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NUPELA MATRIOSCHKA SP. NOV., *NUPELA THURSTONENSIS* COMB. NOV. AND *NUPELA NEOGRACILLIMA* COMB. & NOM. NOV. (BACILLARIOPHYCEAE): CRITICAL ANALYSIS OF THEIR MORPHOLOGY

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Abstract. Light and electron microscopic observations of the diatom flora from the Polistovo-Lovatsky *Sphagnum* bogs (Russia, Novgorod region) revealed the occurrence of an unknown species comparable to *Navicula thurstonensis* Kaczmarska, a taxon described from Hawaii. *Nupela matrioschka* is described here as a species new to science, based on its valve morphology typical for the genus *Nupela* Vyverman & Compère. The major features conforming to *Nupela* are the ultrastructure of the raphe system and areolae. We propose formal transfer of *Navicula thurstonensis* to *Nupela* as *N. thurstonensis* (Kaczmarska) Kulikovskiy, Lange-Bertalot & Witkowski *comb. nov*. Both species are compared to similar taxa belonging to *Nupela* described from temperate climate zones. Also proposed is transfer of *Achnanthes gracillima* Hustedt to *Nupela*. Since the epithet *gracillima* is not available due to the priority of *Nupela gracillima* (Hustedt) Lange-Bertalot 1993, we propose as a necessary new name *Nupela neogracillima* (Hustedt) Kulikowskiy & Lange-Bertalot *comb. nov., nom. nov.*

Key words: taxonomy, diatom morphology, *Nupela*, *Navicula*, *Achnanthes*, new species, new combinations, Polistovo-Lovatsky *Sphagnum* bogs (Russia), Hawaii

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INTRODUCTION

The genus *Nupela* Vyverman & Compère was described based on the ultrastructure of areolae and of the raphe system. As shown by Rumrich *et al.* (2000), Monnier *et al.* (2003) and Potapova *et al.* (2003), areolae in *Nupela* are occluded by external hymens. Likewise the particular raphe structure can only be detected in SEM. The external terminal raphe endings in most cases form a double hook (e.g., Rumrich *et al.* 2000; Monnier *et al.* 2003; Potapova *et al.* 2003) or occasionally a single hook (Lange-Bertalot 1993). The internal proximal raphe endings are variable, either simple or hooked or sometimes T-shaped (Vyverman & Compère 1991; Lange-Bertalot 1993; Potapova *et al.* 2003). Morphological analysis reveals that at present *Nupela* is to a certain extent heterogenous, as it includes frustules with a naviculoid or with a achnanthoid raphe system. In the first case both valves possess fully developed raphe branches; in the second case either the frustule is heterovalvar with one raphid valve and the other one araphid or else the raphe is strongly reduced on the second valve. This problem has already been raised by Monnier *et al.* (2003), Siver *et al.* (2005), Kulikovskiy (2007), Antoniades *et al.* (2008) and others. Since the early 1990s, many naviculoid and achnanthoid species have been either transferred to this genus or described as new to science (e.g., Lange-Bertalot 1993; Lange-Bertalot & Moser 1994; Lange-Bertalot & Metzeltin 1996; Moser *et al.* 1998; Lange-Bertalot & Genkal 1999; Rumrich *et al.* 2000; Kusber & Metzeltin 2001; Monnier *et al.* 2003; Potapova *et al.* 2003; Metzeltin & Lange-Bertalot 1998, 2007; Antoniades *et al.* 2008).

Floristic studies of *Sphagnum* bog diatoms in the European part of Russia resulted in the identification of an unknown species similar to *Navicula thurstonensis* described by Kaczmarska in Rushfort *et al.* (1984) from Hawaii. Both species have principally naviculoid frustule morphology. Based on light and electron microscopic observations we describe a new species *Nupela matrioschka* and propose the transfer of *Navicula thurstonensis* to *Nupela*. Likewise we propose the transfer of *Achnanthes gracillima* Hustedt, which possesses features of achnanthoid taxa in *Nupela*. The general taxonomy of *Nupela* is also briefly discussed.

Material and methods

The material studied was collected from different parts of the Polistovo-Lovatsky *Sphagnum* Bogs (Novgorod region, Russia) in July 2005. Altogether 49 samples were collected including plankton, benthos and periphyton from *Sphagnum* spp. Preparation of the diatoms for microscopic observations followed the methods of Balonov (1975). A part of each sample was placed in glass test-tubes and potassium chromide was added. After 3–5 min of reaction the samples were washed with distilled water by centrifugation, and the supernatant was removed. Centrifugation was repeated several times.

Permanent diatom preparations were mounted with Naphrax®. Light microscopic (LM) observations employed a Nikon Eclipse E600 with a Plan-apochromatic 100× oil immersion objective and a Nikon DS-5M digital camera. Diatom valve ultrastructure was analyzed with a JSM-25S (JEOL, Japan) scanning electron microscope and an H-300 (Hitachi, Japan) transmission electron microscope.

Results and discussion

Nupela matrioschka Kulikovskiy, Lange-Bertalot & Witkowski, ***sp. nov.***

Differens versus Nupela thurstonensis (Kaczmarska) Kulikovskiy, Lange-Bertalot, Witkowski *comb. nov. Valvae distincte late ellipticae apicibus plus minusve late rotundatis* (*nec angustius ellipticeae ad elliptico-lanceolatas apicibus saepe leviter protractis*). *Longitudo 9.7–12.0 μm, latitudo 4.3–6.3* (*non 3.2.–4.2*) *μm. Raphe, area axialis centralisque circiter conformantes. Areolae 30–40* (*non 40–50*) *in 10 μm, quasi irregulariter sitae* (*non fere regulariter*) *inter se cum areis hyalynis apicalibus. Disordinatio Voigtii conspicue latius inter duas strias extendens*.

Type: RUSSIA, Novgorod, Polisto-Lovatsky *Sphagnum* bog, 21 July 2005, *leg. M. Kulikovskiy*. Slide no. 13629 in collection A. Witkowski, Institute of Marine Sciences, University of Szczecin (SZCZ); isotypes: Slide no. 6 in collection M. Kulikovskiy, Institute for Biology of Inland Waters, Russian Academy of Sciences, Borok, Russia; slide no. BMR ZU6/78 deposited in Alfred Wegener Institute, Bremerhaven (BMR), Germany.

Etymology: The epithet may be seen as a neo-Latin substantive referring to traditional Russian dolls.

Differential diagnosis versus *Nupela thurstonensis* (Kaczmarska) Kulikovskiy, Lange-Bertalot & Witkowski *comb. nov*. Valves distinctly broad-elliptical with broad, never protracted apices (not narrower elliptical to elliptical-lanceolate with often slightly protracted ends). Length 9.7–12 μm, breadth 4.3–6.3 (not 3.2–4.2) μm. Raphe, axial and central area approximately conforming. Transapical striae radiate, becoming moderately convergent near the ends on either valve side (this feature is less distinct on the valve side opposite to the Voigt fault in *Nupela thurstonensis*). The Voigt fault is (comparatively) more broadly expanded between two distal striae. Areolae 30–40 (not 40–50) in 10 μm, forming irregular wavy lines apically with narrow hyaline areas in between, as in many other *Nupela* taxa.

TEM and SEM

Valve surface flat, strongly bent towards the very shallow valve mantle. Axial area very narrow, linear; central area weakly developed, as an indistinct expansion of the raphe sternum. A completely developed raphe occurs on both valves of the frustule (Fig. 2: 1). Raphe filiform, straight (Fig. 1: 1–10), external, central raphe endings simple (Fig. 2: 1–4), internally slightly expanded (Fig. 1: 11, 12), ending in a small helictoglossa

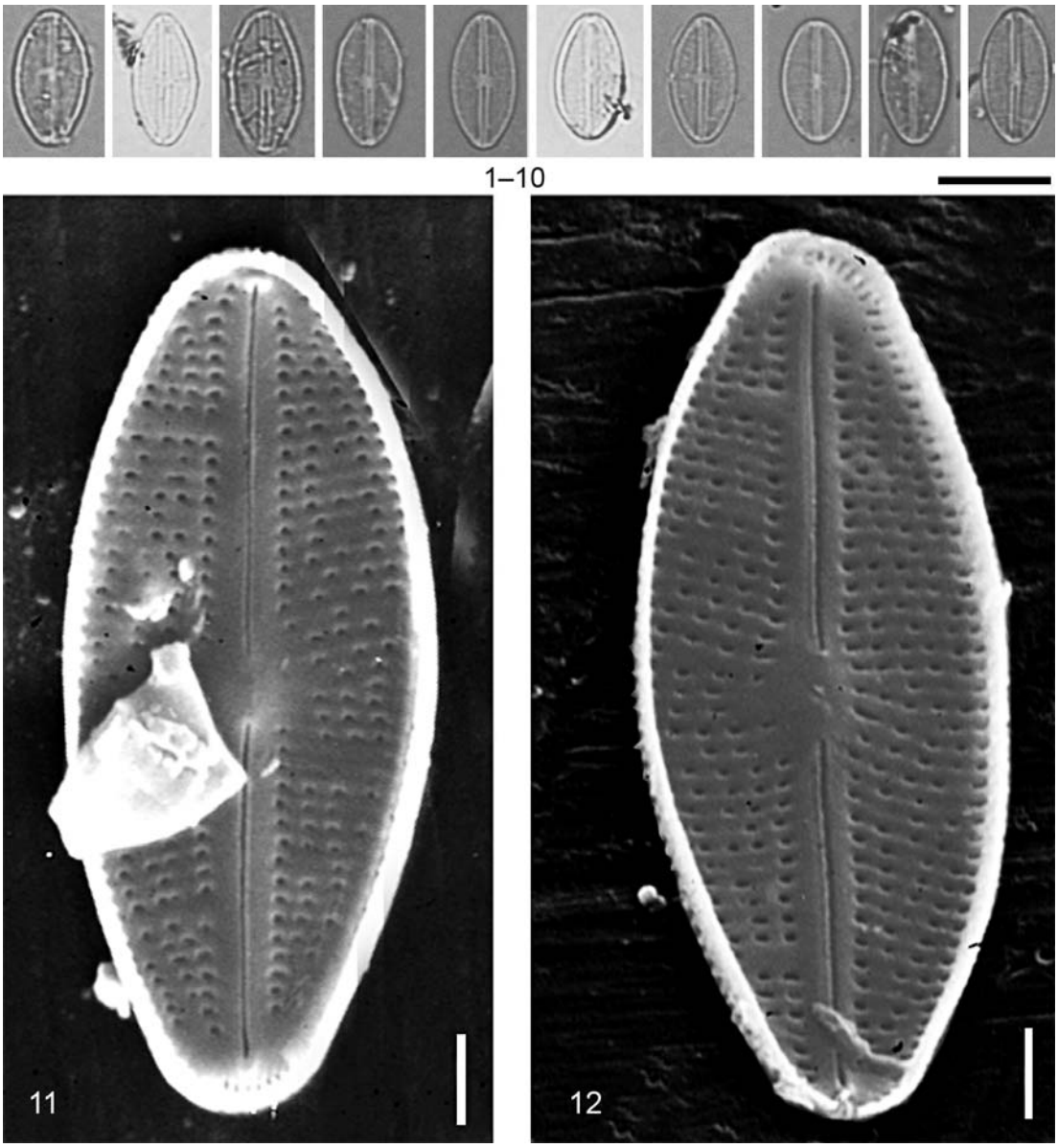

Fig. 1. *Nupela matrioschka* Kulikovskiy, Lange-Bertalot & Witkowski, *sp. nov*. (1–10 – LM, 11 & 12. SEM). Internal views of the valves showing areolae, simple slit-like raphe and a small helictoglossa. Scale bars 1–10 = 10 µm, 11 & 12 = 1 µm.

(Fig. 1: 11, 12). External apical raphe endings on both valves of the frustule strongly doubly hooked towards the same side of the valve (Fig. 2: 1–4). Transapical striae uniseriate, radiate becoming parallel or slightly convergent near the apices, 42–48 in 10 µm. Areolae form 4–5 longitudinal rows on each side of the raphe (Fig. 1: 1–10; 2: 1–4). A row of elongated poroids pervalvar on the valve mantle (Fig. 2: 1–4).

DISTRIBUTION. So far found only at the type locality, Polistovo-Lovatsky *Sphagnum* bogs.

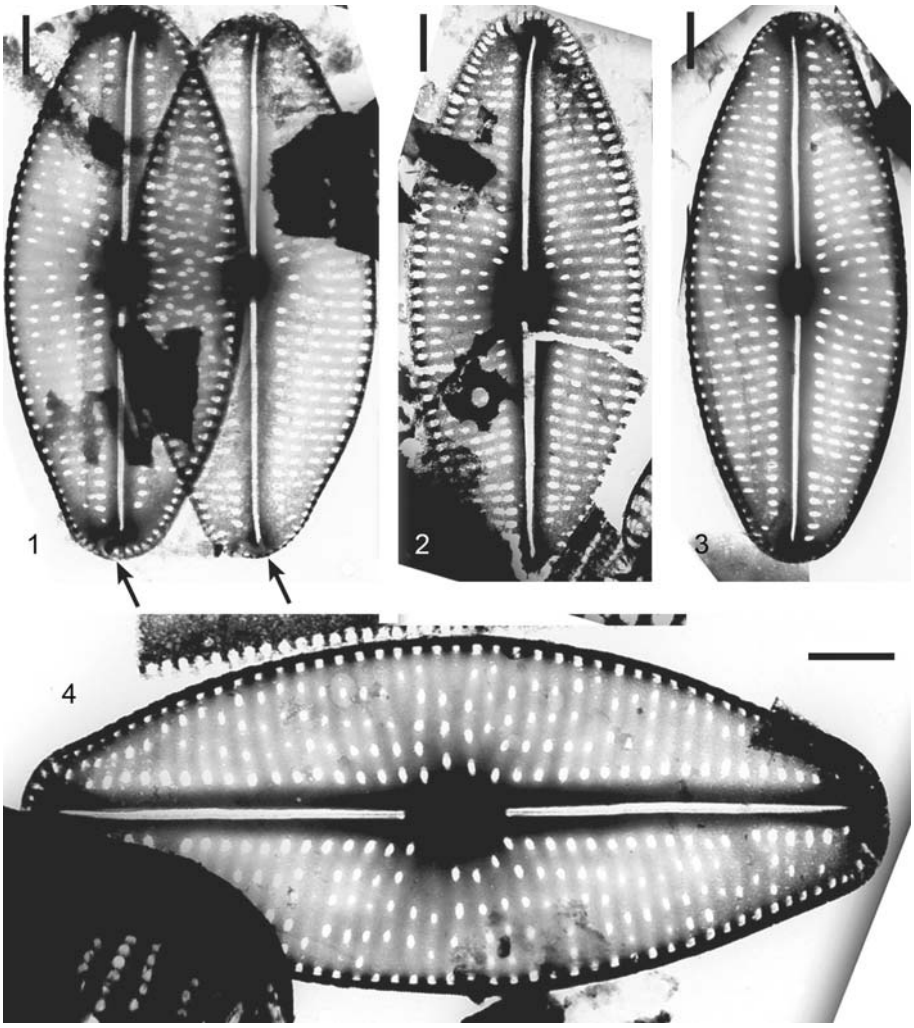

Fig. 2. *Nupela matrioschka* Kulikovskiy, Lange-Bertalot & Witkowski, *sp. nov*. (TEM). 1 – both valves of a cell slightly shifted apart from each other; 1–4 – note slit-like poroids along the valve mantle, and external terminal raphe endings (arrows) strongly hooked to one side. Scale bar = 1 μm.

NOTES. No other established *Nupela* species except *N. thurstonensis* may be confused with the new taxon. The features of three more or less similar taxa from North America are given in Table 1 for comparison.

Nupela thurstonensis (Kaczmarska) Kulikovskiy, Lange-Bertalot & Witkowski, ***comb. nov.***

BASIONYM: *Navicula thurstonensis* Kaczmarska *in* Rushfort, Kaczmarska & Johansen 1984, Bacillaria **7**: 145–146, Figs 81–83, 107–110, 125.

Our proposal to transfer *Navicula thurstonensis* to *Nupela* is based on ultrastructural features of the raphe system and the type of areolation. The ultrastructure of areolae was discussed by Potapova *et al.* (2003), who noted that *Nupela* described from North America have areolae occluded by external hymens and that in specimens after strong cleaning processes the hymenate occlusions are dissolved. Vyverman and Compère (1991) based the generic description of *Nupela* on the presence of perforated hymenate occlusions located on the

valve interior, but they used the term 'hymen' incorrectly. As the number of *Nupela* species is still increasing, raphe ultrastructure can be pointed out as one of the crucial criteria for delimitation of the genus. In *Navicula thurstonensis*, hymenate areolae occlusions were not observed, but the raphe system is typical of species belonging in *Nupela* (cf. Vyverman & Compère 1991; Lange-Bertalot & Moser 1994; Rumrich *et al.* 2000; Potapova *et al.* 2003; Table 1). Hence we propose formal transfer of *Navicula thurstonensis* to the genus *Nupela*.

Most of the more than 40 established *Nupela* species are known from the tropics. Only a few taxa have so far been either described or recorded from the temperate climate zone (e.g., Lange-Bertalot & Metzeltin 1996; Potapova *et al.* 2003). Some of the species originally described from either low or high geographic latitudes have subsequently been found to occur also under temperate or tropical climate conditions (Rumrich *et al.* 2000). It is difficult to characterize *Nupela thurstonensis* autecologically and biogeographically, as the data originate from only one locality.

In terms of the autoecology of *Nupela matrioschka*, it is known only from subaerial habitats with low pH, for example *Sphagnum* bog, which is always characterized by exposed substrate and low pH (e.g., Johanssen 1999; Buczko 2006; Witkowski *et al.* 2006; Kulikoskiy 2007). As pointed out by Rushforth *et al.* (1984), numerous taxa identified in subaerial habitats in Hawaii are also capable of growth in similar conditions worldwide. Included in this group are *Melosira dickiei* (Thwaites) Kützing, *Adlafia bryophila* (Petersen) Lange-Bertalot and *Fallacia insociabilis* (Krasske) D. G. Mann (see also Lange-Bertalot & Metzeltin 1996; Metzeltin & Lange-Bertalot 1998, 2007). In the Polistovo-Lovatsky *Sphagnum* bog ecosystem, *Nupela matrioschka* belongs to a diatom assemblage typical for raised oligotrophic bogs consisting of, for example, *Tabellaria flocculosa* (Roth) Kützing, *Aulacoseira subarctica* (O. Müller) Haworth, *A. tenella* (Nygaard) Simonsen, *Frustulia krammeri* Lange-Bertalot & Metzeltin, *F. saxonica* Rabenhorst, *Eunotia serra* Ehrenberg, *E. meisteri* Hustedt, *Pinnularia subcapitata* var. *elongata* Krammer and *Kobayasiella parasubtilissima* (Kobayasi & Nagumo) Lange-Bertalot (Kulikovskiy 2007).

Both taxa under discussion belong to a group of small-celled forms with elliptic to elliptic-lanceolate valves, which are not difficult to distinguish within *Nupela*. They show close relationships to species like *Nupela exotica* Monnier, Lange-Bertalot & Bertrand, *Nupela neglecta* Ponader, Lowe & Potapova, *Nupela carolina* Potapova & Clason and *Nupela rumrichorum* Lange-Bertalot. These species are very well circumscribed by a complex of features including raphe ultrastructure, which shows different degrees of heterovalvy (e.g., *N. matrioschka*, *N. thurstonensis*, *N. exotica*, *N. carolina*, *N. rumrichorum*, *N. neglecta*; Table 1). The raphe system of *N. matrioschka*, *N. thurstonensis*, *N. exotica*, and *N. carolina* appears to be a criterion typical of naviculoid *Nupela* taxa. Other *Nupela* species have a raphe on only one valve (e.g., *N. rumrichorum*). In *N. matrioschka* and *N. thurstonensis*, autecology is an additional discriminating criterion. They inhabit either intermittently wet habitats (*N. thurstonensis*) or *Sphagnum* bogs (*N. matrioschka*) with low pH, whereas other *Nupela* species occur in habitats with moderately low to higher pH, ranging from 5.4 to 8.5, usually close to or exceeding 7.0 (cf. Table 1).

Achnanthes gracillima Hustedt is a rare species inhabiting oligotrophic water bodies of the Northern Hemisphere (Krammer & Lange-Bertalot 1991). The first SEM images were published by Marciniak (1986), and later by Genkal and Kharitonov (2006). Raphe ultrastructure and the areolae are typical for the genus *Nupela* (Fig. IV: 1–3 in Marciniak 1986; Figs 1: 1–5, 2: 1–8 in Genkal & Kharitonov 2006). Based on these criteria we propose the transfer of *Achnanthes gracillima* to *Nupela*. However, the specific epithet '*gracillima*' is already occupied in the genus, since *Stauroneis gracillima* Hustedt (Hustedt 1943; see also Simonsen 1987) was transferred to *Nupela* as *N. gracillima* (Hustedt) Lange-Bertalot (Lange-Bertalot 1993). Therefore, we propose a new specific epithet '*neogracillima*' to replace '*gracillima*'.

Table 1. Comparison of *Nupela thurstonensis* (Kaczmarska) Kulikovskiy, Lange-Bertalot & Witkowski, *comb. nov.* with other taxa.

Species/ Feature	*Nupela thurstonensis* comb. nov.	*Nupela matrioschka* sp. nov.	*Nupela exotica* Monnier, Lange-Bertalot & Bertrand	*Nupela neglecta* Ponader, Lowe & Potapova	*Nupela carolina* Potapova & Clason
Valve shape	elliptic to elliptic-lanceolate, often with slightly protracted ends	broad-elliptical with broad, never protracted apices	elliptical-lanceolate, ends fairly obtusely to more acutely rounded and often slightly short-protracted	lanceolate to elliptical-lanceolate with slightly protracted apices; slightly asymmetrical about apical and transapical planes	elliptical-lanceolate
Length, µm	7–13	9.7–10.3	8.6–13.3	3–15	5–15
Width, µm	3.2–4.2	4.0–6.3	3.0–4.1	2.6–4.5	2.4–4.4
Stria orientation	radiate, becoming parallel or slightly convergent near the poles	radiate, becoming parallel or slightly convergent near the poles	radiate; striae often contain only a few areolae	slightly radiate, becoming parallel or slightly convergent near the poles	radiate
Stria in 10 µm	(30)35–45	42–48	40–45	40–48	42–54
Axial area	narrow, linear	narrow, linear	narrow, linear	linear-lanceolate	narrow, linear
Central area	rather small ± round, sometimes lacking	rather small ± round, sometimes lacking	barely developed or lacking	small, round or elliptical	square or lyre-shaped, formed by interrupted central striae, often with several isolated areolae
Raphe	long in both valves	long in both valves	long in both valves	differing between valves; one valve with a long raphe, the other with distinctly shortened branches	long in both valves
Proximal raphe ends (externally)	terminate with very small punctiform central pores	terminate with very small punctiform central pores	moderately arcuate with roundish central pores	roundish central pores on long branches and without any visible central pore on short branches	terminal raphe fissure forming a curved opening to the primary side of the valve
Ecology and distribution	wet habitats on rocks, Hawaii	*Sphagnum* oligotrophic bogs (pH 3.7–5.5)	tropical fish aquarium, France	rivers and brooks of USA, pH 5.4–8.5	rivers and brooks of USA, pH 5.4–8.5
Reference	Rushfort *et al*. 1984	This study	Monnier *et al*. 2003	Potapova *et al*. 2003	Potapova *et al*. 2003

Nupela neogracillima (Hustedt) Kulikovskiy & Lange-Bertalot, ***comb. nov. & nom. nov.***

BASIONYM: *Achnanthes gracillima* Hustedt 1927, Arch. Hydrobiol. **18**: 161, Figs 5: 10–11.

With the description of a new species, and the transfer of two additional taxa, the number of species in the genus *Nupela* now exceeds 40 (e.g., Lange-Bertalot 1993; Lange-Bertalot & Moser 1994; Lange-Bertalot & Metzeltin 1996; Moser *et al.* 1998; Lange-Bertalot & Genkal 1999; Rumrich *et al.* 2000; Metzeltin & Kusber 2001; Monnier *et al.* 2003; Potapova *et al.* 2003; Metzeltin & Lange-Bertalot 1998, 2007; Antoniades *et al.* 2008).

To conclude we stress that the results of our study reported here show that further discoveries and transfers in established genera of small-celled taxa, such as *Nupela*, can be expected. This will occur through the routine use of electron microscopes in studies of the ultrastructure of small raphid diatoms.

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