

New combinations and type analysis of *Chamaepinnularia* species (Bacillariophyceae) from aerial habitats

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Abstract – We detail under light and scanning electron microscopy the type materials of three poorly known diatom species first described by Hustedt from aerial habitats in Germany. *Navicula parsura* Hustedt (synonym: *N. obscura* Hustedt), *N. obsoleta* Hustedt, and *N. evanida* Hustedt type materials were observed and compared with populations from Luxembourg. Ultrastructural analysis revealed the presence of striae composed by areolae occluded externally by hymenes and a silica line at the valve face-mantle junction along the apical plane. These taxa also present a naviculoid raphe, which besides overall valve outline, conforms to the genus *Chamaepinnularia* Lange-Bertalot *et* Krammer. Therefore, we propose two new combinations: *Chamaepinnularia obsoleta* (Hustedt) C.E. Wetzel *et* Ector comb. nov. and *C. parsura* (Hustedt) C.E. Wetzel *et* Ector comb. nov. Excepting *C. evanida* (Hustedt) Lange-Bertalot, which is often observed in European rivers and already placed in the genus *Chamaepinnularia*, the remaining two taxa are poorly known and autecological data are scarce. Our results suggest that these species, present in stream drift during flood events, might partially derive from near-stream riparian or upslope terrestrial habitats. In addition, based on literature data, three new combinations are also proposed.

Aerophytic diatoms / Bacillariophyta / Chamaepinnularia / Hustedt / Luxembourg / Taxonomy / Type material

Résumé – **Nouvelles combinaisons et analyse des types d'espèces de *Chamaepinnularia* (Bacillariophyceae) d'habitats aériens.** Nous détaillons ici en microscopie optique et électronique à balayage les matériels types de trois espèces de diatomées mal connues, décrites par Hustedt d'habitats aériens en Allemagne. *Navicula parsura* Hustedt (synonyme : *N. obscura* Hustedt), *N. obsoleta* Hustedt et *N. evanida* Hustedt sont décrits et comparés aux populations du Luxembourg. L'analyse de l'ultrastructure a montré la présence de stries composées d'aréoles extérieurement occluses par des hymens, ainsi qu'une ligne de silice à la jonction face valvaire-manteau le long du plan apical. Ces taxons présentent également un raphé naviculoïde qui, sans tenir compte du contour général des valves, est conforme au genre *Chamaepinnularia* Lange-Bertalot *et* Krammer. Par conséquent, nous proposons deux nouvelles combinaisons: *Chamaepinnularia obsoleta* (Hustedt) C.E. Wetzel *et* Ector comb. nov. et *C. parsura* (Hustedt) C.E. Wetzel *et* Ector comb. nov. Hormis *C. evanida* (Hustedt) Lange-Bertalot qui est souvent observé dans les rivières européennes et déjà placé dans le genre *Chamaepinnularia*, les deux autres taxons sont mal connus et des données autécologiques sont rares. Nos résultats suggèrent que ces espèces, présentes dans les eaux de dérive pendant les épisodes de crue, puissent partiellement dériver des habitats ripariens proches des ruisseaux ou des milieux terrestres des versants ascendants. De plus, sur base des données de la littérature, trois nouvelles combinaisons sont aussi proposées.

Bacillariophyta / Chamaepinnularia / Diatomées aérophytiques / Hustedt / Matériel type / Luxembourg / Taxonomie

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INTRODUCTION

Changes in the species concept and the rarity of many oligotraphentic species in Europe, due to the loss of oligotrophic habitats, are most probably the main reasons that ecological information for a large number of taxa is scarce in the literature (Kapetanović *et al.*, 2011). However, there has been a growing interest in diatoms from pristine areas (springs, peat bogs, spring fens, mountain wetlands) and other habitats less affected by anthropogenic activities (e.g. Cantonati, 1998; Werum & Lange-Bertalot, 2004; Buczkó & Wojtal, 2005; Veselá & Johansen, 2009; Cantonati & Lange-Bertalot, 2010; Kulikovskiy *et al.*, 2010; Cantonati *et al.*, 2011; Reichardt, 2011; Żelazna-Wieczorek, 2011).

Amongst the diatom genera found in these habitats, *Chamaepinnularia* Lange-Bertalot & Krammer is often observed as an important component of diatom communities. This cosmopolitan genus occurs from Arctic and Antarctic regions to Neotropical and Paleotropical environments. *Chamaepinnularia* species are typically found in aerial habitats growing on and around wet mosses, including soil habitats (Metzeltin & Lange-Bertalot, 1998; Wydrzycka & Lange-Bertalot, 2001; Van de Vijver *et al.*, 2002, 2004, 2008, 2010; Cavacini *et al.*, 2006; Cocquyt, 2007; Metzeltin & Lange-Bertalot, 2007; Van de Vijver & Cox, 2013). They also occur in oligotrophic, fresh- to brackish waters and a few species are even found in marine environments (Witkowski *et al.*, 2000) (Table 1).

The genus *Chamaepinnularia* forms a relatively small but heterogeneous group that comprises several taxa previously allocated to the genera *Navicula* Bory or *Pinnularia* Ehrenberg (Lange-Bertalot & Metzeltin, 1996) by previous authors (e.g. Petersen, 1915, 1928; Krasske, 1929; Hustedt, 1934, 1942) and contains currently 62 taxa (including species and varieties) (Fourtanier & Kociolek, 2011). Species have relatively small cells (ca. 25 µm long and 4 µm wide), and ultrastructurally the striae consist of one large areola interrupted by a silica line near the valve face-mantle junction along the apical plane with the external apertures of the areolae occluded by thin unstructured hymenes. The representatives of this genus live as isolated cells and are not chained to form aggregates (Lange-Bertalot & Metzeltin, 1996; Cantonati & Lange-Bertalot, 2009; Kulikovskiy & Lange-Bertalot, 2010).

While studying the diatom flora from aerial environments from northwest Germany, Hustedt (1942) described several new species, and among them three small naviculoid taxa: *Navicula obscura* Hustedt, *Navicula obsoleta* Hustedt and *Navicula evanida* Hustedt [= *Chamaepinnularia evanida* (Hustedt) Lange-Bertalot]. During the study of diatom populations from a preserved small catchment in Luxembourg (Weierbach basin), we encountered several terrestrial and aerophytic diatoms and among them, the three species described by Hustedt. Here, we re-analyse and describe the type material of these species in full detail using both light and scanning electron microscope techniques and we also give information on the distribution and ecological preferences.

MATERIAL AND METHODS

We collected the material used in this study in the Weierbach catchment (40 ha), located in the northwestern part of Luxembourg (Fig. 1). The region is known as the 'Oesling' (northern part of the Grand-duchy of Luxembourg), a high

Table 1. Type locality and ecological preference (broad concept) of species currently placed in the genus *Chamaepinnularia*

Species	Reference*	Type locality	Ecology
<i>Chamaepinnularia abdita</i> (Manguin) Metzeltin et Lange-Bertalot	13	Basse Terre (Guadeloupe)	Freshwater/Aerophytic (bryophytic)
<i>C. aereophila</i> Van de Vijver et Beyens	16	Ile de la Possession (Crozet Archipelago)	Aerophytic
<i>C. alexandrowiczii</i> Witkowski, Lange-Bertalot et Metzeltin	20	Red Sea (Egypt)	Marine
<i>C. aliena</i> (Krasske) Van de Vijver et Le Cohu	16	Wijdebaysite, Spitzbergen (Norway)	Aerophytic/Brackish water
<i>C. amphiborealis</i> Lange-Bertalot et Werum	19	Rohrbach (Germany)	Freshwater
<i>C. australomediocris</i> (Lange-Bertalot et Rol. Schmidt) Van de Vijver	15	King George Island (Antarctica)	Freshwater/Aerophytic (bryophytic)
<i>C. begeri</i> (Krasske) Lange-Bertalot	11	Alpes (Germany)	Freshwater
<i>C. brasiliana</i> Metzeltin et Lange-Bertalot	12	Santos (Brazil)	Freshwater
<i>C. brasilianopsis</i> Metzeltin et Lange-Bertalot	12	Roraima Massif, Paray-Tepui (Venezuela)	Freshwater
<i>C. bremensis</i> (Hustedt) Lange-Bertalot	11	Ochtum, Bremen (Germany)	Freshwater/Aerophytic (bryophytic)
<i>C. bremoides</i> Flower	3	Malvinas Islands (Argentina)	Freshwater
<i>C. brevissima</i> (Hustedt) C.E. Wetzel et Ector comb. nov.	4	Dieng-Plateau, Java (Malay Archipel)	Terrestrial
<i>C. calida</i> (Hendey) Lange-Bertalot	9	British Coastal waters (England)	Marine
<i>C. circumborealis</i> Lange-Bertalot	9	Yugorsky Peninsula (Russia)	Freshwater
<i>C. clamans</i> (Hustedt) Witkowski, Lange-Bertalot et Metzeltin	20	Memmert, Niedersachsen (Germany)	Marine
<i>C. cymatopleura</i> (W. West et G.S. West) P. Cavacini	2	McMurdo Sound, Victoria Land (Antarctica)	Fresh- to brackish water
<i>C. distantepunctata</i> (Simonsen) Witkowski, Lange-Bertalot et Metzeltin	20	Beaufort Bay, Atlantic Coast (U.S.A.)	Marine
<i>C. elongata</i> (Manguin) Metzeltin et Lange-Bertalot	13	Basse Terre (Guadeloupe)	Aerophytic (bryophytic)
<i>C. evanida</i> (Hustedt) Lange-Bertalot	11	Wümmingen, Land Bremen (Germany)	Freshwater/Aerophytic (bryophytic)
<i>C. falkiae</i> Lange-Bertalot et Werum	19	Iffeldorf, Bavaria (Germany)	Freshwater

<i>Species</i>	<i>Reference*</i>	<i>Type locality</i>	<i>Ecology</i>
<i>C. ferrarioana</i> Metzeltin <i>et</i> Lange-Bertalot	12	Demerara River (Guyana)	Freshwater
<i>C. furtiva</i> (Manguin) Metzeltin <i>et</i> Lange-Bertalot	13	Basse Terre (Guadeloupe)	Freshwater/Aerophytic (bryophytic)
<i>C. gandrupii</i> (J.B. Petersen) Lange-Bertalot <i>et</i> Krammer	11	Jan Mayen Island (Norway)	Freshwater
<i>C. gandrupii</i> var. <i>simplex</i> (Krasske) Lange-Bertalot <i>et</i> Krammer	11	Spitzbergen (Norway)	Freshwater
<i>C. gertlachei</i> Van de Vijver <i>et</i> Sterken	17	James Ross Island (Antarctica)	Terrestrial
<i>C. gracilistriata</i> Van de Vijver <i>et</i> Beyens	16	Ile de la Possession (Crozet Archipelago)	Terrestrial
<i>C. gibsonii</i> Van de Vijver	18	Bunger Hills (Antarctica)	Brackish water (saline lake)
<i>C. hassiaca</i> (Krasske) Cantonati <i>et</i> Lange-Bertalot	1	Hessen (Germany)	Freshwater/Aerophytic (bryophytic)
<i>C. hippodontiforma</i> Metzeltin <i>et</i> Lange-Bertalot	13	Cruzeta, Rio grande do Norte (Brazil)	Freshwater
<i>C. justa</i> (Hustedt) Witkowski, Lange-Bertalot <i>et</i> Metzeltin	20	Beaufort, North Carolina (U.S.A.)	Marine
<i>C. krasskei</i> Lange-Bertalot	9	Yugorsky Peninsula (Russia)	Freshwater
<i>C. krookiformis</i> (Krammer) Lange-Bertalot <i>et</i> Krammer	9	North Rhine Westphalia (Germany)	Fresh- to brackish water
<i>C. krookii</i> (Grunow) Lange-Bertalot <i>et</i> Krammer	9	Soos National Reserve (Czech Republic)	Fresh- to brackish water
<i>C. margaritacea</i> (Hustedt) Lange-Bertalot	11	Telaga Pasir (Java)	Aerophytic (bryophytic)
<i>C. margaritana</i> (Witkowski) Witkowski	11	Gulf of Gdansk, Baltic Sea (Poland)	Fresh- to brackish water
<i>C. mediocriformis</i> (M. Coste <i>et</i> Ricard) Lange-Bertalot	14	Mauritius Island, Seychelles (Indian ocean)	Freshwater
<i>C. mediocris</i> (Krasske) Lange-Bertalot	11	Tauern region, Alps (Germany)	Freshwater/Aerophytic (bryophytic)
<i>C. mediocris</i> var. <i>atomus</i> (Hustedt) Lange-Bertalot	11	Singkarak See (Sumatra)	Aerophytic (bryophytic)
<i>C. minutissima</i> (Manguin) Metzeltin <i>et</i> Lange-Bertalot	13	Basse Terre (Guadeloupe)	Freshwater/Aerophytic (bryophytic)
<i>C. obsoleta</i> (Hustedt) C.E. Wetzel <i>et</i> Ector comb. nov.	5	Land Bremen (Germany)	Freshwater/Aerophytic (bryophytic)
<i>C. oculus</i> (Østrup) Lange-Bertalot	9	Hekla Havn, Greenland (Denmark)	Terrestrial
<i>C. parsura</i> (Hustedt) C.E. Wetzel <i>et</i> Ector comb. nov.	7	Land Bremen (Germany)	Freshwater/Aerophytic (bryophytic)
<i>C. perfidissima</i> (Lange-Bertalot) C.E. Wetzel <i>et</i> Ector comb. nov.	10	“Devil’s Hole Cave” (Fife/Scotland)	Freshwater/Aerophytic

<i>Species</i>	<i>Reference*</i>	<i>Type locality</i>	<i>Ecology</i>
<i>C. reinventa</i> Lange-Bertalot et Wydrzycka	21	Julma Ölkky (Finland)	Freshwater
<i>C. reinventa</i> subsp. <i>urtrouquarea</i> Wydrzycka et Lange-Bertalot	21	Alajuela (Costa Rica)	Freshwater
<i>C. resolutata</i> Lange-Bertalot et Wydrzycka	21	Alajuela (Costa Rica)	Freshwater
<i>C. rhombelliptica</i> Lange-Bertalot	11	Julma Ölkky (Finland)	Freshwater
<i>C. rupicola</i> (Hustedt) Lange-Bertalot	11	Ajer Upi (Sumatra)	Freshwater/Aerophytic
<i>C. schaupiana</i> Lange-Bertalot et Metzeltin	11	Julma Ölkky (Finland)	Freshwater
<i>C. soehrensii</i> (Kraske) Lange-Bertalot et Kramer	11	Hessen (Germany)	Freshwater/Aerophytic (bryophytic)
<i>C. soehrensii</i> var. <i>capitata</i> (Kraske) Lange-Bertalot et Kramer	11	Hessen (Germany)	Freshwater/Aerophytic (bryophytic)
<i>C. soehrensii</i> var. <i>musciicola</i> (J.B. Petersen) Lange-Bertalot et Kramer	11	Vestdalur (Iceland)	Freshwater/Aerophytic (bryophytic)
<i>C. submusciicola</i> (Kraske) Lange-Bertalot	19	San Vicente (Chile)	Aerophytic (bryophytic)
<i>C. tongatensis</i> (Hustedt) Lange-Bertalot	11	Tonga-Insel, Nuku'alofa (Tonga)	Freshwater
<i>C. truncata</i> (König) Witkowski, Lange-Bertalot et Metzeltin	20	Gironde (France)	Marine
<i>C. ventosa</i> (Hustedt) C.E. Wetzel et Ector comb. nov.	6	Land Bremen (Germany)	Freshwater/Aerophytic (bryophytic)
<i>C. vyvermannii</i> Lange-Bertalot	11	Galway (Ireland)	Freshwater
<i>C. wetkerii</i> (Manguin) Metzeltin et Lange-Bertalot	13	Basse Terre (Guadeloupe)	Freshwater/Aerophytic (bryophytic)
<i>C. wiktoriae</i> (Witkowski et Lange-Bertalot) Witkowski, Lange-Bertalot et Metzeltin	20	Gulf of Gdansk, Baltic Sea (Poland)	Fresh- to brackish water
<i>C. wiktowskii</i> (Lange-Bertalot et Metzeltin) Kulikovskiy et Lange-Bertalot	8	Gulf of Gdansk, Baltic Sea (Poland)	Fresh- to brackish water

* 1 Cantonati & Lange-Bertalot (2009); 2 Cavacini et al. (2006); 3 Flower (2005); 4 Hustedt (1937); 5 Hustedt (1942); 6 Hustedt (1957); 7 Hustedt (1962); 8 Kulikovskiy & Lange-Bertalot (2010); 9 Lange-Bertalot & Genkal (1999); 10 Lange-Bertalot & Kramer (1989); 11 Lange-Bertalot & Metzeltin (1996); 12 Metzeltin & Lange-Bertalot (1998); 13 Metzeltin & Lange-Bertalot (2007); 14 Moser et al. (1998); 15 Schmidt et al. (1990); 16 Van de Vijver et al. (2002); 17 Van de Vijver et al. (2010); 18 Van de Vijver et al. (2012); 19 Werum & Lange-Bertalot (2004); 20 Witkowski et al. (2000); 21 Wydrzycka & Lange-Bertalot (2001).

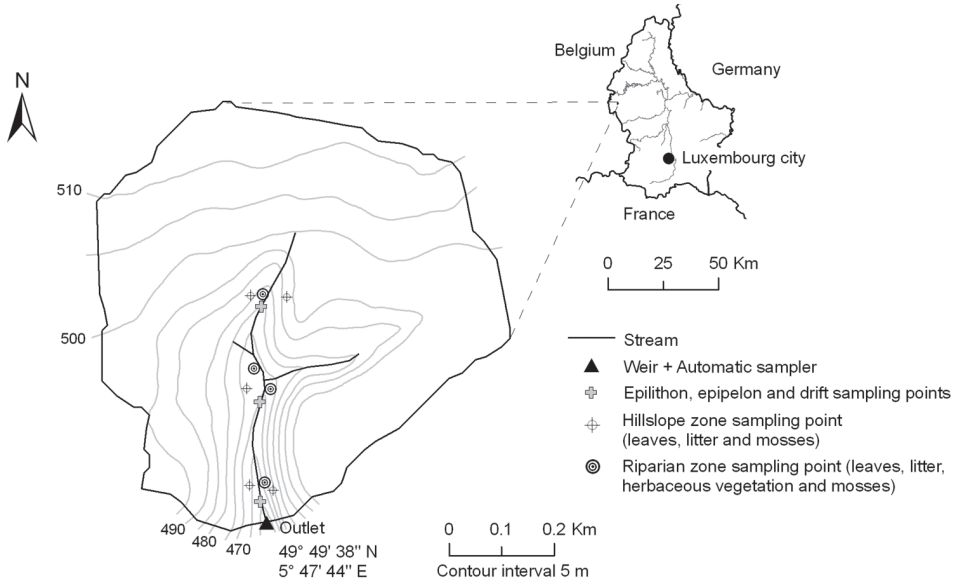


Fig. 1. Location of diatom sampling points (R: riparian zone sample; H: hillslope zone sample; D: drift sampler). Weierbach catchment (Northwest Luxembourg).

sub horizontal plateau with altitudes ranging between 450 and 500 m a.s.l. The lithology of the catchment mainly consists of Devonian rocks (schists, phyllades and quartzite). The catchment is all forested with coniferous (*Picea abies* (L.) Karst.) and deciduous trees (*Fagus sylvatica* L.).

We collected the diatoms manually in several microhabitats. The main available diatom-substrates were identified and sampled. Leaves, litter, mosses and herbaceous vegetation [leaves of several live plants (e.g. *Gramineae* and *Pteridophytae*, exposed to flood inundation events)] were sampled in the riparian zones, whereas litter and mosses were sampled on the hillslopes. Each sample was composed of five sub-samples collected on a 5 m transect parallel to the stream (a subsample collected every meter). We only sampled well-illuminated material from the top surface. Samples were collected in 1-L plastic bottles, labeled with name and date and transported to the laboratory. Sample bottles containing different kinds of substrates (*i.e.* leaves, litter, moss and herbaceous vegetation) were then filled with sparkling water (1-L), carefully shaken and left in the fridge over one night. The sparkling water was used to detach diatoms from the substrate. The next day, we passed the sample through a 1 mm screen. Then, more sparkling water was added to the sample to completely rinse it (0.5-L). The recovered sample was then left in the fridge during a minimum of 8 hours to let diatoms settle down, and the supernatant was then removed by aspiration.

Our collection of epilithic aquatic diatom samples was based on the European standards CEN 13946 and CEN 14407 (European Committee for Standardization, 2003, 2004). Whenever possible, we brushed a minimum of five stones inside the main flow zone and well-lighted river part to collect the diatom biofilm. Epipellic samples were also sampled from the riverbed by revolving the superficial layer of the sediment in different places and placed into a plastic bowl.

We collected drift samples with an automatic sampler (ISCO 6712 FS) located near the weir (Fig. 1). Stream water was sampled at frequent intervals during flood events (0.5-4 h) and less frequently during low flows. Samplers containing 24 bottles (1-L) were linked to the recording stream gauge. The sampler was connected to a differential pressure transducer (ISCO 4120 Flow Logger) monitoring water levels and used to follow discharge fluctuations (via a stage-discharge rating curve). The automatic sampling was triggered by flow conditions via the link with the recording streamgauge.

We also collected water samples bi-weekly at the outlet of the Weierbach catchment (September 2010 to August 2011) and analyzed them for major anions (Cl^- , NO_3^- , SO_4^{2-}) and cations (Na^+ , K^+ , Mg^{2+} , Ca^{2+}), dissolved silica (SiO_2), pH, alkalinity, dissolved organic carbon, dissolved nitrogen, and UV-absorbance (254 nm). Water samples were filtered through WHATMAN GF/C glass fiber filters (0.45 μm), and stored prior to analysis at 4°C. Dissolved anions and cations were analyzed by ion chromatography (Dionex DX 500 and DX 600), SiO_2 by the ammonium molybdate method with a photometer and alkalinity was determined by titration. UV-absorbance was measured by a Beckmann Coulter spectrophotometer. Dissolved organic carbon and dissolved nitrogen were measured simultaneously by the combustion method and using a chemiluminescence detector, respectively (Teledyne TekMar, Apollo 9000). Limnological characteristics of the catchment are presented in Table 2.

We collected a total of 193 diatom samples. All samples were then preserved with 4% formaldehyde. Small aliquots of raw samples were first oxidized by digestion with hot (90 °C) concentrated hydrogen peroxide (H_2O_2) and later with a few drops of concentrated HCl using a sand bath (± 10 hours). Following digestion and decantation, cleaned material was rinsed and diluted with deionized water and mounted permanently on glass slides using Naphrax[®] as mounting medium (Brunel Microscopes Ltd., Chippenham, Wiltshire, UK) for qualitative analysis. Light microscopy (LM) observations, identifications,

Table 2. Water samples collected bi-weekly at the outlet of the Weierbach catchment (September 2010 to August 2011)

	Unit	n	Min	Max	Mean	SD
pH	–	27	5.82	6.95	6.34	0.33
Conductivity	$\mu\text{S cm}^{-1}$	27	48.20	68.20	54.60	5.84
Alkalinity (pH 4.5)	mEq	27	0.05	0.36	0.19	0.10
UV-Absorbance (254 nm)	–	27	0.02	0.33	0.06	0.07
Dissolved organic carbon (DOC)	mg L^{-1}	26	0.73	7.16	2.12	1.47
Dissolved nitrogen (TNd)	mg L^{-1}	26	0.49	2.56	0.99	0.53
Dissolved silica (SiO_2)	mg L^{-1}	25	5.00	10.50	7.00	1.39
Sodium (Na^+)	mg L^{-1}	27	2.23	3.70	2.80	0.38
Potassium (K^+)	mg L^{-1}	27	0.19	1.35	0.36	0.23
Magnesium (Mg^+)	mg L^{-1}	27	2.39	3.13	2.79	0.18
Calcium (Ca^{2+})	mg L^{-1}	27	1.85	3.38	2.44	0.46
Chlorides (Cl^-)	mg L^{-1}	27	2.58	3.59	3.08	0.20
Nitrates (NO_3^-)	mg L^{-1}	27	0.34	1.43	0.71	0.29
Sulphates (SO_4^{2-})	mg L^{-1}	27	5.94	8.91	7.73	0.76

measurements and micrographs were performed with a Leica[®] DMR microscope equipped with a Leica-DFC 500 high-resolution digital camera using Leica Application Suite software (v. 3.7.0, Leica Microsystems[®]). At least 400 valves were identified and counted under the light microscope with a magnification of 1000x.

For scanning electron microscopy (SEM), subsamples of treated diatom suspensions were concentrated on a polycarbonate membrane filter with a 3 µm mesh, attached to aluminium stubs, sputtered with a 30 nm platinum layer and observed with a Hitachi SU-70 field emission scanning electron microscope using an accelerated voltage of 5 kV. All LM and SEM photographic digital images were assembled using Corel Designer X5[®] (Corel Corporation[®]).

In addition to the material collected in Luxembourg, we also observed the following unmounted type material deposited at Hustedt Collection, Bremerhaven (BRM):

– E986. Unmounted material: “Wümmingen, Straßengraben am Weg Rothlake – Hellwege, Lebermoos über Wasser, 12.02.1934”, Land Bremen, Germany (Lat. 53.25, Long. 9.25).

– E1008. Unmounted material: “Hasbruch, Wasserrinne, Rand Moos über Wasser, 03.05.1937”, Land Bremen, Germany (Lat. 53.25, Long. 8.75).

– E1011. Unmounted material: “Hasbruch, Bach b. d. Jagdhütte an Lebermoos über Wasser, 03.05.1937”, Land Bremen, Germany (Lat. 53.25, Long. 8.75).

RESULTS AND DISCUSSION

Chamaepinnularia parsura (Hustedt) C.E. Wetzel *et* Ector *comb. nov.*

Figs 2-25, 73-76

Basionym: *Navicula parsura* Hustedt 1962, p. 240, fig. 1365, *In: Rabenhorst L. (Ed.), Kryptogamen-Flora von Deutschland, Österreich und der Schweiz, Band VII, Teil 3.*

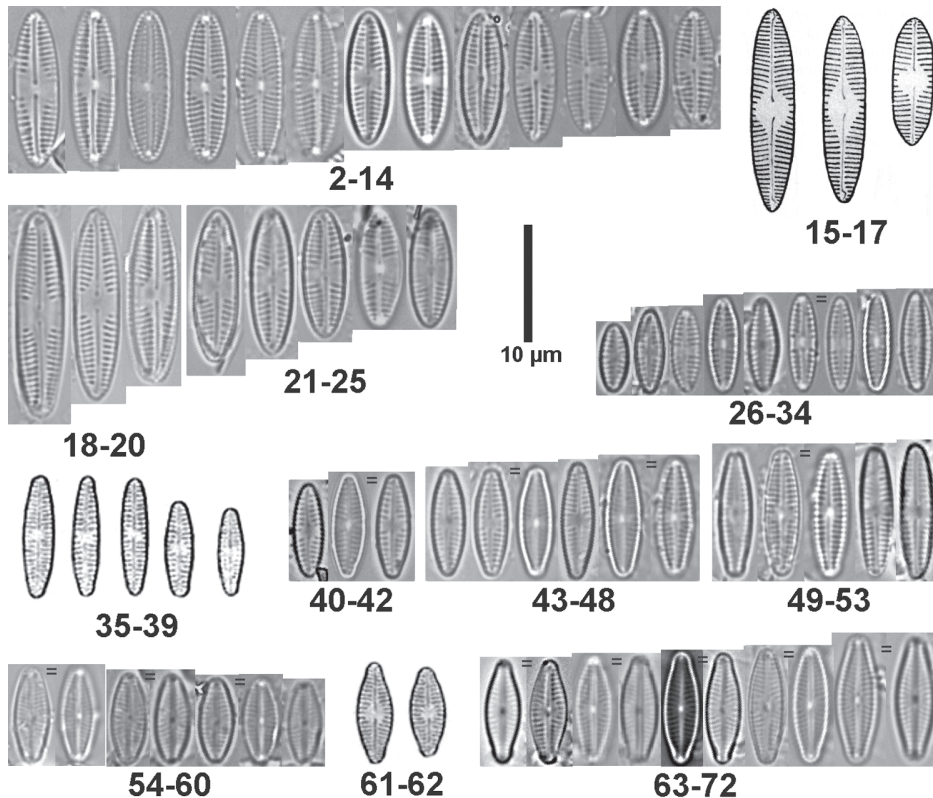
Synonym: *Navicula obscura* Hustedt 1942, *Ber. Deutsch. Bot. Ges.* 60, p. 68, figs 9-11, [*non* Schmidt 1936, *Atlas der Diatomaceenkunde*, pl. 403, figs 25-26; *non* Hustedt 1937, *Archiv für Hydrobiologie*, Suppl. 15, p. 278, pl. 20, fig. 15; *non* Pantocsek 1909, *Verh. des Vereins für Natur-und Heilkunde Pozsony* 19, p. 56, pl. 2, fig. 21].

Lectotype: Designated by Simonsen (1987, p. 267): Slide BRM-N6/11, sample E1008 (Hustedt Collection, Bremerhaven).

Paralectotype: Designated by Simonsen (1987, p. 268): Slide BRM-N2/80, sample E1011 (Hustedt Collection, Bremerhaven).

Type locality: “Hasbruch, Wasserrinne, Rand Moos über Wasser, 03.05.1937”, Land Bremen, Germany (Lat. 53.25, Long. 8.75).

Morphology: Valves elliptic-lanceolate to lanceolate, smaller specimens elliptical; ends cuneiformly rounded. Observed range of valve dimensions (*n*=25): length 8.0-19.0 µm, width 3.5-4.0 µm. Raphe branches slightly curved, filiform, proximal raphe ends with central pores slightly deflected towards the same side. Distal raphe ends terminating in hardly visible terminal fissures. Axial area very narrow. Central area variable, forming a fascia of varying width and shape. Striae slightly radiate in the middle, becoming parallel near the apices, 22-24 striae in 10 µm.



Figs 2-72. Light microscopic micrographs. **2-25.** *Chamaepinnularia parsura* comb. nov.; **2-14.** Lectotype (BRM-E1008); **15-17.** Iconotype of *Navicula parsura* Hustedt; **18-25.** Specimens from Luxembourg (Weierbach basin); **26-53.** *Chamaepinnularia obsoleta* comb. nov.; **26-34.** Holotype (BRM-E1011); **35-39.** Iconotype of *Navicula obsoleta* Hustedt; **40-53.** Specimens from Luxembourg collected during storm events (drift) (figs 40-42) on bryophytes (figs 43-48) and on epipelic material (figs 49-53); **54-72.** *Chamaepinnularia evanida* (Hustedt) Lange-Bertalot. **54-60.** Lectotype (BRM-E986); **61-62.** Iconotype of *Navicula evanida* Hustedt. **63-72.** Population collected on moss vegetation from the riparian zone of the Weierbach catchment (Luxembourg).

Externally, proximal raphe endings weakly expanded towards the same side, distal raphe fissures both hooked to the same side but opposite to the proximal side. Internally, proximal raphe ends unilaterally hooked while distal raphe ends terminating internally with a small helictoglossa. Externally, striae occluded by thin hymenes. Internally, striae consisting of two pores: one small and rounded located on the valve face/mantle junction with the second one, elongated, located on the valve face.

Remarks: The taxon is illustrated in Krammer & Lange-Bertalot (1986, pl. 76, figs 8-10) but has been rarely recorded as can be seen in the sparse literature data. Besides the findings from the type locality (Bremen, Germany), other records are those of Werum (2001) and Werum & Lange-Bertalot (2004, p. 269, pl. 39, figs 1-3) from the Taunus and Spessart mountains (Gelnhausen, Germany) and Loncin *et al.* (1998) from forest catchments in the Belgian area of the Ardennes (close to

Table 3. Maximum relative abundance (%) of selected *Chamaepinnularia* species observed in the stream drift during storm events in the Weierbach catchment (Luxembourg)

Sample type	Date	Code	<i>C. evanida</i> (%)	<i>C. obsoleta</i> (%)	<i>C. parsura</i> (%)
Storm event drift	18-Jul-2011	WEI-683	2.7	5.9	1.0
Storm event drift	6-Aug-2011	WEI-766	8.9	4.7	3.4
Storm event drift	6-Aug-2011	WEI-767	10.2	3.1	4.6

the Weierbach basin, present study). Thus according to Lange-Bertalot & Steindorf (1996) the taxon is considered very rare and aerophilic, typically from bryophytic habitats located nearby acid waters. The correct identification of other records from aerial habitats in Hawaii Islands (Rushforth *et al.*, 1984) and from karstic rivers in China (Wang *et al.*, 2009a, b) needs confirmation.

We found *Chamaepinnularia parsura* in 65 samples collected in mosses, litter, herbaceous vegetation and epipellic sediments from the Weierbach basin, usually in low relative abundances (min = 0.2%, max = 4.6%, mean = 1.1%, SD = 0.92%). The maximum relative abundance was found in drift samples collected during summer storm flood events (Table 3). This taxon is not included in the ecological list of Van Dam *et al.* (1994).

***Chamaepinnularia obsoleta* (Hustedt) C.E. Wetzel *et Ector* comb. nov.**

Figs 26-53, 77-83

Basionym: *Navicula obsoleta* Hustedt 1942, *Ber. Deutsch. Bot. Ges.* 60, p. 69, figs 12-16, [non Hustedt 1945, *Archiv für Hydrobiol.* 40 (4), p. 884 (*sic*)].

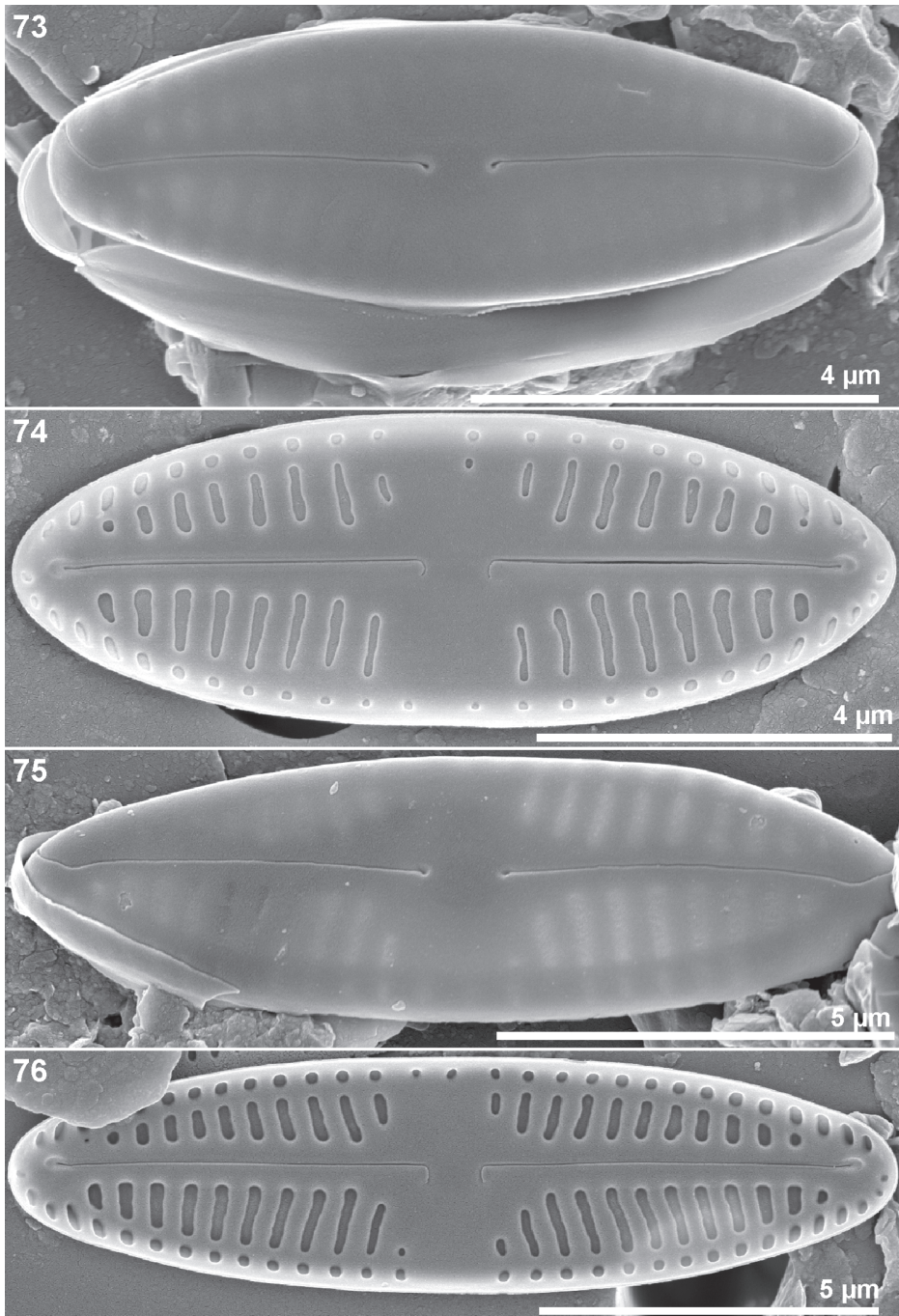
Synonyms: *Navicula perfidissima* Lange-Bertalot 1989 in Lange-Bertalot & Krammer, *Bibliotheca Diatomologica* 18, p. 162, pl. 70, figs 22-25; *Chamaepinnularia rexii* J. Veselá *et* J.R. Johansen 2009, *Diatom Research* 24 (2), p. 465, figs 120-135, 192-194.

Holotype: Slide BRM-N2/80, sample E1011 (Hustedt Collection, Bremerhaven).

Type locality: “Hasbruch, Bach b. d. Jagdhütte an Lebermoos über Wasser, 03.05.1937”, Land Bremen, Germany (Lat. 53.25, Long. 8.75).

Morphology: Valves lanceolate with sharply rounded, rarely protracted ends. Observed range of valve dimensions ($n = 20$): length 5.5.0-12.0 μm , width 2.0-2.5 μm , 23-26 striae in 10 μm . Axial area narrow, linear. Central area distinct, sometimes formed by one or two shortened striae on each side. Raphe branches filiform, proximal raphe ends with central pores slightly expanded, distal raphe ends barely seen in light microscope. Externally, raphe filiform with weakly expanded proximal ends and hooked distal fissures. Internally, proximal raphe ends unilaterally weakly deflected, with small helictoglossae at the distal raphe ends. The striae are slightly radiate and interrupted at the valve face-mantle junction. One elongated pore located on the valve mantle with the second, longer, located on the valve face. Externally valve face hymenes usually perforated on the extremities of the pores (visible on intact valves, e.g. Figs 77, 81-82) giving the impression of a line of perforations along the apical raphe sternum. Connective bands fimbriate, open, lacking perforations.

Remarks: The species was collected originally from bryophytes nearby a stream in Bremen, Germany (Hustedt, 1942) and it has been poorly recorded in the literature since its description. The taxon was found in soil samples from North America (Graveline Bay Marsh, Mississippi, U.S.A) associated with *Juncus*



Figs 73-76. *Chamaepinnularia parsura* comb. nov. SEM of external and internal views; **73-74**. Lectotype (BRM-E1008); **75-76**. Paralectotype (BRM-E1011).

roemerianus Scheele (Sullivan & Moncreiff, 1988) and also recorded in paleolimnological studies of lakes in the region of the Hudson Bay (northern Québec) by Fallu & Pienitz (1999).

European specimens were registered and illustrated by Werum & Lange-Bertalot (2004, pl. 39, figs 4-5) as “(?) *Navicula(dicta) parsura* Hustedt” in samples from the Spessart Mountains (Germany) and by Denys (2009) who found the taxon in sediment samples from “Lake Kraenepoel” (Aalter, Eastern Flanders, Belgium). Also Kapetanović *et al.* (2011, p. 143, fig. 114) illustrate the taxon under SEM, wrongly using the epithet of *Chamaepinnularia evanida*. In the Southern hemisphere the taxon was recorded by Tibby (2004) in southeastern Australian water storages (Victoria and New South Wales) and by Reid (2005) who registered the species in lakes of New Zealand.

Interesting populations of a taxon identified as “*Naviculadicta* (?nov.) spec. cf. *Navicula obsoleta* Hustedt” observed by Rumrich *et al.* (2000, p. 380, pl. 70, figs 19-27) from Chilean samples seem to belong to yet another similar taxon distinguishable mainly by its distinct rhombic central area. Similar taxa were also described from Finland – *Chamaepinnularia reinventa* subsp. *reinventa* Lange-Bertalot *et* Wydrzycka and from Costa Rica – *Chamaepinnularia reinventa* subsp. *urtroquarea* Wydrzycka *et* Lange-Bertalot and *Chamaepinnularia resalutata* Lange-Bertalot *et* Wydrzycka (Wydrzycka & Lange-Bertalot, 2001). *Chamaepinnularia reinventa* and *C. resalutata* were found in both countries under similar ecological conditions: low conductivity, oligo-dystrophic and acid environments (pH ca. 4.0).

Veselá & Johansen (2009) described *Chamaepinnularia rexii* J. Veselá *et* J.R. Johansen from the Kamenice River (Bohemian Switzerland National Park, Czech Republic) and make their diagnosis against *C. evanida* and *C. wiktoriae* (Witkowski *et* Lange-Bertalot) Witkowski *et al.*, a typical fresh to brackish water species from the Gulf of Gdansk, Baltic Sea (Witkowski *et al.*, 2000). However, after the analysis of Hustedt’s type material, no differences (ultrastructural nor morphometric) were found between *Navicula obsoleta* and *Chamaepinnularia rexii*, which henceforth must be treated as a taxonomical synonym of the former species.

Navicula obsoleta shows some resemblances with *Navicula perfidissima* Lange-Bertalot (Lange-Bertalot & Krammer, 1989, p. 162, pl. 70, figs 22-25) that conforms to the concept of Hustedt (1942) and must also be considered a taxonomical synonym. The taxon had a wide morphological concept until recently, when Reichardt (2006, fig. 35) working with samples from Germany (Schwarzachklamm, Northern Bavaria) clarified the previous broad concept of the taxon illustrated by Krammer & Lange-Bertalot (1986, pl. 76, figs 17-20) and Simonsen (1987, pl. 387, figs 14-21), and designated a new lectotype corresponding to the original drawings of Hustedt (1942, figs 8-11), which clearly show more linear forms than those illustrated by the mentioned authors.

Thus, the only illustrations in Krammer & Lange-Bertalot (1986) corresponding to *Navicula obsoleta* Hustedt are the figures 17 and 18 on Plate 76 (excluding figs 19-20), while in Simonsen (1987) *N. obsoleta* is illustrated on Plate 397, figures 14, 18, 19 and 21 (excluding figs 15, 16, 17 and 20). The taxon is considered as very rare and vulnerable in the “Red List” species from Germany and Hungary (Lange-Bertalot & Steindorf, 1996; Németh, 2005).

Chamaepinnularia obsoleta was observed in 78 samples we collected in mosses, litter and herbaceous vegetation and as the previous species usually in low relative abundances (min = 0.2%, max = 5.9%, mean = 1.8%, SD = 1.01%). The maximum relative abundance was found in drift samples we collected during summer storm events (Table 3). This taxon is not included in the ecological list of Van Dam *et al.* (1994).

Chamaepinnularia evanida (Hustedt) Lange-Bertalot**Figs 54-72, 84-88**

Basionym: *Navicula evanida* Hustedt 1942, *Ber. Deutsch. Bot. Ges.* 60, p. 66, figs 20-21.

Synonym: *Navicula ventosa* Hustedt 1957, *Abh. naturw. Ver. Bremen* 3, p. 281, figs 28-31.

Lectotype: Designated by Simonsen (1987, p. 267): Slide BRM-N2/88, sample E986 (Hustedt Collection, Bremerhaven).

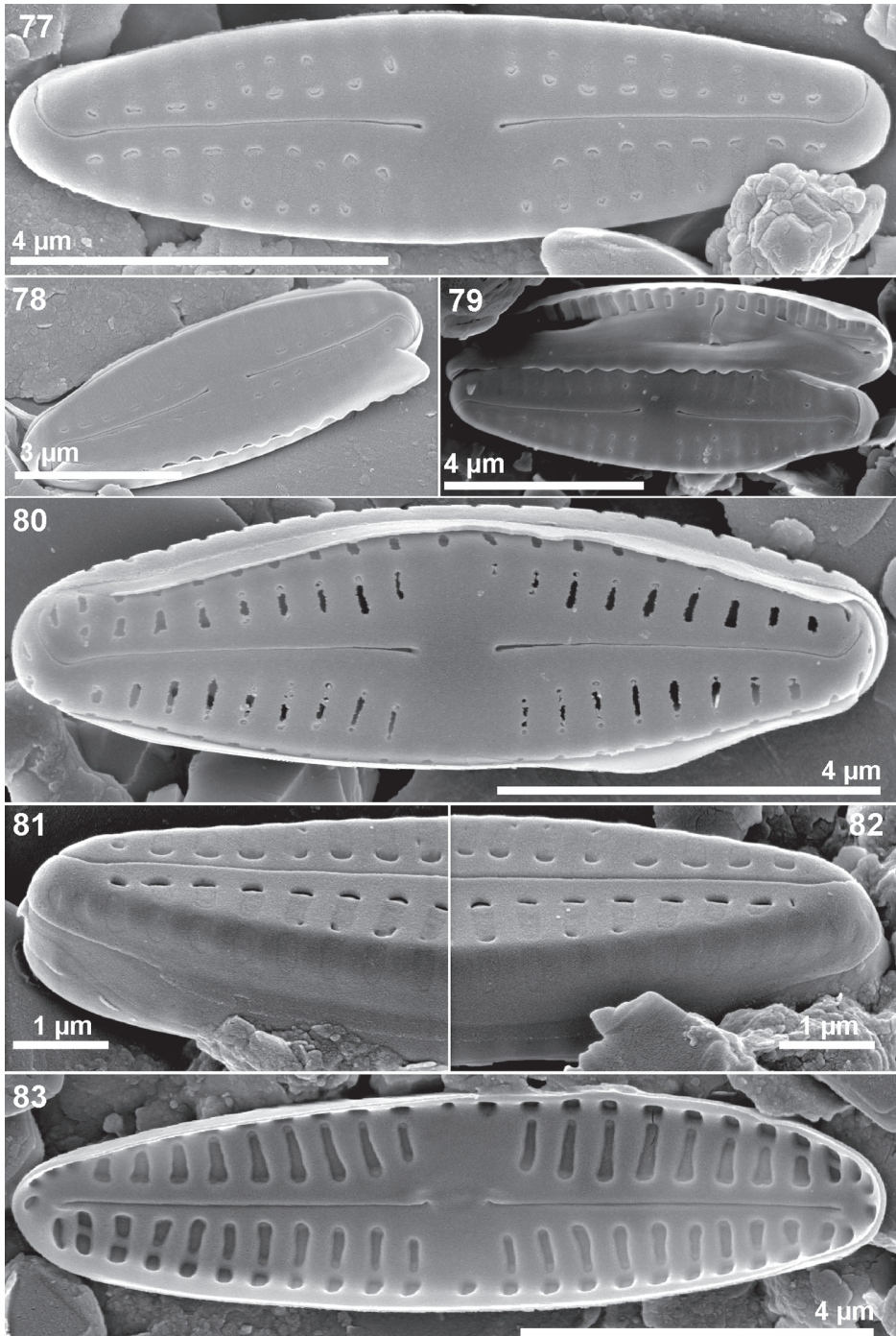
Type locality: “Wümmingen, Straßengraben am Weg Rothlake – Hellwege, Lebermoos über Wasser, 12.02.1934”, Land Bremen, Germany (Lat. 53.25, Long. 9.25).

Morphology: Valves elliptical-lanceolate to rhomboid-lanceolate with obtusely rounded ends. Observed range of valve dimensions ($n = 30$): length 6.8-11.0 μm , width 2.8-3.2 μm , 28-30 striae in 10 μm . Axial area narrow, widening towards the central area. Central area rhomboid to elliptical, no fascia present. Raphe filiform with rounded central pores and hooked terminal fissures. Striae strongly radiate in the central area becoming parallel to slightly radiate near the apices. Sternum clearly visible in LM. In SEM, striae interrupted near the valve face-mantle junction. Externally, striae on the valve face composed by one large pore occluded by thin hymenes usually depressed on the extremities of the pore. Internally, proximal raphe ends almost straight, but weakly deflected and towards the same side while distal raphe ends terminating on a small helictoglossa. Internally, striae consist of one elongated valve face areola and one smaller one located on the valve mantle. A longitudinal line of silica is placed near the valve face-mantle junction between the areolae.

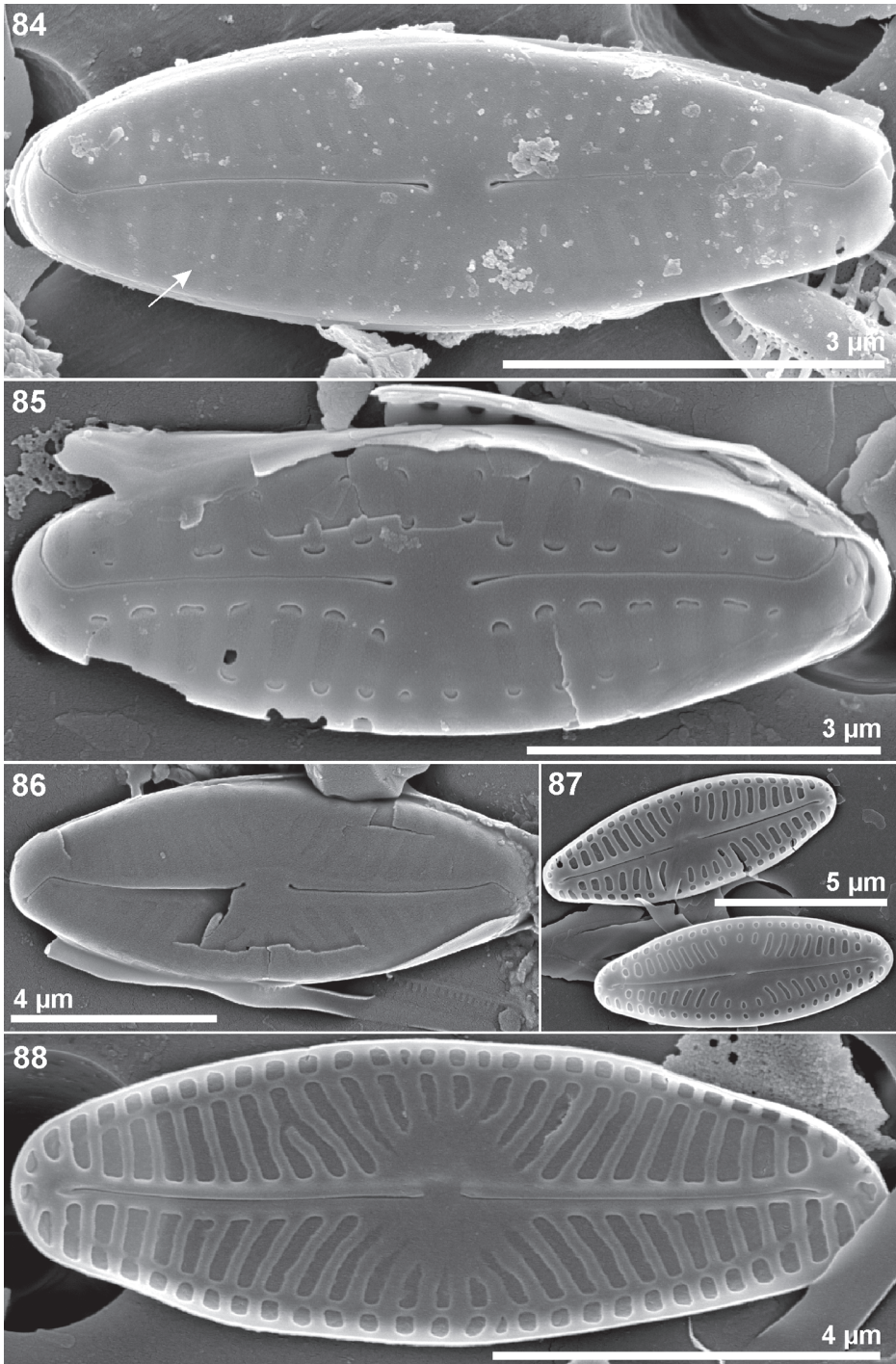
Remarks: The taxon was firstly described from aerial habitats, but has a wide ecological range for several environmental conditions in freshwater running waters (Hofmann *et al.*, 2011). It is considered as an acidophilous diatom (Håkansson, 1993) and it can be found in mesotrophic and oligosaprobic conditions (Van Dam *et al.*, 1994). The species has also been widely reported from soils and moss-inhabiting diatom communities from Antarctic and sub-Antarctic regions (e.g. Van de Vijver *et al.*, 2002, 2004, 2008; Van der Putten *et al.*, 2008; Moravcová *et al.*, 2010).

From South America the taxon is reported by Morales *et al.* (2007, p. 692, fig. 58) from Alpine streams in Bolivia, while in North America Stoermer *et al.* (1999) list the species as occurring in the Laurentian Great Lakes region. The distribution range is large including records from south Australian rivers (Victoria, New South Wales and Queensland) by Chessman *et al.* (2007).

The taxon has an unclear identity and the taxonomical discussions concerning its identity date back to Lange-Bertalot & Rumrich (1981) who illustrated the type material of *Navicula ventosa* Hustedt. Later, Krammer & Lange-Bertalot (1986, p. 232) changed their opinion concerning the placement of the taxon and considered *N. ventosa* as a synonym of *Navicula evanida*. Recently Whittington *et al.* (2003) observed the species in sedimentary samples dating from the Holocene on Shetland Islands. Indeed the LM, TEM and SEM pictures presented by Lange-Bertalot & Rumrich (1981, figs 44-49, 73, 74, 85, 86) correspond to the type material of *Navicula evanida* here analyzed. Werum & Lange-Bertalot (2004, pl. 81, fig. 7) also illustrated *Chamaepinnularia evanida* from Germany using SEM. The same authors also show a second picture under the epithet *C. evanida*; however, the second SEM picture (Werum & Lange-Bertalot, 2004, pl. 83, fig. 6) clearly corresponds to *Chamaepinnularia obsoleta*. Due to its rarity we were unable to obtain more SEM illustrations of *C. evanida* from the type material.



Figs 77-83. *Chamaepinnularia obsoleta* comb. nov. SEM of external and internal views; **77-78, 81-83**. Holotype (BRM-E1011); **79**. Specimen collected on the Weierbach drift during winter (November 2010); **80**. Specimen collected on moss vegetation in the riparian zone of the Weierbach catchment (Luxembourg).



Figs 84-88. *Chamaepinnularia evanida* (Hustedt) Lange-Bertalot. SEM of external and internal details; **84**. Holotype (BRM-E986); **85**. Specimen from moss vegetation from riparian zones in the Weierbach catchment; **86**. Sample from Bremen, Germany (BRM-E1008); **87-88**. Specimens collected on moss vegetation from riparian zone of the Weierbach catchment (Luxembourg).

Chen *et al.* (2008) found that an optimal phosphorus concentration for the taxon is around $90 \mu\text{g L}^{-1}$ for total phosphorus (TP) from lakes in the Irish ecoregion. We observed *C. evanida* in 96 samples (freq. occurrence = 49%) collected on bryophytes (4 samples), drift during baseflow (5 samples), epilithon (11 samples), herbaceous vegetation (4 samples) and on leaves collected in the riparian zone (9 samples). The taxon was observed with low relative abundances in the 96 samples (mean = 2.1%, SD = 0.97%) and was present in 62 samples collected during storm events reaching 10.2% of relative abundance (Table 3).

In spite of not being observed in samples collected in Luxembourg neither from bryophytic material observed by Hustedt from Germany, the following species deserve a new taxonomic placement at the genus level. The combinations are based on bibliography search and analysis of published pictures:

***Chamaepinnularia brevissima* (Hustedt) C.E. Wetzel *et* Ector comb. nov.**

Basionym: *Navicula brevissima* Hustedt 1937, *Archiv für Hydrobiologie*, Suppl. 15, p. 273, pl. 19, figs 22-24.

Taxon described by Hustedt (1937) from a freshwater acid (pH: 4.2-4.5) environment in Java (Telaga Warn). Recently the species was observed by Cocquyt (2007) in samples collected from Hausburg Tam, a glacial lake located in the Alpine zone of Mount Kenya. It clearly presents striation pattern and ultrastructure conforming to the genus *Chamaepinnularia* under scanning electron microscopy. The taxon is a pantropical freshwater species (Cocquyt, 1998) that we have not observed in our catchment.

***Chamaepinnularia perfidissima* (Lange-Bertalot) C.E. Wetzel *et* Ector comb. nov.**

Basionym: *Navicula perfidissima* Lange-Bertalot 1989, *Bibliotheca Diatomologica* 18, p. 162, pl. 70, figs 22-25^{*}.

Although no ultrastructural observations were made from the type material of *Navicula perfidissima* Lange-Bertalot, a species originally described from aerial habitats in Scotland, the taxon shows great resemblance with *Chamaepinnularia obsoleta* (Hustedt) C.E. Wetzel *et* Ector: the striation pattern, valve outline and morphometric values (length, width and number of striae in $10 \mu\text{m}$) are identical in the light microscope. For this reason we propose to place the taxon in the genus *Chamaepinnularia*.

***Chamaepinnularia ventosa* (Hustedt) C.E. Wetzel *et* Ector comb. nov.**

Basionym: *Navicula ventosa* Hustedt 1957, *Abh. naturw. Ver. Bremen* 34, p. 281, figs 28-31.

Based on light, scanning and transmission electronic micrographs provided by Lange-Bertalot & Rumrich (1981), the areolae ultrastructure of *Navicula ventosa* clearly fits with the current concept of the genus *Chamaepinnularia* and for this reason, we propose the combination above.

FINAL CONSIDERATIONS

It is well known that diatoms are a ubiquitous component of most aquatic ecosystems, and they also occur in moist terrestrial habitats, such as soils, rock surfaces or epiphytes (Hoffmann, 1989; Ettl & Gärtner, 1995). As such, the so-called drift diatoms have the potential to link the terrestrial and aquatic worlds and trace water sources and hydrological connectivity at the watershed scale (Pfister *et al.*, 2009).

The taxa presented in this study are typically known as having preferences for terrestrial habitats, mainly living epiphytically on bryophytes (Hustedt, 1942), although some of them can show significant relative abundances in drift samples during storm events (see Table 2). Pfister *et al.* (2009) working in the Attert River basin, from which the Weierbach is a sub-catchment, already showed that during storm events the drift community changes completely, mobilizing diatoms living on wet and moist or temporarily dry terrestrial habitats. The authors suggested a connection between the riparian/upland transition zone and the stream during the rainfall events, whereas during low flow conditions aquatic diatom species dominate the drift samples.

In the Weierbach creek, benthic diatom communities are usually dominated by “well-known” species [e.g. *Achnantheidium kranzii* (Lange-Bertalot) Round *et* Bukthiyarova, *Achnantheidium subatomoides* (Hustedt) O. Monnier, Lange-Bertalot *et* Ector, *Fragilariforma virescens* (Ralfs) D.M. Williams *et* Round, *Eunotia botuliformis* F. Wild, Nörpel *et* Lange-Bertalot, *Eunotia minor* (Kützing) Grunow, *Eunotia paratridentula* Lange-Bertalot *et* Kulikovskiy, *Achnanthes saxonica* Krasske *in* Hustedt, *Planothidium lanceolatum* (Brébisson *ex* Kützing) Lange-Bertalot and *Pinnularia perirrorata* Krammer]. However, many poorly known and rare terrestrial species are quite abundant in this catchment and our future investigations will evaluate their potential for improving our understanding of hydrological and ecological catchment functioning.

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