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A New Species of the Genus *Ensiculifera* (Dinophyceae); Its Cyst and Motile Forms

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Abstract

A new calcareous cyst form attributable to *Ensiculifera*, which is one of the small orthoperidinioid dinoflagellates, is found in surface sediments of central Japan. Other occurrences of the thecate cells are recorded from the Caribbean Sea.

The cysts are spherical, 43-54 μm in diameter and comprise a calcareous outer layer forming a muri and/or large verrucate structure and a smooth inner layer. The paracingulum and parasulcus can be reflected by parallel rows of calcareous muri, but other paraplate features are indistinct. The archeopyle is a therophylic intercalary type, and the archeopyle suture probably runs between the apical and anterior intercalary plate series.

Thecate cells are 18.3-54.2 μm in length by 16.2-38.2 μm in width, and are generally dark brown in color. The epitheca, with a conspicuous apical horn, is triangular in dorso-ventral view and the hypotheca is laterally asymmetrical with a single small and hollow projection (carina) at the triple junction of plates Sp, 1"" and 2"". The Ct plate (cingular transitional plate) has a long spine at its anterior right corner. The plate formula is Po, X, 4', 3a, 7", 5c (4c+t), 5s, 5"", and 2"". Based on these morphological features, this species differs from species of such other genera of small orthoperidinioid dinoflagellates as *Scrippsiella*, *Peridinium* and *Pentapharsodinium*. Therefore, we describe it to be a new species of the genus *Ensiculifera*; *Ensiculifera carinata* MATSUOKA, KOBAYASHI et GAINS sp. nov.

Introduction

The first fossil calcareous dinoflagellate, *Calciodinellum operosum* was described by DEFLANDRE (1947) and additional fossil forms were reported by the same author (DEFLANDRE 1948). WALL & DALE (1968) recorded several Quaternary calcareous dinoflagellate cysts from surface sediments of the North Atlantic Ocean, Mediterranean Sea, Caribbean Sea and western Indian Ocean, and established the theca-cyst relationships of *Peridinium trochoideum* (STEIN) LEMMERMANN and *Scrippsiella sweeneyae* BALECH. Later WALL et al. (1970) suggested

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that the calcareous oblate form of WALL & DALE (1968) is probably a cyst of Ensiculifera cf. mexicana BALECH. Recently, abundant calcareous dinoflagellates which have been previously classified in the calcareous nannoplankton (coccolithophorids) are regarded as important members of pelagic plankton as well as planktonic foraminifers and coccolithophorids (e.g. FÜTTENER 1978). Calcareous cysts produced by some neritic dinoflagellates belonging to the genera Scrippsiella and Ensiculifera should be investigated as well as other organic dinoflagellate cysts for reconstructing paleo marine environments.

The dinoflagellate described herein was first and solely recorded by ODA (1935) as Heterocapsa sp. in a red tide mainly caused by Gymnodinium mikimotoi MIYAKE et KOMINAMI ex ODA in Gokasho Bay of central Japan, which faces to the West Pacific. Recently, it has been found in the British Virgin Islands in the Caribbean Sea by the third Author, G.G. After the examination of the external morphology of both cyst and thecate forms of the Pacific and Caribbean Sea specimens, we recognize this dinoflagellate as a new species belonging to the genus Ensiculifera, E. carinata MATSUOKA, KOBAYASHI et GAINS. This report is the second record to demonstrate the cyst-theca relationship of the genus Ensiculifera. We also discuss the systematics of some related genera; Ensiculifera, Scrippsiella, and Pentapharsodinium.

**Sampling Locations and Methods**

Ensiculifera carinata sp. nov. has been recorded from two areas so far (Fig. 1). The Pacific materials were used for the cyst germination experiment. The studied area in the Pacific was Gokasho Bay (33°40'N, 136°40'E) of central Japan which is in the subtropical oceanographical climatic zone. Surface sediments were collected at eight stations with a small gravity corer which was equipped with an acrylic resin tube of 32cm long and 1.1cm in diameter. The upper 2cm

![Fig. 1. Locations of occurrence of Ensiculifera carinata in Japan (A) and in Virgin Islands (B).](image-url)
of each core was processed under the technique of MATSUOKA et al. (1989) without any chemicals. Living cysts filled with fresh protoplasm were picked under an inverted microscope and inoculated separately in a culture dish containing 1ml of IWASAKI's SWII (IWASAKI 1961). Incubation was carried out in the NK artificial meteostat (Nihon Ikagaku Kikai Seisakusho Model NK LP-100-A) with 20°C and at ca. 100 μE·m⁻²·s⁻¹ under 12 light-12 dark cycle for two weeks for obtaining thecate forms produced throughout asexual reproduction. Morphology of cysts and thecate cells were observed under a Nikon Biophoto microscope with a differential interference optics and an Olympus BH2 microscope with a phase contrast optics.

Other thecate specimens were collected from the coastal waters of the British Virgin Islands (18°32′N, 61°28′W) in the Caribbean Sea and examined with a Zeiss Universal microscope with a differential interference contrast optics and with an ISI Alpha-9 scanning electron microscope at 15kV.

**Observations**

**Cyst Morphology**

The cysts are spherical, 43–54 μm in overall diameter and comprise two thick layers (Pl. I, 1, 3). The outer layer is calcareous, dark brown in color, and 5–8 μm thick, because it has high refractive index in water medium, and disappears after treatment with hydrochloric acid. This layer has a muri and/or large verrucate structure on its surface (Pl. I, 1, 2). It partly reflects a paracingulum and parasulcus, and other indistinct paraplate boundaries (Pl. I, 1). The inner layer is organic, 2–3 μm thick and transparent without any ornament. After removing the outer calcareous layer, the inner capsules are 35–46 μm in diameter (Pl. I, 3, 5). The operculum is never free from the cyst body (adnate type). The archeopyle, therefore, is a therophylic intercalary type with a zigzag archeopyle suture comprising three sides. According to the shape of the archeopyle, two possible positions can be envisaged; apical/anterior intercalary or anterior intercalary/precingular. For estimating the position, the ratio of these three sides of the archeopyle is calculated. It is approximately 0.9–(Fig. 2) 0.7 : 1 : 0.5. On the thecate cells, its ratio is approximately 0.5 : 1 : 0.6 for the apical/

![Fig. 2. Archeopyle suture (heavy line) of the cyst superimposing the plate boundaries of the thecate form of *Ensiculifera carinata*.](image-url)
anterior intercalary series and approximately $0.3 : 1 : 0.4$ for the anterior intercalary/precingular series. The ratio of the cyst is closer to the apical/anterior intercalary series rather than the anterior intercalary/precingular series of the thecate cells. The archeopyle suture, therefore, probably runs between the apical and anterior intercalary plate boundaries (Pl. I, 4; Fig. 4), but sometimes this suture extends after dislocation and consequently becomes half-circular (Pl. I, 3). Living cysts filled with fresh protoplasm are dark brown in color, and

Fig. 3. Plate formula of *Ensiculifera carinata* sp. nov.
usually contain one or two red pigmented bodies and many oil and starch globules.

Thecate Morphology
Totally sixteen thecate cells were germinated after two or three days from twenty-two inoculated cysts. One small thecate cell with active movement initially appeared from each cyst. These small cells were approximately 20 μm long. Each cell reproduced a day after the germination.

The motile cells, excluding germinated small cells from the cysts, are 18.3 ~54.2 μm in length, 16.2~38.2 μm in width and thickness, and broadly spindle-like in shape (Pl. II, 7, 8). The plate formula is Po, X, 4', 3a, 7”, 5c (4c+t), 5s, 5”, and 2”” (Fig. 3).

The epitheca is conical with a broad apical horn comprising a large apical pore plate (Po) and an elongate ventral canal plate (X) (Pl. II, 1A). The apical series consists of four plates which are symmetrically distributed; large rhomboidal 1', hexagonal 2' and 4', and pentagonal 3' (Pl. II, 1c). The anterior intercalary series comprises three plates with approximately equal height; pentagonal 1a and 3a, and hexagonal 2a expanded laterally. But 2a is rarely pentagonal in shape (Pl. II, 1D, E). Seven plates are symmetrically placed in the precingular (Pl. II, 1F).

The suture between 3c and 4c plates is located on the mid-dorsal surface (Pl. III, 3). A long slender spine, which is of the approximately half length of the epitheca, rises up at the right anterior corner of the smallest Ct plate (Pl. II, 5A; Pl. III, 1A). The cingulum is anteriorly displaced by a distance equal to its

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Fig. 4. Plate distribution on the sulcus of *Ensiculifera carinata*. Sa: sulcal anterior plate. Sr: sulcal right plate. Sm: sulcal middle plate, Sl: sulcal left plate, Sp: sulcal posterior plate.
width at the sulcus, and it comprises five plates including t plate (Pl. III, 1B). The sulcus consists of one very large sulcal posterior (Sp) and following four small plates; sulcal anterior (Sa), sulcal right (Sr), sulcal left (Sl) and sulcal middle (Sm) (Pl. II, 4, 8). The cingular plates always attach to the hypotheca when the theca is divided into two parts (Pl. II, 5, 6; Pl. III, 1).

The hypotheca is conical with a truncated antapex and is laterally asymmetrical, because the right half of hypotheca is slightly more convex than the left one. A small carina or keel-like projection rises from a triple junction of the Sp, 1”” and 2”” plates. This projection is ventrally shifted from the saggittal line. The postcingular series has five plates, which are symmetrically distributed. The plate 3”” is the smallest among the precingular plates and pentagonal in shape. It is located on the mid-dorsal surface. Two plates with slightly different size are placed in the antapical area; the 2”” is slightly larger than the 1””.

The thecate cells between the Pacific and the Caribbean Sea are considerably different in size. The former when reproduced during incubation are 25.3 –54.2 μm long (39.5 μm in average for 20 specimens) and 22.1–38.2 μm wide (30.86 μm in average). On the other hand, those collected from the coastal water of Virgin Islands are smaller being 18.3–36.5 μm long (26.9 μm in average for 20 specimens) and 16.2–34.3 μm wide (22.4 μm in average).

Discussion

Comparison with the Related Species

1. Cyst form

Several calcareous cysts have been reported from modern surface sediments (WALL & DALE 1968; Wall et al. 1970). The oblate-type described by WALL & DALE (1968, p. 1406, Text-fig. 3, 10–13, pl. 172, figs. 19–22, 28–30) is considered to be a cyst form of Ensiculifera cf. mexicana (WALL et al. 1970, p. 155). The new cyst described herein differs from that oblate-type in being spherical rather than oblate, and having a distinct parasulcal and paracingular features indicated by muri-structure. The therophylic archeopyle in both cysts is very similar in showing a zigzag margin of archeopyle and having an adnate operculum (WALL & DALE 1968, Text-fig. 3, 10 for E. cf. mexicana and Pl. II, 4–5 in this paper for this new species). WALL & DALE (1968) mentioned that the archeopyle of E. cf. mexicana cyst is apical, probably equivalent to apical and intercalary series. However, that archeopyle is therophylic intercalary according to MATSUOKA (1988), because the principal zigzag archeopyle suture runs along the boundaries between apical and intercalary series rather than intercalary and precingular series.

The tetrahedral-type cyst of WALL & DALE (1968, p. 1403; Text-fig. 3, 1–3, pl. 172, fig. 13) is somewhat similar to the new cyst in having longitudinal and latitudinal septa which incompletely show the paracingulum and parasulcus, but differs from the latter in being tetrahedral rather than spherical in shape.

Some fossil calcareous dinoflagellates also resemble the present new cyst. They are Calciperellum colomi DEFLANDRE, Bicarinellum castaninum DEFLANDRE and Calcigonellum limbatum (DEFLANDRE) KEUPP. C. colomi differs from the present cyst in being smaller in size and lacking paracingular structure. B. castaninum is also distinguishable from the present cyst in being larger in size,
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possessing thicker cyst wall and lacking short muri. *C. limbatum* differs from the present cyst in lacking parasulcus and paracingular structures and also being smaller in diameter.

2. Thecate form

*Ensiculifera mexicana* is another species characterized by the distinct Ct plate with a long spine and five cingular plates. However, the present new species clearly differs from *E. mexicana* in having a more slender epitheca and a short projection or carina at the triple junction of the Sp, 1"", and 2"" plates. The present species is also distinguishable from *E. mexicana* by its broad spindle-like shape in dorso-ventral view.

*Ensiculifera angulata* BALECH recently described from the South Atlantic by BALECH (1988) differs from the new species in lacking a carina and possessing a more elongate 1' plate.

*Peridinium loeblichii* (COX et ARNOTT) DALE (= *Pentapharsodinium loeblichii* INDELICATO et LOEBLICH = *Ensiculifera loeblichii* COX et ARNOTT) is also another species having five cingular plates, but it differs from the present species in lacking a long spine on the Ct plate and short hollow projection on the hypotheca.

*Previous record of* *Ensiculifera carinata* sp. nov.

ODA (1935) described a characteristic dinoflagellate in red tide plankton dominated by *Gymnodinium mikimotoi* MIYAKE et KOMINAMI ex ODA in Gokasho Bay of central Japan, which is the same region of the present study. Although he identified that species as *Heterocapsa* (?) sp., we believe that it is the same species as *Ensiculifera carinata* sp. nov. on the basis of the following morphological features:

i) ODA (1935) reported the plate formula for his species as 4', 3a, 7", 5"", 0p, and 3"", but the 1"" plate which occupies the position below the sulcus in *Heterocapsa* (?) sp. is identical with the sulcal posterior plate of the present new species. Consequently the plate formula of *Heterocapsa* (?) sp. is the same as that of *Ensiculifera carinata* sp. nov.

![Schematic drawings of Heterocapsa (?) sp. from Gokasho Bay, the dotted plate (sulcal posterior plate) was considered to be a member of antapical series by ODA (1935).](image)
ii) *Heterocapsa* (?) sp. is also broadly spindle-like in dorso-ventral view, and bears a single hollow projection or carina at the triple junction of the Sp, 1”” and 2”” plates, which is the same as in the present new species.

Another occurrence of this new species was recorded in the Caribbean Sea. *Ensiculifera cf. mexicana* described by CARLSON (1984) from the Virgin Gorda Islands is identical to the present new species on the basis of its plate formula, elongate spine on the Ct plate and presence of keel-like carina on the hypotheca. However, the specimens of the Caribbean Sea reported by CARLSON (1984) are 25 μm in length, 22 μm in width and 19 μm in thickness and our specimens collected from the same area are 18.3–36.5 μm long and 16.2–34.3 μm wide. Therefore, the specimens of the Caribbean Sea are considerably smaller than the Pacific ones. These size differences could be due to; the Pacific specimens might be larger than the wild ones, because of these specimens provided for measurement being derived from the culture, and secondly, population differences among them are probably included, because of specimens of both regions overlapping in size.

*Taxonomic status of the genus Ensiculifera*

The genus *Ensiculifera* was erected on the basis of *E. mexicana* which possesses five cingular plates with an elongate spine on the Ct plate and the tabulation; Po, X, 4’, 3a, 7”, 4c+t, 5s, 5”, and 2”” by BALECH (1967). However, in the illustration given by BALECH (1967, Figs. 136–138) the cingulum of *E. mexicana* had only four plates including the cingular transitional plate. Later in the discussion of thecal morphology of dinoflagellates, BALECH (1974, Fig. 1, 7–9; 1980, Fig. 4, 9–11) showed schematic illustrations of the genus *Ensiculifera* with six cingular plates including the transitional plate, without any comments on the difference from previous figures. Recently, INDELICATO & LOEBLICH (1986) revised the genera *Ensiculifera* BALECH 1967, *Scrippsiella* BALECH 1959 ex LOEBLICH 1965 and *Peridinium* EHRENBERG 1832, patrim in the special attention to the relationship between the cingular and postcingular plates. They rejected *Ensiculifera*, because the original diagnosis of the type species, *E. mexicana* given by BALECH (1967) was not concordant with his original illustrations of *E. mexicana* and lacked a Latin diagnosis. From a new point of view regarding the hypothecal-cingular plate relationships, INDELICATO & LOEBLICH (1986) realized that the distribution and number of cingular plates in *E. mexicana* are concordant with those of the genus *Scrippsiella*, and transferred this species into the genus *Scrippsiella*, as *S. mexicana* (BALECH) INDELICATO et LOEBLICH. Furthermore, they established a new genus *Pentapharsodinium* on the basis of *Peridinium faeroense* of DALE (1977) characterized by the following plate formula; Po, X, 4’, 3a, 7”, 5c, 5”, 2”” and its organic-walled cysts which were originally reported by DALE (1977). The genus *Pentapharsodinium* includes *Pent. faeroense* (= *Peridinium loeblichii* DALE, 1977 = *Ensiculifera loeblichii* of COX & ARNOTT, 1971).

As mentioned above the number of the cingular plates of *E. mexicana* was different between the original diagnosis and the illustrations. However, in the discussion of the taxonomy of *Peridinium faeroense* PAULSEN, DALE (1977) noted that *Ensiculifera* sp. has one cingular suture seen in the middle of the dorsal
surface and a long conspicuous lance-like projection on the Ct plate, and later he also illustrated the genus *Ensiculifera* consisting of five cingular plates (4c+t) on the basis of thecal morphology of *E. cf. mexicana* (DALE 1978, Text-fig. 1). More recently, BALECH (1988) clearly mentioned the plate formula of the genus *Ensiculifera* to be Po, X, 4', 3a, 7", 5", 2'", 4c+t, when he described another new species of this genus, *E. angulata* BALECH without any comment concerning his previous interpretation on the number of the cingular plates. According to the above-mentioned evidence and our own observations, we think that the genus *Ensiculifera* has five not six cingular plates (4c+t). However, the detailed observations, in particular on the number of the cingular plates of *E. mexicana* leave this interpretation to be confirmed. Under these circumstances, we prefer to keep the genus *Ensiculifera* after proper emendations including its cyst features at the moment.

**Systematics**

Division Pyrrhophyta PASCHER, 1914  
Order Peridiniales HAECKEL, 1894  
Family Calciodinellaceae DEFLANDRE, 1947  
Genus *Ensiculifera* BALECH, 1967 ex MATSUOKA, KOBAYASHI et GAINS emend. herein  

*Emended diagnosis:*  
Orthoperidinioid and photosynthetic. Plate formula Po, X, 7", 5c (or 4c+t), 5s, 5", and 2"". Plate Ct possessing a long spine. Cyst spherical and calcareous, archeopyle therophytic intercalary.  

*Emenda diagnosis:*  
Orthoperidinioides et photosynthetica. Formula plattae Po, X, 7", 5c (vel 4c+t), 5s, 5", et 2"". Platta Ct possidet longam spinam. Cystis sphaerica et calcaria, archeopyla theropylica et intercalaris est.  

*Ensiculifera carinata* MATSUOKA, KOBAYASHI et GAINS sp. nov.  
Plates, I, II, and III; Figs. 3 and 4  

*Synonym:*  
*Heterocapsa* (?) sp. ODA, 1935, p.35, fig. 4  
*Ensiculifera* cf. *mexicana* BALECH; CARLSON, 1984, p. 86, pl. II, figs. j-l.  

*Diagnosis:*  
Thecate cells broadly spindle-like in shape, 18.3-54.2 μm in length, 16.2-38.2 μm in width and thickness. Plate formula Po, X, 4', 3a, 7", 5" (4c+t), 5s, 5", and 2'". Plate Ct bearing a long spine. A single hollow carina raising at the triple junction of plates Sp, 1'" and 2'".  

Cyst spherical, 43-54 μm in diameter and comprising two thick wall layers; calcareous outer layer 5-8 μm thick, having muri and/or verrucate structure, and smooth organic inner layer for 2-3 μm thick. Operculum adnate. Archeopyle therophytic intercalary with a zigzag archeopyle suture line running between the
apical and anterior intercalary plates boundaries.

**Diagnosis:**
The thecate cellae fusoides in vulgari forma, 18.3-54.2 µm in longitudine, 16.2-38.2 µm in latitudine et crassitudine. Formula plattae Po, X, 4’, 3a, 7”, 5c (4c + t), 5s, 5””, et 2””. Platta Ct possidet longam spinam. Singula carina cava arriget in tripli junctione plattae Sp, 1”” et 2””.

Cystis sphaerica 43-54 µm transdiametre est et compono duo coria crassa. Exterius corium quod est 5-8 µm in crassitudine calcarium est, et interius corium leve, organicum est 2-3 µm in crassitudine. Operculum adnatum. Archeopyla theropylica et intercalaris est. Archeopyla sutura tortuosa curret in confinium apicalium et anteriorum plattarum intercaralium.

**Iconotype:**
Figure 3.

**Type locality:**
Gokasho Bay, Mie Prefecture, central Japan.

**Geographic distribution:**
Gokasho Bay, Mie Prefecture; Tanabe Bay, Wakayama Prefecture, Pacific side of Japan. Virgin Gorda Islands, British Virgin Islands.

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Explanation of Plate I
Cysts of Ensiculifra carinata sp. nov.

1. Specimen C-003 (Gokasho Bay), A: ventral surface showing parasulcus (arrow), B: oblique ventral surface showing paracingulum (arrow), C: lateral surface showing paracingulum (arrow), D: dorsal surface (?), E: apical surface (?), F: optical cross section (orientation unknown).

2. Specimen C-002 (Gokasho Bay), A: cyst surface ornamented with many verrucae (orientation unknown), B: optical cross section (orientation unknown).

3. Specimen C-001 (Gokasho Bay), A: optical cross section showing calcareous outer layer with expanded therophytic archeopyle suture, B: calcareous outer and organic inner layers (arrow) during treatment with 1% HCl, C: organic smooth inner layer with expanded therophytic archeopyle after removing calcareous outer layer.

4. Specimen C-006 (Gokasho Bay), A: optical cross section showing many verrucae on the surface, B-E: different focus levels of the oblique dorsal surface; arrow showing archeopyle suture comprising three plate boundaries between apical and anterior intercalary series.

5. Specimen C-006 (Gokasho Bay) after removing calcareous outer layer with 1% HCl, A: lateral view showing therophytic archeopyle on the inner organic layer (arrow) and smooth surface, B: optical cross section.

All figures in phase contrast, scale bar 10 μm.
Explanation of Plate II
Thecae of *Ensiculifera carinata* sp. nov.

1. Specimen TG-001 (Gokasho Bay), A-F: different focus levels of apical view of epitheca.
2. Specimen TG-003 (Gokasho Bay), optical cross section of antapical-apical view, showing plate boundaries of the precingular series (slender arrows) and Ct plate (larger arrow).
3. Specimen TG-002 (Gokasho Bay), ventral surface of the epitheca showing aberrant shape of plate X.
4. Specimen TG-004 (Gokasho Bay), ventral view showing a part of sulcus.
5. Specimen TG-004 (Gokasho Bay), A: ventral view showing Ct plate with a long spine (arrow), B: lateral view showing a long spine on Ct plate.
6. Specimen TG-007 (Gokasho Bay), oblique lateral view showing a small carina (arrow).
7. Specimen TVI-001 (Virgin Islands), ventral surface showing a long spine on Ct plate (arrow).
8. Specimen TVI-002 (Virgin Islands), ventral view showing sulcus posterior plates (Sp), sulcal fin (Sf) and many trichocyst pores on thecal plates, scale bar 5 μm. 1-5 in phase contrast; 6 in bright field; 7 SEM, scale bar 10 μm unless otherwise mentioned.
Explanation of Plate III

Thecae of *Ensiculifera carinata* sp. nov.

1. Specimen TG-005 (Gokasho Bay), A: oblique ventral view showing Ct, 5c and 5" plates, and a long spine on Ct plate (arrow), B: ventral view showing sulcal plates and sulcal fin (arrow), C-D: ventral view showing a large Sp plate, E: dorsal view showing 3"" plate (arrow).

2. Specimen TG-007 (Gokasho Bay), oblique antapical view showing Sp plate (arrow).

3. Specimen TG-008 (Gokasho Bay), dorsal surface of hypotheca showing 3c, 4c, 2"", 3"", 4"" 1"" and 2"" plates; arrow indicating the plate boundary between 3c and 4c plates.

4. Specimen TG-006 (Gokasho Bay), A: lateral view showing 4c and 4"" plates, B: lateral view showing the plate boundaries of 2c/3c and 1""/2"".

5. Specimen TG-008 (Gokasho Bay), antapical view showing Sp, 1"" and 2"" plates, and antapical carina (arrow).

6. Specimen TVI-003 (Virgin Islands), antapical surface showing a carina (arrow).

7. Specimen TVI-004 (Virgin Islands), oblique dorsal view showing a carina (arrow).

8. Specimen TVI-005 (Virgin Islands), ventral view showing sulcal fin (large arrow) and carina (slender arrow).

1-5 in phase contrast; 6-8 SEM, scale bar 10 μm.