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HANNAEA ARCUS (EHRENBERG) R. M. PATRICK: LECTOTYPIFICATION AND NOMENCLATURAL HISTORY

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The original material of *Navicula arcus* Ehrenberg (the type of *Hannaea* R. M. Patrick) was studied and two specimens have been selected as the lectotype and the isolectotype. Since the generic placement of this taxon has been misunderstood for one and a half centuries, its nomenclatural and taxonomic histories are reviewed.

INTRODUCTION

Hannaea arcus (Ehrenberg) R.M. Patrick, the type of the genus *Hannaea* R. M. Patrick, was originally described as *Navicula*? *arcus* by Ehrenberg (1836) from the spring waters of Carlsbad (Karlovy Vary, now in the Czech Republic). Additional information and illustrations were provided in a subsequent publication (Ehrenberg 1838). No type was designated by Ehrenberg; however, micas from Carlsbad containing *Navicula arcus* have been located in the Ehrenberg Collection at the Museum für Naturkunde (BHUPM), Berlin, Germany. These micas, as well as unpublished drawings of *N. arcus* by Ehrenberg, are part of the original material of this taxon and were examined with goals of selecting a lectotype and assessing the accuracy of the modern application of the name. The nomenclatural history of this species is complex and is also reviewed in this paper.

MATERIALS & METHODS

From the Ehrenberg Collection at BHUPM the following materials were investigated: preparation No. 107–5 [old numbering: Trockenpräparate II Polygastrica No. CVII 5]: "- - *arcus γ*" and preparation No. 107–6 [old: CVII 6]: "- - *arcus δ*". In contrast to the preparations No. 107–3 [old: CVII 3]: "*Himantidium arcus α,* jetztlebend ("live")" and No. 107–4 [old: CVII 4]: "- - *β* Degernsfors, fossil" which are *Eunotia* specimens (Ehrenberg 1838: pl. XXI, fig. XXII, published as *Himantidium arcus*), both mica preparations No. 107–5 and 107–6 contain many *Hannaea* specimens that correspond exactly to Ehrenberg's Drawing No. 563 (see Fig. 1) and to his published figures (Ehrenberg 1838, Pl. XXI, Fig. X) published as *Navicula arcus* (both figures illustrated from live material). The "Trockenpräparate" are sandwiched, round mica with strewn dried material in the middle; no Canada Balsam has been

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used as a mountant. No raw material was available from the Carlsbad collections. Photomicrographs in the Ehrenberg Collection were taken with an Olympus DP 50 microscope and BX 51 camera, Objectives: Olympus IC 80x/N.A. = 0.75.

Modern collections of *H. arcus* were examined from the Molalla River, Oregon, U.S.A. (RJB 66 and 403), Panguipulli, Valdavia, Chile (CAS 702233), and Mesta River, Bulgaria (RJB 418). Photomicrographs were taken with a Leica DMRX or Leica TCS SP2 microscope with full immersion objectives (N.A. = 1.40, 1.20 respectively).

OBSERVATIONS

Navicula? *arcus* Ehrenberg

In *Archiv für Naturgeschichte* **2**(1), 243. 1836. Additional information in Ehrenberg, Infusionsthierchen, p. 182, Pl. XXI, Fig. X, 1838.

The lectotype (designated here): preparation No. 107–5; the valve is illustrated in Fig. 5.

The isolectotype (designated here): preparation No. 107–6 (which is the same material from Carlsbad); the valve is illustrated in Fig. 6.

The valves were unable to be marked because of the fragility of the mica.

Locus typicus: zu Carlsbad, am Rande des heißen und im kalten Wasser der Mineralquellen [cold mineral spring water at Carlsbad, Karlovy Vary, Czech Republic].

Ehrenberg's original Latin diagnosis stated "*Navicula*? *Arcus*: arciformis, media inflexa ibique umbonata." The question mark indicated that he was not sure about its future classification within the genus. Additionally, in Ehrenberg's second Latin diagnosis of *N. arcus* (1838: 182), he described *Navicula arcus* as "N. laevis, testula anguste lineari arcuata, media inflexa, ubique umbonata" (translates as "a smooth *Navicula* with a narrowed, linear, arcuate frustule, bent inwards in the middle with a rounded projection in the middle"). Further he writes (translated from German): "this special species reminds in its looks of *Achnanthes* which is often bent. I found it in countless numbers in the water of the mineral springs of Carlsbad which Mr. Fischer has brought to Berlin at my suggestion. I saw it dividing but never moving. From the side, the ends have a constriction and are capitate. Length 1/500 [4.5 µm] up to 1/48 Linie [47 µm] and the length is 2.5 up to 9–10 times of the width."

Ehrenberg's original illustrations of *Navicula arcus* (unpublished) (Fig. 1) are consistent with the specimens found on the mica Nos. 107–5 and 107–6 (Figs 2–8). Although the micas are ordered underneath the name *Himantidium* (ordering had been done at a later time), we are certain that the micas that we examined are the original Carlsbad material of *Navicula arcus* because they corresponds exactly with the drawing sheet (Fig. 1) and are living material, compared to the Degernfors fossil material in 107–3 and 107–4. But the size range of those specimens which Ehrenberg interpreted as *Navicula arcus* is too large; certainly the smallest do not belong to this taxon but to an unidentifiable *Achnanthidium* species (Nos. 44–47 on Fig. 1). Excluding the smaller specimens rules out the size 1/500''' (4.5 µm) and moves the size range to 1/72–1/48''' (= 31.3–47 µm length) which is closer to the size range that we measured in Ehrenberg's specimens: 43–67 µm length and 6–7 µm width. This size range is similar to those of modern collections (i.e., 35.4–80.3 µm length, Figs 9–13). Although Ehrenberg explicitly states in his Infusionthierchen on p. 182 that these drawings are all 300 times enlarged, we believe that two of these illustrations, i.e., # 53, were drawn at a higher magnification. In addition to drawing specimens in valve view, Ehrenberg has included girdle views (Nos. 38 & 50, Fig. 1) and banded colonies in girdle view (No. 43, Fig. 1). The published figures from Ehrenberg (1838) contain identical illustrations of the specimens as the

original drawings but have been rearranged, renumbered, and include two fewer specimen drawings (the two unnumbered specimens in the original drawing). Given the resolution limits of Ehrenberg's micas, we determined that the specimens on mica Nos. 107–5 and 107–6 are the same illustrated by Ehrenberg as *N. arcus* with the dorsiventrally arched valve and unilateral central inflation (Fig. 1).

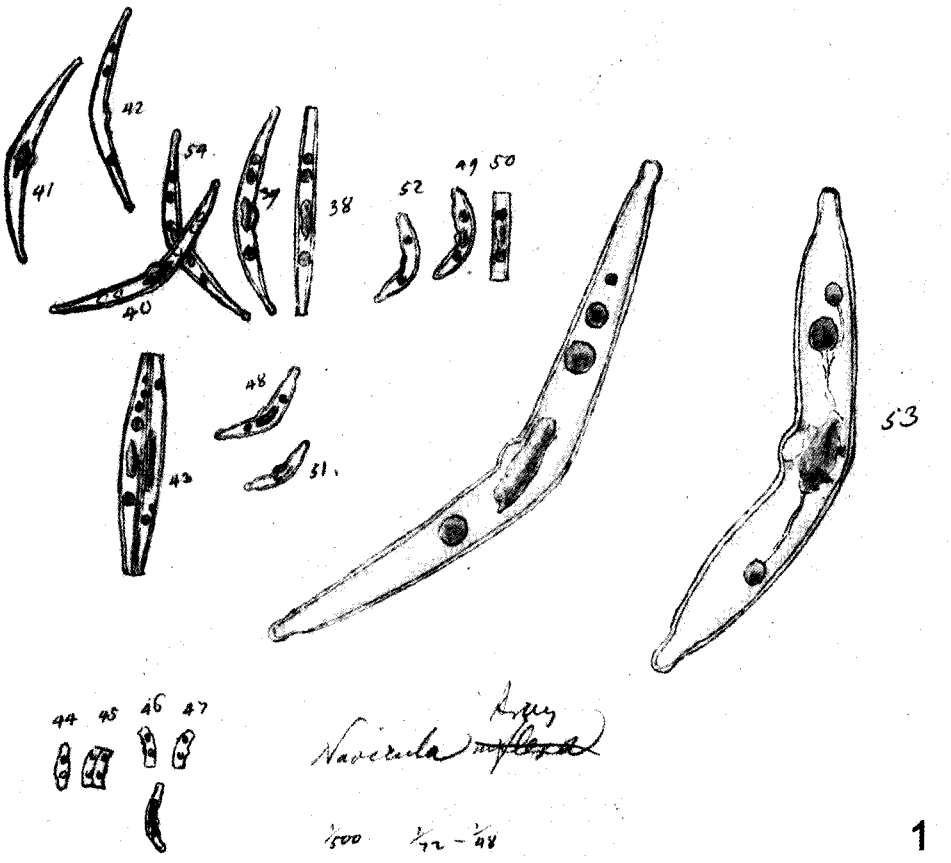


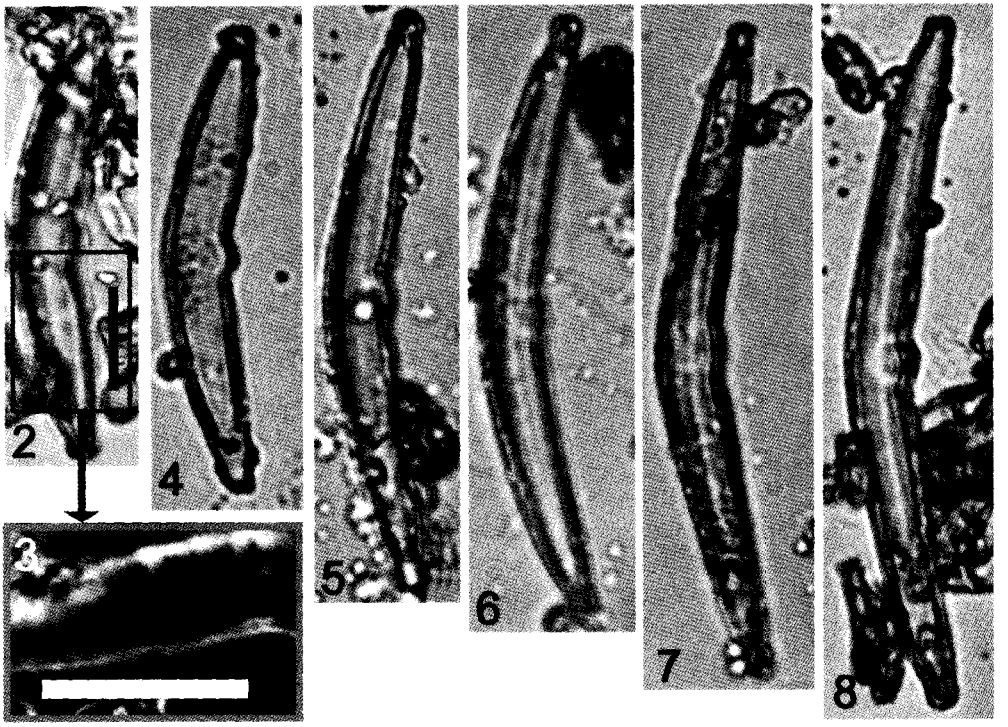
Fig. 1. Ehrenberg's drawing Sheet No. 563 of *Hannaea arcus* (= *Navicula arcus* Ehrenb.), unpublished.

DISCUSSION

Comparison with modern populations

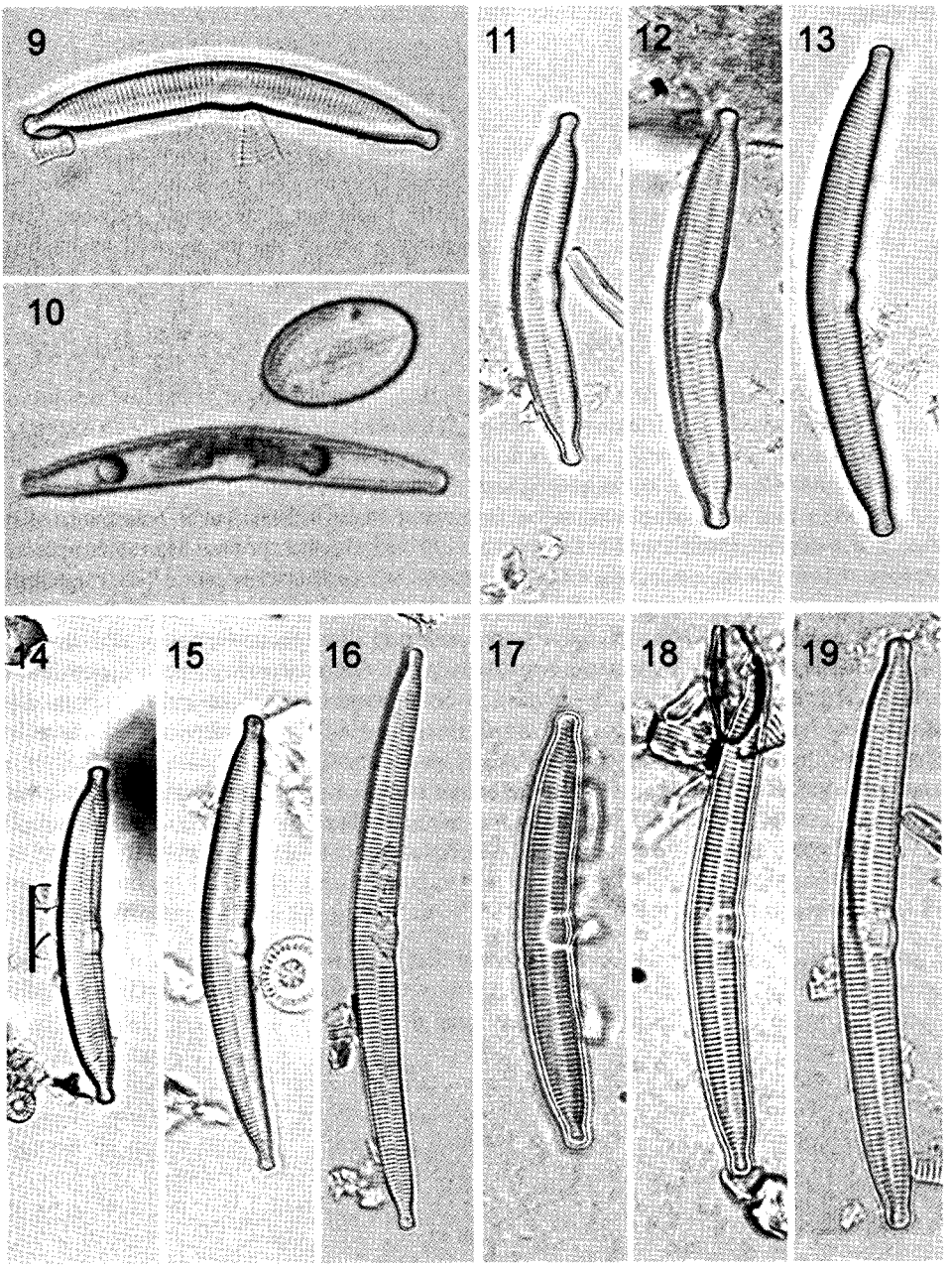
The lectotype and isolectotype, as well as additional specimens from mica Nos. 107–5 and 107–6 and Ehrenberg's drawings, have the valve shape and valve detail as modern exemplars of *H. arcus* (Figs 9–19). Ehrenberg illustrated structures in the cytoplasm of his specimens (Fig. 1) that are consistent with modern live material of *H. arcus* (Fig. 10); the specimens have two lobed chloroplasts extending from the dorsal margin (not particularly obvious in Ehrenberg's drawings) and two or more volutin droplets. The pseudoraphe is visible in all of Ehrenberg's specimens. Some differentiation is also visible around the unilateral inflation in some specimens (Figs 6, 8) which may be buttressing, described as

siliceous thickenings at the margin of the swelling (Bixby 2001). Because of the low resolution of the micas, it is not possible to resolve striae patterns on all valves; however, in Fig. 3, 18–20 striae/10 μm can be counted.



Figs 2–8. Light micrographs of *Hannaea arcus* from Ehrenberg's "Trockenpräparate II Polygastrica" original specimens from Carlsbad mineral spring water. Scale bar = 10 μm. **Fig. 2**. Specimen from No. 107–6. **Fig. 3**. Enlarged area from Fig. 2 illustrating striae density and structure, negative image at 600 d.p.i., contrast adjusted. **Fig. 4**. Further specimen from No. 107–6. **Fig. 5**. No. 107–5, lectotype. **Fig. 6**. No. 107–6, isolectotype. **Fig. 7**. Further specimen from No. 107–5. **Fig. 8**. Further specimen from No. 107–6.

This striae density is consistent with densities for other European *H. arcus* specimens (15–17 striae/10 μm, Figs 17–19) (17 striae/10 μm, Tafel 117: Figs 9–10; text reports 13–16(18) striae/10μm, as *Fragilaria arcus* in Krammer & Lange-Bertalot 1991). Coarser striae densities for *H. arcus* have been recorded in some populations from the Americas (13–14 striae/10 μm at the center to 18 striae/10 μm at apices, Patrick & Reimer 1966). For example, *H. arcus* populations from the Molalla River, Oregon, western U.S.A. had striae densities near the central of the valve that ranged from 12.2–16.5 striae/10 μm (mean 14.5 striae/10 μm) (Figs 11–13, from Bixby 2001). This wide range of striae densities (12–20 striae/10 μm) in European and North and South American populations may be characteristic of naturally occurring morphological variation within a species. Conversely, the North American populations may represent a new species with a lower striae density; this warrants further investigation.



Figs 9–10. *Hannaea arcus*. Molalla River, Oregon, U.S.A. LM. Scale bar = 10 μm. **Fig. 9**. Cleaned material, brightfield optics (RJB 66). **Fig. 10**. Live material, brightfield optics (RJB 403). **Figs 11–19**. *Hannaea arcus*, size ranges from populations. LM. Scale bar = 10 μm. **Figs 11–13**. Molalla River, Oregon, U.S.A. (RJB 66). Size ranges (n=50): 35.4–80.3 μm length (mean 61.5 μm), 5.3–8.2 μm breadth (mean 6.1 μm) and 12.2–16.5 striae in 10 μm (mean 14.5 striae in 10 μm). **Figs 14–16**. Lago Panguipulli, Valdavia, Chile (CAS 702233). Size ranges (n=25): 42.0–101.1 μm length (mean 69.1 μm), 4.9–7.7 μm breadth (mean 6.2 μm) and 13.9–16.4 striae in 10 μm (mean 14.9 striae in 10 μm). **Figs 17–19**. Mesta River, Bulgaria (RJB 418). Size ranges (n=12): 40.0–68.0 μm length (mean 52.2 μm), 5.2–6.4 μm breadth (mean 5.8 μm) and 15–17 striae in 10 μm (mean 16.3 striae in 10 μm).

Autecology

Ehrenberg described his samples from Carlsbad as being from cold water near hot springs. Ehrenberg lists the following taxa from the Carlsbad mineral water including *Surirella striatula* Turpin, *Navicula umbonata* Ehrenb. (=*Nitzschia umbonata*), and *Navicula hippocampus* β *striata* Ehrenb. (*Gyrosigma hippocampus* =*Gyrosigma attenuatum*). He noted that these last two taxa were also found from Wismar, Germany on the Baltic Sea. Concerning *G. hippocampus*, at that time Ehrenberg apparently could not differentiate between species since his composite drawing sheet of *G. hippocampus* shows marine as well as freshwater species (F.A.S. Sterrenburg pers. com.). In contrast, Ehrenberg also records the freshwater taxa *Frustulia appendiculata* C.A. Agardh (=*Pinnularia appendiculata*), *Navicula quadricostata* Ehrenb., *Navicula arcus* Ehrenb. (=*Hannaea arcus*) as well as a bacterium *Monas violacea* Ehrenb. Upon examination of the two preparations (107–5 & 107–6) we were able to verify some taxa on Ehrenberg's list including *N. arcus* although the low resolution of the mica makes species verification difficult. We noted an unknown *Surirella* taxon, (not *S. striatula* Turpin *sensu stricto*), a *Meridion* sp., numerous specimens of an *Achnanthidium* sp. (i.e. Nos. 44–47 on Fig. 1), several *Synedra* spp., *Encyonema* cf. *minutum*, and *Navicula* spp. It appears that this sample contains freshwater taxa, rather than a collection of both marine and freshwater taxa that Ehrenberg states. These freshwater taxa are representative of organisms that might be associated with the habitats where *Hannaea* grows (i.e. oligotrophic, running water, neutral to slightly acidic waters).

Modern samples of *H. arcus* have been collected throughout Germany and the Czech Republic. *Hannaea arcus* is common in streams in the German and Austrian limestone Alps (Rott *et al.* 1999). In contrast, *H. arcus* has not been found in the German lowlands and only in the headwaters of the German Low Mountain range including rivers near Karlovy Vary region of the Czech Republic (G. Hofmann, pers. com., Poulícková *et al.* 2004). The autecology of *H. arcus* in this region is the same as *Hannaea* populations found elsewhere: fast-moving mountain streams, oligotrophic, circumneutral pH (≥6.5), and low nitrates (G. Hofmann, pers. com., Krammer & Lange-Bertalot 1991, Rott *et al.* 1999).

Nomenclature

Soon after its description it became evident that *Navicula arcus* did not fit into the genus *Navicula*. Kützing (1844) placed this taxon into the genus *Ceratoneis* (Greek: "cerato" = horned, referring to the apices) which had been described by Ehrenberg (1839) to include two marine species, *C. closterium* and *C. fasciola*. Kützing (1844) broadened the genus concept with the addition of three very different taxa [*C. arcus* (Ehrenb.) Kütz., *Ceratoneis spiralis* (now *Nitzschia spiralis* (Kütz.) DeToni), and *Ceratoneis laminaris* (now *Mastogloia laminaris* (Ehrenb.) Grunow in Cleve & Möller)] apparently trying to group all horned or attenuated taxa into this genus. Smith (1852, 1853) transferred Ehrenberg's two species to other genera: *Ceratoneis fasciola* to *Pleurosigma fasciola* (Ehrenb.) W. Sm. [now *Gyrosigma fasciola* (Ehrenb.) Griffith & Henfrey; see Jahn *et al.*, 2005] and *C. closterium* to *Nitzschia closterium* (Ehrenb.) W. Sm. (Smith 1853) [now known as *Cylindrotheca closterium* (Ehrenb.) Reimann & Lewin; but see Jahn & Kusber 2005].

For Rabenhorst (1864: 10) *C. arcus* was the typical *Ceratoneis* species, and subsequently he moved all produced/horned nitzschioid taxa in *Ceratoneis* into his newly created genus *Nitzschiella* (Rabenhorst 1864: 16). Grunow (1865) explicitly cites "*Ceratoneis* Kg (nec Ehbg.)" and comments that he does not like using this genus name (*Ceratoneis*) because it is Ehrenberg's genus for the horned *Nitzschia*. Nevertheless, in order to not create any further synonyms, Grunow subdivided the remaining *Ceratoneis* into two subgenera: *Euceratoneis* (fragilarioid taxa: *C. arcus* and *C. amphioxys* Rabenh.) and *Pseudoeunotia* (eleven eunotioid

taxa). All *Pseudoeunotia* taxa were subsequently transferred to *Eunotia* or *Amphicampa*. Boyer (1927) consequently typified the genus *Ceratoneis* with the first taxon in Grunow's list: *Ceratoneis arcus*. Boyer's selection of *C. arcus* is untenable because it was not one of the two species originally included in *Ceratoneis*. Further synonyms for *H. arcus* include *Cymbella arcus* (Ehrenb.) Hassal and *Synedra gibbosa* Ralfs in Pritch.

Patrick (in Patrick & Reimer 1966) correctly stated that "the genus *Ceratoneis* in its present concept cannot stand as it excludes the two species on which it was originally based. I, therefore, propose the name *Hannaea*." The type of the name of the genus *Hannaea* is *Hannaea arcus* (Ehrenb.) var. *arcus* R.M. Patrick as designated in the original publication (Patrick & Reimer 1966, Fourtanier & Kociolek 1999). *H. arcus* var. *amphioxys* (Rabenh.) R.M. Patrick was also transferred to this new genus (Patrick & Reimer 1966). The name *Hannaea* honors Dr G. Dallas Hanna, former curator of geology at the California Academy of Sciences, San Francisco.

Taxonomy

Taxonomically, some diatomists contend that *Hannaea* taxa are part of the concept of the genus *Fragilaria*. Cleve (1898) was the first to place those taxa ("*Ceratoneis*") in *Fragilaria*. Cleve's transfer was resurrected in work by Krammer & Lange-Bertalot (1991), when they pointed out that *Hannaea* has the same characters as *Fragilaria capucina* var. *vaucheriae* (Kütz.) Lange-Bertalot including banded colony structure.

Based on morphological phylogenetics using cladistic analysis, the recognition of *Hannaea* as a separate genus within the Fragilariaceae is supported. The consensus cladogram shows support of the generic separation among Fragilariaceae including *Hannaea*, *Synedra*, *Fragilaria sensu stricto*, and *Fragilaria sensu lato* (i.e., *Staurosira*, *Staurosirella*, *Pseudostaurosira*, and *Fragilariforma*) (Bixby 2001). *Hannaea* is a monophyletic group within a clade containing *Fragilaria sensu stricto* as its sister taxon. This separation is based on a combination of characters including the presence of a unilateral inflation, the lack of striae in that inflation, and a valvocopula with an advalvar crenate margin (Bixby 2001). More research, including molecular phylogenetics, is needed to better understand the generic placement of *Hannaea* within the araphids and species assignment within the genus.

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