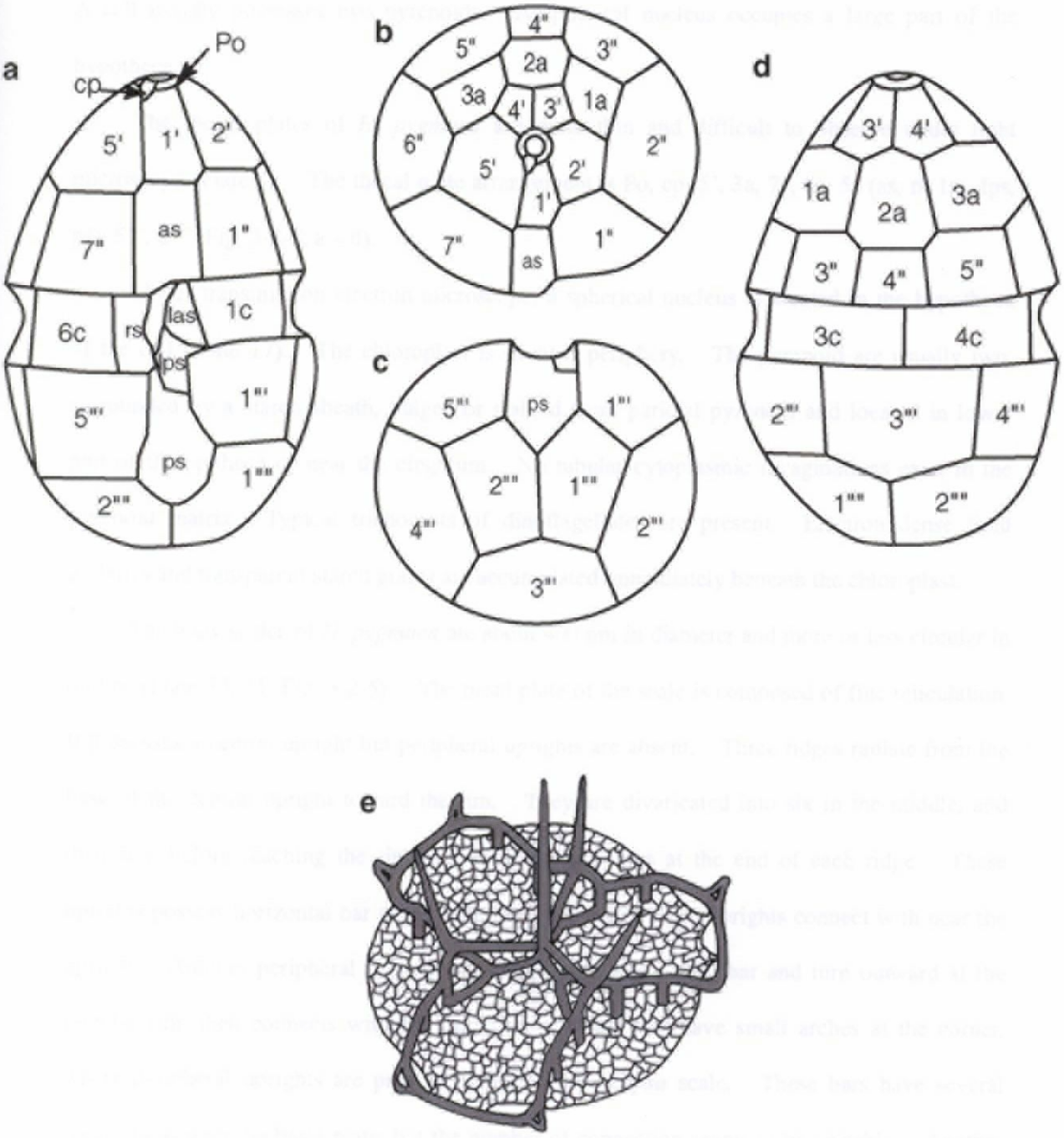

Figure 3-2-5. *Heterocapsa pygmaea* Loeblich III, Schmidt & Sherley.

a-d. Diagmammatic illustrations of thecal plates; **a**, ventral view; **b**, apical view; **c**, antapical view; **d**, dorsal view.
e. Body scale.

A cell usually possesses two pyrenoids. A spherical nucleus occupies a large part of the hypotheca.

The thecal plates of *H. pygmaea* are quite thin and difficult to observe under light microscope (Plate 5). The thecal plate arrangement is Po, cp, 5', 3a, 7", 6c, 5s (as, rs, las, lps, ps), 5'", 2"" (Fig. 3-2-5, a – d).

Under transmission electron microscope, a spherical nucleus is located in the hypotheca of the cell (Plate 17). The chloroplast is situated periphery. The pyrenoid are usually two, surrounded by a starch sheath, bulged or stalked from parietal pyrenoid and located in lower part of the epitheca or near the cingulum. No tubular cytoplasmic invaginations exist in the pyrenoid matrix. Typical trichocysts of dinoflagellates are present. Electron dense lipid globules and transparent starch grains are accumulated immediately beneath the chloroplast.

The body scales of *H. pygmaea* are about 400 nm in diameter and more or less circular in outline (Plate 30, 31, Fig. 3-2-5). The basal plate of the scale is composed of fine reticulation. It possesses a central upright but peripheral uprights are absent. Three ridges radiate from the base of the central upright toward the rim. They are divaricated into six in the middle, and then stop before reaching the rim. A short upright rises at the end of each ridge. These uprights possess horizontal bar at the distal part, by which these uprights connect with near the upright. Another peripheral bar extends to opposite side of the bar and turn outward at the circular rim, then connects with the next one. These bars have small arches at the corner, where peripheral uprights are present in usual *Heterocapsa* scale. These bars have several connections with the basal plate, but the number of connection seems to be unstable. Another bar connects the junction and the most proximal region of central upright.

While the cell shape rather resembles many of *Heterocapsa* species such as *H. niei*, *H. illdefina* and *H. circularisquama*, the cell size differs from each other. This species also differs from *H. horiguchii* in the position of the nucleus. It can be identified by the ultrastructure of the body scale.

The species, *H. pygmaea*, was originally collected from Galveston, Texas in 1957 (Loeblich III, Schmidt & Sherley 1986). This species was also collected at Ligrian Sea, Italy before 1975 (CCMP1490 strain). In the present study, it was recognized as red tide plankton sample from Perdido Bay, Florida and Mersin Bay, Turkey. It was also observed in the seabed core sample collected from Ariake Sound, Nagasaki Prefecture.

3-2-6 *Heterocapsa rotundata* (Lohmann) Hansen (Fig. 3-2-6, Plate 6, 32)

Hansen, 1995, p. 166, Figs. 1-19.

Fukuyo, Inoue & Takayama, 1997, p. 69, pl. 10, Fig. 137.

Horiguchi, 1997, p. 116, pl. 3, Fig. 17

Synonym

Amphidinium rotundatum Lohmann 1908

Lohmann, 1908, Tafel XVII, Fig. 9.

Paulsen, 1908, p. 95, F. 129.

Lemmermann, 1910, p. 615.

Herdman, 1911, p. 71.

Schiller, 1911, p. 31.

Mielck, 1911, p. 20.

Ostenfeld, 1913, p. 338.

Wulff, 1916, p. 103, Tafel II, Fig. 11.

Kofoid & Swezy, 1921, p. 150, Fig. U, 22.

Amphidinium redekei Conrad & Kufferath 1954

Conrad & Kufferath, 1954,

Gymnodinium minutum Lebour 1925

Lebour, 1925, p. 45, Tafel 5, Fig. 4.

Massartia rotundatum (Lohmann) Schiller 1933

Schiller, 1933, p. 438, Fig. 464.

Katodinium rotundatum (Lohmann) Loeblich III 1965

Loeblich III, 1965, p. 16.

Throndsen, 1983, p. 20, Figs. 84, 85.

Steidinger & Tangen, 1996, p. 456, pl. 20.

Konovalova, 1998, p. 120, pl. 25.

Katodinium minutum Sournia 1973

Sournia, 1973, p. 44.

Cells are elliptical or bullet-shape, consisting of a large epitheca and a small hypotheca (Plate 6). The epitheca is two to three times as long as the hypotheca. Cells are quite small as compared to other *Heterocapsa* species, 8.8-12.8 μm (mean 10.4 μm, n = 30) in length, and 7.2-9.6 μm (mean 8.5 μm, n = 30) in width (TK12-D44 strain). The cingulum is rather wide and is displaced by about 1/3 of its width. The sulcus is difficult to observe under light microscope. The chloroplast is located in the cell peripherally, usually appears bilobed. Each lobe of the chloroplast located in the epitheca and the hypotheca. The pyrenoid is spherical and situated in the middle or lower part of the epitheca. The nucleus is ellipsoidal and located in the middle of the cell to the hypotheca.

Cells of *H. rotundata* resemble the gymnodinioid dinoflagellate under light microscope, but it possesses quite thin thecal plates (Plate 6). The thecal plate number are Po, cp, 5', 3a, 7", 6c, 5s (as, rs, las, lps, ps), 5''', 2'''' (Fig. 3-2-6). All thecal plates on the epitheca, viz. the apical series, anterior intercalary series and precingular series are elongated longitudinally due to the long epitheca. In the cingular series, the las plate is relatively smaller than the lps plate.

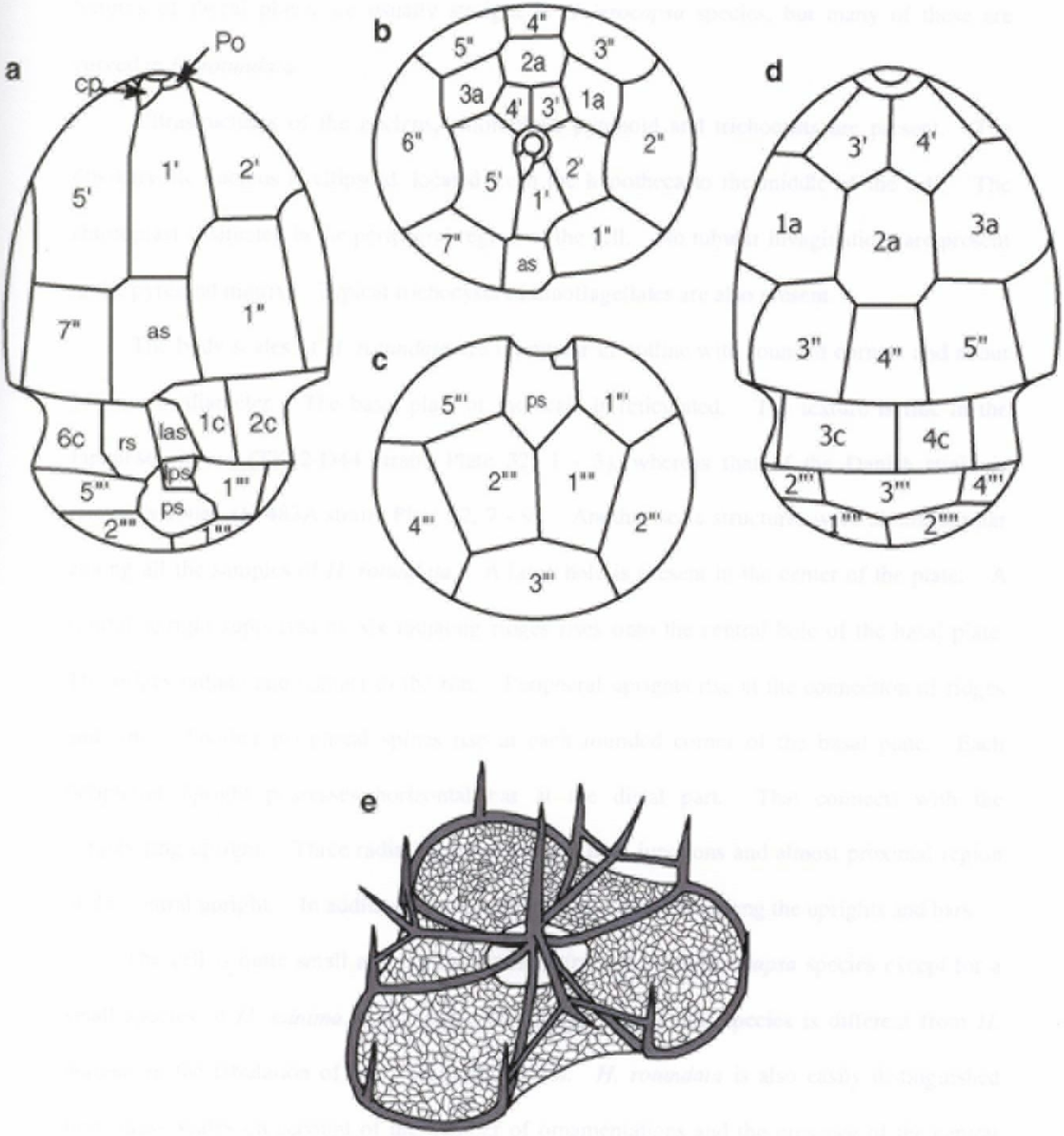

Figure 3-2-6. *Heterocapsa rotundata* (Lohmann) Hansen.

a-d. Diagmammatic illustrations of thecal plates; **a**, ventral view; **b**, apical view; **c**, antapical view; **d**, dorsal view.
e. Body scale.

Sutures of thecal plates are usually straight in *Heterocapsa* species, but many of these are curved in *H. rotundata*.

Ultrastructures of the nucleus, chloroplast, pyrenoid and trichocysts are present. The dinokaryotic nucleus is ellipsoid, located from the hypotheca to the middle of the cell. The chloroplast is situated in the peripheral region of the cell. No tubular invaginations are present in the pyrenoid matrix. Typical trichocysts of dinoflagellates are also present.

The body scales of *H. rotundata* are triangular in outline with rounded corners and about 350 nm in diameter. The basal plate of the scale is reticulated. The texture is fine in the Japanese culture (TK12-D44 strain, Plate 32, 1 - 3), whereas that of the Danish strain is relatively rough (K-483A strain, Plate 32, 7 - 9). Another scale structures were almost similar among all the samples of *H. rotundata*. A large hole is present in the center of the plate. A central upright supported by six radiating ridges rises onto the central hole of the basal plate. The ridges radiate and contact to the rim. Peripheral uprights rise at the connection of ridges and rim. Another peripheral spines rise at each rounded corner of the basal plate. Each peripheral upright possesses horizontal bar at the distal part. That connects with the neighboring upright. Three radiating bars connect these junctions and almost proximal region of the central upright. In addition, spines rise from all junctions among the uprights and bars.

The cell is quite small and clearly different from other *Heterocapsa* species except for a small species of *H. minima*. According to Hansen (1995), this species is different from *H. minima* in the tabulation of the sulcal plate series. *H. rotundata* is also easily distinguished from these scales on account of the number of ornamentations and the presence of the central hole.

Occurrences of *H. rotundata* have been well reported by many authors as some synonyms. It might be distributed along worldwide coastal waters. The Japanese strain (TK12-D44) was established from the pre-culture using sediment surface sample collected from the Tokyo Bay. In this study, this species frequently found in pre-cultures of sediment samples collected during

the season form summer to autumn. This may implies that the species can survive on the bottom of the coastal waters as the temporary cysts. However, the temporary cyst or resting cyst of this species has not been directly found from the sediment samples yet.

3-2-7 *Heterocapsa triquetra* (Ehrenberg) Stein (Fig. 3-2-7, Plate 7, 18, 33)

Stein, 1883, Tafel III, Figs. 30-40

Bütschli, 1885, p. 1007, Pl. 52, Fig. 1.

Schütt, 1895. T. 22, Fig. 62.

Delage & Hréouard, 1896, p. 382. Fig. 563.

Paulsen, 1908, 26, Fig. 32.

Meunier, 1910, T. 45, Fig. 4., Fig. 5-8.

Lindemann, 1924a, 5, 114, Fig. 1-11.

Lindemann, 1924b, 3, 221, Fig. 14.

Lindemann, 1928, p. 88, Fig. 75.

Subrahmanyan, 1971, p. 9.

Campbell, 1973, p. 172, Pl. 12, f. 78a-d; Pl. 28, f. 5-6.

Drebes, 1974, p. 133, abb. 114.

Horiguchi, 1990, p. 119, Figs. A-E.

Steidinger & Tangen, 1996, p. 531, pl. 3, 49.

Konovalova, 1998, p. 251, pl. 59.

Fukuyo, Inoue & Takayama, 1997, p. 70, pl. 22, Fig. 138.

Synonym

Glenodinium triquetrum Ehrenberg 1840

Ehrenberg, 1840,

Peridinium triquetrum (Ehrenberg) Lebour 1925

Lebour, 1925, p. 109, T. 18, Fig. 2.

Schiller, 1937, p. 145, Fig. 147 a-f.

Abé, 1981, p. 298,

Heterocapsa triquetra var. *litoralis*, f. *apiculata* Lindemann 1924

Lindemann, 1924,

Cells of *H. triquetra* are rhomboid (Plate 7). The epitheca and the hypotheca are conical, and almost same in size. An antapical horn is present slightly to the right of the posterior end. Cell sizes are 15.2-26.4 μm (mean 22.1 μm, n = 30) in length, and 10.4-20.8 μm (mean 15.0 μm, n = 30) in width (TK12-D40 strain). The cingulum transverses the equatorial plane of the cell and the displacement is about 1-1/2 of its own width. The sulcus does not reach to the antapex of the cell. The parietal chloroplast is single and occasionally perforated. A spherical pyrenoid surrounded by starch sheaths is situated in the upper part of the hypotheca. No eyespot is present. The nucleus is spherical, and occupies large part of the epitheca.

The thecal plates of *H. triquetra* can be seen under light microscope, but it is difficult to observe its sutures (Plate 7). The typical thecal plate formula is Po, cp, 5', 3a, 7", 6c. 5s (as, rs, las, lps, ps), 5'", 2"" (Fig. 3-2-7). The antapical horn is present on the 2"" plate (Plate 7, f. 5). The thecal plate arrangement in ventral view is typical of *Heterocapsa*, while the epitheca in dorsal view is characteristic. The first anterior intercalar plate (1a) is relatively large and contacts with three precingular plates, 2" – 4". The 2a plate is six-sided and borders to the 4" and the 5" plates. This plate arrangement was found only from this species. The posterior intercalary plate (1p) was rarely observed. Other features of the thecal plates are almost the typical of the genus. The plate arrangement is slightly different from other *Heterocapsa* species, whereas the number is the same.

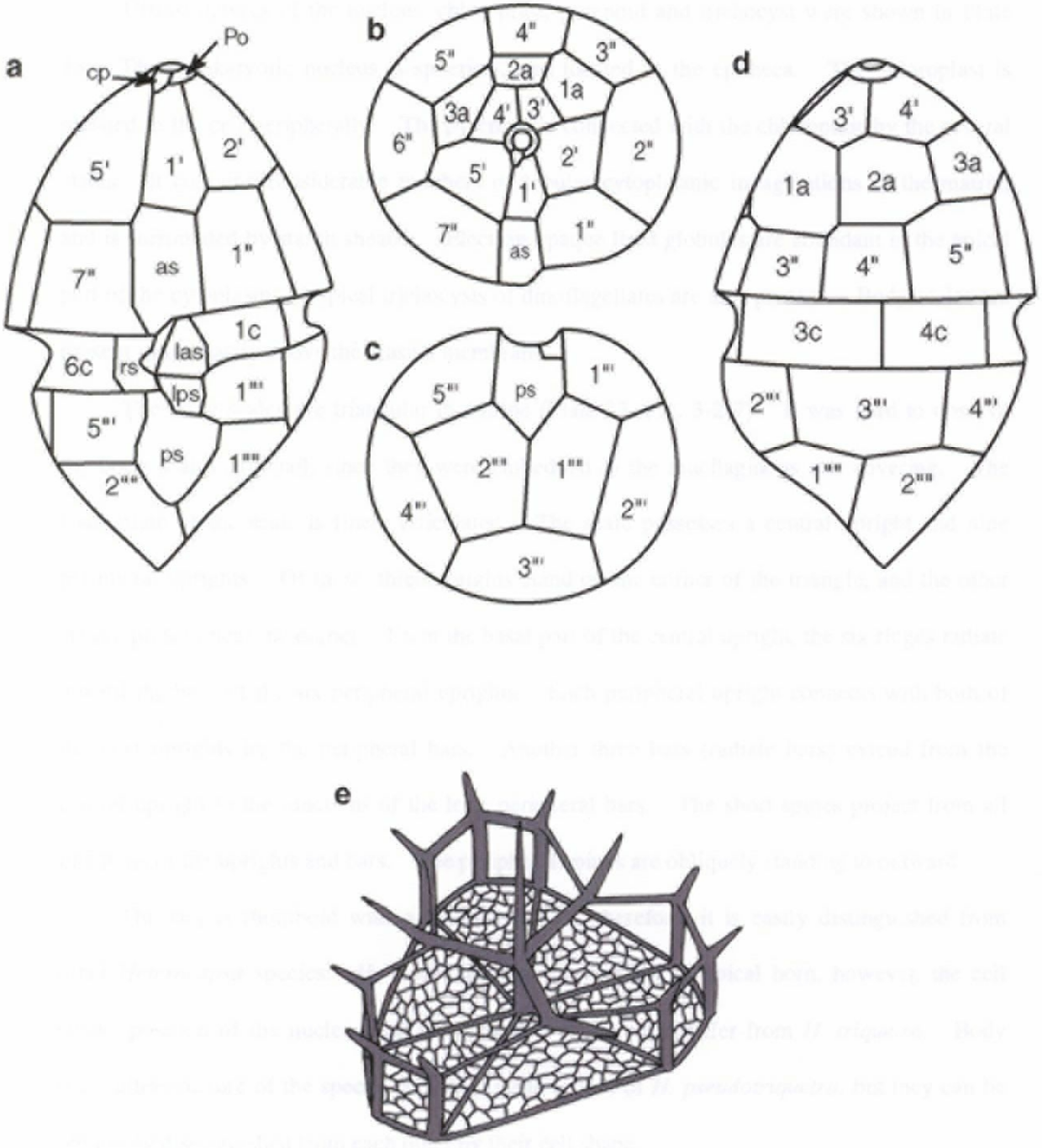

Figure 3-2-7. *Heterocapsa triquetra* (Ehrenberg) Stein.

a-d. Diagmammatic illustrations of thecal plates and body scale. **a**, ventral view; **b**, apical view; **c**, antapical view; **d**, dorsal view; **e**, body scale.

Ultrastructures of the nucleus, chloroplast, pyrenoid and trichocyst were shown in Plate 18. The dinokaryotic nucleus is spherical, and located in the epitheca. The chloroplast is situated in the cell peripherally. The pyrenoid is connected with the chloroplast by the several stalks. It contains considerable numbers of tubular cytoplasmic invaginations in the matrix, and is surrounded by starch sheaths. Electron opaque lipid globules are abundant in the apical part of the cytoplasm. Typical trichocysts of dinoflagellates are also present. Body scales are present immediately above the plasma membrane.

The body scales are triangular in outline (Plate 33, Fig. 3-2-7). It was hard to observe the body scales in detail, since they were embedded in the mucilaginous cell covering. The basal plate of the scale is finely reticulated. The scale possesses a central upright and nine peripheral uprights. Of these, three uprights stand on the corner of the triangle, and the other six are present near the corner. From the basal part of the central upright, the six ridges radiate toward the base of the six peripheral uprights. Each peripheral upright connects with both of the next uprights by the peripheral bars. Another three bars (radiate bars) extend from the central upright to the junctions of the long peripheral bars. The short spines project from all junctions of the uprights and bars. The peripheral spines are obliquely standing to outward.

The cell is rhomboid with an antapical horn, therefore, it is easily distinguished from other *Heterocapsa* species. *H. lanceolata* also possess the antapical horn, however, the cell shape, position of the nucleus and ultrastructure of the scale differ from *H. triquetra*. Body scale ultrastructure of the species is almost same to that of *H. pseudotriquetra*, but they can be obviously distinguished from each other by their cell shape.

H. triquetra is the type species of *Heterocapsa*, and there are many reports on the occurrence of the species since the first description. In the present study, it could be observed the samples from Denmark, U.K., U.S.A. and Japan. It could be considered to be a cosmopolitan species.

3-2-8 *Heterocapsa lanceolata* Iwataki & Fukuyo ms.

(Fig. 3-2-8, Plate 8, 19, 34)

Etymology: lanceolata = lanceolate, from its cell shape.

Synonym

Heterocapsa sp. 1

Iwataki, Takayama, Matsuoka, Hiroishi & Fukuyo (2002)

Cells are lanceolate or angular ovoid with the large epitheca, which is almost twice of the hypotheca in length (Plate 8). The epitheca is conical with truncated apex, while antapex of the conical hypotheca is pointed. Cell size is 16.4-25.0 μm (mean 18.9 μm) in length and 10.0-15.0 μm (mean 11.6 μm) in width (TK6-D57 strain). The cingulum is relatively wide and displaced by almost 1/2 of its own width. A chloroplast is distributed peripherally and frequently perforated. It connects with a pyrenoid, which is situated in the middle of the epitheca and often surrounded by starch sheaths. An ellipsoidal nucleus is situated in the middle of the cell.

Thecal plates are rather thin (Plate 8), and are therefore difficult to observe under light microscope. Thecal plate arrangement of Po, cp, 5', 3a, 7", 6c, 5s, 5'", 2'" could be determined under a fluorescent microscope and a scanning electron microscope (Fig. 3-2-8, f. a - d). Each thecal plate is elongated to longitudinal direction due to the elongate cell body, however, the arrangement is typical of the genus.

In transmission electron microscopy of *H. lanceolata*, mitochondria with tubular cristae, trichocysts, and a chloroplast with three appressed thylakoid lamellae are recognized (Plate 19). The chloroplast is situated in the cell peripherally, and connects with a pyrenoid via an isthmus. The pyrenoid is usually located near the chloroplast, but is sometimes located at some distance

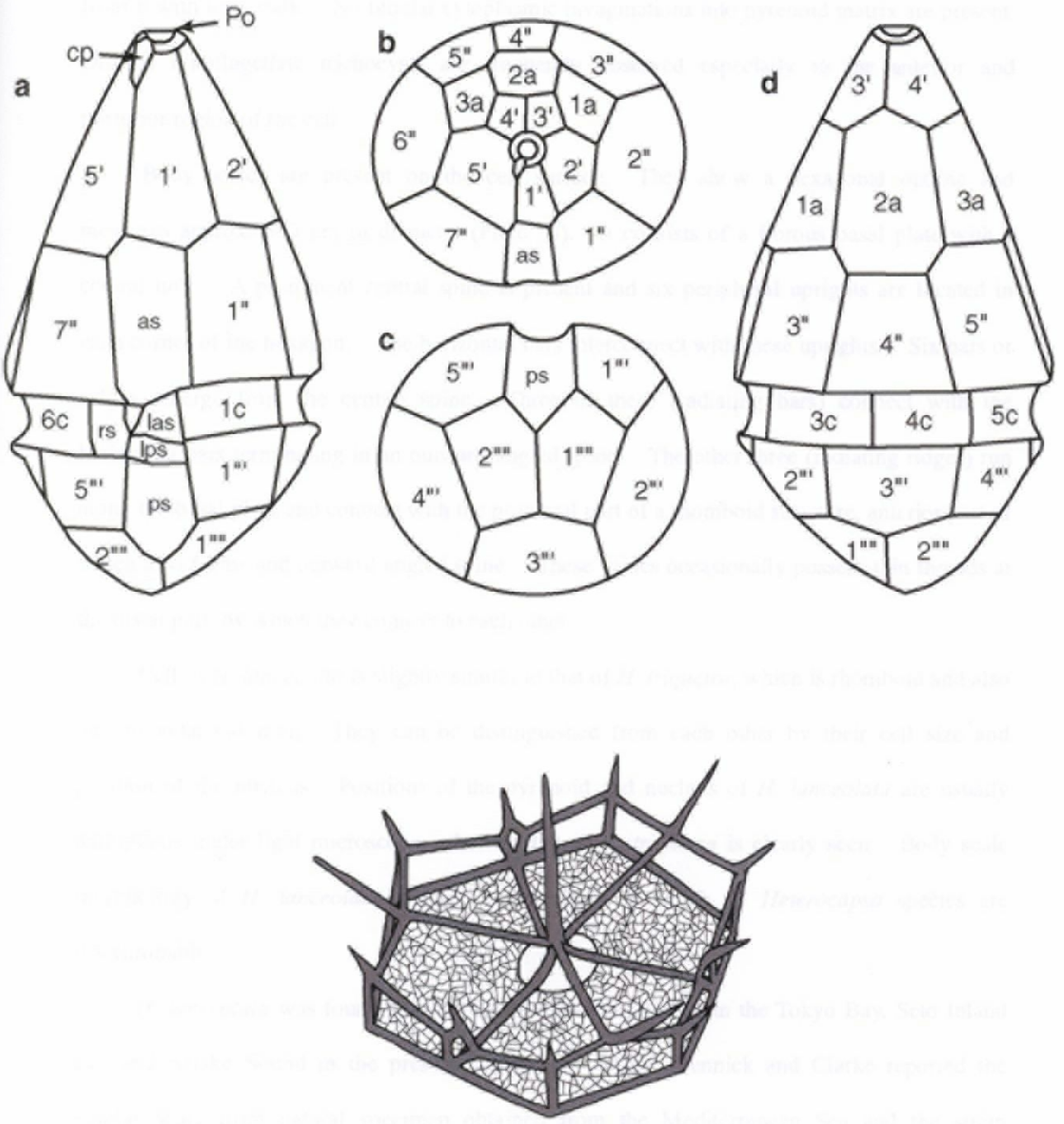

Figure 3-2-8. *Heterocapsa lanceolata* Iwataki & Fukuyo ms.

a-e. Diagmammatic illustrations of thecal plates and body scale; **a**, ventral view; **b**, apical view; **c**, antapical view; **d**, dorsal view; **e,** body scale.

from it with long stalk. No tubular cytoplasmic invaginations into pyrenoid matrix are present. Ordinal dinoflagellate trichocysts are frequently observed especially in the anterior and posterior region of the cell.

Body scales are present on the cell surface. They show a hexagonal outline and measures approx. 500 nm in diameter (Plate 34). It consists of a fibrous basal plate with a central hole. A prominent central spine is present and six peripheral uprights are located in each corner of the hexagon. The horizontal bars interconnect with these uprights. Six bars or ridges emerge from the central spine. Three of these (radiating bars) connect with the horizontal bars terminating in an outward angled spine. The other three (radiating ridges) run along the basal plate and connect with the proximal part of a rhomboid structure, anterior part of which also forms and outward angled spine. These spines occasionally possess thin threads at the distal part, by which they connect to each other.

Cell of *H. lanceolata* is slightly similar to that of *H. triquetra*, which is rhomboid and also has an antapical horn. They can be distinguished from each other by their cell size and position of the nucleus. Positions of the pyrenoid and nucleus of *H. lanceolata* are usually ambiguous under light microscope, whereas that of *H. triquetra* is clearly seen. Body scale morphology of *H. lanceolata* is also characteristic by which all *Heterocapsa* species are discriminable.

H. lanceolata was found as a red tide dominant organism in the Tokyo Bay, Seto Inland Sea and Ariake Sound in the present study. In addition, Pennick and Clarke reported the similar scale from natural specimen obtained from the Mediterranean Sea and the strain LB1116/2 in the CCAP collection (Pennick & Clarke 1977, Fig. 6).

3-2-9 *Heterocapsa horiguchii* Iwataki, Takayama & Matsuoka ms.

(Fig. 3-2-8, Plate 9, 20, 35)

Etymology: horiguchii = Named after Dr. Takeo Horiguchi, who first used the body scale as a diagnostic criterion for *Heterocapsa* species.

Synonyms

Heterocapsa sp. 2

Iwataki, Takayama, Matsuoka, Hiroishi & Fukuyo (2002)

Heterocapsa sp. 4

Iwataki, Takayama, Matsuoka, Hiroishi & Fukuyo (2002)

Cells are elliptical and consisted of a hemispherical epitheca and a hypotheca, both of which are almost equal in size (Plate 9). Cells are relatively small, 13.2-20.8 μm (mean 17.2 μm, n = 30) in length and 10.0-13.6 μm (mean 11.6 μm, n = 30) in width. A cingulum situated on the equatorial plane of the cell is relatively wide, and is displaced by 1/3–1/2 of its own width. The sulcus is shallow and nearly reaches to the antapex of the cell. A parietal chloroplast looks like that of *H. lanceolata* and other *Heterocapsa* species. A pyrenoid surrounded by starch sheathes is situated in the upper part of the hypotheca. A nucleus is spherical or ellipsoidal and located in the epitheca.

Thecal plates of *H. horiguchii* are rather tenuous (Plate 9). Indeed the cell seems gymnodinioid species under light microscope. The thecal plate arrangement is determined as Po, cp, 5', 3a, 7", 6c, 5s, 5'", 2"" (Fig. 3-2-9). The variation of plate 2a was observed, viz. it was usually seven-sided but sometimes substituted with six-sided plate.

The subcellular structure of *H. horiguchii* is typical of dinoflagellates (Plate 20), containing dinokaryotic nucleus, trichocysts, a chloroplast with three appressed thylakoid lamellae and mitochondria with tubular cristae. The pusule containing numerous membranous materials is located near the basal body. The chloroplast is situated in the cell peripherally and connects with the pyrenoid covered with starch sheaths. Tubular invaginations were rarely

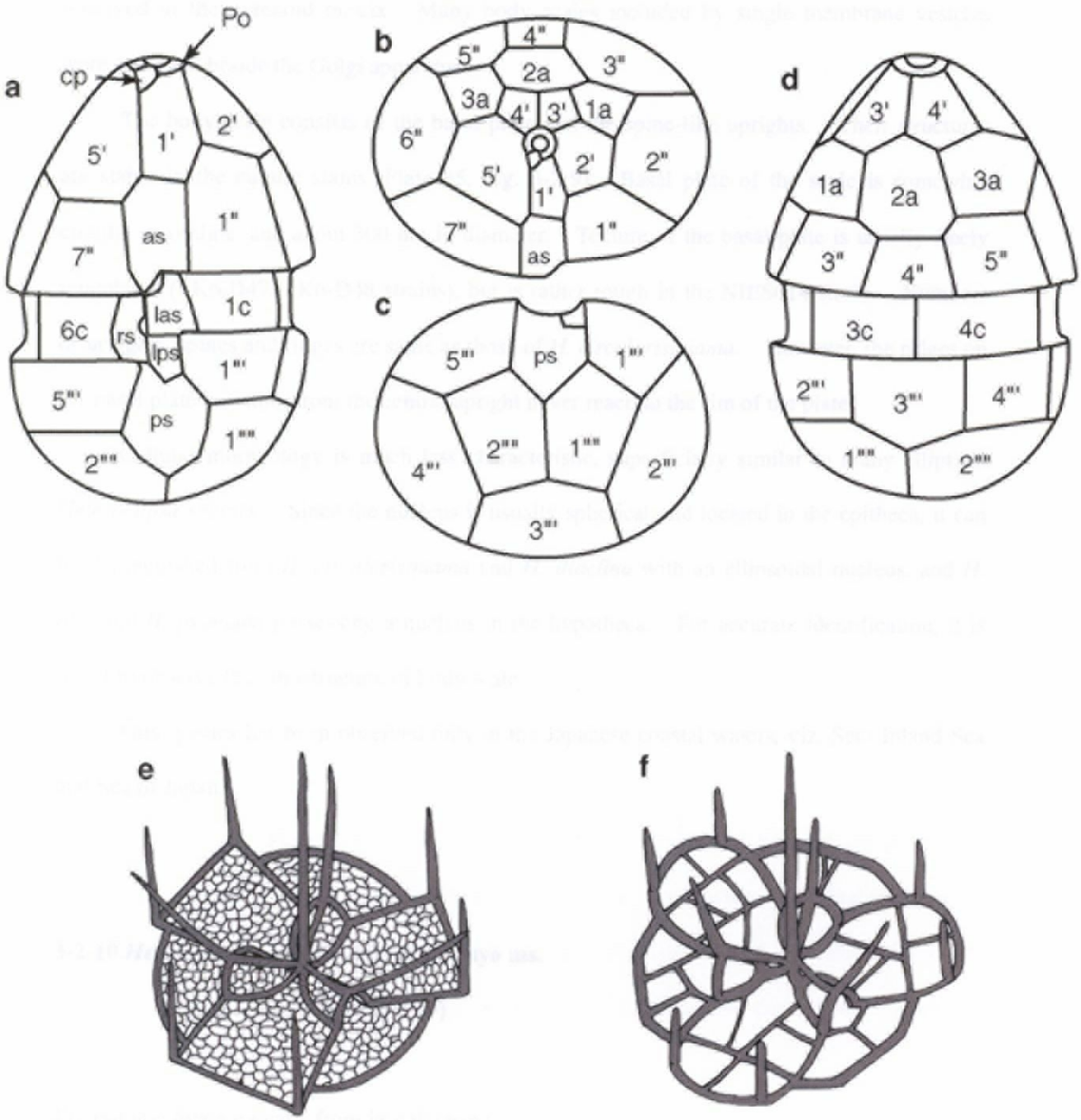

Figure 3-2-9. *Heterocapsa horiguchii* Iwataki, Takayama & Matsuoka ms.

a-d. Diagmammatic illustrations of thecal plates; **a**, ventral view; **b**, apical view; **c**, antapical view; **d**, dorsal view.

e, f. Body scales; **e**, basal plate with fine reticulation; **f**, basal plate with rough reticulation found from old culture.

observed in the pyrenoid matrix. Many body scales included by single membrane vesicles were observed beside the Golgi apparatus.

The body scale consists of the basal plate and the spine-like uprights. Their structures are stable in the culture stains (Plate 35, Fig. 3-2-9). Basal plate of the scale is somewhat circular in outline, and about 300 nm in diameter. Texture of the basal plate is usually finely reticulated (FK6-D47, FK6-D48 strains), but is rather rough in the NIES614 strain. Numbers of uprights, spines and ridges are same as those of *H. circularisquama*. However, the ridges on the basal plate radiating from the central upright never reach to the rim of the plate.

Cellular morphology is much less characteristic, superficially similar to many elliptical *Heterocapsa* species. Since the nucleus is usually spherical and located in the epitheca, it can be distinguished from *H. circularisquama* and *H. illdefina* with an ellipsoidal nucleus, and *H. niei* and *H. pygmaea* possessing a nucleus in the hypotheca. For accurate identification, it is better to observe the ultrastructure of body scale.

This species has been observed only in the Japanese coastal waters, viz. Seto Inland Sea and Sea of Japan.

3-2-10 *Heterocapsa ovata* Iwataki & Fukuyo ms.

(Fig. 3-2-10, Plate 10, 21, 36)

Etymology: ovata = ovate, from its cell shape.

Synonym

Heterocapsa sp. 3

Iwataki, Takayama, Matsuoka, Hiroishi & Fukuyo (2002)

Cells are ovoid with an epitheca and a hypotheca, both of which are hemispherical and almost

equal in size (Fig. 3-2-10). Apex of the epitheca is obtuse, while the antapex is slightly flat. Cells are relatively large, 23.6-33.2 μm (mean 26.9 μm, n = 30) in length and 18.4-28.0 μm (mean 21.4 μm) in width (KZHt-1 strain). The cingulum is relatively narrow and is displaced by about 1/3 of its own width. The sulcus is shallow and almost reaches the antapex of the cell. The chloroplast is located in the cell peripherally and occasionally perforated. The spherical pyrenoid surrounded by starch sheaths is situated in the upper part of the hypotheca. A spherical nucleus is located in the central part of the epitheca.

Presence of the thecal plate of *H. ovata* can be confirmed at light microscopic resolution, however, each plate is relatively thin and determination of the arrangement is rather difficult (Plate 10). The thecal plate arrangement is Po, cp, 5', 3a, 7", 6c, 5s (as, rs, las, lps, ps), 5"', 2"" (Fig. 3-2-10). Among the sulcal plates, the lps plate is larger than the las plate. Other features of thecal plates are almost identical with typical of the genus. Posterior part of the 2a plate usually contacts with 3", 4" and 5" of three precingular series, but sometimes the 2a slightly moves to right direction and contacts only with the 4" and 5" plates.

Under transmission electron microscope, an ellipsoidal nucleus located in the central epitheca was seen (Plate 21). The chloroplast is rather thin and situated periphery. A spherical pyrenoid is located in the center of the hypotheca. It connects with several stalks to the chloroplasts. The pyrenoid includes many tubular invaginations, and surrounded by starch sheaths. Electron dense lipid globules are found in the antapical part of the cytoplasm. Typical trichocysts of dinoflagellate are also present.

The body scales densely surround the cell body (Plate 10, 36, Fig. 3-2-10). It seems to be robust due to its thick ornamentations. The basal plate is rounded triangle in outline, and composed of fine texture of reticulation. A central upright and six peripheral uprights are present. From the base of the central upright, six ridges radiate toward the six peripheral uprights along the basal plate. Three peripheral bars connect with the peripheral uprights at the distal part. As a result, the uprights make three pairs on each corner of the triangle. These

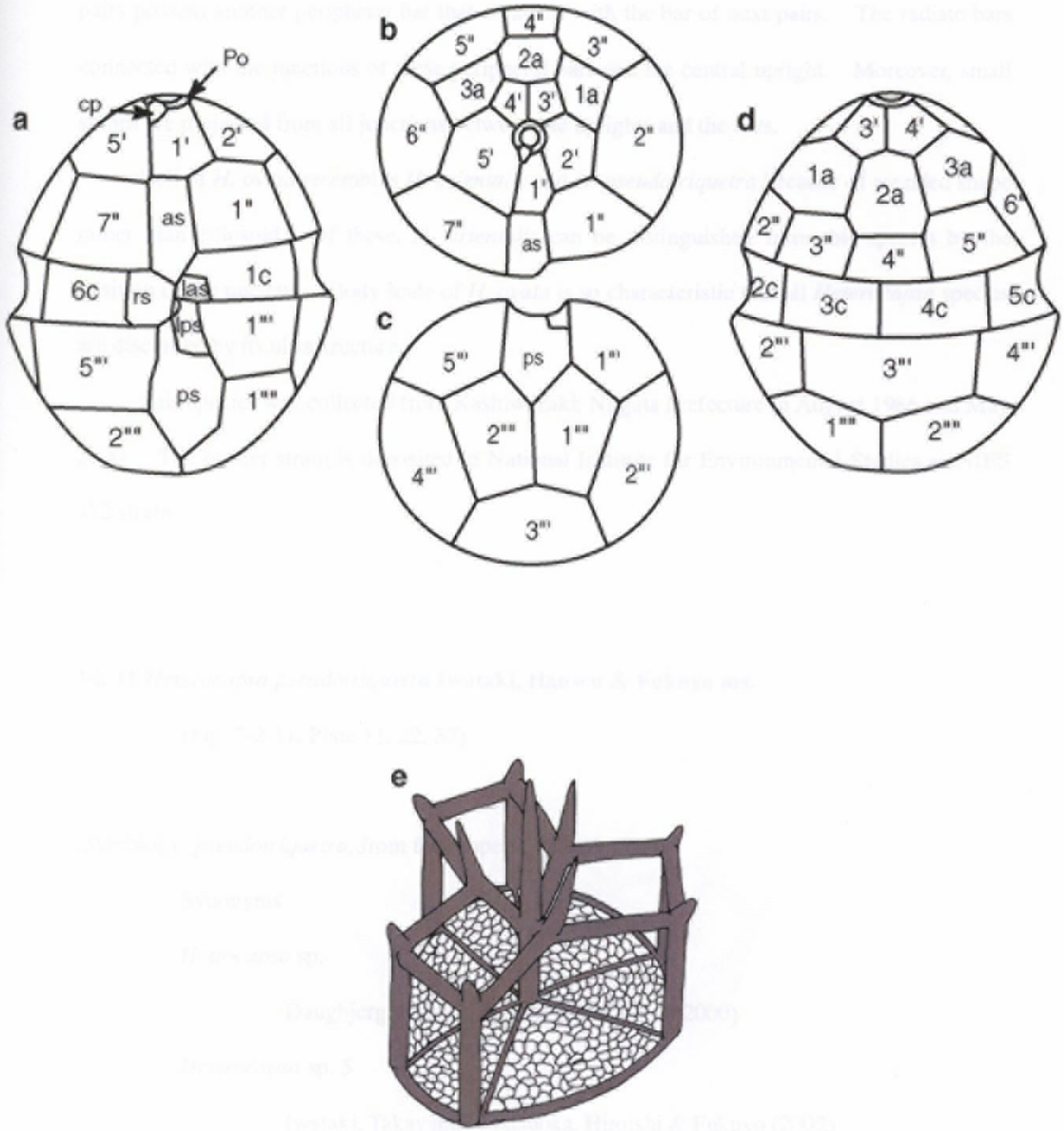

Figure 3-2-10. *Heterocapsa ovata* Iwataki & Fukuyo ms.

a-d. Diagmammatic illustrations of thecal plates; **a**, ventral view; **b**, apical view; **c**, antapical view; **d**, dorsal view.
e. Body scale.

pairs possess another peripheral bar that connects with the bar of next pairs. The radiate bars connected with the junctions of these peripheral bars and the central upright. Moreover, small spines are projected from all junctions between the uprights and the bars.

Cell of *H. ovata* resembles *H. orientalis* and *H. pseudotriquetra* because of rounded shape rather than ellipsoid. Of these, *H. orientalis* can be distinguished from this species by the position of the nucleus. Body scale of *H. ovata* is so characteristic that all *Heterocapsa* species are discerned by its ultrastructure.

This species was collected from Kashiwazaki, Niigata Prefecture in August 1986 and May 2000. The former strain is deposited in National Institute for Environmental Studies as NIES 472 strain.

3-2-11 *Heterocapsa pseudotriquetra* Iwataki, Hansen & Fukuyo ms.

(Fig. 3-2-11, Plate 11, 22, 37)

Etymology: *pseudotriquetra*, from the shape of its body scale.

Synonyms

Hetrocapsa sp.

Daugbjerg, Hansen, Larsen & Moestrup (2000)

Heterocapsa sp. 5

Iwataki, Takayama, Matsuoka, Hiroishi & Fukuyo (2002)

Cells are spherical and consist of the epitheca and the hypotheca, which are hemispherical and equal in size (Plate 11). Cells are 18.4-27.2 μm (mean 22.2 μm, n = 30) in length, and 14.4-21.6 μm (mean 17.2 μm, n = 30) in width (NIES473 strain). The cingulum transverses the equatorial plane of the cell and the displacement is about 1-1/2 of its own width. The sulcus

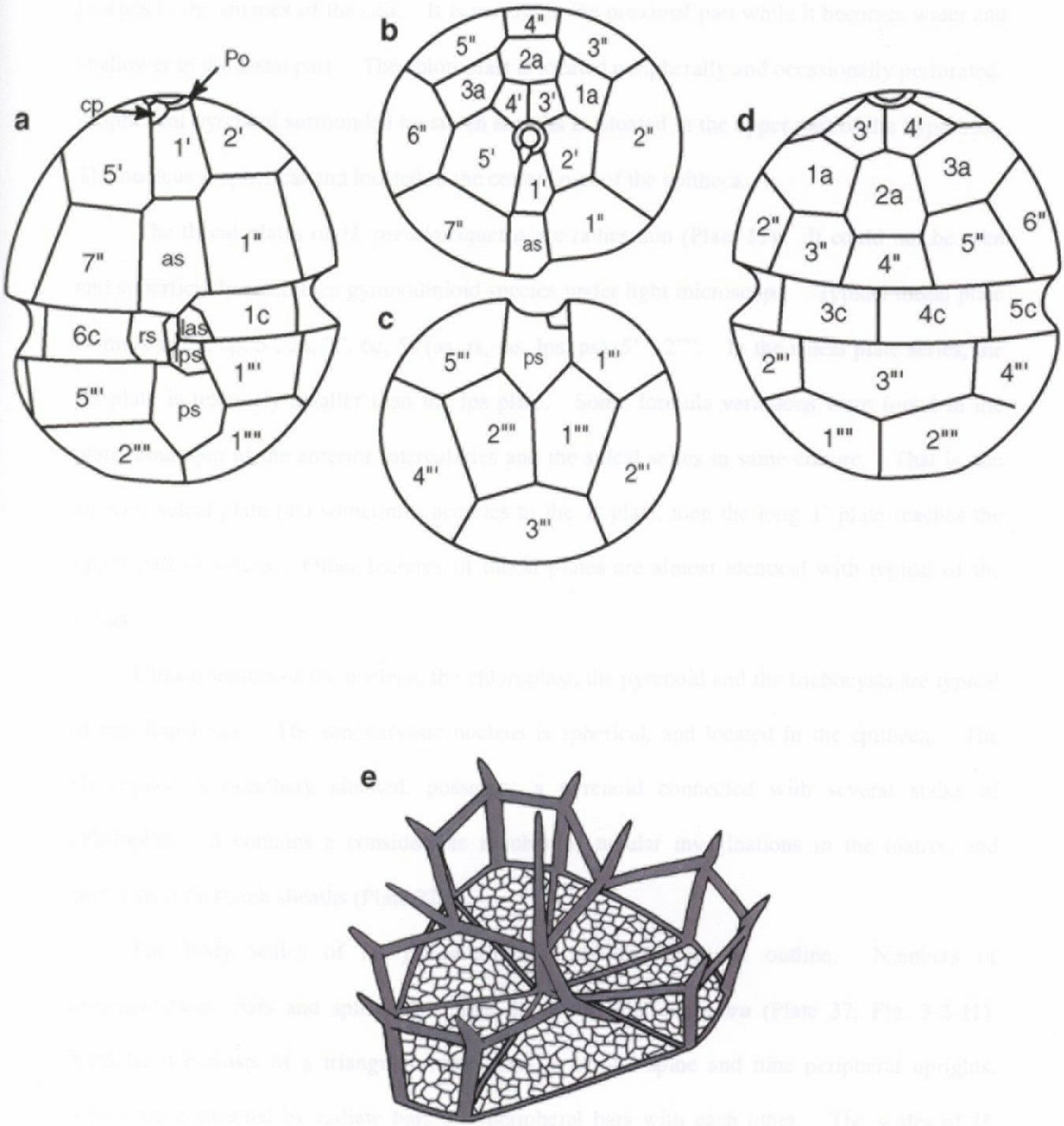

Figure 3-2-11. *Heterocapsa pseudotriquetra* Iwataki, Hansen & Fukuyo ms.

a-d. Diagmammatic illustrations of thecal plates; **a**, ventral view; **b**, apical view; **c**, antapical view; **d**, dorsal view.
e. Body scale.

reaches to the antapex of the cell. It is narrow in the proximal part while it becomes wider and shallower in the distal part. The chloroplast is located peripherally and occasionally perforated. A spherical pyrenoid surrounded by starch sheaths is situated in the upper part of the hypotheca. The nucleus is spherical and located in the central part of the epitheca.

The thecal plates of *H. pseudotriquetra* are rather thin (Plate 11). It could not be seen and superficially resembles gymnodinioid species under light microscope. Typical thecal plate formula is Po, cp, 5', 3a, 7", 6c, 5s (as, rs, las, lps, ps), 5'", 2"". In the sulcal plate series, the las plate is relatively smaller than the lps plate. Some formula variations were found in the plate tabulation of the anterior intercalaries and the sulcal series in same culture. That is, the anterior sulcal plate (as) sometimes accretes to the 1' plate, then the long 1' plate reaches the upper part of sulcus. Other features of thecal plates are almost identical with typical of the genus.

Ultrastructures of the nucleus, the chloroplast, the pyrenoid and the trichocysts are typical of dinoflagellates. The dinokaryotic nucleus is spherical, and located in the epitheca. The chloroplast is periphery situated, possesses a pyrenoid connected with several stalks of chloroplast. It contains a considerable number of tubular invaginations in the matrix, and surrounded by starch sheaths (Plate 22).

The body scales of *H. pseudotriquetra* are triangular in outline. Numbers of ornamentations, bars and spines, are same to those of *H. triquetra* (Plate 37, Fig. 3-2-11). Namely, it consists of a triangular basal plate, a central spine and nine peripheral uprights, which are connected by radiate bars and peripheral bars with each other. The scales of *H. triquetra* were frequently covered by mucilaginous body and difficult to observe in detail, whereas those of *H. pseudotriquetra* were relatively easy to observe.

Another characteristic of this species is abundance temporary cyst (Plate 11, f 3). This species makes the temporary cyst easily under culture conditions. More than half of the cells are observed as temporary cysts in culture condition. Temporary cysts are spherical or slightly

ellipsoid, more or less larger than motile cells, and 18.4-27.2 μm (mean 24.5 μm, n = 20) in diameter.

Cells of *H. pseudotriquetra* are relatively large and spherical, and similar to *H. ovata* and *H. orientalis*. It can be differentiated from *H. orientalis* by the position of nucleus. Body scale structure is different from these two species. On the other hand, the scale structure is almost identical with *H. triquetra*, but cell shapes are quite dissimilar with each other.

Strains of *H. pseudotriquetra* were established using samples collected from the coastal area of Canada, Japan and U.S.A. They possess same cellular and body scale ultrastructures, therefore, they should be the same species. This species seems to distribute all around in the temperate areas of the Pacific Ocean.

3-2-12 *Heterocapsa orientalis* Iwataki & Fukuyo ms.

(Fig. 3-2-12, Plate 12, 23, 38, 39)

Etymology: orientalis = oriental, from its sampling location.

Synonym

Heterocapsa sp. 6

Iwataki, Takayama, Matsuoka, Hiroishi & Fukuyo (2002)

Cells are ovoid and consist of a hemispherical epitheca and hypotheca, which are almost equal in size, or the hypotheca is slightly larger (Plate 12). Cell size is 18.4-34.4 μm (mean 25.7 μm, n = 30) in length and 16.0-24.0 μm (mean 19.6 μm, n = 30) in width (D-127-C-3 strain). The cingulum is relatively deep and displaced by almost 1/2 of its own width. A chloroplast is distributed in the cell peripherally and appears granular. It possesses a pyrenoid, which situated in the epitheca and sometimes surrounded by starch sheaths. An ellipsoidal nucleus is

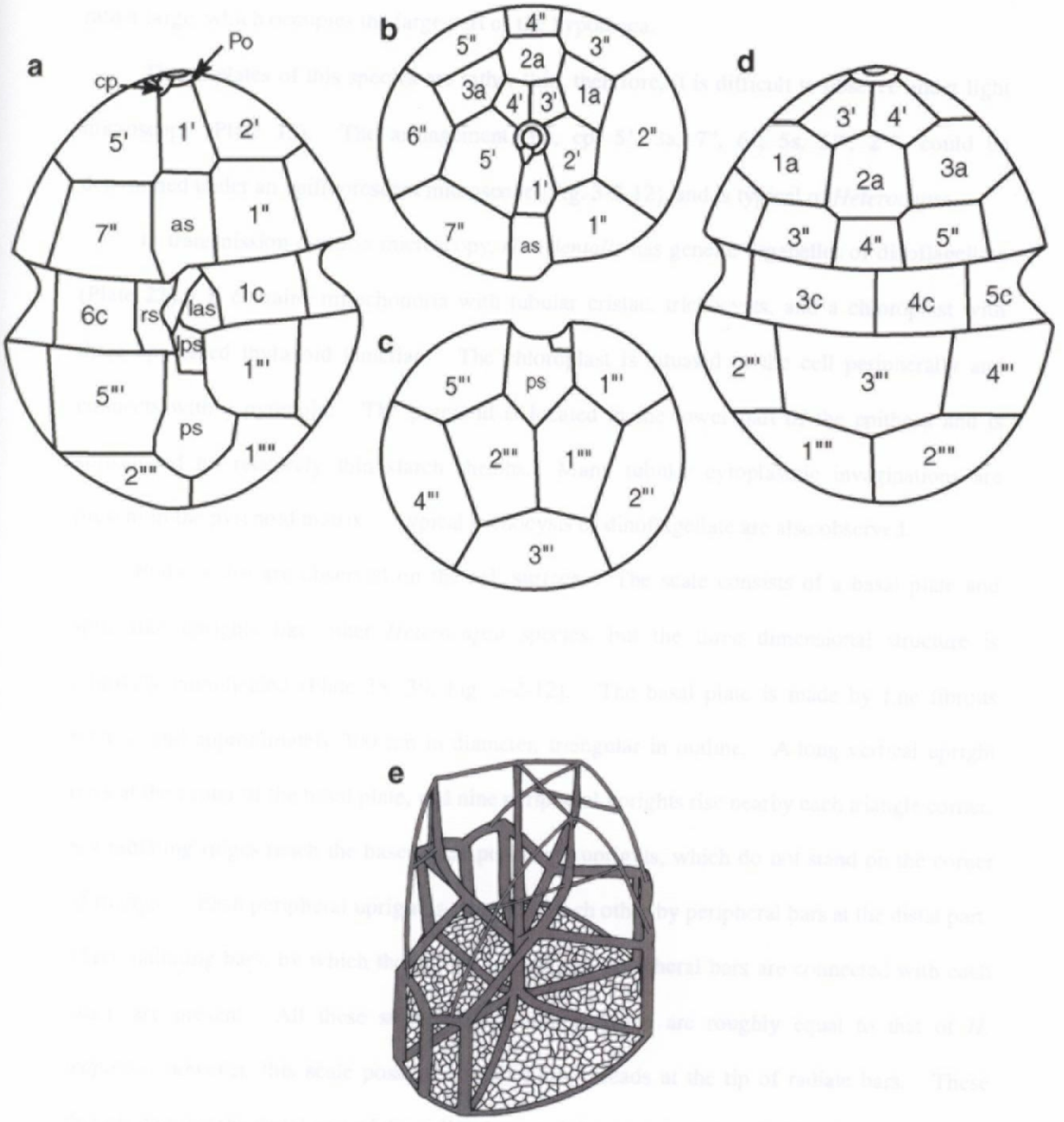

Figure 3-2-12. *Heterocapsa orientalis* Iwataki & Fukuyo ms.

a-d, Diagmammatic illustrations of thecal plates; **a**, ventral view; **b**, apical view; **c**, antapical view; **d**, dorsal view.
e. Body scale.

rather large, which occupies the large part of the hypotheca.

Thecal plates of this species are rather thin, therefore, it is difficult to observe under light microscope (Plate 12). The arrangement. Po, cp, 5', 3a, 7", 6c, 5s, 5"', 2"", could be determined under an epifluorescent microscope (Fig. 3-2-12), and is typical of *Heterocapsa*.

In transmission electron microscopy, *H. orientalis* has general organelles of dinoflagellate (Plate 23). It contains mitochondria with tubular cristae, trichocysts, and a chloroplast with three appressed thylakoid lamellae. The chloroplast is situated in the cell peripherally and connects with a pyrenoid. The pyrenoid is located in the lower part of the epitheca and is surrounded by relatively thin starch sheaths. Many tubular cytoplasmic invaginations are present in the pyrenoid matrix. Typical trichocysts of dinoflagellate are also observed.

Body scales are observed on the cell surface. The scale consists of a basal plate and spine-like uprights like other *Heterocapsa* species, but the three dimensional structure is relatively complicated (Plate 38, 39, Fig. 3-2-12). The basal plate is made by fine fibrous texture, and approximately 300 nm in diameter, triangular in outline. A long vertical upright rises at the center of the basal plate, and nine peripheral uprights rise nearby each triangle corner. Six radiating ridges reach the base of six peripheral uprights, which do not stand on the corner of triangle. Each peripheral upright is connected each other by peripheral bars at the distal part. Three radiating bars, by which the central upright and peripheral bars are connected with each other, are present. All these structures mentioned above are roughly equal to that of *H. triquetra*, however, this scale possesses further thin threads at the tip of radiate bars. These threads connect the distal part of the radiate bars and the central spine. Short spines are absent.

Cells of this species resemble the spherical or ovoid species such as *H. ovata* and *H. pseudotriquetra*, however, it can be distinguished from them by the position of nucleus. The body scale is quite complicated and characteristic, hence this species is easy to identify from the ultrastructure.

This species was recorded only from the coastal area of Iwate Prefecture, Japan.

Heterocapsa species described above could be observed using culture strains. However, culture of the following two species could not be available.

3-2-13 *Heterocapsa minima* Pomroy (Fig. 3-2-13)

Pomroy, 1989, p. 184, Figs. 1-12.

Sournia, 1990, p. 330.

Cell is dorsoventrally compressed. The cingulum displaces half of its width, without the collar. A sulcus reaches the antapex of the cell. Horn and superficial ornamentations are absent. The hypotheca is smaller than the epitheca. Cell is 8.7 μm in length and 6.1 μm in width. Ratio between cell length and width is 1.43. Several chloroplasts are located peripherally. Nucleus is situated in the posterior part of the cingulum. Thecal plates are thin. Sutures are unclear. Numerous trichocysts are present. Thecal plate arrangement is Po, cp, 5', 3a, 7", 6c, 5s (as, rs, las, lps, ps), 5''', 2''''.

This species was described by Pomroy (1989) from the Celtic Sea. Almost all *Heterocapsa* species were reported from coastal waters, while this species collected from offshore. This species was originally described using SEM photomicrographs of preserved cell, and these photos clearly exhibited the typical plate arrangement of the genus *Heterocapsa*. Moreover, its small cell size is rather characteristic among *Heterocapsa* species, and was thus regarded as a new species of *Heterocapsa*. However, body scale was not reported at that time.

It is difficult to be distinguished this species from others only from these characteristics shown by Pomroy (1989). For example, cell sizes of *H. pygmaea* and *H. rotundata* are sometimes less than 10 μm. *H. lanceolata* and *H. rotundata* also possess the larger epitheca.

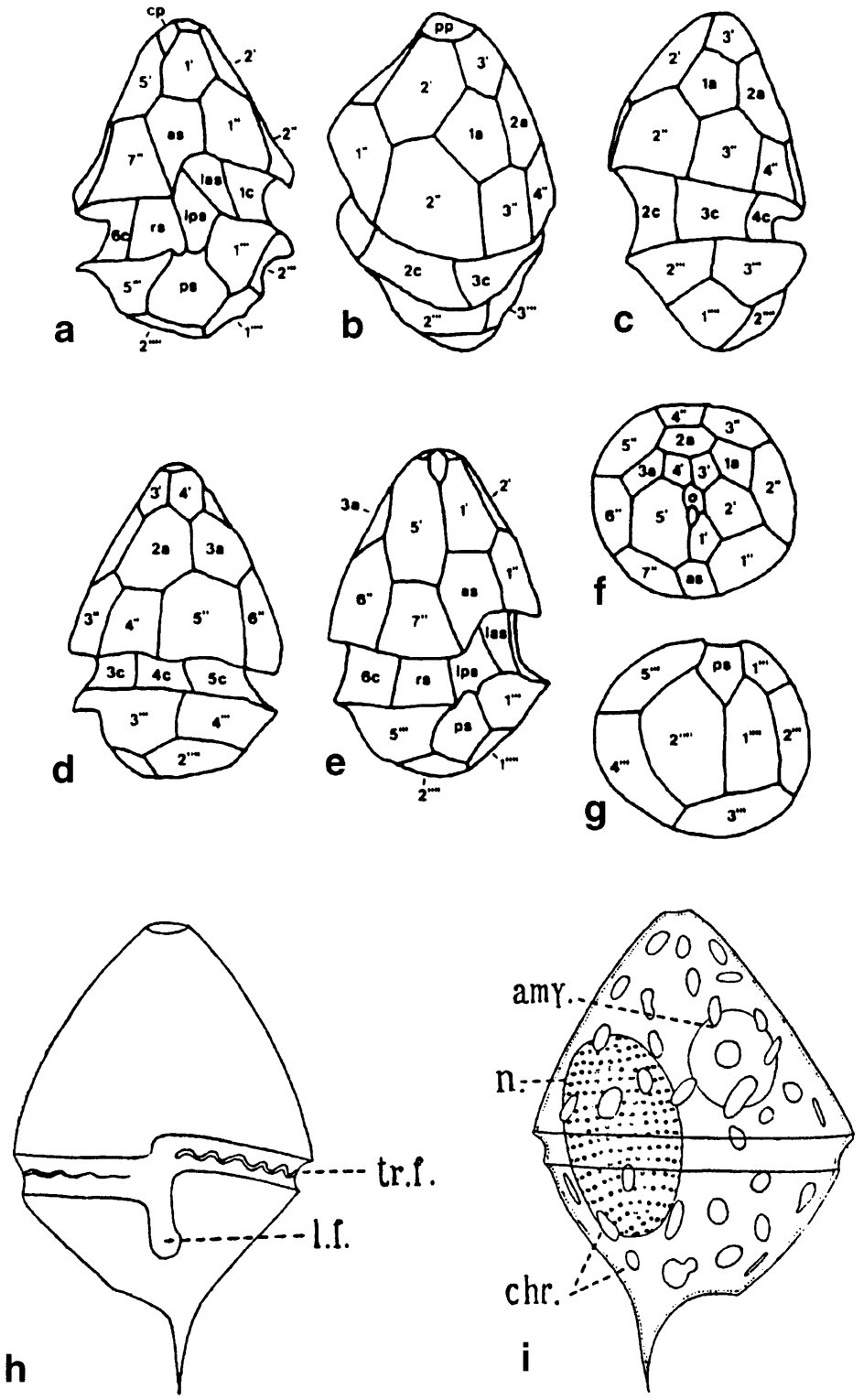

Figure 3-2-13. Original line drawings of *Heterocapsa minima* Pomroy (**a-g**; Pomroy 1989) and *Heterocapsa pacifica* Kofoid (**h-i**; Kofoid 1907).

The nuclei of *H. niei* and *H. pygmaea* are also located in the hypotheca. These characteristics sometimes vary in the culture condition of each species, thus identification of this species seems to be rather difficult. This may be the main reason why *H. minima* has not been reported since the original description was published. Unfortunately, the culture strain of this species is not maintained in Plymouth Marine Laboratory, England, where this species was first observed. It is necessary to recognize the presence of the body scale and to observe the ultrastructure, although this species was listed as the distinct species in the present study.

3-2-14 *Heterocapsa pacifica* Kofoid (Fig. 3-2-13)

Kofoid, 1907, p. 301, Pl. 22, Figs 4, 5

Cells are ovoid, dorsoventrally compressed, with prominent asymmetrical spine. Cell length including spine is 45μm and the width is 30μm. The cell shape resembles *H. triquetra* but is less elongated. The length excluding spine is 1.3 times the width and 2.1 times the dorsoventral one. The epitheca is larger than the hypotheca, its altitude 0.75 of the basal width, its sides slightly convex. Apical pore is present. Hypotheca is less than 0.5 of the transdiameter in height, slightly asymmetrical, the right side more convex than the left, continued posteriorly in a stout acuminate antapical spine a little to the left of the axis. Its base merges gradually into the outline of the hypotheca and its length is 0.3 times of the width. There is a slight elevation on the right side suggestive of a second rudimentary antapical spine. The cingulum is postmedian; the cingulum is impressed, without lists and forms a descending right spiral displaced distally nearly its own width. The sulcus is faint and continues posteriorly for half the length of the hypotheca. Nucleus is ellipsoidal and relatively large, with moniliform chromatin reticulum. A large spherical amyloid body (pyrenoid?) is present

and there are numerous ellipsoidal peripherally located chloroplasts of yellowish color. Thecal plates are hyaline, therefore the suture lines can not be seen under light microscope. Thecal plate arrangement is unknown. This species was found in surface oceanic plankton off San Diego on June.

This species was described as the plankton in the water of offshore of Southern California. As well as *H. minima*, any other authors have not reported the species since the original description of Kofoid (1907). It appears to be a thecate dinoflagellate based on the steady cell body and the antapical spine, but each thecal plate was not observed. This species is difficult to be identified as the genus *Heterocapsa* without information of thecal plate arrangement, and it is also difficult to transfer to other genera of thecate dinoflagellates. According to the original description, cell of *H. pacifica* resembles *H. triquetra*. Moreover, the amyloid body located in the epitheca is somewhat similar to pyrenoid surrounded by starch sheaths of the genus. If this species were one of the numbers of *Heterocapsa*, it is clearly different from other described *Heterocapsa* species. I treat this species as a peculiar species of *Heterocapsa* in the thesis.