

Taxonomy, Ultrastructure, and Biogeography of the *Aulacoseira subarctica* Species Complex

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Abstract We examined the *A. subarctica* species complex using type materials. The type specimen of *A. subarctica* lacks areolae on the valve face, and we recognized individuals with areolae on the valve face as another taxon, *Aulacoseira pusilla* (F.Meister) Tuji et Houki comb. nov. We examined two endemic Japanese *Aulacoseira* taxa, which are very similar to *A. subarctica*, and transferred both to varieties of *A. subarctica* because of their similarity. We also designated several lectotypes for the *A. subarctica* species complex and *A. islandica* species complex.

Key words: *Aulacoseira pusilla* (F.Meister) Tuji et Houki comb. nov., *Melosira pusilla* F.Meister, *Aulacoseira subarctica* var. *logispina* (Hust.) Tuji et Houki stat. nov. et comb. nov., *Melosira logispina* Hust., *Aulacoseira subarctica* var. *tenuis* (Hust.) Tuji et Houki comb. nov., *Melosira longispina* var. *tenuis* Hust., lectotype.

Introduction

Aulacoseira subarctica (O.Müll.) E.Y.Haw. is a very common plankton species (Lund 1971, Amblard and Bourdier 1990) and its taxonomy, biogeography, and ecology have been well studied (Gibson *et al.* 2003). However, a type examination of this species has not been done and the relationships between this species and similar taxa from Japanese lakes have not been examined. Therefore, we examined type specimens of the *A. subarctica* complex using light (LM) and scanning electron microscopy (SEM), and discuss the taxonomy of the *A. subarctica* complex.

Materials and Methods

We examined the following material:

1. A slide labeled “plankton. Heidi, Sud-Island. 28. VIII. 1901” (S)
2. A slide labeled “Thingvallavatn. 23. I. 1903” and “o.m” (S)
3. A slide labeled “Thingvallavatn. 31. III. 1903” and “o.m” (S)
4. A slide labeled “Thingvallavatn. 30. 6.

1903” (S)

The information for these three slides concurs with the sampling date and place in the description in Müller (1906), and these slides should be the syntypes for the six new taxa described in Müller (1906). We could not find any other slide or raw material for Muller (1906).

5. Raw material numbered 54 for Foged (1974), sampled from moss and stone at Thingvallavatn, South-west Island, Iceland, dated “1954. 16/7” in the Foged collection (C)

We used this raw material as the material from type locality for the new taxa described by Müller (1906) for SEM observations.

6. A slide numbered “A2/21” in the Hustedt collection (BRM)
7. Raw material numbered “As163” in the Hustedt collection (BRM)

This slide and a raw material should be used for the new description of *Melosira longispina* Hust. (Simonsen 1987).

8. A slide numbered “A2/22” in the Hustedt collection (BRM)
9. Raw material numbered “As162” in the

Hustedt collection (BRM)

This slide and a raw material should be used for the new description of *Melosira longispina* var. *tenuis* Hust. (Simonsen 1987).

10. A slide numbered "A3/61" with Meister's label in the Hustedt collection (BRM)
11. A slide numbered "A3/30" with Hustedt's label in the Hustedt collection (BRM)

These slides are labeled "*M. pusilla*" and are marked as one individual. These slides should be used for the new description of *Melosira pusilla* F.Meister by Meister.

12. Raw material sampled from Katata Lagoon, Shiga, Japan by A. Tuji in 1998/11/10 (TNS)
13. Raw material sampled from Katata Lagoon, Shiga, Japan by A. Tuji in 2000/3/18 (TNS)
14. Raw material sampled from Lake Biwa, Shiga, Japan by A. Tuji in 1999/6/4 (TNS)

The specimens examined are kept in the Botany Department of the Swedish Museum of Natural History (S), the Botanical Museum and Library of the University of Copenhagen (C), the Friedrich Hustedt Study Centre for Diatoms, the Alfred Wegener Institut für Polar- und Meeresforschung (BRM), and the Department of Botany, National Science Museum, Tokyo (TNS).

Results & Discussion

Müller (1906) described three taxa of *Aulacoseira islandica* (*Melosira islandica* f. *recta*, *M. islandica* f. *curvata*, and *M. islandica* f. *helvetica*) and three *A. subarctica* taxa (*M. italica* ssp. *subarctica* f. *recta*, *M. italica* ssp. *subarctica* f. *curvata*, and *M. italica* ssp. *subarctica* f. *tenuis*). *A. islandica* is easily distinguished from other *Aulacoseira* species using the character of the areolae, the coarse density of the rows, and the pattern of straight rows parallel to the perivalvar axis (Figs 15–22, 36–39, 40).

Taxonomy of *A. islandica*

Müller (1906) described three *Aulacoseira islandica* group taxa: *Melosira islandica* f. *recta*, *M. islandica* f. *curvata*, and *M. islandica* f. *hel-*

vetica. These three taxa were characterized using colony form and cell diameter (Müller 1906). These three types of individuals were seen in syntype slides and we designated the lectotypes for these taxon.

Melosira islandica f. *recta* O.Müll., *Jahrb. f. wiss. Bot.* 43: 56. *pl. I, f. 3.* 1906.

Lectotype (designated here): A slide labeled "Thingvallavatn. 30. 6. 1903" and "o.m" (S).

(Figs 38, 39)

Melosira islandica f. *curvata* O.Müll., *Jahrb. f. wiss. Bot.* 43: 56. *pl. I, f. 1–2.* 1906.

Lectotype (designated here): A slide labeled "Thingvallavatn. 31. III. 1903" and "o.m" (S).

(Fig. 22)

Melosira islandica subsp. *helvetica* O.Müll., *Jahrb. f. wiss. Bot.* 43: 67. *pl. I, f. 8–9 (7, 10, 11?)*. 1906.

Lectotype (designated here): A slide labeled "Thingvallavatn. 30. 6. 1903" and "o.m" (S).

(Figs 36, 37)

The morphological variation within one taxon is thought to be very large in *Aulacoseira* species, and the morphological variation within *A. islandica* described in Müller (1906) should represent the variation within one taxon.

Aulacoseira islandica (O.Müll.) Simonsen, *Bacill.* 2: 60. 1979.

(Figs 15–22, 36–39, 40, 45–51)

Basionym: *Melosira islandica* f. *recta* O. Müll., *Jahrb. f. wiss. Bot.* 43: 56. *pl. I, f. 3–6.* 1906.

Synonym: *Melosira islandica* f. *curvata* O. Müll., *Jahrb. f. wiss. Bot.* 43: 56. *pl. I, f. 1.* 1906.

Synonym: *Melosira islandica* subsp. *helvetica* O. Müll., *Jahrb. f. wiss. Bot.* 43: 67. *pl. I, f. 8–9.* 1906.

Type locality: Thingvallavatn, Iceland.

Valves 7–27 μm in diameter, mantle height 4–21 μm . Valves usually longer than broad. The circular form areolae on the mantle always run in straight rows parallel to the perivalvar axis with 11–12 perivalvar striae/10 μm and 12–13 areolae/10 μm . Linking spine sector form. Sulcus exists. Several rimoportulae exist off sulcus and

sometimes near valve face. This species should not belong to the *A. subarctica* complex.

Taxonomy of *A. subarctica*

Müller (1906) described three *A. subarctica* taxa: *M. italica* ssp. *subarctica* f. *recta*, *M. italica* ssp. *subarctica* f. *curvata*, and *M. italica* ssp. *subarctica* f. *tenuis*. These three taxa were characterized using colony form and cell diameter. These three types of individuals were seen in syntype slides and we designated the lectotype for these taxa. We also examined the ultrastructure of these taxa using the material from the type locality (Thingvallavatn, Iceland).

Melosira italica subsp. *subarctica* f. *recta* O. Müll., *Jahrb. f. wiss. Bot.* 43: 79. *pl. II, f. 7.* 1906.

Lectotype (designated here): A slide labeled “Thingvallavatn. 31. III. 1903” and “o.m” (S).

(Figs 1–2)

Melosira italica subsp. *subarctica* f. *curvata* O. Müll., *Jahrb. f. wiss. Bot.* 43: 79. *pl. II, f. 8.* 1906.

Lectotype (designated here): A slide labeled “Thingvallavatn. 31. III. 1903” and “o.m” (S).

(Fig. 14)

Melosira italica subsp. *subarctica* f. *tenuis* O. Müll., *Jahrb. f. wiss. Bot.* 43. *pl. II, f. 9.* 1906.

Lectotype (designated here): A slide labeled “Thingvallavatn. 31. III. 1903” and “o.m” (S).

(Fig. 9)

The morphological variation within one taxon is thought to be very large for *Aulacoseira* species and this morphological variation within *A. subarctica* is likely the variation seen within one taxon.

Aulacoseira subarctica (O. Müll.) E.Y.Haw., *Dia. Res.* 5: 195. 1988.

(Figs 1–14, 23–35, 41–44, 52–54)

Basionym: *Melosira italica* subsp. *subarctica* f. *recta* O. Müll., *Jahrb. f. wiss. Bot.* 43: 79. *pl. II, f. 7.* 1906.

Synonym: *Melosira italica* subsp. *subarctica* f. *curvata* O. Müll., *Jahrb. f. wiss. Bot.* 43: 79. *pl. II, f. 8.* 1906.

Synonym: *Melosira italica* subsp. *subarctica*

f. *tenuis* O. Müll., *Jahrb. f. wiss. Bot.* 43. *pl. II, f. 9.* 1906.

Type locality: Thingvallavatn, Iceland.

Valves 3–10 μm in diameter, mantle height 5–14 μm . Valves usually longer than broad (Figs 1–14, 23–35, 41–44, 53–54). The circular areolae on the mantle run in a spiral with 16–20 peralvar striae/10 μm and 22–24 areolae/10 μm (Figs 53–54). Valve face areolae do not exist (Fig. 53). Two rows per simple spine (Figs 53–54). Linking spine does not exist. Sulcus exists. Several rimoportulae exist off the sulcus (Figs 5–8, 14, 23–24, 28, 41, 43–44) and sometimes near the valve face (Figs 9, 42).

The morphological variation within this species is thought to be very large. The length/width ratio and density of striae could change with environmental conditions (Kilham *et al.* 1986). Several studies agree with this hypothesis (Edgar & Theriot 2003).

Haworth (1988, 1990) transferred this taxon to the genus *Aulacoseira* using samples from Cambrian waters. She included two morphological types in *A. subarctica*: one lacks areolae on the valve face and usually is not wider than long (Type A) and the other has areolae on the valve face and is markedly wider than long (Type B). Only Type A individuals are found in the syntype from Iceland in this study (Figs 1–14, 23–35, 41–44). Type B is found widely in Japan (Kawashima & Kobayasi 1993, Tuji and Houki 2001; figs 69–105), and Type A is not observed in the same waters. Type A is observed from Lake Shikotsu, Hokkaido, Japan (Tuji personal observation), while we could not find Type B in this lake. Therefore, there are ecological differences between the two types. Furthermore, several morphological differences in the rimoportulae have been observed in the two types. In Type B, rimoportulae are observed only on the sulcus using SEM (Figs 103, 104) and three to five rimoportulae exist per a valve. Unfortunately, we have not succeeded in observing the rimoportulae of Type A directly using SEM and the material from type locality. However, shadows of the rimoportulae are observed using LM. Some exist

near, but not on, the sulcus (Figs 5–8, 14, 23–24, 28, 41, 43–44), and some are distant from the sulcus (Figs 9, 42). Likhoshway & Crawford (2001) observed the rimoportulae of Type A directly using SEM and reported that two rimoportulae occur near, but on, the ringleist per a valve. Although the outline of frustules has large variation, the position of the rimoportulae relative to the sulcus is very stable in the same locality; the position of the rimoportulae should be very useful for the taxonomy of *Aulacoseira* species. Likhoshway & Crawford (2001) also show the importance of rimoportula for the taxonomy of *Aulacoseira* species. Therefore, Type B is another taxon of Type A, which is *A. subarctica*.

Meister (1913) described *Melosira pusilla* from Lake Suwa, Japan. The iconotype of this species is similar to Type B of the *A. subarctica* complex (Tuji & Houki 2001). Two marked specimens labeled “*Melosira pusilla*” are found in the BRM, and should be the slides upon which that type illustrations are based. These specimens were mounted with air, and are difficult to observe in detail (Figs 55–68). Unfortunately, we could not find this taxon from the type locality. However, this species is found in many lakes and ponds in Japan, and we examined materials from Lake Biwa and its lagoon (Katata Lagoon) for this taxon (Figs 69–105). From our examination, we made a new combination for this taxon.

Aulacoseira pusilla (F.Meister) Tuji et Houki comb. nov. (Figs 53–105)

Basionym: *Melosira pusilla* F.Meister, Arch. Hydrobiol. 8: 306. pl. IV, f. 2. 1913.

Lectotype (designated here): A slide numbered “A3/619” with Meister’s label (BRM).

Type locality: Lake Suwa, Nagano Prefecture, Japan.

Valves 6–10 μm in diameter, mantle height 2–10 μm . The circular areolae on the mantle run in a spiral with 20–26 peralvar striae/10 μm and 25–30 areolae/10 μm (Figs 69–99). Valve face areolae exist (Figs 100–102, 105). Two striae per simple spine (Figs 100–101, 105). Linking spine does not exist. Sulcus exists (Figs 103–104). Several rimoportulae exist on the sulcus and not

away from the sulcus (Figs 103–104).

We also examined two taxa that are very similar to *A. subarctica* and Japanese endemic species: *A. longispina* (Hust.) Simonsen var. *longispina* and *A. longispina* var. *tenuis* (Hust.) Simonsen. Hustedt described both taxa from Lake Cyuzenji and Lake Yuno in Huber-Pestalozzi (1942). The water of L. Yuno flows into L. Cyuzenji via the Yukawa River, and both lakes can be thought of as the same body of water. Simonsen (1987) examined the slides upon which that type illustrations are based, and presented photographs of these specimens with the description of “holotype”. However, Hustedt described only the information for type locality (“Japan, Chuzenij-See” and “Japan, Juno-See”) and did not cite any specimen. In this case, these specimens can not be holotype (International Code of Botanical Nomenclature (Saint Louis Code): ICBN, Art 37.3 Note 1), and they can be considered lectotype (ICBN Art 9.8) designated by Simonsen (1987). Although, both lectotype slides include several taxa. these are very pure specimens, and do not cause a problem for the taxonomy of either taxa. Although, both species are very similar under LM, the rimoportulae form differs markedly in the two taxa. The rimoportula of *A. longispina* var. *longispina* is very simple and exists on the sulcus (Figs 128–129), while the rimoportula of *A. longispina* var. *tenuis* has a very complex structure. The rimoportulae are away from the sulcus and exist on a hollow nodule structure (Figs 159–161). These structures can be seen in LM photographs (Figs 131–133, 138–156) and observed from photographs of lectotype specimens (Simonsen 1987). This hollow nodule is not known from other *Aulacoseira* species. Although both taxa are very similar to *A. subarctica*, the long spines and coarse density of the striae differ. These differences may be geological variation and should be at the variety level.

Aulacoseira subarctica* var. *longispina (Hust.) Tuji et Houki stat. nov. et comb. nov.

(Figs 100–130)

Basionym: *Melosira longispina* Hust. in

Huber-Pestalozzi, *Phytopl. Susw.* 2: 388. *pl. 115, f. 469a.* 1942.

Lectotype (designated in Simonsen 1987): A/2/21 in the Hustedt collection (BRM), figs. 460/1–3 in Simonsen (1987).

Type locality: Lake Cyuzenji, Tochigi Prefecture, Japan.

Valves 5–14 μm in diameter, mantle height 12–15 μm (Figs 100–125). The circular areolae on the mantle run in a spiral with 10–12 pervalvar striae/10 μm and 11–14 areolae/10 μm (Fig. 130). Valve face areolae exist (Fig. 127). Two striae per simple spine (Fig. 130). Linking spine does not exist. Sulcus exists. Several rimoportulae exist on the sulcus and not away from the sulcus (Figs 128–129).

Aulacoseira subarctica var. *tenuis* (Hust.) Tuji et Houki comb. nov. (Figs 131–161)

Basionym: *Melosira longispina* var. *tenuis* Hust. in Huber-Pestalozzi, *Phytopl. Susw.* 2: 339. *pl. 115, f. 469b.* 1942.

Lectotype (designated in Simonsen 1987): A/2/22 in the Hustedt collection (BRM), Figs. 460/4, 5 in Simonsen (1987).

Type locality: Lake Yuno, Tochigi Prefecture, Japan.

Valves 4–6 μm in diameter, mantle height 15–18 μm (Figs 131–156). The circular areolae on the mantle run in a spiral with 12–16 pervalvar striae/10 μm and 15–20 areolae/10 μm (Figs 157–160). Valve face areolae exist. Two striae per simple spine (Figs 157–158). Linking spine does not exist. Sulcus exists (Figs 159–160). Several rimoportulae exist away from the sulcus (Figs 160–161).

Conclusions

For *Aulacoseira* species, the morphological variation within one taxon is very large, and there are few taxonomic characters, making it difficult to distinguish *Aulacoseira* species. The morphological characters of the rimoportulae, such as its position relative to the sulcus, number, and form, are very useful for the taxonomy of *Aulacoseira* species (Likhoshway and Crawford

2001). For direct observation of the rimoportulae, it is very important to use SEM and broken frustules. However, it is sometimes difficult to find type material and to break the frustules for observation.

In this study, we could not observe the rimoportulae of *A. subarctica* directly and did not observe North American and European specimens, except from Iceland. We plan to study the taxonomy of the *A. subarctica* complex further.

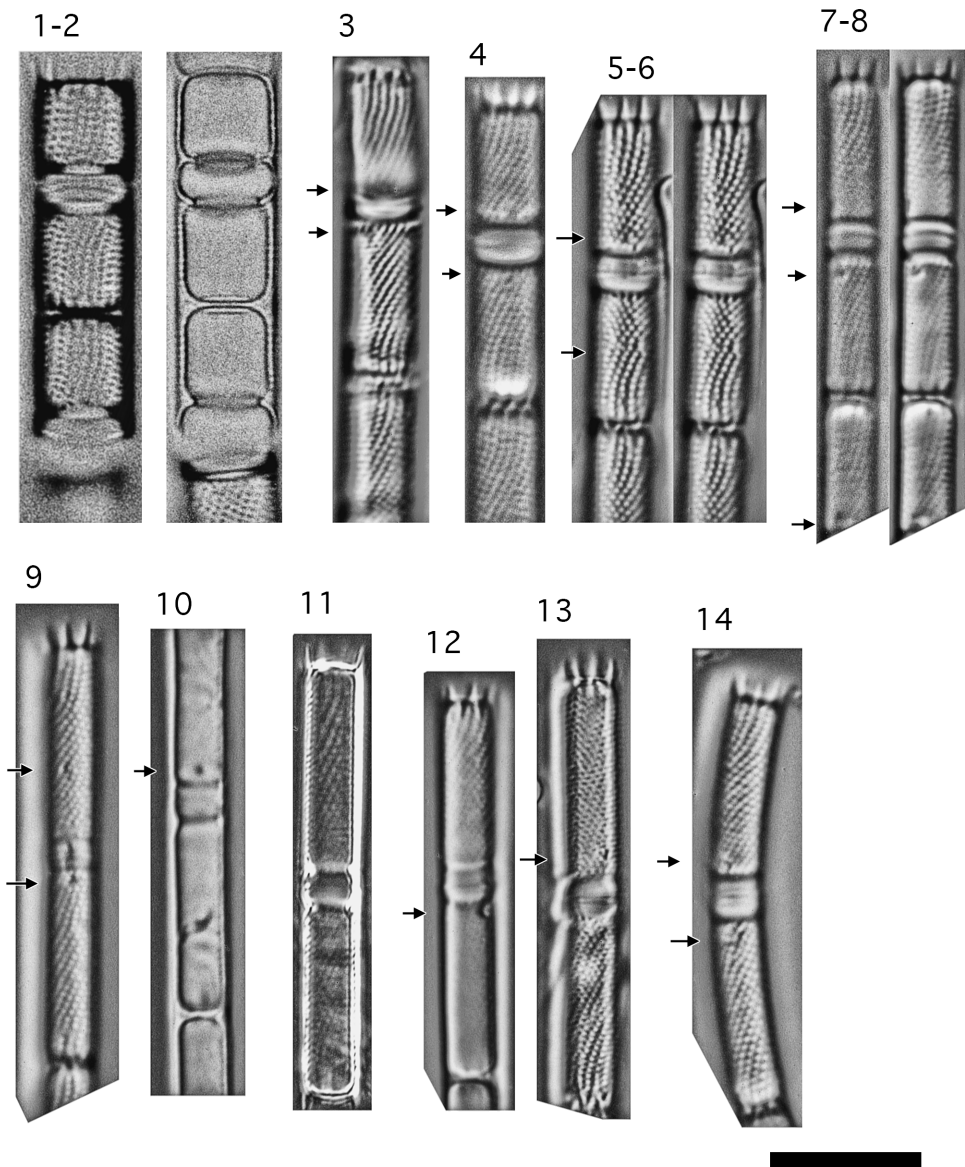
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1-14. *Aulacoseira subarctica* (O.Müll.) E.Y.Haw.

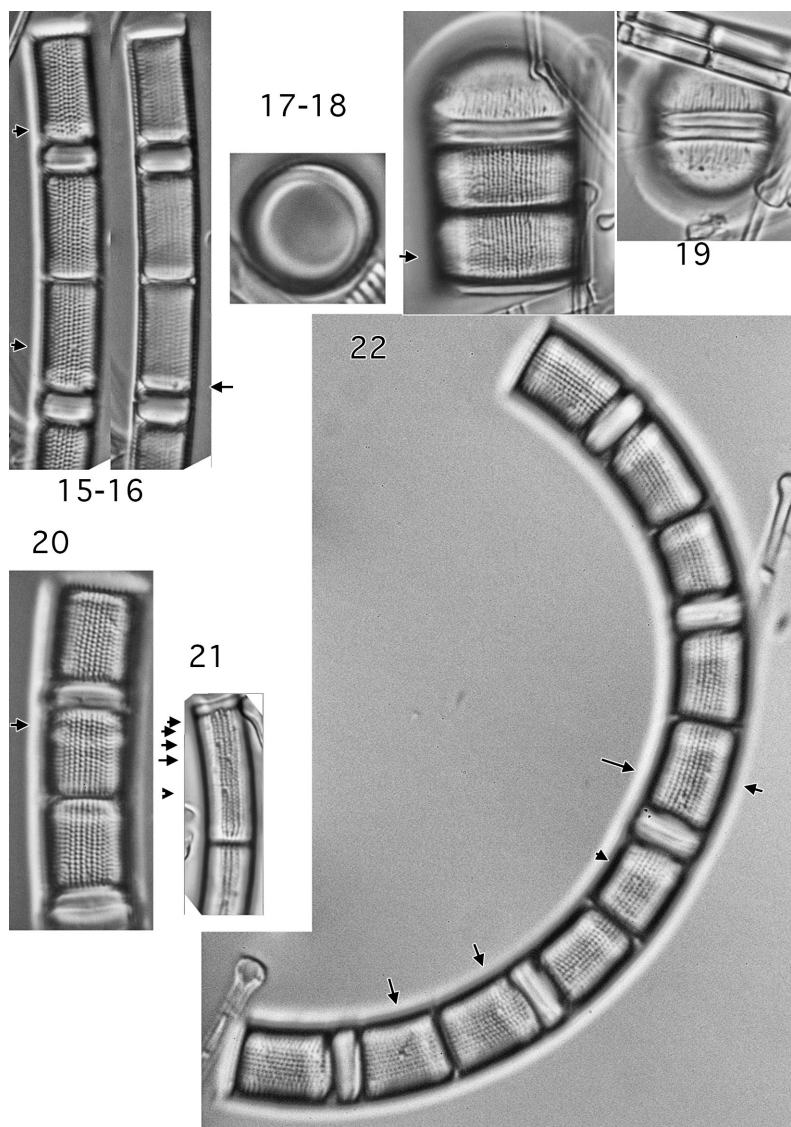
1-14. A slide labeled "Thingvallavatn. 31. III. 1903" and "o.m" (S).

1-14. Bar=10 μm . 1, 2. LM (normal light microscopy image). 3-14. DIC (differential interference contrast image). Arrow=rimoportula.

1, 2. Lectotype. *Melosira italica* subsp. *subarctica* f. *recta* O.Müll.

9. Lectotype. *Melosira italica* subsp. *subarctica* f. *tenuis* O.Müll.

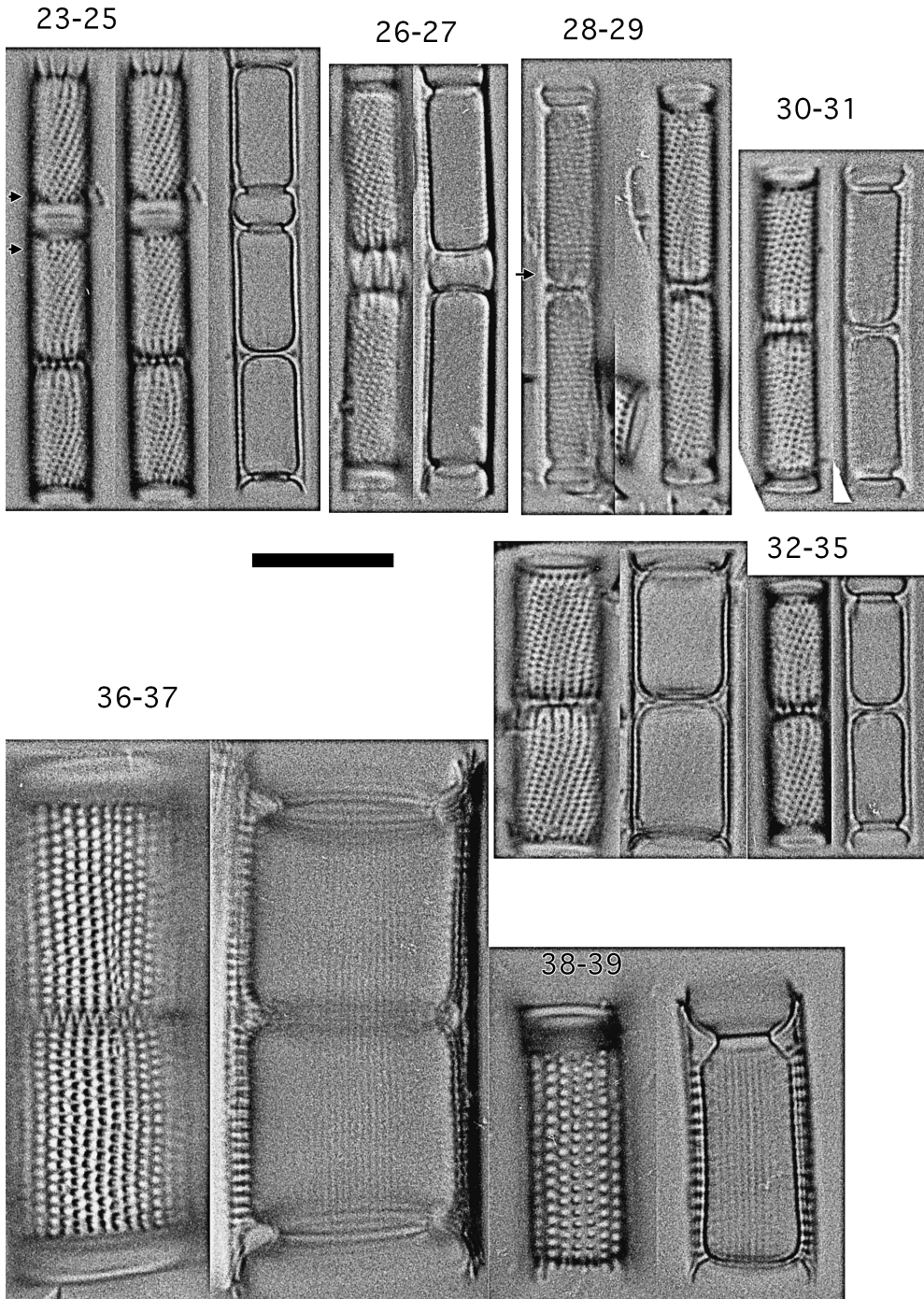
14. Lectotype. *Melosira italica* subsp. *subarctica* f. *curvata* O.Müll.



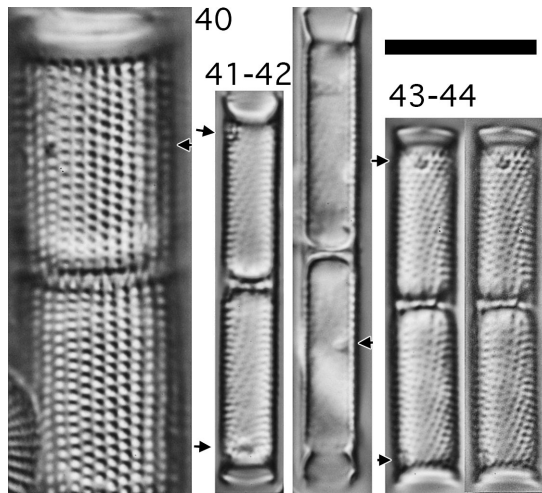
15–22. *Aulacoseira islandica* (O.Müll.) Simonsen. A slide labeled “Thingvallavatn. 31. III. 1903” and “o.m” (S).

15–22. DIC, bar=10 μ m. Arrow=rimoportula.

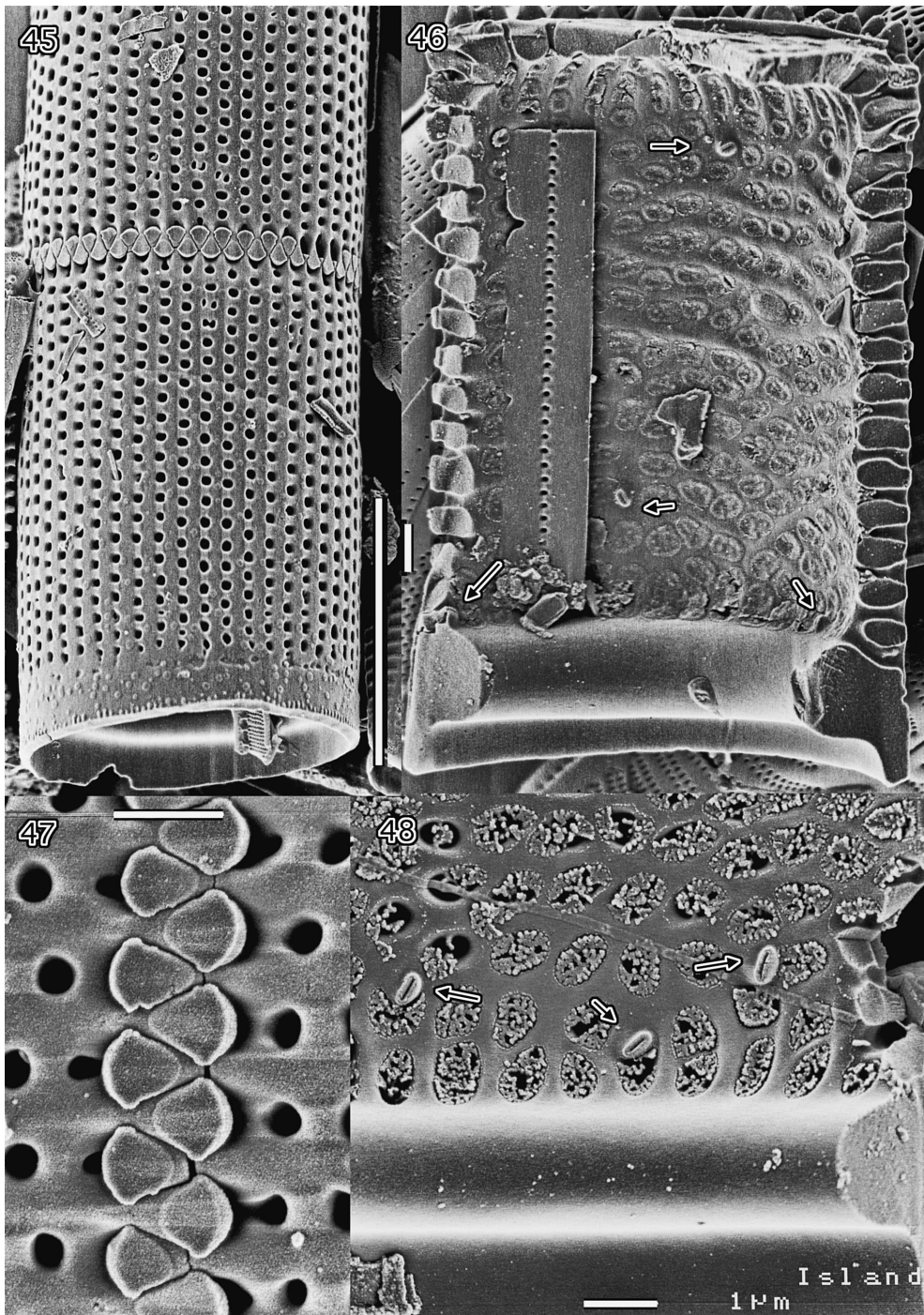
22. Lectotype. *Melosira islandica* f. *curvata* O.Müll.



23–35. *Aulacoseira subarctica* (O.Müll.) E.Y.Haw. 36–39. *Aulacoseira islandica* (O.Müll.) Simonsen.
 23–39. A slide labeled “Thingvallavatn. 30. 6. 1903” (S).
 21–39. LM, bar = 10 μ m. Arrow = rimoportula.
 36–37. Lectotype. *Melosira islandica* subsp. *helvetica* O.Müll.
 38–39. Lectotype. *Melosira islandica* f. *recta* O.Müll.



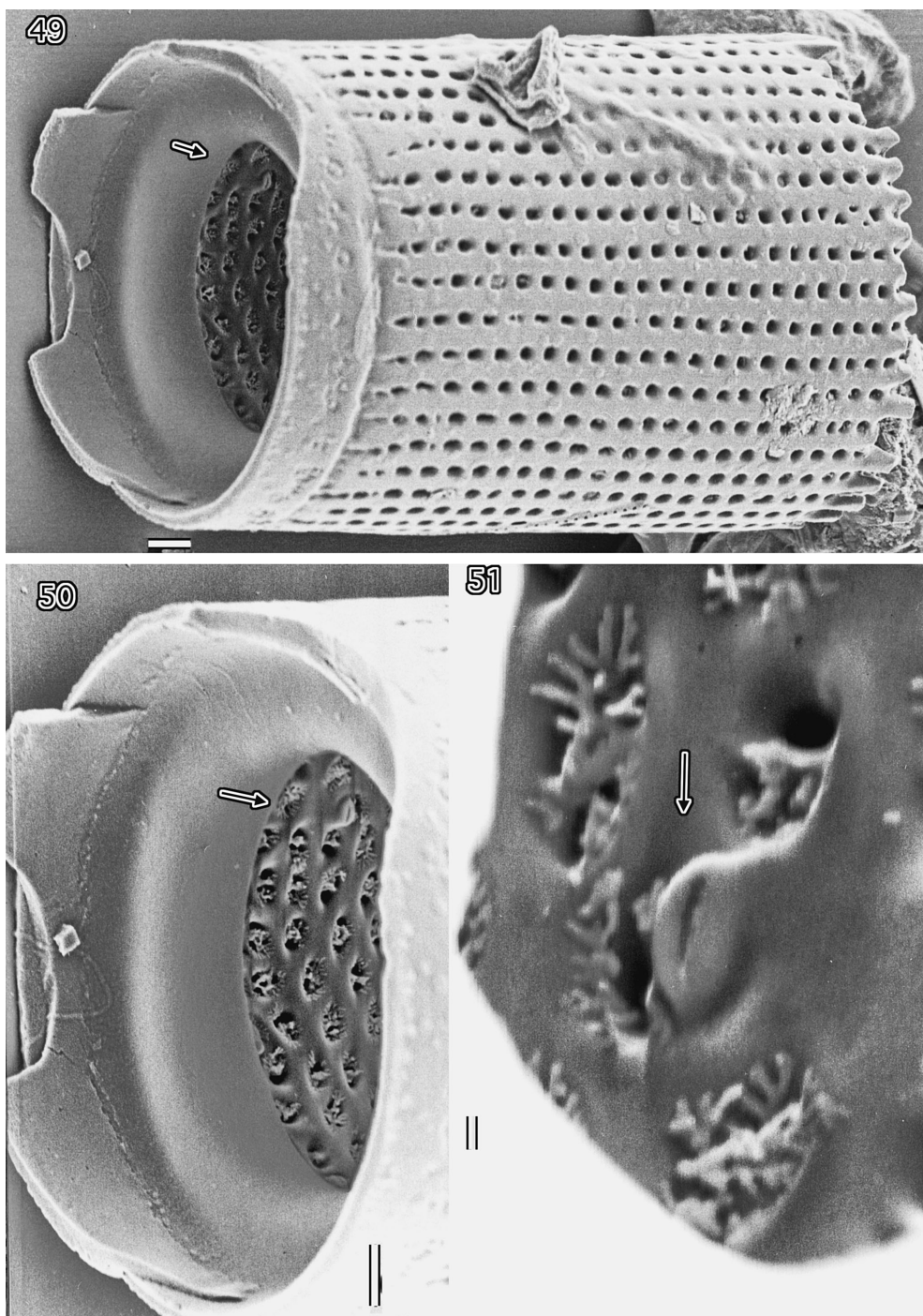
40. *Aulacoseira islandica* (O.Müll.) Simonsen, 41-44. *Aulacoseira subarctica* (O.Müll.) E.Y.Haw.
 40-44. A slide labeled "Thingvallavatn. 30. 6. 1903" (S).
 40-44. DIC, bar=10 μ m. Arrow=rimoportula.



45–48. *Aulacoseira islandica* (O.Müll.) Simonsen.

45–48. “54” for Foged (1974), Thingvallavatn, South-west Island, dated “1954. 16/7” in Foged collection. (C).

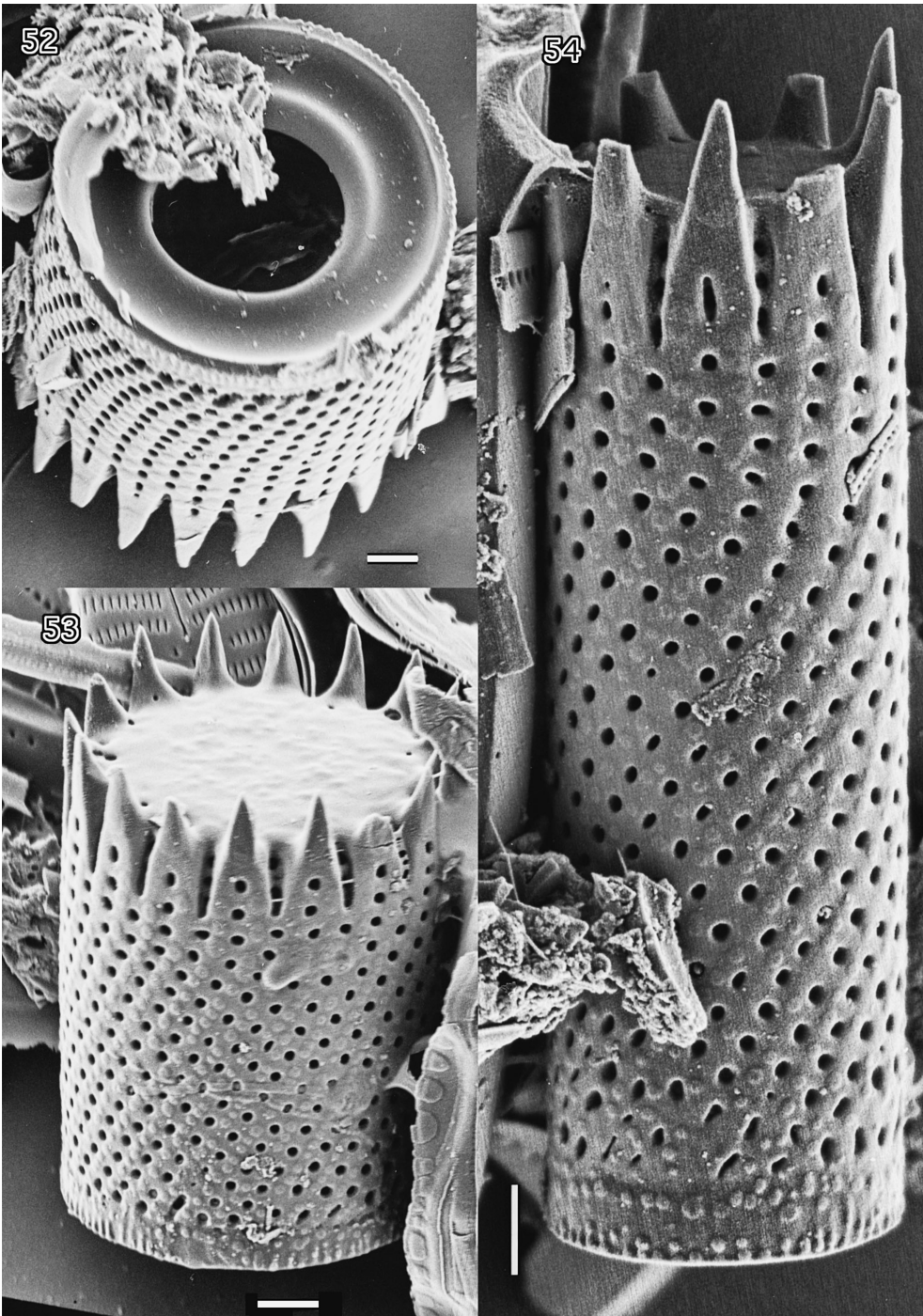
45–48. SEM. Arrow=rimoportula. 45. Whole frustule, bar=10 μm . 46. Rimoportulae exist off the sulcus and sometimes near the valve face, bar=1 μm . 47. Linking spine, bar=1 μm . 48. Rimoportulae exist off the sulcus, bar=1 μm .



49–51. *Aulacoseira islandica* (O.Müll.) Simonsen.

49–51. “54” for Foged (1974), Thingvallavatn, South-west Island, dated “1954. 16/7” in Foged collection. (C)

49–51. SEM. Showing a rimportulae off the sulcus. Arrow=rिमportula. 49–50. A rimportula exist off the sulcus, bar=1 μm . 51. A rimportulae, bar=100 nm.

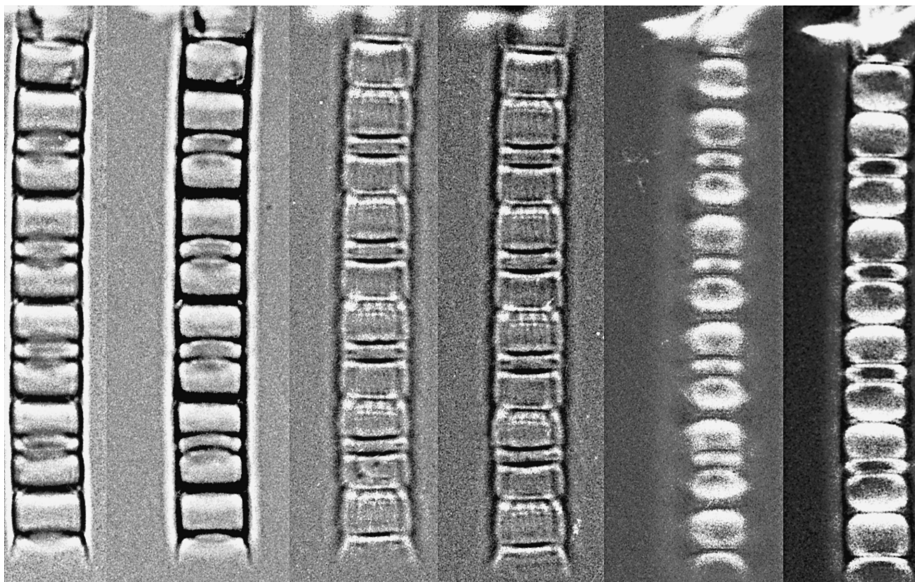


52–54. *Aulacoseira subarctica* (O.Müll.) E.Y.Haw.

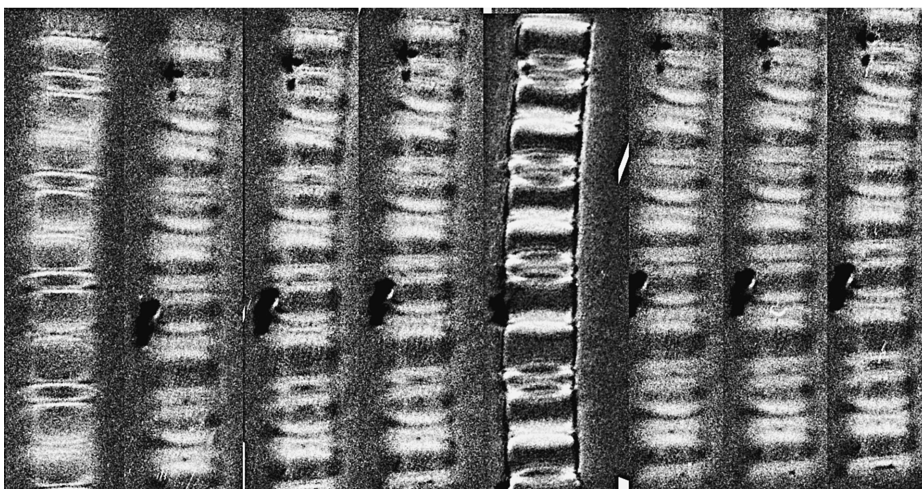
52–54. “54” for Foged (1974), Thingvallavatn, South-west Island, dated “1954. 16/7” in Foged collection. (C)

52–54. SEM, bar=1 μ m. 52. Sulcus. 53. valve face areolae is not exist. 54. whole frustule.

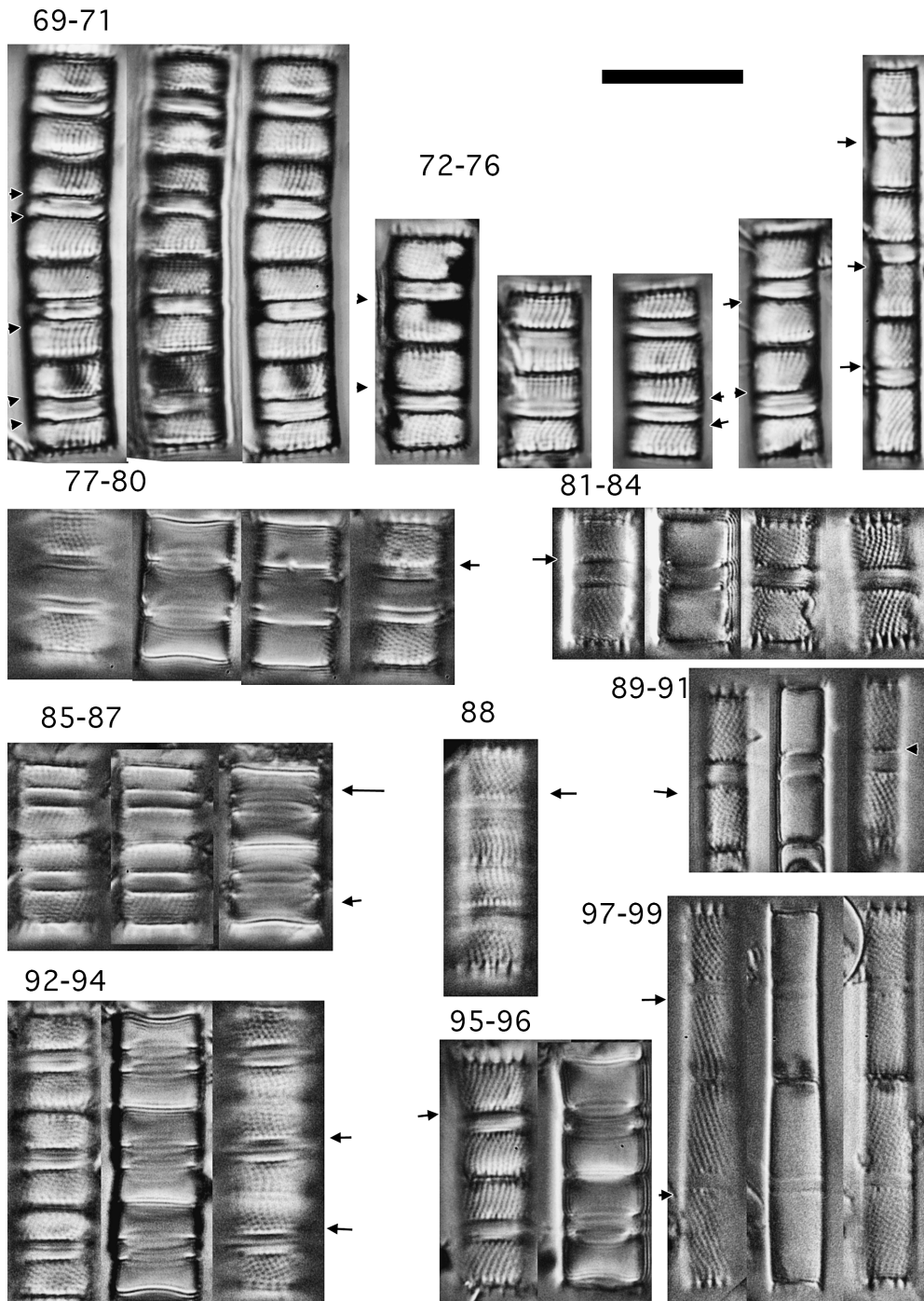
55-60



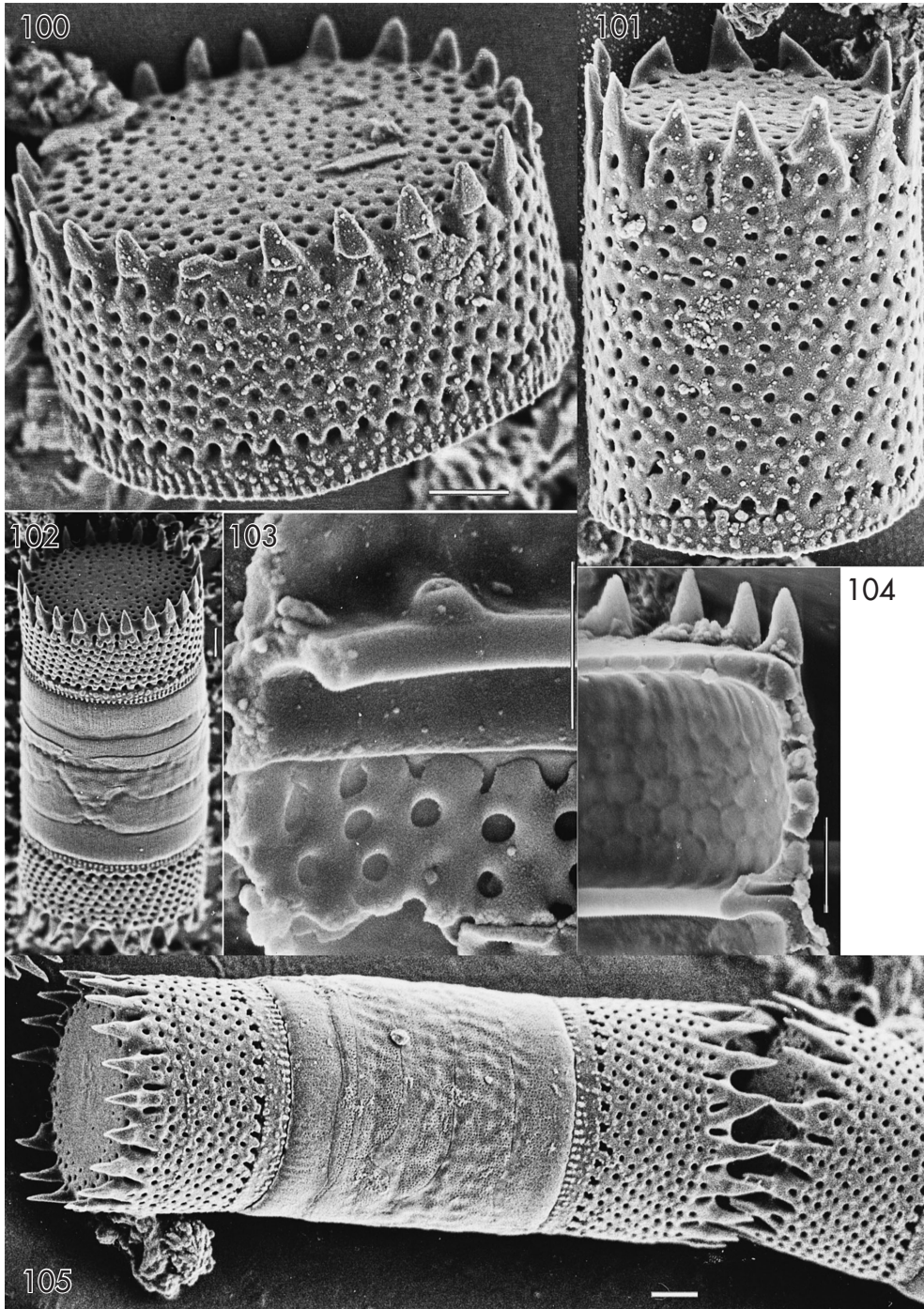
61-68



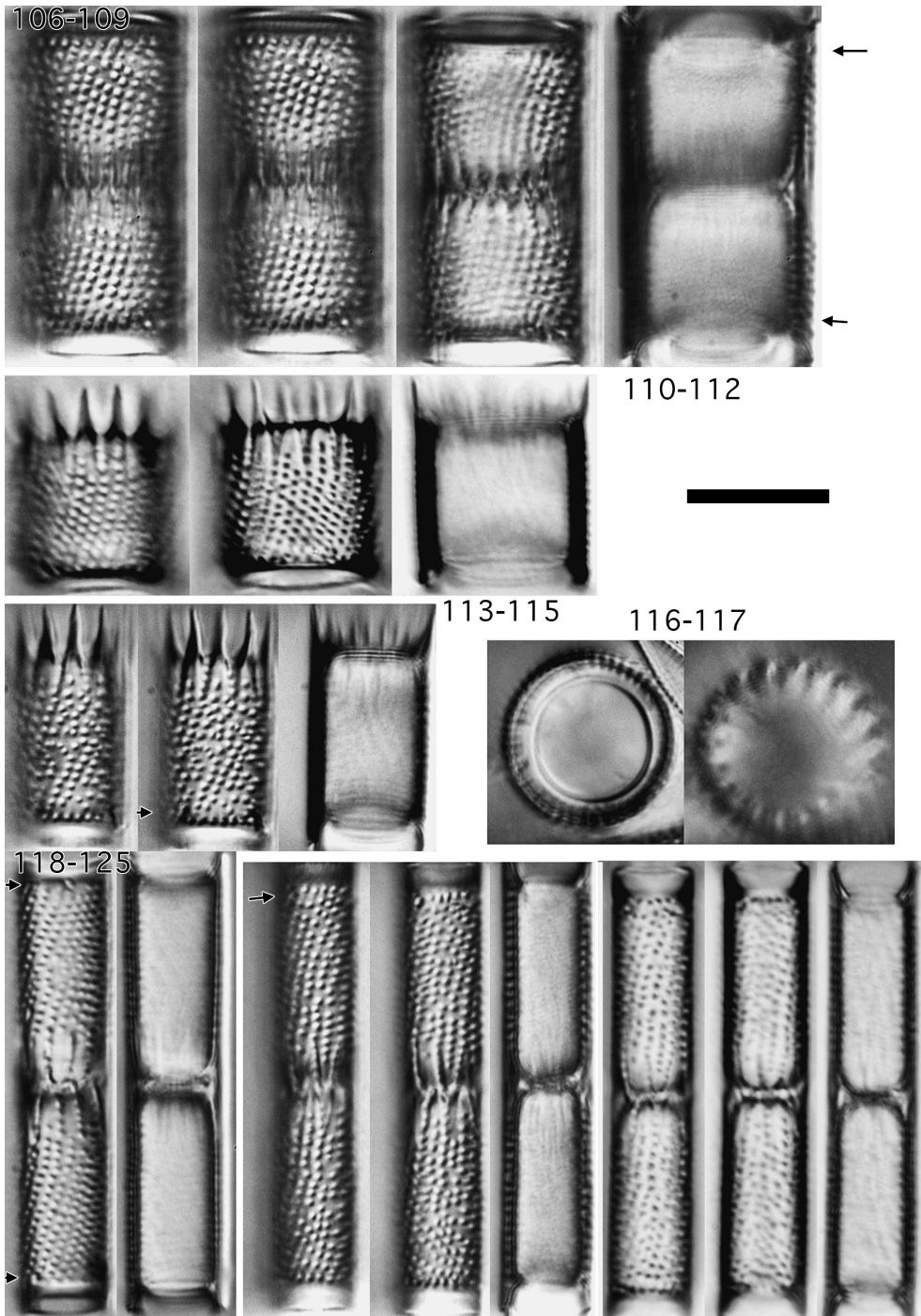
- 55–68. *Aulacoseira pusilla* (F.Meister) Tuji et Houki comb. nov.
 55–68. Bar=10 μm . 55–56. LM. 57–58, 61–68. DIC. 59–60. DC (Dark contrast image).
 55–60. Lectotype. A slide numbered “A3/61” with Meister’s label in Hustedt collection (BRM).
 61–68. A slide numbered “A3/30” with Hustedt’s label in Hustedt collection (BRM).



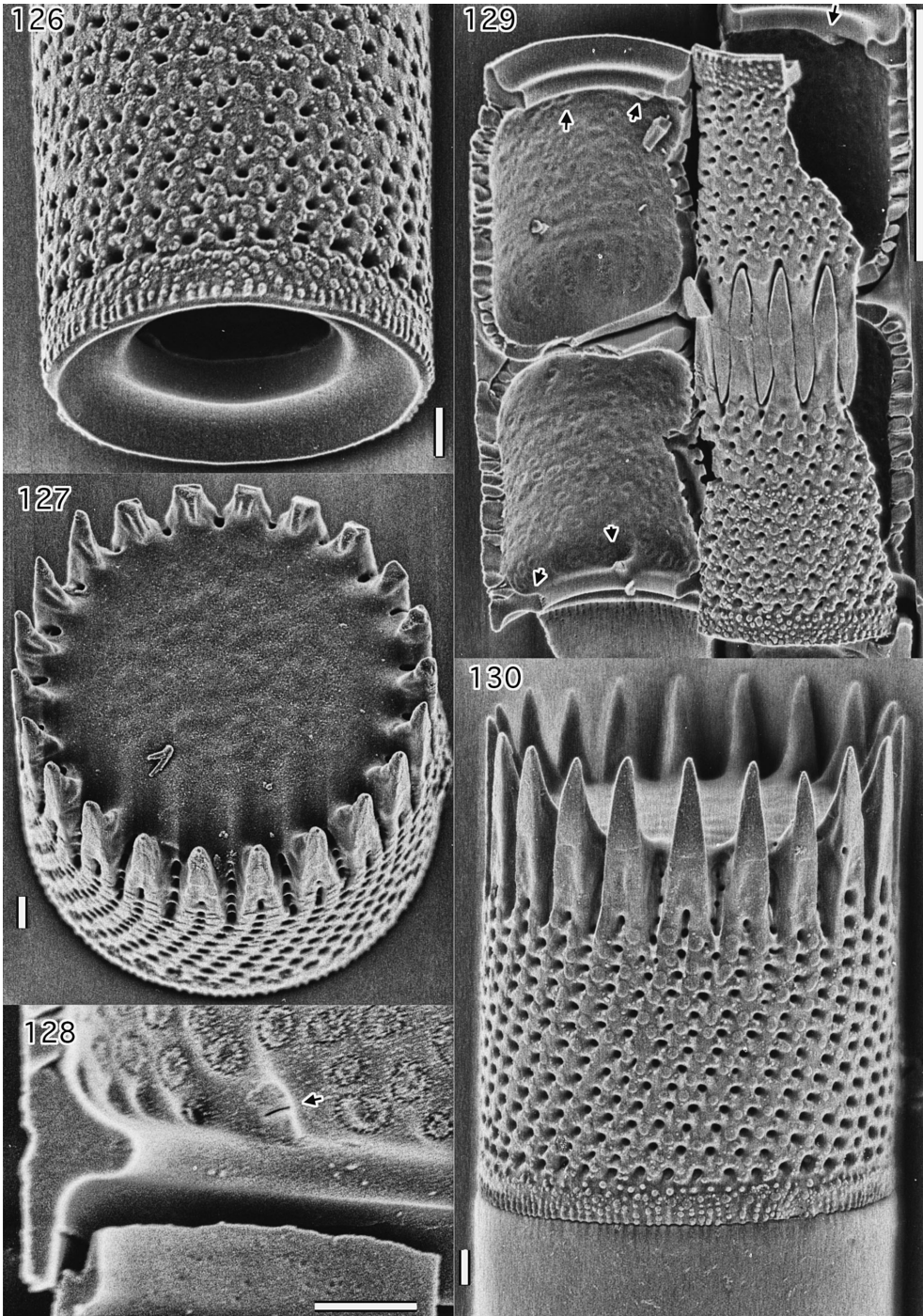
69–99. *Aulacoseira pusilla* (F.Meister) Tuji et Houki comb. nov.
69–99. TNS-AL-55478s (TNS). Katata lagoon dated 2000/3/18.
69–99. DIC, bar=10 μ m. Arrow=rimoportula.



100–105. *Aulacoseira pusilla* (F.Meister) Tuji et Houki comb. nov.
 100–101. Katata lagoon dated 98/11/10. 102,105. Akanoi, Lake Biwa dated 98/06, 103–104. Katata lagoon dated 99/12/10.
 100–105. SEM, bar=1 μ m. 100. Frustule showing areolae on the valve face, 101. frustule of long type. 102, 105. whole frustule and bands. 103–104. rimoportulae on the sulcus.



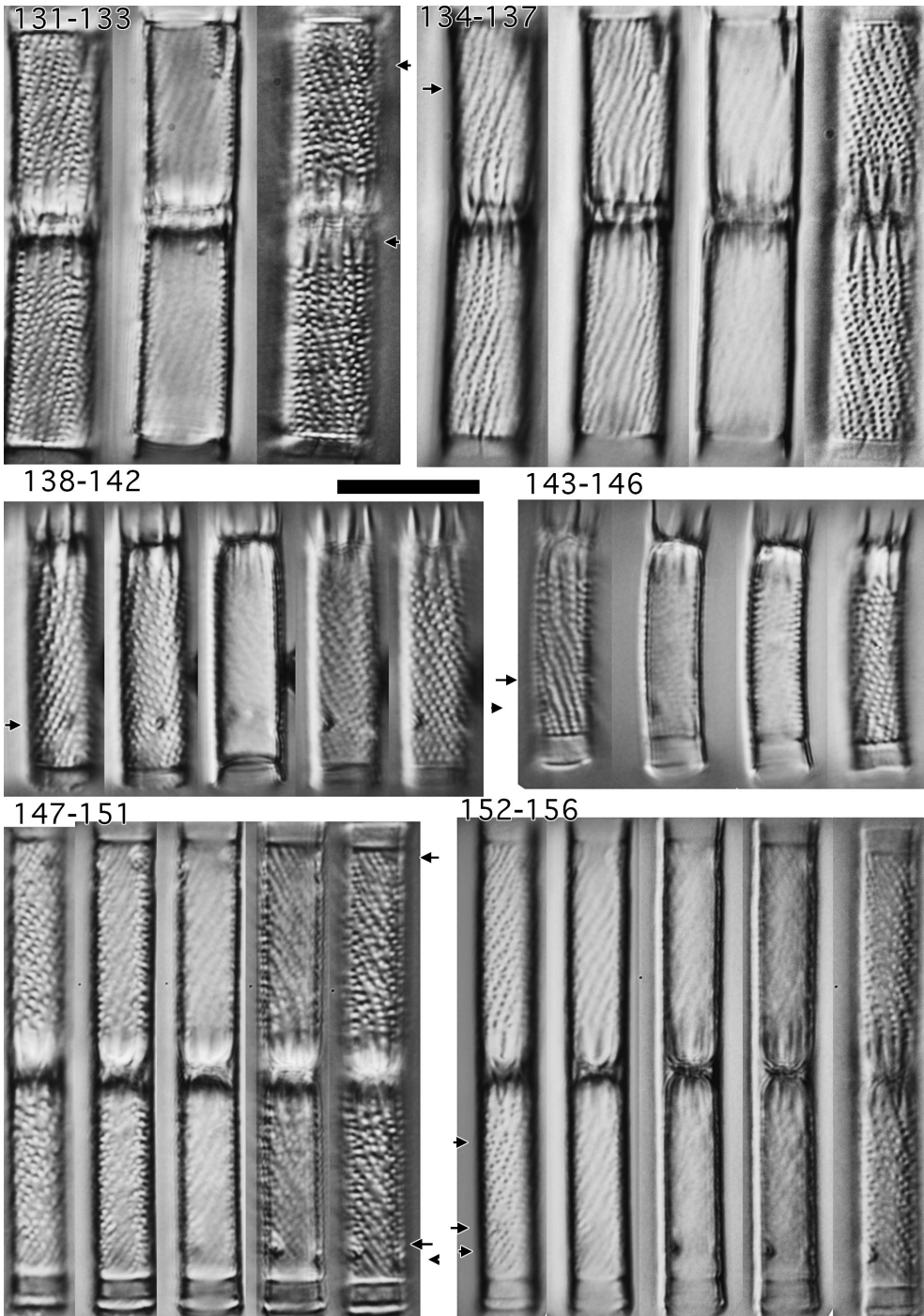
106–125. *Aulacoseira subarctica* var. *logispina* (Hust.) Tuji et Houki stat. nov. et comb. nov.
106–125. TNS-AL-55476s (TNS) from a material As163 (Type material) in Hustedt collection (BRM).
106–125. DIC, bar=10 μ m. Arrow=rimoportula.



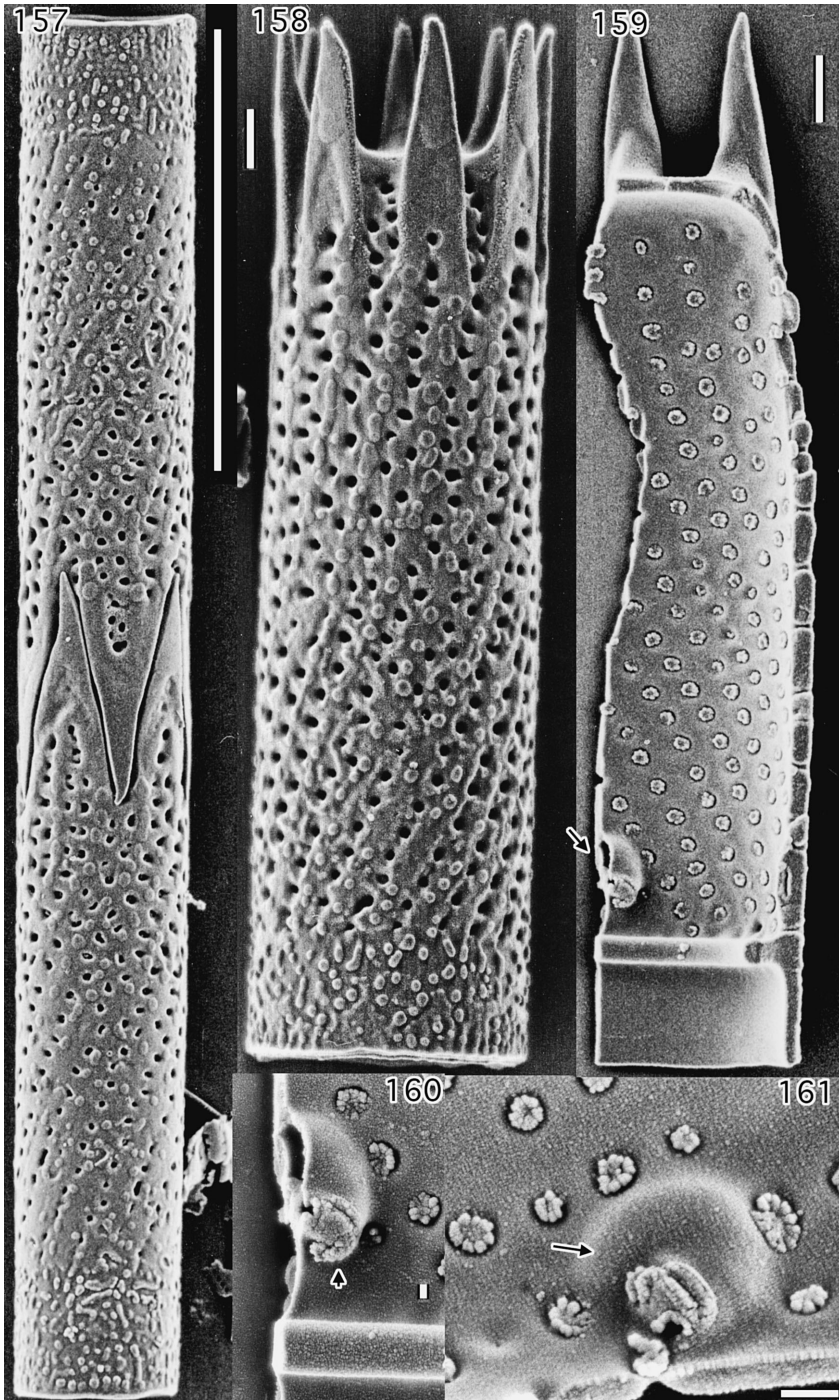
126–130. *Aulacoseira subarctica* var. *logispina* (Hust.) Tuji et Houki stat. nov. et comb. nov.

126–130. As163 (type material) in Hustedt collection (BRM).

126–130. SEM. 126–128. Arrow=rimoportula. Bar=1 μ m. 126. Sulcus. 127. No areolae on the valve face. 128. Rimoportula on the sulcus. 129. Rimoportulae on the sulcus and not off the sulcus, bar=10 μ m. 130. Whole frustule, bar=1 μ m.



131–156. *Aulacoseira subarctica* var. *tenuis* (Hust.) Tuji et Houki comb. nov.
131–156. TNS-AL-55477s (TNS) from a type material As162 in Hustedt collection (BRM)
131–156. DIC, bar=10 μ m. Arrow=rimoportula.



157–161. *Aulacoseira subarctica* var. *tenuis* (Hust.) Tuji et Houki comb. nov.

157–161. As 162 (type material) in Hustedt collection (BRM).

157–161. SEM. Arrow=rimoportula. 157, 158. Whole frustule. 157. Bar=10 μm . 158–160. Bar=1 μm . 159. Rimoportulae exist off the sulcus. 160, 161. Rimoportula exist on the hollow nodule. 160. bar=100 nm.