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A first approach to the study of epizoic diatoms on marine benthic macroinvertebrates in Atlantic Patagonian waters (San Jorge Gulf) with SEM description of the most abundant taxa: *Cocconeis patagonica* sp. nov., *Pseudogomphonema kamtschaticum* and *Tabularia investiens*

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Abstract: Numerous organisms play a host role for a variety of marine and freshwater diatoms and many have yet to be studied in detail. In particular, along the Argentine coast, there have been very few studies on epizoic diatoms. Through the analysis of ascidians, decapods, echinoderms and gastropods sampled from Atlantic Patagonian waters (San Jorge Gulf), this is the first study in the region on epizoic diatoms found on benthic macroinvertebrates. Thirty–one potential host samples, including 14 macroinvertebrates taxa, were examined from different stations. The epizoic diatom taxa found at the highest relative abundance, namely *Cocconeis patagonica* sp. nov., *Pseudogomphonema kamtschaticum* and *Tabularia investiens,* were analyzed using light and electron microscopy, and hence they are described in detail and compared with other species. *Cocconeis patagonica* sp. nov. belongs to the *C. scutellum* complex, but its particular raphe–valve (RV) valvocopula ultrastructure and striation defines it as new. Diagnostic characters are discussed for *T. investiens. Pseudogomphonema kamtschaticum* is reported for the first time in the Atlantic Patagonian waters.

Keywords: Atlantic Patagonian coast, benthic macroinvertebrates, *Cocconeis*, epizoic diatoms, *Pseudogomphonema*, San Jorge Gulf, *Tabularia*

INTRODUCTION

Diatoms play key roles in primary production and the biogeochemical cycles of carbon (C) and silicon (Si) in most oceanic regions, both in planktonic and benthic communities. Benthic diatoms can live freely on and within sediments (epipelic and endopelic communities, respectively), or attached to a substratum such as sand grains, rocks, plants and animals (epipsammic, epilithic, epiphytic and epizoic communities, respectively). Overall, the attached growth forms comprise adnate and erect cells, sometimes forming different types of colonies (Round 1971; Round et al. 1990; Totti et al. 2011).

During the last century, the number of studies on the ecology and taxonomy of marine epizoic diatoms has increased. For example, there are studies on the diatoms found on the skin of cetaceans (Hart 1935; Nemoto 1956, 1958; Nemoto et al. 1977; Holmes 1985; Denys & Van Bonn 2001; Ferrario et al. 2019), on the feathers of diving sea birds (Holmes & Croll 1984), on turtles carapaces (Majewska et al. 2015, 2021; Robinson et al. 2016; Riaux–Gobin et al. 2021a), on small zooplankton such as copepods (Hiromi et al. 1985; Carman & Dobbs 1997; Fernandes & Calixto–Feres 2012; Gómez et al. 2018), and on sessile invertebrates such as hydroids and sponges (Cox & Larkum 1983; Siqueiros–Beltrones et al. 2001; Di Camilo et al. 2005; Totti et al. 2005, 2011; Romagnoli et al. 2007, 2014). There have also been studies on the interactions between diatoms and gastropod or bivalve mollusks (Round 1971 and references therein; Gillan & Cadée 2000; D'Alelio et al. 2011) since their hard shells are favorable to colonization by epizoic microalgae. On the contrary, there is less information on epizoic growth of diatoms in decapods (Madkour et al. 2012; Sanka et al. 2016). Many kinds of animals can play the host role, representing a mosaic of different microhabitats for different species of diatoms, which have not yet been studied (Totti et al. 2011). There are diverse degrees of host specificity for diatoms, and even some species living in a close relationship with their host, have been considered as exclusively epizoic (Riaux–Gobin et al. 2020, 2021a).

For the animal–associated microalgae, the possible benefits derived from their epizoic lifestyle include additional protection against grazing, CO_2 and nutrient supply from the host catabolism, active movement in the water column allowing for a continuous replenishment of nutrients, an elevated position protecting from the sediment resuspension and mechanical abrasion, and access to as yet un–colonized hard surfaces (Romagnoli et al. 2007; Totti et al. 2011; Gomez et al. 2018). On the other hand, whether the hosts are injured by diatoms or not it is still poorly known (Tiffany 2011). Zooplankters can benefit from the oxygen supply or they may be adversely affected by epizoic diatoms reducing their movement and buoyancy, or interfering with their mating (Totti et al. 2011; Gomez et al. 2018).

Particularly in the Argentinean coast only a few studies on epizoic diatoms have been undertaken. Recently, Ferrario et al. (2019) recorded *Bennettella ceticola* (Nelson) Holmes as an epibiont species of the cetacean Franciscana dolphin (*Pontoporia blainvillei*) in Samborombon Bay. Some years ago, Sunesen et al. (2015) recorded *Pseudohimantidium pacificum* Hustedt et Krasske attached to planktonic copepods in the northern coast of Buenos Aires Province. In 2014, Sar & Sunesen emended the description of *Sceptronema orientale* Takano from epizoic specimens of a harpacticoid copepod in coastal waters of Anegada Bay. Earlier, Frenguelli (1939) carried out a study on diatoms in coastal waters of Rada Tilly City, San Jorge Gulf, where they can be interpreted as benthic or epizoic organisms, since they were obtained from the washing of ascidians, crustaceans, echinoderms, mollusks and other benthic invertebrates sampled on soft bottoms at 20 to 30 m depth. Other circumstantial records are diatoms on colonial bryozoans in brackish waters, south of Buenos Aires Province (Frenguelli 1938), and on a gastropod in the southeastern coast of Buenos Aires Province (Frenguelli 1930).

In this study, we present the first account of epizoic diatoms on marine macroinvertebrates (ascidians, decapods, echinoderms and gastropods) in the Argentine inner shelf, based on samples collected in the San Jorge Gulf basin. Using light and electron microscopy, we describe the most abundant diatom taxa: *Cocconeis patagonica* sp. nov., *Pseudogomphonema kamtschaticum* (Grunow) Medlin and *Tabularia investiens* (W. Smith) D.M.Williams et Round. The morphology of each is discussed and compared with other species.

Materials and Methods

As a first exploratory study of epizoic diatoms on benthic macroinvertebrates in the Argentine inner shelf, several groups (ascidians, decapods, echinoderms and gastropods) were sampled in the San Jorge Gulf and adjacent waters. Samples were taken between October 27 and November 6, 2017 onboard the A.R.A. "Puerto Deseado" in the framework of the Argentinean government's Pampa Azul Initiative – San Jorge Gulf Research and Monitoring Program (Dans et al. 2020).

San Jorge Gulf is located in the mid–Atlantic Patagonian waters, between approximately 45° S and 47° S, covering about 40,000 km^2 with a maximum depth of 100 m (Reta 1986). Fine sediments predominate in the central region, whereas

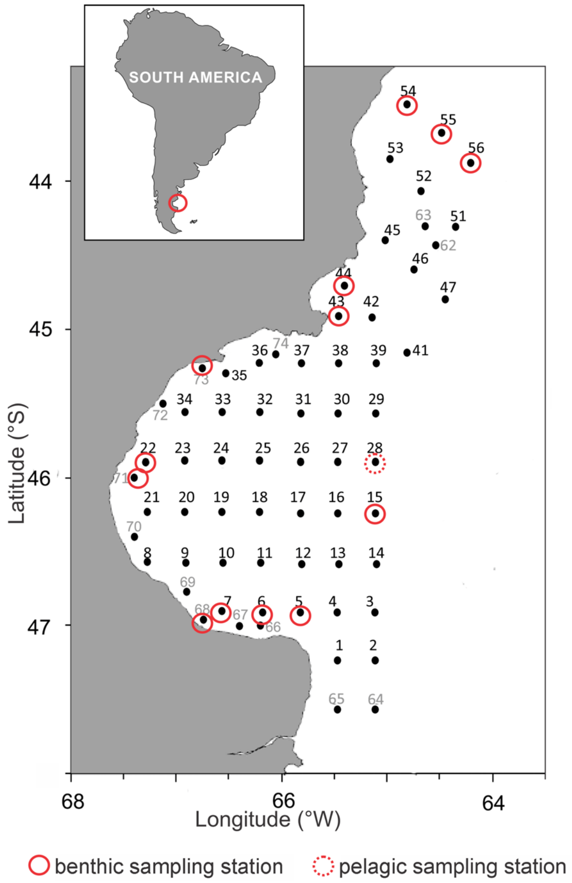


Fig. 1. Maps showing the study area and sampling stations.

Table 1. Positions of the sampling stations in the San Jorge Gulf, including habitat, depth, bottom water temperature (T) and salinity (S).

Station	Date	Lat (°S)	Long (°W)	Habitat	Depth (m)	T (°C)	S (psu)
5	11/06/17	46.92	65.82	benthic	37	10.97	33.18
6	11/06/17	46.88	66.19	benthic	57	10.43	33.23
7	11/06/17	46.90	66.54	benthic	52	10.02	33.16
15	11/05/17	46.23	65.09	benthic	81	10.49	33.43
22	11/04/17	45.90	67.27	benthic	91	8.45	33.31
28	11/03/17	45.57	65.11	pelagic	no data	no data	no data
43	10/31/17	44.91	65.47	benthic	94	11.65	33.43
44	10/31/17	44.68	65.37	benthic	84	11.10	33.44
54	10/27/17	43.47	64.81	benthic	42	12.93	33.54
55	10/28/17	43.71	64.53	benthic	64	11.90	33.49
56	10/28/17	43.89	64.21	benthic	78	11.28	33.47
68	11/06/17	46.91	66.71	benthic	55	9.27	33.27
71	11/04/17	45.98	67.40	benthic	85	8.62	33.41
73	11/01/17	45.29	66.73	benthic	61	9.75	33.45

coarse sediments are present in coastal areas and around Dos Bahías and Tres Puntas capes, northern and southeast extremes of the gulf, respectively (Fernández et al 2005). This gulf is considered to be one of the Southern Hemisphere's most productive ecosystems (Longhurst 2007), its benthic environment supports a great diversity of living organisms.

Samples of macroinvertebrates were taken with an epibenthic trawling net with a mesh size of 20 mm in the codend in locations indicated in the Fig. 1 and Table 1. Sampled invertebrate taxa included *Danielethus patagonicus*, *Eurypodius latreillii*, *Grimothea gregaria* benthic and pelagic morphotypes (Fig. 2), *Libidoclaea granaria*, *Lithodes santolla*, *Peltarion spinulosum*, *Pleoticus muelleri* (Arthropoda, Malacostraca); *Cosmasterias lurida*, *Cycethra verrucosa* (Echinodermata, Asteroidea); *Arbacia dufresnii* (Echinodermata, Echinoidea); *Hemioedema spectabilis* (Echinodermata, Holothuroidea); *Odontocymbiola magellanica* (Mollusca, Gastropoda); *Aplidium* sp., *Paramolgula* sp. (Chordata, Ascidiacea) (Table S1). At station 28, the pelagic morphotype of squat lobsters (*G. gregaria*) was collected with a Bongo paired zooplankton net (by oblique tow). At each station, collected macroinvertebrates were grouped according to their species and rinsed with filtered sea water (0.45 µm) to remove benthic sediments and loose debris.

Diatom samples were obtained by brushing with a damp toothbrush the dorsal body surface of the potential host individual of each species from each station. Toothbrushes and brushed body surfaces were washed with filtered sea water and the biofilm material was collected into separate 100 ml containers and preserved with 4% formaldehyde solution in seawater.

During preliminary microscope observations on water mounts diatoms occurred rarely in most sampled invertebrates except on *G. gregaria* pelagic morphotype, on specimens of the southern king crab *L. santolla* at station 73 and on the spider crabs *L. granaria* at station 43 (Table S1). Given the thin and transparent surface of the carapaces of *G. gregaria* they were also observed on water mounts using light microscopy with the purpose of knowing the diatom arrangement on the carapaces before brushing. After, the fixed material from those samples was washed with distilled water through centrifugation, cleaned with hydrogen peroxide (H_2O_2) at 90 °C, washed and re–centrifuged (Prygiel & Coste 2000). Cleaned material was mounted to make permanent glass slides using Naphrax medium (Ferrario et al. 1995). Aliquots of this material were mounted on stubs, coated with gold–palladium and examined with a Jeol JSM–6510 LV scanning electron microscope (SEM) of the Universidad Nacional de la Patagonia San Juan Bosco, Comodoro Rivadavia, Argentina or with a Jeol JSM–6460LV SEM of Aluar Aluminio Argentino SAIC, Puerto Madryn,

Fig. 2. Specimens of *Grimothea gregaria* (=*Munida gregaria*). The species has two morphotypes, the "gregaria" or pelagic–benthic type (left) and the "subrugosa" or epibenthic type (right).

Argentina. In order to estimate the relative abundance (RA) of diatom taxa in those samples, a minimum of 500 valves per slide were counted and identified at 1000× magnification using a differential interference contrast Olympus BX51 LM and oil immersion, and the results were expressed as percentages (Cefarelli et al. 2010, 2016).

Results and Discussion

From the thirty–one potential host samples examined from the different stations (Tables 1, S1), seven had no epizoic diatoms and in eighteen the number of diatom frustules found was insufficient to perform any detailed diatom analysis, thus excluding them from further analysis with permanent slides. In six host samples, including *Grimothea gregaria* pelagic morphotype (stations 5, 7, 15, 28), *Lithodes santolla* (station 73) and *Libidoclaea granaria* (station 43), the obtained diatom material was sufficient to enable deeper analyses. *Paralia sulcata* (Ehrenberg) Cleve s.l. was found with the greatest frequency (20 out of 31), followed by *Nitzschia* cf. *sigma* (10), *Pleurosigma* aff. *affine* (10), *Psammodictyon panduriforme* (Gregory) Mann in Round et al. (1990) (7) and *Tabularia investiens* (W. Smith) D.M.Williams et Round (7). *Cocconeis patagonica* sp. nov., *Pseudogomphonema kamtschaticum* (Grunow) Medlin and *T. investiens* had the highest relative abundance on *G. gregaria* pelagic morphotype. *Cocconeis patagonica* sp. nov. was closely linked to this arthropod ranging from a RA of 14.9 to 37.1%. It was also found on *L. santolla* at station 73 in a lower proportion (3.5%). *Tabularia investiens* had the greatest RA, reaching 82.8% on *L. santolla* at the same station. *Pseudogomphonema kamtschaticum* had an RA ranged from 3.1 to 42.5% on *G. gregaria* pelagic morphotype and on *L. granaria* (station 43), and it was absent on *L. santolla* (Table S1).

Diatoms found on *G. gregaria* were observed as adnate cells directly attached to the surface of the carapace (e.g., *C. patagonica* sp. nov. formed abundant monospecific gatherings, Fig. 3) or on setae of the carapace occurring mainly as needle–like colonies or in tufts (Fig. 46). For diatoms found on the other macroinvertebrates it could not be specified if they occurred directly on the body of the host or on another epizoic microorganism, such as hydroid colonies, stalked ciliates or filamentous algae, also found from the brushings.

Diatom epibiosis varied considerably among the host groups, among the same host taxa and among sampling stations, possibly in part due to the depths where samples were taken. Cefarelli et al. (2018) found a higher epibiosis on the same host taxa sampled in shallow subtidal environment of the San Jorge Gulf, except in echinoderms where records were very scarce or null in both cases. Diatom growth includes different limitations, among others, light penetration, which is directly related to the water depth (Round et al. 1990; Tiffany 2011). In this sense, it is noteworthy that we observed in *G. gregaria* (Fig. 2), a squat lobster with two morphotypes, one with a benthic habit (*G. gregaria* benthic morphotype) and the other both with benthic and pelagic habits (*G. gregaria* pelagic morphotype) (Williams 1973). We suggest that the reason for epibiosis found on the pelagic morphotype rather than the benthic one is closely associated with their more appropriate environmental conditions. The bentho–pelagic habit of the host possibly allows the diatoms to benefit from better lighting as well as wider nutrient space (Gomez et al. 2018). A noticeable population of *Cocconeis* sp. was also observed on specimens of *G. gregaria* (pelagic morphotype) sampled in open waters around the Falkland/Malvinas Islands – South Atlantic Ocean (A.O. Cefarelli & M. Mascioni, unpublished data). In contrast, ciliates, bryozoans and polychaetes, but no diatoms have been reported as epizoic organisms on *G. gregaria* (benthic morphotype, as *Munida subrugosa*) in the Beagle Channel at the southernmost tip of South America (Martorelli et al. 2003).

When considering the sampled organisms as hosts, there are frequent reports of diatoms on gastropods (Gillan & Cadée 2000; D'Alelio et al. 2011), fewer on decapods (Madkour et al. 2012; Sanka et al. 2016) and ascidians (Lambert et al. 1996; Klöser 1998) and, exceptionally, on echinoderms (McKenzie & Grigolava 1996; Li et al. 2020). Contrary to what we expected, the gastropod *O. magellanica* showed few epizoic diatoms. As mentioned above, the squat lobster *G. gregaria* pelagic morphotype, some samples of the southern king crab *L. santolla* and of the spider crab *L. granaria* presented sufficient epibiosis to perform diatom analyzes. In contrast, *G. gregaria* benthic morphotype, in individual samples or together with the pelagic morphotype, had little or no epibiosis. Ascidians also showed little diatom epibiosis, while echinoderms had the least sign of epibiosis (Table S1). Certain ascidian like *Cystodytes lobatus, Distaplia colligans* and *Aplidium* sp., present bioactivity of secondary metabolites against diatom fouling (Wahl et al. 1994; Koplovitz et al. 2011). However, Cefarelli et al. (2018) found high diatom epibiosis on ascidians sampled in shallower coastal waters of the Gulf, including *Aplidium* sp. Regarding echinoderms, with the exception of the cidaroid sea urchins, which have no epithelium on their primary spines, they rarely act as hosts because all of their body surfaces, even the spines, have a physiologically active tissue with a highly effective antifouling capability (McKenzie & Grigolava 1996; Queiroz 2020). McKenzie & Grigolava (1996) suggest that proteoglycans in the cuticle of echinoderms could develop the function antifouling.

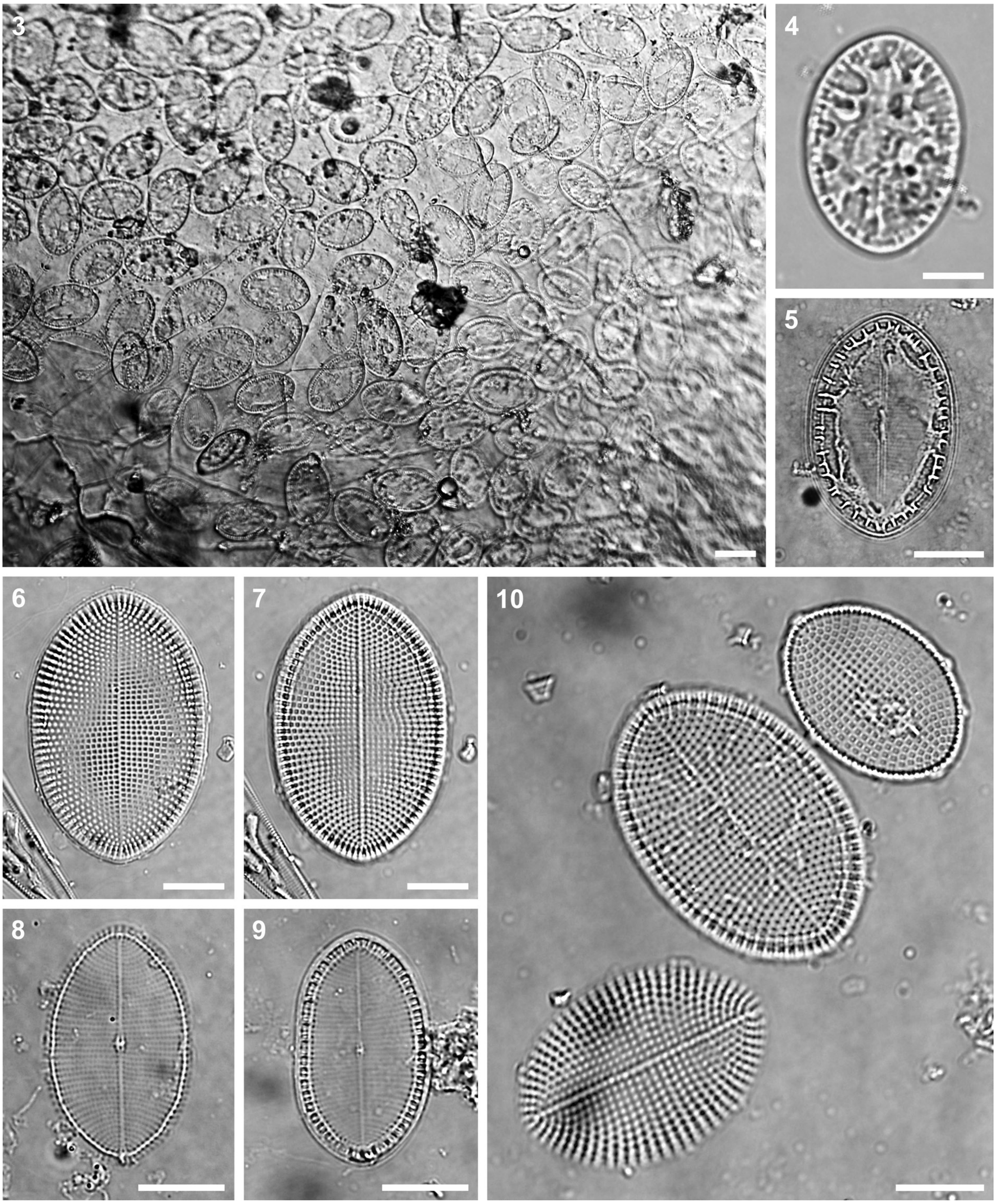
The discovery of a new species of *Cocconeis* Ehrenberg and *P. kamtschaticum,* a species not previously found in the Atlantic Patagonian area, required detailed morphological analyses in order to establish whether the specimens identified as a *Cocconeis* was a new species and to confirm the identity of *P. kamtschaticum*. *Tabularia investiens* was also analyzed in detail in order to discuss its ultrastructure. These three species found in the highest relative abundance on decapods are described below.

Cocconeis patagonica Riaux–Gobin et Cefarelli sp. nov. (Figs 3–28)

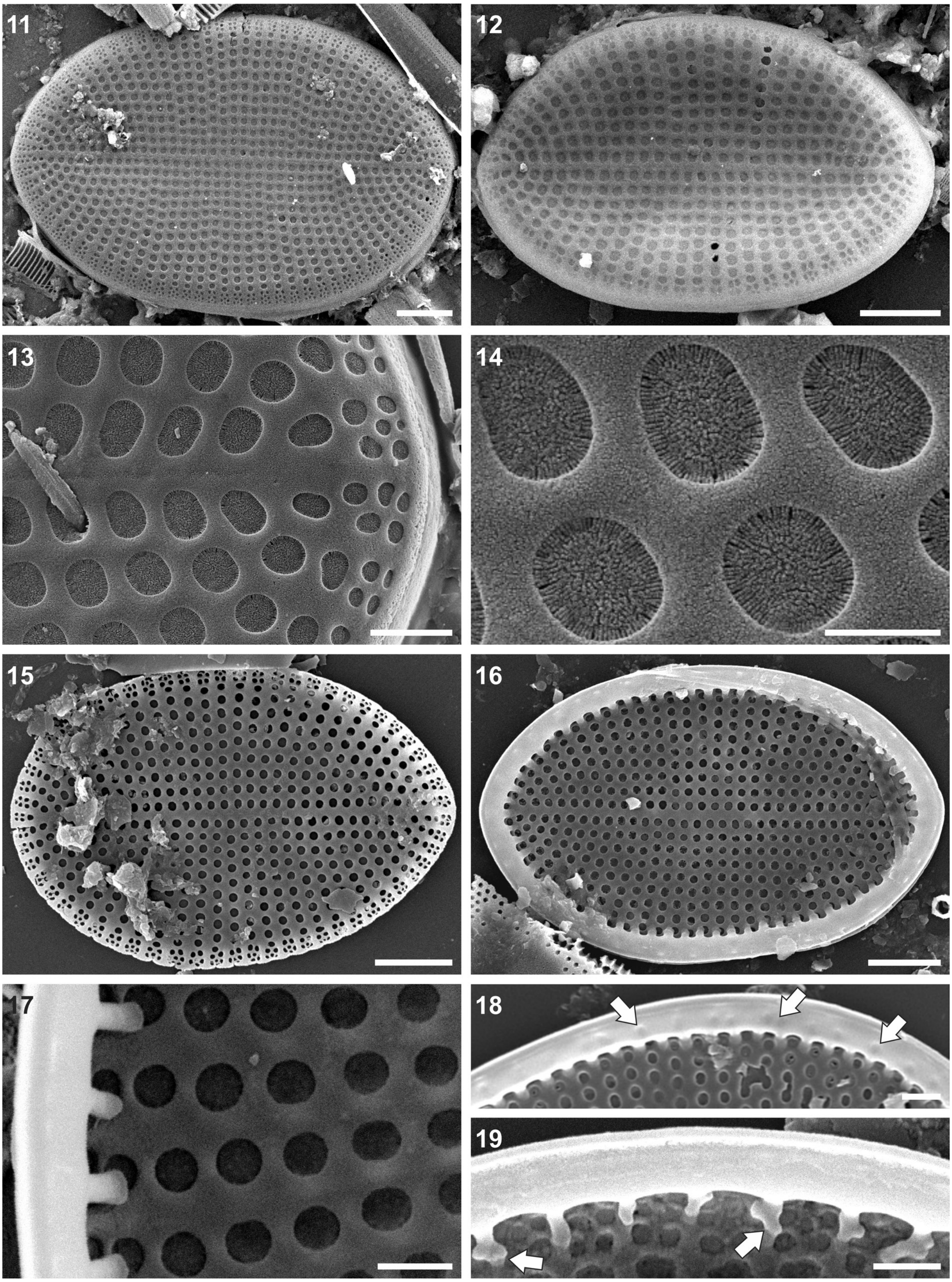
Description

LM (Figs 3–10): Valves elliptical with round or slightly angular poles (Figs 4–10). Valve length 22.5–42.0 µm (x̄ = 29 µm), width 13.5–29.0 µm (x̄ = 19.5 µm*),* average length–to–width ratio 1.5 (n = 56). Areolae square or rectangular in sternum valves (Figs 6, 7, 10). Single, complex multilobed chloroplast per cell (Figs 3–5).

SEM (Figs 11–28): Sternum valve (SV): Externally, valve face flat or slightly concave (Figs 11, 12), sternum linear and relatively narrow. Striae slightly alternate, curved to sharply curved towards apices, regularly spaced, uniseriate on most of valve face becoming bi– to tri–seriate



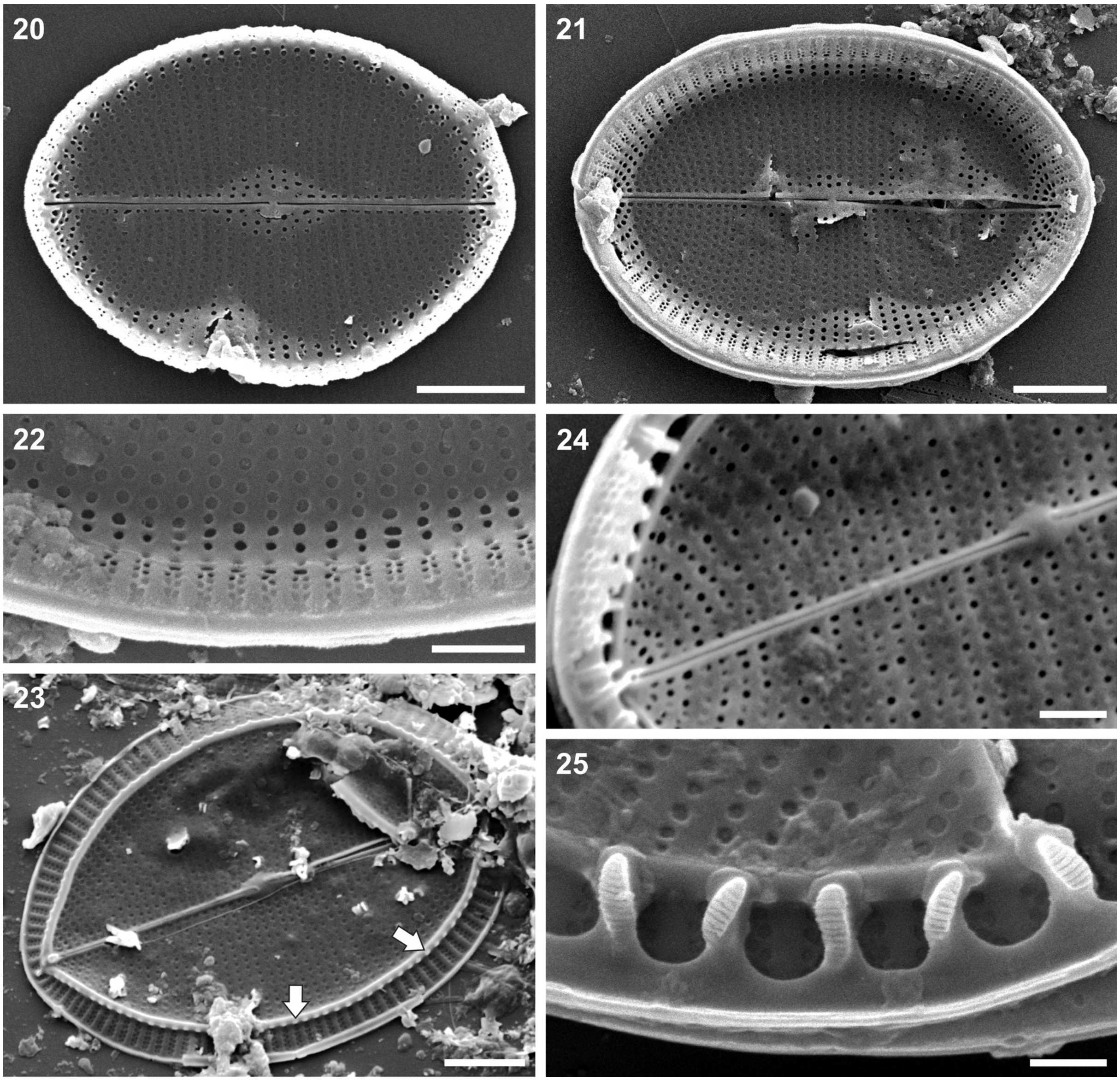
Figs 3–10. (LM) *Cocconeis patagonica* sp. nov.: (3) abundant monospecific gathering attached to surface of carapace of *Grimothea gregaria* pelagic morphotype; (4, 5) cells showing single multilobed chloroplast; (6, 7) SV valve in two different focal planes; (8) RV valve; (9) RV valve with valvocopula; (10) SV valves exemplifying different shapes and sizes. Scale bars 20 µm (3), 10 µm (4–10).



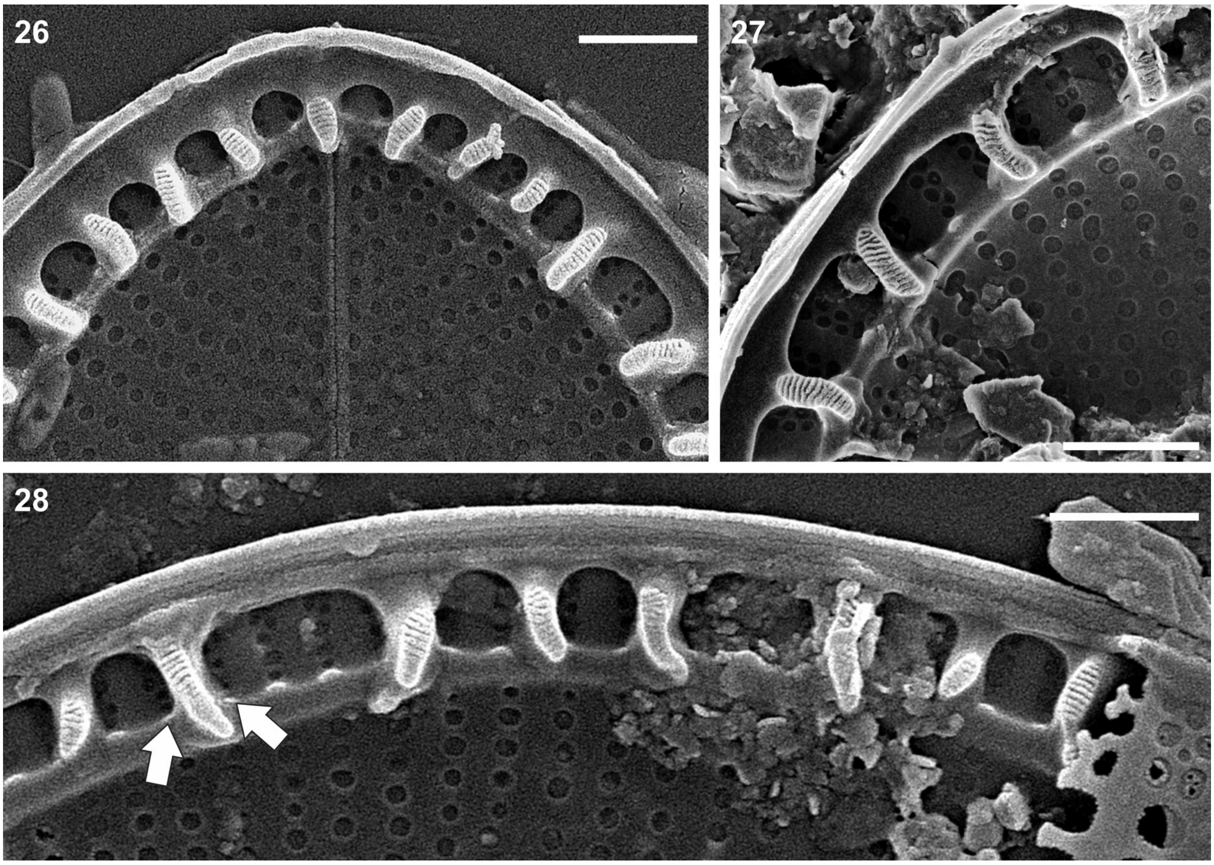
Figs 11–19. (SEM) *Cocconeis patagonica* sp. nov.: (11, 12) SV valves in external view; (13) SV valve end in external view showing details of the areolae; (14) areolae of the same valve showing areola hymenes with short marginal and dense slits; (15) SV valve in internal view; (16) SV valve in internal view with closed valvocopula attached; (17) part of SV valve in internal view showing hymenate areolae and valvocopula; note short fimbriae partially occluding areolae; (18) part of SV valve in internal view showing valvocopula with abvalvar cupules (arrows); (19) part of SV valve in internal view showing valvocopula with branched fimbriae (arrows). Scale bars 5 μm (11, 12, 15, 16), 1 μm (13, 17, 19), 0.5 μm (14), 2 μm (18).

on mantle (Figs 11, 12). Stria density at sternum 9–14 in 10 µm (x̄ = 11.5, n = 45), on valve margin 7–10 in 10 µm (x̄ = 8.5, n = 45). Areola density 9–13 in 10 µm (x̄ = 11, n = 45). Areolae circular, in part transapically elongated, becoming smaller at margin, with pyramidal arrangement (Fig. 13). Areola hymenes with short marginal and dense slits (Fig. 14). Internal valve face with the same structure as the external face (Figs 15, 16). Valvocopula closed showing cupules in abvalvar view, with short fimbriae mostly coinciding with virgae, sometimes partially occluding areolae (Figs 16–18). Valvocopula fimbriae occasionally slightly branched (Fig. 19).

Raphe valve (RV): Externally, valve face flat, becoming concave on margin (Figs 20, 21). Striae opposite, curved towards apices, uniseriate, becoming biseriate towards margins (Figs 21, 22). Stria density by raphe 16–22 in 10 µm (x̄ = 18.5, n = 25), on valve margin 10.5–15.0 in 10 µm (x̄ = 13, n = 25). Areola density 18–26 in 10 µm (x̄ = 22.5, n = 25). Areolae small and circular, smaller at margin; hymenes not observed (Fig. 22). Raphe straight with proximal endings close to each other, straight and very slightly expanded (Figs 20, 21). Internally, narrow submarginal hyaline rim, thickened and raised, with regular bumps coinciding with striae (Fig. 23). Proximal raphe endings slightly deflected to opposite sides. Elliptic, small central area. Distal raphe endings with small and straight helictoglossae (Figs 23, 24). Striae uniseriate, becoming biseriate from hyaline rim to margin (Fig. 23). Valvocopula closed with irregular digitate fimbriae coinciding with each 2–4 virgae and positioned on elevated submarginal hyaline rim,



Figs 20–25. (SEM) *Cocconeis patagonica* sp. nov.: (20, 21) RV valves in external view; (22) margin of RV valve in external view showing details of striae and areolae; (23) RV valve in internal view; note submarginal hyaline rim with regular bumps coinciding with striae (arrows); (24) part of RV valve in internal view showing details of raphe and central area; (25) detail of RV valvocopula in abvalvar view; note digitate fimbriae bearing elongated papillae covered by furrows. Scale bars 5 µm (20, 21, 23), 2 µm (22, 24), 1 µm (25).



Figs 26–28. (SEM) *Cocconeis patagonica* sp. nov.: parts of different RV valves in internal view showing details of valcocopulae; note different shapes and irregularity of fimbriae, papillae and furrows; fimbriae on elevated submarginal hyaline rim, between two bumps (arrows). Scale bars 2 µm.

between two bumps. Fimbriae in abvalvar view bearing irregularly elongated long papillae with furrows resembling fingerprints (Figs 25–28).

Holotype: LPC 15999! (Herbarium of the División Ficología "Dr. Sebastián A. Guarrera", Museo de La Plata, La Plata, Argentina).

Type locality: Argentina, Atlantic Patagonian waters, San Jorge Gulf (45.57° S, 65.11° W).

Habitat: Sea water, epizoic on *Grimothea gregaria* (Fabricius, 1793) pelagic morphotype and *Lithodes santolla* (Molina, 1782).

Etymology: The specific epithet "*patagonica*" refers to Atlantic Patagonian waters where the new taxon was first observed.

Ecology and distribution: Pelagic and benthic zones of the San Jorge Gulf, epizoic on *Grimothea gregaria* pelagic morphotype and *Lithodes santolla*. During sampling, water temperature and salinity were 9.75–10.97 °C and 33.16–33.45 psu, respectively.

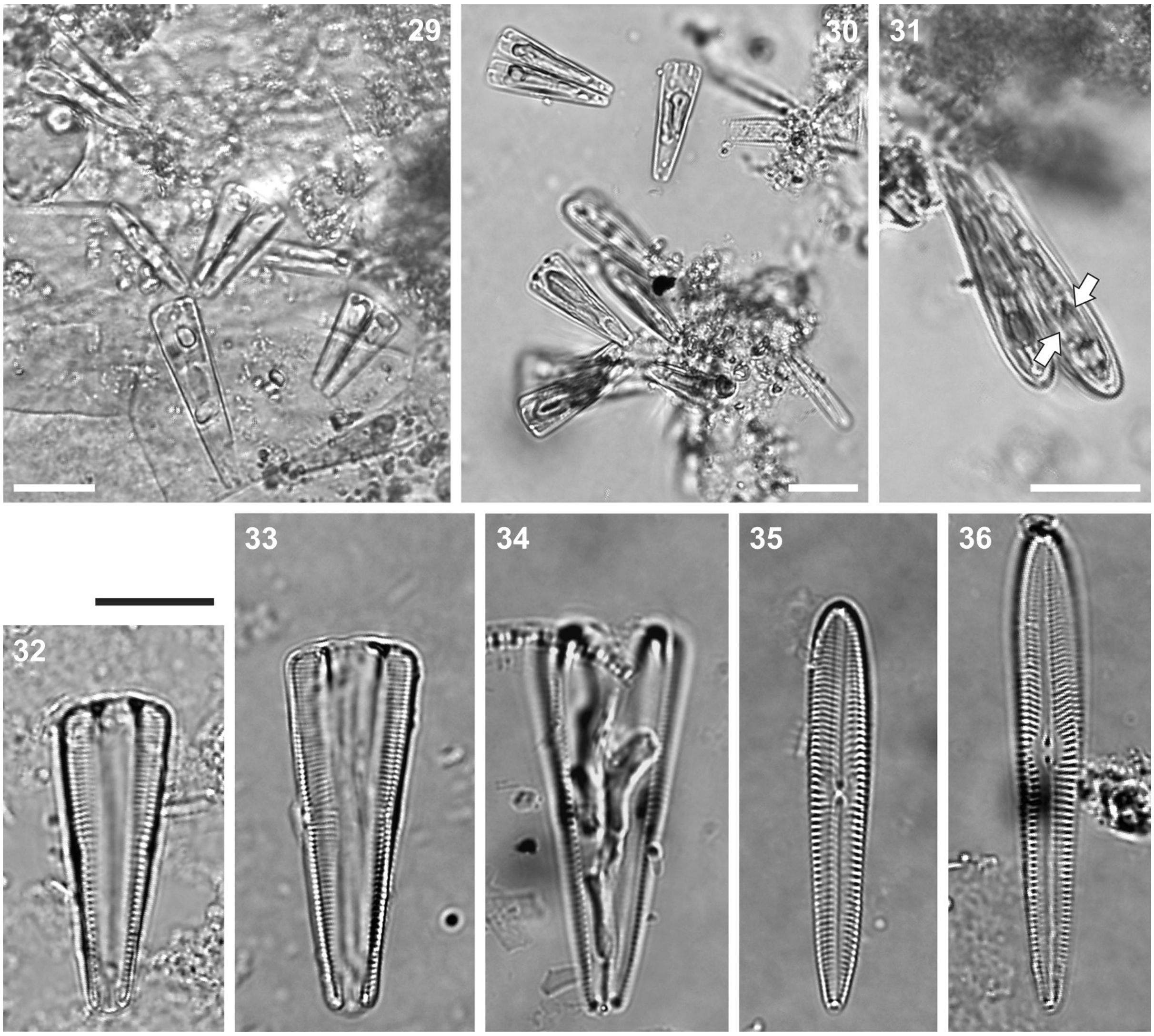
Remarks: *Cocconeis patagonica* is a relatively large taxon with elliptical valves. Some similarities with *C. woodii* Reyes–Vasquez (Reyes–Vasquez 1970), which was originally described as having oblong–elliptic valves with a sigmoid raphe and sigmoid SV sternum and with the same stria densities on both valves (ca. 9–10 in 10 µm) (Reyes–Vasquez 1970), is contrasted with *C. patagonica* which has no sigmoid structures, a more elliptic shaped valve and RV has denser striation than observed on SV. The illustrations of *C. woodii* provided by Witkowski (1998, from Ile des Pins, New Caledonia) and by López–Fuerte et al. (2013), both have a very slightly, but significant, sigmoid structure. The RV, with denser striation on the valve face and biseriate striation on the margin, shares some similarities with that of *C. spina–christi* Riaux–Gobin, Romero, Coste et Galzin (Riaux–Gobin et al. 2013), but the RVVC (RV valvocopula) of the latter has a complex structure, with marginal fenestrae and spines, and bears small round papillae with only a few furrows. The RV of *C. patagonica* has some similarities with that in *C. pseudornata* Riaux–Gobin, Igersheim, Ector et Witkowski (Riaux–Gobin et al. 2019), but again, other features differ. For example, the *C. pseudornata* RVVC has fenestrae, the SV has 'crater–like areolae' in external view, with 'orange–peel like appearance' hymenes, and the SVVC has 'large fimbriae, with undulated edges' (Riaux–Gobin et al. 2019, figs 10–16). The RV of *C. patagonica* also has some similarities with *C. maxima* (Grunow) Peragallo et Peragallo (De Stefano et al. 2000, fig. 27), but many features differ, such as the RVVC with very long fimbriae (De Stefano et al. 2000, fig. 28). The presence of cupules on the abvalvar side of the sternum valve valvocopula of *C. patagonica* (Figs 16–18) is less marked but very similar to that observed in *C. spina–christi* and *C. pseudornata*. The ultrastructure of the SV areola hymenes may be a good character for distinguishing taxa, such as the 'orange–peel appearance' in *C. pseudornata* or the depressed centre, such as observed in *C. scutellum* var. *baldjikiana* (Grunow) Cleve (De Stefano et al. 2008, fig. 38), while flat, with marginal short slits in *C. patagonica* (Fig. 14) and in *C. scutellum* (Riaux–Gobin et al. 2021b, fig. 69).

The most important differences with *C. scutellum* var. *scutellum* Ehrenberg are the stria density higher in RV than in SV, the longer portion of marginal biseriate RV striae, and the elongated long papillae with finger-print–like furrows in the RVVC (Figs 25–28). *Cocconeis patagonica* obviously relates to the *C. scutellum* complex, but its unique characteristics allow its recognition as a new species.

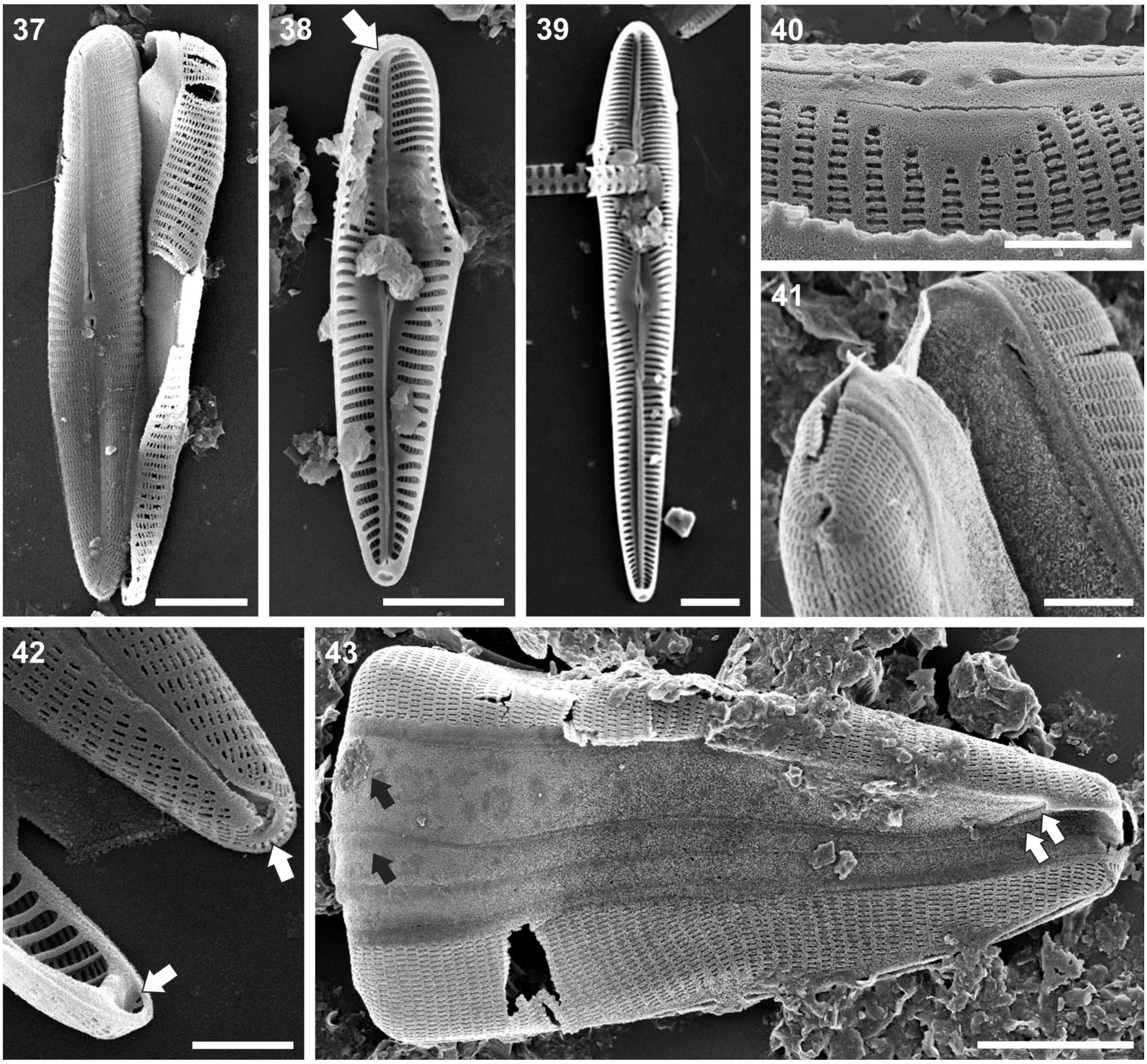
Pseudogomphonema kamtschaticum **(Grunow) Medlin (Figs 29–43)**

Description

Cells solitary, joined in pairs, or forming small tufts, attached to substratum through foot pole (Figs 29–31). Two plate–like chloroplasts, one either side of girdle (Fig. 31). Frustules cuneate in girdle view, height x̄ = 9.0 and 11.5 µm (n = 31), at centre and head pole of frustules, respectively (Figs 32, 33, 43). Valves lanceolate–clavate, with rounded poles (Figs 35–39). Valve length 22.0–54.5 µm (x̄ = 36.0 µm, n = 53), width 4.7–9.0 µm (x̄ = 6.0 µm, n = 13). Valve face flat at centre, curving towards mantle, no clear distinction between face and mantle (Fig. 37). Sternum linear, central area elliptical, with ovoid shape, both slightly asymmetrical about transapical axis, in external and internal views. Raphe system shorter from central area to head pole than to foot pole (Figs 36–39). Externally, raphe straight with proximal endings as enlarged



Figs 29–36. (LM) *Pseudogomphonema kamtschaticum*: (29) living cells on surface of carapace of *Grimothea gregaria* pelagic morphotype.; (30, 31) cells solitary, united in doublets, or forming small tufts, attached to substratum through foot pole; note two plate–like chloroplasts (arrows); (32–34) clean frustules in girdle view exemplifying different sizes; (35, 36) valves showing pseudoseptum with chamber at foot pole. Scale bars 20 µm (29–31), 10 µm (32–36).



Figs 37–43. (SEM) *Pseudogomphonema kamtschaticum*: (37) open frustule in external valve and girdle views showing details of sternum, raphe and central area; (38, 39) valves in internal view showing coarse virgae, raphe slit raised and inclined to one side, helictoglossae, pseudoseptum with chamber at the foot pole and poor development of pseudoseptum at head pole (arrow); (40) central part of valve in external view showing details of proximal raphe endings and different shapes of areolae around central area; (41) head pole in external view illustrating hooked terminal raphe ending; (42) foot poles illustrating pseudoseptum and chamber with slits (arrow) in internal view, and hooked terminal raphe ending and row of slits (arrow) in external view; (43) frustule in girdle view showing wide valvocopula, narrower copula (black arrows) and two short copulae (like ligulae) lying at foot pole (white arrows). Scale bars 5 µm (37–39, 43), 2 µm (40–42).

droplets slightly deflected towards same side (Figs 37, 40). Distal endings hooked to same side of valve (Figs 37, 41, 42). Internally, raphe system raised and inclined to one side, less evident at central area. Proximal raphe endings more or less straight, poorly developed (Figs 38, 39). Both poles with distinct helictoglossa (Fig. 38). Pseudoseptum with distinct chamber or hole at foot pole (Figs 38, 39, 42), clearly visible using LM and oil immersion (Figs 35, 36), opening to outside by a row of slits situated on apex mantle (Figs 42, 43). Poor development of pseudoseptum at head pole (Fig. 38). Striae radiate throughout, more closely spaced towards poles, formed by apically elongate areolae (lineola–like) continuing from valve face to mantle (Figs 37, 40). Internally, striae sunk between coarse virgae (Figs 38, 39). Stria density 15–21 in 10 µm ($\bar{x}$ = 18.0, n = 33) at centre, 18–26 in 10 µm ($\bar{x}$ = 23.0, n = 31) towards head pole. Areolae density c. 53–70 in 10 µm (possible errors due to valve curvature). Cingulum consisting of four open unperforated bands: a wide valvocopula tapering towards foot pole without reaching it, two short and narrower copulae (like ligulae) lying at foot pole, copula as long as valvocopula but narrower (Fig. 43).

Remarks: The genus *Pseudogomphonema* was established by Medlin (in Medlin & Round 1986) to separate some marine gomphonemoid diatoms from the predominantly freshwater genus *Gomphonema* Ehrenberg. The type of the genus is *Pseudogomphonema kamtschaticum* (Grunow) Medlin, its original description, from its basionym *Gomphonema kamtschaticum* Grunow 1878 provided the following data on valve size: length 54–70 µm and width 9–11µm, and striae density of 12–15 in 10 µm. From these measurements it can be concluded that there is great variability in the morphometric data, principally concerning striae density. Our specimen measurements overlap with those of given by Grunow but only at the limits of the values given. Medlin & Round (1986) reported a higher density of striae (16–23 in 10 µm), while Li et al. (2020) had smaller valve sizes and higher stria density (15–19 in 10 µm) that, like our specimens, overlap with those of Grunow at its lower limit. Alternatively, the LM in fig. 25 of *P. kamtschaticum* in Medlin & Round (1986), has a lower striae density than Grunow's original description. Al–Handal & Wulff (2008) also indicated great variability in these measurements comparing their results from Antarctic specimens (10–20 in 10 µm) with those reported by Medlin (1990) from Arctic specimens (10–14 in 10 µm).

Regarding related taxa, Medlin & Round (1986) referred to specimens collected from Bouvet Island, Antarctica, as a possible variety of *P. kamtschaticum* (figs 29, 71, 72) because of its slightly coarser striation (10–11 in 10 µm) and wider axial and central areas. We have also observed something similar in fig. 96 of Al–Handal & Wulff (2008), in fig. 4e of Cefarelli et al. (2016) and in our own unpublished results from Antarctic samples. More data are needed to determine whether or not there is conspecificity between these Antarctic organisms and *P. kamtschaticum. Pseudogomphonema monikae* Witkowski, Metzeltin et Lange–Bertalot also resembles *P. kamtschaticum* but differ from it by having smaller valve size (length 14–38 µm, width 5–7 µm), more elliptical valve shape and higher density of striae (20–28 in 10 µm).

Considering its ecology and distribution, *P. kamtschaticum* is a marine epiphytic and sea ice species principally found in polar and subpolar regions of the Antarctic and the Arctic (Medlin 1990; Scott & Thomas 2005), but also found in coastal waters of Kamchatka, California, South Korea and China (Li et al. 2020). Nemoto (1956) reported the species as an epibiont of whales in the Bering Sea, and Li et al. (2020) also found the species as an epibiont of an ophiuroid in the South Yellow Sea. We report the first occurrence of *P. kamtschaticum* in the Atlantic Patagonian Sea.

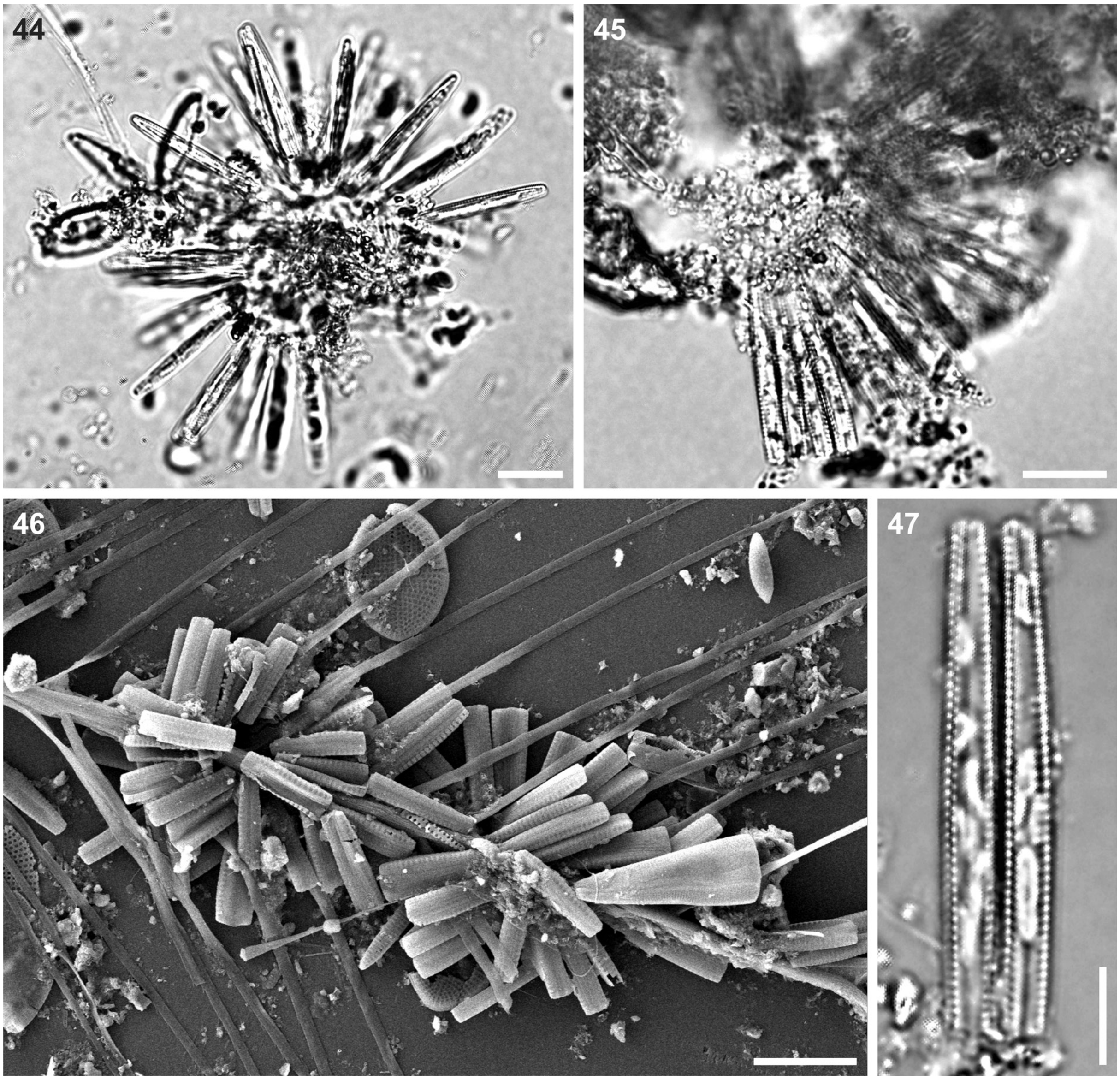
Tabularia investiens (W. Smith) D.M.Williams et Round (Figs 44–65)

Description

Frustules joined to one another at one pole forming tufts or short band–like colonies attached to substratum at poles (Figs 44–46). Chloroplasts elongate, irregularly arranged (Figs 45, 47). Frustules rectangular in girdle view, height $\bar{x}$ = 4.7 µm (n = 19), sometimes slightly arched along longitudinal axis (Figs 47–49). Valves elliptical to narrowly elliptical, isopolar, with rounded or occasionally slightly sub–rostrate ends (Figs 50–58). Valve length 9.8–80.5 µm ($\bar{x}$ = 33.8 µm, n = 65), width 2.3–3.8 µm ($\bar{x}$ = 2.9 µm, n = 28), average length–to–width ratio 9.8 (n = 25). Valve face flat at centre, curving towards mantle, with no clear distinction between face and mantle (Figs 48, 49, 59, 61). Sternum linear (occasionally gently lanceolate, e.g., Fig. 52), variable in width, occupying 8 to 39% of valve width at centre (Figs 52–58, 63). Externally, striae arranged ± parallel, extending from valve face to mantle; broadly elliptical, with apically elongate cribrate areolae and long vimines (not visible with LM). Areolae with finely branched closing plates (Figs 59, 61, 64). Internally, striae elliptical, sunk between coarse virgae (Figs 60, 62, 63). Stria density 9–14 in 10 µm ($\bar{x}$ = 11, n = 64), stria width average 0.55 µm (n = 33), vimines density average 5.2 in 1 µm (n = 23). One rimoportula (hardly discernible with LM) situated at valve pole between the final striae, sometimes off–centre, with transapical to oblique orientation (e.g., Figs 62, 63) and elliptical external opening (Figs 61, 64). Occasionally rimoportula occur at each pole (Figs 53, 54). Single row of simple pores occurring between final polar virga and ocellulimbus. Ocellulimbus sunk into mantle apex, width $\bar{x}$ = 0.95 µm *(*n = 16), with ca. 6–8 rows of 6–8 poroids (Figs 61, 62). Cingulum consisting of open unperforated valvocopula (width $\bar{x}$ = 0.85 µm, n = 23), with irregular crenulate pars interior (Figs 63, 64), ca. 3–4 open copulae (rarely five) with one even row of poroids situated near pars interior. Copulae rarely contain second (incomplete) row of poroids (Figs 63, 65). Width of copulae decreases from 1st to 4th band ($\bar{x}$ = 0.70, 0.50, 0.45 and 0.40 µ*m*, respectively), while poroid density increases in same direction ($\bar{x}$ = 28.5, 31, 34.5 and 35 in 10 µm, respectively).

Remarks: The genus *Tabularia* was established by Williams & Round (1986) and based on the subgenus *Tabularia* Kützing (a subgenus within *Synedra* Ehrenberg). On the basis of morphological characters three sub–groups were proposed: 1) valves with biseriate striae, areolae with simple closing plates; 2) valves with cribra and heavily silicified vimines; and 3) valves with complex cribrate closing plates. *Tabularia investiens* belongs to group 2, having heavily silicified vimines and several copulae.

The areola and their closing plates are not always easy to determine in *Tabularia* and require further study (Williams & Round 1986; Cao et al. 2018). Nevertheless, in the case of *T. investiens* (group 2 of *Tabularia*) an areola that is longitudinally 'elongate' and delimited by the virgae and vimines is, as defined by Williams & Round (1986) for *T. investiens*, "striae parallel with prominent cross–bars (=vimines) set in the depressions between the transapical ribs (= virgae), delimiting longitudinally elongate areolae containing cribra" (with the understanding that 'cribra' means the closing plates are finely branched). Vigneshwaran et

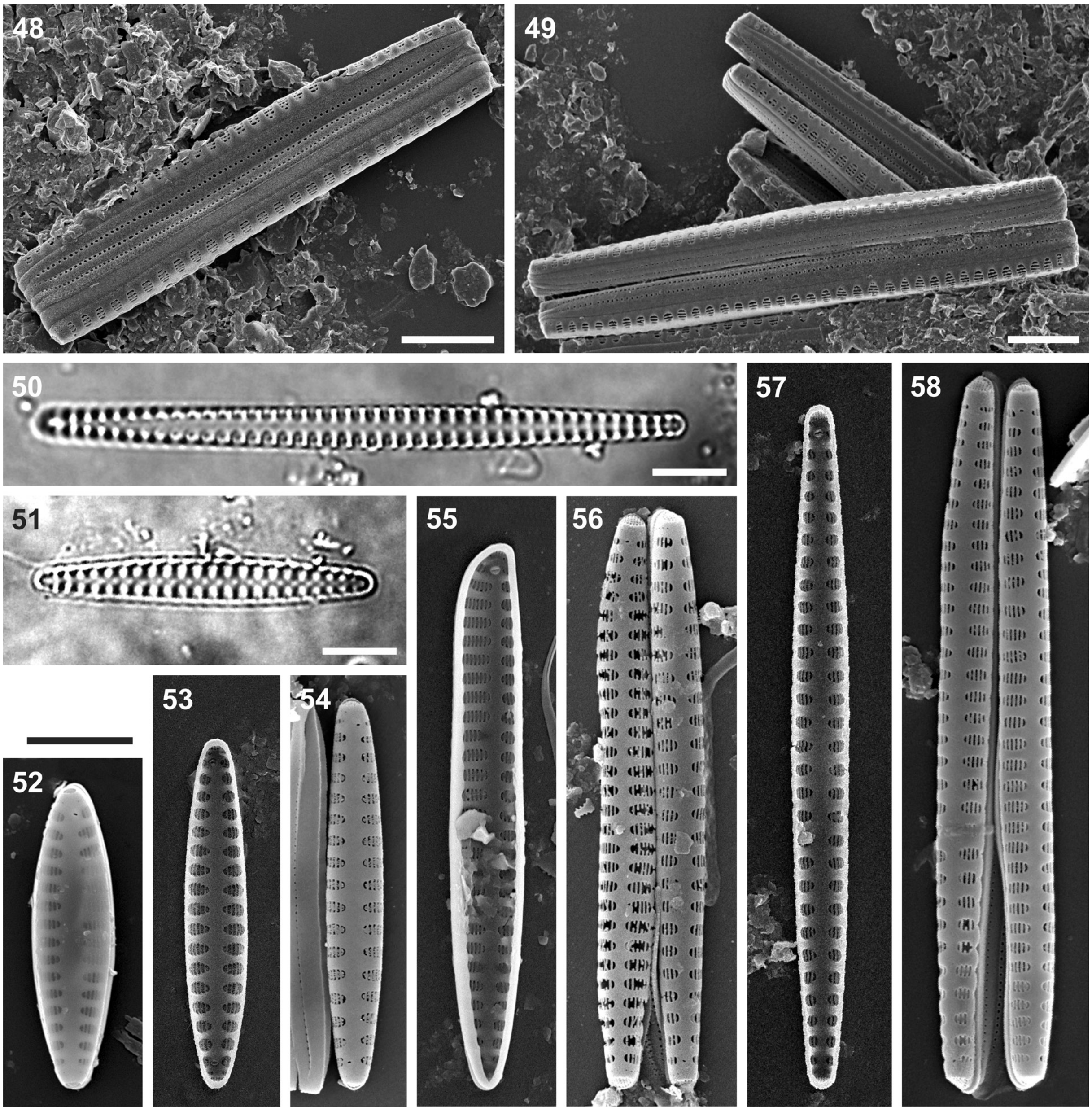


Figs 44–47. *Tabularia investiens*: (44, 45) (LM) living cells forming tufts or short band–like colonies attached to substratum; (46) (SEM) cells forming tufts attached to seta of *Grimothea gregaria* pelagic morphotype; (47) (LM) two whole cells joined to each other at one pole showing irregular arrangement of chloroplasts. Scale bars 20 µm (44–46), 10 µm (47).

al. (2020) also interpreted the areolae in a similar fashion for their species of *Tabularia*. In contrast, taxa in *Tabularia* of group 2, some authors (e.g., Round et al. 1990; Kuriyama et al. 2010; Suzuki et al. 2015) have considered each stria a single cribrate areola. Williams & Round (1986) have a definition that is not sufficiently clear when they characterize the group 2 "cribra with heavily silicified cross–members (= vimines)".

The valve measurements for the specimens identified here as *T. investiens* are similar to previously published data (Smith 1856; Holmes & Croll 1984; Williams & Round 1986; Kuriyama et al. 2010; Suzuki et al. 2015). However, Smith (op. cit.) and Williams & Round (op. cit.) have a smaller size range for valve length: 12.5–30.5 µm and 25–35 µm, respectively. Williams & Round (op. cit.) also have a lower striae density (their fig. 39, 4.5 in 10 µm) while Romagnoli et al. (2014) report up to 29 striae in 10 µm on specimens identified as *T. tabulata* (C.Agardh) Snoeijs, which according to the valves shown in their fig. 2f–j should be identified as *T. investiens* with 11–13 striae in 10 µm. Thus, using these results, the data in the original description (Smith 1856, around 10 striae in 10µm), as well as Holmes & Croll (1984) and Kuriyama et al. (2010), who indicate 8–11 and 7–13 striae in 10 µm, respectively, the valid range of striae in 10 µm for *T. investiens* is between 7 and 14.

Regarding the girdle structure of *T. investiens*, Kuriyama et al. (2010) illustrated it accurately reporting up to eight bands in the cingulum relative to the six for our specimens. In addition, we have provided measurements of the bands and the poroid density of the copulae, and in contrast to Williams & Round 1986, the copulae are regularly perforated by one row of poroids situated close to the pars interior.



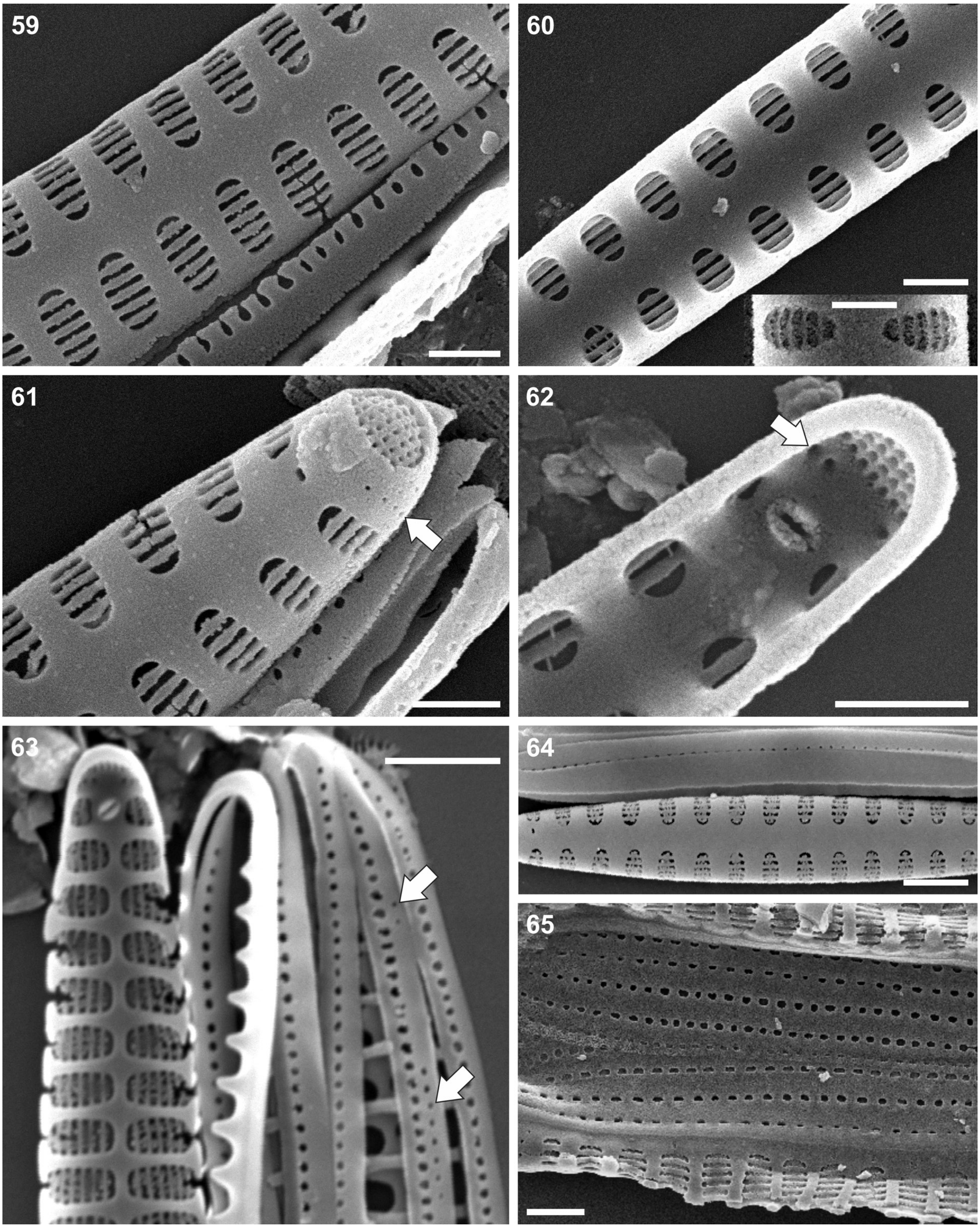
Figs 48–58. *Tabularia investiens*: (48, 49) (SEM) frustules in girdle view; (50, 51) (LM) valves exemplifying different shapes and sizes; (52–58) (SEM) different valves in internal and external views exemplifying different shapes and sizes; note one rimoportula at each pole in Figs 53 and 54. Scale bars 5 µm.

Considering its ecology and distribution, the genus *Tabularia* has a wide geographical distribution, with species being present in fresh, brackish and marine waters, both in temperate and tropical environments (Vigneshwaran et al. 2020); *T. investiens* and *T. tabulata* have also been found in Antarctica (Klöser 1998; Majewska et al. 2013). Species in the genus are primarily epilithic and epiphytic (Round et al. 1990; Snoeijs 1992) and frequently associated with nutrient enrichment (Hillebrand et al. 2000; Kuriyama et al. 2010). *Tabularia investiens* was originally described by Smith (1856) as "marine, thickly covering an *Ectocarpus*" from Kirkaldy, Fifeshire, Scotland. Later, *T. investiens* was found as epizoic attached to the feathers of diving sea birds (Holmes & Croll 1984). In coastal waters of Argentina, *T. investiens* was found for the first time by Frenguelli (1930) as epiphyte of seaweeds and later Frenguelli (1938) found the species in brackish and marine benthic samples, and exceptionally on colonial bryozoans.

Concluding remarks

This work is the first report to specifically address epizoic diatom on macroinvertebrates in the Argentine shelf enlarging the knowledge on epizoic growth of diatoms in decapods.

The degree of diatom epibiosis varies among the



Figs 59–65. (SEM) *Tabularia investiens*: (59) central part of valve in external view illustrating details of striae and areolae; (60) central part of valve in internal view illustrating details of striae, coarse virgae and areolae; note apically elongate areolae with finely branched closing plates; (61, 62) valve poles in external and internal view, respectively; note rimoportula, single row of pores between final virga and ocellulimbus (arrows) and ocellulimbus into mantle apex; (63) part of valve in internal view showing narrow sternum, sunken striae, elongate areolae with closing plates, rimoportula with oblique orientation and cingulum of open copulae; note unperforated valvocopula with crenulate pars interior and four copulae with one row of poroids near pars interior, exceptionally two (arrows); (64) valve in external view and valvocopula with slightly crenulate pars interior; note off-centre opening of rimoportula and branched closing plates of areolae; (65) part of frustule in girdle view illustrating copulae; epicingulum consisting of unperforated valvocopula and five copulae. Scale bars 1 µm (59–62, 65), 2 µm (63, 64).

hosts and sampling stations, possibly due to the environmental conditions where samples were taken. The squat lobster *Grimothea gregaria* pelagic morphotype was the host with the highest diatom epibiosis, possibly due to its bentho–pelagic habit.

Cocconeis patagonica sp. nov., *Pseudogomphonema kamtschaticum* and *Tabularia investiens* were the most representative diatom taxa found, which were thoroughly characterized by using light and electron microscopy.

Cocconeis patagonica sp. nov., a member of the *Cocconeis scutellum* complex, with several ultrastructural specificities, increases the diversity of this group.

Pseudogomphonema kamtschaticum is recorded for the first time in the Atlantic Patagonian waters.

The use of SEM allows the discovery of new taxa, particularly living as an epizoic microflora. Further studies are also needed to evaluate different degrees of host specificity diatom–macroinvertebrates in coastal marine waters.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Presence/absence of diatom taxa in potential host samples of macroinvertebrates. Relative abundance (RA) of diatom taxa (as %) when they occurred at > 3% in samples where the number of diatom cells was sufficient to perform analysis on permanent slides (P*).

This material is available as part of the online article (http://fottea.czechphycology.cz/contents)

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