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Pleurosigma guarreranum, sp. nov. (Pleurosigmataceae, Bacillariophyta), from the Gulf of San Matías, Argentina, and comparison with the allied species *Pleurosigma exemptum* and *P. obesum*

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A new marine diatom, *Pleurosigma guarreranum* Sar, Sterrenburg & Sunesen, *sp. nov.*, is described with light and electron microscopy from material collected in coastal waters of the Gulf of San Matías, Río Negro Province, Argentina. *Pleurosigma guarreranum* resembles *P. exemptum* and *P. obesum* from the Philippines. Isotypes of *P. exemptum* and *P. obesum* deposited in the Albert Mann Collection, National Museum of Natural History, Smithsonian Institution (US), were examined with light microscopy. The observations supported a previous suggestion to include *P. obesum* as a heterotypic synonym of *P. exemptum*, which has priority. Since there is no available unmounted original material of *P. exemptum*, a comparative light microscopical analysis of *P. guarreranum* and the type material of *P. exemptum* was made. Despite some similarities, there are subtle differences in morphometric data, valve outline, raphe sternum pattern, and morphology of the central area. But especially, the two species consistently differ in the angle of intersection of the oblique striae, justifying a separate taxonomic position. *Pleurosigma guarreranum* was also compared with another species belonging to the section *Formosi, P. decorum*, similar in valve outline, raphe sternum pattern and angle of intersection of the oblique striae.

Key words: frustule, new species, *Pleurosigma exemptum*, *Pleurosigma guarreranum sp. nov.*, *Pleurosigma obesum*, taxonomy, type material, ultrastructure

Introduction

Within the framework of an on-going study of the planktonic diatom populations in the Gulf of San Matías (Province of Río Negro, Argentina), numerous species of *Pleurosigma* were found in several net samples and analysed by Sar *et al*. (2013). One of these was a large species that resembled *Pleurosigma exemptum* in the overall shape of the valve, the raphe sternum pattern, the presence of a distinctive central area with bilateral dilation of the central nodule, and stria density.

Mann (1925) described *Pleurosigma exemptum* and *P. obesum* based on material from the Philippine Islands, and designated the slides USNM 43671 and USNM 43673 respectively, as holotypes (Smithsonian Institution, Washington DC, USA). *Pleurosigma exemptum* was characterized in the protologue as follows: 'valve broadly lanceolate, moderately sigmoid, tapering from the broad middle portion to the somewhat blunt ends; raphe more sigmoid than the valve, thereby approaching opposite sides towards the ends; a slight lateral hyaline dilation around the central nodule; markings quincunx … angle between the oblique lines … slightly in excess of 90° …'. In contrast, *P. obesum* was characterized thus: 'valve broad, sigmoid, tapering to the rather blunt rounded ends, raphe strongly oblique to the long axis at the middle of the valve, … curving strongly as it approaches the convex side from which it barely remains separated; marking oblique to the long axis, but crossing each other at right angle …'.

More recently, Stidolph (2002) made a critical re-investigation of the type material of the *Pleurosigma* species described by Mann (1925). According to Stidolph, both holotype slides contained only one specimen and there was no unprocessed material that could be used for further studies with scanning electron microscopy (SEM). Both specimens were comprehensively documented by photomicrographs taken with light microscopy (LM). Based on this analysis, Stidolph (2002) synonymized *P. obesum* under the

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name *P. exemptum*, and his choice establishes the priority of *P. exemptum* under Article 11.5 of the International Code of Nomenclature for algae, fungi and plants (McNeill *et al.*, 2012).

Comparison between the species we found in the Gulf of San Matías and *P. exemptum*, as described in the protologue, reveals subtle differences in the angle of intersection of the oblique striae and Stidolph's (2002) data also indicate important differences between the two taxa concerning this character. However, the fact that Stidolph's data were obtained from only two specimens suggested the desirability of an analysis of additional type material of *P. exemptum* and *P. obesum*, if available, to assess the range of morphological variation in the original populations. It would also be helpful to examine other material reported to contain either *P. exemptum* or its synonym *P. obesum* but there appear to be very few records of these species. As far as we can determine *P. exemptum* has been reported only by Tynni (1986), from tidal flat sediments at Long Beach (Washington State, USA), while *P. obesum* has never been found after the original description. Material from the Gulf of San Matías shows similarities with Tynni's (1986) data as regards stria density, the bilateral dilatation around the central nodule, and the angle of intersection of the oblique striae, though Tynni's illustrated fragmentary specimen is narrower than ours and Mann's.

The aims of this study were therefore to investigate the Gulf of San Matías *Pleurosigma* using light and scanning electron microscopy and to compare it with type material of other *Pleurosigma* species, including the morphologically similar *P. exemptum* and *P. obesum*, and also *P. decorum* (Smith, 1853), to which the Argentinian specimens show some similarities in general appearance.

Materials and methods

The material from the Gulf of San Matías (Río Negro Province) was collected at several stations: Punta Orengo, Las Garzas, Banco Reparo, San Antonio Oeste, Los Álamos, Las Grutas, El Sótano and El Fuerte (Fig. 1), from March 2006 to April 2007.

Qualitative samples were taken from the surface layer of the water column (between 0 and 5 m) with net hauls (30 µm mesh) and fixed with 4% formalin. In the laboratory, the preserved samples were rinsed with distilled water to remove salt and preservatives, and then the organic matter was oxidized according to Prygiel & Coste (2000). The cleaned material was mounted for LM and SEM after Ferrario *et al.* (1995). Permanent mounts were made with Naphrax (Brunel Microscopes, Chippenham, U.K.). Samples have been deposited in the Herbarium of the División Ficología 'Dr. Sebastián A. Guarrera', Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata under the numbers LPC 13648 to 13685.

The material examined from the Philippine Islands belonged to the Albert Mann Collection, deposited in the National Museum of Natural History, Smithsonian Institution, Washington D.C., USA (herbarium abbreviation US). *Pleurosigma exemptum* was analysed from two isotype slides, catalogue numbers US D3289 and US D3292 (original numbers 3071 and 3074 respectively), for which the date and collector are unknown. *Pleurosigma obesum* was analysed from one isotype slide, catalogue number US D3309 (original number 3091), dated January 1919; again, the collector is

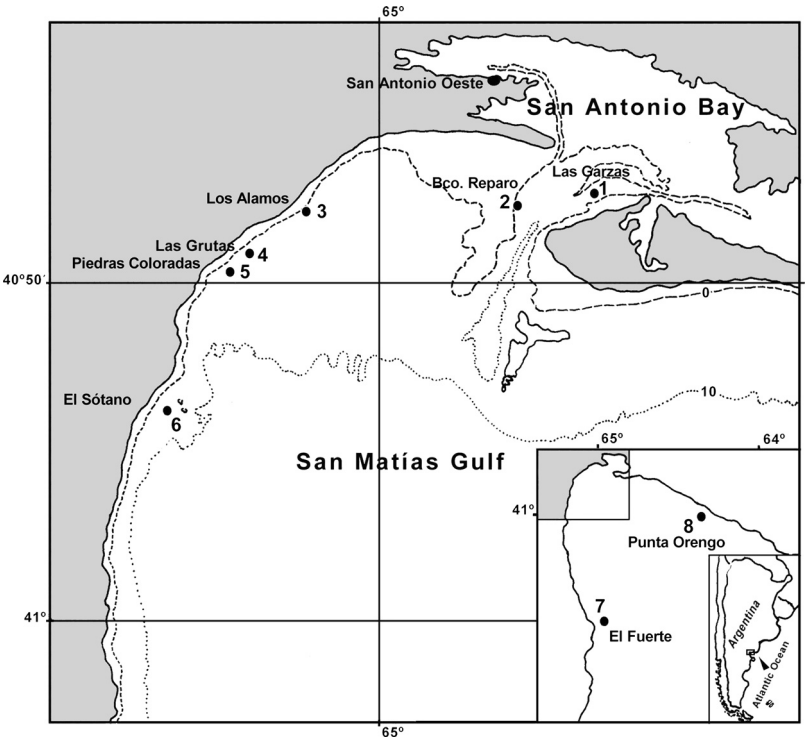


Fig. 1. Map of the northern region of the Gulf of San Matías showing the nine sampling stations and locations in the study area of Argentina.

unknown. As in the case of the holotype slides, each isotype slide contains only one specimen. No further material, in particular unmounted material for SEM, was available. To check the morphometric data for the holotype specimens, we examined original enlargements of the holotype microphotographs published by Stidolph (2002), kindly made available to us by that author.

Observations and photomicrographs were made using Leica DM 2500 light microscopes (Leica Microsystems, Wetzlar, Germany), under phase contrast and differential interference contrast, and a JEOL JSM 6360 LV scanning electron microscope (JEOL, Tokyo, Japan). Terminology follows Ross *et al*. (1979), Round *et al*. (1990), Sterrenburg (1991*a*, 1991*b*) and Reid (2012). The procedure for the measurement of intersection angle of the oblique striae and raphe angle was as detailed in Sterrenburg (1991*a*).

Results and discussion

Although the need to describe a new species became evident only after comparison with type material of *P. exemptum* and *P. obesum*, reported below, we will describe *P. guarreranum* first, to avoid referring to the 'Gulf of San Matías' specimens or taxon.

Pleurosigma guarreranum Sar, Sterrenburg & Sunesen, *sp. nov.*

(Figs 2–27)

Description: Valves sigmoid-lanceolate, vaulted, with sub-obtuse apices (Figs 2, 3), 600–681 µm long and 76–90 µm wide. Ratio length : width 6.2–7.8. Raphe-sternum eccentric, with a single sigmoid curvature, crossing the centre of the valve diagonally and closer to the convex sides towards the apices (Figs 2, 3). Raphe angle +8° to +12° (Figs 2, 3). Central area circular, small, with a thick saddle-shaped central nodule, which is bilaterally dilated (Figs 4–7). Central nodule surrounded by two symmetrical, almost parallel bars (Fig. 4). Internal central raphe endings coaxial and slightly dilated (Fig. 4). Central external raphe fissures very long, slightly undulate, overlapping and more or less parallel for a short distance (Figs 5–7). Terminal areas unilaterally dilated, funnel-shaped, in apical position (Figs 8, 9) with twisted helictoglossae (Fig. 10). Terminal raphe fissures not reliably visible in LM. Striation pattern dominated by oblique striae, 11–12 in 10 µm, slightly curved, intersecting between 80–86°, crossed by less obvious transverse striae, 14–16 in 10 µm (Figs 4–8).

In external SEM views, the valve is vaulted, flatter at the centre than towards the ends, and angled at the raphe (Fig. 11). The valve surface is verrucose in untreated material (Figs 12, 13, 16, 17). The valve mantle hardly differentiated from the valve face and the valve margin is non-porous (hyaline) (Figs 15–18). The raphe is bordered by a hyaline area, which is delimited by areolae that are smaller than on the rest of the valve face (Fig. 18). The central external raphe fissures project markedly into the central area and vary in undulation among valves, overlapping for some distance and curving towards opposite sides (Figs 12, 14). The terminal raphe fissures are hook-shaped (Figs 16–18) and bent in opposite directions, each turning towards the concave side of the valve. The areolae are loculate (Fig. 19) and arranged in decussate striae, and open by apically elongate, slit-like foramina in treated material (Figs 14, 15).

In internal views, the raphe sternum is narrow, slightly thickened, and delimited by a row of small areolae (Figs 20, 22, 24). The central area is conspicuous and saddle-shaped, and forms a short stauros-like structure, which is laterally excavated near the sternum to form small overhangs (Fig. 24, arrowheads), and bears slender, symmetrical, central bars surrounding the oval, central nodule (Figs 20, 21, 24). The central raphe endings are coaxial and slightly dilated (Figs 24). At each pole, the raphe terminates in a helictoglossa, which is turned towards the concave side of the valve and is bordered by an area of thicker non-perforated silica and surrounded laterally by a discontinuous row of apical slits (Figs 25–27). The areolae open internally by circular pores (probably occluded by hymenes), which are crossed by a bar recessed below the internal surface of the valve (Figs 19, 23 arrows). Scattered on the valve surface are some pairs of pores that are slightly larger and lack bars (Figs 19, 23 arrowheads).

Holotype: Slide LPC 13671 (1), labelled 'holotipo de *Pleurosigma guarreranum*, Piedras Coloradas, 05/08/2006', deposited in the Herbarium of the División Ficología 'Dr. Sebastián A. Guarrera'.

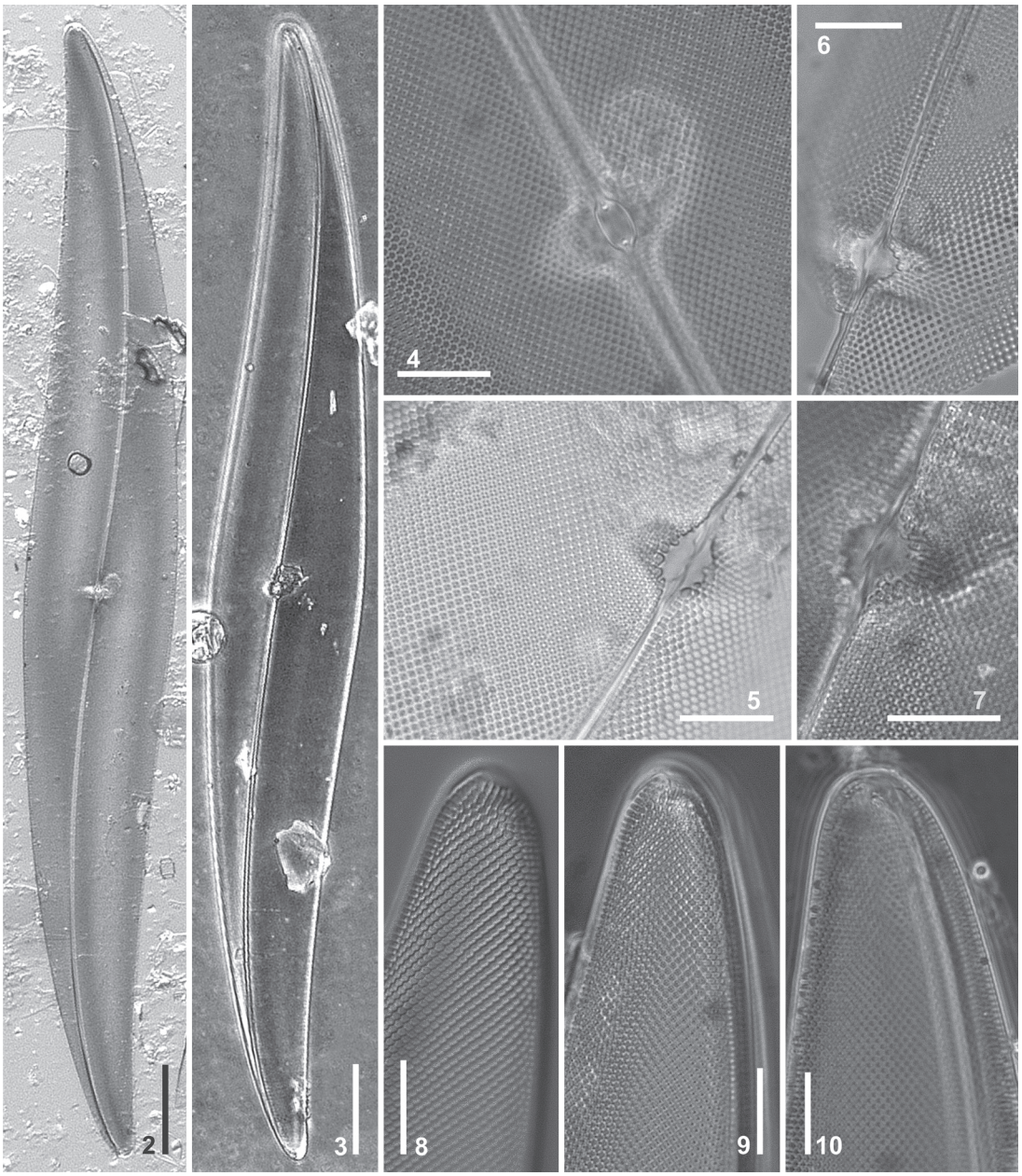
Isotype: Slide LPC 13671 (2), labelled 'isotipo de *Pleurosigma guarreranum*, Piedras Coloradas, 05/08/2006', deposited in the Herbarium of the División Ficología 'Dr. Sebastián A. Guarrera'.

Paratype: Slide LPC 13672 (1), labelled 'paratipo de *Pleurosigma guarreranum*, Las Grutas, 05/08/2006', deposited in the Herbarium of the División Ficología 'Dr. Sebastián A. Guarrera'.

Type locality: Piedras Coloradas, 40° 50′ 33″ S, 65° 06′ 54″ W, Provincia de Río Negro, Argentina.

Distribution: Known thus far only from the Gulf of San Matías (Río Negro Province, Argentina), where it was collected at several stations (Fig. 1). In this area the seawater temperature is 7–23.5°C and the salinity varies from 34 to 36 psu (Pascual *et al*., 2001). This zone is characterized by strong re-suspension of bottom material caused by tidal currents in the shallow waters of the San Antonio Bay and neighbouring coastal environments, which explains the frequent occurrence of benthic diatom cells in the plankton.

Etymology: This species was given the epithet '*guarreranum*' in honour of Emeritus Professor Dr. Sebastián A.

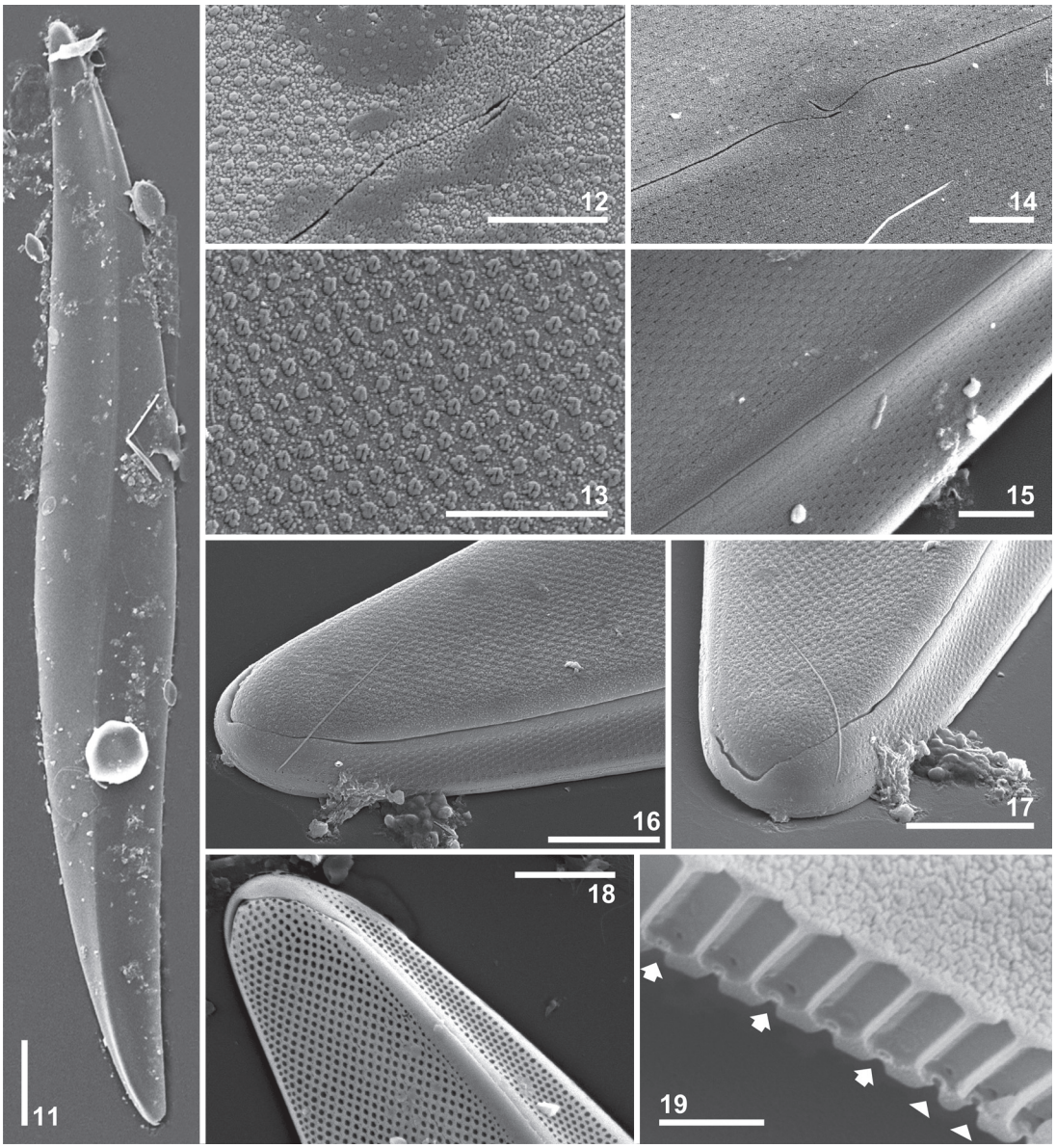


Figs 2–10. *Pleurosigma guarreranum*, holotype: LPC 13671, Piedras Coloradas (Figs 3, 7–10); paratype: LPC 13672, Las Grutas (Figs 2, 4–6). LM. **2, 3.** Valve showing the central area with bilateral dilatation. **4–7.** Details of central areas. Figure 4 shows the central nodule, containing the central raphe endings, surrounded by two symmetrical, almost parallel bars (cf. Fig. 24); Fig. 7 is focused on the external raphe fissures (cf. Figs 12, 14). **8–10.** Details of the valve apex, including two different focuses of the same apex (Figs 8, 9). Note that the terminal area is unilaterally dilated and funnel-shaped in apical position (Fig. 9); Fig. 10 shows the helictoglossa (cf. Figs 25–27). Scale bars = 50 µm (Figs 2, 3) and 10 µm (Figs 4–10).

Guarrera, one of the first Argentinian phycologists, who created the División Ficología at the Museo de La Plata.

The status of Pleurosigma exemptum *and* P. obesum*, based on analyses of type material*

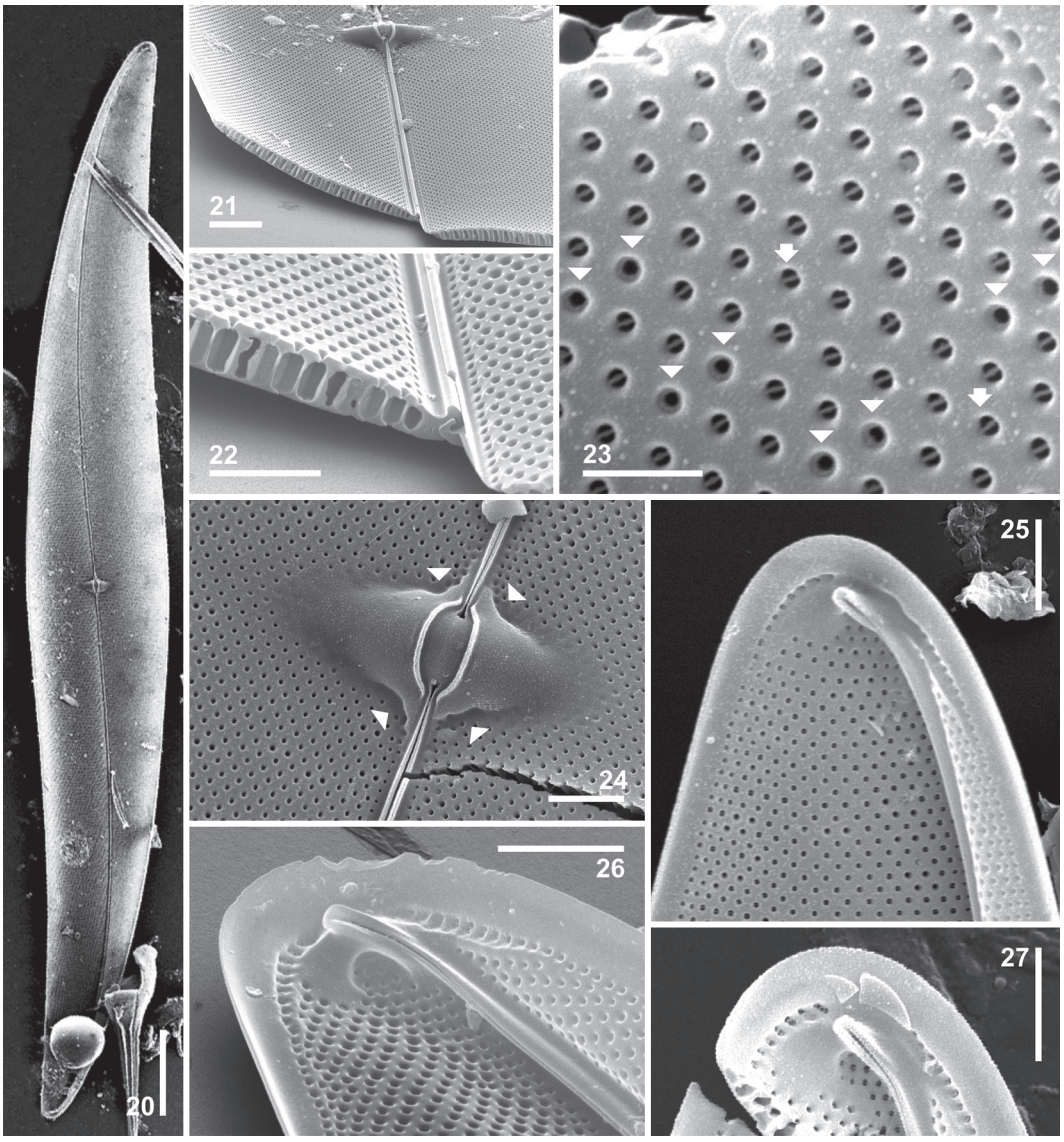
The valves found in the isotype slides were sigmoid-lanceolate, vaulted, with sub-obtuse apices (Figs 28–30), those corresponding to *P. exemptum* (Figs 28, 29) being 500 and 644 µm long and 92 and 100 µm wide, while that corresponding to *P. obesum* (Fig. 30) was smaller, 315 µm long and 63 µm wide. The ratio of length : width of specimens was 5.43 and 6.44 for the isotypes of *P. exemptum* and 5.00 for the isotype of *P. obesum*. The raphe-sternum was similar in all three type specimens, being sigmoid, slightly diagonal in the middle part of the valve, and approaching opposite convex sides towards the apices (Figs 28–30). The raphe angle was +9 and +10° for the isotypes of *P. exemptum* (Figs 28, 29, respectively) and +11° for the isotype of *P. obesum* (Fig. 30). The central areas were similar in the type material of both species, being small with a thick, saddle-shaped, central raphe nodule that was bilaterally dilated (Figs 28, 29, 31 and 30, 33, respectively). The isotypes also showed similarities in the central raphe endings, which were coaxial and slightly dilated (Figs 31 and 33, respectively) and in the morphology of the



Figs 11–19. *Pleurosigma guarreranum* from the Gulf of San Matías: isotype material, Piedras Coloradas. External views, SEM. **11.** Whole valve, angled (vaulted) at the raphe. **12, 13.** Valve surface, which is verrucose. Note the undulate and overlapping central raphe fissures (Fig. 12). **14, 15.** Valve face showing apically elongated slit-like foramina. Note the central raphe fissures (Fig. 14) and the raphe bordered by a hyaline area limited by a row of small areolae (Fig. 15). **16–18.** Valve apex showing hook-shaped terminal raphe fissures. **19.** Broken valve showing loculate areolae with internal occluded pores with recessed bars (arrows) and a pair of bigger pores lacking the central bar (arrowheads). Scale bars = 50 µm (Fig. 11), 10 µm (Figs 16–18), 5 µm (Figs 12–15) and 2 µm (Fig. 19).

terminal areas, which were unilaterally dilated, funnel-shaped (Figs 28, 29, 32 and 30, 34, respectively). The striation pattern was the same for all specimens, being dominated by the oblique striae (i.e. the oblique striae are more obvious than the transverse striae), of which there were 10 in 10 µm in *P. exemptum* (Figs 31, 32) and 11 in 10 µm in *P. obesum* (Figs 33, 34); the oblique striae were slightly curved and crossed by transverse striae, of which there were 14 in 10 µm in both species. The intersection angle of the oblique striae was 95–102° in *P. exemptum* (Figs 31, 32) and 94–95° in *P. obesum* (Figs 33, 34).

Comparison of the isotypes of *P. exemptum* and *P. obesum* analysed in this study and the holotype of the same species analysed by Stidolph (2002, pl. 2, figs 1–5, and pl. 3, figs 5–9) shows that all specimens have the following features in common: a sigmoid-lanceolate valve outline, a similar raphe sternum shape (forming a simple sigmoid curve, slightly diagonal to the valve margins in the middle part of the valve, and approaching opposite convex sides towards the apices), a central area with a thick, saddle-shaped, bilaterally dilated central nodule, a similar stria pattern with slightly curved oblique striae, and a similar stria density. The valve outline and the length : width ratio of the isotype of *P. exemptum* (slide US D3092: Figs 28, 29, 31, 32; Table 1) is less similar to the holotype specimen (Stidolph, 2002, pl. 2, figs 1–5)

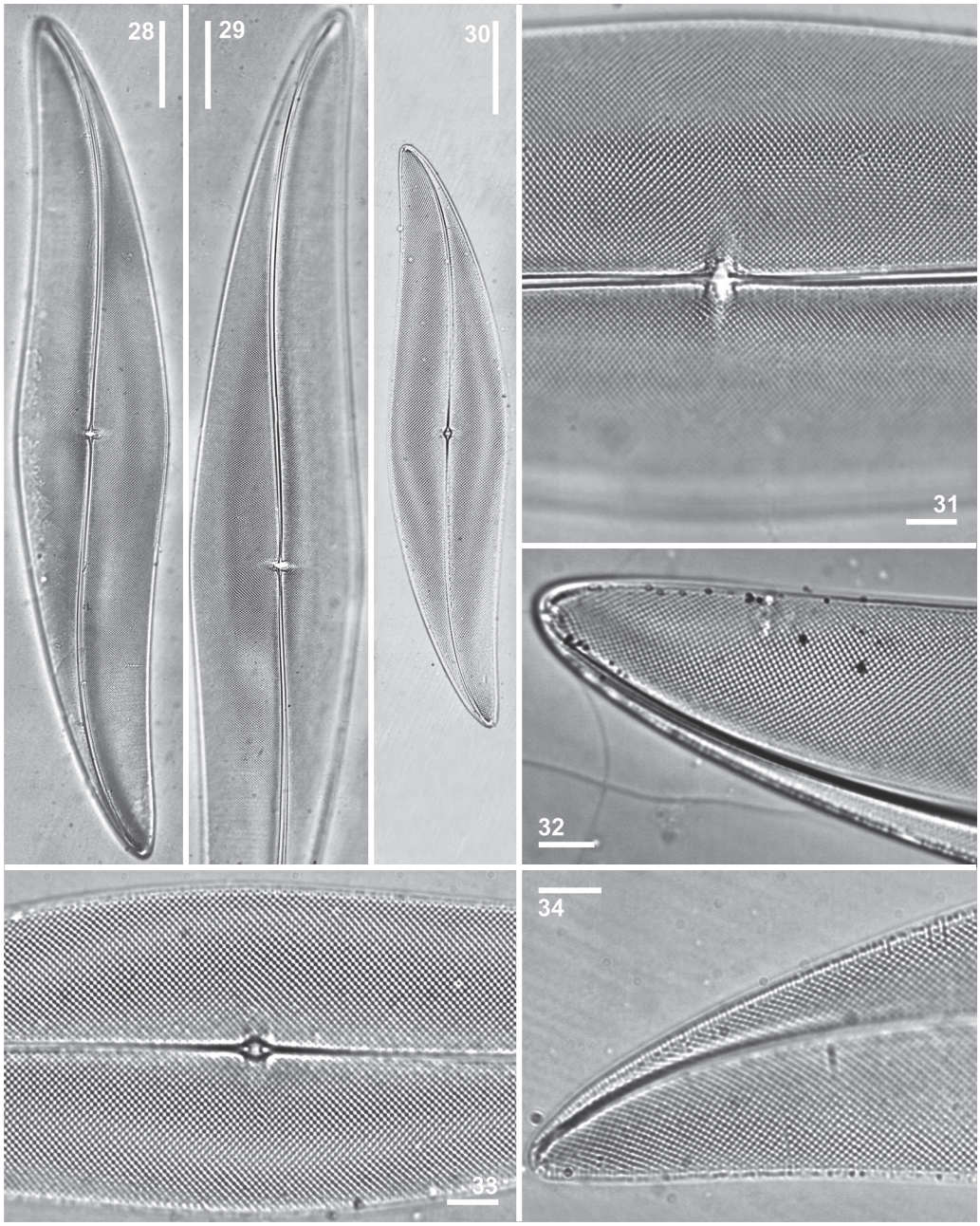


Figs 20–27. *Pleurosigma guarreranum* from the Gulf of San Matías: isotype material, Piedras Coloradas (Figs 20, 23–25, 27); paratype material, Las Grutas (Figs 21, 22, 26). Internal views, SEM. **20.** Valve showing saddle-shaped central area. **21.** Valve broken and tilted showing raphe sternum and central area. **22.** Detail of Fig. 21, showing raphe sternum bordered by a row of small areolae. **23.** Circular pores (probably occluded by hymenes) crossed by a recessed bar (arrows). Note the pairs of pores lacking the central bar (arrowheads). **24.** Detail of the saddle-shaped central area showing central bars surrounding the central nodule. Arrowheads show lateral excavations of the stauros-like structure. **25–27.** Valve apex showing polar endings finishing in helictoglossae bordered by an unperforate area; note also the discontinuous row of apical slits (Fig. 27). Scale bars = 50 µm (Fig. 20), 10 µm (Fig. 21); 5 µm (Figs 22, 24, 25, 27) and 2 µm (Figs 23, 26).

than to the holotype specimen of *P. obesum* (Stidolph, 2002, pl. 3, figs 5–9). A similar situation can be observed in the case of the raphe sternum pattern in the middle part of the valve: the isotype of *P. exemptum* (slide US D3092) agrees better with the holotype of *P. obesum* (Stidolph's 2002, fig. 5) than with the holotype of the *P. exemptum* (Stidolph's 2002, fig. 1).

Table 1 shows data on the size, length : width ratio, angle of intersection of the oblique striae, and the angle of the raphe in the isotypes and holotypes of *P. exemptum* and *P. obesum*. Analysis of the five type specimens (the only ones known that can be confirmed to represent Mann's concept of these two species) shows that there is no significant discontinuity in size between the two species; there is also no discontinuity as regards the raphe angle, the angle of intersection of the oblique striae, or the length : width ratio. Specimens of *P. exemptum* as long as those mentioned in Mann's (1925) protologue, with a putative ratio length : width of about 10, were not found.

Hence, taking into account our new LM comparison of the type materials of *Pleurosigma exemptum* and *P. obesum*, we agree with Stidolph (2002) in considering *P. obesum* as a heterotypic synonym of *P. exemptum*. Thus the range of morphological variation of the species should be enlarged in size, length/



Figs 28–34. *Pleurosigma exemptum, sensu emend.*, LM. *Pleurosigma exemptum*, isotype slides US D3092 (Fig. 28) and US D3289 (Figs 29, 31, 32); and *P. obesum* isotype slide US D3309 (Figs 30, 33, 34). **28–30.** Valves showing the central area with bilateral dilatation. **31.** Detail of central area of valve in Fig. 29. **32.** Detail of the apex of valve in Fig. 29. **33.** Central part of valve. Note the coaxial central raphe endings. **34.** Apex, showing terminal area funnel-shaped. Scale bars = 50 µm (Figs 28–30) and 10 µm (Figs 31–34).

width ratio, angle of intersection of oblique striae and raphe angle. An emended description of *P. exemptum* is as follows:

Pleurosigma exemptum A. Mann, *emend.* Stidolph (2002) and Sar, Sterrenburg & Sunesen

(Figs 28–34)

Synonym: *P. obesum* A. Mann (1925, p. 136, pl. 29, fig. 9: see also Stidolph, 2002, p. 278, figs 5–9).

Original description: A. Mann (1925, p. 134, pl. 29, figs 7, 8: see also Stidolph, 2002, p. 276, figs 1–3).

Emended description: Valves broadly sigmoid-lanceolate, vaulted, with sub-obtuse apices, 315–1160 µm long and 63–116 µm wide. Ratio length : width 5.0–7.3 (10). Raphe-sternum eccentric, with a single sigmoid curvature, crossing the centre of the valve more or less diagonally and closer to the convex sides towards the apices. Raphe angle +8° to +12°. Central area small with a thick, saddle-shaped, central raphe nodule bilaterally dilated. Internal central raphe endings coaxial and slightly dilated. Terminal areas unilaterally dilated, funnel shaped, with twisted helictoglossae. Striation pattern dominated by oblique striae, 10.0–11.2 in 10 µm, slightly curved, intersecting between 94–102°, crossed by less obvious transverse striae, 14.0–15.5 in 10 µm.

Table 1. Morphometric data obtained from specimens of *Pleurosigma guarreranum* and from type material, protologues and literature of *P.exemptum, P. obesum* and *P. decorum*. Abbreviations: nd, no data given by the original author; *, measured from pictures in the literature cited; *n* gives the number of valves measured.

Taxon	Reference	Length (µm)	Width (µm)	Length : width ratio	Transverse striae in 10 µm	Oblique striae in 10 µm	Stria angle	Characteristics of raphe sternum	Morphology of the apices	Valve outline
P. guarreranum	This study (*n* =12)	600–681	76–90	6.2–7.8	14.0–16.0	11.0–12.0	80–86°	sigmoid, approaching opposite sides towards the apices raphe angle +8° to +12°	sub-obtuse	sigmoid-lanceolate
P. exemptum	Mann (1925)	504–1160	90–116	nd *7.3	nd	10.3–11.0	in excess of 90°	sigmoid, approaching opposite sides towards the apices	somewhat blunt ends	valve broadly lanceolate, moderately sigmoid
	Stidolph (2002: type material) (*n* = 1)	758.5	108.4	7.1	15.0	10.0	100° *95–97°	sigmoid, eccentric towards the apices raphe angle +8°	sub-obtuse	sigmoid-lanceolate
	This study (type material) (*n* = 2)	500–644	92–100	5.4–6.4	14.0	10.0	95–102°	sigmoid, approaching opposite sides towards the apices raphe angle +9° to +10°	sub-obtuse	sigmoid-lanceolate
P. obesum	Mann (1925)	312–351	63–67	nd *5.0	nd	11.2	90°	sigmoid, strongly oblique to the apical axis at mid-valve, approaching opposite sides towards the ends	blunt rounded ends	valve broad, sigmoid
	Stidolph (2002: type material) (*n* = 1)	347.2	66.5	5.2	15.5	11.0	95°	sigmoid and eccentric towards ends raphe angle +12°	*sub-obtuse	*sigmoid-lanceolate
	This study (type material) (*n* = 1)	315	63	5.0	14.0	11.0	94–95°	sigmoid, approaching opposite sides towards the ends raphe angle +11°	sub-obtuse	sigmoid-lanceolate
P. decorum	Smith (1853)	248–317 *279	nd *31	nd *9.0	nd	14	nd	not central *raphe angle +15	acute	lanceolate, twisted
	Sterrenburg *et al.* (2014, in press)	254–260	27–33	7.8–9.4	18–20	13–14	81–83°	sigmoid and strongly eccentric towards the ends of the valves raphe angle +15°	sub-acute	sigmoid-lanceolate

Holotype: US D3288, 'Philippine Islands' (formerly numbered as USNM 43671).

Other specimens: US D3308 (formerly numbered as USNM 43673), US D3289, US D3292, US D3309.

Known distribution: Philippine Islands (Mann, 1925); tidal flats at Long Beach, Washington, USA (unconfirmed report by Tynni, 1986).

Separation of Pleurosigma guarreranum *from* P. exemptum

Based on the morphological data obtained from type material of *Pleurosigma exemptum*, which somewhat extend the intraspecific morphological variation known from previous data (Mann, 1925; Stidolph, 2002), some morphological differences between this species and *P. guarreranum* can be summarized. *Pleurosigma guarreranum* presents an angle of intersection of the oblique striae between 80° and 86°, while in *P. exemptum* this angle is between 94° and 102°. According to Sterrenburg (1991*a*), the angle of intersection of the oblique striae is a stable feature in *Pleurosigma*, with a small intraspecific variation (within a few degrees) and often marked interspecific variation. Thus, the difference found between the species, with ranges that are clearly separated, is sufficient to distinguish them in LM. Additionally, valves of *P. guarreranum* are slimmer and clearly taper towards the apices, while those of *P. exemptum* are broader and taper only slightly towards the apices.

Pleurosigma guarreranum belongs to the section *Formosi sensu* Peragallo (1891), where the intersection angle of the oblique striae is defined as 'somewhat less than 90°'.

Comparison with Pleurosigma decorum

The new species has a valve outline and an angle of intersection of the oblique striae similar to those of another species in the section *Formosi, Pleurosigma decorum* (Smith 1853, pl. 21, fig. 196), but *P. guarreranum* is larger, has a lower stria density and smaller raphe angle (Table 1). Furthermore, an ultrastructural comparison of *P. guarreranum* and of type material of *P. decorum* (Sterrenburg *et al*., 2014 [in press]) shows that these species share several morphological features, such as a thick and strongly elevated saddle-shaped central area, very long overlapping central raphe fissures, short hook-shaped terminal raphe fissures, and similar morphology of the internal hymen-occluded pores crossed by a recessed bar. In addition, both species have small numbers of irregularly distributed pairs of internal areolar pores that lack bars and are slightly larger. This character is also present in the type species of section *Formosi, P. formosum* (Sterrenburg *et al*., 2014 [in press]). Despite the similarities to *P. decorum, P. guarreranum* clearly differs ultrastructurally from it by having a thick unperforated area around the helictoglossa that is delimited by a row of slit-like areolae, which is absent in *P. decorum*; a more prominent and laterally excavated saddle-shaped nodule; the fact that the two symmetrical central bars delimiting the central nodule are almost parallel in *P. guarreranum* but not parallel and more curved in *P. decorum*; and the row of smaller, densely spaced areolae bordering the raphe sternum in *P. guarreranum*, which is absent in *P. decorum*.

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