

Asterionella Hassall (Heterokontophyta, Bacillariophyceae) Taxonomic history and quantitative methods as an aid to valve shape differentiation

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Abstract

The taxonomic history of the diatom genus *Asterionella* is sketchy at best. At present, delimitation of the genus, and species within it, are unclear. This is presented in a compilation of the taxonomy of *Asterionella*. In regard to species determination, valve shape variation is important. With the proliferation of splitting diatom taxa at the species level, the need for revision of *Asterionella* is apparent. We have provided some initial results concerning application of quantitative methods to valve shape variation in *Asterionella*. Seven shape variants may be present in the Great Lakes.

Key index words

Asterionella, diatoms, morphology, shape variation, taxonomy

Asterionella morphology and speciation

In 1850, A. H. Hassall described *Asterionella* in "Microscopic Examination of the Water supplied to the Inhabitants of London" (Patrick & Reimer 1966, Körner 1970, Round *et al.* 1990). This ubiquitous, freshwater diatom (Heterokontophyta, Bacillariophyceae) genus has cells that are elongate and asymmetric which are joined to form stellate colonies (Round *et al.* 1990) in life. The head pole, where attachment occurs in colony formation, is usually wider than the foot pole. Cell attachment in colonies occurs by adhesion of mucilage pads (Round *et al.* 1990).

Asterionella is one of the least conspicuously ornamented diatoms, having few characters distinguishable by light and/or scanning electron microscopy (Körner 1970, Round *et al.* 1990). In valve view, *Asterionella* frustules are bilobate, having inflated ends (Barber & Haworth 1981). Apices have been described as capitate (Patrick & Reimer 1966, Round *et al.* 1990), but vary in shape. There are no septa or intercalary bands present (Patrick & Reimer 1966). Areolae (striae) are uniseriate, the sternum is narrow, and vela are indistinct (Round *et al.* 1990). Apical pore fields may be present at either end of

both valves (Round *et al.* 1990). These fields may be lost during size diminution (Round *et al.* 1990, Mann 1999). Rimoportulae at either end of both valves are oriented in a transverse to the apical axis. The external opening of this process is a pore that is larger than the areolae (Round *et al.* 1990) without any external extension. Spines may be present along the edge of the valve, and several copulae which appear as rows of pores may occur on the advalvar side of the frustule (Round *et al.* 1990). Compared to other diatom genera, *Asterionella* is especially character-poor.

Hassall's description did not distinguish between *Asterionella* the genus and the description of the type species, *Asterionella formosa* (Patrick & Reimer 1966). Unfortunately, prepared slides and/or material of the type species are not known to exist. This taxon is described as having unequal-sized capitate apices and fine striae, 24–28 in 10 μm , length of 40–130 μm , and width of 1–3 μm (Patrick & Reimer 1966, Krammer & Lange-Bertalot 1991). The type locality is described as Thames at Brentford, where *Asterionella* was found in drinking water supplied by the Grand Junction Company (Patrick & Reimer 1966). In general, this taxon is described as planktonic and cosmopolitan with respect to its distribution in freshwater systems (Hustedt 1949,

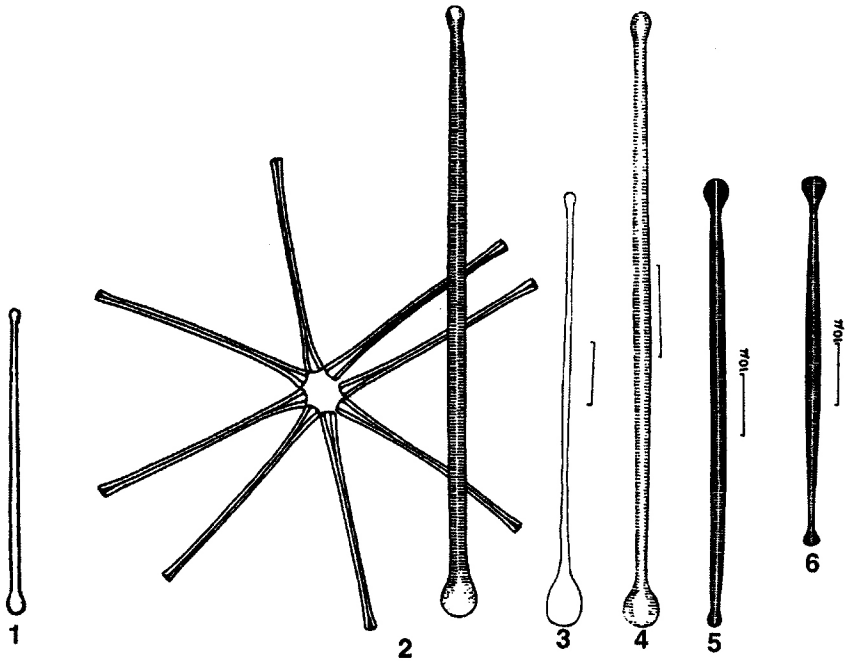


Fig. 1. *Asterionella formosa* in valve view illustrated in Van Heurck 1880-1885, p. 154, Pl. 51, Fig. 19. **Fig. 2.** *Asterionella formosa* in valve and girdle view illustrated in Huber-Pestalozzi 1942, p. 445, Pl. 132, Figs 531a and b. **Fig. 3.** *Asterionella formosa* in valve view illustrated in Cleve-Euler 1953, p. 155, Fig. 401a. **Fig. 4.** *Asterionella formosa* in valve view illustrated in Cleve-Euler 1953, p. 155, Fig. 401d. **Fig. 5.** *Asterionella formosa* in valve view illustrated in Patrick & Reimer 1966, p. 159, Pl. 9, Fig. 1. **Fig. 6.** *Asterionella formosa* in valve view illustrated in Patrick & Reimer 1966, p. 159, Pl. 9, Fig. 2.

Patrick & Reimer 1966). *Asterionella formosa* often occurs in mesotrophic to eutrophic waters (Patrick & Reimer 1966, Lowe 1974, Beaver 1981).

Asterionella formosa Hassall has been found in the Great Lakes. Specimens from Lake Michigan are described as having a very narrow valve body. Sides are parallel in large specimens, while in small specimens, sides taper towards the foot pole. In addition, the width of the mid-valve region is less than one-half the head pole width (Stoermer & Yang 1969).

Asterionella formosa is one of the dominant taxa found in southern Lake Michigan (Stoermer & Kopczynska 1967, Stoermer & Yang 1969). High abundances have been recorded during the spring, in August, and in October (Stoermer & Kopczynska 1967, Stoermer & Yang 1970). This taxon is tolerant of temperature extremes with relative abundance peaks at 3-6°C and 15-17°C

(Stoermer & Ladewski 1976). Two possibilities were given as an explanation of its bimodal occurrence pattern. One was that *A. formosa* is eurythermal and grew at two temperatures in response to other factors. The other explanation is that *A. formosa* exhibits cryptic speciation or has races with different temperature optima.

Asterionella formosa has been said to exist in a wide variety of habitats and exhibit considerable morphological variation in southern Lake Michigan. This led to the comment by Stoermer & Yang (1970) that "*A. formosa* may have) a number of ecological races or even that its present circumscription may include a number of separate species which are difficult to distinguish from morphological criteria. Close observation of populations from Lake Michigan shows considerable variability, but we have been unable to separate them on the basis of any consistent feature. This problem bears further investigation."

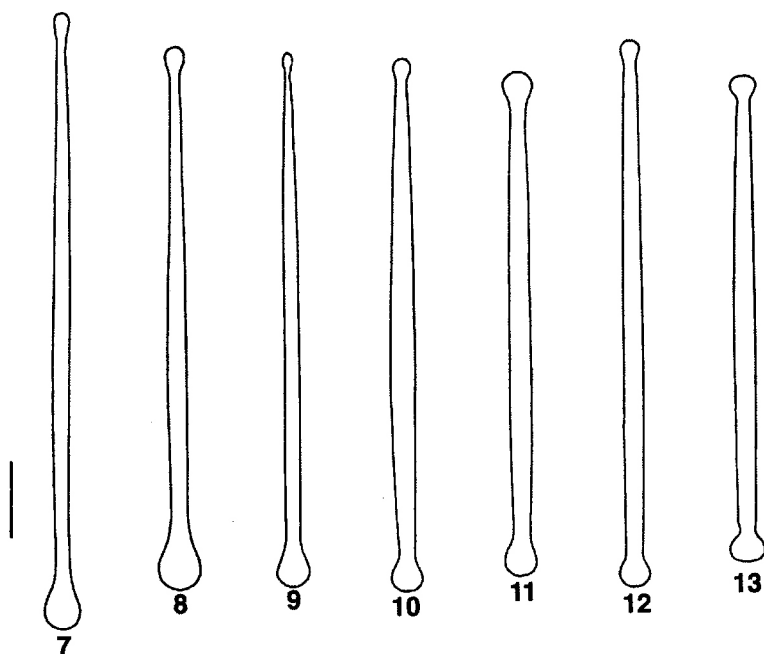


Fig. 7. *Asterionella formosa* in valve view illustrated in Körner 1970, pp. 571-600, Fig. 1. **Fig. 8.** *Asterionella formosa* in valve view illustrated in Körner 1970, pp. 571-600, Fig. 2. **Fig. 9.** *Asterionella formosa* in valve view illustrated in Körner 1970, pp. 571-600, Fig. 3. **Fig. 10.** *Asterionella formosa* in valve view illustrated in Körner 1970, pp. 571-600, Fig. 4. **Fig. 11.** *Asterionella formosa* in valve view illustrated in Körner 1970, pp. 571-600, Fig. 5. **Fig. 12.** *Asterionella formosa* in valve view illustrated in Körner 1970, pp. 571-600, Fig. 6. **Fig. 13.** *Asterionella formosa* in valve view illustrated in Körner 1970, pp. 571-600, Fig. 7.

Many illustrations of this taxon in valve view depict *A. formosa* with a wide range of shape variation (Van Heurck 1880-1885, Huber-Pestalozzi 1942, Cleve-Euler 1953, Patrick & Reimer 1966, Körner 1970, Sims 1996 (Figs 1-14)). Even light micrographs of *A. formosa* show the wide range of valve shape variation (Krammer & Lange-Bertalot 1991 (Figs 15-19)). Two varieties of *A. formosa*, *A. formosa* var. *subtilis* Grunow in Van Heurck 1881 and *A. formosa* var. *subtilissima* Grunow in Van Heurck 1881 (Figs 20, 21), are difficult to distinguish from the nominate variety. In some cases, the written description does not match the illustration or light micrograph depicting *A. formosa* (e.g., Figs 14, 15, 16, and 18).

Another taxon from this genus has been described from Lake Michigan. *A. bleakeleyi* W.Sm. 1856 has an asymmetric head pole and less expanded foot pole. The mid-valve region of the valve margins is slightly convex, with the mid-

valve width greater than one-half the head pole width. This taxon is commonly found in polluted harbors (Stoermer & Yang 1969).

Other accounts of this taxon have been given. According to Patrick & Reimer (1966), *A. bleakeleyi* in girdle view has unequal inflated ends, is swollen in the middle, and has a more distinctly capitate head pole than *A. formosa*. They illustrate this taxon in girdle view (Patrick & Reimer 1966). Illustrations in girdle view are presented in Smith (1856), Van Heurck (1880-1885), and Hustedt (1932) as well. The only valve view illustration is presented in Peragallo & Peragallo (1897-1908 (Fig. 22)). This illustration does not depict *A. bleakeleyi* having an asymmetrical head pole. Van Heurck (1896) distinguishes *A. formosa* var. *bleakeleyi* (from *A. bleakeleyi* W.Sm.) as having short frustules with an enlarged, dilated base. *A. bleakeleyi* is a marine taxon (Smith 1856, Van Heurck 1896, Pat-

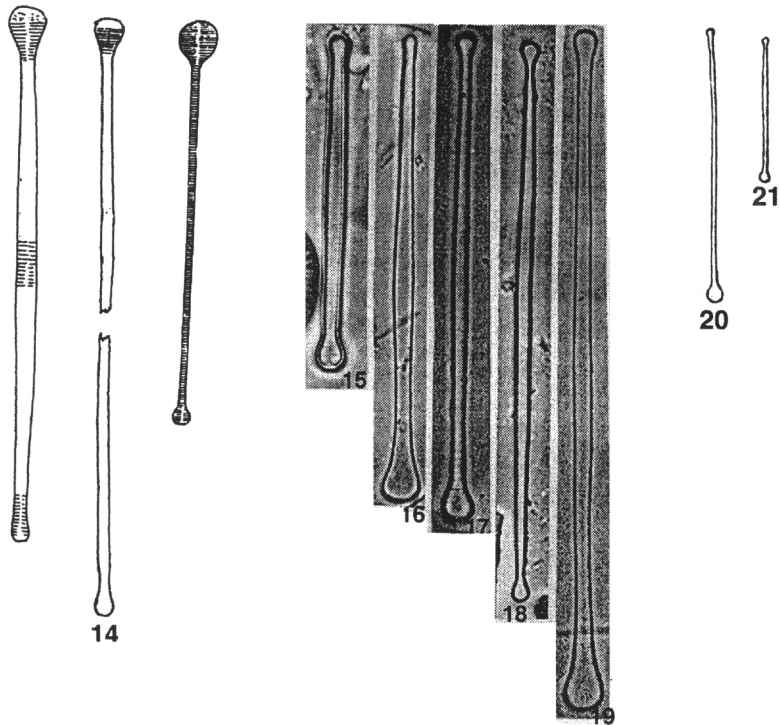


Fig. 14. *Asterionella formosa* in valve view illustrated in Sims 1996, Barber & Carter's illustrations, p. 72, Pl. 28, Fig. 2, three illustrations. **Fig. 15.** Light micrographs of *A. formosa* in valve view in Krammer & Lange-Bertalot 1991, p. 103, Pl. 103, Fig. 4. **Fig. 16.** Light micrographs of *A. formosa* in valve view in Krammer & Lange-Bertalot 1991, p. 103, Pl. 103, Fig. 5. **Fig. 17.** Light micrographs of *A. formosa* in valve view in Krammer & Lange-Bertalot 1991, p. 103, Pl. 103, Fig. 6. **Fig. 18.** Light micrographs of *A. formosa* in valve view in Krammer & Lange-Bertalot 1991, p. 103, Pl. 103, Fig. 7. **Fig. 19.** Light micrographs of *A. formosa* in valve view in Krammer & Lange-Bertalot 1991, p. 103, Pl. 103, Fig. 8. **Fig. 20.** *Asterionella formosa* var. *subtilis* in valve view illustrated in Van Heurck 1880-1885, p. 154, Pl. 51, Fig. 21. **Fig. 21.** *Asterionella formosa* var. *subtilissima* in valve view illustrated in Van Heurck 1880-1885, p. 154, Pl. 51, Fig. 24.

rick & Reimer 1966, Round *et al.* 1990).

Asterionella bleakeleyi var. *notata* Grunow has become the type specimen for the genus *Bleakeleya* (Round *et al.* 1990). The name of this genus is based on *A. bleakeleyi* W.Sm. as it is the earliest synonym of *B. notata* (Round *et al.* 1990). *Bleakeleya* has valve ultrastructure unlike *Asterionella* (Round *et al.* 1990). Van Heurck (1880-1885) separates *A. notata* Grunow from *A. bleakeleyi* var. *notata* (Fig. 23) in addition to recognizing *A. formosa* var. *bleakeleyi* (Van Heurck 1896). Peragallo & Peragallo (1897-1908 (Fig. 24)) and Körner (1970 (Fig. 25)) identify *A. bleakeleyi* var. *notata* as *A. notata* which does not resemble *A. bleakeleyi* W.Sm. (Fig. 22). In

addition, Körner (1970) states that he is unsure that *A. bleakeleyi* is the same as *A. bleakeleyi* var. *notata*. Grunow (1867) identified both taxa from specimens found in *Sargassum* near Honduras. Apparently, there is considerable confusion with respect to the true identity of *A. bleakeleyi*.

Asterionella gracillima (Hantzsch) Heib. 1863 has been recognized as a distinct species and as a variety of *A. formosa*, *A. formosa* var. *gracillima* (Hantzsch) Grunow in Van Heurck 1881 (Patrick & Reimer 1966, Körner 1970). This taxon has head and foot poles almost equal in size (Patrick & Reimer 1966). Illustrations of *A. gracillima* show that this taxon has a narrow range of morphological variability (Van Heurck

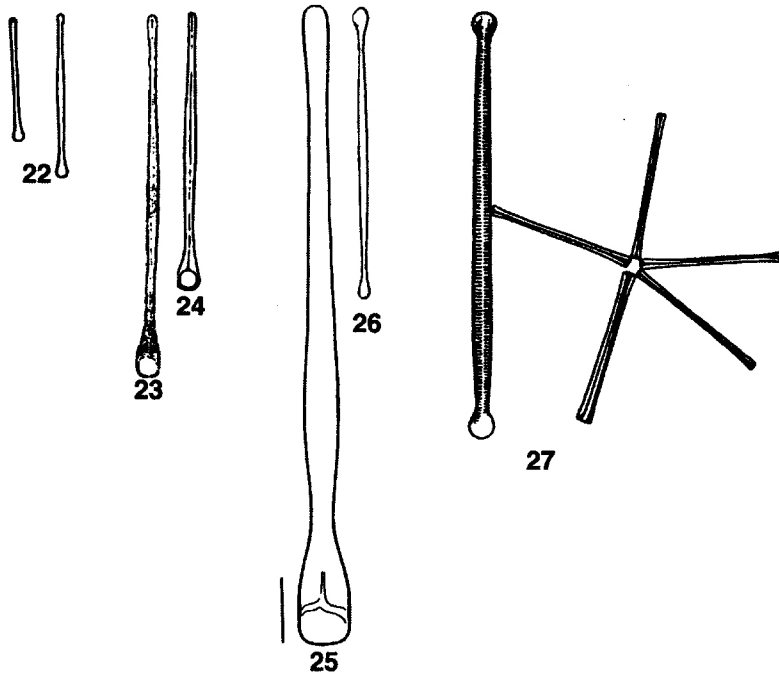


Fig. 22. *Asterionella bleakeleyi* in valve view illustrated in Peragallo & Peragallo 1897-1908, p. 322, Pl. 81, Fig. 11, 2 illustrations. **Fig. 23.** *Asterionella notata* in valve view illustrated in Van Heurck 1880-1885, Pl. 52, Fig. 3. **Fig. 24.** *Asterionella notata* in valve view illustrated in Peragallo & Peragallo 1897-1908, pp. 322-323, Pl. 81, Fig. 12. **Fig. 25.** *Asterionella notata* in valve view illustrated in Körner 1970, pp. 640-652, Fig. 42. **Fig. 26.** *Asterionella formosa* var. *gracillima* in valve view illustrated in Van Heurck 1880-1885, p. 155, Pl. 51, Fig. 22. **Fig. 27.** *Asterionella gracillima* in valve and girdle view illustrated in Huber-Pestalozzi 1942, p. 446, Pl. 133, Figs 532a and b.

1880-1885, Huber-Pestalozzi 1942, Cleve-Euler 1953, and Patrick & Reimer 1966 (Figs. 26-29)). According to Patrick & Reimer (1966), *A. formosa* var. *gracillima* occurs commonly in the winter. In an early study of southern Lake Michigan, identification of *A. gracillima* was uncertain since that taxon was so rare (Stoermer & Kopczynska 1967). In a later Lake Michigan study, *A. gracillima* was also found to be rare (Stoermer & Yang 1969). Stoermer & Yang (1969) conclude that from their observations of natural populations, this taxon is not a growth form of *A. formosa*. This taxon has been reported from waters of all pH ranges except for the most alkaline waters (Lowe 1974, Beaver 1981).

Even as early as 1967, *Asterionella* was considered to be under revision (Stoermer 1967). Körner (1970) in his revision studied freshwater forms *A. formosa* Hassall and *A. ralfsii* W.Sm. as

well as marine forms *A. notata* Grunow, *A. glacialis* Castrac. (syn. *A. japonica* Cleve), and *A. kariana* Grunow. However, Körner (1970) did not separate taxa at the generic level, despite morphological differences. *Asterionella glacialis* and *A. kariana* have since been transferred to the genus *Asterionellopsis* (Round *et al.* 1990). Subsequently, *Asterionellopsis kariana* has been transferred to the genus *Asteroplanus* based on fine structure (Crawford & Gardner 1997). According to Körner (1970), *Asterionella notata* had been considered to be a morphologically intergrading taxon between the freshwater and marine forms. New taxa described by Körner were *A. ralfsii* var. *hustedtiana*, *A. ralfsii* var. *americana*, and *A. notata* var. *reticostata*. In addition, the validity of other taxa included in the genus *Asterionella* was examined by him.

Of the freshwater forms, Körner (1970) described three valve types of *Asterionella*. The

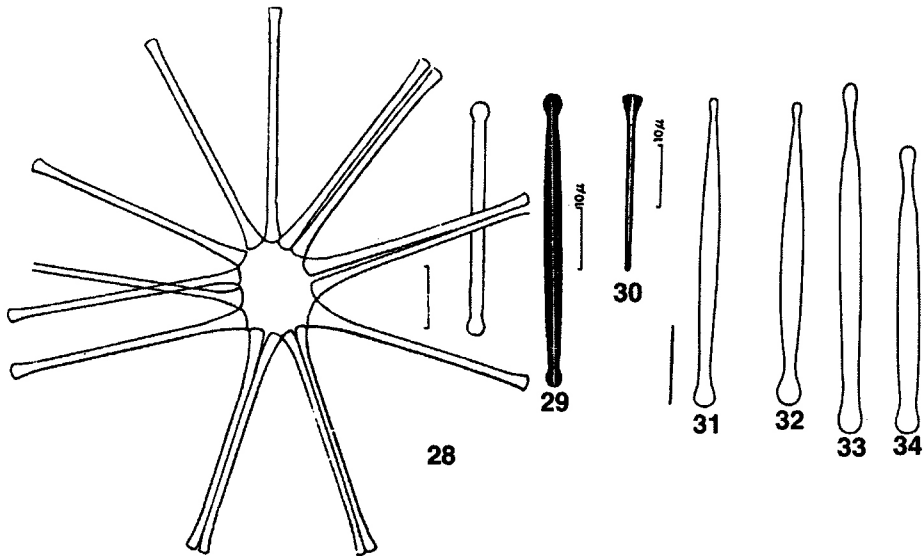


Fig. 28. *Asterionella gracillima* in valve and girdle view illustrated in Cleve-Euler 1953, p. 155, Figs 401Ba-b. **Fig. 29.** *Asterionella formosa* var. *gracillima* in valve view illustrated in Patrick & Reimer 1966, p. 159, Pl. 9, Fig. 4. **Fig. 30.** *Asterionella ralfsii* in valve view illustrated in Patrick & Reimer 1966, p. 160, Pl. 9, Fig. 5. **Fig. 31.** *Asterionella ralfsii* in valve view illustrated in Körner 1970, pp. 601-610, Fig. 20. **Fig. 32.** *Asterionella ralfsii* in valve view illustrated in Körner 1970, pp. 601-610, Fig. 21. **Fig. 33.** *Asterionella ralfsii* in valve view illustrated in Körner 1970, pp. 601-610, Fig. 24. **Fig. 34.** *Asterionella ralfsii* in valve view illustrated in Körner 1970, pp. 601-610, Fig. 25.

first represents valves having large pyriform footpoles, mid-valve region not expanded or contracted, headpole small and circular, and in girdle view the footpole has angular corners. When in colonial form, cells join at the footpoles in a stellate fashion. *A. formosa* belongs to this group (Körner 1970).

The second represents valve views with rounded or somewhat pyriform equal foot and head poles and is rarely constricted in the middle. In girdle view, small spines are present at the foot pole. Cells are not joined at the flat edges when in colonies. Colonies are partially helical and zig-zag such as *A. gracillima sensu* Hustedt (Körner 1970).

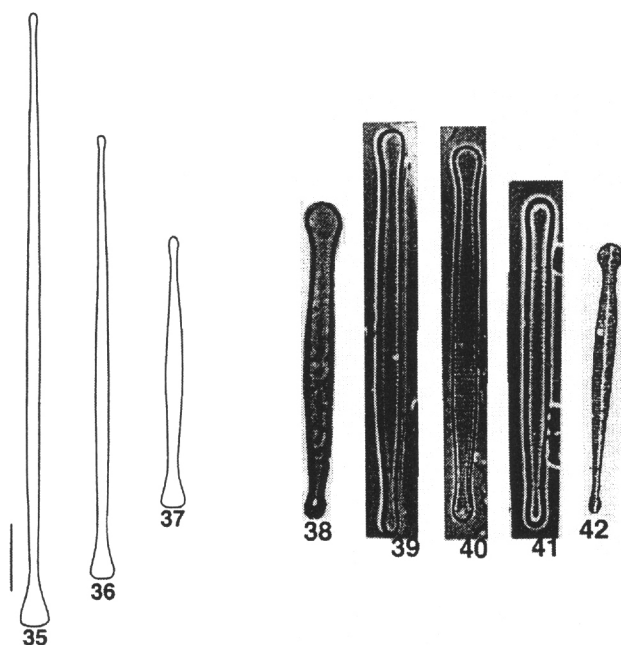
The third represents valve view with approximately equal-size ends which are somewhat twisted along the apical axis. The mid-valve region is constricted. In girdle view, foot pole edges have small spines. Colonies are helical and zig-zag and include *A. gracillima sensu* Heiberg (Körner 1970). Körner (1970) concluded from observations of specimens in culture that *A.*

gracillima was a growth form of *A. formosa*.

Asterionella ralfsii W.Sm. prefers low pH waters and dystrophic conditions (Patrick & Reimer 1966). This taxon is distinguished from other members of *Asterionella* by its small size range, 20-50 μm , and the shape of its valve (Patrick & Reimer 1966, Körner 1970). In fact, *A. ralfsii* valve shape is depicted in various ways (Patrick & Reimer 1966, Körner 1970, Krammer & Lange-Bertalot 1991, Sims 1996 (Figs 30-42)). *Asterionella ralfsii* has been found only extremely rarely in the Great Lakes (Stoermer *et al.* 1999).

Valve shape variation

Diatom valve shape variation occurs as a result of at least two processes. One process is size diminution during the vegetatively reproductive part of the diatom life cycle (Geitler 1932). As daughter cells are produced from mother cells, valve shape is slightly changed. As cell division continues, valve shape tends to converge on a more ovoid form, thereby producing shape variation within a species (Mann 1999). Size re-



- Fig. 35.** *Asterionella ralfsii* in valve view illustrated in Körner 1970, pp. 601-610, Fig. 29.
Fig. 36. *Asterionella ralfsii* in valve view illustrated in Körner 1970, pp. 601-610, Fig. 30.
Fig. 37. *Asterionella ralfsii* in valve view illustrated in Körner 1970, pp. 601-610, Fig. 31.
Fig. 38. Light micrographs of *A. ralfsii* in valve view in Krammer & Lange-Bertalot 1991, p. 103, Pl. 104, Fig. 4. **Fig. 39.** Light micrographs of *A. ralfsii* in valve view in Krammer & Lange-Bertalot 1991, p. 103, Pl. 104, Fig. 5. **Fig. 40.** Light micrographs of *A. ralfsii* in valve view in Krammer & Lange-Bertalot 1991, p. 103, Pl. 104, Fig. 6. **Fig. 41.** Light micrographs of *A. ralfsii* in valve view in Krammer & Lange-Bertalot 1991, p. 103, Pl. 104, Fig. 7. **Fig. 42.** *Asterionella ralfsii* in valve view illustrated in Sims 1996, Barber & Carter's illustrations, p. 72, Pl. 28, Fig. 3.

duction occurs in *Asterionella* cultures (Happy-Wood & Hughes 1980). Misshapen or aberrant forms rarely occur in nature, but do occur in culture (Round *et al.* 1990). An almost oval valve shape from size reduction has been observed in cultures of *A. formosa* (Körner 1970, Jaworski *et al.* 1988).

Sometimes, size reduction was not observed to occur. Some populations of *A. formosa* seem to maintain a constant size, such as *A. formosa* "var. *hypolimnetica*," in contrast to other populations such as *A. gracillima* (Mann 1988). *Asterionella gracillima* has a very long life cycle with size reduction at 2 μm per year in Danish lakes (Mann 1988). Auxosporulation has not been observed in *Asterionella* (Mann 1988). For some species, *Asterionella* size ranges (e.g., Patrick & Reimer 1966) include smallest specimens approximately 30 to 40% of the maximum size.

This suggests that size restoration via sexual reproduction does occur (Edlund & Stoermer 1997), if optimum environmental conditions are present. Mann (1988) has speculated that the life cycle of *Asterionella* is 2-40 years, but sexual reproductive activity may last only a few weeks. According to Mann (1988), this may explain the lack of observed auxosporulation in *Asterionella* species.

The second process involves environmental influences on valve shape (Edlund & Stoermer 1997). Environmental changes are evident in phenotypic plasticity of the cell (Mann 1999). As already discussed, *Asterionella* species are generally described as cosmopolitan, able to tolerate wide ranging conditions (Patrick & Reimer 1966, Lowe 1974, Beaver 1981).

Asterionella ralfsii is especially tolerant of low pH (Patrick & Reimer 1966). In an acidified en-

vironment with aluminum present and at higher growth rates, *A. ralsii* var. *americana* cells become more heavily silicified (Gensemer 1990). At higher aluminum levels, smaller cells increase in number, and higher growth rates occur with increasing rates in size reduction (Gensemer 1990).

In freshwater habitats such as the Great Lakes, cold water forms are generally found to be long specimens. Vegetative reproduction must occur slowly since smaller specimens are rarely found. At colder temperatures, diatoms may be more heavily silicified (Edlund 1992). Low light intensities and low levels of total dissolved solids produce conditions apparently favoring the presence of more heavily silicified cells (Edlund 1992).

Silica availability also affects *Asterionella* valve shape (Lund 1962, Schelske & Stoermer 1971, Lund & Reynolds 1982). In freshwater habitats where silica is depleted, smaller, more finely silicified cells are found (Edlund 1992). During silica limitation, degree of silicification may induce polymorphic forms. Changes in valve shape are gradual in response to gradual changes in silica levels (Mann 1999).

Degree of silicification probably affects valve shape by influencing growth rate and consequent size reduction (Mann 1999). Silica uptake by diatoms occurs at the amount required for frustule formation just before cell wall formation and cell division (Edlund 1992). Larger cells are more heavily silicified than smaller cells in response to silica levels when reproductive rate is high (Theriot 1987, Edlund 1992). That is, variation in silicification is related to cell size (Theriot 1987). Rapid size reduction in *A. formosa* may occur in response to silica limitation and excess phosphorus (Kling 1993). Silica levels also affect the number of cells per colony and colony morphology in *Asterionella* (Kilham, 1975, Tilman *et al.* 1976, Holm & Armstrong 1981, Jaworski *et al.* 1988).

Cell wall flexibility is affected by degree of silicification (Mann 1994). Changes in salinity affect turgor pressure which affects valve shape (Mann 1999). In response to salinity, brackish water forms may exhibit polymorphism and less silicification (Edlund 1992). However, valve shape integrity is maintained within a narrow limit. This occurs because the silica cell walls must be able

to withstand turgor pressure despite physical and chemical fluctuations in the environment (Mann 1988, 1999). Environmental changes may affect valve shape changes during the life cycle in a gradual manner (Mann 1994, 1999).

Genetic diversity in *A. formosa* (Soudek & Robinson 1983) may be accompanied by morphological and ecological differences as well as reproductive isolation. Individual groups may deserve recognition as separate species (Mann 1999). Genetic differences in *A. formosa* between lakes may produce distinct populations in approximately 100 years (Soudek & Robinson 1983). A high frequency of diatom endemism exists in ancient habitats; time and isolation appear to promote endemism (Mann 1999).

Directions in diatom classification

In the past few years, there has been a proliferation in the number of diatom genera (Round *et al.* 1990). Splitting at the generic level has occurred largely based on gross valve morphology but increasingly on valve cytoplasmic ultrastructure and cytology. This is evident by the genera *Asterionella*, *Bleakeleya*, *Asterionellopsis*, and *Asteroplanus* which used to be conscribed to *Asterionella*. The category "genus" is supposed to be broad enough to include similar taxa, species, but narrow enough to exclude entities with obvious morphological differences (Round *et al.* 1990).

The number of diatom species has increased as well. The number of species has almost certainly been underestimated (Mann 1999). Valve morphology, symmetry, and complexity are used as distinguishing features. Increasingly, other modes of evidence are used in this realm of taxonomic decision-making including cytological, physiological, molecular, and genetic. Estimates for the number of diatom species may be as much as 10^5 or 10^6 (Round *et al.* 1990, Mann 1994, 1999). *Asterionella* is one of many diatom genera in need of revision.

Results from application of quantitative methods

In some diatom studies, application of quantitative methods has been useful in discerning shape variation within a genus (e.g., Stoermer & Ladewski 1982) as well as variation between groups (e.g., Stoermer *et al.* 1984, Theriot &

Ladewski 1986). Using quantitative methods requires two steps. First, valve outline must be quantified. Second, numerical values from valve outline analysis must be used as data to determine the extent of shape variation among all specimens.

To accomplish the first task, valve shape of each specimen is represented by orthogonal polynomial coefficients calculated from Legendre polynomial expansion (e.g., Farrell & Ross 1963) or Fourier expansion (e.g., Zahn & Roskies 1972). To determine shape groups, principal components analysis (PCA (e.g., Cooley & Lohnes 1971, Green & Carroll 1978)), among other multivariate statistical methods, has been used (e.g., Stoermer *et al.* 1986). Sometimes, distinct shape groups with crisp boundaries were not determined. Rather, highly overlapping groups were evident (e.g., Steinman & Ladewski 1987) or little shape differentiation was found (e.g., Goldman *et al.* 1990).

Some differentiation of shape groups was found to be related to geographic isolation (e.g., Stoermer *et al.* 1986). Shape variation between groups was only found in the most general way (e.g., Stoermer *et al.* 1984, Mou & Stoermer 1990). That is, comparison of type specimens to a population of specimens (e.g., Theriot & Ladewski 1986) or comparison of modern and fossil specimens quasi-shape groups were determined (e.g., Stoermer & Ladewski 1982). Sometimes results from PCA were explainable on one component, but not on others (e.g., Stoermer & Ladewski 1982). Sometimes interpretation of results were clouded by uncertainties regarding size diminution for a single taxon or overlapping size ranges for a species complex (Steinman & Ladewski 1987). Comparisons between results from shape analysis and visual inspection were made, and agreement was not always evident (Stoermer & Ladewski 1982).

For *Asterionella*, we calculated Fourier shape coefficients for specimens from the Great Lakes, and we differentiated shape groups by PCA and specimen membership tested using fuzzy measures (Wang & Klir 1992) in classification integration (Sugeno 1977) based on fuzzy set theory (e.g., Zadeh 1978, Dubois & Prade 1980, Novák 1989, Zimmerman 1991). Ninety-six specimens were used in which seven shape groups were

identified (Pappas 2000). The first three shape groups were distinct from the next three. The seventh shape group was unlike all other specimens, in that the head pole is extremely asymmetrical. There was some similarity among proximal shape groups in PCA shape space. These shape groups overlapped to different degrees, determined by fuzzy analysis. In no case was shape group overlap greater than 60% (Pappas 2000). Except for two specimens, membership in each shape group was greater than 60% (Pappas 2000). Each shape group is sufficiently distinct, and these groups may represent taxonomically different entities.

The first shape group has wedged-shaped head and foot poles. The second shape group had similarly shaped head and foot poles, but these are slightly more rounded. The third shape group had rounded head and foot poles, where the head pole was smaller than that for the first two shape groups. In contrast to the first three shape groups, the fourth shape group has rounded head poles with a nearly uninflated foot pole. The fifth shape group has rounded head and foot poles, where the valve width throughout is much greater than that for any other shape group. This shape group does not overlap with the third shape group. The sixth shape group is somewhat similar to the fifth shape group except for a much more narrow valve width. Specimens of similar size have been described here to negate the complication of comparing different life cycle stages (Pappas 2000).

Shape and form in diatoms is an ontogenic property. During vegetative reproduction, shape is an inherited property by daughter cells from the mother cell (Mann 1994). During auxosporulation, shape is restored *de novo* (Mann 1994). One distinct valve shape cannot change into another distinct valve shape implying different shaped valves belong to different species groups. Most of the current subdividing of genera has been based on differences in shape and symmetry (Round *et al.* 1990, Mann 1994).

History of *Asterionella* taxonomy reveals that little work has been performed in the naming process at the species level. Much confusion still exists with regard to species designations versus varietal designations. The scant literature refer-

ences to and descriptions of taxa in this genus as well as the lack of existence of type specimens except the designated neotype of *A. formosa* (Körner 1970) adds to the vagueness of *Asterionella* taxonomy.

It is evident that much more work is necessary to adequately describe the extent of variation in *Asterionella*. The potential to determine differences is enhanced by using quantitative methods. Such methods are necessary to augment the difficulties encountered when trying to study taxonomically sketchy and character-poor taxa such as *Asterionella*.

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