Dinophyceans were originally classified solely as Protozoa. At the present time some still classify them as Dinoflagellida Bütschli, class Mastigophora Diesing. In this class there are more colorless, heterotrophic algal species present than among all the other algae. These protists sometimes produce strong toxins and may act as parasites or phagotrophs. Dinoflagellates are probably more phagocytic than is commonly known (Kudo 1971, Grell 1973). Two marine species *Kryptoperidinium foliaceum* and *P. balticum* are known to possess a second eukaryotic nucleus as well as the usual dinokaryon present in dinoflagellages (Dodge 1971, Tomas et al. 1973) *Peridiniopsis balticum* has a chrysophycean chloroplast (Tomas and Cox 1973). Thus some believe that this represents an invasion of an autotrophic organism into a dinoflagellate cell which otherwise would be apochloric (Raikov 1978) or on the other hand the dinoflagellate cell could store certain of its prey's organelles or storage products for food or maintain them functioning as a reserve metabolic mechanism.

Following Klebs (1912) work Pascher (1927) placed the Dinophyceae in the phylum Pyrrhophyta together with the Cryptophyceae and Desmokontae on the basis of certain similar morphological features, photosynthetic and accessory pigments and the presence of starch. Chadefaud (1960) and Christensen (1962) placed the class Dinophyceae and Cryptophyceae into the phylum Chromophyta. Fott (1971) excluded the Cryptophyceae from the Chromophyta thus emphasizing their nonrelatedness to the Dinophyceae. The position of the Dinophyceae as an isolated group in the algae is unusual. Thus, at the present time it seems appropriate to classify the Dinophyceae among the Protozoa (Mycetozoa) since the presence of coccal and trichal forms is questionable.

2. Cell structure

2.1. Cell covering

Naked dinoflagellate cells have definitive body shapes or forms (some monads) during certain phases of their life cycles or are metamorphic in shape such as *Dinamoebidium,* dinococcalian members and their rhizopodial stages (Popovský and Pfiester 1982). The cell covering of all dinophyceans is called the amphiesma (Schütt 1895, Loeblich 1968) or theca. In naked members (unarmored or athecated) the theca is composed of several membrane layers as seen with an electron microscope and may be passively metabolic. Some species of the genera *Gymnodinium, Katodinium* and *Amphidinium* have a delicate cell cover which is sensitive to chemical and physical changes in the environment. These genera cannot be well preserved. In other naked taxa the cell cover is rather rigid and often sculptured. This protects the cell against chemical and physical changes in the environment. They retain their cell shape when preserved.

Flattened thecal vesicules may be found between the outer membrane and the plasma membrane. Armored forms have structural cellulose or other polysachrides in these vesicules. The inner membrane is interpreted as the plasma membrane. Microtubules occur on the inner side of the plasma membrane. A 5th membrane that may represent a cytoplasmic vesicular component can occur below the microtubules. Those armored species which shed the epi- and hypothecae at cell division often have a pellicular layer. There is disagreement on whether the outermost or inner membrane is the functional plasmalemma (Loeblich 1968).

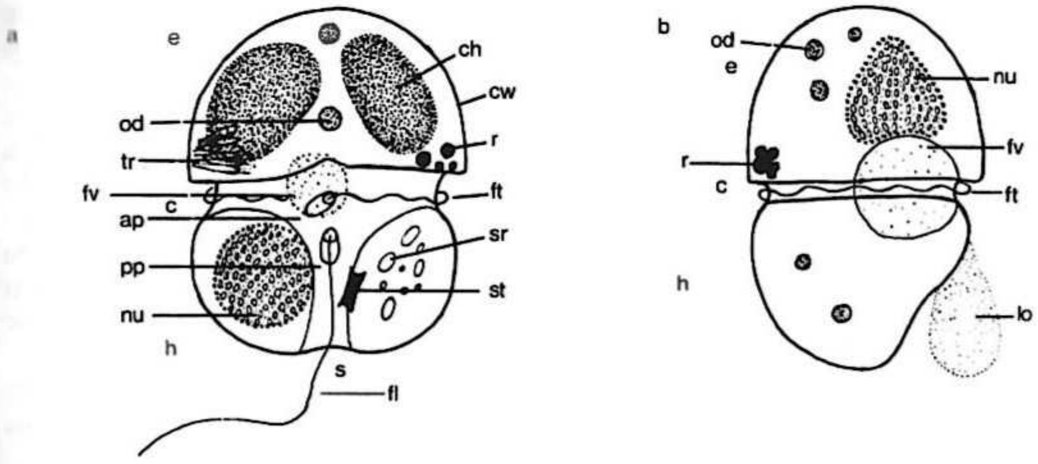


Fig. 2. Cell body, diagrammatic; *a.* ventral, *b.* lateral section; e epicone, h hypocone, c cingulum or girdle, s sulcus, ft transverse flagellum, fl longitudinal flagellum, ap anterior flagellar pore, pp posterior flagellar pore, ch chloroplast, r red remnants, red oil droplets, sr starch, fv food vacuole, nu nucleus, tr trichocyste, cw cell wall, lo lobopode. Organelles and structures that may be present but are not illustrated here include: contractile vacuole and all types of pseudopodia and tentacles.

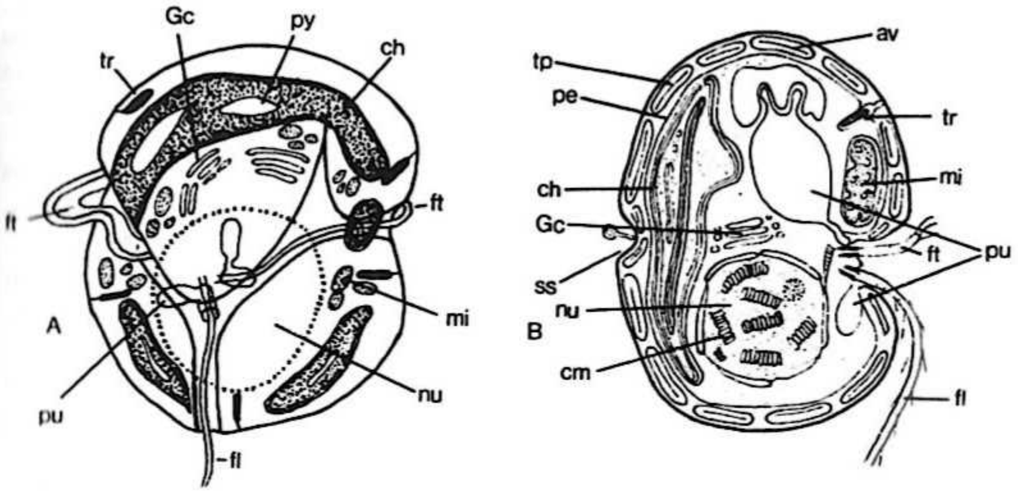


Fig. 3. A. Ultrastructure of marine *Woloszynskia micra* (ventral view); ch chloroplast, py pyrenoid, nu nucleus, tr trichocyst, Gc Golgi complex, mi mitochondria, pu pusule, ft transverse flagellum, fl longitudinal flagellum (after Leadbeater and Dodge).

B. Ultrastructure of a gymnodinioid dinoflagellate (diagrammatic lateral section); av amphiesmal vesicle, ch chloroplast, cm chromosome, Gc Golgi complex, ft transverse flagellum, fl longitudinal flagellum, ss striated strand, mi mitochondrion, nu nucleus, pe pellicular layer, pu pusule, tp thecal plate, tr trichocysts (after Taylor).

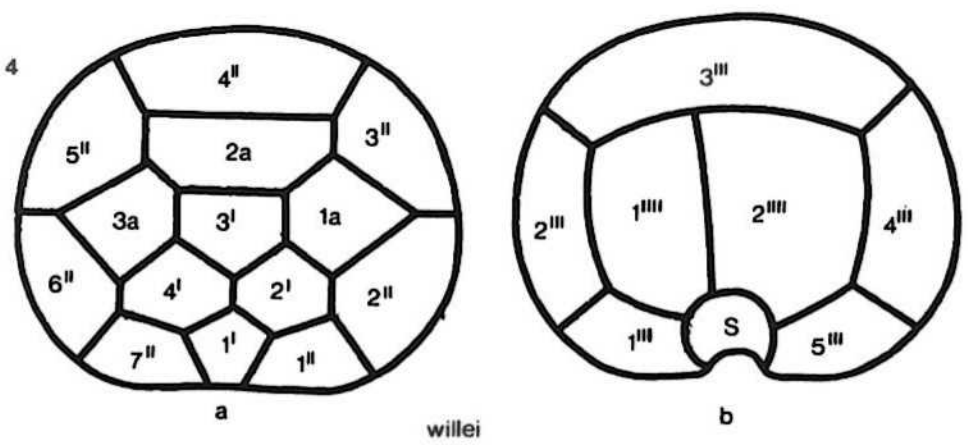
In the dinococcalians the cell wall is composed of cellulose and is relatively thick. In *Cystodinedria, Stylodinium* and *Cystodinium* the cell wall of the phagocytic phase is metabolic enabling the cell to move by changing its shape and to enlarge its cell volume during predation. These cells also possess haustoria at some stages in their life history (figs. 54, 55). In *Stylodinium* and *Cystodinium* the stalk (haustorium) is similar to that found in suctorians. It may be short or three times the cell diameter (see chapter 2.6.) *Cystodinedria inermis* rarely exhibits a rhizopodium (haustorium) by means of which it phagocytizes *Oedogonium* cells (Popovský and Pfiester 1981). One of the horns in *Cystodinium* probably has an opening through which very short pseudopodia anchor it as shown on figures of *C. cornifax* (fig. 243). Stalks figured on drawings of *Dinococcus* (figs. 236–238) and *Tetradinium* (figs. 239–241) probably function as haustoria. However, at this stage of investigation into the now recognized complex life of members of the order Dinococcales one cannot be certain that these latter two genera are not zygotic stages within the life histories of the other previously mentioned dinococcalian genera. *Stylodinium tarnum* at times produced a single zoospore (Baumeister 1943) which has a plate pattern formula identical to that of *Peridiniopsis dinobryonis* (fig. 221). In our opinion it is a monad, which forms a haustorium through its apical pore which it uses in

---

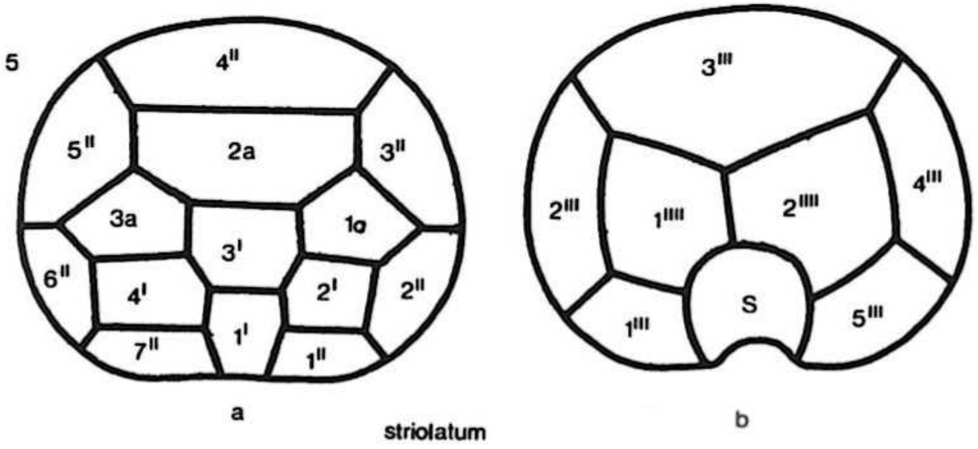
Figs. 4–31. Diagrammatic plates arrangements in the following genera and species. Projections of the epitheca *(a)* and hypotheca *(b)*. Each projection in the genera *Peridinium and Peridiniopsis* represents a section of species which exhibits the same plate formula. Symbols used: S sulcus, G girdle, Xa anterior intercalary plates , X' apical plates, X'' precingular plates, X''' postcingular plates, X'''' antapical plates, X_p accessory posterior intercalary plate, sa upper ventral plate in the junction, sp lower plate, sd right plate, ss left plate, c_x cingulum plates, po pore plate; i. e. *Peridinium willei* plate formula is: 4', 3a, 7''; 5''', 2''''. Plates are numbered in a counter clockwise fashion in apical view and clockwise in the antapical view. In the formula, however, they are ordered from the cingulum to the (a) apical pole, and (b) the antapical pole.

Fig. 4. *Peridinium,* section *willei* (Cleistoperidinium), Fig. 5. *Peridinium,* section *striolatum,* Fig. 6. *Peridinium,* section *cinctum,* Fig. 7. *Peridinium,* section *palatinum,* Fig. 8. *Peridinium,* section *bipes* (Poroperidinium), Fig. 9. *Peridinium,* section *gutwinskii,* Fig. 10. *Peridinium,* section *umbonatum,* Fig. 11. *Peridinium,* section *lomnickii,* Fig. 12. *Peridinium,* section *allorgei,* Fig. 13. *Peridiniopsis,* section *polonicum,* Fig. 14. *Peridiniopsis* section *lindemannii,* Fig. 15 *Peridiniopsis,* section *elpatiewskyi,* Fig. 16. *Peridiniopsis,* section *cunningtonii,* Fig. 17. *Peridiniopsis,* section *penardii,* Fig. 18. *Glenodiniopsis steinii,* Fig. 19. *Peridiniopsis,* section *quadridens,* Fig. 20. *Peridiniopsis,* section *borgei,* Fig. 21. *Peridiniopsis,* section *thompsonii.* Fig. 22. *Sphaerodinium cinctum,* Fig. 23. *Diplopsalis acuta,* Fig. 24. *Dinosphaera palustris.* Fig. 25. *Peridiniopsis,* section *dinobryonis,* Fig. 26. *Gonyaulax apiculata,* Fig. 27. *Thompsodinium intermedium.* Fig. 28. shows the numbered plates in *Hemidinium nasutum, a* ventral view, *b* dorsal view, *c* apical projection, *d* antapical projection. Fig. 29. shows the numbered plates in *Ceratium hirundinella, a* ventral view, *b* dorsal view, *c* apical projection, *d* antapical projection. Fig. 30. the numbered plates in *Peridinium bipes,* a view from the *a ventral, b* dorsal, *c* lateral position. Fig. 31. the arrangement of the sulcus and girdle juction in *a Peridinium willei, b P. cinctum, c P. palatinum.*

4



5



6

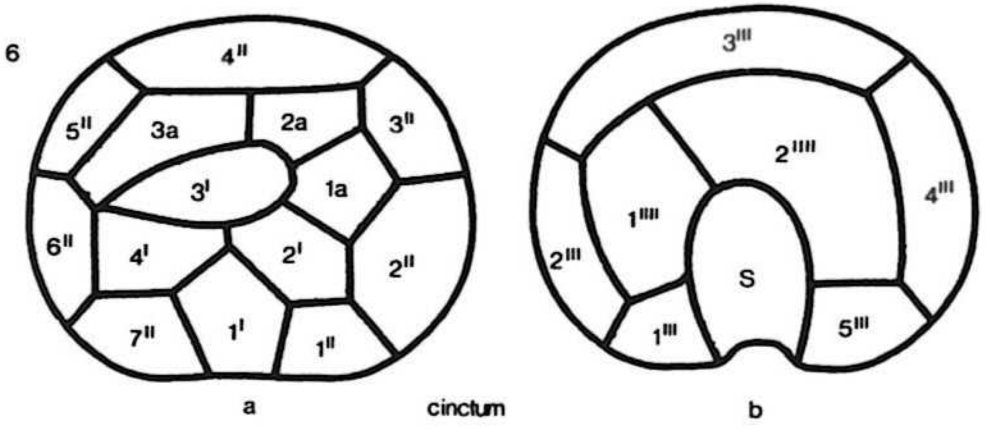


Fig. 4–6

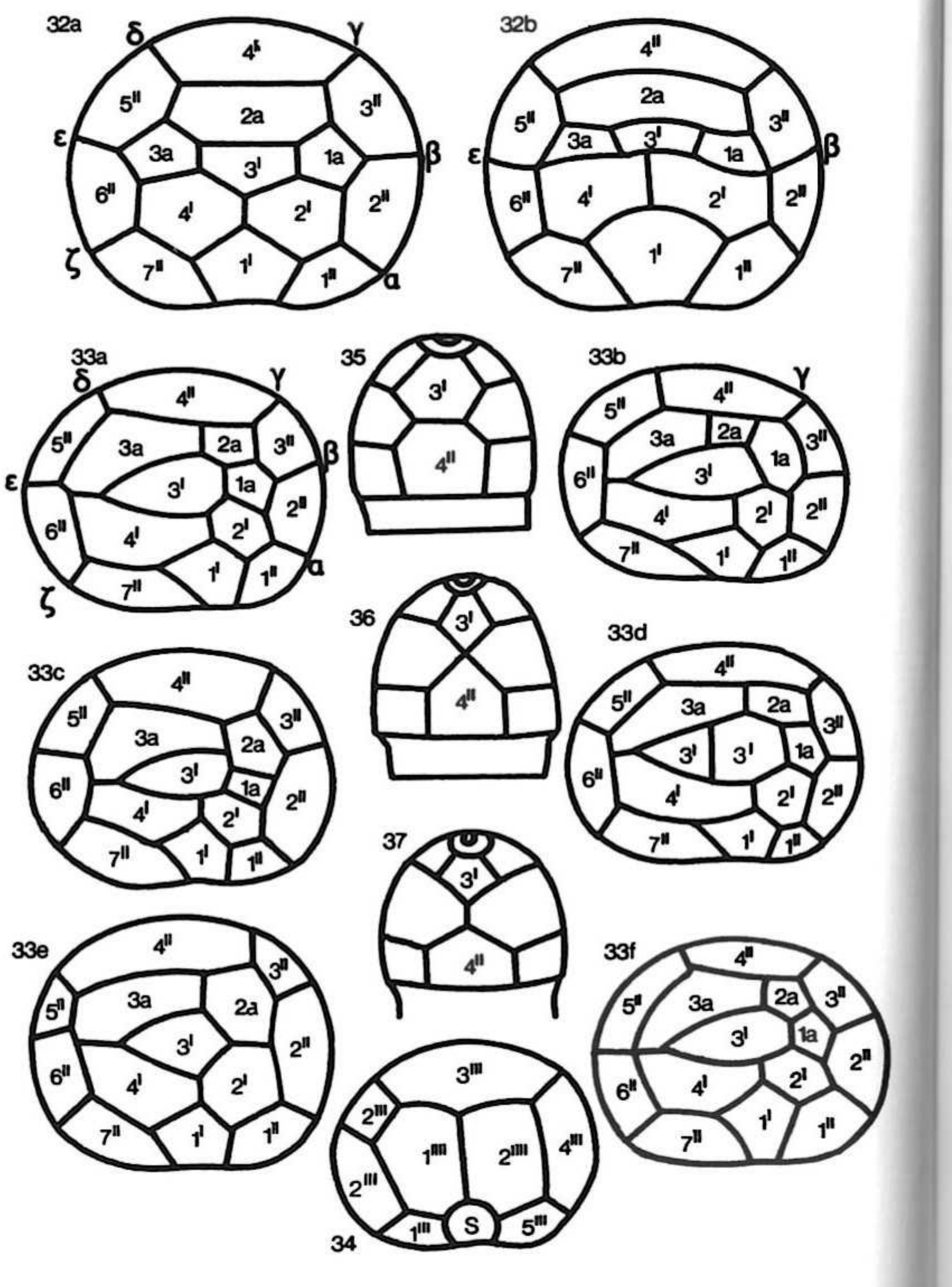


Fig. 32.—37. Projections on the epitheca of *Peridinium willei* and *P. cinctum* show the variations which may occur along the sutures, and in the numbers and position of the plates. Greek script of. sutures for plates 1″ and 7″ differ except for plate 1′ (the rhomboidal plate). This is also true for the hypotheca. Fig. 32. *a Peridinium willei, b P. willei* β ε bicollineatum, Fig. 33. *a Peridinium cinctum, b P. cinctum* γ travectum, *c P. cinctum* travectum, *d P. cinctum* 23′ complexum (the apical plate 3′ is double) *e P. cinctum* 1a simplex (the intercalary plate 1a is absent), *f. P. cinctum* ε collineatum, Fig. 34. shows the doubled plate on the hypotheca-22'''' complexum in *Peridinium cinctum*, Fig. 35—37, three variations are shown for *Peridinium umbonatum* from the dorsal view and depict the arrangement of sutures of plates 3′ and 4″ referred to as — 35 conjunctum, 36 contactum, 37 remotum.

predation. *Stylodinium polymorphum* also produces a single "zoospore" with plates and an apical pore. Its plate formula, however, is unknown and thus cannot be compared to existing formulae for other taxa (Baumeister 1957).

Spiromonas perforans also has a metabolic cell covering by means of which it phagocytizes *Chilomonas paramaecium*. This species possesses a haustorium (rostrum) during its trophozoid habit in its life history (fig. 60).

In armored species the celullose wall is very thick and may contain some chitin. As stated previously the cell covering is composed of a number of membranes as viewed through the transmission electron microscope: (1) an outer membrane which is common to all species, (2) a vesicular layer which is also common to all taxa. This layer is composed of flattened vesicles which stain with silver and appear to have a hexangular structure; the cellulosic plates are contained in these vesicles, (3) another membrane which is probably the plasma membrane and (4) a pellicular layer of acid polysaccharides (Loeblich 1969) common only to armored species. This layer is homogenous and structureless. This complex membrane system composes the amphiesma or theca. In some genera such as *Woloszynskia, Glenodiniopsis* and *Hemidinium* the theca appears to be divided into thin hexagonal plates, supposedly of uniform thickness (Bold and Wynne 1978). *Woloszynskia reticulata* (fig. 142) is unusual in the genus by having a thin, smooth, bell-shaped epitheca with a carina (ridge formed by small plates) over the apex from the ventral to the dorsal margin of the girdle and a hemispherical hypotheca composed of smooth, concave plates (fig. 134b, c) (Pfiester et al. 1980) with thick ridges. These plates differ from those found in such genera as *Peridinium, Peridiniopsis, Gonyaulax, Ceratium, Sphaerodinium, Diplopsalis,* and *Dinosphaera* in lacking suture bands joining polyangular plates. The sutures represent zones of thecal growth (figs. 38e, 153, 170). A such they enable the cell wall to accommodate protoplast enlargement. This is extremely important during sexual reproduction when the planozygote doubles in size. Thus in the latter stages of planozygote development the sutures are extremely widened and striated (Pfiester and Skvarla 1979, 1980).

Resting vegetative cysts possess a two layered cell wall and hypnozygotes have a three layered cell wall. The exact chemical composition of these walls is as yet unknown but it has been suggested that hypnozygotic walls may possess chitin (Pfiester 1975) and/or sporopollenin (Spector et al. 1981). That opening which forms in the zygote through which the meiocyte "escapes" is termed the archeopyle. It is formed when one or more plates disassociate and create an opening or pore. If these plates remain attached to the theca along one suture they form what is called an operculum or lid. The plates which separate from the theca forming the archeopyle are species specific. No information is as yet available concerning the cell wall structure of the Adinophycidae, Protaspidaceae and rhizopodial stages (trophozoides and sporocytes) of the Dinococcales.

The number, shape and arrangement of thecal plates is the main taxonomic character used in the identification of armored dinoflagellates (Desmokontae excepted – see chapter 3.1). We have used the epithecal and/or hypothecal plate formulae in our key. These plate formulae are genera and species specific. There are numerous freshwater *Peridinium* and *Peridiniopsis* species, each of which has a distinct plate pattern. Some possess an apical pore. These genera are subdivided into sections on the basis of plate pattern formulae and the presence of apical pore. Figures 4–29 show the generalized epi- and hypothecal plate arrangements for the following genera: *Peridinium, Peridiniopsis, Sphaerodinium, Diplopsalis, Dinosphaera, Gonyaulax, Thompsodinium, Hemidinium,* and *Ceratium.* Figures 30 and 31 show plates from the ventral, dorsal, and lateral views.

Plates are numbered in a counter clockwise fashion in apical view and clockwise in antapical view. In the formula, however, they are ordered from the cingulum to (a) the apical pole, and (b) the antapical pole; i. e. *Peridinium willei* plate formula is: $4', 3a, 7''; 5''', 2''''$ – four apical plates, three anterior intercalary plates, seven precingular plates, five postcingular plates, and two antapical plates.
Several systems for naming and numbering plates have been used in the older literature. In Bütschli's system *Peridinium willei* would be given as: 7pr + 1r + 2vap + 3map + 1dap; 5pst + 2at – seven precingular, one rhomboidal ventral ("Rautenplatte"), two ventral, three medium, one dorsal plates; five postcingular, and two antapical plates. Accordingly Lefèvre's system the same formula would read: p_7 a a_3 p'_5 a'_2 – seven precingular, one rhomboid ventral, three apical, three medium plates, five postcingular, and two antapical plates. Kiselev would list it as 7pr + 4a + 4sr; 5zb + 2a′ – seven precingular, four apical, three medium plates; five postcingular, and two antapical plates.
Most plates are ornamented with spines and ridges. Pores, poroid, and trichocysts pores may also be present and arranged in rows. Plate reticulation is common in many species (fig. 38). The margins of furrows are sometimes ornamented with hyaline ridges and wings. There is a great deal of variability found on small structures on the epi -and hypothecae. Common examples have been illustrated by Lefèvre (1927) and are referred to in many textbooks. Because these variations, common though they may be, are usually present in low numbers in a population or when present are seldom documented, they have not been credited with taxonomic value. Only a few such variations are depicted in figures 32–37. Recently more attention is being given to the plate formula in the girdle and sulcus. Plates forming the junction of the sulcus and girdle have two flagellar pores or openings. The number of plates forming the girdle or cingulum is usually the same as the number of postequatorial plates on the hypotheca. The arrangement of plates forming the junction between the girdle and sulcus is given in figures 29–31.
In contrast to the external theca of most Dinophyceae, a complex internal skeleton (a dominant taxomomical feature for the Foraminifera) is present in the family Actiniscaceae (Zimmermann 1930, Schiller 1933/37). Composition of this internal skeleton consists of opaline silica in freshwater species of the genus *Actiniscus* Ehrenberg and *Pseudoactiniscus* Bursa. Adachi (1965) described an internal plate-like structure located beneath the theca in *Peridiniopsis polonicum.* This "internal skeleton" is in contact with the ventral side of the cell and has the following formula: $3', t, 2c, 4c, 2''$. Its origin and position is quite different from that of the internal skeleton in the Actiniscaceae.

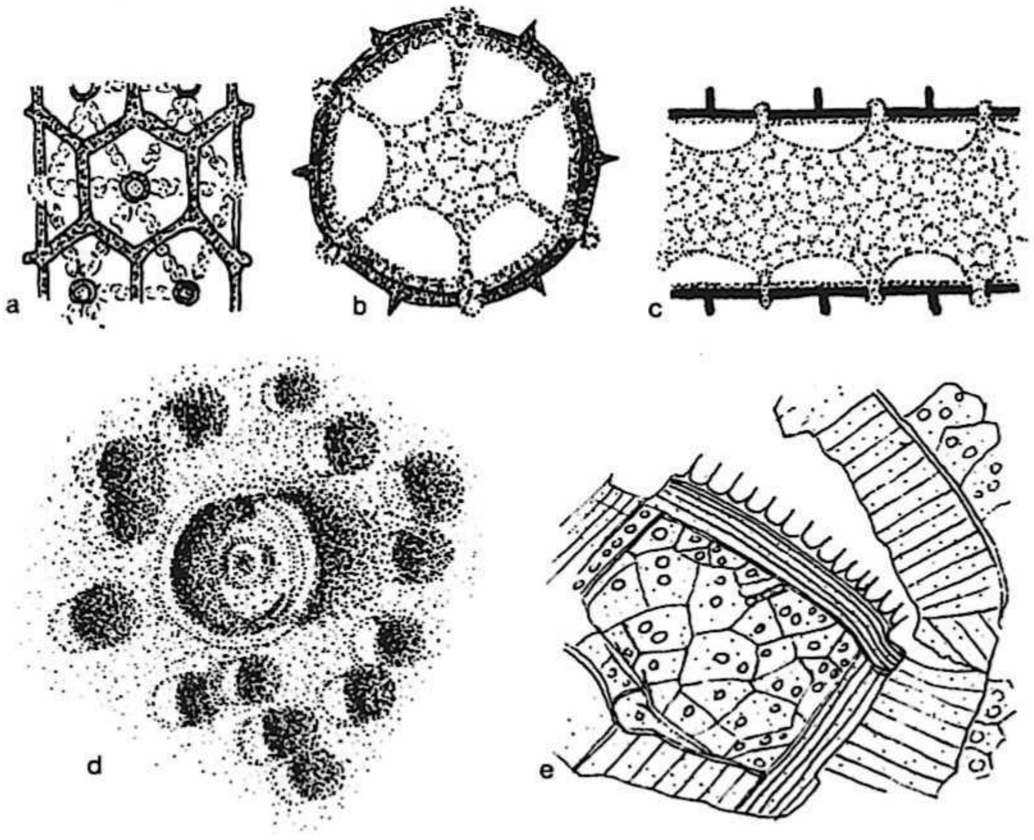


Fig. 38. Arrangement of pores and cytoplasm in the apical horns of *Ceratium hirundinella; a* plate reticulation with pores (dark lines) and cytoplasmic connection (light lines), *b* cross section near the apex, *c* longitudinal section (after Entz), *d* single trichocyst pore surrounded by spines in marine *Ensiculifera loeblichii,* 500×, *e* single plate of *Peridinium cinctum* showing reticulations and trichocysts pores and region of plates expansion – 4650× (redrawn from EM microphotographs in Bold and Wynne).

2.2. Flagella and motion

Monads have two flagella. They may be apical as in *Desmomastix globosa* (fig. 1a) or subapical in *Protaspis metarhiza* (fig. 1b) and *Spiromonas perforans* (fig. 60). Most commonly the flagella are inserted in pores on the ventral side of the organism where the sulcus and cingulum join as in *Ceratium hirundinella.* The longitudinal flagellum is either used to pull the organism trough the water (as in the Desmomastigales) or to push it (Peridiniales). The other flagellum encircles the monad lying within the cingulum (fig. 2). Its movement causes the cell to rotate or swirl as it moves through the water.
The longitudinal flagellum is coiled in the sulcus when the cell is at rest and stretches out past the antapex trailing the cell when it is in motion. Its length which varies with specific taxa may reach a length two and a half times the length of the cell. Hypnozygotes may be recognized also by the presence of two trailing flagella. The transverse flagellum arises from a pore located just above the pore for the longitudinal flagellum (fig. 2). It encircles