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Floristics and Biogeographical Affinity of Diatoms Attached to *Sargassum fluitans* (Børgesen) Børgesen and *Sargassum natans* (Linnaeus) Gaillon Arriving on Mexico's Caribbean Coasts

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Abstract: The environmental contingency caused by the recent massive arrivals of pelagic sargasso (*Sargassum natans* and *S. fluitans*) on Mexico's Caribbean coasts have given rise to several areas of scientific research. Our work proposed identifying the diatom flora adhered to the thalli of these two sargasso species collected on the coasts of Cancun, Isla Mujeres, and Puerto Morelos. We recorded 184 diatom taxa (all illustrated) from 68 genera. Taxa from the genera *Mastogloia* (37), *Cocconeis* (11), *Nitzschia* (10), *Diploneis* (8), and *Amphora* (9) represented 41% of the total, while 44 of these genera were represented by a single species. In the total floristic count, 41 taxa occurred exclusively on *S. fluitans*, 53 exclusively on *S. natans* (22 and 29%, respectively) and 90 (49%) were found on both. Species of *Navicula* were scarce, and *Navicula barbara* var. *densestriata* was here transferred to the genus *Lyrella* (*Lyrella barbara* var. *densestriata* (Foged) López-Fuerte & Siqueiros Beltrones comb. nov.). Overall, 17 (9%) of the identified taxa were new recordings for Mexico's coasts. Supporting the hypothesis proposed, the 37 *Mastogloia* taxa suggested a tropical affinity, while the high species richness denoted that the surfaces of both sargasso species constituted favorable substrata for the growth of diatom assemblages.

Keywords: Bacillariophyta; epiphytes; invasive species; new combination; new records

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1. Introduction

Historically, it has been observed that naturally occurring environmental variations bring physical and chemical changes that can cause radical modifications in the abundance and distribution of certain taxa. In addition, anthropogenic activities can cause disturbances that displace taxa to regions distant from their original environments where they may settle as invasive species [1]. The massive arrivals of the pelagic sargassos *Sargassum fluitans* (Børgesen) Børgesen and *Sargassum natans* (Linnaeus) Gaillon to the coasts of the Mexican Caribbean fall into this condition and category [2]. Although the original oceanographic distribution of these species is broad, extending from the Atlantic Ocean to the southern Asia Sea, studies have identified massive invasions in the North Equatorial Region (NERR) between the coasts of Africa and Brazil, where conditions (mainly temperature and nutrient concentrations) are adequate for their growth. That movement eventually brought them to the coasts of Mexico [3–6]. Finally, a possible sub-equatorial origin of these arrivals [7] unrelated to the Sargasso Sea is posited [8].

Floating ecosystems such as these rafts of *S. natans* and *S. fluitans* have diverse ecological properties, including a high taxonomic richness of the epibionts they harbor [2]

and serving as transport vessels that allow epibionts to potentially colonize distant habitats as exotic or invasive species. Diatoms stand out among these epibiont assemblages because macroalgae thalli exhibit especially high levels of diatom epiphytism [9,10], a mechanism for dispersal and colonizing habitats with favorable conditions for settlement and growth. Studies of epiphytic diatoms from *Sargassum* species are, however, scarce and outdated [11–14], especially in the case of *S. fluitans* and *S. natans*, for which there are only two published studies [15,16]. For these reasons, the aim of this work was to describe the floristic and biogeographical affinity of the diatom flora (epiphytes) attached to rafts of *S. fluitans* and *S. natans* that arrive at the coasts of the Mexican Caribbean. Based on the proposed origin of the floating masses of these sargassos (NERR) and the suggested tropical affinity of the dominant genera/species recorded earlier for the targeted diatom flora, we hypothesized that the diatom assemblages would also show a tropical affinity.

2. Materials and Methods

Thalli of *S. fluitans* and *S. natans* were collected 50 to 100 m offshore on the coasts of Quintana Roo, Mexico, in the Mexican Caribbean. The massive arrival of these sargasso species is linked to oceanographic dynamics, specifically the currents which determine that they first reach Isla Mujeres, with a significant number of thalli detaching and moving towards Punta Cancún until they affect the coasts near Isla Cozumel and Puerto Morelos [17]. The geographic locations of the sampling sites were Cancun (21°03′46″ N, 86°46′36″ W), Isla Mujeres (21°09′54″ N, 86°43′30″ W), and Puerto Morelos (20°51′12″ N, 86°52′18″ W) (Figure 1).

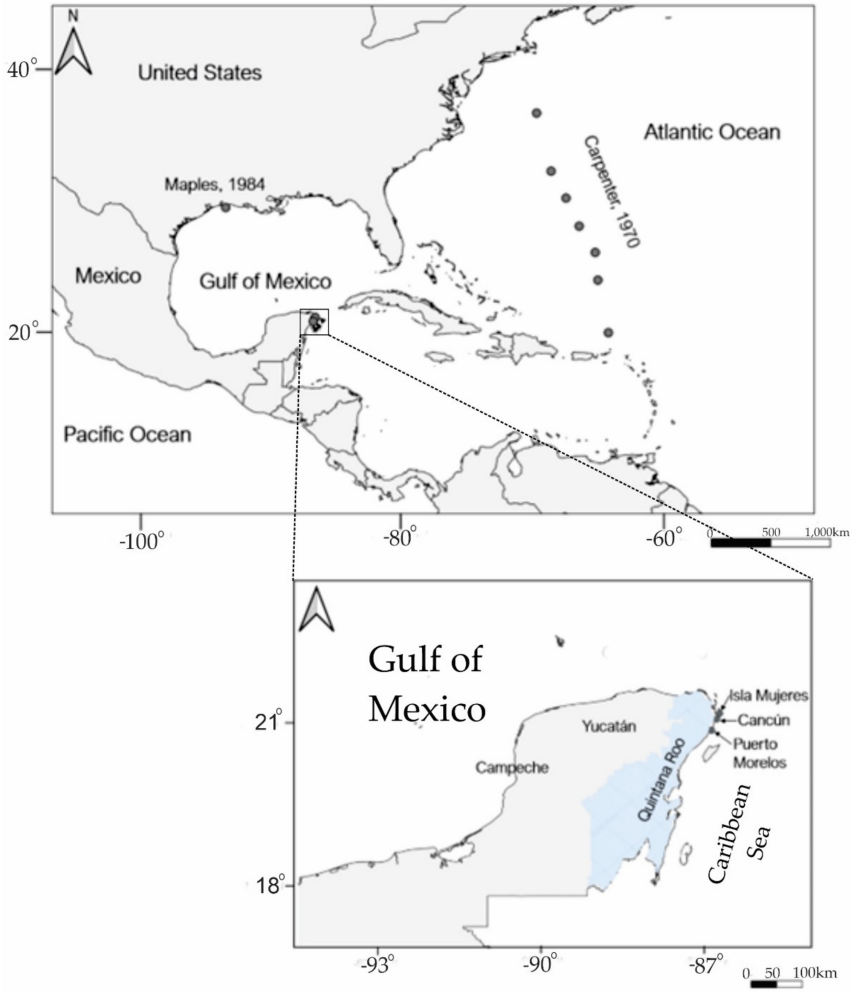

Figure 1. Location of sampling sites of *Sargassum fluitans* and *S. natans* on the Mexican's Caribbean coast and previous works.

During September, October, and November 2021, five thalli of *S. fluitans* and *S. natans* (each) were collected at Delfines beach, Cancún. Five others were gathered at Isla Mujeres and Puerto Morelos in October 2021 and January–February 2022. Specimens were still fresh and were inspected before processing. Species identification of the macroalgae was done following [18].

For the epiphytic diatoms, we selected one thallus of each sargasso species having ~200 phylloids and one with ~150–200, for *S. fluitans* and *S. natans*, respectively. The macroalgae thalli were rinsed with purified freshwater to wash-off loose organisms and other matter. The diatoms were then separated using a toothbrush and rinsed with 250 mL of purified water. The end product was collected in 16, 15 mL Falcon tubes and centrifuged for 5 min at 4000 rpm. The supernatant was decanted to concentrate the brushed-off material into 15 mL samples. From that concentrate, 3 mL aliquots were taken for oxidation treatment (frustule cleaning) of all organic matter using a mixture of nitric acid and commercial alcohol at a 3:1:1 ratio [10]. The remaining oxidized material was then rinsed by diluting repeatedly with purified water until reaching a pH $\geq$ 6. Using the cleaned samples of diatoms from each sargasso species, three permanent slides were mounted using the synthetic resins Zrax and Pleurax® (RI = 1.7) (made and distributed by Bill Daily, University of Pennsylvania, Philadelphia, USA).

The slides were inspected under a Zeiss Axio Lab-A1 (Zeiss, Germany) optical microscope with phase contrast illumination, equipped with a Canon EOS Mark II digital camera (Canon Inc., Tokyo, Japan). Taxonomic identification was carried out by frustule morphology following classic and regional literature as references, as well as recent articles [10,19–33]. The classification system in [34] was followed, and the systematic list was elaborated and updated according to two web platforms: www.algaebase.org (accessed on 23 June 2020) [35] and www.marinespecies.org (accessed on 23 June 2022) [36].

3. Results

Overall, 184 specific and infraspecific diatom taxa were identified for both *Sargassum* species. The taxa comprised 26 orders, 40 families, and 68 genera, of which 44 were represented by a single taxon. The genera with higher species richness were *Mastogloia* (37), *Cocconeis* (11), *Nitzschia* (10), *Diploneis* (8), and *Amphora* (9), as they accounted for 41% of all taxa. At the class level, 70% (129) of the taxa recorded were Bacillariophyceae, 15% (28), Coscinodiscophyceae, and 15% (27) Fragilariophyceae.

Exclusively, for *S. fluitans*, 41 taxa (22% of the total) were identified from 23 genera, of which 15 (64%) were represented by a single taxon. The dominant genera in terms of the number of taxa were *Mastogloia* (8), *Halamphora* (4), *Diploneis* (4), and *Nitzschia* (3), as they accounted for 46% of all the taxa recorded. Exclusively for *S. natans*, 53 (29%) of all taxa were accounted for from 29 genera, of which 19 (66%) were represented by a single taxon. The dominant genera were *Lyrella* (7), *Mastogloia* (5), *Nitzschia* (5), *Amphora* (4), and *Cocconeis* (3), as they accounted for 44% of all taxa identified for *S. natans*.

Ninety taxa (49% of the total) from 40 genera occurred on both *Sargassum* species, 65% (26) represented by a single taxon. In general, the predominant genera were *Mastogloia* (24), *Cocconeis* (7), *Plagiogramma,* and *Pleurosigma*, each with four taxa, and *Navicula* (3). These accounted for 48% of all the genera identified in the two *Sargassum* species. Overall, 17 taxa (9%) were new recordings for the coasts of Mexico: *Amphora inelegans* var. *polita* Cleve, *A. floridae* Wachnicka & Gaiser, *A. graeffei* var. *minor* Peragallo, *Climaconeis lorenzii* Grunow, *Dictyoneis marginata* var. *maxima* Boyer, *Mastogloia lineata* var. *albifrons* (Brun) Hustedt, *M. mauritiana* var. *capitata* Voigt, *M. pseudoelegans* Hustedt, *M. stephensiana* Yohn & Gibson, *Mastoneis biformis* (Grunow) Cleve, *Lyrella barbara* var. *densestriata* (Foged) López-Fuerte & Siqueiros Beltrones nov. com., *Nitzschia insignis* var. *lanceolata* Hustedt nom. inval., *Petroneis subdiffusa* (Hustedt) D. G. Mann, *Pleurosigma obscurum* var. *diminuta* H. Peragallo, *Rhaphoneis amphiceros* var. *elegans* Foged, *Rhoicosigma parvum* Hein & Lobban and *Surirella manca* Janisch 1877. The most frequent epiphytic diatom species or infraspecific taxon for both *Sargassum* species were *Mastogloia binotata* (Grunow) Cleve, *Mastogloia crucicula* var. *crucicula* Cleve, *Mastogloia ovata* Grunow, and *Mastogloia pusilla* var. *subcapitata* Hustedt.

The following is a systematic list of the diatom taxa found on *Sargassum fluitans** and *S. natans*• from the Mexican Caribbean, where bold indicates new recordings for the Mexican coasts. Information on identification references is also included. The slides containing the diatom taxa recorded are referred to as *Sargassum* spp. and housed at the Phycological Herbarium of the Universidad Autónoma de Baja California Sur [FBCS-20142,20143,20263–20266].

CLASS: COSCINODISCOPHYCEAE F.E. Round & R.M. Crawford 1990.
Order: Hemiaulales Round & Crawford 1990.
Family: Isthmiaceae Schütt.
ISTHMIA Agardh, 1832.
Isthmia minima Harvey & Bailey 1862 • (Figure 6a–c).
Reference illustrate (Ref. illus.): Lobban, C.S.; Schefter, M.; Jordan R. W.; Arai Y.; Sasaki, A.; Theriot, E.C; Ashworth, M.; Ruck, E.C.; Pennesi, C. 2012. p. 251, pl. 7, Figures 4–6.

Order: Asterolamprales Round & Crawford 1990.
Family: Asterolampraceae Smith 1872.
ASTEROLAMPRA Ehrenberg, 1844.
Asterolampra marylandica Ehrenberg 1844 • (Figure 5g).
Ref. illus.: Hustedt, F. 1929, p. 485, Figures 270 and 271.

Order: Coscinodiscales Round & Crawford 1990.
Family: Coscinodiscaceae Kützing 1844.
COSCINODISCUS Ehrenberg, 1839.
Coscinodiscus asteromphalus Ehrenberg 1844 * (Figure 2a–f).
Ref. illus.: Hustedt, F. 1928, p. 452, Figure 250.
Coscinodiscus radiatus Ehrenberg 1840 * (Figure 3e–j).
Ref. illus.: Hustedt, F. 1928, p. 420, Figure 225a,b.

Order: Anaulales Round & Crawford 1990.
Family: Anaulaceae (Schütt) Lemmermann 1899.
EUNOTOGRAMMA Weisse 1855.
Eunotogramma dubium Hustedt 1939 * (Figure 4j,k).
Ref. illus.: Hustedt, F. 1939, p. 592, Figures 8–10.

Order: Biddulphiales Krieger 1954.
Family: Biddulphiaceae Kützing 1844.
LAMPRISCUS Schmidt, 1882.
Lampriscus shadboltianus (Greville) Peragallo & Peragallo 1902 *• (Figure 6d,e).
Ref. illus.: Peragallo, H.; Peragallo, M. 1897–1908, p. 389, pl. 106, Figure 1.

BIDDULPHIA Gray 1821.
Biddulphia biddulphiana (J. E. Smith) Boyer 1900 *• (Figure 4d,e).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 25, pl. 8, Figures 8 and 9 (as *Biddulphia pulchella*).

NEOHUTTONIA Kuntze 1898.
Neohuttonia reichardtii (Grunow) Kuntze 1898 *• (Figure 8o–p).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 33, pl. 3, Figures 10 and 11 (as *Huttoniella reichardtii*).

Family: Hemidiscaceae Hendey ex Hasle 1996.
ACTINOCYCLUS Ehrenberg 1837.
Actinocyclus crassus (W. Smith) Ralfs ex Pritchard 1861 • (Figure 3a–d).
Ref. illus.: Van Heurck, H. 1880, pl. 124, Figures 6–8.
Actinocyclus gallicus Meister 1937 *• (Figure 4a–c).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 20, pl. 4, Figure 4.
Actinocyclus octonarius var. *sparsus* (Gregory) Hendey 1954 • (Figure 3k,l).
Ref. illus.: Stidolph, S.R., Sterrenburg, F.A.S., Smith, K.E.L., Kraberg, A. 2012, pl. 4, Figure 92.

AZPEITIA M. Peragallo 1912.
Azpeitia nodulifera (A. W. F. Schmidt) Fryxell & Sims 1986 *● (Figure 3m–q).
Ref. illus.: Fryxell, G.A.; Sims, P.A.; Watkins, T.P. 1986, p. 19, Figures 17, 18 and 30.

ROPERIA Grunow ex Pelletan 1889.
Roperia tesselata (Roper) Grunow ex Pelletan 1889 * (Figure 5a–e).
Ref. illus.: Roper, F.C.S. 1858, p. 19, pl. 3, Figure 1.

Order: Cymatosirales Round & Crawford 1990.
Family: Cymatosiraceae Hasle, von Stosch & Syvertsen 1983.
CYMATOSIRA Grunow 1862.
Cymatosira lorenziana Grunow 1862 *● (Figure 9q,r).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 27, pl. 11, Figures 12–15.

Order: Paraliales R.M. Crawford 1990.
Family: Paraliaceae R.M. Crawford 1988.
PARALIA P.A.C. Heiberg 1863.
Paralia sulcata (C.G. Ehrenberg) P.T. Cleve 1873 ● (Figure 7j–n).
Ref. illus.: Hendey, N.I. 1964, p. 73, pl. 23, Figure 5.

Family: Stephanodiscaceae I.V. Makarova 1986.
CYCLOTELLA (F.T. Kützing) A. de Brébisson 1838.
Cyclotella atomus Hustedt 1937 ● (Figure 7q).
Ref. illus.: Hustedt, F. 1937, p. 143, pl. 9, Figures 1–4.
Cyclotella litoralis Lange & Syvertsen 1989 ● (Figure 7o,p).
Ref. illus.: Moreno, J.L.; Licea, S.; Santoyo, H. 1996, p. 61, pl. 18, Figure 10 (as *C. stylorum*).

Order: Thalassiosirales Glezer & Makarova 1986.
Family: Thalassiosiraceae M. Lebour 1930.
SHIONODISCUS A.J. Alverson, S.H. Kang & E.C. Theriot, 2006.
Shionodiscus oestrupii (Ostenfeld) Alverson, Kang & Theriot 2006 *● (Figure 3r–t; Figure 4f–i).
Ref. illus.: Hasle G.R., Syvertsen E.E. 1996, p. 83, pl. 12, Figure b (as *Thalassiosira oestrupii*).

Order: Triceratiales Round & Crawford 1990.
Family: Plagiogrammaceae De Toni 1890.
DIMEREGRAMMA Ralfs 1861.
Dimeregramma marinum (Gregory) Ralfs 1861 * (Figure 9c,d).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 28, pl. 3, Figure 9.

GLYPHODESMIS Greville, 1862.
Glyphodesmis eximia Greville 1862 ● (Figure 9e–h).
Ref. illus.: Greville, R.K. 1862, p. 235; pl. 10, Figures 7–10.

NEOFRAGILARIA Desikachary, Prasad & Prema, 1987.
Neofragilaria anomala (Giffen) Witkowski & Dabek 2015 ● (Figure 9l).
Ref. illus.: Li, C.; Ashworth, M.P.; Witkowski, A.; Dąbek, P.; Medlin, L.K.; Kooistra, W.H.C.F.; Sato, S.; Zgłobicka, I.; Kurzydłowski, K.J.; Theriot, E.C.; Sabir, J.S.M.; Khiyami, M.A.; Mutwakil, M.H.Z.; Sabir, M.H,; Alharbi, N.S.; Hajarah, N.H.; Qing, S.; Jansen, R.K.; 2015, p. 10, Figure 6. Witkowski, A.; Dabek, P. 2015, p. 10, Figure 6.

PLAGIOGRAMMA Greville 1859.
Plagiogramma minus (Gregory) Li, Ashworth & Witkowski 2020 *● (Figure 9i–k).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 29, pl. 11, Figures 3–9 (as *Dimeregramma minor* var. *minor*).
Plagiogramma rhombicum Hustedt 1955 *● (Figure 9n).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 38, pl. 11, Figure 33.
Plagiogramma pulchellum var. *pulchellum* Greville 1859 *● (Figure 9p).
Ref. illus.: Peragallo, H.; Peragallo, M. 1897–1908, p. 338, pl. 82, Figures 1 and 2.
Plagiogramma wallichianum Greville 1865 *● (Figure 9m).
Ref. illus.: Schmidt, A.W.F. 1886, pl. 209, Figure 20.
Plagiogramma pulchellum var. *pygmaeum* (Greville) Peragallo & Peragallo 1901 *● (Figure 9o).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 38, pl. 10, Figure 13, pl. 11, Figures 29 and 30.

TALARONEIS Kooistra & De Stefano, 2004.
Talaroneis furcigera (Grunow) Sterrenburg 2004 • (Figure 6f–i).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 29, pl. 11, Figures 10 and 11 (as *Dimeregrammopsis furcigerum*).

Family: Triceratiaceae (Schütt) Lemmerm 1899.
TRICERATIUM Ehrenberg 1839.
Triceratium biquadratum Janisch 1886 • (Figure 5f).
Ref. illus.: Schmidt, A.W.F. 1886, pl. 98, Figures 4–6.

CLASS: FRAGILARIOPHYCEAE F.E. Round 1990.
Order: Rhaphoneidales Round 1990.
Family: Rhaphoneidaceae Forti 1912.
PERISSONOË Andrews & Stoelzel 1984
***Perissonoë trigona* (Grunow) Andrews & Stoelzel 1984** *• (Figure 8j–m).
Ref. illus.: Foged, N. 1984, p. 90, pl. 27, Figure 5 (as *Rhaphoneis amphiceros* var. *elegans*).

RHAPHONEIS Ehrenberg 1844.
Rhaphoneis amphiceros var. *amphiceros* (Ehrenberg) Ehrenberg 1844 *• (Figure 8e–i).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 77, pl. 22, Figures 3–6.

Order: Ardissoneales Round 1990.
Family: Ardissoneaceae Round 1990.
ARDISSONEA De Notaris 1870.
Ardissonea formosa (Hantzsch) Grunow 1880 * (Figure 10r).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 43, pl. 30, Figure 12.
Ardissonea fulgens (Greville) De Toni 1892 • (Figure 10c,f).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 44, pl. 31, Figures 9–11.

Order: Climacospheniales Round 1990.
Family: Climacospheniaceae Round 1990.
CLIMACOSPHENIA Ehrenberg 1841.
Climacosphenia elongata Bailey 1854 * (Figure 11a).
Ref. illus.: Round, F.E. 1982, Figures 4–6 and 14.

Order: Fragilariales Silva 1962.
Family: Fragilariaceae Greville 1833.
FRAGILARIA Lyngbye 1819.
Fragilaria cf. *tenera* (W. Smith) Lange-Bertalot 1980 * (Figure 10e).
Ref. illus.: Patrick, R. M.; Reimer, C.W. 1966, p. 137, pl. 5, Figure 5 (as *Synedra tenera* var. *tenera*).

PODOCYSTIS Bailey 1854.
Podocystis adriatica (Kützing) Ralfs 1861 *• (Figure 8a–d).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 74, pl. 21, Figures 1–4. (as *Podocystis americana*).

SYNEDRA Ehrenberg 1830.
Synedra bacillaris (Grunow) Hustedt 1932 *• (Figure 10q).
Ref. illus.: Foged, N. 1984, p. 96, pl. 30, Figure 6.

TABULARIA (Kützing) Williams & Round 1986.
Tabularia cf. *fasciculata* (Agardh) Williams & Round 1986 *• (Figure 10i–l).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 80, pl. 30, Figures 4 and 5 (as *Fasciculata fasciculata*).

Family: Staurosiraceae Medlin 2016.
OPEPHORA Pettit 1888.
Opephora mutabilis Sabbe & Wyverman, nom. inval. 1995 • (Figure 6m,n).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 72, pl. 25, Figures 10–17.

Order: Licmophorales Round 1990.
Family: Licmophoraceae Kützing 1844.
HYALOSYNEDRA Williams & Round 1986.
Hyalosynedra laevigata (Grunow) D.M. Williams & Round 1986 *• (Figure 10d,m).
Ref. illus.: Foged, N. 1984, p. 97, pl. 28, Figure 13 (as *Synedra laevigata*).

LICMOPHORA Agardh 1827.
Licmophora cf. *communis* (Heiberg) Grunow 1881 *• (Figure 27l,m).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 63, pl. 20, Figures 1 and 2.
Licmophora gracilis (Ehrenberg) Grunow 1867 *• (Figure 27k).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 65, pl. 18, Figures 12–15; pl. 19, Figures 7–15.
Licmophora paradoxa (Lyngbye) Agardh 1828 *• (Figure 27j).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 67, pl. 18, Figures 4–10, pl. 19, Figure 5.
Licmophora remulus (Grunow) Grunow 1867 * (Figure 27i,k).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 68, pl. 19, Figures 1 and 2.

Family: Rhabdonemataceae Round & Crawford 1990.
RHABDONEMA Kützing 1844.
Rhabdonema adriaticum Kützing 1844 *• (Figure 5h,i).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 76, pl. 13, Figures 10–12.

Order: Rhaphoneidales Round 1990.
Family: Psammodiscaceae Round & Mann 1990.
PSAMMODISCUS Round & Mann 1980.
Psammodiscus calceatus Watanabe, Nagumo & Tanaka 2013 • (Figure 7a–c,h,i).
Ref. illus.: Watanabe, T; Nagumo, T; Sun, Z; Hasegawa, K; Miyagawa, T; Kumada, M; Tanaka, J. 2013, p. 5, Figures 19–52.
Psammodiscus nitidus (Gregory) Round & D. G. Mann 1980 *• (Figure 7d–g).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 75, pl. 23, Figures 12–14.

Family: Rhaphoneidaceae Forti 1912.
DELPHINEIS Andrews 1977.
Delphineis surirella (Ehrenberg) Andrews 1981 • (Figure 9a,b).
Ref. illus.: Navarro, J.N. 1982, p. 19, pl. 14, Figures 1–3.

Order: Striatellales Round 1990.
Family: Striatellaceae Kützing 1844.
GRAMMATOPHORA Ehrenberg 1840.
Grammatophora oceanica var. *oceanica* Ehrenberg 1840 • (Figure 12a–c).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 59, pl. 15, Figures 13 and 4; pl. 16, Figure 12; pl. 17, Figures 3 and 4.
Grammatophora hamulifera Kützing 1844 • (Figure 12g–i).
Ref. illus.: Hustedt (1931–1959), p. 40, Figure 566.
Grammatophora marina (Lyngbye) Kützing 1844 *• (Figure 12f,j,l).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 58, pl. 15, Figures 9–12.
Grammatophora oceanica var. *subtilissima* (Bailey) Grunow 1881 * (Figure 12e).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 59, pl. 13; Figure 1, pl. 15, Figures 12 and 13; pl. 17, Figure 1.
Grammatophora serpentina Ehrenberg 1844 *• (Figure 12d,k,m,n).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 59, pl. 16, Figures 1–3.

STRIATELLA Agardh 1832.
Striatella unipunctata (Lyngbye) Agardh 1832 • (Figure 11b).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 78, pl. 23, Figures 5–7.

Order: Toxariales Round 1990.
Family: Toxariaceae Round 1990.
TOXARIUM Bailey 1854.
Toxarium undulatum Bailey 1854 * (Figure 10a,b).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 83, pl. 31, Figures 5 and 6.
Toxarium hennedyanum (Gregory) Pelletan 1889 *• (Figure 10g,h).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 83, pl. 30, Figure 11, pl. 31, Figure 7.

CLASS: BACILLARIOPHYCEAE E. Haeckel 1878.
Order: Dictyoneidales D.G. Mann 1990.
Family: Dictyoneidaceae D.G. Mann 1990.
DICTYONEIS Cleve 1890.
***Dictyoneis marginata* var. *maxima* Boyer 1916** • (Figure 16m–p).
Ref. illus.: Boyer, C.S. 1916, p. 79, pl. 20, Figure 1.

Order: Achnanthales Silva 1962.
Family: Achnanthaceae Kützing 1844.
ACHNANTHES Bory 1822.
Achnanthes brevipes var. *intermedia* (Kützing) Cleve 1895 * (Figure 14r).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 86, pl. 43, Figures 1–5.

Family: Cocconeidaceae Kützing 1844.
ANORTHONEIS Grunow 1868.
Anorthoneis excentrica (Donkin) Grunow 1868 • (Figure 6j–l).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 97, pl. 42, Figure 20; pl. 54, Figures 9 and 10.

COCCONEIS Ehrenberg 1838.
Cocconeis britannica Naegeli ex Kützing 1849 *• (Figure 13t–v).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 102, pl. 39, Figures 21–23.
Cocconeis comis Schmidt 1894 • (Figure 13q,r,z,aa).
Ref. illus.: Siqueiros Beltrones, D. A.; Y. J. Martínez; Aldana-Moreno, A. 2019, p. 104, Figure 103.
Cocconeis decipiens Cleve 1873 • (Figure 13s).
Ref. illus.: Cleve, P.T. 1873, p. 14, pl. 1, Figure 6.
Cocconeis diruptoides Hustedt 1933 *• (Figure 13k,l).
Ref. illus.: Foged, N. 1975, p. 40, pl. 14, Figure 3.
Cocconeis krammeri Lange-Bertalot & Metzeltin 1996 • (Figure 13e,f,m–p).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 109, pl. 33, Figures 1–5; pl. 34, Figures 4–5; pl. 42, Figure 34.
Cocconeis maxima (Grunow) Peragallo & Peragallo 1897 * (Figure 13a–d).
Ref. illus.: Peragallo, H.; Peragallo, M. 1897, pl. 3, Figures 1–4.
Cocconeis heteroidea Hantzsch 1863 *• (Figure 13i,j).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 108, pl. 35, Figures 4 and 5.
Cocconeis scutellum var. *parva* (Grunow) Cleve 1895 *• (Figure 13w).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 114, pl. 38, Figure 10; pl. 42, Figures 17–19.
Cocconeis speciosa Gregory 1855 *• (Figure 13x).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 112, pl. 36, Figure 10; pl. 38, Figures 38–40.
Cocconeis scutellum var. *scutellum* Ehrenberg 1838 *• (Figure 13y).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 114, pl. 36, Figures 1–7; pl. 38, Figure 11.
Cocconeis thalassiana Romero & López-Fuerte 2013 *• (Figure 13g,h).
Ref. illus.: Romero, O.; López-Fuerte, F.O. 2013, p. 2, Figures 1–25.

Order: Bacillariales Hendey 1937.
Family: Bacillariaceae Ehrenberg 1831.
NAGUMOENA Kociolek & Witkowski, 2011.
Nagumoea vallus (Nikolaev) Majewska & Van de Vijver 2020 *• (Figure 7r,s).
Ref. illus.: Sullivan, M.J. 2010, p. 175, Figures 1, 2 and 4–8 (as *Denticula vallus*).

NITZSCHIA Hassall 1845.
Nitzschia bicapitata Cleve 1901 • (Figure 29p,q).
Ref. illus.: Fryxell, G. 2000, p. 46, Figures 1–11.
Nitzschia carnicobarica Desikachary & Prema 1987 • (Figure 29k,l).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 373, pl. 183, Figures 9 and 10.
Nitzschia angularis W. Smith 1853 • (Figure 29n).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 368, pl. 199, Figures 5 and 6.
Nitzschia fluminensis Grunow 1862 *• (Figure 29o).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 381, pl. 202, Figures 6–9.
***Nitzschia insignis* var. *lanceolata* (Hustedt) Simonsen 1987** • (Figure 29c–f).
Ref. illus.: Schmidt, A.W.F. 1921, pl. 333, Figures 16 and 17.
Nitzschia longissima f. *costata* Hustedt ex Simonsen 1987 • (Figure 29b).
Ref. illus.: Foged, N. 1978, p. 107, pl. 46, Figures 9 and 10.
Nitzschia nienhuisii Sterrenburg & Sterrenburg 1990 * (Figure 29g).
Ref. illus.: Lobban, C.S. 2015, p. 10, Figures 89–94.
Nitzschia pellucida Grunow 1880 * (Figure 29r).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 399, pl. 191, Figures 1–7 and 11.
Nitzschia sicula (Castracane) Hustedt 1958 *• (Figure 29aa–cc).
Ref. illus.: Hasle G.R., Syvertsen E.E. 1996, p. 327, pl. 75, Figures a–d.
Nitzschia sigma (Kützing) Smith 1853 * (Figure 29a).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 404, pl. 206, Figures 1–10.

Order: Cymbellales D. G. Mann 1990.
Family: Lyrellaceae D. G. Mann 1990.
LYRELLA Karayeva 1978.
Lyrella approximatoides (Hustedt) D. G. Mann 1990 • (Figure 25e).
Ref. illus.: Foged, N. 1984, p. 60, pl. 49, Figure 1 (as *Navicula approximatoides*).
Lyrella barbara (Heiden) D. G. Mann 1990 • (Figure 25g).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 231, pl. 95, Figure 7 (as *Lyrella* cf. *barbara*).
Lyrellabarbara* var. *densestriata* (Foged) López-Fuerte and Siqueiros Beltrones *comb. nov. • (Figure 25f).
Basionym: *Navicula barbara* var. *densestriata* Foged, in Foged 1984. Freshwater and littoral diatoms from Cuba. *Biblioth. Diatom*, p. 60, pl. 49, Figure 6.
Type locality: The tidal zone of the northern coast near Hotel Oasis at Varadero, Cuba.
Ref. illus.: Foged, N. 1984, p. 60, pl. 49, Figure 6.
Lyrella excavata (Greville) D. G. Mann 1990 • (Figure 25h).
Ref. illus.: Siqueiros Beltrones, D.A. 2017, p. 16, Figures 34 and 37.
Lyrella diffluens (A. W. F. Schmidt) D. G. Mann 1990 * (Figure 25c).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 232, pl. 96, Figure 7.
Lyrella lyra var. *lyra* (Ehrenberg) Karayeva 1978 • (Figure 26a).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 234, pl. 158, Figure 8.
Lyrella lyra var. *constricta* Siqueiros-Beltrones 2020 • (Figure 26b).
Ref. illus.: Peragallo, H.; Peragallo, M. 1897, pl. 23, Figure 3 (as *Navicula lyra* var. *constricta*) Hustedt, F. 1961–1966, p. 507, Figure 507.
Lyrella granulata (Grunow) Nevrova, Witkowski, Kulikovskiy & Lange-Bertalot 2013 • (Figure 26c–f).
Ref. illus.: Siqueiros Beltrones, D.A; Argumedo-Hernández, U; López-Fuerte, F.O. 2017, p. 17, Figures 46–57, 60, 61 and 64.

PETRONEIS Stickle & D. G. Mann 1990.
Petroneis granulata D. G. Mann nom. illeg. 1990 • (Figure 25b).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 327, pl. 97, Figures 1 and 2.
Petroneis plagiostoma (Grunow) D. G. Mann 1990 * (Figure 25d).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 329, pl. 102, Figures 5 and 6.
***Petroneis subdiffusa* (Hustedt) D. G. Mann 1990** • (Figure 25a).
Ref. illus.: Hustedt, F. 1955, p. 24, pl. 8, Figure 22 (as *Navicula subdiffusa*).

Order: Mastogloiales D. G. Mann 1990.
Family: Mastogloiaceae Mereschkowsky 1903.
TETRAMPHORA Mereschkowsky 1903.
Tetramphora intermedia (Cleve) Stepanek & Kociolek 2016 *• (Figure 28a).
Ref. illus.: Wachnicka, A.H.; Gaiser, E.E. 2007, p. 419, Figure 118 (as *Amphora rhombica* var. *intermedia*).
Tetramphora securicula (Peragallo & Peragallo) Stepanek & Kociolek 2016 *• (Figure 28b).
Ref. illus.: Peragallo, H. and Peragallo, M. 1897–1908. p. 224, pl. 50, Figure 2.

MASTOGLOIA Thwaites 1856.
Mastogloia angulata Lewis 1861 *• (Figure 19b–g).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 238, pl. 80, Figures 1 and 2.
Mastogloia angusta Hustedt 1933 • (Figure 22f,g).
Ref. illus.: Hustedt, F. 1933, p. 512, Figure 940.
Mastogloia bahamensis Cleve 1893 * (Figure 23f).
Ref. illus.: Cleve, P.T. 1893, p. 16, pl. 1, Figure 17.
Mastogloia beaufortiana Hustedt 1955 * (Figure 22a–c).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 239, pl. 84, Figures 1 and 2.
Mastogloia binotata (Grunow) Cleve 1895 *• (Figure 22l–o).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 240, pl. 75, Figures 15–17.
Mastogloia delicatissima Hustedt 1933 *• (Figure 22d,e).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 244, pl. 76, Figures 12–15.
Mastogloia biocellata (Grunow) Novarino & Muftah 1991 • (Figure 21w,x).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 240, pl. 77, Figures 19, 20.
Mastogloia borneensis Hustedt 1933 • (Figure 23c,d).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 241, pl. 76, Figures 28 and 29.
Mastogloia cf. *elegans* Lewis 1865 • (Figure 19a).
Ref. illus.: Schmidt, A.W.F. 1893, pl. 185, Figure 40.
Mastogloia cocconeiformis Grunow 1860 * (Figures 17f–k and 18c).
Ref. illus.: Grunow, A. 1860, p. 578, pl. 7, Figure 14.
Mastogloia corsicana Grunow 1878 *• (Figure 20l,m and Figure 24a–e).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 242, pl. 77, Figures 15–18.
Mastogloia cribrosa Grunow 1860 *• (Figure 18g–i).
Ref. illus.: Navarro, J.N. 1983, Figures 28 and 29.
Mastogloia crucicula var. *crucicula* Cleve 1895 *• (Figure 19l,m).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 242, pl. 75, Figure 3.
Mastogloia crucicula var. *alternans* Zanon 1948 • (Figure 19n–q).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 243, pl. 75, Figures 4 and 5.
Mastogloia cuneata (Meister) Simonsen 1990 *• (Figure 20n,o).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 243, pl. 74, Figures 19–26, pl. 81, Figures 15–18.
Mastogloia erythraea var. *erythraea* Grunow 1860 *• (Figure 21a–i,m–r).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 246, pl. 82, Figures 7 and 8.
Mastogloia erythraea var. *grunowii* Foged 1984 *• (Figure 21s–v).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 246, pl. 76, Figures 2–7.
Mastogloia fimbriata (Brightwell) Grunow 1863 *• (Figure 18d–f).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 247, pl. 77, Figures 1–4; pl. 83, Figures 1–4.
Mastogloia ignorata Hustedt 1933 *• (Figure 20j,k, Figure 23g,h and Figure 24f,g).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 250, pl. 76, Figures 8–11, pl. 77; Figures 13 and 14; pl. 81, Figures 5–8.
Mastogloia jelineckii (Grunow) Grunow 1877 *• (Figure 22h,i).
Ref. illus.: Peragallo, H.; Peragallo, M. 1897, p. 32, pl. 6, Figure 1.
Mastogloia lacrimata Voigt 1963 *• (Figure 22p,q).
Ref. illus.: Voigt, M. 1963, p. 116, pl. 24, Figure 6.
***Mastogloia lineata* var. *albifrons* (Brun) Hustedt 1933** *• (Figure 19h,i).
Ref. illus.: Hustedt, F. 1933, p. 539, Figure 972.
Mastogloia mauritiana var. *mauritiana* Brun 1893 *• (Figure 20h,i; Figure 23e).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 254, pl. 79, Figures 9 and 10.

***Mastogloia mauritiana* var. *capitata* Voigt 1942** *• (Figure 20e–g).
Ref. illus.: Voigt, M. 1942, p. 14, Figure 35.
Mastogloia ovata Grunow 1860 *• (Figure 18a,b, Figure 19j,k, and Figure 20a,b,u).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 255, pl. 82, Figure 1.
Mastogloia ovulum Hustedt 1933 *• (Figure 19r,s).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 255, pl. 75, Figure 14.
Mastogloia parva Hustedt 1933 * (Figure 23i).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 256, pl. 83, Figure 11 and 12.
***Mastogloia pseudoelegans* Hustedt 1955** * (Figure 20c,d).
Ref. illus.: Hustedt, F. 1955, p. 19, pl. 6, Figure 10.
Mastogloia pseudolatecostata Yohn & Gibson 1982 *• (Figure 20v,w).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 258, pl. 77, Figures 5 and 6.
Mastogloia punctatissima (Greville) Ricard 1975 * (Figure 17a–e).
Ref. illus.: Greville, R.K. 1857, p. 8; pl. 3, Figure 1.
Mastogloia pusilla var. *subcapitata* Hustedt 1933 *• (Figure 20r).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 259, pl. 80, Figure 16.
Mastogloia rhombica Cleve 1883 *(Figure 21j–l).
Ref. illus.: Cleve, P.T. 1893, p. 494, pl. 35, Figure 9.
Mastogloia rostellata (Grunow) Grunow 1877 *• (Figure 22j,k).
Ref. illus.: Foged, N. 1984, p. 56, pl. 32, Figure 15.
Mastogloia similis Hustedt 1933 *• (Figure 22r,s).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 261, pl. 79, Figures 9 and 10.
***Mastogloia stephensiana* Yohn & Gibson 1982** * (Figure 23a,b,j).
Ref. illus.: Yohn, T.A.; Gibson, R.A. 1982, p. 44, Figures 30a,b and 31a,b.
Mastogloia urveae Witkowski, Lange-Bertalot & Metzeltin 2000 *• (Figure 20s,t).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 263, pl. 84, Figures 22 and 23.
Mastogloia varians Hustedt 1933 *• (Figure 20p,q).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 263, pl. 82, Figures 5 and 6.

Order: Naviculales Bessey 1907.
Family: Pinnulariaceae D. G. Mann 1990.
PINNULARIA C.G. Ehrenberg, 1843.
Pinnularia cf. *rectangulata* Kociolek & Wang 2018 • (Figure 15i).
Ref. illus.: Hendey, N.I. 1964, p. 233, pl. 34, Figure 10.

OESTRUPIA Heiden 1935.
Oestrupia powellii (Lewis) Heiden 1935 *• (Figure 11c–f).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 318, pl. 155, Figure 1.
Oestrupia zanardiniana (Grunow) Hendey 1964 * (Figure 11g).
Ref. illus.: Peragallo, H.; Peragallo, M. 1897, p. 79, pl. 14, Figure 10 and 11 (as *Navicula zanardiniana*).

Family: Amphipleuraceae Grunow 1862.
HALAMPHORA (Cleve) Levkov 2009.
Halamphora acutiuscula (Kützing) Levkov 2009 * (Figure 28r).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 128, pl. 161, Figures 10–13 (as *Amphora acutiuscula*).
Halamphora exigua (Gregory) Levkov 2009 * (Figure 28q).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 137, pl. 161, Figures 15–17 (as *Amphora exigua*).
Halamphora lineata (Gregory) Levkov 2009 * (Figure 28o).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 142, pl. 167, Figure 22 (as *Amphora lineata*).
Halamphora turgida (Gregory) Levkov 2009 * (Figure 28v).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 153, pl. 166, Figures 16 and 17 (as *Amphora turgida*).

Family: Berkeleyaceae D. G. Mann 1990.
BERKELEYA Greville 1827.
Berkeleya scopulorum (Brébisson) Cox 1979 *• (Figure 10p).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 157, pl. 62, Figure 6 (as *B. scopulorum* (?) var.).

CLIMACONEIS Grunow 1862.
***Climaconeis lorenzii* Grunow 1862** *• (Figure 10n,o).
Ref. illus.: Hustedt, F. 1961, Figure. 1188.

Family: Diadesmidaceae D. G. Mann 1990.
DIPLONEIS Ehrenberg 1844.
Diploneis gemmatula (Grunow) Cleve 1894 * (Figure 14g–i).
Ref. illus.: Hustedt, F. 1931–1959, p. 527, Figure 1038.
Diploneis didyma (Ehrenberg) Ehrenberg 1839 *• (Figure 14q).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 185, pl. 87, Figure 19.
Diploneis littoralis var. *clathrata* (Østrup) Cleve 1896 * (Figure 14l).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 188, pl. 89, Figures 5 and 7–13.
Diploneis smithii var. *smithii* (Brébisson) Cleve *• (Figure 14m).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 193, pl. 88, Figures 2–5; pl. 89, Figure 1.
Diploneis suborbicularis (Gregory) Cleve 1894 *• (Figure 14o,p).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 195, pl. 93, Figures 9 and 10.
Diploneis parca (Schmidt) Boyer 1927 * (Figure 14e,f,j,k).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 191, pl. 89, Figures 4–6.
Diploneis vacillans (Schmidt) Cleve 1894 • (Figure 14n).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 196, pl. 89, Figure 14; pl. 90, Figures 11 and 12; pl. 91, Figures 9 and 10.
Diploneis weissflogii (Schmidt) Cleve 1894 * (Figure 14a–d).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 197, pl. 92, Figures 4 and 5; pl. 12, Figure 12,13.

CALONEIS Cleve 1894.
Caloneis excentrica (Grunow) Boyer 1927 *• (Figure 15a–c,h).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 744, pl. 151, Figures 5 and 6 (as *Caloneis* spec. (?nov.) cf. *excentrica*).
Caloneis liber var. *umbilicata* (Grunow) Cleve 1894 • (Figure 15d).
Ref. illus.: Schmidt, A. 1877, pl. 50, Figure 32 and 33.
Caloneis linearis (Grunow) Boyer 1927 *• (Figure 15e–g).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 166, pl. 160, Figure 12.

Family: Naviculaceae Kützing 1844.
TRACHYNEIS Cleve, 1894.
Trachyneis aspera (Ehrenberg) Cleve 1894 *• (Figure 16k,l).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 355, pl. 159, Figure 9.

MASTONEIS Cleve 1894.
***Mastoneis biformis* (Grunow) Cleve 1894** *• (Figure 19t).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 264, pl. 101, Figure 5.

NAVICULA Bory 1822.
Navicula bipustulata A. Mann 1925 • (Figure 16i,j).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 268, pl. 144, Figures 8–12.
Navicula longa var. *longa* (Gregory) Ralfs 1861 *• (Figure 16b).
Ref. illus.: Foged, N. 1984, p. 66, pl. 45, Figure 4.
Navicula longa var. *irregularis* Hustedt 1955 *• (Figure 16a,c,h).
Ref. illus.: Hustedt, F. 1955, p. 28, pl. 9, Figure 1.

Navicula pennata Schmidt 1876 *• (Figure 16f,g).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 296, pl. 141, Figures 27 and 28.
Navicula transitans Cleve 1883 *• (Figure 16d,e).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 309, pl. 127, Figures 6–8.

SEMINAVIS Mann 1990.
Seminavis delicatula Wachnicka & Gaiser 2007 *• (Figure 28j–l).
Ref. illus.: Wachnicka, A.H.; Gaiser, E.E. 2007, p. 442, Figures 228–234.
Seminavis robusta Danielidis & D. G. Mann 2002 • (Figure 28i).
Ref. illus.: Wachnicka, A.H.; Gaiser, E.E. 2007, p. 442, Figures 221–225.

Family: Pleurosigmataceae Mereschowsky 1903.
RHOICOSIGMA Grunow 1867.
***Rhoicosigma parvum* Hein & Lobban 2015** • (Figure 27g,h).
Ref. illus.: Hein, M.K.; Lobban, C.S. 2014, p. 77, Figures 1–32.

PLEUROSIGMA Smith 1852.
Pleurosigma formosum Smith 1852 *• (Figure 27a,b).
Ref. illus.: Moreno, J.L.; Licea, S.; Santoyo, H. 1996, p. 113, pl. 28, Figure 18.
***Pleurosigma obscurum* var. *diminuta* H. Peragallo 1891** *• (Figure 27d).
Ref. illus.: Peragallo, H.; Peragallo, M. 1897, p. 5; pl. 1, Figures 15 and 16.
Pleurosigma salinarum (Grunow) Grunow 1880 *• (Figure 27c).
Ref. illus.: Foged, N. 1984, p. 88, pl. 5, Figure 3; pl. 39, Figure 2.
Pleurosigma rostratum Hustedt 1955 *• (Figure 27e,f).
Ref. illus.: Hustedt, F. 1955, p. 35, pl. 12, Figure 4.

Family: Sellaphoraceae Mereschkowsky 1902.
FALLACIA Stickle & D. G. Mann 1990.
Fallacia vittata (Cleve) D. G. Mann 1990 *• (Figure 25i).
Ref. illus.: Hein, M.k.; Winsborough, B.M.; Sullivan M.J. 2008, p. 56, pl. 28, Figures 4 and 5.

Order: Rhopalodiales D. G. Mann 1990.
Family: Rhopalodiaceae (karsten) Topachevs'kyj & Oksiyuk 1960.
EPITHEMIA Kützing 1844.
Epithemia guettingeri (Krammer) Lobban & Park 2018 *• (Figure 29u–z).
Ref. illus.: Lobban C.S.; Park, J.S. 2018, p. 132, Figures 171–173.

RHOPALODIA Müller 1895.
Rhopalodia gibberula Mereschkowsky 1906 *• (Figure 29s,t).
Ref. illus.: Foged, N. 1984, p. 92, pl. 14, Figure 7, pl. 55, Figure 8.

Order: Surirellales D. G. Mann 1990.
Family: Entomoneidaceae Reimer 1975.
ENTOMONEIS Ehrenberg 1845.
Entomoneis paludosa (Smith) Reimer 1975 *• (Figure 11h).
Ref. illus.: Peragallo, H.; Peragallo, M. 1897, pl. 38, Figures 12–15.

Family: Surirellaceae Kützing 1844.
CORONIA (Ehrenberg) Ehrenberg 1912.
Coronia decora (Brébisson) Ruck & Guiry 2016 *• (Figure 30c).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 412, pl. 214, Figure 15 (as *Campylodiscus decorus*).

CAMPYLODISCUS Ehrenberg 1844.
Campylodiscus cordatus Hagelst 1939 *• (Figure 30f–h).
Ref. illus.: Foged, N. 1984, p. 27, pl. 60, Figure 6.
Campylodiscus neofastuosus Ruck & Nakov 2016 * (Figure 30b).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 414, pl. 215, Figures 1–3.
Campylodiscus subangularis Cleve & Möller 1891* (Figure 30d,e,i,j).
Ref. illus.: López-Mejía, D.; Siqueiros Beltrones, D.A.; López-Fuerte, F.O.; Gutiérrez-Mendieta, F. 2021, p. 32, Figure 6k.

SURIRELLA Turpin 1828
***Surirella manca* Janisch 1877** * (Figure 30a)
Ref. illus.: Schmidt, A. 1877, pl. 56, Figure 9.

PSAMMODICTYON Mann 1990.
Psammodictyon constrictum (Gregory) D. G. Mann 1990 * (Figure 29m).
Ref. illus.: Peragallo, H.; Peragallo, M. 1897, pl. 270, Figures 8–10.
Psammodictyon panduriforme var. *continuum* (Grunow) Snoeijis 1998 * (Figure 29h–j).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 398, pl. 183, Figure 6 (as *Nitzschia panduriformis* var. *continua*).

Order: Thalassiophysales D. G. Mann 1990.
Family: Catenulaceae Mereschkowsky 1902.
AMPHORA Ehrenberg 1844.
***Amphora inelegans* var. *polita* Cleve** *• (Figure 28p).
Ref. illus.: Cleve, P. T. 1895, p. 111, pl. 4, Figure 39. Peragallo, H.; Peragallo, M. 1898, p. 209; pl. 46, Figure 10.
Amphora caroliniana Giffen 1980 *• (Figure 28d).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 132, pl. 167, Figure 2.
Amphora corpulenta var. *capitata* Tempère & Peragallo 1909 • (Figure 28e,f).
Ref. illus.: A.H. Wachnicka & E.E. Gaiser, 2007, p. 407, Figures 62 and 63.
***Amphora floridae* Wachnicka & Gaiser 2007** • (Figure 28c).
Ref. illus.: A.H. Wachnicka & E.E. Gaiser, 2007, p. 414, Figures 90–93.
***Amphora graeffei* var. *minor* Peragallo 1897** • (Figure 28u).
Ref. illus.: Peragallo, H.; Peragallo, M. 1897, p 211, pl. 46, Figures 14 and 15.
Amphora laevissima Gregory 1857 * (Figure 28t).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 142, pl. 168, Figures 5–7.
Amphora proteoides Hustedt 1955 * (Figure 28s).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 147, pl. 162, Figures 3 and 4.
Amphora proteus Gregory1857 *• (Figure 28m,n).
Ref. illus.: Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. 2000, p. 148, pl. 161, Figures 1 and 2; pl. 162, Figures 5 and 6.
Amphora robusta Gregory 1857 • (Figure 28g,h).
Ref. illus.: Gregory, W. 1857, p. 516, pl. 13, Figure 79.

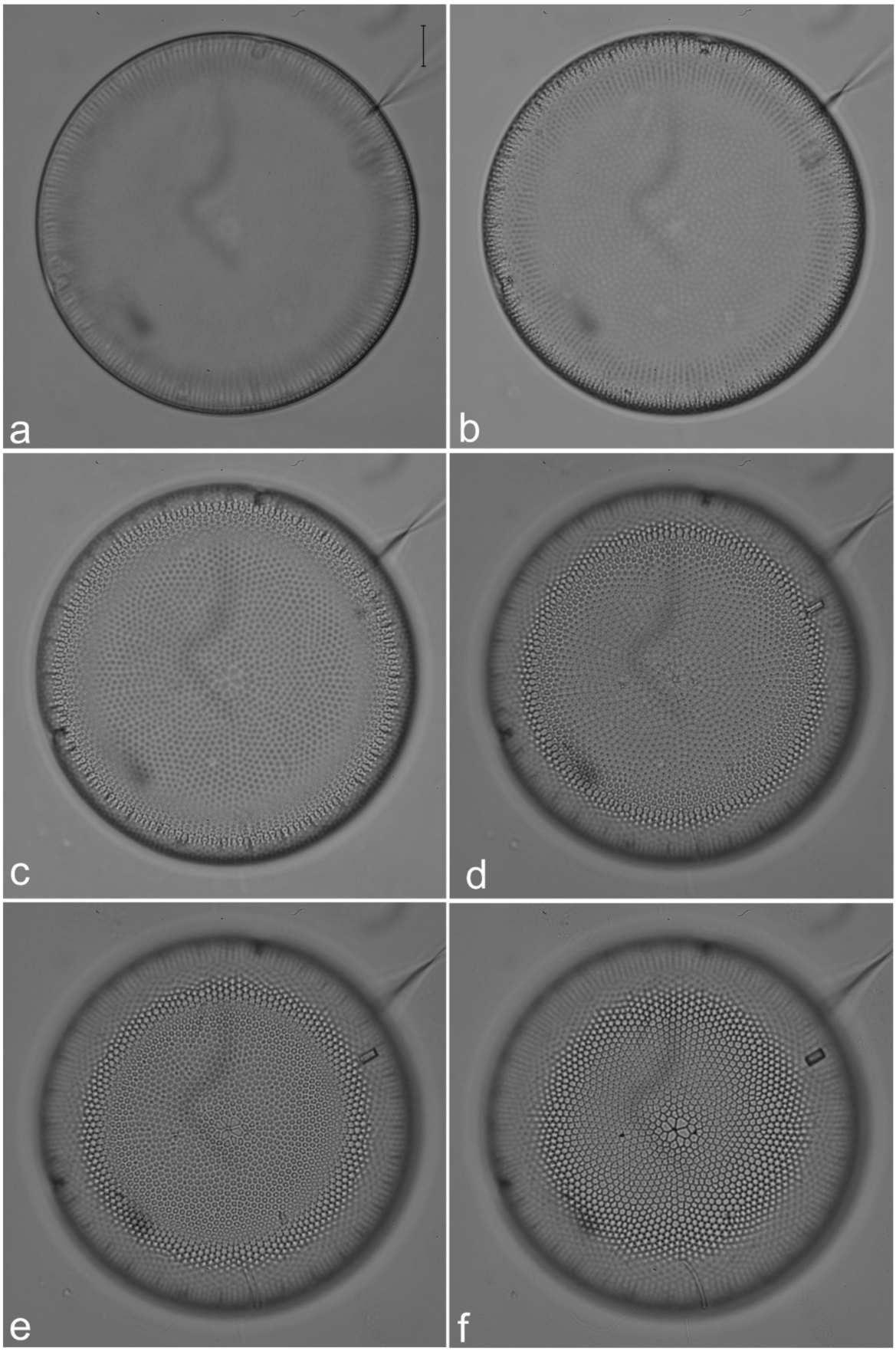

Figure 2. (**a**–**f**) *Coscinodiscus asteromphalus* in different focal planes. Scale bar = 10 μm.

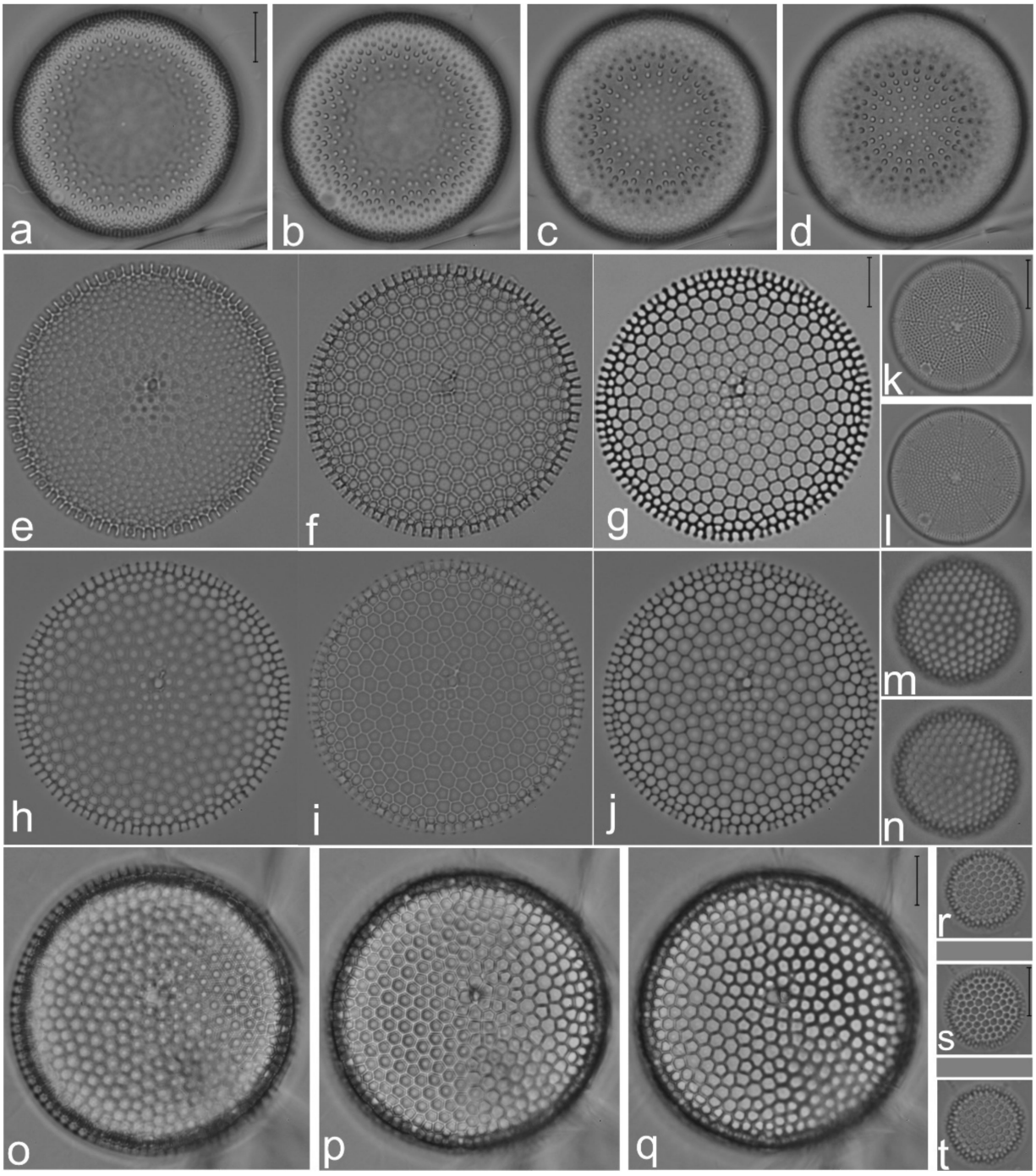

Figure 3. (**a**–**d**) *Actinocyclus crassus* valves in different focal views; (**e**–**j**) *Coscinodiscus radiatus* in different focal planes; (**k**,**l**) *Actinocyclus octonarius* var. *sparsus*; (**m**–**q**) *Azpeitia nodulifera*; (**r**–**t**) *Shionodiscus oestrupii* in different focal planes and showing a range in size. Scale bar = 10 µm.

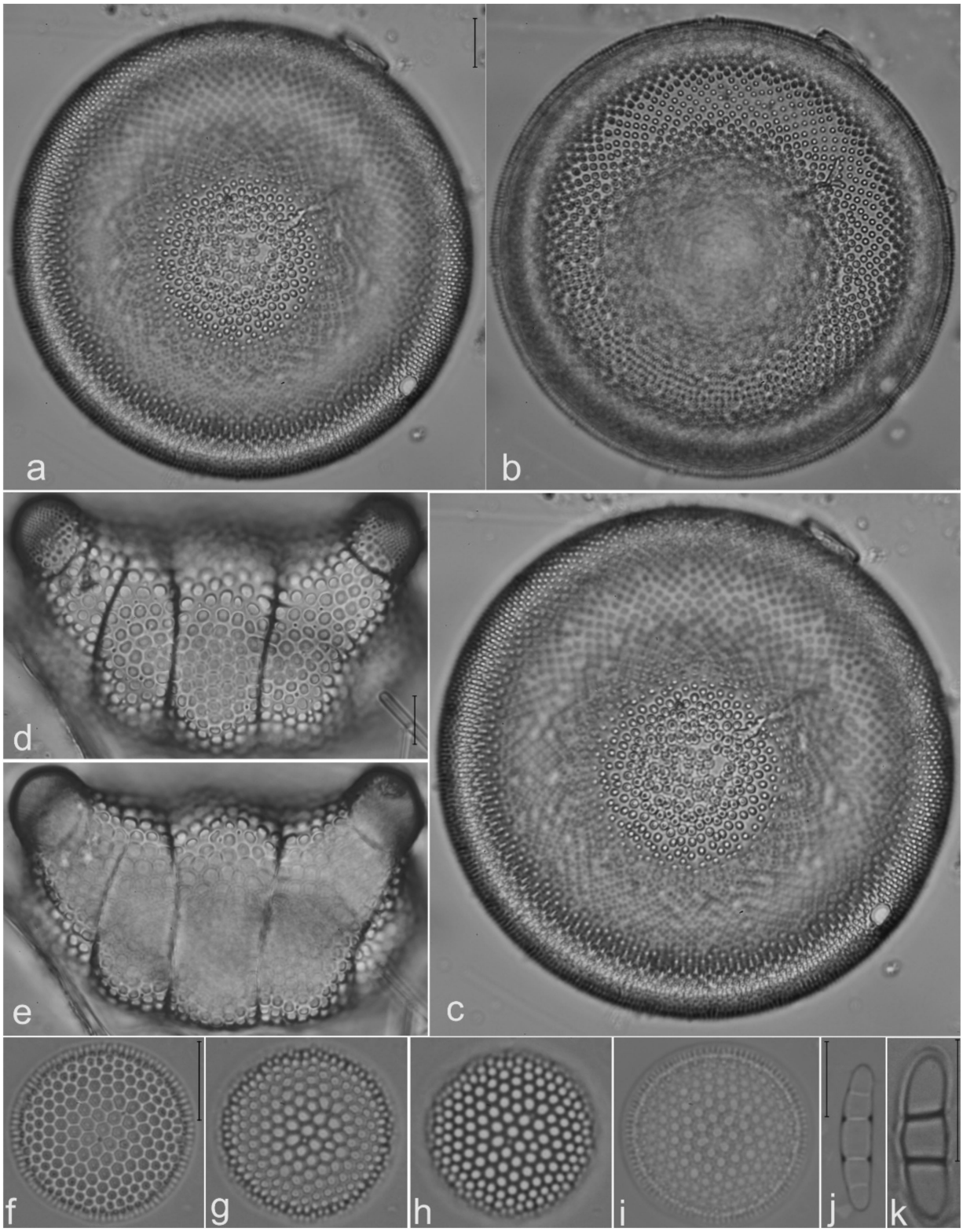

Figure 4. (**a**–**c**) *Actinocyclus gallicus* in different focal views; (**d**,**e**) *Biddulphia biddulphiana*; (**f**–**i**) *Shionodiscus oestrupii* in different focal views; (**j**,**k**) *Eunotogramma dubium*. Scale bar = 10 µm.

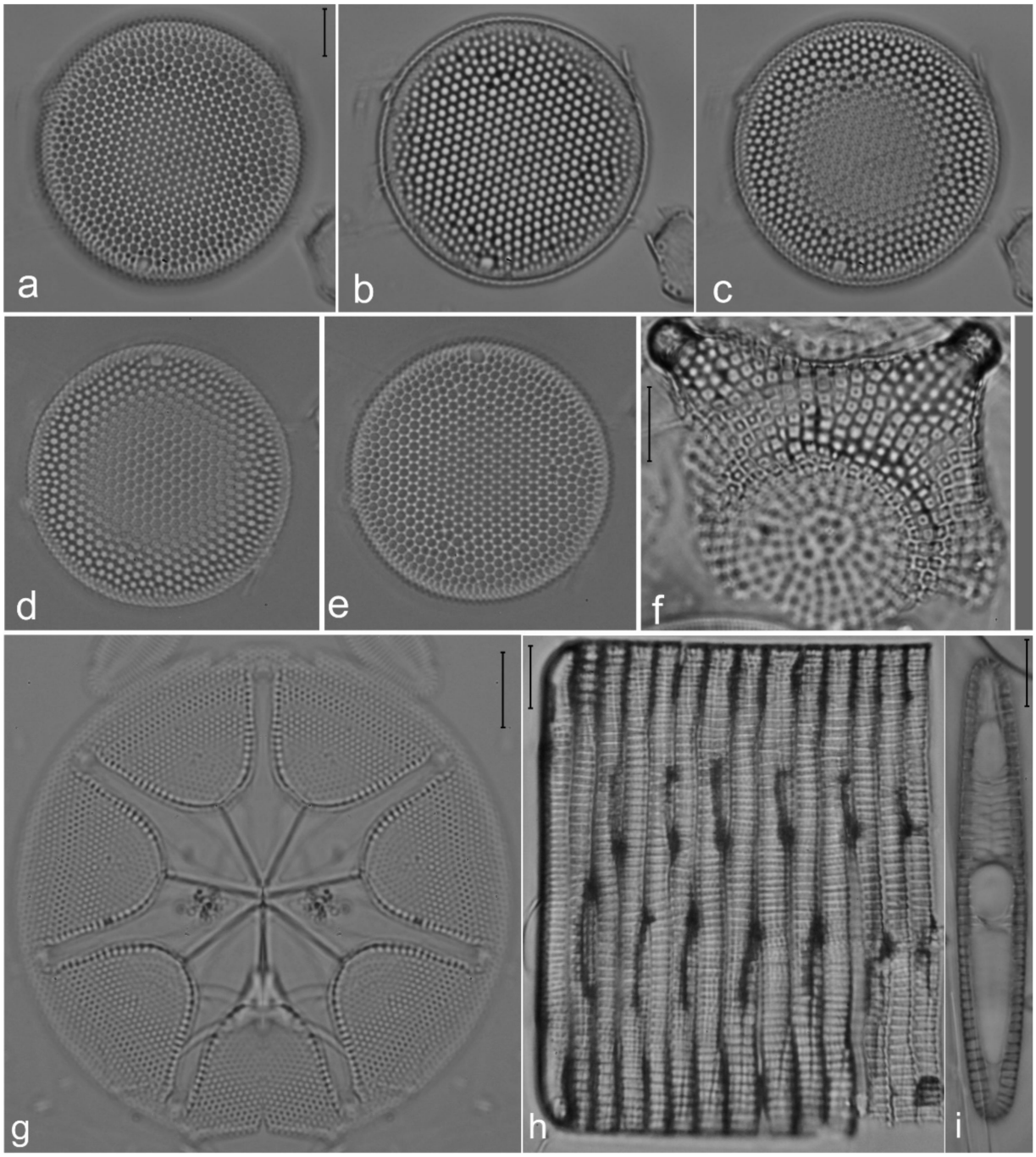

Figure 5. (**a**–**e**) *Roperia tesselata* valves in different focal views; (**f**) *Triceratium biquadratum*; (**g**) *Asterolampra marylandica*; (**h**,**i**) *Rhabdonema adriaticum*, image h frustule in girdle view. Scale bar = 10 μm.

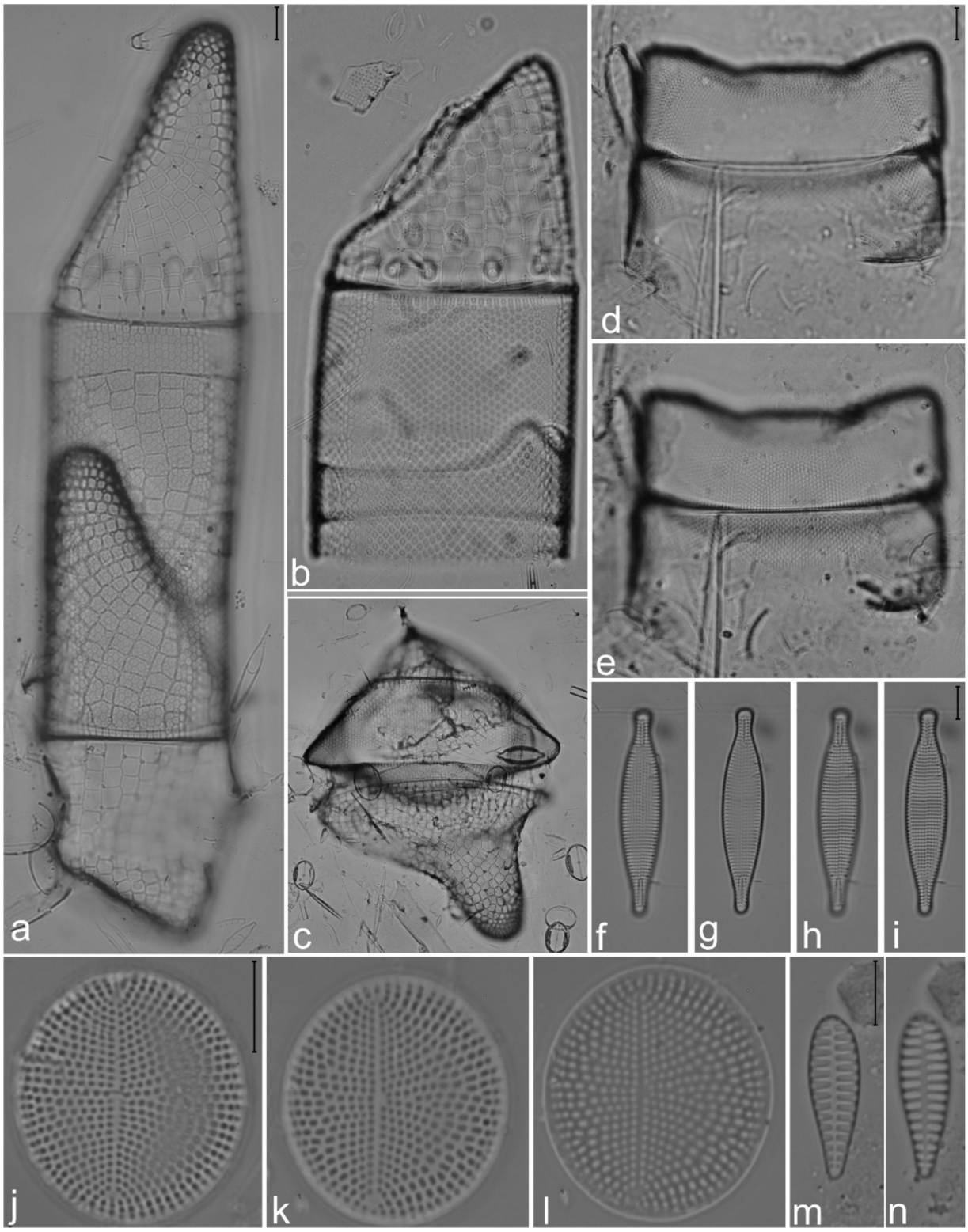

Figure 6. (**a**–**c**) *Isthmia minima* images a, b frustule showing the cingulum with full set of girdle bands; (**d**,**e**) *Lampriscus shadboltianus*; (**f**–**i**) *Talaroneis furcigera* valves in different focal views; (**j**–**l**) *Anorthoneis excentrica* valves in different focal views; (**m**,**n**) *Opephora mutabilis* in different focal views. Scale bar = 10 µm.

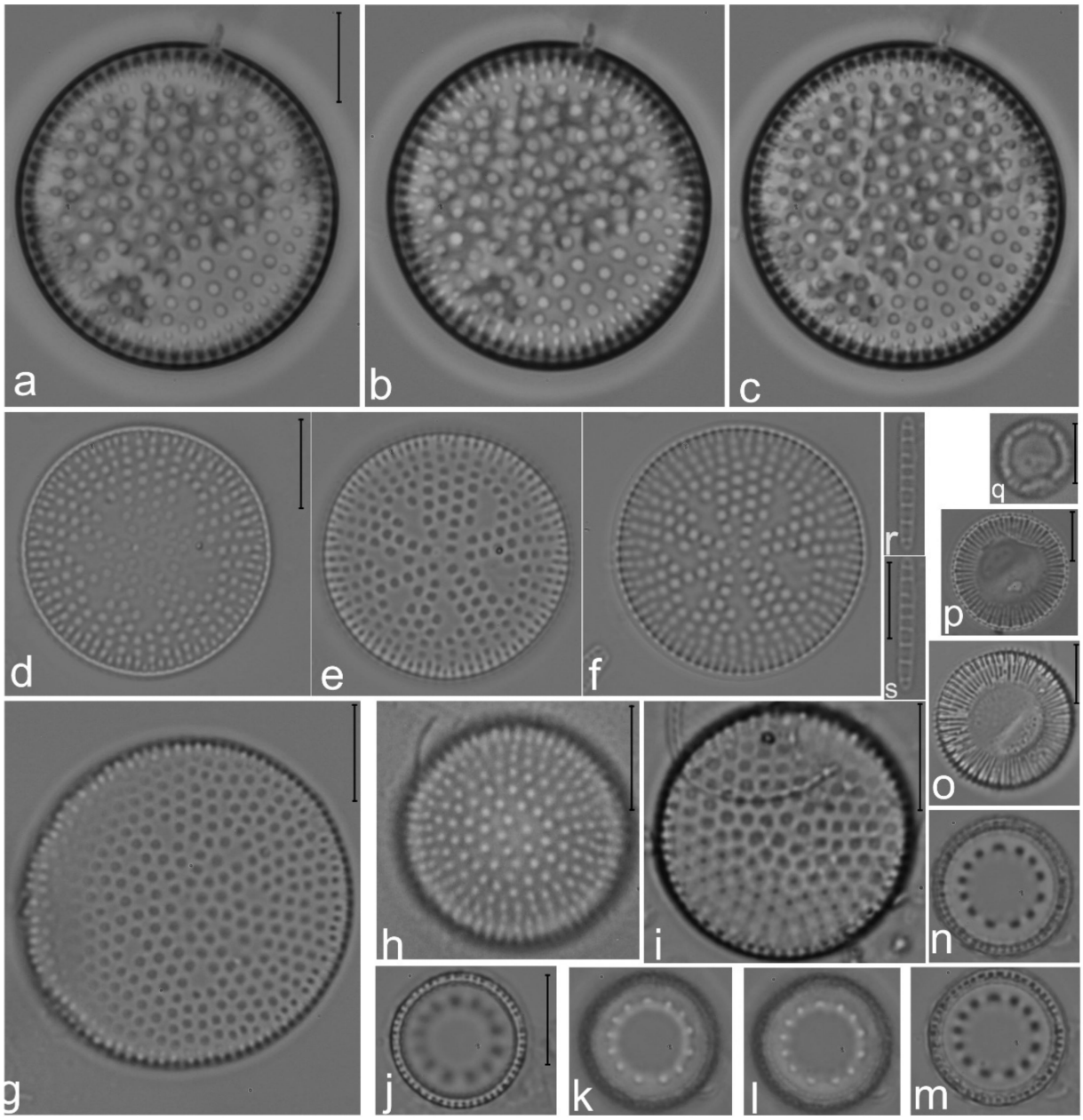

Figure 7. (**a**–**c**,**h**,**i**) *Psammodiscus calceatus* in different focal views; (**d**–**g**) *P. nitidus* valves in different focal views; (**j**–**n**) *Paralia sulcata* valves in different focal views; (**o**,**p**) *Cyclotella litoralis* (**q**) *Cyclotella atomus*; (**r**,**s**) *Nagumoea vallus*. Scale bar = 10 μm; q = 5 μm.

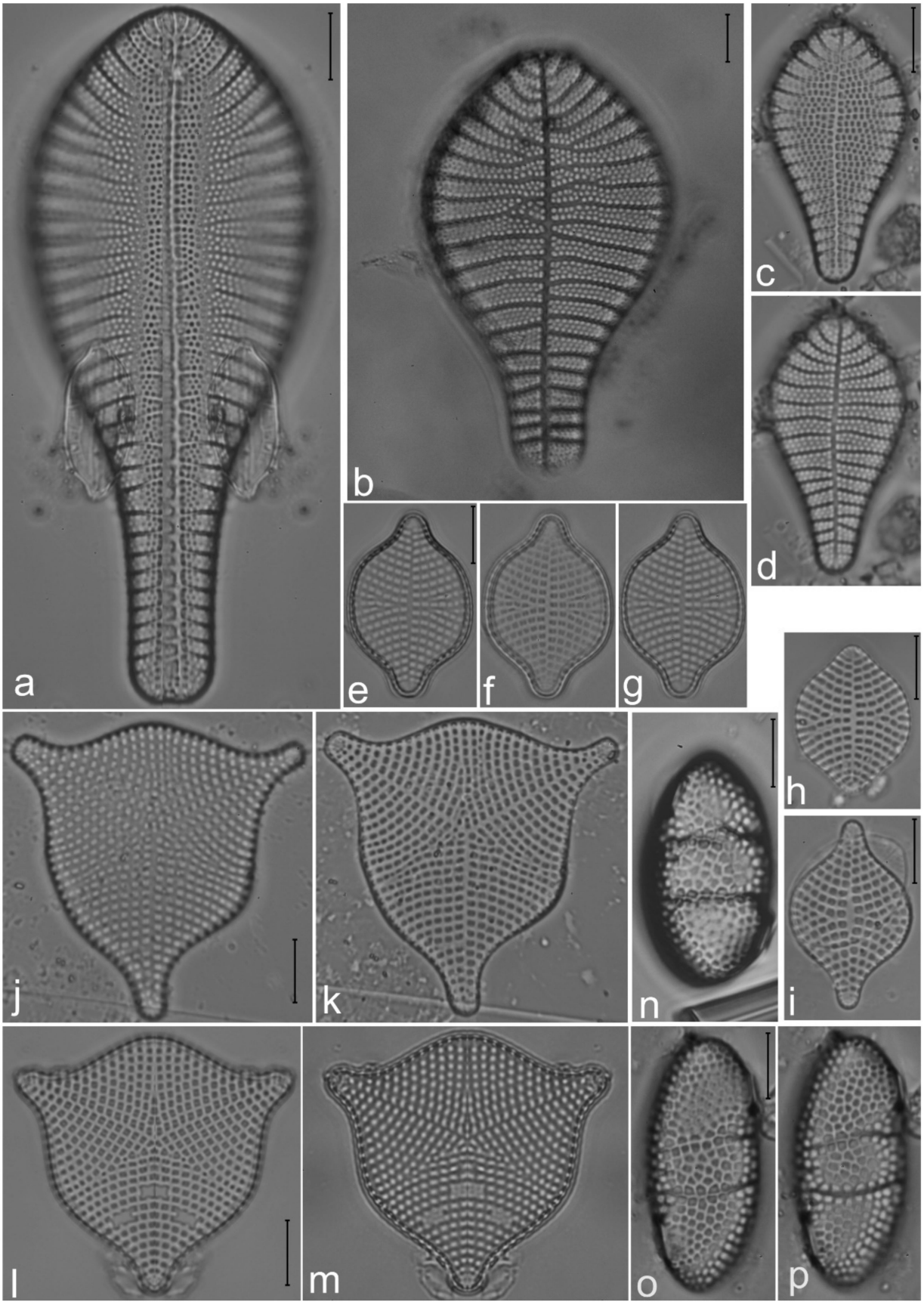

Figure 8. (**a**–**d**) *Podocystis adriatica* showing range in size; (**e**–**i**) *Rhaphoneis amphiceros* var. *amphiceros*; (**j**–**m**) *Perissonoë trigona*; (**n**–**p**) *Neohuttonia reichardtii*. Scale bar = 10 μm.

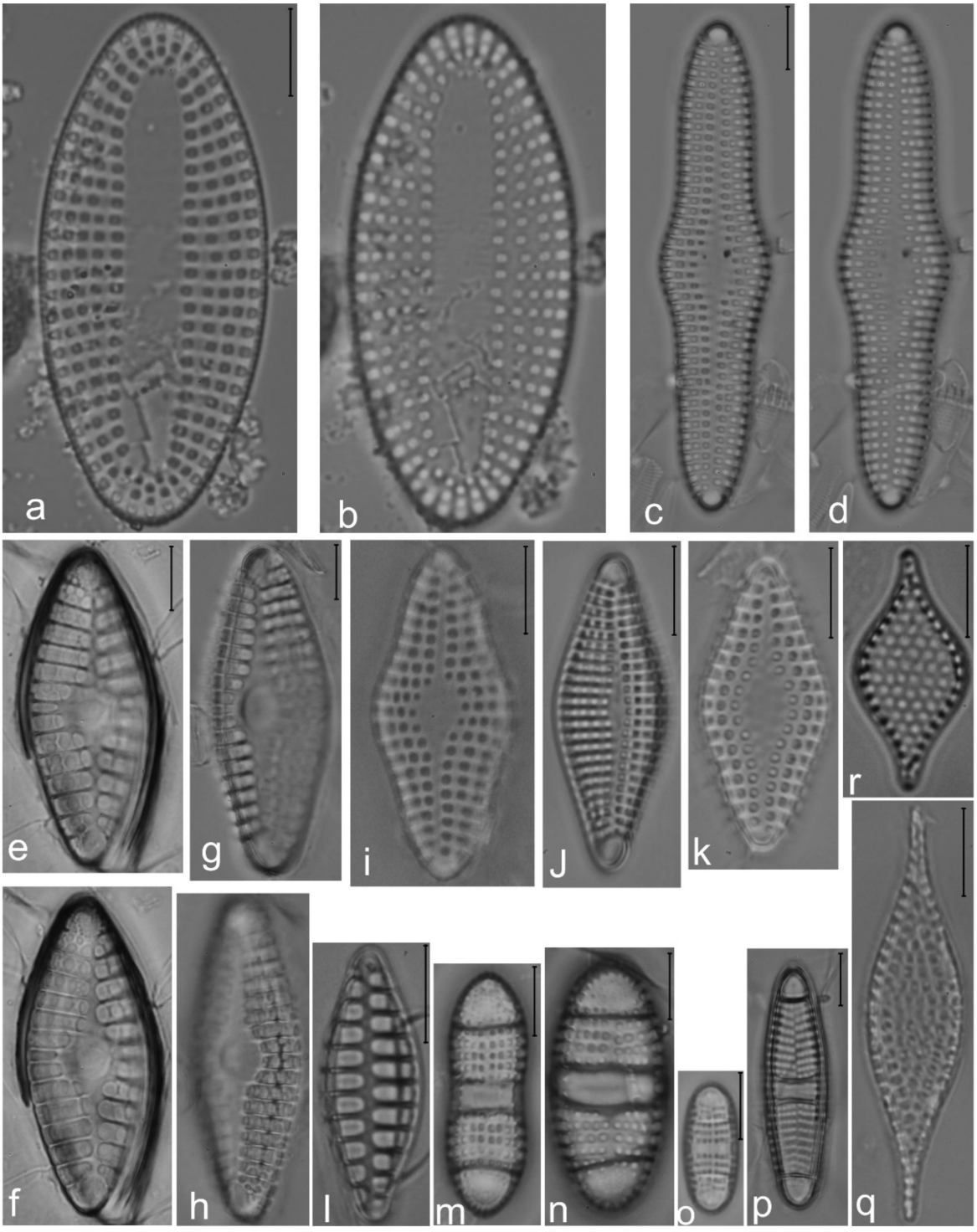

Figure 9. (**a**,**b**) *Delphineis surirella*; (**c**,**d**) *Dimeregramma marinum*; (**e**–**h**) *Glyphodesmis eximia*; (**i**–**k**) *Plagiogramma minus*; (**l**) *Neofragilaria anomala*; (**m**) *Plagiogramma wallichianum*; (**o**) *P. pulchellum* var. *pygmaeum*; (**n**) *P. rhombicum*; (**p**) *P. pulchellum* var. *pulchellum*; (**q**,**r**) *Cymatosira lorenziana*. Scale bar = 10 μm.

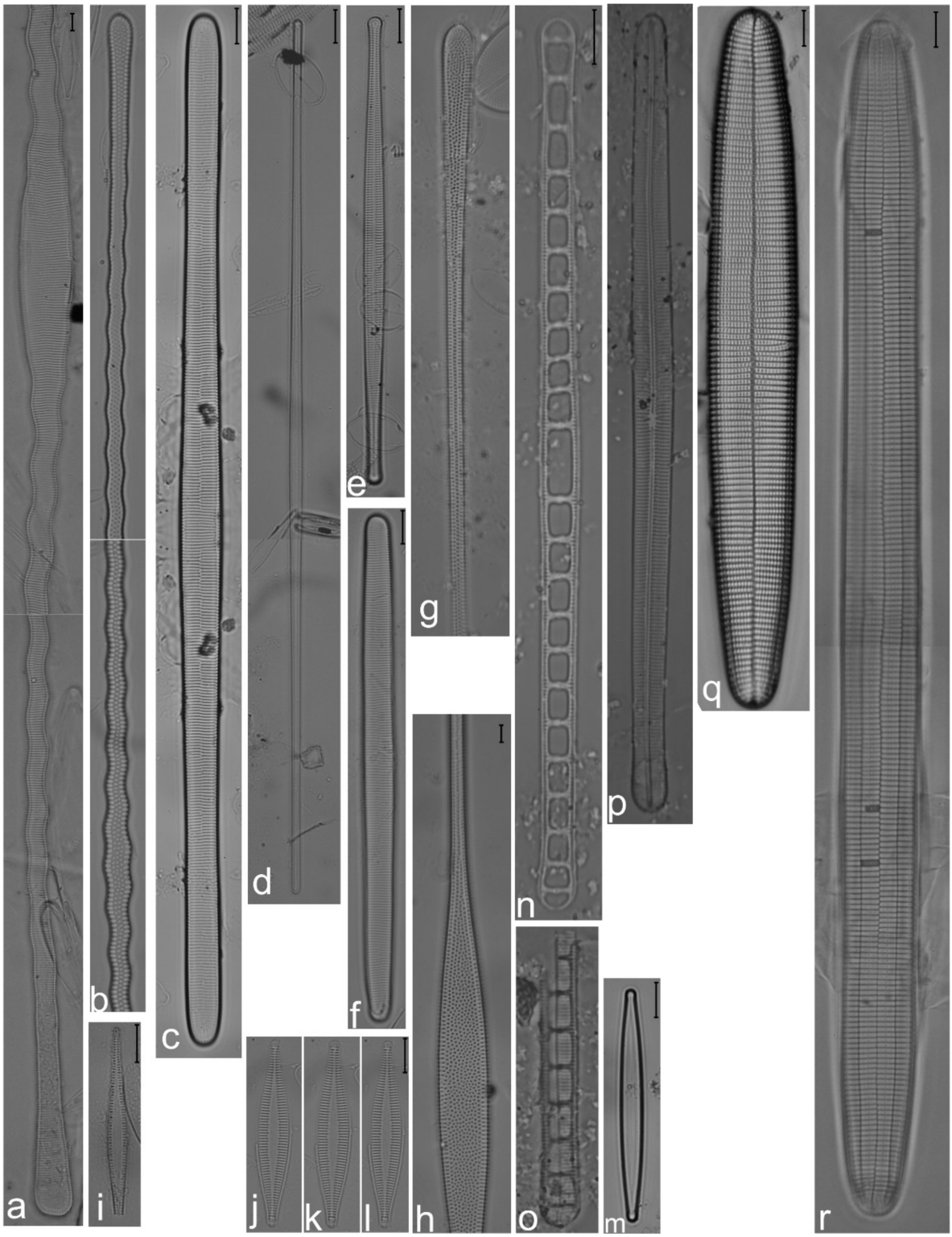

Figure 10. (**a**,**b**) *Toxarium undulatum*; (**c**,**f**) *Ardissonea fulgens*; (**e**) *Fragilaria* cf. *tenera*; (**g**,**h**) *Toxarium hennedyanum*; (**i**–**l**) *Tabularia* cf. *fasciculata*; (**d**,**m**) *Hyalosynedra laevigata*; (**n**,**o**) *Climaconeis lorenzii*; (**p**) *Berkeleya scopulorum*; (**q**) *Synedra bacillaris*; (**r**) *Ardissonea formosa*. Scale bar = 10 μm.

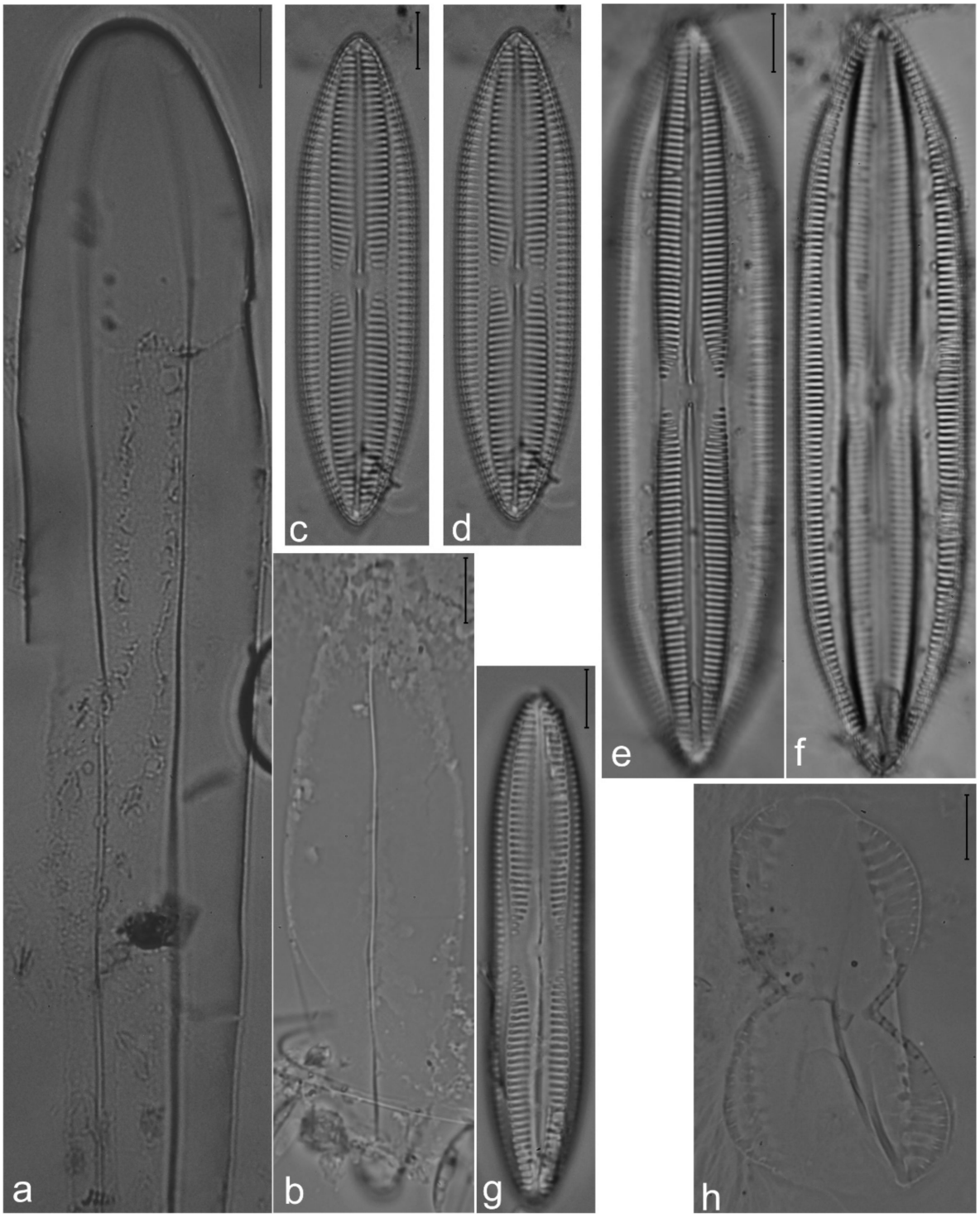

Figure 11. (**a**) *Climacosphenia elongata*; (**b**) *Striatella unipunctata*; (**c**–**f**) *Oestrupia powellii*; (**g**) *O. zanardiniana*; (**h**) *Entomoneis paludosa*. Scale bar = 10 µm.

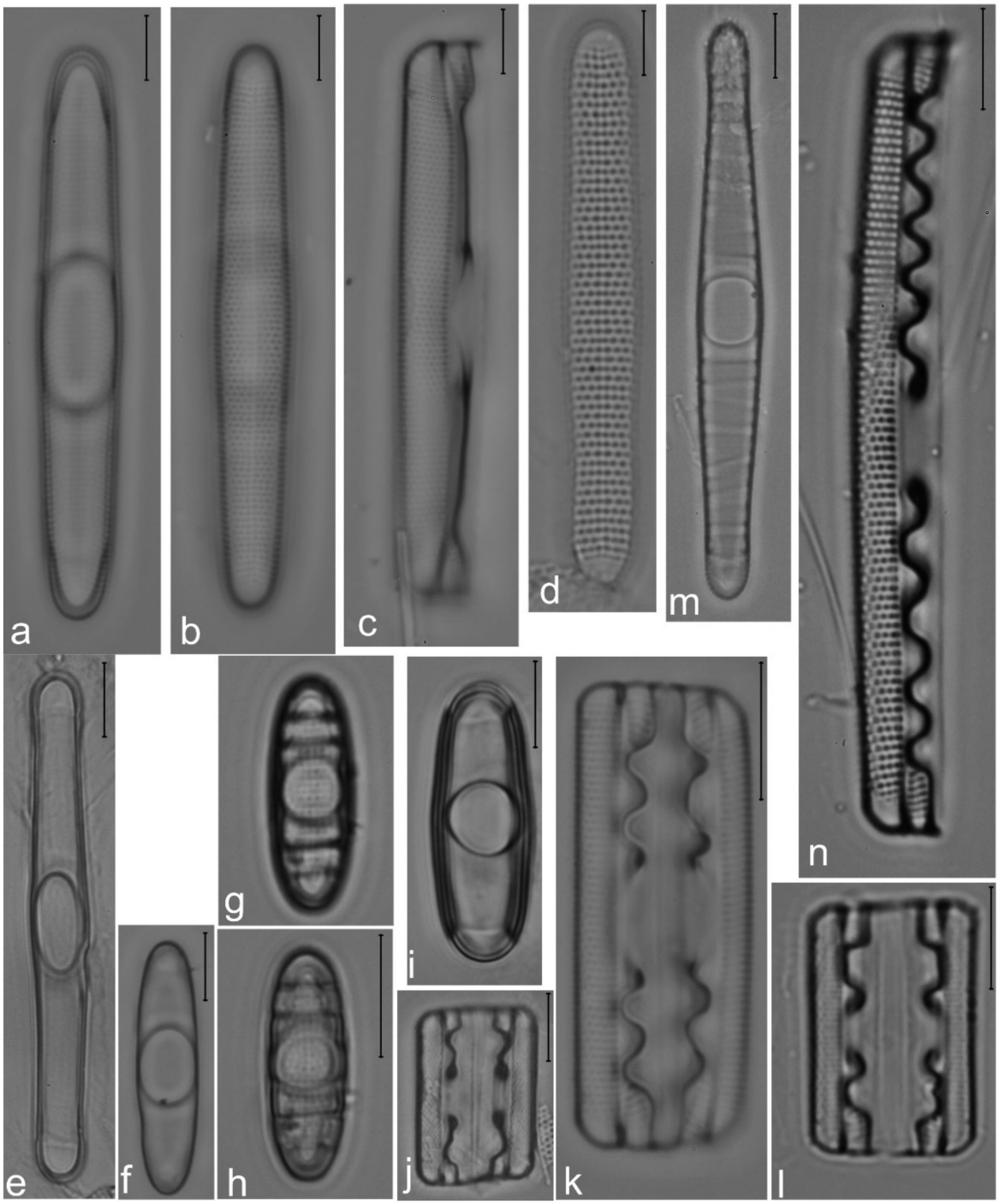

Figure 12. (**a**–**c**) *Grammatophora oceanica* var. *oceanica*; (**d**,**k**,**m**,**n**) *G. serpentina*; (**e**) *G. oceanica* var. *subtilissima*; (**f**,**j**,**l**) *G. marina*; (**g**–**i**) *G. hamulifera*. Scale bar = 10 μm.

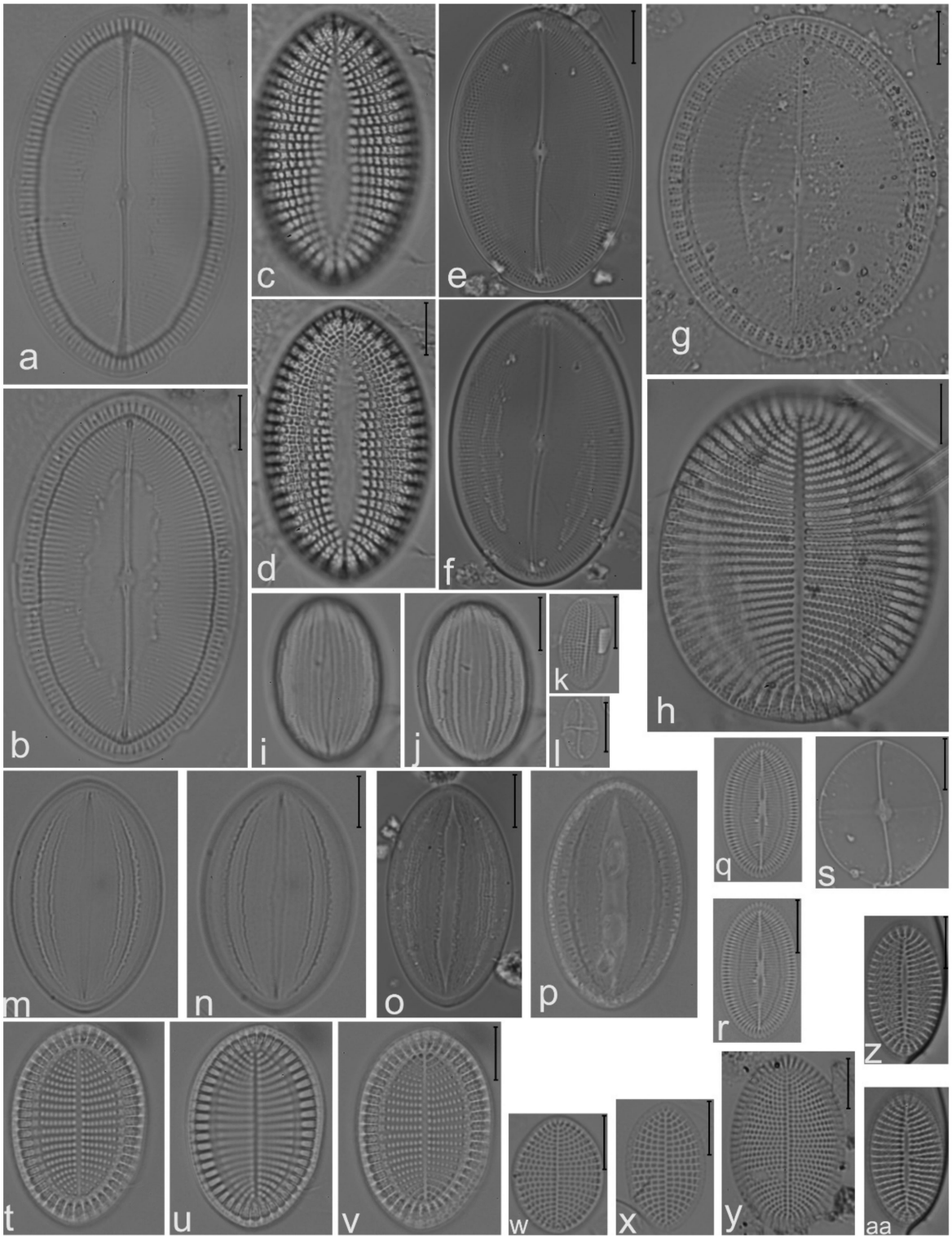

Figure 13. (**a**–**d**) *Cocconeis maxima*; (**e**,**f**,**m**–**p**) *C. krammeri*; (**g**,**h**) *C. thalassiana*; (**i**,**j**) *C. heteroidea*; (**k**,**l**) *C. diruptoides*; (**q**,**r**,**z**,**aa**) *C. comis*; (**s**) *C. decipiens*; (**t**–**v**) *C. britannica*; (**w**) *C. scutellum* var. *parva*; (**x**) *C. speciosa*; (**y**) *C. scutellum* var. *scutellum*. Scale bar = 10 μm.

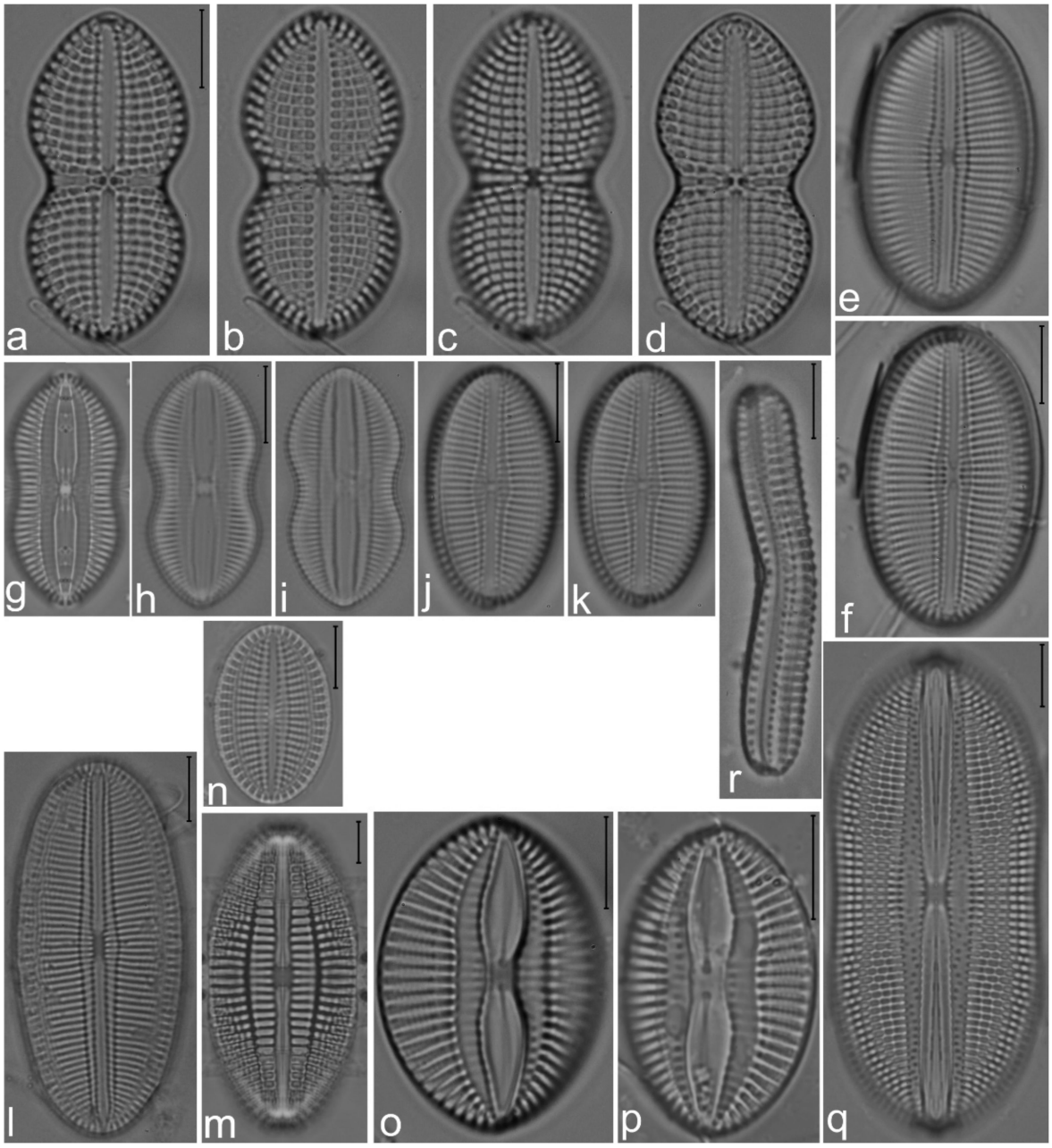

Figure 14. (**a**–**d**) *Diploneis weissflogii*; (**e**,**f**,**j**,**k**) *D. parca*; (**g**–**i**) *Diploneis gemmatula*; (**l**) *D. littoralis* var. *clathrata*; (**m**) *D. smithii* var. *smithii*; (**n**) *D. vacillans*; (**o**,**p**) *D. suborbicularis*; (**q**) *D. didyma*; (**r**) *Achnanthes brevipes* var. *intermedia*. Scale bar = 10 μm.

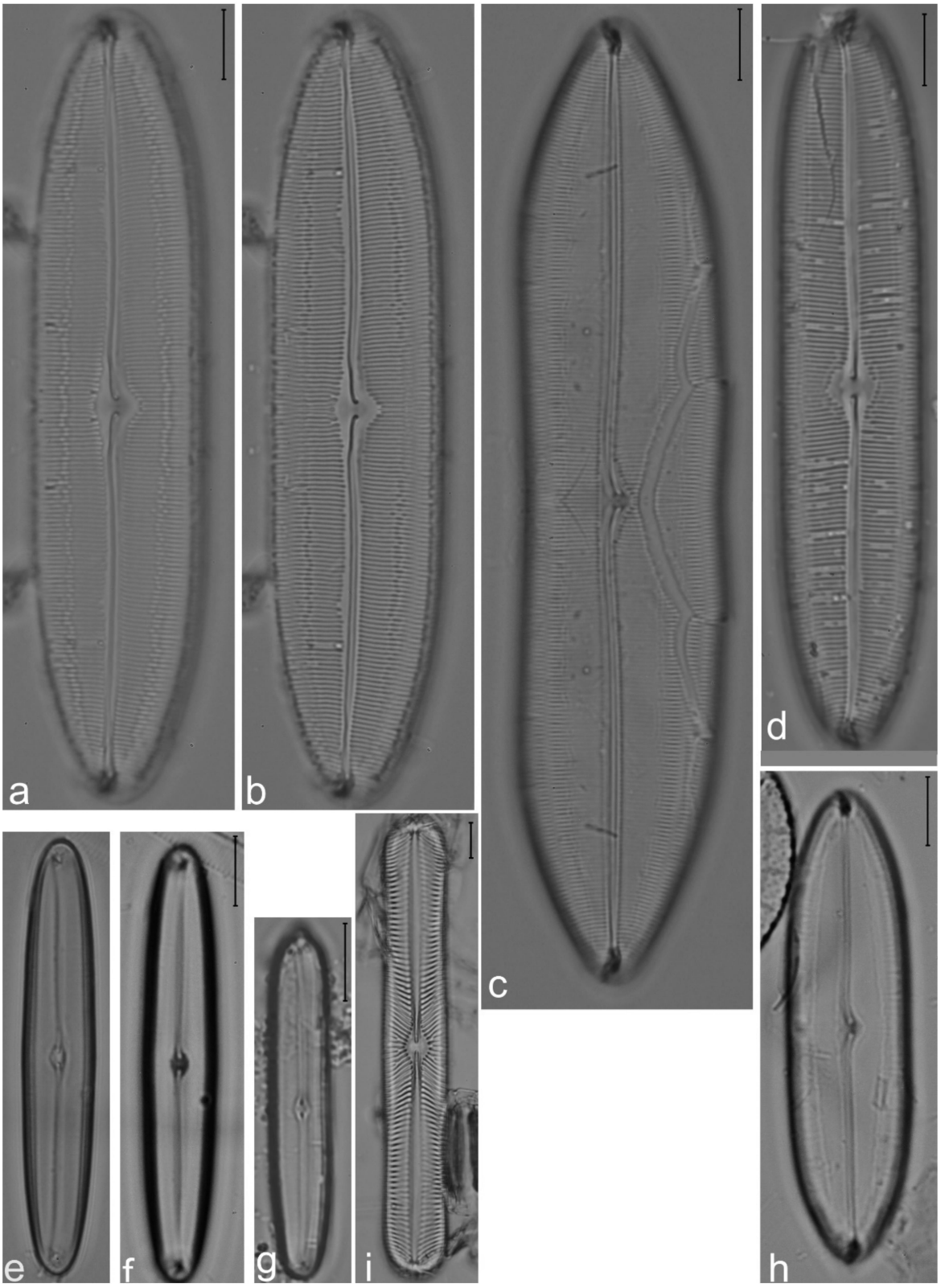

Figure 15. (**a**–**c**,**h**) *Caloneis excentrica*; (**d**) *C. liber* var. *umbilicata*; (**e**–**g**) *C. linearis*; (**i**) *Pinnularia* cf. *rectangulata*. Scale bar = 10 μm.

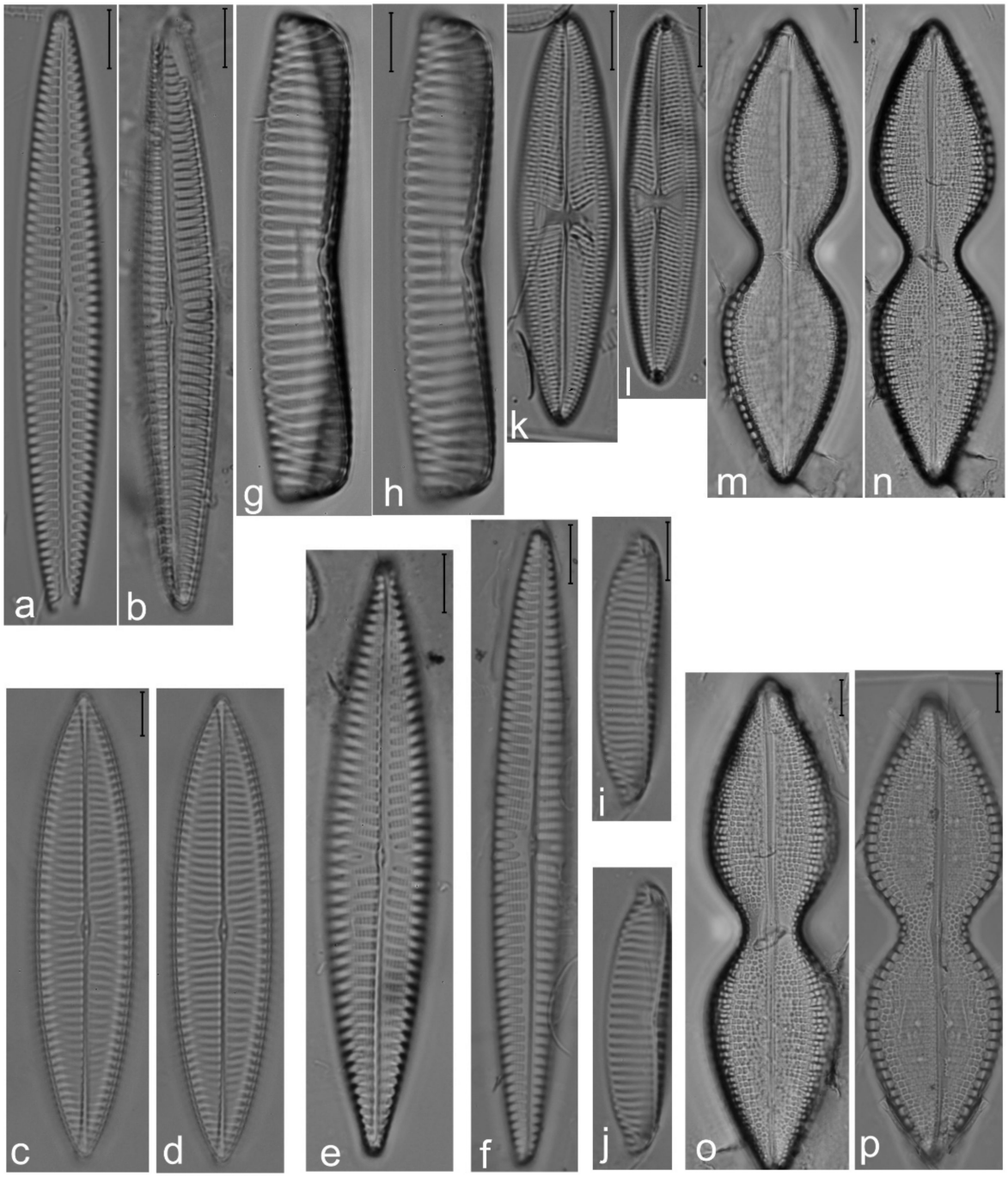

Figure 16. (**a**,**c**,**h**) *Navicula longa* var. *irregularis*; (**b**) *N. longa* var. *longa*; (**d**,**e**) *N. transitans*; (**f**,**g**) *N. pennata*; (**i**,**j**) *N. bipustulata*; (**k**,**l**) *Trachyneis aspera*; (**m**–**p**) *Dictyoneis marginata* var. *maxima* in different focal planes. Scale bar = 10 μm.

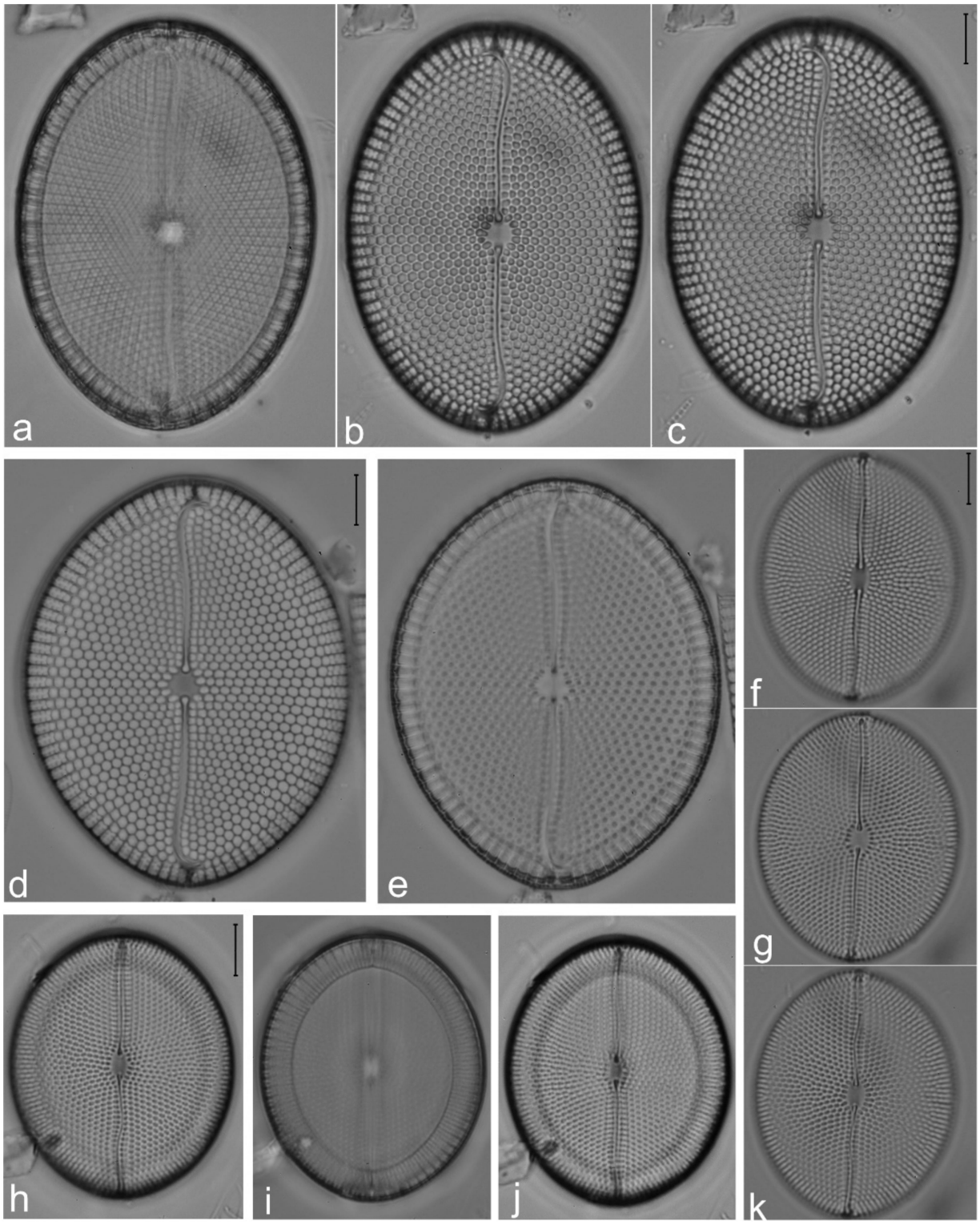

Figure 17. (**a**–**e**) *Mastogloia punctatissima* in different focal planes; (**f**–**k**) *M. cocconeiformis* valve in different focal planes. Scale bar = 10 μm.

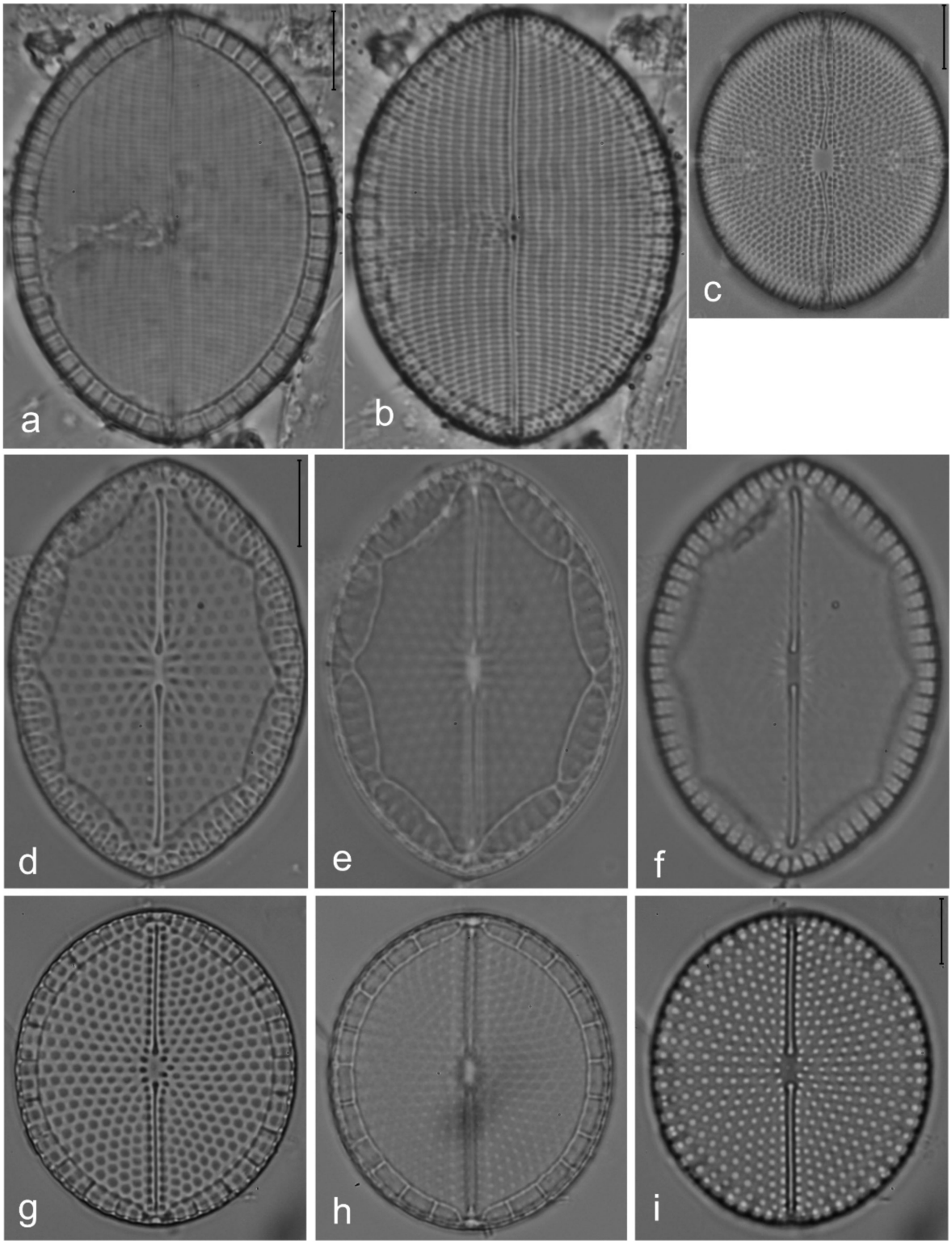

Figure 18. (**a**,**b**) *Mastogloia ovata*; (**c**) *M. cocconeiformis*; (**d**–**f**) *M. fimbriata* in different focal planes; (**g**–**i**) *M. cribrosa* valve in different focal planes. Scale bar = 10 μm.

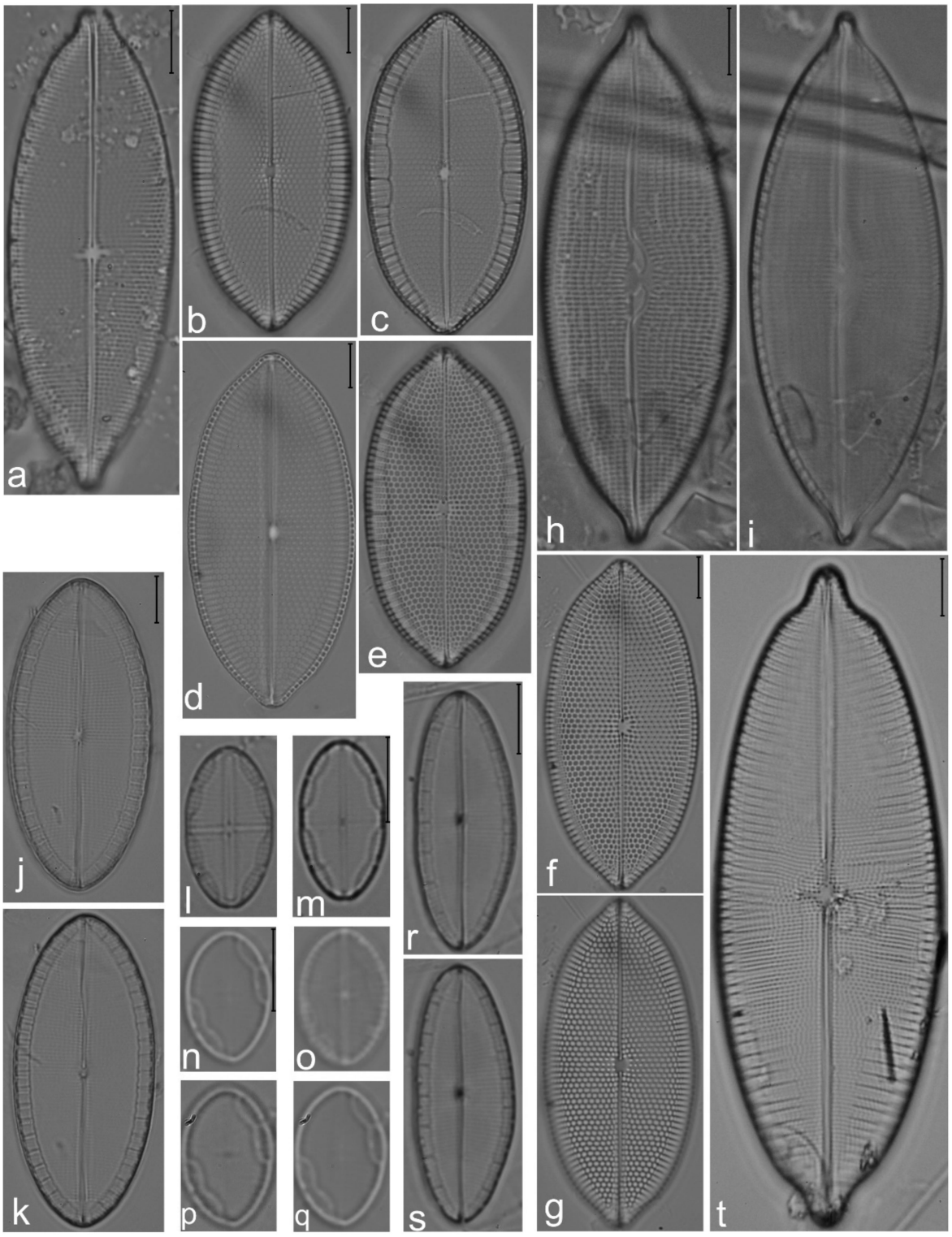

Figure 19. (**a**) *Mastogloia* cf. *elegans*; (**b**–**g**) *M. angulata* in different focal planes; (**h**,**i**) *M. lineata* var. *albifrons*; (**j**,**k**) *M. ovata*; (**l**,**m**) *M. crucicula* var. *crucicula*; (**n**–**q**) *M. crucicula* var. *alternans*; (**r**,**s**) *M. ovulum*; (**t**) *Mastoneis biformis*. Scale bar = 10 µm.

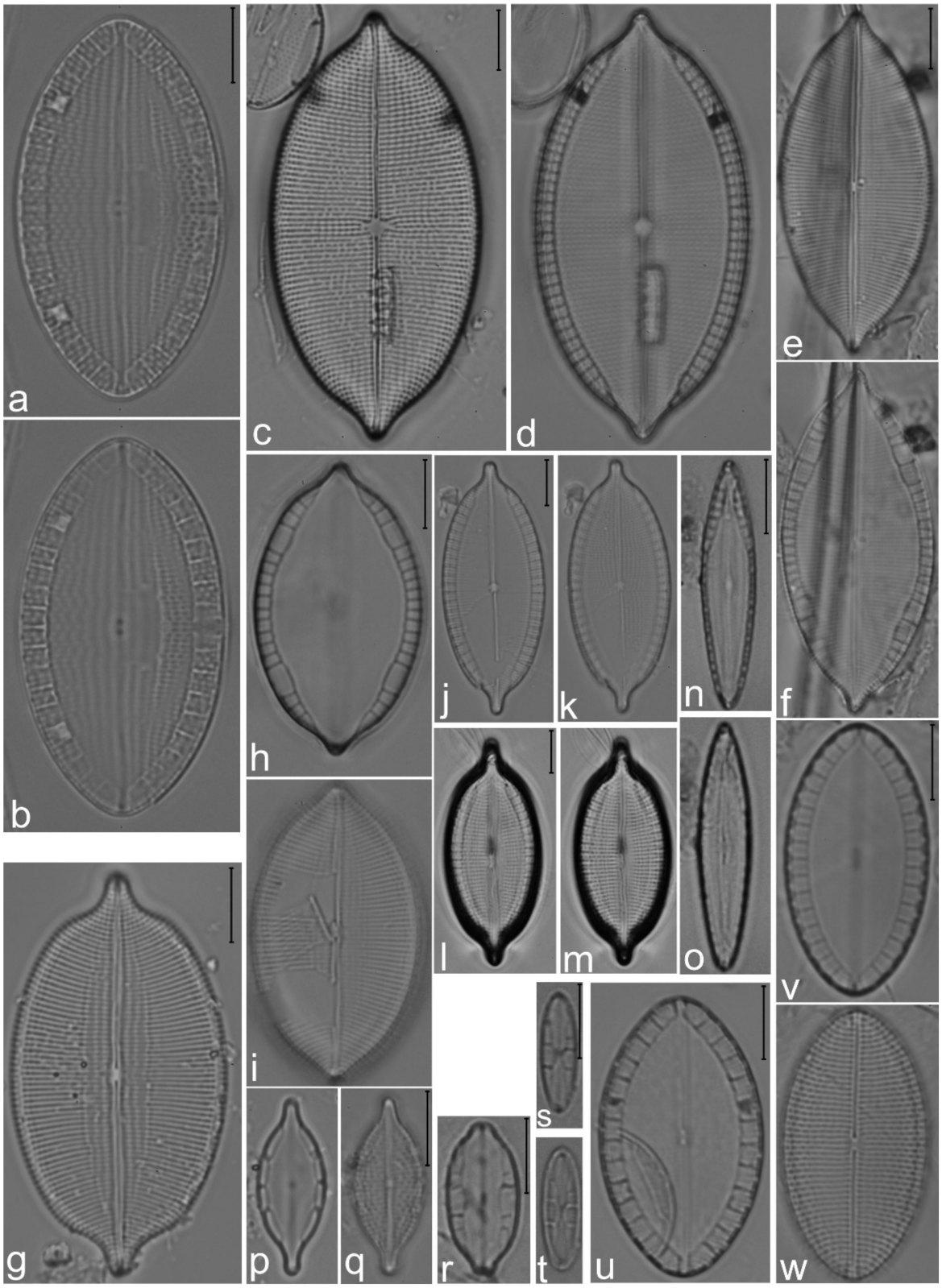

Figure 20. (**a**,**b**,**u**) *Mastogloia ovata*; (**c**,**d**) *M. pseudoelegans*; (**e**–**g**) *M. mauritiana* var. *capitata*; (**h**,**i**) *M. mauritiana* var. *mauritiana*; (**j**,**k**) *M. ignorata*; (**l**,**m**) *M. corsicana*; (**n**,**o**) *M. cuneata*; (**p**,**q**) *M. varians*; (**r**) *M. pusilla* var. *subcapitata*; (**s**,**t**) *M. urveae*; (**v**,**w**) *M. pseudolatecostata*. Scale bar = 10 μm.

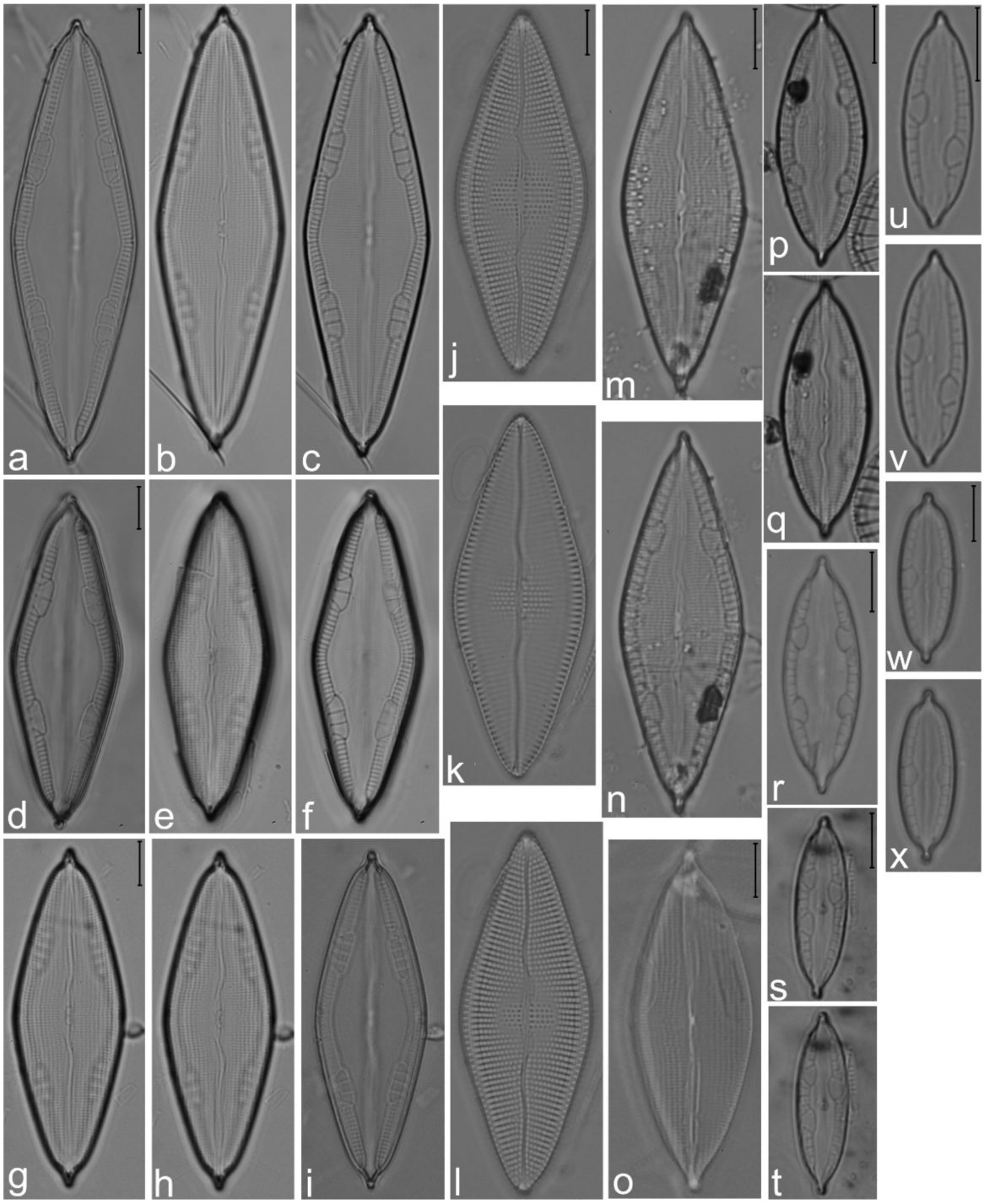

Figure 21. (**a**–**i**,**m**–**r**) *Mastogloia erythraea* var. *erythraea* in different focal planes; (**j**–**l**) *M. rhombica*; (**s**–**v**) *M. erythraea* var. *grunowii* in different focal planes and showing a range in size; (**w**,**x**) *M. biocellata*. Scale bar = 10 μm.

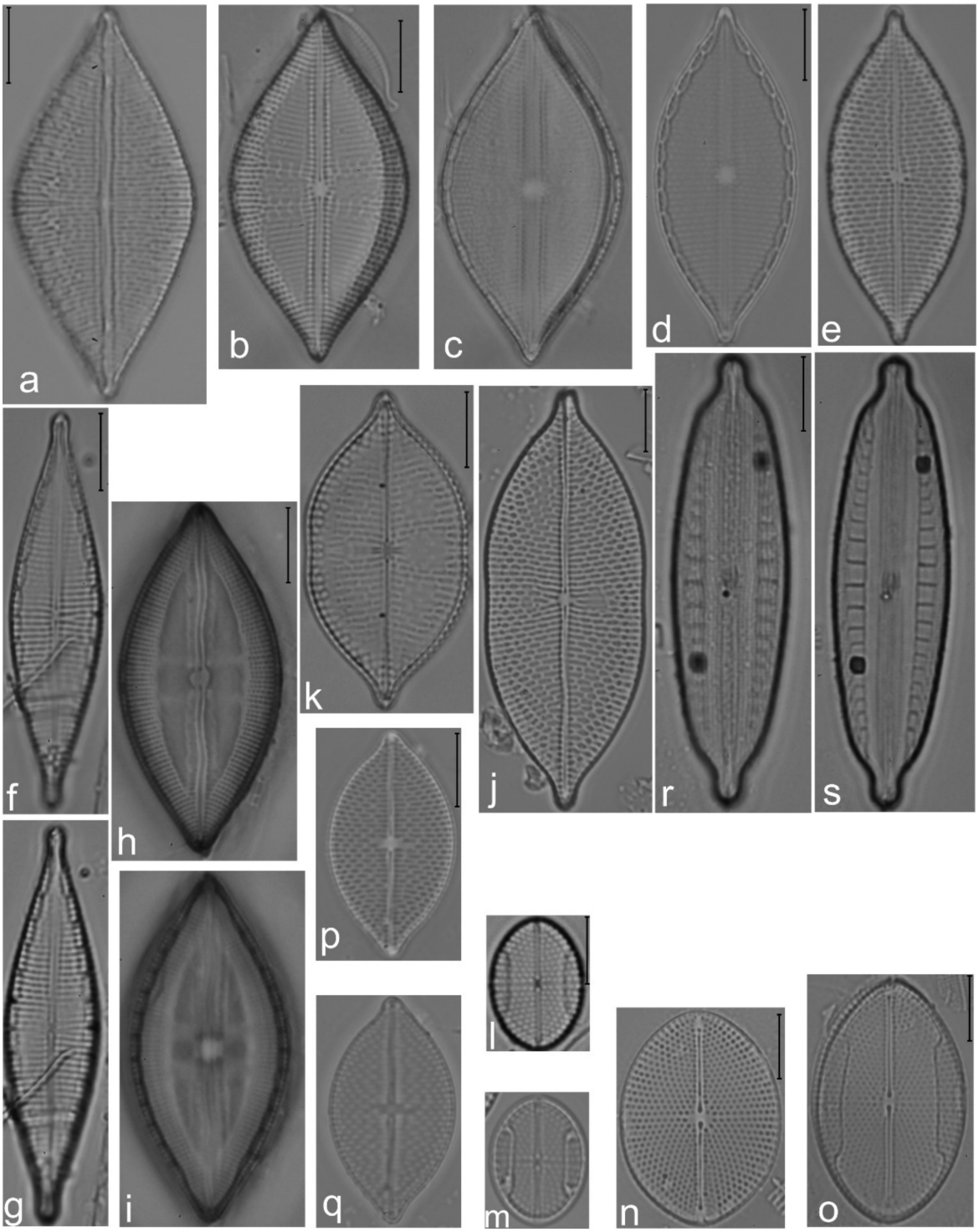

Figure 22. (**a**–**c**) *Mastogloia beaufortiana*; (**d**,**e**) *M. delicatissima*; (**f**,**g**) *M. angusta*; (**h**,**i**) *M. jelinekii*; (**j**,**k**) *M. rostellata*; (**l**–**o**) *M. binotata* in different focal planes and showing a range in size; (**p**,**q**) *M. lacrimata*; (**r**,**s**) *M. similis*. Scale bar = 10 μm.

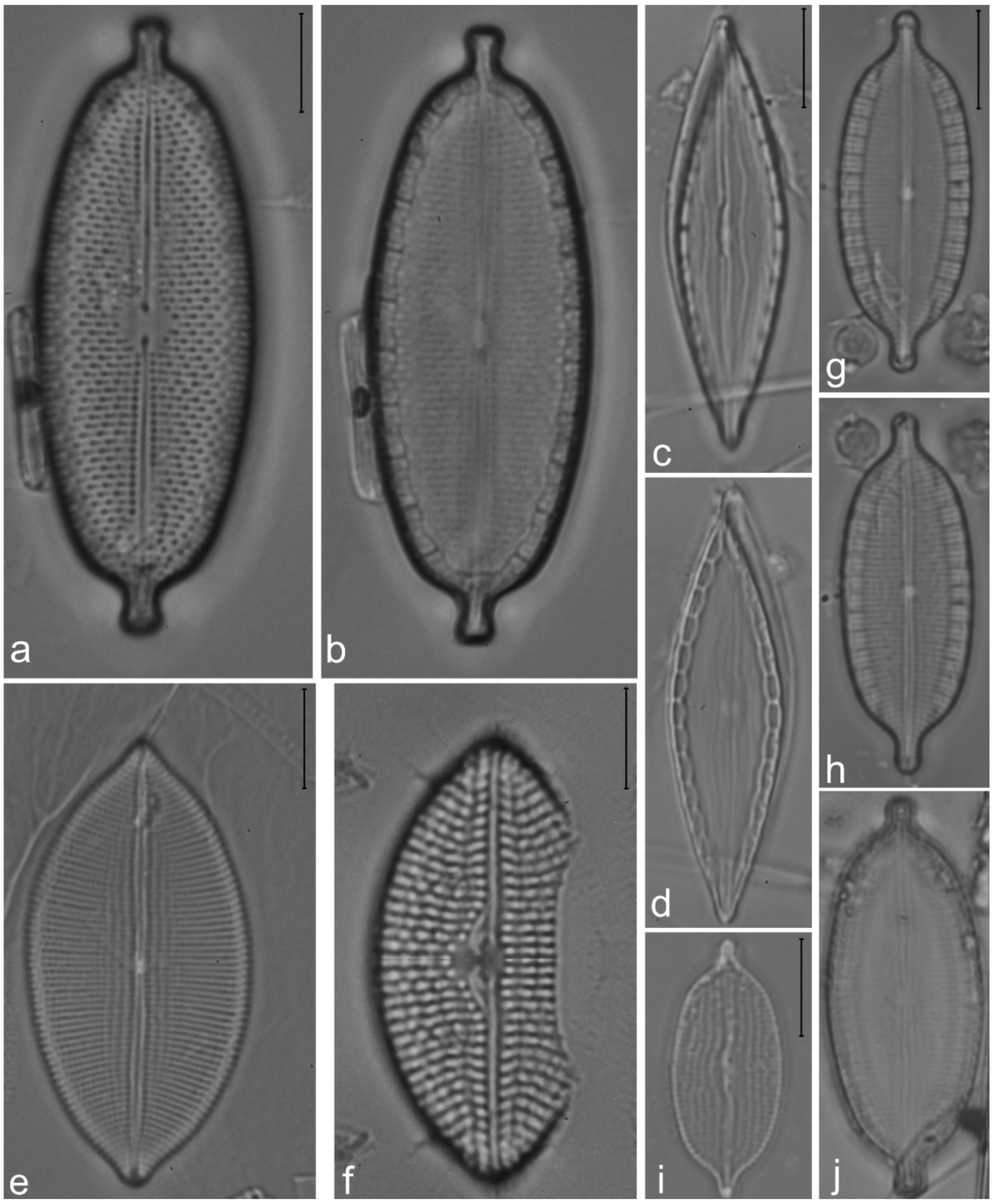

Figure 23. (**a**,**b**,**j**) *Mastogloia stephensiana*; (**c**,**d**) *M. borneensis*; (**e**) *M. mauritiana* var. *mauritiana*; (**f**) *M. bahamensis*; (**g**,**h**) *M. ignorata*; (**i**) *M. parva*. Scale bar = 10 μm.

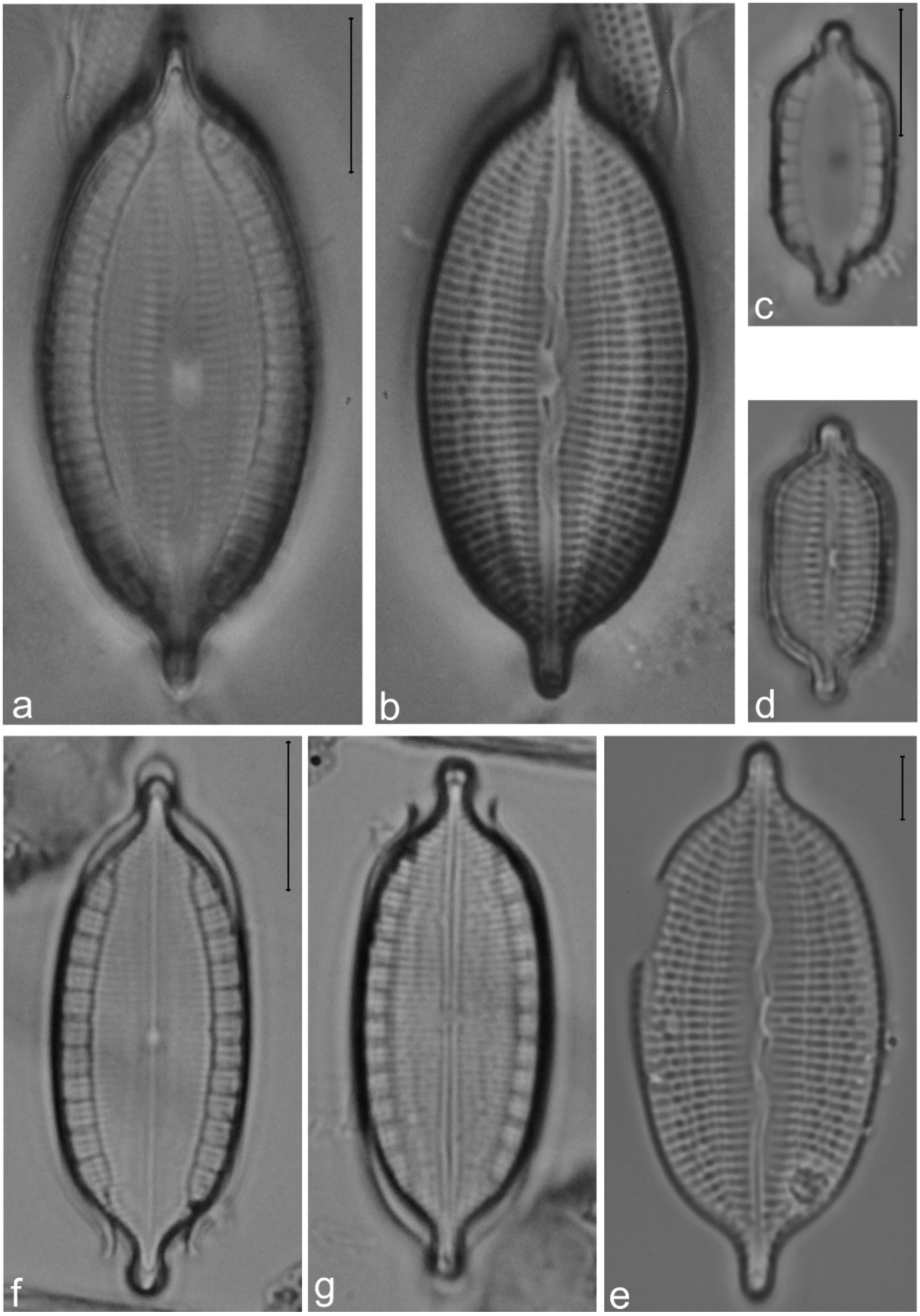

Figure 24. (**a**–**e**) *Mastogloia corsicana* in different focal planes and showing a range in size; (**f**,**g**) *M. ignorata*. Scale bar = 10 μm.

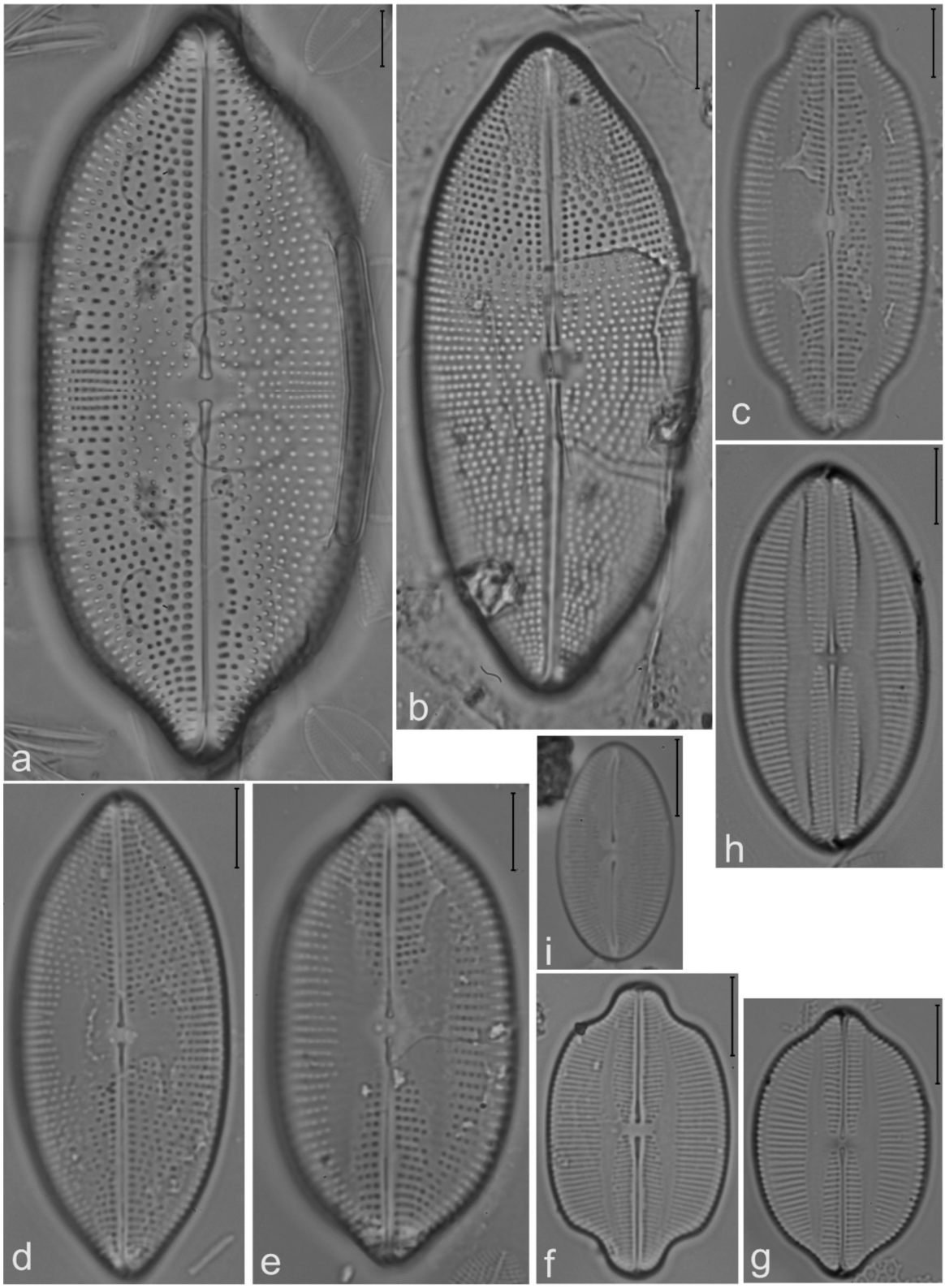

Figure 25. (**a**) *Petroneis subdiffusa*; (**b**) *P. granulata*; (**c**) *Lyrella diffluens*; (**d**) *Petroneis plagiostoma*; (**e**) *Lyrella approximatoides*; (**f**) *L. barbara* var. *densestriata*; (**g**) *L. barbara*; (**h**) *L. excavata*; (**i**) *Fallacia vittata*. Scale bar = 10 μm.

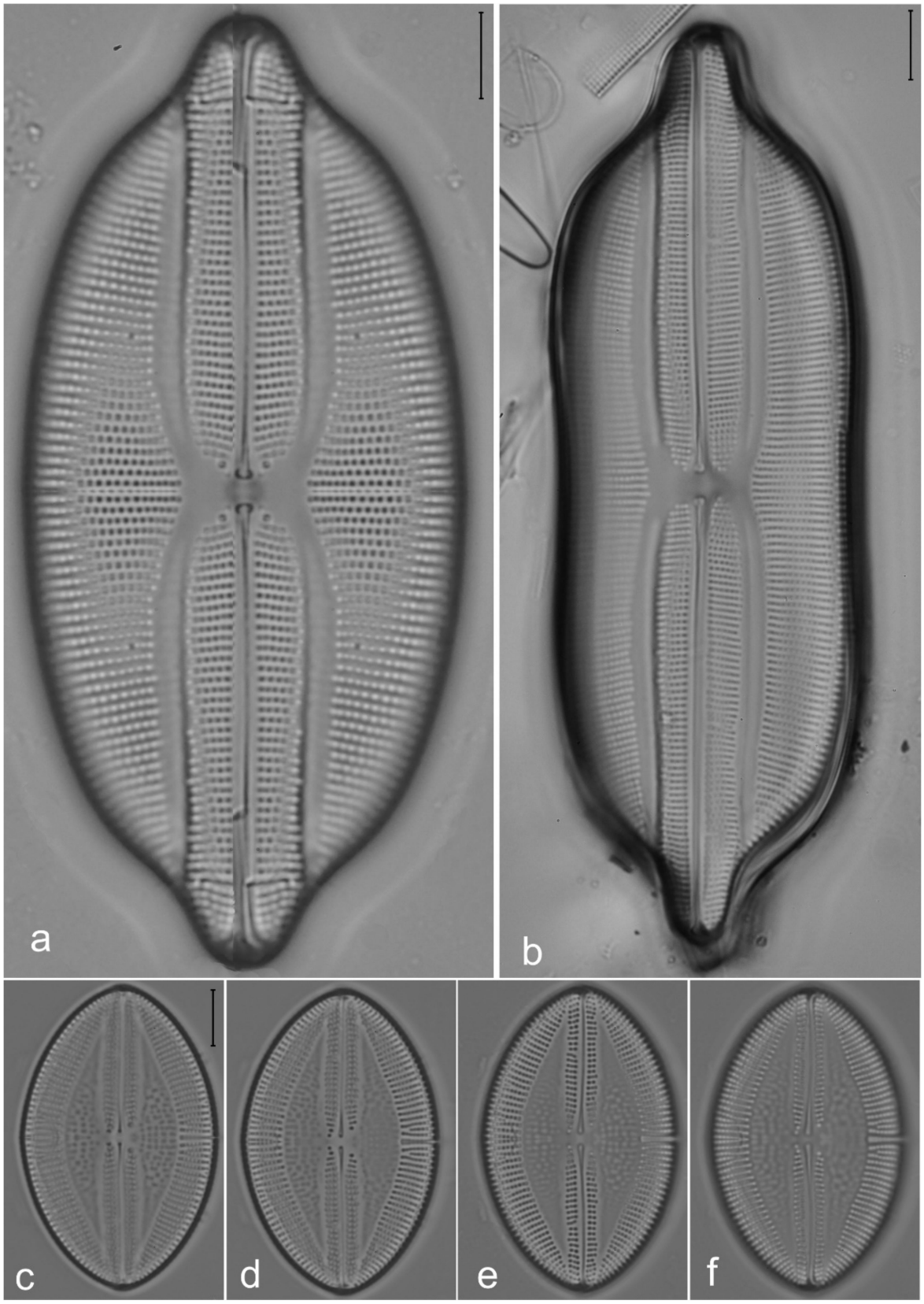

Figure 26. (**a**) *Lyrella lyra* var. *lyra*; (**b**) *L. lyra* var. *constricta*; (**c**–**f**) *L. granulata* in different focal planes. Scale bar = 10 μm.

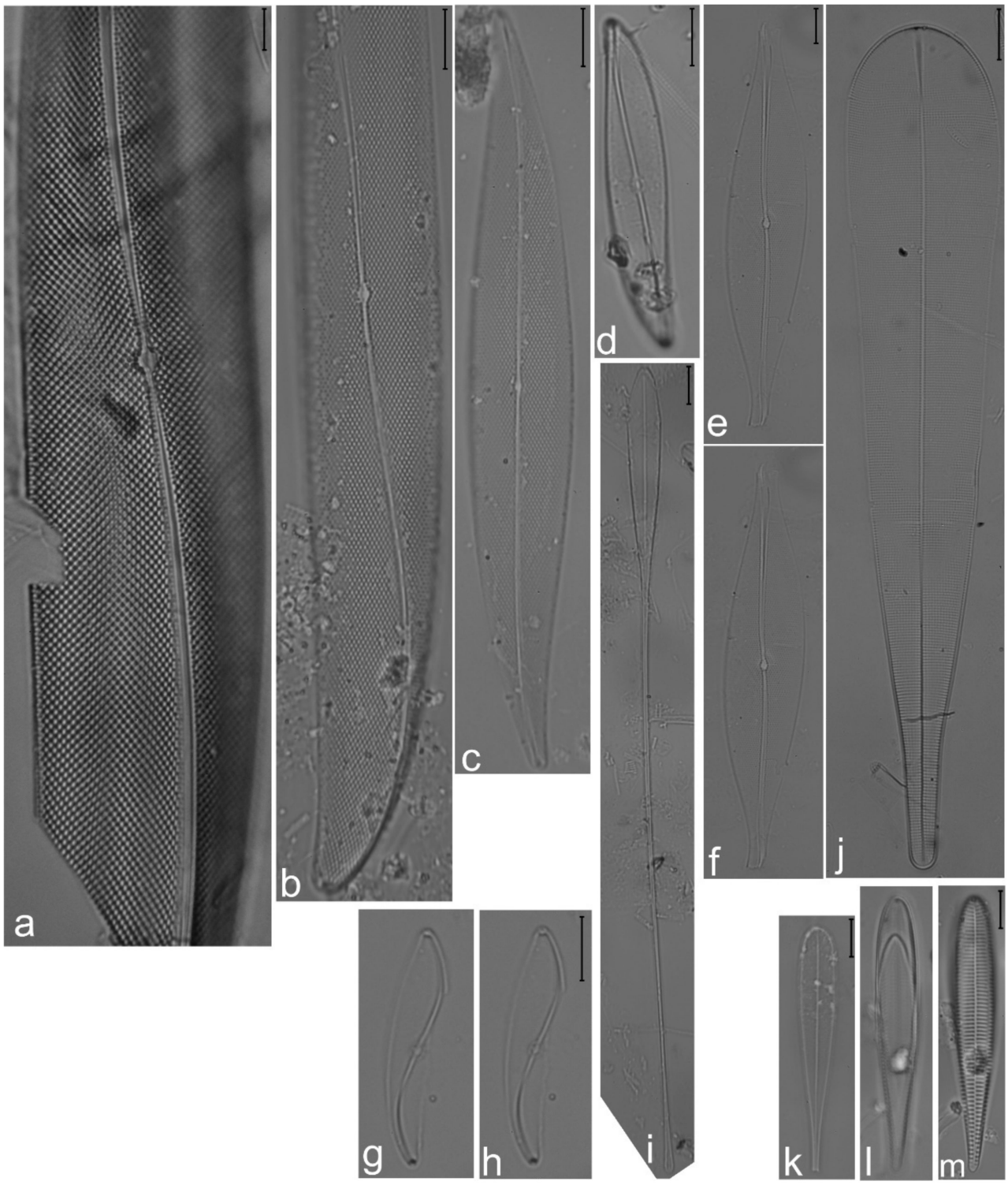

Figure 27. (**a**,**b**) *Pleurosigma formosum*; (**c**) *P. salinarum*; (**d**) *P. obscurum* var. *diminuta*, (**e**,**f**) *P. rostratum*; (**g**,**h**) *Rhoicosigma parvum*; (**i**,**k**) *Licmophora remulus*; (**j**) *L. paradoxa*; (**l**,**m**) *L.* cf. *communis*. Scale bar = 10 μm.

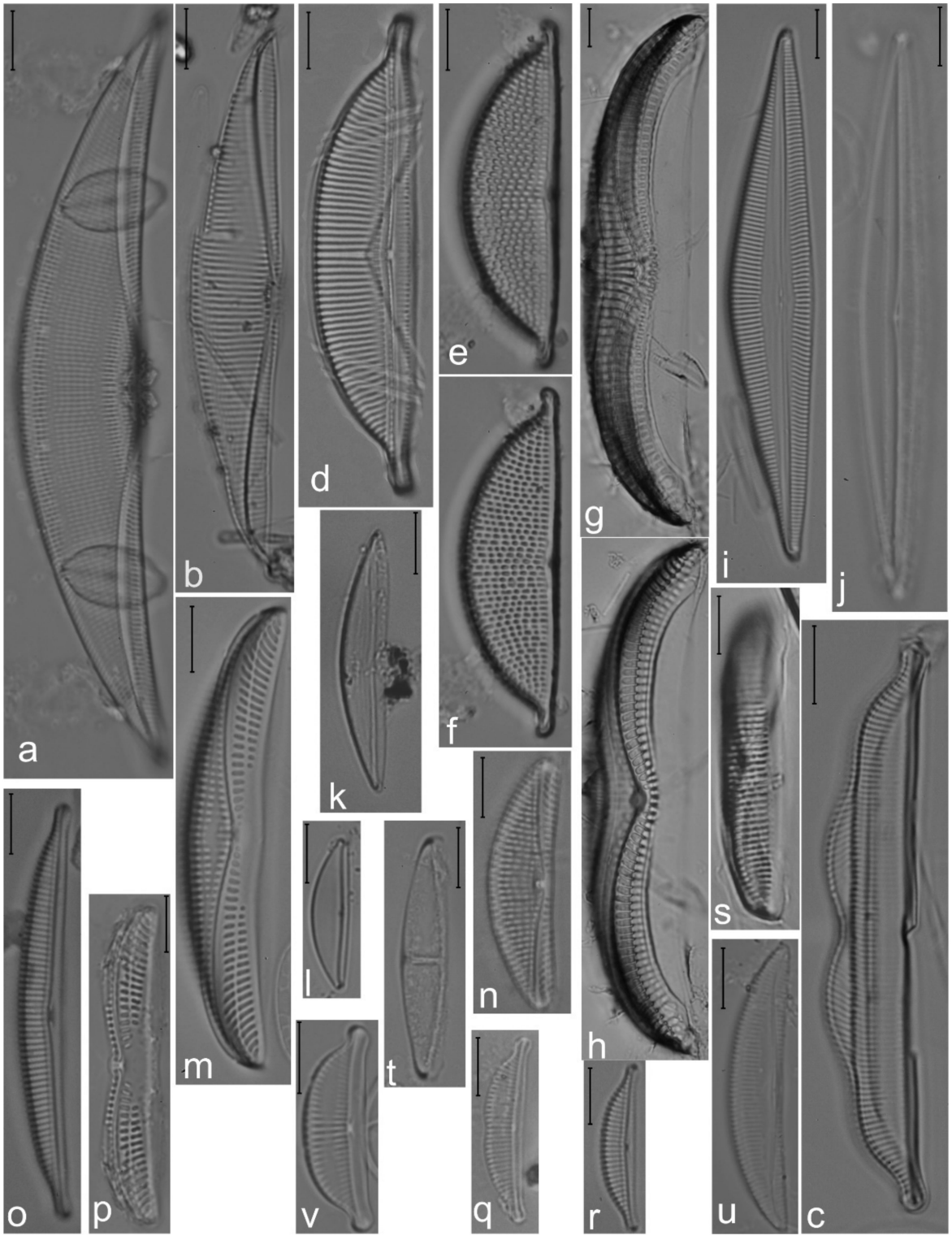

Figure 28. (**a**) *Tetramphora intermedia*; (**b**) *T. securicula*; (**c**) *Amphora floridae*; (**d**) *A. caroliniana*; (**e**,**f**) *A. corpulenta* var. *capitata*; (**g**,**h**) *A. robusta*; (**i**) *Seminavis robusta*; (**j**–**l**) *S. delicatula*; (**m**,**n**) *Amphora proteus*; (**q**) *Halamphora exigua*; (**o**) *H. lineata*; (**p**) *Amphora inelegans* var. *polita*; (**r**) *Halamphora acutiuscula*; (**s**) *Amphora proteoides*; (**t**) *A. laevissima*; (**u**) *A. graeffei* var. *minor*; (**v**) *Halamphora turgida*. Scale bar = 10 µm.

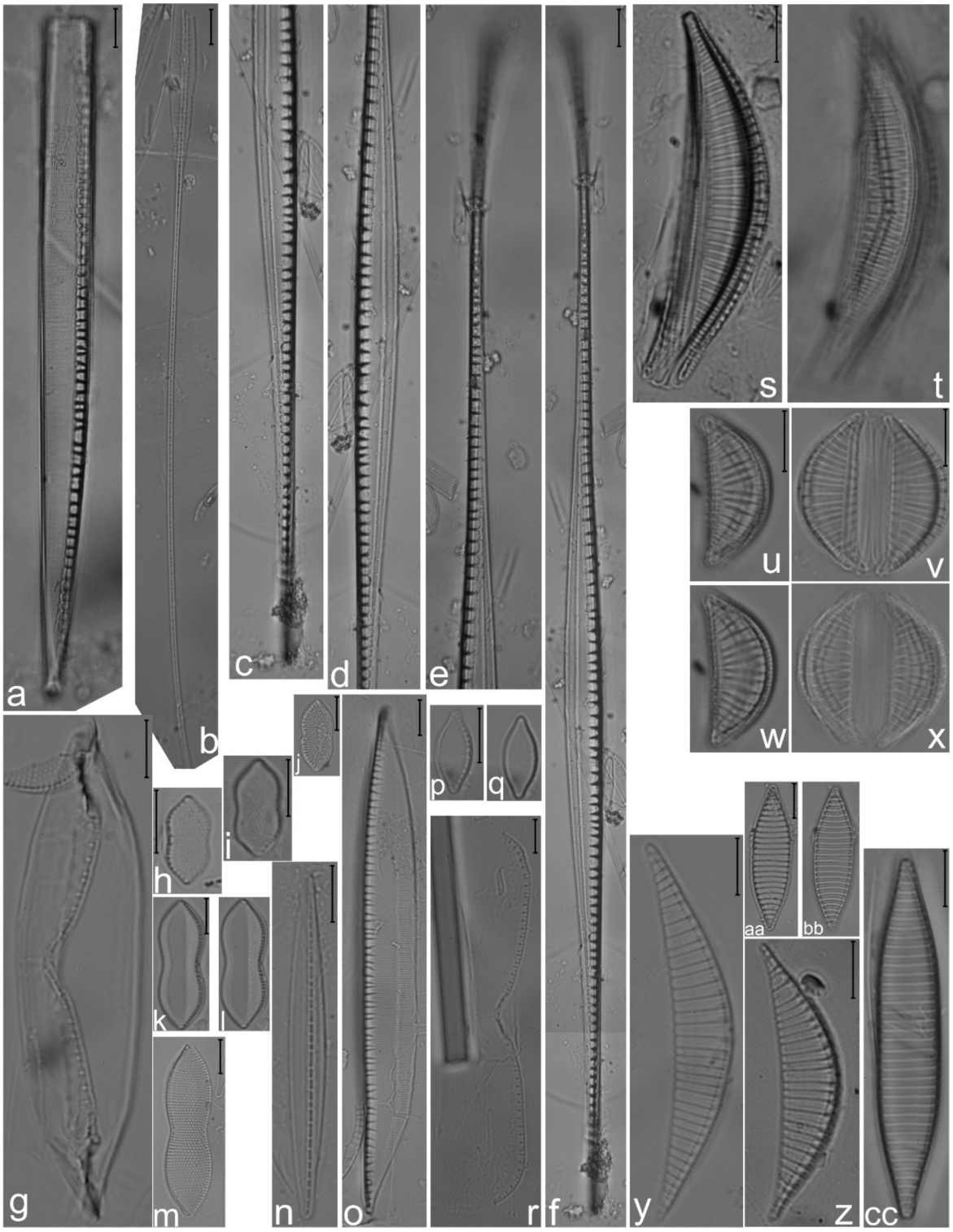

Figure 29. (**a**) *Nitzschia sigma*; (**b**) *N. longissima* f. *costata*; (**c**–**f**) *N. insignis* var. *lanceolata*; (**g**) *N. nienhuisii*; (**h**–**j**) *Psammodictyon panduriforme* var. *continuum*; (**k**,**l**) *Nitzschia carnicobarica*; (**m**) *Psammodictyon constrictum*; (**n**) *Nitzschia angularis*; (**o**) *N. fluminensis*; (**p**,**q**) *N. bicapitata*; (**r**) *N. pellucida*; (**s**,**t**) *Rhopalodia gibberula*; (**u**–**z**) *Epithemia guettingeri*; (**aa**–**cc**) *Nitzschia sicula*. Scale bar = 10 μm.

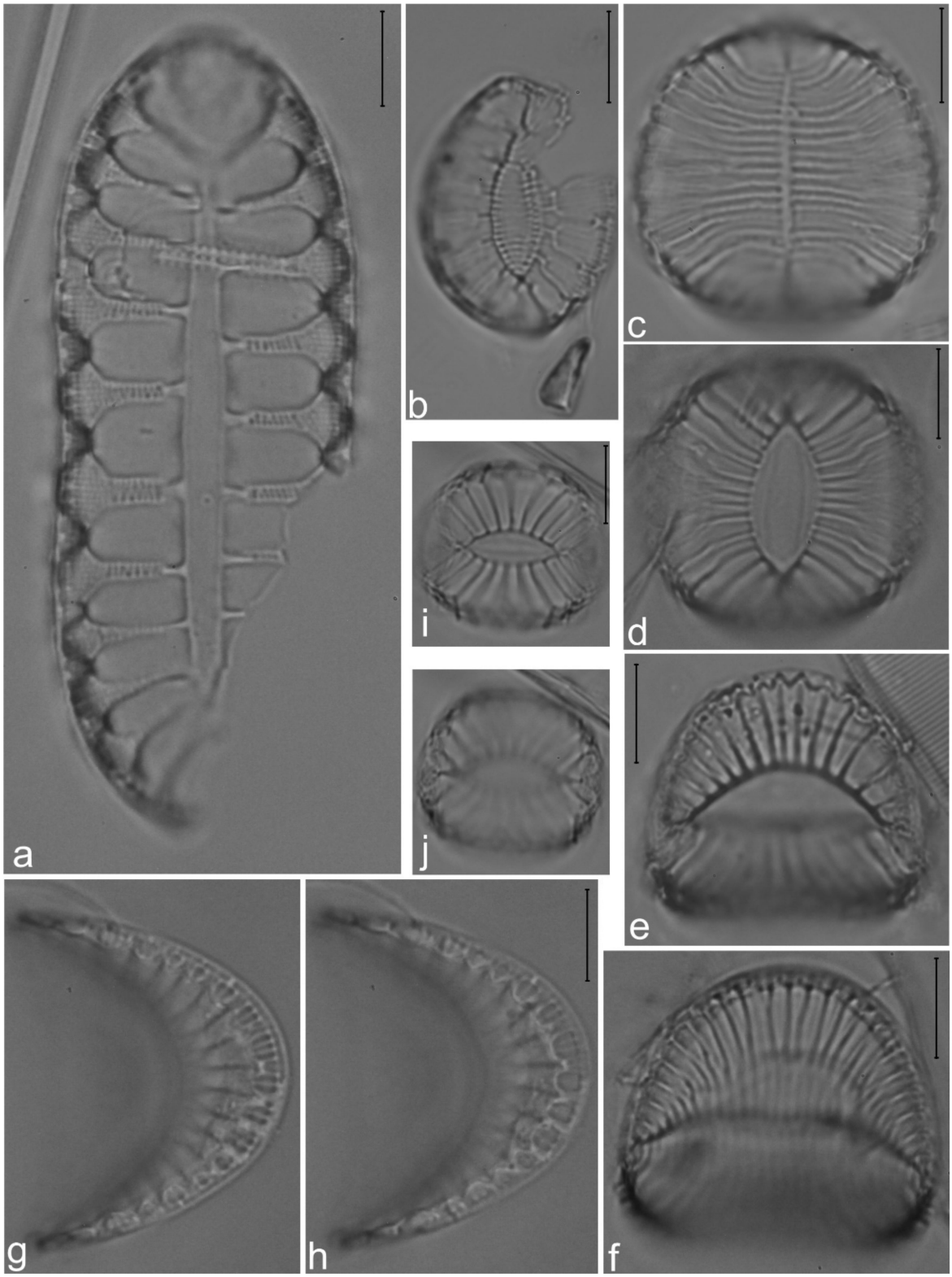

Figure 30. (**a**) *Surirella manca*; (**b**) *Campylodiscus neofastuosus*; (**c**) *Coronia decora*; (**d**,**e**,**i**,**j**) *Campylodiscus subangularis* in different focal planes; (**f**–**h**) *C. cordatus.* Scale bar = 10 μm.

4. Discussion

Although benthic diatoms in general have been little studied as epiphytes of sargasso species, or in the study region, a basic floristic account has been presented that comprises several substrata and localities [37–41] and allows for certain types of comparisons and contrasts that may support the hypothesis posed. One of the first studies of epiphytic diatoms of *Sargassum* spp. [11] recorded 35 species and 18 genera, while others [13,14] reported 7 taxa on *Sargassum* sp. and *S. thunbergia*. Prior to the present study, only two published works [15,16] on the epiphytic diatoms of *S. fluitans* and *S. natans* existed, one on thalli from the Gulf of Mexico, the other on findings in the Sargasso Sea. Overall, 63 taxa were recorded in the two studies, but only four were identified in both (*Cyclotella meneghiniana* Kutz., *Mastogloia binotata* (Grun.) Cl. *M. erythraea* Grun., and *M. pusilla* Grun.).

The low number of diatom species (10) reported in [15] on *S. fluitans* and *S. natans* suggested that these sargasso species were not propitious substrata for the settlement and growth of diatom assemblages. However, the 184 taxa recorded in the present work indicate otherwise, as this figure surpasses the 107 diatom taxa recorded for *Thalassia testudinum* samples from a nearby area [42]. On the other hand, previous studies inspected samples collected further offshore while we collected as close as 50 m from the beach. However, the observed differences seem more an issue of floristic effort. Besides, the rinsing of the sargasso specimens should have washed away any loosely deposited elements from the shore, leaving only the firmly attached forms. Although certain risks of washing away attached stalked forms should be considered in future studies. Notwithstanding, adding all the taxa from the three studies gives a total of 220 in 71 genera of epiphytic diatoms from *S. fluitans* and *S. natans*.

However, only 19 of these taxa were found in all three studies: *Achnanthes brevipes* var. *intermedia*, *Cocconeis scutellum* var. *scutellum*, *Coscinodiscus radiatus*, *Cyclotella atomus*, *Diploneis weissflogii*, *Grammatophora oceanica* Ehrenberg, *Halamphora exigua*, *Licmophora remulus*, *Mastogloia angulata*, *M. binotata*, *M. crucicula* (Grunow) Cleve, *M. erythraea* var. *erythraea*, *M. ovulum*, *M. pusilla* var. *subcapitata*, *Pleurosigma salinarum*, *Psammodiscus nitidus*, *Rhopalodia gibberula*, *Striatella unipunctata*, and *Tabularia* cf. *fasciculata*. At the level of genus, only *Bacillaria*, *Thalassionema* and *Trachysphenia* did not appear in our samples.

In contrast, the percentage of genera with a single taxon (species/infraspecies [54%]) in this study was lower than for other substrata recorded on the Yucatan Peninsula [37,39,41,42]. This suggests that the differences observed are due to floristic effort, and that the taxa common to all studies are the most abundant ones in the assemblages. One finding that stands out is that the number of taxa of *Nitzschia* (10), *Amphora* (9), and *Navicula* (6) was very low, though they usually contributed the highest number of species and infraspecies of benthic diatoms [10]. This suggests that these sargasso species are not a favorable habitat for species of the "most frequent" diatom genera. This seems to be especially true for *S. natans*, as only two *Navicula* species were found on that material. This suggests that these sargasso species are sui generis habitats.

In addition to the above, the identification of *Amphora floridae*, one of 21 new taxa recorded earlier from Florida [43], could indicate the importance of contrasting the subequatorial origin of the sargasso [8], by comparing diatom floristics from strategic localities using specific taxa. Unfortunately, the time scale involved in the circulation system around the NERR would likely cloud any possible connectivity among the diatom taxocoenoses.

Turning to specific taxa as biogeographical indicators, *Mastogloia* species have been proposed as being of tropical affinity based on a high number of taxa recorded on Mexican littorals [37,39,44]. Thus, the 37 *Mastogloia* taxa recorded here, which represented a dominant component of the assemblages described from the two sargasso species, seem to indicate tropical affinity and thus support the hypothesis. However, these taxa were mostly dissimilar to those described in other tropical regions, such as the Revillagigedo Archipelago, for which the first exploratory studies yielded 51 *Mastogloia* taxa [40,45]. Moreover, other genera, such as *Grammatophora* and *Caloneis*, also considered tropical [38], were poorly represented in the sargasso assemblages.

It should be noted however, that during the identification process, the infraspecies taxon *Navicula barbara* var. *densestriata* was here transferred to the genus *Lyrella*, as *Lyrella barbara* var. *densestriata*, thus a new combination, based on the obvious lyra characterizing this genus.

With regard to other factors, it has been suggested in general that *S. natans* and *S. fluitans* are natives of oligotrophic environments, so a continental supply of nutrients would be required for these massive proliferations to occur [46,47]. In this sense, the low number of taxa (13) recorded earlier [15] for samples from the Sargasso Sea would correspond to a nutrient-poor environment. In addition, it could be assumed that the 50 taxa recorded in samples from the Gulf of Mexico [16] might reflect similar conditions. However, the high species richness of diatoms in this study (184 taxa) does not concur with an oligotrophic environment, which may be deemed extreme, and where the species richness of benthic diatoms is low [10]. This condition is attributed to the Gulf of Mexico, even though the coastal zone and the existence of a nutricline renders it a moderate-to-high productive zone [4,48]. Finally, high concentrations of phosphates have been reported in the water column between the pelagic sargasso beds, suggesting that this nutrient may favor the growth of the holobionts associated with this sargasso, including diatoms [49].

5. Conclusions

According to these findings, a thorough floristic effort showed that epiphytic diatom assemblages currently thrive on the substrata provided by the pelagic populations of *S. natans* and *S. fluitans*, indicating that favorable conditions exist there, including nutrient availability. The overall high species richness, especially that of the genus *Mastogloia*, suggests that these diatom assemblages are of tropical affinity and originated in a region distinct from the Sargasso Sea, most likely in an area between the coasts of Africa and Brazil in the North Equatorial Region.

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References

1. Capdevila-Argüelles, L.; Zilletti, B.; Suárez Álvarez, V.A. *Cambio Climático y Especies Exóticas Invasoras en España. Diagnóstico Preliminar y Bases de Conocimiento Sobre Impacto y Vulnerabilidad*; Oficina Española de Cambio Climático, Ministerio de Medio Ambiente y Medio Rural y Marino: Madrid, Spain, 2011; p. 146.
2. Vázquez-Delfín, E.; Freile-Pelegrín, Y.; Salazar-Garibay, A.; Serviere-Zaragoza, E.; Méndez-Rodríguez, L.; Robledo, D. Species composition and chemical characterization of Sargassum influx at six different locations along the Mexican Caribbean coast. *Sci. Total Environ.* **2021**, *795*, 148852. [CrossRef] [PubMed]
3. Dawes, C.J.; Mathieson, A.C. *The Seaweeds of Florida*; University Press of Florida: Gainesville, FL, USA, 2008; p. 592.

4. Gower, J.; Young, E.; King, S. Satellite images suggest a new Sargassum source region in 2011. *Remote Sens. Lett.* **2013**, *4*, 764–773. [CrossRef]
5. De Széchy, M.T.M.; Guedes, P.M.; Baeta-Neves, M.H.; Oliveira, E.N. Verification of Sargassum natans (Linnaeus) Gaillon (Heterokontophyta: Phaeophyceae) from the Sargasso Sea off the coast of Brazil, western Atlantic Ocean. *Check List* **2012**, *8*, 638–641. [CrossRef]
6. Johnson, D.R.; Dong, K.O.; Franks, J.; Moreno, P.; Sánchez-Rubio, G. The Sargassum Invasion of the Eastern Caribbean and Dynamics of the Equatorial North Atlantic. In Proceedings of the 65th Gulf and Caribbean Fisheries Institute, Santa Marta, Colombia, 5–9 November 2012.
7. Franks, J.; Johnson, D.; Ko, D. Pelagic Sargassum in the tropical North Atlantic. *Gulf Carib. Res.* **2016**, *27*, SC6–SC11. [CrossRef]
8. Franks, J.S.; Johnson, D.J. *Summary Report Describing Pelagic Sargassum Seaweed Growth, Abundance and Mass Transport within the North Equatorial Recirculation Region (NERR) and Eastern Caribbean for 2014 and 2015*; Food and Agriculture Organization of the United Nations (FAO) By Center for Fisheries Research and Development (CFRD), The University of Southern Mississippi School of Ocean Science and Engineering Gulf Coast Research Laboratory (GCRL): Ocean Springs, MS, USA, 2018; p. 9.
9. Tiffany, M.A. Epizoic and epiphytic diatoms. In *The Diatom World. Cellular Origin, Life in Extreme Habitats and Astrobiology*; Seckbach, J., Kociolek, J.P., Eds.; Springer: New York, NY, USA, 2011; Volume 19, pp. 197–209. [CrossRef]
10. Siqueiros Beltrones, D.A. *Diatomeas Bentónicas de la Península de Baja California, Diversidad y Potencial Ecológico*; IPN-CICIMAR-UABCS: La Paz, Mexico, 2002; p. 102.
11. Grunow, A. Diatomeen auf Sargassum von Honduras, gesammelt von Lindig. *Hedwegia* **1867**, *6*, 17–37.
12. Hentschel, E. Uber den Bewuchs auf den Treibenden Tagen der Sargassosee. *Mitteil. Zool. Staatsinst. Mus. Hamburg.* **1921**, *38*, 1–26.
13. Takano, H. Epiphytic diatoms upon Japanese agar sea-weeds. *Bull. Tokai Reg. Fish. Res. Lab.* **1961**, *31*, 269–274.
14. Takano, H. Notes on epiphytic diatoms upon seaweeds from Japan. *J. Oceanogr. Soc. Jpn.* **1962**, *18*, 29–33. [CrossRef]
15. Carpenter, E.J. Diatoms attached to floating Sargassum in the western Sargasso Sea. *Phycologia* **1970**, *9*, 269–274. [CrossRef]
16. Maples, R.S. The epiphytic diatom flora of two Sargassum species. *Gulf Res. Rep.* **1984**, *7*, 373–375. [CrossRef]
17. Dreckmann, K.M.; Sentíes, A. Los arribazones de algas marinas el caribe mexicano: Evento biológico natural o basura en las playas. *Conabio Biodiversitas* **2013**, *107*, 7–11.
18. Littler, D.S.; Littler, M.M. *Caribbean Reef Plants: An Identification Guide to the Reef Plants of the Caribbean, Bahamas, Florida and Gulf of Mexico*; Offshore Graphics: Washington, DC, USA, 2000; p. 542.
19. Peragallo, H.; Peragallo, M. *Diatomées Marines de France et des Districts Maritimes Voisins*; Tempère, J., Ed.; Micrographe-Editeur: Grez-sur-Loing, France, 1908; pp. 1–491.
20. Hein, M.K.; Winsborough, B.M.; Sullivan, M.J. *Bacillariophyta (Diatoms) of the Bahamas*; A.R.G. Gantner Verlg, K.G.: Ruggell, Liechtenstein, 2008; p. 302.
21. Hustedt, F. *Marine Littoral Diatoms of Beaufort, North Carolina*; Duke University Press: Durham, NC, USA, 1955; p. 67.
22. Cleve-Euler, A. *Die Diatomeen von Schweden und Finnland. Part III. Monoraphideae, Biraphideae 1*; Kongliga Svenska Vetenskaps-Akademiens Handligar: Stockholm, Sweden, 1953; p. 255.
23. Schmidt, A.W.F.; Schmitz, M.; Fricke, F.; Müller, O.; Heiden, H.; Hustedt, F. *Atlas der Diatomaceen-Kunde*; 4 Bands, pls. 1–480; Koeltz Scientific Books: Königstein, Germany, 1972; pp. 1874–1959.
24. Foged, N. Some littoral diatoms from the coasts of Tanzania. *Biblioth. Phycol.* **1975**, *16*, 1–127.
25. Foged, N. Diatoms in Eastern Australia. *Biblioth. Phycol.* **1978**, *41*, 1–243.
26. Foged, N. Freshwater and littoral diatoms from Cuba. *Biblioth. Diatom.* **1984**, *5*, 1–243.
27. Moreno, J.L.; Licea, S.; Santoyo, H. *Diatomeas del Golfo de California*; Universidad Autónoma de Baja California Sur-SEP-FOMES-PROMARCO: Tijuana, Mexico, 1996; p. 273.
28. Witkowski, A.; Lange-Bertalot, H.; Metzeltin, D. Diatom Flora of Marine Coasts. In *Iconographia Diatomologica*; Lange-Bertalot, H., Ed.; Koeltz Scientific Books: Königstein, Germany, 2000; pp. 1–925.
29. Novelo, E.; Tavera, R.; Ibarra, C. Bacillariophyceae from karstic wetlands in Mexico. *Biblioth. Diatom.* **2007**, *54*, 136.
30. López-Fuerte, F.O.; Siqueiros Beltrones, D.A.; Navarro, J.N. *Benthic Diatoms Associated with Mangrove Environments in the Northwest Region of Mexico*; CONABIO-UABCS-IPN: La Paz, Mexico, 2010; p. 217.
31. Stidolph, S.R.; Sterrenburg, F.A.S.; Smith, K.E.L.; Kraberg, A.; Stuart, R. Stidolph Diatom Atlas. U.S. Geological Survey Open-File Report 2012-1163. Available online: http://pubs.usgs.gov/of/2012/1163/ (accessed on 16 April 2022).
32. Loir, M.; Novarino, G. *Marine Mastogloia Thwaites ex W. Sm. and Stigmaphora Wallich Species from the French Lesser Antille*; Diatom Monographs, Koeltz Scientific Books: Königstein, Germany, 2013; Volume 16, p. 133.
33. Lobban, C.S.; Schefter, M.; Jordan, R.W.; Arai, Y.U.; Sasaki, A.S.; Theriot, E.C.; Ashworth, M.A.; Ruck, E.C.; Pennesi, C.H. Coral-reef diatoms (Bacillariophyta) from Guam: New records and preliminary checklist, with emphasis on epiphytic species from farmer-fish territories. *Micronesica* **2012**, *43*, 237–479.
34. Round, F.E.; Crawford, R.M.; Mann, D.G. *The Diatoms: Biology & Morphology of the Genera*; Cambridge University Press: Cambridge, UK, 1990; p. 747.
35. Guiry, M.D.; Guiry, G.M. Algaebase. Available online: http://www.algaebase.org (accessed on 23 June 2020).
36. WoRMS Editorial Board. World Register of Marine Species. Available online: http://www.marinespecies.org (accessed on 23 June 2022).

37. López-Fuerte, F.O.; Siqueiros-Beltrones, D.A.; Veleva, L.; Huerta-Quintanilla, D.A. Species composition and association structure of microfouling diatom assemblages growing on fiber-glass plates off the coast of Yucatán, México. *Hidrobiologica* **2017**, *27*, 23–37. [CrossRef]
38. Siqueiros Beltrones, D.A.; Martínez, Y.J. Prospective floristics of epiphytic diatoms on Rhodophyta from the southern Gulf of Mexico. *Cicimar Oceánides* **2017**, *32*, 35–49. [CrossRef]
39. López-Fuerte, F.O.; Siqueiros Beltrones, D.A.; Veleva, L. Diatoms (Bacillariophyta) from artificial substrates and sediments in the Caribbean Sea off Yucatan, Mexico. *Phytotaxa* **2019**, *406*, 1–54. [CrossRef]
40. Siqueiros Beltrones, D.A.; López-Fuerte, F.O.; Martínez, Y.J.; Altamirano-Cerecedo, M.C. A first estimate of species diversity for benthic diatom assemblages from the Revillagigedo Archipelago, México. *Diversity* **2021**, *13*, 458. [CrossRef]
41. López-Mejía, D.; Siqueiros-Beltrones, D.A.; López-Fuerte, F.O.; Gutiérrez-Mendieta, F. Floristics of epiphytic diatoms on Thalassia testudinum from the southern Gulf of Mexico. *Cymbella* **2021**, *7*, 18–35.
42. López-Fuerte, F.O.; Siqueiros-Beltrones, D.A.; Hernández-Almeida, O.U. Epiphytic diatoms of Thalassia testudinum in Yalahau lagoon, Quintana Roo, Mexico. *Mar. Biodivers. Rec.* **2013**, *6*, e107. [CrossRef]
43. Wachnika, A.H.; Gaiser, E.E. Characterization of Amphora and Seminavis from South Florida, U.S.A. *Diatom Res.* **2007**, *22*, 387–455. [CrossRef]
44. Siqueiros-Beltrones, D.; López-Mejía, D.; Gutiérrez-Mendieta, F. High species richness of epiphytic Mastogloia Thwaites ex W. Sm. (Mastogloiales; Bacillariophyceae) on Thalassia testudinum K.D. Koenig from the southern Gulf of México. *Rev. Mex. Biodivers.* **2020**, *91*, e9129763. [CrossRef]
45. Siqueiros Beltrones, D.A.; López-Fuerte, F.O.; Martínez, Y.J.; Altamirano-Cerecedo, M.C. Additions to the Mastogloia (Bacillariophyceae: Mastogloiales) of the Revillagigedo Archipelago, Mexico. *Rev. Mex. Biodivers.* **2022**, *93*, e934033. [CrossRef]
46. Lapointe, B.E. A comparison of nutrient-limited productivity in Sargassum natans from neritic vs. oceanic waters of the western North Atlantic Ocean. *Limnol. Oceanogr. Bull.* **1995**, *40*, 625–633. [CrossRef]
47. Fernández, F.; Boluda, C.J.; Olivera, J.; Guillermo, L.A.; Gómez, B.; Echavarria, E.; Mendis, A. Análisis elemental prospectivo de la biomasa algal acumulada en las costas de la República Dominicana. *Rev. Cent. Azúcar.* **2017**, *44*, 11–22.
48. Biggs, D.C.; Muller-Karger, F.E. Ship and satellite observations of chlorophyll stocks in interacting cyclone-anticyclone eddy pairs in the western Gulf of Mexico. *J. Geophys. Res.* **1994**, *99*, 7371–7384. [CrossRef]
49. Culliney, J.L. Measurements of reactive phosphorus associated with pelagic Sargassum in the northwest Sargasso Sea. *Limnol. Oceanogr.* **1970**, *15*, 304–306. [CrossRef]