Diatom biodiversity in Mongolia: A new amphoroid diatom from saline lakes in western Mongolia, *Amphora soninkhishigae* sp. nov.

MARK B. EDLUND¹*, AVERY L. C. SHINNEMAN², ZLATKO LEVKOV³

¹ St. Croix Watershed Research Station, Science Museum of Minnesota, Marine on St. Croix, Minnesota 55047, USA

² Department of Geology, University of Minnesota, 310 Pillsbury Dr. SE, Minneapolis, Minnesota 55455, USA

³ Institute of Biology, Faculty of Natural Sciences, Gazi Baba bb, 1000 Skopje, Republic of Macedonia

A new *Amphora* species, *Amphora soninkhishigae* sp. nov. is described from the saline lakes, Oigon Nuur and Uvs Nuur, in western Mongolia. *Amphora soninkhishigae* is characterized by its small size (valves $12-28 \,\mu m \log_2 2.9-3.8 \,\mu m$ wide), fine ornamentation, and a broad, internally thickened central area on the dorsal side of the valve (dorsal stauros) that branches along the dorsal margin. Among the amphoroid diatoms, *Amphora soninkhishigae* belongs in the subgenus *Oxyamphora* Cleve, where it is allied with other small *Amphora* taxa bearing a dorsal stauros including *Amphora staurophora* Juhlin-Dannfelt, *Amphora abludans* Simonsen, *Amphora laevissima* var. *perminuta* Grunow, and *Amphora laevis* var. *minuta* Cleve.

Key words: Diatom, taxonomy, ultrastructure, biogeography, systematics, *Amphora soninkhishigae*, Mongolia

Introduction

The amphoroid diatoms have long been recognized to be an unnatural group. Early workers recognized morphological groups within "*Amphora*" (e.g., 23 groups by SMITH 1873) and CLEVE (1895–1896) formally recognized nine groups at the subgenus level (e.g., subgenera *Amphora*, *Halamphora* Cleve, *Psammamphora* Cleve). ROUND et al. (1990) recognized that *Amphora* needed revision and described the segregate marine genus *Seminavis* D.G. Mann in Round et al. to accommodate the *Amphora angusta*-group (subgenus *Cymbamphora* Cleve) and resurrected *Catenula* Mereschowsky (MERESCHOWSKY 1902–1903) to accommodate the tiny-celled *C. adhaerens* and *C. pelagica*-group. VYVERMAN et al. (1998) erected the new eunotioid genus *Eunophora*, a southern hemisphere endemic that only superficially resembled *Amphora*. WILLIAMS and REID (2006) described *Collicu*-

^{*} Corresponding author, e-mail: mbedlund@smm.org

loamphora, a new eunotioid genus, to accommodate two amphoroid taxa, including the previously known *A. reichardtiana* Grunow. *Eunophora* and *Colliculoamphora* are only superficially related to *Amphora sensu stricto*, and are more closely allied with the eunotioid diatoms. Most recently, LEVKOV (2009), in the first step toward a revision of *Amphora*, elevated the subgenus *Halamphora* Cleve to the genus level.

The amphoroid diatoms are species-rich in Mongolia with more than 25 taxa reported to date (EDLUND et al. 2001, SHINNEMAN 2008, LEVKOV 2009) including five taxa formally described from Mongolia's ancient Lake Hövsgöl (*Amphora mongolica* Østrup, *A. dentata* Edlund et Levkov, *A. hovsgoliana* Levkov et Edlund, *A. neglectiformis* Levkov et Edlund, and *A. paracopulata* Levkov et Edlund). In a recent hydrobiological survey of the Valley of the Great Lakes in western Mongolia, we undertook a first detailed study of the diatom flora from lakes in this ecologically and culturally significant region (DULMAA 1979, OLSON and DINERSTEIN 1998, FERNANDEZ-GIMENEZ 2000, SHINNEMAN et al. 2009). Among the 15 amphoroid taxa reported by SHINNEMAN (2008), an unidentified *Amphora* was noted in two saline lakes and is herein formally described.

Study area

The Valley of the Great Lakes lies in the far west of Mongolia, bounded by the Altai Mountains to the west, the Khangai Mountains to the east, and the Gobi Desert to the south. The Great Lakes region is part of the endorheic Central Asian Basin and includes several smaller closed drainage basins with lakes ranging from fresh to hypersaline (DULMAA 1979, SHINNEMAN et al. 2009). Many of the large terminal basins in the valley are believed to be remnants of large Tertiary or Quaternary paleo-lakes (GRUNERT et al. 2000). There are three large terminal basins in the area, Khyargus, Uvs, and Uureg Nuur, and numerous large and small ephemeral ponds, playa lakes, floodplain lakes, and dune-blocked lakes.

Lakes sampled in summer 2004–2005 ranged from dilute to hyper-saline (40–200,000 μ S cm⁻¹). Saline lakes (SC>3000 μ S cm⁻¹) were common in the region (SHINNEMAN et al. 2009). Terminal large lakes in the central valley were saline and many small lakes and pools were also highly saline. At the highest concentrations, ionic composition was dominated by sodium chloride, whereas dilute lakes were more commonly composed of sulfate and carbonate salts. Trophic status index (TSI) calculations (CARLSON 1977) made using TP and Secchi depth measurements indicated that most lakes, fresh and saline, were eutrophic to hyper-eutrophic at the time of sampling in late summer. Nitrogen to phosphorus ratios showed that most lakes were strongly P-limited (SHINNEMAN et al. 2009).

Material and methods

During two field seasons (August 2004 and August 2005) we sampled over 60 lakes in western Mongolia. At each lake a surface sediment sample (0–1 cm sediment depth) was collected from the deepest site accessible by canoe using a line-operated "Wiegner" gravity corer. The sediment was preserved in 10% formaldehyde solution and prepared for microscopy following RENBERG (1990). Cleaned material was mounted on microslides with Zrax and random transects examined with an Olympus BX50 microscope (magnification 1250 times and n.a. 1.40) until 300–400 valves were counted. Digital light micrographs were captured using a SPOT Insight QE camera (Diagnostic Instruments). Cleaned material was

also mounted on carbon coated aluminum stubs, coated with 20 nm Au, and examined with a JEOL JSM-6060LV scanning electron microscope (SEM) at 15–20 kV operating voltage. Descriptive terminology follows LEVKOV (2009).

Results

Amphora soninkhishigae Edlund, Shinneman, Levkov sp. nov. (Figs. 1–12)

Holotype: Marked specimen (Fig. 6) on ANSP slide M1468 (G.C. 36334), ANSP material M1468 (G.C. 24046).

Isotypes: Slides and material of collection M1468 deposited in California Academy of Sciences (M1468c), National University of Mongolia Diatom Herbarium (M1468b), and in M.B. Edlund collection (M1468a; Science Museum of Minnesota).

Paratypes: Slides and material of collection M1461 deposited in CAS (M1461c), M1461b in National University of Mongolia Diatom Herbarium, M1461a in M.B. Edlund collection (Science Museum of Minnesota). Uvs Nuur, Uvs aimag, Mongolia, site 63, surficial sediment from 6.3 m depth, 759 m elevation, (50.25172°N, 93.26403°E), coll: M1461 by M. Edlund, A.L.C. Shinneman, N. Soninkhishig, 08 August 2005 (Figs. 13–24).

Type locality: Oigon Nuur (lake), Zavkhan aimag, Mongolia, site 82, surficial sediment from 5 m water depth, 1680 m elevation, (49.20750°N, 96.61932°E), coll: M1468 by M. Edlund, A.L.C. Shinneman, N. Soninkhishig, 12 August 2005.

Etymology: This taxon is named in honor of Dr. N. Soninkhishig, Biology Faculty, National University of Mongolia, for her long friendship and pivotal role in developing a diatom research and training program in Mongolia.

Descriptio: Cellulae solitariae, valde dorsiventrales, aspectu cincurae lanceolatae ad anguste elipticae. Valvae semilanceolatae quoad specimina maxima, ad semi-lanceolatae quoad specimina minima, margine dorsali leniter convexa, margine ventrali leviter recta vel leviter inflata. Apices valvarum acuti quoad specimina maxima anguste rotundati quoad specimina minima. Longitudo valvae 12–28 μ m, latidudo 2.9–3.8 μ m. Area axialis angusta, linearis. Area centralis ad latus dorsale angustam fasciam formans ad marginem valvae extensa, ad latus ventrale indistincta. Ramis raphis rectis, excentrica ad marginem ventralem positis, fissuris proximalibus rectis. Striae ventrales vix aspectabiles microscopio photonico, ca. 50 in 10 μ m. Chromatophora ignotae.

Description: Cells solitary, frustules lanceolate to narrowly elliptical with amphoroid symmetry (Fig. 24). Valves semi-lanceolate in larger specimens to semi-elliptical in smaller specimens (Figs. 1–12). Dorsal margin convex, ventral margin straight to slightly gibbous (Figs. 1–12). Valve ends acute in larger specimens to narrowly rounded in smaller specimens (Figs. 1–12). Valve length 12–28 μ m, valve breadth 2.9–3.8 μ m (Figs. 1–12). Axial area narrow, linear (Figs. 1–12). Central area on dorsal side narrow fascia expanding and branching near dorsal margin, on ventral side indistinct (Figs. 1–12). Raphe branches straight, running near the ventral margin, proximal raphe endings straight (Figs. 1–12). Striae indistinct, hard to resolve with LM, ca. 50 in 10 μ m. Plastids unknown.

Ultrastructure: In the SEM, frustules are lanceolate to narrowly elliptical, sometimes gibbous in the middle (Fig. 25). A very narrow marginal ridge is present along the junction of the valve face and dorsal margin (Fig. 27). The transition from valve face to valve mantle



Figs. 1–24. Light micrographs (DIC) of Amphora soninkhishigae. 1–12 – Size diminution series from Oigon Nuur, Mongolia (Fig. 6 is the holotype). 13–23 – Size diminution series from Uvs Nuur, Mongolia. 24 – Complete frustule, Uvs Nuur, Mongolia. Scale bar = 10 μm

AMPHORA SONINKHISHIGAE SP. NOV.

is abrupt (Figs. 25, 27). The raphe is located near the ventral valve margin. A distinct raphe ledge is absent; however, a slightly elevated sternum is apparent in the mid-valve on the dorsal valve side. The raphe branches are straight with simple, straight or weakly dorsally bent proximal endings and strongly dorsally deflected distal fissures (Figs. 25–27). The central area on dorsal side is narrow, rectangular, and bordered with strongly shortened striae near the dorsal margin (Fig. 27). These striae are composed of elongated areolae which are occluded internally ("ghost" areolae). The central area on ventral side is semi-lanceolate and extends to the ventral margin (Fig. 27). Striae are uniseriate, composed of small round areolae, except for a few on the central dorsal side that comprise strongly transapically elongated areolae (Fig. 27). Ventral striae are interrupted in the mid-valve



Figs. 25–30. Scanning electron micrographs of A. soninkhishigae from Oigon Nuur, Mongolia. 25 – Ventral side of complete frustule. 26 – End of frustule showing dorsal deflection of terminal raphe endings (arrow). 27 – Ventral side of frustule, mid-valve, showing slight dorsal deflection of proximal raphe endings, uniseriate dorsal and ventral striae, central area as a dorsal stauros with transapically elongated areolae along dorsal margin of valve (arrow). 28 – Internal view of valve with linear internal raphe slits and branching dorsal stauros (arrow). 29 – Internal view of valve center showing dorsal stauros that branches at the dorsal margin of valve, absence of central helictoglossae on proximal raphe ending in a small helictoglossa (arrow). Scale bar: 5 μm (Fig. 25), 2 μm (Fig. 28), 1 μm (Figs. 26, 27, 29, 30).

(Fig. 29). Internally, the most remarkable feature is the strongly thickened central area that extends costa-like as a dorsal stauros onto the dorsal mantle, as where it is branches and is even more thickened (Figs. 28, 29). This feature can be observed also externally as a slight inflation in the valve middle (Fig. 25). Internally, the raphe branches are linear and terminate distally in poorly developed helictoglossae (Fig. 30). The internal proximal raphe endings are simple (Fig. 29) without tongue-like extensions (central helictoglossae). Striae are uniseriate and the areolae are not occluded with hymens on the valve interior (Fig. 29).

Diagnosis: It is the combination of characters associated with frustule shape, the linear raphe branches, and the central area or dorsal stauros that branches at the dorsal margin that differentiates Amphora soninkhishigae from other Amphora species. Only few small--celled Amphora taxa have a lanceolate-elliptical frustules with a prominent dorsal stauros similar to Amphora soninkhishigae. Two taxa that bear a strong resemblence to A. soninkhishigae are A. staurophora Juhlin-Dannfelt 1882 [=A. dannfeltii Berg (BERG 1952), non A. staurophora (Castracane) Cleve (CLEVE 1895–1896), the latter has rostrate valve ends] and A. laevissima var. perminuta Grunow. Amphora staurophora is illustrated by Bérard-Therriault et al. (1986: fig. 85) with elliptical frustules of length 9–14 μm, breadth 5–8 μ m, and valve width of 2–3 μ m, which corresponds closely to the JUHLIN-DANNFELT (1882) description, but the raphe branches are slightly dorsally arched and the dorsal stauros broadens approximately mid-valve on the dorsal side without branching. In contrast, the dorsal stauros of A. soninkhishigae widens and branches only very near the dorsal margin and the raphe branches are linear. SCHOEMAN and ARCHIBALD (1986: fig. 19) illustrate a specimen identified as Amphora laevissima var. perminuta that is possibly conspecific with A. soninkhishigae. However, they compare it to the type of Amphora laevissima var. perminuta Grunow (in VAN HEURCK 1884-1887, see ARCHIBALD and SCHOEMAN 1986: figs. 22, 23) which has raphe branches that are slightly dorsally arched and a dorsal staursos more similar to A. staurophora. Amphora abludens Simonsen (SIMONSEN 1960) in the type description and as illustrated by Bérard-Therriault et al. (1986: figs. 50–52) is larger and more coarsely ornamented than A. soninkhishigae and has weakly dorsally arched raphe branches. The virgae of A. abludens also become fibulae-like along the entire dorsal margin, a character not present in A. soninkhishigae. Amphora sublaevis Hustedt (HUSTEDT 1955) is more coarsely ornamented and has dorsally arched raphe branches. Lastly, an illustration of Amphora laevis var. minuta Cleve by BÉRARD-THERRIAULT et al. (1986: 417, fig. 76) is larger and does not have the obvious branching of the dorsal stauros seen in A. soninkhishigae. However, there is taxonomic confusion with Amphora laevis var. minuta. CLEVE (1895–1896: 130) notes that this taxon is based on H. L. SMITH (1876–1888) exsiccatum No. 615 (as A. laevissima Gregory); however, examination of Smith's slide (EDLUND unpublished) shows this taxon to have rectangular frustules, recurved raphe branches, and a convex ventral margin, which is quite different than the specimen illustrated by Bérard-Therriault et al. (1986: fig. 76).

Apart from the thickened, branching dorsal stauros, *Amphora soninkhishigae* shares a combination of characters with *Amphora* spec. (J) sensu LEE et al. (1989: fig. 2: 9) including: straight raphe branches with weakly dorsally bent proximal raphe fissures; a weakly developed raphe ledge; dorsal striae opposite the central area composed of strongly transapically elongated areolae; and ventral striae composed of a series (2–4) of small round poroids. The internal structure of *Amphora* spec. (J) view is not known. Differences between these two taxa include valve size, with *Amphora* spec. (J) having smaller valves

Taxon	Author	habitat	frustule shape	length	frustule val breadth brea	valve breadth	striae density	stauros	raphe branches
				(µm)	(µm)	(µm)	(no/10 µm)	•	
Amphora soninkhishigae Edlund, Shinneman et Levkov	1	inland saline lakes, Mongolia	lanceolate to narrow-elliptical	12–28	_	2.9–3.8	50	branching near dorsal margin	straight
A. staurophora Juhlin-Dannfelt	2	Baltic Sea	elliptical-oval	14	9.2	3.3	not resolved	widens toward dorsal side	slightly dorsally arched
A. staurophora Juhlin-Dannfelt	3	Gulf of St. Lawrence	small- lanceolate	9–14	5–8	2–3	indistinct	widens toward dorsal side	slightly dorsally arched
A. laevissima v. perminuta Grunow in Van Heurck	4	Swansea Dock, Wales	lanceolate- truncate ends	16–21.3	7.6–8	3–3.3	not resolved	widens toward dorsal side	slightly dorsally arched
Amphora abludens Simonsen	5	Baltic Sea	elliptical	13–30	10-14	2.5–5	38	present	weakly dorsally arched
Amphora sublaevis Hustedt	6	E. coast USA	elliptical- truncate	25–60	10–20	5–6	40	widens toward dorsal side	dorsally arched
Amphora laevis v. minuta Cleve	7	Gulf of St. Lawrence	lanceolate	13–42	7–20	3–8	not resolved	widens toward dorsal side	straight
Amphora sp.	8	endosymbiont	lanceolate	8.8	5.4	2.1	>60	not present	straight

Tab. 1. Morphological and habitat characteristics of Amphora soninkhishigae and allied Amphora species.

Authors:

1 EDLUND et al. (this study)

2 JUHLIN-DANNFELT (1882, type)

3 Bérard-Therriault et al. (1985)

4 SCHOEMAN and ARCHIBALD (1986)

5 SIMONSEN (1960)

6 HUSTEDT (1955)

7 BÉRARD-THERRIAULT et al. (1895–1896) 8 LEE at al. (1989)

ACTA BOT. CROAT. 68 (2), 2009

 $(\sim 10 \,\mu\text{m})$, higher striae density ($\sim 60 \,\text{per} \, 10 \,\mu\text{m}$), and different habitat preference. *Amphora* spec. (J) is endosymbiotic in large foraminifera (LEE et al. 1989).

Distribution and ecology: *Amphora soninkhishigae* was abundant (>5% relative abundance) in the epipelon of only two of the survey lakes in western Mongolia. In Oigon Nuur and Uvs Nuur, *A. soninkhishigae* was found at 13.5% and 6.25% relative abundance, respectively. It was also found in lower abundance in a third saline lake, Khyargus Nuur. Oigon Nuur is a large, shallow terminal basin with total phosphorus 0.058 mg L⁻¹, specific conductivity 32276 μ S cm⁻¹, and pH 9.26. Uvs Nuur is the largest (by surface area) lake in Mongolia; in 2005, it had total phosphorus of 0.023 mg L⁻¹, specific conductivity 20363 μ S cm⁻¹, and pH 9.43. Khyargus Nuur had total phosphorus of 0.031 mg L⁻¹, specific conductivity 9400 μ S cm⁻¹, and pH 9.41.

Discussion

Recent studies confirm the long-held view that *Amphora sensu lato* is a heterogeneous group and have resulted in recognition or resurrection of several segregate genera (MERESCH-KOWSKY 1902–1903, ROUND et al. 1990, VYVERMAN et al. 1998, WILLIAMS and REID 2006). Initial steps have also been taken to formally reconsider or recognize Cleve's *Amphora* subgenera at the genus level (LEVKOV 2009). Furthermore, targeted survey efforts on several geographic regions have highlighted the underappreciated diversity of this group and resulted in the recent discovery and description of many new amphoroid taxa (NAGUMO 2003, LEVKOV 2009). In Mongolia, recent surveys have resulted in the description of four new *Amphora* species from ancient Lake Hövsgöl (LEVKOV 2009), numerous new distributions (EDLUND et al. 2001, SHINNEMAN 2008, LEVKOV 2009), and the discovery of *A. soninkhishigae* in saline lakes in western Mongolia.

The systematic position of *Amphora soninkhishigae* among the amphoroid diatoms must be considered. Taxa that are closely allied with *A. soninkhishigae*, including *A. staurophora*, *A. abludans*, *A. sublaevis*, and *A. laevis* var. *minuta*, have generally been placed in the marine subgenus *Oxyamphora* Cleve. These taxa share lanceolate to elliptical frustules, +/– a dorsal stauros, linear to weakly dorsally arched raphe branches near the ventral margin, no longitudinal lines or keels, and fine ornamentation. These characters, in part, define the subgenus *Oxyamphora* (see CLEVE 1895–1896), the subgenus where we propose *A. soninkhishigae* is best accommodated.

However, a solid, strongly thickened central structure or dorsal stauros, which characterizes *Amphora soninkhishigae*, is present in several species belonging to different amphoroid subgenera (sensu Cleve 1895–1896). For example, in the subgenus *Psammamphora* Cleve, the central structure of *Amphora delphinea* L.W. Bailey (see METZELTIN and LANGE-BERTALOT 1998: figs 145: 3 and 164: 5) continues onto the dorsal valve mantle where it is perforated by few striae. A similar structure was observed in *Amphora delphineiformis* Levkov (LEVKOV 2009: fig. 253: 1). In members of *Psammamphora*, the dorsal structure differs from *A. soninkhishigae* by continuing onto the dorsal mantle; in broken valves it appears as a structure extending and widening towards the valve mantle (LEVKOV unpublished observation). Several representatives of *Halamphora* Cleve also have a semi-stauros on the dorsal side. In *Amphora montana* Krasske the semi-stauros is spatulate and flattened internally, but it is perforated with a few strongly shortened striae (CARTER and ROUND 1993: figs. 25, 26). Similar features can also be observed in *A. normanii* Rabenhorst (CARTER and ROUND 1993: fig. 35).

Additional features aligning *Amphora soninkhishigae* with *Oxyamphora* include lack of tongue-like extensions (central helictoglossae *sensu* LEVKOV 2009) on the internal proximal raphe endings. In most *Halamphora* species, the proximal raphe endings terminate internally with fused central helictoglossae, except in *A. chilensis* (SALA et al. 2007), whereas in *Amphora sensu stricto* (i.e. subgenus *Amphora* Cleve) each raphe branch terminates with separate central helictoglossae (see KRAMMER 1980). In some, but not all representatives of other subgenera (e.g. *Oxyamphora*, *Diplamphora* and *Psammamphora*) the proximal raphe endings are also simple without extensions. On the other hand, in representatives of *Psammamphora* and *Oxyamphora* the raphe distally terminates with fully developed helictoglossae, a feature that is poorly developed in *A. soninkhishigae*.

Lastly, in *Amphora soninkhishigae* the raphe lies in a weakly elevated external raphe ledge that is present only dorsally, a feature shared by the subgenera *Halamphora* and *Oxyamphora* (ARCHIBALD and BARLOW 1983). In most subgenus *Amphora* taxa the raphe lies in a raphe ledge elevated along both sides (GUSLYAKOV 1985: figs. A, B). A strongly developed raphe ledge on both valve sides is also present in representatives of subgenus *Diplamphora* (GUSLYAKOV 1985: fig. 1), while in subgenus *Psammamphora* this structure is absent.

What is perhaps more intriguing is that a member of the subgenus *Oxyamphora* can be found in Mongolia over 2000 km from any marine habitat. *Oxyamphora* taxa are generally considered marine, although some representatives inhabit estuarine habitats (BÉRARD-THERRIAULT et al. 1986). Inland or athallassic saline lakes, although not always sodium chloride-dominated systems, can provide inland habitats for more typical marine species of microalgae. The larger Mongolian saline lakes where *Amphora soninkhishigae* was found are sodium chloride-dominated but also have ample magnesium and sulfate ion content. Typical marine diatom taxa such as *Achnanthes brevipes* C.Agardh, *Melosira moniliformis* var. *octogona* (Grunow) Hust., and *Haslea spicula* (Hickie) Bukht. can be found in Mongolia's Valley of the Great Lakes (EDLUND et al. 2001). Other saline *Amphora* species in Mongolia include *Amphora commutata* Grunow in Van Heurck, *A. coffeaeformis* (C.Agardh) Kütz., and *A. coffeaeformis* var. *angularis* (Van Heurck) Cleve; however, *A. soninkhishigae* is the first member of subgenus *Oxyamphora* reported from Mongolia.

The Valley of the Great Lakes is a culturally and ecologically significant region (DULMAA 1979, OLSON and DINERSTEIN 1998, FERNANDEZ-GIMENEZ 2000) that is currently under threat from climate warming and political and economic drivers of change (SHINNEMAN 2008). People of the region follow the millennia-old traditions of pastoral nomadism; however, increases in herd size, changes in herd makeup, and more sedentary households have resulted in increased eutrophication of surface waters in the region (SHINNEMAN 2008). The Valley is also home to several critically endangered wildlife species and an important stop-over for migratory birds (OLSON and DINERSTEIN 1998). Threats to the ecology and culture of the region make biodiversity surveys, especially those targeting important bioindicator groups, critical and time-sensitive. Initial results from our hydrobiological surveys indicate that the aquatic biodiversity of this region of Mongolia can be used for assessment of modern and historical ecological assessment (SHINNEMANN et al. 2009), and that the biodiversity is underappreciated, as evidenced by the discovery of new diatom taxa (SHINNEMAN 2008) including *Amphora soninkhishigae*.

Acknowledgements

We thank our Mongolian colleagues, Drs N. Soninkhishig, Y. Khand, and G. Tserenkhand, and especially our drivers, cooks, and field crew for their help and generosity during two field expeditions. We thank Dr. Matthew Julius, St. Cloud State University, for providing scanning electron microscope facilities. This material is based upon work supported by the National Science Foundation (NSF) under grants DEB-0316503 and DEB-0431529 to MBE. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the NSF. Dr. Levkov acknowledges support from the Alexander von Humboldt Foundation.

References

- ARCHIBALD, R. E. M., BARLOW, D. J., 1983: On the raphe ledge in the genus *Amphora* (Bacillariophyta). Bacillaria 6, 257–266.
- BÉRARD-THERRIAULT, L., CARDINAL, A., POULIN M., 1986: Les Diatomées (Bacillariophyceae) Benthiques de Substrats durs des eaux Marines et Saumâtres du Québec. 6. Naviculales: Cymbellaceae et Gomphonemaceae. Le Naturaliste Canadien 113, 405–429.
- BERG, Å., 1952: Eine Diatomeengemeinschaft an der schwedischen Ostküste. Arkiv för Botanik, Series 2, 2, 1–39.
- CARLSON, R. E., 1977: A trophic state index for lakes. Limnology and Oceanography 22, 361–369.
- CARTER, J. R., ROUND, F. E., 1993: Studies on freshwater *Amphora* species. V. A. montana and A. normanii. Diatom Research 8, 1–11.
- CLEVE, P. T., 1895–1896: Synopsis of the naviculoid diatoms. Kungliga Svenska Vetenskaps-Akademiens Handlingar, 27, 1–220.
- DULMAA, A., 1979: Hydrobiological outline of the Mongolian lakes. International Revue der Gesamten Hydrobiologie 64, 709–736.
- EDLUND, M. B., SONINKHISHIG, N., WILLIAMS, R. M., STOERMER, E. F., 2001: Biodiversity of Mongolia: Checklist of diatoms, including new distributional reports of 31 taxa. Nova Hedwigia 72, 59–90.
- FERNANDEZ-GIMENEZ, M. E., 2000: The role of Mongolian nomadic pastoralists' ecological knowledge in rangeland management. Ecological Applications 10, 1318–1326.
- GRUNERT, J., LEHMKUHL, F., WALTHER, M., 2000: Paleoclimatic evolution of the Uvs Nuur basin and adjacent areas (Western Mongolia). Quaternary International 65, 171–192.
- GUSLYAKOV, N. E., 1985: O morfologii pantsirei nekotorykh predstabitelei roda *Amphora* (Bacillariophyta) from the Black Sea. Botanicheskii Zhurnal 70, 1478–1481.
- HUSTEDT, F., 1955: Marine littoral diatoms of Beaufort, North Carolina. Duke University Press, Durham, North Carolina.
- JUHLIN-DANNFELT, H., 1882: On the diatoms of the Baltic Sea. Academical Dissertation. Kongl. Boktryckeriet, P.A. Norstedt and Söner, Stockholm.
- KRAMMER, K., 1980: Morphologic and taxonomic investigations of some freshwater species of the diatom genus Amphora Ehr. Bacillaria 3, 197–226.

- LEE, J. J., MCENERGY, M. E., TER KUILE, B., EREZ, J., ROETGER, R., ROCKWELL, R. F., FABER, W., LAGZIEL, A., 1989: Identification and distribution of endosymbiotic diatoms in larger foraminifera. Micropaleontology 35, 353–366.
- LEVKOV, Z., 2009: *Amphora* sensu lato. In: LANGE-BERTALOT, H. (ed.), Diatoms of Europe: Diatoms of European inland waters and comparable habitats elsewhere. Koeltz, Koenigstein.
- MERESCHKOWSKY, C., 1902–1903: Le types de l'endochrome chez les Diatomées. Scripta Botanica, Horti Universitalis Imperialis Petropolitanae 21, 1–106 (in Russian); 107–193 (in French).
- METZELTIN, D., LANGE-BERTALOT, H., 1998: Tropical diatoms of South America, 1. Iconographica Diatomologica 5, 1–695.
- METZELTIN, D., LANGE-BERTALOT, H., GARCIA-RODRIGUEZ, F., 2005: Diatoms of Uruguay. Iconographica Diatomologica 15, 1–737.
- NAGUMO, T., 2003: Taxonomic studies of the subgenus *Amphora* Cleve of the genus *Amphora* (Bacillariophyceae) in Japan. Bibliotheca Diatomologica 49, 1–265.
- OLSON, D. M., DINERSTEIN, E., 1998: The Global 200: A representation approach to conserving the Earth's most biologically valuable ecoregions. Conservation Biology 12, 502–515.
- RENBERG, I., 1990: A procedure for preparing large sets of diatom slides from sediment cores. Journal of Paleolimnology 4, 87–90.
- ROUND, F. E., CRAWFORD, R. M., MANN, D. G., 1990: The Diatoms. Biology and morphology of the genera. Cambridge University Press, United Kingdom.
- SALA, S., GUERRERO, J. M., COSTE, M., 2007: Valve morphology of *Amphora chilensis* Hustedt (Bacillariophyceae). Nova Hedwigia 85, 353–364.
- SCHOEMAN, F. R., ARCHIBALD, R. E. M., 1986: Observations on Amphora species (Bacillariophyceae) in the British Natural History Museum I. Some species from the subgenus Oxyamphora Cleve. Nova Hedwigia 43, 113–127.
- SHINNEMAN, A. L. C., 2008: Climatic and anthropogenic influences on aquatic ecosystems in the valley of the Great Lakes, Mongolia. Ph.D. thesis University of Minnesota, Minneapolis, Minnesota.
- SHINNEMAN, A. L. C., EDLUND, M. B., ALMENDINGER, J. E., SONINKHISHIG, N., 2009: Diatoms as indicators of water quality in Western Mongolian lakes: a 54-site calibration set. Journal of Paleolimnology. 42, 373–389.
- SIMONSEN, R., 1960: Neue Diatomeen aus der Ostsee II. Kieler Meeresforschungen 16, 126–130.
- SMITH, H. L. 1873: Conspectus of the Diatomaceae. Analysis of the species of the genus *Amphora*. The Lens 2, 65–91.
- SMITH, H. L., 1876–1888: Diatomacearum species typicae. Centuries 1–6, numbers 1–600; Supplement numbers 601–750. Stodder, Boston.
- VAN HEURCK, H., 1884–1887: Types de synopsis de Belgique. Serie 1–22. 550 slides, Text of A. Grunow.

- VYVERMAN, W., SABBE, K., MANN, D., VYVERMAN, R., HODGSON, D., VANHOUTTE, K., KILROY, C., 1998: *Eunophora gen. nov.* (Bacillariophyta), a new genus of amphoroid diatoms from Tasmanian highland lakes with close affinities to the genus *Eunotia*. European Journal of Phycology 33, 95–111.
- WILLIAMS, D. M., REID, G., 2006: Fossils and the tropics, the Eunotiaceae (Bacillariophyta) expanded: A new genus for the Upper Eocene fossil diatom *Eunotia reedi* and the recent tropical marine diatom *Amphora reichardtiana*. European Journal of Phycology 41, 147–154.