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Review Article

The Croatian National Diatom Collection – an overview and future challenges

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Abstract – Knowledge of the importance of algae in the Earth's hydrosphere emerged after the discovery of the microscope and microorganisms at the beginning of the 18th century. Due to the beauty and morphological distinctiveness of diatoms, the majority of protist research has been focused on those intriguing silicate cells. Today, the vast species diversity of diatoms can only be estimated, but the taxa that have been explored over the years are stored in collections that represent an important resource for modern taxonomy, phylogeny and evolution, ecology, paleoecology, biogeography, phylogeography, applied biology, monitoring and conservation. The Croatian National Diatom Collection (HRNDC) was established in 2018 on the basis of long-term work by Croatian algologists. Today it represents a collection of 2883 permanent specimens that store valuable information on the diatom biodiversity of all waterbodies and store important holotypes, isotypes and paratypes of described new species for science. The future brings the challenge of keeping the collection sustainable, digitalized, and more accessible to the scientific community as well as capable of meeting the challenge of the omics era. The HRNDC is a priceless contribution to the legacy of the Croatian natural heritage.

Keywords: diatoms, collection, freshwater and marine environment, natural heritage

Introduction

Over the years, scientists have tried to gather as much information about nature as they possibly could. The biodiversity of the different ecosystems on Earth has always been one of the main topics in biological studies. In order to preserve their findings about different species, biologists organise the collected specimens in biological collections that help us to understand the taxonomic and phylogenetic background of each published species. Collections such as herbaria or zoological collections in their core keep records of extant and extinct species through a certain period of time and serve as historical evidence that will teach generations about the characteristics of examined samples. Collections will allow easier identification of any specimen found in the future. They can also provide more accurate categorisation of newly discovered species through the morphological or molecular studies of already recorded specimens. Collections enable biodiversity in the ecosystems studied to be tracked by providing evidence of living species and comparing them with deposited specimens. All of these benefits contribute to the fact that the study of the life-form diversity is considerably improved by the systematisation that biological collections provide.

Diatom collections

Diatom collections are an important resource for modern taxonomy, phylogeny and evolution, ecology, biogeography, phylogeography, applied biology, monitoring and conservation. Diatom specimens provide valuable information for taxonomists to be able to answer scientific questions about basic morphological characteristics and variation of species and genera as well as providing a basis for the establishment of the phylogenetic relationships of diatom species and their geographic distribution and ecology. They contain representatives of diatoms from freshwater, brackish water and marine environments, both fossil and recent, therefore representing an irreplaceable treasure and biorepositories of diatom diversity.

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The documentation of diatoms requires the preparation of permanent specimens, and in the older diatom collections consisted mainly of permanent glass slides and micas. Today, the term diatom collection is also used for collections of living cultures, and thus the collection of diatoms has gained a new dimension in the research processes. Having a live culture allows not only the study of morphological variations to find breaks in the pattern of variations leading to definition and naming of diagnosable entities (Mann and Droop 1996), but also allows us to perform molecular research and resolve phylogenetic relationships, metabolic pathways in order to screen specific compounds and to evaluate their biotechnological potential and to use diatoms as model organisms (Rotter et al. 2021).

Diatoms are not usually collected in the same way as other organisms, due to their microscopic size and spatial and temporal occurrence, patchiness in the environment. Instead, they are often analysed using water samples or sediment/periphyton composites from aquatic environments containing a span of different organisms, which are then deposited as samples and permanent slides. Renowned universities, botanical gardens and institutes around the world maintain collections of diatoms. In addition to Husted's, the most extensive diatom collection, notable collections include: the Natural History Museum Diatom collection, Macedonian National Diatom Collection, Van Heurck diatom collection housed at the National Botanic Garden of Belgium, Academy of Natural Sciences of Drexel University, the diatom collection of Albert Grunow at the herbarium of the Natural History Museum Vienna, the Szczecin Diatomological Collection of the University of Szczecin, Poland. Some of them are prominent in terms of the number of samples, some of them for the quantity of different habitats and others have collections of more significant authors. Motivated by awareness of diatom biodiversity in the diverse waterbodies in Croatia, the importance of research conducted to date and the importance of keeping the national heritage in the country the Croatian National Diatom Collection (HRNDC) was established on 1st March 2018 at the University of Zagreb, Faculty of Science (Gligora Udovič and Ljubešić 2021).

Historical highlights – two important diatomologists for the Croatian diatom flora

Dr. Friedrich Hustedt (Bremen, 15 December 1886 – Bremen, 1 April 1968)

Friedrich Hustedt is one of the best-known diatom researchers and has described around 2000 new diatom taxa worldwide. During the excursion organised after the 7th Congress of Limnologists in 1934, he visited Croatia and collected samples from the River Krka and the Plitvice Lakes. From these samples, Hustedt (1945) described many new species for science such as *Achnanthes fonticola* Hustedt, *Cocconeis semiaperta* Hustedt, *Cyclotella stelligeroides* Hustedt, *Cyclotella plitvicensis* Hustedt, *Navicula exiguiformis* Hustedt, *Navicula obsita* Hustedt, etc. All these diatom taxa were illustrated and documented in Simonsen (1987) and type slides have been deposited in the Hustedt collection, which was previously located at the Alfred Wegener Institute for Polar and Marine Research in Bremerhaven but was recently transferred to the Botanical Garden and Museum in Berlin. Hustedt (1945) is one of the most important papers in the diatom taxonomy of the whole of SE Europe and emphasizes the significance of karstic areas in Croatia as centres for the diversity and endemism of diatoms.

Dr. Anto Jurilj (Komarica, Bosnia and Herzegovina, 19 February 1910 – Zagreb, 1 April 1981)

Anto Jurilj was a Croatian botanist and phycologist. He graduated from grammar school in 1933, obtained a diploma in biology in 1937 and finally completed his PhD in Zagreb in 1949 on the subject of New diatoms of Lake Ohrid and their phylogenetic importance. In the 1950s, he worked first as an assistant and then as a professor at the Faculty of Science in Zagreb. In 1961, Jurilj began working in the Laboratory of Biology with Technical Microscopy at the Technical Faculty of Zagreb, where he became head of the laboratory. He retired in 1980. One of Jurilj's most important contributions to science was his research on diatoms in Lake Ohrid. He described 50 new endemic taxa for the lake and recorded 30 relict taxa that were only considered fossils from the Miocene and Pliocene. Particularly important for phylogeny and evolution was an array of six branching events between the genera *Surirella* and *Campylodiscus*. He described five new genera and one of these, *Iconella*, is now widely accepted for many members of *Surirella sensu lato* (Ruck et al. 2016). His influence on diatom research can also be recognised in the naming of 13 different species described by various authors (e.g. *Actinoptychus juriljii* Molinari & Guiry (Molinari-Novoa and Guiry 2021), *Campylodiscus jurilji* Hajós (Hajós 1973), *Cyclotella juriljii* Skvortsov (Skvortsov 1971), *Cymbella jurilji* Husted (Hustedt 1955), *Cymbopleura juriljii* Z. Levkov & D. Metzeltin (Levkov et al. 2007) *Placoneis juriljii* A. Miho & Lange-Bertalot (Miho and Lange-Bertalot 2006). A part of his diatom collection concerning Lake Ohrid diatoms has been found and is now deposited in the Croatian National Diatom Collection. Although he published his work in various scientific journals such as Acta Biologica, Acta Botanica Croatica, Archiv für Hydrobiologie und Mikroskopie, his most comprehensive work on fossil diatoms called Diatomophyta fossilia, which was commissioned for the first part of the palaeobotanical encyclopaedia Traite de paleobotanique, remains unpublished. In this work, Jurilj studied 320 genera of diatoms with 12,000 species and discovered nine new genera with 30 new species during his research. His original handwritten paper is kept in the National Library of the University of Zagreb.

Diatom diversity

Diatoms are considered one of the most diverse groups of algae, with estimates of the number of diatom species ranging from 20,000 to 2.000,000 (Mann and Droop 1996, Spaulding et al. 2021). Some of the most recent works estimate the number of diatoms at 100,000–200,000 species, divided into the three classes Bacillariophyceae, Mediophyceae and Coscinodiscophyceae (Medlin and Kaczmarska 2004). There are currently 14,867 diatom species listed in the global algae database AlgaeBase (Guiry and Guiry 2024, https://www.algaebase.org/), while the Diatoms of North America database (Spaulding et.al. 2021, https://diatoms.org/) contains 1,099 described species. The wide range of diatom diversity is due to the continuous discovery and classification of new species and/or revisions of already described species and genera and the complex taxonomy of diatoms, which frequently leads to revisions and reclassifications. In addition, the use of different methods contributes to this complexity. In the 1970s, the scanning electron microscope revolutionized the systematics of diatoms by revealing taxonomically important ultrastructural features that were not visible with the light microscope (Hasle and Fryxell 1970, Alverson 2008). For some species of diatoms there was the necessity of introducing transmission electron microscopy (TEM), especially for those lightly silicified cells often found in marine environments (e.g., *Pseudo-nitzschia*, *Entomoneis*) (Burić et al. 2008, Mejdandžić et al. 2018). Finally, molecular methodology such as environmental DNA (eDNA) sequencing and genotyping of specific marker genes are now providing new insights into the systematics of diatoms and helping in the daily discovery of new species (Alverson 2008).

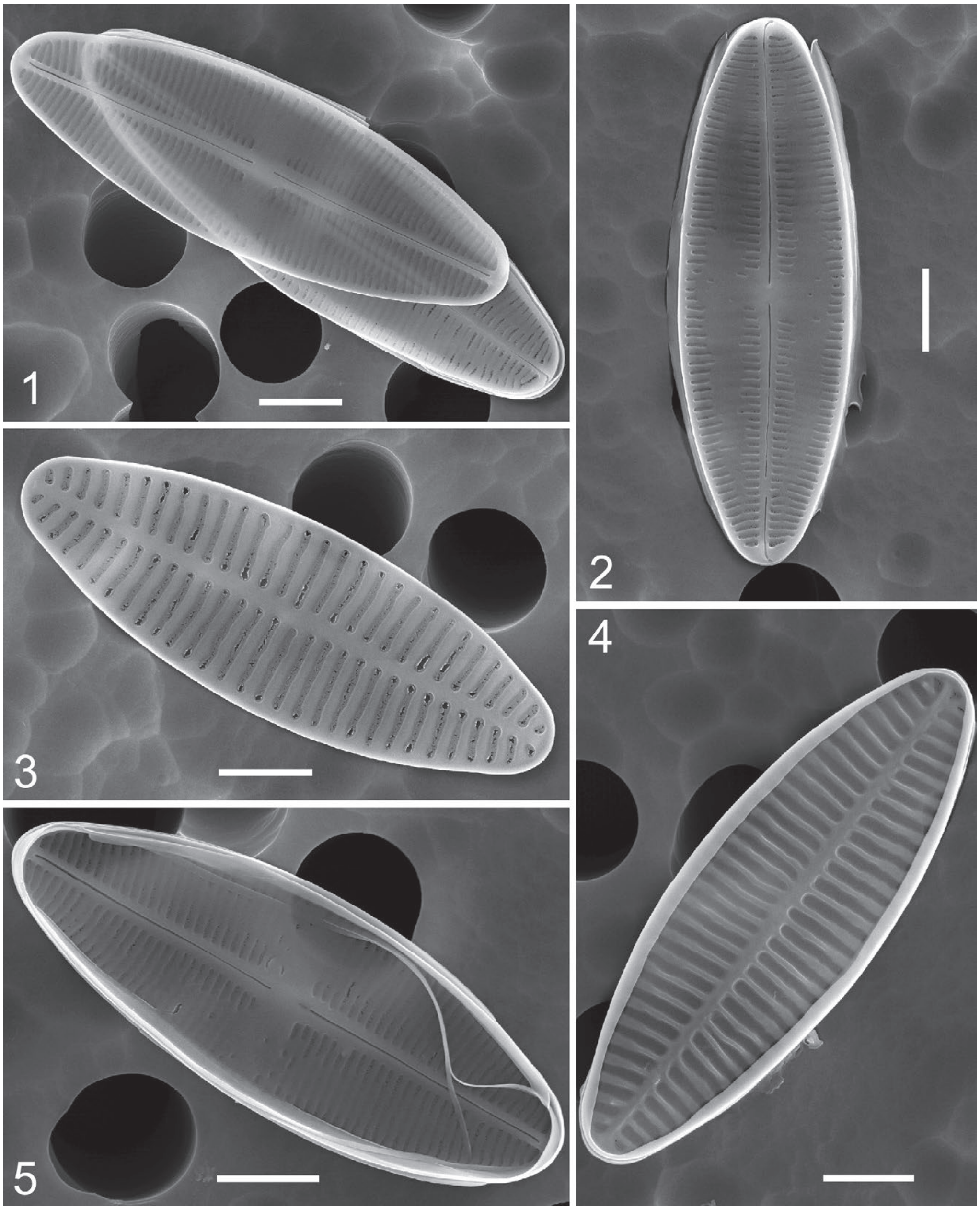
Overview of diatom research in the Eastern Adriatic Sea

Diatom research in the Adriatic Sea started very early, and some of the first described diatoms were *Bacillaria adriatic* Lobarzewski (von Lobarzewski 1840), *Berkeleya adriatica* Kützing (Kützing 1844) and *Amphitetras adriatica* Kützing (Kützing 1845). The beginnings of Adriatic research were focused on the northern Adriatic, where due to the influence of Italy and the Austro-Hungarian Monarchy, researchers came from different European countries (Casellato 2008). The first record of phytoplankton in the Adriatic Sea was at the end of the 19th century and it reports on the diatom *Nitzschia closterium* (Ehrenberg) W. Smith bloom in the northern Adriatic (Hauck 1872). Some of the pioneering important work of phytoplankton investigation, but focused on diatoms, is the results of the research expeditions "Rudolf Virchow" (Schröder 1911), "Naiads" (Schiller 1913a, b, 1925a, b, 1933, Schussnig 1914), and "Thor" (Jörgensen 1920, 1923) which resulted in numerous publications that are to a large extent still valuable keys for determining diatom species. But the main step in diatom research was the work of German botanist Friedrich Hustedt. He published the determination key for planktonic diatoms that was partly based on the analysis of Adriatic samples and many editions of that work are still relevant today (Hustedt 1927-1966). Croatian diatomologist Anto Jurilj, and Friedrich Hustedt collaborated and exchanged publications.

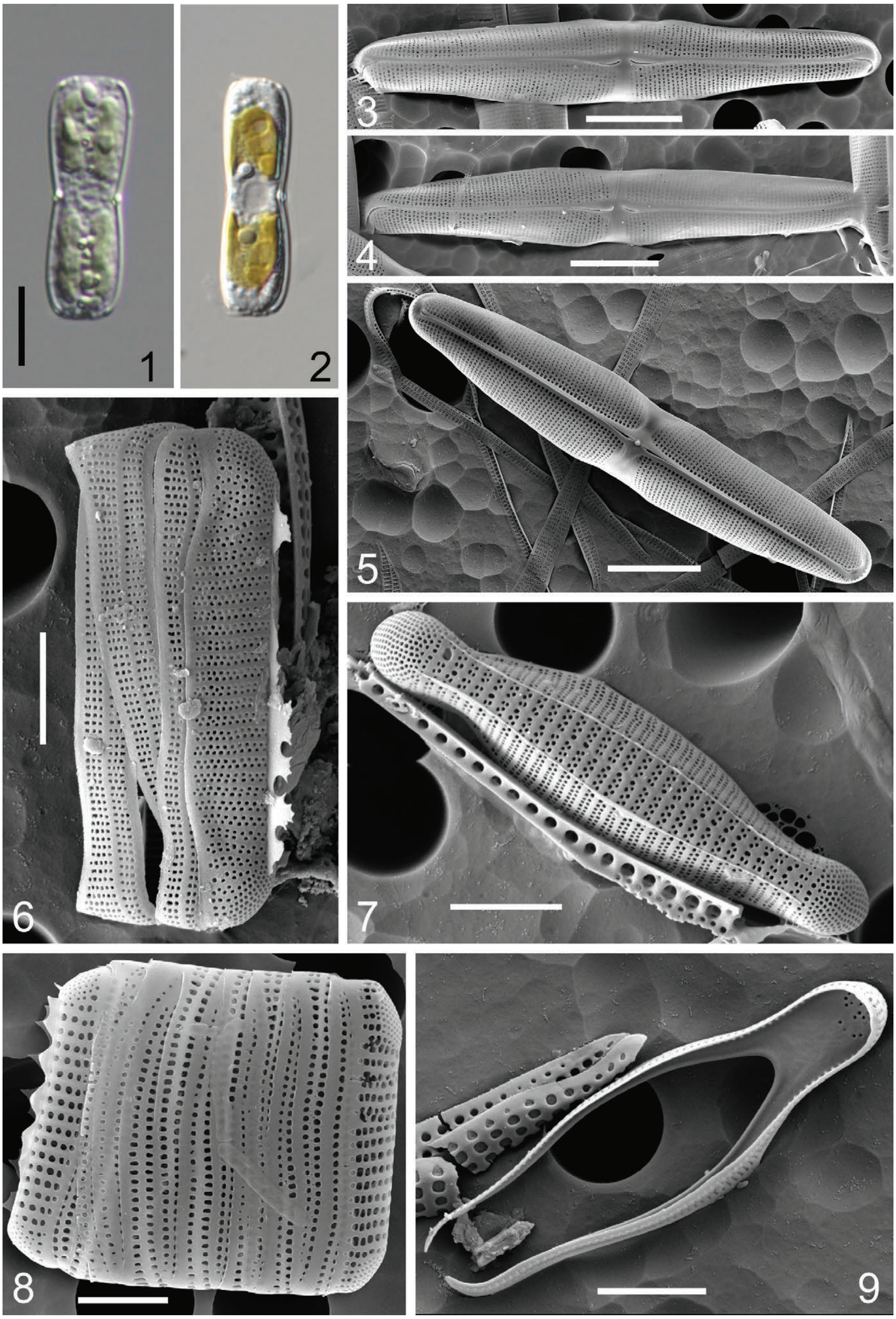
The research of phytoplankton taxonomy and ecology in the Adriatic Sea was continuous during the 20th century following the up-to-date literature and methods (Ercegović 1936, Viličić and Ljubešić 2017 and references therein). A comprehensive overview of eastern Adriatic phytoplankton taxonomy research and an updated checklist was published by Viličić et al. (2002) showing the great diatom diversity, of 518 diatom species. It must be added that 266 diatom species from this list, mostly benthic were recorded only by Revelante (1985). More recently an updated checklist of phytoplankton from 12 ports in the Adriatic was published recording 330 diatom taxa (Mozetič et al. 2019). Diatom diversity in the Adriatic Sea is high, probably due to its shallow parts and habitat heterogeneity and the long tradition of skilled diatomists. New species are constantly described not only those from the water column, but also those attached to a substrate (Car et al. 2012, Van De Vijver et al. 2020, Lobban et al. 2021). The diversity of periphytic diatoms has been investigated on natural and artificial substrates and submerged plants (Burić et al. 2004, Caput Mihalić et al. 2008, Car et al. 2012, 2019a, b, 2020, 2021, Mejdandžić et al. 2015, Nenadović et al. 2015, Hafner et al. 2018a, b, Kanjer et al. 2019, Seveno et al. 2023, 2024).

By the beginning of the 2010s, molecular methods came into traditional diatom taxonomy research. The first published sequences of diatoms from the Adriatic Sea were of the well-established species *Cylindrotheca closterium* (Ehrenberg) W. Smith (Pletikapić et al. 2012), and of the newly described species *Bacteriastrum jadranum* Godrijan, Maric & Pfannkuchen (Godrijan et al. 2012). In 2019 a complete chloroplast genome sequence was published of the small pennate diatom *Nanofrustulum shiloi* (J.J.Lee, Reimer & McEnery) Round, Hallsteinsen & Paasche collected from the Adriatic Sea (Li et al. 2019). It is also important to mention studies that used quick molecular identification for species that were difficult to resolve with traditional microscopy or that were treated as a threat for human health during harmful algal blooms (HABs): toxic specimens of the genus *Pseudo-nitzschia* (Penna et al. 2013, Grbin et al. 2017, Arapov et al. 2020, Smodlaka Tanković et al. 2022). Electron microscopy has proved a great tool for obtaining an insight into this genus heterogeneity (Burić et al. 2008, Ljubešić et al. 2011). Processes of diatom cultivation significantly endorsed the use of the molecular approach in taxonomical research into planktonic diatoms in the Adriatic Sea. With cultures established through several projects in the past decade, the number of cultivated diatoms from the Adriatic Sea increased exponentially, and consequently, multiple sequences were deposited in primary genetic databases such as GenBank, European Nucleotide Archive (ENA) or within in-house databases (Ruđer Bošković Institute, Marine Research Centre Rovinj; Institute of Oceanography and Fisheries, Split). One newly described diatom genus *Majewska* (Van de Vijver et al., 2020), with type species *Majewska istriaca* (Pl. 1) and several other genera were revised and supplemented with new taxa decribed from the Adriatic Sea, including *Entomoneis* (Mejdandžić et al. 2017, 2018, Al-Handal et al. 2020, 2020a, 2023), *Proschkinia* (Majewska et al. 2019), *Nitzschia* (Mucko et al. 2020), *Hyalosira* (Lobban et al. 2021) and *Craspedostauros* (Majewska et al. 2021) (Pl. 1-8). Description of images in plates are shortened and with commonly known diatom terminology. For detailed terminology explanation and description of each species please see original publications. eDNA sequencing and genotyping of cultivated diatoms in parallel enabled the first metabarcoded diatom checklist of North Adriatic Sea to be published (Grižančić et al. 2023).

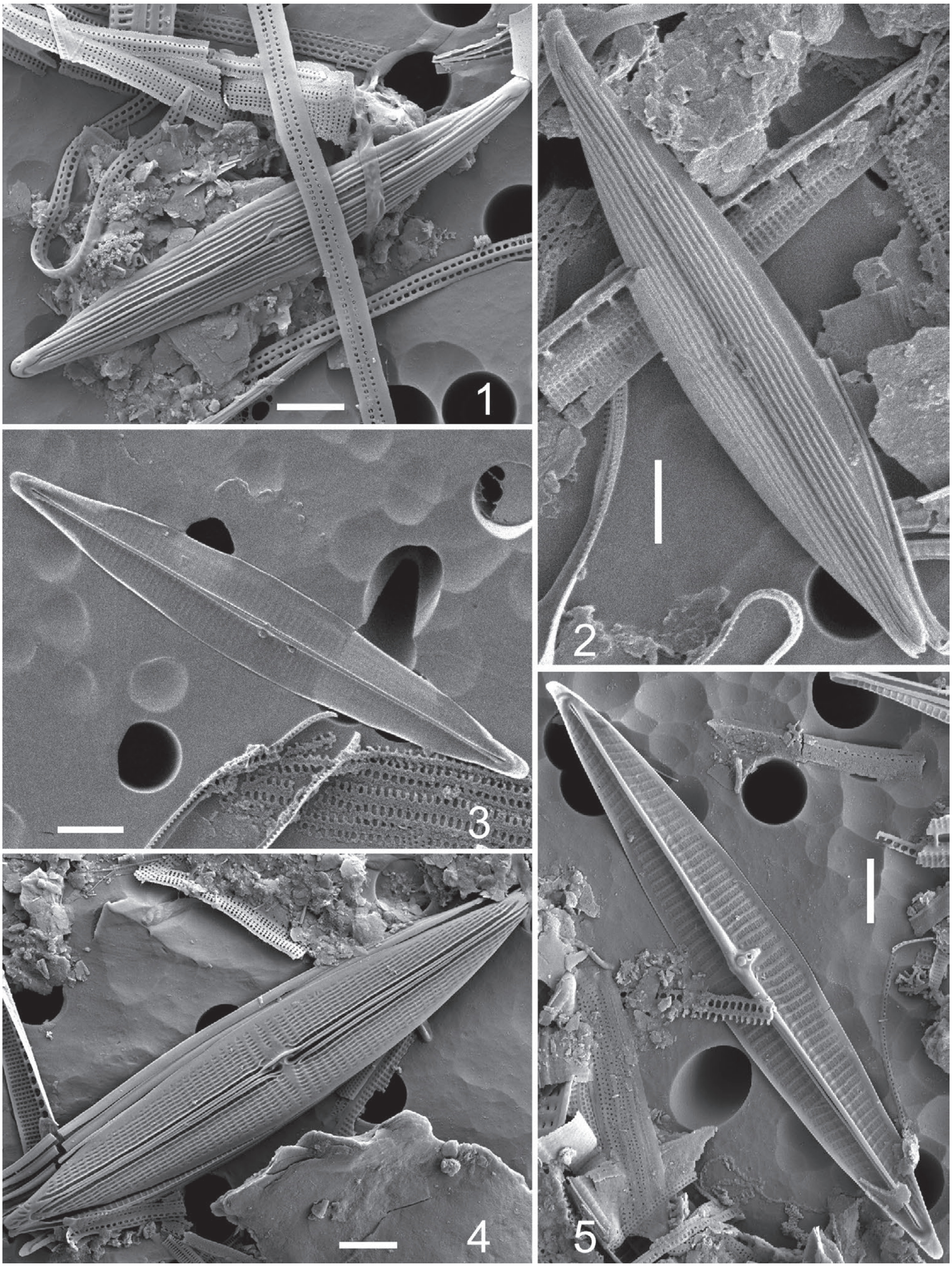
Today, phytoplankton in the Adriatic Sea is continuously metabarcoded and investigated with traditional microscopy for the purposes of whole-phytoplankton community and diatom community research (Mucko et al. 2018, Matek et al. 2023, Turk Dermastia et al. 2023, Baricevic et al. 2024), which is generating knowledge for future studies.



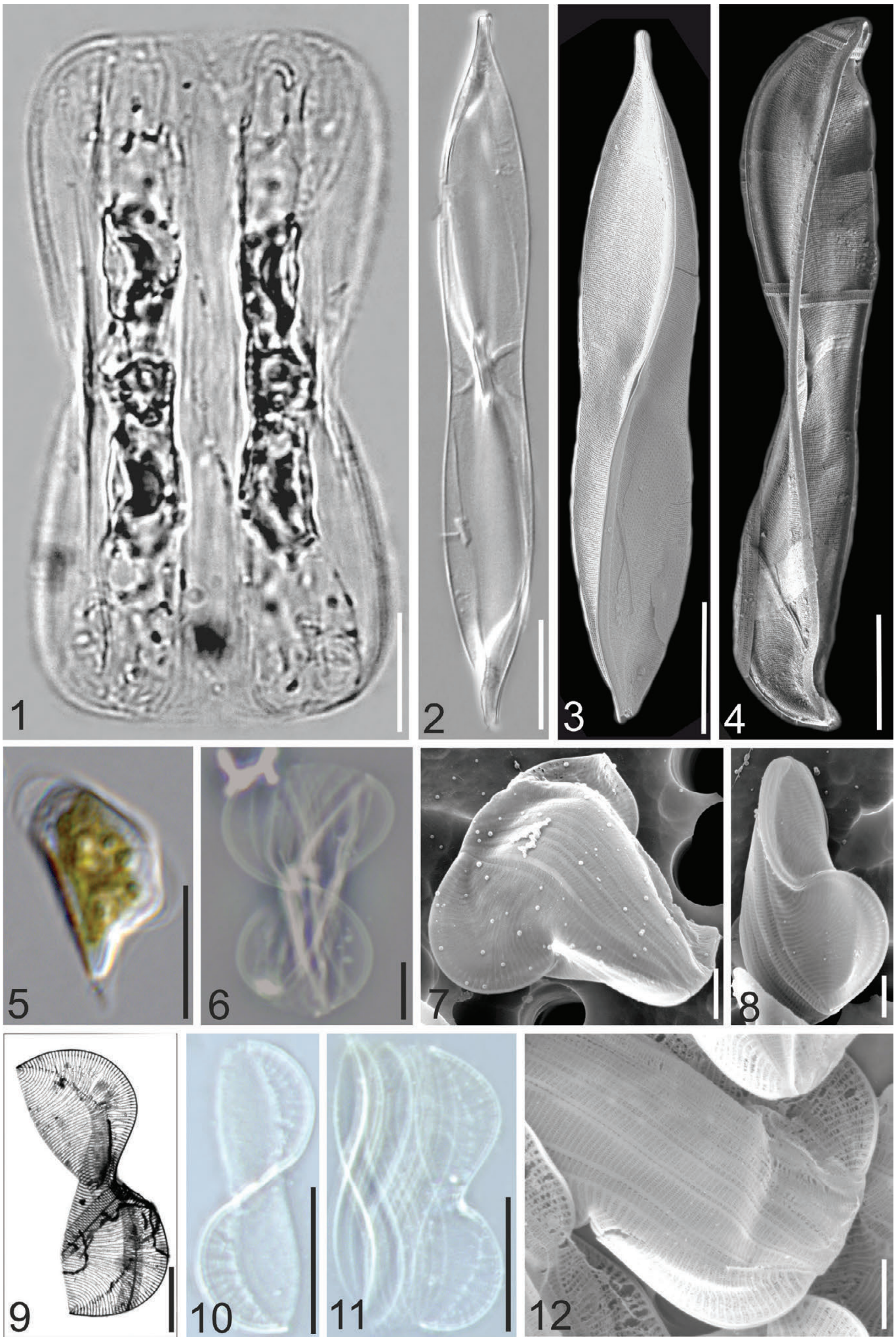
Pl. 1. SEM micrographs of *Majewskaea istriaca* from the PMFTB0125 culture material (Figs. **1–5**): **1** – Two overlaying raphe valves with the upper valve in the internal valve view and the lower in the external valve view; **2** – Internal view of the raphe valve; **3** – External view of the sternum valve; **4** – Internal view of the sternum valve with well-developed silica ridge surrounding the entire valve; **5** – Internal view of the raphe valve with partially attached open, narrow, unperforated girdle bands. SEM scale bar = 2 µm. Abbreviations: SEM–Scanning electron microscopy.



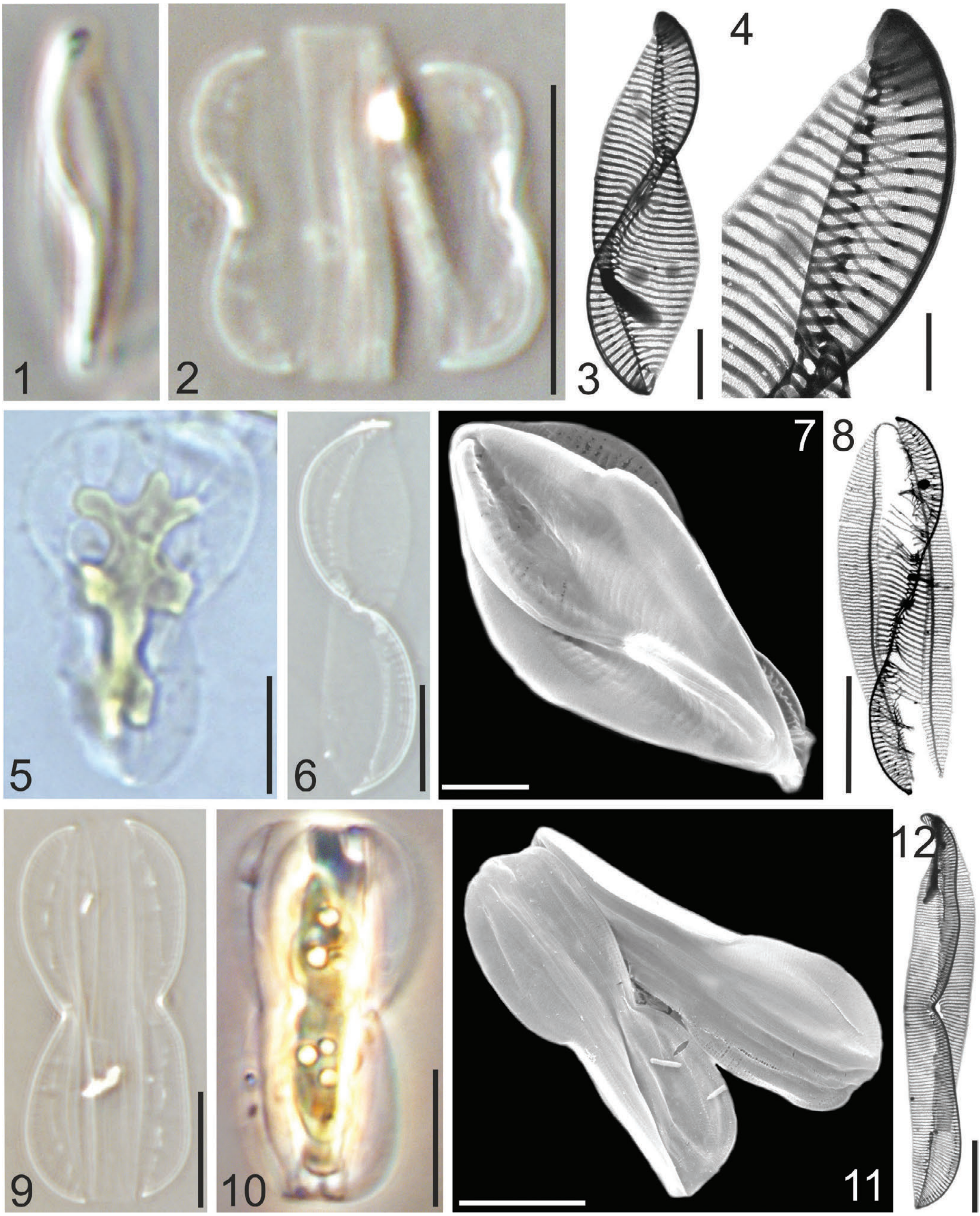
Pl. 2. *Craspedostauros legouvelloanus* PMFTB0003 culture material (Figs. **1–5**): **1,2** – LM micrographs of live cells in girdle view; **3,4** – SEM micrographs of external valve view showing the raphe and stria morphology; **5** – SEM micrograph of complete valve showing the internal valve structure (modified from Majewska et al. 2020.). SEM micrographs of *Hyalosira septata* from the type material (Figs. **6–9**): **6** – Girdle view of valve with prominent cristae and partially detached girdle bands (modified from Lobban et al. 2021.); **7** – External valve view showing stria morphology; **8** – Girdle view of a complete frustule; **9** – Open girdle band with prominent septa. LM scale bar = 10 µm (Figs. **1, 2**). SEM scale bar = 5 µm (Figs. **3–5**) and 2 µm (Figs. **6–9**). Abbreviations: LM–Light microscopy, SEM–Scanning electron microscopy.



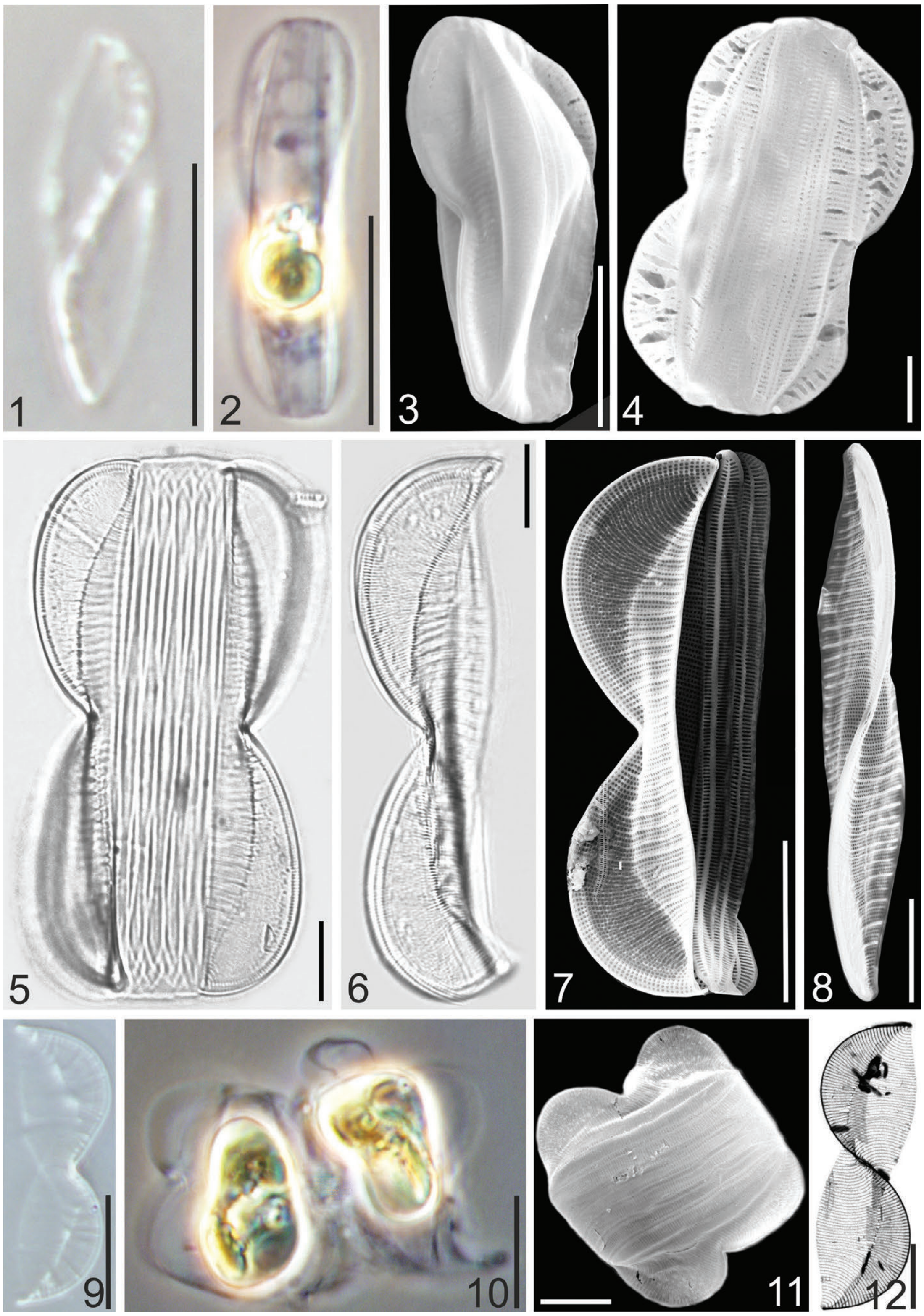
Pl. 3. SEM micrographs of *Proschkinia sulcata* from the type material (Figs. **1–3**): **1,2** – External valve view, note the valve central area with fistula opening hidden beneath the pocket-like silica thickening; **3** – Internal valve view showing stria pattern and a central fistula occluded by one domed hymen forming a ball-like structure. SEM micrographs of *Proschkinia torquata* from the type material (Figs. **4–5**): **4** – External valve view showing the longitudinal silica strips over the valve central area and a pocket-like rimmed silica flap obscuring the external fistula opening; **5** – Internal valve view with a distinctive fistula opening composed of several circular domed hymenes raised on the lateral expansion of the central nodule. SEM scale bar = 2 μm. Abbreviations: SEM–Scanning electron microscopy.



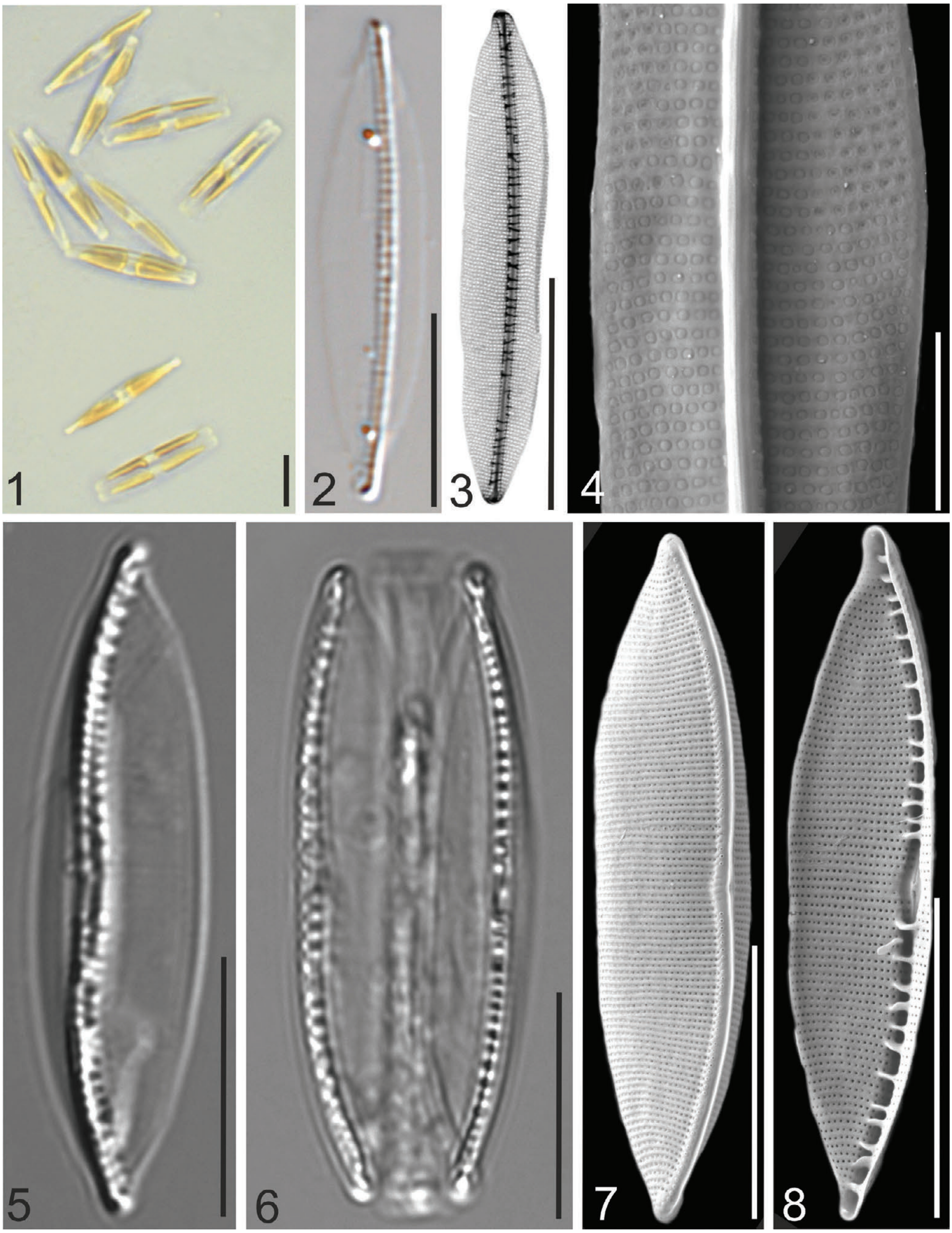
Pl. 4. LM and SEM micrographs of *Entomoneis annagodheae* from the field and type material (Figs. **1–4**): **1** – LM micrograph of live cell from field material; **2** – LM micrograph of external valve with prominent oblique transapical fascia; **3,4** – SEM micrographs of external and internal valve view. LM and SEM micrographs of *Entomoneis tenera* from culture and type material (Figs. **5–8**): **5** – LM micrograph of live apically torsioned cell from culture material, strain PMFEN1; **6** – LM micrograph of torsioned frustule in girdle view; **7** – SEM micrograph of torsioned frustule in girdle view; **8** – SEM micrograph of external valve with elevated bilobate keel. LM, SEM and TEM micrographs of *Entomoneis umbratica* from the type material (Figs. **9–12**): **9** – TEM micrograph of valve in girdle view; **10** – LM micrograph of valve with sigmoid raphe-bearing keel; **11** – LM micrograph of valve in girdle view with valvocopulae and copulae; **12** – SEM micrograph of showing girdle details. LM scale bar = 10 µm (Figs. **1,2,10,11**) and 5 µm (Figs. **5,6**), SEM scale bar = 10 µm (Figs. **3,4**), 5 µm (Fig. **12**) and 2 µm (Figs. **7,8**), TEM scale bar = 4 µm (Fig. **9**). Micrographs **1–4** are modified from Al-Handal et al. 2020; Micrographs **5–8** are modified from Mejdandžić et al. 2017; Micrographs **9–12** are modified from Mejdandžić et al. 2018. Abbreviations: LM–Light microscopy, SEM–Scanning electron microscopy.



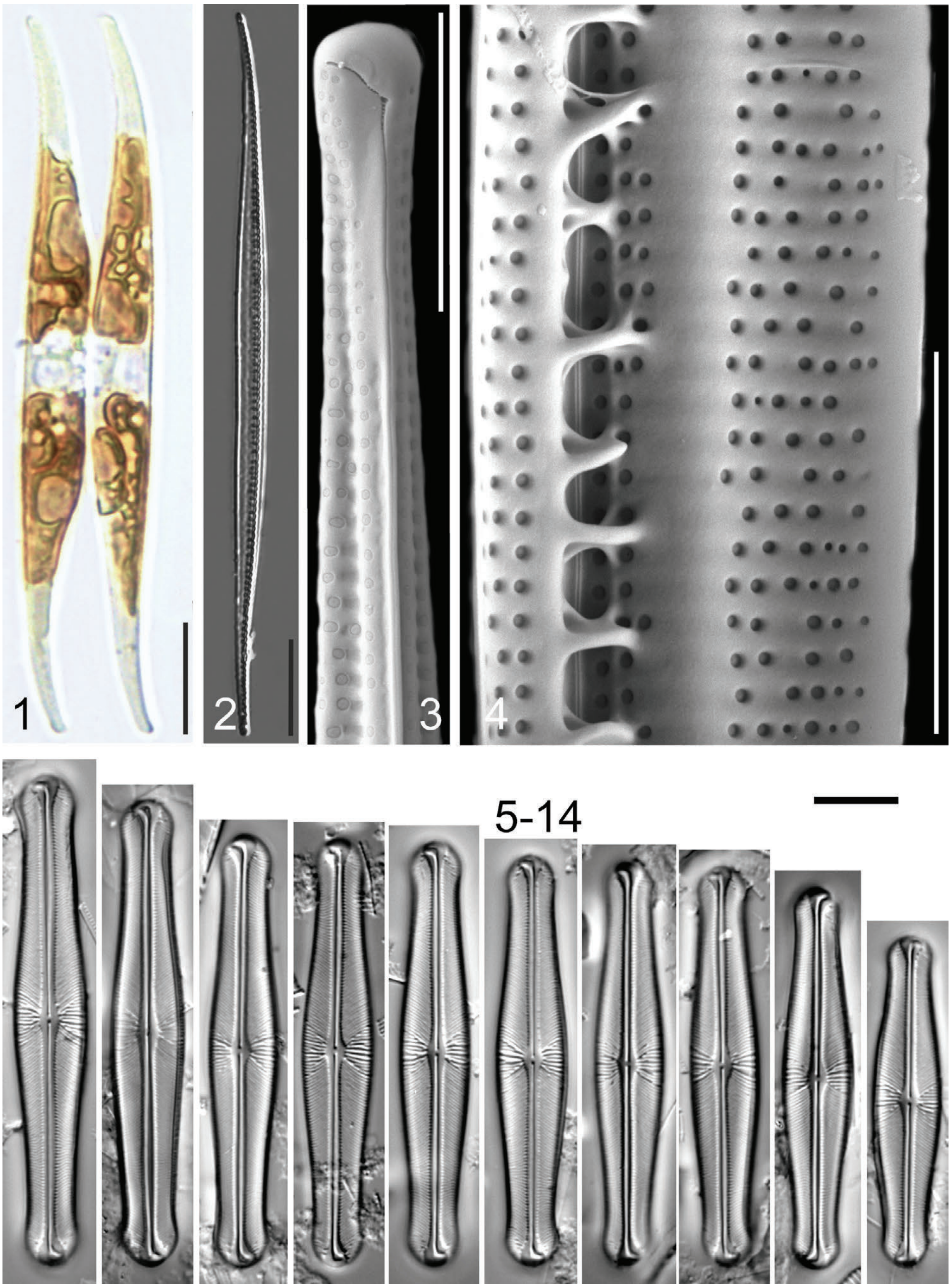
Pl. 5. LM and TEM micrographs of *Entomoneis pusilla* from the type material (Figs. **1–4**): **1** – LM micrograph of valve with sigmoid raphe-bearing keel; **2** – LM micrograph of frustule in girdle view; **3, 4** – TEM micrographs of valves with striae and keel details. LM, SEM and TEM micrographs of *Entomoneis adriatica* from the type material (Figs. **5–8**): **5** – LM micrograph of live apically torsioned cell from culture material, strain BIOTAII-49; **6** – LM micrograph of valve with sigmoid raphe-bearing keel; **7** – SEM micrograph of external valve; **8** – TEM micrograph of valve with valvocopulae. LM, SEM and TEM micrographs of *Entomoneis vilicicii* from culture and type material (Figs. **9–12**): **9** – LM micrograph of frustule in girdle view; **10** – LM micrograph of live cell from culture material, strain PMFBION4A; **11** – SEM micrograph of two partially torsioned frustules; **12** – TEM micrograph of valve with acute valve apices. LM scale bar = 10 µm (Figs. **1,2,5,6,9**), SEM scale bar = 2 µm (Fig. **7**) and 10 µm (Fig. **11**), TEM scale bar = 5 µm (Figs. **8,12**), 2 µm (Fig. **3**) and 1 µm (Fig. **4**). Micrographs **1,3,4,5,7** and **9–12** are modified from Mejdandžić et al. 2018. Abbreviations: LM–Light microscopy, SEM–Scanning electron microscopy.



Pl. 6. LM and SEM micrographs of *Entomoneis gracilis* from culture and type material (Figs. **1–4**): **1** – LM micrograph of valve with sigmoid raphe-bearing keel; **2** – LM micrograph of live cell from culture material, strain BIOTAII-60a; **3** – SEM micrograph of torsioned frustule with elevated raphe-bearing keel; **4** – SEM micrograph of frustule in girdle view. LM and SEM micrographs of *Entomoneis grisslehamnensis* from the type material (Figs. **5–8**): **5** – LM micrograph of frustule in girdle view; **6** – LM micrograph of valve with scalpelliform apices in girdle view; **7** – SEM micrograph of valve and accompanying valvocopulae in girdle view; **8** – SEM micrograph of external valve with sigmoid keel. LM, SEM and TEM micrographs of *Entomoneis infula* from culture and type material (Figs. **9–12**): **9** – LM micrograph of valve in girdle view; **10** – LM micrograph of two live cells from culture material, strain BIOTAII-68; **11** – SEM micrograph of frustule in girdle view; **12** – TEM micrograph of valve with scalpelliform apices. LM scale bar = 10 µm (Figs. **1,2,5,6,9,10**), SEM scale bar = 10 µm (Figs. **7,8**), 5 µm (Figs. **3,11**) and 2 µm (Fig. **4**), TEM scale bar = 10 µm (Fig. **12**). Micrographs **1–4** and **9–12** are modified from Mejdandžić et al. 2018; Micrographs **5–8** are modified from Al-Handal et al. 2023. Abbreviations: LM–Light microscopy, SEM–Scanning electron microscopy.



Pl. 7. LM, SEM and TEM micrographs of *Nitzschia adhaerens* from culture and type material (Figs. **1–4**): **1** – LM micrograph of live cells in culture material, strain BIOTAII-60; **2** – LM micrograph of spindle-shaped valve with cuneate apices; **3** – TEM micrograph of with pronounced raphe sternum and fibulae; **4** – SEM micrograph of with details of continuous raphe and striae areolae. LM and SEM micrographs of *Nitzschia dalmatica* from the type material (Figs. **5–8**): **5** – LM micrograph of linear to lanceolate valve; **6** – LM micrograph of frustule in girdle view; **7,8** – SEM micrographs of external and internal valves with eccentric elevated keel. LM scale bar = 10 µm (Figs. **1,2,5,6**), SEM scale bar = 10 µm (Figs. **4,7,8**), TEM scale bar = 10 µm (Fig. **3**). Micrographs **1–8** are modified from Mucko et al. 2020. Abbreviations: LM–Light microscopy, SEM–Scanning electron microscopy.



Pl. 8. LM and SEM micrographs of *Nitzschia inordinata* from culture and type material (Figs. **1–4**): **1** – LM micrograph of live cells from culture material, strain BIOTAII-44; **2** – LM micrograph of sigmoid valve with protracted apices; **3** – SEM micrograph of external valve with details of protracted apex with bent raphe fissure; **4** – SEM micrograph of internal valve with fibulae and areolae details. LM micrographs of *Envekadea hedinii* (Figs. **5–14**): LM micrographs of external view of the valves. LM scale bar = 10 µm (Figs. **1,2**), SEM scale bar = 5 µm (Figs. **3,4**). Micrographs **1–4** modified from Mucko et al. 2020. Abbreviations: LM–Light microscopy, SEM–Scanning electron microscopy.

Overview of the diatom research in the freshwater bodies in Croatia

Research on freshwater algae in Croatia began in the early 20th century (Brunnthaler 1900, Car 1906). Initially, the focus was on the floristic recording, taxonomy and description of the species (Krmpotić 1914, Pevalek 1919, 1925, 1935, 1938, Ercegović 1925, Vouk 1936, 1947, 1948, Jurilj 1957, Emili 1958), but with the acquisition of new knowledge, research expanded to the ecology of species, seasonal dynamics, spatial distribution, role in water treatment processes and primary organic production. Most diatom research was conducted in the context of comprehensive community diversity studies. This led to more comprehensive research on the diversity of algae, including diatoms, in the second half of the 20th century, and the first list of diatoms was published in 1995 (Plenković-Moraj 1995).

Firstly, algal and diatom research in Croatia was conducted mainly in karstic lakes and the tufa barriers of karst rivers, but today, due to the mandatory monitoring programme for surface waters under the Water Framework Directive (WFD) (European Community, 2000), research has expanded to the whole country and contributed to the discovery of new species. More advanced approaches to the study and biomonitoring of freshwaters brought new findings on diatoms and on periphyton community colonisation on natural and artificial substrates in the Zrmanja, Krka and Ombla rivers (Kralj et al. 2006, Caput Mihalić et al. 2008, Levkov et al. 2010) as well as on the study of the epiphytic community on sawgrass in the Plitvice Lakes National Park (Caput and Plenković-Moraj 2000). Studies have used a range of methods to assess species composition, abundance and distribution, often emphasising high species diversity and unique community structures. Therefore, general research on periphytic diatoms has focussed on various aspects such as diversity and community structure (Plenković et al. 1989, Plenković-Moraj 1996, Plenković-Moraj et al. 2008) in different freshwater habitats, including rivers, lakes and streams.

Diatoms were further analysed and recorded as part of extensive ecological studies on the taxonomy and ecology of phytoplankton in the Danube floodplains and along the Danube River, regarding the influence of the flooding of the Danube on species composition (Mihaljević et al. 2009, 2010, 2013, 2015, Stević et al. 2013). Phytoplankton was also studied in other large rivers such as the Mura, Drava and Sava (Stanković et al. 2012) and karst lakes (Žutinić et al. 2014, Gligora Udovič et al. 2015, 2017) using a novel morpho-functional approach and functional groups. The phytoplankton community in the context of Reynolds functional groups is well researched in Croatia and used as a bioindicator for assessing the water quality and ecological status of freshwater systems (Žutinić et al. 2020, Hanžek et al. 2021, 2023, Šimunović et al. 2022). All these phytoplankton studies included lists of diatom species and expanded the knowledge of diatom diversity and ecology, from phytobenthos to phytoplankton. The exploration of new habitats, such as mires with a narrow pH gradient, has also led to an increase in the list of recorded diatom species in Croatia (Stanković et al. 2022)

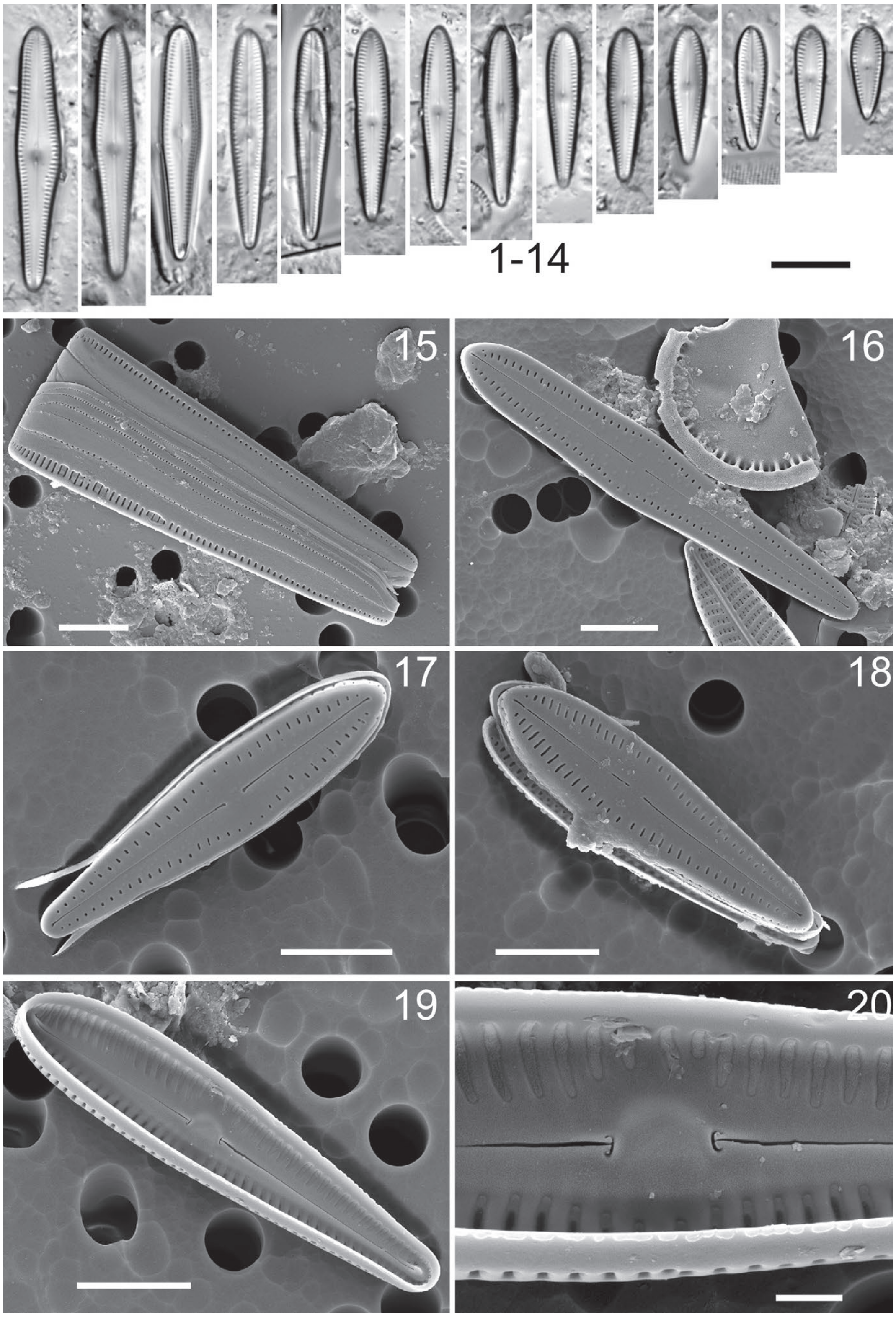
Today, the list of diatom species comprises 897 species and is used as the official operational list of diatoms in the national freshwater monitoring system and in assessing the ecological status of Croatian freshwater ecosystems. Studies in Croatia have developed and applied methods based on phytobenthos and phytoplankton to assess the ecological status of rivers and lakes and thus contribute to effective water management and protection strategies resulting in scientific articles in the field of ecology and benthic diatom assemblages along freshwater typology (Kralj Borojević et al. 2017).

The use of molecular methods and new genomic tools as well as the combination of morphological and molecular approaches in the analysis of phytoplankton and phytobenthos has provided new insights into algal diversity, including diatoms and also greatly improved phytobenthos and phytoplankton research in freshwater, embedded in the standardised bioassessment of the water quality and ecological status of regularly monitored water bodies (Kolda et al. 2019, Hanžek et al. 2021, Kulaš et al. 2021, 2022).

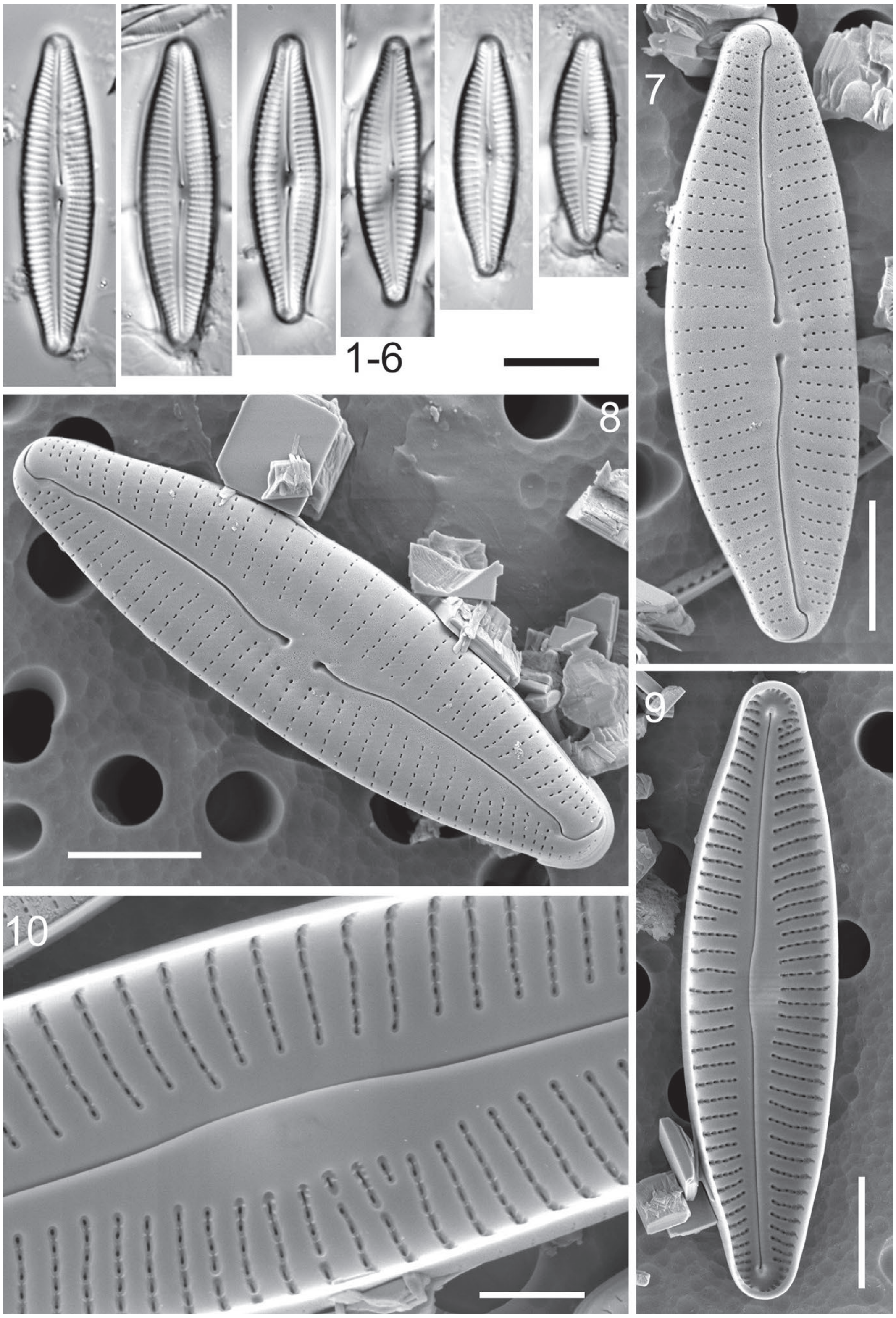
Analyses of the diatom material in all of these comprehensive studies led to comparison of some species to the type material (Kulaš et al. 2020, Trábert et al. 2019), to more detailed morphological studies (Gligora Udovič et al. 2017) and also the description of several new freshwater species. The ecological study of the phytoplankton community in the shallow Vrana Lake resulted in the study by Gligora et al. (2009) of the population of an unknown naviculoid diatom and the characterisation of the new genus *Envekadea* in 2009 in Vrana Lake near the town of Biograd, Dalmatia (Pl. 8).

The description was based on morphological characteristics of *Navicula hedinii* Hustedt. Furthermore, extensive paleo research was conducted on Vrana Lake in Croatia, which resulted in the identification of a new species, *Envekadea vranaensis* Caput Mihalić, Galović & Levkov (Caput Mihalić et al. 2020), which was described from Holocene sediments. Another new species *Tetramphora croatica* Gligora Udovič, Caput Mihalić, Stanković & Levkov, was observed and described from contemporary and core samples of Lake Vransko (Caput Mihalić et al. 2019). The first successful dive to the bottom of the karstic lake Crveno jezero, near the town of Imotski in the southern part of Croatia, resulted in the discovery of a diatom species new to science *Gomphosphenia plenkoviciae* Gligora Udovič & Žutinić (Gligora Udovič et al. 2018) (Pl. 9).

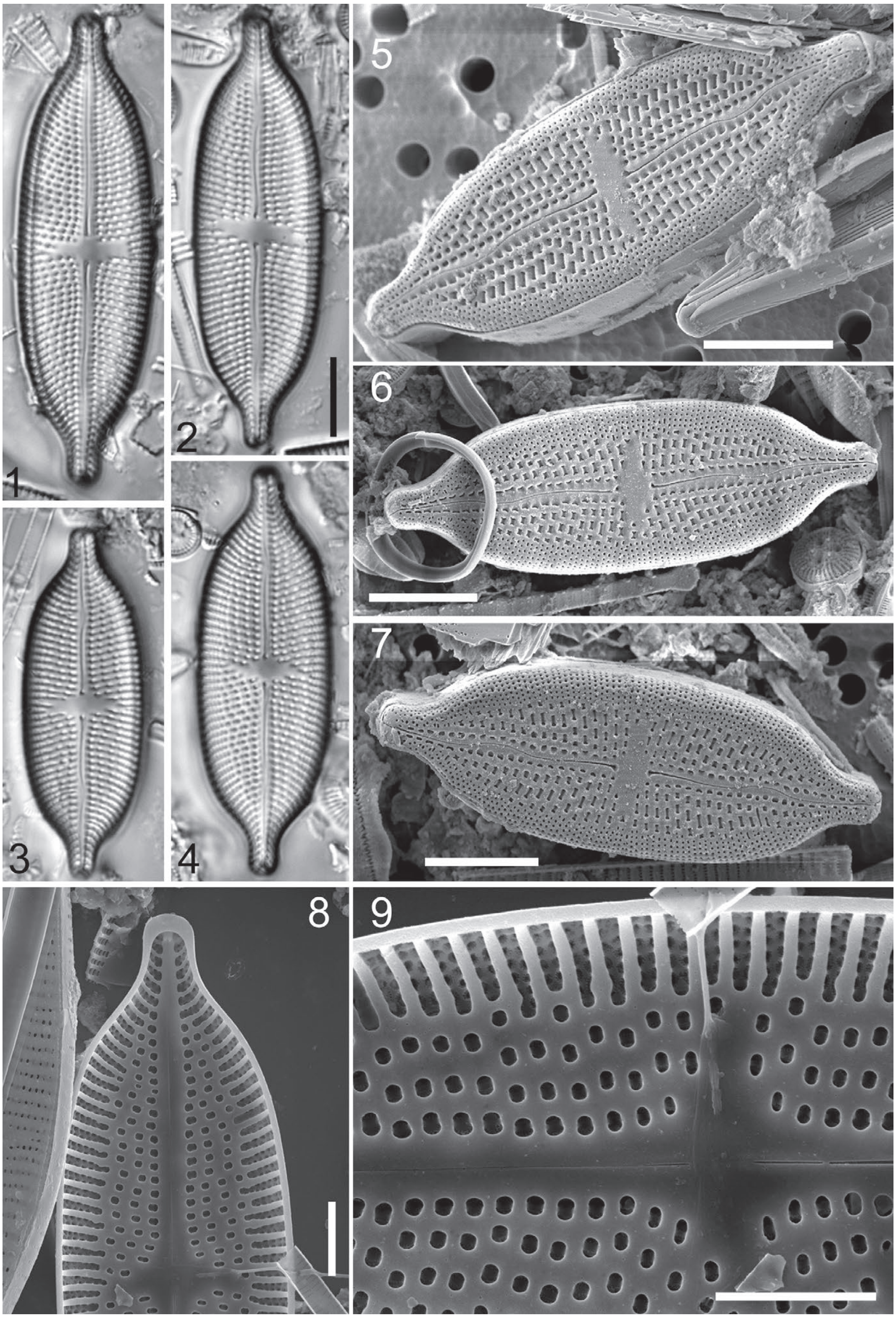
During the research in Krka National Park and establishment of the Krka diatom collection two new species were described *Cymbopleura amicula* Gligora Udovič, Kulaš, Šušnjara, Arapov, Blanco & Levkov (Gligora Udovič et al. 2022) and *Aneumastus visovacensis* Gligora Udovič et Levkov (Gligora Udovič et al. 2023) (Plate 10, 11).



Pl. 9. Light micrographs of *Gomphosphenia plenkoviciae* from the type material (Figs. **1–14**). External girdle view of the whole frustule (Fig. **15**). External view of the whole valve. Note the simple proximal and distal raphe ends and striae composed of a single areola located near valve margin (Figs. **16–18**). Internal view of the whole valve. Internally, areolae are occluded by hymens. Distally, raphe terminates in helictoglossae (Fig. **19**). Internal detailed view of mid-valve showing the internal structure of proximal raphe ends (T-shaped) and areolae (Fig. **20**). LM scale bar = 10 µm (Figs. **1–14**). SEM scale bar = 5 µm (Figs. **15–19**); 2 µm (Fig. **20**). Abbreviations: LM–Light microscopy, SEM–Scanning electron microscopy.



Pl. 10. Light micrographs of *Cymbopleura amicula* from river Krka (Figs. **1–6**). External view of the whole valve showing the areola and raphe structure. Areolae have slit-like external opening. Distal raphe ends are dorsally deflected. Proximally raphe terminates with expanded central pores (Figs. **7, 8**). Internal view of the whole valve. Note the small struts present across the vimines (Fig. **9**). Internal detailed view of mid-valve showing the internal structure of raphe and areolae. Raphe "lacking an intermissio" or proximal raphe ends are covered by overgrowth of silica that hides the deflected endings (Fig. **10**). LM scale bar = 10 μm (Figs. **1–6**). SEM scale bar = 5 μm (Figs. **7–9**) and 2 μm (Fig. **10**). Abbreviations: LM–Light microscopy, SEM–Scanning electron microscopy.



Pl. 11. Light micrographs of *Aneumastus visovacensis* from the type material (Figs. **1–4**). External view of the whole valve. Striae near raphe uniseriate are composed of large elongated, bone–shaped or X–shaped areolae, becoming biseriate near the valve margin and composed of small, round areolae. Areolae are complex, occluded, opened into deep pits via sieves of small pores (Figs. **5–7**). Internal valve view. Raphe is very narrow linear with indistinct and straight proximal raphe ends (Fig. **8**). Internal detailed view of midvalve showing the internal structure of raphe and areolae. Areola openings round to ellipsoidal near axial area becoming elongate towards valve margin (Fig. **9**). LM scale bar =10 µm (Figs. **1–4**). SEM scale bar = 10 µm (Figs. **5–7**) and 5 µm (Figs. **8, 9**). Abbreviations: LM–Light microscopy, SEM–Scanning electron microscopy.

Based on the presented long-term research on diatoms in Croatia, the Department of Biology founded the Croatian National Diatom Collection (HRNDC), the first institutional collection of permanent microscopic specimens of diatoms in Croatia, currently comprising 2,883 microscopic slides and 23 type specimens (Tab. 1).

Tab. 1. List of newly (2009-2023) described species deposited in the Croatian National Diatom Collection (HRNDC).

Species	Habitat	Described by	Region	Reference	Accession number
Entomoneis pusilla	marine plankton	Sunčica Bosak, Maja Mejdandžić	Adriatic Sea, south–eastern coast, Croatia	Mejdandžić et al. 2018	HRNDC000001
Entomoneis gracilis	marine plankton	Sunčica Bosak, Maja Mejdandžić	Adriatic Sea, south–eastern coast, Croatia	Mejdandžić et al. 2018	HRNDC000002
Entomoneis vilicicii	marine plankton	Sunčica Bosak, Maja Mejdandžić	Adriatic Sea, south–eastern coast, Croatia	Mejdandžić et al. 2018	HRNDC000003
Entomoneis infula	marine plankton	Sunčica Bosak, Maja Mejdandžić	Adriatic Sea, south–eastern coast, Croatia	Mejdandžić et al. 2018	HRNDC000004
Entomoneis adriatica	marine plankton	Sunčica Bosak, Maja Mejdandžić	Adriatic Sea, south–eastern coast, Croatia	Mejdandžić et al. 2018	HRNDC000005
Entomoneis umbratica	marine plankton	Sunčica Bosak, Maja Mejdandžić	Adriatic Sea, south–eastern coast, Croatia	Mejdandžić et al. 2018	HRNDC000006
Proschkinia torquata	sea water	Sunčica Bosak, Bart Van de Vijver, Roksana Majewska	Marine Turtle Rescue Centre, Pula, Croatia	Majewska et al. 2019	HRNDC000007
Proschkinia sulcata	sea water	Roksana Majewska, Bart Van de Vijver, Sunčica Bosak	Marine Turtle Rescue Centre, Pula, Croatia	Majewska et al. 2019	HRNDC000007
Gomphosphenia plenkoviciae	freshwater	Marija Gligora Udovič, Petar Žutinić	Crveno jezero, Croatia	Gligora Udovič et al. 2018	HRNDC000008
Tetramphora croatica	brackish water	Marija Gligora Udovič, Katarina Caput Mihalić, Igor Stanković, Zlatko Levkov	Lake Vransko, Croatia	Mihalić et al. 2019	HRNDC000009
Nitzschia dalmatica	marine plankton	Maja Mucko, Sunčica Bosak	Southeast Adriatic Sea, Croatia	Mucko et al. 2020	HRNDC000010
Nitzschia adhaerens	marine plankton	Maja Mucko, Sunčica Bosak	Southeast Adriatic Sea, Croatia	Mucko et al. 2020	HRNDC000011
Nitzschia inordinata	marine plankton	Maja Mucko, Sunčica Bosak	Southeast Adriatic Sea, Croatia	Mucko et al. 2020	HRNDC000012
Cymbopleura amicula	freshwater	Marija Gligora Udovič, Antonija Kulaš, Mirela Šušnjara, Jasna Arapov, Saul Blanco, Zlatko Levkov	Krka River, Croatia	Gligora Udovič et al. 2022	HRNDC000026
Aneumastus visovacensis	freshwater	Marija Gligora Udovič, Zlatko Levkov	Lake Visovac, Croatia	Gligora Udovič et al. 2023	HRNDC000046
Entomoneis tenera	marine plankton	Maja Mejdandžić, Sunčica Bosak	Adriatic Sea, Croatia	Mejdandžić et al. 2017	HRNDC000435
Entomoneis annagodheae	marine plankton	Adil Y. Al-Handal, Maja Mucko	Kungälv fjord, West coast of Sweden	Al-Handal et al. 2020	HRNDC000436
Majewskaea istriaca	marine benthos	Bart Van de Vijver, Käthe Robert, Andrzej Witkowski, Sunčica Bosak	Adriatic Sea, Croatia	Van De Vijver et al. 2020	HRNDC000437
Craspedostauros legouvelloanus	marine benthos	Roksana Majewska, Sunčica Bosak	Kosi Bay, South Africa Adriatic Sea	Majewska et al. 2021	HRNDC000502
Hyalosira septata	marine benthos	Sunčica Bosak, Bart Van de Vijver, Nihavet Bizsel	Pula Aquarium, Croatia	Lobban et al. 2021	HRNDC000850
Entomoneis grisslehamnensis	sea water	Adil Y. Al-Handal, Maja Mucko	Sweedish coast of Baltic Sea: Grisslehamn and Juniskär	Al-Handal et al. 2023	HRNDC001665
Pinnularia furatensis	brackish water	Adil Y. Al-Handal	Euphrates River, Southern Iraq	Al-Handal 2022	HRNDC001666
Envekadea hedinii sp.nov	brackish water	Van de Vijver, Gligora, F. Hinz, Kralj & Cocquyt	Lake Vransko, Croatia	Gligora et al. 2009	HRNDC002157

Future challenges

Having in mind the variety and quantity of data being published every year and considering the intensity of diatom research (especially new species descriptions), the existence and professional sustainability and curation of diatom collections is of the utmost importance. However, neither a database nor a diatom collection is free from daily and long-term challenges that need to be overcome with professional staff (scientists and collaborators). One of the main challenges we would like to address is the stability of funding and staff employment to ensure that the collection is continuously available for research, teaching and public use. We often face uncertain funding and rely on scientific (or professional monitoring) projects that have an expiry date, but the collection is here to stay. The frequent turnover of personnel working for a collection introduces uncertainty and potential errors within the database and provides fertile ground for errors in publications that collect data from the same collections.

Considering the omics era and the description of new species with the deposition of material, collections should also be careful to register peer-reviewed data only, ensuring the quality of taxonomy. However, we can still register one specimen as species A and revise it further to a strain of species B, subspecies of species A or entirely other species C, as long as personnel keeps track of the annotation. Eukaryotic tree of life (Adl et al. 2019) is expanding daily and currently establishes nine taxonomic levels (according to pr2 database, Vaulot et al. 2022) and many taxa are changing in their higher systematic ranks, as well as shifting from one genus to other. Phylogenetic papers often confront key aspects of species definition to be faulty when dealing with monophyly vs. paraphyly and support in clade differentiation spanning one species or species complex. There is also sensitivity in cryptic species descriptions that needs to be addressed, and diatoms have many examples of such behaviour (Pinseel et al. 2019) and plasticity in terms of morphological *vs*. phylogenetical concept of species (Alverson 2008 and references therein). Thus, revisions of existing historical material deposited in collections often can shed light on complex species relationships.

The availability of a collection directly depends on its housing the collection if it is not digitalized. Well into the technological era, most research, in view of the exploitation and comparison of data, can be done online, through available, well curated collections such as the Croatian National Diatom Collection (HRNDC). To meet this challenge, the collection is set to be digitalized in 2025 as part of the newly established BIOFIT data platform. BIOFIT is an internal web database application designed for the collection and management of ecological research data. The information about a collection(s) housed within BIOFIT will be made publicly accessible in a curated format on the Flora Croatia Database (Nikolić 2024) and the HRNDC web page https://www.diatoms.biol.pmf.hr/collection. Once this process is done, valuable data will be ready for use by members of academia and scholars. However, digital availability is not sufficient if the collections not well curated. Experts in taxonomy, phylogeny and evolution, whether they act as authors of a publication and depositors, or as second-hand curators, have a tremendously important job – to correct the taxonomical annotation of specimens. Biocurators need to ensure that relevant specimens are reliable, reusable and accessible by other researchers. With this in mind, every revised taxonomy annotation must be tracked and acknowledged on every collection milestone, ensuring up-to-date lists and systematics. Many collections have therefore established workflows which ensure fulfilment of the tasks biocurators do, so nothing is left unattended (Odell et al. 2017). Within this process of curation, newly established collections such as HRNDC can benefit from networking, sharing of best practices, developing collaboration and promoting interactions with other similar (and more experienced) diatom collections.

Finally, it is important to emphasise that collections often help generate solutions to societal challenges by stimulating interaction among academia, the public and bioindustry. The popularization of science through collections as valuable resource in which parties can observe, experience, touch and acknowledge scientific work ensures that the efforts required in their establishment have been worthwhile within the framework of the Croatian natural heritage.

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Author contribution statement

Z. LJ. – conceptualization, writing - original draft; D. J. – writing - original draft, writing - review and editing; T.P.

– data curation, investigation, writing - original draft; M.Ž. – data curation, investigation, writing - original draft; Z. Le. – visualization, writing - original draft; M.M. – writing - review and editing; S.B. – writing - review and editing; M.G.U. – conceptualization, writing - original draft.

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