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## ***Cabra reticulata* sp. nov. (Dinophyceae), a new sand-dwelling dinoflagellate from the Atlantic Ocean**

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### **Abstract:**

A new sand-dwelling dinoflagellate species, *Cabra reticulata* sp. nov., is described from sandy habitats in the south of Brittany (northwestern France). This new species possesses the characteristics of the 'unusual' genus, *Cabra* Murray et Patterson. The thecal plate formula is Po Pt 3' 1a 4" 'x' 3c ?s 5''' 1'''' (or alternatively interpreted as Po Pt 4' 0a 4" 'x' 3c ?s 5''' 1''''). Because of the strong lateral compression, cells of *C. reticulata* are frequently seen laterally and have a polygonal shape, with three prominent antapical pointed flanges and a dorsal spine in the anterior part of the hypotheca. The cingulum is ascending and incomplete. The thecal surface is ornamented with strong reticulations forming polygonal areolae, which differs from *C. matta* Murray et Patterson, the type species of the genus. In addition to their different size and shape, a detailed study of *C. reticulata* by scanning electron microscopy also revealed several different plate features. Plates of the cingulum,  $c_1$  and  $c_3$ , have no reticulations and are ornamented with shallow round areolae, while  $c_2$  is only faintly reticulated. Plate 1'''' is also characteristic because dorsally it forms a prominent pointed flange and ventrally bears a peculiar small area of densely arranged pores or tiny areolae. A similar finding has previously been described in *Roscoffia capitata* Balech. In the description of the genus, it was suggested that *Cabra* is closely related to species of the genus *Roscoffia*, and our observations strengthen this hypothesis. Prior to this study, *C. reticulata* was probably observed in the Virgin Islands, Caribbean Sea, but was tentatively identified as *Thecadinium* sp. and not fully described. Thus, *C. reticulata* appears to be present on both sides of the Atlantic Ocean and to occupy benthic habitats in temperate and tropical areas.

**Keywords:** benthic; Dinophyceae; marine; Podolampaceae; protists; Roscoffia; sand-dwelling; taxonomy

## Introduction

Benthic, sand-dwelling dinoflagellates have been known since early in the last century, when Herdman (1922, 1924a,b) published a remarkable series of papers on species causing the discoloration of sand on the Isle of Man. Then, apart from the significant work of Balech (1956), who described several new taxa from the northern part of French Brittany, these organisms were only poorly studied until the last 20-30 years. The known diversity of benthic dinoflagellates has recently increased considerably and several new taxa have been described not only from the tropics (e.g. Fukuyo, 1981; Faust, 1993; 1997; Quod *et al.*, 1999; Ten-Hage *et al.*, 2000; Faust *et al.*, 2008) but also from temperate regions (e.g. Saunders & Dodge, 1984; Murray & Patterson, 2002; Selina & Hoppenrath, 2004; Murray *et al.*, 2007; Hoppenrath & Leander, 2008; Chomérat *et al.*, 2009).

Several genera of thecate, sand-dwelling dinoflagellates have a very 'unusual' plate pattern and are monotypic, i.e. comprise only the type of the genus. These include *Adenoides* Balech 1956, *Amphidiniella* Horiguchi 1995, *Cabra* Murray et Patterson 2004, *Herdmania* Dodge 1981, *Pileodinium* Tamura et Horiguchi 2005, *Plagiodinium* Faust et Balech 1993, *Planodinium* Saunders et Dodge 1984, *Pseudothecadinium* Hoppenrath et Selina 2006, *Rhinodinium* Murray *et al.* 2006 and *Sabulodinium* Saunders et Dodge 1984. Owing to their peculiar plate patterns, showing affinities with peridinioids and gonyaulacoids, they are difficult to circumscribe and categorize based on existing taxonomic criteria. Hence, it is difficult to assign them to existing families. Even when molecular data are available, their evolutionary relationships have not always been clear (Murray *et al.*, 2006; Hoppenrath *et al.*, 2007).

Among these, the genus *Cabra* is poorly known and its single species, *Cabra matta* Murray et Patterson, has been very rarely observed. It has been found in Australia

(Murray & Patterson, 2004) and a recent study mentioned its possible presence in the Gulf of Mexico (Okolodkov *et al.*, 2007). From a taxonomic point a view, this genus has morphological affinities with the genus *Roscoffia* Balech and the family Podolompaceae Lindemann, but some characters are too divergent to support its inclusion in this family. Thus, its exact systematic position remains uncertain (Murray & Patterson, 2004; Murray *et al.*, 2006).

During the course of a study of benthic dinoflagellates in sand habitats from the south of Brittany, we encountered some specimens of a very peculiar dinoflagellate with the morphological characters of *Cabra*. Using light and scanning electron microscopy, we observed that this species differs markedly from *C. matta*. The present paper provides a detailed morphological description of *Cabra reticulata* sp. nov., revising the monotypic status of this unusual genus.

## **Material and methods**

**Study area.** Two main areas situated in the southern part of Brittany (northwestern France) were prospected. Samples from the Glénan archipelago, at the east of the Moutons Island (47°46 00' N, 4°00 00' W) and samples from the Groix Island, collected at the east of the island (47°38 00' N, 3°27 44' W), were also studied (Chomérat *et al.*, 2009). Sampling was carried out annually from 2003, during the summer period (June-September) between 5 and 13 m deep (at mid-tide). For each sample, a diver scraped the sand surface to a depth of 3 to 5 mm using 50 ml Falcon tubes in several places. After a dilution with an equal volume of seawater, the samples were fixed with acidic Lugol's solution.

**Observations.** For observation, the tubes were shaken vigorously and a subsample diluted in filtered seawater (1:1000). Then, depending on the density of organisms and

particles, 100 to 250  $\mu$ l of solution were put in sedimentation chambers and filled with filtered seawater. After complete settling, cells were isolated with a micropipette under either a Zeiss Invertoscope D (Carl Zeiss, Oberkochen, Germany) or an Olympus IX51 (Olympus, Tokyo, Japan) inverted microscope and placed between a glass slide and a coverslip. Light microscopical observations were performed with a Zeiss Universal microscope fitted with Nomarski Differential Interference Contrast (DIC) optics, a drawing tube and a digital camera, or an Olympus IX70 inverted microscope equipped with a digital camera. For scanning electron microscopy cells were isolated individually and then concentrated in 0.2 ml tubes containing water and a drop of formaldehyde to prevent development of fungi. Cells were then filtered, rinsed in deionised water and prepared according to Chomérat & Couté (2008). After gold-coating, SEM examination was carried out with a Quanta 200 (FEI, Eindhoven, The Netherlands) scanning electron microscope.

Cells were measured in LM using a calibrated micrometer on each microscope or from SEM digital micrographs using ImageJ software (Rasband, 1997–2006). SEM images were presented on a uniform background using Adobe Photoshop CS2 (V. 9.0.2, Adobe Systems). The terminology used in this paper follows Balech (1980; 1988) for thecal plates and Carbonell-Moore (1994) for the plates of the apical pore complex (APC).

## Results

### *Cabra reticulata* Chomérat et Nézan sp. nov. (Figs 1–28)

DIAGNOSIS: Organismus sine stigma, polygonius in latere visu et manifeste compressus in fronte visu. Cellulae longitudo : 44–49  $\mu\text{m}$  ; latitudo : 35–43  $\mu\text{m}$ . Epitheca deminuta ; hypotheca major cum tribus antapicalibus prominentibus acuminibus et spina in anteriore dorsale parte. Crista continuat spinam dorsalem cum cingulo curvato et concavo. Cingulum maxime ascendens imperfecte cellulam cingens, cum tribus lamellis dissimiliter ornatis. Lorica valde reticulata cum polygoniis areolis instructis aut non cum poris. Duo typi pororum. Tabulatio : (APC) 3' 1a (4' 0a) 4'' 'x' 3c ?s 5''' 1'''' . Laminae 1''' et 5''' angustae et cum duabus spinis utrinque sulco. Laminae 3''' et 4''' latae, longitudinaliter plicatae in dorsale parte. Lamina 1'''' cum in dorsale parte spina et in fronte parte minima superficie proxime poris dispositis.

Organism without stigma, polygonal in lateral view and compressed in front view. Length 44–49  $\mu\text{m}$ , width 35–43  $\mu\text{m}$ . Epitheca small, hypotheca large, with three antapical prominent pointed flanges and a spine in its anterior dorsal part. Margin between the dorsal spine and the cingulum curved and concave. Cingulum strongly ascending, incompletely encircling the cell and composed by three plates with a different ornamentation. Theca strongly reticulate, with polygonal areolae with or without pores. Two kinds of pores. Plate formula: (APC) 3' 1a (4' 0a) 4'' 'x' 3c ?s 5''' 1'''' . Plates 1''' and 5''' narrow bearing a prominent pointed flange on both sides of the sulcus. Plates 3''' and 4''' large, longitudinally folded in the dorsal part. Plate 1'''' forming an antapical dorsal pointed flange and with a small area of densely arranged pores in the ventral part.

HOLOTYPE: Fig. 12 (collected in 2007, SEM stub 08–B11 has been deposited in the National Museum of Natural History, Paris, FR).

ISOTYPES: Figs 6–7, 13.

TYPE LOCALITY: Sands of Groix Island (South Brittany, France).

ETYMOLOGY: The epithet *reticulata* refers to the reticulations on the thecal surface, forming polygonal areolae. Since the gender of this monotypic genus has not been defined by its authors and its etymology is without a botanical tradition, we use it as a feminine noun, according to article 62.3 of the International Code of Botanical Nomenclature (McNeill *et al.*, 2006).

#### Description

Cells are mostly observed in lateral view in which they appear polygonal, with three prominent pointed flanges in the posterior part and one spine in the dorsal anterior part of the hypotheca (Figs 1–3, 6–8, 12–13). The shape is somewhat different when seen from the left or the right lateral sides. In the right lateral view, the cingulum is straight and short (Figs 1–2, 12), while in the left view, it is oblique and extends the whole cell width (Figs 3, 9, 13). Cells of *C. reticulata* are strongly laterally compressed (Figs 4–5, 15, 17–18). In apical or antapical views, cells are almost oval (Figs 4–5, 17–18). They are 44–49  $\mu\text{m}$  long (mean 47.7  $\mu\text{m}$ , s.d. 1.8  $\mu\text{m}$ ,  $n = 8$ ), the dorso-ventral diameter varies from 35–43  $\mu\text{m}$  (mean 39.7  $\mu\text{m}$ , s.d. 2.4  $\mu\text{m}$ ,  $n = 8$ ), and width measured between lateral sides is 17–28  $\mu\text{m}$  (mean 20.8  $\mu\text{m}$ , s.d. 3.9  $\mu\text{m}$ ,  $n = 6$ ). The nucleus is located posteriorly, in the dorsal part of the hypotheca (Figs 1, 8–9). Apart from some coloured or colourless granules, probably food-bodies (Fig. 9), no plastids or stigma have been observed in fixed material.

The epitheca is much smaller than the hypotheca, which is relatively large (Figs 1–3, 12–13). It is asymmetrical and composed by an apical pore plate (Po), a cover plate

(Pt), three apical plates, an intercalary plate, four precingular plates and a 'x' plate, since the cingulum does not completely encircle the cell. The apical pore complex (APC) appears to be formed by a pore plate (Po) that is almost oval and bears a ring of small pores and a hook-shaped cover plate (Pt), lying on a raised protrusion in the centre of Po (Figs 22–23). Plates of the apical series (') are very different, 1' being very narrow, long and with a short contact with the apical area (Fig. 24), while the others are small and surround the APC (Figs 22–23). Plates that encircle the apical area on its left and right sides are 'C'-shaped, while the 1a plate, located dorsally, has short contacts with 2' and 3' plates (Fig. 22). In some specimens, this plate is in contact with the APC (Fig. 23). Plates 1'' and 2'' are rather large, trapezoidal and form the left side of the epitheca (Fig. 17). Plates 3'' and 4'' are smaller and form the right side of the epitheca (Figs 16–17). The 'x' plate is long and occupies the position of a fifth precingular plate, but as the cingulum is not closed, part of its right side is in contact with the postcingular series (''') and cannot therefore be a true precingular (Figs 10, 16, 27). The cingulum is strongly ascending, resulting in its oblique orientation in left lateral view (Figs 3, 13). It is bordered by short smooth lists that form a gutter containing pores on plates of the precingular and postcingular series (Figs 20, 27). Three plates compose the cingulum, c<sub>1</sub> and c<sub>3</sub> being larger than c<sub>2</sub>, which is rather short and located on the left side of the cell (Fig. 26). The sulcus is rather short and indents the hypotheca obliquely, about one third of the dorsoventral diameter (Figs 5, 18). It is deep and narrow (Figs 14, 18), so that it is impossible to identify sulcal plates in SEM. The hypotheca is formed of only two plate series: five postcingular plates and one antapical. Three postcingular plates (1''', 2''' and 3''') form the left lateral side of the cell (Figs 3, 13, 18), while only two (4''' and 5''') form the right side (Figs 2, 12, 18). Plate 1''' is longer than wide, and forms the left side of the sulcal area, bearing a narrow left list (Figs 12, 14). Posteriorly, this plate forms a

prominent pointed flange (Figs 14, 21). Plate 2''' is rather large and quadrangular (Figs 3, 13). Plate 3''' is large, pentagonal, and dorsally bears a spine in its anterior part (Figs 19–20). The margin joining this spine to the cingulum is concave (Figs 3, 13, 19). This plate is folded longitudinally in its median part, forming an angle so that the cell tapers dorsally (Figs 13, 18–19). Plate 4''' is the largest plate of the theca, covering almost all the right lateral side of the hypotheca. It is six-sided, has a long contact with plate 'x' (Figs 12, 16). Plate 5''' is longer than wide, bears a narrow right sulcal list, and posteriorly forms a prominent pointed flange (Figs 12, 14, 21). The unique antapical plate 1'''' is longer than wide, polygonal, and contacts all plates of the postcingular series and the posterior sulcal plate (Figs 5, 18, 25). Plate 1'''' forms a prominent, dorsally directed, pointed flange (Fig. 21).

Most plates, except the narrow 1', which is smooth (Fig. 24), are strongly ornamented with reticulations, forming shallow polygonal areolae with raised borders (Figs 11–28). Some areolae contain one or several pores (Fig. 28). Cingular plates are ornamented but the pattern is different from the other plates of the theca. Plates  $c_1$  and  $c_3$  are areolated, with shallow circular depressions without raised borders and devoid of pores (Figs 26–27). In contrast, plate  $c_2$  has only faint reticulations and its surface has very shallow golf ball-like dimples (Figs 20, 26). Pores are of two types: large and small. Larger pores ( $0.27 \pm 0.03 \mu\text{m}$ ), probably trichocyst pores, are scattered on the surface of the theca and form marginal rows (Fig. 24). Alongside the borders of the cingulum, large pores are aligned in one or two rows in the gutter formed by elongated areolae (Fig. 26). Small pores ( $0.14 \pm 0.02 \mu\text{m}$ ) are scattered over the surface and are sometimes present in the same areolae as large pores (Fig. 28). Some are on the raised reticulations, but this is rare (Fig. 28). An unusual area of about twenty densely arranged pores, or tiny areolae, is observed near the sulcus curve on plate 1'''' (Fig. 25).



This was not observed elsewhere on the cell. In some cells, large (up to 8  $\mu\text{m}$ ) megacytic growth bands are present (Figs. 15, 18, 21). They are smooth and striated transversely by thickenings that appear like rungs of a ladder (Figs 15, 18, 21). They are always devoid of ornamentation and pores (Figs 15, 18, 25).

Cells of *C. reticulata* were found in the sand from the two locations and in samples from different years. The abundance of this species was always very low in comparison with benthic diatoms and other sand-dwelling dinoflagellates, such as *Prorocentrum* spp. Of the latter, the most abundant species was the recently described *Prorocentrum tsawwassenense* Hoppenrath et Leander (Hoppenrath & Leander, 2008).

## **Discussion**

Taxonomy of *Cabra reticulata* and differences from *C. matta*

Prior to this study, our new species may have been observed by Carlson (1984) who illustrated some specimens of *Thecadinium* sp. with a similar shape and a reticulate ornamentation from the Virgin Islands, Caribbean Sea, (cf. figs k-p, pl. VII in Carlson, 1984). Although Carlson (1984) mentioned that this new taxon would be described, no ICBN effective publication (McNeill *et al.*, 2006) has been found and this is still a 'new' species. Specimens from the Caribbean Sea were somewhat smaller than those from Brittany (Table 1), but apart from their size, they are in perfect agreement with the description of *C. reticulata*. Nevertheless, we never observed cells with such prominent antapical pointed flanges as represented by Carlson (Carlson, 1984). He also interpreted the thecal plates quite differently although he was aware that the plate pattern did not correspond to any existing genus. For this reason, he placed this species only tentatively in the genus *Thecadinium*.

At present, the genus *Cabra* has only one known species, *Cabra matta* (Murray & Patterson, 2004), but from the detailed morphological study of *C. reticulata*, there is evidence that it also belongs to this genus (Table 1). However, there are several discrepancies between these species. *Cabra matta* is smaller and has a convex rounded dorsal margin, while *C. reticulata* has a dorsal margin with distinct edges, and the small dorsal edge between the dorsal spine and the cingulum is concave. One of the most conspicuous discrepancies between these species is their thecal ornamentation. *Cabra matta* has shallow round depressions (areolae) without raised sides, whereas *C. reticulata* possesses strong reticulations that form polygonal areolae. This surface ornamentation is comparable to some other benthic species, such as *Roscoffia capitata* Balech (Balech, 1956), *Sinophysia canaliculata* Quod (Quod *et al.*, 1999), *Coolia areolata* Ten-Hage, Turquet, Quod et Couté (Ten-Hage *et al.*, 2000), and to the ubiquitous planktonic species *Gonyaulax grindleyi* Reinecke [= *Protoceratium reticulatum* (Claparède et Lachmann) Bütschli] (Faust, 2000). The ornamentation of cingular plates, which differs from the rest of the theca and also among plates of the series, was not reported for *C. matta*, apart from a note on the absence of pores (Murray & Patterson, 2004). The presence of two kinds of pores, as well as the area of densely arranged pores or tiny areolae on the antapical plate were also not reported for *C. matta* (Table 1). In addition, the thecal pattern is not exactly the same between these two species.

First, we observed specimens in which the interpretation of the apical plates is not obvious because the 1a equivalent plate is displaced and can be considered as a 3' plate owing to its contact with the APC. As a consequence, the epithecal plate formula can be interpreted quite differently, depending on the 1a plate contacts (Table 1). This feature has not been shown yet in *C. matta*. Moreover, we observed that the 3''' plate is

wider than the 2''' in *C. reticulata*, while it is the opposite in *C. matta*. So, the suture between 2''' and 3''' is more ventral and distant from the suture  $c_1/c_2$  in *C. reticulata* than in *C. matta*. Approximately at the position of the 2'''/3''' suture in *C. matta*, the 3''' plate in *C. reticulata* is longitudinally folded, while no fold was reported in *C. matta*. Finally, the 2''' plate of *C. matta* appears to be in contact with the sulcus (cf. Fig. 18 in Murray & Patterson, 2004) but in *C. reticulata*, only plates 1''', 5''' and 1'''' contact the furrow. Based on all these comparisons, it appears that *C. reticulata* is a new species.

Like *C. matta*, which was described as heterotrophic, our observations on fixed material did not reveal the presence of any plastids, but the non-photosynthetic status and heterotrophy of *C. reticulata* need to be validated.

Relationships with species of other genera.

As reported for the genus, *C. reticulata* is similar to species of the genus *Roscoffia*, with a general plate pattern of Po 3-4' 0-1a 5'' 3c 3-4s 5''' 1'''' (Balech, 1956; Hoppenrath & Elbrächter, 1998; Murray & Patterson, 2004). The epithecal pattern of *C. reticulata* shows affinities with *R. minor* described with 3' and 1a plates (Horiguchi & Kubo, 1997) and with *R. capitata*, having only four or three apical and no intercalary plates (Balech, 1956; Hoppenrath & Elbrächter, 1998). In addition to the very similar hypothecal plate arrangement, the presence of three cingular plates, the narrow first apical plate and the ascending cingulum described for *C. matta* (Murray & Patterson, 2004), other characters of *C. reticulata* strengthen the relationship with *Roscoffia*, especially *R. capitata*. The different cingular plate ornamentation is similar to the observations on *R. capitata* made by Hoppenrath & Elbrächter (1998) who found that  $c_2$  is smooth, whereas  $c_1$  and  $c_3$  are areolated. In *C. reticulata*,  $c_2$  also differs from  $c_1$  and  $c_3$ , having only faint reticulations and no areolae. Moreover, the peculiar area of very

densely arranged pore-like structures on the antapical plate was also reported in *R. capitata*. Balech (1956) first described this area of small areolae resembling the ornamentation of some *Coscinodiscus* species, and referred to it as a 'petit pentagone' or 'tache'. Hoppenrath & Elbrächter (1998) observed it in SEM, demonstrating the constancy of this feature. In *C. reticulata*, it is present and occupies roughly the same position on the 1<sup>'''</sup> plate, which suggests a strong affinity with *Roscoffia capitata*.

However, as for *C. matta*, some characters of *C. reticulata* differ from *Roscoffia*. In *Cabra*, the cingulum is incomplete and does not encircle the cell, and an 'x' plate is present in the epitheca, which is not found in *Roscoffia*. Moreover, as in *C. matta*, due to the narrow and deep sulcus, the sulcal plate pattern of *C. reticulata* could not be elucidated. The systematic position of *Roscoffia* has long been problematic and, using a SSU rDNA study, it has been shown to be a sister species of the monotypic genus, *Lessardia* Saldarriaga et Taylor (Saldarriaga *et al.*, 2003). *Lessardia* belongs to the family Podolampaceae and this phylogenetic study seems to confirm the suggested relationship of *Roscoffia* to this family (Horiguchi & Kubo, 1997; Hoppenrath & Elbrächter, 1998). Considering the typical plate formula of the Podolampaceae, given as Po Pt X 3' 1a 5'' 3c 4-5s 4-5''' 1'''' (Carbonell-Moore, 1994), *Cabra* species have affinities with this family with respect to the number of cingular plates and the hypothecal pattern. The most obvious discrepancy between *Cabra* and the Podolampaceae concerns the epithecal pattern. In *C. reticulata*, as in *C. matta* (depending on the interpretation), the APC is very similar to that observed in the Podolampaceae, except that the canal plate (X) seems to be lacking. However, because of the shape of plate 2', it remains possible that this is present and hidden in *C. reticulata*. Based on the variation in the apical/intercalary series, *C. reticulata* either agrees with *C. matta* in having four apical plates, or with the Podolampaceae, having

three apical and one intercalary plates, although there are examples in this family where the ‘dorsal plate’ touching the dorsal precingular plates is interpreted as an intercalary plate, even if it is in contact with the APC (Carbonell-Moore, 1994). Given the morphological affinities of *Cabra* with the Podolampaceae, we follow this interpretation of the plate pattern but this may need to be revised if new data become available. The apparent difference between *Cabra* and the Podolampaceae in the number of precingular plates can result from the interpretation of the plate ‘x’. In other genera, such as *Amphidiniopsis*, such a plate has been considered an additional precingular plate (Toriumi *et al.*, 2002). In *Cabra*, it could be equivalent (homologue) to a displaced fifth precingular, and the number of plates in the series would then be in agreement with the Podolampaceae. Since species of the genus *Lissodinium* Matzenauer (also this family) are laterally compressed, *Cabra* could be closely related to this genus (Murray & Patterson, 2004). Nevertheless, in spite of these similarities based on plate formulae, strong discrepancies exist between *Cabra* and the Podolampaceae, the most conspicuous being the deep cingulum present in both *Cabra* species.

According to Fensome *et al.* (1993), the Podolampaceae comprise ‘Peridiniineans in which the cingulum is not readily apparent but in which a series of three plates occur posterior to the equator of the cell’. It is obviously very different in *Cabra*. For this reason, and until new data argue differently, it is not possible to place *Cabra* in the family, and we follow the proposition of Murray & Patterson (2004) to keep it in the order Peridinales, family uncertain.

Distribution of *Cabra* species

With respect to the geographic distribution of *Cabra* species, *C. matta* has only very scarcely been reported. Except by its authors, who discovered it in Australia, it has only otherwise been observed in the Gulf of Mexico, although the identification is doubtful as the authors indicated its name with a question mark (Okolodkov *et al.*, 2007). *Cabra reticulata* has been found in sediments from the south of Brittany (this study), and if we consider the species observed by Carlson (1984) to be the same, also in the Caribbean Sea. These observations concern both sides of the Atlantic Ocean, which is an interesting fact. For this reason, it may be interesting to make a detailed comparison among specimens from various locations, as it has been done for another benthic species, *Sabulodinium undulatum* Dodge et Saunders (Hoppenrath *et al.*, 2007).

In our samples, *C. reticulata* was very rare among other abundant benthic diatoms and dinoflagellates, but it has been observed in sediment from two locations in the South of Brittany. Carlson (1984) also mentioned that it was rarely observed at two stations, associated with sediment and macroalgae and at different times. Similarly, *C. matta* was rarely observed and its authors collected it in only three samples (Murray & Patterson, 2004). Thus, *Cabra* species are infrequently observed but it cannot be excluded that some others are still to be discovered. To assign the genus to a particular family, further studies are required, using molecular, ultrastructural or biochemical tools, since morphology is obviously not sufficient, but owing to the rarity of these organisms, such works is likely to be difficult to conduct.

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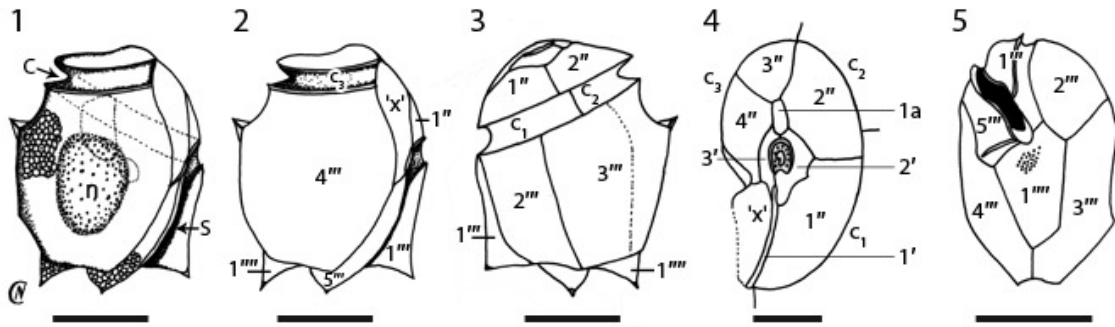
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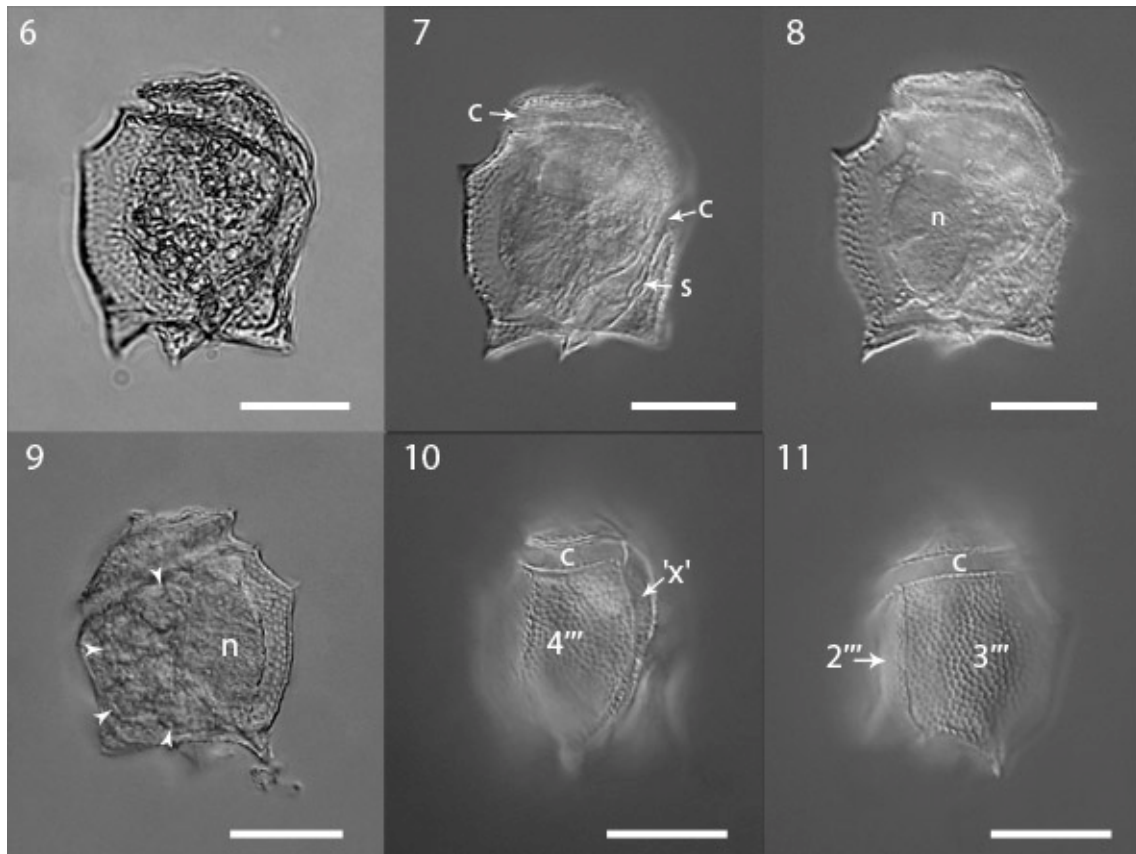
Table 1: Morphological features of *Cabra reticulata* sp. nov. compared with *C. matta*

Species	<i>Cabra reticulata</i> <sup>a, b</sup>	<i>Cabra matta</i> <sup>c</sup>
Length (µm)	44 – 49 <sup>a</sup> 39 <sup>b</sup>	32 – 40
Dorsoventral diameter (µm)	35 – 43 <sup>a</sup> 31 <sup>b</sup>	23 – 33
Epitheca	Po Pt 3' 1a 4'' 'x' (alternatively Po Pt 4' 0a 4'' 'x')	Po 4' 4'' 'x'
Cingulum	3c	3c
Sulcus	?s	?s
Hypotheca	5''' 1''''	5''' 1''''
Thecal ornamentation	Reticulations forming polygonal areolae with raised borders on thecal plates, except the cingulum shallow round areolae on c <sub>1</sub> and c <sub>3</sub> c <sub>2</sub> smooth, embossed	shallow circular depressions
Pores	Two types: large (0.27 ± 0.03 µm) and small (0.14 ± 0.02 µm) Group of densely arranged pores (or tiny areolae) on plate 1''''	One type (0.15 µm) –
Megacytic growth bands	Smooth, striated transversely	smooth
Spines	3 antapical 1 dorsal	3 antapical 1 dorsal
Distribution	temperate <sup>a</sup> , tropical <sup>b</sup>	temperate <sup>c</sup> , possibly tropical <sup>d</sup>

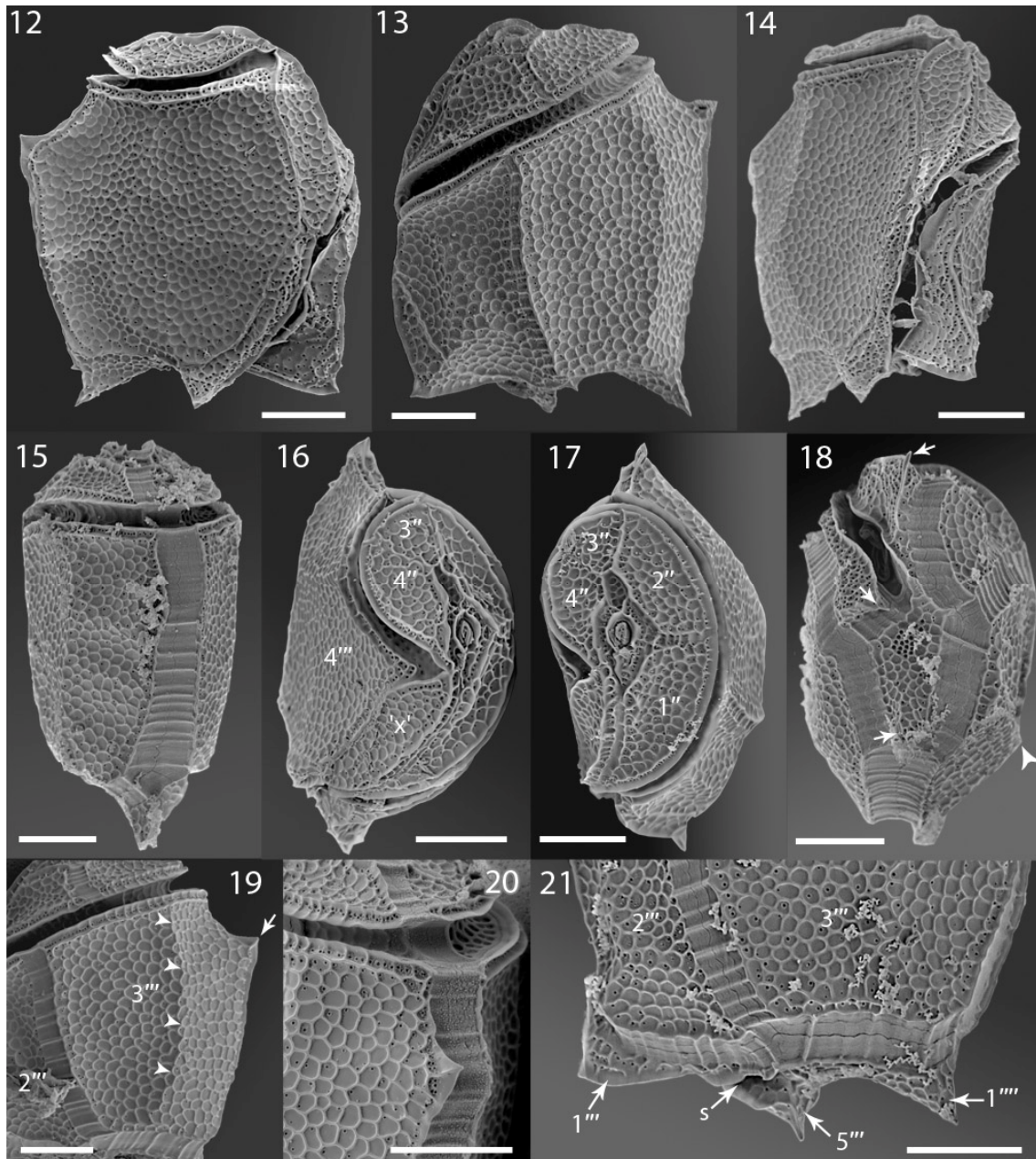
<sup>a</sup>this study; <sup>b</sup>Carlson, 1984 (as *Thecadinium* sp.); <sup>c</sup>Murray & Patterson, 2004; <sup>d</sup>Okolodkov *et al.*, 2007.



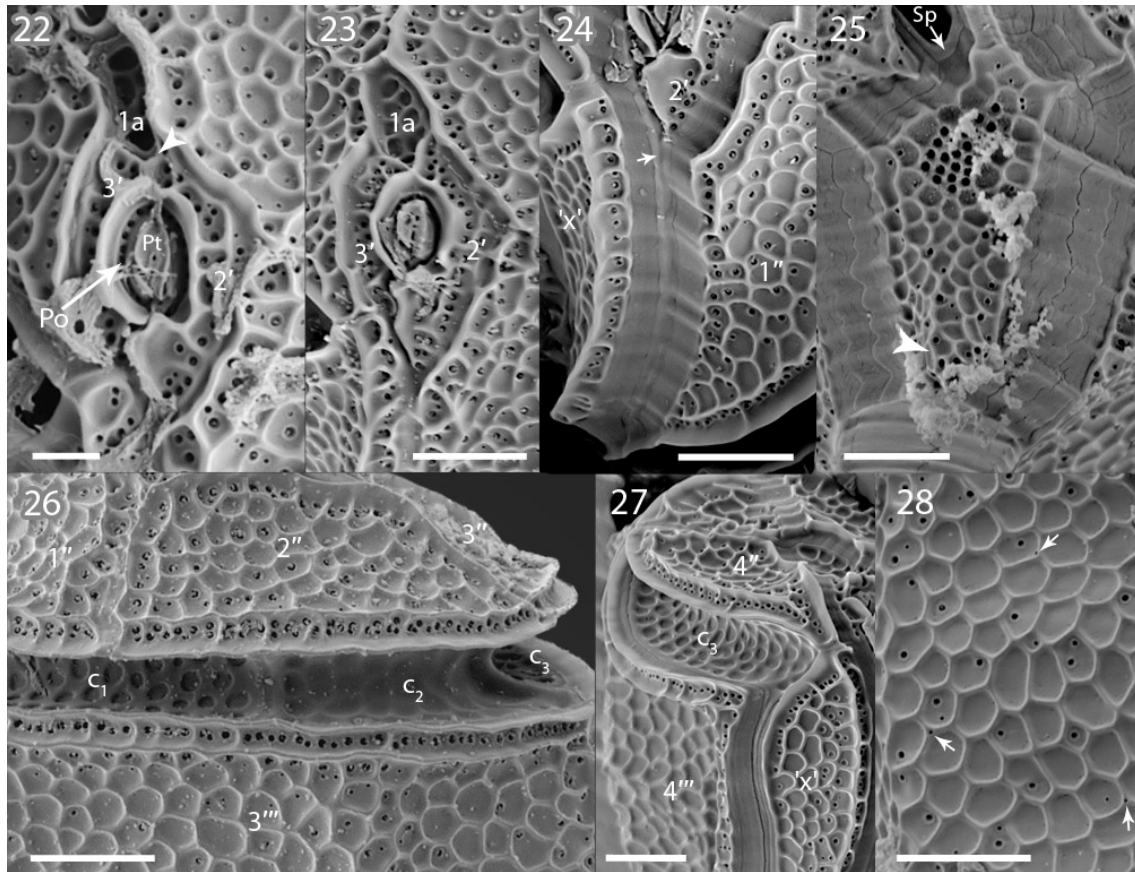
Figs 1–5. *Cabra reticulata* Chomérat *et* Nézan sp. nov.: line drawings. Fig. 1. Right lateral view showing the outline shape, the location of the cingulum (C), the sulcus (S) and the nucleus (n). Figs 2–5. Drawings showing the thecal plates arrangement. Fig. 2. Right lateral view. Fig. 3. Left lateral view. Fig. 4. Apical view. Fig. 5. Antapical view. Scale bars represent: Figs 1–3, 5, 10  $\mu$ m; Fig. 4, 5  $\mu$ m.



Figs 6–11. *Cabra reticulata* Chomérat *et* Nézan sp. nov.: photomicrographs in light microscopy. Fig. 6. Cell viewed laterally in bright field. Fig. 7. Cell with focus on the sulcus (s) and parts of the cingulum (c). Fig. 8. Cell in left lateral view with focus on the nucleus (n). Fig. 9. Cell in right lateral view showing the nucleus (n) and globular bodies (food vacuoles ?) in the cytoplasm (arrowheads). Fig. 10. Cell in ventral right lateral view with focus on plate 4'''. Note the right-end of the cingulum (C) and the 'x' plate of the epitheca. Fig. 11. Cell in left lateral view. Scale bars represent 20  $\mu$ m.



Figs 12–21. *Cabra reticulata* Chomérat *et* Nézan sp. nov.: photomicrographs in scanning electron microscopy. Fig. 12. Cell in right-lateral view (holotype). Fig. 13. Cell in left-lateral view. Note the oblique cingulum. Fig. 14. Ventro- right lateral view showing the cingulum and the sulcus. Fig. 15. Left dorsal view. Note the large megacytic growth band striated transversally. Fig. 16. Right apical view showing the cingulum displacement and the 'x' plate of the epitheca. Fig. 17. Apical view. Fig. 18. Antapical view. Note the position of the antapical pointed flanges (arrows) and the fold on plate 3''' (arrowhead). Fig. 19. Detail of the 3''' plate showing the longitudinal fold (arrowheads) and the dorsal spine (arrow). Fig. 20. Detail of the dorsal spine supported by the left lateral plate 3''' of the hypotheca. Fig. 21. Detail of the three antapical pointed flanges, seen from the left side (s: sulcus). Scale bars represent 10  $\mu$ m.



Figs 22–28. Details of *Cabra reticulata* Chomérat *et* Nézan sp. nov. in SEM. Figs 22–23. Apical pore complex of two different cells. Fig. 22. Specimen with a 1a plate distant from the APC (arrowhead). Note the organization of the APC formed by a pore plate (Po) with a ring of pores and a cover plate (Pt) on a raised protrusion in the centre of Po. Fig. 23. Specimen with a 1a plate contacting shortly the APC and which could be interpreted as an apical plate. Fig. 24. First apical plate 1' (arrow). Note the absence of ornamentation. Fig. 25. Detail of plate 1''' forming dorsally the antapical dorsal spine (arrowhead) and bearing ventrally a small area of very densely arranged pores or tiny areolae. Note the posterior sulcal plate (Sp). Fig. 26. Detail of the cingulum in the left dorsal view showing plate  $c_2$  with a faint reticulation while  $c_1$  and  $c_3$  have round and shallow areolae. Note the presence of elongated areolae and a row of marginal large pores on plates bordering the cingulum. Fig. 27. Ventral view of the right end of the cingulum and of the anterior part of plate 'x'. Fig. 28. Detail of the reticulated surface of thecal plates. Note the presence of large pores in some areaolae while small pores are in areaolae or on the reticulations (arrows). Scale bars represent: Fig. 22, 2  $\mu\text{m}$ ; Figs 23–28, 5  $\mu\text{m}$ .