Chapter 4
Alpine Lake Environments and Psychrophile Diatoms Around the World with a Particular Emphasis on Turkish Glacial Lakes

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Abstract Cold environments are considered extreme biomes and historically thought to be barren and unproductive. However, investigations show that some of the coldest regions in the world represent unique biodiversity hotspots. In this review, the prominent diatom communities of alpine lakes and ponds across different parts of the world, including the Arctic, Antarctic, and alpine regions, are evaluated. Glacial lakes in western Asia (Turkey) are specifically examined as a proxy for extreme cold aquatic systems between the primary mountainous areas of the Alps and the Himalaya. Biogeographically, Turkey is a subtropical region with two prominent glacial ecozones (southern Taurus and northeastern Anatolian Mountains). In this study, glacial lakes in the Kaçkar Mountains, northeastern Anatolia, are evaluated noting the importance of genera with smaller diatom taxa including *Genkalia*, *Psammothidium*, and *Eunotia*. The presence of genera like *Genkalia*

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and cold environment species like *Psammothidium subatomoides* highlight the isolation of alpine biomes in subtropical regions. Broad biogeographic distributions of biological diversity from polar to alpine are considered, and a number of taxa within *Eunotia* and *Psammothidium* are recorded for the first time in this region.

Keywords Antarctica · Arctic · Kaçkar Mountains · *Psammothidium subatomoides* · Swiss Alps

4.1 Alpine Environments and Biomes

Extreme biomes have hidden mysteries that intrigue our sense of curiosity and understanding. Few get to see these environments, and even fewer have the chance to study them. Of the extreme biomes, glacial, Arctic, Antarctic, and alpine ecozones are globally the most prominent and significant to Earth's well-being. The capture and control of surficial water supplies hinges on the availability of water over Milankovitch orbital cycles of global cooling and warming (glacial and interglacial) (Bennett 1990; Huybers and Curry 2006). Through historical time, humans and human cultures have passed through or established living communities in cold biomes, although to-date sustainable living in these environments is limited. The most notable example of humans interacting with extreme cold environments is the migration of *Homo sapiens* from Africa to northern Asia (Russia) and then migrating across the Bering Strait, between the Chukchi and Bering Seas, to North America (Fladmark 1979; O'Rourke and Raff 2010). Paleo-Inuit and Indigenous Peoples of the North established living communities that survived and even thrived in cold environments across the Arctic. The successful survival of these early peoples and cultures is with the understanding that to survive means knowing the living conditions and biota of cold environments and using them in a sustainable way. Likewise, isolated cultures living in alpine ecobiomes around the world have an understanding of their restricted conditions (Rhoades and Thompson 1975; Viazzo 1989). Early cultures recognized the importance of living in cold environments without disturbing or with limited disturbances to the ecosystem. This knowledge, historic (traditional) understanding of cold extremes, is now becoming available to society at large and will become more incorporated into our scientific knowledge of extreme cold systems.

Data from the World Bank (2021) highlights the fact that mountains cover 25% of the Earth's land surface, supply freshwaters to more than 3.5 billion people, and maintain 12% of the human population. Alpine environments are found on every continent where continental uplift and volcanic activity occurred. The Antarctic is an extreme cold environment which is primarily ice coved and not considered to have alpine environments distinct from the rest of the continent. The prominent alpine ecobiomes are found across the Andes (South America), Rocky Mountains (North America), Alps (Europe), Eastern Rift Mountains (Africa), and Himalayans (Asia) (Figs. 4.1 and 4.2). In the western part of China, significant additional alpine ecobiomes are found in the Kunlunshan, Tianshan, Taihangshan, Qilianshan, and

Fig. 4.1 Selected high alpine, alpine, and peri-alpine lakes and ponds. Top: Lake Orsirora (Switzerland), a high alpine cirque lake with sapphire blue (dark blue) waters surrounded by moss, grass, sedge, and boulder terrain. Second row from top: the Enchantments, Washington State, USA, a high alpine cirque lake with blue-green-colored waters surrounded by exposed

Hengduanshan mountains. The southern Alps of New Zealand have alpine ecobiomes, although the notable waterbodies associated with the Southern Alps are alpine and below treeline. Indeed, there are countless number of alpine lakes, ponds, and waterways around the world. WIKIpedia (2021) lists 40 famous alpine lakes, and it is no surprise that the majority is from the extensive Asian mountains with historical links to global trade and the Silk Road (lakes: 15, Pakistan; 7, India; 2, Nepal).

Alpine ecozones are identified as high-altitude regions above treeline (Pechlaner 1971). This ecozone is geographically characterized by steep slopes with high runoff (seepage, streams, and rivers) and variable conditions of unstable to stable biological growth. Water is retained in sections of flattened terrain (e.g., cirques or flatted meadows) across the alpine zone, and in these areas biological communities have more sustainable living conditions. Although sustainable, alpine wetlands, pond, and lakes are considered extreme biomes (Catalán et al. 2006; Hinder et al. 1999). In this chapter, alpine ecobiomes are separated into to three categories: (1) high alpine (high altitude cirques and valley meadows) (above treeline, >2500 m), (2) alpine (forested slopes and valleys) (1500–2500 m), and (3) peri-alpine (lakes and wetlands in the foothills of mountains) (below treeline, <1500 m).

In shallow waters, ice forms to the bottom sediments with no living life in the ice, except microbes. In these shallow frozen waters, sediments below the ice maintain a vast diversity of life which annually reappears in the warm seasons with primary production again feeding the food web. In deeper alpine lakes, with ice-covered water, the long winter seasons have extended thickened ice (up to 2 m) and snow cover which minimizes light availability for low lotic biological productivity (Ventelä et al. 1998). During the shortened growing season, there is an elevated level of solar radiance with altitude, which supports lotic productivity across the food web (Billings and Mooney 1968; Rose et al. 2009).

4.2 Cryoconite Holes

Small holes, water-filled depressions, and westage areas are commonly observed on the surface of glaciers. These cryoconite holes take their name from the presence of sediment-cryoconite or cold rock dust (Wharton et al. 1985). Arctic explorer A. E.

Fig. 4.1 (continued) bedrock and ion salt precipitate deposits (white). Third row from top, left: Trift Lake (Switzerland), high elevation alpine lake with turquoise (floured)-colored waters surrounded by a mix of exposed bedrock and vegetation. The sediment flour comes from the glacial stream at the top of the picture. Fourth row from top, right: Lake Colorada (Bolivia), a high alpine lake with extensive plankton and benthic invertebrate productivity (red colorations) associated bird and mammal wildlife. Bottom left: Unnamed Lake (Washington State, USA), an alpine lake with surrounding tree cover. Bottom right: Lake Lucerne (Switzerland), a large peri-alpine lake with a distinct limnion-layered structure. Image Copyright license agreements acquired from Gettyimages.com, 123rf.com, and share images from unsplash.com

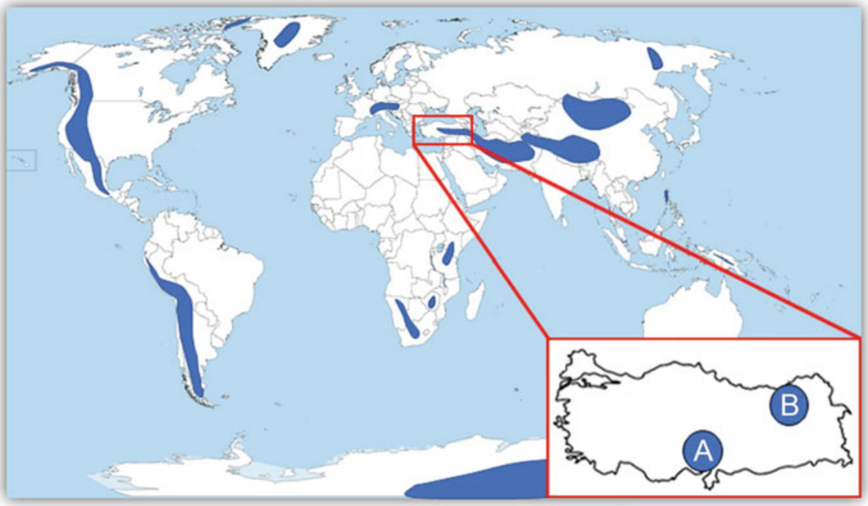


Fig. 4.2 Antarctic, Arctic, and high alpine mountain areas at different latitude zones. Insert map of Turkey ((**a**) southern Taurus Mountains in Turkey; (**b**) northeastern Anatolian Mountains). Modified base map from Google, Creative Commons CCO Licence, GNU Free Document Licence

Nordenskjöld created this term in his first trip to the Greenland Ice Cap in 1870 (Leslie 1879). He chose to name it from the Greek: *kruos* (ice) and *konis* (dust) (Gajda 1958). Wharton et al. (1985) noted that cryoconite holes may result partly from biothermal energy released by algal metabolism and microorganisms. Further, biological life in cryoconite holes could play a role in the colonizing of newly exposed habitats following glacial retreat. The holes can be in different sizes (less than 1 cm to 1 m in width) and rarely deeper than 60 cm (Steinböck 1936; Von Drygalski 1897). They have been reported throughout the world (in Greenland by Poser 1934; Svalbard by De Smet and Van Rompu 1994; Canada by Adams 1966; Antarctica by Wharton et al. 1985; glaciers of the Rocky Mountains by McIntyre 1984; Ecuador by Chamorro et al. 2021; and Himalayas by Takeuchi et al. 2000).

Previously, glaciers were considered as unproductive environments. However, this coldest of Earth's biomes has biodiversity hotspots of psychrophiles (Anesio and Laybourn-Parry 2012; Buda et al. 2020). Living organisms in these holes have been investigated since the 1930s (Charlesworth 1957; Gerdel and Drouet 1960; Mueller et al. 2001; Steinböck 1936; Wharton et al. 1981). In a comprehensive study, Mueller et al. (2001) compared southern (Canada Glacier) and northern (White Glacier) cryoconite holes in Antarctica. They reported that coccoid cyanobacteria were dominant in the southern cryoconite holes, whereas desmids were dominant in northern cryoconites. Further, there were a greater number of taxa observed in the Canada Glacier cryoconite. Regarding the diatoms, Chamorro et al. (2021) found 278 diatom taxa in 54 surface holes in the Antisana Glacier (Ecuador), and they reported that cryoconite holes are sites of high diversity. Moreover, the diatom *Muelleria cryoconicola* was described from the Commonwealth Glacier in Taylor Valley, Antarctica (Van de Vijver et al. 2010).

4.3 Alpine Lakes and Ponds

Although the African continent is relatively flat and dry, it has some of the oldest mountain ranges including extensive alpine ecobiomes. The Barberton Greenstone belt in South Africa, with an estimated age of 490 million years, is the oldest mountain range in the world (De Ronde and De Witt 1994). Other South African ranges (Waterberg, 2.7 billion years; Magaliesberg, 2.4 billion years; Pilansberg, 1.2 billion years) compliment the ancient continental formation of Africa. Mount Kenya, at 9 degrees south latitude, is an old mountain range (ca. 3 million years) which has been extensively eroded across today's glacial interglacial cycles forming a rugged topography with high altitude alpine lakes and ponds (Eggermont and Verschuren 2007). In the nearby Rwnnzori Mountains, close to the Equator, most of the alpine lakes are at high altitude (>3500 m) with glacial meltwater inputs in exposed bedrock catchments and scattered alpine terrestrial vegetation (Eggermont et al. 2007). Biological studies on African alpine lakes are limited (Barker et al. 2001).

The majority of freshwater lakes in South America were created through glacial activity and tectonic-volcanic events in the alpine areas of the Andes or in the surrounding foothills (Llames and Zagarese 2009). Lake Titicaca with an elevation of 3,812 m can be considered an alpine lake, although it is below treeline in the foothill's region (peri-alpine) and water temperatures do not fall below zero. Lake Titicaca is one of South America's largest lakes at 190 km long and up to 80 km wide. Historically, the lake has undergone significant water level changes over glacial and interglacial cycles (Fritz et al. 2007), and more recently (<2500 yBP), the land experienced human settlement. Evapotranspiration, caused by intense light, wind, and regional climate, accounts for ca. 90% water loss. Lake Titicaca has been investigated by different diatomists (Frenguelli 1939; Servant-Vildary 1991; Tapia et al. 2003), and some new centric and araphid diatom taxa have been described, *Cyclotella andina*, *Pseudostaurosira decipens*, *P. sajamaensis*, *Staurosira kjotsunarum*, *Ulnaria titicacaensis*, and *U. macilenta* (Morales et al. 2012, 2014; Theriot et al. 1985). The highest alpine ponds (pools) in the world are present in the Andes (Tsarenko et al. 2021). Lake Licancabur (Chile/Bolivia) at 5916 m a.s.l. is the highest lake covering a 6000 m^2 area. The lake is slightly saline and may have some geothermal heat sources. Ojos del Salado (Chile/Argentina) is the highest pond (pool) in the world at 6390 m a.s.l. Ojos del Salado is 100 m in diameter and shallow with turquoise (floured) water color. Acamarachi Pool (Chile) at 5950 m a.s.l. was the 5th highest pond, last known to be 10–15 m in diameter and now may be extinct. The status of Cerro Walter Penck pool(s) (Argentina), 6th highest in the world, is uncertain although reported with possible high sulfur content (Scanu 2013). Other high alpine glacial Andean lakes include Tres Cruces Norte (Chile); Lagunas Palcacocha, Perolcocha, and Tullpacocha (Parque Nacional Huascaran, Peru); and

Lagunas Huarmicocha, Colorcocha, Challhuacocxha, and Purectishgo from the Huanuco Lima Region (Peru). Biological studies on high alpine lakes in South America are limited (e.g., Aszalós et al. 2020).

The North American Rock Mountains have uncounted high alpine and alpine lakes, ponds, and wetlands scattered across the western marginal regions of the United States and Canada. Crater Lake, in the state of Oregon (USA), is the 2nd deepest lake in North America and 9th deepest lake in the world. Crater Lake (alpine) freezes every year and is considered a glacial lake (glaciers on adjacent mountains) with minimal lake outflow. Evaporation, rainfall, and snow fall are the modulating factors for water retention (Redmond 2007). The lake is below 3000 m (1884 m) and in the tree zone. The largest alpine lake in North America is Lake Tahoe with a surface area of 490 km^2 at an elevation of 1898 m (Gardner et al. 2000). Lake Tahoe is the second deepest lake in the United States with a depth of 501 m. The lake is below 3000 m (1898 m) a.s.l. and within the tree zone. Lake Tahoe does not freeze over during the winter. Other notable glacial alpine lakes include Tenaya Lake (2484 m a.s.l., max. depth 35 m), Yellowstone Lake (2357 m a.s.l., max. depth 120 m), Moraine Lake (1885 m a.s.l., max. depth 14 m), and Lake Louise (1768 m a.s.l., max. depth 70 m). Tenaya Lake is an isolated glacial lake, while Yellowstone has extensive tourist activity, and lakes Louisa and Moraine maintain local communities plus tourism. The Volcanogenic Garibaldi Lake (1484 m a.s.l., 109 m mean depth) is a more undisturbed natural alpine lake, semi-isolated with minimal camping and hiking activity. A high alpine lake of note, Thousand Island Lake (3001 m a.s.l., max depth 27 m, USA) is an isolated lake with hiking activity, formed at the bottom of a cirque after glacial retreat (Schoenherr 1992). A lot of research has been conducted on North American alpine lakes (selected references presented in text below) with many new diatom species described (as an example, Bahls 2010).

The Tibetan plateau and Himalayan Mountains comprise a countless plethora of alpine lakes ranging from ultra-freshwater to salt (or soda) lakes. The average elevation of the Tibetan Plateau is 4300 m a.s.l., and most of the lakes are categorized as salt lakes with varying levels of mineral loading. Snowmelt and rain are the primary water sources for lakes on the plateau. The largest lake, Namtso (4718 m a.s.l.), is an old lake, formed during the Paleogene age, and although without major settlements, the lake is surrounded by pastoral lands and is considered one of the holiest by Buddhist pilgrims (Li et al. 2008). In addition to snow and rain, Namtso Lake also has glacial water inputs. Lake color and mineral content vary greatly across the plateau, with sapphire blue (dark blue) lakes (e.g., Namtso Lake) the most evident using Landsat Copernicus imagery (Google Earth 2021). Turquoise (flour lakes) are the next prominent and located within valleys with high glacial mineral sediment loading. Some examples of these flour lakes include Tong Tso (4399 m a.s.l.), Zhaxi Co (4421 m a.s.l.), Gopug Co (4723 m a.s.l.), Chagbo Co (4518 m a.s.l.), and Changtiao Lake (4954 m a.s.l.). Green-colored lakes (light to dark) are also scattered across the Tibetan Plateau, represented by Yibug Lake (4562 m a.s.l.), Pongyin Co (4735 m a.s.l.), and Serbug Co (4524 m a.s.l.). Both turquoise and green-colored lakes have notable precipitated salt deposits in and around the lake basin. Qinghai Lake (3198 m a.s.l.) is the largest alpine lake in China with an average depth of 21 m. The lake is located in a contained basin (endorheic) with high salt and sediment accumulation (Rongxin et al. 2018; Zhang et al. 2011). In this lake, five permanent streams supply 80% of the water (Rhode et al. 2010). Qinghai Lake has extensive agricultural activity and, in the past, has had religious significance.

The alpine lakes in Pakistan, in contrast to the Tibetan Plateau, are situated within the Himalayan Mountains and are freshwater. The highest elevational lakes in Pakistan are Pakistan Lake and Shimshal Lake; both are at altitudes over 4,755 m. Other notable high alpine lakes over 3800 m include: Ansoo Lake (4126 m a.s.l.), Barah Lake (4512 m a.s.l.), Dakholi Lake (4771 m a.s.l.), Ghanche Lake (4600 m a.s.l.), Hrkolong Lake (4126 m a.s.l.), Karambar (4272 m a.s.l.), Rush Lake (4693 m a.s.l.), and Sheosar Lake (4142 m a.s.l.) (WIKIpedia 2021). These glacial lakes have sparse to limited terrestrial vegetation, are clear to turquoise colored (floured), and are shallow. Another series of alpine lakes (2500–3800 m, a.s.l.) are above treeline but have more biomass and diversity in terrestrial vegetation compared to the high alpine lakes. These lakes from Pakistan include, Dudipatsar Lake (3800 m a.s.l.), Lulusar Lake (3410 m a.s.l., Mahodand Lake (2900 m a.s.l.), Payee Lake (2895 m a.s.l.), Pyala Lake (3410 m a.s.l.), Ratti Lake (3700 m a.s.l.), and Saiful Muluk Lake (3224 m a.s.l.) (WIKIpedia 2021). Biological studies, on high alpine lakes in Pakistan are few (e.g., Barinova et al. 2013).

The Alps are layers of rock of European, oceanic, and African origin (De Graciansky et al. 2011). The specific folding and fracturing of the rock, coupled with erosion, form the steep vertical peaks of the central Alps (Gerrard 1990). These formations create enhanced runoff with fewer high alpine lake environments. The prominent lakes of the Alps are at the foothills of these steep vertical peaks with lower elevations and referred to as peri-alpine lakes. Lakes Geneva (372 m a.s.l., average depth 154 m), Lugano (282 m a.l.s., average depth 134 m), Garda (62 m a.s.l., average depth 136 m), Zurich (402 m a.s.l., average depth 49 m), and Konstance (396 m a.s.l., average depth 90 m) are examples of peri-alpine lakes below treeline in the foothills of the central alps. Higher elevated alpine lakes like Resia Reschen (1499 m a.s.l.), Kratzberger (2122 m a.s.l.), and Lago di Vernago (1692 m a.s.l.) are still below treeline and with human settlements. Across the Central Alps, there are scattered pockets of cirque and shallow valley ponds and lakes. In the Parco Naturale Gruppo di Tessa region (South of Innsbrück, Austria), high altitude ponds and small lakes of note are evident (e.g., Egret lakes) which are <3000 m a.s.l. but above treeline with minimal terrestrial vegetation. The Parco dell'Alpe Veglia e dell' Aple Devero region of Italy has a mixture of high latitude ponds and lakes above treeline with turquoise (floured) and sapphire blue (dark blue) colored waters (e.g., Lago del Sabbione, 2460 m a.s.l.; Lago del Narèt, 2305 m a.s.l.). The biology and ecology of alpine lakes across Europe have been studied (references presented in text below). Many new diatom species have been described from the Alps; as an example, Hustedt (1943) described four species new to science from high mountain lakes around Davos Switzerland.

4.4 Turkey and Area

Turkey is located between temperate forest zone mountains (southern Taurus Mountains) and subtropical sclerophyllous forest zone mountains (northeastern Anatolian Mountains) (Nagy and Grabherr 2009; Solak et al. 2012, Fig. 4.2). The mean elevation is less than 500 m in the western Anatolia, about 1000 m in the central Anatolia, and over 3000 m in the mountanous area of eastern Anatolia. There are three main glacial areas: the Taurus Mountains, the Kaçkar Mountains, and some high mountains in Anatolia Plateau (Sarıkaya and Çiner 2019, Fig. 4.3). A number of investigations have studied the morphological and biological aspects of Alpine lakes in Turkey (e.g., Atıcı 2018; Aygen et al. 2009; Şahin et al. 2020; Yıldız et al. 2012; Yıldız-Gürbüzer 2016). For instance, the morphometrical features of selected lakes in Kaçkar and Soğanlı Mountains (northern eastern Anatolian mountains) have been evaluated by Sarı et al. (2015), and the reported max. depths of the lakes were between 0.5 and 49.0 m (mean 7.4 m), max. length of the lakes ranged between 25.2 and 497.4 m (216.8 m), and max. widths between 15.5 and 297.9 m (mean 135.0 m). At present, diatom assemblages of some glacial lakes have been studied. Among them, Atıcı (2018) reported *Cymbella affinis* as abundant in the Artabel Lakes of Eastern Blacksea. In Aygır Lake (also Eastern Black Sea), Taş (2016) noted *Achnanthidium minutissimum*, *Lindavia bodanica*, *L. comensis*, and *Diatoma mesodon* were abundant in the plankton.

4.4.1 Van and Urmia Lakes

The soda lakes Van and Urmia are recognized under 40 famous alpine lakes in the world (WIKIpedia 2021). The lakes are located in the "*Irano-Anatolian Mountains of Central Asia*" region, considered in the top 35 biodiversity hotspots of the world (Marchese 2015).

Van Lake, the largest lake in Turkey, is located at a high altitude (1648 m a.s.l.) in Eastern Anatolia. It is 450 m deep with a volume of 576 km^3, thus the largest soda lake and third largest closed lake in the world. This saline lake is defined by its elevated sodium and potassium levels, with a balance of bicarbonate and carbonate ions along with other alkaline earth ions, giving a $Na\text{-}CO_3\text{-}Cl\text{-}(SO_4)$ chemistry (Reimer et al. 2009). The lake has a high specific conductance of 22.9–26.7 $mS.cm^{-1}$ and a pH of 9.3–9.8. The presence of diatoms in sediment deposits and characteristics in terms of hydrology and water chemistry of Van Lake and associated rivers were detailed by Reimer et al. (2009). Van Lake is famous for a special type of sediment called microbialites, carbonate forming crusts (Kempe et al. 1991; Kempe and Kaźmierczak 2003; López-García et al. 2005). Unique in regard to these geochemical characteristics, Van Lake also hosts endemic species such as the pearl mullet *Alburnus tarichi* (Guldenstaedtii, 1814). About 80 years ago, Legler and Krasske (1940) described several diatom species from Van Lake: *Amphiprora*

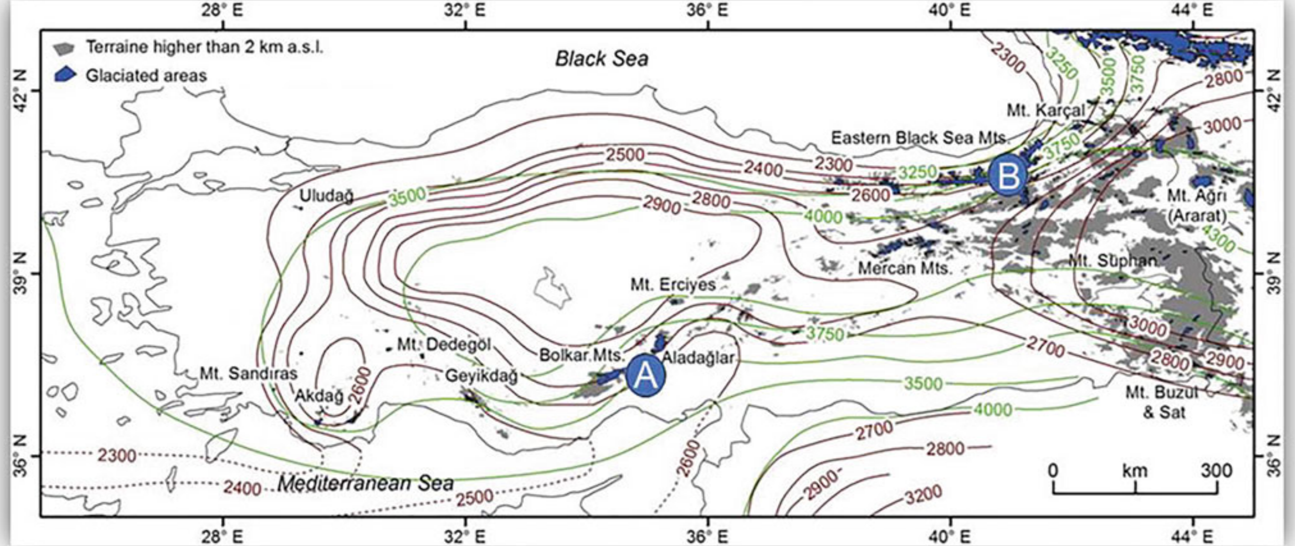


Fig. 4.3 Altitude map of Turkey showing high elevation terranes (grey, alpine environments) and glacial areas (blue, high alpine environments ((**a**) southern Taurus Mountains in Turkey; (**b**) northeastern Anatolian Mountains). With permission and modified from Sarıkaya and Çiner 2019)

paludosa var. *densestriata* (Syn. *Entomoneis densestriata*), *Rhopalodia musculus* var. *supresemicirculatus* (Syn: *Rhopalodia supresemicirculata*), *Nitzschia incognita*, and *Surirella invicta.* Other species have also been documented, including *Nitzschia vitrea*, *N. frustulum*, *N. frustulum* var. *subsalina*, *N. fonticola*, *N. inconspicua*, *N. kuetzingiana*, and *N. communis*, in a review of Van Lake phytoplankton and littoral diatoms species (Gessner 1957). The lake community has a selective emphasis for taxa from the orders Bacillariales, Rhopalodiales, and Surirellales. Some of the described taxa were later reinvestigated and imaged by Lange-Bertalot et al. (1996). Also, reports have been published on diatoms from the surrounding area (e.g, Solak et al. 2012). Recently, a new species from the genus *Nitzschia* was found in the lake (Solak et al. 2021). Additional investigations on benthic diatom assemblages of Van Lake show a potential presence of more endemic taxa (unpublished data).

Lake Urmia is the second largest hypersaline lake in the world, located in northwest Iran. Due to its unique biodiversity, the lake was declared a National Park, Ramsar Site, in 1971 and a Biosphere Reserve by UNESCO starting in 1976 (Khatami and Berndtsson 2013; Nhu et al. 2020). The elevation of the lake is 1278 m a.s.l. with a maximum water depth of 16 m and salinity range of 217–300 g L^{-1}. The pelagic zone of the lake is inhabited by brine shrimp (e.g., *Artemia urmiana*), bacteria, archaea, and phytoplankton (Eimanifar and Mohebbi 2007). Recently, the water quality of the southern part was investigated by Goshtasbi et al. (2021). They report that dissolved oxygen levels in the lake were quite low (2.99–3.37 mg L^{-1}), and intensive cyanobacteria blooms were present. Annually, the climate is semiarid with evaporation pressures on Lake Urmia. The lake basin contains 204,000 ha of agricultural land and gardens. Most of the agricultural pressures are linked to irrigation. The main sources for agricultural water are both surface and underground water (Nhu et al. 2020). A comparison of diatom assemblages between Van Lake and lakes from the Tibetan region shows no similarities. Yang et al. (2003) investigated forty lakes from the Tibetan region between 2797 m and 5180 m a.s.l. and reported *Achnanthidium minutissimum*, *Amphora libyca*, *Cymbella affinis*, *Nitzschia perminuta*, *Sellaphora pupula*, and *Staurosirella pinnata* as common. Moreover, *Anomoeoneis sphaerophora*, *Surirella peisonis*, *Mastogloia elliptica*, and *Navicymbula pusilla* were characteristic saline species. In contrast, *Berkeleya* sp., *Nitzschia incognita*, *Surirella invicta*, and *Rhopalodia supresemicirculata* are the characteristic saline taxa in Van Lake (unpublished data).

4.5 The Holocene

Extreme cold biomes, like the Arctic and Antarctic, have a short extant history of ecosystem development and sustainability, which comprises the latest interglacial period of the Holocene (Jersabek et al. 2001). There are exceptions where isolated regions in the Arctic survived the last glaciation with Arctic lakes extending back to previous interglacial periods (e.g., marine isotope stage (MIS 5)) (Crump et al. 2021;

Hughes et al. 2013). Biological records in the sediments of past interglacials are limited, and age models need further validation (Wilson et al. 2012). The Holocene epoch is divided into three stages, recognizing changing climate conditions during the melting and retreating of the glaciers and current climate state at the end of the Little Ice Age (Walker et al. 2018, 2019). Global alpine biomes were slow to develop during the Greenlandian stage (8300–11,700 YBP) gradually warming with glacial melt highlighted by evaporation regime changes. The development of temporary and permanent glacial and alpine waterbodies was extensive through this period with fluctuations in climate impacting biological productivity (e.g., Smol et al. 2005). The Northgrippian stage (8300–4200 YBP) documents an initial cooling followed by a drier period with accelerated glacial ice melt. The development of temporary glacial pond lakes likely declined during this stage with extended cold seasons and ice cover (e.g., Zhang et al. 2020). The Meghalayan stage (4200–60 YBP) represents periods of reduced precipitation across Asia and a colder climate (Walker et al. 2018). Alpine lakes and ponds have experienced dramatic water level changes, periods of drought, and pond/lake extinctions throughout the Holocene (Zhang et al. 2020). Through these stages of the Holocene, terrestrial biomes also developed and advanced or retreated quickly from low altitudes extending up mountain range slopes with the present-day tree line delineating the advancement of biome production up to the alpine. The initiation of the Anthropocene epoch (International Commission on Stratigraphy) proposed for some time in 2022/2023 will document continued warming of the global climate after 1950 with implications for changes in alpine ecosystems.

4.6 Chemistry

The primary elements impacting high alpine lakes and ponds are the dominant anions and cations in the region. These are coupled with other erosional elements from rock and soils to create a broad range of observed water color. Clear waters with low ion and inorganic elemental content have the classic dark to sapphire blue (dark blue)-colored waters in contrast to lakes with high ion and/or inorganic element loading creating the turquoise to green (floured) waters (suspended particles reflecting light). This water color is ultimately determined by type of local bedrock, erosional patterns, and water retention time in the waterbody. In lower peri-alpine lakes, organic matter further contributes to darken water color (particles absorbing light). Available nutrients and organic matter can further contribute to water color through the growth of plankton and littoral-related tychoplankton. This algae growth typically gives a green color due to the absorption of sunlight by chlorophyll. However, other color pigments, like pink (cyanobacteria secondary pigments) and golden brown (diatom lipids), can be observed in the plankton and on the bottom of ice covers (e.g., Frenette et al. 2008).

Nutrients are low in high alpine aquatic systems, with both nitrogen and phosphorus often limiting. In high elevation cirque and valley lakes above tree line, the source of nutrients is bedrock and soil, local biological activity with decaying organic matter, and atmosphere deposition through rain, snow, and glaciers. Studies from around the world have shown atmospheric nitrogen as a primary seed for this nutrient in high alpine aquatic primary production (e.g., Liu et al. 2015; Rogora et al. 2008; Wolfe et al. 2003). However, atmospheric N sources will vary depending on geographic location and global wind circulation conditions. Alpine biomes close to anthropogenic sources or regions of high lowland productivity (e.g., Alps in Europe) will have higher nitrate levels, while at the other extreme, more remote locations (Andes, South America) with minimal atmospheric N sources will have enhanced local cycling of organic nitrogen (Rogora et al. 2008). Glaciers are excellent sinks for the accumulation of nitrogen over long periods of time. Detailed studies show nitrogen sources from glaciers (long-term sinks) are more plentiful compared to snowmelt (annual sinks) (Slemmomon and Saros, 2012; Saros et al. 2010). On the Tibetan Plateau with paleo-marine sediments, the groundwater for Ximen Co Lake was found to be an important source of dissolved inorganic nitrogen relative to total phosphorus (Luo et al. 2018), ultimately driving this lake system toward phosphorus limitations. Phosphorus is consistently a limiting nutrient in alpine aquatic systems (Camarero and Catalan 2012; Tiberti et al. 2010). Since dissolved organic phosphorus (DOP) is not readily available in most alpine lakes, dissolved inorganic phosphorus (DIP) is the primary source for algal growth (Hudson et al. 2000). Like nitrogen, atmospheric sources of phosphorus through rain, snow, and glacial melt are substantial even in the Tibetan Plateau (Rongxin et al. 2018; Zhang et al. 2019). However, as illustrated above, nutrient loading and cycling in high alpine lakes varies globally. Since many alpine lakes are both N and P limited (Cook et al. 2020; Zhang et al. 2019), it is the specific colimitation interaction (not N/P ratio) between these nutrients and ions that will determine nutrient availability for primary productivity (Harpole et al. 2011). Wildlife plays a minimal role in nutrient cycling, although, as observed in Lago Colorada, Bolivia (Fig. 4.1), wildlife can have some specific influences on lake nutrient loading and cycling (Sarnelle and Knapp 2005).

The ionic and nutrient composition of high elevation lakes on the Tibetan Plateau (old marine seabeds) is heavily influenced by soils and bedrock (Li et al. 2021; Luo et al. 2018). Alpine lakes on the plateau are predominantly brackish to soda lakes (Ma et al. 2011) with nutrient interactions alleviating salinity limitation for bacteria and plankton growth (Jiang et al. 2007; Li et al. 2021; Yue et al. 2019). Therefore, salinity effects on phytoplankton composition are more complex than previously reported (Ferreira et al. 2019). These findings from the Tibetan Plateau further highlight the complexities of changing nutrient and ion-salt sources in directing stochastic and deterministic biological diversity and primary production.

The majority of high alpine lakes are oligotrophic, limited by light and nutrients (Liu et al. 2011; Mitamura et al. 2003). High alpine ponds and lakes also experience elevated UV levels (Caldwell et al. 1980) with deeper photic zone in clear waters due to nutrient limitations and low productivity (Scully and Lean 1994). Thus, these alpine lakes and ponds have poorly developed planktic and tychoplanktic communities associated with the littoral zone (Doyle and Saros 2005). The particulate-rich turquoise and green-colored lakes further reduce the photic zone, limiting phytoplankton productivity in the surface waters (Sommaruga 2015). In contrast, peri-alpine lakes have more complex planktic communities with a broad tropic structure. In a global examination of planktic assemblages in alpine systems (Europe, Chile, Ethiopia), Filker et al. (2015) observed a broad spectrum of taxa in the plankton with dinoflagellates more prominent in Europe, mixotrophic cryptophytes in Chile, and chlorophytes and heterokonts (including diatoms) in Ethiopia and Chile. Tolotti et al. (2006) also noted the prominence of dinoflagellates, cryptophytes and chrysophytes in European alpine phytoplankton. Other researchers have observed the importance, abundance, and diversity of chrysophytes in alpine and Arctic aquatic systems (Betts-Piper et al. 2004; Charvet et al. 2012; Duff et al. 1992; Kamenik and Schmidt 2005; Lotter et al. 1998). The green chlorophyte algae (including desmids) are present but not abundant in alpine lakes and ponds, unless elevated levels of nutrient are present (Lepori and Robin 2014; Oleksy et al. 2021; Priddle and Happey-Wood 1983; Tolotti et al. 2006).

With respect to alpine plankton ecology, factors controlling growth are mixed. Catalán et al. (2009), in a 235 alpine lake study in Europe, identified four factors controlling biotic growth in alpine systems: (1) lake size was linked to rotifers; (2) pH correlated to diatoms, (3) ice cover was associated with chydorids and planktic crustaceans, and (4) Trophic statue (structure) was linked to chironomids. Tolotti et al. (2006) in a similar 70-lake study observed catchment vegetation, geochemistry (acidity/alkalinity), and nitrate to be correlated with phytoplankton and trophic status linked to the zooplankton community. Other alpine lake systems, Tibetan Plateau, for example, have shown phytoplankton community diversity to be higher in more saline habitats (Lozupone and Knight 2007; Zhong et al. 2016). In another study, Marchetto et al. (2009) noted that lake size and catchment type correlated with phytoplankton. Jacquemin et al. (2019) also observed that small rocky catchments reduced functional richness of phytoplankton, while increasing total phosphorus increased the autotrophic component of the phytoplankton, and lower phosphorus levels encouraged mixotrophic communities. Anneville et al. (2005) studying peri-alpine lakes further noted the preference of mixotrophic communities with reduced phosphorus loading. Also, Lotter et al. (1998) observed that total phosphorus was linked to diatom growth but not with chrysophytes and cladocerans. In other studies, nitrogen has been identified as a controlling factor (Liu et al. 2015; Rogora et al. 2008; Tolotti et al. 2006). In peri-alpine lake systems, cyanobacteria can be dominant as blooms or even toxic blooms (Monchamp et al. 2019). The control of cyanobacteria blooms in lakes can be achieved simply by the reduction of carbon and nutrients (Dokulil and Teubner 2000). Monchamp et al. (2019) using sediment genetic markers in peri-alpine lakes found cyanobacteria phylogeny associations with air temperature and water column and little to no correlation to elevated levels of phosphorus and nitrogen. Finally, Vogt et al. (2021) studying 256 lakes across an elevational gradient document that protists showed decreasing richness and diversity with increasing altitude as well as a high proportion of region-specific specialists. In summary, many factors are selectively driving plankton productivity and diversity. First, altitude matters, and climate is driving many of the determining factors. Phytoplanktons are correlated to catchment size (including vegetative development) and nutrients. Higher nutrients align with autotrophic dominant communities, whereas lower nutrients associate with mixotrophic communities. Zooplanktons are correlated to lake size, climate, and phytoplankton composition.

Cyanobacteria play a significant role in benthic alpine aquatic biodiversity and productivity (Jungblut and Vincent 2017; Mez et al. 1998; Sommaruga and Garcia-Pichel 1999). As an example, the diversity of algae and cyanobacteria as bioindicators of Lake Nesamovyte (Eastern Carpathians, Ukraine) was investigated by Tsarenko et al. (2021), and they recorded 234 species in the lake. In alkaline environments, cyanobacteria are common and scattered on the substratum or in mats and sediment crusts. When nitrogen is limiting, nitrogen fixing cyanobacteria mats and crusts are observed in the lake benthos (Dickson 2000). Since climate and reduced levels of carbon and nitrogen can determine planktic cyanobacteria growth, it would be no surprise that benthic cyanobacteria are also under the control of these factors. Further, cyanobacteria are susceptible to UV exposure, and benthic crusts act as shields in addition to UV protection compounds to sustain communities (Castenholz and Garcia-Pichel 2012). In a novel study, it was demonstrated that selected cyanobacteria can migrate within crusts and mats in shallow waters, optimizing living conditions (Garcia-Pichel et al. 1994). Given the broad global distribution of cyanobacteria, it is not surprising that there is genetic similarity in cyanobacteria taxa between Arctic, Antarctic, and alpine ecoregions (Jungblut et al. 2009). The significance of biotic crusts in alpine lakes, especially ion-rich lakes, is yet to be determined.

Diatoms are a common assemblage in the plankton of oligotrophic to mesotrophic alpine to high alpine lake environments with depths >10 m. In shallower lakes and ponds, productivity is predominant in the benthos (Wunsam et al. 1995). In harsh polar and glacial environments, diatoms can also be found on ice in surface pools, under the ice as attached mats and in terrestrial environments with sporadic water exposure (Bashenkhaeva et al. 2015; Van Kerckvoorde et al. 2000; Vincent et al. 2000). The reported number of species in alpine environments varies depending on the criteria used to define alpine. A range from 109 to 719 taxa of diatoms, primarily benthic, have been reported (Clarke et al. 2005; Feret et al. 2017; Robinson and Kawecka 2005). Numbers on the higher side (350 plus) are currently in-line with species numbers reported from the Arctic (Antoniades et al. 2008; Foged 1974, 1981) and Antarctic (Verleyen et al. 2021).

Diatoms are well adapted to poor environments with limited nutrients and correlate with phosphorus (Bigler et al. 2005; Lotter et al. 1998; Murphy et al. 2010), nitrogen (Hobbs et al. 2011; Tolotti et al. 2007), pH (Koinig et al. 1998; Psenner and Schmidt 1992), salinity (Yang et al. 2003), silicates (Tolotti et al. 2007), and even UV light (Vinebrooke and Leavitt 1996). However, the statistical sensitivity of nutrient-diatom correlations for phosphorus (as an example) below detection limit or even <10 ug L^{-1} may not be effective at giving consistent relationships over spatial scales (Berthon et al. 2013). At present, there is no one environmental factor that can explain the growth of diatoms across globally spaced alpine systems, although chemical factors are prominent (Rivera-Rondón and Catalán 2020).

4.7 Diatom Biodiversity in Extreme Environments

Many studies in cold regions around the world have documented the biogeography and taxonomy of diatoms (e.g., Van de Vijver et al. 2004; Zidarova et al. 2016; Spaulding et al. 2021, in Antarctica; Foged 1974; Antoniades et al. 2008; Zimmermann et al. 2010; Pla-Rabés et al. 2016; Zgrundo et al. 2017, in the Arctic; Patrick and Freese 1961; Foged 1981; Bahls and Luna 2018, in Alaska; Skvortzow (1929, 1937, 1938a, 1938b), Lange-Bertalot and Genkal 1999; Laing et al. 1999; Reichardt 2009; Genkal et al. 2010; Kulikovskiy et al. (2012); Kulikovskiy, Kociolek, et al. 2015a; Potapova et al. 2014; Pestryakova et al. 2018; Potapova 2018, in Siberia; Rumrich et al. 2000; Morales et al. 2009; Blanco et al. 2013; García et al. 2021, in the Andes; Dickie 1882; Suxena and Venkateswarlu 1968; Jüttner et al. (2000, 2004, 2010, 2011, 2017, 2018); Bhatt et al. 2008; Van de Vijver et al. 2011; Krstić et al. 2013; Verma et al. 2017; Mohan et al. 2018; Wetzel et al. 2019; Radhakrishnan et al. 2020, in the Himalayan Mountains; Van de Vijver et al. 2010, in South African glaciers; Lin et al. 2018; Zhang et al. 2019, in China, and Levkov et al. 2005; Kawecka and Robinson 2008; Buczkó et al. 2010; Cantonati et al. 2012; Buczkó 2016; Feret et al. 2017; Heudre et al. 2019, in Europe).

4.7.1 Antarctica

The first notable diatom work on extreme environments was done by Reinsch (1879) in the Antarctic region, and then many diatom studies followed (*detailed in* Zidarova et al. 2016). In a bipolar study of the Antarctic and Arctic, Van de Vijver et al. (2004) examined the genus *Stauroneis* and described 40 new taxa. Van de Vijver et al. (2010) also worked on the genus *Muelleria* from Antarctic and South African glaciers and, in that study, observed more than 15 taxa with some of them new to science. Over the last two decades, Van de Vijver and his colleagues have conducted extensive work on maritime Antarctic and Antarctic diatoms with the description of many new taxa Verleyen et al. (2021). To further assist in diatom identifications, Zidarova et al. (2016) prepared a taxonomic monograph using LM and SEM images. More recently, Spaulding et al. (2021) established a website on Antarctic freshwater diatoms.

In a preliminary examination of 13 samples from the maritime Antarctic, South Shetland Islands (Robert, Ardley, Livingstone, Horseshoe, and Galindez Islands), we identified ca. 100 freshwater taxa from ponds and lakes. Abundant taxa included *Chamaepinnularia krookiformis*, *Navicula australoshetlandica*, *Planothidium australe*, *P. renei*, and *Psammothidium subatomoides.* Overall, most of the identified taxa are small forms belonging to the genera *Chamaepinnularia*, *Luticola*, *Microcostatus*, and *Psammothidium*, while also some big forms exist belonging to *Navicula*, *Nitzschia*, *Stauroneis*, and especially *Pinnularia*. Among the taxa, *Navicula gregaria, Nitzschia gracilis*, and *N. homburgiensis* were interesting because *N. gregaria* (for example) is documented from polluted inland waters in Turkey. *Nitzschia gracilis* and *N. homburgiensis* are not abundant; however, the taxa are also observed across different regions in Turkey.

4.7.2 Arctic

Early investigations on Arctic diatoms were done by Ehrenberg (1844), Lagerstedt (1873), and Cleve (1896). Cleve continued to study Arctic diatoms, marine and freshwater, from the circumpolar Arctic region into the early 1900s. Since then, a plethora of diatom research has been conducted on the Arctic biome considering everything from taxonomy to climate change (*detailed in* Antoniades et al. 2008; Smol et al. 2005). More recently, diatom assemblages in the Canadian Arctic Archipelago were archived in monographs by Antoniades et al. (2008), Zimmermann et al. (2010), and Bahls et al. (2018). Antoniades et al. (2008) investigated the diatoms of freshwater ponds and lakes in the Prince Patrick, Ellef Ringnes, and northern Ellesmere Islands from the Canada Arctic Archipelago and identified 362 taxa with 7 new species across 6 genera (Antoniades et al. 2008). They along with Bouchard et al. (2004) and others have documented the richness and abundance of small araphid and monoraphid diatoms in cold environments. In contrast, Zimmermann et al. (2010) examined a Pliocene–Pleistocene freshwater diatom flora on Bylot Island documenting the historical diatom flora from this extreme environment.

Despite the large area of Alaska, there are limited works about freshwater diatoms in the region (e.g., Bahls and Luna 2018; Hein 1990; Patrick and Freese 1961). Foged (1981) investigated 258 samples from 218 localities in Alaska and identified 987 taxa with the description of 9 species, 20 varieties, and 16 formae as new for science. The diatoms from Wrangell-St. Elias National Park in the southwest side of Alaska were more recently examined by Bahls and Luna (2018) with 139 taxa identified. Most of the Wrangell-St. Elias National Park diatoms (84%) were reported from Europe, and a rare taxon *Surirella arctica* was also noted.

Greenland, Iceland, Spitzbergen, and Franz-Josef Land represent real islands or island clusters of biogeological importance. Lagerstedt (1873) made the first diatom survey for Spitzbergen, and our examination of original material found many small species from the genera *Humidophila*, *Navicula*, *Eunotia*, *Staurosira*, *Staurosirella*, *Achnanthidium*, and *Planothidium*. Zgrundo et al. (2017) observed 96 taxa (excluding subspecies, varieties and formae) in aquatic habitats of northern Spitsbergen, including the smaller taxa *Achnanthidium minutissimum*, *Staurosirella pinnata*, and *Nitzschia alpina*. Foged (1974) examined 244 samples from Iceland and recorded 689 freshwater diatom taxa (excluding forms). In the Iceland study, there were

37 small araphid taxa, and 55 small monoraphids. Also, the diatom structure and diversity in Franz Josef Land Archipelago was investigated by Pla-Rabés et al. (2016), and *Diatoma tenuis* was the most abundant taxon with several circumpolar taxa observed such as *Chamaepinnularia gandrupii*, *Cymbella botellus*, *Psammothidium* spp., and *Humidophila laevissima*.

Historically, Skvortzow (1929, 1937, 1938a, 1938b) published extensive floristic surveys of diatoms from Siberia. Genkal et al. (2010) examined centric diatoms of some water bodies in northeastern West Siberia and noted circumpolar planktic diatoms: *Aulacoseira subarctica, Cyclotella arctica, C. comensis, Stephanodiscus invisitatus*, and *S. triporus*. Later, Genkal et al. (2012) identified the Pennatophyceae members of the region with unidentified taxa from the genera *Amphora, Cavinula, Eunotia, and Navicula*. Diatom assemblages from Yakutian lakes in northeastern Siberia were documented by Pestryakova et al. (2018) reporting 157 taxa. In addition, a monograph was prepared by Lange-Bertalot and Genkal (1999) from Vaygach, Mestnyi, Matveev Islands, and Yugorsky Peninsula in northwest Siberia. Lake Baikal is the largest freshwater lake in the World with about 10% of the planktonic algae recorded as endemic (Kozhov 1962, 1972). Genkal and Bondarenko (2006) also confirmed endemic diatom assemblages in the lake. In a volumetric treatise, Kulikovskiy et al. (2012) and Kulikovskiy, Lange-Bertalot, and Kuznetsova (2015b) documented 10 new genera and 382 new species from Lake Baikal. Additional taxa and some genera have also been described in separate articles (e.g., Kociolek et al. 2013, 2018; Kulikovskiy et al. 2016; Kulikovskiy, Gluschenko, Genkal, et al. 2020a; Kulikovskiy, Gluschenko, Kuznetsova, et al. 2020b; Kulikovskiy, Kociolek, et al. 2015a). Reichardt (2009) underlined that diatom studies across the Russian Arctic were limited with respect to the large area, and he described some new *Gomphonema* taxa (*G. demersum*, *G. jergackianum*, *G. marvanii*). Potapova et al. (2014) recently described a scattered selection of four new taxa, from the Yakutia region in Siberia. Potapova (2018) also documented the distribution of *Psammothidium* species by describing *Psammothidium onufrii* from northeastern Siberia.

Laing et al. (1999) investigated 23 lakes located near Norilsk, Siberia, and found the prominent diatom communities were very similar to Canadian and Fennoscandian lakes, supporting the findings of a circumpolar distribution in the Arctic diatom flora. Taxonomically, an interesting work was conducted by Paull et al. (2008) using small fragilarioid (*Staurosira* and *Staurosirella*) taxa from the Canadian Arctic, Siberia, and Fennoscandia; they found different morphological forms of *Staurosirella pinnata* sensu lato and *Staurosira venter* could be distinguished and that these groups (morphs/taxa) were distributed across the circumpolar Arctic.

4.7.3 Andes and Patagonia

The early diatom flora from Andean Patagonia was documented with drawings and species lists by Frenguelli (1924, 1936, 1942) and Frenguelli and Orlando (1956). However, diatom floras of the Andes have received little attention in comparison with North temperate freshwaters (Blanco et al. 2013). Rumrich et al. (2000) reported that many different cosmopolitan taxa, typical from Holarctic and temperate areas in Europe, were present in the Andes, while common European species were not. The epilithic diatoms from cloud forest and alpine streams in Bolivia were investigated by Morales et al. (2009), and they described two new species (*Fragilaria cochabambina* and *Achnanthidium sehuencoensis*) and underlined that totally 118 species were found and 42 of them were newly observed for the region. Some recently described taxa include: *Navicula venetoides*, *Pinnularia boliviana*, *Nitzschia sansimoni*, *Surirella striatula* var. *halophila*, and *S. moralesii* from a saline lake in Lopez Area (Argentina) (Blanco et al. 2013). García et al. (2021) also described four small species including *Pseudostaurosira australopatagonica*, *P. catalinae*, *P. tehuelcheana*, and *P. zolitschkae* from four shallow lakes in Santa Cruz Province on the east side (Argentina) of the Andes and one shallow lake from the Magallanes Region on the west side (Chile).

4.7.4 Himalaya and Tibetan Plateau

In the Himalaya, diatom studies began early with Dickie (1882), the results detailed in Suxena and Venkateswarlu (1968) with an extensive list of the diatoms. Compère (1983) also published a list of algae from Kashmir and Ladakh in Western Himalaya. Nautiyal, Kala, and Nautiyal (2004) reported 200 diatom taxa (including 77 of them as first records) from the Mandakini basin. Then, Nautiyal, Nautiyal, et al. (2004) investigated the streams in Garhwal region in India and documented 58 as first records for the area. Some years later, the distribution of diatoms within the family Acanthaceae from the Himalayan highlands was published by Verma et al. (2017). In 2008, Bhatt et al. (2008) reported the invasive species *Didymosphenia geminata* (Lyngbye) Schmidt as abundant in Western Himalaya.

After Himalaya was recognized as a hotspot (Jüttner et al. 2000), many new taxa were described. Taxonomic studies have centered around the genus *Oricymba* (3 new species), and the older *Gomphonema* (8 new species), along with *Odontidium* (4 new species). Additional species were also described from the genera *Achnanthidium*, *Cymbopleura*, *Navicula*, and *Synedra* (Table 4.1).

Table 4.1 A list of new diatom taxa described from the Himalaya region after 2000

Taxon	Length (µm)	Width (µm)	Reference
Achnanthidium coxianum I. Jüttner, L. Ector, and C.E. Wetze	8.1–12.9	2.5–3.0	Wetzel et al. (2019)
A. rostropyrenaicum Jüttner and E.J. Cox	18.0–24.5	4.3–4.5	Jüttner et al. (2011)
Cymbopleura emoda Jüttner and Van der Vijver	35.0–40.0	6.8–7.7	Van de Vijver et al. (2011)
C. gokyoensis Jüttner and Van de Vijver	20.1–21.7	2.7–3.7	
Eunotia igorii S. Krstic, Z. Levkov, and A. Pavlov	38.2–72.7	12.6–15.3	Krstić et al. (2013)
E. panchpokhariensis S. Krstic, Z. Levkov, and A. Pavlov	23.4–32.6	2.4–3.3	
E. paramuscicola Krstić, Z. Levkov, and A. Pavlov	9.5–29.0	2.0–3.3	
E. zechii Krstić, Z. Levkov, and A. Pavlov	20.3–55.3	3.1–5.6	
Gomphonema adhikharyi C. Radhakrishnan, Sudipta K. Das, Kociolek J, B. Karthick	28.0–34.0	5.0–6.0	Radhakrishnan et al. (2020)
G. chubichuense I. Jüttner and E.J. Cox	11.0–22.0	3.0–5.0	Jüttner et al. (2000)
G. pararhombicum Reichardt, Jüttner, and E.J. Cox	20.0–70.0	6.5–11.0	Jüttner et al. (2017)
G. nepalense Reichardt, Jüttner, and E.J. Cox	18.0–55.0	6.0–8.0	
G. nediense Reichardt, Jüttner, and E.J. Cox	19.0–31.0	5.0–6.0	
G. incognitum Reichardt, Jüttner and E.J. Cox	17.0–39.0	4.0–6.5	
G. makaluense Reichardt, Jüttner, and E.J. Cox	26.0–62.0	6.0–9.5	
G. saccatum Reichardt, Jüttner, and E.J. Cox	12.5–45.3	5.2–7.0	
G. sinestigma Reichardt, Jüttner, and E.J. Cox	17.0–22.0	3.0–4.0	
Navicula obtecta I. Jüttner and E.J. Cox	41.0–60.0	7.0–9.5	Jüttner et al. (2000)
Odontidium nepalese I. Jüttner, Gurung, Van de Vijver, and D.M. Williams	22.0–63.5	8.5–12.0	Jüttner et al. (2017)
O. himalongissimum I. Jüttner, D.M. Williams, and E.J. Cox	10.0–56.5	5.5–8.5	
O. longiovalum I. Jüttner, D.M. Williams, and E.J. Cox	10.5–61.0	6.0–10.0	
O. parvoapiculatum I. Jüttner, D.M. Williams, and E.J. Cox	12.5–38.5	6.0–8.5	
Oricymba japonica (Reichelt) Jüttner, E.J. Cox, Krammer, and Tuji	30.0–55.0	9.0–13.0	Jüttner et al. (2010)
O. latirotundata I. Jüttner and Van de Vijver	54.0–71.0	13.0–16.0	
O. subaequalis I. Jüttner, Krammer, E.J. Cox, Van de Vijver, and Tuji	33.0–43.0	9.0–11.0	
O. subovalis I. Jüttner, Krammer, and E.J. Cox	25.0–55.0	9.0–11.0	
Synedra inaequalis var. *jumlensis* I. Jüttner and E.J. Cox	37.0–48.0	7.5–11.0	Jüttner et al. (2000)

4.7.5 *European Alps*

High-altitude lakes from the European Alps have been well studied. Hustedt conducted many microscopic examinations of diatoms from Germany, Austria, and Switzerland, which included alpine waters (e.g., Hustedt 1931, 1943). More recently, a taxonomic study by Levkov et al. (2005) documented diatoms from the highlands of the Shara and Nidze Mountains (North Republic of Macedonia) and noted the common presence of smaller diatoms which included *Cavinula pseudoscutiformis, Eunotia incisa*, and the larger *Tabellaria flocculosa*. Also, diatom composition in low conductivity lakes (5.7–23.9 μS cm^{-1}) in Polish (Tatra Mnt.) and the Swiss Alps (Macun Lakes) were compared by Kawecka and Robinson (2008). They found *A. minutissimum*, *Eunotia exigua*, *Fragilaria capucina/gracilis* group, *Psammothidium marginulatum*, and *Tabellaria flocculosa* were the most frequent taxa along with *Psammothidium subatomoides* in streams within the Macun Lakes area. The diatoms of glacial lakes in the South Carpathians, Romania, were investigated by Buczkó et al. (2010) and Buczkó (2016), with *Aulacoseira* species well documented using LM and SEM images. Buczkó (2016) prepared a monograph with 119 taxa, noting that small *Psammothidium* species were very abundant and diverse in the study.

Cantonati et al. (2012) investigated springs from the southeastern Italian Alps and recorded *Achnanthidium pfister, A. pyreaicum, A. lineare, Gomphonema elegantissimum,* and *Nitzschia fonticola* in carbonate rheocrenes. Feret et al. (2017) sampled 62 natural lakes above 1300 m a.s.l. in the French Alps and noted *Achnanthidium*, *Encyonema*, *Encyonopsis*, *Denticula*, *Staurosirella*, and *Navicula* taxa to be prominent. Among the taxa, *Achnanthidium minutissimum*, *Encyonema minutum*, *Encyonopsis subminuta*, and *Denticula tenuis* were dominant. Of special interest, *Psammothidium abundans* an Antarctic species was reported in Longemer Lake (Vosges Mountain, France) by Heudre et al. (2019).

4.7.6 *Taurus Mountains and Anatolian Mountains in Turkey*

4.7.6.1 Primary Producers

Turkey alpine biomes are geographically located in a mid-zone between subtropical and temperate regions (Solak et al. 2012). At present, studies on the diatom flora of alpine lakes are still in progress, and we have limited knowledge on the biogeography and diversity. In the Black Sea Region, the planktic community, and ecological state of Aygır Lake in the Karagöl Mountains, was examined by Taş (2016); she reported 48 algae in the lake (Bacillariophyta (21), Chlorophyceae (10), Cyanobacteria (7), Ochrophyta (3), Euglenophyta (3), Charophyta (2), Cryptophyta (1), and Miozoa (1)). Atıcı (2018) observed 96 taxa (Bacillariophyta (58), Chlorophyta (17), Cyanobacteria (15), Euglenophyta (2), Pyrrhophyta (2), and

Cryptophyta (2)) in the Artabel Lakes. Subsequent ecological studies of the Artabel Lakes were conducted by Şahin et al. (2020) with 95 diatom taxa from 15 lakes in the region; they further reported that the lakes were not polluted.

4.7.6.2 Biodiversity in the Alpine Lakes of Turkey

The distribution of aquatic oligochaetes in high alpine lakes of the eastern Black Sea Region has been examined by Yıldız et al. (2012) with 28 taxa in 59 lakes. Yıldız (2011) also investigated the zooplankton fauna of some alpine lakes in Verçenik Valley (Rize, Turkey) and documented 29 species belonging to Rotifera (17), Cladocera (9), and Copepoda (3). Ten of the rotifera species have also been reported from Antarctic glacial lakes. Then, she studied alpine lake zooplankton faunas in the Kaçkar Mountains (northern eastern Anatolian mountains) and Aladağlar (southern Taurus), recognizing 28 species of Rotifera (20), Cladocera (5), and Copepoda (3) in the lakes (Yıldız-Gürbüzer 2016). Ustaoğlu et al. (2008) studied glacial lakes in the Uludağ Mountains and found 36 zooplankton, 38 benthic macroinvertebrates, and 8 vertebrates, with a Rotifera, *Microcodides hertha*, documented as a new record for the Turkish fauna. Zooplankton composition and abundance in Alpine Lake Eğrigöl (Antalya) was investigated by Aygen et al. (2009), reporting 41 species (Rotifera (30), Cladocera (8), and Copepoda (3)) in the lake.

4.7.6.2.1 Diatom Biodiversity

In Turkey, the dominant diatom genera include *Cymbella*, *Gomphonema*, *Navicula*, and *Nitzschia*. In contrast, the glacial lakes have a diverse collection of genera but different in dominance. The dominant genera include *Cavinula*, *Eunotia*, *Genkalia*, *Nupela*, *Psammothidium*, *Stauroneis*, and *Tabellaria*. Like diatoms from the Alps, taxa from these genera are not typical for the lowlands of Turkey. Moreover, a number of taxa in the alpine lakes of the Kaçkar Mountains are also present in the Antarctic and Arctic regions (e.g., *Cavinula pseudoscutiformis* and *Psammothidium subatomoides*). Species in the genus *Psammothidium* are rarely found in low elevation Turkish freshwaters (only *P. perpusillum* is reported in Taşkın et al. 2019). However, species in this genus exist with a high diversity in Turkish alpine lakes.

In total, about 150 species are currently recognized from alpine lakes and ponds in Turkey, with many more rare taxa still to be discovered. New records or common diatom taxa from the alpine lakes and ponds are listed in Table 4.2. The genus *Eunotia* has the greatest number of new or common species (7) followed by *Psammothidium* (7) and *Stauroneis* (5).

Five prominent taxa, *Tabellaria flocculosa*, *Caloneis vasileyevae*, *Cavinula pseudoscutiformis*, *Genkalia digitulus*, *and Genkalia boreoalpina* are present in Turkish alpine lakes (Figs. 4.4 and 4.5). *Cavinulapseudoscutiformis* is also present in Scotland and in the northern and alpine regions of Canada and the United States (Cvetkoska et al. 2014; Jüttner et al. 2021). Morales et al. (2007) also found

Table 4.2 New or common taxa recorded for alpine lakes and ponds across Turkey

Taxon	Length (μm)	Width (μm)
Caloneis vasileyevae Lange-Bertalot, Genkal, and Vekhov[a]	15.0–17.3	4.3–4.6
Cavinula pseudoscutiformis (Hustedt) DGMann, and Stickle[a]	6.0–11.1	6.0–10.0
Eunotia bilunaris (Ehrenberg) Schaarschmidt[b]	47.5–69.8	4.3–5.7
Eunotia boreoalpina Lange-Bertalot and Nörpel-Schempp[a,c]	12.0–30.9	4.5–5.2
Eunotia botuliformis F. Wild, Nörpel, and Lange-Bertalot[a]	10.2–34.1	3.7–3.8
Eunotia crista-galli Cleve[a]	23.9–27.4	4.3–6.2
Eunotia curtagrunowii Nörpel-Schempp and Lange-Bertalot[a]	20.4–29.8	7.0–8.9
Eunotia islandica Østrup[a]	21.0–38.7	7.3–10.0
Eunotia minor (Kützing) Grunow[c]	19.9–34.1	4.0–5.2
Eunotia subarcuatoides Alles, Nörpel, and Lange-Bertalot[a]	14.0–23.3	2.9–3.7
Eunotia valida Hustedt[b]	35.9–74.9	5.4–6.4
Genkalia digitulus (Hustedt) Lange-Bertalot and Kulikovskiy[a]	10.4–16.8	3.8–4.9
Genkalia boreoalpina Wojtal, C.E. Wetzel, Ector, Ognjanova-Rumenova, and Buczkó[a]	13.9–15.9	4.0–4.2
Psammothidium daonense (Lange-Bertalot) Lange-Bertalot[a]	8.8–17.9	5.5–6.8
Psammothidium didymium (Hustedt) Bukhtiyarova and Round[a,c]	6.9–9.0	3.6–4.0
Psammothidium helveticum (Hustedt) Bukhtiyarova and Round[a]	11.8–21.5	4.0–7.1
Psammothidium levander i(Hustedt) Bukhtiyarova and Round[a]	9.1–9.6	5.1–5.5
Psammothidium microscopicum (Cholnoky) S. Blanco[a,c]	5.7–8.0	3.6–4.2
Psammothidium rossii (Hustedt) Bukhtiyarova and Round[a]	9.0–15.9	4.9–6.2
Psammothidium subatomoides (Hustedt) Bukhtiyarova and Round[a,c]	7.3–11.2	4.6–5.0
Psammothidium ventrale (Krasske) Bukhtiyarova and Round[a]	10.6–11.0	4.8–5.2
Stauroneis agrestis J.B. Petersen[b]	31.2	7.0
Stauroneis intricans Vijver and Lange-Bertalot[a]	29.7–32.6	6.6–6.9
Stauroneis reichardtii Lange-Bertalot, Cavacini, Tagliaventi, and Alfinito [a]	39.9–43.2	8.7–8.9
Stauroneis subgracilis Lange-Bertalot and Krammer[a]	69.9–72.8	13.3–13.4
Stauroneis thermicola (J.B. Petersen) J.W.G. Lund[a]	14.2–16.8	3.3–4.0
Tabellaria flocculosa (Roth) Kützing[c]	23.5–26.5	8.0–9.1

[a] New record taxa
[b] Present
[c] Common taxa

C. pseudoscutiformis in high altitude mountains streams in Bolivia. Beside *C. cocconeiformis, C. pseudoscutiformis* has also been reported from Spitsbergen (Svalbard), by Zgrundo et al. (2017). *Genkalia* is another notable group in high altitude regions. The genus was described by Kulikovskiy et al. (2012) with the type species from Lake Baikal. *Genkalia* is identified by a solitary isopolar valve with

Fig. 4.4 Map of the Western Mediterranean and Black Sea region. Locations of Lake Urmia (Iran) and Lake Van (Turkey). Inset. Outlines of the lakes and satellite image showing water color and lake basin morphology. Scale bars on the figure. Modified base maps from Google, Creative Commons CCO Licence, GNU Free Document Licence

weak sigmoid raphes, and areolae are covered by fine membranes on the external face. Wojtal et al. (2014) noted that *Genkalia digitulus* (Syn. *Navicula digitulus*) is a common taxon in high altitude lakes of the Holarctic region and northern Europe. They also described an additional species *Genkalia boreoalpina* from Switzerland. Both *Genkalia* taxa exist in the Kaçkar Mountain lakes. However, the distribution of *G. boreoalpina* is still poorly known, along with *Caloneis vasileyevae*. The later species was described by Østrup from Denmark, currently reported as rare in different studies across Europe (Veselá and Johansen 2009; Wojtal 2013). In this study, *C. vasileyevae* was present but rarely found in the Black Sea glacial lake region. *Psammothidium daonense* was recorded as new for Turkish diatom flora. The taxon was originally described from Italy by Lange-Bertalot (1999). *Encyonema minutum* and *E. silesiacum* were commonly found in Turkish alpine lakes while very rare across other regions in Turkey. *Encyonema* taxa were quite abundant in Turkish glacial lakes while commonly reported to "exist (about %1)" in other waterbodies around the country (Solak et al. 2012). We believe that *Achnanthidium* and *Planothidium* populations need to be investigated further to document the forms.

Six new records of *Eunotia* are reported here, and two species are common. These taxa represent simple lunate shapes of moderate size (23–75 μm length range, Table 4.2, Figs. 4.6, 4.7, and 4.8). In the high Arctic, 18 species of *Eunotia* have been documented, although most species are rare with 2 species (*E. rostellata* and *E.*

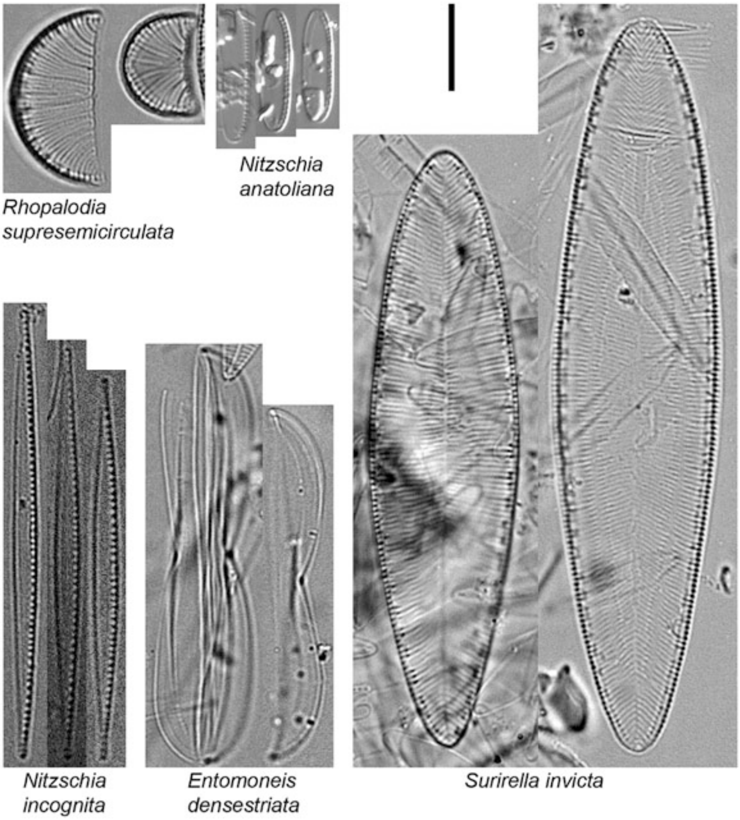


Fig. 4.5 Light microscope images of described soda taxa from Van Lake. Scale bar: 10 μm

boreotenuis) showing populations up to 3% relative abundance. In Turkey, *E. minor* and *E. boreoalpina* (both acidophilic taxa) have prominent population with 5–10% relative abundances. Although there are problems with the taxonomy of *E. minor* (Lange-Bertalot et al. 2011), this taxon is documented to have a Holarctic distribution that can live in higher altitude springs and headwaters within circumneutral to acidic waters. *Eunotia crista-galli*, *E. islandica*, and *E. boreotenuis* are noted from extreme Arctic environment, while *E. curtagrunowii*, *E. subarcuatoides*, and *E. valida* have Holarctic distributions and can occur in spring and higher altitude headwaters under circumneutral to lower pH, with low nutrient conditions (Lange-Bertalot et al. 2011). *Eunotia minor* and *E. boreoalpina* are also documented as acidophilous mire taxa observed in siliceous seepages and pool springs in the Italian Alps (Cantonati et al. 2012). *Eunotia* species (17) have also been commonly

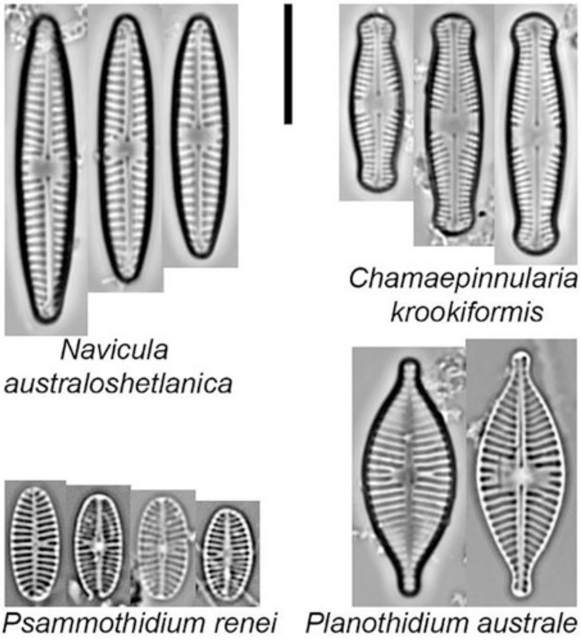
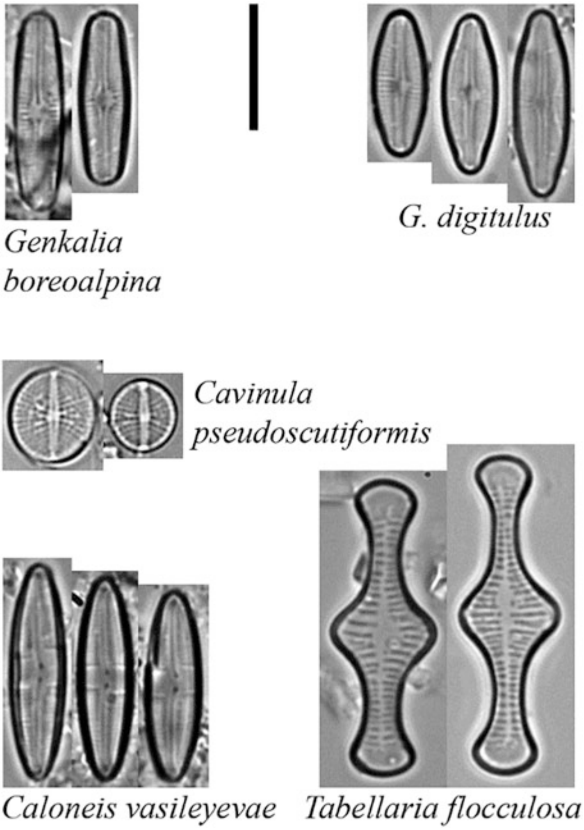


Fig. 4.6 Abundant taxa in the maritime Antarctic samples from the South Shetland Islands. Scale bar: 10 μm

observed in high altitude lakes in Macedonia, including *E. bilunaris*, and *E. minor* (Pavlov and Levkov 2013). In general, *Eunotia* species are regarded as good indicators of circumneutral to low pH and low conductivity (Krammer and Lange-Bertalot 2004; Rimet et al. 2007; Siver et al. 2004).

Monoraphid (one valve with raphe, one valve without a raphe) species are typically small forms that can be found in harsher environments. Eleven genera to date (*Achnanthidium*, *Eucocconeis*, *Gololobovia*, *Gogorevia*, *Karayevia*, *Lemnicola*, *Planothidium*, *Platessa*, *Psammothidium*, *Rossithidium*, *Skabitschewskia*) have been documented from extreme cold environments. *Psammothidium* species are not typically dominant but consistently found across cold study regions. The seven *Psammothidium* species documented from Turkey are similar in numbers to Antoniades et al. (2008) from the Arctic with 9 taxa (Table 4.2, Figs. 4.9, 4.10, 4.11, 4.12, 4.13, 4.14, and 4.15). More specifically, *Psammothidium didymium*, *P. helveticum*, *P. levanderi*, *P. subatomoides*, and *P. ventrale* are species found in both high alpine Turkish lakes and high Arctic freshwater systems. Surprisingly, Foged (1981) in his extensive study of diatoms from Alaska only found 5 *Psammothidium* (as *Achnanthes*) species with no matches to the species from Turkish alpine lakes. *Psammothidium helveticum*, *P. levanderi*, and *P. subatomoides* have also been recorded from Spitsbergen (Svalbard) (Zgrundo et al. 2017), while

Fig. 4.7 Light microscope images of five prominent diatoms from glacial lakes in Turkey. Four taxa are small motile diatoms, with one (*Tabellaria flocculosa*) littoral tychoplanktic taxon. Scale bar: 10 µm



Pla-Rabés et al. (2016) recorded 11 *Psammothidium* species from Franz Josef Land Archipelago with two similar taxa (*P. subatomoides*, *P. ventrale*) to the Turkish alpine lakes. Both *P. subatomoides* and *P. ventrale* are found in circumneutral to alkaline waters with moderate conductivity levels (species optima 82–97 µS cm^{-1}) and moderate dissolved organic carbon levels (ca. 2 mg L^{-1}) (Antoniades et al. 2008). Hofmann et al. (2013) further document that these taxa can be observed in low mountain ranges. *Psammothidium didymium* (Syn. *Achnanthes didyma*), *P. helveticum* (Syn. *A. helvetica*), and *P. levanderi* (Syn. *A. levanderi*) were found in low alkalinity lakes in Northeastern United States by Camburn and Charles (2000). Also, Spaulding et al. (2021) reported that *P. levanderi* occurred in İle da la Possession and Crozet Archipelago. The latter taxon and *P. didymium* were also tentatively given in the checklist of Great Lakes diatoms by Stoermer et al. (1999) (Figs. 4.16, 4.17, 4.18, 4.19, and 4.20).

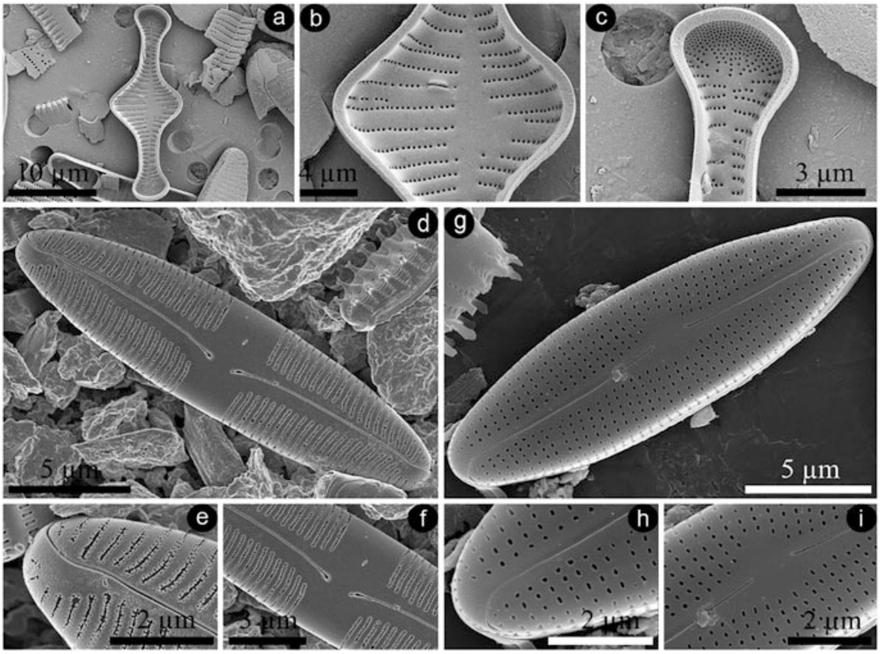


Fig. 4.8 Scanning electron microscope images of three prominent diatoms from glacial lakes in Turkey: *Tabellaria flocculosa, Caloneis vasileyevae, Genkalia digitulus*. (**a–c**) Internal views of *T. flocculosa*. (**b**) Shows the center with a special flattened tubular structure (the rimoportulae); (**c**) shows the end of the valve with a fine punctate apical pore field. (**d–f**) External views of *C. vasilevevae*. The central region lacks markings with a broadly curved slit (raphe) extending from end to end with an interruption in the middle. (**e**) Shows two rows of very small pores which are interrupted by unnatural cracks forming after the death of the diatom. (**g–i**) External views of *G. digitulus* showing raphe slits running down the middle and round to elliptic pore holes extending to both sides. Scale bars are presented on each figure

Among these prominent taxa, some preliminary observations on *P. subatomoides* show differences between the specimens of alpine glacial lakes and Antarctic lakes. A single sample from each region was examined, and 30 specimens of *P. subatomoides* in each sample was measured. The average size of Antarctic specimens was slightly smaller (Table 4.3, Fig. 4.21). In this comparison, specimens from a Swiss alpine lake (about 2400–2600 m. a.s.l.) and Turkish glacial lake (about 3000 m. a.s.l.) were on average larger than specimens from the Antarctic lake. Moreover, areolae (pore) sizes in the Turkish forms are larger than Antarctic forms, while areolae numbers are higher in Antarctic forms (6 areolae) compared to Turkish forms (4 areolae) in central area of raphe valves (Fig. 4.17). These could be different species which are difficult to separate or populations showing differ-

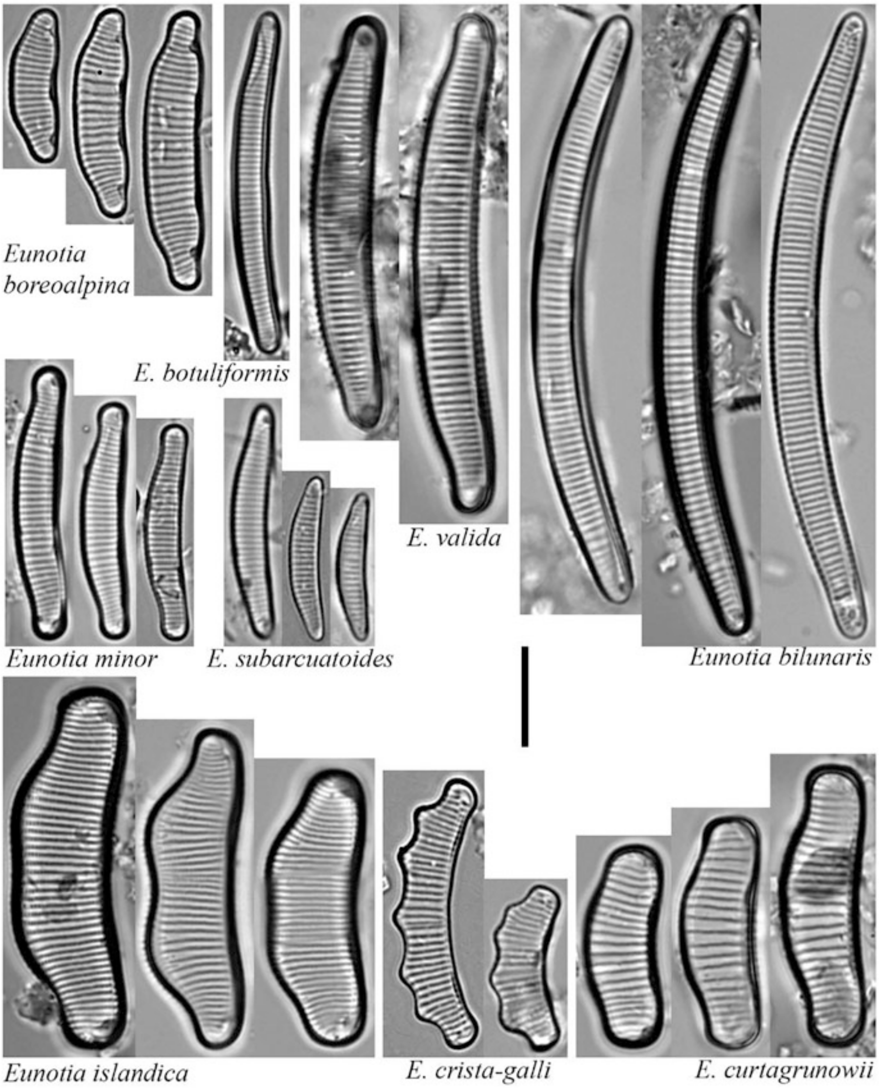


Fig. 4.9 Light microscope images of different *Eunotia* species found in Turkish alpine lakes. Scale bar: 10 μm

ences in phenotypic expression. What environmental differences between polar and mid-latitude extremes might control population size? Possible factors would include light regimes (photosynthetic active radiation, positive; UV light, negative), growing season temperatures, and duration of the growing season.

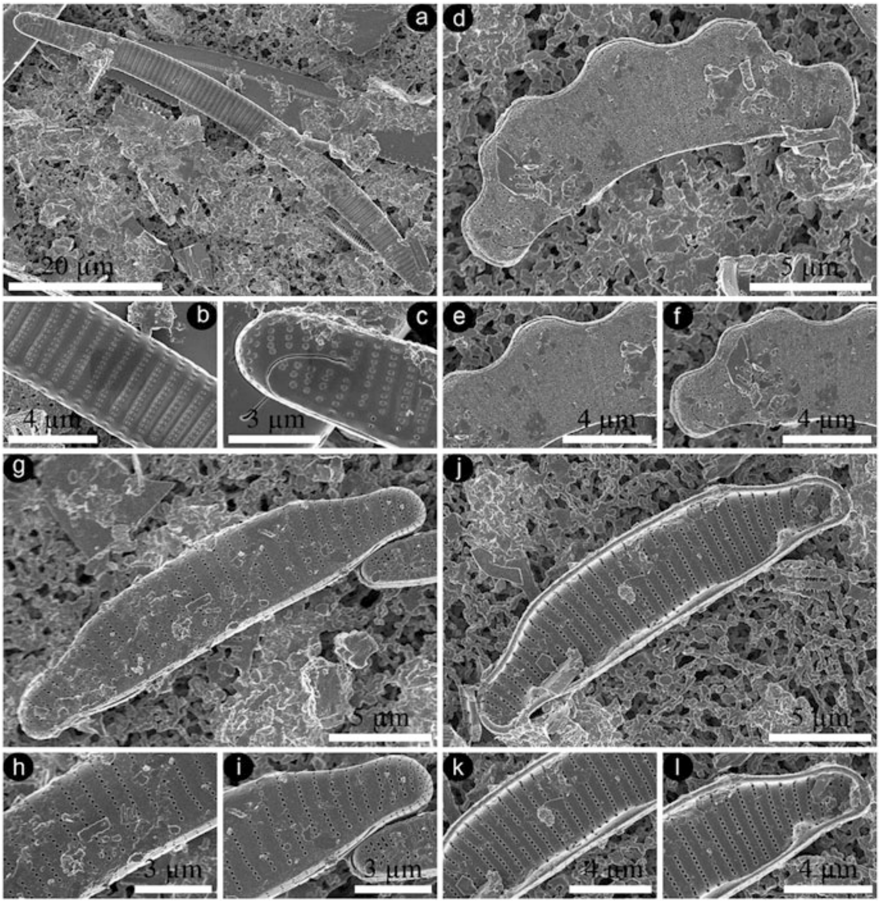


Fig. 4.10 Scanning electron microscope images of *Eunotia bilunaris, E. crista-galli,* and *E. boreoalpina*. (**a**–**c**) External views of *E. bilunaris*, whole valve, center and apex. (**d**–**f**) External views of *E. crista-galli*, whole valve, center and apex. (**g**–**i**) External valve surface of *E. boreoalpina*, whole valve, center and apex. (**j**–**l**) Internal views of *E. boreoalpina*, whole valve, center and apex. Scale bars on each figure

The genus *Stauroneis* represents larger taxa from extreme environments which are not common but show a high level of species richness. Van de Vijver et al. (2004) recognized 63 taxa from Antarctic and Arctic environments with an average maximum valve length of 75.5 µm compared to 36.5 for *Eunotia* species from Turkish alpine lakes. However, there is a broad range in *Stauroneis* valve sizes with polar species as small as 17 µm (maximum length). In Turkish alpine waters, the largest species (*S. subgracilis*) was 72 µm in length with the other species all less

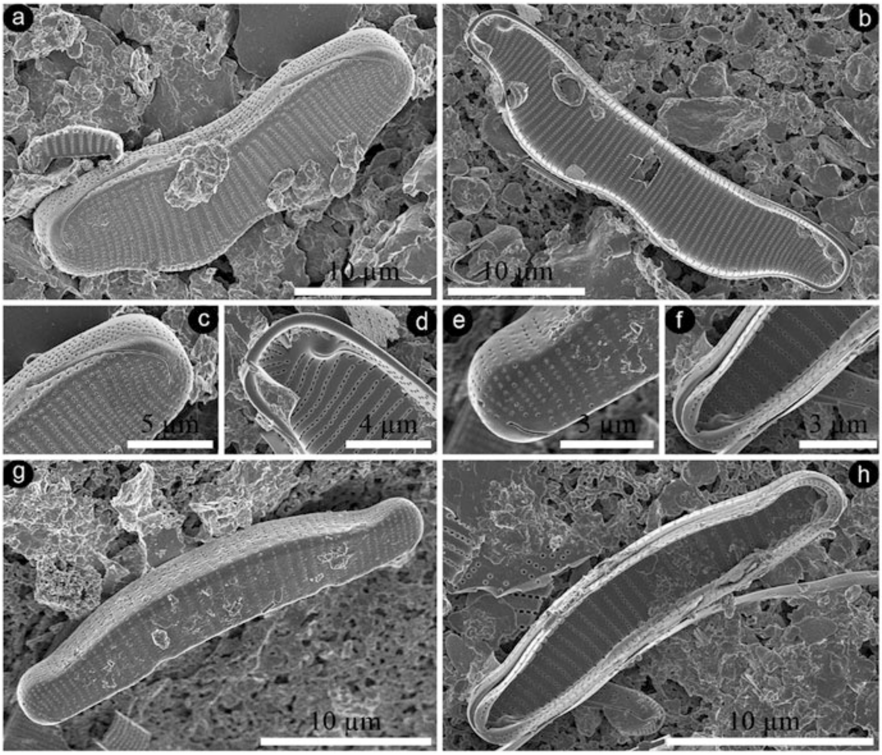


Fig. 4.11 Scanning electron microscope images of *Eunotia islandica* and *E. minor*. (**a**, **c**) External views of *E. islandica*, whole valve and apex. (**b**, **d**) Internal views of *E. islandica*, whole valve and apex. (**d**, **g**) External views of *E. minor*, whole valve, and apex. (**f**, **h**) Internal views of *E. minor*, whole valve, and apex. Scale bars on each figure

than 40 µm (Figs. 4.19 and 4.20). None of the species were abundant. The larger species, *Stauroneis intricans*, *Stauroneis reichardtii*, and *Stauroneis subgracilis* were found in the lakes as new records for the Turkish diatom flora. The smaller *Stauroneis thermicola* was also found in alpine environments from the North American Rocky Mountains (Bahls 2010). Four of the recorded species in Turkey are found across the Arctic, and one species (*S. subgracilis*) is found at both poles. *Stauroneis reichardtii* was originally described from Sardinia, Italy, by Lange-Bertalot et al. (2003) and then recorded from Jan Mayen Island, Norway (Van de Vijver et al. 2005). The higher link of Turkish alpine diatoms with Arctic species, compared to Antarctic species, indicates biogeographic dispersal and distribution patterns favoring the northern hemisphere (Figs. 4.22 and 4.23).

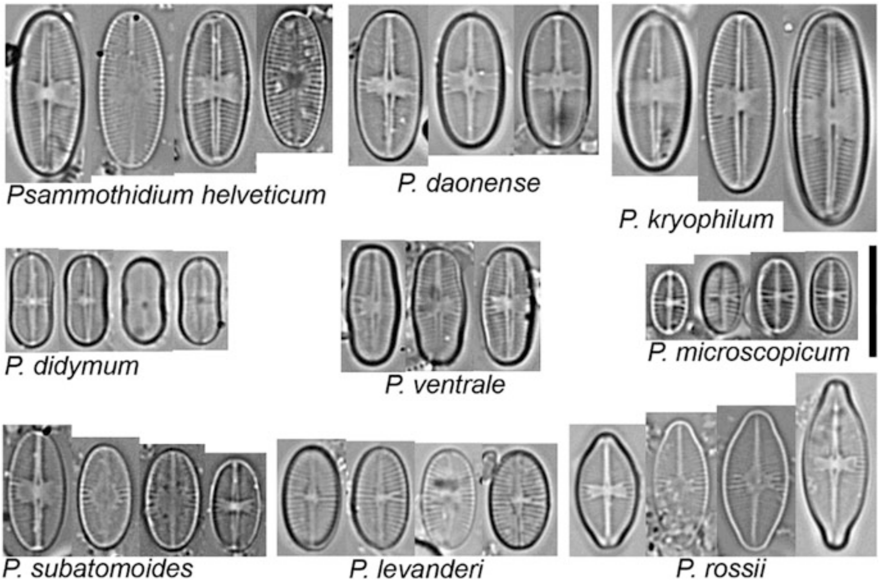


Fig. 4.12 Light microscope images of *Psammothidium* species from glacial lakes in Turkey. Scale bar: 10 μm

4.8 Environmental DNA and Cold Extremes

Environmental DNA (eDNA) analyses have exploded in the scientific literature over the last 10 years, and studies in alpine and Arctic regions have shown changing environments (climate) based on eDNA distributional patterns (Hou et al. 2014). In diatom research, eDNA studies on the Arctic Lake in Siberia found 163 verified diatom sequences, while 176 morphological species were identified by Hudson et al. (2000). Projected out to regional surveys, total species estimates would be in line with the works of Foged and others (>350 species). Within the generic complexes of *Staurosira* and *Staurosirella* (dominant polar taxa), a DNA study revealed that multiple haplotypes could be distinguished with a latitudinal and climate gradient (Stoof-Leichsenring et al. 2014, 2015). This research has direct implications for biogeographic studies, especially in alpine and polar biomes that have clear disjunct separation. In another study of recent and ancient sedimentary DNA, Stoof-Leichsenring et al. (2020) found that selected diatom genera are more resilient and able to adapt to environmental change. In extreme cold environments, this could suggest that the more prominent smaller monoraphid genera are better able to adapt to harsher conditions but may not have the same competitive advantage when other genera are not displaced by the environment. Rules of assemble structured by the

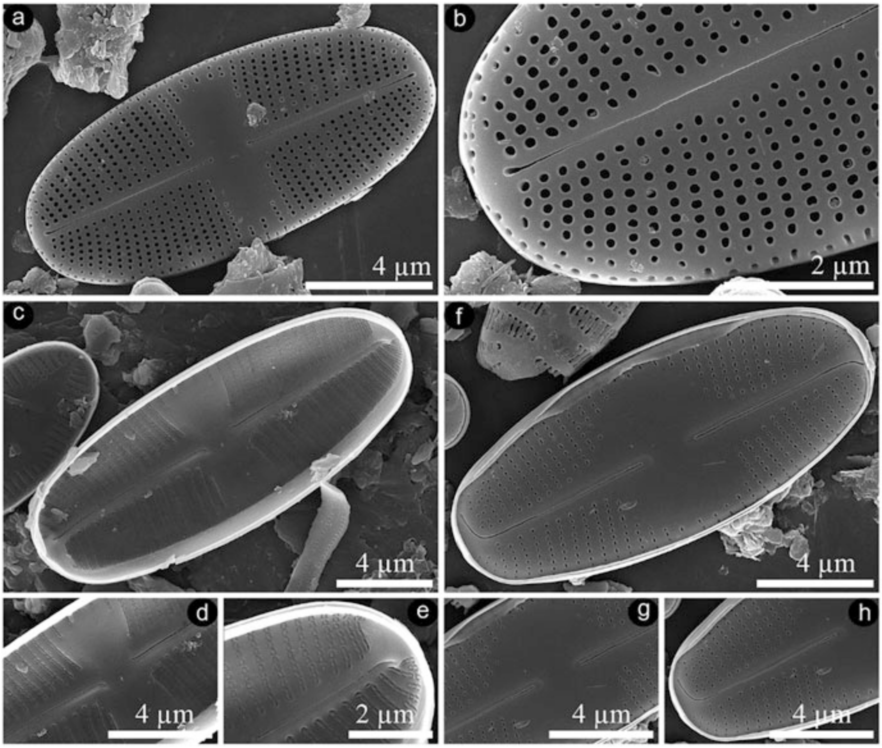


Fig. 4.13 Scanning electron microscope images of *Psammothidium daonense* and *P. helveticum*. (**a**) External view of *P. daonense*. (**b**) Internal view of *P. daonense*. (**c–e**) Internal view of *P. helveticum*. (**f–h**) External view of *P. helveticum*. Scale bars are presented on the plate

environment, with deterministic processing, may have significance when determining diatom assembles of alpine and polar biomes.

4.9 Trends in Biogeography for Alpine Lakes and Ponds

At present, there are no clear trends in global equatorial to polar biogeography when considering high alpine, alpine, and even peri-alpine environments. The somewhat random distribution of alpine biomes including differences in elevations and bedrock chemistry introduces another layer of factors pressuring stochastic and deterministic colonization processes. Further niche size has a very important role to play in determining the ultimate success of community composition. In this chapter, we

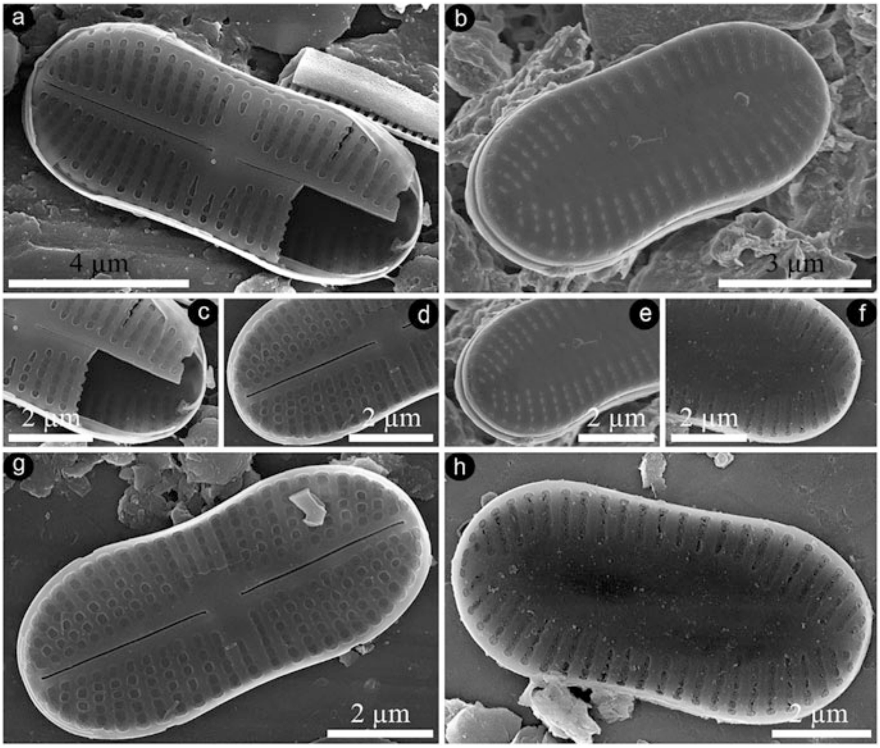


Fig. 4.14 Scanning electron microscope images of *Psammothidium didymium*. (**a**, **c**) External views of the raphe valve. (**b**, **e**) External views of the raphe valve. (**d**, **g**) Internal views of the rapheless valve. (**f**, **h**) Internal views of the rapheless valve. Scale bars are presented on the plate

examined the current state of the scientific literature and used diatoms as a proxy for community, regional systems, and broader scale biogeographic distributions. Diatoms tell us that high elevation alpine communities near the equator have some commonalities with polar environments. Many variables are impacting diatom community development, in decreasing order of importance: climate, physical factors, and chemical factors. In addition to natural factors, there are anthropogenic factors from atmospheric deposition of contaminants to regional agriculture which alter the biology. It is interesting to note that different forms of nitrogen will be deposited through atmospheric deposition in alpine biomes depending on distances from source, thus linking the impacts of nutrients directly with climate. Apart from the complexity of competing environmental factors, there are some trends that in the future can be explored. Under similar physical conditions: (1) species diversity decreases with increasing exposure to cold extremes (increasing latitude or eleva-

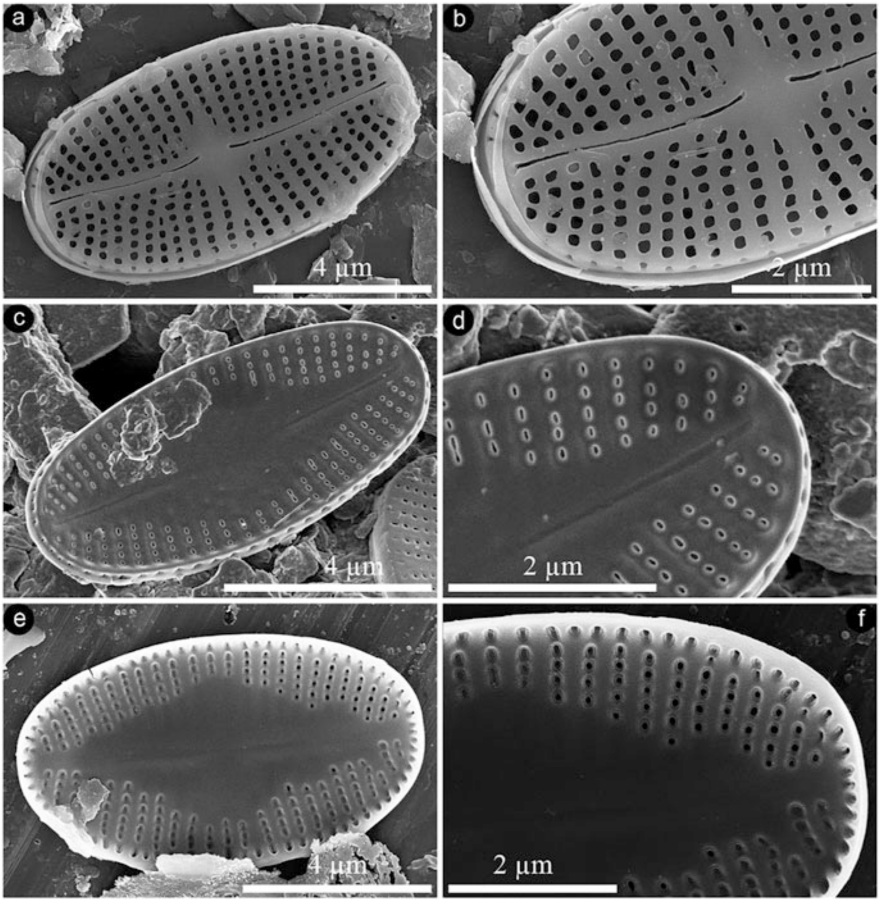


Fig. 4.15 Scanning electron microscope images of *Psammothidium levanderi.* (**a**, **b**) External views of the raphe valve. (**c**, **d**) External views of the rapheless valve. (**e**, **f**) Internal views of the rapheless valve. Scale bars are presented on the plate

tion); (2) prominent populations of smaller species, or smaller sizes of a single species, trend with increased exposure to colder environments; (3) in diatoms, the structural complexity of valve morphology decreases with increasing exposure to harsher (colder) environments; (4) again in diatoms, there is a trending change from biraphid species to monoraphid species and then to araphid species with increasing exposure to extreme conditions; (5)examples of species radiations (long-term projections in species evolution) are not documented from cold environments (i.e.,

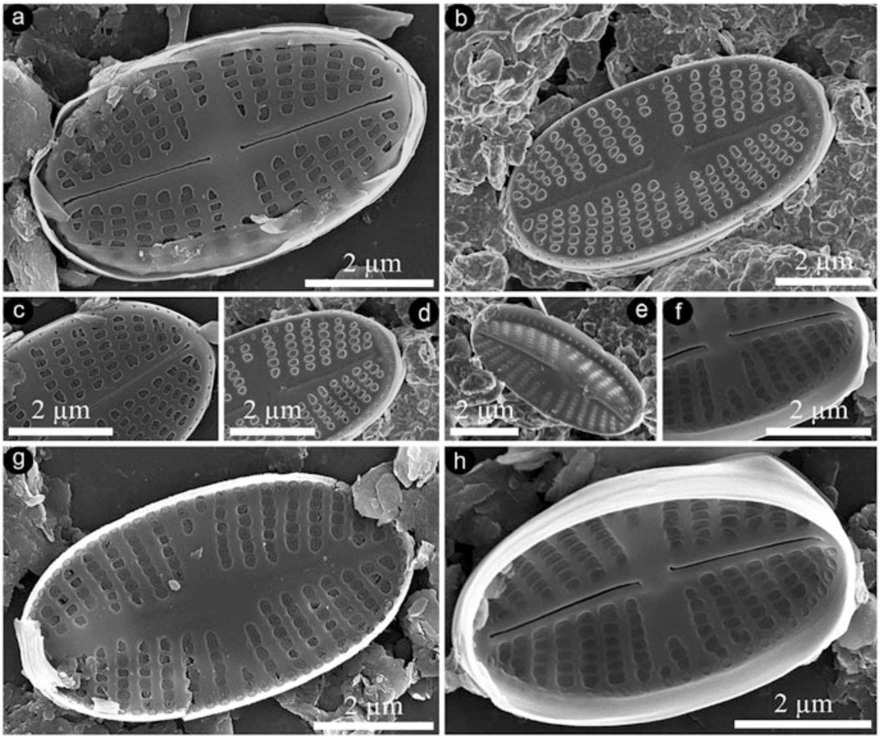


Fig. 4.16 Scanning electron microscope images of *Psammothidium microscopicum*. (**a**, **c**) External views of the raphe valve. (**b**, **d**) External views of the rapheless valve. (**e**) Shows slit-like areolae in the mantle. (**g**) Internal view of the rapheless valve. (**f**, **h**) Internal views of the raphe valve. Scale bars are presented on the plate

species surviving and radiating over glacial exposure cycles). Thus, extreme environments are constraining biodiversity and limiting evolutionary processes.

Although there are interesting trends in biogeographic distributions, noted exceptions should be considered. Foged (1981) conducted an extensive study of the diatoms from Alaska and documented 987 species, and varieties, beyond what might be expected. In another study of diatoms from Iceland, Foged (1974) documented 689 taxa which are in line with more recent taxa studies from the Arctic. These results challenge the overriding idea of decreasing diversity with increasing latitude. Foged examined more sample material (microscope slides from a single sample) and habitats than other research studies which could, in part, explain the higher recorded number of species. The justifications presented are still not enough to explain the high diversity of diatom taxa from Alaska. In the future,

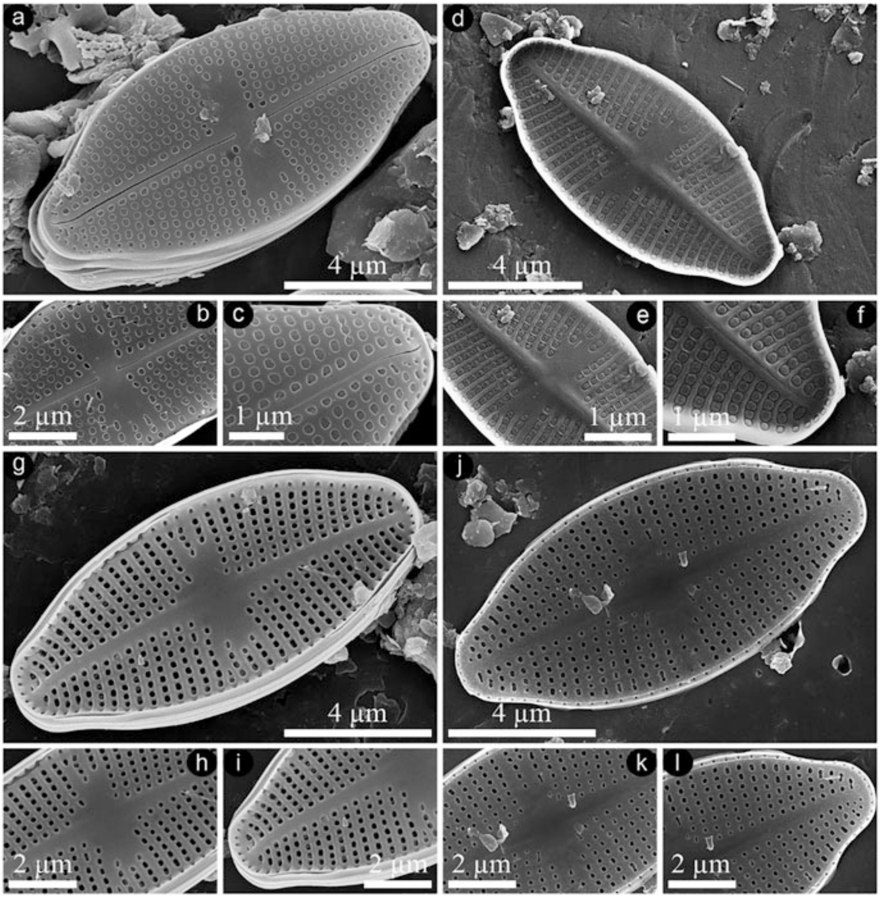


Fig. 4.17 Scanning electron microscope images of *Psammothidium rossi*. (**a**–**c**) External views of the raphe valve. (**d**–**f**) Internal views of the raphe valve. (**g**–**i**) Internal views of the rapheless valve. (**j**–**l**) External views of the rapheless valve. Scale bars are presented on the plate

can we find this level of diversity in alpine biomes with intense study? The answer is yes. Another interesting anomaly is paleo-sediment sea beds at high altitudes (e.g., Tibetan Plateau (Asia), Lake Urmia (Iran)). The paleo-sediments are a primary seed for ions and nutrients, creating a more insular and stable biome. Since the aquatic lakes and ponds are similar and diversity of habitats more limited, these alpine environments may be less diverse (alpha, beta biodiversity), although with more morphologically complex diatom taxa. However, high inorganic sediment loads in selected lakes will influence regional diversity. Finally, the presence of similar taxa

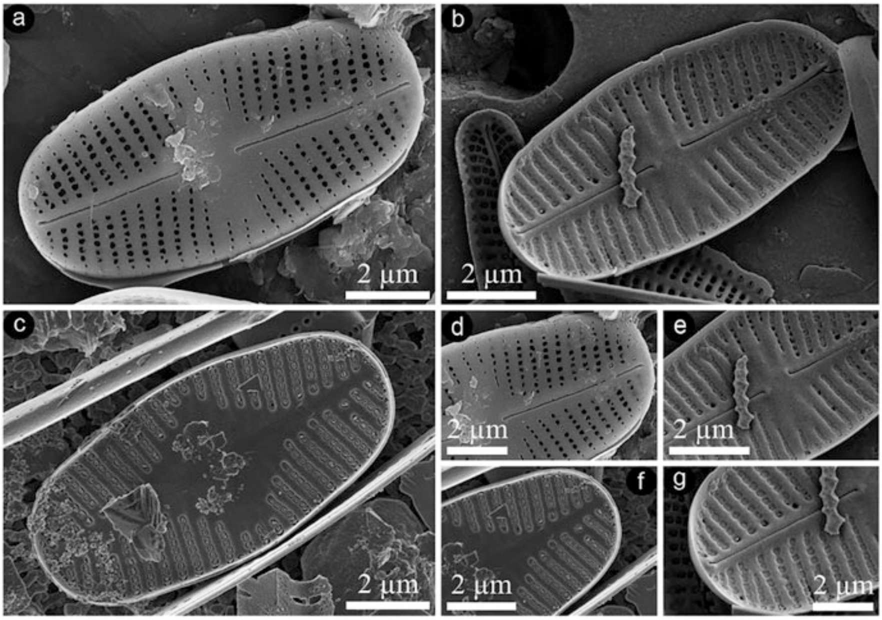


Fig. 4.18 Scanning electron microscope images of *Psammothidium ventrale*. (**a**, **d**) External views of the raphe valve. (**b**, **e**, **g**) Internal views of the raphe valve. (**c**, **f**) Internal views of the rapheless valve. Scale bars are presented on the plate

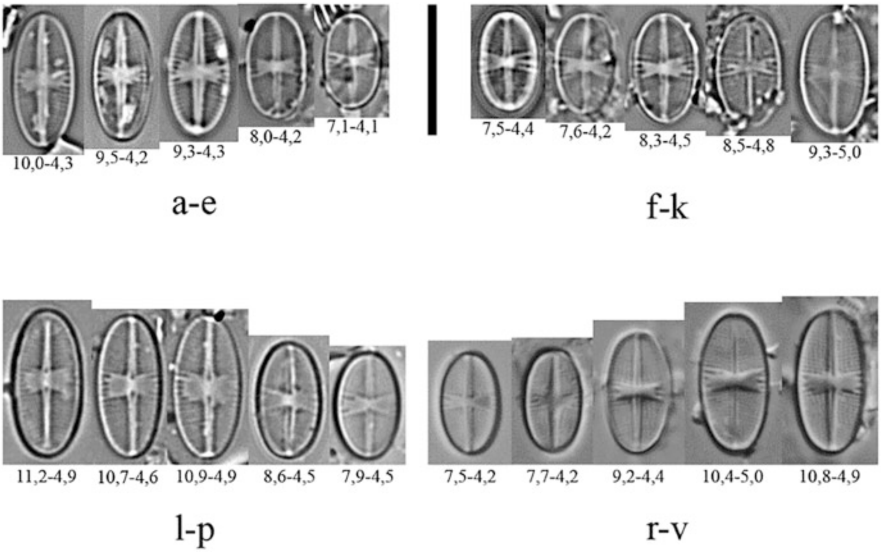


Fig. 4.19 Light microscope images of *Psammothidium subatomoides* in glacial lakes from maritime Antarctica (**a**–**e**, Robert Island; **f**–**k**, Horseshoe Island), Turkish glacial lakes (**l**–**p**), and Swiss alpine lakes (**r**–**v**). Scale bar: 10 µm

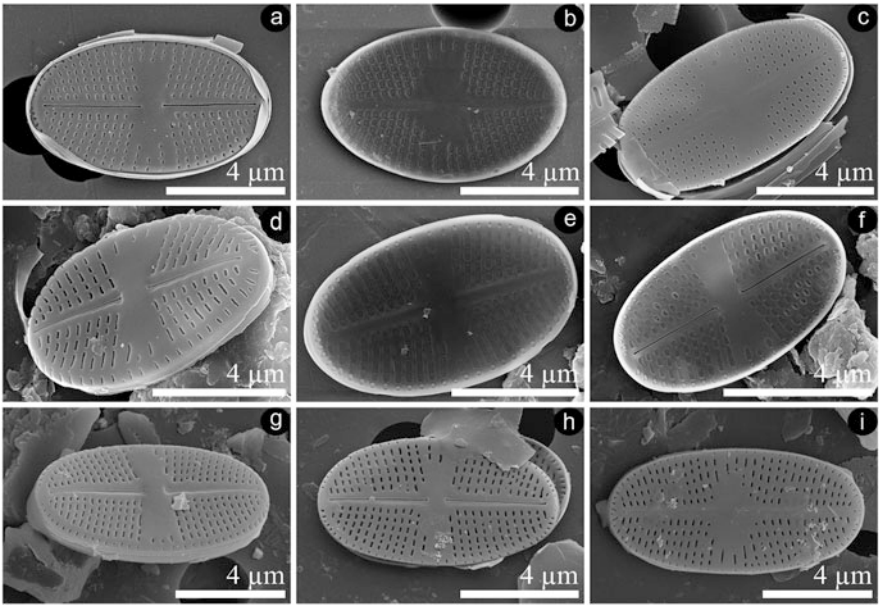


Fig. 4.20 Scanning electron microscope images of *Psammothidium subatomoides* in glacial lakes from maritime Antarctica (**a**–**c**), Turkish glacial lakes (**d**–**f**), and Swiss alpine lakes (**g**–**i**). Specimens of this species have two enclosing valves (shells) with different surface structures. (**a**, **d**, **g**, **h**) outside view of the valve with a raphe. (**f**) inside view of the valve with a raphe. (**c**, **i**) outside view of valve without the raphe. (**b**, **e**) inside view of the valve without a raphe. Scale bars: 4 µm

in equatorial alpine systems with aquatic freshwaters at both poles (Antarctic and Arctic) supports the idea that there is some level of connectivity between these distantly spaced biomes. The level and significance of this connectivity is yet to be determined, although genetics gives us the tools to examine this question.

4.10 Climate and the Anthropocene

Climate change will, in the future, greatly impact extreme environments, especially polar and alpine biomes. The Great Acceleration (1950s–1980s) has been documented with diatom proxies in Arctic (e.g. Gajewski et al. 1997; Kaufman et al. 2009) and alpine aquatic systems (e.g., Sommaruga-Wögrath et al. 1997). Due to their extreme environmental conditions (i.e., low temperatures and strong solar radiation) and simple trophic structure, lake and pond biodiversity will be more

Table 4.3 *Psammothidium subatomoides* specimen measures from three distinct regions: maritime Antarctic, Turkish glacial lakes, and Swiss Alps

	Antarctic_lakes			TR_glacial lakes			Swiss alpine lakes		
	L	W	L/W	L	W	L/W	L	W	L/W
1	10.0	4.3	2.3	10.7	4.6	2.3	9.4	4.8	2.0
2	9.5	4.2	2.3	10.9	4.9	2.2	9.2	5.1	1.8
3	9.3	4.1	2.3	10.2	4.7	2.2	7.2	3.8	1.9
4	9.2	4.0	2.3	10.3	5.0	2.1	9.2	4.9	1.9
5	9.1	4.1	2.2	10.1	4.8	2.1	9.6	4.6	2.1
6	9.3	4.3	2.2	9.9	4.9	2.0	7.3	4.2	1.7
7	8.6	4.5	1.9	10.0	4.5	2.2	10.0	5.0	2.0
8	8.1	4.1	2.0	9.7	4.4	2.2	10.4	5.2	2.0
9	8.0	4.2	1.9	8.9	4.5	2.0	6.3	3.8	1.7
10	7.7	4.2	1.8	9.3	4.5	2.1	7.9	4.0	2.0
11	7.1	4.1	1.7	9.2	4.3	2.1	9.2	4.5	2.0
12	9.3	5.0	1.9	8.9	4.6	1.9	9.6	4.1	2.3
13	8.5	4.8	1.8	8.4	4.5	1.9	10.4	5.1	2.0
14	8.2	4.4	1.9	8.1	4.3	1.9	8.0	4.3	1.9
15	8.3	4.3	1.9	7.3	4.6	1.6	11.1	5.5	2.0
16	8.4	4.4	1.9	11.2	4.9	2.3	8.8	4.6	1.9
17	8.3	4.5	1.8	8.9	4.9	1.8	9.0	4.6	2.0
18	8.3	4.6	1.8	8.5	4.9	1.7	8.7	4.6	1.9
19	8.1	4.5	1.8	8.1	4.6	1.8	11	5.8	1.9
20	8.0	4.3	1.9	7.9	4.4	1.8	6.5	3.8	1.7
21	8.1	4.7	1.7	7.9	4.5	1.8	9.1	4.3	2.1
22	7.6	4.4	1.7	9.2	4.1	2.2	10.6	4.8	2.2
23	7.7	4.7	1.6	8.1	4.0	2.0	7.8	4.3	1.8
24	8.0	4.1	2.0	10.1	4.9	2.1	10	4.7	2.1
25	7.9	4.5	1.8	8.3	4.6	1.8	9.3	4.6	2.0
26	7.9	4.4	1.8	9.1	4.3	2.1	6.7	3.9	1.7
27	7.7	4.4	1.8	8.6	4.5	1.9	10.7	5.2	2.1
28	7.6	4.4	1.7	9.6	4.9	2.0	10.8	5.2	2.1
29	7.6	4.2	1.8	7.8	4.1	1.9	8.1	3.9	2.1
30	7.5	4.4	1.7	7.8	4.6	1.7	8.7	4.4	2.0
Mean	8.3	4.4	1.9	9.1	4.6	2.0	9.0	4.6	2.0
Max	10.0	5.0	2.3	11.2	5.0	2.3	11.1	5.8	2.3
Min	7.1	4.0	1.6	7.3	4.0	1.6	6.3	3.8	1.7

Underlined valve lengths greater than 10 μm. All measurements are in μm

sensitive to environmental change (Arndt et al. 2013). Future changes in alpine lakes and ponds will be related to precipitation, glacial melt (Barker et al. 2001), and solar irradiance (Lean et al. 1995). Globally, the impact of climate change will vary among regions. Some regions, like the alps, will experience different levels of acidification

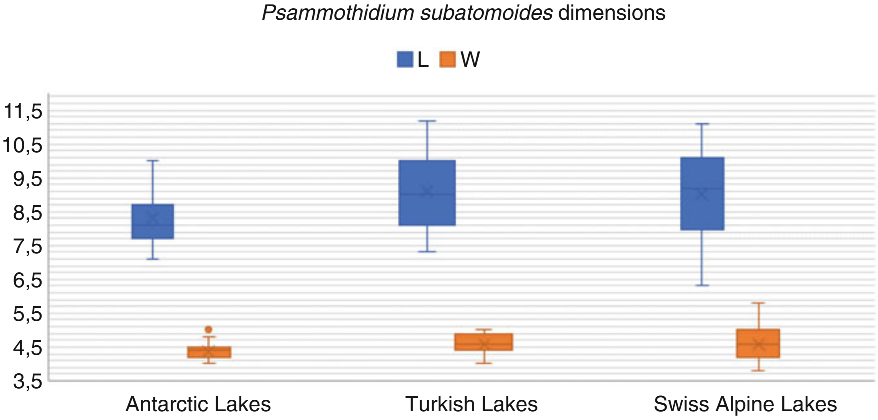


Fig. 4.21 The maximum, minimum, and mean lengths of *Psammothidium subatomoides* specimens from glacial lakes in maritime Antarctic, Turkish glacial lakes, and Swiss alpine lakes (*L* length; *W* width). Scale on *Y*-axis in μm

(Gąsiorowski and Sienkiewicz 2010; Sommaruga-Wögrath et al. 1997), and more isolated regions will be impacted by growing season and nutrification (Wolfe et al. 2003), while other regions will experience evapotranspiration and drought with waters becoming more salty (ion rich) (Barker et al. 2001; Calanca 2007).

In regions with enhanced nutrification through glacial melt, shifts in community structure will occur within phyla and between phyla, even with minor changes in nutrients (Saros et al. 2003). Specifically, there will be a shift from mixotrophic (e.g., cryptophytes) and oligotrophic communities (diatoms, chrysophytes) to meso- (all microbe groups) and eutrophic communities favoring chlorophytes and cyanobacteria. Under most impact scenarios (excluding drought), within phyla, there will be increases in species richness, biodiversity, and a shift to larger morphologically complex taxa. Over the last 100 years, the Arctic diatom flora has shown increasing richness and diversity with a trend toward larger taxa (Overpeck et al. 1997). At present, smaller taxa are still predominant. Similarly, the alpine lakes and ponds of Turkey also show a dominance of smaller species, although diatom survey studies are not extensive (Bouchard et al. 2004). Regarding the Turkish freshwater diatom flora, *Cymbella affinis*, *Navicula cryptotenella*, *N. tripunctata*, *Nitzschia dissipata*, *N. media*, *Pantocsekiella ocellata*, and *P. delicatula* are generally abundant taxa except in the Inner Anatolia glacial region (Solak et al. 2012). Due to the high conductivity, inland waters have different diatom compositions. For this reason, brackish species *Conticribra weissflogii*, *Craticula halophila*, *Craticula anatoliana*, *Ctenophora pulchella*, *Navicula recens*, *Navicula phylleptosoma*,

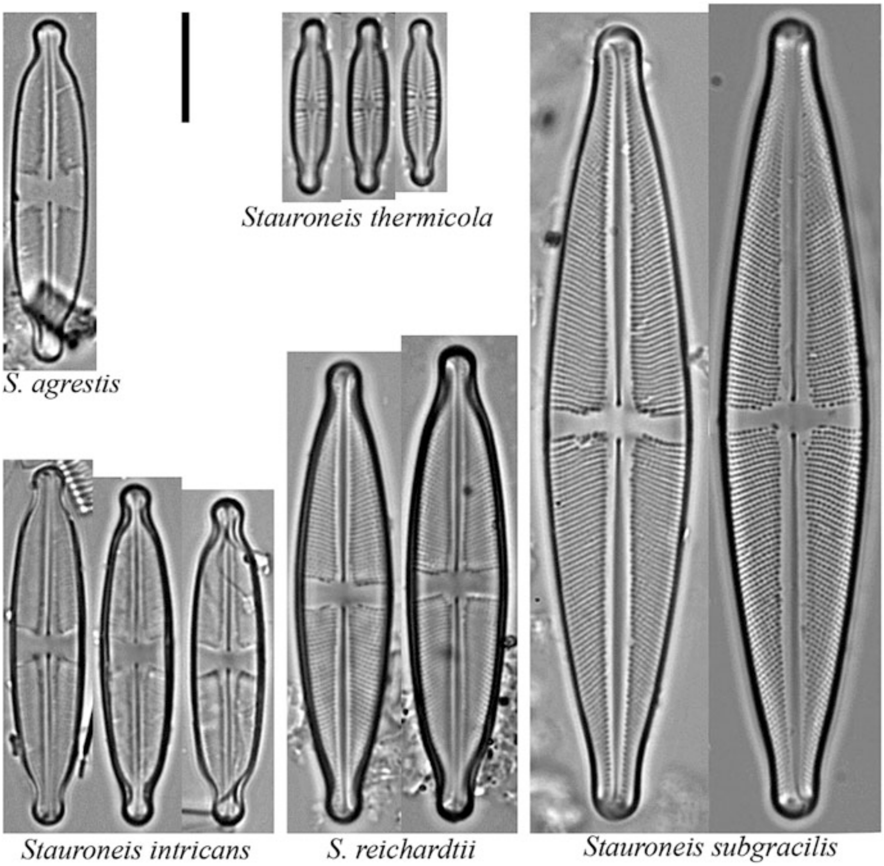


Fig. 4.22 Light microscope images of *Stauroneis* species found in glacial lakes in Turkey. Scale bar: 10 μm

Tabularia fasciculata, and *Halamphora coffeaeformis* are quite common in the region (Çetin et al. 2021).

The stress of human disturbance in alpine biomes, especially in peri-alpine and alpine systems, has been evident for a long period of time (Salmsao et al. 2018). Agriculture is the top stressor in alpine biomes across every continent, and alpine lakes on the Tibetan Plateau would be an excellent example. Additional environment stressors, but less disturbing, include hydroelectric development, mining, forestry, human settlements, and tourism. In the future, agriculture and other human disturbances will continue to be globally significant factors in peri-alpine and alpine aquatic systems. In more isolated (high alpine), typically smaller, and exposed aquatic systems, local conditions will continue to be a limitation, although atmospheric depositions of nutrients and contaminants (current and past captured in glaciers) will become more significant. Climate change is creating a large laboratory experiment to which many hypotheses will be tested.

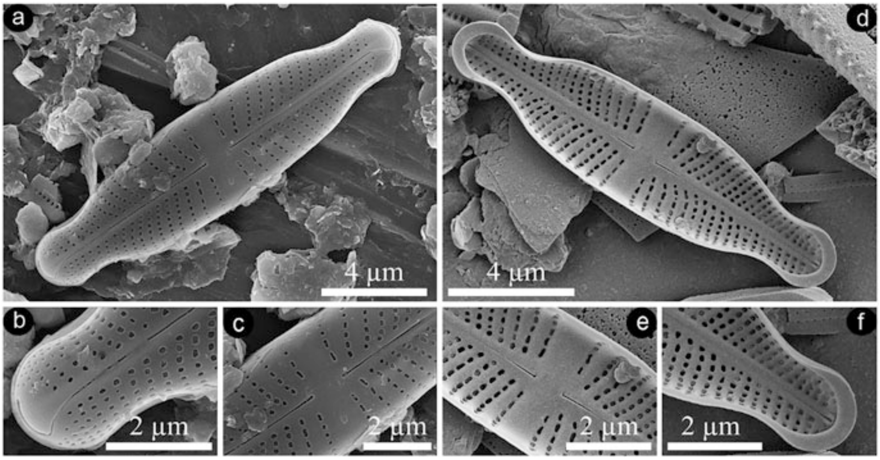


Fig. 4.23 Scanning electron microscope images of *Stauroneis thermicola*. (**a–c**) External views of the valve. Note the central space across the valve and the "?" shaped ends of the raphe slit at the poles. (**d–f**) Internal view of the valve. Note the thickened rim at each apex of the valve. Scale bars are on the images

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