



***Homoeocladia* C.Agardh reinstated for bilaterally symmetrical conopeate *Nitzschia* species
(*Bacillariaceae*, *Bacillariophyta*)**

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Mann (1986) formally defined *Nitzschia* Hassall, *nom. cons.*, subgenus *Nitzschia* to include all species with conopea within this large, polyphyletic genus. Among these is the generitype, *Nitzschia sigmoidea* (Nitzsch) W.Smith (= *Nitzschia elongata* Hassall, *nom. illeg.*). Subsequently, focusing on cell division, Mann & Trobajo (2014) recognized four symmetry categories in *Hantzschia* and *Nitzschia*: (1) all cells hantzschoid; (2) hantzschoid and nitzschoid cells in a 2:1 ratio; (3) hantzschoid and nitzschoid cells in a 1:1 ratio; and (4) all cells nitzschoid. Geitler (1968) and Pickett-Heaps (1983) had already established that *N. sigmoidea* produces both hantzschoid and nitzschoid cells. Mann & Trobajo (2014) added three new conopeate species of *Nitzschia* whose cells are always hantzschoid (*N. dicrogramma* D.G.Mann & Trobajo, *N. brachygramma* D.G.Mann & Trobajo, and *N. parkii* D.G.Mann & Trobajo). The hantzschoid and nitzschoid symmetries both depend on a strongly eccentric keel: two keels on the same side classically assigned to *Hantzschia* and on opposite sides to *Nitzschia*. However, there appear to be two groups of conopeate *Nitzschia*.

Lobban & al. (2019) found great diversity in ultrastructure of a subgroup of conopeate *Nitzschia* spp. with a distinctive set of characters they referred to as the “tholophora (canopy-bearing) morphology”, neither hantzschoid nor nitzschoid because the keel is central; these are bilaterally symmetrical conopeate *Nitzschia* species. Several were already known from electron microscopy (Lobban & Mann 1987, Witkowski & al. 2015, 2016, Liu & al. 2015). Lobban & al. (2019) described 14 new species, mostly marine but one freshwater; showed that light microscopy (LM) was inadequate to identify species; and analyzed molecular and morphological data cladistically.

As we are discovering many more of these bilaterally symmetrical conopeate species, there is a need to be able to distinguish them from congeners without having to first state the characters of “tholophora morphology”, as we did with all the new species in Lobban & al. (2019), and to have a taxonomically meaningful handle to refer to them. It will also allow us to place unidentified species in the group—operational taxonomic units, for community analysis—by giving the genus name. The genus *Nitzschia* is “ripe for reassessment” (Mann & al. 2021); major changes are anticipated but it is not yet clear what those changes might involve. We make a case here on morphological grounds for a separate genus to be recognized at least for pragmatic reasons to distinguish the bilaterally symmetrical conopeate diatoms from those of *Nitzschia sensu stricto*.

Morphology of *Nitzschia sigmoidea* (Mann 1986: fig. 2): Frustules sinuous in girdle view, isosceles trapezium or rhombus in cross section, with strongly eccentric keels bearing conopea on each side (Mann 1978; Mann 1980, fig. 28; Knattrup & al. 2007; Mann & al. 2021, fig 6A). *Nitzschia sigmoidea* division results in both hantzschoid cells and nitzschoid cells (Geitler 1968, Pickett-Heaps 1983, Mann 1986, Knattrup & al. 2007, Mann & Trobajo 2014).

Homoeocladia redefined on valve characters “tholophora morphology” (Lobban & al. 2019: fig. 6): Frustules rectangular in cross section. Keel central or nearly so, valve with longitudinal depressions along keel, conopea extending from wall of raphe canal over the depressions (Fig. 1). The extreme



variation in valve and girdle bands stems from multiple states for areolae, presence and extent of external transverse costae and ribs, etc.

Among the conopeate *Nitzschia* spp., the symmetrical morphology is consistent and well established, and readily distinguished from the asymmetrical hantzschoid–nitzschoid morphologies. Mann (1986) and Mann & Trobajo (2014) observed a uniting feature in the conopea across subgenus *Nitzschia*, but we contend that the differences between “tholophora morphology” and cells with eccentric keels are sufficient to establish a separate genus for the former. Lobban & al. (2019) deferred to unpublished genetic data that suggested *Nitzschia sigmoidea* was within the “tholophora” clade, and described them as species of *Nitzschia*, rather than pursue the separate genus originally presented at a symposium (Lobban & al. 2017). DNA data remain scarce as, while Mann & al. (2021) included *N. sigmoidea* and several other conopeate strains with eccentric raphes in their dataset, only two symmetrical conopeate strains were included, so a robust molecular phylogeny of nitzschoid and symmetrical strains has yet to be established. DNA data from only a single *Hantzschia* strain was included in both the Lobban & al. (2019) and Mann & al. (2021) datasets, suggesting that further sampling from this genus should be pursued to resolve a clear molecular phylogeny of the conopeate nitzschoid and hantzschoid taxa.

Unfortunately, proposing a new genus name for this assemblage is not possible because one of the species included is *N. martiana* (C.Agardh) Schütt, the basionym of which, *Homoeocladia martiana* C.Agardh, is the generitype (monotype) of *Homoeocladia* Agardh, 1827, *nom. rejic.* While this is a rejected name in favour of *Nitzschia* Hassall, 1845, *nom. cons.*, its use is only prevented when its generitype is included in *Nitzschia*. If *Nitzschia sigmoidea*, the correct name for the type of *Nitzschia*, *Nitzschia elongata* Hassall, and *Homoeocladia martiana* C.Agardh are considered to represent separate genera, as we propose here, then the genus name *Homoeocladia* becomes available and must be adopted (Turland & al. 2018, Arts 14.6, 14.10). This requires redefining *Homoeocladia* from habit characters to valve characters and rejecting the assortment of diatoms that was added later, many of which are not even tube-dwelling. A search for *Homoeocladia* in AlgaeBase (Guiry & Guiry 2022) produced 230 names, of which the 18 still remaining in *Homoeocladia* are listed here in Appendix I.

In the bigger picture, other Bacillariaceae with central keels occur outside *Nitzschia*, i.e., *Bacillaria* and *Gomphotheca* (*G. marciae* Lobban & Prelosky 2022 also has conopea). [*Gomphotheca* (as *Gomphonitzschia*) was originally separated from *Nitzschia* solely because of heteropolarity.] Comparing all these characters, we can draw a tentative classification scheme (Fig. 2) where *Bacillaria*, *Homoeocladia* and *Gomphotheca* group together based on the shared central raphe, with *Homoeocladia* sister to *Gomphotheca* based on the conopeum. The eccentric-raphe Bacillariales genera can then be diagnosed by the positions of the keels across the frustule, as discussed previously. Several other genera have already been described from *Nitzschia* sensu lato, of course, but these are not discussed here because they all can be distinguished from *Nitzschia* sensu stricto and *Homoeocladia* based on the keel position.

Homoeocladia C.Agardh *emend.* Lobban & Ashworth.

Description: Bilaterally symmetrical valves with central keel subtended by fibulae, longitudinal valve depressions on each side of the keel and conopea extending from wall of keel canal over depressions to form conopeal canals open at the apices.

Type (monotype): *Homoeocladia martiana* C.Agardh, 1827, *Flora oder Botanische Zeitung, Regensburg* 10: 629 (as 'Martiana'). Synonym: *Nitzschia martiana* (C.Agardh) Schütt, 1896: 145



Since Agardh (1827) characterized the genus (monotypic at the time) by the tube-dwelling habit with frustules in parallel longitudinal rows, many species added subsequently were also tube-dwelling but otherwise of varied forms, including many transfers by Kuntze (1898). In emending the genus definition to focus on the valve morphology, we purposely omit reference to the tube-dwelling character of the type species, since it appears to be unusual for the genus. We also omitted reference to internal costae because, although none have been seen yet in some 50 taxa documented, the range of characters and the discovery of additional characters (including biseriate striae) suggests that species with internal costae could exist.

Included species, based on SEM:

Homoeocladia abelmanniae (Witkowski & Lange-Bertalot) Lobban & Ashworth, comb. nov.

Basionym: *Nitzschia abelmanniae* Witkowski & Lange-Bertalot in Witkowski & al., *Nova Hedwigia Beihefte* 144: 216, figs 17–37, 2015

Phycobank registration: <http://phycobank.org/103549>

Homoeocladia alcyoneae (Lobban, Ashworth, Calaor & E.C.Theriot) Lobban & Ashworth, comb. nov.

Basionym: *Nitzschia alcyoneae* Lobban, Ashworth, Calaor & E.C.Theriot, *Phytotaxa* 401: 218, figs 75–82, 2019.

Phycobank registration: <http://phycobank.org/103550>

Homoeocladia angularis (W.Smith) Kuntze *Revisio generum plantarum. Pars III (3)*: 408, 1898.

Basionym: *Nitzschia angularis* W.Smith, 1853, *A Synopsis of the British Diatomaceae*, p. 40, pl. 13, fig. 117, 1853

Homoeocladia arierae (Bing Liu, S. Blanco & B.Q.Huang) Lobban & Ashworth, comb. nov.

Basionym: *Nitzschia arierae* Bing Liu, S. Blanco & B.Q.Huang, *Phytotaxa* 231: 261, figs 1–22, 2015.

Phycobank registration: <http://phycobank.org/103551>

Homoeocladia asteropeae (Lobban, Ashworth, Calaor & E.C.Theriot) Lobban & Ashworth, comb. nov.

Basionym: *Nitzschia asteropeae* Lobban, Ashworth, Calaor & E.C.Theriot, *Phytotaxa* 401: 219, figs 17, 89–94, 2019.

Phycobank registration: <http://phycobank.org/103552>

Homoeocladia carahii (Lobban, Ashworth, Calaor & E.C.Theriot) Lobban & Ashworth, comb. nov.

Basionym: *Nitzschia carahii* Lobban, Ashworth, Calaor & E.C.Theriot, *Phytotaxa* 401: 221, figs 12, 95–99, 2019.

Phycobank registration: <http://phycobank.org/103553>

Homoeocladia celaenoae (Lobban, Ashworth, Calaor & E.C.Theriot) Lobban & Ashworth, comb. nov.

Basionym: *Nitzschia celaenoae* Lobban, Ashworth, Calaor & E.C.Theriot, *Phytotaxa* 401: 231, figs 11, 145–148, 2019.

Phycobank registration: <http://phycobank.org/103554>



Homoeocladia dagmannii (Lobban, Ashworth, Calaor & E.C.Theriot) Lobban & Ashworth, comb. nov.

Basionym: *Nitzschia dagmannii* Lobban, Ashworth, Calaor & E.C.Theriot, *Phytotaxa* 401: 223, figs 20, 100–106, 2019.

PhycoBank registration: <http://phycobank.org/103555>

Homoeocladia distans (W.Gregory) Kuntze, *Revisio generum plantarum. Pars III (3)*: 409, 1898.

Basionym: *Nitzschia distans* W.Gregory *Transactions of the Microscopical Society of London* 5: 79, 1857a, and W.Gregory 1857b in *Transactions of the Royal Society of Edinburgh* 21: 530, pl. 14, fig. 103 and 103b. [Gregory 1857b (read 19 Jan. 1857) refers to the London paper (read 26 March 1856), from which the figure was omitted; he used “n. sp.” in both papers.

Comment: Our recommendation is based on Gregory’s (1857a, b) descriptions and Poulin et al.’s (1990, p. 81, figs 38–41) SEM images, which establish a central keel.

Homoeocladia electrae (Lobban, Ashworth, Calaor & E.C.Theriot) Lobban & Ashworth, comb. nov.

Basionym: *Nitzschia electrae* Lobban, Ashworth, Calaor & E.C.Theriot, *Phytotaxa* 401: 228, figs 22, 130–140, 2019.

PhycoBank registration: <http://phycobank.org/103556>

Homoeocladia guamensis (Lobban, Ashworth, Calaor & E.C.Theriot) Lobban & Ashworth, comb. nov.

Basionym: *Nitzschia guamensis* Lobban, Ashworth, Calaor & E.C.Theriot, *Phytotaxa* 401: 223, figs 107–111, 2019.

PhycoBank registration: <http://phycobank.org/103557>

Homoeocladia jordanii (Lobban, Ashworth, Calaor & E.C.Theriot) Lobban & Ashworth, comb. nov.

Basionym: *Nitzschia jordanii* Lobban, Ashworth, Calaor & E.C.Theriot, *Phytotaxa* 401: 213, figs 52–55, 2019.

PhycoBank registration: <http://phycobank.org/103558>

Homoeocladia lasrucensis (Lobban & C.E.Wetzel) Lobban & Ashworth, comb. nov.

Basionym: *Nitzschia lasrucensis* Lobban & C.E.Wetzel, 2019 in Lobban, Ashworth, Calaor & Theriot, *Phytotaxa* 401: 211, figs 46–51, 2019.

Comment: We have included this species despite a “slightly eccentric keel” because of very strong similarities in valve and conopeum morphology with other species, and because both the LM and SEM images of whole valves (Lobban & al. 2019, figs 46, 47) suggest the isolated valves had twisted and that the apparent eccentricity may be an artefact (contrast *N. maiae* comment on p. 6).

PhycoBank registration: <http://phycobank.org/103559>

Homoeocladia meropeae (Lobban, Ashworth, Calaor & E.C.Theriot) Lobban & Ashworth, comb. nov.

Basionym: *Nitzschia meropeae* Lobban, Ashworth, Calaor & E.C.Theriot, *Phytotaxa* 401: 217, figs 16, 19, 69–74, 2019.

PhycoBank registration: <http://phycobank.org/103561>

Homoeocladia nanodissipata (Chunlian Li & Witkowski) Lobban & Ashworth, comb. nov.



Basionym: *Nitzschia nanodissipata* Chunlian Li & Witkowski in Witkowski & al., *Journal of Coastal Research, Special Issue 74*: 188, fig. 12, 2016.

Phycobank registration: <http://phycobank.org/103562>

Homoeocladia schefferae (Lobban, Ashworth, Calaor & E.C.Theriot) Lobban & Ashworth, comb. nov.

Basionym: *Nitzschia schefferae* Lobban, Ashworth, Calaor & E.C.Theriot, *Phytotaxa* 401: 229, figs 7, 8, 141–144, 2019.

Phycobank registration: <http://phycobank.org/103563>

Homoeocladia spathulatoides (Lobban, Ashworth, Calaor & E.C.Theriot) Lobban & Ashworth, comb. nov.

Basionym: *Nitzschia spathulatoides* Lobban, Ashworth, Calaor & E.C.Theriot, *Phytotaxa* 401: 227, figs 121–129, 2019.

Phycobank registration: <http://phycobank.org/103564>

Homoeocladia tarangensis (Lobban) Lobban & Ashworth, comb. nov.

Basionym: *Nitzschia tarangensis* Lobban, *Phytotaxa* 508: 257, figs 103–110, 2021.

Phycobank registration: <http://phycobank.org/103565>

Homoeocladia taygeteae (Lobban, Ashworth, Calaor & E.C.Theriot) Lobban & Ashworth, comb. nov.

Basionym: *Nitzschia taygeteae* Lobban, Ashworth, Calaor & E.C.Theriot, *Phytotaxa* 401: 219, figs 12, 21, 83–88, 2019.

Phycobank registration: <http://phycobank.org/103566>

Homoeocladia volvendirostrata (Ashworth, Dąbek & Witkowski) Lobban & Ashworth, comb. nov.

Basionym: *Nitzschia volvendirostrata* Ashworth, Dąbek & Witkowski in Witkowski & al., *Journal of Coastal Research Special Issue 74*: 188, fig 13, 2016.

Phycobank registration: <http://phycobank.org/103567>

We exclude 18 *Homoeocladia* names apparently not yet assigned to currently accepted genera (Appendix I). We also specifically exclude *Nitzschia dissipata* (Kützinger) Rabenhorst, which has an eccentric keel as shown by Mann (1978, figs 253–254, 808–811), even though Poulin & al. (1990) show specimens identified as this with a central keel. In addition, we reserve judgement on two species in which the keel is “often” or “somewhat” eccentric: (1) *N. spathulata* Brébisson ex W.Smith, for which Mann (1978: 222) stated that the raphe was “often eccentric.” Smith (1853) did not indicate the raphe position of this species and it is very difficult to find valve views (all our images of it are in girdle view; Lobban & al. 2019). (2) *Nitzschia maiae* Lobban, Ashworth, Calaor & E.C.Theriot, which can be somewhat eccentric and lacks the valve depressions alongside the keel characteristic of other *Homoeocladia* taxa. A cladistic analysis of morphological features put it sister to the other species in cladistic analysis (Lobban & al. 2019); we have no sequence data for this species. Finally, we reserve judgement on *Nitzschia gaoi* Bing Liu, S.Blanco & B.Q.Huang (2015) until we complete analysis of several bilaterally symmetrical conopeates that also have external T-shaped costae like *N. gaoi* and the distinctly eccentric and conopea-less species *Nitzschia incurva* Grunow (= *N. lorenziana* Grunow, *nom. illeg.*).

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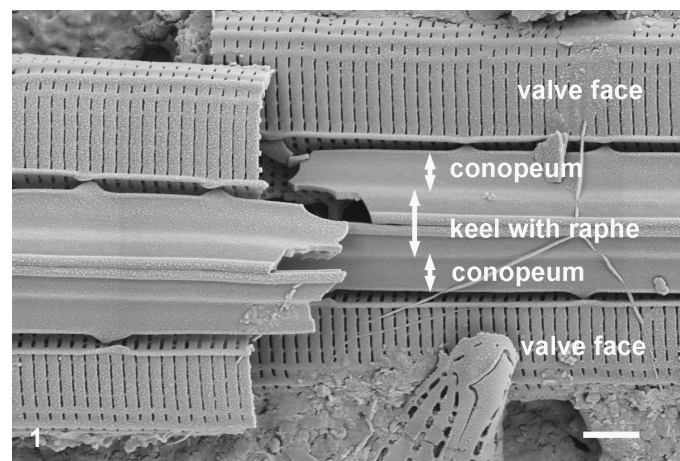


Fig. 1. Detail of representative *Homoeocladia* showing conopea arising from central keel above valve depression (*H. dagmanii*, Palau, sample PW1990-47). Scale bar = 1 μ m.

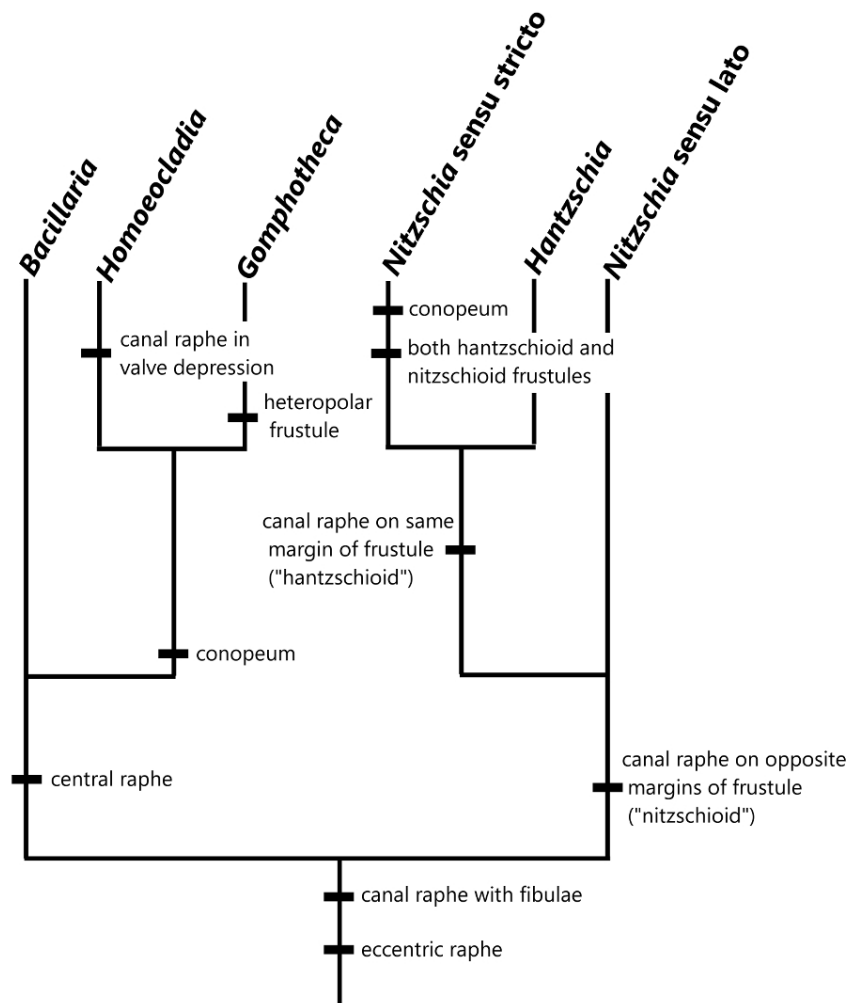


Fig. 2. Tree diagram outlining a classification of some of the bacillarialean genera based on canal raphe position and structure.



Appendix I. List of *Homoeocladia* names apparently not currently referred to another genus. Source: AlgaeBase, 7 Dec. 2022 (Guiry & Guiry 2022). Places of publication and dates are provided there.

Homoeocladia anglica C.Agardh
Homoeocladia arbuscula Kützing
Homoeocladia capitata H.L.Smith
Homoeocladia congesta Meunier
Homoeocladia dilatata Kützing
Homoeocladia dufourii De Notaris
Homoeocladia filiformis Carruthers
Homoeocladia filiformis f. *parva* Rabenhorst
Homoeocladia fimbriata Eichwald
Homoeocladia glomerata Meunier
Homoeocladia helioides Meneghini
Homoeocladia mucicola Meunier
Homoeocladia radula Kuntze
Homoeocladia rossica Kuntze
Homoeocladia subcohaerens var. *chinensis* Grunow
Homoeocladia taeniata Meunier
Homoeocladia tenuis Meunier
Homoeocladia vidovichii var. *nodulosa* Hagelstein