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MORPHOLOGY AND IDENTITY OF AULACOSEIRA ITALICA AND TYPIFICATION OF AULACOSEIRA (BACILLARIOPHYTA)

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MORPHOLOGY AND IDENTITY OF *AULACOSEIRA ITALICA* AND TYPIFICATION OF *AULACOSEIRA* (BACILLARIOPHYTA)

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Original material of Ehrenberg's from Santa Fiora (Tuscany, Italy) was examined to establish the identity of the diatom to which Ehrenberg gave the name *Gaillonella italica*. It was compared with other Ehrenberg material, notably from New England, and with numerous other samples, both fossil and recent, with a view to understanding the taxonomy of this species. Although Ehrenberg later discarded the name, it was validly published and we consider it synonymous with *G. crenulata*. However, despite the earlier publication of *G. italica*, *G. crenulata* remains the type of the name of the genus *Aulacoseira*. New observations on the rimoportulae and the velum together with recent illustrations of separation valves have been added to the features used to distinguish the species from others in the genus, of which, the most important, though hitherto neglected, is the curving of the pore rows to the left (sinistrorse). We draw attention to the fact that *A. italica* has often been confused with *A. valida*.

Key index words: *Aulacoseira italica*; *Aulacoseira crenulata*; *Aulacoseira crenata*; Bacillariophyta; morphology; nomenclature, systematics.

INTRODUCTION

The genus name *Aulacoseira* was first used by Thwaites in 1848. He based the genus on *Melosira crenulata* Kützing 1844 which Kützing had presented, presumably as a form of *M. italica*, even though he reported the former (living) from flowing waters and the latter from diatomaceous earth. Kützing, in turn, had based *Melosira crenulata* on *Gaillonella crenulata* Ehrenberg 1843. Thwaites' proposal appears to have been largely ignored. The species remained within *Melosira* with many new species being described in the interim until, in 1979, Simonsen drew attention to the validity of *Aulacoseira* and made many new combinations.

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Thwaites (1848) had considered *Melosira crenulata* Kützing 1844 conspecific with *M. orichalcea* Ralfs 1843 and in 1981a, Crawford reported material that Thwaites had labelled as *Aulacoseira crenulata*. He found a diatom that did not correspond to the group of mainly planktonic species but to a genus of “aerophilic species” illustrated in Round *et al.* (1991) as *Orthoseira* (though the nomenclature of that group of species also has a number of problems – see Spaulding & Kociolek 1998). Accordingly, Crawford made new combinations of these aerophilic species with *Aulacoseira* but these changes were rendered unsound by changes in the ICBN (see Greuter *et al.* 2000). We quote from a letter from Dr Paul Silva to RMC in 1981 in response to his publication: “First...the type of a generic name is not a species or the name of a species, as everyone had assumed, but a specimen. Second, it was agreed that this specimen is not the one in hand, but the type specimen of the species indicated by the author of the generic name. Hence, the application of *Aulacoseira* Thwaites 1848 is determined not by the material in hand,... but by the type of material of Ehrenberg’s *Gaillonella crenulata*”.

Simonsen was therefore correct in using the name *Aulacosira*, albeit with changed orthography, for the freshwater, mainly planktonic species and this has since been widely accepted. Simonsen had chosen *Gaillonella italica* Ehrenberg as type of the name of the genus by synonymizing *Gaillonella crenulata* Ehrenberg and *Aulacoseira crenulata* (Ehrenberg) Thwaites with this taxon (Simonsen 1979, p. 60).

Since both epithets *crenulata* and *italica*, were introduced by Ehrenberg, we are investigating Ehrenberg’s types in order to establish both the identity of these species which are considered synonymous, and the type of the name of the genus *Aulacoseira*. Ehrenberg in the course of his research had changed his concepts of these taxa and included a third epithet in 1844, *crenata*, which was legitimized with a figure in 1849 although later synonymized with *crenulata* in 1875.

We now have the chance to resolve the taxonomic confusion since the Ehrenberg collection in Berlin has recently been brought into order (Lazarus & Jahn 1998). We began with the first species of *Aulacoseira* that Ehrenberg introduced, *A. distans* (Ehrenberg) Simonsen (Crawford & Likhoshtway 1999) and intend to continue chronologically through the genus. We believe this is the best approach to alleviate the present systematic confusion. Our sources of information include the publications of Ehrenberg, his drawings (Zeichenblätter), his types on mica (Glimmerplättchen), his original material, and the index books of his daughter Clara.

MATERIALS AND METHODS

Material from the following sources has been examined.

Ehrenberg Collection (BHUPM) Institut für Paläontologie, Museum für Naturkunde, Humboldt Universität zu Berlin:

1. Diatomite from Santa Fiora, Tuscany, Italy; obtained by Ehrenberg from the Klapproth Collection (see Ehrenberg 1836: 53); Micastrips in Kasten 29 Buch 7 labelled Santafiore; Zeichenblatt No. 2322; Klapproth’s sample 282/99 housed at the Institut für Mineralogie, Museum für Naturkunde, Berlin is the original material for *G. italica*. Part of this material has been re-deposited in the Ehrenberg collection.
2. Diatomite from West Point, New York, USA; supplied by Bailey to Ehrenberg (see Ehrenberg 1843: 330); Micastrips in Kasten 26 Buch 3 labelled Westpoint (01–08); Zeichenblatt No. 2233; sample No. 1756. This is original material for *G. crenulata*.
3. Soil on a plant from Cayenne, French Guyana; supplied by Schomburgk to Kunth (see Ehrenberg 1843: 306). Micastrips in Kasten 18 Buch 5 labelled Commeline (09–16); Zeichenblatt No. 2053; sample No. 1108.

4. Diatomite under peat from Pelham, Massachusetts, USA; collected by Hitchcock (see Ehrenberg 1843: 352); Micastrips in Kasten 26 Buch 3 labelled Pelham (09–16); Zeichenblatt No. 2237; sample No. 1767.
5. Trübender Staubregen im hohen atlantischen Ocean bei 17° 43' N. 26° W., collected on 9 March 1838 on the ship "Sprey" and sent by Charles Darwin to Ehrenberg (see Ehrenberg 1844: 194 and 1849: 451, plate IV A & B); Micastrips in Kasten 47 Buch 1 & 2; Zeichenblatt No. 2171 & 2170; sample No. 2894 & 2895. Original material for *G. crenata*.

Hustedt Collection (BRM), Alfred-Wegener Institut, Bremerhaven:

6. Waldtümpel im Holm am Dieksee, an Algen, 7.10.1921 (E4277).
7. Eulengebirge, Sturzbach? Wüste Giersdorf, Schroeder 1884, (Div 857).
8. Veermoor, Bremerhaven collected 1912 by Hustedt. Slide BRM 214/93.
9. Lake Sumner, Canterbury, New Zealand. Material AT64 as *Melosira decipiens* Grove.

Collection of Vaclav Houk:

10. Kutnar Pool, S. Maravia, Czech Republic, collected by O. Skácelova.

Specimens were examined by LM and SEM according to standard methods. For LM, a Zeiss Axioplan was used (for the figures 18–20 kindly supplied by Vaclav Houk, see Skácelova & Houk 1993). ISI DS130 and Cambridge 360 scanning electron microscopes were used. When views of the inner surface of the valves were required, the specimens were dried onto a cover-slip and subjected to gentle pressure beneath a second cover-slip until they split along their length. One other non-standard method was used for LM. In order to see the linking spines of intact sibling cells clearly, cleaned valves were dried onto a slide, coated with gold in a sputter-coater and examined without cover-slip but under immersion oil.

RESULTS AND DISCUSSION

Ehrenberg's types, material and concept

Between 1836 and 1859, Ehrenberg introduced a number of new names for the diatom genus *Gaillonella* which, in 1838, p. 166, he attributed to Bory de Vincent (1825) and named after Mr Gaillon from Dieppe. Ehrenberg often used an alternative spelling, *Gallionella* in dealing with a number of organisms, not all of them diatoms. The spelling *Gaillonella* was conserved by the bacteriologists (Buchanan *et al.* 1958); when writing of diatoms the spelling has to be corrected to *Gaillonella* (P. Silva, personal comm.). Most of his contemporaries, like Kützing (1844), preferred the genus name *Melosira*.

Gaillonella italica Ehrenberg

Infusionsthierchen: 171 (1838). [First mentioning of name only (*Gaillonella italica* n. sp.): Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin, 1836, 53 (1836)].

Lectotype (designated here): BHUPM Ehrenberg-Collection: 290706 a red (see Fig. 1b).

Type locality: Diatomaceous earth from Santa Fiora, collected by Klaproth.

Further original material: Ehrenberg's Zeichenblatt No. 2322 (partly reproduced here as Fig. 1a). Ehrenberg's sample No. 1932 is missing.

Epitype (designated here): BHUPM ECO-007, (Fig. 2, England finder S 37). Isoepitype: BRM Zu5/42, (Fig. 4, finder number 286.5).

Original material of the epitype: Klaproth-Collection Sample Nr. 282/99 (San Fiore, Toscana) (Institut für Mineralogie, Museum für Naturkunde, Berlin). Part of this material has been redeposited in the Ehrenberg collection.

Ehrenberg first mentioned the name as a new species in 1836 where he also mentioned the locality – “Bergmehl von Santa Fiora (San Fiore)”. This is a locality in Tuscany, Italy, and the material was from Klaproth's collection. The name was validated by Ehrenberg in 1838 (p. 171) when he provided a differentiating diagnosis: “Sie unterscheidet sich durch einen gekerbten Circelrand von *G. distans* ...Grösse 1/384 Linie” (It differs from *G. distans* by a crenulated edge of the valve. The size is equivalent to 6µm).

The first drawing of *italica* appeared on Ehrenberg's Zeichenblatt 2322, labelled Santa Fiora on the reverse (Fig. 1a). There are girdle views of two sibling pairs, both of them with distinct markings where one would expect the linking spines to be, and a valve view with a very wavy outline. The lectotype, see Fig. 1b, illustrates clearly the characters depicted by Ehrenberg in his drawing. Kützing (1844: 55) added a Latin description, which can be translated as: “Smaller *Melosira* with cylindrical articulation, length double the diameter, at the margin the nodes are finely denticulated; the margin of the disk is radially punctate”. Kützing reports this diatom from “Bergmehl von San Fiore”, i.e. the same locality as Ehrenberg's material. Most of Kützing's drawings, (his plate 2 fig. VI), show a diatom with visible linking spines and one, fig VI 8, shows the hemispherical outline of a resting spore valve. Kützing extends the range of the diameter to 1/300–1/150 lines (7,5–15µm).

Because the original sample No. 1932 that Ehrenberg had obtained from Klaproth could not be found, and due to the limited information provided by the light micrographs of the micas, we located Klaproth's material of Santa Fiora at the Institut für Mineralogie (Museum für Naturkunde, Humboldt Universität zu Berlin), and declared a specimen of this material as epitype. Here we present light and electron microscopy of this material. Further information on the diatom is provided from other sources and illustrated on separate plates.

Light microscopy

Valves of *A. italica* in the material from Santa Fiora are in the size range of 5–14µm broad (valve diameter) and 11–20µm long (mantle length). The great majority of the cells are united in pairs as siblings. Uncommonly, one complete cell and two attached sibling valves are found and rarely, two complete cells. In the larger of the valves, the linking spines can easily be seen *in situ*. When sibling valves fall apart after some of the linking spines on both valves are broken, the individual spines may be seen in profile. Relative to those of many other species of *Aulacoseira* the spines have long basal shafts that expand sharply to a broad, anvil-shaped terminal part. The spines were described by Barinova (1988) as T-lobed on short or long cylindrical stalks. This taxon also differs from most other species of the genus because the pore rows curve to the left away from the mantle edge, i.e. they are sinistrorse.

In mid-focus the ringleist can be seen as a small v-shaped projection on the inner surface of the otherwise thin, straight mantle (Figs 3, 4). The rimoportula can be seen about 1/6 of the distance away from the ringleist but only by using phase contrast optics (Fig. 2). In the Santa Fiora material this feature is very difficult to detect and many valves must be examined before a suitable specimen is found. This is true to a lesser extent in other material because we have found that there are only two

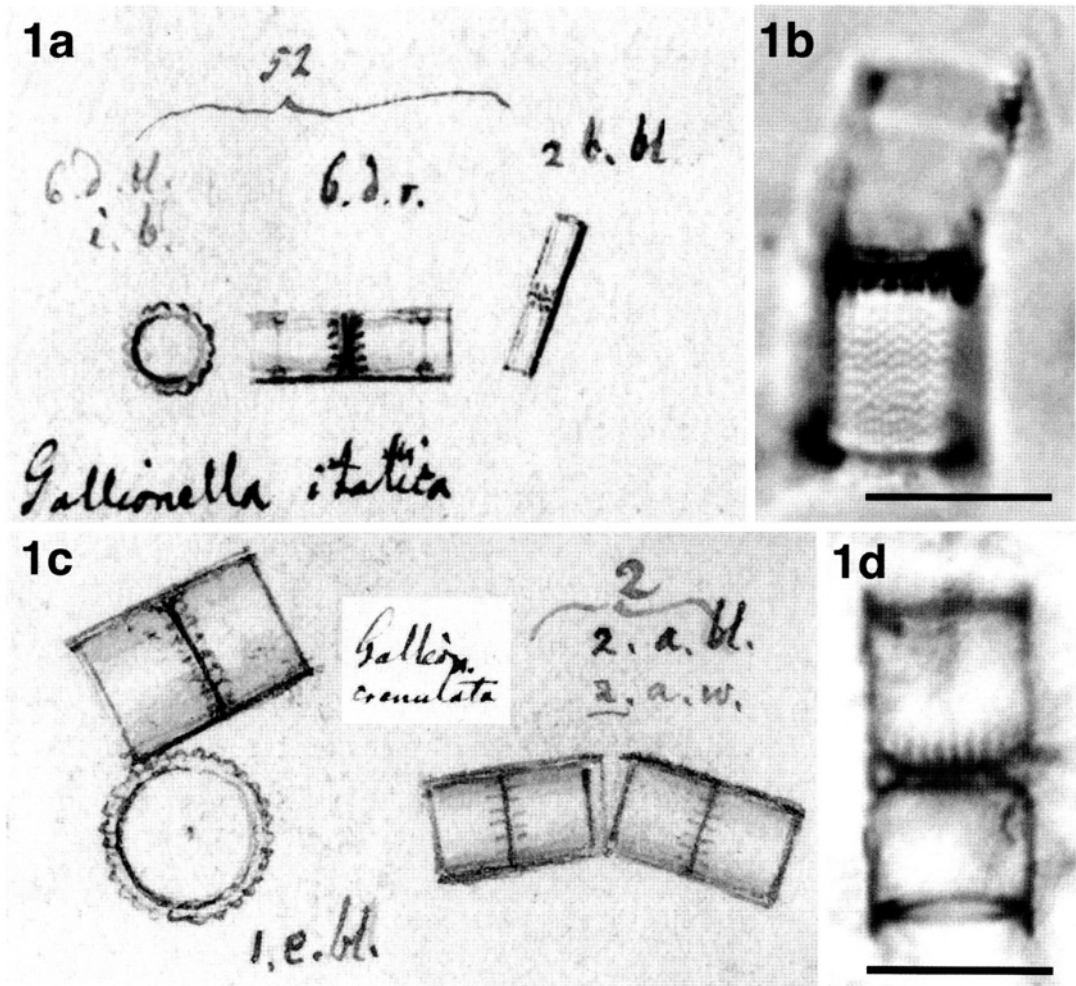


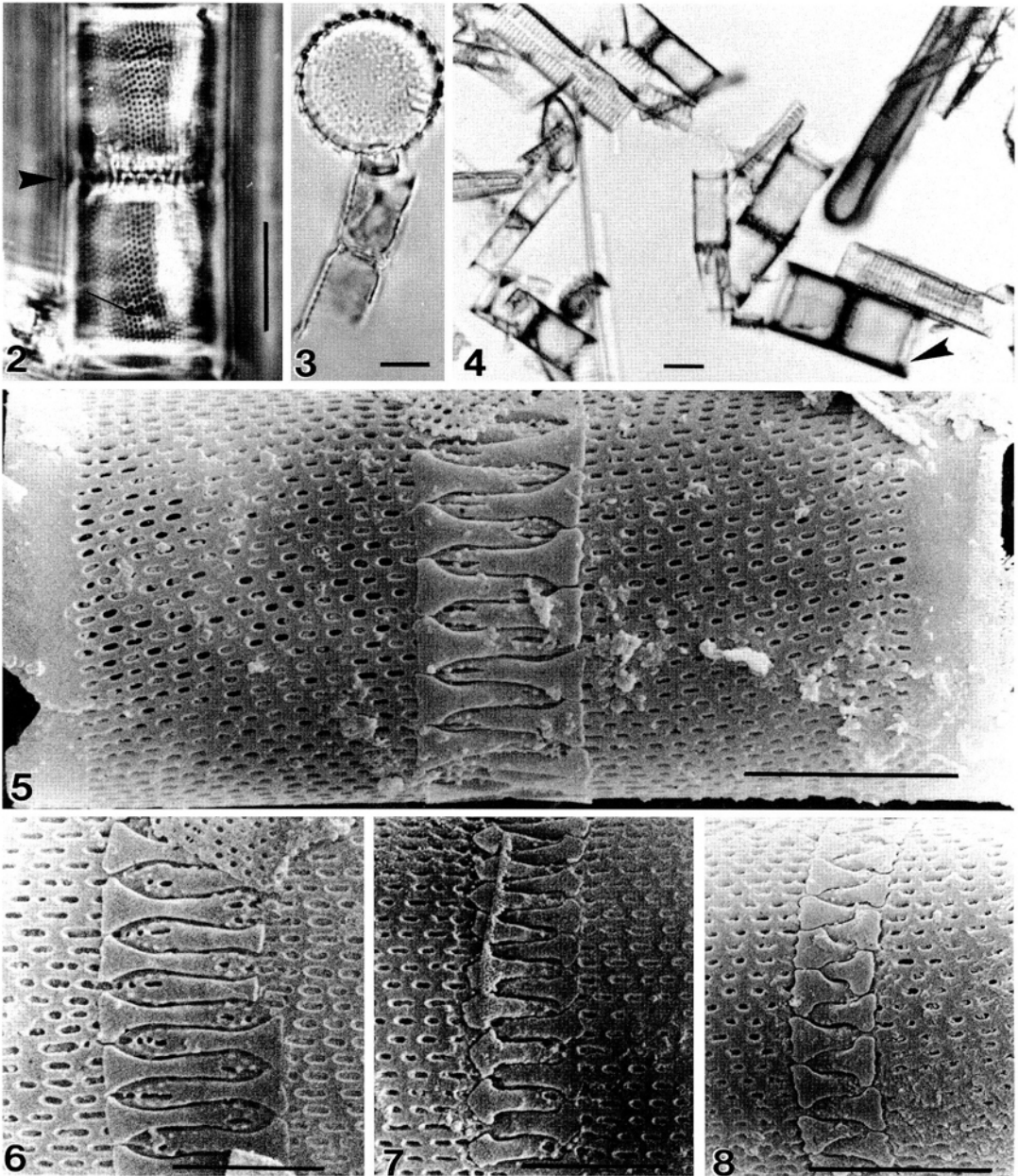
Fig. 1. Ehrenberg's original material. **Figs 1a & 1b.** *Gaillonella italica*. **Fig. 1a.** Part of Ehrenberg's Zeichenblatt No. 2322 from Santa Fiora. **Fig. 1b.** Designated lectotype. **Figs 1c & 1d.** *Gaillonella crenulata*. **Fig. 1c.** Part of Ehrenberg's Zeichenblatt No. 2233 from Westpoint, New York. **Fig. 1d.** Designated lectotype. Drawings are not to scale, scale bars Fig. 1b = 10 μ m, Fig. 1d = 16 μ m.

processes in each valve and they must be positioned optimally to avoid being obscured by the light scattering within the mantle.

Because of the geometry of the valves, the face is not often seen unless the valve is damaged in some way. Consequently the outline of those that are found is irregularly crenulate and resembles a crown when viewed from above. The surface of the valve face may be plain or variously and unevenly poroid (Fig. 3) but flat in all cases except for the spore forms (see below).

Scanning electron microscopy

A. italica is usually seen in girdle aspect as sibling pairs of valves because of the effectiveness of the linking spines in forming a long cylinder. These spines vary between extremes of length, thickness and breadth and in the shape of the distal part. Some of this variation is shown in Figs 6–8 where the

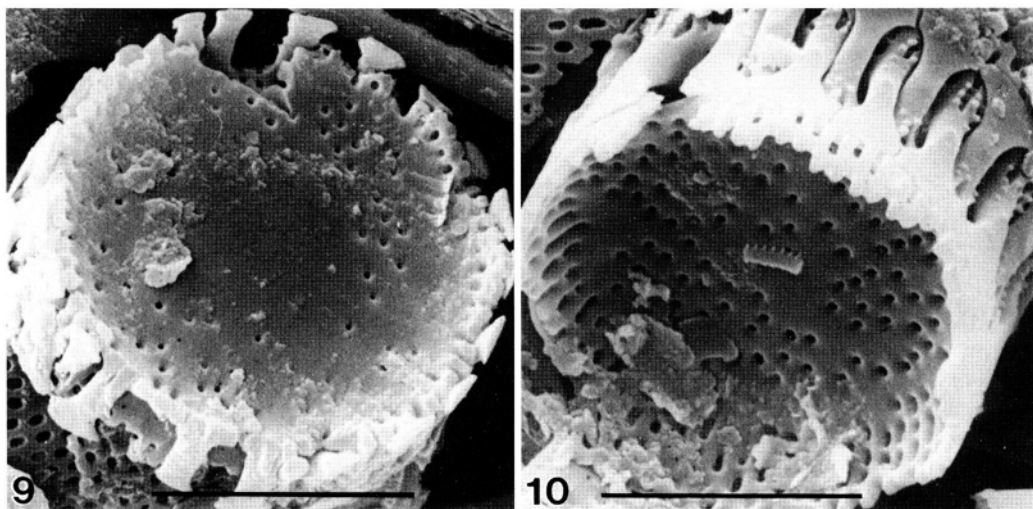


Figs 2–8. All Santa Fiora specimens of *Aulacoseira italica*. Figs 2–4 LM, scale bar = 10 μ m. **Fig. 2.** Designated epitype. Phase contrast of two sibling valves showing sinistrorse spiral rows of areolae and rimoportula, arrow. Note area of linking spines, arrowhead. **Fig. 3.** Valve view with irregular coverage of areolae. **Fig. 4.** Mid focus of several sibling pairs showing poorly defined ringleist, arrow. Figs 5–8, SEM, scale bar = 5 μ m. **Fig. 5.** Sibling pair showing pore row curvature and absence of obvious rimoportula exit pore. **Figs 6–8,** details of linking spines from different specimens. Note variation of form, length and ornament but also variation in areola outline.

form is either anvil-shaped or spade-like at the extremes. One, rarely two, rows of areolae run up into the shaft of the spine which may often be coated with small granules of silica.

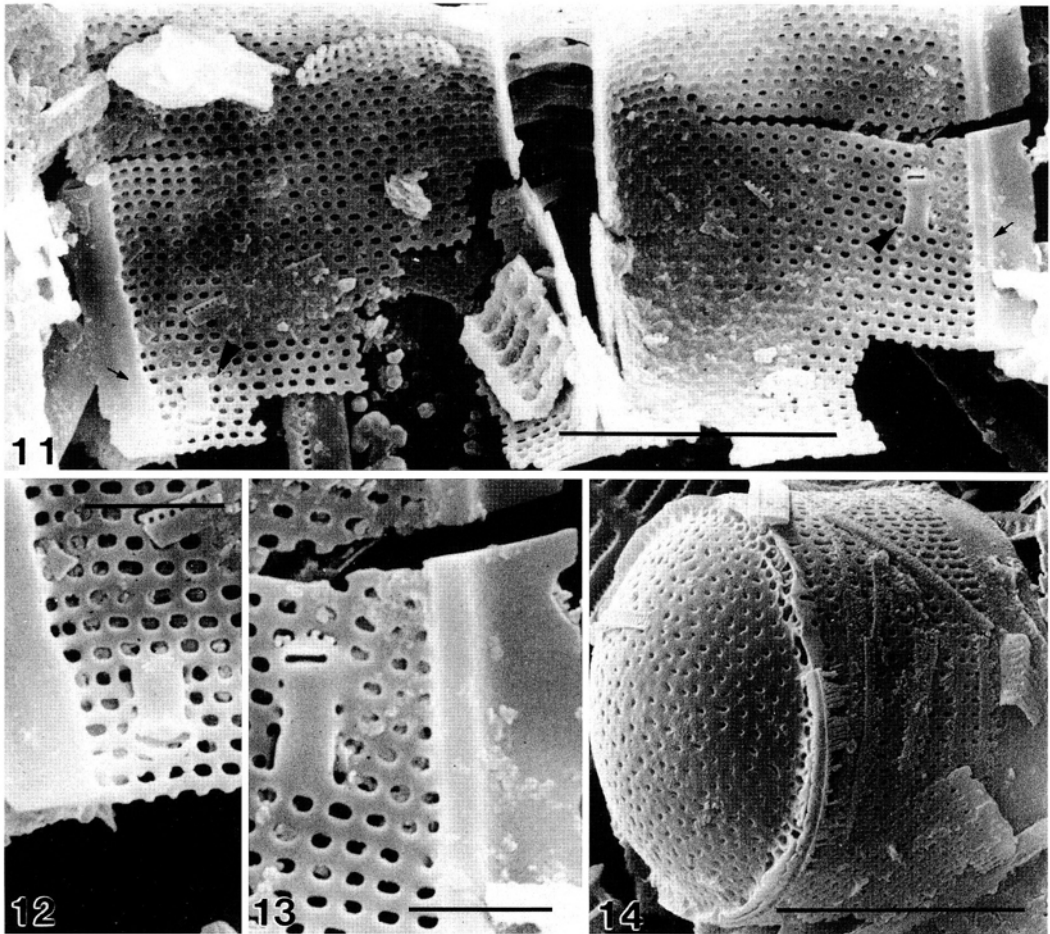
The collar is plain and there is no sharp demarcation between it and the areolar zone (Fig. 5). The shape of the areolae varies between sibling pairs, more rarely from one valve to the other and even more uncommonly, within the valve between slit-like ovals to circular apertures. The velum is deep-seated and visible only with difficulty from the outside. The curvature of the rows of areolae is such that they begin almost straight as they leave the linking spines, curve to the left and meet the collar at an oblique angle. No indication of the external apertures of the rimoportulae can be seen. On some valves a step can be seen which is either on the mantle or on the collar – the Müller step (Figs 22, 29). This is the imprint of the end of the cingulum that overlies one of the new sibling valves during its formation and one would expect such a feature to appear in accord with observations in other species (Müller 1884, Crawford 1981b). Why it may be absent as in Fig. 5 is not clear but in *Aulacoseira* species generally the imprint is neither strong nor regular in position (Crawford & Likhoshway 1999).

Other information must be gained from observation of fragments. The valve face can be seen only when at least some of the spines are broken on both of the sibling valves or when the valve itself is broken (Figs 9, 10). The valve face is variously covered with areolae, which are randomly distributed. In some cases the surface has no areolae (Fig. 33). Those that are present appear to differ from the areolae on the valve mantle in not having the velar apparatus. In the Santa Fiora material the velum has not been preserved and the inside surface shows only the areolae (Figs 9–13).



Figs 9–10. Santa Fiora specimens of *Aulacoseira italica*. Fragment of the inner surface of the valve face. Note variation of areola distribution. Scale bar = 5 μm .

The position and nature of the rimoportulae can only be appreciated in the SEM of the inner surface (Fig. 11). In this species the structure is remarkable in consisting of a long tube that is part of the valve, oriented usually parallel to the edge of the mantle and transverse to the areolar rows, that opens by a slit typical of other rimoportulae in the genus. In detail it may be significant that in both processes in Figs 12, 13, the tube seems to be partly separate from the valve surface. It is as if in the course of evolution, a long, straight tube has slowly become integral with the valve. In *A. granulata* a similar structure is coiled (Likhoshway & Crawford 2002). In the light of this SEM information one can distinguish the tube as a blurred strip and the end of the process as a bright spot in the specimens under the light microscope (Fig. 2). There appears to be no consistency as to whether the tube runs left or right.



Figs 11–14. Santa Fiora specimens of *Aulacoseira italica*, SEM. **Fig. 11.** Fracture of sibling pair, inner surface, showing rimoportulae, arrowheads and ringleists, arrows. Scale bar = 10 μm . **Figs 12, 13.** Detail of rimoportulae, fuller explanation in text. Scale bars 2.5 μm and 2 μm respectively. **Fig. 14.** Resting spore with rounded valve face and flange on margin with no spines. Scale bar = 10 μm .

Valves that are commonly regarded as resting spores have been found in all gatherings of this species except for sample Div. 857 from Eulengebirge. They may be more common in some gatherings than in others; for example they are scarce in Santa Fiora and illustrated here from the SEM (Fig. 14) and LM (Figs 35, 36). Areolae are usually, though not invariably, in more or less straight lines on the mantle. This is separated by a more-or-less well-defined ridge from the convex valve face which has evenly scattered areolae. In some cases rudimentary spines form the ridge. So far, we have found no rimoportulae on the inner surface of the mantle of these resting spores.

***Gaillonella crenulata* Ehrenberg**

Abh. Königl. Akad. Wiss. Berlin 1841, 376 (no description), pl. IV/I, fig. 31 (1843). [First published mentioning of name only: Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin, 1841, 205 (1841)].

Lectotype (designated here): BHUPM Ehrenberg-Collection: 260302 a blue (see Fig. 1d).

Type locality: Diatomite from Westpoint, New York.

Further original material: Ehrenberg's sample No. 1756; Ehrenberg's Zeichenblatt No. 2233 (partly reproduced here as Fig. 1c).

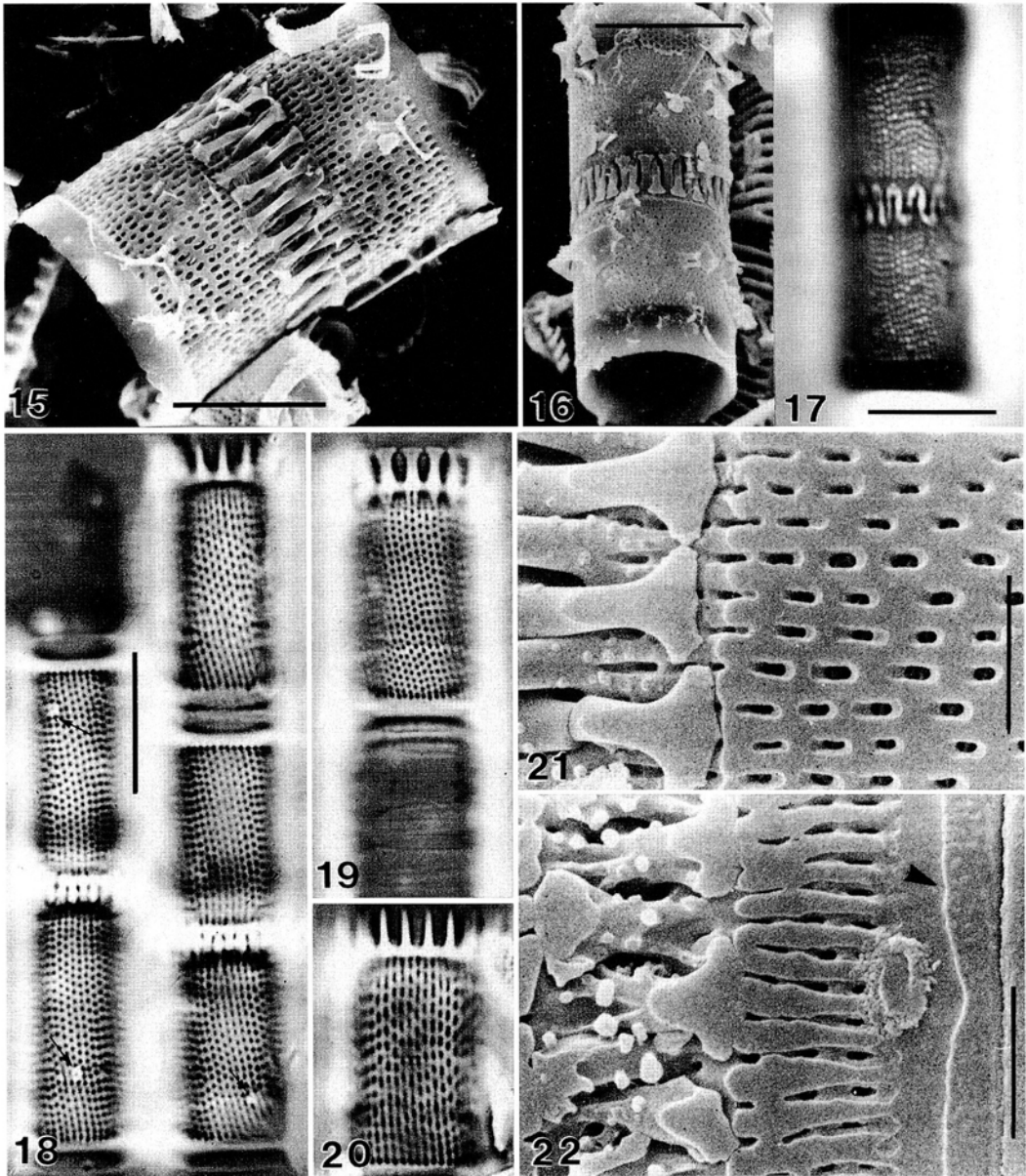
As is often the case with Ehrenberg's new taxa, the name *Gaillonella crenulata* was first mentioned in the Monthly Reports of the Royal Berlin Academy of Sciences of 1841 which appeared mostly in the same year as the reports were given (1841: 205). The validation took effect in 1843 when he illustrated this taxon in the Abhandlungen of 1841 (published in 1843) in which are shown only a valve view from Cayenne (Tafel II/I, fig. 41) and a girdle view of a chain of cells with characteristic marking (linking spines) from New York, (Tafel IV/I, fig. 31) (Ehrenberg 1843). We have chosen the type for this name from the mica of Westpoint, New York (Fig. 1d) and further illustrate it from original material (sample No. 1756) in the SEM (Fig. 15). Although Ehrenberg does not supply a description, Kützing (1844: 55, pl. 2, fig. 8) describes *Melosira crenulata*: as: "articulis diametro 2–4plo longioribus, exacte cylindris; ad marginem evidenter denticulatis."

We have examined material from Ehrenberg's collection from both of these syntype-localities and from Pelham, Massachusetts (another site from which Ehrenberg reported this taxon in 1843) and we conclude that this diatom taxon is the same as that named *G. italica* by Ehrenberg from Santa Fiore. We have gathered more information on this species from a number of sources that also show some of the variation. Two pairs of sibling valves are illustrated in Figs 15, 16 from West Point, New York and from Pelham, Massachusetts respectively. There is considerable variation in both samples and these figures should not be taken as typical but they do show some of the extremes. The long, slender linking spines of the eroded specimen in Fig. 15 would probably cause some workers to call it *A. crenulata*. However, we have also examined a slide from Kützing's material marked *Melosira crenulata* (Kützing slide number 108, BM number 18968) and found it to be consistent with what we have illustrated in this paper as *A. italica*. We have examined further recent material which we will discuss later in this paper.

***Gaillonella crenata* Ehrenberg**

As an added complication, Ehrenberg introduced the name *G. crenata* in 1844, when he was presenting his findings of diatoms in atmospheric dust deposited on the ship "Sprey" in the Atlantic Ocean which he had received from Charles Darwin. In his paper of 1849 he summarized his findings and presented several figures of *G. crenata* from many different localities, but without adding a diagnosis as he had done for many other new species in this paper. Apparently he used this name instead of *G. crenulata* for in 1875 he wrote on page 186: *G. crenata* = *G. crenulata*. Further, one of the girdle views and the valve view shown on Zeichenblatt 2322 as *G. crenulata* then appears again as being from Santa Fiore (the type locality of *G. italica*) under the name *Gaillonella crenata* on Zeichenblatt 646. This sheet is a composite of published drawings from many sources and is clearly later than 2322. Nevertheless, this name, *G. crenata*, has been introduced and a figure published. It therefore needs to be typified. To this end we examined the "Sprey" material of Darwin's that was sent to Ehrenberg and to which the latter gave the sample numbers 2894 and 2895. Neither of these samples, nor the mica samples made from them, contained what we have recognized as *A. italica* although a number of other *Aulacoseira* species were found. We believe, therefore, that Ehrenberg was mistaken in believing these specimens to be synonymous with the other two species and we shall return to consider the name *A. crenata* at a later date.

Why Ehrenberg introduced these three names for what appeared to him to be the same taxonomic entity is not explained by Clara's Taxonomic Index (Lazarus & Jahn 1998). *G. italica* is not listed at all and *G. crenulata* and *G. crenata* have two different entries for pictures and sites which do not coincide with the valid date of publication of these two names. What happened to *G. italica*, a taxon



Figs 15–16. Specimens of *Aulacoseira crenulata* from Ehrenberg material. **Fig. 15.** Original material from the lectotype locality West Point, New York. **Fig. 16.** From Pelham, Mass, SEM. The former is a little eroded but nevertheless has relatively longer linking spines than the latter. Scale bars 10 μ m. **Figs 17–22.** Further specimens of *Aulacoseira italica* from other material. **Fig. 17.** Kutnar Pool, S. Moravia. Sibling valves coated with gold/palladium and viewed with LM phase-contrast under oil. Note clarity of linking spines, scale bar 10 μ m. **Figs 18–20.** Phase contrast LM specimens supplied by Vaclav Houk. Note rimoportulae, arrows, spatulate linking spines, tapered separation spines and the strong curvature of pore rows. Scale bar = 10 μ m. **Figs 21, 22.** Eulengebirge, SEM. Detail of valve surface showing change of surface areolar outline with thickening of the valve – both valves from the same chain. Original round areolae are visible at bottom of the opening. The Müller step on the mantle is arrowed in Fig. 22. Scale bars = 2 μ m.

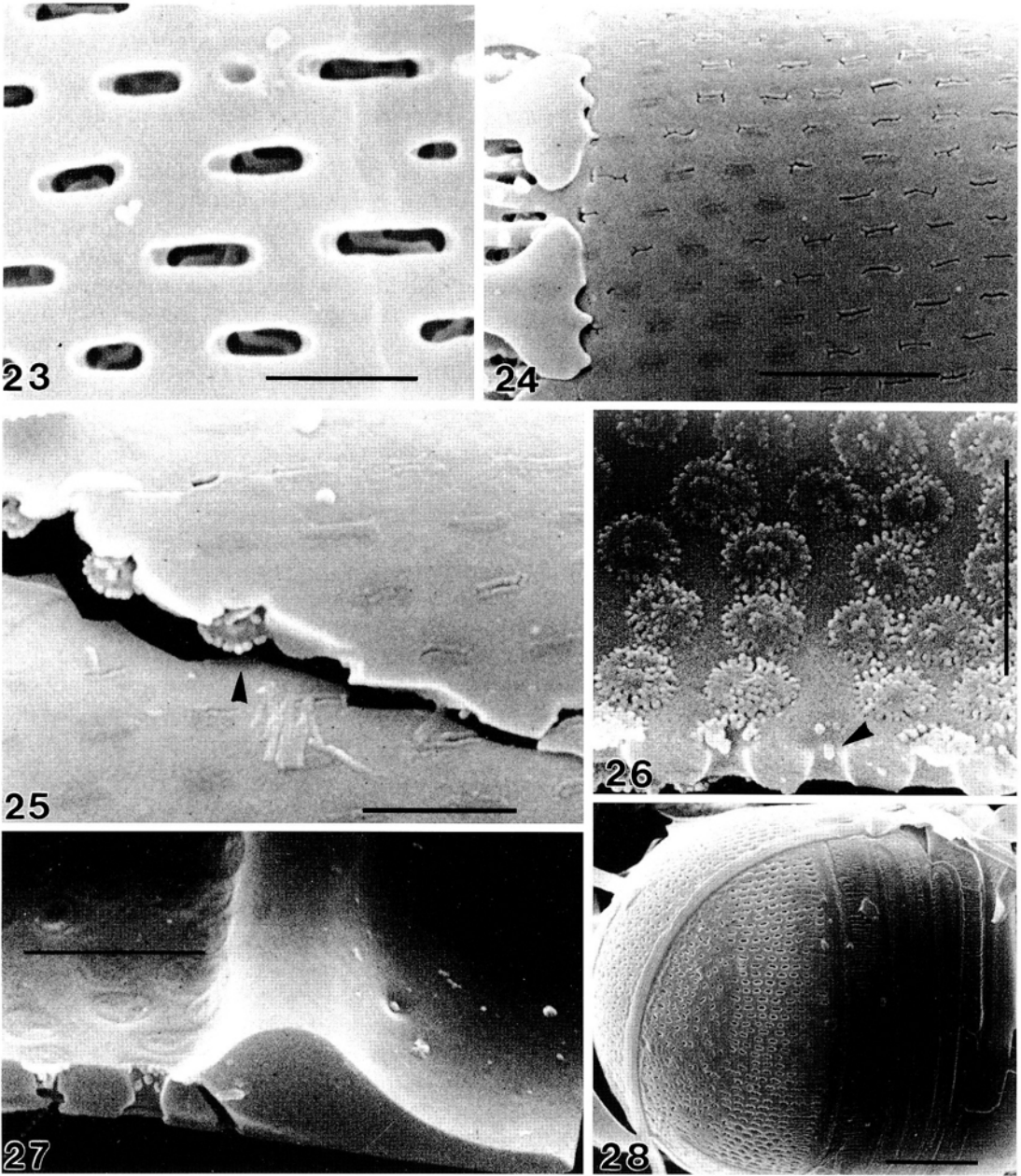
that was taken up by Kützing and used by many workers since? In his scrap-book Ehrenberg had listed *G. italica* = *G. distans*, and in 1836 Ehrenberg was uncertain about the differences between *G. distans* and *G. italica* but in 1838 he had published a differentiating diagnosis. By 1843 he seems to have discarded *G. italica* in favour of *G. crenulata*. In his report on South and North American diatoms (1843) a number of times he reports *G. distans* and *G. crenulata*, the later illustrated by him for the first time in 1843.

Reference to his Zeichenblatt 2322 (from the type locality of *G. italica*, Santa Fiora and labelled "Santa Fiora" on the reverse) shows clear evidence of linking spines in his description of *G. italica*. This feature only appears in *G. crenulata* (or *G. crenata*) in later drawings and therefore it is reasonable to conclude that he considered *crenulata* and *italica* to be the same diatom. Why Ehrenberg discarded the earlier name may never be known. Part of the difficulty may lie with the microscopes available to Ehrenberg at the time. Also, owing to their different geometry, he may not have appreciated that he was often looking at girdle and valve views of *G. distans* but rarely the valve views of *italica* /*crenulata*. The crenulate outline of the valves can be obtained in all of these taxa, especially in eroded fossil material. Be that as it may, Ehrenberg continued to use *G. crenulata* and *G. distans*. Following these names through Ehrenberg's Zeichenblätter, 2233 from West Point, New York is a good example, *G. distans* consistently shows the thickened ringleist and *G. crenulata* what we now know to be the linking spines. Later, Ehrenberg composed a composite Zeichenblatt, number 646, where he arranged the drawings he had earlier made under the names *G. distans* and *G. crenata* (but not *G. crenulata*). Clearly *G. crenata* was intended to replace *G. crenulata* for some reason best known to Ehrenberg because several drawings that had previously appeared under the name *G. crenulata* are recognizable here. For example, the girdle and valve views from Zeichenblatt 2237 from Pelham, Massachusetts, which is easily distinguishable by an error Ehrenberg made in showing linking spines on the open end of one of the sibling valves. Incidentally, the post-auxospore group of cells from that drawing are moved to *G. distans* on drawing 646 (see also Crawford & Likhoshway 1999). It seems then, that ultimately Ehrenberg was confident and more or less consistent about the naming of these specimens by the time he made his composite drawing 646.

Further material and other characters

In 1986 Genkal & Korneva reported for the first time separation spines on what they called terminal valves of (*Melosira*) *A. italica* from Russian waters. This report was confirmed by Skácelová & Houk in 1993, who described this feature in a sample provided from a small pool in southern Czech Republic. Houk has kindly allowed us to reproduce three of his micrographs (Figs 19, 20 were published by them, *loc. cit.*). Neither Genkal & Korneva, nor Skácelová & Houk comment on the frequency of these separation valves, but we have been unable to find any in the many samples in our collections, including material provided by Houk. They must be considered very rare in this species and, perhaps produced in very specific environmental conditions. Figs 18, 20 show how slender they are when compared to the linking spines in Fig. 19. Figs 18, 19 show the well-developed spatulate linking spines though they are best seen when the sibling valves are broken, Fig. 19. If the specimen is sputter-coated after mounting on a slide, however, these spines can easily be seen *in situ*, Fig. 17. The regular appearance of rimoportulae, arrowed, is clear in Fig. 18.

Figs 21, 22 illustrate how the original, sub-circular outline of the areolae can be obscured by the thickening of the valve. As silica is added, so the areolae appear more and more as slits. This possibly explains why some areolae appear as slits in the light microscope and may have led some authors to consider *A. crenulata* to be a separate species. Fig. 22 also shows the Müller step (arrow) in the mantle formed by the edge of the overlying girdle band and Figs 21, 23 show the deep-seated velum or part of it. In some samples valves have been found where the velum is almost obscured by silica and all that remains is a very narrow slit (Figs 22, 24). Fractures of these valves reveal the form of the velum to be a perforated disc held in place by a small number of struts that bend down from the wall of the



Figs 23–28. Further specimens of *Aulacoseira italica* from other material. Figs 23–25, 27, 28, Waldtümpel im Holm am Dicksee; Fig. 26, Eulengebirge. SEM. **Fig. 23.** Detail of slit-like areolae and the supporting struts of the vela below. Scale bar = 1 μm . **Fig. 24.** Outer aperture of the areola closed to an extreme slit. Scale bar = 2 μm . **Fig. 25.** Fracture through valve showing disc-shaped vela with supporting struts and fimbriate fringes, arrowhead. Scale bar = 1 μm . **Fig. 26.** View of velar plates on the inner surface. Note broken vela support, arrowhead. Scale bar = 10 μm . **Fig. 27.** Fracture through valve in region of the ring-leist. Note vella supports in two areolae. Scale bar = 2 μm . **Fig. 28.** Auxospore initial valve and several girdle bands. Note “mantle” pattern of straight rows of areola and random arrangement on the valve “face”. Scale bar = 10 μm .

foramen (Fig. 25). The view from the inside shows the spongy nature of the velum (Fig. 26) and a fracture near the ringleist shows an areola from which the velum has been lost leaving three fragments of the velar support (Fig. 27). For a review of velum structure in *Aulacoseira* see Crawford & Likhoshway (2002).

The auxospore of *A. italica* resembles other species of the genus in having hemispherical initial valves lacking linking valves and covered entirely with areolae but with those on the mantle arranged in rows (Fig. 28). At least one rimoportula has been found on an initial valve (RMC, unpubl.).

Nomenclatural results

Whatever the reasons for Ehrenberg discarding the name *Gaillonella italica* in favour of *G. crenulata*, *G. italica* was validly published by him in 1838. Having examined Ehrenberg's type material for *Gaillonella italica* and *G. crenulata* and compared it with other samples, we believe that the fine variation in morphology is continuous over a range as will be seen in the revised taxonomy below that includes some other authors concepts of *crenulata*. For example, Krammer & Lange Bertalot (1991) treated *A. crenulata* and *A. italica* as separate species, not having seen the original Ehrenberg material. Like Ehrenberg, we see no reason for distinguishing these taxa, but even though the epithet, *italica*, was discarded by Ehrenberg, it has priority over the other name and must be retained. *G. crenulata* is therefore a later heterotypic synonym (=) of *G. italica* and we recognize the validity of the genus *Aulacoseira* Thwaites with its type *Aulacoseira crenulata* (Ehrenberg) Thwaites, which is synonymized with *A. italica* (Ehrenberg) Simonsen.

Aulacoseira Thwaites

Ann. Mag. Nat. Hist., ser.2,1: 167 (1848).

Type: *Aulacoseira crenulata* (Ehrenberg) Thwaites

Basionym: *Gaillonella crenulata* Ehrenberg, Abh. Königl. Akad. Wiss. Berlin 1841: 376, pl. IV/I, fig. 31 (1843).

= *Aulacoseira italica* (Ehrenberg) Simonsen (*Gaillonella italica* Ehrenberg) see below.

Aulacoseira italica (Ehrenberg) Simonsen

Basionym: *Gaillonella italica* Ehrenberg, Infusionsthierchen: 171 (1838).

Synonyms: = *Melosira italica* (Ehrenberg) Kützing 1844

= *Gaillonella crenulata* Ehrenberg 1843

= *Melosira crenulata* (Ehrenberg) Kützing 1844

= *Aulacoseira crenulata* (Ehrenberg) Thwaites 1848

= *Aulacoseira italica* f. *crenulata* (Ehrenberg) Ross 1986

For designated lectotypes of these two Ehrenberg taxa see above.

A revised taxonomic concept of *Aulacoseira italica*

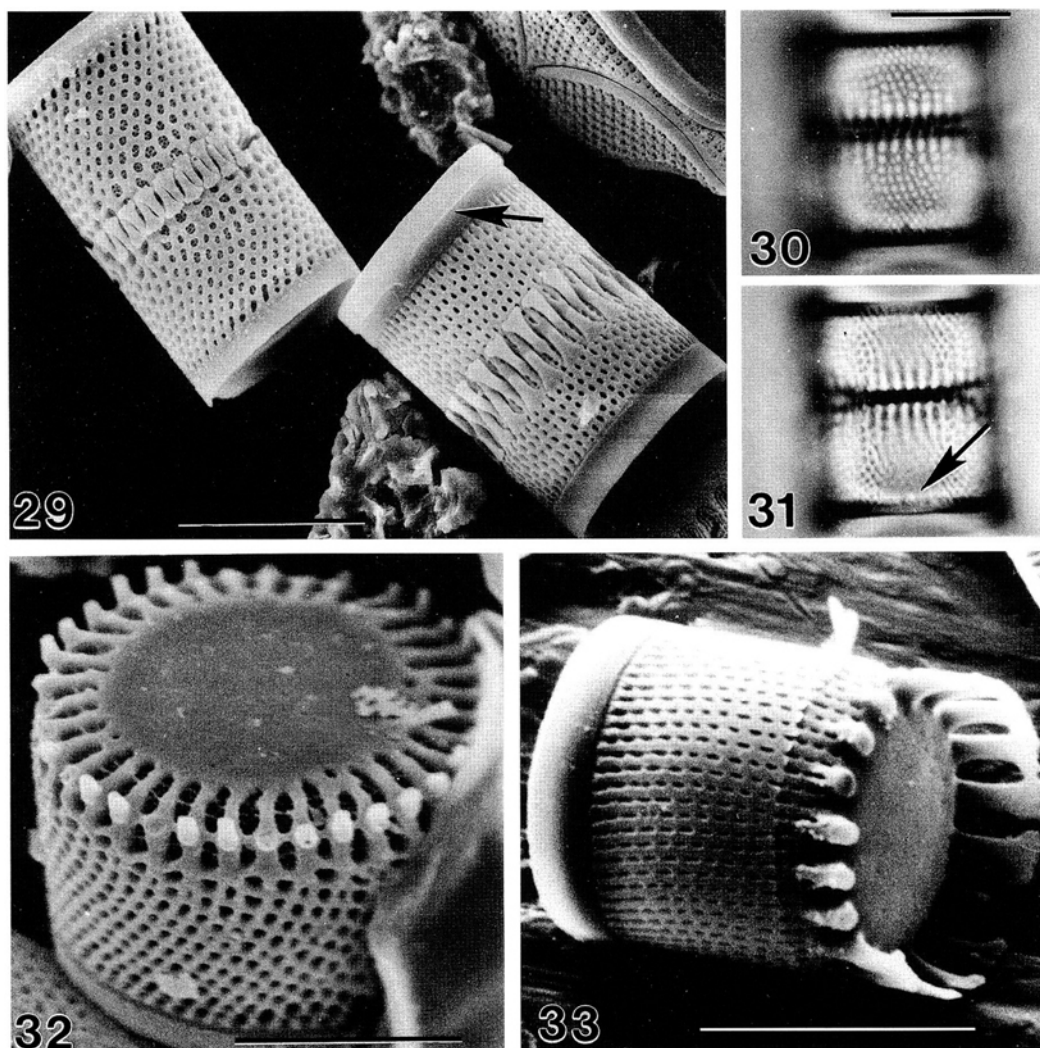
During the course of this study it has become clear that *A. italica* is being confused with another species of the same genus in modern literature, *A. valida* (Grunow) Krammer, even though they can be easily distinguished on the basis of the curvature of the rows of areolae. This confusion is partly due to the fact that *A. italica* is alone among the species with a sinistrorse direction of curvature (to the left away from the linking spines) but when first described it was only the second species of what is now

Aulacoseira. Thus there was no reason for Ehrenberg to think the direction of curvature was particularly significant. However, the second element of confusion dates from Grunow's drawing of a specimen from Lac de Gerardmer in the Voges, published in 1884, plate 88, fig. 8 as *M. crenulata* var. *valida*. This pair of sibling valves are shown with sinistrorse curvature rather than the reality, dextrorse, that Krammer (1991) illustrates in several valves of his new combination *Aulacoseira valida* from Grunow's type locality, Gerardmer. Why Grunow reversed the curvature is not clear. It is possible that he focused on the lower surface of the mantle and this might also explain why he did the same for other species, e.g. *A. ambigua* (Grunow) Simonsen. However it is more likely that he used a *camera lucida* that inverted the image. R. Simonsen has drawn our attention to the fact that Grunow's illustrations of *Odontella* are similarly inverted (see Simonsen 1979). Photographic inversion is out of the question for Grunow of course, but something to be guarded against more recently. At this point we considered dealing in detail with *A. valida* but prefer to continue with our policy of working through the species as they were described chronologically because of so much nomenclatural confusion in the genus. Instead we illustrate what we believe to be *A. valida* (Figs 29–32) in order to support our comments here and suggest looking at the figures of Krammer (1991) (Figs 29–33). We are leaving a detailed comparison with *A. italica* for a later publication.

Hustedt's figures for *Melosira italica* in his *Kryptogamenflora* (1930, fig. 109) are correct in showing sinistrorse spirals for *M. italica* itself and dextrorse spirals for the variety *valida*. However Hustedt gives no comment as to the direction of curvature and distinguishes between the varieties using other features, chiefly in a greater robustness of the valve and its features such as the ringleist. Hustedt's slides of "*Melosira italica* var. *valida*" match the images of Krammer from Gerardmer very well but slides labelled "*M. italica*" itself also have dextrorse pore rows! The only slides we can find in the Hustedt collection that match *A. italica* are those from Veermeer, presented below. Illustrations in Krammer & Lange-Bertalot (1991) are correct with the exception of plate 25, figs 1, 8. The former may well be inverted because the possible bright spots of rimoportulae are in the right position for *italica* though the curvature is wrong. As for the fig. 8, the curvature and the position of the rimoportula – a dark spot on the ringleist of the uppermost valve (compare with our Figs 30, 31) – suggest *valida*; see plate 28, fig. 9. Figures 42–45 of Siver & Kling (1997), purporting to be of *A. italica*, are in fact of *A. valida* and figs 53, 54 of Haworth (1988) are of *A. valida* rather than *A. italica* as stated. Genkal & Korneva (1986) and Barinova (1988) both illustrate *A. italica* and *A. valida* correctly even though they do not mention the feature that we believe so important for recognition of *A. italica* – the pore-row curvature. There are many more examples in the literature where this character has been overlooked. These were chosen because they are considered some of the more important recent works on the genus. Siver & Kling (1997) do draw attention to the direction of curvature of the pore rows (striae) always to the right and wonder if there are exceptions in other species. They were unlucky not to have had true *A. italica* to hand!

As a result we believe that *A. italica* may have been over-reported in the literature and that Skácelova & Houk (1993) may be correct in fearing that *A. italica* may not now be as common as in the fossil record. Perhaps both are true. Certainly, our attempts to find *A. italica* growing locally have failed. It should also be noted that the planktonic *A. subarctica* (O Müller) Haworth may also have been confused in the literature though only in name; it was a variety of *A. italica* until removed by Haworth (1988).

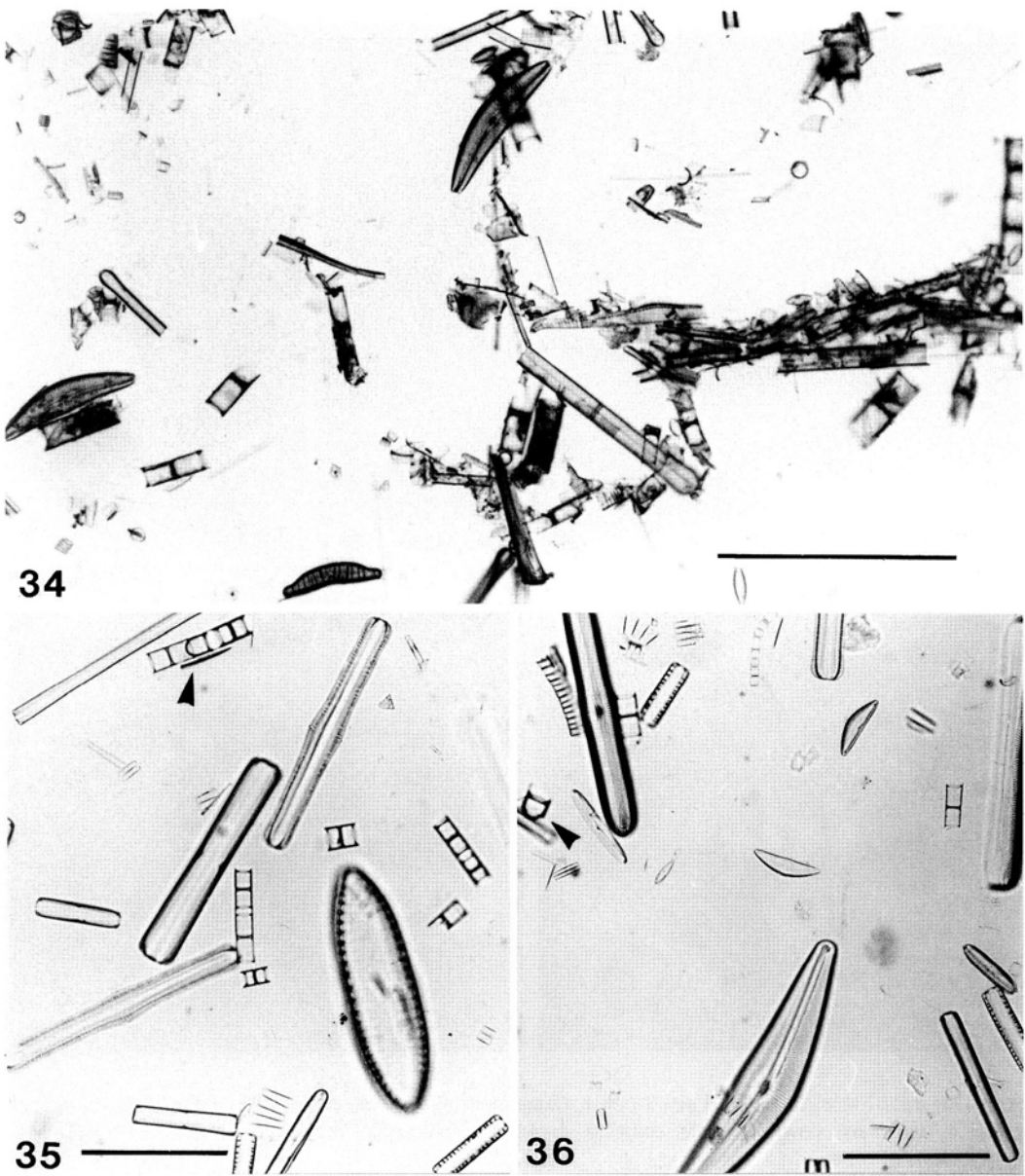
After examining many microscope slides it has become apparent that the diatom flora associated with *A. italica* is distinctive. Commonly found genera include: *Gomphonema*, *Rhopalodia*, *Epithemia*, *Cymbella*, *Encyonema*, *Eunotia*, *Pinnularia*, *Neidium*, *Synedra*, *Surirella* and *Stauroneis*; all of them essentially benthic and characteristic of a very different environment from the open water plankton of *A. ambigua* and *A. granulata* (Ehrenberg) Simonsen for example. Fig. 34 shows some of the taxa in the Santa Fiora sample and Figs 35, 36 are examples from Veermeer. Also shown in the latter two figures are spore valves of the *A. italica*, arrows. Initial valves of post-auxospore cells measuring 26–30 µm have been found in a sample from Dieksee, Schleswig-Holstein BRM slide 24/3. This size range is



Figs 29–33. *Aulacoseira valida*(?), Lake Sumner, Canterbury, New Zealand. **Fig. 29.** Sibling pairs of *A. valida*, left, and *A. italica* are shown, the latter showing one Müller step, arrow. **Figs 30, 31.** Two focuses of *A. valida* with two views of rimoportula arrowed in Fig. 31. **Fig. 32.** Single valve of *A. valida* for comparison with *A. italica* in Fig. 33. All scales = 10 μm .

extended at the bottom end for *A. italica* generally by Krammer & Lange-Bertalot (1991) who report valves as narrow as $3\mu\text{m}$. In one sample, Diecksee, there are large valves that appear to be perfect hemispheres. We believe these to be post-auxospore initial valves although their association with a conventional valve with the same orientation is unexpected. If the latter is one of the subsequent progeny of the initial cell then the valve should be facing in the other direction. However, at up to $30\mu\text{m}$, these valves lie at the upper limit of the size range for the species.

In addition to the distinctive sinistrorse spiralling of the rows of areola, we have established the uniqueness of the rimoportulae in the electron microscope and shown it can be seen with light microscopy (Kobayasi & Nozawa 1982 illustrated the feature with SEM but gave no LM image).



Figs 34–36. General view of the assemblages together with *Aulacoseira italica*. **Fig. 34.** Original material of *Aulacoseira italica* from Santa Fiora which includes species of *Cymbella*, *Synedra*, *Epithemia* and *Rhopalodia*. Scale bar = 100 μ m. **Figs 35, 36.** Veermor, Bremerhaven showing general assemblage including resting stages, arrowheads, and *Surirella*, *Synedra*, *Pinnularia* *Rhopalodia*, *Epithemia*, *Cymbella* and *Encyonema*. Scale bars = 100 μ m.

Separation spines have now been recorded twice in *A. italica* (Genkal & Korneva 1986, Skácelová & Houk 1993) although it appears they are very rarely formed and this prompts questions as to the ecology of the species. Again we echo the fears of Skácelová & Houk that *A. italica* may not be as common as it once was. A revised description follows:

***Aulacoseira italica* (Ehrenberg) Simonsen emend. R.M.Crawford, Y.E. Likoshway & R. Jahn**

Valves united by broadly anvil- or spade-shaped linking spines that vary in length among sibling valve pairs. A single row (rarely two) of areolae run up into the stem of the spine which may bear a number of granules. Separation spines of the same length as linking spines but tapering to a fine point are formed very rarely. Areolae are subcircular, or more usually, angust-elliptic to fine slits and arranged in sinistrorse, spiralling rows. Velum a spongiform plate covering the inner aperture of the areola and suspended by 3 or 4 supports from the sides of the areola. Valve face more or less covered by randomly arranged areolae or areolae absent. Rimoportulae one or more, usually two, per valve, visible with difficulty in the LM and positioned 4–5 areolae distant from the ringleist. Outer aperture of rimoportula not distinguishable in SEM from areolae; inside aperture terminates a straight tube lying flat against the valve surface and oriented transverse to the areolar rows. Ringleist solid, narrow and shallow. Valves 3–30µm wide, areolae 10–20 in 10µm, pores rows 18–25 in 10µm. This species forms resting spores.

The ecology of *A. italica* is not well known but clearly differs from the planktonic species in occurring with species of the genera listed above. Why it forms resting spores/cells and separation spines and under what environmental conditions needs to be investigated. The species promises to be a valuable environmental indicator if accurate records can be made.

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