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TAXONOMY, MORPHOLOGY AND DISTRIBUTION OF SOME *AULACOSEIRA* TAXA IN GLACIAL LAKES IN THE SOUTH CARPATHIAN REGION*

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Abstract. The morphology and taxonomy of *Aulacoseira* taxa, the dominant group of diatoms in a small glacial lake in the Retezat Mts (TDB-1) were studied in specimens from late glacial and Holocene sediments. Seven species were identified and evaluated by light and scanning electron microscopy. The results of these observations showed some variability of morphological features within the mountain species populations from a poorly investigated part of Europe. *Aulacoseira laevissima*, *A. perglabra* and *A. pfaffiana* are new for the Romanian flora as well as for this region. We confirm the existence of a low-mantle *Aulacoseira* species, published earlier but not described formally, in the South Carpathian mountain region.

Key words: *Aulacoseira*, diatoms, oligotrophy, Retezat Mountains, paleolimnology

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Introduction

The taxa of the genus *Aulacoseira* are among the most successful and most widely distributed diatoms. They are the oldest non-marine diatoms; the history of the genus extends back to the latest Cretaceous (Ambwani *et al.* 2003). They are also abundant in Quaternary lake sediments (Koinig 1994; Lotter & Hölzer 1994; Koinig *et al.* 1998; Gibson *et al.* 2003; Lotter & Hofmann 2003; Buczkó *et al.* 2009). The diversity and abundance of these cylindrical diatoms makes them useful and prominent elements of paleoenvironmental reconstructions. The most frequent *Aulacoseira* species are commonly used in biomonitoring studies; not only diatomists but also many environmental experts use them. This means that many analysts need to know the main features of *Aulacoseira* species. Due to the demand for better understanding of the taxonomy and diversity of the genus *Aulacoseira*, they have been in the focus of interest in the last few years. Clearly, however, we are far from knowing enough about them to make accurate reconstructions. Oligotraphenic, low-mantle *Aulacoseira* taxa are particularly in need of more study, but their geographical distribution has been the focus of several works recently (Lange-Bertalot & Metzeltin 1996; Trifonova & Genkal 2001; Potapova *et al.* 2008; English & Potapova 2009; Monoylov *et al.* 2009).

The first species of *Aulacoseira* was described by Ehrenberg in 1836 as *Gallionella distans* (Krammer 1991). The genus *Aulacoseira* was established by Thwaites in 1848 with *Aulacoseira crenulata* Ehrenberg (Crawford 1981). For decades, *Aulacoseira* species were grouped to the genus *Melosira*; not until 1979 did Simonsen reactivate the genus name, by splitting *Melosira* sensu lato (Krammer 1991; Crawford *et al.* 2003).

* Dedicated to Dr. Kurt Krammer on the occasion of his 85th birthday

Frustules of *Aulacoseira* species are cylindrical due to the depth of the valve mantle; consequently they are often seen in girdle view (high-mantle species). The frustules frequently form chains. The areolae on the mantle are clearly visible by LM, and are arranged in straight or curved rows; they are dextrorse when the areolae curve to the right, and sinistrorse when they curve to the left (Takano 1981). The areolae are simple, round to rectangular. Spines may be present around the junction of the valve face and mantle, particularly in end cells (i.e., at the end of a chain). Two types of spines, namely linking and separation spines, can be distinguished; linking spines are spatulate and firmly connect sibling valves, and separation spines are tapering. Sibling valves with separation spines can easily separate from each other (Houk & Klee 2007). A furrow is usually visible, often forming a thickening (ringleist) at the junction between the plain mantle edge and the areolate section. The valve view is circular and the valve face is either plain or bearing puncta (Kelly *et al.* 2005).

Historically, classification of species within this genus relied primarily on (1) the ratio of mantle height to valve diameter, (2) the orientation of the pervalvar rows of areolae (Takano 1981), and (3) details of separating spines (Siver & King 1997). As a second phase of classification, some other features have also been considered, such as (4) valve face morphology, (5) ringleist structure, (6) linking spine shape and (7) velum structure (Le Cohu 1991; Crawford & Likhoshway 1998). Recently another character, (8) the position of rimoportulae, has been studied in detail, and sometimes it has been crucial to the distinction of a species (*A. distans*, one of the most often recorded species, seems to be relict on the basis of number and position of rimoportulae; Likhoshway & Crawford 2001).

This characteristic genus is often the most important part of diatom assemblages (Koinig 1994; Lotter & Hölzer 1994; Buczkó *et al*. 2009). In spite of its importance, species-level identification is almost impossible, since the most characteristic features are so small that they are indistinguishable by light microscopy (Houk 2003; Houk & Klee 2007). Many taxa can only be identified or determined with confidence using SEM. The co-occurrence of several similar representatives of the genus in a given locality or sample is responsible for difficulties during the counting procedure.

Many taxa have yet to be examined by SEM to see how different morphologically they are, as the relationships among of *Aulacoseira* taxa remain unexplored. The aim of this paper is to contribute towards the better understanding of the biogeography and chronological distribution of *Aulacoseira* species in a poorly investigated part of the Europe. We hope that detailed LM and SEM documentation will help us gain a better overview of this genus on a world-wide scale. In this study we present an unidentified *Aulacoseira* specimen, the identity of which is unclear.

Materials and methods

Study sites

The Retezat is the wettest massif in the Romanian Carpathians (1400 mm/yr at 1500–1600 m a.s.l.) due to its Mediterranean and oceanic influences. As a result, the effects of the last glaciation have been more significant here than elsewhere in the Southern Carpathians. Numerous glacial lakes appear in the subalpine and alpine belts, formed following the retreat of the ice, mainly during the late glacial. For a detailed multi-proxy investigation of paleolimnological changes, Lake Tăul dintre Brazi on the northern slopes was selected (TDB, core TDB-1; 45°23′47″N, 22°54′06″E; 0.5 ha; 1740 m a.s.l.; 1 m water depth); this lake is situated in the subalpine belt. For more details see Magyari *et al.* (2010).

Methods

A five-meter sediment core was taken with a Livingston piston corer from the deepest part of the lake in 2007. For sub-sampling, the plastic pipes containing the sediment were cut into halves and sub-samples were taken at 1–4 cm intervals. For siliceous algae analyses the samples were prepared using standard digestion procedures (Battarbee 1986). Aliquot-evaporated suspensions were embedded in Zrax (refractive index 1.7). For light microscopy a LEICA DM LB2 (100× HCX PLAN APO) and Fujifilm Digital Camera (FinePix S2 Pro) were used. Scanning electron microscopy was performed with a Hitachi S-2600N. We followed mainly the nomenclature of Takano (1981) Krammer (1991), Krammer and Lange-Bertalot (1991), Siver and Kling (1997), Houk (2003), Houk and Klee (2007), Potapova *et al.* (2008) and English and Potapova (2009). Evaluation of the diatom flora of glacial lakes in the Retezat Mts in relation to other Romanian floras was greatly supported by an exhaustive treatment of the algae of Romania by Caraus (2002).

RESULTS

Eight representatives of the genus *Aulacoseira* were distinguished during study of the late glacial and Holocene sediments of TDB-1. Seven taxa were identified at species level, and a form remains unidentified.

Aulacoseira ambigua (Grunow) Simonsen 1979
Figs 1–12

'Valve mantle with hollow ringleist'

Aulacoseira ambigua is a relatively easily recognizable diatom in LM, because it is the only *Aulacoseira* species with a hollow ringleist (Figs 1–8, 11), although this feature is rarely visible in SEM (Fig. 9).

Valves 4–15 µm in diameter and 3.5–15.0 µm high (Houk 2003), so valves longer than wide. The ratio of mantle height to valve diameter is more than 1 (high mantle). It has dextrorse-running areolae on the valve mantle, arranged into spiral pervalvar rows (Takano 1981; Houk 2003). The areolae usually are round to square, but less often elongate. The areolae often have internal reticulation of the ribs (Fig. 9; Le Cohu 1991). Linking spines are small, spatulate or flared, described by different authors as 'triangular,' 'bifurcate' or 'bicuspidate' (Potapova *et al*. 2008). The spines of *A. ambigua* are positioned at the end of each pervalvar mantle costa (Houk 2003). Siver and Kling (1997) reported that the valve faces of most *A. ambigua* valves do not have areolae, but a single ring of areolae might be found on the valve face of separation valves. According to Houk (2003) the valve faces are flat, with randomly arranged finer pori at the valve face margin. The valves have two rimoportulae, which are located at the ringleist (Fig. 9) and are opposite each other (Likhoshway & Crawford 2001); their external openings are also well visible (Fig. 9).

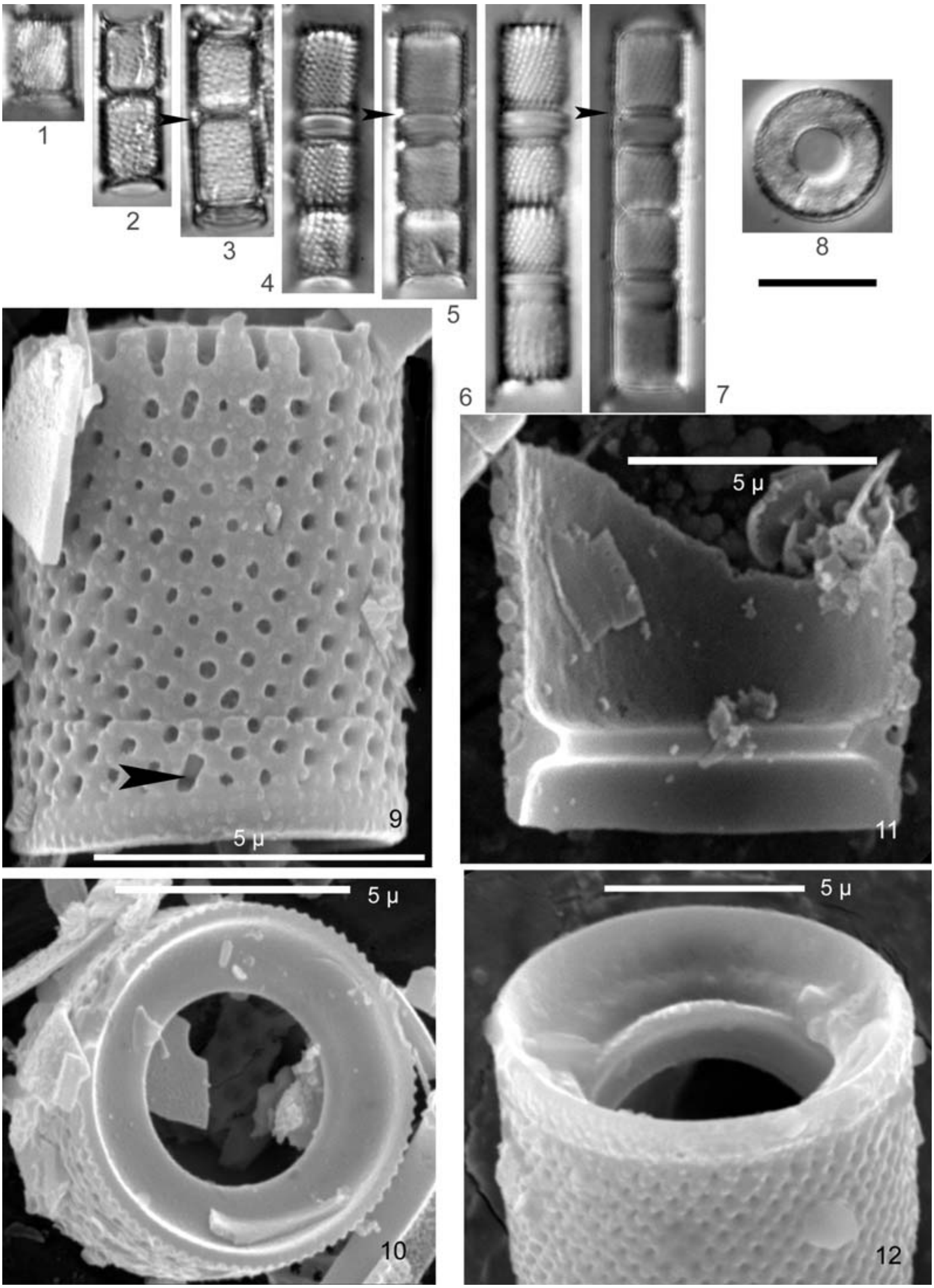
DISTRIBUTION. *Aulacoseira ambigua* is common in plankton of meso- and eutrophic stagnant waters (Houk 2003), frequent in the Holocene sediment of Lake Balaton, and often dominant (Korponai *et al.* 2010). In the Retezat Mts it is also reported from Lake Zenoga (Halász 1941). In TDB-1 this species is more abundant in samples representing the Late Holocene than the Early Holocene. *A. ambigua* is absent in the late glacial part of the core.

Aulacoseira alpigena (Grunow) Krammer 1990
Figs 13–22

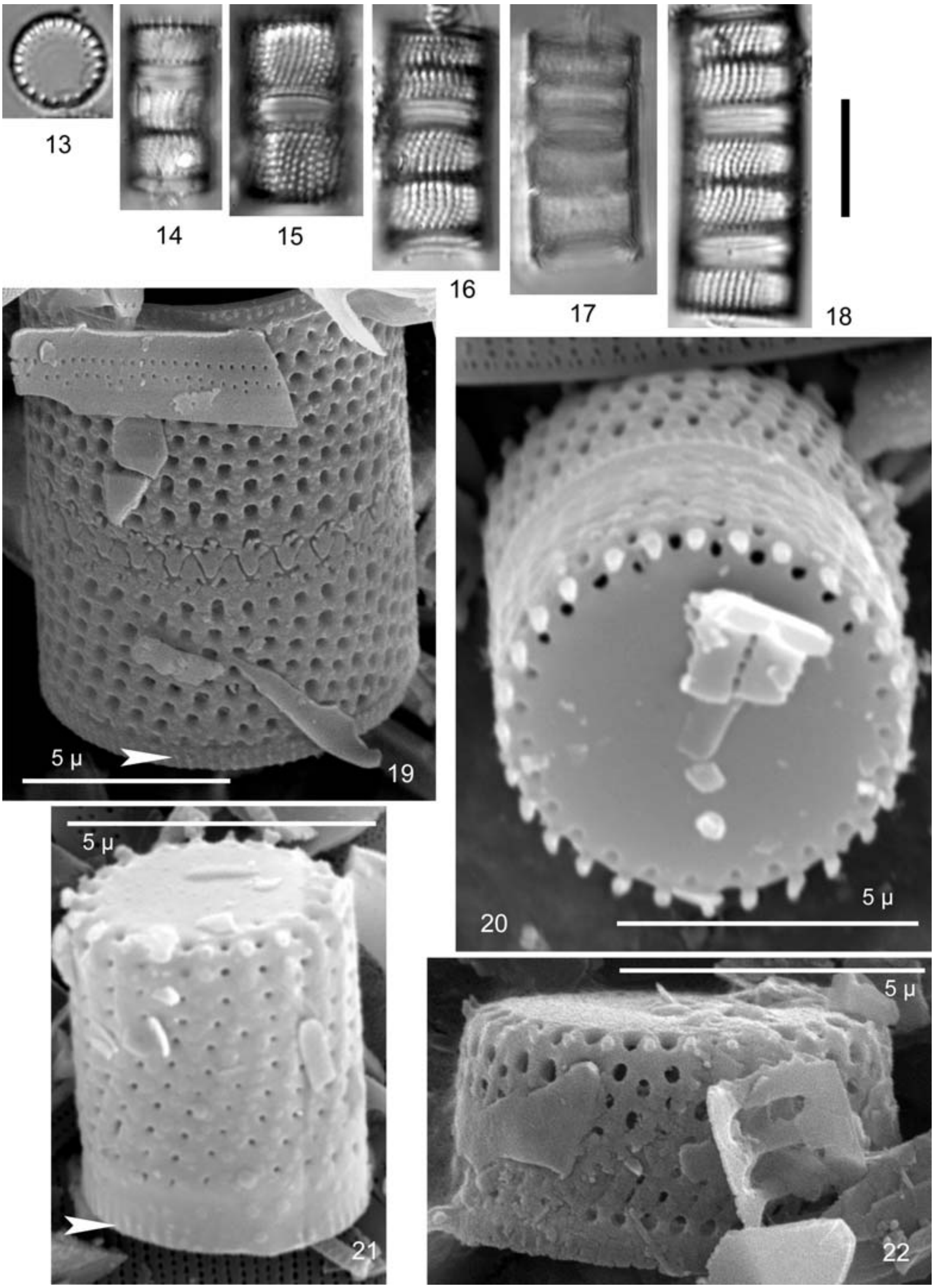
'Valve face with one row of marginal areolae, and mantle rows of areolae are curved'

Aulacoseira alpigena has cylindrical cells 4–15 µm in diameter and with mantle height 4–7 µm. The ratio of mantle height to valve diameter is less than 1 (low mantle). The areolae rows are dextrorse, 15–22 in 10 µm. The valve face is plain and smooth, with one row of marginal areolae (Figs 13, 20 & 21). The spines are at the end of each pervalvar costa (Figs 14 & 21–23). The linking spines are small (Figs 21–23) but there can be finger-like projections at the ends (Fig. 19, Siver & Kling 1997). The linking spines can have lateral ramifications on the spatulate anchors (Krammer 1991). The collum bears small dots in irregular rows (Fig. 19). The ringleist is small. The valve view of *A. alpigena* is very distinctive because most of the valve face is plain and only 1–2 peripheral rows of areolae may be present. Although *A. alpigena* is the low-mantle species most often reported and is an abundant member of the genus, we found its identification to be problematic, and for this reason precise counting is difficult.

DISTRIBUTION. Cosmopolitan species, preferring oligotrophic lakes with low conductivity. It is abundant in the lake sediment of Taul dintre Brazi (TDB-1). *A. alpigena* was found in a paleolimnological study of Zanoguta peat bog (Péterfi 1974). This species was also published from Lake Zenoga



Figs 1–12. *Aulacoseira ambigua* (Grunow) Simonsen. 4–5 & 6–7 are of the same specimens at different focal planes; 8 & 10–12 – ringleist; 9 – mantle view. Arrow indicates the external opening of the rimoportula. 1–8 – LM, 9–12 – SEM. Scale bar = 10 µm for LM.



Figs 13–22. *Aulacoseira alpigena* (Grunow) Krammer. 16 & 17 are of the same specimens at different focal planes; 19 – mantle view with finger-like projections, note the curved rows of areolae (arrow indicates the dots on the collum); 20 – plain valve face with one peripheral row of areolae; 21 – small atypical form; 23 – flat form. 13–18 – LM, 19–22 – SEM. Scale bar = 10 µm for LM.

(Halász 1941). *A. alpigena* is the first representative of the genus that appears in the late glacial period in TDB-1.

Aulacoseria sp. 1 Figs 23–28

'Valve face with only one ring of areolae, and mantle rows of areolae are parallel'

These cells have valve diameter of 7–10 µm and mantle height of 2–4 µm. The ratio of mantle height to valve diameter is *ca* 0.1–0.4 (low mantle). The mantle rows of areolae are typically parallel or slightly oblique to the pervalvar axis. They contain only a few areolae, 11–16 rows in 10 µm. The valve face is flat, with only one ring of areolae. The spines are situated at the end of each pervalvar costa. The collum is very small. The spines are thin and tapered, and have an anchor-shaped end. The ringleist is very small. This species is very similar to that was published by Houk (2003, Tab. XXXIX, Figs 1–14) as *Aulacoseira* sp.

Aulacoseira laevissima (Grunow) Krammer 1990 Figs 29–38

'Dots on the valve face/valve mantle junction'

Cells are cylindrical, tightly linked into long chains, with valves 6–17 µm in diameter and 5–10 µm high. The ratio of mantle height to valve diameter is less than 1 (low mantle). Valve faces are flat (Figs 33, 34 & 36) or convex (Figs 31, 37 & 38), with fine, irregularly spaced pori. Small pointed spines are situated at the valve face/valve mantle junction, usually one spine between two or three longitudinal rows of areolae (Figs 51, 54 & 57), a feature well seen in LM. The collar is high, with no structure on it, with a poorly developed ringleist internally. The mantles with longitudinal, straight (or slightly dextrorse) thick rows of very fine areolae, 22–28 rows in 10 µm, 23–30 areolae in 10 µm in a row. A rimoportula was not observed.

DISTRIBUTION. According to Houk (2003) it is a rarely observed taxon, known from Scotland. Siver and Kling (1997) also mentioned it as a rare taxon in two Connecticut waterbodies with low specific conductivity. According to our preliminary results, *A. laevissima* is absent in the late glacial, flourished in the Early Holocene, and present throughout the Holocene. It can also be found in surface sediment samples. The ecological indicator role of *A. laevissima* is poorly understood due to its rarity. New species for Romania.

Aulacoseira nivalis (W. Smith) English & Potapova 2009 Figs 46–56

'The valve face is covered by relatively large areolae arranged in regular tangential rows.'

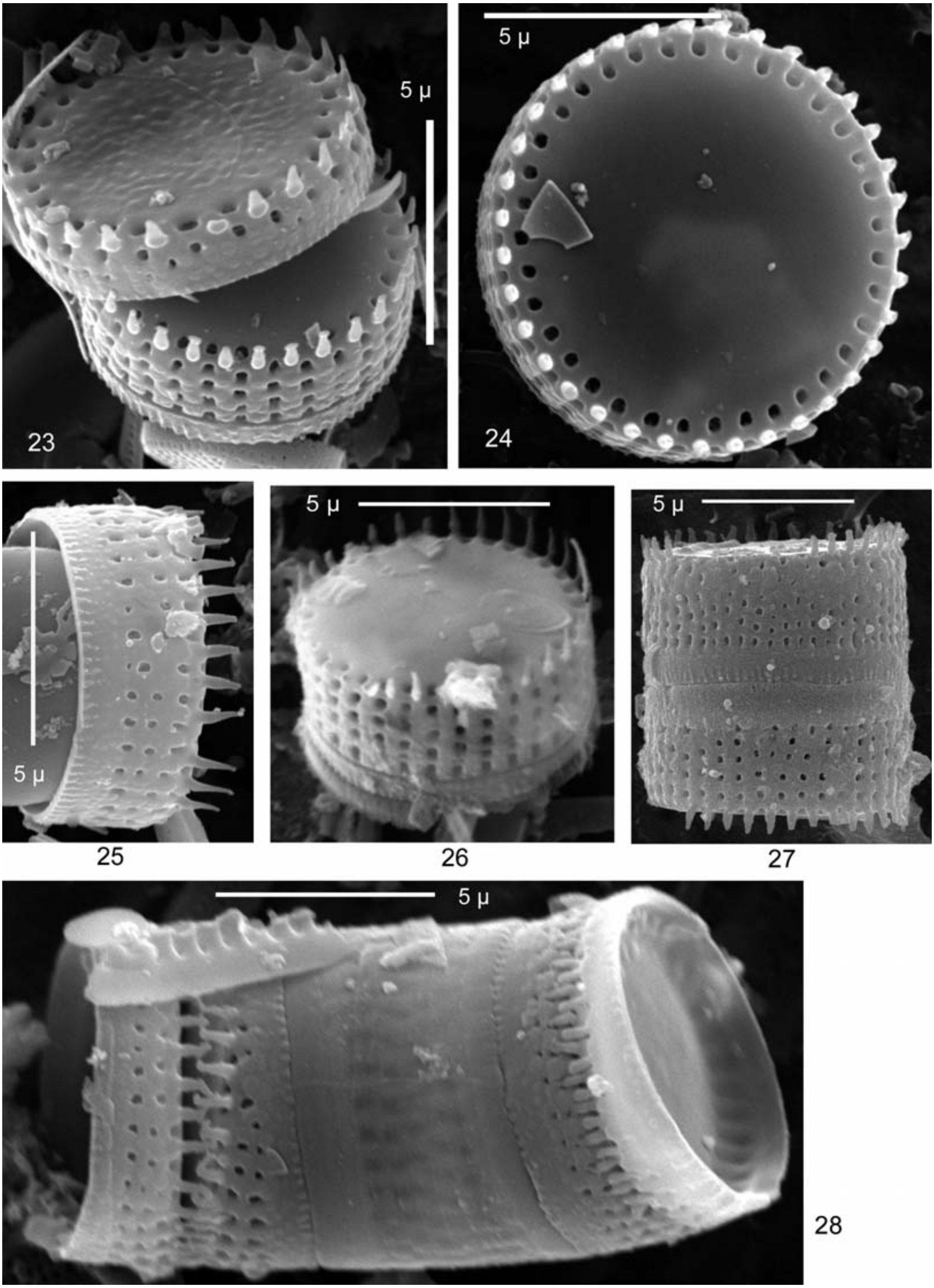
We observed specimens with diameter (4) 6–12 µm and mantle height 2.5–4.0 µm, smaller than given in published data (Krammer & Lang-Bertalot 1991; English & Potapova 2009). The mantle areolae are in straight rows which are slightly dextrorse, with 12–16 striae in 10 µm and 2–6 areolae in each row (Figs 50–52, 54 & 56). The spines are at the end of each pervalvar costa (Figs 53–56), but some irregularity can be seen in Figure 54. The ringleist is shallow and there is only one rimoportula on the mantle near the ringleist (Figs 47 & 53). The most significant differentiating character for *Aulacoseira nivalis* is the structure of the valve face, which is covered by relatively large areolae covering the whole valve face and arranged in regular tangential rows (Krammer 1991 as *A. distans* var. *nivalis*). *A. nivalis* has areolae *ca* 0.5 to 0.7 µm in diameter in our material (Figs 54–56), less than English and Potapova reported (2009).

DISTRIBUTION. *Aulacoseira nivalis* is known as a diatom characteristic of alpine and northern regions (Krammer & Lange-Bertalot 1991); frequent in western North America (English & Potapova 2009) and also abundant in the lake sediment of Taul dintre Brazi (TDB-1).

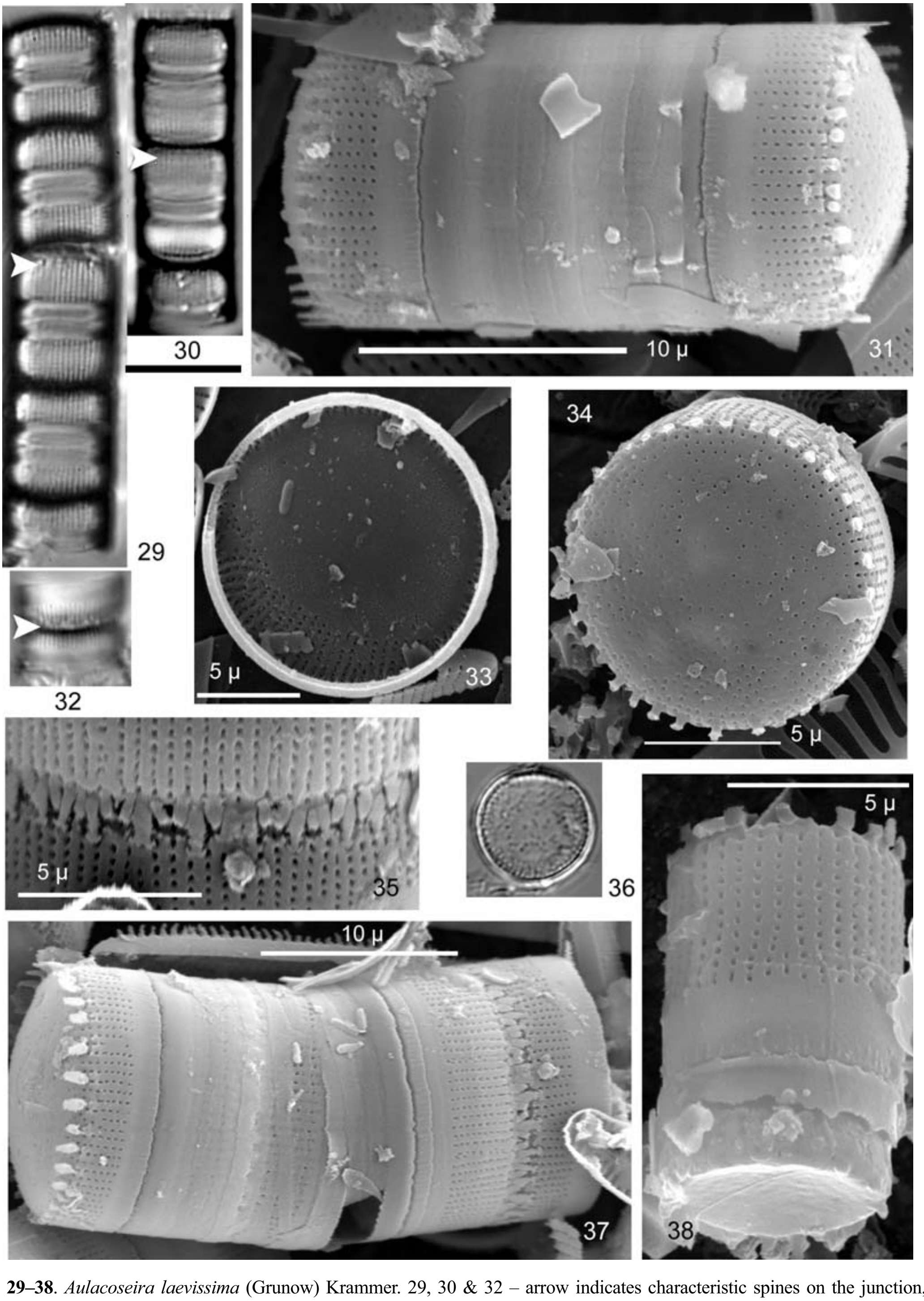
Aulacoseria perglabra (Østrup) Haworth 1988 Figs 39–45

'No visible structure on mantle in LM'

Cells low cylindrical, cell walls medially thick. with valves 8–17 µm in diameter and mantle height



Figs 23–28. *Aulacoseira* sp. 23, 24 & 26 – plain valve face with one peripheral row of areolae; 23 & 25–27 – mantle view with parallel rows of areolae; 25, 27 & 29 – linking spines are T-shaped, thin, tapered, and have an anchor-shaped end; all SEM.



Figs 29–38. *Aulacoseira laevissima* (Grunow) Krammer. 29, 30 & 32 – arrow indicates characteristic spines on the junction, as well-visible dots; 33, 34 & 36 – flat valve face with fine, irregularly spaced pori; 35 – hook-like linking spines. 38 – *Aulacoseira* cf. *laevissima*: atypical form. 29, 30, 32 & 36 – LM, 31, 33–35 & 37–38 – SEM. Scale bar = 10 μm for LM.

2–4 µm. The ratio of mantle height to valve diameter is *ca* 0.3–0.4 (low mantle). The valve face is more or less flat, with variable ornamentation: from pattern consisting of only one ring of coarse areolae at the valve margin to a pattern consisting of coarser puncta on the whole surface (Houk 2003). Spines are short and pointed. There is no structure on the high collar, and no ringleist is visible in LM. According to Houk (2003), 20–28 rows in 10 µm, but we found fewer, 16–20 in 10 µm. We have only LM documentation of the occurrence of *A. perglabra*, so the other features of the species cannot be described. More observations are required.

DISTRIBUTION. This species is known from marine sediments (!) (Lange-Bertalot & Krammer 1991; Houk 2003) as well as from lakes in England and Bohemia. Rare in our samples. New species for Romania.

Aulacoseira pfaffiana (Reinsch) Krammer 1991
Figs 57–64

'The valve faces have large, coarse areolae; those on the edge of the valve face are elongated'

The valve is cylindrical, 5–23 µm in diameter, with mantle height 3–11 µm. The ratio of mantle height to valve diameter is 0.25–0.80 (Krammer 1991). The cell walls are quite thick. The mantle areolae are in straight rows which are slightly oblique to the pervalvar axis (Figs 61 & 62). There are 12–15 rows of areolae in 10 µm and 16–18 areolae in 10 µm. There are 2–5 circular or pervalvar-elongated areolae in a row, often incomplete (Figs 61 & 62). The valve faces are flat and have large, coarse areolae (Figs 57–60 & 62–64). The areolae in the central part of the valve face are round, and those on the edge of the valve face elongated. Spines are thin, pointed, continuing from the ribs between the pervalvar rows of valve mantle areolae. The structureless collar is high; typically the collar of the epi-and hypotheca are as high as the areolate part of the valve mantle (Krammer 1991). One small rimoportula could be observed near the very shallow ringleist (Figs 61 & 64).

DISTRIBUTION. Cosmopolitan form, abundant in lake Taul dintre Brazi (TDB-1). The specimens found in TDB-1 (247 cm) have clearly visible elongated areolae on the valve face. It is a new species for the Romanian flora.

Aulacoseira valida (Grunow) Krammer 1990
Figs 65–71

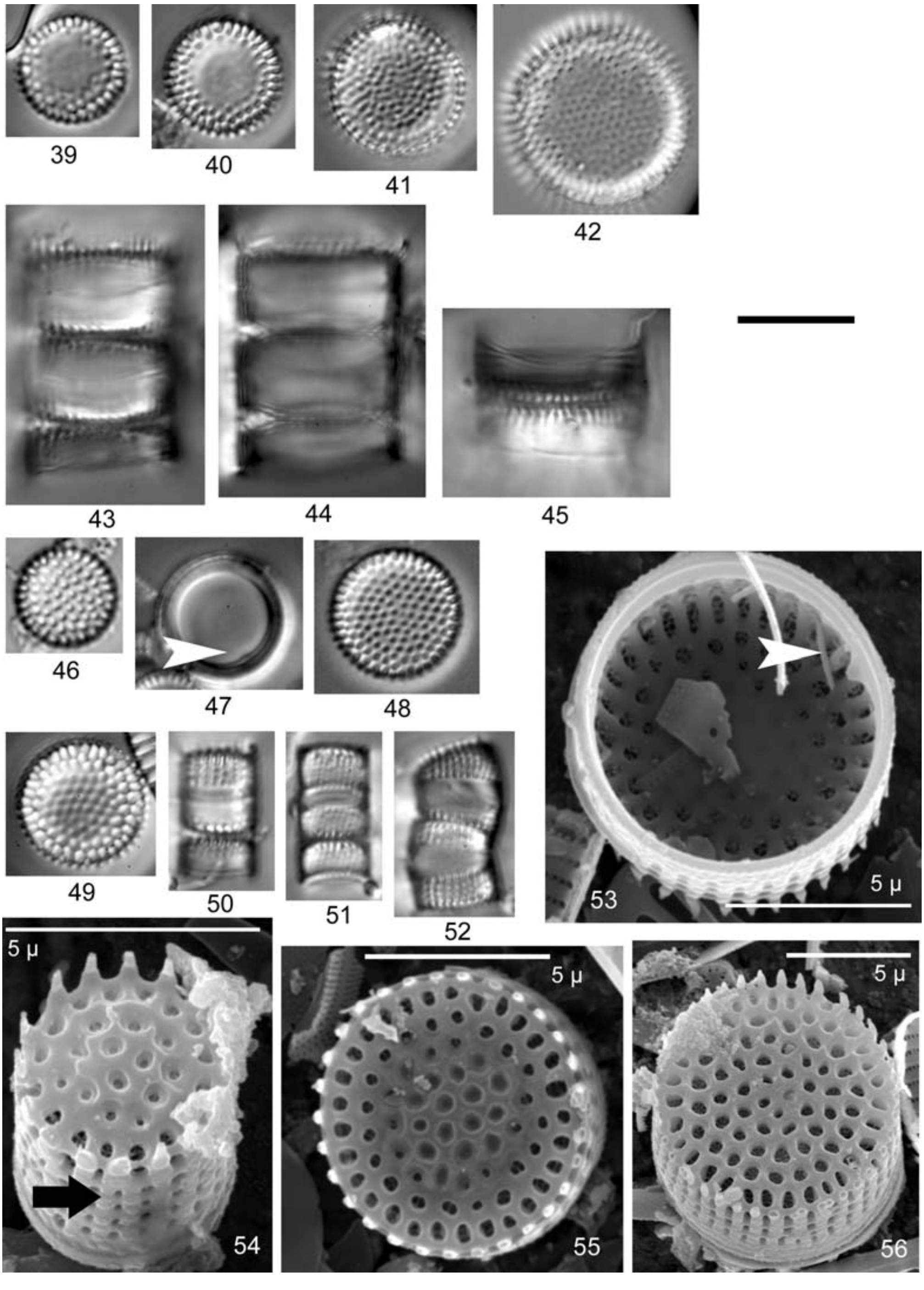
'The pervalvar areolae becoming larger at the valve face'

The cells are cylindrical, 10–25 µm in diameter and 10–18 µm high. Cell walls are thick. The height/diameter ratio is 0.6 to 3, but usually more than 1. The slightly convex valve face has fine areolae and distinct short grooves between the marginal spines. A characteristic feature of the species is the pervalvar areolae, smaller near the collum and becoming larger at the valve face, a pattern well visible in LM. There are 12–15 pervalvar rows of areolae in 10 µm, running dextrorse. The ringleist is medially developed. The linking spines are long, T-shaped (Houk 2003) and/or dendritic. *Aulacoseira valida* is best distinguished from other species of *Aulacoseira* by having long and thick spines, right-curved (dextrorse) pervalvar rows of areolae, and pervalvar areolae smaller near the collum and becoming larger at the valve face.

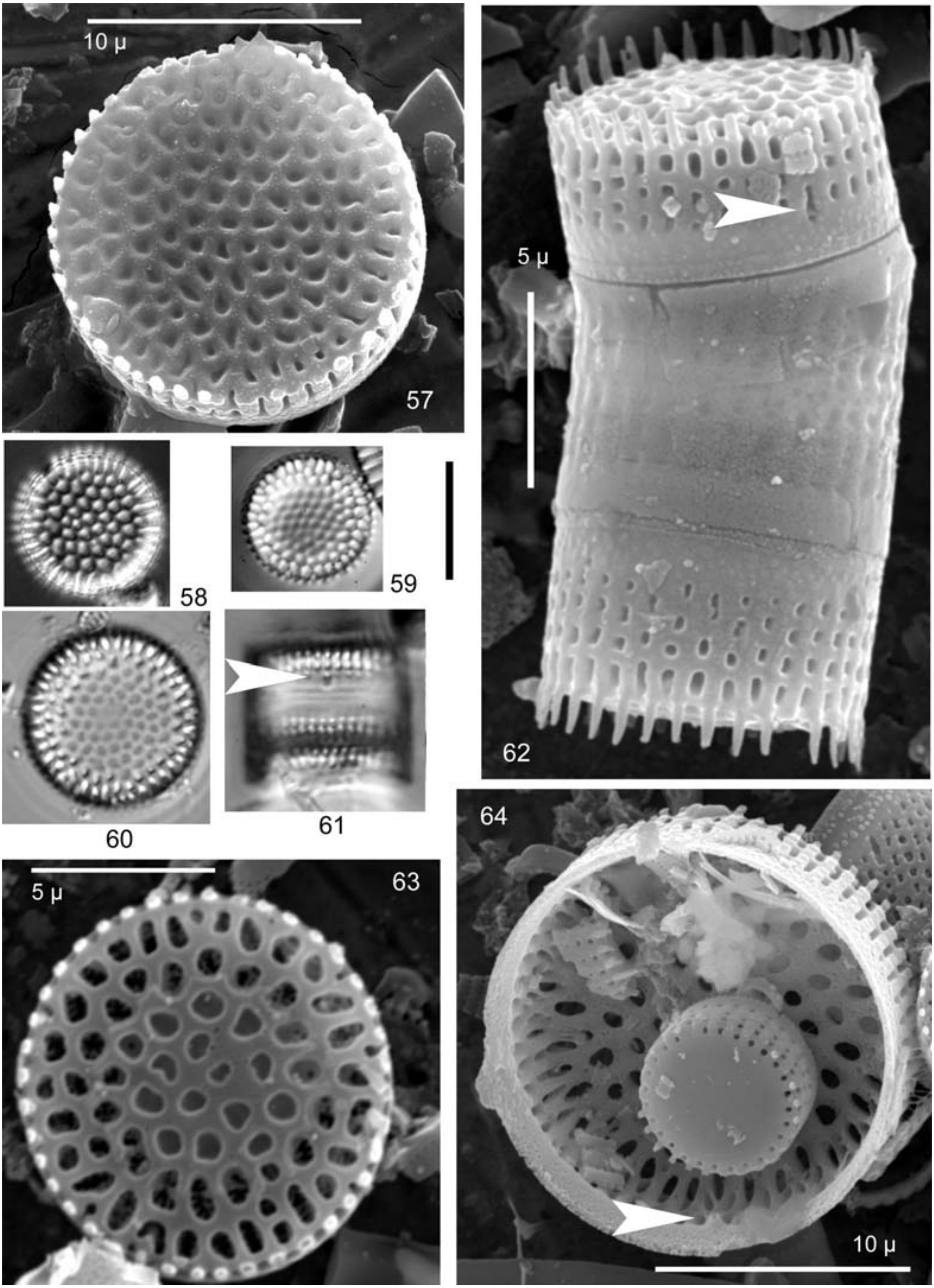
DISTRIBUTION. According to Houk (2003), *A. valida* is a Nordic-alpine cosmopolitan species, relatively infrequent, occurring in dystrophic and oligotrophic lakes and pools. In our samples, *A. valida* is common and abundant in the Holocene part of TDB-1. Also known from Zanoguta peat bog (Péterfi 1974), and abundant in the Rila and Pirin Mts in Bulgaria.

DISCUSSION

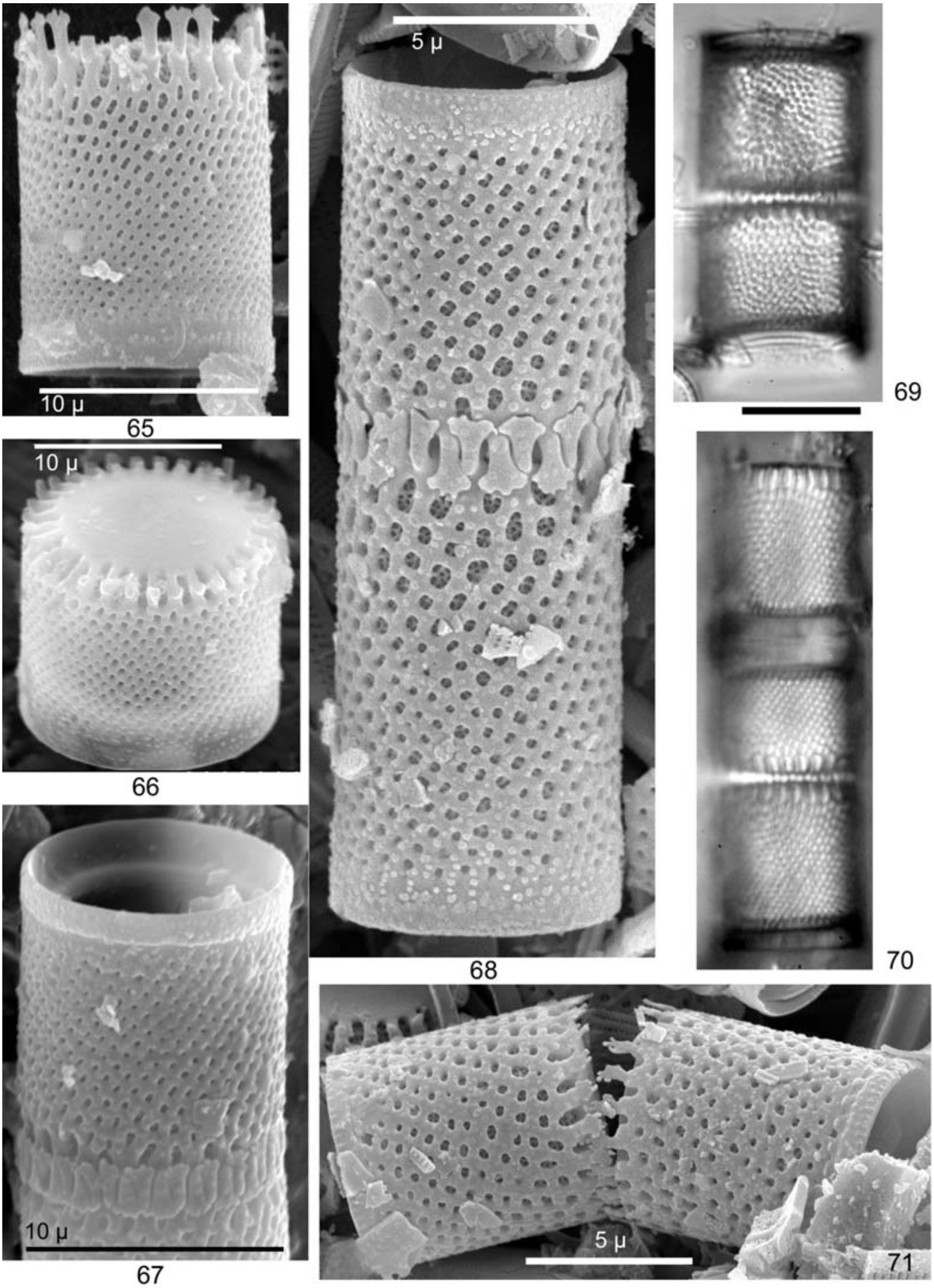
It is well known that *Aulacoseira* taxa are globally distributed, forming a considerable component of phytoplankton assemblages. They can also be abundant in lake bottoms (sediment surface) and on lakeshores, as well as among mosses and macrophytes. Some *Aulacoseira* taxa (mainly high-mantle ones) are characteristic for eutrophic and human-impacted waters, while others (many low-mantle forms) are restricted to less dis-



Figs 39–56. 39–45 – *Aulacoseira* cf. *perglabra* (Østrup) Haworth. 39–42 – valve face with variable ornamentation; 43–45 – structureless mantle view. 46–56 – *Aulacoseira nivalis* (W. Smith) English & Potapova. 46–49 – plain valve face with coarse areolae; 50–52 – mantle view; 53 – arrow indicates the rimoportula; 54 – irregular pattern, usually the spines are at the end of each pervalvar costa but here is one spine joined to two rows (arrow). 39–52 – LM, 53–56 – SEM. Scale bar = 10 μm for LM.



Figs 57–64. *Aulacoseira pfaffiana* (Reinsch) Krammer. 58–60 – valve faces, with coarse areolae (note elongated areolae on the edge of valve face); 61 & 62 – mantle view. 64 – a small *A. alpigena* valve interior *A. pfaffiana* valve (note the difference in dimensions; arrow indicates the rimoportula); 62 – spines are thin, pointed, continuing from ribs between pervalvar rows of valve mantle areolae. 58–61 – LM, 57 & 62–64 SEM. Scale bar = 10 µm for LM.



Figs 65–71. *Aulacoseira valida* (Grunow) Krammer. 65 & 68 – mantle view with pervalvar areolae that are smaller near the collum and becoming larger at the valve face; 67 – ringleist; 68 – deep-lying vela in irregular areolae in mantle view. 65–68 & 71 – SEM, 69 & 70 – LM. Scale bar = 10 µm for LM.

turbed, pristine habitats. Recently more attention has been paid to oligotrophic habitats because of global environmental concerns, but the taxonomy of oligotraphenic diatoms living there is unclear (Lange-Bertalot & Metzeltin 1996).

Based on the currently available descriptions in the literature we had difficulty distinguishing between *A. nivalis* and *A. pfaffiana* because of the overlap in character descriptions, and because we often found these two similar taxa together. *Aulacoseira pfaffiana* is strikingly similar to *A. nivalis*. The descriptions differ only in the arrangement of valve face areolae; the main feature distinguishing between the two taxa is that in *A. pfaffiana* the areolae in the central part of the valve face are round, and those on the edge of valve face elongated, whereas in *A. nivalis* the valve face areolae are round everywhere. These two forms of areolae are illustrated in the original figure of Reinsch (discussed in Tuji & Williams 2006). Potapova *et al*. (2008) are uncertain about the difference between *A. nivalis* and *A. pfaffiana*, and leave the question open. Our observations lead us to accept the original concept, confirming the difference between *A. pfaffiana* and *A. nivalis*. Detailed study of the spines may help define these similar forms more precisely. *A. nivalis* probably has two different kinds of spines, linking and separating, whereas *A. pfaffiana* has only one type of spine which looks like a separating spine (V. Houk, pers. com).

Aulacoseira alpigena has been a frequent and abundant species during the Holocene history of lake Taul dintre Brazi. Three forms were distinguished during preliminary counting: 'nominate' (Figs 13–20), 'small' (Fig. 21) and 'flat' (Fig. 22) form. Our findings correspond to the observations of Koinig (1994) in Schwarzsees. These three forms can easily be distinguished in LM. One more form closely related to the *A. alpigena* group was found in the study. An unidentified *Aulacoseira* species is documented in Figures 23–28. A similar taxon was published by Houk (2003), and it is also found in the Rila Mts (N. Ognjanova, unpubl.). This form is similar to *A. tethera* described from a Cumbrian lake and accepted by Krammer (1991) due to features clearly distinguishing it from *A. alpigena*. Houk and Klee (2006) did not mention this taxon, and its presence could not be confirmed in North America (Potapova *et al.* 2008). The linking spines are thin and tapered, and the form presented here has an anchor-shaped end distinguishing it from *A. tethera*, which has spatulate spines. We agree that this form is separated from the earlier-described species.

The late glacial and Holocene data (Buczkó *et al.* 2009) clearly show that *Aulacoseira* taxa are restricted in or almost absent from the late glacial period in lake Taul dintre Brazi, but they flourish in the Holocene. The indicator value of *Aulacoseira* taxa is problematic. Usually they are regarded as tychoplanktonic forms, but several *Aulacoseira* are often found among aquatic macrophytes in lake margins, ponds and ditches. Given the potential of *Aulacoseira* species as indicators of environmental conditions, it is important to ensure the consistency of their species-level identification (Camburn & Kingston 1986; Potapova *et al.* 2008).

The growing database of *Aulacoseira* species makes it clear that their distribution is characteristic on smaller and larger geological scales, as well as on the evolutionary scale. An example of the smaller-scale differences is from the Alps, where a sharp difference in the abundance of *Aulacoseira alpigena* between lakes situated on northern and southern slopes was noted. The northern slope lakes had much higher abundances of *A. alpigena* than southern slope lakes (Robinson & Kawecka 2005). The distribution of *Aulacoseira pseudamericana* is restricted to North America, illustrating world-scale differences (Manoylov *et al.* 2009).

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