

***Aulacoseira subborealis* stat. nov. (Bacillariophyceae):
a common but neglected plankton diatom**

by

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With 30 figures and 1 table

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Abstract: *Aulacoseira subarctica* f. *subborealis* differs from *A. subarctica* var. *subarctica* by a number of morphological features (smaller linking spines without areolae on their base, shorter spine grooves, discus always areolated, shallower mantle and different 'Formwechsel', considerably finer structure, rimoportula on the inner side of the pseudoseptum), as well as its ecological preferences. It is therefore considered to represent a separate species: *A. subborealis* stat. nov. Characteristics that differ from those of the similar species, *A. alpigena*, include the non-spathulate linking spines, each one originating from two peralvar ribs, more numerous areolae on the disci, smaller dimensions, finer areolation of the mantle and, in the LM, absence of more marked mantle areolae next to the collum. In the LM, confusion may further arise with *A. laevissima*, *A. distans* or *A. nygaardii*, which also show some resemblance to *A. subborealis*. *Aulacoseira subborealis* is widely distributed in rivers and lakes in W-Europe and Australia, and presumably occurs in New Zealand and North America as well, but has been reported only rarely because of confusion with other taxa. It appears to develop especially well in more alkaline and rather eutrophic, highly turbid fresh water. Yet, this planktonic species is unable to withstand extremely severe eutrophication or pollution.

Key words: diatoms, *Aulacoseira*, morphology, taxonomy, eutrophication, plankton.

Introduction

Aulacoseira species are important diatoms in a range of freshwater systems throughout the world. They often attain high biomass in eutrophic rivers (e.g. Hotzel & Croome 1996; Yang et al. 1997) and lakes (e.g. Haberyan 1985; Håkansson 1989; Donar et al. 1996), but are also an important component of the diatom communities in oligotrophic waters (e.g. Petrova 1986; Haworth et al. 1988; van Dam & Mertens 1995; Hall & Smol 1996). Because the dominant *Aulacoseira* species vary with lake trophic status, they are particularly useful indicator organisms in actuo-ecological and palaeolimnological studies (e.g. Lepistö 1990; Sabater & Haworth 1995; Donar et al. 1996; Bradbury & Van Metre 1997; Kling 1998; Meriläinen et al. 2000). Obviously, this requires a firm taxonomic basis, which has not yet been attained for all known members of the genus in spite of several detailed studies (e.g. Florin 1981; Camburn & Kingston 1986; Haworth 1988; Krammer 1991a, 1991b; Siver & Kling 1997; Crawford & Likoshway 1999; Likoshway & Crawford 2001).

Aulacoseira subarctica (O. Müller) Haworth f. *subborealis* (Nygaard) Haworth, described originally by Nygaard (1956) as *Melosira italica* Ehrenberg var. *subborealis* Nygaard from the sediments of Lake Gribssø, is one of those taxa that have remained in relative obscurity. Haworth (1988) recombined the taxon as a form of *Aulacoseira subarctica*, arguing that its basic morphology agrees entirely with that of *A. subarctica* var. *subarctica*, and that only differences in size and spine length are observed. Krammer & Lange-Bertalot (1991a) consider *A. subarctica* f. *subborealis* as insufficiently described and provide no clues to its identification. Other literature reports also indicate that its status is in need of further clarification. Stevenson et al. (1991), for instance, did not differentiate *A. subarctica* f. *subborealis* from *A. subarctica* in their data set, due to the apparent lack of clear morphological criteria. Turkia & Lepistö (1999) mention this *Aulacoseira* from a lake in Finland, but indicate that the diatom they found in sediment material may actually be the same as the one they identified as *A. distans* var. *alpigena* (Grunow) Simonsen in phytoplankton collections.

Positive identifications of *Aulacoseira subarctica* f. *subborealis* are mostly from Scandinavia, and especially from core material. In addition to Nygaard (1956), Renberg (1976, 1978), reports the taxon in lake stratigraphies from northern Sweden. Outside Scandinavia, Haworth (1988) mentions its occurrence in a Scottish lake (re-identified material from Pennington et al. 1972), and in samples from Michigan and New Zealand lakes. Jones et al. (1997) present a diatom diagram from Loch Ness sediments featuring '*Aulacoseira subborealis*' (sic). As *Aulacoseira subarctica* type 2, Anderson & Korsman (1990), Anderson et al. (1997) and Rosén et al. (2000) indicate its wider distribution in central and northern Sweden, whereas Sorvari & Korhola (1998) recorded it in the sediments of a Finnish lake.

Recent observations by the authors indicate that *Aulacoseira subarctica* f. *subborealis* can be an important phytoplankton diatom in W-European rivers and lakes, and that it is also widely distributed elsewhere. This suggests that *A. subarctica* f. *subborealis* often remains unidentified or is mistaken for other taxa, due to identification problems and its absence in standard reference works. In order to prevent further confusion, we present a detailed morphological study of this taxon based on collections from different localities to address the range of frustular variation, and discuss relationships with neighbouring or similar taxa. The results of this study provide arguments for a reassessment of *A. subarctica* f. *subborealis* as a distinct species. Furthermore, an overview of the distribution and ecology of this diatom is given by means of published and new observations.

Material and methods

Nygaard (1956) indicates that *Melosira italica* var. *subborealis* occurs in the Subboreal sediments of Stora Gribsø (Denmark, Hillerød) between levels VII-IXa, corresponding to the samples 79 and 85. Type material is absent in the Nygaard collection, kept in the Botanical Museum, University of Copenhagen, as well as in the V. Mikkelsen legacy at the Department of Ecology in the Veterinary and Agricultural University, Copenhagen. At present we assume that no type material is available. However, in view of articles 8.3 and 8.4 of the Botanical Code (Greuter et al. 2000), figures 13-19 on plate 2 of the protologue (Nygaard 1956), representing specimens from sample 85, can be considered as the icono-lectotype validating this taxon. This series of transmission electron micrographs shows the major valve characteristics allowing discrimination against other *Aulacoseira* species.

Morphological observations on material identified as *Aulacoseira subarctica* f. *subborealis* presented in this paper were made on a sediment-core sample taken in the Blankaart Reservoir (Woumen, Belgium), samples of surface sediment from several ponds in Flanders, Belgium (L. Denys), recent phytoplankton and surface-sediment collections from the rivers Schelde (Belgium; K. Muylaert), Maas and Rijn (The Netherlands; T. Joosten), lakes in the the French Massif Central (P. Rioual), a lake at Asserbos (Assen, The Netherlands; T. Joosten) and billabongs and reservoirs in the River Murray Basin (south-east Australia; M. Reid).

Samples were cleaned with concentrated hydrogen peroxide or sulphuric acid. Cleaned residue was mounted in water, Naphrax or Hyrax, and observed with Leitz Orthoplan and Zeiss Universal light microscopes (LM), using interference contrast. For scanning electron microscopy (SEM) Philips SEM 515, JEOL JSM-840 and JEOL JSM-5600 LV microscopes were used. Nomenclature and most of the terminology follow Krammer & Lange-Bertalot (1986, 1988, 1991a, 1991b) and Krammer (1991a, 1991b). Following Haworth (1988), ring ledge ('Ringleiste') and pseudoseptum are considered synonyms.

Observations

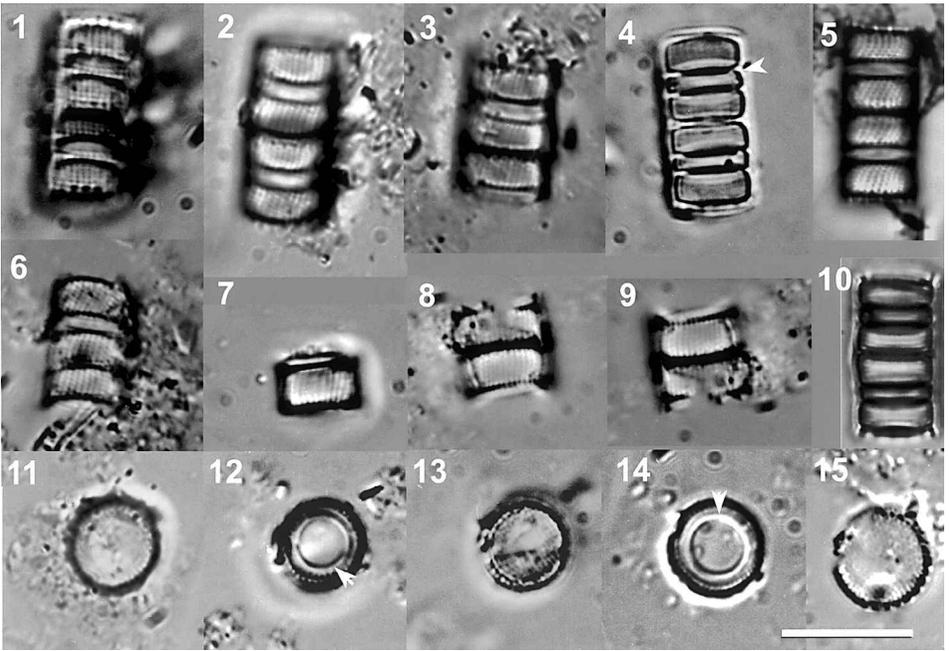
Aulacoseira subborealis (Nygaard) Denys, Muylaert & Krammer stat. nov.

Basionym: *Melosira italica* Ehrenberg var. *subborealis* Nygaard 1956 in *Folia Limnologica Scandinavica* 8, p. 74, plate 1, fig. 8, plate 2, figs 13-19 (icono-lectotype), plate 6, figs 24-25.

Synonym: *Aulacoseira subarctica* (O. Müller) Haworth f. *subborealis* (Nygaard) Haworth (Haworth 1988; Haworth 1990). Also reported as *A. italica* subsp. *subarctica* type II, *A. subarctica* type 2 (Anderson & Korsman 1990; Stevenson et al. 1991; Anderson et al. 1997; Weckström et al. 1997; Sorvari & Korhola 1998; Rosén et al. 2000) and *Aulacoseira subborealis* (sic, Jones et al. 1997).

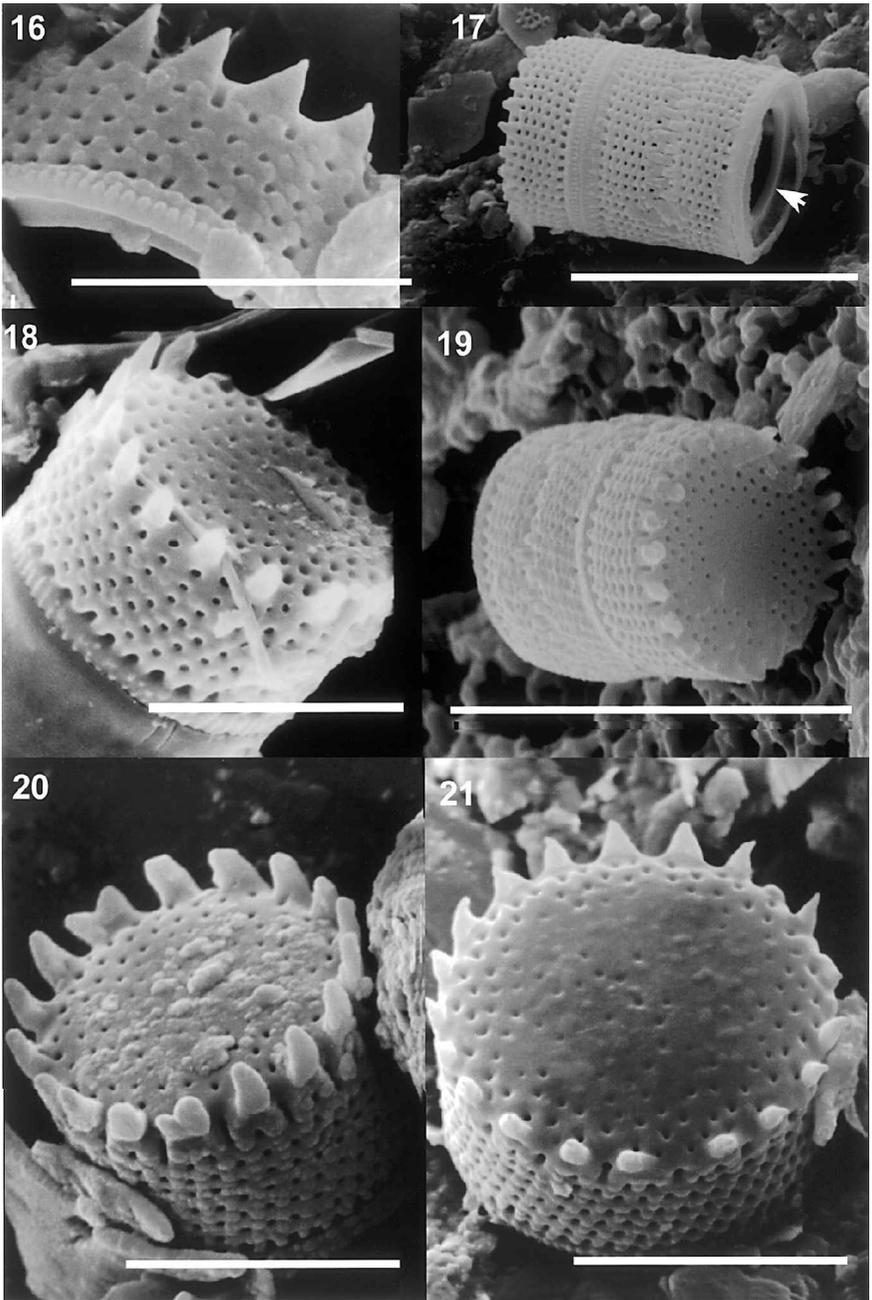
VALVE MORPHOLOGY (Pl. I-III, Figs 1-27, Table 1)

Only vegetative cells, often still in short filaments of 2 to 4 cells, are observed. Their frustules are cylindrical and measure ca. 5.5 to 9.0 μm in diameter (mostly 6-7 μm) and are about 2 to 4 μm high (Figs 1-10). The ratio between mantle height and diameter varies from 0.39 to 0.55, increasing with size. Some variation is observed in the degree of silicification of the frustule. The inner and outer sides of the mantle are slightly convex; both being parallel to each other. At its edge with the valve face, the mantle is more or less rounded off. The so-called 'pseudosulcus' – an optical delusion on the mantle at the position of the pseudoseptum, caused by light refraction – appears shallow, 'opening' with an angle of about 30° (Fig. 4). The solid pseudoseptum is about 1.0-1.5 μm wide (Figs 4, 12, 14). The ratio between pseudoseptum width and valve diameter is fairly constant (0.23-0.25). The pseudoseptum bears a reinforced inner rim (Figs 17, 23-24, 27), making it almost T-shaped in section. This rim is also conspicuous in the LM (Figs 12, 14). The collum is only ca. 0.5 to 1.0 μm high; the ratio between its height and the rest of the mantle varies from 0.20 to 0.43. In the SEM its regular surface ornamentation with low and closely spaced transverse ridges, often partly reduced to small warts, becomes apparent (Figs 16-22, 24). The areolae on the mantle are fairly distinct and appear as more or less round in the LM. The SEM observations confirm this shape (Figs 16-22). Their density amounts to ca. 35 to 40 in 10 μm . The pervalvar rows of areolae, 23.5 to 28.0 in 10 μm , are generally somewhat inclined (sinistrorse and up to ca. 20°) and curved, but may sometimes be almost straight and parallel to the pervalvar axis. In the LM all the mantle areolae appear equally large. With the SEM, however, it can be seen that those adjacent to the sulcus are somewhat enlarged (Figs 18, 22). The pervalvar ribs bear low, rounded knobs, one at each crossing with a connecting rib, so that each areola is surrounded by four knobs (Figs 16, 18-22). The spines are rather small, but distinct in the LM. Their density amounts to ca. 12-14 in 10 μm . The spines, which all appear to be of the same type, do not appear to be completely straight, even when cells have not yet been separated, but are slightly curved inwards. They are pointed, tapering from the base, and without anchors or projections (Figs 16, 18-22). Occasionally, their base appears to be somewhat broadened (Fig 16), but this largely depends on the viewpoint, as illustrated by Fig. 21. The spines are about 2.5 times as long as wide, giving them a rather stout appearance. Their length does not exceed ca. 1.2 μm . SEM observations show that they emanate from two pervalvar ribs, a feature also discernable in the LM. In material from the Murray river billabongs, spines emerging from 3 or 4 pervalvar ribs were sometimes observed, in

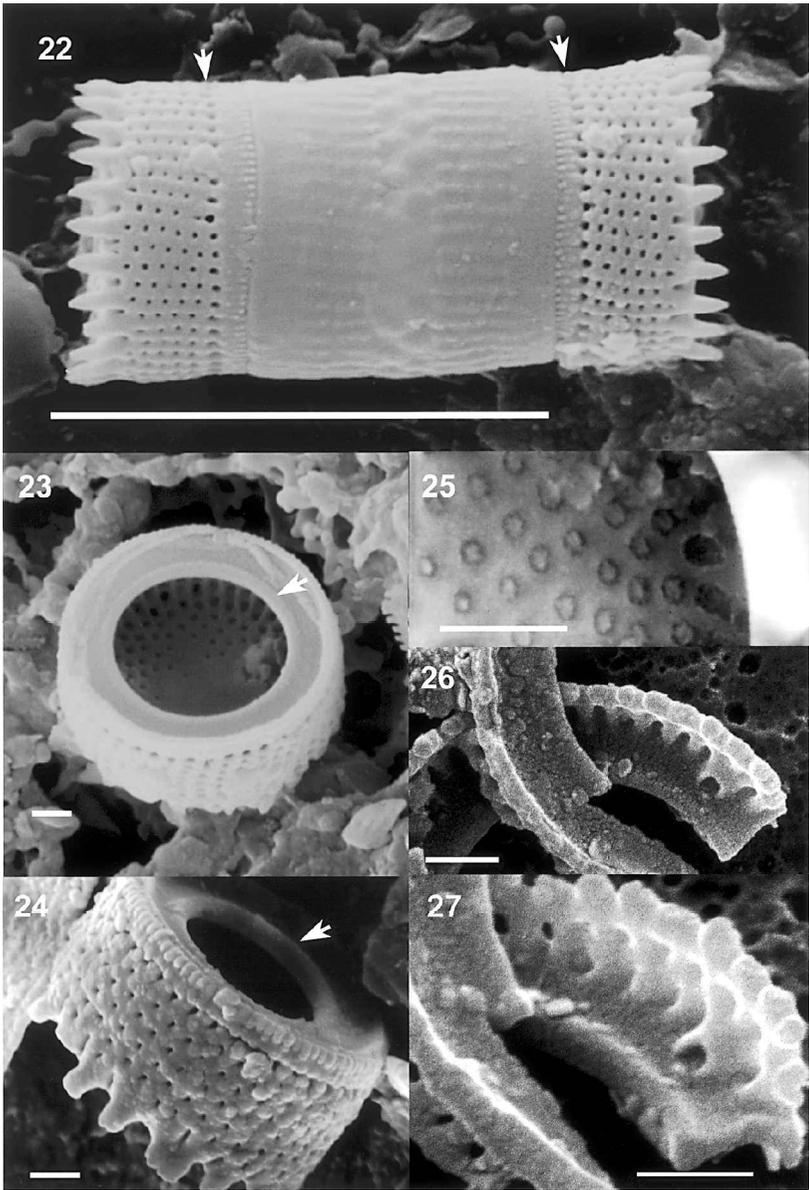


Pl. I: Figs 1-15. *Aulacoseira subborealis*, material from Blankaart (Figs 1-4, 6-9, 11-15) and Asserbos (Figs 5, 10) (LM). Figs 1-10: Mantle views at different focus in the LM. Arrow indicates pseudosulcus in Fig. 4. Figs 11-15: Valve face views at different focus in the LM. Arrow indicates thickened rim of pseudoseptum in Figs 12, 14. Scale bar = 10 μm .

which case the spines were bifurcated (Figs 20, 24). Only exceptionally, a small and rounded areola occurs on the base of a spine (Fig. 24). Between the spines, short spine grooves are present (Figs 16, 20-22). Pervalvar rows of areolae end both at the base of each spine and in the spine grooves. The external valve surface bears no rugosities and is flat or very slightly sunken in the middle (Figs 18-19). Fine areolae are present on the entire valve face, where they are often placed in a more or less radial pattern in continuation of the rows of areolae on the mantle. In some valves the areolae are occluded ('blind') towards the exterior or, altogether, lacking in the central part of the discus, in which case only a broad marginal zone is fully areolated (Figs 19, 21, 23). The areolae become progressively smaller towards the centre. The areolae appear to be closed by simple rotae (see Round et al. 1990), slightly sunken beneath the internal valve surface and with about 5 supporting ribs (Fig. 25). However, technical limitations may have obscured their actual structure, and more detailed observations are necessary for confirmation. The rimoportula is situated at the base of a row of areolae on the inner side of the pseudoseptum, with which it is merged (Figs 26-27). It is directed perpendicular to the mantle, quite stout (slightly less than 0.5 μm wide) and extends halfway the pseudoseptum. The external opening is inconspicuous and probably represented by or associated with an areola. The exact number of rimoportulae could not be established but appears to be low.



Pl. II: Figs 16-21. *Aulacoseira subborealis*, material from Blankaart (Figs 17, 19), Asserbos (Fig. 18), Murray billabong (Fig. 20) and Schelde estuary (Figs 16, 21) (SEM). Figs 16-17: Mantle views. Arrow indicates thickened rim of pseudoseptum in Fig. 17. Figs 18-21: Oblique views showing the external valve face. Scale bars 5 (Figs 16, 18-21) or 10 μ m (Fig. 17).



Pl. III: Figs 22-27. *Aulacoseira subborealis*, material from Blankaart (Figs 22-23), Murray billabong (Fig. 24), Schelde estuary (Fig. 25) and Groenendaal, Belgium (Figs 26-27) (SEM). Fig. 22. Mantle view of two frustules with cingulum. Arrows mark rows of slightly larger areolae. Figs 23-24: Oblique views showing part of the valve interior. Note the reinforced rim of the pseudoseptum (arrows). Fig. 25. Detail of the areolae seen from the interior. Figs 27-28. Interior of broken valve showing rimoportula and section of the pseudoseptum. Scale bars 10 μm (Fig. 22) or 1 μm (Figs 23-27).

Table 1: Characteristics of *Aulacoseira subborealis* and some similar species (vegetative cells; from literature data and own observations).

	<i>A. subborealis</i> (own observations)	<i>A. subborealis</i> (protologue)	<i>A. subarctica</i>	<i>A. alpigena</i>	<i>A. laevissima</i>	<i>A. nygaardii</i>	<i>A. distans</i>
mantle height (µm)	2.5-4.0	2.6-3.7	2.5-18.0	4-7	5-10	4-19	3.5-8.5
diameter (µm)	5.5-9.0	4-7	3-15	4-15	6-17	5-11	4-20
mantle height/diameter	0.39-0.55	0.45-0.75	0.55-4.10	0.35->1	0.38-0.69	0.56-1.07	0.3-1.6
perivalvar striae/10 µm	23.5-28.0	20-26	17-21	15-22	22-28	20-22	10-16
prevalent orientation	± inclined	inclined	inclined	inclined	± inclined	not inclined	not inclined
perivalvar striae							
mantle areolae/10 µm	28-38	25-31	17-22	15-22	23-30	25-30	13-22
height collum/areolated mantle	0.20-0.43	0.20-0.25	0.12-0.18	0.23-0.50	0.33-0.57	0.29-0.60	0.27-0.50
mantle sides	convex	variable?	straight	convex	convex	slightly convex	convex
spine type	simple, fairly stout	simple, fairly stout	simple, slender	spathulate, anchors	small anchors	?	simple, short
perivalvar ribs at spine base	2	2	2	1, or spines and ribs alternating	1	?; 1 spine/2-3 perivalvar striae	1
areolae on valve face	over entire surface or broad marginal zone	over entire surface	none, over entire surface or broad marginal zone	1-2 marginal rows	over entire surface	marginal zone of < 1 µm wide	over entire surface

In material from the Lac Chauvet (Massif Central, France) and Lac Gerardmer (Vosges, France) a morphologically very similar diatom occurs (observations P. Rioual), which appears to differ only by a slightly larger diameter (8-10 μm) and coarser areolation (ca. 20 striae in 10 μm). The specimen illustrated by Krammer (1991a, fig. 28) from Gerardmer most probably corresponds to this form as well. Typical more delicate *Aulacoseira subborealis* is also present in Lac Chauvet, without intergradation between both. This larger morphotype requires further examination to establish its relations to *A. subborealis* and *A. subarctica*. The short spines, however, rather suggest that it is closer to the former.

Occurrence

Sediment records

On the basis of the inferred pH values for the period of maximum development and subsequent waning in the Holocene record from Lake Gribbsø, *A. subborealis* was provisionally classified as alkaliphilous by Nygaard (1956). The high abundances of the species in the post-isolation phases of Lake Prästsjön and Lake Rudetjärn observed by Renberg (1976, 1978) also point to a preference for alkaline and relatively nutrient-rich conditions. Conversely, Lake Saanajärvi is neutral, very dilute and extremely nutrient-poor (TP 3-5 $\mu\text{g.l}^{-1}$; Sorvari & Korhola 1998). Anderson et al. (1997) report high abundances of *A. subarctica* type 2 in sediments of the boreal forest lake Sjösjön, central Sweden, deposited prior to ca. 1900 when diatom-inferred pH was slightly above 6. In the ultra-oligotrophic Loch Ness it appeared only in the last few decades (Jones et al. 1997). *Aulacoseira subborealis* was also present in the early part of the recent (post-1925) sediments of Lake Culluleraie, NW Victoria, a shallow, turbid and eutrophic off-river storage basin (J. Fluin, personal communication).

A more complete picture of the trophic range of *Aulacoseira subborealis* is given by its occurrence in the sediment record of the shallow (< 2 m) Blankaart Reservoir, Belgium. This site underwent severe eutrophication and pollution in the course of the 20th century due to the inflow of untreated sewage and agricultural drainage (Denys 1994). Fig. 28 shows the relative abundance of common diatoms in the core with highest abundance of *Aulacoseira*. From 26 to 32 cm depth *Aulacoseira subborealis* attains a frequency of 0.2 to 6.8% in a transition phase from an assemblage dominated by epiphytic and epipellic diatoms (incl. *Planothidium frequentissimum* (Lange-Bertalot) Lange-Bertalot, *Cocconeis placentula* Ehrenberg, *Gomphonema micropus* Kützing, *Gyrosigma acuminatum* (Kützing) Rabenhorst and *Navicula* spp.) and small *Fragilaria* spp. (*F. brevistriata* Grunow, *F. construens* (Ehrenberg) Grunow and *F. construens* f. *venter* (Ehrenberg) Grunow) to a plankton-dominated assemblage, typical of hyper-eutrophic and polluted conditions (*Cyclotella atomus* Hustedt, *C. meneghiniana* Kützing, *Nitzschia* spp., *Stephanodiscus hantzschii* Grunow, *S. parvus* Stoermer & Håkansson, *Thalassiosira pseudonana* Hustedt). *Aulacoseira subborealis* culminates at the same level as *Cyclostephanos dubius* (Fricke) Round, a species indicating alkaline and nutrient-enriched water (Clarke 1989; van Dam et al. 1994) for which Bennion (1994) observed a TP (total phosphorus) optimum of 215 $\mu\text{g L}^{-1}$.

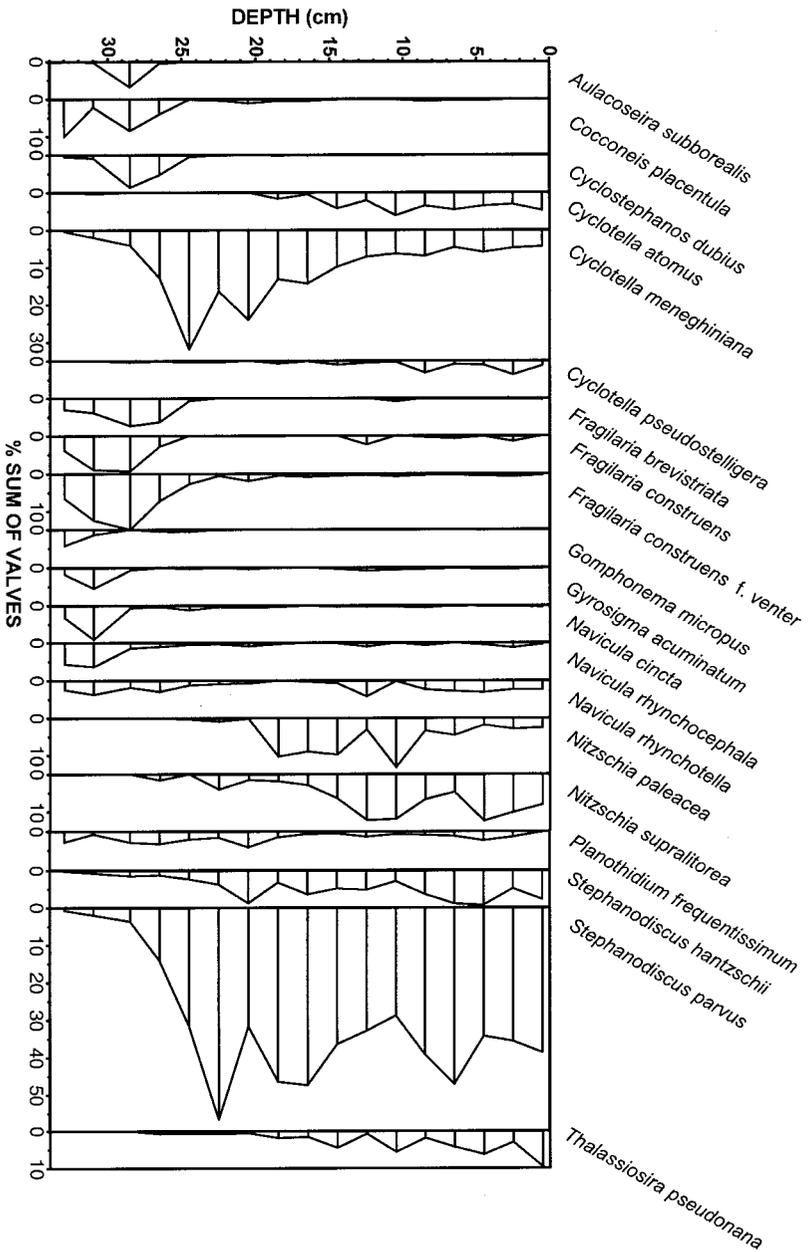


Fig. 28. Diatom diagram of Blankaart core 5 (selected taxa only; percentages are based on counts of at least 500 valves).

Recent observations

Aulacoseira subborealis is a minor constituent of the phytoplankton communities in the freshwater tidal reaches of the Schelde estuary. It was found mainly in the uppermost estuarine zone during autumn, contributing less than 1% of the total phytoplankton biomass with a maximum of 180 cells mL⁻¹. *Aulacoseira subborealis* occurred in the most upstream reaches of the Schelde estuary together with *A. granulata* (Ehrenberg) Simonsen, which contributed on average 5% to the total phytoplankton biomass and occurred in winter and from late summer to early autumn (Fig. 29). The spatial distribution of both species suggests that *A. subborealis* was imported into the estuary from the river while *A. granulata* was probably autochthonous within the estuary. The co-dominant species was *Cyclotella scaldensis* Muyaert & Sabbe whereas *Aulacoseira subarctica* was absent. In the freshwater tidal estuary, TP concentration ranges between 75 and 235 µg L⁻¹ and turbidity is very high (Secchi depth 20-40 cm and concentrations of suspended particulate matter of about 100 mg L⁻¹). In the tributaries, turbidity is lower (Secchi depth > 50 cm) while TP concentrations are comparable (average 110 µg L⁻¹; data from Muyaert et al. 1997).

In the Dutch part of the River Maas, *A. subborealis* was observed together with the closely related *A. subarctica*. Neither species was dominant. *Aulacoseira subborealis* bloomed in late summer at the most upstream station sampled (Eijsden; Fig. 30). Further downstream, it occurred in much lower numbers but densities were highest here during the same season. *Aulacoseira subarctica* was not observed at Eijsden but displayed a pronounced bloom at the more downstream station Keizersveer in spring. It was also found to be relatively abundant at Belfeld near Venlo, about halfway both other sites, around the same time. Both species were also present in the Dutch part of the River Rijn, again never as a dominant component of the phytoplankton. As in the Maas, both species displayed different optima in space and time.

In The Netherlands, *A. subborealis* was also found in several eutrophic lakes in the catchment area of the Rivers Maas and Rijn. In neighbouring Belgium, *A. subborealis* was noted in surface sediment samples from 17 eutrophic ponds and oxbow lakes, always without any trace of *A. subarctica*. In 13 of them, ranging in average pH from 6.5 to 7.9 and in average TP from 110 to 350 µg L⁻¹, it occurred within a count of 500 valves (max. 17.8%). The weighted average (WA) TP optimum calculated for these samples amounted to 210 µg L⁻¹.

In a survey of diatoms in the surface sediments of 57 billabongs in the River Murray basin, *A. subborealis* was found to be an important component of the diatom community. It occurred in 42 billabongs, contributing to more than 10% of total abundance in 24 of these, and was the most abundant species in 11. It was most common in the billabongs along the middle reaches of the Murray River, below Lake Hume, where it often occurred together with *A. granulata*, the dominant phytoplankton in this river (Hotzel & Croome 1996). The billabongs where *A. subborealis* occurred are characterised by shallow depth (< 4 m), high turbidity and very high phosphorus concentrations (mean TP concentrations from 67 to 1680 µg L⁻¹). In those billabongs which receive summer irrigation flows of the River Murray,

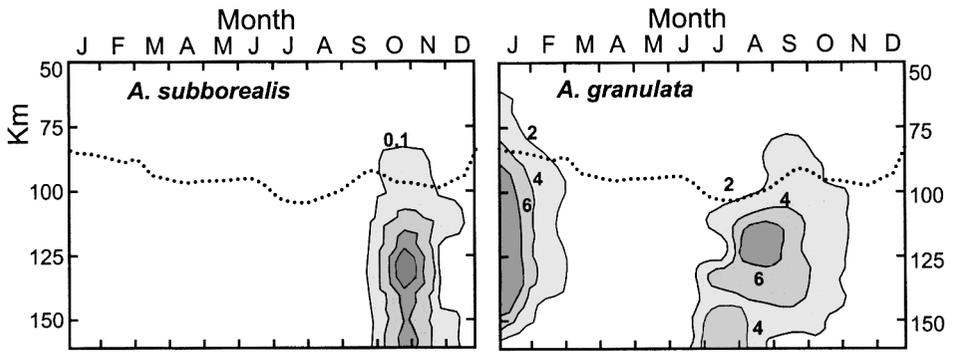


Fig. 29. Spatio-temporal distribution of *Aulacoseira granulata* and *A. subborealis* in the upper reaches of the Schelde estuary, Belgium (biomass in mg C L^{-1}); months are indicated along the horizontal axis while distance from the mouth of the estuary is displayed along the vertical axis. The position of the 0.5 psu isohaline (broken line) is indicated to show the relation of diatom distribution to salinity.

A. granulata was usually the dominant species, whereas in lakes receiving riverine inputs only during flooding, *A. subborealis* generally dominated. *Aulacoseira subborealis* also occurs in 25 lakes in Victoria and New South Wales (personal communication John Tibby and Jenny Fluin), where it is most abundant at high turbidity and mean TP concentrations of 27 to 40 $\mu\text{g L}^{-1}$ but also occurs in more transparent and nutrient-poorer waters.

A study in the French Massif Central revealed *A. subborealis* in nine lakes. Highest abundance (up to 60%) was noted in the plankton of the Lac de la Landie, a 21 m deep, tea-coloured (~ 20 Hazel units), lake of glacial origin at 1000 m.a.s.l., where it occurred together with *Aulacoseira ambigua* (Grunow) Simonsen, *Cyclotella pseudostelligera* Hustedt, *C. radiosa* (Grunow) Lemmermann and *C. stelligera* (Cleve & Grunow) Van Heurck. *A. subborealis* also amounts to significant percentages in Lac Crégut, a 26 m deep glacial lake at 900 m.a.s.l., and in Lac Chambon, a shallow lake (max. depth 4 m) of volcanic origin at 880 m.a.s.l. The plankton assemblage in Lac Crégut consists of *Asterionella formosa* Hassall, *Aulacoseira subarctica*, *Cyclotella pseudostelligera*, *C. stelligera* and *Fragilaria crotonensis* Kitton. In the more eutrophic Lac Chambon (annual mean TP 42.6 $\mu\text{g L}^{-1}$), *A. subborealis* was part of a very diverse planktonic assemblage with *Asterionella formosa*, *Aulacoseira subarctica*, *Cyclostephanos tholiformis* Stoermer, Håkansson & Theriot, *Cyclotella pseudostelligera*, *Stephanodiscus parvus* Stoermer & Håkansson, *Fragilaria delicatissima* (W. Smith) Lange-Bertalot and *F. nana* (Meister) Lange-Bertalot. In these lakes, the TP optimum calculated by WA for *Aulacoseira subborealis* and *A. subarctica* amounted to 15 and 19 $\mu\text{g L}^{-1}$, respectively. *A. subarctica* sometimes co-occurred with *A. subborealis*, but displayed a different distribution pattern, occurring more abundantly at higher alkalinity, nitrate and silica levels. Growth of *A. subborealis* in nutrient-poor conditions is also evident from its presence in 12 such lakes in northern Sweden (Rosén et al. 2000).

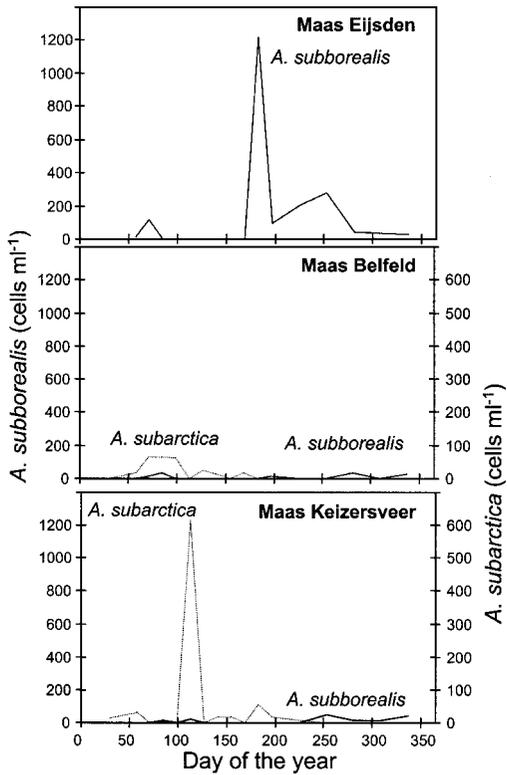


Fig. 30. Seasonal occurrence of *Aulacoseira subborealis* and *A. subarctica* in the River Maas, The Netherlands, at three sampling stations: Eijsden (most upstream), Belfeld and Keizersveer (most downstream).

Discussion

Taxonomy

Electron microscopic observations on the valve morphology of *A. subarctica* have been published by, among others, Crawford (1979), Haworth (1988), Canter & Haworth (1991), Krammer & Lange-Bertalot (1991a), Genkal (1992) and Le Cohu (1996). They reveal a large similarity in the structure of this species and that of *A. subborealis*, e.g. with regard to the form and arrangement of mantle areolae, and the overall shape as well as the implantation of the linking spines. As in *A. subborealis*, the mantle areolae of *A. subarctica* are generally surrounded by four knobs each. Similar knobs are observed in other *Aulacoseira* species, but with different arrangements (e.g. Davey & Crawford 1986; Haworth & Sabater 1993; Krammer 1991a; Le Cohu 1991). Apart from these similarities, however, the spines are considerably longer and more slender in *A. subarctica*, and the spine grooves correspondingly extend further on the mantle. Also, the areolae commonly extend far

onto the base of the spines where they may become quite elongate. This is never the case in *A. subborealis*. According to Le Cohu (1991, pers. comm. 1997) and personal observations, *A. subarctica* presents two types of spines: separation spines, with a somewhat widened base and a length of about 2.8 μm , and longer linking spines of 3.3 to 4.0 μm . Only one type of spine is observed in *A. subborealis*. Probably due to the limited spine length (only ca. 1.2 μm), neighbouring cells separate easily and filaments remain short (mostly 2-3 or single cells only) in this species. Crawford & Likoshway (2002) report that the vela of *A. subarctica* are set very deep in the areolar foraminae and supported by 1-3 downwardly directed supports. At an SEM enlargement of up to 40,000 we could not ascertain the fine structure of the velum in *A. subborealis* and further studies using more appropriate techniques remain necessary. It may be, however, that the number of supporting ribs is somewhat higher than in *A. subarctica*. The abundant terminal valves of *A. subarctica* show unperforated discs. The other cells, however, have valves that are areolated as in *A. subborealis* (cf. Genkal 1992; Le Cohu 1996; Le Cohu, pers. comm. 1997; and K. Krammer, unpublished observations). Valves with unperforated discs were not observed in *A. subborealis*. Variation in the areolation of the valve face was also noted in other *Aulacoseira* species (cf. Haworth & Sabater 1993) and a varying degree of importance is attributed to the areola pattern of the valve face (e.g. Haworth 1988; Krammer & Lange-Bertalot 1991a). A more straightforward distinction between both taxa is found in the density of mantle areolae, with *A. subarctica* having only 17-22 pervalvar areolae and 17-21 pervalvar striae in 10 μm (Krammer & Lange-Bertalot 1991a, Table 1). Although some populations of *A. subborealis* show somewhat more heavily silicified cells, no overlap is observed with regard to this feature. Environmental conditions, such as light or nutrient availability, may affect size, pore size and the degree of silicification in *Aulacoseira* spp. (see e.g. Stoermer et al. 1985; Kilham et al. 1986; Gomez et al. 1995; Turkia & Lepistö 1999), but this does not explain the observed discontinuous variation between *A. subarctica* and *A. subborealis*, which also remains when both occur together. Moreover, the cells of *A. subarctica* tend to have less convex mantle margins and are usually longer in relation to their width. The valve height to diameter ratio tends to vary substantially in *A. subarctica* populations (Krammer & Lange-Bertalot 1991a; Jewson 1992; Siver & Kling 1997). In a detailed morphometric study, Jewson (1992) reported that while cell diameter was highly variable, cell height remained more or less constant. Thus, small cells of *A. subarctica*, of which the cell diameter might overlap with that of *A. subborealis*, will usually have a valve height to diameter ratio exceeding 1 (Krammer & Lange-Bertalot 1991a; Siver & Kling 1997), whereas this ratio is always markedly below 1 in *A. subborealis*. Consequently, *A. subborealis* is not merely a small form of *A. subarctica*. Siver & Kling (1997) and Likoshway & Crawford (2001) have drawn particular attention to the species-characteristic position and morphology of the rimoportula in *Aulacoseira* and documented this feature for *A. subarctica*. In this species, the rimoportula is situated next to the pseudoseptum but completely separate from it, penetrating the mantle into a large exterior opening. According to Likoshway & Crawford (2001) the rimoportula in *A. subarctica* classifies as 'occurring next to the Ringleiste, without stalk and external opening large, visible in LM'. In *A. subborealis*, this structure is merged with the pseudoseptum and has an external

opening that remains inconspicuous. Also, its internal aperture appears larger. Overall, its morphology strongly resembles that illustrated for *Melosira californica* Ehrenberg by Likoshway & Crawford (2001, fig. 22) and could be described in their classification as ‘occurring only on the inner side of the Ringleiste, without stalk and external opening small, (probably) open into areola’. Unless the variation of rimoportula features is much greater in *A. subarctica* than presently conceived, its structure represents a major distinction between both taxa. A final morphological difference is found in the pseudoseptum, of which the inner margin is less conspicuously thickened in *A. subarctica* or not thickened at all (Le Cohu, pers. comm. 1995; Siver & Kling 1997, figs 21-22; Crawford & Likoshway 2002, fig. 21). Finally, *A. subborealis* also differs from *A. subarctica* in its ecological requirements, since the latter is more typical of more or less acid oligo- to mesotrophic conditions, and does not extend into very nutrient-rich, alkaline waters (Krammer & Lange-Bertalot 1991a; van Dam et al. 1994). All these differences indicate that *A. subborealis* is quite distinct from *A. subarctica* var. *subarctica* and this to such a degree that a separation at the species rather than forma level is warranted.

Characteristics of some other taxa that could give rise to confusion are gathered in Table 1. In the LM, *A. subborealis* resembles *A. alpigena* (Grunow) Krammer rather strongly; both having valves that are wider than high, convex mantle margins, inclined/curved rows of mantle areolae, and small linking spines. The latter, however, has a distinctly coarser mantle areolation (15-22 striae in 10 µm and areolae of similar density; Krammer & Lange-Bertalot, 1991a). Another distinction in the LM is that in *A. alpigena*, the areolae in the row next to the collum appear distinctly larger than the remaining ones. Also, collum and mantle are separated by a more strongly refractive ring (the pseudoseptum or ring ledge). In valve view, *A. alpigena* is distinguished easily by having only one or two rows of marginal areolae. In the SEM, the very different linking spines (spathulate or with marginal anchors), their different implantation and the absence of spine grooves are important differential characteristics (see Haworth 1988; Marciniak 1988; Krammer & Lange-Bertalot 1991a). *Aulacoseira laevissima* (Grunow) Krammer presents an almost equally fine areolation and similar cell shape as *A. subborealis*. Generally, however, it has a larger diameter and the collum is higher relative to the remainder of the mantle. Also, the valve face presents more marked and equally large areolae over the entire surface, the linking spines possess small terminal anchors, and the pseudoseptum is less well developed (Haworth 1988; Krammer 1991b; Krammer & Lange-Bertalot 1991a). The less known N-American *Melosira nygaardii* Camburn has longer cells, only 20-22 striae in 10 µm, which also run parallel to the pervalvar axis, and an unperforated valve face (Camburn & Kingston 1986). As mentioned, *Melosira californica* from the same continent possesses very similar rimoportulae, but these are separated by only 2 to 4 rows of areolae. Moreover, this species is about twice as large as *Aulacoseira subborealis*, has 5 µm long slender spines and presents a considerably coarser structure (viz. Likoshway & Crawford 2001). *Aulacoseira distans* should especially be mentioned here, because *A. subborealis* repeatedly has been reported under this name. Actually, *A. subborealis* could be placed in the ‘*distans* group’ (Krammer 1991a) on the basis of the low ratio of mantle height to valve diameter. *A. distans* was described (as *Galionella distans*) by Ehrenberg (1836)

from fossil samples ('Biliner Polierschiefer'). Material from the type location is also present in other collections, e.g. in the Kützing collection (sample nr. 107 from the BM [NH]). Krammer (1991a) presents a series of light-microscopical photographs of the type material from the Ehrenberg collection and Crawford & Likoshway (1999) present a detailed account of both LM and SEM observations (see also Likoshway & Crawford 2001). Material from the Kützing collection has been examined by R.M. Crawford and was found to contain a morphologically identical *Aulacoseira* species (personal communication 1998). SEM photographs of *A. distans* from the Kützing collection are published in Haworth et al. (1988) and Haworth (1988). *Aulacoseira distans* specimens from the type locality differ substantially from *A. subborealis* in having mantle areolae predominantly arranged in parallel rows, a peralvar striae density of 12-15 in 10 μm , larger areolae on the entire surface of the discus, a rugose valve-face surface, rimoportulae next to the pseudoseptum, and – probably most decisive – spines which emerge from a single peralvar rib. Until recently, however, diatoms possessing marginal spines that emerge from two peralvar ribs in stead of one and with mantle areolae essentially arranged in oblique rows were often identified as *A. distans* (see e.g. Cassie 1981; Eloranta 1986; Krammer 1991a; Krammer & Lange-Bertalot 1991a; Siver & Kling 1997). These specimens clearly differ from the *A. distans* type material but show similarities to *A. subborealis*, particularly the specimens illustrated by Cassie (1981), Eloranta (1986) and Krammer (1991a, fig. 28), which appear identical. Doubts that illustrations given by Eloranta (1986) would pertain to *A. distans* were already voiced by Crawford & Likoshway (1999). Although the present knowledge of *A. distans* and *A. subborealis* makes future confusion between these taxa less likely, further studies appear necessary to sort out some of the similar *Aulacoseira* morphs that have been reported in the literature.

Ecology

We observed *Aulacoseira subborealis* in recent and sub-recent material from rivers and lakes in the northern as well as the southern hemisphere. Previous studies have reported this taxon from Scandinavia, Scotland, North America and New Zealand (Cassie 1981; Haworth 1988). It therefore seems to be a widespread and common taxon of cosmopolitan distribution.

Based on the present data, it does not seem that *A. subborealis* is an extremely useful indicator species for trophic conditions. Although it is often associated with fairly nutrient-rich conditions, especially with TP concentrations of ca. 100 $\mu\text{g L}^{-1}$ or more, its trophic range apparently extends into ultra-oligotrophic conditions in some areas as well. Possibly, regional infraspecific variation or interaction with other environmental factors may be occurring. In the Schelde and Murray basins, it co-occurs with *A. granulata*, which also reflects more eutrophic conditions (e.g. Donar et al. 1996; Kling 1998). Interestingly, *A. subborealis* was found to mark the onset of hyper-eutrophication in the Blankaart Reservoir. In the Rivers Maas and Rijn, it was observed with the closely related *A. subarctica*, a species which marks the onset of nutrient enrichment in oligotrophic systems (Haworth 1988; Sabater & Haworth 1995), but generally occurs in less eutrophic environments than *A. granulata*.

(Krammer & Lange-Bertalot 1991a; van Dam et al. 1994). Development of *A. subarctica* and *A. subborealis* differed markedly in time and space, demonstrating substantial differences in their ecological requirements. This also shows from the subfossil records and present distribution of *A. subborealis* and *A. subarctica* in European lakes.

Although *A. subborealis* occurs in the estuarine reach of the Schelde, this does not imply adaptation to increased salinities, since it was only found in the freshwater tidal zone and disappeared rapidly even before a notable increase in salinity occurred. Moreover, its distribution suggests that it is derived here from the Schelde River, as it was most common in the most upstream part of the estuary and occurred in periods when river discharge was highest. *A. subborealis* was also found in the lower reaches of other rivers (Rijn, Maas), as well as in turbid shallow lakes (e.g. Blankaart Reservoir and Murray River billabongs), and deeper lakes with water coloured by humic substances (Lac de la Landie). Lowland rivers are strikingly similar in terms of light climate to turbid shallow lakes (Reynolds 1994; Reynolds et al. 1994), suggesting that *A. subborealis* is particularly well adapted for low-light environments.

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References

- ANDERSON, N.J., P. BLOMQUIST & I. RENBERG (1997): An experimental and palaeoecological study of lake responses to lake acidification and liming in three central Swedish lakes. - *Eur. J. Phycol.* **32**: 35-48.
- ANDERSON, N.J. & T. KORSMAN (1990): Land-use change and lake acidification: Iron Age desettlement in northern Sweden as a pre-industrial analogue. - *Philos. Trans. R. Soc., Lond. B* **327**: 373-376.
- BENNION, H. (1994): A diatom-phosphorus transfer function for shallow, eutrophic ponds in southeast England. - *Hydrobiologia* **275/276**: 391-410.
- BRADBURY, J.P. & P.C. VAN METRE (1997): A land-use and water-quality history of White Rock Lake reservoir, Dallas, Texas, based on paleolimnological analyses. - *J. Paleolimnol.* **17**: 227-237.

- CAMBURN, K.E. & J.C. KINGSTON (1986): The genus *Melosira* from soft-water lakes with special reference to northern Michigan, Wisconsin and Minnesota. - In: SMOL, J.P, R.W. BATTARBEE, R.B. DAVIS & J. MERILÄINEN (eds): Diatoms and lake acidity: 17-34. Junk, Dordrecht.
- CANTER, H.M. & E. HAWORTH (1991): The occurrence of two new planktonic diatom populations in the English Lake District: *Aulacoseira islandica* subspecies *helvetica* and *A. ambigua*. - *Freshw. Forum* **1**: 39-48.
- CASSIE, V. (1981): The fossil and living freshwater diatom flora of New Zealand. - In: ROSS, R. (ed.): Proceedings of the sixth symposium on recent and fossil diatoms: 321-338. Koeltz, Koenigstein.
- CLARKE, K. (1989): The distribution of *Cyclotephanos dubius* in Norfolk. - *Diatom Res.* **4**: 207-215.
- CRAWFORD, R.M. (1979): Filament formation in the diatom genera *Melosira* C.A. Agardh and *Paralia* Heiberg. - *Nova Hedwigia Beih.* **64**: 121-133.
- CRAWFORD, R.M. & Y. LIKOSHWAY (1999): The frustule structure of original material of *Aulacoseira distans* (Ehrenberg) Simonsen. - *Diatom Res.* **14**: 239-250.
- CRAWFORD, R.M. & Y.V. LIKOSHWAY (2002): The velum of species of the diatom genus *Aulacoseira* Thwaites. - In: JOHN, J. (ed.): Proceedings of the 15th International Diatom Symposium: 275-287. A.R.A. Gantner Verlag, Ruggell, Liechtenstein.
- DAVEY, M.C. & R.M. CRAWFORD (1986): Filament formation in the diatom *Melosira granulata*. - *J. Phycol.* **22**: 144-150.
- DENYS, L. (1994): Palaeolimnology of the hypertrophic man-made Lake Blankkaart (Belgium); the diatom record. - In: Abstract book 13th International Diatom Symposium, Stazione Zoologica "Anton Dohrn", Naples: 164.
- DONAR, C.M., R.K. NEELY & E.F. STOERMER (1996): Diatom succession in an urban reservoir system. - *J. Paleolimnol.* **15**: 237-243.
- EHRENBERG, C.G. (1836): Nachrichten über das Vorkommen fossiler Infusorien. - Bericht über die zur Bekanntmachung geeigneten Verhandlungender königlichen preuss. Akademie der Wissenschaften zu Berlin **1**: 50-54.
- ELORANTA, P. (1986): *Melosira distans* var. *tenella* and *Eunotia zasuminensis*, two poorly known planktonic diatoms in Finnish lakes. - *Nord. J. Bot.* **6**: 99-103.
- FLORIN, M.-B. (1981): The taxonomy of some *Melosira* species. A comparative morphological study. - In: ROSS, R. (ed.): Proceedings of the sixth symposium on recent and fossil diatoms: 321-338. Koeltz, Koenigstein.
- GENKAL, S.I. (1992): Atlas diatomovych vodoroslej reki Volgi. - Gidrometeoizdat, St. Petersburg, 128 pp.
- GOMEZ, N., J.L. RIERA & S. SABATER (1995): Ecology and morphological variability of *Aulacoseira granulata* (Bacillariophyceae) in Spanish reservoirs. - *J. Plankt. Res.* **17**: 1-16.
- GREUTER, W., J. McNEILL, F.R. BARRIE, H.M. BURDET, V. DEMOULIN, T.S. FILGUEIRAS, D.H. NICOLSON, P.C. SILVA, J.E. SKOG, P. TREHANE, N.J. TURLAND & D.L. HAWKSWORTH (2000): International Code of Botanical Nomenclature (Saint Louis Code). - *Regnum Vegetabile* 138: 1-474. Koeltz Scientific Books, Koenigstein, Germany.
- HABERYAN, K.A. (1985): The role of copepod fecal pellets in the deposition of diatoms in Lake Tanganyika. - *Limnol. Oceanogr.* **30**: 1010-1023.
- HALL, R.I. & J.P. SMOL (1996): Paleolimnological assessment of long-term water-quality changes in south-central Ontario lakes affected by cottage development and acidification. - *Can. J. Fish. Aquat. Sci.* **53**: 1-17.
- HÅKANSSON, H. (1989): Diatom succession during Middle and Late Holocene time in Lake Krageholmssjön, southern Sweden. - *Nova Hedwigia* **48**: 143-166.

- HAWORTH, E.Y. (1988): Distribution of diatom taxa of the old genus *Melosira* (now mainly *Aulacoseira*) in Cumbrian waters. - In: ROUND, F.E. (ed.): *Algae and the aquatic environment*: 138-167. Biopress Ltd. Bristol.
- HAWORTH, E.Y. (1990): Diatom name validation. - *Diatom Res.* **5**: 195-196.
- HAWORTH, E.Y., K.M. ATKINSON & P.S. NEWELL (1988): Distribution of certain diatom taxa in the waterbodies of Cumbria, U.K. - In: ROUND, F.E. (ed.): *Proceedings of the 9th International Diatom Symposium*: 17-28. Biopress, Bristol and Koeltz, Koenigstein.
- HAWORTH, E.Y. & S. SABATER (1993): A new Miocene *Aulacoseira* species in diatomite from the ancient lake in la Cerdanya (NE Spain). - *Nova Hedwigia Beih.* **106**: 227-242.
- HOTZEL, G. & R. CROOME (1996): Population dynamics of *Aulacoseira granulata* (Ehr.) Simonson (Bacillariophyceae, Centrales), the dominant alga in the Murray River, Australia. - *Arch. Hydrobiol.* **136**: 191-215.
- JEWSON, D.H. (1992): Size reduction, reproductive strategy and the life cycle of a centric diatom. - *Philos. Trans. R. Soc., Lond. B* **336**: 191-213.
- JONES, V.J., R.W. BATTARBEE, N.L. ROSE, C. CURTIS, P.G. APPLEBY, R. HARRIMAN & A.J. SHINE (1997): Evidence for the pollution of Loch Ness from the analysis of its recent sediments. - *Sci. Total Environm.* **203**: 37-49.
- KILHAM, P., S.S. KILHAM. & R.E. HECKY (1986): Hypothesized resource relationships among African planktonic diatoms. - *Limnol. Oceanogr.* **31**: 1169-1181.
- KLING, H.J. (1998): A summary of past and recent plankton of Lake Winnipeg, Canada, using algal fossil remains. - *J. Paleolimnol.* **19**: 297-307.
- KRAMMER, K. (1991a): Morphology and taxonomy in some taxa of the genus *Aulacoseira* Thwaites (Bacillariophyceae) I. *Aulacoseira distans* and similar taxa. - *Nova Hedwigia* **52**: 89-112.
- KRAMMER, K. (1991b): Morphology and taxonomy in some taxa of the genus *Aulacoseira* Thwaites (Bacillariophyceae) II. Taxa in the *A. granulata*, *italica*- and *lirata*-groups. - *Nova Hedwigia* **53**: 477-496.
- KRAMMER, K. & H. LANGE-BERTALOT (1986): Bacillariophyceae. 1. Teil: Naviculaceae. - In: Ettl, H., J. Gerloff, H. Heynig & D. Moltenhauer (eds): *Süßwasserflora von Mitteleuropa*. Band 2/1. Gustav Fischer Verlag, Stuttgart. 876 pp.
- KRAMMER, K. & H. LANGE-BERTALOT (1988): Bacillariophyceae. 2. Teil: Bacillariaceae, Epithemiaceae, Surirellaceae. - In: Ettl, H., J. Gerloff, H. Heynig & D. Moltenhauer (eds): *Süßwasserflora von Mitteleuropa*. Band 2/2. Gustav Fischer Verlag, Stuttgart. 596 pp.
- KRAMMER, K. & H. LANGE-BERTALOT (1991a): Bacillariophyceae. 3. Teil: Centrales, Fragilariaceae, Eunotiaceae. - In: Ettl, H., J. Gerloff, H. Heynig & D. Moltenhauer (eds): *Süßwasserflora von Mitteleuropa*. Band 2/3. Gustav Fischer Verlag, Stuttgart. 576 pp.
- KRAMMER, K. & H. LANGE-BERTALOT (1991b): Bacillariophyceae 4. Teil: Achnanthaceae. Kritische Ergänzungen zu *Navicula* (Lineolatae) und *Gomphonema*. - In: Ettl, H., J. Gerloff, H. Heynig & D. Moltenhauer (eds): *Süßwasserflora von Mitteleuropa*. Band 2/4. Gustav Fischer Verlag, Stuttgart. 437 pp.
- LE COHU, R. (1991): Morphologie des valves et du cingulum chez *Aulacoseira ambigua* (Grun.) Simonsen (Bacillariophycées). Quelques observations sur les phases pré- et postauxospores. - *Nova Hedwigia* **53**: 409-421.
- LE COHU, R. (1996): Further observations and some comments on the fine structure of the centric diatom *Aulacoseira islandica* (Bacillariophyceae). - *J. Phycol.* **32**: 333-338.
- LEPISTÖ, L. (1990): Some centric diatoms as indicators of water quality in Finnish lakes. - In: SIMOLA, H. (ed.): *Proceedings of the 10th International Diatom Symposium*: 499-504. Koeltz Scientific Books, Koenigstein.

- LIKOSHWAY, Y.V. & R.M. CRAWFORD (2001): The rimoportula - a neglected feature in the systematics of *Aulacoseira*. - In: ECONOMOU-AMILLI, A. (ed.): Proceedings of the 16th International Diatom Symposium: 33-47. University of Athens, Athens.
- MARCINIAK, B. (1988): Diatoms from the Late Quaternary sediments of the Bedowo Lake, Central Poland. Preliminary report. - In: MILLER, U. & A.-M. ROBERTSSON (eds): Proceedings of the Nordic Diatomist Meeting 1987. USDQR Report **12**: 57-65.
- MERILÄINEN, J.J., J. HYNYNEN, A. TEPPÖ, A. PALOMÄKI, K. GRANBERG & P. REINKAINEN (2000): Importance of diffuse nutrient loading and lake level changes to the eutrophication of an originally oligotrophic boreal lake: a palaeolimnological diatom and chironomid analysis. - *J. Paleolimnol.* **24**: 251-270.
- MUYLAERT, K., A. VAN KERKVOORDE, W. VYVERMAN & K. SABBE (1997): Structural characteristics of phytoplankton assemblages in tidal and non-tidal freshwater systems: a case-study from the Schelde basin. - *Freshw. Biol.* **38**: 263-276.
- NYGAARD, G. (1956): The ancient and recent flora of diatoms and Chrysophyceae in Lake Gribsø. - *Folia Limnol. Scand.* **8**: 32-94, 253-262.
- PENNINGTON, W., E.Y. HAWORTH, A.P. BONNY & J.P. LISHAM (1972): Lake sediments in Northern Scotland. - *Philos. Trans. R. Soc., Lond. B* **264**: 191-294.
- PETROVA, N.A. (1986): Seasonality of *Melosira*-plankton of the great northern lakes. - *Hydrobiologia* **138**: 65-73.
- REINBERG, I. (1976): Palaeolimnological investigations in Lake Prästsjön. - *Early Norrland* **9**: 113-159.
- REINBERG, I. (1978): Palaeolimnology and varve counts of the annually laminated sediment of Lake Rudetjärn, northern Sweden. - *Early Norrland* **11**: 63-92.
- REYNOLDS, C.S. (1994): The long, the short and the staled: on the attributes of phytoplankton selected by physical mixing in lakes and rivers. - *Hydrobiologia* **289**: 9-21.
- REYNOLDS, C.S., J.-P. DESCY & J. PADISÁK (1994): Are phytoplankton dynamics in rivers so different from those in shallow lakes? - *Hydrobiologia* **289**: 1-7.
- ROSÉN, P., R. HALL, T. KORSMAN & I. REINBERG (2000): Diatom transfer-functions for quantifying past air temperature, pH and total organic carbon concentration from lakes in northern Sweden. - *J. Paleolimnol.* **24**: 109-123.
- ROUND, F.E., R.M. CRAWFORD & D.G. MANN (1990): The diatoms. Cambridge University Press, Cambridge, 747 pp.
- SABATER, S. & E.Y. HAWORTH (1995): An assessment of recent trophic changes in Windermere South Basin (England) based on diatom remains and fossil pigments. - *J. Paleolimnol.* **14**: 151-163.
- SIVER, P.A. & H. KLING (1997): Morphological observations of *Aulacoseira* using scanning electron microscopy. - *Canad. J. Botany* **75**: 1807-1835.
- SORVARI, S. & A. KORHOLA (1998): Recent diatom assemblage changes in subarctic Lake Saanajärvi, NW Finnish Lapland, and their paleoenvironmental implications. - *J. Paleolimnol.* **20**: 205-215.
- STEVENSON, A.C., S. JUGGINS, H.J.B. BIRKS, D.S. ANDERSON, N.J. ANDERSON, R.W. BATTARBEE, F. BERGE, R.B. DAVIS, R.J. FLOWER, E.Y. HAWORTH, V.J. JONES, J.C. KINGSTON, A.M. KREISER, J.M. LINE, M.A.R. MUNRO & I. REINBERG (1991): The surface waters acidification project palaeolimnology programme: modern diatom/lake-water chemistry dataset. - ENSIS Publishing, London, 86 pp.
- STOERMER, E., J. WOLIN, C. SCHELSKE & D. CONLEY (1985): Variations in *Melosira islandica* valve morphology in Lake Ontario sediments related to eutrophication and silica depletion. - *Limnol. Oceanogr.* **30**: 414-418.

TURKIA, J. & L. LEPISTÖ (1999): Size variations of planktonic *Aulacoseira* Thwaites (Diatomae) in water and in sediment from Finnish lakes of varying trophic state. - *J. Plankton Res.* **21**: 757-770.

VAN DAM, H. & A. MERTENS (1995): Long-term changes of diatoms and chemistry in headwater streams polluted by atmospheric deposition of sulphur and nitrogen compounds. - *Freshw. Biol.* **34**: 579-600.

VAN DAM, H., A. MERTENS & J. SINKELDAM (1994): A coded checklist and ecological indicator values of freshwater diatoms from the Netherlands. - *Neth. J. Aquat. Ecol.* **28**: 117-133.

WECKSTRÖM, J., S. SORVARI, N. CAMERON, K. KOINIG & A. LOTTER (1997): MOLAR: a programme of MOUNTAIN LAKE Research. Diatom taxonomic workshop in Helsinki, 18-19.10 1996. - In: WATHNE, B. (ed.): MOLAR Progress Report 1996-1997, Norwegian Institute for Water Research, Oslo, 8 pp.

YANG, J.R., B.K. BASU, P.B. HAMILTON & F.R. PICK (1997): The development of a true riverine phytoplankton assemblage along a lake-fed lowland river. - *Arch. Hydrobiol.* **140**: 243-260.

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