields in *Asterionellopsis* and *Asteroplana* are considered ocelli (Round & al. 1990,

[*] "*Ulnariaceae*" E.J.Cox is an invalid designation (ICN Art. 36.1) as it was introduced as a *nomen provisorium* ("nom. prov.")

Crawford & Gardner 1997, Kaczmarska & al. 2014) and in *Asterionellopsis* has slits rather than pores. By contrast, *Bleakeleya, Perideraion* and *Koernerella* have more gradually tapered apices and the basal pore fields are perforated by small pores.

Because the *Bleakeleya*, *Perideraion* and *Koernerella* clade is consistently resolved in the molecular phylogenetic trees, but its relationship to the *Plagiogrammales* and *Rhaphoneidales* is less consistently resolved, we feel it is most appropriate at this time to classify the *Bleakeleya* clade to a level equivalent to these more well-established orders. We therefore propose *Koernerellaceae fam. nov.*, and *Koernerellales ord. nov.*, which reflect the constituent genera without creating confusion with similar described family names (*Berkeleyaceae* vs. "*Bleakeleyaceae*") or basing the name on a genus that appears to be paraphyletic in the molecular phylogeny.

Koernerellales Lobban & Ashworth, *ord. nov.*
Description: Heteropolar cells tapering from a broad base in girdle and valve views, forming necklace-like colonies (Fig. 2). Basal pore fields occupying the entire basal valve face, separated from striae by hyaline bar or ring and not organized as elevated ocelli; apical poles with smaller pores not organized into a distinct field.
Type: *Koernerella* Ashworth, Lobban & E.C.Theriot, 2011
PhycoBank registration: http://phycobank.org/103381
Notes: The term "Basal pole" is employed here for the broader, attached end, as in Round & al. (1990), Lobban & al. (2011) and Kaczmarska & al. (2014), not the other way around as claimed by Medlin & Desdevises (2016). Although Lobban & al. (2011) referred to smaller pores at the apices as a pore field, Round & al. (1990) did not classify them as a pore field and, following our consideration of the similar situation in *Hyalosira* (Lobban et al. 2021), we now follow Round & al. (1990).

Koernerellacae Lobban & Ashworth, *fam. nov.*
With the characters of the order *Koernerellales*.
Type: *Koernerella* Ashworth, Lobban & E.C.Theriot, 2011
PhycoBank registration: http://phycobank.org/103382

Cox, E.J. (2015). Diatoms, Diatomeae (Bacillariophyceae s.l., Bacillariophyta). *In*, W. Frey (ed.) *Engler's Syllabus of Plant Families, 13th ed.*, part 2/1, pp. 64–103. Borntraeger Science Publishers, Stuttgart, Germany.

Crawford, R.M. & Gardner, C. (1997). The transfer of *Asterionellopsis kariana* to the new genus *Asteroplanus* (Bacillariophyceae), with reference to the fine structure. *Nova Hedwigia* 65: 47–57.

Grunow, A. (1867). Diatomeen auf *Sargassum* von Honduras gesammelt von Lindig. *Hedwigia* 6: 1–8, 17–37.

Kaczmarska, I., Mather, I., Luddington, I.A., Muise, F. & Ehrman, J.M. (2014). Cryptic diversity in a cosmopolitan diatom known as *Asterionellopsis glacialis* (Fragilariaceae): implications for ecology, biogeography, and taxonomy. *American Journal of Botany* 101: 267–286.

Körner, H. (1970). Morphologie und Taxonomie der Diatomeengattung *Asterionella*. *Nova Hedwigia* 20: 557–724.

Li, C.L., Ashworth, M.P., Witkowski, A., Dąbek, P., Medlin, L.K., Kooistra, W.H.C.F., Sato, S., Zgłobicka, I., Kurzydłowski, K.J., Theriot, E.C., Sabir J.S.M., Khiyami, M.A., Mutwakil M.H.Z., Sabir, M.J., Alharbi, N.S., Hajarah, N.H., Qing. S. & Jansen, R.K. (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., Ashworth, M.P, Mackiewicz, P., Dąbek, P., Witkowski, J., Górecka, E., Krzywda, M. & Witkowski, A. (2020). Morphology, phylogeny, and molecular dating in Plagiogrammaceae family focused on *Plagiogramma-Dimeregramma* complex (Urneidophycideae, Bacillariophceae). *Molecular Phylogenetics and Evolution* 148 (106808: 1-23, 15 figs.

Lobban, C.S. & Pérez, C.O. (2016). A second species of bleakeleyoid diatoms (Bacillariophyta, Fragilariales), *Koernerella grunowii*, from Grunow's Honduras *Sargassum* materials. *Nova Hedwigia* 102: 547–552.

Lobban, C.S., Ashworth, M.P., Arai, Y., Jordan, R.W. & Theriot, E.C. (2011). Marine necklace-chain Fragilariaceae (Bacillariophyceae) from Guam, including descriptions of *Koernerella* and *Perideraion*, genera nova. *Phycological Research* 59: 175–193.

Lobban, C.S., Majewska, R., Ashworth, M., Bizsel, N., Bosak, S., Kooistra, W.H.C.F., Lam, D.W., Navarro, J.N., Pennesi, C., Sato, S., Van de Vijver, B. & Witkowski, A.. (2021). Diatom genus *Hyalosira* (Rhabdonematales emend.) and resolution of its polyphyly in Grammatophoraceae and Rhabdonemataceae with a new genus, *Placosira*, and five new *Hyalosira* species. *Protist* 172, 125816. 37 p.

Lobban, C.S., Ashworth, M.P., Camacho, T., Lam, D.W. & Theriot, E.C. (2022). Revision of Ardissoneaceae (Bacillariophyta, Mediophyceae) from Micronesian populations, with descriptions of two new genera, *Ardissoneopsis* and *Grunowago*, and new species in *Ardissonea*, *Synedrosphenia* and *Climacosphenia*. *PhytoKeys* 208: 103–184.

Medlin, L.K. & Desdevises, Y. (2016). Phylogeny of 'araphid' diatoms inferred from SSU & LSU rDNA, RBCL & PSBA sequences. *Vie et Milieu.* 66: 129-154

Round, F.E., Crawford, R.M. & Mann, D.G. (1990). *The diatoms* biology and morphology of the genera. pp. [i-ix], 1-747. Cambridge: Cambridge University Press.

Sato, S., Watanabe, T., Crawford, R.M., Kooistra, W.H.C.F. & Medlin, L.K. (2008). Morphology of four plagiogrammacean diatoms; *Dimeregramma minor* var. *nana*, *Neofragilaria nicobarica*, *Plagiogramma atomus* and *Psammogramma vigoensis* gen. et sp. nov., and their phylogenetic relationship inferred from partial large subunit rDNA. *Phycological Research* 56: 255–268.

Van Heurck, H. (1881). *Synopsis des Diatomées de Belgique* Atlas. pls XXXI-LXXVII [31-77]. Anvers: Ducaju et Cie.

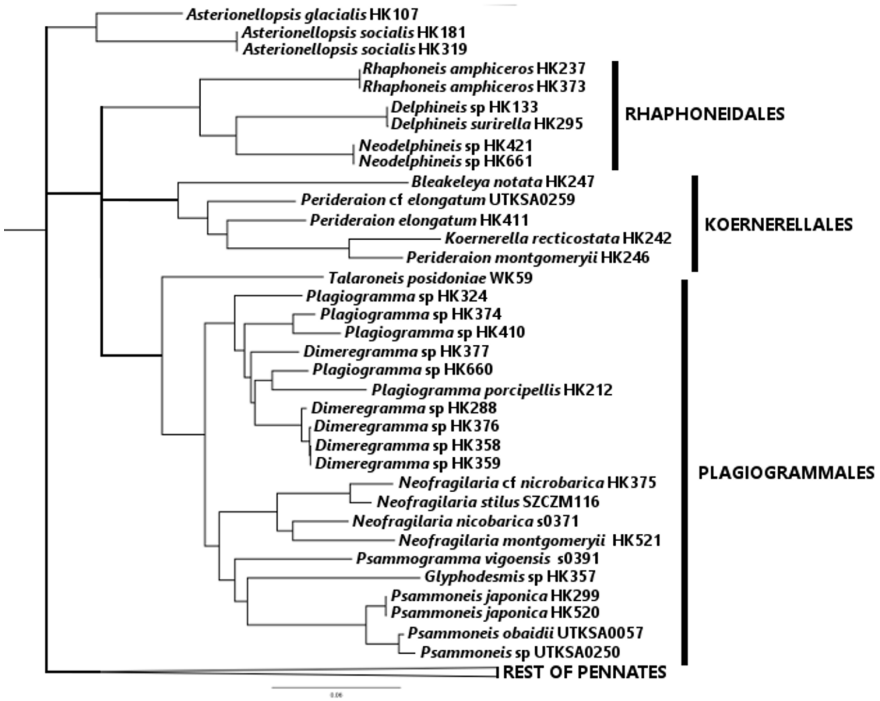

Fig. 1. Strict consensus tree of the results of phylogenetic analyses of a recent DNA sequence dataset, showing the *Bleakeleya–Perideraion–Koernerella* clade exclusive of the *Asterionellopsis*, *Rhaphoneidales* and *Plagiogrammales* clades. The full trees are available in Ashworth & Lam Supplementary Material 5–7 for Lobban et al. (2022).

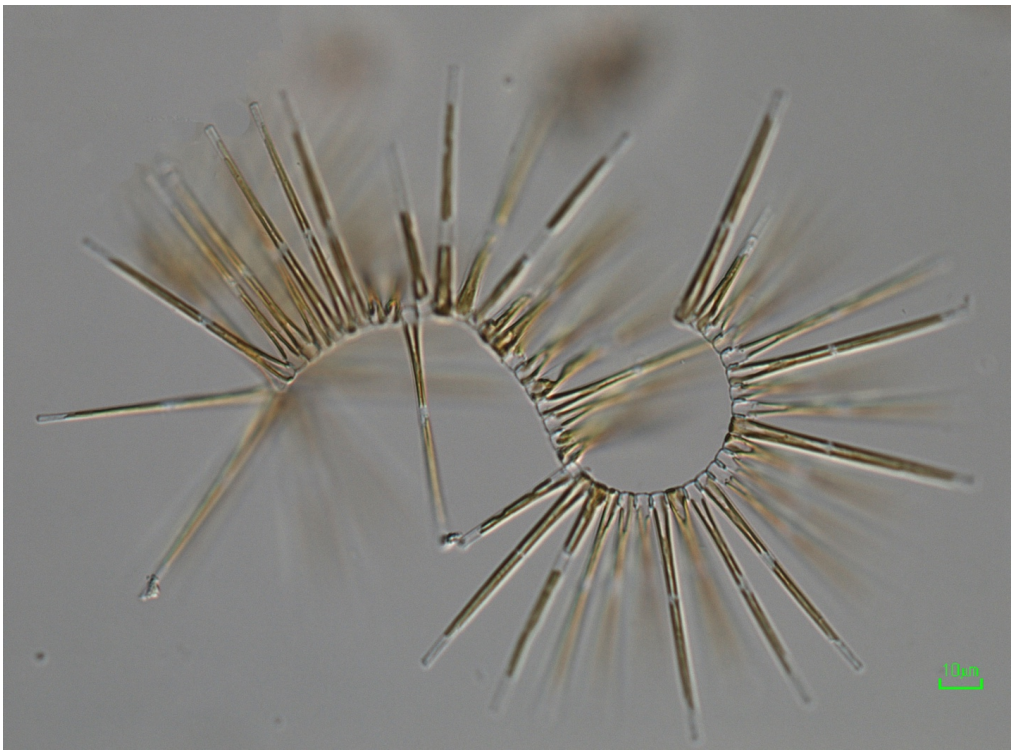

Fig. 2. *Perideraion elongatum* R.W.Jordan, Y.Arai & Lobban: "necklace chain" colony from Guam.