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A First Estimate of Species Diversity for Benthic Diatom Assemblages from the Revillagigedo Archipelago, Mexico

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Abstract: Recent investigations at previously unexplored localities on the Mexican coast have confirmed the high taxonomic potential of benthic marine diatom assemblages (BMDA) in the region. An exploratory study of epiphytic diatoms of macroalgae in the Revillagigedo Archipelago (RA) suggested that further studies would yield many more taxa, prompting the hypothesis that diversity measurements, based on ecological indices, would be among the highest in pristine environments. Thus, the aim of this research was to enrich the record of epiphytic diatom floristics of the RA, and to estimate species diversity based on information theory (H'). Floristically, 167 identified taxa are added here to the BMDA species list of the RA, bringing the total to 397 taxa overall, including 52 taxa that are potentially new records for the Mexican Pacific coast. Among the most conspicuous genera are *Mastogloia* with five new taxa and it remains the most diverse genus with 55 taxa overall, followed by *Cocconeis* (27), *Nitzschia* (24), *Amphora* (23), *Navicula* (19), *Diploneis* (17) and *Grammatophora* (15). As expected for a pristine environment, the computed species diversity values for the BMDA were high, ranging from $H' = 3.92–5.2$, depicting stability. Future surveys are expected to further increase the species richness of BMDA for the RA.

Keywords: Bacillariophyceae; benthic diatom assemblages; floristics; islands; protected natural areas

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1. Introduction

The ecological significance of benthic diatoms has distinguished them as a suitable referential for estimating biodiversity in marine protected areas [1] and as useful references for assessing environmental impact [2]. Thus, both diversity and ecological aspects of benthic diatoms should be considered essential in order to have an adequate ecological prospect of any aquatic ecosystem, particularly when developing management plans for protected areas. The high floristic potential of benthic diatoms (Bacillariophyceae) for Mexican littorals has recently been confirmed through surveying new substrata and by studies in hitherto unexplored areas that have yielded numerous new records for the region [3–7] and have enriched the overall species list for the region [6]. According to [8], in some parts of the biosphere where diatoms are abundant, there is very little known about them. Thus, a good case can be made that at least some diatom species and even a few genera are endemics, but many such claims are still weak. Such claims about diatom distributions and endemism must be treated with skepticism.

In this sense, the potential endemism and particularities of benthic diatom taxocenoses from remote locations such as the Revillagigedo Archipelago (RA) encouraged the first floristic study of epiphytic diatom assemblages on macroalgae from that region, yielding a species richness of 208 diatom taxa [6].

Although macroalgal surfaces harbor numerous species of epiphytic diatoms, the above study relied on the inspection of only two macroalgae specimens of *Laurencia* sp. (Rhodophyta). Thus, it was assumed that further observations comprising a larger sample of macroalgae hosts would yield at least twice the number of diatom taxa [6]. However, in spite of the fact that most taxa had been recorded elsewhere [9], it comprised of 50 additions to the benthic diatom flora for Mexican littorals, including 16 undetermined taxa that are likely new species. In addition, because certain diatom taxa may constitute useful references while addressing various ecological and biogeographical issues, the *Mastogloia* species, which were the most diverse diatom taxa in the above study in the RA, were surveyed separately [10] yielding 23 new records, i.e., an increase of approximately 75%, adding up to 50 *Mastogloia* taxa and 231 taxa overall. Thus, a similar increase could be expected for the overall diatom floristics. In this way, further research on diatom floristics in the RA could eventually lead to finding over 500 epiphytic taxa for the 190 macroalgae taxa documented [11], including a significant number of new and likely endemic diatom taxa, which would imply a formal taxonomic endeavor.

After constructing reliable diatom floristics, estimating relative or proportional abundances of the recorded taxa can be used for the calculation of ecological parameters to better describe the assemblages. Ecological studies through the joint analyses of classical parameters such as species richness, diversity, dominance and equitability, aid in detecting patterns in taxocenoses that can reflect the ecological status in pristine environments or reflect various types of impact [2]. Unlike species richness alone, species diversity analysis depicts a structure in communities. Comparing the structure of benthic diatom assemblages (species richness, diversity, dominance) may serve to assess environmental conditions in protected areas [4].

So, because diversity (H′) values estimated in undisturbed environments and protected areas have been observed to surpass those comprised within usual intervals of statistical parameters such as average, median and mode [4,12], our hypothesis dictated that diversity estimates (H′) would vary between 4–5 bits/taxon and species richness (S) may approximate 400 taxa overall in the RA. Thus, the aim of this study was to make the first numerical estimate of species diversity for epiphytic diatoms sampled from macroalgal hosts in the RA resorting to ecological indices and concomitantly seeking to estimate the overall species richness while adding to the taxonomic list of nonrecorded species in Mexican waters.

2. Materials and Methods

The Revillagigedo Archipelago comprises San Benedicto, Socorro, Roca Partida and the Clarion islands located 386 km south of Cabo San Lucas, Baja California Sur, under the jurisdiction of the state of Colima, México. In July 2016, UNESCO declared it a World Heritage Site [13], and recently there was an *ex professo* study for justifying its declaration as a national park [14,15]. Seasonal variations in the RA region seem to be determined by the alternating influence of the California Current and the North Equatorial Current, whilst the rest of the year a transition between both states may be observed [16]. The archipelago rocky coasts harbor a rich macroalgal community of 190 to 200 macroalgae taxa [11,17], and on the surfaces of these macroalgae, floristic rich assemblages of epiphytic diatoms have been identified [6]. Environmental conditions suggest that the biogeographical affinity of the epiphytic diatom taxocenoses is strongly tropical, although has important temperate components [6].

During an opportune (recreational) trip to the Revillagigedo Islands, from 10 to 15 February 2019, 15 macroalgae thalli were collected manually by scuba diving at 7–27 m depths on the rocky shore of San Benedicto and the Socorro islands (RA).

Specific sampling points included El Boiler (19°19′38.30″ N, 110°48′17.16″ W) and El Cañon (19°17′40.48″ N, 110°48′40.92″ W) on San Benedicto, and Cabo Pearce (18°45′57.24″ N, 110°54′00.30″ W) and Punta Tosca (18°46′33.46″ N, 111°03′26.01″ W) on Socorro Island (Figure 1). The macroalgae specimens were sun dried, transported in plastic Ziploc bags, and identified in the laboratory following [18]. Diatoms were brushed off from each algae specimen while rinsing with purified water, washing the brush after each use. The brushed-off material was placed in a 150 mL test tube and left to settle. Thereafter, the precipitates were collected and oxidized using a mixture of commercial alcohol and nitric acid at a ratio of 1 (sample): 2 (alcohol): 5 (acid), according to [2]. Thereafter, the oxidized material was rinsed repeatedly with purified water until it reached a pH $\geq$ 6. After that, for each sample, two double permanent slides were mounted using the synthetic resin Pleurax (RI = 1.7). The slides were inspected under several magnifications (including 250×, 400×, 630× and 1000×) for general recognizance of diatom taxa and forms. Diatom identification was conducted at 1000× under an Olympus CH-2 compound microscope with brightfield illumination, following [1,2,6,19–45]. Taxonomic status was updated according to the Algaebase Web site at http://algaebase.org/search/species/ (accessed on 1 August 2021) [46]. Images of selected specimens were captured with a CMOS Konus digital lens at 630× (oil) and 1000× (oil) and used to construct an iconographic catalog to back the reliability of the identifications. Thus, images of previously recorded taxa in [6] were also included that show no correspondence with the list of new additions to the Revillagigedo diatomological flora but were observed during the quantitative analysis.

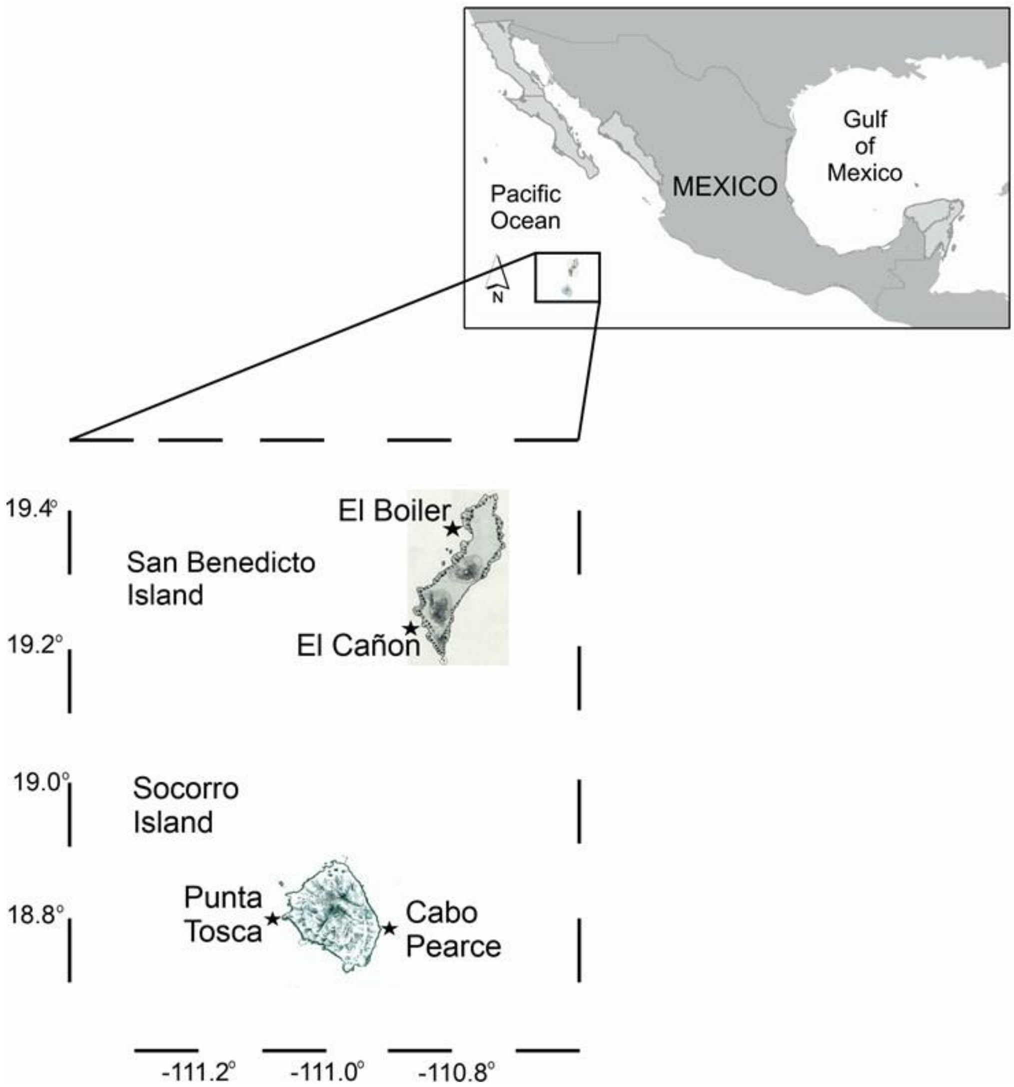

Figure 1. Location of sampling sites at the Revillagigedo Archipelago.

Species diversity estimations of the epiphytic diatom assemblages were based on information theory [47,48]. Values of Shannon's index H′ using $\log_2$ in the form of bits/taxon were computed, supported by species richness and values of other diversity indices such as Pielou's equitability (J′), Simpson's dominance (λ) and diversity (1 − λ) [12]. For this, based on diatom abundances observed in the mounted slides, the samples from 12 sites were selected, and relative abundances of all diatom taxa estimated based on a sample size (N) of 500 valves per mounted slide (sub-sample), including a replicate. Finally, the similarity between all the samples and their replicates was measured using the Bray–Curtis indices to gain an insight into the taxa distribution among the sampling sites relying first on solely the presence/absence of taxa and considering their relative abundances. Clusters were derived from the Bray–Curtis similarity values from each matrix. All calculations were performed using program Primer 6 [49].

3. Results

The inspected macroalgae specimens from the Revillagigedo Archipelago included phaeophytes (*Canistrocarpus cervicornis* (J.V. Lamouroux) De Paula and De Clerck; *Dictyota crenulata* J. Agardh; *D. dichotoma* (Hudson) J.V. Lamouroux; *Sargassum liebmannii* J. Agardh); and rhodophytes (*Amphiroa beauvoisii* J.V. Lamouroux, *Asparagopsis* sp. and cf. *Laurencia* sp.); besides which there were several other macroalgae specimens not identified to a genus or species level but as either phaeophytes or rhodophytes.

The floristic survey of diatoms collected from the inspected macroalgae thalli yielded 167 taxa (Table 1; Figures 2–35) which constitute new records for the RA, and 52 potential new records for the Mexican Pacific coast. The genera with most taxa were: *Amphora* (14), *Navicula* (14), *Cocconeis* (10), *Diploneis* (10), *Nitzschia* (7), *Halamphora* (7) and *Grammatophora* (6). Additionally, six new *Diploneis* and five *Mastogloia* taxa were recorded during the quantitative phase. Overall, 29 taxa could not be identified to species level, 13 were proposed as cf. and 17 remained as sp., such as *Planothidium* sp. 1, *Achnanthes* sp. 2, *Caloneis* sp. 6, *Mastogloia* sp. 1. Others, such as one identified as cf. *Staurosirella martyana*, were not comparable within the available literature consulted.

During the quantitative analysis, it was noted that the abundance of valves in all the mounted preparations was low. Notwithstanding, 12,443 valves were counted, and 276 taxa were included, 47 of which were *Mastogloia* species. Eighty percent of the counted valves belonged to only 35 taxa (Table 2), while 20% of the valves comprised the other 241 taxa. The most frequent were *Achnanthidium exiguum* var. *heterovalvata*, *Cocconeis krammeri*, *Mastogloia crucicula*, *Cocconeis scutellum* var. *parva* and *Epithemia pacifica* (Table 2). The number of taxa per sub-sample (replicate) ranged from 47 to 87 taxa, with a maximum spread of 16 between sub-samples from the same locality. According to their relative abundances, either as independent taxocenoses of each sampling locality or an overall taxocenoses, the diatom assemblages showed a typical structure of a few abundant taxa, more common taxa and many uncommon and rare taxa. Said classification is arbitrary in terms of the number of valves for each category but fits the whole species list with most of the taxa being uncommon and rare (88%), and thus excluded from Table 2.

Table 1. Floristic list of epiphytic diatoms (Bacillariophyceae) found on thalli of rhodophytes and phaeophytes collected at Revillagigedo Islands, Mexico, that constitute new records for the archipelago. Bold = potential new records for the Mexican Pacific coast. * Corrected synonymies from [6].

Achnanthes apiculata Riaux-Gobin, Compère, Hinz and Ector (Figure 15e,f)
Achnanthes pseudogroenlandica Hendey (Figure 16j)
***Planothidium* sp. 1** (Figure 16c–f,h,i)
***Achnanthes* sp. 2** (Figure 16a,b)
Achnanthes trachyderma (F. Meister) Riaux-Gobin, Compère, Hinz and Ector (Figure 15a–d)
Achnanthidium exiguum var. *heterovalvata* (Krasske) Czarnecki (Figure 16k–m)
Actinocyclus cf. *subtilis* (W. Gregory) Ralfs No image
Actinocyclus octonarius (Ehrenberg) Kützing (Figure 4b; Figure 6f,g)
Actinocyclus octonarius var. *ralfsii* (W. Smith) Hendey (Figure 4a)

Table 1. *Cont.*

Actinocyclus subtilis (W. Gregory) Ralfs (Figure 6d)
Alveus marinus (Grunow) Kaczmarska and Fryxell (Figure 31b)
Amphicocconeis debesii (Hustedt) De Stefano (Figure 14t,u)
Amphicocconeis disculoides (Hustedt) Stefano and Marino (Figure 14s)
Amphora alternata A. Mann (Figure 25b,c)
Amphora arenaria Donkin (Figure 27k)
Amphora bigibba var. *interrupta* (Grunow) Cleve (Figure 27a)
Amphora biundulata Bérard-Therriault, Cardinal and Poulin (Figure 27d)
Amphora capensis A.W.F. Schmidt (Figure 25h,i)
Amphora cf. *obtusa rectangulata* H. Peragallo and M. Peragallo (Figure 27n)
Amphora cf. *praelata* Hendey (Figure 25g)
Amphora crassa* var. *campechiana Grunow (Figure 25a)
Amphora grevilleana* var. *campechiana Grunow (Figure 25f)
Amphora immarginata Nagumo (Figure 26a,b,e–g)
Amphora laevissima W. Gregory (Figure 25e)
Amphora marina W. Smith (Figure 26h,i,l)
Amphora mexicana A.W.F. Schmidt (Figure 26c,d)
Amphora novaecaledonica Grunow (Figure 25d)
Anaulus* cf. *balticus Simonsen (Figure 8p–s)
Ardissonea crystallina (C. Agardh) Grunow (Figure 9f,h)
Azpeitia neocrenulata (VanLandingham) Fryxell and T.P. Watkins (Figure 4d,e)
Azpeitia nodulifera (A.W.F. Schmidt) G.A. Fryxell and P.A. Sims (Figure 4c)
Bacillaria socialis (W. Gregory) Ralfs (Figure 32f)
Biremis ambigua (Cleve) D.G. Mann (Figure 21h; Figure 28n)
Biddulphia biddulphiana (J.E. Smith) Boyer (Figure 3a)
Biddulphia subaequa (Kützing) Ralfs (Figure 3d)
Caloneis egena (A.W.F. Schmidt) Cleve (Figure 22f)
Caloneis liber (W. Smith) Cleve (Figure 21g)
Caloneis maxima var. *bicuneata* (Grunow) Amoss (Figure 21a; Figure 23l)
Caloneis elongata (Grunow) Boyer (Figure 23m)
***Caloneis* sp. 6** (Figure 21e,f)
Campylodiscus ralfsii W. Smith (Figure 34g)
Campylodiscus simulans Gregory (Figure 35g)
***Campylodiscus* sp. 1** (Figure 34h,i)
***Campyloneis* sp.** No image
***Catenula* sp.** (Figure 26r–t)
Catenula pelagica Mereschkowski No image
Cocconeis hauniensis Witkowski (Figure 14h)
Cocconeis cf. *placentula* Ehrenberg No image
Cocconeis contermina A.W.F. Schmidt (Figure 13h)
Cocconeis guttata Hustedt and Aleem (Figure 14a–g)
Cocconeis hoffmannii Simonsen (Figure 12d; Figure 16g)
Cocconeis latecostata Hustedt (Figure 14i)
Cocconeis neodiminuta (Pantocsek) Hustedt * No image
Cocconeis peltoides Hustedt (Figure 14q,r)
Cocconeis pinnata W. Gregory ex Greville (Figure 12h)
Cocconeis speciosa W. Gregory (Figure 14j,k,p)
Colliculoamphora minima (Hustedt) D.M. Williams and G. Reid (Figure 25k,l)
Coronia ambigua (Greville) Ruck and Guiry (Figure 35a–f)
Coronia decora (Brébisson) Ruck and Guiry * No image
Coscinodiscus oculus-iridis (Ehrenberg) Ehrenberg (Figure 5b)
Coscinodiscus sp.1 (Figure 3f)
Cymatosira lorenziana Grunow (Figure 8o)
Delphineis surirella (Ehrenberg) G.W. Andrews No image
Delphineis surirelloides (Simonsen) G.W. Andrews No image
***Diatom* sp.** (cf. Neosynedra) (Figure 7d)
***Dickieia* sp.** (Figure 28i)
Diploneis bombus Ehrenberg (Figure 23a,b)

Table 1. *Cont.*

Diploneis cf. *didyma* Ehrenberg (Figure 23j,k)
Diploneis gemmata* var. *pristiophora (C. Janisch) Cleve (Figure 24g)
Diploneis litoralis (Donkin) Cleve var.? (lanceolate form) (Figure 21p)
Diploneis papula (A. Schmidt) Cleve (Figure 21l)
Diploneis papula var. *constricta* Hustedt (Figure 21m)
Diploneis smithii var. *recta* M. Peragallo (Figure 24b)
***Diploneis* sp. 1** (Figure 24f)
***Diploneis* sp. 2** (Figure 21n)
Diploneis suborbicularis (W. Gregory) Cleve (Figure 22h)
Carinasigma minutum (Donkin) G. Reid (Figure 31h)
Ehrenbergiulva hauckii (Grunow) Witkowski, Lange-Bertalot and Metzeltin (Figure 5f)
Entomoneis punctulata (Grunow) K. Osada and H. Kobayasi (Figure 30f)
Epithemia guettingeri (Krammer) Lobban and J.S. Park (Figure 34j,k)
Eunotogramma laevis Grunow (Figure 7p)
Eunotogramma variabile Grunow (Figure 7q)
Fallacia forcipata (Greville) Stickle and D.G. Mann (Figure 17i)
Fallacia ny (Cleve) D.G. Mann (Figure 17h)
Fallacia oculiformis (Hustedt) D.G. Mann (Figure 17g)
Fragilariopsis doliolus (Wallich) Medlin and P.A. Sims (Figure 33g)
***Glyphodesmis* sp.** (Figure 7j,k)
Grammatophora hamulifera Kützing (Figure 11k,l)
Grammatophora marina var. *subundulata* Grunow (Figure 10m)
Grammatophora ovalauensis Grunow (Figure 10p)
Grammatophora serpentina Ehrenberg (Figure 11m–o)
Grammatophora oceanica var. *subtilissima* (Bailey) Grunow (Figure 11i,j)
Grammatophora undulata* var. *gibba (Ehrenberg) Grunow (Figure 10i,j)
Gyrosigma cf. *parvulum* Hustedt (Figure 30d)
Halamphora acutiuscula (Kützing) Levkov (Figure 27i)
Halamphora clara (A.W.F. Schmidt) Levkov (Figure 25j)
Halamphora holsatica (Hustedt) Levkov (Figure 27f,g)
Halamphora pseudohyalina (Simonsen) J.G. Stepanek and Kociolek (Figure 28z)
Halamphora subangularis (Hustedt) Levkov (Figure 27e)
Halamphora terroris (Ehrenberg) P. Wang (Figure 27j)
Halamphora yundangensis W.W. Wu, C.P. Chen and Y.H. Gao (Figure 26j)
***Hemidiscus* sp.**? (Figure 6a)
Hyalodiscus ambiguus (Grunow) Tempère and Peragallo (Figure 5a)
Hyalodiscus scoticus (Kützing) Grunow (Figure 4f)
Luticola mutica (Kützing) D.G. Mann (Figure 28g)
Lyrella abrupta (W.Gregory) D.G. Mann (Figure 17a,e,f)
Lyrella rudiformis (Hustedt) E. Nevrova, A. Witkowski, M. Kulikovskiy and Lange-Bertalot (Figure 17d)
Margaritum terebro (Leuduger-Fortmorel) Moreira Filho (Figure 5e)
Mastogloia jelinecki Grunow (Figure 18q,r)
Mastogloia* cf. *latericia (A.W.F. Schmidt) Cleve (Figure 18d,e)
Mastogloia pseudoexigua Cholnoky (Figure 19a–f)
Mastogloia punctifera Brun (Figure 18f,g)
***Mastogloia* sp. 1** (Figure 18a)
Mastogloia subaffirmata Hustedt (Figure 18h,i)
Navicula arenaria var. *rostellata* Lange-Bertalot (Figure 28u)
Navicula athenae Witkowski, Lange-Bertalot and Metzeltin (Figure 28t)
Navicula bipustulata A. Mann (Figure 28e)
Navicula (Lyrella) clavata* var. *proxima (Janisch) Cleve (Figure 17j)
Navicula digitoconvergens Lange-Bertalot (Figure 28p)
Navicula digitoradiata (W. Gregory) Ralfs (Figure 28k)
Navicula inflexa (W. Gregory) Ralfs (Figure 28o)
Navicula pennata A.W.F. Schmidt (Figure 28d)
Navicula platyventris F. Meister (Figure 28h)
Navicula sp. 1 (Figure 28j)

Table 1. *Cont.*

***Navicula* sp. 2** (Figure 28s)
***Navicula* sp. 3** (Figure 28l)
Navicula sparsistriata Hustedt (Figure 17b,c)
Navicula subrostellata Hustedt (Figure 28m)
Neodelphineis silenda (M.H. Hohn and J. Hellerman) N. Desianti and M. Potapova (Figure 8l)
Neosynedra tortuosa (Grunow) D. M. Williams and Round (Figure 9i)
Nitzschia angularis W.S. Smith (Figure 33k,l)
Nitzschia behrei Hustedt (Figure 32b–d)
Nitzschia insignis W. Gregory (Figure 32e)
Nitzschia jelineckii Grunow (Figure 29l)
Nitzschia nienhuisii F.A.S. Sterrenburg and F.J.G. Sterrenburg (Figure 33m)
Nitzschia punctata var. *coarctata* (Grunow) Hustedt No image
Nitzschia tenerifa Lange-Bertalot (Figure 33j)
Odontella aurita (Lyngbye) C. Agardh (Figure 3b,c)
Paralia sulcata (Ehrenberg) Cleve (Figure 4g)
Parlibellus cf. *delognei* (Van Heurck) E.J. Cox (Figure 28x)
Plagiogramma* cf. *gregorianum Grevillei (Figure 7m)
Plagiogramma interruptum (W. Gregory) Ralfs (Figure 7l)
Pleurosigma angulatum (J.T. Quekett) W. Smith (Figure 31f,g)
Pleurosigma barbadense Grunow (Figure 30e)
Pleurosigma intermedium W. Smith (Figure 31c–e)
Podocystis spathulata (Shadbolt) Van Heurck (Figure 8a)
Podosira baldjickiana Grunow (Figure 6b)
Progonoia musca (W. Gregory) H.J. Schrader (Figure 24a)
Psammodictyon panduriforme (W. Gregory) D.G. Mann (Figure 29e)
Psammodictyon pustulatum (Voigt ex Meister) C.S. Lobban (Figure 29i)
Psammodictyon roridum (M.H. Giffen) D.G. Mann (Figure 29a–c)
Psammodiscus nitidus (W. Gregory) Round and D.G. Mann (Figure 3e)
Pseudodictyota dubia (Brightwell) P.A. Sims and D.M. Williams (Figure 3g–i)
Pseudotriceratium punctatum (Wallich) Simonsen (Figure 2f)
Rhabdonema adriaticum Kützing (Figure 7a–c)
Rhaphoneis amphiceros (Ehrenberg) Ehrenberg (Figure 8h,i)
Rhaphoneis elegantula Hustedt (Figure 7i)
Seminavis basilica D.B. Danielidis (Figure 27m)
cf. *Staurosirella martyi* (Héribaud) E.A. Morales and K.M. Manoylov (Figure 8m,n)
Synedra bacillaris (Grunow) Hustedt (Figure 7h)
***Talaroneis* sp.** (Figure 7r)
Thalassionema nitzschioides var. *parvus* Moreno-Ruíz (Figure 8f)
Thalassiosira eccentrica (Ehrenberg) Cleve (Figure 6e)
Trachyneis velata (A.W.F. Schmidt) P.T. Cleve (Figure 21j; Figure 22c–e)
Triceratium biquadratum Janisch (Figure 2c,d)
Trigonium diaphanum A. Mann (Figure 2b)
Trigonium formosum* f. *quadrangularis (Greville) Desikachary and Sreelatha (Figure 2e)
Tryblionella didyma (Hustedt) D.G. Mann (Figure 30a,b)
Tryblionella nicobarica (Grunow) D.G. Mann (Figure 29d)

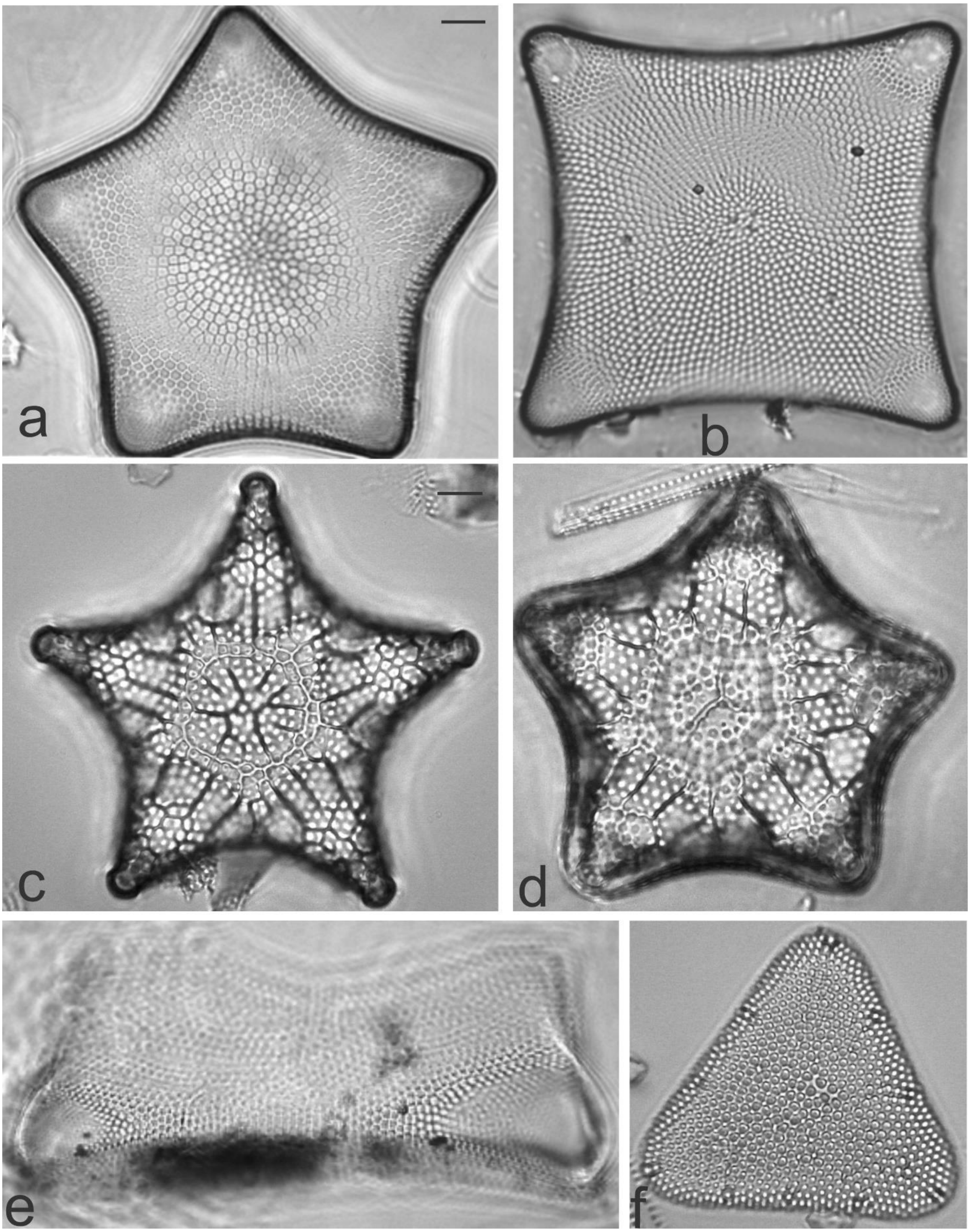

Figure 2. (**a**) *Triceratium formosum* var. *quinquelobatum*; (**b**) *Trigonium diaphanum*; (**c**,**d**) *Triceratium biquadratum*; (**e**) *Trigonium formosum* f. *quadrangularis*; (**f**) *Pseudotriceratium punctatum*. Scale bars: (**a**–**d**,**f**) = 10 µm, (**e**) = 15 µm.

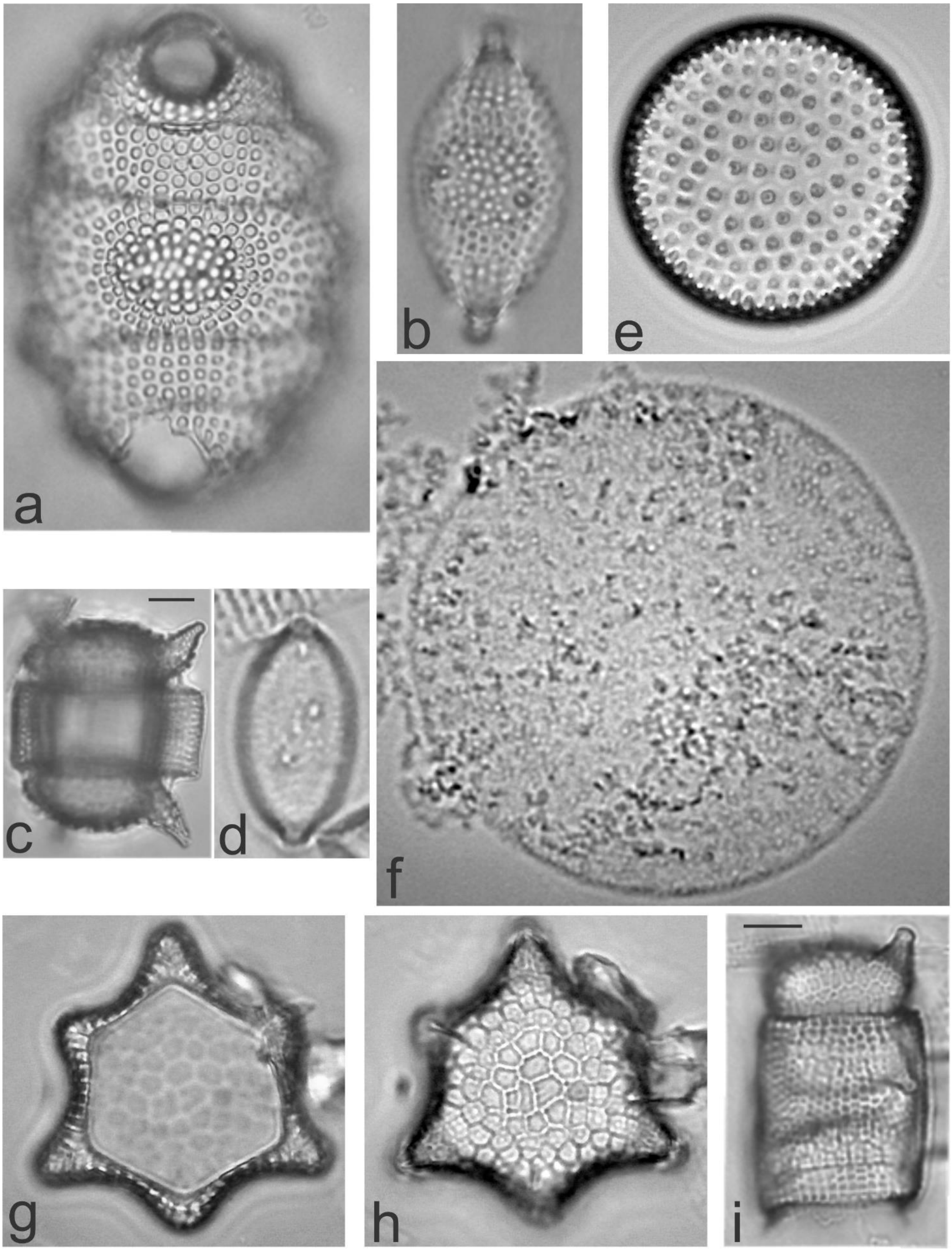

Figure 3. (**a**) *Biddulphia biddulphiana*; (**b**,**c**) *Odontella aurita*; (**d**) *Biddulphia subaequa*; (**e**) *Psammodiscus nitidus*; (**f**) *Coscinodiscus* sp. 1; (**g**–**i**) *Pseudodictyota dubia*. Scale bars: (**b**–**d**,**e**–**i**) = 10 μm; (**a**) = 15 μm.

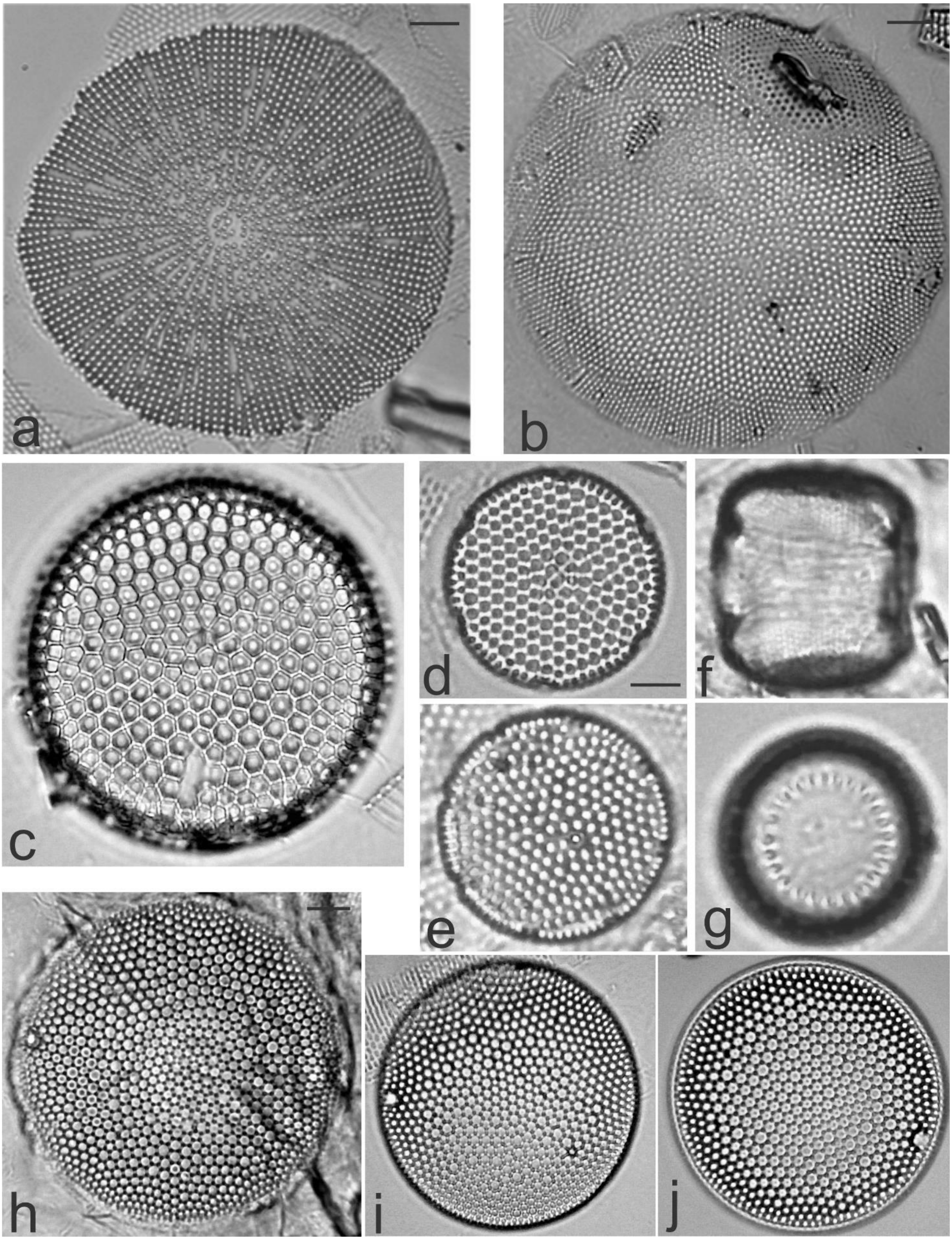

Figure 4. (**a**) *Actinocyclus octonarius* var. *ralfsii*; (**b**) *Actinocyclus octonarius*; (**c**) *Azpeitia nodulifera*; (**d**,**e**) *Azpeitia neocrenulata*; (**f**) *Hyalodiscus scoticus*; (**g**) *Paralia sulcata*; (**h**–**j**) *Roperia tesselata*. Scale bars = 10 μm.

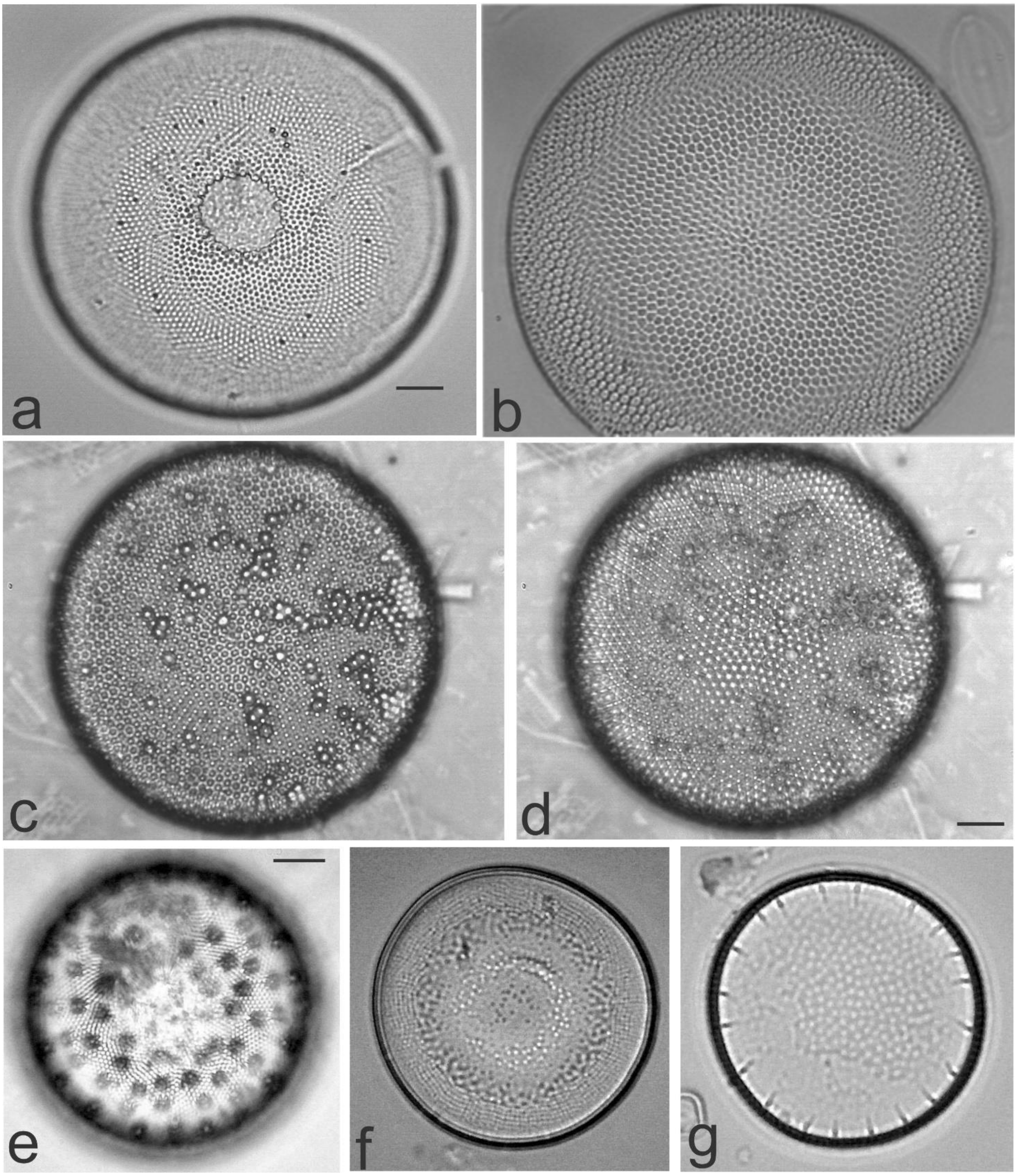

Figure 5. (**a**) *Hyalodiscus ambiguus*; (**b**) *Coscinodiscus oculus-iridis*; (**c**,**d**) *Actinocyclus alienus*; (**e**) *Margaritum terebro*; (**f**) *Ehrenbergiulva hauckii*; (**g**) *E. granulosa*. Scale bars = 10 μm.

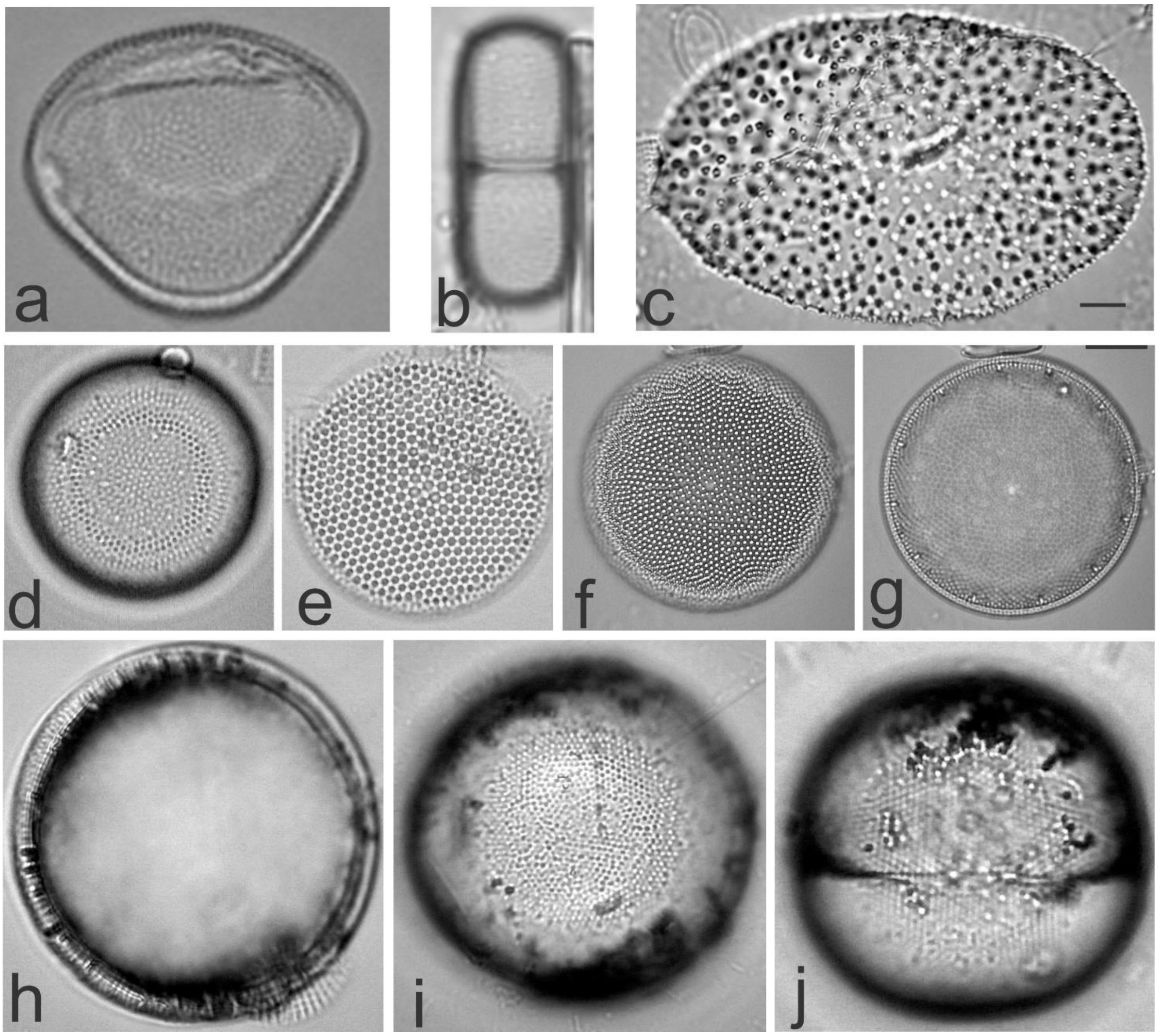

Figure 6. (**a**) *Hemidiscus* sp.?; (**b**) *Podosira baldjickiana*; (**c**) resting spore; (**d**) *Actinocyclus subtilis*; (**e**) *Thalassiosira eccentrica*; (**f**,**g**) *A. octonarius*; (**h**–**j**) *Podosira montagnei*. Scale bars: (**c**) = 15 μm; rest = 10 μm.

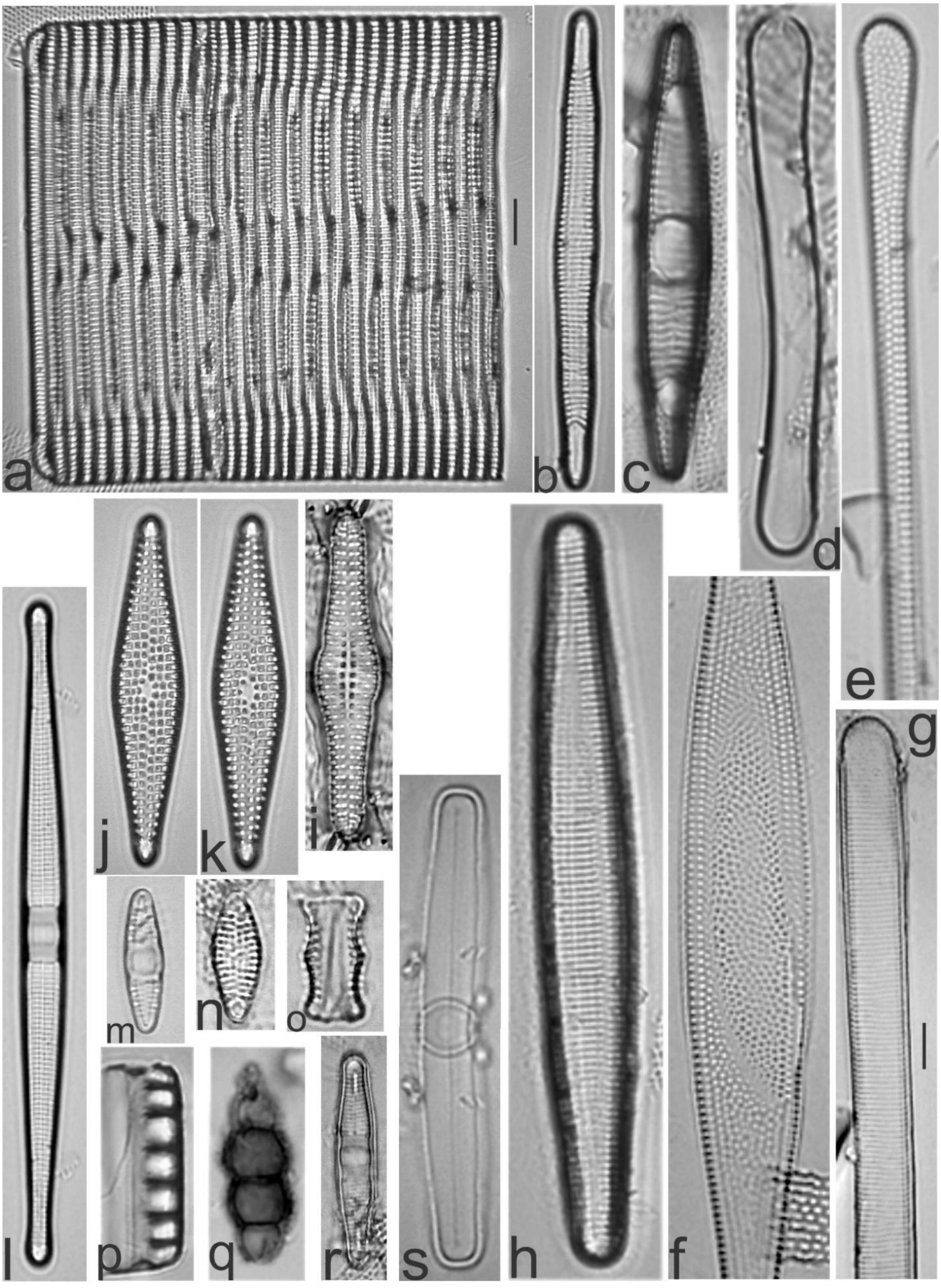

Figure 7. (**a**–**c**) *Rhabdonema adriaticum*; (**d**) *Diatom* sp.; (**e**,**f**) *Toxarium hennedyanum*; (**g**) *Ardissonea fulgens*; (**h**) *Synedra bacillaris*; (**i**) *Rhaphoneis elegantula*; (**j**,**k**) *Glyphodesmis* sp.; (**l**) *Plagiogramma interruptum*; (**m**) *Plagiogramma* cf. *gregorianum*; (**n**,**o**) *Dimeregramma minor* var. *nana*; (**p**) *Eunotogramma laevis*; (**q**) *E. variabile*; (**r**) *Talaroneis* sp.; (**s**) *Cyclophora tenuis*. Scale bars = 5 μm.

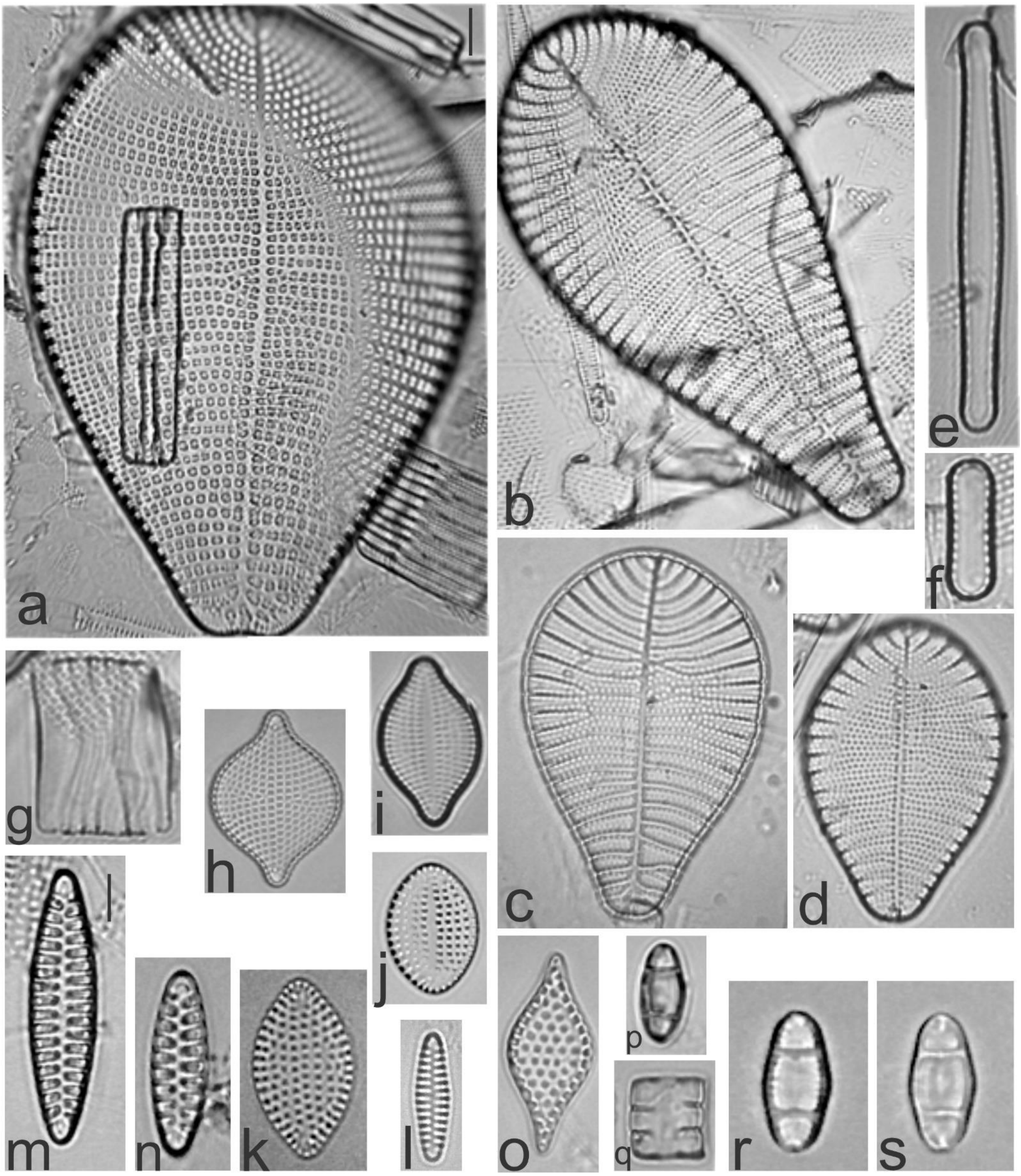

Figure 8. (**a**) *Podocystis spathulata*; (**b**–**d**) *P. americana*; (**e**) *Thalassionema nitzschioides*; (**f**) *T. nitzschioides* var. *parvus*; (**g**) *Hyalosira tropicalis*; (**h**,**i**) *Rhaphoneis amphiceros*; (**j**,**k**) *Delphineis minutissima*; (**l**) *Neodelphineis silenda*; (**m**,**n**) cf. *Staurosirella martyi*; (**o**) *Cymatosira lorenziana*; (**p**–**s**) *Anaulus* cf. *balticus*. Scale bars = 5 μm.

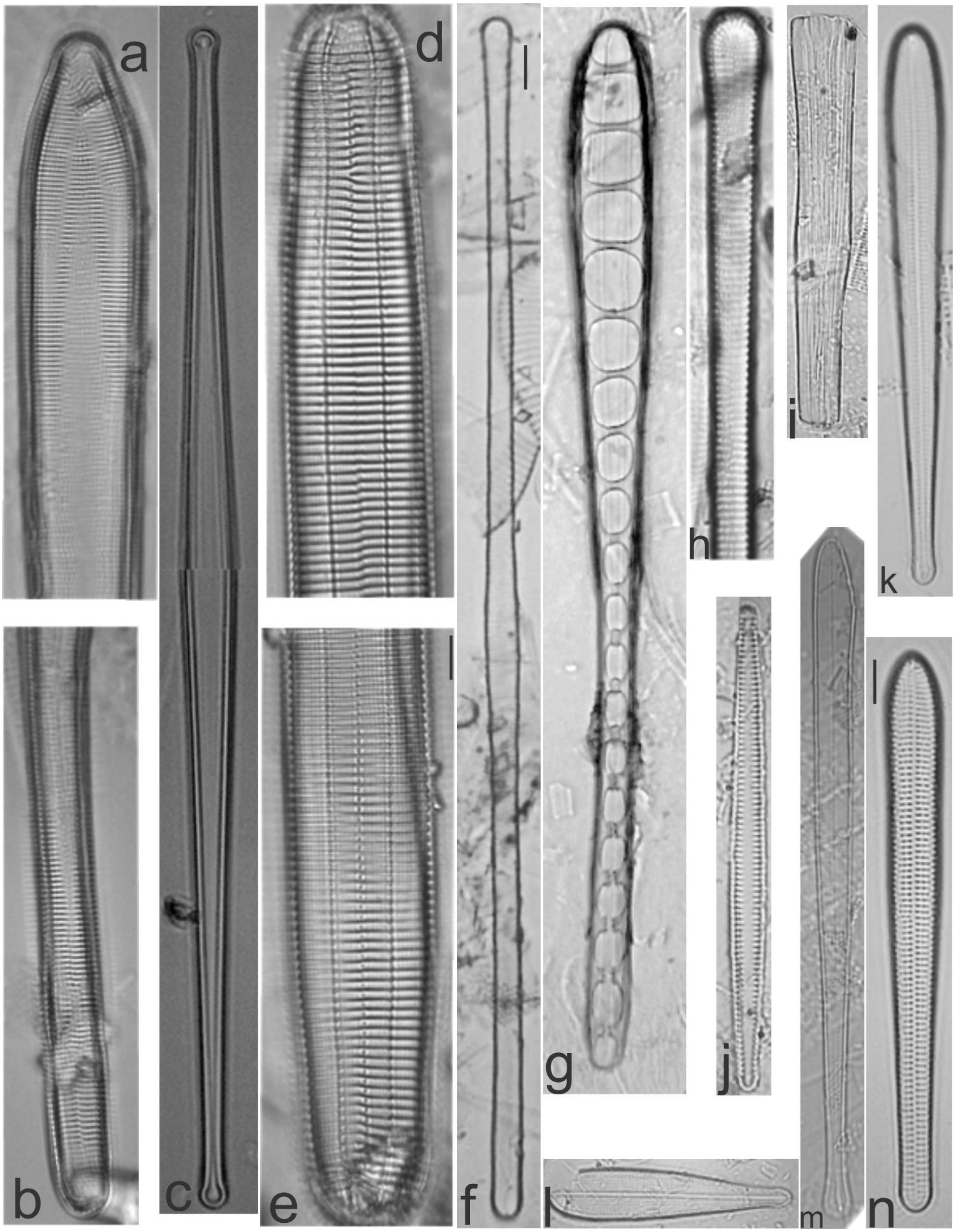

Figure 9. (**a**,**b**) *Synedrosphenia cuneata*; (**c**) *Hyalosynedra laevigata*; (**d**,**e**) *Ardissonea robusta*; (**f**,**h**) *Ardissonea crystallina*; (**g**) *Climacosphenia moniligera*; (**i**) *Neosynedra tortuosa*; (**j**) *Tabularia fasciculata*; (**k**) *Licmophora debilis*; (**l**) *L. gracilis*; (**m**) *L. flabellata*; (**n**) *L. paradoxa*. Scale bars = 5 μm.

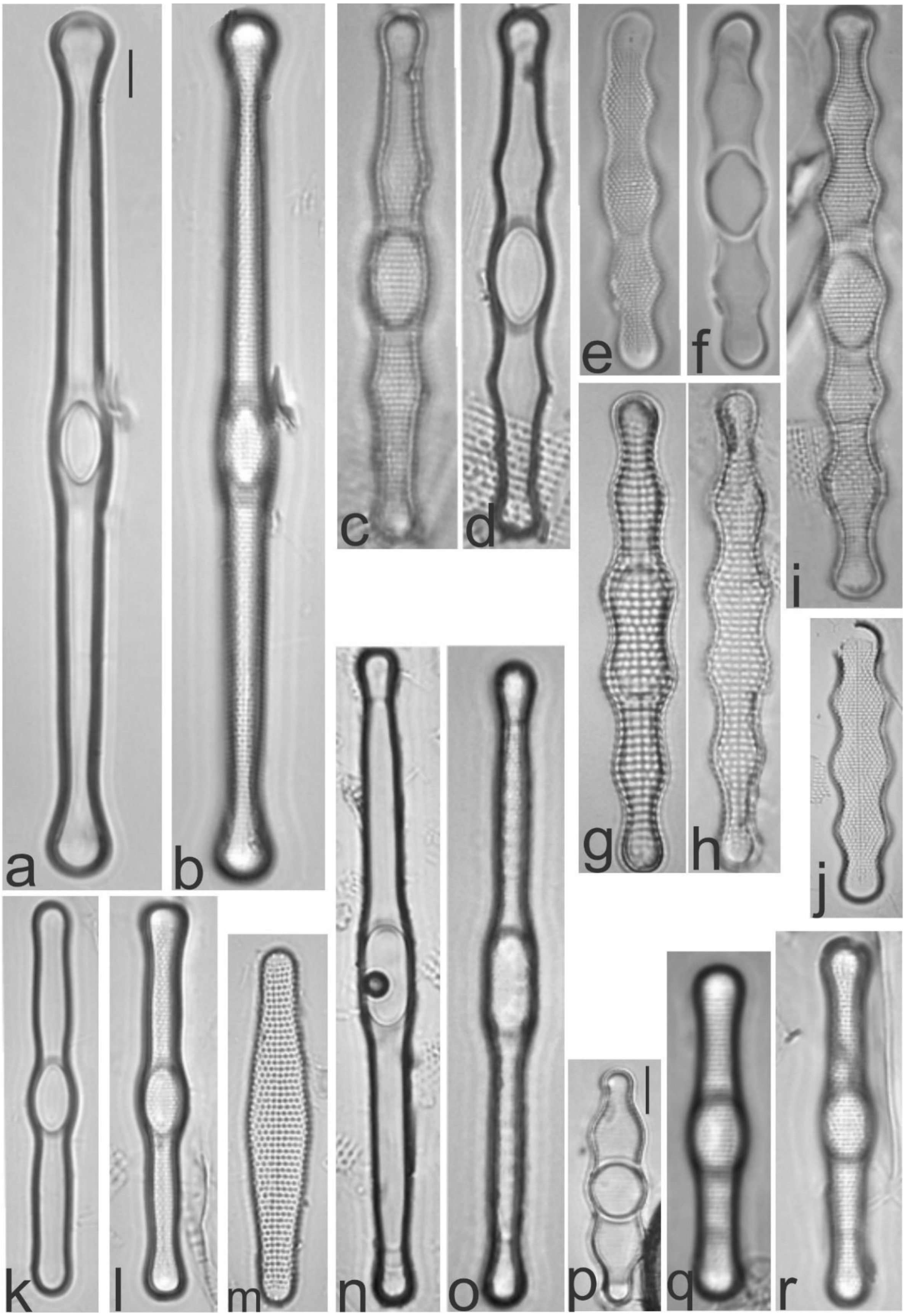

Figure 10. (**a**,**b**,**q**,**r**) *Grammatophora monilifera*; (**c**–**f**) *G. undulata*; (**g**,**h**) *G. undulata* var. *gallopagensis*; (**i**,**j**) *G. undulata* var. *gibba*; (**k**,**l**) *G. merletta*; (**m**) *G. marina* var. *subundulata*; (**n**,**o**) *G. caribaensis*; (**p**) *G. ovalauensis*. Scale bar: (**p**) = 7.5 μm; all others = 5 μm.

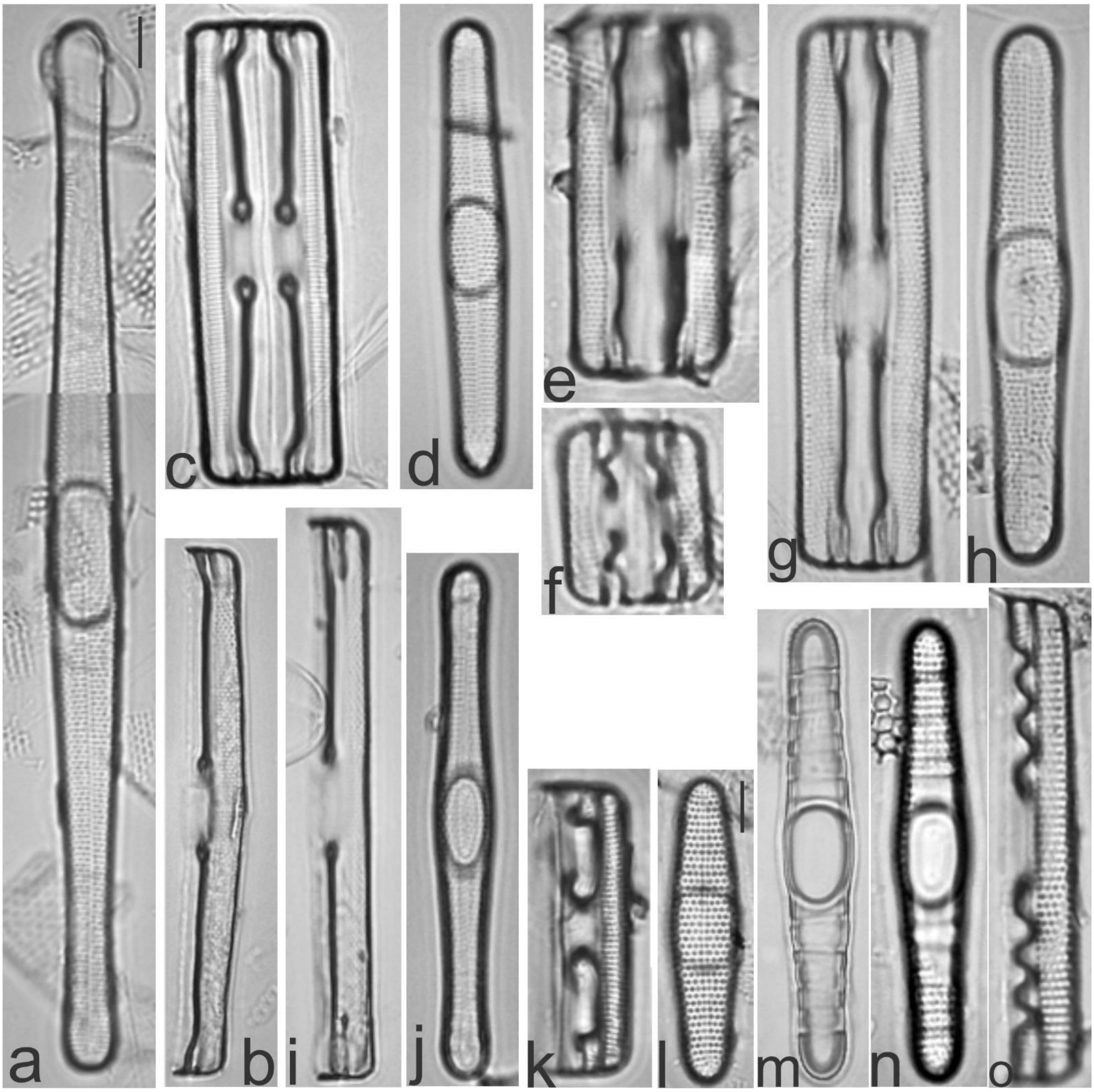

Figure 11. (**a**,**b**) *Grammatophora macilenta*; (**c**,**d**) *G. oceanica*; (**e**,**f**) *G. marina*; (**g**,**h**) *G. maxima*; (**i**,**j**) *G. oceanica* var. *subtilissima*; (**k**,**l**) *G. hamulifera*; (**m**–**o**) *G. serpentina*. Scale bar = 5 µm.

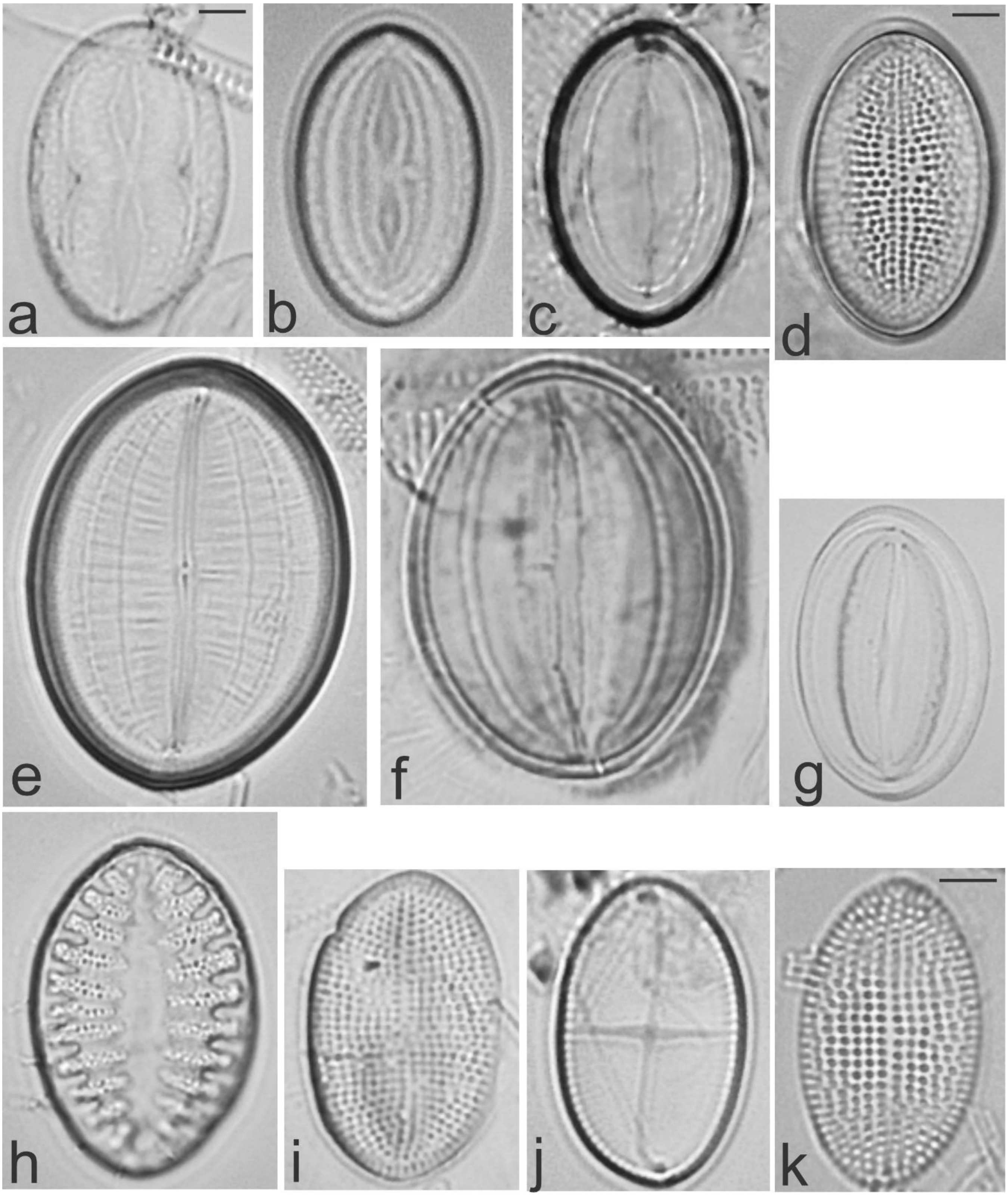

Figure 12. (**a**) *Cocconeis caribensis*; (**b**,**c**) *C. comis*; (**d**) *C. hoffmannii*; (**e**) *C. heteroidea*; (**f**,**g**) *C. krammeri*; (**h**) *C. pinnata*; (**i**,**j**) *C. pseudodiruptoides*; (**k**) *C. diruptoides*. Scale bar = 5 μm.

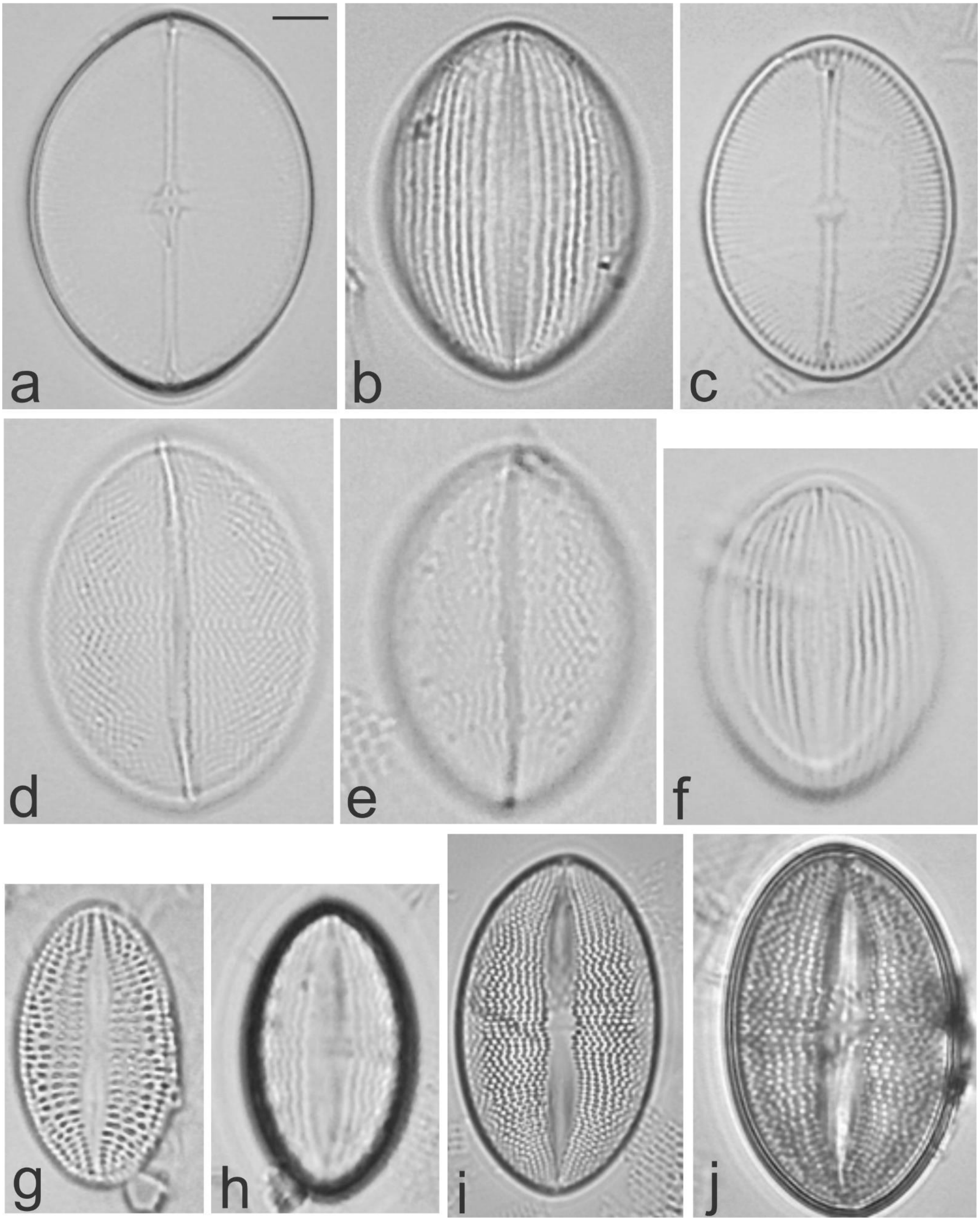

Figure 13. (**a**–**c**,**f**) *Cocconeis convexa*; (**d**,**e**,**i**,**j**) *C. dirupta*; (**g**) *C. dirupta* var. *flexella*; (**h**) *C. contermina*; Scale bar = 5 µm.

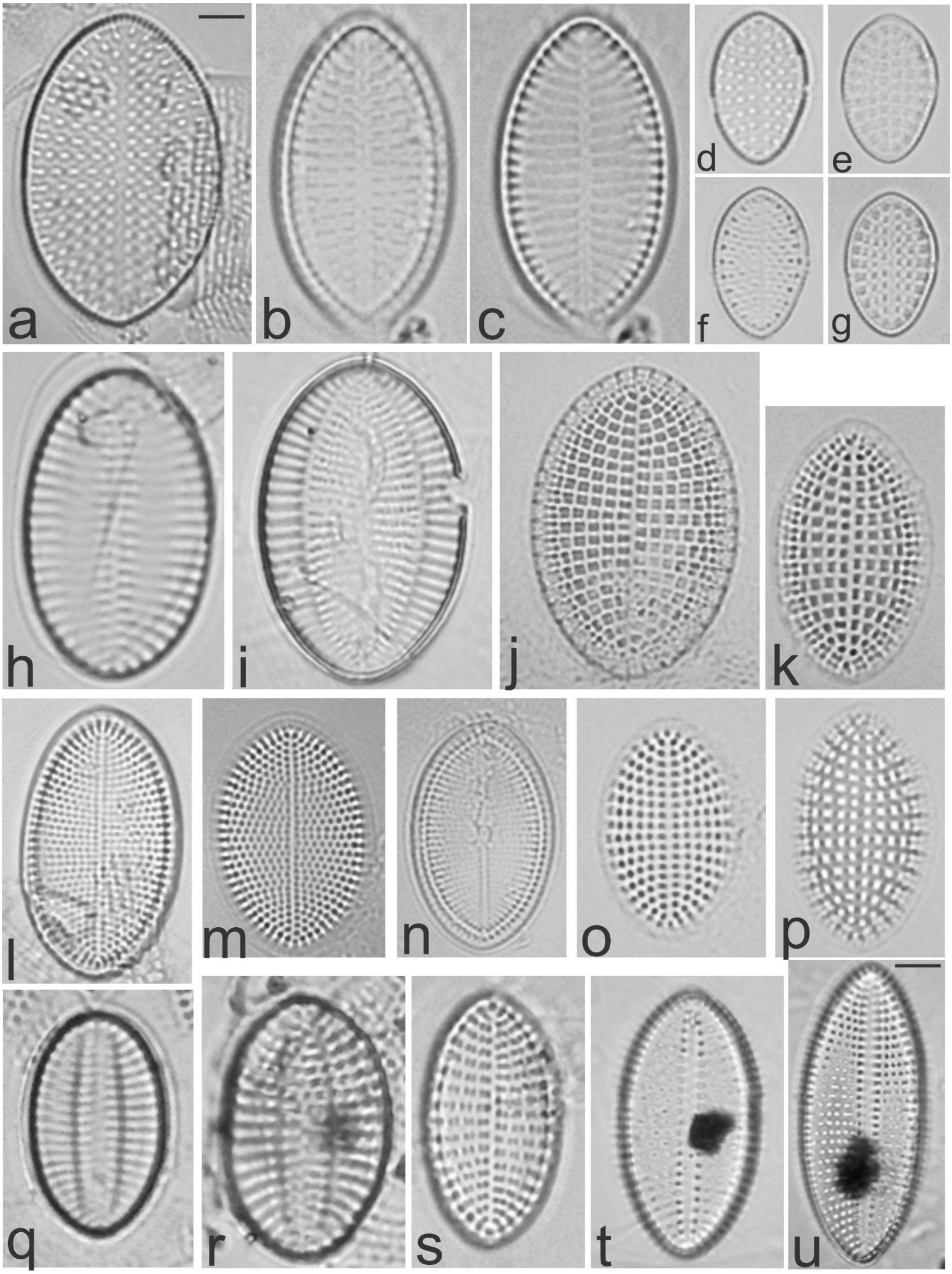

Figure 14. (**a**–**g**) *Cocconeis guttata*; (**h**) *C. hauniensis*; (**i**) *C. latecostata*; (**j**,**k**,**p**) *C. speciosa*; (**l**–**n**) *C. placentula*; (**o**) *C. scutellum* var. *parva*; (**q**,**r**) *C. peltoides*; (**s**) *Amphicocconeis disculoides*; (**t**,**u**) *A. debesii*. Scale bar = 5 µm.

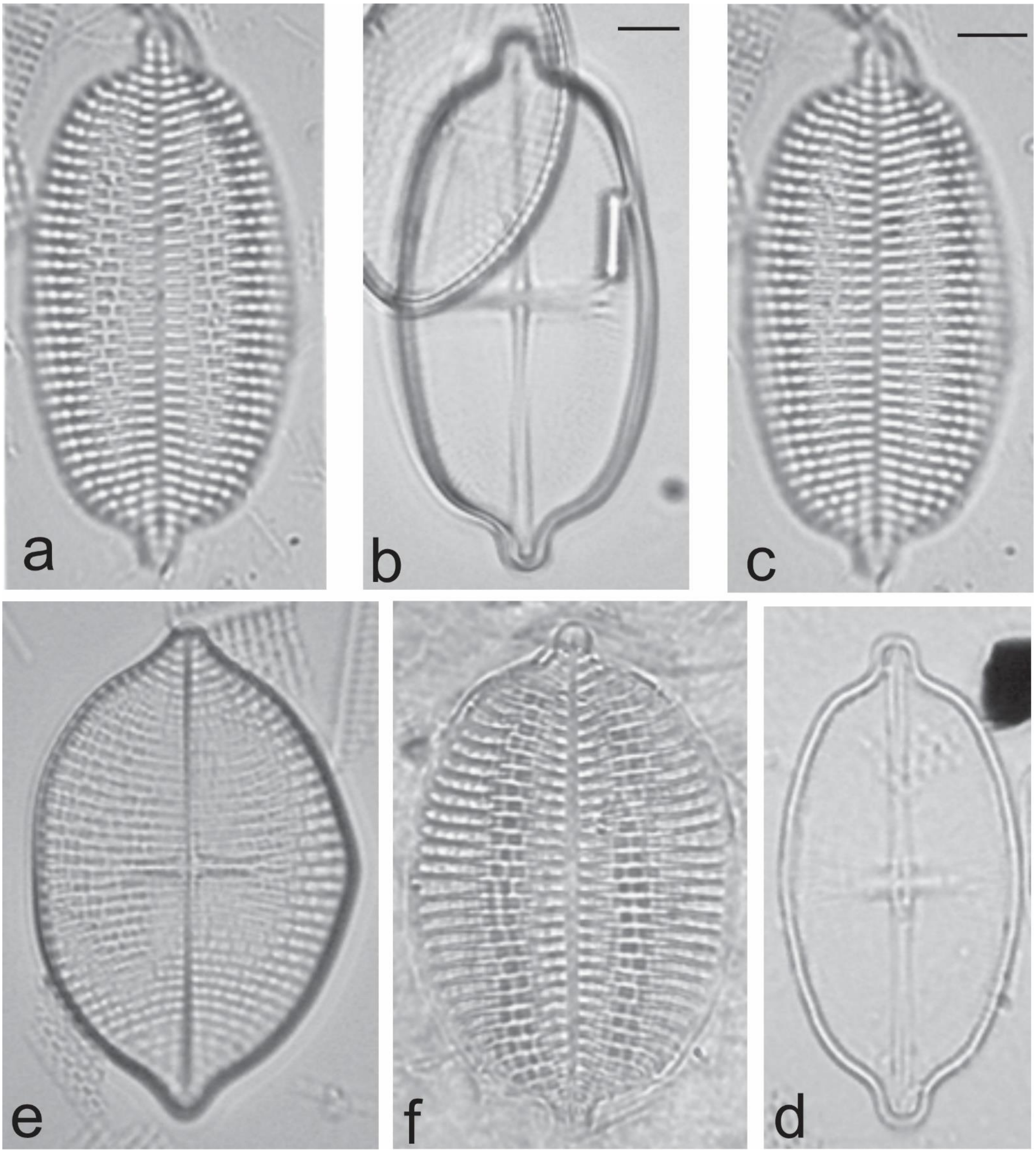

Figure 15. (**a**–**d**) *Achnanthes trachyderma*; (**e**,**f**) *A. apiculata*. Scale bar = 5 µm.

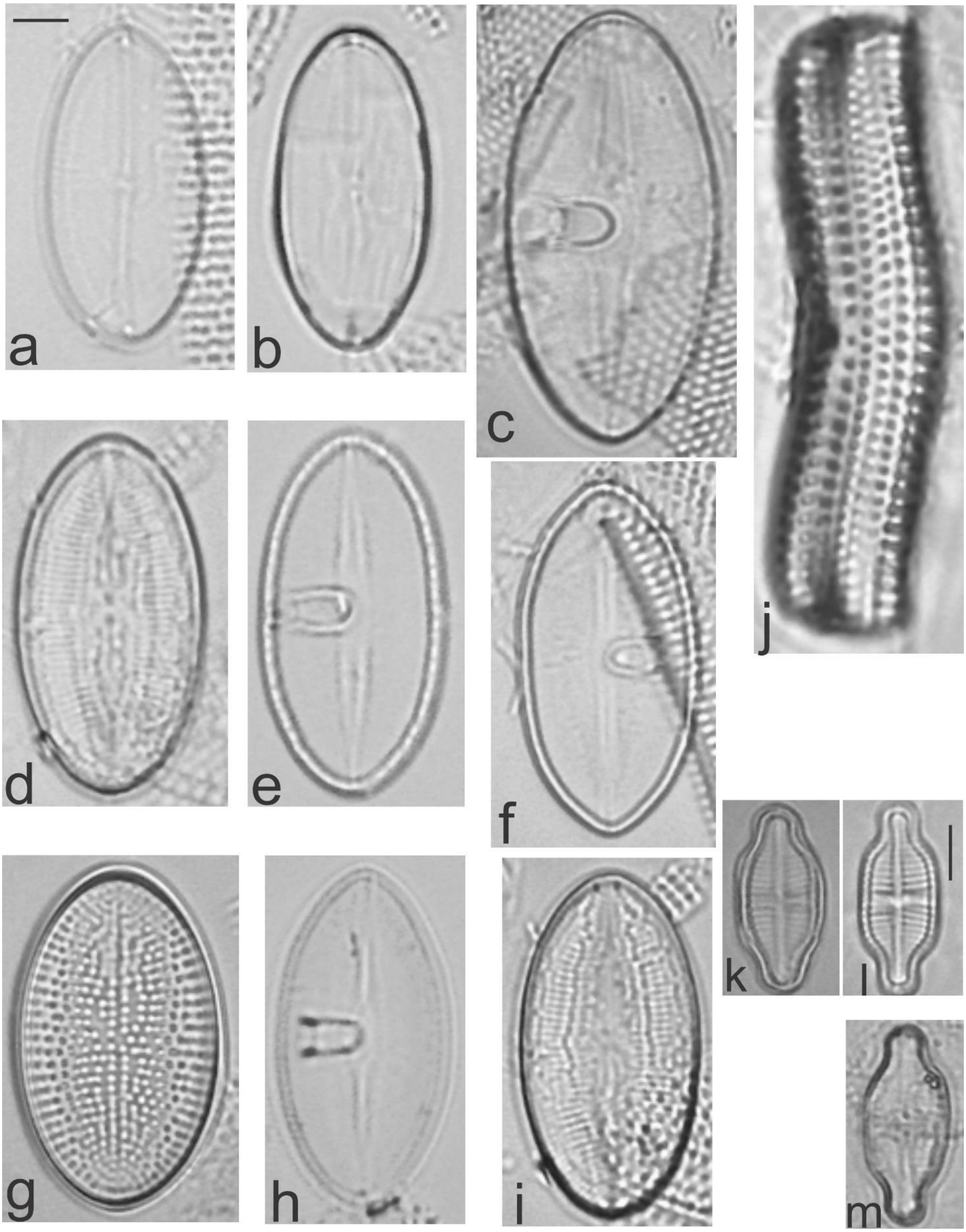

Figure 16. (**a**,**b**) *Achnanthes* sp. 2; (**c**–**f**,**h**,**i**) *Planothidium* sp. 1; (**k**–**m**) *Achnanthidium exiguum* var. *heterovalvata*; (**g**) *Cocconeis hoffmannii*; (**j**) *Achnanthes pseudogroenlandica*. Scale bar = 5 µm.

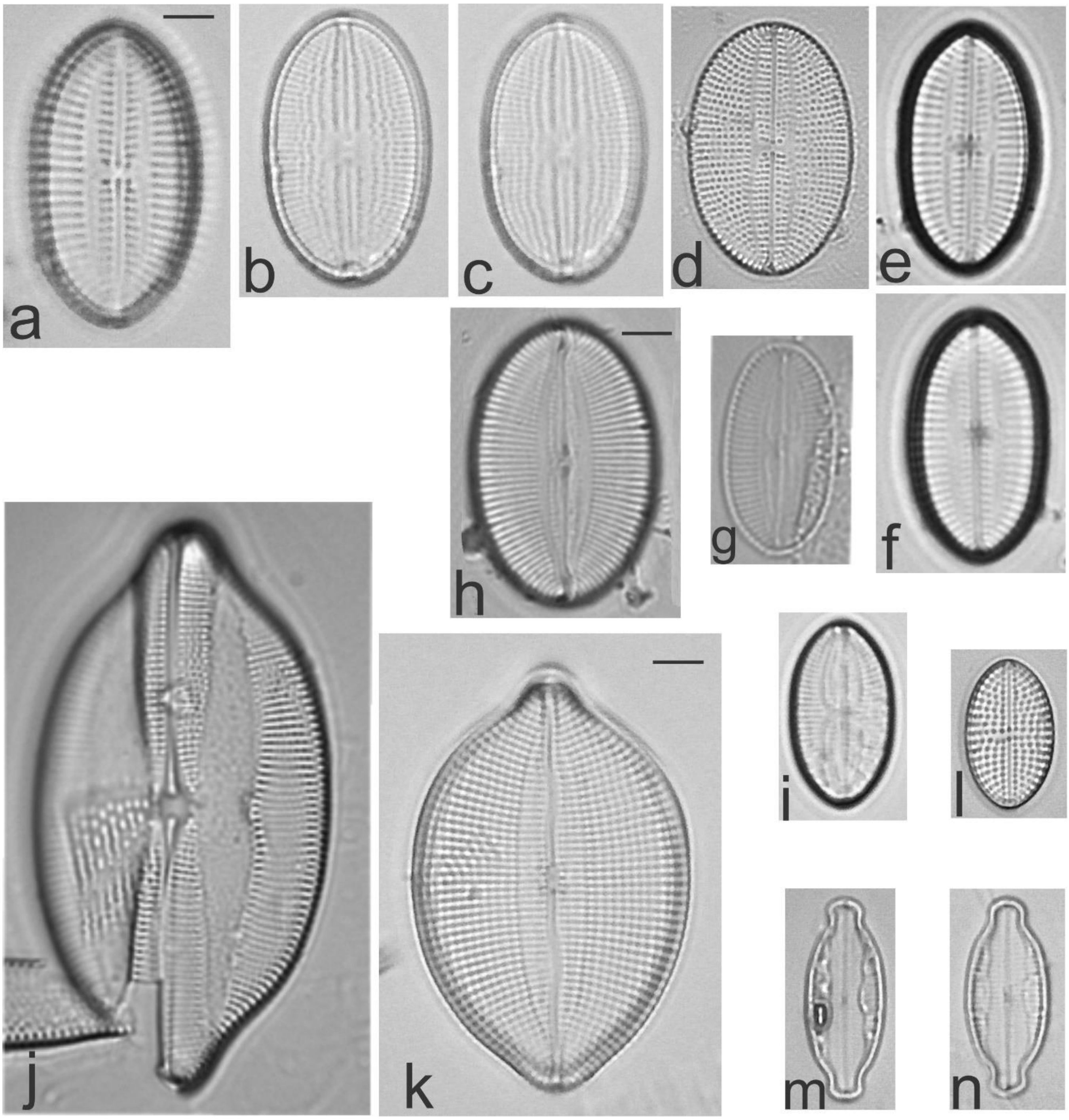

Figure 17. (**a**,**e**,**f**) *Lyrella abrupta*; (**b**,**c**) *Navicula sparsistriata*; (**d**) *Lyrella rudiformis*; (**g**) *Fallacia oculiformis*; (**h**) *Fallacia ny*; (**i**) *Fallacia forcipata*; (**j**) *Navicula* (*Lyrella*) *clavata* var. *proxima*; (**k**) *Mastogloia peragalli*; (**l**) *Mastogloia ovalis*; (**m**,**n**) *Mastogloia manokwariensis*. Scale bars = 5 µm.

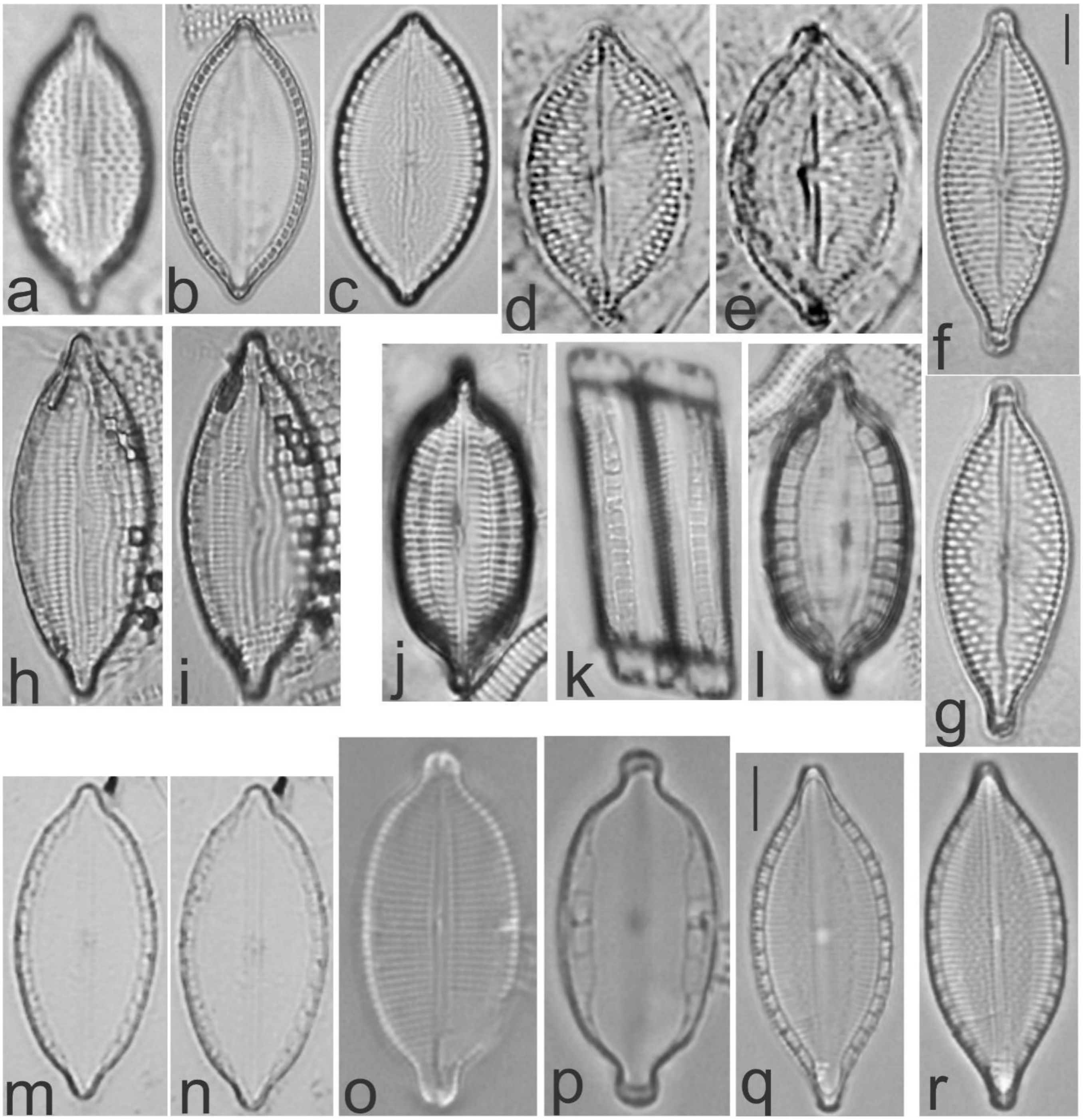

Figure 18. (**a**) *Mastogloia* sp. 1; (**b**,**c**) *M. cannii*; (**d**,**e**) *Mastogloia* cf. *latericia*; (**f**,**g**) *Mastogloia punctifera*; (**h**,**i**) *M. subaffirmata*; (**j**–**l**) *M. corsicana*; (**m**,**n**) *M. delicatissima*; (**o**,**p**) *Mastogloia acutiuscula* var. *elliptica*; (**q**,**r**) *M. jelinecki*. Scale bars = 5 μm.

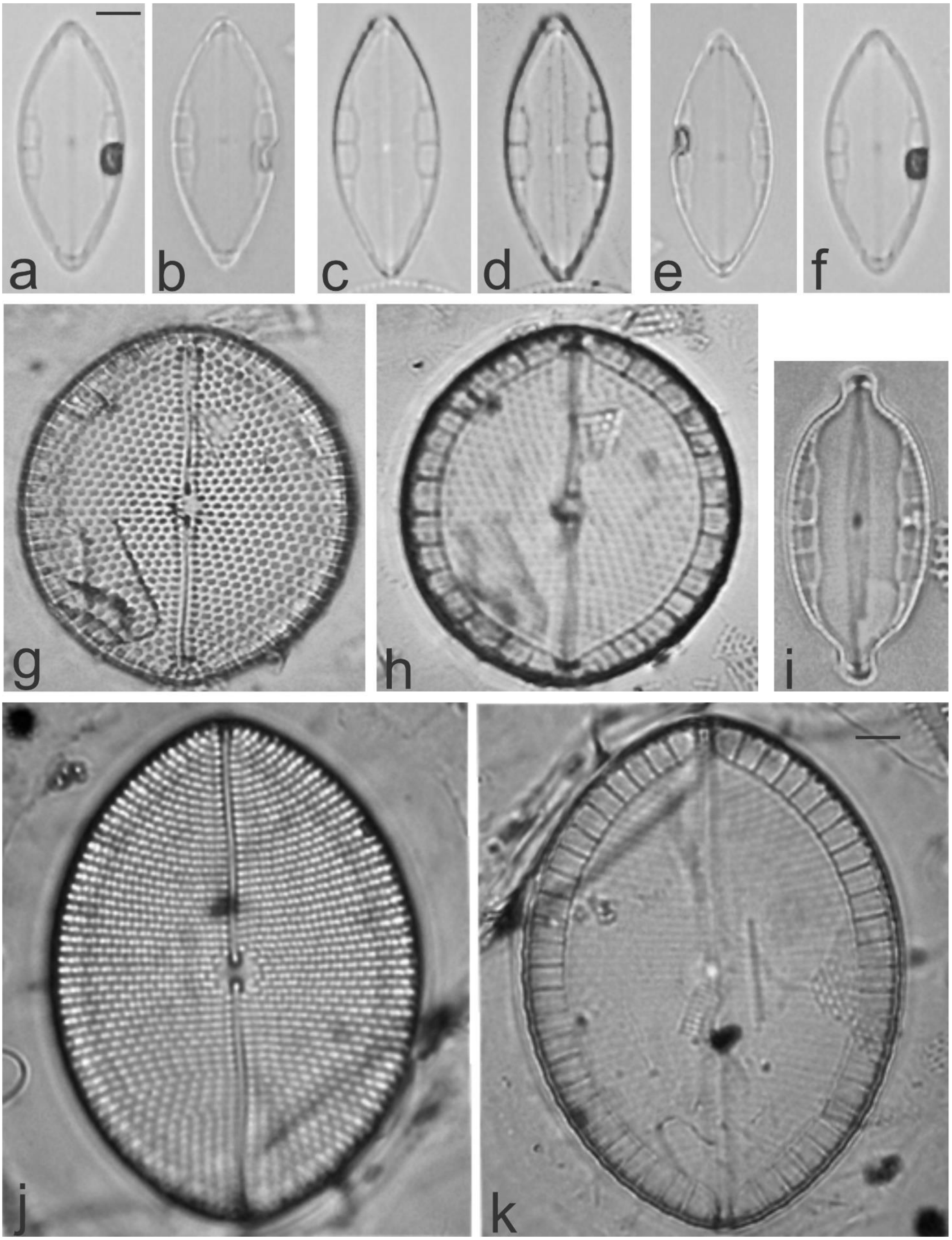

Figure 19. (**a**–**f**) *Mastogloia pseudoexigua*; (**g**,**h**) *M. cribrosa*; (**i**) *M. acutiuscula* var. *elliptica*; (**j**,**k**) *M. pseudolatecostata*. Scale bars: (**j**,**k**) = 5 µm; all others = 4 µm.

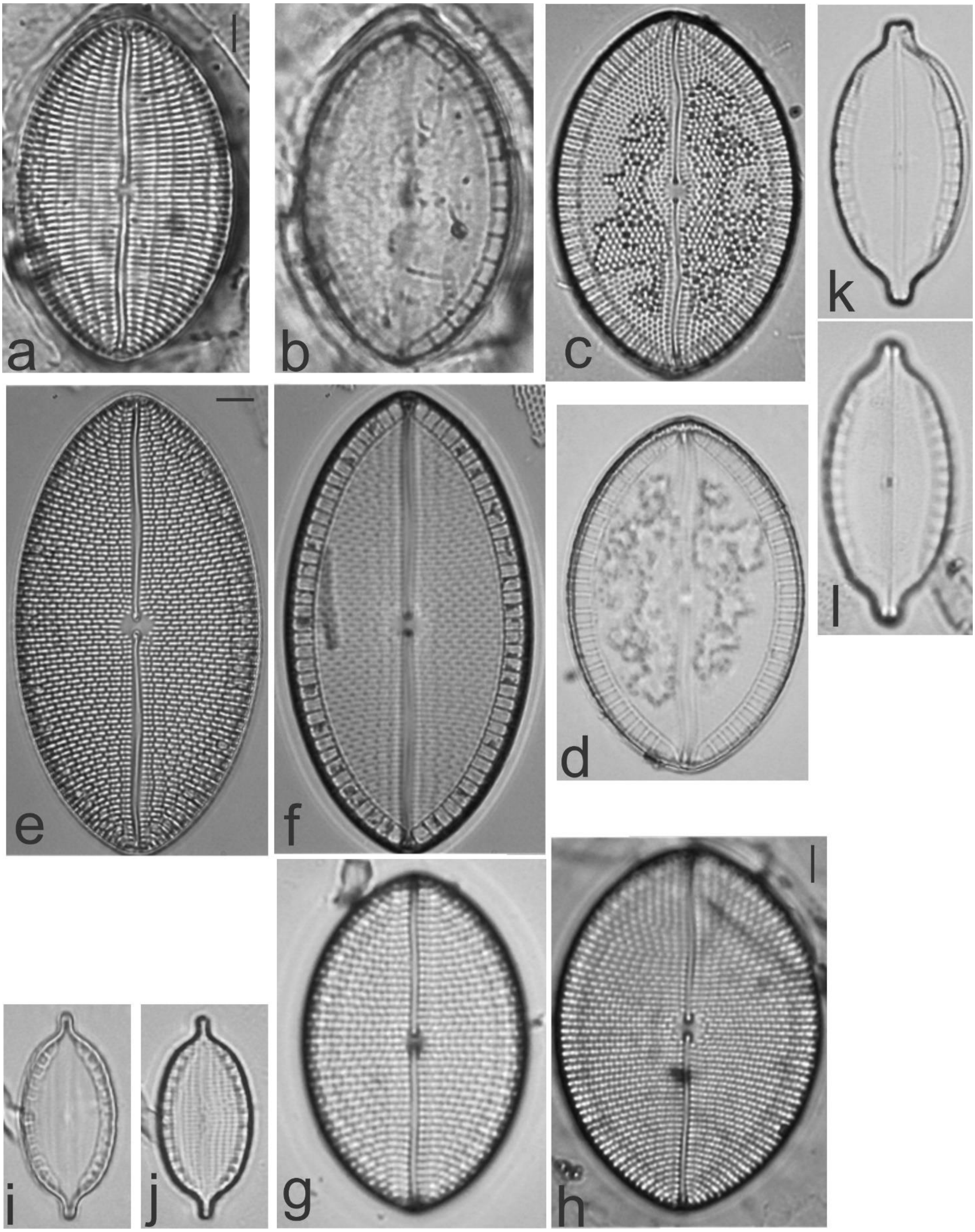

Figure 20. (**a**–**d**) *Mastogloia ovata*; (**e**–**g**) *M. ovum-paschale*; (**h**) *M. pseudolatecostata*; (**i**,**j**) *M. parva*; (**k**,**l**) *M. decipiens*. Scale bar = 5 µm.

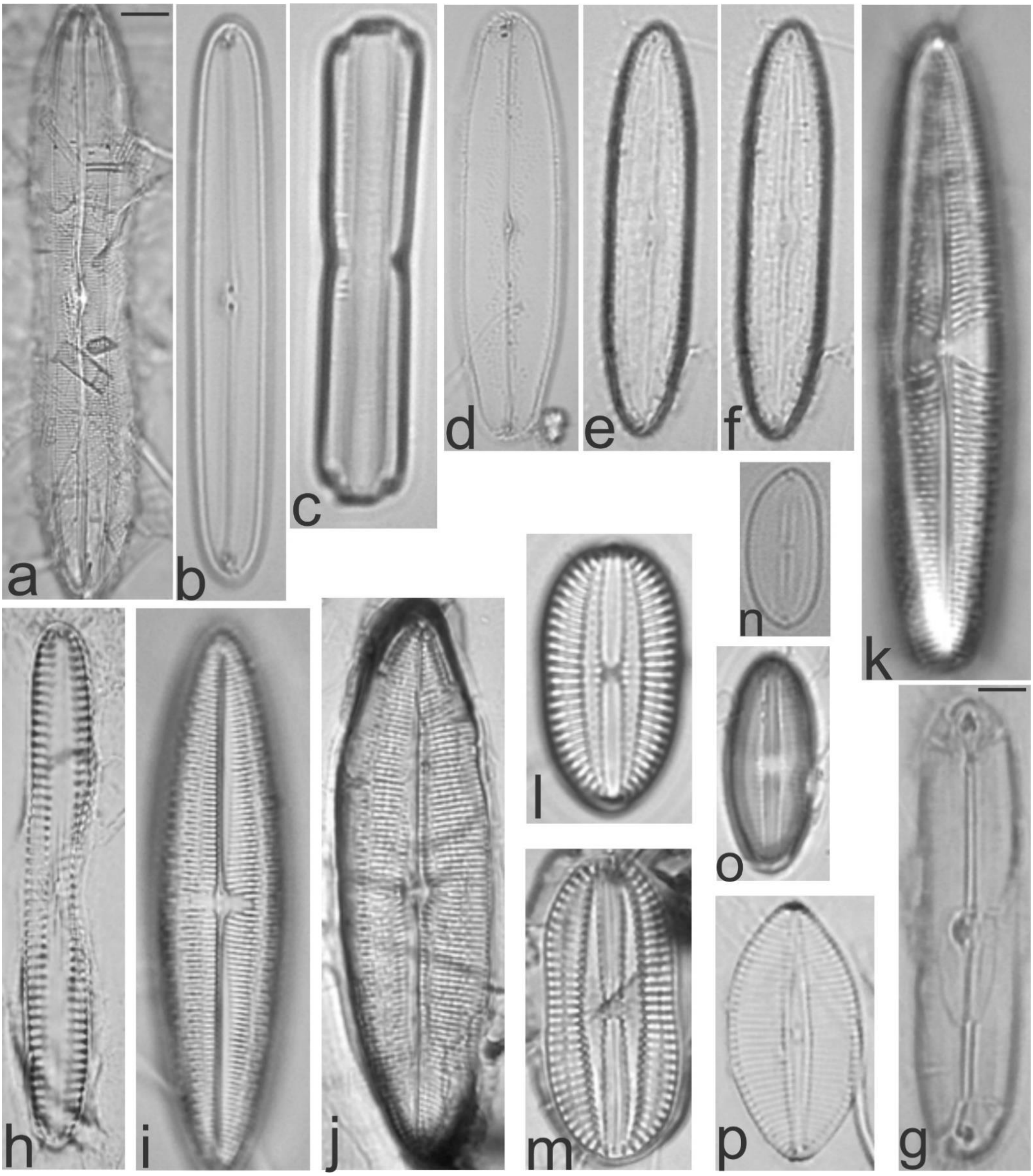

Figure 21. (**a**) *Caloneis maxima* var. *bicuneata*; (**b**,**c**) *C. linearis*; (**d**) *Caloneis* sp. 3; (**e**,**f**) *Caloneis* sp. 6; (**g**) *C. liber*; (**h**) *Biremis ambigua*; (**i**) *Trachyneis aspera*; (**j**) *T. velata*; (**k**) *T. aspera* var. *oblonga*; (**l**) *Diploneis papula*; (**m**) *D. papula* var. *constricta*; (**n**) *Diploneis* sp. 2; (**o**) *Diploneis* cf. *petersenii*; (**p**) *D. litoralis* var.? (lanceolate form). Scale bar = 10 µm.

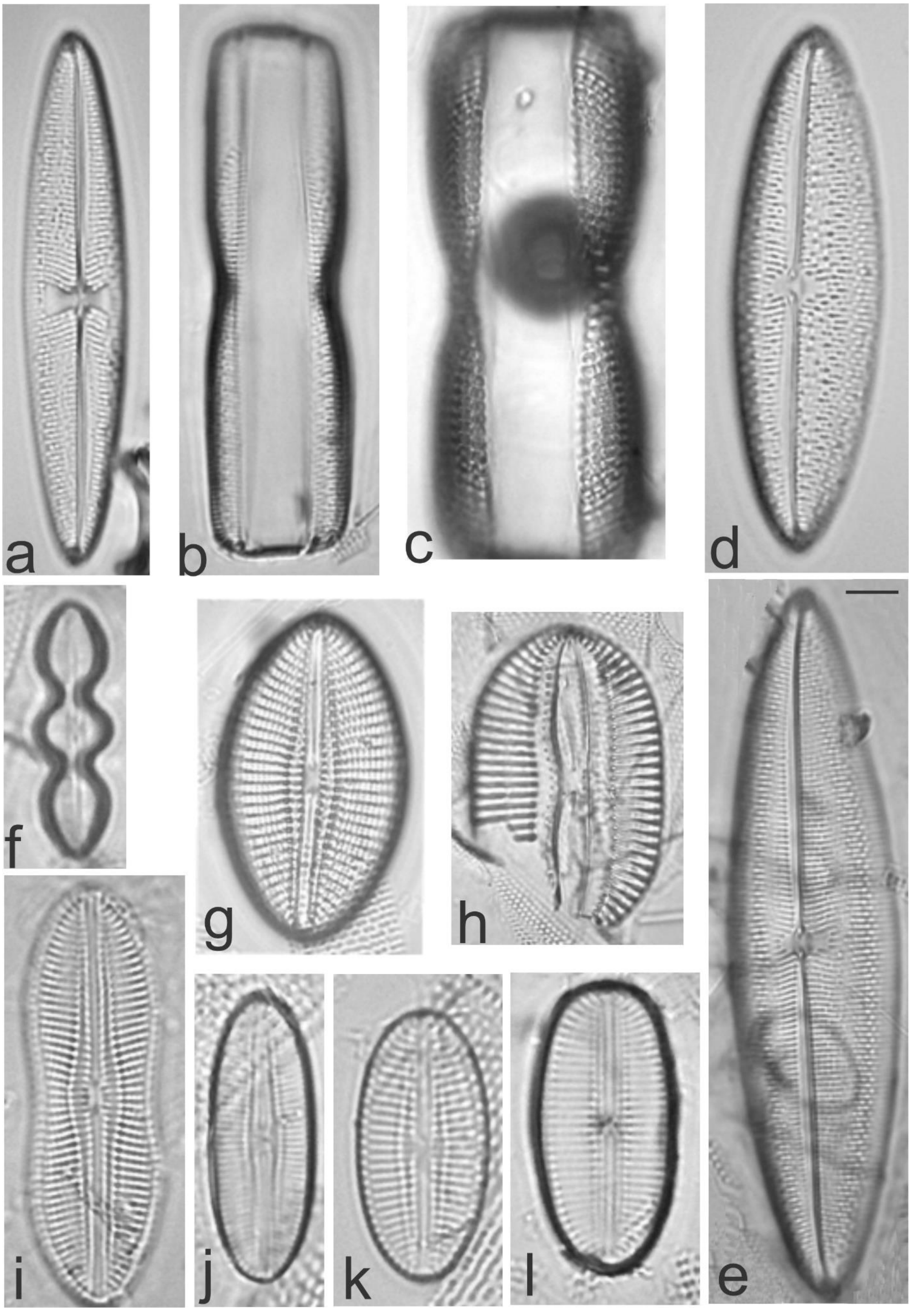

Figure 22. (**a**,**b**) *Trachyneis aspera*; (**c–e**) *T. velata*; (**f**) *Caloneis egena*; (**g**) *Diploneis smithii*; (**h**) *D. suborbicularis*; (**i**) *D. vacillans* var. *renitens*; (**j**) *D. vacillans* var. *vacillans*; (**k**) *Diploneis parca*; (**l**) *D. litoralis* var. *clathrata*. Scale bar = 5 μm.

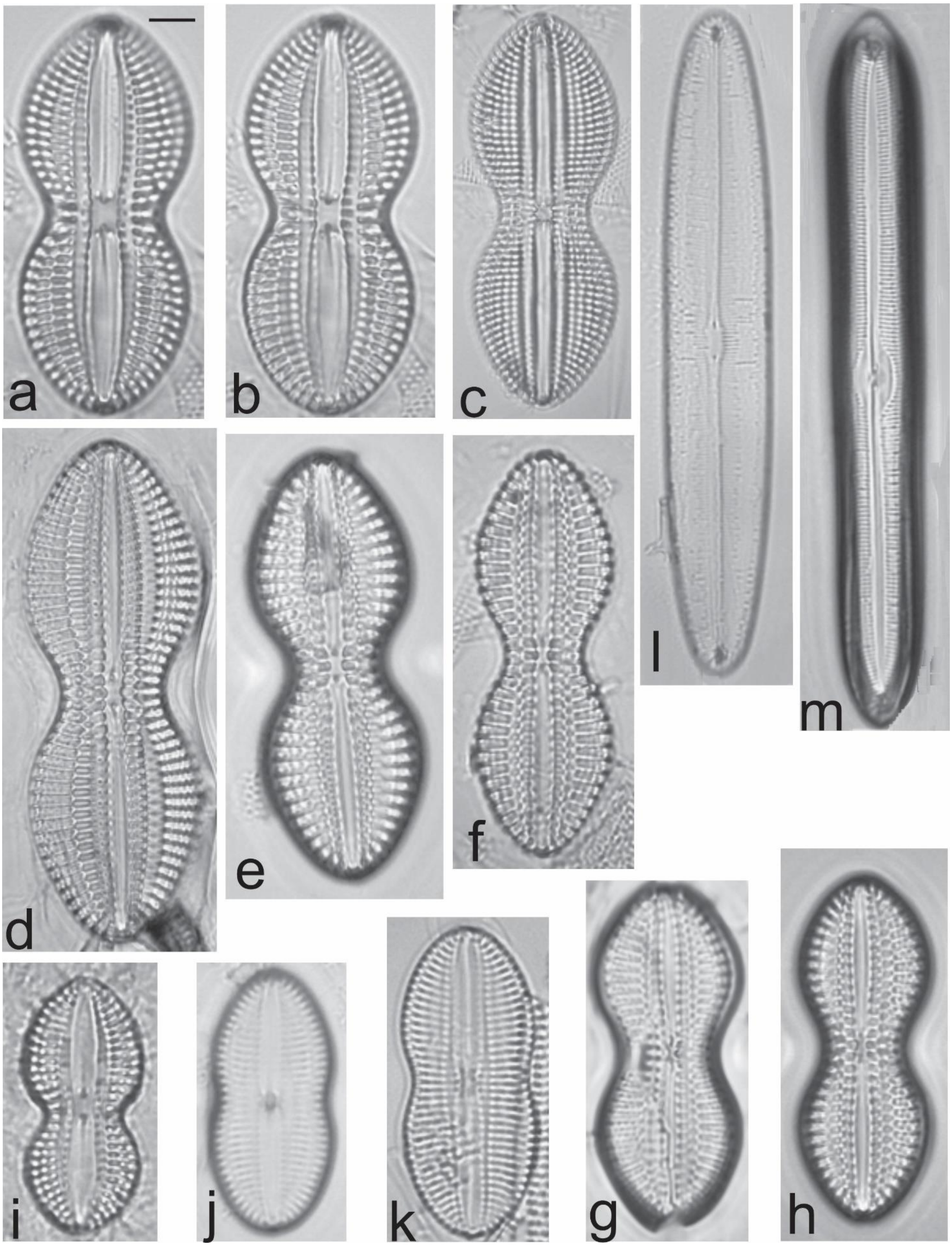

Figure 23. (**a**,**b**) *Diploneis bombus*; (**c**) *D. chersonensis*; (**d**–**h**) *D. crabro*; (**i**) *D. gruendleri*; (**j**,**k**) *Diploneis* cf. *didyma*; (**l**) *Caloneis maxima* var. *bicuneata*; (**m**) *C. elongata*. Scale bar = 6 μm.

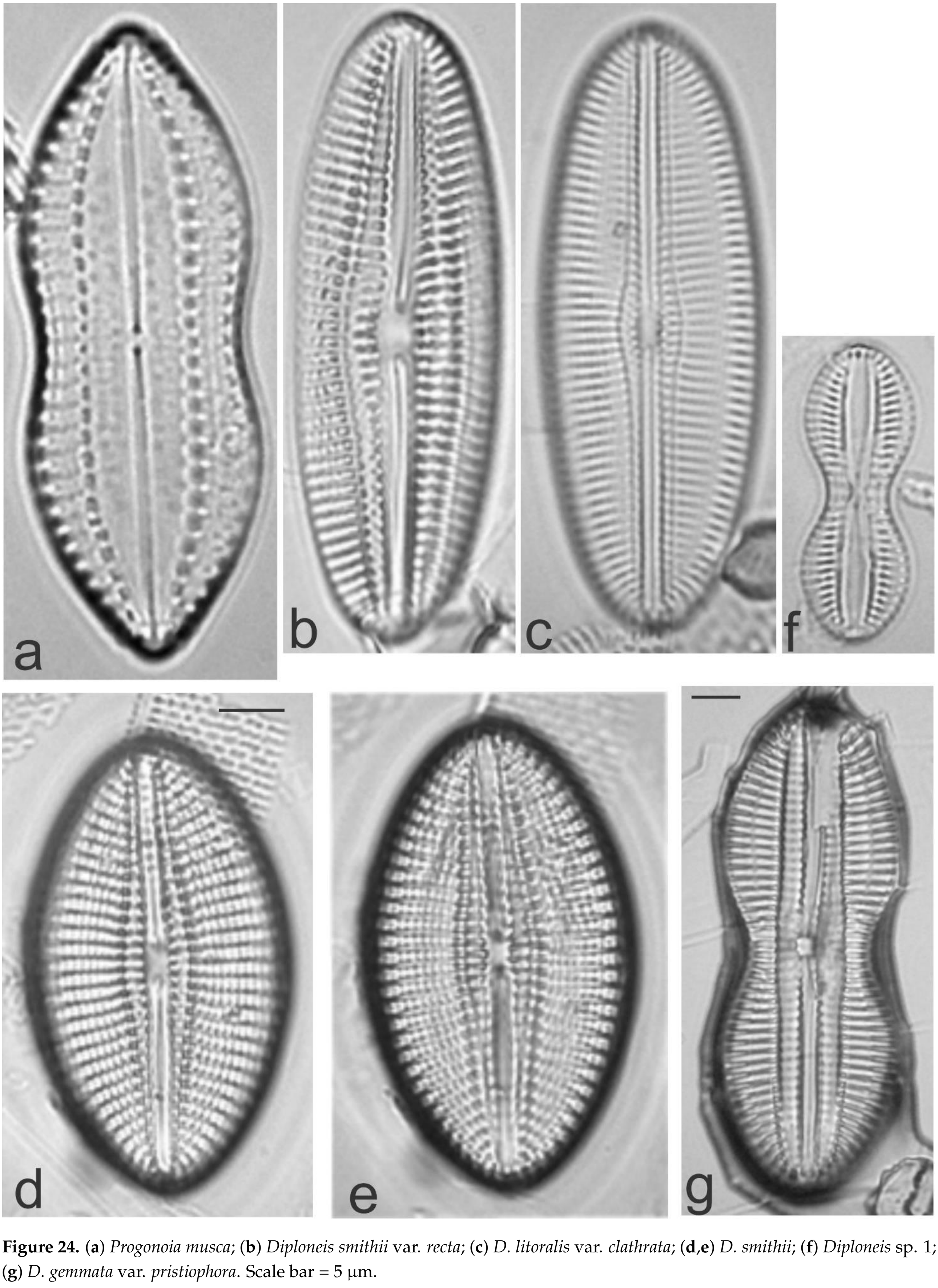

Figure 24. (**a**) *Progonoia musca*; (**b**) *Diploneis smithii* var. *recta*; (**c**) *D. litoralis* var. *clathrata*; (**d**,**e**) *D. smithii*; (**f**) *Diploneis* sp. 1; (**g**) *D. gemmata* var. *pristiophora*. Scale bar = 5 μm.

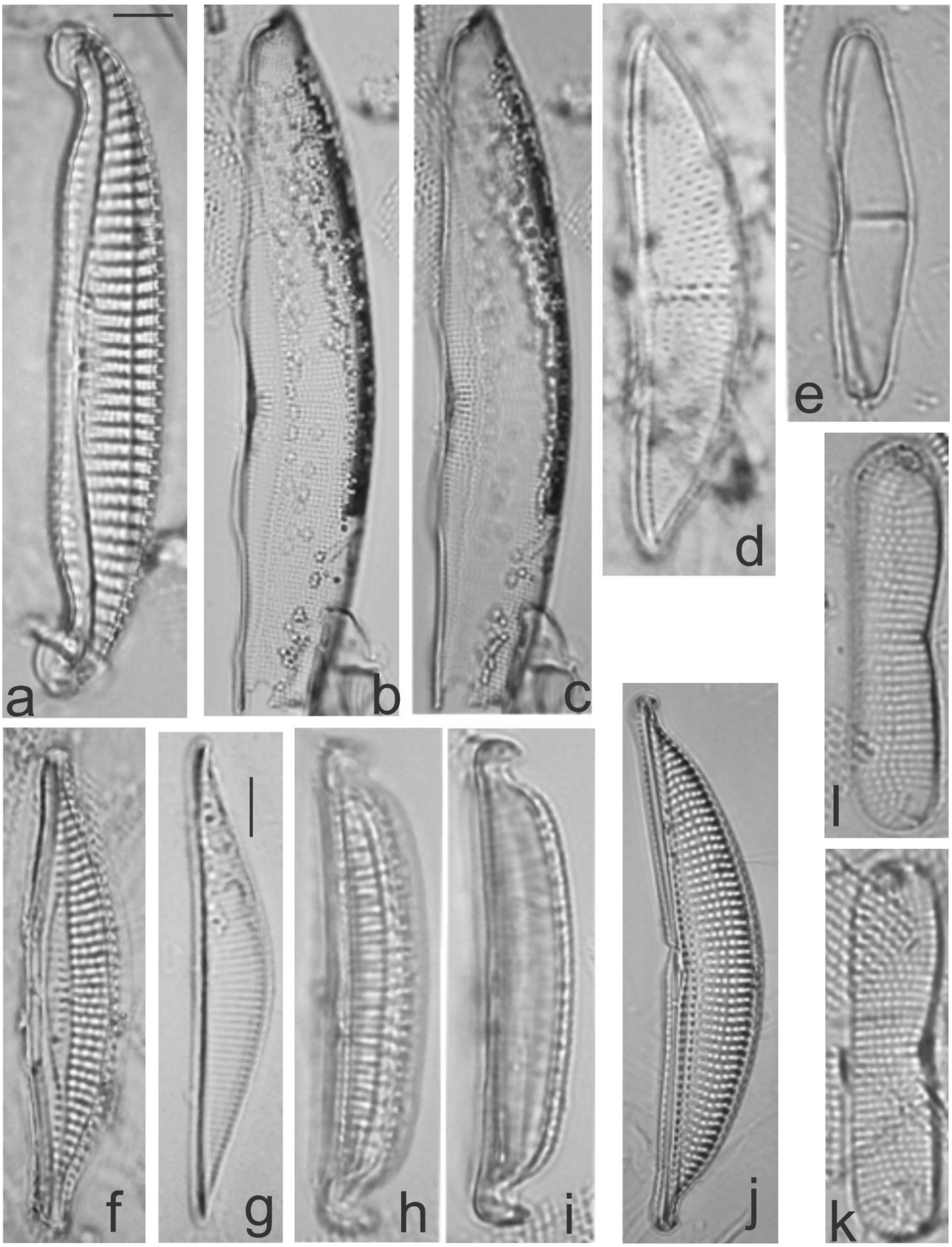

Figure 25. (**a**) *Amphora crassa* var. *campechiana*; (**b**,**c**) *A. alternata*; (**d**) *A. novaecaledonica*; (**e**) *Amphora laevissima*; (**f**) *A. grevilleana* var. *campechiana*; (**g**) *Amphora* cf. *praelata*; (**h**,**i**) *A. capensis*; (**j**) *Halamphora clara*; (**k**,**l**) *Colliculoamphora minima*. Scale bar = 5 μm.

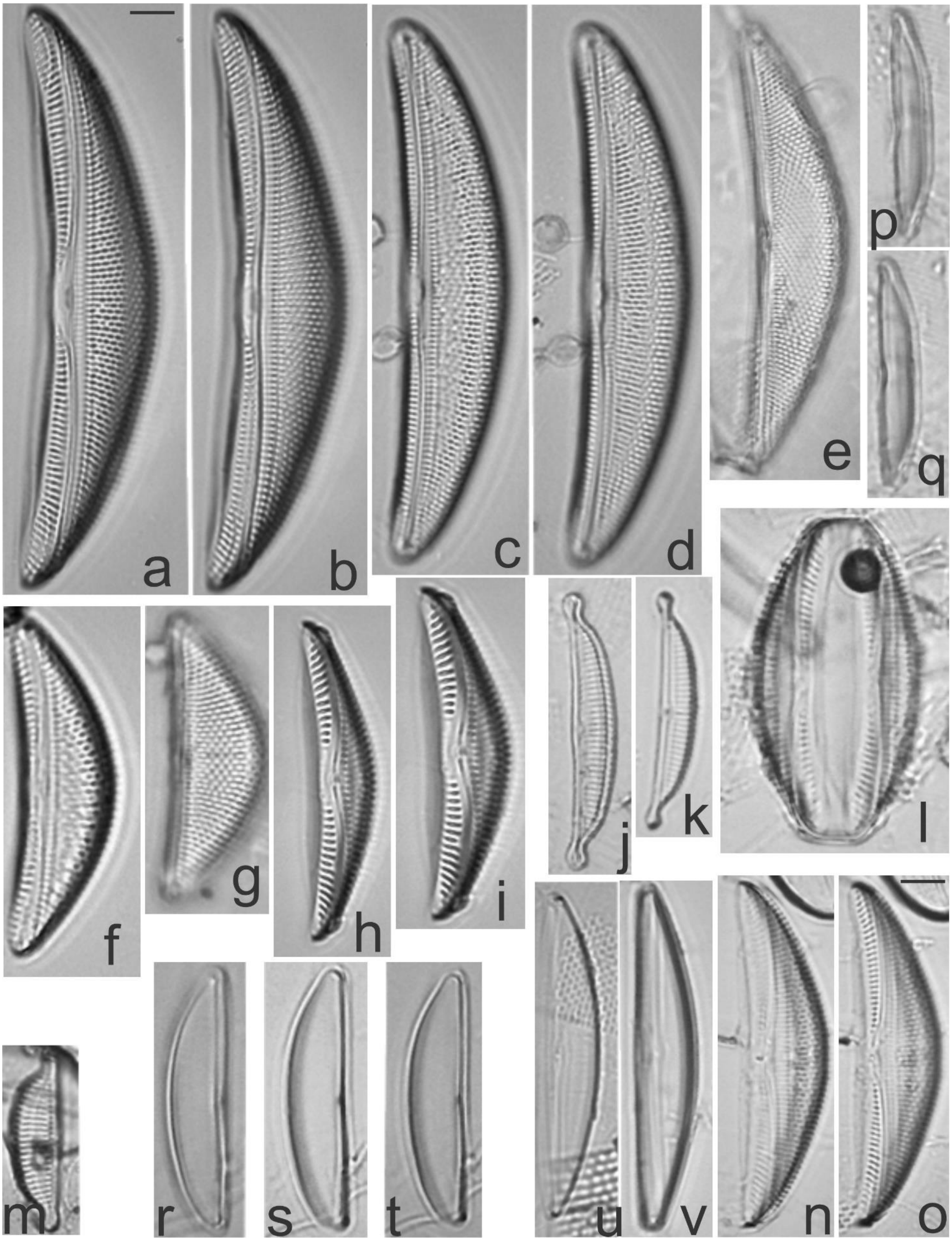

Figure 26. (**a**,**b**,**e**–**g**) *Amphora immarginata*; (**c**,**d**) *A. mexicana*; (**h**,**i**,**l**) *A. marina*; (**j**) *Halamphora yundangensis*; (**k**) *H. coffaeiformis* (**m**) *H. turgida*; (**n**,**o**) *Amphora proteus*; (**p**,**q**) *Catenula adhaerens*; (**r**–**t**) *Catenula* sp.; (**u**,**v**) *Seminavis delicatula*. Scale bar = 5 µm.

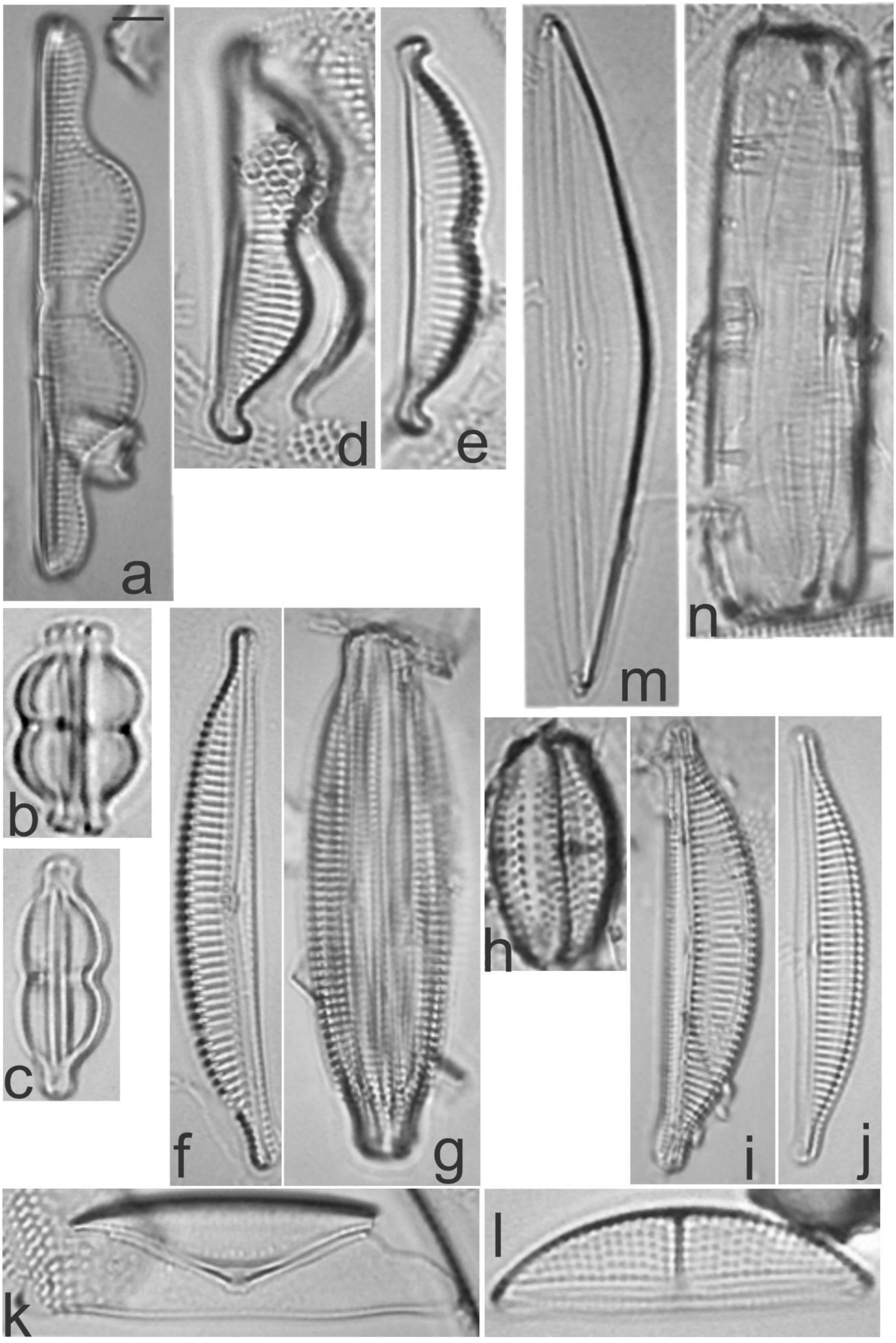

Figure 27. (**a**) *Amphora bigibba* var. *interrupta*; (**b**,**c**) *A. bigibba*; (**d**) *A. biundulata*; (**e**) *Halamphora subangularis*; (**f**,**g**) *H. holsatica*; (**h**) *A. maletractata* var. *constricta*; (**i**) *H. acutiuscula*; (**j**) *H. terroris*; (**k**) *A. arenaria*; (**l**) *Tetramphora ostrearia*; (**m**) *Seminavis basilica*; (**n**) *Amphora* cf. *obtusa* var. *rectangulata*. Scale bar = 5 μm.

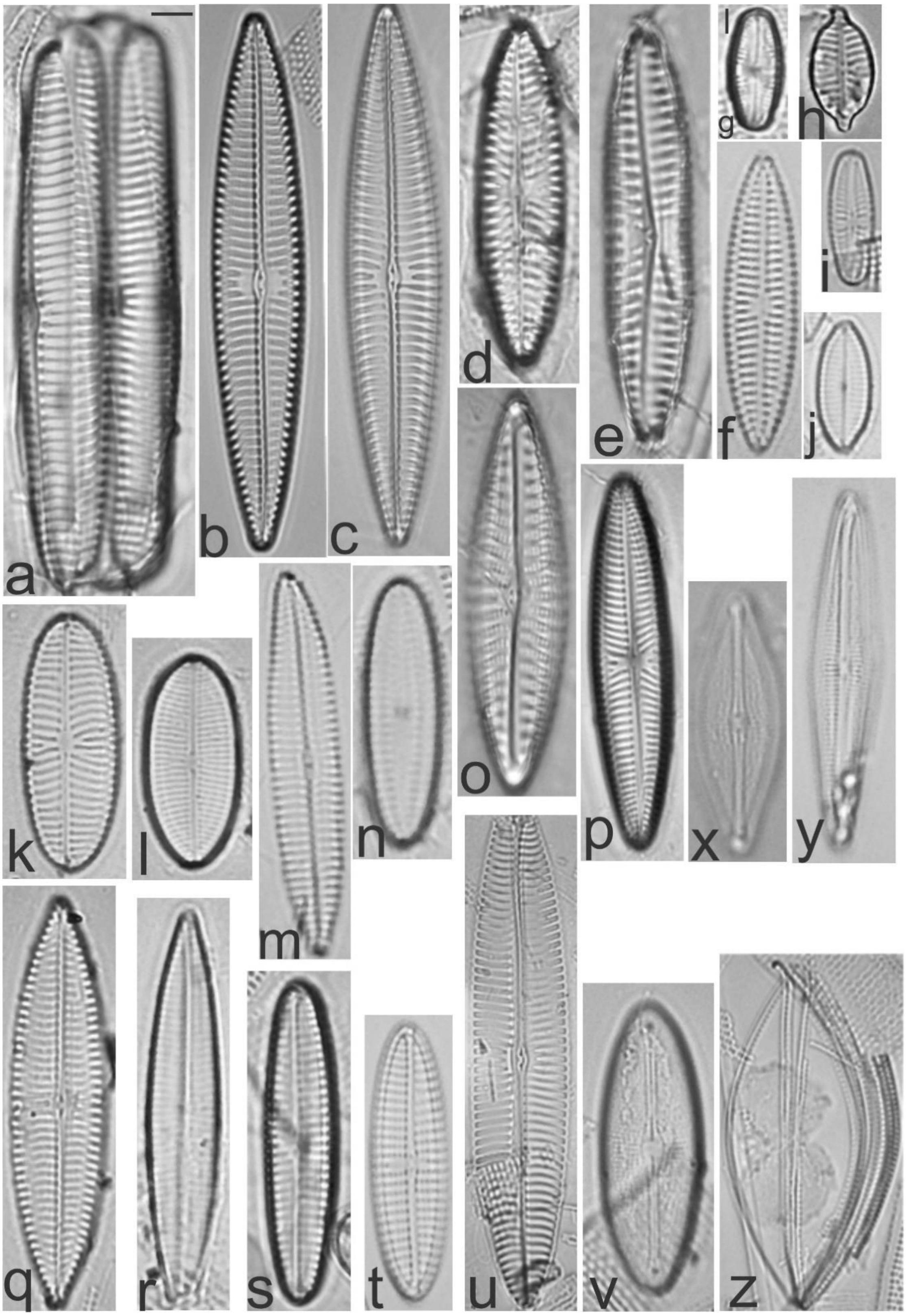

Figure 28. (**a**–**c**) *Navicula longa*; (**d**) *N. pennata*; (**e**) *N. bipustulata*; (**f**) *N. zostereti*; (**g**) *Luticola mutica*; (**h**) *Navicula platyventris*; (**i**) *Dickieia* sp.; (**j**) *Navicula* sp. 1; (**k**) *N. digitoradiata*; (**l**) *Navicula* sp. 3; (**m**) *Navicula subrostellata*; (**n**) *Biremis ambigua*; (**o**) *Navicula inflexa*; (**p**) *N. digitoconvergens*; (**q**) *N. johanrossii*; (**r**) *Craticula halophila*; (**s**) *Navicula* sp. 2; (**t**) *Navicula athenae*; (**u**) *N. arenaria* var. *rostellata*; (**v**) *Parlibellus* cf. *phoebeae*; (**x**) *P.* cf. *delognei*; (**y**) *P. cruciculoides*; (**z**) *Halamphora pseudohyalina*. Scale bar = 5 μm.

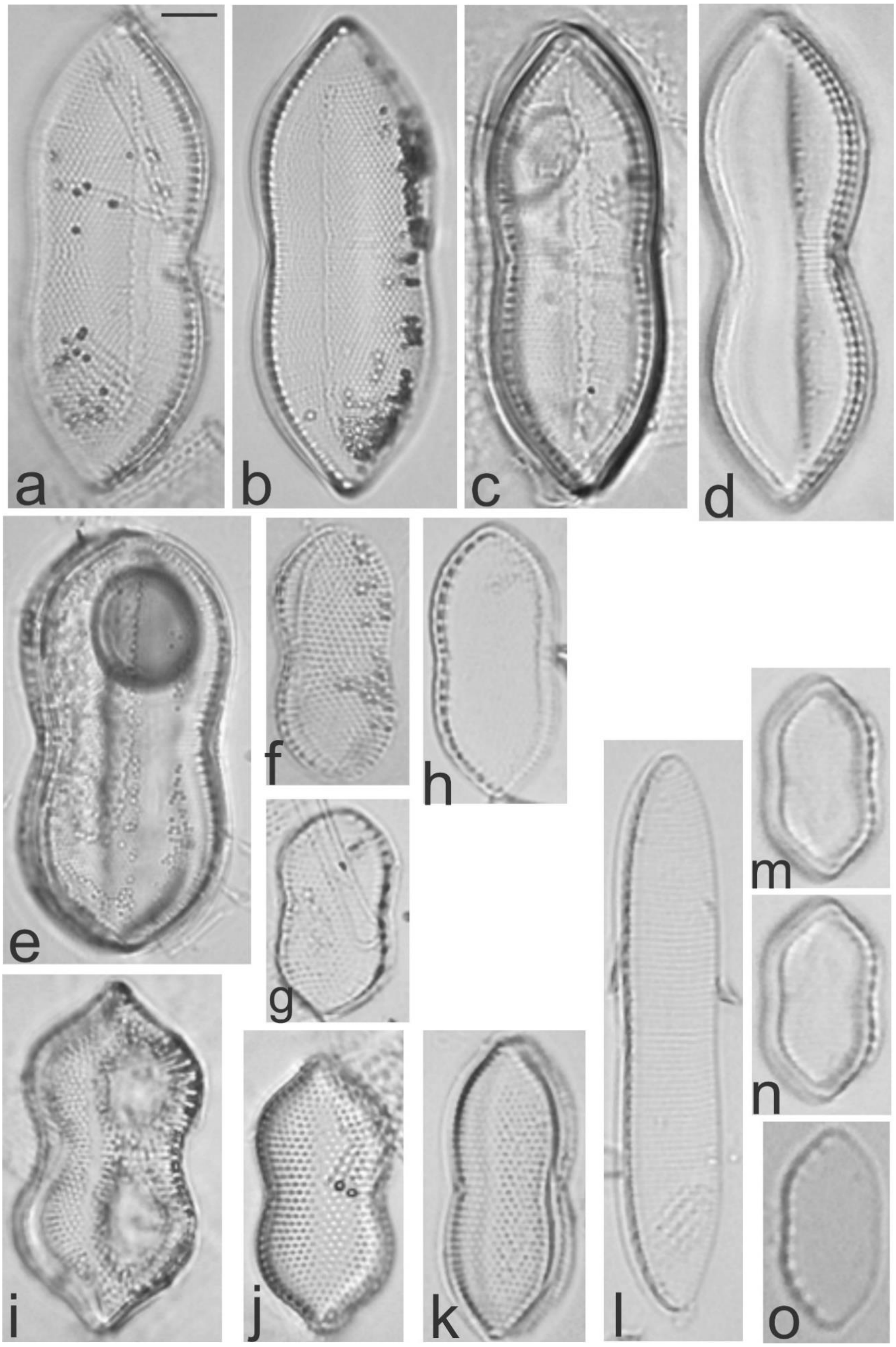

Figure 29. (**a**–**c**) *Psammodictyon roridum*; (**d**) *Tryblionella nicobarica*; (**e**) *Psammodictyon panduriforme*; (**f**,**g**,**k**) *P. constrictum*; (**h**) *Tryblionella persuadens*; (**i**) *Psammodictyon pustulatum*; (**j**) *Tryblionella coarctata*; (**l**) *Nitzschia jelineckii*; (**m**,**n**) *Psammodictyon panduriforme* var. *continuum*; (**o**) *P. rudum*. Scale bar = 5 μm.

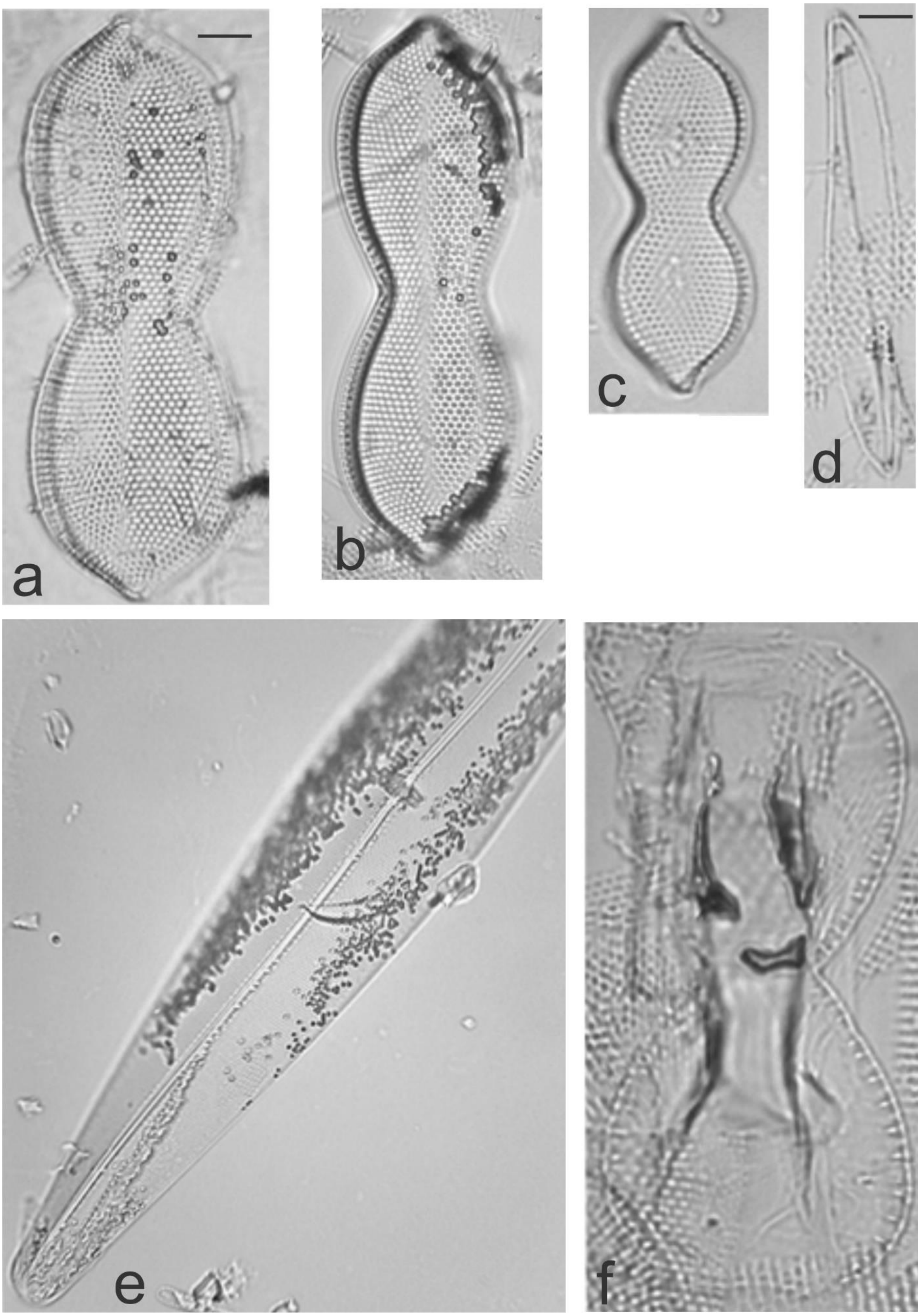

Figure 30. (**a**,**b**) *Tryblionella didyma*; (**c**) *Nitzschia bombiformis*; (**d**) *Gyrosigma* cf. *parvulum*; (**e**) *Pleurosigma barbadense*; (**f**) *Entomoneis punctulata*. Scale bars: (**e**) = 10 μm; all others = 5 μm.

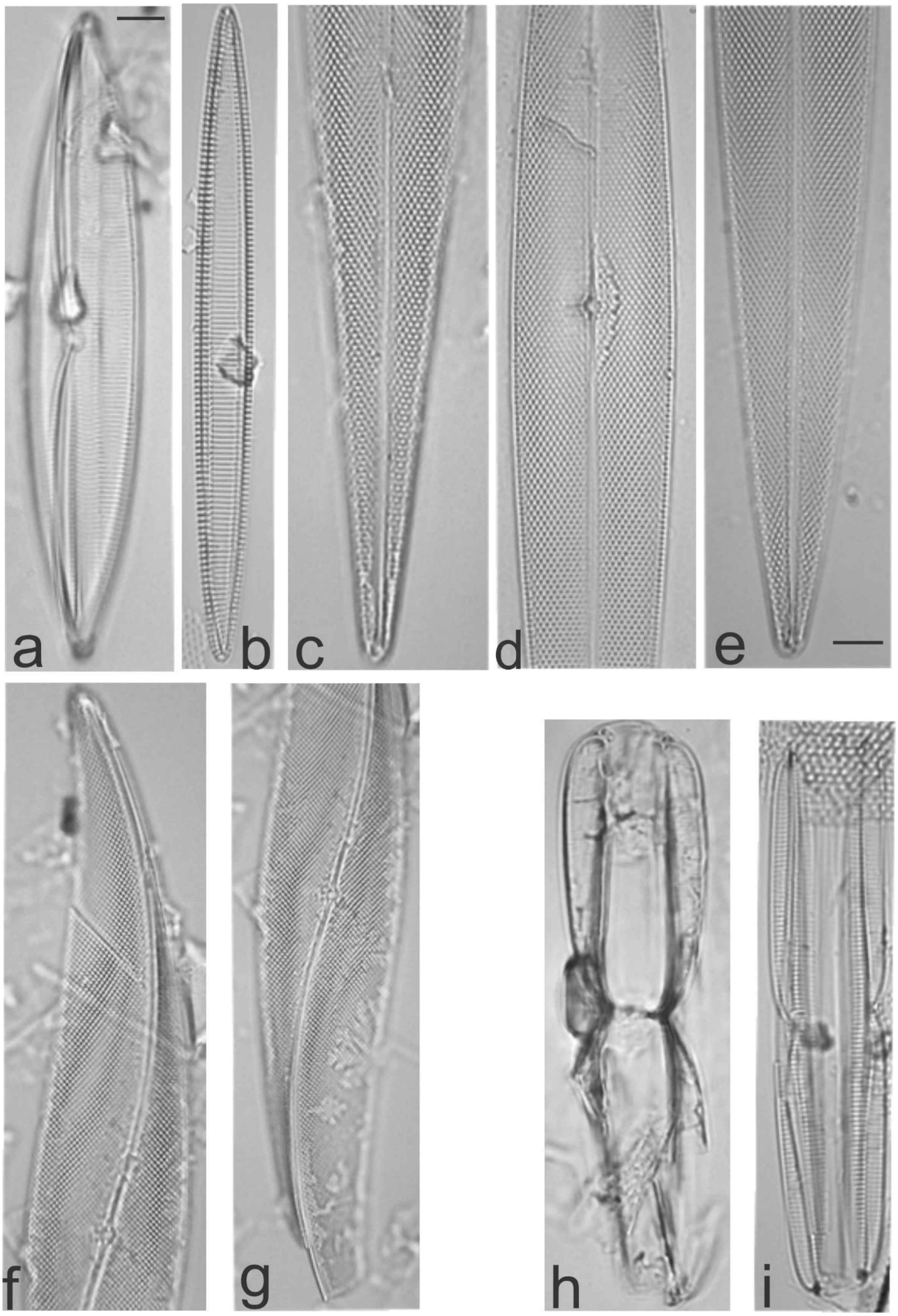

Figure 31. (**a**) *Plagiotropis pusilla*; (**b**) *Alveus marinus*; (**c**–**e**) *Pleurosigma intermedium*; (**f**,**g**) *P. angulatum*; (**h**) *Carinasigma minutum*; (**i**) *Tropidoneis* sp. Scale bars: (**c**–**e**,**f**,**g**) = 10 µm; all others = 5 µm.

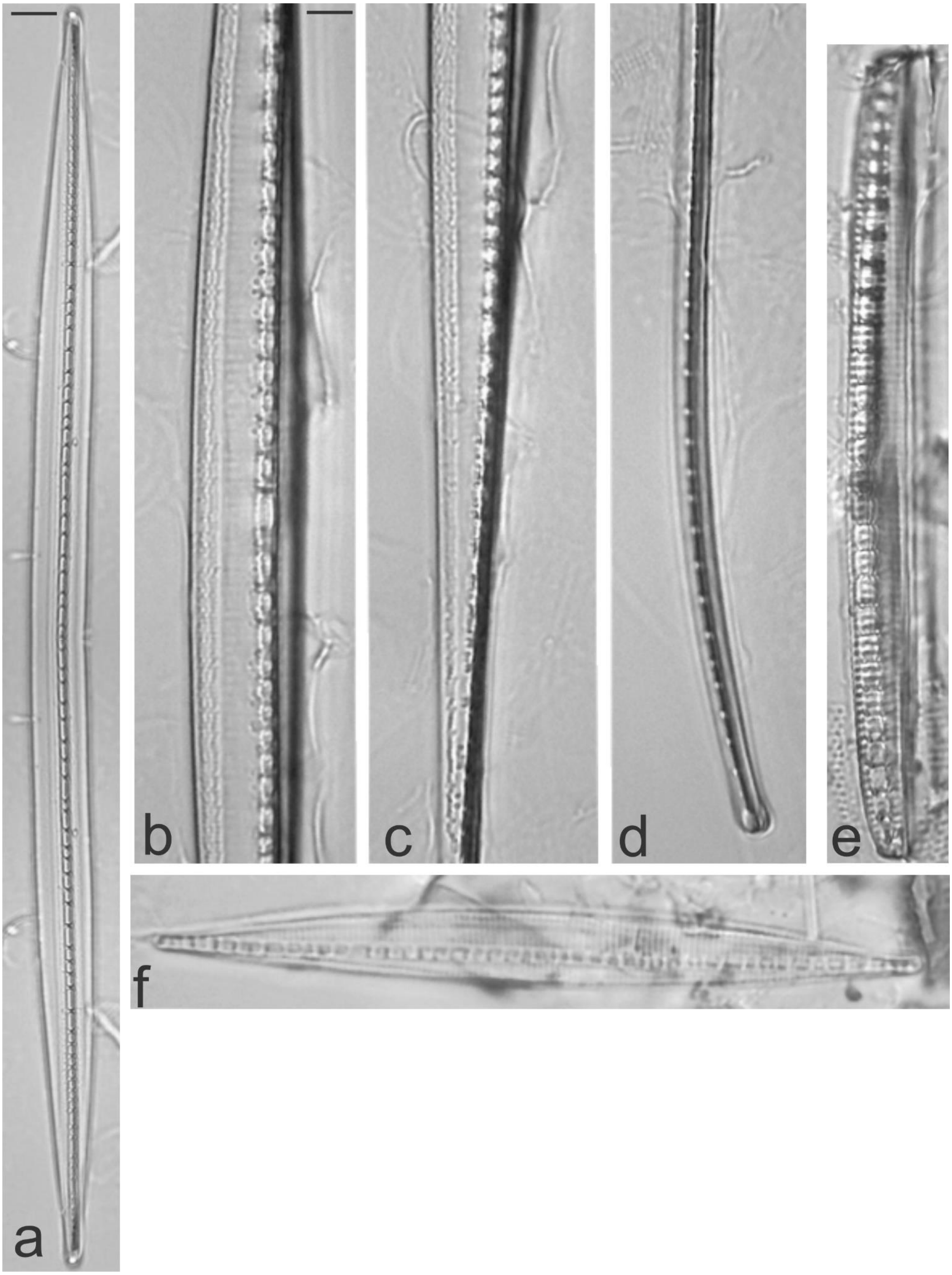

Figure 32. (**a**) *Nitzschia distans*; (**b–d**) *N. behrei*; (**e**) *N. insignis*; (**f**) *Bacillaria socialis*. Scale bar = 5 µm.

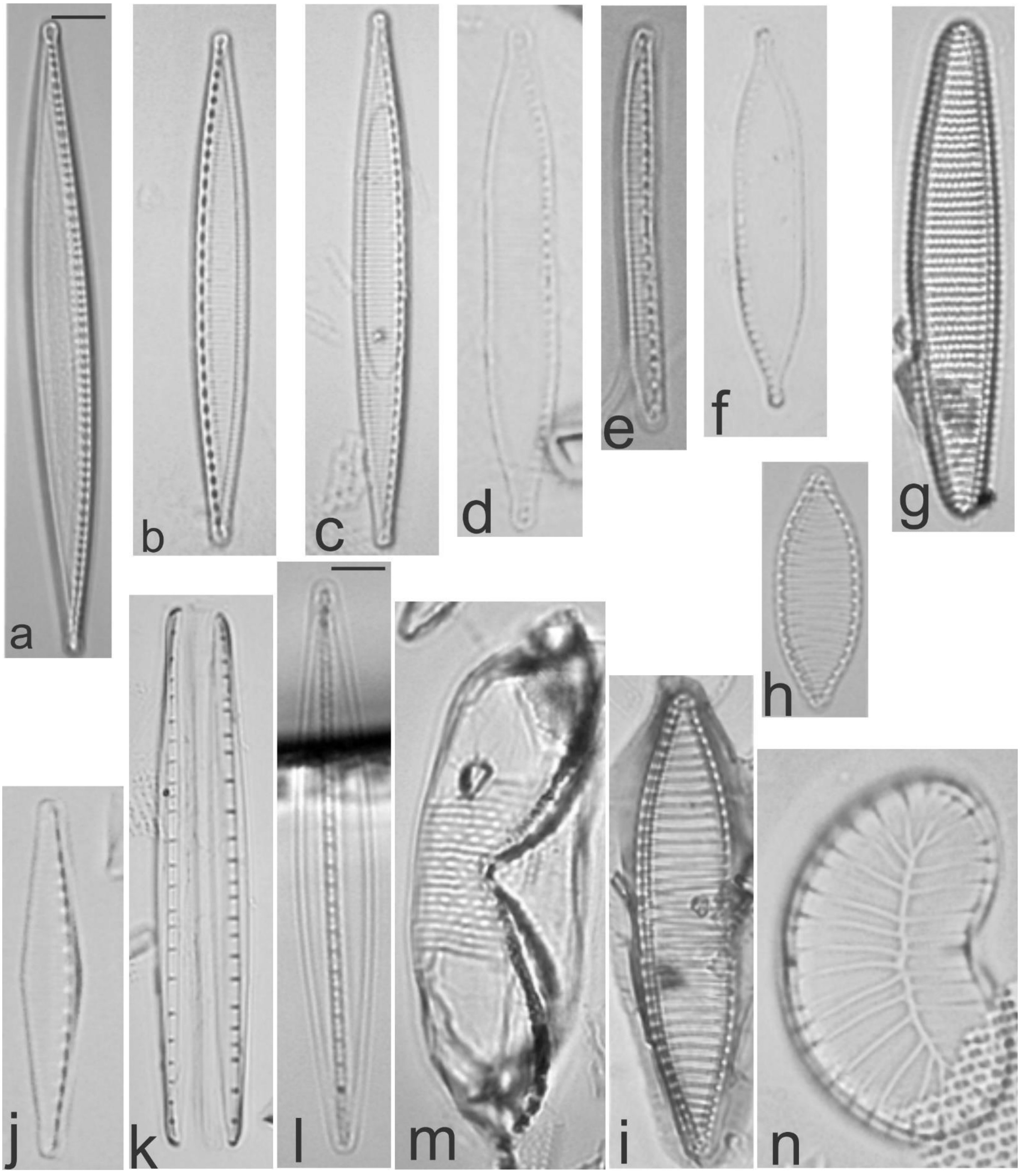

Figure 33. (**a**) *Nitzschia sigma*; (**b**,**c**) *N. subacuta*; (**d**,**f**) *N. tubicola*; (**e**) *Cymbellonitzschia banzuensis*; (**g**) *Fragilariopsis doliolus*; (**h**,**i**) *Nitzschia sicula*; (**j**) *N. tenerifa*; (**k**,**l**) *N. angularis*; (**m**) *N. nienhuisii*; (**n**) *Plagiodiscus nervatus*. Scale bar = 5 µm.

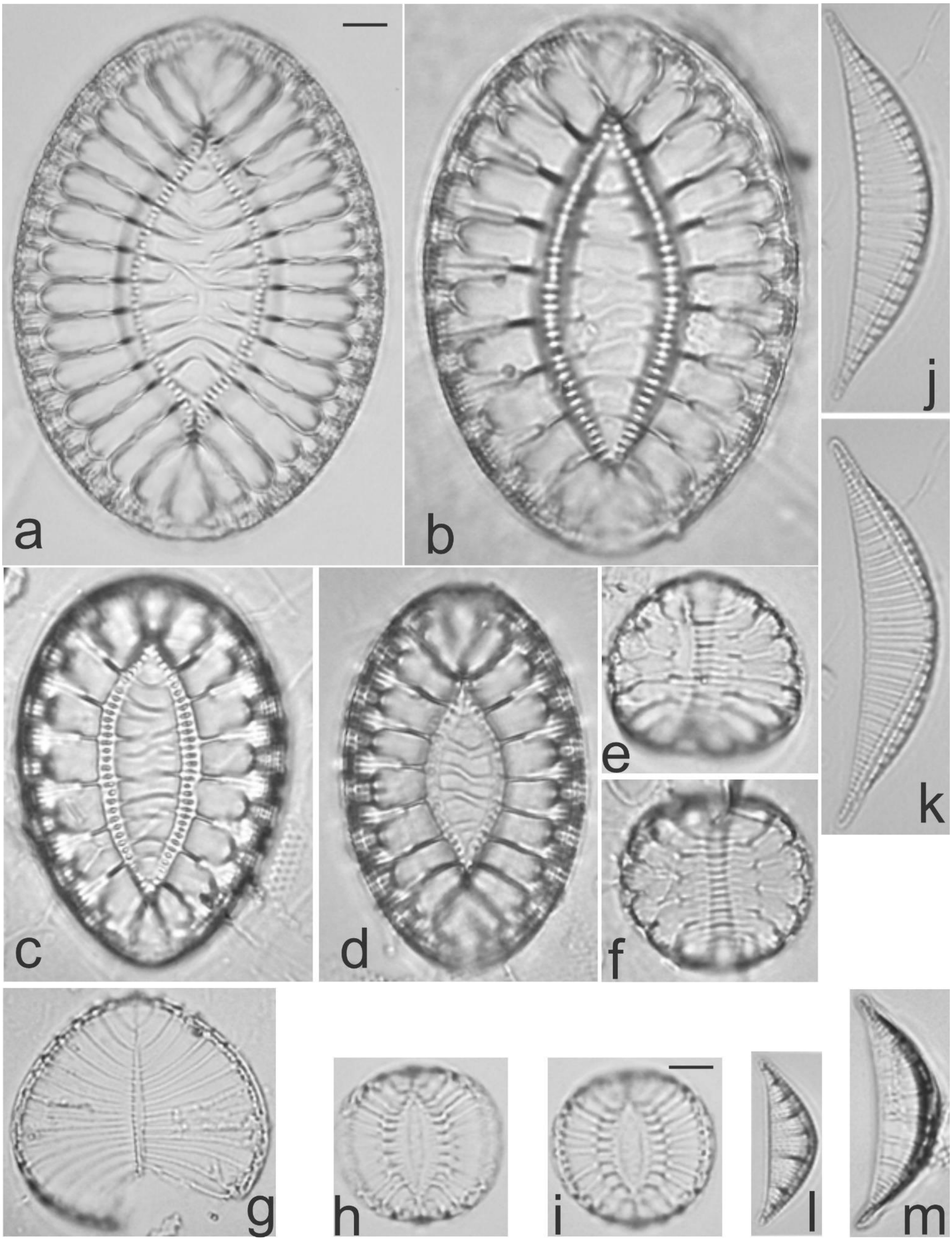

Figure 34. (**a**–**d**) *Campylodiscus neofastuosus*; (**e**,**f**) *C. thuretii*; (**g**) *C. ralfsii*; (**h**,**i**) *Campylodiscus* sp. 1; (**j**,**k**) *Epithemia guettingeri*; (**l**) *Rhopalodia gibberula* var. *producta*; (**m**) *Epithemia pacifica*. Scale bar = 5 µm.

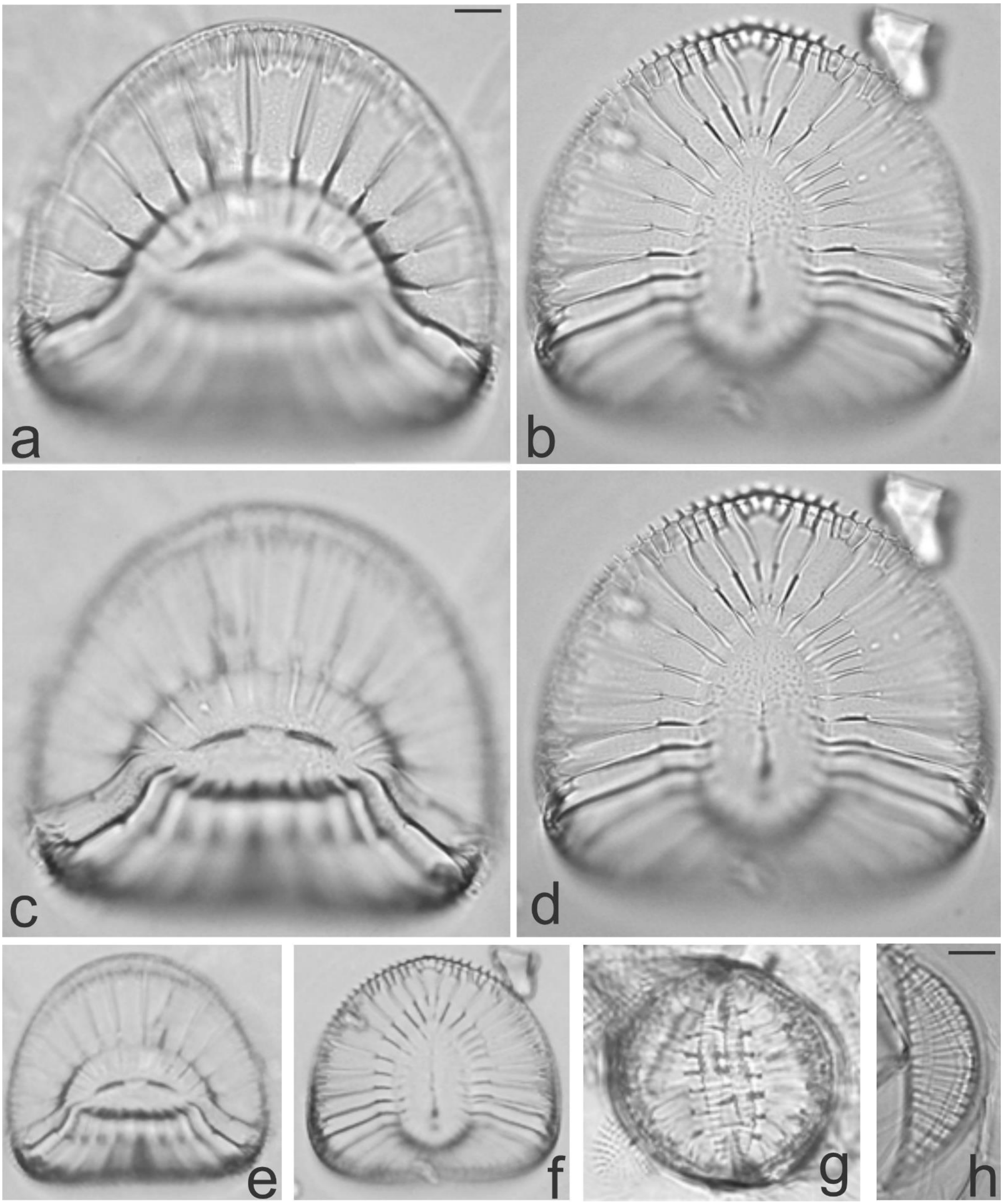

Figure 35. (**a**–**d**,**e**,**f**) *Coronia ambigua*; (**g**) *Campylodiscus simulans*; (**h**) *Epithemia pacifica*. Scale bars: (**e**,**f**) = 10 μm; all others = 5 μm.

Table 2. Estimated relative abundances (RA) for the benthic marine diatom taxa found on macroalgae hosts from the Revillagigedo Archipelago, Mexico (N = 12,443). Taxa comprising 80% of the total valves counted. ARA = accumulative relative abundances.

TAXA	Valves	RA	ARA
Achnanthidium exiguum var. *heterovalvata*	1054	8.471	8.471
Cocconeis krammeri	927	7.450	15.921
Mastogloia crucicula	812	6.526	22.446
Cocconeis scutellum var. *parva*	802	6.445	28.892
Epithemia pacifica	670	5.385	34.276
Mastogloia binotata	497	3.994	38.271
Hyalosynedra laevigata	429	3.448	41.718
Amphora exilitata	359	2.885	44.603
Tabularia fasciculata	329	2.644	47.247
Cocconeis comis	326	2.620	49.867
Rhabdonema adriaticum	310	2.491	52.359
Grammatophora oceanica	278	2.234	54.593
Podocystis americana	221	1.776	56.369
Mastogloia crucicula var. *alternans*	215	1.728	58.097
Cocconeis pseudodiruptoides	205	1.648	59.744
Bleakeleya notata	202	1.623	61.368
Cocconeis placentula	200	1.607	62.975
Cocconeis sp. 2	184	1.479	64.454
Mastogloia fimbriata	181	1.455	65.909
Halamphora coffeaeformis	176	1.414	67.323
Mastogloia cuneata	155	1.246	68.569
Mastogloia emarginata	133	1.069	69.638
Nitzschia bicapitelata	130	1.045	70.682
Seminavis delicatula	130	1.045	71.727
Cocconeis pediculus	125	1.005	72.732
Navicula cincta	123	0.989	73.720
Cocconeis convexa	120	0.964	74.685
Cocconeis neodiminuta	114	0.916	75.601
Toxarium undulatum	107	0.860	76.461
Gomphonemopsis pseudexigua	103	0.828	77.288
Mastogloia graciloides	88	0.707	77.996
Mastogloia tenuis	84	0.675	78.671
Cocconeis dirupta var. *flexella*	78	0.627	79.298
Cocconeis diruptoides	70	0.563	79.860
Mastogloia exilis	70	0.563	80.423

Notwithstanding the depicted distribution, the average species diversity value was $H' = 4.68$ bits/taxon, ranging from high $H' = 3.92$ ($S = 55$) to very high 5.2 ($S = 87$). Furthermore, between the lowest and richest sub-samples (replicates) the H' values were both high, 4.11 ($S = 57$) vs. 4.62 ($S = 73$), with all community parameter values showing good correspondence between them, particularly with low values of dominance, high values of equitability and species richness (Table 3).

Table 3. Diversity values computed for the diatom taxa found on macroalgae hosts from the Revillagigedo Archipelago, Mexico.

Sub-Samples	Macroalgal Host	S	N	J′	H′	λ	1 − λ
1a	*Sargassum liebmanii*	80	535	0.79	5.01	0.06	0.94
1b	*Sargassum liebmanii*	80	461	0.79	5.01	0.06	0.94
2a	*Amphiroa beauvoisii*	83	553	0.80	5.09	0.05	0.95
2b	*Amphiroa beauvoisii*	79	483	0.80	5.07	0.05	0.95
4a	*Dictyota crenulata*	87	508	0.81	5.20	0.05	0.95
4b	*Dictyota crenulata*	72	491	0.79	4.90	0.06	0.94
5bI	*Asparagopsis* sp.	71	497	0.72	4.45	0.10	0.90
5bII	*Asparagopsis* sp.	74	518	0.71	4.40	0.10	0.90
6a	*Dictyota* sp.	73	512	0.77	4.74	0.08	0.92
6b	*Dictyota* sp.	59	504	0.76	4.49	0.09	0.91
10a	*Dictyota dichotoma*	82	582	0.77	4.92	0.07	0.93
10b	*Dictyota dichotoma*	77	564	0.76	4.75	0.08	0.92
11a	*Canistrocarpus cervicornis*	85	535	0.77	4.92	0.07	0.93
11b	*Canistrocarpus cervicornis*	73	501	0.75	4.61	0.09	0.91
12a	Rhodophyte	47	547	0.79	4.39	0.07	0.93
12b	Rhodophyte	51	532	0.85	4.80	0.05	0.95
13a	*Dictyota* sp.	75	543	0.74	4.63	0.07	0.93
13b	*Dictyota* sp.	66	488	0.77	4.64	0.07	0.93
14a	*Dictyota* sp.	64	512	0.80	4.81	0.06	0.94
14b	*Dictyota* sp.	70	533	0.78	4.80	0.06	0.94
16a	Rhodophyte	73	515	0.75	4.62	0.09	0.91
16b	Rhodophyte	57	535	0.70	4.11	0.14	0.86
17a	*Laurencia* sp.	55	500	0.68	3.92	0.18	0.82
17b	*Laurencia* sp.	57	494	0.68	3.99	0.16	0.84
Range/Mean		47–87	461–582	0.76	4.68	0.082	0.92

In terms of similarity, measurements for all the collected samples indicate a dissimilarity between the different diatom assemblages, showing around or over 50% similarity based on the presence/absence of taxa; this is compared to the values between replicates that depict the same assemblage and varied at around 0.7 similarity (Figure 36). Whilst, based on the taxa relative abundances, values ranged from just below to just above 0.3 (Figure 37), this is compared to the similarity between replicates which varied at around 0.8. All this indicates that much of the taxa, which compose the assemblages, are different including the most numerous ones.

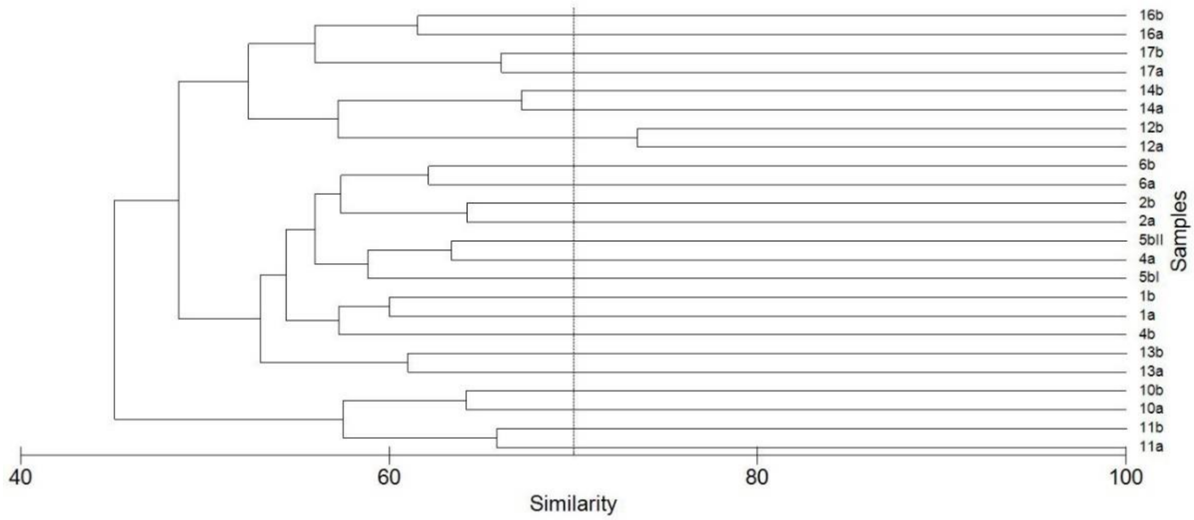

Figure 36. Similarity between the epiphytic diatom assemblages from Revillagigedo Archipelago according to the Bray–Curtis index based on the presence/absence of taxa.

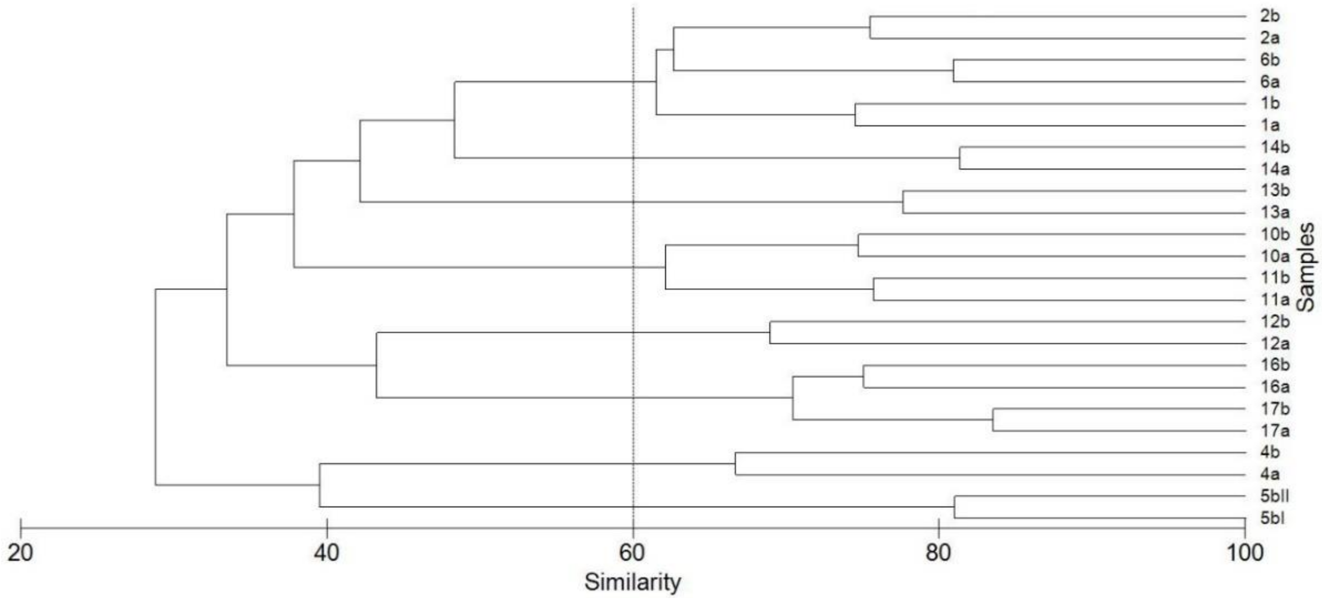

Figure 37. Similarity between the epiphytic diatom assemblages from Revillagigedo Archipelago according to the Bray–Curtis index based on the relative abundances of the shared taxa.

4. Discussion

With the new records from this study (167), the species richness of diatoms found on macroalgae from the Revillagigedo Archipelago reaches a total of 397 taxa. This implies an increase of >75% in this report alone, not including the independently recorded species of the genus *Mastogloia* whose species richness had previously increased by approximately 75% [10]. Thus, an overall increase in species richness of 90%, including the previously recorded *Mastogloia* taxa, is attained.

Considering the previous study of the RA [6], the five new *Mastogloia* taxa recorded make this genus the most diverse, with 55 taxa in the study area, followed by the *Cocconeis* (27), *Nitzschia* (24), *Amphora* (23), *Navicula* (18), *Diploneis* (17) and *Grammatophora* (15). It does seem valid to remark that such an increase in species richness, which is only four less than the predicted number, supports our hypothesis on the potential species richness of benthic diatoms in the RA. Moreover, some of the taxa were also recorded recently from the Gulf of California, such as *Achnanthes apiculata*, *Caloneis egena*, *Coronia ambigua*, *Grammatophora undulata* var. *gallopagensis*, *Gyrosigma parvulum*, *Psammodictyon pustulatum*, *Psammodictyon roridum*, *Seminavis basilica*, *Trachyneis aspera* var. *oblonga* and *Tryblionella nicobarica*, among others [7,50]. This indicates a biogeographical connectivity between regions where warm conditions determine the presence of species with a tropical affinity. It thus seems that long-distance dispersal is, in many cases, effective enough for species to establish across large geographic areas [8]. This, however, should also be examined relying on the *Mastogloia* taxa that they share.

Moreover, the unidentified species such as *Planothidium* sp. 1, *Achnanthes* sp. 2, *Caloneis* sp. 6 (*Caloneis* species 1–5 in [6]) and *Mastogloia* sp. 1, including the one identified as cf. *Staurosirella martyana* and 13 others, are likely new (undetermined) taxa and, added to the previous 16 in [6], require formal taxonomic treatment.

Regarding other taxonomic issues, in certain cases apparent synonymies in the identified taxa were not updated and the names from the literature were kept. These included *Amphora novaecaledonica*, which is deemed a synonymy of *Amphora ostrearia* var. *vitrea* Cleve [46]. Our specimen, however, closely resembles the *A. novaecaledonica* in [39] but differs from *A. ostrearia* var. *vitrea* in several modern references. Additionally, our *Nitzschia punctata* var. *coarctata* is considered synonymous with *Tryblionella coarctata* (Grunow) D.G. Mann, which was recorded in the previous floristics for the RA [6]; the forms were different, and the assigned names were consistent with several modern references. Furthermore, in the case of *Thalassionema nitzschioides* var. *parvus*, we opted for this authority vs. Heiden and Kolbe 1928 [46], provisionally.

On the other hand, also backing our hypothesis are the species diversity values which ranged from H′ = 3.92–5.2 bit/taxon, with an average value of 4.68. Typical diatom assemblages are shaped by a few abundant and very common species, and many rare and uncommon species. Variations in this distribution pattern are reflected in the mathematical values of diversity derived from information theory calculated with Shannon's index (H′). Estimated values of H′ have been observed to vary mainly between (modal) values of 2.6–3.8 bits/taxon (median, 2.4–4.6) benthic diatom assemblages [51] and have been interpreted as usual or moderately high values of diversity that indicate stability of the assemblages. Although higher ($H' \approx 5$) and lower ($H' < 2$) values are not uncommon, these have been interpreted as indicative of a tendency towards an improbable and thus unstable state of the assemblages in nature [12]. Thus, the primary high estimates of species diversity for the inspected benthic (epiphytic) diatom assemblages of the RA may reflect the pristine conditions of the islands due to the combined factors of remoteness and enforced policies as a protected natural area. When compared to diversity values from other protected areas, such as the Guerrero Negro lagoon, certain equivalence is noted with the average values of H′ = 4.96 bits/taxon, and range of 3.7–5.9, computed for the epipelic diatom assemblages of that lagoon [3]. So, according to the latter study, the high values of diversity depict pristine or undisturbed conditions (independent of whether the habitat is protected or not), but species richness and the corresponding diversity values are expected to be as high as those in both studies. Whatever the case, the assessed attributes of the diatom assemblages inspected indicate that the Revillagigedo Archipelago is free from any environmental impact.

Finally, the low similarity between various compared samples is typical of benthic diatom taxocenosis that exhibit a patchy or aggregate distribution in which the species composition and the main taxa that they are composed of are both different and are most likely alternating these components on a successional basis [2]. More precise descriptions of space distribution require a hypothesis-based sampling design, preferably coupled with temporal variations of the diatom assemblages.

In terms of limitations of this study, the 29 taxa that could not be identified are added to those in the previous survey [4], making a total of 61 taxa for the RA that are expected to be undetermined species requiring formal taxonomic treatment. Some of the reference images are deemed in need to of improving and further sampling is likely to provide better specimens to replace them. Meanwhile, they are considered to adequately serve as backup for the identifications made.

On the other hand, the generated ecological parameter estimates are based on the inspection of a few host specimens with very few macroalgal taxa (<10) out of the >200 macroalgal taxa recorded from the RA [17]. Besides this, other substrates such as sediments or rock or a number of other localities in the area were not considered. Thus, the potential number of taxa [6] and concomitant ecological diversity parameter values that can be expected by inspecting a more representative number of samples from the aforementioned substrates may surpass the S and H values observed in this study.

Furthermore, the taxonomic relevance on classification, determination and identification issues of benthic diatoms in these types of environments show the benefits of focusing on remote protected areas worldwide. The bearing that this observation can have on ecological and biogeographical topics clearly justifies further research of benthic diatoms in these protected areas.

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(M.d.C.A.-C.) identified the macroalgal specimens, reviewed and formatted the original draft. All authors have read and agreed to the published version of the manuscript.

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