

HANNAEA SUPERIORENSIS SP. NOV., AN ENDEMIC DIATOM FROM THE LAURENTIAN GREAT LAKES

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Hannaea superioensis sp. nov. is formally described from benthic and tychoplanktonic locations in the North American (Laurentian) Great Lakes, primarily from Lake Superior. This taxon has previously been reported as *Ceratoneis arcus* (Ehrenb.) Kütz., *Hannaea arcus* (Ehrenberg) Patrick or *Hannaea arcus* var. *linearis* (Holmboe) Ross in Hartley; however, significant morphological and ecological differences support the separation of *Hannaea superioensis* as a new species. Length-width-curvature triplots demonstrate the greater length and length: width ratio of this taxon compared with other *Hannaea* populations. Morphologically, *H. superioensis* most closely resembles *H. arcus* var. *linearis*. Finally, the habitat preferences of *H. superioensis* are distinctive compared to the riverine nature of *H. arcus* and its varieties; *Hannaea superioensis* is primarily found as epilithon in the littoral wave zone of Lake Superior. This species can also be found secondarily in the tychoplankton of Lake Superior and is occasionally transported as tychoplankton to other Laurentian Great Lakes. *Hannaea superioensis* does not appear to be sympatric with *H. arcus* in the modern Great Lakes, but it may have speciated from local river populations of *H. arcus* during the Late Pleistocene–Early Holocene to become adapted to the cold, high-energy wave zone of Lake Superior.

Key words: Laurentian Great Lakes, Lake Superior, *Hannaea*, araphid, endemism, lentic environments, rapid speciation

INTRODUCTION

The freshwater araphid diatom genus *Hannaea* Patrick is characterized by a dorsiventrally bent valve and a ventral unilateral central inflation. Along with a distinctive valve shape, a restrictive ecological tolerance traditionally separates *Hannaea* from other similar diatom genera (e.g., *Fragilaria sensu lato* and *Synedra*). Typically, *Hannaea* is associated with oligotrophic, high altitude riverine systems and is found in lake systems only as lotic inputs. In North America, most *Hannaea* populations have been recorded from higher elevations in the western United States and Canada (Bixby 2001). In the eastern United States,

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collections of *Hannaea arcus* have been collected in the Great Smoky Mountains of eastern Tennessee (Kociolek 1982).

The genus name *Hannaea* was proposed by Patrick in Patrick and Reimer (1966) for these bent araphid taxa originally in the genus *Ceratoneis* after the two original taxa described under *Ceratoneis* were transferred to other genera. The type of the genus *Hannaea* is *H. arcus* (Ehrenb.) R.M. Patrick by original designation (Patrick & Reimer 1966). The basionym of this species is *Navicula arcus* Ehrenb. (Ehrenberg 1836), Kützing (1844) later transferred *N. arcus* to *Ceratoneis*. The current concept of *Hannaea* includes one species (*H. arcus*) and its three common varieties [*H. arcus* var. *amphioxys* (Rabenh.) Patrick in Patrick and Reimer, *H. arcus* var. *linearis* (Holmboe) Ross in Hartley, and *H. arcus* var. *recta* nom. nud.].

A *Hannaea* taxon found in the Laurentian Great Lakes that has previously been reported as *Ceratoneis arcus* (Fox *et al.* 1969, Holland 1969), *H. arcus* (Stoermer 1980, Millic & Lowe 1981) or *H. arcus* var. *linearis* (Stoermer 1980) has different morphological structure than these entities. The Great Lakes *Hannaea* species primarily grows epilithically in the near shore wave zone of Lake Superior, rather than in the typical lotic environments commonly associated with the genus *Hannaea*; this Great Lakes taxon also grows in rosette colonies rather than in ribbon-like colonies more typical of other *Hannaea* taxa. We present morphological and ecological evidence that show *Hannaea* populations from Lake Superior differ significantly from *Hannaea arcus* and its recognized varieties, and formally propose these populations to represent a new species, *H. superiorenensis* sp. nov.

METHODS

Light microscopy (LM) and scanning electron microscopy (SEM) were used to study material from collections of the authors, colleagues, and museum collections (Table 1). Collections designated EFS are currently being accessioned at the California Academy of Science, San Francisco; original EFS collection numbers are cited in this work. Material was processed by boiling for one hour in nitric acid followed by rinsing with distilled water to remove oxidation by-products. Cleaned material was dried on cover slips and mounted onto slides with NaphraxTM. Specimens were imaged with a Leica DMRX microscope with full immersion objectives (N.A. = 1.40). For SEM analysis, cleaned material was air-dried on MilliporeTM 0.45 µm filters or cover slips and mounted on stubs for SEM analysis. Stubs were coated with 25 nm of Au-Pd and examined on a JEOL JSM-T100 or LEO 1430VP scanning electron microscope (25 kV).

To examine morphological differences among *Hannaea* taxa, including the specimens collected from the Laurentian Great Lakes, morphometrics from nine populations of *Hannaea* were analyzed. Populations were chosen that represented diverse examples of morphology within the genus (Table 2). Measurements were taken on a Leitz Dialux 20 microscope; analysis performed on a Macintosh computer using the public domain NIH Image program (developed at the U.S. National Institutes of Health and available on the Internet at <http://rsb.info.nih.gov/nih-image/>) (Stoermer 1996).

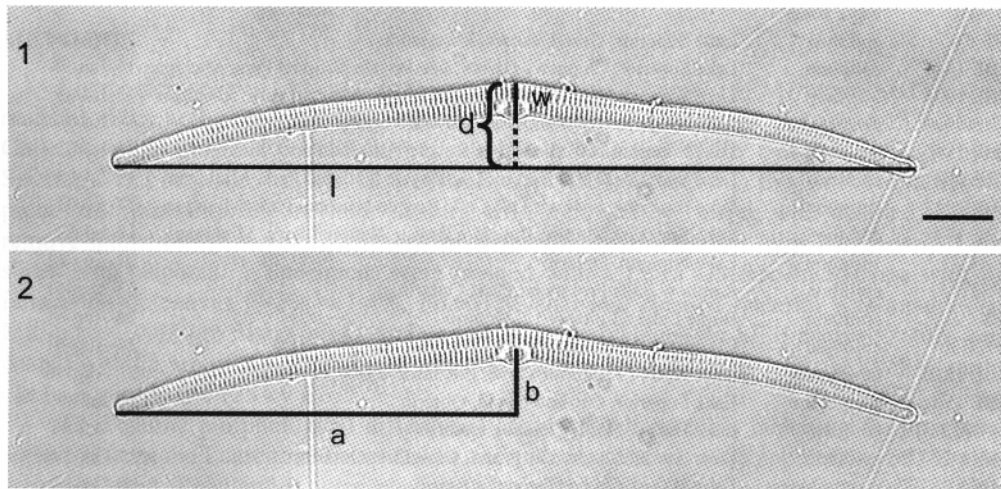
Metrics included valve length, valve breadth, striae density in 10 µm measured to the right of the inflation, and valve curvature. Length was measured as the chord between the two apices; breadth was measured at the central inflation. Curvature (inverse radius) was estimated by measuring valve length, valve breadth, and valve deflection (Fig. 1). These values were incorporated in the equation $c = 2b(a^2 + b^2)^{-1/2}$ (where c = valve curvature, a = half of the total length, and b = height of center line) to estimate curvature of the center line (Fig. 2). In several instances, collections contained two or more morphologically different taxa; these taxa were treated as separate populations. Three-dimensional scatter plots of length vs. width vs. curvature from *Hannaea* populations were plotted with Sigma Plot (Version 8.02).

Table 1. Collections examined for *Hannaea superiorenensis* and *Hannaea arcus*.

Collection number	Habitat	Locality	Date collected
JLG 01	dock piling	Sugar Island, Lake George, St. Mary's River, Michigan	20-Jun-97
JLG 02	periphyton	Lake Superior, Whitefish Point, Michigan	20-Jul-93
JLG 03	epilithon	Lake Superior, Grand Marais, Michigan	08-Apr-95
MBE 1972	periphyton	Lake Superior, Munsing, Michigan	12-Sep-02
RJB 147	plankton	Lake Superior, Eagle Harbor, Michigan	17-May-98
RJB 149	plankton	Lake Superior, Portage Channel, near Houghton, Michigan	17-May-98
MBE 1970	epipelon	Lake Superior, Presque Isle River, Michigan	10-Sep-02
MBE 1971	periphyton	Lake Superior, Ashland, Wisconsin	11-Sep-02
MBE 1221	periphyton	Lake Superior, Ashland, Wisconsin	01-Jul-96
MBE 1967	periphyton	Lake Superior, Apostle Islands, Wisconsin	10-Sep-02
RJB 428	epipelon in wave zone	Lake Superior, Two Harbors, Minnesota	22-Sep-01
MBE 1500	periphyton	Lake Superior at Gooseberry River, Minnesota	29-Sep-98
CAS 607313	stick scrape	Lake Superior, St. Louis County, Minnesota	24-Jun-84
DBC 01	periphyton	Lake Superior at Baptism River, Minnesota	DBC, pers. comm.
DBC 02	periphyton	Lake Superior at Temperance River, Minnesota	DBC, pers. comm.
EFS C3	epilithon	Cascade River, Cook County, Minnesota	20-Aug-61
CAS 625017	epilithon in wave zone	Lake Superior, Grand Marais, Minnesota	04-Jul-92
EFS C6	epilithon	Lake Superior, Grand Marais, Minnesota	20-Aug-61
MBE 1441	epilithon	Lake Superior, Chippewa Harbor, Isle Royale National Park, Michigan	15-Jun-98
MBE 1938	epilithon	Lake Superior, Davidson Island, Isle Royale National Park, Michigan	15-Jul-03
MBE 1939	periphyton	Lake Superior, NW shore, Isle Royale National Park, Michigan	16-Jul-03
MBE 1940	periphyton	Lake Superior, NW shore, Isle Royale National Park, Michigan	16-Jul-03
MBE 1941	epilithon	Lake Superior, Todd Harbor, Isle Royale National Park, Michigan	17-Jul-03
MBE 1943	epilithon	Lake Superior, Siskiwit Lake, Isle Royale National Park, Michigan	17-Jul-03
MBE 1945	epilithon	Lake Superior, Malone Bay, Isle Royale National Park, Michigan	18-Jul-03
EFS C12	epilithon	Lake Nipigon, Ontario	23-Aug-61
EFS C15	epilithon	Rainbow Falls Provincial Park, Ontario	23-Aug-61
EFS C23	epilithon	Bogle Lake, Highway 17, Ontario	24-Aug-61
EFS C30	epilithon	Chippewa River, Ontario	24-Aug-61
MBE 1220	periphyton	Lake Huron, Katherine Cove, Bachawana Bay, Ontario	21-Aug-96
MBE 150	periphyton	Lake Superior, Caribou Island, Ontario	16-Jul-89
CANA 28772	epilithon	Lake Huron, North Channel, Ontario	19-Oct-84
CANA 28776	epilithon	Lake Huron, Manitoulin Island, Gore Bay, Ontario	19-Oct-84
CANA 28777	macrophytes	Lake Huron, Coche Channel, Ontario	20-Oct-84
CANA 28778	epilithon	Lake Huron, Bay of Islands near Whitefish River, Ontario	20-Oct-84
CANA 28780	epilithon	Lake Huron, Manitoulin Island, Sheguiandah, Ontario	19-Oct-84
CANA 28792	epilithon	Lake of the Woods, Ontario	15-Jul-84
CANA 28794	benthos	Lake of the Woods, South Narrow Lake near Whitefish Bay, Ontario	15-Jul-84
MBE 1975	periphyton	Lake Huron, Mackinac Island, Michigan	14-Sep-02
EFS 1161	epilithon, 10 foot depth	Lake Michigan near South Fox Island, Michigan	16-Jun-66
EFS 1244	plankton (# 20 net)	Lake Michigan, Station F-1, 45 21 45 N, 85 19 45 W	11-Jun-64
EFS 1258	plankton (# 20 net)	Lake Michigan, Station F-1, 45 21 45 N, 85 19 45 W	06-Jul-64
EFS 1403	plankton (# 20 net)	Lake Michigan, Charlevoix Harbor entrance	10-May-67
NAA	plankton (# 20 net)	Lake Huron near Alpena, Michigan	NAA, pers. comm.

Table 2. Collections used in population analysis. Table includes collection abbreviations, collection numbers, taxon measured, and geographic locations for each population.

Abbreviation	Collection #	Taxon	Location
ORG	RJB 66	<i>Hannaea arcus</i>	Molalla River, Oregon, USA
MNT	RJB 168	<i>Hannaea arcus</i>	Hyalite Canyon, Montana, USA
SUP	CAS 625017	<i>Hannaea superiorenensis</i>	Lake Superior, Minnesota, USA
BUL	RJB 418	<i>Hannaea arcus</i> var. <i>linearis</i>	Mesta River, Bulgaria
ANG	EFS 4221	<i>Hannaea</i> sp. undescribed	Angara River/Lake Baikal, Russia
HOV	MS 97B	<i>Hannaea</i> sp. undescribed	Lake Hövsgöl, Mongolia
TUR	MS 115a	<i>Hannaea arcus</i> var. <i>recta</i> (nom. nud.)	Tuul River, Mongolia
TUL	MS 115a	<i>Hannaea</i> sp. undescribed	Tuul River, Mongolia
ALK	RJB 35	<i>Hannaea arcus</i> var. <i>amphioxys</i>	Atigun River, Alaska, USA



Figs 1–2: Light micrograph of a *Hannaea* sp. showing valve dimensions for curvature calculation. Scale bar = 10 μ m. **Fig. 1.** Measurements in light microscope: l = length from apex to apex, w = valve breadth at inflation, d = valve deflection from dorsal margin to length chord. **Fig. 2.** Chords for curvature calculations, c = valve curvature which was calculated with the formula $c = 2b(a^2 + b^2)^{-1/2}$ where a = half of total length, and b = height of center line.

Additionally, stereo pairs were plotted with a rotation of 7° between graphs, using methods similar to Droop *et al.* (2000). Graphs can be viewed with a standard stereo viewer or by focusing beyond the images and moving the graphs into the line of sight to create a three-dimensional image from the two graphs.

OBSERVATIONS

Hannaea superiorenensis R. J. Bixby & M. B. Edlund, sp. nov.

Other citations:

Hannaea arcus (Ehrenb.) Patrick in Patrick & Reimer, STOERMER, E. F. & YANG, J. J. (1969), p. 101.

Hannaea arcus (Ehrenb.) Patrick in Patrick & Reimer, STOERMER, E. F. (1980), p. 41.

Hannaea arcus (Ehrenb.) Patrick in Patrick & Reimer, MILLIE, D.F. & R.L. LOWE (1981), p. 202 (unconfirmed, no material available).

Hannaea arcus var. *linearis* (Holmboe) Ross in Hartley, STOERMER, E. F. (1980), p. 41.

Ceratoneis arcus (Ehrenb.) Kütz., FOX, J. L., ODLAUG, T. O. & OLSON, T. A. (1969), p. 116, pl. 14.

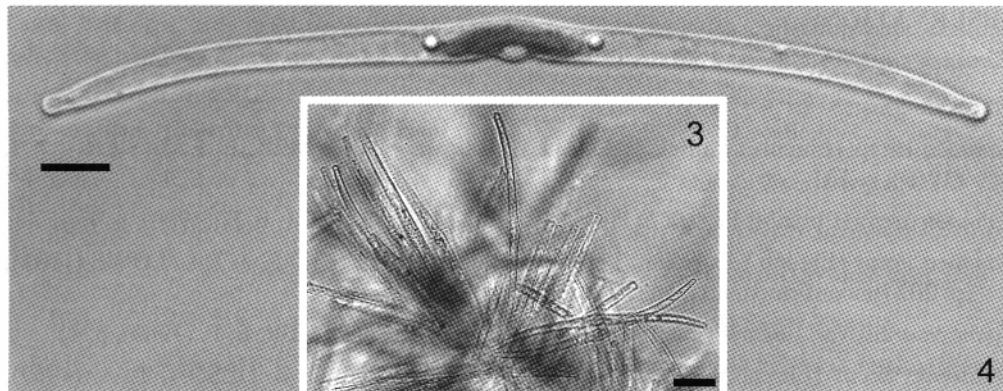
Ceratoneis arcus Kütz. (nom. nud.) HOLLAND, R. E. (1969), p. 431, (unconfirmed, no material available).

Diagnosis: Differt a *Hannaea arcus* longitudine longiore, ratione major longitudinis/latitudinis, valvis secundariter reflexis ad marginem dorsalem et habitationis characteribus. Differt a varietatibus cognitis et civiis indscriptis *H. arcus* forma valvae, amplitudine valvae, grado curvaturae et ratione longitudinis/latitudinis.

Description: Cellulae affixae ad apices, colonias rosulatas facientes. Chloroplastus centralis, laminiiformis, secus latum dorsale frustuli. Nucleus centralis, ventraliter locatus. Guttulae una vel plus, ad extrema distalia chloroplasti locata. Cingula aperta, valvocopula in margine advalvari crenato, serie punctarum abvalvari marginem crenatum. Valvae arcuatae secundariter reflexae versus marginem dorsalem, apicibus capitatis, tumore centrali unilaterali. Valvae 111.8–170.2 μm in longitudino, 4.9–7.8 μm in latitudine (ad inflationem), ratione longitudinis/latitudinis propinquus 22:1, grado curvaturae 0.0033–0.0065 μm^{-1} . Raphe absens. Area axialis angusta. Tumor centralis striis oclclusis. Striae punctatae et parallelae, uniseriatae in superficie et limbo valvae, 10.3–15.1 in 10 μm . Spinae inter strias interdum adsunt. Rimoportula polaris sessilis ad apicem valvam, ocellulimbis mutatis in limbo amborum apicum valvarum.

Diagnosis: Differs from *Hannaea arcus* by its longer length, greater length to width ratio, secondary reflexion towards dorsal margin, and ecological traits. Differs from known varieties and undescribed populations of *H. arcus* by valve shape, valve size, degree of curvature, and length/width ratio.

Description: Cells attached at the end forming rosette colonies (Fig. 4). Chloroplast central, plate-like, along the dorsal side of frustule (Fig. 3). Nucleus central, ventrally located (Fig. 3). Lipid droplets one or more, positioned at distal ends of the chloroplast. Cingula open with valvocopula crenate on advalvar margin, with single row of punctae abvalvar to crenate margin. Valves arcuate with secondary reflexion towards dorsal margin, capitate ends, central unilateral inflation (Figs 3–9). Valves 111.8–170.2 μm length, 4.9–7.8 μm breadth (at inflation), length/breadth ratio approximately 22:1, degree of curvature 0.0033–0.0065 μm^{-1} . Raphe absent. Axial area narrow. Central inflation with occluded striae. Striae punctate and parallel, uniseriate on valve face and mantle, 10.3–15.1 in 10 μm (Figs 10–11). Spines between striae, occasional (Fig. 11). Valve apices with a single polar, sessile rimoportula per valve (Figs 9–10), with modified ocellulimbi on mantle of both valve apices (Fig. 10).



Figs 3–4. *Hannaea superiorenensis*, uncleaned material, LM. **Fig. 3:** Live cell with a central plate-like chloroplast aligned along the dorsal side of the frustule, a central ventrally displaced nucleus, and a droplet at the distal ends of the chloroplast, Lake Superior; scale bar = 10 μm . **Fig. 4.** Rosette colony from epilithon, Lake Superior, Minnesota (MBE 1553); scale bar = 20 μm .

Holotype here designated: Holotype specimen circled on slide CAS 221080 (Fig. 6), material: CAS 625017. Type locality: epilithon, wave zone, Lake Superior, Grand Marais, Cook County, Minnesota, U.S.A., 04 July 1992, collector: M.B. Edlund

Isotypes: MBE 498, RJB 167. *Paratype:* CAS 607313, stick scrape, Lake Superior, St. Louis County, Minnesota, U.S.A., 24 June 1984, collector: J.P. Kociolek

Distribution: *Hannaea superiorenensis* (Table 1, Fig. 12). Laurentian Great Lakes, North America, including Lakes Superior, Michigan, Huron, and Lake Erie.

A triplot of length, width, and curvature demonstrates clear separation of *Hannaea superiorenensis* from other populations of *Hannaea* (Figs 13–15). Notably, valve length of *H. superiorenensis* is greater than most *Hannaea* populations, and the length: breadth ratio separates *H. superiorenensis* from longer specimens of *Hannaea* from lakes in the Baikal Rift Zone. Curvature of *H. superiorenensis* is relatively small compared with other *Hannaea* populations.

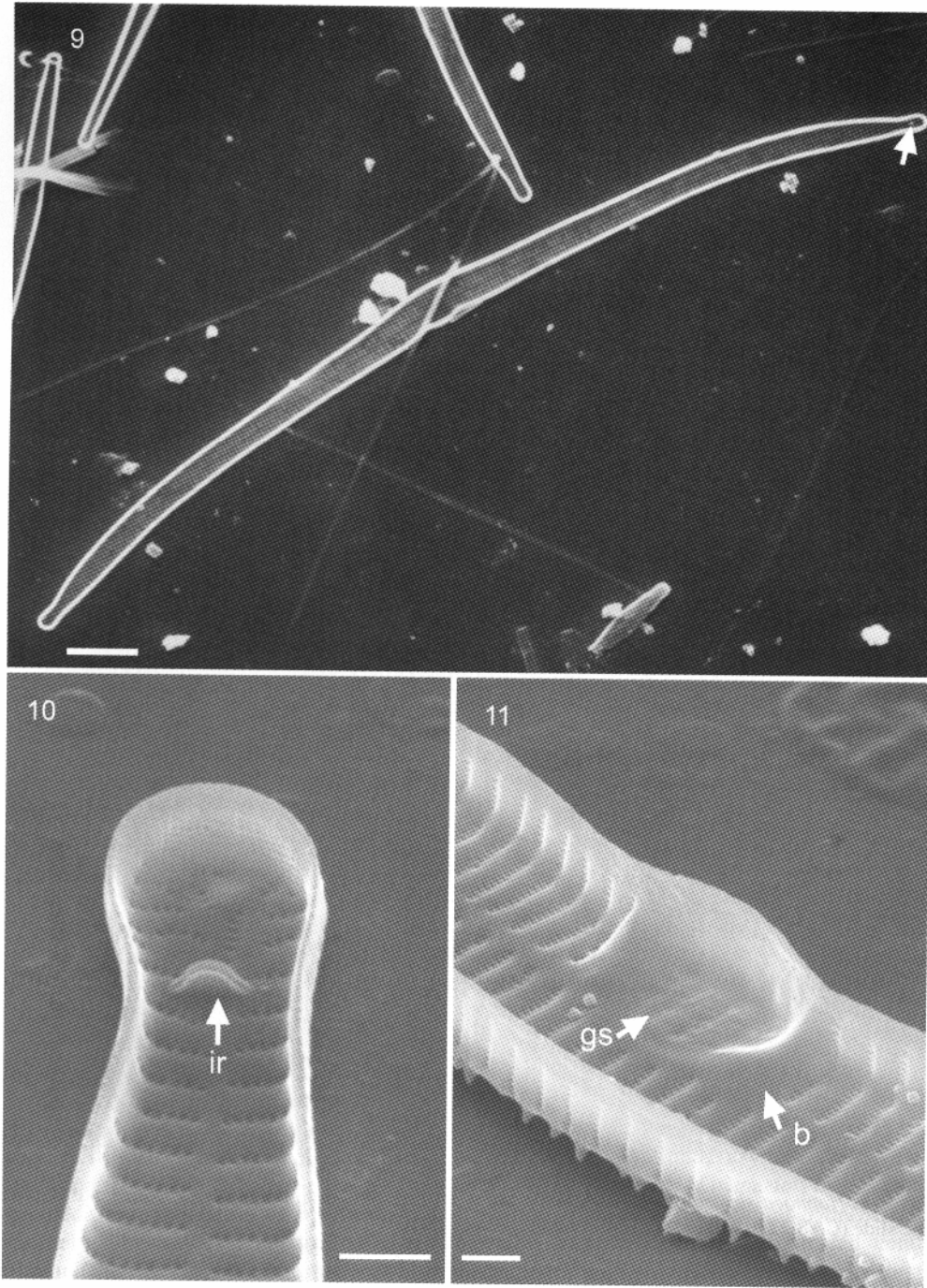
DISCUSSION

Hannaea superiorenensis has a morphology that most closely resembles *H. arcus* var. *linearis*. It also bears a superficial resemblance to an abnormal, asymmetric *Synedra* population that inhabits Lake Superior (Feldt *et al.* 1973); however, *H. superiorenensis* is easily separated from this *Synedra* by its unilateral ventral inflation. *Hannaea superiorenensis* has extremely long valves compared to other *Hannaea* taxa and a more pronounced ventral inflation (Figs 16–31). The shortest valves in the Superior populations are considerably longer than the length of the type population of *H. arcus* var. *linearis* (80 μm length, Holmboe 1899) and are nearly as large than the longest valves in other populations of *H. arcus* var. *linearis* (Figs 28–29). The overall valve outline differs from *H. arcus* var. *linearis*; starting in the valve center, the outline of *H. superiorenensis* is initially curved toward the ventral side, then is secondarily reflexed toward the dorsal side, and finally the distal ends of the valve are further bent toward the ventral side. Valves also have a much narrower width compared to other



Figs 5–8. *Hannaea superiorenensis*. LM. Scale bar = 10 μm . Size diminution series from Lake Superior type slide (CAS 221080). Fig. 6: LM of holotype specimen.

Hannaea taxa. *Hannaea superiorenensis* also has a smaller curvature compared to other *Hannaea* populations (Fig. 13). Whereas there is an overall decrease in curvature with increasing length among the populations measured, it is clear that curvature differences distinguish populations independent of size. For example, populations of similarly sized *H. arcus* var. *recta* (nom. nud.) and an undescribed *Hannaea* from the Tuul River are differentiated by valve curvature alone (Fig. 13).



Figs 9–11. *Hannaea superiorenensis*. SEM, Lake Superior, Grand Marais, Minnesota. Scale bar = 10 μm (Fig. 9) and 1 μm (Figs 10–11). Holotype material from CAS 625017. **Fig. 9.** Internal valve view. Arrow = polar rimoportula. **Fig. 10.** Internal view of rimoportula (ir) and modified ocellulimbus (o). Note uniseriate striae. **Fig. 11.** Internal view of central area with ghost striae (gs) and buttressing (b). Uniseriate striae on valve face and mantle. Spines visible along face-mantle interface.

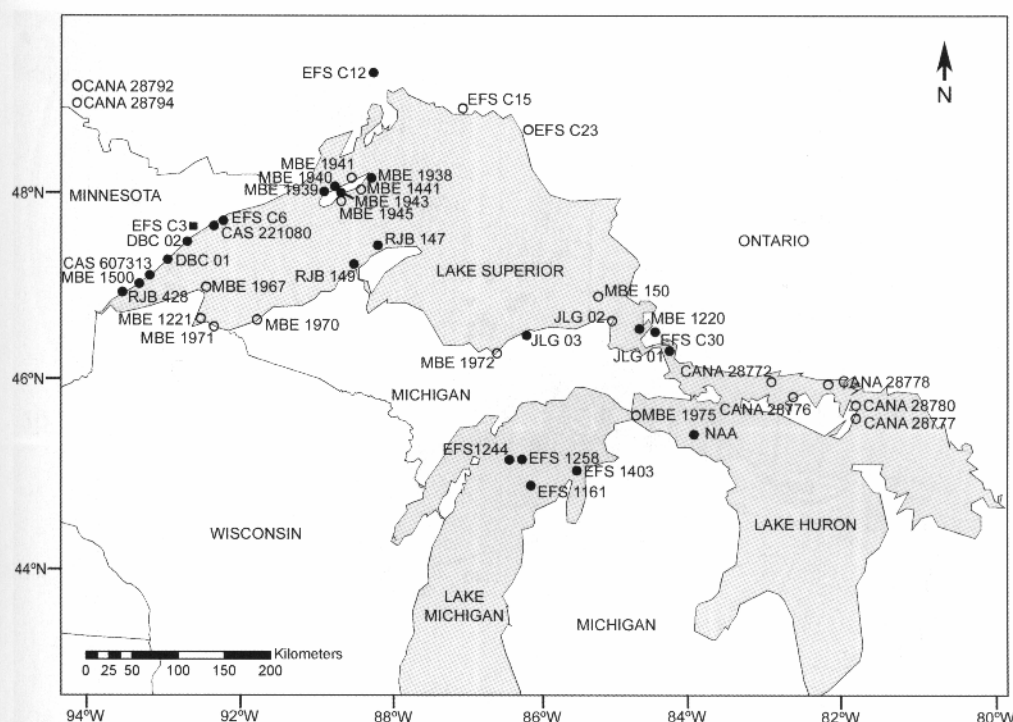
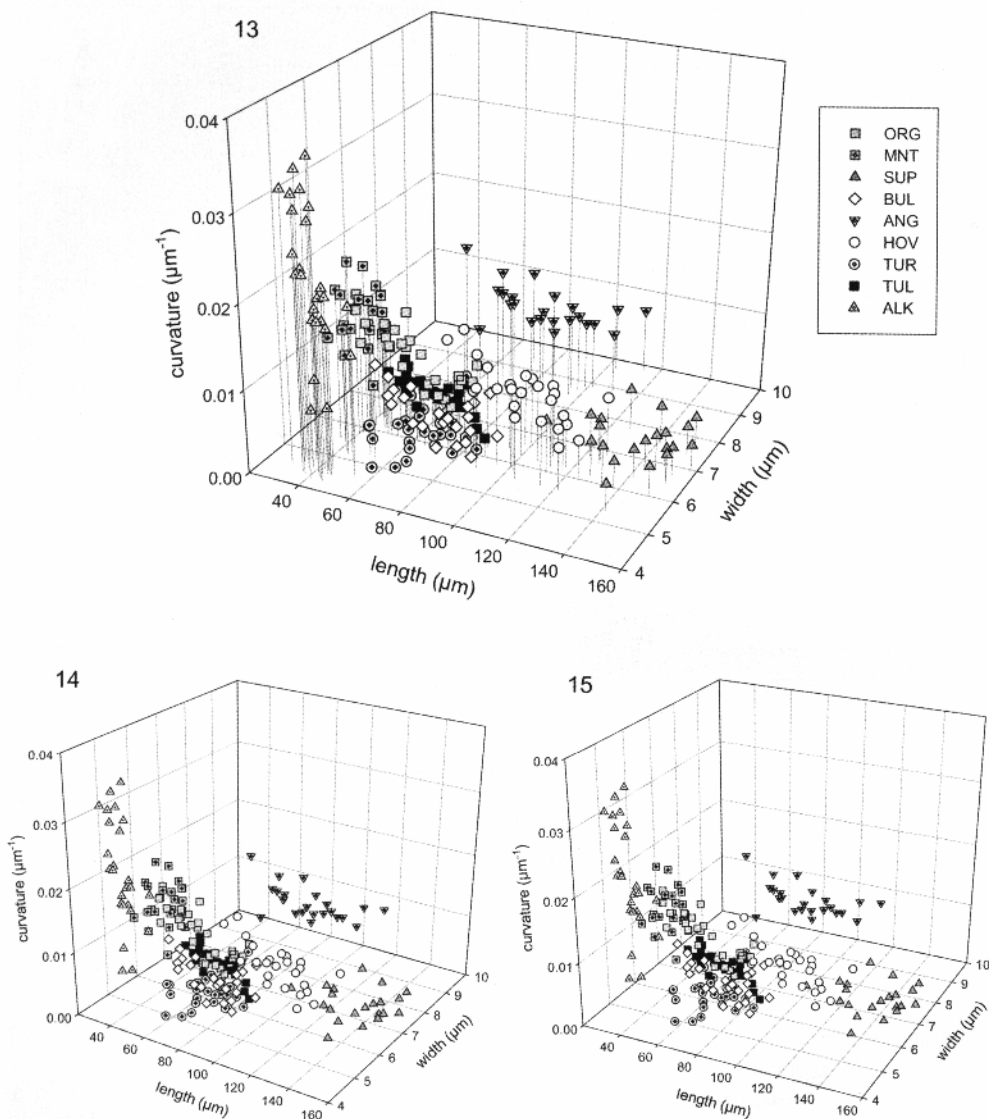


Fig. 12. Distribution map of *Hannaea* taxa in the Laurentian Great Lakes region. Solid circles = *Hannaea superiorenensis* only in collection, solid square = *Hannaea arcus* only in collection, empty circles = no *Hannaea* taxa in collection. Additional collection information is located in Table 1.

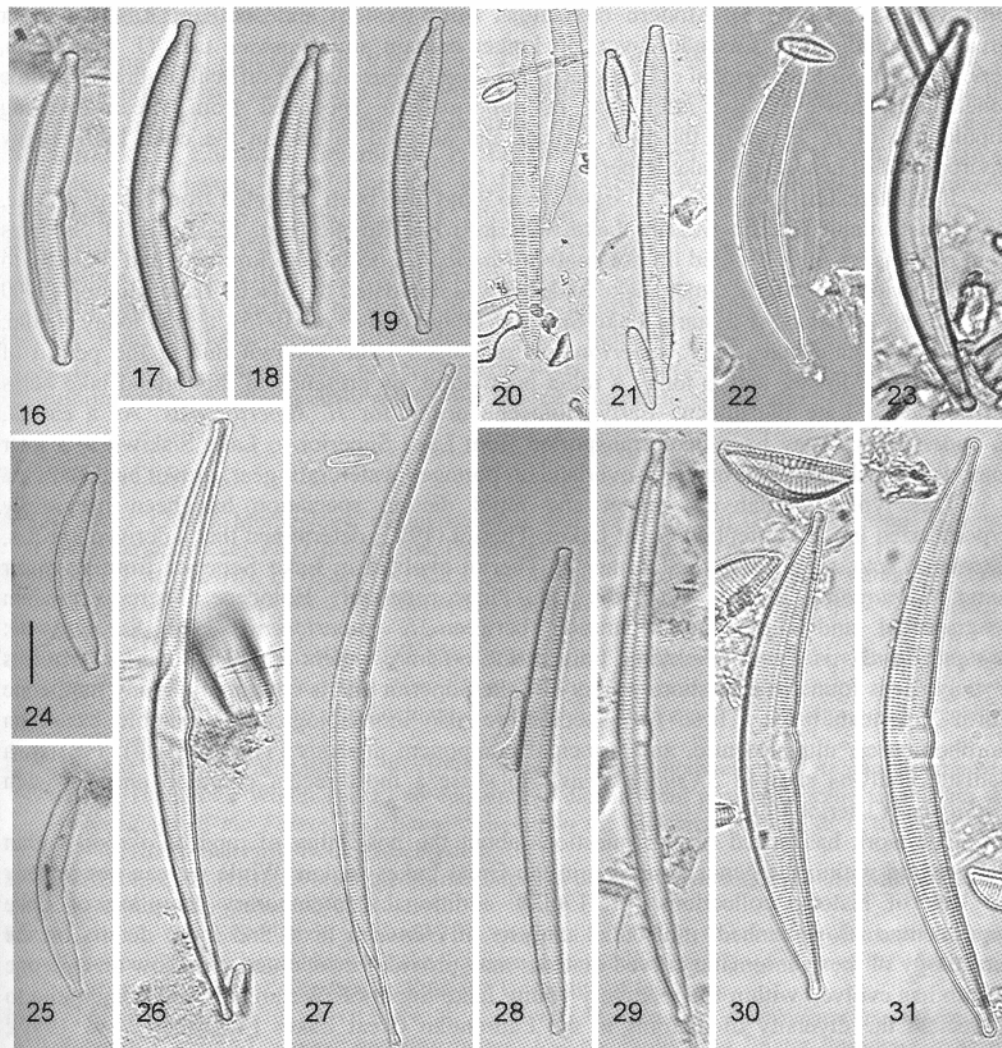
Frustular ultrastructure is similar to that of *H. arcus* and its varieties, with uniseriate striae, ghost striae in a buttressed ventral inflation, one polar rimoportula per valve, and a modified ocellulimbus at each apex. *Hannaea superiorenensis* also forms rosette colonies, attaching to a common mucilage pad (Fig. 3). Other *Hannaea* taxa grow singly or in ribbon-like bands attached valve face to face. Ribbon-like colonies have not been reported from collections of *H. superiorenensis*.

Hannaea superiorenensis in Lake Superior further differs from other *Hannaea* taxa in its general habitat preference (except two undescribed species in lakes Baikal and Hövsgöl, Baikal Rift Zone, see below). *Hannaea superiorenensis* primarily grows as nearshore epilithon in Lake Superior and in two lakes that drain to Lake Superior. It is, on occasion, secondarily entrained in the tycho plankton of Lake Superior and is an uncommon tycho plankton in the other Great Lakes (Fig. 12, Table 1). We believe that tycho planktonic *H. superiorenensis* in the Great Lakes originates as periphyton in Lake Superior and travels by current to other areas within the basin. *Hannaea superiorenensis* is notably absent from streams that flow into western Lake Superior (J. Thompson, pers. comm., J. Kingston, pers. comm.), where one might expect to find *Hannaea* spp. living, although the cold, high energy, and highly oxygenated wave zone of Lake Superior has characteristics similar to those associated with high elevation riverine environments. Two undescribed *Hannaea* populations have been similarly found growing in the wave-zone epilithon of Lakes Baikal and Hövsgöl, large ancient lakes in the Baikal Rift Zone (Bixby 2001, Edlund *et al.* in press). Although inhabiting similar habitats, the three lentic *Hannaea* species are easily separable when viewed in the light microscope.



Figs 13–15: Three-dimensional scatter plot of length vs. width vs. curvature for nine populations of *Hannaea* taxa. Data are untransformed. Population abbreviations listed in Table 2. **Fig. 13.** Length (μm) vs. width (μm) vs. curvature (μm^{-1}). **Figs 14, 15.** Stereo pairs of length vs. width vs. curvature with a rotation of 7° on the horizontal axis between plots.

The Laurentian Great Lakes are relatively young features on the earth's surface; they began to fill during the Late Wisconsin only 13,300 years ago (Holman 1995). As no distributional or fossil records report *Hannaea superiorenensis* outside of the Great Lakes basin, this species may have evolved allopatrically from *H. arcus* in the short time period since the formation of the Laurentian Great Lakes. Several lines of evidence support this assertion. First, a cladistic analysis showed *H. arcus* and *H. superiorenensis* to be sister taxa (Bixby 2001). Second, *H. superiorenensis* grows primarily in the wave zone of Lake Superior where thermal



Figs 16–31. Exemplar specimens from populations used in morphometric analysis (excluding population from Lake Superior, see Figs 5–8), LM. Scale bar = 10 μ m. See Table 2 for additional information. **Figs 16, 17.** *Hannaea arcus*, Molalla River, Oregon, USA. **Figs 18, 19.** *Hannaea arcus*, Hyalite Canyon, Montana, USA. **Figs 20, 21.** *Hannaea arcus* var. *recta* (nom. nud.), Tuul River, Mongolia. **Figs 22, 23.** *Hannaea* sp., undescribed, Tuul River, Mongolia. **Figs 24, 25.** *Hannaea arcus* var. *amphioxys*, Atigun River, Alaska, USA. **Figs 26, 27.** *Hannaea* sp., undescribed, Lake Hövsgöl, Mongolia. **Figs 28, 29.** *Hannaea arcus* var. *linearis*, Mesta River, Bulgaria. **Figs 30, 31.** *Hannaea* sp., undescribed, Angara River/Lake Baikal, Russia.

and energy conditions are similar to higher elevation, cold, riverine systems where *H. arcus* is normally found. Third, contemporary and historical collections from Lake Superior and streams draining into Lake Superior demonstrate that *H. arcus* and *H. superiorensis* are not sympatric and inhabit disparate ecological niches (Fig. 12, Table 1). Collections made between 1961 and 2003 from around and within Lake Superior showed that these two taxa never occurred in the same collections. At present, *H. arcus* is likely only surviving at the edge of its range; a single sample with *H. arcus* was found in the Cascade River, Minnesota in

1961 (Fig. 12; EFS C3). Modern collections from western and southern Lake Superior streams, including the Cascade River, no longer contain any *Hannaea* taxa (J. Thompson, pers. comm.). So few regional collections of *Hannaea arcus* make it difficult to draw absolute conclusions; however, we infer that *H. superiorensis* speciated from stream-dwelling populations of *H. arcus* in the Late Glacial and adapted to live in the cold, high-energy environment of near-shore Lake Superior.

It is interesting to note that *H. superiorensis* has also been collected from Siskiwit Lake, the largest inland lake on western Lake Superior's Isle Royale (Fig. 12, Table 1). Samples from other lakes on the island do not contain *Hannaea*. Located 0.5 km from and draining to Lake Superior by a single outlet, Lake Siskiwit was inundated by Glacial Lake Minong (9000 y BP) as an embayment of early Lake Superior (Raymond *et al.* 1975), and is today a cold, deep, oligotrophic lake. If *H. superiorensis* colonized Lake Siskiwit during the period of Glacial Lake Minong and is today a relict population, its presence in this inland lake helps corroborate a Late Pleistocene–Early Holocene origin for *H. superiorensis*. As a caveat, *H. superiorensis* may have been transported from Lake Superior to Lake Siskiwit at a later date via the Lake Siskiwit outlet or overland on portaged watercraft, gear, or bait buckets.

This type of relatively recent and rapid diatom speciation has been previously hypothesized in the Laurentian Great Lakes. Theriot (1992) determined that a derived species, *Stephanodiscus superiorensis* Stoermer & Theriot evolved in Lake Superior from its sister taxon, *S. niagarae* Ehrenb. since the Late Pleistocene/early Holocene. There is modern geographical and ecological separation between *S. superiorensis* and *S. niagarae*; *S. superiorensis* is found planktonic only in the offshore waters of Lake Superior, whereas *S. niagarae* is found in near shore waters of Lake Superior and is common in many temperate North American lakes. These two species are also morphologically separable based on morphometrics, ultrastructure, and principal component analysis (Theriot 1984). Finally, a cladistic analysis showed *S. superiorensis* to share a most recent common ancestor with *S. niagarae* (Theriot 1992).

Our work has raised further questions about the possibility of rapid evolution within diatoms and within the genus *Hannaea* in the Great Lakes region. While we can not remedy the lack of historic collections (pre-1960s), additional contemporary sampling of Lake Superior and its watershed, molecular analysis of *Hannaea* taxa, and more details on the autecology of these enigmatic curved diatoms may provide better clues as to how an endemic diatom has evolved within the relatively young Lake Superior. We are still only beginning to appreciate the diversity of diatoms in the Laurentian Great Lakes (Stoermer *et al.* 1999); recent studies have reported rare taxa (Edlund & Stoermer 1999), new taxa (Kociolek & Stoermer 1991), extinctions (Stoermer & Smol 1999), and cryptic species groups (Pappas & Stoermer 2003). Apart from *Stephanodiscus superiorensis* and *Hannaea superiorensis*, few diatoms have been described as endemic or potentially endemic to the Great Lakes (Stoermer & Yang 1971, Kociolek & Stoermer 1991). An interesting endemic, *Cyclotella americana* A. Schmidt [non *Cyclotella americana* (Ehrenb.) Kütz.], was once common in the deepwater plankton of lakes Erie and Ontario. Anthropogenic impacts brought on by European settlement and development in the basin, and in particular elevated nutrient loading, appear to have led to collapse of the deepwater plankton community in the Lower Great Lakes and the eventual extinction of *C. americana* by about 1880 A.D. (Stoermer *et al.* 1996). Similar cultural impacts and demands on the Great Lakes led to extinction of other endemic organisms including several fishes (Smith & Todd 1984, Jude & Leach 1993). As we continue to describe the diatom diversity of the Great Lakes, the discovery of novel species and extant endemics highlights the need to more quickly document the diversity of this unequalled natural resource in a fast changing world and to realize that endemic species deserve greater attention as they are often most sensitive to ecological change.

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