

無殻渦鞭毛藻の上錐溝について

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Apical Grooves of Unarmored Dinoflagellates^{1), 2)}

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Abstract

The external morphology was studied by the light and scanning electron microscopes for 22 species of unarmored dinoflagellates: 6 species of *Gymnodinium*, 7 species of *Gyrodinium*, 2 species of *Polykrikos*, 3 species of *Warnowia*, 3 species of *Nematodinium* and 1 species of *Erythropsioidinium*. In all of these species, one or two narrow grooves were found in the upper part of epicone in addition to the cingulum and the sulcus. Generally, the groove is neither connected with the cingulum nor the sulcus. In some species it is connected with these furrows, but it is easily distinguishable from the furrows because of its narrow and shallow structure. The paracingular lines of *Erythropsioidinium* (= *Erythropsioidinium*) (KOFOID & SWEZY 1921), the "acrobase" of 7 species of unarmored dinoflagellates (BIECHELER 1934, 1952, CHATTON & HOVASSE 1934), the carinal groove of *Ptychodiscus brevis* (= *Gymnodinium breve*) (STEINDINGER 1979) and the apical groove of *Gymnodinium nagasakiense* and *Gym. breve* (TAKAYAMA 1981, TAKAYAMA & ADACHI 1984) seem to be homologous with the groove. Here, the name of "apical groove" is proposed again in common use for unarmored dinoflagellates. The apical groove frequently makes an inward or an outward left spiral around the apex in varying degrees. In a species of *Gymnodinium* it does not make a circuit but its distal end makes a leftward arch. In many species of *Gymnodinium*, *Gyrodinium* and *Polykrikos*, the apical groove goes around in one time, while those of several species of *Warnowia*, *Nematodinium* and *Erythropsioidinium* make more than one time.

The unarmored dinoflagellates have been known to have two furrows: a cingulum and a sulcus. TAKAYAMA (1981) and TAKAYAMA & ADACHI (1984) found that a narrow and shallow groove is present in the epicone of *Gymnodinium nagasakiense* and *Gymnodinium breve* in addition to these two "traditional" furrows, and tentatively named it as apical groove. Other authors also suggested similar grooves for some species. KOFOID & SWEZY (1921) reported that the cingulum of *Erythropsioidinium* (= *Erythropsioidinium*) is bordered by the paracingular lines. BIECHELER (1934, 1952) and CHATTON & HOVASSE (1934) noted a structure named "acrobase" which subdivides the epicone of unarmored dinoflagellates into "acromere" and "prosomere." STEINDINGER (1979b) found a carinal groove at the apex of *Ptychodiscus brevis* (= *Gymnodinium breve*). These structures have some features in common: they are narrower and shallower than the cingulum or the sulcus and turn counter-clockwise around the apex if they turn. Subsequent observations performed with the scanning electron and the light microscopes showed that such narrow grooves are found in many unarmored dinoflagellates.

Materials and Methods

The dinoflagellates were collected with a bucket from the coastal areas of the Inland Sea of

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²⁾ 無殻渦鞭毛藻の上錐溝について

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Japan along Hiroshima Prefecture. Six species of *Gymnodinium*, 7 species of *Gyrodinium*, 2 species of *Polykrikos*, 3 species of *Warnowia*, 3 species of *Nematodinium* and 1 species of *Erythrospidinium* were used in the present study. Living cells were observed by light microscope (LM) with or without differential interference contrast. Specimens for scanning electron microscope (SEM) observations were fixed with 2% filtered seawater solution of osmic acid, adhered to the poly-lisin coated glass plates according to the procedure by TSUTSUI et al. (1976), rinsed with distilled water, dehydrated in a series of ethanol (30, 50, 70, 90, 95 and 100%), transferred to amyl acetate, critical point-dried using liquid carbon dioxide and ion-sputter-coated with gold or platinum-palladium. Observations were made with a SEM (Hitachi S-430).

Results

A narrow and shallow groove is situated on the epicone of *Gymnodinium* sp. 1 (Pl. I, 1). The groove originates from the right side of the proximal end of cingulum, extends to the right side of the apex, veers to the left, crosses the ventral surface to the left margin, curves in a leftward arch and then reaches to the dorsal surface. Such a narrow groove extends nearly straightly from dorsal to ventral side in the epicone of *Gymnodinium nagasakiense* Takayama et Adachi (Pl. I, 7), but it encircles the apex in many other species of *Gymnodinium* and *Gyrodinium*. The groove of *Gyrodinium glaucum* Lebour (Pl. II, 10-12) makes an incomplete circuit at the apex. The tongue-shaped lobe bordered by the groove rises the surface at the apex. The minute groove runs around the apex of *Gymnodinium sanguineum* Hirasaka (Pl. I, 8). The groove of *Gymnodinium abbreviatum* Kofoid et Swezy (Pl. I, 2) rotates about one time around the apex and its distal end is slightly involuted. In *Gyrodinium instriatum* Freudenthal et Lee (Pl. I, 9), a narrow groove originates from the upper junction of cingulum and sulcus, extends to the left side of the apex, crosses the dorsal surface, leads downward and reaches to the right side of its proximal end. The sulcus of *Gymnodinium aureum* Kofoid et Swezy (Pl. II, 4 and 5), *Gyrodinium dominans* Hulburt (Pl. I, 6), *Gyrodinium pepo* (Schütt) Kofoid et Swezy (Pl. II, 14) and *Gyrodinium* sp. 1 (Pl. II, 13) invades deeply into the epicone. A narrow and shallow groove starts above the anterior end of the sulcus and encircles entirely the apex of these species. *Gym. aureum*, *Gyr. pepo* and *Gyrodinium* sp. 1 have a ridge at the apex surrounded by the groove. The cells of *Gyrodinium spirale* (Bergh) Kofoid et Swezy (Pl. II, 15) and *Gyrodinium* sp. 2 (Pl. II, 16) are tapering anteriorly with a pointed apex. A minute groove makes a circuit around the base of the pointed apex. *Gymnodinium* sp. 2 have two narrow grooves (Pl. I, 3). Such a narrow groove is also present at the apex of *Polykrikos kofoidii* Chatton (Pl. II, 17) and *Polykrikos hartmannii* Zimmermann (Pl. II, 18).

Three species of *Warnowia* and 3 species of *Nematodinium* were observed during the present study. The cingulum of each of these species originates from slightly below the apex, turns around the cells more than one time and reaches to the antapex. The sulcus of *Nematodinium armatum* Dogiel (Pl. II, 19) and *Nematodinium* sp. 1 (Pl. III, 28) starts from the proximal end of the cingulum and descends more steeply than the cingulum. The sulcus of

Warnowia sp. 3 (Pl. III, 24 and 25) commences from the proximal end of the cingulum and two furrows take about 0.5 turn around the cell side by side. Reaching to the ocellus, they separate. The cingulum passes above the ocellus and descends in a uniform left spiral to the antapex. The sulcus descends steeply there, passes under the ocellus and contacts again with cingulum which precedes one more turn. In *Warnowia* sp. 1 (Pl. III, 20 and 21), *Warnowia* sp. 2 (Pl. III, 22 and 23) and *Nematodinium* sp. 2 (Pl. III, 26 and 27), the relatively narrow sulcus begins from the halfway of the cingulum. The transverse flagellum of *Warnowia* sp. 1 emerges from the anterior end of the cingulum. However, each transverse flagellum of *Warnowia* sp. 2 and *Nematodinium* sp. 2 emerges from near the upper junction of cingulum and sulcus, and the anterior end of cingulum has no flagellum. Besides the cingulum and the sulcus, these *Warnowia* and *Nematodinium* have the narrow grooves encircling the apex. The grooves of *N. armatum* (Pl. II, 19) and *Nematodinium* sp. 1 (Pl. III, 28) encircle about one time, and their distal ends are located on the outside of their own proximal ends. The narrow groove forms an inward left spiral about 1.5 turns in *Warnowia* sp. 1 (Pl. III, 21), and it takes 2 turns in *Warnowia* sp. 2 (Pl. III, 23). In *Nematodinium* sp. 2 (Pl. III, 27), the groove starts from just above the proximal end of the cingulum, turns leftward around the apex, then descends at the center between the cingulum and forms an outward left spiral. *Warnowia* sp. 3 (Pl. III, 24 and 25) have 2 narrow grooves. One of them is an inward left spiral such as *Warnowia* sp. 1 and *Warnowia* sp. 2, and the other is an outward left spiral such as in *Nematodinium* sp. 2. Since the apical part of this species is somewhat complex, the schematic representation of its apex is shown in Fig. 1.

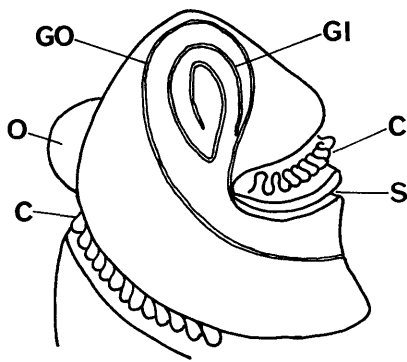


Fig. 1. Schematic representation of the apex of *Warnowia* sp. 3. C: Cingulum, G: Apical groove, GI: Inward-looping apical groove, GO: Outward-looping apical groove, O: Ocellus, R: Apical ridge, S: Sulcus. Scale bar=10 μ m.

The sulcus of *Erythrospidinium agile* (Hertwig) Silva (Pl. III, 29 and 30) extends nearly straightly from near the apex to the antapex with a small apical horn above its proximal end. The cingulum originates from proximal end of the sulcus and descends in a left spiral of about 1.5 turns around the cell. The narrow groove originates from the base of the apical horn (a

in Pl. III, 30), goes round leftward about 3/4 turn along the margin of the epicone (b), veers abruptly before reaching the sulcus (c), goes to the apex (d), then curves rightward around the proximal end of the sulcus (e), veers again leftward (f), and goes round the cell parallel to the original course (g).

Discussion

As mentioned above, many species of unarmored dinoflagellates have the grooves in the upper part of epicone in addition to the cingulum and the sulcus. Generally, they are neither connected with the sulcus nor the cingulum. In some species, i.e. *Gyr. instriatum*, *Poly. kofoidii*, *Poly. hartmannii*, *Warnowia* sp. 3 and *N. armatum*, they appear to be connected with the cingulum or the sulcus. However, these grooves can be distinguished from traditional furrows because they are much narrower and shallower than the latter. The groove is also visible in living cells under most careful observations using the light microscope (Pl. I, 4 and Pl. II, 10).

TAKAYAMA (1981) and TAKAYAMA & ADACHI (1984) found that *Gym. nagasakiense* and *Gymnodinium breve* Davis have a narrow and shallow groove on the epicone and tentatively named it as apical groove. Although the apical grooves of *Gym. nagasakiense* (Pl. I, 7) and *Gym. breve* extend almost straightly to near the apex to reach the dorsal side, the narrow grooves examined in the present study can be regarded as the structures homologous to the apical grooves from their position and morphological characteristics. The present author proposes again here the name of "apical groove" for these structures. TAKAYAMA (1981) once noted that the apical groove is absent in *Gym. sanguineum* (cited as *Gymnodinium nelsoni*). However, this species does have the apical groove as shown in Pl. I, 8. Most species of unarmored dinoflagellates appear to have the apical groove, although this should be examined more extensively.

The apical groove frequently rotates leftward around the apex in varying degrees. In *Gymnodinium* sp. 1 (Pl. I, 1), it first extends to the right side of the apex, but its distal end makes a leftward arc around the apex. In many other species it encircles about one time around the apex. In some species of specialized genera such as *Warnowia*, *Nematodinium* and *Erythrospidinium* it rotates more than 1 turn making an inward or an outward spiral. *Warnowia* sp. 1 (Pl. III, 20 and 21) and *Warnowia* sp. 2 (Pl. III, 22 and 23) have an inward-looping groove. The apical groove of *E. agile* (Pl. III, 29 and 30) is slightly deformed but it forms an inward left spiral. In *Gym. abbreviatum* (Pl. I, 2) it is also classified into the inward-looping groove. *Nematodinium* sp. 2 (Pl. III, 26 and 27) have an outward-looping apical groove. The apical groove of *Gyr. instriatum* (Pl. I, 9), *Poly. kofoidii* (Pl. III, 17), *Poly. hartmannii* (Pl. II, 18), *N. armatum* (Pl. II, 19) and *Nematodinium* sp. 1 (Pl. III, 28) belong to this type, because the distal end of each apical groove is situated on the outside of its own proximal end. However, it is difficult to judge whether the apical groove of some species, for example, *Gym. aureum* (Pl. I, 5), *Gyr. dominans* (Pl. I, 6), *Gyr. pepo* (Pl. II, 14) and *Gyrodinium* sp. 2 (Pl. II, 16), should be classified into the inward or outward type, because they make a nearly complete circuit.

The apex crowned by the apical groove is sometimes notched or ridged. This seems to have been observed by some authors but with very few attention. KOFOID & SWEZY figured a circle at the apex of *Gyr. pepo* (KOFOID & SWEZY 1921, fig. DD 2). It appears to show the apical groove but they did not make any comment about it. KOFOID & SWEZY (1921) also noted the apex of *Gym. aureum* to be truncate-acuminate with a median and two lateral elevations on the summit. The median elevation is corresponding to the apical ridge and the lateral ones are attributed to the courses of the apical groove as shown in Pl. I, 4 and 5. The teeth-like projections at the apex of *Gymnodinium helveticum* Penard (KOFOID & SWEZY 1921, fig. Y 11) and *Gymnodinium tridentatum* Schiller (SCHILLER 1933, 422, figs. 443 a-c) appear to indicate the presence of the same structures. KOFOID & SWEZY (1921) described that the apex of *Gyr. glaucum* is flexed to the left with a rounding-up of the right side resulted. HULBURT (1957) and DODGE (1982) reported the apex of this species to be pointed and sometimes slightly twisted. The tongue-shaped lobe bordered by the apical groove rises the surface of the apex of this species (Pl. II, 11 and 12), and the apical features vary, being pointed, twisted or notched according to the angle of observation. The apical grooves perhaps pass through the apical notches of some species, for example, *Gymnodinium hamulum* Kofoid et Swezy (KOFOID & SWEZY 1921, fig. Y5), *Gymnodinium agile* Kofoid et Swezy (KOFOID & SWEZY 1921, fig. Y9), *Massartia glandula* (Herdman) Schiller (SCHILLER 1933, fig. 461a) or *Katodinium glandulum* (Herdman) Loeblich (DODGE 1982, fig. 15c), *Massartia asymmetrica* (Massart) Schiller (HULBURT 1957, figs. 10 and 14) or *Katodinium asymmetricum* (Massart) Loeblich (DODGE 1982, fig. 15d) and *Herdmania litoralis* Dodge (DODGE 1982, figs. 15g-h). Also, the apical groove may surround the apical mammillate process of *Gym. abbreviatum* (DREBES 1974, fig. 96a) and *Gymnodinium J* (STEIDINGER 1970, fig. 72).

Some authors suggested that some species of unarmored dinoflagellates had the other grooves in addition to the cingulum and sulcus. KOFOID & SWEZY (1921) described that the cingulum of *Erythroopsis* (= *Erythropsidinium*) might be bordered by the precingular and postcingular grooves which were designated as the paracingular grooves or lines. *Erythroopsis extrudens* Kofoid et Swezy (KOFOID & SWEZY 1921, fig. TT3) has both the precingular and postcingular lines, of which the precingular line runs sinistrally inward more than one time around the apex. It is very similar to the apical groove of *E. agile* (Pl. III, 29 and 30). The precingular line of *Erythropsidinium* corresponds to the inward-looping apical groove. A few species, for example, *Gymnodinium* sp. 2 (Pl. I, 3) and *Warnowia* sp. 3 (Pl. III, 24 and 25), have two apical grooves. The postcingular line may be another apical groove, perhaps the outward-looping apical groove, although it cannot be surely decided because *E. agile* has an inward-looping groove only. KOFOID & SWEZY (1921) reported that *Pouchetia* (= *Warnowia*) and *Nematodinium* do not have paracingular lines. In the present study, however, the same structures have been found to be present in the species of these genera.

BIECHELER (1934, 1952) and CHATTON & HOVASSE (1934) described a narrow groove called "acrobases" in some species of *Amphidinium*, *Gymnodinium*, *Gyrodinium* and *Polykrikos*. They divided the cells of unarmored dinoflagellates into four parts: "acromere," "prothomere,"

“mesomere” and “opisthomere.” The opisthomere is almost synonymous with the hypocone and the mesomere indicates the cingulum. The epicone is subdivided into the acromere and the prothomere by the acrobasis which encircles counter-clockwise the apex. The acrobasis seems to be synonymous with the apical groove in its location, narrowness, shallowness and looping manner.

STEIDINGER (1979a, 1983) has moved *Gym. breve* to the genus *Ptychodiscus*. TAKAYAMA (1981) and DODGE (1982) did not agree with this new classification, because the cells of this species have different features from *Ptychodiscus*. Apart from this taxonomical problem, STEIDINGER (1979b) found that *Gym. breve* has a structure named carinal groove at the apex. TAKAYAMA (1981) suggested the carinal groove of this species to be recognized as the structure homologous with the apical groove.

KOFOID & SWEZY (1921) described an apical loop in some species of *Cochlodinium*, *Pouchetia* (= *Warnowia*) and *Nematodinium*. They considered it equally as the anterior extension of sulcus above the upper junction of the cingulum and the sulcus. However, the apical loop may be classified into 3 types from their figures. The apical loop of *Cochlodinium cereum* Kofoid et Swezy (357-358, fig. GG 5), *Cochlodinium conspiratum* Kofoid et Swezy (361-362, fig. GG 10), *Cochlodinium scintillans* Kofoid et Swezy (381-382, fig. GG 11), *Cochlodinium strangulatum* Schütt (382-382, fig. GG 8) is relatively short. It is probably the sulcus. The apical loop of many species of *Pouchetia*, for example, *Pouchetia atra* Kofoid et Swezy (439-440, fig. PP 5), *Pouchetia pouchetii* Kofoid et Swezy (455-456, fig. PP 4), *Pouchetia subnigra* Kofoid et Swezy (469-471, fig. OO1), *Pouchetia violescens* Kofoid et Swezy (469-471, fig. OO1), and *Nematodinium partitum* Kofoid et Swezy (425-426, figs. MM and NN 4), forms an ascending right spiral around the apex. The apical loops of these species are similar to the anterior extension of cingulum of *Warnowia* sp. 2 (Pl. III, 22 and 23) and *Nematodinium* sp. 2 (Pl. III, 26 and 27). In these species, the cingulum commences from just below the apex and descends in a left spiral. The sulcus starts from the halfway of the cingulum as in *Warnowia* sp. 1 (Pl. III, 20 and 21). The origin of the cingulum of *Warnowia* sp. 1 is very clear because the transverse flagellum emerges from its anterior end. However, each transverse flagellum of *Warnowia* sp. 2 and *Nematodinium* sp. 2 originates from near the upper junction of the cingulum and the sulcus, and the anterior portion of the cingulum has no flagellum. Therefore, a question may arise whether the anterior end of the furrow belongs to the cingulum or to the sulcus. They should be treated as the anterior extensions of the cingulum but not sulcus. On the other hand, the apical loop of *Cochlodinium miniatum* Kofoid et Swezy (372-373, fig. GG 6) is narrower than the sulcus or cingulum, and turns leftward around the apex. It shows prominent features of the apical groove. The counter-clockwise apical loops in some species described by other authors, i.e. *Cochlodinium vinctum* Kofoid et Swezy (LEBOUR 1925, 63, pl. IX 5a-b), *Katodinium dorsalisulcum* Hulburt et al. (HULBURT et al. 1960, 323-326, figs. 1-9), *Cochlodinium heterolobatum* Silva (SILVA 1963, pl. 1 A), *Gymnodinium gracile* Bergh (ELBRÄCHTER 1979, 6-8, fig. 12) and *Gymnodinium striatissimum* Hulburt (ELBRÄCHTER 1979, 9-10, figs. 18-23), correspond to the apical groove for the same reasons.

KOFOID (1920) and KOFOID & SWEZY (1921) noted that the sulcus of *Noctiluca scintillans* (Macartney) Ehrenberg consisted of two main regions, namely, the oral pouch and the apical groove or apical trough. TAKAYAMA (1983) suggested that rod organ (=apical trough) of this species might be a variation of the apical groove but it was not a component of sulcus.

The synonymous or the confusing terms with the apical groove mentioned above are listed in Table 1.

TABLE 1. SYNONYMOUS AND CONFUSING TERMS WITH APICAL GROOVE.

Term	Species	Authors	Original authors' interpretations	Present author's interpretations
Apical trough (Apical groove)	<i>Noctiluca scintillans</i>	KOFOID (1920), KOFOID & SWEZY (1921)	Anterior component of sulcus	Apical groove
Apical loop (Anterior loop)	<i>Cochlodinium cereum</i> <i>Cochlodinium conspiratum</i> <i>Cochlodinium scintillans</i> <i>Cochlodinium strangulatum</i>	KOFOID & SWEZY (1921)	Anterior extension of sulcus	Anterior extension of sulcus
Apical loop (Anterior loop)	<i>Cochlodinium clarissimum</i> <i>Nematodinium partitum</i> <i>Pouchetia</i> (= <i>Warnowia</i>) spp.	KOFOID & SWEZY (1921)	Anterior extension of sulcus	Anterior extension of cingulum
Apical loop (Anterior loop)	<i>Cochlodinium miniatum</i> <i>Cochlodinium vinctum</i> <i>Katodinium dorsalsulcum</i> <i>Cochlodinium heterolobatum</i> <i>Gymnodinium gracile</i> <i>Gymnodinium striatissimum</i>	KOFOID & SWEZY (1921) LEBOUR (1925) HULBURT et al. (1960) SILVA (1963) ELBRÄCHTER (1979)	Anterior extension of sulcus	Apical groove
Acrobase	<i>Gyrodinium pavillardii</i> <i>Amphidinium subsalsum</i> <i>Gymnodinium splendens</i> <i>Gymnodinium maquelannese</i> <i>Gymnodinium holophilum</i> <i>Massartia asymmetrica</i> <i>Polykrikos schwartzi</i>	BIECHELER (1934) BIECHELER (1952) CHATTON & HOVASSE (1934)	Different structure from sulcus	Apical groove
Carinal groove	<i>Ptychodiscus brevis</i> (= <i>Gymnodinium breve</i>)	STEIDINGER (1979)	Different structure from sulcus	Apical groove

The apices of some *Gymnodinium* and *Gyrodinium* surrounded by the apical groove are similar to the apical features of fossil *Dinogymnium* which has an opening at the apex. EVITT (1967) and EVITT et al. (1967) noted that the fossils were cysts and the opening at the apex was the archeopyle from which the motile cell excysted. MAY (1976) suggested, however, that *Dinogymnium* showed a striking similarity in morphology to the motile stages of recent *Gymnodinium* and *Gyrodinium*, and *Dinogymnium* might represent ancestral motile stages but not cysts. Although it is still obscure whether the fossils are motile stages or cysts, the external features of these dinoflagellates present much interest in comparative morphology.

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Explanation of Plates

Plate I. Light and scanning electron micrographs showing apical grooves of unarmored dinoflagellates.

1. *Gymnodinium* sp. 1 (SEM), 2. *Gymnodinium abbreviatum* (SEM), 3. *Gymnodinium* sp. 2 (SEM), 4. *Gymnodinium aureum* (LM), 5. *Gym. aureum* (SEM), 6. *Gyrodinium dominans* (SEM), 7. *Gymnodinium nagasakiense* (SEM), 8. *Gymnodinium sanguineum* (SEM), 9. *Gyrodinium instriatum* (SEM). For explanation of symbols, see legend of Fig. 1. Scale bar=10 μ m.

Plate II. Light and scanning electron micrographs showing apical grooves of unarmored dinoflagellates.

10. *Gyrodinium glaucum* (LM with differential interference contrast), 11 and 12. *Gyr. glaucum* (SEM), 13. *Gyrodinium* sp. 1 (SEM), 14. *Gyrodinium pepo* (SEM). 15. *Gyrodinium spirale* (SEM), 16. *Gyrodinium* sp. 2 (SEM), 17. *Polykrikos kofoidii* (SEM), 18. *Polykrikos hartmannii* (SEM), 19. *Nematodinium armatum* (SEM). For explanation of symbols, see legend of Fig. 1. Scale bar=10 μ m.

Plate III. Scanning electron micrographs showing apical grooves of unarmored dinoflagellates.

20 and 21. *Warnowia* sp. 1 (SEM), 22 and 23. *Warnowia* sp. 2 (SEM), 24 and 25. *Warnowia* sp. 3 (SEM), 26 and 27. *Nematodinium* sp. 2 (SEM), 28. *Nematodinium* sp. 1 (SEM), 29 and 30. *Erythroapsidinium agile* (SEM). For explanation of symbols, see legend of Fig. 1. Scale bar=10 μ m.

PLATE I

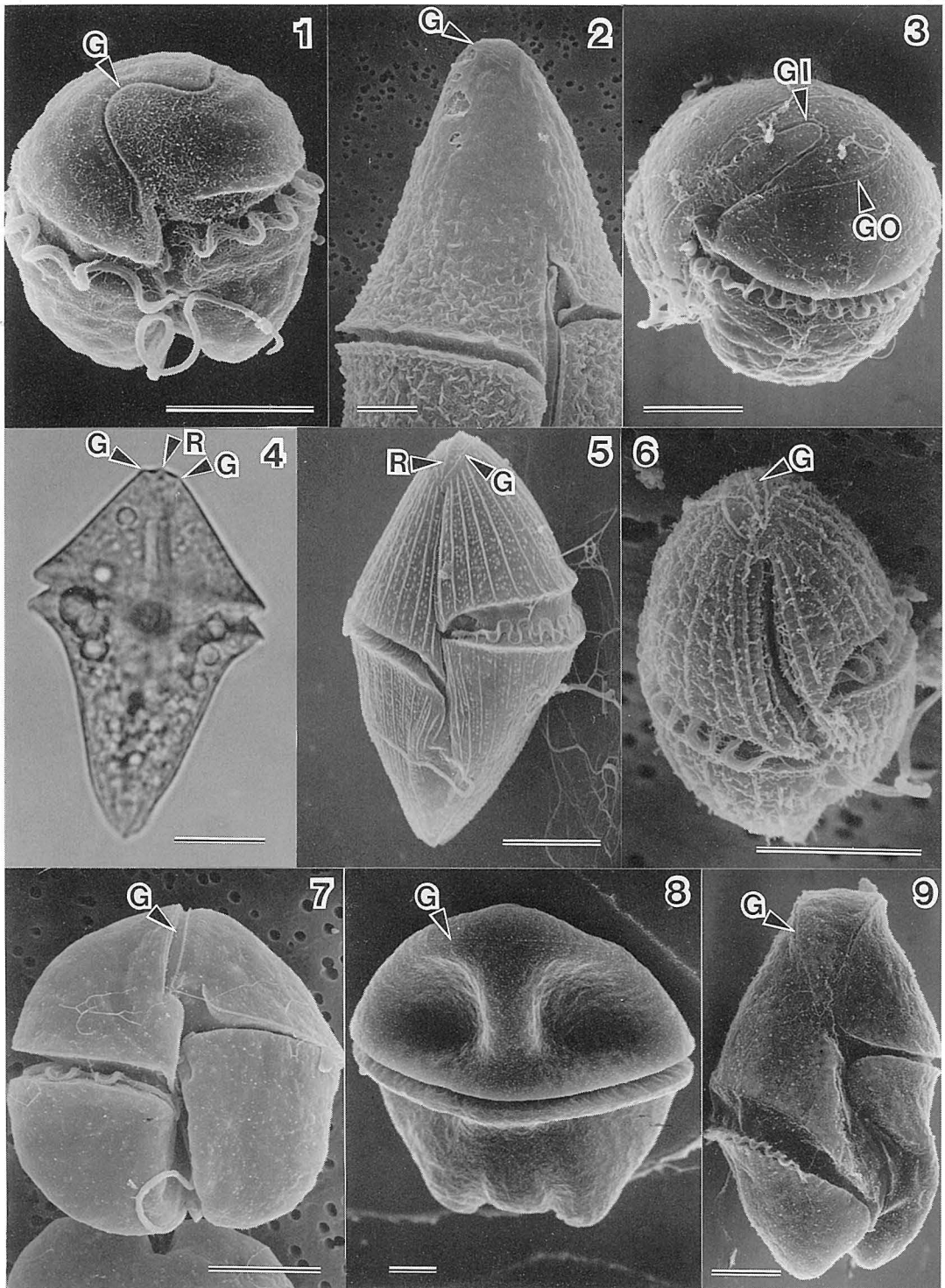


PLATE II

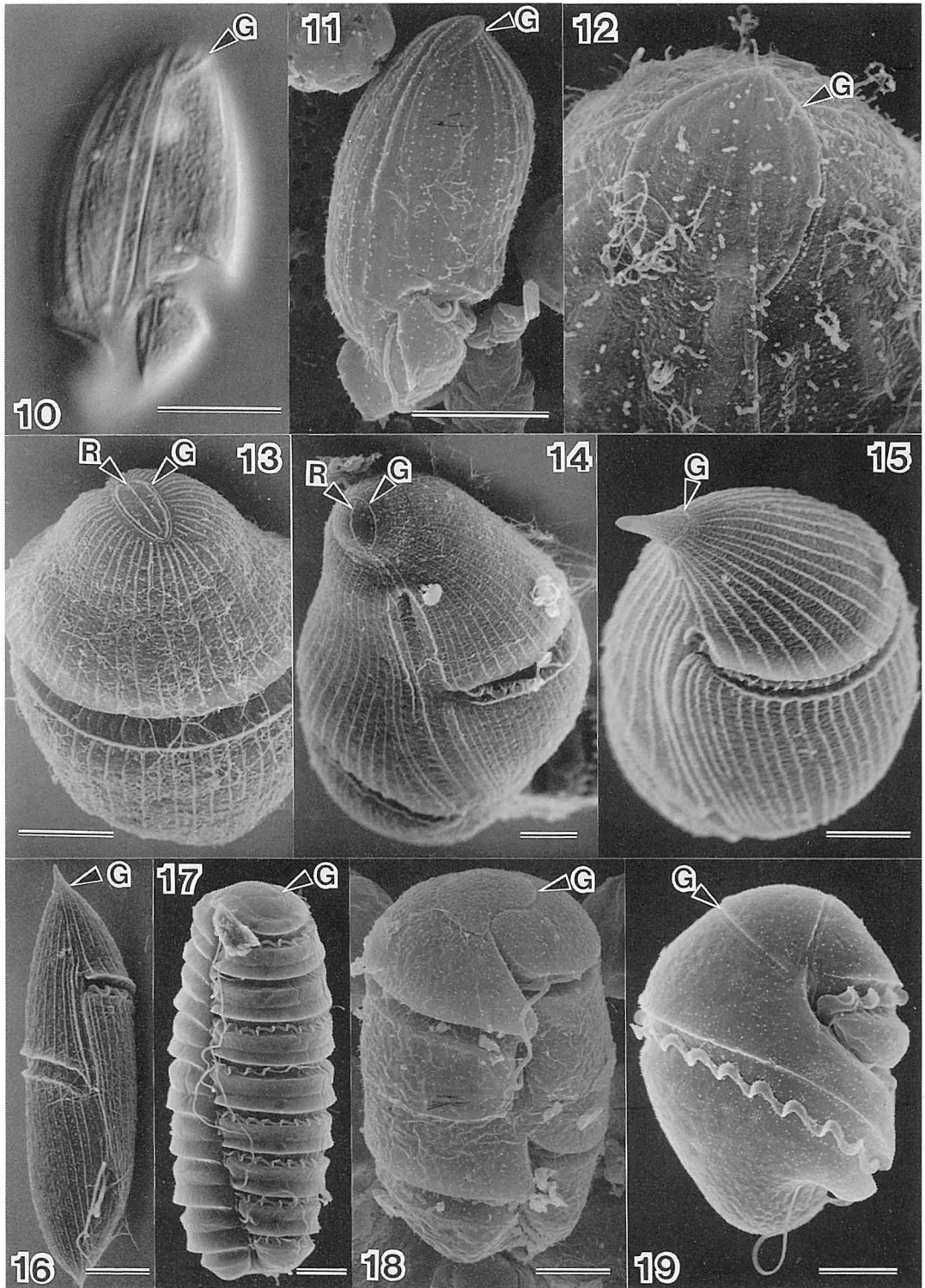


PLATE III

