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Ekologie a diverzita půdních rozsivek ostrova Nový Amsterdam a ostrova Svatého Pavla (TAAF, Jižní Indický oceán)

Diplomová práce

Bc. Tereza Cahová

Vedoucí práce: Mgr. Barbora Chattová, Ph.D.

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Ecology and diversity of soil diatoms on Ile Amsterdam and Ile Saint-Paul (TAAF, Southern Indian Ocean)

Master Thesis

Bc. Tereza Cahová

Supervisor: Mgr. Barbora Chattová, Ph.D.

Department of Botany and Zoology

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Autor:	Bc. Tereza Cahová Přírodovědecká fakulta, Masarykova univerzita Ústav botaniky a zoologie
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Abstrakt

V této diplomové práci se věnujeme druhové bohatosti a biogeografii půdních rozsivek dvou malých izolovaných ostrovů vulkanického původu, ostrova Nový Amsterdam a ostrova Svatého Pavla. Práce se věnuje složení rozsivkových společenstev a faktorům prostředí, které je ovlivňují. V průběhu terénních prací byly měřeny fyzikálně-chemické parametry prostředí. Součástí práce je i srovnání zjištěné rozsivkové flóry ostrova Nový Amsterdam s ostatními ostrovy jižního Indického oceánu. Během práce bylo analyzováno 76 půdních vzorků z ostrova Nový Amsterdam a 18 půdních vzorků z ostrova Svatého Pavla. Celkem bylo na obou ostrovech zjištěno 193 taxonů rozsivek. Výsledky analýz společenstev ukazují že mezi hlavní faktory ovlivňující složení rozsivkových společenstev patří vlhkost, pH a konduktivita. Podle biogeografické analýzy patří minimálně 15 % všech nalezených taxonů mezi endemity obou ostrovů a dalších téměř 14 % vykazuje omezený subantarktický výskyt.

Abstract

In this thesis we examine species richness and biogeography of soil diatoms of two small isolated volcanic islands called Amsterdam Island and Saint-Paul Island. The thesis deals with the composition of diatom communities and environmental factors influencing them. A series of physicochemical variables have been measured on Amsterdam Island. Part of the thesis is also a comparison of observed diatom flora with diatom flora of other sub-Antarctic islands located in Southern Indian Ocean. During the study, 76 soil samples from Amsterdam Island and 18 soil samples from Saint-Paul Island were analysed. All 193 diatom taxa were found on both islands. The results of community analysis showed that moisture, pH and conductivity are the major factors influencing the composition of diatom communities of Amsterdam Island. According to biogeographical analysis, at least 15 % of all observed taxa are endemic species of the studied islands and nearly 14 % have a limited sub-Antarctic distribution.

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Oficiální zadání: Výzkum subantarktických rozsivek ve spolupráci s odborníky z Národní botanické zahrady v Bruselu má na algologickém pracovišti MU dlouholetou tradici. V minulosti byly z těchto dvou malých, vulkanických a izolovaných ostrovů zpracovány vzorky sladkovodních a mechy obývajících rozsivek. Výzkum půdních rozsivek vhodně doplní chybějící informace o terestrické rozsivkové flóře obou ostrovů. Studentka zpracuje minimálně 60 vzorků půdních rozsivek. V každém preparátu se pokusí determinovat a následně spočítat 400 rozsivkových valv, minimálně však 200. Během výzkumu provede fotodokumentaci. Cílem práce je zaznamenání aktuální diverzity půdní rozsivkové flóry, která bude následně porovnána nejen mezi oběma studovanými ostrovy, ale i s rozsivkovou flórou ostatních subantarktických ostrovů. Jedním z cílů práce je zjistit, jaké faktory nejvíce ovlivňují druhové složení společenstev půdních rozsivek na ostrově Nový Amsterdam, kde byly při terénních pracech v sezóně 2016/2017 měřeny pH, konduktivita a vlhkost. Studentka se pokusí zhodnotit i vliv vegetačního pokryvu druhové složení společenstev půdních rozsivek. K zobrazení hlavních trendů v získaných datech a k zjištění, do jaké míry dané faktory prostředí ovlivňují druhové složení půdních společenstev rozsivek, budou použity vhodné statistické metody programů R a CANOCO.

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Chattová, B.,Lebouvier, M., & Van de Vijver, B. 2014: Freshwater diatom communities from Ile Amsterdam (TAAF, southern Indian Ocean). Fottea 14: 101–119.
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Vedoucí pracovní skupiny: doc. Mgr. Michal Hájek, Ph.D.

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prof. RNDr. Milan Chytrý, Ph.D.
ředitel Ústavu botaniky a zoologie

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Podpis studenta

Poděkování

Na tomto místě bych chtěla poděkovat v první řadě celé svojí rodině za nekonečnou lásku a podporu, díky čemuž mohu studovat to, co mě doopravdy baví, a jmenovitě svému mladšímu bráškovi Bímu, bez něhož by tato práce byla napsána mnohem horším jazykem. Dále nejlepšejší vedoucí na světě Barče Chattové za příležitost věnovat se jedinečné oblasti vědy, za vstřícnost, laskavost, online poradenství 24/7 a mimo jiné i nejlepší scénku Vánočního večírku. Svému příteli Kubovi za všechny teplé večeře a čaje, bez nichž by nebyla nejen tato práce, ale ani zkoušky nebo cokoliv jiného. Stejně tak bych ráda poděkovala Kubově rodině za podporu a příležitosti vycestovat, díky nimž se mi rozšiřují nejen obzory, ale získala jsem i kontakty ke své budoucí stáži. Další obrovské díky musím směřovat k Víťovi Syrovátkovi za laskavost a čas a rady, bez nichž bych se se statistickými analýzami trápila mnohem déle. Profesoru Chytrému, vyučujícím a všem lidem z ÚBZ za jedinečnou atmosféru, kde se dobře pracuje a člověk se sem rád vrací.

Prohlášení

Prohlašuji, že jsem svoji diplomovou práci vypracovala samostatně s využitím informačních zdrojů, které jsou v práci citovány.

Brno 30. dubna 2019 ………………………………

Tereza Cahová

Contents

1. General introduction

1.1. Diatoms

Diatoms (Bacillariophyceae) are unique group of unicellular algae easily identifiable under the light microscope by the yellow-brown colour of their chloroplast.

They are characterised by the silica impregnated cell wall, making ornamented shell known as a frustule. The frustule consists of two almost equal halves called epivalve and hypovalve, which are connected by the girdle elements. The girdle elements are enclosing the cell and there are two sets called epicingulum and hypocingulum (Fig. 1).

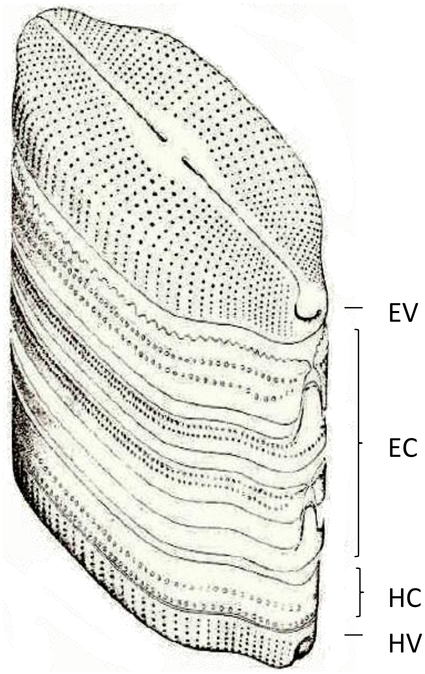

Fig. 1: Frustule of naviculoid diatom showing (EV) epivalve, (EC) epicingulum, (HC) hypocingulum and (HV) hypovalve (Round et al., 1990)

Each frustule is made of the older valve, which may have existed for several or many cell cycles, and the newer one, which was formed immediately after cell separation. The older valve with one set of girdle elements is called epitheca and the newer valve, which is usually smaller, with second set of elements is called hypotheca (Round et al.1990).

Diatom classification largely depends on ornamentation of valves, which can be seen better after removing the organic material. One of the most important features of many genera is the presence of the raphe system, consisting of one or two longitudinal slits through the valve. The length, position and structure of the raphe and its endings are important taxonomic characters. Other characteristics for diatom classification and determination are the shape of valve, striae density, presence of stigma etc (Chattová 2017a).

Detailed protoplast structure may vary in pennate and centric diatoms (Bellinger and Sigee, 2010), but as other eukaryotic organisms, the diatoms have diploid nucleus in protoplast and its position may differ in dependence to the taxa, Golgi apparatus, endoplasmic reticulum or chloroplast. Outside the plastids there are chrysolaminaran and lipid bodies functioning as food reserves.

Diatom chloroplast has yellow-brown colour and contains photosynthetic pigments chlorophylls a + c1, c2, c3 and fucoxanthin. Apart from these "light-harvesting", pigments diatoms also have group of photoprotective pigments containing β-carotene and the xanthophylls, diatoxanthin, diadinoxanthin, violaxanthin, antheraxanthin, and zeaxanthin (Kuczynska et al.2015).

Under the light microscope we can observe diatoms as single non-flagellate cells, simple colonies or chains of connected cells. The form of diatom cell wall makes any organisation other than simple colonies difficult to imagine, because the wall does not allow the cells to stay in close association during the growth. But it has great compressional strength allowing to form simple colonies held by interlocking siliceous spines, processes or ridges. The colonies also can be formed by pads or stalks of mucilage, or by threads of polysaccharide (Round et al.1990)

Reproduction

Diatoms reproduce primarily vegetatively via asexual mitotic division. After the separation, both epitheca and hypotheca of the mother cell will become epitheca, one for each daughter cell. That leads to one cell with the same size as the mother cell and another smaller. It also leads to decreasing mean cell size in population in every new generation (Smol and Stoermer 2010). Size restoring is usually via auxospore, its formation is usually associated with sexual reproduction (vegetative size restoring is possible, yet extremely rare, for example *Skeletonema costatum* (Greville) Cleve 1873 (Gallagher 1980 in Round et al.1990). The auxospore further develops into single, maximally sized cell called initial cell, which may differ from the vegetative cell in valve outline or structure (Werner 1977).

Ecology

Diatoms can be found in almost all water habitats except the hottest and most hypersaline. They can be found in the phytoplankton (in open water) and phytobenthos (on moist or submerged surfaces) of marine and freshwater without dependence on latitude and it is hard to find a sample without any diatom cell.

Benthic diatoms are more diverse, both in terms of numbers of species and the present life forms. But unfortunately, benthic communities are more difficult to sample and quantify than planktonic. Benthic communities may be classified according to their substrata: epi- and endopelic associated with mud, epipsammic with sand, epilithic growing on the surface of stones, epiphytic attached to plants and epizoic attached to animals. There are two categories of attached diatoms, first group's cells are closely appressed to the substrata as the *Amphora, Epithemia* or *Cocconeis*, the species of second category lives on stalks or pads of mucilage, like *Gomphonema* or *Cymbella* (Round et al.1990). Beside epizoic diatoms, there is also group of species living endosymbiotically in Foraminifera, mainly from genus *Nitzschia* (Lee et al.2000). Diatoms play a great role in primary production; they provide at 20 – 25 % of the world net primary production and at least 40 % of the oceanic net primary production. They are also important elements of biochemical cycles of several elements, mainly silica and carbon (Mann 1999).

Even though the majority of diatom species can be found mostly in aquatic habitats, there is significant number of taxa able to survive in dry areas e.g. dry mosses, humid rocks and soils. As all soil algae, in the soil food web, diatoms are sources of food for heterotrophic soil protozoa and micro- and meio fauna, such as nematodes or collembolants. Moreover, diatoms as primary producers are thought to be important contributors to the organic carbon content of soil. The algae cement soil particles together and thus contribute to soil stabilization. Beside bryophytes and lichens, soil algae play an important role as pioneer organism during colonization of raw soil (Heger, et al.2012, Stanek-Tarkowska and Noga 2012).

There are also a small number of diatom species, which can host endosymbiotic organisms. The freshwater populations of *Epithemia* and *Rhopalodia* possess a special ability to fix atmospheric nitrogen using a unicellular, nitrogen-fixing cyanobacterial endosymbiont. (DeYoe et al. 1992).

Applications of diatoms

Diatoms can be used in wide range of applications in the environmental and earth sciences. They can help to analyse ecological problems related to climate change, eutrophication or acidification. Diatoms can also function as indicators of ecological assessments of water quality or can be used for assessing chemical and biological conditions, diagnosing stressors of ecosystem, or determining biodiversity, because they respond sensitively to many changes in ecosystems, such as temperature, nutrient concentrations and herbivory (Smolt and Stoermer 2010). Also, there are promising attempts to create diatom index similar to existing aquatic indices, which can help to judge soil quality. Currently is known, that soil diatom communities can be used as indicators of anthropic disturbances in soil (Stanek-Tarkowska and Noga 2012, Antonelli et al.2017).

But diatoms also can be helpful in other fields of study such as forensics, nanotechnology and archaeology. In criminology and forensic medicine, diatoms are very useful in cases of drowning or immersing the body in the water post-mortem, in which diatoms have great diagnostic significance in fragmented or rotting bodies (Hirt and Vorel 2015). In archaeology diatoms can be useful in locating prehistoric settlement or clay sources for pot manufacture, or in reconstructing salinity and tidal regimes in estuaries (Battarbee 1988). This can serve for revealing ancient routes of the trade and communication, forgotten catastrophes or for paleoecological reconstructions. Diatoms can function as markers of atmospheric transport, can be used for tracking fish and seabirds and help with oil and gas exploration (Stoermer and Smol 2010). As mentioned above, oil and gas are mainly composed of dead diatoms cells, but also their frustules are important. Frustules are used as a soft, porous, fine-grained, lightweight, siliceous sedimentary rock called diatomite. Diatomite can be acquired by accumulation and compaction of diatom frustules. Those Diatom-rich sediments can be found in marine deposits, where they have been since the Late Cretaceous (~80 million years ago). Rich deposits are also in large lakes, where they have been accumulating since at least the Eocene (~50 million years ago) (Harwood et al. 2007). Mankind use diatomite for at least two thousand years and today diverse industries tries to make use of diatoms – food, pharmaceutical, chemical, agricultural etc. Diatomite is mainly used as filtration, insulation, absorption or building materials, mineral fillers, as a pesticide, catalysts, food additive etc. (Smol and Stoermer 2010).

Taxonomy

As mentioned, the traditional taxonomy and identification of diatoms is based mostly on the frustule morphology (valve size and outline, raphe system, stria density). Although additional ecological molecular, physiological and reproductive behavioural data are being increasingly collected together with molecular genetics method, which is becoming inexpensive, more widespread and easy, it is still doubtful whether they will ever entirely replace morphology, which provides continuity with past taxonomies, is easily to describe, cheaper and more accessible than other methods (Mann 2010).

Unfortunately, the current diatom taxonomy is "messy" according to David Mann (1999). For example, Spammer (1997) discuss the problem of diatom taxonomy using a reference to a group of small celled *Stephanodiscus* species. Here, misinformation, repetition of published mistakes and unadvised 'corrections' lead to cosmopolitan species *Stephanodiscus minutulus* (Kützing) Cleve & Möller 1882 (the current taxonomic concept of the basionym *Cyclotella minutula* Kiitzing) 1844 or *S. minutus* Pantocsek, which in fact consisted of at least eleven taxonomically distinct species in two genera. Second example proving difficulty of diatom taxonomy is case of *Thalassiosira rotula* Meunier 1910 and *T. gravida* Cleve 1896. Originally, there were two species with different valve structure and ecology. *Thalassiosira rotula,* was common species in colder seas, while *T. gravida* in warmer seas. But they also coexisted in spring diatom bloom in Scotland. After series of experiment, it was found that *T. rotula* is only heterotypic synonym of *T. gravida* and the differences in morphology are caused by water temperature or amounts of nutrients (Sar et al.2011).

In the world there is currently known over 75 000 described diatom taxa (Kociolek et al.2019), but some studies presume, that number of diatom species is above 200 000, which means that with assumed amount of 72 500 species of algae, there are 4-5 diatom species on one from any other group of algae (Guiry 2012). Also, the Bacillariales has more described species than all of the mammals combined (Kociolek et al.2019).

Currently, diatoms belong to infrakingdom of Stramenopila (syn. Heterokonta) and superclass Diatomea (syn. Bacillariophyta). Centric diatoms with radial symmetry belong to group Coscinodiscophytina and the pennate to group Bacillariophytina (Adl et al.2012)

Biogeography and dispersal of diatoms

As other microorganisms, diatoms disperse between localities using passive mechanisms. Diatoms can disperse by animals, wind, water and people (Kristiansen 1996). As example of dispersal by human activities can serve spreading diatoms such as *Bacteriastrum furcatum* Shadbolt 1854, *Odontella aurita* (Lyngbye) C. Agardh 1832 or *Thalassiosira pacifica* Gran & Angst 1931 (Hallegraeff and Bolch 1992). The ability to disperse differs amongst species and depends on a whole range of factors e.g. its morphological and physiological characteristics (adaptations to factors causing stress, the presence of resting cells tolerant to stress and active motion) and on the characteristics of the habitat which has to be overcome during the dispersal. Diatoms should be resistant to a large amount of adverse conditions when dispersing over a long distances, such as desiccation, sudden temperature changes and UV irradiance (Souffreau et al. 2010, 2013). With unfavourable condition are usually connected specialized resting cells and spores, differencing from vegetative cells in appearance as well as physiology, having thicker frustule of rounder shape and less elaborate surficial pattern. The term resting cell identifies cells that have undergone physiological changes but remain morphologically very similar to vegetative cells (McQuoid and Hobson 1996). There are also special summer/winter and cold/warm water cell types produced by Antarctic species as *Thalassiosira antarctica* Comber 1896 or *Eucampia antarctica* (Castracane) Mangin 1915, which are usually morphologically distinct from vegetative cells. These forms are an important adaptation to survive extreme seasonality of the polar regions (Allen 2014).

According to the ubiquity hypothesis, diatoms have unlimited dispersal abilities. That means diatoms are a cosmopolitan group of microorganisms with weak or absent latitudinal diversity gradients (Baas-Becking 1934, Finlay 2002, Fenchel and Finlay 2004). Recent studies showed, that microorganisms, including diatoms have similar distribution patterns to those known from higher plants and animals, which reflect historical, ecological and continental/local conditions. Beside the persisting lack of data, it is realistic to assume, that at 30 % of the all protists are endemic. (Foissner 2006). For example, presence of latitudinal gradient was proved by Vyverman et al.(2007) using a global freshwater diatom data set, together with highly asymmetric regional genus richness between both hemispheres.

With regard to Antarctic and sub-Antarctic region, according to several fine-grained taxonomic revisions of regional diatom flora there are some areas with at least 40 % of endemic taxa varying in their geographical ranges, although Antarctic and sub-Antarctic regions are significantly less diverse than (sub-)Arctic regions (Vyverman 2010).

1.2. Diatom research in sub-Antarctic region

History of diatom research in Sub-Antarctic region

The historic collections of diatom samples from sub-Antarctic region are dated to the end of the eighteen century. The first man, who investigated diatom content of some samples, was Reinsch (1876, 1879). He investigated samples from Kerguelen Islands, collected by the Rev. A. E. Eaton, and identified twenty-one species, belonging to thirteen genera. O'Meara (1877) lead a less productive research and found only three diatom species on the nearby Marion Island. Samples from the Kerguelen Islands were also investigated by Hemsley (1885), who listed 14 taxa. First paper treating with composition of composition of South Georgia Islands was published by Reinsch (1890), listing ten diatom taxa. However, most of the taxa in these studies were cosmopolitan species (as for example *Pinnularia viridis* (Nitzsch) Ehrenberg 1843).

Typical sub-Antarctic diatom species were not observed until the first detailed studies at the beginning of the 20th century. Carlson (1913) studied freshwater diatoms of South Georgia near the coast of South America and listed fifty-five species and made considerable efforts to compare the recorded flora with nearby Falkland Islands, Southern Chile and Tierra del Fuego. Later, Fukushima (1965) observed forty-nine species from various sampling in South Georgia.

The present-day research

In past two decades, there was number of papers investigating terrestrial and freshwater diatom flora published from different sub-Antarctic islands – Keguelen Islands (Van de Vijver et al. 2001, Le Cohu 2005), Crozet Islands (Van de Vijver et al. 2002a), Heard Island (Van de Vijver et al. 2004), Tristan da Cunha (Van de Vijver and Kopalová 2008) and the Prince Edward Islands (Van de Vijver and Gremmen 2006, Van de Vijver et al. 2008b). In these works, the entire sub-Antarctic diatom flora is being revised using more fine-grained taxonomy based on a better analysis and interpretation of the morphological observations. This approach leads to description of many new species across the sub-Antarctic zone.

First published results of preliminary survey of the terrestrial and freshwater diatom flora of Amsterdam Island were published by Van de Vijver and Beyens (1999c), during this research, 90 taxa in 24 samples were observed. Further research of Amsterdam Island led also to description of new species, 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). Beside new species, also new genera were described. First one, *Microfissurata*, based on two species, one of them *Microfissurata australis* Van de Vijver & Lange-Bertalot 2009 was found in Museau de Tanche on Amsterdam Island (second in Italian Alps, Cantonati et al.2009). Second, *Ferocia*, found in lava tunnels of sub-Antarctic islands - *Ferocia setosa* (Greville) Van de Vijver & Houk 2017 from Amsterdam Island and *F. ninae* Van de Vijver & Houk 2017 from Crozet Archipelago (Van de Vijver et al.2017).

On the other hand, there is only few works from Saint-Paul, mostly taxonomic describing new species from genera *Luticola* (Van de Vijver et al.2002b, Chattová et al.2017b), *Humidophila* (Chattová et al.2018). Preliminary results of ecological study of moss-inhabiting and soil diatom communities on Saint-Paul were published by Chattová (2017a).

2. Material and Methods

2.1. Study site

Both, Amsterdam Island and Saint-Paul Island belong to The French Southern and Antarctic Lands (in French Terres australes et antartiques françaises, TAAF). In sub-Antarctic region, its parts are also Kerguelen Islands and Crozet Islands.

The sub-Antarctic region is an area between the Antarctica and area about 45° latitude, it consists of islands in the southern Atlantic, Indian and Pacific Oceans (Van de Vijver B.and Beyens L. 1999a) and can be divided to cold-temperature and warm-temperature sub-Antarctic zones.

The first sub-zone is characterized by cold temperate, strongly influenced by the sea during whole year. The precipitation exceeds 1 metre during the year, average monthly temperatures are above 0°C, rarely stays snow. The winds are strong, usually coming from the west. Kerguelen Islands and Crozet Islands belong to this sub-zone. The second sub-zone is warm with strong maritime influence during the year with mean monthly temperatures above + 10 °C. In this area is not permanent ice, precipitation exceeds 1 metre. In this sub-zone we can find Amsterdam Island and Saint-Paul Island (Stonehouse 1982).

2.1.1. Amsterdam Island

Amsterdam Island (37°50'S, 77°30'E) is located in Indian Ocean close to the East Indian mid-oceanic ridge, north of the subtropical convergence, 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). With Saint-Paul Island it is one of the most isolated islands in the world, being 3200 km from Australia, 4200 km from South Africa and 3300 km from Antarctica.

Amsterdam Island was discovered in 1522 by Sebastien Del Cano, but the first recorded landing was by Willem van Vlaming in 1696. The island is a 55 km^2 volcanic dome rising to 881 m (Mont de la Dives), elliptic in shape. Geologically, the island is very young and was probably formed during the last 700,000 years (Giret 1987). Much of the island is surrounded by steep cliffs and the only landing place is in the north. The climate is temperate oceanic with mean annual temperature of 13,8 °C.

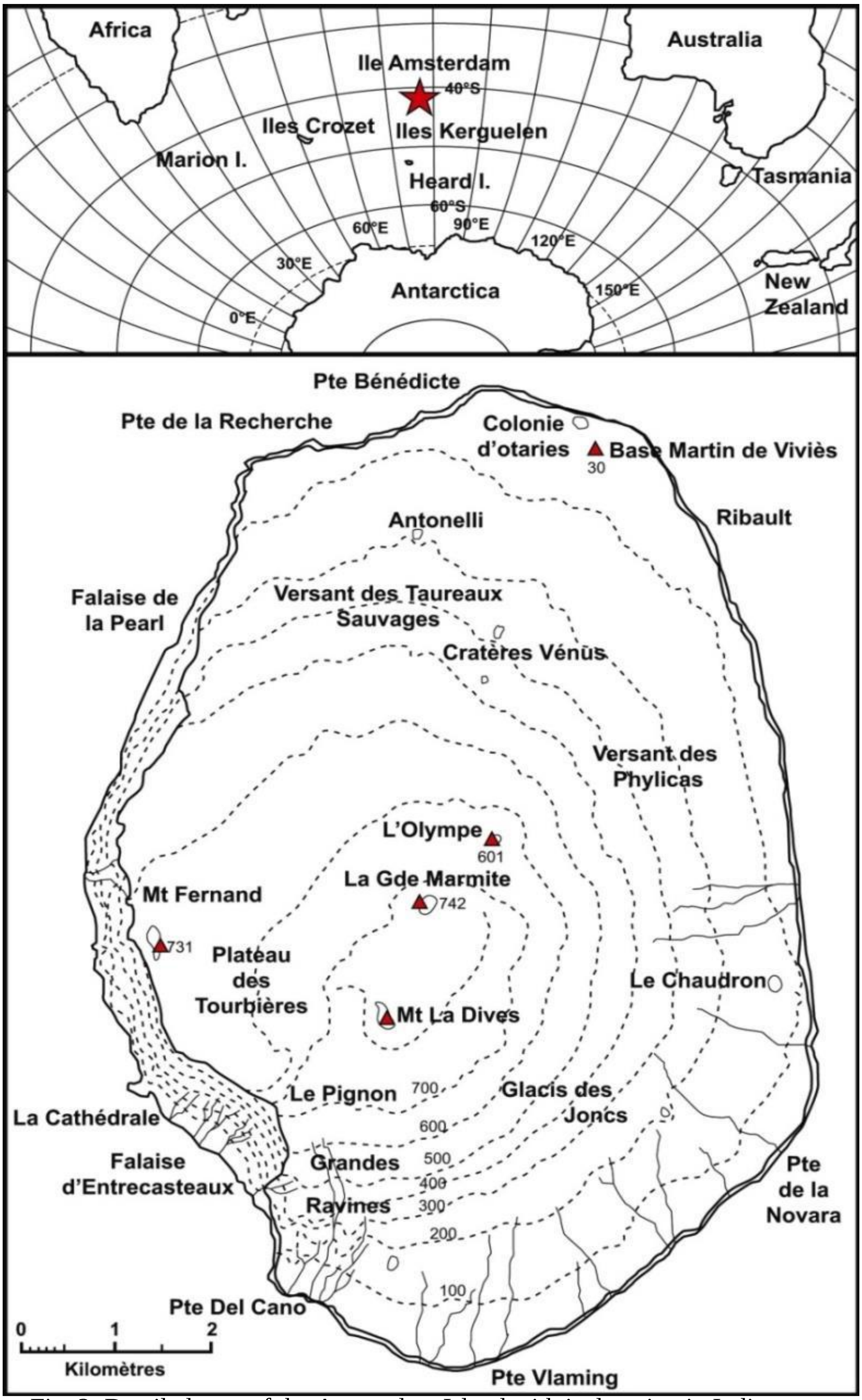

Fig. 2: Detailed map of the Amsterdam Island with its location in Indian Ocean (Chattová 2014).

The coldest month is August with a mean of 11,2 °C, while the warmest is February with a mean of 17,0 °C (data from the Meteorological Office Recording Station on Amsterdam Island; Micol & Jouventin 1995). Relative humidity is generally high (> 80%) due to the frequency of low cloud. Precipitation is usually high with an annual average of 1127 mm distributed over 239 days and falling primarily as rain. Permanent waterbodies are scarce and restricted to the higher plateau in the centre of the island and the southwestern part of the island (Van de Vijver et al.2008a).

Flora and fauna of Amsterdam Island

Among the French islands of the Southern Indian Ocean, Amsterdam Island is the richest in endemic species, but its native terrestrial ecosystem has been drastically modified. Although the island has not stable settlement, sealer and transoceanic voyagers caused irreversible damage to the native flora and fauna, either directly by fires and culling, or indirectly by introduced mammals (Micol & Jouventin 1995).

In the lowland there are patches of native tree *Phylica arborea* Thouars 1808, which is endemic to Amsterdam Island and Tristan Da Cunha Islands (Richardson et al.2003). The largest of these patches is called Grand Bois Phylica. But also individuals of introduced trees are found (*Cryptomeria japonica* (L. f.) D. Don 1923, *Pinus* sp., *Cupressus* sp., *Malus domestica* Borkh. 1803, *Mimosa* sp., *Prunus domestica* L. 1753, *Prunus persica* (L.) Batsch 1801). On the higher plateaus, the vegetation has the typical sub-Antarctic outlook, and consists of ferns, grasses, *Lycopodium* and mosses (Aproot et al.2011). The number of native vascular plants is currently 43 and there is 56 introduces species (Frenot et al.2001).

After centuries of anthropic influence, endemic fauna is rather poor and comprises a few marine bird species such as the rare, endemic Amsterdam albatross (*Diomedea amsterdamensis* Roux et al.1983), although early account by visitors and analysis of subfossil bones showed in the past rich avifauna containing 18 taxa, three of which were endemic to Amsterdam and Saint-Paul – a small flightless duck *Anas amsterdamensis*, a storm-petrel, two petrels of the genera *Pterodroma* and one prion (Micol & Jouventin 1995).

In 1871 the first sealers visiting Amsterdam had to disperse fur seals (*Arctocephalus tropicalis* Gray 1872) before landing, because the shore was completely covered by them. But after years of hunting fur seals for their skin, there are only several larger colonies on the island. Other big mammals are represented by elephant seals (*Mirounga leonina* L. 1758).

In mentioned year 1871 five individuals of cattle (*Bos taurus* L. 1758) were brought on the island and lately abandoned. After century they have made one of the few feral cattle herds in the world, but they have caused huge ecological damage on the native flora. Same as rats, cat and dog introduced by sealers, who threatened local avifauna (Micol & Jouventin 1995).

2.1.2. Saint-Paul Island

Saint-Paul Island is smaller island of 8 km^2, consisting of former calderra – eroded top of single volcano rising up to 268 m, located 80 km south of the Amsterdam Island. Now is island ear-shaped as on the lower east side, the rim of the crater has broken down and been invaded by the sea. In the past, this amphitheatre of bare rocks has been a favoured spot for fur seal (*Arctocephalus tropicalis*) and elephant seals (*Mirounga leonina*) to breed and bear their offspring. Apart from the inner shores of this shallow crater, the terrain is very broken and hard to traverse. There are some springs of hot water and other signs of active volcanic activity smouldering beneath the surface. As Amsterdam Island, Saint-Paul Island lies too far north to be within the true sub-Antarctic zone, but has a relatively mild, wet oceanic climate, with mean sea-level temperature of 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 exceeds 1100 mm with short dry season in summer, when evaporating exceeds rainfall (Data from Meteorological Office Recording Station on Amsterdam Island; Micol and Jouventin 2002).

Saint-Paul was discovered in 1559, but first description of it, and probably first landing, was by Willem van Vlaming in 1696. From its discovery, island has never been permanently inhabited, but was visited by sealer, who almost exterminated the sub-Antarctic fur seals. They also decimated the original flora and fauna through repeated carelessness with fire and introduction of non-native species, such as rats, mice and cats (Richards 1984). But through account of sealers, fisherman or sails, it is possible to provide general description of the early flora and fauna. The shore was covered with a multitude of seals, that visitors had to disperse them before landing. The whole island was covered with kind of coarse long grass or reeds and yielded various seabirds (Micol and Jouventin 2002).

2.2. Sampling

The fieldwork on Amsterdam Island and Saint-Paul Island was conducted during November and December 2016. A total of 287 diatom samples were collected, among them 76 soil samples. Sampling locations were chosen to represent a maximum variability of habitat types. All samples were localized using GPS and were accompanied by detailed site description. If possible, pH, specific conductance, soil temperature and moisture were measured.

Fig. 3: Map of the Amsterdam Island with samples locations. (Modified by MyMaps.google.com)

2.3. Slide preparation

To investigate detailed structure of ornamentation of siliceous frustule, it is necessary to remove all organic material. Diatom samples were prepared following the method described in Van der Werff (1955), which is effective and gentle. All 76 soil samples were prepared this way and further surveyed for diatoms.

Small amount of the samples was cleaned by adding 37% H_2O_2 and heated up to 80 °C for about 1 hour. The reaction was completed by adding $KMnO_4$. After that, digestion and centrifugation (three times 10 minutes at 3700 x g) was used. The resulting clean material was diluted with distilled water to avoid excessive concentrations of diatom valves that may hinder reliable observations. Then it was dried on cover slips and adhered to a microscope slide with high refracting index medium Naphrax®.

2.4. Determination and counting

All samples were observed at 1000x magnification on a random transect using an Olympus BX51 light microscope. In most samples was counted a standard quantity of 400 diatom valves, some samples yielded less than 300 valves. Considering the extreme environments involved, these numbers seemed acceptable (Beyens 1989).

Moreover, microphotographs of observed species in all samples were done by microscope and camera, and from these microphotographs plates for every sample were made, each of them containing microphotographs of species observed in the sample.

Identification was based on a numerous of publications, but mainly on following literature:

Chattová et al.(2017b), Chattová et al.(2018), Van de Vijver and Cox (2013), Van de Vijver et al.(2002a), Van de Vijver et al.(2008a), Van de Vijver et al.(2012), Van de Vijver et al.(2014), Van de Vijver et al.(2017).

In the resulting tables, the nomenclature was unified according to international AlgaeBase database.

2.5. Data analysis

For a pair wise comparison of the diatom flora of Amsterdam Island with those of the other sub-Antarctic Islands (Kerguelen Islands, Crozet Islands, Prince Edward Islands and Heard Islands) the Community Coefficient of Sørensen was used. This index has the following formula:

$$\frac{2c}{(a+b+2c)}$$

where *a* is number of exclusively observed species of the first site, *b* is number of exclusively observed species from the second site and *c* is the number of species shared by these two sites.

Non-metric Multidimensional Scaling (NMDS) was performed to reduce the multidimensional species data matrix in two dimensions best reflecting sites dissimilarities given by diatom species composition. NMDS was based on Bray-Curtis 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 and using the extended Indicator Species Analysis, indicator species were identified. The indicator value (IV) is product of two components, called 'A' and 'B', where component 'A' is the probability that the surveyed sites belongs to the target group given the fact that the species has been found. Component 'B' is the probability of finding the species in sites belonging to the site group (De Cáceres et al. 2010).

For statistical analyses the R environment was used (R Core Team 2018) with packages vegan, cluster and indicspecies (Oksanen et al.2019, Maechler 2018, De Cáceres and Legendre 2009).

3. Results

3.1.1. Species richness and diversity

Amsterdam Island

The analysis of 76 samples revealed the presence of 130 diatom taxa which belong to 36 genera and 6, where the genus was not determined. Seventeen additional taxa were observed outside the counts bringing the total number of soil diatoms up to 147. One sample contained almost no diatoms, even after counting the entire slide, and two samples contained only conidia and one sample was completely empty. These four samples (numbers S053, S078, S079, S101) have been removed from further analysis.

The distribution of species numbers per sample (Fig. 4) showed that most samples contained between 11 and 15 species. The average number (and standard deviation) of taxa per sample was 16 ± 8, with median number 11. Species richness per sample ranged from 2 to 39. The lowest species richness was recorded in the sample S036, which was almost monospecific with 398 valves of *Humidophila brekkaensis* (Petersen) R.L. Lowe et al.2014 and only 2 valves of *Luticola beyensii* Van de Vijver, Ledeganck & Lebouvier 2002. The most species rich sample (39 taxa) was sample S109.

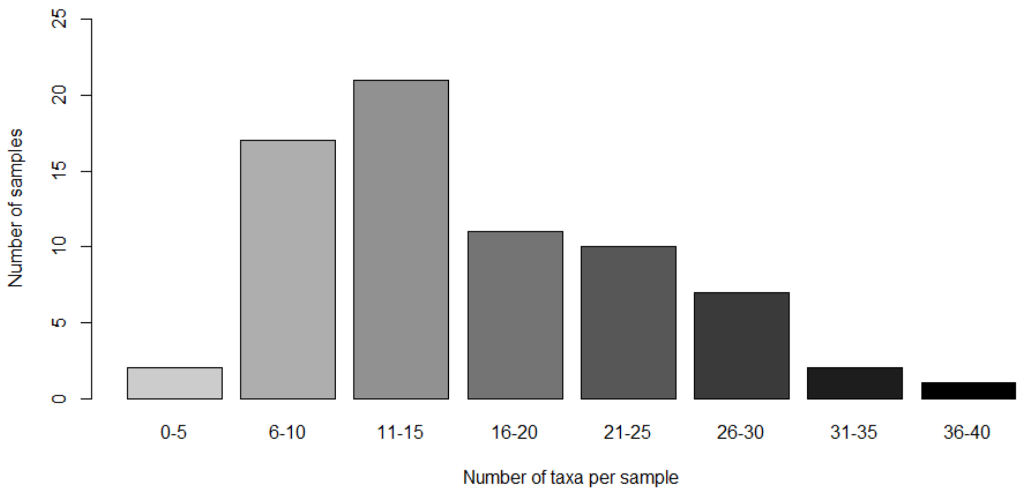

Fig. 4: Distribution of species richness per sample.

The five most abundant species accounted for 56.6 % of all counted valves. The dominant species were *Humidophila brekkaensis* (13.2 %), *Eunotia paludosa* var. *paludosa* Grunow (8.7 %), *Ferocia setosa* (6.6 %), *Humidophila rouhaniana* Chattová & Van de Vijver 2018 (5.5 %) and *Kobayasiella subantarctica* Van de Vijver & Vanhoutte 2002 (5.5 %). On the other hand, 104 taxa (more than 69.8 % of all counted taxa) had a total relative abundance of less than 1 %. From 129 taxa found during counting, there is actually 30 taxa (20.1 % of counted species), which could 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*, *Pinnularia*, *Pinnunavis* and *Sellaphora*). As mentioned, there is also 6 taxa (4 %) for which no genus was identified, all of these taxa appear to be new for science, but further research is needed.

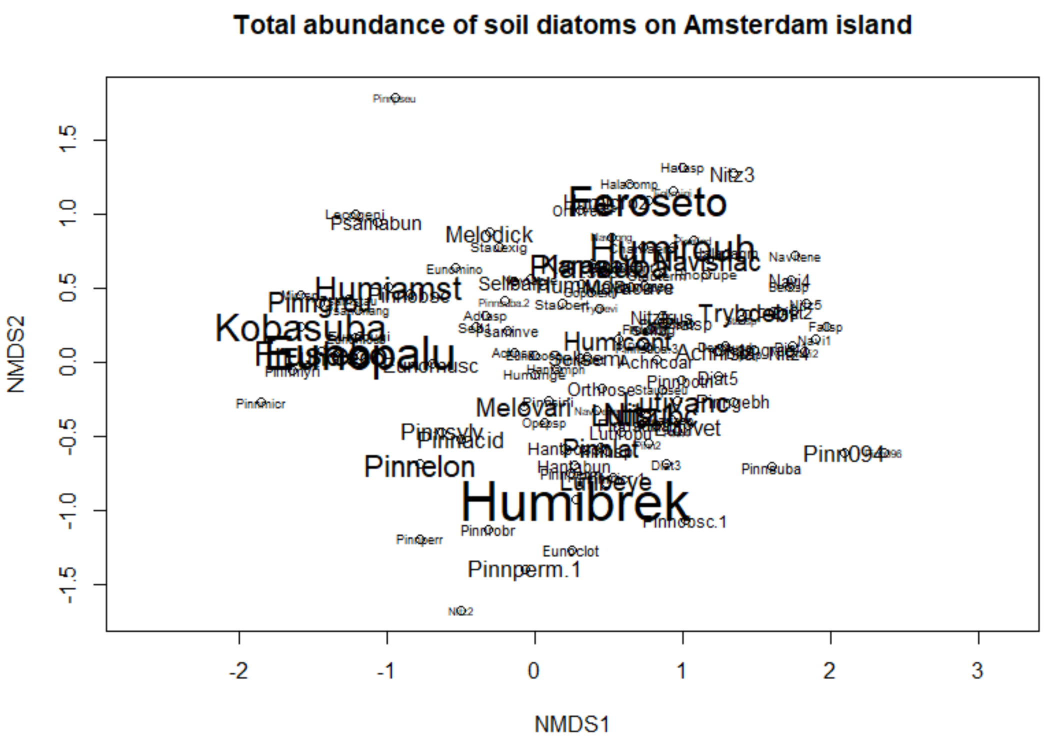

Fig. 5: Total abundance of soil diatoms on Amsterdam Island

Genus	n	%
Pinnularia	30	83,3
Eunotia	8	22,2
Navicula	8	22,2
Nitzschia	8	22,2
Humidophila	7	19,4
Sellaphora	7	19,4
Luticola	6	16,7
Stauroneis	5	13,9
Halamphora	4	11,1
Psammothidium	4	11,1
Achnanthes	3	8,3
Gomphonema	3	8,3
Hantzschia	3	8,3
Frustulia	2	5,6
Chamaepinnularia	2	5,6
Mayamaea	2	5,6
Melosira	2	5,6
Orthoseira	2	5,6
Pinnunavis	2	5,6
Platessa	2	5,6
Tryblionella	2	5,6
Adlafia	1	2,8
Achnanthidium	1	2,8
Berkeleya	1	2,8
Denticula	1	2,8
Diploneis	1	2,8
Fallacia	1	2,8
Ferocia	1	2,8
Kobayasiella	1	2,8
Lecohuia	1	2,8
Microfissurata	1	2,8
Opephora	1	2,8
Placoneis	1	2,8
Planothidium	1	2,8
Rhopalodia	1	2,8
Stauroforma	1	2,8

Tab. 1: Amsterdam Island genera ordered by decreasing percentil portion (%) calculated on the number of the taxa (n).

Saint-Paul Island

In 18 soil samples from Saint-Paul Island were found 53 diatom taxa in 20 genera. The distribution of species number per sample (Fig. 6) showed that most samples contained between 11 and 15 taxa per sample. The average number (and standard deviation) of taxa per sample was 14 ± 5, with a median number 15. Species richness per sample ranged from 6 to 24. The highest species richness was recorded in sample A6, and the lowest in the sample A17.

The 5 most abundant species were accounted for 60.1 % of all counted valves. The dominant species were *Luticola vancampiana* Chattová & B. Van de Vijver 2017 (18,2 %), *Humidophila contenta* (Grunow) R.L. Lowe et al.2014 (17.8 %), *Humidophila brekkaensis* (13.7 %), *Luticola beyensii* (5.9 %) and *Luticola subcrozetensis* Van de Vijver, Kopalová, Zidarova & Levkov 2013 (5.3 %). In contrast to Amsterdam Island, there were 38 species which had a total relative abundance of less than 1 % and accounted only for 9.6 % of all counted valves. Thirteen taxa (24.5 %) were identified only up to the genus level, and some of them appear to be new to science and are yet to be formally described (especially within the genera *Nitzschia* and *Hantzschia*).

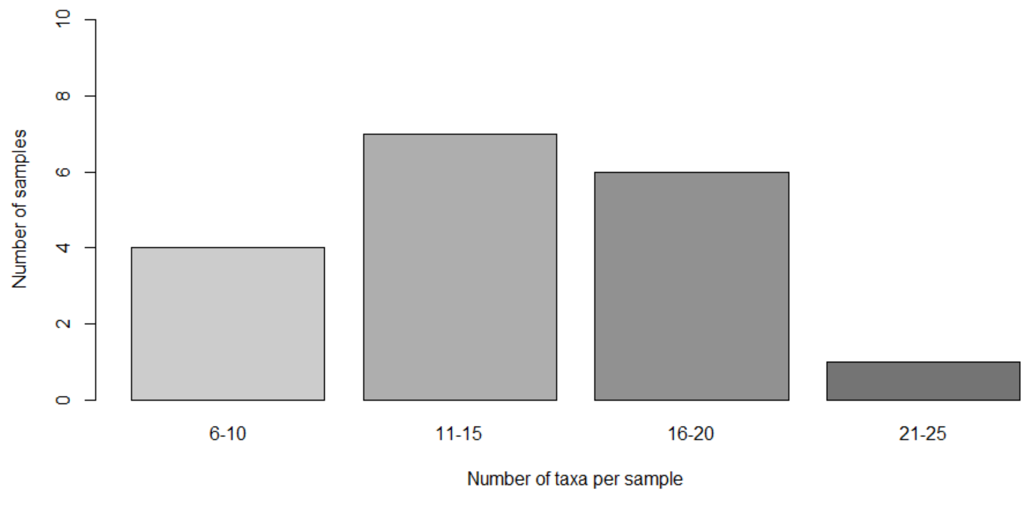

Fig. 6: Distribution of species richness per sample.

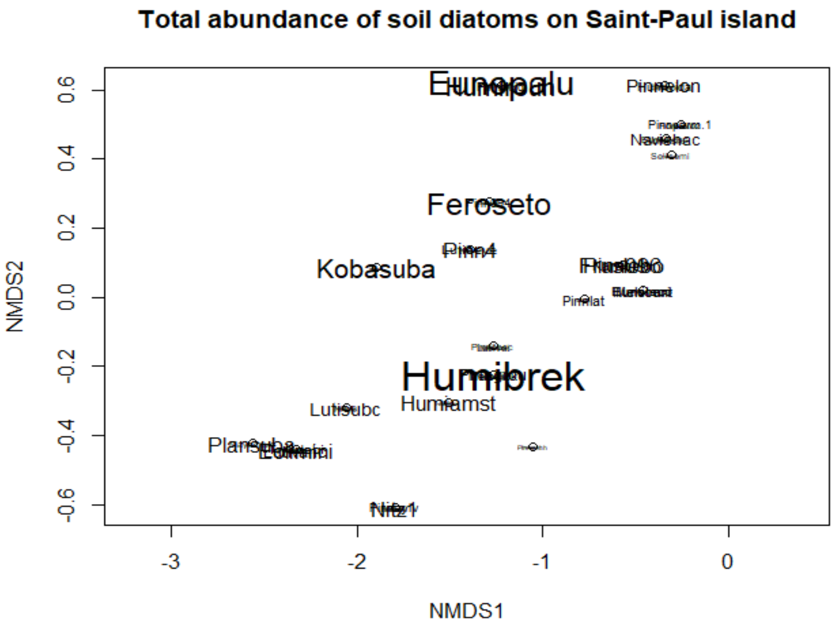

Fig. 5: Total abundance of soil diatoms on Sain-Paul Island

genus	n	%
Pinnularia	14	70,0
Nitzschia	6	30,0
Hantzschia	5	25,0
Humidophila	4	20,0
Luticola	4	20,0
Achnanthes	2	10,0
Eunotia	2	10,0
Mayamaea	2	10,0
Navicula	2	10,0
Pinnunavis	2	10,0
Achnanthidium	1	5,0
Aulacoseira	1	5,0
Denticula	1	5,0
Diploneis	1	5,0
Epithemia	1	5,0
Melosira	1	5,0
Orthoseira	1	5,0
Planothidium	1	5,0
Rhopalodia	1	5,0
Sellaphora	1	5,0

Tab. 2: Saint-Paul Island genera ordered by decreasing percentil portion (%) calculated on the number of the number of the taxa (n).

Figure 8 shows the biogeographical distribution of the diatom flora observed on Amsterdam Island and Saint-Paul Island. 25 % of the soil diatom taxa of both islands have typical cosmopolitan distribution, whereas 13.75 % of the species have restricted sub-Antarctic distribution. More than 10 % of all observed species can be considered endemic to Amsterdam Island, while another 3.47 % to be endemic to both studied islands. There is also 16.25 % of species, which can be considered endemic to both islands, and to one of the islands, but are yet undescribed. For more than 30 % of all observed taxa, biogeographical distribution is yet unknown.

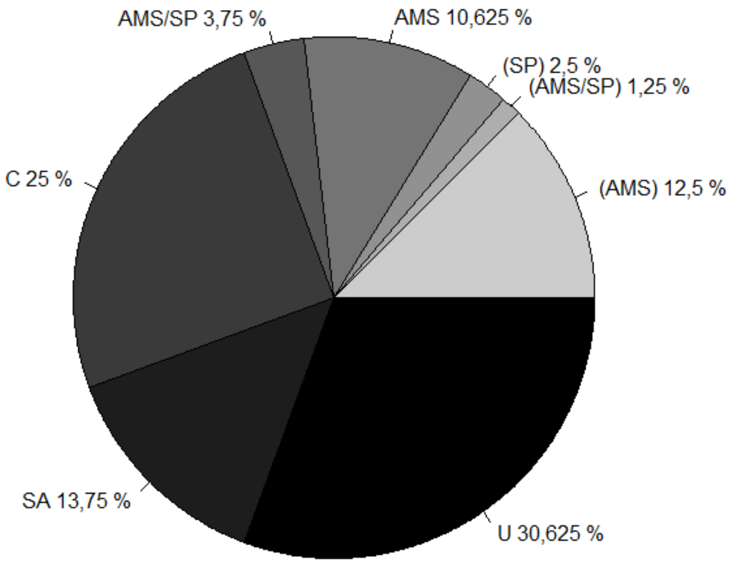

Fig. 8: Distribution of soil diatom taxa observed on Amsterdam Island and Saint-Paul Island according to their biogeographical distribution: (SA) sub-Antarctic, (C) cosmopolitan, (AMS/SP) Amsterdam Island and Saint-Paul Island, (AMS) Amsterdam Island, ((SP)) Saint-Paul but yet undescribed, ((AMS/SP)) Amsterdam Island and Saint-Paul Island but yet undescribed, ((AMS)) Amsterdam but yet undescribed, (U) unknown distribution.

The similarity analysis based on presence/absence data indicates that diatom flora of Amsterdam Island shows only a limited affinity to other sub-Antarctic islands, with Sørensen index values ranging from 0.21-0.36 (Tab. 3). The most similar island is, without big surprise, Saint-Paul Island, although the value of Sørensen index is quite low.

	Amsterdam Island	Kerguelen Islands	Crozet Islands	Prince Edward Islands	Heard Island	Saint-Paul Island
Number of taxa	180	231	235	188	191	53
Index of Sørensen		0,33	0,21	0,22	0,23	0,36

Tab. 3: Similarty analysis based on Sørensen index between Amsterdam Island and other sub-Antarctic islands.

Table 4 shows the results of the similarity analysis of different diatom floras within Amsterdam Island and Saint-Paul Island. Species list of soil samples from Amsterdam Island was compared with moss and water species from Amsterdam and with moss and soil species from Saint-Paul. Amsterdam Island's soil diatom flora is, according to Sørensen index, quite similar to mosses and water, but not identical and is also significantly species richer.

Amsterdam soil diatom flora also shows higher affinity to Saint-Paul diatom flora, but Sørensen index is still not very high. Although it is clear, that Saint-Paul's soil diatom flora is more similar to Amsterdam's soil, than the moss diatom flora.

	Amsterdam soil	Amsterdam moss	Amsterdam water	Saint-Paul moss	Saint-Paul soil
Number of taxa	147	123	99	41	53
Index of Sørensen		0,66	0,61	0,35	0,42

Tab. 4: Similarty analysis based on Sørensen index between soil diatom flora of Amsterdam Island and water and moss Amsterdam diatom flora and Saint-Paul diatom flora.

1.1.2. Community analysis

The NMDS analysis, based on a cluster dendrogram divides the samples into 5 main groups (Fig. 9). The distinction between 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 indicator value (IV) ranging from 0,89 – 0,99 (Fig. 9, De Cáceres 2010).

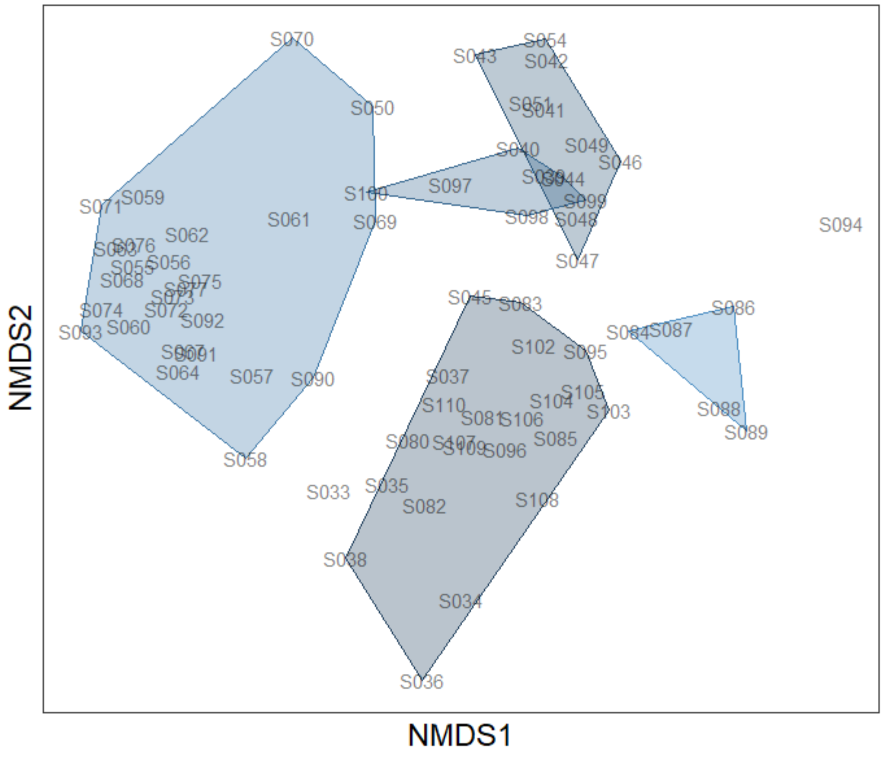

Fig. 9: NMDS diagram showing 5 main groups of samples.

The first group is formed in the bottom of the diagram, and consists mainly from the samples from Del Cano. Indicator species of this group is *Luticola beyensii* (IV 0,909, p-value 0,01). Beside *Luticola beyensii*, in samples of this group are also abundant *Achnanthes* aff. *islandica* Østrup 1918, *Humidophila brekkaensis*, *Luticola subcrozetensis* and *L. vancampiana* or *Nitzschia frustulum* (Kützing) Grunow *1880*. These samples are from localities with mostly dry soil and poor vegetation of *Spartina* or *Scirpus*, few of them are influenced by seaspray. In the lower-left part of the group are samples from Grand Bois Phylica with dominant *Humidophila brekkaensis.* To the first group belongs also sample S082 from Entercasteaux, dominated by *Humidophila brekkaensis* and *Nitzschia* sp. 1.

Second group, the biggest one on the left side of the diagram, is mostly composed of samples from Plateau Museau de Tanche, and so from higher altitudes, slightly acidic. Indicator species are *Frustulia lebouvieri* Van de Vijver & Gremmen 2006 (IV 0,928, p-value 0,005) and *Kobayasiella subantarctica* (IV 0,885, p-value 0,01). In this group are also abundant species as *Eunotia paludosa* subsp. *paludosa*, *Humidophila amsterdamensis* Chattová & Van de Vijver 2018 or various *Eunotia* (*E. manguinii* Van de Vijver & Jüttner 2018, *E. lecohui* Van de Vijver 2008) and *Pinnularia* (*P. microstauron* (Ehrenberg) Cleve 1891, *P. acidicola* Van de Vijver & Le Cohu 2002, *P. myriamiae* Van de Vijver, Chattová & Metzeltin 2012) species.

The third group in the upper right part of the diagram shows group of samples with indicator species *Ferocia setosa* (IV 0,925, p-value 0,005). These samples were collected in the Grand Tunnel, a lava tube, where is enough moisture, but lack of light. Besides mentioned *Ferocia setosa*, in these samples were abundant also various species of the genus *Humidophila* (mostly *H. rouhaniana*, less *H. contenta* or *H. crozetikerguelensis* (Le Cohu & Van de Vijver) Lowe et al.2014) and in a few samples *Orthoseira roeseana* (Rabenhorst) Pfitzer 1871 or *Platessa oblongella* (Østrup) C.E.Wetzel, Lange-Bertalot & Ector 2017.

Fourth group in the middle of the diagram contains slightly acidic samples from rock walls of Del Cano. Indicator species here are *Platessa oblongella* (IV 0,948, p-value 0,005) and *Planothidium subantarcticum* B. Van de Vijver & C.E.Wetzel 2013 (IV 0,928, p-value 0,005). This group is also interesting, because it is composed technically from only four samples from Del Cano (S097, S098, S099 and S100), from moist localities with mosses and liverworts. All these samples are dominated by mentioned indicator species, but they are also species rich and contain high concentration of diatom valves. Abundant species of this group are also *Sellaphora seminulum* (Grunow) D.G.Mann 1989 or various species of the genus *Humidophila.*

Last group, fifth, located in the right part of the diagram is composed of Entercasteaux samples. As indicator species *Chamaepinnularia gracilistriata* Van de Vijver & Beyens 2002 (IV 0,961, p-value 0,005), *Tryblionella debilis* Arnott ex O'Meara 1873 (IV 0,927, p-value 0,045) and *Navicula* sp. 4 (IV 0,894, p-value 0,03) were marked. These samples are from dry, rocky localities almost without vegetation, but rich of nutrient from near albatross colony. Besides indicator species, *Achnanthes* aff. *islandica, Humidophila rouhaniana* or *Luticola vancampiana,* are abundant.

The cluster analysis also shows three samples, which stand isolated from the mentioned five groups. Due to the unique species composition, the indicator species analysis identified distinct indicator species for these three samples.

First of these samples is S033 from the tractor road near Grand Bois Phylica with moist soil and vegetation (*Juncus*, *Scirpus*, *Isolepis*). On the NMDS diagram, the sample can be found between the two biggest groups on the left bottom. As indicator species, *Pinnularia perirrorata* Krammer 2000 (IV 0,989, p-value 0,05), *Pinnularia robbrechtii* Van de Vijver 2012 (IV 0,98, p-value 0,05) and *Pinnularia perminor* M. Kulikovskiy, Lange-Bertalot & Metzeltin 2010 (IV 0,971, p-value 0,02) were marked.

Second sample is S094 from the rock in the fur seal colony, with moist soil and without any vegetation. This sample is dominated by *Pinnularia* sp. 094 (IV 0,995, p-value 0,01) together with *Pinnularia subacoricola* Metzeltin, Lange-Bertalot & García-Rodríguez 2005 (IV 0,979, p-value 0,01).

Third sample is S108 from Del Cano. On the NMDS diagram it is hidden under the first group on the bottom, but according to the cluster dendrogram it stands aside. The sample was collected on the red soils affected with seaspray with little vegetation and cyanobacteria and moss crusts. Three indicator species were identified: *Pinnularia* cf. *obscura* Krasske 1932 (IV 0,993, p-value 0,25), *Pinnunavis* sp. (IV 0,920, p-value 0,025) and *Pinnularia microcapitata* Van de Vijver, Chattová & Metzeltin 2012 (IV 0,908, p-value 0,045).

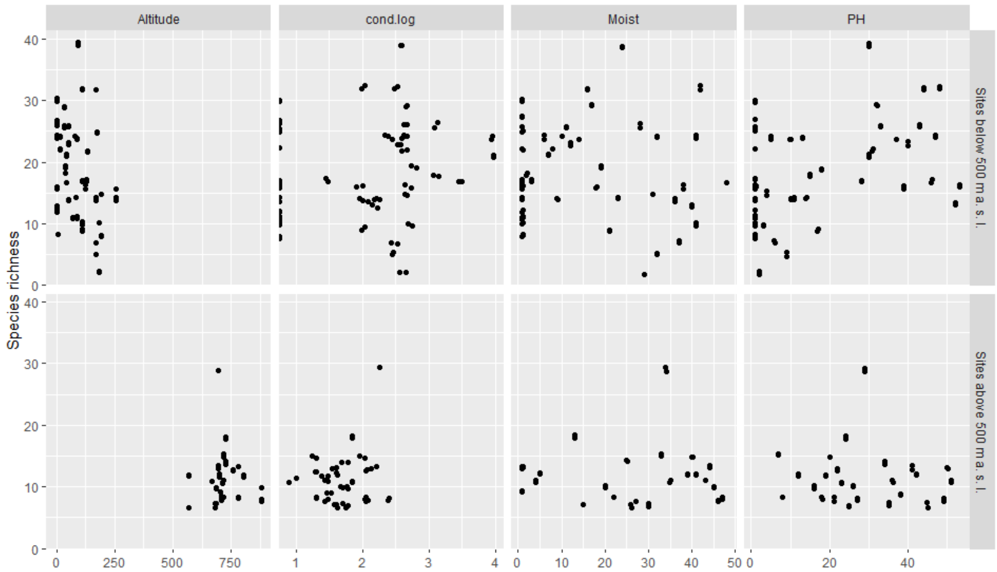

Fig. 10: A scatter plot showing a relation between species richness and environmental variables (altitude, conductivity, moisture and pH)

Analysis of relationship between species richness and environmental variables on the Amsterdam Island was analysed with the samples divided in two main groups, according to altitude (Fig. 10). The analysis shows barely recognizable trend of increasing species richness with growing pH in the higher altitudes. In the lower altitudes unfortunately shows no significant trend.

2. Discussion

Species composition

When talking about Amsterdam Island, the most crucial species was *Humidophila brekkaensis,* a cosmopolitan species often found on mosses (even dry) or liverworts, occurring with *Luticola beyensii* or *Eunotia paludosa* (Chattová et al.2018). Within five most abundant taxa, three were cosmopolitan (*Humidophila brekkaensis, Eunotia paludosa* var. *paludosa* and *Ferocia setosa*), one species with a typical sub-Antarctic distribution (*Kobayasiella subantarctica*) and one endemic to Amsterdam Island (*Humidophila rouhaniana*).

Species with the highest frequency of occurrence were *Nitzschia* sp. 1, which was found in 39 samples (of 76 total), with high probability endemic species to Amsterdam Island. Within five most common species are also represented cosmopolitan species (*Humidophila brekkaensis*, 34 samples, *Eunotia paludosa* var. *paludosa*, 38 samples), sub-Antarctic species (*Luticola subcrozetensis*, 35 samples) and species with unknown distribution (*Melosira* aff. *varians* C.Agardh 1827, 32 samples).

The most abundant species of Saint-Paul Island was *Luticola vancampiana*, which is so far endemic to the Amsterdam/Saint-Paul Islands. Within five most abundant species of soil diatom flora of Saint-Paul Island are species of typical soil genera *Luticola* (*L. beyensii* and *L. subcrozetensis*) and *Humidophila* (*H. contenta* and *H. brekkaensis*).

Soil genera play the biggest role on scale of frequency of occurrence. The five most common species are *Humidophila brekkaensis* (18 samples), *Humidophila contenta* (16 samples), *Luticola beyensii* (16 samples), *Hantzschia amphioxys* (Ehrenberg) Grunow 1880 (14 samples) and *Luticola subcrozetensis* (14 samples).

The unique thing about Amsterdam Island's diatom flora is occurance of several genera (*Pinnularia, Nitzschia, Humidophila*) with amount of differentiated species, often new for science and for now looking like endemic, at least for Amsterdam Island and Saint-Paul Island. This can be a consequence of geographical isolation and volcanic origin of both islands, which favours high levels of speciation (Chattová 2017a).

Biogeography

The low similarity values based on presence/absence data between Amsterdam Island and other sub-Antarctic islands are not surprising, especially considering the large distance between the islands, the isolated position of Amsterdam Island, the differences in the microhabitat diversity, and also the relatively young geological age. Although the closest to Amsterdam Island based on its diatom flora was the neighbouring Saint-Paul Island, the similarity values were quite low. This can be caused by relatively small number of observed species on Saint-Paul Island, most of which are common on Amsterdam Island and just few unique for Saint-Paul. In similarity values, Saint-Paul Island is followed by Kerguelen Islands.

The reasons of low similarity values can be illustrated on several examples. Whereas on Amsterdam Island and Saint-Paul Island species of *Pinnularia* and *Eunotia* dominated in the soil communities, the situation is a bit different on Ille de la Possession (Crozet Archipelago), where the most important genera (beside *Pinnularia*) are *Humidophila, Achnanthes, Fragilaria* and *Navicula* (Van de Vijver et al.2002c). The diatom floras dominated with species of genus *Achnanthes* are also reported from Kerguelen Islands (Van de Vijver et al.2001) and South Georgia (Van de Vijver & Beyens 1997).

Community analysis

The analysis of relationship between species richness and environmental variables did not show significant trend, but that does not mean, that environment does not influence the species composition. The diatom distribution indicates, that the major factors involving the structure of the soil diatom communities of Amsterdam Island are especially pH and moisture.

The acidic diatom communities represented by the second (the biggest) group can be found especially in the higher altitudes (above 500 m a. s. l.) on locations characterized by peat-bogs with higher moisture levels and acidic pH. These samples are dominated by *Frustulia lebouvieri, Humidophila amsterdamensis* and several *Eunotia* species (especially *E. paludosa* var. *paludosa*), accompanied with various *Psammothidium* taxa. Almost identical communities were observed from same locations in freshwater samples (Chattová et al.2014) and in mosses (Chattová

2017a). Also, similar diatom communities characterized by the dominance of *Eunotia paludosa* var. *paludosa* were reported from South Georgia (Van de Vijver & Beyens 1997) or Ile de la Possession (Van de Vijver & Beyens 1999b) and Kerguelen Islands (Van de Vijver et al.2002c). However, differences can be found in species, which accompany the dominant one, for example as co-dominant on Ile de la Possession was reported *Chamaepinnularia muscicola* (J.B. Petersen) Kulikovskiy et al.2010 and *Achnanthes aueri* Krasske 1949 with *Fragilaria maillardii* Le Cohu 1986 on Kerguelen Islands (Van de Vijver & Beyens 1999b; Van de Vijver et al.2002c).

Another acidic samples can be found in Entercasteaux and Del Cano in lower altitudes (about 220 m a. s. l.). These localities are both characterized by steep cliffs with small ravines. Samples from these localities are in groups 1, 4 and 5. In the first group most of the species are similar, these samples are dominated by *Humidophila brekkaensis* accompanied by *Nitzschia* sp. and *Luticola species* in contrast with moss-inhabiting communities with species preferring alkaline conditions (Chattová 2017a). Groups 4 and 5 completely differ. Group five is represented by only a few samples from soils strongly influenced by animals (albatrosses and fur seals) with indicator species *Chamaepinnularia gracilistriata* and *Tryblionella debilis* accompanied by abundant *Achnanthes* aff. *islandica*, *Humidophila rouhaniana* and *Luticola* species. Completely different diatom communities on soils influenced by animals were also studied on Kerguelen Islands, where the most typical species were *Staurosirella pinnata* (Ehrenberg) D.M. Williams & Round 1988, *Pinnularia kolbei* Fukushima, Kobayashi & Yoshitake 2000 and *Planothidium delicatulum* (Kützing) Round & Bukhtiyarova 1996. Group 4 shows more affinity to samples from Grand Tunnel, very likely because of the habitat similarity. This group consists of species of wet rock walls with abundant *Planothidium subantarcticum* and *Platessa oblongella.* This type of sample was not recorded on Kerguelen Island, but similar communities dominated by *Planothidium subantarcticum* were observed in mosses of Ile de la Possession, together with various fragilarioid taxa, such as *Frankophila maillardii* (R.Le Cohu) Lange-Bertalot 1997 or *Distrionella germainii* (Reichardt & Lange-Bertalot) Morales, Bahls & Cody 2005, in the contrary to the Amsterdam Island where only a few araphid taxa can be found (in soils were found *Pseudostaurosira* *trainorii* E.A.Morales 2001 and *Stauroforma* aff. e*xiguiformis*; Van de Vijver and Beyens 1999b).

The major factors determining the soil diatom communities of Amsterdam Island are pH, moisture and specific conductance and their combination. There are clearly distinct groups of samples of acidic wet soils, acidic dry soils, wet rock walls (and lava tunnel) and nutrient rich soils influenced by animals. The most species rich samples are found in all groups, usually on moist localities with slightly acidic pH.

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4. Appendix

Tab. 3: Taxonomical list of all observed taxa with their distribution: (SA) sub-Antarctic, (C) cosmopolitan, (AMS/SP) Amsterdam Island and Saint-Paul Island, (AMS) Amsterdam Island, ((SP)) Saint-Paul but yet undescribed, ((AMS/SP)) Amsterdam Island and Saint-Paul Island but yet undescribed, ((AMS)) Amsterdam Island but yet undescribed, (U) unknown distribution. Species found outside the counts are marked with an asterisk.

Species	Distri-bution	AMS moss	AMS water	AMS soil	SP moss	SP soil
Adlafia sp.	U			X		
Achnanthes aff. *islandica* Østrup	U		X	X		
Achnanthes brevipes var. *intermedia* (Kützing) Cleve	C					X
Achnanthes coarctata (Brébisson) Grunow	C	X	X	X	X	X
Achnanthes muelleri Carlson	SA	X	X	X		
Achnanthes naviformis Van de Vijver & Beyens	SA	X	X		X	
Achnanthes sp. 1	U			X*		
Achnanthidium sieminskae Witkowski, Kulikovskiy & Riaux-Gobin	SA	X	X			X
Achnanthidium sp.	U	X		X		
Amphora cf. *pediculus* (Kützing) Grunow	U			X*		
Aulacoseira sp	(SP)					X
Berkeleya sp.	U			X		
Caloneis bacillum (Grunow) Cleve	C	X	X			
Cosmioneis sp.	U			X*		
Craticula submolesta (Hustedt) Lange-Bertalot	C	X	X			
Cyclotella sp.	U			X*		
Denticula cf. *sundaysensis* Archibald	U	X	X	X	X	X
Diatom sp. 1	(AMS)			X		
Diatom sp. 2	(AMS)			X		
Diatom sp. 3	(AMS)			X		
Diatom sp. 4	(AMS)			X		
Diatom sp. 5	(AMS)			X		
Diatom sp. 6	(AMS)			X		
Diatomella balfouriana Greville	C	X				
Diploneis sp.	U			X		X
Epithemia sp.	(SP)					X
Eunotia aff. *minor* (Kützing) Grunow	U	X		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	X
Eunotia cocquytiae Van de Vijver	AMS	X	X	X		
Eunotia lecohui Van de Vijver	SA	X	X	X		
Eunotia manguinii Van de Vijver & Jüttner	SA	X	X	X		X
Eunotia mourotii B.Van de Vijver, M.de Haan & Lange-Bertalot	U			X		
Eunotia paludosa var. *paludosa* Grunow group	C	X	X	X		
Eunotia pugilistica Van de Vijver	AMS	X	X	X		
Eunotia sp.	U			X*		
Fallacia sp.	U			X		
Ferocia setosa (Greville) Van de Vijver & Houk	C	X	X	X		
Fistulifera sp.	U	X				
Frustulia lebouvieri Van de Vijver & Gremmen	SA	X	X	X		
Frustulia vulgaris (Thwaites) De Toni	C	X	X	X		
Geissleria sp.	U	X				
Gomphonema aff. *exilissimum* Grunow	U	X	X	X		
Gomphonema cf. *montanum* (J.Schumann) Grunow	U	X	X	X		
Gomphonema parvulum (Kützing) Kützing group	C	X	X	X*		
Halamphora compereana Van de Vijver & Levkov	AMS	X	X	X		
Halamphora dagmarobbelsiana Van de Vijver & Levkov	AMS	X		X		

Species	Distri-bution	AMS moss	AMS water	AMS soil	SP moss	SP soil
Halamphora sp.	U			X		
Halamphora veneta (Kützing) Levkov	C	X	X	X*		
Hantzschia abundans Lange-Bertalot	C	X		X	X	X
Hantzschia amphioxys (Ehrenberg) Grunow	C	X	X	X	X	X
Hantzschia possessionensis Van de Vijver & Beyens	SA	X	X	X	X	X
Hantzschia sp. 1	U	X			X	X
Hantzschia sp. 2	(SP)					X
Humidophila amsterdamensis Chattová & Van de Vijver	AMS	X	X	X		
Humidophila brekkaensis (Petersen) Lowe et. al.	C	X	X	X	X	X
Humidophila contenta (Grunow) Lowe et. al.	C	X	X	X	X	X
Humidophila crozetikerguelensis Le Cohu & Van de Vijver) Lowe et. al.	SA	X	X	X		X
Humidophila gallica (W. Smith) Lowe et al.	C	X	X			
Humidophila ingeae (Van de Vijver) Lowe et. al.	U			X		
Humidophila rouhaniana Chattová & Van de Vijver	AMS	X	X	X		
Humidophila vidalii (Van de Vijver, Ledeganck & Beyens) Lowe et al.	SA	X	X	X	X	X
Chamaepinnularia aerophila Van de Vijver & Beyens	SA	X	X	X		
Chamaepinnularia evanida (Hustedt) Lange-Bertalot	C	X				
Chamaepinnularia soehrensis var. *muscicola* (J.B.Petersen) Lange-Bertalot & Krammer	C	X				
Chamaepinnularia gracilistriata Van de Vijver & Beyens	SA			X		
Kobayasiella subantarctica Van de Vijver & Vanhoutte	SA	X	X	X		
Lecohuia geniculata (H.Germ.) Lange-Bertalot & U.Rumrich	C	X	X	X		
Luticola beyensii Van de Vijver, Ledeganck et Lebouvier	SA	X	X	X	X	X
Luticola ivetaiana Chattová & Van de Vijver	AMS/SP	X	X	X	X	X
Luticola robusta Van de Vijver, Ledeganck & Beyens	SA			X		
Luticola sp.	AMS/SP			X		X
Luticola subcrozetensis Van de Vijver et al.	SA	X	X	X	X	X
Luticola vancampiana Chattová & Van de Vijver	AMS/SP	X	X	X	X	X
Mayamaea cavernicola Van de Vijver & Cox	AMS	X	X	X		
Mayamaea cf. *agrestis* (Hustedt) Lange-Bertalot	U	X	X			
Mayamaea fossalis (Krasske) Lange-Bertalot group	C	X		X*		
Mayamaea sp.	(SP)					X
Mayamaea permitis (Hustedt) K.Bruder & Medlin	C	X	X	X*		X
Mayamaea sp. 2	U			X		
Melosira aff. *dickiei* (Thwaites) Kützing	U	X	X	X		
Melosira aff. *varians* C. Agardh	U	X		X		
Melosira sp.	U				X	X
Microfissurata australis Van de Vijver & Lange-Bertalot	AMS	X		X		
Navicula aff. *shackletonii* West & G.S.West	(AMS)	X		X		
Navicula cf. *bicephala* Hustedt	U	X				
Navicula cf. *cincta* (Ehrenberg) Ralfs	U					X
Navicula cf. *cryptotenella* Lange-Bertalot	U	X	X	X	X	X
Navicula cf. *longicephala* Hustedt group	U			X		
Navicula cf. *veneta* Kützing	U			X		
Navicula gregaria Donkin	C	X	X	X		
Navicula longicephala Hustedt group	C	X				
Navicula sp. 1	(AMS)			X		
Navicula sp. 2	(AMS)			X		
Navicula sp. 3	(AMS)			X*		
Navicula sp. 4	(AMS)			X		
Navicula veneta Kützing	C	X	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			

Species	Distri-bution	AMS moss	AMS water	AMS soil	SP moss	SP soil
Nitzschia dissipata (Kützing) Rabenhorst	C				X	
Nitzschia fonticola (Grunow) Grunow	C	X	X			
Nitzschia frustulum (Kützing) Grunow	C	X	X	X	X	X
Nitzschia palea (Kützing) W. Smith group	C	X	X		X	X
*Nitzschia soratensi*s Morales & Vis	C	X	X			X
Nitzschia sp. 1	(AMS/SP)	X	X	X	X	X
Nitzschia sp. 2	(AMS)			X		
Nitzschia sp. 3	(AMS/SP)			X		X
Nitzschia sp. 4	(AMS)			X		
Nitzschia sp. 5	(AMS)			X		
Nitzschia sp. 6	(AMS)			X		
Nitzschia sp. 7	(AMS)			X*		
Nitzschia sp. 8	(AMS)			X		
Opephora sp.	U			X		
Orthoseira roeseana (Rabenhorst) O'Meara	C	X	X	X	X	X
Orthoseira verleyenii Van de Vijver	AMS	X	X	X		
Pinnularia acidicola var. *acidicola* Van de Vijver & Beyens	SA	X	X	X	X	X
Pinnularia aff. *acidicola* var. *elongata* Van de Vijver & Beyens	U	X		X		
Pinnularia aff. *amsterdamensis* Chattová, Van de Vijver & Metzeltin	U	X			X	
Pinnularia aff. *microstauron* (Ehrenberg) Cleve	U	X		X		
Pinnularia aff. *subacoricola* Metzeltin, Lange-Bertalot & García-Rodríguez	U			X	X	X
Pinnularia amsterdamensis Chattová, Van de Vijver & Metzeltin	AMS	X	X			
Pinnularia australogibba Van de Vijver, Chattová & Metzeltin	AMS	X	X	X		
Pinnularia australogibba var. *subcapitata* Van de Vijver, Chattovà & Metzeltin	AMS	X	X	X*		
Pinnularia borealis Ehrenberg complex	C	X	X	X	X	X
Pinnularia bottnica Krammer	C	X	X	X		X
Pinnularia cf. *obscura* Krasske	U			X		
Pinnularia cf. *obscuriformis* Krammer	U			X	X	X
Pinnularia cf. *subacoricola* Metzeltin, Lange-Bertalot & García-Rodríguez	U			X		
Pinnularia cf. *vixconspicua* Chattová, Metzeltin & Van de Vijver	U				X	
Pinnularia lindanedbalovae B.van de Vijver & A.Moravcová	SA	X	X	X	X	X
Pinnularia microcapitata Van de Vijver, Chattová & Metzeltin	AMS/SP	X		X	X	X
Pinnularia microstauron (Ehrenberg) Cleve group	C	X	X	X		X
Pinnularia myriamiae Van de Vijver, Chattová & Metzeltin	AMS	X	X	X		
Pinnularia perirrorata Krammer	C			X		
Pinnularia perminor M.Kulikovskiy, Lange-Bertalot & Metzeltin	C	X	X	X		X
Pinnularia pseudohilseana Van de Vijver, Chattová & Metzeltin	AMS	X	X	X		
Pinnularia rabenhorstii var. *subantarctica* Van de Vijver & Le Cohu	SA	X	X	X		
Pinnularia robbrechtii Van de Vijver	AMS	X	X	X		
Pinnularia sinistra Krammer	C	X	X	X	X	X
Pinnularia sp. 1	U			X		
Pinnularia sp. 2	U			X		
Pinnularia sp. 3	U			X*		
Pinnularia sp. 4	U			X		
Pinnularia sp. S094	U			X		
Pinnularia sp. S096	U			X		
Pinnularia sp. S108	U			X*		
Pinnularia subacoricola Metzeltin, Lange-Bertalot & García-Rodríguez	C	X	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		X		
Pinnularia vixconspicua Chattová, Metzeltin & Van de Vijver	AMS	X	X			
*Pinnularia whinamia*e Van de Vijver	SA	X	X			
Pinnularia aff. *vlaminghii* Van de Vijver, Chattová & Metzeltin	U			X		
Pinnularia cf. *perminor* M.Kulikovskiy, Lange-Bertalot & Metzeltin	U			X		

Species	Distri-bution	AMS moss	AMS water	AMS soil	SP moss	SP soil
Pinnularia vlaminghii Van de Vijver, Chattová & Metzeltin	AMS	X	X	X*	X	X
Pinnunavis elegans (W.Smith) Okuno	C	X	X			
Pinnunavis gebhardii (Krasske) Van de Vijver	SA	X	X	X	X	X
Pinnunavis sp.	AMS/SP	X	X	X	X	X
Placoneis anglica (Ralfs) E.J.Cox	C	X	X	X	X	
Planothidium delicatulum (Kützing) Round & Bukhtiyarova	C		X			
Planothidium pericavum (J.R.Carter) Lange-Bertalot	C	X	X			
Planothidium subantarcticum B.van de Vijver & C.E.Wetzel	SA	X	X	X	X	X
Platessa oblongella (Østrup) C.E.Wetzel, Lange-Bertalot & Ector	C	X	X	X	X	X
Platessa sp.	U			X		
Psammothidium abundans (Manguin) Bukhtiyarova & Round	C	X	X	X		
Psammothidium incognitum var. *stauroneioides* (Manguin) Le Cohu	C	X	X	X		
Psammothidium investiens (J.R.Carter) L.Bukhtiyarova	C	X	X	X		
Psammothidium manguinii (Hustedt) Van de Vijver	C	X		X		
Pseudostaurosira naveana (Le Cohu) Morales & Edlund	C	X	X			
*Pseudostaurosira trainori*i E.A.Morales	C	X	X	X*		
Rhopalodia rupestris (W.Smith) Krammer	C	X	X	X		X
Sellaphora arvensis (Hustedt) C.E.Wetzel & L.Ector	C	X	X	X		
Sellaphora cf. *nigri* (De Notaris) Wetzel et Ector	U	X		X	X	
Sellaphora seminulum (Grunow) D.G.Mann	C	X	X	X	X	X
Sellaphora sp	(AMS)	X	X			
Sellaphora sp. 1	(AMS)			X		
Sellaphora sp. 2	(AMS)			X		
Sellaphora sp. 3	(AMS)			X		
Sellaphora barae B.van de Vijver & E.J.Cox	AMS	X	X	X		
Stauroforma aff. *exiguiformis* (Lange-Bertalot) R.J.Flower, V.J.Jones & Round	U	X	X	X		
Stauroneis cf. *bertrandii* Van de Vijver & Lange-Bertalot	U			X		
Stauroneis kriegeri Patrick	C	X	X			
Stauroneis pseudomuriella Van de Vijver & Lange-Bertalot	SA	X	X	X		
Stauroneis sp.	U			X		
Stauroneis thermicola (J.B.Petersen) J.W.G.Lund	C	X	X	X		
Stauroneis bertrandii Van de Vijver & Lange-Bertalot	SA	X	X	X		
Staurosira neoproducta (Lange-Bertalot) Chudaev & Gololobova	C	X				
Tryblionella aff. *levidensis* W.Smith	U			X		
Tryblionella debilis Arnott ex O'Meara	C	X	X	X	X	X

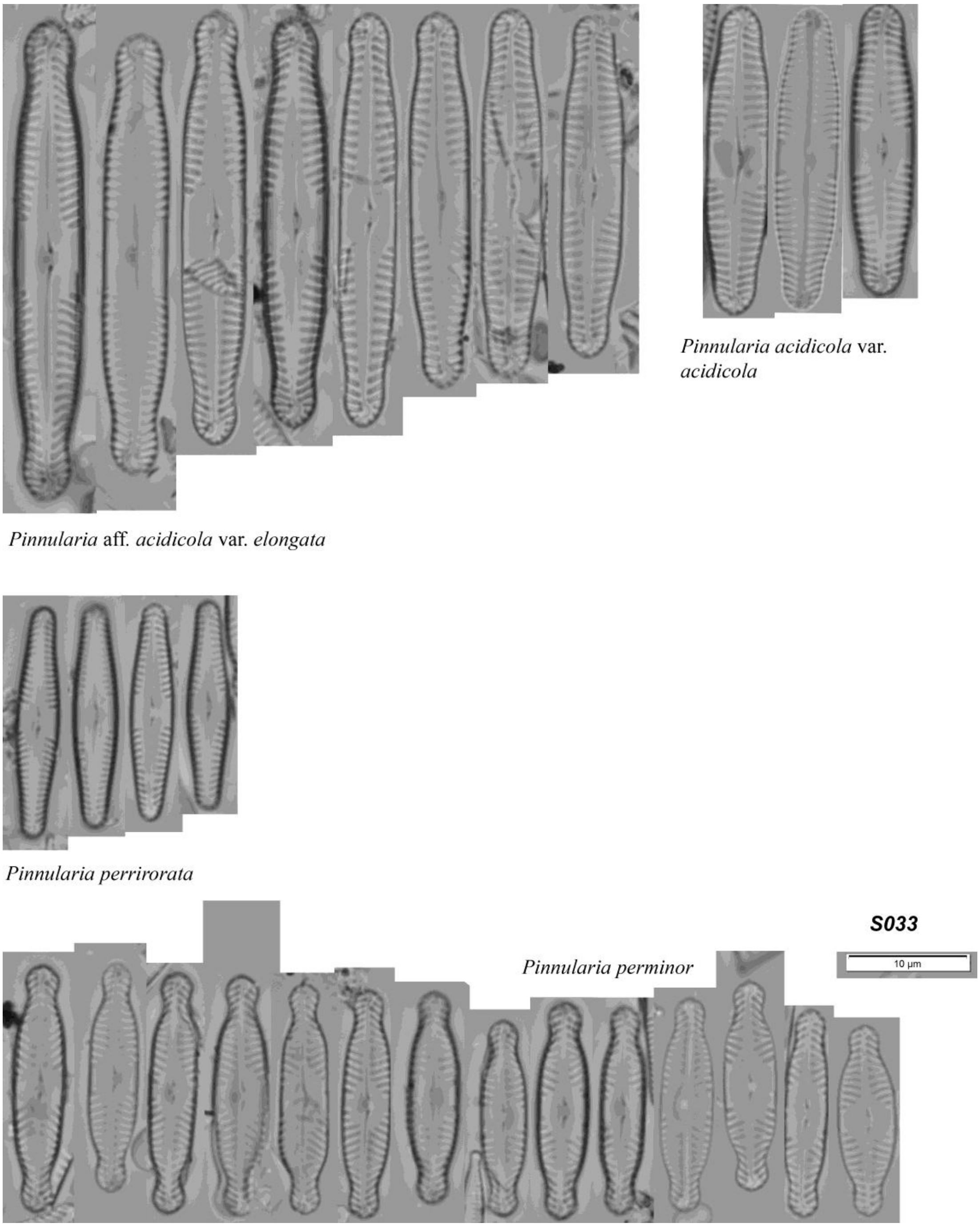


Fig. 11: Microphotographs of species observed in sample S033.

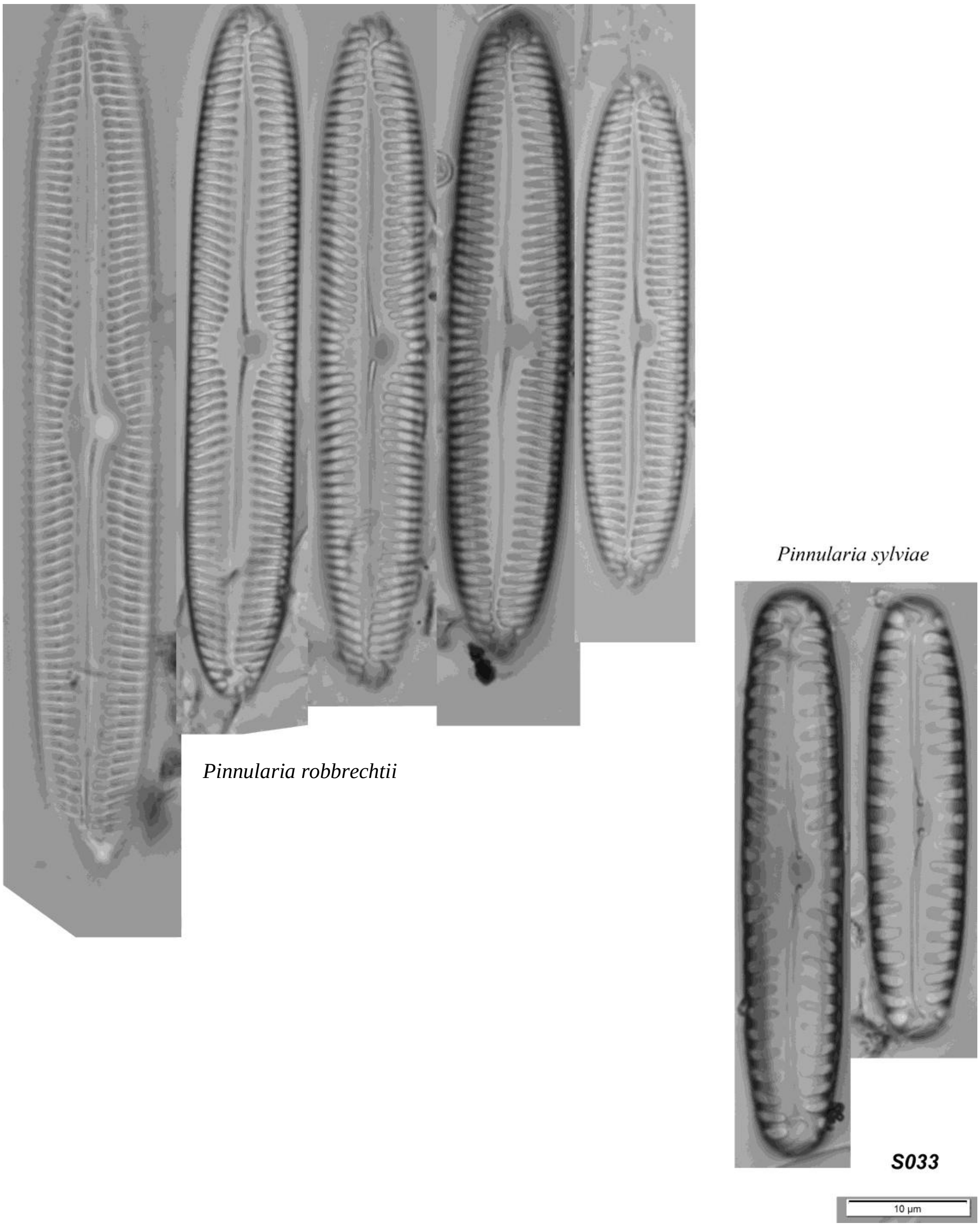


Fig. 12: Microphotographs of species observed in sample S033.

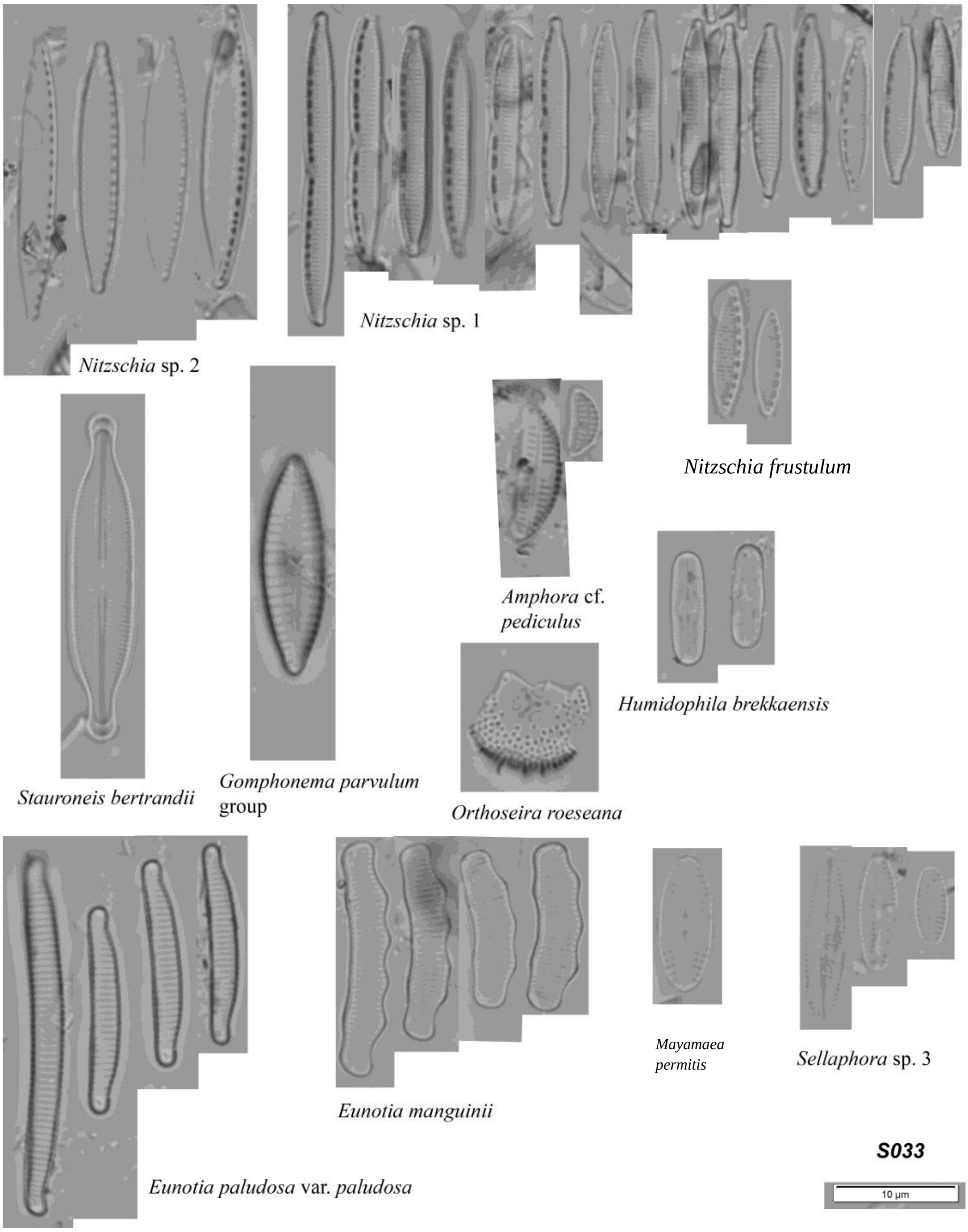


Fig. 13: Microphotographs of species observed in sample S033.

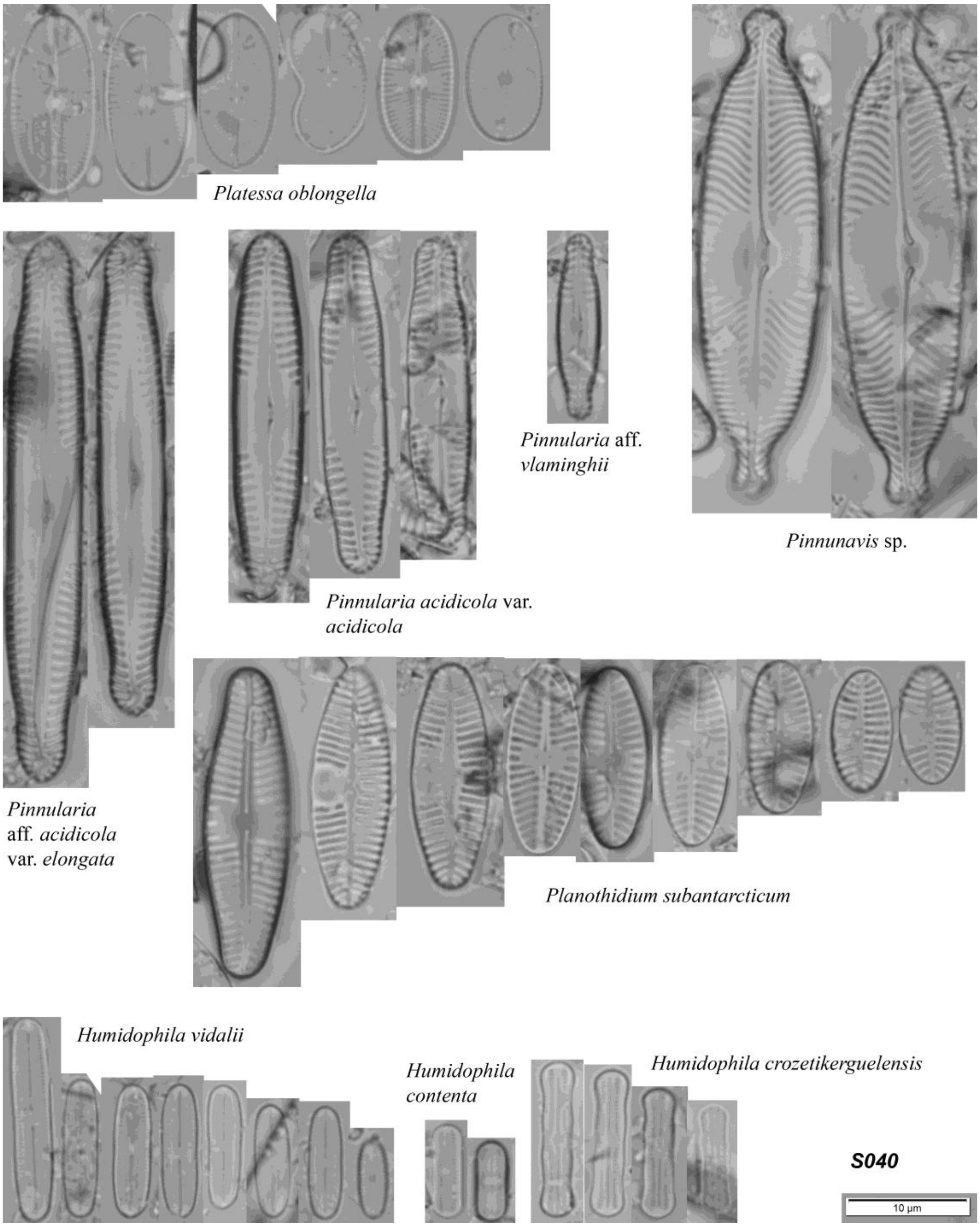


Fig. 14: Microphotographs of species observed in sample S040.

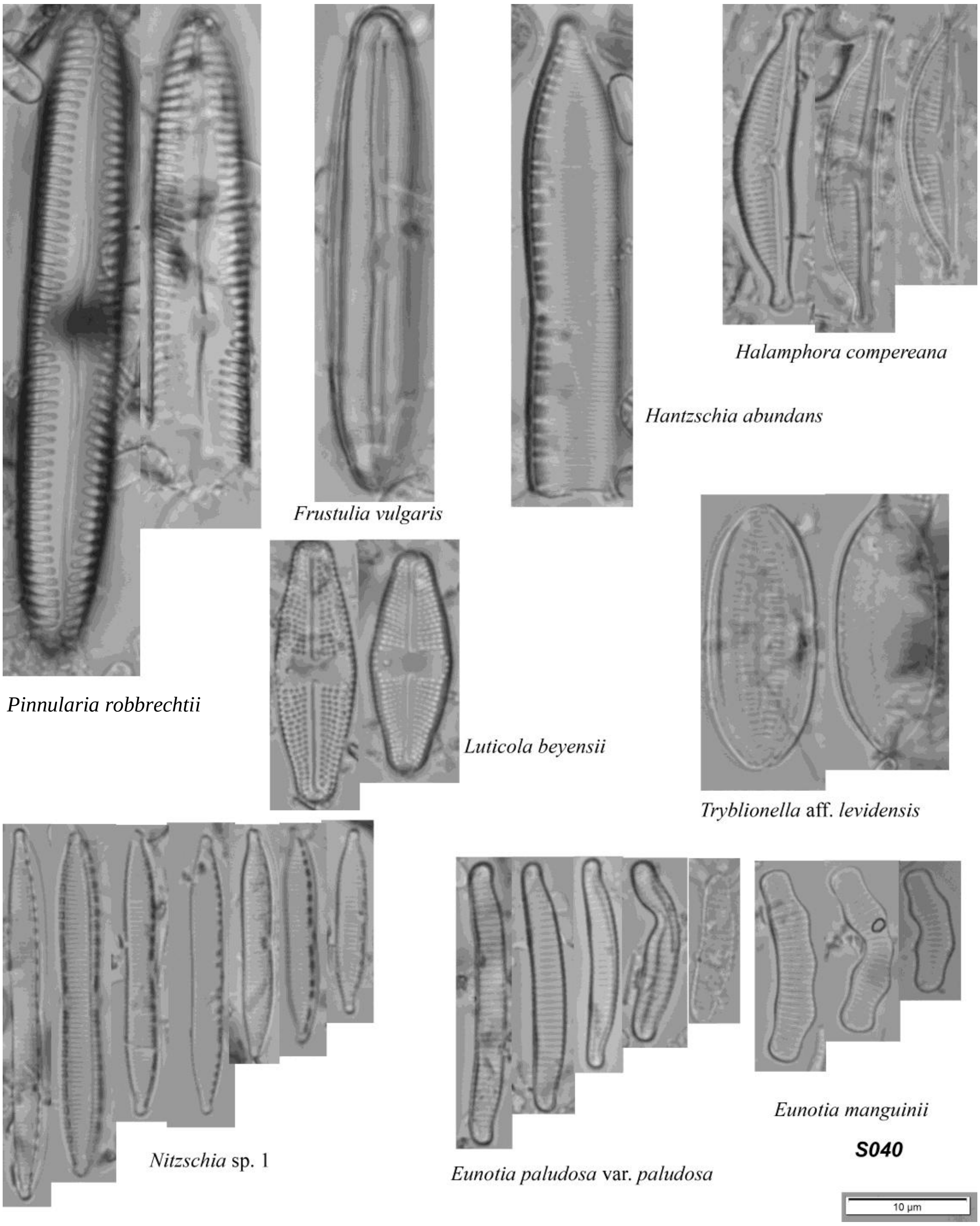


Fig. 15: Microphotographs of species observed in sample S040.

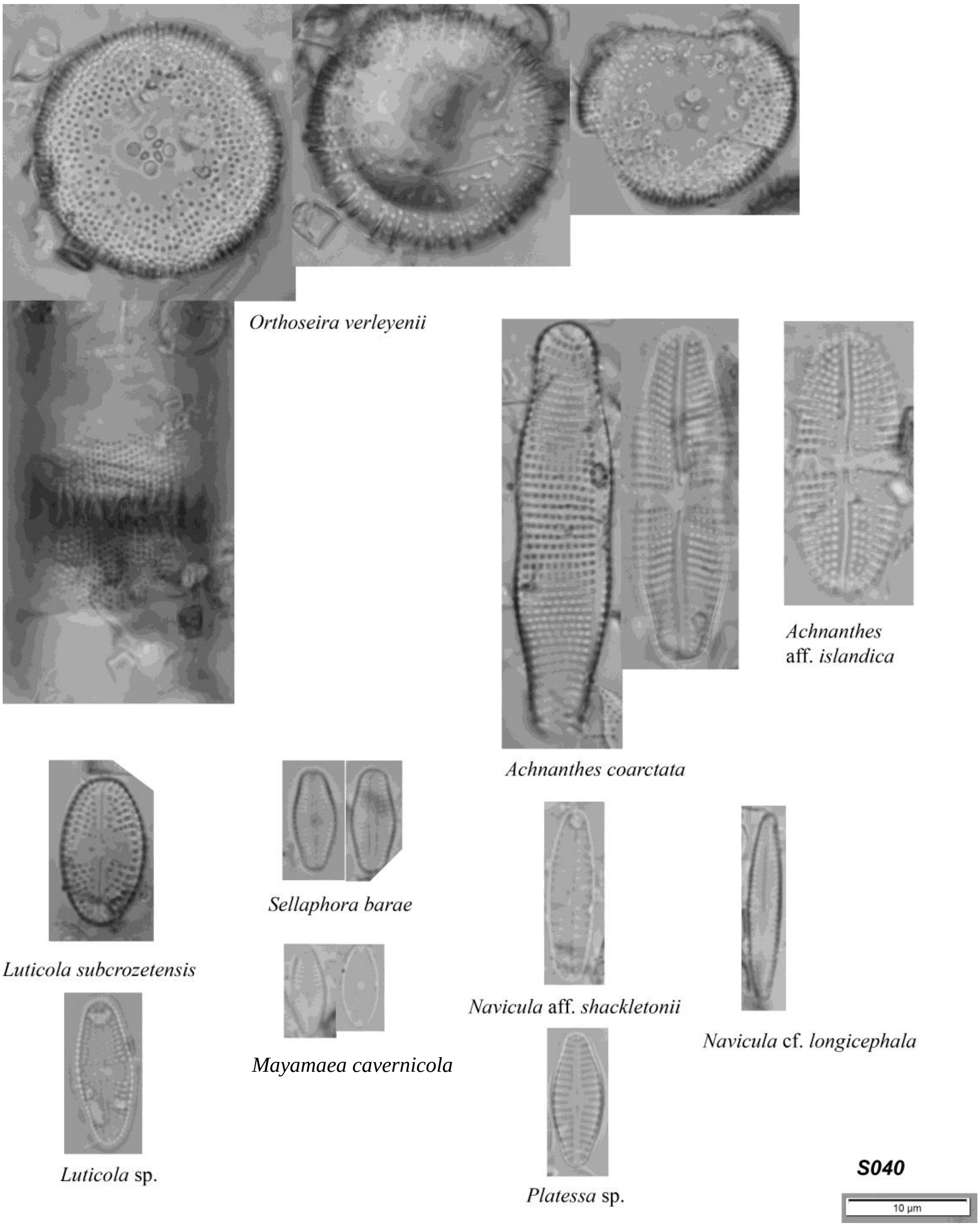


Fig. 16: Microphotographs of species observed in sample S040.

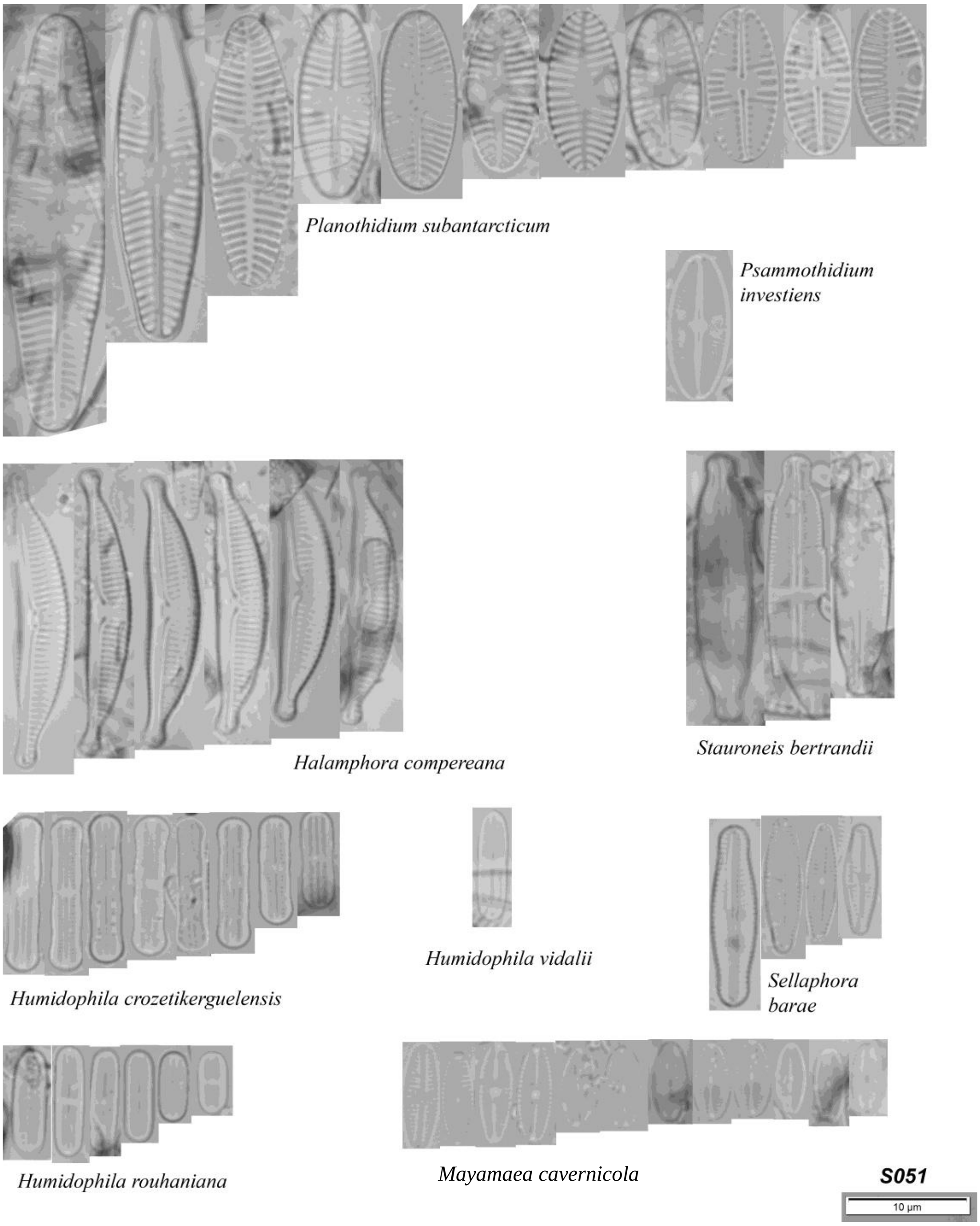


Fig. 17: Microphotographs of species observed in sample S051.

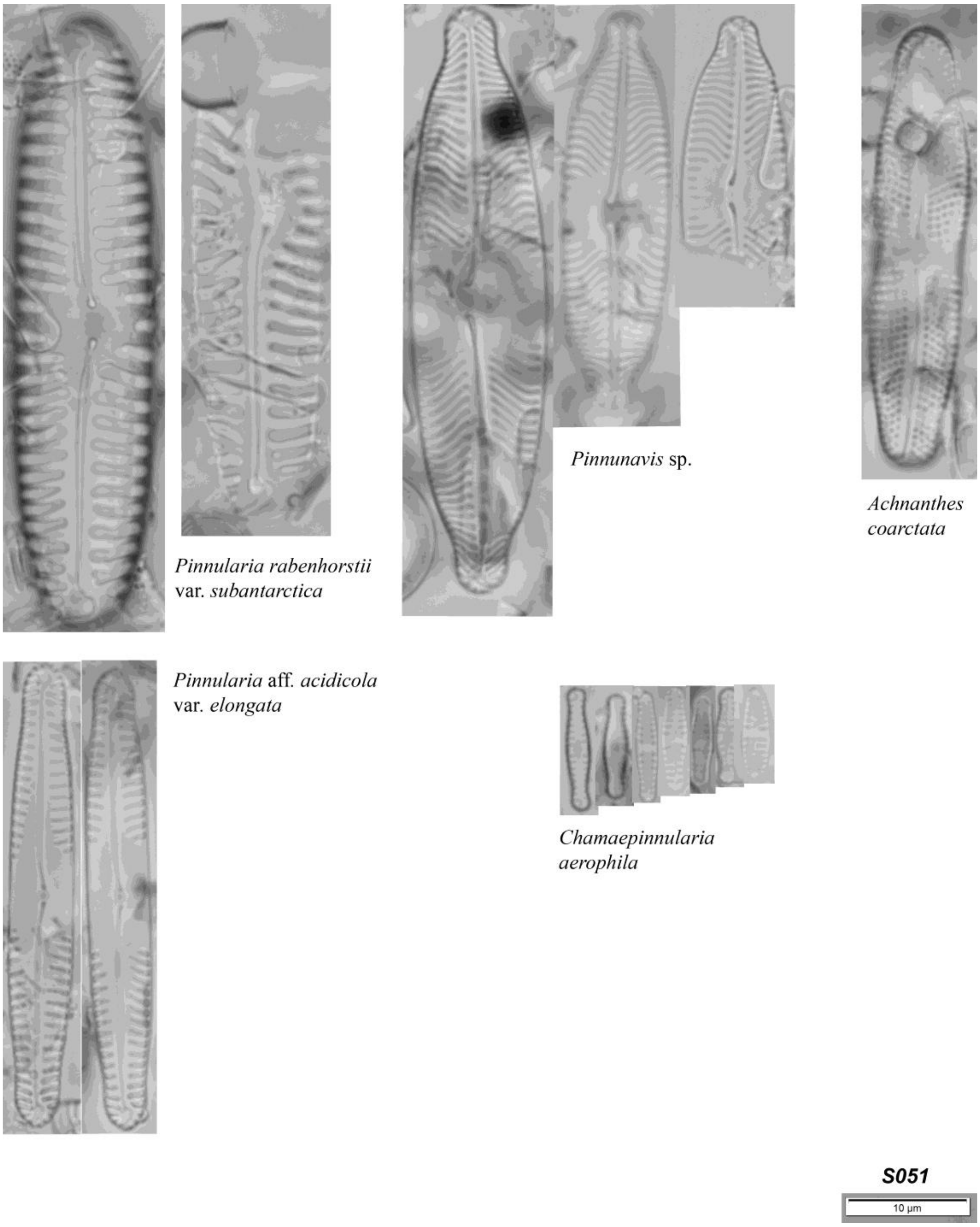
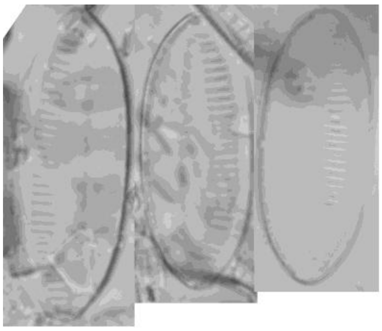
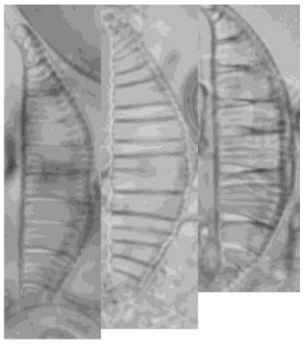


Fig. 18: Microphotographs of species observed in sample S051.

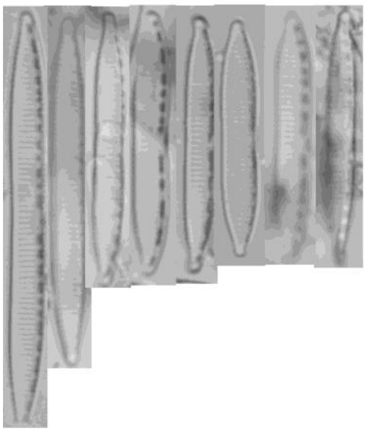


Tryblionella aff. *levidensis*

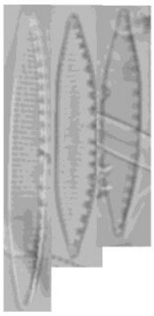
Tryblionella debilis



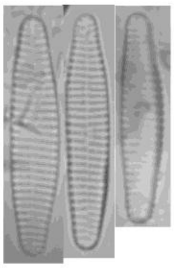
Rhopalodia rupestris



Nitzschia sp. 1



Nitzschia frustulum



Stauroforma aff. *exiguiformis*

S051

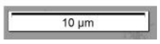


Fig. 19: Microphotographs of species observed in sample S051.

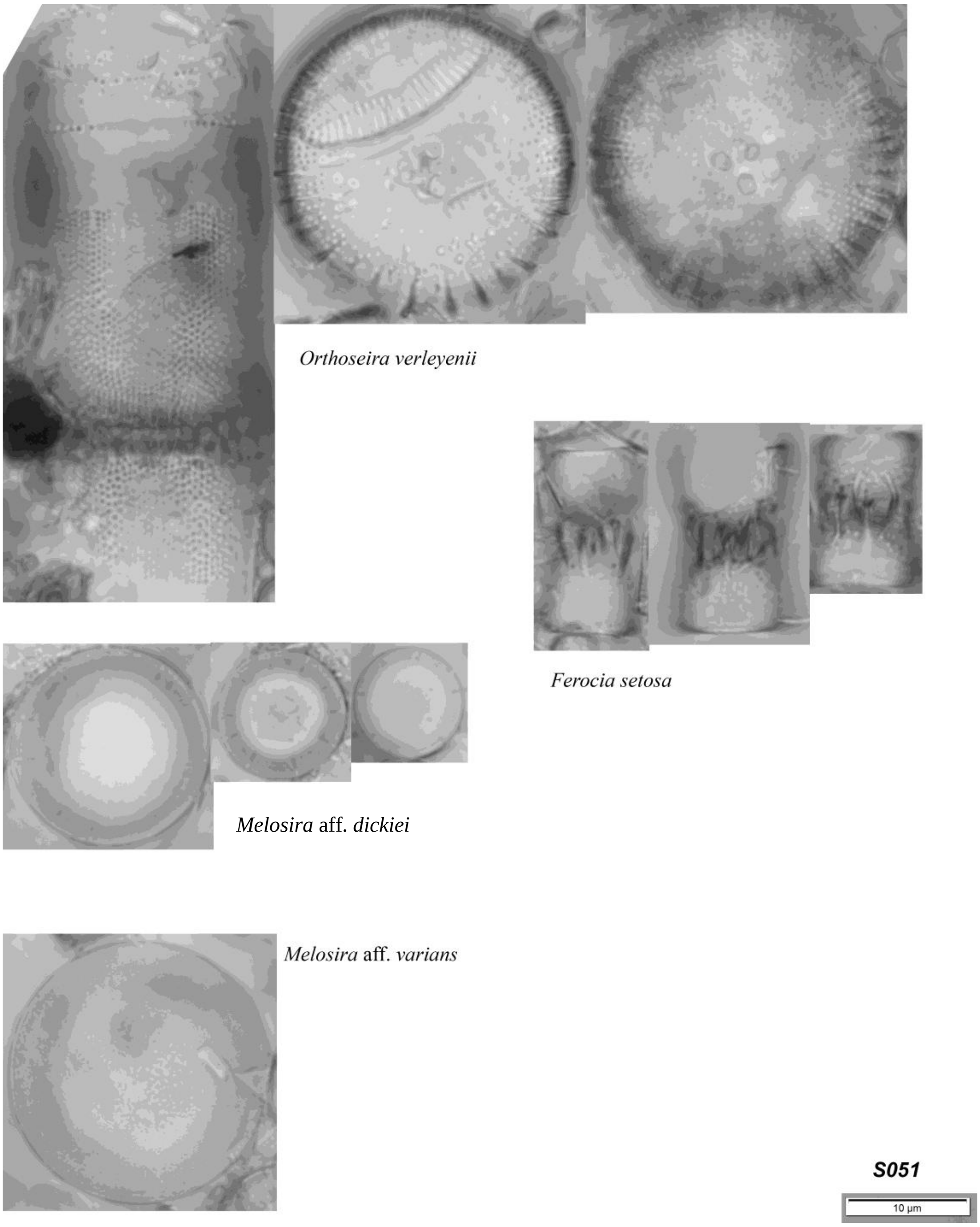


Fig. 20: Microphotographs of species observed in sample S051.

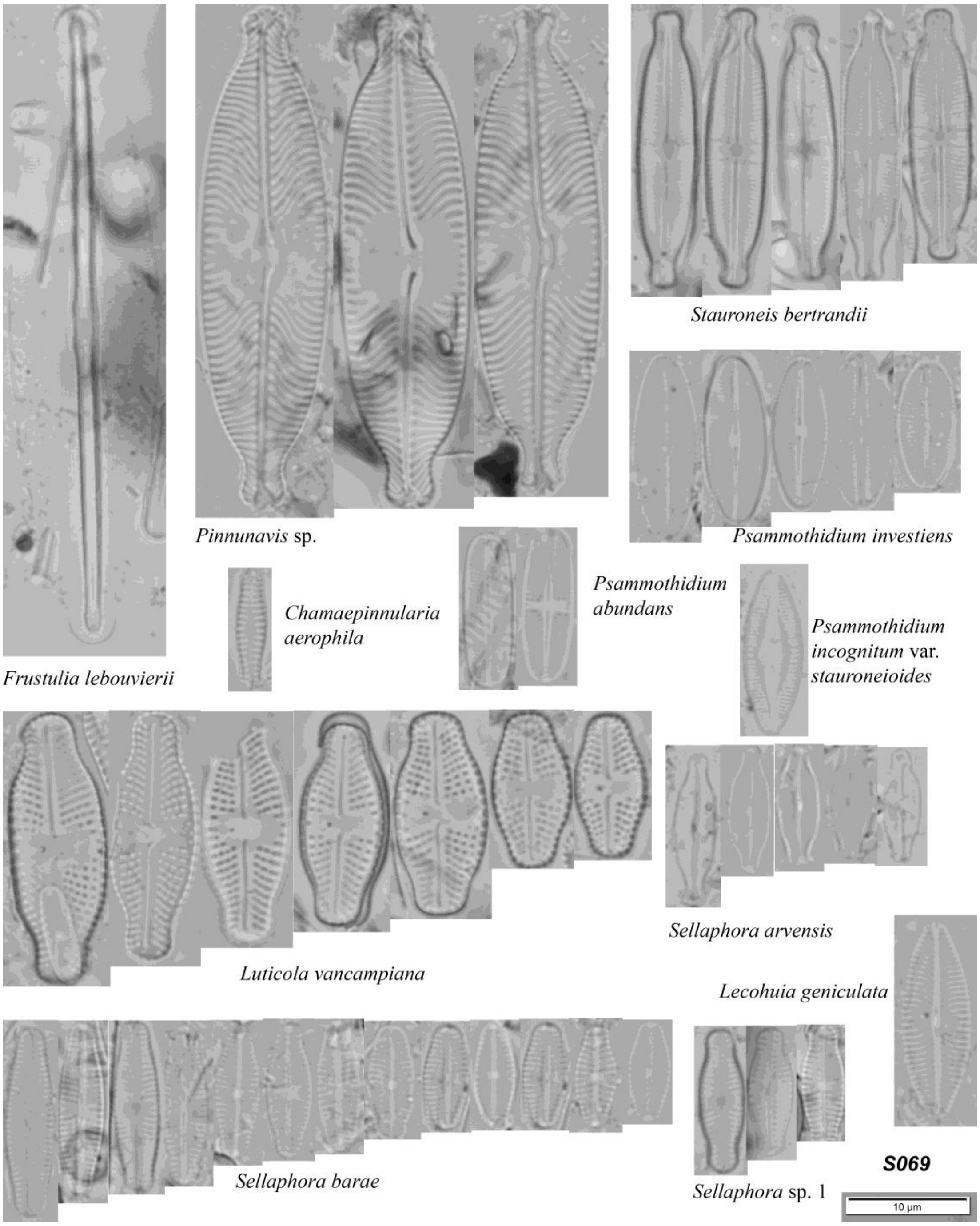


Fig. 21: Microphotographs of species observed in sample S069.

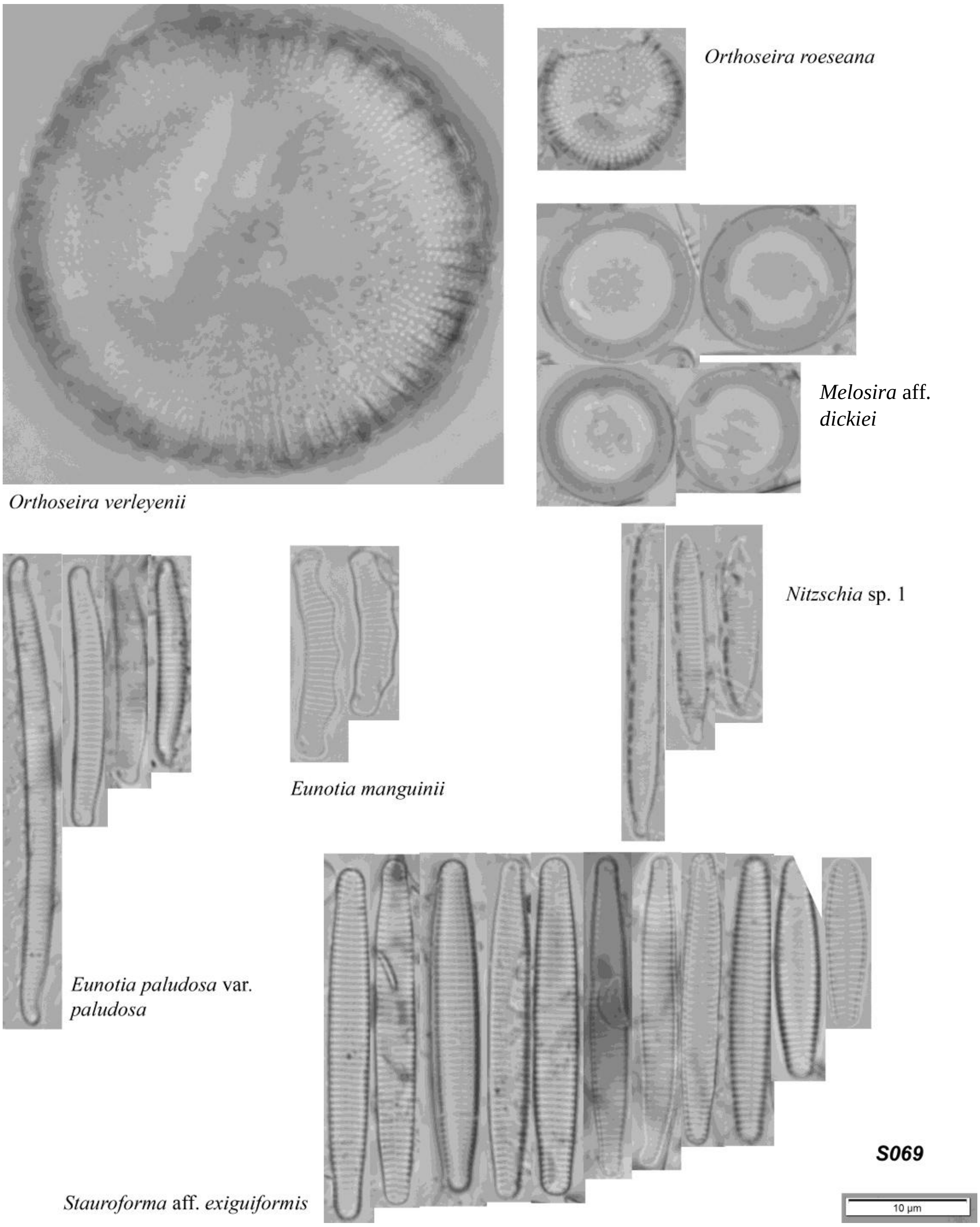


Fig. 22: Microphotographs of species observed in sample S069.

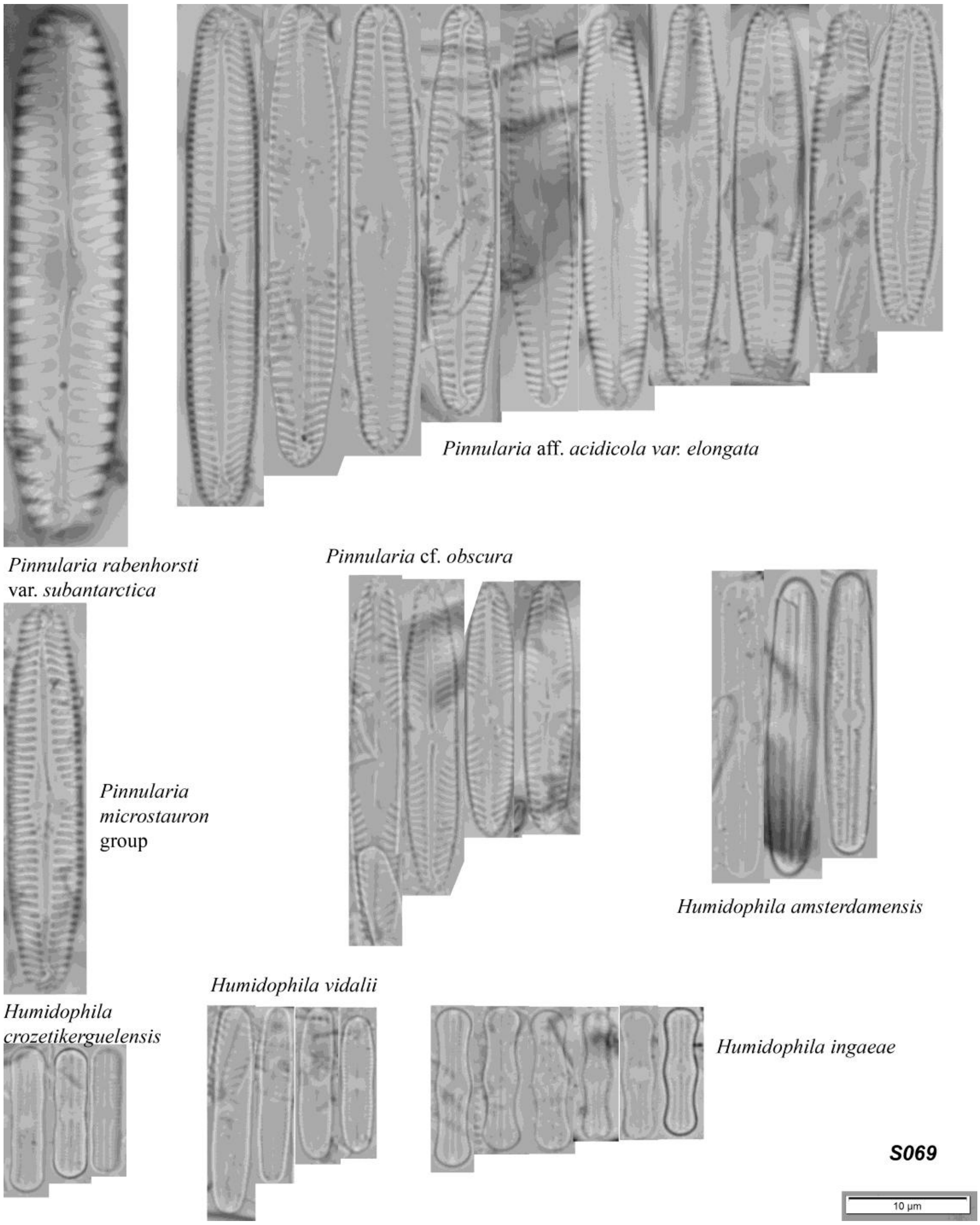


Fig. 23: Microphotographs of species observed in sample S069.

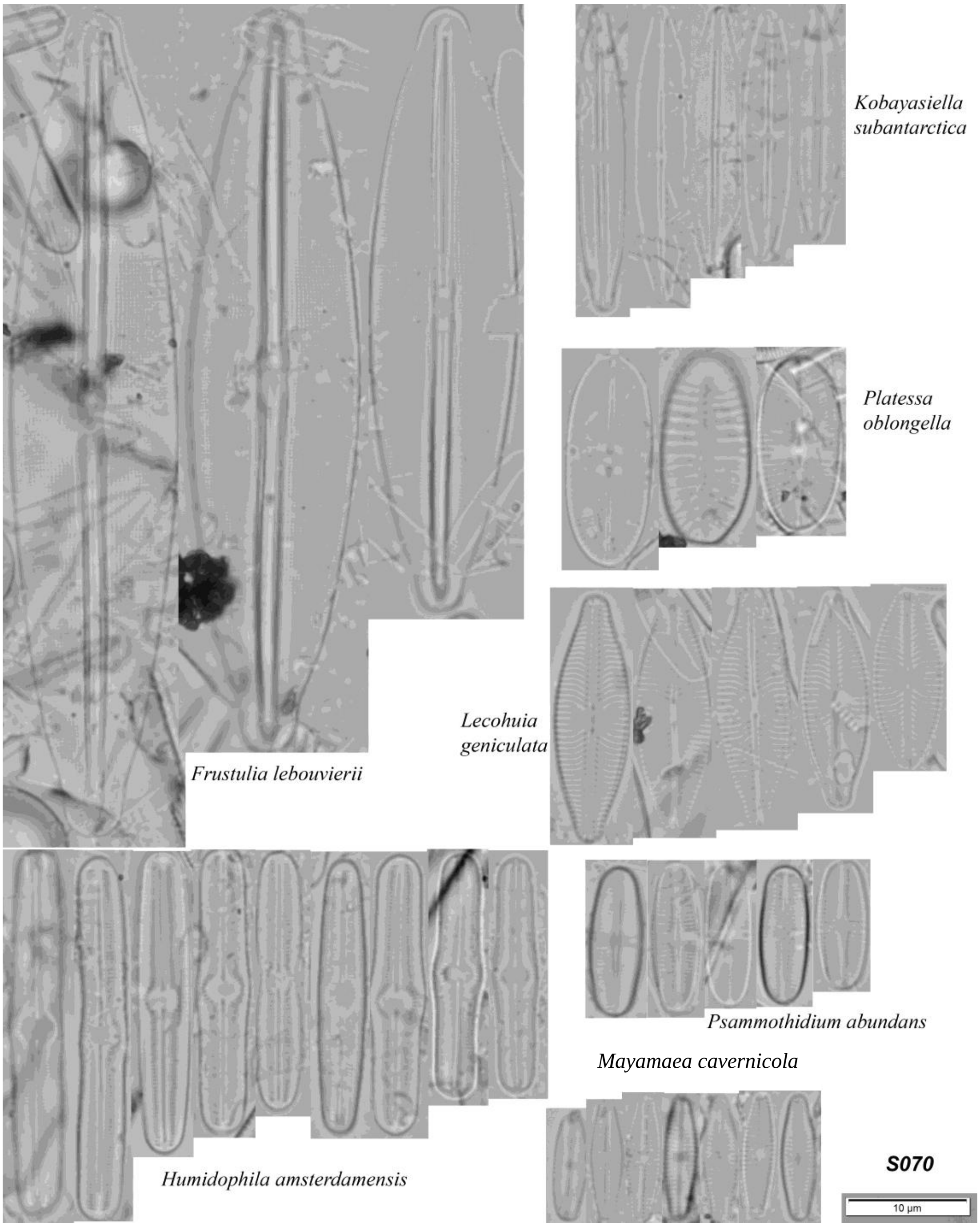


Fig. 24: Microphotographs of species observed in sample S070.

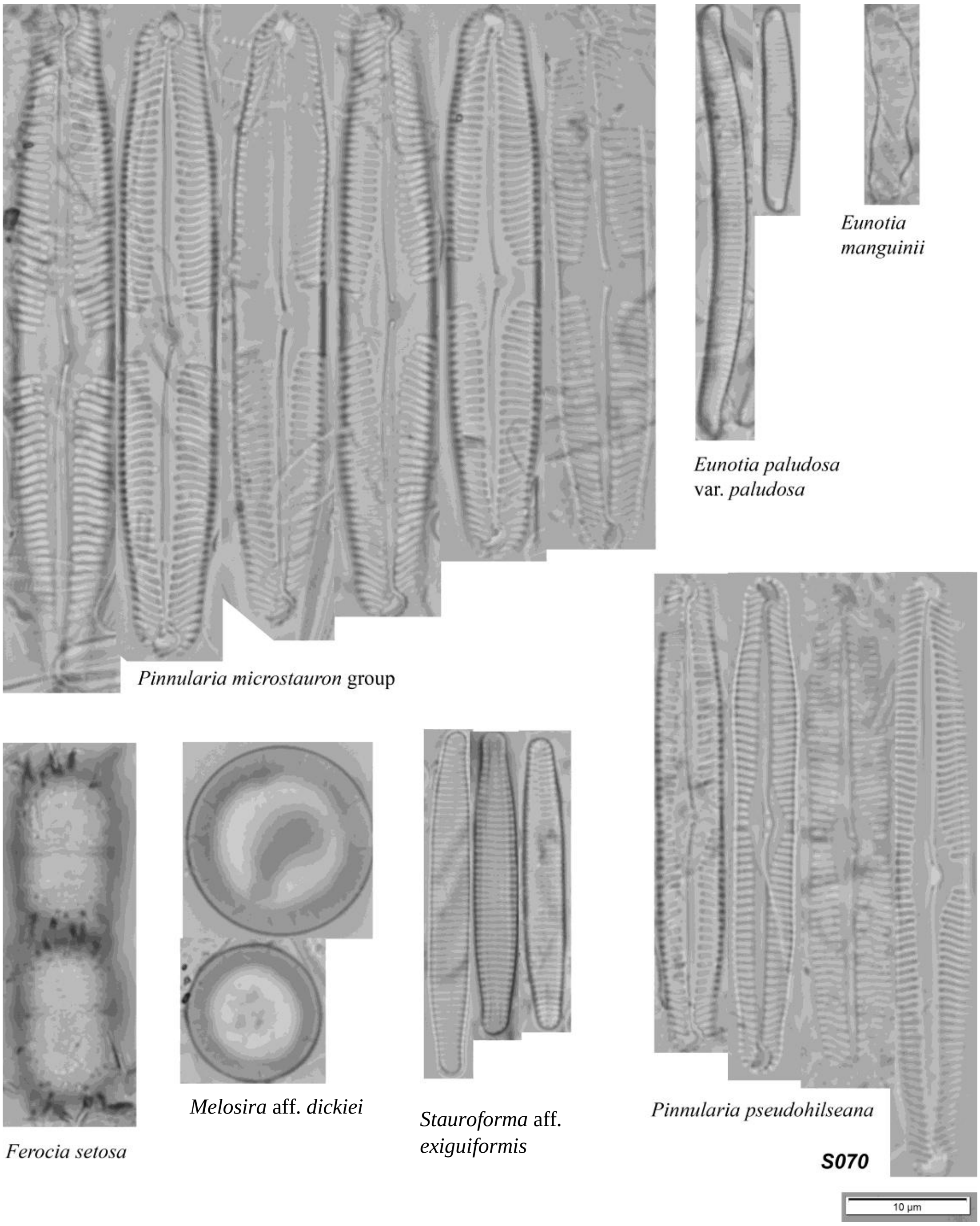


Fig. 25: Microphotographs of species observed in sample S070.

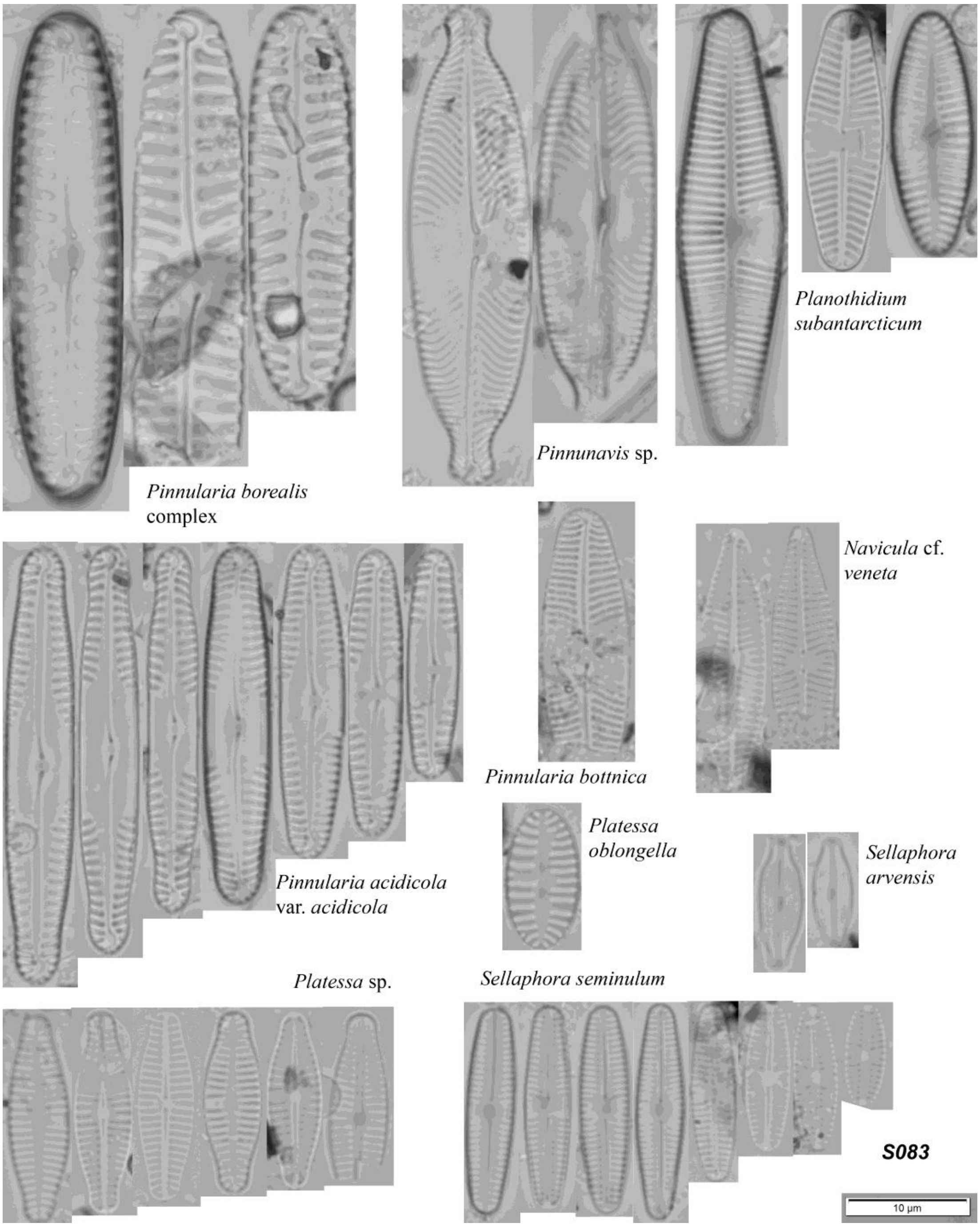


Fig. 26: Microphotographs of species observed in sample S083.

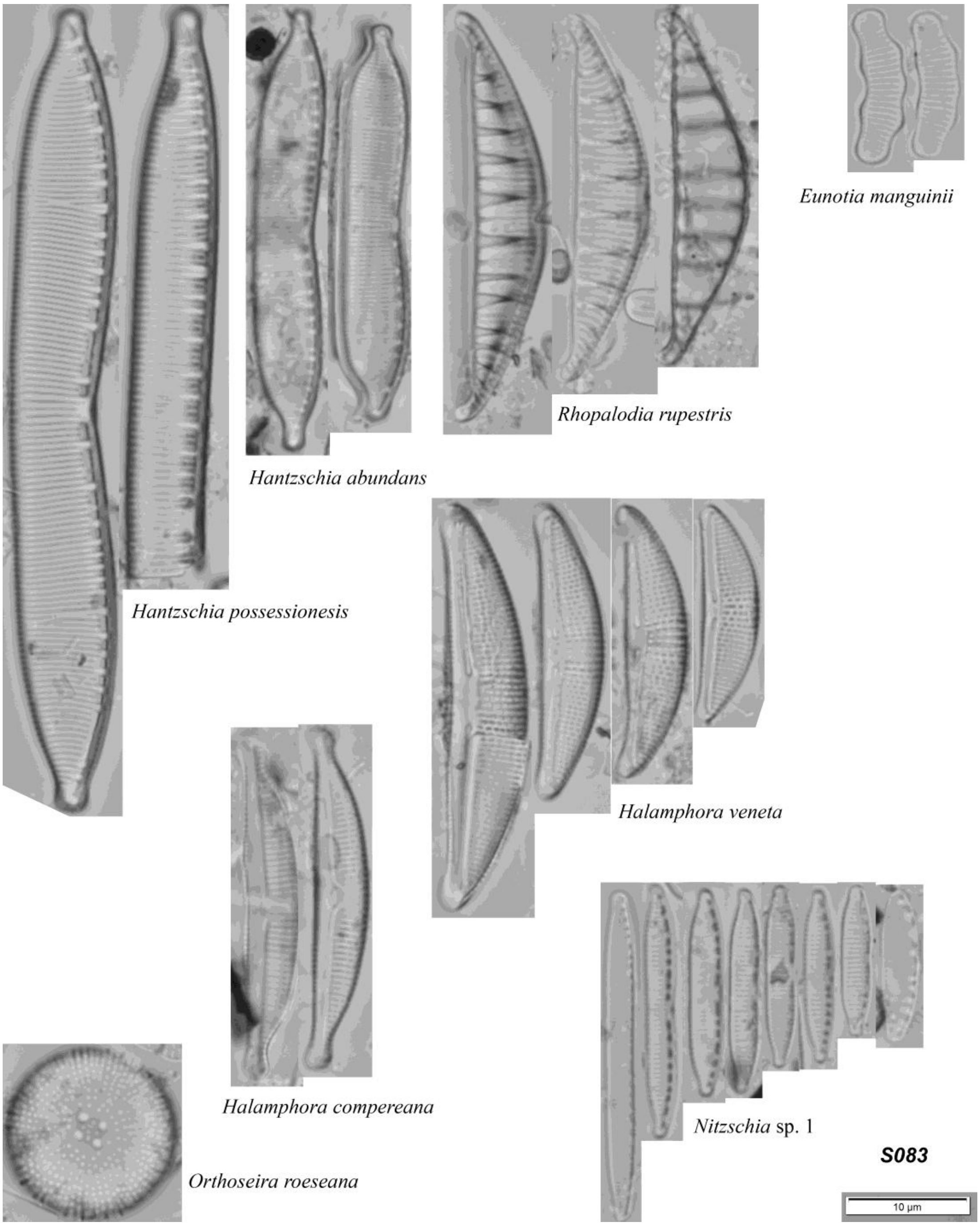


Fig. 27: Microphotographs of species observed in sample S083.

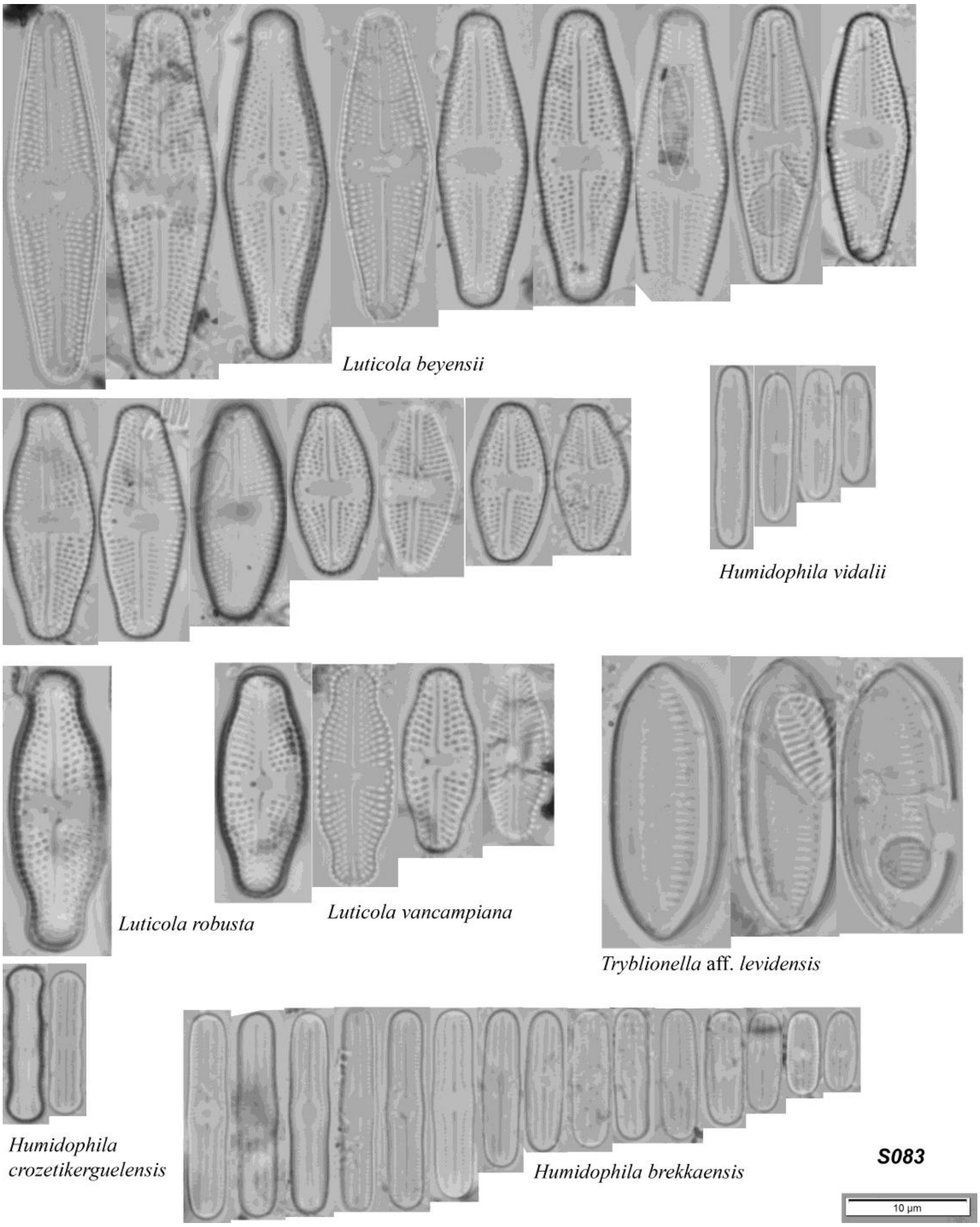


Fig. 27: Microphotographs of species observed in sample S083.

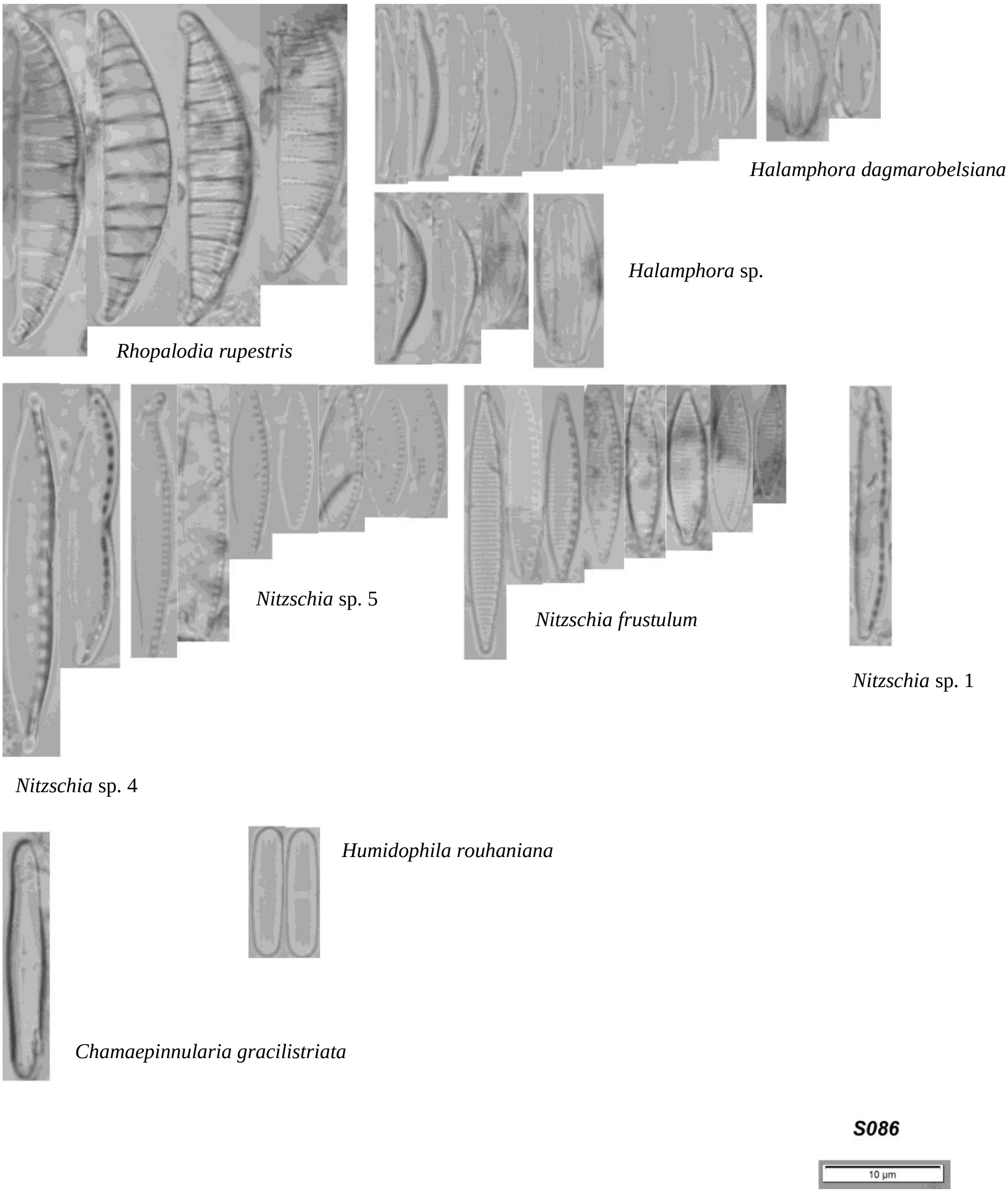


Fig. 28: Microphotographs of species observed in sample S086.

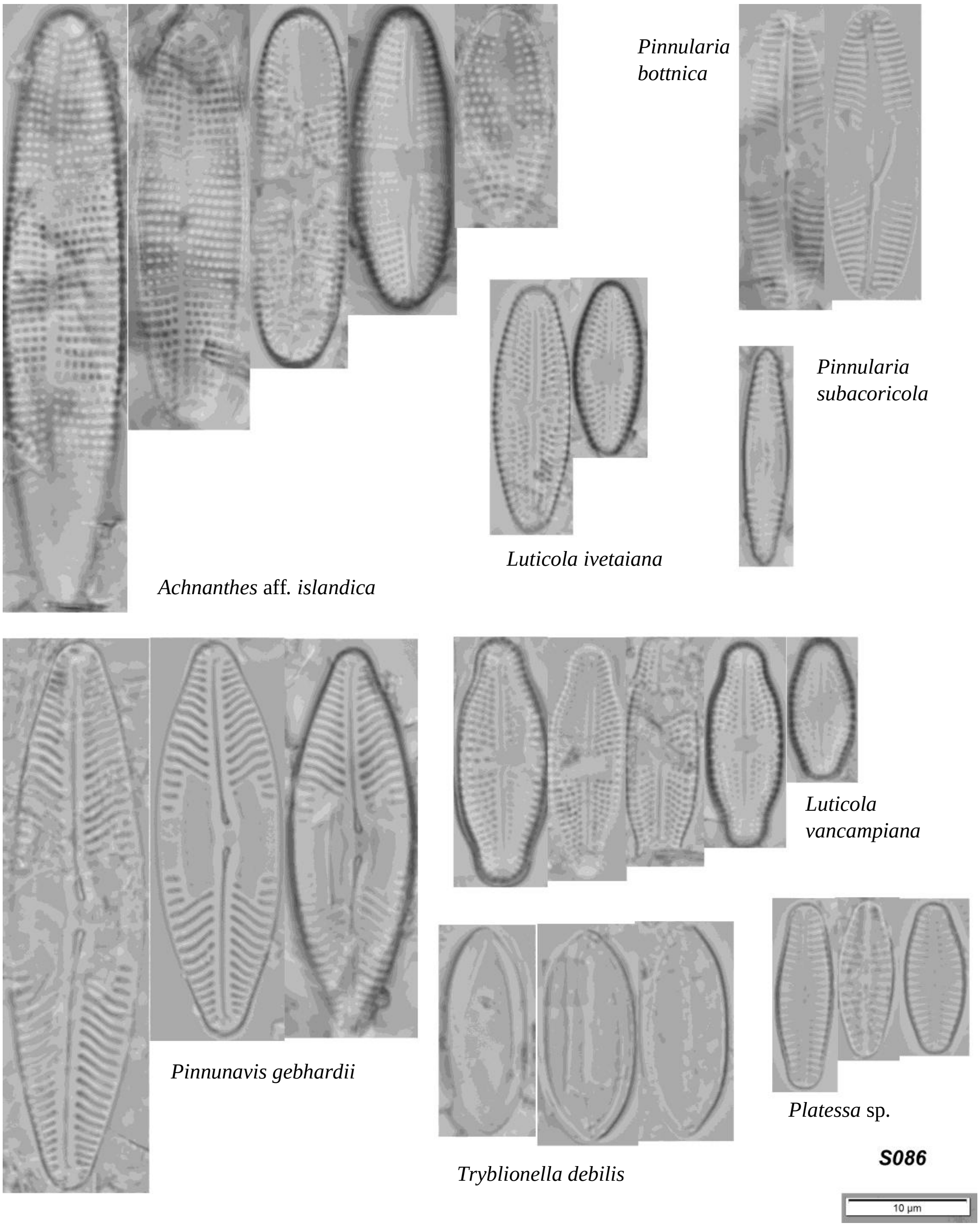


Fig. 29: Microphotographs of species observed in sample S086.

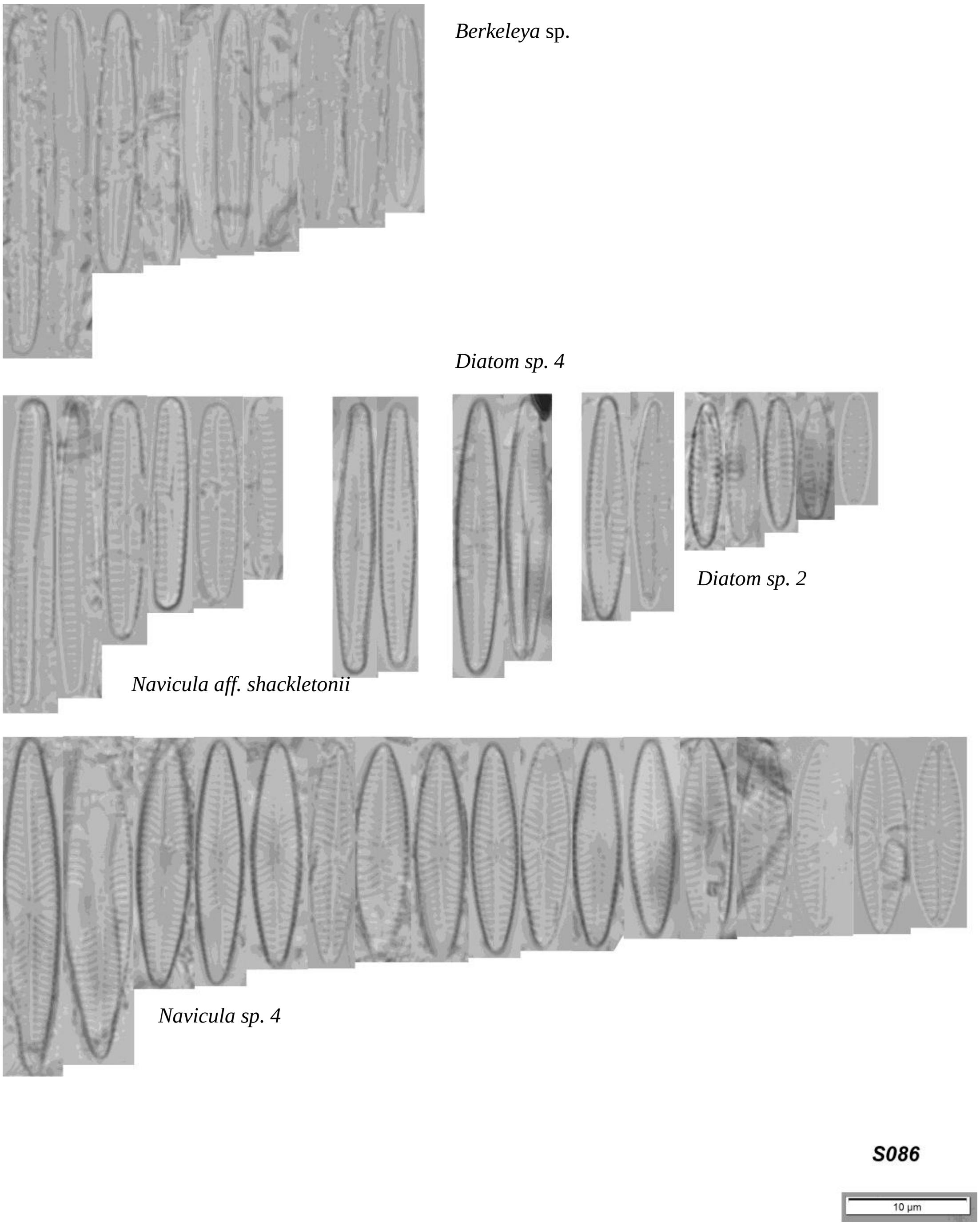


Fig. 30: Microphotographs of species observed in sample S086.

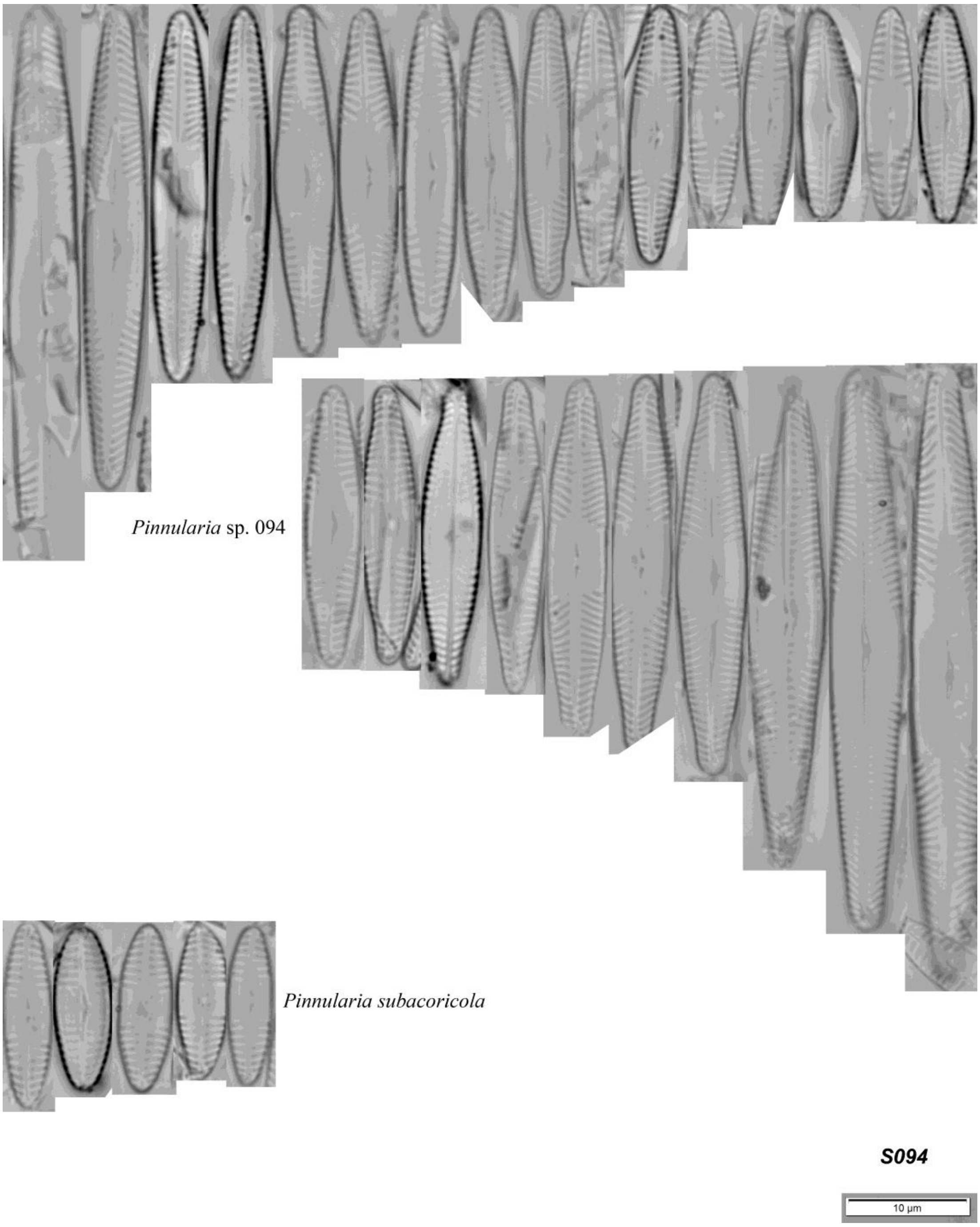


Fig. 31: Microphotographs of species observed in sample S094.

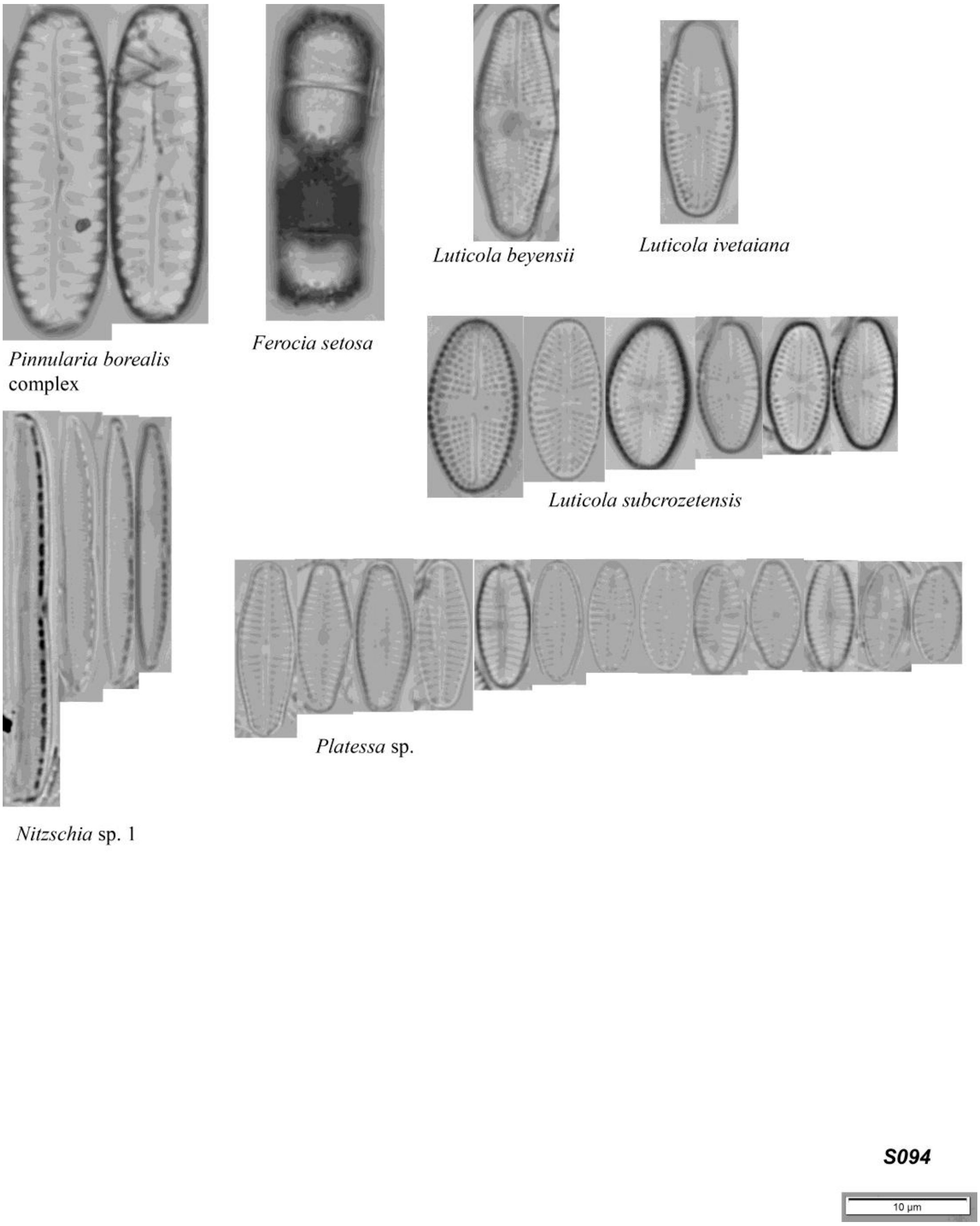


Fig. 32: Microphotographs of species observed in sample S094.

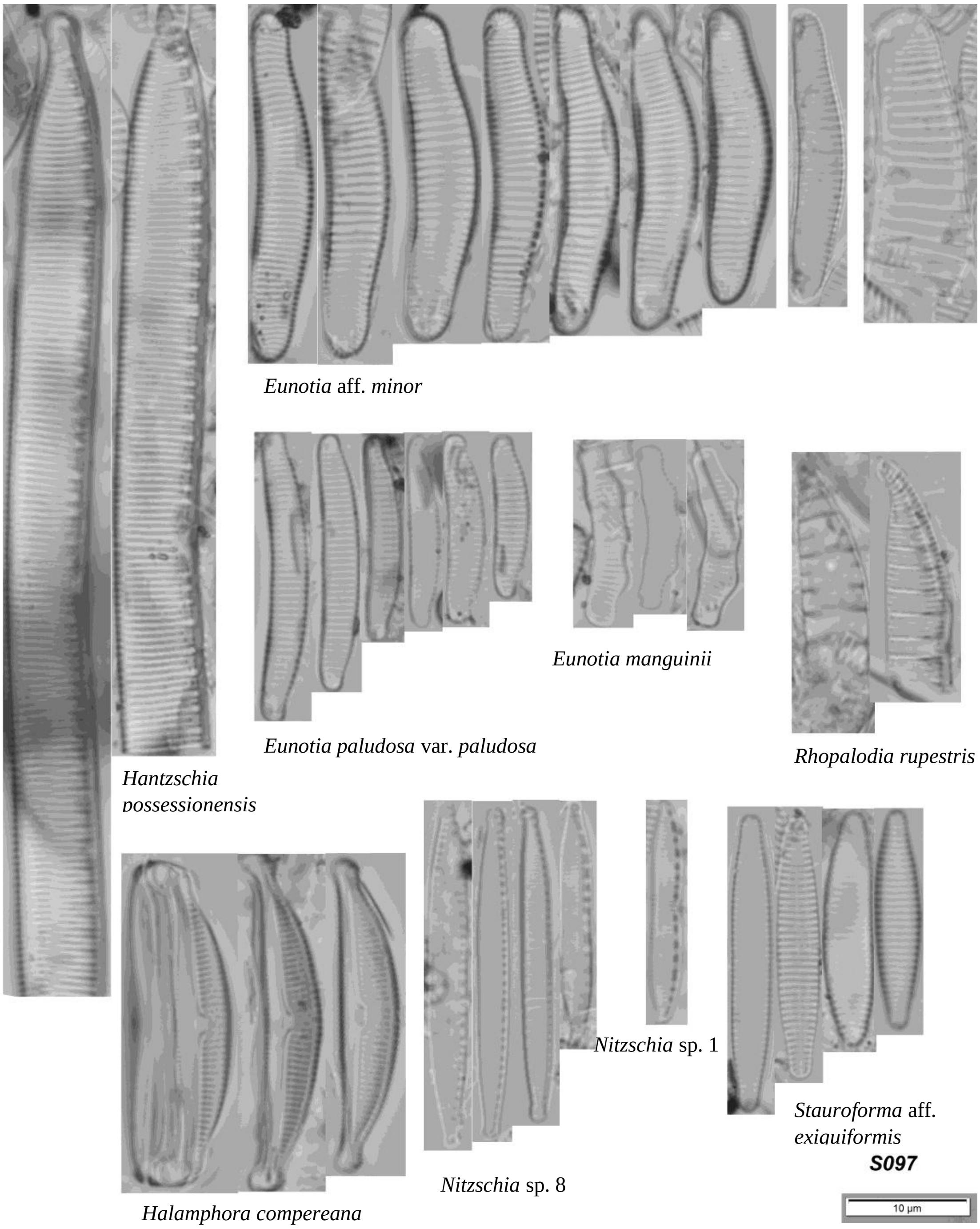


Fig. 33: Microphotographs of species observed in sample S097.

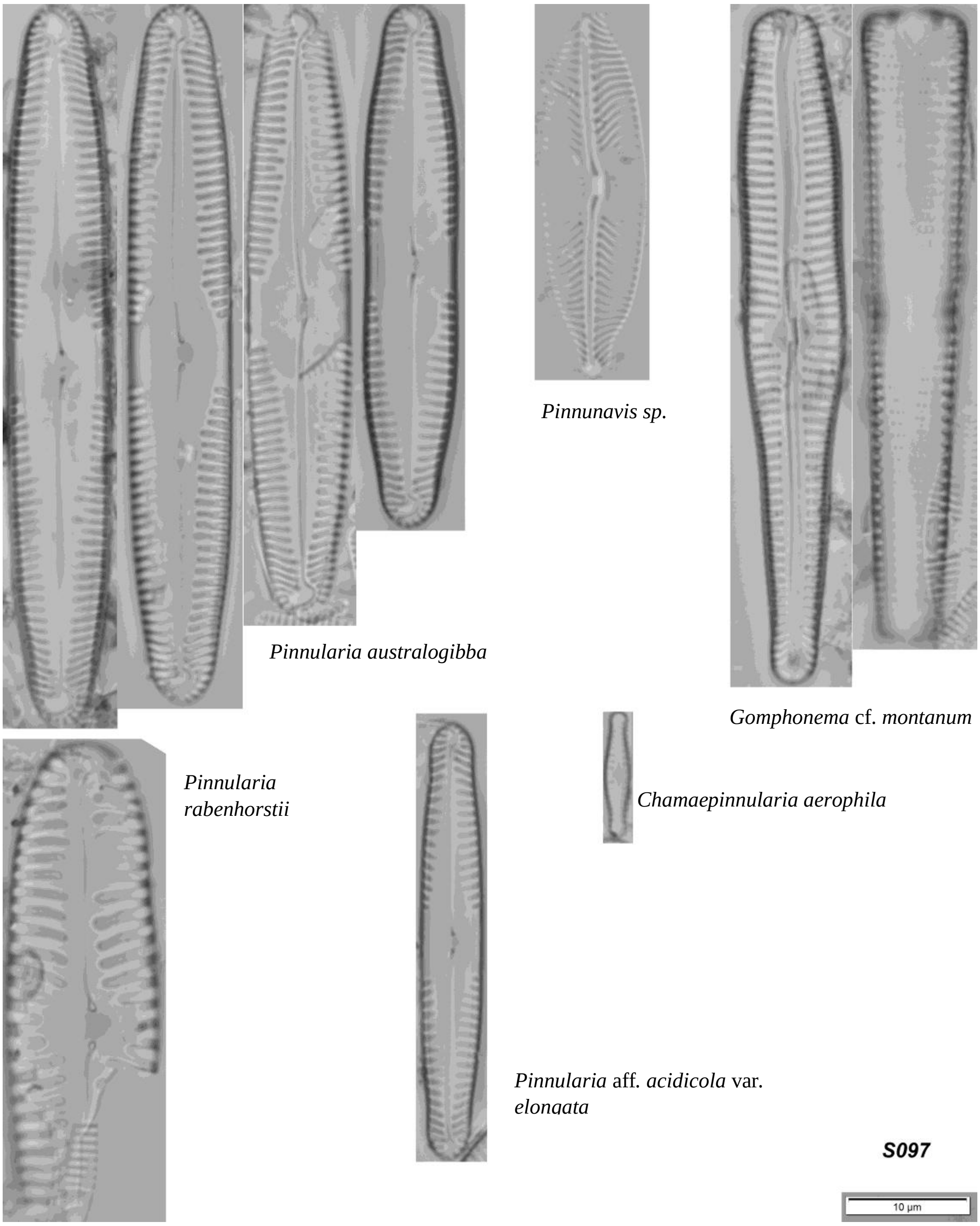


Fig. 34: Microphotographs of species observed in sample S097.

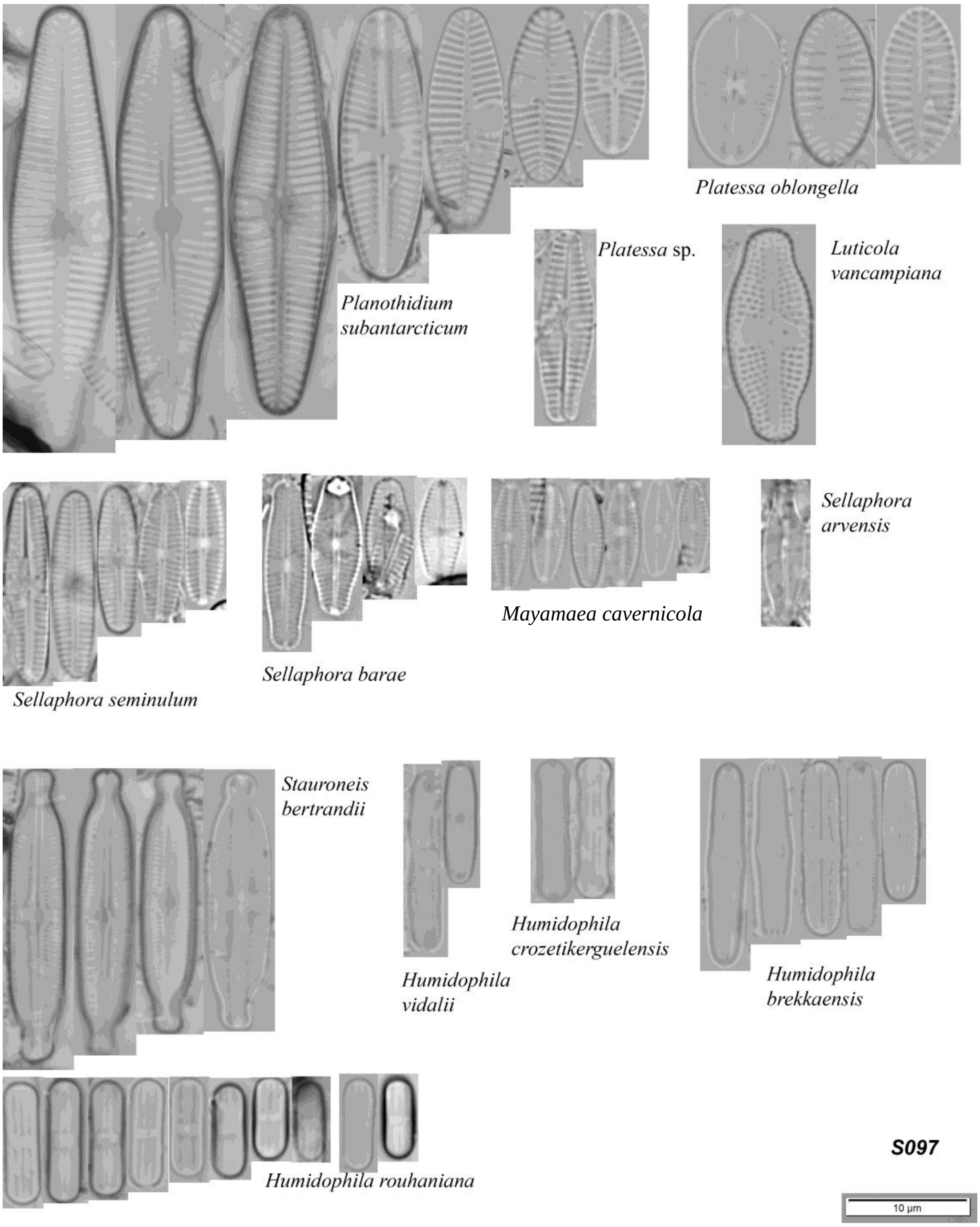


Fig. 35: Microphotographs of species observed in sample S097.

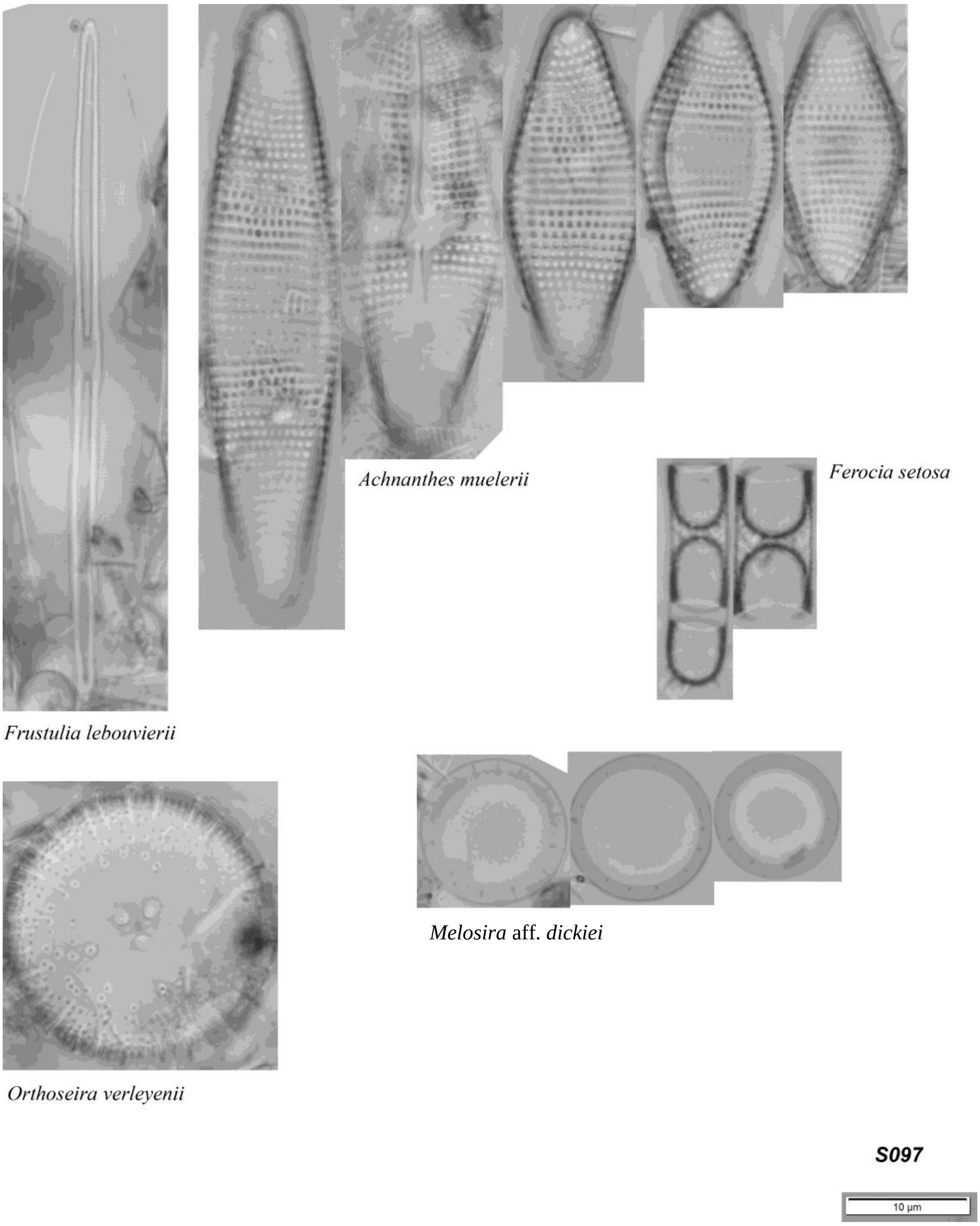


Fig. 36: Microphotographs of species observed in sample S097.

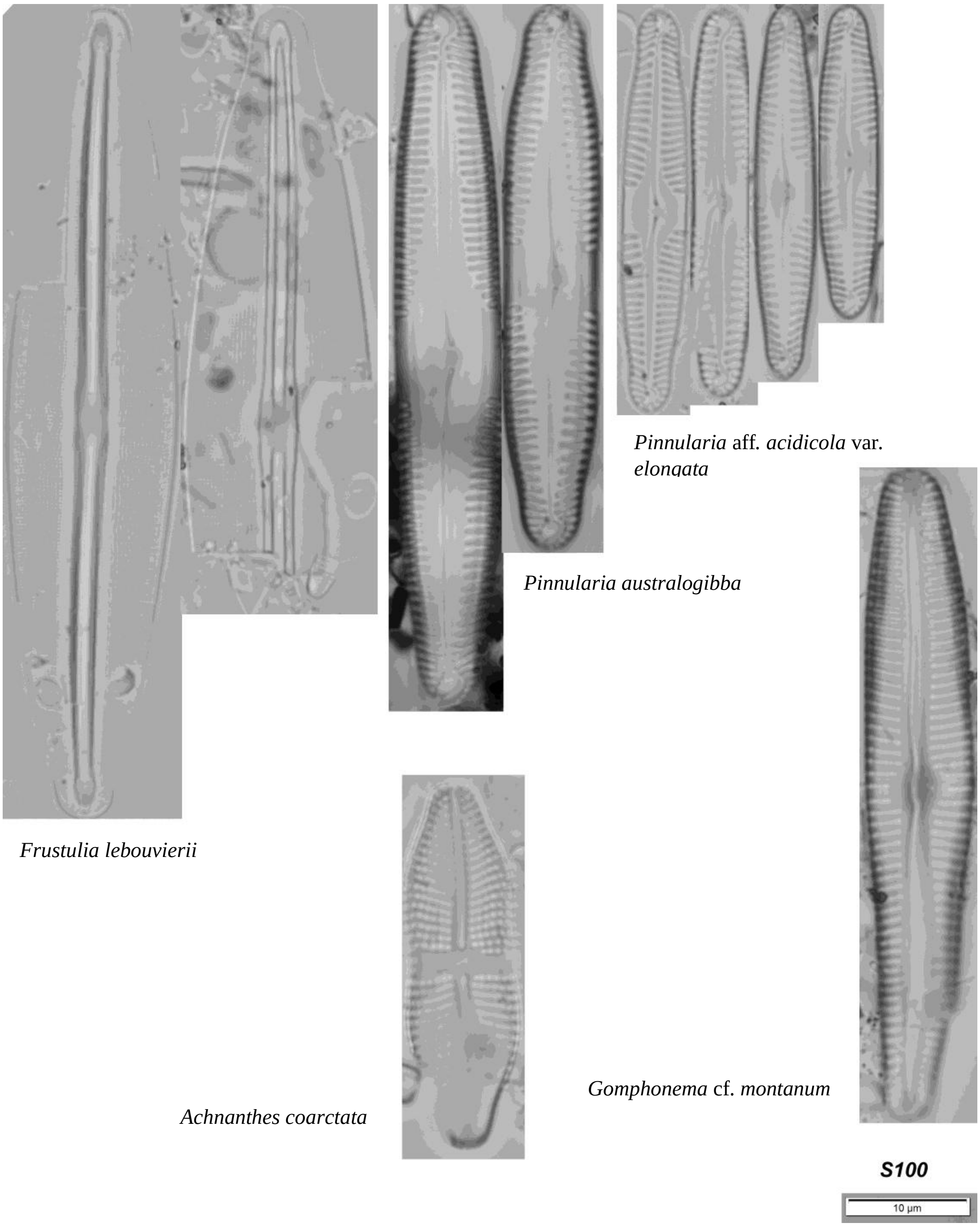


Fig. 37: Microphotographs of species observed in sample S100.

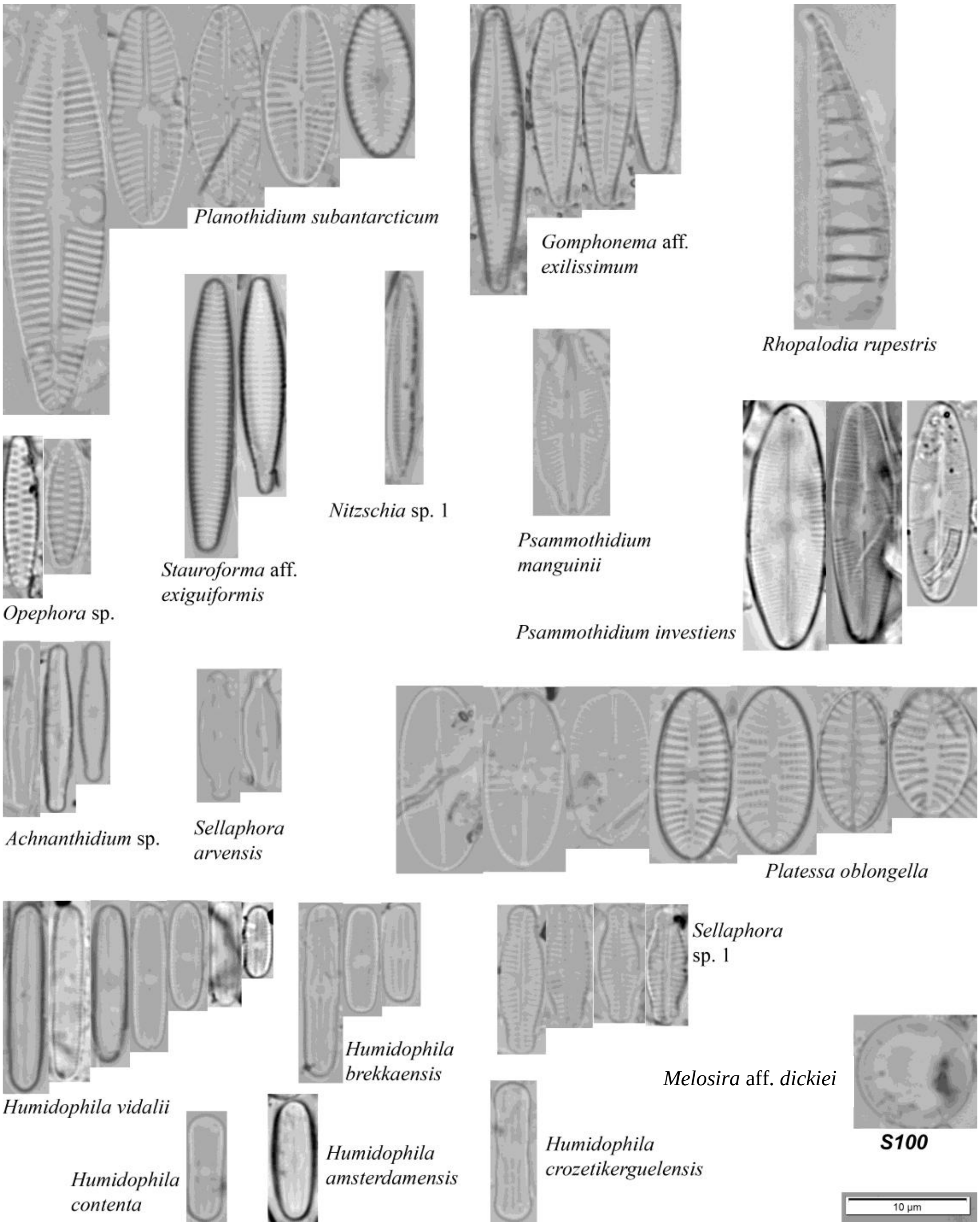


Fig. 38: Microphotographs of species observed in sample S100.

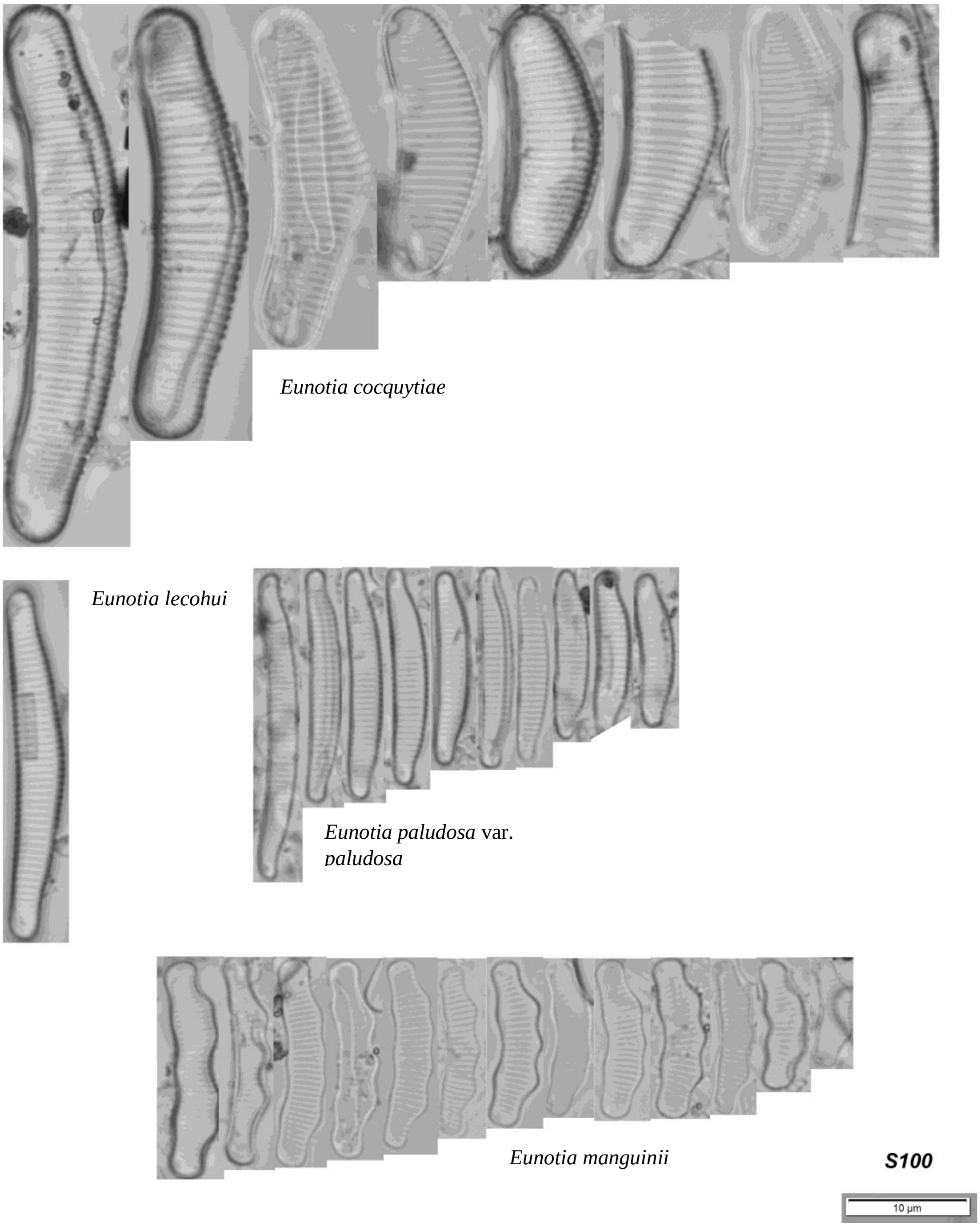


Fig. 39: Microphotographs of species observed in sample S100.

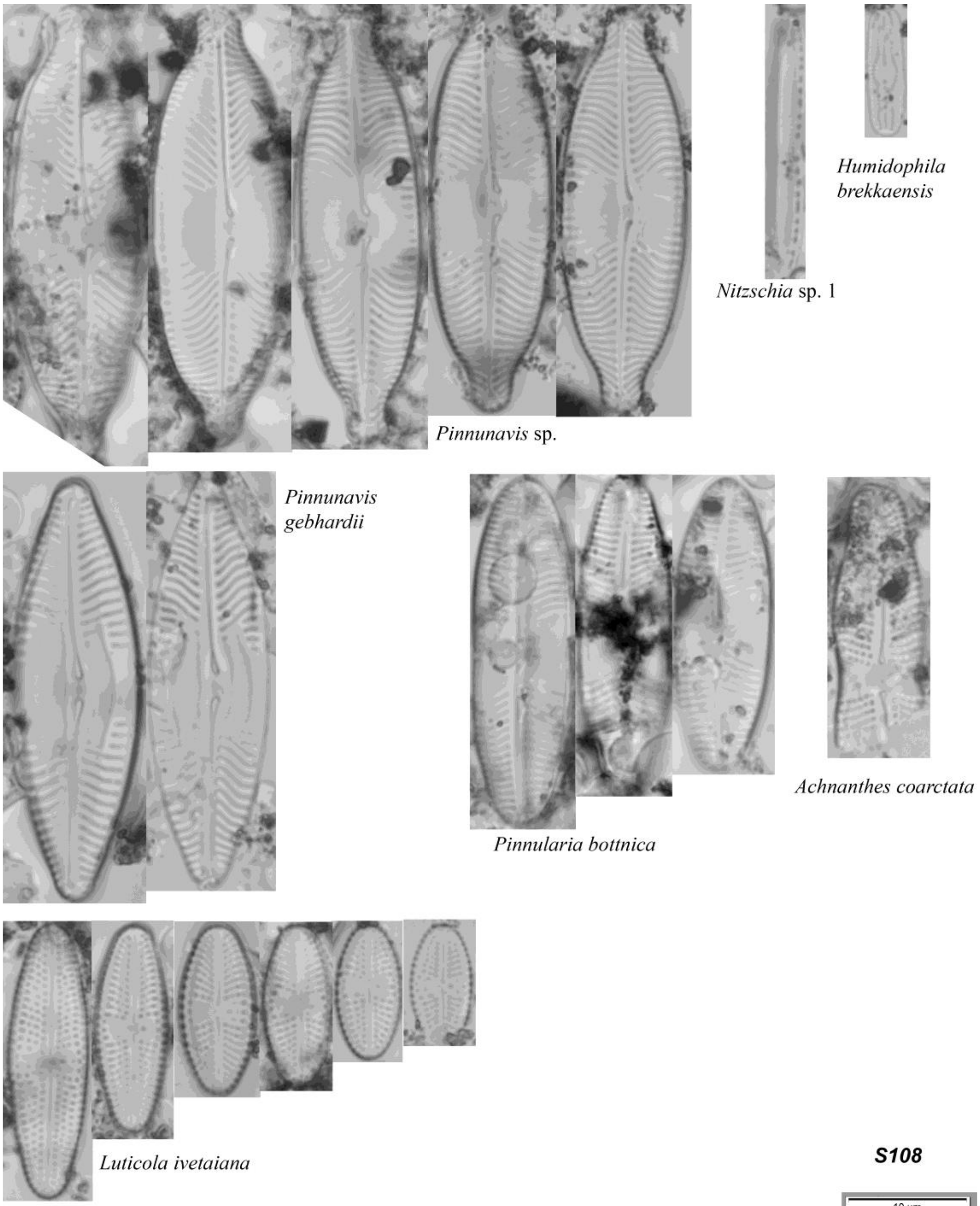


Fig. 40: Microphotographs of species observed in sample S108.

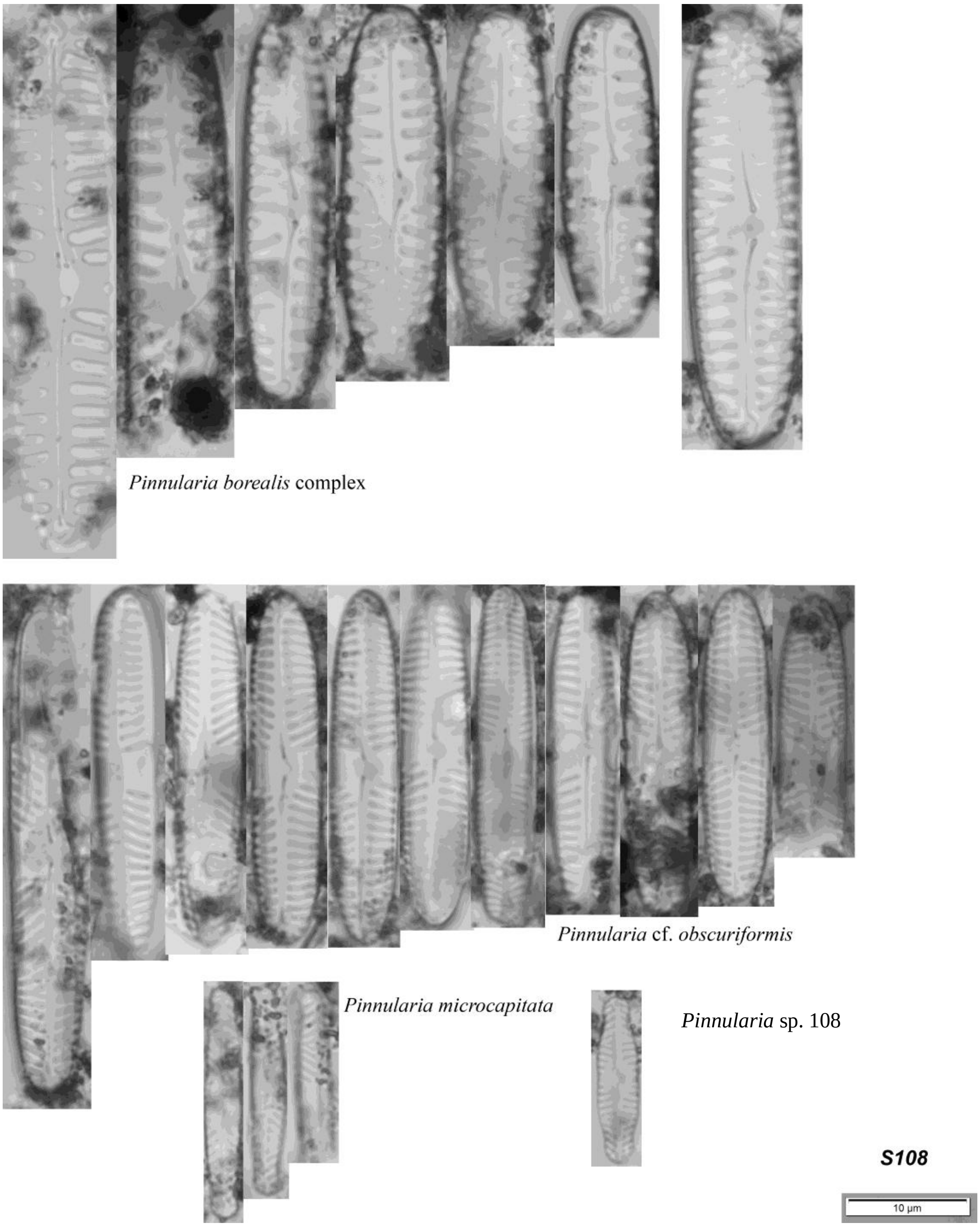


Fig. 41: Microphotographs of species observed in sample S108.