

Uncommon species diversity values in epiphytic diatom assemblages of the kelp *Eisenia arborea*Valores poco comunes de diversidad de especies en asociaciones de diatomeas epifitas del kelpo *Eisenia arborea*David A. Siqueiros Beltrones¹, Uri Argumedo Hernández² and Cristina Landa Cansigno³¹Departamento de Plancton y Ecología Marina, Centro Interdisciplinario de Ciencias Marinas del Instituto Politécnico Nacional. Av. IPN s/n, Col. Playa Palo de Santa Rita, La Paz, B.C.S. 23096. México²Dpto. Economía, UAB.C.S., Km 5.5. Carretera al Sur, La Paz, B.C.S. 23091. México³Departamento de Biotecnologías, Centro Interdisciplinario de Ciencias Marinas del Instituto Politécnico Nacional. Av. IPN s/n, Col. Playa Palo de Santa Rita, La Paz, B.C.S. CP 23096. México
e-mail: dsiquei@ipn.mxSiqueiros Beltrones D. A., U. Argumedo Hernández and C. Landa Cancigno. 2015. Uncommon species diversity values in epiphytic diatom assemblages of the kelp *Eisenia arborea*. *Hidrobiológica* 26 (1): 61-76.

ABSTRACT

Macroalgae are an ideal substratum for multiple species of diatoms that are ingested along with their hosts by many species of grazers including abalones (*Haliotis* spp.). Much of the diet of abalones along the western coast of the Baja California peninsula (Mexico) depends on blades of the kelp *Macrocystis pyrifera* that is heavily colonized by diatoms. Although the kelp *Eisenia arborea* (its ecological alternative) is an acceptable food-source for *Haliotis* spp., the epiphytic diatom flora living on this kelp was hitherto unknown. Thus, the association structure of the epiphytic diatoms growing on blades of *E. arborea* from the western coast of Baja California Sur (B.C.S.) was determined. We tested the hypothesis that the epiphytic diatom assemblages on blades of *E. arborea* collected at different dates would show low species diversity and taxa representing distinct stages of succession. We identified 99 diatom taxa that represent the first floristic list of diatoms living on *E. arborea*. Values of diversity (H') were lower than usual and, together with an extremely high dominance of *Pteroncola inane* (a new record for the region), the structure of the diatom assemblage is regarded atypical, similar to those measured for assemblages from extreme environments. However, structure analysis did not permit distinction of succession stages in the epiphytic diatom assemblage.

Key words: Bacillariophyceae, first record, floristics, kelps, macroalgae.

RESUMEN

Las macroalgas constituyen un sustrato ideal para muchas especies de diatomeas, algunas de las cuales proliferan y son ingeridas junto con su hospedero por varias especies de herbívoros entre las que se hallan los abulones *Haliotis* spp. Gran parte de la alimentación de los abulones en la costa occidental de la Península de Baja California, México, depende de láminas de *Macrocystis pyrifera* colonizadas por diatomeas. Aunque el kelpo *Eisenia arborea* (su alternativa ecológica) es un alimento aceptable para *Haliotis* spp., hasta ahora se desconocía qué especies de diatomeas epifitas albergaba. De acuerdo con esto se determinó la estructura de las asociaciones de diatomeas epifitas de *E. arborea* de la costa oeste de B.C.S. Se contrastó la hipótesis de que las asociaciones de diatomeas epifitas de *E. arborea*, recolectadas en diferentes fechas presentarían una baja diversidad de especies, y se encontrarían diatomeas (especies) representativas de etapas de sucesión distintas. Así, se elaboró la primera lista florística representativa de diatomeas epifitas de *E. arborea* que redujo 99 taxa para la costa occidental de B.C.S. En conclusión, la estructura de la taxocenosis es considerada atípica y semeja aquellas de ambientes extremos con valores bajos de diversidad (H'), destacando la dominancia extrema del taxón *Pteroncola inane*, el cual constituyó un nuevo registro para la región. El análisis de la estructura de las taxocenosis de diatomeas epifitas en láminas de *E. arborea* y sus variaciones no permitió distinguir etapas de sucesión.

Palabras clave: Bacillariophyceae, florística, kelpos, macroalgas, primer registro.

INTRODUCTION

Macroalgae are an ideal substratum for many species of Bacillariophyceae. Over two hundred diatom taxa living as epiphytes on multispecies macroalgal assemblages have been recorded for the southern Baja California peninsula, both along the west coast (Siqueiros Beltrones and Valenzuela Romero, 2004; Siqueiros Beltrones and López-Fuerte, 2006) and the east coast (Siqueiros Beltrones and Hernández Almeida, 2006). However, a high number of diatom taxa has also been recorded living on a single species of macroalgae, such as in the giant kelp *Macrocystis pyrifera* L. (C. Agardh) where the number of diatom species surpassed 170 taxa for several sampling dates (Siqueiros Beltrones *et al.*, 2002; Siqueiros Beltrones and Argumedo-Hernández, 2005; Argumedo-Hernández and Siqueiros Beltrones, 2008). Moreover, in a recent study where a single specimen of the rhodophyte *Plocamiun cartilagineum* (Lamoroux) Dixon was examined, as many as 42 diatom taxa were recorded (Siqueiros Beltrones and Argumedo-Hernández, 2014a).

Multiple species of diatoms colonize macroalgal substrates and are ingested along with their hosts by many species of grazers, including abalone (*Haliotis* spp.). In particular, the main interest surrounding epiphytic diatoms of *M. pyrifera* comes from its role as the main food-source for several abalone species whose diets depend strongly on its heavily epiphytized blades, which is the most abundant kelp on the western coast of the Baja California peninsula (Mexico).

Based on the above, we were interested in determining which diatom taxa were to be found living on other macroalgae that are also grazed by abalone (Siqueiros Beltrones *et al.*, 2002); the phaeophyte *Eisenia arborea* Areschoug seemed as the next-best option, inasmuch as it is the second most abundant kelp along the western coast of the peninsula (Hernández-Carmona *et al.*, 2009), and would represent an ecological alternative, particularly when the *M. pyrifera* forests disappear during El Niño events. Like *M. pyrifera*, *E. arborea* is distributed from British Columbia, Canada, down to Bahía Magdalena, Mexico, in the intertidal zone where it forms dense beds over rocky substratum (Pedroche *et al.*, 2008). We thus assumed that the epiphytic diatom assemblage it harbored would be similar to that of *M. pyrifera* in species composition and structure, *i.e.*, species richness, diversity, dominance. However, the first *ex profeso* observations made on *E. arborea* blades from the same region did not support such expectations because diatoms were not found (Siqueiros Beltrones *et al.*, 2002). Nonetheless, the presence of diatoms on blades of *E. arborea* from the same region was recently noted when samples of this kelp were processed for biochemical assays (Muñoz, M., IPN-CICIMAR, com. pers.). After verifying the report, we established our objective to describe the diatom assemblages on the basis of their species composition and association structure. Thus, based on previous observations in epiphytic diatoms of *M. pyrifera* (Argumedo Hernández and Siqueiros Beltrones, 2008,) we tested the hypothesis that, on the blades of *E. arborea* from different

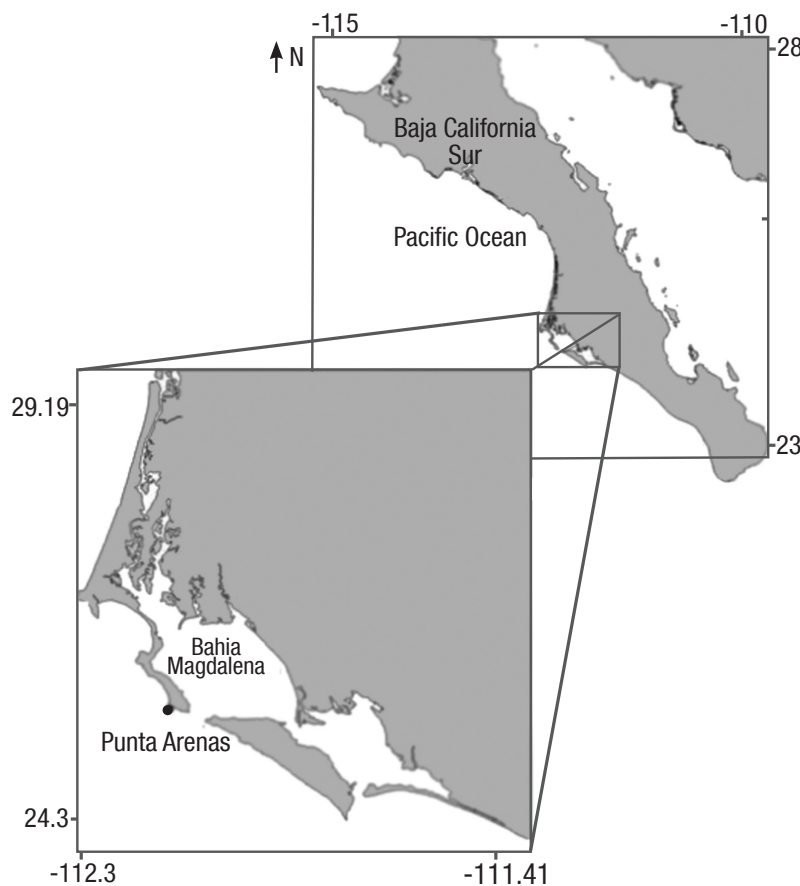


Figure 1. Location of sampling site Punta Arenas off Isla Magdalena, B.C.S., México.

Table 1. Diatom taxa living on blades of *Eisenia arborea* off Isla Magdalena, B.C.S., Mexico collected from September 2013 to May 2014. * New record for the Mexican NW region; **Record reported in Siqueiros Beltrones and Argumedo Hernández (2014b) for the same survey.

TAXA	Presence	TAXA	Presence
<i>Achnanthes manifera</i> Brun	rare	<i>Grammatophora macilenta</i> W. Smith	common
<i>Achnanthes yaquiniensis</i> McIntire <i>et</i> Reimer	rare	<i>Grammatophora marina</i> (Lyngbye) Kützing	common
<i>Actinocyclus curvatulus</i> Janisch	common	<i>Grammatophora marina</i> var. <i>subundulata</i> Grunow	rare
<i>Actinoptychus aster</i> Brun	common	<i>Grammatophora oceánica</i> (Ehrenberg) Grunow	common
<i>Actinoptychus senarius</i> (Ehrenberg) Ehrenberg	rare	<i>Grammatophora undulata</i> Ehrenberg	rare
<i>Amphicocconeis disculoides</i> (Ehr.) Ehrenberg	common	<i>Hantzschia amphioxys</i> (Ehrenberg) Grunow	rare
<i>Amphora angustissima</i> Heiden in Heiden <i>et</i> Kolbe	less common	<i>Hyalosynedra laevigata</i> (Grunow) Williams <i>et</i> Round	common
<i>Amphora angusta</i> Gregory	common	<i>Licmophora gracilis</i> (Ehrenberg) Grunow	rare
<i>Amphora</i> cf. <i>exilitata</i> Giffen	common	<i>Licmophora communis</i> (Helberg) Grunow	rare
<i>Amphora holsaticoides</i> Naguma <i>et</i> Kobayashi	less common	<i>Lyrella exsul</i> (A. Schmidt) D.G. Mann	rare
<i>Amphora proteus</i> var. <i>contigua</i> Cleve	common	<i>Mastogloia macdonaldii</i> Grevillei	rare
<i>Anaulus</i> cf. <i>minutus</i> Grunow	rare	<i>Melosira</i> sp.	rare
<i>Asteromphalus arachne</i> (Brébisson) Ralfs	rare	<i>Navicula cancellata</i> Donkin	less common
<i>Azpeitia nodulifera</i> (Schmidt) Fryxell <i>et</i> Sims	common	<i>Navicula</i> cf. <i>agnita</i> Hustedt	less common
<i>Berkeleya rutilans</i> (Trentenpohl ex Roth) Grunow	abundant	<i>Navicula</i> cf. <i>feuenbornii</i> Hustedt	less common
<i>Biddulphia biddulphiana</i> (Boyer) J.E. Smith	rare	<i>Navicula</i> cf. <i>incerta</i> Grunow	less common
<i>Biddulphia grundleri</i> A. Schmidt	rare	<i>Navicula</i> cf. <i>mollissima</i> Hustedt	rare
<i>Caloneis</i> cf. <i>linearis</i> (Grunow) Boyer	common	<i>Navicula clavata</i> var. <i>caribaea</i> Cleve	rare
<i>Campyloneis grevillei</i> (Wm. Smith) Grunow <i>et</i> Eulenstein	rare	<i>Navicula directa</i> (Smith) Ralfs	common
<i>Campylopyxis garkeana</i> (Grunow) Medlin	abundant	<i>Navicula diversistriata</i> Hustedt	less common
<i>Campylodiscus</i> cf. <i>simulans</i> Gregory	rare	<i>Navicula longa</i> Gregory	common
<i>Cocconeis contermina</i> A. Schmidt	rare	<i>Navicula pennata</i> Schmidt	less common
<i>Cocconeis convexa</i> Giffen	rare	<i>Navicula</i> sp. 1	rare
<i>Cocconeis diminuta</i> (Pantocsek) Hustedt	common	<i>Nitzschia dissipata</i> (Kützing) Grunow	less common
<i>Cocconeis dirupta</i> var. <i>flexella</i> (Gregory) Janisch	common	<i>Nitzschia distans</i> Gregory	less common
<i>Cocconeis krameri</i> Lange-Bertalot <i>et</i> Metzeltin	less common	<i>Nitzschia hybrida</i> Grunow	less common
<i>Cocconeis latecostata</i> Hustedt	rare	<i>Nitzschia</i> sp. 1	rare
<i>Cocconeis pseudodisruptoides</i> Foged	rare	<i>Nitzschia punctata</i> var. <i>coarctata</i> (Grunow) Hustedt	common
<i>Cocconeis scutellum</i> Ehrenberg	common	<i>Nitzschia sicula</i> (Castracane) Hustedt	common
<i>Cocconeis speciosa</i> Gregory	common	<i>Parlibellus</i> sp.	rare
<i>Cocconeis vetusta</i> A. Schmidt	rare	<i>Paralia sulcata</i> f. <i>radiata</i> Grunow	common
<i>Coscinodiscus crenulatus</i> Grunow	rare	<i>Paralia sulcata</i> var. <i>crenulata</i> Grunow	common
<i>Coscinodiscus radiatus</i> Ehrenberg	common	<i>Podosira stelliger</i> (Bailey) Mann	common
<i>Coscinodiscus rothii</i> (Ehrenberg) Grunow	rare	<i>Psammodiscus nitidus</i> (Gregory) Round <i>et</i> Mann	common
<i>Cyclotella litoralis</i> Lange <i>et</i> Syvertsen	common	<i>Pteroncola inane</i> (Giffen) Round	very abundant
<i>Delphineis surirella</i> var. <i>australis</i> (Petit) Tsarenko	rare	<i>Raphoneis surirella</i> var. <i>ceylanica</i> (Cleve) N. Foged	rare
<i>Denticula kuetzingii</i> Grunow	rare	<i>Rhoicosphenia adolphii</i> Schmidt	common
<i>Diploneis aestuarii</i> Hustedt	rare	<i>Rhoicosphenia</i> cf. <i>marina</i> (Smith) M. Schmidt	abundant
<i>Diploneis bombus</i> Ehrenberg	rare	<i>Rhoicosphenia genuflexa</i> (Kützing) Medlin	abundant
<i>Diploneis</i> cf. <i>chersonensis</i> (Grunow) Cleve	rare	<i>Roperia tessellata</i> (Roper) Grunow	common
<i>Diploneis crabro</i> Ehrenberg	rare	<i>Seminavis ventricosa</i> (W. Gregory) M. García-Baptista	common
<i>Diploneis didyma</i> (Ehrenberg) Cleve	rare	<i>Staurophora</i> sp.	common
<i>Diploneis litoralis</i> (Donkin) Cleve	less common	<i>Tabularia barbatula</i> (Kützing) D.M. Williams <i>et</i> Round	rare
<i>Diploneis obliqua</i> (Brun) Hustedt	rare	<i>Tabularia investiens</i> (W. Smith) Williams <i>et</i> Round	common
<i>Diploneis papula</i> (A. Schmidt) Cleve	common	<i>Tabularia tabulata</i> var. <i>fasciculata</i> (Kütz.) Williams <i>et</i> Round	rare
<i>Diploneis papula</i> var. <i>constricta</i> Hustedt	rare	<i>Thalassiosira eccentrica</i> (Ehrenberg) Cleve	common
<i>Diploneis smithii</i> (Brébisson) Cleve	rare	<i>Thalassiosira</i> sp.	common
<i>Gomphonemopsis pseudexigua</i> (Simonsen) Medlin	common	<i>Trachyneis aspera</i> Ehrenberg	common
<i>Gomphoseptatum aestuarii</i> (Cleve) Medlin	abundant	<i>Trachyneis velata</i> Schmidt	common
<i>Grammatophora hamulifera</i> Kützing	abundant		

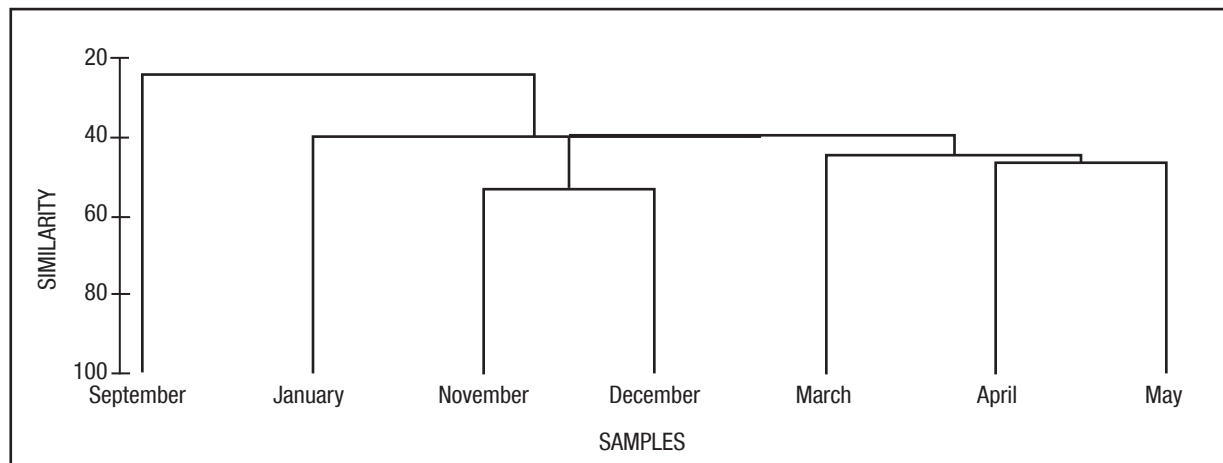


Figure 2. Similarity between samples of epiphytic diatom assemblages living on blades of *Eisenia arborea* from B.C.S., measured with the Jaccard index.

dates, diatom taxa representing distinct stages of succession would be found together with either abundant pioneer taxa such as *Cocconeis* spp., or naviculoid opportunistic species that depict advanced stages of colonization, in both cases associated with low values of diversity. We conclude that the structure of the diatom assemblage is unusual, similar to those of assemblages from extreme environments. However, structure analysis did not permit the distinction of succession stages in the epiphytic diatom assemblage.

MATERIALS AND METHODS

Blades of *E. arborea* were collected at Punta Arenas (24° 33' 2" N and 112° 05' 28" W), off Isla Magdalena (Fig. 1), in the west coast of B.C.S. Samplings were gathered in September, November, and December, 2013, and in January, March, and May, 2014, at a depth of 5-10 m by scuba diving. The blades were dried before being transported to the laboratory, where the most noticeable epiphytized blades were selected among those having few or no bryozoans. Epiphytes on the surface of the *E. arborea* blades from each date were scraped off using a glass slide while rinsing with purified water into a dissecting tray. The resul-

ting epiphyte concentrate was stored in assay tubes; decanted water was eliminated and then a sample of each concentrate was oxidized in assay tubes using a mixture of commercial ethanol and nitric acid at a ratio of 1:3:5 that varied depending on the amount of organic matter in each sample (Siqueiros-Beltrones, 2002). Afterwards, repeated rinsing was done using purified water until a pH ≥ 6 was reached. From each cleaned diatom sample five (double) permanent preparations and a repetition were mounted using the synthetic resin Pleurax (RI=1.7).

Diatom taxa were identified under a phase contrast compound microscope with planapo-chromatic lenses at 1000 $\times$, following the references of Cleve-Euler (1968); Desikachary (1988); Hende (1964); Hustedt (1959; 1961-66); López-Fuerte *et al.* (2010); Peragallo and Peragallo (1908); Round *et al.* (1990); Schmidt *et al.* (1874-1959); Siqueiros Beltrones (2002); Siqueiros Beltrones and Valenzuela-Romero (2001); Siqueiros Beltrones *et al.* (2004); Siqueiros Beltrones and Hernández-Almeida (2006); Witkowski *et al.* (2000). A representative micro-photographic record of the diatom taxa is provided.

In order to describe the structure of the epiphytic diatom assemblages of *E. arborea*, the relative abundances of the taxa were estimated

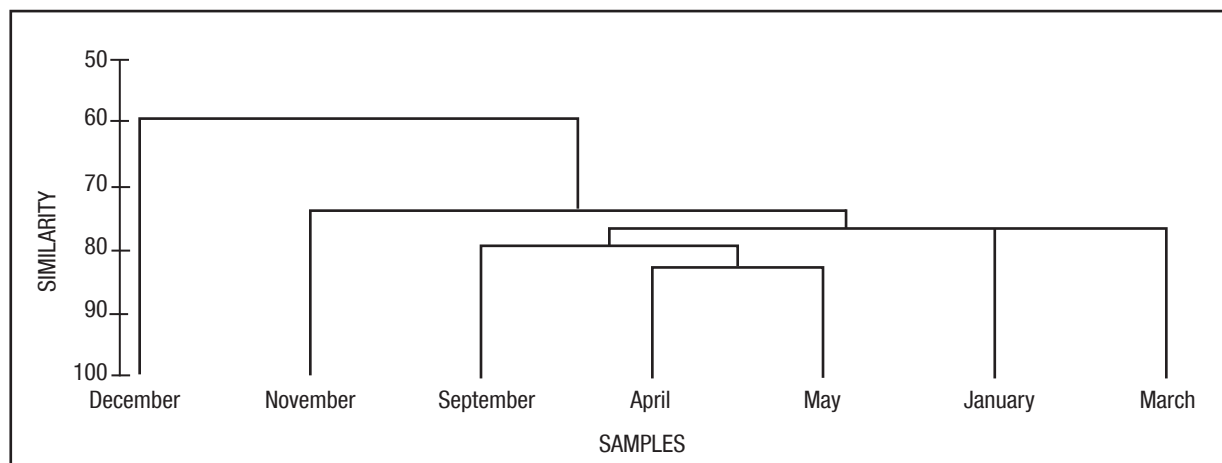


Figure 3. Similarity between samples of epiphytic diatom assemblages living on blades of *Eisenia arborea* in B.C.S., measured with the Bray-Curtis index.

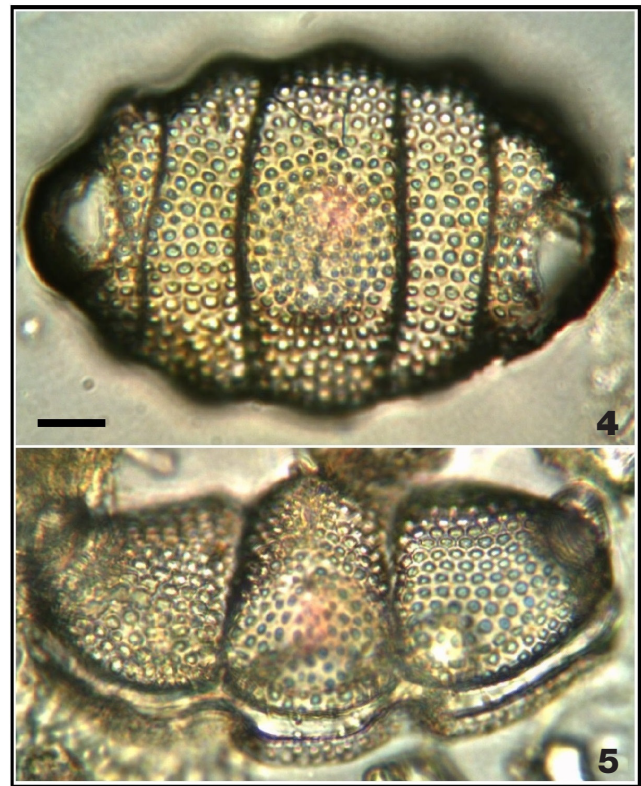
Table 2. Relative abundance of the main diatom taxa in the epiphytic assemblages living on blades of *Eisenia arborea* collected in B.C.S., Mexico from September 2013 to May 2014.

TAXA	%
<i>Pteroncola inane</i>	66.37
<i>Campylopyxis garkeana</i>	4.89
<i>Anaulus cf. minutus</i>	3.67
<i>Rhoicosphenia adolphii</i>	3.08
<i>Berkeleya rutilans</i>	2.86
<i>Gomphoseptatum aestuarii</i>	2.61
<i>Gomphonemopsis pseudexigua</i>	2.42
<i>Amphicocconeis disculoides</i>	1.97
<i>Tabularia investiens</i>	1.72
<i>Gramatophora marina</i>	1.47
<i>Navicula incerta</i>	1.42
Cumulative relative abundance	92.47

based on an approximate sample size (n) of 500 valves (Siqueiros Beltrones, 2002) per sample (N = 3600). With these, the following indices for estimating diversity were calculated: Shannon's (H'), Pielou's (J'), Simpson's (λ); and the Bray-Curtis index for measuring similarity between samples, which was complemented using the Jaccard index. All computations were done using program Primer 6 v 6.1.6.

RESULTS

Floristics. The resulting floristic list shows a total of 99 diatom taxa living on blades of *E. arborea* (Table 1). A photographic catalogue including most of the taxa is provided (Figs. 4-158). Most taxa, either common or rare, are epiphytic forms, except for certain taxa like the *Lyrella* forms and *Diploneis* spp. that are epipellic. Others, such as the centric forms *Biddulphia biddulphiana* (Boyer) J.E. Smith, *Paralia sulcata* f. *radiata* Grunow, *Paralia sulcata* var. *crenulata* Grunow, and *Podosira stelliger* (Bailey) Mann are typical epiphytes of the region; biraphids forms such as *Campylopyxis garkeana* (Grunow) Medlin, *Gomphonemopsis pseudexigua* (Simonsen) Medlin, *Gomphoseptatum aestuarii* (Cleve) Medlin, and *Rhoicosphenia genulifera* (Kützinger) Medlin are characteristic epiphytes of *M. pyrifera* and were proportionally re-



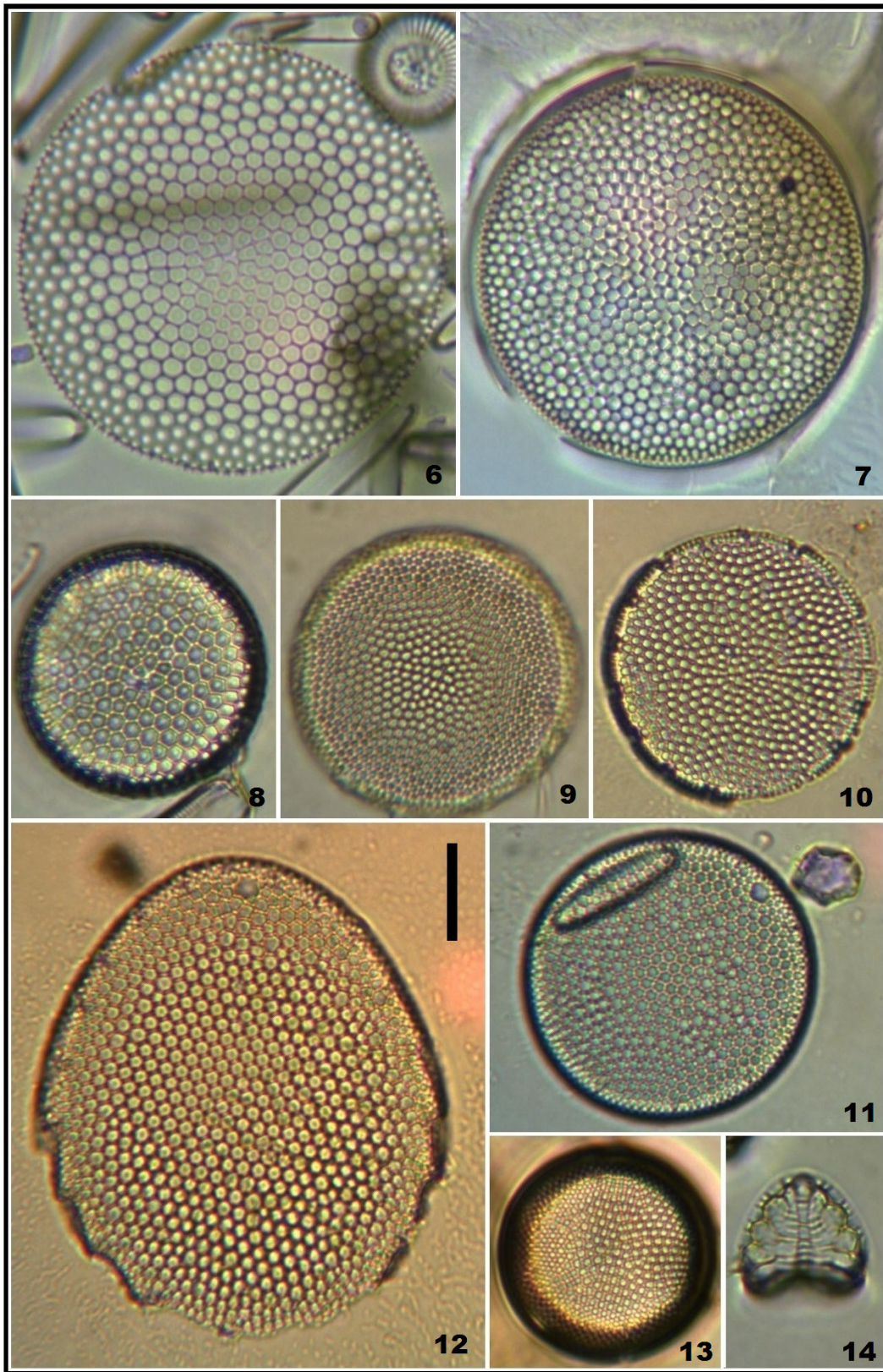
Figures 4-5. 4) *Biddulphia biddulphiana*; 5) *Biddulphia grundleri*. Scale bar = 10 μ m for both specimens.

presented; however, others such as *Grammatophora* spp., which are common epiphytes were not as conspicuous as in other macroalgae of the region. On the other hand, the araphid *Pteroncola inane* (Giffen) Round (Siqueiros Beltrones and Argumedo Hernández, 2014b) and the centric *Biddulphia grundleri* A. Schmidt constitute new records for the Mexican NW region. The former was extremely abundant in most samples, while the latter was rare.

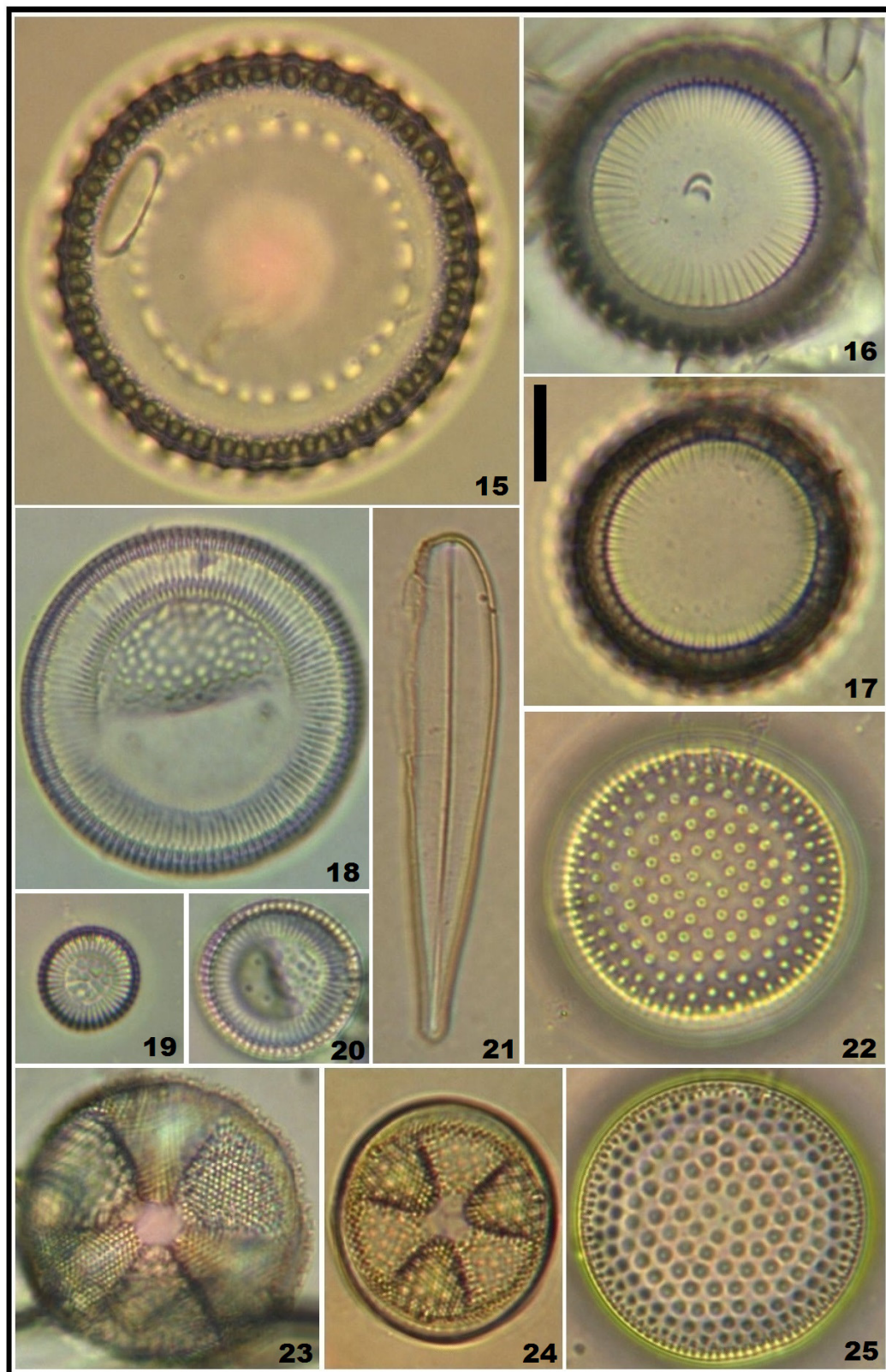
As implied above, the epiphytic diatom assemblage on *E. arborea* was characterized by the extreme dominance by a single taxon, *P. inane* (Figs. 50, 52-55), which represented between 33% and 94% of the

Table 3. Diversity values estimated for the epiphytic diatom assemblages found on blades of *Eisenia arborea* in Isla Magdalena, B.C.S. from September 2013 to May 2014. S= species richness; N= valves counted; J'= equitability; H'= Shannon's diversity; λ = Simpson's dominance; 1- λ = Simpson's diversity.

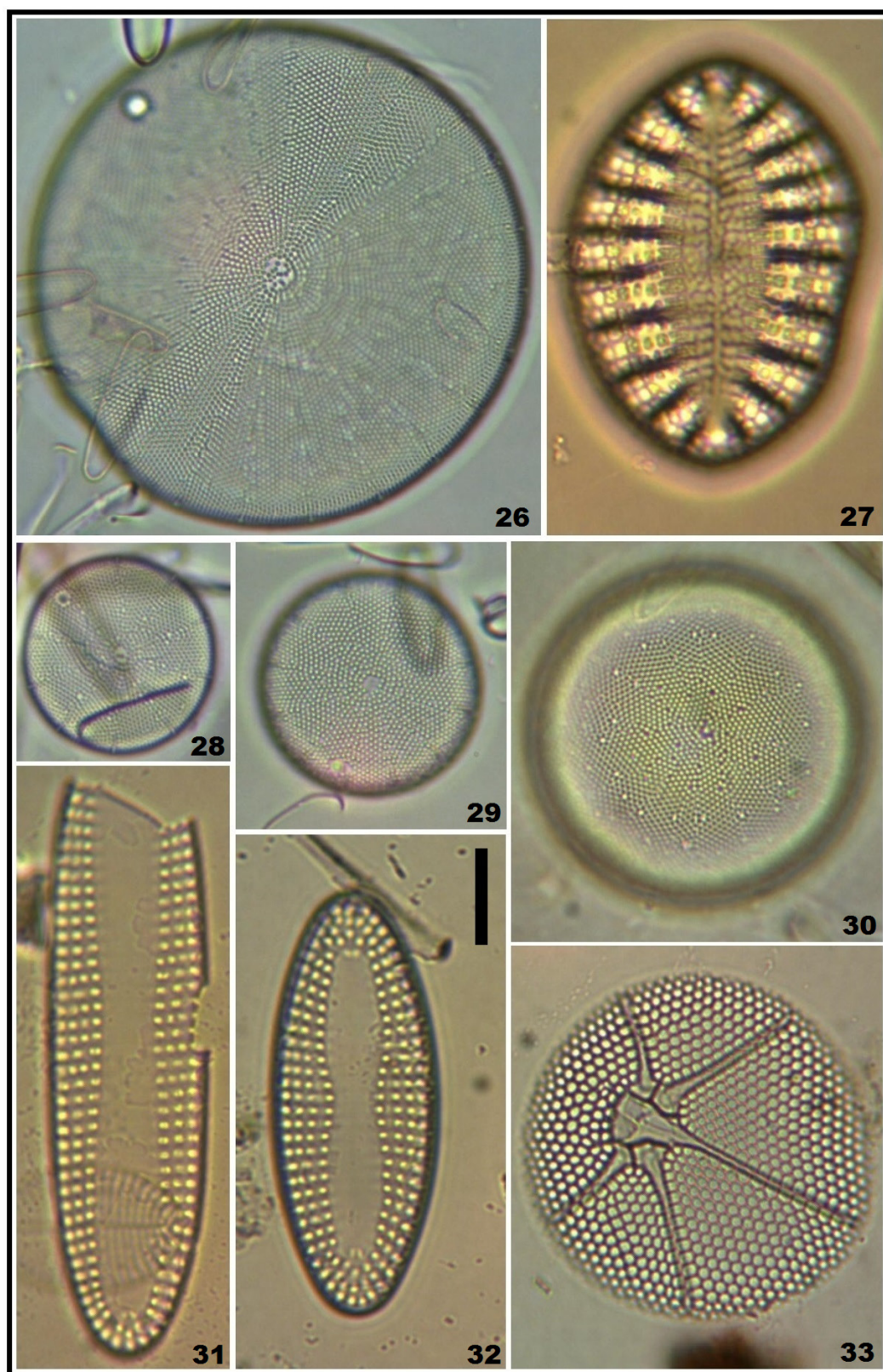
FECHA	S	N	J'	H'	λ	1- λ	Valve abundance
September	6	478	0.12	0.30	0.93	0.07	very abundant
November	24	497	0.53	2.42	0.38	0.62	scarce
December	28	505	0.61	2.93	0.21	0.79	scarce
January	15	582	0.47	1.83	0.47	0.53	less abundant
March	24	530	0.53	2.43	0.38	0.62	scarce
April	22	557	0.41	1.84	0.49	0.51	scarce
May	25	452	0.31	1.44	0.64	0.36	very scarce



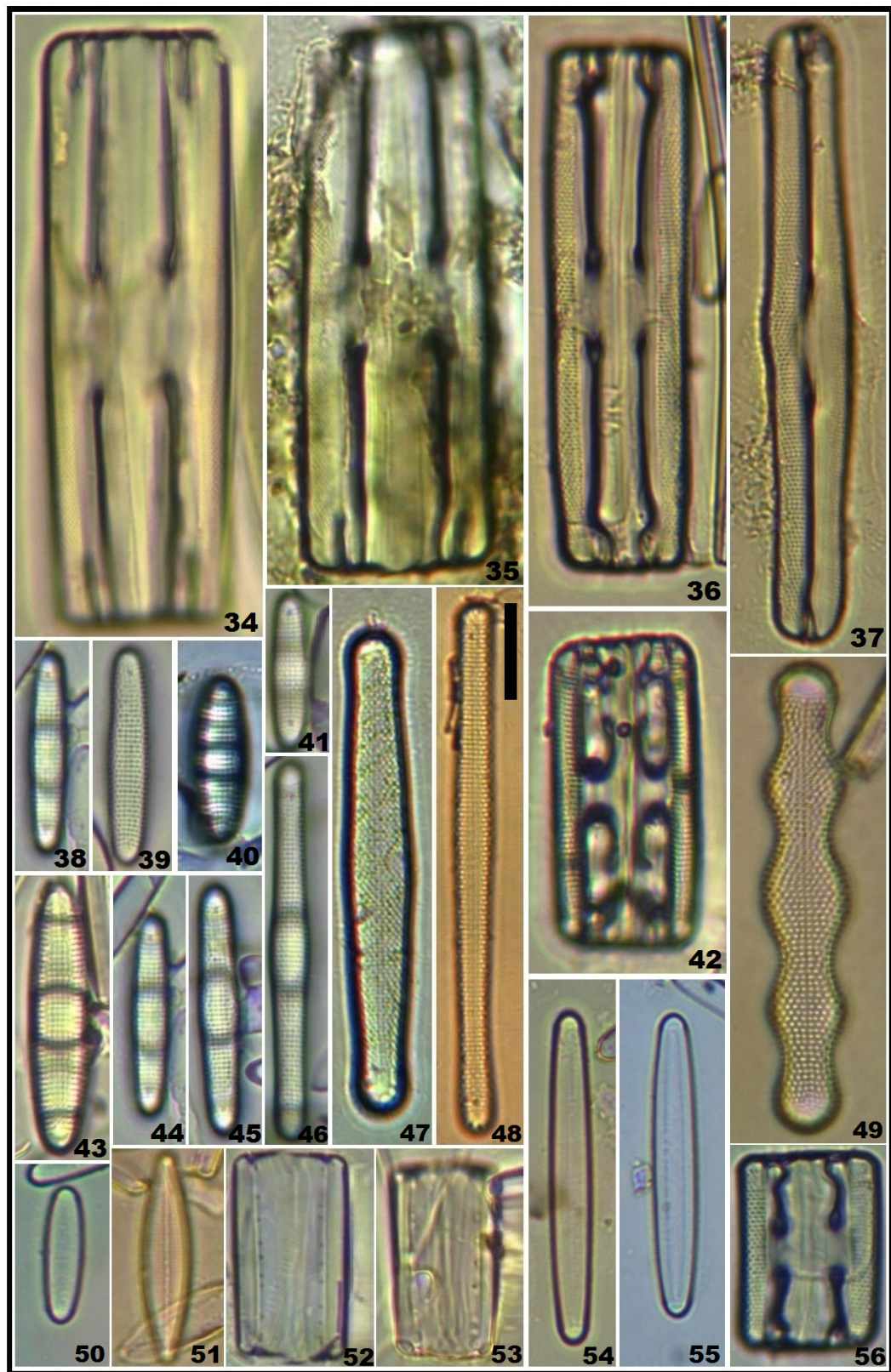
Figures 6-14. 6, 9) *Coscinodiscus radiatus*; 7) *Coscinodiscus rothii*; 8) *Azpeitia nodulifer*; 10) *Coscinodiscus crenulatus*; 11-12) *Roperia tessellata*; 13) *Thalassiosira eccentrica*; 14) *Campylodiscus* cf. *simulans*. Scale bar = 10 μ m for all specimens.



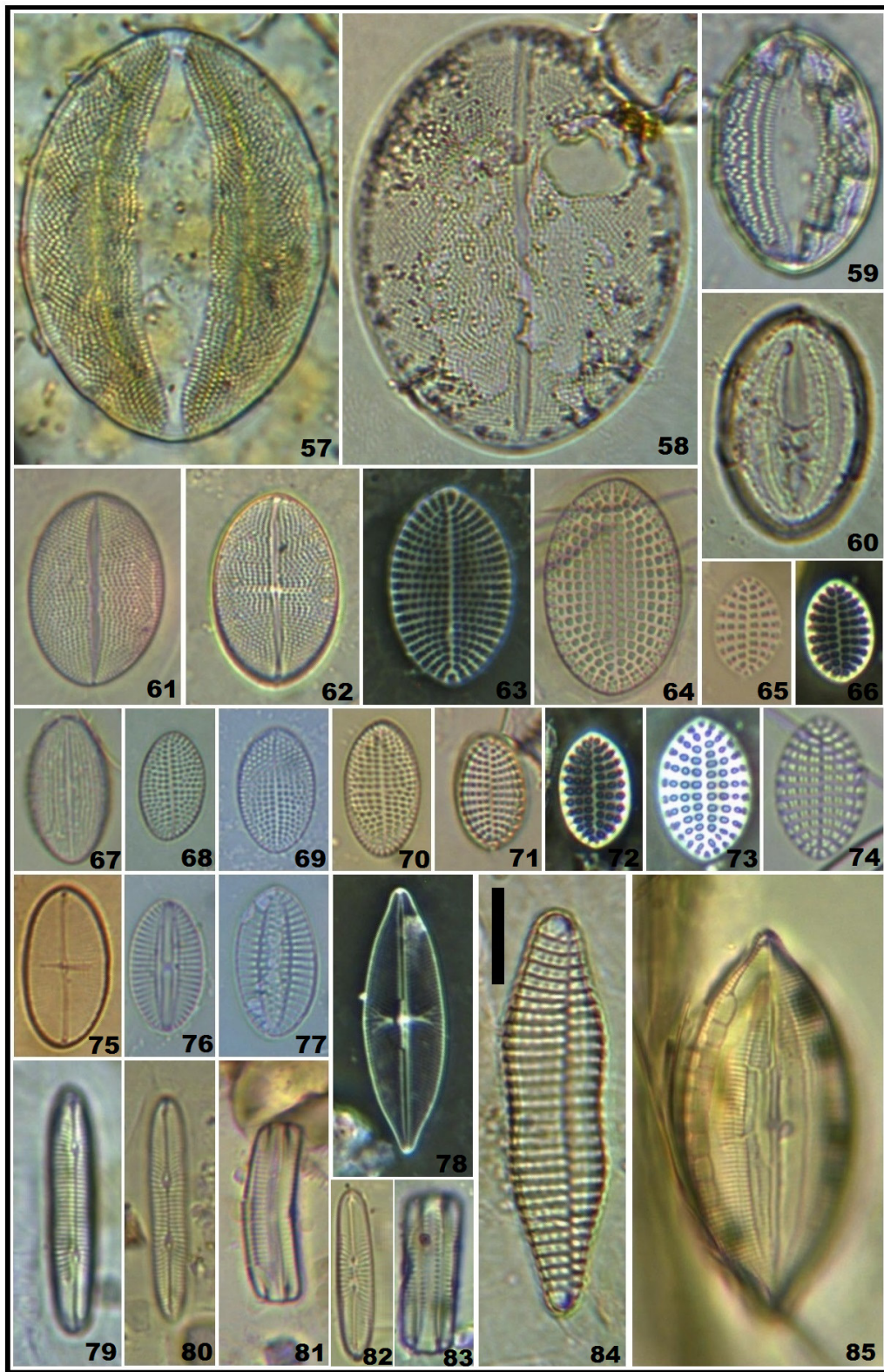
Figures 15-25. 15) *Paralia sulcata* var. *crenulata*; 16-17) *Paralia sulcata* f. *radiata*; 18-20) *Cyclotella litoralis*; 21) *Licmophora gracilis*; 22, 25) *Psammodiscus nitidus*; 23) *Actinopterychus aster*; 24) *Actinopterychus senarius*. Scale bar = 10 μ m for all specimens.



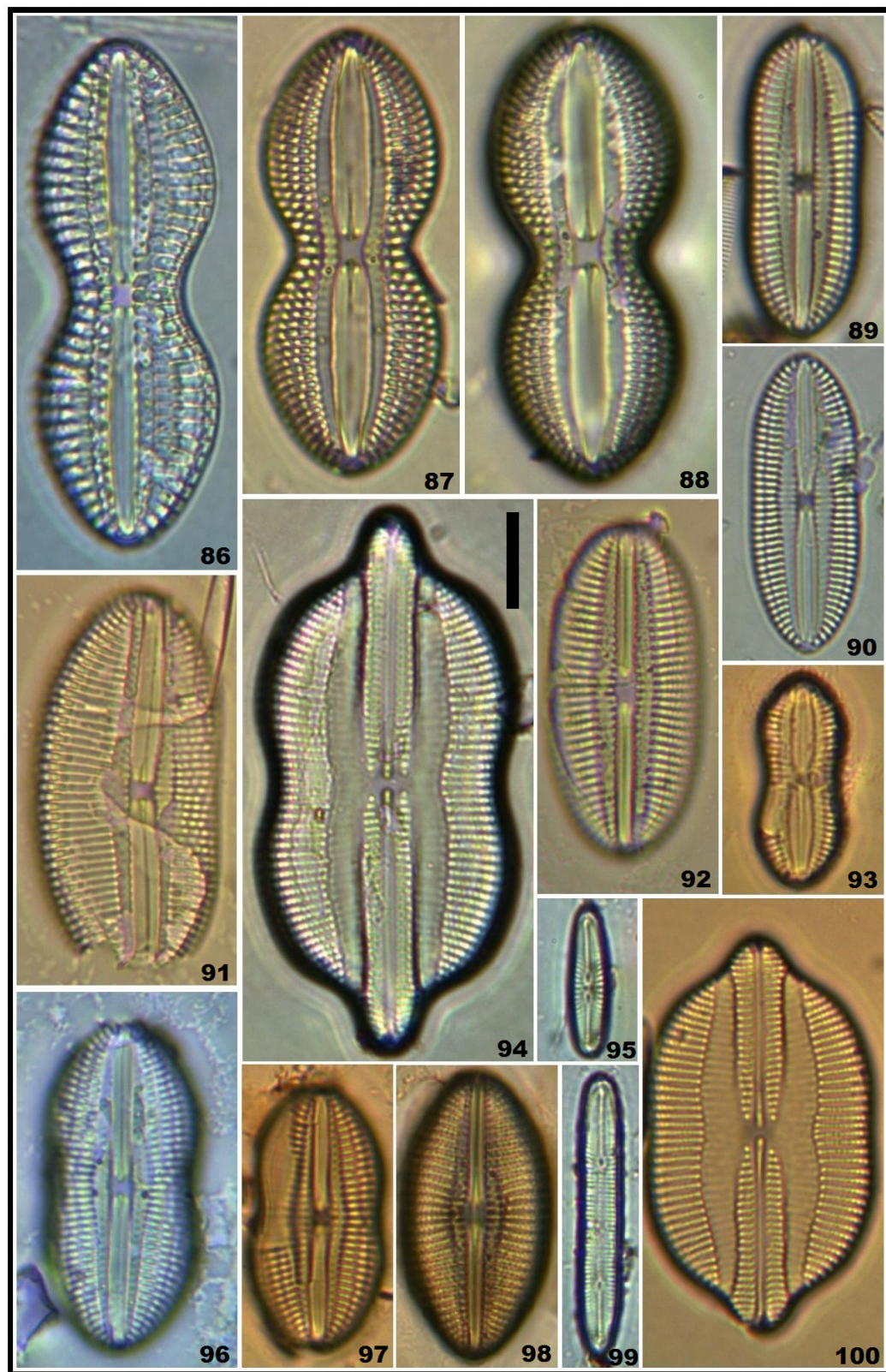
Figures 26-33. 26, 28-30) *Actinocyclus curvatulus*; 27) *Campyloneis grevillei*; 31) *Raphoneis surirella* var. *ceylanica*; 32) *Delphineis surirella* var. *australis*; 33) *Asteromphalus arachne*. Scale bar = 10 μ m for all specimens.



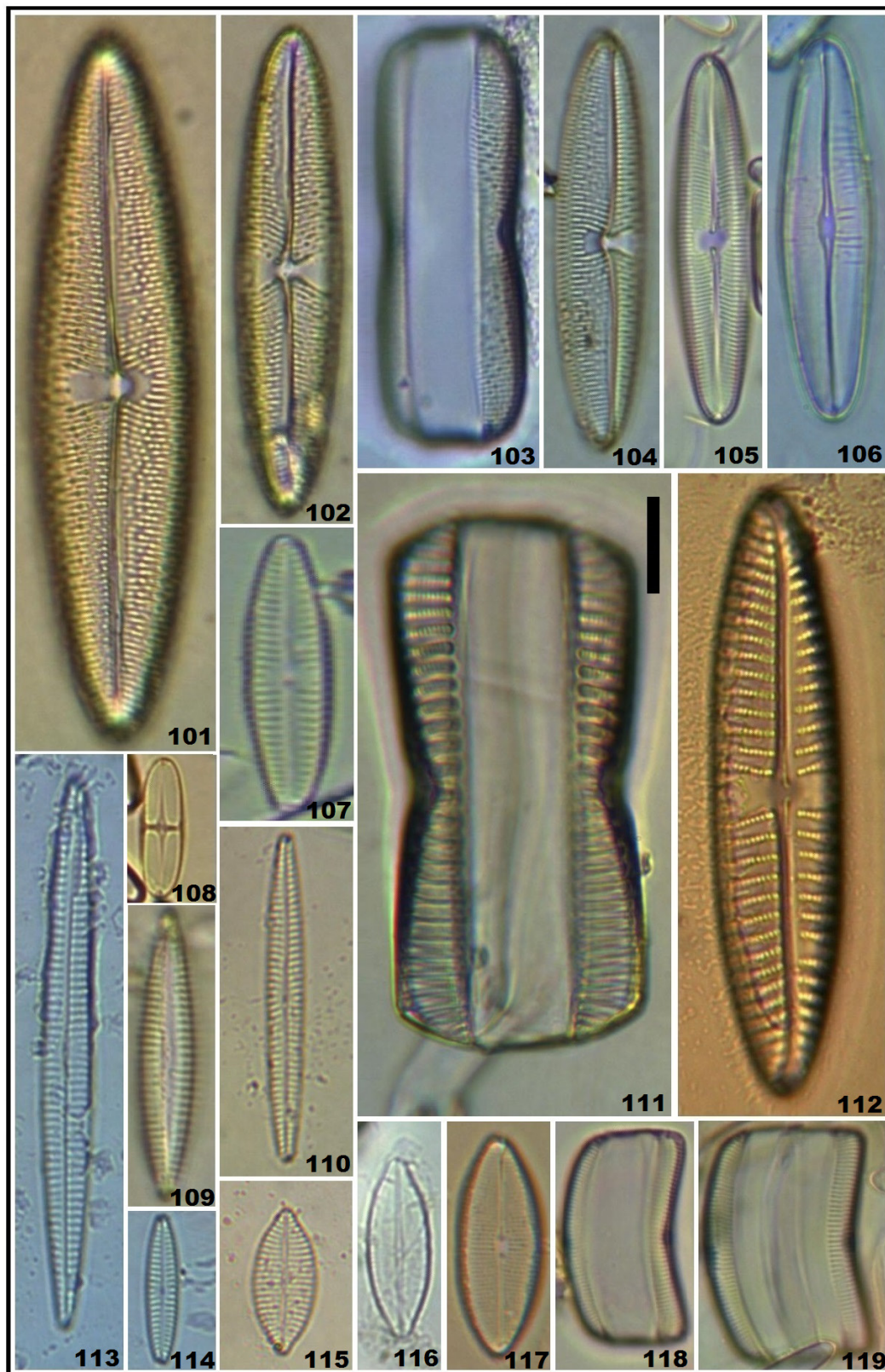
Figures 34-56. 34-35) *Grammatophora macilenta*; 36-37, 48) *Grammatophora oceanica*; 38-39, 41, 44-46, 56) *Grammatophora marina*; 40, 42-43) *Grammatophora hamulifera*; 47) *Grammatophora marina* var. *subundulata*; 49) *Grammatophora undulata*; 50, 52-55) *Pteroncola* sp.; 51) *Synedra barbatula*. Scale bar = 10 μ m for all specimens.



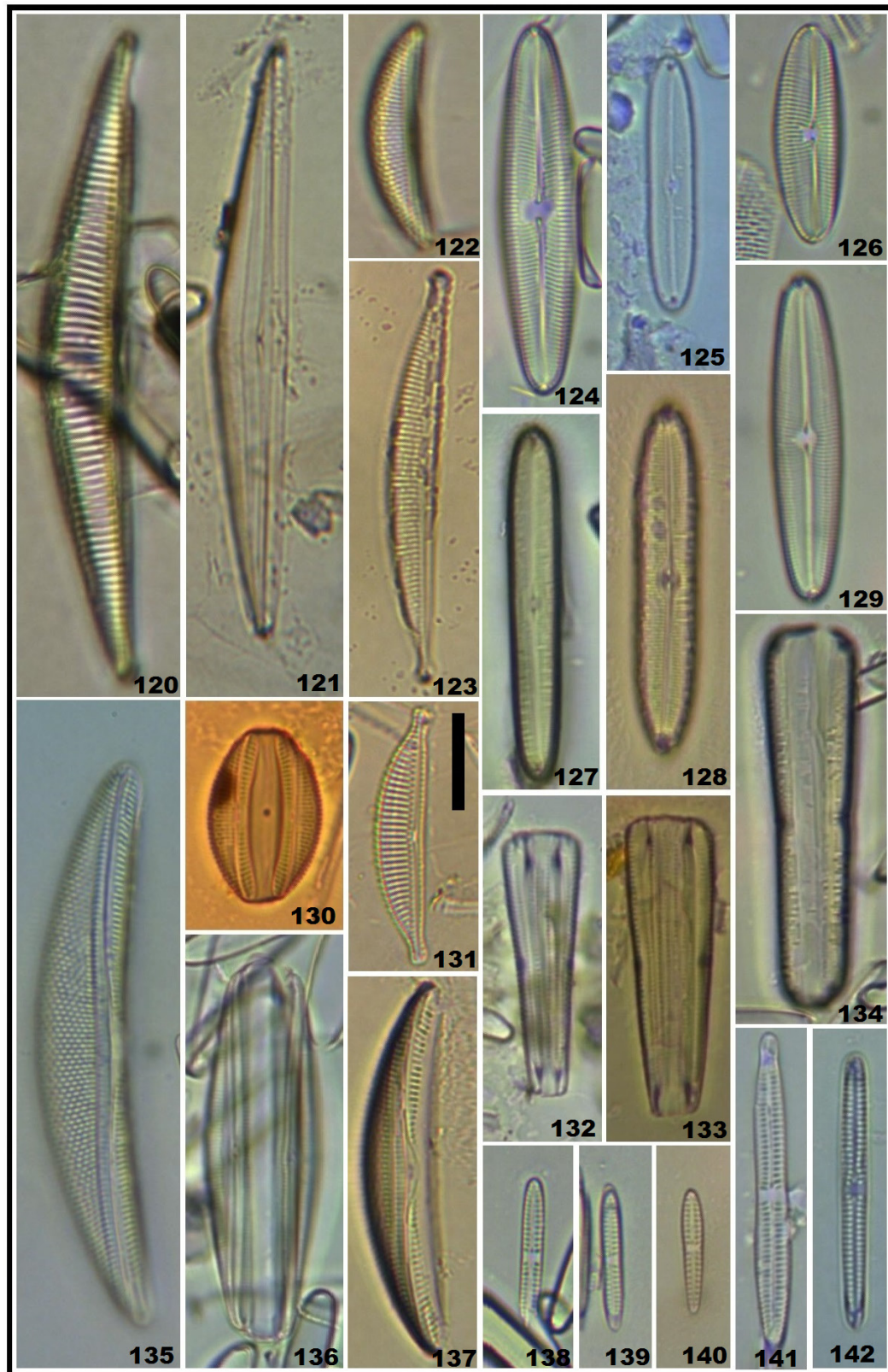
Figures 57-85. 57) *Cocconeis vetusta*; 58, 59-62, 75) *Cocconeis dirupta* var. *flexella*; 59) *Cocconeis contermina*; 60) *Cocconeis krameri*; 63-64) *Cocconeis scutellum*; 65, 74) *Amphicocconeis disculoides*; 67) *Cocconeis convexa*; 68-70) *Cocconeis pseudodiruptoides*; 69) *Cocconeis diminuta*; 66, 72-73) *Cocconeis speciosa*; 76) *Diploneis aestuarii*; 77) *Cocconeis latecostata*; 78) *Achnanthes manifera*; 79-80) *Berkeleya rutilans*; 81-83) *Rhoicosphenia genuflexa*; 84) *Achnanthes yaquinensis*; 85) *Mastogloia macdonaldii*. Scale bar = 10 μ m for all specimens.



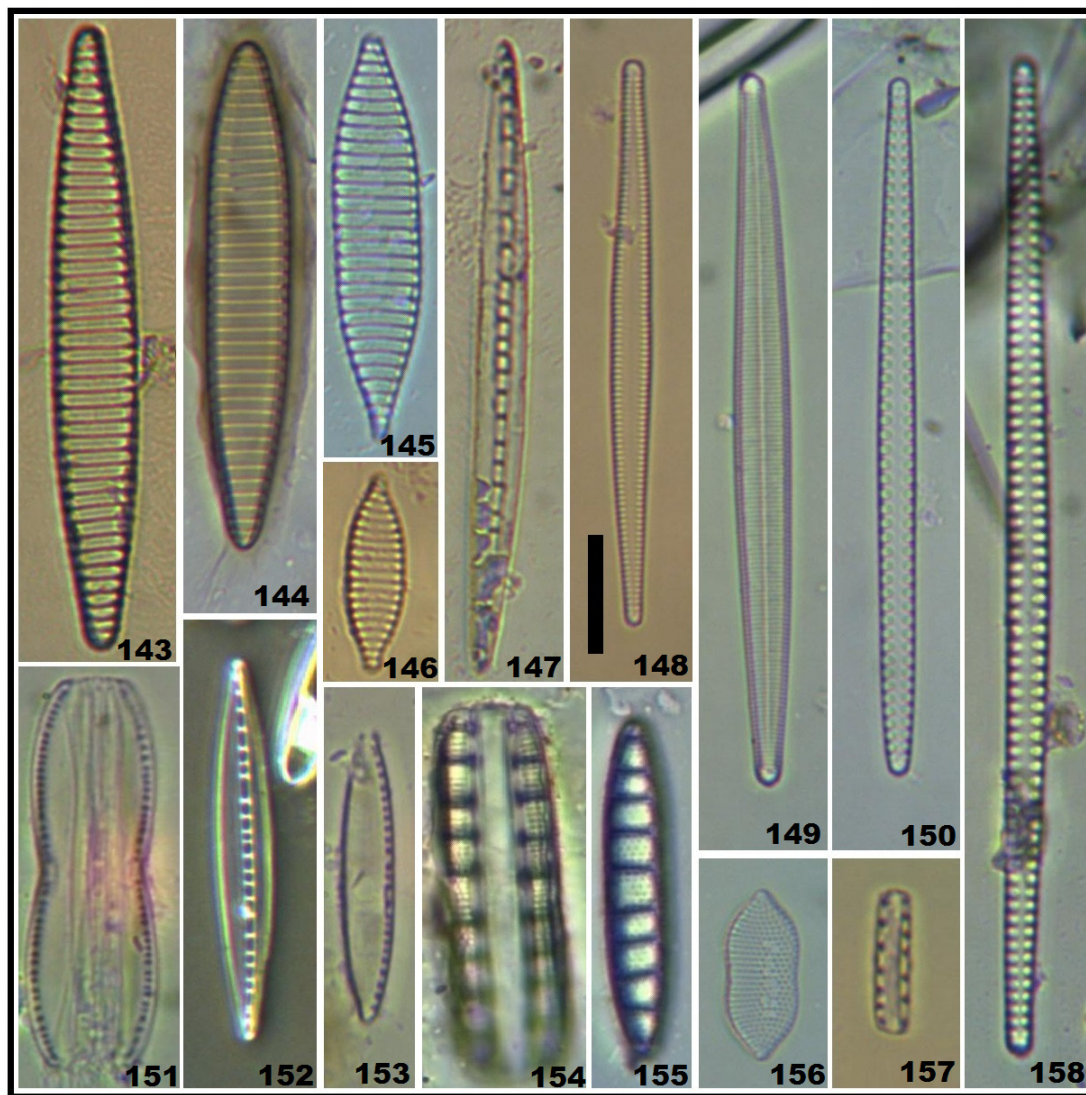
Figures 86-100. 86) *Diploneis crabro*; 87-88) *Diploneis bombus*; 89-90) *Diploneis papula*; 91) *Diploneis obliqua*; 92) *Diploneis litoralis*; 93) *Diploneis papula* var. *constricta*; 94) *Lyrella exsul*; 95) *Rhoicosphenia genuflexa*; 96-97) *Diploneis didyma*; 98) *Diploneis smithii*; 99) *Berkeleya rutilans*; 100) *Navicula clavata* var. *caribaea*. Scale bar = 10 μ m for all specimens.



Figures 101-119. 101, 103) *Trachyneis velata*; 102, 104) *Trachyneis aspera*; 105) *Campylopyxis garkeana*; 106) *Navicula* cf. *mollissima*; 107) *Navicula incerta*; 108) *Staurophora* sp.; 109) *Navicula* cf. *feuenbornii*; 110, 114) *Navicula cincta*; 111) *Navicula cancellata*; 112) *Navicula pennata*; 113) *Navicula directa*; 115) *Navicula diversistriata*; 116) *Navicula* sp. 1; 117) *Parlibellus* sp.; 118-119) *Campylopyxis garkeana*. Scale bar = 10 μ m for all specimens.



Figures 120-142. 120) *Seminavis ventricosa*; 121) *Amphora angusta*; 122, 130, 135, 137) *Amphora proteus* var. *contigua*; 123) *Amphora angustissima*; 124, 126, 129) *Campylopyxis garkeana*; 125, 127-128, 134) *Caloneis linearis*; 131) *Amphora holsaticoides*; 132-133, 141-142) *Gomphoseptatum aestuarii*; 138-140) *Gomphonemopsis pseudexigua*. Scale bar = 10µm for all specimens.



Figures 143-158. 143-146) *Nitzschia sicula*; 147, 152) *Nitzschia distans*; 148) *Tabularia tabulata* var. *fasciculata*; 149) *Hyalosynedra laevigata*; 150, 158) *Tabularia investiens*; 151) *Nitzschia hybrida*; 153) *Nitzschia* sp. 1; 154-155) *Denticula kuetzingii*; 156) *Nitzschia punctata* var. *coarctata*; 157) *Anaulus* cf. *minutus*. Scale bar = 10 μ m for all specimens.

counted valves in the different dates, and more than 66% overall ($N = 3600$); by contrast, the second abundant taxon, *Campylopyxis garkeana* (Figs. 105, 118, 119) represented less than 5% of the total valves (Table 2). Moreover, the quantitative phase yielded only 54 species, most of the taxa being rare or uncommon (Table 1). In spite of the above, according to the estimated relative abundances, the described diatom assemblage exhibits a typical pattern, *i.e.*, many rare and uncommon species, and few abundant (or very common) ones. In this case, however, it is unusual that a single species contributes 66% of the total abundance.

Species diversity. The estimated values of species diversity ranged in general from low to very low (Table 3), with the lowest value corresponding to the September sample ($H' = 0.3$; $S = 6$), in which *Pteroncola inane* was more abundant. However, in other samples where the cell concentration in the preparations was either abundant (January) or very

low (April, May), due to *P. inane*, diversity values were also very low; unlike the diversity values of the samples from November, December, and March (Table 3), which are similar to those from normal (favorable) environments, as a result of their species richness ($S = 24, 28, 24$, respectively) and equitability (J') higher than 0.5, which are in fact atypically lower.

Similarity. The similarity values between samples of epiphytic diatom assemblages living on blades of *Eisenia arborea* based on presence/absence of species (Jaccard's index) show that September is the most distinct sample (<20%), mainly because of the absence of taxa ($S = 6$). The rest show a similarity of around 40% which, according to other studies and the characteristics of the index, is only slightly low (Fig. 2). In contrast, when also considering the relative abundance of each taxon (Bray-Curtis index), the minimum similarity was 60% (Fig. 3), but was

generally high (approximate 80%), mainly due to the abundance of *P. inane* in most of the samples; the segregation of the December sample, however, has to do with an increase in the abundance of *C. garkeana* (Table 2).

The main components in the low values of diversity were thus the high abundance of *P. inane*, the scarcity of the other taxa (low S), and the low equitability. These parameters did vary between the samples (dates) but were in general atypical of benthic diatom assemblages; such low values resemble those that characterize diatom assemblages from extreme environments. According to these data, our hypothesis that diatom taxa from different dates representing distinct stages of succession would be found on the blades of *E. arborea*, together with abundant pioneer taxa or species from advanced stages of colonization, was not supported, although low values of diversity were observed. We conclude that the structure of the diatom assemblage is atypical, similar to those of assemblages from extreme environments, because of the uncommon (very) low diversity values (S, H', J'). However, structure analysis did not permit the distinction of succession stages in the epiphytic diatom assemblage.

DISCUSSION

Although macroalgae are considered an ideal substratum for many species of diatoms and recent studies in NW Mexico have proven this to be so, in this case the brown alga *E. arborea* represents a good substratum only for a few diatom taxa, particularly *P. inane*, but not for most of the recorded taxa in this study. The scarcity of diatom cells and low species richness, along with the pioneer observation showing no diatoms on *E. arborea* blades (Siqueiros Beltrones *et al.*, 2002) suggest a *sui generis* substratum whose study requires at least high-frequency observations. The iconographic catalog in this report may prove to be a useful reference when undertaking future studies on the epiphytic diatoms of *E. arborea*, inasmuch as the frequency of the diatom taxa and their time variation can be monitored in order to infer changes in the epiphytic diatom assemblages.

The observed species richness was approximately half of what has been recorded in similar floristic studies for either a single or for multiple macroalgae species (Siqueiros Beltrones, 2002; Siqueiros Beltrones and Hernández Almeida, 2006; Argumedo Hernández and Siqueiros Beltrones, 2008). In contrast, the floristic study mentioned earlier of a single specimen of *P. cartilagineum* showed it to be heavily epiphytized by many of the 42 taxa recorded, and coupled to a much higher value of diversity ($H' = 3.52$), a low dominance and a high equitability, indicating that the environment provided by the host is very favorable (Siqueiros Beltrones and Argumedo Hernández, 2014a). Meanwhile, the low values of diversity observed for the diatom assemblages on *E. arborea* blades resemble those observed in diatom assemblages from extreme environments (Siqueiros Beltrones, 2002). The subtidal habitat is characterized by high energy which causes very dynamic movement of the *E. arborea* thalli, affecting the settlement of diatoms on the violently moving blades. Colonization is expected to be higher during periods of calm waters.

Because similarity values were high in subsamples from a same sample (Siqueiros Beltrones and Argumedo-Hernández, 2014a), they represent the same structure and ensure that the subsamples did not differ from the overall epiphytic assemblage. This suggests that the

examined samples represent but one assemblage that does not show important temporal variations on the basis of species composition and association structure strongly influenced by *Pteroncola inane*. Accordingly, the abundance of *P. inane* determines the basic structure of the assemblage.

It is thus strange that, in spite of being so abundant, *P. inane* set a new record for the region during this investigation (Siqueiros Beltrones and Argumedo Hernández, 2014b). Such monospecific proliferations have been observed on blades of *M. pyrifera* e.g., *Cocconeis costata* var. *pacifica* (Grunow) Grunow (Siqueiros Beltrones *et al.*, 2002) and *Rhoicosphenia genuflexa* (Kützinger) Medlin (Argumedo Hernández and Siqueiros Beltrones, 2008); in these cases, however, the monospecific dominance has not been that extreme.

Based on the above, an expected succession of the taxa in the assemblage could not be observed because, although the abundance of *P. inane* was highest in the September sample, in the other dates most taxa also remained rare or uncommon. That is, the abundance of cells depended heavily on the proliferation of *P. inane*. Given the objective of this study, this property (abundance) was not quantified, but it may be inferred from the valve concentration in the examined permanent mounts (Table 2).

As noted above, the initial reported absence of diatoms on *E. arborea* (Siqueiros Beltrones *et al.*, 2002), and the scarcity of most diatom taxa in the present study merely suggests that distinct stages of succession occur on the *E. arborea* blades as proposed in our hypothesis, but it precludes its confirmation. It is tempting to suggest that the abundance of *Pteroncola inane* in the examined samples represents the proliferation of a pioneer species that conditions the blade surface of *E. arborea* for other taxa, serving as an alternate substrate to *E. arborea* which could be hostile to the other diatoms. Epiphytism between diatoms is a common phenomenon (Round *et al.*, 1990), and has been documented for this region in epiphytic diatom assemblages of *M. pyrifera* (Siqueiros Beltrones *et al.*, 2002) and of *P. cartilagineum* (Siqueiros Beltrones and Argumedo Hernández, 2014a). To contrast this new hypothesis, an *ex profeso* design is required, including a higher frequency sampling species, i.e., several samplings within a single season to contrast said hypothesis, which may also prove useful in monitoring other diatoms.

From a pragmatic point of view, in spite of the low species diversity of epiphytic diatoms observed on blades of *E. arborea*, the sole proliferation of *Pteroncola inane* combined with many rare or uncommon taxa are expected to enrich the kelp's nutritional value which would favor various species of grazers including those of economic importance like abalones (*Haliotis* spp.). In fact, much of the interest in the study of *M. pyrifera* focuses on its role as food for abalone. As with other macroalgae, epiphytic diatoms are considered to be enriching their food value (Siqueiros Beltrones and Argumedo Hernández, 2005; Siqueiros Beltrones and Argumedo Hernández, 2014a), inasmuch as many epiphytic diatoms have been observed within the gut contents of juveniles and adults of abalone collected in the wild (Siqueiros Beltrones, 2002; Siqueiros Beltrones *et al.*, 2004; Siqueiros Beltrones *et al.*, 2005). Thus our intention to determine what diatom taxa would be found on other macroalgae, such as *E. arborea*, which represents the ecological alternative for *M. pyrifera* in the region. The assumption that *E. arborea* blades may be grazed by abalone is supported by recent experiments that show that abalone juveniles from the region successfully feed on *E. arborea* (Mazariegos-Villarreal *et al.*, 2012).

Knowing the taxonomic identity of the main epiphytic diatoms that are being ingested by *Haliotis* spp. together with their hosts offers an alternative to a better management of abalone under culture conditions. It should also prompt studies on the nutritious properties of these taxa in order to pinpoint their specific role in the diet of the many grazers that depend on them.

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