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,
despite its rarity. It seems that this diatom is a constant member of oligotrophic 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 oligotrophic 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 striaion 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 striaion 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 (Magyar 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
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 μm (average 9.5±0.4) long, 2.6–3.2 μm (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 μm (average 9.4±0.4) long, 2.6–3.3 μm (average 3.0±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 μm (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 μm in length and 2.5 μm in width).
Figs 10–17. Scanning electron microscopy of the type material of *Navicula schmassmannii* Hust. 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 μm).
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 μm (average 8.3±1.7) long, 2.1–3.8 μm (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 μm (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 slit-like 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](image)

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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 μm).](image)

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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 Metzeltin (1996) referred to it as Naviculadiicta schmassmannii (Hustedt) Lange-Bertalot (Pl. 28, figs 1–5), although this combination has not been formally published. Moreover the validity of genus Naviculadiicta is generally not accepted by diatomists, (e.g. Kociolek 1996), so the transfer of H. schmassmannii in a „catch-all”, 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.
Table 1. Comparison of morphological features among similar taxa of the *Humidophila schmassmannii* complex (length, width, stria density and pattern, outline, and distribution). (* = Lange-Bertalot et al. 1996; ** = Lange-Bertalot and Metzeltin 1996)

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Length</th>
<th>Width</th>
<th>Striae</th>
<th>Slit-like striae</th>
<th>Outline</th>
<th>Distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Diadesmis schmassmannii</em> type material in this study</td>
<td>8.5–10.5, average 9.5</td>
<td>2.6–3.3, average 3</td>
<td>34–42, average 36.5</td>
<td>yes</td>
<td>elliptic to linear-elliptic or lanceolate-elliptical</td>
<td>Alpine lake sediment, Switzerland</td>
</tr>
<tr>
<td><em>Navicula leptidissima</em> Cleve-Euler 1953, p. 165, fig. 840c</td>
<td>10–12</td>
<td>2.2–2.4</td>
<td>invisible in LM</td>
<td>unknown</td>
<td>very small and narrow sublinear valves with central pores distictively far located from each other, ends capitate</td>
<td>Calcium-rich peat bog, Sweden</td>
</tr>
<tr>
<td><em>Navicula stolida</em> Krasske 1939*</td>
<td>9–10</td>
<td>2.5–3</td>
<td>~40</td>
<td>unknown</td>
<td>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</td>
<td>Lago Riso Patron, Chile</td>
</tr>
<tr>
<td><em>Achnanthes stolida</em> (Krasske) Krasske 1949*</td>
<td>9–13</td>
<td>2.5–3.5</td>
<td>35–40</td>
<td>unknown</td>
<td>elliptical to elliptic-lanceolate or (?) linear with broadly rounded elongated (subcapitate) apices. Three striae in the middle portion of a valve more distantly located</td>
<td>Chile, Patagonia, peat bog, Chile</td>
</tr>
<tr>
<td><em>Achnanthes carissima</em> Lange-Bertalot **</td>
<td>5–9 (5.5–14.5)</td>
<td>2.3–3 (2.5–3.0)</td>
<td>45–50</td>
<td>yes</td>
<td>slightly subcapitate ends and tumid middle portion of the valve</td>
<td>Schleswik-Holstein Garrense, Germany, Julma Ölkky, Finland</td>
</tr>
</tbody>
</table>
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. schmassmannii* 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 μg/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, chydrorids, 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%. (Bitušík et al. 2009). Altogether, it remains unclear whether *Humidiphila 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, Bitušík *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 ice-free 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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