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New species and combinations in the genus *Geissleria* (Bacillariophyceae)

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Abstract – Two new *Geissleria* species are described from Portugal based on their morphological and ultrastructural characteristics. *Geissleria tagensis* Novais *et* Ector sp. nov. has rhombic-elliptical valves with broadly rounded to slightly protracted apices and lacks an isolated pore. *Geissleria lusitanica* Novais *et* Ector sp. nov. has linear-elliptical to elliptical valves with slightly to markedly protracted ends and two isolated pores. The type analysis of similar species (*Geissleria acceptata* (Hustedt) Lange-Bertalot *et* Metzeltin, *G. schoenfeldii* (Hustedt) Lange-Bertalot *et* Metzeltin and *Navicula modica* Hustedt) allowed their better characterization and illustration, supporting the delimitation of the new Portuguese species. A new taxon present in the type material of *G. schoenfeldii, G. hinziae* Novais *et* Ector is also described. Three new combinations are also proposed: *Geissleria capitata* (H. Kobayasi *in* Kobayasi *et* Ando) Ector *et* Novais comb. nov., *G. modica* (Hustedt) C.E. Wetzel, Novais *et* Ector comb. nov. and *G. taishanica* (Y.Q. Guo *et* S.Q. Xie) Ector *et* Novais comb. nov. A checklist of the species and a thorough survey of the literature available on *Geissleria* are provided.

Bacillariophyta / *Geissleria* / *Navicula* / new species / Portugal / taxonomy / type material

Résumé – Deux nouvelles espèces de *Geissleria* sont décrites du Portugal sur base de leurs caractéristiques morphologiques et ultrastructurales. *Geissleria tagensis* Novais *et* Ector sp. nov. possède des valves rhombo-elliptiques avec des apex largement arrondis à légèrement protractés et sans pore isolé. *Geissleria lusitanica* Novais *et* Ector sp. nov. a des valves linéaires-elliptiques à elliptiques avec des extrémités légèrement à nettement protractées et possède deux pores isolés. L'analyse des types d'espèces semblables (*Geissleria acceptata* (Hustedt) Lange-Bertalot *et* Metzeltin, *G. schoenfeldii* (Hustedt) Lange-Bertalot *et* Metzeltin et *Navicula modica* Hustedt) a permis leur meilleure caractérisation et illustration, soutenant la délimitation des nouvelles espèces du Portugal. Un nouveau taxon présent dans le matériel type de *G. schoenfeldii*, *G. hinziae* Novais *et* Ector est également décrit. Trois nouvelles combinaisons sont aussi proposées : *Geissleria capitata* (H. Kobayasi *in* Kobayasi *et* Ando) Ector et Novais comb. nov., *Geissleria modica* (Hustedt) C.E. Wetzel, Novais *et* Ector comb. nov. et *G. taishanica* (Y.Q. Guo *et* S.Q. Xie) Ector *et* Novais comb. nov. Une liste des espèces ainsi qu'un aperçu complet de la littérature sur les *Geissleria* sont fournis.

Bacillariophyta / *Geissleria* / *Navicula* / matériel type / nouvelle espèce / Portugal / taxonomie

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INTRODUCTION

The genus *Geissleria* was erected in 1996 by Lange-Bertalot & Metzeltin to include all species from the section *Annulatae* of the genus *Navicula* (Hustedt, 1937). Its main differential characteristic is the presence of the subpolar elongated areolae forming a structure called an annulus (Lange-Bertalot & Metzeltin, 1996), usually quite discernible even using light microscopy. Despite the presence of simple external areolar openings and the lack of pores on the girdle bands, several other structures suggest that an inclusion of *Geissleria* within *Navicula s.s.* should not be considered. Several species of *Geissleria* possess an isolated pore in the central area, a feature never observed in *Navicula s.s.* Moreover, in *Navicula*, the raphe opens laterally in an internal rib. This internal rib has never been observed in *Geissleria* (Lange-Bertalot, 2001). The lack of internal hymenes, present in *Navicula s.s.* and the presence of additional small props between the pores are reminiscent of cymbelloid diatoms (E.J. Cox, pers. comm.). The exact taxonomic position of *Geissleria* species will only be clarified using advanced molecular techniques.

The genus currently comprises 71 taxa, distributed worldwide, from Europe (Lange-Bertalot & Metzeltin, 1996; Lange-Bertalot, 2001; Levkov *et al.*, 2007; Cantonati & Lange-Bertalot, 2009; Van de Vijver *et al.*, 2012), Asia (Metzeltin *et al.*, 2009, Kulikovskiy *et al.*, 2012), South America (Metzeltin & Lange-Bertalot, 1998; Rumrich *et al.*, 2000; Torgan & Oliveira, 2001; Metzeltin *et al.*, 2005), North America (Potapova & Winter, 2006) and the Maritime Antarctic and sub-Antarctic regions (Van de Vijver & Le Cohu, 2003; Zidarova *et al.*, 2009). *Geissleria* species have been found in different freshwater habitat types such as rivers, lakes, springs, waterfalls and can occur epilithically, epiphytically or in soils.

Until now, only five *Geissleria* species were reported from Portugal: *Geissleria acceptata* (Hustedt) Lange-Bertalot *et* Metzeltin, *G. declivis* (Hustedt) Lange-Bertalot, *G. decussis* (Østrup) Lange-Bertalot et Metzeltin, *G. ignota* (Krasske) Lange-Bertalot *et* Metzeltin and *G. schoenfeldii* (Hustedt) Lange-Bertalot *et* Metzeltin. From these, *G. declivis* and *G. ignota* were only cited for the Azores Archipelago; *G. acceptata* and *G. schoenfeldii* were cited for the Region Centre and *G. decussis* was cited for the Regions Alentejo, Centre and the Azores Archipelago and is the most often reported taxon (Gil, 1988; Rino & Gil, 1989; Calado, 1990; Almeida, 1998; Nunes, 2007; Gonçalves, 2008; Gonçalves *et al.*, 2010; Novais, 2011).

During a survey of benthic diatoms sampled in watercourses from mainland Portugal, two unknown *Geissleria* species were found. The presence of these species in various sites (even if always in low abundance), led us to perform a detailed analysis of their morphology using both light (LM) and scanning electron microscopy (SEM), to compare them with the type material of the morphologically similar species *Navicula acceptata* Hustedt, *N. modica* Hustedt and *N. schoenfeldii* Hustedt and to perform a thorough literature analysis. This allowed us to propose these two Portuguese *Geissleria* species as new for science.

Geissleria acceptata and *G. schoenfeldii* are among the most common *Geissleria* species. Both were originally described by Hustedt as *Navicula acceptata* in 1950 and *N. schoenfeldii* in 1930, under the section *Annulatae*. The analysis of the type material of *N. schoenfeldii* revealed the existence of two morphs, one corresponding to the original description and a second one that proved to be a new species, described and illustrated hereby. *Navicula modica* was also described by Hustedt (1945), but it was placed in the section *Minusculae.* The illustrations of *N. modica* Hustedt in Simonsen (1987) led us to hypothesise that this could also be ascribable to *Geissleria*. Therefore a thorough analysis of its type material has been performed and the results are presented in the current paper.

Furthermore, during the literature analysis, two other *Navicula* species (*Navicula taishanica* Y.Q. Guo *et* S.Q. Xie and *Navicula schoenfeldii* var. *capitata* H. Kobayasi *in* Kobayasi *et* Ando) revealed the presence of typical *Geissleria* characteristics and new combinations are proposed.

MATERIALS AND METHODS

Benthic epilithic diatoms were sampled in spring and summer 2006 and 2007 in streams and rivers from mainland Portugal, following standard methodology (AFNOR, 2003; European Committee for Standardization, 2003; INAG, 2008) and preserved with a formaldehyde solution (4% v/v) immediately after sampling.

At each sampling site, water samples from lotic zones were collected for chemical analysis, and environmental variables such as temperature (°C), pH, dissolved oxygen (mg L^{-1}), oxygen saturation (% O_2), conductivity (µS cm^{-1}) and water velocity (m s^{-1}) were measured *in situ* with portable meters calibrated in the field. Standard methods for water chemical analysis were carried out according to APHA (1995) and comprise the following parameters: total hardness (mg $CaCO_3$ L^{-1}), N-NH_4^+ (µg N-NH_4^+ L^{-1}), Cl^- (mg Cl^- L^{-1}), N-NO_3^- (µg N-NO_3^- L^{-1}), N-NO_2^- (µg N-NO_2^- L^{-1}), P-PO_4^{3-} (µg P-PO_4^{3-} L^{-1}), soluble reactive phosphorus (SRP) (µg P L^{-1}), total phosphorus (µg P L^{-1}), Na^+ (mg Na^+ L^{-1}), Ca^{2+} (mg Ca^{2+} L^{-1}), SO_4^{2-} (mg SO_4^{2-} L^{-1}) and total organic carbon TOC (mg CL^{-1}).

Details of the sampling sites where the Portuguese *Geissleria* species were found are shown in Table 1.

In addition to the material collected in Portugal, the type material of *Navicula acceptata*, *N. modica* and *N. schoenfeldii* was obtained from the Friedrich Hustedt Diatom Study Centre in the Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, Germany (BRM) (detailed information is presented in Table 2).

Both field samples and type material were treated by oxidation using hot hydrogen peroxide (35%) and dilute HCl (37%) in order to obtain a suspension of clean frustules. Permanent slides were mounted with Naphrax®. LM observations and morphometric measurements were performed using a Leica® DMRX brightfield microscope with 100 × oil immersion objective and light micrographs were taken with a Leica® DC500 camera. Samples selected for scanning electron microscopy were filtered through polycarbonate membrane filters with a pore diameter of 3 µm, mounted on stubs using double side carbon tape and sputtered with platinum (30 nm) in a Modular High Vacuum Coating System (BAL-TEC MED 020) and studied with a Hitachi SU-70, operated at 5.0 kV and 10 mm distance. Micrographs were manipulated digitally and plates containing LM and SEM pictures were mounted using Corel Draw X5®.

Morphological terminology follows Ross *et al.* (1979), Round *et al.* (1990) and Krammer & Lange-Bertalot (1991).

Based on an extensive literature review, we have collated published taxonomic information on all *Geissleria* species and summarised this within the paper (Table 3). All *Geissleria* species described until now are presented, together with their basionym, references, type locality and morphometry of the type population as mentioned in their original description. This information was also used for comparison with the new Portuguese taxa. Among the numerous publications analysed, the following were examined in detail: Hustedt (1930, 1945, 1950), Simonsen (1987), Lange-Bertalot & Metzeltin (1996), Lange-Bertalot (2001), Levkov *et al.* (2007), Cantonati & Lange-Bertalot (2009), Le Cohu *et al.* (2009), Zidarova *et al.* (2009) and Van de Vijver *et al.* (2012).

In the course of the literature review, *Navicula taishanica, N. modica* and *N. schoenfeldii* var. *capitata* showed typical *Geissleria* characteristics and new combinations are proposed hereby.

Table 1. Environmental characterization of the sampling sites where the new Portuguese *Geissleria* species have been identified

Taxon	*Geissleria tagensis* Novais et Ector			*Geissleria lusitanica* Novais et Ector				
Site	*Marachão*	*Lanheses*	*Amieira*	*Casal Rei*	*Chamusca*	*Monte das Águias*	*Tua*	*Amieira*
Watercourse	Cávado River	Lima River	Tagus River	Zêzere River	Tagus River	Divôr Stream	Tua River	Tagus River
Hydrographic basin	Cávado	Lima	Tagus	Tagus	Tagus	Tagus	Tua/Douro	Tagus
Sampling date	22/09/2007	21/09/2007	06/07/2006	26/06/2006	06/07/2006	03/07/2006	16/08/2007	06/07/2006
Latitude	41º 30' 10.187'' N	41º 43' 39.800'' N	39º 31' 20.272'' N	39º 30' 39.277'' N	39º 21' 31.311'' N	38º 52' 30.316'' N	41º 23' 12.765'' N	39º 31' 20.272'' N
Longitude	08º 43' 04.136'' W	08º 40' 14.500'' W	07º 50' 03.736'' W	08º 19' 45.662'' W	08º 29' 25.605'' W	08º 07' 13.711'' W	07º 12' 03.892'' W	07º 50' 03.736'' W
Altitude (m a.s.l.)	10	5	50	21	13	87	200	50
Catchment area (km^2)	1332.8	1690.2	116629.2	5033.9	122879.7	266.32	2989.2	116629.2
Current velocity ($m\ s^{-1}$)	0	0	0.04	0.4	0.11	0	0.73	0.04
Water temperature (°C)	20.9	21.2	18.13	16.34	28.25	28.64	24.9	18.13
Conductivity ($\mu S\ cm^{-1}$)	280	307	718	102	714	803	96.4	718
pH	6.9	6.2	7.7	7.2	7.4	7.8	7.0	7.7
OD (% sat)	72.5	93.3	76	102.8	95	114.4	92.8	76
OD ($mg\ L^{-1}$)	6.96	7.94	7.1	10.1	7.4	8.8	7.52	7.1
Total hardness ($mg\ CaCO_3\ L^{-1}$)	16	15	203	–	216	222	25	203
N-NH_4^+ (μg N-$NH_4^+\ L^{-1}$)	50	6	130	2	40	2	140	130
Cl^- ($mg\ Cl^-\ L^{-1}$)	68	85	90.8	8.4	79.9	139	12	90.8
N-NO_3^- (μg N-$NO_3^-\ L^{-1}$)	2410	3850	800	950	920	870	120	800
N-NO_2^- (μg N-$NO_2^-\ L^{-1}$)	1	2	140	20	60	10	5	140
P-PO_4^{3-} (μg P-$PO_4^{3-}\ L^{-1}$)	25	6	9	61	3	6	8	9
SRP ($\mu g\ P\ L^{-1}$)	8	2	3	20	1	2	3	3
Total phosphorus ($\mu g\ P\ L^{-1}$)	15	9	3	29	8	4	9	3
Na^+ ($mg\ Na^+\ L^{-1}$)	40.6	39.3	8.8	2.7	8.8	11.8	8.08	8.8
Ca_2^+ ($mg\ Ca^{2+}\ L^{-1}$)	4	4	63	12	57	53	6	63
SO_4^{2-} ($mg\ SO_4^{2-}\ L^{-1}$)	9.05	11.9	126.2	12.7	168.1	31.6	4.36	126.2
TOC ($mg\ CL^{-1}$)	2.85	2.09	8.92	3	–	8.8	1.82	8.92

Table 2. Type material information

	Navicula acceptata *Hustedt 1950*	***Navicula modica*** *Hustedt 1945*	***Navicula modica*** *Hustedt 1945*	***Navicula schoenfeldii*** *Hustedt 1930*
Material	Unmounted material number E6459	Unmounted material number E723	Unmounted material number E717/DIV405	Unmounted material number E6841
Collector(s)	U. Rein and W. Selle	F. Hustedt	F. Hustedt	G. Schönfeld
Type locality	diatomaceous earth, interglacial, Oberohe, Lüneburger Heath, Lower Saxony, Germany	lime mud in the northern part of Lake Ohrid, Macedonia	epiphyte on *Chara* sp. in the northern part of Lake Ohrid, Macedonia	Seewiesen b, Kaditz in Dresden, Saxony, Germany
Collection date	–	01/09/1934	01/09/1934	01/01/1922
Type	Lectotype designated by Simonsen, 1987: slide No. N14/33	Lectotype designated by Simonsen, 1987: slide No. N17/46	Paralectotype designated by Simonsen, 1987: slide No. N17/44	Lectotype designated by Simonsen, 1987: slide No. N7/50

Table 3. Compiled information on the taxa belonging to the genus *Geissleria*. Morphometric measurements are from the original protologue

Taxon	*Basionym*	*Reference*	*Type locality*	*Morphometry*	*Isolated pore*
Geissleria acceptata (Hustedt) Lange-Bertalot *et* Metzeltin 1996	*Navicula acceptata* Hustedt 1950	Hustedt, 1950; Lange-Bertalot & Metzeltin, 1996	Oberohe, Lüneburger Heide, Niedersachsen, Germany	Length 6.0-11.0 µm, width 3.0-5.0 µm, 16 striae/10 µm	One isolated pore facultatively present
Geissleria aikenensis (Patrick) Torgan *et* M.A. Oliveira 2001	*Navicula aikenensis* Patrick 1959	Patrick, 1959; Torgan & Oliveira, 2001	Savannah River, South Carolina, USA	Length 20.0-23.0 µm, width 6.0-8.0 µm, 18.0-19.0 striae/10 µm	One isolated pore at the end of the median stria on one side of the valve
Geissleria annulata (Grunow) Lange-Bertalot *et* Metzeltin 1996	*Navicula annulata* Grunow *in* Cleve et Grunow 1880	Cleve & Grunow, 1880; Lange-Bertalot & Metzeltin, 1996	Demerara River, Guyana	Length 58.0-76.0 µm, width 25.0-30.0 µm, 7 striae/10 µm	No isolated pore
Geissleria arkonensis Lange-Bertalot 2001	–	Lange-Bertalot, 2001	Arkona Basin, Baltic Sea	Length 14.0-20.0 µm, width 7.3-8.5 µm, 17-19 striae/10 µm	One isolated pore regularly present in the central nodule
Geissleria badarma Kulikovskiy, Metzeltin *et* Lange-Bertalot 2012	–	Kulikovskiy *et al*., 2012	Bolshoi Ushkaniy Island, Lake Baikal, Russia	Length 25.3-26.7 µm, width 8.0-8.7 µm, 9-10 striae/10 µm	No isolated pore
Geissleria badma Kulikovskiy, Metzeltin *et* Lange-Bertalot 2012	–	Kulikovskiy *et al*., 2012	Bolshoi Ushkaniy Island, Lake Baikal, Russia	Length 16.7-20.0 µm, width 8.0-8.6 µm, 1 5-16 striae/10 µm	No isolated pore
Geissleria boo Kulikovskiy, Metzeltin *et* Lange-Bertalot 2012		Kulikovskiy *et al*., 2012	Bolshoi Ushkaniy Island, Lake Baikal, Russia	Length 44 µm, width 11.3 µm, 8 striae/10 µm	No isolated pore
Geissleria boreosiberica Lange-Bertalot, Genkal *et* Vekhov 2001	–	Lange-Bertalot, 2001	Yugorsky-Shar-Strait, Siberia, Russia	Length 23.0-29.0 µm, width 7.5-8.5 µm, 14-16 striae/10 µm	One isolated pore present close to the central nodule
Geissleria bourbonensis Le Cohu, Ten-Hage *et* M. Coste 2009	–	Le Cohu *et al.*, 2009	Du Mât River, Reunion Island, Indian Ocean	Length 6.5-13.0 µm, width 4.0-6.0 µm, 16-18 striae/10 µm	One isolated pore more or less visible
Geissleria capitata (H. Kobayasi) Ector *et* Novais comb. nov.	*Navicula schoenfeldii* var. *capitata* H. Kobayasi *in* Kobayasi *et* Ando 1977	Kobayasi & Ando, 1977	Nishida-numa (an irrigation pond in Musashikyuryo-shinrin Park), Saitama Prefecture, Japan	Length 18.0-21.5 µm, width 6.5-7.0 µm, 14-16 striae/10 µm	No isolated pore
Geissleria craticuloides Metzeltin, Kulikovskiy *et* Lange-Bertalot 2012	–	Kulikovskiy *et al*., 2012	Lake Baikal, station no. 29, 52°71.825N, 107°71.961E, Cape Tonkij, Russia	Length 35.5-39.0 µm, width 11.6-12.0 µm, 11-13 striae/10 µm	One isolated pore close to the central nodule

Taxon	*Basionym*	*Reference*	*Type locality*	*Morphometry*	*Isolated pore*
Geissleria creolorum Le Cohu 2009	–	Le Cohu *et al.*, 2009	St Gilles ravin, Reunion Island, Indian Ocean	Length 13.0-27.0 µm, width 5.0-7.0 µm, 15-17 (18) striae/10 µm	One isolated pore more or less visible in the central nodule
Geissleria cummerowii (Kalbe) Lange-Bertalot 2001	*Navicula cummerowii* Kalbe 1973	Kalbe, 1973; Lange-Bertalot, 2001	Kummerower lake, Mecklenburg-Vorpommern, Germany	Length 8.0-17.0 µm, width 4.0-6.5 µm, 14-16 striae/10 µm	No isolated pore
Geissleria decliviformis Metzeltin, Kulikovskiy *et* Lange-Bertalot 2012	–	Kulikovskiy *et al.*, 2012	Lake Baikal, station no. 31, 52°56.464N, 107°11.893E, Cape Sukhinskij, Russia	Length 19.3-21.3 µm, width 6.1-6.5 µm, 17-20 striae/10 µm	Isolated pore lacking or not clearly discernible
Geissleria declivis (Hustedt) Lange-Bertalot 1996	*Navicula declivis* Hustedt 1934	Hustedt, 1934; Lange-Bertalot & Metzeltin, 1996	Poggenpohls Moor, Niedersachsen, Germany	Length 19.0-22.0 µm, width 6.0-7.0 µm, 16 striae/10 µm	One isolated pore near the central nodule
Geissleria decussis (Østrup) Lange-Bertalot *et* Metzeltin 1996	*Navicula decussis* Østrup 1910	Østrup, 1910; Lange-Bertalot & Metzeltin, 1996	Fiskebæk, Denmark	Length 16.0-22.0 µm, width 6.0-7.0 µm, 16-20 striae/10 µm	One isolated pore
Geissleria diversestriata (Jasnitsky) Kulikovskiy 2012	*Navicula diversestriata* Jasnitsky 1936	Jasnitsky, 1936; Kulikovskiy *et al.*, 2012	Lake Baikal, Russia	Length 5.0-64.0 µm, width 19.0-24.0 µm, 6-9 striae/10 µm	No isolated pore
Geissleria dolomitica (W. Bock) Lange-Bertalot *et* Metzeltin 1996	*Navicula dolomitica* W. Bock 1970	Bock, 1970; Lange-Bertalot & Metzeltin, 1996	Italian dolomites, Italy	Length 11.0-20.0 µm, width 4.0-5.0 µm, 16-19 striae/10 µm	No isolated pore
Geissleria dungar Kulikovskiy, Lange-Bertalot *et* Metzeltin 2012	–	Kulikovskiy *et al.*, 2012	Bolshoi Ushkaniy Island, Lake Baikal, Russia	Length 31.3-33.0 µm, width 10.0-12.0 µm, 9-12 striae/10 µm	No isolated pore
Geissleria gabrielae Van de Vijver *et* Zidarova *in* Zidarova *et al.* 2009	–	Zidarova *et al.*, 2009	South Shetland Islands, Deception Island, near Crater Lake	Length 15.3-23.8 µm, width 5.3-6.2 µm, 14-16 striae/10 µm	No isolated pore
Geissleria gereckei Cantonati *et* Lange-Bertalot 2009	–	Cantonati & Lange-Bertalot, 2009	Val Lovatel Spring, Dolomiti Bellunesi National Park, Italy	Length 11.0-16.0 µm, width 4.5-5.5 µm, 13-17 striae/10 µm	One simple isolated pore with an elongated foramen placed almost at the centre of the central nodule
Geissleria hinziae Novais *et* Ector sp. nov.	–	This study	Kaditz, Saxony, Germany	Length 11.3-15.7 µm, width 4.8-5.7 µm, 15-18 striae/10 µm	One small isolated pore is present near the central nodule

Taxon	*Basionym*	*Reference*	*Type locality*	*Morphometry*	*Isolated pore*
Geissleria hustedtii Metzeltin, Lange-Bertalot *et* García-Rodríguez 2005	–	Metzeltin *et al.*, 2005	Jurucui Lake, epiphytic, Brazil	Length 24 µm, width 9 µm, 18 striae/10 µm	One isolated pore
Geissleria ignota (Krasske) Lange-Bertalot *et* Metzeltin 1996	*Navicula ignota* Krasske 1932	Krasske, 1932; Lange-Bertalot & Metzeltin, 1996	Between Fusch and Ferleiten, Salzburg, Austria	Length 17.0-25.0 µm, width 4.5-5.0 µm, 12-14 striae/10 µm	No isolated pore
Geissleria irregularis Kulikovskiy, Lange-Bertalot *et* Metzeltin 2012	–	Kulikovskiy *et al*., 2012	Bolshoi Ushkaniy Island, Lake Baikal, Russia	Length 6.7-10.7 µm, width 4.7-4.7 µm, 16-18 striae/10 µm	No isolated pore
Geissleria kriegeri (Krasske) Lange-Bertalot 1996	*Navicula kriegeri* Krasske 1943	Krasske, 1943; Lange-Bertalot & Metzeltin, 1996	Kilpisjärvi, Lapland, Finland	Length 14.0-19.0 µm, width 6.0-7.0 µm, 16 striae/10 µm	No isolated pore
Geissleria lacusbaicalensis Kulikovskiy, Lange-Bertalot *et* Metzeltin 2012	–	Kulikovskiy *et al*., 2012	Bolshoi Ushkaniy Island, Lake Baikal, Russia	Length 22.5-28 µm, width 6.3-6.8 µm, 14-15 striae/10 µm	Isolated pore apparently lacking
Geissleria lange-bertalotii Metzeltin *in* Metzeltin *et* Witkowski 1996	–	Metzeltin & Witkowski, 1996	Tapajós River, Santarém, Pará, Brazil	Length 18.0-37.5 µm, width 9.0-11.5 µm, 16-18 striae/10 µm	One isolated pore
Geissleria lateropunctata (J.H. Wallace) Potapova *et* D.M. Winter 2006[1]	*Navicula lateropunctata* J.H. Wallace 1960	Wallace, 1960; Potapova & Winter, 2006	Upper Three Runs, Aiken County, South Carolina, USA	Length 17.0-22.0 µm, width 8.0 µm, 22-24 striae/10 µm	One isolated pore near the central nodule
Geissleria lusitanica Novais *et* Ector sp. nov.	–	This study	Tagus River at Amieira, municipality of Nisa, subregion Alto Alentejo, Portugal, 39º 31' 20.272''N, 07º 50' 03.736''W	Length 11.3-17.0 µm, width 5.0-5.9 µm, 14-15 striae/10 µm	Two isolated pores
Geissleria mafatensis Le Cohu, Ten-Hage *et* M. Coste 2009	–	Le Cohu *et al.*, 2009	Galets River, Reunion Island, Indian Ocean	Length 10.0-20.0 µm, width 4.5-5.5 µm, 16-18 (20) striae/10 µm	One isolated pore always present in the central nodule
Geissleria magna Kulikovskiy *et* Lange-Bertalot 2012	–	Kulikovskiy *et al*., 2012	Lake Baikal, station no. 25, 53°82.141N, 108°83.040E, Cape Orlovyj, Russia	Length 42.7-65.3 µm, width 18-22 µm, 6-7 striae/10 µm	One isolated pore is present unilaterally in prolongation of the median stria
Geissleria mascarenicensis Le Cohu, Ten-Hage *et* M. Coste 2009	–	Le Cohu *et al.*, 2009	Bras de Ste Suzanne stream, Reunion Island, Indian Ocean	Length 12.0-24.0 µm, width 5.0-6.0 µm, 16-17 (18) striae/10 µm	One isolated pore always present in the central nodule

Taxon	*Basionym*	*Reference*	*Type locality*	*Morphometry*	*Isolated pore*
Geissleria matrioschka Kulikovskiy, Metzeltin *et* Lange-Bertalot 2012	–	Kulikovskiy *et al*., 2012	Bolshoi Ushkaniy Island, Lake Baikal, Russia	Length 11.6-12.7 µm, width 4.5-4.7 µm, 15-17 striae/10 µm	One isolated pore clearly visible in close to central nodule
Geissleria merinensis Metzeltin, Lange-Bertalot *et* García-Rodríguez 2005	–	Metzeltin *et al.*, 2005	Merín Lagoon, Uruguay	Length 28.0-41.0 µm, width 14.0-17.0 µm, 13-15 striae/10 µm	One isolated pore present near the central nodule
Geissleria meyeri (Jasnitsky) Kulikovskiy, Metzeltin *et* Lange-Bertalot 2012	*Navicula meyeri* Jasnitsky 1936	Jasnitsky, 1936; Kulikovskiy *et al*., 2012	Chivyrkuysky Gulf, Lake Baikal, Russia	Length 22.0-37.0 µm, width 8.0-12.0 µm, 7-11 striae/10 µm	No isolated pore
Geissleria mirabilis (Krasske) Metzeltin *et* Lange-Bertalot 1998	*Stauroneis mirabilis* Krasske 1951	Krasske, 1951; Metzeltin & Lange-Bertalot, 1998	S. Francisco River, Jatobá, Brazil	Length 35.0-44.0 µm, width 9.0 µm, 16 striae/10 µm	One isolated pore present near the central nodule
Geissleria modica (Hustedt) C.E. Wetzel, Novais *et* Ector comb. nov.	*Navicula modica* Hustedt 1945	Hustedt, 1945	Ohrid Lake, Macedonia	Length 10.0-13.0 µm, width 5.0-6.0 µm, ca. 18 striae/10 µm	One small isolated pore, sometimes difficult to discern in LM
Geissleria mongolica Metzeltin, Lange-Bertalot *et* Nergui 2009	–	Metzeltin *et al.*, 2009	Ynegtiin River, Khentii Aimag, Mongolia	Length 19.0-20.0 µm, width 7.0 µm, 14-15 striae/10 µm	No isolated pore
Geissleria moseri Metzeltin, Witkowski *et* Lange-Bertalot *in* Lange-Bertalot *et* Metzeltin 1996	–	Lange-Bertalot & Metzeltin, 1996	Skutilen, Bear Island, Svalbard, Norway	Length 22.0-25.0 µm, width 7.0-8.0 µm, 15-17 striae/10 µm	No isolated pore
Geissleria nanobadma Kulikovskiy, Metzeltin *et* Lange-Bertalot 2012	–	Kulikovskiy *et al*., 2012	Bolshoi Ushkaniy Island, Lake Baikal, Russia	Length 12.0-16.7 µm, width 5.3-6.0 µm, 14-17 striae/10 µm	No isolated pore
Geissleria neosubtropica Metzeltin, Lange-Bertalot *et* García-Rodríguez 2005	–	Metzeltin *et al.*, 2005	Merín Lagoon, Uruguay	Length 21.0-28.0 µm, width 8.6-10.6 µm, 16-18 striae/10 µm	One isolated pore present near the central nodule
Geissleria neotropica Metzeltin *et* Lange-Bertalot 1998	–	Metzeltin & Lange-Bertalot, 1998	Tapajós River, Santarém, Brasilia, Brazil	Length 13.5-27.0 µm, width 6.0-9.0 µm, 18.5-21 striae/10 µm	One isolated pore near the central nodule
Geissleria ochigma Metzeltin, Kulikovskiy *et* Lange-Bertalot 2012	–	Kulikovskiy *et al*., 2012	Lake Baikal, station no. 30, 52°69.778N, 107°52.637E, between Cape Baklanij and Cape Tolstyi, Russia	Length 23.0-46.0 µm, width 9.0-11.3 µm, 12-14 striae/10 µm	No isolated pore

Taxon	*Basionym*	*Reference*	*Type locality*	*Morphometry*	*Isolated pore*
Geissleria ohridana Levkov *in* Levkov *et al.* 2007	–	Levkov *et al.*, 2007	Lake Ohrid, near St. Naum springs, Macedonia	Length 10.0-15.0 µm, width 5.0-6.0 µm, 16-20 striae/10 µm	One isolated pore near the central nodule
Geissleria ovisimilis Kulikovskiy, Lange-Bertalot *et* Metzeltin 2012	–	Kulikovskiy *et al.*, 2012	Bolshoi Ushkaniy Island, Lake Baikal, Russia	Length 10.7-18.7 µm, width 4.7-6.0 µm, 10-11 striae/10 µm	One isolated pore
Geissleria paludosa (Hustedt) Lange-Bertalot *et* Metzeltin 1996	*Navicula lagerstedtii* var. *palustris* Hustedt 1934	Hustedt, 1934; Lange-Bertalot & Metzeltin, 1996	Poggenpohls Moor, Doetlingen, Niedersachsen, Germany	Length 16.0-20.0 µm, width 5.0-6.0 µm, 15 striae/10 µm	One isolated pore near the central nodule is usually present
Geissleria paucistriata Kulikovskiy, Lange-Bertalot *et* Metzeltin 2012	–	Kulikovskiy *et al.*, 2012	Bolshoi Ushkaniy Island, Lake Baikal, Russia	Length 20.0-27.0 µm, width 4.7-5.0 µm, 8-10 striae/10 µm	Isolated pore is not clearly to discern from the median stria or is lacking
Geissleria perelegans (Hustedt) Metzeltin *et* Lange-Bertalot 1998	*Navicula perelegans* Hustedt 1952	Hustedt, 1952; Metzeltin & Lange-Bertalot, 1998	Cachoeira Flechal, Cupari River, Brazil	Length 34.0 µm, width 14.0 µm, 15 striae/10 µm	One isolated pore
Geissleria pseudobadma Kulikovskiy, Metzeltin *et* Lange-Bertalot 2012	–	Kulikovskiy *et al.*, 2012	Bolshoi Ushkaniy Island, Lake Baikal, Russia	Length 24.7-39.0 µm, width 8.7-9.3 µm, 13-14 striae/10 µm	No isolated pore
Geissleria pseudoshanaga Kulikovskiy, Lange-Bertalot *et* Metzeltin 2012	–	Kulikovskiy *et al.*, 2012	Bolshoi Ushkaniy Island, Lake Baikal, Russia	Length 21.5-30.0 µm, width 5.6-7.0 µm, 15-17 striae/10 µm	No isolated pore
Geissleria pseudozula Metzeltin, Kulikovskiy *et* Lange-Bertalot 2012	–	Kulikovskiy *et al.*, 2012	Lake Baikal, station no. 25, 53°82.141N, 108°83.040E, Cape Orlovyj, Russia	Length 43.3-51.3 µm, width 15.3-16.7 µm, 8 striae/10 µm	Isolated pore close to the central nodule unilaterally
Geissleria pumila Kulikovskiy, Lange-Bertalot *et* Metzeltin 2012	–	Kulikovskiy *et al.*, 2012	Bolshoi Ushkaniy Island, Lake Baikal, Russia	Length 8.0-10.0 µm, width 4.0-4.2 µm, 15-16 striae/10 µm	No isolated pore
Geissleria pumilolinearis Kulikovskiy, Lange-Bertalot *et* Metzeltin 2012	–	Kulikovskiy *et al.*, 2012	Bolshoi Ushkaniy Island, Lake Baikal, Russia	Length 9.3-11.0 µm, width 3.5-3.9 µm, 16-17 striae/10 µm	Isolated pore absent or difficult to discern
Geissleria punctifera (Hustedt) Metzeltin, Lange-Bertalot *et* García-Rodríguez 2005[2]	*Navicula punctifera* Hustedt 1952	Hustedt, 1952; Metzeltin *et al.*, 2005	Cachoeira Flechal, Cupari River, Brazil	Length 15.0-23.0 µm, width 6.0-9.0 µm, 16-18 striae/10 µm	One isolated pore

Taxon	*Basionym*	*Reference*	*Type locality*	*Morphometry*	*Isolated pore*
Geissleria rostrata (Jasnitsky) Kulikovskiy, Metzeltin *et* Lange-Bertalot 2012	*Navicula meyeri* var. *rostrata* Jasnitsky 1936	Jasnitsky, 1936; Kulikovskiy *et al*., 2012	Chivyrkuysky Gulf, Fertik Bay, Lake Baikal, Russia	–	No isolated pore
Geissleria scaniae Van de Vijver, Ector *et* Jarlman 2012	–	Van de Vijver *et al.*, 2012	Verkeån, Skåne, southern Sweden	Length 10.0-15.0 µm, width 3.0-4.0 µm, 15-18 striae/10 µm	One isolated pore very close to the central nodule
Geissleria schmidiae Lange-Bertalot *et* Rumrich 2000[3]	–	Rumrich *et al.*, 2000	Gala River, Ecuador	Length 16.0-28.0 µm, width 6.0-7.0 µm, 14-16 striae/10 µm	One isolated pore present in the central nodule and usually 4 isolated poreta in a square position in the central area
Geissleria schoenfeldii (Hustedt) Lange-Bertalot *et* Metzeltin 1996	*Navicula schoenfeldii* Hustedt 1930	Hustedt, 1930; Lange-Bertalot & Metzeltin, 1996	Kaditz, Saxony, Germany	Length 12.0-25.0 µm, width 6.0-8.0 µm, 12-14 striae/10 µm	No isolated pore
Geissleria schoenfeldii var. *tahitiensis* (M. Coste *et* Ricard) Lange-Bertalot 1996	*Navicula ignota* var. *tahitiensis* M. Coste *et* Ricard 1990	Coste & Ricard, 1990; Lange-Bertalot & Metzeltin, 1996	Moorea and Tipaerui Islands, French Polynesia	Length 16.5-20.0 µm, width 5-5.8 µm, 12-13 striae/10 µm	No isolated pore
Geissleria seseg Kulikovskiy, Lange-Bertalot *et* Metzeltin 2012	–	Kulikovskiy *et al*., 2012	Bolshoi Ushkaniy Island, Lake Baikal, Russia	Length 12.7-15.3 µm, width 4.0-4.7 µm, 16-18 striae/10 µm	Isolated pore absent or difficult to discern
Geissleria shanaga Kulikovskiy, Metzeltin *et* Lange-Bertalot 2012	–	Kulikovskiy *et al*., 2012	Bolshoi Ushkaniy Island, Lake Baikal, Russia	Length 20.0-29.0 µm, width 5.8-7.0 µm, 16-18 striae/10 µm	No isolated pore
Geissleria similis (Krasske) Lange-Bertalot *et* Metzeltin 1996	*Navicula similis* Krasske 1929	Krasske, 1929; Lange-Bertalot & Metzeltin, 1996	Königswartha, Saxony, Germany	Length 14.0-18.0 µm, width 6.0-7.0 µm, 16 striae/10 µm	One isolated pore more or less visible in the central nodule
Geissleria skvorzowii Kulikovskiy, Metzeltin *et* Lange-Bertalot 2012	–	Kulikovskiy *et al*., 2012	Bolshoi Ushkaniy Island, Lake Baikal, Russia	Length 22.7-27.3 µm, width 4.7-5.0 µm, 10-12 striae/10 µm	One isolated pore present near the central nodule consistently
Geissleria subantarctica Van de Vijver *et* Le Cohu 2003	–	Van de Vijver & Le Cohu, 2003	Vallée des Branloires, Ile de la Possession, Crozet Archipelago	Length 18-23 µm, width 6.0-7.0 µm, 16-18 striae/10 µm	No isolated pore
Geissleria subdecussis (Hustedt) Lange-Bertalot 2001	*Navicula subdecussis* Hustedt 1942	Hustedt, 1942; Lange-Bertalot, 2001	Luzon, Philippine Islands	Length 22.0-27.0 µm, width 7.0-8.0 µm, 18 striae/10 µm	One isolated pore

Taxon	*Basionym*	*Reference*	*Type locality*	*Morphometry*	*Isolated pore*
Geissleria submagna Metzeltin, Kulikovskiy *et* Lange-Bertalot 2012	–	Kulikovskiy *et al*., 2012	Lake Baikal, station no. 29, 52°71.825N, 107°71.961E, Cape Tonkij, Russia	Length 28.0-53.0 µm, width 13.0-18.6 µm, 7-10 striae/10 µm	One isolated pore is present unilaterally in prolongation of the median stria
Geissleria taafiana Van de Vijver *et* Le Cohu 2003	–	Van de Vijver & Le Cohu, 2003	Vallée des Branloires, Ile de la Possession, Crozet Archipelago	Length 21.0-40.0 µm, width 5.5-7.5 µm, 16-17 striae/10 µm	No isolated pore
Geissleria tagensis Novais *et* Ector sp. nov.	–	This study	Tagus River at Amieira, municipality of Nisa, subregion Alto Alentejo, Portugal, 39º 31' 20.272''N, 07º 50' 03.736''W	Length 7.7-14.9 µm, width 4.3-5.5 µm, 15-18 striae/10 µm	No isolated pore
Geissleria taishanica (Y.Q. Guo *et* S.Q. Xie) Ector *et* Novais comb. nov.	*Navicula taishanica* Y.Q. Guo *et* S.Q. Xie 1994	Guo & Xie, 1994	Taishan of Shandong, China	Length 12.7-15.3 µm, width 4.5-6.4 µm, 12 striae/10 µm in the centre and 20 striae/ 10 µm in the poles	One isolated pore
Geissleria tectissima (Lange-Bertalot) Lange-Bertalot 1996	*Navicula tectissima* Lange-Bertalot *in* Lange-Bertalot *et al.* 1996	Lange-Bertalot *et al*., 1996	Rügen Island, Baltic seacoast, Germany	Length 37.0 µm, width 14.0 µm, 10 striae/ 10 µm in the centre to ca. 14 striae/10 µm in the poles	One isolated pore
Geissleria thingvallae (Østrup) Metzeltin *et* Lange-Bertalot 1996	*Navicula thingvallae* Østrup 1918	Østrup, 1918; Lange-Bertalot & Metzeltin, 1996	Thingvallatn Lake, Iceland	Length 25.0 µm, width 7.2 µm, 16 striae/10 µm	One isolated pore present near to the middle of the central nodule
Geissleria tumefacta Metzeltin, Kulikovskiy *et* Lange-Bertalot 2012	–	Kulikovskiy *et al*., 2012	Lake Baikal, station no. 24, 53°94.222N, 109°33.9411E, near mouth of Kedrovaya, Russia	Length 13.3-17.5 µm, width 6.3-7.3 µm, 17-19 striae/10 µm	Isolated pore absent or difficult to discern
Geissleria zula Metzeltin, Kulikovskiy *et* Lange-Bertalot 2012	–	Kulikovskiy *et al*., 2012	Lake Baikal, station no. 25, 53°82.141N, 108°83.040E, Cape Orlovyj, Russia	Length 25.0-40.7 µm, width 9.5-14.7 µm, 11-13 striae/10 µm	One isolated pore close to the central nodule consistently present

1. *Geissleria lateropunctata* (J.H. Wallace) Potapova *et* D.M. Winter is considered as synonym of *G. neotropica* Metzeltin *et* Lange-Bertalot 1998, according to Potapova & Winter (2006).
2. *Geissleria punctifera* (Hustedt) Metzeltin, Lange-Bertalot *et* García-Rodríguez is considered as synonym of *G. aikenensis* (Patrick) Torgan *et* M.A. Oliveira and maybe of *G. schmidiae* Lange-Bertalot *et* Rumrich, according to Metzeltin *et al.* (2005).
3. *Geissleria schmidiae* Lange-Bertalot *et* Rumrich is considered as synonym of *G. aikenensis* (Patrick) Torgan *et* M.A. Oliveira, according to Torgan & Oliveira (2001).

RESULTS AND DISCUSSION

Type material analyses and new combinations

LM illustrations of the type materials of *Navicula acceptata*, *N. modica* and *N. schoenfeldii* are shown in Figures 1-53 and the morphometric features are summarized in Table 4.

Geissleria schoenfeldii (Hustedt) Lange-Bertalot *et* Metzeltin 1996 Figs 1-17, 80-83

Hustedt (1930) originally described *Geissleria schoenfeldii* as *Navicula schoenfeldii*. The species is characterized in the protologue as having elliptical to elliptic-lanceolate valves with broadly rounded, almost truncated, non-protracted apices. Valves are 12-25 µm long and 6-8 µm wide. The axial area is narrow and the central area moderately large, transversally enlarged. Transapical striae are robust, radiate throughout, 12-14/10 µm, and alternately short and long at the middle of the valve.

This taxon has been reported and illustrated by several authors, such as Stoermer & Kreis (1978), Lange-Bertalot & Metzeltin (1996, pl. 123, figs 5, 6: SEM, pl. 124, figs 1-4: SEM), Potapova & Charles (2007), Antoniades *et al.* (2008, pl. 50, figs 15-18: LM, pl. 116, figs 1-3: SEM), Coste *et al.* (2009) and Hofmann *et al.* (2011, pl. 51, figs 35-39: LM). Nevertheless, its type material was only illustrated by Simonsen (1987, pl. 133, figs 7-12: LM).

Two different morphs are present in the type material of *Navicula schoenfeldii* (Figs 1-17 and 19-27). However, the original description and drawings (Fig. 18) (Hustedt, 1930) correspond only to the morph illustrated in Figures 1-17 (the second morph, illustrated in Figs 19-27, is smaller and narrower, 11.3-15.7 µm long and 4.8-5.7 µm wide). This is in accordance with the comments by Lange-Bertalot (2001), who excluded the fig. 7 in plate 133 of Simonsen (1987) from the lectotype specimens due to narrower valves. Therefore, only specimens illustrated in Figs 1-17 were considered for the present definition of the taxon.

Our type material analysis revealed a smaller range of valve dimensions than the protologue (11.3-18.3 µm long and 6.3-6.7 µm wide). The central area is variable, ranging from moderately large (as mentioned in the original description) to small (e.g. Fig. 7), resulting from irregularly shorter or longer striae. An isolated pore is always absent, contrarily to the SEM illustration of Lange-Bertalot & Metzeltin (1996, plate 123, fig. 5) where an isolated pore is clearly visible near the central nodule. Striae are uniseriate and radiate throughout the entire valve. Areolae externally present as short slits (ca. 70 in 10 µm) (Figs 80, 82). The raphe is filiform and almost straight. External proximal endings are slightly expanded, bent in the same direction to the distal ends (Fig. 80). Internally, the raphe endings are simple, terminating proximally on a raised central nodule (Figs 81, 83). The central nodule is formed by two masses of siliceous material, but is lacking slit-like grooves characteristic for *G. decussis* (Lange-Bertalot, 2001). The distal ends are hooked externally (Fig. 80) and internally slightly deflected onto small helictoglossae (Fig. 81). One to three apically elongated subpolar areolae with warty outgrowths are present per stria in two striae near the raphe (Figs 80, 81). Internally no hymenes or occlusions have been observed on the areolae (Fig. 83).

Further literature analysis revealed that the second morph (Figs 19-27) was a species not yet described in the literature and we describe it hereby.

Table 4. Morphological features of the studied taxa

	Geissleria acceptata (Hustedt) Lange-Bertalot *et* Metzeltin	*Geissleria modica* (Hustedt) C.E. Wetzel, Novais *et* Ector	*Geissleria* sp.	*Geissleria schoenfeldii* (Hustedt) Lange-Bertalot *et* Metzeltin	*Geissleria hinziae* Novais *et* Ector	*Geissleria lusitanica* Novais *et* Ector	*Geissleria tagensis* Novais *et* Ector
	Type material (this study)	Type material (this study)	Type material of *N. modica* (this study)	Type material (this study)	Type material of *G. schoenfeldii* (this study)	This study	This study
Length (µm)	7.2-10.0	9.7-12.5	7.2-10.1	11.3-18.3	11.3-15.7	11.3-17.0	7.7-14.9
Width (µm)	3.7-4.0	5.3-5.4	4.2-5.0	6.3-6.7	4.8-5.7	5.0-5.9	4.3-5.5
Valve shape	Rhombic-elliptical	Elliptical	Elliptical	Elliptical to elliptical-lanceolate	Linear-elliptical to elliptical	Linear-elliptical to elliptical	Rhombic-elliptical
Central area	Small	Small	Variable, expanded due to irregularly shorter or longer striae	Variable, expanded due to irregularly shorter or longer striae	Variable, expanded due to irregularly shorter or longer striae	Small, sometimes expanded due to 1 or 2 shorter striae	Variable, expanded due to irregularly shorter or longer striae
Isolated pore	One isolated pore facultatively present	One isolated pore of small dimensions, sometimes difficult to discern in LM	Absent	Absent	One isolated small pore (sometimes difficult to discern in LM)	Two isolated pores	Absent
Striation pattern	Radiate, becoming less radiate to almost parallel near the centre	Radiate	Radiate to almost parallel in the centre	Strongly radiate	Radiate throughout	Slightly radiate, almost parallel in the centre	Radiate
Number of striae/10 µm	16-18	18-20	18	13-14	15-18	14-15	15-18
Subpolar areolae	2	–	2-3	2	2-3	2-3	2

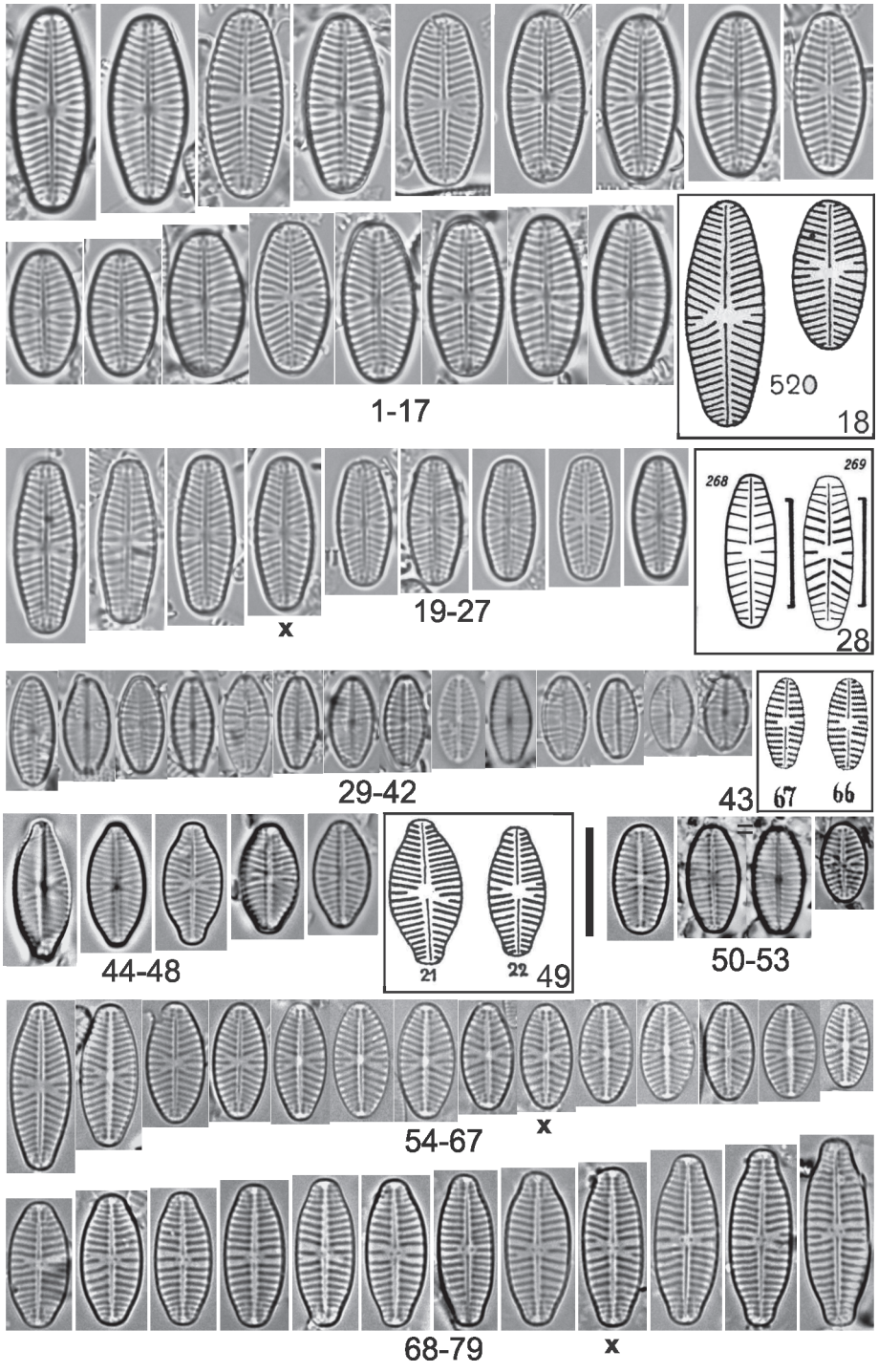
***Geissleria acceptata* (Hustedt) Lange-Bertalot *et* Metzeltin 1996 Figs 29-42, 84-89**

This species was originally described by Hustedt (1950) as *Navicula acceptata* and characterized as having linear-elliptical valves, 6.0-11.0 µm long and 3.0-5.0 µm wide, with broad, rounded, usually blunt and slightly protracted apices. The raphe is straight, filiform, the axial area is narrow, linear and the central area is small. The transapical striae are radiate, becoming less radiate to almost parallel near the valve centre, ca. 16/10 µm, denser near the apices.

The taxon has been reported and illustrated by several authors, such as Stoermer & Kreis (1978), Krammer & Lange-Bertalot (1986, pl. 64, figs 22-24: LM, fig. 25: SEM), Metzeltin & Witkowski (1996), Lange-Bertalot (2001, pl. 97, figs 1-12: LM), Werum & Lange-Bertalot (2004), Potapova & Charles (2007), Coste *et al.* (2009), Metzeltin *et al.* (2009, pl. 62, figs 27, 28: LM), Dorigo *et al.* (2010), Zimmermann *et al.* (2010, pl. 46, fig. 5: LM), Hofmann *et al.* (2011, pl. 51, figs 52-56: LM) and Żelazna-Wieczorek (2011, pl. 74, figs 11-14: LM, figs 18, 19: SEM). Nevertheless, its type material was only illustrated by Krammer & Lange-Bertalot (1986, pl. 64, figs 22-25; with fig. 25 a SEM micrograph illustrating the elongated areolae), Simonsen (1987, pl. 543, figs 12-16: LM) and Lange-Bertalot (2001, pl. 97, figs 1, 2: LM). There is therefore only one SEM micrograph of the taxon, and that only shows the valve apices.

Analysis of the type material revealed a smaller range of valve dimensions than the protologue. The striae are uniseriate and radiate, becoming less radiate to almost parallel near the valve centre, 15-18/10 µm. Areolae externally present as short slits (ca. 80 in 10 µm) (Figs 84, 88). The raphe is filiform and almost straight. External proximal endings are slightly expanded, bent in the opposite direction to the distal ends (Fig. 84). Internally, the raphe endings are simple, terminating proximally on a raised central nodule (Fig. 89). The central nodule is formed by two masses of siliceous material, but is lacking slit-like grooves characteristic for *G. decussis* (Lange-Bertalot, 2001). The distal ends are hooked externally (Fig. 84) and internally slightly deflected onto small helictoglossae (Fig. 85). One to two apically elongated subpolar areolae, with warty outgrowths per stria are present in two striae near the raphe (Figs 84, 85). Warty outgrowths are visible along the long sides of the subpolar areolae and between some other areolae on the rest of the valve (Figs 85, 89), even if the material is corroded.

In the fossil type material of *G. acceptata* one isolated pore can be present or not, as can be seen in LM (Figs 31, 37) and SEM micrographs (Figs 85, 86, 87) where an isolated pore is visible, while it is not discernible in the other LM micrographs and its absence is confirmed by SEM (Figs 84, 88, 89). Also the type material micrographs provided by Lange-Bertalot (2001) show that this feature is not constant (in pl. 97, fig. 1 shows an isolated pore while it is absent in fig. 2), even if the original drawing in Hustedt (1950) shows the absence of an isolated pore (as can be seen in Fig. 43). Until now, to our knowledge, this is the only *Geissleria* species that can have or not an isolated pore. Indeed, this fact raised the hypothesis that two different species were present in the same sample; nevertheless, the absence of other differential characters did not allow us to prove this hypothesis. Consequently originates the question whether the presence/absence and number of isolated pores are a good character to distinguish *Geissleria* species. Nevertheless, our observations revealed the constancy of this character in all other analyzed species, as can be seen by the LM and SEM micrographs presented and by the literature analysis (Table 3). Even when sometimes an isolated pore is difficult to discern in LM, it is due to its small size or position near the central nodule and SEM micrographs prove its presence, as is the case of *G. hinziae* here described.


1-17
520
18
x
19-27
268
269
28
29-42
43
67
66
44-48
21
22
49
50-53
54-67
x
68-79
x

Geissleria capitata* (H. Kobayasi *in* Kobayasi *et* Ando) Ector *et* Novais comb. nov. *et stat. nov.

Basionym: *Navicula schoenfeldii* var. *capitata* H. Kobayasi *in* Kobayasi *et* Ando 1977, *Bulletin of Tokyo Gakugei University ser. IV Mathematics and Natural Sciences* 29, p. 241, pl. 5, figs 40-43

Navicula schoenfeldii var. *capitata* was validly described by Kobayasi in Kobayasi & Ando (1977) from Nishida-numa (an irrigation pond in Musashikyuryo-shinrin Park), Saitama Prefecture, Japan. It is characterized by linear-lanceolate valves, 18-21.5 µm long and 6.5-7 µm wide, with broadly rostrate capitate apices. The axial area is narrow and the central area rectangular. The raphe is straight and thread-like, with terminal fissures curved in the same direction. The transapical striae are radiate, 14-16/10 µm in the middle of the valve, parallel towards the apices, up to 18-22/10 µm; the two terminal striae on both sides of the terminal fissures are divided into two parts. Kobayasi & Ando (1977) distinguished it from the nominate variety by its rostrate capitate ends.

The LM illustrations in the original publication (Kobayasi & Ando, 1977) (Figs 40-43) and specially the drawing in Fig. 41, clearly show the typical subpolar areolae characteristic of *Geissleria*. Furthermore, Kobayasi described it as a variety of *Navicula schoenfeldii*, a taxon already transferred to *Geissleria* by Lange-Bertalot & Metzeltin (1996). We raise it to species level based on the rostrate capitate ends, which are not present in *Geissleria schoenfeldii* (Figs 1-17).

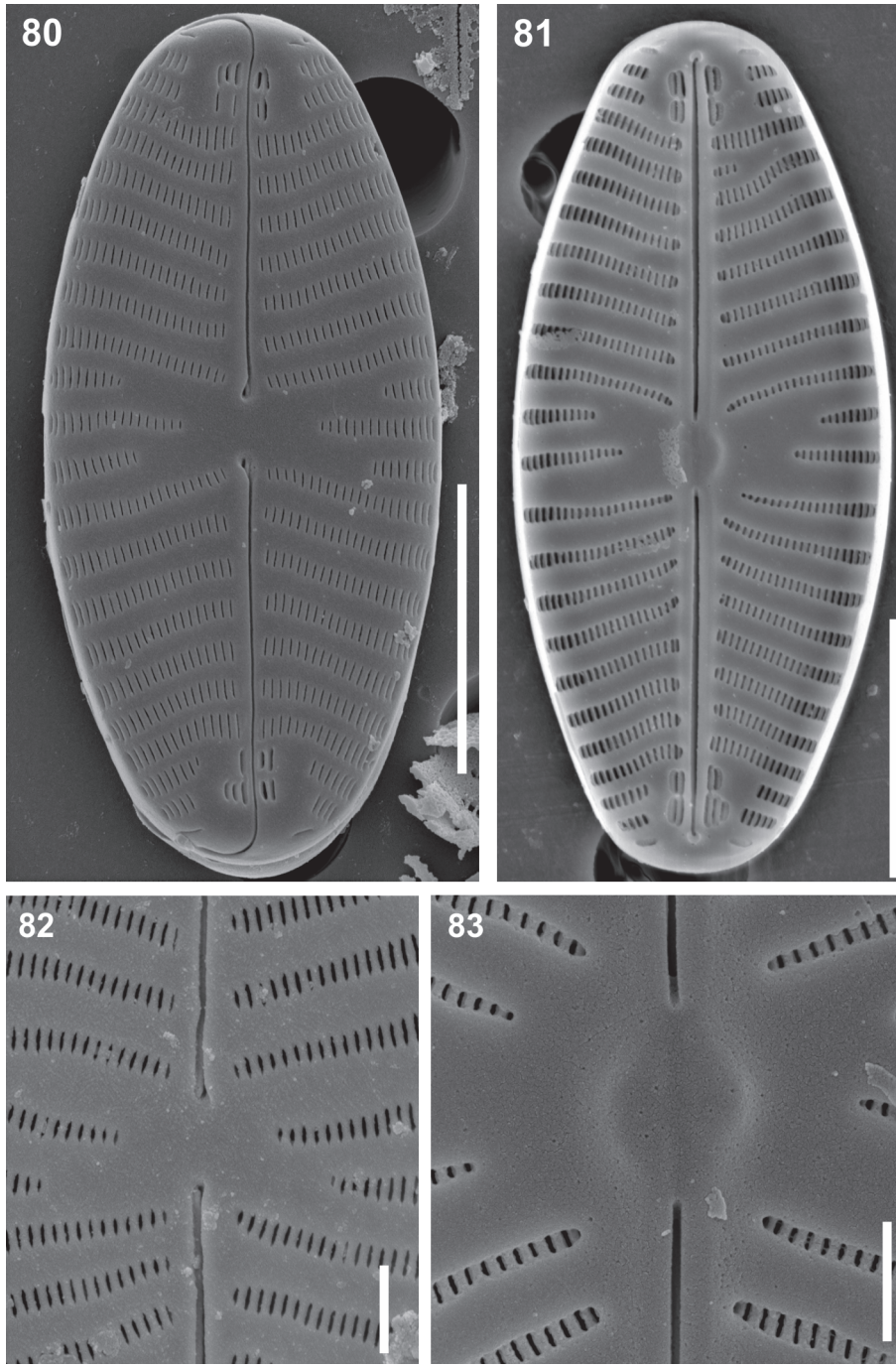
***Geissleria modica* (Hustedt) C.E. Wetzel, Novais *et* Ector comb. nov. Figs 44-48**

Basionym: *Navicula modica* Hustedt 1945, *Archiv fur Hydrobiologie* 40 (4), p. 916, pl. 41, figs 21-23
Synonym: *Geissleria ohridana* Levkov *in* Levkov *et al.* 2007, *Iconographia Diatomologica* 16, p. 59, pl. 88, figs 1-15

Navicula modica was described by Hustedt (1945) from Lake Ohrid and is originally characterized as having elliptical valves, a valve length of 10.0-13.0 µm long and a valve width of 5.0-6.0 µm, with short and widely protracted, smoothly rounded apices. The raphe is straight and filiform. The axial area is linear and narrow, widening in the middle of the valve to form a small, irregularly expanded transversally central area. The transapical striae are radiate throughout, ca. 18/10 µm, alternately short and long at the middle of the valve.

Since no valves of this taxon could be found in the unmounted material designated as lectotype (E723), the paralectotype sample (E717/DIV405) was used to illustrate the species. In this sample, two different morphs were illustrated using light microscopy (Figs 44-48 and 50-53). These two morphs are also illustrated by Simonsen (1987), where pl. 507, fig. 19 represents the second morph. The drawings in the original publication (Hustedt, 1945, pl. 43, figs 21-23,

◀ Figs 1-79. Original drawings of the type materials and LM micrographs of the type materials and the new *Geissleria* species. **1-17.** *Geissleria schoenfeldii*, LM micrographs of the type material. **18.** Original drawing of *G. schoenfeldii* in Hustedt (1930, fig. 520). **19-27.** *G. hinziae*, the Fig. 22 represents the iconotype. **28.** Original drawing of *G. cummerowii* in Kalbe (1973, figs 268, 269). **29-42.** *G. acceptata*, LM micrographs of the type material. **43.** Original drawing of *G. acceptata* in Hustedt (1950, figs 66, 67). **44-48.** *G. modica*, LM micrographs of the type material. **49.** Original drawing of *G. modica* in Hustedt (1945, figs 21, 22). **50-53.** *Geissleria* sp. in the type material of *G. modica*. **54-67.** *G. tagensis*, type population, Fig. 62 represents the iconotype. **68-79.** *G. lusitanica*, type population. Fig. 76 represents the iconotype. Scale bars = 10 µm.



Figs 80-83. SEM micrographs of the type material of *Geissleria schoenfeldii*. **80.** External valve view. **81.** Internal valve view. **82.** Detail of the central area in external view, the absence of an isolated pore can be noticed. **83.** Detail of the central area in internal view, the absence of an isolated pore can be noticed. Scale bars = 5 µm in Figs 80 & 81 and 1 µm in Figs 82 & 83.

presented in Fig. 49) correspond to the first morph only, based on valve shape. The analysis of the type material of this taxon revealed the presence of the annulus, the most characteristic feature of this genus. Therefore a new combination is proposed. The second morph (Figs 50-53) is similar to our new species *Geissleria tagensis* in valve outline and dimensions. However, the strongly radiate striae in the central area of *G. tagensis* differ from the undescribed Hustedt morph from Lake Ohrid, which also clearly belongs to *Geissleria* (see SEM Fig. 90).

Our literature review revealed that a species with identical morphology and morphometry as *Navicula modica* had been described by Levkov (Levkov *et al*., 2007) from Lake Ohrid, as *Geissleria ohridana*. According to Levkov *et al*. (2007), the latter is 10.0-15.0 µm long, 5.0-6.0 µm wide and has 16-20 striae/10 µm, corresponding well to the above description of *G. modica*. Therefore, *G. ohridana* should be synonymised with *G. modica*, since the latter was described first, following the Article 11 of the International Code of Nomenclature for algae, fungi, and plants (McNeill *et al.*, 2011).

Geissleria taishanica (Y.Q. Guo *et* S.Q. Xie) Ector *et* Novais comb. nov.

Basionym: *Navicula taishanica* Y.Q. Guo *et* S.Q. Xie 1994, *Acta Phytotaxonomica Sinica* 32 (3), p. 271, pl. 1, figs 1-5

Navicula taishanica was described by Guo & Xie (1994) from Taishan of Shandong (China) and is characterized by linear to linear-lanceolate valves, 12.7-15.3 µm long, 4.5-6.4 µm wide, the apices are narrowly rostrate and slightly capitate, the axial area is narrow and the central area rectangular. The raphe is straight, filiform, presenting hooked distal ends; the transapical striae are radiate, 12/10 µm in the middle of the valve, slightly parallel at the apices, 20/10 µm; one isolated pore is present near the central nodule.

The SEM figures in the original publication (Guo & Xie, 1994) clearly illustrate the typical characteristics of *Geissleria*, especially the presence of the apically elongated subpolar areolae with warty outgrowths on each side. There are similar outgrowths across the centre of the other areolae. We therefore propose the new combination *Geissleria taishanica*.

Description of the new species

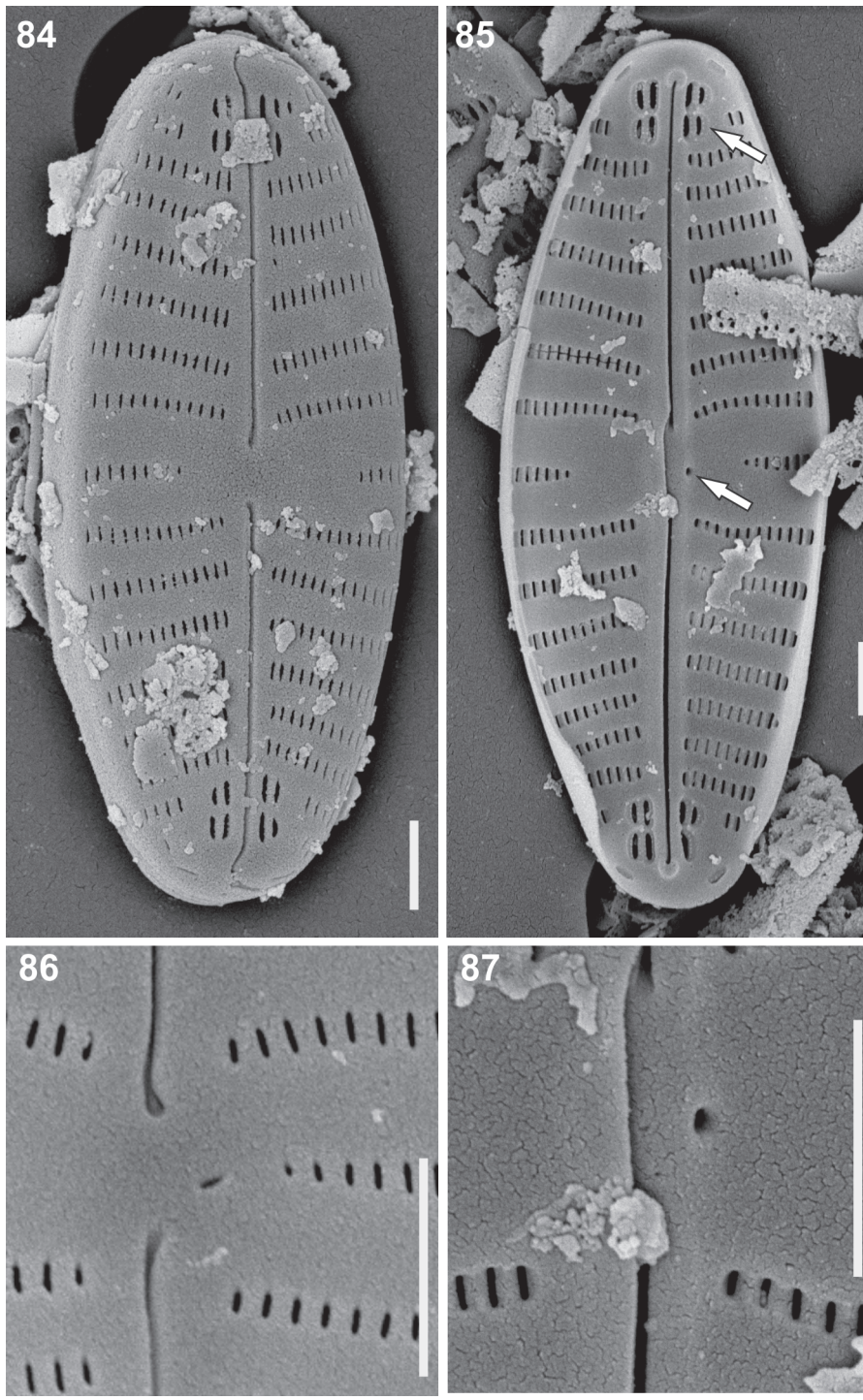
Geissleria hinziae Novais *et* Ector sp. nov. Figs 19-27, 91-94

Holotype: BR-4304 (National Botanic Garden, Meise, Belgium), microscopic slide.

Isotype: slide N7/50 and unmounted material number E6841 (Hustedt Collection, Bremerhaven, Germany), slide corresponding to the type material of *Navicula schoenfeldii*.

Type locality: Seewiesen b, Kaditz in Dresden, Saxony, Germany (coll. G. Schönfeld, coll. date 01/01/1922).

Etymology: The specific epithet *hinziae* refers to Friedel Hinz (Friedrich Hustedt Diatom Study Centre in the Alfred Wegener Institute for Polar and Marine Research, Bremerhaven), to whom we gratefully dedicate this species, acknowledging her valuable help with the Hustedt Collection.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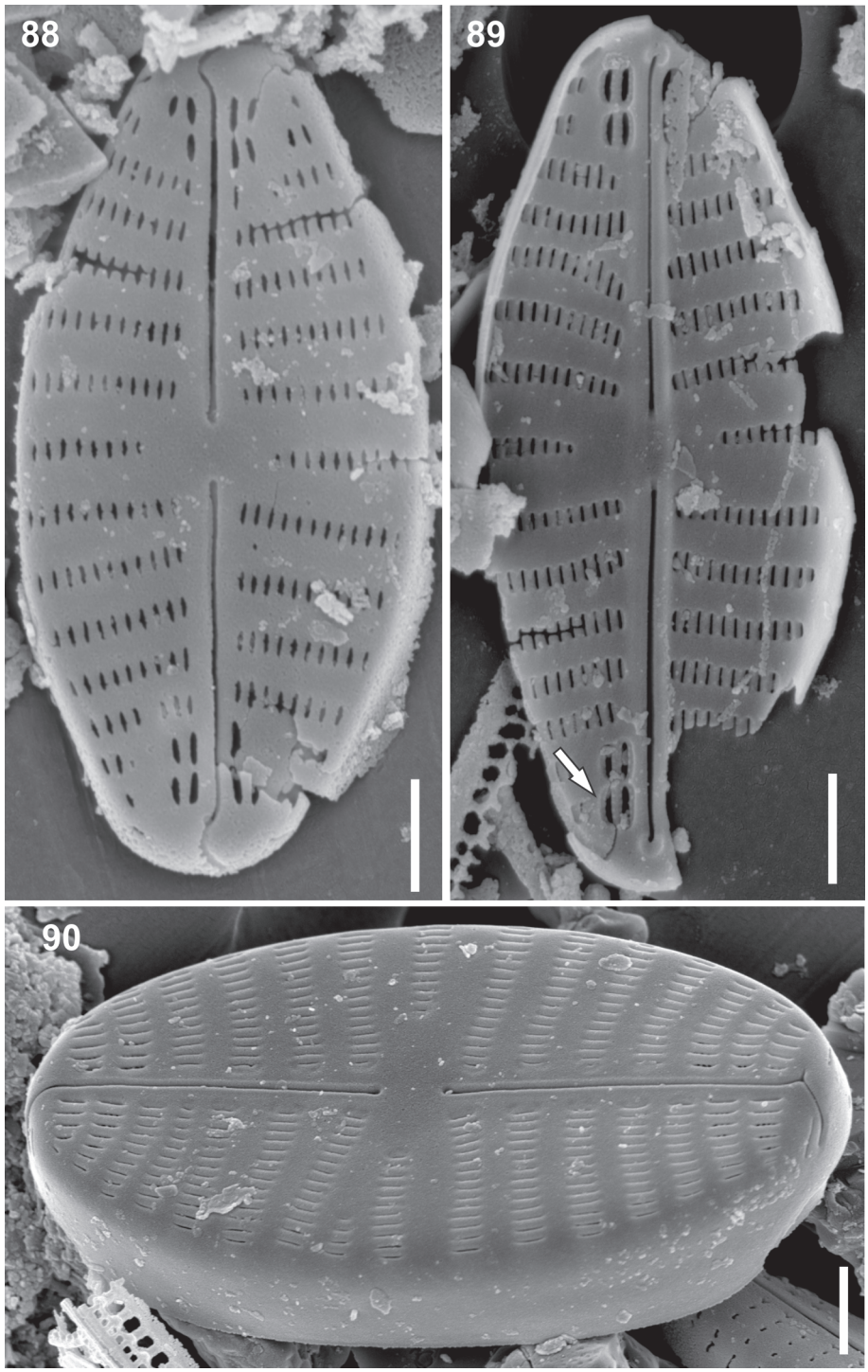
Description: Valves are linear-elliptical to elliptical, 11.3-15.7 µm long and 4.8-5.7 µm wide, with slightly protracted, broad, blunt and rounded apices. Axial area is narrow and linear. The central area is characterized by the presence of two or three more or less markedly shorter striae, alternating between longer and shorter striae. One isolated pore is present near the central nodule, small, especially in external view (Figs 91, 93), what makes it sometimes difficult to discern in LM (e.g. Figs 21-23). Striae are uniseriate and radiate throughout the entire valve, 15-18/10 µm. Areolae present externally as short slits (*ca* 90 in 10 µm) (Figs 91, 93). The raphe is filiform and almost straight. External proximal endings are slightly expanded, bent in the opposite direction to the distal ends (Fig. 91). Internally, raphe endings are simple, terminating proximally on a raised central nodule (Fig. 94). Central nodule is formed by two masses of siliceous material, but is lacking slit-like grooves characteristic for *G. decussis* (Lange-Bertalot, 2001). The distal ends are hooked externally (Fig. 91) and internally slightly deflected onto small helictoglossae (Fig. 92). One to two apically elongated subpolar areolae with warty outgrowths per stria are present in two striae near the raphe (Fig. 92). Warty outgrowths are also present between the other areolae (Figs 92, 94). Internally no hymenes or occlusions are observed on the areolae (Fig. 94).

Comparison with similar species: This species has been previously identified as *G. cummerowii* (Kalbe) Lange-Bertalot due to its clear resemblance in valve outline and dimensions. In fact, it was already illustrated in fig. 7 in plate 133 of Simonsen (1987) and fig. 15 in pl. 94 of Lange-Bertalot (2001), where it was considered to be *G. cummerowii* (identified from the type material of *G. schoenfeldii*). Nevertheless, there is a set of distinctive characters that allow its separation: the density of striae (*G. hinziae*: 15-18/10 µm throughout vs. *G. cummerowii*: 8-10/10 µm in the middle and 14-16/10 µm near the apices); the valve apices very slightly or not protracted in *G. cummerowii*, by opposition to the always slightly protracted apices in *G. hinziae*; the transapical striae are radiate becoming parallel to even slightly convergent at the apices in *G. cummerowii* and are radiate throughout in *G. hinziae*; the isolated pore near the central nodule (clearly visible in SEM, but sometimes difficult to discern in LM due to its small dimensions, see Figs 90, 92) in *G. hinziae*, which is absent in *G. cummerowii*, as can be seen in the LM micrographs of its type material (pl. 94, figs 18, 19, 21-23 in Lange-Bertalot, 2001) and in the original drawings (figs 268, 269 in Kalbe, 1973, presented here in Fig. 28).

This taxon is described from the type material of *G. schoenfeldii*; nevertheless it has sufficient characters that allow its clear separation: *G. hinziae* is narrower, has linear-elliptical to elliptical valves while these are elliptical to elliptical-lanceolate in *G. schoenfeldii*; the apices are slightly protracted in *G. hinziae* and non-protracted in *G. schoenfeldii*; and an isolated pore is always present in *G. hinziae* and absent in *G. schoenfeldii* (Table 4). Unfortunately, until now there is no clear information about the ecological preferences of *G. hinziae*, but they are probably similar to those of *G. schoenfeldii*, since *G. hinziae* was always found together with *G. schoenfeldii* until now.

◀ Figs 84-87. SEM micrographs of the type material of *Geissleria acceptata*. **84.** External valve view, showing the central area without isolated pore. **85.** Internal valve view, showing the isolated pore (arrow) and the elongated subpolar areolae with warty outgrowths (arrow). **86.** Detail of the central area in external view, showing the isolated pore. **87.** Detail of the central area in internal view, showing the isolated pore. Scale bars = 1 µm.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***Geissleria tagensis* Novais *et* Ector sp. nov.** **Figs 54-67, 95-98**

Holotype (here designated): BR-4275 (National Botanic Garden, Meise, Belgium), microscopic slide and preserved sample.

Isotypes: BM-101644 (Natural History Museum, London, UK), ZU8/37 (Hustedt Collection, Bremerhaven, Germany), microscopic slides.

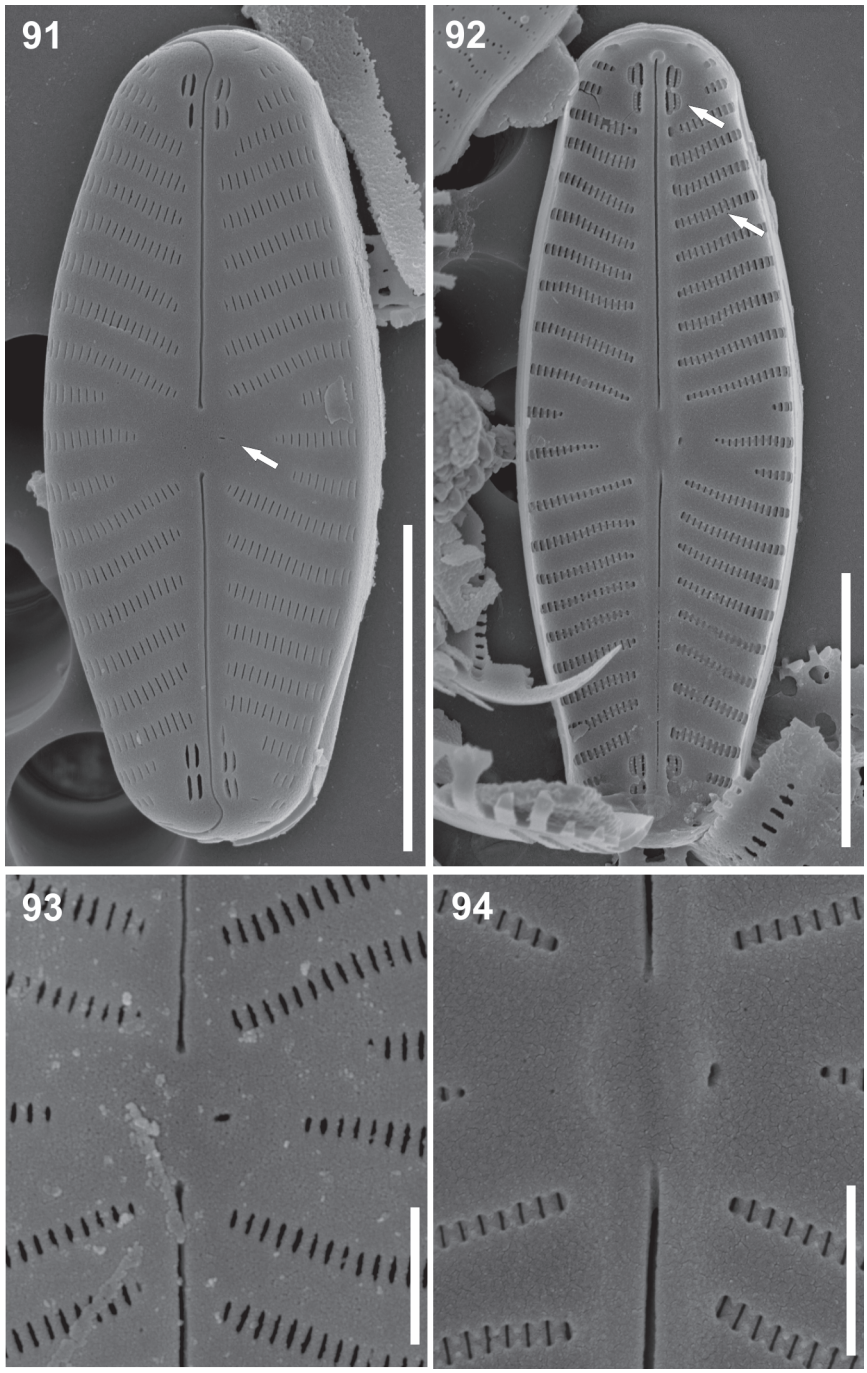
Type locality: Tagus River at Amieira, municipality of Nisa, subregion Alto Alentejo (District: Portalegre), Portugal (coll. Novais, coll. date 06/07/2006), coordinates 39º 31' 20.272''N, 07º 50' 03.736''W.

Etymology: The specific epithet *tagensis* refers to Tagus River, where the type material of this species has been collected.

Description: Valves rhombic-elliptical, 7.7-14.9 µm long and 4.3-5.5 µm wide, with broadly obtusely rounded apices. Axial area is narrow and linear but slightly widening towards the central area. The central area is characterized by the presence of two or three more or less markedly shortened striae, alternating between longer and shorter striae. No isolated pore present near the central nodule. Striae are uniseriate and radiate throughout the entire valve, 15-18/10 µm, slightly more densely arranged near the poles. Areolae present externally as short slits (*ca* 70 in 10 µm) (Figs 95, 97). The raphe is filiform and almost straight. The external proximal endings are slightly expanded, bent in the opposite direction to the distal ends (Fig. 95). Internally, the raphe endings are simple, terminating proximally on a raised central nodule (Fig. 98). The central nodule is formed by two masses of siliceous material, but is lacking slit-like grooves characteristic for *G. decussis* (Lange-Bertalot, 2001). The distal ends are hooked externally (Fig. 95) and internally are slightly deflected onto small helictoglossae (Fig. 96). Two to three apically elongated subpolar areolae, with warty outgrowths per stria are present in two striae near the raphe (Figs 95, 96). Warty outgrowths are present along the long sides of the subpolar areolae and between the areolae on the rest of the valve (Figs 96, 98). Internally no hymenes or occlusions are observed on the areolae (Fig. 98).

Comparison with similar species: In terms of valve dimensions *Geissleria tagensis* is closely related to *G. acceptata*, *G. bourbonensis*, *G. cummerowii*, *G. dolomitica*, *G. gabrielae*, *G. gereckei*, *G. mafatensis*, *G. modica*, *G. scaniae* and *G. taishanica*. Nevertheless, it differs from *G. acceptata* by its wider valves, the presence of a wider central area and more radiate striae. It can be easily distinguished from *G. bourbonensis*, *G. gereckei*, *G. hinziae*, *G. mafatensis*, *G. scaniae*, *G. taishanica* due to the existence of one isolated pore in all these species. *Geissleria cummerowii* does not have an isolated pore, but it has linear-elliptical valves while *G. tagensis* has more rhombic-elliptical valves, especially in small specimens, and denser striation. The valve shape is the main difference between *G. tagensis* and *G. dolomitica*, since the latter has linear-elliptical to elliptical-lanceolate valves. *Geissleria gabrielae* also exhibits linear-elliptical to elliptic-lanceolate valves with rostrate (smaller valves) to subcapitate (larger valves) apices. *Geissleria modica* is more similar in valve shape, but has a smaller central area, shortly protracted, subcapitate, obtusely rounded ends and denser striation throughout the whole valve.

◀ Figs 88-90. SEM micrographs of *Geissleria acceptata* type material (Figs 88, 89) and *Geissleria* sp. (Fig. 90). **88, 90.** External valve view. **89.** Internal valve view, showing the characteristic expanded areolae presenting the warty outgrowths on each side (arrow). Scale bars = 1 µm.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***Geissleria lusitanica* Novais *et* Ector sp. nov. Figs 68-79, 99-102**

Holotype (here designated): BR-4276 (National Botanic Garden, Meise, Belgium), microscopic slide and preserved sample.

Isotypes: BM-101644 (Natural History Museum, London, UK), ZU8/37 (Hustedt Collection, Bremerhaven, Germany), microscopic slides.

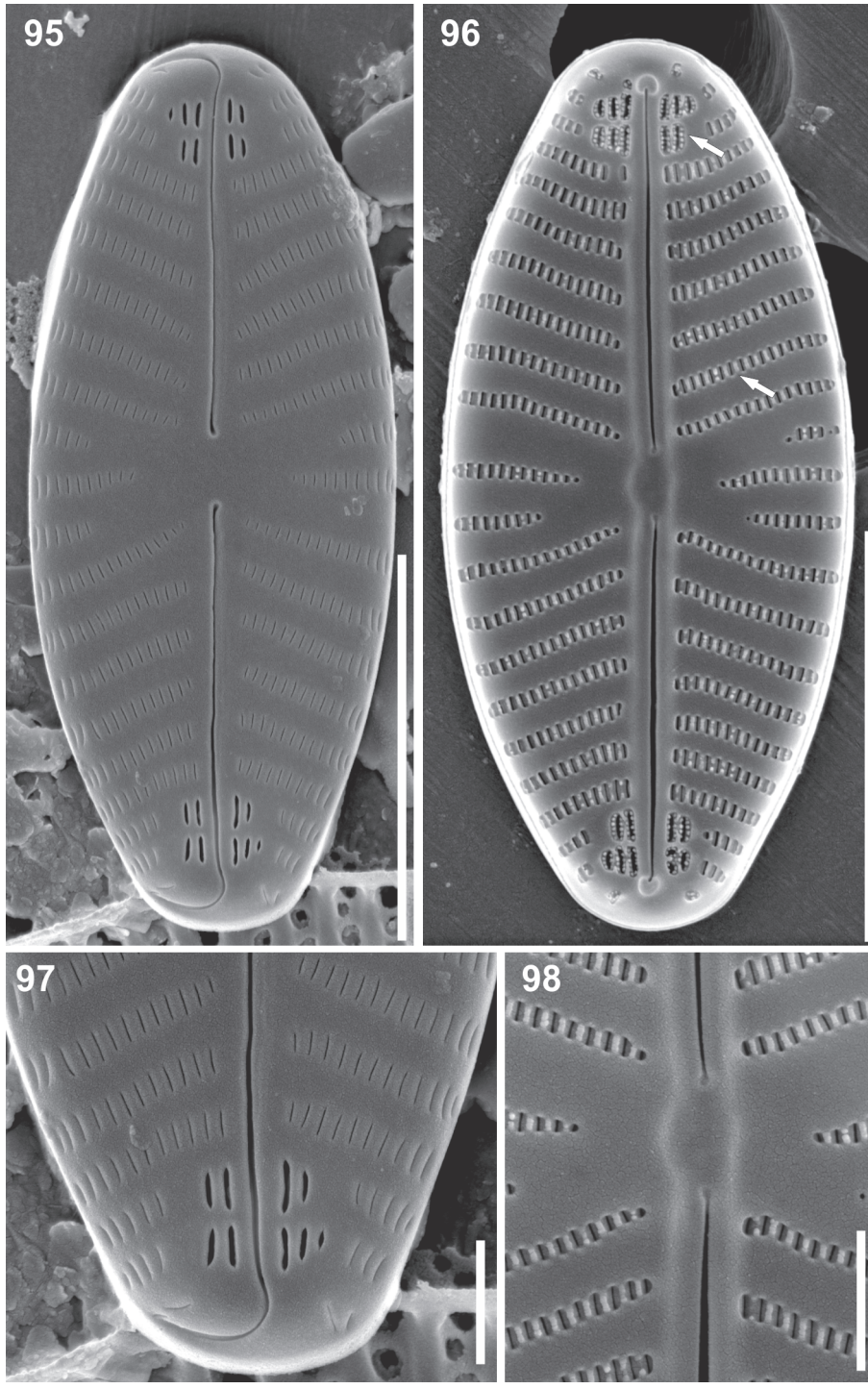
Type locality: Tagus River at Amieira, municipality of Nisa, subregion Alto Alentejo (District: Portalegre), Portugal (coll. Novais, coll. date 06/07/2006), coordinates 39º 31' 20.272''N, 07º 50' 03.736''W.

Etymology: The specific epithet *lusitanica* refers to Portugal (Latin: Lusitania), country from where it is being described.

Description: Valves linear-elliptical to elliptical, 11.3-17.0 µm long and 5.0-5.9 µm wide, with slightly convex lateral margins and slightly protracted to protracted ends. The axial area is narrow, linear but widening towards the central area. Central area is variable, sometimes delimited by one slightly shorter stria up to two or three markedly shorter and alternating striae. Two isolated pores are always present near the central nodule. The striae are uniseriate, ranging from slightly radiate to almost parallel near the central area, 14-15/10 µm, more densely arranged near the poles. Areolae externally are slit-like (*ca* 60 in 10 µm) (Fig. 99). The raphe is filiform and almost straight. The external proximal raphe endings are expanded and bent to the same side as the distal endings (Fig. 99). Internally, the raphe endings are simple, proximally terminating on a raised central nodule (Figs 100, 101). The distal ends are hooked externally (Fig. 99), internally terminating on small helictoglossae (Fig. 102). The central nodule is formed by two masses of siliceous material, with slit-like grooves clearly visible externally (Fig. 99). The subpolar areolar fields are occupying two or three striae, starting from the penultimate. Two to three apically elongated areolae are present per stria near the raphe (Figs 99-100). Several warty outgrowths are present along the long sides of these areolae, and these structures are also present between the areolae in the rest of the valve (Figs 100-102). Internally no hymenes or occlusions are observed on the areolae (Figs 101, 102).

Comparison with similar species: The presence of two isolated pores on opposite sides of the central nodule allows clear distinction between *G. lusitanica* and other *Geissleria* species, as can be seen in Table 3. The only other taxon with several isolated pores is *G. schmidiae*, which differs from *G. lusitanica* in its larger dimensions, valve shape and more parallel and denser striation. If morphometric characteristics only are considered, the new taxon can be compared with other taxa such as *G. creolorum*, *G. cummerowii*, *G. gabrielae*, *G. gereckei*, *G. hinziae*, *G. ignota*, *G. kriegeri*, *G. mafatensis*, *G. mascarenicensis*, *G. modica*, *G. paludosa*, *G. schoenfeldii* var. *tahitiensis* and *G. taishanica*. *Geissleria lusitanica* can be distinguished from *G. creolorum* by a central area bordered by three striae. *Geissleria cummerowii* and *G. hinziae* have less protracted and broader apices. *Geissleria gabrielae* has weakly protracted and broadly rounded, rostrate valve apices in smaller valves to subcapitate in larger valves. *Geissleria gereckei* has

◀ Figs 91-94. SEM micrographs of the type population of *Geissleria hinziae*. **91.** External valve view, showing the isolated pore (arrow). **92.** Internal valve view, showing the elongated subpolar areolae with warty outgrowths (arrow) and the warty outgrowths between the other areolae (arrow). **93.** Detail of the central area in external view, showing the small isolated pore. **94.** Detail of the central area in internal view, showing the isolated pore. Scale bars = 5 µm in Figs 91 & 92 and 1 µm in Figs 93 & 94.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slightly convex, straight or slightly concave lateral margins and characteristically protracted, often subcapitate ends. *Geissleria ignota* has undulate valve margins and a larger central area bordered by one short stria. *Geissleria kriegeri* has an axial area that does not or only slightly widens around the central nodule. *Geissleria mafatensis* and *G. mascarenicensis* have denser striation and linear valves. *Geissleria modica* valves are broadly elliptical and its central area is smaller than in *G. lusitanica*. *Geissleria paludosa* has a different valve shape, the middle part of the valve is swollen, and the larger central area is flanked only by one short stria. *Geissleria schoenfeldii* var. *tahitiensis d*iffers in shape, being more elliptical with convex margins and more radiate striae. *Geissleria taishanica* has rostrate, slightly capitate ends and a rectangular central area, bordered by only one shorter stria.

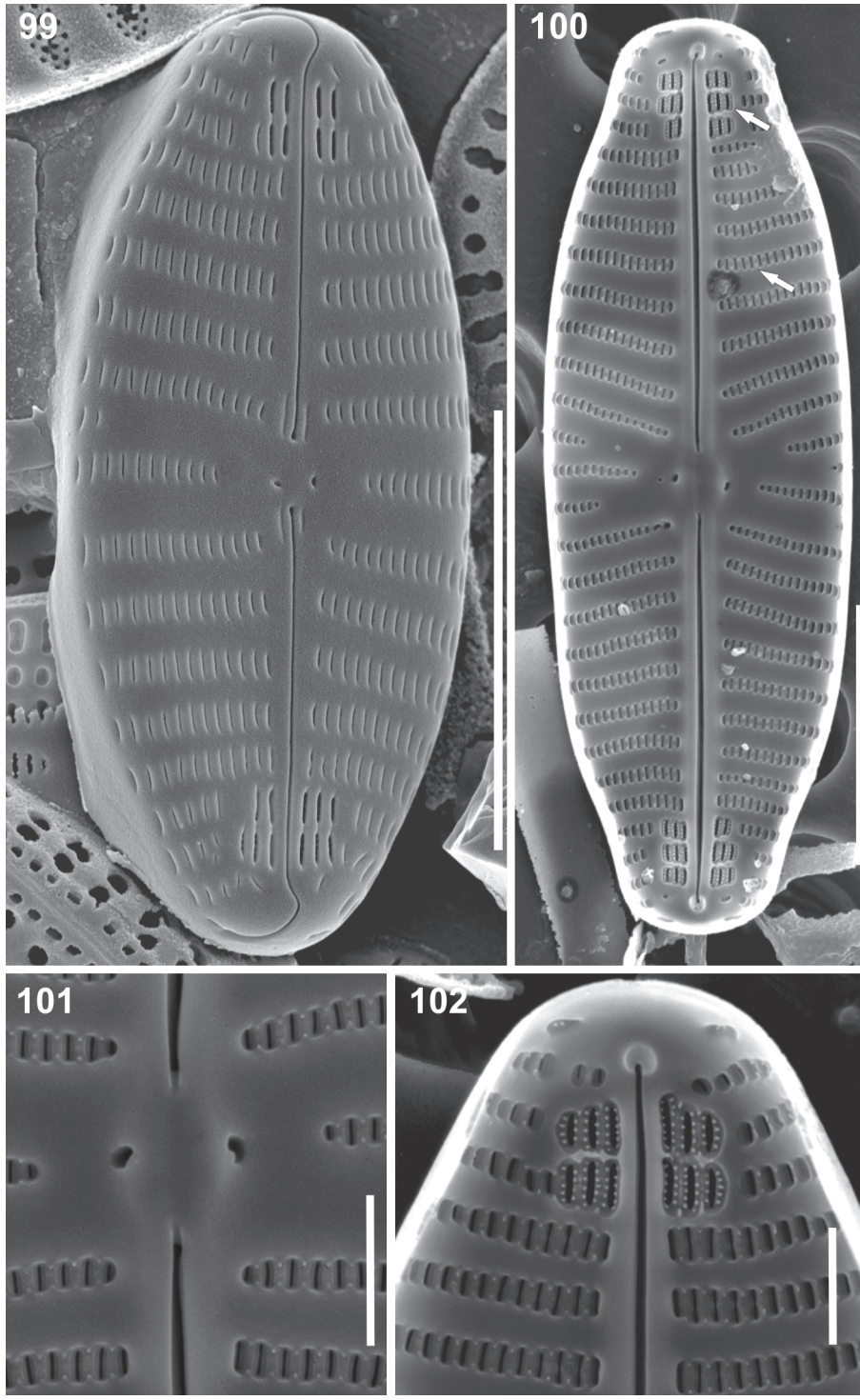
Ecology, distribution and associated diatom flora: Both *Geissleria tagensis* and *G. lusitanica* were present in the epilithon at various sampling sites in Portugal (Table 1), but always in low relative abundances. *Geissleria tagensis* was found at three sampling sites in the Cávado, Lima and Tagus watersheds. *Geissleria lusitanica* was identified from five sampling sites in the Tagus and Douro watersheds. It is noticeable that both species were found in large rivers (except the Divôr stream), where they were sampled from the shore. These are all permanent lowland rivers, with low current velocity, high water temperature and a wide range of environmental characteristics (Table 1). *Geissleria tagensis* was present in poor mineralized rivers with moderate conductivity (280-718 µS cm^{-1}) and slightly acidic to slightly alkaline pH (6.2-7.7). *Geissleria lusitanica* occurred in poor to moderately mineralized rivers with moderate to high conductivity and circumneutral to slightly alkaline pH (Table 1). The diatom assemblage of the type locality of both species was dominated by *Nitzschia soratensis* E. Morales *et* Vis, with *Amphora pediculus* (Kützing) Grunow, *Eolimna minima* (Grunow) Lange-Bertalot, *Fallacia clepsidroides* Witkowski, *Geissleria decussis* (Østrup) Lange-Bertalot *et* Metzeltin, *Nitzschia amphibia* Grunow, *N. fonticola* (Grunow) Grunow, *N. inconspicua* Grunow, and *Planothidium delicatulum* (Kützing) Round *et* Bukhtiyarova as subdominants; these are mainly subaerial, meso-eutraphentic to eutraphentic, and alkaliphilous taxa.

CONCLUSION

Based on the presence of the subpolar elongated areolae of the annulus, the three new species clearly belong to the genus *Geissleria* (Lange-Bertalot & Metzeltin, 1996).

Geissleria hinziae, G. lusitanica and *G. tagensis* are characterized by a set of morphological and ultrastructural features that separate them well from all the

◀ Figs 95-98. SEM micrographs of the type population of *Geissleria tagensis*. **95.** External valve view. **96.** Internal valve view, presenting the elongated subpolar areolae with warty outgrowths (arrow) and the warty outgrowths between the other areolae (arrow). **97.** Detail of the apice in external view, showing the deflected raphe. **98.** Detail of the central area in internal view, showing the absence of the isolated pore. Scale bars = 5 µm in Figs 95 & 96 and 1 µm in Figs 97 & 98.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other similar *Geissleria* species. Both *G. lusitanica* and *G. tagensis* occur in various Portuguese rivers; there is therefore a high probability that they also occur commonly in other European watercourses, but have not yet been recorded, probably due to misidentification as other similar *Geissleria* species, such as *G. acceptata* or *G. schoenfeldii*. *Geissleria hinziae*, on the other hand, has been identified as *G. cummerowii* and *G. schoenfeldii*, but with the separation from these taxa it will probably be recorded in the future from several European watercourses.

The new combinations proposed indicate that there are probably still other *Navicula* species that, after thorough analysis, could be transferred to the genus *Geissleria*.

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◀ Figs 99-102. SEM micrographs of the type population of *Geissleria lusitanica*. **99.** External valve view. **100.** Internal valve view, presenting the elongated subpolar areolae with warty outgrowths (arrow) and the warty outgrowths between the other areolae (arrow). **101.** Detail of the central area in internal view, showing the two isolated pores. **102.** Detail of the apice in internal view, with the characteristic expanded areolae presenting the warty outgrowths on each side. Scale bars = 5 µm in Figs 99 & 100 and 1 µm in Figs 101 & 102.

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