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FACULTY OF SCIENCE
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Ecology, taxonomy and biogeography of diatoms (Bacillariophyta) of Ile Amsterdam and Ile Saint-Paul (TAAF, Southern Indian Ocean)

Ph.D. Dissertation

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Abstract

This thesis brings information about the diatom diversity and taxonomy of two isolated, volcanic islands, Ile Amsterdam and Ile Saint-Paul (TAAF, Southern Indian Ocean).

The first part of the thesis focuses on the ecological preferences of the freshwater and moss-inhabiting diatom flora of Ile Amsterdam, its biogeographical position within the southern Indian Ocean Province, and the different diatom communities in relation to several habitat characteristics. One chapter is devoted to the preliminary results of the terrestrial diatom flora of Ile Saint-Paul. A series of physicochemical variables have been measured (if possible) on Ile Amsterdam to allow specific characterisation of the ecological preferences of the observed diatom flora. During this study, more than 400 samples from three different habitat types (freshwater habitats, mosses and soils) have been analysed, resulting in the observation of a total number of 146 diatom taxa, belonging to 41 genera. Main factors influencing species composition of diatom assemblages appeared to be specific conductance, sulphate, pH and moisture content. The biogeographical analysis showed that 19% of all observed taxa can be considered endemic to Ile Amsterdam or Ile Saint-Paul, with an additional 14% showing an exclusive sub-Antarctic distribution.

One of the main objectives of this study was to revise the diversity of the dominant genera (*Pinnularia*, *Humidophila* and *Luticola*) on Ile Amsterdam and Ile Saint-Paul based on a modern morphological species concept. The outcomes of this revision can be found in the second part of this thesis. The study resulted in the description of sixteen new taxa. Detailed morphological descriptions of these taxa are given based on both light (LM) and scanning electron microscopy (SEM) observations. The new taxa are morphologically and ecologically characterized comparing each of them with all at present known species and notes on their ecology, biogeography and associated diatom communities are added. Finally, a description of a new centric diatom genus, *Ferocia*, is presented in Appendix 1.

A comparison with the other sub-Antarctic islands in the southern Indian Ocean clearly demonstrated the unique floristic situation of the islands. The results of this thesis indicate

the presence of a highly specific diatom flora on the investigated islands, containing a large number of species with a very restricted, even sometimes endemic distribution, contrary to the generally accepted ideas about the cosmopolitan nature of micro-organisms worldwide. All results will be used in further (paleo)-ecological and taxonomical research.

Abstrakt

Tato práce přináší informace o druhové bohatosti a taxonomii rozsivek dvou malých, izolovaných vulkanických ostrovů, ostrova Nový Amsterdam a ostrova Svatého Pavla, které jsou součástí francouzského zámořského teritoria v jižním Indickém oceánu.

V první části práce najdeme výsledky ekologické studie sladkovodních a mechy obývajících rozsivek ostrova Nový Amsterdam. Práce se věnuje zejména zhodnocení vlivu podmínek prostředí na složení různých rozsivkových společenstev na ostrově. V průběhu terénních prací byly měřeny fyzikálně-chemické parametry prostředí. Součástí studie je srovnání biogeografických vztahů a rozsivkové flóry ostrova Nový Amsterdam s ostatními ostrovy v jižním Indickém oceánu. Jedna kapitola je věnována předběžným výsledkům ekologické studie terestrických rozsivek ostrova Svatého Pavla. Během této disertační práce bylo analyzováno více než 400 vzorků, které byly odebrány ze tří různých typů habitatů (sladkovodní, půdní a vzorky odebrané z mechů). Celkově bylo na obou ostrovech nalezeno 146 druhů rozsivek náležících k 41 rodům. Výsledky analýz ukazují, že mezi hlavní faktory ovlivňující druhové složení rozsivkových společenstev patří konduktivita, obsah síranů, pH a vlhkost. Dle biogeografické analýzy patří 19% všech nalezených druhů k endemitům sledovaných ostrovů a dalších 14% druhů vykazuje omezený subantarktický výskyt.

Jedním z hlavních cílů práce bylo provést taxonomickou revizi dominantních rodů (*Pinnularia*, *Humidophila* a *Luticola*) obou ostrovů, založenou na moderním morfologickém konceptu. Výsledkem této revize je popis šestnácti nových rozsivkových druhů. V práci je uveden jejich detailní morfologický popis na základě pozorování jak ve světelném, tak ve skenovacím elektronovém mikroskopu. Morfologie a ekologie nových druhů je srovnána s podobnými, již popsanými taxony. Ke každému nově popsanému druhu jsou připojeny poznámky o jeho ekologii, biogeografii a charakteristických rozsivkových společenstvech, ve kterých se daný druh nejčastěji vyskytuje. Studii doplňuje Příloha č. 1, která obsahuje popis nového rodu centrických rozsivek, *Ferocia*.

Výsledky srovnání s ostatními subantarktickými ostrovy dokazují vysokou specifitu rozsivkové flóry ostrova Nový Amsterdam. Rozsivková flóra obou ostrovů se vyznačuje

vysokým podílem nových (endemických) druhů a druhů s omezeným subantarktickým výskytem. Jedinečnost rozsivkové flóry těchto dvou malých izolovaných ostrovů tak vytváří další trhlinu v teorii kosmopolitního výskytu organismů. Výsledky práce budou použity v dalším (paleo)-ekologickém a taxonomickém výzkumu obou ostrovů.

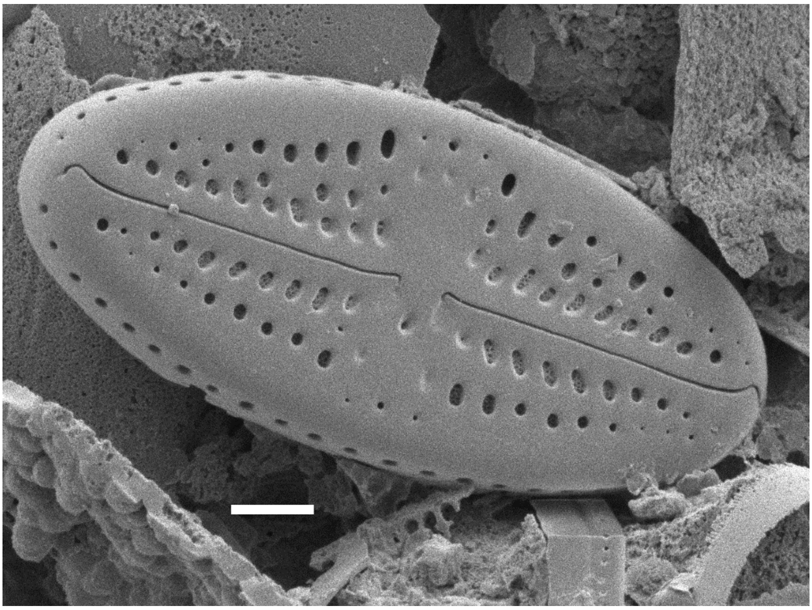
What did the mermaid wear to her math class? An algae-bra

Preface

England, 1703

Once upon a time and a very good time it was there was a man looking with his simple microscope at roots of the pond-weed *Lemna* and ' ... saw adhering to them (and sometimes separate in the water) many pretty branches, composed of rectangular oblongs and exact squares'. And this was the day, the first diatom was recorded.

Nowadays, more than 3 centuries later, we can examine the finest ultrastructure of the diatom frustule in SEM, observe precise cross sections in TEM, sequence the diatom genes and still, every time I look into the light microscope at a new sample, I have the exact thrilling feeling of excitement the anonymous English gentleman must have had in 1703.



Luticola ivetaiana Chattová & Van de Vijver, scale bar = 1 µm

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Smart and beautiful? She must be an algologist!

My special thankful thoughts go to Markétka Fránková, my first teacher who introduced me to the fantastic microscopic world of algae and for providing the opportunity to join the ERASMUS exchange program, an internship at the University of Antwerp and in the algology lab of Bart Van de Vijver, in Botanic Garden Meise. I would like to thank Myriam de Haan for preparing the slides and for help with the scanning electron microscopy. Christine, Anneke and Eveline are thanked for making my stay in Belgium much more pleasant. Sincere thanks go to Prof. Louis Beyens and Prof. Ivan Nijs for their help with the student affairs at the University of Antwerp. I am especially grateful to my consultant, Bart, for all the help, energy, time, opinions and advices he gave me. He knows the best that without his help and support this thesis would not have been possible. Ik ben jou zeer dankbaar, dank je wel, Bart!

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I am grateful to my family for all the support, endless freedom and love they gave me, not only during this thesis, but during my whole studies.

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Picture of the arriving deck at Ile Amsterdam (©Bart Van de Vijver)

Content

Author contributions to the papers presented in the Ph.D. Dissertation 13

Introduction 15

Main aims of the Ph.D. Dissertation 23

Methods 25

General results and conclusion.. 33

References 45

Paper I 54

Paper II 74

Paper III 109

Paper IV 146

Paper V 175

Appendix 1: Paper VI..198

Curriculum vitae 216

Author contributions to the papers presented in the thesis

Paper I

Chattová, B., Lebouvier, M., & Van de Vijver, B. 2014: Freshwater diatom communities from Ile Amsterdam (TAAF, southern Indian Ocean). *Fottea* 14: 101–119.

BCH and BVDV conceived the ideas and led the writing, BCH did the microscopical observations, photographed and analyzed the diatom flora, ML and BVDV performed the field sampling, ML commented on the manuscript.

Paper II

Chattová, B., Lebouvier, M., Syrovátka, V. & Van de Vijver, B. 2017. Moss-inhabiting diatom communities from Ile Amsterdam (TAAF, southern Indian Ocean) (manuscript)

BCH and BVDV conceived the ideas, BCH analysed the diatom flora and led the writing, ML performed the field sampling, VS did the statistical analyses, BVDV performed the field sampling and is a co-author of the text.

Paper III

Van de Vijver, B., Chattová, B., Metzeltin D., & Lebouvier M. 2012. The genus *Pinnularia* (Bacillariophyta) on Ile Amsterdam (TAAF, Southern Indian Ocean). *Nova Hedwigia Beiheifte* 141: 201–236.

BVDV conceived the ideas and led the writing, BCH analysed part of the diatom data and is author or co-author of the new species descriptions and a co-author of the text, DM provided stimulating discussions, is co-author of the text of new species descriptions, ML performed the field sampling, discussed the data and made important comments to the text. All authors discussed the ideas and commented on the manuscript.

Paper IV

Chattová, B., Lebouvier, M., & Van de Vijver, B. 2017. Morphological and taxonomical analysis of the terrestrial diatom genus *Humidophila* (Bacillariophyta) on Ile Amsterdam and Ile Saint-Paul (Southern Indian Ocean). *Phytotaxa* (in review)

BCH and BVDV conceived the ideas, BCH led the writing, ML and BVDV performed the field sampling, BVDV discussed the data and made important comments to the text. All authors discussed the ideas and commented on the manuscript.

Paper V

Chattová, B., Lebouvier, M., De Haan, M., & Van de Vijver, B. 2017. The genus *Luticola* (Bacillariophyta) on Ile Amsterdam and Ile Saint-Paul (Southern Indian Ocean) with the description of two new species. *European Journal of Taxonomy* (submitted)

BCH and BVDV conceived the ideas, BCH led the writing, ML and BVDV performed the field sampling, MDH prepared the samples, BVDV discussed the data and made important comments to the text. All authors discussed the ideas and commented on the manuscript.

Paper VI

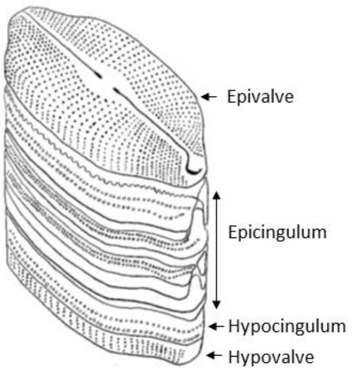
Van de Vijver, B., Chattová, B., Lebouvier, M., & Houk, V. 2017. *Ferocia* gen. nov., a new centric diatom genus (Bacillariophyceae) from the sub-Antarctic region. *Phytotaxa* (submitted)

BVDV collected the data, conceived the ideas and wrote the manuscript, BCH contributed in analyzing the samples and commented on the manuscript, ML performed the field sampling and commented on the text, VH is a co-author of the text and of the new genus description. All authors discussed the ideas and commented on the manuscript.

Introduction: Diatoms

Diatoms are eukaryotic unicellular microorganisms, characterised by their unique, silica-impregnated cell wall known as a frustule. This frustule consists of two equal halves called epivalve and hypovalve, connected by girdle elements enclosing the algal cell. The two sets of girdle elements are referred to as the epicingulum and hypocingulum (Fig. 1).

Each frustule has one valve formed immediately after the last cell division and an older valve. One set of elements is associated with the older valve, and one with the newer. The older valve, together with the girdle elements (cingulum) associated with it, is called the epitheca while the newer valve and its associated elements is the hypotheca (Round *et al.* 1990). Diatom classification depends to a great extent upon the valve structure (Fig. 2).



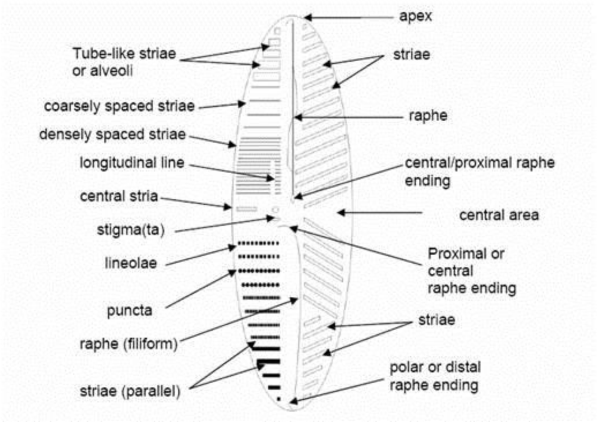


Fig. 1: Frustule of a raphid diatom showing the epivalve, epicingulum containing 4 bands, the incomplete hypocingulum and the hypovalve. Modified according to Round *et al.* 1990

Fig. 2: The detailed valve structure of a raphid pennate diatom (figure taken from the diatom cell gallery http://keywordsuggest.org

A characteristic feature of many genera is the presence of one or two longitudinal slits through the valve, together constituting the raphe system. The length, position and structure of the raphe and its endings are important taxonomic characters.

The most noticeable components of the protoplast are the chromatophores, which are usually brown because other pigments (carotenoids, diatoxanthin, diadinoxanthin and fucoxanthin) mask the colour of the chlorophylls (a, c2, and c1 or c3) (Stauber & Jeffrey 1988). Diatoms convert photosynthetic products into high-energy lipids. The lipid reserves produced by diatoms play a crucial role in the aquatic food web (Arts *et al.* 2009).

Although most diatoms are pigmented and photosynthetic, some species within the genera *Nitzchia* and *Hantzschia* can be (facultative) heterotrophic (Round *et al.* 1990).

Diatoms are the most species-rich group of algae on Earth (Mann 1999). According to Mann & Vanormelingen (2013), there are likely to be at least 30,000 and probably even ca. 100,000, diatom species by extrapolation from an eclectic sample of genera and species complexes.

The first physical remains of diatoms are from the Jurassic, and well-preserved, diverse floras are available from the Lower Cretaceous. Pennate diatoms appear in the late Cretaceous and raphid diatoms in the Palaeocene, though molecular phylogenies imply that raphid diatoms did in fact evolve considerably earlier (Sims *et al.* 2006).

The recent classification system of the eukaryotes places diatoms into the ‘Stramenopiles’ next to other heterokont protists such as Chrysophyceae and Xanthophyceae (Adl *et al.* 2012). According to valve outline and valve pattern (radial organization vs bilateral organization), diatoms are further subdivided into two main groups: Bacillariophytina and Coscinodiscophytina. Coscinodiscophytina have circular (rarely elliptical) valve outline, with valve pattern radiating from a central or subcentral circular annulus and oogamous sexual reproduction. Bacillariophytina are characterized by a bipolar or multipolar valve outline with valve pattern radiating from a central circular or elongate annulus or from a sternum and by oogamous (Mediophyceae) or isogamous (Bacillariophyceae) sexual reproduction.

Reproduction

Diatoms reproduce primarily via asexual mitotic division. After the division, both epitheca and hypotheca of the mother cells will become epitheca in the next generation, one for each daughter cell. The mitotic products result in one daughter cell equal in size to the mother cell and one daughter cell smaller than the mother cell. Repeated division results in a gradual decrease in population mean cell size over time (Stoermer & Smol 2010). Size is restored via an auxospore. Auxospore formation is usually associated with sexual reproduction. The auxospore further develops into a single, maximally sized, cell. This initial cell may differ from the vegetative cell in valve outline and structure.

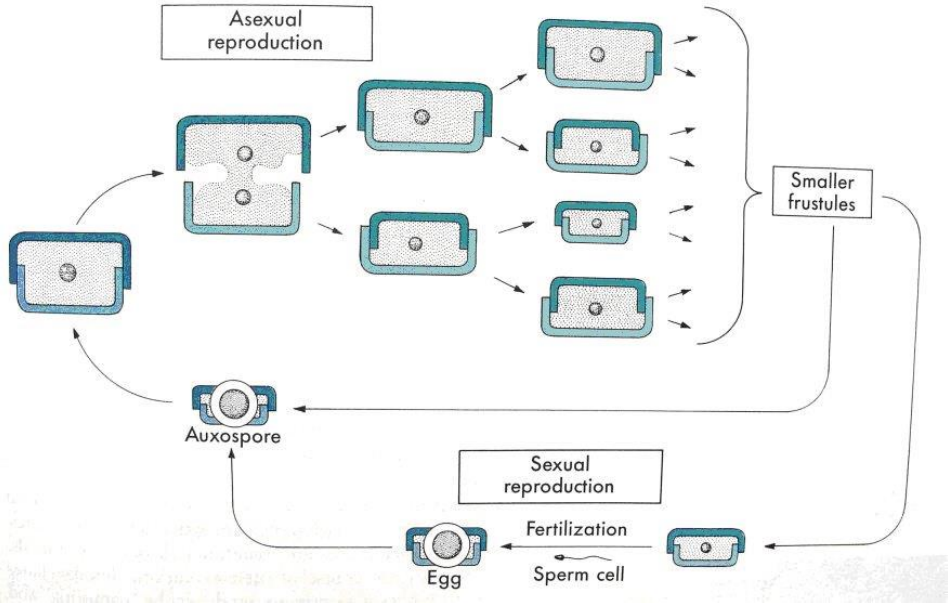


Fig. 3: Simplified diagram of a diatom life cycle. Each daughter cell keeps one half of the frustule and grows a smaller half. As a result, the average size of diatom cells gets smaller after each division cycle. In order to restore the cell size of a diatom population, sexual reproduction and the production of an auxospore must occur. (figure taken from www.bio.vu.nl)

Ecology and applications of diatoms

Diatoms are abundant in almost all aquatic habitats except the hottest and most hypersaline, where they occupy two major habitats: open water (planktonic) and moist or submerged surfaces (benthic). Benthic diatoms are much less understood ecologically than planktonic diatoms. The benthos is more diverse than the plankton, both in terms of the numbers of species and the life forms present. The attached communities may be classified according to their substrata: epipsammic (attached to sand grains), epilithic (attached to stones), epiphytic (attached to plants) and epipelic (associated with mud). By growth habit, except planktonic and benthic, we further distinguish species with adaptations for tychoplanktonic and subaerial existences (Round *et al.* 1990). Diatoms have global significance in biogeochemical cycles of several elements, in particular silica and carbon, and provide at least 40 % of the oceanic net primary production and 20 – 25 % of the world net primary production (Mann 1999). Cells are mainly solitary but some taxa form colonies and these are held together by interlocking siliceous spines, processes or ridges, by pads or stalks of mucilage, or by threads of polysaccharide.

Although the majority of diatom species are bound to aquatic habitats, a large number of diatom taxa are able to survive in non-submerged or even dry habitats such as dry mosses, humid rocks and soils. A few diatoms act as hosts for endosymbiotic organisms. The freshwater populations of *Epithemia* and *Rhopalodia* possess a unicellular, nitrogen-fixing, cyanobacterial endosymbiont in order to fix atmospheric nitrogen (DeYoe *et al.* 1992). To extend the possible habitats of diatoms, there are also a few species (mainly in the genus *Nitzschia*) living endosymbiotically in Foraminifera (Lee *et al.* 2000).

Diatoms can be used in a wide range of applications in the environmental and earth sciences. Diatoms can help us not only to analyse ecological problems related to climate change, eutrophication or acidification, but also in other fields of study such as forensics, nanotechnology and archaeology. Furthermore, we can use diatoms as excellent markers of atmospheric transport, for tracking fish and seabirds and in oil and gas exploration (Stoermer & Smol 2010). Another economic use of diatoms is the exploitation of diatomite, a soft, porous, fine-grained, lightweight, siliceous sedimentary rock produced by accumulation and compaction of diatom frustules. Diatom-rich sediments have been accumulating in marine deposits since the Late Cretaceous (~80 million years ago) and in large lakes since at least the Eocene (~50 million years ago) (Harwood *et al.* 2007). The distinctive properties of high absorption, low density and high porosity have led to the use of diatomite in filtration processes and as a light-weight filler.

Diatoms have proven to be extremely powerful indicators to explore and interpret many ecological conditions, problems and trends. Moreover, diatom remains in oceanic and freshwater sediments are valuable indicators of past environments and have been recently used to detect pH changes, in stratigraphic correlations and paleoecological reconstructions (Stoermer & Smol 2010).

Taxonomy

Traditionally, most diatom species delineation and identification is based on valve morphology (valve size, stria density, raphe structure, valve outline, striation pattern and shape of the central area), but additional ecological, molecular, physiological and reproductive behavioural data are being increasingly collected to assess species boundaries. Although molecular genetic methods are becoming widespread, easy, and inexpensive, it is doubtful whether they will ever entirely replace morphology for the primary characterization and identification of diatom species and populations. Valve morphology provides continuity with past taxonomies, is easily described, can be assessed more quicklyand cheaply than other aspects of the phenotype and is readily available (Mann 2010).

Unfortunately, the current diatom taxonomy is not without problems, David Mann (1999) did not hesitate to use the term “messy”. The paper by Spamer & Theriot (1997) discusses the problems of diatom taxonomy using a reference to a group of small celled *Stephanodiscus* Ehrenberg species. Here, misidentification, nomenclatural errors, changes in the circumscription of taxa, and a failure to document research properly have created an impressive body of information about a cosmopolitan diatom that does not exist (Mann 1999).

Moreover, recent studies show that diatoms are substantially underclassified at the species level, with many semicryptic or cryptic species (morphologically similar, but reproductively isolated) to be recognized (Sims *et al.* 2006). Studies devoted to species complexes (Mann 1989, Mann *et al.* 1999, Behnke *et al.* 2004, Mann *et al.* 2004, Beszteri *et al.* 2007, Vanormelingen *et al.* 2008a, Kermarrec *et al.* 2013, Trobajo *et al.* 2009) suggest, that many diatom species contain several subtly distinct, (semi)-cryptic entities, that are worth taxonomic recognition at the species level, and that, as a consequence, diatom species diversity has been severely underestimated rather than overestimated. It is clear that further work, using various genetic markers and isolates, will be needed to determine the full extent of cryptic speciation in many other species. Especially important is to investigate whether the segregate species are ecologically differentiated and whether they have value as indicators.

Biogeography and dispersal

Diatoms, such as other microorganisms, use passive mechanisms of dispersal between localities. Diatoms can be dispersed by animals, wind, water and humans (Kristiansen 1996). The dispersal ability of a species depends on a whole range of factors, including its morphological and physiological characteristics (adaptations for stress factors, the presence of stress tolerant resting cells and active motion) and on the characteristics of the habitat they have to overcome during the dispersal. In order to be able to disperse over long distances, diatoms should be resistant to a wide range of unfavourable conditions, such as desiccation, sudden temperature changes and UV irradiance (Souffreau *et al.* 2010, 2013).

Diatoms were believed to have unlimited dispersal capabilities and therefore to be a cosmopolitan group of microorganism, showing weak or absent latitudinal diversity gradients (Fenchel and Finlay 2004) according to the ubiquity hypothesis (Baas-Becking 1934, Finlay 2002). In contrast, using a global freshwater diatom data set, Vyverman *et al.* (2007) were able to demonstrate, that latitudinal gradients in local and regional genus richness are present and are highly asymmetric between both hemispheres. They strongly suggest that historical processes (i.e., colonization and extinction, dispersion and migration) are responsible for global patterns in regional and local diatom diversity and explain significantly more of the observed geographic patterns in genus richness than do contemporary environmental conditions.

It has been clear for some time now that cosmopolitan diatom species are not the rule and a considerable degree of endemism is apparent (Vanormelingen *et al.* 2008b). This statement is confirmed both by the recent findings of high levels of endemism among diatoms, particular in isolated areas, especially in the (sub)-Antarctic (Spaulding *et al.* 1999, Le Cohu

& Van de Vijver 2002, Van de Vijver *et al*. 2002a, 2002b, 2005, 2008a, 2010, 2012, 2014, Sabbe *et al.* 2003) and after all by the results of this thesis, contradicting the ubiquity hypothesis and indicating that the diatom communities are shaped by similar processes as those controlling macro-organism communities (Vanormelingen *et al*. 2008b).

In past, the degree of endemicity was probably masked by the historic force-fitting (Tyler 1996) of European and North American names to (sub)-Antarctic species. Force-fitting had severe consequences for our understanding of the ecology, diversity and biogeographical distribution of diatoms, as it not only stretched the morphological boundaries of many species, but also reinforced the idea that most diatom species have cosmopolitan distributions and are ecologic generalists (Kociolek & Spaulding 2000). To prevent the incorrect identifications, diatomologists should not hesitate to label unknown taxa as unknown rather than forcing it into an existing species category (Stoermer 2001).

Some may still ask, why we keep on describing more and more new species. The basic taxonomic research is extremely important for people working in “special“ habitats. More and more scientists are working in polar regions and we want to make their (and our) work more comfortable by converting those ‘cf.’s’ , aff.’s, and sp.’s to more certain, new, knowledge. Or, can any of my colleagues from our vegetation science group imagine working in the South American mountains equipped just with the central European floras?

Diatom research in the sub-Antarctic region

The early (historic) collections of diatoms from sub-Antarctic islands date back to the end of the eighteenth century. Reinsch (1876, 1879) was the first to investigate the diatom content of some samples, collected by the Rev. A. E. Eaton, who visited Kerguelen. He identified twenty-one species, belonging to thirteen genera. Two species appeared to be new. O’Meara (1877) recorded only three diatom species on nearby Marion Island. Another study of early diatomaceous gatherings on Kerguelen was made by Hemsley (1885) who listed 14 taxa. A few years later, Reinsch (1890) published a first paper on the diatom composition of South Georgia, listing ten diatom species. Most of the diatoms, however, in these studies were cosmopolitan species (e.g. *Stauroneis phoenicentreon* (Nitzsch)

Ehrenberg, and *Pinnularia viridis* (Nitzsch) Ehrenberg). Diatom species, typical of the sub-Antarctic region, were not observed. One of the first detailed studies on freshwater diatoms in this area was published by Carlson (1913). He listed fifty-five species from South Georgia and made considerable efforts to compare the recorded flora with nearby Falkland Islands, Southern Chile & Tierra del Fuego. Fukushima (1965) recorded forty-nine species from various sampling sites on South Georgia.

The terrestrial and freshwater diatom floras of the sub-Antarctic islands have been intensively studied in recent years on Kerguelen (Van de Vijver *et al.* 2001, Le Cohu 2005), Crozet Archipelago (Van de Vijver *et al.* 2002a), Heard Island (Van de Vijver *et al.* 2004b), Tristan da Cunha (Van de Vijver & Kopalová 2008, Vinšová, unpublished results) and the Prince Edward Islands (Van de Vijver & Gremmen 2006, Van de Vijver *et al.* 2008b). In 1999, Van de Vijver & Beyens published results of a preliminary survey on the terrestrial and freshwater diatoms of Ile Amsterdam. They listed 90 taxa from 24 samples. Since the taxonomy of the sub-Antarctic diatoms was not yet fully updated at that time, a new and more elaborate study on the non-marine diatom flora of the island was extremely important. Recently, the entire sub-Antarctic diatom flora is being revised using a more fine-grained taxonomy based on a better analysis and interpretation of the morphological observations. This led to the description of a large number of new species (Van de Vijver *et al.* 2002a, Van de Vijver *et al.* 2004a), some of them, especially within the genera *Eunotia* (Van de Vijver *et al.* 2008a), *Pinnularia* (Van de Vijver *et al.* 2012), *Sellaphora* (Van de Vijver & Cox 2013), *Halamphora* (Van de Vijver *et al.* 2014) being described directly from Ile Amsterdam. Furthermore, a new genus, *Microfissurata* Lange-Bertalot *et al.*, was described based on two species of which one was found on Ile Amsterdam (i.e. *Microfissurata australis* Van de Vijver & Lange-Bertalot, [Cantonati *et al.* 2009]).

Despite the many taxonomic studies published from Ile Amsterdam, the diatom flora of Ile Saint Paul remains poorly known, due to its remoteness and inaccessibility limiting fieldwork on the island. The only paper presenting diatom results on Ile Saint Paul is the description of a new *Luticola* species, *Luticola beyensii* Van de Vijver & Ledeganck (Van de Vijver *et al.* 2002b).

Main aims of the dissertation

The present thesis improves our knowledge and understanding of the diatom diversity of two small, volcanic islands, belonging to the most remote places in the world, focusing on the ecological and taxonomical characterization of freshwater and moss-inhabiting diatom communities on Ile Amsterdam and on the taxonomical analysis of two important terrestrial genera (*Humidophila* and *Luticola*) on Ile Saint-Paul. Within this work, special attention was devoted to the identification of the main environmental variables influencing the distribution of freshwater and moss-inhabiting diatom assemblages on Ile Amsterdam.
To be able to answer research questions regarding biogeography, diversity and structure of the diatom diversity on the islands, a thorough taxonomical revision of the main dominant genera was necessary. The results of such a new study provide important data especially in the light of more correct biogeographic hypotheses and may clarify the biogeographical position of the islands within the southern Indian Ocean Province.

More particularly, this thesis will focus on several key subjects:

1. What is the diatom diversity and species richness of Ile Amsterdam and Ile Saint-Paul? Is this diatom flora characteristic for isolated, oceanic islands? Can all the species be identified using the currently available literature? Do the new species have to be described?
    - ➢ To answer these questions, the morphology and taxonomy of several selected diatom genera will be analysed in more detail, together with a complete (more general) analysis of all diatoms in samples from different (micro-)habitats. Comparisons with known taxa worldwide, often after analysis of type material, will be made.

2. Is there a relation between the observed diatom community composition and the main habitat characteristic? Can typical assemblages be identified within the entire

diatom flora on Ile Amsterdam and Ile Saint Paul? Are the diatom communities influenced by specific environmental conditions?

  - ➢ These questions will be addressed by analysing and characterizing the freshwater and moss-inhabiting diatom communities of Ile Amsterdam and the terrestrial diatom communities from Ile Saint-Paul. The ecological preferences determining the freshwater and moss-inhabiting diatom communities of Ile Amsterdam will be thoroughly analysed.

3. Is the observed diatom flora mainly composed of cosmopolitan, sub-Antarctic, or even endemic taxa? How important is the proportion of unique (i.e. endemic) species? What are the similarities with other sub-Antarctic islands?
   - ➢ This important question will be answered by comparing the observed diatom flora of Ile Amsterdam with those of other Southern Ocean and sub-Antarctic islands.

General Material and Methods

A brief description of the study area and a summary of the methods used in this thesis are outlined here. More details about the statistical analyses of the data can be found in the Methods section of each paper.

Study area

The sub-Antarctic Region

The sub-Antarctic region consists of several, relatively small islands and archipelagos, situated in the southern part of the Atlantic, Indian and Pacific Ocean. According to Stonehouse (1982), the sub-Antarctic region can be subdivided into a cold-temperate sub-Antarctic part (including the Crozet archipelago, Kerguelen and Marion Island) and more warm-temperate sub-Antarctic part that is situated north of the sub-tropical convergence. The latter comprises islands such as Ile Amsterdam, Saint-Paul Island in the Indian Ocean, Gough Island and Tristan da Cunha in the Atlantic Ocean and Bounty and Snares Island in the Pacific Ocean. The oceanic islands situated in the sub-Antarctic biogeographical province are of a major interest because they remained free of human disturbance up to a recent period and their pristine specific diversity is exceptionally low, many of them with a high rate of endemism in flora and invertebrate fauna (Frenot *et al.* 2001).

Ile Amsterdam

Ile Amsterdam (77°30'E, 37°50'S) is located in the Indian Ocean close to the East Indian mid-oceanic ridge, north of the subtropical convergence (Fig. 4). In this sense, it is not a true sub-Antarctic island but its native flora growing at high altitude belongs mainly to the sub-Antarctic province (Frenot *et al.* 2001). It is one of the most isolated islands in the world, located 4200 km from South Africa, 3300 km from Antarctica and 3200 km from Australia. The closest landmass is Ile Saint-Paul situated 80 km to the south.

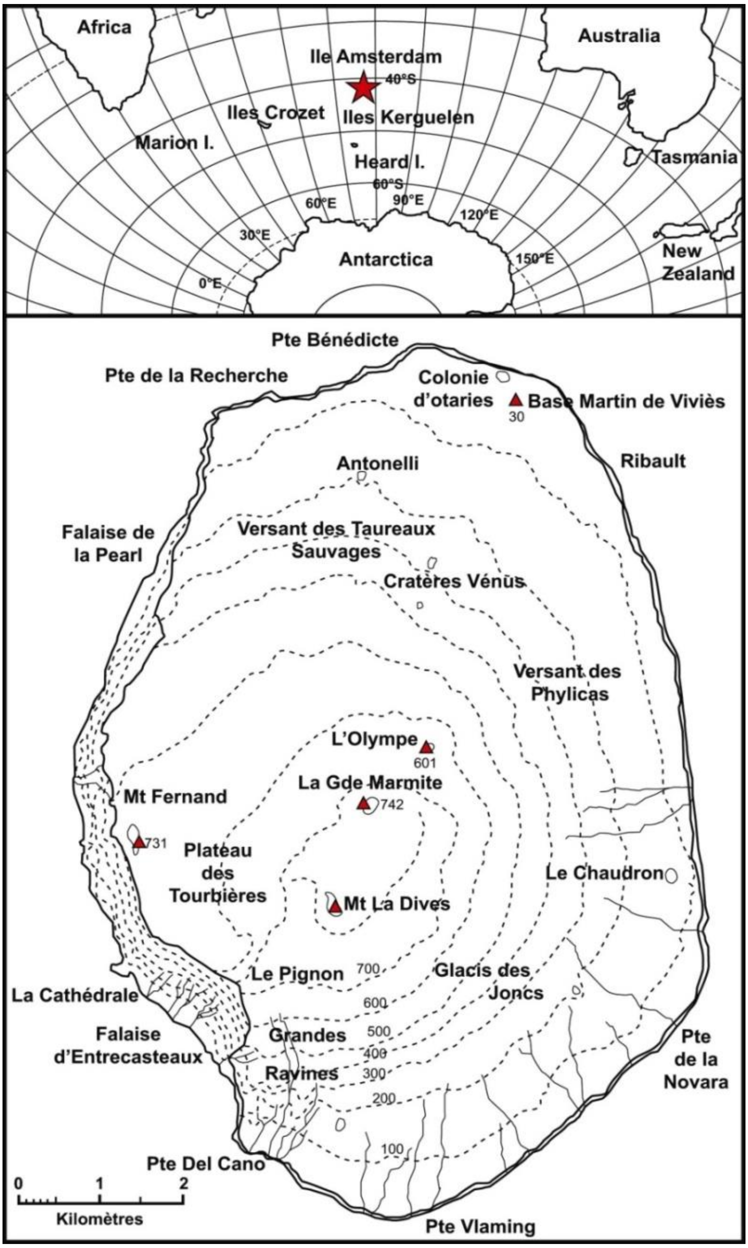


Fig. 4: Geographical position of Ile Amsterdam in the Southern Indian Ocean and detailed map of the island

History

Ile Amsterdam was discovered in 1522 by Juan Sebastián Elcano (Del Cano), a travelling companion of Magellan, on the way back to Europe after the first circumnavigation of the globe. The first recorded landing was by Willem de Vlamingh in 1696 (Micol & Jouventin 1995). Together with Ile Saint Paul, the island forms one of the districts within the Terres Australes et Antarctiques Françaises (TAAF). The TAAF is responsible for the (French) sovereignty of these islands, the French Polar Institute (IPEV) on the other hand is the central agency for research, and the Committee for the Polar Environment (CEP) provides advice on environmental protection and management issues (Lebouvier & Frenot 2007).

Physical characteristics

Ile Amsterdam is elliptical in shape, about 9.2 km long by 7.4 km wide, with a total surface of 55 km^2, culminating in the Mont de la Dives (881m a.s.l.). The entire coastline, except for two sites in the northwest, is surrounded by steep cliffs, commonly 30-60 m high, rising up to 700 m in the western part. Geologically, the island is very young and was probably formed during the last 700,000 years (Giret 1987). It is entirely volcanic. Amsterdam Island has a temperate oceanic climate with a mean annual temperature of 14°C. Relative humidity is generally high (> 80%) due to the frequency of low cloud ceilings. Precipitation is usually high with an annual average of 1127 mm distributed over 239 days and falling primarily as rain (Van de Vijver *et al.* 2008a). The austral summer (January-March) is drier (78 mm month^{-1}) than the other seasons (100 mm month^{-1}). Permanent waterbodies can only be found at the higher plateau (Fig. 5) in the central and in the south-western part of the island. Almost no other areas have (semi-permanent) waterbodies due to the steepness of the slope and the permeability of the lava tunnels, holes and fissures. Due to high relative humidity, the summit is often foggy and these conditions have allowed extensive peat development in the volcanic Caldera (Heger *et al.* 2009)

Fig. 5: The upper plateau of Ile Amsterdam with a view on Mont de la Dives, the highest point on the island (881 m) (© Bart Van de Vijver)

Flora and fauna

The vegetation, composed of only a few species reflecting its extreme isolation, is dominated by both endemic sub-Antarctic and introduced species. Only 43 native vascular plant species have been found. The number of alien species is 56 (Frenot *et al.* 2001). *Sphagnum* mosses, although absent from the other sub-Antarctic islands in the southern Indian Ocean, are omnipresent on the island, mainly on higher grounds. In the lower parts of the island, small patches of the once very extensive *Phylica nitida* Lamarck forest can be found. On the higher central plateau, the vegetation has a typical sub-Antarctic character and consists of mosses, small ferns, grasses and *Lycopodium* L. ssp. The endemic fauna is rather species-poor and comprises a few marine bird species such as the rare Amsterdam albatross (*Diomedea amsterdamensis* Roux *et al.*) and several large fur seal colonies (*Arctocephalus tropicalis* Gray) (Van de Vijver *et al.* 2008a). Other big mammals are represented by elephant seals (*Mirounga leonina* Linnaeus). Introduced mammals such as rats (*Rattus norvegicus* Berkenhout) and cats (*Felis catus* Linnaeus) have threatened the avifauna on the island. There were also numerous peat fires, often caused by sealers during the history of the island. Some of them are known to have lasted several months and caused serious damage to the vegetation, especially to the *Phylica* forest. Further damage was caused by grazing and trampling by cattle, which were introduced by a farmer in 1871 (and finally removed in 2014).

Conservation and management

The first restoration program was implemented in 1988 (Micol & Jouventin 1995): cattle were removed from the larger part of the island, a fence was erected to protect the peat bogs at altitude and the breeding area of the Amsterdam albatross, and about 10 000 *Phylica* seedlings were planted between 1988 and 1993. In 2006 the island gained the status of Nature Reserve and a new management plan is currently in place to provide greater protection for the environment and biota (Lebouvier & Frenot 2007).

Ile Saint-Paul

Ile Saint-Paul (77°31’ E, 38°43’S), a small volcanic island (Fig. 6) of only 7 km^2, is part of the Amsterdam District, the smallest of the five districts of the so-called TAAF, Terres Australes et Antarctiques Francaises. The island is situated in the southern Indian Ocean, 80 km south from Ile Amsterdam and consists of the eroded top of a single volcano, rising to 268 metres. Parts of the collapsed ancient crater resulted in the formation of a circular bay forming a protected lagoon, 1.6 km in diameter (Postec *et al.* 2010). The main feature of the island is the presence of fumaroles and so-called ‘terres chaudes’, hot places where the soil temperature can reach about 100°C (Van de Vijver & *et al.* 2002b). Around these warmer places, a subtropical flora and fauna can be observed (Gressit & Weber 1959, Trave 1974). The climate is relatively mild, wet oceanic like as on Tasmania and New Zealand, located at the same latitude. Mean sea-level temperature is 13.8°C. The coldest month is August with a mean of 11.2°C, while the warmest is February with a mean of 17.0°C. Mean annual rainfall is 1115 mm with a short dry season in summer (February-March) when evaporation exceeds rainfall (Micol & Jouventin 2002). Ile Saint-Paul was discovered in 1559. The first detailed description of it, and perhaps the first landing, was by Willem de Vlamingh in 1696 (Richards 1984).

Fig. 6: The lagoon of Ile Saint-Paul seen from the rockhopper penguin rookery (© Bart Van de Vijver)

Fieldwork

During two short visits (1998 & 1999) and two fieldwork seasons on the volcanic islands Ile Amsterdam and Ile Saint-Paul in 2007 and 2016/2017, more than 400 samples have been collected from various habitats including waterbodies, soils and moss vegetation. Sampling sites were chosen in order to represent maximum variability of habitat types. The samples were collected in PVC bottles and fixed with 3% formalin.

For Papers I and II, each sample was geographically localized using GPS and was accompanied by a detailed site description. In situ, pH, specific conductance, water temperature and oxygen have been measured using a WTW 340i Multimeter. For 46 samples, water has been collected 20 cm below the surface, filtered in situ and deep-frozen to be subsequently analysed in the laboratory at the University of Antwerp. In the frozen water samples NO_2^-+NO_3^{2-}N, NH_4^+-N, PO_4^{3-}-P, SO_4^{2-}, Cl^-, Na^+, K^+, Mg^{2+}, Ca^{2+}, Fe^{2+} were analysed at the Laboratory for Ecosystem Management (University of Antwerp, Belgium) using a continuous flow analysis (CFA-SKALAR).

In order to determine the moisture content of the sample (Papers II, IV, V) the F-value, referring to the F-classification of Jung (1936) was selected as representative for moisture and used for each sample. It is a humidity scale based on water content as follows:

FI = submerged mosses, FII = free floating mosses, FIII = very wet (water drips from the samples without pressure), FIV = wet (water drips with a slight pressure), FV = quasi-wet (water drips after moderate pressure), FVI = moist (little water produced after high pressure), FVII = quasi-dry (only a few drops of water can be squeezed out), FVIII = dry (contains no water).

Sample preparation and counting

To investigate the siliceous frustule in any detail, it is necessary to remove the protoplasm and all organic material. An effective but gentle treatment with hydrogen peroxide was used, followed by washing with distilled water (Van der Werff 1955). Cleaned material was dried onto cover slips and then adhered to a microscope slide with Naphrax®, a high refracting index medium. Slides were observed at 1000X magnification on a random transect. The cleaned sample can be used for both light and electron microscopy. For scanning electron microscopy (SEM) in Papers IV, V and VI, parts of the oxidized suspensions were filtered through a 1 μm Isopore™ polycarbonate membrane filter (Merck Millipore). The stubs were sputter-coated with a Gold-Palladium, or Gold layer of 20 nm and studied in a JEOL JSM-7100F SEM microscope at 1kV (Botanic Garden Meise, Belgium).

The fixed material and permanent slides are preserved and stored for potential re-examination at the BR-collection (Botanic Garden Meise).

The diatom taxa were identified as much as possible up to species level or variety. When the taxonomic status of a taxon was uncertain, abbreviations ‘cf.’ (confer: probably belongs to the species identified), ‘aff.’ (affinis: it bears some similarity to this taxon, but it is not conspecific), or ‘sp.’ (species of genera given) were used.

For identification, mainly the following publications were consulted: Bourrelly & Manguin (1954), Le Cohu & Maillard (1986), Le Cohu (2005), Van de Vijver *et al.* (2002a, 2002b, 2002c, 2004, 2008a, 2012, 2014), Van de Vijver & Zidarova (2011), Van de Vijver & Cox (2013), Lowe *et al.* (2013) and Wetzel *et al.* (2015).

The new species were compared with similar taxa using the most current literature: Moser *et al.* (1998), Lange-Bertalot & Genkal (1999), Rumrich *et al.* (2000), Lange-Bertalot & Werum (2001), Werum & Lange-Bertalot (2004), Van de Vijver *et al.* (2002a, 2011), Van de Vijver & Mataloni (2008), Kopalová *et al.* (2011, 2009, 2015), Levkov *et al.* (2013), Zidarova *et al.* (2014), Kohler *et al.* (2015) and Lowe *et al.* (2017).

Nomenclature follows Van de Vijver et al. (2002a). Terminology of valve morphology is based on Ross *et al.* (1979), Round *et al.* (1990), Krammer (2000), Van de Vijver & Mataloni (2008), Lowe *et al.* (2014) and Levkov *et al.* (2013).

General results and conclusion

Overview of the studied material

During this study three specific diatom habitats (freshwater habitats, mosses and soils) were analysed. An overview of the observed diatom flora is presented below.

More than 400 samples were examined, in each sample a standard quantity of 400 diatom valves was counted. The combined diatom flora of Ile Amsterdam and Ile Saint-Paul obtained during the different studies revealed a total of 146 diatom species belonging to 41 genera. Table 1 provides an overview of all observed taxa, together with their biogeographical distribution.
The moss-inhabiting diatom flora of Ile Amsterdam is the most species rich (125 species in 38 genera) in the whole data set, compared to the 104 taxa recorded from the freshwater samples on the same island, and to the 60 taxa observed in the terrestrial samples of Ile Saint-Paul. This higher species richness is most likely the result of a higher diversity of moss and aquatic habitats (such as caves, bog ponds and small streams) and from a higher number of investigated samples.

Figure 7 shows the biogeographical distribution of the diatom flora observed on Ile Amsterdam and Ile Saint-Paul. Following the application of a more fine-grained taxonomy, it is clear that almost one third of all observed taxa showed a restricted sub-Antarctic distribution with 19% of taxa confined only to the two observed islands. This is in strong contrast to the (past) ideas about the ubiquity of microorganisms (Baas-Becking 1934, Finlay 2002, Fenchel and Finlay 2004).

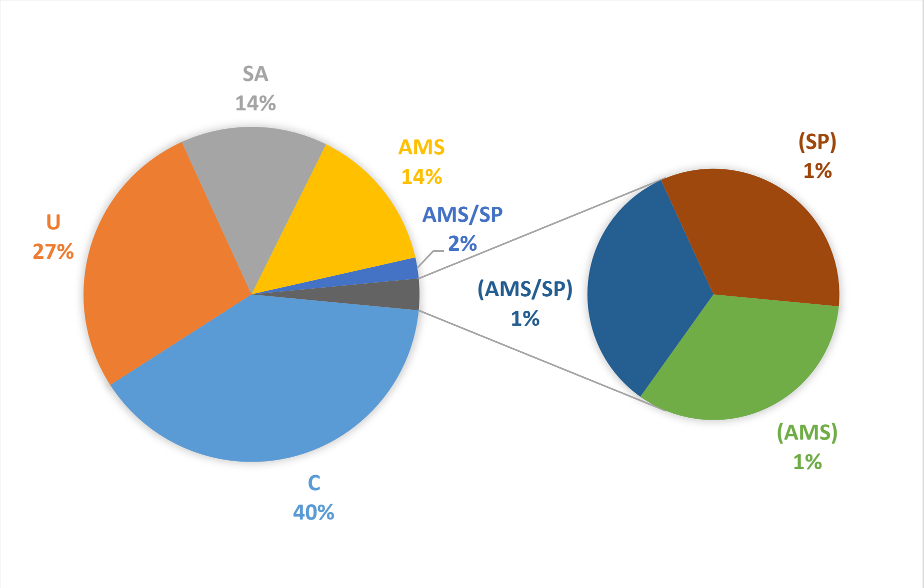


Fig. 7: Biogeographical distribution of the species recorded during this study. [Distribution: (C) cosmopolitan, (SA) sub-Antarctic region, (U) unknown, (AMS) Ile Amsterdam, (AMS/SP) Ile Amsterdam and Ile Saint Paul. The smaller pie chart on the right shows the proportion of unknown, potentially new species ((AMS)) Ile Amsterdam but yet undescribed, ((SP)) Ile Saint Paul but yet undescribed, ((AMS/SP)) Ile Amsterdam and Ile Saint Paul but yet undescribed].

Typical sub-Antarctic species include *Humidophila vidalii* (Van de Vijver *et al.*) Lowe *et al.*, *Hantzschia possessionensis* Van de Vijver & Beyens, *Luticola beyensii*, *Luticola subcrozetensis* Van de Vijver *et al.* and *Pinnularia acidicola* var. *acidicola* Van de Vijver & Beyens, whereas *Luticola ivetaiana* Chattová & Van de Vijver, *Luticola vancampiana* Chattová & Van de Vijver, *Pinnularia subsinistra* Van de Vijver *et al.* and *Pinnularia vlaminghi* Van de Vijver *et al.* were so far observed only on Ile Amsterdam or Ile Saint-Paul. Four cosmopolitan species were recorded from all habitats on both islands: *Achnanthes coarctata* (Brébisson) Grunow, *Hantzschia amphioxys* (Ehrenberg) Grunow, *Humidophila brekkaensis* (Petersen) Lowe *et al.* and *Humidophila contenta* (Grunow) Lowe *et al.*

Figure 8 shows the most important genera (based on the number of recorded taxa) observed in the diatom flora of Ile Amsterdam and Ile Saint-Paul. The two most diverse genera on both islands are *Pinnularia* and *Nitzschia*, followed by *Eunotia* and *Humidophila* on Ile Amsterdam and by *Luticola* and *Hantzschia* on Ile Saint-Paul.

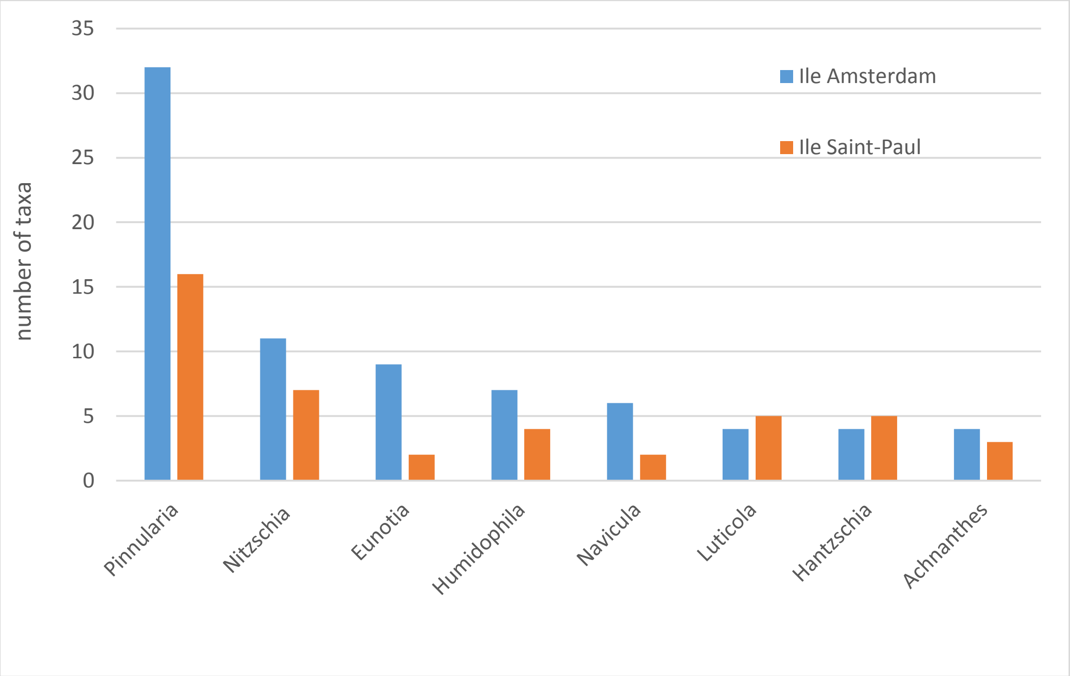


Fig. 8: The principal genera based on species richness on Ile Amsterdam and Ile Saint-Paul.

When comparing the most important genera of both islands, it is clear that samples on Ile Saint-Paul are dominated by typical terrestrial genera. The freshwater genera *Eunotia* and *Navicula*, although belonging to the 5 most species rich genera on Ile Amsterdam, play only a minor role on Ile Saint-Paul. The same pattern can be seen on the species level, where the two most abundant species from Ile Amsterdam *Eunotia paludosa* Grunow var. *paludosa* (23% of all counted valves) and *Frustulia lebouvieri* Van de Vijver & Gremmen (21% of all counted valves) are even lacking on Ile Saint-Paul. This situation is not surprising considering the limited water sources on Ile Saint-Paul.

Tab 1: Taxonomical list of all observed taxa in this study. Unidentified species are given a provisional letter code. [Distribution: (C) cosmopolitan, (SA) sub-Antarctic region, (U) unknown, (AMS) Ile Amsterdam, (AMS/SP) Ile Amsterdam and Ile Saint Paul, ((AMS)) Ile Amsterdam but yet undescribed, ((SP)) Ile Saint Paul but yet undescribed, ((AMS/SP)) Ile Amsterdam and Ile Saint Paul but yet undescribed].

	Distribution	AI Moss	AI Water	SP Soil	SP Moss
Achnanthes brevipes var. *intermedia* (Kützing) Cleve	C			x	
Achnanthes cf. *islandica* Oestrup	U		x		
Achnanthes coarctata (Brébisson) Grunow	C	x	x	x	x
Achnanthes muelleri Carlson	SA	x	x		
Achnanthes naviformis Van de Vijver & Beyens	SA	x	x		x
Achnanthidium sp	U	x			
Achnanthidium sieminskae Witkowski, Kulikovskiy & Riaux-Gobin	SA	x	x	x	
Aulacoseira sp	U			x	
Caloneis bacillum (Grunow) Cleve	C	x	x		
Craticula submolesta (Hustedt) Lange-Bertalot	C	x	x		
Denticula cf. *sundaysensis* Archibald	U	x	x	x	x
Diatomella balfouriana Greville	C	x			
Diploneis sp	U			x	
Eolimna cf. *minima* (Grunow) Lange-Bertalot	U	x			x
Epithemia sp	U			x	
Eunotia aff. *minor* (Kützing) Grunow	U	x			
Eunotia cf. *arcus* Ehrenberg	U	x			
Eunotia cf. *pectinoides*Carter	U	x			
Eunotia clotii Van de Vijver, de Haan & Lange-Bertalot	SA	x		x	x
Eunotia cocquytiae Van de Vijver	AMS	x	x		
Eunotia lecohui Van de Vijver	SA	x	x		
Eunotia muscicola var. *muscicola* Krasske	C	x	x	x	
Eunotia paludosa var. *paludosa* Grunow group	C	x	x		
Eunotia pugilistica Van de Vijver	AMS	x	x		
Ferocia setosa (Greville) Van de Vijver & Houk	C	x	x		
Fistulifera sp	U	x			
Fragilaria neoproducta Lange-Bertalot	C	x			
Frustulia lebouvieri Van de Vijver & Gremmen	SA	x	x		
Frustulia vulgaris (Thwaites) De Toni	C	x	x		
Geissleria sp	U	x			
Gomphonema aff. *exilissimum* Grunow	U	x	x		

	Distribution	AI Moss	AI Water	SP Soil	SP Moss
Gomphonema cf. *montanum* (J.Schumann) Grunow	U	x	x		
Gomphonema parvulum (Kützing) Kützing group	C	x	x		
Halamphora compereana Van de Vijver & Levkov	AMS	x	x		
Halamphora dagmarobbelsiana Van de Vijver & Levkov	AMS	x			
Halamphora veneta (Kützing) Levkov	C	x	x		
Hantzschia abundans Lange-Bertalot	C	x		x	x
Hantzschia amphioxys (Ehrenberg) Grunow	C	x	x	x	x
Hantzschia possessionensis Van de Vijver & Beyens	SA	x	x	x	x
Hantzschia sp1	U	x		x	x
Hantzschia sp2	U			x	
Humidophila amsterdamensis Chattová & Van de Vijver	AMS	x	x		
Humidophila brekkaensis (Petersen) Lowe *et al.*	C	x	x	x	x
Humidophila contenta (Grunow) Lowe *et al.*	C	x	x	x	x
Humidophila crozetikerguelensis Le Cohu & Van de Vijver) Lowe *et al.*	SA	x	x	x	
Humidophila gallica (W. Smith) Lowe *et al.*	C	x	x		
Humidophila rouhaniana Chattová & Van de Vijver	AMS	x	x		
Humidophila vidalii (Van de Vijver, Ledeganck & Beyens) Lowe *et al.*	SA	x	x	x	x
Chamaepinnularia aerophila Van de Vijver & Beyens	SA	x	x		
Chamaepinnularia evanida (Hustedt) Lange-Bertalot	C	x			
Chamaepinnularia soehrensis var. *muscicola* (J.B.Petersen) Lange-Bertalot & Krammer	C	x			
Karayevia oblongella (Østrup) Aboal	C	x	x		
Kobayasiella subantarctica Van de Vijver & Vanhoutte	SA	x	x		
Lecohuia geniculata (Germain) Lange-Bertalot & Rumrich	C	x	x		
Luticola beyensii Van de Vijver, Ledeganck & Lebouvier	SA	x	x	x	x
Luticola ivetaiana Chattová & Van de Vijver	AMS/SP	x	x	x	x
Luticola sp	(SP)			x	
Luticola subcrozetensis Van de Vijver, Kopalová, Zidarova & Levkov	SA	x	x	x	x
Luticola vancampiana Chattová & Van de Vijver	AMS/SP	x	x	x	x
Mayamaea atomus var. *permitis* (Hustedt) Lange-Bertalot	C	x	x	x	
Mayamaea cavernicola Van de Vijver & Cox	AMS	x	x		
Mayamaea cf. *agrestis* (Hustedt) Lange-Bertalot	U	x	x		
Mayamaea fossalis (Krasske) Lange-Bertalot group	C	x			
Mayamaea sp	U			x	
Melosira aff. *dickiei* (Thwaites) Kützing	U	x	x		
Melosira aff. *varians* Agardh	U	x			
Melosira sp	U			x	x

	Distribution	AI Moss	AI Water	SP Soil	SP Moss
Microfissurata australis Van de Vijver & Lange-Bertalot	AMS	x			
Navicula aff. *shackletonii* West & G.S.West	(AMS)	x			
Navicula cf. *bicephala* Hustedt	U	x			
Navicula cf. *cincta* (Ehrenberg) Ralfs	U			x	
Navicula cf. *cryptotenella* Lange-Bertalot	U	x	x	x	x
Navicula gregaria Donkin	C	x	x		
Navicula longicephala Hustedt group	C	x			
Navicula veneta Kützing	C	x	x		
Nitzschia acidoclinata Lange-Bertalot	C		x		
Nitzschia cf. pseudofonticola Hustedt	U	x	x		
Nitzschia cf. *pusilla* Grunow	U		x		
Nitzschia communis Rabenhorst	C	x	x		
Nitzschia commutata Grunow	C	x	x		
Nitzschia debilis (Arnott ex O'Meara) Grunow	C	x	x	x	x
Nitzschia dissipata (Kützing) Rabenhorst	C				x
Nitzschia fonticola (Grunow) Grunow	C	x	x		
Nitzschia frustulum (Kützing) Grunow	C	x	x	x	x
Nitzschia palea (Kützing) W. Smith group	C	x	x	x	x
Nitzschia soratensis Morales & Vis	C	x	x	x	
Nitzschia sp1	(AMS/SP)	x	x	x	x
Nitzschia sp2	U			x	
Orthoseira roeseana (Rabenhorst) O'Meara	C	x	x	x	x
Orthoseira verleyenii Van de Vijver	AMS	x	x		
Pinnularia acidicola var. *acidicola* Van de Vijver & Beyens	SA	x	x	x	x
Pinnularia aff. *acidicola* var. *elongata* Van de Vijver & Beyens	U	x			
Pinnularia aff. *amsterdamensis* Chattová, Van de Vijver & Metzeltin	U	x			x
Pinnularia aff. *microstauron* (Ehrenberg) Cleve	U	x			
Pinnularia aff. subacoricola Metzeltin, Lange-Bertalot & García-Rodríguez	U			x	x
Pinnularia amsterdamensis Chattová, Van de Vijver & Metzeltin	AMS	x	x		
Pinnularia australogibba Van de Vijver, Chattová & Metzeltin	AMS	x	x		
Pinnularia australogibba var. *subcapitata* Van de Vijver, Chattová & Metzeltin	AMS	x	x		
Pinnularia borealis Ehrenberg complex	C	x	x	x	x
Pinnularia bottnica Krammer	C	x	x	x	
Pinnularia cf. *obscuriformis* Krammer	U			x	x
Pinnularia cf. *vixconspicua* Chattová, Metzeltin & Van de Vijver	U				x
Pinnularia lindanedbalovae Van de Vijver & Moravcová	SA	x	x	x	x

	Distribution	AI Moss	AI Water	SP Soil	SP Moss
Pinnularia microcapitata Van de Vijver, Chattová & Metzeltin	AMS	x		x	x
Pinnularia microstauron (Ehrenberg) Cleve	C	x	x	x	
Pinnularia myriamiae Van de Vijver, Chattová & Metzeltin	AMS	x	x		
Pinnularia perminor Kulikovskiy, Lange-Bertalot & Metzeltin	C	x	x	x	
Pinnularia pseudohilseana Van de Vijver, Chattová & Metzeltin	AMS	x	x		
Pinnularia rabenhorstii var. *subantarctica* Van de Vijver & Le Cohu	SA	x	x		
Pinnularia robrechtii Van de Vijver	AMS	x	x		
Pinnularia sinistra Krammer	C	x	x	x	x
Pinnularia sp1	U	x			x
Pinnularia sp2	U	x			x
Pinnularia sp3	U	x			
Pinnularia sp4	U	x			
Pinnularia sp5	U			x	
Pinnularia subacoricola Metzeltin, Lange-Bertalot & García-Rodríguez	C	x	x		
Pinnularia subcommutata Krammer	C	x			
Pinnularia subsinistra Van de Vijver, Chattová & Metzeltin	AMS/SP	x	x	x	x
Pinnularia sylviae Van de Vijver	AMS	x			
Pinnularia vixconspicua Chattová, Metzeltin & Van de Vijver	AMS	x	x		
Pinnularia vlaminghi Van de Vijver Chattova & Metzeltin	AMS	x	x	x	x
Pinnularia whinamiae Van de Vijver	SA	x	x		
Pinnunavis elegans (W.Smith) Okuno	C	x	x		
Pinnunavis gebhardii (Krasske) Van de Vijver	SA	x	x	x	x
Pinnunavis sp	(AMS/SP)	x	x	x	x
Placoneis anglica (Ralfs) Cox	C	x	x		x
Planothidium delicatulum (Kützing) Round & Bukhtiyarova	C		x		
Planothidium pericavum (J.R.Carter) Lange-Bertalot	C	x	x		
Planothidium subantarcticum Van de Vijver & Wetzel	SA	x	x	x	x
Psammothidium abundans (Manguin) Bukhtiyarova & Round	C	x	x		
Psammothidium investians (Carter) Bukhtiyarova	C	x	x		
Psammothidium manguini (Hustedt) Van de Vijver	C	x			
Psammothidium stauroneioides (Manguin) Bukhtiyarova	C	x	x		
Pseudostaurosira naveana (Le Cohu) Morales & Edlund	C	x	x		
Pseudostaurosira trainorii Morales	C	x	x		
Rhopalodia rupestris (W. Smith) Krammer	C	x	x	x	
Sellaphora arvensis (Hustedt) Wetzel & Ector	C	x	x		
Sellaphora barae Van de Vijver	AMS	x	x		

	Distribution	AI Moss	AI Water	SP Soil	SP Moss
Sellaphora cf. *seminulum* Grunow	U	x	x	x	x
Sellaphora sp	(AMS)	x	x		
Stauroforma aff. *exiguiformis* (Lange-Bertalot) Flower, Jones & Round	U	x	x		
Stauroneis bertrandii Van de Vijver & Lange-Bertalot	SA	x	x		
Stauroneis kriegeri Patrick	C	x	x		
Stauroneis pseudomuriella Van de Vijver & Lange-Bertalot	SA	x	x		
Stauroneis thermicola (Petersen) Lund	C	x	x		

Main results

This thesis is mainly based on 6 papers, which cover two important fields in diatom research- ecology and taxonomy. The overview of the main results can be found below.

Ecological part

This part of the thesis focuses on the analysis, characterization and ecological preferences of the freshwater and moss-inhabiting diatom communities of Ile Amsterdam, its biogeographical position within the southern Indian Ocean Province, and the different diatom communities on the island in relation to several habitat characteristics. The last chapter is devoted to the preliminary results of the terrestrial diatom communities of Ile Saint-Paul.

During a survey of 95 freshwater samples, a total of 104 diatom taxa belonging to 33 genera has been found. The samples were dominated by several *Pinnularia* taxa, *Frustulia lebouvieri*, *Kobayasiella subantarctica* Van de Vijver & Vanhoutte, *Eunotia paludosa* var. *paludosa*, *E. muscicola* and *Planothidium subantarcticum*. The biogeographical analysis showed that the Ile Amsterdams freshwater diatom flora is composed of cosmopolitan, sub-Antarctic and endemic elements. Almost 17% of all recorded taxa can be considered endemic to Ile Amsterdam, most of them belonging to the genus *Pinnularia*, with an additional 14% of taxa showing an exclusive sub-Antarctic distribution. A series of physicochemical variables were measured (if possible) to allow a specific determination of the ecological preferences of the observed diatom flora. Based on their chemical characteristic a classification of samples was conducted using a Canonical Component Analysis, revealing that specific conductance, sulphate and pH play a primary role in determining the composition of the diatom communities, apart from the impact of altitude. (Paper I)

The analysis of 148 moss samples revealed a presence of 125 diatom taxa belonging to 38 genera. Species richness per sample ranged from 1 to 40. The dominant species were *Eunotia paludosa* var. *paludosa* with more than 35% of all counted valves, followed by *Frustulia lebouvieri* (10.5%), *Planothidium subantarcticum* (7.4%), *Eunotia muscicola* var. *muscicola* (5.6%) and *Kobayasiella subantarctica* (5.6%). At present, eleven taxa (9%) could at only be identified up to the genus level. Some of them appear to be new to science and are awaiting a formal description (mainly in the genera *Nitzschia*, *Navicula*, *Pinnunavis* and *Sellaphora*). From a biogeographical point of view, 42% of taxa have a typical cosmopolitan distribution, whereas 18% of all observed species can be considered endemic to Ile Amsterdam, with another 16% species having a restricted sub–Antarctic distribution. The similarity analysis based on presence/absence data indicates that the moss diatom flora of Ile Amsterdam shows only a limited affinity to other sub-Antarctic islands, with Sørensen (1948) index values ranging from 0.24–0.48. The NMDS analysis, based on a cluster dendrogram, divided the samples into 6 main groups. For each group, indicator species were determined. Both environmental data and diatom distributions indicate that apart from altitude, specific conductance, pH and moisture are the major factors involving the structure of moss-inhabiting diatom communities on Ile Amsterdam. (Paper II)

Taxonomical part

The isolated geographic position and physical features of both islands have resulted in the presence of a very typical diatom flora, dominated by species belonging to the genus *Pinnularia*. The taxonomy of this genus altogether with other two important genera *Humidophila* and *Luticola* was not updated at this time, requiring a precise analysis and revision before reaching the final species list that could be used in further ecological work.

The thorough morphological analysis resulted in a presence of sixteen taxa which did not correspond to any of the currently known species and were described as new to science. For all newly described taxa, detailed morphological descriptions are provided and their ecology, biogeography and separation from similar taxa are discussed.

The taxonomical analysis of the genus *Pinnularia*, one of the most widespread and most diverse diatom genera in the entire sub-Antarctic Region, typical for oligotrophic, acid stagnant waterbodies, wet mosses and wet non-biotic soils, revealed the presence of 22 different taxa. After a thorough morphological analysis, 12 taxa could not be identified using the currently available literature and are described as new to science: *Pinnularia amsterdamensis* Chattová *et al.*, *Pinnularia australogibba* Van de Vijver *et al.*, *Pinnularia australogibba* var. *subcapitata* Van de Vijver *et al.*, *Pinnularia microcapitata* Van de Vijver *et al.*, *Pinnularia myriamiae* Van de Vijver *et al.*, *Pinnularia pseudohilseana* Van de Vijver *et al.*, *Pinnularia robrechtii* Van de Vijver, *Pinnularia subsinistra* Van de Vijver *et al.*, *Pinnularia sylviae* Van de Vijver, *Pinnularia vixconspicua* Chattová *et al.*, *Pinnularia vlaminghi* Van de Vijver *et al.* and *Pinnularia whinamiae* Van de Vijver.

The genus *Pinnularia* is frequently reported from other, more southerly positioned, sub-Antarctic islands where another 23 *Pinnularia* species were described from. However, comparing the overall *Pinnularia* flora of Ile Amsterdam with other sub-Antarctic islands, only seven, mostly cosmopolitan species are shared. The fact that, apart from *P. acidicola*, none of the sub-Antarctic endemics was found on Ile Amsterdam, highlights the unique floristic situation of this island and of the entire region, and may add valuable information to the ongoing discussion whether micro-organisms are cosmopolitan or not. (Paper III)

The elaborate taxonomic analysis of the material further revealed the presence of seven species belonging to the terrestrial diatom genus *Humidophila*. Apart from five previously known taxa (*Humidophila contenta*, *H. crozetikerguelensis*, *H. gallica*, *H. brekkaensis*, *H. vidalii*), two taxa didn't correspond to any of the known species and are described as new to science: *Humidophila amsterdamensis* Chattová & Van de Vijver and *Humidophila rouhaniana* Chattová & Van de Vijver. (Paper IV)

Paper V continues with the taxonomical revision and reports the results of the analyses of 5 species of the terrestrial genus *Luticola*. Apart from the 2 already known *Luticola* species *Luticola beyensii* Van de Vijver *et al.* and *Luticola subcrozetensis* Van de Vijver *et al.*, two new species are described: *Luticola ivetaiana* Chattová & Van de Vijver and *Luticola vancampiana* Chattová & Van de Vijver. Observation of the material in LM revealed the presence of the fifth unknown *Luticola* taxon with a highly asymmetrical central area. As the taxon could not be found during SEM analysis, we have insufficient data regarding its morphological ultrastructure and therefore the decision was taken not to describe it as new to science.

Species of the genera *Humidophila* and *Luticola* belong to the dominant components of the diatom flora in terrestrial habitats on sub-Antarctic Islands. These habitats show a diverse and very characteristic terrestrial diatom flora with high degree of regional endemism in the entire Antarctic region. However, the correct taxonomy and biogeography of those genera in the (sub)-Antarctic region was hampered due to species drift, and the degree of endemism was probably masked by the historic force-fitting (Tyler 1996) of European and North American names to (sub)-Antarctic species. Due to the lack of appropriate literature, the first studies mainly reported typical cosmopolitan taxa, which resulted into stretched biogeographical distributions of the reported species.

In order to show as detailed picture of the studied material as possible, a description of a new centric diatom genus, *Ferocia* Van de Vijver & Houk is presented in Appendix 1.

Overall conclusion

The diatom flora of both islands can be considered as typical for oceanic islands, based on its disharmonic composition with several genera lacking and other being overrepresented. All results point to the presence of a very unique diatom flora, with an important proportion of new species and are valuable for understanding the biodiversity and biogeography of the sub-Antarctic diatoms. The high number of newly described taxa is not surprising, considering the fact that the islands are geographically very isolated and have a volcanic origin, which favours a high level of speciation. The results of this thesis will be further used in another taxonomical, ecological and planned paleo-ecological studies.

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Ecological part

Paper I

Chattová, B., Lebouvier, M., & Van de Vijver, B. 2014: Freshwater diatom communities from Ile Amsterdam (TAAF, southern Indian Ocean). *Fottea* 14: 101–119.

Freshwater diatom communities from Ile Amsterdam (TAAF, southern Indian Ocean)

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Abstract: Diatom and water chemistry samples were collected during the austral summer of 2007 from lakes, streams and bogponds on Ile Amsterdam (TAAF), a small island located in the southern Indian Ocean. A diverse diatom flora of 104 taxa was found, dominated by several *Pinnularia* taxa, *Frustulia lebouvieri*, *Kobayasiella subantarctica*, *Eunotia paludosa*, *E. muscicola* and *Planothidium subantarcticum*. Biogeographically, the Ile Amsterdam freshwater diatom flora is composed of cosmopolitan, sub–Antarctic and endemic elements. The biogeographical analysis showed that almost 17% of all observed taxa can be considered endemic to Ile Amsterdam with an additional 14% showing an exclusive sub–Antarctic distribution. The flora can be considered as typical for oceanic islands based on its disharmonic composition with several genera lacking and other being overrepresented.

Canonical Component Analysis was used to classify the samples based on their chemical characteristics, revealing that, specific conductance, sulphate and pH were the main factors dividing the samples into four different groups. The geological history of the island in combination with the climate and the specific environmental features of the main habitat in the Caldera most likely shaped the composition of the actual diatom communities.

Key words: Bacillariophyta, biogeography, ecology, Ile Amsterdam, southern Indian Ocean, sub–Antarctic region

Introduction

Diatoms (Bacillariophyceae) are one of the most abundant and species–rich algal groups in freshwater and terrestrial ecosystems in the (sub–)Antarctic region (Jones 1996; Van de Vijver & Beyens 1999a; Sabbe et al. 2003). The past few years, there has been an increasing effort in revising the freshwater and limno–terrestrial diatom flora of the entire (sub–) Antarctic region. Especially the diatom flora on the islands in the southern Indian Ocean has been the subject of intensive taxonomic studies (a.o. Romero & Van de Vijver 2011; Van de Vijver et al. 2002a, 2002b, 2011, 2013; Witkowski et al. 2012) followed by detailed ecological surveys of the diatom communities inhabiting these islands [e.g., Iles Kerguelen (Van de Vijver et al. 2001); Iles Crozet (Van de Vijver & Beyens 1999b; Van de Vijver et al. 2002a), Heard Island (Van de Vijver et al. 2004a) and the Prince Edward Islands (Van de Vijver et al. 2008a)].

The results of these studies clearly indicated the presence of a highly specific diatom flora on all investigated islands containing a large number of species with a very restricted, even sometimes endemic distribution, contrary to the generally accepted ideas about the cosmopolitan nature of micro–organisms worldwide (Finlay & Clarke 1999).

Just north of the sub–Antarctic islands in the southern Indian Ocean, two small volcanic islands can be found, Ile Amsterdam (77°30'E, 37°50'S) and Ile Saint Paul (77°31' E, 38°41'S). The first results of a survey on the terrestrial and freshwater diatoms of Ile Amsterdam have been published in 1999 (Van de Vijver & Beyens 1999c) reporting 90 taxa from 24 samples. Based on these results, two sampling campaigns have been undertaken in 1999 and 2007 in order to investigate in–depth the diatom flora of both islands. A new *Luticola* species was published based on material collected in 1999 from Ile Saint Paul (Van de Vijver et al. 2002b). In 2008, a paper describing three *Eunotia* Ehrenberg species was published (Van de Vijver et al. 2008b) followed by the description of a new genus, *Microfissurata* Lange–Bertalot, Cantonati et Van de Vijver, based on two species of which one was found on Ile Amsterdam (i.e. *Microfissurata australis* Van de Vijver et Lange–Bertalot; Cantonati et al. 2009). Several years later, 23 different *Pinnularia* Ehrenberg taxa have been observed during a taxonomic analysis of aquatic, moss and soil samples, of which twelve did not correspond to any other currently known species and were described as new species (Van de Vijver et al. 2012). Special attention was further given to the different lava tube diatom communities that are present on the island. As a result of this, several unknown taxa were found and described as new for science (Van de Vijver & Cox 2013; Lowe et al. 2013). Despite this growing interest and the handful of taxonomic papers, little is known on the ecology and composition of the diatom communities of Ile Amsterdam.

The present paper focusses on the ecological preferences of the freshwater diatom flora of Ile Amsterdam, its biogeographical position within the southern Indian Ocean Province, and the different diatom communities on the island in relation to several habitat characteristics.

Material and Methods

Study Site. Ile Amsterdam is an entirely volcanic island located in the southern Indian Ocean, halfway between the African continent and Australia (Fig. 1) and is one of the most remote and isolated oceanic islands in the world. The island, with a total surface of 55 km², presents the shape of a small cone culminating at 881m (Mont de la Dives) and is geologically spoken, very young, with its main part arisen during the period 400–200 kyr BP (Giret 1987, Doucet 2003). Ile Amsterdam has a temperate oceanic climate with a mean annual temperature of 14.0°C with minimum and maximum temperatures of 11.2 °C in August and 17.4 °C in February respectively (Lebouvier & Frenot 2007). Strong westerly winds are frequent, especially in winter. Relative humidity is generally high (> 80%) due to the frequency of low cloud ceilings. Precipitation, falling primarily as rain, is usually high with an annual average of 1114 mm distributed over more than 220 days at the meteorological station (Martin de Viviès, 27 m a. s. l.); a dry period occurs in summer (c. 70 mm in February). According to a one year record (Frenot & Valleix 1990) in the Caldera at 700 m a.s.l. the mean temperature is lower by 7 °C while the precipitation is almost twice as high.

Permanent waterbodies are restricted to the higher plateau (Caldera, Plateau des Tourbières) in the centre and the west–southwestern part of the island (Falaises d'Entrecasteaux, Grandes Ravines). Almost all other areas lack (semi–permanent) waterbodies due to the steepness of the slope and the permeability of the lava tunnels, holes and fissures. Due to frequent fog and clouds, and high relative humidity in the upper areas (from 500 m a.s.l.), extensive peat formations have been developed, especially in the volcanic caldera (Heger et al. 2009).

Ile Amsterdam is not truly sub–Antarctic. Nevertheless, on the higher central plateau, the vegetation has a typical sub–Antarctic character consisting of mosses, small ferns [e.g., *Blechnum penna–marina* (Poiret) Kuhn], grasses, sedges (e.g., *Uncinia brevicaulis* Thouars) and *Lycopodium* ssp. (Trehen et al. 1990). The rather species–poor vegetation is dominated by both native (43) and introduced (56) species, reflecting the isolation of the island (Frenot et al. 2001). The vegetation differs however in two aspects from the other islands in the southern Indian Ocean. The lower part of the island used to be covered by dense *Phylica arborea* Thouars forests, a native tree restricted to the Tristan da Cunha archipelago and Ile Amsterdam, patches of which are still present on the island. Secondly, the native flora includes also several (endemic) *Sphagnum* species, forming extensive peatlands above 500 m a.s.l. However, *Sphagnum* peatlands are absent on the other sub–Antarctic islands (Flatberg et al. 2011). Although the diversity of the lichen flora is rather poor (77 species), recently a new lichen species, *Caloplaca amsterdamensis* Aptroot et Ertz was described (Aptroot et al. 2011).

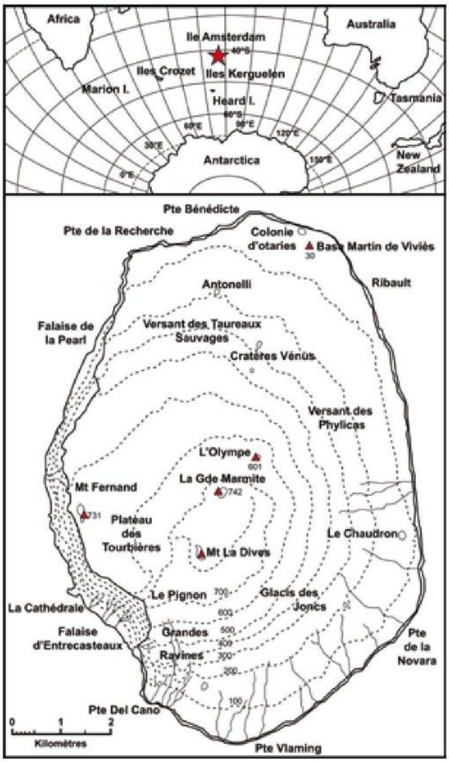

Fig. 1. (a) Location of Ile Amsterdam in the southern hemisphere; (b) Ile Amsterdam with the main topographic indications used in the text.

The endemic fauna is composed of a few marine bird species such as the rare Amsterdam albatross (*Diomedea amsterdamensis* Roux et al.) and several large fur seal colonies (*Arctocephalus tropicalis* Gray). Fires, past human activities and the introduction of cattle (*Bos taurus* Linnaeus) have caused serious ecological damage and altered significantly the biodiversity of the island (Micol & Jouventin 1995) although it is unclear what the effects are on the micro–flora and –fauna of the island.

Table 1. Physico–chemical characteristics (when available) of samples collected on Ile Amsterdam, temperature in °C, conductivity in µS.cm^{-1}, altitude in m.a.s.l., other variables in mg.l^{-1}

sample	NO^{2-} +$N0^{3-}$	NH_4^+	PO_4^{3-}	SO_4^{2-}	Cl^-	pH	cond	T	altitude	Na^+	K^+	Ca^{2+}	Mg^{2+}
W001	2.3	0.25	0.01	8	34	5.56	136	10.2	750	17.0	0.6	1.0	1.73
W003	2.1	0.12	0.09	2	103	4.67	73	12.0	711	4.6	0.4	0.2	0.39
W004	2.1	0.22	0.01	4	18	5.91	64	14.3	717	3.6	0.1	0.2	0.35
W005						5.91	64	14.3	710				
W006						5.86	63	14.3	710				
W007	1.0	0.05	0.13	2	153	5.15	68	11.8	714	5.6	0.4	0.3	0.45
W009	3.8	1.10	0.05	13	24	4.80	66	15.0	711	4.1	0.3	0.2	0.39
W010						4.50	115	14.6	709				
W011	1.4	0.27	0.01	4	13	5.08	86	13.8	710	5.5	0.5	0.3	0.55
W012	1.3	0.12	0.01	4	22	5.57	80	13.8	700	12.9	1.0	0.8	1.14
W013						5.57	80	13.8	700				
W016						5.54	84	17.2	701				
W017	10.2	0.54	0.17	14	49	5.39	56	14.5	706	6.5	0.4	0.5	0.59
W018						5.39	56	14.5	706				
W019	1.05	0.05	0.01	2	19	5.03	62	15.5	710	6.7	0.1	0.4	0.53
W020						5.03	62	15.5	710				
W022	2.3	0.05	0.01	2	12	5.84	40	14.8	713	6.1	0.1	0.5	0.43
W023						5.84	40	14.8	713				
W025	2.9	0.26	0.01	2	13	5.58	50	13.9	716	4.4	0.1	0.2	0.28
W027	1.7	0.12	0.01	2	19	5.48	57	13.6	715	6.4	0.3	0.5	0.58
W028						5.48	57	13.6	715				
W030						5.24	56	13.2	715				
W031	5.3	15.2	1.58	56	247	6.90	1057	19.5	10	126	33.8	6.0	9.96
W032						6.90	1057	19.5	10				
W033	0.31	0.09	0.06	10	63	5.81	239	17.0	220	35.5	1.3	4.1	4.62
W034						5.81	239	17.0	220				
W035	0.29	0.05	0.01	6	42	4.14	167	17.1	386	24.2	1.8	1.6	2.48
W036						4.35	138		398				
W037	2.0	0.05	0.20	20	63	7.82	627	13.0	20	41.0	4.2	22.2	12.6
W038						7.82	627	13.0	20				
W039	2.1	0.05	0.07	19	61	7.94	1126	12.0	73	42.1	4.1	20.7	12.8
W040						7.94	1126	12.0	73				
W041	0.21	0.05	0.08	21	34	8.49	316	12.0	132	25.5	3.2	20.2	12.2
W042						8.58	325	11.0	78				
W043	0.07	0.05	0.06	22	33	8.58	325	11.0	78	25.4	3.2	20.3	12.3
W044						7.83	293	13.0	69				
W045	0.28	0.20	0.11	17	39	7.83	293	13.0	69	19.1	2.0	9.5	6.15

Table 1 Cont.

sample	N O^{2-} +N0^{3-}	NH_4^+	PO_4^{3-}	SO_4^{2-}	Cl^-	pH	cond	T	altitude	Na^+	K^+	Ca^{2+}	Mg^{2+}
W046						6.18	444	14.0	600				
W047	0.02	0.05	0.01	7	28	6.18	444	14.0	600	16.2	0.4	1.1	1.60
W048	0.13	0.05	0.01	5	17	5.40	67	8.5	739	10.3	0.4	0.7	0.95
W049						5.40	67	8.5	739				
W050	0.60	0.05	0.0	6	17	6.70	69	14.0	570	11.4	0.1	0.7	0.98
W051						6.70	69	14.0	570				
W052						6.76	54	17.0	757				
W053						6.10	68	16.0	758				
W056						6.44	68	15.0	759				
W058						6.03	46	16.0	748				
W059	0.02	0.05	0.08	7	27	6.80	46	14.0	742	9.8	12.5	0.6	0.76
W060						6.80	46	14.0	742				
W062	0.02	0.05	0.01	6	15	6.59	46	16.0	749	8.8	0.1	0.7	0.76
W063						6.59	46	16.0	749				
W064						6.13	88	13.0	711				
W065	0.02	0.05	0.04	7	27	6.13	88	13.0	711	12.2	7.9	1.1	1.21
W067	0.02	0.05	0.01	7	17	6.47	62	15.0	720	12.1	0.1	1.0	1.06
W068						6.47	62	15.0	720				
W069	0.02	0.05	0.01	7	20	5.75	81	15.0	706	14.0	0.4	1.0	1.35
W070						5.75	81	15.0	706				
W072						5.94	74	13.0	676				
W074						5.47	43	14.0	697				
W076	0.02	0.05	0.01	5	14	5.06	55	13.0	717	9.6	0.4	0.6	0.93
W078						5.02	47	12.0	717				
W080						4.98	78	15.0	717				
W082	0.02	0.05	0.01	6	17	5.22	48	15.0	724	9.1	0.4	0.4	0.76
W084						4.93	57	15.0	724				
W085						5.22	47	14.0	725				
W087						5.30	76	15.0	724				
W089						5.39	44	15.0	727				
W091						5.79	57	16.0	725				
W093						5.78	76	14.0	725				
W095	0.02	0.05	0.01	10	13	5.58	45	15.0	724	8.0	0.1	0.7	0.62
W097	0.02	0.05	0.01	7	19	4.98	67	13.0	739	10.3	0.4	0.6	0.78
W098						4.98	67	13.0	739				
W100						4.76	62	13.0	743				
W101	0.02	0.05	0.01	8	18	4.71	69	13.0	738	7.4	0.4	0.5	0.66

Table 1 Cont.

sample	N O^{2-} +N0^{3-}	NH_4^+	PO_4^{3-}	SO_4^{2-}	Cl^-	pH	cond	T	altitude	Na^+	K^+	Ca^{2+}	Mg^{2+}
W104						5.32	83	11.0	804				
W108						5.13	50	13.0	738				
W111	0.02	0.05	0.01	8	19	5.19	73	12.0	745	12.0	0.5	0.8	1.12
W113	0.02	0.05	0.01	8	18	4.89	71	13	742	12.6	0.1	0.8	1.09
W116	0.02	0.05	0.01	7	18	5.54	55	15.0	726	11.1	0.1	0.8	0.94
W118	0.02	0.05	0.01	5	15	5.42	60	14.0	707	9.9	0.1	0.7	0.86
W119						5.42	60	14.0	707				
W121						7.15	329	15.0					
W122						7.15	329	15.0					
W123	0.18	0.05	0.01	5	17	5.03	62	12.0	675	7.6	0.1	0.6	0.71
W124	0.27	0.05	0.02	17	143	6.21	487	14.0	131	77.6	1.9	7.0	9.64
W125	0.02	0.05	0.01	21	171	6.05	595	13.0	135	58.7	1.1	4.5	7.84
W126							240	14.0	121				
W127	0.02	0.05	0.01	10	63	6.38	240	14.0	121	40.0	1.0	3.1	4.72
W128	0.02	0.05	0.01	9	55	6.14	223	13.0	121	36.9	1.0	2.6	4.04
W129	0.02	0.05	0.01	12	96	6.36	358	14.0	163	52.5	1.7	5.7	6.24
W130	0.02	0.05	0.35	137	1062	6.44	3440	17.0	78	632	23.0	30.2	63.9
W131						6.44	3440	17.0	78				
W132						8.46	235	16.0	59				
W133						8.46	235	16.0	59				

In 1949, a scientific and meteorological station, Martin–de–Viviès, was established on the north–eastern coast. Since 2006 the island gained the status of Nature Reserve and a management plan is currently in place to provide greater protection for the environment and its biota (Lebouvier & Frenot 2007).

Sampling. A total of 133 diatom samples were collected during November and December 2007. Sampling locations were chosen in order to represent a maximum variability of habitat types ranging from small streams, lakes, bogponds and temporary pools from all over the island. The samples were collected in PVC bottles and fixed with 3% formaldehyde. Each sample was geographically localized using GPS and was accompanied by a detailed site description. In situ, pH, specific conductance, water temperature and oxygen have been measured for all samples using a WTW 340i Multimeter. For 46 of them, water has been collected 20 cm below the surface, filtered in situ and deep–frozen to be subsequently analysed in the laboratory at the University of Antwerp. Table 1 lists all samples together with their chemical characteristics. In the frozen water samples NO_2^-+NO_3^-N, NH_4^+–N, PO_4^{3-}–P, SO_4^{2-}, Cl^-, Na^+, K^+, Mg^{2+}, Ca^{2+}, Fe^{2+} were analysed at the Laboratory for Ecosystem Management (University of Antwerp, Belgium) using a continuous flow analysis (CFA–SKALAR).

Slide preparation and counting. A selection of 95 samples (out of 133) was further surveyed for diatoms, including all 46 samples with full chemical analysis. Diatom samples were prepared following the method described in Van der Werff (1955). Small quantities of the samples were cleaned by adding 37% H_2O_2 and heating to 80 °C for about 1 h. The reaction was completed by addition of $KMnO_4$. Following digestion and centrifugation, the resulting clean material was diluted with distilled water to avoid excessive concentrations of diatom valves that may hinder reliable observations. Cleaned diatom valves were mounted in Naphrax®. Samples and slides are stored at the National Botanic Garden of Belgium (BR), Department of Bryophytes and Thallophytes. In each sample, 400 diatom valves were identified and enumerated on random transects at 1 000× magnification using an Olympus BX51 microscope equipped with Differential Interference Contrast (Nomarski) optics. Slides have been scanned after doing the 400 valves counts in order to find rare species. Identifications of Antarctic and sub–Antarctic species are based on descriptions by Bourrelly & Manguin (1954), Le Cohu & Maillard (1983, 1986), Schmidt et al. (1990), Oppenheim (1994), Van de Vijver et al. (2002a, 2004b, 2008b, 2011, 2012) and Le Cohu (2005).

Nomenclature follows Van de Vijver et al. 2002a.

Data analysis. For a pair wise comparison of the diatom flora of Ile Amsterdam with those of the other sub–Antarctic islands of the southern Indian Ocean Province (Prince Edward Islands, Iles Crozet, Iles Kerguelen, Heard Island) the Community Coefficient of Sørensen (1948) is used. This index has the following formula: 2c/(a+b+2c) where a and b are the numbers of species exclusively observed in each of the two sites and c is the number of species shared by these sites.

To evaluate the extent to which our sampling effort represented the diatom flora in the waterbodies of Ile Amsterdam, we calculated the incidence–based species richness estimator (ICE, Chao et al. 2000) and the mean Chao2 richness estimator (Chao 1984), both using the EstimateS program version 8.2 (Colwell 2009). Shannon–Wiener diversity index (log10–based) and Hill's evenness index were calculated using the statistical package MVSP. Ordination was used to show the patterns in species composition. The statistical analysis was performed using CANOCO version 4.5 (ter Braak & Šmilauer 2002). Square root–transformed abundance data were used in the ordinations.

Principal Components Analysis (PCA) was used to determine the main directions of variation in the water chemistry dataset. Fe was removed from the original data set since most of its values were below the limit of detection. All environmental variables, except for pH and temperature, were log–transformed since they had skewed distributions. After this transformation, no skewed distributions were shown. Detrended Correspondence Analysis (DCA) was carried out to estimate gradient length. The results showed that two samples (W031, W032), subject to excessive marine influence (sampled from a pool in the middle of a large fur seal colony) were considered to be outliers. A DCA with the outliers omitted showed gradient lengths for the first four axes of 4.5, 3.8, 2.3, and 2.9, suggesting that methods based on unimodal models (Canonical Correspondence Analysis) would be appropriate for a subsequent ordination (ter Braak & Prentice 1988). A CCA with 46 samples (for which physic–chemical data were available) was used to detect patterns of variation in the species data that can be explained by environmental variables. All other samples were added as passive samples. Since not all of the 13 environmental variables influence the diatom distributions independently, we used Canonical Correspondence Analysis (CCA) with forward selection and unrestricted Monte Carlo permutation tests (999 permutations, $P \leq 0.05$). All statistical and numerical techniques used in this study are described in full detail in Jongman et al. (1995).

RESULTS

Water chemistry

The major patterns of variation within the chemistry data are revealed based on a Principal Component Analysis (Fig. 2). Based on its extreme high conductivity value, sample W130 was removed from the analysis. Small angles between biplot arrows indicate generally high positive correlations. Environmental variables that explain most of the variation, are represented by the longest arrows aligned along the axes and hence are more important. PCA axis 1 accounts for 64% of the variance (λ_1=0.643) in the data set and reflects two, strongly negatively correlated main gradients: on one hand altitude and on the other pH and specific

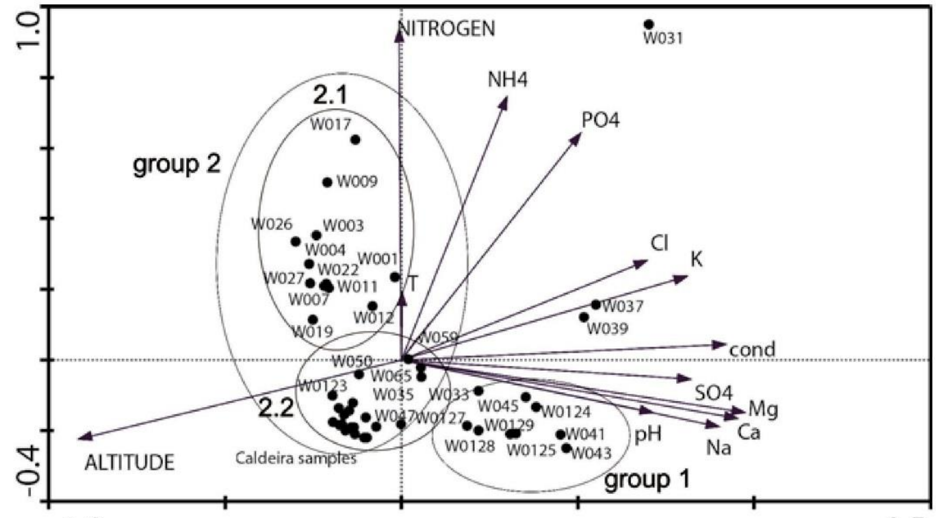

Fig. 2. A correlation biplot of samples and environmental variables resulting from the Principal Components Analysis of the water chemistry dataset.

conductance, the latter being highly linked to Cl^-, Na^+, Ca^{2+}, K^+, Mg^{2+} and SO_4^{2-}. Axis 2 seems less important and accounts for only 17% of the variance (λ_2=0.165) and is most likely reflecting a nitrogen gradient. Sample W031, situated in the upper left part of the diagram, is set somewhat apart from the other samples without being considered a complete outlier. This sample has the highest ammonium (NH_4^+–N) and phosphate (PO_4^{3-}–P) load most likely caused by animal influence as the sample was taken from a pool in the fur seal colony close to the sea. Two major groups of samples can be recognized. A first group contains all samples collected at Pointe Del Cano and Pointe d'Entrecasteaux showing high amounts of the above mentioned ions, whereas the second group is composed of all samples taken from the Caldera region in the centre of the island. The latter group can be subdivided into two parts. A first subgroup (2.1) contains only samples from the lowest plateau in the Caldera, immediately in the vicinity of the Museau de Tanche crater. These samples are characterized by elevated nitrogen values (1.0–10.2 mg/l) and are separated from all other samples in the Caldera region forming subgroup 2.2, characterized by low nitrogen values (<0.8 mg.l^{-1}).

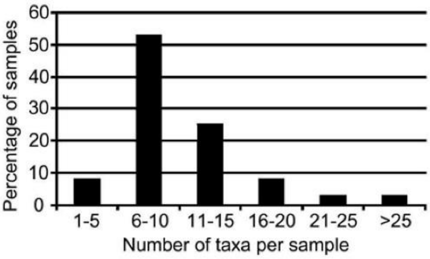

Fig. 3. Frequency distribution of diatom taxa in studied samples.

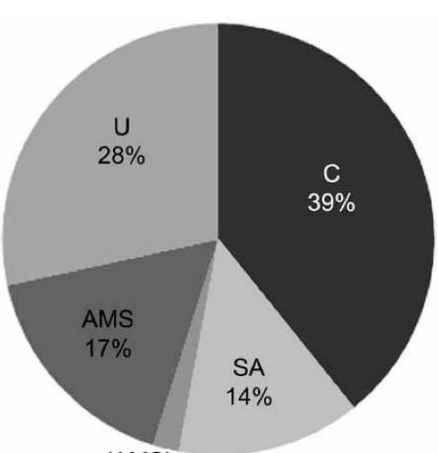

Fig. 4. Distribution of the species according to their biogeographical distribution [Distribution: (C) cosmopolitan, (AMS) Ile Amsterdam, (SA) subantarctic region, (U) unknown, ((AMS)) – Ile Amsterdam but yet undescribed].

Species composition and the similarity analysis. A total of 98 diatom taxa (including species, varieties and forms) belonging to 33 genera has been found during the analysis of 95 freshwater samples. Six additional taxa were observed outside the counts bringing the total number of diatoms in our samples up to 104. Table 6 provides a full list of all species observed in this study together with the biogeographical distribution of the taxa.

Using species richness estimators, it is possible to evaluate how well the sampling effort reflected the true diatom species richness. The expected total number of taxa in all samples is 110 (ICE) or 113 (Chao2), suggesting that the counting protocol scored between 87 and 89% of the total taxa present in the samples overall.

Species richness per sample ranged from 1 to 27. Two samples were entirely monospecific, composed of only *Eunotia paludosa* Grunow (W007 & W009). The distribution of species numbers per sample (Fig. 3) showed that most samples contained between 6 and 10 taxa per sample with an average number of taxa per sample of 11 ± 5. Table 2 lists all genera arranged according to their species number. The most species rich genera include *Pinnularia* (20 species), *Nitzschia* (11 species), *Diadesmis* (9 species), *Luticola* (6 species) and *Eunotia* (5 species). The five most abundant species made up 66.2% of all the diatoms counted: *Frustulia lebouvieri* Van de Vijver et Gremmen (30.8%), *Eunotia paludosa* (9.8%), *Kobayasiella subantarctica* Van de Vijver et Vanhoutte (9.7%), *Planothidium subantarcticum* Van de Vijver et C.E.Wetzel (8.6%) and *Eunotia muscicola* Krasske (7.3%). On the other side of the abundance scale, 83 taxa (more than 85% of all counted taxa) had a total relative abundance of less than 1%.

Detailed scanning electron microscopy analysis observations revealed the presence of several recently described species, mostly within the genus *Pinnularia* such as *P. australogibba* Van de Vijver, Chattová et Metzeltin or *P. amsterdamensis* Chattová, Metzeltin et Van de Vijver. Additionally, three recently described species were found during a survey of lava tube sample W033: *Mayamaea cavernicola* Van de Vijver, *Sellaphora barae* Van de Vijver and *Orthoseira verleyenii* Van de Vijver. A large number of taxa (12%) could at present only be identified up to the genus level, mostly within the genera *Amphora*, *Diadesmis* and *Luticola*.

Based on the biogeographic distribution of the

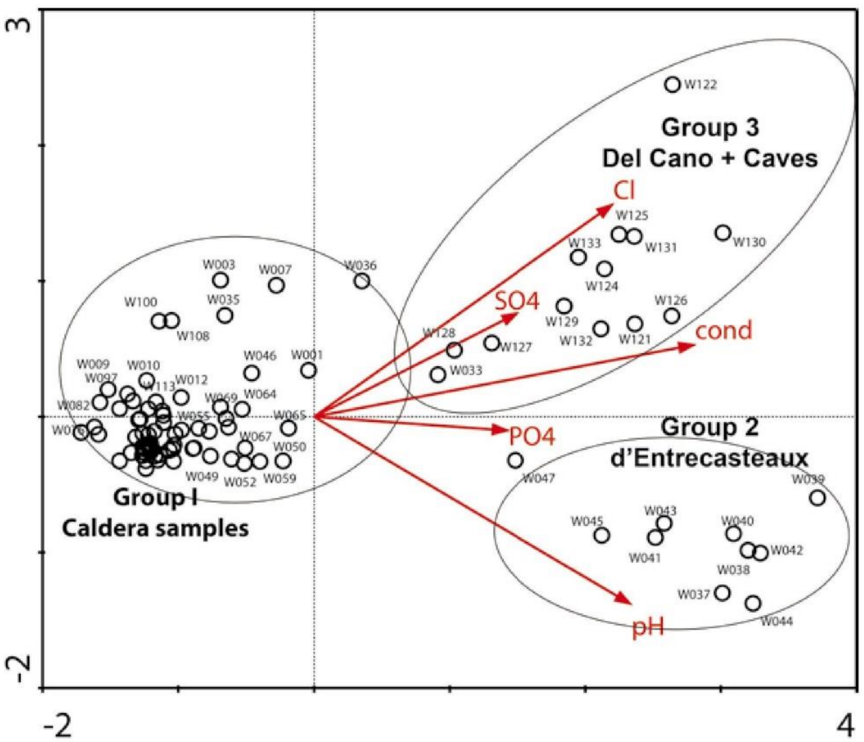

Fig. 5. Canonical Correspondence Analysis (CCA) correlation biplot of samples versus environmental variables based on species relative abundance data. The different groups (except group 4) are indicated on the diagram. The CCA–analysis was based on 46 samples for which a complete set of physic–chemical data were available. The other samples were added as passive samples.

taxa, it is clear that the Amsterdam freshwater diatom flora is composed of cosmopolitan, sub–Antarctic and endemic elements (Fig. 4). Almost 17% of all recorded taxa can be considered endemic to Ile Amsterdam, most of them belonging to the genus *Pinnularia*. An additional 14% of the taxa show an exclusive sub–Antarctic distribution such as *Achnanthes naviformis* VAN DE VIJVER et BEYENS, *Frustulia lebouvieri* and *Kobayasiella subantarctica*.

A similarity analysis based on presence/absence data was performed between the Ile Amsterdam diatom flora with the floras from the other islands in the southern Indian Ocean Province (Prince Edward Islands, Iles Crozet, Iles Kerguelen and Heard Island). Based on this presence/absence list of the Ile Amsterdam taxa, the Ile Amsterdam diatom flora shows a low affinity with the diatom floras of the true sub–Antarctic islands in the southern Indian Ocean with SØRENSEN similarity coefficients ranging between 0.28 and 0.29 (Table 3). The low similarity values are most likely the consequence of both a low total number of species on Ile Amsterdam and a low number of shared species. Typical shared sub–Antarctic taxa include *Achnanthes muelleri* CARLSON, *Achnanthes naviformis*, *Chamaepinnularia aerophila* VAN DE VIJVER et BEYENS, *Diadesmis vidalii* VAN DE VIJVER, LEDEGANCK et BEYENS and *Diadesmis crozetikerguelensis* LE COHU et VAN DE VIJVER.

Diatom community analysis. The initial dataset of 95 samples and 98 diatom taxa was used in the multivariate analysis. After a first analysis, two samples were removed from the analysis as outliers (W031 & W032). The original set of 13 environmental variables was reduced to five. Potassium (K$^+$), Sodium (Na$^+$), Magnesium (Mg^{2+}) and Calcium (Ca^{2+}) were highly correlated to specific conductance and therefore removed from the analysis. Forward selection with Monte Carlo unrestricted permutations (999 permutations) identified specific conductance, Cl$^-$, SO$_4^{2-}$, PO$_4^{2-}$and pH as the environmental variables that explain significant variation in the diatom data ($P<0.05$). The CCA restrained to these five selected variables explained only 28.7% of the species variance. This is low but typical for noisy data sets with many blank values (STEVENSON et al. 1991). The first two

Table 2. Genera ordered by decreasing percentual portion (%) calculated on the number of the taxa (n).

	n	%
Pinnularia	21	20.2
Nitzschia	10	9.6
Diadesmis	9	8.7
Luticola	6	5.8
Eunotia	5	4.8
Achnanthes	4	3.8
Navicula	4	3.8
Stauroneis	4	3.8
Gomphonema	3	2.9
Mayamaea	3	2.9
Pinuavis	3	2.9
Planothidium	3	2.9
Psammothidium	3	2.9
Sellaphora	3	2.9
Amphora	2	1.9
Frustulia	2	1.9
Hantzschia	2	1.9
Orthoseira	2	1.9
Achnanthidium	1	1.0
Caloneis	1	1.0
Chamaepinularia	1	1.0
Craticula	1	1.0
Denticula	1	1.0
Karayevia	1	1.0
Kobayasiella	1	1.0
Lecohuia	1	1.0
Melosira	1	1.0
Opephora	1	1.0
Placoneis	1	1.0
Pseudostaurosira	1	1.0
Rhopalodia	1	1.0
Stauroforma	1	1.0
Tryblionella	1	1.0
Total	104	

axes account for 79.6% of the cumulative variance. The first two axes ($\lambda_1 = 0.709$, $\lambda_2 = 0.228$) were highly significant ($p<0.001$) (ter Braak & Šmilauer 2002). CCA axis 1 is strongly correlated with specific conductance (inter–set correlation = 0.88) and to a lesser extent with pH (0.73) and Cl^- (0.68) whereas CCA axis 2 is correlated with Cl^- (0.52) and negatively with pH (–0.46). The CCA diagram (Fig. 5) shows three main groups of samples. Table 4 lists the relevant (measured) ecological parameters, together with mean species diversity, mean evenness and mean number of taxa. Samples W031 and W032, considered outliers and not taken into account in the CCA, were added as a fourth group since both were taken from the same pool in the fur seal colony. The dominant and subdominant species observed in each group are shown in Table 5.

The first group, situated in the left part of the diagram, is composed exclusively of high–altitude very acid lakes with low specific conductance, nutrient and ion values. These lakes are characterized by *Eunotia muscicola*, *Frustulia lebouvieri* and *Kobayasiella subantarctica*. Additionally, *Pinnularia vixconspicua* Chattová, Van de Vijver et Metzeltin and *E. lecohui* Van de Vijver, though in general rather rare on the island, show a remarkable abundance in these lakes. The second group, found in the lower right part of the diagram, contains all samples collected from streams and pools in the vicinity of Falaise d'Entrecasteaux, located in the southern part of the island. These samples have higher pH values (8.2±0.4) and a higher conductivity, SO_4^{2-}, Mg^{2+}, Ca^{2+} and K^+ values. Dominant taxa include *Planothidium subantarcticum*, *Navicula gregaria* Donkin, *Navicula veneta* Kützing and *Sellaphora seminulum* (Grunow) D.G.Mann. The third group is composed of samples from two localities: all samples from the Del Cano region in the southern part of the island together with four samples taken in small cave pools located in the Grand Tunnel near the scientific base in the northern part of Ile Amsterdam. The samples are characterized by a slightly acid pH, higher specific conductance values and higher Cl^- and Na^+ values, possibly the result of increased sea–spray input. The samples are dominated by *Planothidium subantarcticum*, *Karayevia oblongella* (Østrup) M.Aboal, *Achnanthidium* cf. *minutissimum* (Kützing) Czarnecki, *Melosira* sp. and several *Diadesmis* taxa. The last group (not represented in the Canoco Analysis) is based on only two samples (W031 and W032) that were left out as outliers. Both samples, showing very high specific conductance, SO_4^{2-}, N and PO_4^{2-} concentrations, were taken from a large rocky pool in the middle of a large fur seal colony and are dominated by *Pinnularia subacoricola* Metzeltin, Lange–Bertalot et García–Rodríguez, *Nitzschia palea* (Kützing) W.Smith and *Luticola* sp1 with *Mayamaea permitis* (Hustedt) K.Bruder et Medlin and *Pinnularia australogibba* var. *subcapitata* Van de Vijver, Chattová et Metzeltin often being subdominant.

DISCUSSION

Species composition and general biogeography

The low similarity values based on presence/absence data between Ile Amsterdam and the other islands are not surprising considering the low number of species observed at the sites, the differences in the microhabitat diversity, the rather large distance between the islands, the very isolated position of Ile Amsterdam and the relative young geological age. Similar results can be found in the species composition of other organisms such as higher plants, mosses and lichens (APTROOT et al. 2011). The sub–Antarctic islands, grouped by STONEHOUSE (1982) in the so–called "cold–temperate sub–Antarctic Region" whereas Ile Amsterdam is located in the "warm–temperate sub–Antarctic Region", show a higher diversity of microhabitats such as different types of bogponds, animal wallows, fellfields and lakes, where different diatom floras could develop (VAN DE VIJVER et al. 2008). On Ile Amsterdam, the number of stagnant waterbodies is limited to the acid, *Sphagnum*–dominated, pools and lakes in the caldera region, showing a rather uniform diatom composition.

It is however true that based on relative abundance data, the situation is somewhat different. Within the five most abundant taxa, three are typical sub–Antarctic taxa and two can even be considered to have a worldwide distribution. The three sub–Antarctic taxa are confined only to the southern Indian Ocean islands and absent on all other studied Antarctic localities (KOPALOVÁ & VAN DE VIJVER 2013; KOPALOVÁ et al. 2013). *Frustulia lebouvieri* was so far only found on the Prince Edward Islands, the most northerly situated sub–Antarctic Islands (VAN DE VIJVER et al. 2008a) whereas the other two species are absent from the most southern sub–Antarctic island (Heard Island; VAN DE VIJVER et al. 2004). Both cosmopolitan taxa belong to the most common taxa in the southern hemisphere and are present, usually in large abundances, on merely every analysed Antarctic locality (KELLOGG & KELLOGG 2002). This may indicate that these 5 taxa probably a rather broad environmental tolerances, easily capable of adapting to prevailing environmental conditions. It also might indicate that their dispersal to and colonisation of Ile Amsterdam was therefore facilitated. Their overall dominance on Ile Amsterdam is not necessarily related to possible anthropogenic impact although the only way to clearly demonstrate this will be the analysis of Holocene sediment and peat to identify the evolution of the diatom communities on the island. Hypotheses on the human impact is therefore at the moment high speculative and therefore not relevant.

A typical feature of oceanic islands is the fact that the flora and fauna on these islands are usually disharmonic (GILLESPIE 2007). Some genera tend to be overrepresented whereas others are missing or show only a reduced diversity. The diatom flora of Ile Amsterdam proved to be a good example of this rule. As can be seen in Table 2, *Pinnularia* accounts for more than 20% of all recorded taxa whereas other typical species–rich genera such as *Navicula*, *Nitzschia* or *Eunotia* are less abundantly present on the island or even completely absent as is the case for *Fragilaria*. One of the reasons might be the highly specific nature of the Ile Amsterdam environment dominated by the acid *Sphagnum*–dominated peatland area in the upper Caldera. However, in comparable northern hemisphere environments, genera such as *Neidium*, *Brachysira*, *Eunotia* and *Frustulia* co–dominate bogponds and heathland fens, often represented by a high number of taxa (e.g., FRÁNKOVÁ et al. 2009; LANGE–BERTALOT et al. 2011; POULÍČKOVÁ et al. 2013). The main reason for this disharmony is most likely the reduced dispersion and colonisation success of these genera followed by an increased speciation of the successful genera. VYVERMAN et al. (2007) already stated that the effect of isolation was particularly high on Ile Amsterdam reducing the genus diversity compared to the other islands, contradicting that way the ongoing discussion on the possible ubiquity of diatoms (FINLAY & CLARKE 1999). The effect is apparently even more striking based on species level. Only a very low number of taxa are shared with the other islands. Most remarkably is the fact that more than 75% of these shared taxa show a cosmopolitan, even worldwide, distribution. Typical examples such as *Navicula gregaria* or *Amphora veneta* are widespread in the world and seem to be present on every continent (KELLOGG & KELLOGG 2002; METZELTIN et al. 2009; HOFMANN et al. 2011). Whether these taxa are also genetically similar is an open question. Recent results on the cosmopolitan *Pinnularia borealis* EHRENBERG showed the presence of several genetically different lineages including a typical Antarctic lineage (SOUFFREAU et al. 2013). Only a minority of the shared species have a restricted sub–Antarctic distribution, confirming previous biogeographic results on the sub–Antarctic flora (VAN DE VIJVER et al. 2005, 2011). The low similarity also indicates the presence of a highly specific diatom flora on Ile Amsterdam. It is clear from the large number of cf. and sp. taxa in the species list (Table 6) that a large part of the observed species show some affinity with known taxa but at the same time sufficient differences to be separated as independent taxa. Several have been described recently (VAN DE VIJVER et al. 2012; VAN DE VIJVER & COX 2013; LOWE et al. 2013) whereas some others still await a formal description. Additional morphological analysis will be necessary to reveal their true taxonomic status and it is likely that some of them will need a formal description as new taxa.

It is possible that the geographic isolation combined with the special environmental and climatic conditions resulted in an increased speciation rate, as is often seen on oceanic islands (FLEISCHER et al.

Table 3. Similarity analysis (Sørensen index) between Ile Amsterdam and other sub–Antarctic localities.

	Amsterdam Island	**Prince Edward Islands**	**Kerguelen**	**Crozet**	**Heard Island**
Number of taxa	104	196	210	220	191
Index of Sørensen	–	0.29	0.29	0.28	0.28

Table 4. Water chemistry and diversity features in the different sample groups identified by the CCA analysis (mean and standard deviation).

	1	**2**	**3**	**4**
number of samples (#with physico–chemical data)	70(31)	9(6)	14(8)	2(1)
number of taxa	9±3	15±5	18±6	16±2
number of genera	5±2	12±2	13±2	10±2
diversity	1.3±0.4	1.5±0.2	1.74±0.6	2±0.1
Evenness	0.58±0.17	0.55±0.07	0.59±0.17	0.73±0.08
pH	5.5±0.6	8.1±0.3	6.7±0.9	6.9
specific conductance	74±68	562±326	312±113	1057
$(NO_2^- + NO_3^-)N$	0.9±1.9	0.9±0.9	0.11±0.1	5.3
NH_4^+–N	0.1±0.11	0.08±0.1	0.06±0.01	15.2
PO_4^{3-}P	0.02±0.03	0.1±0.1	0.02±0.01	1.58
SO_4^{2-}	6±2.5	19.8±1.7	13±4.3	56
Cl^-	23±17	46±13.2	99±44	247
Na^+	10±3	31±9	50±15	126
K^+	1±0.1	3.3±0.8	1.3±0.3	33.8
Ca^{2+}	0.7±0.2	19±5	4.5±1.4	6.0
Mg^{2+}	0.9±0.3	11.2±2.5	6.2±1.9	9.96

2008, Buckley et al. 2009). Important genera such as *Pinnularia* and *Eunotia* show more than 60% of taxa that are only found on Ile Amsterdam (Van de Vijver et al. 2009, 2012). Some of these taxa present affinities with cosmopolitan taxa for instance *P. australogibba* is strongly related to *P. gibba* Ehrenberg but differs in several important details to justify a separation as an independent species. Molecular research should make clear how long these taxa have been separated. The analysis of the *Pinnularia borealis* populations in Souffreau et al. (2013) already discussed this phenomenon. Rapid speciation has been shown before within diatoms. Theriot et al. (2006) reported, although sometimes contested, on the rapid morphological evolution of the endemic *Stephanodiscus yellowstonensis* Theriot et Stoermer that evolved within several thousands of years from *S. niagarae* Ehrenberg. Similar results can be seen in other organisms on Ile Amsterdam. Among the seventeen native phanerogamic species reported from Ile Amsterdam, six are endemic to Ile Amsterdam and Ile Saint–Paul (Tréhen et al. 1990; Galley et al. 2007). A lot of these species are nowadays mainly present in the Caldera region, which is quite isolated from the rest of the island. Typical examples of higher plants in the Caldera region include *Plantago stauntoni* Reichardt (Rønsted et al. 2002) and *P. pentasperma* Hemsley. Recently, several new *Sphagnum* taxa have been described from Ile Amsterdam (Flatberg et al. 2011) with all reported species showing a restricted distribution to Ile Amsterdam and/or the neighbouring Ile Saint–Paul. The same applies for the Hepaticae and Anthocerotae flora of the island (Grolle 2002; Váňa et al. 2010), despite the fact that the island is rather understudied for these groups.

Freshwater diatom communities

Both chemistry data and diatom distributions indicate that specific conductance and pH are the major factors separating the freshwater diatom communities on Ile Amsterdam. The presence of $PO4^{3-}$–P as one of the determining factors is yet unclear. A possible explanation is the presence of marine mammals at lower altitude in combination with soil erosion, high winds and seaspray. This may cause a higher phosphorus load in the investigated samples. As can be seen, the samples from the fur seal colony show high levels of phosphorus whereas in the caldera, phosphorus levels are always quite low. The waterbodies in the region near Falaises d'Entrecasteaux and Pointe Del Cano all have a slightly acid to clearly alkaline pH whereas in the Caldera the waterbodies are strictly acidic. d'Entrecasteaux and Del Cano present a similar habitat on very steep cliffs, the latter more or less taken in the small ravines that were cut out by the rivers. The similar physicochemical characteristics of the small brooks confirm this. Subsequently, the diatom communities also present a high similarity. They are dominated by taxa preferring circumneutral to alkaline conditions such as *Planothidium subantarcticum*, *Sellaphora seminulum*, *Amphora veneta*, several *Nitzschia* taxa and *Rhopalodia rupestris* (LEVKOV 2009; HOFMANN et al. 2011; VAN DE VIJVER et al. 2013). Rivers on Ile de la Possession (Crozet Archipelago) and Iles Kerguelen on the contrary have very high frequencies of various *Fragilaria* taxa, such as *Fragilaria capucina* DESMAZIÈRES, *Frankophila maillardii* (R.LE COHU) LANGE–BERTALOT and *Fragilaria germainii* E.REICHARDT et LANGE–BERTALOT (VAN DE VIJVER & BEYENS 1999b) whereas lotic waters on Ile Amsterdam completely lack any *Fragilaria* taxa. The acid diatom community in the Caldera regions differs considerably from similar communities on sub–Antarctic islands. On Ile de la Possession, acid pools such as bogponds and peatland lakes are dominated by *Chamaepinnularia soehrensis* var. *muscicola* (J.B.PETERSEN) LANGE–BERTALOT et KRAMMER, *Eunotia paludosa* and *E. muscicola* (VAN DE VIJVER & BEYENS 1999b), the latter two also present in relatively large numbers on Ile Amsterdam. On the contrary, *Frustulia lebouvieri* and most of the *Pinnularia* taxa that dominate the Ile Amsterdam peatlands, play a less important role on the sub–Antarctic islands. On the Prince Edward Islands, lakes and ponds are dominated by *Aulacoseira principissa* VAN DE VIJVER, *Psammothidium abundans* (MANGUIN) BUKHTIYAROVA et ROUND and *Eunotia paludosa* (VAN DE VIJVER et al. 2008b). Moving southwards, the acid diatom communities change even more with *Stauroforma exiguiformis* (LANGE–BERTALOT) FLOWER, JONES et ROUND and *Aulacoseira principissa* as dominant taxa on Iles Kerguelen (VAN DE VIJVER et al. 2001). A major habitat difference between the Caldera region and the sub–Antarctic islands is the overall dominance of *Sphagnum* taxa as peat forming mosses on Ile Amsterdam whereas on the sub–Antarctic Islands, *Sphagnum* taxa are completely lacking (FLATBERG et al. 2011). On these islands, the peatland moss vegetation is mostly composed of *Rhacomitrium* and *Sanionia* (VAN DE VIJVER et al. 2004a).

The PCA analysis indicated altitude as a contributor to the variation in the sample diversity. This is probably a rather artificial contribution as in the analysis most samples originate either from the Caldera region (at an altitude of 700 m) or from the southern part of the island (at almost sea–level). Intermediate samples are not numerous in the analysis. On the other hand, there is a striking difference between the physic–chemical composition of the Caldera region and the southern part of the island and as such can altitude be used to indicate the nature of the samples. It is however unclear whether the geological history of the island influenced the chemistry of the waterbodies and subsequently the shaping of their diatom communities on Ile Amsterdam. But based on this history it is possible to develop a plausible hypothesis. Ile Amsterdam has been shaped by two consecutive volcanic episodes. The volcanism on Ile Amsterdam is characterized by the formation of a mostly subalkaline tholeiitic basalt with a high concentration of magnesium (DOUCET et al. 2004). This geochemical composition probably resulted in the formation of the alkaline and slightly acid diatom communities found in the d'Entrecasteaux and Del Cano areas and probably might represent the original habitat for diatom communities on the island. All sampled streams in these areas seep out of the bedrock in the steep cliffs that form the southern shore of Ile Amsterdam and then run for several tens of meters on the lowland area towards the ocean. Most likely, the water originates from the upper Caldera region penetrating the porous underlying basaltic bedrock only to reappear almost at sea level as small but fast–flowing streams (VAN DE VIJVER, pers. obs.). The high levels of Na^+ and Cl^- most likely result from seaspray that is deposited continuously in the streams and on the lowlands in combination with soil erosion and strong winds. Whether this is also the case for Ca^{2+} is unclear. There is no indication of calcareous rocks on the entirely volcanic island. A possible source of the Ca^{2+} may be the huge colony of the yellow–nose albatross nearby but this is highly speculative and needs to be tested before it can be put forward as an hypothesis. Precipitation at sea level is rather limited (FRENOT & VALLEIX 1990) making it a less probable source for the continuous streams in the d'Entrecasteaux and Del Cano areas. The large Caldera that was formed during the last volcanic phase (DOUCET et al. 2003) constantly receives year round a large amount of precipitation (LEBOUVIER & FRENOT 2007) enabling the development of thick peat layers, almost exclusively

Table 5. List of diatom species and their abundance in the four groups (1 to 4) of samples identified by the CCA analysis [(X) >10%, (O) 5–10%, (+) 2–5%, (o) 2–0.5 %, (·) < 0.5%)].

Taxon name	**1**	**2**	**3**	**4**
Frustulia lebouvieri	X		.	
Kobayasiella subantarctica	X		.	
Eunotia muscicola var. *muscicola*	X		+	
Eunotia paludosa var. *paludosa*	X		o	
Eunotia lecohui	O			
Pinnularia vixconspicua	O		.	+
Pinnularia perminor	+		.	
Planothidium subantarcticum	o	X	X	.
Navicula gregaria	.	X	o	
Navicula veneta		O	.	.
Nitzschia frustulum	.	O	o	
Sellaphora seminulum	.	O	o	o
Amphora veneta	.	+		
Tryblionella debilis		o	o	
Karayevia oblongella	o	+	X	.
Achnanthidium cf. *minutissimum*	.	.	O	
Melosira sp	.	.	O	
Nitzschia sp1			O	
Planothidium pericavum		.	+	
Diadesmis contenta		.	+	
Diadesmis crozetikerguelensis		.	+	
Diadesmis sp1	.	o	+	
Diadesmis sp2	.	o	+	+
Diadesmis vidalii			+	
Psammothidium investians	.		+	
Achnanthes coarctata			o	
Pinnularia subacoricola			.	X
Nitzschia palea		.		X
Luticola sp1			.	X
Mayamaea permitis			.	O
Pinnularia australogibba var. *subcapitata*		.		+
Craticula submolesta	.			+

Table 6. Taxonomical list of all diatom taxa observed in this study. Unidentified species are given provisional letter codes or numbers [Distribution: (C) cosmopolitan, (AMS) Ile Amsterdam, (SA) Subantarctic region, (U) unknown, ((AMS)) Ile Amsterdam but yet undescribed].

Taxon name	**Distribution**
Achnanthes coarctata (Brébisson) Grunow	C
Achnanthes cf. *islandica* Oestrup	U
Achnanthes muelleri Carlson	SA
Achnanthes naviformis Van de Vijver et Beyens	SA
Achnanthidium cf. *minutissimum* (Kützing) Czarnecki	U
Amphora sp.	(AMS)
Amphora veneta Kützing	C
Caloneis aff. *bacillum* (Grunow) P.T.Cleve	U
Chamaepinularia aerophila Van de Vijver et Beyens	SA
Craticula submolesta (Hustedt) Lange–Bertalot	C
Denticula sundaysensis Archibald	C
Diadesmis aff. *comperei* Le Cohu et Van de Vijver	U
Diadesmis aff. *ingeae* Van de Vijver	U
Diadesmis contenta (Grunow) D.G.Mann	C
Diadesmis crozetikerguelensis Le Cohu et Van de Vijver	SA
Diadesmis gallica W.Smith	C
Diadesmis sp1	U
Diadesmis sp2	U
Diadesmis subantarctica Le Cohu et Van de Vijver	SA
Diadesmis vidalii Van de Vijver, Ledeganck et Beyens	SA
Eunotia cocquytiae Van de Vijver	AMS
Eunotia lecohui Van de Vijver	AMS
Eunotia muscicola Krasske var. *muscicola*	C
Eunotia paludosa Grunow var. *paludosa*	C
Eunotia pugilistica Van de Vijver	AMS
Frustulia aff. *vulgaris* (Thwaites) De Toni	U
Frustulia lebouvieri Van de Vijver et Gremmen	SA
Gomphonema cf. *exilissimum* Grunow	U
Gomphonema cf. *montanum* Schumann	U
Gomphonema parvulum Kützing	C
Hantzschia amphioxys (Ehrenberg) Grunow	C
Hantzschia possessionensis Van de Vijver et Beyens	SA
Karayevia oblongella (Oestrup) M.Aboal	C
Kobayasiella subantarctica Van de Vijver et Vanhoutte	SA
Lecohuia sp	U
Luticola beyensii Van de Vijver, Ledeganck et Lebouvier	SA
Luticola cf. *cohnii* (Hilse) D.G.Mann	U

Table 6 Cont.

Taxon name	**Distribution**
Luticola sp1	U
Luticola sp2	U
Luticola sp3	U
Luticola sp4	U
Mayamaea cavernicola Van de Vijver	AMS
Mayamaea cf. *agrestis* (Hustedt) Lange–Bertalot	U
Mayamaea permitis (Hustedt) K.Bruder et Medlin	C
Melosira sp	(AMS)
Navicula arvensis Hustedt	C
Navicula cf. *tenelloides* Hustedt	U
Navicula gregaria Donkin	C
Navicula veneta Kützing	C
Nitzschia acidoclinata Lange–Bertalot	C
Nitzschia cf. *liebetruthii* Rabenhorst	U
Nitzschia cf. *pseudofonticola* Hustedt	U
Nitzschia cf. *pusilla* Grunow	U
Nitzschia communis Rabenhorst	C
Nitzschia commutata Grunow	C
Nitzschia frustulum (Kützing) Grunow	C
Nitzschia inconspicua Grunow	C
Nitzschia palea (Kützing) W. Smith	C
Nitzschia sp1	U
Opephora naveana Le Cohu	C
Orthoseira roeseana (Rabenhorst) O'Meara	C
Orthoseira verleyenii Van de Vijver	AMS
Pinnularia acidicola var. *acidicola* Van de Vijver et Le Cohu	SA
Pinnularia amsterdamensis Chattová, Van de Vijver et Metzeltin	AMS
Pinnularia australogibba Van de Vijver, Chattová et Metzeltin	AMS
Pinnularia australogibba var. *subcapitata* Van de Vijver, Chattová et Metzeltin	AMS
Pinnularia borealis s.l. Ehrenberg	C
Pinnularia borealis var. *subislandica* Krammer	C
Pinnularia bottnica Krammer	C
Pinnularia cf. *obscuriformis* Krammer	U
Pinnularia microstauron (Ehrenberg) Cleve	C
Pinnularia myriamiae Van de Vijver, Chattová et Metzeltin	AMS
Pinnularia perminor Kulikovskiy, Lange–Bertalot et Metzeltin	C
Pinnularia pseudohilseana Van de Vijver, Chattová et Metzeltin	AMS
Pinnularia rabenhorstii var. *subantarctica* Van de Vijver et Le Cohu	SA

Table 6 Cont.

Taxon name	**Distribution**
Pinnularia robrechtii Van de Vijver	AMS
Pinnularia sinistra Krammer	C
Pinnularia sp [cf. *divergentissima* (Grunow) Cleve]	U
Pinnularia subacoricola Metzeltin, Lange–Bertalot et García–Rodríguez	C
Pinnularia subsinistra Van de Vijver, Chattová et Metzeltin	AMS
Pinnularia vixconspicua Chattová, Metzeltin et Van de Vijver	AMS
Pinnularia vlaminghii Van de Vijver, Chattová et Metzeltin	AMS
Pinnularia whinamiae Van de Vijver	AMS
Pinnunavis elegans (W. Smith) Okuno	C
Pinnunavis gebhardii (Krasske) Van de Vijver	SA
Pinnunavis sp	U
Placoneis cf. *anglica* (Ralfs) R.Lowe	U
Planothidium delicatulum (Kützing) Round et Bukhtiyarova	C
Planothidium pericavum (Carter) Lange–Bertalot	C
Planothidium subantarcticum Van de Vijver et C.E.Wetzel	SA
Psammothidium abundans (Manguin) Bukhtiyarova et Round	C
Psammothidium staroneioides (Manguin) Bukhtiyarova	C
Psamnothidium investians (Carter) Bukhtiyarova	C
Pseudostaurosira trainorii E.A.Morales	C
Rhopalodia rupestris (W. Smith) Krammer	C
Sellaphora barae Van de Vijver	AMS
*Sellaphora seminulum (*Grunow) D.G.Mann	C
Sellaphora sp1	U
Stauroforma exiguiformis (Lange–Bertalot) Flower, Jones et Round	C
Stauroneis bertrandii Van de Vijver et Lange–Bertalot	AMS
Stauroneis pseudomuriella Van de Vijver et Lange–Bertalot	SA
Stauroneis cf. *thermicola* (J.B.Petersen) Lund	U
Stauroneis kriegeri Patrick	C
Tryblionella debilis (Arnott) Grunow	C

composed of *Sphagnum* mosses. *Sphagnum* is well known for acidifying its environment (Clymo 1963, 1964; Munson & Gherini 1993) and this activity in the isolated Caldera region in combination with the flat geomorphology of the Caldera most likely created the highly acid and oligotrophic habitat where the acid diatom community could develop. Other regions on Ile Amsterdam where *Sphagnum* could be found (e.g., near the Pignon area), the *Sphagnum* vegetation is often found on more or less steep slopes where peat formation is less likely.

CONCLUSION

The freshwater diatom flora on Ile Amsterdam is unique in many aspects. This study showed the presence of a rather species poor diatom flora although for some genera such as *Pinnularia* a remarkable high diversity was found. The latter unbalanced diversity is most likely the result of the biogeographical isolation and the oceanic nature of the island. The combination of the subalkaline volcanism that shaped the island and the acidifying properties of *Sphagnum* most likely resulted in the actual composition of these quite contrasting diatom communities that were observed in this study.

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Paper II

Moss-inhabiting diatom communities from Ile Amsterdam (TAAF, southern Indian Ocean)

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(manuscript)

Abstract

The present study shows the results of a taxonomic and ecological survey on the moss-inhabiting diatom flora of Ile Amsterdam (TAAF), a small volcanic island in the southern Indian Ocean. The analysis of 148 samples revealed the presence of 125 diatom taxa belonging to 38 genera. The specificity of the Ile Amsterdam's diatom flora is mainly reflected in the species composition of the dominant genera *Pinnularia*, *Nitzschia*, *Humidophila* and *Luticola*, with a large number of new species. This highly specific diatom flora, together with differences in sampling habitats and the isolated position of the island, resulted in very low similarity values between Ile Amsterdam and the other islands of the Southern Ocean. From a biogeographical point of view, 42% of the taxa have a typical cosmopolitan distribution, whereas 18% of all observed species can be considered endemic to Ile Amsterdam, with another 16% species showing a restricted sub–Antarctic distribution. The NMDS analysis, based on a cluster dendrogram, divides the samples into 6 main groups. For each group, indicator species were determined. Both environmental data and diatom distributions indicate that apart from altitude, specific conductance, pH and moisture are the major factors involving the structure of moss-inhabiting diatom communities on Ile Amsterdam.

Key words: Bacillariophyta, diatoms, ecology, mosses, Ile Amsterdam, southern Indian Ocean, sub-Antarctic region

Introduction

Ile Amsterdam (77°30’E, 37°50’S) is located north of the sub-Antarctic islands in the southern Indian Ocean, halfway between South Africa and Australia and is one of the most remote islands in the world. This study is the second in a series of three papers characterizing the diatom diversity of freshwater, moss and soil habitats on Ile Amsterdam. The first paper describes the ecological preferences of the freshwater diatom flora (Chattová *et al.* 2014) while the third paper dealing with the soil diatom communities is currently being prepared. The ecological analysis of the diatom communities from Ile Amsterdam are accompanied by a thorough morphological and taxonomical revision, which led to a description of many new species (Van de Vijver *et al.* 2008a, 2012, 2014b, Van de Vijver & Cox 2013, Lowe *et al.* 2013).

One of the first papers discussing the sub-Antarctic moss-inhabiting diatom flora provided an analysis of epiphytic diatom communities from Campbell Island (Hickman & Vitt 1974), reporting the presence of 59, mostly cosmopolitan, diatom species. In recent years, the moss diatom flora of sub-Antarctic islands was increasingly well studied. In 1997 Van de Vijver & Beyens reported 104 taxa from South Georgia, followed by a study of moss diatom communities from Ile de la Possession (Van de Vijver & Beyens 1999b). The richest moss inhabiting diatom flora was reported from Kerguelen (Van de Vijver *et al.* 2001), while another 192 diatom taxa were collected from bryophyte samples from Heard Island (Van de Vijver *et al.* 2004b). In 2007, Gremmen et al. examined the distribution of moss-inhabiting diatoms along an altitudinal gradient on Kerguelen. A last paper describing the diversity and distribution patterns of moss-inhabiting diatoms on the Prince Edward Islands was published a year later (Van de Vijver *et al.* 2008b). All published results showed a high species diversity characterized by a high level of endemicity.

Diatoms (Bacillariophyceae), one of the most abundant and species–rich algal groups in the (sub–)Antarctic region (Jones 1996; Van de Vijver & Beyens 1999a; Sabbe *et al.* 2003) are able to survive in non-submerged or even dry habitats, such as terrestrial mosses (Van de Vijver & Beyens 1999b). Bryophyte communities represent an important part of the sub-

Antarctic vegetation. Surprisingly, *Sphagnum* peatlands are absent on almost all sub–Antarctic islands, except Ile Amsterdam where several (endemic) *Sphagnum* species, forming extensive peatlands above 500 m a.s.l., have been discovered (Flatberg *et al.* 2011).

The main objective of this study is to determine the diatom communities living in mosses on Ile Amsterdam, to reveal the principal factors influencing the diatom diversity and to compare the moss diatom flora of Ile Amsterdam with that of other sub-Antarctic islands.

Material and Methods

Study site

Ile Amsterdam, an isolated, entirely volcanic island is located in the southern Indian Ocean, halfway between the African continent and Australia. The island, with a total surface of 55 km², presents the shape of a small cone culminating at 881m (Mont de la Dives) and is, geologically spoken, very young, with its main part arisen during the period 400–200 kyr BP (Giret 1987, Doucet 2003). Permanent waterbodies are restricted to the higher plateau (Caldera, Plateau des Tourbières) in the centre and the west–southwestern part of the island (Falaises d'Entrecasteaux, Grandes Ravines). Almost all other areas lack (semi–permanent) waterbodies due to the steepness of the slope and the permeability of the lava tunnels, holes and fissures. Due to frequent fog, clouds, and high relative humidity in the upper areas (from 500 m a.s.l.), extensive peat formations have been developed, especially in the volcanic caldera (Heger *et al.* 2009). On the higher central plateau, the vegetation has a typical sub–Antarctic character, consisting of mosses, small ferns [e.g., *Blechnum penna–marina* (Poiret) Kuhn], grasses, sedges (e.g., *Uncinia brevicaulis* Thouras) and *Lycopodium* ssp. (Trehen *et al.* 1990). The rather species–poor vegetation is dominated by both native (43) and introduced (56) species, reflecting the isolation of the island (Frenot *et al.* 2001). Although the diversity of the lichen flora is rather poor (77 species), recently a new lichen species, *Caloplaca amsterdamensis* Aptroot & Ertz was described (Aptroot *et al.* 2011).

Sampling

Almost 150 moss samples were collected during a field campaign in November and December 2007. The samples were collected in PVC bottles and fixed with 3%

formaldehyde. Each sample was geographically localized using GPS and was accompanied by a detailed site description. If possible, pH, specific conductance and water temperature were measured in situ using a WTW 340i Multimeter. For 25 of them, water was collected 20 cm below the surface, filtered in situ and deep-frozen to be subsequently analysed in the laboratory at the University of Antwerp. Appendix 1 lists all samples together with their characteristics. In order to determine the moisture content of the sample, the F-value, referring to the F-classification of Jung (1936), was selected as representative for moisture and used for each sample. It is a humidity scale based on water content as follows: FI = submerged mosses, FII = free floating mosses, FIII = very wet (water drips from the samples without pressure), FIV = wet (water drips with a slight pressure), FV = quasi-wet (water drips after moderate pressure), FVI = moist (little water produced after high pressure), FVII = quasi-dry (only a few drops of water can be squeezed out), FVIII = dry (contains no water).

Sample preparation and counting

Samples were prepared for further analysis following the method described in Van der Werff (1955): small parts of the samples were cleaned by adding 37% H_2O_2 and heating to 80 °C for about 1 h. The reaction was completed by addition of an excessive amount of $KMnO_4$. Following digestion and centrifugation (three times 10 minutes at 3700 × g), cleaned material was diluted with distilled water to avoid excessive concentrations of diatom valves on the slides. Cleaned diatom valves were mounted in Naphrax®. Samples and slides are stored at the BR-collection, property of the Belgian federal government and given in permanent loan to the Botanic Garden Meise (Belgium). In each sample, 400 diatom valves were identified and enumerated on random transects at 1000× magnification using an Olympus BX53 microscope, equipped with Differential Interference Contrast (Nomarski) optics and Olympus UC30 Imaging System. Slides were scanned after doing the 400 valves counts in order to find rare species. For identification of Antarctic and sub-Antarctic species mainly the following publications were consulted: Van de Vijver *et al.* 2002a, 2002b, 2004a, 2008a, 2012, 2014b, Van de Vijver & Cox 2013, Lowe *et al.* 2013 and Wetzel *et al.* 2015).

Data analysis

For a pair wise comparison of the diatom flora of Ile Amsterdam with those of the other sub–Antarctic islands (Prince Edward Islands, Iles Crozet, Iles Kerguelen, Heard Island and Gough Island) the Community Coefficient of Sørensen (1948) was used. This index has the following formula: 2c/(a+b+2c) where a and b are the numbers of species exclusively observed in each of two sites and c is the number of species shared by these sites.

Non-metric Multidimensional Scaling (NMDS) was performed to reduce the multidimensional species data matrix into two dimensions best reflecting sites dissimilarities given by diatom species composition. NMDS was based on Bray-Curtis (Sørensen) dissimilarity calculated on square root transformed species data.

Classical agglomerative clustering was employed to group diatom assemblages according to the same Bray-Curtis distances using the unweighted per group average algorithm (UPGMA).

Resulting groups were projected into the NMDS ordination as well as best indicator species of the (combinations of) site groups. Indicator species were identified using the extended Indicator Species Analysis. The indicator value (IV) of an indicator species is a number calculated as the product of two quantities, called A and B, ranging from 0 to 1. Quantity A gives the probability of a site being a member of the site-group combination when the species was found at that site. Quantity B informs of how frequently (and hence how easily) the species is found at sites of the site-group combination under study (*De Cáceres et al. 2010).* Statistical analyses were performed using the R statistical environment (R Core Team 2017, RStudio Team 2015). For better classification of the individual groups, indicator species were used to characterize the community types of the individual groups. The indicator value (IV) of an indicator species is a number calculated as the product of two quantities, called A and B, ranging from 0 to 1. Quantity A gives the probability of a site being a member of the site-group combination when the species was found at that site. Quantity B informs of how frequently (and hence how easily) the species is found at sites of the site-group combination under study (*De Cáceres et al. 2010).*

Results

Species composition and diversity

The analysis of 148 samples revealed the presence of 122 diatom taxa belonging to 38 genera. Three additional taxa were observed outside the counts bringing the total number of moss-inhabiting diatoms up to 125. Twenty-one samples contained (almost) no diatoms, even after counting an entire slide. Subsequently, these samples have been removed from further analysis. The distribution of species numbers per sample (Fig. 1) showed that most samples contained between 11 and 15 taxa per sample. The average number (and standard deviation) of taxa per sample was 12 ± 7, with a median number of 11. Species richness per sample ranged from 1 to 40. Two samples were entirely monospecific, composed of only *Eunotia paludosa* Grunow var. *paludosa* (M026 & M157). The highest species richness was recorded in sample M203 (40 taxa). The 5 most abundant species accounted for 64.3% of all counted valves. The dominant species were *Eunotia paludosa* var. *paludosa* with more than 35% of all counted valves, followed by *Frustulia lebouvieri* Van de Vijver & Gremmen (10.5%), *Planothidium subantarcticum* Van de Vijver & Wetzel (7.4%), *Eunotia muscicola* Krasske var. *muscicola* (5.6%) and *Kobayasiella subantarctica* Van de Vijver & Vanhoutte (5.6%). On the contrary, 108 taxa (more than 87% of all counted taxa) had a total relative abundance of less than 1%. Appendix 1 provides an alphabetical list of all observed species together with their biogeographical distribution. The genera *Pinnularia* (twenty-nine taxa), *Eunotia* (nine taxa), *Nitzschia* (eight taxa) and *Humidophila* (seven taxa) were the most species rich genera. Other important genera include *Hantzschia*, *Luticola*, *Psammothidium*, *Sellaphora* and *Stauroneis* (four taxa). Table 1 lists all genera arranged according to their species number. Eleven taxa (9%) could at present only be identified up to the genus level. Some of them appear to be new to science and are yet to be formally described (mainly in genera *Nitzschia*, *Navicula, Pinnunavis* and *Sellaphora*).

Tab. 2: Genera ordered by decreasing percental portion (%) calculated on the number of the taxa (n).

genus	n	%
Pinnularia	29	23
Eunotia	9	7,1
Nitzschia	8	6,3
Humidophila	7	5,6
Navicula	6	4,8
Hantzschia	4	3,2
Luticola	4	3,2
Mayamaea	4	3,2
Psammothidium	4	3,2
Sellaphora	4	3,2
Stauroneis	4	3,2
Achnanthes	3	2,4
Gomphonema	3	2,4
Halamphora	3	2,4
Chamaepinnularia	3	2,4
Pinnunavis	3	2,4
Achnanthidium	2	1,6
Frustulia	2	1,6
Melosira	2	1,6
Orthoseira	2	1,6
Planothidium	2	1,6
Pseudostaurosira	2	1,6
Caloneis	1	0,8
Craticula	1	0,8
Denticula	1	0,8
Diatomella	1	0,8
Eolimna	1	0,8
Ferocia	1	0,8
Fistulifera	1	0,8
Fragilaria	1	0,8
Geissleria	1	0,8
Karayevia	1	0,8
Kobayasiella	1	0,8

genus	n	%
Lecohuia	1	0,8
Microfissurata	1	0,8
Placoneis	1	0,8
Rhopalodia	1	0,8
Stauroforma	1	0,8

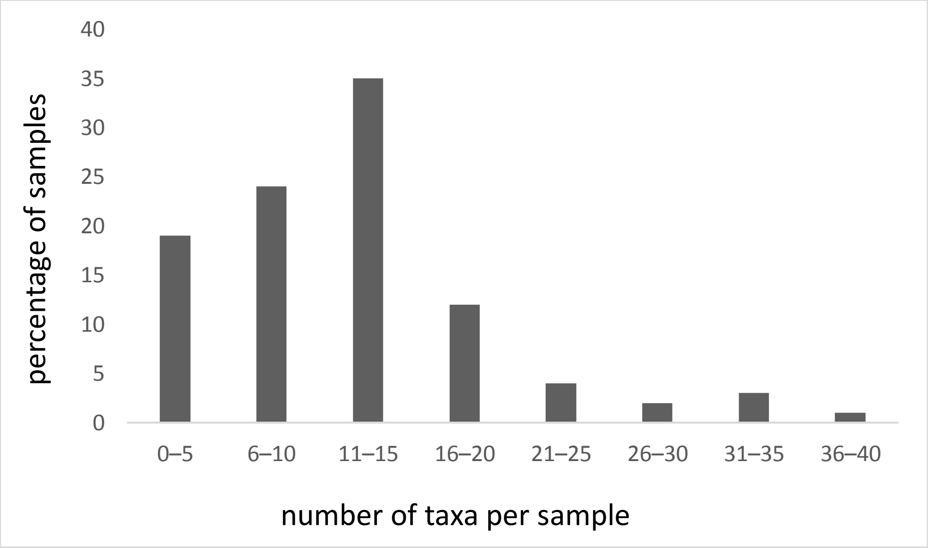

Fig. 1: Distribution of the taxon richness per sample.

Similarity analysis and distribution

From a biogeographical point of view, 42% of taxa have a typical cosmopolitan distribution whereas 18% of all observed species can be considered endemic to Ile Amsterdam, with another 16% species having a restricted sub–Antarctic distribution (Fig. 2).

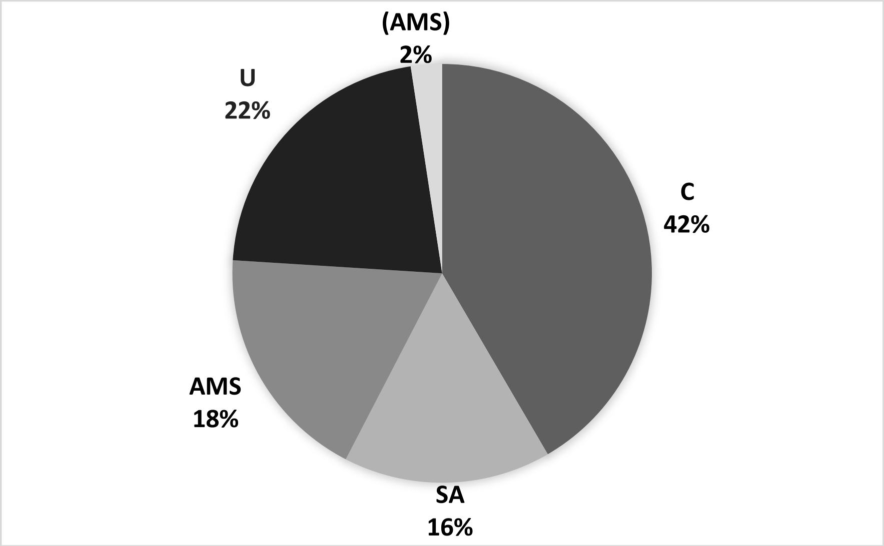

Fig. 2: Distribution of the species according to their biogeographical distribution [Distribution: (C) cosmopolitan, (SA) sub-Antarctic region, (AMS) Ile Amsterdam, (U) unknown, ((AMS)) Ile Amsterdam but yet undescribed].

The similarity analysis based on presence/absence data indicates that the moss diatom flora of Ile Amsterdam shows only a limited affinity to other sub-Antarctic islands, with Sørensen index values ranging from 0.24–0.48 (Tab. 2).

Tab. 2: Similarity analysis (Sørensen index) between Ile Amsterdam and other sub-Antarctic islands

	Ile Amsterdam	Prince Edward Islands	Crozet	Heard Island	Kerguelen	Gough Island	Saint-Paul
Number of taxa	125	198	160	181	210	141	60
Index of Sørensen		0.29	0.33	0.30	0.31	0.24	0.48

Community analysis

The NMDS analysis, based on a cluster dendrogram (not shown) divides the samples into 6 main groups (Fig. 2). The distinction between these groups is clearly reflected in the species composition. For each group, indicator species were determined. A strong relation between the indicator species and the groups was observed with the IV ranging from 0.8–0.99 (Fig. 3) (*De Cáceres et al. 2010).*

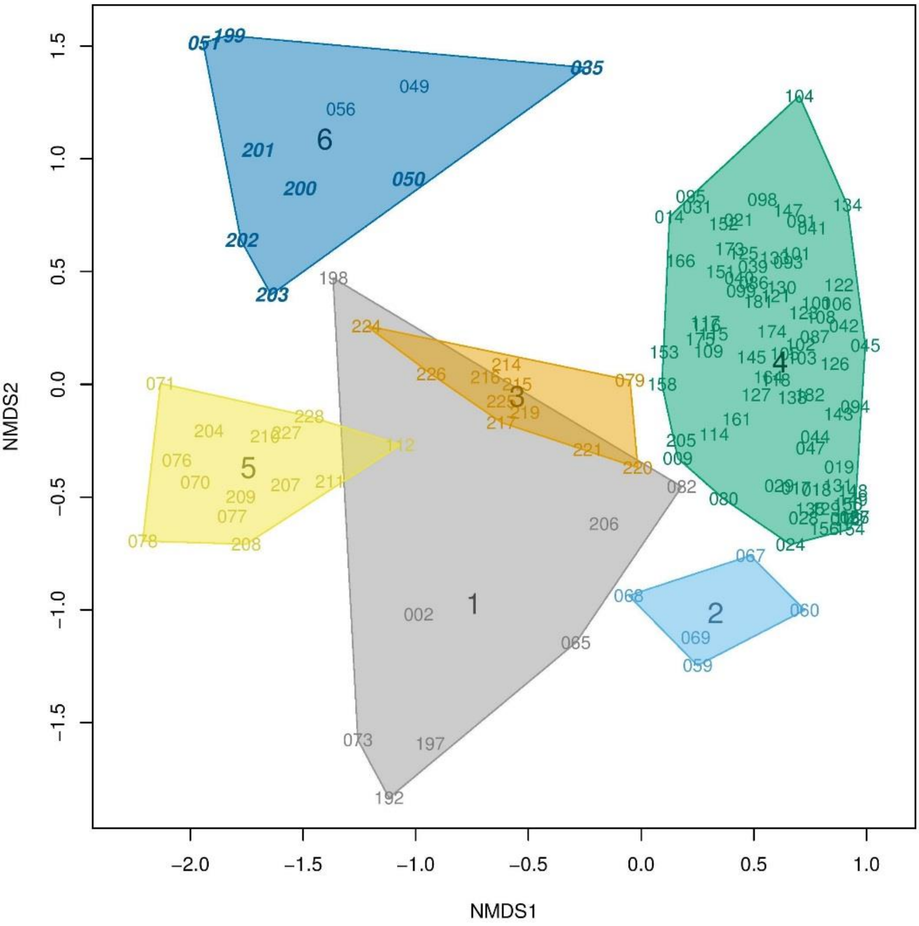

Fig. 2: NMDS diagram showing the 6 main groups of samples

The first group is formed in the bottom of the diagram, containing species-poor, dry samples, from moisture categories VI–VIII, with indicator species *Humidophila brekkaensis* (Petersen) Lowe *et al.* (IV 0.94), *H. contenta* (Grunow) Lowe *et al.* (IV 0.83) and *Pinnularia borealis* Ehrenberg complex (IV 0.89). To this group also belongs the detached sample M198, characterized by a high abundances of *Melosira* aff. *dickiei* (Thwaites) Kützing (placing it in the upper parts of the diagram) and *Humidophila contenta*. Five samples on the bottom right form a second group with acid, species-poor, mostly dry samples. The indicator species is *Pinnularia whinamiae* Van de Vijver (IV 0.99). The samples are further dominated by *Eunotia paludosa* var. *paludosa* and *Pinnularia microstauron* (Ehrenberg) Cleve. The third group formed in the middle, contains slightly acid samples from Del Cano and is characterized by a dominance of *Karayevia oblongella* (Østrup) Aboal (IV 0.9), *Psammothidium investians* (Carter) Bukhtiyarova (IV 0.99) and by high frequencies of *Eunotia paludosa* var. *paludosa*, *Sellaphora* cf. *seminulum* Grunow, *Sellaphora arvensis* (Hustedt) Wetzel & Ector and *Eunotia muscicola* var. *muscicola*. On the right side, a big group of high altitude, mostly acidic samples can be found. This fourth group is characterized by extremely high abundances of its indicator species *Frustulia lebouvieri* (IV 0.84) and *Eunotia paludosa* var. *paludosa* (IV 0.97). The samples are further dominated by *Kobayasiella subantarctica* and various *Eunotia* (*E. muscicola* var. *muscicola*, *E. lecohui* Van de Vijver) and *Pinnularia* taxa (*P. amsterdamensis* Chattová *et al.*, *P. vixconspicua* Chattová *et al.*, *P. myriamiae* Van de Vijver *et al.*). Almost all coastal samples from the Falaises d'Entrecasteaux and the Pointe Del Cano, with the highest pH and conductivity values, can be found in the left site of the diagram, forming a fifth group. The samples are almost exclusively dominated by *Planothidium subantarcticum* (IV 0.97) with. *Sellaphora* cf. *seminulum*, *Nitzschia soratensis* Morales & Vis and *Halamphora veneta* (Kützing) Levkov as co-dominant taxa. The last group in the upper half of the diagram comprises dry samples (moisture categories IV-VII), taken mainly from caves. The samples are dominated by *Melosira* aff. *dickiei* (IV 0.99), *Melosira* sp. (IV 0.94), *Orthoseira verleyenii* Van de Vijver (IV 0.89), *Humidophila rouhaniana* Chattová & Van de Vijver, *Chamaepinnularia aerophila* Van de Vijver & Beyens, *Mayamaea cavernicola* Van de Vijver & Cox, *Luticola ivetaiana* Chattová & Van de Vijver and various *Humidophila* taxa (*H. amsterdamenis* Chattová & Van de Vijver, *H. crozetikerguelensis* (Le Cohu & Van de Vijver) Lowe *et al.* and *H. gallica* (W. Smith) Lowe *et al.*). The relationship between species richness and environmental variables was analyzed with the samples divided into two main groups, according to altitude (Fig. 4). The majority (84) of samples belong to the group of the higher altitude samples (above 500 m a.s.l), whereas the rest of the samples originate from lower altitudes (0-500 m a.s.l). The species richness clearly increases with increasing pH and conductivity in the samples of the lower altitudes, whereas no apparent trend can be observed in the higher altitude samples.

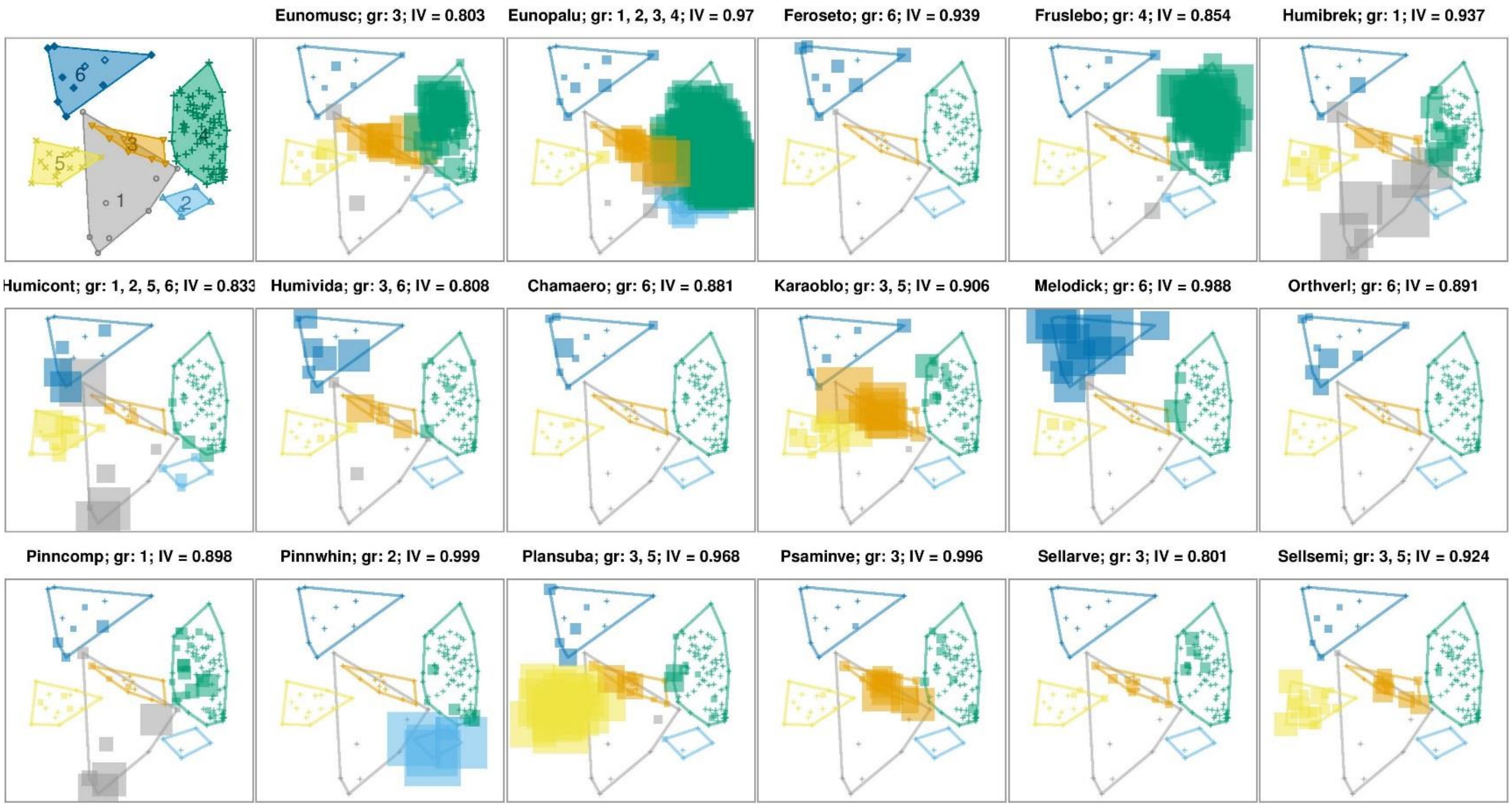

Fig. 3: Indicator species for different groups of samples

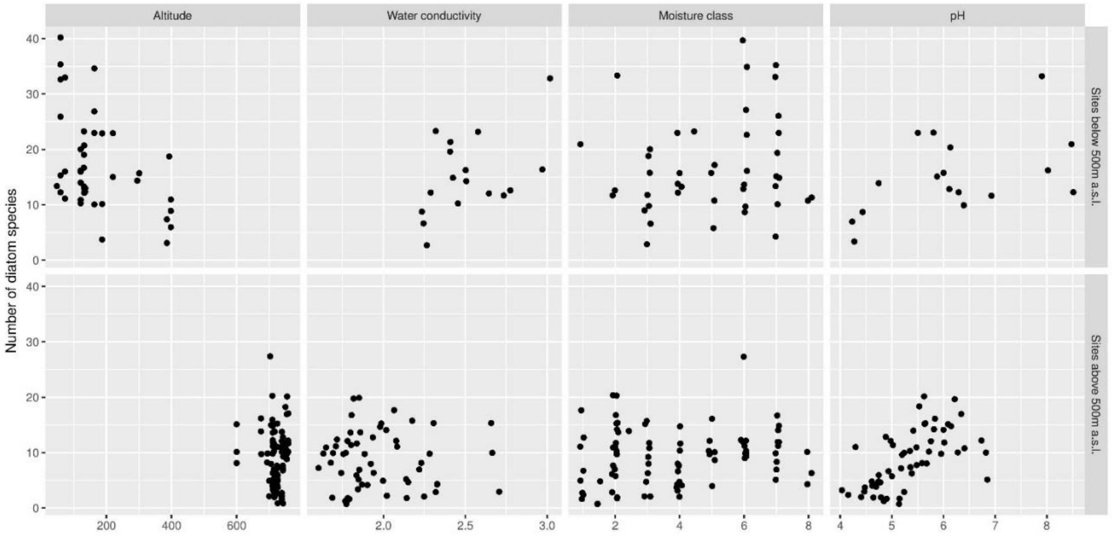

Fig. 4: A scatterplot showing a relation between species richness and environmental variables (altitude, pH, moisture and conductivity).

Discussion

Species composition and general biogeography

Based on the relative abundance data, the principal taxon was *Eunotia paludosa* var. *paludosa*, a cosmopolitan species, frequently reported from sub-Antarctica and typically found in semi-wet terrestrial mosses or small acid pools with lower conductivity values (Van de Vijver *et al.* 2014a).

Within the five most abundant taxa, three are typically sub-Antarctic (*Frustulia lebouvieri*, *Planothidium subantarcticum* and *Kobayasiella subantarctica*) and two can be considered to have a cosmopolitan distribution (*Eunotia paludosa* var. *paludosa* and *Eunotia muscicola* var. *muscicola).*The specificity of the Ile Amsterdam’s diatom flora is mainly reflected in the species composition of several highly diversified genera, such as *Pinnularia*, *Nitzschia*, *Humidophila* and *Luticola*, with a large number of new species.

The low similarity values (except from Ile Saint-Paul) based on presence/absence data between Ile Amsterdam and the other islands are not surprising, considering the differences in the microhabitat diversity, rather large distance between the islands, the isolated position of Ile Amsterdam and the relative young geological age. The closest to Ile Amsterdam, based on its diatom flora, identified was the neighbouring Ile Saint-Paul followed by Ile de la Possession from the Crozet Archipelago. Illustrative analyses of terrestrial diatom communities from Ile Saint-Paul (further in this thesis) revealed an additional 15 taxa not presented in the mosses of Ile Amsterdam, but an otherwise highly similar flora. The situation is different on Ile de la Possession, where the species of Achnanthoid genera (*Psammothidium*, *Planothidium*), *Fragilaria* and *Navicula* dominate. Diatom floras dominated by species of genera *Achnanthes* were previously also reported from South Georgia (Van de Vijver & Beyens 1997) and Kerguelen (Van de Vijver *et al.* 2001).

Moss inhabiting diatom communities

Both environmental data and diatom distributions indicate that apart from altitude, specific conductance, pH and moisture are the major factors involving the structure of moss-inhabiting diatom communities on Ile Amsterdam. The mosses in the region near the Falaises d’Entrecasteaux and Pointe Del Cano were taken from waterbodies showing a slightly acid to clearly alkaline pH, whereas in the upper Caldera the waterbodies are strictly (very) acidic. Since the area of d’Entrecasteaux and Del Cano, in our data set represented by groups 3 and 5, represent a similar habitat showing very steep cliffs with small ravines, the diatom communities of both groups show some clear similarities. Samples of both groups are dominated by taxa preferring circumneutral to alkaline conditions such as *Sellaphora* cf. *seminulum, Rhopalodia rupestris* (W. Smith) Krammer and several *Nitzschia* taxa (Hofmann *et al.* 2011). However, the groups significantly differ in the dominant (indicator) species, with *Karayevia oblongella* and *Psammothidium investians* characterizing the third group of the slightly acid to circumneutral samples from Del Cano, while *Planothidium subantarcticum* almost exclusively dominates the alkaline samples of the fifth group. On the contrary the alkaline moss-inhabiting diatom communities on Ile de la Possession and Iles Kerguelen, have a very high frequency of various *Fragilaria* (fragilaroid) taxa such as *Frankophila maillardii* (Le Cohu) Lange-Bertalot, *Fragilaria vaucheriae* (Kützing) Petersen and *Distrionella germainii* (Lange-Bertalot & Reichardt) Flower, whereas the diatom flora on Ile Amsterdam is extremely poor in fragilaroid taxa. The only araphids on Ile Amsterdam are *Pseudostaurosira naveana* (Le Cohu) Morales & Edlund, *Pseudostaurosira* cf. *trainorii* Morales, *Stauroforma* aff. *exiguiformis* (Lange-Bertalot) Flower, Jones & Round and *Fragilaria* cf. *neoproducta* Lange-Bertalot, found in the caves or the coastal habitats.

The acidic diatom communities represented by the high altitude samples from the fourth group, are dominated by *Frustulia lebouvieri* and *Eunotia paludosa* var. *paludosa*. This group is typical for locations found at higher altitudes (above 500 m a.s.l.) characterized by peat-bogs with higher moisture levels and acidic pH. Similar communities characterized by the dominance of *Eunotia paludosa* var. *paludosa* were reported from Gough Island (Vinšová, unpublished results), South Georgia (Van de Vijver & Beyens 1997) and Ile de la Possession (Van de Vijver & Beyens 1999b). However, differences can be found in the associated diatom flora of the dominant species. The *Eunotia paludosa* var. *paludosa* dominated assemblages were on Ile de la Possession co-dominated by *Chamaepinnularia soehrensis* var. *muscicola* (Petersen) Lange-Bertalot & Krammer, *Aulacoseira alpigena* (Grunow) Krammer and *Adlafia bryophyla* (Petersen) Lange-Bertalot, whereas on Gough Island by *Eunotia* cf. *fallax* (Cleve) and *Chamaepinnularia* cf. *begeri* (Krasske) Lange-Bertalot (Van de Vijver & Beyens 1999b, Vinšová, unpublished results).

The typical terrestrial taxa such as *Hantzschia amphioxys*, *Humidophila brekkaensis*, *Pinnularia borealis* complex or *Orthoseira roeseana*, forming the driest assemblages of group 1, play only a minor role or are completely absent on Ile de la Possession and Gough Island (Van de Vijver & Beyens 1999b, Vinšová, unpublished results). The only similar feature of the Ile Amsterdam's terrestrial diatom flora with those on Ile de la Possession is the dominance of *Humidophila contenta*. Differences can be found in the associated diatom flora of this communities, mainly composed of *Planothidium aueri* and *Fragilaria* cf. *vaucheriae*. The most similar terrestrial diatom flora was found in dry mosses of South Georgia, with the samples dominated mainly by well known, cosmopolitan taxa, such as

Hantzschia amphioxys, *Pinnularia borealis* complex, *Orthoseira roeseana* and *Humidophila contenta* (Van de Vijver & Beyens 1997).

Moisture content is one of the prinicpal factors determining the diatom assemblages in moss communities in (sub)-Antarctic (Van de Vijver & Beyens 1999b, Kopalová *et al*. 2014) and is one of the factors co-responsible for the classification of the main groups of moss-inhabiting diatom communities on Ile Amsterdam. A clear difference between diatom communities growing in wetter mosses and those from dry mosses was found. Moisture can be therefore considered as an important factor, even when the wettest samples aren't the most species rich on the island, resulting most likely from the fact that the majority of wet samples belong to the most acidic, with lower conductivity values. Moreover, the species richest cave samples are at the same time one of the driest at the island. For future research, that is to reveal the influence and specificity of the cave and lava tube microhabitat, an entire large dataset of lava tube and cave samples was collected on Ile Amsterdam during the recent field campaign.

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Appendix 1

Physico–chemical characteristics (when available) of samples collected on Ile Amsterdam, temperature in °C, conductivity in µS.cm–1, altitude in a.s.l., other variables in mg.l^{-1}

sample	$(NO_2^-+NO_3^-)N$	NH_4^+-N	PO_4^{3-}-P	SO_4^{2-}	Cl^-	pH	cond	T	altitude	Na^+	K^+	Ca^{2+}	Mg^{2+}	moisture
M002									301					VI
M009						4,81	360		295					IV
M014	2,3	0,25	0,01	8	34	5,56	136	10,2	750	17,0	0,6	1,0	1,73	I
M015	2,1	0,12	0,09	2	103	4,44	243	12,0	711	4,6	0,4	0,2	0,39	II
M017						4,71	96		711					III
M018						4,7	121		711					III
M019									711					VIII
M021	2,1	0,22	0,01	4	18	5,91	64	14,3	717	3,6	0,1	0,2	0,35	II
M024	1,0	0,05	0,13	2	153	5,15	68	11,8	714	5,6	0,4	0,3	0,45	II
M026						5,17	64	13,5	726					I-II
M028	1,4	0,27	0,01	4	13	4,66	90	13,8	710	5,5	0,5	0,3	0,55	IV
M029						4,79	80		710					I-II
M031	1,3	0,12	0,01	4	22	5,57	80	13,8	710	12,9	1,0	0,8	1,14	II
M035									703					VI
M039	10,2	0,54	0,17	14	49	6,00	168	14,5	706	6,5	0,4	0,5	0,59	IV
M040									710					V
M041									714					IV
M042									714					VII
M044						4,72	82		716					IV
M045						5,24	56	13,2	715					VI
M047									715					VII
M049									715					VII
M050	0,31	0,09	0,06	10	63	5,81	239	17,0	220	35,5	1,3	4,1	4,62	IV-V
M051						5,81	239	17,0	220					VII
M056									393					VII
M059	0,29	0,05	0,01	6	42	4,14	167	17,1	386	24,2	1,8	1,6	2,48	III
M060						4,34	169		386					III
M065									398					VIII
M067									398					V
M068						4,35	138		398					VI
M069									398					III

sample	$(NO_2^-+NO_3^-)N$	NH_4^+-N	PO_4^{3-}-P	SO_4^{2-}	Cl^-	pH	cond	T	altitude	Na^+	K^+	Ca^{2+}	Mg^{2+}	moisture
M070	2,1	0,05	0,07	19	61	7,94	1126	12,0	73	42,1	4,1	20,7	12,8	II
M071						7,94	1126		73					V
M073									73					VIII
M076	0,21	0,05	0,08	21	34	8,49	316	12,0	132	25,5	3,2	20,2	12,2	I
M077						6,96	454		132					III
M078									132					IV
M079	0,02	0,05	0,01	7	28	6,18	444	14,0	600	16,2	0,4	1,1	1,60	III
M080									600					IV
M082	0,02	0,05	0,01	7	28	6,18	444	14,0	600	16,2	0,4	1,1	1,60	VI
M086	0,13	0,05	0,01	5	17	5,40	67	8,5	739	10,3	0,4	0,7	0,95	II-III
M087						5,4	67	8,5	739					VI
M091	0,02	0,05	0,0	9	15	6,80	54	17,0	757	10,1	0,1	0,7	0,82	II
M093						6,10	68	16,0	758					VI
M094									758					VIII
M095	0,02	0,05	0,01	7	19	6,14	65	13,0	755	12,1	0,1	1,1	1,22	II
M098						6,44	68	15,00	759					II
M099						5,85	116		759					III
M100									758					IV
M101						6,03	46	16,00	748					V
M102	0,02	0,05	0,08	7	27	6,80	46	18,0	742	9,8	12,5	0,6	0,76	VI
M103						5,43	152		742					IV
M104						5,53	102		742					III
M105									752					VII
M106									752					VI
M108									752					VI
M109						5,63	78		711					II
M112									711					V
M114									711					V
M115									711					VI
M116						5,92	122		711					II
M117						5,69	83		711					II
M118									711					VII
M121						6,47	62	15	720					II
M122						5,74	211		706					IV
M123						5,71	70	18	695					VII
M125									676					II

sample	$(NO_2^-+NO_3^-)N$	NH_4^+-N	PO_4^{3-}-P	SO_4^{2-}	Cl^-	pH	cond	T	altitude	Na^+	K^+	Ca^{2+}	Mg^{2+}	moisture
M126									694					VII
M127						6,94	57	14	700					I
M129						4,43	119		700					IV
M130						4,93	57	15	726					II
M131						3,96	487		726					IV
M133						5,22	47		726					II
M134						5,3	76	15	724					II
M135						4,64	219	15	727					IV
M138									725					VIII
M143						4,42	230		725					V
M145									725					VII
M147	0,02	0,05	0,01	10	13	5,58	45	15,0	724	8,0	0,1	0,7	0,62	II
M148						4,88	56	15	716					I
M149						4,15	144		716					III
M150									716					II
M151	0,02	0,05	0,01	7	19	4,98	67	13,0	739	10,3	0,4	0,6	0,78	II
M152						4,98	67	13	739					II
M153						4,32	116	13	739					III
M154						4,84	59	13	739					II
M155						4,65	110		739					III
M156									739					I
M157						4,76	62	13	743					I-II
M158						5,24	238		754					V
M161									754					V
M164									754					VI
M166									754					VII
M172						5,13	50	13	738					I
M173									743					III
M174	0,02	0,05	0,01	8,00	18,00	4,89	71	13	742	12,6	0,1	0,8	1,09	I
M175	0,02	0,05	0,01	8,00	18,00	4,89	71	13	742	12,6	0,1	0,8	1,09	I
M181	0,02	0,05	0,01	7	18	5,54	55	15,0	726	11,1	0,1	0,8	0,94	I
M182						4,56	159	15	727					IV
M192									187					VII
M197									187					VII
M198									187					VII
M199									59					VII

sample	$(NO_2^-+NO_3^-)N$	NH_4^+-N	PO_4^{3-}-P	SO_4^{2-}	Cl^-	pH	cond	T	altitude	Na^+	K^+	Ca^{2+}	Mg^{2+}	moisture
M200									59					VII
M201									59					VII
M202									59					VI
M203									59					VI
M204									48					VII
M205						5,8	152		675					III
M206									675					VII
M207									131					III
M208									131					VI
M209									131					V
M210									131					VI
M211	0,02	0,05	0,01	21	171	6,05	595	13,0	135	58,7	1,1	4,5	7,84	II
M214						6,23	650		135					IV
M215									121					III
M216						6,05	286		121					IV
M217									121					V
M219	0,02	0,05	0,01	9	55	6,14	223	13,0	121	36,9	1,0	2,6	4,04	III
M220									121					VI
M221									121					VI
M224	0,02	0,05	0,01	12	96	6,36	358	14,0	163	52,5	1,7	5,7	6,24	III
M225						5,51	435		163					IV
M226									163					VII
M227									163					VI
M228						8,46	235	16	59					II

Appendix 2

Taxonomical list of all observed taxa in this study. Unidentified species are given a provisional letter code. [Distribution: (C) cosmopolitan, (SA) sub-Antarctic region, (U) unknown, (AMS) Ile Amsterdam, ((AMS)) Ile Amsterdam but yet undescribed].

species	Distribution
Achnanthes coarctata (Brébisson) Grunow	C
Achnanthes muelleri Carlson	SA
Achnanthes naviformis Van de Vijver & Beyens	SA
Achnanthidium sieminskae Witkowski, Kulikovskiy & Riaux-Gobin	SA
Achnanthidium sp	U
Caloneis bacillum (Grunow) Cleve	C
Craticula submolesta (Hustedt) Lange-Bertalot	C
Denticula cf. *sundaysensis* Archibald	U
Diatomella balfouriana Greville	C
Eolimna cf. *minima* (Grunow) Lange-Bertalot	U
Eunotia aff. *minor* (Kützing) Grunow	U
Eunotia cf. *arcus* Ehrenberg	U
Eunotia cf. *pectinoides* J.R.Carter	U
Eunotia clotii Van de Vijver, de Haan & Lange-Bertalot	SA
Eunotia cocquytiae Van de Vijver	AMS
Eunotia lecohui Van de Vijver	SA
Eunotia muscicola Krasske var. *muscicola*	C
Eunotia paludosa var. *paludosa* Grunow group	C
Eunotia pugilistica Van de Vijver	AMS
Ferocia setosa (Greville) Van de Vijver & Houk	C
Fistulifera sp	U
Fragilaria neoproducta Lange-Bertalot	C
Frustulia lebouvieri Van de Vijver & Gremmen	SA
Frustulia vulgaris (Thwaites) De Toni	C
Geissleria sp	U
Gomphonema aff. *exilissimum* Grunow	U
Gomphonema cf. *montanum* (J.Schumann) Grunow	U
Gomphonema parvulum (Kützing) Kützing group	C
Halamphora compereana Van de Vijver & Levkov	AMS
Halamphora dagmarobbelsiana Van de Vijver & Levkov	AMS

species	Distribution
Halamphora veneta (Kützing) Levkov	C
Hantzschia abundans Lange-Bertalot	C
Hantzschia amphioxys (Ehrenberg) Grunow	C
Hantzschia possessionensis Van de Vijver & Beyens	SA
Hantzschia sp	U
Humidophila amsterdamensis Chattová & Van de Vijver	AMS
Humidophila brekkaensis (Petersen) Lowe, Kociolek, Johansen, Van de Vijver, Lange-Bertalot & Kopalová	C
Humidophila contenta (Grunow) Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange-Bertalot & Kopalová	C
Humidophila crozetikerguelensis (Le Cohu & Van de Vijver) Lowe, Kociolek, Johansen, Van de Vijver, Lange-Bertalot & Kopalová	SA
Humidophila gallica (W.Smith) Lowe, Kociolek, You, Wang & Stepanek	C
Humidophila rouhaniana Chattová & Van de Vijver	AMS
Humidophila vidalii (Van de Vijver, Ledeganck & Beyens) Lowe, Kociolek, Johansen, Van de Vijver, Lange-Bertalot & Kopalová	SA
Chamaepinnularia aerophila Van de Vijver & Beyens	SA
Chamaepinnularia evanida (Hustedt) Lange-Bertalot	C
Chamaepinnularia soehrensis var. *muscicola* (J.B.Petersen) Lange-Bertalot & Krammer	C
Karayevia oblongella (Østrup) Aboal	C
Kobayasiella subantarctica Van de Vijver & Vanhoutte	SA
Lecohuia geniculata (H.Germ.) Lange-Bertalot & U.Rumrich	C
Luticola beyensii Van de Vijver, Ledeganck et Lebouvier	SA
Luticola ivetaiana Chattová & Van de Vijver	AMS
Luticola subcrozetensis Van de Vijver, Kopalová, Zidarova & Levkov	SA
Luticola vancampiana Chattová & Van de Vijver	AMS
Mayamaea atomus var. *permitis* (Hustedt) Lange-Bertalot	C
Mayamaea cavernicola Van de Vijver & Cox	AMS
Mayamaea cf. *agrestis* (Hustedt) Lange-Bertalot	U
Mayamaea fossalis (Krasske) Lange-Bertalot group	C
Melosira aff. *dickiei* (Thwaites) Kützing	U
Melosira aff. *varians* C.Agardh	U
Microfissurata australis Van de Vijver & Lange-Bertalot	AMS
Navicula aff. *shackletonii* West & G.S.West	U
Navicula cf. *bicephala* Hustedt	U
Navicula cf. *cryptotenella* Lange-Bertalot	U

species	Distribution
Navicula gregaria Donkin	C
Navicula longicephala Hustedt group	C
Navicula veneta Kützing	C
Nitzschia communis Rabenhorst	C
Nitzschia commutata Grunow	C
Nitzschia debilis (Arnott ex O'Meara) Grunow in Cleve & Grunow	C
Nitzschia fonticola (Grunow) Grunow	C
Nitzschia frustulum (Kützing) Grunow	C
Nitzschia palea (Kützing) W. Smith group	C
Nitzschia soratensis Morales & Vis	C
Nitzschia sp	(AMS)
Orthoseira roeseana (Rabenhorst) O'Meara	C
Orthoseira verleyenii Van de Vijver	AMS
Pinnularia acidicola var. *acidicola* Van de Vijver & Beyens	SA
Pinnularia aff. *acidicola* var. *elongata* Van de Vijver & Beyens	U
Pinnularia aff. *amsterdamensis* Chattová, Van de Vijver & Metzeltin	U
Pinnularia aff. *microstauron* (Ehrenberg) Cleve	U
Pinnularia amsterdamensis Chattová, Van de Vijver & Metzeltin	AMS
Pinnularia australogibba Van de Vijver, Chattová & Metzeltin	AMS
Pinnularia australogibba var. *subcapitata* Van de Vijver, Chattová & Metzeltin	AMS
Pinnularia borealis Ehrenberg complex	C
Pinnularia bottnica Krammer	C
Pinnularia lindanedbalovae Van de Vijver & Moravcová	SA
Pinnularia microcapitata Van de Vijver, Chattová & Metzeltin	AMS
Pinnularia microstauron (Ehrenberg) Cleve	C
Pinnularia myriamiae Van de Vijver, Chattová & Metzeltin	AMS
Pinnularia perminor Kulikovskiy, Lange-Bertalot & Metzeltin	C
Pinnularia pseudohilseana Van de Vijver, Chattová & Metzeltin	AMS
Pinnularia rabenhorstii var. *subantarctica* Van de Vijver & Le Cohu	SA
Pinnularia robrechtii Van de Vijver	AMS
Pinnularia sinistra Krammer	C
Pinnularia sp1	U
Pinnularia sp2	U
Pinnularia sp3	U

species	Distribution
Pinnularia sp4	U
Pinnularia subacoricola Metzeltin, Lange-Bertalot & García-Rodríguez	C
Pinnularia subcommutata Krammer	C
Pinnularia subsinistra Van de Vijver, Chattová & Metzeltin	AMS
Pinnularia sylviae Van de Vijver	AMS
*Pinnularia vixconspicu*a Chattová, Metzeltin & Van de Vijver	AMS
Pinnularia vlaminghi Van de Vijver Chattova & Metzeltin	AMS
Pinnularia whinamiae Van de Vijver	SA
Pinnunavis gebhardii (Krasske) Van de Vijver	SA
Pinnunavis sp	(AMS)
Placoneis anglica (Ralfs) Cox	C
Planothidium pericavum (J.R.Carter) Lange-Bertalot	C
Planothidium subantarcticum Van de Vijver & Wetzel	SA
Psammothidium abundans (Manguin) Bukhtiyarova & Round	C
Psammothidium investians (Carter) Bukhtiyarova	C
Psammothidium manguini (Hustedt) Van de Vijver	C
Psammothidium stauroneioides (Manguin) Bukhtiyarova	C
Pseudostaurosira naveana (Le Cohu) Morales & Edlund	C
Pseudostaurosira trainorii Morales	C
Rhopalodia rupestris (W. Smith) Krammer	C
Sellaphora arvensis (Hustedt) Wetzel & Ector	C
Sellaphora barae Van de Vijver	AMS
Sellaphora cf. *seminulum* Grunow	U
Sellaphora sp	(AMS)
Stauroforma aff. *exiguiformis* (Lange-Bertalot) Flower, Jones & Round	U
Stauroneis kriegeri Patrick	C
Stauroneis pseudomuriella Van de Vijver & Lange-Bertalot	SA
Stauroneis thermicola (Petersen) Lund	C
Stauroneis bertrandii Van de Vijver & Lange-Bertalot	SA

Preliminary analysis of diatoms from Ile Saint-Paul

Diatom analyses of Ile Saint Paul diatom flora are limited to terrestrial (moss-inhabiting and soil) diatom communities, due to the absence of waterbodies on the island, altogether with the limited number of diatom fieldwork done on this island. More thorough research of Ile Saint-Paul is underway, promising to bring complete result in future.

Almost 50 samples were analysed during a preliminary observation of the biodiversity of the soil and moss inhabiting diatom flora of Ile Saint-Paul. Thirty-two (18 soil and 14 moss) samples contained a sufficient amount of diatom valves and were retained for further analysis whereas 17 samples were almost empty and therefore removed from the dataset. In 18 soil samples 53 taxa were found, whereas in 14 moss samples (including one lichen sample) only 42 species were identified. The combined diatom flora of Ile Saint Paul comprises a total of 60 species belonging to 20 genera. The identification of 9 taxa was uncertain (indicated with ‘cf.’, ‘aff.’ or ‘group’) and another 13 taxa could be identified up to the genus level only. A full list of all diatom taxa can be found in Table 1 in the general results of this thesis. Taxa identified upon genus level only were referred to by their genus name followed by ‘sp’. The species richness per sample varied between 6 and 24, with the mean number of taxa per sample being 14. The highest species richness was recorded in soil sample A6 (24 taxa). The distribution of species numbers per sample (Fig. 1) showed that most samples contained between 11 and 15 taxa per sample.

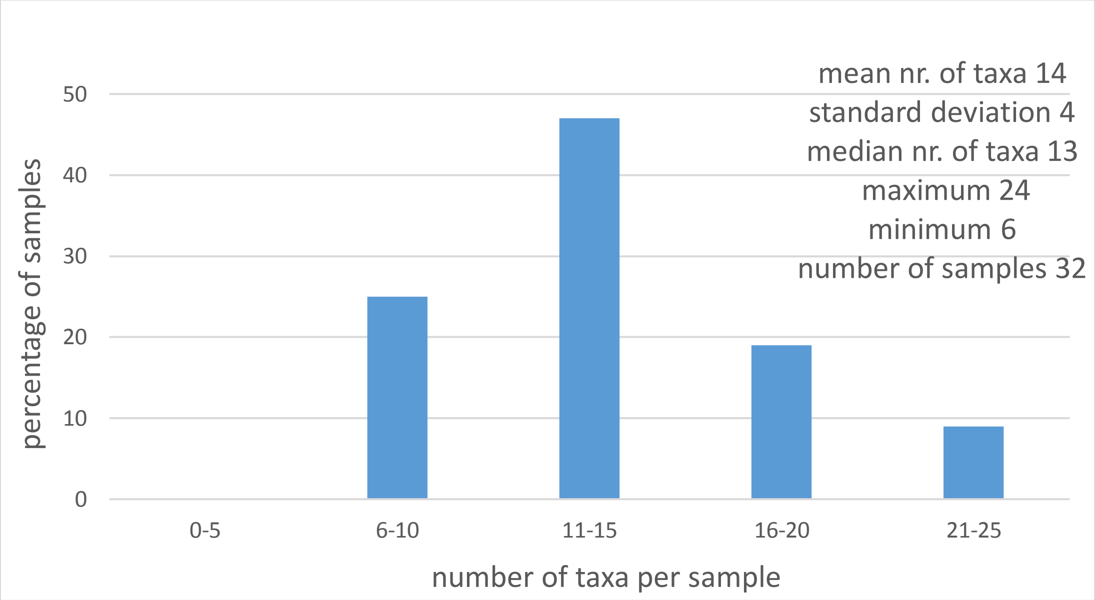

Fig. 1: Distribution of the taxon richness per sample.

The most common taxa on Ile Saint-Paul are: *Humidophila brekkaensis* (Petersen) Lowe *et al. (*15%), *H. contenta* (Grunov) Lowe *et al.* 15%, *Luticola vancampiana* Chattová & Van de Vijver 12%, *Pinnularia acidicola* var. *acidicola* Van de Vijver & Beyens 9 % and *P. borealis* Ehrenberg complex 8%. Other frequently found species include *Luticola beyensii* Van de Vijver, Ledeganck & Lebouvier, *Hantzschia amphioxys* (Ehrenberg) Grunow, *Achnanthes brevipes* var. *intermedia* (Kützing) Cleve, *Nitzschia* sp1 and *Pinnularia sinistra* Krammer. *Humidophila brekkaensis* is the only taxon which was observed in all samples. Figure 2 represents the most species rich genera: *Pinnularia* (16 taxa), *Nitzschia* (7 taxa), *Luticola* (5 taxa), *Hantzschia* (5 taxa), *Humidophila* (4 taxa) and *Achnanthes* (3 taxa). Some of the dominant genera on Ile Saint Paul and the neighbouring Ile Amsterdam (*Pinnularia*, *Luticola* and *Humidophila*) have recently been taxonomically revised, resulting in the description of several new species (Van de Vijver *et al.* 2012, Chattová *et al.* unpublished results). Details can be found in the taxonomical part of this thesis. It is however clear that near-future planned, more detailed analysis of the material, will reveal that more taxa need a formal description (mainly within the genera *Nitzschia*, *Mayamaea* and *Achnanthes*).

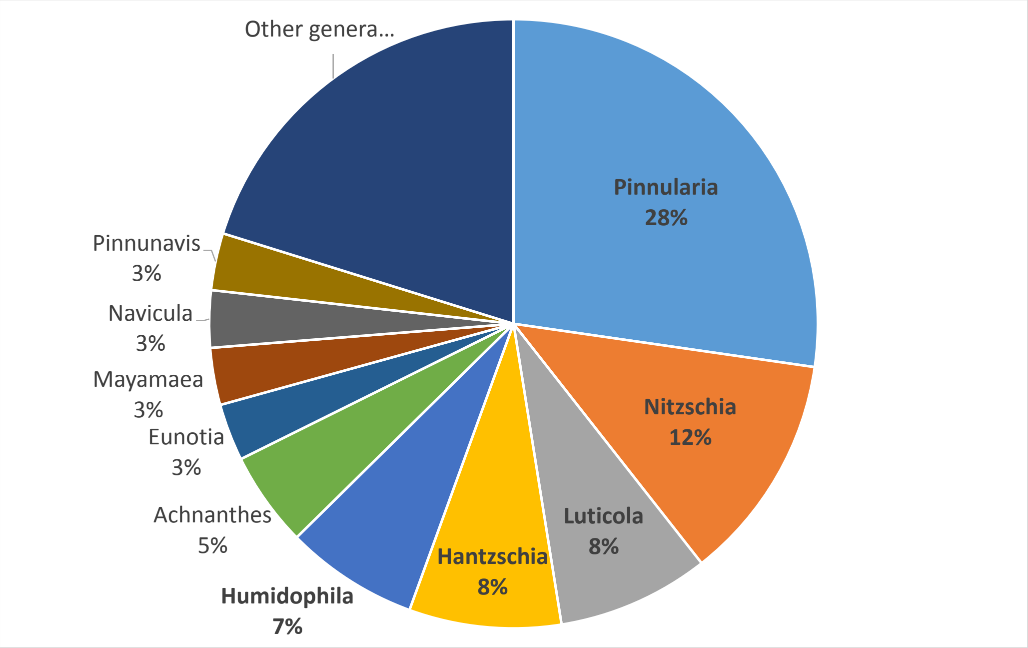

Fig. 2: Composition of Ile Saint-Pauls diatom community (genera level) based on species richness

Almost 34% of all observed taxa are cosmopolitan species, 18% of taxa have a restricted sub-Antarctic distribution and 10% of taxa can be considered endemic to Ile Amsterdam or Ile Saint-Paul, with additional 8% of potentially endemic taxa which are unidentified (undescribed) at the moment (Fig. 3).

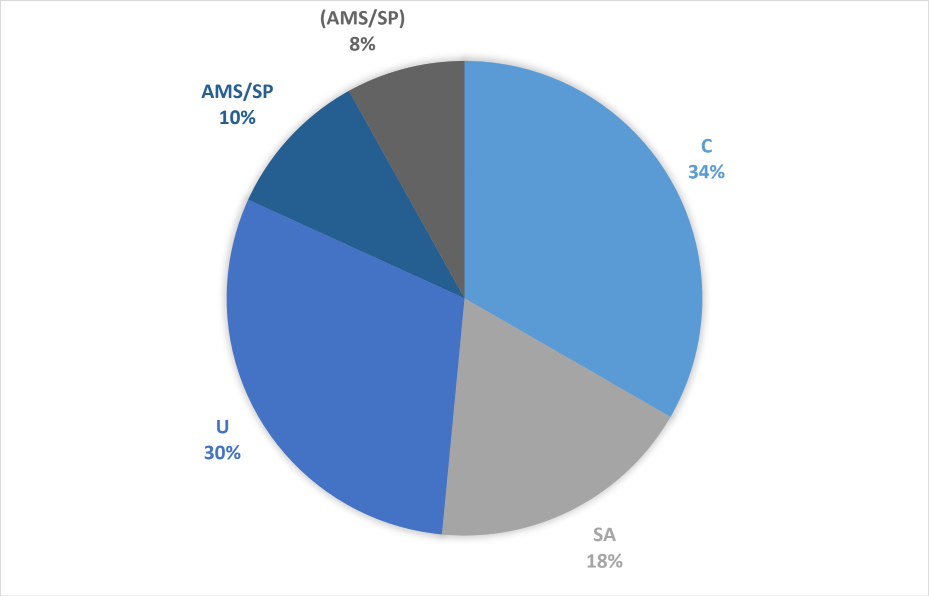

Fig 3: Distribution of the species according to their biogeographical distribution [Distribution: (C) cosmopolitan, (AMS/SP) Ile Amsterdam or Ile Saint Paul, (SA) sub-Antarctic region, (U) unknown, ((AMS/SP)) – Ile Amsterdam/Ile Saint Paul but yet undescribed].

The result of a similarity analysis with Ile Amsterdam (Index of Sørensen=0.48) indicates a high affinity of both diatom floras. The moss diatom flora of both islands is almost identical, with only two species (*Nitzschia dissipata* (Kützing) Rabenhorst and *Pinnularia* aff. *subacoricola* Metzeltin, Lange-Bertalot & García-Rodríguez) which were exclusively observed in mosses of Ile Saint-Paul. The situation is somewhat different in the case of soil samples, where 13 typical species for Ile Saint-Paul were found (e.g., *Achnanthes brevipes* var. *intermedia*, *Mayamaea* sp, *Luticola* sp or *Diploneis* sp). Highly probably due to the uncomplete analyses of the Ile Amsterdam's soil diatom flora.

The PCA analysis (Fig. 4) was performed on the log transformed data set (32 samples). The first two PCA axes ($\lambda_1 = 0.25$, $\lambda_2 = 0.13$) explained 37.5% of the variation in the diatom composition with an additional 16.2% explained on the next two axes. The samples on the upper right site of the diagram form a group of samples taken in the crater, belonging to the wetter (moisture categories VI–VII) and most species rich on the island, dominated by

Pinnularia acidicola, *Nitzschia* sp1, *Pinnularia sinistra* and *Luticola beyensii*. A small group of 3 soil samples, of temperature 24–33°C, dominated by *Humidophila contenta*, *Hantzschia amphioxys*, *Nitzschia frustulum* (Kützing) Grunow, *Nitzschia debilis* (Arnott ex O'Meara) Grunow and *Luticola beyensii* is formed in the bottom right. On the left side, two main groups can be observed. The upper half is comprised of soil samples, with some of them clearly influenced by animals, dominated by *Luticola vancampiana*, *Luticola subcrozetensis* Van de Vijver *et al.*, *Pinnunavis gebhardii* (Krasske) Van de Vijver and *Humidophila brekkaensis*, whereas the lower half is formed by dry moss samples of moisture category VIII, characterized by a high frequency of the *Pinnularia borealis* complex, *Humidophila contenta* and *Luticola subcrozetensis*. Finally, soil samples in the middle part of the diagram, mainly taken at the coast near the former lobster factory, are characterized by high abundances of *Humidophila contenta*, *Humidophila brekkaensis*, *Luticola subcrozetensis* and *Hantzschia amphioxys*. The sample A7 is taken from the upper part of the island of the area of fumaroles and so-called ‘terres chaudes’ reaching the temperature of 58°C. In this sample,an unidentified, unique *Luticola* sp. was found (see Paper V).

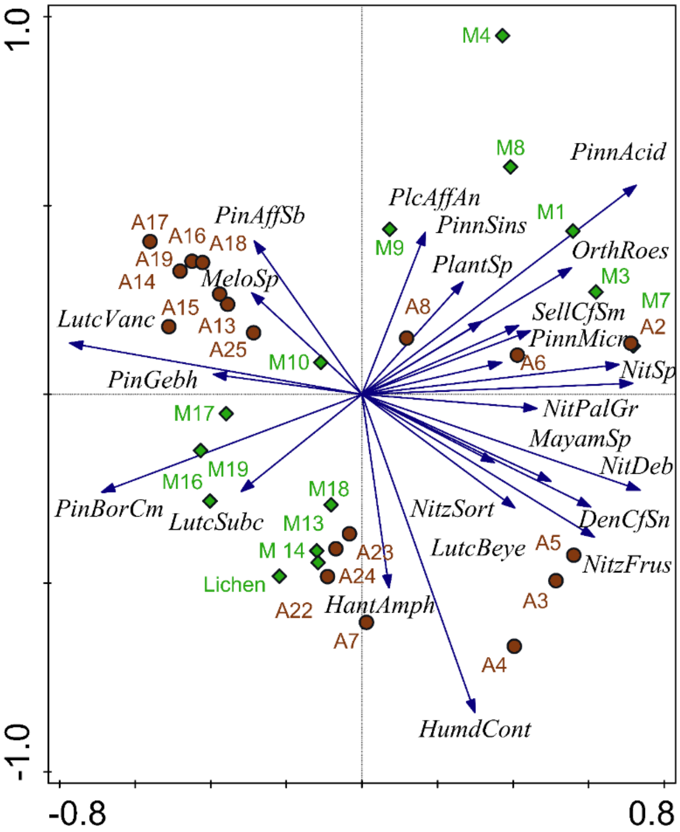

Fig 4.: Principal component analysis (PCA) correlation biplot of the Saint-Paul islands data set showing moss samples (green diamonds), soil samples (brown circles) and species (abbreviations: DentcfSn – *Denticula* cf. *sundaysensis*, HantAmph – *Hantzschia amphioxys*, HumdCont – *Humidophila contenta*, LutcBeye – *Luticola beyensii*, LutcVanc – *Luticola vancampiana*, LutcSubc – *Luticola subcrozetensis*, MayamSp – *Mayamaea* sp., Melosp – *Melosira* sp, NitDeb – *Nitzschia debilis*, NitFrust – *Nitzschia frustulum*, NitzSort – *Nitzschia soratensis*, NitPalGr – Nitzschia palea group, NitSp – *Nitzschia* sp., OrthRoes – *Orthoseira roeseana*, PinBorCm – *Pinnularia borealis* complex, PinMicr – *Pinnularia microstauron*, PinnAcid – *Pinnularia acidicola*, PinnAffSb – *Pinnularia* aff. *subacoricola*, PinnSins – *Pinnularia sinistra*, PlcAffAn – *Placoneis* aff. *anglica*, PlantSp – *Planothidium* sp, PinGebh – *Pinnunavis gebhardii*, SellCfSm – *Sellaphora* cf. *seminu*

Taxonomical part

Paper III

Van de Vijver, B., Chattová, B., Metzeltin D., & Lebouvier M. 2012. The genus *Pinnularia* (Bacillariophyta) on Ile Amsterdam (TAAF, Southern Indian Ocean). *Nova Hedwigia Beiheifte* 141: 201–236.

Nova Hedwigia, Beiheft 141, 201–236
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Article

The genus *Pinnularia* (Bacillariophyta) on Ile Amsterdam (TAAF, Southern Indian Ocean)

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With 253 figures and 2 tables

Abstract: Ile Amsterdam (77° 34′ E, 37° 47′ S), a young, small volcanic island situated in the southern Indian Ocean has a very isolated geographic position and is one of the remotest places in the world. The geographic and physical features of the island have resulted in the presence of a very typical diatom (Bacillariophyta) flora dominated by species belonging to the genus *Pinnularia*. A total of 22 different *Pinnularia* taxa were observed during a taxonomic analysis of aquatic, moss and soil samples. Twelve taxa did not correspond to any of the currently known species and are described as new species. The new taxa are morphologically and ecologically characterized comparing each of them with all at present known species. The other *Pinnularia* species are briefly discussed. A comparison with the other sub-Antarctic islands in the southern Indian Ocean clearly demonstrated the unique floristic situation of Ile Amsterdam.

Key words: Diatoms, Ile Amsterdam, new species, *Pinnularia*, sub-Antarctica

Introduction

The past decade, the non-marine diatom flora of the southern Indian Ocean islands Crozet (e.g. Van de Vijver et al. 2002), Kerguelen (e.g. Van de Vijver et al. 2001, Le Cohu 2005), Heard Island (e.g. Van de Vijver et al. 2004 a) and Marion Island (e.g. Van de Vijver et al. 2008 a) was the subject of a major intensive morphological, taxonomic and biogeographic study. The islands and archipelagos in this area are characterized by having a relatively young geological age, a rather small surface area and a remote, isolated position from any major continent. They all belong to the so-called sub-Antarctic region, bordered by the Antarctic Convergence in the south and the Subtropical Convergence in the north (Stonehouse 1982). According to Stonehouse (1982), this

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region can further be subdivided into a cold-temperate sub-Antarctic part (including Crozet, Kerguelen and Marion) and a more warm-temperate sub-Antarctic part that is situated north of the sub-tropical Convergence comprising Ile Amsterdam and Ile Saint-Paul.

The result of an elaborate taxonomic analysis of the non-marine diatom flora of the southern Indian Ocean islands resulted in the description of a large number of new species (Van de Vijver et al. 2002, 2004 b, Van de Vijver & Gremmen 2006). Although the presence of most of these species was already reported in earlier publications (Germain 1937, Pierre 1977; Le Cohu & Maillard 1983, 1986, Van de Vijver & Beyens 1999 a, b), their unique character was obscured due to force-fitting (Tyler 1996) and taxonomic drift. Detailed morphological analysis comparing the sub-Antarctic populations with well-known temperate species, revealed sufficient morphological differences to justify in most cases the separation as independent species.

Despite the many taxonomic studies on the sub-Antarctic diatoms, the non-marine diatom flora of Ile Amsterdam, the most northerly positioned of the islands, is only poorly known. Pierre & Noel (1971) published a first study on the waterbodies on the island. Although several algal species are mentioned, no indication is given on the presence of diatoms. In 1999, Van de Vijver & Beyens (1999 c) presented a first but limited survey of the Amsterdam non-marine diatoms since based on only 24 samples, mostly collected in the vicinity of the scientific base Martin-de-Viviès. Ninety taxa including six marine contaminants were reported. However, the taxonomy of the sub-Antarctic diatoms was not updated at that time, requiring a new study on the Ile Amsterdam diatom flora. The results of such a new study can provide important data especially in the light of more correct biogeographic hypotheses (Vyverman et al. 2007, Verleyen et al. 2009) dealing with on one hand the southern Indian Ocean and on the other hand the entire Antarctic region.

In 2007, a large field campaign was conducted on Ile Amsterdam, aiming at a better characterization of the diatom flora of the island. A first paper, describing three new *Eunotia* species was published in 2008 (Van de Vijver et al. 2008 b). The present paper shows the results of the taxonomical analysis of the genus *Pinnularia*, one of the most widespread and most diverse diatom genera in the entire sub-Antarctic Region, typical for oligotrophic, acid stagnant waterbodies, wet mosses and wet non-biotic soils. On Ile de la Possession for instance, the main island of the Crozet Archipelago, 40 different species, including 14 new ones, were found (Van de Vijver et al. 2002).

Study site

Ile Amsterdam (77° 34′ E, 37° 47′ S) is a small oceanic island, situated halfway between the African continent and Australia in the southern part of the Indian Ocean. Together with the smaller Ile Saint-Paul, they form a separate district within the Terres Australes et Antarctiques Françaises (TAAF) and are among the most remote islands in the world. Ile Amsterdam, with a total surface area of 55 km², has a volcanic origin and is, geologically, very young: the main part of Ile Amsterdam arose during the period 400–200 kyr BP (Giret 1987, Doucet et al. 2003). The island has the shape of a small cone culminating at 880 m (Mont de la Dives) and has a temperate oceanic climate (Lebouvier & Frenot 2007) with a mean annual temperature of 14.0 °C with minimum and maximum temperatures of 11.2 °C in the coldest month (August) and 17.4 °C in the warmest month (February). Relative humidity is high (> 80 %) throughout the year due to the frequency of low cloud ceilings. Precipitation, falling primarily as rain, is usually high with an annual average of 1.114 mm distributed over more than 220 days at the meteorological station (Martin-de-Viviès, 27 m a.s.l.); a dry period occurs in summer (c. 70 mm in February). According to records over one year (Frenot & Valleix 1990) the mean temperature is lower by 7 °C and the precipitation is double in the Caldera at 700 m a.s.l. Permanent water bodies are scarce and restricted to the higher plateau in the centre of the island (Caldera, Plateau des Tourbières) and the W-SW part of the island (Falaises d'Entrecasteaux, Grandes Ravines). Almost all other areas do not have (semi-) permanent water bodies due to the steepness of the slopes and the permeability of the lava tunnels, holes and fissures.

The vegetation on Ile Amsterdam is dominated by both endemic sub-Antarctic and introduced species. There are no large forests on the island but some patches of one native tree (*Phylica arborea* Thouars) (the largest of which is called Grand Bois), as well as groves or isolated individuals of introduced trees [*Cryptomeria japonica* (L. f.) D. Don, *Pinus* sp., *Cupressus* sp., *Malus domestica* Borkh., *Mimosa* sp. *Prunus domestica* L. and *Prunus persica* (L.) Batsch] (Jolinon 1987, Frenot et al. 2001). On the higher plateau, the vegetation is a typical sub-Antarctic flora and consists of ferns, grasses, *Lycopodium* and mosses. *Sphagnum*, although absent from the other sub-Antarctic islands in the southern Indian Ocean, is omnipresent on the island, mainly on higher (= wetter) grounds above 400 m a.s.l.

The endemic fauna is rather poor and comprises a few marine bird species such as the rare, endemic Amsterdam albatross (*Diomedea amsterdamensis* Roux et al.) and several larger fur seal colonies (*Arctocephalus tropicalis* Gray). The introduction of cattle (*Bos taurus* L.) on the island in 1871 has caused major ecological changes, especially at low altitude, but the population, controlled since 1988 (Micol & Jouventin 1995), is now being eradicated. A small, permanently occupied base (Martin-de-Viviès) is situated on the northern shore.

Material and methods

During two short visits (1998 and 1999) and one fieldwork season on Ile Amsterdam in 2007 more than 250 samples were collected. Sampling locations were chosen to represent a maximum variability of habitat types ranging from small streams, lakes, bogponds and temporary pools from all over the island. The samples were collected in PVC bottles and fixed with 3 % formalin. Due to logistic constraints during the two short visits in 1998 and 1999, the number of measured environmental parameters was limited. In 2007, water was collected 20 cm below the surface at each site, filtered in situ and deep-frozen to be analysed in the laboratory at the University of Antwerp. In situ, pH, specific conductance, water temperature and oxygen were measured using a WTW 340 i multimeter. NO_2^- +NO_3^-–N, NH_4^+–N, PO_4^{3-}–P, SO_4^{2-}, Cl^-, Na, K, Mg, Ca, Fe were analysed from the frozen samples at the Laboratory for Ecosystem Management (University of Antwerp). A complete overview of the samples will be published separately (Chattová et al., unpublished results). Samples in which new species were found are listed in Table 1 together with their main physical and chemical characteristics.

The samples were prepared following the method described in Van der Werff (1955). Small parts of the samples were cleaned by adding 37 % H_2O_2 and heated to 80 °C for about 1 h after which the reaction was completed by addition of $KMnO_4$. Following digestion and centrifugation (3 times 10 minutes at 3500 rpm), the material was diluted with distilled water to avoid excessive concentrations of diatom valves that could hinder reliable observations. Cleaned diatom valves were mounted in Naphrax®. The samples and slides were deposited at the National Botanic Garden of Belgium (BR), Department of Bryophytes and Thallophytes. Light microscope observations were conducted using an Olympus BX51 microscope equipped with Nomarski optics.

Identifications of Antarctic species are compared with descriptions in Bourrelly & Manguin (1954), Le Cohu & Maillard (1983) and Van de Vijver et al. (2002, 2004 b). Terminology of valve morphology is based on Barber & Haworth (1981), Hendey (1964), Round et al. (1990) and Krammer (2000).

Table 1. List of samples in which new *Pinnularia* species were found, together with their physical and chemical properties ('–' = not measured)

Sample	Sampling date	Sampling locality	Altitude (m)	pH	spec. cond. (µS/cm)	Temp (°C)	$(NO_2^-+NO_3^-)N$ (mg/l)	NH4⁺-N (mg/l)	PO_4^{3-}-P (mg/l)	SO_4^{2-} (mg/l)	Cl^- (mg/l)	Na (mg/l)	K (mg/l)	Ca (mg/l)	Mg (mg/l)	Fe (mg/l)
AMS7	2/12/1998	Pointe Goodenough	15	–	–	–	–	–	–	–	–	–	–	–	–	–
AMS15	2/12/1998	Base Martin-de-Viviès	20	–	–	–	–	–	–	–	–	–	–	–	–	–
BM413	12/15/1999	Plateau du Museau de Tanche	720	–	–	–	–	–	–	–	–	–	–	–	–	–
BM435	12/15/1999	Otarie Club, Base Martin-de-Viviès	20	–	–	–	–	–	–	–	–	–	–	–	–	–
BW442	12/15/1999	Plateau du Museau de Tanche	725	4,8	138	19,0	–	–	–	–	–	–	–	–	–	–
BA128	12/15/1999	Plateau du Museau de Tanche	690	–	–	–	–	–	–	–	–	–	–	–	–	–
W003	11/29/2007	Plateau du Museau de Tanche	711	4,67	73	12,0	2,1	0,12	0,09	<4	103	4,6	0,4	0,2	0,39	<0,01
W037	12/6/2007	Pointe d'Entrecasteaux	20	7,82	627	13,0	2,0	<0,08	0,20	20	63	41,0	4,2	22,2	12,6	<0,01
W085	12/11/2007	Plateau du Museau de Tanche	725	5,22	47	14,0	<0,05	<0,08	<0,02	6	13	8,3	<0,3	0,6	0,75	0,05
W113	12/12/2007	Plateau du Lac Bleu	742	4,89	71	13,0	<0,05	<0,08	<0,02	8	18	12,6	<0,3	0,8	1,09	0,03
M200	12/15/2007	Base Martin-de-Viviès	25	–	–	–	–	–	–	–	–	–	–	–	–	–
W124	12/17/2007	Ravines Del Cano	131	6,21	487	14,0	0,27	<0,08	0,02	17	143	77,6	1,9	7,0	9,64	0,02

Observations

A total of 250 samples were analysed resulting in the observation of 22 *Pinnularia* taxa (including species, varieties and forms). After a thorough morphological analysis, 12 taxa could not be identified using the currently available literature and will be described as new taxa.

Pinnularia borealis Ehrenb. sensu lato (Figs 1–18)

MORPHOLOGY: For more details regarding the overall morphology, see Krammer (2000). Observed range of dimensions: length 25–50 µm, width 6.4–10.0 µm. Raphe linear to weakly lateral. Proximal raphe endings deflected, clearly expanded. Striae radiate in the middle, parallel to convergent near the apices, 5–7 striae in 10 µm.

REMARKS: Two distinct morphodemes were distinguished in the *P. borealis* populations of Ile Amsterdam. A first group (Figs 1–8) contains rather large valves (length: 30–50 µm) that are relatively broad (8–10 µm) with a broadly elliptical-lanceolate outline. A second group (Figs 9–18) is composed of smaller valves (length: 25–35 µm) with a more linear, rectangular valve outline and a lower valve width (6–7 µm). No difference in raphe structure, stria density or orientation was observed. The first morphodeme shows some resemblance to *P. borealis* var. *subislandica* Krammer although the valves are somewhat narrower, the valve apices are broadly rounded and not truncate and the number of striae is higher. The second deme most probably represents the nominate variety of *P. borealis*.

A large number of varieties already exist within the *P. borealis*-complex and some show overlapping features making a thorough revision of all these varieties highly

Figs 1–8. *Pinnularia borealis* Ehrenb. large morphodeme; **9–18**. *Pinnularia borealis* Ehrenb. small morphodeme; **19–20**. *Pinnularia rabenhorstii* var. *subantarctica* Van de Vijver & Le Cohu. Scale bar represents 10 µm.

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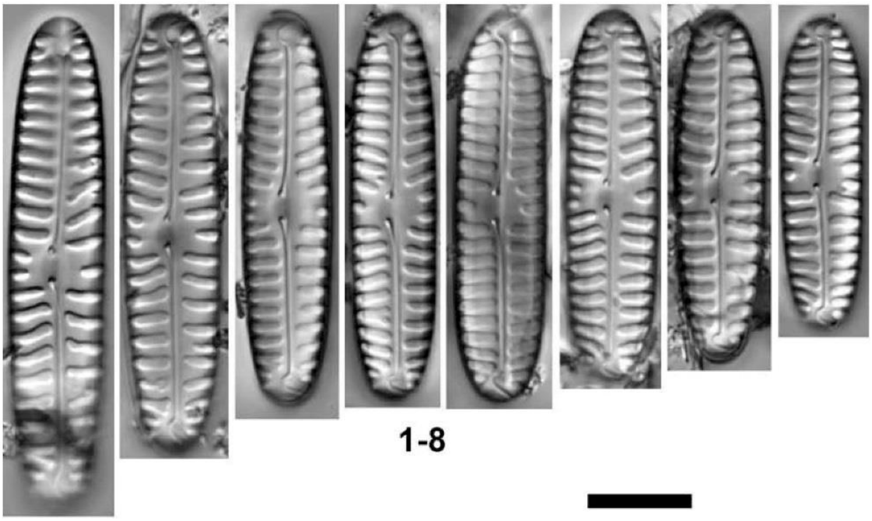
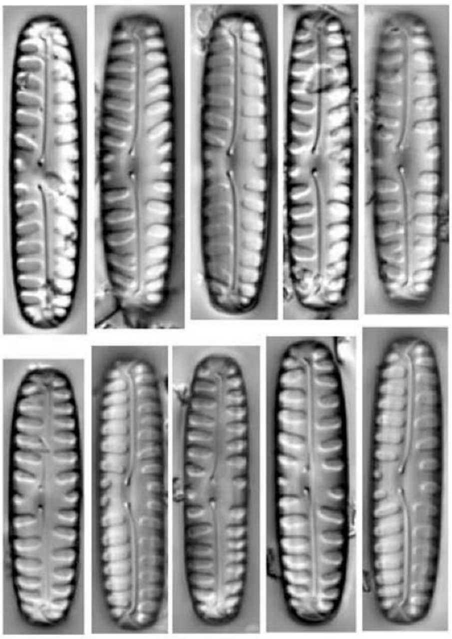


1-8



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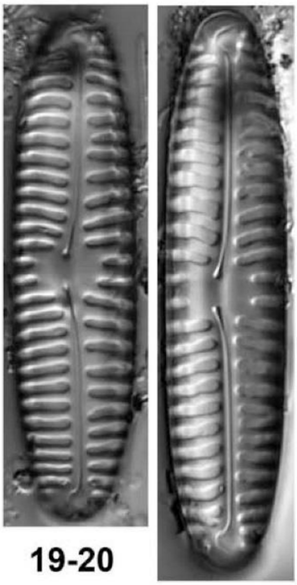


19-20

necessary. Therefore we refrain from subdividing the *P. borealis* populations of Ile Amsterdam until the correct identity of all varieties is clear.

Ecology and associated diatom flora: *Pinnularia borealis* s.l. is a widespread species on Ile Amsterdam, present in almost every terrestrial habitat ranging from semi-wet to even dry soils and mosses. The species is associated with several *Luticola*, *Diadesmis*, *Hantzschia* and *Orthoseira* species, all typical for the terrestrial habitat. No habitat differences were observed for the larger and smaller morphodemes.

***Pinnularia rabenhorstii* var. *subantarctica* Van de Vijver & Le Cohu** (Figs 19–20)

Morphology: For more details regarding the overall morphology, see Van de Vijver et al. (2002). Observed range of dimensions: length 50–55(72) µm, width 12–13 µm. Raphe weakly to moderately lateral. Proximal raphe endings deflected, clearly expanded. Striae radiate in the middle, parallel to convergent near the apices, 5–6 striae in 10 µm.

Remarks: One of the observed valves of *P. rabenhorstii* var. *subantarctica* is larger than mentioned in the original description (72 vs. 58 µm). The type population of this *P. rabenhorstii* variety was described from the neighbouring Crozet archipelago where sometimes fairly large populations were observed (Van de Vijver et al. 2002).

Ecology and associated diatom flora: *Pinnularia rabenhorstii* var. *subantarctica* is a rare species on Ile Amsterdam and was only observed in several aquatic and wet moss samples from the Del Cano area in the southern part of the island. The area is characterized by a slightly acid to almost circumneutral pH (6–6.5), a moderately high specific conductance value (400–500 µS/cm), low nutrient but high Na-values. The dominant diatom flora is composed of *Planothidium lanceolatum* (Bréb.) Lange-Bert., *Karayevia oblongella* (Østrup) Aboal, *Diadesmis contenta* (Grunow) D. G. Mann, *Eunotia muscicola* Krasske and several *Pinnularia* taxa.

***Pinnularia sylviae* Van de Vijver sp. nov.** (Figs21– 33)

Diagnosis: Valvae stricte lineares marginibus parallelis apicibusque late rotundatis, non-protractis sed leviter contractis. Longitudo 42–80 µm, latitudo 8.5–11.5 µm. Area axialis angusta, linearis. Area centralis asymmetrica, elliptica ad rectangularis, leviter dilatata striis centralibus irregulariter abbreviates, numquam attingens margines. Striae centrales semper praesentes. Raphe clare lateralis ramis rectis ad leviter curvatis. Terminationes raphis proximales unilateraliter deflexae cum poris leviter expansis. Terminationes raphis distales fortiter uncinatae. Striae latae, distantes, leviter radiatae in media parte valvae, parallelae ad etiam convergentes ad apices, 4–5 in 10 µm. Lineae speciosae longitudinales nullae.

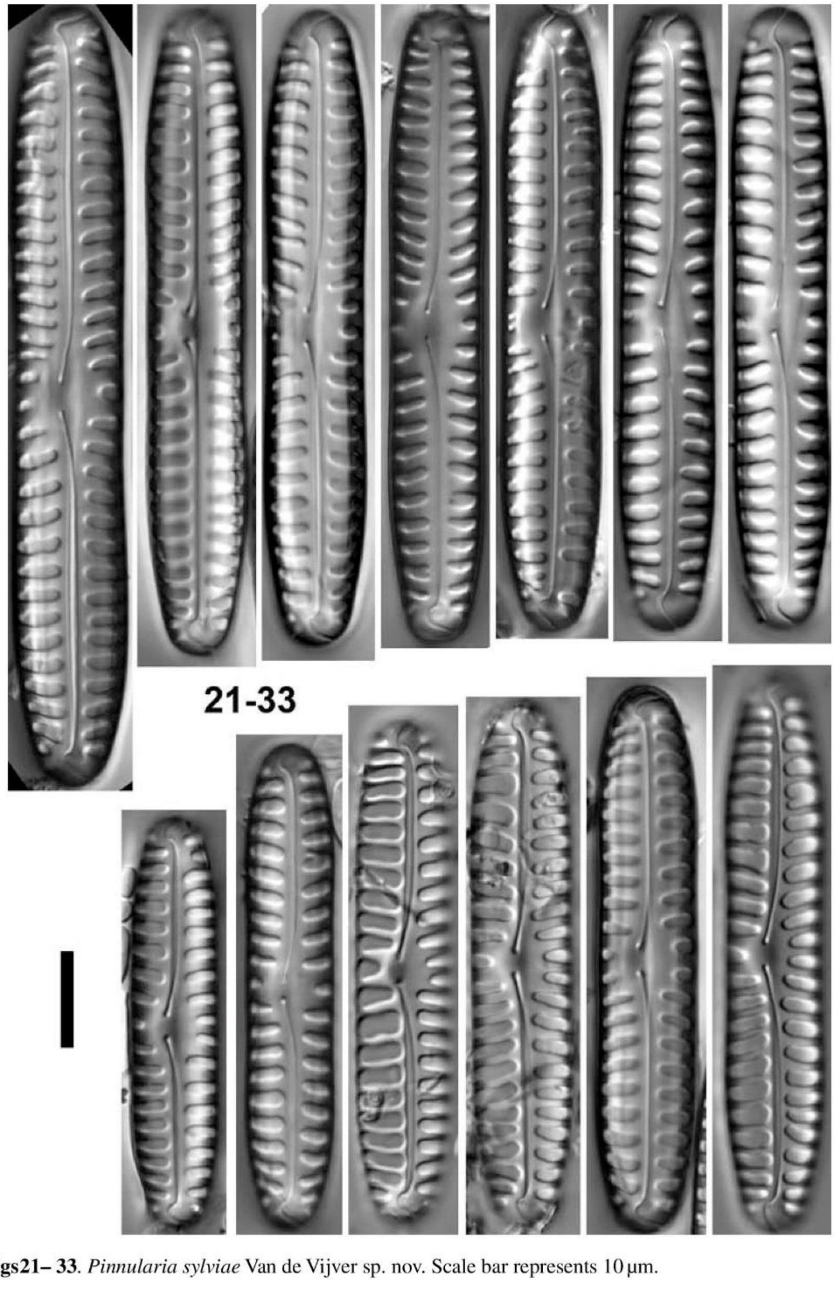
Holotypus: Slide no. BR-4215 (holotype here designated see Fig. 23) deposited in National Botanic Garden, Meise, Belgium, leg. B. Van de Vijver, coll. date 15/12/1999.

Isotypi: PLP-165 (UA, University of Antwerp, Belgium), BRM-ZU7/62 (Hustedt Collection, Bremerhaven, Germany)

Type locality: Plateau du Museau de Tanche, Ile Amsterdam, TAAF, southern Indian Ocean, sample BM413.

Etymology: The species is named in honor of my dear friend Dr. Sylvie Geiger (Université de Strasbourg, France) on the occasion of her PhD defense in September 2010, to thank for her kind help during the Antarctic sampling campaigns of 2004 and 2007.

Morphological observations: Valves strictly linear with parallel margins and broadly rounded, non-protracted but slightly tapering apices. Valve dimensions (n = 18): length 42–80 µm, width



Figs21– 33. *Pinnularia sylviae* Van de Vijver sp. nov. Scale bar represents 10 µm.

8.5–11.5 µm. Axial area narrow, linear. Central area asymmetrical, elliptical to rectangular, slightly enlarged due to irregular shortening of the central striae, never reaching the margins to form a fascia. Central striae never absent. Raphe clearly lateral with straight to weakly curved raphe branches. Proximal raphe endings unilaterally deflected terminating in slightly expanded pores. Distal raphe endings strongly hooked ('sickle-shaped') opposite to the proximal endings. Striae broad, distant, usually 4, occasionally 5 in 10 µm, slightly radiate in the middle, parallel to convergent towards the apices. Longitudinal lines crossing the striae and spot-like appearing depressions in the centre absent.

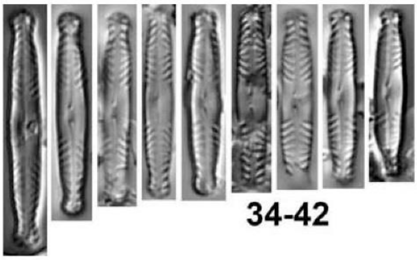
REMARKS: *Pinnularia sylviae* belongs to the former section Distantes (Cleve) Patrick characterized by their flat broad striae that are distantly placed from each other (Patrick & Reimer 1966). The most typical species in this section are *Pinnularia borealis* Ehrenb. and *P. rabenhorstii* (Grunow) Krammer, both widespread in the (sub-)Antarctic Region (Kellogg & Kellogg 2000) and also present on Ile Amsterdam. *Pinnularia sylviae* presents morphological features shared with either *P. borealis* or *P. rabenhorstii* but differs also from both species. The valve dimensions are intermediate between the two mentioned species. The maximum length of *P. borealis* is only 42 µm whereas the smallest specimens of *P. rabenhorstii* have a minimum length of 40 µm. *Pinnularia sylviae* ranges from 42 to 80 µm. On the other hand, the valve width never exceeds 12 µm, consistent with the width of *P. borealis* but much narrower than *P. rabenhorstii* (12–18 µm). The raphe structure corresponds more with the lateral raphe in *P. rabenhorstii* while *P. borealis* has a more filiform to only weakly lateral raphe. The valve outline is more similar to *P. borealis* than to *P. rabenhorstii*. The number and orientation of the striae is comparable to both species. Both similar species present a large number of varieties or formas but apart from *P. borealis* var. *islandica* Krammer, none of the *P. borealis* varieties presents comparable valve dimensions (length 40–52 µm, width 10–12 µm). Other Distantes species such as *P. subrabenhorstii* Krammer differ in valve outline, being more rectangular with truncated apices. *Pinnularia lata* (Bréb.) Rabenh. and *P. alpina* W. Smith are a lot larger with more elliptic-lanceolate valves.

ECOLOGY AND ASSOCIATED DIATOM FLORA: The type population of *P. sylviae* was found in a relatively dry *Sphagnum* sample, collected in the vicinity of the Museau de Tanche crater in the caldera region on top of the island on the edge of a small pool. The species was also present in soil samples collected in the same area. These are relatively wet soil samples collected under a vegetation of grasses, mosses and pink-coloured *Sphagnum* sp. Dominating taxa in the samples include *Eunotia paludosa* Grunow, *Frustulia lebouvieri* Van de Vijver, *Pinnularia vixconspicua* and several *Diadesmis* species.

***Pinnularia microcapitata* Van de Vijver, Chattová & Metzeltin sp. nov.** (Figs 34–42)

DIAGNOSIS: Valvae lineares ad anguste lanceolatae marginibus parallelis ad leviter convexis sed semper undulatis apicibusque capitatis. Longitudo 17–24 µm, latitudo 2.8–3.3 µm. Area axialis angustissima, linearis. Area centralis formans fasciam rectangularem latam. Striae centrales absunt. Raphe filiformis. Terminationes raphis proximales deflexae cum poris leviter expansis. Terminationes raphis distales fortiter uncinatae. Striae radiatae in media parte valvae, abrupte fortiter convergentes ad apices, 12–13 in 10 µm. Lineae speciosae longitudinales nullae.

Figs 34–42. *Pinnularia microcapitata* Van de Vijver, Chattová & Metzeltin sp. nov.; **43–53**. *Pinnularia subacoricola* Metzeltin, Lange-Bertalot & García-Rodríguez; **54–62**. *Pinnularia obscura* Krasske; **63–72**. *Pinnularia vlaminghii* Van de Vijver, Chattová & Metzeltin sp. nov.; **73–79**. *Pinnularia* sp. [cf. d*ivergentissima* (Grunow) Cleve]; **80–83**. *Pinnularia whinamiae* Van de Vijver sp. nov.; **84–93**. *Pinnularia perminor* Kulikovskiy, Lange-Bertalot & Metzeltin. Scale bar represents 10 µm. ►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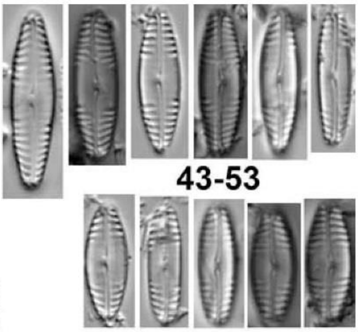
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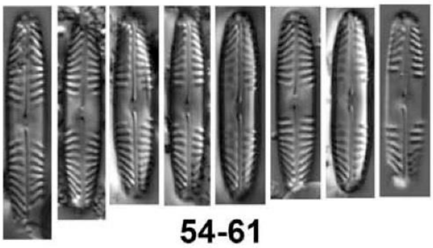
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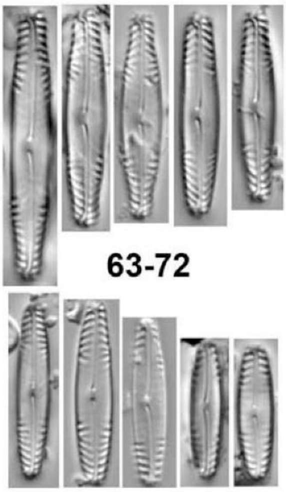
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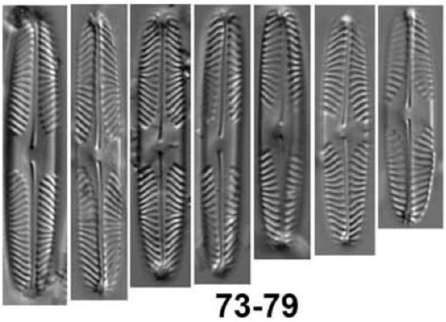
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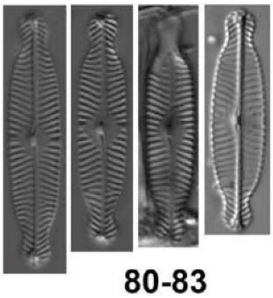
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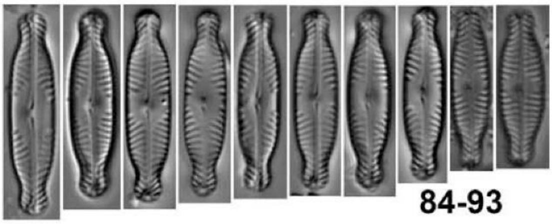

84-93

HOLOTYPUS: Slide no. BR-4216 (holotype here designated see Fig. 35) deposited in National Botanic Garden, Meise, Belgium, leg. B. Van de Vijver, coll. date 12/02/1998.

ISOTYPI: PLP-166 (UA, University of Antwerp, Belgium), BRM-ZU7/62 (Hustedt Collection, Bremerhaven, Germany)

TYPE LOCALITY: Pointe Goodenough, Ile Amsterdam, TAAF, southern Indian Ocean, sample AMS7.

ETYMOLOGY: The specific epithet *microcapitata* refers to the small size of the capitate apices.

MORPHOLOGICAL OBSERVATIONS: Valves linear to narrowly lanceolate with parallel to slightly convex but always undulating margins and capitate apices. Valve dimensions (n = 12): length 17–24 µm, width 2.8–3.3 µm. Axial area very narrow, linear. Central area forming a large, rectangular fascia. Central striae absent. Raphe filiform. Proximal raphe endings deflected, terminating in slightly expanded pores. Distal raphe endings strongly hooked (= 'sickle-shaped'). Striae clearly radiate in the valve middle, abruptly becoming strongly convergent, 12–13 in 10 µm.

REMARKS: *Pinnularia microcapitata* can be confused with several small-sized *Pinnularia* species such as *Pinnularia joculata* (Manguin) Krammer and *Pinnularia schroeterae* Krammer, but can be distinguished by the combination of valve dimensions, valve outline, shape of the central area and stria density. *Pinnularia joculata*, described from Guadeloupe (Bourrelly & Manguin 1952), has similar valve dimensions but lacks the undulated valve margins and the abrupt change in stria orientation and has a higher striae density (14–16 vs. 12–13 in 10 µm in *P. microcapitata*). *Pinnularia schroeterae* has a larger valve width (4.3–5.4 µm vs. 2.8–3.3 µm), more convex margins, contrary to the undulating, straight margins in *P. microcapitata*, a smaller central area and a different striation pattern, lacking the abrupt change in orientation. Other *Pinnularia* taxa such as the group of species around *P. divergentissima* Grunow, *P. acidophila* Hofmann & Krammer or *P. obscura* Krasske differ sufficiently in valve outline and shape of the apices to exclude all confusion with *P. microcapitata*. The most similar of these three is *P. divergentissima* var. *hustedtiana* Ross but the latter can be easily distinguished by its more rhombic-lanceolate outline and its larger valve dimensions (length 24–28 µm).

ECOLOGY AND ASSOCIATED DIATOM FLORA: *Pinnularia microcapitata* is a fairly rare species on Ile Amsterdam and so far, the species was only found on the type locality, a small lithotelm close by the Indian Ocean, overgrown with dry mosses, occasionally moistened by rainwater. The sample is dominated by *Achnanthes coarctata* (Bréb.) Grunow, several (so far unidentified) *Luticola* species and *P. borealis*.

Pinnularias ubacoricola **Metzeltin, Lange-Bertalot & García-Rodríguez** (Figs 43–53)

MORPHOLOGY: For more details regarding the overall morphology, see Metzeltin et al. (2005: p. 163). Valves narrowly lanceolate to rhombic-lanceolate. Observed range of dimensions: length 12–20 µm, width 3.0–4.2 µm. Central area forming a large fascia. Raphe filiform. Proximal raphe endings deflected, weakly expanded. Striae parallel, quickly becoming convergent near the apices, 12–14 striae in 10 µm.

REMARKS: Metzeltin et al. (2005) distinguished three different morphotypes, apparently related to differences in pH values. The morphologically rather variable populations on Ile Amsterdam are however difficult to classify within one of these morphotypes. Most similar is morphotype B, found under slightly acid pH circumstances. The habitat preferences of *P. subacoricola* in Uruguay seem to be similar to the Ile Amsterdam populations (Metzeltin et al. 2005). *Pinnularia oominensis* Kobayasi has shorter striae and a different central area (Yamagishi & Kobayasi 1971).

Ecology and associated diatom flora: All populations of *P. subacoricola* on Ile Amsterdam were found growing on mosses in shaded volcanic caves, scattered over the northern part of the island. All caves had a reduced light regime and the mosses growing near the entrances, where the samples were taken, were continuously, although not extensively, moistened by dripping water. The dominant diatom flora in the samples is composed of several *Diadesmis* species such as *D. crozetikerguelensis* Le Cohu & Van de Vijver and *D. vidalii* Van de Vijver & Ledeganck, *Planothidium lanceolatum*, *Amphora* cf. *veneta* Kütz., *Melosira* sp., *Nitzschia frustulum* (Kütz.) Grunow and several so far unidentified *Luticola* species.

Pinnularia obscura **Krasske** (Figs 54–62)

Morphology: For more details regarding the overall morphology, see Krammer (2000: p. 50). Valves linear to narrowly lanceolate with gradually tapering, non protracted, broadly rounded apices. Observed range of dimensions: length 17–22 µm, width 3.4–4.2 µm. Central area forming a large fascia. Raphe filiform. Proximal raphe endings deflected, weakly expanded. Striae slightly radiate in the middle, becoming strongly convergent near the apices, 11–13 striae in 10 µm.

Remarks: Krammer (2000) distinguished three different morphotypes based on shape of the apices and valve width. Based on our observations, the Ile Amsterdam populations belong to morphotype 2 since the apices are not rostrate as is the case in morphotype 1. *Pinnularia osoresanensis* (Negoro) Fukushima, Yoshitake & Ts. Kobayasi, described from Japan (Fukushima et al. 2002), shows some resemblance but has more convex valve margins with more acutely rounded apices.

Ecology and associated diatom flora: *Pinnularia obscura* was found in dry terrestrial habitats on Ile Amsterdam such as dry soils and only temporarily moistened mosses. The observed populations are usually small and are accompanied by typical aerophilic species such as *Pinnularia borealis*, various *Luticola* and *Diadesmis* species and *Achnanthes coarctata*.

Pinnularia vlaminghii **Van de Vijver, Chattová & Metzeltin sp. nov.** (Figs 63–72)

Diagnosis: Valvae anguste lanceolatae marginibus leviter convexis. Valvae maiores apicibus late rostratis, valvae minores apicibus leviter protractis. Longitudo 13–29 µm, latitudo 3.3–4.0 µm. Area axialis angusta, linearis. Area centralis formans fasciam rectangularem maximam. Striae centrals absunt. Raphe filiformis terminationibus proximalibus deflexis, extensis ultra strias ultimas centrales, cum poris expansis, terminationibusque distalibus fortiter uncinatis. Striae solum praesentes prope apices, radiatae in parte proxima, convergentes ad apices, 12–14 in 10 µm. Lineae speciosae longitudinales nullae.

Holotypus: Slide no. BR-4217 (holotype here designated see Fig. 64) deposited in National Botanic Garden, Meise, Belgium, leg. B. Van de Vijver, coll. date 15/12/1999.

Isotypi: PLP-167 (UA, University of Antwerp, Belgium), BRM-ZU7/63 (Hustedt Collection, Bremerhaven, Germany)

Type locality: Otarie Club, Base Martin-de-Viviès, Ile Amsterdam, TAAF, southern Indian Ocean, sample BM435.

Etymology: The species is named after Willem de Vlamingh, a Dutch captain and explorer, who was the first person to set footh on land on Ile Amsterdam in 1696.

Morphological observations: Valves narrowly lanceolate with weakly convex margins. Larger valves with broadly rostrate apices, smaller valves with only weakly protracted apices. Valve dimensions (n = 20): length 13–29 µm, width 3.3–4.0 µm. Axial area narrow, linear. Central area forming a very large rectangular fascia. Central striae absent. Raphe filiform with deflected proximal raphe endings terminating in expanded central pores. Proximal raphe endings extending well beyond the last central striae. Distal raphe endings strongly hooked, not always well visible in LM. Striae only present near the apices, radiate in the first part close to the central area, becoming strongly convergent at the apices, 12–14 in 10 µm. Longitudinal lines on the striae absent.

REMARKS: *Pinnularia vlaminghii* belongs to the complex of species around *P. obscura*. The large central area and the proximal raphe endings that extend well beyond the last central striae however, separate the species from *P. obscura*. Other species such as *P. joculata*, *P. acidophila* and *P. intermedia* are all sufficiently different based on valve outline, striation pattern and valve dimensions to exclude conspecificity.

ECOLOGY AND ASSOCIATED DIATOM FLORA: So far, two relatively large populations of *P. vlaminghii* were found on Ile Amsterdam growing on mosses in shaded volcanic caves near the scientific base Martin-de-Viviès. The dominant diatom flora in the samples is composed of several *Diadesmis* species such as *D. crozetikerguelensis* and *D. vidalii*, *Planothidium lanceolatum*, *Amphora* cf. *veneta*, *Melosira* sp., *Nitzschia frustulum* and several so far unidentified *Luticola* species.

***Pinnularia* sp. [cf. *divergentissima* (Grunow) Cleve]** (Figs73 –79)

MORPHOLOGY: Valves linear to narrowly lanceolate with non protracted, obtusely rounded apices. Observed range of dimensions: length 22–30 µm, width 4.3–4.2 µm. Axial area very narrow, linear, widening towards the central area. Central area forming a small to moderately large, asymmetrical fascia. Isolated central striae sometimes present. Raphe filiform. Proximal raphe endings weakly deflected, terminating in slightly expanded pores. Distal raphe endings strongly hooked. Striae strongly radiate in the middle, abruptly becoming strongly convergent near the apices with an acute angle between the two striae groups, 14–16 striae in 10 µm. Longitudinal lines on the striae absent.

REMARKS: The most similar species is *P. divergentissima*. The correct identity of the latter is currently under debate since apparently in the type slide, two *Pinnularia* species are present. The drawing made by Grunow in Van Heurck (1880) of *P. divergentissima* does not correspond with the generally accepted idea of *P. divergentissima* but on the contrary corresponds with the second species in the type slide. The taxonomy of *P. divergentissima* is currently under investigation reanalysing the type material and comparing the species with species from the same complex such as *P. martinii* Krasske and *P. fottii* Bily & Marvan. The first results of this analysis showed that the sub-Antarctic populations, including the Ile Amsterdam populations, should be described as a separate species. The results of this analysis together with the description of the new sub-Antarctic species will be the subject of a separate publication (Moravcová et al., unpubl. results).

ECOLOGY AND ASSOCIATED DIATOM FLORA: This *Pinnularia* species, although widespread on the sub-Antarctic islands of the southern Indian Ocean (Van de Vijver et al. 2002, under the name of *P. divergentissima*), is a rare species on Ile Amsterdam. The largest population was found in a relatively dry soil sample collected under a *Blechnum penna-marina* (Poir.) Kuhn vegetation in the Grand Bois de Phylicas, the last remaining forest of the native tree *Phylica arborea* Thouars. The diatom flora in the sample is rather scarce and apart from *Diademis* cf. *ingeae* Van de Vijver and some fragments of *Pinnularia* sp. and *Luticola* sp., no other diatoms were found.

Pinnularia whinamiae **Van de Vijver sp. nov.** (Figs 80–83)

DIAGNOSIS: Valvae lineares marginibus parallelis apicibusque capitatis. Longitudo 22–26 µm, latitudo 5–5.5 µm. Area axialis angustissima, linearis, graduatim dilatata ad aream centralem. Area centralis rotundata ad rhombica, numquam formans fasciam striis centralibus abbreviates. Raphe filiformis. Terminationes raphis proximales leviter deflexae cum poris expansis, locatis in nodulo centrali conspicuo. Striae radiatae in media parte valvae, fortiter convergentes ad apices, 14–15 in 10 µm. Lineae speciosae longitudinales nullae.

HOLOTYPUS: Slide no. BR-4218 (holotype here designated see Fig. 80) deposited in National Botanic Garden, Meise, Belgium, leg. B. Van de Vijver, coll. date 29/11/2007.

ISOTYPI: PLP-168 (UA, University of Antwerp, Belgium), BRM-ZU7/64 (Hustedt Collection, Bremerhaven, Germany)

TYPE LOCALITY: Plateau du Museau de Tanche, Ile Amsterdam, TAAF, southern Indian Ocean, sample W003.

ETYMOLOGY: The species is named in honor of my colleague and friend Dr. Jennie Whinam (Hobart, Tasmania) to thank for the wonderful fieldtrip we spent together on Ile Amsterdam in 2007.

MORPHOLOGICAL OBSERVATIONS: Valves linear with parallel margins and capitate apices. Valve dimensions (n = 15): length 22–26 µm, width 5–5.5 µm. Axial area very narrow, linear, gradually widened towards the central area. Central area rounded to rhomboid, never forming a fascia due to shortened striae in the central area. Raphe filiform. Proximal raphe endings only weakly deflected terminating in expanded pores, located on a well-developed central nodule. Striae radiate in the middle of the valve, becoming strongly convergent towards the apices, 14–15 in 10 µm. Longitudinal lines on the striae absent.

REMARKS: *Pinnularia whinamiae* can be confused with several small, capitate *Pinnularia* species such as *P. subinterrupta* Krammer & Schroeter, *P. schroeterae*, *P. streckerae* Krammer and *P. divergentissima* var. *minor* Krammer. The most similar is *P. subinterrupta*, described from the Swedish Sarek Mountains. The latter has narrower valves (width 4.3–4.6 vs. 5.0–5.5 µm) giving the species a more slender outline with a different, rather large central area. In *P. whinamiae*, the central area gradually getting shorter whereas in *P. subinterrupta* almost all central striae are equally shortened. *Pinnularia schroeterae* and *P. streckerae* both possess a distinct fascia with *P. streckerae* also being narrower than *P. whinamiae*. Finally, *P. divergentissima* var. *minor* has a distinct, abrupt change in stria orientation, typical for the *P. divergentissima*-group but lacking in *P. whinamiae*.

ECOLOGY AND ASSOCIATED DIATOM FLORA: So far two populations of *Pinnularia whinamiae* were found on Ile Amsterdam. Both populations were collected in small, acid (pH 4.7–5.0), almost dystrophic pools near the Museau de Tanche crater in the caldera on top of the island. The samples were dominated by *Eunotia paludosa* and *E. muscicola*.

Pinnularia perminor **Kulikovskiy, Lange-Bertalot & Metzeltin** (Figs 84–93)

MORPHOLOGY: For more details regarding the overall morphology, see Krammer (2002: p. 45). Valves linear-elliptical to lanceolate with capitate apices. Observed range of dimensions: length 16–20 µm, width 3.5–4.5 µm. Central area rather large, rounded, forming an asymmetrical fascia. Raphe filiform. Proximal raphe endings deflected, weakly expanded. Striae radiate in the middle, abruptly becoming strongly convergent near the apices, 14–16 striae in 10 µm.

Ecology and associated diatom flora: The largest population of *P. perminor* (> 90 % of all counted valves) was found in a small, temporary pool at 400 m altitude near the Vénus craters. It is a very acid (pH 4.1) shallow pool with a rather low specific conductance value (170 µS/cm) and a vegetation of *Scirpus* and *Juncus*. In several other samples, only a few valves were found, almost always in acid, oligotrophic pools in the caldera region on top of the island.

***Pinnularia australogibba* Van de Vijver, Chattová & Metzeltin sp. nov.** (Figs94 –101)

Diagnosis: Valvae lanceolatae ad anguste lanceolatae marginibus convexis apicibusque leviter protractis, rostratis, late rotundatis. Longitudo 45–60 µm, latitudo 7.8–9.4 µm. Area axialis moderate lata, lanceolate, clare dilatata ad aream centralem. Area centralis magna, rhombico-rotundata, formans fasciam latam. Striae isolatae in area centrali nullae. Cum quattuor aeris nubilis circum nodulo centrali. Raphe clare lateralis. Terminationes raphis proximales leviter deflexae cum poris distincte expansis. Terminationes raphis distales fortiter uncinatae. Striae radiatae in medio parte valvae ad parallelae et etiam convergentes ad apices, 12–13 in 10 µm. Lineae speciosae longitudinales nullae.

Holotypus: Slide no. BR-4219 (holotype here designated see Fig. 94) deposited in National Botanic Garden, Meise, Belgium, leg. B. Van de Vijver, coll. date 17/12/2007.

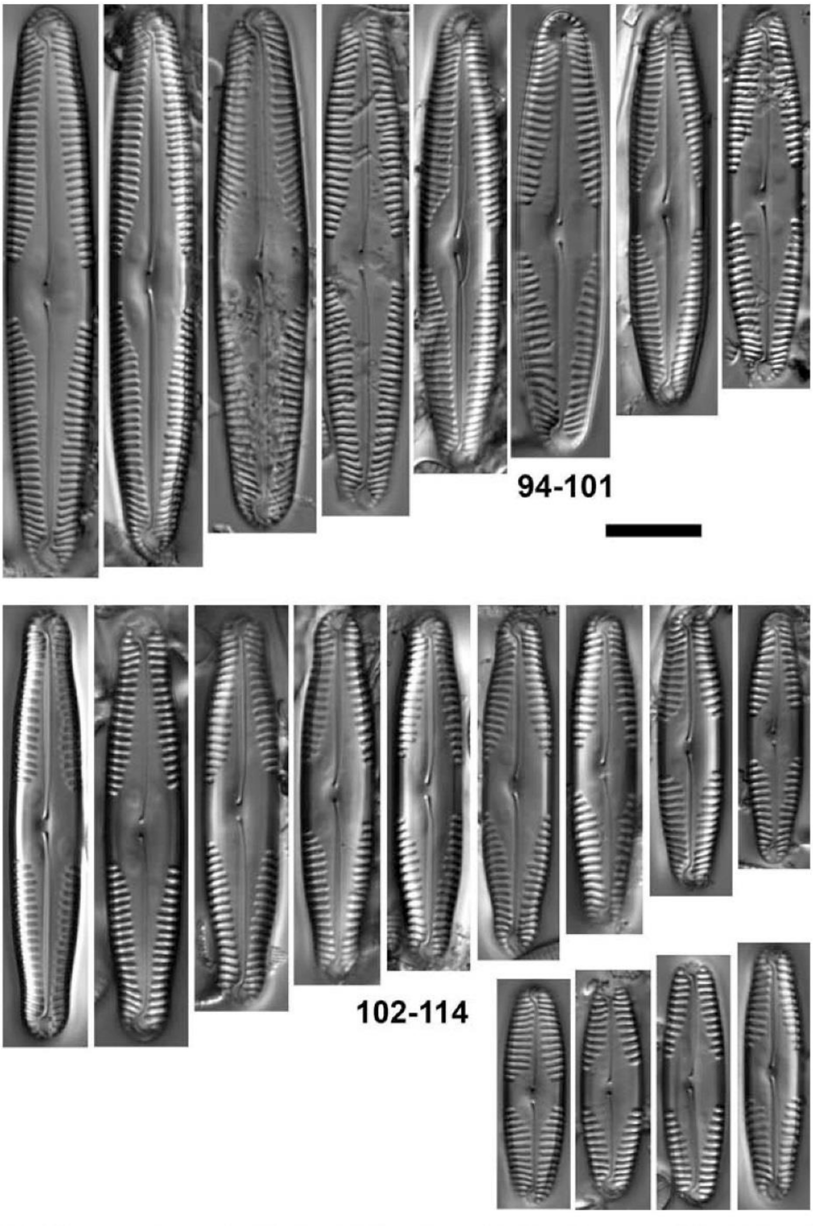
Isotypi: PLP-169 (UA, University of Antwerp, Belgium), BRM-ZU7/65 (Hustedt Collection, Bremerhaven, Germany)

Type locality: Ravines Del Cano, Ile Amsterdam, TAAF, southern Indian Ocean, sample W124.

Etymology: The specific epithet refers to the resemblance to *Pinnularia gibba* Ehrenb., a species that is not present in the sub-Antarctic region.

Morphological observations: Valves lanceolate to narrowly lanceolate with convex margins and weakly protracted, rostrate, broadly rounded apices. Valve dimensions (n = 20): length 45–60 µm, width 7.8–9.4 µm. Axial area moderately broad, lanceolate, clearly widening towards the central area. Central area large, rhombic-rounded, forming a broad fascia. No isolate central striae present. Several large shallow depressions present in the central area. Raphe clearly lateral. Proximal raphe endings weakly deflected, terminating in distinctly expanded pores. Distal raphe endings strongly hooked. Striae radiate near the valve middle, becoming parallel to even moderately convergent towards the apices, 12–13 in 10 µm. Longitudinal lines absent.

Remarks: The valve outline and the presence of the four depressions in the central area are two features that link this new species to the complex of species around *Pinnularia gibba*. This complex is quite large with a lot of infraspecific taxa (mostly varieties and formas), some of which that are now separated as independent species such as *P. subbrevistriata.* Krammer (former *P. gibba* var. *brevistriata* Grunow in Van Heurck) or *P. subgibba* Krammer that was formerly known as *P. gibba* var. *linearis* sensu Hustedt. Despite this high number of already identified species in this complex, the Ile Amsterdam population could not be assigned to any of them. *Pinnularia gibba* s. str. presents typically broadly rounded, capitate apices [see Krammer (2000), Figs 68: 1–8] whereas all Ile Amsterdam populations typically only show rostrate, broadly rounded apices. Moreover, *P. gibba* is much larger (length 60–110 µm) than the Ile Amsterdam populations where the largest observed specimen is only 60 µm long and most of the populations ranges between 40 and 50 µm. *Pinnularia parvulissima* Krammer has broader valves (10–12 µm vs. 7.8–9.4 µm) with less convex, rather parallel margins. *Pinnularia monicae* Metzeltin & Lange-Bertalot is likewise much larger (length 70–120 µm) with a more rhombic-lanceolate valve outline and only very weakly protracted, rostrate apices. Two other South American species, *P. denotata* Metzeltin & Krammer in Metzeltin & Lange-Bertalot and *P. angustistriata*



Figs 94–101. *Pinnularia australogibba* Van de Vijver, Chattová & Metzeltin sp. nov.; **102–114**. *Pinnularia australogibba* var. *subcapitata* Van de Vijver, Chattová & Metzeltin var. nov. Scale bar represents 10 µm.

Metzeltin & Krammer in Metzeltin & Lange-Bertalot have similar valve outlines, but differ in lacking the central markings (i.c. *P. denotata*) or lacking rostrate endings and having a different striation pattern (i.c. *P. angustistriata*). *Pinnularia subbrevistriata* is probably the most similar species but differs in having broader valves (10–11 µm vs. 7.8–9.4 µm), a lower number of striae (8–10 in 10 µm vs. 12–13 in 10 µm) and less protracted, rostrate apices.

ECOLOGY AND ASSOCIATED DIATOM FLORA: *Pinnularia australogibba* is widespread in the small brooks flowing out of the ravines of Del Cano, located in the southern part of Ile Amsterdam. These brooks are characterized by a rather weakly acid pH (6–6.5), moderate specific conductance values (250–500 µS/cm) and low nutrient values. The type population was sampled in a small, shaded pool on the foot of a small waterfall covered with ferns, mosses and grasses. The dominating flora in the sample consists of *Planothidium lanceolatum*, *Karayevia oblongella*, *Achnanthes coarctata*, *Diadesmis contenta*, various (so far unidentified) *Luticola* species and *Sellaphora seminulum* (Grunow) D. G. Mann. A small, isolated population was also found in the Mare aux Eléphants, a pool located in the middle of the largest fur seal (*Arctocephalus tropicalis* Gray) colony of the island, close to the scientific base Martin-de-Viviès. This was a highly eutrophic, circumneutral (pH 6.9) shallow, turbid lake with a high specific conductance value (1075 µS/cm).

Pinnularia australogibba var. *subcapitata* Van de Vijver, Chattová & Metzeltin var. nov. (Figs 102 –114)

DIAGNOSIS: Differt a varietate nominata dimensionibus valvae semper minoribus (longitudo 22–45 µm, latitudo 5.3–7.3 µm), apicibusque typice subcapitatis. Striae transapicales 11–12 in 10 µm.

HOLOTYPUS: Slide no. BR-4220 (holotype here designated see Fig. 104) deposited in National Botanic Garden, Meise, Belgium, leg. B. Van de Vijver, coll. date 6/12/2007.

ISOTYPI: PLP-170 (UA, University of Antwerp, Belgium), BRM-ZU7/66 (Hustedt Collection, Bremerhaven, Germany)

TYPE LOCALITY: Pointe d'Entrecasteaux, Ile Amsterdam, TAAF, southern Indian Ocean, sample W037.

ETYMOLOGY: The variety epithet *subcapitata* is derived from the shape of the apices that are more subcapitate contrary to the nominate variety that has rostrate apices.

MORPHOLOGICAL OBSERVATIONS: Compared to the nominate variety, valves generally smaller (length 22–45 µm, width 5.3–7.3 µm, n = 15) with typically subcapitate apices. Smaller valves with non protracted-, broadly rounded apices. Axial area, central area and raphe structure not significantly different with proximal raphe endings slightly more deflected. Striae radiate near the central area, becoming convergent near the apices, 11–12 in 10 µm.

REMARKS: The variety *subcapitata* differs from the nominate variety in valve outline and dimensions. Contrary to *P. australogibba* that has typically weakly protracted, rostrate, broadly rounded apices, the variety *subcapitata* has distinct subcapitate apices with a clear constriction of the valve before the apices. The variety is also markedly smaller (22–45 µm vs. 45–60 µm for *P. australogibba*). Both varieties have never been observed in the same samples although both are present in the southern part of the island (Entrecasteaux and Del Cano).

ECOLOGY AND ASSOCIATED DIATOM FLORA: *Pinnularia australogibba* var. *subcapitata* is present in almost all aquatic and moss samples taken in the area around Pointe d'Entrecasteaux. This area is formed by the remains of the first volcanic phase that shaped Ile Amsterdam and is characterized by several small, fast-flowing brooks, the only running water on the island. The pH of these brooks is rather alkaline (pH 7.8–8.5) with a moderate specific conductance value (300–350 µS/cm) and low nutrient values. The dominant diatom flora is composed of *Planothidium lanceolatum*, *Halamphora* cf. *paraveneta* (Lange-Bertalot, Cavacini, Tagliaventi & Alfinito) Levkov, *Nitzschia commutata* Grunow, *Karayevia oblongella*, *Sellaphora seminulum*, *Navicula gregaria* Donkin and several so far unidentified *Nitzschia* and *Luticola* species.

Pinnularia amsterdamensis Chattová, Metzeltin & Van de Vijver sp. nov. (Figs 115 –131)

DIAGNOSIS: Valvae lineares-lanceolatae ad rhombicae-lanceolatae in media parte valvae leviter inflatae, apicibus subcapitatis, cuneatim rotundatis. Longitudo (45) 56–63 (69) µm, latitudo 6.6–8.0 µm. Ratio longitudinis/latidudinis 6.7–9.7. Raphe lateralis, recta ad leviter curvata, terminationibus centralibus raphis distinctis, unilateraliter deflexis, poris distinctis, leviter bulbiformibus. Fissurae terminales falcatae. Area axialis angusta, ad aream centralem versus dilatata, fasciam leviter latam saepe asymmetricam formans. Striae transapicales in media parte valvae fortiter radiantes, ad apices fortiter convergentes, 13–14 in 10 µm. Lineae speciosae longitudinales nullae.

HOLOTYPUS: Slide no. BR-4221 (holotype here designated see Fig. 115) deposited in National Botanic Garden, Meise, Belgium, leg. B. Van de Vijver, coll. date 11/12/2007.

ISOTYPI: PLP-171 (UA, University of Antwerp, Belgium), BRM-ZU7/67 (Hustedt Collection, Bremerhaven, Germany)

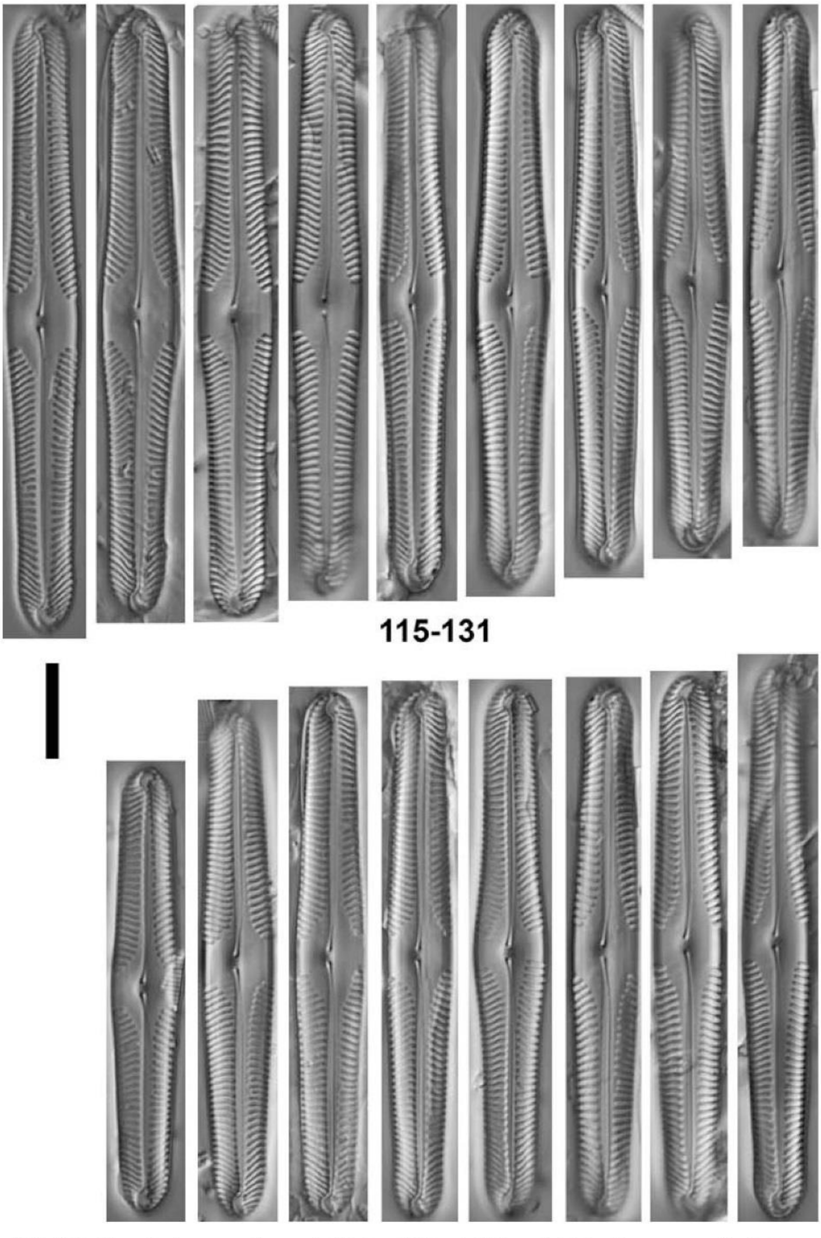
TYPE LOCALITY: Plateau du Museau de Tanche, Ile Amsterdam, TAAF, southern Indian Ocean, sample W085.

ETYMOLOGY: This taxon is named after Ile Amsterdam (southern Indian Ocean) where it was found to be growing abundantly in the caldera area.

MORPHOLOGICAL OBSERVATIONS: Frustules in girdle view rectangular. Valves narrowly linear-lanceolate to rhombic-lanceolate in larger valves, tapering gradually from the swollen, convex middle to the subcapitate, rounded to slightly cuneate ends. Valve dimensions (n = 25): length (45) 56–63 (69) µm, valve width 6.6–8.0 µm, length/width ratio 6.7–9.7. Axial area narrow, lanceolate, slightly widening towards the central area. Central area forming a more or less broad, rhombic, commonly slightly asymmetrical fascia. Raphe lateral with straight to slightly curved raphe branches. Central raphe endings unilaterally deflected with slightly inflated, distinctly visible central pores, rather close to each other. Terminal raphe fissures typically sickle-shaped. Transapical striae strongly radiate in the middle up to strongly convergent near the apices, 13–14 in 10 µm. Longitudinal lines absent.

REMARKS: *Pinnularia amsterdamensis* belongs to the group of taxa around *Pinnularia gibba*, although *P. gibba* itself can be very easily distinguished based on the irregular markings in the central area, the larger and more pronounced capitate apices and the short striae resulting in a wide axial area. The new species can be separated from *P. gibbiformis* Krammer by a different length/width ratio (6.7–9.7 in *P. amsterdamensis* vs. 10–13 in *P. gibbiformis*), the presence of a distinct fascia (absent in *P. gibbiformis*) and the strongly convergent striae near the apices. *Pinnularia macilenta* Ehrenb. has much larger valve dimensions (length up to 134 µm) whereas *P. subgibba* Krammer and its variety *undulata* Krammer, have more linear valves lacking the central inflation.

ECOLOGY AND ASSOCIATED DIATOM FLORA: *Pinnularia amsterdamensis* is so far only found on Ile Amsterdam. On the other archipelagos and islands in the southern Indian Ocean, the species has never been found (Van de Vijver et al. 2001, 2002, 2004 a, 2008 a). All populations observed



Figs 115–131. *Pinnularia amsterdamensis* Chattová, Van de Vijver & Metzeltin sp. nov.; Scale bar represents 10 μm.

during the survey, were found in lakes and pools of the caldera region on top of the island (alt. 700–800 m). All lakes and pools had very similar physico-chemical characteristics with a pH ranging from 5.00 to 6.80, a specific conductance of 40–86 µS/cm, very low nutrients and ion concentrations and low chloride and sulphate concentrations (< 20 mg/l). Dominating taxa in the samples include *Frustulia lebouvieri*, *Eunotia paludosa*, *Eunotia muscicola*, *Kobayasiella subantarctica* Van de Vijver & Vanhoutte and various *Pinnularia* taxa.

Pinnularia vixconspicua **Chattová, Metzeltin & Van de Vijver sp. nov.** (Figs 132 –159)

DIAGNOSIS: Valvae lineares marginibus paene parallelis apicibusque rostratis ad leviter cuneatis. Longitudo 23–50 µm, latitudo 6–6.6 µm. Ratio longitudinis/latitudinis 4.1–9.8. Area axialis angusta, lanceolata. Area centralis formans fasciam irregularem. Raphe lateralis, recta ad leviter curvata, terminationibus centralibus raphis distinctis, unilateraliter deflexis poris centralibus raphis guttiformibus. Fissurae terminales falcatae. Striae transapicales in media parte valvae radiatae ad parallelae in speciminibus parvis, ad apices leviter convergentes, 15–16 in 10 µm. Lineae speciosae longitudinales nullae.

HOLOTYPUS: Slide no. BR-4222 (holotype here designated see Fig. 136) deposited in National Botanic Garden, Meise, Belgium, leg. B. Van de Vijver, coll. date 12/12/2007.

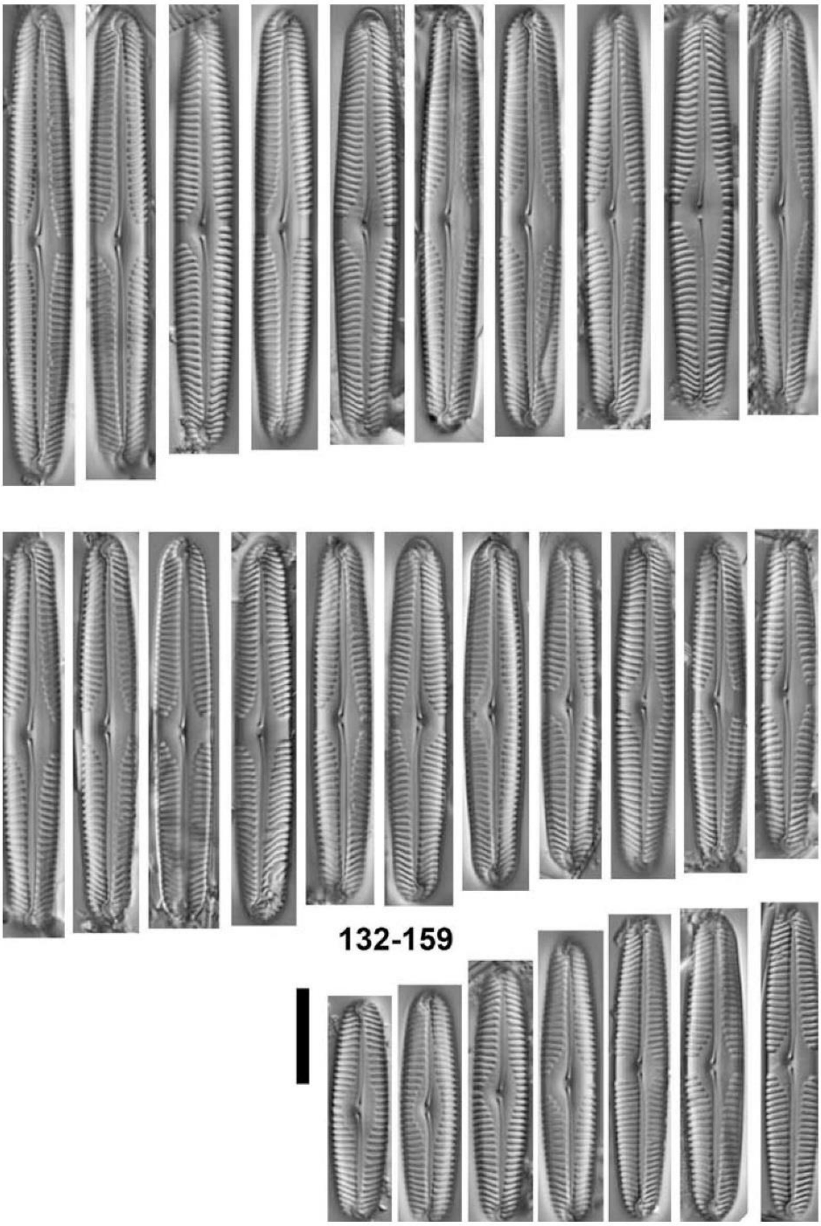
ISOTYPI: PLP-172 (UA, University of Antwerp, Belgium), BRM-ZU7/68 (Hustedt Collection, Bremerhaven, Germany)

TYPE LOCALITY: Plateau du Lac bleu, Ile Amsterdam, TAAF, southern Indian Ocean, sample W113.

ETYMOLOGY: Latin: *vix-* meaning 'hardly' and *conspicuous* meaning 'conspicuous', pointing to the fact that this new taxon has no typical features but can be distinguished by its unique character combination.

MORPHOLOGICAL OBSERVATIONS: Frustules in girdle view rectangular. Valves linear with almost parallel margins lacking any central inflation and broadly rostrate to sometimes even very slightly cuneate apices. Valve dimensions (n = 30): length 23–50 µm, width 6–6.6 µm, length/width ratio 4.1–9.8. Axial area narrow, lanceolate to linear-lanceolate, slightly widening towards the central area. Central area small, usually forming a narrow unilateral or bilateral fascia due to the irregular shortening of the central striae. Valves lacking a fascia present in the population and even within the same frustule. Raphe clearly lateral, straight to slightly curved. Central raphe endings unilaterally deflected with distinctly visible, drop-like central pores, strikingly close to each other. Terminal raphe fissures typically sickle-shaped. Transapical striae weakly radiate to almost parallel in small specimens near the valve centre becoming strongly convergent near the apices, 15–16 in 10 µm. Longitudinal lines absent.

REMARKS: *Pinnularia vixconspicua* has hardly any typical features distinguishing the species from other *Pinnularia*-taxa but the combination of morphological features is nevertheless unique and makes its separation from other, similar *Pinnularia*-taxa quite obvious. *Pinnularia microstauron* (Ehrenb.) Cleve and *Pinnularia microstauropsis* Kulikovskiy, Lange-Bertalot & Metzeltin, *P. nanomicrostauron* Kulikovskiy, Lange-Bertalot, Metzeltin show a slight resemblance but has protracted valve apices, a different central area with less shortened central striae, more radiate striae (contrary to the almost parallel striae in *P. vixconspicua*), a filiform raphe (whereas *P. vixconspicua* has a clearly lateral raphe) and larger valve dimensions (valve width 7–15 µm vs. 6.0–6.6 µm in *P. vixconspicua*). *Pinnularia submicrostauron* Schroeter has similar valve dimensions but a lower stria density (12–14 vs. 15–16 in 10 µm) and lacks the typical irregular fascia. Other taxa such as *Pinnularia tirolensis* (Metzeltin & Krammer) Krammer and *P. sub-*



132-159

Figs 132–159. *Pinnularia vixconspicua* Chattová, Van de Vijver & Metzeltin sp. nov.; Scale bar represents 10 µm.

capitata var. *subrostrata* Krammer sufficiently differ to be excluded from conspecificity.

Ecology and associated diatom flora: *Pinnularia vixconspicua* is so far only found on Ile Amsterdam and at present absent on the nearby archipelagos of Crozet and Kerguelen and the islands of Marion, Prince Edward and Heard (Van de Vijver et al. 2001, 2002, 2004 a, 2008 a). All populations observed during the survey, were found in lakes and pools of the caldera region on top of the island (alt. 700–800 m) where *P. vixconspicua* is one of the dominating species in the diatom communities. All lakes and pools had very similar physico-chemical characteristics with a pH ranging from 5.0 to 6.8, a specific conductance of 40–86 µS/cm, very low nutrients and ion concentrations and low chloride and sulphate concentrations (< 20 mg/l). Dominating taxa in the samples include *Frustulia lebouvieri*, *Eunotia paludosa*, *E. muscicola*, *E. lecohui* Van de Vijver, *Kobayasiella subantarctica* and several *Pinnularia* taxa such as *P. amsterdamensis*.

***Pinnularia pseudohilseana* Van de Vijver, Chattová & Metzeltin sp. nov.** (Figs 160–171)

Diagnosis: Valvae stricte lineares marginibus parallelis apicibusque rostratis-capitatis. Longitudo 35–45 µm, latitudo 4.8–5.5 µm. Area axialis angusta ad moderate lata, linearis, graduatim dilatata ad aream centralem. Area centralis rotundata ad rhombica, plerumque formans fasciam sed valvae sine fascia et com fascia asymmetrica aliquando praesentes. Raphe clare lateralis. Terminationes raphis proximales deflexae poris centralis expansis, approximatis. Terminationes raphis distales fortiter uncinatae. Striae radiatae in media parte valvae, graduatim parallelae ad fortiter convergentes ad apices, 13–15 in 10 µm. Lineae speciosae longitudinales nullae.

Holotypus: Slide no. BR-4223 (holotype here designated see Fig. 162) deposited in National Botanic Garden, Meise, Belgium, leg. B. Van de Vijver, coll. date 15/12/1999.

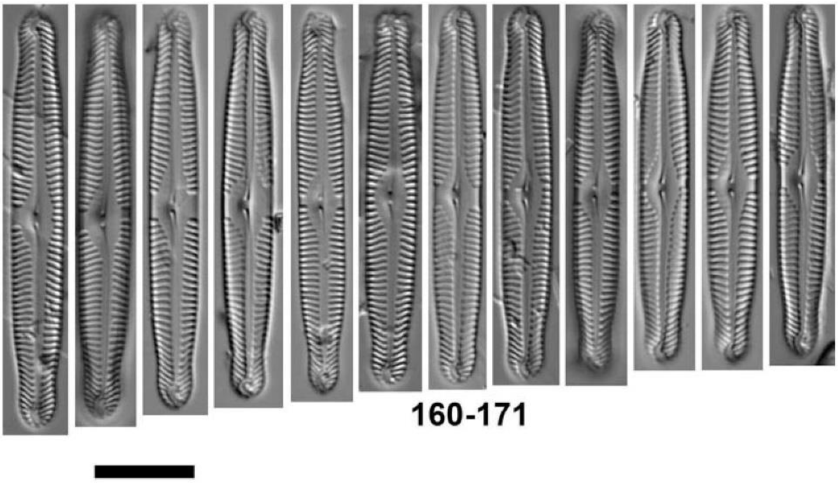
Isotypi: PLP-173 (UA, University of Antwerp, Belgium), BRM-ZU7/69 (Hustedt Collection, Bremerhaven, Germany)

Type locality: Plateau du Museau de Tanche, Ile Amsterdam, TAAF, southern Indian Ocean, sample BW442.

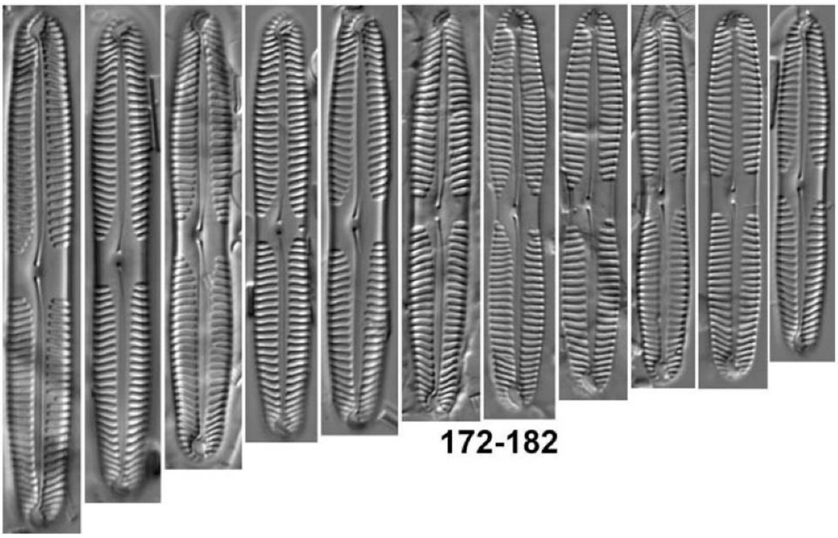
Etymology: the specific epithet refers to the resemblance with *P. hilseana* Janisch.

Morphological observations: Valves strictly linear with parallel margins and rostrate-capitate apices. Valve dimensions (n = 27): length 35–45 µm, width 4.8–5.5 µm. Axial area narrow to moderately broad, linear, gradually widening towards the central area. Central area rounded to rhomboid, usually forming a fascia reaching the valve margins but valves lacking a fascia or only with an asymmetric fascia also present. Raphe clearly lateral. Proximal raphe endings deflected, terminating expanded pores, positioned closely together. Distal raphe endings strongly hooked ('sickle-shaped'). Striae radiate near the central area, becoming gradually parallel to strongly convergent towards the apices, 13–15 in 10 µm. Longitudinal lines absent.

Remarks: The species shows some resemblance to *P. hilseana*, *P. subcapitata* var. *elongata* Krammer, *P. subcapitata* var. *semicruciata* Metzeltin & Krammer in Metzeltin & Lange-Bertalot, *P. pisciculus* var. *angusta* Metzeltin & Krammer in Metzeltin & Lange-Bertalot and *Pinnularia microstauron* var. *tenuirostris* Manguin in Bourrelly & Manguin but can be distinguished based on valve outline, valve dimensions and striation pattern. *Pinnularia hilseana*, a species that was later synonimized with *P. subcapitata* Greg., has a typical rectangular fascia contrary to the asymmetrical fascia in *P. pseudohilseana* and more typically capitate apices whereas *P. pseudohilseana* has rostrate-capitate apices. *Pinnularia subcapitata* var. *elongata* is usually longer (up to 57 µm) with broader valves (5.4–6.6 µm), a distinct rectangular fascia and well-developed capitate apices. *P. subcapitata* var. *semicruciata*, described from Guyana (Metzeltin & Lange-Bertalot 1998), has a similar fascia and valve apices but with slightly smaller dimensions (length



160-171



172-182

Figs 160–171. *Pinnularia pseudohilseana* Van de Vijver, Chattová & Metzeltin sp. nov.; **172–182**. *Pinnularia myriamiae* Van de Vijver, Chattová & Metzeltin sp. nov.; Scale bar represents 10 µm.

26–37 µm) and a much narrower axial area. *P. pisciculus* var. *angusta* (from Guyana; Metzeltin & Lange-Bertalot 1998) and *P. microstauron* var. *angusta* (described by Manguin from Guadeloupe; Bourrelly & Manguin 1952) also have capitate (and not rostrate-capitate) apices and both have much larger valves (length up to 64 µm, width up to 7.7 µm). Therefore, the description of *P. pseudohilseana* as an independent species is justified.

Ecology and associated diatom flora: *Pinnularia pseudohilseana* is rather widespread in the caldera region on top of the island. The populations are usually rather small but a fairly large population was found in sample BW442, taken from small acid (pH 4.8) pool with low specific conductance value (< 140 µS/cm) in the vicinity of the Museau de Tanche. The accompanying diatom flora is composed of *Frustulia lebouvieri*, *Kobayasiella subantarctica*, *Pinnularia amsterdamensis* and several *Eunotia* species.

Pinnularia myriamiae **Van de Vijver, Chattová & Metzeltin sp. nov.** (Figs 172 –182)

Diagnosis: Valvae stricte lineares marginibus parallelis clare constrictis in media valvae apicibus rostratis, leviter protractis. Longitudo 35–55 µm, latitudo 4.5–6.0 µm. Area axialis angusta ad moderate lata, lanceolate, graduatim dilatata ad aream centralem. Area centralis formans fasciam rectangularem. Striae isolatae aliquando praesentes in area centrali. Raphe clare lateralis. Terminationes raphis proximales deflexae poris centralis expansis. Terminationes raphis distales fortiter uncinatae. Striae leviter ad moderate radiatae in media parte valvae, graduatim parallelae et fortiter convergentes ad apices, 12–13 in 10 µm. Lineae speciosae longitudinales nullae.

Holotypus: Slide no. BR-4224 (holotype here designated see Fig. 173) deposited in National Botanic Garden, Meise, Belgium, leg. B. Van de Vijver, coll. date 15/12/1999.

Isotypi: PLP-174 (UA, University of Antwerp, Belgium), BRM-ZU7/70 (Hustedt Collection, Bremerhaven, Germany)

Type locality: Plateau du Museau de Tanche, Ile Amsterdam, TAAF, southern Indian Ocean, sample BA128.

Etymology: The species is dedicated to our colleague Mrs. Myriam de Haan (Nat. Botanic Garden of Belgium), to thank her for all her technical and practical assistance in the algology lab.

Morphological observations: Valves strictly linear with parallel margins showing a distinct constriction in the valve middle and weakly protracted, rostrate apices. Valve dimensions (n = 18): length 35–55 µm, width 4.5–6.0 µm. Axial area narrow to moderately broad, lanceolate, gradually widening towards the central area. Central area forming a rectangular fascia. Isolated striae sometimes present in the central area. Raphe clearly lateral. Proximal raphe endings deflected with expanded central pores. Distal raphe endings strongly hooked. Striae weakly to moderately radiate near the valve middle, gradually becoming parallel and towards the apices, strongly convergent, 12–13 in 10 µm. Longitudinal lines absent in the striae.

Remarks: Only a few *Pinnularia* species show a similar central constriction in combination with a linear valve outline. *Pinnularia lange-bertalotii* Krammer and *P. paralange-bertalotii* Fukushima, Yoshitake & Ts. Kobayasi are clearly constricted but have both broad, more rostrate-capitate apices, contrary to the rostrate apices in *P. myriamiae*. Both species are also much wider (up to 10 µm) with a larger, less rectangular central area and a broader axial area. Other species, lacking a central constriction but with a similar valve outline, are *P. tirolensis* (Metzeltin & Krammer) Krammer, *P. ivaloensis* Krammer and *Navicula wilmani* Fritsch. *Navicula wilmani*, described from South Africa (Fritsch & Rich 1929), clearly belonging to *Pinnularia*, shows some resemblance to *P. myriamiae* but the valves are much broader (width 7–8.5 µm) with, based on Fritsch's drawings, more parallel striae almost throughout the entire valve. *Pinnularia tirolensis* has broader valves (width 6.4–9.4 µm) with slightly convex margins lacking any constriction whereas *P. ivaloensis* has a longitudinal line visible on its striae.

Ecology and associated diatom flora: *Pinnularia myriamiae* was found in several samples collected near the Museau de Tanche crater in the caldera region on top of Ile Amsterdam. The largest population was found in a very wet peaty soil sample taken under a vegetation of grasses and *Sphagnum*, indicating its acid, oligotrophic character. Other species present in the sample include *Frustulia lebouvieri*, *Eunotia paludosa*, *Eunotia lecohui* and *Pinnularia vixconspicua*.

***Pinnularia* cf. *obscuriformis* Krammer** (Figs 183–193)

MORPHOLOGY: Valves linear with parallel to slightly convex margins and non protracted, cuneately rounded apices. Valve dimensions (n = 11): length 28–40 µm, width 5.5–6.8 µm). Axial area narrow, linear, widening towards the central area. Central area forming a broad fascia. No isolated central striae present. Raphe filiform, almost straight with only weakly deflected proximal raphe endings terminating in expanded pores. Distal raphe endings hooked, ?-shaped. Striae radiate in the valve middle, gradually becoming convergent near the apices, 10–11 in 10 µm. No longitudinal lines present on the striae.

REMARKS: The populations observed on Ile Amsterdam differ slightly from the drawing in Van Heurck (1880) and from the description in Krammer (2000). In Krammer (2000), most probably two species are represented under the name *P. obscuriformis*: the Figs 28–30 represent the true *P. obscuriformis* whereas the valves from Finland (Figs 31–35) most probably belong to a different species. Only the Figs 28–30 are taken into account for comparison with the Ile Amsterdam populations. The Ile Amsterdam valves are slightly larger [28–40 µm vs. 15–34 µm in Krammer (2000)], with less cuneate but instead broadly rounded apices, and less convergent striae near the apices. Nevertheless are these differences too small to justify a separation from *P. obscuriformis*. *Pinnularia brebissonii* (Kütz.) Rabenh. is larger with more convex valve margins, more broadly rounded apices and a different striation pattern with a higher stria density.

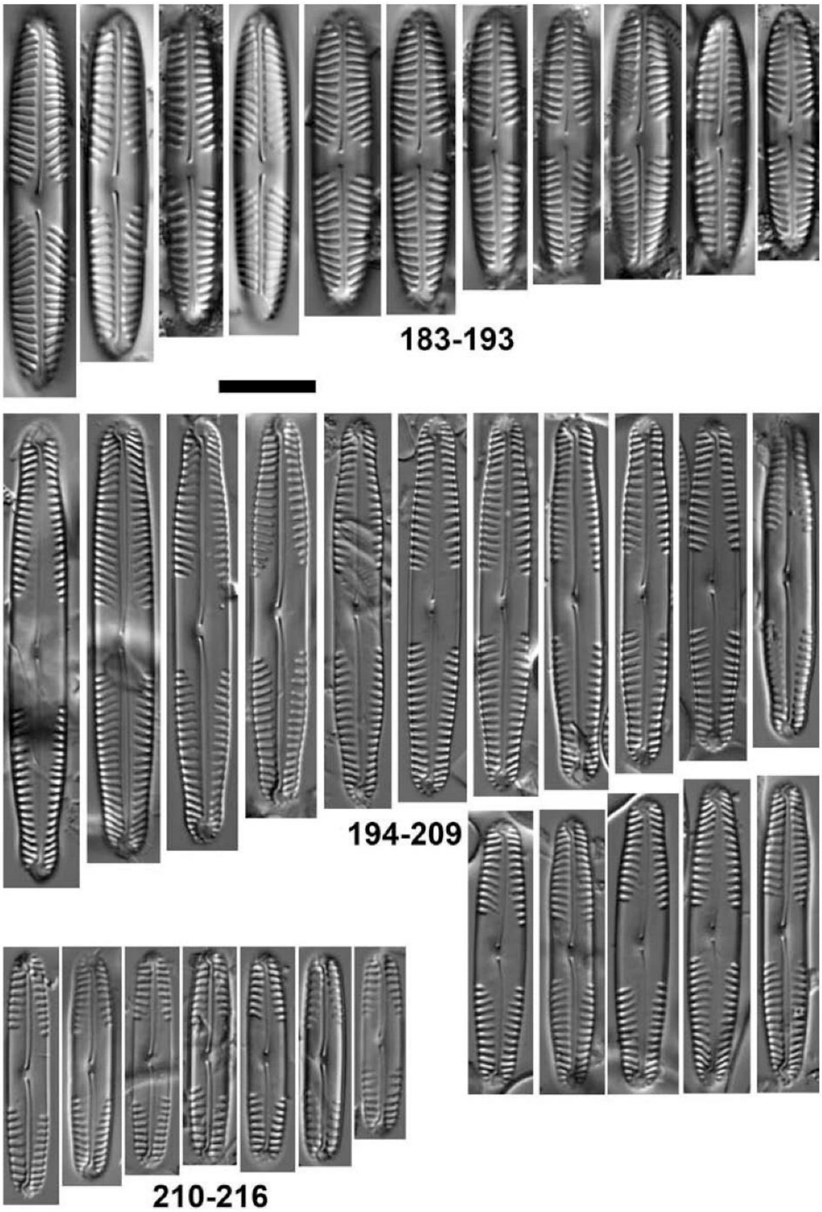
ECOLOGY AND ASSOCIATED DIATOM FLORA: *Pinnularia* cf. *obscuriformis* is a fairly rare species on Ile Amsterdam. The largest population was found in a small lithotelm close by the Indian Ocean, overgrown with dry mosses, occasionally moistened by rainwater. The sample is dominated by *Achnanthes coarctata*, several (so far unidentified) *Luticola* species and *P. borealis*.

***Pinnularia sinistra* Krammer** (Figs194 –209)

MORPHOLOGY: Valves linear with parallel to slightly convex to even concave margins and clearly protracted, subcapitate apices. Valve dimensions (n = 27): length 28–50 µm, width 5–6 µm. Axial area moderately broad, lanceolate, clearly widening towards the central area. Central area forming a broad-, sometimes asymmetrical fascia. Raphe filiform in smaller specimens, clearly lateral in larger valves with curved outer fissures. Proximal raphe endings deflected, terminating in expanded central pores. Distal raphe endings strongly hooked. Striae radiate in the middle, becoming parallel and weakly convergent towards the apices, 10–11 in 10 µm. Longitudinal bands on the striae absent.

REMARKS: The *P. sinistra* populations observed on Ile Amsterdam are almost similar to *P. sinistra* shown in Krammer (1992, 2000). The valve dimensions are within the reported range but the axial area is somewhat different being broader whereas *P. sinistra* has a more narrow axial area.

ECOLOGY AND ASSOCIATED DIATOM FLORA: *Pinnularia sinistra* is only found in a few samples. The largest population was observed in a small pool in a cave in the Grand Tunnel, a large lava tunnel of which certain parts collapsed forming shallow caves. The sample was taken in a small, very shallow pool of only 30 cm in diameter, with a pH of 5.8 and a specific conductance of 239 µS/cm. The dominating diatom flora in the sample was composed of *Diadesmis vidalii*, *D. crozetikerguelensis*, *Melosira* sp., *Planothidium lanceolatum*, *Karayevia oblongella* and *Orthoseira* sp. In other caves on the island, smaller populations of this species were observed.



Figs 183–193. *Pinnularia* cf. *obscuriformis* Krammer; **194–209**. *Pinnularia sinistra* Krammer; **210–216**. *Pinnularis subsinistra* Van de Vijver, Chattová & Metzeltin sp. nov.; Scale bar represents 10 µm.

Pinnularia subsinistra **Van de Vijver, Chattová & Metzeltin sp. nov.** (Figs 210–216)

DIAGNOSIS: Valvae lineares marginibus parallelis apicibusque late rotundatis, non protractis. Longitudo 19–26 µm, latitudo 3.8–4.2 µm. Area axialis angusta, lanceolata, dilatata ad aream centralem. Area centralis formans fasciam rectangularem latam, paene ⅓ longitudinis valvae. Raphe filiformis, ramis curvatis terminationibus proximalis raphis deflexis cum poris parvis, leviter expansis terminationibusque distalis fortiter uncinatis. Striae parallelae ad levissime radiatae in media parte valvae, leviter convergentes ad apices, 12–14 in 10 µm. Lineae speciosae longitudinales nullae.

HOLOTYPUS: Slide no. BR-4225 (holotype here designated see Fig. 210) deposited in National Botanic Garden, Meise, Belgium, leg. B. Van de Vijver, coll. date 15/12/2007.

ISOTYPI: PLP-175 (UA, University of Antwerp, Belgium), BRM-ZU7/71 (Hustedt Collection, Bremerhaven, Germany)

TYPE LOCALITY: Base Martin-de-Viviès, Jardin Météo, Ile Amsterdam, TAAF, southern Indian Ocean, sample M200.

ETYMOLOGY: The specific epithet refers to the close resemblance to *P. sinistra*.

MORPHOLOGICAL OBSERVATIONS: Valves linear with parallel margins and broadly rounded, non protracted apices. Valve dimensions (n = 12): length 19–26 µm, width 3.8–4.2 µm. Axial area narrow, lanceolate, widening towards the central area. Central area forming a broad, rectangular fascia, almost ⅓ of the total valve length. Raphe filiform with curved raphe branches and deflected proximal raphe endings terminating in small, weakly expanded pores. Distal raphe endings strongly hooked. Striae parallel to very weakly radiate in the middle, becoming very weakly convergent near the apices, 12–14 in 10 µm. Longitudinal lines absent.

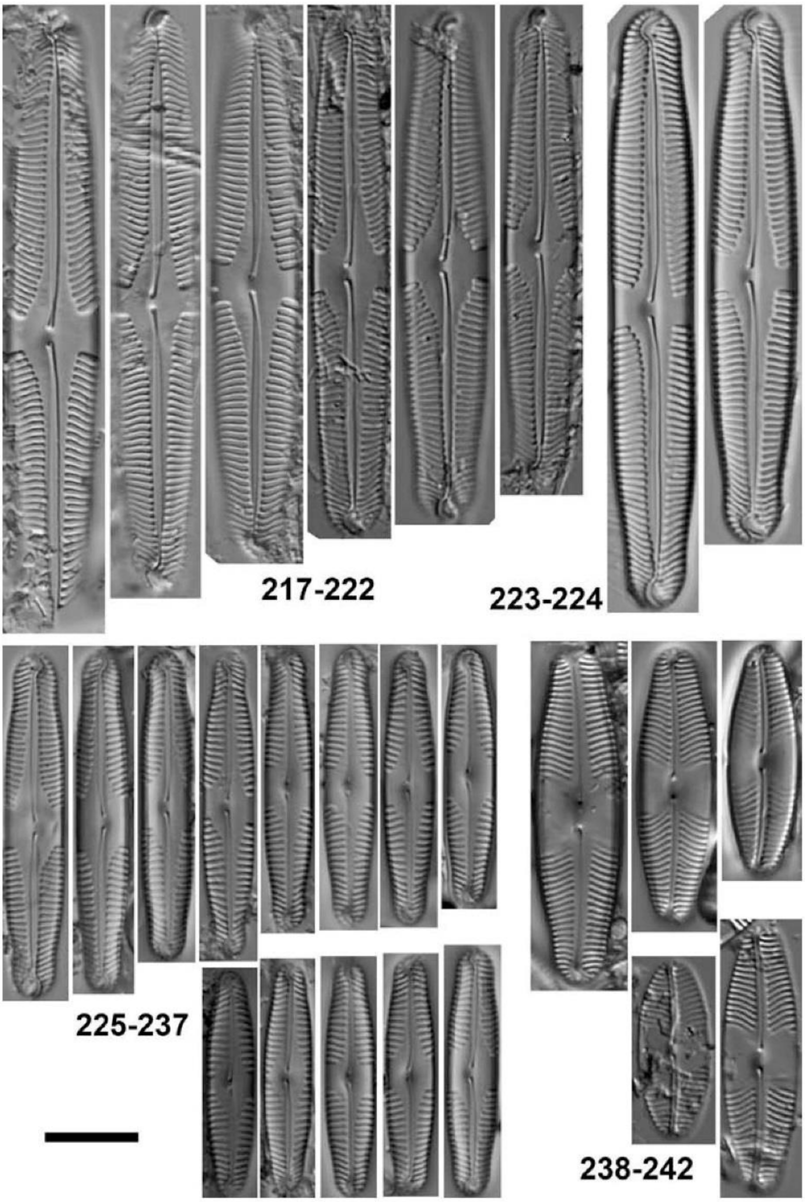
REMARKS: *Pinnularia subsinistra* might be considered belonging to *P. sinistra* representing the smallest valves of the species range. On Ile Amsterdam, both species occur together allowing the differentiation of both species. The largest specimens of *P. subsinistra* are always smaller than the smallest *P. sinistra* valves (26 µm vs. 28 µm) showing a very broad fascia reaching almost 1/3 of the valve length. The striae in *P. subsinistra* are more parallel and only very weakly radiate whereas in *P. sinistra*, the striae are parallel but more likely radiate becoming convergent towards the apices. In *P. subsinistra*, the striae are less convergent near the apices. Finally, the apices in *P. subsinistra* are broadly rounded and never protracted, contrary to *P. sinistra* that has protracted, subcapitate apices. These differences are sufficiently large to justify the separation of both species.

There are hardly any other *Pinnularia* species that show some similarities with *P. subsinistra. Pinnularia lagerstedtii* (Cleve) Cleve-Euler, *P. schimanskii* Krammer and *P. incognita* Krasske show a different striation pattern with less striae (max. 10 in 10 µm vs. 12–14 in 10 µm), a smaller central area and a linear axial area.

ECOLOGY AND ASSOCIATED DIATOM FLORA: *Pinnularia subsinistra* is so far only found on its type locality in a small cave (Jardin Méteo) near the scientific base Martin-de-Viviès. The sample was taken from wet mosses at the bottom of a narrow tunnel leading to the cave where light penetrated to the bottom. The accompanying diatom flora consisted of *Melosira* sp., *Diadesmis crozetikerguelensis*, *D. vidalii*, *Pinnularia sinistra* and several so far unidentified *Luticola* and *Nitzschia* species.

Pinnularia microstauron **(Ehrenb.) Cleve** (Figs217– 224)

MORPHOLOGY: For more details regarding the overall morphology, see Krammer (2000). Observed range of dimensions: length 50–75 µm, width 8.4–10.0 µm. Central area rhomboid form-



Figs 217–224. *Pinnularia microstauron* (Ehrenb.) Cleve; **225–237**. *Pinnularia acidicola* Van de Vijver & Le Cohu; **238–242**. *Pinnularia bottnica* Krammer sensu Van de Vijver et al. (2002); Scale bar represents 10 µm.

ing an asymmetric fascia. Isolated central striae sometimes present. Raphe clearly lateral with deflected proximal raphe endings and expanded pores. Striae radiate in the middle, parallel to strongly convergent near the apices, 12–14 striae in 10 µm.

REMARKS: *Pinnularia microstauron* is a variable, widespread species. Contrary to what is mentioned in Krammer (2000), the raphe of the Ile Amsterdam valves is clearly lateral and not narrowly lateral. Nevertheless, the similarity between the Ile Amsterdam populations and the generally accepted idea of *P. microstauron* is very large justifying the proposed identification.

ECOLOGY AND ASSOCIATED DIATOM FLORA: *Pinnularia microstauron* was found in samples taken on the southern side of the island, at an altitude of 600 m, outside the caldera area. The small pool where the largest population was observed, is part of a small brook with a pH of 6.2 and a rather high specific conductance of 440 µS/cm. The pool was vegetated with several moss species with black filamentous algae on the edges. The diatom flora in the sample is dominated by *Frustulia lebouvieri*, *Eunotia paludosa* and *Pinnularia vixconspicua*.

***Pinnularia acidicola* Van de Vijver & Le Cohu** (Figs225 –237)

MORPHOLOGY: For more details regarding the overall morphology, see Van de Vijver et al. (2002: p. 78). Observed range of dimensions: length 23–37 µm, width 4.8–6.3 µm. Axial area narrow, lanceolate, widening towards the central area. Central area rhomboid forming a large fascia. Raphe narrowly lateral with deflected proximal raphe endings and expanded pores. Striae parallel to weakly radiate in the middle, parallel to clearly convergent near the apices, 13–15 striae in 10 µm.

REMARKS: The only difference between the Ile Amsterdam populations and the type population of *P. acidicola*, described from the Crozet archipelago (Van de Vijver et al. 2002), is the number of striae (13–15 in 10 µm vs. 11–12 in 10 µm in *P. acidicola*). Since all other morphological features match, the proposed identification can be justified.

ECOLOGY AND ASSOCIATED DIATOM FLORA: All populations of *P. acidicola* on Ile Amsterdam were found in the brooks flowing out of the ravines of Del Cano, in the southern part of the island. These brooks are characterized by a slightly acid to almost circumneutral pH (6–6.5), a moderately high specific conductance value (400–500 µS/cm), low nutrient but high Na-values. The dominant diatom flora is composed of *Planothidium lanceolatum*, *Karayevia oblongella*, *Diadesmis contenta*, *Eunotia muscicola* and several *Pinnularia* taxa.

***Pinnularia bottnica* Krammer sensu Van de Vijver et al. (2002)** (Figs 238–242)

MORPHOLOGY: For more details regarding the overall morphology, see Van de Vijver et al. (2002: p. 81). Valves elliptical. Smaller valves with non protracted, broadly rounded ends, larger valves with broadly rostrate, protracted apices. Observed range of dimensions: length 19–36 µm, width 7.5–9.5 µm. Axial area narrow, linear, almost not widened towards the central area Central area rhomboid forming a large, wedge-shaped fascia. Raphe filiform with curved branches and deflected proximal raphe endings with expanded pores. Striae radiate in the middle, parallel to very weakly convergent near the apices, 14–16 striae in 10 µm.

REMARKS: On the Crozet Archipelago, a similar *Pinnularia* species was found. In Van de Vijver et al. (2002) these populations were identified as *P. bottnica* whereas the more narrowly rostrate valves were identified as *P. kolbei* Manguin. In 2001, Fukushima et al. renamed *P. kolbei* as *P. parakolbei* Fukushima, Kobayashi & Yoshitake since the name *P. kolbei* Manguin appeared to be a homonym of *P. kolbei* Mölder. Unfortunately, the *P. parakolbei* valves shown in Fukushima et al. (2001) (reported from the Falkland Islands) do not correspond to the original drawing and description of the type of *P. kolbei* from the sub-Antarctic Iles Kerguelen but correspond more to *P. bottnica* Krammer. It is however not clear if *P. bottnica* and *P. parakolbei* sensu Fukushima et al. belong to the same species representing different parts of the cell cycle. Until the correct identity and morphology of *P. parakolbei* sensu Fukushima et al. is not determined, we suggest to identify all broadly rounded, not clearly rostrate valves as *P. bottnica*.

ECOLOGY AND ASSOCIATED DIATOM FLORA: *Pinnularia bottnica* is present in some of the small brooks flowing out of the ravines of Del Cano, located in the southern part of Ile Amsterdam, characterized by a rather weakly acid pH (6–6.5), moderate specific conductance values (250–500 µS/cm) and low nutrient values. The dominating diatom flora in the sample consists of *Planothidium lanceolatum*, *Pinnularia australogibba*, *Karayevia oblongella*, *Achnathes coarctata*, *Diadesmis contenta*, various (so far unidentified) *Luticola* species and *Sellaphora seminulum* (Grunow) D. G. Mann.

***Pinnularia robbrechtii* Van de Vijver sp. nov.** (Figs 243–253)

DIAGNOSIS: Valvae lineares marginibus rectis, parallelis, numquam gibbosis, graduatim contractis ad apices cuneatim rotundatos, non protractos. Longitudo 40–105 µm, latitudo 8.0–12.8 µm. Area axialis lata, ½–⅓ latitudinis valvae, linearis ad lanceolate ad apices. Area centralis rotundata ad rhombico-rotundata, asymmetrica, paene ⅔ latitudinis valvae. Raphe lateralis fissures externis curvatis terminationibus proximalibus rectis ad deflectis cum poris graduatim expansis terminationibusque distalis raphis magnis, formatis similibus *P. viridis*. Striae radiatae in media parte valvae, parallelae ad fortiter convergentes ad apices, 9–10 in 10 µm. Lineae speciosae longitudiales conspicue apparentes.

HOLOTYPUS: Slide no. BR-4226 (holotype here designated see Fig. 244) deposited in National Botanic Garden, Meise, Belgium, leg. B. Van de Vijver, coll. date 12/02/1998.

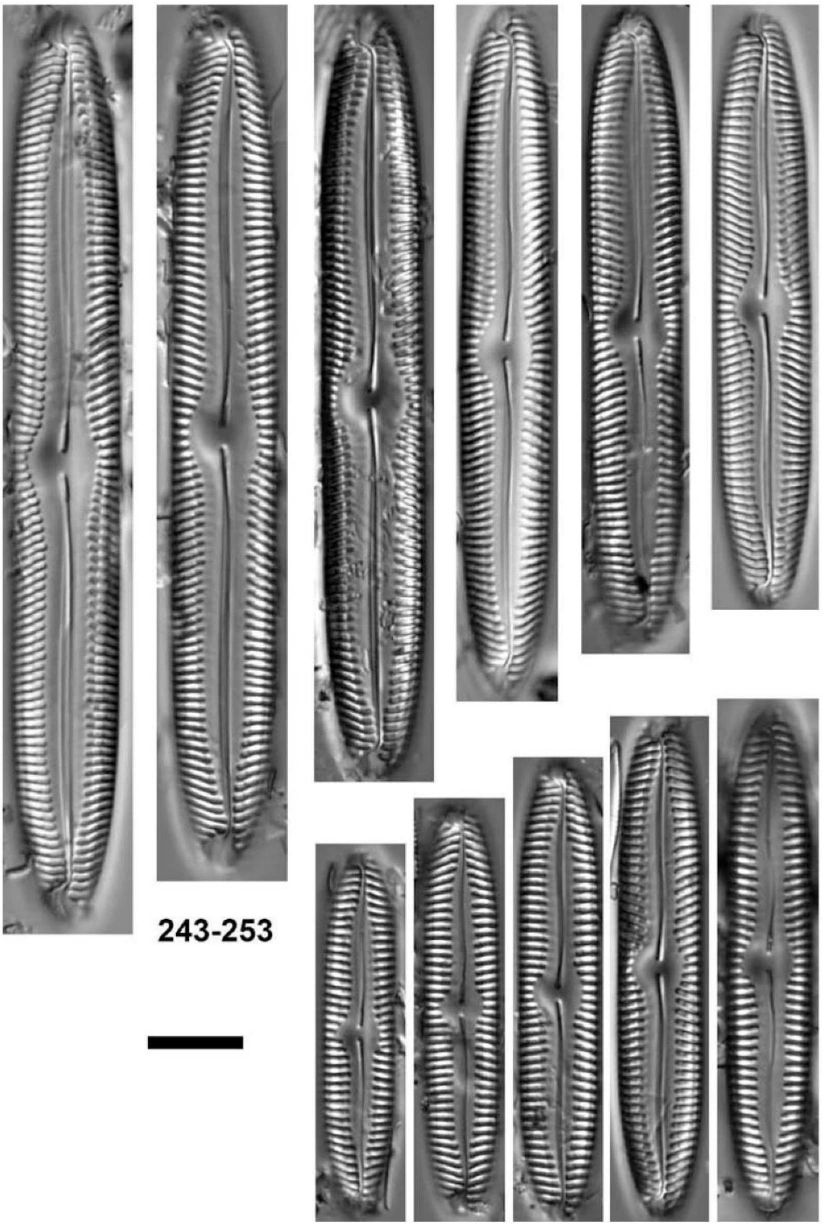
ISOTYPI: PLP-176 (UA, University of Antwerp, Belgium), BRM-ZU7/72 (Hustedt Collection, Bremerhaven, Germany)

TYPE LOCALITY: Base Martin-de-Viviès, Ile Amsterdam, TAAF, southern Indian Ocean, sample AMS15.

ETYMOLOGY: The species is named in honor of our colleague, Prof. Dr. Elmar Robbrecht (National Botanic Garden of Belgium) on the occasion of his retirement (01/03/2011).

MORPHOLOGICAL OBSERVATIONS: Valves linear with straight, parallel, never gibbous margins, near the apices gradually tapering to the cuneately rounded, not protracted apices. Valve dimensions (n = 26): length 40–105 µm, width 8.0–12.8 µm. Axial area broad, ½–⅓ of the valve width, linear to lanceolate towards the apices. Central area rounded to rhombic-rounded, asymmetrical, almost ⅔ of the valve width. Raphe lateral with curved outer fissures and almost straight to deflected proximal endings terminating in gradually expanding pores. Distal raphe endings large, viridis-like. Striae radiate near the valve middle, becoming parallel to strongly convergent near the apices, 9–10 in 10 µm. A longitudinal band clearly present on the striae.

REMARKS: In the past, a large number of *Pinnularia* species with similar valve dimensions and outlines were described but they never present the same combination of morphological characters as *P. robbrechtii*. *Pinnularia subrupestris* Krammer is smaller (length 35–77 µm), the longest specimens present a more gibbous middle portion of the valves and the striae lack the typical longitudinal line, clearly present in *P. robbrechtii*. *Pinnularia peracuminata* Krammer is also smaller (length 40–85 µm) with a narrower axial area and, in larger specimens, a slightly swollen central part. This gibbous central part has never been observed in *P. robbrechtii*. On the other hand, *P. percuneata* var. *minor* Krammer is larger (width 13–21 µm). Other species such



Figs 243–253. *Pinnularia robbrechtii* Van de Vijver, Chattová & Metzeltin sp. nov.; Scale bar represents 10 µm

as *P. esoxiformis* Fusey or *P. viridiformis* var. *minor* Krammer have a complex raphe contrary to the lateral raphe in *P. robbrechtii*. Therefore we believe that the description of *P. robbrechtii* as an independent species is justified.

ECOLOGY AND ASSOCIATED DIATOM FLORA: *Pinnularia robbrechtii* was found in only small numbers in several samples taken around the scientific base Martin-de-Viviès. The largest population was found growing on temporarily moistened mosses. The diatom flora in the sample was dominated by a large number of species such as *Planothidium lanceolatum*, *Navicula* cf. *tenelloides* Hustedt, *Nitzschia* cf. *hantzschiana* Rabenh., *Tryblionella debilis* (Arnott) Grunow and *Sellaphora seminulum*.

Discussion

When comparing the *Pinnularia* flora of Ile Amsterdam with the more southerly positioned sub-Antarctic islands (Prince Edward Islands, Archipel Crozet, Iles Kerguelen, Heard Island), it is clear that only a few species are shared. Table 2 shows the *Pinnularia* species found on the various islands (based on data from Van de Vijver et al. 2001, 2002, 2004 a, 2008 a). Of the 22 species, only seven are shared with the other sub-Antarctic islands. Most (5 out of 7) of these shared species present a cosmopolitan distribution. This result is confirmed by other biogeographic studies dealing with the sub-Antarctic diatom flora. In 2005, a biogeographic survey of the genus *Stauroneis* showed the presence of only one unknown species on Ile Amsterdam whereas on the other sub-Antarctica more than 10 new species were described (Van de Vijver et al. 2004 c, 2005). A similar result was found in the genus *Eunotia* where only two out of five species were shared between Ile Amsterdam and the other sub-Antarctic islands (Van de Vijver et al. 2008 b). The two species shared by the islands were considered to have a cosmopolitan distribution whereas the three species restricted to Ile Amsterdam seem to be true endemic species. Finally, in 2009, a new genus, *Microfissurata*, was described based on two species of which one was restricted to Ile Amsterdam (i.e. *Microfissurata australis* Van de Vijver & Lange-Bertalot) (Cantonati et al. 2009).

The genus *Pinnularia* is well represented on the sub-Antarctic islands. Based on Table 2, 63 *Pinnularia* species were observed on the five islands and archipelagos. Apart from the Ile Amsterdam endemics, another 23 *Pinnularia* species were described from the true sub-Antarctic islands, most of them occurring on all four islands/archipelagos (Van de Vijver et al. 2002, 2004 b, 2006). The fact that, apart from *P. acidicola*, none of these sub-Antarctic endemics was found on Ile Amsterdam highlights the unique floristic situation of this island and of the entire region and may add valuable information to the ongoing discussion whether micro-organisms are cosmopolitan or not (Vyverman et al. 2007, Verleyen et al. 2009).

Moreover, twelve out of fifteen species, restricted on Ile Amsterdam can be considered being truly endemic for the island. Only *Pinnularia sinistra*, *P.* cf. *obscuriformis* and *P. subacoricola* were also found in Europe. The large number of new *Pinnularia* species described from this small island is hardly surprising considering on one hand the unique features of Ile Amsterdam but on the other hand, the lack of detailed taxonomic studies on the Ile Amsterdam diatom flora. The oceanic island is volcanic in origin and, geologically spoken, very young with an age of less than 750.000 years. One of the key-features of the organisms on oceanic islands, is the presence of an imbalanced flora and fauna with some genera being overrepresented and some even lacking. The island is very isolated with the nearest larger landmasses more than 1500 km away. Human occupation on the island dates from 1696 when the Dutch sea-captain and explorer Willem de Vlamingh first set foot on the island. The environmental conditions in the caldera area where most of the *Pinnularia* species were found, are rather stable and well-isolated from the other

Table 2. List of all *Pinnularia* taxa found on the Southern Indian Ocean islands. New species are bold-faced.

	Ile Amsterdam	Prince Edward Islands	Crozet archipelago	Iles Kerguelen	Heard Island
Pinnularia acidicola Van de Vijver & Le Cohu	X	X	X	X	X
Pinnularia acidicola var. *elongata* Van de Vijver & Le Cohu		X	X	X	X
Pinnularia acoricola Hustedt				X	X
Pinnularia alpiniformis Van de Vijver & Beyens			X		
Pinnularia amae Van de Vijver, Ledeganck & Beyens		X	X		
***Pinnularia amsterdamensis* Chattová, Van de Vijver & Metzeltin**	X				
Pinnularia angliciformis Van de Vijver & Beyens		X	X	X	X
***Pinnularia australogibba* Van de Vijver, Chattová & Metzeltin**	X				
***Pinnularia australogibba* var. subcapitata Van de Vijver, Chattová & Metzeltin**	X				
Pinnularia borealis s.l. Ehrenberg	X	X	X	X	X
Pinnularia bottnica Krammer	X	X	X	X	X
Pinnularia carteri Krammer		X	X	X	
Pinnularia crozetii Van de Vijver & Le Cohu		X	X	X	X
Pinnularia cuneorostrata (Manguin) Van de Vijver & Le Cohu		X	X	X	X
Pinnularia decrescens var. *kerguelensis* (Manguin) Van de Vijver & Le Cohu		X	X	X	X
Pinnularia cf. *divergentissima* Grunow	X	X	X	X	X
Pinnularia dulcicola (Manguin) Van de Vijver & Le Cohu		X	X	X	
Pinnularia extralonga Van de Vijver, Beyens & Le Cohu			X		
Pinnularia intermedia (Lagerstedt) Cleve		X		X	X
Pinnularia kerguelensis Germain		X		X	
Pinnularia kolbei Manguin		X	X	X	X
Pinnularia laperousei Van de Vijver & Beyens		X	X		
Pinnularia lecohui Van de Vijver			X	X	
***Pinnularia microcapitata* Van de Vijver, Chattová & Metzeltin**	X				
Pinnularia microstauron (Ehrenberg) Cleve	X	X	X	X	
Pinnularia microstauron var. *nonfasciata* Krammer		X	X		X
Pinnularia microstauron var. *rostrata* Krammer		X	X		
***Pinnularia myriamiae* Van de Vijver, Chattová & Metzeltin**	X				
Pinnularia neomajor Krammer			X		
Pinnularia obscura Krasske	X	X	X	X	X
Pinnularia cf. *obscuriformis* Krammer	X				
Pinnularia peracuminata Krammer			X		

Table 2 (continued).

	Ile Amsterdam	Prince Edward Islands	Crozet archipelago	Iles Kerguelen	Heard Island
Pinnularia perirorrata Krammer		X	X	X	X
Pinnularia perminor Kulikovskiy, Lange-Bertalot & Metzeltin	X	X	X	X	X
Pinnularia petersenii Krammer & Lange-Bertalot			X	X	X
Pinnularia pisciculus Ehrenberg		X	X		
***Pinnularia pseudohilseana* Van de Vijver, Chattová & Metzeltin**	X				
Pinnularia rabenhorstii (Grunow) Krammer		X	X	X	X
Pinnularia rabenhorstii var. *franconica* Krammer			X		
Pinnularia rabenhorstii var. *raphecurvata* Van de Vijver & Beyens		X	X	X	
Pinnularia rabenhorstii var. *subantarctica* Van de Vijver & Le Cohu		X	X	X	X
Pinnularia rhombarea var. *serrata* Van de Vijver & Beyens			X		
***Pinnularia robbrechtii* Van de Vijver**	X				
Pinnularia rupestris Hantzsch				X	
Pinnularia sagittiformis Van de Vijver & Beyens		X	X	X	X
Pinnularia schoenfelderi Krammer		X	X	X	X
Pinnularia silvatica Petersen		X			
Pinnularia similiformis Krammer		X		X	
Pinnularia sinistra Krammer	X				
Pinnularia sofiae Van de Vijver et al.		X			
Pinnularia subacoricola Metzeltin, Lange-Bertalot & García-Rodríguez	X				
Pinnularia subantarctica var. *elongata* (Manguin) Van de Vijver & Le Cohu		X	X	X	X
Pinnularia subantarctica var. *subantarctica* (Manguin) Van de Vijver & Le Cohu		X	X	X	X
Pinnularia subcommutata Krammer			X	X	
***Pinnularia subsinistra* Van de Vijver, Chattová & Metzeltin**	X				
***Pinnularia sylviae* Van de Vijver**	X				
Pinnularia thoenii Van de Vijver		X			
Pinnularia vatii Van de Vijver & Beyens		X	X		
***Pinnularia vlaminghii* Van de Vijver, Chattová & Metzeltin**	X				
Pinnularia viridiformis Krammer			X		
Pinnularia viridiformis var. *minor* Krammer			X	X	
***Pinnularia vixconspicua* Chattová, Van de Vijver & Metzeltin**	X				
***Pinnularia whinamiae* Van de Vijver**	X				
total number of *Pinnularia* species	22	35	40	32	23

habitats on the island. Endemic species on Ile Amsterdam are known in vascular plants (e.g. *Plantago stauntoni* Reichardt; Ronsted et al. 2002), in birds (the Amsterdam albatross *Diomedea amsterdamensis*; Roux et al. 1983, Jouventin & Roux 1983), in insects (Tréhen et al. 1990) and in diatoms (Van de Vijver et al. 2008 b). Recently, a new lichen species, *Caloplaca amsterdamensis* Aptroot & Ertz was described (Aptroot et al. 2011). This suggests that Ile Amsterdam and Ile Saint Paul are sufficiently old and isolated for a speciation to occur in several biological groups. On the other hand, no endemism was found among testate amoebae from Ile Amsterdam (Heger et al. 2009), but this is probably more the result of an uncertain and only poorly understood taxonomy than a real biogeographical fact.

It is clear that further research will be necessary to investigate if similar biogeographical conclusions can be drawn for the entire diatom flora present on the island. The present study was only intended to investigate the possible uniqueness of this island with regard to one genus.

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Paper IV

Morphological and taxonomical analysis of the terrestrial diatom genus *Humidophila* (Bacillariophyta) on Ile Amsterdam and Ile Saint-Paul (Southern Indian Ocean)

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(Phytotaxa in review)

Abstract

During a survey of the non-marine diatom flora of the volcanic islands, Ile Amsterdam and Ile Saint-Paul (southern Indian Ocean), seven species belonging to the terrestrial diatom genus *Humidophila* have been recorded. Apart from five previously known taxa (*Humidophila contenta*, *H. crozetikerguelensis*, *H. gallica*, *H. brekkaensis*, *H. vidalii)*, two taxa could not be identified based on the currently available literature and are described as new to science: *Humidophila amsterdamensis* sp. nov. and *Humidophila rouhaniana* sp. nov.

Detailed morphological descriptions of these taxa are given based on both light (LM) and scanning electron microscopy (SEM) observations. The morphological features of each taxon have been compared with similar species and notes on their ecology and associated diatom communities have been added.

Key words: Bacillariophyta, diatoms, *Humidophila*, new species, morphology, ecology

Introduction

The volcanic Islands Ile Amsterdam (77°30’E, 37°50’S) and Ile Saint Paul (77°31’ E, 38°43’S), forming a separate district within the Terres Australes et Antarctiques Françaises (TAAF), are among the most remote islands in the world, situated in the southern Indian Ocean, north of the sub-Antarctic islands, halfway between South Africa and Australia. Both islands are, geologically spoken, very young with the main part of Ile Amsterdam formed during the period 400-200 kyr BP. Ile Saint Paul is even younger (< 50 kyr) and still shows some volcanic activity in the form of hot ground and fumaroles (Giret 1987, Doucet et al. 2003).

Despite numerous taxonomic studies on sub-Antarctic non-marine diatoms (see Van de Vijver et al. 2002a and references therein), the freshwater and terrestrial diatom flora of Ile Amsterdam and Ile Saint Paul, is only poorly known. Apart from some older algal and diatom inventories such as Pierre & Noel (1971) and Van de Vijver & Beyens (1999) most data on the diatom flora of both islands were only recently acquired. In 2004, Van de Vijver et al. described one new *Stauroneis* (Ehrenberg 1843: 45) species (i.e. *Stauroneis bertrandii* Van de Vijver & Lange-Bertalot in Van de Vijver et al. 23) in a monography on the genus *Stauroneis* in the Arctic and Antarctic regions. In 2008, a paper describing three *Eunotia* Ehrenberg (1837: 44) species was published (Van de Vijver et al. 2008) followed by the description of a new genus in 2009: *Microfissurata* Lange-Bertalot, Cantonati & Van de Vijver (in Cantonati et al. 2009: 733) based on two new species of which one was found on Ile Amsterdam (i.e. *Microfissurata australis* Van de Vijver & Lange-Bertalot in Cantonati et al. 2009: 738). Several years later, 23 different *Pinnularia* Ehrenberg (1843: 45) taxa were observed during a taxonomic analysis of aquatic, moss and soil samples, of which twelve were described as new species (Van de Vijver et al. 2012). Special attention was further given to the different lava tube diatom communities that are present on the island. As a result of this, several unknown taxa were found and described as new for science (Van de Vijver & Cox 2013, Lowe et al. 2013).

Diatom analyses of Ile Saint Paul diatom flora are even more scarce due to its remoteness, the absence of waterbodies on the island and the limited number of diatom fieldwork done on this island. The only paper discussing its diatom flora dates already from 2002 when Van de Vijver et al. described a new *Luticola* D.G. Mann (in F.E. Round, R.M. Crawford & D.G. Mann 1990: 670) species, *Luticola beyensii* Van de Vijver, Ledeganck & Lebouvier (2002b: 236) from relatively dry soil samples (Van de Vijver et al. 2002b).

All results pointed to the presence of a very unique and mostly unknown diatom flora. The present paper reports on further diatom observations made in samples taken during field work on Ile Amsterdam and Ile Saint Paul in 1998, 1999 and 2007, especially within the genus *Humidophila* Lowe et al. (2014: 352), recently established to accommodate most taxa originally placed in the genus *Diadesmis* Kützing (1844: 109) (subgenus *Paradiadesmis* Lange-Bertalot & Le Cohu). *Humidophila* taxa are characterized in having small valve dimensions, rarely protracted apices and striae composed of one, usually transapically elongated, elliptical to ovoid areola, internally occluded by a porous hymen. The raphe is filiform with simple, always straight, drop-like or anchor-shaped, external proximal and distal endings (Lowe et al. 2014). Several taxa of this genus were observed and studied using detailed light and scanning electron microscopy observations, resulting in the description of two new taxa. For all taxa detailed morphological descriptions are provided and their ecology, biogeography and separation from similar taxa are discussed.

Material and Methods

Study site

Ile Amsterdam presents the shape of a small cone culminating at 881 m (Mont de la Dives). On Ile Saint Paul, the main crater is low (max. 256 m a.s.l.) opening on one side to the sea, forming thus a sheltered ocean bay. Both islands have a temperate oceanic climate (Lebouvier & Frenot 2007) with a mean annual temperature of 14.0°C. Relative humidity is high (> 80%) throughout the year due to the frequency of low cloud ceilings. Precipitation is usually high with an annual average of 1.114 mm distributed over more than 220 days at the meteorological station (Martin de Viviès, 27 m a.s.l.) with a dry period occurring in summer (ca. 70 mm in February). On Ile Amsterdam, permanent waterbodies are restricted to the higher plateau in the centre of the island (Caldeira, Plateau des Tourbières) and the W-SW part of the island (Falaises d'Entrecasteaux, Grandes Ravines). Almost all other areas do not have (semi-) permanent waterbodies due to the steepness of the slopes and the permeability of the lava tunnels, holes and fissures. Ile Saint Paul has no permanent waterbodies.

The vegetation on the islands is dominated by both endemic sub-Antarctic and introduced species. There are no trees on Ile Saint Paul, but patches of one native tree (*Phylica arborea* Thouars) can be found on Ile Amsterdam (Jolinon 1987, Frenot *et al.* 2001, Richardson et al. 2003). On the higher plateau, the vegetation has a typical sub-Antarctic outlook and consists of ferns, grasses, *Lycopodium* and mosses. *Sphagnum*, although absent from the other sub-Antarctic islands in the southern Indian Ocean, is omnipresent on the island, mainly on higher (=wetter) grounds above 400 m asl (Flatberg et al. 2011).

Sampling

During two short visits (1998 & 1999) and one fieldwork season on Ile Amsterdam and Ile Saint Paul in 2007 more than 200 samples have been collected from various habitats including waterbodies, soils and moss vegetation. Sampling locations were chosen in order to represent a maximum variability of habitat types. The samples were collected in PVC bottles and fixed with 3% formalin.

In order to determine the moisture content of the sample, the F-value, referring to the F-classification of Jung (1936) was selected as representative for moisture and used for each sample. It is a humidity scale based on water content as follow: FI = submerged mosses, FII = free floating mosses, FIII = very wet (water drips from the samples without pressure), FIV = wet (water drips with a slight pressure), FV = quasi-wet (water drips after moderate pressure), FVI = moist (little water produced after high pressure), FVII = quasi-dry (only a few drops of water can be squeezed out), FVIII = dry (contains no water).

Sample preparation

Samples were prepared for further analysis following the method described in Van der Werff (1955): small parts of the samples were cleaned by adding 37% H_2O_2 and heating to 80 °C for about 1 h. The reaction was completed by addition of an excessive amount of $KMnO_4$. Following digestion and centrifugation (three times 10 minutes at 3700 × g), cleaned material was diluted with distilled water to avoid excessive concentrations of diatom valves on the slides. Cleaned diatom valves were mounted in Naphrax®. Light microscopy (LM) observations were done using an Olympus BX53 microscope and Olympus UC30 Imaging System. Samples and slides are stored at the BR-collection, property of the Belgian federal government and given in permanent loan to the Botanic Garden Meise (Belgium). For scanning electron microscopy (SEM), parts of the oxidized suspensions were filtered through a 1 µm Isopore™ polycarbonate membrane filter (Merck Millipore). The stubs were sputter-coated with a Gold-Palladium layer of 20 nm and studied in a JEOL JSM-7100F SEM microscope at 5 kV (Botanic Garden Meise, Belgium). Diatom terminology follows Ross et al. (1979), Round et al. (1990) and Lowe et al. (2014). For the new taxa, the number of specimens measured on the type slide is indicated (n). The new species were compared with similar taxa from the Antarctic Region (Van de Vijver et al. 2002a, Kopalová et al. 2009, 2015), Europe (Lange-Bertalot & Genkal 1999, Lange-Bertalot & Werum 2001, Werum & Lange-Bertalot 2004), South America (Rumrich et al. 2000), Asia (Lowe et al. 2017) and New Caledonia (Moser et al. 1998).

Results

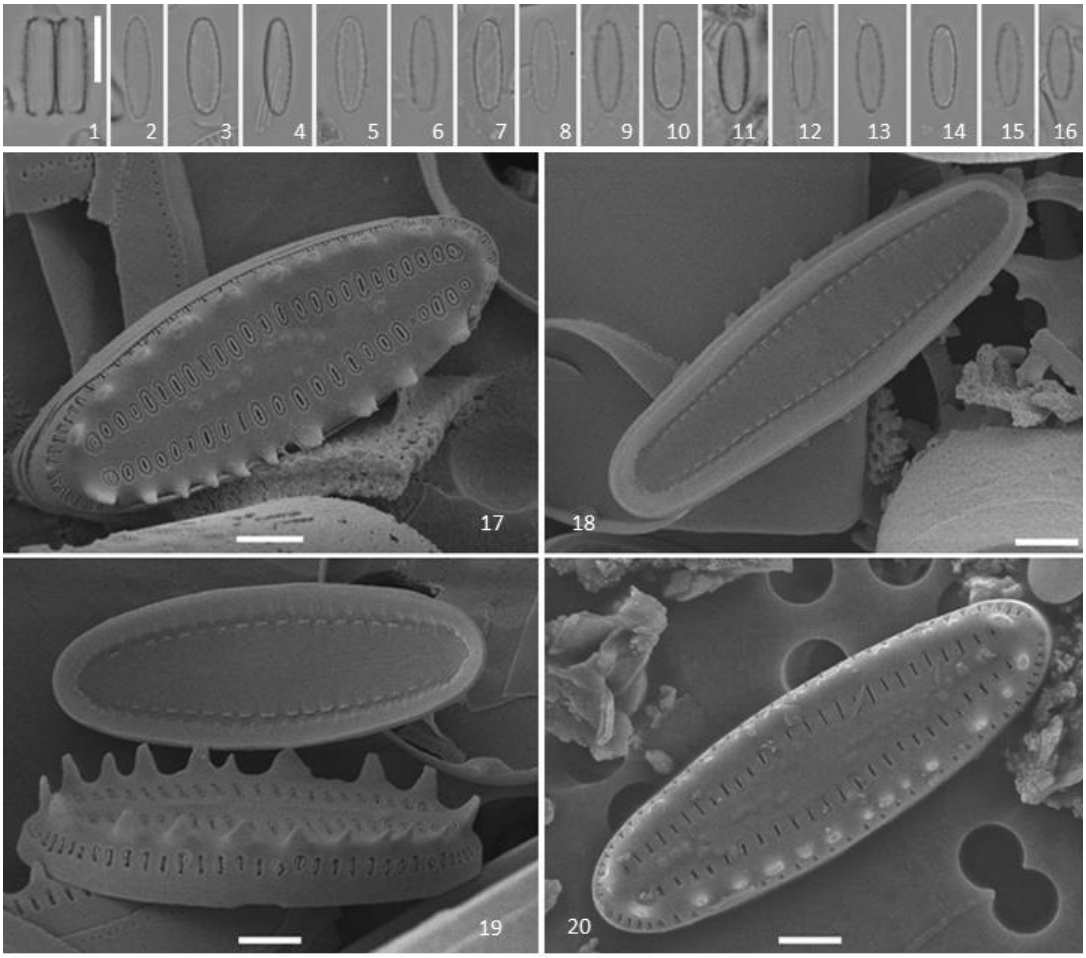
In total, seven different *Humidophila* taxa have been observed. Four of these had been previously identified: *Humidophila contenta* (Grunow in Van Heurck 1885: 109) R.L.Lowe et al. (2014: 357), *H. crozetikerguelensis* (Le Cohu & Van de Vijver 2002: 124) R.L.Lowe et al. (2014: 357), *H. vidalii* (Van de Vijver, Ledeganck & Beyens 2002c: 334) R.L.Lowe et al. (2014: 359), *H. brekkaensis* (Petersen 1928: 389) R.L.Lowe et al. (2014: 357) and *H. gallica* (W.Smith 1857: 11) R.L.Lowe et al. (2017: 281). The two remaining *Humidophila* species could not be identified using the available literature and are described as new species: *Humidophila amsterdamensis* sp. nov. and *H. rouhaniana* sp. nov.

Humidophila gallica (W.Smith) R.L.Lowe et al. (Figs 1–20)

Morphological observations: –Frustules rectangular in girdle view, usually forming long, bandlike colonies, connected by linking spines. Valves linear-elliptical with bluntly rounded, rarely subcapitate apices. Valve dimensions (n=25): length 8–11.5 µm, width

1.9–3.2 µm. Two contrasting valves morphologies observed. Most valves lacking a raphe system but showing well-developed marginal spines. Occasionally valves with a normally developed raphe system lacking marginal spines observed. Striae not discernible in LM, 34–42 in 10 µm, composed (SEM) of one large, transapically elongated areola.
The associated diatom community is composed of other *Humidophila* species (*Humidophila amsterdamensis*, *H. rouhaniana*, *H. vidalii*, *H. contenta*), *Eunotia paludosa*, *Achnanthes coarctata* (Brébisson ex W.Smith 1855: 8) Grunow in Cleve & Grunow (1880: 20), *Frustulia lebouvieri* and *Eunotia muscicola*.

Ecology and associated diatom flora: –*Humidophila gallica* is a cosmopolitan species, common in terrestrial biotopes such as bryophyte vegetations, wet to semi-dry rock faces, soils and in caves (Falasco et al. 2014, 2015, Lowe et al. 2017). On Ile Amsterdam, this species was abundantly present in lava tubes, accompanied by other *Humidophila* species (mainly *H. vidalii* and *H. contenta*), *Rhopalodia rupestris* (W.Smith 1853: 14) Krammer in Lange-Bertalot & Krammer (1987: 86) and *Orthoseira roeseana* (Rabenhorst 1848-1860: 383) O'Meara (1875: 255).

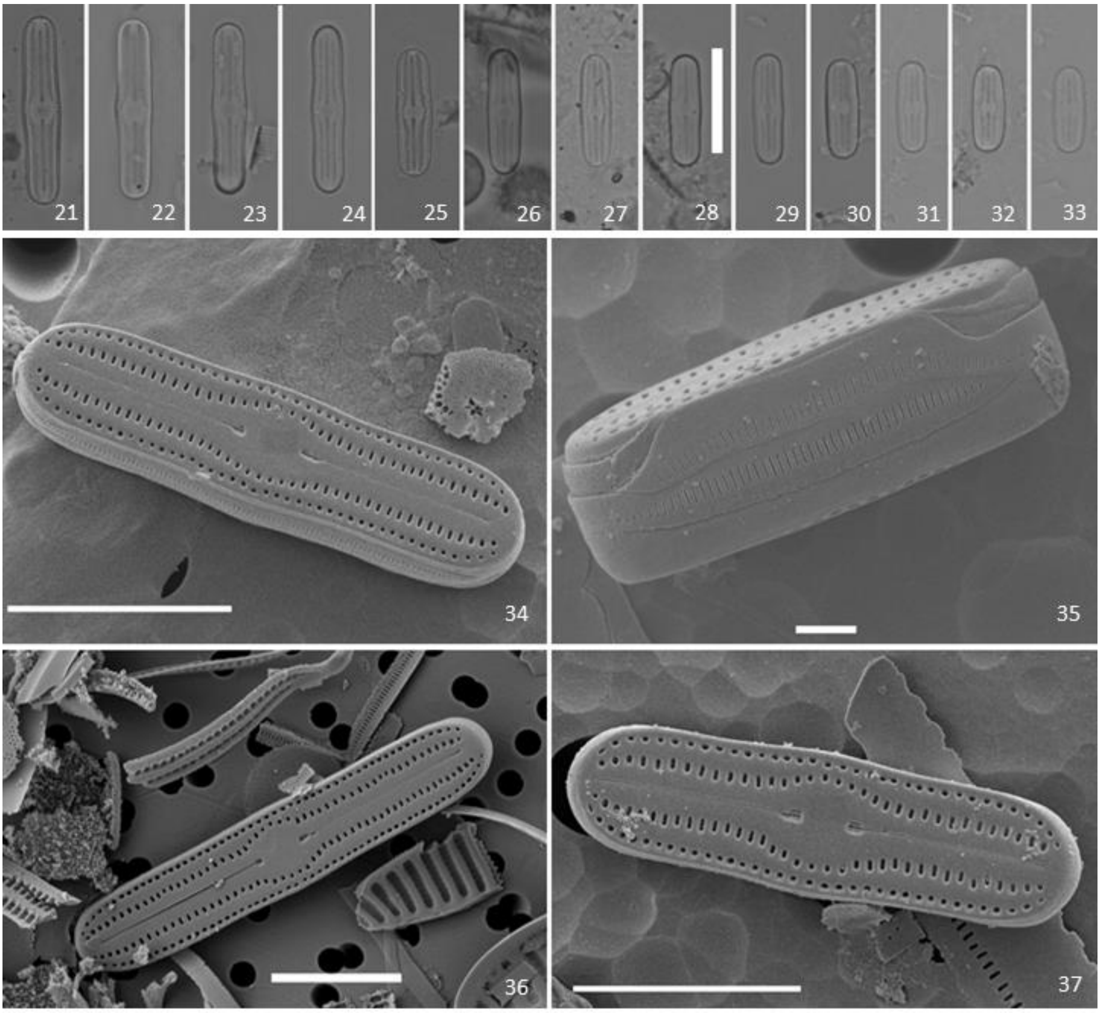


FIGURES 1–20**.** *Humidophila gallica* (W.Smith) R.L. Lowe et al.
Light (LM) and scanning electron micrographs (SEM). 1. LM of a girdle view of two frustules, connected by linking spines. 2–16. LM of valve face views. 17. SEM of an entire valve (externally). 18. SEM valve (internally). 19. SEM valve (internally) and SEM of a valve with marginal spines (externally). 20. SEM of an entire valve (externally). LM scale bar = 10 µm. SEM scale bars = 1 µm.

***Humidophila brekkaensis* (Petersen) R.L. Lowe et al. (Figs 21–37)**

Morphological observations: –Valves linear, with a slightly gibbous central part, convex margins and bluntly rounded apices. Valve dimensions (n=20): length 7.5–18.0 µm, width 3.0–4.5 µm. Raphe filiform, straight with simple straight proximal and distal endings. Striae parallel throughout the entire valve, 28–33 in 10 µm, easy to resolve even with light microscope. In SEM, striae composed of one transapically elongated areola. In contrast to other *Humidophila* species, mantle areolae not separated from the valve face by an edge but positioned on the same level as the areolae of the valve face.

Ecology and associated diatom flora: –Most *H. brekkaensis* valves have been found in moss samples, almost exclusively taken from the driest mosses (*Campylopus* Brid.) (F-value: VIII) or on liverworts, usually associated with *Eunotia paludosa* Grunow (1862: 22), *Frustulia lebouvieri* Van de Vijver & Gremmen (2006: 435), *Pinnularia microstauron* (Ehrenberg 1843b, pl. 1/4, fig. 1) Cleve (1891: 28), *Luticola beyensii* and other *Humidophila* species.



FIGURES 21–37. *Humidophila brekkaensis* (Petersen) R.L.Lowe et al.
Light (LM) and scanning electron micrographs (SEM). 21–33. LM of valve views. 34. SEM of an entire valve (externally). 35. SEM girdle view. 36–37. SEM of an entire valve (externally).
Note the mantle areolae positioned on the same level as the areolae of the valve face. LM scale bar = 10 µm. SEM scale bars = 5 µm, 1 µm for the SEM girdle view.

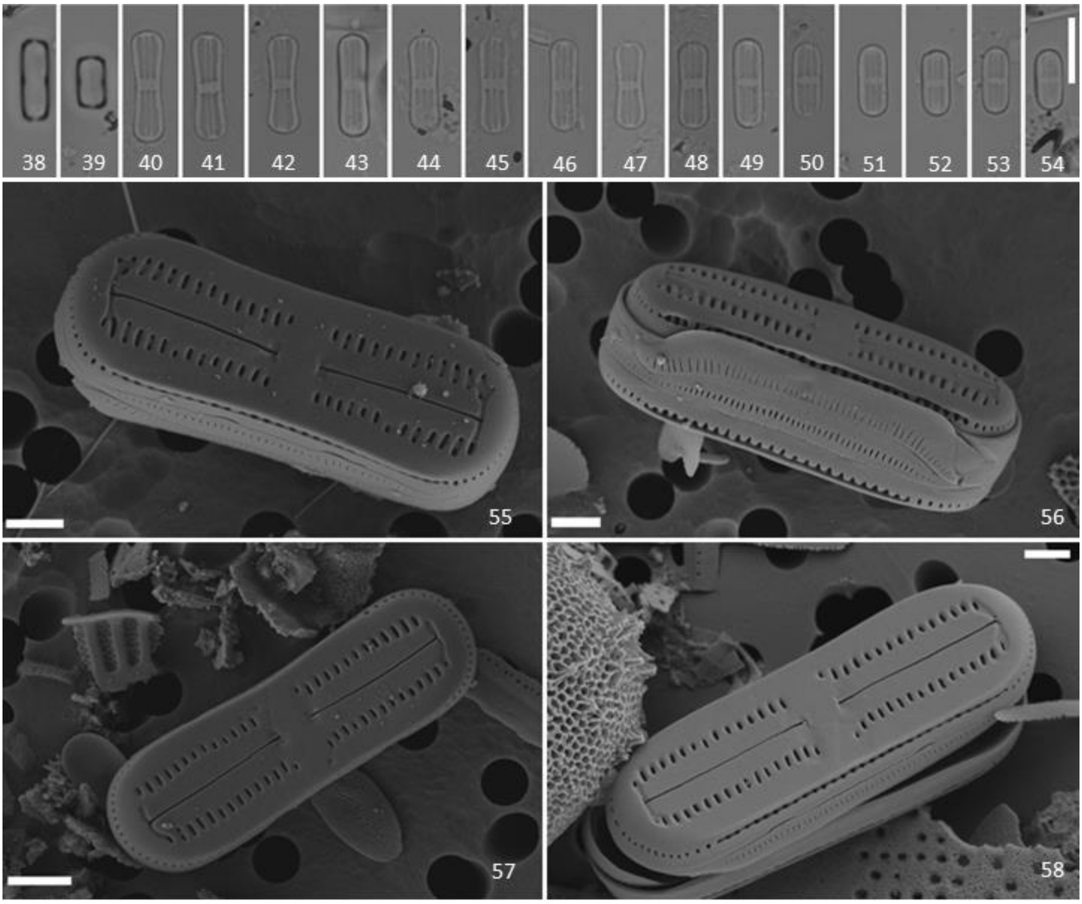
***Humidophila contenta* (Grunow) R.L. Lowe et al. (Figs 38–58)**

Morphological observations: –Valves linear to elliptical with slightly concave margins and broadly rounded, never (sub-)capitate ends. Valve dimensions (n=25): length 6.1–11.6

µm, width 2.1–2.9 µm. Axial area narrow, linear. Central fascia clearly present, extending from the central nodule to the valve margins. Raphe filiform, straight with distinct T-shaped central and terminal endings. Transapical striae parallel, interrupted centrally, almost not discernible in LM, 34–49 striae in 10 µm.

***Taxonomical remarks**: –Humidophila contenta* is quite similar to *Humidophila paracontenta* (Lange-Bertalot & Werum in Lange-Bertalot & Genkal 1999: 41) Lowe et al. (2014: 358), described from freshwater in Siberia, but differs in stria density and raphe structure. *H. paracontenta* typically shows 27–30 striae in 10 µm whereas *H. contenta* usually has more than 35 striae (Van de Vijver et al. 2002a). The proximal and distal raphe endings in *H. contenta* typically shows small depressions next to the raphe pores whereas these depressions seem to be absent in *H. paracontenta* (see Werum & Lange-Bertalot 2004, plate 65).

Ecology and associated diatom flora: – *Humidophila contenta* is one of the few cosmopolitan species of this genus. It has been reported worldwide in soils, subaerial habitats, in small bodies of oligotrophic acidic water and in biotopes with greatly reduced light intensity (Werum & Lange-Bertalot 2004, Poulíčková & Hašler 2007). On Ile Amsterdam and Ile Saint Paul *H. contenta* has been found living on moss species of the genus *Anthoceros* L., *Brachythecium* Schimp. and *Sphagnum* L. showing a specific moisture value ranging from F-V to F-VII, and in soils, usually accompanied by *Humidophila vidalii, H. amsterdamensis* sp.nov., *Eunotia muscicola* Krasske (1939: 366), *Pinnularia borealis* Ehrenberg (1843b: 420) s.l., *Pinnularia perminor* Kulikovskiy, Lange-Bertalot & Metzeltin (2010: 359), *Luticola beyensii* and *Tryblionella debilis* Arnott ex O'Meara (1873: 310).

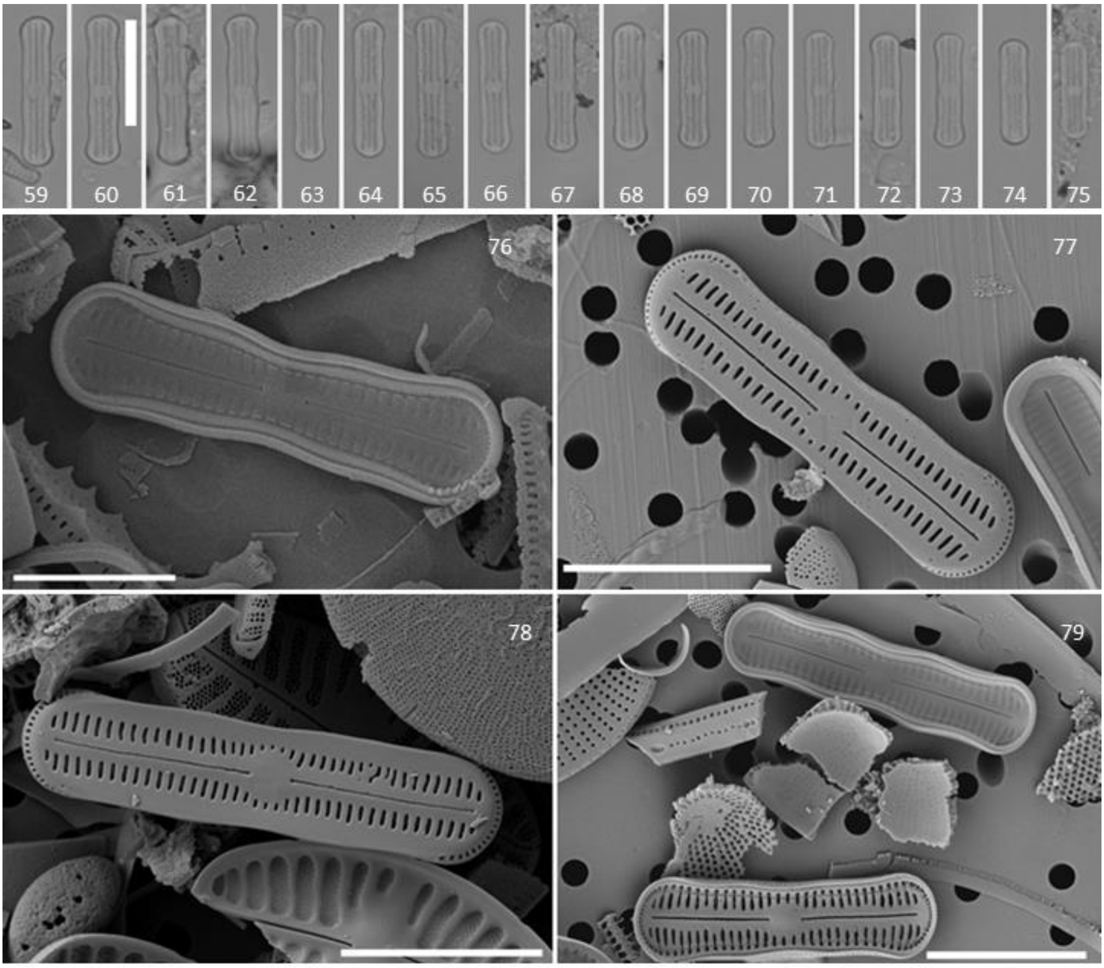


FIGURES 38–58. *Humidophila contenta* (Grunow) R.L.Lowe et al.
Light (LM) and scanning electron micrographs (SEM). 38–39. LM of a girdle view. 40–54. LM of valve views showing variation in size. 55. SEM of an entire valve (externally). 56. SEM of a girdle view. 57–58. SEM of an entire valve (externally). Note the proximal and distal raphe endings showing small depressions next to the raphe pores. LM scale bar = 10 µm. SEM scale bars = 1 µm.

***Humidophila crozetikerguelensis* (Le Cohu & Van de Vijver) R.L.Lowe et al. (Figs 59–79)**

Morphological observations: – Valves linear with strongly undulating margins and broadly rounded subcapitate apices. Valve dimensions (n=20): length 11.2–14.9 µm, width 2–3.2 µm. Width of the apices never extending beyond the valve undulations. Axial area well-defined, linear. Central area widened, generally bordered by 3 striae. Raphe straight filiform with only slightly marked endings. Distal raphe endings terminating near the last striae. Striae slightly radiate in the middle, becoming more convergent towards the apices, 32–34 in 10 µm.

Ecology and associated diatom flora: *–Humidophila crozetikerguelensis,* originally described from Kerguelen, is quite common on Ile Amsterdam, present on both wet and terrestrial mosses with a wide F-value range of II-VII, and occasionally on wet mosses and soils on Ile Saint Paul.



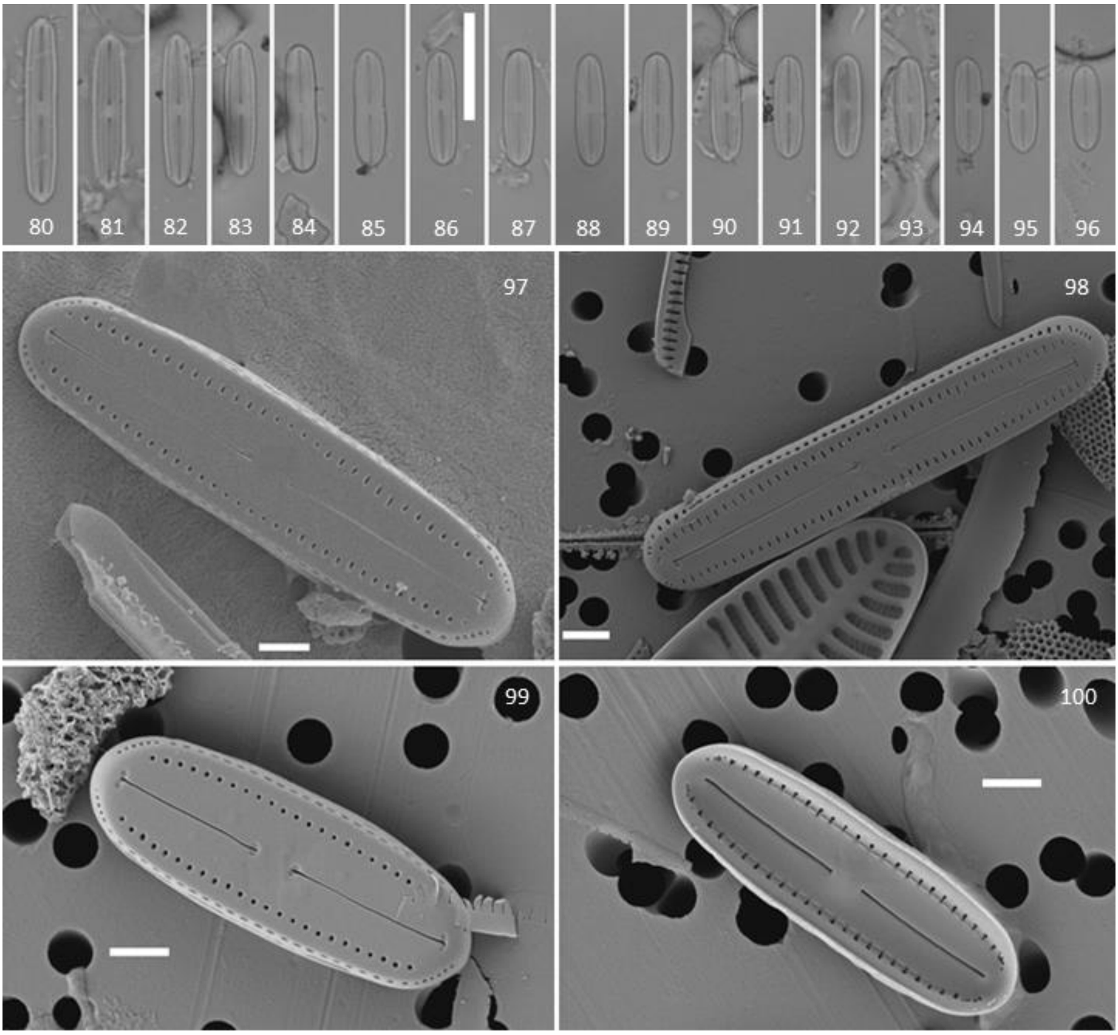
FIGURES 59–79. *Humidophila crozetikerguelensis* (Le Cohu & Van de Vijver) R.L.Lowe et al. Light (LM) and scanning electron micrographs (SEM). 59–75. LM of valve views.

76. SEM of internal valve view. 77–78. SEM of an entire valve (externally). 79. SEM of internal valve view. LM scale bar = 10 µm. SEM scale bars = 5 µm.

Humidophila vidalii (Van de Vijver, Ledeganck & Beyens) R.L.Lowe et al. (Figs 80–100)

Morphological observations: –Valves always linear with broadly rounded, never protracted apices. Larger valves with clear concave margins. Valve dimensions (n=30): length 7.2–17.6 µm, width 2–3.5 µm. Axial area linear, broad, slightly narrowing towards the poles. Central area absent. Raphe straight, filiform with clearly depressed distal and proximal raphe pores. Occasionally, T-shaped endings present. Striae composed of very short, almost rounded areolae, located close to the valve margins, 33–36 in 10 µm. Areolae on the mantle equidistant, more closely together towards the poles.

Ecology and associated diatom flora: –The species seems to have an overall preference for wet to quasi-dry terrestrial bryophytes especially in the areas of Grand Tunnel, Jardin Météo and Del Cano. The samples are quite often dominated by *Humidophila crozetikerguelensis*, *H. amsterdamensis*, *Eunotia paludosa*, *Sellaphora barae* Van de Vijver & E.J.Cox (2013: 40), *Orthoseira verleyenii* Van de Vijver (in Lowe et al. 2013: 41), *Mayamaea cavernicola* Van de Vijver & E.J.Cox (2013: 40), an at present unidentified *Nitzschia* Hassall (1845: 435) species and a centric diatom species belonging at present to an undescribed new genus (Van de Vijver et al., unpubl. data), closely related to *Melosira* C.Agardh (1824: 14).



FIGURES. 80–100. *Humidophila vidalii* (Van de Vijver, Ledeganck & Beyens) R.L.Lowe et al. Light (LM) and scanning electron micrographs (SEM). 80–96. LM of valve views. 97–99. SEM of an entire valve (externally). 100. SEM of internal valve view. Note the missing central area. LM scale bar = 10 µm. SEM scale bars = 1 µm.

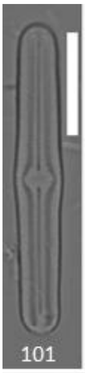
***Humidophila amsterdamensis* Chattová &Van de Vijver sp. nov. (Figs 101–121)**

Light microscopy (Figs 101–115): Frustules rectangular in girdle view. Valves linear with gibbous central part and broadly rounded, non-protracted apices. Valve dimensions (n = 50): length 13.5–32.5 µm, width 3–5.5 µm. Axial area linear, fairly wide. Central area round, slightly widened due to the shortening of the central striae, never forming a fascia. Raphe filiform, straight with simple straight proximal and distal endings. Striae parallel throughout the entire valve, not interrupted in the middle. SEM (Figs 116–121): Striae parallel, composed of one short, transapically elongated areola, not interrupted near the proximal raphe pores, but curving convexly around the central nodule, 31–32 in 10 μm. In smaller specimens, striae near the apices terminating at the same level as the distal raphe endings. In larger specimens striae terminating beyond the distal raphe endings. Raphe filiform with weakly expanded proximal and straight distal pores. Mantle areolae enlarged, positioned in a longitudinal groove running from one apex to the other. Grooves disappearing near the apices, revealing areolae on the mantle. Mantle areolae becoming smaller and rounded near the apices, continuing around the apices usually without or with a small interruption. External raphe branches straight with simple proximal endings. T-shaped distal and proximal never observed. Distal raphe endings short, terminating on the valve face, well before the apices, never exceeding on the valve mantle. Internally, areolae appearing much larger than externally, occluded by porous hymens. Well-developed central nodule present. Internal raphe endings straight with distal endings terminating on very weakly developed helictoglossae. Girdle composed of three open copulae, perforated by two rows of very small rounded poroids. Poroids in the second row more widely spaced.

Type:– ILE AMSTERDAM, TAAF sample AMS-M035, B. Van de Vijver, 4 December 2007 (holotype: BR! slide no. 4488; isotype: PLP! slide no. 326, University of Antwerp, Belgium).

Etymology: –The specific epithet refers to the Ile Amsterdam, the island where the new species is described from.

Ecology and associated diatom flora: – *Humidophila amsterdamensis* was found in a sample taken from semi-dry mosses with F-value VI, taken from a small cave bog-pond with a pH of 6.1 and a conductivity value of 220 μS cm^{-1}. The sample was dominated by *Eunotia lecohui* Van de Vijver (in Van de Vijver et al. 2008: 117), *Chamaepinnularia aerophila* Van de Vijver & Beyens (in Van de Vijver et al. 2002a: 26), *Microfissurata australis* Van de Vijver & Lange-Bertalot, *Orthoseira verleyenii* and *Pinnularia* *amsterdamensis* Chattová et al. (in Van de Vijver et al. 2012: 217). So far, the species was not observed on Ile Saint Paul.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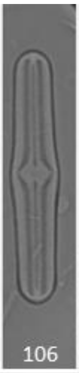
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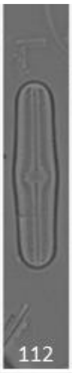
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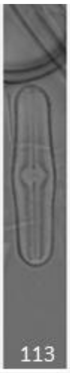
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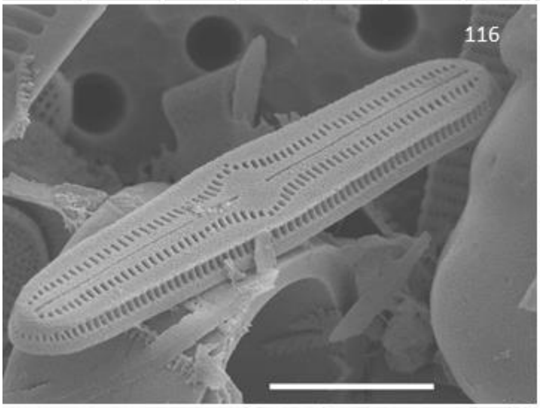
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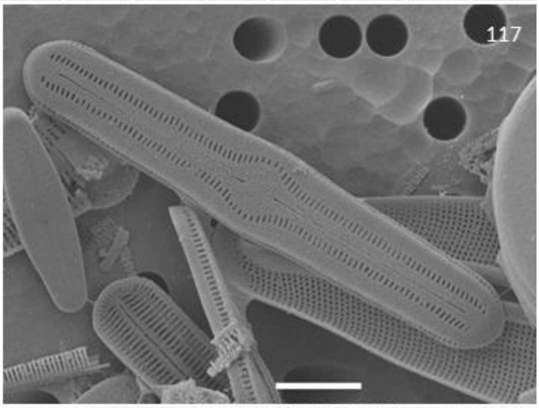
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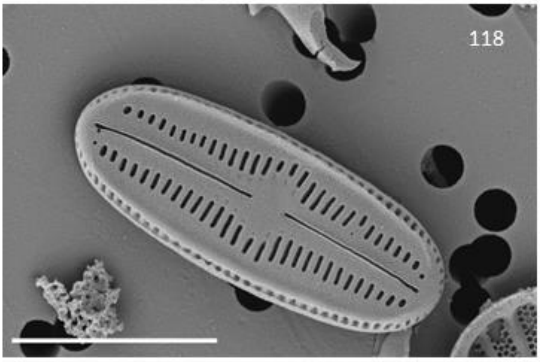
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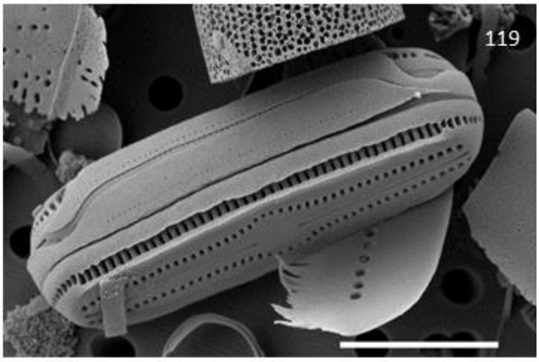
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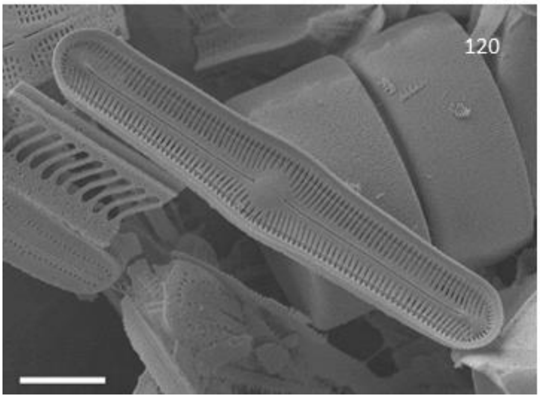
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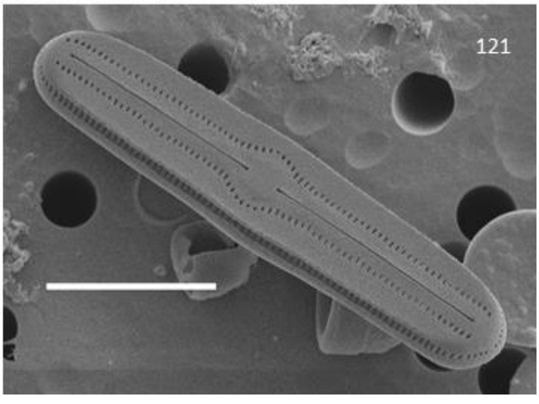
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FIGURES 101–121. *Humidophila amsterdamensis* Chattová &Van de Vijver sp. nov. Light (LM) and scanning electron micrographs (SEM). 101–115. LM of valve views of the type population from Ile Amsterdam. 116–118. SEM of an entire valve (externally). 119. SEM of a girdle view. 120. SEM of internal valve view. 121. SEM of an entire valve (externally). LM scale bar = 10 µm. SEM scale bars = 5 µm.

Humidophila rouhaniana **Chattová & Van de Vijver sp. nov. (Figs 122–144)**

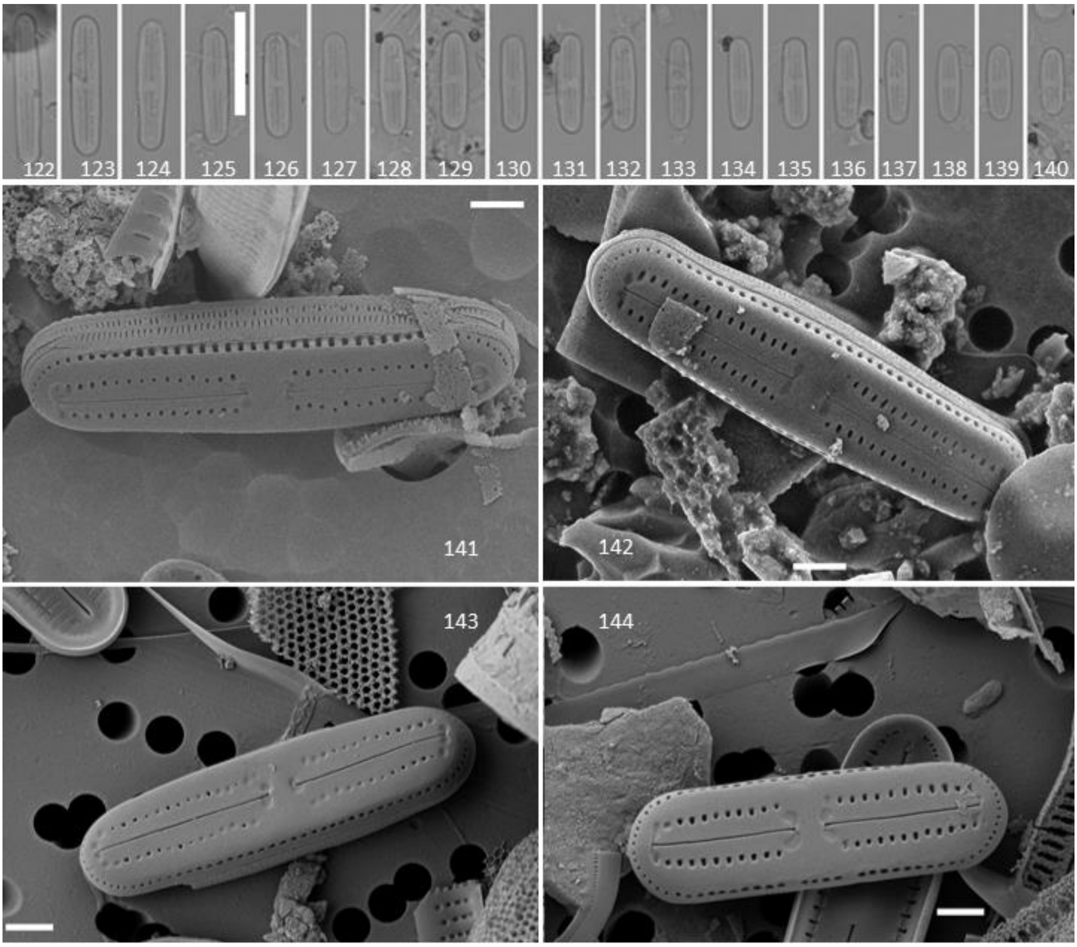
Light microscopy (Figs 122–140): Frustules rectangular in girdle view. Valves linear with almost parallel to sometimes even slightly asymmetrical margins and broadly rounded apices. Smaller specimens occasionally with a more linear–elliptic valve outline. Valve dimensions (n = 50): length 7.4–15.7 µm, width 1.7–3.1 µm. Axial area linear, rather broad, slightly narrowing towards the poles. Raphe filiform, straight. Central area stauroform, reaching the valve margins. Transapical striae not discernible in LM, interrupted centrally. SEM (Figs 140–144)*:* Striae composed of one transapically weakly elongated, near apices almost rounded areola, ca. 45 in 10 µm. At the apices, striae usually terminating near the distal raphe endings, sometimes beyond the distal raphe endings. Mantle areolae continuing around the apices. External raphe branches straight with clearly depressed proximal and distal pores with distinct bow-tie endings. Internal structure not observed. Valve face and mantle areolae separated by a narrow longitudinal groove. Girdle composed of three copulae, perforated by a single row of elongated, slit-like pores.

Type:– ILE AMSTERDAM, TAAF sample AMS-M201, B. Van de Vijver, 15 December 2007 (holotype: BR! slide no. 4489; isotype: PLP! slide no. 327, University of Antwerp, Belgium).

Etymology: The new species is named after Dr. Germinal Rouhan (Muséum National d’Histoire Naturelle, Paris, France) to thank him for the wonderful joint field work on Ile Amsterdam in November-December 2016.

Ecology and associated diatom flora: –The type population of *Humidophila rouhaniana* was found in an almost dry moss sample (F-value VII) taken from the Jardin Météo on the vicinity of the base Martin-de-Viviès. The associated community is composed of several

Humidophila species (such as *H. amsterdamensis* and *H. vidalii*), *Halamphora dagmarobbelsiana* Van de Vijver & Levkov (in Van de Vijver et al. 2014: 384), *Chamaepinnularia aerophila* and an at present unidentified *Nitzschia* species.



FIGURES 122–144. *Humidophila rouhaniana* Chattová & Van de Vijver sp. nov.
Light (LM) and scanning electron micrographs (SEM). 122–140. LM of valve views of the type population from Ile Amsterdam. 141–144. SEM of external valve view showing the stauroform central area and the raphe with depressed proximal and distal pores with distinct bow-tie endings. LM scale bar = 10 µm. SEM scale bars = 1 µm.

Discussion

The main objective of this study was to revise the diversity of the terrestrial diatom genus *Humidophila* on two sub-Antarctic Islands, based on a modern morphological concept. The study resulted in the description of two new taxa whose identification was based on detailed LM and SEM microscopical research. The genus *Humidophila* shows a strong preference for wet or semi-dry terrestrial habitats such as wet soils, moss vegetation, moist rock faces or cave habitats. The high diversity is probably related to the greater diversity in aerophilic microhabitats on both islands, where water sources are limited. *Humidophila* are presented worldwide, with a large number of presumably endemic taxa restricted only to the (sub)-Antarctic region. It has been clear for some time now that cosmopolitan diatom species are not the rule and that a considerable degree of endemism is apparent (Vanormelingen et al. 2008). In the past, the degree of endemism was probably masked by the historic "force-fitting" (Tyler 1996) of European names to (sub)-Antarctic species. Recently, the entire sub-Antarctic diatom flora is being revised using a more fine-grained taxonomy based on a better analysis and interpretation of the morphological observations. This led to the description of a large number of new species (Van de Vijver et al. 2002a, Van de Vijver et al. 2004), some of them, especially within the genera *Eunotia, Pinnularia, Sellaphora, Halamphora,* being described directly from Ile Amsterdam (Van de Vijver et al. 2008, 2012, Van de Vijver & Cox. 2013, Van de Vijver et al. 2014) and *Luticola* from Ile Saint Paul (Van de Vijver et al. 2002b). The description of two new *Humidophila* taxa from Ile Amsterdam follows the previous descriptions of 8 *Humidophila* (former *Diadesmis*) species from the sub-Antarctic region (Le Cohu & Van de Vijver 2002, Van de Vijver et al. 2002c). The high number of newly described taxa is not surprising, considering the fact that the islands are geographically very isolated and have a volcanic origin which favours a high level of speciation. Similar results were found for other islands at the same latitude. A new aerophilic *Orthoseira* species was described from Gough Island (Van de Vijver & Kopalová 2008), whereas on Ile de la Possession (Crozet Archipelago) almost 25% of the species were described as new (Van de Vijver et al. 2002a).

A comparison of the new species with morphologically similar species shows marked differences. *Humidophila amsterdamensis* bears some similarities with *Humidophila* *australoshetlandica* Kopalová et al. (in Kopalová et al. 2015: 121), but the former is much larger with a more gibbous central valve part. Additional morphological differences can be observed in the ultrastructure. *Humidophila australoshetlandica* shows a much shorter groove on the mantle in which the mantle areolae are placed. The mantle areolae always continue entirely around the apices in *H. australoshetlandica* contrary to the usually interrupted areolae near the apices of *H. amsterdamensis*. The girdle bands of *H. amsterdamensis* show a double row of poroids, lacking in *H. australoshetlandica*. Another comparable taxon is *Humidophila arcuata* (Heiden in Heiden & Kolbe 1928: 628) R.L.Lowe et al. (2014: 357). *H. amsterdamensis* can be separated from *H. arcuata* by its valve outline lacking the gibbous protracted apices and the typical narrow ridge that surrounds the raphe in *H. arcuata*. Transapical striae are slightly radiate to convergent near the apices in *H. arcuata* but always parallel in *H. amsterdamensis*. The axial area in *H. arcuata* is also convergent near the apices, in the contrary to the linear axial area in *H. amsterdamensis.*

The smaller forms of *H. amsterdamensis* were in previous studies (Chattová et. al 2014) reported as *Diadesmis subantarctica* Le Cohu & Van de Vijver (2002: 128), (now *Humidophila subantarctica* (Le Cohu & Van de Vijver 2002: 128) R.L.Lowe et al. (2014: 359), a sub-Antarctic taxon described from other islands in the southern Indian Ocean such as Iles Kerguelen and Ile de la Possession, which seems to be missing on Ile Amsterdam and Ile Saint Paul. *H. subantarctica* has a different valve outline, being more elliptical, shorter and narrower, with a different shape of the central area which is wider than longer.

Based on valve outline, *Humidophila rouhaniana* closely resembles *H. vidalii*, described from Ile de la Possession (Crozet Archipelago) in the southern Indian Ocean. However, both taxa can be easily separated based on the different central area and on the structure of the areolae. *Humidophila rouhaniana* always has a clear stauroform central area, never present in *H. vidalii*. Transapical striae in case of *H. rouhaniana* are interrupted centrally, unlike *H. vidalii* whose areolae are uninterrupted. Moreover in *H. rouhaniana*, the mantle areolae entirely surround the apices, whereas in *H. vidalii* the mantle areolae are interrupted. The new species can also be separated from another taxon with a fascia, *H. contenta*, by the valve shape. *H. contenta* has more elliptical valves with concave margins in the contrary to the linear shape of *H. rouhaniana*. *Humidophila contenta* has centrally constricted valve margins, whereas constricted valves have never been observed in *H. rouhaniana*.

Conclusions

It is clear that based on the LM and SEM observations, the description of both new taxa is justified. These results prove again the high specificity of the sub-Antarctic diatom flora and are valuable for understanding the biodiversity and biogeography of the sub-Antarctic diatoms. Additionally, more thorough research of Ile Amsterdam and Ile Saint Paul is underway, which may result in the description of many more new taxa. The results will be further used in another taxonomical, ecological and planned paleo-ecological studies.

Acknowledgements

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Paper V

The genus *Luticola* (Bacillariophyta) on Ile Amsterdam and Ile Saint-Paul (Southern Indian Ocean) with the description of two new species.

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Running title: The genus *Luticola* on Ile Amsterdam and Ile Saint-Paul

(EJT, submitted)

Abstract

Five species of the terrestrial diatom genus *Luticola* were found during a taxonomic survey of two small volcanic islands, Ile Amsterdam and Ile Saint-Paul (Southern Indian Ocean). Apart from the 2 already known *Luticola* species *Luticola beyensii* Van de Vijver *et al.* and *Luticola subcrozetensis* Van de Vijver *et al.*, two new species are described: *Luticola ivetaiana* Chattová & Van de Vijver sp. nov. and *Luticola vancampiana* Chattová & Van de Vijver sp. nov. Finally, one, up to now unknown, *Luticola* species is briefly discussed and illustrated. Detailed morphological descriptions of these taxa are provided based on both light and scanning electron microscopy observations. Morphological features of the new species are compared to morphologically similar taxa, and notes on their ecology and biogeography are added.

Key words: Bacillariophyta, diatoms, *Luticola*, new species, morphology

Introduction

The genus *Luticola* D.G.Mann is one of the dominant genera in the Antarctic terrestrial diatom flora. *Luticola* taxa can be distinguished in having uniseriate striae, composed of rounded to transapically elongated areolae covered internally by perforated hymenes, a usually distinct isolated pore in the central area, a longitudinal canal positioned within the valve wall and by a simple, filiform raphe with variable raphe endings (Round *et al.* 1990, Levkov *et al.* 2013). However, the correct taxonomy and biogeography of this genus in the (sub)-Antarctic region was hampered due to species drift and force fitting the Antarctic species into European and North American names (Tyler 1996). Due to the lack of appropriate literature, the first studies mainly reported typical cosmopolitan taxa such as *L. cohnii* (Hilse) D.G.Mann (in Round *et al.* 1990) or *L. nivalis* (Ehrenberg) D.G.Mann (in Round *et al.* 1990) and taxa described in the early 20th century such as *Luticola gaussii* (Heiden) D.G.Mann (in Round *et al.* 1990) and *Luticola suecorum* (G.W.F.Carlson) Van de Vijver (Van de Vijver & Mataloni 2008). Moreover, *Luticola muticopsis* (Van Heurck) D.G. Mann (in Round *et al.* 1990) was used as a catch-all taxon for all capitate *Luticola* specimens, while the non-capitate forms were usually force-fitted into *L. mutica* (Kützing) D.G.Mann (in Round *et al.* 1990). This resulted into stretched biogeographical distributions of those species, making them the most widespread in the entire Antarctic Region.

Recently, all (sub)-Antarctic *Luticola* species have been the subject of a thorough taxonomic and morphologic revision, in order to unravel the correct diversity of this genus. This resulted in the description of more than 25 new Antarctic *Luticola* taxa, mainly from the Maritime Antarctic Region and the Antarctic Continent (Van de Vijver *et al.* 2006, 2011, Kopalová *et al.* 2011, Levkov *et al.* 2013, Zidarova *et al.* 2014, Kohler *et al.* 2015). Several new taxa were also found in the sub-Antarctic region. In 2002, *Luticola beyensii* Van de Vijver *et al.* (Van de Vijver *et al.* 2002b) was described from Ile Saint-Paul, whereas *L. ledeganckii* Van de Vijver (Van de Vijver *et al.* 2002a), *L. robusta* Van de Vijver *et al.* (Van de Vijver *et al.* 2002a), *L. crozetensis* Van de Vijver *et al.* (in Levkov *et al.* 2013), *L. ipevii* Van de Vijver & Levkov (in Levkov *et al.* 2013), and *L. subcrozetensis* Van de Vijver *et al.* (in Levkov *et al.* 2013), were described from Ile de la Possession, the main island of the Crozet Archipelago.

The present paper continues this revision of the genus *Luticola* with an analysis of 5 taxa observed on Ile Amsterdam and Ile Saint-Paul, two islands in the southern Indian Ocean. Two *Luticola* taxa are described as new based on detailed light and scanning electron microscopy whereas a fifth unidentified taxon could only be found in LM and is illustrated and discussed but due to the lack of sufficient observations, it is still unclear whether it also represents a new species.

Material and Methods

Sampling

During two short visits (1998 & 1999) and two fieldwork seasons on the volcanic islands Ile Amsterdam (77°30'E, 37°50'S) and Ile Saint-Paul (77°31' E, 38°43'S) in 2007 and 2016, more than 300 samples were collected from various habitats including waterbodies, soils and moss vegetations. Both islands are among the most remote islands in the world, situated in the southern Indian Ocean, north of the sub-Antarctic islands, halfway between South Africa and Australia, and form a separate district within the Terres Australes et Antarctiques Françaises (TAAF). In geological terms, these lands are very young, with the main part of Ile Amsterdam formed during the period 400-200 kyr BP and Ile Saint-Paul being even younger (< 50 kyr). More information regarding climate, vegetation and geology can be found in Lebouvier & Frenot (2007).

Sampling sites were chosen in order to represent a maximum diversity of habitat types. The samples were collected in PVC bottles and fixed with 3% formalin. In order to determine the moisture content of the sample, the F-value, referring to the F-classification of Jung (1936) was selected as representative for moisture and used for each sample. It is a humidity scale based on water content as follow: FI = submerged mosses, FII = free floating mosses, FIII = very wet (water drips from the samples without pressure), FIV = wet (water drips with a slight pressure), FV = quasi-wet (water drips after moderate pressure), FVI = moist (little water produced after high pressure), FVII = quasi-dry (only a few drops of water can be squeezed out), FVIII = dry (contains no water).

Samples were prepared for microscopy analysis following the method described in Van der Werff (1955): small parts of the samples were cleaned by adding 37% H_2O_2 and heating to

80 °C for about 1 h. The reaction was completed by addition of an excessive amount of $KMnO_4$. Following digestion and centrifugation (three times 10 minutes at 3700 × g), cleaned material was diluted with distilled water to avoid excessive concentrations of diatom valves on the slides. Cleaned diatom valves were mounted in Naphrax®. Light microscopy (LM) observations were done at Olympus BX53 microscopes, equipped with Differential Interference Contrast (Nomarski) optics. LM micrographs were taken using Olympus UC30 camera connected to the Cell Sense Standard program. Samples and slides are stored at the BR-collection (Botanic Garden Meise, Belgium). For scanning electron microscopy (SEM), parts of the oxidized suspensions were filtered through a 1 µm Isopore™ polycarbonate membrane filter (Merck Millipore). The stubs were sputter-coated with a Platinum layer of 2 nm and studied in a JEOL JSM-7100F SEM microscope at 1 kV (Botanic Garden Meise, Belgium).

Morphological terminology follows Round *et al.* (1990), Van de Vijver & Mataloni (2008) and Levkov *et al.* (2013). The morphology of the new species is discussed based on detailed light and scanning electron microscopy observations and has been compared with known *Luticola* species using the most current literature: Rumrich *et al.* (2000), Van de Vijver & Mataloni (2008), Kopalová *et al.* (2011), Van de Vijver *et al.* (2011), Levkov *et al.* (2013), Zidarova *et al.* (2014) and Kohler *et al.* (2015).

For the typification of the new species, we chose to use the entire slide as the holotype. Diatoms show a broad variability along their cell cycle making the choice for the entire population on the slide more obvious.

Results

Five *Luticola* taxa were found in the samples during the survey. Two taxa, *Luticola beyensii* and *L. subcrozetensis* could be identified using the currently available literature. Based on a morphological analysis, two taxa are described as new species: *Luticola ivetaiana* Chattová & Van de Vijver sp. nov. and *Luticola vancampiana* Chattová & Van de Vijver sp. nov. Observation of the material in LM revealed the presence of a fifth unknown *Luticola* taxon with a highly asymmetrical central area. As the taxon could not be found during SEM analysis, we have insufficient data regarding its morphological ultrastructure and therefore the decision was taken not to describe it as new to science.

Class Bacillariophyceae Haeckel emend. Medlin & Kaczmarska (Medlin & Kaczmarska 2004)
Subclass Bacillariophycidae D.G.Mann in Round *et al.* (1990)
Order Naviculales Bessey (Bessey 1907)
Family Diadesmidaceae D.G.Mann in Round *et al.* (1990)
Genus *Luticola* D.G.Mann in Round *et al.* (1990)

Luticola beyensii **Van de Vijver, Ledeganck & Lebouvier**

Figs 1–12

Description

Light microscopy (Figs 1–10)

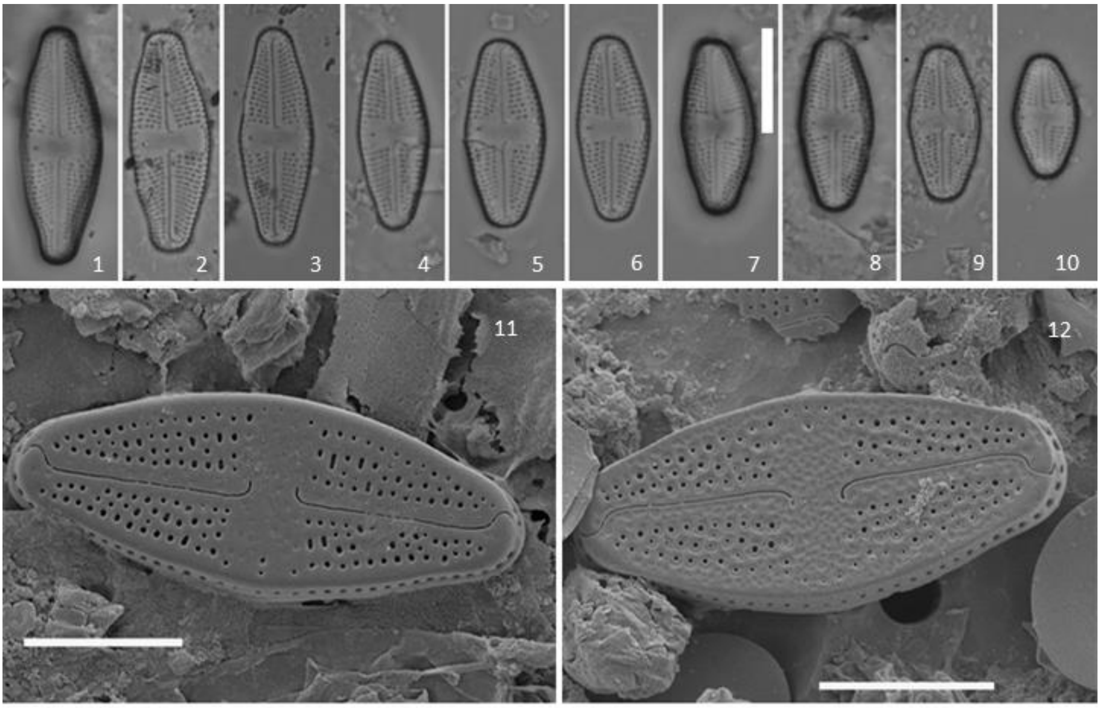
Valves rhombic-lanceolate with clearly convex margins. Larger individuals with more or less rostrate apices, in smaller specimens apices more broadly rounded. Valve dimensions (n=25): length 14.5–22.0 µm, width 6.0–8.5 µm. Axial area relatively narrow, linear. Central area with a large fascia, rarely reaching the valve margins, due to a series of small areolae bordering the central area near the margins. Isolated pore solitary, round, located close to the valve margin, never connected to a stria. Raphe filiform, straight, with simple, bent proximal raphe endings, away from the isolated pore. Terminal raphe fissures clearly hooked. Striae weakly radiate near the central area, becoming more radiate towards the apices, 22–24 in 10 µm. Areolae well visible in LM.

Scanning electron microscopy (Figs 11–12)

Striae composed of 2–4 rounded areolae (Figs 11, 12). Occasionally areolae fused within one stria forming transapically enlarged areolae (Fig. 11). Terminal raphe fissures clearly hooked, first deflected towards the side opposite the isolated pore, then hooked into the other side, weakly continuing onto the valve mantle (Fig. 12).

Ecology and associated diatom flora

Luticola beyensii was found in relatively dry, bare soils and on dry mosses (F-value VII-VIII) on both islands. The samples with *L. beyensii* were dominated by several *Humidophila taxa (H. amsterdamensis* Chattová & Van de Vijver (Chattová *et al*., submitted), *H. contenta* (Grunow) R.L.Lowe *et al.* in Lowe *et al.* 2014, *H. brekkaensis* (Petersen) R.L.Lowe *et al.* in Lowe *et al.* 2014), *Pinnularia borealis* Ehrenberg (Ehrenberg 1843) and *Hantzschia amphioxys* (Ehrenberg) Grunow (Cleve & Grunow 1880).



Figs 1–12. *Luticola beyensii* Van de Vijver, Ledeganck & Lebouvier. Light and scanning electron micrographs of a population from Ile Amsterdam. Figs 1–10. LM of valve face views. Figs 11–12. SEM of external view of entire valve, showing raphe structure, position of the isolated pore and striae structure. LM scale bar = 10 µm. SEM scale bars = 5 µm.

Luticola subcrozetensis Van de Vijver *et al.*

Figs 13–26

Description

Light microscopy (Figs 13–22)

Valves rhombic-lanceolate to elliptic-lanceolate and even elliptic in smaller specimens with clearly convex margins and broadly rounded, non-protracted apices. Valve dimensions (n=25): length 12–29 µm, width 7.0–8.5 µm. Axial area linear, slightly widening towards apices and central area. Central area bow–tie shaped, wider opposite the isolated pore, bordered by shortened striae on both sides. An isolated pore present in the central area, located halfway between the valve centre and the valve margin. Raphe branches straight, bent away from the isolated pore at both proximal and distal ends. Striae radiate throughout the entire valve, 15–17 in 10 µm.

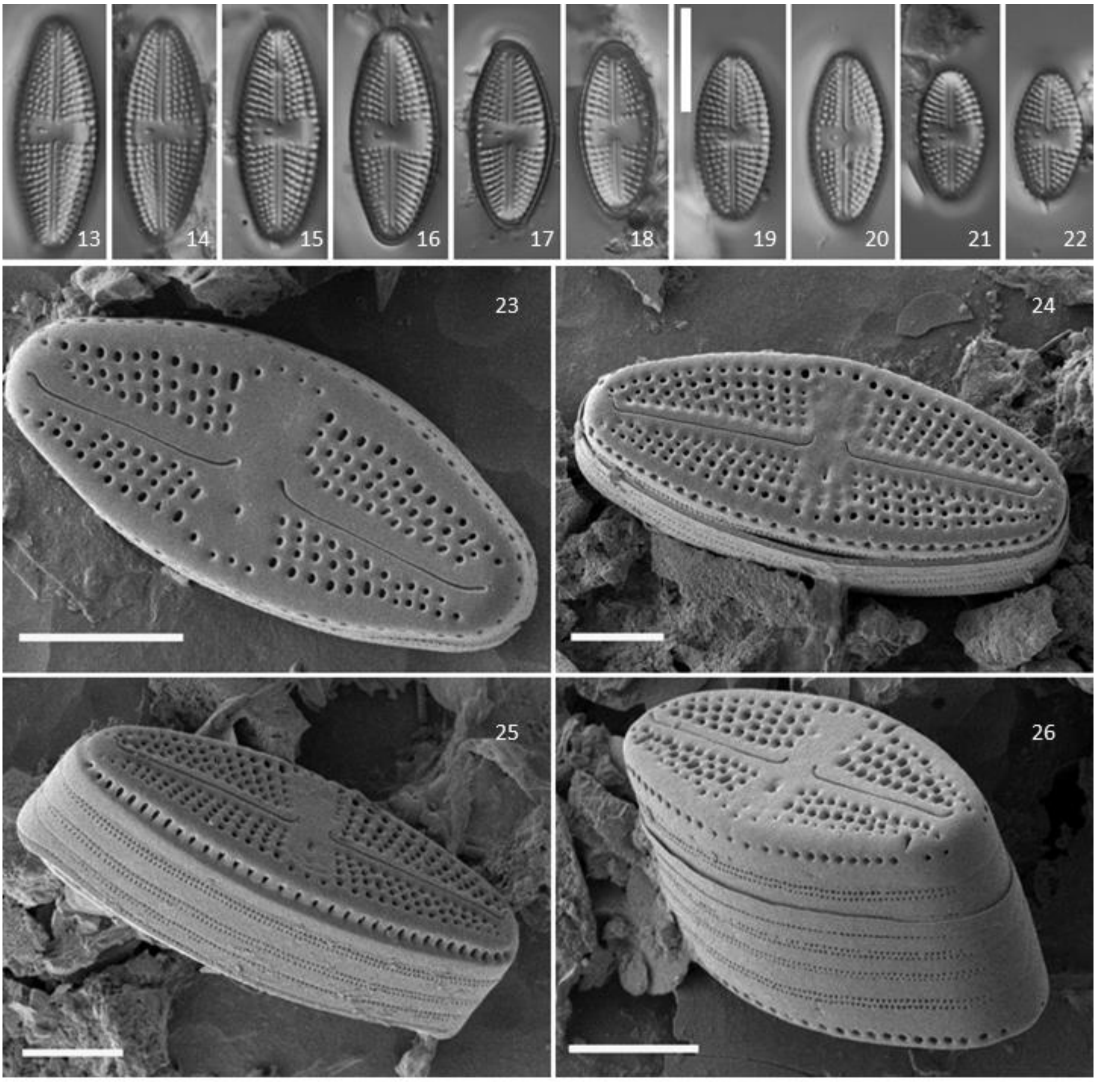
Scanning electron microscopy (Figs. 23–26)

Striae composed of 3–5 small, rounded to slightly elongated areolae at the apices, only 1–2 rounded areolae per stria, extending past the terminal raphe fissures on the valve face (Fig. 23). A single row of rounded areolae present along entire valve mantle, interrupted at apices (Fig. 26). Isolated pore rounded, slightly elongated, not associated with a stria. Central area usually bordered by one, rarely two, series of small, rounded areolae. Raphe branches straight to slightly curved. Proximal raphe endings bent to the side opposite the isolated pore, terminating into weakly developed pores. Terminal raphe fissures bent to the same side as the proximal endings terminating on the valve face, not extending onto the mantle (Fig. 24).

Ecology and distribution

Luticola subcrozetensis is a typical sub-Antarctic and Maritime Antarctic species. Originally described from Ile de la Possession (Crozet archipelago), the species was also reported from Livingston Island (Zidarova *et al.* 2016), one of the major South Shetland Islands, located in the southern Atlantic Ocean. The species was recently found in moss samples from Gough Island (Vinšová, unpublished results). It was present in samples from both Ile Saint-Paul and Ile Amsterdam.

The largest population was observed in a soil sample collected near the rockhopper penguin rookery of Ile Saint-Paul, at an altitude of 110 m, hidden in cracks in the rocks that border the penguin rookery.



Figs 13–26. *Luticola subcrozetensis* Van de Vijver *et al.* Light (LM) and scanning electron micrographs (SEM). Specimens from Ile Saint-Paul. Figs 13–22. LM of valve face views.

Figs 23–24. SEM of external view showing composition of striae and typical raphe structure. Figs 25–26. SEM girdle view. LM scale bar = 10 µm. SEM scale bars = 5 µm.

Luticola ivetaiana Chattová & Van de Vijver sp. nov.

Figs 27–43

Etymology

The new species was named after Mrs. Iveta Chattová, mother of the first author, on the occasion of her 50th birthday.

Type

Entrecasteaux, Ile Amsterdam, TAAF, sub-Antarctica, sample W030 (37°51′18.6″ S 77°31′23.5″ W) (leg. B. Van de Vijver), coll. date: 21 Dec. 2016 (holo-: slide no. BR–4495,; iso-: slide PLP–330, University of Antwerp, Belgium)

Description

LM observations (Figs 27–36)

Valves elliptic-lanceolate with convex margins and broadly rounded, non-protracted apices. Valve dimensions (n=50): length 11.0–25.5 µm, valve width 6.0–7.5 µm. Axial area narrow, linear, almost not widening towards the apices and central area. Central area forming a bow-tie shaped stauros. One isolated pore present in the central area, positioned close to the valve centre. Raphe filiform, straight with weakly deflected simple proximal raphe endings and elongated terminal raphe fissures. Striae radiate throughout the entire valve, 16–18 in 10 µm.

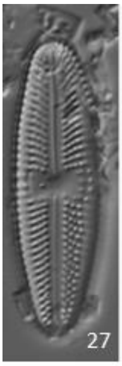
Scanning electron microscopy (Figs 37–43)

Striae composed of 2–4 round to elongated areolae, clearly enlarged near the central area and the valve margins (Figs. 37, 43). Mantle areolae very large, rounded, never slitlike (Fig. 39). Central area bordered by 1–2 rounded to weakly transapically elongated areolae.

Isolated pore elliptic, clearly isolated from the central striae (Fig. 38). Raphe branches straight with short proximal raphe endings bent towards the side with the isolated pore (Fig. 42). Terminal raphe fissures hooked, continuing onto the valve mantle (Fig. 41). Internally, poroids of valve face occluded by hymens forming a continuous strip on each stria. Distinct stauros visible. Internal proximal raphe endings straight, terminating on the edge of the stauros. Distal raphe endings terminating onto small helictoglossae (Fig. 40).

Ecology and distribution

So far, *Luticola ivetaiana* was observed on Ile Amsterdam only. The type locality where a large population of this new species was observed was a small crack in a rock face at Entrecasteaux, clearly under the permanent influence of seaspray. A very thin film of water was present in the crack together with wet mud. The sample was taken by scraping off the mud and the water from the crack. Another large population where *L. ivetaiana* was found is a lava cavern in the partly collapsed Grand Tunnel, running from the Cratères Vénus to the northern coast. The sample was taken from wet mosses (F-value IV-V), growing on the wall of the cavern, close to the entrance, in a population of *Blechnum australe* L. The sample was dominated by a centric diatom species belonging at present to an undescribed new genus closely related to *Melosira* Agardh (Van de Vijver *et al.*, unpubl. data) with *Orthoseira verleyenii* Van de Vijver (Lowe *et al.* 2013), *Sellaphora barae* Van de Vijver & E.J.Cox (Van de Vijver & Cox 2013) and various *Humidophila* Lowe *et al.* species.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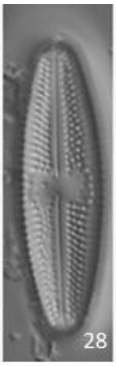
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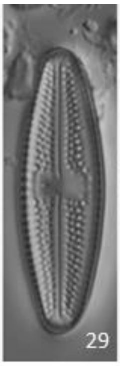
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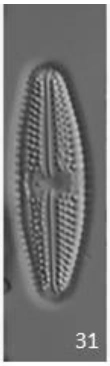
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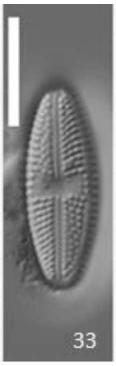
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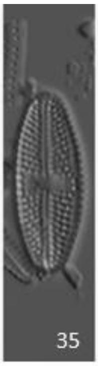
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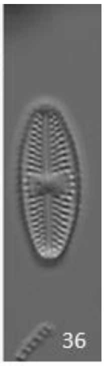
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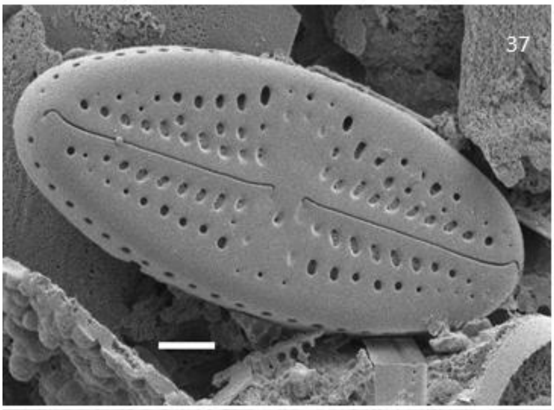
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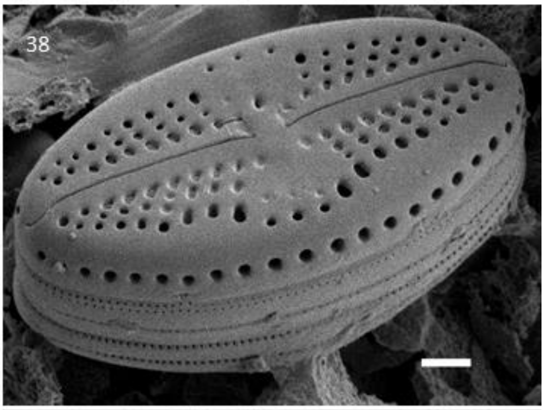
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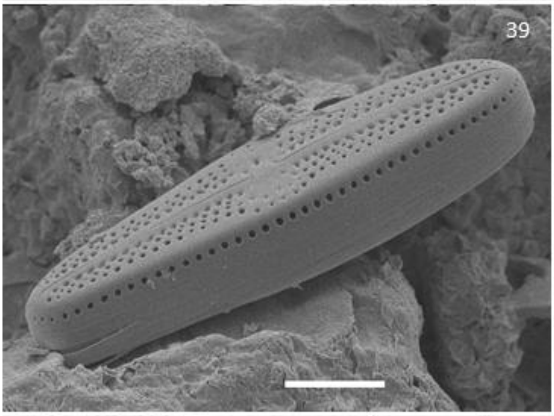
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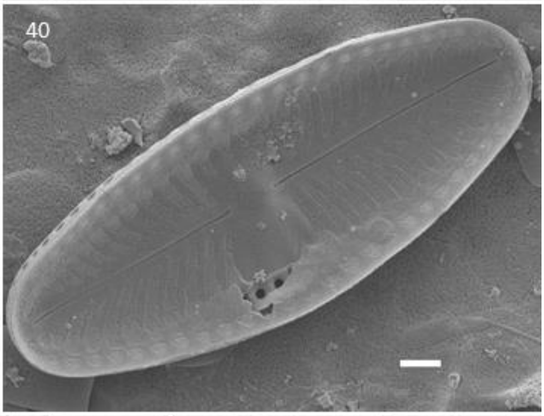
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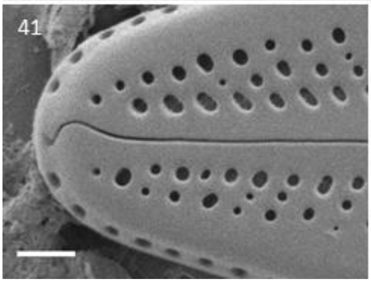
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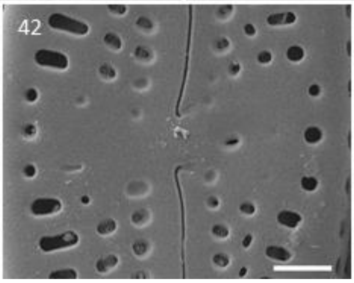
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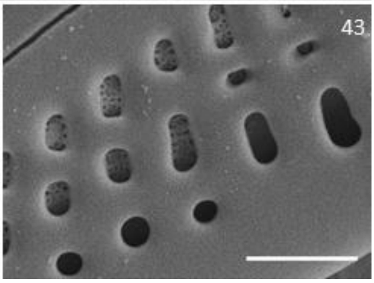
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Figs 27–43. *Luticola ivetaiana* Chattová & Van de Vijver sp. nov. Light (LM) and scanning electron micrographs (SEM). Specimens from the type population from Entrecasteaux on Ile Amsterdam. Figs 27–36. LM of valve face views. Figs 37–38. SEM of external valve view. Fig 39. SEM girdle view. Fig 40. SEM of internal valve view. Fig 41. SEM of external detail of hooked terminal raphe fissures. Fig 42. SEM of external detail view of central area showing the typical deflection of proximal raphe endings. Fig 43. SEM of external detail view of areolae structure. LM scale bar = 10 µm. SEM scale bars = 1 µm except for Fig 39, where scale bar = 5 µm.

***Luticola vancampiana* Chattová & Van de Vijver** sp. nov.

Figs 44–71

Etymology

The species is named after Prof. Dr. Karel Van Camp (University of Antwerp, Belgium), to thank him for his efforts in conserving the Van Heurck Collection and his broad interest in diatom research.

Type

Conserverie, Ile Saint-Paul, TAAF, sub-Antarctica, sample S029 (38°42′52.0″ S 77°31′55.5″ W) (leg. B. Van de Vijver), coll. date: 24 Nov. 2016 (holo-: slide no. BR–4496,; iso-: slide PLP–331, University of Antwerp, Belgium)

Description

Light microscopy (Figs 44–67)

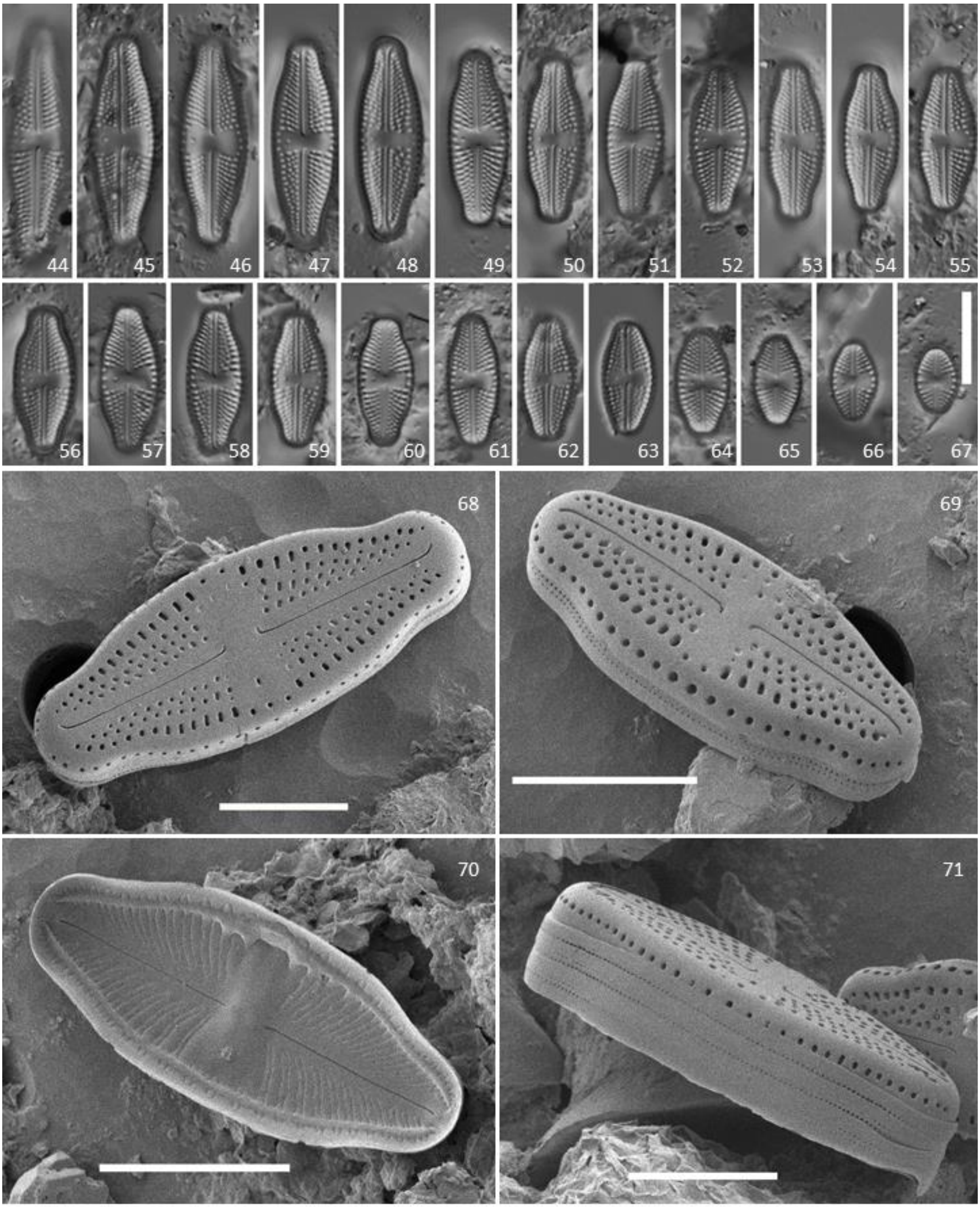
Valves linear-lanceolate to elliptic-lanceolate, elliptic in the smallest specimens, with protracted, subcapitate to rostrate apices. In smaller specimens, valve ends not as protracted, only subrostrate or obtusely rounded. Initial cells rhombic-lanceolate. Valve dimensions (n=35): length 10.0–26.0 µm, width 5.0–8.5 µm. Axial area linear, narrow. Single, rounded isolated pore present in the central area, located halfway between the valve centre and margin, sometimes attached to a stria. Central area wide, bow–tie shaped, bordered on both sides with a series of 3–5 round areolae. Raphe branches straight, deflected away from the isolated pore at both proximal and distal ends. Transapical striae radiate throughout, 16–19 in 10 µm.

Scanning electron microscopy (Figs 68–71)

Valve mantle with a single row of round areolae (Fig. 71), interrupted at the apices. Striae composed of 3–4 areolae, 1–2 areolae at the apices. Areolae round to elongated, clearly enlarged and prolonged close to the valve margins (Fig. 68). Internally, areolae occluded by hymens, forming a continuous strip across the valve (Fig. 70). Isolated pore showing an elliptic external opening. Internally, central nodule thickened, expanding into stauros. Isolated pore with semi-lunar opening formed by tongue-like structure. Raphe branches straight. Proximal raphe endings short, deflected to side opposite to the isolated pore. Terminal raphe fissures deflected to the same side as the proximal endings, not extending onto the mantle (Fig. 69). Internally, proximal raphe endings straight, while distally, raphe branches terminating on small helictoglossae.

Ecology and distribution

So far *Luticola vancampiana* was found on both Ile Amsterdam and Ile Saint-Paul. The largest population was found in a wet soil covered by green algae close to the ocean on Ile Saint-Paul. The sampling site is frequently visited by fur seals and penguins, as was visible in the macroremains (feathers, excrements). The sample was almost entirely dominated by the new *Luticola* species. Other (smaller) populations were found in soil samples collected near penguin rookeries where similar conditions (considerable biotic influence, considerable salinity input) prevailed.



Figs 44–71. *Luticola vancampiana* Chattová & Van de Vijver sp. nov. Light (LM) and scanning electron micrographs (SEM). Specimens from the type population from Conserverie on Ile Saint-Paul. Figs 44–67. LM of the type population showing the variation

in size and shape of the valve apices. Figs 68–69. SEM of external valve view. Fig 70. SEM of internal valve view. Fig. 71. SEM girdle view. LM scale bar = 10 µm. SEM scale bars = 5 µm.

***Luticola* sp.**

Figs 72–82

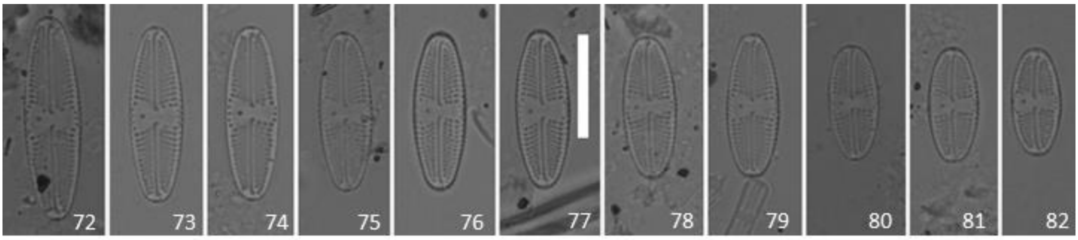
Description

Light microscopy (Figs 72–82)

Valves linear-lanceolate to elliptic-lanceolate in smaller specimens, with rounded, non-protracted apices. Valve dimensions (n=12): length 10.7–20.5 µm, width 4.5–6.5 µm. Axial area narrow, linear. Central area wide, bow-tie shaped, clearly asymmetrical with the side bearing the isolated pore markedly wider. Isolated pore present in the central area, located halfway between the valve centre and margin. Raphe branches straight, deflected away from the isolated pore at both proximal and distal ends. Transapical striae punctate, radiate throughout the entire valve, 20–24 in 10 µm.

Remarks

So far, the specimens of this species have been observed only with light microscopy. Further studies and SEM observations will be necessary to determine its correct taxonomic position. The species is characteristic by its asymmetrical central area, narrow valves and consistently linear-lanceolate outline, a combination of features that is almost never encountered within the genus *Luticola*. Based on the valve shape and striae density, the most similar species is *Luticola frequentissima* Levkov *et al.* (in Levkov *et al.* 2013). Both species can be differentiated by their proximal raphe endings which are deflected towards the isolated pore in *L. frequentissima*. Moreover, *Luticola* sp. has slightly narrower valves for any given valve length when compared to *L. frequentissima*. The central area of *Luticola similis* Levkov *et al*. (in Levkov *et al.* 2013) is slightly asymmetrical, but always wider on the side opposite to the isolated pore. *Luticola mutica* has a more variable valve outline, a narrower central area and coarser striae (16–18 in 10 µm).The species was so far found in only two soil samples (A6 and A7) taken from Ile Saint-Paul. Both samples are dominated by *Luticola beyensii, Humidophila brekkaensis*, *Pinnularia acidicola* Van de Vijver & Le Cohu (Van de Vijver *et al.* 2002a) and *Hantzschia amphioxys*.



Figs 72–82. *Luticola* sp. Light micrographs of a population from Ile Saint-Paul. Scale bar represents10 µm.

Discussion

The genus *Luticola* is one of the dominant components of the diatom flora in terrestrial habitats on sub-Antarctic Islands. These habitats show a diverse and very characteristic terrestrial flora with high degree of regional endemism in the entire Antarctic region, as is demonstrated by the large number of endemic taxa in typical terrestrial genera such as *Microfissurata* Lange-Bertalot, Cantonati & Van de Vijver (Cantonati *et al.* 2009), *Orthoseira* Thwaites (Van de Vijver & Kopalová 2008, Lowe *et al.* 2013), *Humidophila* (Kopalová *et al.* 2015, Chattová *et al.*, submitted), *Hantzschia* (Zidarova *et al.* 2010) and *Muelleria* Frenguelli (Frenguelli) (Van de Vijver *et al.* 2010, 2014).

The morphological and taxonomical analysis of the genus *Luticola* on Ile Amsterdam and Ile Saint-Paul revealed the presence of two new species. A wide combination of morphological features such as valve outline, shape of the valve apices, shape of the central and axial area, position and shape of the isolated pore, stria pattern and density and raphe and areola structure has been used for comparison with all similar taxa known worldwide so far. Sufficient morphological differences have been found to justify the separation of both taxa as new to science.

Luticola ivetaiana resembles several *Luticola* species with elliptic lanceolate valves, however the new species can be easily distinguished by the proximal raphe endings typically bent towards the isolated pore. There are only a few species showing a similar deflection such as *L. ledeganckii*, *L. frequentissima* and *L. raynae* Zidarova & Van de Vijver (Van de Vijver *et al.* 2011). *Luticola raynae* and *L. ledeganckii* have typical capitate apices, always lacking in *L. ivetaiana*. The most similar is *L. frequentissima*, but the latter species can be differentiated by shape of the central area, which is much smaller in *L. ivetaiana* and by the stria composition. *Luticola frequentissima* has transapical striae composed of 4–6 areolae per stria contrary to *L. ivetaiana* that has only 2–4 areolae per stria. The two species also differ ecologically, *L. ivetaiana* seems to be an aerophilic and most likely even slightly brackish taxon given the habitat in Entrecasteaux where it was found, while *L. frequentissima* always occurs in freshwater habitats. *Luticola mutica* and *L. imbricata* (Bock) Levkov *et al.* (in Levkov *et al.* 2013) have longer proximal raphe endings curved doubly, a feature lacking in *L. ivetaiana. Luticola imbricata* additionally differs from the new taxon by the shape of isolated pore (rounded versus elliptical) and by the apices that are narrowly rounded versus broadly rounded. *Luticola mutica* does not only differ by the shape and deflection of the raphe endings but also by the different shape of central area and the structure of the striae. Smaller specimens of *L. ivetaiana* also resemble *L. pseudoimbricata* Levkov *et al.* (in Levkov *et al.* 2013) based on their valve shape, but can however be separated by the different shape and deflection of both raphe proximal and distal fissures. *Luticola similis* Levkov *et al.* can be differentiated from *L. ivetaiana* by the wide and asymmetrical central area, by its lanceolate valve outline and its narrowly rounded valve apices.

The largest specimens of *L. vancampiana* bear some similarities to *L. robusta*. However, both taxa significantly differ in stria density (13–14 in 10 µm in *L. robusta* versus 16–19 in 10 µm in *L. vancampiana*). Additionally, *L. robusta* has a markedly wider axial area. *L. vancampiana* may also resemble *L. ledeganckii* based on valve shape and stria density. The main difference between these two species can be observed in the direction of proximal raphe endings, which are deflected towards the isolated pore in *L. ledeganckii*. *Luticola montana* Levkov, Metzeltin & Pavlov (in Levkov *et al.* 2013) has a similar valve shape compared to *L. vancampiana*, but can be easily differentiated from the latter species by its stria and areola density. *Luticola montana* has finer (19–22 in 10 µm) striae composed of 5–8 areolae, contrary to *L. vancampiana* that has only 3–5 areolae per stria. Additionally, the distal raphe fissures in *L. montana* continue onto the valve mantle, interrupting the row of areolae. *Luticola suecorum* has similar valve shape and protracted apices. Nevertheless, both species can be hardly confused and are easily distinguished by their valve dimensions and stria density. *L. suecorum* is much larger (20–42 µm, 7.5–13 µm) with coarser striae (13–14 in 10 µm). Additional differences can be observed in the SEM. *Luticola suecorum* has doubly hooked distal raphe endings that extend onto the valve mantle and an ornamented central area with surface depressions. *Luticola ipevii* can be differentiated from *L. vancampiana* by its slender, elongated valve outline and non-protracted, broadly rounded apices. Finally, *L. muticopsis* and *L. permuticopsis* Kopalová & Van de Vijver (Kopalová *et al.* 2011) have both more capitate apices. Moreover, *L. permuticopsis* has a higher striae density (18–22 in 10 µm).

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Appendix 1

Ferocia gen. nov., a new centric diatom genus (Bacillariophyceae) from the sub-Antarctic region

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Abstract

A new centric diatom genus, *Ferocia* Van de Vijver & Houk gen. nov. is described based on *Melosira setosa* Greville. Several large populations of the latter were observed in lava tunnels on Ile Amsterdam, a small isolated, volcanic island in the southern Indian Ocean. The new genus is characterized in having heavily silicified, spherical frustules, connected into long chains by large, complex linking spines. Valves are dome-shaped with a high mantle with rounded to irregularly shaped areolae. Numerous small rimoportulae forming a marginal ring are present near the mantle edge. The cingulum is composed of a large number of narrow, open copulae. A second, newly described, species, *Ferocia ninae* Van de Vijver & Houk sp. nov., is described from the nearby Crozet archipelago. Both *F. ninae* and *F. setosa* were found in shaded lava tunnels with a sparse moss vegetation. The two species are illustrated and discussed based on detailed LM and SEM observations.

Key-words: centric diatoms, new genus, *Melosira*, *Ferocia*, sub-Antarctic Region

Introduction

The number of centric diatoms in the Antarctic Region (including the sub-Antarctic islands combined with the Tristan da Cunha Archipelago, Ile Amsterdam and Ile Saint Paul, Maritime Antarctic Region and the Antarctic Continent) is rather limited. Van de Vijver (2012) gives an overview of the different species that have been reported in the past. Most species belong to the genera *Melosira* C.Agardh (1824: 14), *Orthoseira* Thwaites (1848: 167) and *Aulacoseira* Thwaites (1848: 167). In the recent years, several new species in these genera were described such as *Aulacoseira principissa* Van de Vijver (2012: 35), *Orthoseira biportulata* Van de Vijver & Beyens (in Van de Vijver et al 2002a: 75) and *O. limnopolarensis* Van de Vijver & Crawford (2014: 248). Most of these species had been force-fitted in the past into European or North American names (Tyler 1996) obscuring the real diatom biodiversity in the Antarctic Region.

During a survey of the terrestrial diatom flora of several sub-Antarctic islands, two unknown, but clearly related, centric taxa were observed. Both taxa show a clear affinity with the genus *Melosira*. They form colonies in which the frustules are linked not by mucilage pads but by well-developed linking spines. Comparison of these sub-Antarctic populations with previously described *Melosira* taxa possessing linking spines (such as *M. setosa* Greville 1866: 436 and *M. echinata* Manguin 1941: 154) showed that at least one of the taxa (observed on Ile Amsterdam) is conspecific with *M. setosa* whereas the other taxon (observed on Ile de la Possession, Crozet archipelago), showed sufficient differences to separate it as a new species. Further morphological analysis of both taxa and comparison with typical *Melosira* taxa forming colonies joined by mucilage pads, indicated several important differences suggesting that the two spine-bearing taxa should be separated from *Melosira* and placed in a new genus.

The present paper describes and discusses the new genus *Ferocia* based on light and scanning electron microscopy to accommodate the two taxa found on Ile Amsterdam and Ile de la Possession. Since it was the most similar taxon, the type material of *Melosira setosa* was investigated to determine conspecificity. The transfer of *M. setosa* to the new genus is proposed, *Ferocia setosa* (Greville) Van de Vijver & Houk comb. nov. and a new species, *Ferocia ninae* Van de Vijver & Houk sp. nov. is described.

Material & Methods

During the austral summers of 1999 and 2007-2008, several samples were taken in accessible caverns of the collapsed lava tunnel Grand Tunnel on Ile Amsterdam and in some shallow caves on the Pointe Basse area in the north-western part of Ile de La Possession, the main island of the Crozet Archipelago. Detailed information on the sampling localities can be found in Chattová et al. (2014) for Ile Amsterdam and Van de Vijver et al. (2002b) for Ile de la Possession.

Small subsamples were prepared for light microscopy (LM) observation following the method described in Van der Werff (1955). Small parts of the samples were cleaned by adding 37% H_2O_2 and heating to 80°C for about 1h. The reaction was completed by addition of $KMnO_4$. Following digestion and centrifugation (three times 10 minutes at 3700 x g), cleaned material was diluted with distilled water to avoid excessive concentrations of diatom valves on the slides. Cleaned diatom material was mounted in Naphrax®. For scanning electron microscopy (SEM), part of the cleaned suspension was pipetted onto small coverglasses glued to aluminium stubs, and sputter coated with a 20 nm thick layer of gold-palladium. Observations and photomicrography were performed at the Natural History Museum in London (UK) using a Zeiss® Ultra plus scanning electron microscope at 3 kV. Samples, slides and stubs are stored at the BR-collection (Botanic Garden Meise, Belgium).

Williams (1988) investigated three syntypes (BM 3532, BM 3533 and BM 3534) of *M. setosa* without officially designating a lectotype. One of the slides (BM 3532) has been investigated in the present study in more detail. The slide was taken from material collected at Aneitum, New Hebrides. Unfortunately, no unmounted material was conserved so SEM analysis could not be performed on the type material.

Terminology follows Round et al. (1990) and Houk (2003).

Results

Ferocia Van de Vijver & Houk, gen. nov.

Frustules heavily silicified, cylindrical, ellipsoid to often spherical, connected by large, complex spines forming long chains. Valve structure usually very fine, rarely discernible in LM. Valves hemispherical to dome-shaped with a high mantle, often thickened near the mantle edge. Granules and a combination of large and numerous small spines, scattered all over the valve face and parts of the mantle, present. Areolae rounded to irregularly shaped, covered by an external velum. Numerous small rimoportulae forming a marginal ring near the mantle edge. Fultoportulae absent.

Cingulum composed of a large number of narrow, open copulae with a fimbriate pars interior. Internal valves sometimes present. Numerous small chloroplasts present.

Type: – *Ferocia setosa* (Greville) Van de Vijver & Houk (vide infra)

Etymology: – the new genus name *Ferocia* is derived from the Latin word *ferox* which means fierce, referring to the spiny outlook of the composing taxa.

Ferocia setosa (Greville) Van de Vijver & Houk comb. nov. (Figs 1–27)

Basionym: – *Melosira setosa* Greville (1866) Transactions of the Botanical Society of Edinburgh 8, p. 436; pl. 6, fig. 17-19.

Lectotype (designated here): – slide BM 3532 (Aneitum, New Hebrides, in Coll. Greville, Natural History Museum, London, UK)

Type material

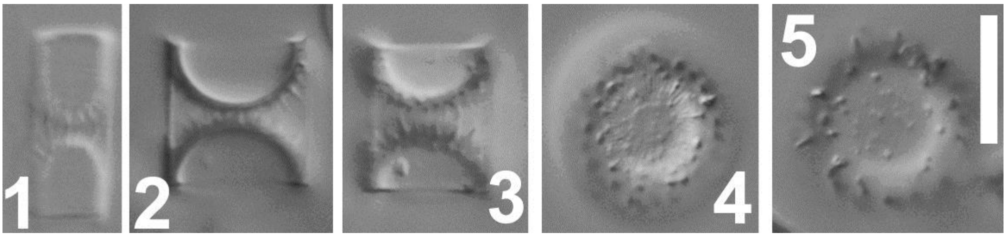
LM (Figs 1–5): Valves hemispherical connected to each other via well developed, acute linking spines (Figs 1–3). Valve diameter 3–7 µm, Valve height 2–4 µm. Valves dome-shaped. Linking spines of variable height, scattered over the entire valve face.

Ile Amsterdam population

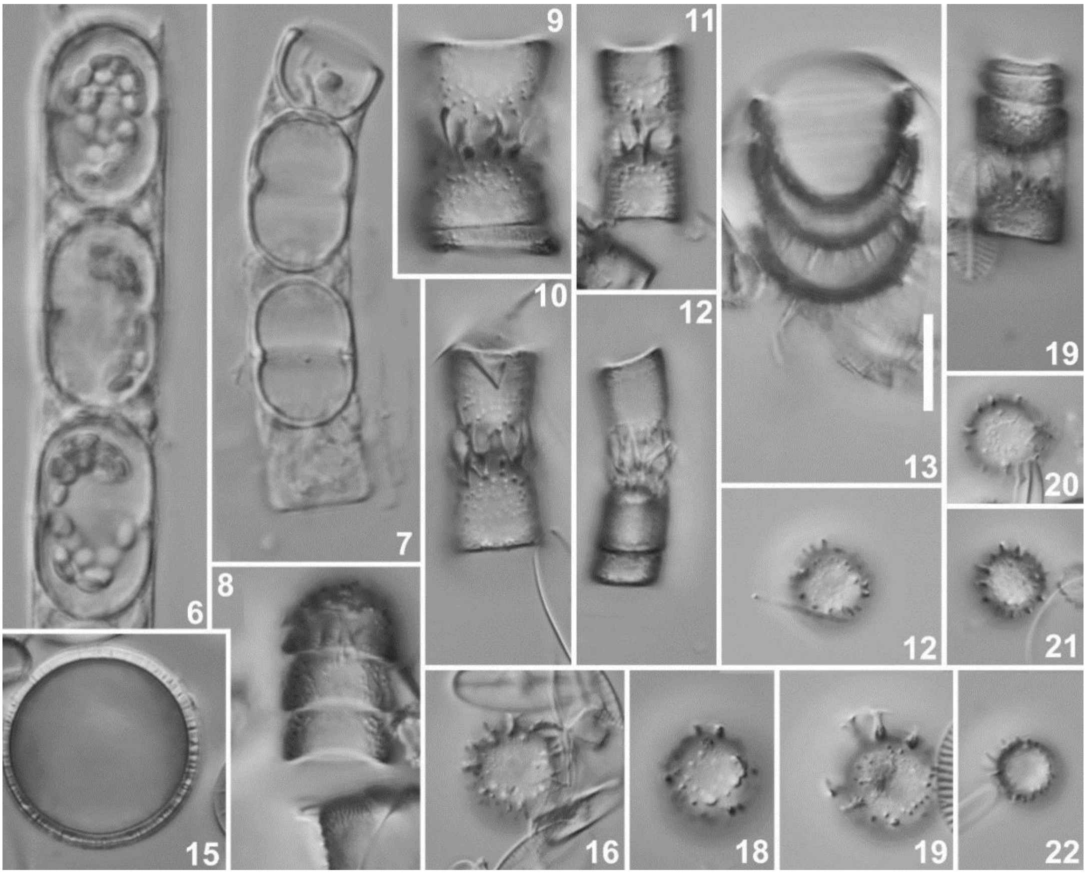
LM (Figs 6–22): Frustules with hemispherical valves bearing robust, often plate-like acute linking spines connecting the frustules forming long chains of up to 15 cells (Figs 6, 7). Numerous chloroplasts present (Fig. 6).Valve diameter (n=50): 5.5–22.0 µm, valve height 4.0–8.5 µm. Valves dome-shaped with a relatively high mantle and rounded valve face (Figs 8–14). Internal valves often present (Figs 8, 13). Cingulum composed of several narrow copulae, often visible as a regular, parallel striping of the valve mantle (Fig. 11). SEM (Figs 23–27): Valves clearly hemispherical (Fig. 25). Linking spines very large, irregularly shaped, often plate-like with sharp, acute endings (Figs 24, 25). Smaller spines and granules positioned between the large linking spines, often bluntly terminating close to the copulae (Fig. 23). Müller step often very large (Fig. 24). Cingulum composed of a large number of narrow, open, unperforated, ligulate copulae (Fig. 23). Pars interior of the copulae fimbriate (Fig. 23). Areolae on the mantle edge small, rounded, arranged in irregular rows, parallel to the pervalvar axis (Fig. 24). On the valve face, areolae often slit-like, arranged in star-shaped patterns around the spines (Fig. 25). Internally, ring of slit-like rimoportulae present near the mantle edge (Figs 26, 27). Rimoportulae never equidistant (Fig. 26).

Remarks: – The type population of *Melosira setosa*, originally described from Aneityum, one of the islands of Vanuatu (Greville 1866), shows lower valve dimensions compared to the Ile Amsterdam populations that are always larger in every morphometric aspect. However, apart from these slight differences, the Ile Amsterdam population shows no morphological separation with the type material and can therefore be considered conspecific. Another population of *Melosira setosa*, originating from New South Wales (material AT68 from the Hustedt collection, Alfred Wegener Institute for Polar and Marine Research (BRM)) was recently studied by Houk et al. (unpubl. res.) as part of their new revision of the genera *Melosira*, *Orthoseira* and *Aulacoseira*. All morphological features such as shape, size and position of linking spines, arrangement of mantle and valve face areolae, number and structure of the copulae and number and arrangement of the rimoportulae are almost identical (Houk, pers. comm.).

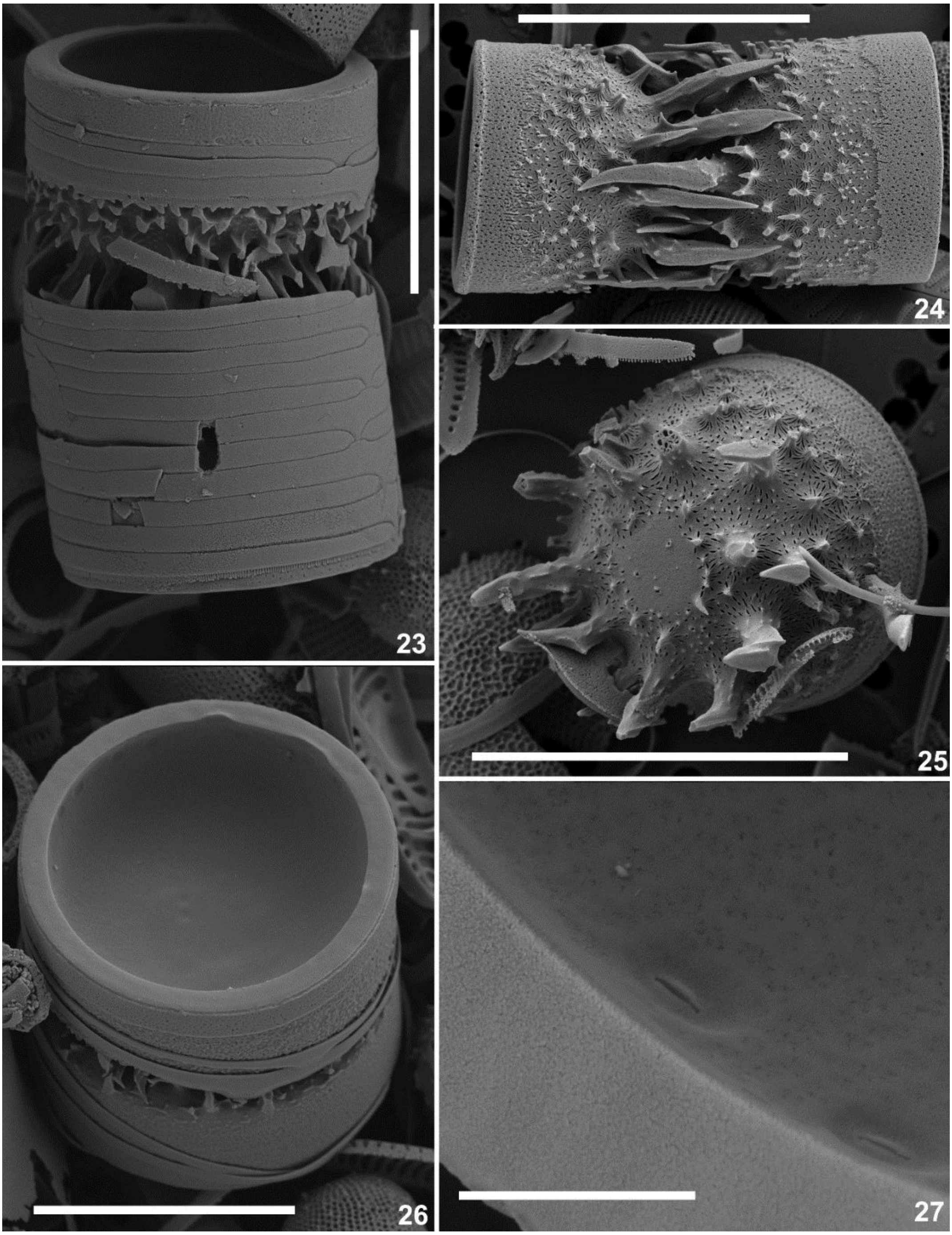
Ecology & Distribution: – *Ferocia setosa* is a common species on Ile Amsterdam inhabiting a very specific biotope: lava caves and tunnels. The species was observed in almost every sampled lava tunnel and cave on the island under low light conditions. All samples in which *F. setosa* was observed were collected from wet moss, continuously moistened by dripping or seeping water. The samples were dominated by several species of *Humidophila* R. L. Lowe et al (2014: 354), *Planothidium lanceolatum* (Brébisson ex Kützing 1846: 247) Lange-Bertalot (1999: 287), *Sellaphora barae* Van de Vijver & E.J.Cox (2013: 40) and *Mayamaea cavernicola* Van de Vijver & E.J.Cox (2013: 40).



Figures 1–5. *Melosira setosa* Greville. LM pictures taken from the type population (Aneitum, New Hebrides, lectotype slide BM 3532, Natural History Museum, London, UK). Scale bar represents 5 µm.



Figures 6–22. *Ferocia setosa* (Greville) Van de Vijver & Houk comb. nov. LM pictures taken from the Ile Amsterdam population (sample AMS-W033). Figs 6–7. Chains of up to 4 frustules linked by linking spines. Fig. 1 shows numerous chloroplasts. Figs. 8–14. Valves linked via linking spines. Note the internal cells in Figs 8, 13 & 14 and the numerous copulae in Fig. 11 (see arrows). Fig. 15. Valve view showing the cell contours. Figs 16–22. Several valves in valve view showing linking spines. Scale bar represents 10 µm.



Figures 23–27. *Ferocia setosa* (Greville) Van de Vijver & Houk comb. nov. SEM pictures taken from the Ile Amsterdam population (sample AMS-W033). Fig. 23. Two valves

connected by linking spines with the cingulum composed of numerous narrow, ligulate open copulae. Fig. 24. Two valves connected by linking spines. Note the large spines, the numerous granules and the areolae on the mantle. Müller step clearly visible. Fig. 25. View of an entire valve showing spines, valve face areolae and mantle. Fig. 26. Internal view of an entire valve showing the ring of rimoportulae (arrows). Fig. 27. Internal detail of the rimoportulae. Scale bar represents 10 µm except for fig. 27 where scale bar = 1 µm.

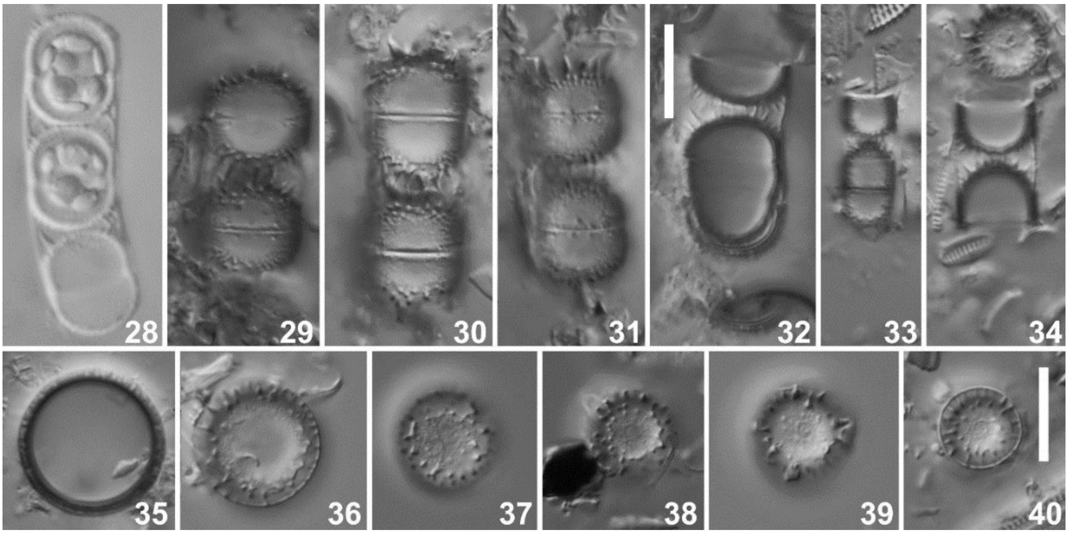
Ferocia ninae **Van de Vijver & Houk sp. nov.** (Figs 28–45)

LM (Figs 28–40): Frustules cylindrical to almost spherical with hemispherical valves bearing a large number of acute linking spines connecting the frustules forming short chains of up to 3–5 cells. Valve diameter (n=50): 4.5–19.0 µm, valve height 4.0–6.0 µm. Spines usually arranged around the valve face. Valves dome-shaped with a relatively low mantle and rounded valve face. Internal valves occasionally present. SEM (Figs 41–45): Valves clearly hemispherical with a low mantle (Fig. 43). Linking spines relatively large, irregularly shaped, with sharp, acute endings (Figs 42, 43). Valve face entirely covered by a large number of smaller spines and irregularly shaped granules positioned between the large linking spines (Fig. 43). Müller step often very large (Fig. 43). Cingulum composed of a large number of narrow, open, unperforated ligulate copulae (Fig. 41). Pars interior of the copulae fimbriate (Fig. 41). Areolae on the mantle edge small, rounded, arranged in irregular rows, parallel to the pervalvar axis (Fig. 43). On the valve face, areolae often slit-like, arranged in star-shaped patterns around the spines (Fig. 42). Internally, ring of slit-like, equidistantly placed rimoportulae present near the mantle edge (Fig. 44, arrows). Areolae internally individually covered by vela (Fig. 45).

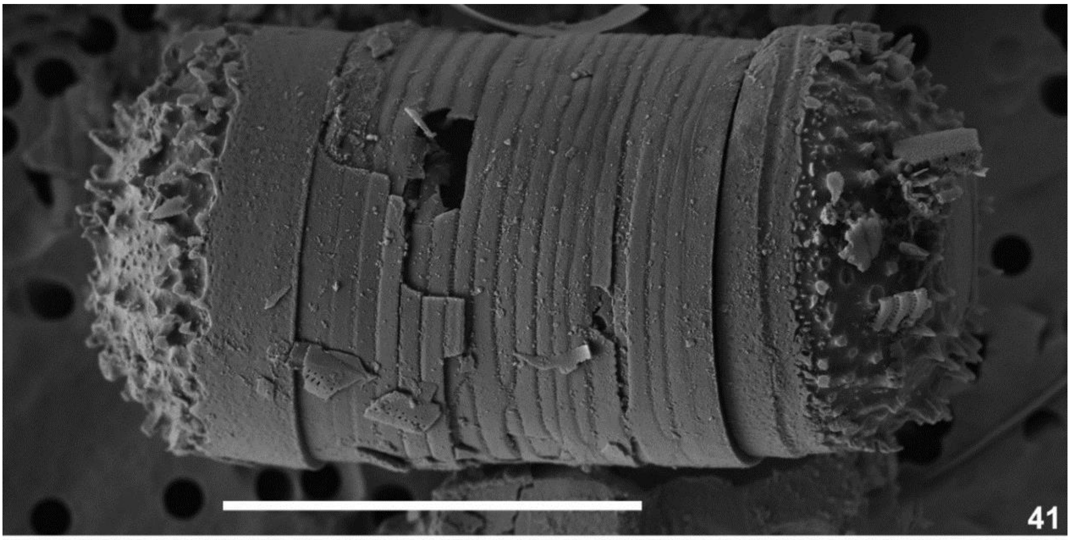
Type:– Pointe Basse, Ile de la Possession, Crozet Archipelago, Sub-Antarctica, sample BA61, (leg. B. Van de Vijver), coll. date 21/11/1999 (holotype BR!, slide no. 4498, isotype PLP! slide no. 332, University of Antwerp, Belgium).

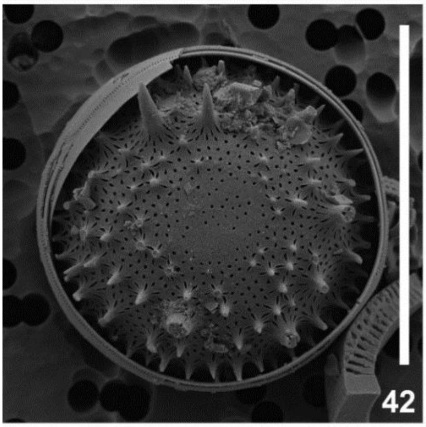
Etymology:– The species is named after Mrs. Nina Marchand (IPEV, France) to thank her for the help during the sampling campaigns on Ile Amsterdam (2007 & 2016) and Ile de la Possession (2012).

Ecology & Distribution:– The new species was found in dry soil samples collected from several shallow lava caves and caverns on the border of the small river that is flowing in the Pointe Basse Region. The samples were dominated by *Planothidium aueri* (Krasske 1949: 77) Lange-Bertalot (1999: 281), several *Humidophila* taxa such as *H. subantarctica* (Le Cohu & Van de Vijver 2002: 128) R.L.Lowe et al. (2014: 359) and *H. arcuata* (Heiden in Heiden & Kolbe 1928: 628) R.L.Lowe et al. (2014: 357) and *Chamaepinnularia aerophila* Van de Vijver & Beyens in Van de Vijver et al. (2002a: 26).



Figures 28–40. *Ferocia ninae* Van de Vijver & Houk sp. nov. LM pictures taken from the Ile de la Possession type population (sample BA061). Fig. 28 Chain of up to 3 frustules linked by linking spines, showing numerous chloroplasts. Figs. 29–34. Valves linked via linking spines. Note the internal cells in Fig. 33. Fig. 35. Valve view showing the cell contours. Figs 36–40. Several valves in valve view showing linking spines. Scale bar represents 10 µm.


41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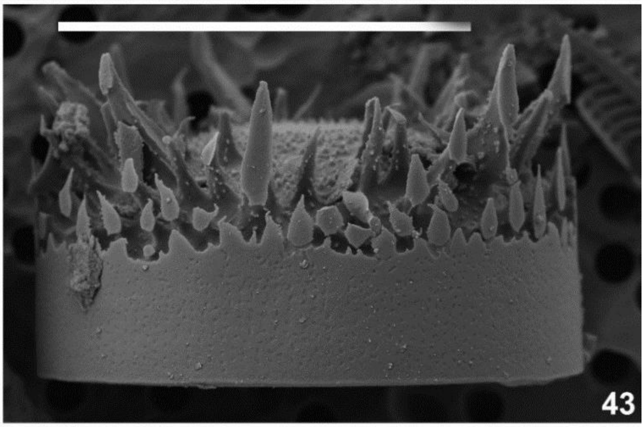
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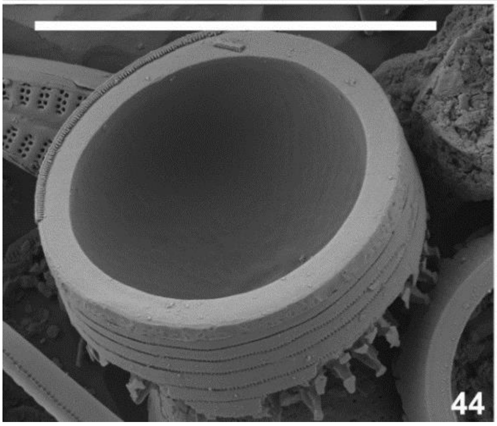
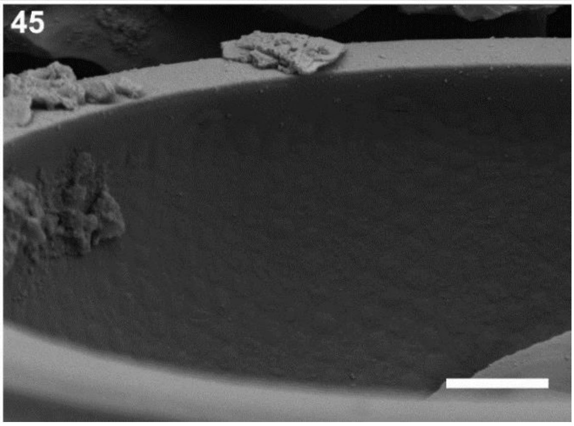

44


45

Figures 41–45. *Ferocia ninae* Van de Vijver & Houk sp. nov. LM pictures taken from the Ile de la Possession type population (sample BA061). Fig. 41. Two frustules connected by linking spines with the cingulum composed of numerous narrow, ligulate open copulae. Fig. 42. View of an entire valve showing spines and valve face areolae. Fig. 43. External view of a hemispherical valve in girdle view showing the spines and the rather low mantle with areolae. Fig. 44. Internal view of an entire valve showing the ring of rimoportulae (arrows). Fig. 45. Internal detail of the rimoportulae. Scale bar represents 10 µm except for fig. 45 where scale bar = 1 µm.

Discussion

Ferocia setosa was firstly described as *Melosira setosa*, as it corresponded with the generally accepted idea of the genus *Melosira*. A large number of taxa was originally placed within *Melosira* but thorough morphological and taxonomical research resulted in a transfer of most of these taxa to other, often newly described, genera such as *Ellerbeckia* Crawford (1988: 421), *Aulacoseira* Thwaites (1848: 167) or *Liparogyra* Ehrenberg (1848: 217). Nevertheless, several taxa such as *M. setosa* and *M. dickiei* remained in *Melosira* although they did not entirely fit the original description.

Several important differences separate *Ferocia* from *Melosira* (Round et al. 1990, Houk, 2003, Houk & Klee 2007). The cingulum in *Melosira* is composed of rather broad, ligulate copulae, perforated by several rows of small poroids (see Round et al. 1990, p. 155, Fig. i), contrary to *Ferocia* that possesses narrow, unperforated copulae. The valve face in *Melosira* is usually flat whereas *Ferocia* only shows domed valves. The rimoportulae, arranged in a marginal ring on the mantle in *Ferocia*, are often organized in a marginal ring in *Melosira* on the mantle plus lying scattered or grouped on the valve face, a feature never observed in *Ferocia*. Spines are only rarely observed in *Melosira* and never serve to link cell into a colony, whereas in *Ferocia* they are clearly used to link frustules in the colony. Instead, *Melosira* colonies are united in filaments by mucilagous pads (Round et al. 1990).

Other *Melosira* species such as *M. dickiei* Thwaites (1848: 168) present several features that do not correspond to the description of the genus *Melosira* such as the presence of numerous, narrow, unperforated, ligulate girdle bands, the formation of internal valves and the ring of rimoportulae on the valve mantle. These species will be placed in a new genus

(Houk, pers. comm.) that is however different from *Ferocia* in lacking the domed valve shape with the high mantle, the absence of the complex linking spines and differences in the areola shape, placement and structure. Shared features include the ring of rimoportulae and the structure of the cingulum.

Another genus showing robust linking spines is *Clipeoparvus* Woodbridge et al. in Woodbridge et al. (2010: 198), described in 2010 from Cappadocia, Turkey. The latter shows hemispherical valves entirely covered with granules and linking spines and numerous ligulate, non-perforated, narrow copulae. *Clipeoparvus* differs however from *Ferocia* in the absence of rimoportulae in the former, a feature well present in *Ferocia* (Woodbridge et al. 2010). *Clipeoparvus* only has two small chloroplasts whereas *Ferocia* has numerous chloroplasts. *Clipeoparvus* never forms long colonies and has a paired or solitary life-form contrary to *Ferocia* that forms long chains of up to 15 cells.

Other genera such as *Podosira* Ehrenberg (1840: 161) and *Hyalodiscus* Ehrenberg (1845: 71), both strictly marine, differ sufficiently (for instance in the placement of the rimoportula, the cingulum structure and the absence of spines) to be excluded as host genus for both *Ferocia* taxa.

Ferocia setosa and *F. ninae* show a high degree of similarity but differ nevertheless sufficiently to justify their separation as two independent taxa. Several populations on both Ile Amsterdam and Ile de la Possession have been investigated. Both taxa thrive in shaded lave tubes and lava caves. Both show irregularly shaped spines linking the frustules into long (*F. setosa*) or short (*F. ninae*) chains. On Ile Amsterdam, all populations show long colonies of up to 15 cells whereas on Ile de la Possession, colonies never exceeded 5 linked cells. Both *Ferocia* species have a marginal ring of short, slit-like rimoportulae but in *Ferocia setosa*, the rimoportulae are irregularly distributed along the ring whereas in *F. ninae*, the rimoportulae are almost equidistant. The valves in *F. setosa* always have a higher mantle whereas *F. ninae* has a lower mantle height. The frustules in *F. setosa* are always linked by larger, more complex linking spines compared to the smaller spines in *F. ninae*.

No differences could be found in the number and structure of the copulae and the structure of the areolae. Nevertheless, the observed differences are sufficient to separate both taxa.

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Curriculum vitae

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- **2007-2010** Faculty of Science, MU, Brno, Department of Botany and Zoology
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    - Thesis: Chattová, B. (2010): Taxonomy and ecology of freshwater diatoms of Ile Amsterdam (TAAF, South Indian Ocean)

- **2005-2007 F**aculty of Science, MU, Brno, Department of Botany and Zoology
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    - Theses: Chattová, B. (2007): Algological study of fens at fishpond margins in the Třeboň basin

Study abroad

- **Sept. 2009 – Jan. 2010** Erasmus programme at the University of Antwerp
    - Algological lab, Prof. Dr. Bart Van de Vijver at National Botanic Garden of Belgium)
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Language skills

English	Very good knowledge reading, speaking and writing
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Employment

- Sept. 2010 – now Faculty of Science, Masaryk University
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Pedagogical activities

- Teacher or a co-responsible person of courses on algae at the Masaryk University
- Since 2010 Plant phylogeny and diversity-practical course, Phylogeny and diversity of algae and fungi-practical course
- Since 2012 Basic diatomology, Diatomology-identification course
- Since 2014 Ecology of algae and cyanobacteria, Methods of field phycology, Plant phylogeny and diversity, Phylogeny and diversity of algae and fungi, Algal and fungal system for advanced, Phycological excursion
- Supervisor, consultant and opponent of bachelor and master theses at the Masaryk University and at the Charles University in Prague

Organizational skills

- Member of the organizing committee of Conference of Czech Algological Society, September 2007, Nivnice
- Member of the organizing committee of 11th Central European diatom meeting, **22 – 25 March 2017, Prague**
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Other activities

- Member of Czech Algological Society
- Reviewer of Nova Hedwigia
- Polar ecology field course, July 2013, Petunia Bukta, Svalbard (algology group)
- Field work in Maritime Antarctica- James Ross Island, January-February 2015

Publications in peer-reviewed journals

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Conference contributions

International conferences

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