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MORPHOLOGY AND DISTRIBUTION OF NAVICULA SCHMASSMANNII AND ITS TRANSFER TO GENUS HUMIDOPHILA

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Abstract: A small diatom with a peculiar shape is often identified as *Navicula schmassmannii* in samples collected from alpine lakes and the Arctic region. Due to its characteristic outline, it is relatively well-identifiable, but scanning electron microscope (SEM) confirmation is essential for proving species identity. This species likely has a palaeoecological indicator value of warming climate in mountain lakes, although it is generally a minor component of the diatom assemblages. Here we re-investigate its type material to clarify its identity and taxonomic position. We provide an emended description based on SEM observation, including new information on girdle morphology. Furthermore, another population of *N. schmassmannii* was studied. Detailed morphological observations using light microscope (LM) and SEM were done on specimens from a sediment core obtained from Lake Brazi in the Southern Carpathian Mountains. Late-glacial and early Holocene populations of the diatom resembling *N. schmassmannii* showed high morphological variability in comparison with the type material. On the basis of details of type material and the different morphotypes from Lake Brazi, the transfer of *N. schmassmannii* Hustedt to the genus *Humidophila* is proposed as *H. schmassmannii* (Hustedt) Buczkó et Wojtal.

Key words: bioindication, *Humidophila*, *Navicula schmassmannii*, new combination, oligotrophy, palaeolimnology, Retezat Mountains, taxonomy, type material

INTRODUCTION

A tiny naviculoid diatom with a peculiar outline, occurring in alpine regions is usually identified as *Navicula schmassmannii* Hustedt. Due to its characteristic outline and slit-like striae, it is a frequently mentioned and illustrated diatom,

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despite its rarity. It seems that this diatom is a constant member of oligotraphentic diatom assemblages (e.g., SABATER and ROCA 1992, GÜTTINGER 1996, FALLU *et al.* 2000, TOLOTTI 2001, RÜHLAND *et al.* 2003, WERUM and LANGE-BERTALOT 2004, BRINER *et al.* 2006, CATALAN *et al.* 2009, JUGGINS 2010, ANSP 2015). Because of its oligotraphentic character and restricted distribution, the species can be regarded as a valuable bioindicator. However, its type material has never been investigated using electron microscopy, and its systematic position is regarded as unresolved (KRAMMER and LANGE-BERTALOT 1986, WERUM and LANGE-BERTALOT 2004, CANTONATI *et al.* 2009).

There are also uncertainties regarding the range of natural morphological variability of Navicula schmassmannii. In 1934 HUSTEDT published drawings of a new member of the Navicula genus in the A. Schmidt Atlas (SCHMIDT 1874-1959). The detailed description of the morphology of the species was provided only nine years later (HUSTEDT 1943), and was illustrated by drawings of two specimens. These were characterized by elliptical and linear-elliptical valves with distinctively capitate apices, and (generally) equidistantly located striae that were slightly radiate in the central area of the valves. According to the distribution notes (HUSTEDT 1943), the species was found only at a few localities, mainly in lakes. HUSTEDT (1962) recapitulated the morphological range of the species and mentioned another tiny diatom, N. leptidissima Cleve-Euler described from Sweden, as similar to or even conspecific with N. schmassmannii. In 1987, the Atlas and Catalogue of the Diatom Types of Friedrich Hustedt was published by SIMONSEN, who lectotypified N. schmassmannii using several slides from the Davos area with specimens marked and named by Hustedt. The four individuals photographed by SIMONSEN (1987a, b) clearly correspond to those depicted by the drawings published by Hustedt (in SCHMIDT et al. 1934). The drawings (HUSTEDT 1934, pl. 400, figs 48-52 in SCHMIDT 1874-1959) illustrated specimens that originated from Hochseen near Davos (Switzerland). Four of them had linear-elliptical valves with subcapitate apices, slightly radiate striation in the middle part of the valves and lanceolate axial area. The fifth illustrated valve (HUSTEDT 1934, pl. 400, fig. 48) looks somewhat different, despite having a similar outline: it is much smaller and its striation is not discernible. Two additionally illustrated specimens were presented by KRAMMER and LANGE-BERTALOT (1986, pl. 70, figs 8-13) in one of the most commonly used identification books. These pictures differed from Simonsen's lectotypes: having pronounced radiate striae in the central part of the valves and more convex margins.

For clarifying the identity of *N. schmassmannii* the type material from the Hustedt Diatom Study Centre in Bremerhaven was studied by means of LM and

SEM material. The high morphological variability of a population resembling *N. schmassmannii* in the context of its ecological and palaeoecological indicator value was also investigated from a poorly studied alpine region, the Southern Carpathian Mountains. The time window of this sediment spans *ca* 6,000 yrs, between *ca* 9,500–15,500 cal yrs BP. In consonance with this aim, we scanned large number of diatom samples and particularly searched for tiny diatoms with slit-like striae in this period.

MATERIAL AND METHODS

Methods for type material

The following information is available on the vial containing the type material of *Navicula schmassmannii*: "E1324 Davos, Schweiz 129 Kleiner Flüelasee, grund, Oktober 1932" The cleaned material has been stored with formalin and glycerin, before the re-investigation it was washed several times and used for making new glass slides. A light microscope (LEICA DM LB2 with 100 HCX PLAN APO) and Fujifilm Digital Camera (FinePix S2 Pro) was used for observations. Some additional LM pictures were taken using Nikon Eclipse 600 LM equipped with differential interference contrast and DS-Fi 1 camera (Figs 1–4, 9, 18, 20). Furthermore, the type material was mounted on stubs, coated with gold–palladium, and examined with a Hitachi S-2600N scanning electron microscope. Permanent glass slides are stored in the Diatom Collection of the Hungarian Natural History Museum, BP 2220–2221 and in the Institute of Nature Conservation, Polish Academy of Sciences, No DW 15.

Study site of the late-glacial and early Holocene population

Lake Brazi (TDB-1; 45.39639° N, 22.90167° E, 1740 m) is a small, glacial lake in the Retezat Mts, Romania. It is positioned below the upper tree limit, in a mixed *Picea abies – Pinus cembra* forest. On the lakeshore of TDB, *Sphagnum* species, *Juncus filiformis* L., *Eriophorum vaginatum* L., *Vaccinium myrtillus* L., *V. vitis-idaea* L. and *Rhododendron myrtifolium* Schott et Kotschy form floating carpet with *Pinus mugo* Turra. During the discussed time period, i.e. the late-glacial and early Holocene (15,500–9500 cal yr BP), Lake Brazi was a shallow alpine lake (inferred water depth 3–5 m). It was situated just below the upper treeline during the late-glacial interstadial. The lake itself was surrounded by mixed coniferous open forest since 14,500 cal yr BP and closed larch-spruce-pine forest after *ca* 11,200 cal yr BP (MAGYARI *et al.* 2010).

Methods for the late-glacial and early Holocene population

The 490 cm long sediment core was taken in 2007 with a Livingston piston corer from the deepest part of Lake Brazi (1 meter average water depth at the core location). For sub-sampling, the plastic tubes containing the sediment were cut into halves and sub-samples were taken from every centimetre for mul-



Figs 1-9. Navicula schmassmannii HUSTEDT, type material. Valves with subcapitate apices LM Figs 1-5, 9. Valve view, Figs 6-8. Girdle view.

ti-proxy analyses, including pollen, macrofossils, cladocera, chironomid, geochemical and siliceous algae (MAGYARI *et al.* 2010). For siliceous algae analyses, samples were prepared using standard digestion procedures (BATTARBEE 1986). Aliquot-evaporated suspensions were embedded in Naphrax. The sequence, spanning from 15,700 cal yr BP to 9500 cal yr BP was analyzed in high resolution, and counted using LM as well as SEM. At least 300 valves were counted in each sample. To obtain morphometric data for the slit-like striated diatoms, the valve width as well as width of the mantle and the girdle bands were measured at the middle part of non-tilted frustules.

RESULTS

Observations on type material

Light microscopy (Figs 1–9): Valves are elliptic to linear-elliptic (Fig. 3) with capitate ends, 8.8–10.4 μ m (average 9.5±0.4) long, 2.6–3.2 μ m (average 2.9±0.2; n = 31) wide. Raphe (filiform, straight) simple, threadlike with simple terminals, the proximal terminals are well visible. Axial area is hardly visible. Central area is of different size, rhomboid and a bit asymmetric. Striae are hardly discernible; they are slightly radiate in the middle part and become parallel at the end of the valve.

Scanning electron microscopy (Figs 10-17). The valve face is plane with a hyaline area between the face and mantle (Figs 14, 15), 8.4–10.1 μ m (average 9.4±0.4) long, 2.6–3.3 μ m (average 3.0 \pm 0.2; n = 24) wide. Raphe is filiform, simple, usually without any terminals externally (Fig. 10), but occasionally slightly curved (Fig. 14). Externally, both proximal raphe ends bend in the same direction. Internally, distal raphe ends are simple, not expanded, with small helictoglossa (Figs 11, 13). Proximal raphe terminals are simple or sometimes bent in the same direction. Axial area is narrow, widening slightly towards the central area. Striae are closely located, about 36 in 10 μ m (34–42, average 36.5 ± 3.2, n = 24). The striae are simple, slit-like alveoli, usually slightly radial, or rarely almost parallel (Figs 10-15). The valve mantle has one row of poroids (Figs 15-17). The striae on the mantle correspond well in number and width with those on the valve face. Some small irregular poroids can occasionally be observed on the mantle of the epivalve (Fig. 16). The cingulum is composed of different number of bands (copulae). The valvocopula and copulae are unperforated (Figs 15–17). The alveoli are internally closed by hymens (Figs 11-13), but often corroded.

Remarks. Our observed morphometric data of *Navicula schmassmannii* type material correspond well to the description by Hustedt, except that he reported smaller specimens than the smallest we observed (i.e., $6 \mu m$ in length and 2.5 μm in width).



Figs 10–17. Scanning electron microscopy of the type material of *Navicula schmassmannii* Hustedt. Figs 10, 14. External view of valve face, with slightly curved raphe, the proximal raphe ends bend in the same direction Figs 11–13. Internal view of valves, note the curved proximal raphe ends. Fig. 12. Partly corroded hymen and an open band cover the central area. Fig. 13. Note bent raphe ends (arrows), and alveoli internally closed by hymens Figs 15–17. Girdle view with different numbers of bands. The valve mantle is structured like the valve face, with one row of poroids. Fig. 16.

Note the smaller, irregular poroids on the epitheca (small white arrows) (scale bars = 2 μ m).

On the basis of SEM morphological features of *N. schmassmannii* Hustedt (the basic valve structure and in particular the slit-like striae, both on the valve face and mantle) we propose to transfer it to *Humidophila* genus as *Humidophila schmassmannii* (Hustedt) Buczkó et Wojtal comb. nov.

Humidophila schmassmannii (Hustedt) Buczkó et Wojtal comb. nov.

Basionym: *Navicula schmassmannii* Hustedt, Schmidt's Atlas der Diatomaceen-Kunde: pl. 400: figs. 48–52. 1934.

Type locality: Hochseen near Davos (Switzerland).

Observations on the late-glacial and early Holocene population

Light microscopy (Figs 18–28). Valves are of a highly variable outline, elliptical to linear-elliptical or lanceolate-elliptical to lanceolate, 4.6–13.4 μ m (average 8.3±1.7) long, 2.1–3.8 μ m (average 2.7±0,4; n = 31) wide. Ends are also variable from capitate to rostrate, somewhat asymmetric/irregular. Raphe (filiform, straight) simple, threadlike with simple terminals, the proximal terminals are well visible. Axial area is hardly visible, central area is variable and of different size, rhombic and slightly asymmetric. Striae are rarely discernible on the valve.

Scanning electron microscopy (Figs 29–37): The valve face is plane with a hyaline area between the face and mantle. Raphe is filiform, simple, without any terminals externally. Internally, distal raphe ends are simple, not expanded, with small helictoglossa. Axial area is narrow, widening slightly towards the central area. Striae are closely located about 42 in 10 μ m (36–46, average 42.4 ± 3.2, n = 36). The striae are simple, slit-like alveoli, usually parallel or slightly radial. The striae on the mantle correspond well in number and width with those on the valve face. Neither hymenes nor copulae were observed. A frustule with a shallow mantle is presented in Figure 32. The central area can be asymmetric in terms of length, width and shape along apical axis.

Small naviculoid diatoms with slit-like striae from the sediment of the Lake Brazi show a high morphological variability in terms of all features that can characterize a diatom valve, including length, width, striae density and their pattern, valve outline, shape of apices, size and shape of central area. The orientation of striae also varies from parallel to radiate.

The first occurrence of diatoms with slit-like striae was detected at 566 cm (12,490 cal yrs BP) and it was present up to 552 cm (11,480 cal yrs BP). Notably, their late-glacial occurrence is confined to the Younger Dryas, which is known as a cold period during the late-glacial (AMMANN *et al.* 2000). Their relative abundance was always < 2%. Following a *ca* 1,000 year long gap, they reappeared at 532 cm (10,510 cal yrs BP) and were present until only 416 cm (*ca* 9500 cal yrs BP).

DISCUSSION

The most characteristic feature of *Humidophila schmassmannii* is the slitlike striae pattern, which implies that it does not belong to *Navicula* sensu stricto. Only a few diatom species, spread over multiple genera, have similar slit-like striae instead of areolae. Examples include two species from the recent-



Figs 18-28. High morphological variability of slit-like striated diatoms of the Navicula schmassmannii - complex (Lake Brazi), LM

ly described genus *Microfissurata* Lange-Bertalot, Cantonati et Van de Vijver (CANTONATI *et al.* 2009; the name of the genus indeed refers to these slit-like striae). CANTONATI *et al.* (2009) also discuss and illustrate further examples for the occurrence of slit-like striae in other genera like *Diadesmis* subgenus *Paradiadesmis*, recently elevated to the genus rank as *Humidophila* by LOWE *et al.* (2014), *Chamaepinnularia, Gomphosphenia* and *Kobayasiella*. This compilation



Figs 29–37. Slit-like striated diatoms from Lake Brazi. SEM Figs 29–33. External view of the valves Fig. 32. Note the shallow mantle, the girdle elements are missing. Figs 35–37. Internal view. Note the simple proximal raphe ends. (Scale bars = $2 \mu m$).

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also mentions *H. schmassmannii* as a separate entity, indicating that it bears a curious set of features. CANTONATI *et al.* (2009) refer to unpublished observations stating that the alveoli of *H. schmassmannii* are closed on the exterior part of the valves, distinguishing it from *Diadesmis/Humidophila*. Our investigation of type material clearly shows alveoli internally closed by hymens (Figs 11–13), i.e. the same type of structure as in the genus *Humidophila*.

That *Humidophila schmassmannii* is not a member of *Navicula* s.s. because of its alveoli structure was recognized previously. LANGE-BERTALOT and MET-ZELTIN (1996) referred to it as *Naviculadicta schmassmannii* (Hustedt) Lange-Bertalot (Pl. 28, figs 1–5), although this combination has not been formally published. Moreover the validity of genus *Naviculadicta* is generally not accepted by diatomists, (e.g. KOCIOLEK 1996), so the transfer of *H. schmannannii* in a "catchall", not well defined genus could result in more trouble than good.

WERUM and LANGE-BERTALOT (2004, Pl. 34, figs, 1–6) published SEM images of valves identified as *Navicula schmassmannii* from Lower Triassic sandstone from the Black Forest. They noted that the frustules observed appeared rather similar to *Diadesmis* at first glance, but the unperforated and comparatively narrow girdle elements and the broad valve mantle make their "congenerity unlikely".

Recently, the subgenus *Paradiadesmis* of *Diadesmis* was erected to the generic rank by LOWE *et al.* (2014) as *Humidophila* Lowe, Kociolek, Johansen, Van de Vijver, Lange-Bertalot et Kopalová. The basic valve structure and in particular the slit-like striae, both on the valve face and mantle, clearly link *Navicula schmassmannii* to this new genus. Although the somewhat deflected proximal raphe endings and the unperforated girdle bands differ from what has been reported for other *Humidophila* species, for the moment, the transfer of *N. schmassmannii* into the genus *Humidophila* seems the best nomenclatural solution. It is of course possible that in the future, observation of a similar combination of features will make the erection of a new genus for *H. schmassmannii* and allies necessary.

Similar taxa

Two other species similar to *Humidophila schmassmannii* are *Navicula leptidissima* (CLEVE-EULER 1953) and *N. stolida* Krasske. The main characteristics of these species are presented in Table 1. Without an examination of their type material with SEM, their conspecificity remains unclear. It is noteworthy that ten years after its description, Krasske transferred *N. stolida* to the genus *Achnanthes*, because he recognized in LM that this species has rapheless valves, a feature commonly observed in *Humidophila* spp. Additionally, information on *Achnanthes carissima* Lange-Bertalot is also presented in Table 1. This is a further diatom taxon with slit-like striae which often co-occurs with *H. schmassmannii* in oligotrophic waters.

	Length	Width	Striae	Slit-like striae	Outline	Distribution
<i>Diadesmsis schmassmannii</i> type material in this study	8.5–10.5, average 9.5	2.6–3.3, average 3	34–42, average 36.5	yes	elliptic to linear-elliptic or lanceolate-elliptical	Alpine lake sedi- ment, Switzerland
<i>Navicula leptidissima</i> Cleve- Euler 1953, p. 165, fig. 840c	10-12	2.2-2.4	invisible in LM	unknown	very small and narrow sublin- ear valves with central pores distinctively far located from each other, ends capitate	Calcium-rich peat bog, Sweden
Navicula stolida Krasske 1939*	9-10	2.5-3	~ 40	unknown	elliptic to elliptic-linear with broadly rounded elongated (subcapitate) apices. 3 striae in the middle portion of a valve, widely located. Axial area lanceolate without central area enlargement	Lago Riso Patron Chile
Achnanthes stolida (Krasske) Krasske 1949*	9–13	2.5-3.5	35-40	unknown	elliptical to elliptic-lanceolate or(?) up to (?) linear with broadly rounded elongated (subcapitate) apices. Three striae in the middle portion of a valve more distantly located	Chile, Patagonia, peat bog, Chile
<i>Achnanthes carissima</i> Lange- Bertalot **	5–9 2.3–3 (5.5–14.5) (2.5–3.0)	2.3–3 (2.5–3.0)	45-50	yes	slightly subcapitate ends and tumid middle portion of the valve	Schleswik-Hols- tein Garrensse, Germany, Julma Ölkky; Finland

MORPHOLOGY AND DISTRIBUTION OF NAVICULA SCHMASSMANNII

Present distribution, habitat preference

Navicula schmassmannii was characterized in Hustedt's original description as a boreal diatom. The growing amount of data point out that an alpine-Nordic distribution seems to be a better biogeographic description. RÜHLAND *et al.* (2003) detected *N. schmassamnnii* on 19 occasions in surface-sediment samples of 77 lakes across the subarctic Canadian region, including arctic-tundra, forest-tundra and boreal-forest lakes. They found that *N. schmassmannii* was especially common in arctic-tundra lakes with low DIC and low DOC. They determined the optimum of the taxon for DIC at 0.5 mg/l; for DOC at 4.1 mg/l; for depth at 7.5 m; for SiO₂ at 0.3 mg/l and surprisingly high value for total nitrogen at 219.8 μ g/l.

Recently performed analyses featured *N. schmassmannii* as a characteristic member of diatom assemblages in some alpine regions (CATALAN *et al.* 2009). In this comprehensive study, the ecological threshold of diatoms, rotifers, chydorids, planktonic crustaceans and chironomids were studied in 235 alpine lakes in the Alps, Pyrenees, Tatras (Western Carpathians), Retezat (Southern Carpathians) and Rila Mts (Balkans), but diatom assemblages were only studied from 142 lakes. On the basis of diatom occurrences, all assemblages showed a high score of acid neutralising capacity and correlated variables. Twenty-one lakes were situated in the Central Swiss Alps, Piedmont-Ticino, Tyrol and Tatra Mts, all above the treeline. From Retezat Mts only 4 lakes were included in the study but none of them was grouped in the cluster that can be characterized by the presence of *N. schmassmannii* and the co-occurring diatom taxa.

The contribution of *N. schmassmannii* to diatom assemblages rarely reaches 2% (JUGGINS 2010, ANSP 2015), its occurrence is often sporadic, and only one or two valves are detected in a sample. According to the European Diatom Database, *N. schmassmannii* was found in 80 European lakes, but its relative abundance exceeded 2% only in 5 lakes (max 14.2% in Terianske Pleso in Slovenia; CAMERON *et al.* 1999, JUGGINS 2010).

In lakes on Victoria Island in the Canadian High Arctic, MICHELUTTI *et al.* (2003) found this taxon to occur exclusively in moss habitats (albeit in low relative abundances), and it is considered by some to be aerophilic (PAUL *et al.* 2010). In Tatra lakes it is abundant only in deeper lakes >20 m where its relative abundance can reach 20%. (BITUŠIK *et al.* 2009). Altogether, it remains unclear whether *Humidophila schmassmannii* prefers the shallow or deep waters or even it can be regarded as aerophilic and/or moss inhabiting species. The widely varying ecological preferences recorded might also be caused by taxonomic force-fitting or reporting different cryptic taxa under the name *N. schmassmannii*.

Palaeoecological significance

Navicula schmassmannii has commonly been found in palaeolimnological studies on arctic and alpine regions (e.g., HAWORTH 1976, PIENITZ et al. 1995, FALLU et al. 2002, RÜHLAND et al. 2003, MICHELUTTI et al. 2003, BRINER et al. 2006, BITUŠIK et al. 2009, PAUL et al. 2010, ANSP 2015), but generally as a minor component of the diatom assemblage. Its highest relative abundance was observed in the Tatra Mts (Slovakia), reaching about 40% in Nižné Terianske pleso in the first half of the 20th century (BITUŠÍK et al. 2009). Recent substantial increase in the relative abundance of N. schmassmannii in a Slovakian (ŠPORKA et al. 2002) and in a Norwegian alpine lake (LARSEN et al. 2006), was interpreted to have been driven by recent warming. In the Tatra study, similar clear N. schmassmannii signals were not observed (BITUŠÍK et al. 2009).

Several findings refer to *Navicula schmassmannii* as a warm bioindicator in alpine lakes above the treeline, but the taxon is also often reported from cooler periods at low elevation forested sites. It is abundant in deep lakes but there are evidences about aerophilic preferences. This taxon was reported to have increased notably in relative abundance with the onset of the Holocene Thermal Maximum in a lake on Baffin Island (BRINER *et al.* 2006). PAUL *et al.* (2010) also detected the presence of *N. schmassmannii* in the early Holocene sediments of Lake TK-2, which he interpreted as a consequence of warming resulting in prolonged icefree periods of sufficient duration to initiate the establishment of mosses in the littoral zone. ROBINSON (2004) also found a connection between warming and increasing abundance of *N. schmassmannii* in Shetland Island.

To the contrary, in Lake Krakenes (Norway), *N. schmassmannii* was most abundant (close to 20%) during the Younger Dryas (*ca* 12,700 cal yr BP), which is characterized by an abrupt and significant cooling (BRADSHAW *et al.* 2000). HAWORTH (1976) also reports *N. schmassmannii* to occur in the late-Devensian age in her late-glacial study. This is a period when an *Artemisia* pollen zone, together with chemical indicators of soil erosion in the catchment area, indicated a cooler period.

CONCLUSIONS

Transfer of *Navicula schmassmannii* Hustedt to *Humidophila* genus is proposed as *Humidophila schmassmannii* (Hustedt) Buczkó et Wojtal on the basis of re-investigation of the type material.

A broad range of morphological variability has been documented in diatoms with slit-like striae closely resembling *Humidophila schmassmannii* in the sediment of Lake Brazi, in terms of such features as length, width, striae density

and pattern, outline including the shape of apices, the length, width and shape of the central area. The orientation of striae exhibits certain change from parallel to radiate. The asymmetry of valves is also rather well expressed. The question arises whether this variation represents natural, random phenotypic diversity; phenotypic plastic responses to differing environmental conditions; or the presence of more than one taxon.

Reports of the taxon from apparently contrasting habitat types and with opposite interpretations in terms of its palaeoecological indicator value, might point to an as yet unrecognized diversity, and/or to an unrecognized environmental factor related to temperature changes.

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Összefoglaló: Magas hegyi tavak és arktikus területek jellemző kovaalgája az apró termetű Navicula schmassmannii Hustedt. Bár fénymikroszkópban is jellegzetes, a pontos határozáshoz a szkenning elektronmikroszkópos vizsgálatok elengedhetetlenek. Paleoökológiai rekonstrukciókban a melegebb időszakok indikátorának tartják. Az itt bemutatott munkában a faj típusanyagát vizsgáltuk fény- és elektronmikroszkóp segítségével, részletes leírást adunk a finomszerkezetéről, külön hangsúlyt fektetve a ritkán tanulmányozott oldalnézetre. A típusanyag vizsgálatán túl bemutatjuk a Déli-Kárpátok Fenyők-közti-tavából gyűjtött populáció morfológiai variabilitását is, ami jóval meghaladja a típusanyagét. A finomszerkezet vizsgálata alapján nyilvánvaló, hogy ez a faj nem a Navicula nemzetségbe tartozik. Javasoljuk átsorolását a Humidophila nemzetségbe, mint H. schmassmannii (Hustedt) Buczkó et Wojtal.

REFERENCES

- AMMANN, B., BIRKS, H. J. B., BROOKS, S. J., EICHER, U., VON GRAFENSTEIN, U., HOFMANN, W., LEMDAHL, G., SCHWANDER, J., TOBOLSKI, K. and WICK, L. (2000): Quantification of biotic responses to rapid climatic changes around the Younger Dryas – a synthesis. – *Palaeogeogr, Palaeoclimatol., Palaeoecol.* 159: 313–347. http://dx.doi.org/10.1016/S0031-0182(00)00092-4
- ANSP (2015): Algae image database from the Phycology Section, Patrick Center for Environmental Research, The Academy of Natural Sciences of Drexel University. – http://diatom.acnatsci. org/AlgaeImage/ (accessed 27.01.2015)
- BATTARBEE, R. W. (1986): Diatom analysis. In BERGLUND, B. E. (ed.): Handbook of Holocene palaeoecology and palaeohydrology. John Wiley and Sons, Chichester, New York, Brisbane, Toronto, Singapore, pp. 527–570.
- BITUŠÍK, P., KUBOVČÍK, V., ŠTEFKOVÁ, E., APPLEBY, P. G. and SVITOK, M. (2009): Subfossil diatoms and chironomids along an altitudinal gradient in the High Tatra Mountain lakes: a multi-proxy record of past environmental trends. *Hydrobiologia* 631(1): 65–85. http://dx.doi.org/10.1007/s10750-009-9802-0

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- BRADSHAW, E. G., JONES, V. J., BIRKS, H. J. B, and BIRKS, H. (2000): Diatom responses to late-glacial and early-Holocene environmental changes at Kråkenes, western Norway – *J. Paleolimnol.* 23: 21–34. http://dx.doi.org/10.1023/A:1008021016027
- BRINER, J. P., MICHELUTTI, N., FRANCIS, D. R., MILLER, G. H., AXFORD, Y., WOOLLER, M. J. and WOLFE, A. P. (2006): A multi-proxy Holocene climate change on northeastern Baffin Island, Arctic Canada. – *Quatern. Res.* 65: 431–442. http://dx.doi.org/10.1016/j.yqres.2005.10.005
- CAMERON, N. G., BIRKS, H. J. B., JONES, V. J., BERGE, F., CATALAN, J., FLOWER, R. J., GARCIA, J., KAWECKA, B., KOINIG, K. A., MARCHETTO, A., SÁNCHEZ-CASTILLO, P., SCHMIDT, R., ŠISKO, M. SOLOVIEVA, N., ŠTEFKOVÁ, E. and TORO, M. (1999): Surface-sediment and epilithic diatom pH calibration sets for remote European mountain lakes (AL:PE Project) and their comparison with the Surface Waters Acidification Programme (SWAP) calibration set. J. Paleolimnol. 22: 291–317. http://dx.doi.org/10.1023/A:1008025928509
- CANTONATI, M., VAN DE VIJVER, B. and LANGE-BERTALOT, H. (2009): Microfissurata gen. nov. (Bacillariophyta), a new diatom genus from dystrophic and intermittently-wet terrestrial habitats. – J. Phycol. 45(3): 732–741. http://dx.doi.org/10.1111/j.1529-8817.2009.00683.x
- CATALAN, J., BARBIERI, M. G., BARTUMEUS, F., BITUŠÍK, P., BOTEV, I., BRANCELJ, A., COGĂLNICEANU, C., MANCA, M., MARCHETTO, A., OGNJANOVA-RUMENOVA, N., PLA, S., RIERADEVALL, M., SORVARI, S., ŠTEFKOVÁ, E., STUCHLÍK, E. and VENTURA, M. (2009): Ecological thresholds in European alpine lakes. – *Freshwater Biol.* 54: 2494–2517. http://dx.doi.org/10.1111/j.1365-2427.2009.02286.x
- CLEVE-EULER, A. (1953): Die Diatomeen von Schweden und Finnland. Part III. Monoraphideae, Biraphideae 1 – Kongl. Sv. Vetensk.-Akad. Handl., ser. 4, 4: 1–255, figs 484–970.
- FALLU, M. A., ALLAIRE, N. and PIENITZ, R. (2000): Freshwater diatoms from northern Québec and Labrador (Canada). Species-environment relationships in lakes of boreal forest, forest-tundra and trunda regions. – In: LANGE-BERTALOT, H. and KOCIOLEK, P. (eds): Bibliotheca Diatomologica 45. J. Cramer, Berlin, Stuttgart, pp. 1–200.
- FALLU, M. A., ALLAIRE, N. and PIENITZ, R. (2002): Distribution of freshwater diatoms in 64 Labrador (Canada) lakes: species-environment relationships along latitudinal gradients and reconstruction models for water colour and alkalinity. – Can. J. Fish. Aquatic Sci. 59: 329–349. http://dx.doi.org/10.1139/f01-211
- GÜTTINGER, W. (1996): Collection of SEM micrographs of diatoms. 8: 47 pls. Pura, Switzerland, self published
- HAWORTH, E. Y. (1976): Two Late-Glacial (Late Devensian) diatom assemblage profiles from Northern Scotland. *New Phytol.* 77: 227–256.
- HUSTEDT, F. (1943): Die Diatomeenflora einiger Hochgebirgseen der Landschaft Davos in den Schweizer Alpen. Arch. f. Hydrobiol. 43: 124–197.
- HUSTEDT, F. (1962): Die Kieselalgen Deutschlands, Österreichs und der Schweiz unter Berücksichtigung der übrigen Länder Europas sowie der angrenzenden Meeresgebiete. – In: RABENHORST, L. (ed.): Kryptogamen Flora von Deutschland, Österreich und der Schweiz. Akademische Verlagsgesellschaft m.b.h. Leipzig, 7(3): 161–348, figs 1295–1456.
- JUGGINS, S. (2010): The European Diatom Database. http://craticula.ncl.ac.uk/Eddi/ (accessed 17.07.2014)
- KOCIOLEK, J. P. (1996): Comment: taxonomic instability and the creation of Naviculadicta Lange-Bertalot in Lange-Bertalot & Moser a new catch-all genus of diatoms. – *Diatom Research* 11(1): 219–222. http://dx.doi.org/10.1080/0269249X.1996.9705373
- KRAMMER, K. and LANGE-BERTALOT, H. (1986): Bacillariophyceae 1. Teil: Naviculaceae. In: ETTL, H., GERLOFF, J., HEYNIG, H. and MOLLENHAUER, D. (eds): Die Süsswasserflora Mitteleuropa 2/1. G. Fischer, Stuttgart, 876 pp.

- LANGE-BERTALOT, H. and METZELTIN, D. (1996): Indicators of oligotrophy. 800 taxa representative of three ecologically distinct lake types. – In: LANGE-BERTALOT, H. (ed.): Iconographia Diatomologica. Annotated diatom micrographs 2. Koeltz Scientific Books, Königstein, 390 pp.
- LANGE-BERTALOT, H., KULBS, K., LAUSER, T., NORPEL-SCHEMPP, M. and WILLMANN, M. (1996): Dokumentation und revision der von Georg Krasske beschriebenen Diatomeen-Taxa.
 In: LANGE-BERTALOT, H. (ed.): Iconographia Diatomologica. Annotated diatom micrographs 3. Koeltz Scientific Books, Königstein, 358 pp.
- LARSEN, J. L., JONES, V. J. and EDIE, W. (2006): Climatically driven pH changes in two Norwegian alpine lakes. J. Paleolimnol. 36: 175–187. http://dx.doi.org/10.1007/s10933-006-0013-7
- LOWE, R. L., KOCIOLEK, P., JOHANSEN, J. R., VAN DE VIJVER, B., LANGE-BERTALOT, H. and KOPALOVÁ, K. (2014): Humidophila gen. nov., a new genus for a group of diatoms (Bacillariophyta) formerly within the genus Diadesmis: species from Hawaii, including one new species. – *Diatom Research* 29: 351–360.

http://dx.doi.org/10.1080/0269249X.2014.889039

- MAGYARI, E. K., BRAUN, M., BUCZKÓ, K., HUBAY, K. and BÁLINT, M. (2010): Radiocarbon chronology of glacial lake sediments in the Retezat Mts (S Carpathians, Romania): a window to Lateglacial and Holocene climatic and palaeoenvironmental changes. – *Central Eur. Geol.* 52(3-4): 225-248. http://dx.doi.org/10.1556/CEuGeol.52.2009.3-4.2
- MICHELUTTI, N., HOLTHAM, A. J., DOUGLAS, M. S. V. and SMOL, J. P. (2003): Periphytic diatom assemblages from ultra-oligotrophic and UV transparent lakes and ponds on Victoria Island and comparisons with other diatom surveys in the Canadian Arctic. – J. Phycol. 39: 465–480. http://dx.doi.org/10.1046/j.1529-8817.2003.02153.x
- PAUL, C. A., RÜHLAND, K. M. and SMOL, J. P. (2010): Diatom-inferred climatic and environmental changes over the last 9000 years from a low Arctic (Nunavut, Canada) tundra lake. – *Paleogeogr., Palaeoclimatol., Palaeoecol.* 291: 205–216. http://dx.doi.org/10.1016/j.palaeo.2010.02.030
- PIENITZ, R., SMOL, J. P. and BIRKS, H. J. B. (1995): Assessment of freshwater diatoms as quantitative indicators of past climatic change in the Yukon and Northwest Territories, Canada. – J. Paleolimnol. 13: 21–49. http://dx.doi.org/10.1007/BF00678109
- ROBINSON, M. (2004): A Late glacial and Holocene diatom record from Clettnadal, Shetland Islands, northern Scotland. – *J. Paleolimnol.* **31**: 295–319.
 - http://dx.doi.org/10.1023/B:JOPL.0000021716.49552.da
- RÜHLAND, K. M., SMOL, J. P. and PIENITZ, R. (2003): Ecology and spatial distributions of surfacesediment diatoms from 77 lakes in the subarctic Canadian treeline region. – *Can. J. Bot.* 81(1): 57–73. http://dx.doi.org/10.1139/b03-005
- SABATER, S. and ROCA, J. R. (1992): Ecological and biogeographical aspects of diatom distribution in Pyrenean springs. – *British Phycol. J.* 27: 203–213. http://dx.doi.org/10.1080/00071619200650201
- SCHMIDT, A. (1874–1959): Atlas der Diatomaceen-Kunde. Parts 1–120, Pls. 1–460. Aschersleben, Leipzig.
- SCHMIDT, A., SCHMIDT, M., FRICKE, F., HEIDEN, H., MÜLLER, O. and HUSTEDT, F. (1934): Atlas der Diatomaceen-Kunde. Aschersleben, Leipzig, Tafel 395.
- SIMONSEN, R. (1987*a*): Atlas and catalogue of the diatom types of Friedrich Hustedt. Vol. 1. Catalogue. – J. Cramer, Berlin, 525 pp.
- SIMONSEN, R. (1987b): Atlas and catalogue of the diatom types of Friedrich Hustedt. Vol. 2. Atlas, Plates. J. Cramer, Berlin, 395 pp.
- Šporka, F., Štefková, E., Bitušík, P., Thompson, A. R., Agustí-Panareda, A., Appleby, P. G., Grytnes, J. A., Kamenik, C., Krno, I., Lami, A., Rose, N. and Shilland, N. E. (2002):

The paleolimnological analysis of sediments from high mountain lake Nižné Terianske pleso in the High Tatras (Slovakia). – *J. Paleolimnol.* **28**: 95–109. http://dx.doi.org/10.1023/A:1020376003123

- TOLOTTI, M. (2001): Phytoplankton and littoral epilithic diatoms in high mountain lakes of the Adamello-Brenta Regional Park (Trentino, Italy) and their relation to trophic status and acidification risk. J. Limnol. 60: 171–188.
- WERUM, M. and LANGE-BERTALOT, H. (2004): *Iconographia Diatomologica. Annotated diatom micrographs.* Vol. 13. Diatoms from springs. – A. R. G. Gantner Verlag, K. G. Ruggell, 480 pp.

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