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Discovery of living populations of a purported fossil diatom: *Aulacoseira scalaris* from two lakes in the Vosges Mountains (France)

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Résumé – Découverte de populations vivantes d'une prétendue diatomée fossile : *Aulacoseira scalaris* dans deux lacs du Massif des Vosges (France). Dans le cadre du Programme de Surveillance répondant à la Directive européenne Cadre sur l'Eau, un suivi du phytoplancton des plans d'eau de plus de 50 hectares est réalisé dans le bassin Rhin-Meuse. C'est lors de ce suivi que la diatomée centrique *Aulacoseira scalaris* (Grunow *in* Van Heurck) Houk, Klee & Passauer a été identifiée dans les lacs de Longemer en 2010 (Xonrupt-Longemer, France) et de Gérardmer en 2011 (Gérardmer, France). Sa présence a été à nouveau détectée dans les échantillons prélevés en 2014 sur ces deux lacs. *Aulacoseira scalaris* n'avait été jusqu'à présent trouvée que dans des échantillons fossiles à subfossiles des U.S.A. (État de l'Oregon, et Virginia City de l'État du Nevada) et de France (Lac de Gérardmer, Vosges, France). Cette espèce ayant été retrouvée vivante dans le phytoplancton de ces deux lacs des Vosges, elle ne doit plus être considérée comme uniquement une diatomée fossile. Des informations sur son autécologie sont proposées grâce aux données physicochimiques des deux lacs, et sa morphologie est comparée avec les espèces d'*Aulacoseira* semblables présentes dans la littérature.

***Aulacoseira scalaris* / Diatomées / France / lacs / Vosges**

Abstract – As a part of the Monitoring Program of the European Water Framework Directive, the phytoplankton of water bodies over 50 hectares have been studied in the Rhine-Meuse river basin. During the analysis, the centric diatom *Aulacoseira scalaris* (Grunow *in* Van Heurck) Houk, Klee & Passauer was identified from Longemer Lake in 2010 (Xonrupt-Longemer, France) and Gérardmer Lake in 2011 (Gérardmer, France). The presence of this diatom was again confirmed in samples collected in 2014 from both lakes. Interestingly, *Aulacoseira scalaris* until recently has been found only in fossil to subfossil materials from U.S.A. (State of Oregon and Virginia City, State of Nevada) and France (Vosges Mountains, Gérardmer Lake). The species has been observed for the first time in live material and should no longer be considered as strictly fossil or subfossil. Information on its autecology is provided using the physicochemical data of the lakes, and its morphology is compared with similar species of *Aulacoseira* in available literature.

***Aulacoseira scalaris* / Diatoms / France / lake / Vosges**

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INTRODUCTION

The genus *Aulacoseira* Thwaites is one of the most common in freshwater, especially abundant in plankton of lakes and large rivers (Spaulding & Edlund, 2008). It has been established by Thwaites in 1848 with *Aulacoseira crenulata* (Ehrenberg) Thwaites as generitype, which in turn is based on *Gaillonella crenulata* Ehrenberg (1843). Until Simonsen (1979) the name *Aulacoseira* was largely forgotten and most of the species currently placed in this genus were included within *Melosira* C. Agard (Siver & Kling, 1997; Potapova *et al*., 2008).

The genus *Aulacoseira* is currently described as having short to long cylinder-shaped cells, joined by spines present on the valve face periphery forming chains. These spines are of two types in most species: separating spines and linking spines. The valve mantle that makes a right angle to the planar valve face may be high or short, with a structure of straight or curved pervalvar rows of areolae. At least one rimoportula can be found on the inner side of the ringleist (Round *et al*., 1990; Houk, 2003; Potapova *et al*., 2008).

Melosira (*distans* var.) *scalaris* Grunow in Van Heurck (1882, pl. 86, figs 30BB, 31) was recombined in the genus *Aulacoseira* by Houk *et al*. (2007). *Aulacoseira scalaris* (Grunow in Van Heurck) Houk, Klee & Passauer is described as having short, rounded or conical spines, forming mostly short chains and having a low mantle. The valve face is flat, with rounded and irregularly spaced areolae. The rows of areolae on the valve mantle are straight. There are about 18 rows in 10 µm and 22 areolae in 10 µm along a row. The ringleist extends to about 2/5 of valve diameter, containing a ring of widely spaced rimoportulae on its inner side (Houk *et al*., 2007). This species was found in Grunow's material from two locations of the United States of America and one from France as fossil or subfossil materials. The type population was described from an Oregon deposit. The species was also found in a Nevada deposit and in Gérardmer Lake sediments, Vosges, France (Houk & Klee, 2007; Houk *et al*., 2007). Genkal *et al.* (2010, p. 29, pl. 1, fig. 3) and Tanaka *et al.* (2011, p. 125, figs 8-12) illustrated valves of *Aulacoseira* sp., which resemble *Aulacoseira scalaris* from phytoplankton of the Svisloch River (Minsk City, Belarus) and from a lacustrine fossil deposit (Atagi Formation) in Owashi (northern Gujo City, Gifu Prefecture, Japan), respectively.

During the survey of phytoplankton communities of the Rhine-Meuse river basin, as a part of the biomonitoring program for the European Water Framework Directive, *A. scalaris* was found in two glacial lakes in the Vosges Mountains. This article presents the morphology and ultrastructure of the two populations using light and scanning electron microscopy. Based on the physicochemical data and features of the lakes, information on its autecology are provided and compared with morphologically similar *Aulacoseira* species.

MATERIALS AND METHODS

The two lakes (Longemer and Gérardmer), are located in northeastern France, in the Vosges Mountains (Fig. 1). They are situated in the upstream section of the Vologne River, a tributary of the Moselle River. Both are glacial lakes on granitic substratum. Their watersheds are similar in terms of size and land cover

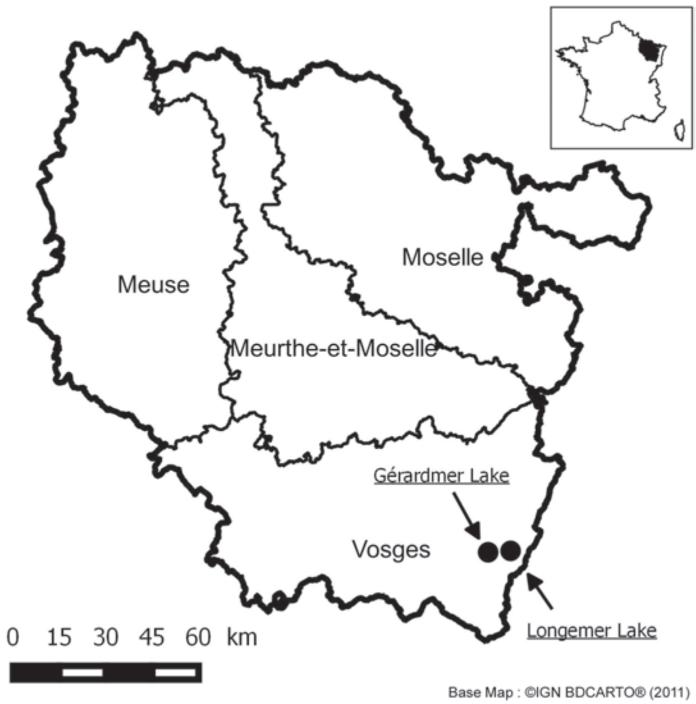


Fig. 1. Location of Gérardmer Lake and Longemer Lake in the French region of Lorraine.

Table 1. Features of the lakes (Centre Technique du Génie Rural des Eaux et Forêts (CTGREF), 1979)

	Altitude	*Length*	*Width*	*Surface area*	*Volume*	*Maximum depth*	*Average turnover time*	*Surface area of the watershed*
Gérardmer Lake	660 m	2000 m	750 m	115.5 ha	$19.5\ 10^6\ m^3$	36.2 m	1 year	$12.39\ km^2$
Longemer Lake	750 m	1900 m	520 m	76.2 ha	$10.8\ 10^6\ m^3$	29.5 m	0.4 year	$12.63\ km^2$

(mostly resinous forest with small urban pressure). Their altitude and surface area are similar as well as their maximum depth (Table 1). On the other hand, the average water turnover time is much shorter in Longemer Lake (Table 1).

Four phytoplankton samples were collected from Longemer Lake from April to September, 2010 and 4 samples from Gérardmer Lake from March to October, 2011 by a public (Direction Régionale de l'Environnement, de l'Aménagement et du Logement (DREAL) Lorraine) and a private (GREBE: Groupe de Recherche et d'Étude Biologie et Environnement) organizations in charge of monitoring water quality control networks. Samples were collected in the euphotic zone with a water sampler (Niskin Type) and fixed in the field with Lugol's solution, according to the French national protocol (Laplace-Treyture *et al.*, 2009).

Diatoms slides were made according to the French diatom protocol (AFNOR, 2007). The samples were treated by oxidation with hot 37% hydrogen peroxide (H_2O_2) and hydrochloric acid (HCl), and rinsed three times with deionized water. For light microscopy (LM) observations, cleaned diatoms were mounted in Naphrax®. LM and morphometric measurements were performed with an OLYMPUS BX50 microscope using a ×100 oil immersion objective and a MOTIC MOTICAM 2000 camera. For each lake, measurements were taken from more than 50 individuals. For scanning electron microscopy (SEM), parts of the oxidized suspensions were filtered with additional deionized water through a 3-µm Isopore™ polycarbonate membrane filter (Merck Millipore). Filters were mounted on aluminium stubs and coated with platinum using a Modular High Vacuum Coating System BAL-TEC MED 020 (BAL-TEC AG, Balzers, Liechtenstein). An ultra-high-resolution analytical field emission (FE) scanning electron microscope, Hitachi SU-70 (Hitachi High-Technologies Corporation, Japan), operated at 5 kV and 10 mm distance, was used for the analysis. SEM images were taken using the lower (SE-L) detector signal and a tilting of up to 28°. Micrographs were digitally manipulated and plates containing light and scanning electron microscopy images were created using CorelDraw X5®.

Physicochemical data were taken from the "Système d'Information sur l'Eau Rhin-Meuse (S.I.E.R.M.)" (http://www.rhin-meuse.eaufrance.fr/). Physicochemical samples were collected together with plankton samples, thus, only 4 measures per year are available in 2010 for Longemer Lake and in 2011 for Gérardmer Lake (Table 2).

Table 2. Minimum and maximum values of physicochemical parameters for each lake DOC: Dissolved Organic Carbon; COD: Chemical Oxygen Demand; BOD_5: Biochemical Oxygen Demand after 5 days

	Longemer Lake	*Gérardmer Lake*		*Longemer Lake*	*Gérardmer Lake*
NH_4^+ (mg.l^{-1})	0.05	0.05-0.06	Pheopigments (µg.l^{-1})	0.2-1.5	0.5-1.2
NO_2^- (mg.l^{-1})	0.01	0.01	Ca^{2+} (mg.l^{-1})	4.2-5.8	4.2-4.6
NO_3^- (mg.l^{-1})	1.1-1.4	0.5-1.4	Cl^- (mg.l^{-1})	28-29	27
Kjeldahl Nitrogen (mg.l^{-1})	0.5-1.3	0.7-0.9	Mg^{2+} (mg.l^{-1})	0.8-1.3	0.7-0.9
Total Nitrogen (mg.l^{-1})	0.32-1.6	0.7-1.2	K^+ (mg.l^{-1})	0.4-0.5	0.5-0.7
PO_4^{3-} (mg.l^{-1})	0.02	0.02	SiO_2 (mg.l^{-1})	3.7-4.3	3.1-4.1
Total phosphorus (mg.l^{-1})	0.02	0.01-0.02	Na^+ (mg.l^{-1})	16-18	16-18
SO_4^{2-} (mg.l^{-1})	2.9-3.3	3.4-3.9	Conductivity (µS.cm^{-1})	85-134	119-120
DOC (mg.l^{-1})	1.6-1.9	2.3-2.8	Suspended Matter (mg.l^{-1})	2 (40)	2
COD (mg.l^{-1})	4-7	5-11	pH	5.6-9.4	7.03-8
BOD_5 (mg.l^{-1})	0.9-1.9	1.1-1.7	Dissolved Oxygen (mg.l^{-1})	9.5-11.2	9.2-11.8
Chlorophyll *a* (µg.l^{-1})	0.5-3.8	1.1-3.8	Dissolved Oxygen saturation (%)	75-104	88-99

RESULTS

Morphology

Discoid plastids typical of the genus *Aulacoseira* (Cox, 1996) were observed in living material (Figs 2-3). Treated samples of *Aulacoseira scalaris* (Figs 4-12) tend to form short chains of between 2 to 5 cells. Chains of up to 14 cells were however observed in the living material.

The valve face is always flat, with irregularly spaced areolae (Figs 13-25 and 34). Numerous spines can be found on the valve face rim (Figs 27-30, 32 and 36). Cells have either rounded and short spines (Figs 28, 30 and 32) or conical and thick ones (Figs 27, 29, 30 and 36).

The valves are short in height (2.5-5 µm) and have a diameter of 5-14 µm. The ratio valve height/diameter ranges from 0.35 to 0.6.

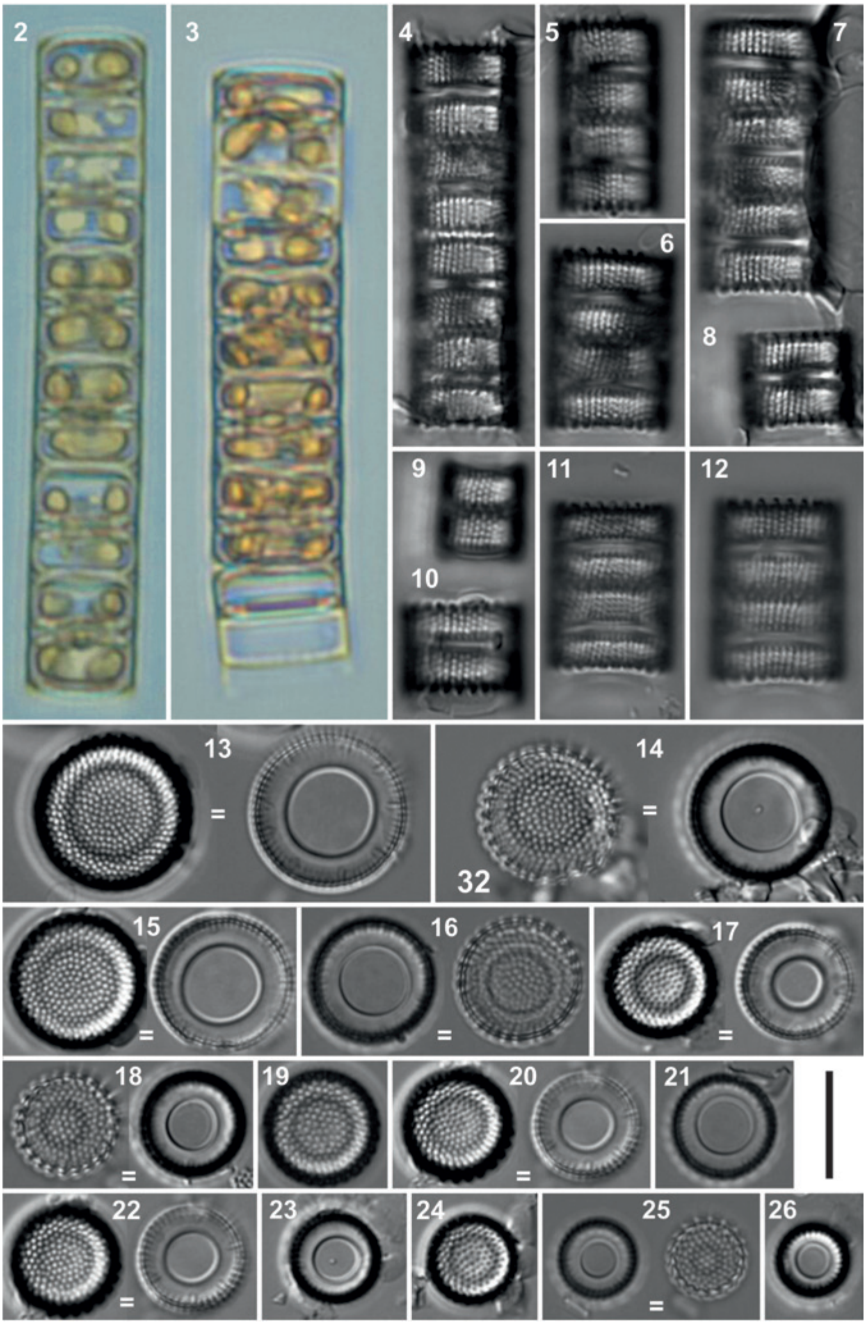
The two studied populations have very close similar morphometric measurements (Table 3), even when in Gérardmer Lake *A. scalaris* had a higher frequency of valves with bigger diameter (12 to 14 µm).

The valve mantle has rows of areolae, which are straight and abundant with about 18 rows in 10 µm. However, anomaly may occur: one valve was found with curved rows (Fig. 29). The areolae density is average with 18-21 areolae in 10 µm. There are twice as many rows of areolae than spines (Figs 32 and 36).

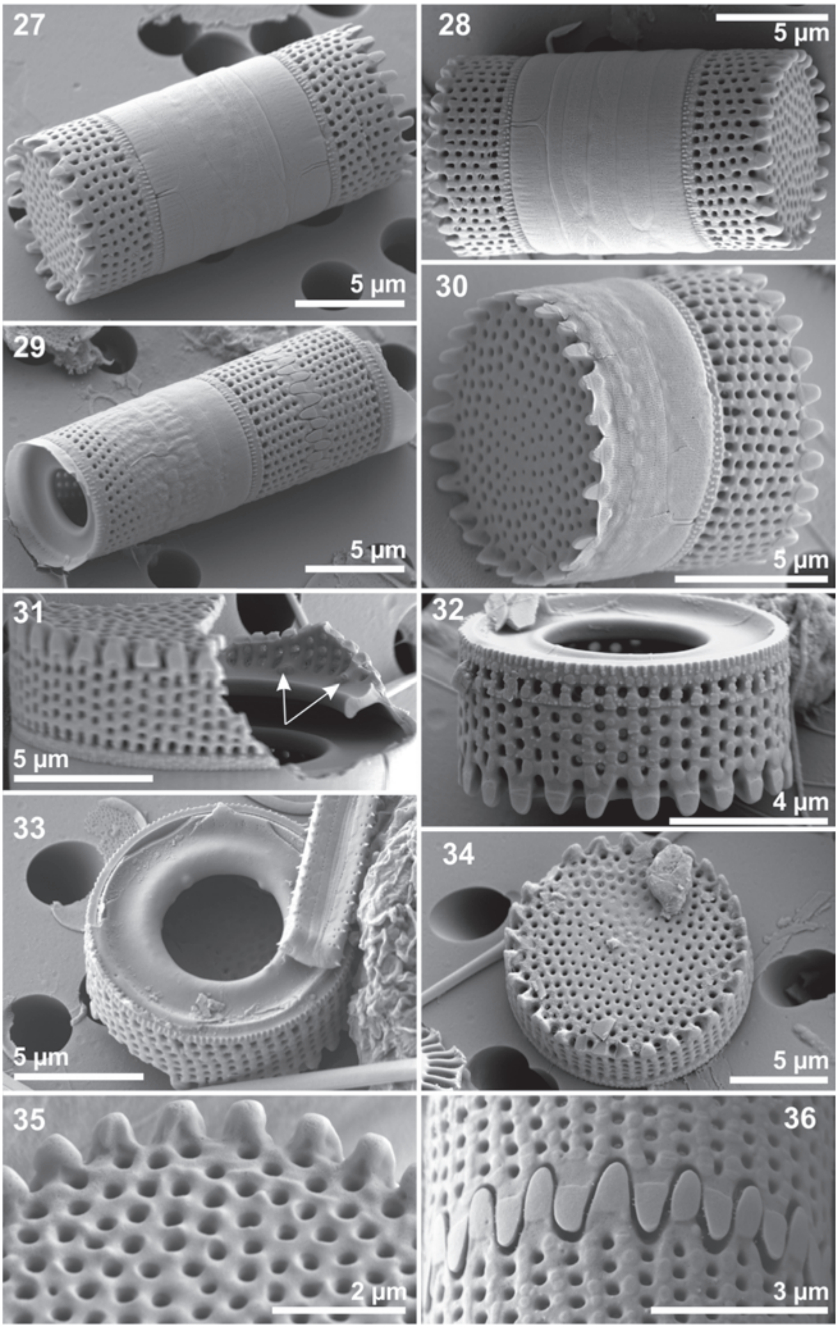
Table 3. Comparison of biometric data and morphological features of *Aulacoseira scalaris* between our recent freshwater material and the fossil type material

	Aulacoseira scalaris[1] (recent material from Longemer Lake)	*Aulacoseira scalaris*[1] (recent material from Gérardmer Lake)	*Aulacoseira scalaris*[2] (fossil type material from Oregon)
Ringleist	1/3-1/2 of the diameter	2/5-1/2 of the diameter	~2/5 of the diameter
Ratio *N* striae / *n* spines	2	2	2
Spines	Rounded and short or conical and thick	Rounded and short or conical and thick	Rounded and short or conical and thick
Striae orientation	Parallel	Parallel	Parallel
Valve face	Flat with thin areolae	Flat with thin areolae	Flat with thin areolae
Mantle height (µm)	2.5-5 M: 3.5 SD: 0.6	2.5-5 M: 3.3 SD: 0.5	3-6
Valve diameter (µm)	5-10 (12) M: 7.8 SD: 1.8	6-14 M: 8.8 SD: 1.9	5-16
Ratio mantle height / valve diameter	0.35-0.6 M: 0.4 SD: 0.1	(0.25) 0.35-0.4 (0.6) M: 0.4 SD: 0.1	0.4-0.6
Striae density (/10 µm)	18	18	18
Areolae density (/10 µm)	18-21	20	22
Rimoportulae	Long (1/2 of ringleist), forming a ring inside the ringleist	Long (1/2 of ringleist), forming a ring inside the ringleist	Long (1/2 of ringleist), forming a ring inside the ringleist

1: This study; 2: Houk *et al.*, 2007; M: mean; SD: standard deviation



Figs 2-26. *Aulacoseira scalaris* LM girdle (Figs 2-12) and valve (Figs 13-26) views. **2-3.** Live material from Longemer Lake (France) fixed with Lugol´s solution. **4-26.** Treated material from Gérardmer Lake (France). Scale bar = 10 µm.



Figs 27-36. *Aulacoseira scalaris* SEM views (Material from Longemer Lake). **27-30.** External girdle view of full frustules. **31.** Girdle view of a broken specimen showing rimoportulae (arrows) and the reinforcing rib of the ringleist. **32.** Girdle external view of a valve. **33-34.** Internal (Fig. 33) and external (Fig. 34) views of a valve face. **35.** Focus on spines and valve face from valve view. **36.** Focus on spines from girdle view.

The ringleist extends from about 1/3 to 1/2 of valve diameter in the case of small specimens (Figs 13-26), but 2/5 is the most frequent occurrence (Fig. 33). This ringleist has a reinforcing rib near the margin (Fig. 31). A ring of spaced rimoportular canals runs inside the ringleist. They are quite long, extending to approximately 1/2 of the ringleist (Fig. 31), and can be seen in valve view under light microscopy (Figs 13 and 22).

Ecology and associated flora

In this manuscript, we illustrated and described for the first time living cells of *A. scalaris* from two lakes of the Vosges Mountains. However, some assumptions based on the similarities of Longemer Lake and Gérardmer Lake can be made. In their euphotic zone, both have water of relatively low conductivity, poor mineralization, good oxygenation and low chlorophyll concentration. They are both mesotrophic environments on granitic substratum, with moderate anthropogenic pressure.

Aulacoseira scalaris did not show strong seasonality since it was found through the seasons in similar abundance (30 to 100 cells/ml) in all samples.

The phytoplankton communities were mainly composed of very small chroococcalean cyanobacteria (such as *Aphanothece* sp. and *Snowella* sp.), colonial Chlorophyceae (mostly *Sphaerocystis* sp.), Cryptophyceae (*Cryptomonas* spp. and *Plagioselmis nannoplanctica* (H. Skuja) Novarino, I.A.N. Lucas & S. Morrall) and Chrysophyceae (*Dinobryon* spp., *Kephyrion* sp. and *Mallomonas* sp.).

Aulacoseira scalaris was associated with *Discostella stelligera* (Cleve & Grunow) Houk & Klee, *Tabellaria flocculosa* (Roth) Kützing, and needle-shaped *Fragilaria* spp. likely belonging to the *Fragilaria tenera* (W. Smith) Lange-Bertalot species complex were found in all samples.

DISCUSSION

Based on available literature, *A. scalaris* was compared with morphologically similar taxa (Table 4). The morphological characters used to delineate *Aulacoseira* species include: mantle height/valve diameter ratio, striae and areola density, curvature of striae, location and structure of the ringleist, spine morphology, location of rimoportulae, morphology of the valve face, and position of spines in relation to striae (Siver & Kling, 1997; Potapova *et al*., 2008).

Aulacoseira alpigena (Grunow) Krammer had valves in mantle view similar to *A. scalaris* in height/diameter ratio, density of striae and areolation. However, *A. alpigena* striae are clearly curved and the valve face is plain with only one or two peripheral rows of areolae. It also differs by less numerous and prominent rimoportulae, making them invisible in light microscopy.

Aulacoseira scalaris can be easily differentiated from *Aulacoseira distans* (Ehrenberg) Simonsen by having a clearly shorter mantle height, different spine morphology, number of mantle's rows of areolae in 10 µm and the number of rows in front of each spine.

Aulacoseira nivalis (W. Smith) English & Potapova, like *A. distans*, has different spine morphology and number of rows of areolae in front of each spine. It

Table 4. Comparison of biometric data and morphological features of *Aulacoseira scalaris* with closely related taxa from the literature

	Aulacoseira scalaris[1]	*Aulacoseira alpigena*[2,3]	*Aulacoseira distans*[4,5,6]	*Aulacoseira nivalis*[2,7,8,9]	*Aulacoseira nivaloides*[7,10]	*Aulacoseira pusilla*[11,12]	*Aulacoseira subborealis*[13]	*Aulacoseira subarctica*[11,14,15]
Ringleist	~2/5 of the diameter	Shallow to very shallow (< 1 µm)	1/3 to 1/2 of the diameter	Shallow to very shallow (< 1 µm)	Shallow to very shallow (< 1 µm)	1/5 to 2/5 of the diameter	1/4 of the diameter	to 1/2 of the diameter
Ratio *N* striae / *n* spines	2	1	1	1	2	2	2	2
Spines	Rounded and short or conical and thick	Small and thin	Conical and thin	Conical and thin	Conical and thin	Conical and thin	Conical, rather thick (L/W ~2.5)	Conical and long
Striae orientation	Parallel	Curved to parallel	Parallel	Slightly curved	Parallel	Curved	More or less curved	Curved
Valve face	Flat with thin areolae	Flat and plain (1 row of marginal areolae)	Flat with thin areolae	Flat with large areolae	Concave or convex with thin areolae	Flat with thin areolae	Flat with thin areolae	Flat and plain
Mantle height (µm)	3-6	4-7	8-10	2.5-6	4-6	3.5-5	2.5-4	2.5-14
Valve diameter (µm)	5-16	4-15	4-20	6-18	4-11	5-7.5	5.5-9	3-6 (14)
Ratio mantle height / valve diameter	0.4-0.6	0.5-1	0.5-2	0.4-0.6	0.5-1	0.6-0.7	0.39-0.55	(0.3) 1-2
Striae density (/10 µm)	18	15-22	12-14	12-16	16-22	20-27	23-28	15-22
Areolae density (/10 µm)	22	~20	~20	~9-10	15-21	27-29	28-38	22-25
Rimoportulae	Long (1/2 of ringleist), forming a ring inside the ringleist	Unknown, but none visible in LM	Long (1/2 of ringleist), 4 to 12, one for 4 or 5 areolae	Only one rimoportula on the mantle near the ringleist	Unknown, but none visible in LM	Very long (all the ringleist), form a ring inside the ringleist	Long (1/2 of ringleist), number unknown but low	Short, low number

1: Houk *et al.*, 2007; 2: Buczkó *et al.*, 2010; 3: Potapova, 2009; 4: Crawford & Likhoshway, 1999; 5: Krammer, 1991; 6: Tuji, 2006; 7 : English & Potapova, 2009; 8: Potapova & English, 2011; 9 : Tuji, 2010; 10: Potapova & English, 2010a; 11: Tuji & Houki, 2004; 12: Tuji & Williams, 2006; 13: Denys *et al.*, 2003; 14: Kobayasi *et al.*, 2006; 15: Potapova & English, 2010b.

can also be differentiated from *A. scalaris* by specific features: a shallow ringleist to the point of being nearly invisible in light microscopy, only one rimoportula on the mantle near the ringleist, a developed collar (structureless distal part of the valve mantle), and a valve face covered by relatively large areolae arranged in regular tangential rows. *Aulacoseira nivaloides* (Camburn) English & Potapova share discriminating characteristics with *A. nivalis* like the shallow ringleist, but in addition it has a clearly concave or convex valve face.

Aulacoseira subborealis (Nygaard) Denys *et al.* and *Aulacoseira pusilla* (F. Meister) Tuji & Houki have a different number of rows of areolae in 10 µm, with a much higher density of areolae. Moreover, the rows tend to be curved rather than parallel.

Finally, *Aulacoseira subarctica* (O. Müller) E.Y. Haworth has a higher average ringleist size, different spine features and a greater mantle height/diameter ratio. This species also has mantle areolae in a clearly curved pattern, except at the beginning of every second row which start straight in the spine base. Another useful criterion to differentiate *A. scalaris* from similar species as *A. subarctica* is the clearly visible presence of two types of spines in LM in *A. scalaris* (Figs 5-6, 11-12 showing some separation spines, Figs 7-8 showing only linking spines). Because of this characteristic, the observer can at first glance think there are perhaps two species in the sample.

In Denys *et al*. (2003, p. 415), a reference is made to a diatom found in Chauvet Lake (Puy-de-Dôme, Massif Central, France) and Gérardmer Lake (Vosges, France); this *Aulacoseira* was said to be close to *A. subborealis*, but with much coarser areolae (around 20 in 10 µm) and slightly higher diameter (8-10 µm). Additionally, the specimen from Gérardmer Lake has been illustrated by Krammer (1991, fig. 28) as *A. distans* var. *distans.* Even though only one figure is available it is assumed both specimens could belong to *A. scalaris.*

Despite slight differences between the living material found by us from France and the fossil type population from Oregon concerning maximum diameter and variability of ringleist size (Table 3), it was confirmed that living cells of *A. scalaris* were found. Interestingly, Gérardmer Lake is among the three localities initially observed by Grunow (Houk *et al.*, 2007).

Aulacoseira scalaris was so far found in a limited number of localities (U.S.A., and France). This sporadic distribution may result of misidentification: this species is not familiar to phytoplankton analyst due to its “fossil” status. In future assessments, *A. scalaris* should no longer be considered as a fossil or subfossil diatom species. It could be more widespread, especially in mesotrophic lakes lying on granitic bedrock.

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