Taxonomic appraisal of *Melosira arctica* Dickie and description of a new variety (Bacillariophyta)

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Abstract

Original material of *Melosira arctica* was examined. Species circumscription is emended to include detailed frustule fine structure and, for the first time, the basic morphometrics of the population from original material have been established using light and electron microscopy. This original population, collected in 1850, was compared to three contemporary populations of this taxon, collected at Arctic Ocean stations ranging from latitude of 71° to 76° N and from longitude 77° to 173° W. As a result of morphometric examination, a new variety, *M. arctica* var. *krembsii*, is proposed. The new variety differs from the nominate variety by finer perforation of the valvocopulae, by fewer marginal rimoportulae in 10 μm located further above the mantle margin, by fewer rimoportulae on the valve face, and by finer striation of the valves. Based on published illustrations, we suggest that *M. arctica* var. *krembsii* may be more common at latitudes south of 70° N, while the nominate variety occurs in more polar seas.

Keywords: centric diatoms; Ehrenberg collection; new taxon; sea ice; SEM.

Introduction

Melosira arctica Dickie has been reported from numerous locations along the arctic coast of Eurasia, North America and associated islands (e.g., Gran 1904, Cleve-Euler 1951, Syvertsen and Hasle 1988, Syvertsen 1991, Booth and Horner 1997, Gosselin et al. 1997, Hasle and Syvertsen 1997, Cremer 1998, Krembs et al. 2002, Lovejoy et al. 2002). This species has been recorded from ice-floes (Gran 1904), attached as long strands under the ice (Syvertsen and Hasle 1988, Melnikov 1997, Krembs et al. 2002) and from surface sediment (Ehrenberg 1853), at latitudes ranging from 70° N to 85° N and at longitudes varying between 162° E and 154° W. This diatom is also reported from more southerly latitudes. For example, it is known from the Baltic Sea (e.g., Hustedt 1930, Mölder and Tynni 1966, 1967, Plinski 1979, Syvertsen and Hasle 1988, Snoeijs 1993), the Oslofjord in Norway (Syvertsen

and Hasle 1988) and the northeastern part of the Gulf of St. Lawrence in eastern Canada (Bérard-Therriault et al. 1999). Despite the circumarctic distribution and relatively frequent occurrence in massive (macroscopic) growth in some of these locations (Figures 1 and 2; Gran 1904, Gutt 1995, Melnikov 1997, Krembs et al. 2002), surprisingly little is known regarding frustule fine structure of this diatom. Only three studies have documented some aspects of *M. arctica* morphology using electron microscopic technology (Heimdal 1973, Syvertsen and Hasle 1988, Sakson and Miller 1993).

The original diagnosis of the species by Dickie (1852) gives only the frustule shape; Ehrenberg, who had received some of Dickie's original material, was a little more elaborate in his description, including also the size range (1853 as *Gaillonella arctica*) plus an illustration (1854). Since few details of the frustule microstructure can be seen by light microscopy (LM), only the electron microscope offers the possibility of differentiating minute, but diagnostic features. Heimdal (1973) examined *Melosira arctica* from the Gulf of Finland using transmission (TEM) and scanning electron microscopy (SEM), but in those early years of electron microscopy, several details of the valve structure, i.e., density of the loculae, were still unresolved. Finally, nearly two decades ago, a preliminary note on *M. arctica* by Syvertsen and Hasle (1988), using Dickie's original material, showed some important morphological features, i.e., the rimoportulae, and discussed a possible geographic infra-specific variability within this species.

In this paper, we used light and electron microscopy to examine the original material sent by Dickie to Ehrenberg as well as recent populations of *Melosira arctica* from various Arctic locations, in order to update the circumscription of the species, to establish basic morphometrics of the original population, and to resolve confusion regarding the authorities for the binomial.

In addition to this report, the information on the taxa discussed will be made available via the AlgaTerra Information System (Jahn and Kusber 2006).

Materials and methods

Ehrenberg's original material is curated at the Institute of Paleontology, Museum of Natural History, Humboldt University Berlin (BHUPM) (see Figures 3–10). It includes the mica strip preparation 271711 (Figure 5) and Ehrenberg's illustration on Drawing Sheet No. 2264 (reproduced in part here as Figure 3). The original sample No. 1796 (Figure 4) is a piece of mica on which material is dried (Figure 6) and labelled: "Schleim-Massen auf Glimmer" [mass of mucilage on mica]. Ehrenberg's LM preparations (mica strips, see Figure 5) are diatom material placed on mica which is embedded in Canada balsam (see Figures 7–10;
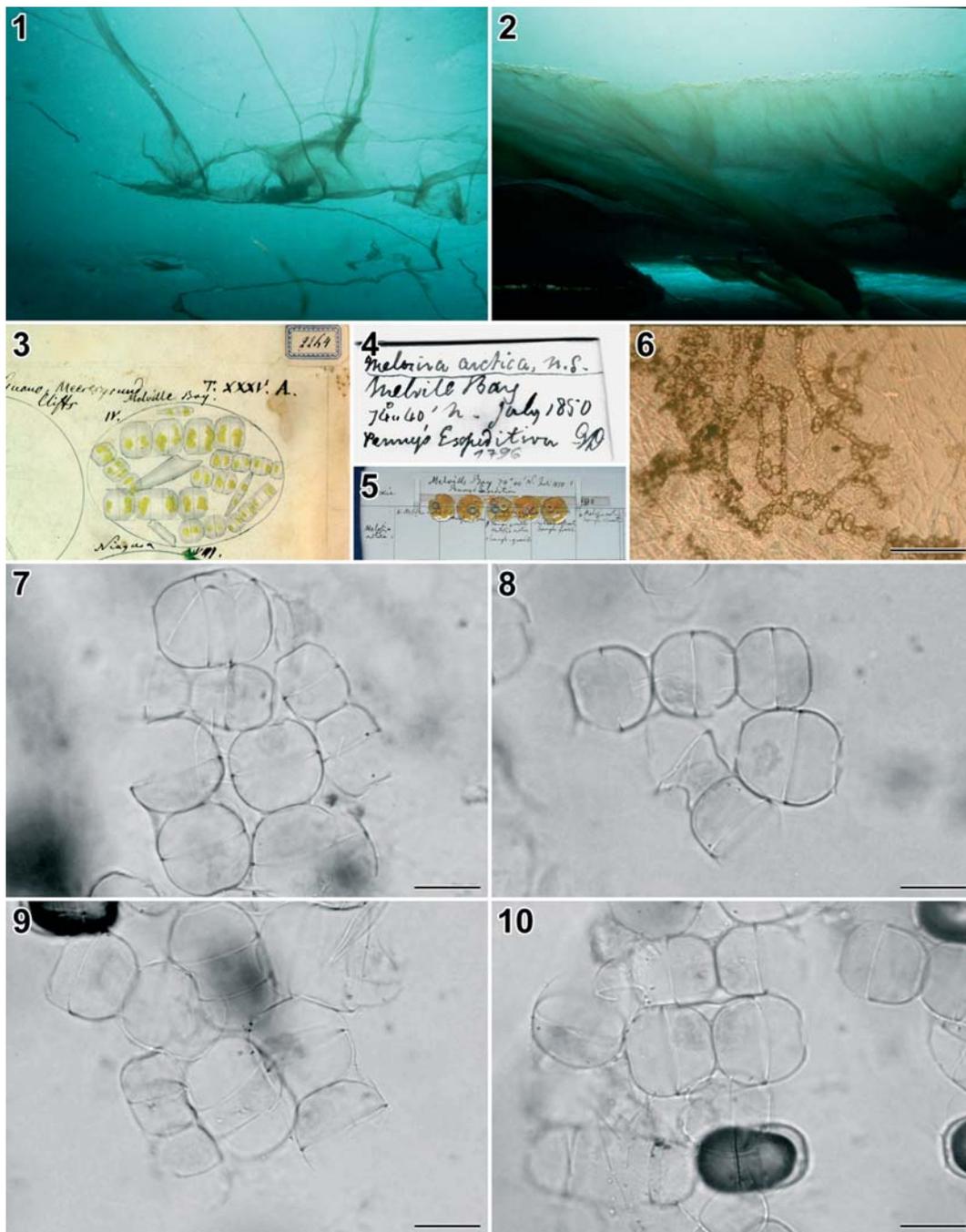
Figures 1–10 *Melosira arctica*: live and historical collections.
(1–2) Macroscopic growth of *Melosira arctica* attached to the under-surface of sea ice, photographed by J. Gutt, Alfred Wegener Institute, Germany on 8 June 1993 at 80° 17′ N by 13° 39′ W; further details provided in Gutt (1995). (1) *Melosira*-strands about 3 m long by 2 cm wide. (2) Full growth of *Melosira*-strand occupying approximately 200 cm by 40 cm. (3–10) Original material of *Melosira arctica* var. *arctica* from the Ehrenberg Collection at BHUPM. (3) Ehrenberg's drawing of *Melosira arctica* as part of Drawing Sheet No. 2264. (4) G. Dickie's hand-written label on Sample No. 1796. (5) Photograph of Ehrenberg's preparation mica strip No. 271711; the voucher specimen is the first mica disc (-a), blue ring. (6) Image of the dried material in sample No. 1796, showing colonies of *M. arctica* on the mica fragment. Scale bar=200 μm. (7–10) Specimens from the voucher mica (271711-a blue), showing the size range of frustules in the population from which the voucher specimen was taken. Scale bars=20 μm.

for further details on the collection see Lazarus and Jahn 1998, Jahn and Kusber 2004). We also studied some unmounted original material (peeled off from the mica of sample No. 1796), which we placed onto a glass slide and examined with LM (see Figure 6). All original material was comprised almost exclusively of *Melosira arctica*. For SEM examination, filters with a minute amount of the peeled-off material from the mica sample No. 1796 were first soaked and then rinsed in distilled water under gentle vacuum in a filtration tower to dissolve sea salts and rinse off particles and debris. The prepared material was then mounted on aluminium stubs as in Kaczmarska et al. (2000) and observed using a JEOL JSM-5600 SEM (Tokyo, Japan) operating at 10 kV and 8 mm working distance at the Digital Microscopy Facility at Mount Allison University. Because even gentle oxidation in hydro-

gen peroxide at room temperature proved too destructive for this fragile original material (and is thus not recommended for this type of old material), in SEM preparations of original samples, frustules were still covered with dried organic matter ("Schleim"), obscuring some details of the siliceous frustule micro-architecture.

Because of this unavoidable shortcoming of the 155-year-old original material, we also obtained three samples of contemporary populations of this species, and these were cleaned chemically, following Kaczmarska et al. (2005). These three samples contained great quantities of *Melosira arctica* and were collected in 1998 in the North Water polynya, northern Baffin Bay (sample 54-B, 76° 57′ N, 77° 19′ W, sub-ice habitat) and in 1994 from the Chukchi Sea (snagged from the side of the ship while on transit from station 6; 75° 21′ N by 170° 39′ W to station 7, 76° 39′ N by 173° 20′ W).

The third sample was collected by Dr. Christopher Krembs off the Alaskan shore in the Chukchi Sea and served as the source for the live culture isolated from sub-ice (71° 20′ N 156° 40′ W) from which our new taxon var. *krembsii* is proposed. Detailed description of the stations, oceanographic conditions and associated biota at these stations can be found in Gosselin et al. (1997), Krembs et al. (2002) and Michel et al. (2002), respectively. Vouchers of the new variety and associated material is deposited at the Berlin-Dahlem Botanical Garden and Botanical Museum, Germany (B), the Canadian Museum of Natural History, Ottawa, Canada (CANA), and at the Hustedt Collection, Alfred Wegener Institute for Polar Research, Bremerhaven, Germany (BRM).

Terminology follows that of Stosch (1975), Ross et al. (1979) and Round et al. (1990). SEM biometrics were based on at least 30 measurements (unless otherwise indicated) and are meant to establish the mean and the range of the morphological variability of the type population. The range of SEM-based valve diameter and pervalvar axis is augmented with additional LM observations. These are included in the ranges cited below, but not the means.

Results

Melosira arctica Dickie

Melosira arctica Dickie, *Journal of a voyage in Baffin's Bay and Barrow Straits in the years 1850–1851, II.* Appendix: cxcvi. 1852. [Often cited as: *Melosira arctica* (Ehrenberg) Ralfs *in*: Pritchard, *A history of infusorial animalcules*, 4th edition, 1861: 819].

Gaillonella arctica (Dickie) Ehrenberg, *Bericht* über *die zur Bekanntmachung geeigneten Verhandlungen der Königlich-Preussischen Akademie der Wissenschaften zu Berlin*, 1853: 528. (Basionym is indicated as "Dickie in litt.").

Dickie's very short diagnosis reads (1852: cxcvi): "*Melosira arcticum n.s.* Frustules transversely elliptical; central line rather faint. The young frustules are nearly spherical. At first I supposed it to be a variety of *M. Borreri*; but, on more careful examination, I now agree with Rev. W. Smith in believing it to be new. Dr. Sutherland … communicating a brown tinge to the water in Melville

Bay, off the Devil's Thumb, in shreds of mucilaginous consistence, and infested with numerous microscopic animals; N. lat. 74° 40′; 11th July, 1850."

Lectotype, as designated by Syverstsen and Hasle (1988), is their SEM pictures 4 and 6 from the original material, obtained from the Natural History Museum (BM).

Apparently, Ehrenberg had been unaware of Dickie's (1852) publication as his diagnosis reads (1853: 528): "…*Gaillonella arctica* Ehrenberg (= *Melosira arctica* Dickie *in litteris*) *articulis globosis laevibus, linea suturali media plurimis unica, in divisione subcutanea duplicata, cingulo laevi intercedente. Diameter articulorum majorum 1/96′″, minimorum observatorum 1/182′″,*. Melville Bay *et* Hingston-Bay. *Longis catenis socialis est*." In translation: "….with smooth spherical segments, most with a single median suture line, doubled with subcutaneous division, with the smooth girdle lying in between. The diameter of the larger segments is 24 µm, and of the smallest observed 12 µm. Melville Bay and Hingston Bay. Living in long chains." Moreover, Ehrenberg (1853: 522) wrote about Dickie and the origin of the sample: "Through the Russian academician Mr. von Hamel, Dr. Dickie from Aberdeen in England has sent me three samples of high Nordic microscopical life which were collected during the expedition of Captain Penny from 1850–1851." (translated from German).

Although the label of the sample reads *Melosira arctica* in G. Dickie's handwriting (Figure 4), Ehrenberg (1853) published it under the genus name *Gaillonella* as *Gaillonella arctica*. Since G. Dickie published a diagnosis (Dickie 1852), the name "*Melosira arctica* Dickie" is validly published according to the International Code of Botanical Nomenclature (Greuter et al. 2000), rendering Hustedt (1930), Syvertsen and Hasle (1988), Snoeijs (1993) correct in citing Dickie as author. This is in contrast to other authors following Ralfs (in Pritchard 1861) who transferred Ehrenberg's name "*Gaillonella arctica*" to the genus *Melosira*, creating therefore the author combination (Ehrenberg) Ralfs which is incorrect.

Since we are using Dickie's original material from the Ehrenberg Collection for the documentation of *Melosira arctica*, we are here designating the vouchers, which can be consulted for further studies.

Vouchers   Mica preparation 271711-a blue, Ehrenberg Collection, BHUPM (illustrated here in Figures 7–10; the entire mica strip is Figure 5); and SEM preparation B 400 040 257, Berlin-Dahlem Botanic Garden and Botanical Museum (Figures 11–28).

Further material   Illustrations from Ehrenberg's drawing sheet 2264 (Figure 3) were published in Ehrenberg (1854, pl. 35 A IV Figures 1–2).

Locality   Tiefgrund [seabed], Melville Bay 74° 40′ N, July 1850, Penny's Expedition.

Original material (Figures 3–28)

Melosira arctica is a colonial species where the cells are mechanically held together in long filaments or chains by interlocking collars (carinae) and persisting parental girdle
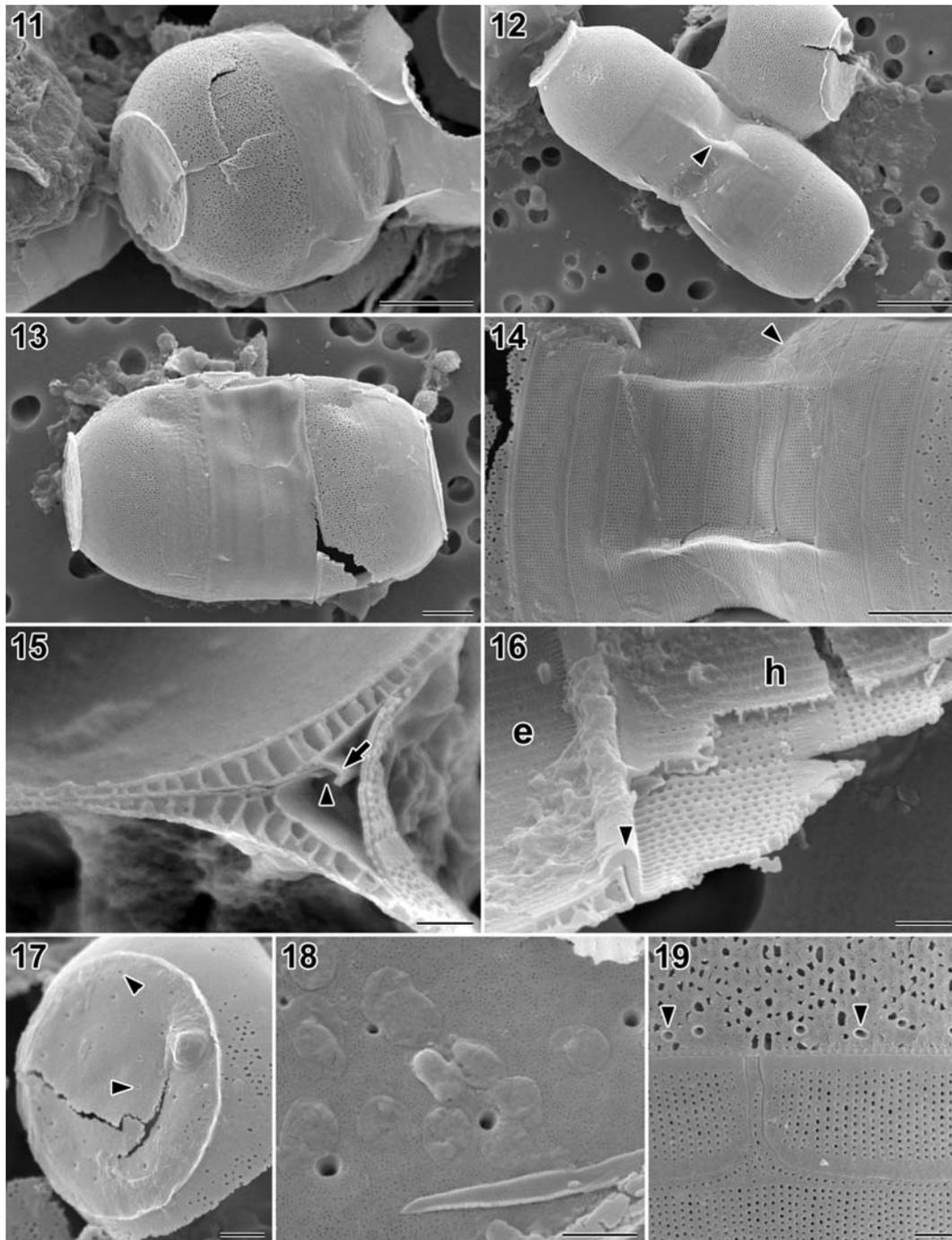
Figures 11–19   Original material of *Melosira arctica* var. *arctica* from the Ehrenberg Collection at BHUPM: external views in SEM, Ehrenberg's sample No. 1796.

(11) Newly divided globular valve. Scale bar=10 μm. (12) Two cells remaining attached after division. Note wrinkled parental cingulum (arrowhead). Scale bar=10 μm. (13) Cell strongly elongated by addition of copula, ready to divide; note the size difference of collars (carinae). Scale bar=5 μm. (14) Parental cingulum after division (sibling valve outline discernible underneath, arrowhead). Scale bar=5 μm. (15) A section of a sibling valve junction, the overlapping larger carina (arrow) on the top of a smaller one (arrowhead). Scale bar=1 μm. (16) Junction between valves and a valvocopula (arrowhead); note that the copula underlaps the epivalve (e) and overlaps the hypovalve (h). Scale bar=1 μm. (17) Valve centre with the carina, note 2 rings of rimoportulae (arrowheads). Scale bar=2 μm. (18) External openings of central rimoportulae, note difference in sizes. Scale bar=1 m. (19) Junction of valve mantle with copulae. Note external openings of irregularly spaced marginal portulae (arrowheads); ligula lies beneath the ends of the copula. Scale bar=1 μm.

bands (Figures 6–10, 11–12, 15). Chloroplasts are golden-yellow (based on Ehrenberg's drawing, Figure 3), numerous and polygonous (as preserved in the original material and discernible in SEM preparations).

The frustules are nearly spherical in girdle view (Figures 6–10), becoming ellipsoidal (Figures 7, 9–10, 12) as new girdle bands are added as the cells grow in preparation for division (Figure 13). Young frustules consist of two
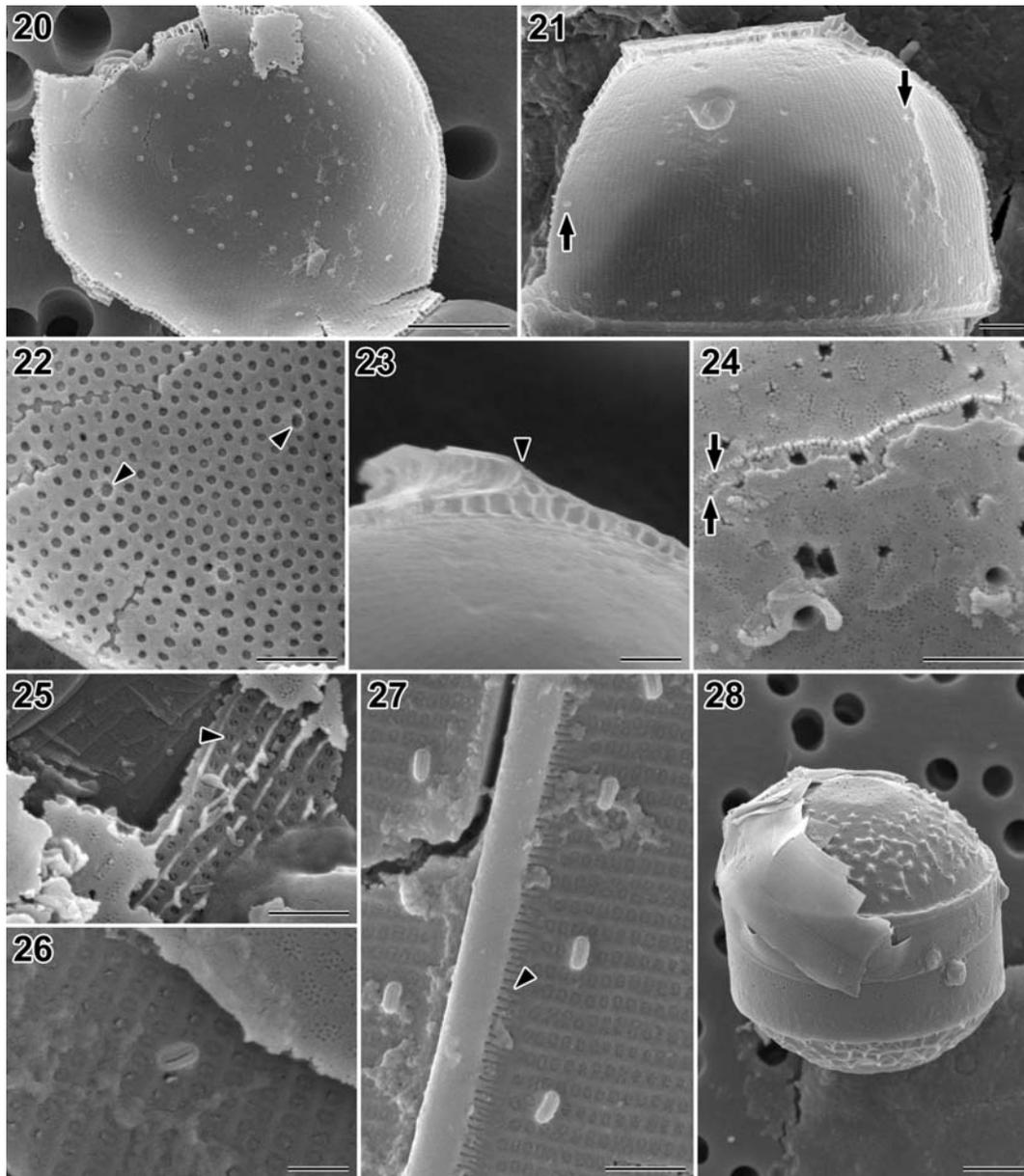
Figures 20–28 Original material of *Melosira oarctica* var. *arctica* from the Ehrenberg Collection at BHUPM: internal and external views in SEM, sample No. 1796.

These 150-year-old specimens are partially covered with dried, natural mucilaginous matter. The material was too fragile to subject it to chemical oxidation. Consequently, resolution of the finest frustule microstructures is imperfect. For these details recent frustules from Chukchi Sea and Baffin Bay are shown in Figures 33–41. (20) Internal valve showing the distribution and the number of rimoportulae towards the valve centre. Scale bar=5 μm. (21) Internal view of the valve mantle exhibiting the ring of marginal rimoportulae; note the irregularly located rimoportulae in the upper part of the mantle (arrows). Scale bar=2 μm. (22) Internal view of basal silica layer showing the large openings which will become rimoportulae (arrowheads) and the areolation in the valve face centre. Scale bar=1 μm. (23) A fractured carina (arrow) showing internal locula, note the absence of projected extensions of the walls of underlying loculae seen in *M. nummuloides* (Crawford 1975, his Figures 6 and 7 and Round et al. 1990, their Figure h). Scale bar=1 μm. (24) External view of the valve face showing the clusters of minute pores and the remnants of a broken carina. Note minute pores underneath the carina (arrows). Scale bar=1 μm. (25) Broken valve showing exposed external surface of basal silica layer with longitudinal thickenings between loculae and pores with rota (arrowhead). Scale bar=1 μm. (26) Inner opening of the rimoportula. Scale bar=0.5 μm. (27) Internal view at the junction of the valve with the copula showing the ring of rimoportulae and the fimbriate edge of the valvocopula (arrowhead), compare to Crawford 1975, his figure 4. Scale bar=1 μm. (28) Spore with thick stellate markings, similar to those reported in Crawford 1975, his figures 9–11. Scale bar=5 μm.

valves and a valvocopula. One margin of the valvocopula (Figure 16, arrowhead), which carries delicate fimbria (Figure 27, arrowhead), underlaps the epivalve and lines up internally the distal edge of the valve mantle. The other margin of the valvocopula overlaps the hypovalve externally. Prior to cell division, new open bands are added (Figures 13 and 14) which overlap and carry a long and narrow ligula (Figure 19). The ornamentation pattern of the bands is considerably finer than those on the valve (Table 1) and consists of straight, parallel rows of minute

Table 1 *Melosira arctica*: summary of morphometrics for *M. arctica* v. *arctica* and *M. arctica* v. *krembsii* from original material (Melville Bay) and recent populations from Baffin Bay, Chukchi Sea and off the Alaskan coast.

Variety	Source		Valve width (μm)	Valve height (μm)	Rows of loculae (in 10 μm)	Pores (in 1 μm)	Rimoportulae (in 10 μm)	Number of pores below rimoportula	Rows of pores on copulae (in 10 μm)
v. *arctica*	Melville Bay	N	46	45	80	49	69	19	54
		Min	17.3	9.1	32.7	5.0	4.0	0.0	39.6
		Max	32.9	15.0	43.2	6.2	8.8	3.0	49.5
		Mean	23.1	12.2	36.4	5.5	6.1	1.2	43.3
		SD	3.5	1.5	1.9	0.3	1.2	0.8	2.1
	Chukchi Sea	N	46	41	52	32	45	30	41
		Min	17.1	13.3	31.1	4.8	3.4	0.3	33.9
		Max	41.9	20.7	39.7	6.1	6.5	4.3	46.7
		Mean	29.1	17.1	35.0	5.3	4.8	1.6	42.9
		SD	5.8	1.7	1.8	0.3	0.8	0.9	1.9
	Baffin Bay	N	40	41	53	31	53	48	30
		Min	14.4	11.3	31.7	5.1	3.5	0.0	39.7
		Max	27.7	16.5	40.5	6.1	6.9	3.5	45.7
		Mean	17.7	13.5	35.5	5.5	5.2	1.3	42.0
		SD	2.7	1.2	1.9	0.2	0.8	0.7	1.3
v. *krembsii*	Culture from offshore Alaska	N	44	35	45	40	26	26	30
		Min	5.0	5.3	39.7	4.7	2.2	1.5	54.7
		Max	17.5	15.3	51.4	6.0	4.3	9.5	74.9
		Mean	12.0	9.4	44.3	5.2	3.1	4.0	63.6
		SD	3.8	1.7	2.8	0.3	0.5	1.9	5.9

N: number of specimens measured; Min: minimum value; Max: maximum value; SD: one standard deviation.

pores, 40–50 rows in 10 μm (Figures 13, 14, 16 and 19). The bands appear lightly silicified and often collapse onto the sides of the sibling valves (Figures 12 and 14).

In girdle view, the valves are hemispherical (Figures 7–11) with the valve face gently sloping into the mantle, 17–33 μm in diameter and 9–15 μm high (Table 1). A few larger valves with a diameter of about 40 μm were observed on the original mica preparation, but these large specimens were not retrieved in SEM. In the type material, both small and large valves have a hemispherical shape. The pervalvar axis of the valve is consistently about one half of the valve diameter.

The external valve surface is smooth (Figures 7–13), except that each valve carries a single, narrow carina (collar) consisting of a circular thickening located about mid-way or less to the valve's diameter (Figures 11–13, 17). Adjacent valves interlock their collars (Figure 15, arrow and arrowhead) with one margin overlapping its sibling (Figure 15). The different structure of the locking carinae in sibling valves may result in heterovalvy of the frustule (Figures 12, 13). Carinae are made of a thin, slightly raised siliceous fold of the external layer of the valve (Figure 23, arrowhead). Internally, carinae are not supported by extensions of lateral walls of locular areolae present in a morphologically similar species, *Melosira nummuloides* (Dillwyn) Agardh.

The valve is loculate (Figures 15, 23) forming elongate rectangular chambers with the longest sides of the loculae running between the single rows of pores and appearing more silicified (Figure 25). One loculus (or chamber) may be occluded externally by more than one field of minute pores and internally by several larger pores with rotae (Figure 25, arrowhead).

The outer layer of silica is ornamented with parallel (on the mantle) and radial (on the valve face) rows of irregularly sized clusters of minute pores (Figures 19, 24) also discernible under the carina (Figure 24, arrows). The basal silica layer of the valve is perforated by larger pores with rotae, 32–43 rows in 10 μm (Figures 21, 26, 27). Along one row, there are 5–6 pores in 1 μm (Table 1). A ring of inconspicuous external openings of the rimoportulae occurs near the margin of the mantle (Figure 19, arrowheads). Additionally, rimoportulae are scattered throughout the circumference of the whole mantle (Figure 21, arrows). On the valve face, two to three irregular rings of rimoportulae occur more or less centrally with respect to the carina (Figure 17, arrowheads; Figure 20; Figure 22, arrowheads); 17–28 rimoportulae on vegetative valves, much less on the spores. External openings of the valve rimoportulae vary in size (Figures 17 and 18), but internally they are identical on the valve and the mantle. Rimoportulae consist of a short internal lipped tube (Figures 26 and 27), which opens externally in a simple circular pore with no tube or rim (Figures 17–19). Rimoportulae are irregularly spaced along the margin of the mantle (Figure 21). Marginal rimoportulae are located close to the valve margin, on average 1.2 pores with rotae above the structure-less margin (Table 1).

Occasionally a few strongly silicified cells, called spores (e.g., Gran 1904), were observed, usually in pairs. Spores carried no carina and had distinct stellate thickenings on the valve mantle (Figure 28). Each spore car-

ried one valvocopula and rings of rimoportulae in numbers and distribution patterns similar to those of the vegetative cells.

Contemporary material (Figures 29–41)

Representative specimens from the Chukchi Sea are presented in Figures 29–33, 35, 38 and 40, while those from the North Water polynya in Baffin Bay are shown in Figures 34, 36, 37, 39 and 41. Both samples contained lightly silicified cells and spores (Figure 32). The morphological characteristics of the frustules were similar to those of the original material. The size range differed somewhat between these samples and the original material, but scatter plots of the biometrics of all three populations indicate that the valve features overlap in all measurable characters (Table 1); plots of selected characters are shown in Figures 42–45. The Chukchi Sea sample contained auxospores and initial cells. This allows us to postulate that the maximum valve diameter for this species is close to 45–50 μm. The presence of post-reproductive cells in this population likely accounts for slightly greater means of some biometric data.

Emended description of *Melosira arctica* Dickie var. *arctica* emend. Kaczmarska *et* R. Jahn

Cells are spherical (shortly after division) to ellipsoidal (prior to division), 14–45 μm in diameter. Valves hemispherical, 9–21 μm in pervalvar axis, with sometimes very small carinae. Carinae of the sibling valves interlock. Carinae are absent on spores. Vegetative valves loculate, with 31–43 rows of loculae in 10 μm and 5–6 rotae pores in 1 μm along a row. Rimoportulae are small, simple, irregularly disposed in a ring along the mantle margin, 3–9 in 10 μm, and sparsely dispersed along the mantle circumference in the upper half of the mantle height, and aggregated again in 2–3 loose rings at the valve face centre. External openings of the valve face rimoportulae decrease in size towards the centre. Mantle rimoportulae positioned close to the valve margin, 0–4.3 pores above its edge. Copulae are open, ligulate; valvocopulae perforated by parallel rows of pores, 34–50 rows of pores in 10 μm.

Description of a new variety (Figures 46–58)

In addition to the populations presented above, we also examined a culture of a diatom significantly different from *Melosira arctica* var. *arctica*.

Melosira arctica var. *krembsii* Kaczmarska *et* R. Jahn, var. nov.

Holotype   SEM-Preparation No. B 400 040 258 (illustrated here in Figure 48) *ex* culture. Further original raw material from this culture is also deposited at the Botanic Garden and Botanical Museum Berlin-Dahlem, Germany: B 400 040 259 SEM- and B 400 040 260 LM-preparation.

Isotypes   Preparation CANA 79393 (Canadian Museum for Nature, Ottawa, Canada) and preparation BRM Zu6/01 (Hustedt Collection, Alfred Wegener Institute, Bremerhaven) *ex* culture.

Locus typicus   Off the Alaskan coast in Chukchi Sea, from 10 cm long sea-ice core taken from the bottom segment of the sea-ice chunk; the material was collected by Dr. Christopher Krembs in February 2001 (71° 20′ N, 156° 40′ W).

Habitat   At the time of collection *in situ* temperature varied between -1.9 and -2.7°C. In culture the cells survived from 4 to -20°C in darkness (Krembs et al. 2002) and growth was detected in salinities ranging from about 20 to 90 psu (Krembs, unpublished data). When grown on agar with f/2 medium (Guillard and Ryther 1962), the chloroplasts appeared emerald-green rather than golden-brown. Living original material from which the culture was isolated is no longer available.

Diagnosis   *A varietate typica differt ornamentatione valvocopularum tenuiore, cum 54–75 poris per 10 μm, cingula unica rimoportularum paucarum isodiametricarum in parte centrali frontis valvae (in varietate typica 34–49 poris per 10 μm et 2–4 cingulis rimoportulis pluribus); rimoportulis marginalibus paucioribus, 2–4 per 10 μm, in distantia grandiore a margine; ordinibus striarum loculatarum tenuioribus.*

Short differential diagnosis   This variety differs from the nominate variety by the finer ornamentation of the valvocopulae with 54–75 pores in 10 μm, and a single ring of few, equally sized rimoportulae in the central part of the valve face (the nominate variety has 34–49 girdle band pores in 10 μm, and 2–4 rings with many rimoportulae within each ring); it has fewer marginal rimoportulae, 2–4 in 10 μm, located further from the valve margin; rows of loculate striae are finer.

Detailed description   *Melosira arctica* var. *krembsii* is also a colonial diatom (Figures 46 and 47). Large cells contain numerous chloroplasts while small cells have fewer, larger, lobate plastids. Cells are linked together into a filament by mucilaginous pads (in larger cells, Figure 48) or a ring of spiny protrusions (in smaller cells, Figures 49, 52). Small carinae are evident in larger vegetative valves (Figure 57), but they do not press or fit within each other as seen in the nominate variety (compare Figure 48 to Figure 15). Consequently, valves of neighbouring cells touch each other over a smaller part of the valve face (Figure 48) than in the nominate variety (Figures 7–10). The girdle band shows a structure and patterning which is similar to that observed in the nominate variety, but the rows of pores are significantly finer in the var. *krembsii* with 54–74 rows in 10 μm (Figures 49, 53 and 55).

   Large cells are nearly spherical, but become more cylindrical as the cultured cells become smaller, 5–17 μm in diameter, and 5–15 μm in pervalvar axis. With decreasing diameter, the valve outline from the girdle view becomes more conical as well (compare Figures 48 and 49). Valves are also loculate, with 40–51 rows of
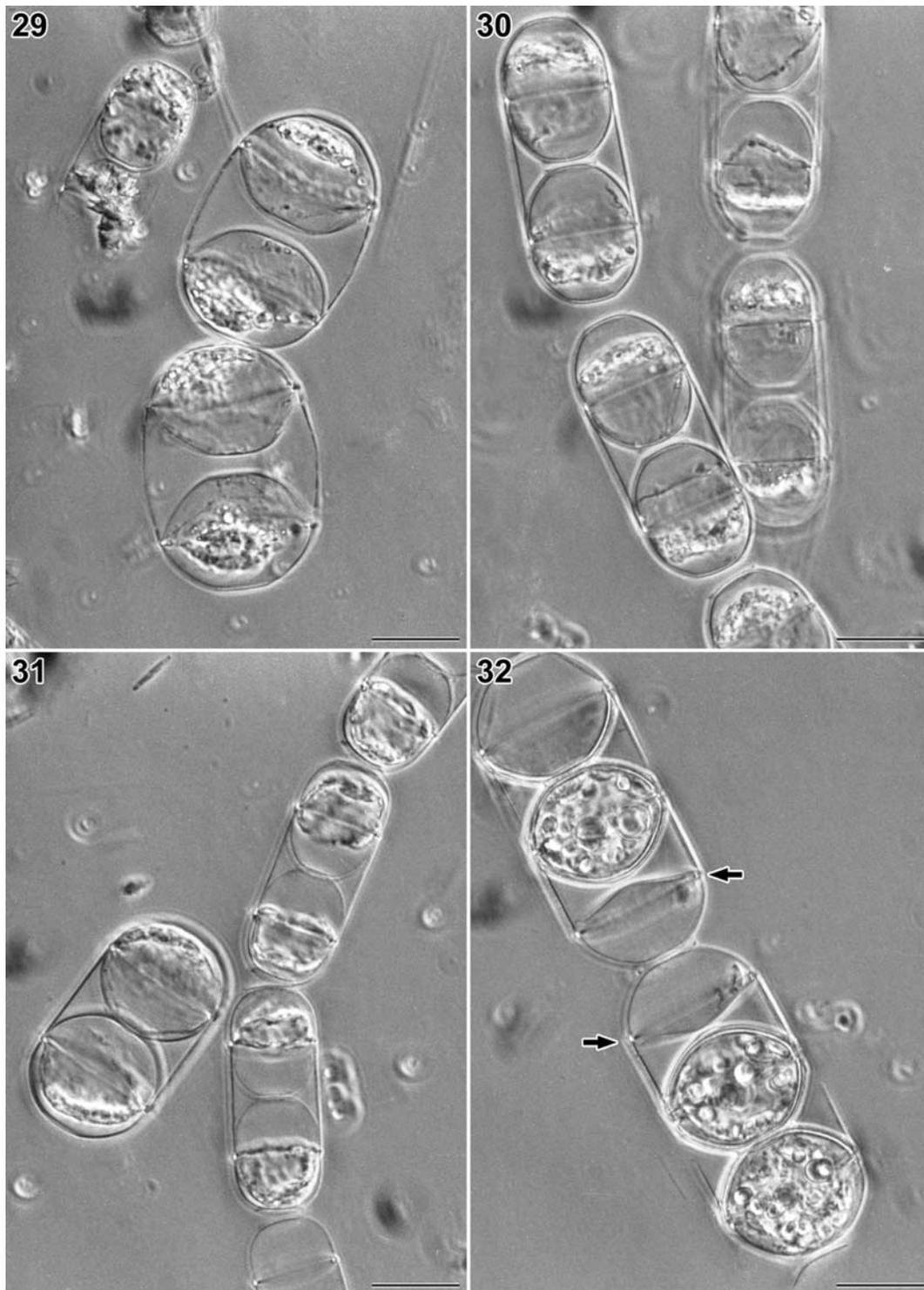
Figures 29–32   Specimens of *Melosira arctica* var. *arctica* in LM from the Chukchi Sea.
Note the size and shape range of the progressively smaller frustules. (32) Spores with supernumerary valves (arrows) in the residual cell produced during sporogenesis. All scale bars=10 μm.

loculae in 10 μm, and 5–6 pores with rotae in 1 μm along a row. The external openings of the valve face rimoportulae are often slit-shaped rather than circular as in the nominate variety (compare Figures 51 to 18). Central rimoportulae are few (most often 4–6) and are organised in one irregular ring in larger specimens (Figures 50, 51 and 54), while there is only one rimoportula on smallest valves (Figure 58). There are 2–4 marginal rimoportulae in 10 μm (Figure 55) which are located further from the mantle edge than seen in the nominate variety, a mean of 4 pores lie between the valve edge and the process (Figure 53, Table 1). Spores were also present in the culture and the supernumerary valves resulting from sporogenesis carried grossly distorted perforation patterns (Figure 56). Other characters of the frustules are the same as those observed in the nominate variety.
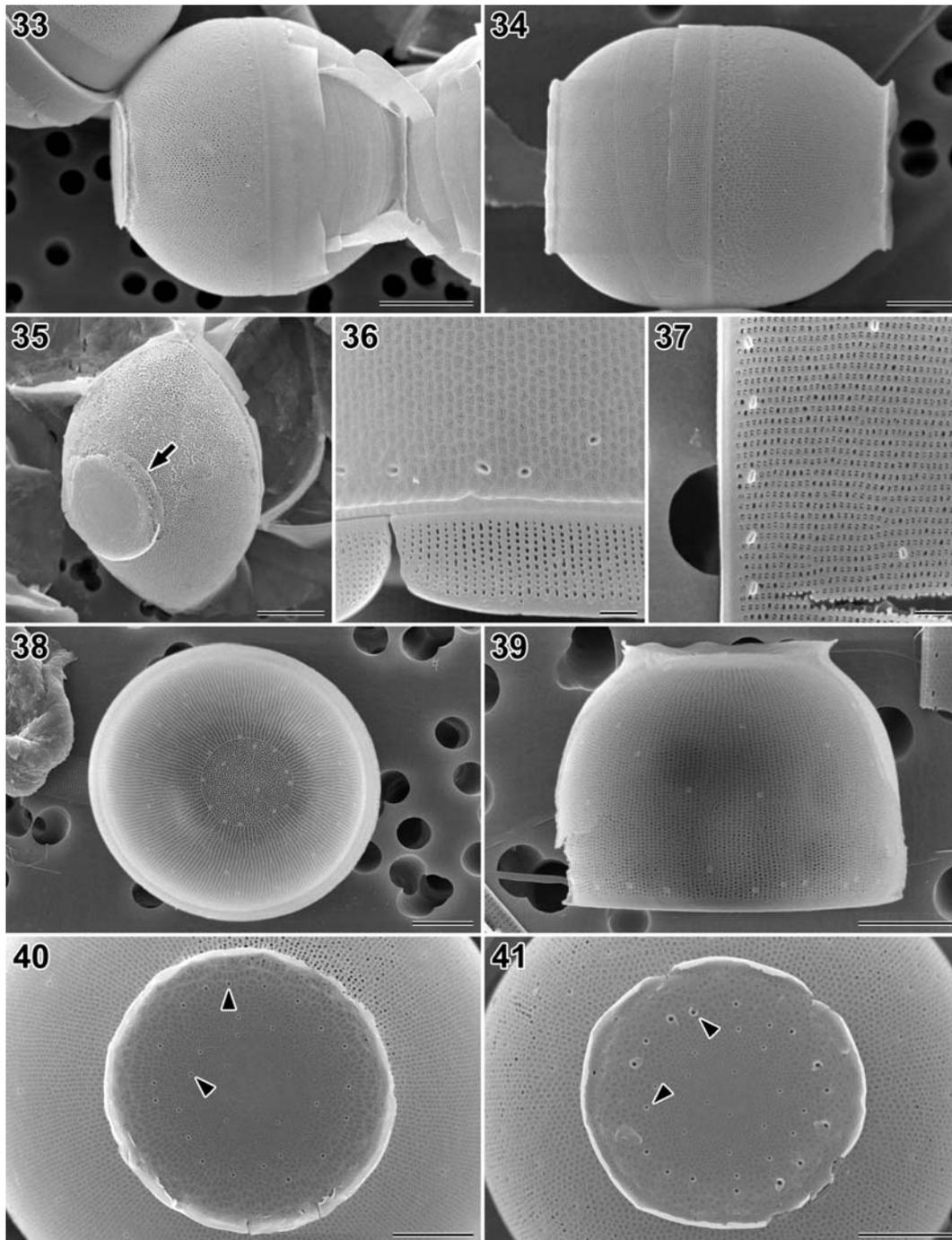
Figures 33–41 Internal and external views in SEM of *Melosira arctica* var. *arctica* from Chukchi Sea (Figures 33, 35, 38 and 40) and northern Baffin Bay (Figures 34, 36, 37, 39 and 41).
(33) External view of a spherical frustule. Scale bar=10 μm. (34) External view of an elliptical frustule. Scale bar=5 μm. (35) External view of a valve shows broken carina (arrow). Scale bar=10 μm. (36) External openings of marginal rimoportulae and ligulate valvocopula. Scale bar=1 μm. (37) Interior view of the valve mantle showing the ring of rimoportulae close to the valve margin. Scale bar=1 μm. (38) Internal valve showing radial orientation of the rows of pores with rota on the mantle and less organised pattern in the valve centre. Note the rings of central rimoportulae. Scale bar=5 μm. (39) Broken valve showing the marginal ring of rimoportulae and the dispersed rimoportulae in the upper part of the mantle. Scale bar=5 μm. (40) Valve face with the carina and a ring of external openings of rimoportulae (arrowheads) from a Chukchi Sea specimen. Scale bar=5 μm. (41) Valve face showing the carina and the ring of rimoportulae openings (arrowheads) from a Baffin Bay specimen. Note the opening is progressively smaller toward the valve centre. Scale bar=5 μm.

Discussion and conclusion

The occurrence of a carina (collar) and the absence of a corona are the two most striking criteria used to discriminate between similar species of *Melosira* (e.g., Gleser et al. 1992, Hasle and Syvertsen 1997). The only taxon carrying just a carina is *M. arctica*, but note the exceptional case reported by Stidolph (1993) and discussed below. The current concept of *M. arctica* is very broad, as it is based on features discernible using LM, i.e., the frustule

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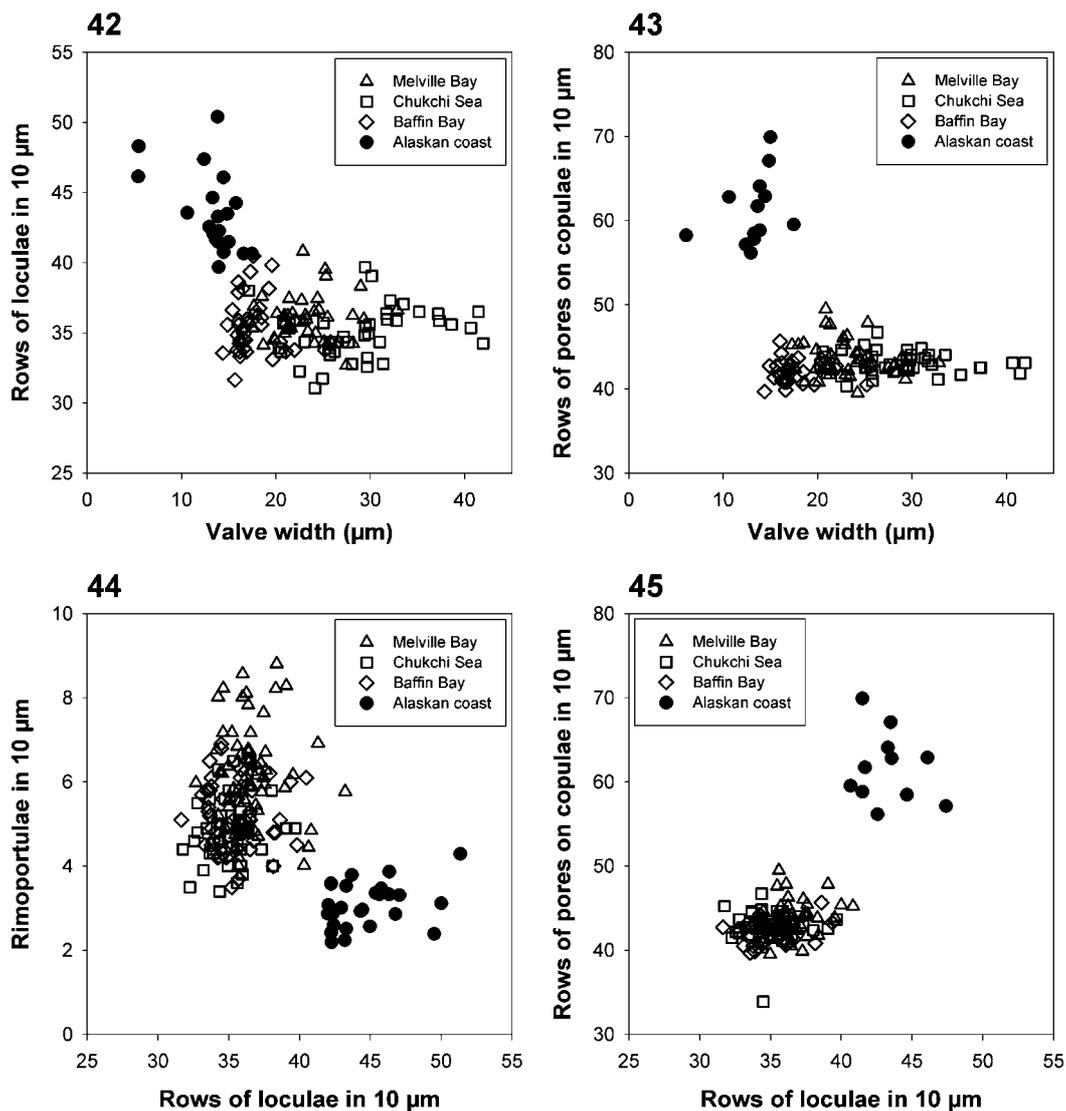
Figures 42–45   *Melosira arctica*: scatter plots showing relationships between selected biometric features measured in all populations of *Melosira arctica* var. *arctica* and var. *krembsii*.
(42) Valve width versus density of rows of loculae. (43) Valve width versus the number of pores on valvocopulae in 10 μm. (44) Number of rows of loculae in 10 μm versus density of marginal rimoportulae. (45) Number of rows of loculae versus the number of rows of pores on valvocopulae in 10 μm. Note clear separation of var. *krembsii* (Alaskan coast) in all plots.

shape and size. *M. arctica sensu lato* is relatively easy to confuse with other brackish species when only shape and size are available for comparison (Gleser et al. 1992, Hasle and Syvertsen 1997, Cremer 1998) and frustules carry only small carinae. The ornamentation of the valve is unresolvable in LM, as is the case in many species of *Melosira*. Only a few species of this genus have been examined in depth using electron microscopy, rendering comparative analysis of the frustule fine structure among the species tentative (Crawford 1971, 1975, 1978).

The diatoms closest to *Melosira arctica* are *M. nummuloides*, which has both a carina and corona, and *M. dubia* Kütz. and *M. moniliformis* (O.F. Müller) C.A. Agardh, which lack both carina and a corona. They instead may possess irregular spiny protrusions and/or papilla scattered throughout the valve. Stidolph (1993) documented exceptional specimens of possible *M. moniliformis* (as *Hyalodiscus pustulatus* Schmidt) showing a small, rim-like carina, but more taxonomic work is needed to fully

ascertain taxonomic affinity of this diatom. The vegetative valves of *M. arctica* possess a carina, but it may be reduced to a low rim in some valves. Among the four taxa mentioned above, the frustules of *M. arctica* and *M. dubia* are globular in shape rather than cylindrical. *M. arctica*, *M. nummuloides* and *M. dubia* have parallel rows of loculae, in contrast to *M. moniliformis*, which shows a reticulate pattern. *M. dubia*, however, has also a distinct concentric areolation pattern, absent in the three other species. In all three species, valve ornamentation is coarser (only up to 30 rows of areolae in 10 μm, Gleser et al. 1992) than in *M. arctica*. Other non-cylindrical members of the genus have not been investigated (and published) in sufficient detail to compare fine structures of their frustules.

The overall architecture of the frustule in *Melosira arctica* var. *krembsii* shows a clear similarity to *M. arctica* var. *arctica*. The most obvious similarities are the loculate structure of the valves, loculae with one row of rotate
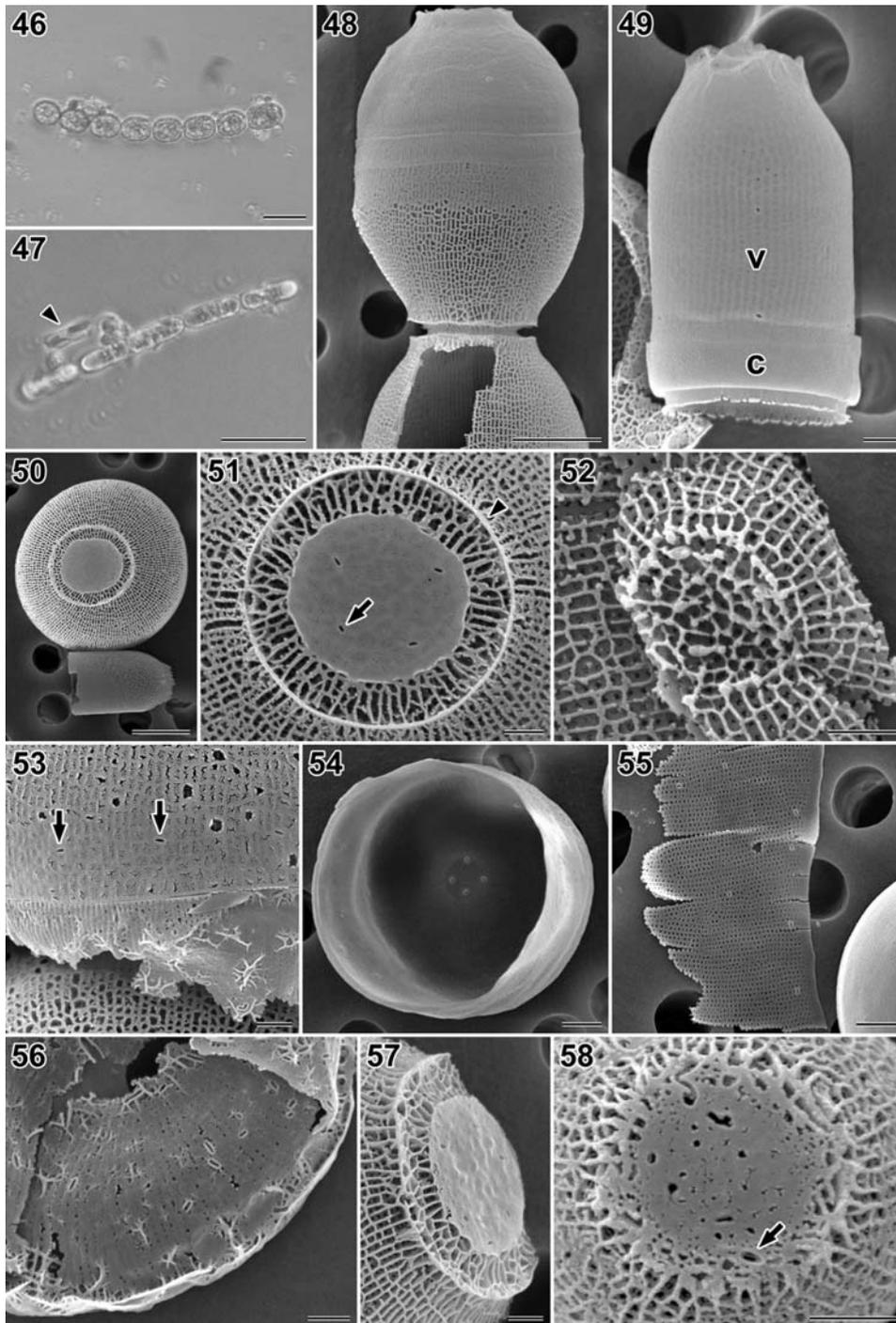
Figures 46–58   Culture specimens of *Melosira arctica* var. *krembsii* in LM (Figures 46 and 47) and SEM (Figures 48–58) from the Alaskan coast (71° 20′ N, 156° 40′ W).

(46) Colonial spherical and elliptical cells with chloroplasts. Scale bar=10 μm. (47) Colonial cylindrical cells with fewer, larger plastids. A specimen of *Attheya septentrionalis* (Østrup) Crawford (arrowhead) is positioned parallel to the chain of var. *krembsii*. Scale bar=10 μm. (48) Specimen showing one hemispherical and one hemi-ellipsoidal valve with somewhat conical upper valve, representing the holotype. Scale bar=5 μm. (49) Girdle view of a tubular hypovalve (v) and a copula (c). Scale bar=1 μm. (50) Two valves of different size, one in face view, the other in mantle view. Scale bar=5 μm. (51) Valve face centre of the large specimen from the previous figure showing carina (arrowhead) and the external openings of four rimoportulae (arrow). Scale bar=1 μm. (52) Valve face centre of a small, incomplete valve showing spiny projections off the loculae walls which in completed form may look like spines seen on the valve face in Figure 49. Scale bar=1 μm. (53) Edge of the valve mantle with external openings of marginal rimoportulae (arrows). Scale bar=1 μm. (54) Interior of the valve showing a cluster of four central rimoportulae. Scale bar=2 μm. (55) Piece of the mantle with marginal rimoportulae and pores with rotae. Scale bar=2 μm. (56) Fragment of the thin, abnormally ornamented, supernumerary valve from a residual cell produced during sporogenesis, compare to LM image of the same structure in Figure 32. Scale bar=1 μm. (57) An oblique view of a valve centre showing the low relief of the carina. Scale bar=1 μm. (58) Valve face centre of a small individual without a carina, note the single rimoportula (arrow). Scale bar=1 μm.

pores and absence of a corona and presence of a carina, albeit only on larger valves. However, several quantifiable characters distinguish var. *krembsii* from the nominate variety (Figures 42–45, Table 1). We consider the copulae pore density of particular significance because the girdle characteristics often show considerable uniformity within higher taxa (Mann 1999). It is only infrequently used even to discriminate between species (Fryxell et al. 1981). In addition, the difference in density of loculae, number and distribution of the rimoportulae are largely valve size-independent and thus noteworthy. We propose var. *krembsii* in an attempt to draw attention to the morphological heterogeneity within the species complex of *M. arctica*. We take a conservative approach and define this new taxon as a variety rather than a new species, because at this time we only have one monoclonal culture, which clearly limits the range of morphological variability that can be investigated. An earlier attempt to draw attention to existing infra-specific variability within the diatom called *M. arctica* (Syvertsen and Hasle 1988) did not, unfortunately, lead to taxonomic revision.

A review of LM-based documentation of *Melosira arctica* (e.g., Cleve-Euler 1951, figures 29d, e, g–i, k, l; Mölder and Tynni 1967, figure 2; Bérard-Therriault et al. 1999, figure 12c) indicates that the shape of the valve and the size range do not fully conform to the characteristics of the original population to which the name is tied. For example, Cleve-Euler (1951) included cylindrical valves into her concept of this species. The difference in the size of the frustules is interpreted as a result of a greater reduction in the valve diameter relative to its pervalvar axis due to successive vegetative divisions. Such a trend has not been seen in the original population, or the two others examined in this study, where the valve outline is consistently hemispherical in specimens ranging from 45 to 17 μm. We thus speculate that some of those specimens may represent our new variety.

Published SEM-based documents are rare and even combined do not provide a full assessment of the frustule structure either for *M. arctica* var. *arctica* or var. *krembsii*. A preliminary report on the fine structure of six specimens was attributed to *M. arctica* from the Barents Sea, Melville Bay, Oslofjord and the vicinity of Helsinki in the Baltic Sea (Syvertsen and Hasle 1988). The authors showed that three different morphotypes existed within their collection of specimens, and suggest that in addition to the nominate variety (specimens from the Barents Sea and the Canadian Arctic), there were two others that may represent different taxa at the rank of variety or form. Specimens from the Baltic Sea are of particular importance for this study because they carry strongest similarity to our var. *krembsii*. They also are smaller in diameter, the valves are cylindrical with conical valve face profile, they carry fewer central rimoportulae and fewer marginal rimoportulae in 10 μm, which are positioned further from the mantle margin. The most distinct diagnostic character, the density of copular pores, remains unknown, however.

Also for Baltic Sea specimens, Heimdal (1973) showed valves with tubular outlines, few central rimoportulae and sparse marginal rimoportulae, which could represent var. *krembsii*. Unfortunately, girdle patterning of Heimdal's

specimens and var. *krembsii* cannot be compared because copulae are not illustrated in her publication. It is suggested, however, that both the valve mantle and the copulae carry about 40 longitudinal rows of locular areolae. In the original material from Ehrenberg's collection, the valve mantle shows 33–43 rows of loculae in 10 μm and 40–49 rows in 10 μm for the rows of pores on the copulae. Marginal rimoportulae are more distant from each other in Heimdal's (1973) specimens and they are positioned every 10 rows of pores with rotae in two images (op. cit.). The distance between rimoportulae is more variable in Ehrenberg's material, with one such process every 3–14 rows.

In addition to the frustule morphology, *Melosira arctica* var. *krembsii* may also have a distribution pattern different from that of the nominate variety. *M. arctica* var. *krembsii* is reported mainly from more southern, subarctic regions as opposed to the clearly arctic distribution of *M. arctica* var. *arctica*. If we consider, for instance, the conical-cylinder shape of the cells as an indicator, specimens illustrated in Cleve-Euler (1951, figures 29 d, e, g–i, k, l), Mölder and Tynni (1967, figure 2), Heimdal (1973, figures 23, 29a), Sakson and Miller (1993, figure 2c) and Bérard-Therriault et al. (1999, figure 12c) show a strong similarity to our new var. *krembsii*. Wherever it has been possible for us to make clear observations in published illustrations, tubular specimens have been reported more commonly at sites south of 70° N. However, due to the small number of works providing illustration of specimens this pattern may be an artefact and supports the need for further detailed studies of these and similar taxa.

In conclusion, we emphasise that, although the name *Melosira arctica* can be found in a growing number of ecological studies (e.g., Melnikov 1997 and references therein, Harvey et al. 2004), in many cases the available documentation does not provide a clear concept of which diatom(s) this name represents. In part, this has been undoubtedly due to the lack of a detailed morphological and taxonomical study of the type population as a reference for its modern species concept.

It is also possible that we are confronted here again with a taxon (Sammelart) which includes further "cryptic" species discernible only by use of electron microscopy (Kaczmarska et al. 2005). Environmental assessment research, for example, now uses SEM routinely to discriminate between small fragilarioids (Morales et al. 2001) and soon may need to include also centric taxa such as *Melosira*. Certainly, more research is needed on the current taxonomic concept of *M. arctica* in order to ascertain the existence of cryptic species within the *M. arctica* morphology, and to establish its true geographic distribution as well as its ecological preferences.

Acknowledgements

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