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805. CYST AND THECATE FORMS OF *PYROPHACUS STEINII* (SCHILLER) WALL ET DALE, 1971*

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Abstract. The cyst form of *Pyrophacus steinii* (Schiller) Wall et Dale is clarified as a result of both field and laboratory observations. Thecate forms germinated from living cysts identified as *Tuberculodinium vancampoae* (Rossignol) Wall are assignable to *Pyrophacus steinii* on the basis of detailed observation of their plate distribution. Furthermore, many thecate specimens of *P. steinii* including living cysts identical with *T. vancampoae* were found in the summer plankton of Omura Bay.

According to these data, *T. vancampoae* is regarded as a resting cyst of not only *P. vancampoae* (Rossignol) but also *P. steinii*, and *P. vancampoae* is concluded to be a subspecies of *P. steinii*.

Introduciton

Tuberculodinium vancampoae (Rossignol) Wall 1967 has a lenticular body and a hypocystal archeopyle. Owing to these characteristic features, this species is easily distinguishable from other fossil dinoflagellate cysts.

T. vancampoae is also regarded as an useful indicator of the tropical to warm temperate environment based on the modern distribution in the Atlantic (Wall and Dale, 1971; Harland, 1982) and in the Pacific (Matsuoka, 1985). In Japan, this species has been reported from the middle Miocene to Early Pleistocene sediments in the Niigata area (Matsuoka, 1983) and in the Kinki area (Harada, 1984; Matsuoka, 1976). These two evidences suggest that *T. vancampoae* has a possibility to be an useful fossil as a tropical to warm temperate marine environment since the Neogene in Japan.

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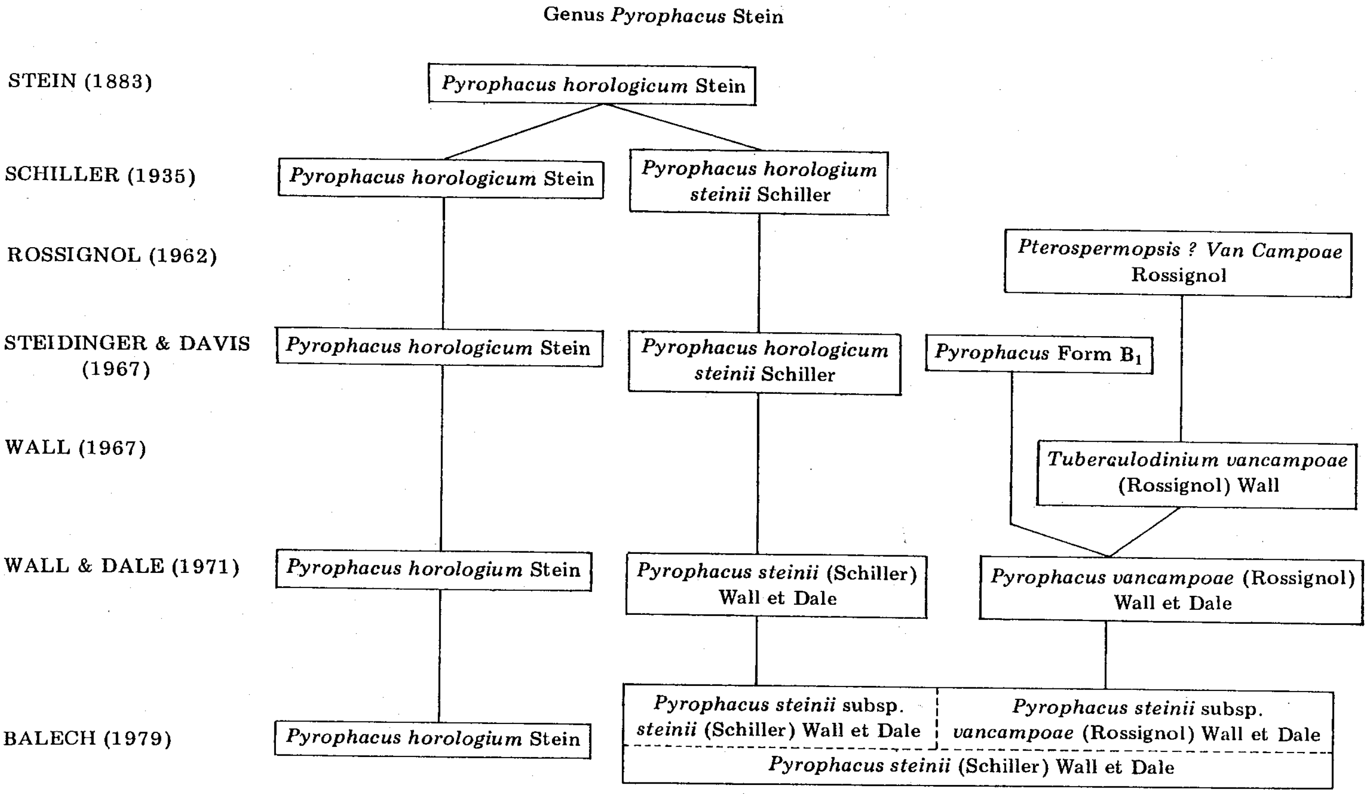
But the correlative thecate form of this cyst species have never been fixed until the present, because the plate formula (plate distribution pattern) which is the most important character for the thecate dinoflagellates is extremely variable in number and shape and is not useful in case of its parent thecate genus *Pyrophacus*. On the contrary, recent studies of modern dinoflagellate cysts reveal that the cyst morphotype (=cyst species) probably appear to be a natural species (Wall and Dale, 1968).

The present paper documents that the real taxonomic position of the thecate form of *T. vancampoae* is confirmed on the basis of the modern biological methodology and the paleontological account to be cyst form. And through the consideration about this species, the taxonomical significance in both modern and fossil dinoflagellate cysts will be clarified.

Historical review of study of *Pyrophacus* and *Tuberculodinium*

The genus *Pyrophacus* was first established



Text-fig. 1. Taxonomic history of the genus *Pyrophacus*.

by Stein (1883) and at that time this genus contained only one species, *P. horologium* Stein. Schiller (1935) recognized one species and one variety, *P. horologicum* Schiller and *P. horologicum* var. *steinii* Schiller based on difference of thecal plate formula in the genus.

Apart from plankton research, Rossignol (1962) found a peculiar fossil species from the Pleistocene sediments and named it *Pterospermopsis ? van campoae*. Later, Wall (1967) also obtained this species from deep sea core samples of the Caribbian Sea and erected the new cyst genus *Tuberculodinium* with emendation of *P. vancampoae*.

Steidinger and Davis (1967) noticed the presence of a characteristic form consisting of more plates than other varieties of *P. horologicum* and called this form *P.* Form B_1.

Wall and Dale (1971) carried out an incubation experiment of several cyst forms of the genus *Pyrophacus* and reexamined the classification of this genus. They concluded that *Tuberculodinium vancampoae* (Rossignol) is a cyst form of living *P.* Form B_1 of Steidinger and Davis, and as a result, they recognized the following three *Pyrophacus* species; *P. horologium* Stein, *P. steinii* (Schiller) Wall et Dale and *P. vancampoae* (Rossignol) Wall et Dale. But they did not find a cyst form for *P. steinii* (Schiller) Wall et Dale.

Recently, Balech (1979) reexamined the plate morphology of the genus *Pyrophacus* and recognized two species and one subspecies. He concluded that *P. vancampoae* (Rossignol) Wall et Dale is a subspecies of *P. steinii* (Schiller) because the difference in plate distribution between these two is rather than minor.

The taxonomic history of these species, subspecies, and varieties is shown in Text-fig. 1.

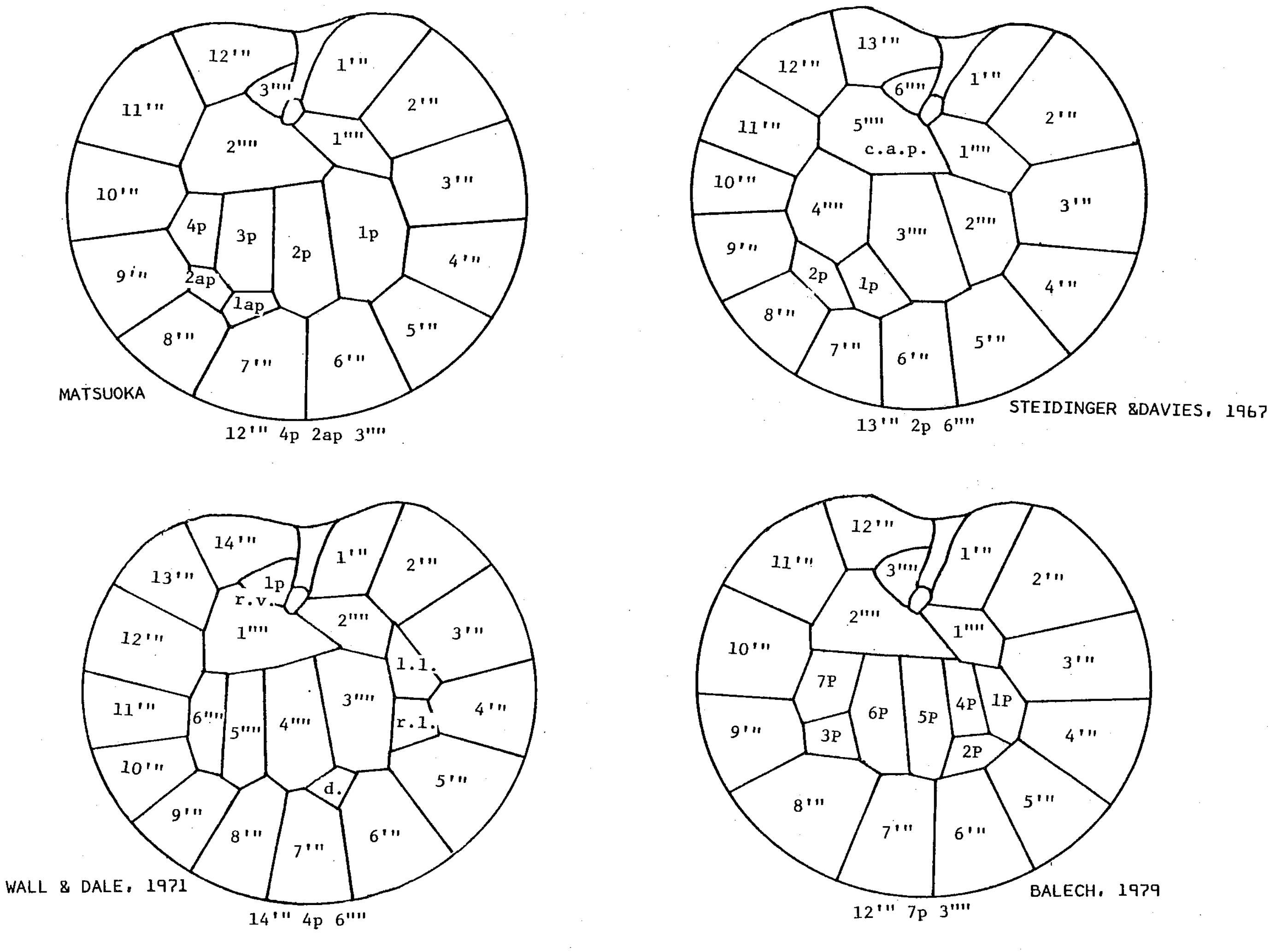
Materials and method

Samples containing various dinoflagellate cysts were collected in gravity cores from Omura Bay (Lat. 32°53′N, Long. 129°54′E, water depth −18 m), Nagasaki Prefecture, west Japan on 12 March, 1981. This bay is influenced by the warm Tushima Current, and its surface water temperature and chlorinity are as follows; 9 ± 2°C in winter, 30 ± 2°C in summer and 17.5—19‰ (Nagasaki Univ., 1976). The sediments are black and saplopelic mud sometimes containing small shell fragments.

Until the start of the incubation experiment, the samples were stored in the refrigerator for three to four months. The upper 2 cm of the core was provided for the investigation. Before incubation, the material (about 1.9 *ml*) was cleaned by sonification and sieved between 125 μm and either 37 μm or 20 μm stainless steel screen. The materials retained on the latter screens was washed in filtered sea water passed several times through a Whatman GF/C glass filter.

The isolated cysts picked up by a capillary pipet were placed in a culture dish containing ca. 1 *ml* filtered sea water. The incubation was carried out under the following condition; temperature 20—22°C, fluorescent light about 4,000 lux, light-dark cycle 14—10 hours.

For small thecate forms described in detail later, a vegetative newly formed cell was individually placed into another chamber. This operation was repeated until the appearance of the small thecate forms. The materials remaining after the incubation experiment was used for the investigation of cyst morphology. For palynological analysis, the usual procedure (Matsu-



Text-fig. 2. Hypothecal labeling systems of several authors and proposal of a new system. Abbreviation in Wall and Dale (1971) . . . r.v.; right ventral, l.l.; left lateral, r.l.; right lateral, d.; dorsal intercalary plate.

oka, 1985) was adopted.

Many vegetative cells included in surface plankton were also provided for the present study for taking the information of the plate formula in situ. These samples were collected from the surface water of Omura Bay (Lat. 32°54′N, Long. 129°52′E) in June of 1983 and July of 1984 by net haul. At that time, the surface temperature was 20°C and 33.5‰ in salinity.

Labeling on the antapiral plates of the genus *Pyrophacus* — Difference of labeling among several authors

Since Stein (1883) first described the genus *Pyrophacus*, the plate formula of this genus has not been fixed, because it has considerable variation in plate number. In the description of *Pyrophacus* Form B_1, Steidinger and Davis (1967) noticed that a large and nearly triangular plate is always present just below the sulcus, and named it coupling antapical plate (C.A.P.) (Text-fig. 2). Wall and Dale (1971) proposed a new labeling system and later Balech (1979) suggested another one. But there are major differences between these two in the antapical series (Text-fig. 2). According to Wall and Dale (1971), the distinctive and larger triangular plate which always contacts the small elliptical posterior sulcal platelet is the first antapical plate (1′′ ′′), the plate which constantly occupies the left position of the 1′′ ′′ plate is the second antapical plate (2′′ ′′) and the plate placed above the 1′′ ′′ plate is the right ventral posterior intercalary plate (r.v.p.). The plates which always contact the 1′′ ′′ and 2′′ ′′ plates are other antapical plates, and those between these and the postcingulars are posterior intercalary plates.

Balech's system is as follows; the antapical series consists of three plates which always surround the sulcal posterior platelet. The left plates is the first antapical plate (1′′ ′′), the center is the second (2′′ ′′) and the right is the third (3′′ ′′). Other plates between these and the postcingular series are posterior intercalary plates.

A new nomenclature, especially in the hypotheca

In all species of *Pyrophacus*, three plates are always present around the small posterior sulcal platelet. These three plates are regarded as the first, second and third antapical plates. The second one is the same as C.A.P. of Steidinger and Davis (1976). One to five, or occasionally more plates occupy the position between the antapical and postcingular series. These are regarded as members of the posterior intercalary series.

In the cyst, two to four, occasionally five paraplates similar to these intercalary plates in shape and position form an archeopyle. This suggests that these intercalary plates are of one plate series.

In *P. steinii*, additional plates that are usually smaller than the posterior intercalaries are present between the posterior intercalary and postcingular series. In the present work, these plates are newly named as additional posterior intercalary plates (a.p.). They have never developed in other thecate dinoflagellates.

Similarity of the plate formula in related taxa

Fragilidinium heterolobum Balech ex Loeblich, which is closely related to the genus *Pyrophacus* in having a similar plate distribution in the hypotheca. The plate formula of this species was first suggested by Balech (1979) as follows; Po, 4′, 9′′, 12c, 7′ ′′, 2′′ ′′, 1p and 6s. But in the figure shown by Balech (1979, Fig. 3), the 12c platelet is different in shape from other cingular platelets and occupies the position between the cingulum and sulcus. If this platelet is not seen as a part of the cingulum but as a part of the sulcus, the 7′ ′′ plate which directly contacts this platelet is not a postcingular. Based on this viewpoint, three antapical plates surround the small sulcal posterior platelet and the plate formula in the hypotheca should be corrected as follows; 11c, 6′ ′′, 3′′ ′′, 1p and 7s. This plate distribution around the sulcus is fundamentally the same in both *Fragilidinium* and *Pyrophacus*.

Observation in unialgal culture

Many and various dinoflagellate cysts were recovered from the surface sediments of Omura Bay. Based on the morphological characteristics, mentioned later in detail, the cysts identifiable as *T. vancampoae* (Rossignol) were selected for unialgal culture. For morphological investigations, both living and empty cysts were observed under optical microscope. Living cysts were selected for germination and incubation experiments. Twenty living cysts were placed in a single chamber of the culture dish and then eighteen cysts were excysted and developed in thecate vegetative cells. Most of these vegetative cells were reproduced asexually, produced many vegetative daughter cells. Furthermore, several cells were continued to divide for about two weeks. After several divisions, these thecate cells became small spherical thecate cells.

Living cyst (Pl. 36, Figs. 4a, b):—Living cysts which are pale brown with many small spherical oil or starch particles and one large red pigmented body are selected for the germination experiment. Even cysts with breaks in the distal extremities of large processes or the autophragm are excysted and produced normal thecal plates.

The cysts are ca. 80 μm in lateral diameter and ca. 55 μm in length. They are flattened and nearly circular in apical-antapical view. Many large barrel-shaped processes ornament the cyst body. The paratabulation indicated by the processes and archeopyle is 5—8′, 9—11″, 0c, 10—11′″ and (4—5)″″ + 2—4@ (Table 1). The symbol (@) indicates the number of paraplates consisting of the operculum in the cyst, and is common in this text and figures. The morphological features closely resemble those of the empty cysts recovered from Omura Bay. Based on these features, the living cysts are clearly identified as *T. vancampoae*.

Thecate form (Pl. 37, Figs. 2—8, 10a—12; Pl. 38, Figs. 1, 3, 5—7, 10—13; Pl. 39, Figs. 2, 4, 5—7):—Most of the living cysts were germinated within two to five days. After excystment, only one thecate vegetative cell (=germinated cell) appeared in the culture chamber. This cell was larger than any of the subsequent vegetative daughter cells. The plate formulae of many thecate specimens produced from living cysts were investigated. As compared with the same observations made of many thecate specimens collected from the plankton in Omura Bay.

As a result, the laboratory-excysted vegetative cells show a relatively wide variation in number of plates (Table 1). The cultured specimens have more plates than those obtained from the plankton. In vegetative cells derived from the plankton and excystment, however, the plates are arranged in the usual apical, precingular, cingular, postcingular and antapical series. The fundamental plate pattern in these specimens is as follows.

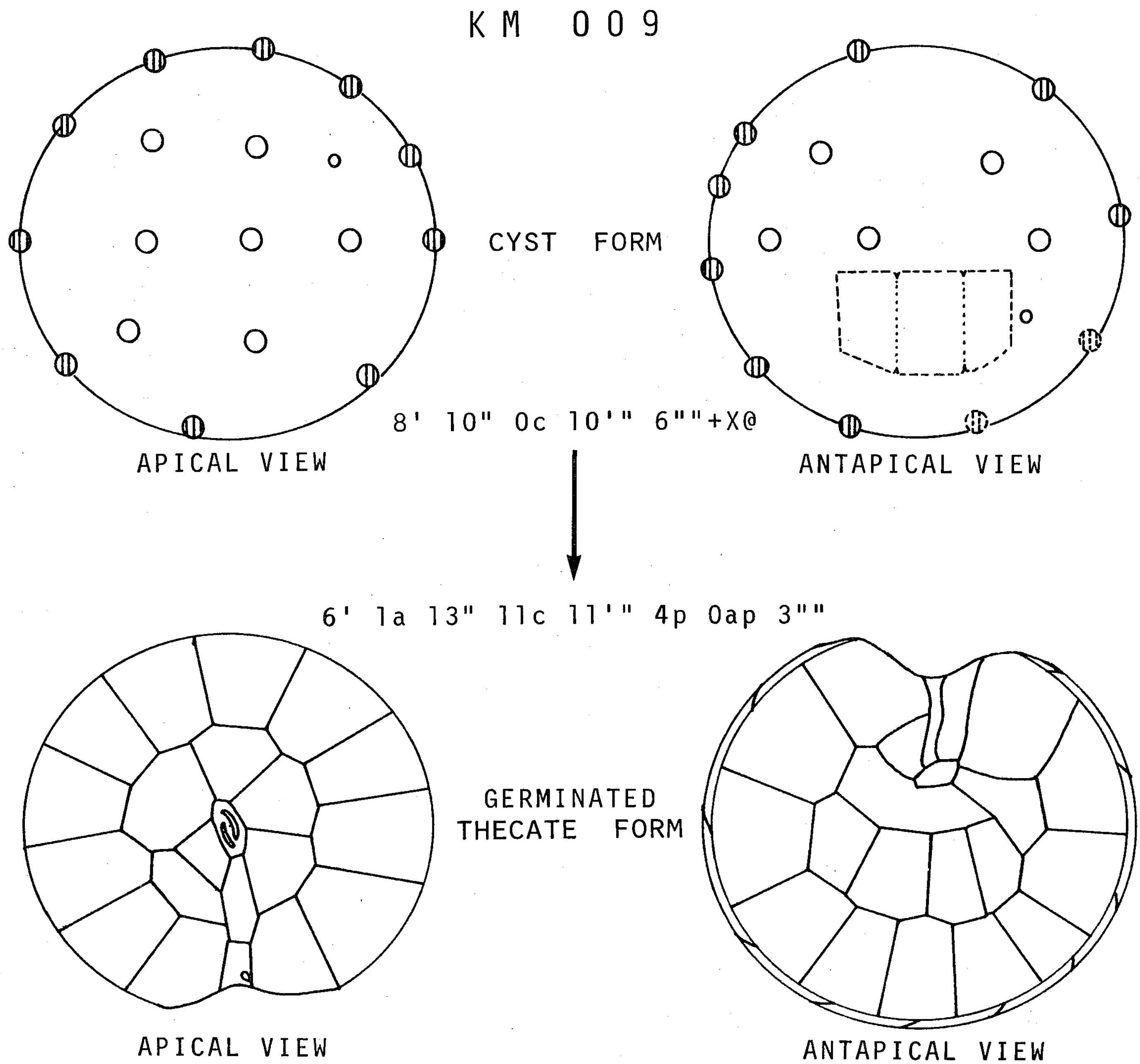
The apical pore platelet is roughly ellipsoidal, but polygonal in detail, and its longest axis is slightly oblique (Pl. 36, Fig. 7). The two apical pores are linear and arched in shape, and the dorsal one is larger than the other. The apical series consists of six to eight plates. The 1′ plate was asymmetrical and antero-posteriorly romboidal in shape and bears a small pore, probably the "ventral pore", in its posterior part. Other apical plates are pentagonal or hexagonal in shape and similar in height. One to two intercalary plates, which are usually smaller than the apicals, are observed in some specimens. The precingular series is made up of nine to fourteen plates. The first (1″) and the last (9″, 10″, 11″, 12″, 13″ or 14″) plates are shorter and always trapezoidal. The other plates are trapezoidal or pentagonal in shape.

The cingulum is slightly indented and the number of platelets in it is basically the same as the number of postcingulars. They always remain connected to the hypotheca, when the theca splits into two hemispherical parts. Each plate has perforations arranged nearly parallel to the shallow cingular list. The postcingular series consists of ten to fourteen plates. The first (1′″) plate is nearly orthogonal and the last (10′″, 11′″, 12′″, 13′″ or 14′″) plate is roughly triangular but irregularly trapezoidal in detail. The ventral plates are usually shorter than the dorsal ones. The postcingular plates

Table 1. Paratabulation of living cysts used in incubation experiment and plate formula of germinated and subsequent daughter cells.

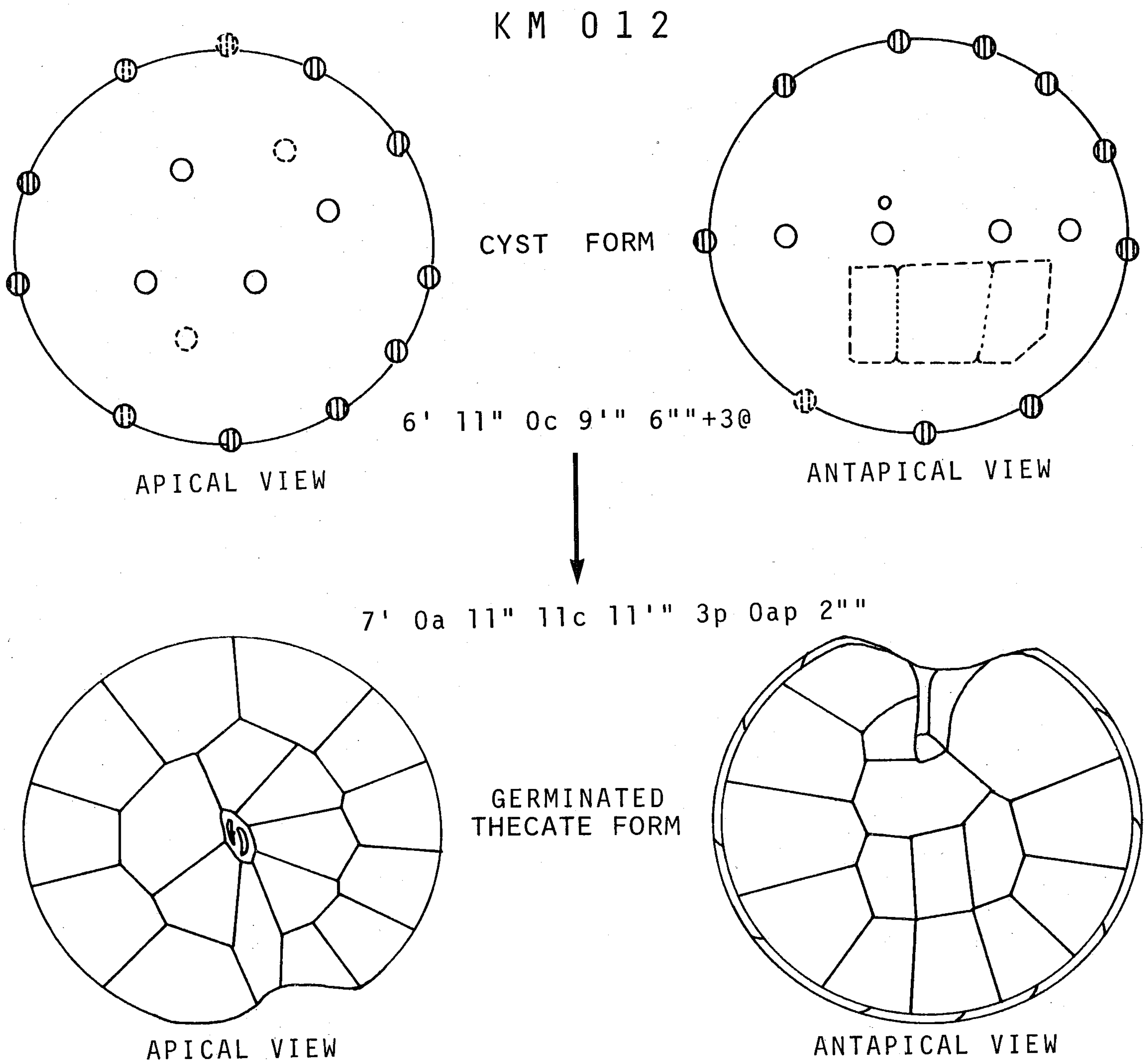
Speciman	Paratabulation of cyst	Plate formula of germinated cell	Plate formula of daughter cells
KM 001	not determined	7′ 1a 13″ 12c 12‴ 2p 1ap 3⁗	not produced
KM 002	not determined	8′ 0a 13″ 11c 11‴ 4p 0ap 3⁗	8′ 0a 13″ 11c 11‴ 4p 0ap 3⁗ 8′ 0a 11″ 11c 11‴ 3p 0ap 3⁗
KM 003	7′ 9″ 0c 10‴ 4⁗+X@	8′ 0a 12″ 11?c 11‴ 3p 1ap 3⁗	7′ 0a 12″ 12c 12‴ 3p 0ap 3⁗
KM 004	6?′ 10″ 0c 10‴ ?⁗	not germinated	
KM 005	not determined	7′ 0a 12″ 12?c 12‴ 4p 1ap 3⁗	7′ 0a 12″ 12c 12‴ 4p 0ap 3⁗ 7′ 0a 12″ 12c 12‴ 3p 1ap 3⁗
KM 006	not determined	6′ 1a 9″ 10?c 10‴ 2p 0ap 3⁗	7′ 0a 12″ 10?c 10‴ 4p 0ap 3⁗ 7′ 0a 12″ 12?c 12‴ 2p 0ap 3⁗
KM 007	6′ 10″ 0c 10‴ 5⁗+2@	7′ 1a 12″ 12?c 12‴ 3p 1ap 3⁗	7′ 1a 12″ 12c 12‴ 3p 1ap 3⁗ 8′ 0a 12″ 12c 12‴ 3p 0ap 3⁗ 8′ 2a 12″ 12c 12‴ 4p 0ap 3⁗ 8′ 2a 12″ 12c 13‴ 4p 1ap 3⁗ 8′ 2a 12″ 12c 13‴ 4p 1ap 3⁗
KM 008	7′ 10″ 0c 11‴ 4⁗+3@	7′ 0a 12″ 12c 12‴ 3p 0ap 3⁗	7′ 0a 12″ 12c 12‴ 3p 0ap 3⁗
KM 009	8′ 10″ 0c 10‴ 6⁗+3@	6′ 1a 13″ 11c 11‴ 4p 0ap 3⁗	7′ 0a 12″ 12?c 12‴ 3p 1ap 3⁗ 7′ 0a 11″ 11?c 11‴ 3p 0ap 3⁗ 7′ 0a 12″ 12c 12‴ 4p 0ap 3⁗ 6′ 1a ?″ 12c 11‴ 3p 0ap 3⁗ ---------- 12c 12‴ 5p 0ap 3⁗ ---------- 11c 11‴ 5p 0ap 3⁗ ---------- 11c 11‴ 5p 0ap 3⁗ ---------- 11c 11‴ 3p 1ap 3⁗
KM 010	6′ 11″ 0c 10‴ 4⁗+3@	7′ 0a 11″ 11c 11‴ 4p 0ap 3⁗	7′ 0a 12″ 12c 12‴ 3p 1ap 3⁗ 7′ 0a 11″ 11?c 11‴ 2p 0ap 3⁗ 7′ 0a 12″ 12c 12‴ 4p 0ap 3⁗ 7′ 0a 13″ 13c 13‴ 4p 0ap 3⁗ 7′ 0a 12″ 13?c 13‴ 4p 0ap 3⁗ ---------- 11c 11‴ 4p 0ap 3⁗ ---------- 11c 11‴ 3p 0ap 3⁗ ---------- 12c 12‴ 4p 0ap 3⁗ ---------- 13c 13‴ 3p 0ap 3⁗
KM 011	5?′ 10″ 0c 10‴ 4⁗+X@	7′ 0a 11″ 12c 12‴ 2p 0ap 3⁗	not produced
KM 012	6′ 11″ 0c 10‴ 5⁗+X@	7′ 0a 11″ 11c 11‴ 3p 0ap 2⁗	7′ 0a 11″ 11c 11‴ 3p 0ap 3⁗ 7′ 0a 12″ 12c 12‴ 3p 0ap 3⁗ 7′ 1a 11″ 11c 11‴ 3p 0ap 3⁗ ---------- 12c 12‴ 3p 1ap 3⁗ ---------- 12c 12‴ 3p 0ap 2⁗ ---------- 13c 13‴ 3p 0ap 3⁗ ---------- 10c 10‴ 2p 0ap 3⁗
KM 013	7′ 10″ 0c 10‴ 5⁗+3@	7′ 1a 13″ 14c 14‴ 4p 1ap 3⁗	7′ 1a 13″ 14c 14‴ 4p 0ap 3⁗ 7′ 1a 13″ 14c 13‴ 4p 0ap 3⁗ ---------- 12c 12‴ 2p 1ap 3⁗ ---------- 12c 12‴ 3p 0ap 3⁗ ---------- 14c 14‴ 4p 1ap 3⁗
KM 014	not determined	7′ 2a 11″ 10c 10‴ 3p 0ap 3⁗	not produced
KM 015	not determined	---------- 12c 12‴ 3p 0ap 3⁗	---------- 12c 12‴ 3p 0ap 3⁗
KM 016	not determined	7′ 0a 12″ 12c 12‴ 3p 0ap 3⁗	7′ 1a 12″ 12c 12‴ 3p 0ap 3⁗ 7′ 0a 12″ 12c 12‴ 3p 1ap 3⁗ 7′ 0a 12″ 12c 12‴ 2p 0ap 3⁗ ---------- 12c 12‴ 4p 1ap 3⁗ ---------- 12c 12‴ 4p 0ap 3⁗
KM 018	6?′ 8″ 0c 8‴ 5⁗+X@	7′ 1a 12″ 13c 13‴ 3p 0ap 3⁗	7′ 1a 12″ 12?c 12‴ 3p 0ap 3⁗ 6′ 1a 12″ 13c 13‴ 3p 0ap 3⁗
KM 019	not determined	7′ 2a 13″ 12c 12‴ 4p 0ap 3⁗	not produced
KM 020	7′ 10″ 0c 10‴ 4?⁗+X@	7′ 0a 10″ 10c 10‴ 2p 0ap 3⁗	7′ 0a 10″ 11c 11‴ 2p 0ap 3⁗ 7′ 0a 12″ 12c 12‴ 3p 0ap 3⁗ 6′ 4a 12″ 11c 11‴ 3p 1ap 3⁗ 7′ 0a 11″ 11c 10‴ 2p 0ap 3⁗ ---------- 11c 11‴ 4p 0ap 3⁗
Composite	5—8′ 9—11″ 0c 10—11‴ 4—5⁗+2—3@	6—8′ 0—2a 9—14″ 10—14c 10—14‴ 2—4p 0—2ap 2—3⁗	6—8′ 0—4a 11—13″ 10—14c 10—14‴ 2—5p 0—1ap 2—3⁗
C 949*	data not provided	7′ 3a 15″ Xc 13‴ 2p 5⁗	
C 955*	data not provided	7′ 2a 13″ Xc 13‴ 1p 5⁗	8′ 0a 13″ --------------------

*Incubated specimens of Wall and Dale (1971)



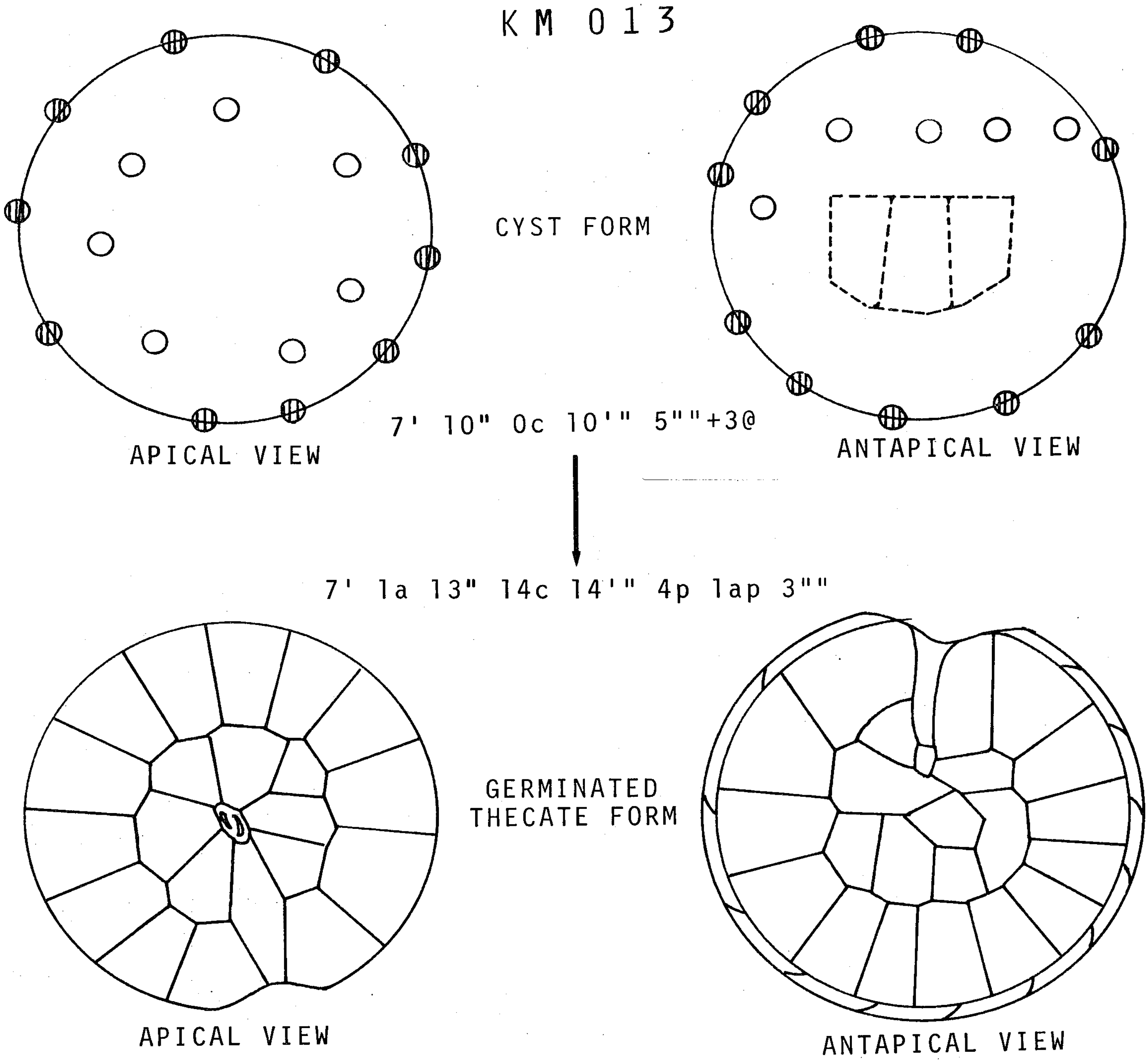
Text-fig. 3a. Cyst-theca relationships of *Pyrophacus steinii* (Schiller) Wall et Dale based on incubation experiments. 3a; Specimen KM 009, 3b; Specimen KM 012, 3c; Specimen KM 013, 3d; Specimen KM 020.

are also covered with coarse granules and perforated many small pores linearly arranged near the cingulum. The plates possess distinct growth or intercalary bands in mature spcimens. There are three antapical plates that always surrounded the small posterior sulcal platelet. The 1′′′′ plate is an irregularly pentagonal to hexagonal shape equatorially expanded. The characteristic 2′′′′ plate is the largest and is nearly triangular in shape. The triangular and smaller 3′′′′ plates is also nearly in the sulcus and contacts the last postcingular plate and 2′′′′. The posterior intercalary plates are also variable in number from two to five. The 1p plate is usually nearly trapezoidal and always contacts the 1′′′′ and 2′′′′ plates and a few postcingular plates. The



Text-fig. 3b.

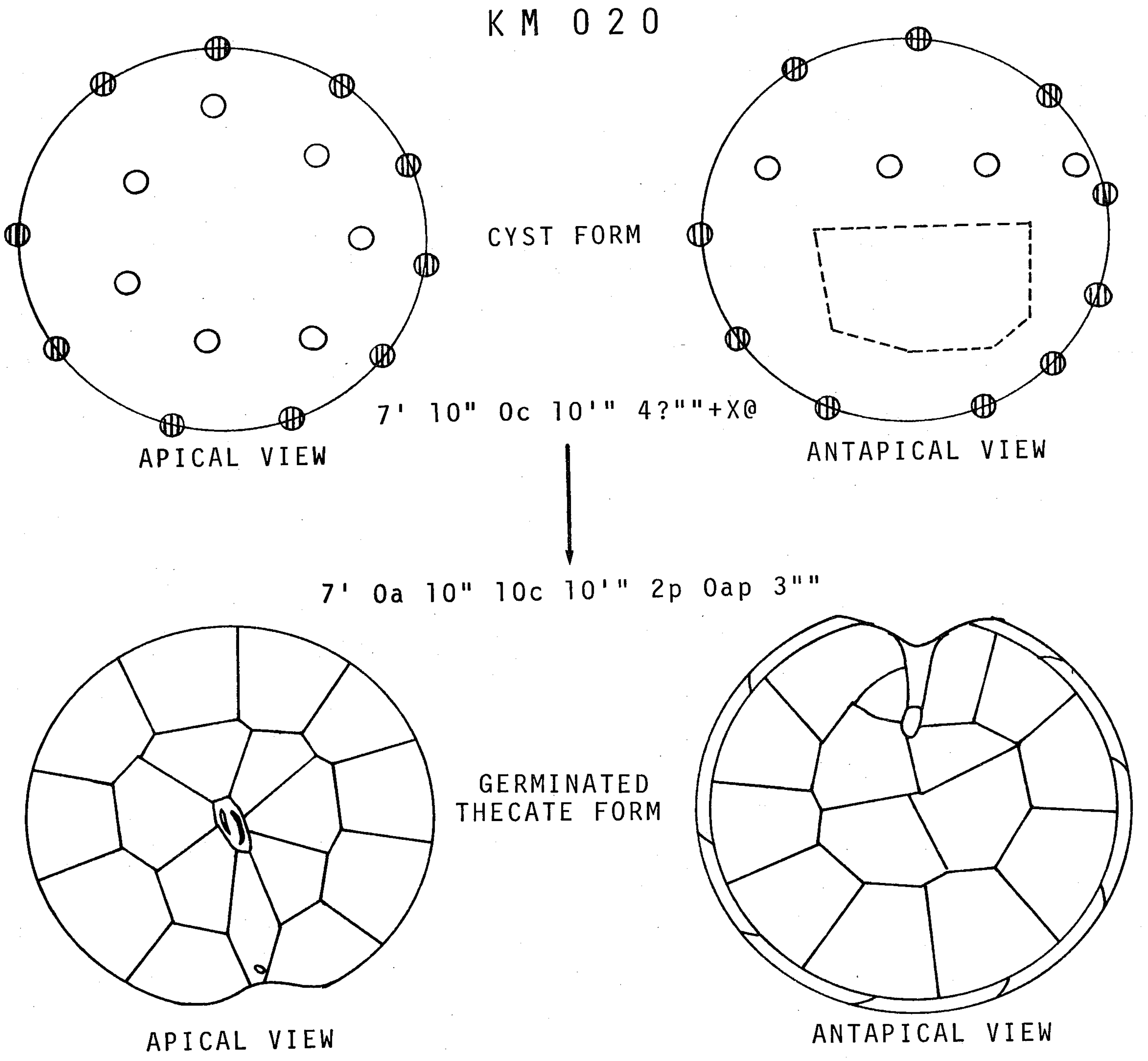
last posterior intercalary plate is irregularly hexagonal and occupies the position between the 2″ plates and dorsal postcingulars. The other plates are elongated trapezoids and are situated between the antapical and ventral postcingulars. There are a few additional plates between the posterior intercalary and/or antapical plates and the postcingulars. These additional posterior intercalary plates are usually smaller than the other posterior intercalaries and are variably pentagonal to hexagonal in shape. The sulcal region consists of eight platelets (Pl. 36, Fig. 6; Text-fig. 4). The rectangular anterior sulcal platelet is the largest and obliquely contacted the first and last cingular platelets. The posterior sulcal platelet is roundly triangular to ovoid in shape, and consistently surrounded by three antapical plates. The left sulcal platelet is larger than the right one. Both platelets are situated just anterior sulcal platelet. The right sulcal accessory platelet is roundly rectangular, and larger, and is located between the last



Text-fig. 3c.

cingular plate and the right sulcal platelet. The left sulcal accessory platelet has a round triangular shape. Two other small platelets are occurred in the middle of the sulcal region: median sulcal and anterior accessory platelets.

Small thecate form (Pl. 40, Figs. 1—12, Text-fig. 6):—The vegetative cell germinated from the incubated cyst becomes gradually smaller in diameter during asexual reproduction (Text-fig. 5). After six to eight divisions, the protoplasm is divided into four or eight smaller masses inside the parent theca (Pl. 36, Fig. 1). Subsequently, four or eight small cells appear in the culture chamber. These small forms are also covered with many thin thecal plates and platelets, but they are very different from the parent cells in size and shape. These small cells are ovoidal in shape, 36—37.2 μm long, 32—36 μm wide and 32—36 μm thick (dorso-ventrally) (Pl. 40, Figs. 1—4). Although there are slight

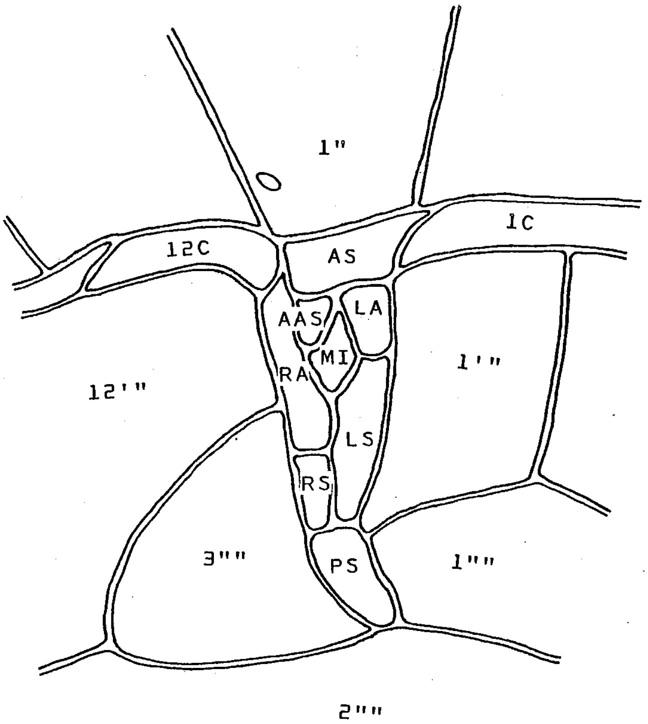


Text-fig. 3d.

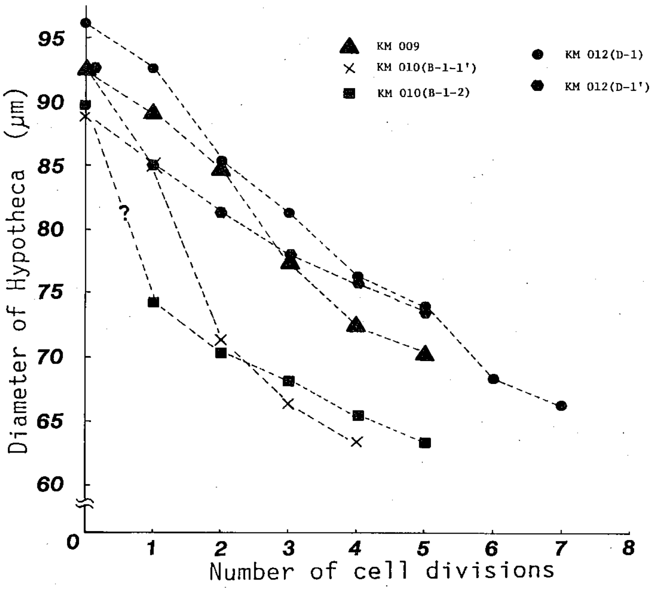
variations in number of plates, they total 38 to 39, excluding the sulcal and apical pore platelets. The plates are smooth and transparent without any ornamentation under optical microscope.

The apical pore plate is round hexagonal and has many very small perforations scattered around the margin, and two large arched slits in the centre (Pl. 40, Figs. 5, 10a, 11). The apicals consist of six to seven plates. The 1′ plate is nearly pentagonal in shape, but strongly expands antero-posteriorly and has a small and elongate perforation, possibly "ventral pore" on its posterior part (Pl. 40, Figs. 5, 12). Other apical plates are irregularly pentagonal or hexagonal in shape and of similar height.

There are no anterior intercalary plates. The precingular series consists of nine plates of similar height. The 3″, 4″, 6″ and 7″ plates are pentagonal and others trapezoidal.



Text-fig. 4. Plate and platelet distribution in the sulcus.



Text-fig. 5. Decrease in thecal diameter in relation to number of cell divisions.

The cingulum is relatively wide (0.11 to 0.13 of the cell length), laevorotary (left handed) displacement of one cingular width. When the

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Explanation of Plate 35

Figs. 1—3. *Tuberculodinium vancampoae* (Rossignol) Wall

Fig. 1. Fossil specimen from the Pleistocene upper Nishiyama Formation; apical view, showing apical and precingular barrel-shaped processed, Loc. Haizume, Niigata Prefecture, × ca. 250.

Fig. 2. Fossil specimen from the Pliocene lower Nishiyama Formation, antapical view, showing attached operculum and antapical processes, and a somewhat damaged archeopyle (arrow), Loc. Haizume, Niigata Prefecture, × ca. 250.

Fig. 3. Fossil specimen from the late Miocene Shiiya Formation, antapical view, showing attached operculum composed of three rectangular paraplates, Loc. Ishiji, Niigata Prefecture, × ca. 250.

Figs. 4a—5b. *Pyrophacus steinii* (Schiller) Wall et Dale from plankton sample of Omura Bay.

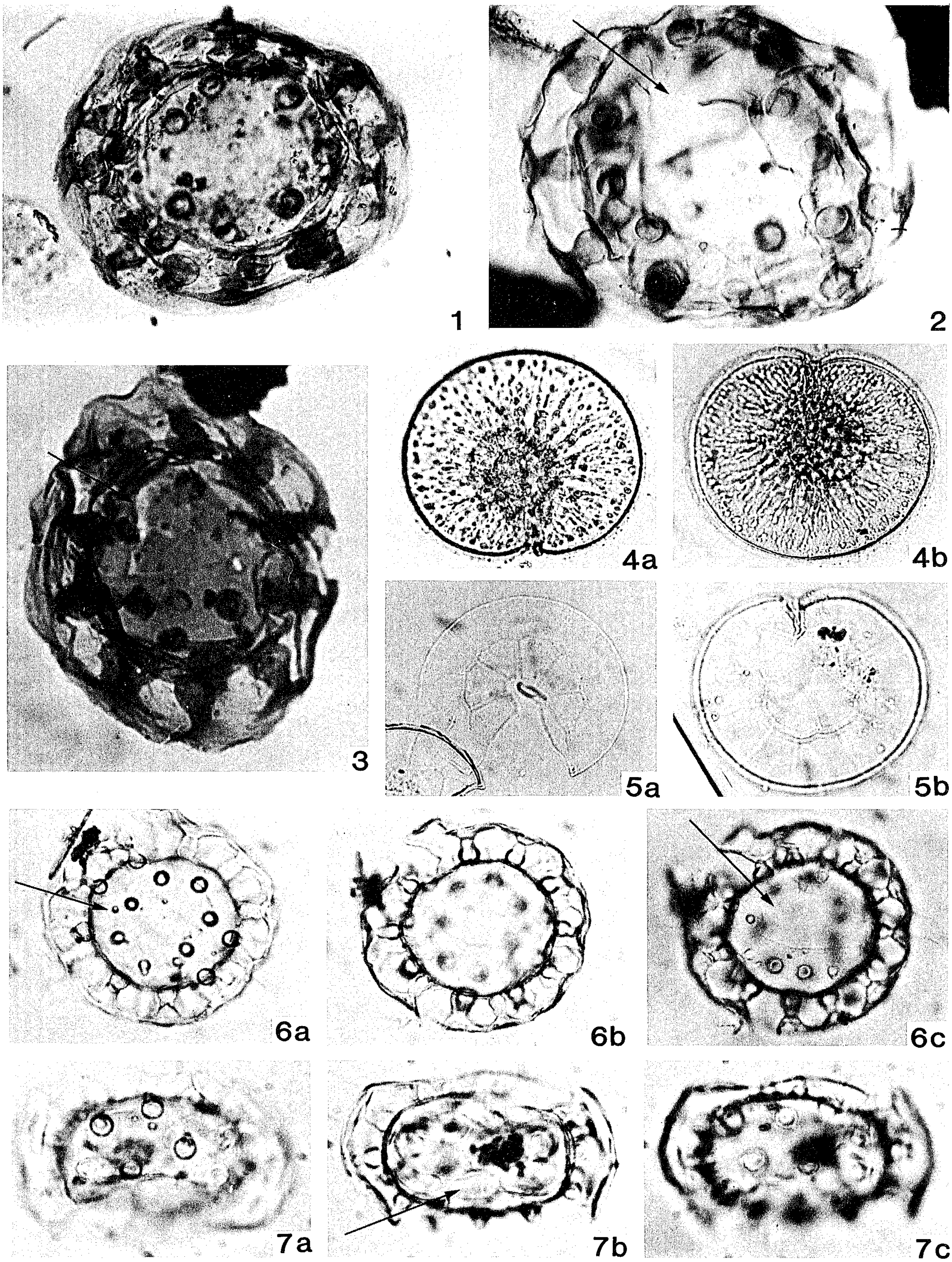
Figs. 4a—b. Living thecate vegetative cell containing a large nucleus, many chromatophores and food reserves. a; apical view, × ca. 310, b; antapical view, × ca. 310.

Figs. 5a—b. Vegetative cell theca, showing the distribution of major plates: 5a; apical view, 5b; antapical view; plate formula, Po, 7′, 0a, 12″, 12c, 12′ ″, 3p, 0ap and 3″ ″, × ca. 310.

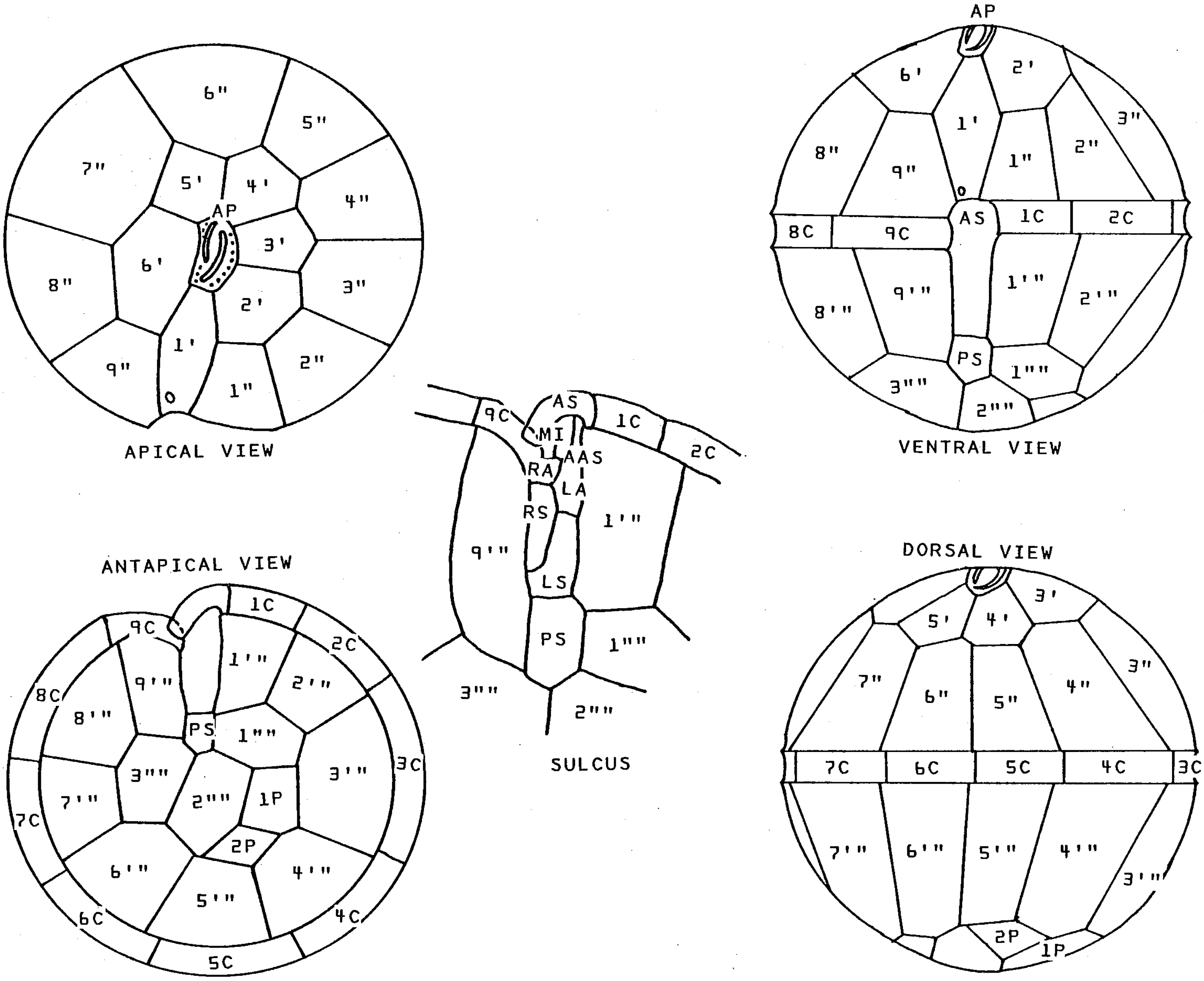
Figs. 6a—7c. *Tuberculodinium vancampoae* (Rossignol) Wall from surface sediments of Omura Bay.

Figs. 6a—c. Polar view, 6a; apical view, showing large apical and precingular processes and additional small, spherical apical processes (arrow), × ca. 235, 6b; optical cross section, 6c; antapical view, showing hypocystal archeopyle (arrow), × ca. 235.

Figs. 7a—c. Lateral view, 7b; optical cross section, showing hypocystal archeopyle (arrow), × ca. 235.


1
2
3
4a
4b
5a
5b
6a
6b
6c
7a
7b
7c

complete theca is broken and split into two the cingulum remained attaches to the hypotheca. The cingulum consists of nine rectangular platelets, wider than tall, and equatorially expanded. The 9c platelet somewhat invades the sulcus. The postcingulum also possesses nine plates. Some are trapezoidal, and similar in height to the precingulars. Other parts of the hypotheca are insufficiently clear in detail because it is easily deformed. Judging from relationships with the adjacent plates, there are one or two posterior intercalary plates. Three antapical plates always surround the posterior sulcal platelets, and these are variable in shape. The sulcus is narrow and almost straight, and did not reach the centre of the hypotheca. This area comprises of eight platelets of various shapes and sizes. The anterior sulcal platelet is the largest in shallow U-shape. The posterior sulcal platelet is also large and irregularly hexagonal. This platelet contacts the 1′″, 9′″, 1″″, 2″″ and 3″″ plates and the left sulcal platelet. The left sulcal platelet is large, L-shaped and occupies the position just anterior the posterior sulcal platelet. The elongated rectangular right sulcal platelet does not contact the posterior sulcal platelet. Four other small platelets are located between the left and right



Text-fig. 6. Diagram of the small thecate from of *Pyrophacus steinii* (Schiller) Wall et Dale. Specimen KM 012 D1-1.

sulcals and the anterior sulcal platelet.

The plate formula of these small thecate forms is interpreted as Po, 6—7′, 9″, 9c, 9‴, 1—2p, 3⁗ and 8s.

Cyst and thecate forms obtained from net haul and sediment samples

Cyst form:—The polar view in *T. vancampoae* is very different from the equatorial view. In the polar view, in which orientation most cysts are observed, the cyst is circular to roundly reniform, while in the equatorial view, it is a slightly round rectangular with weakly developed shoulders. The cyst wall consists of a thin, smooth and nearly transparent autophragm. The processes are hollow, and intratabular of two types. One is large and barrel- to dumbell-shaped, because it consists of two spherical parts with different diameters. In well-preserved specimens, the distal extremities of these processes are expanded to be flare-like and connected with adjacent ones. In this way, they often make an outer cyst wall. The other type of processes, a simple sphere, is rare. The walls of both types of processes are thin and smooth. These processes do not have any parasutural features at the proximal bases. These processes are regularly distributed in four latitudinal lines surrounded the cyst body. Judging from their position relative to the archeopyle and the plate distribution in the thecate form, these lines correspond to the apical, precingular, postcingular and antapical paraplate series. The apical area consists of six to eight large processes and sometimes a few small spherical processes as well. There is no process representing the apical pore platelet in the thecate form. The precingular area begins at the epicystal shoulder of the cyst body and includes eight to ten large processes. This area contained hardly any small spherical processes. The postcingulum is relatively variable in number of processes and is composed of nine

Table 2. Paratabulation of empty cysts recovered from the surface sediments of Omura Bay. The symbol @ indicates opercula in the hypocyst. 'S' means small spherical processes on the epicyst.

Paratabulation					Total number of processes
8′	12″	0c	12‴	5⁗+3@	37 + 3@
7′+1s	10″	0c	10‴	4⁗+3@	31 + 3@
7′+1s	10″	0c	12‴	4⁗+3 or 4@	33 + 3 or 4@
6′	10″	0c	11‴	4⁗+3@	31 + 3@
7′	10″	0c	9‴	3⁗+3@	29 + 3@
14s	9″	0c	9‴	5—6⁗+X@	-------
7′	10″	0c	12‴	3⁗+3@	32 + 3@
7′	9″	0c	12‴	3⁗+3@	31 + 3@
6′	9″	0c	9‴	4⁗+3@	28 + 3@
8′	11″	0c	11‴	5⁗+3@	33 + 3@
7′	10‴	0c	13‴	5⁗+3@	35 + 3@
*6—8′	9—12″	0c	9—13‴	3—5(6)⁗+3—4@	28—35+3—4@
**5—8′	8—13″	—	6—13‴	3—11⁗	
(7′	10″		10‴	8⁗)	

*composite paratabulation of empty cysts of Omura Bay

**composite paratabulation of cysts of Ivory Coast (Wall & Dale, 1971)

Explanation of Plate 36

Modern cyst and thecate forms of *Pyrophacus steinii* (Schiller) Wall et Dale collected from surface plankton of Omura Bay.

Figs. 1a—b. Gamete formation (?) showing eight small cells included within a normal vegetative cell, × ca. 310.

Fig. 2. Hypnozygote (?), theca containing a living cyst identified as *Tuberculodinium vancampoae* (Rossignol) Wall showing archeopyle suture preparing for germination (arrow) (interference contrast optics), × ca. 310.

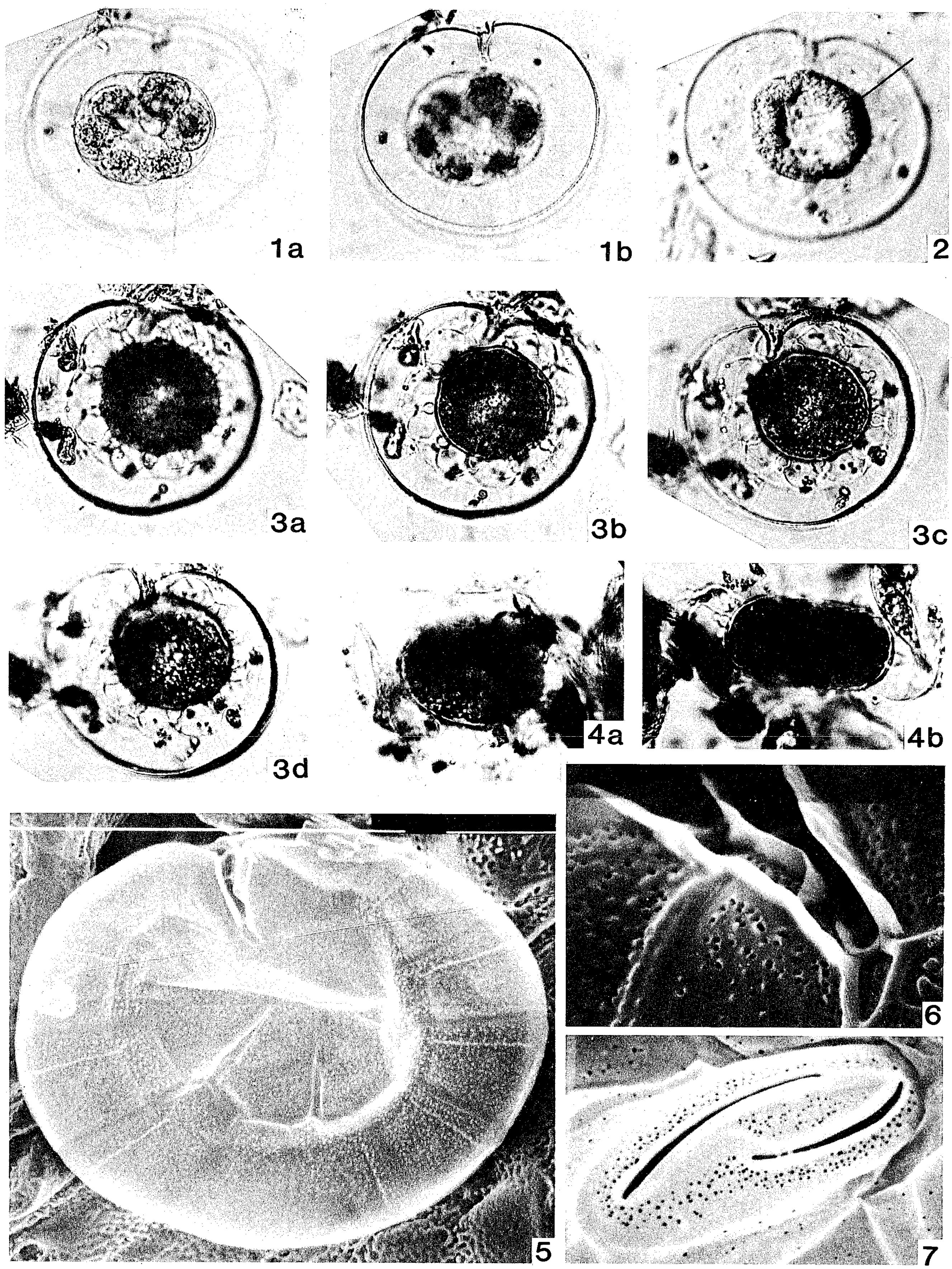
Figs. 3a—b. Hypnozygote (?), theca containing a living cyst, × ca. 310.

Figs. 4a—b. Living cyst probably recently freed from its parent theca. 4a; apical-antapical view, × ca. 310, 4b; lateral view, × ca. 310.

Fig. 5. Hypotheca of vegetative cell, showing well developed growth band and many small surface granules. SEM photograph, × ca. 700.

Fig. 6. Sulcus of the thecate cell. SEM photograph, × ca. 2500.

Fig. 7. Apical pore platelet of thecate cell. SEM photograph, × ca. 2500.


1a
1b
2
3a
3b
3c
3d
4a
4b
5
6
7

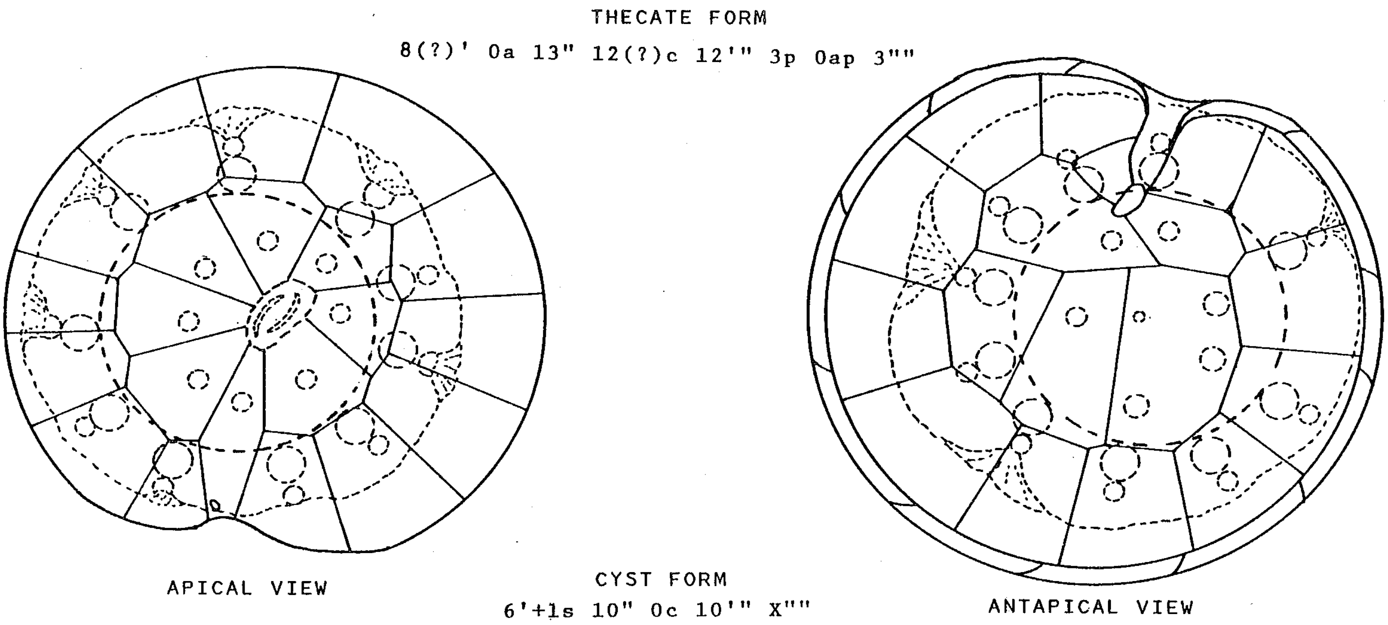
to thirteen large processes. These processes occur at another hypocystal shoulder. The antapical area has three to five large processes and the archeopyle, consisting of two to three, rarely four or five paraplates which are released at excystment. There are no processes or ornamentation between the pre- and post-cingular series. Therefore, the paracingulum is represented by the space between these two rows of processes. The parasulcal area is also not reflected by any morphological features.

Based on this evidence, most cysts recovered from Omura Bay possess 27 to 37 processes, including large and small spherical types and two to five paraplates corresponding to the archeopyle.

Thecate cell bearing living cyst (Pl. 36, Figs. 2, 3; Text-fig. 7):—The plankton sample collected from Omura Bay in June, 1983 and July, 1984 contained not only many thecate specimens identifiable as *P. steinii* (Schiller) but also a few living forms of *T. vancampoae* (Rossignol). Furthermore, rare of thecate cells filled not with protoplasm as observed at the motile stage but with a cyst were found in it (Pl. 36, Figs. 2, 3). Two thecate specimens enclosing the living cysts were examined for thecal tabulation and cyst paratabulation. One consists of eight apicals, thirteen precingular, twelve cingulars, twelve postcingular, three posterior intercalaries, three antapical plates and one apical pore platelet. Its plate formula is 8′, 0a, 13″, 12‴, 3p, 0ap and 3⁗. The paratabulation of the cyst included within the thecate cell is 6′ with one small process, 10″, 0c, 10‴ and ?⁗, and its archeopyle is not clear. In another specimen, although the plate formula in the epitheca can not be determined, the hypotheca contains twelve

Table 3. Plate formulae of thecae and paratabulation of living cysts contained within, from plankton samples of Omura Bay in June, 1983.

Plate formulae of thecae								Paratabulation on living cyst				
8(?)′	0a	13″	12(?)c	12‴	3p	0ap	3⁗	6′+1s	10″	0c	10‴	X⁗
---------?---------				12‴	3p	0ap	3⁗	8′+5(?)s	10″	0c	10‴	6⁗+3@



Text-fig. 7. Diagram of a theca containing a living cyst, collected from Omura Bay in June, 1983.

postcingulars, three posterior intercalaries and three antapicals. The paratabulation of the cyst is interpreted as 8′ (+ a few small processes), 10″, 0c, 10‴ and 4⁗ + 3@. The archeopyle consists of three nearly rectangular opercula, and has been already indicated by the boundary of three paraplates. Trabecula or small spherical processes are completely lacking. These paraplates are closely similar to the posterior intercalary plates in general shape, but smaller. Also, the orientation of the opercula is clearly different from that of the thecate form. The diameter of the cyst is nearly half of the thecate cell and resembles that of the temporary cyst produced by the usual asexual reproduction.

Morphological variation in thecate form

Variations in the cell shape and the plate pattern are seen in both field-collected and cultured specimens. Plates show wide variations in shape and number, while the cell shape was relatively consistent.

Cell shape:—All field specimens and most cultured specimens are lenticular in dorso-ventral view and roundly reniform in polar view. This is one of the most stable characters in the thecate form. But in speicmen labelled as KM 018 for example, all of the thecate cells derived from one cultured cyst are different from the progeny of the other cysts in cell shape (Pl. 38, Fig. 9). They have a normal-lenticular epitheca and a roundly conical hypotheca, and these features makes them longer than normal forms. On the other hand, the plate formula of these specimens 6—7′, 1a, 12″, 13c, 12—13‴, 3p, 0ap and 3⁗ with minor variability in number of plate; but this variation is quite similar to that of other cells.

Aberrant shape of plate:—The first apical plate is occasionally divided in the middle into two plates. In this case, the 1′ plate does not reach the cingulum and the ventral pore appears on the 1″ plate (Pl. 37, Fig. 2a; Pl. 39, Fig. 2a).

Explanation of Plate 37

Modern cyst and thecate forms of *Pyrophacus steinii* (Schiller) Wall et Dale obtained in unialgal culture.

Figs. 1—5. *Pytophacus steinii* (Schiller) Wall et Dale, Specimen KM 009.

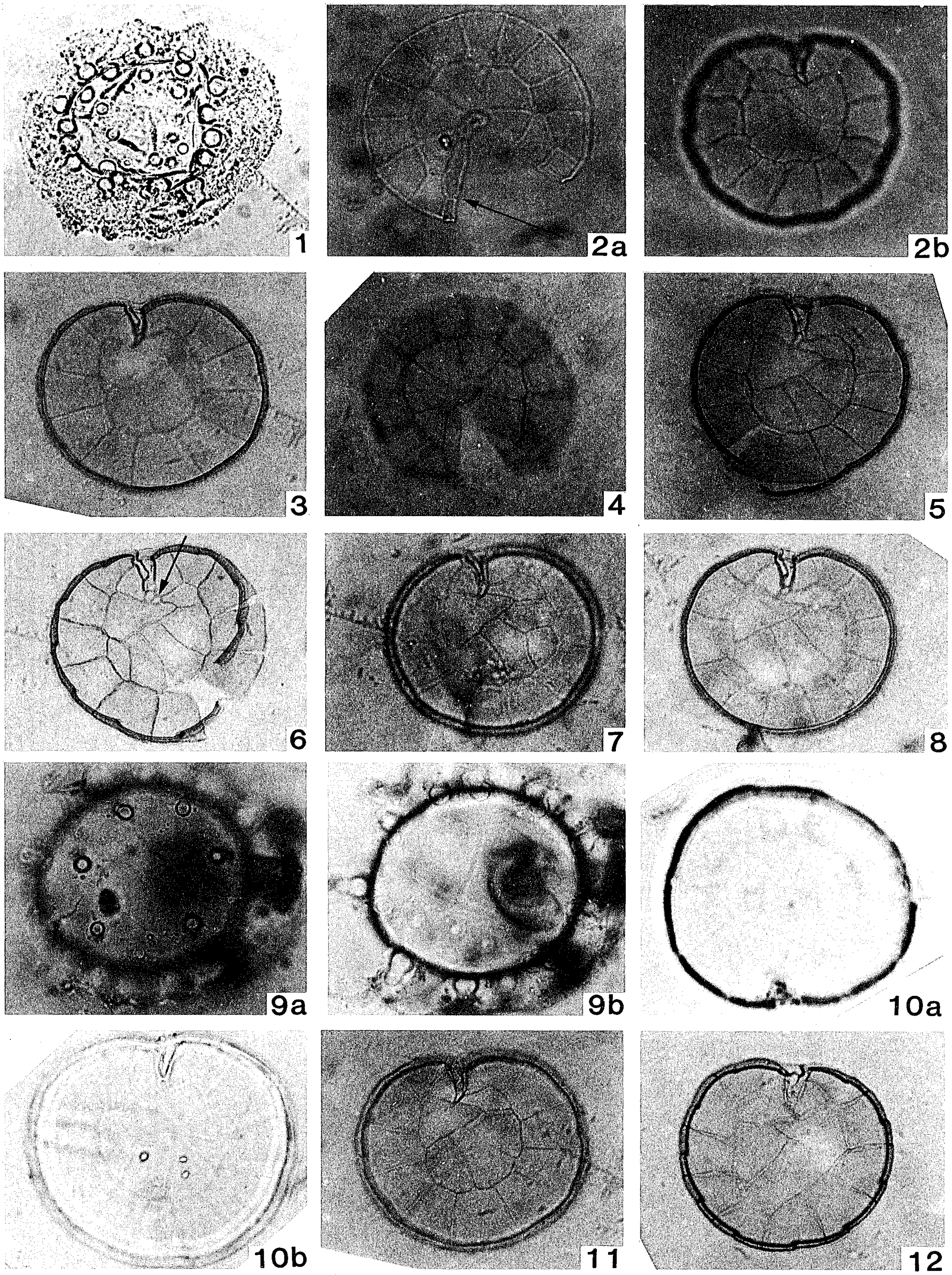
- Fig. 1. Cyst after germination, showing much compressed cyst body, × ca. 330.
- Figs. 2a—b. Newly germinated vegetative cell, 2a; epitheca, apical surface in antapical view, showing aberrant shape of the 1′ plate (arrow), × ca. 330, 2b; hypotheca, antapical surface in apical view, × ca. 330.
- Fig. 3. Hypotheca of daughter cell, antapical surface in antapical view, × ca. 330.
- Fig. 4. Epitheca of daughter cell, apical surface in antapical view, × ca. 330.
- Fig. 5. Hypotheca of daughter cell, antapical surface in antapical view, × ca. 330.

Figs. 6—8. *Pyrophacus steinii* (Schiller) Wall et Dale, Specimen KM 010.

- Fig. 6. Hypotheca of newly germinated vegetative cell, antapical surface in antapical view, showing additional small posterior sulcal platlet (arrow), × ca. 330.
- Fig. 7. Hypotheca of daughter cell, antapical surface in antapical view, × ca. 330.
- Fig. 8. Hypotheca of daughter cell, antapical surface in antapical view, × ca. 330.

Figs. 9a—12. *Pyrophacus steinii* (Schiller) Wall et Dale, Specimen KM 012.

- Fig. 9. Cyst after germination, 9a; apical surface, × ca. 360, 9b; antapical surface, showing attached operculum corresponding to three rectangular paraplates, × ca. 360.
- Figs. 10a—b. Newly germinated vegetative cell, 10a; epitheca, apical surface in apical view, × ca. 400, 10b; hypotheca, showing two antapical plates, antapical surface in apical view, × ca. 400.
- Fig. 11. Hypotheca of daughter cell, antapical surface in antapical view, × ca. 330.
- Fig. 12. Hypotheca of daughter cell, antapical surface in apical view, × ca. 330.


1
2a
2b
3
4
5
6
7
8
9a
9b
10a
10b
11
12

The posterior intercalary plates are normally rectangular or elongatedly pentagonal. But this plate series occasionally consists of two large septagonal and one nearly triangular plates. Furthermore, in specimens possessing extra posterior intercalary plates, the shape of the posterior intercalary plates also becomes irregular (Pl. 38, Fig. 13).

The second antapical plate was rarely absent (*e.g.* specimen labelled as KM 011) and then the first postcingular plate touched the second antapical plate (Pl. 37, Fig. 10b).

These aberrant plates appeared only in cultured specimens.

Number of plates:—The number of major plates and cingular platelets is more variable than the cell shape. The total number of plates ranges from 31 to 41. The plate formulae of freshly germinated cells vary. The composite formula is 6—8′, 0—2a, 9—14″, 10—14c, 10—14‴, 2—4p, 0—2ap and 2—3″″. The most common pattern is 7′, 0a, 11—12″, 12c, 12‴, 3—4p, 0ap and 3″″.

The progeny of these first cell has composite plate formulae 6—7′, 0—4a, 11—13″, 10—14c, 10—14‴, 2—5p, 0—1ap and 2—3″″. The most common pattern is 7′, 0a, 12″, 12c, 12‴, 3p, 0ap and 3″″ (52 out of 155 specimens). The total number of plates ranges from 31 to 43.

Clearly then, the plate formula of the daughter cells are frequently different from those of the first germinated cells. For example, in specimen labelled as KM 020, the first germinated cell has the formula 7′, 2a, 11″, 10c, 10‴, 2p, 0ap and 3″″. Within several days, more than ten daughter cells are produced with plate formula as follows: 7′, 0a, 10″, 11c, 11‴, 2p, 0ap and 3″″; 7′, 0a, 12″, 12c, 12‴, 3p, 0ap and 3″″; 6′, 4a, 12″, 11c′, 11‴, 3a, 1ap and 3″″; 7′, 0a, 11″, 11c, 10‴ or 11‴, 2p, 0ap and 3″″.

The composite formulae of field specimens are 6—7′, 0a, 9—12″, 11—13c, 11—13‴, 2—3p, 0ap and 3″″, and the total number of plates ranges from 31 to 37. Among them, the most frequent formula is 7′, 0a, 12″, 12c, 12‴, 3p, 0ap and 3″″ for a total of 37 plates (in 76 out of 83 specimens).

These data indicate that the cultured specimens are more in number of plates and variable than the field spcimens.

Table 4. Variation in numbers of plate of germinated cells and subsequent daughter cells in incubation experiments and of normal vegetative cells in plankton sample.

Plate series	Germinated cells	Daughter cells	Cells in plankton
Apical plates	6—8 (7)	6—8 (7)	6—7 (7)
Anterior intercalary plates	0—2 (0)	0—4 (0)	0
Precingular plates	9—14 (11, 12)	11—13 (12)	9—12 (12)
Total plates in epitheca	16—22 (20)	17—22 (19)	16—19 (19)
Cingular platelets	10—14 (12)	10—14 (12)	11—13 (12)
Sulcal platelets	8	8	8
Postcingular plates	10—14 (12)	10—14 (12)	11—13 (12)
Antapical plates	2—3 (3)	2—3 (3)	3
Posterior intercalary plates	2—4 (3, 4)	2—5 (3)	2—3 (3)
Additional post. inter. plates	0—2 (0)	0—1 (0)	0
Total plates in hypotheca	15—21 (18)	15—21 (18)	16—19 (18)
Total plates	31—41 (39)	33—43 (39)	33—37 (37)
Number of specimens	17	155	83

Discussion

Cyst morphology:—Based on morphological characteristics, the living cysts provided for incubation experiments were clearly identified as *T. vancampoae*. In addition, several new morphological features are noted as a result of the present study.

As Wall and Dale (1971) have already mentioned, the number of paraplates corresponding to the operculum is variable in number. It ranges from two to five in the present cyst specimens. The fossil *Tuberculodinium rossignolae* Drugg is known to have two opercular paraplates which consiered to be an important character (Drugg 1970). But the Miocene specimens of this species shown by Williams and Brideaux (1975, pl. 34, figs. 2, 3) clearly has three opercular paraplates similar to those of *T. vancampoae*. Therefore, this character is not diagnostic for *T. rossignolae*.

Small spherical "processes" are also present on the fossil species *Tuberculodinium wallii* Drugg. But this species has these processes more densely not only on the apicals but also on the postcingulars, including the opercular paraplates, and the antapicals.

The paratabulation of the specimens collected from Omura Bay is as follows; 5—7′, 9—10″, 10—11‴ and 4—5⁗ + 2—3@. This is within the range of variation indicated by Wall and Dale (1971). In the specimens used in the in-

Explanation of Plate 38

Modern cyst and thecate forms of *Pyrophacus steinii* (Schiller) Wall et Dale obtained in unialgal culture.

Fig. 1. *Pyrophacus steinii* (Schiller) Wall et Dale, Specimen KM 012, hypotheca of daughter cell, showing aberrant shape of the 2⁗ plate (arrow), antapical surface in antapical view, × ca. 330.

Fig. 2. *Pyrophacus steinii* (Schiller) Wall et Dale, Specimen KM 011, cyst after germination, lateral view, × ca. 400.

Fig. 3. *Pyrophacus steinii* (Schiller) Wall et Dale, Specimen KM 009, hypotheca of newly germinated vegetative cell, antapical surface in antapical view, × ca. 330.

Figs. 4a—6. *Pyrophacus steinii* (Schiller) Wall et Dale, Specimen KM 013.

Figs. 4a—c. Cyst after germination, 4a; apical surface, × ca. 260, 4b; optical cross section of antero-posterior view, × ca. 260, c; antapical surface showing attached operculum composed of three rectangular paraplates, × ca. 260.

Fig. 5. Epitheca of newly germinated vegetative cell, apical surface in antapical view, × ca. 260.

Fig. 6. Hypotheca of daughter cell, antapical surface in antapical view, × ca. 260.

Fig. 7. *Pyrophacus steinii* (Schiller) Wall et Dale, Specimen KM 002, hypotheca of daughter cell, antapical surface in apical view, × ca. 335.

Figs. 8—11. *Pyrophacus steinii* (Schiller) Wall et Dale, Specimen KM 018.

Fig. 8. Cyst after germination, showing somewhat damaged autophragm, × ca. 325.

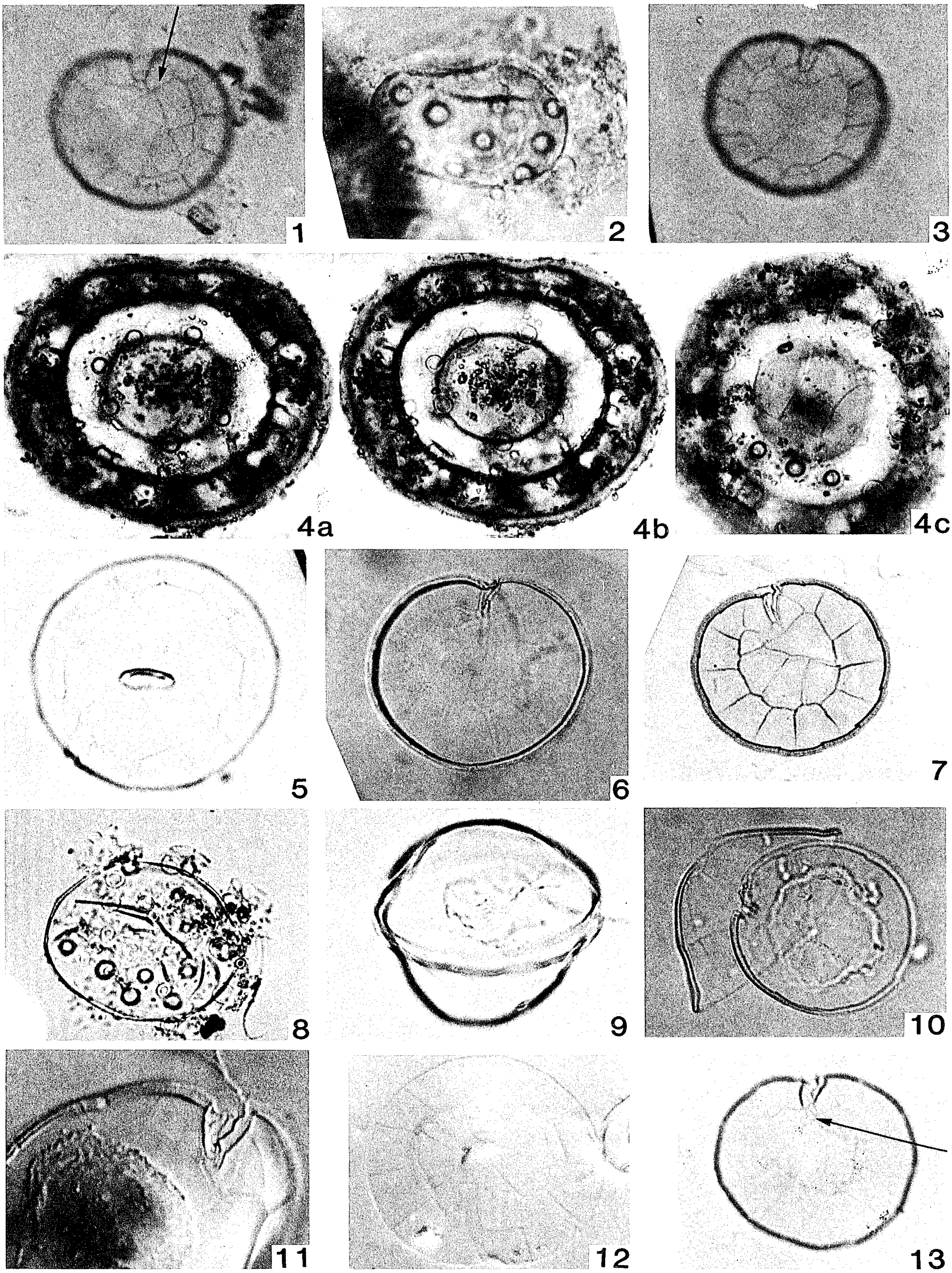
Fig. 9. Lateral view of newly germinated vegetative cell, showing relatively normal epitheca and subspherical aberrant hypotheca, × ca. 325.

Fig. 10. Epitheca and hypotheca of daughter cell, showing lenticular epitheca, × ca. 325.

Fig. 11. Sulcus of daughter cell, apical surface in oblique apical view (interference contrast optics), × ca. 640.

Fig. 12. *Pyrophacus steinii* (Schiller) Wall et Dale, Spcimen KM 003, epitheca of newly germinated vegetative cell, apical surface in antapical view, × ca. 325.

Fig. 13. *Pyrophacus steinii* (Schiller) Wall et Dale, Spcimen KM 006, hypotheca of daughter cell, showing additional sulcal posterior platelet (arrow), antapical surface in apical view, × ca. 330.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4a
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13

cubation experiment, the paratabulation represented by the intratabular processes and the archeopyle corresponds only roughly to the tabulation of the thecate form, except for the cingulum and sulcus (which does not correspond at all). The number of processes plus opercular paraplates is usually fewer than the number of thecal plates. These facts suggest that such morphological information as the number and structure of plates and platelets in the thecate stage are poorly reflected in the cyst stage.

Plate formula of Pyrophacus steinii, and P. vancampoae:—There are three taxonomic units in the genus *Pyrophacus*, as several authors have agreed, but the taxonomic positions of these units are uncertain.

Steidinger and Davis (1967) recognized one species, one variety and one form as follows; *Pyrophacus horologicum*, *P. horologicum* var. *steinii* and *P.* Form B_1. According to their observations, the plate formula of *P. horologicum* var. *steinii* is 6—7′, 0—1a, 11—13″, 11—13′ ″, 0—1p and 5—8″ ″ (6—7′, 0—1a, 11—13″, 11—13′ ″, 2—5p, 0—1ap and 3″ ″ in my nomenclature), and *P.* Form B_1 has 7—9′, 2—8a, 13—15(16?)″, 13—16′ ″, 0—6p and 7—11″ ″ (7—9′, 2—8a, 13—15(16?)″, 13—16′ ″, 4—8p, 0—6ap and 3″ ″ in my nomenclature). Based on these data, they suggested that *P.* Form B_1 is either another variety of *P. horologicum* or is an aberrant form.

Wall and Dale (1971) carried out a precise statistical study of the plate formulae of these three taxa, and divided them into three species; *P. horologium*, *P. steinii*, and *P. vancampoae*. The plate formula of *P. steinii* is 6—7′, 0a, 11—13″, 12c, 11—14′ ″, 1—2p and 4—6″ ″ (6—7′, 0a, 11—13″, 12c, 11—14′ ″, 1—3p, 1—2ap and 3″ ″ in my nomenclature) plus an apical pore platelet with about eight sulcal platelets. *P. vancampoae* is more variable in plate number and its formula is 7—9′, 0—9a, 13—15″, 12—16c, 12—17′ ″, 1—9p and 5—7″ ″ (7—9′, 0—9a, 13—15″, 12—16c, 12—17′ ″, 2—4p, 1—9ap and 3″ ″ in my nomenclature) plus an apical pore platelet with eight sulcal platelets. Its most common formula is represented as 8′, 0a, 14″, 14c, 14′ ″, 1p and 6″ ″ (8′, 0a, 14″, 14c, 14′ ″, 3p, 1ap and 3″ ″ in my nomenclature). Although they recognized the presence of the morphologically intermediate forms between *P. steinii* and *P. vancampoae*, and furthermore the possibility that these two species may be biological ecotypes, they considered that these species are different enough to warrant separation.

Balech (1979) rearranged these three species described by Wall and Dale (1971) into two species, but with *P. vancampoae* reduced to a subspecies under the code of International

Table 5. Summarized plate formula of *Pyrophacus steinii* (Schiller) and its related taxa, according to several authors.

Taxon	Plate formula								Author or locality
Pyrophacus Form B_1	7—9′	2—8a	13—15(16)″		13—16‴	0—6p [4—5p	7—11⁗ 0—5ap	 3⁗]	Steidinger & Davis (1967)
Pyrophacus horologicum var. *steinii*	6—7′	0—1a	11—13″		11—13‴	0—1p [3—5p	5—8⁗ 0—1ap	 3⁗]	
Pyrophacus vancampoae	7—9′ (8′	0—9a 0a	13—15″ 14″	12—16c 14c	12—17‴ 14‴	1—9p 1p	5—7⁗ 6⁗)		Wall & Dale (1971)
Pyrophacus steinii	6—7′ (7′	0a 0a	11—13″ 12″	12c 12c	11—14‴ 12‴	1—2p 1p	4—6⁗ 6⁗)		
Pyrophacus steinii subsp. *vancampoae*	8′		12—14″	12c	12—14‴		3⁗		Balech (1979)
Pyrophacus steinii subsp. *steinii*	7′		12″	12c	12‴	3p	3⁗		
Present specimens	6—8′ (7′	0—4a 0a	9—14″ 12″	10—14c 12c	10—14‴ 12‴	2—5p 3p	0—2ap 0ap	3⁗ 3⁗)	From Omura Bay

Zoological Nomenclature, because the differences between *P. steinii* and *P. vancampoae* are smaller than those between *P. horologium* and *P. steinii*. According to him, the normal plate formula of *P. steinii* is Po, 7′, 12″, 12c, 12‴, 3⁗, 3p and 8s, and that of *P. vancampoae* is basically Po, 8′, 12—14″, 12—14c, 12—14‴, 3⁗, 8s and 8—11p. Based on this, he considered that *P. vancampoae* is a subspecies of *P. steinii*.

In the specimens germinated from living cysts of Omura Bay, only a few may have formula like that of *P. vancampoae*; Specimen labelled as KM 002 was 8′, 0a, 13″, 11c, 11‴, 4p, 0ap and 3⁗; specimen labelled as KM 013 was 7′, 2a, 13″, 12c, 12‴, 4p, 0ap and 3⁗. These formulae do not agree with the most common formula of *P. vancampoae* indicated by Wall and Dale (1971). Furthermore, in the case of specimen KM 013, progeny of the first germinated cell had the formula 7′, 1a, 13″, 13c, 13‴, 4p, 0ap and 3⁗. This formula is well within the range of *P. horologicum* var. *steinii* sensu Steidinger and Davis (1967), *P. steinii* sensu Wall and Dale (1971) and *P. steinii* subsp. *steinii* sensu Balech (1979).

Cyst form of Pyrophacus steinii:—Based on the morphological characters, systs used in the incubation experiments and those acquired by palynological method can all be assigned to *T. vancampoae*. There are not significant morpholgical differences between cysts from Phosphorescent Bay (Wall and Dale 1971) and from Omura Bay. Although the vegetative cells obtained from the incubation experiments showed greater individual variation in the plate formula, they were clearly identifiable as *P. steinii*. Furthermore, theca containing living *T. vancampoae* cysts were found in the plankton. These theca had the plate formula of *P. steinii*, as well only *P. horologium* and *P. steinii* motile cells were found in the plankton. No plankton cells could be identified as *P. vancampoae*. This means that *T. vancampoae* is also the cyst form of *Pyrophacus steinii*.

Based on their incubation experiments, Wall and Dale (1971) concluded that *T. vancampoae* is the cyst form of *P. vancampoae* but they did not discuss the cyst of *P. steinii*. Germinated

Explanation of Plate 39

Modern cyst and thecate forms of *Pyrophacus steinii* (Schiller) Wall et Dale obtained in unialgal culture.

Figs. 1a—2c. *Pyrophacus steinii* (Schiller) Wall et Dale, Specimen KM 009.

Figs. 1a—f. Cyst after germination, 1a; apical surface, × ca. 285, 1b; optical corss section in antero-posterior view, × ca. 285, 1c; antapical surface, showing attached operculum composed of three paraplates, 1d; enlargement of 1e, showing archeopyle, × ca. 570, 1e and 1f; lateral surface, × ca. 285.

Figs. 2a—c. Newly germinated vegetative cell, 2a; epitheca lacking the apical pore platelet, showing aberrant shape of the 1′ plate (arrow), apical surface in apical view, × ca. 285, 2b; epitheca, showing lenticular shape, oblique lateral view, × ca. 285, 2c; hypotheca, antapical surface in apical view, × ca. 285.

Figs. 3—7. *Pyrophacus steinii* (Schiller) Wall et Dale, Specimen KM 020.

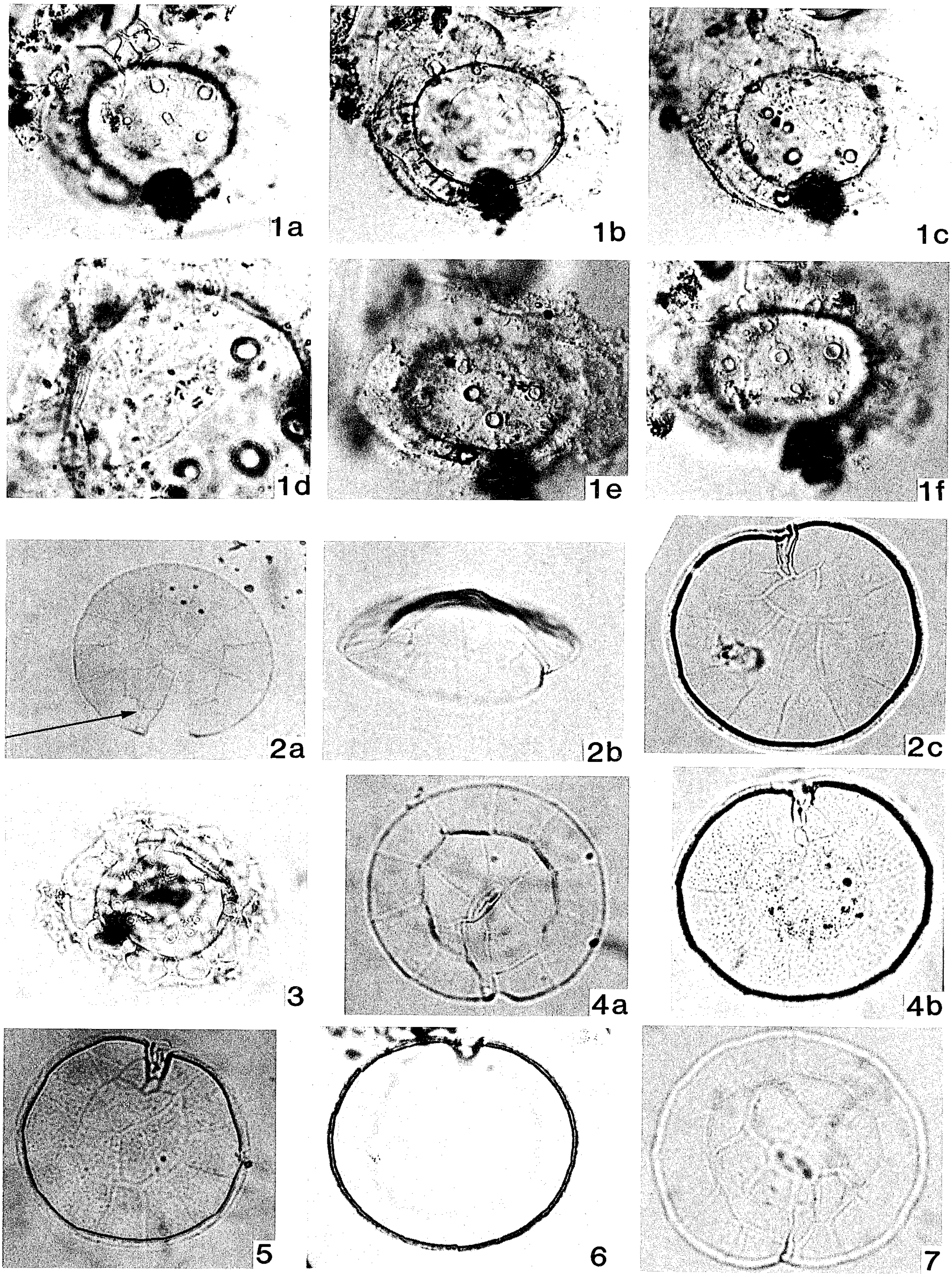
Fig. 3. Cyst after germination, apical surface, × ca. 260.

Figs. 4a—b. Newly germinated vegetative cell, 4a; epitheca, apical surface in antapical view, × ca. 260, 4b; hypotheca, showing the aberrant shape of the 1⁗ and 2⁗ plates, antapical surface in apical view, × ca. 260.

Fig. 5. Hypotheca of daughter cell, showing only two antapical plates; antapical surface of antapical view, × ca. 260.

Fig. 6. Hypotheca of daughter cell, showing cingular platelets, optical cross section in antero-posterior view, × ca. 260.

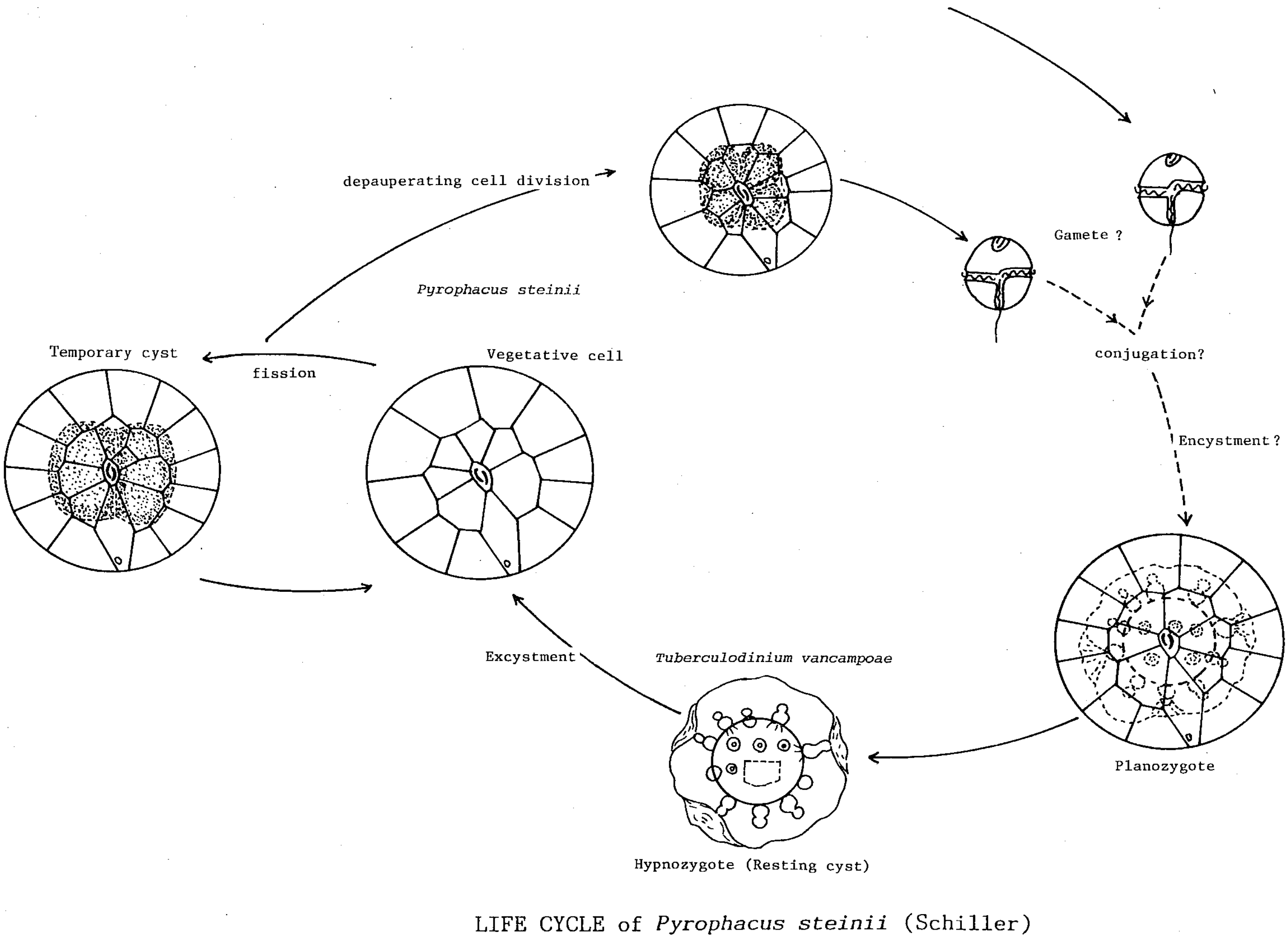
Fig. 7. Epitheca of daughter cell, apical surface in apical view, × ca. 260.


1a
1b
1c
1d
1e
1f
2a
2b
2c
3
4a
4b
5
6
7

thecate cells obtained from Phosphorescent Bay have following plate formula; C949 · · · 7′, 3a, 15″, 15‴, 2p and 5⁗, and C955 · · · 7′, 2a, 13‴, 1p, and 5⁗, and 8′, 0a, 13″ (hypotheca unknown) according to Wall and Dale (1971). The plate number of these specimens are larger than the normal form of *P. steinii*; but in my opinion, one of them, C955, is clearly included within the range of *P. steinii.* Therefore, no clear separation can be made based on vegetative cell plate formulae, between *P. steinii* and *P. vancampoae* obtained from Phosphorescent Bay and Omura Bay.

Significance of small thecate form in life cycle of Pyrophacus steinii (Text-fig. 8):—The small thecate form of *P. steinii* is different from normal vegetative cells of *P. steinii* (Schiller) in plate formula and cell shape, and most closely resembles *P. horologium* except for the number of apical plates. The latter species has only five to six plates, while the former form possesses six to eight.

Steidinger and Davis (1967) reported that *P. horologicum* is more spherical than *P. steinii* and that smaller cells are found. The small thecate forms derived from incubation are similar in shape to these small and spherical cells of *P. horologium*, but they are distinguishable from the latter in being ovoid in cell shape and having a wider cingulum. This small forms also differ form *P. horologium* in the plate and platelet distribution of the antapicals and sulcus. *P. horologium* possesses three antapical plates surrounding the posterior sulcal plates, one of



Text-fig. 8. Life cycle of *Pyrophacus steinii* (Schiller) Wall et Dale. Solid line; observed process, dotted line; hypothesized process.

which is characteristically large and triangular, and others having consistent shapes and positions. These characters are also found in *P. steinii.* Though this small thecate form also possesses three antapical plates, none are large and triangular. Furthermore, the structure of the sulcus is different in the two. The anterior sulcal platelet of the small thecate form is shallow U-shape, while this platelet of *P. horologium*, is nearly rectangular. The posterior sulcal platelet of the small thecate form is irregularly hexagonal, but the corresponding platelet of *P. horologium* is nearly ellipsoidal. In the former, the last cingular platelet clearly invades the sulcus, but the platelet of the latter does not.

Metzenauer (1933) reported the occurrence of *P. horologium* sensu lato from the Indian Ocean. The figured specimen (Matzenauer 1933, p. 481, fig. 78) is noteworthy in no being lenticular but rather subspherical, with a theca composed of many plates and platelets as observed in normal vegetative cells. This spherical form is also smaller (57 μm in length and 59.5 μm in width) than normal cells and apparently resembles the present small thecate form. Unfortunately its plate formula is not clear and cannot be reconstructed in detail from his original figure, so we cannot determine which species of the genus *Pyrophacus* that specimen is assignable to. However, the species of Matzenauer differs from the small thecate form in being more spherical and in having a cingulum without displacement. With respect to the life cycle in *P. steinii*, it is significant that the small thecate form appeared in the unialgal culture. Stosch (1973) reported the appearance of smaller and light colored cells in cultures of the

Explanation of Plate 40

Small thecate form of *Pyrophacus steinii* (Schiller) Wall et Dale obtained in unialgal culture.

Figs. 1—2. Ventral surface in dorsal view, showing the displacement of the cingulum. Both specimens are somewhat elongated antero-posteriorly; 1, specimen KM 012-1, × ca. 690; 2, specimen KM 012-2, × ca. 550.

Figs. 3—4. Optical cross section in lateral view, showing the theca; 3, specimen KM 012-2, × ca. 650; 4 specimen KM 012-2, × ca. 600.

Figs. 5—6, 10a—b. Plate distribution on epitheca.

Fig. 5. Apical surface in antapical view, showing small ventral pore in the 1′ plate (arrow), specimen KM 012-3, × ca. 570.

Fig. 6. Apical surface in oblique apical view, specimen KM 012-4, × ca. 660.

Figs. 10a—b. Apical surface in antapical view, showing the apical pore platelet and apical plates (10a), × ca. 590, and precingular plates (10b), × ca. 590, specimen KM 012-2.

Figs. 7—9. Plate distribtuion on hypotheca.

Fig. 7. Nearly optical corss section of hypotheca, showing the sulcus and postcingular plates, specimen KM 012-3, × ca. 770.

Fig. 8. Antapical surface in oblique antapical view, showing the 6′ ″, 7′ ″ and 8′ ″ plates, specimen KM 012-3, × ca. 770.

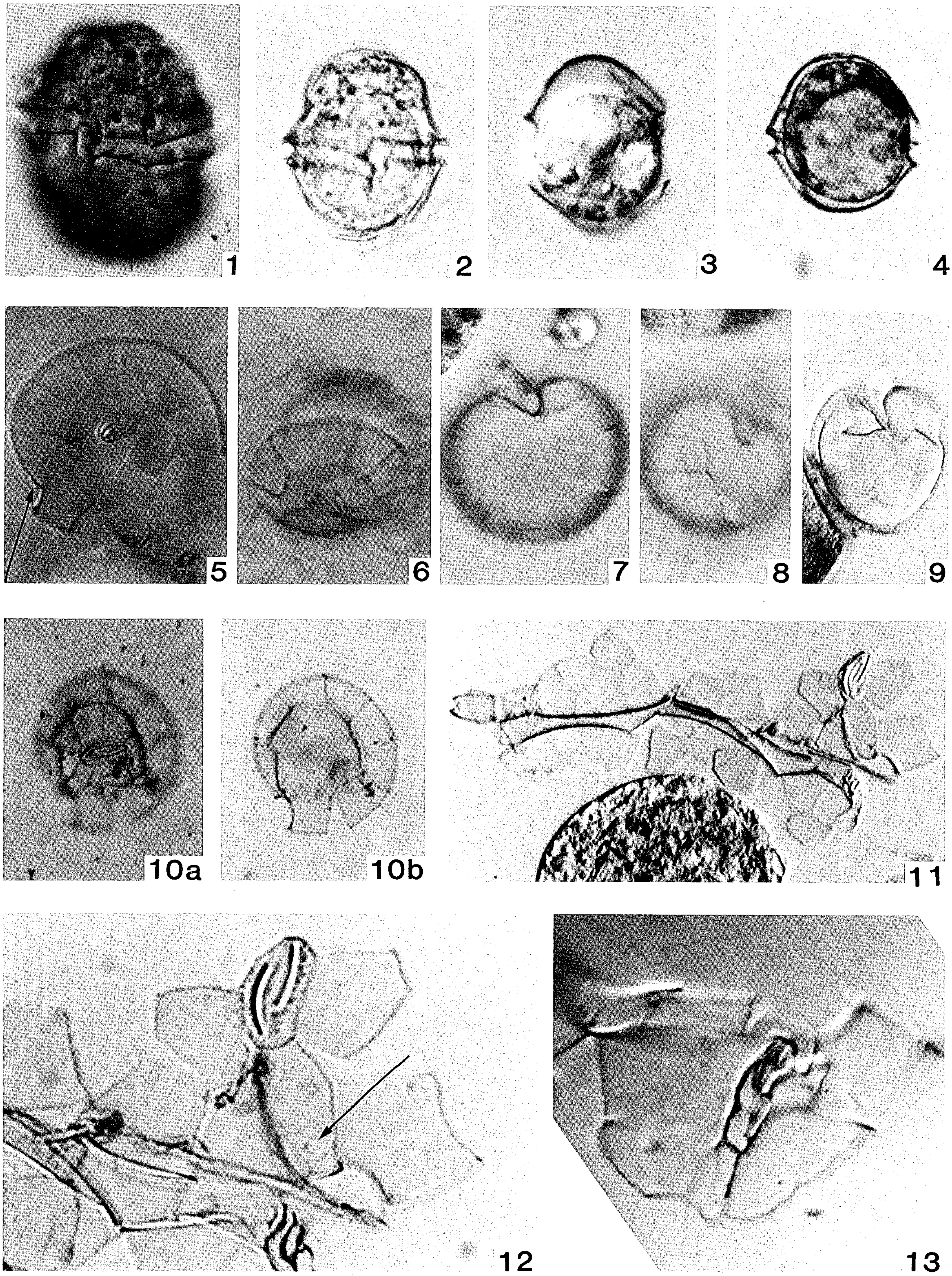
Fig. 9. Antapical surface in oblique antapical view, showing right precingular plates and some antapicals, specimen KM 012-2, × ca. 630.

Figs. 11—13. Cell pressed under coverslip, ventral surface in dorsal view.

Fig. 11. Thecal plates and platelets constituting the theca, a few plates and platelets are missing, specimen KM 012-1, × ca. 600.

Fig. 12. Enlargement of anterior ventral part, showing an apical pore platelet and the 1′, 2′, 7′, 1″, 2″, 3″ (part) and 8″ plates, and a ventral pore on the 1′ plate (arrow), specimen KM 012-1, × ca. 1400.

Fig. 13. Enlargement of posterior ventral part, showing the distribution of sulcal platelets, specimen KM 012-1, × ca. 1325.


1
2
3
4
5
6
7
8
9
10a
10b
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12
13

freshwater gymnodinialean species, *Gymnodinium pseudopalsutre* Schiller and concluded that this form was a gamete formed by depauperating cell division. Later, Dale (1977) also observed such smaller cells in the thecate species, *Peridinium faeroense.* The present smaller form is very different from the normal vegetative cell in its smaller size and more spherical shape. This strongly suggests that this smaller form may be a gamete of *P. steinii*, but confirmation of this will need to investigate on its nuclear phase and to observe a zygote formation.

Conclusion

Living cyst identical with the fossil dinoflagellate *Tuberculodinium vancampoae* (Rossignol) Wall produced the thecate species *Pyrophacus steinii* (Schiller) Wall et Dale in incubation experiments.

In the plankton of Omura Bay, thecate form of *Pyrophacus steinii* (Schiller) Wall et Dale contained living cysts assignable to *Tuberculodinium vancampoae* (Rossignol) Wall.

These facts indicate that *Tuberculodinium vancampoae* is also the cyst form of *Pyrophacus steinii* Wall et Dale.

Pyrophacus vancampoae (Rossignol) is concluded to be a subspecies of *P. steinii* as follows: *Pyrophacus steinii* (Schiller) Wall et Dale subsp. *vancampoae* (Rossignol) Balech.

In the unialgal culture of *Pyrophacus steinii* germinated from living cysts, a small thecate form appeared. This form is very different from the normal vegetative cell in being smaller and more ovoid. The plate formula of this from is more similar to that of *Pyrophacus horologium* than to that of *P. steinii.*

The morphological characteristics of this form strongly suggest that it is a gamete.

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Pyrophacus steinii (Schiller) Wall et Dale, 1971 のシストと游泳体: *Pyrophacus steinii* (Schiller) Wall et Dale のシストが室内及び野外観察の結果から明らかにされた。*Tuberculodinium vancampoae* (Rossignol) と同定される生シストから発芽した游泳・有殻体は，鎧板配列の詳細な観察に基づいて *Pyrophacus steinii* に属するとされた。さらに *T. vancampoae* と同定され得る生シストを包含した *Pyrophacus steinii* の游泳・有殻体が大村湾の夏季のプランクトン群集から数多く得られた。これらの資料によると，*T. vancampoae* は *P. vancampoae* だけでなく *P. steinii* のシストでもあり，また *P. vancampoae* は *P. steinii* の亜種であると結論される。

松岡数充
