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The Diatom Genus *Navicula* in Spring Ecosystems with the Description of *Navicula aquaesuavis* sp. nov.

María Cid-Rodríguez [1], Marco Cantonati [2,*], Nicola Angeli [3], Olena Bilous [4,5], Maha Al-Harbi [6], Horst Lange-Bertalot [7], Zlatko Levkov [8], Lucia Piana [2], Daniel Spitale [9] and Abdullah A. Saber [10]

[1] Department of Ecology and Animal Biology, University of Vigo, 36310 Vigo, Spain; maria.cid@uvigo.es
[2] Department of Biological, Geological and Environmental Sciences, Alma Mater Studiorum—University of Bologna, 40126 Bologna, Italy; lucia.piana@studio.unibo.it
[3] Research & Collections Department (Limnology & Phycology), MUSE—Museo delle Scienze, 38123 Trento, Italy; nicola.angeli@muse.it
[4] Institute of Hydrobiology and Aquatic Ecosystem Management (IHG), University of Natural Resources and Life Sciences, 1180 Vienna, Austria; olena.bilous@boku.ac.at
[5] Institute of Hydrobiology of NAS of Ukraine, Volodymyra Ivasiuka Ave, 12, 04210 Kyiv, Ukraine
[6] Department of Biology, College of Science, Princess Nourah bint Abdulrahman University, Riyadh 11671, Saudi Arabia; maalharbi@pnu.edu.sa
[7] Biologicum, Goethe Universität Frankfurt, 60438 Frankfurt, Germany
[8] Institute of Biology, Faculty of Natural Sciences and Mathematics, Ss. Cyril and Methodius University, 1000 Skopje, North Macedonia; zlevkov@pmf.ukim.mk
[9] BMT BioMonitoring Team, 38095 Trento, Italy; spitale@biomonitoraggi.it
[10] Botany Department, Faculty of Science, Ain Shams University, Cairo 11566, Egypt; abdullah_elattar@sci.asu.edu.eg
* Correspondence: marco.cantonati@unibo.it

Abstract: Given the limited understanding of species diversity and ecological preferences of diatoms of the genus *Navicula* in spring ecosystems, herein we present and describe as species new to science, *Navicula aquaesuavis* Lange-Bert., Levkov, Cid-Rodríguez, A.A.Saber and Cantonati sp. nov. This species was collected from a mountain spring located above the tree line at 1613 m a.s.l. in the Northern Apennines. The *Fontana del Vescovo* (Bishop's spring), which is the *locus classicus* of the new species, has a low conductivity (60–70 µS cm^{-1}), temperature of ca. 5 °C, circumneutral pH (7.3–7.5), relatively low nitrate (ca. 1 mg L^{-1}), and also suffered from a discharge reduction from 1 to 0.1 L s^{-1} from 2011 to 2023. The putative new species was confirmed by a second finding in Northern Macedonia, and we thoroughly document this second population as well. We seized the opportunity to describe this new *Navicula* and review the global literature on the diatom genus *Navicula* in spring ecosystems. Using the results of this review and our own databases on springs and wells in central Europe and Egypt, we discuss the main *Navicula* species and their environmental preferences in spring habitats.

Keywords: diatoms; *Navicula*; springs; ecological preferences; distribution; new species

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1. Introduction

Spring ecosystems are unique habitats that are increasingly at risk because of the exploitation of strategic water resources, the availability of which is reduced in many geographic areas due to climate change [1]. Diatoms in springs have been investigated more than other components of the biota, but still, new species (sometimes even new genera) are described from springs in the frame of in-depth research on diatom communities (e.g., [2]).

The genus *Navicula* Bory is usually well-represented in springs; however, it is typically not prominent from a quantitative standpoint, likely because of environmental features of such ecosystems, such as, for instance, low trophic levels (e.g., *Navicula dealpina* Lange-Bert.) [2].

Representatives of the genus occur more commonly and abundantly in springs at low elevations, in urban areas, with higher nitrates, and with sandy, muddy substrata (e.g., [3]). For instance, in the karstic *Su Gologone* spring (central-eastern Sardinia, Italy), the *Navicula-Nitzschia-Surirella* Index indicated low physical disturbance [4].

Fazlutdinova et al. [5] studied diatom communities in soils near thermal springs and found that they included both aquatic and terrestrial species. *Navicula* was one of the most common diatom genera. Kamberović et al. [6] investigated twenty springs of Mt. Konjuh (Bosnia and Herzegovina) from contrasting bedrocks (limestones and different ophiolitic lithologies, respectively) and noted that the most common alkaliphilic, circumneutral, and eutraphentic diatoms were represented by the genera *Gomphonema*, *Nitzschia* and *Navicula*. Finally, *Navicula*, *Fragilaria*, *Nitzschia*, *Cymbella* and *Gomphonema* were the most species-rich genera in the limnocrenic spring Zelenci in Slovenia [7].

At low altitudes, in urban springs, even a *Navicula* species-flock, morphotypes in the vicinity of *N. cincta* (Ehrenb.) Ralfs) appear to have developed, including *Navicula domiciliensis* E.Reichardt [8], *N. veronensis* Lange-Bert. and Cantonati [2], and *Navicula fontana* Żelazna-Wieczorek, Lange-Bert., Olszynski and Witkowski [9].

Considering the pivotal importance of the correct knowledge of the taxonomy and ecological preferences of the species occurring in mountain (low conductivity) freshwater ecosystems to use diatoms as reliable indicators of environmental and climate change (e.g., ref. [10]), in this paper, we contribute to fill the gap of the limited understanding of species diversity and ecological preferences of diatoms of the genus *Navicula* in spring ecosystems. Our objectives were to describe a putative new *Navicula* species from a spring in the Northern Apennines, review the global literature on *Navicula* in springs, including arid and semi-arid regions, and use our own selected databases to calculate ecological preferences for the main *Navicula* species in the mountains of southern central Europe.

2. Materials and Methods

2.1. Study Area, Sampling

Fontana del Vescovo (Bishop's spring), Northern Apennines, Italy, is a small flowing (rheocrenic) spring shaded only by tall grasses [1]. It has a low conductivity (60–70 µS cm^{-1}), temperature of ca. 5 °C, circumneutral pH (7.3–7.5), relatively low nitrate (ca. 1 mg L^{-1}), and suffered from a discharge reduction from 1 to 0.1 L s^{-1} from 2011 to 2023 (MC, unpublished data). *Fontana del Vescovo* is depicted on a map in [1]. All details, including the co-occurring photoautotrophs from cyanobacteria to angiosperms, are available in Cantonati et al. [11]. In general, the photoautotrophic communities are typical of small, mountain, oligotrophic, low-conductivity but well-buffered, flowing springs.

Lake Bogovinsko is the largest permanent glacial lake in North Macedonia, located on Shara Mountain between Bresovec and Mala Smreka at an altitude of 1936 m (shown on a map in [12]). It is located in a rocky area with siliceous geology. The lake is 471 m long and 195 m wide with a shoreline of 1246 m. It is relatively shallow, with a maximum depth of 2.2 m. In the past, Lake Bogovinsko was larger, but due to the anthropogenic regulation (widening) of the river Bogovinska, its size significantly decreased. Several small springs, streams, and snowmelt feed the lake. The water loss is caused by evaporation and surface runoff from the River Bogovinska.

Epilithic diatoms were collected by brushing seven to ten cobbles or small boulders. For the epibryon, entire plantlets of the dominant bryophyte species (submerged or closest to the water) were collected.

2.2. Diatom Preparation, Identification and Counting

The diatom samples were treated with hydrogen peroxide and hydrochloric acid to remove organic material. The cleaned valves were then mounted with Naphrax® (Brunel Microscopes Ltd., Chippenham, Wiltshire, UK). For each sample, three coverslips were prepared and mounted on glass slides, with a total of 400 valves counted to determine relative abundances. The identification and nomenclature primarily followed Lange-Bertalot [13].

Observations were conducted using a Zeiss Axioskop 2 optical microscope (Carl Zeiss Microscopy GmbH, Jena, Germany) equipped with phase contrast and a digital Axiocam camera (Carl Zeiss JSC, Milan, Italy). SEM observations on gold-coated prepared material were primarily carried out at the University of Frankfurt using a Hitachi S-4500 (Hitachi Ltd., Tokyo, Japan). Additional SEM observations were performed at the Museo delle Scienze—MUSE in Trento with an LEO XVP (Carl Zeiss SMT Ltd., Cambridge, UK) under a high vacuum. All observations and micrography mentioned in this note were based on epibryon samples.

Materials, including slides, prepared samples, and aliquots of the original specimens, along with the holotypes of the two new species and the epitype, were stored at the Diatom Collection of MUSE—Museo delle Scienze (TR) in Trento, Northern Italy.

Isotype slides and aliquots of prepared material from the same locality and substratum were deposited at the Diatom Collection of the Natural History Museum, London (BM), and the Diatom Collection of the Botanical Garden and Botanical Museum of the Freie University of Berlin (B), Germany. Measurements from 55 different specimens representing the size-diminution series were taken to obtain ranges and averages of the morphological and ultrastructural features.

2.3. Data Processing and Statistical Analysis

The eight primarly databases that were used to find out the main *Navicula* species, and their ecological preferences that occur in mountain springs of southern central Europe were as follows: CRENODAT (110 springs): 'Biodiversity assessment and integrity evaluation of springs of Trentino—Italian Alps—and long-term ecological research (2004–2008) and 16 springs in the adjacent Dolomiti Bellunesi National Park (2004) [14,15]; EBERs; diatoms (sampled in 2022) from 15 springs selected in the Berchtesgaden National Park (Bavaria, Germany) to be sentinel environments of climate change (the paper [16] provides a description of the same dataset but based on samples taken in 2018); diatoms (sampled in 2022) from 14 springs selected in the Bavarian Forest (*Bayerischer Wald*) National Park (Bavaria, Germany) to be sentinel environments of climate change (twin project to the previous one, M.C. unpublished data); application of the standard methodology developed in the previous project to other protected areas of southern Germany: Rhön UNESCO Biosphere Reserve (nine springs) and Steigerwald Nature Park (six springs) [17], Fichtelgebirge Nature Park (six springs) and Spessart Nature Park (six springs) (M.C. unpublished data).

To study the environmental preferences of all the *Navicula* taxa, we computed the weighted averages using the *WA* function in the *vegan* package in R. The technique calculates the average value of an environmental variable weighted by the relative abundance of the species. By leveraging the species' abundance data, the weighted average approach allows us to infer the optimal conditions for species based on their distribution across different sites.

3. Results

Division: Bacillariophyta.
Class: Bacillariophyceae Haeckel, 1878 (emend. D.G. Mann, in Round et al., 1990 [18]).
Subclass: Bacillariophycidae D.G. Mann, in Round et al. [18].
Order: Bacillariales D.G. Mann, in Round et al., 1990 [18].
Family: Bacillariaceae Kütz. 1844.
Genus: *Navicula* Bory de Saint-Vincent, 1822.

Navicula aquaesuavis **Lange-Bert., Levkov, Cid-Rodríguez, A.A. Saber and Cantonati sp. nov.**

Description: LM (Figure 1): Valves lanceolate, ends shortly protracted, subrostrate. Length 14–26 µm, breadth 5.0–6.5 µm. The average length is 18.7 µm with a standard deviation of 2.2 µm, and the average width is 6.0 µm with a standard deviation of 0.3 µm. Raphe filiform with distinct central pores appearing indistinctly or not deflected. The axial area is narrowly linear but somewhat expanded proximally. The central area is moderately large, variable in shape, and mostly of an approximately rhombical shape. Striae radial and slightly arcuate up to the strongly developed Voigt discontinuity, becoming straight and less radial, then parallel, and finally convergent near the apices, 13 in 10 µm. Striae at the central area do not regularly alternate shorter/longer, but one or two shorter ones may be intercalated irregularly. Areolae discernible at least with oblique lighting, 30–40 in 10 µm.

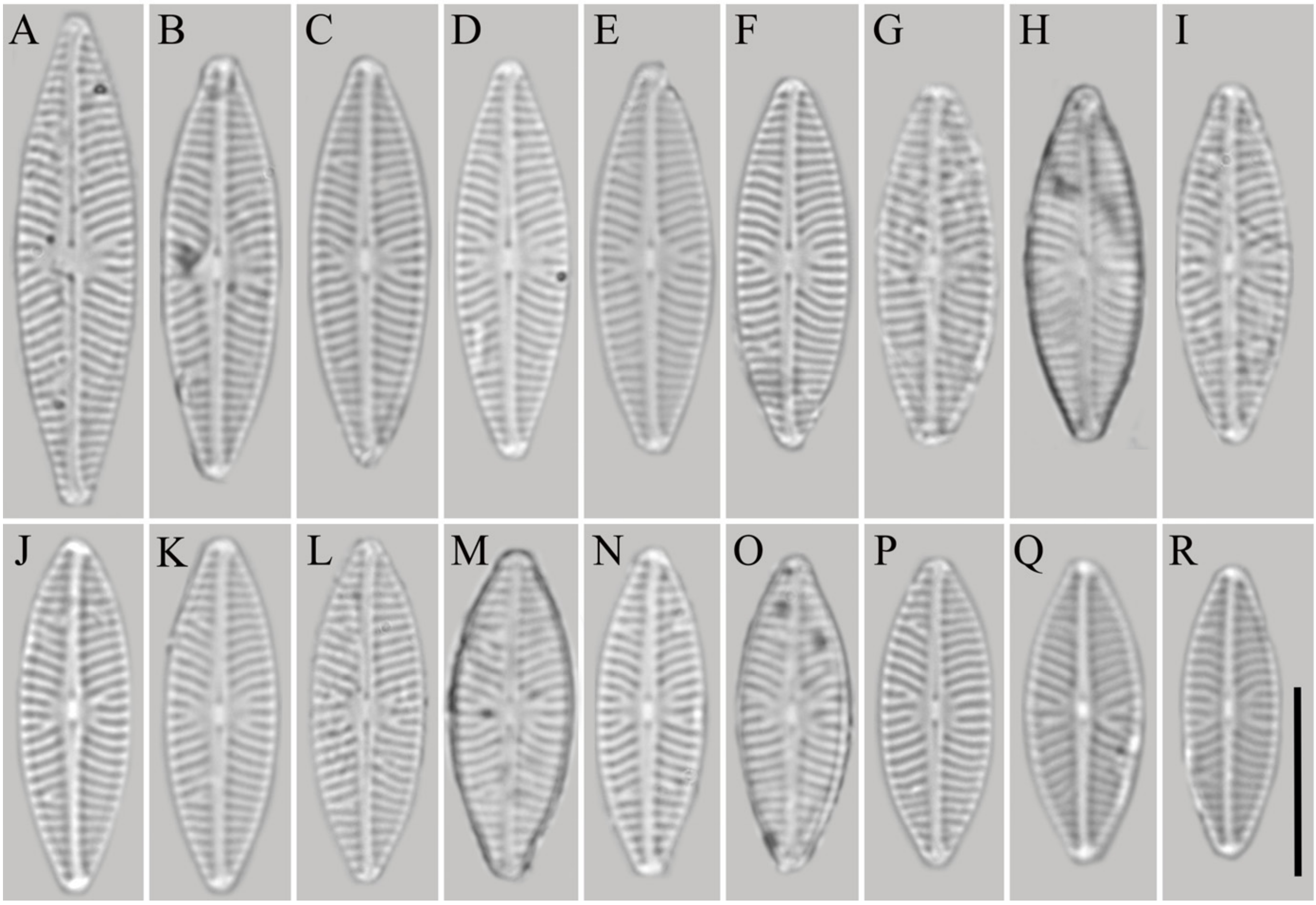

Figure 1. (**A**–**R**) Type material of *Navicula aquaesuavis* sp. nov. from a spring in the Apennines, Italy. LM micrographs of valves showing the size diminution series. Scale bar = 10 µm.

SEM external view, see Figure 2A,B. The raphe sternum with extended central nodule relief-like elevated above the smooth valve face, just even in slightly oblique view (black arrow). The asymmetry of the central area and nodule, respectively, is scarcely developed. Raphe branches are gently curved. The drop-shaped central pores are slightly deflected to the primary side of the valve, opposite to the distal endings and Voigt fault. This feature occurs in most specimens but is sometimes not clearly marked. Terminal raphe fissures commonly form a complicated double curve, never being simply fish-hook-shaped (white arrow). Voigt discordances are commonly marked by a gap in the stria pattern or by a reduced series of less and shortened lineolae.

SEM internal view, see Figure 2C. The fine structure pattern conforms to the large majority of comparable *Navicula* s. str. Species, and therefore does not provide exclusive characters that might be useful for identification. The raphe slits are twisted in the narrow internal raphe sternum, with free central ends lying in a distinct apically elongated nodule (white arrow), and distal ends in small helictoglossae (black arrow) that are more or less circular to shortly elliptical areolae, which are occluded by hymens lying in troughs between rather equally broad virgae.

Holotype: 31 July 2011, M. Cantonati s.n. (holo-: TR, slide cLIM007 DIAT 1984, partly shown here in Figures 1 and 2A–C (holotype specimen: Figure 1P).

Isotypes: B, slide B 40 0045802, cleaned material B 40 0045803, raw material B 40 0045804; BM; slide BM 92453.

Registration—http://phycobank.org/104897.

Type locality: Rheocrenic mountain spring *Fontana del Vescovo*, Italy, Northern Apennines, Province of Parma, Municipality of Corniglio in the Upper Parma Valley, lithology: Siliciclastic sandstones (44°22′44.767″ N, 10°2′26.790″ E, 1613 m a.s.l.).

Etymology: The Latin epithet *aquae suavis* is the genitive of "soft water" in free translation and refers to the water quality of the habitat.

Synonymy: To exclude from synonymy: *Navicula reichardtiana* var. *crassa* Lange-Bert. and Hofmann [19].

Distribution: *Navicula aquaesuavis* sp. nov. was found only in two sites: the type locality of *Fontana del Vescovo* in northern Italy and Lake Bogovinsko (the population found at this site is illustrated in Figures 3 and 4) in Northern Macedonia (see Section 2.1 Study area for their environmental characteristics). At the type locality, the new species was found, though with very low numbers of specimens (<0.25% = not counted), both in the epilithon and in the epibryon, but was more abundant in the latter.

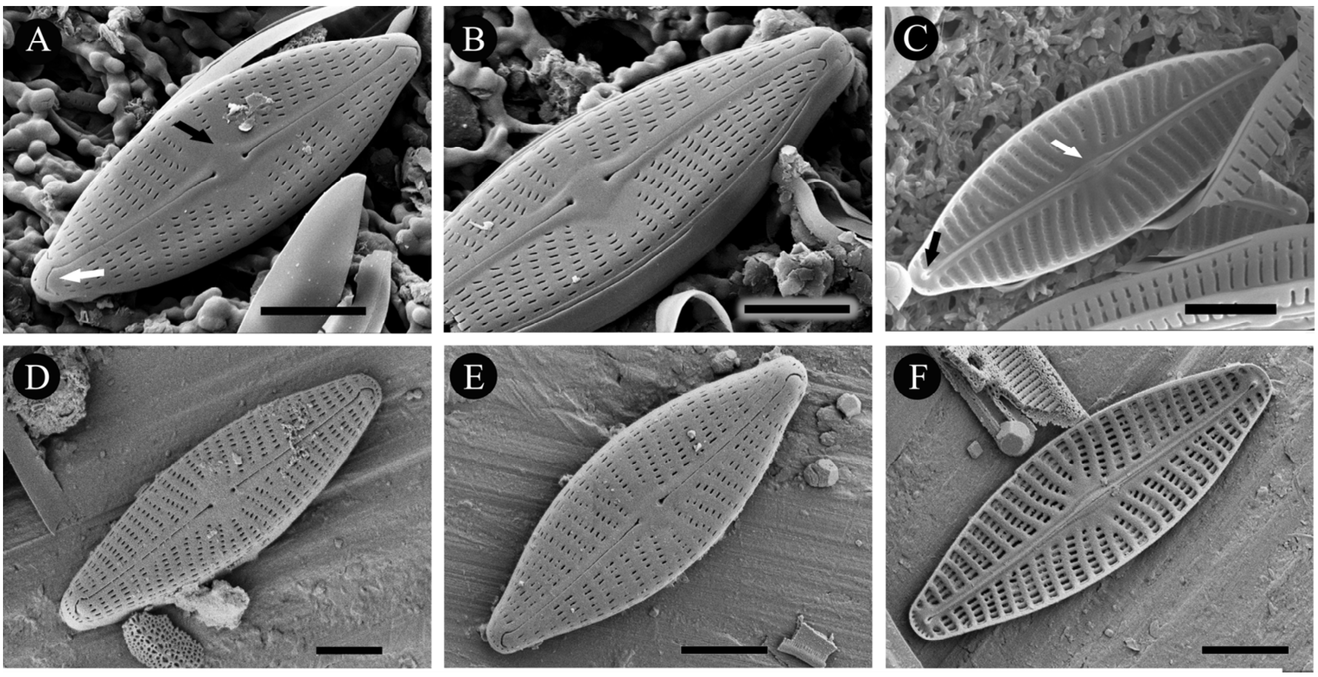

Figure 2. (**A**–**C**) SEM micrographs of *Navicula aquaesuavis* sp. nov.; (**D**–**F**) SEM micrographs of *Navicula metareichardtiana* shown for comparison. (**A**,**B**,**D**,**E**) outside view. Black arrow: central nodule. White arrow: distal raphe endings; (**C**,**F**) inside view. Black arrow: distal raphe endings terminate in a helictoglossa. White arrow: central ends lying in an elongated nodule. Scale bars = 4 µm.

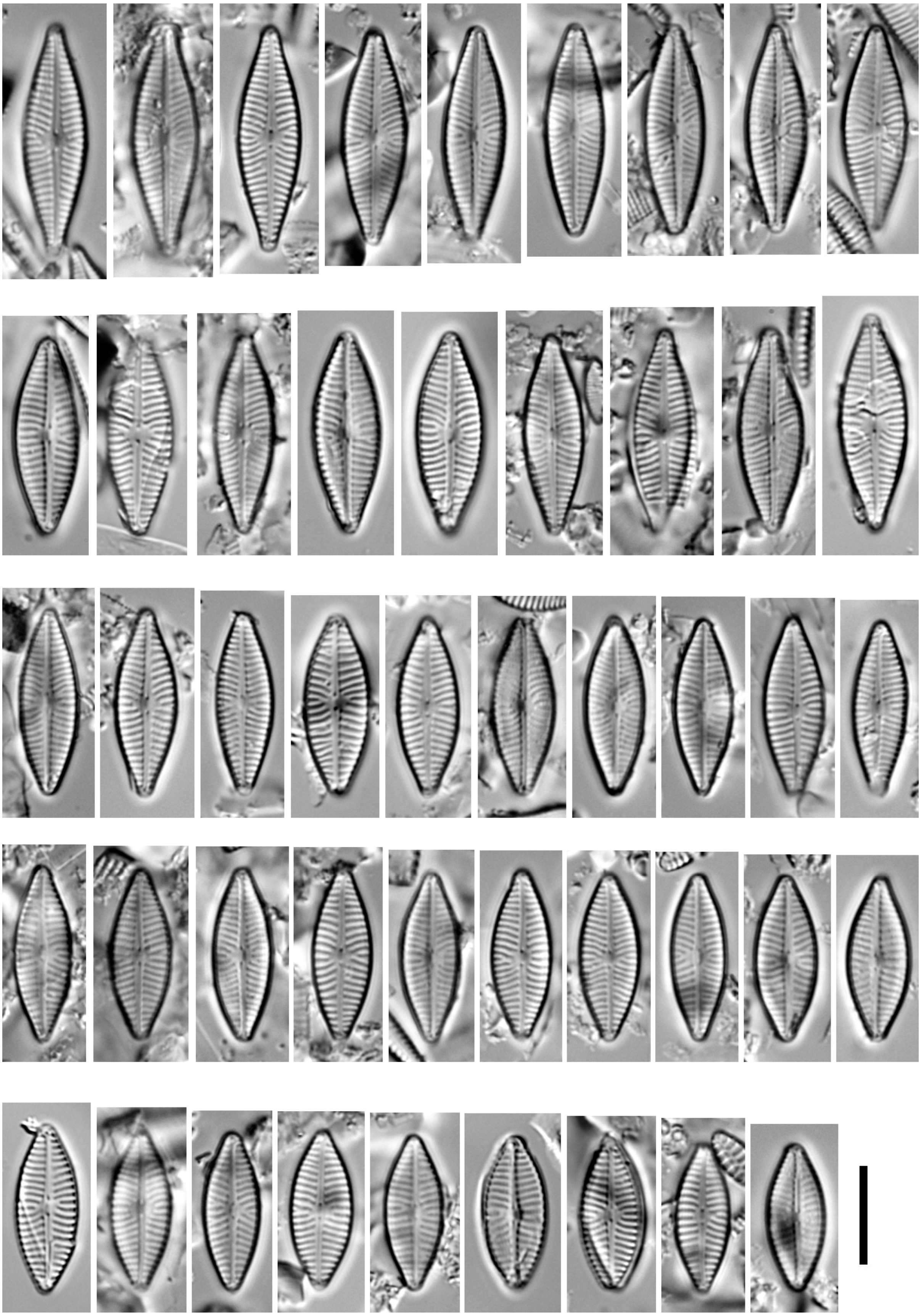

Figure 3. LM micrographs of *Navicula aquaesuavis* from Lake Bogovinsko on Shara Mountain, North Macedonia. Scale bar = 10 µm.

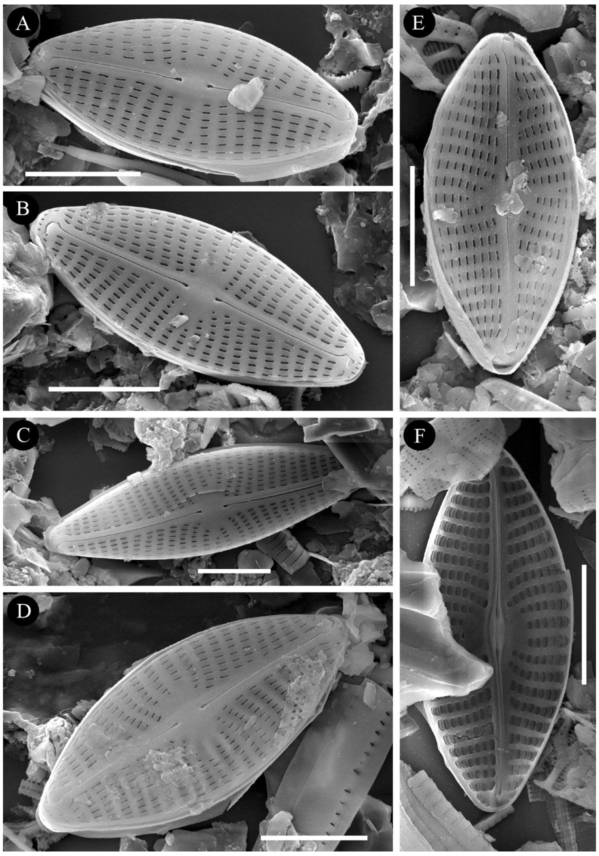

Figure 4. (**A**–**F**) SEM micrographs of *Navicula aquaesuavis* from Lake Bogovinsko on Shara Mountain, North Macedonia. Scale bars = 2 µm.

Co-occurring diatom species and ecology

Fontana del Vescovo: Associated diatom species were *Achnanthidium minutissimum* (Kütz.) Czarn., *A. lineare* W.Smith, *Planothidium lanceolatum* (Bréb. ex Kütz.) Lange-Bert., *Amphora indistincta* Levkov, *A. inariensis* Krammer, *Navicula exilis* Kütz., and *Odontidium mesodon* (Kütz.) Kütz.

Lake Bogovinsko: *Cymbella neocistula* Krammer, *Cymbopleura macedonica* Levkov & Krstic, *Diploneis mollenhaueri* Lange-Bert. and Fuhrmann, *Navicula oligotraphenta* Lange-Bert. & G.Hofm., *Placoneis opportuna* (Hustedt) Chudaev and Gololobova, *Platessa ziegleri* (Lange-Bert.) Lange-Bert., *Pseudostaurosira pseudoconstruens* (Marciniak) D.M. Williams and Round, *Sellaphora utermoehlii* (Hustedt) C.E.Wetzel and D.G.Mann, *Planothidium joursacense* (Héribaud-Joseph) Lange-Bert., *Staurosira construens* (Ehrenb.) D.M.Williams and Round, *Staurosira neoproducta* (Lange-Bert.) Chudaev and Gololobova, *Staurosira sviridae* Kulikovskiy, Genkal smf Mikheyeva and several unidentified fragilaroid species.

From the environmental assessments at the two verified sites where the new species occurs, from physical and chemical measurements and analyses at the type locality, and from the autecological preferences of the co-occurring diatom species, the new species appears to be typical of oligotrophic, mountain inland waters, with good light conditions and relatively low-conductivity but well-buffered waters.

3.1. The Ecological Preferences of the Main Navicula Species in Mountain Springs of Southern Central Europe as Represented in Own Selected Databases

Nine species were found to be relevant in the epibryon with the set criteria (Table 1), whilst six were important in the epilithon (Table 2). Of these, six were in common, and three were relevant in the epibryon only: *Navicula dealpina*, *N. lundii*, and *N. moenofranconica*.

Table 1. List of *Navicula* species selected with >three records and >1.2% max abundance with their weighted averages in the epibryon. In bold are species that were relevant only in the epibryon.

Navicula Species	Elevation [m a.s.l.]	T [°C]	Discharge [L s^{-1}]	pH	Conductivity [μS cm^{-1}]	N-NO_3^- [μg L^{-1}]	SO_4^{2-}	Cl^-	Ca^{2+}	Mg^{2+}	Na^+	K^+
N. antonii	1247	7.5	4.3	7.7	1095	0.6	603.5	2.8	233.5	44.1	3.6	1.4
N. cryptocephala	712	6.9	68.6	7.7	192	0.4	4.4	1.2	29.2	6.5	1.1	0.4
N. cryptotenella	669	8.9	3.6	7.9	268	0.6	3.5	0.8	42.7	12.0	0.5	0.3
N. dealpina	625	9.9	0.9	7.7	358	1.3	11.4	8.8	61.0	12.9	5.0	1.5
N. exilis	893	7.4	32.0	6.5	86	0.7	6.6	4.7	9.0	1.2	3.2	1.0
N. leistikowii	1435	5.5	8.3	7.8	181	0.5	5.7	0.7	31.6	6.1	1.1	0.4
N. lundii	1542	5.5	8.2	6.7	48	0.3	11.9	0.4	15.7	5.4	1.0	0.6
N. moenofranconica	719	8.1	1.4	7.8	394	1.0	11.0	16.4	62.4	10.4	8.8	1.0
N. tripunctata	464	9.7	1.6	7.8	282	1.0	10.5	1.7	41.7	12.7	1.4	0.5

Table 2. List of *Navicula* species selected with >three records and >1.2% max abundance with their weighted averages in the epilithon.

Navicula Species	Elevation [m a.s.l.]	T [°C]	Discharge [L s^{-1}]	pH	Conductivity [μS cm^{-1}]	N-NO_3^- [μg L^{-1}]	SO_4^{2-}	Cl^-	Ca^{2+}	Mg^{2+}	Na^+	K^+
N. antonii	809	8.4	0	7.6	564	2.0	70.8	4.9	83.3	21.5	3.2	0.9
N. cryptocephala	686	6.5	119	7.9	179	0.3	1.9	0.5	32.6	5.9	0.2	0.2
N. cryptotenella	449	9.6	5	7.6	316	1.1	6.7	2.8	66.6	4.4	2.0	0.6
N. exilis	899	7.7	104	6.6	109	0.7	4.1	5.8	10.6	1.8	2.3	0.9
N. leistikowii	685	9.0	7	7.9	268	0.3	1.7	0.5	44.8	11.6	0.3	0.3
N. tripunctata	422	10.3	1	7.5	699	2.8	35.1	4.9	60.5	24.6	5.0	2.3

Considering all records, i.e., both epibryon and epilithon, the two species with the highest numbers of occurrences were *Navicula exilis* and *N. cryptotenella*, with 33 and 32 records, respectively, and the two with the highest relative abundances were *N. cryptocephala* (64%) and *N. cryptotenella* (16%).

3.2. The Genus Navicula in Spring Ecosystems as Represented in the Global Literature

The global literature on the diatom genus *Navicula* in spring ecosystems is still scarce. Papers from our review related to springs as habitats (global literature) were integrated with 2–3 books on the topic and by specifically searching the Web of Science for *Navicula* in springs. These efforts, combined with the articles on arid land springs cited below, hardly yielded twenty papers relevant to the topic.

In typically oligotrophic and often fast-flowing mountain springs, *Navicula* is not a prominent diatom genus. The only indicator species found by Cantonati et al. [15] working on spring types of the Alps was *Navicula exilis* for 'well-buffered siliceous rheocrenes'.

Many of the mountain springs in North Macedonia are under hydromorphological pressures since the water is used for human consumption [20]. Several *Navicula* appear frequently and abundantly in alkaline springs: *N. hintzii* Lange-Bert., *N. exilis* Kütz., and *N. moenofranconica* Lange-Bert. In circumneutral springs, *N. radiosa* Kütz. and *N. metareichardtiana* Lange-Bert. and Kusber are most commonly found, while the diversity of *Navicula* species is the lowest in slightly acidic springs (*N. angusta* and *N. heimansioides* Lange-Bert.). In a few cases, rare species, such as *N. umida* Bock and *N. odiosa* Wallace, have been recorded from mountain springs. All species observed in mountain springs are typically oligotrophentic and sensitive to pollution, except *N. cryptotenella*, which might tolerate moderate pollution levels and eutrophication. A few *Navicula* species might be found in temporary springs or subaerial habitats (*N. lundii* Reichardt). The highest species diversity has been noticed in helocrenic springs where various microhabitats are present (humic substrate, sand and silt, and bryophytes), enabling varied diatom communities where different ecological traits can find their place. In general, *Navicula* species, being motile, prefer springs with low and permanent currents, while they are extremely rare in rheocrenes with fast flow or temporary springs. Such ecological preferences of *Navicula* species make them quite vulnerable to climate change. A decrease in precipitation (15–20% annually), especially in the quantity of snow during the winter and draughts during the summer, might change the water regime of springs, thus strongly influencing species distribution.

Navicula is one of the most numerous genera of diatoms present in the areas with low-elevation springs in Central [3] and Southern [21] Poland. *N. cincta* inhabit waters with a broad range of nitrate concentrations and high levels of calcium, magnesium, potassium, sodium, and moderate dissolved oxygen [21]. *N. striolata*, listed as endangered in the Polish Red List of Algae [3,22], has the narrowest range of environmental variables. It is primarily found in sandy-bottomed springs with limestone bases and moderate magnesium and sodium concentrations while also tolerating a broad range of nitrate levels and showing tolerance to some increased content of nitrate [3]. This species, classified as alkalibiontic taxon by Van Dam et al. [23], also occurs in calcareous springs in the Brenta Dolomites [24]. Werum [25]. *Navicula angusta* Grunow was found in less polluted springs with low conductivity, nitrate content, alkalinity, calcium concentration, and high dissolved oxygen. *Navicula reinhardtii*, common in rheocrenes with higher discharge, is found in slightly alkaline waters and is positively influenced by sodium, chloride, and pH levels. The occurrence of species like *N. cryptocephala* Kütz., *N. cryptotenella* Lange-Bert., *N. radiosa* Kütz., *N. reichardtiana* Lange-Bert. (currently *Navicula metareichardtiana*) is promoted by human impacts. These species were all recorded in calcium-rich springs with moderate–high specific conductivity. *N. metareichardtiana* was observed in the Krakowsko-Częstochowska Upland in lightly alkaline, highly alkaline and moderate–very high chlorides and high–very high nitrate concentrations [3].

Navicula gregaria Donkin, a very high-nutrient taxon, is observed in calcium-rich waters with moderate–high specific conductivity and is positively influenced by sodium and chloride ion concentrations. *N. antonii* is common in alkaline waters with a broad range of specific conductivity, calcium, and nitrate concentrations, which are most prevalent in waters with high nitrate levels. This species is affected positively by potassium and nitrate ion concentrations and redox potential but negatively by silica concentration. These last two species are indicators of increased trophic status in springs of Southern Poland [3]. *Navicula aquaedurae*, *N. catalanogermanica* Lange-Bert. and G.Hofm., *N. cataracta-rheni* Lange-Bert., and *N. moenofranconica* Lange-Bert. are all vulnerable/rare diatom taxa in Poland. The occurrence of *N. moenofranconica* was negatively influenced by sodium, nitrate, and phosphate ion concentrations and redox potential. *N. veneta* Kütz., and *N. wiesneri* Pant. are rare taxa found in sulphide springs with slightly alkaline waters [3].

The genus *Navicula* can also occur and even be prevalent in some special kinds of springs, such as naturally radioactive mineral springs, where Baker et al. [26] found *Navicula sanctamargaritae* to be one of the dominant amplicon sequence variants (ASV). Beauger et al. [27] found *Navicula sanctamargaritae* to be also associated with the highest potassium concentration in mineral saline springs in the French Massif Central.

Our knowledge of the diversity of species of the genus *Navicula* in arid and semi-arid springs is still limited. In South America, Angel et al. [28] studied the diatom inventory in the high-altitude arid and semi-arid thermal springs in the El Tatio geothermal field (Altiplano, Chile), one of the least known major geothermal systems in the southern hemisphere, and pinpointed that the water conductivity of these springs varied from 4860 to 12,150 $\mu S \cdot cm^{-1}$, except for the freshwater fumarole spring where conductivity showed the lowest range from 440 to 810 $\mu S \cdot cm^{-1}$. *Navicula cincta*, *N. cryptocephala*, *N. cryptotenella*, *N. lauca* U.Rumrich and Lange-Bert., *N. microdigitoradiata* Lange-Bert., *N. parinacota* U.Rumrich and Lange-Bert., *N. pseudogracilis* Hust., *N. salinicola* Hust., *N. tripunctata* (O.F.Müller) Bory, *N. veneta*, and *N. viridula* (Kütz.) Ehrenb. were recorded. *N. salinicola* was the most common diatom species in these springs, reflecting its tolerance to the water chemistry of these saline groundwater-dependent systems.

Very little is known about diatoms from the arid and semiarid springs in the Middle East countries. Springs in this hot and dry region of the world are common and the main water supply for local populations. In Saudi Arabia, Abdelwahab and Amin [29], for instance, studied the diatom diversity of the arid mineral-rich hot springs (temp.: up to

60 °C and T.D.S.: up to 4000 mg L^{-1}) in the southwest region and identified 23 different diatom taxa. Both *N. cincta* and *N. radiosa* were among the dominant diatom taxa in these springs. In northern Israel, Barinova and Romanov [30] also only recorded *N. recens* and *N. rhynchocephala* in the ambient freshwater spring 'Ein El Balad' located on the northern slope of the Mount Carmel, confirming the rare occurrence of species of the genus *Navicula* in the arid and semiarid springs of this region. Similarly, Gerloff et al. [31], on their preliminary list of diatoms from Jordan, only reported *N. veneta*, *N. rhynchocephala* var. *amphiceros* (currently regarded as *N. rhynchotella*), and *N. radiosa* var. *tenella* in the nutrient-rich freshwater springs studied. In Iran, very little attention has also been given to the diatom assemblages in the spring ecosystems. In their study on the hydrochemistry and diatom diversity in three arid springs in NE Iran, Mirzahasanlou et al. [32] stressed that the springs' diatom assemblages are mainly shaped by the size and morphology of the springs. *Navicula broetzii* Lange-Bert., E.Reichardt, *N. capitatoradiata*, *N. cryptotenella*, *N. rostellata* Kütz, *N. trivialis* Lange-Bert. and *N. tripunctata*. These *Navicula* species are widely distributed, have a wide range of tolerance to pollution, and usually prefer eutrophic waters. Both *N. cryptotenella* and *N. rostellata* were among the most abundant diatom species in the springs studied.

In Africa, Coste et al. [33], for instance, studied the diatom assemblages from three thermal springs in the semi-arid Merguellil Wadi located in Central Tunisia and found a few taxa of the genus *Navicula*, mostly with low relative abundances, including *N. recens* (Lange-Bert.) Lange-Bert., *N. radiosa*, *N. rostellata*, and *N. veneta*. Ecologically, the latter diatom species was classified as N-heterotrophic, with a low water quality signature.

Our understanding of the diversity and distribution of the genus Navicula in the arid springs of the largest oasis in the world, Egypt, is still limited. All the previous studies on the Egyptian Navicula species mostly depended on light microscopical observations, using complex taxonomic and nomenclatural history in species identification. In this sense, the real picture of the diversity and distribution of the genus Navicula in Egypt, especially in the spring habitats, is still unconfirmed, and thus, more in-depth taxonomic studies are still needed using modern diatom taxonomy standards. Shaaban [34], Hamed [35], and Saleh [36] are among the reliable taxonomic literature available as an aid for the identification of the Egyptian diatoms, including the Navicula species, but the nomenclatural system applied is nowadays obsolete, overlooking the interesting and small-sized species. For instance, Shaaban and Hamed [37] studied the diatom diversity of the euthermal mineral-rich spring 'Ain El-Sokhna', located on the western side of the Suez Gulf, and identified thirty-six different diatom species, out of them N. disjuncta Hust. (currently known as Myriactula pulvinata (Kütz.) Kuntze), N. erifuga Lange-Bert., N. leptostriata E.G.Jørg., N. stankovicii Hust., and N. tenelloides Hust. In the Egyptian desert springs, the occurrence of Navicula species has rarely been observed. For example, N. erifuga was only reported in the inventory of diatoms of Ain Kidies and Ain El-Godyrate at El-Arish Valley in North Sinai, Egypt [38]. The same observations were documented by Shaaban [39] in an investigation of the desert thermal mineral springs of the Siwa Oasis (the Western Desert of Egypt), where he only recorded N. menisculus Schum. and N. radiosa. The same findings were recently confirmed by Saber (unpublished data). Similarly, N. cryptocephala and N. heufleri var. leptocephala (Bréb. ex Grunow) H.Perag. and Perag. (currently known as N. erifuga) were only documented in three thermal and hot springs of the El-Bahariya Oasis. Hamed [35] summarized the geographical distribution of the Egyptian diatoms in different aquatic habitats, including thermal and hot arid springs, and reported eight taxonomically accepted Navicula species in all the springs, including N. cincta, N. cryptocephala, N. erifuga, N. halophila var. leptocephala (currently considered a synonym of N. erifuga Lange-Bert.), N. leptostriata, N. stankovicii, N. tenelloides, and N. veneta. In our recent taxonomic and ecological investigation on diatoms of El-Farafra Oasis springs and drilled wells, the most common Navicula species identified were N. cf. arctotenelloides, N. cryptocephala, N. cryptotenelloides, N. rhynchocephala, N. tenelloides, and N. veneta (Saber and Cantonati, unpublished data) (Figure 5). In general, the most common and distributed Navicula species in the Egyptian arid springs and their counterpart artificial habitats, 'drilled wells', are N. cryptocephala and N. veneta ([34–36,40]; A.A. Saber, unpublished data). These Navicula species usually colonize the freshwater mineral springs and could tolerate increased nutrient (N and P) concentrations (meso- to eutraphentic species), reflecting different human impacts on the springs they colonize.

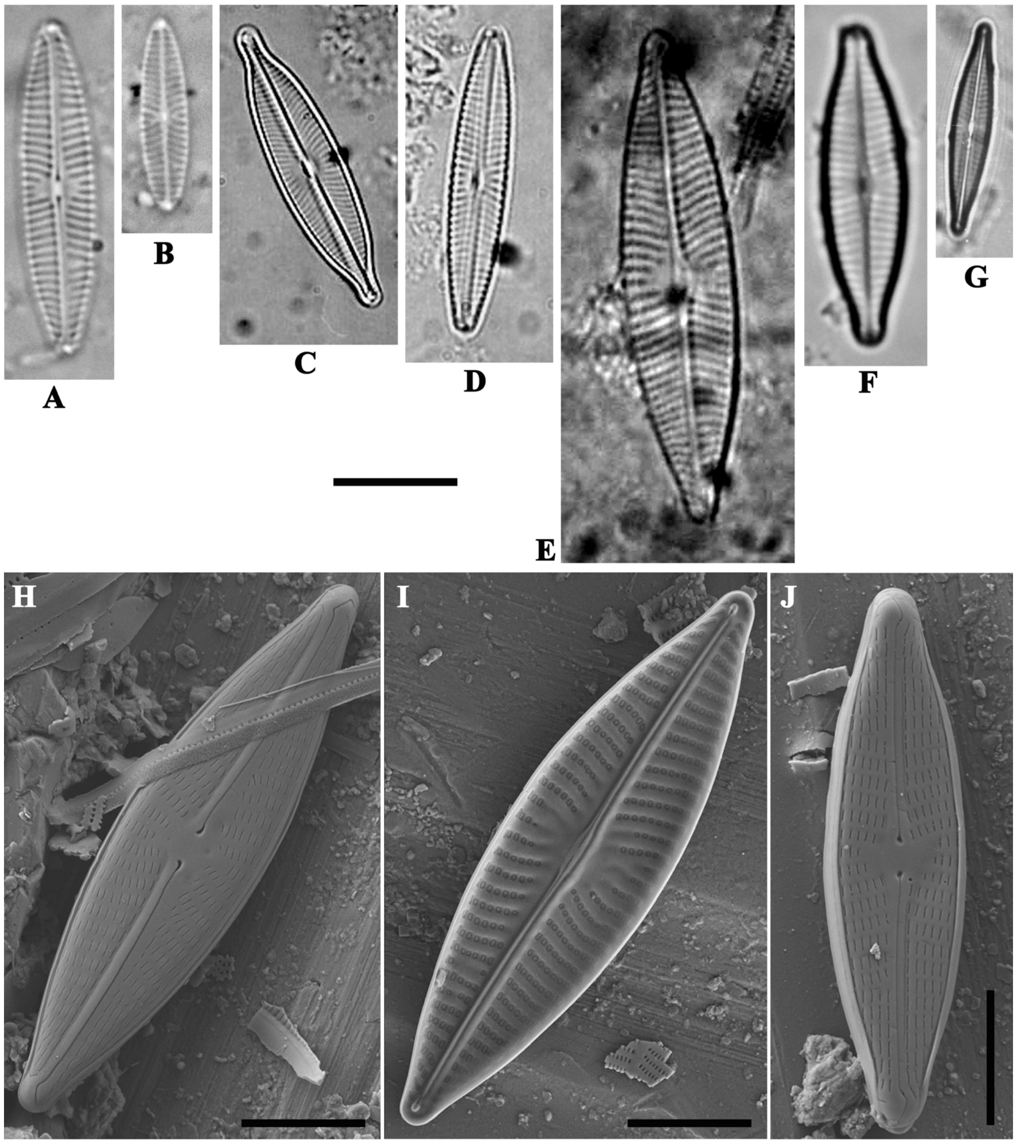

Figure 5. Light and SEM micrographs of the most common *Navicula* species inhabiting the Egyptian springs and drilled wells. (**A**) *Navicula* cf. *arctotenelloides* from a thermal freshwater drilled well known as 'Bir Sitta' in El-Farafra Oasis. (**B**) *N. cryptotenelloides* from a slightly hot freshwater drilled well known as 'Bir 1B' at Abu Minqar village in El-Farafra Oasis. (**C**) *N. cryptocephala* from a freshwater spring in the Bahariya Oasis. (**D**) *N. erifuga* from the thermal mineral-rich spring 'Hammam Musa'. (**E**) *N. rhynchocephala* from the rheocrenic, slightly hot freshwater spring 'Ain El-Balad' in the El-Farafra Oasis. (**F**) *N. tenelloides* from a slightly hot freshwater drilled well known as 'Bir 3A' at Esha Abd El-Rahman village in the El-Farafra Oasis. (**G**) *N. veneta* from the rheocrenic thermal mineral-rich spring 'Ain Helwan', south of Cairo, Egypt. (**H**,**I**) External and internal valve views of *N. cryptocephala* at 'Bir Sitta' in El-Farafra Oasis. (**J**) External valve of an entire valve of *N. veneta* at 'Bir Sitta' in El-Farafra Oasis. All the micrographs were taken from diatom specimens collected in 2015 from the El-Farafra Oasis (the Western Desert of Egypt), except Figures (**C**,**D**,**G**), which were obtained after Hamed [35]. Scale bars: LM = 10 µm; SEM = 5 µm.

4. Discussion

The newly described species superficially resembles the allied *Navicula* species listed in the following, in particular *N. metareichardtiana*, but still can be separated by combinations of morphological (and ecological) characters.

Navicula metareichardtiana is commonly recorded from eutrophic, beta-meso-saprobic, alkaline waters. As the most resembling species, it differs mainly by the following morphological characteristics: Valves moderately narrower on average, 5.0–5.5, rarely up to 6.0 (vs. 5.5–6.5) µm; stria density higher on average, 14–16 (vs. 13–15) in 10 µm; areola density higher on average, 35–40 in 10 µm, difficult to discern in LM (vs. 30–35) in 10 µm. The central area is not extended and is approximately rhombical but is smaller. Under the SEM external views, the central nodule and other proximal parts of the sternum do not appear relief-like elevated at any angle of view (by tilting). The slits (areolae, foramina, and lineolae) are apically longer and the alternating virgae and, therefore, narrower than in *N. acquaesuavis.*

Navicula caterva Hohn and Hellerman exists in alkaline, euthrophic waters with medium–high electrolyte content, differing by valve breadth commonly lower than 5 µm and a higher stria and areola density, 18–21 and ca. 40 in 10 µm, respectively. The central area is conspicuously smaller.

Navicula associata Lange-Bert. is distinguished by almost elliptical valves and longer rostrate protracted ends. In SEM, proximal raphe ends clearly deflected to the secondary valve side; striae more radiated proximally; the lineolae were therefore arranged notably concentrically around the central area; central pores were elongated apically. This species is ecologically adapted to eutrophic alkaline lakes and lake outflows with medium to higher conductivity.

Navicula reichardtiana var. *crassa* Lange-Bert. and Hofmann is clearly different and separated from the newly described species both morphologically and ecologically. *Navicula reichardtiana* var. *crassa*, as the variety epithet suggests, is broader than *Navicula metareichardtiana*, whilst *Navicula aquaesuavis* sp. nov. is narrower (see above). *Navicula reichardtiana* var. *crassa*, was described from a eutrophic lake (Waginger See) with much higher nitrate contents as compared to the sites from which the newly described species is known [19].

Overall, the statistical analysis of the ecological optima of the main *Navicula* species in springs of southern central Europe confirms that the epilithon is more suitable for discussing relationships between diatom species and water-quality variables because the epibryon represents a particular, partly buffered, microenvironment. In this way, in our data, nitrates confirm *Navicula antonii* and *N. tripunctata* as classical eutraphentic species in the epilithon only. Contrastingly, our analyses focused on *Navicula* in spring ecosystems confirm the epibryon to be the substratum hosting the most diverse associations, also including rare and Red List species. Out of the three species that were relevant in the epibryon only in our databases, two are in high-threat categories of the Red List [41]: *Navicula dealpina* (threat category "2") and *N. moenofranconica* (t.c. "3"). All of the three *Navicula* species (*N. cryptocephala*, *N. cryptotenella*, *N. exilis*) most frequent and abundant in our spring databases are included in the list of terrestrial species of Foets et al. [42], highlighting once more that many springs with small discharge are deeply influenced by the effects of discharge fluctuations and desiccation episodes (e.g., ref. [17]).

The results of the study of the ecological preferences of *Navicula* species in the mountain springs of southern central Europe are also in good agreement with the picture emerging from our synthesis of the global literature on the diatom genus *Navicula* in spring habitats. The focus on the poorly known diatom assemblages of arid land springs appears to suggest that common species that are typical eutraphentic elements in central Europe (e.g., *N. cryptotenelloides*, *N. erifuga*, and *N. veneta*) might be widespread representatives of diatom assemblages of not necessarily polluted desert springs and wells. However, due to important human impacts on almost all oasis springs in North Africa, more in-depth and focused studies are needed to clarify this point.

Springs are unique but fragile habitats that need to be known as natural biota refugia and sites where the potential of diatoms as indicators particularly unfolds and to be protected because they increasingly face the insults of exploitation and climate change globally [1]. Our study of the species diversity and ecological preferences of diatoms of the genus *Navicula* in spring ecosystems, also including the description of a new species, is a small but significant contribution to filling the gap of knowledge on this genus in springs, which is important to achieve a correct knowledge of the taxonomy and ecological preferences of the species occurring in near-natural mountain (low conductivity) freshwater ecosystems to use diatoms as reliable indicators of environmental and climate change (e.g., ref. [10]).

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