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ORIGINAL PAPER

Morphology and taxonomy of a new marine sand-dwelling *Amphidiniopsis* species (Dinophyceae, Peridiniales), *A. aculeata* sp. nov., from Cap Feret, France

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Abstract A new dinoflagellate species within the benthic, heterotrophic, and thecate genus *Amphidiniopsis* was discovered in a fixed sediment sample taken at Cap Feret, France, in 1994. The cells within this sample were manually isolated and characterized by light and scanning electron microscopy. The thecal plate pattern and overall ornamentation demonstrate that this taxon is different from all other described species within the genus. *Amphidiniopsis aculeata* sp. nov. is dorsoventrally flattened, 37.5-40.3 μm long and 31.7-35.3 μm wide. The plate formula is APC 4′ 2a 7″ 3c 5s 5‴ 2⁗. The thecal plates possess pores of two different size classes and are ornamented with conspicuous spines of different lengths.

Keywords *Amphidiniopsis* · Benthic · Biodiversity · Dinoflagellates · Morphology · Taxonomy

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Introduction

The genus *Amphidiniopsis* was introduced by Woloszynska (1928) with the type species *A. kofoidii*. The history of records, nomenclatural changes and classification schemes of *Amphidiniopsis* species were summarized in Hoppenrath (2000). The genus includes 13 validly described species: *A. arenaria* Hoppenrath, *A. cristata* Hoppenrath, *A. dentata* Hoppenrath, *A. galericulata* Hoppenrath, *A. hexagona* Yoshimatsu, Toriumi et Dodge, *A. hirsutum* (Balech) Dodge, *A. kofoidii* Woloszynska, *A. korewalensis* Murray et Patterson, *A. pectinaria* Toriumi, Yoshimatu et Dodge, *A. sibbaldii* Nicholls, *A. swedmarkii* (Balech) Dodge, *A. urnaeformis* Gail 1950, and *A. uroensis* Toriumi, Yoshimatu et Dodge (Balech 1956; Dodge 1982; Gail 1950; Hoppenrath 2000; Murray and Patterson 2002; Nicholls 1998, 1999; Toriumi et al. 2002; Yoshimatsu et al. 2000). Records of two additional species exist, but these have yet to be formally named. For instance, Yoshimatsu et al. (2000) published a taxon named "*A. swedmarkii*", but as explained earlier (Hoppenrath 2000; Selina and Hoppenrath 2007), this species was misidentified. Silva (1952) reported a species—referred to as "*Amphidinium* sp."—that is very similar to *A. hirsutum*; this was also recognized by Balech (1956, footnote p. 47). All of these species are heterotrophic sand-dwellers with diverse cell morphologies, including morphological variability within the same species (Bursa 1963; Selina and Hoppenrath 2007).

Records of marine benthic, sand-dwelling dinoflagellates from France are rare. Balech (1956) was the first to investigate this habitat in Roscoff, and he found several new species and genera of dinoflagellates, such as *Adenoides* Balech (Hoppenrath et al. 2003) and *Roscoffia*

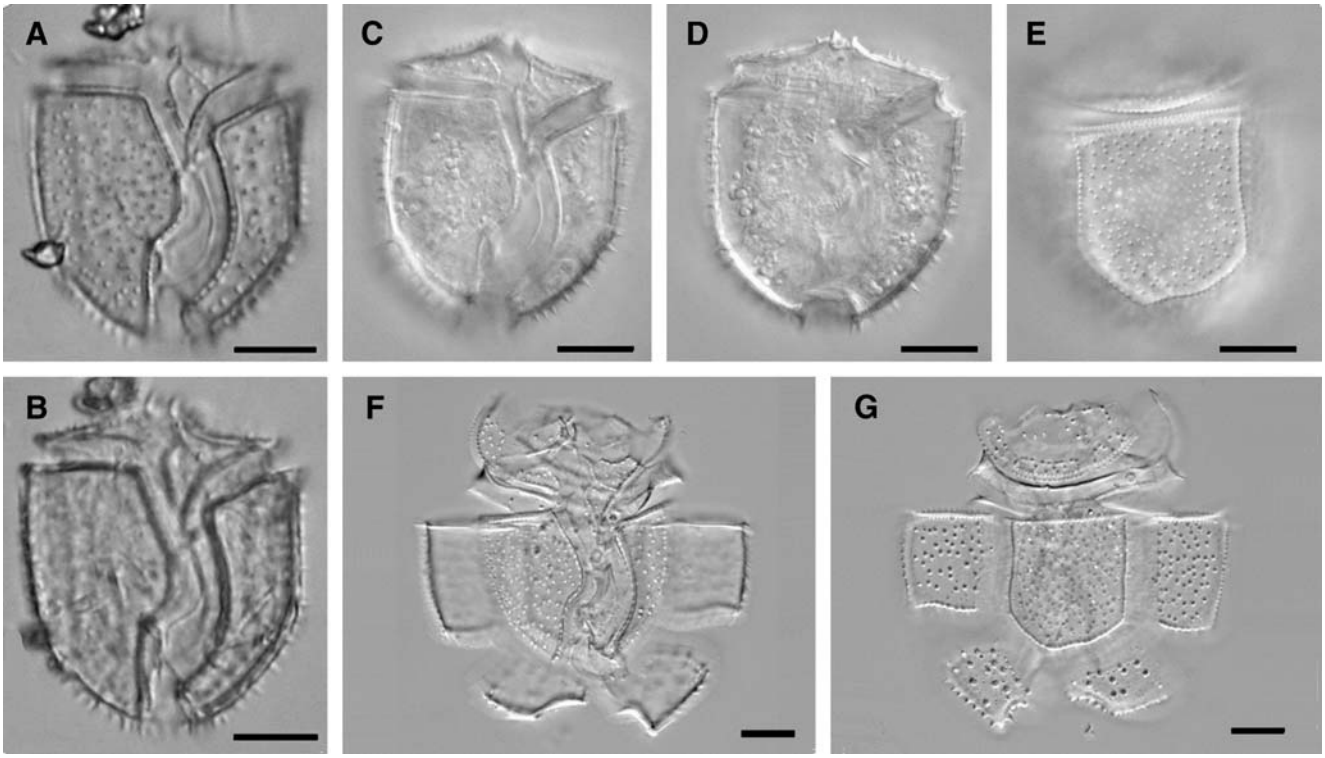


Fig. 1 Light micrographs of *Amphidiniopsis aculeata* sp. nov. **A, B** Ventral view of the same cell **A** Focus on ventral cell surface **B** Mid-cell focus **C–E** Same cell **C** Ventral view **D** Ventral view, mid-cell focus **E** Dorsal view, focus on dorsal cell surface **F, G** Smashed cell showing the thecal plates **F** Ventral view **G** Dorsal view*Scale bars* 10 μm

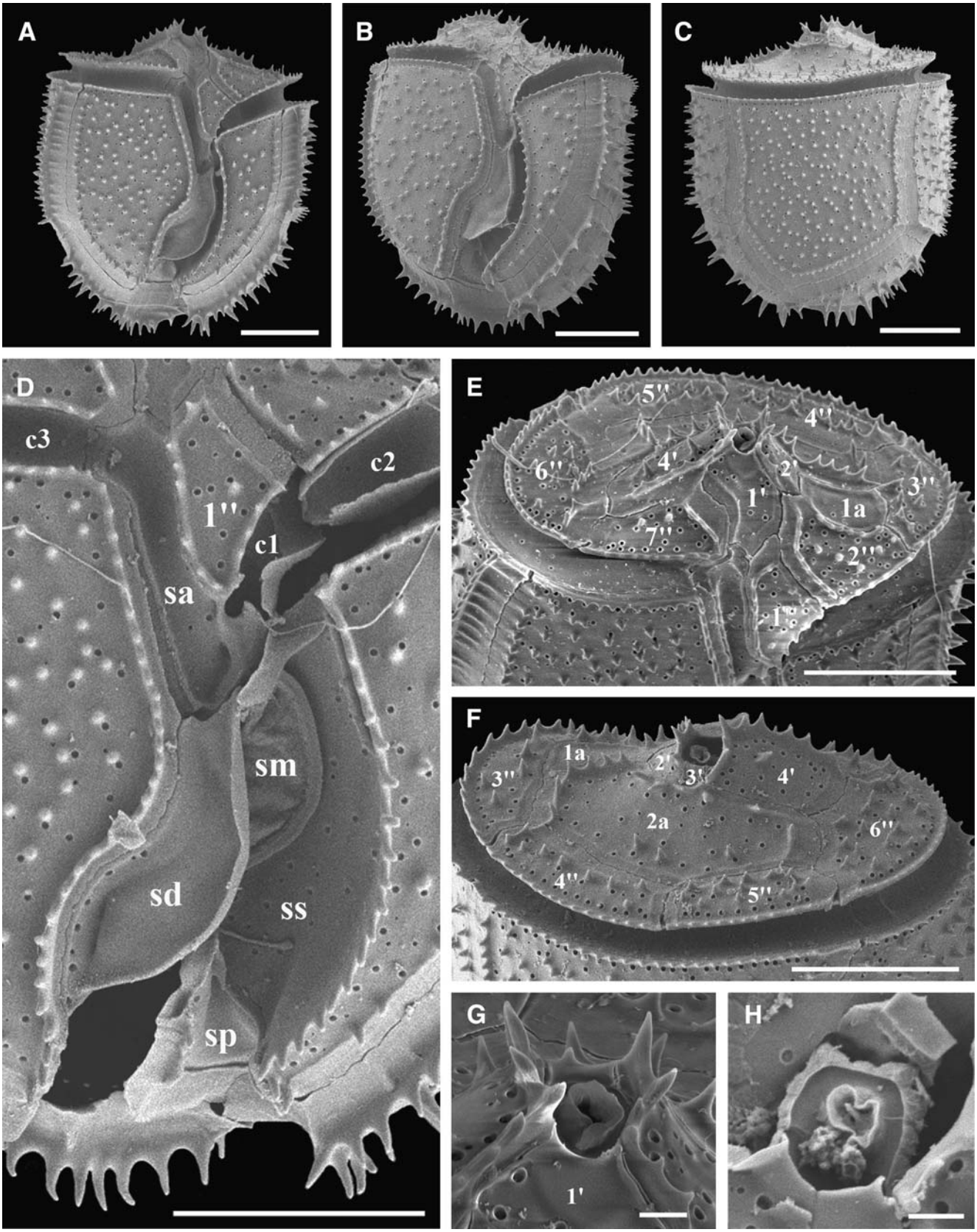
Balech (Hoppenrath and Elbrächter 1998). Dragesco (1965) subsequently studied sand-dwelling flagellates collected from the beaches of Brittany. Dodge and his colleagues made some additional discoveries of new benthic taxa in samples from Northern France (Dodge and Lewis 1986; Saunders and Dodge 1984), such as *Planodinium* Saunders et Dodge and *Sabulodinium* Saunders et Dodge (Hoppenrath et al. 2007). A few benthic species have also been recorded from the coast of Normandy (Paulmier 1992).

This study addresses a new taxon that is similar in many respects to *A. hirsutum* and *A. swedmarkii*, and that was recorded previously but was either misclassified (Silva 1952) or misidentified (Paulmier 1992). This new *Amphidiniopsis* species was rediscovered in a fixed, sediment sample taken in 1994 and is formally described here using light and scanning electron microscopy (SEM).

Material and methods

The sediment sample was collected by R.P.T. Koeman on July 29, 1994 on Cap Feret beach (44°38′25.10″N 01°15′ 36.17″W). The sand was taken from a moist spot, with a faint brownish discoloration (caused by the presence of diatoms and photosynthetic dinoflagellates), near the lower eulittoral tidal zone. The upper centimetre of sand was obtained with a spoon and deposited into a bottle (approximately 50 ml of sand was collected in total). An equal volume of filtered seawater was added to the sand and subsequently stirred vigorously for 15 s. The supernatant was quickly decanted into a separate bottle and fixed with Lugol's solution. The sample was stored in the dark at room temperature, and a subsample was reinvestigated in 2006/2007. The fixed material was screened under an inverted light microscope at 40–250× magnification (Leica DMIL, Wetzlar, Germany), and single cells were isolated in preparation for differential interference contrast (DIC) optics and high-magnification photomicroscopy. Light micrographs were made using a Zeiss Axioplan 2 imaging microscope (Carl-Zeiss, Oberkochen, Germany) connected to a Leica DC500 color digital camera (Leica, Wetzlar, Germany).

Fig. 2 Scanning electron micrographs of *Amphidiniopsis aculeata* sp. nov. **A, B** Ventral view **C** Dorsal view **D** Detail of the sulcus showing all sucal plates **E** Ventral view of the epitheca **F** Dorsal view of the epitheca **G** Outside view of the apical pore complex **H** Inside view of the pore plate *Scale bars* 10 μm in **A–F**, 1 μm in **G, H** *c1, c2, c3* first, second, third cingular plate; *sa* anterior sulcal plate; *sd* right sulcal plate; *sm* middle sulcal plate; *ss* left sulcal plate; *sp* posterior sulcal plate; *1′* first apical plate; *2′* second apical plate; *3′* third apical plate; *4′* fourth apical plate; *1a* first anterior intercalary plate; *2a* second anterior intercalary plate; *1″–7″* first to seventh precingular plate ▶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Cells prepared for SEM were transferred onto a 5-µm polycarbonate membrane filter (Corning Separations Div., Acton, Mass.), washed with distilled water and gradually dehydrated with increasing concentrations of ethanol. After dehydration in 100% ethanol, the cells were rinsed twice in hexamethyldisilazane (HMDS) and then dried for 5 min at 60°C. The dried cells were mounted on an aluminum SEM stub, sputter-coated with gold and examined under a Hitachi S4700 Scanning Electron Microscope (Hitachi, Tokyo, Japan). Some SEM images were placed on a black background using Adobe Photoshop 6.0 (Adobe Systems, San Jose, Calif.).

About 20 cells were observed in the light microscope, but only five cells were measured from scanning electron micrographs.

Results

Cells are rectangular, rounded posteriorly, dorsoventrally flattened, 37.5-40.3 µm long and 31.7-35.3 µm wide (Fig. 1A–E). The small epitheca is slightly narrower than the hypotheca and is cap-like and pointed at the anterior end (Fig. 1B–D). The sulcus is characteristically curved and ascending about two cingular widths (Figs. 1A,C, 2A). There are conspicuous spiny lists at the thecal plate margins, and are especially visible at the lateral and posterior cell border at mid cell focus (Fig. 2, 4). The spiny appearance of the apical pore area is also striking (Fig. 1B,D). Thecal plate morphologies, especially plate borders, are visible in the light microscope in both intact and crushed cells (Fig. 1A,B,D–G).

Molecular sequence data (e.g. DNA barcodes) and morphological data pertaining to the positions of the nucleus and pusules are not reported because only the robust theca of dead cells was available for investigation.

The epithecal and hypothecal plates are all ornamented with spines, except for the first anterior intercalary plate (Fig. 2A–F). The spines vary in length. Spiny lists are present on the margins of the epithecal and hypothecal plates (Fig. 2A–G). Pores of two size classes are scattered over all of the plates (Fig. 2A–H). Large pores are 0.23-0.28 µm in diameter and small pores are 0.10-0.14 µm in diameter. Rows of large pores are arranged along the precingular and postcingular margins of the precingular and postcingular plates, respectively (Fig. 2E,F). The cingular and sulcal plates are smooth with scattered pores (Fig. 2A–F). The sutures are broad and free of spines (e.g. Fig. 2E).

The plate formula is APC 4′ 2a 7″ 3c 5s 5‴ 2⁗ (Figs. 2A–F, 3A c). The epitheca consists of 14 plates (Figs. 2E–G, 3A; Table 1). The almost circular apical pore plate (Po) (Fig. 2G,H) has a central ring-like flange at the cell outside surrounding the apical pore (Fig. 2G). A smaller ridge surrounds the apical pore near the inside of the plate and a thin finger-like projection is directed across the opening (Fig. 2H). The Po plate is encircled by four apical plates, of which plate 1′ is in contact with the sulcus and plate 3′ is very tiny (Fig. 2E,F, 3A c). There are two anterior intercalary (syn. apical intercalary, epithecal intercalary) plates (Fig. 3A c). Plate 1a is quadrangular (syn. square, four-sided) and smooth (Fig. 2E, 3A c). Plate 2a is large and ornamented with spines and is positioned on the dorsal side of the epitheca (Figs. 2F, 3A c). There are seven precingular plates (Figs. 2E,F, 3A c). The ascending cingulum consists most probably of three smooth plates with scattered pores (Figs. 2D–F, 3A), but the sutures are difficult to discern. Five smooth sulcal plates with pores were identified (Fig. 2D), but an unobstructed view of the mid sulcal plate (sm) is not visible because it is hidden behind the right sulcal plate (sd) (Figs. 2A,B, 3A a). The anterior sulcal plate (sa) is narrow and elongated (Figs. 2A,B,D,E, 3A a). The broad right sulcal plate (sd) is positioned in the middle of the sulcus, and the right and left margins of this plate are curved (Figs. 2A,B,D, 3A a). The left sulcal plate (ss) is elongated and characteristically curved (Figs. 2A,B,D, 3A a). The left margin of the mid sulcal plate (sm) is also curved (Fig. 2D), and this plate is positioned near the centre of the sulcus behind the sd plate. The posterior sulcal plate (sp) is relatively small and reaches the antapex (Figs. 2A,D, 3A a). The flagella pore (s) are obscured from view. The hypotheca consists of seven plates: five postcingular plates and two antapical plates (Figs. 2A–C, 3A a,b). The first (1‴) and fifth (5‴) postcingular plates are large and cover most of the ventral side of the hypotheca (Figs. 2A,B, 3A a). The extremely large, asymmetrical third postcingular plate (3‴) is pentagonal and covers nearly the complete dorsal hyposome (Figs. 1E, 2C, 3A b). The two, antapical plates are asymmetrical, and their antapical margins are ornamented with spines that were visible with light microscopy (Figs. 2C, 3A b).

Taxon description

Amphidiniopsis aculeata Hoppenrath, Koeman et Leander sp. nov.

Figs. 1A–G, 2A–H, 3A

Diagnosis Cellula 37.5-40.3 µm longae, 31.7-35.3 µm latae, rectangulares, dorsoventraliter complanatae. Formula scutelli: APC 4′ 2a 7″ 3c 5s 5‴ 2⁗. Cingulum adscendens duplo altiore quam latitudinis ipsius. Theca baculis ornata. Bacula lateralia et antapicalia longitudine differentes. Area pori apicalis elevata baculis marginata.

Cells 37.5-40.3 µm long, 31.7-35.3 µm wide, rectangular, rounded posteriorly, dorsoventrally flattened. Plate

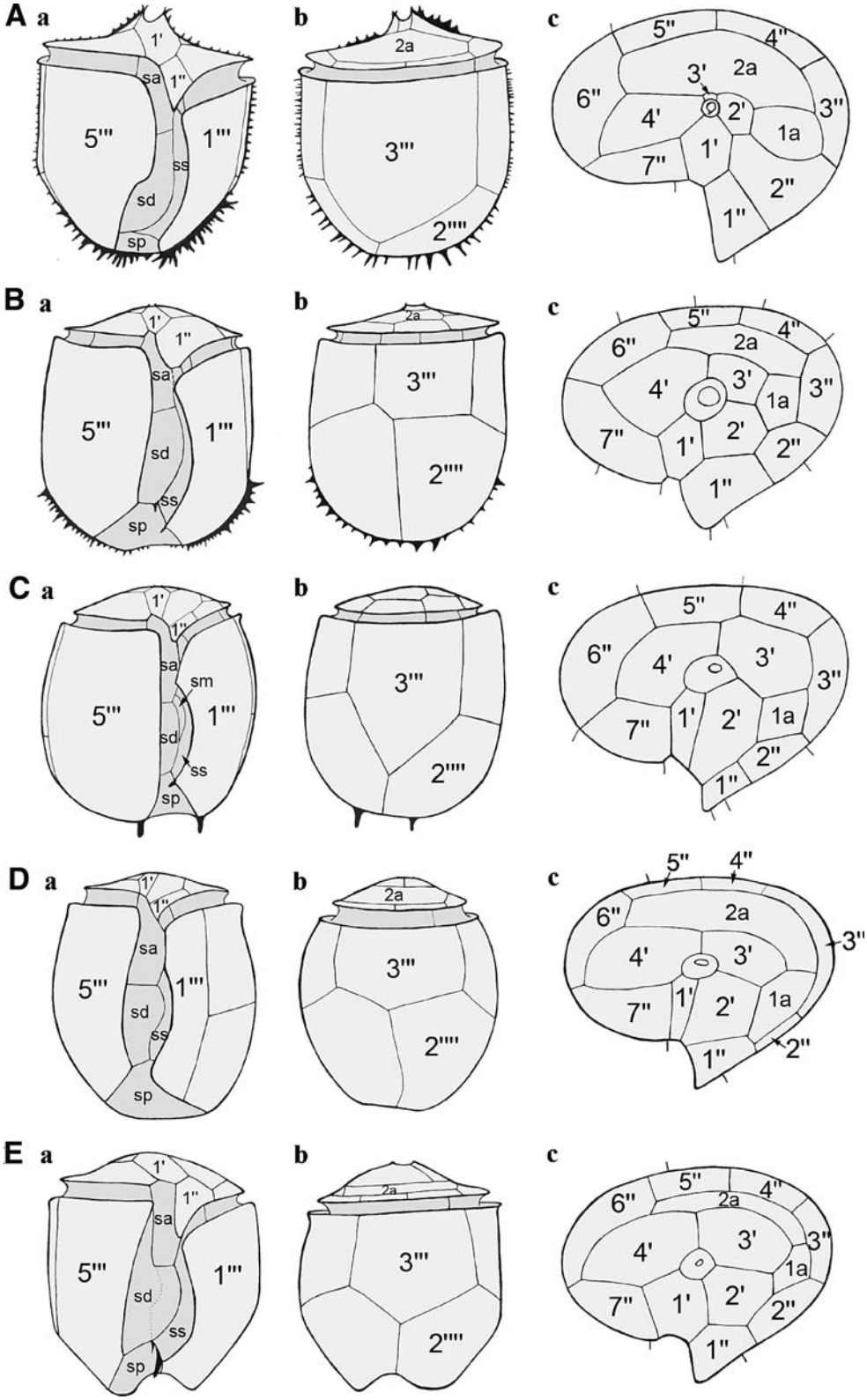

Fig. 3 Line drawings of the thecal plate patterns of the *Amphidiniopsis* species similar to *A. aculeata* sp. nov. a Ventral cell side; b dorsal cell side; c epitheca **A** a–c *A. aculeata* **B** a–c *A. hirsutum* **C** a–c *A. swedmarkii* **D** a–c *Amphidiniopsis* sp. (‘*swedmarkii*’) drawn from SEM figures published in Yoshimatsu et al. (2000) **E** a–c *A. hexagona* drawn from SEM figures published in Yoshimatsu et al. (2000)*1′-4′*apical plate series; *1a, 2a*anterior intercalary plates; *1″-7″*precingular plate series; *1‴-5‴*postcingular plate series; *2″″*second antapical plate; *sa*anterior sulcal plate; *sd* right sulcal plate; *sm*middle sulcal plate; *ss*left sulcal plate; *sp* posterior sulcal plate

formula: APC 4′ 2a 7″ 3c 5s 5‴ 2″″. Cingulum ascending about two cingular widths. Theca ornamented with spines, lateral and antapical rows/ridges of spines of different lengths. Raised apical pore area bordered with spines.

Holotype SEM stub (designation CEDiT2008H3) deposited at the Senckenberg Research Institute and Natural History Museum, Centre of Excellence for Dinophyte Taxonomy, Germany.

Table 1 Plate formulae of morphologically similar, dorsoventrally flattened *Amphidiniopsis* species

	APC	′	a	″	c	s	‴	⁗
A. aculeata	APC	4	2	7	3	5	5	2
A. hirsutum	APC	4	2	7	8?	4	5	2
A. swedmarkii	APC	4	1	7	6?	5	5	2
A. sp (‘*swedmarkii*’)	APC	4	2	7	3	4[a]	5	2
A. hexagona	APC	4	2	7	3	4[a]	5	2
Amphidiniopsis	APC	3-4	1-3	6-8	3-8	3-5	5	2

[a] Our interpretation of the images provided by Yoshimatsu et al. (2000)

Iconotype Fig. 3A a-c.

Type locality Beach sand at Cap Feret (44°38′25.10″N 01° 15′36.17″W), France

Etymology Latin *aculeus* = spine, referring to the spiny ornamentation of the theca

Further references Silva (1952, p. 29, pl. II, figs. 6, 6a) as *Amphidinium* sp.; Paulmier (1992, p. 59, pl. 70, figs. 7–9) as *Amphidiniopsis swedmarkii*.

Discussion

Species of the genus *Amphidiniopsis* are heterotrophic, sand-dwelling dinoflagellates from marine and freshwater sites. The described cell morphologies within the genus are diverse: laterally or dorso-ventrally flattened, with complete or incomplete cingulum, with or without an apical hook (Balech 1956; Dodge 1982; Gail 1950; Hoppenrath 2000; Murray and Patterson 2002; Nicholls 1998, 1999; Toriumi et al. 2002; Woloszynska 1928; Yoshimatsu et al. 2000). The described number of anterior intercalary, precingular, cingular, and sulcal plates varies between species (Hoppenrath 2000; Toriumi et al. 2002). Because of the morphological heterogeneity one could hypothesize that the genus is polyphyletic, consisting of more than one genus. This needs to be analysed and verified with molecular phylogenetic data. At the moment, the genus *Amphidiniopsis* is characterized by an ascending cingulum, the typically curved sulcus morphology and the hypothecal plate pattern. Similarities with other genera and the systematic placement within the order Peridiniales have been discussed in Hoppenrath (2000).

The new species is clearly a member of the genus *Amphidiniopsis* because of its overall morphology, thecal plate pattern (Fig. 3A, Table 1), ascending cingulum and characteristically curved sulcus (e.g. Hoppenrath 2000; Selina and Hoppenrath 2007; Yoshimatsu et al. 2000). In addition to *A. aculeata*, four other dorsoventrally flattened *Amphidiniopsis* species with similar thecal plate morphologies and plate formulae (Fig. 3A–E, Table 1) are known: *A. hirsutum*, *A. swedmarkii*, *Amphidiniopsis* sp. (‘*swedmarkii*’) and *A. hexagona* (Balech 1956, Hoppenrath 2000, Yoshimatsu et al. 2000). The cell size ranges are overlapping and, therefore, not useful taxonomic markers. These five species can be distinguished from one another by their thecal plate morphologies and ornamentation. *Amphidiniopsis aculeata* is the only species with prominent spines on the thecal plates and spiny lists at their margins. *Amphidiniopsis hirsutum* has a row of irregular spines at its antapical cell margin (Balech 1956; Hoppenrath 2000; Fig. 3B), and *A. swedmarkii* has two antapical spines (Balech 1956; Hoppenrath 2000; Fig. 3C). *Amphidiniopsis aculeata* can be distinguished from *A. hirsutum* by its extremely large and differently shaped 3‴ plate, its quadrangular 1a plate (pentagonal in *A. hirsutum*) and the very tiny 3′ plate (compare Fig. 3A,B). *Amphidiniopsis aculeata* can be distinguished from *A. swedmarkii* by the smaller and more pointed 3‴ plate (in *A. swedmarkii*), the separation between the 2′ plate and the sulcus (connected in *A. swedmarkii*), and the number of anterior intercalary plates (i.e. two in *A. aculeate* and one in *A. swedmarkii*) (compare Figs. 3A,C). *Amphidiniopsis* sp. (‘*swedmarkii*’) can be distinguished from the other species by the following features: a relatively narrow 1‴ plate, causing the sutures between plates 1‴, 2‴ and 1⁗ to be visible in ventral view; a very distinctive size and shape of plate 3‴; a hexagonal 1a plate; and a connection between plate 2′ and the sulcus (Yoshimatsu et al. 2000; compare Figs. 3A,D). *Amphidiniopsis hexagona* is distinctive in having a smaller 3‴ plate, a pentagonal 1a plate, and a large 3′ plate (Yoshimatsu et al. 2000; compare Figs. 3A,D).

In summary, all five dorsoventrally flattened species of *Amphidiniopsis* can be differentiated by (1) the shape and size of plate 3‴, (2) the shape of the 1a plate, (3) the

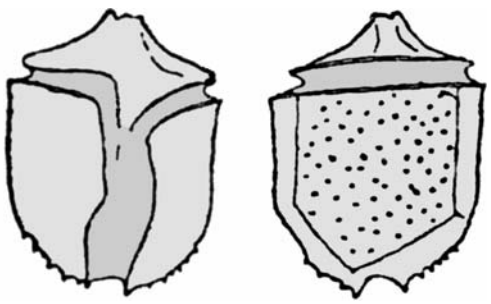

Fig. 4 Line drawing of *Amphidiniopsis aculeata* sp. nov. reproduced and colored from Silva (1952)

connection or separation between the 2′ plate and the sulcus, (4) the size of plate 3′, and (5) the presence or absence of antapical projections. *Amphidiniopsis aculeata* can be distinguished from all other dorsoventrally flattened species by having a complete cingulum and no apical hook projecting over the apical pore (Murray and Patterson 2002; Toriumi et al. 2002). The remaining of the known *Amphidiniopsis* species are laterally flattened, and differ in thecal plate formulae and morphologies and ornamentation.

Amphidiniopsis aculeata was recorded previously by Silva (1952), who described this taxon as "*Amphidinium* sp." from Lagoa de Óbidos, Portugal. Balech (1956, footnote p. 47) also recognized that this taxon was similar to *A. hirsutum*. The drawings given by Silva (1952, plate II, figs. 6, 6a; reproduced here as Fig. 4) clearly show a thecate species with the characteristic cell shape, spiny edges and third postcingular plate morphology that is demonstrated here for *A. aculeata* (Figs. 1E,G, 4). Paulmier (1992, p. 59, pl. 70, figs. 7–9) subsequently misidentified *A. aculeata* as *A. swedmarkii*. The light micrographs in this report show cells with the diagnostic features for *A. aculeata* (Paulmier 1992, figs. 7–9). The cell recorded by Silva (1952) was 45 μm long and 32 μm wide and Paulmier (1992) gave the size of 44 μm long and 36 μm wide. The cells were only slightly bigger than recorded in this study. These data taken together indicate that the known distribution of *A. aculeata* is restricted to northern France (Paulmier 1992), the west coast of France, Cape Feret (present study), and the coast of Portugal (Silva 1952).

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